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HYDRICHTHYS PIETSCHI, NEW SPECIES, (COELENTERATA) PARASITIC ON THE FISH, *CERATIAS HOLBOELLI*

W. E. MARTIN[1]

ABSTRACT: A new hydroid, *Hydrichthys pietschi*, was found on a myctophid fish, *Ceratias holboelli* Krøyer, collected off the leeward shore of Oahu, Hawaii. The basal plate of the hydroid erodes the pigmented epidermis and underlying tissues of the host. The literature on commensal and parasitic hydroids is reviewed.

Although the phenomenon is relatively rare, commensalism and parasitism involving hydroids and fish have been found in Russia (Ussow, 1887); Rumania (Dimitru, 1961); India (Alcock, 1893; Lloyd, 1907); Africa (Warren, 1916); European Atlantic Ocean (Damas, 1934; Jones, 1966); New England Atlantic (Fewkes, 1887, 1888; Gudger, 1928); Eastern Pacific (Heath, 1910; McCormick, Laurs, and McCawley, 1967); Japan (Franz and Stechow, 1908; Komai, 1932; Miyashita, 1941); New Zealand (Hand, 1961); and Hawaii (present paper). Some of these associations apparently are commensal without invasion of the host, with the polyps possessing tentacles and obtaining nourishment as do free-living species. Others are parasitic with invasion of the host, with polyps lacking tentacles and with reduction or loss of nematocysts. How the parasites obtain their food is of some interest. Warren (1916) reported that the non-tentacled polyps of *Hydrichthys boycei* ingested host red corpuscles and even connective tissue. Jones (1966) found that a hydroid, which he thought probably was *Ichthyocodium sarcotretis* Jungersen, 1911, attached to copepods, *Sphyrion lumpi* (Krøyer), parasitic on the redfish, *Sebastes mentella* Travin, fed on the fish hosts' blood and tissue. Damas (1934) suggested that the inner ectoderm of *Hydrichthys cyclothonis*, which is much thicker than the outer ectoderm, absorbed nutrients from the fish host, *Cyclothone signata* (Garman). The ribbon-like stolon of *Polypodium hydriforme*, which occurs in the ovarian eggs of certain Russian and Rumanian sturgeons, must be nourished through its outer layer which is believed to be endoderm! The latter species has a remarkable life history with some aspects still unknown. The cycle has been reviewed by Raikova (1958), and Smol'yanov and Raikova (1961). A young stage invades the ovarian eggs of sturgeons in the Volga, neighboring rivers, and the Danube, then develops into a ribbon-like stolon which undergoes multiple budding. The buds form polyps by developing tentacles internally from the ectoderm, detaching from the stolon and turning inside out to bring the body layers to their usual position. After the fish spawns, the polyps and what remains of the stolon escape from ruptured eggs. The polyps usually bear 6, 12, or 24 tentacles (Lipin, 1909). Most polyps become male or female but a few are hermaphroditic. Eggs are released into the gastrovascular cavity. Male polyps, each bearing four testes near the aboral end, can become attached to small sturgeons. The ectoderm over each testis produces adhesive material which firmly attaches this area. Then the testes are released from the polyp and resemble buttons attached to the fish. After the four testes are released the polyp seems to disintegrate. Raikova (1965) used Feulgen cytophotometry to determine the deoxyribonucleic acid content of the various cells of this hydroid. Ectoderm and endoderm have the diploid content.

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The two nuclei of the "spermatids" are unequal, the smaller haploid (n), the larger 2 to 6 n. Nurse cells of the ovary are 8–32 n but the eggs are diploid when released. The youngest stage found in the sturgeon egg has two unequal nuclei, one about 400 n that forms a capsule around the embryo cells, and the other haploid. The early embryo cells also are haploid. This led Raikova to conclude that there is no fertilization and that diploidy is restored in later embryogenesis. Questions remain unanswered. If there is no fertilization, what role is played by "spermatids?" How is diploidy restored in later embryogenesis, etc.? It is apparent that further work needs to be done on this unusual type of development. Are sturgeons in parts of the world other than Russia and Rumania hosts of this parasite?

The assignment of specific names to such hydroids is difficult because of the relative paucity of diagnostic characters. If host specificity exists the problem would be greatly simplified. McCormick, *et al.*, (1967) argued against host specificity because they found presumably the same species of hydroid on two species of fish, *Tarletonbaenia crenularis* (Jordan and Gilbert, 1880) and *Diaphus theta* (Eigenmann and Eigenmann, 1890). Also they found the hydroid on a copepod, *Cardiodectes medusaeus* (Wilson, 1908) parasitic on *D. theta* and another fish, *Lampanyetus leucopsarus* (Eigenmann and Eigenmann, 1890). The attachment of the hydroid to a parasitic copepod may not be relevant to host specificity because Jones (1966) found that a hydroid attached to a copepod parasite still fed on the fish hosts' blood and other tissues. McCormick, *et al.*, (1967) examined more than 2000 Pacific specimens of the fish genus *Cyclothone* including *C. signata* without finding any hydroids. Yet Damas (1934) found 24 hydroid colonies on 21 of over 2000 *Cyclothone signata* from the Atlantic. If host specificity does not exist, why did not McCormick, *et al.*, find hydroids on *C. signata*? Warren (1916) also reported finding several species of fish hosts to *Hydrichthys boycei*. But again was only one species of hydroid involved? In support of host specificity, Alcock (1893) found *Stylactis minoi* on the fish, *Minous inermis*, but not on *Minous coccineus* or other fish in the same trawl. Komai (1932) found this hydroid also only on *Minous inermis* in Japan. The following have been reported from only one species of fish: *Hydrichthys mirus* Fewkes, 1888 on *Seriola zonata*; *H. cyclothonis* Damas, 1934 on *Cyclothone signata*; *Podocoryne bella* Hand, 1961 on *Congiopodus leucopaecilus*; *Perigonimus pugetensis* Heath, 1910 on *Hypsagonus quadricornis*; *Stylactis piscicola* Komai, 1932 on *Erosa erosa*; *Nudicola monocanthi* Lloyd, 1907 on *Monocanthus tomentosus*; *Hydrichthys pacificus* Miyashita, 1941 on *Xesurus* sp. *Polypodium hydriforme* Ussov, 1885 parasitizes only sturgeons. It is possible, however, that a wider search might show more than one species of fish hosting the same hydroid. The question of host specificity has not been settled.

Ecological factors may determine whether or not a species of fish plays host to hydroids. Heath (1910) found twenty-five per cent of the fish, *Hypsagonus quadricornis*, bearing the same hydroid, *Perigonimus pugetensis*, in Puget Sound but outside the sound the same species of fish was negative. McCormick, *et al.*, (1967) stated that the rate of infection with hydroids was higher in species of fish that migrated to the surface at night.

The purpose of this paper is to describe another hydroid parasitic on a fish. Theodore Pietsch, presented a lantern fish, *Ceratias holboelli* Krøyer, 1844, about 15 cm long, that had a small patch of tiny, finger-like polyps dorsal and slightly anterior to the left eye (Fig. 1). This fish was collected with an Isaacs-Kidd midwater trawl at a depth of about 95 meters off the leeward side of Oahu, Hawaii on March 1, 1971. A few polyps were stained with Mayer's paracarmine and mounted in Canada balsam. A portion of the colony was sectioned, stained with hematoxylin and triosin and mounted in Canada balsam. Drawings were made with the aid of a camera lucida unless

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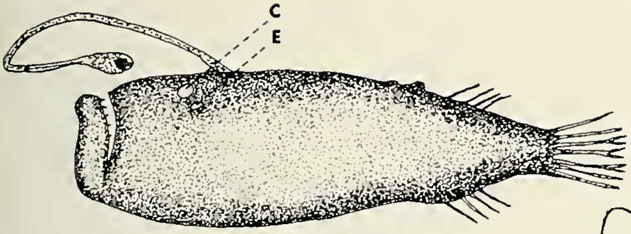
Figure 1. Sketch of *Ceratias holboelli*, C, location of coelenterate colony; E, eye. *Figure 2.* Section of uninfected fish skin, EP, pigmented epidermis; S, spine-like scale. Magnification scale same as figure 4. *Figure 3.* Part of coelenterate colony and surrounding host skin, B, basal plate; P, polyp. *Figure 4.* Section through part of basal plate and host skin, I, inner ectoderm; O, outer ectoderm; S, spine-like scale; T, host cell response. *Figure 5.* Optical section of bud and stalk, projecting from polyp wall, EC, ectoderm; EN, endoderm.



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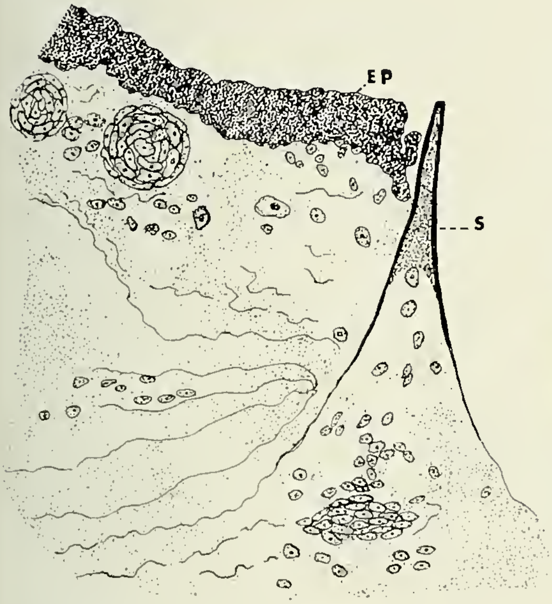

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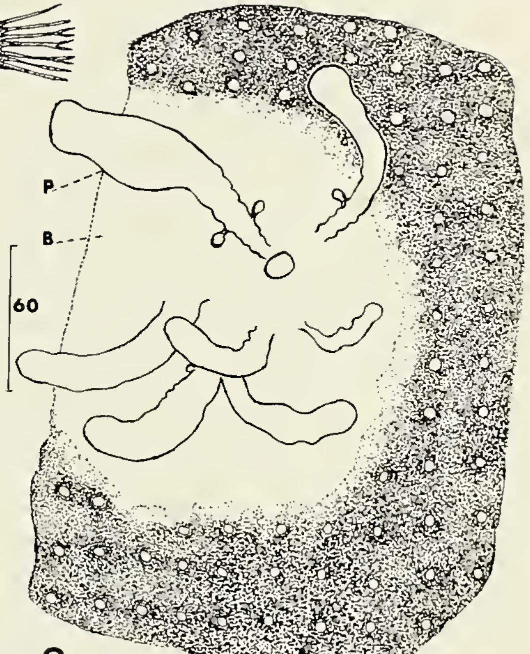

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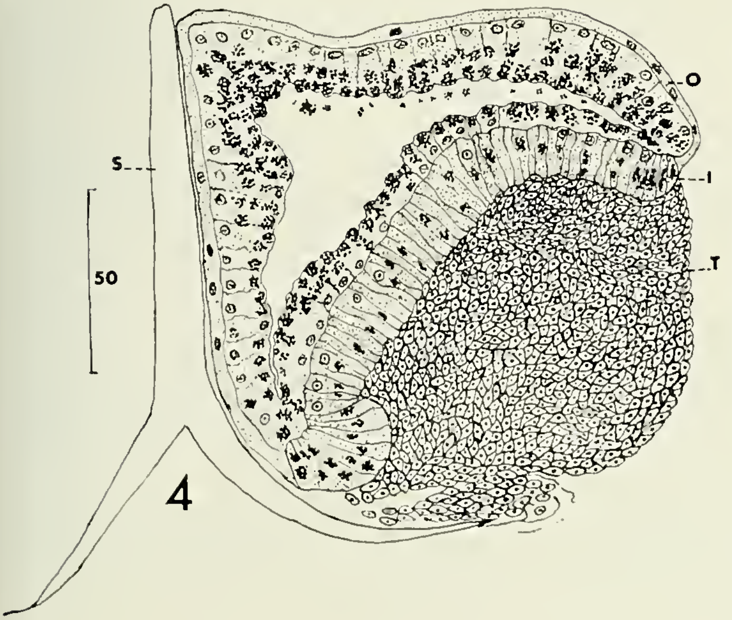

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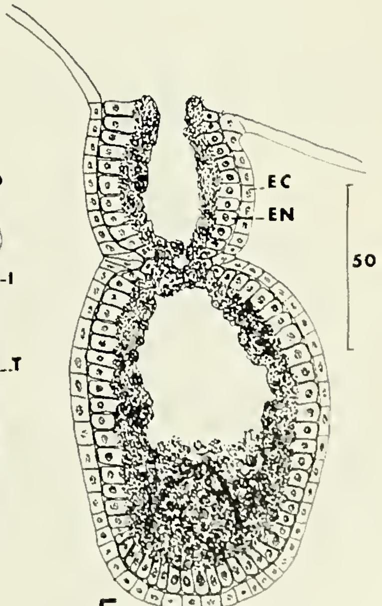

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otherwise indicated. Measurements are expressed in microns unless otherwise indicated.

Hydrichthys pietschi, new species

Figures 3–5

Polyps project from basal plate, some bearing buds on the aboral half of body (Fig. 3). Polyp 490–1,010 long; 112–168 wide. Ectoderm thin (about 3) endoderm 8–9 thick enclosing many granules 0.8–.9 in diameter. Nematocysts and mesoglea not seen. Medusa bud (Fig. 5) stalked, 87–106 long, 68 wide. Mass of cells at distal end probably developing manubrium. Bud endoderm also contains granules. Bud stalk 40–50 long; 47 wide.

Basal plate (Fig. 4) approximately 4,800 in diam. with outer thin, 3, and inner thick, 16–22, ectoderm. Thickened inner ectoderm contains granules and may function in digestion as suggested by Damas (1934). Endoderm thickness 8–25, with numerous granules, encloses shallow gastrovascular cavity. Maximum plate thickness 137 which is about equal to the greatest penetration into the host. In this penetration the pigmented epidermis and some of the underlying tissues of the host are eroded. The granules of the hydroid and of the host epidermis are very nearly the same size. Possibly the hydroid obtains its granules from the host. There is a definite tissue response of the host to the parasite with a massing of cells beneath the inner ectoderm (Fig. 4) which is not seen in uninfected skin (Fig. 2).

Host: *Ceratias holboelli* Krøyer, 1844.

Habitat: Skin.

Type locality: Leeward side of Oahu, Hawaii.

Holotype: No. 7115, deposited in the Hancock Parasitology Collection, University of Southern California.

DISCUSSION

Hydrichthys pietschi differs from other members of the genus in apparently lacking nematocysts and mesoglea, in having a thicker inner ectoderm of the basal plate, and in a deeper penetration of the host. The only other report of a hydroid on a myctophid fish is that of McCormick, *et al.*, (1967), a species which has a thick mesoglea, a thinner inner ectoderm and only slight invasion of the host.

After this paper was accepted for publication, *Polypodium sp.* was reported in *Acipenser fulvescens* collected in the Black River near Cheboygan, Michigan (Hoffman, Raikova, and Yoder. J. Parasit., 60:548–550. 1974).

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INFESTATION OF THE SANDY BEACH AMPHIPOD *ORCHESTOIDEA CORNICULATA* BY *GAMMARIDACARUS BREVISTERNALIS* (ACARI: LAELAPTIDAE)

Donna Scurlock[1]

Abstract: The mesostigmatid mite, *Gammaridacarus brevisternalis* has been found on both decomposing wrack and on the beach amphipods *Orchestoidea corniculata* and *O. californiana*. The percentage infestation of the host population increased with size of hosts and varied from 1.5 percent (hosts 3–7.9 mm) to 83.07 percent (hosts 16–19.9 mm). Mites showed no preference for male or female hosts. The number of mites per infested host increased slightly with amphipod size. Mites were found attached by gnathosoma exclusively on the ventral side of the host. The mites left hosts within 2–9 hours after death of the host and mites without hosts can crawl over sand at an average rate of 3 inches per minute. After leaving dead hosts, *G. brevisternalis* attach to new, living hosts. The mites traveled at least 30 cm in finding new hosts and observations suggest that the mites possess chemotactic senses for locating hosts at a distance.

In California sandy beach communities, members of the amphipod genus *Orchestoidea* are among the most abundant macrofauna. At night these beach hoppers leave their sand burrows and feed in large numbers on stranded seaweed. As early as 1912 small, apparently ectoparasitic mites had been found on these gammarids (Hull, 1912), and in later studies of *Orchestoidea* both McClurkin (1953) and Bowers (1954) noted their occurrence. In Oregon and Washington, Canaris (1962) found *Orchestoidea californiana* Brandt, 1851, infested with males, females, and deutonymphs of a mesostigmatid mite which he named *Gammaridacarus brevisternalis* Canaris,

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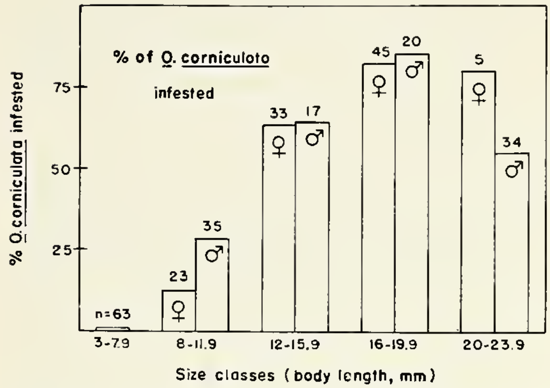

Figure 1. Percentage of the *Orchestoidea corniculata* population, by size class and sex, found infested with mites. Sex of members of the smallest size class could not be determined. Females of the largest size are scarce.

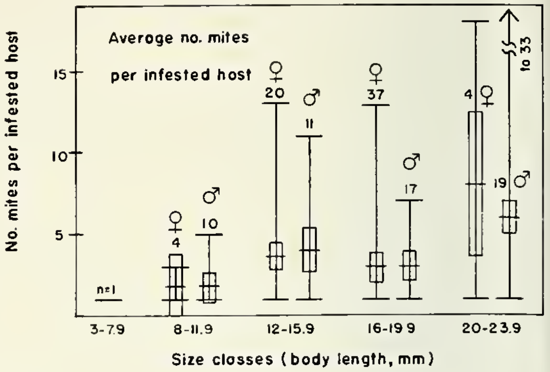

Figure 2. Average number of mites per host on infested *Orchestoidea corniculata,* according to host size class and sex. Each column shows mean, range, and 95 percent confidence limits of the mean. Sex of members of the smallest size class could not be determined.

1962. These mites have also been found in sandy beach wrack by Newell (pers. comm., 1972) and the author.

This investigation was undertaken to extend our knowledge of the relationship between the parasite and host. Studies were carried out at Hopkins Marine Station of Stanford University, Pacific Grove, California from April to June, 1972. All collections were made on the Monterey Boatworks beach located just east of Mussel Point, Pacific Grove. This beach was found by Bowers (1964) to contain a beach hopper population consisting solely of *Orchestoidea corniculata* Stout 1913. All amphipods collected were identified using keys in Bousfield (1959). Only *O. corniculata* was found on this beach.

Occurrence of mites on the host.—Investigations were made to discover the extent to which the host population was infested by mites, and to see whether or not the mites showed a preference for hosts of a particular size or sex. A total of 275 hosts was collected. Each amphipod was immediately placed in a separate vial of 75 percent ethyl alcohol, thus any mites that became detached could be counted and attributed to a single amphipod.

In the laboratory, the contents of each vial were examined under a dissecting microscope. Each amphipod was identified by species and sex, and the number of mites and their positions on the host were noted. Occasionally mites were found to have come free of their hosts and were loose in the vials of alcohol. The sex of the youngest hosts could not be determined. In the case of brooding female hosts, the eggs or young were also checked for mites. The body length of each amphipod was then measured by straightening the body and recording the distance from the front of the rostrum to the tip of the telson. The *O. corniculata* collected ranged in length from 3 mm, the size when the young first leave the marsupium (McClurkin, 1953), to 24 mm, the size of the largest males.

Results of the survey (Fig. 1) show there is a positive correlation between host body size and the percentage of the host population infested. In fact, only one mite (a deutonymph) was found among the 63 amphipods of the smallest size class examined. The smallest amphipods have less exposed ventral surface area for mite attachment, and also show a pattern of behavior slightly different from that of the larger hosts. The youngest amphipods are more active than the larger ones during the days and can sometimes be found hopping above the surface at that time (Bowers, 1964, and pers. observations). Mites are very susceptible to desiccation (Cheng, 1964: 545) and conceivably, this host daytime behavior could subject the mites to desiccation.

The percentage of infested males of the largest size class was lower than that of the next smallest size class. The females of the two largest sizes showed similar percentages of infestation. The decrease found in the largest males might be attributed to their tougher outer covering. Females of the largest size class were close to the lower length limit of this range (20 mm) and so were almost members of the next smaller class.

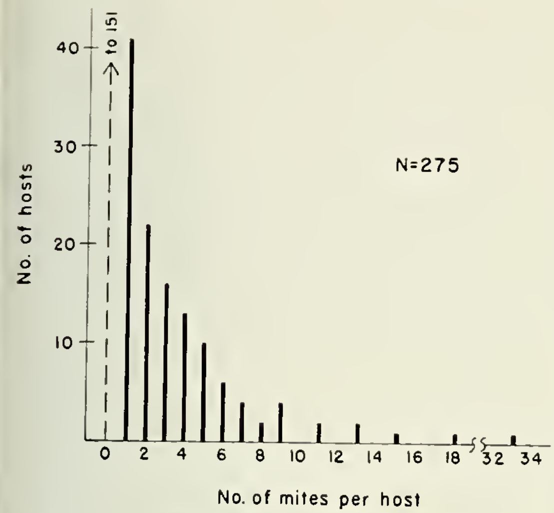

Figure 3. Degree of infestation with mites of all *O. corniculata* examined.

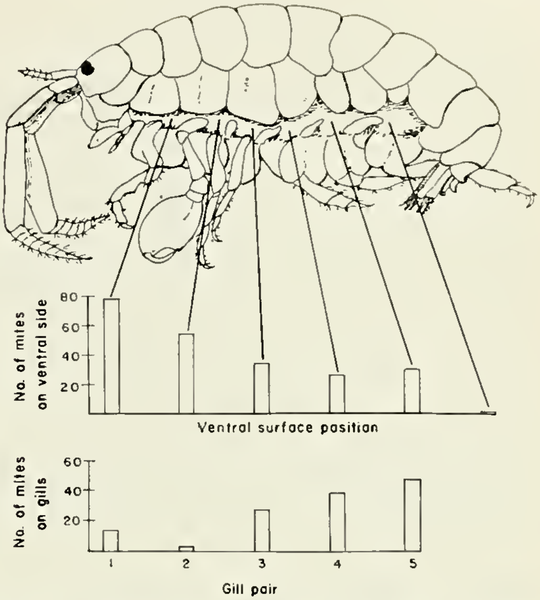

Figure 4. Positions on host body at which attached mites were found in a survey of 275 amphipods. An *O. corniculata* (male) is shown with appendages of the left side removed. Gill pairs are numbered 1 through 5 from front to rear. In addition, eight mites were found on female oostegites.

The average size of the mite population on individual infested hosts increased slightly with host body size (Fig. 2). This is not surprising since larger hosts have more room for parasites, and have had a longer time in which to acquire them. One male in the largest size class carried 33 mites. Among those *O. corniculata* which were infested, small mite loads were more common than large loads (Fig. 3).

Distribution and attachment of mites on the host body.—When live hosts were examined, unattached mites occasionally were observed crawling on the ventral or dorsal side of the host, or on its appendages. This probably explains why mites were sometimes found detached from their hosts following preservation in alcohol.

Attached mites, however, when observed on hosts preserved in alcohol, were found only ventrally on the amphipod body; here they ranged longitudinally from the area between the first gnathopods to a position directly above the first pleopods. Mites were found in every possible position on this flat, thin skinned surface, and also on sites on the five pairs of gills (Fig. 4). The ventral surface forms part of a protected and probably humid chamber when the amphipod curls its body and crosses its gnathopods and peraeopods across its ventral side during its daily resting period in its sand burrow.

The number of mites on the ventral surface was greater anteriorly on the hosts while the number on the gills was higher posteriorly, where the gills are larger. In heavily infested hosts, mites tended to cluster into dense packs in the ventral mid-line. The ventral surface of the host is weakly sclerotized; also, a large blood sinus passes close to the cuticle (Cussans, 1904). The five pairs of gills also offer a rich blood supply. If the mites feed on blood, better sites could not be found on the host.

Mites were never found attached to the host's abdomen or telson, probably because of the amphipods' mode of locomotion. When a beach hopper jumps, it curls its posterior end forward under the body, then straightens it suddenly in springing away.

On brooding females, mites (8) were also found on the four pairs of oostegites or brood plates which retain the eggs or young. No mites were found on eggs or young of brooding females.

Mites were found most often attached to the host by their mouth parts; their remaining appendages were held extended, but not attached. This position suggests feeding. However, even the more heavily infested hosts showed no obvious signs of weakness, damage, or even inconvenience caused by the mites.

The behavior of mites during molting of the host was not observed, but it seems likely that this presents few problems to the ectoparasites.

Orchestoidea, after molting, remain dormant for a period and then proceed to eat their shed exoskeletons (McClurkin, 1955). This behavior would appear to permit the mites to detach from the old cuticle and find a place on the new, soft cuticle.

Transfer between healthy hosts.—Experiments were conducted to determine if mites shift from one living host to another, or from dead to living hosts. One investigation was initiated to discover if the mites remain with their hosts even in the presence of other living amphipods. Live amphipods were first anesthetized with ethyl ether fumes and then were examined very carefully under a dissecting microscope. Both mites and amphipods quickly recovered from the anesthetic.

Amphipods were maintained in the laboratory using the methods of McClurkin (1953). Cotton pads moistened with seawater were placed in two 2 × 9 cm glass vials and the tops of the vials were covered with cotton gauze to prevent escape of the amphipods. One infested and one uninfested *O. corniculata* were placed in each of the two containers. After one to two days, each previously uninfested amphipod bore at least one mite.

The mites are quite motile. They can shift from one living host to another, at least when the hosts are close together. This physical proximity occurs in the field especially during the night, when many closely packed *O. corniculata* can be found feeding on wrack.

Mite reaction to host death.—A similar experiment was set up to determine the reaction of mites to the death of their host. Two live *O. corniculata* infested with two mites each were killed by stabbing. They were immediately placed in two McClurkin vials and left overnight. The dead hosts bore no mites the next morning, and even the cotton in the vials appeared to be free of mites.

The experiment was repeated in an aquarium tank filled with four inches of damp sand similar to that in which the amphipods burrow during the day. Five infested *O. corniculata* were killed by stabbing and placed overnight in shallow holes in the sand to simulate the death of amphipods in their burrows. All the amphipods were found the next day to have no mites.

Finding a new host.—Since mites leave after death of the host, other experiments were performed to determine whether mites can locate new, healthy hosts. In one experiment, two dead infested amphipods were placed in separate McClurkin vials, and a live uninfested *O. corniculata* added to each vial. One dead amphipod bore one mite, and the other two mites, at the start of the experiments, but after 12 hours all the mites had transferred to the living amphipods.

A similar experiment was carried out in the sand tank. Five infested *O. corniculata* with one mite each were killed and placed in holes in the sand, then three uninfested live amphipods were added. After nine hours, one living *O. corniculata* individual bore all five mites and the remaining live and dead amphipods had no parasites.

In these experiments, contact between the dead and living hosts was possible. In the field, *O. corniculata* have been observed eating individuals of their own species, which should provide good opportunity for mite transfer.

Experiments were also performed to discover if mite transfer could take place without close contact between hosts. Under normal beach conditions this might involve mite movement across the beach. In order to test the mites' capabilities of locomotion in sand, a round dish of beach sand was prepared. A mite was introduced at a marked spot on the sand, and allowed to move freely. The mite's progress was observed under the dissecting microscope, and it appeared to have no great difficulty traveling on sand. The several mites timed averaged 3 inches per minute. When a living *O. corniculata* was placed at a point across the dish of sand from the mite, the mite was observed to crawl directly across the sand and climb on the amphipod, suggesting chemotaxis.

With these results in mind, a more complex experiment was performed to test mite transfer from dead to living hosts over varying distances. A large aquarium tank was divided by metal sheets into four separate compartments or runways measuring about 8 × 42 cm. Sand from the normal environment, treated with steaming hot water for fifteen minutes to kill any mites, was drained, dried to the dampness *O. corniculata* prefers, then placed in each runway, and the surface roughly leveled. Living, uninfested *Orchestoidea* were caged in cylinders of plastic screen of 1 mm square mesh, two animals to a cage. A cage of amphipods was placed at one end of each of the aquarium runways. Three fresh *O. corniculata*, each with three mites, were killed by piercing and placed on sand in separate runways of the aquarium. One dead infested amphipod was placed 10 cm away from the cage in runway A, one was placed 20 cm away in runway B, and one at 30 cm in runway C. Runway D contained live caged uninfested hosts and no dead host with parasites. After nine hours (overnight, in darkness), the cage in runway A contained one amphipod with two mites and one with one mite (no loss of mites over 10 cm). In runway B, one caged amphipod bore three mites, the other none (no loss of mites over 20 cm). In runway C, each caged amphipod bore one mite (loss of one mite over 30 cm). No mites were found on the caged amphipods in control runway D.

The results suggest the mites possess chemoreceptors enabling them to locate hosts over considerable distances.

Mites in environments other than the host.—The foregoing observations suggest that some part of the mite population exists apart from the *O. corniculata* population. Possible alternative environments for these mites are: 1) other host species; 2) damp sand; and 3) damp wrack on the beach. As previously noted, mites also infest the *O. californiana* population. Mites that had the appearance of those infesting *O. corniculata* were found in older, partially buried wrack. Newell (pers. comm., 1972) has identified them as *G. brevisternalis*, and noted that he has found these mites in southern California exclusively in wrack. Mites from Pacific Grove wrack, which appeared identical to the amphipod mites, were introduced into a vial with live uninfested amphipods. A day later, they were found attached to the *O. corniculata*. The mites can live for prolonged periods apart from the host. *Gammaridacarus brevisternalis* can live more than a month on decomposing wrack placed in closed plastic bags (Helen Kompfner, pers. comm., 1972). I have kept the mites in stoppered vials containing only tiny bits of beach wrack, and also in vials containing only a pad of sea water soaked cotton for at least 3.5 weeks. In contrast, mites held overnight in an empty, corked glass vial were all dead the next morning, evidently of desiccation.

Perhaps when the mites do not locate an amphipod quickly, they find in the wrack a humid environment where they can survive until they find a new host. The relationship of the mites to the wrack requires further study.

ACKNOWLEDGMENTS

I thank Irwin M. Newell of the University of California, Riverside, for identifying the mite, and for his helpful suggestions. Marty Mendelson of the State University of New York at Stony Brook assisted me with the later stages of my diagrams. Sam Johnson, a graduate student at Hopkins Marine Station at the time of this study, answered many questions about amphipods. Especially, I would like to express my deep appreciation to Donald P. Abbott for his enthusiastic guidance.

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OBSERVATIONS ON TWO SPECIES OF HYPERIID AMPHIPODS ASSOCIATED WITH THE CTENOPHORE *PLEUROBRACHIA BACHEI*

Marilyn Flores[1] and Gary J. Brusca[2]

ABSTRACT: Two species of hyperiid amphipods (*Hyperoche medusarum* and *H. mediterranea*) were found in symbiotic associations with the ctenophore *Pleurobrachia bachei. H. mediterranea* has not previously been reported from this ctenophore. Adult amphipods were most frequently encountered on the exterior of the host, or forming excavations in the surface. Immatures were most abundant within the mesoglea of the ctenophore. Behavioral observations on living specimens are discussed and related to the method of entrance into the host by the amphipods.

Symbiotic relationships between pelagic hyperiid amphipods and various host organisms (medusae, ctenophores, salps) have been noted by several authors (Bowman, Meyers, and Hicks, 1963; Brusca, 1967, 1971; Hardy, 1965; Laval, 1963, 1966, 1968; Schellenberg, 1942; Stephensen, 1923; Steuer, 1911), but few of these reports discuss the nature of the associations. In at least one instance, (*Hyperia galba* on the scyphomedusa *Cyanea capillata*), post mortem gut analyses of the amphipod revealed nematocyst capsules and the relationship was reported as parasitic (Dahl, 1959). Bowman *et al.*, (1963) reported on observations of living specimens of *H. galba* on a live *C. capillata*, but actual feeding by the hyperiid was not seen, and Dahl's conclusions remain unsupported by direct evidence. Most of the related literature consists of reports of occurrence of members of the family Hyperiidae.

We intend to elaborate on the association between *Hyperoche medusarum* and the ctenophore *Pleurobrachia bachei*, previously reported by Brusca (1971), and to present observations on the association between *H. mediterranea* and *P. bachei*. We have found no mention of the latter relationship in the literature. All of the specimens discussed here were collected from northern California waters either with plankton nets aboard the RV/CATALYST within a few miles of the entrance to Humboldt Bay, or by finding freshly stranded ctenophores on the mud and sand flats of the bay itself. Collections were made during the months of June and July, 1972.

SYSTEMATICS OF *H. MEDUSARUM* AND *H. MEDITERRANEA*

The genus *Hyperoche* is distinguished from other members of the family Hyperiidae by having gnathopods one and two chelate, with the carpal prolongation of the second pair compressed and blade-like. In the two species discussed here, the carpal process of the first gnathopods are similar in shape.

Only about 45 specimens collected during this study were large enough to identify with certainty. The remaining individuals were unpigmented juveniles (less than 1 mm in length) and immatures (1–3 mm in length), and could not be identified or sexed. The epimeral plates of these young amphipods were observed under 430× magnification, but could not be assigned to either species as described below.

The separation of *H. medusarum* from *H. mediterranea* is based upon the shape of the epimeral plates of pleonites 1–3. Hurley (1955) described these two species from specimens taken in New Zealand waters. Figures 1 and 2 picture the epimeral plates and gnathopods from males and females, and illustrate the specific traits as observed in the animals collected during the present study.

Pleonites 1–3 possess postero-ventral points in *H. medusarum* (Fig. 1 A, D), whereas, these plates are generally rounded and blunt in *H. mediterranea* (Fig. 2 A, D). Some variation was noted when examining individuals for this characteristic, and the specimens figured are individuals which show the described shapes. Some of the amphipods displayed less prominent, but distinct points, and in one instance a point was seen on the second plate; none was present on either the first or the third plate. The extent to

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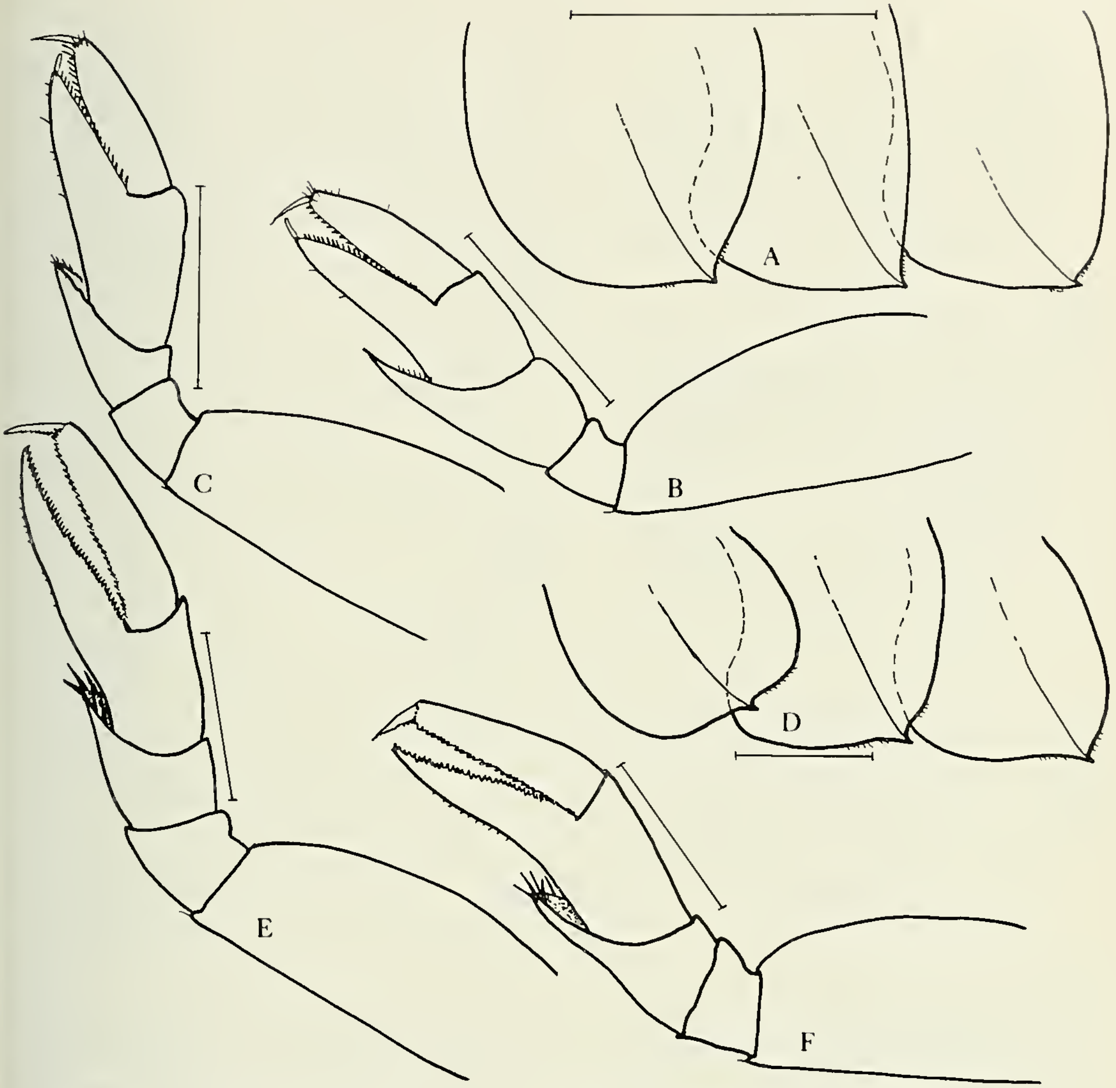

Figure 1. Hyperoche medusarum. A (♀), epimera of pleonites 1, 2, 3; B (♀), gnathopod 1; C (♀), gnathopod 2; D (♂), epimera of pleonites 1, 2, 3; E (♂), gnathopod 2; F (♂), gnathopod 1. Total length of ♀ = 4 mm, total length of ♂ = 6.5 mm. All scale lines = 0.5 mm.

which these intermediate forms are present in the natural population is unknown, but it should be of interest to examine a larger series for possible taxonomic implications.

The gnathopods of both species are similar, with the following differences. The meeting edges of the chelae appear quite heavily toothed in *H. medusarum* (Fig. 1 B, C, E, F) when compared with the fine setation of the respective claw margins on *H. mediterranea* (Fig. 2 B, C, E, F). In addition, the extension of the merus along the posterior edge of the carpus bears 5–7 large distal spines in *H. medusarum* (males), which are absent from *H. mediterranea.* Hurley (1955) reported these spines in female *H. medusarum* as well, but the specimens studied here showed only a fine to moderate setation.

Although *H. medusarum* has been reported from the northeastern Pacific, *H. mediterranea* was previously known only from the Mediterranean Sea, and the south Pacific near New Zealand. It is likely that these species will be shown to have wider distributions as more samples become available from around the world.

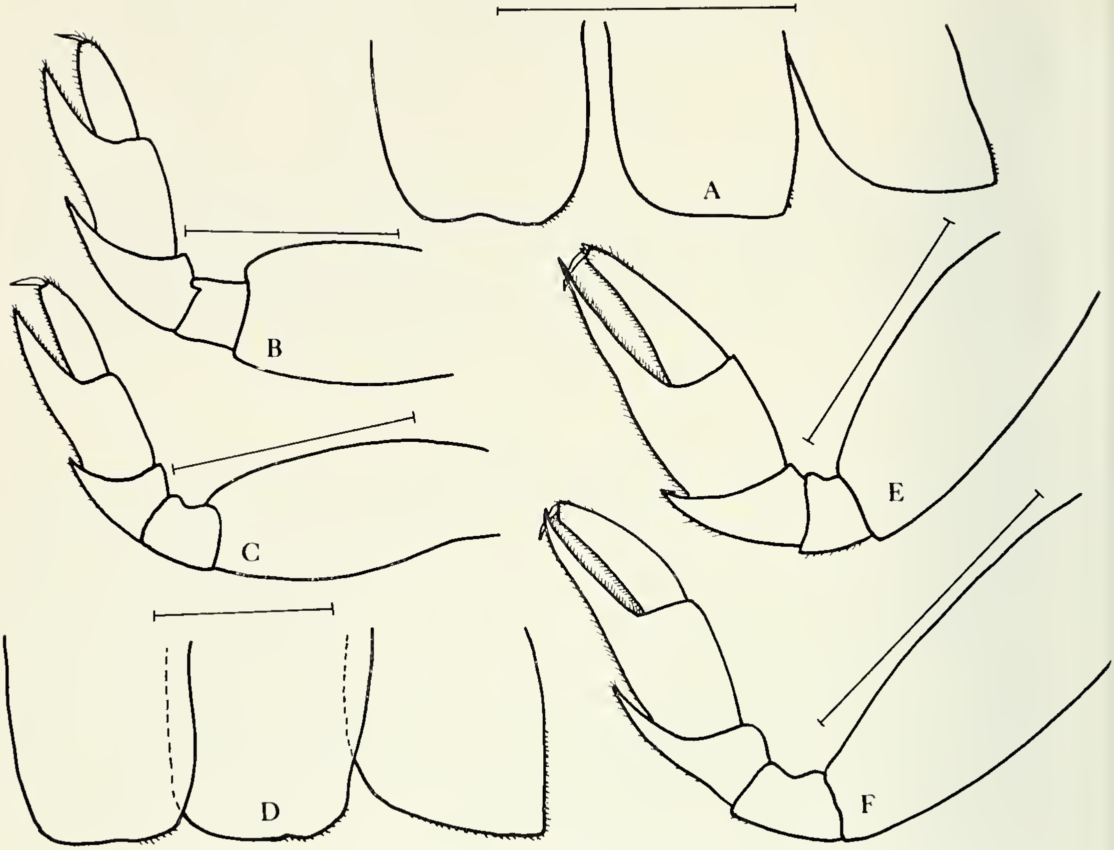

Figure 2. Hyperoche mediterranea. A (♀), epimera of pleonites 1, 2, 3; B (♀), gnathopod 1; C (♀), gnathopod 2; D (♂), epimera of pleonites 1, 2, 3; E (♂), gnathopod 2; F (♂), gnathopod 1. Total length of ♀ = 3 mm, total length of ♂ = 5.5 mm. All scale lines = 0.5 mm.

MATERIAL EXAMINED AND LOCATION WITHIN THE HOST

Detailed counts were made of the amphipods associated with 50 preserved *Pleurobrachia bachei.* Every ctenophore housed at least one hyperiid, and one individual contained five. Thirty-two amphipods had dropped from the hosts during preservation (17 adults and 15 young) and 107 were removed from inside the ctenophores (106 young and 1 adult). The examination of the 50 specimens thus yielded a total of 139 hyperiids. This is a marked increase in density over the 1971 report by Brusca of 24 hyperiids in 135 *P. bachei.* Unfortunately, earlier work analyzed undated samples, so any seasonal significance to the difference remains unclear.

The specific locations of the amphipods removed from the preserved ctenophores were as follows: Adults (total = 18)—*H. medusarum,* (6 specimens; dropped from surface); *H. mediterranea,* (12 specimens; 11 dropped from surface, 1 in mesoglea). Unidentifiable young (total = 121)—15 specimens, dropped from surface; 101 specimens, in mesoglea; 2 specimens, imbedded in surface; 2 specimens, partially imbedded in gut wall (aboral canal); 1 specimen, inside pharynx.

In addition to the above data on preserved individuals, several living adult amphipods were observed on freshly collected ctenophores. Counts were not made during these behavioral studies.

OBSERVATIONS ON LIVING SPECIMENS

About 20 living ctenophores were examined in a search for active hyperiids. Most of the amphipods noted were immature and imbedded in the mesoglea; these remained stationary while slowly moving their peraeopods and gnathopods. While some of these young hyperiids moved the gnathopods around the area of their mouthparts, definite feeding activity could not be confirmed.

In two instances live, unpigmented juveniles (less than 1 mm long) were seen moving about within the gut canals of the host. Although small crustaceans frequently are eaten by *P. bachei*, neither of these amphipods seemed to be affected by the digestive action of the gut. In the above two cases there was no visible damage to the gut wall. Evidence presented earlier mentioning two preserved amphipods partially imbedded in the canal walls, indicates that these young hyperiids may actually burrow into the lumen of the gut from the surrounding mesoglea. This combination of data suggests that the ctenophores must heal rapidly enough to prevent serious interference with feeding and digestion.

Brusca (1971) reported that the three adult *H. medusarum* he found in *P. bachei* were imbedded in the mesoglea. Two of these specimens were completely encased and the hosts showed no evidence of external damage. The third had contact with the exterior through a hole in the surface of the ctenophore. This opening was oval and about the size of the amphipod's head, quite unlike the excavations observed during the present study. As is suggested for the gut wall, the body surface must also heal without permanent damage to the host.

We independently made observations on the behavior of live hyperiids located on or in the surface of the ctenophores. Upon comparing records of these separate observations, it was found that some actions of the amphipods followed consistent patterns. Two common situations were encountered and described for males and females of both species of *Hyperoche*. Some of the females were carrying ova or young in their brood pouches. Many of the amphipods crawled slowly over the surface of the host, using the posterior three pairs of peraeopods. These individuals paused frequently, picking at the ctenophore with their gnathopods. It appeared that these appendages transferred material to the area of the mouthparts, but feeding could not be confirmed.

A second, more complex condition was noted in which amphipods were excavating the surface of the ctenophores. Figure 3 diagrammatically represents two specimens observed during such activities. Amphipods were seen digging in virtually all parts of their hosts, with the exception of the area immediately surrounding the mouth. In several instances, excavation broke through comb rows, or was near tentacular sheaths. In one case, tentacles of the ctenophore were wrapped around the amphipod for several minutes with no apparent effect or evidence of colloblast release.

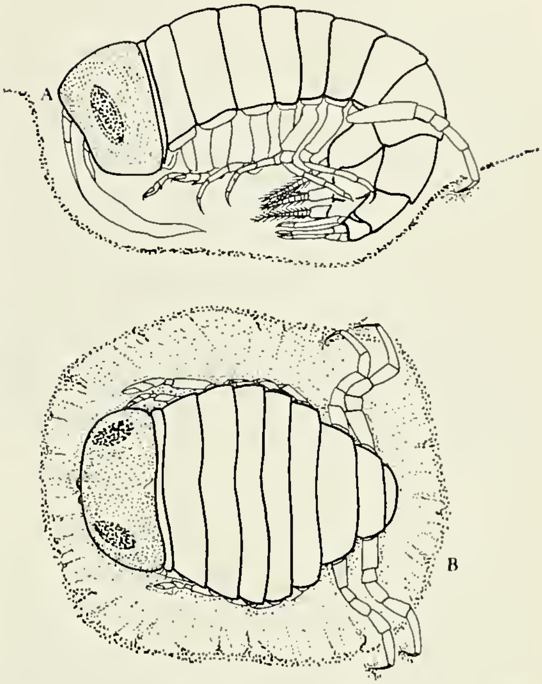

Figure 3. A, diagrammatic lateral view of 5.5 mm ♂ *H. medusarum* forming an excavation in the surface of *P. bachei*. This individual was attached only by the last pair of peraeopods. B, diagrammatic dorsal view of 3 mm ♀ *H. medusarum* positioned over an excavation site. This amphipod was attached by peraeopods 4 and 5.

The hyperiids fixed themselves in position by imbedding the dactyli of any combination of the last three pairs of peraeopods into the epidermis of the host. The abdomen was flexed ventrally and forward. The head and front portion of the thorax were, at this point, suspended above the excavation site. After positioning, the most common sequence of events was as follows: The head was lowered and the gnathopods picked for a few seconds at the exposed mesoglea in the depression. Some indications of passing material to the mouth were noted. Following these movements, the head was raised and the gnathopods were extended laterally. Holding this position, the pleopods were vigorously fanned for two or three seconds during which time small bits of detritus were carried out under the head in the resultir current. Then the head was lowered and the sequence repeated.

Several less consistent behavioral patterns were noted by both observers. Occasionally the tail fan was moved in a posterior to anterior scooping motion, followed by the typical "picking and digging" activity. Other instances included pushing the sides of the excavation outward by a lateral extension of the gnathopods as the pleopods were fanned. Nearly every hyperiid which was observed for a few minutes engaged in what appeared to be a cleaning activity. The first pair of gnathopods were placed over the dorsum of the body at about the junction of the head and thorax, then brought forward over the surfaces of the cephalon and the antennae.

CONCLUSIONS

At least during the summer months, the incidence of amphipods in *P. bachei* is high (100 percent in the material examined). Most of the adult *Hyperoche* were found on the exterior of their hosts and exhibited excavating behavior, as described above. This activity may represent an invasionary process by which the amphipods enter the mesoglea of the ctenophores. This suggestion is supported by the fact that the adults are sometimes found completely imbedded within the host with no communication to the outside.

The high frequency of juveniles within the bodies of the ctenophores may be the result of releasing young either on the surface of the host or within the mesoglea after burrowing. Some mature females in this study carried ova or young, and Brusca (1971) located one female with eggs within the mesoglea. The two juveniles which were found imbedded in the surface of ctenophores could have been entering or leaving the hosts. Perhaps the relationship provides a protective nursery environment for the young amphipods. The two live hyperiids located within the gut canals of the ctenophores either entered through the mouth or burrowed through the wall from the mesoglea. The latter is suspected to be the case since those which were partially imbedded in the canal walls were in a "digging" position, with the heads deeper into the gut than the posterior portion of the body.

There does not appear to be any difference between the activities of *H. medusarum* and *H. mediterranea* in their association with *P. bachei*, and neither seems to cause permanent damage to the host.

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HANNEMANIA (ACARINA: TROMBICULIDAE) AND THEIR ANURAN HOSTS AT FORTYNINE PALMS OASIS, JOSHUA TREE NATIONAL MONUMENT, CALIFORNIA

W. Calvin Welbourn, Jr., and Richard B. Loomis[1]

Abstract: The larval stage of *Hannemania hylae* (Ewing) embeds in the California Tree Frog *Hyla cadaverina* Cope and *Hannemania bufonis* Loomis and Welbourn parasitizes the Red-Spotted Toad, *Bufo punctatus* Baird and Girard at Fortynine Palms Oasis, San Bernardino County, Joshua Tree National Monument, California. Studies from May 1969 to April 1971 revealed estimated average populations of 288 frogs and 300 toads around three small ponds.

Approximately 98.9 percent of the frogs had a mean of 21.4 *H. hylae* per frog and the estimated larval populations varied from 4250 in the spring to 8500 larvae in July to September. One life cycle is completed each year, but unengorged larvae were found on frogs throughout the summer. Nearly 41 percent of the toads possessed a mean of 8 *H. bufonis* and the estimated low was 840 larvae in May to July and the high was 1350 larvae in September. Only one life cycle per year was determined, and unengorged larvae were observed only in the late summer months.

A conspicuous parasite of amphibians is the larval trombiculid mite commonly called a chigger. Larvae of four genera have adapted to amphibian hosts by embedding in the skin. Two genera, *Vercammenia* (Audy and Nadchatram, 1958) and *Anouracarus* (Vercammen-Grandjean, 1973) are known from the Asiatic-Pacific Region, whereas a third, *Endotrombicula* (Ewing, 1925), is found on amphibians in South Africa. The fourth genus, *Hannemania* Oudemans, is certainly the best developed of the intradermal chiggers, and has been found only in the New World.

The length of time as a parasite seems long for *Hannemania* larvae when compared to most other trombiculid mites. Hyland (1961) observed that in the laboratory *Hannemania hegeneri* Hyland remained for at least six months on frogs of the genus *Rana*. Ewing (1926) stated that *H. hylae* was trapped in the skin, and Loomis (1956) believed that *H. eltoni* Sambon overwintered in the skin of the hosts.

The following study involves the populations and natural cycles of *Hannemania hylae* (Ewing) found on the California Tree Frog, *Hyla cadaverina* Cope, and *Hannemania bufonis* Loomis and Welbourn taken only from the Red-Spotted Toad, *Bufo punctatus* Baird and Girard at Fortynine Palms in Joshua Tree National Monument, San Bernardino County, California. This locality was selected because both the hosts and their respective chiggers were found in the same small protected area. The oasis is about 610 meters in elevation and consists of nine major ponds. This study centered around the upper three ponds.

The trees at the oasis consisted largely of California Fan Palms (*Washingtonia filifera*), Cottonwoods (*Populus fremontii*), Willow (*Salix*), and Mesquites (*Prosopis*) (Miller and Stebbins,

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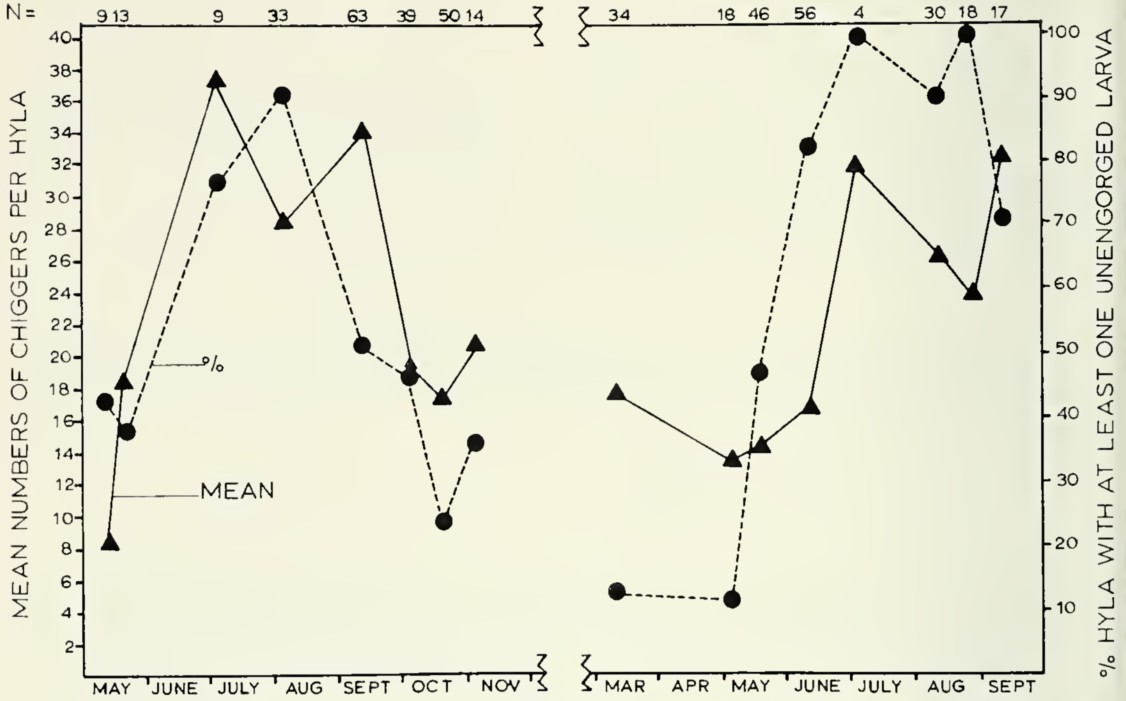

Figure 1. The occurrence of *Hannemania hylae* on *Hyla cadaverina* at Fortynine Palms Oasis, from May 1969 through September 1970. N = number of frogs examined, triangles and solid lines indicate mean numbers of larvae per frog, and dots and dashed lines show the percent of *Hyla* with at least one unengorged chigger.

1964). Other plants in and around the ponds were cattails, reeds, numerous herbs, and algae.

Pond one, the largest and deepest (1 m), contained the most *Hyla cadaverina* and *Bufo punctatus.* The tree frogs were in evidence around the pond by day and night in the spring and fall, whereas on summer days they regularly retreated into rock crevices at the west end of the pool.

Pond two, a small depression filled with cattails and water about 0.2 m deep, contained few *Hyla cadaverina* and *Bufo punctatus.*

Pond three, the most stable of all oasis ponds, contained nearly 0.5 m of water and varied less than 0.03 m in depth all year. This pond was shaded by palms nearly all day and harbored few *Hyla cadaverina* or *Bufo punctatus.*

METHODS

Twenty-two visits to Fortynine Palms Oasis were made between May 1969 and April 1971, to locate and capture *Hyla cadaverina* and *Bufo punctatus.* These anurans were released soon after the toes were clipped (Jameson, 1955) and the numbers of unengorged and engorged larvae were recorded.

The amphibian populations were estimated using the Schnabel Method of accumulative capture and recaptures (Smith, 1966).

$$N = \frac{\Sigma(A)\ (B)}{\Sigma(C)}$$

A = number of amphibians captured
B = number of amphibians marked
C = number of recaptures
N = population estimate
Σ = sum

With this method the total estimate of the amphibians was obtained by averaging the last four population estimates. The larval population of each species was determined by using the mean host population estimate and mean number of chiggers counted per host each visit. These data were arranged by months and plotted in figures 1 and 2.

In addition, two attempts were made to locate unfed, free-living chigger larvae using ten un-

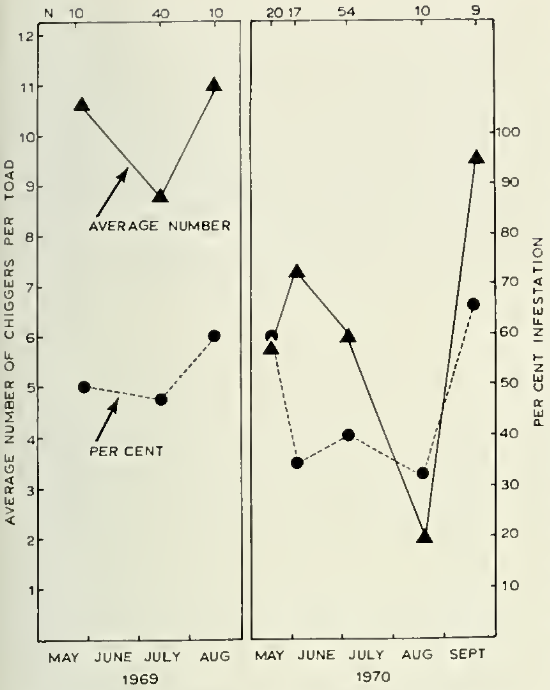

Figure 2. The occurrence of *Hannemania bufonis* on *Bufo punctatus* at Fortynine Palms Oasis, from May 1969 through September 1970. N is the number of toads examined, triangles and solid lines denote the mean numbers of larvae per toad, and dots and dashed lines indicate percent of chigger infestation on the toads.

infested *Hyla cadaverina* in screen cages placed in selected sites around the oasis.

HYLA CADAVERINA AND THE CHIGGER *HANNEMANIA HYLAE*

In the vicinity of the upper three ponds, 256 *Hyla cadaverina* were marked and 197 of these were recaptured at least once. Using the Schnabel Method the mean frog population was estimated to be approximately 288 individuals.

No territoriality was detected as marked frogs were captured at various sites. However, the frogs seemed to prefer rocks located at the western margins of ponds 1 and 3, whereas few frogs were found in pond 2. The tree frogs showed little movement between ponds, as only 15 individuals (5 percent) were captured in more than one pond. In July of 1969 and 1970 when the oasis was subjected to thunderstorms, *Hyla cadaverina* seemed to virtually disappear. However in July 1970, after a thunderstorm, several *H. cadaverina* were heard calling and one tree frog was captured high up on an adjacent hillside. This migration from the canyon bottom was noted only during thundershower activity.

The number of *Hannemania hylae* on *Hyla cadaverina* varied seasonally. The mean for 1969 and 1970 was 21.4 larvae per frog with 98.9 percent infestation. In the spring (March, May, and early June) there was a mean of 15 chiggers (range 8–18) per frog with an estimated population of 4250 larvae. During the summer (July, August, and September) the mean per host doubled to nearly 31 larvae (range 24–37), and the estimated population of embedded chiggers was 8500 larvae. In the fall the mean dropped to 19 chiggers (range 17–20) per frog or approximately 5400 chiggers. This represented a reduction from the peak summer population to nearly 3000 chiggers in the fall and even fewer larvae were present the following spring. Therefore some engorged larvae dropped off between late fall and early spring.

When the percentage of tree frogs infested with at least one unfed *Hannemania hylae* was plotted with the mean number of chiggers per frog per month (Fig. 1) it showed that the increase of chiggers per frog in the summer resulted from more unengorged larvae. This would seem to indicate that most of the active unfed larvae emerge and find a host in the summer, as verified by finding most but not all unengorged larvae on the tree frogs during the summer.

In September 1969, all chiggers were removed from 29 toe-clipped *Hyla cadaverina* before their release. Recaptures showed few if any new chiggers until June, and by August and September of 1970 the recaptured frogs had the expected numbers of larvae. This also indicated that the unfed larvae became embedded in the hosts from late June through August.

Two attempts were made to locate unfed larvae of *H. hylae* and a single chigger was found on each of two frogs placed among the rocks. This suggests that unfed larvae and probably the nymphs and adults live in rock crevice retreats of the frogs.

BUFO PUNCTATUS AND THE CHIGGER *HANNEMANIA BUFONIS*

At the oasis, adult toads were found from May through September. They breed in Ma

June, and July, and were especially numerous in breeding congresses after dark following thundershowers in July of 1969 and 1970. This breeding pattern has been noted by Stebbins (1954), Tevis (1966), Mayhew (1968) and others.

A total of 131 toads were marked and 39 of these were recaptured at least once. The mean population in and around the upper three ponds was estimated at approximately 300 toads using the Schnabel Method (Smith, 1966). Most of the toads were found at pond 1, although some toads were found, but not marked, at ponds 4 and 9.

The infestation rate of *Hannemania bufonis* on *Bufo punctatus* was 46.8 percent, with a range of 33 to 70 percent infestation, with a mean number of eight chiggers per toad and there was seasonal variation (Fig. 2). The infestation percentage was low when compared to that of *Hyla.*

The greater numbers of chiggers were recorded in May, late August, and September, whereas fewer chiggers were seen in June, July, and early August. In 1969, when only 60 toads were examined, the infestation remained unchanged (50 percent in May and 47.5 percent in July) until late August when it increased to 70 percent. However the mean number of chiggers remained relatively unchanged as the low of 8.8 chiggers per toad in July was only two chiggers less than in August. In 1970, 100 toads were examined from late May to mid-September, and although the infestation rate was similar to that of 1969, there was a greater range of infestation percentages. The highs were in May with 60 percent and September with 66 percent infestation, whereas the lowest was 30 percent in August. The mean number of chiggers per toad ranged from two in August to 9.6 in September.

The mean yearly population of larval *H. bufonis* on *B. punctatus* was estimated to be 1224 chiggers. In 1969 the population dropped to approximately 840 larval chiggers in May to July and increased to approximately 1060 chiggers (45.8 percent) in August. The few unengorged larvae found were observed only in August and September. In 1970 the larval population was estimated to be approximately 1100 in May, dropping to a mean of 550 in June, July, and August. The reduction was approximately 50 percent, whereas a 71 percent increase, to 1350 chiggers occurred in September.

Apparently the active unfed larva parasitized a toad in August and September, engorged and overwintered on the host. The engorged larva probably dropped off the toad between early May and August after spending at least eight months or longer embedded in the host. Some of the larvae were embedded throughout the year. As a free-living mite it goes through three nymphal stages, emerges as an adult and the inseminated female lays eggs that hatch in the summer. Therefore the unfed larvae emerge while the toads are active around the pools.

SUMMARY

Hannemania hylae and *H. bufonis* have definite life cycles correlated with the activity cycles of their hosts. Although engorged larvae were present on the hosts throughout the year, the active unfed and embedded unengorged larvae were found in the summer months from July to September.

Although these two sympatric species are morphologically similar (Loomis and Welbourn, 1969) each annual cycle appeared to be different. *Hannemania hylae* had an extended summer period of larval abundance (July, August, September) on hosts, whereas *H. bufonis* reached its greatest abundance in late August and early September. However each species seems to complete only a single life cycle per year, although engorged larvae may spend more than one year on the host. *Hannemania bufonis* appears to have a longer parasitic period than *H. hylae* with larvae remaining on their hosts from August-September to May or August the following year. *Hannemania hylae* attached on their host in the summer but there was a significant reduction in engorged larvae in the fall.

Estimates of the percent infestation and the mean annual larval populations of the two chigger species were significantly different, although the estimated host populations were similar. The percent infestation for *H. hylae* on *Hyla* was 98.9 percent whereas the infestation of *H. bufonis* on *Bufo* was 46.8 percent. The population estimates were 6063 larval *H. hylae* per year on 288 *H. cadaverina* as compared to only 1224 larvae of *H. bufonis* on 300 *B. punctatus.*

The unengorged larval *H. hylae* and presumably nymphs and adults occur in rock crevice retreats of the host.

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CIRCADIAN ACTIVITY RHYTHM IN THE HORN SHARK, *HETERODONTUS FRANCISCI*: EFFECT OF LIGHT INTENSITY

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Abstract: Activity onsets of horn sharks, *Heterodontus francisci*, were studied in the natural environment at Santa Catalina Island, California. The mean of activity onsets of these nocturnal sharks occurred 76 min after sunset which corresponded to an approximate light level of 0.03 lux. During laboratory studies under a fixed LD 12:12 (12 hr light–12 hr dark) regime, the L phase of which was 8 lux, *H. francisci* showed anticipation of the D phase. Under 23 days of constant dim light, *H. francisci* exhibited a drifting circadian rhythm with period lengths, for one individual, of 20.8 hr under 2.0 lux, and 23.0 hr under 0.13 lux. Under 15 days of constant darkness, the sharks showed a high level of aperiodic activity. During laboratory experimental dusk transitions, the light intensity eliciting onset of activity was: 1), proportional to the amount of time sharks spent in the L phase of the LD regime, and 2), independent of the level of light during the L phase of the LD regime.

Many studies have been published concerning the effect of light intensity on the diel behavior of fish. Among those conducted in the natural environment were Cummings, Brahy, and Herrnkind (1964), Starck and Davis (1966), Collette and Talbot (1972), Emery (1973), and Hobson (1965, 1968). Their observations indicated that individual species and often whole families tend to be consistent in their periods of activity, vocalization, or predatory behavior, being diurnal, nocturnal, or crepuscular. Hobson (1972) described fish activity on a Hawaiian coral reef during the transition between daylight and darkness. Three major periods were recognized: 1), shelter-seeking of diurnal fishes, ending 15 min after sunset (10 lux); 2), an interim "quiet" period, 13 to 33 min after sunset (10 to estimated .01 lux); and 3), emergence of nocturnal fishes, 33 to 50 min after sunset (estimated .01 to .0001 lux).

Laboratory experiments involving the effects of light on the diel behavior of teleosts have been numerous, including those of Jones (1956), Davis (1962), Kruuk (1963), Lissman and Schwassmann (1965), Lane (1967), and Olla and Studholme (1972).

There is little literature on the effect of light intensity on diel behavior in sharks. Observational notes on various species have been published by Springer (1963), Limbaugh (1963), Randall (1967), and Hobson (1968). Springer and Randall have noted that some species of tropical sharks, e.g., the tiger shark, *Galeocerdo cuvieri*, avoid shallow water during the day, apparently because of high light intensity. Clarke (1971) suggests that small hammerhead pups, *Sphyrna lewini*, respond to bright light by seeking the darkness of greater depths. Underwater investigations in Australia of the Port Jackson shark, *Heterodontus portusjacksoni*, have shown that it is nocturnal and spends much of the day inactive in caves and trenches of oceanic reefs (McLaughlin and O'Gower, 1971). Utilizing ultrasonic telemetry, Standora (1972) determined the Pacific angel shark, *Squatina californica*, to be basically nocturnal in activity.

Nelson and Johnson (1970) found that *H. francisci* and the swell shark, *Cephaloscyllium ventriosum*, were distinctly nocturnal (night active, day inactive) in the natural environment and under laboratory LD 12:12 regimes. The swell shark showed a drifting circadian rhythm under constant darkness and under constant light of 515 lux. The horn shark, however, showed only aperiodic activity of high level under constant darkness, and of low level under 515 lux.

The above study contains the only published laboratory experiments on activity rhythms in sharks, but includes no investigation of the effects of varying light intensities. This paper addresses this subject and is a further contribution to the understanding of activity rhythms in sharks.

METHODS

The underwater research was conducted at Ship Rock, a small rocky pinnacle 2 km north of the

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Isthmus, Santa Catalina Island, California. The study area, in a kelp-bed community averaging 10 to 20 m deep, consisted of steep, rocky slopes with many caves in which the horn sharks spent their daylight hours.

Underwater clocks (battery-powered Westclox TR-3, in waterproof housings) were used to determine the time at which the sharks left their daytime refuges to begin nighttime swimming activity. A clock would be attached to a nearby resting shark's dorsal spine via a short monofilament line and alligator clip. A pull on the line would move an external magnet, causing opening of an internal reed switch, thereby stopping the clock at the time of shark departure. Light levels were recorded underwater by a photographic-densitometric technique, using an underwater 35mm Nikonos camera and neutral-density filters.

The laboratory experiments, using male sharks of 31 to 63 cm total length, were conducted in a light-proof, temperature-controlled laboratory at California State University, Long Beach. Four circular vinyl pools (1.5 m diameter, .35 m deep) were located within the laboratory, and held one experimental shark each. The primary light source was a 300 watt projector lamp (Sylvania CRT, 3200° Kelvin) which provided a maximum light level of 8 lux in the pools. The light projector was placed on the floor at the common center of the four pools and projected to the white ceiling, thereby reflecting downward equally into each pool. An additional 300 watt incandescent bulb with reflector and rheostat control was used only when levels above 8 lux were needed.

The level of the primary light source was controlled by neutral-density filters (Kodak Wratten N.D., 0.3 log) which were placed in a felt-lined container over the projector aperture. Each filter when placed over the aperture reduced the light level by 50%; when simulating dusk transitions, this was done by hand every 5 min. Light levels of 2 lux and over were measured with a selenium-cell photometer (G.M. Mfg. and Instrument Co., Model 15MO4). Readings were taken at the bottom center of each pool. Levels below 2 lux were calculated extrapolations based on the number of filters used.

Electro-mechanical activity sensors similar to those used by Spoor (1941) and Nelson and Johnson (1970) were used to detect the activity of the sharks. Activity in each of the pools was recorded simultaneously on separate tracks of an Esterline-Angus event recorder, as was the condition of the primary light, i.e., on or off.

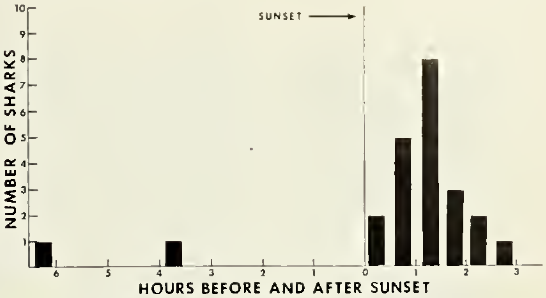

Figure 1. Activity onset times (in relation to sunset) of 24 *H. francisci* in the natural environment.

In experiments involving dusk transitions, all filters were removed after activity-onset data were obtained from all sharks being tested. This restored the normal L-phase light level for the remainder of the 12-hr L phase. An activity onset during these regimes was defined as the start of a minimum of 10 min of continuous activity, preceded by a minimum of 2 hr with no continuous activity exceeding 2 min. During regimes without dusk transitions, activity onset was determined by inspection as the start of the primary period of activity.

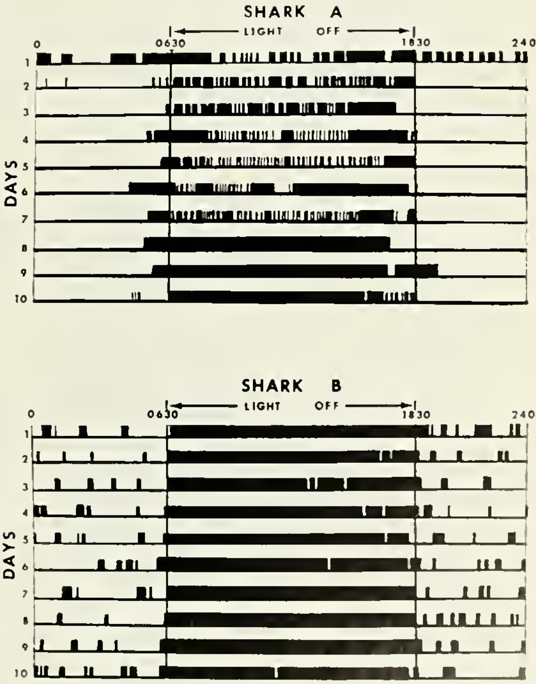

Figure 2. Laboratory activity records of 2 *H. francisci* under an LD 12:12 regime, the L phase of which was 8 lux.

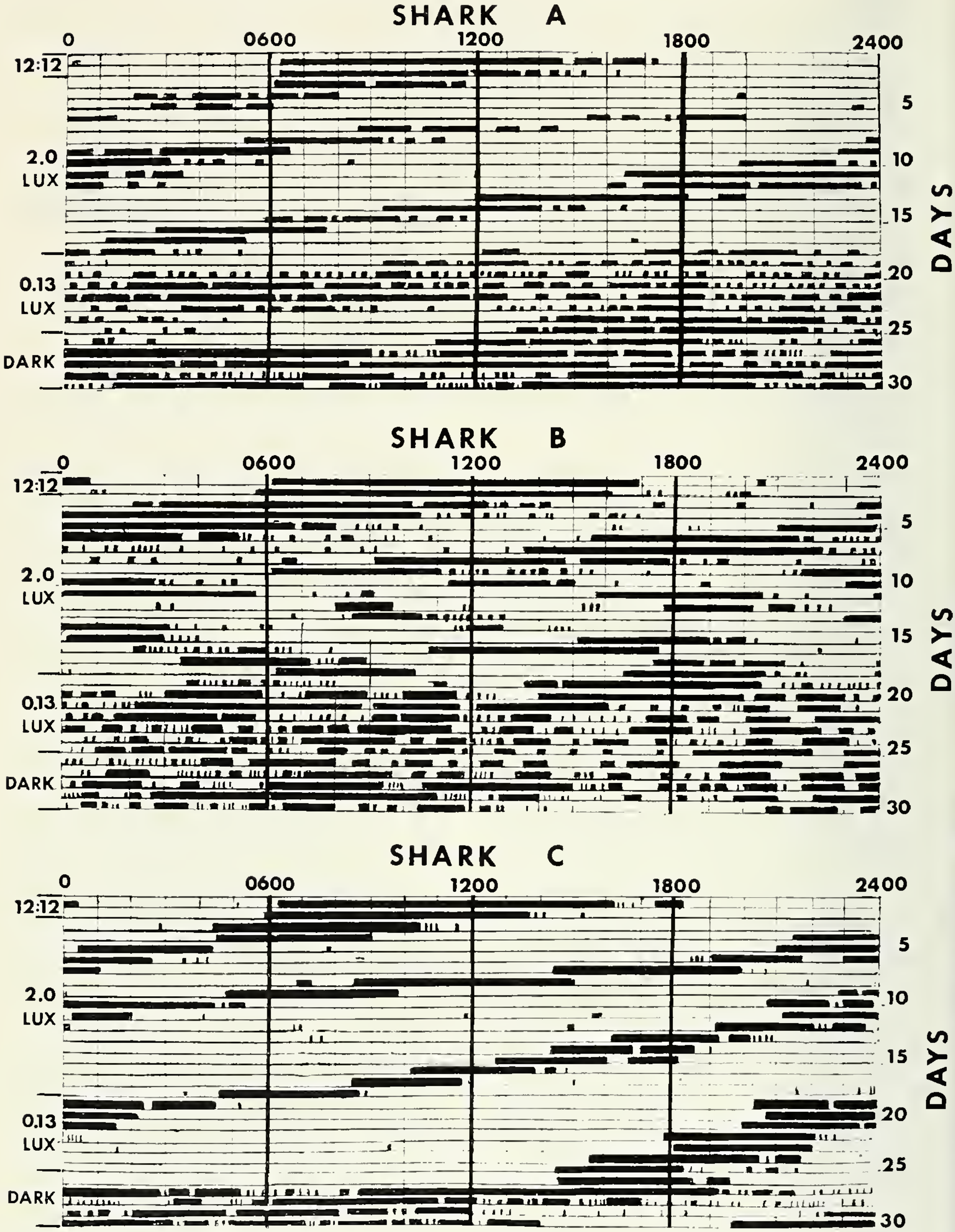

Figure 3. Laboratory activity records of 3 *H. francisci* under several lighting conditions. Days 1–2: LD 12:12, the light phase (1800–0600 hr) of which was 8 lux. Days 3–18: Constant light of 2.0 lux. Days 19–25: Constant light of 0.13 lux. Days 26–30: Constant darkness.

RESULTS

Activity onsets of 24 *H. francisci* were recorded in the natural environment at a mean depth of 10.5 m (Fig. 1). The mean time for onset of activity was 76 min after sunset (not counting two mid-day onsets) with a range of 19–156 min; the greatest concentration of onsets occurred between 60 and 90 min after sunset. The mean light level at 10 m depth at 75 min after sunset was approximately 0.03 lux.

One shark, tested 26 March 1970, remained inactive for 24 hr. On examination, this shark's stomach was relatively full, containing 2 blacksmith, *Chromis punctipinna* (Pomacentridae), and one squid, *Loligo opalescens*. Two sharks became active during full daylight, and two others became active relatively early at 19 and 24 min after sunset. These four onsets occurred during the annual early-summer occurrence at Ship Rock of numerous dead and dying blacksmith, found on the bottom at depths of 5 to 20 m.

Laboratory activity data are shown in figure 2 for two sharks held 10 days under an LD 12:12 regime, the light (L) phase of which was 8 lux, and the dark (D) phase of which was total darkness. Shark A showed definite anticipation of the D phase on every day except day 10 and possibly day 2 (the animal appeared not yet acclimated to the situation on day 1). Shark B showed anticipation on days 4, 5, 6, 8, 9, and 10. During 15 subsequent days of constant darkness, both sharks showed a high level of aperiodic activity.

The activity of three sharks under constant low-light is shown in figure 3. Days 3–18 were held at 2.0 lux, days 19–25 at 0.13 lux, and days 26–30 were in total darkness. A drifting circadian rhythm of less than a 24-hr period was observed for all three sharks under 2.0 lux. Under the lower intensity of 0.13 lux, Shark A's activity became erratic and nearly aperiodic except for the last several days. Under 0.13 lux, Shark B became totally aperiodic. Shark C, which exhibited the clearest periodicity, maintained a definite rhythm under 0.13 lux. Under 2.0 lux, Shark C averaged a circadian period length of 20.8 hr, i.e., drifting earlier 3.2 hr/day. Under 0.13 lux, however, the same shark increased its period to 23.0 hr, i.e., drifting 1.0 hr earlier/day. In total darkness all three sharks appeared arhythmic. In Shark C, lengthened periods of activity were associated with shorter circadian periods, whereas shortened activity periods occurred with longer circadian periods.

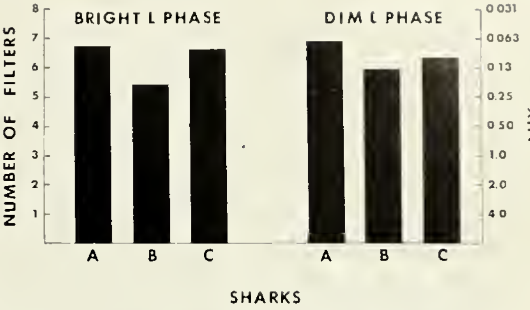

Figure 4. Mean light levels during laboratory dusk transitions eliciting activity onset in 3 *H. francisci* spending 12 days in an LD 12:12 regime. The L phase was alternated on successive days between bright (180 lux) and dim (8 lux).

The effect of L-phase light intensity is shown in figure 4. Three sharks were subjected to an LD 12:12 regime for 12 days. A high light level (180 lux) and a low light level (8 lux) were provided on alternate days during the light-on phase. At the 8th hr of the L phase, the light intensity was reduced from 8 lux at the rate of 50 percent (one filter)/5 min until activity onset occurred. On the days of high illumination, the reduction process was started 20 min early to reduce from 180 lux down to 8 lux at the rate of about 50 percent/5 min. A mean of 0.14 lux

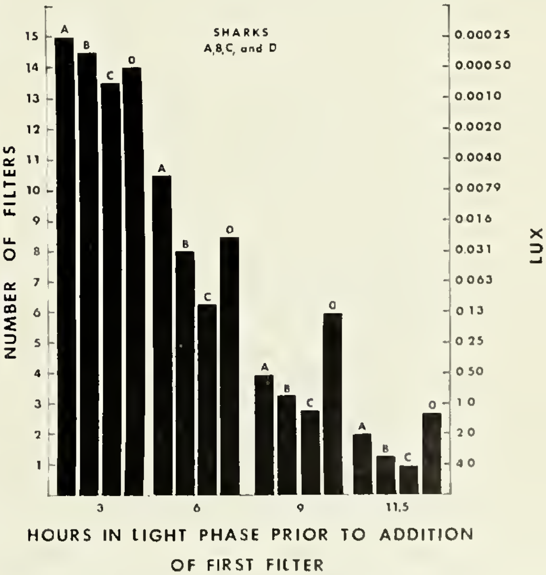

Figure 5. Mean light levels during laboratory dusk transitions eliciting activity onset in 4 *H. francisci* as a function of number of hours spent in the L phase of an LD 12:12 regime. Based on 16 days of testing each shark (4 days/hour group).

was required to elicit activity onset following L-phase levels of 180 lux, and a mean of 0.12 lux was required after L-phase levels of 8 lux. Statistical analysis (*t* test) showed no significant difference between these means.

The effect of number of hours spent in the L-phase on the light level eliciting activity onset in four sharks is shown in figure 5. A marked increase in this light level, i.e., decrease in amount of dimming necessary, occurred with an increase in the number of hr spent in the L phase. The mean light levels eliciting activity onsets for 3, 6, 9, and 11.5 hr in the L phase were 0.00040, 0.021, 0.50, and 2.3 lux respectively. From figure 5 it can also be seen that the individual sharks differed in their relative response to the light stimulus. For example, in all four cases, Shark C required the least dimming to elicit activity, and the relationships between Sharks A, B, and C were maintained in all four cases.

DISCUSSION

Although *H. francisci* clearly exhibited a circadian rhythm under laboratory conditions of constant dim light, shark activity during LD cycles was synchronized closely with the onset of darkness (during abrupt changeovers), or with a particular light level (during artificial dusk transitions). In the natural environment, therefore, it seems that activity would be closely synchronized to some light intensity (at the shark) during the natural dusk transition. Since these sharks are found to considerable depths, and are often quite far back in caves during the day, both of which affect the amount of light reaching the shark, some range of activity onset times relative to sunset would be expected. A shark initiating activity deep in a cave, however, may be inhibited from actually departing by the brighter light at the cave mouth. Because of the depth and cave-dwelling habits of this species, it would also seem necessary that it be capable of synchronizing to diel cycles of quite low L-phase levels.

In this study, *H. francisci* in the natural environment became active at an average of 76 min after sunset at about 0.03 lux. Those nocturnal Hawaiian reef fishes observed by Hobson (1972) began their mass emergence about 33 min after sunset at about 0.01 lux—a light level of similar order of magnitude. The lower light level relative to sunset is at least partly due to the shorter twilight at the more southerly latitude of Hawaii.

Activity onsets in the field, however, are not always correlated with a particular light level, as was shown by the two sharks which became active during full daylight, and the two which started swimming relatively soon after sunset. These early activities, however, occurred during the presence of large numbers of dead and dying blacksmith and may represent a response to this unusual feeding opportunity. Standora (1972), working with angel sharks, *Squatina californica*, another primarily nocturnal species occurring at Ship Rock, found these sharks to be day-active also only when dead and dying blacksmith were abundant.

Laboratory studies on *H. francisci* by Nelson and Johnson (1970), showed that under an LD 12:12 regime, the L phase of which was 515 lux, no anticipation of the D phase was exhibited, and under a constant 515 lux activity was greatly reduced and aperiodic. Rhythm studies on certain other species, however, indicate that excessively bright light can inhibit activity or extinguish circadian rhythmicity (Harker, 1958). In the present study, using a lower L-phase intensity of 8 lux, anticipation of the D phase clearly occurred (Fig. 2), indicating the existence of at least a "short-term" internal timer. The drifting periodicity of the three sharks (Fig. 3) under constant low-light (2.0 lux), definitely shows the presence of a circadian rhythm and supports the existence of long-term endogenous control. These results also indicate that the relatively bright light used previously by Nelson and Johnson was indeed inhibitory of activity and rhythmicity.

According to Aschoff's rule, a decrease in the intensity of constant light causes a shortening of the circadian period in nocturnal organisms (Aschoff, 1960; Pittendrigh, 1960). Data from the present study does not follow this rule as the one shark which remained clearly rhythmic at 0.13 lux showed a lengthening of its period relative to that at 2.0 lux. Sufficient data on this matter was not obtained from the other two sharks tested under constant conditions as they became erratic or arhythmic at 0.13 lux. Further testing would be desirable, therefore, before concluding that *H. francisci* typically behaves contrary to Aschoff's rule. Harker (1964) has shown, however, that there are species which have been studied for long periods of time which do appear to be exceptions to Aschoff's rule.

As demonstrated in figure 4, the L-phase light level prior to the dusk transition did not affect the light level at activity onset. Because the experiment started 20 min earlier on days of bright light, a greater change in intensity occurred on these days than on days of dim light. Because the sharks became active at the same light level, they appeared to be responding not to a relative amount of change of intensity, but rather to a specific absolute light level. These results suggest that *H. francisci* in the natural environment may tend to become active at the same underwater dusk light level regardless of fluctuations in daytime light intensities due to cloud cover or water turbidity.

Laboratory experiments (Fig. 5) also showed that the light level releasing activity is very dependent on the amount of time the shark had spent in the L phase of an LD 12:12 regime. The sharks' sensitivity to dimming of the light increased with the number of hours it had spent in the light. Their "readiness" to swim appeared much stronger after the 11th hr in light than after, for instance, the 3rd hr. This difference, however, does not appear explainable simply on the basis of recovery from physical fatigue from the previous night's swim, as sharks in constant darkness typically swim almost continuously for at least several days before fatigue appears to reduce activity. The shark's change in responsiveness to light might be thought of as regulated from within by a short-term (at least ½ diel cycle) rhythm in phase with the LD cycle. These findings are in accordance with those of Davis (1962) in which recovery time of bluegills, *Lepomis macrochirus*, from a light shock during the D phase of an LD 12:12 regime decreased with an increased amount of time spent in the dark.

The main advantages to *H. francisci* of nocturnal activity are probably to obtain nocturnally active prey and possibly to escape diurnally active predators. Many invertebrates, especially crustaceans and echinoderms, are night active and away from their daytime refuges and would therefore become more available as prey. The sea urchins, starfish, and bivalve molluscs found in stomachs of this species by Taylor (1972) support this idea. That the food of the Port Jackson shark, *H. portusjacksoni*, includes crustaceans and echinoderms also supports this hypothesis (McLaughlin and O'Gower, 1971). Present predators of *H. francisci* are unknown, but the elephant seal, *Mirounga angustirostris*, according to Daugherty (1966), was once more abundant in California and does feed on small sharks. The daytime seclusion of *H. francisci* in deep caves could have served as protection from this or other predators.

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A NEW SPECIES OF PALEOCENE CHIMAEROID FROM CALIFORNIA

SHELTON P. APPLEGATE[1]

ABSTRACT: A new species of Chimaeroid from the Paleocene of California is described which is the first New World record for the genus *Ischyodus*. The relationships of the present new species within the genus *Ischyodus* is discussed.

The ratfishes of Chimaeroids are elasmobranch fishes known from the Devonian to the Recent. The suborder Chimaeroidei is known from the Jurassic. The oldest member being *Ischyodus aalensis* Reuss 1887. In these fishes the jaw elements are frequently preserved and are of taxonomic importance. The genus *Ischyodus* is extinct.

CLASS: HOLOCEPHALI

Order: Chimaeriformes

Suborder: Chimaeroidei

Family: Edaphodontiae Owen, 1845

Genus *Ischyodus* Egerton, 1843

Ischyodus zinsmeisteri, new species

Holotype: LACM 37206, a lower right mandible, (Figs. 1, 2).

Horizon and Locality: The locality where the specimen was collected is LACM Loc. number 3216, a dark rusty brown concretion in a limestone at lat. 34°14′58″ N, and long. 118°42′52″ W, T2N R18W, elevation 1200 to 1225 feet above sea level on a ridge between Meier and Runkle Canyons, Calabasas Quadrangle 1942, 7.5 minute series scale 1:24,000 Simi Hills, Ventura Co, California. The collector was William Zinsmeister. The rocks are mapped as being marine and of Paleocene age (Jennings and Strand, 1969).

Diagnosis: A mandible with an elongate and pointed beak. The symphyseal tritor is placed near the base of the jaw and is the smallest tritor.

Description: The type (Fig. 2) is characterized by a long, straight beak which is inclined at an angle of approximately 45° from the vertical. Below and behind the beak are two well defined ridges which are directed anteriorly in the same manner as the beak. The ridges end in a raised cutting edge (Fig. 2B). The lateral side of the mandible (Fig. 2A) is flat except where the anterior one-half of the beak curves toward the symphysis. The inner side of the beak possesses a thick ridge that originates just below the lip and runs to the base of the tooth (Fig. 2B). The cutting edge of the tooth (Fig. 2A) shows a high beak followed by two rounded protuberances formed at the top of the two ridges (Fig. 2B). Tritors are columns of calcified hard tissue which are less subject to normal wear than the surrounding soft calcified tissue of the jaw plate. They are visibly distinct and represent important taxonomic entities. There are five tritors (Fig. 2B): 1), a beak tritor, shown in detail in (Fig. 2D); 2), a symphyseal tritor; 3), an anterior dorsal tritor; 4), a posterior dorsal tritor and 5), a median tritor. The last four are seen in (Fig. 2B). The beak tritor consists of a tritoral

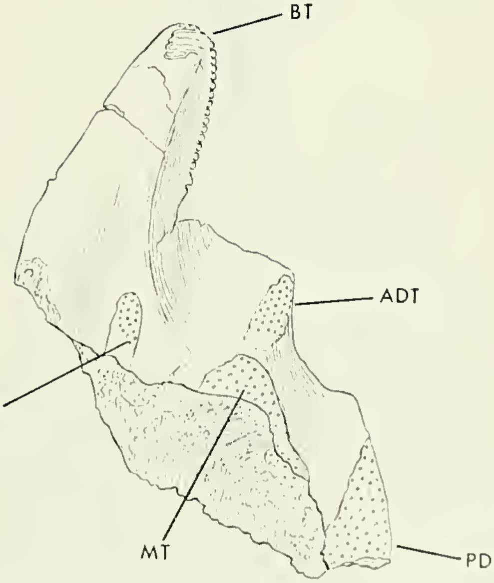

Figure 1. Ischyodus zinsmeisteri, new species, a diagrammatic sketch of LACM 37206 (holotype), right mandible enlarged × 3.6: bt. beak tritor; st. symphyseal tritor; adt. anterior dorsal tritor; pdt. posterior dorsal tritor; mt. median tritor.

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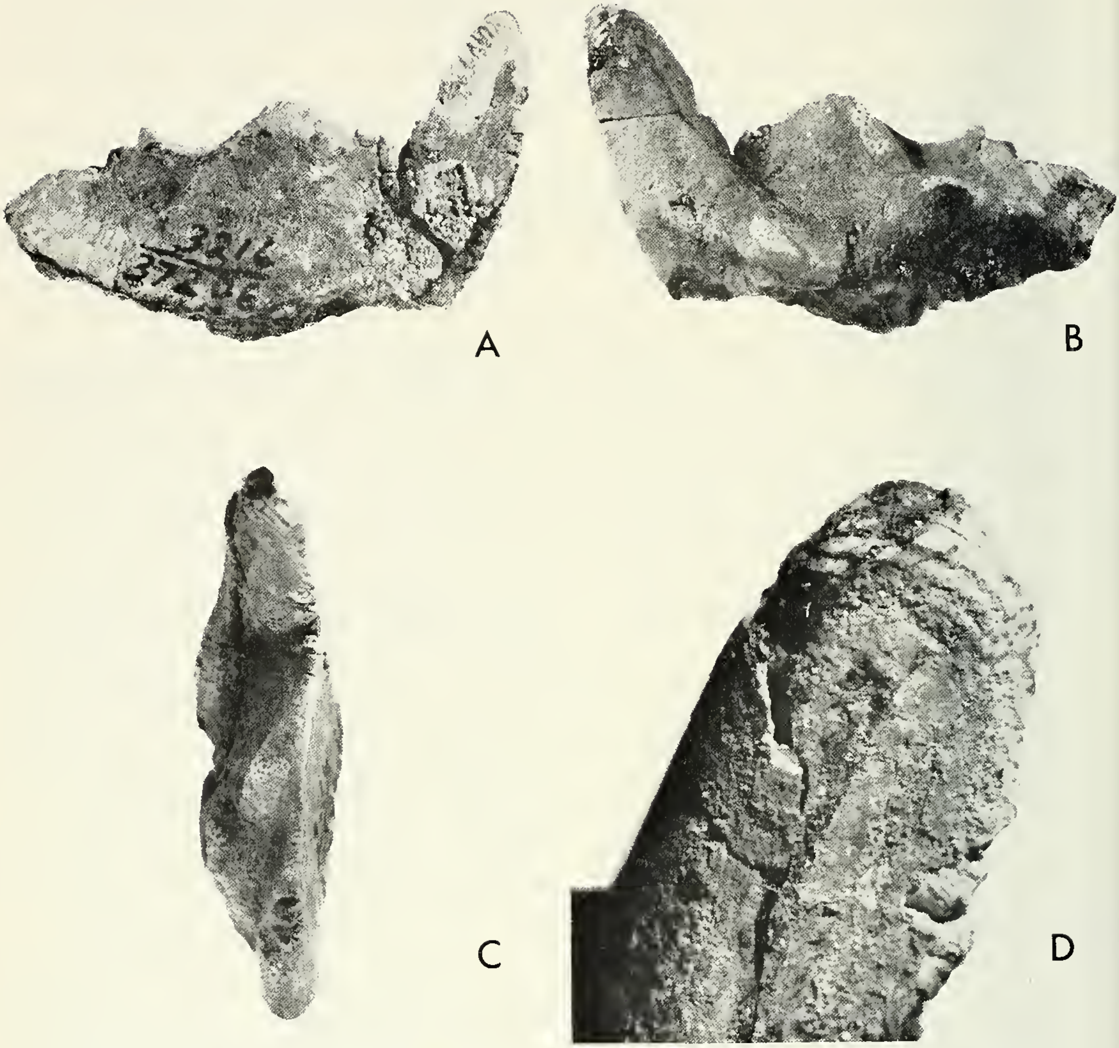

Figure 2. A, Holotype, LACM 37206, view of lateral surface of mandible (enlarged × 2.5); B, view of internal side of mandible (enlarged × 2.5); C, superior view of mandible (enlarged × 2.5); D, inner tip of beak (enlarged × 9.2).

column with pteromic hard tissue (Orvig, 1967), in the form of plates. The posterior tip of the beak shows exposed canals surrounded by radiating calcifications as with the other tritoral areas. The inner dorsal side near the tip shows four plates (Fig. 2D) and the posterior edge of the beak shows 15 platelets seal (Fig. 1). At the base of the beak ridge (Fig. 2B) is the symphyseal tritor. The symphyseal tritor is roughly elongate oval in shape and about one-half the size of the anterior dorsal tritor; as such, it is the smallest tritoral area. The anterior dorsal tritor lies near the top of the first ridge below the border of the cutting edge. The cutting edge of the first ridge in front of this tritor does, however, seem to be composed of a hard tissue. The anterior tritor is elongate oval and rests atop the upper portion of the first ridge as mentioned. The posterior dorsal tritor is incomplete, but rests on the posterior side of the second ridge and occupies one-half of the cutting edge. The median tritor lies at the base of the first ridge posterior to the anterior dorsal tritor and below the posterior dorsal tritor. The median tritor is incomplete yet it is the largest tritoral area.

Measurements in (mm): Total length, 32.1; height, 22.1; thickness, 9.0; height of beak, 11.0. Symphyseal tritor, length, 4.0; width, 2.0. Anterior dorsal tritor, length, 6.0; width, 2.0. Posterior dorsal tritor (incomplete), length (greatest), 10.0+; width (greatest), 4.0. Median tritor (incomplete), length, 8.0+; width, 5.0+.

DISCUSSION

The present fossil mandible is referable to the ratfish genus *Ischyodus*. Several conflicting systems have been used for naming tritors in this genus. More recent among the workers suggested systems are Woodward (1911), Gurr (1962), and Radwanski (1968). Woodward (1911) refers to a beak tritor which is the apical dentine of Gurr (1962). The symphyseal tritor of Leriche (1902) and Radwanski (1968) is the internal anterior tritor of Gurr (1962). The internal posterior tritor of Gurr is the median tritor of Woodward (1891) and Radwanski (1968). The median tritor of Gurr (1962) does not occur in studies by either Woodward (1891) or Radwanski (1968), therefore, this tritor should be given a different name, perhaps intermediate tritor would be appropriate. The external anterior tritor and the external posterior tritor have similar usage by all of the above authors so they present no real problem. I have followed the terminology of Woodward (1891), Leriche (1902), and Radwanski (1968).

The genus *Ischyodus* was erected by Egerton (1843). It ranges from the Jurassic to the Eocene. *Ischyodus* differs from the related genus *Edaphodon* in that there is a hard layer on the outer aspect immediately below the oral margin (Woodward, 1891). The symphyseal facet is narrow. There is a beak tritor, a median tritor which is undivided and two external tritors. Woodward does not mention a symphyseal tritor and Applegate (1970) is in error in stating that this genus has only four tritoral areas since *I. thurmanni*, Pictet and Campeche, 1858, has at least five and *I. dolloi*, Leriche, 1902 has, according to Gurr (1962) six tritors. The large size of the upper part of the beak, the small size and low placement of the symphyseal tritor separate *Ischyodus zinsmeisteri* from any of the closely related Tertiary or Cretaceous species. It is closest to *Ischyodus dolloi*, whose lower jaw was described by Gurr (1962).

This specimen is the first member of the genus to be described from the New World; only two other Tertiary species being known. *Ischyodus thurmanni* is a species that bridges the Cretaceous-Tertiary gap, being known from the Cretaceous of Europe and the Paleocene of New Zealand. *Ischyodus dolloi* is known from the Paleocene of Belgium and the lower Eocene of England.

Ischyodus zinsmeisteri was etched from a limestone which contains an important, but as yet, undescribed Paleocene shark fauna. Tentative identifications of this fauna suggests that it has shark species known from North Africa and Europe. Stratigraphic studies in progress will hopefully place the beds from which *Ischyodus zinsmeisteri* was collected more precisely in the Paleocene.

Mr. Zinsmeisteri states in a letter (14 May 1973) that the *Ischyodus* specimen was collected from a small, dark rusty-brown concretion. Associated with *Ischyodus* were several species of mollusks, *Retipirula crassitesta* and *Amauropsis martinezensis*. The locality is 428 feet above the contact between the Martinez marine member and the underlying Simi conglomerate. To be more specific, Zinsmeister says this is what he calls the lower concretionary horizon of the Martinez marine member.

ACKNOWLEDGMENTS

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PREDATION ON THE ISOPOD CRUSTACEAN *PORCELLIO SCABER* BY THE THERIDIID SPIDER *STEATODA GROSSA*

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Abstract: A population of the theridiid spider *Steatoda grossa* in Pacific Grove, California was studied to observe its predatory behavior towards the terrestrial isopod *Porcellio scaber* and subsidiary prey items. The isopod and spider are both found to be nocturnally active. The carcasses of consumed prey are cut from the spider's web to collect in a debris pile which can be examined for an indication of long term dietary consumption. The isopod, though rejected as prey by most spiders because of repugnant tegumental glands, composes 84 percent of the diet of this spider as determined by web analysis. The spider from laboratory experiments was found to average 5.0 days between meals but able to tolerate periods of three weeks or more without feeding.

Cloudsley-Thompson (1958), reported birds, reptiles, amphibia, and many other insectivorous animals including spiders, harvestmen, mites and centipedes as predators of terrestrial isopods. For central Californian woodlice, Miller (1938) listed as vertebrate predators "at least two species of salamanders, several species of reptiles, birds, and insectivores; among the invertebrates, the black widow spider (*Latrodectus mactans*) and various species of centipedes." Gorvett (1956) has stressed the importance of the tegumental glands as defense mechanisms in isopods; these organs only occur in terrestrial species and the fact that their secretions are distasteful to many spiders suggests that spider predation has provided the strongest selective pressure for their evolution. Spiders thus appear to be at least potentially the major predators on woodlice, yet detailed studies of spider predation on isopod populations are almost non-existent.

Porcellio scaber Latreille, 1804 is the terrestrial isopod which shows the greatest development of the tegumental glands (Gorvett, 1951). This species is a member of the cryptozoan community, a term coined by Dendry (1895) to describe the assemblage of small terrestrial animals found dwelling in darkness beneath stones, rotten logs, bark of trees, and other similar situations. Though cosmopolitan in distribution, and one of the commonest isopods in the United States, little study

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has been devoted to its interspecific relationships, particularly those of predation.

Several groups of arachnids were initially observed in their contacts with *P. scaber* under laboratory conditions; these included solpugids, harvestmen, wolf spiders, orb weavers, pholcids and theridiids. The theridiid house spider *Steatoda grossa* (C. L. Koch) was found to be the most active predator on *P. scaber* of all arachnids studied. It is the purpose of this paper to discuss the natural history of this spider, particularly its predatory behavior towards *P. scaber*.

All studies were carried out at the Hopkins Marine Station and around private homes in Pacific Grove, California during the period April to September, 1973.

Porcellio scaber populations were collected from both the grounds of the marine station and from a private estate near Asilomar Beach. The populations were maintained in the laboratory in 30 × 20 × 10 cm plastic tubs. A thin layer of dirt was spread over damp paper towels on the bottom; this was covered with a layer of grass and pine needles; and this in turn topped with small pieces of decaying wood and bark. Tubs were covered with aluminum foil and humidity was maintained at a high level. As long as the paper towels were kept damp an ideal environment was maintained.

Most work on *S. grossa* was conducted in garages and other human habitats. The main study area consisted of one wall of a garage of a private home near Asilomar Beach, which supported 115 individual webs with 76 observed spiders.

Methods used in specific investigations are indicated in the appropriate sections which follow.

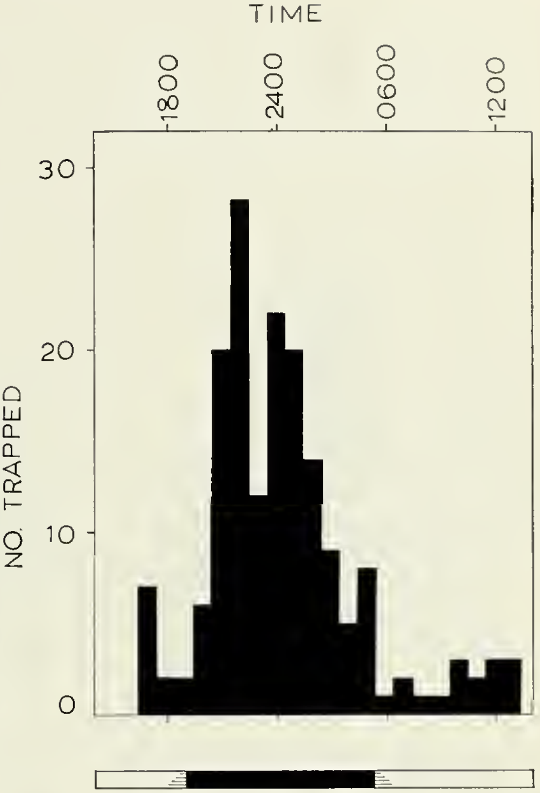

Figure 1. Graph showing number of *P. scaber* caught in traps as an indication of relative activity level during a 24 hour period on April 26 to 27, 1973.

Activity patterns of Porcellio scaber.—Initially activity patterns of the isopod were monitored in a natural environment on the grounds of the Hopkins Marine Station. Twenty-two traps consisting of plastic drinking cups were buried, with the lip of each cup at ground level, in dirt and sand surrounding a large patch of *Mesembryanthemum* bordering the east beach on Mussel Point. These traps effectively captured and retained all isopods which wandered over the lip. In addition, four 0.25 m^2 areas of nearby granite rock surface were also monitored. Counts were made every hour for 24 hours on numbers of *P. scaber* trapped in cups or detected on the rock surface. Since activity proved largely nocturnal, these populations were subsequently monitored on three successive nights, and data gathered on physical parameters. Temperature readings were taken with a thermocouple heat probe and relative humidity with a Honeywell portable relative humidity indicator from 5 cm above the ground surface. Temperature was also recorded from the iceplant habitat proper.

The results of these studies (Figs. 1 and 2) show that activity in the *P. scaber* population increases at sunset and ceases with approaching sunrise. Relative humidity consistently shows a peak near 0300, with a corresponding temperature minimum. Activity is maximum earlier and is declining at this time. Activity from sunrise to sunset is negligible.

Porcellio scaber is sensitive to desiccation (Heeley, 1941); in this connection it maintains a nocturnal activity pattern, avoids dry places, and remains in a humid environment. Judging from the data in figure 2, activity is most closely related to the absence of light rather than to particular conditions of temperature or humidity. The light regime provides the most constant parameter of the environment and one easiest for

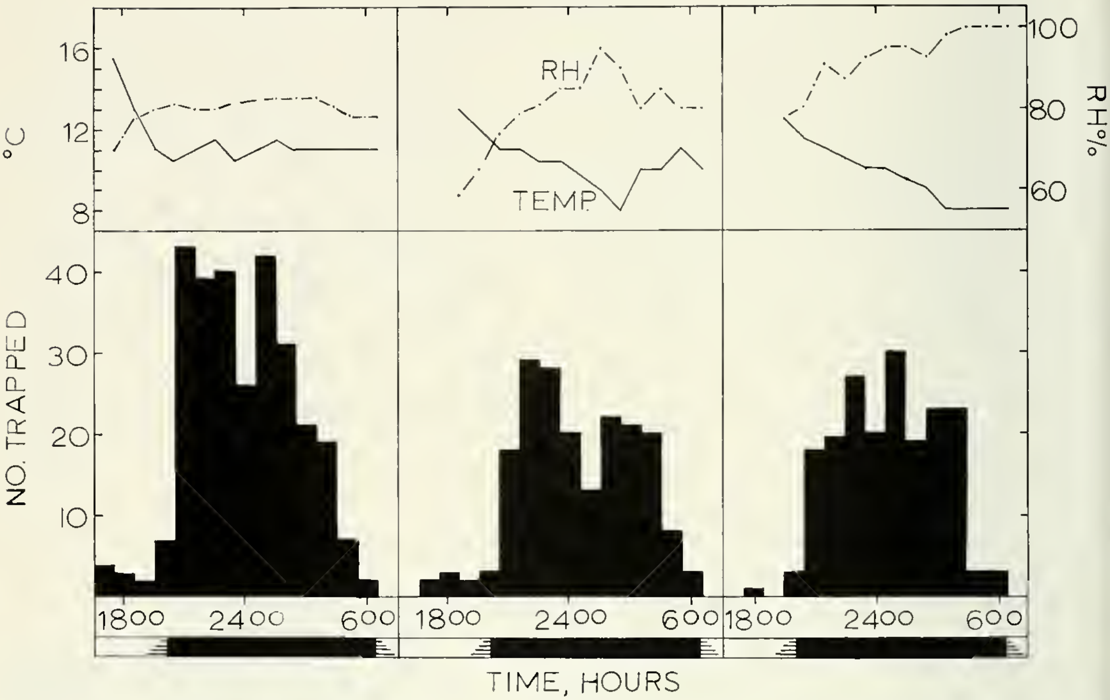

Figure 2. Graph showing number of *P. scaber* caught in traps as an indication of relative activity level on three successive nights, April 30 to May 3, 1973. Lines above show the relative humidity (RH), and temperature 5 cm above the ground in the *Mesembryanthemum* habitat (TEMP).

them to detect. Humidity may also be of importance, however; on the second night, and especially on the third night of study (when because of heavy fog, the humidity remained close to 100 percent) nocturnal activity continued until a later hour at night.

Activity pattern of Steatoda grossa.—The activity patterns of 76 *S. grossa* were monitored in the garage study area near Asilomar Beach. An atomizer which sprayed a very fine mist of water was used to delineate the extent of each web. The droplets adhered to the web without damaging it and without harm to the spider, and refracted the light brilliantly. Within 20 minutes evaporation restored the web to its original state.

Each spider was observed every two hours over a 24 hour period. Spiders were scored as inactive if hiding in their daytime retreats, and as active if they were in a typical predatory stance in the web or were out actively moving about. Temperature, relative humidity and light exposure were recorded every hour from one typical web. During the night spiders were observed with a flashlight covered with a red filter, a procedure which appeared not to disturb them.

There was much variance among the individual spiders with respect to their periods of activity. Some individuals were active in the predatory stance during the whole observational period; others were not active at all although they had been seen previously. However, on the whole the population showed much greater activity between sunset and sunrise than during the day (Fig. 3). Relative humidity and temperature showed a correlated maximum and minimum respectively, between 0600–0800.

Thus it was found that *S. grossa*, like *P. scaber*, is principally nocturnal. Spiders are potentially diurnal having an integument containing a waxy epicuticle which acts to prevent desiccation. The more primitive groups of spiders are secondarily adapted to nocturnal habits, probably as a result of competition with more efficient species (Cloudsley-Thompson, 1958). The fact that *S. grossa* feeds upon *P. scaber*, a species rejected by more advanced spiders, may further indicate its inability to compete with these forms. In *S. grossa* as in *P. scaber*, the period of activity corresponds best with the period of darkness rather than the temperature or humidity directly, emphasizing that behavior is cued mainly to light.

Predatory behavior is dealt with in a separate section to follow, but a few observations of other aspects of *S. grossa* activity and behavior are included here.

Several of the spiders maintained in the lab were observed to spin egg cocoons, one spinning a second two and a half weeks after the first. One typical egg sac contained 129 eggs. The eggs are enclosed within a hollow silk sac with a cavity of larger volume than the eggs. When rotated the sac shows the eggs to sometimes be tightly packed together in a mass or else loose and able to roll around. Four weeks after formation of the cocoon, the eggs within had hatched and gone through at least one molt to produce unpigmented pre-spiderlings with definite body form and capable of limited movement.

Steatoda grossa spiderlings upon emergence from the cocoon spin a common web encompassing parts of the old web supporting the cocoon. But within two weeks, if confined to a small area, they begin to prey upon one another until eventually one spider remains. If in an open area they leave the common web in search of suitable locations to spin their own webs. In view of the large number of annual offspring this cannibalistic activity would function to limit the population size to that suitable for the amount of available prey in the environment.

The spiders are reported to have a six-year lifespan (Kaston, 1953). The sizes of the middens of old prey below webs suggests that they remain in the same web as long as there is a good food supply and they are not disturbed. Should they be disturbed, they readily spin a new one in a suitable location as seen by those collected for the laboratory. The webs are discreet units separated from neighboring webs. Two adult spiders do not share the same web. When ten hungry spiders were placed together they were found to be extremely cannibalistic, killing off each other until one remained. It then sat down to consume the dead losers.

Since *S. grossa* is sedentary, the question of where and how it obtains water is of interest. During experiments with the fine mist atomizer, the spiders were observed to drink water droplets from the threads of the web. The legs and pedipalps were also used to collect droplets from the web and bring them to the mouth. This suggests that collection of dew condensing on the webs provides an important source of water for the spider.

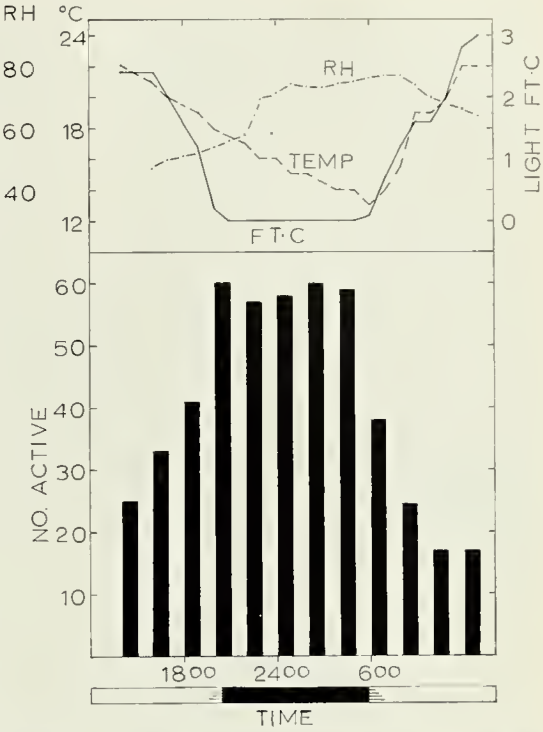

Figure 3. Graph showing periods during which the population of spiders in the garage wall study area were active in the characteristic predatory stance over a 24 hour period, May 28–29, 1973. Blackened vertical bars indicate the number of spiders active in an hourly period.

Predatory behavior of Steatoda grossa.—Members of the family Theridiidae characteristically build irregular webs from the threads of which they suspend themselves in an inverted position while they await their prey (Levi, 1968). This is what I term the predatory stance in *S. grossa.* Both males and females were observed to spin webs, sex determined in males by the presence of pedipalps swollen at the distal end with the reproductive apparatus. All of the larger web spinners were females as evidenced by egg laying activity. The web of *S. grossa* is a more or less closely woven sheet extending in a single plane and consisting of threads running in all directions with no apparent regularity (Fig. 4). The sheet extends outwards from a hidden retreat in a crack or crevice, in which the spider is generally found when not in the predatory stance. These are the two basic states of activity. Occasionally a spider prowls its web laying new threads and actively repairing damaged portions of the web. Litter or dead carcasses are cut out of the web and dropped, where they form an accumulated garbage heap.

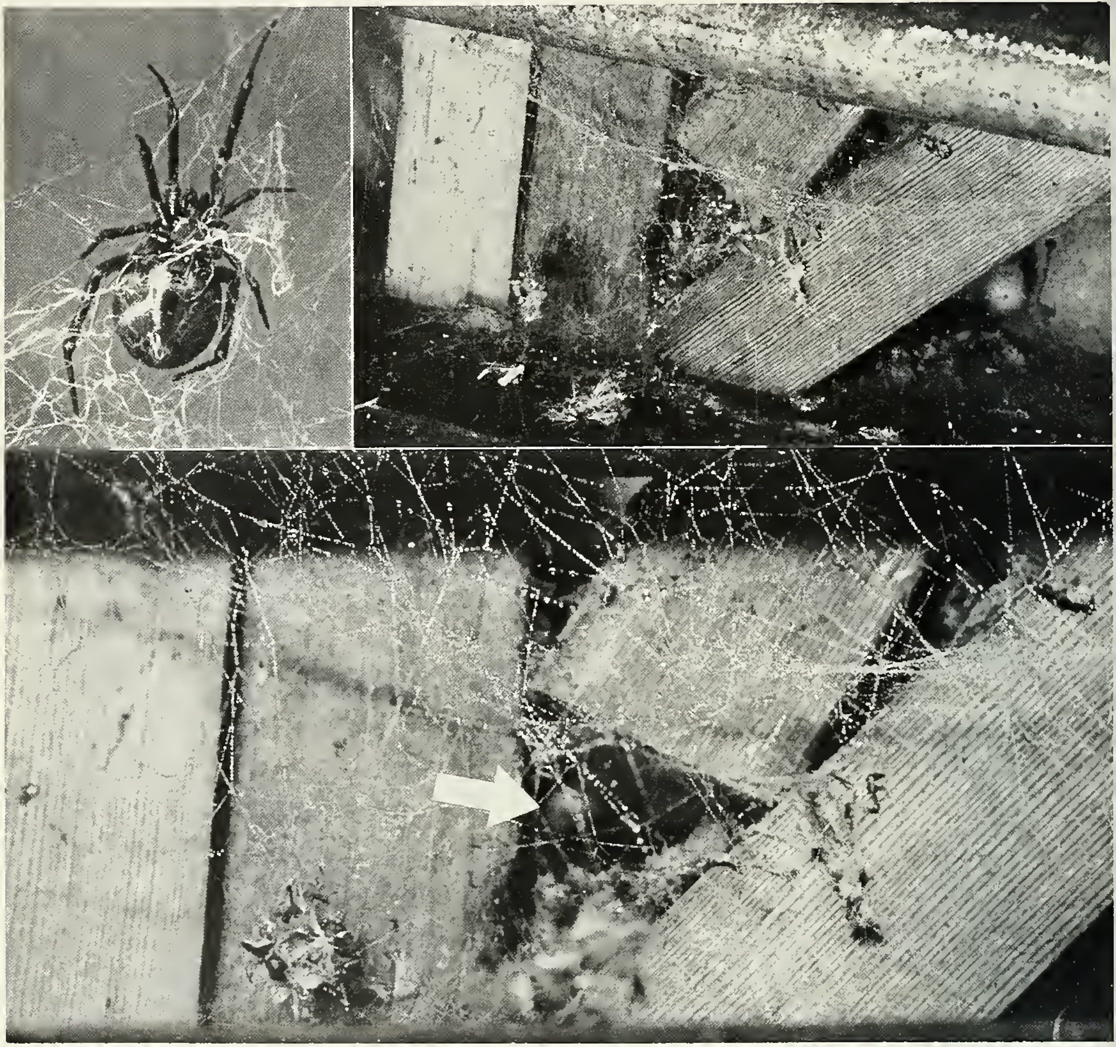

Figure 4. Upper left, photograph of *S. grossa* in its predatory stance, hanging inverted from its web of irregular threads. Upper right, photograph of web of *S. grossa* in garage wall study area showing main sheet, scaffolding lines, drop lines, and daytime retreat. Bottom, closeup view of upper right photo, web freshly misted. The arrow points to the abdomen of an individual *S. grossa* hidden in its lair.

As is typical of primitive web builders (Kullman, 1972), the web is used only as a means of getting information about the position of approaching prey, and does not use special viscid threads to snare its victims. Much silk is required and the webs are rather complicated and irregular. Vertical tangles of interconnecting scaffolding lines above, and drop lines below and to the sides anchor the main sheet of the web in place and provide additional means for detecting and entangling passing prey. Sometimes the webs are so compacted in a corner that they lose their characteristic shape.

Once alerted to the presence of prey by vibrations of the web, the spider advances rapidly and touches the isopod or other prey with the pedipalps and first pair of walking legs. At this point the prey may be either accepted or rejected. If accepted, *S. grossa* proceeds to swath the ventral surface of *P. scaber* with viscid threads pulled from the spinnerets by the fourth pair of walking legs. The prey is not rotated as seen in species of *Araneus*, and not even held, but rather is crisscrossed ventrally with silk in the place of entanglement. The spider places occasional guy lines to the dorsal surface of the prey and attaches them to its web, acting to hitch the prey up into the web. It may pause occasionally and if the struggling is strong it continues to swath the prey in silk.

A series of short bites with the fangs is then made through the ventral surface. One assumes venom is being injected but it is not always sufficient to kill *P. scaber*. The spider may then move a short distance away from the prey for a period of several minutes or less. If struggles continue it adds additional silk. It then sinks its chelicerae through the ventral surface of the prey and remains in this position for 1½–3 hours. Details of the feeding process were not followed; presumably enzymes are injected, and suction applied to ingest the organic soup created. The dead carcass is eventually cut from the main sheet of the web.

If the packaged prey is small it may be carried from the web periphery to the center of the main sheet for consumption. While walking the spider carries the package with one of its third pair of walking legs, and it is held in a position between the spider and the web. If the prey is larger (and isopods up to five times the size of the spider were effectively preyed upon) then it is consumed in the place of capture.

Additional details of predatory behavior were gained from a study of 25 specimens of *S. grossa*, 2–10 mm in body length, which were kept in the laboratory for observation and experiment. I attempted to feed these nightly between the hours of 2200–0200. *Porcellio scaber* of weight 20–35 mg were introduced either by dropping them into the mainsheet of the web in the vicinity of the spider, or by placing them in peripheral parts, or wholly outside the web.

Records of prey taken by lab specimens were kept for 19 *S. grossa*. Predation is relatively infrequent and the spiders averaged 5.0 days between meals. Some spiders endured at least three weeks without feeding despite the presence of food and there is no reason to believe they could not starve for longer periods.

The spiders were observed to have a poor sense of vision. Isopods walking even within 5 cm of the spider never elicited a response unless the web was touched indicating that detection of prey relies primarily on vibratory stimulus. The isopods can alert the spider to their presence in several ways. They can fall directly into the web, or become entangled in drop lines or outlying guy lines. Subsequent struggles alert the spider to a stereotyped response. Isopods contacting the web are not necessarily trapped. It was observed that *P. scaber* can walk upside down either up or down a single thread of the web without too much difficulty.

The habit of *S. grossa* of discarding its old prey in a tangled heap below the mainsheet of the web made it easy to determine longterm diets for representative spiders. Accumulated carcasses from ten webs were taken from the garage study area and analyzed for contents. Similar collections were made from the webs of *S. grossa* in two other locations, an open carport and a closed woodbox from a home on Jack's Point in New Monterey. The animals most commonly found and their percent occurrence are: *P. scaber* (84), moths (5), ants (2.4), beetles (1.9), millipedes (1.1), and others (5). The animals classified under others are those less abundant than one percent and consist mainly of flying insects such as horse flies, beach flies, dragon flies, etc. but there were also a few earwigs and other spiders.

The same animals were found fairly consistently in the webs, but by far the primary prey of *S. grossa* as determined from the webs is *P. scaber*. Moths form the second most commonly taken prey, but only because of two very exceptional webs, occurring near window ledges; the primary prey found here were moths and other flying insects, undoubtedly attracted to lights shining through the windows.

Aside from these two webs, the main prey of *S. grossa* clearly consists of crawling arthropods, which blunder into the web on foot. I expected to find dietary differences between spiders with webs close to the floor and those high on the walls, but no such differences were found. Webs were very abundant occupying almost every available corner or crevice in the study area, and everywhere except in the window webs, *P. scaber* is the major prey. Two points are of special interest in this regard. First, *P. scaber* is probably the main food here because it is most available rather than the most attractive prey. In feeding experiments in the laboratory I concluded that *S. grossa* does have a relative distaste for *P. scaber*. On several occasions when an isopod had been refused, a fly was introduced and elicted a complete predatory response resulting in consumption.

A second point of interest is that *P. scaber* seems equally available to spiders of the floor and those near the ceiling. When *P. scaber* was released on the garage floor they were observed to have no difficulties climbing the garage walls, and on several occasions marked isopods released the floor were captured as early as four hours later in webs halfway up the walls. Climbing is probably part of the normal nocturnal foraging habits of *P. scaber*. Bristowe (1941) found that specimens in captivity would eat spiders eggs. They also are observed to consume dead and decaying matter including dead members of the species. The largest number found climbing on the walls were observed around 0400 when the humidity was reaching a maximum. It is reported that *P. scaber* prefers vertical surfaces where moisture collects but does not become excessive (Heeley, 1941).

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THE BIOLOGY OF THE SOCIAL SPIDER *ANELOSIMUS EXIMIUS* (ARANEAE: THERIDIIDAE)

VINCENT BRACH[1]

ABSTRACT: The social spider *Anelosimus eximius* has evolved advanced subsocial behavior which increases the efficiency of web construction, the capture of large prey, and defense. Colonies were observed in the field and in the laboratory. Communication between colony members is effected by apparently tactile signals. Cannibalism usually follows a breakdown in the communication mechanism and most frequently involved juveniles preying on sick or dead adults, and also on broodmates. Since cannibalism on nonfunctional and redundant colony members conserves energy, this trait may have been maintained by selection and should not necessarily be considered primitive.

The majority of spiders are intolerant of their own kind during much of their lives, although there are a few situations other than mating in which individuals are known to come together peaceably for the performance of some specific function. Some spiders, for example, are known to overwinter in species-specific clusters (Kaston, 1953). In many families (especially the Pisauridae, Lycosidae, and Theridiidae), the mother spider typically guards and may even feed her offspring; the mother and brood all living together in the same web or the young may be carried on the back of the mother. However, this behavior reflects tolerance rather than sociability and is typically short-lived. After the maternal instinct has disappeared, contacts between mother and young may result in the latter being eaten, and the spiderlings themselves will usually become cannibalistic if prevented from dispersing.

In contrast to this merely tolerant behavior of spiders, are the few known cases of advanced subsocial behavior. The natural history of the Asian and African species of *Stegodyphus* (Eresidae) has been described by Jambunathan (1905), Savory (1928), and Kullman, Nawabi, and Zimmerman (1972). These spiders form large, permanent webs, containing hundreds or thousands of individuals, over bushes in arid places; web construction, prey capture, and feeding are performed cooperatively. Recent and extensive observations on the Gabonese *Agelena consociata* (Agelenidae), by Darchen (1965) and Krafft (1970) have shown that a similar situation occurs in this species. Certain Neotropical spiders such as *Uloborus republicanus* (Uloboridae), *Coenothele gregalis* (Dictynidae), and *Araneus bandelieri* (Araneidae) also have forms of social behavior. These range from short-term association of the females for the cooperative construction of a communal egg cocoon (*A. bandelieri*) to the formation of permanent colonies of large size (*C. gregalis*) (Millot, 1949; Kullman, 1968).

The New World genus *Anelosimus* (Theridiidae) contains several species of spiders exhibiting different degrees of sociability. Archer (1946) and Comstock (1948) describe the North American *A. studiosus* as a loosely social species which constructs a communal web around dead leaves and twigs; the leaves being used for common retreats. The Neotropical species *A. eximius* is described by several authors (Simon, 1891; F. O. P. Cambridge, quoted by Comstock, 1948) as having communal webs of much larger size than those of *A. studiosus* which sometimes cover many cubic yards and contain hundreds or even thousands of spiders. The purpose of this investigation was to make a detailed study of the behavior and natural history of the social spider *Anelosimus eximius* and to attempt to determine the possible adaptive significance of the remarkable sociability of this species.

METHODS

For a period of ten days in late January 1973, a colony of approximately 200 *A. eximius* was observed in the rainforest on the grounds of the Rio Palenque Biological Station, Prov. Los Rios, Ecuador, 220 m, km 56 Quevedo to Sto. Domingo. At the conclusion of my stay in Ecuador, 40 adult spiders were collected alive and taken to my

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Figure 1. Field web of *Anelosimus eximius* (diagrammatic). Actual size about two cubic feet. Redrawn from a field sketch.

laboratory at the University of Miami, Coral Gables, Florida. The spiders were housed in various glass containers until finally a large chromatography jar measuring 46 × 20 cm was employed as a permanent cage. The jar was filled with a thin layer of moist sand and potting soil to provide humidity. A large branched twig was placed in the jar to provide support for the web. An inch-wide ring of vaseline was applied to the inside rim of the jar, and the entire undersurface of the glass plate which was used as a cover was smeared with vaseline so that the cage could be open for inspection and cleaning without damaging the web or injuring the spiders. The spiders were fed insects of several sizes to determine prey size preference, but were most often fed large mealworms every three or four days.

RESULTS

Field observations.—The field colony of *A. eximius* was located at the side of an unpaved road cut through the rainforest which surrounded the station. The web was spun around the top of an unidentified woody shrub that measured about two meters in height. The web occupied about two cubic feet, but had no definite shape, since additions and deletions were made almost nightly. The web is shown diagrammatically in figure 1. The outside portions consisted of fine, loosely spun silk, whereas the interior was divided into several tiers by flat sheets of more densely spun silk. These silk "platforms" were perforated at intervals by silk-reinforced holes about 25 mm in diameter. The spiders used the undersides of the green leaves spun into the web for retreats. The overall appearance of the web was not unlike that of webs made by the tent caterpillars (*Malacosoma* spp.) of the United States, but was not as dense nor as regular in outline as that of caterpillars. The web was free of dead leaves and did not closely resemble the web figured by Millot (1949) for *Theridion socialis* (= *A. eximius*).

The spiders were not restricted to any particular portion of the web and were often seen patrolling the "platforms" in an apparently aimless fashion. Frequently, large numbers of spiders were seen sitting motionless underneath leaves. Rains produced a great burst of activity; the spiders hurriedly retreated to the undersides of the leaves until the rain stopped, after which they resumed patrolling the web. Spiders were often seen drinking from drops of water caught in the web. They were never seen outside the web unless the web was violently shaken.

Very few juveniles and only three adult males were observed. Males of *A. eximius* are quite sluggish and do not appear to participate in many of the cooperative activities of the colony. The males were considerably thinner than any of the females, which may indicate that the males do not feed often or at all after the last molt.

While I made several attempts to locate additional colonies, none were found during my stay at the station. After my departure, one other colony of similar size was discovered by the station director. This second colony was located in a bush at a site quite distant from the study colony. I was told by the station director that the study colony had occupied the same spot for at least three years preceding my visit, being little changed during this time.

Spinning behavior.—*Anelosimus eximius* prefers to spin at night. Portions of the web which were damaged by rain or falling forest debris were always repaired by the next day; the silk "platforms" were the last structures to be repaired. However, work was not begun until after dark. The reluctance of the spiders to expose themselves while spinning near or on the outside of the web or in open, damaged areas during the day is probably an adaptation to avoid predation by spider-eating birds and wasps. Selection for this behavior may be quite strong. The station director told me of an instance where he observed a hermit hummingbird (*Phaethornis* sp.) attempting to pluck spiders from the web while hovering next to it.

When spinning a new web in the laboratory, several spiders will follow one another about laying down foundation lines, from which an irregular meshwork is spun as the spiders move off in every direction. Webs are constantly reinforced as the spiders move through them, since the spiders lay down draglines wherever they go. Communicating holes between "platforms" are cut out of the web by several spiders working together, and the edges are reinforced with silk. Field and laboratory webs were always begun at the very tops of supporting twigs and leaves.

Feeding behavior.—Large insects which flew into the field web usually penetrated it somewhat before becoming severely entangled. A struggling insect elicits an immediate response with the spiders swiftly converging on the prey from all directions. When slightly less than one centimeter away from the prey, the spiders assume a vertical attitude and rapidly pull masses of sticky silk from their spinnerets with alternating strokes of the last pair of legs. The prey is soon covered with a tangle of sticky silk. When the prey is sufficiently immobilized, the spiders crawl onto it and deliver several prolonged bites. Potentially dangerous or very large prey are usually bitten on an extremity from a position of safety. This phenomenon was noted and photographed by Kullman *et al.* (1972) in *Stegodyphus pacificus*. When the prey is motionless, the already well-fed spiders usually leave it to resume their patrolling while the hungry spiders remain to feed. Large beetles are soon sucked dry by the combined efforts of several dozen spiders. The carcass may be disjointed and the parts moved about by cooperative effort. This increases the available surface area of the prey for feeding and often brings the prey to spiders which did not participate in the killing. Large carcasses usually are cut out of the web after several days, although lighter refuse frequently remains until completely consumed by mold.

There is a definite decrease in the efficiency of prey capture as the size of the prey decreases. Mosquito-sized or smaller insects are often ignored and usually escape after landing on the web, their feeble struggles attracting few or no spiders. The optimal prey size appears to be about 2.5 cm. In the laboratory colony, which at times contained many small juveniles, but virtually no adults, *Drosophila* flies were captured in the extremely fine webbing spun by these spiders. One *Drosophila* was sufficient food for several freshly-hatched spiderlings, although such tiny prey was ignored by spiders older than the third molt. In the field web, the few juveniles present fed upon pieces of larger prey captured and disjointed by the adults.

Defense.—Anelosimus eximius is quite aggressive. A large-scale disturbance of the web, such as resulted from putting my hand in the web to collect spiders, resulted in a concerted attack from the majority of the spiders. Web defense differs from prey capture in that no attempt is made to throw silk; the spiders simply bite the intruding object upon contact. If the disturbance is sufficiently great, many spiders will temporarily abandon the web by dropping to the ground, spinning out a dragline as they fall. Web abandonment was especially common in the laboratory webs containing mostly juveniles.

Reproduction and development.—Mating behavior was not observed in the field, and the two adult males brought into the laboratory died soon afterward. One empty egg case was collected in the field and two were made by different females in the laboratory, on 27 February and 4 March 1973. These egg cases were spherical, 4 mm in diameter, and were dull grey in color. The mother spiders carried their egg cases about with their chelicerae, or temporarily attached them to the web or a twig. The spiderlings emerged in 24 and 23 days, the cases yielding 21 and 24 young, respectively. Both egg cases were dissected after the spiders had emerged and were found to contain no dead individuals and very few unhatched eggs. The lack of dead spiderlings is unusual, considering the normally cannibalistic behavior of young spiders within the egg case. The young remained in a fairly dense cluster for several days, after which they dispersed to all corners of the web. No maternal behavior (*e.g.*, regurgitation feeding, remaining with the young) was displayed by the mother spiders. Ballooning by the dispersed young was not observed. Within one week of emergence, young spiders were seen feeding upon the weaker and dead of the broods, sick adults, and captured insects. By the third molt, which in most cases occurred in late April or early May, only 20 spiders remained from the two broods; more than half succumbing to their broodmates. All of the remaining spiders except one survived to adulthood, the majority attaining adult size in late June. Of these, only one was a male. The colony remained in good health until late August, when it was accidentally destroyed by heat.

Communication and species recognition.—The spiders frequently encountered one another while patrolling the web but went on their respective ways with no hostilities after a brief investigative tapping of each other with the first pair of legs. The manner in which the front legs are carried by patrolling spiders is decidedly antenniform, producing a rather ant-like appearance. During prey capture, spiders sometimes collided on the way to the prey but were never observed to attack one another. However, a wounded or dead spider was usually soon sucked dry by juveniles. Molting individuals are ignored unless a serious injury is sustained during molting. Enemies and prey are usually identified at a distance by their shaking and tearing the web. For smaller "invaders," actual contact is necessary to evoke an attack. As a test of species recognition, several spiders of the genera *Theridion* and *Leucage* having a size roughly equivalent to *A. eximius* were placed in the laboratory web. These foreign spiders were ignored unless they were actually touched by a patrolling *A. eximius*. Such contact usually evoked an unsuccessful attack, the "invader" dropping out of the web before it could be wrapped in silk. There appears to be little difference between the treatment given to a dead (hence, unresponsive) *A. eximius* and a dead spider of some other genus; both are sucked dry, usually by juveniles. While other species of spiders have been recorded from the webs of *A. eximius* (Levi, 1955), none were observed in the field colony. Foreign species introduced into the laboratory colony soon left the web by themselves if not made to drop out of the web by an attacking *A. eximius*.

DISCUSSION

The social behavior of *Anelosimus eximius* appears to improve efficiency of large prey capture and defense. In the rainforest at the Rio Palenque Biological Station, large flying insects, particularly euglossine bees and scarabeid beetles, are quite common but are not readily captured by the smaller, solitary web-spinning spiders. *Anelosimus eximius* is able to capture such large prey with its fine, extensive web and the cooperative efforts of the members of the colony. It is unlikely that a web of the type spun by this spider could be constructed or efficiently utilized by a solitary spider without consuming large amounts of time and energy. The social behavior of *A. eximius* reduces the energy demand on each colony member while permitting the exploitation of an energy source unavailable to solitary spiders of similar size. An interesting adaptation which probably increases the effectiveness of all the cooperatively-performed activities in this species is the greatly reduced proportion of males to females. This phenomenon was also observed in the social *Stegodyphus* by Savory (1928).

The evolution of social behavior in the Theridiidae is believed by Kullman (1968; 1971, 1972) to stem from an extension of the periodically social behavior of the mother and her brood. This author ranked *Theridion eximium* (= *A. eximius*) at the top of an evolutionary scale of social behavior in which cooperative labor and specialized brood care involving regurgitation feeding were considered to be the most advanced characteristics, along with the more general requirement for a complete lack of intraspecific aggression. However, my observations indicate that cannibalism in *A. eximius* is a common event which is often the result of a breakdown in the apparently tactile species recognition mechanism. Cannibalism of this sort does not necessarily represent an activistic or "primitive" condition. In fact, such behavior conserves energy within the colony while selecting for species recognition behavior. It is possible that the mechanism for generating the imbalance between males and females in *A. eximius* is the cannibalism of the possibly less responsive or weaker male spiderlings by their female broodmates. This would explain the apparently incongruous cannibalism exhibited by the spiderlings in the laboratory colony.

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RESEARCH NOTES

THE OCCURRENCE OF THE POLYNOID *HARMOTHOE* cf. *LUNULATA* FROM THE TUBE OF THE MALDANID *AXIOTHELLA RUBROCINCTA* (POLYCHAETA)

Axiothella rubrocincta (Johnson, 1901), is a tubicolous maldanid polychaete that is distributed from western Canada southwards along the Pacific coast into the Gulf of California (Hartman, 1961; Reish, 1968; Kudenov, 1973). In central California, *A. rubrocincta* is found intertidally, and is the well known host for the commensal pinnotherid crab, *Pinnixa longipes* (Lockington). No other commensals have ever been reported from the tube of this bamboo worm (Ricketts, *et al.*, 1968).

While the author was at the Pacific Marine Station, Dillon Beach, California, a series of collections of *A. rubrocincta* were taken at Lawson's Flat in Tomales Bay. Sampling began in July, 1969, and terminated in June, 1970. During December, 1969, and January, 1970, a total of eight *Harmothoe* cf. *lunulata* (delle Chiaje, 1841) were collected from the tubes of *A. rubrocincta*. Usually only a single *H.* cf. *lunulata* occupied a single tube. In one case a pair of polynoids were captured from the same tube. I did not find *H.* cf. *lunulata* at any other time of the year.

Family Polynoidae

Harmothoe cf. *lunulata* (delle Chiaje, 1941)

Figure 1a–g

Material examined: Lawson's Flat, Tomales Bay, California, 31 January 1970, coll. J. Kudenov (1).

Description: The specimen of *Harmothoe* cf. *lunulata* consists of 33 segments, and is 9 mm long by 2 mm wide without setae. The elytra completely conceal the body and imbricate with one another.

The prostomium is longer than wide, and has a middorsal incision that is incomplete posteriorly (Fig. 1a). The anterior prostomial margin is produced into two conical processes between which the unpaired median and the paired lateral antennae are visible. The lateral antennae are conical and taper distally to abrupt points. The median antenna has been lost, but a distinct basal cirrophore is present. There are two pairs of eyes. The anterior pair is set wide apart, and each eye is situated along the dorsolateral margin of the prostomium. The posterior pair is closer together, and each eye is near the posterior margin of the prostomium.

The peristomial tentacles are cirriform, cylindrical in cross-section, and sharply pointed (Fig. 1a). Cirrophoral seta are present. Parapodia are pronounced structures with truncate hemispherical notopodial lobes and laterally compressed, yet prolonged neuropodial lobes (Fig. 1b). The neuropodium has a slender, superior acicular lobe and an entire, rounded postsetal lobe. The postsetal lobe is completely obscured by the acicular lobe. The ventral cirrus is inserted on the proximal half of the parapodium. A basal papillar thickening is present on the outer margin of the ventral cirrus (Fig. 1b).

There are 15 pairs of elytra. All are subcircular and smooth with entire margins (Fig. 1c). The elytral scar is oriented along the longitudinal body axis. All such scars bear elytral pigmentation either as isolated patches or as a continuation of the existing pattern (Fig. 1c). Elytral coloration is submarginal. The anterior pair and two posterior pairs of elytra have ellipsoidal color patterns in which the centralmost region is translucent. The pigmentation pattern on all other elytra represents an "S" restricted to the posterior elytral hemicircle (Fig. 1c).

Notopodial fascicles are disposed as tufts of similar notosetae (Fig. 1b) that vary in length. Superior notosetae are shorter than the inferior ones. The latter bristles nearly touch the neuropodial fascicles. All notosetae are subdistally serrated and grade distally into blunt apices (Fig. 1d). The notosetae are larger in diameter than the neurosetae. The neuropodial fascicles are fan-like (Fig. 1b). Superior and intermediate neurosetae have moderately long accessory teeth and distal hooks (Fig. 1e–f). The inferior neurosetae (Fig. 1g) have sharp, slightly recurved apices but lack accessory teeth. These neurosetae are generally much smaller than the superior and intermediate neurosetae. All neurosetae, however, have well developed dorsolateral spinules. Transverse dorsal rows of pectinae were not observed.

Remarks: *Harmothoe* cf. *lunulata* differs subtly from *H. lunulata* in having an incomplete middorsal prostomial incision, cirriform prostomial tentacles, presetal lobes that obscure the postsetal lobes, an "S" type pigmentation pattern restricted to the posterior half of most elytra, and in having neurosetae with a moderately well defined, but short, accessory tooth and two dorsolateral rows of subdistal spinules. Transverse rows of pectinae were not observed in *H.* cf. *lunulata*. These two species share low numbers of body segments, and have imbricating, entire elytra with smooth margins. The elytra completely conceal the dorsum. The arrangement of eyes and the structure of the setal fascicles are similar. The notosetae resemble one another, and are larger than the neurosetae. The ventral cirri have similar basal papillar thickenings at the outer margin.

Fauvel (1923:70), Hartman (1944:244) and Day (1967:71) present descriptions of *H. lunulata*. Fauve (*op. cit.*) has also listed numerous varieties of *H*

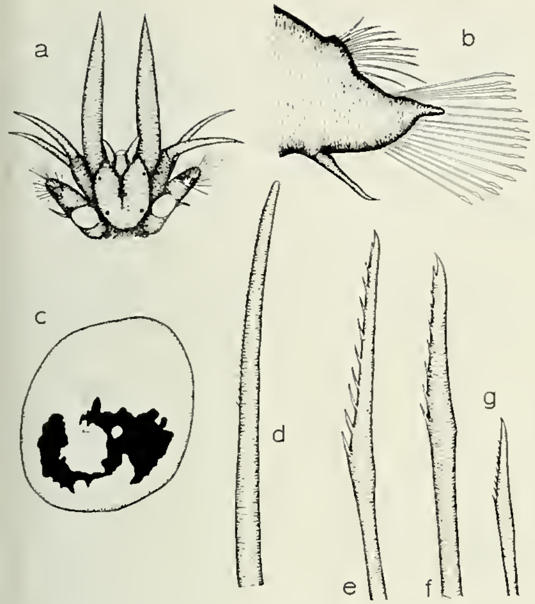

Figure 1. Harmothoe cf. *lunulata* (delle Chiaje): a, anterior segments, dorsal view, × 8; b, left parapodium of segment 16, anterior view, × 45; c, elytron, dorsal view, × 8; d, notoseta, lateral view, × 322; e, superior neuroseta, lateral view, × 322; f, intermediate neuroseta, lateral view, × 536; g, inferior neuroseta, lateral view, × 322.

lunulata from Europe, and Monro (1928) named another from the Galapagos Islands. *H. lunulata* is known from widespread areas such as the Mediterranean, Europe, Saudi Arabia and the west coast of North America. It occurs under rocks, or as a commensal of holothurians and tubicolous polychaetes. The current concept of *H. lunulata*, however, is so confused that this species must be redefined on a worldwide basis. Pending such an investigation, I prefer not to name this specimen from Tomales Bay. It is now deposited in the Allan Hancock Foundation of the University of Southern California.

This commensal relationship between *H.* cf. *lunulata* and *A. rubrocincta* may be fortuitous, or may actually represent a temporary, seasonal habitat for the former species. There has not been a great deal of attention given to maldanid commensals. Sanders, *et al.* (1962) have recorded the amphipod *Listriella clymenellae* Mills, and the bivalve, *Monacuta* (*Aligena*) *elevans* Stimpson, from the tubes of *Clymenella torquata* (Leidy) in Massachusetts.

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LEAST AND LONG-TAILED WEASELS (*MUSTELA NIVALIS* AND *M. FRENATA*) COLLECTED IN GRUNDY COUNTY, ILLINOIS

The distribution of the least weasel (*Mustela nivalis*) is restricted to the northern half of Illinois where it is occasionally captured. This weasel is known to occur in most of the northern three tiers of counties in the western part of the state, and south into Champaign County in the eastern part (records from eight of the 15 northern counties). Various other recent southern records are mentioned in this paper. *Mustela frenata,* the long-tailed weasel, occurs throughout the state and Hall (Univ. Kansas Publ., Mus. Nat. Hist., 4:1–466, 1951) illustrates (in Fig. 10) the approximate southern limits of color change for this weasel involving an area in a band which covers the northern one-third of Illinois.

On 10 November, 1973, Tom Thompson brought to Fran Harty a small mammal that he found while while hunting pheasants near Kinsman, Grundy County, Illinois. This specimen, identified as the seldom captured least weasel, was preserved as a study skin and skull. Warnock and Warnock (Trans. Illinois State Acad. Sci., 66:115–116, 1973) review captures of the least weasel in Illinois and add several recent records and specimens reported taken by Calhoun from Kendall County. and Parmalee and Hoffman from Woodford County. The Grundy County specimen, obtained by Harty, was taken between Kendall and Woodford Counties and is a new county record.

Although this specimen of the least weasel was taken in early November, there is no indication of a change in color from its brown summer coat to a white winter coat. Several specimens of least weasels from Sauk County, in south-central Wisconsin, are housed in the mammal collection at Southern Illinois University. One of these specimens, taken between November 10–14 (1943), has a totally white coat.

On 30 November, 1973, Jim Thompson, also of Kinsman, caught a long-tailed weasel which was given to Harty. This specimen also did not show a color change in its pelage. Grundy County falls near the center of the band of color change illustrated by Hall in his figure 10. If this one specimen is indicative of the color change of other long-tailed weasels, the line of demarcation for such color change should lie somewhere within the distance of about 150 miles between Grundy County, Illinois, and southern Wisconsin. Hall indicates, however, that males may not turn color in areas where females change color in the winter; our specimens of both weasels are males.

Note: Since submission, four additional unreported specimens of *M. nivalis* were found in the collection of the Illinois Natural History Survey collection: 1 white (2 December 1959) and 1 brown (13 March 1968) from Carroll County, 1 brown (27 July 1939) from Lee County, and 1 white (6 February 1956) from Livingston County which is south of Grundy County.

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NOTES ON THE METABOLISM OF THE CUCKOO OWLET AND HAWK OWL

Despite the many recent studies of the metabolism of birds, there still exists a relative paucity of data on non-passerines and particularly carnivores. The owls (Strigiformes) represent a partial exception due to several recent studies (Graber, 1962; Collins, 1963; Ligon, 1968, 1969; Coulombe, 1970; Gessaman, 1972; Johnson, 1974). This paper presents data on the metabolism of two additional species of owls, the Cuckoo Owlet, *Glaucidium cuculoides,* of southeast Asia and the Hawk Owl, *Surnia ulula,* of the holarctic boreal zone. Metabolic values obtained from single individuals, as true here, should be considered preliminary values for the species. Such values are however useful, particularly when considering the unavailability of additional individuals for study. The data presented here supplements our knowledge of the metabolic rate of diurnal owls; most previous work has been done on largely or entirely nocturnal species.

Both owls were maintained on a diet of beef heart tissue and laboratory mice, *Mus musculus.* A food deprivation period of at least 12 hours insured that the owls were post absorptive during testing. Oxygen consumption values were corrected to standard temperature and pressure and a factor of 4.71 kcal/l O_2 (Graber, 1962) was used to calculate the caloric equivalent of oxygen consumed.

The Cuckoo Owlet was obtained from a commercial pet dealer in 1971 and maintained in captivity in a large flight cage at California State University, Long Beach, until testing in July 1973. This bird, an adult female, was similar in pattern and coloration to specimens of *G. c. rufescens.* Twelve oxygen consumption determinations were obtained at five ambient temperatures between 27° and 30°C using a closed system and modified Zollinhofer manometer apparatus (Dabney and Zollinhofer, 1968). The body weight of the bird varied from 159.7 to 166.3 gms (average: 162.7 gms) during the test period. The oxygen consumption values averaged 0.978 cc O_2/gm/hr (17.99 kcal/day) with a range of 0.918 to 1.026 cc O_2/gm/hr. The mean cloacal temperature of this owl, as determined with a Schultheis mercury thermometer was 40.1°C (range: 39.0° to 40.8°C) between ambient temperatures of 1° to 27°C.

The Hawk Owl was captured (by Collins) near Seney, Schoolcraft Co., Michigan in December 1962.

Large numbers of these birds were reported that winter far south of their normal more northerly winter range. The bird, an adult female, was maintained at the University of Michigan at normal outdoor temperatures. The metabolic determinations were made within two weeks of capture by means of a paramagnetic oxygen analyzer used in conjunction with a recording potentiometer as described by Dawson (1958). Two determinations, at 24°C were both 0.93 cc O_2/gm/hr (35.0 kcal/day) when the bird weighed 333 gms. Later observations of the body weight of this bird indicated it could fluctuate between 293 to 375 gms without apparent ill effects to the bird (Collins, unpublished). Resting body temperature, also measured with a Schultheis thermometer, was later observed to range from 38.2° to 41.8°C being slightly higher in the daytime than at night (Collins, unpublished).

The metabolic rate of the Hawk Owl is very similar to that predicted by the metabolism-weight equation of Lasiewski and Dawson (1967) for non-passerines, whereas that of the Cuckoo Owlet is appreciably lower. The relationship between metabolism and body weight has been analyzed for owls alone by Ligon (1968) and corrected by Coulombe (1970). However, due to the accidental use of some erroneous values (Lasiewski and Dawson, 1967: Table 2) and the subsequent availability of values for additional species this relationship is presently being reanalyzed (Collins and Johnson, manuscript).

We thank the late Robert C. Lasiewski for assisting with the oxygen consumption determinations of the Hawk Owl and Richard Zembal for his help with the care and feeding of the Cuckoo Owlet.

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A CALIFORNIA GRAY WHALE CALF (*ESCHRICHTIUS ROBUSTUS*) BORN OUTSIDE THE CALVING LAGOONS

Gilmore (1961) reported seven observations of California gray whale (*Eschrichtius robustus*) calves off San Diego, California during the months of the southward migration from 1955–1961 and (1974 pers. comm.) reported several similar records for the years since 1961. Sund and O'Connor (1974) added a single record of a gray whale mother and calf off Monterey, California in January 1973.

Despite these few records of the occurrence of calves during the southward migration, however, and despite a detailed description of a birth in Magdalena Bay, Baja California (Balcomb, 1974), we are unaware of any published details of the birth of a gray whale calf outside its traditional calving grounds.

On 17 January 1974, while accompanying a filming crew off the coast of San Diego, the authors observed what was thought to be the birth of a gray whale. This birth is of significance both because of the location and because of the time of its occurrence.

A gray whale, assumed to be a female, approximately 35–40 ft (10.7–12.2 m) long was sighted at 32°45′N, 117°19′W about three and a half miles west of the entrance to Mission Bay, San Diego. The water at this location was 54°F (12°C) in temperature and 40 fms (73 m) in depth, and the bottom was flat and sandy. When first encountered the whale was on its side at the surface, approximately 600 yds (0.55 km) from the working boat, sculling its flukes slowly back and forth but moving forward very little. Periodically, the animal lurched forward with violent tail spasms approximately 30 seconds apart. One of us (Leatherwood) has previously observed similar behavior in Scammon's Lagoon and assumed it to be advanced stages of labor.

During a period of about five minutes, our vessel closed from 600 yds (0.55 km) to within a 100 yds (92 m) of the animal. At that point, the whale suddenly righted itself and began to swim away, its back barely awash and the strokes of the flukes leaving large swirls on the surface. Gulls which had been floating and flying nearby moved quickly to the area of the first swirl and began following the whale's tracks, sweeping down at the area of each swirl. As we approached the gulls, we were able to determine that they were picking up small fragments of bloody tissue from the water.

As the whale began to swim away, a small calf surfaced to its left, swam across its barely awash back, and assumed a swimming position just in front of the large whale's right tail fluke. The calf swam jerkily and unsteadily at first, seeming to have trouble maintaining its stability.

We remained behind the two animals during the next few minutes, filming their swimming behavior. The calf remained close beside its mother for the majority of the time observed. At one point it turned on its side, exposing its belly and exhibited an 8–10 inch (20–25 cm) length of reddish pink umbilical cord. As we continued to track the whales, pieces of tisssue, including one nearly 4 ft^2 and a series of smaller chunks, apparently part of the placenta, were seen drifting about the area. Gulls were seen taking the smaller fragments. Attempts to retrieve portions of the material were unsuccessful.

The field estimate of approximately 10 ft (3 m) for the calf's size appears too small considering the mean size of 15 ft (4.9 m) reported for full-term fetuses (Rice and Wolman, 1971). Nevertheless the calf did appear appreciably smaller than newborn commonly observed in the Baja lagoons.

In addition to its small size and the still bloody umbilicus the animal was identifiable as a newborn by white foetal folds along each side of the body and by the presence of numerous bristles along the very slender snout.

The authors thank Erwin Verity of Disney Studios and Ralph White of Coronado Productions for the opportunity to participate in the filming activities, and Dale W. Rice, Forrest G. Wood, Raymond M. Gilmore, and William C. Cummings for reading the manuscript.

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Brattstrom, B. H. 1969. The Condor in California. Pp. 369–382 *in* Vertebrates of California. (S. E. Payne, ed.), Univ. California Press, xii + 635 pp.

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RESEARCH NOTES

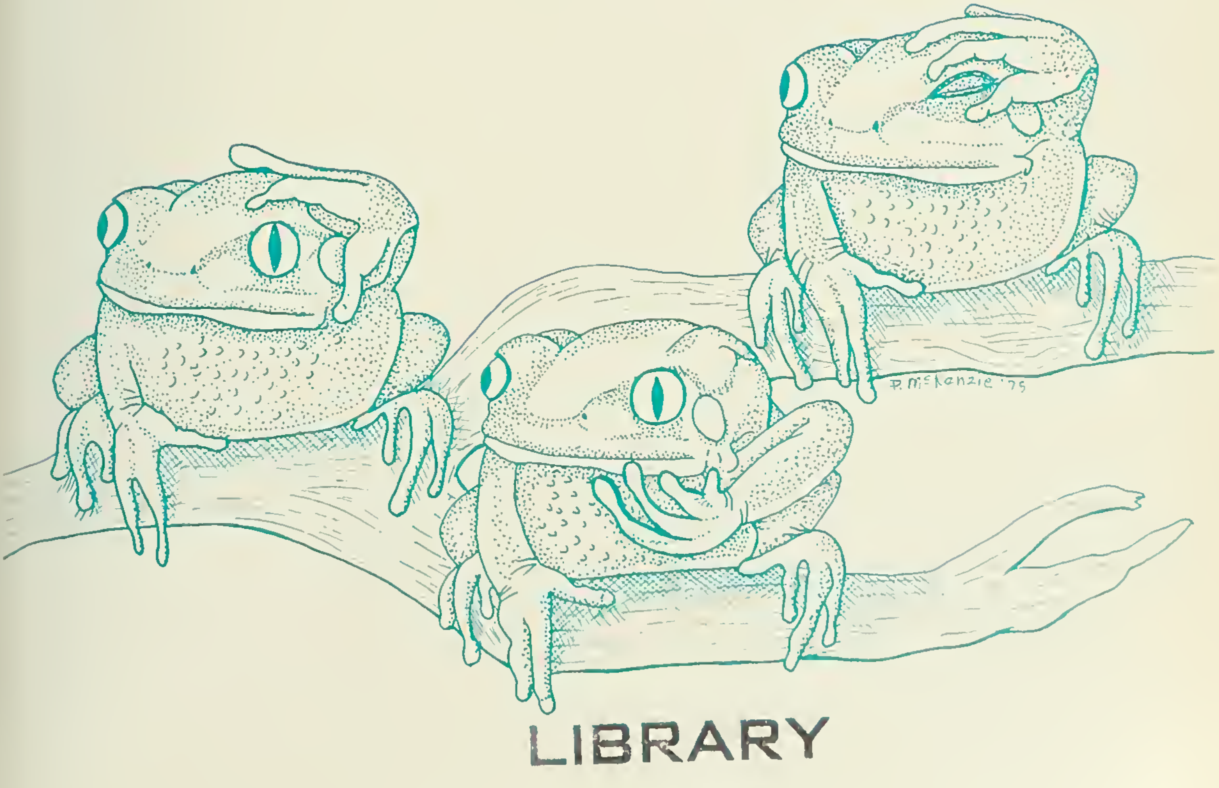
COVER: *Evening bat,* Nycticeius humeralis, *from Homestead, Florida.*

Photography by Vincent Brach, Univ. Miami.

SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

BULLETIN

Volume 74 Number 2



BCAS-A74(2) 49–96 (1975) AUGUST 1975

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BULLETIN OF THE SOUTHERN CALIFORNIA
ACADEMY OF SCIENCES

VOLUME 74 AUGUST 26, 1975 NUMBER 2

TAXONOMIC CHARACTERS OF THE GENUS *OCHODAEUS* SERVILLE WITH DESCRIPTIONS OF TWO NEW SPECIES IN THE *O. PECTORALIS* LECONTE SPECIES COMPLEX (COLEOPTERA: SCARABAEIDAE)

DAVID C. CARLSON[1]

ABSTRACT: The mandibles, stridulatory peg, and male genitalia of the adults of eight species of *Ochodaeus* found in the United States have useful characters for the delineation of species and are described and figured. The most useful taxonomic feature of the male genitalia is the aedeagal sac. The taxonomic characters of *Ochodaeus* are reviewed and a key to the species of the *O. pectoralis* species complex is presented.

The *Ochodaeus pectoralis* species complex is erected to contain the nominate species *O. pectoralis* LeConte and two new species which are described. The other five species considered are *O. biarmatus* LeConte, *O. inarmatus* Schaeffer, *O. kansanus* Fall, *O. praesidii* Bates, and *O. simplex* LeConte. A lectotype is designated for *O. inarmatus* Schaeffer.

The genus *Ochodaeus* Serville is one of six genera included in the subfamily Ochodaeinae. Approximately half of the sixty species of *Ochodaeus* occur in the New World (Arrow, 1912) and of these, twenty are from the United States, ten from Mexico and Central America, and five from South America. Species of *Ochodaeus* are distributed throughout North America with the greatest number occurring in the arid southwestern United States and northern portions of Mexico. Only three species are recorded from Canada (Howden, 1968). Previously, only a few species were known to be common to the United States and Mexico. Examination of several thousand specimens from the southwestern United States and northern Mexico discloses that many species are common to both areas.

The adults are nocturnal. In most areas where *Ochodaeus* have been collected, more than one species usually is taken, and it is not uncommon to take three or four species at the same locality on the same night. Very little is known about their biology or immature stages.

The last revisionary work on the United States species of *Ochodaeus* was by Fall (1909) and the genus is currently in need of revision. The present work is an attempt to discover new taxonomic characters and to evaluate their potential for use in revising the genus.

Serville (1828) described *Ochodaeus* and Westwood (1852) published the initial synoptic work. The New World species have been revised by LeConte (1868), Horn (1876), Fall (1909), and Arrow (1911).

Arrow (1904) described the position and morphology of the stridulatory peg and pectinate mesotibial spur (Fig. 15). Using characters associated with these structures he erected the subfamily Ochodaeinae with *Ochodaeus* as its only included genus. Previously, *Ochodaeus* was placed in the Orphniidae. The relationships of *Ochodaeus* to other Scarabaeidae have been considered by Ritcher (1969a, b) and Holloway (1972).

METHODS

Preparation of the male genitalia.—When studying the aedeagal sac, it is best to have the genitalia dissected from the specimen, with the aedeagal sac completely everted. In this condition, the sclerotized structures on the aedeagal sac are fully exposed.

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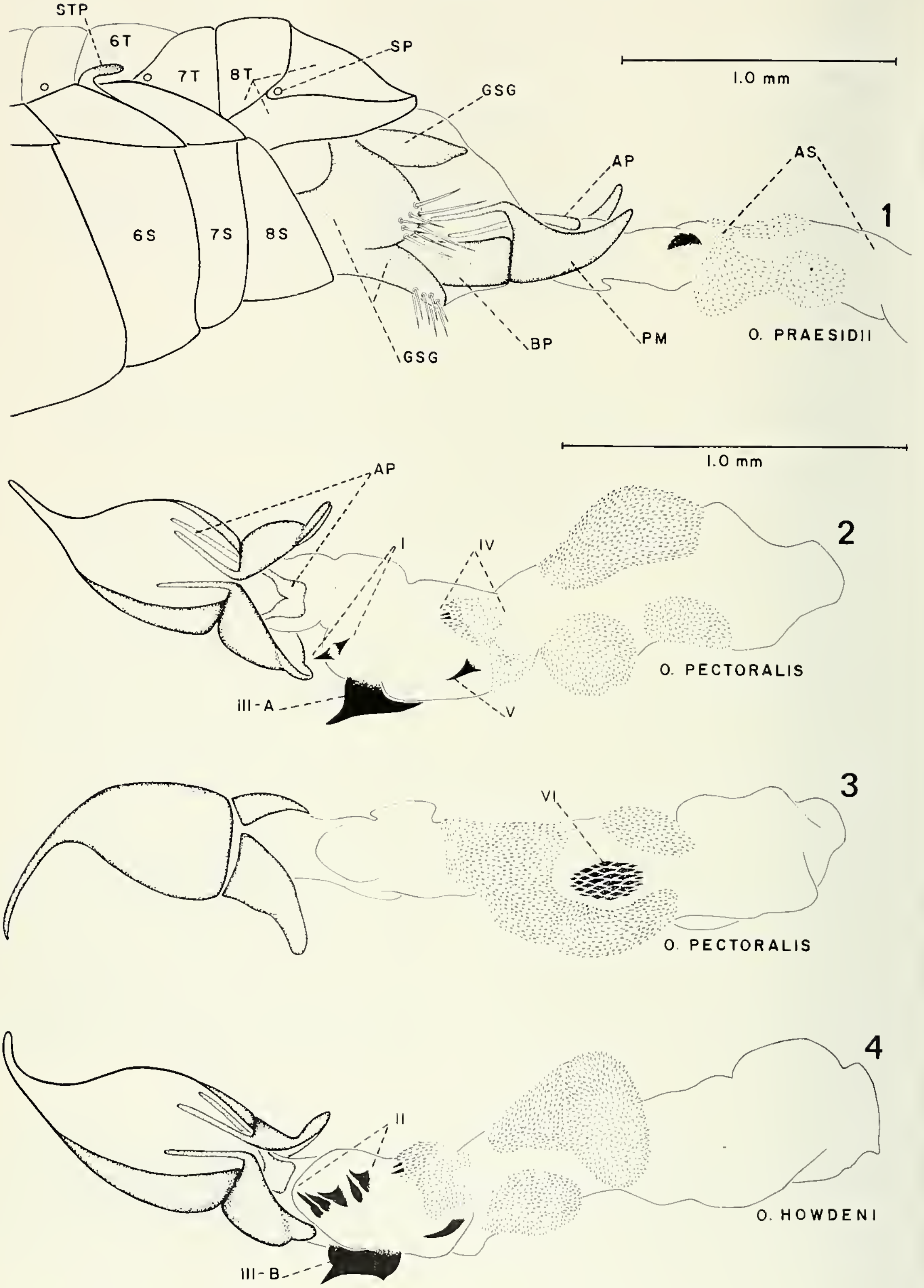

Figures 1–4. Male genitalic structures of *Ochodaeus* species: 1, *O. praesidii* Bates, abdomen with aedeagus everted; 2, *O. pectoralis* LeConte, aedeagus, dorsal view; 3, *O. pectoralis* LeConte, aedeagus, ventral view;

The best genitalic preparations were made from live specimens by squeezing the specimen between the thumb and index finger until the aedeagus was extruded and aedeagal sac everted. The specimen was then killed and preserved in 70 percent ETOH. Genitalia prepared by this method usually required no further dissection, were easy to study, and displayed the correct spatial relationships of the sclerotized structures.

Preserved specimens were less satisfactory for genitalic preparations. Dried specimens were relaxed and the genitalia removed from the specimen. All genitalic preparations were placed in 60°C KOH for a few minutes, washed in tap water, and then placed in 10 percent acetic acid for a few seconds to neutralize the KOH.

If the aedeagal sac was not everted at all, the inverted sac was slipped inside out over a minuten pin and cut longitudinally. Once the spatial arrangement of the structures for a particular species had been determined from an inflated sac, this type of preparation was used for studying and tabulating variations in the sclerotized structures.

If the aedeagal sac was partially everted, it was manually turned right-side-out using a hooked minuten pin. A fine glass micropipet was then inserted into the sac through the ostium and the sac fully inflated with glycerine. This technique was initially suggested by R. L. Wenzel (pers. comm., P. O. Ritcher).

The flattened aedeagal sac served well for examination and comparison purposes, but an inflated and completely everted sac was used for illustrations.

Preparation of the mouthparts.—The mouthparts were studied on microscope slides or on intact specimens. When a specimen was relaxed for genitalic dissection the mandibles were spread, exposing all of the medial edges, except the basal regions of the molar surfaces. No further dissection was necessary.

Preparation of the stridulatory peg.—In order to study the stridulatory peg it was necessary to lift an elytron slightly or prepare a microscope slide of one side of the abdomen. Slides were prepared by the same method used by Ritcher (1969a) to study abdominal spiracles.

TAXONOMY OF THE GENUS *OCHODAEUS*

The taxonomy of *Ochodaeus* has been worked out primarily at the species level. Previously, no attempt was made to establish infrageneric groups. The *O. pectoralis* complex is erected to contain the nominate species, *O. pectoralis* LeConte, and the two new species described herein. Although no other complexes are designated at this time, a number of currently recognized species are probably complexes of several closely related species.

Taxonomic Characters

The taxonomic characters previously used included the armature of the legs and head, punctation of the elytra, sculpturing of the clypeus, shape of the mentum and outer margin of the mandibles, and the nature of the sutural angle of the elytra. The shape of the stridulatory peg and dentition of the mandibles were used in the descriptions of a few Old World species in the early literature, but have not been used for New World species. Genitalic characters have not been used previously in *Ochodaeus*.

Male genitalia.—The terminology used is that of Lindroth and Palmén (1970). The male genitalia in *Ochodaeus* consists of a sclerotized genital segment (gsg) and a group of sclerites and membranous parts which form the aedeagus. The aedeagus consists of the tegmen, formed by the basal piece (bp) and paired parameres (pm), and the penis which is formed by the V-shaped apophysis (ap) and internal sac (as).

The genital segment is presumably derived from the ninth abdominal segment and surrounds and supports the aedeagus (Fig. 1). The aedeagus is attached to the genital segment by membranes at the point of articulation of the basal piece and parameres. When the aedeagus is extended and the internal sac everted, the parameres and internal sac project distad of the genital segment; the basal piece remains enclosed and supported by the genital segment. The shape of the genital segment was similar in all *Ochodaeus* species examined and is of no taxonomic value at the species level.

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4. *O. howdeni*, n. sp. aedeagus, dorsal view. Abbreviations: AP, V-shaped apophysis; AS, aedeagal sac; BP, basal piece; GSG, genital segment; PM, paramere; SP, spiracle; STP, stridulatory peg; 6S, sixth sternite; 6T, sixth tergite.

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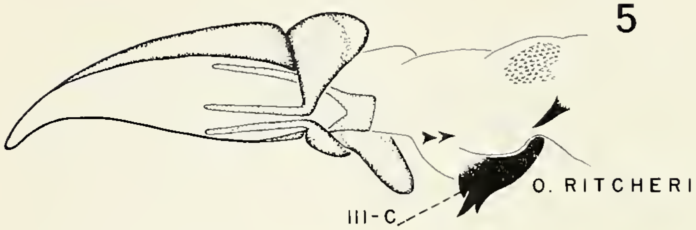

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The basal piece in *Ochodaeus* is an elongate sclerotized process, tapering to a point at the proximal extremity, and enlarged into a semicircular channel at its distal end where it articulates with the parameres (Figs. 2–4). This structure is the same shape in *Chaetocanthus* Péringuey, *Codocera* Eschscholtz, and *Pseudochodaeus* Carlson and Ritcher (Carlson and Ritcher, 1974). It does not form a continuous tubular structure as in the vaginate type of aedeagus (Lindroth and Palmén, 1970). There is little structural diversification of the basal piece in *Ochodaeus* and consequently it does not provide useful taxonomic characters for distinguishing species. It does, however, provide characters which are useful for assessing generic relationships in the Ochodaeinae.

The parameres articulate with the distal end of the basal piece and form a complete tubular structure through which the aedeagal sac is everted. They are sclerotized, symmetrical, evenly pigmented, and are capable of opening and closing. The points of articulation are in the median plane at the dorsal and ventral surfaces of the aedeagus. The parameres are simple in shape, show little structural diversity, and do not provide useful characters for distinguishing species.

A V-shaped apophysis is attached to the dorsal surface of the aedeagal sac and has a distal margin which is either truncate (Fig. 2) or pointed (Fig. 12). The arms of the apophysis extend cephalad, back through the ostium to about the midpoint of the basal piece. The arms are free of specific articulation with the tegmen, but are attached to a membrane which covers the dorsal surface of the basal piece. The apophysis is sclerotized, evenly pigmented, and gives support to the basal portion of the aedeagal sac when it is everted. The shape of this apophysis is similar in all species considered except *O. biarmatus* LeConte in which its distal margin is pointed (Fig. 12). It does not provide characters for distinguishing other species.

The aedeagal sac is an elongate, membranous structure often bearing numerous sclerotized areas or processes. These processes vary in number, size, and position in each species and may be hooks, barbs, spines, serrate plates, stellate structures, or groups of spinules. No attempt was made to adopt a terminology or means of coding the various structures and their positions at the generic level. However, a coding system was adopted for the *O. pectoralis* species complex which was useful in determining variation in these structures. Each position on the sac bearing sclerotized structures was given a roman numeral beginning at the basal (proximal) end of the sac. For each position, the number of structures was recorded after the roman numeral. Each shape of a particular process at each position was given a letter, and this was listed, if applicable, after the number of processes present. Thus, the aedeagal sac formula for a species might appear as: I-0, II-1-A, III-3 to 5, IV-1 to 4, V-present, etc.

The structures on the aedeagal sac exhibited characters which were useful for distinguishing species. These characters were less variable than many of the external morphological characters and were consequently more reliable for distinguishing species. In most cases other nongenitalic characters supported the differences found in genitalic structures, but these were less apparent. It appears that characters associated with the aedeagal sac will be useful for distinguishing species and indicating relationships between species.

Mouthparts.—Taxonomic characters associated with the mouthparts have been used extensively in *Ochodaeus*. The shape of the mentum is most often used (Horn, 1876; Fall, 1909), and provides characters which are useful for distinguishing the species of the *O. pectoralis* complex.

Although the shape of the labrum was mentioned in the early literature (Westwood, 1852; Horn, 1876), it has not been used in subsequent works. It is used here as a means of distinguishing species in the *O. pectoralis* complex, in which the sculpturing of the dorsal surface is unique (Figs. 28–30).

Westwood (1852) was the only author to figure and use characters associated with the maxillae in

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Figures 5–13. Aedeagi and associated structures of *Ochodaeus* species: 5, *O. ritcheri*, n. sp., aedeagus, dorsal view; 6, *O. howdeni*, n. sp., type-D structure from position III; 7, *O. howdeni*, n. sp., type-E structure from position III; 8, *O. inarmatus* Schaeffer, aedeagus, dorsal view; 9, *O. inarmatus* Schaeffer, aedeagus, ventral view; 10, *O. kansanus* Fall, aedeagus, left lateral view; 11, *O. kansanus* Fall, aedeagus, dorsal view; 12, *O. biarmatus* LeConte, aedeagus, dorsal view; 13, *O. inarmatus* Schaeffer, bifurcate basal structure.

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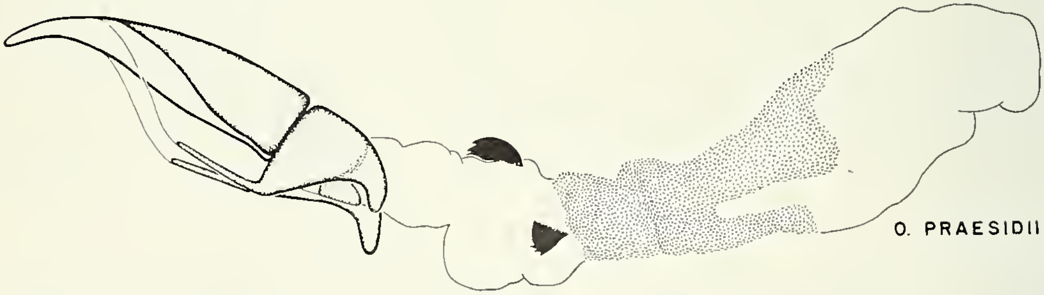


Figures 14–19. 14, *O. biarmatus* LeConte, aedeagus, dorsal view; 15, *O. repandus* Fall, mesotibial spur; 16, *O. simplex* LeConte, aedeagus, dorsal view; 17, *O. simplex* LeConte, aedeagus, right lateral view; 18, *O. praesidii* Bates, aedeagus, left lateral view; 19, *O. praesidii* Bates, aedeagus, right lateral view.

species descriptions. The maxillae were considered in this study, but no useful characters were found.

Horn (1876) and Fall (1909) considered the shape of the outer margin of the mandibles and Westwood (1852) figured and described the medial edges and dentition of the mandibles of several Old World species. The dentition and sculpturing of the inner margin of the mandibles provide excellent taxonomic characters in *Ochodaeus*. This portion of the mandible is subject to wear, but none of the specimens examined had mandibles which were worn to the extent that the dentition was obscured.

The mandibles are asymmetrical and the shape of the left mandible may be used in conjunction with other characters to divide the genus into species complexes. The mandibular dentition of the *O. pectoralis* complex is unique for each species and remains constant despite wear, with the right mandible offering the best characters. Overall size of the mandibles varies with the size of the adult and is not a reliable character.

A system of categorizing the shape of the left mandible was adopted and has been used in the species descriptions. Three types of left mandibles are apparent: type I, unidentate, with apical tooth only, lacking any secondary subapical teeth (Fig. 26); type II, bidentate, with apical portion broad and bladelike, the secondary subapical tooth small, just distad of the membranous prostheca (Figs. 20–21, 24–25, 27); type III, tridentate, apical portion produced into a sharp tooth, secondary and tertiary teeth distad of the prostheca (Fig. 23).

The third tooth of the type III mandible apparently arises from the emarginate apical portion of the type II mandible. The left mandible of *O. kansanus* Fall (Fig. 22) appears to be intermediate between the typical type II mandible (Fig. 20) and the type III mandible (Fig. 23). The left mandible of this species seems to indicate the development of the secondary tooth from the apical portions of the mandible. In the type II mandible, the apical scissorial portion varies from being quite flat to distinctly emarginate.

Stridulatory peg.—Horn (1876) was the first to mention stridulation in *Ochodaeus*, but Arrow (1904) first identified the stridulatory peg, which is located on the sixth sternite (Fig. 1). This peg projects posteriorly and is covered with small tubercles. The area of the elytron adjacent to the peg is thicker than the rest of the elytron and is covered with fine teeth. This appears to be the area which works against the peg to produce sound.

Chaethocanthus Péringuey and *Pseudochodaeus* Carlson and Ritcher lack stridulatory pegs, but do possess the pectinate mesotibial spur (Carlson and Ritcher, 1974). Examination of a number of *Ochodaeus* in the present study revealed at least one species (*O. mandibularis* Linell) which lacks the stridulatory peg.

Arrow (1904) used the shape of the peg as a character in his description of *O. maculipennis* Arrow and figured the pegs of two European species. *Ochodaeus maculipennis* was found to have a straight projection terminated by numerous sharp teeth while the European species has a bent, rounded club with the apex slightly bulbous. This is the same basic type found in the New World species I examined.

The shape of the stridulatory peg is distinct for each of the species considered (Figs. 40–47) and is the same in both sexes of each species. The magnitude of differences between species in the *O. pectoralis* complex was less apparent than that observed between this complex and the other species considered.

Descriptions of Species

The *O. pectoralis* species complex is considered first as an assemblage and then the three species of the complex are described. The salient characters of five other species are included for comparison and illustrate the variability of these characters within *Ochodaeus*. The holotypes of all the species discussed, except *O. praesidii* Bates, were examined. In the case of *O. praesidii*, a specimen compared with the type at the British Museum (Natural History) by H. F. Howden was examined.

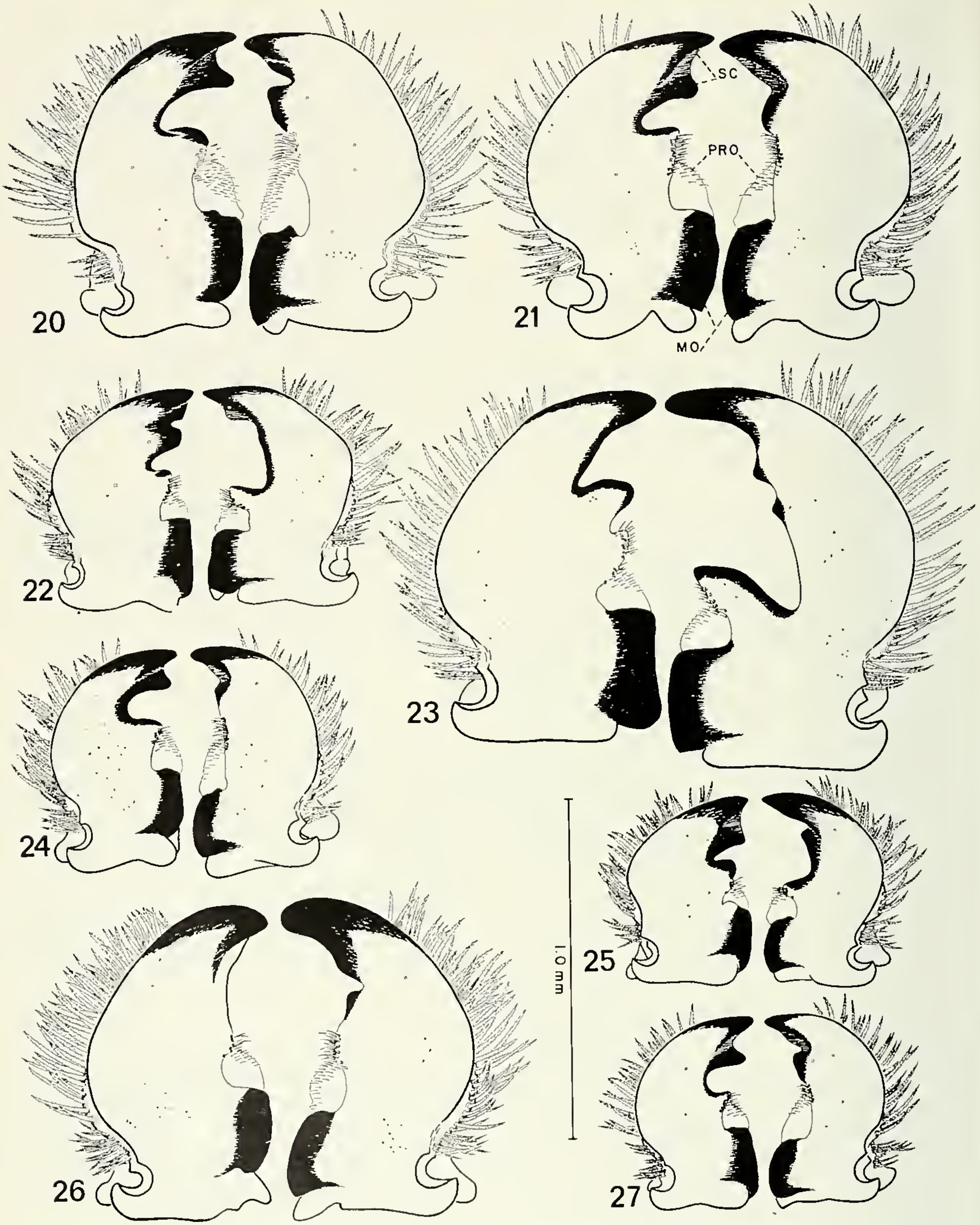
Ochodaeus pectoralis complex

Ochodaeus pectoralis LeConte and the two new species described below are included in the *O. pectoralis* complex. A coding system has been adopted for this complex to facilitate discussion and comparison of the characters of the aedeagal sac (Figs. 2–7).

Description: *Male genitalia.* V-shaped apophysis truncate. Aedeagal sac with six sclerotic positions I through VI as follows:

I. Basal series of singular, unipointed spines varying in number from zero to three (Fig. 2).

II. Secondary basal series of singular, uni-



Figures 20–27. Right and left mandibles of *Ochodaeus* species, dorsal view: 20, *O. howdeni*, n. sp.; 21, *O. inarmatus* Schaeffer; 22, *O. kansanus* Fall; 23, *O. praesidii* Bates; 24, *O. pectoralis* LeConte; 25, *O. biarmatus* LeConte; 26, *O. simplex* LeConte; 27, *O. ritcheri*, n. sp. Abbreviations: MO, molar area; PRO, prostheca; SC, scissorial area.

pointed spines varying in number from zero to six (Fig. 4).

III. Large, singular, basal sclerotized structure always present, but varying in shape. Five shapes recognized:
   A. Simple (Fig. 2).
   B. One small basal tooth (Fig. 4).
   C. Two small basal teeth (Fig. 6).
   D. Two small distal teeth (Fig. 7).
   E. Apex bidentate (Fig. 5).

IV. Medially located patch of spiculi; varying in the number of heavily sclerotized and pigmented spiculi from zero to five (Fig. 2).

V. Solitary, simple spine always present, but varying in size (Fig. 2).

VI. Ventrally located patch of heavily pigmented and sclerotized spiculi near distal end of sac. Always present in all three species (Fig. 3).

Mouthparts. Mandibles (Figs. 20, 24, 27): Left mandible type II, with apical portion modified into scissorial structure; midpoint of this area evenly indented; secondary tooth set off by large, deep indentation; prostheca located between this tooth and basal molar area. Right mandible bidentate, with apical portion produced into sharp tooth; secondary tooth set off by distinct indentation between it and primary tooth; shape of secondary tooth unique for each species; prostheca anterior to basal molar area, varying in size in each species. Sculpturing and setation of *labrum* (Figs. 28–30) unique for each species. Shape of *mentum* (Figs. 31–34, 36) unique for each species, particularly in degree to which it is produced ventrally. *Stridulatory peg* (Figs. 40–42): Peg similarly shaped in three species, but varies in size, angle of projection, and degree to which apex is enlarged; distal end bluntly rounded.

Remarks: Externally the species of this complex can most easily be distinguished by the sculpturing of the labrum and shape of the mentum. Only one of the series of spines at positions I and II on the aedeagal sac is present in any one species.

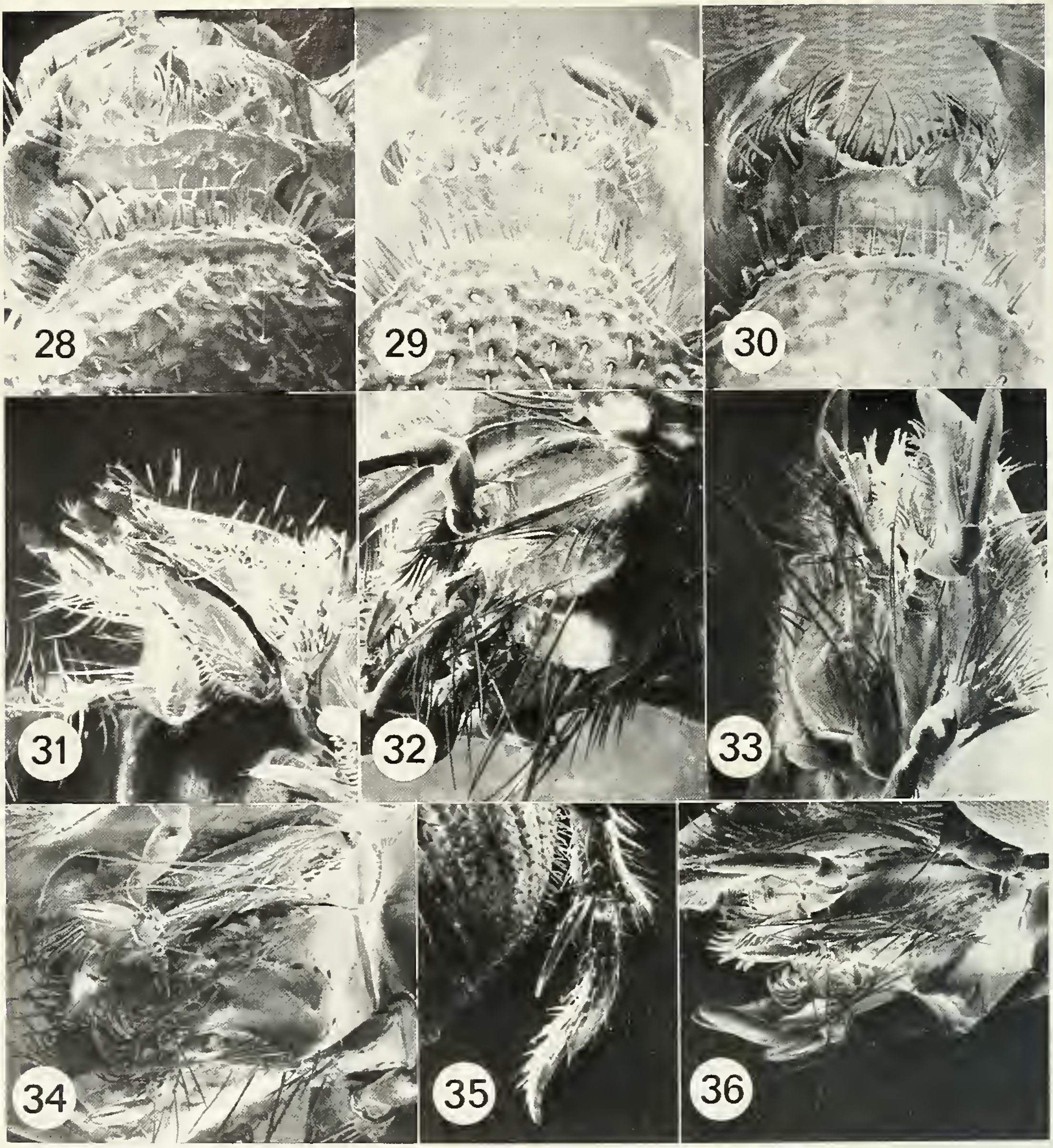
Ochodaeus pectoralis LeConte

Figures 2–3, 24, 28, 31, 35, 37, 40, 48

Ochodaeus pectoralis LeConte, 1868:51; Horn, 1876: 181; Fall, 1909:32; Arrow, 1912:23.

Since two new species closely related to *O. pectoralis* LeConte are being described, it is redescribed in detail below.

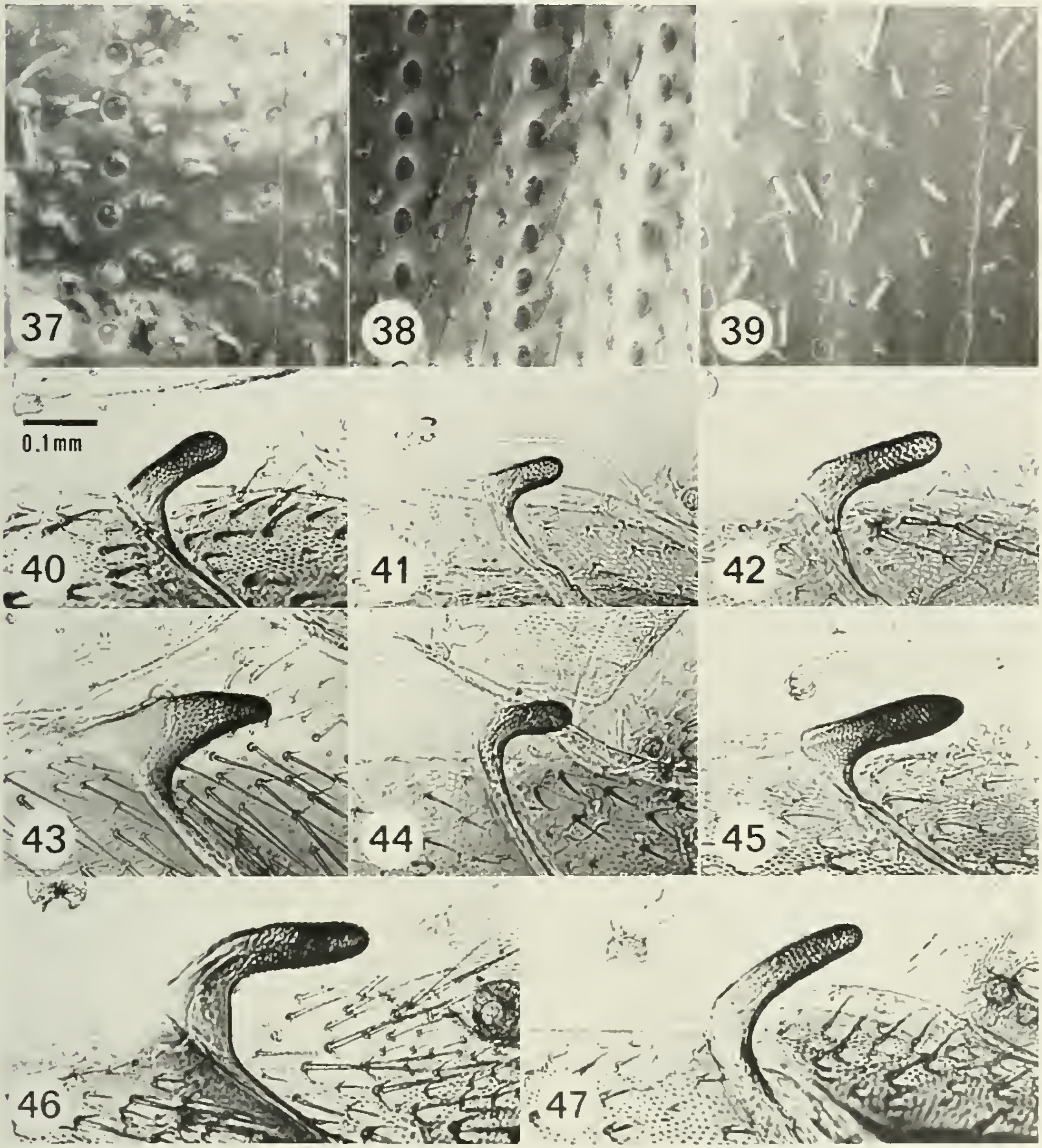
Description: *Male (Holotype)*. N.M.; Type, M.C.Z., 3335; *O. pectoralis* Lec.; *Ochodaeus pectoralis* Lec. Length 7.5 mm, width through midpoint of elytra 3.9 mm. Mandibles, labrum, clypeus, pronotum, elytra, ventral surfaces, and legs reddish-brown. Frons and vertex mostly reddish-brown, areas adjacent to eyes shading into black. Labrum, clypeus, vertex, pronotum, and elytra covered with yellowish, uniformly short, semi-erect setae. Ventral surfaces, legs, and first antennal segment covered with longer, relatively fine, yellow setae. Mandibles evenly arcuate along outer margin. Labrum (Fig. 28) distinctly emarginate distally, almost bilobed; dorsal surface covered with moderately long setae, each seta set in shallow depression, separated from adjacent setae by raised ridges; proximal half lacks sculpturing, but with transverse row of short, fine setae, anterior to distal margin of preclypeus; postero-lateral margins of labrum concave. Clypeus elevated above labrum, lacking lateral or medial horns; anterior margin slightly reflexed, covered with dense patch of setae. Surface of clypeus and vertex evenly setose, each seta arising just posterior to small tubercle. Posterior margin of head behind eyes lacking setae, closely punctate. Pronotum with marginal bead entire; surface strongly convex, irregularly punctured, and evenly setose, each seta arising from base of small tubercle. Scutellum flat, surface closely punctate, sparsely setose. Each elytron with five punctate striae between median suture and humeral umbone, areas between striae covered with three irregular rows of setae, each seta with basal puncture and tubercle, distance between punctures less than or equal to diameter of individual punctures (Fig. 37). Sutural apex of each elytron dentiform. Propygidium with two tubercles, one on each side of midline. Mentum (Fig. 31) produced ventrally to form transverse wedge, projecting well below ventral edge of maxillae, emarginate anteriorly; anterior surface nearly flat, lacking median ridge; posterior surface of wedge nearly vertical; anterior surface sloping at about 45-degree angle. Prosternum produced anteriorly to form blunt point. Fore tibia tridentate, with proximal tooth median in position; hind femur and tibia lacking dentition, tibia only slightly dilated distally; hind tarsi with first segment arcuate, longer than remaining four segments together; angulation of first metatarsal segment occurring at about apical third. The holotype was not dissected. The descriptions of the genitalia, mandibles, and stridulatory peg which follow are composite descriptions of all of the specimens examined. *Male genitalia* (Figs. 2–3): Basal piece and parameres not distinctive, distal end of V-shaped apophysis truncate. Aedeagal sac formula: I-0 to 3, II-0, III-A, IV-0 to 2, V-present, VI-present. *Mandibles* (Fig. 24): Left mandible type II, apical scissorial portion with shallow, median indentation partially dividing this area into two small teeth; large deep indentation posterior to apical



Figures 28–36. 28, *O. pectoralis* LeConte, labrum, dorsal view; 29, *O. ritcheri*, n. sp., labrum, dorsal view; 30, *O. howdeni*, n. sp., labrum, dorsal view; 31, *O. pectoralis* LeConte, mentum, ventro-lateral view; 32, *O. howdeni*, n. sp., mentum, ventro-lateral view; 33, *O. howdeni*, n. sp., mentum, ventro-lateral view; 34, *O. ritcheri*, n. sp., mentum ventro-lateral view; 35, *O. pectoralis* LeConte, metatarsal segments, dorsal view; 36, *O. ritcheri*, n. sp., mentum, ventro-lateral view.

scissorial area separating this area from poorly developed secondary tooth; secondary tooth produced into blunt projection; prostheca posterior to secondary tooth and anterior to basal molar area. Right mandible unidentate, with pointed apical tooth; shallow indentation at base of apical tooth delimiting poorly developed secondary projection; large prostheca adjacent to large basal molar area. Molar area of each mandible evenly convex. *Stridulatory peg* (Fig. 40): Peg of medium length, projecting dorso-caudad with neck not parallel to longitudinal body axis, distal end bluntly rounded and slightly bulbous.

Female. Females are similar to males in all respects except that the venter of the abdomen is distinctly convex when viewed laterally as compared to the concave venter of males. The first metatarsal



Figures 37–47. 37–39, Dorsal surface of elytra of species in the *O. pectoralis* species complex (200×): 37, *O. pectoralis* LeConte; 38, *O. ritcheri*, n. sp.; 39, *O. howdeni*, n. sp.: 40–47, Stridulatory pegs of *Ochodaeus* species (all same scale as Fig. 40): 40, *O. pectoralis* LeConte; 41, *O. ritcheri*, n. sp.; 42, *O. howdeni*, n. sp.; 43, *O. simplex* LeConte; 44, *O. biarmatus* LeConte; 45, *O. kansanus* Fall; 46, *O. praesidii* Bates; 47, *O. inarmatus* Schaeffer.

segment in some females appears to be slightly less arcuate than in males.

Variation. In males, length ranges from 4.0 mm to 9.4 mm and width from 2.2 mm to 4.2 mm. In females, length ranges from 4.2 mm to 8.2 mm and width from 2.2 mm to 3.6 mm. Color varies from light brown to dark reddish-brown. The majority of the specimens are dark reddish-brown. Variations in the sclerotized structures on the aedeagal sac are as indicated in the sac formula above. Of the sixty-two males dissected, the structures at positions I and IV vary most. The most common condition is I-2 and IV-2. The proportions of the structure at position III vary, but retain a basic shape and show no addition of extra teeth. The size of all sclerotized structures vary to a limited extent, but does not affect thei

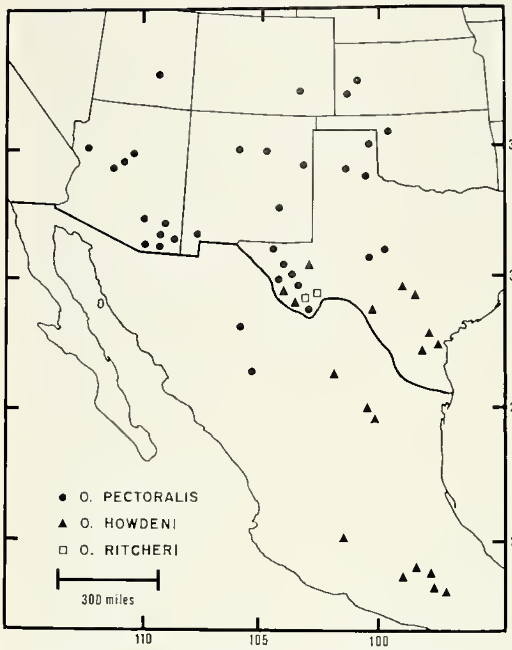


Figure 48. Distribution of species of the *O. pectoralis* species complex in North America and Mexico.

basic shape. The mandibles were quite constant in shape, with only slight variation due to abrasion. The shape of the mentum and stridulatory peg are constant.

Other specimens examined (112 ♂, 159 ♀): UNITED STATES ARIZONA: *Cochise Co* Chiricahua Mts: Cave Creek Ranch, Pinery Cyn, Portal, Southwestern Research Station, Turkey Creek; Dragoon Mts; Cochise Stronghold; Huachuca Mts: Garden Cyn, Flying H Ranch; Sierra Vista; Tombstone; 8 mi E Wilcox. *Coconino Co* Midgley Bridge, Oak Creek Cyn; Sedona. *Mohave Co* 6 mi SE Kingman. *Navajo Co. Pima Co* Stratton, S Catalina Mts, 6700 ft. *Pinal Co* near Oracle. *Santa Cruz Co* Canelo. *Yavapai Co* Jerome, Red Rock Camp, Prescott, 4 mi W Prescott. COLORADO: *Otero Co* Rocky Ford. KANSAS: *Kearny Co* Kendal. *Scott Co.* NEW MEXICO: *Chaves Co* Roswell. *Eddy Co* Guadalupe Mts: Sitting Bull Falls. *Luna Co* 26 mi W Deming. *Quay Co* San Jon. *Sandoval Co* Jemez Spgs: Sulphur Dam, 5 mi N Jemez Spgs. *San Miguel Co* Las Vegas. OKLAHOMA: *Woodard Co* Woodard. TEXAS: Hot Spgs. *Brewster Co* Alpine: Big Bend National Park; Tornillo Flat: S. G. Ranch. *Coleman Co* Hords Creek Res. *Culberson Co* Kent. *Hall Co* 5 mi W Memphis. *Hemphill Co* Canadian. *Hudspeth Co* Guadalupe Pass. *Jeff Davis Co* Davis Mts: Limpia Cyn, Madera Cyn Park; Ft. Davis; 1 mi W Ft. Davis; Valentine. *Randall Co* Palo Dura Cyn State Park. *Reeves Co* 40 mi W Ft. Stockton. *Tom Green Co* Highland Park Cmpgnd near San Angelo. *Val Verde Co.* UTAH: *Wayne Co* Bull Creek, 5000 ft, 15 mi S Hanksville; Fairview Ranch, 5000 ft, 13 mi S Hanksville. MEXICO CHIHUAHUA: Arroyo Catarinas, 15 mi S Matamoras; Catarinas; 12 mi N Chihuahua; Valle de Olivos, 5500 ft. COAHUILA: Rancho la Encontada, 5200 ft, Sierra del Carmen. DURANGO: Nombre de Dios, 5900 ft; Pedricena, 4500 ft. Collection dates range from April 15 through October 30, with the largest numbers in July and August.

Remarks: This species, as well as the two new species, will key to *O. pectoralis* LeConte in Fall's (1909) key. *Ochodaeus pectoralis* LeConte can be distinguished from them by the greatly produced mentum, by the large size of elytral punctures relative to the distance between punctures, by the first metatarsal segment which is angulate at the apical third, and by its labrum which lacks a median projection. These species can also be distinguished from each other by differences in the sclerotized structures on the aedeagal sac (Figs. 2–5).

Ochodaeus howdeni, new species
Figures 4, 6–7, 20, 30, 32–33, 42, 48

Description: *Male* (*Holotype*). Mexico, near Jame, Coahuila, 33 mi SE Saltillo, 7500 ft, 25 July 1963, H. F. Howden (CNC #13,467). Length 8.9 mm, width through midpoint of elytra 4.3 mm. Mandibles, labrum, clypeus, pronotum, elytra, ventral surfaces, and legs largely dark reddish-brown. Frons and vertex mostly brown, areas adjacent to eyes shading into black. Labrum, clypeus, vertex, pronotum, and elytra covered with yellowish, uniformly short, semi-erect setae. Ventral surfaces and legs covered with longer, relatively fine, yellow setae. Mandibles (Fig. 20) evenly arcuate along outer margin. Left mandible type II, apical scissorial portion with median indentation partially dividing this area into two small teeth; large, deep indentation posterior to apical scissorial area delimiting secondary tooth, this tooth only slightly developed; relatively large prostheca just anterior to large molar area. Right mandible bidentate, apical piercing tooth with shallow basal indentation separating it from bilobed secondary tooth just anterior to large prostheca, molar area smaller than left mandible. Molar areas of each mandible evenly convex. Labrum (Fig. 30) distinctly emarginate distally, almost bilobed; dorsal surface covered with sparse, moderately long setae, each seta set in shallow depression, separated from adjacent setae by raised ridges; proximal half lacks sculpturing, but has transverse row of short, fine setae, anterior to distal margin of preclypeus; postero-lateral margins of labrum concave. Clypeus elevated above labrum, lacking lateral or medial horns; anterior margin slightly reflexed, covered with dense patch of setae. Surface of clypeus and vertex evenly setose, each seta arising just posterior to small tubercle. Posterior margin of head behind eyes lacking setae, closely punctate. Pronotum with marginal bead entire: surface strongly convex, irregularly punctured, and evenly setose, each seta arising from base of small tubercle. Scutellum flat, surface closely punctate, sparsely setose. Each elytron with five punctate striae between median suture and humeral umbone, areas between striae covered with three irregular rows of setae, each seta with basal puncture and tubercle, distance between punctures greater than diameter of individual punctures (Fig. 39), sutural apex of each elytron dentiform. Propygidium with two tubercles, one on each side of midline. Mentum (Figs. 32–33) produced ventrally to form shallow transverse wedge, projecting only slightly below ventral edge of maxillae, emarginate anteriorly, and longitudinally impressed. Prosternum produced anteriorly to form blunt point, posterior margin with projection at midline. Fore tibia tridentate, with proximal tooth median in position: hind femur and tibia lacking dentition, tibia only slightly dilated distally; hind tarsi with first segment arcuate, longer than remaining four segments together; angulation of first metatarsal segment even, bend occurring near middle. *Genitalia* (Figs. 4, 6–7): Basal piece and parameres not distinctive, distal end of V-shaped apophysis truncate. Aedeagal sac formula: I-0, II-5, III-B, IV-4, V-present, VI-present. *Stridulatory peg* (Fig. 42): Peg long, projecting dorso-caudad with neck not parallel to longitudinal body axis, distal end bluntly rounded, not bulbous. Edges of peg parallel, not tapering distally.

Female (*Allotype*). Mexico, Coahuila, near Jame, 33 mi SE Saltillo, 7500 ft, 25 July 1963, A. T. Howden (HFH). Length 7.6 mm, width through midpoint of elytra 3.6 mm. Color uniformly reddish-brown except for darkening around eyes. First metatarsal segment less stout and arcuate than male, venter of abdomen evenly convex when viewed laterally; similar to male in other respects.

Paratypes (52 ♂ 33 ♀): UNITED STATES TEXAS: 1 ♂ (AMNH); 1 ♂, Horn collection H5577 (ANSP). *Brewster Co* Big Bend National Park: 1 ♂ 1 ♀, 10 June 1948, L. J. Bottimer (CNC); 4 ♂ 2 ♀, Basin, 13 August 1950, R. F. Smith (AMNH); 1 ♂, Chisos Basin, 16–17 July 1973, F. T. Hovore (DCC); 1 ♀, Chisos Mts, 4–6 July 1961, R. L. Westcott (RLW); 1 ♂ 3 ♀, Dugout Wells, 27 August 1965, A. Blanchard (ARH); 1 ♀, Green Gulch, Chisos Mts, 25–27 August 1965, A. Blanchard (LACM); 2 ♀, Green Gulch, 5700 ft, 3 August 1968, J. E. Hafernik (TAMU); 2 ♂, Juniper Cyn, Chisos Mts, 13–14 July 1928, F. M. Gaige (HFH, UM); Chisos Mts: 1 ♂, 17 July 1946, D. J. and J. N. Knull (OSU); 1 ♀, 28 July 1962, D. J. and J. N. Knull (HFH); 1 ♂ 22 June 1967, D. J. and J. N. Knull (OSU): 1 ♂ 1 ♀, Big Bend, 2–4 July 1946, VanDyke collection (CAS). *Duval Co* 1 ♀, Sepulveda Ranch, 6 June 1970, C. W. Griffin (ORSU). *Jeff Davis Co* 1 ♀, Davis Mts St Park, 18–21 July 1973, F. T. Hovore (DCC). *Kendal Co* 1 ♂ 1 ♀, vicinity "Cave without Name" near Boerne, 30 July 1968, G. E. Ball (AMNH). *Kerr Co* 1 ♂, Kerrville, 27 May 1906, J. D. Mitchell (USNM). *Kinney Co* 1 ♂ 1 ♀, 7 mi E Brackettville, 25 September 1971 R. Turnbow (RHT). *Maverick Co* 3 ♂ 2 ♀, 24 May 1940, M. Marquis (CAS). *Nueces Co* 1 ♂. Corpus Christi, 6 October 1951, O. L. Cartwright and A. B. Gurney (USNM). *Presidio Co* 1 ♂ 1 ♀, Shafter, 2 August 1968, M. L. Allender (TAMU). *San Patricio Co* 4 ♀, Mathis, 4 June 1964, H. R. Burke (TAMU). MEXICO COAHUILA: same locality as holotype; 3 ♂, 7500 ft, 18 July 1963, H. and A. Howden (CNC); 3 ♂, 7000 ft, 18 July 1963, A. Howden (HFH); 3 ♂ 1 ♀, 7500 ft, 18 July 1963, A. T. Howden (HFH): 1 ♂ 1 ♀, 7500 ft, 18 July 1963, Arnett and Van Tassell (HFH, CNC); 2 ♂ 2 ♀, 7500 ft, 25 July 1963, H. F. Howden (CNC); 5 ♂, 20 mi SE Saltillo, 6000 ft Rt. 015, 20–21 June 1971, H. F. Howden (HFH); 1 ♀, 9 mi E Quatro Cienegas, 2200 ft, 24 September 1958, T. J. Cohn (UM); 1 ♂, Coahuila, Horn collection, H5577 (ANSP). DURANGO: 1 ♂ 2 mi S Menores de Arriba, 14 September 1950, R. F. Smith (AMNH). GUANAJUATO: 3 ♂ 3 ♀, 22 mi E Penjamo, 5200 ft, 20 September 1968, A. R. Hardy, L. Espinosa, and J. P. Abrayaya (ARH). GUERRERO: 1 ♀, vicinity Acuitlapan, 10 mi NE Taxco, 5000 ft, 4–5 September 1970, E. M. and J. L. Fisher (ARH). MORELOS: 3 ♂ 1 ♀, Cañon del Lobos, 3 mi W Yautepec, 12–13 July 1970, E. Fisher and P. Sullivan (ARH). PUEBLA: 1 ♂, 13 mi SE Acatlan, 25 August 1964 (ARH); 3 ♂, 34 mi S Atlixco, 27 June 1957, J. A. Chemsak and B. J. Rannels (UCB, HFH); 1 ♂, 7 mi N Izucar de Matamoros, 4000 ft, 8–9 June 1971, H. F. Howden (HFH); 1 ♂, 12 mi SE Izucar Matamoros, 5 September 1969, S. and J. Peck (HFH).

Variation: In males length ranges from 5.8 mm to 8.9 mm and width from 2.9 mm to 4.3 mm. In females length ranges from 5.1 mm to 7.8 mm and width from 2.7 mm to 4.3 mm. Color varies from tan to a dark reddish-brown. Variation in the sclerotized structures on the aedeagal sac is: II-3 to 6, III-A or B or C or D, IV-0 to 5. The structures at positions II and IV are constant in shape, but vary in number. In some specimens the two faintly raised tubercles on the vertex are not visible. Variation in the mouthparts and stridulatory peg is slight.

Remarks: This species will key to *O. pectoralis* LeConte in Fall's (1909) key. *Ochodaeus howdeni* can be distinguished from *O. pectoralis* LeConte by the slightly produced mentum, by the small size of elytral punctures relative to the distance between punctures, and by the first metatarsal segment which is angulate at its midpoint. The secondary tooth of the right mandible reaches its greatest development in this species of the

O. pectoralis complex. These species can also be distinguished by differences in the sclerotized structures on the aedeagal sac (Figs. 2–4). The holotype is in the Canadian National Collection (CNC #13,467) and the allotype is in the personal collection of H. F. Howden (HFH). The paratypes are in the collections indicated in parentheses.

I am pleased to name this species after Henry F. Howden who collected a large part of the type material and assisted me with this study.

Ochodaeus ritcheri, new species
Figures 5, 27, 29, 34, 36, 38, 41, 48

Description: *Male* (*Holotype*). Texas, Big Bend National Park, Panther Jct, 4000 ft, 12 May 1959, Howden and Becker (CNC #13,468). Length 6.7 mm, width through midpoint of elytra 3.4 mm. Mandibles, labrum, clypeus, head, pronotum, ventral surfaces, and legs dark reddish-brown. Elytra slightly lighter in color. Labrum, clypeus, head, pronotum, and elytra covered with yellowish, uniformly short, semi-erect setae. Ventral surfaces and legs covered with longer, relatively fine setae. Mandibles (Fig. 27) evenly arcuate along outer margin. Left mandible type II, apical scissorial portion with median indentation partially dividing this portion into two small teeth; large, deep indentation posterior to apical scissorial area, delimiting secondary tooth, this tooth developed only slightly, rounded and narrow; relatively small prostheca anterior and adjacent to basal molar area. Right mandible bidentate, apical piercing tooth with shallow, basal indentation separating it from secondary tooth, not bilobed, just anterior to large prostheca. Basal molar area of each mandible evenly convex. Labrum (Fig. 29) distinctly emarginate anteriorly, almost bilobed; small pointed projection arising at midpoint of emargination on dorsal surface; anterior dorsal surface covered with sparse setae, each seta arising from shallow depression, separated from adjacent setae by fine ridges; posterior half of labrum lacking sculpturing, but with transverse row of very small, fine setae, anterior to distal margin of preclypeus; postero-lateral margins of labrum concave. Clypeus elevated above labrum, lacking lateral or medial horns; anterior margin slightly reflexed, covered with dense patch of setae. Surface of clypeus and vertex evenly setose, each seta arising at base of small tubercle. Vertex evenly convex, except for shallow depression at center just anterior to eyes; two slightly elevated areas on head between eyes. Posterior margin of head closely punctured, lacking setae and tubercles. Pronotum with marginal bead entire, surface strongly convex, irregularly punctured, and evenly setose, each seta arising at base of small tubercle. Scutellum flat, closely punctured, and sparsely setose. Each elytron with five punctate striae between median suture and humeral umbone, areas between striae with three irregular rows of setae, each seta arising from base of small tubercle, distance between punctures in elytral striae equal to or less than diameter of individual punctures (Fig. 38), sutural apex of each elytron dentiform. Propygidium with two tubercles, one on each side of midline. Mentum (Figs. 34, 36) produced ventrally to form transverse wedge extending considerably below ventral edge of maxillae, emarginate anteriorly, longitudinally impressed, with slight ridge at midpoint. Prosternum produced anteriorly to form blunt point, posterior margin with projection at midpoint. Fore tibia tridentate, basal tooth located approximately at midpoint between base of tibia and apical tooth, hind femur lacking apical unciform tooth, posterior apical margin with slightly produced edge, hind tibia lacking dentition and dilated only slightly at apex, hind tarsus with first segment as long as remaining four segments together, triangular in cross section, and arcuate, angulation occurring at approximately one-third distance from apex. *Genitalia* (Fig. 5): Basal piece and parameres not distinctive, distal end of V-shaped apophysis truncate. Aedeagal sac formula: I-2, II-0, III-E, IV-0, V-present, VI-present. *Stridulatory peg* (Fig. 41): Peg short, projecting caudad and slightly dorsal, with neck not quite parallel to longitudinal body axis, distal end bluntly rounded, not bulbous. Edges of peg parallel, not tapering distally.

Female (*Allotype*). Same data as holotype. Length 7.2 mm, width through midpoint of elytra 3.3 mm. Color uniformly dark reddish-brown with setation similar to male, labral projection same as in male. Similar to holotype in all other respects, except that venter of abdomen is evenly convex when viewed laterally.

Paratypes (2 ♂ 8 ♀): UNITED STATES TEXAS: *Brewster Co* Big Bend National Park: 1 ♂, Panther Jct, 4000 ft, 12 May 1959, Howden and Becker (CNC); 1 ♀, Tornillo Flat, 3200 ft, 5 May 1959, Howden and Becker (CNC); 1 ♂ Tornillo Flat 3200 ft, 20 May 1959, Howden and Becker (CNC); 4 ♀, Oak Springs, 25 August 1965, A. Blanchard (LACM); 2 ♀, Big Bend Oak Springs, 26 August 1965, A. and M. E. Blanchard (ARH); 1 ♀, Chisos Basin, 16–17 July 1973, F. T. Hovore (DCC).

Variation: A complete indication of the variation is difficult due to the limited amount of type material available. In males, length ranges from 6.1 mm to 6.7 mm and width from 3.1 mm to 3.5 mm. In females, length ranges from 5.1 mm to 6.7 mm and width from 2.7 mm to 3.3 mm. Color varies from light to very dark reddish-brown with some variation resulting from the type of treatment given to relax and remove the genitalia. The only variation in the male genitalia occurs at position III. The sclerotized structure at this position varies in the degree to which the apical teeth are produced. In one specimen the subapical tooth is greatly reduced. The two faintly raised tubercles on the vertex are visible in some specimens and completely lacking in others. Variation in the mouthparts and stridulatory peg is slight.

Remarks: This species will key to *O. pectoralis* LeConte in Fall's (1909) key. *Ochodaeus ritcheri* can be distinguished from *O. pectoralis* LeConte by the median projection of the labrum occurring in *O. ritcheri.* The secondary tooth on the left mandible in *O. ritcheri* is smaller and more rounded than in the other species of the *O. pectoralis* species complex. The shape of the right mandible in *O. ritcheri* more closely resembles the right mandible of *O. howdeni* than that of *O. pectoralis* LeConte. *Ochodaeus ritcheri* can also be distinguished from *O. howdeni* and *O. pectoralis* LeConte by the sclerotized structures on the aedeagal sac (Figs. 2–5). The holotype (CNC #13,468) and allotype are in the Canadian National Collection. Paratypes are in the collections indicated in parentheses.

I am pleased to name this species after my major professor, Paul O. Ritcher, who assisted me a great deal with this study. I am indebted to him for suggesting the topic, making the preliminary investigations into the possibility of using the aedeagal sac, and for accompanying me on collecting trips.

KEY TO THE SPECIES OF THE *OCHODAEUS PECTORALIS* SPECIES COMPLEX (ADULTS)

1a. First metatarsal segment arcuate, longer than remaining four segments together; mentum produced ventrally to form transverse wedge; sutural angle of elytra dentiform (*O. pectoralis* complex) 2
b. First metatarsal segment not arcuate, not longer than remaining four segments together; mentum not produced ventrally to form transverse wedge (if mentum is produced ventrally then sutural angle of elytra not dentiform) .. all other species.
2a. Labrum with median projection on dorsal surface .... *O. ritcheri*, new species.
b. Labrum without median projection on dorsal surface 3
3a. Mentum produced well below ventral surface of maxillae; first metatarsal segment with angulation occurring at apical one-third; distance between elytral punctures approximately equal to diameter of individual punctures .... *O. pectoralis* LeConte.
b. Mentum produced only slightly below ventral surface of maxillae; first metatarsal segment with angulation occurring at midpoint; distance between elytral punctures larger than diameter of individual punctures .... *O. howdeni*, new species.

Five species other than those of the *O. pectoralis* species complex were examined to determine the array of structural differences found in the aedeagal sac, mandibles, and stridulatory peg. Differences are briefly outlined below. For a key to these species see Fall (1909).

Ochodaeus inarmatus Schaeffer
Figures 8–9, 13, 21, 47

Ochodaeus inarmatus Schaeffer, 1906:270; Fall, 1909: 34; Arrow, 1912:22.

Type material: Two Cotypes: Males. United States National Museum. Type; Huachuca Mts., Ariz., Brooklyn Museum, Coll., 1929; Catal. No. 924; Cotype, No. 42575, USNM: *Ochodaeus inarmatus* Schaef., type; *Ochodaeus inarmatus* Schaef. I designate this specimen as lectotype. The other cotype, which is undissected, has an additional mentum mounted on a point below the specimen and lacks the second determination label.

Description: *Male genitalia* (Figs. 8–9, 13): V-shaped apophysis truncate. Aedeagal sac with four distinct sclerotic regions. *Mandibles* (Fig. 21): Left mandible type II; right mandible bidentate. *Stridulatory peg* (Fig. 47): Peg long, slightly arcuate, projecting dorso-caudad with neck not parallel to longitudinal body axis; distal end bluntly rounded, not bulbous; sides of peg parallel, not tapering distally.

Other specimens examined (76): UNITED STATES ARIZONA. MEXICO DURANGO.

Remarks: The only apparent variation in the sclerotized structures on the aedeagal sac is in the first basal structure. In some specimens the distal end of this structure is bifurcate (Fig. 13). The illustrations are of specimens taken at the Southwestern Research Station, 5 mi W Portal, Arizona.

Ochodaeus kansanus Fall
Figures 10–11, 22, 45

Ochodaeus kansanus Fall, 1909:34; Arrow, 1912:23.

Type material: *Holotype*: Male. Museum of Comparative Zoology, Harvard. Hamilton Co., Ks. 3350 ft, F. H. Snow; ♂; Type *kansanus*: M.C.Z. Type 24778.

Description: *Male genitalia* (Figs. 10–11): V-shaped apophysis truncate. Aedeagal sac with three serrate and one stellate, heavily pigmented, sclerotized structures; variable number of simple spines at distal end. *Mandibles* (Fig. 22): Left mandible type II, intermediate in shape between type II and type III mandibles; right mandible bidentate. *Stridulatory peg* (Fig. 45): Peg long, projecting caudad with neck parallel to longitudinal body axis; sides not parallel.

but narrow at base, bulbous at midpoint, and tapering to blunt point at apex.

Other specimens examined (200): UNITED STATES ARIZONA, COLORADO, KANSAS, NEBRASKA, NEW MEXICO, TEXAS. MEXICO CHIHUAHUA, DURANGO.

Remarks: There is little variation in the sclerotized structures on the aedeagal sac except in the simple structures at the distal end and the stellate structure. The simple teeth vary in number and shape and the stellate structure is lacking in some specimens bearing the same label as the type. Other specimens identical in all other respects possess this stellate structure. More than one distinct form keys out to this species in Fall's (1909) key. The illustrations are of specimens taken 26 mi W Deming, New Mexico.

Ochodaeus biarmatus LeConte
Figures 12, 14, 25, 44

Ochodaeus biarmatus LeConte, 1868:51; Horn, 1876: 182; Fall, 1909:35; Arrow, 1912:21.

Type material: *Holotype*: Male. Museum of Comparative Zoology, Harvard. N.M.; *O. biarmatus* Lec.; Type, M.C.Z., 3338.

Description: *Male genitalia* (Figs. 12, 14): V-shaped apophysis pointed. Aedeagal sac with two stellate patches, basally; series of nine or ten spines medially; series of three spines distally. *Mandibles* (Fig. 25): Left mandible type II; right mandible tridentate. *Stridulatory peg* (Fig. 44): Peg small, projecting caudad with neck parallel to longitudinal body axis; apex bluntly rounded, not bulbous; sides of peg parallel, not tapering distally.

Other specimens examined (740): UNITED STATES ARIZONA, COLORADO, NEW MEXICO, TEXAS. MEXICO CHIHUAHUA, COAHUILA, DURANGO, SONORA.

Remarks: Several distinct forms key to this species in Fall's (1909) key. Some of the specimens which key to this species lack acute dentition on the hind femur and some lack tubercles on the anterior clypeal margin. The illustrations are of specimens taken at the Southwestern Research Station, 5 mi W Portal, Arizona.

Ochodaeus simplex LeConte
Figures 16–17, 26, 43

Ochodaeus simplex LeConte, 1854:222; Horn, 1876: 182; Fall, 1909:32; Arrow, 1912:24.

Type material: *Holotype*: Female. Museum of Comparative Zoology, Harvard. C; *O. simplex* Lec., Webb, Copper Mines; Type 3340.

Description: *Male genitalia* (Figs. 16–17): V-shaped apophysis truncate. Aedeagal sac with two simple structures basally; spinous plate medially; elongate serrate structure distally. *Mandibles* (Fig. 26): Left mandible type I; right mandible bidentate. *Stridulatory peg* (Fig. 43): Peg medium in length, projecting caudad with neck parallel to longitudinal body axis; apex bluntly pointed; sides of peg not parallel, but tapering from broad base to bluntly pointed apex.

Other specimens examined (56): UNITED STATES ARIZONA, COLORADO, MONTANA, NEW MEXICO, OREGON, TEXAS, UTAH. MEXICO CHIHUAHUA.

Remarks: The only apparent variation in the structures on the aedeagal sac is in the pigmentation and development of the teeth of the spinous plate. The illustrations are of specimens taken 13 mi SE Sisters, Oregon.

Ochodaeus praesidii Bates
Figures 1, 18–19, 23, 46

Ochodaeus praesidii Bates, 1887:106; Fall, 1909:36; Arrow, 1912:23.

Type material: The holotype is in the British Museum of Natural History, London, and was not examined. A specimen compared with the holotype at the British Museum by Henry F. Howden was examined and dissected. This specimen was taken at Tuxpan, Nayarit, Mexico. According to H. F. Howden (pers. comm.) the holotype is a male. The type locality is Praesidio, Mexico.

Description: *Male genitalia* (Figs. 1, 18–19): V-shaped apophysis truncate. Aedeagal sac with three serrate plates occurring basally. *Mandibles* (Fig. 23): Left mandible type III; right mandible with two large and two small teeth. *Stridulatory peg* (Fig. 46): Peg long, acutely arcuate with distal two-thirds projecting caudad, parallel to longitudinal body axis; apex bluntly rounded, not bulbous; sides of peg divergent at base, becoming parallel along apical two-thirds.

Other specimens examined (820): UNITED STATES ARIZONA, TEXAS. MEXICO CHIHUAHUA, DURANGO, NAYARIT, SINALOA, SONORA.

Remarks: The sclerotized structures on the aedeagal sac of the specimen compared with the holotype are identical to those figured. The illustrations are of specimens taken at the Southwestern Research Station, 5 mi W Portal, Arizona.

ACKNOWLEDGMENTS

I thank Paul O. Ritcher, my major professor, for suggesting the topic and for providing support and guidance throughout this study. I also thank Henry F. Howden for helping to formulate the scope of this study, for providing the scanning electron micrographs, and for reviewing the manuscript.

Approximately four thousand specimens of *Ochodaeus* were borrowed from museums, institutions, and individuals. I am indebted to the following for the generous loan of these specimens: American Museum of Natural History (AMNH); British Museum of Natural History (BM); California Academy of Sciences (CAS); Canadian National Collection (CNC); Carnegie Museum (CM); Field Museum of Natural History (FMNH); Los Angeles County Museum (LACM); Academy of Natural Sciences of Philadelphia (ANSP); United States National Museum (USNM); Arizona State University, Tempe (AS); California State College, Long Beach (CSLB); Cornell University (CU); Harvard University (Museum of Comparative Zoology) (MCZ); Ohio State University (OSU); Oregon State University (ORSU); Stephen F. Austin State University (SASU); Texas A. and M. University (TAMU); University of Arizona (UA); University of California, Berkeley (UCB), Davis (UCD), Riverside (UCR); University of Idaho (UI); University of Kansas (Snow Entomological Museum) (KU); University of Michigan (UM); University of Nebraska (UNEB); A. R. Hardy (ARH); F. T. Hovore (FTH); H. F. Howden (HFH); F. H. Parker (FHP); R. H. Turnbow (RHT); R. L. Westcott (RLW). The letters in parentheses are the abbreviations used in the text.

I also thank the American Museum of Natural History for the use of their facilities at the Southwestern Research Station and especially V. Roth, Resident Director, for many favors during my visits.

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A STUDY OF THE MORPHOLOGICAL AND PHYSIOLOGICAL CHANGES IN THE LAMELLIBRANCH, *MYTILUS EDULIS*, AFTER 6-OH-DOPA ADMINISTRATION

Anthony A. F. Paparo[1] and Judith A. Murphy[2]

Abstract: Lateral ciliary activity was studied on gill preparations of the mussel *Mytilus edulis.* Electrical stimulation of the branchial nerve accelerated ciliary beating. The cilio-excitatory effect of electrical stimulation of the branchial nerve on the lateral ciliated cell decreased after intramuscular injection of 6-OH-DOPA. Scanning electron microscopic observations of the branchial nerve and visceral ganglion show degeneration of neuronal structures. Therefore, it appears likely that the lateral ciliated cell is dependent on the branchial nerve and visceral ganglion for its neuronal regulation.

Activity of the lateral ciliated cell is dependent upon the branchial nerve (Aiello, 1960, 1970: Paparo, 1973). Branchial nerve fibers were traced from the visceral ganglion to the lateral ciliated cell on the gill of *Mytilus* (Aiello and Guideri, 1965; Paparo, 1972). Dopamine (DA) was found to inhibit the lateral ciliated cell (Paparo and Aiello, 1970). DA has been localized within the visceral ganglion, branchial nerve, and lateral ciliated cell (Paparo and Finch, 1972; Malanga, Wenger, and Aiello, 1972). The visceral ganglion and gill were found to metabolize L-[^{3}H] tyrosine and L-[^{3}H] DOPA to [H^3] DA (Paparo and Finch, 1972). Selective depletion and destruction of DA in nerves is caused by 6-OH-DOPA in the visceral ganglion and branchial nerve of *Mytilus* (Paparo and Tate, 1973) and in the rat brain (Jocobowitz and Kostrzewa, 1971). The use of 6-OH-DOPA as an experimental tool in the destruction and functional elimination of an organ to characterize its physiological role is a well established principle that has found wide application in the investigation of the physiology and pharmacology of the nervous system (De Champlain and Nadeau, 1971). The purpose of this study was to ascertain the effect of administration of 6-OH-DOPA on (1) the lateral ciliated cell and (2) the morphology of the visceral ganglion and branchial nerve.

METHODS

All experiments were performed on the mussel, *Mytilus edulis,* obtained from the Marine Biological Laboratory; Woods Hole, Massachusetts. The specimens were kept from one to two weeks in artificial sea-water (Rila Marine Mix) in a Dayno Ocean Aquarium (temperature 16° C, pH 7.5–8.0, density 1.025). Before each experiment mussels were placed in finger bowls of the same sea-water, the posterior adductors were cut, and each gill with its branchial nerve, visceral ganglion, and piece of adductor muscle for support was isolated. This ganglion-nerve-gill preparation was pinned to rubber mats glued in the bottom of a Petri dish containing sea-water. The dish was placed in a holder fastened to the adjustable stage of a microscope. Under the ten power objective, the gill was seen to consist of numerous parallel filaments. Three major types of ciliated cells are clearly distinguished: frontal, laterofrontal, and lateral. This study is concerned with the rate of beating of lateral ciliated cell whose metachronal rate of beating is expressed in beats per second (bps). The bps was estimated by synchronizing the rate of flashing of a calibrated, stroboscopic light used in place of the substage lamp, with the rate of beating of the lateral ciliated cell. Synchronization was achieved when the metachronal wave appeared to stand still.

The dish was perfused with sea-water at 21° C, pH 7.5 and density 1.025, at a rate of about 0.5 ml per minute. Constant temperature was maintained by means of a tubular system built into the holder fastened to the adjustable stage of a microscope and cooled by means of circulating water from a Haake Kryomat. A thermoprobe was placed in the dish to a tele-thermometer. At 21° C ciliary activity was fairly rapid, well-coordinated, and of fairly constant rate after about two hours of equilibration.

When nerve stimulation was part of the ex-

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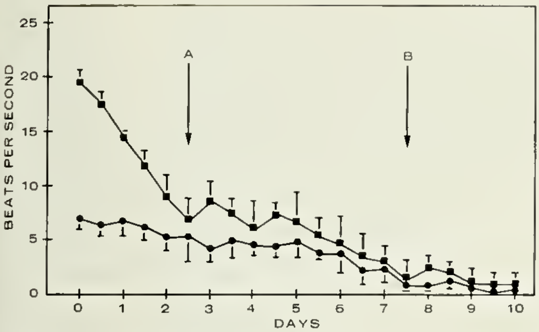


Figure 1. The effect of 6-OH-DOPA on the rate of beating of the lateral ciliated cell before (dots) and after (squares) branchial nerve stimulation. The letters A and B represent specimens taken for scanning electron microscopic examination.

periment, the mounted preparation was further dissected under four-power magnifying lens to expose the branchial nerve and a concentric electrode was placed at its point of emergence from the visceral ganglion just before it passed posteriorly into the gill. The electrode was held in place by a micro-manipulator fastened to the same holder that held the Petri dish. The pulse characteristics were: 10 V, 10 biphasic pulses per second, 2 m sec. pulse duration for three minutes.

The following drug was used 6-OH-DOPA (6-OH-3,4-dihydroxyphenylalanine: 10^{-6}M.) as a selective depletor and destructor of dopamine (DA) nerve fibers.

Specimens prepared for scanning electron microscopy were dissected in normal saline and immediately immersed into three percent glutaraldehyde (EM Sciences) in 0.05 M. S-collidine buffer, pH 7.4. Samples were fixed thirty minutes, washed three times in buffer, postfixed in Parducz fixative (six parts two percent OsO_4: one part saturated $HgCl_2$) for twenty minutes, washed five times in distilled water and dehydrated through graded series of alcohols to 100 percent then in Freon TF (Texwipe Co.). Critical point drying was carried out in a Bomar 900 EX CPD unit with Freon 13 and mounted on Cambridge type specimen stubs with double sided sticky tape. Samples were made conductive by coating with carbon followed by high and low angle evaporations of a 40:60 gold palladium alloy while being simultaneously rotated and tilted to obtain an even coating. A Cambridge Mark IIA Scanning Electron Microscope operated at 20 KV was used for examination.

RESULTS

Intramuscular injection of 6-OH-DOPA caused the rate of beating of lateral ciliated cell to decrease in response to branchial nerve stimulation (Fig. 1). Electrical stimulation of the branchial nerve in the control (zero time: Fig. 1) increased the rate of beating from 7.1 bps to 19.7 bps ($p < 0.002$). There was a rapid decrease in the response to electrical stimulation of the branchial nerve with no significant increase in rate of beating after two and one-half days. The basal rate of beating was maintained for six days with subsequent decrease after this time: no recovery was observed.

Scanning electron microscopic observations of cross-sections of the branchial nerve at times specified by letters A and B in figure 1 are shown in figures 2A and 2B, respectively. These investigations reveal progressive destruction of axons present in the branchial nerve subsequent to 6-OH-DOPA administration.

Nerve cells were observed on the ventral surface of the visceral ganglion prior to the injection of 6-OH-DOPA (Figs. 3 and 4). Seven days subsequent to intramuscular injection of 6-OH-DOPA degenerated nerve cells were observed (Fig. 5). Higher magnification of the surface of nerve cell body revealed numerous degenerative changes (Fig. 6). Ten days subsequent to administration of 6-OH-DOPA revealed massive destruction of nerve cells (Fig. 7).

DISCUSSION

The experiments with 6-OH-DOPA described in in this study indicate that the rate of beating of the lateral ciliated cell in *Mytilus* is under the control of the branchial nerve. The progressive destruction of the branchial nerve as revealed under the scanning electron microscope correlates well with the gradual decrease in the cilioexcitatory effect of electrical stimulation of the branchial nerve after 6-OH-DOPA administration. This study provides the morphological and physiological evidence to support other published results which show a decrease in the decarboxylase enzyme in visceral ganglion and gill in *Mytilus* after injection of 6-OH-DOPA (Paparo and Tate, 1973). This enzyme is needed for the formation of DA (Sourkes, 1966). DA has been identified in the nervous tissue of many molluscs (Sweeney, 1963; Kerkut, Sedden, Walker, 1966; Cottrell, 1967). It seems likely that DA is the principal physiologically active catecholamine that acts inhibitorily on the

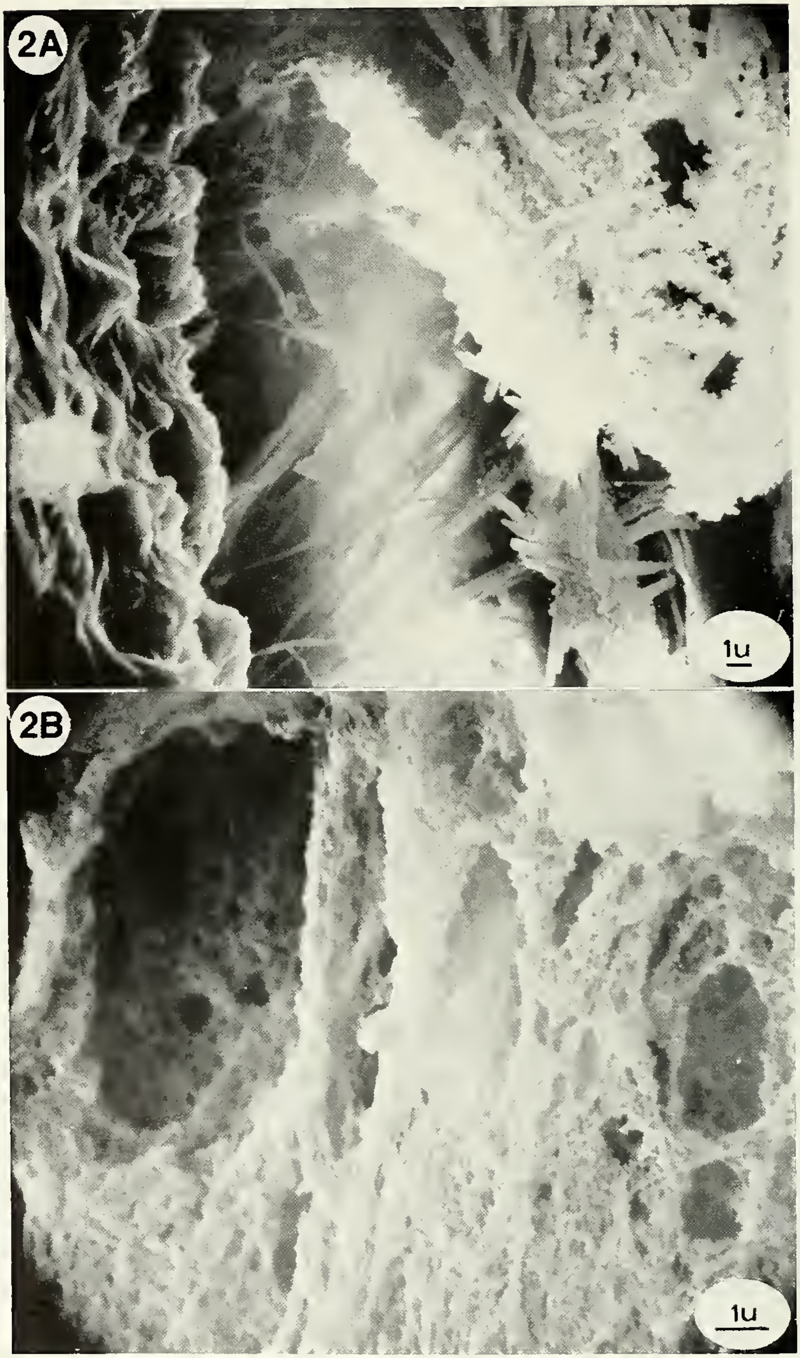
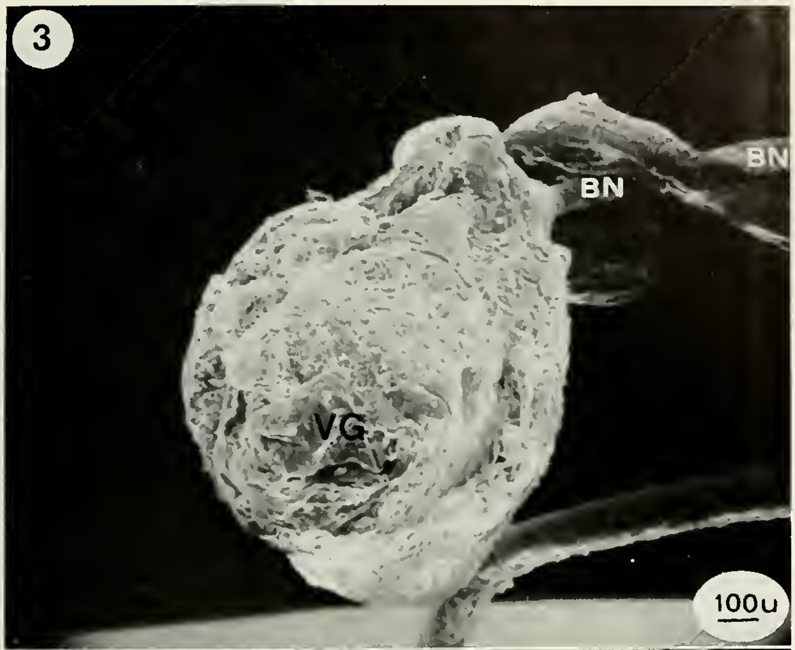


Figure 2. Scanning electron microscopic examinations cross-sections of the branchial nerve. Photographs A and B represent samples of the branchial nerve taken from specimens at intervals specified by letters appearing in figure 1.

lateral ciliated cell in *Mytilus edulis* (Parparo and Aiello, 1970) since no other catecholamine could be demonstrated by chemical measurements (Paparo and Finch, 1972).

CONCLUSION

6-OH-DOPA is a useful experimental tool in *Mytilus edulis* because of its selective elimination



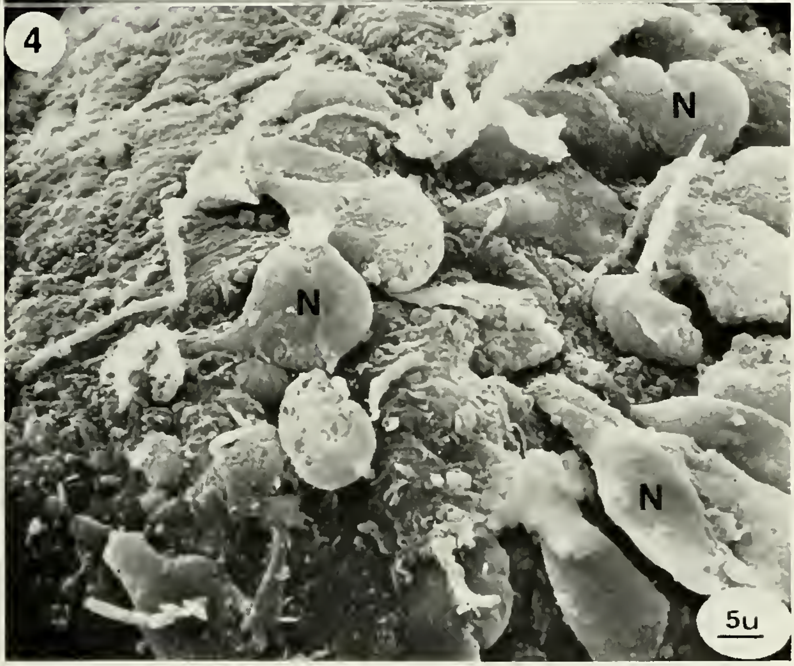


Figure 3. Scanning electron microscopic examination of the visceral ganglion (VG). The branchial nerve (BN) is shown emanating from the ventral surface of this ganglion.

Figure 4. A group of nerve cells (N) on the ventral surface of the visceral ganglion.

of specific parts of the dopaminergic system. This may further be used to elucidate the physiological importance of DA in the regulation of lateral ciliary activity.

ACKNOWLEDGMENTS

The center for Electron Microscopy of Southern Illinois is acknowledged for the use of its facilities

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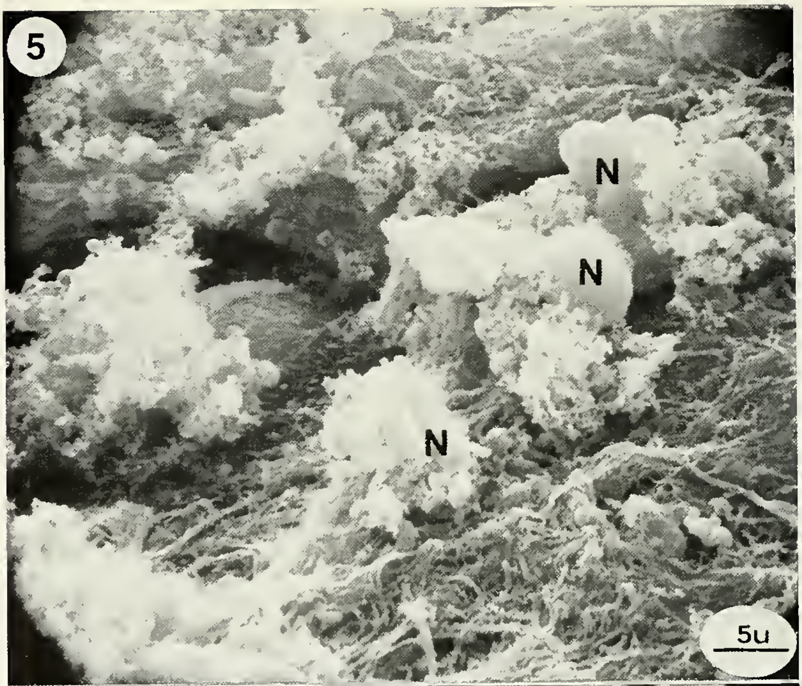

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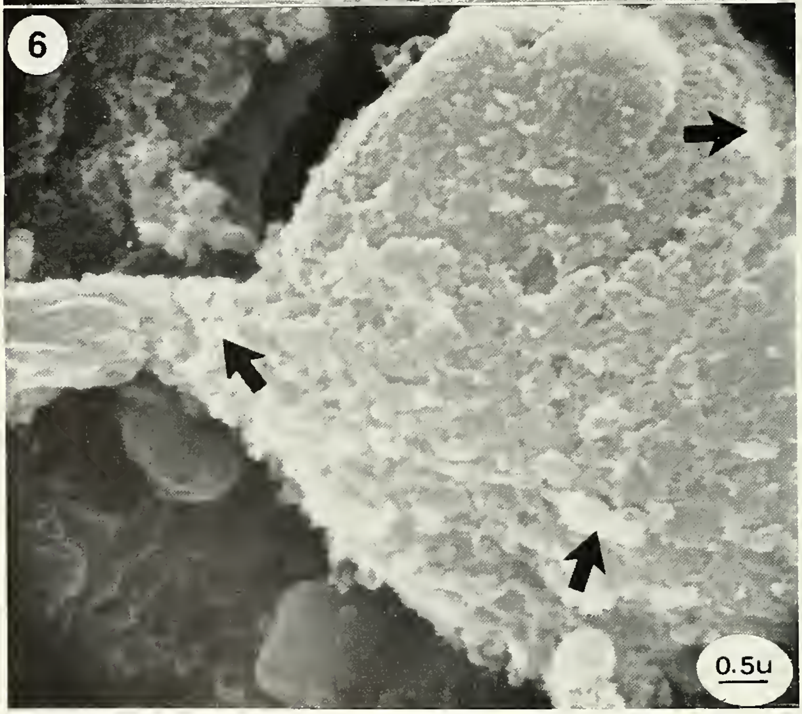

Figure 5. Degeneration of nerve cells (N) on the ventral surface of the visceral ganglion. Samples taken for scanning electron microscopic examination seven days after intramuscular injection of 6-OH-DOPA.

Figure 6. A nerve cell showing surface evaginations (arrows) of the perikaryon. Sample taken for scanning electron microscopic examination seven days after injection of 6-OH-DOPA.

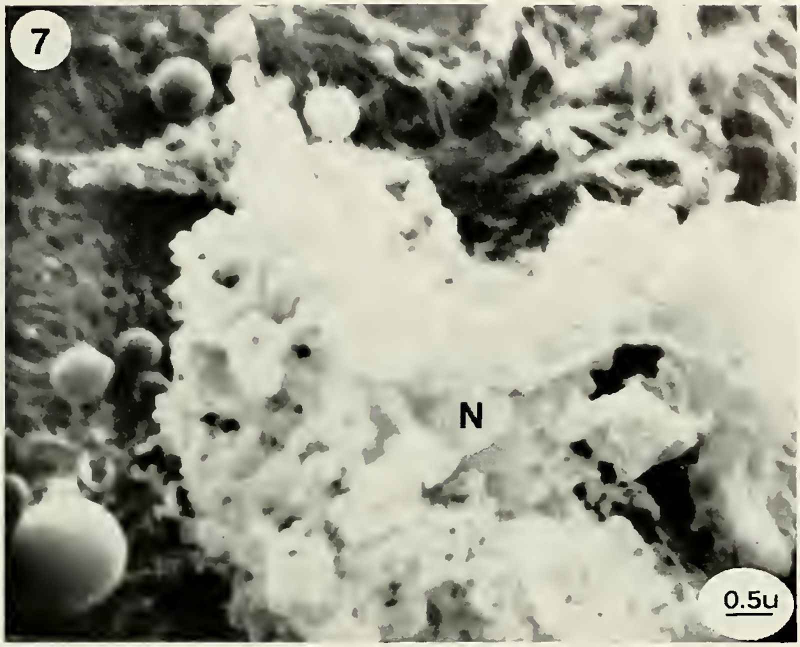

Figure 7. A nerve cell (N) with complete destruction of surface morphology. Sample taken for electron microscopic examination ten days after administration of 6-OH-DOPA.

including a Cambridge Mark IIA Stereoscan Scanning Electron Microscope purchased with the Biomedical Sciences Support Grant No. FR-1 SO5 FRO7118-0.

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PARASITISM AS AN INDICATOR OF FOOD SOURCES IN A CAVE-ADAPTED SALAMANDER HABITAT

William G. Dyer[1]

Abstract: Samples of the grotto salamander, *Typhlotriton spelaeus* Stejneger, 1893, comprising 119 specimens. colleced in Wet Cave, Shannon Co, Missouri, were examined for gastrointestinal parasites. The parasites recovered included *Haptophyra gigantea* Maupas, 1879; *Brachycoelium salamandrae* (Froelich, 1789) Lühe, 1909; *Capillaria inequalis* Walton, 1935; *C.* sp.; *Falcaustra catesbeianae* Walton, 1929; and *Oswaldocruzia* sp. Comparison of parasitological findings and feeding habits revealed a definite correlation between intestinal parasitocoenosis of postmetamorphic *T. spelaeus* and food sources in the habitat.

Large samples of cave-adapted salamanders are arduous and perhaps undesirable to obtain and specimens are often quite difficult to find during some seasons of the year. Because of this, it is highly desirable to obtain as much data as possible from captured specimens. Comparatively little information is available on cave-adapted salamanders beyond their morphology and taxonomy (Poulson, 1974). Most studies on salamander biology are restricted to a single aspect neglecting observations that might possibly contribute to a better understanding of other aspects.

With the exception of comprehensive surveys conducted by Harwood (1932), Mann (1932), Rankin (1937, 1945), and Fischthal (1955) little is known of salamander parasites in general and even less of the parasites of cave-adapted species. In all questions concerning the intestinal parasites of salamanders the food factor of the host is of primary importance. The use of parasites as "ecological labels" or "biologic tags" can render valuable information concerning the habits and habitats of their host (see Audy, 1960).

Observations on intestinal parasites are often excluded from studies on digestive tract contents. One reason for this may be that salamander parasites are difficult to identify and special procedures are required for proper fixation and preparation of specimens for study. Correlations which may exist between gastrointestinal parasitocoenosis of salamanders and food sources in their habitats is a topic on which little information is available.

Brandon (1971) investigated the reproduction, seasonal abundance, and feeding habits of a population of grotto salamanders, *Typhlotriton spelaeus* Stejneger, 1893, from a single cave in southeastern Missouri. The present report is based on a collection of helminths recovered from the gastrointestinal tracts of these salamanders and the results correlated with the feeding activity data contained in Brandon's previous report.

METHODS

According to Brandon (1971), Wet Cave is a small muddy passage in Ordovician dolomite located 30 to 40 ft above the floor of Sinking Creek Valley in northeastern Shannon Co, Missouri. It lies at an elevation of 820 ft in the southeastern drainage of the Salem Plateau (Current River drainage). The cave is small, inconspicuous and apparently seldom or never visited by cave

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explorers. It is not noted by Vineyard and Brod (1968) in their list of Missouri caves.

Between 1964 and 1967, 119 postmetamorphic grotto salamanders were collected from Wet Cave by Ronald A. Brandon, Department of Zoology, Southern Illinois University, Carbondale, Illinois. Since the primary purpose for collecting these salamanders involved studies on feeding and reproductive activity, the animals were killed in a solution of chloretone within one to two hr, fixed in 10 percent formalin, and stored in 65 percent ethyl alcohol. Standard parasitological procedures were utilized in the preservation, staining, and mounting of specimens. Protozoans were stained with Heidenhain's iron haematoxylin. Termatodes were stained with Grenacher's alcoholic borax-carmine or Harris' haematoxylin, cleared in beechwood creosote and studied in temporary mounts. Nematodes were cleared in glycerine and also studied in temporary mounts. The anterior ends of some specimens were removed and mounted in glycerine-jelly for *en face* studies.

RESULTS

The variety of gastrointestinal parasites encountered and the incidence of infections are presented in table 1. Of the 119 hosts examined only 14 (11.8 percent) were infected with parasites. Concurrent infections were not observed. *Haptophyra gigantea* Maupas, 1879, was the only protozoan species detected. Trematode infections were sparse with *Brachycoelium salamandrae* (Froelich, 1789) Lühe, 1909, being the only species of fluke encountered. More salamanders were infected with nematodes than any other group of parasites. Nematodes found included *Capillaria inequalis* Walton, 1935; *C.* sp.; *Oswaldocruzia* sp.; and *Falcaustra catesbeianae* Walton, 1929. All hosts examined were negative for cestodes and acanthocephalans. As indicated in table 1, the intensity of infections were low with no more than ten specimens in any single infection.

DISCUSSION

Brandon's (1971) observations on the feeding habits of *Typhlotriton spelaeus* in Wet Cave revealed that organisms suitable as salamander food were scarce. The relative scarcity of food was reflected by four nonbreeding adult males which were noticeably starved and emaciated, and also in the small size of adults compared with those in other, food-rich caves. The only abundant terrestrial invertebrates were heleomyzid flies, *Amoebaleria defessa*, although mosquito larvae and beetles were found in gut contents of transformed *T. spelaeus*. *Amoebaleria defessa* is commonly found in caves of eastern United States (Gill, 1962), as are adult mosquitoes (Barr, 1961). Smith (1948) noted the probable importance of *A. defessa* as food for terrestrial cave-dwelling amphibians.

TABLE 1. Intestinal parasites of 119 *Typhlotriton spelaeus* collected in Wet Cave, Shannon Co. Missouri.

Species of parasite	No. parasites per salamander	No. infected	Per cent infected
Protozoa:			
Haptophyra gigantea	6–10	2	1.7
Trematoda:			
Brachycoelium salamandrae	1–2	2	1.7
Nematoda:			
Capillaria inequalis	1–3	4	3.4
C. sp.	1	3	2.5
Falcaustra catesbeianae	1	1	0.8
Oswaldocruzia sp.	1–3	2	1.7

Aquatic invertebrates were not observed by Brandon in Wet Cave, but the few larval *T. spelaeus* whose gastrointestinal tracts were examined contained dipteran larvae and pieces of snail shell in addition to many pieces of unidentified invertebrate exoskeleton. That aquatic crustaceans were not observed by Brandon is not surprising on the basis of the paucity of parasites encountered.

Previous studies on salamander parasites have revealed that species of *Brachycoelium* are the most common flukes encountered and in the present study *B. salamandrae* was the only fluke detected. To my knowledge, only two life histories have been reported, namely, those of *B. obesum* and *B. mesorchium* by Cheng (1960) and Jordon (1962), respectively. Both species utilize terrestrial snails as intermediate hosts. Flukes utilizing aquatic intermediate hosts were not detected in the present study.

All salamanders examined were negative for tapeworms. Previous investigations on salamander parasites have demonstrated that cestodes are essentially correlated with an aquatic environment and copepods are known to serve as intermediate hosts for salamander cestodes (Thomas, 1927). Smith (1948) reported nine of 31 larval salamanders of *T. spelaeus* from a small cave near Waynesville in Pulaski Co, Missouri infected with proteocephalid cestode of the genus *Ophiotaenia*, probably *O. amphiumae*. Investigation of stomach contents proved an isopod, *Lyrecus happinae* to be the most dominant food of the larval salamanders. Smith concluded that since this isopod appeared to be not only the most abundant animal in the cave but also the only crustacean, other than *Cambarus*, it probably served as the intermediate host.

The absence of acanthocephalan infections in salamanders from Wet Cave is not surprising as few species of acanthocephalans have been reported from salamanders in North America. The occurrence of acanthocephalans in salamanders also appears to be essentially correlated with an aquatic environment and as Pearse (1932) suggests they are probably confined to strictly aquatic salamanders because of their dependence on particular arthropod intermediate hosts.

All of the nematodes found in the present study, to my knowledge, probably have direct life cycles and hence do not utilize invertebrate hosts.

The absence of tapeworms, acanthocephalans and certain flukes from salamanders in Wet Cave substantiates the report by Brandon on the absence of aquatic invertebrates and hence the dependence of these postmetamorphic cave-dwellers on terrestrial organisms as food sources.

While this study may demonstrate that correlations exist between intestinal parasitocoenosis of salamanders and food sources in their habitats it is not without criticism. This study would certainly be more informative had the results been compared to data obtained from a study on salamanders living in a food-rich cave. Unfortunately data of this type were not available and the recommendation that future studies extract as much data as possible from autopsies considered urgent. Furthermore, the parasites were not fixed according to standard parasitological procedures and this practice is not condoned. The placing of the entire gastrointestinal tract in formalin usually results in distortion of the parasites which in turn may render them unidentifiable. Adherence to acceptable procedures of fixing will be well worth the effort.

ACKNOWLEDGMENT

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TWO NEW SPECIES OF ERRANT POLYCHAETES FROM THE GULF OF CALIFORNIA, MEXICO

JERRY D. KUDENOV[1]

ABSTRACT: Two new species of errant polychaetes from the Gulf of California, Mexico, are described. A key to the species of *Malmgrenia* is presented.

The Aphroditid polychaetes are frequently collected by shrimp trawlers in the Gulf of California, Mexico. *Aphrodita mexicana* Kudenov, in press, was described from such material. A new species from the northern Sea of Cortez is described. During comparisons of these two species, a small polynoid was discovered in the lateral setae of *A. mexicana.* Subsequent examination revealed that it too is a new species of a genus unreported previously from the Gulf. These materials are deposited in the Allan Hancock Foundation, University of Southern California.

FAMILY APHRODITIDAE

Aphrodita sonorae, new species

Figure 1

Material examined: 31° 14′ N, 113° 55′ W, 36 m, silty sand, 9 November 1973, coll. Ramon Durazo (4, TYPE).

Description: The body is elliptical. The caudal region is attenuate. There are 45 segments. The average length of four specimens is 47 mm and the width is 28 mm. The type specimen is 50 mm × 28 mm. The dorsum is somewhat encrusted with debris; all notosetae are visible above the felt. The lateral setae are whitish yellow to coppery colored. The ventrum is moderately covered with very small tubercles.

The prostomium is globulate in shape (Fig. 1a). There are two pairs of eyes; each pair is located on a distinct peduncle. A median ridge terminates as an inflated lobe on the posterior margin of the prostomium. The palpi are four times as long as the prostomium. They are coarsely ciliated, particularly along palpal ridges. The median tentacle is reduced to a small tubercle. The facial tubercle is as long as the prostomium; it is lightly tuberculate.

There are 15 pairs of translucent elytra (Fig. 1b). They are petaloid anteriorly and elliptical posteriorly. A lateral notch is present where each elytron is attached to the body. Venation is absent. Fine tubercles are present on the posterior surface of each elytron. Elytral margins are entire.

There are 19 pairs of branchiae (Fig. 1c). They are present on cirriferous segments 6–36, and are best developed from segments 12–20 as four lobed processes.

The notosetae are pale copper in color. They are long, curved and slender; all terminate in straight points (Fig. 1d). The neurosetae are arranged in three tiers (Fig. 1e). The superior tier has 2 large, reddish brown hirsute setae (Fig. 1f); the intermediate tier has 5–6 lighter reddish brown ones (Fig. 1g); the inferior tier has 16–19 golden brown ones (Fig. 1h). All setae are essentially straight; the inferior neurosetae are distally constricted.

Remarks: *Aphrodita sonorae* resembles *A. mexicana* because the median tentacle is reduced to a

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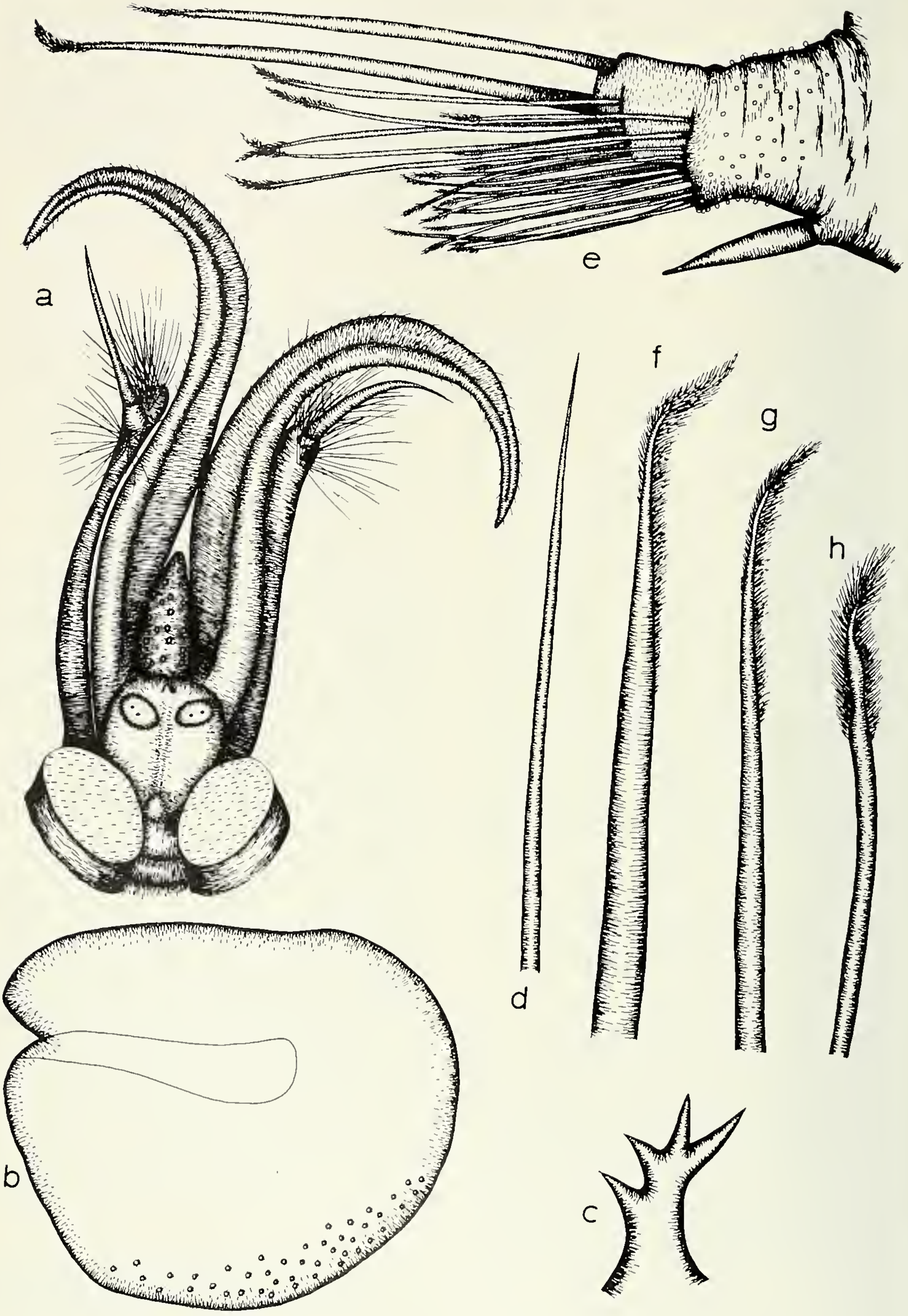
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tubercle. *Aphrodita sonorae* is separable from *A. mexicana* because the former species has ocular peduncles; the latter has sessile eyes. The palpi of *A. sonorae* are relatively short and coarsely ciliated; they are longer and finely ciliated in *A. mexicana*. The elytra of the latter species are circular to elliptical, white and smooth. Those of *A. sonorae* are petaloid to elliptical, translucent and tuberculate. The notosetae of *A. sonorae* penetrate the dorsal felt and terminate in straight, slender tips; those of *A. mexicana* do not penetrate the felt and are distally recurved. There are 2 superior, 5–6 intermediate and 16–19 inferior neurosetae in *A. sonorae*; *A. mexicana* has 2, 3–8 (usually 4–5) and 9–19 (usually 13–14). The neurosetae of both species are essentially straight and distally pilose. The inferior neurosetae of *A. sonorae* are distally constricted; such shapes are absent in *A. mexicana*.

FAMILY POLYNOIDAE

Malmgrenia hartmanae, new species

Figure 2

Material examined: 31° 10′ N, 113° 50′ W, 40 m, 28 February 1971, coll. R. C. Brusca (2); found in the lateral setae of *Aphrodita mexicana* by K. Zimmerman (1, TYPE).

Description: The body is elongate and flat; it is 6 mm long by 1.75 mm wide. There are 30 segments. The elytra imbricate with one another and nearly cover the body. Only the sensory appendages and setae are exposed. A pair of cylindrical anal cirri are present.

The prostomium is elliptical (Fig. 2a); it is divided into two equal lobes by a median groove. The anterior pair of eyes is larger than the posterior pair. The frontal antennae are nearly continuous with the anterior margin of the prostomium, but are inserted on its ventral surface. The facial tubercle is longer than wide; the median antenna is distally inflated. The frontal antennae are two-thirds the length of the median antenna. The palpi are twice as long as the prostomium. They are cirriform and round in cross section. Cirrophoral setae are present.

The parapodia are well defined (Fig. 2b). The notopodia are small lobes set on top of the larger, laterally compressed neuropodial lobes. The acicular lobe of the neuropodium is distally rounded. A flat superior lobe is present on the acicular lobe. The postsetal lobe is nearly obscured by the acicular lobe. The distal inferior margin of the neuropodium is folded. Each neuropodium is dorsoventrally excavate where the neurosetae emerge. The dorsal cirri are cirriform and smooth; they extend beyond the neurosetae. The dorsal cirrophores are longer than wide. The ventral cirri are subulate, and are inserted on the proximal half of the neuropodium.

There are 15 pairs of elytra. Anterior and posterior elytra are elliptical; middle elytra are "D" shaped (Fig. 2c). The inner lateral margin of each middle elytron is straight. An anterior patch of submarginal tubercles is present on each elytron. All elytra are entire, reticulated (Fig. 2d), and are light brown in color.

Notopodial fascicles resemble whorls of thin, yellow colored notosetae (Fig. 2e). A single row of spinules is present on each notoseta. The inferior notosetae are longer than superior ones. The neurosetal fascicles resemble fans. The neurosetae are longer and wider than the notosetae. A series of 4–6 transversely serrated plates are present on each neuroseta (Fig. 2f,g). All neurosetae are bidentate: the accessory tooth is conical and stout; the distal hook is slightly recurved.

Remarks: *Malmgrenia hartmanae* resembles *M. marquesensis* (Monro, 1928) and possibly also *M. whiteavesii* McIntosh, 1874, because the notosetae have single rows of denticles. McIntosh's description of *M. whiteavesii* is brief, and it is not clear whether the notosetae have single rows of spinules. *Malmgrenia hartmanae* differs from *M. marquesensis* because its neurosetae are larger than the notosetae. The notosetae of the latter species are much larger than the neurosetae. The neurosetae of *M. whiteavesii* are of two kinds. *Malmgrenia hartmanae* differs from *M. whiteavesii* because it has one kind of neuroseta. *Malmgrenia hartmanae* has diagnostic elytra that are completely reticulated and "D" shaped. *Malmgrenia nigralba* Berkeley, 1923, has white reticulae restricted to posterior elytral surfaces,

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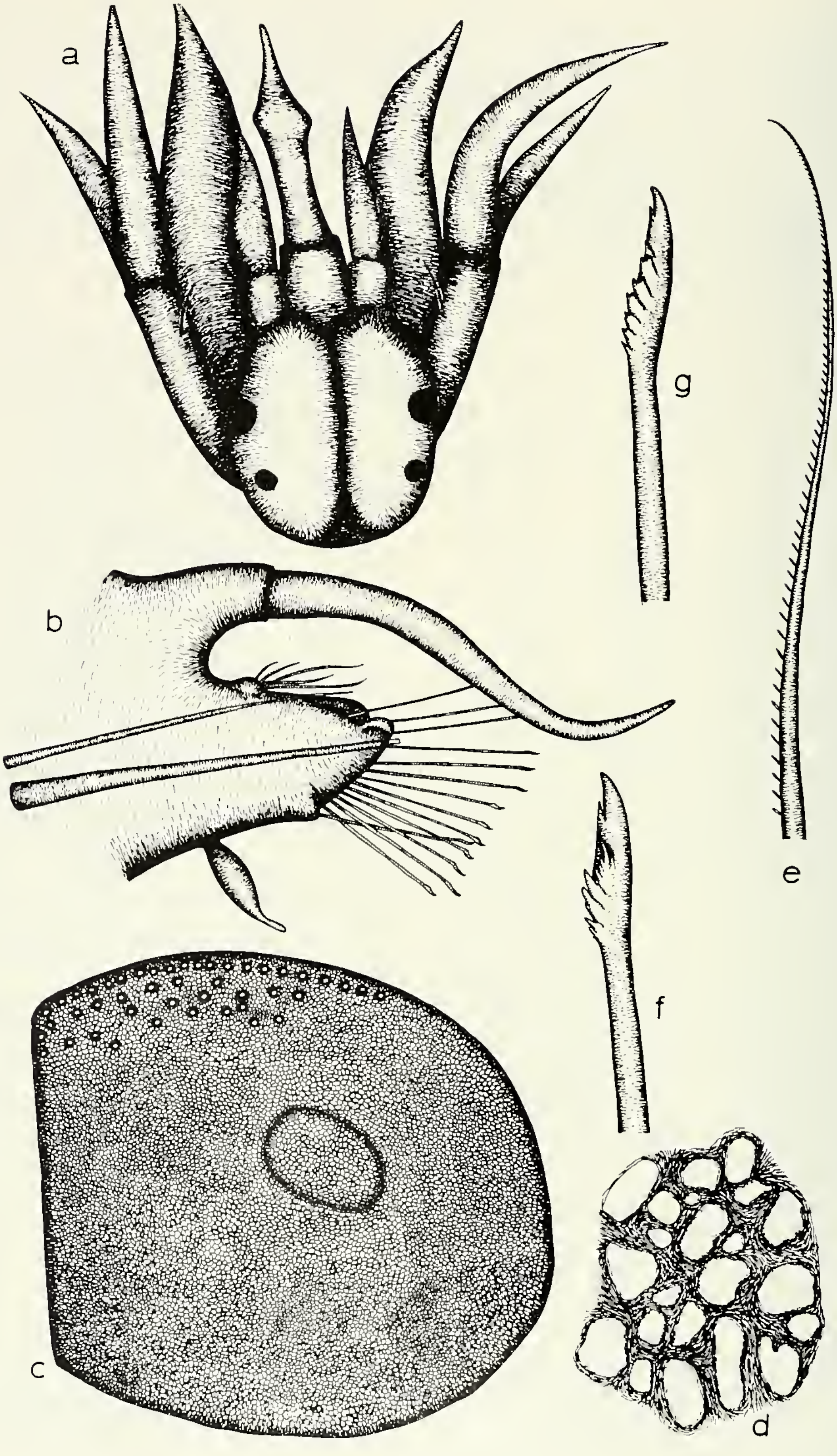
Figure 1. *Aphrodita sonorae*, new species: a, anterior segments, dorsal view, × 22; b, left elytron from segment 11, dorsal view, × 6.6; c, right branchia from segment 12, anterior view, × 22; d, notoseta, dorsal view, × 79; e, left parapodium from segment 16, posterior view, × 22; f, superior neuroseta, lateral view, × 79; g, intermediate neuroseta, lateral view, × 79; h, inferior neuroseta, lateral view, × 79.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but its elytra are circular to reniform. This species is named in honor of the late Olga Hartman, Allan Hancock Foundation, University of Southern California.

A total of 11 species are now present in *Malmgrenia.* The affinities of three species, *M. alba* (Malmgren, 1865), *M. ampulliferoides* Uschakov and Wu, 1959, and *M. castanea* McIntosh, 1876, are not clear. These species need to be re-examined. According to Hartman (1959), the generic status of *M. castanea* is confused. Specimens of these and other *Malmgrenia* species could not be obtained for detailed examinations. A key to this genus is presented below. Since it is based upon literature descriptions, some of which are incomplete, the key must be considered preliminary and tentative pending first hand examination of the type materials. *Malmgrenia alba, M. ampulliferoides,* and *M. castanea* have not been included in this key.

KEY TO THE SPECIES OF *MALMGRENIA*

1a. Notosetae are distally bidentate .... *M. curacaöensis* Augener, 1927
b. Notosetae are distally entire 2
2a. Notosetae with transverse plates along the convex margin 3
Notosetae with transverse serrations along the convex margin 4
b. Notosetae with a single row of denticles along the convex margin 5
3a. Bidentate neurosetae with 12–20 transverse plates distributed all along the cutting surface .... *M. micropoides* Augener, 1918
b. Bidentate neurosetae with 7–10 transverse plates restricted to the posterior half of the cutting surface .... *M. nesiotes* (Chamberlin, 1919)
4a. Neurosetae with 25 transverse rows of spinules; accessory tooth minute and sometimes absent; elytra not reticulated .... *M. purpura* Day, 1960
b. Neurosetae with less than 25 transverse rows of spinules; accessory tooth minute and generally absent; elytra reticulated .... *M. nigralba* Berkeley, 1923
5a. Neurosetae are of two types .... *M. whiteavesii* McIntosh, 1874
b. Neurosetae are of one type 6
6a. Neurosetae thicker than notosetae; elytra reticulated .... *M. hartmanae*, new species
b. Neurosetae thinner than notosetae; elytra not reticulated .... *M. marquesensis* (Monro, 1928)

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Figure 2. Malmgrenia hartmanae, new species: a, anterior segments, dorsal view, × 72; b, left parapodium from segment 16, anterior view, ×72; c, right elytron from segment 15, dorsal view, × 72; d, detail of right elytron from segment 15, dorsal view, × 325; e, notoseta from segment 16, lateral view, × 325; f–g, neurosetae from segment 16, lateral view, × 325.

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STUDY ON THE DEVELOPMENT OF THE PRIOR RESIDENCE EFFECT IN RAINBOW TROUT (*SALMO GAIRDNERI*)

Thomas R. Payne[1]

Abstract: Hatchery-raised rainbow trout (*Salmo gairdneri*, Richardson) were placed singly in small aquarium tanks for varying periods of time before the addition of a second fish. The effect of prior residence upon dominance between two fish became evident after 12 hours or more had elapsed before the addition of the second fish. The resident was more likely than the intruder to attack first, attacked in a shorter time, and had a higher potential for final dominance. The results may be applicable to the estimation of the carrying capacity of natural waterways and artificial propagation enclosures.

Successful methods for rearing fish in artificial ponds as a commercial enterprise have received a great deal of attention recently. The main cost involved in fish propagation is almost always food, and for this reason, alternative sources of nutrition are constantly being sought. In a continuing study on Humboldt Bay in northern California, an attempt is being made to raise fingerling salmonids to commercial size by utilizing tertiary treated sewage water to stimulate primary productivity in rearing ponds.

Initial difficulties with the project have led to analysis of factors involved in the dynamics of self-supporting ecosystems, and as a result aspects of territorial and dominance behavior in fish were examined. The obvious success of existing private and state hatchery programs employing high-density fish culture indicates that any adverse effects of fish behavior can be overcome by a regimen of heavy supplemental feeding and rapid water exchange.

Aggressive behavior could still possibly play a significant role in determining the carrying capacity of fish ponds which depend on natural or fertilized food sources. With the aim of better understanding the effects of behavior, this study was initiated to analyze the "prior residence effect," which states that a fish familiar with an area has a competitive advantage over a newcomer. If prior residence develops strongly and quickly, then planted fish should tend to remain in small, familiar areas where they are dominant, which is, in effect, territoriality. If territoriality could then be shown to affect carrying capacity, it should be possible to use the strength of the prior residence effect as an indicator of the potential carrying capacity of an artificial pond.

Intraspecific competition and aggression among animal populations serve to establish and maintain the stability and integrity of social structures (Collias, 1944). Chapman (1966) reviewed the most apparent feature of social structure, territoriality, and concluded that it regulates salmonid population density in terms of food and space requirements. Fish which defend territory, apart from the breeding season, have a definite advantage in obtaining food and shelter, grow faster, and survive longer.

An important contributing factor to the outcome of a territorial contest seems to be prior residence. Noble (1939) stated that "mere familiarity with an area gives the resident a decided advantage over a newcomer" in the cichlid jewelfish, *Hemichromis bimaculatus*. Braddock

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(1949) studied the effect of prior residence upon dominance in the poeciliid topminnow, *Platypoecilus maculatus*, and found that residents were more likely to be initially dominant, even over larger intruders. Several workers, notably Gerking (1953), Chapman (1962), Mason and Chapman (1965), and Jenkins (1968), have since noted the effect in observations on salmonids. Miller (1958) concluded that the stress of competition with resident fish was a cause of high mortality among planted hatchery trout.

These observations support the existence of the prior residence effect, but only one worker (Newman, 1959) has reported a quantitative description. He isolated sockeye salmon smolts, *Oncorhynchus nerka*, for varying lengths of time before adding intruders and found that aggressiveness increased with time of residence. Attacks on intruders were more frequent and more violent the longer the smolts were in residence. Braddock (1949) noted that the effect of prior residence was strongest after at least 36 hours of residence in aquaria. This paper is an attempt to further describe the prior residence effect by testing how the duration of residence can influence dominance in hatchery-raised rainbow trout, *Salmo gairdneri*.

METHODS

Experiments were conducted in five 20 gallon glass-walled aquarium tanks (35 cm × 35 cm × 75 cm) at the Humboldt State College Fish Hatchery. The area provided a semi-isolated location and could be darkened for observations. Each tank was screened by black curtains and illuminated with 15-watt lamps one foot above water level. A single glass-wool-and-charcoal filter recirculated water in each tank for aeration and to control turbidity. The slate bottoms of the tanks were left bare and kept free of debris to reduce distractions from foreign objects and to minimize the tendency of trout to associate with the physical features of their environment (Gerking, 1959). Each tank was covered by a screen of ¼″ mesh hardware cloth to prevent fish from jumping out.

The tanks were filled with water from an underground source that normally empties into the hatchery water system. Chemical analysis showed the water to be high in dissolved oxygen, low in hardness, and free of phosphates, nitrates, and dissolved solids. This underground source was chosen for the quality of the water and because behavior experiments can be influenced by water in which fish had lived previously (Shaw, 1932). The water was changed after each use of the tanks to eliminate the possible transfer of chemical stimuli such as urea or pheromones between experiments (Bardach and Todd, 1970).

Tests were run using immature rainbow trout taken from normal hatchery stock. The fish came from two-year-old brood stock (4 female, 12 male) and were raised at high density in standard incubators and hatchery troughs under constant lighting, using Oregon Moist Pellets for diet. They were transferred to an exterior circular raceway at 10 months of age, and were a year old at the start of the experiment (20 fish/pound, 135 mm average total length).

The experimental design was selected to generate a curve of the prior residence effect as it developed with time. One resident fish was placed in each tank for a period of time before an intruder was added and their interactions recorded. Ten pairs of fish were tested in this way at each of seven time periods (0, 1, 6, 12, 18, 24, and 36 hours of residence). Time of residence was plotted against the number of pairs which established a dominant-subordinate relationship within the first half-hour of observation time. As the time between the introductions of residents and intruders increased, it was expected that the effect of prior residence would become stronger and that resident fish would dominate intruders in a significantly greater number of cases.

Determination of dominance was a subjective appraisal of agonistic behavior, including charging, nipping, chasing, frontal display, lateral display, and fleeing. Dominant and submissive fish behave in characteristically stereotyped patterns: a dominant fish will threaten, chase, and nip a subordinant fish, which will submit and flatten its fins against its body (Keenleyside and Yamamoto, 1962). A "stable dominance relationship" was judged to exist when one fish would submit to the nipping of the other without threatening or nipping in return (Braddock, 1949). Size and weight, fighting ability, health and endurance, aggressiveness, and experience all influence the outcome of a dominance contest (Baerends and Baerends-van Roon, 1950).

To reduce the effect of fish size on dominance and to emphasize the effect of experience, only healthy fish were chosen and were graded to a five percent maximum size difference. Residents and intruders were distinguished for observational purposes by small marks of dye. A hypodermic syringe filled with National Fast Blue dye was used to scrape a spot of skin near the pelvic fins of fish anaesthetized with MS-222 at 100 ppm concentration. The technique produced a bright blue spot which lasted clearly for over three months and had no discernable effect on either the behavior or the health of the fish.

Marked fish were held in groups of ten in a darkened holding trough prior to each experiment for 24 hours. A single resident was introduced into each experimental tank at half-hour intervals. This procedure allowed a half-hour observation time for each tank and kept the length of residence time constant. After each experiment all fish were measured and returned to a holding trough separate from the inexperienced fish so that no fish was used more than once. Experienced fish were later returned to the hatchery stock.

Since the duration of each experiment was short, no food was administered, except during the 36 hour interval when all fish were fed.

A preliminary experiment was performed to observe basic behavior patterns and to test the persistence of the prior residence effect. Fish were added one at a time to each tank at continuous 24 hour intervals. From previous experience, I believed that hatchery fish would school and cease agonistic activity when they reached a certain density in relation to water volume. The present experiment was continued for two weeks until there were 14 fish in each tank. All fish were fed every day.

Water temperatures during all experimentation were maintained at approximately 14° C in the holding troughs and at 15° C in the aquarium tanks.

RESULTS

In the preliminary experimentation, resident fish in four of the five tanks dominated all introduced fish. The intruders were constantly attacked and physically herded into a tight group in one corner by the resident, which would remain in the center of the tank when not so occupied. If an intruder ventured to leave the group he was immediately attacked by the resident and chased back into the group. In one of these tanks the resident was deposed and replaced by the seventh intruder after a protracted battle. The fifth tank had no dominant fish; the resident and all intruders quietly schooled. The residents and the dominant intruder in the four tanks showed no signs of fatigue or reduced aggressiveness after two weeks and 13 intruders, and even appeared to become more efficient at dominating the groups of submissive fish. Increased efficiency of dominance most probably is a result of learning, just as mice can be taught to be dominant or submissive with a series of victories or defeats (Scott and Fredericson, 1951).

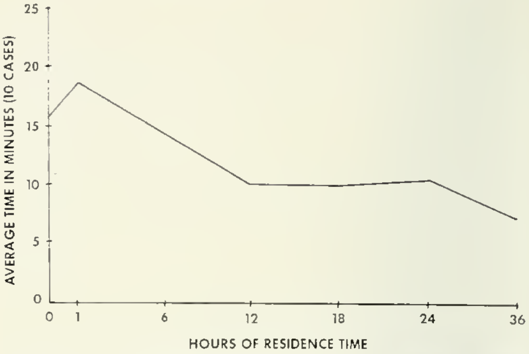

Figure 1. Relationship between average time elasped between introduction of intruder and initiation of first attack and length of residence time prior to introduction of intruder.

The preliminary experiment was terminated when it was apparent that aggression was not abating and because the persistence of the prior residence effect was confirmed.

Agonistic behavior in the preliminary and major experiments was very similar to the descriptions of salmonid behavior reported by Fabricius (1953), Newman (1956), Kalleberg (1958), and Keenleyside and Yamamoto (1962). The most common threat posture between two unequally aggressive fish was the "frontal threat display" (Fabricius, 1953), where one fish would slowly approach the other, with its fins stiffly erect and its body bent at a downward angle. The approach, usually to within 6 or 7 cm, was repeated often, and almost always was followed within a few moments by a rushing attack, regardless of the behavior of the threatened fish.

An attack consisted of a very fast darting motion, originating about 12 cm from the victim and culminating in a bite along the flanks or posterior fins, which usually loosened several scales in the region bitten. An attacked fish often would make escape movements by trying to swim through the confines of the glass-walled tank.

Equally aggressive fish would engage in "lateral threat display" (Fabricius, 1953) and "reciprocal circling" (Newman, 1956), where two fish would approach each other laterally, most often head-to-tail, with fins erect and bodies slightly bent, and

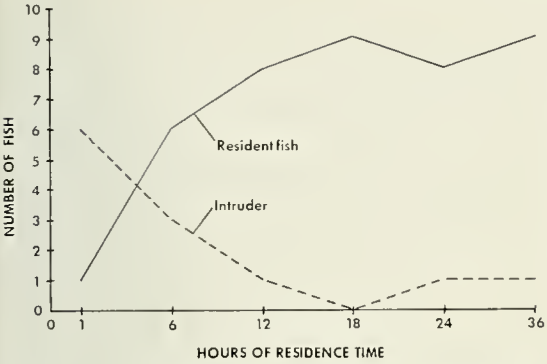

Figure 2. Comparison of numbers of residents and intruders initiating first attack as a function of residence time prior to introduction of intruder.

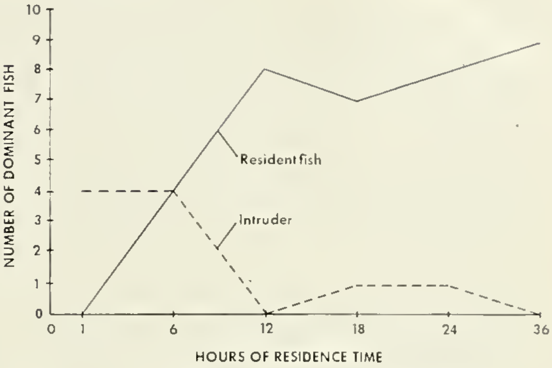

Figure 3. Comparison of "stable dominance relationships" established between residents and intruders as a function of residence time prior to introduction of intruder.

attempt to turn upon one another. This behavior would then result in either rapid whirling movements until one fish managed to bite the other, or, more commonly, in direct attack. In the latter case, one fish would back away while slowly turning and then make an attack. Circling would continue with each fish alternating attack until one would flee with the other in pursuit. Once a fish made escape movements, either as a result of frontal display and attack, or from reciprocal circling, its subordinate status was firmly established. In no case did a fish which had fled once from attack ever turn on its aggressor and return an attack.

Since reciprocal circling or threat behavior did not in themselves create stable dominance relationships, the first incident of physical contact was chosen as the initial indication of a dominance encounter (Fig. 1). In the shorter periods of residence the first attack was delayed, with time spent in threat behavior or mutual avoidance. As the time in residence increased, the time to the initiation of the first attack became shorter. In 35 out of 40 cases in which the resident had been isolated 12 or more hours, the attack was initiated within 15 minutes, in 29 out of 40 cases within 10 minutes, and in 15 out of 40 cases within 5 minutes. In 18 out of 30 cases in which residents were isolated less than 12 hours, attack was initiated within 15 minutes, in 10 out of 30 cases within 10 minutes, and in only one out of 30 cases in less than five minutes (Table 1).

Similar to what Braddock (1949) reported for *P. maculatus*, the resident fish in the present experiments were more likely than the intruders to initiate attack behavior (Fig. 2). In only three out of 37 cases in which the resident was isolated for more than 12 hours did the intruder make the first attack, whereas the intruder was the initial aggressor in 9 out of 16 cases in which the resident was isolated for less than 12 hours (Table 2).

The pattern of first stable dominance relationships (Fig. 3) followed much the same pattern as the first attacks (Fig. 2). The effect of prior residence seemed fully developed after 12 hours of residence, since 32 out of 34 residents became dominant after that time. Only four of 12 residents isolated for less than 12 hours exhibited dominance.

The total number of stable dominance relationships formed within a half-hour at each time interval remained about the same, even though the resident fish became dominant more often than the intruders at the longer time intervals (Fig. 4). Except for a variation at the one-hour interval, the fish tended to form stable relationships more often and in shorter times as the time in residence increased.

Several experiments were discarded due to aberrant behavior of non-normal test fish. In these tests one or more fish were sick and died or behaved erratically, losing equilibrium and swimming abnormally. These experiments were repeated with new fish to assure that there was a total of ten pairs for each time period.

DISCUSSION

When juvenile rainbow trout are placed in residence in small aquarium tanks and intruders are added at varying time intervals, prior residence becomes a significant factor in the establishment

TABLE 1. Relative numbers of fish initiating the first attack within specified time limits after introduction of intruder.

Hours of Residence	Time elapsed between introduction of intruder and initiation of first attack (minutes)							
	< 5		< 10		< 15		< 30	
	No.	%	No.	%	No.	%	No.	%
< 12 (30 encounters)	1	3.3	10	33.3	18	60.0	23	76.7
⩾ 12 (40 encounters)	15	37.5	29	72.5	35	87.5	37	92.5

of dominance relationships. After 12 hours of residence, the resident fish in my experiments was found more likely than the intruder to initiate an attack, attacked in a shorter time, and had a higher potential for final dominance.

These results suggest that the effect of prior residence is an innate phenomenon and that the outcome of a dominance struggle is greatly influenced by its expression. Whether it becomes a factor in the carrying capacity of an artificial pond is another question. The assumption is that prior residence is a direct indication of territorial behavior, and that territorial behavior will limit carrying capacity. Braddock (1949) stated that, while prior residence and territoriality have features in common, they also have some differences. Both are related to the defence of an area; however, prior residence is a cause of dominance and territoriality is a result of dominance. The end result is the same: a fish will tend to remain in the area where it is dominant and the effect of prior residence will perpetuate its dominance.

The difference may be one of degree, a dominant fish will tolerate the presence of subordinate fish if they stay in a submissive group (Baerends and Baerends-van Roon, 1950), whereas a territorial fish, as the term is generally defined (Greenberg, 1947), will maintain an area exclusively for itself. The present experiment cannot distinguish between the formation of a dominance hierarchy and the formation of a true territory since it did not provide an avenue of escape for submissive fish. In future studies the experimental tanks would have to be either larger than a single territory or would have to be partitioned for visual isolation. Even so, the experiment definitely indicates a sizable potential for aggression in hatchery trout that can be released when the opportunity arises.

TABLE 2. Relative numbers of residents and intruders which initiated the first attack within 30 minutes after introduction of intruder.

Hours of Residence	Residents Initiating First Attack		Intruders Initiating First Attack	
	No.	%	No.	%
< 12 (16 encounters)	7	43.8	9	56.2
⩾ 12 (37 encounters)	34	91.9	3	8.1

Another interesting question is whether this aggression will limit the number of fish that will survive and grow in an artificial pond. Kalleberg (1958) found that increasing numbers of fish will compress territory size to a minimal limit, at which time excess fish will be forced into schools. Keenleyside and Yamamoto (1962) stated that aggressive behavior is suppressed under crowded conditions, provided that food is available. When fish must depend on a natural food supply it is uncertain how their behavior is affected by crowding. It may be that trout will adjust territory size to the available food supply (Slaney, pers.

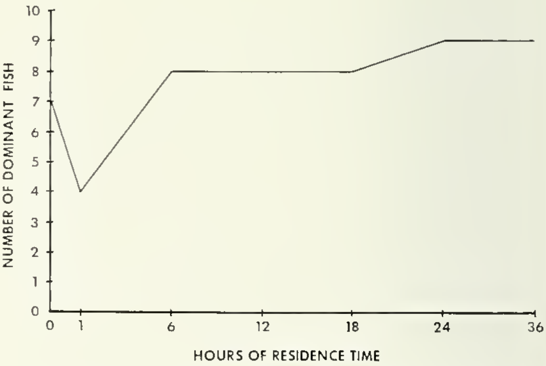

Figure 4. Total number of "stable dominance relationships" established between residents and intruders as a function of residence time prior to introduction of intruder.

comm.), or that hunger will increase aggression and mortality (Symons, 1968; Fenderson, Everhart, and Muth, 1968). In a recent experiment, Jenkins (1971) planted different size-groups of hatchery rainbows in a near-natural stream and concluded that aggression and density may not even be related. Aggression, then, is apparently imprecisely related to population levels, and may not be the mechanism that initially will set the optimum population size.

The probable result of stocking hatchery fish in a fertilized pond should be the creation of individual territories by some and the formation of schools by the remainder. Growth should be a function of the general availability of food and not by the agonistic activities of territorial fish.

The present experiment can be used as a basis for comparison to test the effects on behavior of the water chemistry, bottom type, and turbidity found in a potential pond. For the sewage fish pond on Humboldt Bay, for example, the species and size of fish to be planted should be tested using the pond water and the oyster shell substrate. Turbid water and oyster shells both would increase visual isolation and reduce the incidence of intraspecific aggression. Water chemistry possibly could interfere with the known ability of some fish to communicate chemically (Bardach and Todd, 1970). If the results of the tests are comparable (that is, if prior residence still develops strongly within 12 hours), then it still might be possible for territorial behavior to affect the population as a whole. Final confirmation would have to be direct observation of the fish while they are in the pond, if that is possible.

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NATURAL HYBRIDIZATION BETWEEN *HULSEA HETEROCHROMA* AND *HULSEA VESTITA* ssp. *CALLICARPHA*

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Abstract: Three hybridizing populations involving *Hulsea heterochroma* A. Gray and *H. vestita* Gray ssp. *callicarpha* (Hall) Wilken were discovered in the San Jacinto Mountains, Riverside Co, California. Population structure was investigated by means of morphological analyses, flavonoid chemistry, meiotic chromosome behavior and pollen fertility. Synthetic F_1 and BC_1 hybrids were employed in assessing the degree of hybridization in the three populations. F_1 hybrids were found to be heterozygous for a single reciprocal translocation and their pollen fertility was relatively high. Synthetic backcross hybrids displayed normal meiosis and high pollen fertility. On the basis of correlative studies, the hybridizing populations were found to comprise plants of both parental taxa, F_1 hybrids and backcross hybrids with *H. vestita* ssp. *callicarpha* as the recurrent parent. The inability to readily distinguish most putative backcross hybrids from plants of the recurrent parent in natural populations indicates that introgression involving the two taxa should prove difficult to substantiate by traditional techniques.

The genus *Hulsea* (Asteraceae) comprises eleven self-incompatible taxa with an allopatric distribution throughout much of montane western North America (Wilken, 1971). *Hulsea* populations occur on ecologically disturbed sites, including talus slopes, forest clearings, road cuts and recent burns. All taxa possess a diploid complement of 38 chromosomes. Evidence from an extensive crossing program (Wilken, in press) indicates that *Hulsea* species are cross-compatible and that their F_1 hybrids are relatively fertile. Natural hybridization, however, is a rare event because of the isolation imposed by ecological and geographical barriers. Nevertheless, three instances of intraspecific hybridization have been discovered and investigated. These cases of hybridization involve *H. heterochroma* A. Gray and *H. vestita* A. Gray ssp. *callicarpha* (Hall) Wilken and occur in the San Jacinto Mountains of Riverside County, Cali-

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fornia. It is the purpose of this paper to describe the structure of the hybridizing populations with respect to meiotic chromosome behavior, fertility and variation of specific morphological and biochemical characters.

Hulsea heterochroma is characterized as a leafy-stemmed, robust biennial ranging from 3 to 10 dm in height and possessing glandular, dentate, oblanceolate leaves. This species is further distinguished by narrow, red, ray corolla ligules and the presence of short, uniseriate trichomes on the ray and disc corollas. *Hulsea heterochroma* typically occurs in chaparral clearings and burns at elevations from 300 to 1500 meters. *Hulsea vestita* ssp. *callicarpha* is readily distinguished from *H. heterochroma* by a scapose, perennial habit and spatulate, entire, lanate leaves. Furthermore, the ray corolla ligules are yellow or merely tinged with red pigmentation and uniseriate trichomes are absent from the ray and disc corollas. *Hulsea vestita* spp. *callicarpha* occurs in forest clearings and talus slopes at elevations from 1000 to nearly 2500 meters in the San Jacinto Mountains.

METHODS

A sample was collected of each flowering plant from the three populations wherein hybridization was suspected. The localities of these populations were: (1) Chalk Hill, along May Valley Road, 3.3 miles north of Mountain Center; (2) near Stone Creek, along County Road R1, 9.2 miles northwest of Idyllwild; and (3) near Lake Fulmor, along County Road R1, 12.9 miles northwest of Idyllwild. Populations 1 and 2 were discovered and sampled in June, 1972; population 3 was first discovered and sampled in June, 1968.

The following morphological character states were measured and recorded for each plant: leaf length, leaf indumentum, phyllary length, phyllary width, ray flower number, ray flower pigmentation, morphology of corolla trichomes, and achene length. These data were used in the construction of pictorialized scatter diagrams following the method of Anderson (1949). Scatter diagrams of the three populations are depicted in figure 1.

An extensive series of crossing attempts have produced numerous F_1 hybrids and several backcross progenies involving both parental species. Crossing attempts were accomplished by applying pollen to the stigmas of the seed parent with the aid of a sterilized camel's hair brush. All plants employed in the crossing program were maintained under conditions free from potential pollinators. Since *Hulsea* species are self-incompatible, the chance of contamination by illegitimate pollen was considered minimal. A total of 26 F_1 hybrids, 12 first generation backcross (BC_1) hybrids with *H. heterochroma* as the recurrent parent, and 36 BC_1 hybrids with *Hulsea vestita* ssp. *callicarpha* as the recurrent parent were available for study.

Dried capitula were removed from individual plant samples and were extracted in 80 percent aqueous methanol for a minimum of 48 hours. The extract was partitioned against petroleum ether to remove lipophilic compounds and the aqueous phase was applied to Whatman No. 3 chromatography paper. Development of the chromatograms was accomplished in two dimensions by employing the descending method (Harborne, 1967). The first dimension solvent system was composed of a mixture of t-butanol: acetic acid: water (4:1:1 v/v) followed by a second dimension system employing acetic acid: water (3:17 v/v). Dried chromatograms were examined in the presence and absence of ammonia vapor under ultraviolet light. Investigations employing the techniques of of co-chromatography in different solvent systems and spectral analyses (Harborne, 1967; Mabry, Markham and Thomas, 1972) indicated that the majority of compounds detected in *Hulsea* species are glycosides of the flavonoids quercetin, apigenin, cyanidin and diometin. Complete characterization was difficult because insufficient quantities of each compound were unavailable. The patterns of flavonoid compounds within *H. heterochroma*, *H. vestita* ssp. *callicarpha*, putative natural hybrids and synthetic F_1 and BC_1 hybrids were determined and are diagrammatically depicted in figure 2.

Meiotic chromosome behavior was examined in selected parental strains, putative natural hybrids and all synthetic hybrids. Immature capitula were fixed in a solution of ethanol: chloroform: acetic acid (4:3:1 v/v) for a minimum of 24 hours followed by storage in 60% aqueous ethanol at −10°. Anthers were dissected from flower buds and the contents squeezed into a drop of acetocarmine. The cytological preparations were made permanent in Hoyer's medium (Beeks, 1955). All observations were made with freshly prepared slides. Pollen stainability with cotton blue in lactophenol was taken as a measure of pollen fertility. A minimum of 300 grains were examined in each plant obtained from the three population samples and in all synthetic hybrids. Grains which appeared deeply stained were considered viable.

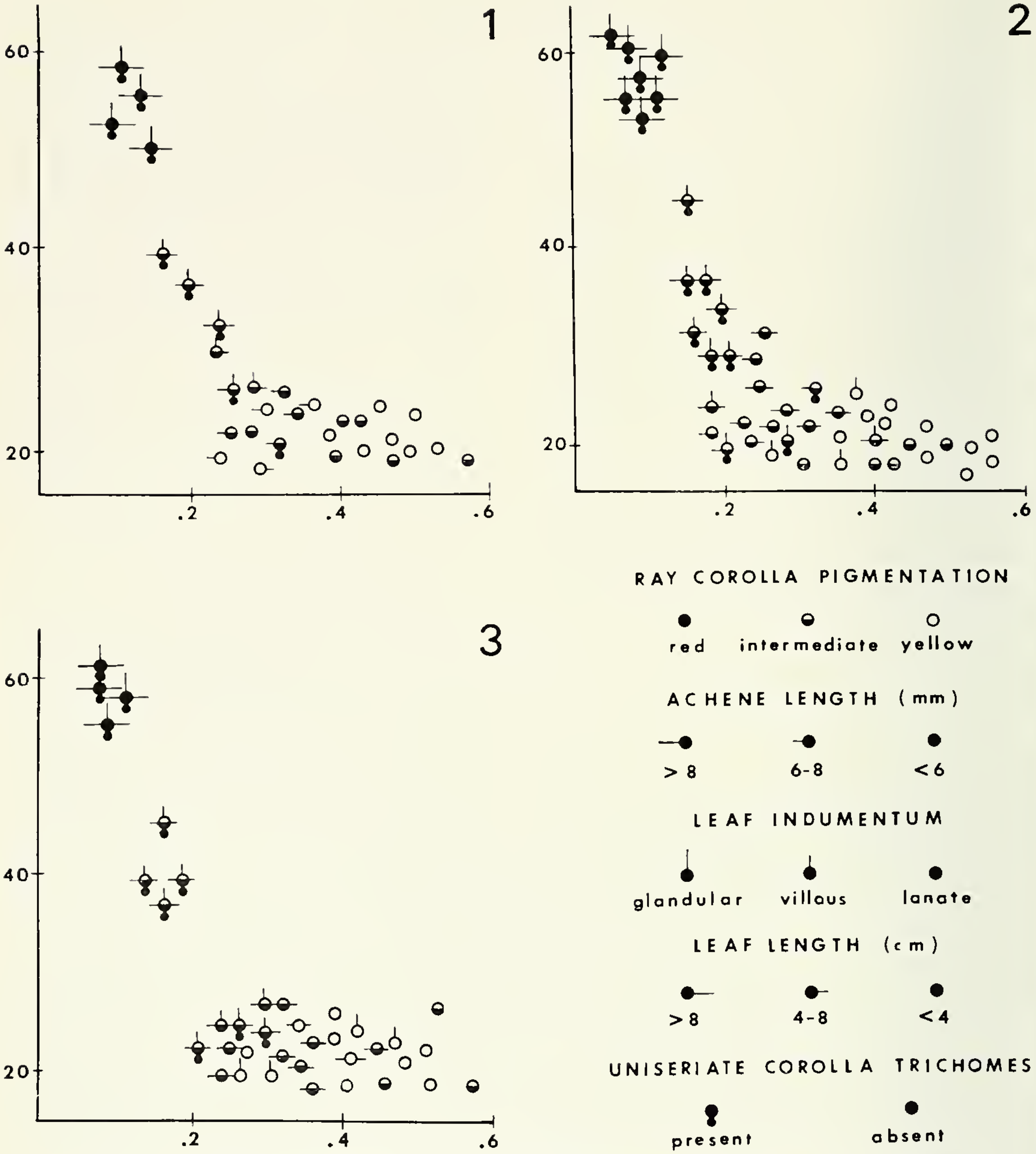

Figure 1. Pictorialized scatter diagrams of hybridizing populations. Vertical axis represents mean ray flower number; horizontal axis represents phyllary length/width ratio. See text for localities of populations 1, 2, and 3.

whereas unstained or weakly stained grains were considered infertile.

RESULTS

Synthetic Hybridization.—Crossing attempts involving strains of *H. heterochroma* and *H. vestita* ssp. *callicarpha* revealed the presence of weak cross-compatibility barriers. A total of 48 reciprocal crosses were accomplished. The average seed-set (expressed as No. of filled achenes/No. of flowers pollinated) from these crosses was 39 percent as compared to 58 percent from over 40 interpopulational crosses within each of the two taxa. Germination of F_1 seed (43 percent of all achenes) proved as high as that obtained from

Figure 2. Diagrammatic representation of the chromatographic patterns of *H. v.* ssp. *callicarpha* and *H. heterochroma.* The first dimension solvent (BAW) consisted of butanol: acetic acid: water; the second dimension solvent (WAC) consisted of acetic acid: water. Compounds common to both species are blackened, those of *H. heterochroma* are outlined. Compound 1 was determined to be diosmetin (4′ O-methyl luteolin); compounds 2 and 4 were cyanidin glycosides; compounds 3, 5, 6, 7, 8, 10, and 11 were quercetin glycosides and compound 9 was apigenin 7-glucoside.

seeds of the parental strains (49 percent). The differences between seed germination of parental strains and that of synthetic F_1 hybrids were insignificant at $p = 0.05$. A total of 26 synthetic F_1 hybrids were grown to maturity. These hybrids were intermediate to the parental strains with respect to all morphological characters examined (Table 1). Significantly, the flavonoid patterns in most F_1 hybrids were found to be complementary to those expressed by the parental strains. Of the three compounds inherited from *H. heterochroma*, compound 9 was absent from only 3 of the 26 hybrids and compounds 10 and 11 occurred in all F_1 hybrids although represented by a noticeably reduced spot size. All synthetic F_1 hybrids displayed evidence of heterozygosity for a single translocation between two nonhomologous chromosomes. In 59 percent of all pollen mother cells examined at meiotic metaphase there occurred 17 bivalents and a chain or ring of four chromosomes. Normal meiosis characterized the remaining cells. Average pollen stainability in all F_1 hybrids was 71 percent within a range from 38 to 85 percent. The differences between pollen stainability of synthetic F_1 hybrids and the parental strains were significant at $p = 0.05$.

Backcrosses to strains of both parental taxa were attempted by employing synthetic F_1 hybrids as pollen donors and egg parents. The average seed set from 32 reciprocal crosses involving *H. vestita* ssp. *callicarpha* was 43 percent. Average seed set from 17 reciprocal crosses involving *H. heterochroma* was 39 percent. The progeny of the combination F_1 × *callicarpha* comprised 36 plants. The progeny as a whole displayed a relatively narrow range of morphological variation (Table 1) and differed statistically (significant at $p = 0.05$) from both parental taxa and F_1 hybrids with respect to leaf length, achene length, ray flower number and phyllary length/width ratio. Twenty-one of the F_1 × *callicarpha* progeny possessed uniseriate corolla trichomes. Fifteen of the progeny possessed reddish ray corollas with the remaining 21 plants displaying yellow ray corollas at anthesis. Chromatography of flavonoid extracts revealed the inheritance of both cyanidin glycosides as a block in the red flowered members of the progeny. All 36 BC_1 hybrids lacked compounds 9, 10, and 11. Cytological examination revealed normal meiosis in all but one plant, which exhibited 19 bivalents and one univalent in 46 percent of cells examined at meiotic metaphase. Pollen stainability averaged 98 percent within a range from 85 to 100 percent.

BC_1 hybrids derived from the combination F_1 × *heterochroma* differed statistically (significant at $p = 0.05$) from both parental taxa and F_1 hybrids with respect to leaf length, achene length, ray corolla number and phyllary length/width ratio. The flavonoid patterns of the 12 BC_1 hybrids were identical to that exhibited by *H. heterochroma.* Meiosis appeared normal in all plants and the average pollen stainability was 97 percent within a range from 93 to 100 percent.

Natural Hybridization.—Examination of population structure as determined by morphological analysis revealed the presence of putative hybrids in each of the three populations. The Chalk Hill population (1, Figure 1) included a number of plants representing either F_1 or BC_1 hybrids with *H. vestita* ssp. *callicarpha* as the recurrent parent. However, only two of the putative hybrids possessed a flavonoid profile complementary of the parental taxa and each displayed evidence of a

TABLE 1. Morphological Character Expressions of Cultivated Parental Strains and Synthetic F_1 and BC_1 Hybrids. Ranges of quantitative expressions are given, followed by mean values in parentheses.

	H. heterochroma	F_1 × *heterochroma*	F_1	F_1 × *callicarpha*	*H. callicarpha*
Leaf length, cm	9.3–16.5 (12.7)	8.4–13.3 (10.9)	6.4–10.3 (8.0)	4.8–7.6 (5.9)	4.0–6.3 (5.1)
Leaf indumentum	glandular	lightly villous	villous	lanate	lanate
Phyllary length/ width ratio	.08–.12 (.11)	.10–.15 (.13)	.14–.22 (.18)	.26–.38 (.30)	.42–.60 (.59)
Number of ray flowers/capitulum	48–65 (53)	41–53 (49)	34–45 (38)	21–35 (29)	17–23 (21)
Ray flower pigmentation	red	red	red to orange	red in 15/36 yellow in 21/36	yellow
Uniseriate corolla trichomes	present in all	present in all	present in all	present in 21/36	absent
Achene length, mm	8.0–10.6 (9.4)	7.5–10.4 (8.4)	6.4–8.6 (7.9)	4.5–6.4 (6.2)	4.3–6.6 (5.1)

single heterozygous translocation. Mean pollen stainabilities in the two hybrids were 58 percent and 67 percent. These putative F_1 hybrids expressed a phyllary length/width ratio of less than 0.2 and their average ray flower numbers were 37 and 39. Examination of the remaining putative hybrids revealed normal meiosis, pollen stainabilities exceeding 90 percent and a flavonoid pattern indistinguishable from that of *H. vestita* ssp. *callicarpha.* At least three plants in the Chalk Hill population were judged to be BC_1 hybrids, based on the occurrence in these plants of uniseriate corolla trichomes. Furthermore, an additional number of plants, clustered near the BC_1 hybrids in the scatter diagram, cannot be rejected as possible backcross hybrids on the basis of morphological variation.

As compared to populations 1 and 3, the Stone Creek population (2, Figure 1) appeared more complex with respect to morphological variation. A broad attenuation of the recombination spindle at the *callicarpha* pole suggests the presence of F_1 hybrids and numerous backcross hybrids. Five of these putative hybrids displayed complementary flavonoid patterns and each displayed evidence of a heterozygous translocation at meiotic metaphase. The average ray flower number in these putative hybrids ranged from 33 to 45 and the phyllary length/width ratio was less than 0.2 in all five plants. This evidence suggests that all five plants were F_1 hybrids. Each of the remaining putative hybrids displayed normal meiosis, pollen stainability exceeding 90 percent and a flavonoid pattern indistinguishable from that of *H. vestita* ssp. *callicarpha.* The occurrence of uniseriate corolla trichomes, anthocyanin pigmentation and intermediate morphological expressions suggest that at least four and perhaps more of these plants comprised a BC_1 progeny.

The Lake Fulmor population (3, Figure 1) was characterized by a relatively narrow recombination spindle. All four plants located in the center of the spindle displayed 17 bivalents and a chain of four at meiotic metaphase. Pollen stainability ranged between 59 and 83 percent and each of the four hybrids possessed a complementary flavonoid pattern. The occurrence of reddish ray corollas and intermediate character expressions appear skewed within the distribution of plants at the *callicarpha* pole of the spindle. Judging solely on the presence or absence of uniseriate corolla trichomes, at least three of these plants could be considered as BC_1 hybrids.

DISCUSSION

A number of recent studies have demonstrated the necessity for an eclectic approach in the interpretation of natural hybridization. Levin (1967a,b) provided evidence, for example, which indicated that certain plants, judged to be backcross hybrids by morphological criteria, could not be confidently distinguished from the recurrent parents with respect to flavonoid chemistry. On the other hand, Crawford (1972) has demonstrated the usefulness of flavonoid chemistry in detecting hybrids when the morphological evidence indicated no discordant variation with respect to the parental taxa. In addition, Crawford convincingly demonstrated the value of synthetic hybrids in establishing the identity of putative natural hybrids.

On the basis of morphological criteria alone,

one might have assumed a higher proportion of F_1 hybrids in at least two of the natural populations investigated in this study. Comparative studies of synthetic F_1 and BC_1 hybrids with respect to flavonoid chemistry, meiotic chromosome configurations and pollen stainability suggest, however, that a number of putative natural hybrids may be excluded as F_1 types and are to be regarded as advanced generation or backcross types. The absence of phenotypes similar to synthetic hybrids derived from the combination $F_1 \times$ *H. heterochroma* and the broadened recombination spindles at the *callicarpha* pole suggest that most of the non-F_1 hybrids are derived from backcrossing to *H. vestita* ssp. *callicarpha.* It is interesting, however, that data derived from studies of chromosome behavior, pollen stainability and flavonoid chemistry did not allow positive identification of backcross hybrids. Meiosis appeared regular in a high proportion of the synthetic backcross progeny and pollen stainability averaged as high as that of parental strains.

Two contrasting patterns of flavonoid inheritance occurred with respect to BC_1 hybrids obtained from the cross $F_1 \times$ *H. vestita* ssp. *callicarpha.* Although both anthocyanins were inherited as a block in approximately half the progeny, the flavonoids 9, 10, and 11 did not appear in chromatograms of any of the synthetic BC_1 plants. Inasmuch as anthocyanins have been detected in pure populations of *H. vestita* ssp. *callicarpha* it is difficult to assess the degree to which genes derived from *H. heterochroma* are involved in their inheritance in hybrid progenies. The absence of compounds 9, 10, and 11 in synthetic BC_1 hybrids suggest that flavonol and flavone inheritance may be under relatively complex genetic control. The general patterns of flavonoid inheritance observed in the synthetic backcross progeny did not, however, aid in the detection of natural backcross hybrids.

A relatively narrow range of morphological variation and strong correlation between intermediate character expressions were exhibited by synthetic hybrid progenies. One was able to readily distinguish synthethic F_1 and BC_1 hybrids from each other and from cultivated strains of the parental taxa. Although morphological criteria allowed the detection with some confidence of F_1 hybrids in natural populations, the identification of natural backcross hybrids proved difficult. The inheritance of uniseriate corolla trichomes thus provided the only conclusive evidence for detecting the degree of backcross hybridity in natural populations. The variation displayed by plants clustered at the *callicarpha* pole of the recombination spindle suggest that, under natural conditions, both backcross hybrids and plants of *H. vestita* ssp. *callicarpha* exhibit considerable phenotypic plasticity.

It is surprising that none of the hybridizing populations displayed evidence of backcrossing in the direction of *H. heterochroma.* Populations of *H. heterochroma* are presumably favored by the ecological conditions which characterized the sites of hybridized populations. Synthetic backcrosses to *H. heterochroma* were performed with ease and the BC_1 progeny exhibited normal meiosis and high pollen fertility. The synthetic progeny was readily distinguished from F_1 hybrids and strains of the parental species. Although critical studies of pollinator fidelity were not undertaken, general observations indicated that the principal pollinating agents (unidentified Megachilidae, Halictidae, and Syrphidae) moved indiscriminately throughout the hybridized populations. The absence of backcrosses to *H. heterochroma* suggests, however, that the contribution of *H. heterochroma* to the gene pool in each of the populations may have been much less than that of *H. vestita* ssp. *callicarpha.* The number of *H. heterochroma* plants represented less than 15 percent of the total number of plants in each of the populations. Based on this evidence, the most likely hypothesis indicates that a higher proportion of backcrosses to the numerically dominant species would be expected.

The combination of self-incompatibility, relatively high fertility of F_1 and BC_1 hybrids, the occurrence of hybrid populations on disturbed sites and the relatively broad geographical distribution of hybrid populations within the San Jacinto Mountains suggests the potential for introgressive hybridization. Studies of variation within populations of *H. vestita* ssp. *callicarpha* have supplied little evidence to support the hypothesis of introgression by genes from *H. heterochroma.* The results of this investigation clearly show that, regardless of the potential for extensive gene flow, the detection of introgression beyond the first backcross generation would prove difficult on the basis of morphological and biochemical criteria.

In general, the relatively uniform morphological patterns which characterize interspecific variation within *Hulsea* do not pose significant taxonomic problems. The systematic relationships of the 11 taxa within *Hulsea* are characterized by relatively high cross-compatibility and relatively high fertility of synthetic F_1 hybrids (Wilken, 1971; Wilken, in press). The absence of strong barriers to gene exchange, an allopatric distribution, and the occurrence of hybridization following species contact, as exemplified in the present study, suggests that the taxonomy of *Hulsea* reflects a pattern of gradual differentiation associated with geographical and ecological isolation.

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ERRATUM

Martin, W. E. 1975. Hydrichthys pietschi, *new species, (Coelenterata) parasitic on the fish,* Ceratias holboelli. *Bull. So. California Acad. Sci., 74(1):1–5.*

I erroneously stated that the fish host of *Hydrichthys pietschi* was a myctophid [abstract] whereas, it is a ceratiid. A transposition occurred in *Tarletonbeania* (page 2, line 8, 2nd paragraph). Also, on page two, the third line of the last paragraph should read: [presented an angler fish, *Ceratias holboelli* Krøyer,]. On page four, the fifth line under discussion should read: [the host. The only report of a hydroid on]. W. E. Martin, *Dept. Biology, Univ. Southern California, Los Angeles, California 90007.*

RESEARCH NOTES

ON THE AFFINITIES OF *MONADENIA CHURCHI* HANNA AND SMITH (GASTROPODA: STYLOMMATOPHORA)

Pilsbry (Monogr. 3, Acad. Nat. Sci. Philadelphia, 1:33, 1939) divided the northwest American helicoid genus *Monadenia* Pilsbry, 1895 (type-species, *Helix fidelis* Gray, 1834) into two groups of species, based on proportions of the mucus glands, atrium, and "flagellum," as well as conchological characters. The second of these groups was named *Corynadenia* by Berry (Bull. So. California Acad. Sci., 38:204, 1940a), with type-species *M. hillebrandi* (Newcomb, 1864). Both authors recognized that the distribution of the two groups was largely allopatric. Berry (J. Entomol. and Zool., 32:1, 1940b) characterized the range of the genus as resembling "an inverted tuning fork, the stem end arising somewhere in or near the southern end of Alaska, the divarication in the general vicinity of Mount Shasta, and the tines extending southward on either side of the great California valley," with *Monadenia, sensu stricto*, inhabiting the stem and western, or Coast Range, tine, and *Corynadenia* the eastern, Sierran tine.

Monadenia churchi Hanna and Smith (Nautilus, 46:79, pl. 5, figs. 1–5, pl. 6, fig. 8, 1933), which occupies a fairly wide range around the north end of the Sacramento Valley, at the divarication of the fork, was placed with qualification in the inland group by Pilsbry. Berry (1940a) considered this species "somewhat anomalous" and remarked (1940b) that its placement in *Corynadenia* had not been positively established. Material to clarify the systematic position of *M. churchi* has been available for some time in the Departments of Geology and Invertebrate Zoology, California Academy of Sciences, as (a) the dissected paratype whose genitalia were originally figured by Hanna and Smith, and (b) three lots of wet-preserved specimens collected during the 1930's and early 1940's by Allyn G. Smith.

Reexamination of the paratype (CASG 5806a) and fresh dissections show that *Monadenia churchi* combines characters of both *Monadenia, s.s.*, and *Corynadenia*. I dissected four specimens from a large lot (AGS 7824) collected near a small creek along the former road to Copper City, near the McCloud River, Shasta Co. (probably in sec. 23, T. 34 N, R. 4 W, Mt. Diablo Base and Meridian); this locality is now under the waters of Shasta Lake. In these specimens the epiphallic caecum ("flagellum" of Pilsbry), borne in five to seven helical coils, is slender, decidedly longer than penis plus epiphallus, and tapers to a fine distal end tipped by a minute bulb. The mucus gland is 10–15 mm long, five to seven times as long as the dart sac, with a constriction near the middle and another 2–2.5 mm from the free end. The dart sac is small (ca. 2 mm), perched on a broad, saccular atrium. A penial retractor muscle inserts on the outside of a medial crook in the epiphallus.

Substantially the same characters occur in specimens from Shasta Springs (AGS 7906), and from the west slope of Mount Shasta, near Wagon Camp (AGS 4768), both localities in Siskiyou Co. The longest dart sac (3 mm) was found in the Wagon Camp specimen, which has a 13 mm long mucus gland. In all examples opened, the relative proportions of the organs are quite constant—more so than shell size, which ranges from 32 mm major diameter in the largest of the McCloud River specimens to 19.5 mm in an apparently mature individual from Wagon Camp.

Hanna and Smith suggested that their paratype might not have been entirely sexually mature, and the new dissections would seem to bear this out. In comparison to the paratypic anatomy, the latter have a much larger spermatotheca, longer epiphallic caecum, more prominent penis, and considerably larger mucus gland. The paratype has a distinct penis, not shown in the original figure. As in the new dissections, the distal 2 mm section of its mucus gland is bent at a sharp angle to the rest of that organ.

Conchologically, the embryonic sculpture of spirally elongate, occasionally confluent granules differs from both the clothlike texture found on Coast Range species and the more discrete granulation of the Sierran *M. hillebrandi* and *M. mormonum* but may be somewhat nearer the latter. In both *M. mormonum* and *M. churchi* the early teleoconch whorls are almost as densely granulose as the protoconch; early teleoconch whorls of *Monadenia* (*Monadenia*) species are much more sparsely granulated.

Most of the anatomic characters cited are those of the nominate subgenus. The principal *Corynadenia*-like features are the very long epiphallic caecum and the persistence of granular sculpture. Since genital anatomy is considered the better indicator of supraspecific relationships, I would assign *M. churchi* to *Monadenia, sensu stricto*.

If the present distribution and morphologic relations of forms of *Monadenia* are interpreted as direct expressions of the group's evolutionary history, then *M. churchi* might be regarded as preserving an intermediate stage in the divergence of *Corynadenia* from *Monadenia, s. s.* Hanna (Univ. Oregon Publ., 1(6): 3, 1920) has suggested that *Helix* (*Zonites*) *marginicola* Conrad, 1871, from the John Day Basin in Oregon (where *fidelis*-type fossil forms are known), is related to the Sierran group of *Monadenia*. This implies that the two groups were already differentiated in the Miocene, and in quite a different geographic setting. Without further examination of this poorly known fossil species, and of the Recent monadenias living in Shasta and Siskiyou Counties, either conclusion would be premature.

I am grateful to Allyn Smith for the loan of comparative specimens.

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DESCRIPTION OF A NEW TERRESTRIAL SNAIL FROM SAN NICOLAS ISLAND, CALIFORNIA (GASTROPODA: STYLOMMATOPHORA)

The presence of terrestrial snails, both living and subfossil, on San Nicolas Island, approximately 65 miles from the southern California mainland, has been remarked by numerous authors (Cooper, 1869; Bowers, 1890; Hemphill, 1901; Lowe, 1903; Vedder and Norris, 1963; among others). In April 1974, in connection with a study of land snails of the California Channel Islands, conducted for the Office of Endangered Species and International Activities, Department of the Interior, I received some specimens of *Micrarionta* from San Nicolas Island which could not be referred to any species previously described. The specimens were sent by Jan K. Larson, wildlife biologist with the Naval Undersea Center, San Clemente Island, and were collected by him, Philip J. Regal, and Roger Anderson. Additional material of the same species was located in the collections of the Academy of Natural Sciences, Philadelphia, and the Department of Geology, California Academy of Sciences. Allyn G. Smith of the latter department kindly loaned comparative material from his personal collection. In October 1974, Mr. Larson sent additional, living, specimens, which have furnished the basis for an anatomical description.

Micrarionta opuntia, new species

Figure 1

Diagnosis: A *Micrarionta* of 4¾ to 5¼ whorls, lacking spiral sculpture, with upper surface punctate, umbilicus open but narrow, and ends of peristome strongly convergent.

Description: Shell small, depressed-globose, openly but narrowly umbilicate, of 4¾ to 5¼ whorls, moderately thin; spire low-conic, whorl profile convex, sutures impressed. Surface glossy to silky, very finely granular, with low, irregular, radial wrinkles more or less papillose on early whorls. Protoconch radially wrinkled. Whorls of spire punctate; punctations arranged in diagonal lines, less regular on later whorls, becoming spirally elongate on penultimate and body whorl, sparse on base and around umbilicus. Whorls enlarging slowly; body whorl slightly constricted and descending behind aperture. Peristome subcircular, its ends strongly convergent; lip sharply turned outward, not greatly thickened, moderately reflected at base, encroaching on umbilicus for less than ¼ of its diameter. Parietal wall convex, lightly calloused between ends of peristome. Color, under a light tan periostracum, pale brown with a purplish tinge, with chestnut-brown peripheral band bordered with white; base lighter; lip pinkish tan within.

Figure 1. Micrarionta opuntia, new species. Top, basal, and apertural views of holotype, 55212 CASGTC.

Dimensions of holotype: Height 6.5 mm; maximum diameter 10.5 mm; umbilicus 1.2 mm; whorls 5.

Type locality: Northeastern San Nicolas Island, Ventura Co, California, in depression or small burrow at base of prickly-pear plant (*Opuntia littoralis*); collected by J. K. Larson, P. J. Regal, R. Anderson, April 1974. The type lot (13 specimens) was found in a region of isolated prickly-pear and *Lycium* patches among annual grasses, with bare ground comprising approximately 40 percent of a unit area. The snails were found beneath the surface either covered by soil or clinging to the sides of the burrow.

Type material: Holotype, No. 55212, California Academy of Sciences Geology Type Collection; paratype, No. 55213 CASGTC. Additional paratypes in collections of Academy of Natural Sciences, Philadelphia, Field Museum of Natural History, Natural History Museum of Los Angeles County, and the private collections of W. B. Miller, A. G. Smith, S. S. Berry, and the author.

Referred material: Eight specimens, California Academy of Sciences locality 42909, San Nicolas Island, collected by George Willett; one of these is mature at a maximum diameter of only 8.2 mm. Two specimens, No. 86608, Academy of Natural Sciences, Philadelphia, San Nicolas Island, collected by Henry Hemphill before 1904. Thirty-five specimens from an old dump area 0.2 mi NE of military compound, San Nicolas Island, below wreckage of a jet plane and under boards, collected by J. K. Larson, 22–23 October 1974; California Academy of Sciences and the author's collection.

Anatomy: Mantle pale gray with extensive patches of black; mantle collar grayish white. Sole of foot whitish; dorsal integument light grayish tan, darker in head region. Right ocular apparatus passing between male and female genitalial systems. Atrium short; penis capacious, containing short, spherical verge, separated from epiphallus by a slight constriction. Epiphallic caecum long, complexly coiled. Dart sac absent. Single mucus gland present, its duct inserting about half way up vagina. Duct of spermatotheca stout; no spermatothecal diverticulum present.

Discussion: The genus *Micrarionta*, *sensu stricto* (type species, *Helix facta* Newcomb, 1864), comprises a taxonomically difficult group of species restricted to the southern members of the California Channel Islands—San Clemente, Santa Catalina, San Nicolas and Santa Barbara Islands—and Guadalupe Island, Baja California, Mexico. The most recent revision of the genus is that by Pilsbry (1939), who recognized 13 specific and infraspecific taxa. Extreme endemism (only one species, *M. feralis*, definitely occurs on more than one island) and significant differences between living and Quaternary subfossil populations attest to a rapid rate of evolution. Present discrimination of taxa by shell characters depends on size, sculpture, number of whorls and tightness of coiling, breadth of umbilicus and lip, as well as on less easily quantified details of shape. For many years the bulk of material available for study was that taken by the ardent (and at times intemperate) collector, Henry Hemphill, who did not localize his material except by island and habitually sent out specimen lots selected for uniformity—thus obscuring any evidence of population structure. (Hemphill did state [1901:137] concerning San Nicolas Island, "my time and operations were limited while there to the south end of that island.") Genitalial dissections, important for reckoning affinities in helminthoglyptid snails, have not been published for most of the taxa now recognized. A serological study, which could be valuable in showing relationships between the living species, would necessarily exclude the several taxa known only from subfossil specimens.

Micrarionta opuntia averages smaller than *Micrarionta facta* (Newcomb, 1864) of Santa Barbara Island, which in addition has from five to 5¾ whorls and less obvious punctation on the spire. *Micrarionta facta* frequently has faint incised spiral lines on the body whorl, particularly behind the outer lip, and the lip nearly covers the umbilicus. James G. Cooper (1869) reported *M. facta* from San Nicolas Island, and Cooper material in the University of California Museum of Paleontology contains five specimens so labeled. Seven other specimens are in the collection of A. G. Smith (No. 1938, *ex* Cooper collection). *Micrarionta facta* has not been reported recently from San Nicolas Island, and the record needs confirmation. The "larger, heavier, extinct variety" of *M. facta* cited from San Nicolas by Binney (1885: 149) is presumably *Micrarionta feralis* (Hemphill, 1901).

The extinct *Micrarionta sodalis* (Hemphill, 1901) of San Nicolas Island, a possible progenitor of *M. opuntia*, resembles the new species in that the ends of the peristome converge strongly and the umbilicus is open; its umbilicus, however, is wider than that of *M. opuntia*, the shell is more depressed, and a thicker callus connects the ends of the peristome. Gregg (1960) reported the absence of dart sac and descending mucus gland in "*Micrarionta sodalis*"; as other workers have not found *M. sodalis* living, he probably had *M. opuntia*.

"*Micrarionta sodalis* form *micromphala*" Pilsbry (1939:211; on p. viii as *Micrarionta sodalis micromphala*) was described as "higher than *sodalis*, approaching the form of *feralis*, the umbilicus very small, partially covered; shoulder band wanting or very weak; the lip-margins converging somewhat, but less than in *sodalis*. Lip rather narrow, thickened within, ivory-yellow to pinkish buff, with an ochraceous-tawny internal border. 9.7 × 14 mm, 5½ whorls; also running down to about 9 mm diameter. San Nicolas; only fossil specimens" (Pilsbry, 1939). The type lot was collected by Henry Hemphill before 1904. Only the holotype (ANSP 86833a) matches Pilsbry's description. It is a large, sturdy shell with much narrower umbilicus than either *M. sodalis* or *M. opuntia*. The paratype (ANSP 86833), although somewhat sandblasted, shows traces of incised spiral lines over much of the body whorl and is undoubtedly a specimen of *M. feralis*. The other specimens examined by Pilsbry (ANSP 86608), "running down to about 9 mm. diameter," are typical *Micrarionta opuntia*.

Micrarionta guadalupiana ("Dall" Pilsbry and Vanatta, 1898) has a more open, funnellike umbilicus, flatter whorl profile, and subangulate periphery. The ends of the nearly circular peristome approach each other closely. Like *M. opuntia* it lacks incised spiral sculpture and has a thin shell with papillose early whorls.

Other species and subspecies of *Micrarionta* are less similar. *Micrarionta rufocincta* (Newcomb, 1864) and *M. r. beatula* Cockerell, 1929, both from Santa Catalina Island, and *M. gabbi* (Newcomb, 1864) from San Clemente Island, are distinctly spirally striate. In *Micrarionta feralis* (Hemphill, 1901) from from San Clemente and San Nicolas Islands, which is also spirally striate, the lip covers the umbilicus and the ends of the peristome converge only weakly.

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EDITORIAL: REQUEST FOR COVER ILLUSTRATIONS

On the cover of each issue of the Bulletin an illustration is printed. Usually this illustration pertains to an article in the issue or it may be one of general scientific interest. There is a marked shortage of such illustrations available for consideration and I would like to request that members of the Academy submit illustrations for consideration. These may be line-drawings or black and white photographs. The background of photographed subjects should be light and highly contrasted and submitted on black and white glossy paper. A brief, but informative, caption, including scientific name(s) of subject(s) and relevant points of interest, should accompany each illustration. In addition, the illustration should appropriately fill the space provided (see covers of past Bulletins). Please do not submit black and white negatives or color transparencies. James Dale Smith, Managing Editor.

INSTRUCTIONS FOR AUTHORS

The BULLETIN is published three times each year (April, August, and November) and includes articles in English in any field of science. **Non-members will be assessed a page charge of $40.00 per page.** Manuscripts submitted for publication should contain results of original research, embrace sound principles of scientific investigation, and present data in a clear and concise manner. The current AIBS *Style Manual for Biological Journals* is recommended as a guide for contributors. Consult also recent issues of the BULLETIN. Authors should strive for directness and lucidity, achieved by use of the active voice. Special attention should be given to consistency in tense, unambiguous reference of pronouns, and logically placed modifiers.

MANUSCRIPT PREPARATION

It is strongly recommended that, before submitting a paper, the author ask qualified persons to review it. The author is requested to submit *at least one additional copy with the original,* on 8½ × 11 opaque, nonerasable paper, double spacing the entire manuscript. ***Do not break words at right-hand margin anywhere in the manuscript.*** Footnotes should be avoided. **Manuscripts which do not conform to the style of the BULLETIN will be returned to the author.**

An abstract summarizing in concise terms the methods, findings, and implications discussed in the paper *must* accompany a *feature article. Abstract should not exceed 100 words.*

A feature article comprises approximately five to thirty typewritten pages. Papers should usually be divided into the following sections: abstract, introduction, methods, results, discussion and conclusions, acknowledgments, and literature cited. Avoid using more than two levels of subheadings.

A research note is usually one to six typewritten pages and rarely utilize subheadings. Consult a recent issue of the BULLETIN for the format of *notes.* Abstracts are not used for notes.

Abbreviations: Use of abbreviations and symbols can be determined by inspection of a recent issue of the BULLETIN. **Omit periods after standard abbreviations:** 1.2 mm, 2 mi, 30 cm, but Figs. 1–2. Use numerals *before* units of measurements: 5 ml, but nine spines (10 or numbers above, such as 13 spines). The metric system of weights and measurements should be used wherever possible.

Taxonomic procedures: Authors are advised to adhere to the taxonomic procedures as outlined in the International Code of Botanical Nomenclature (Lawjouw *et al.*, 1956), the International Code of Nomenclature of Bacteria and Viruses (Buchanan *et al.*, 1958), and the International Code of Zoological Nomenclature (Stoll, *et al.*, 1961). Special attention should be given to the description of new taxa, designation of holotype, etc. Reference to new taxa in titles and abstract should be avoided.

The literature cited section should include six or more references; entries for books and articles should take these forms.

McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.
Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus.* J. Mamm., 54: 452–458.
Brattstrom, B. H. 1969. The Condor in California. Pp. 369–382 *in* Vertebrates of California. (S. E. Payne, ed.), Univ. California Press, xii + 635 pp.

If fewer than six references are cited they should be inserted in text as follows:

(McWilliams, Insect mimicry, p. 216, 1970); (Holmes and Speak, J. Mamm., 54: 452–458, 1971); (Brattstrom, The Condor in California, Pp. 369–382, *in* Vertebrates of California, 1969).

Tables and figures (line drawings, graphs, or black and white photographs) **should not repeat data contained in the text.** The author must provide *numbers* and *short legends* for tables and figures and place reference to each of them in the text. Legends should be typed on a separate sheet of paper and placed at the end of the manuscript. **Illustrations and lettering thereon should be of sufficient size and clarity to permit reduction to standard page size;** ordinarily they should be no more than twice the size of intended reduction and should not exceed 8½ by 11 inches in size. Photographs *must* be printed on glossy paper. Submit one photoduplicated copy of each illustration. All illustrations accompanying **Research Notes** will be reduced to one column width. **All half-tone illustrations will have light screen (grey) backgrounds. Special handling such as dropout half-tones, special screens, etc., must be requested by and will be charged to authors.**

A cover illustration pertaining to an article in the issue or one of general scientific interest will be printed on the cover of each issue. Such illustrations along with a brief caption should be sent to the technical editor for review.

PROCEDURE

All manuscripts should be submitted to the Technical Editor, James Dale Smith, Department of Biology, California State University, Fullerton, California 92634. **Evaluation of a paper** submitted to the BULLETIN begins with a critical reading by the technical editor; several referees also check the paper for scientific content, originality, and clarity of presentation. Judgments as to the acceptability of the paper and suggestions for enhancing it are sent to the author at which time he may be requested to rework portions of the paper considering these recommendations. The paper is then resubmitted and may be re-evaluated before final acceptance after which it is sent to the managing editor.

Proof: The galley proof and manuscript, as well as reprint order blanks, will be sent to the author. He should **promptly and carefully read** the proof sheets for errors and omissions in text, tables, illustrations, legends, and bibliographical references. He marks corrections on the galley (copy editing and proof procedures in *Style Manual*) and **promptly returns both galley and manuscript** to the managing editor, James Dale Smith, Department of Biology, California State University, Fullerton, California 92634. Manuscripts and original illustrations will not be returned unless requested at this time. **All changes in galley proof attributable to the author (misspellings, inconsistent abbreviations, deviations from style, etc.) will be charged to the author. Reprint orders are placed with the printer, not the Managing Editor.**

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RESEARCH NOTES

COVER: *Anterior limb wiping sequence in* Phyllomedusa sauvagi; *ongoing research by William Presch, Department of Biological Sciences, California State University, Fullerton.*

Illustration by Paula McKenzie, Department of Biological Sciences, California State University, Fullerton.

SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

BULLETIN

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BULLETIN OF THE SOUTHERN CALIFORNIA
ACADEMY OF SCIENCES

VOLUME 74 JANUARY 16, 1976 NUMBER 3

DEVELOPMENT OF THE WHIPSCORPION *SCHIZOMUS FLORIDANUS*, WITH NOTES ON BEHAVIOR AND LABORATORY CULTURE

VINCENT BRACH[1]

ABSTRACT: The embryonic and larval stages of *Schizomus floridanus* are described, with special emphasis on the morphology of the larval tarsi. *Schizomus floridanus* is facultatively if not completely parthenogenetic. Females are capable of producing young after being raised apart from males for over a year. Breeding specimens were found in south Florida in August. The lack of a nesting chamber and the small number of embryos found on the brooding females resembles the situation reported for cavernicolous members of the order. A simple method of long-term culture is described, and additional notes on ecology and behavior are given.

The order Schizomida comprises less than 100 species of tiny, eyeless arachnids which inhabit leaf litter and rotten logs in tropical and subtropical regions (Kaestner, 1968). Little is known of their biology, and few investigators have had the opportunity to observe them over prolonged periods in the laboratory. While most schizomids are difficult to collect, *Schizomus floridanus* (Muma, 1968) is common in many moist forest-litter and rotten-log habitats in south Florida. In this report, the larva, behavior and ecology of this species are described.

METHODS

Schizomids were collected by hand with the aid of a small brush on Key Biscayne, Dade Co. Florida on 10 January 1973. Specimens were taken to my laboratory at the University of Miami. Twelve adult schizomids were housed in a plastic shoe box filled four cm deep with natural humus taken from the collection site and sprinkled with rotten log fragments. Water was added to the culture whenever it appeared dry. Once a month, several maimed *Drosophila* flies or other small arthropods were added to the culture for food. No special attention was given to either lighting or temperature.

The larvae were photographed while alive and attached to the parent. Larvae were prepared for microscopy by formalin fixation and alum-cochineal staining. Both larvae and adults were mounted as whole mounts using Turtox CMC medium.

RESULTS AND DISCUSSION

Schizomus floridanus was found to be exceptionally abundant under the bark of rotten palm logs in mixed *Casuarina-Cocos* stands at the collection site. A fairly large population was also discovered under pine needle litter on the University of Miami campus.

Schizomus floridanus is a highly active creature. Specimens uncovered in the field usually succeeded in escaping into crevices, moving in abrupt rushes as do solpugids. The highly flexible antenniform first pair of legs and numerous trichobothria appear to be the major sense organs. A schizomid in motion constantly explores the ground ahead with its antenniform legs and will frequently investigate potential food or crevices with prolonged, delicate touches of these appendages.

Feeding was not observed in the field, but captive specimens fed upon virtually any small insect. Freshly killed or maimed prey is preferred to intact prey unless the prey is extremely small

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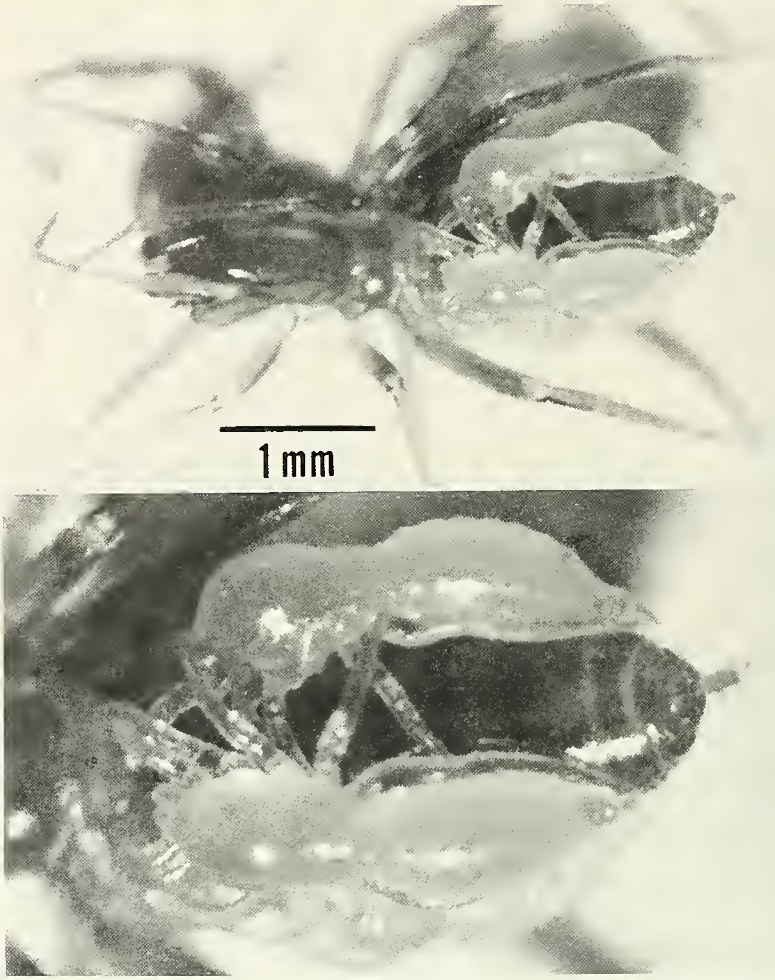

Figure 1. Top: Female *Schizomus floridanus* with larvae. Bottom: Closeup of *S. floridanus* larvae attached to the abdomen of the mother. An additional larva is attached to the undersurface of the abdomen.

(<0.5 mm). Prey is seized by the raptorial pedipalps and is carried to a crevice before being eaten. Small termites, psocids, and zorapterans were favorite food items and may comprise part of the natural diet. Schizomids have been found in association with termites in the field by others (Briggs and Hom, 1966; McDonald and Hogue, 1957; Kaestner, 1968) and a laboratory colony of *Prorhinotermes simplex* at the University of Miami, which was originally collected in Dade Co, Florida, was found to be literally infested with *S. floridanus*. However, it is not known whether *S. floridanus* is tolerated within the occupied termite galleries.

Schizomus floridanus appears to be somewhat gregarious, as dozens of individuals may live under the same log. However, burrows or crevices may be defended by individuals. Defense consists of agonistic displays involving short, abrupt advances and retreats, the antenniform legs and pedipalps being raised in a threatening manner. Accidental intraspecific encounters while exploring result in a sudden backward rush by both individuals, after which different courses are taken.

On 6 August 1974, a female was collected with eight embryos attached to the underside of the abdomen in a loosely-compacted mass. The embryos were spherical, measuring approximately 0.2 mm. They were not attached by any markedly sticky secretion and were shed by the female shortly after capture. Another female was captured later in the day from the same site carrying a mass of several larval exuviae on the dorsal surface of the abdomen. This mass also was shed shortly after capture. In neither case were nesting chambers found. During the rest of the month of

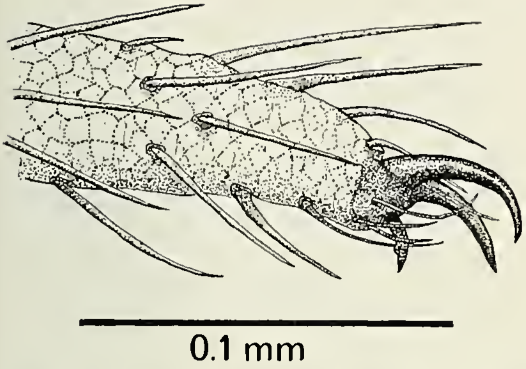

Figure 2. Tarsus of the third walking leg of adult *S. floridanus.*

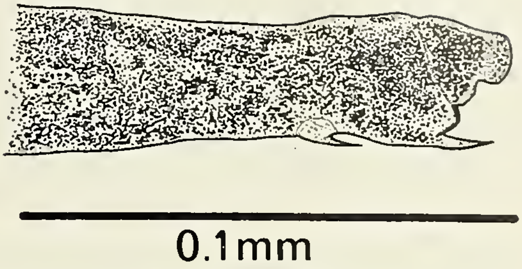

Figure 3. Tarsus of third walking leg of larval *S. floridanus.* Alum-cochineal stained specimen.

August, exceptionally large numbers of second-instar young were seen in the forest litter, suggesting a definite breeding season.

On 21 April 1974, a schizomid in the laboratory colony was found in a shallow, unmodified crevice with three larvae attached to its abdomen (Fig. 1). The larvae were pale white and translucent, superficially similar to the adult but lacking extensive spination. They were much larger in comparison to the mother than those figured by Rowland (1972) for *Trithyreus pentapeltis.* The larvae were sticky on their ventral surfaces and were completely motionless, even when removed from the parent. No protective envelope, such as is secreted by the thelyphonids (Millot, 1949) was seen, and the abdomen of the mother was not carried erect.

The morphology of the larval tarsi is quite different from that of all subsequent stages (Figs. 2, 3). The end of the tarsus is equipped with an adhesive disc as in the larvae of uropygids (Millot, 1949) and bears a pair of spines. Attachment of the larvae to the parent is accomplished by means of the modified tarsi and the sticky ventral surface. The last pair of legs is kept closely appressed to the abdomen and does not appear to be used for attachment.

No muscle fibers were visible in stained whole mounts of the larvae. Instead, the cellular material appeared diffuse and undifferentiated. It is probable, therefore, that the immobility of the larvae is physiological rather than behavioral. This implies that the young are positioned by the mother and do not crawl onto her abdomen by themselves.

There are five post-embryonic molts in *S. floridanus*, as in *T. pentapeltis* (Rowland, 1972). The post-larval instars closely resemble the adult but are not as heavily sclerotized and are therefore much lighter in color. The small number of rather large young observed contrasts with the situation described for *S. crassicaudatus* (Millot, (1949) and *T. pentapeltis* (Rowland, 1972). Rowland mentions that female cavernicolous schizomids from Mexico were found to carry relatively small broods and were collected at large, as were the brooding *S. floridanus.* The lack of a nesting chamber in *S. floridanus* is not certain, however, as such structures are fragile and might have been destroyed when the field specimens were uncovered.

No males of *S. floridanus* have been found, despite extensive collecting by myself and by Muma (1968). Since the female in figure 1 was raised in the absence of males for 15 months, it is highly probable that this species is parthenogenetic.

Schizomus floridanus is both hardy and long-lived in culture. Longevity may be true of schizomids generally. Briggs and Hom (1966) record keeping *T. pentapeltis* for many months under simple culture conditions. Rowland (1972) also kept this species alive for a considerable period but was unable to induce it to feed. The durability of *S. floridanus* in culture, combined with its longevity and abundance in nature, should stimulate further research into the biology of this interesting arachnid order.

ACKNOWLEDGMENTS

I thank H. F. Strohecker for critically reading the manuscript.

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Accepted for publication March 25, 1975.

FIRST RECORDS AND RANGE EXTENSIONS OF CRABS IN CALIFORNIA WATERS

JANET HAIG AND MARY K. WICKSTEN[1]

ABSTRACT: Range extensions are reported for 14 species of anomuran and brachyuran crabs (Crustacea: Decapoda), six of them new to California waters. Three cold-temperate species not previously known south of the Monterey Bay area were found to occur south of Point Conception at San Miguel and Santa Rosa Islands, where a strong northern element is present in the fauna. Two species with their known northern limit of range near San Francisco Bay, and one species known only as far south as Oregon, were collected in the area of unusually cold water around Cape Mendocino.

Since publication of Schmitt's (1921) comprehensive review, information on Californian decapod Crustacea has continued to appear. In this paper we report six additions to the crab fauna of California, and extend the known distribution within the state of eight other species. Records are based on material in the Allan Hancock Foundation, from collections made by the "Velero III" and "Velero IV," "Searcher," California Fish and Game vessels, and several individuals, including SCUBA divers.

Measurements refer to carapace length unless there is an indication to the contrary. When two measurements are given for a single specimen, they are differentiated as carapace length (cl.) and carapace breadth (cb.).

SPECIES UNREPORTED FROM CALIFORNIA

Family ALBUNEIDAE

Lophomastix diomedeae Benedict, 1904

Lophomastix diomedeae Benedict, 1904:621, fig. 1.

Recorded distribution: "Albatross" sta. 2913, off Cortes Bank, Baja Cfa., Mexico, 32°25′30″N, 119°03′30″W; 48 m (Benedict).

Material examined: "Velero IV" sta. 14121-70, 3 mi from Blue Banks anchorage, Santa Cruz I., 33°58′50–56″N, 119°35′58″–36′35″W; 29–31 m; 17 Apr. 1970; 1♂ 18.0 mm — "Velero III" sta. 976-39, N of Santa Barbara I., 33°31′N, 119°01′50″W; 27–37 m, sand; 28 May 1939; 1♂ 14.2 mm — "Velero III" sta. 1120-40, off San Nicolas I., 33°18′20″N, 119°28′45″W; 53–60 m, sand and shell; 11 Apr. 1940; 3♂ 17.9–22.5 mm — "Velero III" sta. 1122-40, off San Nicolas I., 33°18′N, 119°24′10″W; 55 m, sand, rock, shell; 11 Apr. 1940; 2♀ 12.7 and 25.6 mm — "Velero III" sta. 1327-41, ½ mi W of Castle Rock, San Clemente I., 33°02′N, 118°37′20–35″W; 40–68 m, fine broken shell; 8 June 1941; 1♀ 23.7 mm.

Remarks: This is the third genus and species in family Albuneidae to be reported from California waters. The following key will distinguish it from *Lepidopa californica* Efford (*L. myops*

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[1] Allan Hancock Foundation, Univ. Southern California, Los Angeles, California 90007.

Holmes of earlier authors; see Efford, 1971:74) and *Blepharipoda occidentalis* Randall:

1. a. Carapace with a single lateral spine; eyes broad, compressed, scale-like, with a rudimentary cornea .... *Lepidopa californica*
   b. Carapace with more than one lateral spine; eyes slender, elongate, cylindrical, with a distinct cornea 2
2. a. Carapace with four lateral spines; eyes divided into two sections by a submedian articulation .... *Blepharipoda occidentalis*
   b. Carapace with three lateral spines; eyes not articulated submedially .... *Lophomastix diomedeae*

Family PAGURIDAE

Pagurus ochotensis Brandt, 1851

Pagurus ochotensis—McLaughlin, 1974:57, figs. 15, 16.

Not *Pagurus ochotensis*—Schmitt, 1921:130, fig. 84 [= *Pagurus armatus* (Dana)].

Recorded distribution: Sea of Japan to Okhotsk Sea; Pribilof Ids., Alaska, to Tillamook Head, Oregon (McLaughlin).

Material examined: Just S of Trinidad Head; 12–15 m, soft mucky bottom with patches of boulders; 4 Aug. 1971; Camm Swift; 1 ♂ (juv.) 13.1 mm — "Searcher" sta. 208, about 12 mi S of Point Arena [exact position not recorded]; 90 m or less; 9 Aug. 1971; 1 ♂ 39.0 mm.

Remarks: The only precise Oregon locality that we have been able to find for this species is Tillamook Head (McLaughlin, 1974). The collections of the Allan Hancock Foundation contain Oregon material from off Ocean Park, Winchester Bay, and Coos Bay.

Pagurus aleuticus (Benedict, 1892)

Pagurus aleuticus—McLaughlin, 1974:72, figs. 17–19.

Recorded distribution: Japan to Kamchatka Peninsula; Bering Sea (latitude of Pribilof Ids.) southward to Oregon at 46°01.5′N, 124°43.2′W (McLaughlin).

Material examined: "MV Scofield" sta. 69-S-6-9, off Crescent City, 41°40′N, 124°26.7′W; 164–166 m; 6 Sept. 1969; presented by Howard Ness, Calif. Fish and Game; 2 ♂ 22.0 and 22.3 mm, 2 ♀ 17.7 and 20.0 mm — Off Eureka, 40°41′N, 127° 31.7′W; 208–283 m; 5 Feb. 1969; presented by Don Hendrick, Calif. Fish and Game; 1 ♂ 37.3 mm.

Pagurus caurinus Hart, 1971

Pagurus caurinus Hart, 1971:1528, figs. 1–7. McLaughlin, 1974:132, figs. 33, 34.

Recorded distribution: Kodiak I., Alaska, to Washington (McLaughlin).

Material examined: South Jetty, Bodega Bay; shore, –0.9′ tide; 8 Aug. 1949; L. O. Miles and W. K. Emerson; 1 ♂ 8.8 mm, 3 ♀ 6.3–8.9 mm — Los Angeles Breakwater, San Pedro; 6 m, rock; 18 Feb. 1974; Mary K. Wicksten, SCUBA diving at night; 1 ♀ 9.9 mm.

Remarks: In the field, this species should be easy to distinguish from other small intertidal and subtidal *Pagurus* by the bright orange antennae and the broad, intensely white band on the distal part of the propodus of the walking legs.

Family GALATHEIDAE

Munidopsis diomedeae (Faxon, 1893), new combination

Galacantha diomedeae—Faxon, 1895:79, pl. 25 figs. 1, 1a–e.

Recorded distribution: Gulf of California, Mexico, 27°34′N, 110°53′40″W (Faxon) to off Peru, 18°23′S, 71°13′W (Del Solar, 1972); 1100–3433 m.

Material examined: "Velero IV" sta. 8791-63, 20.3 mi 258° from Castle Rock Light, San Clemente I., 32°54′29″–33°01′40″N, 118°55′00″–119°05′20″W; 1719–1738 m, mud; 17 July 1963; 6 ♂ 13.8–28.3 mm, 3 ♀ 15.0–23.0 mm, 1 juv. 11.0 mm.

Remarks: We follow those writers (e.g. Chace, 1942; Pequegnat and Pequegnat, 1970) who consider *Galacantha* to be synonymous with *Munidopsis*.

Munidopsis scabra Faxon, 1893

Munidopsis scabra—Faxon, 1895:93, pl. 21 figs. 1, 1a.

Recorded distribution: Off Tres Marias Ids., Mexico, 21°19′N, 106°24′W (Faxon) to off Peru, 11°50′S, 77°58′W (Garth and Haig, 1971); 907–1243 m.

Material examined: "Velero IV" sta. 1989-50, 4¼ mi 066° from Avalon, Santa Catalina I., 33°22′05–26″N, 118°14′55–56″W; 604 m, rubble; 12 Aug. 1950; 1 ♀ 12.6 mm — "Velero IV" sta. 1865-49, 14-mile Bank ESE of Santa Catalina I., 33°11′20″–12′00″N, 118°03′32″–04′40″W; 567–640 m, mud; 11 July 1949; 1 ♀ *ca.* 14.0 mm (rostrum broken).

EXTENSIONS OF RANGE WITHIN CALIFORNIA

Family LITHODIDAE

Phyllolithodes papillosus Brandt, 1848

Phyllolithodes papillosus—Schmitt, 1921:153, pl. 22 fig. 2, text-fig. 99.

Recorded distribution: Unalaska, Alaska (Schmitt) to Carmel. Calif. (McLean, 1962).

Material examined: "Velero III" sta. 1415-41, 1½ mi E of Cardwell Point, San Miguel I., 34°00′45–55″N, 120°15′00″–16′30″W; 37–38 m, sand and rocks; 16 Sept. 1941; 1 ♀ (juv.) 13.5 mm.

Cryptolithodes typicus Brandt, 1848

Cryptolithodes typicus—Schmitt, 1921:154, pl. 20 figs. 1, 2.

Recorded distribution: Amchitka I., Alaska (Barr, 1973) to Monterey Bay, Calif. (Schmitt).

Material examined: "Velero III" sta. 1003-39, Bechers Bay, Santa Rosa I., 34°01′15–45″N, 120°00′14–30″W; 26 m, sand and shell; 18 Aug. 1939; 1 ♂ cl. 15.9 mm, cb. 27.1 mm.

Family DIOGENIDAE

Paguristes parvus Holmes, 1900

Paguristes parvus—Schmitt, 1921:124, pl. 17 fig. 1, text-fig. 83.

Recorded distribution: White's Point near San Pedro, Calif. (Schmitt); Arrecife Sacramento, Baja Cfa., Mexico (Haig, Hopkins, and Scanland, 1970).

Material examined: Naples Reef (20–22 km W of U. C. Santa Barbara campus, ½–1 mi offshore); 14–18 m, in kelp bed; 18 Oct. 1970; C. Swift, W. Stewart, D. Divins; 1 ♀ 4.4 mm — "Velero IV" sta. 4822-57, 11 mi 089° from Point Conception Light, 34°27′15″N, 120°14′45″W; 16 m; 17 Jan. 1957; 1 ♂ 3.9 mm — "Velero IV" sta. 5562-58, 5½ mi 092° from Point Conception Light, 34°26′47″N, 120°21′35″W; 19 m, rocky; 28 Jan. 1958; 3 ♂ to 4.7 mm, 5 ♀ to 3.3 mm — "Velero IV" sta. 5164-57, 4½ mi 089° from Point Conception Light, 34°26′40″N, 120°21′45″W; 21 m, shaley rocks; 2 July 1957; 2 ♂ to 4.0 mm, 9 ♀ to 4.1 mm — "Velero IV" sta. 6694-59, 2 mi 262° from Santa Barbara Point Light, 34°24′15″N, 119°45′40″W; 9 m, sand; 3 Dec. 1959; 1 ♀ 4.5 mm — Within or near Big Fisherman's Cove, Santa Catalina I.; 3–12 m; June–July 1973; Mary K. Wicksten; 4 ♂ 6.2–7.8 mm — "Velero IV" sta. 1646-48, Long Point, Santa Catalina I.; shore, rocky headland at −1.2′ tide; 30 Nov. 1948; 1 ♂ 4.4 mm — "Velero IV" sta. 1648-48, White Cove, Santa Catalina I.; 16–20 m; 1 Dec. 1948; 1 ♂ 3.4 mm.

Isocheles pilosus (Holmes, 1900)

Holopagurus pilosus—Schmitt, 1921:127, pl. 17 fig. 2.

Recorded distribution: San Francisco, Calif. (Schmitt) to Estero de Punta Banda, Baja Cfa., Mexico (Ricketts and Calvin, 1939); possibly S to Bahía de Santa María, Baja Cfa. (Haig, Hopkins, and Scanland, 1970).

Material examined: Doran Beach Co Park, Bodega Bay: 1 m, on sand; 16 Aug. 1974; Mary K. Wicksten; 1 ♂ 12.1 mm, 2 juv. 5.5 and 7.1 mm.

Family PAGURIDAE

Pagurus hemphilli (Benedict, 1892)

Pagurus hemphillii—Schmitt, 1921:142, fig. 92.

Pagurus hemphilli—McLaughlin, 1974:149, figs. 37, 38.

Recorded distribution: Queen Charlotte Ids., British Columbia (McLaughlin) to near Carmel, Calif. (McLean, 1962).

Material examined: Diablo Cove, San Luis Obispo Co; 3–6 m; 23 Sept. 1970; C. Swift and R. Lavenberg; 2 ♂ 12.7 and 18.6 mm, 3 ♀ 9.9–16.0 mm — "Velero III" sta. 894-38, S of San Miguel I., 34°01′N, 120°24′W; 9–27 m, rock with kelp; 10 Aug. 1938; 1 ♀ 14.0 mm.

Pylopagurus diegensis Scanland and Hopkins, 1969

Pylopagurus diegensis Scanland and Hopkins, 1969: 257, fig. 1.

Recorded distribution: La Jolla, Calif. (Scanland and Hopkins).

Material examined: About 2 mi W of Twin Harbors, Santa Cruz I.; 9 m, in pile of rocky rubble at base of reef; 29 Sept. 1974; Mary K. Wicksten; 1 ♂ 7.5 mm — Just E of Fisherman's Cove, Santa Catalina I.; 12–14 m, rock rubble; 16 Aug. 1970; C. Swift, K. Hooker, and C. Gage; 1 ♂ 10.0 mm — Between Blue Cavern Point and Big Fisherman's Cove, Santa Catalina I.; 8 m, in pile of rocks under kelp bed; 9 July 1973; Mary K. Wicksten; 1 ♂ 11.5 mm — Farnsworth Bank, off Santa Catalina I.; 20–34 m; 12 Dec. 1970; Nat. Hist. Mus. of Los Angeles Co. Calif. Fish and Game; 4 ♂ 7.2–11.2 mm, 1 ♀ 6.5 mm.

Family CALAPPIDAE

Mursia gaudichaudii (H. Milne-Edwards, 1837)

Mursia gaudichaudii—Schmitt, 1921:190, fig. 118. Rathbun, 1937:220, pls. 66, 67.

Recorded distribution: Gulf of the Farallones, Calif. (Rathbun) to Talcahuano, Chile (Garth, 1957).

Material examined: "Searcher" sta. 187, 5 mi SW of Point Delgada, Humboldt Co., 39°56′N, 124°07′W; 91 m; 6 Aug. 1971; 1 ♂ cl. 38.4 mm, cb. 54.0 mm (not including lateral spines).

Remarks: A specimen from still farther north was seen by one of us (M. K. Wicksten) in the collection of the California Academy of Sciences. Data are as follows: 18.7 mi WSW of the Klamath River, 41°27′N, 124°29′W; 210–218 m; 10 Sept. 1964; coll. Peter Isaacson.

Family MAJIDAE

Loxorhynchus crispatus Stimpson, 1857

Loxorhynchus crispatus—Schmitt, 1921:213, fig. 133. Rathbun, 1925:200. pls. 66, 67. Garth, 1958:260, pl. P fig. 3, pl. 27 fig. 2, pl. 28 fig. 1.

Recorded distribution: California, off Cordell Bank, Marin Co, and S to San Diego (Garth).

Material examined: "Searcher" sta. 156, Tolo Banks, 3 mi S of Shelter Cove, Mendocino Co; 21–30 m; 28 July 1971; 1 ♂ 29.7 mm — "Searcher" sta. 150, Arena Rock, 1½ mi N of Point Arena; 24–30 m; 26 July 1971; 2 ♂ 98.7 and 100.5 mm.

DISCUSSION

The occurrence of four of these species outside their recorded ranges may be due to localized regions of cold water. A mixture of fauna typical of both cold- and warm-temperate waters has been reported in the northern Channel Islands of California, where the cold California Current swings offshore from the mainland coast (Hewatt, 1946; Neushul, Clarke, and Brown, 1967). Three cold-temperate species, *Phyllolithodes papillosus*, *Pagurus hemphilli*, and *Cryptolithodes typicus*, were found in this region. Ekman (1953) called attention to the water mass around Cape Mendocino, which is lower in temperature than at any other point on the northeast Pacific coast up to southern Alaska. Within the 11 degree isotherm surrounding this water mass was found the southern extension of the range of the northern species *Pagurus aleuticus*. This mass of cold water may serve as the northern boundary of the ranges of the southern species *Loxorhynchus crispatus* and *Mursia gaudichaudii*.

Since this paper was submitted for publication, our attention has been called to two checklists in a 1972 work edited by A. T. Pruter and D. L. Alverson: The Columbia River estuary and adjacent ocean waters. Bio-environmental studies. Univ. Washington Press, 882 pp. The first of these (J. E. McCauley, A preliminary checklist of selected groups of invertebrates from ottertrawl and dredge collections off Oregon: 409–421) lists *Mursia gaudichaudii* from off Oregon in 100 m (p. 414). The second (W. T. Pereyra and M. S. Alton, Distribution and relative abundance of invertebrates off the northern Oregon coast: 444–474) lists *Munidopsis scabra* from northern Oregon in 1463 m (p. 450). No precise locality was given in either case.

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DIAGNOSIS, SYSTEMATICS, AND NOTES ON *GRANDIDIERELLA JAPONICA* (AMPHIPODA: GAMMARIDEA) AND ITS INTRODUCTION TO THE PACIFIC COAST OF THE UNITED STATES

John W. Chapman[1] and Julie A. Dorman[2]

Abstract: The introduction of *Grandidierella japonica* Stephensen, 1938 (Corophiidae) from Japan to Tomales Bay, Bolinas Lagoon and San Francisco Bay, California, is recorded for the first time. A diagnosis and a list of associate species are given. The possible synonymy of the genera *Grandidierella* and *Neomicrodeutopus* is indicated. This species probably arrived with oyster spat transplants from Japan.

Early in 1971, the authors discovered an amphipod from San Francisco Bay, California, that could not be readily identified. James T. Carlton of the California Academy of Sciences, San Francisco, pointed out a description of a Japanese species, *Grandidierella japonica* Stephensen, 1938 (Corophiidae), that proved to match the amphipod in question. *Grandidierella japonica* has previously been recorded only from Japan. This is the first record of this genus and species on the Pacific Coast of the United States.

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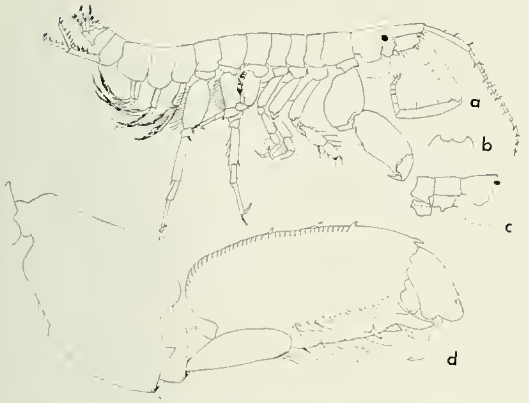

Figure 1. Male *Grandidierella japonica*: a, body; b, rostrum; c, medioventral spine on pereonite 1; d, medial view of gnathopod 1.

Figure 2. Female: a, rostrum; b, body; c, urosome.

Grandidierella japonica Stephensen, 1938
Figures 1–4

Diagnosis: Because Stephensen's description of *Grandidierella japonica* is incomplete and lacks certain critical details, a more thorough diagnosis is presented here.

Body (Figs. 1a, 3b): slightly cylindrical; urosomite segments separate, with no dorsal depression; no elongation of urosomite 1 (Fig. 3c). Mature males possessing a medio-ventral spine on first pereonite (Fig. 1c).

Head: one-fourth longer than pereonite 1, cuboidal; lateral lobes rounded, projecting slightly beyond a short acute rostrum (Figs. 1b, 3a). Eyes large and dark.

Antenna 1: greater than one-half body length, with 20 articles total; flagellum with 17 articles. Accessory flagellum consisting of one minute article with short distal hairs. Article 1 of peduncle with ventral spines.

Antenna 2: from three-fourths length to longer than antenna 1; article 2 barely visible from lateral view; spines on articles 3, 4, and 5; male antenna stout.

Mouthparts: form subquadrate bundle. Mandible (Fig. 4) with large triterative molar; incisors and lacina mobila toothed. Mandibular palp tri-articulate, article 2 longest, article 3 slightly longer than article 1, setation heaviest medio-distally on article 3.

Maxillipeds: generalized, inner plates of normal size, with distal setation; outer plates twice the length of inner plates with heaviest setation on medial sides. Maxilliped palp, four-articulate; article 2 twice length of articles 1 and 3; terminal palp claw-like; when extended, palp twice length of outer plate.

Male gnathopod 1 (Fig. 1d): massive, carpochelate; articles 2 and 5 greatly enlarged; article 2, length one and one half times width, broad and ovate, subequal in length to article 5, medial side concave, anterior edge sharp; article 3 small; article 4 elongate; article 5 length twice its width with three distal posterior teeth, one tooth enlarged, forming a thumb, anterior edge with short transverse grooves and four anterior spines; article 6 subquadrangular, one-third length of article 5.

Female gnathopod 1 (Fig. 5a): reduced, articles 4 and 5 possessing posterior hairs with pinnate barbs: article 6 with three posterior spines; article 7, serrated claw forming acute angle with article 6.

Male gnathopod 2 (Fig. 5c): subchelate, smaller than gnathopod 1, article 2 twice length of article 5; articles 4, 5, and 6 possessing posterior hairs with pinnate barbs, serrated subchelate claw forms transverse angle with article 6; sexual dimorphism apparent, male with elongate article 2 (Fig. 5c). Pereopods 1–5 as described by Stephensen, 1938 (as pereiopods 3–7), coxae reduced, 1–4 subquadrate.

Female gnathopod 2 (Fig. 5b): similar to male gnathopod 2 but with shortened article 2.

Uropod 1 and 2 biramous; uropod 3 uniramous; numerous spines on all uropods; uropod 1 projecting posteriorly slightly beyond uropod 2 and 3, prominent distal peduncular process on uropod 1, urosomite 1 with two spines on antero-lateral surface (Fig. 3c).

Figure 3. Right mandible and mandibular palp.

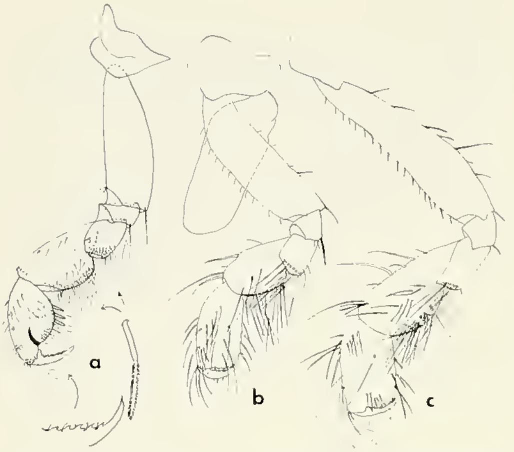

Figure 4. a, female gnathopod 1; b, female gnathopod 2; c, male gnathopod 2.

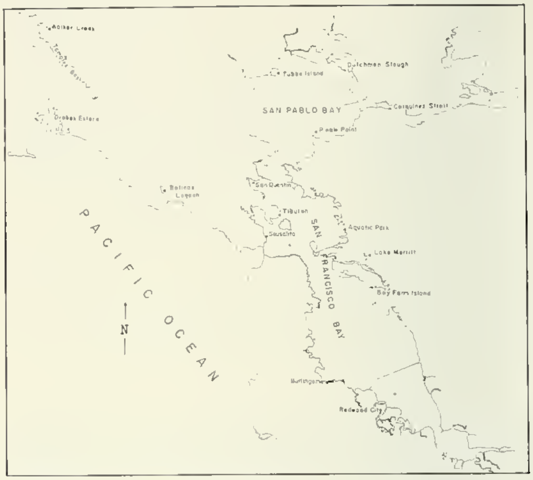

Figure 5. Collecting sites in San Francisco and Tomales Bay areas, California.

Telson small, button-like, with pronounced medial groove.

Largest male examined 22 mm in length, largest female 13 mm; cuticle mottled gray to gray brown, color retained in 70 percent isopropyl alcohol, flesh becoming apaque.

Material examined: Specimens have been deposited in the California Academy of Sciences, Department of Invertebrate Zoology, Type Series, no. 585 (Male, Fig. 1a) and no. 586 (Female, Fig. 3b). Additional material has been deposited at the Academy and at the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Remarks: *Grandidierella japonica* builds U-shaped tubes in muddy bottoms in which one male and one female often are found together. Males have been observed wandering about in tide pools at low tide.

Males observed in aquaria were noted to scrape the grooves on article 5 of gnathopod 1 rapidly against the sharp anterior edge of article 2. It has been suggested that these grooves function as "stridulating organs" (Stephensen, 1938).

Systematic discussion: Although originally placed in the genus *Grandidierella* by Stephensen, 1938, *Grandidierella japonica* cannot confidently be assigned to that genus or to the closely related genus, *Neomicrodeutopus*. Schellenberg, 1925, and Barnard, 1969; 1973, p. 14, distinguish the two genera by the length of mandibular palp article 1 (elongate in *Grandidierella*, short in *Neomicrodeutopus*). Since at least three species currently assigned to *Grandidierella* are now known to have a short palp article 1 (*G. dentimera* Myers, 1970, *G. japonica* Stephensen, 1938 and *G. perlata* Schellenberg, 1938), this character alternative appears to have no value in distinguishing the two genera (J. L. Barnard, April, 1973 *in litt.*). Barnard, 1973, has indicated the probable synonymy of *Grandidierella* and *Neomicrodeutopus*. Since the described species of both genera must be throughly reexamined to establish clear generic distinctions, if such exist, we consider it beyond the scope of the present paper to argue the correct generic placement of *G. japonica.*

Records: The following collection sites (Fig. 5) of *Grandidierella japonica* in central California are given with substratum, water depth, relative abundance, collection date and collector. The more common associated species are included where possible.

TOMALES BAY: Walker Creek delta, Marin Co: mud-sand, intertidal near Japanese oyster beds, abundant: 23:VII:1969: Coll. James Blake and Edmund Smith. Associates: polychaete, *Capitella* sp.; amphipods, *Ampelisca milleri, Ampithoe valida, Anisogammarus* sp. cf. *ramellus*, and *Corophium spinicorne.*

BOLINAS LAGOON: Marin Co: mud-sand, intertidal, moderately abundant: VIII: 1971: Coll. J. Chapman and J. F. Gustafson. Associates: polychaetes, *Capitella capitata* and *Streblospio benedicti*; amphipods, *Allorchestes angustus, Ampelisca milleri, Ampithoe valida, Corophium acherusicum* and *Corophium insidiosum*; isopod, *Gnorimosphaeroma lutea*; bivalves, *Cryptomya californica*, and *Gemma gemma.*

SAN FRANCISCO BAY: Carquinez Straits, Contra Costa Co: Construction site of barge loading facilities for brick works; mixed mud and brick fragments, 3 m, moderately abundant: 21:IX:1971: Coll. J. Chapman. Associates: polychaete, *Neanthes suc-*

cinea; barnacle, *Balanus improvisus*; amphipods, *Corophium acherusicum* and *Corophium spinicorne*.

Dutchman Slough, Solano Co: 100 m W Napa Val Fishing Resort; mud, intertidal, moderately abundant: 1966: Coll. Jean Chapman. Associates: amphipod, *Corophium spinicorne*; bivalve, *Macoma* sp.

Tubbs Island, Sonoma Co: northeast side, facing San Pablo Bay; mud, intertidal, moderately abundant: 19:III:1972: Coll. J. Chapman. Associates: polychaetes, *Neanthes succinea* and *Heteromastus filiformis*; bivalves, *Macoma balthica* and *Macoma nasuta*.

Pinole Point, Contra Costa Co: mud, 3 m, abundant: 20:II:1971: Coll. J. F. Gustafson. Associates: polychaete, *Glycinde* sp.; amphipods, *Ampelisca milleri* and *Corophium* sp.; bivalves *Gemma gemma*, *Macoma nasuta*, and *Mya arenaria*.

San Quentin, Marin Co: 100 m south of prison; mud-shell, intertidal, abundant: 28:II:1971: Coll. J. F. Gustafson. Associates: polychaete, *Glycinde* sp.; amphipods, *Ampelisca milleri* and *Corophium insidiosum*; bivalve, *Macoma nasuta*.

Tiburon, Marin Co: east cove on Tiburon Point; mud-sand, 2 m, moderately abundant: 28:II:1971: Coll. J. F. Gustafson. Associates: polychaete, *Glycinde* sp.; amphipods *Ampelisca milleri* and *Corophium insidiosum*; bivalve, *Macoma nasuta*.

Sausalito, Marin Co: from Ondine's Restaurant to sewage treatment plant; mud-sand, 2–6 m, scarce: 2:II:1971: Coll. J. F. Gustafson. Associates: polychaetes, *Glycinde* sp. and *Platynereis bicanaliculata*; amphipods, *Ampelisca milleri*, *Corophium acherusicum*, and *Photis brevipes*; bivalves, *Macoma balthica* and *Macoma nasuta*.

Aquatic Park, Berkeley, Alameda Co: among *Ruppia*, 0.5 m: 29:VII:1967: Coll. J. T. Carlton.

Lake Merritt, Oakland, Alameda Co: in fouling, 0.5 m: 22:XII:1966: Coll. J. T. Carlton. Associates: polychaete, *Mercierella enigmatica*; amphipod, *Melita* sp.; insect, Corixidae.

Lake Merritt, Oakland, Alameda Co: Sailboat Clubhouse, in fouling; intertidal, abundant: 19:IX:1970: Coll. J. T. Carlton.

Bay Farm Island, Alameda Co: 100 m N Bay Farm Island Bridge (State Highway 61); mud-sand, intertidal, abundant; 15:III:1972: Coll. J. Chapman. Associates: polychaetes, *Capitella capitata* and *Pseudopolydora kempi*; amphipods, *Ampelisca milleri* and *Corophium acherusicum*; bivalves, *Ostrea lurida* and *Tapes japonica*.

Burlingame, San Mateo Co: 1 mi W Coyote Point; hard mud, intertidal, abundant: 13:III:1972: Coll. J. Chapman and J. Dorman. Associates: polychaetes, *Capitella capitata*, *Glycinde* sp. and *Pseudopolydora kempi*; amphipod, *Corophium insidiosum*.

Redwood City, San Mateo Co: 2 mi S San Mateo Bridge, 1 mi W west bay shore; in mud and oyster (*Ostrea lurida*) beds, 4–13 m, moderately abundant: 12:II:1972: Coll. J. Chapman and J. F. Gustafson. Associates: anemone, *Haliplanella luciae*; polychaetes, *Glycinde* sp. and *Harmothoe imbricata*; barnacle, *Balanus improvisus*; amphipods *Ampelisca milleri* and *Corophium acherusicum*.

Mode of introduction: *Grandidierella japonica* was first recorded from the benthos of the brackish waters of the Abasiri River, Hokkaido and Mokoto-numa Lake (near Abasiri) in Japan (Stephensen, 1938). Nagata (1960) found *G. japonica* in great abundance in mud substratum in a *Zostera* region throughout the brackish waters of Mihara Bay, Japan. The North American *G. japonica* is also found in estuarine environments typified by brackish water and mud substratum.

Grandidierella japonica probably arrived on the west coast through passive dispersal means. Since all life stages are found together in the benthos (indicating little or no planktonic dispersal) and this amphipod appears to be restricted to estuaries, introduction due to transoceanic drift seems unlikely. It is probable that *G. japonica* was introduced with commercial oyster (*Crassostrea gigas*) spat transplants from Japan (see Barrett, 1963). Japanese oysters were widely introduced in large numbers into bay environments on the Pacific Coast, and introductions still continue. It is probable that *G. japonica* was also introduced with the oysters.

A large number of Japanese estuarine invertebrates, judged to have been introduced similarly with commercial oyster plantings, are also now well established on the Pacific Coast. These include the flatworm, *Pseudostylochus ostreophagus* (Hyman, 1955), the gastropods, *Batillaria zonalis* and *Ocenebra japonica*, the bivalves, *Musculus senhousia* and *Tapes japonica* (as *Paphia philippinarum*) (Hanna, 1966), the endoparasitic copepod, *Mytilicola orientalis* (Odlaug, 1946), the isopod *Gnorimosphaeroma rayi* (Hoestlandt, 1969), possibly the amphipod *Corophium uenoi* (Barnard, 1952; Barnard and Reish, 1959), additionally several spionid polychaetes and the ctenostome bryozoan *Victorella pavida* (J. T. Carlton, pers. comm.).

If *Grandidierella japonica* was introduced with oyster transplants, it could have arrived in central California as early as 1928 with the first Japanese oyster spats transplanted to Tomales Bay. There are no collections dating earlier than 1966 at hand, but judging from its wide distribution in San Francisco Bay at that date, *G. japonica* was probably introduced well before that time.

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A STUDY OF *BRYOTHINUSA* (COLEOPTERA: STAPHYLINIDAE), COMPARING A TABULAR AND A DICHOTOMOUS KEY TO THE SPECIES

Ian Moore[1] and E. F. Legner[1]

Abstract: Comparison of a tabular with a dichotomous key to the species of *Bryothinusa* demonstrates advantages of the former. *B. rothi* n. sp., Mexico and *B. fluenta* n. sp., Hong Kong are described.

Tabular keys have been in use for a number of years (Newell 1951, 1953, 1957, 1959) but it was not until 1970 that their construction was described in detail. Further improvements in the structure of tabular keys followed (Newell 1972).

Tabular keys have advantages over dichotomous keys in that they are open-ended allowing for easy additions, all desired useful characters of a taxon are expressed, and missing characters do not exclude a taxon from the key. Exceptions within a taxon are easily handled without hindering the function of the key. Tabular keys are useful beyond the function of identification in that they are useful tools in revisional studies, information storage and retrieval, and in communication.

We present here for comparison a dichotomous key and a tabular key to the genus *Bryothinusa*. It is at once apparent that the information content of the tabular greatly exceeds that of the dichotomous key. In the last review of the genus (Moore, Legner, and Chan, 1973) it was necessary to append the dichotomous key by a paragraph for each species detailing characters not mentioned in the key. All of these characters are listed in the tabular key given here and are available by quick scanning.

Further details of the use of tabular keys may be obtained by reference to Newell (1970, 1972).

Bryothinusa was described by Casey (1904) on the basis of a single species, *catalinae*, from the seabeach at low tide in southern California. Casey's original description was inadequate so that when Sawada (1955) described four more species from Japan he placed them in a new genus, *Halasthenus*. Moore (1956) redescribed the genus and the genotype, *catalinae*. Sawada (1971) synonymized *Halasthenus* with *Bryothinusa*, added another Japanese species and synonymized one of his previously described species. Moore and Legner (1971) described a single species from Hong Kong and Moore, Legner, and Chan (1973) reviewed the entire genus and added three additional species from Hong Kong. All species known through 1973 were from the intertidal ocean. In this paper we add two more species, one intertidal species from the Gulf of California and a fresh water species from a stream in Hong Kong. The latter is remarkable in being the only staphylinid known to us which lives beneath the surface in fresh water.

STATEMENT OF CHARACTERS

1. Ratio of eye length to tempora length = RAT. LEN. TEMP. EYE (1.3 to 8.1)
2. Relative length of tenth antennomere = REL. LEN. 10TH ANTEN.
   longer = elongate, longer than wide.
   equal = width equals length, as long as wide.
   wider = transverse, wider than long.
3. Color of elytra = COL. ELY.
   pice = piceus.
   ferr = ferrugineus.
4. Ratio of length to width of third segment of maxillary palpus = RAT. LEN. WID. 3 M.P. (2.1 to 5.2).
5. Ratio of length to conjoint width of elytra = RAT. LEN. WID. ELY.
   wider = wider than long.
   equal = as wide as long.
   longer = longer than wide.
6. Total length of insect in mm. = TOTAL LEN. (1.48 to 2.20.).

Distribution
CAL. = California.
MEX. = Gulf of California.
H.K. = Hong Kong.
JAP. = Japan.

DICHOTOMOUS KEY TO THE SPECIES OF *Bryothinusa*

1.	Tenth antennomere longer than wide	2
	Tenth antennomere not longer than wide	5

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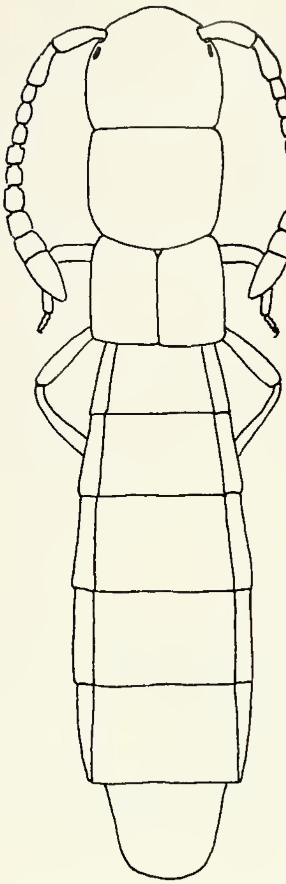

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Figure 1. Habitus of *Bryothinusa rothi*, new species.

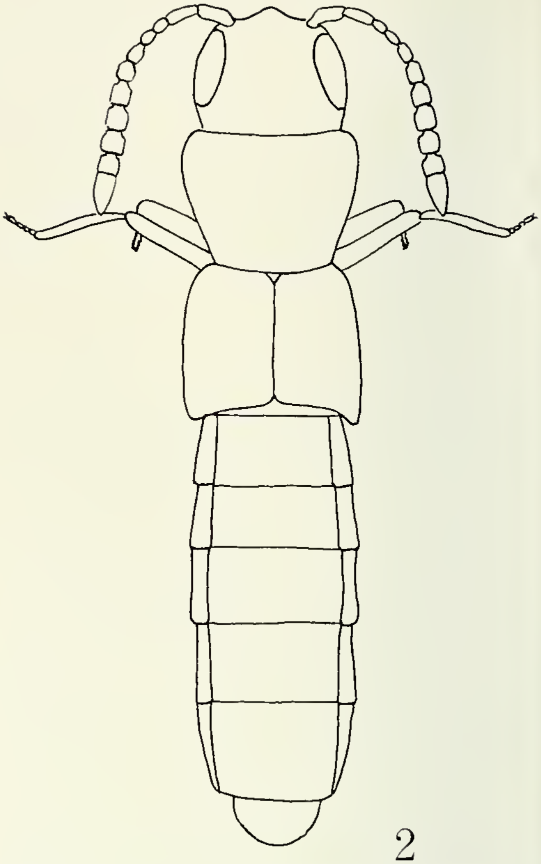

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Figure 2. Habitus of *Bryothinusa fluenta*, new species.

2. Head concave .... *catalinae* Casey
   Head convex 3
3. Tempora as long as eye ....
   .... *sawadai* Moore, Legner, and Chan
   Tempora longer than eye 4
4. Elytra shorter than pronotum; length 1.50 mm. .... *minuta* Sawada
   Elytra equal in length to pronotum; length 2.50 mm .... *algarum* Sawada
5. Tempora longer than eye 6
   Tempora shorter than eye 8
6. Tempora five times as long as eye ....
   .... *rothi* New Species
   Tempora two times as long as eye 7
7. Tenth antennomere quadrate .... *tsutsuii* Sawada
   Tenth antennomere transverse .... *nakanei* Sawada
8. Third segment of maxillary palpus not more than three times as long as wide; tenth antennomere quadrate 9
   Third segment of maxillary palpus more than three times as long as wide: tenth antennomere transverse ....
   .... *sinensis* Moore, Legner, and Chan
9. Elytra conjointly longer than wide ....
   .... *hongkongensis* Moore, Legner, and Chan
   Elytra conjointly wider than longer 10
10. Eye three times as long as tempora ....
    .... *fluenta* New Species
    Eye two times as long as tempora ....
    .... *chani* Moore and Legner

In *tsutsuii* the tenth antennomere is definitely quadrate, not elongate as stated in previous key in Moore, Legner, and Chan, 1973.

Bryothinusa rothi, new species
Figure 1

Description of holotype.—Color entirely pale ferrugineus except fourth tergite piceus, base of fifth tergite very dark ferrugineus and fourth and fifth sternites infuscate.

Head one-sixth wider than long; disc nearly flat, finely reticulate, with a fine short sparse pubescence; eyes very small, of about five or six facets; tempora about five times the length of eye, gently arcuate; surface beneath finely reticulate and pubescent as above. Antennae almost as long as head, pronotum

TABULAR KEY TO THE SPECIES OF *BRYOTHINUSA*

1 RAT. LEN. TEMP. EYE	2 REL. LEN. 10TH ANTEN.	3 COL. ELY.	4 RAT. LEN. WID. 3 M.P.	5 RAT. LEN. WID. ELY.	6 TOT. LEN. IN MM.	DISTR.	REFERENCE	NAME
5.1	Equal	ferr	3.1	wider	1.90	MEX.	Holotype	*rothi*
3.1	longer	ferr	3.1	wider	2.00	CAL.	Moore 56	*catalinae*
8.1	longer	ferr	2.1	wider	1.50	JAP.	Saw. 55, 71	*minuta*
5.1	longer	ferr	3.1	wider	2.50	JAP.	Saw. 71	*algarum*
2.1	equal	ferr	3.1	wider	2.20	JAP.	Spm.	*tsutsuii*
1.1	longer	ferr	3.1	wider	2.00	H.K.	Paratype	*sawadai*
1.3	equal	pice	3.1	wider	2.30	H.K.	Holotype	*fluenta*
1.2	equal	pice	3.1	equal	2.00	H.K.	Paratype	*chani*
1.3	wider	ferr	5.1	wider	2.20	H.K.	Paratype	*sinensis*
2.1	wider	ferr	4.1	wider	2.20	JAP.	Saw. 55, 71	*nakanei*
1.2	wider	ferr	5.2	longer	1.48	H.K.	Paratype	*honkongensis*

and elytra; first segment about three times as long as wide; second segment about as wide as first, about two times as long as wide; third segment narrower than second and a little more than half as long; fourth segment as wide as third and a little shorter; fifth through tenth segments of about equal length but very gradually wider to tenth which is quadrate; eleventh segment as wide as tenth and nearly twice as long, pointed in apical third.

Pronotum about one-fifth wider than long, widest at about apical fourth, base and apex straight, apex a little wider than base, sides gently arcuate, apical angles nearly rectangular, basal angles narrowly rounded; surface reticulation and pubescence very similar to that of head.

Elytra quadrate, slightly narrower and somewhat shorter than pronotum, one-third wider than long, humeri narrowly rounded, sides almost straight to the rectangular outer apical angles, apices nearly straight to the very narrowly rounded inner apical angles; surface reticulation and pubescence as on head.

Abdomen nearly parallel-sided although slightly wider to fifth segment, segments of about equal length; surface reticulation above and beneath much as on the head. Apices of apical tergites and sternites unmodified.

Length 1.90 mm.

Sex unknown.

Puenta Cuevas (29.48° – 112.35°), Sonora, Mexico, September 24–25, 1973, intertidal "probably from beneath rock," Vincent D. Roth and W. Brown collectors. Deposited in American Museum of Natural History, New York.

Remarks.—This species most resembles *minuta* and *algarum* from Japan with its very small eyes but differs from the above in that the tenth antennomere is quadrate rather than elongate. It is named in honor of one of its collectors, Vincent D. Roth.

Bryothinusa fluenta, new species
Figure 2

Description of holotype.—*Color* above piceus with the undersurface and femora very dark ferrugineus and the mouthparts, antennae, tibiae and tarsi paler.

Head one-fifth wider than long; disc slightly convex, strongly finely reticulate with a fine short pubescence; eyes very large, occupying three-fourths of side of head; surface sculpture and pubescence beneath much as above. Antennae a little longer than head and pronotum; first segment about three times as long as wide, second segment almost as long and as wide as first, third segment about half as long and slightly narrower than second, fourth through tenth segments each about as long as and slightly wider than the preceding, the tenth quadrate, eleventh two and one-half times as long as tenth, pointed in apical third.

Pronotum about one-third wider than long, widest at apical fifth, apex straight, apical angle almost rectangular; sides gently arcuate, converging to the broadly arcuate apical angles, base gently arcuate, about two-thirds as wide as apex. Surface reticulation and pubescence similar to that of head with the pubescence denser.

Elytra conjointly about as wide as pronotum and one-fifth longer than pronotum, humeri narrowly rounded, sides subparallel but gently arcuate to the narrowly arcuate outer apical angles, apices somewhat oblique to the obtusely rounded inner apical angles; surface reticulation and pubescence as on pronotum.

Abdomen subparallel, widest at fifth tergite, tergites of nearly equal length, reticulation and pubescence above and beneath much as on pronotum. Apices of apical tergites and sternites unmodified.

Length 2.30 mm.

Sex unknown.

New Territory, Hong Kong, fresh water stream about 500 meters from bay shore line in water of zero salinity. Tai-din Chan collector. Deposited in California Academy of Sciences, San Francisco.

Two paratypes with same data as holotype in the collection of the University of California at Riverside.

Remarks.—This species is similar to *sawadai* but has the tenth antennomere quadrate rather than elongate as in that species. The upper surface is entirely piceus whereas ferrugineus is the predominant color in most species of the genus.

The habitat of this species is unique among Staphylinidae. It presumably lives beneath the surface of a fresh water stream a short distance from the seashore. All of the other species of the genus are strictly marine and live in intertidal habitats. *Bryothinusa fluenta* seems to have invaded a fresh water habitat directly from salt water.

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THE EVOLUTION OF LIMB REDUCTION IN THE TEIID LIZARD GENUS *BACHIA*

William Presch[1]

Abstract: The reduction pattern of limbs in the teiid lizard genus *Bachia* is described and discussed. The pattern which has emerged for *Bachia* is as follows: Reduction of the limb and girdles can be correlated with the length of the limb and the terminal structures of the appendage; the reduction is greater in the hindlimbs than the forelimbs, with the complete loss of hindlimb externally. The forelimbs are greatly reduced (down to 2–3 mm in length), but are not lost externally. Comparison of the limbs of the species of *Bachia* suggests that the pattern of limb formation is a result of paedomorphic development. Comparison of the limb structure with other genera of limb-reduced or limbless forms results in the construction of two possible models: 1) the loss of hindlimbs first with reduction or loss of forelimbs and 2) loss of the forelimbs with reduction, loss or modifications of the hindlimbs. The first model may represent the stages leading to the amphisbaenians, whereas, the second model probably represents the mode of limb loss in the ancestry of snakes.

Limb reduction and loss has occurred independently in eight families of lizards. In five of these families (Anniellidae, Feylinidae, Pygopodidae, Anelytropsidae, and Dibamidae), the limbs and associated girdles are greatly reduced and may be absent. Among the Scincidae, Cordylidae, and Teiidae, several genera (e.g., *Brachymeles*, *Tetradactylus*, and *Bachia*) include members that exhibit intermediate stages of limb and girdle reduction.

The purpose of this study is to examine the evolutionary reduction trends in the limbs and girdles within the genus *Bachia*, to determine a sequence in the reduction process of the appendages and to present a model upon which a comparison with other limbless groups can be made. It is assumed that limbed forms are primitive and that the limblessness condition is a derived state. The morphoclines presented for the genus was constructed by viewing existing species.

The genus *Bachia* (subfamily Gymnophthalminae, Presch, 1970, MacLean, 1974) contains 15 described species. All the species are rather small and secretive forms with varying degrees of adaptation for a fossorial habitat. The dominant feature of this genus is the elongation of the body and the associated reduction in limb length. The gymnophthalmines can be divided into two groups on the basis of snout-vent length vs number of presacral vertebrae (Fig. 1). Two trends are clearly present: 1) as the snout-vent length increases the number of presacral vertebrae remains constant and 2) as the snout-vent length increases the number of presacral vertebrae increases. The first group includes forms with 25–27 presacral vertebrae and a well developed set of appendages, containing a complete set of osteological elements (e.g., *Leposoma*, *Ptychyglossus*, and *Pholodobolus*). The second group includes lizards which exhibit a reduction in the size and structure of the appendages both in osteological and myological elements, correlated with an increase in vertebral number.

The second group contains several genera: *Anotosaura*, *Bachia*, *Colobodactylus*, *Colobosaura*, *Gymnophthalmus*, *Heterodactylus*, *Iphisa*, *Micrablepharus*, and *Tretioscincus*. In these genera some reduction occurs in one or both sets of appendages; reduction of the inner toe and wrist elements of the forelimb (*Gymnophthalmus* and *Iphisa*), to the absence of external hind appendages and reduction of the anterior appendages to small nub-like structures (*Bachia*).

Bachia ranges from southern Costa Rica through Panama; across the northern coasts of Colombia, Venezuela, and the Guianas; south into the Amazonian basin of Brazil, Ecuador, Peru, and Bolivia. The genus is characterized by having a narrow and elongated body; countersunk lower jaw; short to nubby, and no appendages, with a varying finger formula of from 4-4 to 1-0 on the fore and hindlimbs when present. Reduction in scales, toes, and elongation of the body are adaptive modifications for the fossorial habit in which the animal is found. The group is associated with leaf-litter or debris and with sandy soils. They

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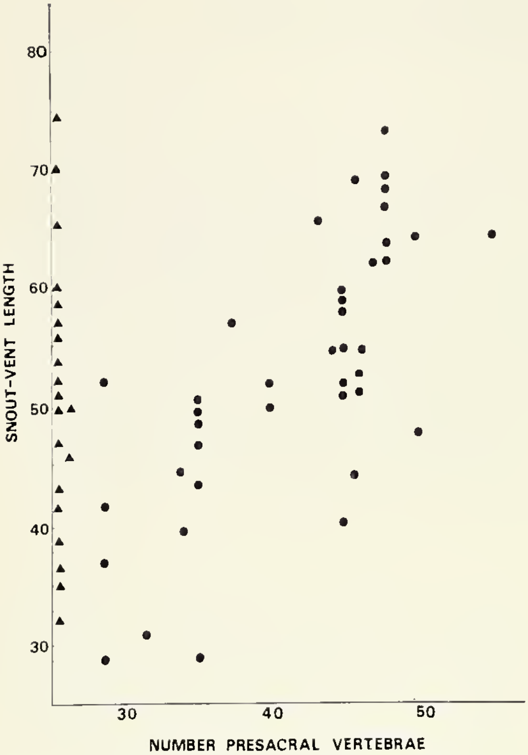

Figure 1. The number of presacral vertebrae plotted against the snout-vent length (mm) for 20 genera of microteiid lizards.

are frequently found among the root systems of large trees and grasses in compact or sandy clay.

Dixon (1973) reviewed the systematics of the genus and proposed a phylogenetic arrangement for the included species, based on the number and arrangement of the head shield, toes, and general scale patterns of the body.

METHODS

The osteological descriptions and data are based on the examination of dry skeletons and radiographs following the procedure of Presch (1969). When possible, cleared and stained material was prepared following the method of Zug and Crombie (1970). The following species of *Bachia* were examined (each species is followed by the number of specimens examined): *barbouri* (4); *bicolor* (4); *dorbignyi* (6); *flavescens* (1); *heteropa* (35); *intermedia* (2); *monodactylus* (1); *pallidiceps* (7); *panoplia* (9); *peruana* (2); *scolecoides* (1); *talpa* (3); *trisanale* (22). In addition, one specimen of *Heterodactylus imbricatus* was examined.

RESULTS

The length of the appendage, as measured from the distal tip of the appendage to the point of contact with the body wall, was plotted against the number of presacral vertebrae, and reveals the amount the appendages are reduced (Figs. 2 and 3). The number of sacral vertebrae for a particular species may vary from 0 to 2. In several species, the hindlimbs are so reduced or absent that these could not be measured. Nonmeasurable limbs were not included in the figures causing a reduction in the number of points plotted. It should be noted that the hindlimbs are reduced a greater amount than the forelimbs and that in some specimens no hindlimbs are present externally. The data suggests that the initial reduction of the forelimbs is more rapid than for the hindlimbs and reaches a stabilized point beyond which no further reduction occurs. The hindlimb reduction is initially slower but continues through a steady reduction series to an end point where no external limb is present. The average reduction rate appears greater for the hindlimbs but the maximum rate is exhibited by the forelimbs. The forelimbs are never lost externally but may be reduced to a nub-like projection of 2–3 mm length. The data imply that limb reduction reflects a definite pattern of reduction correlated with the size of the animal (as measured by the number of presacral vertebrae).

Forelimbs and Girdles.—The least reduced state of the forelimb and pectoral girdle is seen in *Bachia heteropa, panoplia, pallidiceps,* and *scolecoides.* The pectoral girdle (Figs. 4 and 5) contains all elements, but the sternum is narrow and cartilaginous. The interclavicle is a long narrow rod without lateral processes. The clavicles are ossified, do not enclose a fenestra and lack posterior hooks. The scapulocoracoid is ossified but the scapular foramen is absent. Two sternal ribs articulate with the sternum and a well developed post-xiphisternum is present. The pectoral girdle is less reduced than the pelvic girdle, retaining the clavicles and interclavicle but showing reduction in overall size and amount of ossification rather than in number of elements.

The forelimb consists of a humerus, ulna and reduced radius, two carpal elements and four metacarpal elements articulating with four sets of well developed phalanges (Fig. 6A). A fifth and single phalangeal element is present but is greatly reduced and does not protrude through the skin. This description is compatible with other saurian forelimbs, but *Bachia* exhibits an overall minia-

Figure 2. The number of presacral vertebrae plotted against the length of the forelimb (mm) for 13 species of *Bachia.*

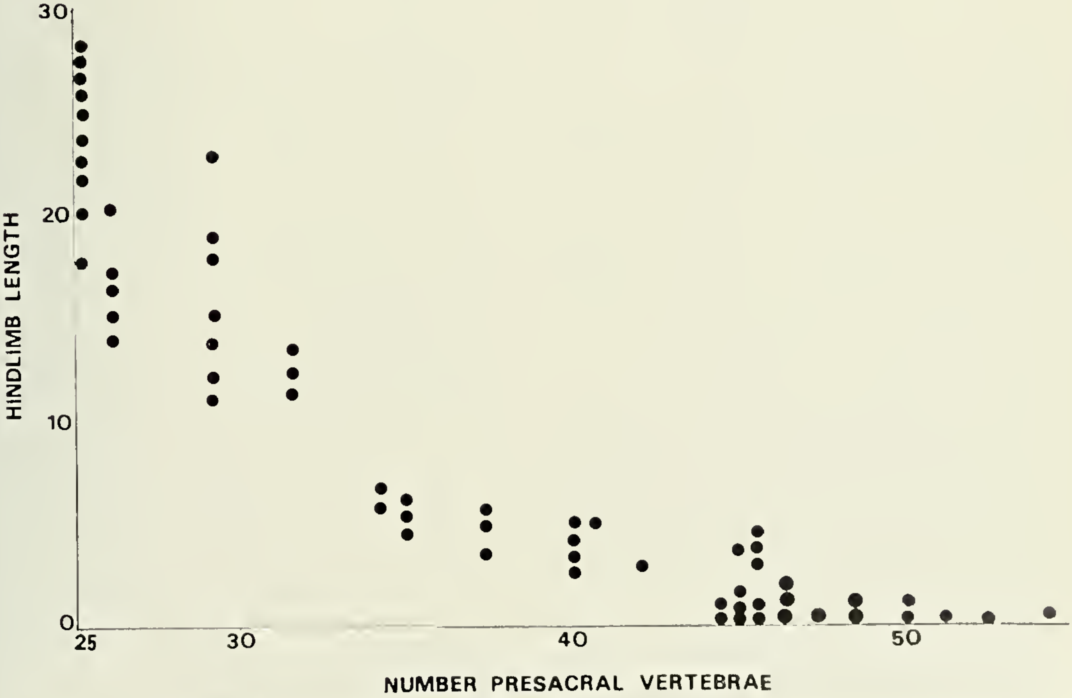

Figure 3. The number of presacral vertebrae plotted against the length of the hindlimb (mm) for 13 species of *Bachia.*

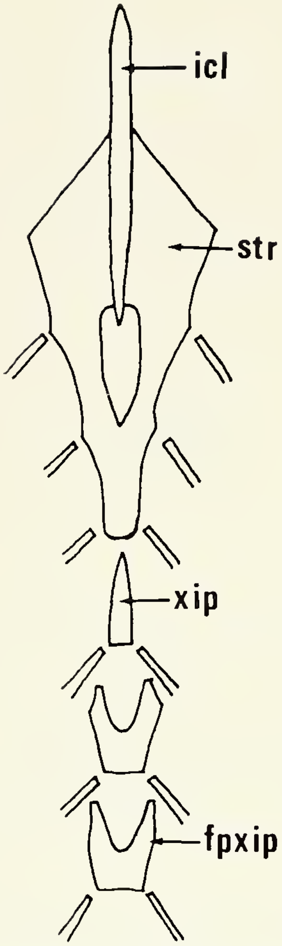

Figure 4. Ventral view of the interclavicle (icl), sternum (str), xiphisternum (xip) and fragmented postxiphisternum (fpxip) of the genus *Bachia.*

turization of the elements. Length and width of the individual elements are greatly reduced over the condition exhibited by closely related genera (e.g., *Heterodactylus*, *Colobosaura*, and *Colobodactylus*).

Bachia dorbignyi has reduced the metacarpals and wrist elements to 2 or 3 with the loss of the fifth phalange. *Bachia intermedia*, and *peruana* exhibit reduction to three sets of phalange elements externally, but *B. intermedia* retains the fourth phalangeal element subcutaneously. Only two carpal elements are present. *Bachia bicolor*, *barbouri*, and *trisanale* exhibit reduction and loss of phalanges, the carpal elements articulating distally with one or two elongated metacarpals. *Bachia monodactylus* retains a greatly reduced humerus, ulna-radial complex, one or two carpal elements, and four metacarpal elements.

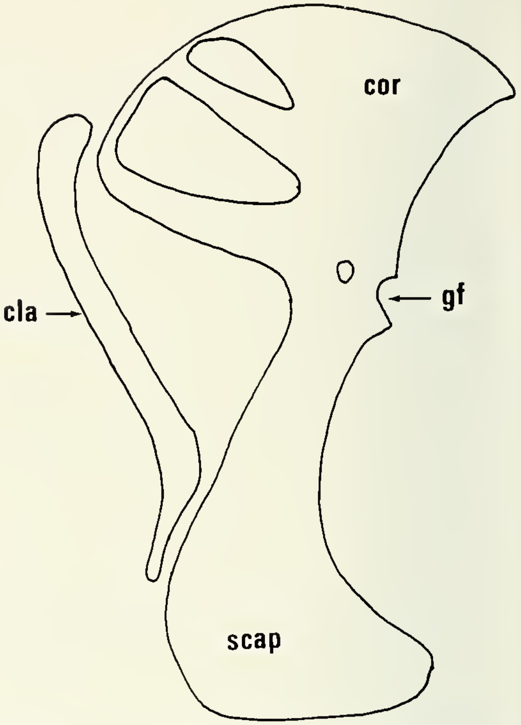

Figure 5. Lateral view of the pectoral elements of the genus *Bachia* (cla-clavicle; scap-scapula; cor-coracoid; gf-glenoid fossa).

Hindlimb and Girdle.—The hindlimb in the least reduced state consists of a femur, tibia, a very slender fibula, two ankle elements, and several fused metatarsals which articulate with three or four sets of phalangeal elements (Fig. 7A). The number of external toes exhibited is highly variable in *Bachia heteropa.* Depending on the subspecies (Dixon, 1973), there may be 4, 3 or 2 toes visible externally. Internally, beneath the skin, four phalanges are present but may show reduction in size corresponding to the external condition. This difference in number of toes on the external hindlimb appears to be correlated with the occurrence of species in drier, sandy soil types.

The hindlimb is reduced in *Bachia dorbignyi* to three elements, arranged in linear fashion from the pelvic girdle distally. The elements are a femur, tibia-fibula and a single carpal element. The lack of metacarpals and phalanges is not surprising as these elements are reduced and lost very early in the forelimb. A similar condition is exhibited in the genus *Tetradactylus* and *Chamaesaura* (Family Cordylidae).

Bachia bicolor, *B. intermedia*, *B. monodactylus*, and *B. peruana* have smaller distal elements (fused

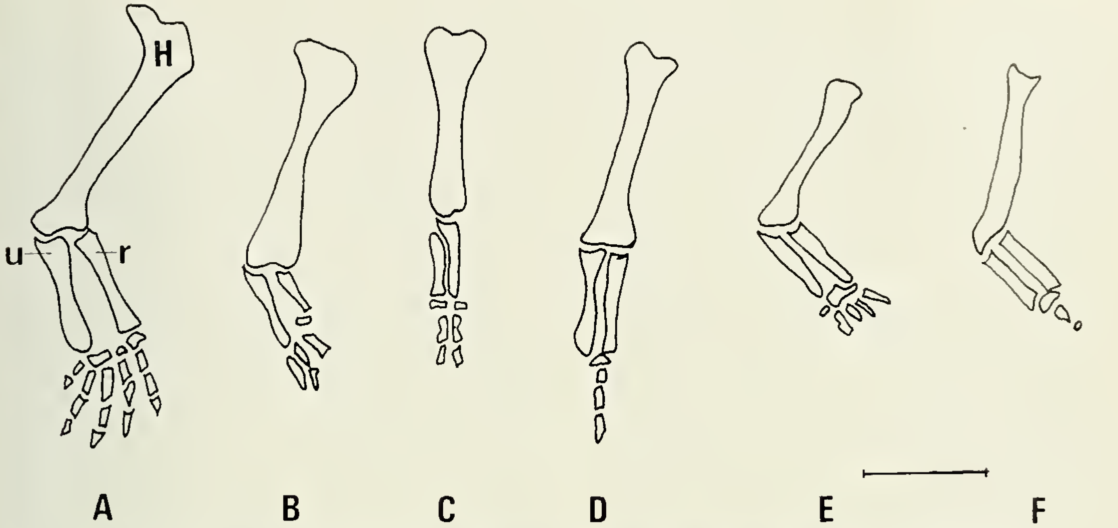

Figure 6. Diagrammatic view of the forelimb (H) humerus, ulna, radius, of six species of *Bachia*: A, *heteropa*; B, *dorbignyi*; C, *barbouri*; D, *bicolor*; E, *monodactylus*; F, *trisanale*: line equals 1 mm.

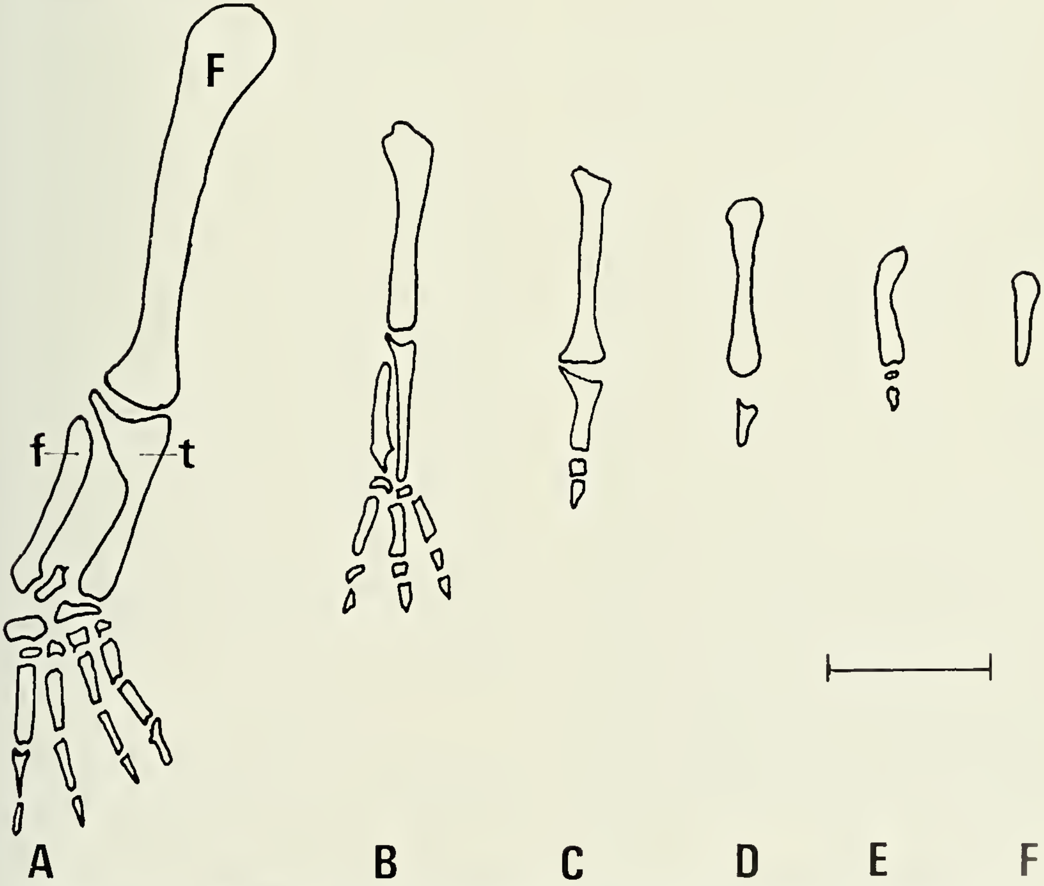

Figure 7. Diagrammatic view of the hindlimb (F) femur, (f) fibula, (t) tibula, of six species of *Bachia*: A, *heteropa*; B, *pallidiceps*; C, *dorbignyi*; D, *intermedia*; E, *monodactylus*; F, *trisanale*; line equals 1 mm.

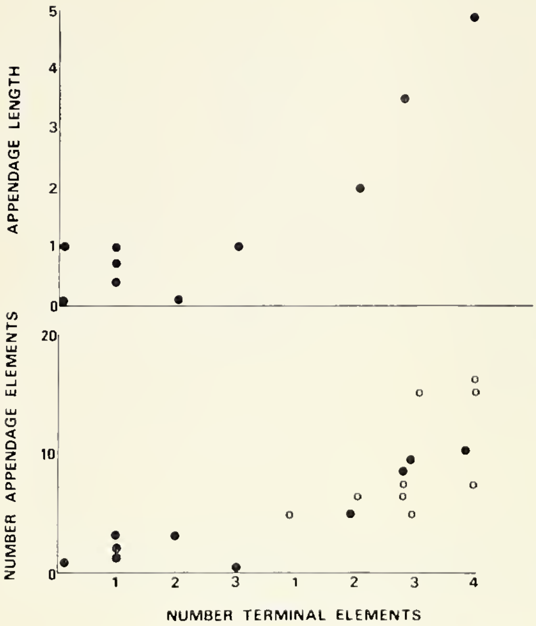

Figure 8. Number of appendage elements and appendage length plotted against the number of external terminal elements (scales or phalanges) for eight species of *Bachia*. Open circles represent forelimbs; closed circles, hindlimbs. See text for explanation.

tibia and fibula and tarsal elements) with loss of the tarsal elements in *bicolor* and *peruana. Bachia trisanale* has a femoral and tibia-fibula element while *bicolor* has no hindlimb element or only a very short femoral element (based on its position).

The pelvic girdle articulates with two sacral vertebrae and consists of an ilium oriented ventroanteriorly, a posteroventrally projecting ischium and an anteroventral projecting pubis. Unlike the pectoral girdle, the pelvic girdle is much reduced including the reduction and/or loss of the ischium and pubis (*B. trisanale*) as well as reduction in the sacral diapophysis and finally, complete loss of both sacral diapophyses (*B. monodactylus*). In all specimens examined, a single, dorsally positioned, anteroventrally oriented element was present, which I believe to be the ilium. The interpretation of this element as an ilium is supported by work on other limbless forms and by some embryological evidence (Cope, 1892a; Essex, 1927; Stokely, 1947).

A correlation between a reduction in number of skeletal elements and the shortening of the appendage is indicated in figure 8. In both cases, as the number of distal external structures (i.e., toes or terminal scales on a single blunt appendage) or number of internal skeletal elements are reduced, the total length of the appendage is reduced. This may seem obvious at first but it is not necessarily the case as reduction in the tarsal elements and phalanges in the genus *Teius* does not result in the shortening of the limb, (Presch, 1970). The expression of these data in a linear form (Figs. 2 and 3) suggests that the pattern of reduction follows a particular sequence.

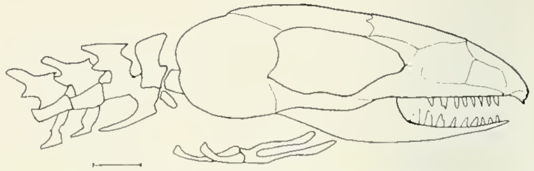

Figure 9. Lateral view of the skull and four cervical vertebrae of *Bachia trisanale*; line equals 1 mm.

The pattern of reduction in the number of osteological elements in an appendage suggests that reduction and loss of elements begins at the distal end of the appendage and progresses proximally. The variation in the number of carpals, metacarpals, tarsals, and metatarsals present, suggests the lack of a step by step reduction pattern at an element by element level. However, the orderly reduction of the phalanges first, followed or accompanied by reduction of the metacarpals, metatarsals, and tarsals, carpals, distal long bones with later reduction of the more proximal long bones suggests a pattern of reduction with respect to the major divisions of the appendage (Romer, 1956). Nelsen (1953) presented the sequence of internal limb bone formation for vertebrates. The data presented here indicates that arrested development of the normal bone formation sequence is occurring, suggesting that developmental stages of limb formation are missing and that the limb develops only to that point of the developmental stage exhibited by the adult, that is, reduction is the result of arrested embryonic development (paedomorphic development as defined by Wake, 1966).

DISCUSSION

The problems of saurian osteology and particularly reduction in the limbs and girdles has been investigated by many workers (Cuvier, 1825; Gegenbaur, 1864, 1865; Fürbringer, 1870, 1900; Cope, 1892a, 1892b; Siebenrock, 1895; and more recently by Krieg, 1919; Larsell, 1926; Underwood, 1957; Gasc, 1967, 1968; and Stokely, 1947a, 1947b). Series of lizards exhibiting reduction in limbs have been investigated by Essex (1927), Mosauer (1932), and Sewertzoff (1931). Cope (1892a) and Fürbringer (1870) agreed that the reduction of limbs began at the digits and progressed proximally. Siebenrock (1895) offered additional support, but Krieg (1919) suggested that the reduction of limbs and girdles and the sternal apparatus were two independent processes with no bearing on one another. Sewertzoff (1931) examined the problem from an embryological perspective and concluded that the organ undergoing reduction is first miniaturized and then a subtraction of the end-stages of ontogeny occurs. He suggested that the sequence of reduction corresponded inversely to the sequence of formation of the normal adult structure in unrelated forms. I cannot be certain as to the exact mode of limb reduction in *Bachia*, as I have not examined embroyological material. However, I disagree with Krieg's (1919) view that the sternal reduction and limb reduction are independent; at least in all cases. They are interrelated in *Bachia* as shown by the data presented above.

The pattern that has emerged for *Bachia* is as follows: Reduction of the limb and girdles can be correlated with the length of the limb and the terminal structures of the appendage; the rate of reduction is greater in the hindlimbs than the forelimbs, with the complete loss of hindlimb externally. The forelimbs are greatly reduced (down to 2–3 mm in length) but are not lost externally. The reduction of the skeletal elements agrees with the findings of Cope (1892a), and Fürbringer (1870) for other reduced limb forms; the reduction begins distally and progresses proximally, and with Sewertzoff (1931) who noted that the reduction appears to be inversely related to normal ontogenetic development.

The reduction in size and number of limbs in *Bachia* correlates with the evolution of the group towards a fossorial habitat. Accompanying the loss of limbs and elongation of the body are the countersunk lower jaw; modification of the atlas-axis and anterior cervical vertebrae (Fig. 9); the wedge-shaped appearance of the skull (in lateral view) with the widest portion of the entire body just posterior to the head; the smooth head plates, the smooth or imbricate body scales (Dixon, 1973) with no scutes or annuli.

The variation of hindlimb structure in the subspecies of *Bachia heteropa* suggests that this species is in the process of limb reduction. Dixon (1973) pointed out the change in and correlation of size reduction and loss of prefrontal scales and hindlimb toe reduction extending in an eastern direction from Trinidad to La Luz, Barinas, Venezuela. There is also a trend from wet to dry habitats along this same transect. The subspecies of *B. heteropa* may eventually be recognized as species, depending on their continued restriction and separation.

The *Bachia* with greatly reduced appendages move by lateral undulation of the body starting at the head and passing posteriorly. This method, described as serpentine by Gans (1962), is similar to that seen in many other forms (*Anniella* and *Ophisaurus*) (Miller, 1944). The anterior limbs, though small in *Bachia*, may be used as a structural support to provide a purchase against the substrate during the initial movement in locomotion perhaps in the way the annuli of amphisbaenians are used (Gans, 1968, 1969).

In the genus *Bachia* the posterior limbs are reduced more than the anterior limbs with eventual complete absence of posterior limbs in *B. bicolor* and *trisanale*. Body elongation is correlated with limb reduction and increased flexibility. This same pattern of limb reduction is implied in the amphisbaenians. The genus *Bipes* retains forelimbs which are well developed and are used to pull the body along the surface of the substrate. Hindlimbs are absent. However, the three species of *Bipes* exhibit reduction in the number of forelimb toes, from 4 to 3 to 2 with accompanying reduction in the carpal elements. All limbs and most girdle elements are absent in all other amphisbaenians.

Among the scincids, *Brachymelas*, *Ophiomorus*, and *Rhodona* exhibit varying degrees of limb reduction but a second pattern is seen. Hindlimb reduction is less extensive than the forelimb reduction and there may be complete loss of forelimb. A similar pattern is seen in *Tetradactylus* and *Chamaesaura* (Cordylidae) with *Chamaesaura macrolepis* retaining small hindlimbs (16 mm long) with anterior limbs absent, externally.

Among the anguids, *Anguis* and *Ophisaurus* lack external limbs, but remnants of the pelvic girdle are present. *Anniella* (Anniellidae) shows a similar pattern with a single pelvic bone element, the ilium present (Cope, 1892a); and cartilaginous clavicles in the pectoral region (Camp, 1923).

The pygopodids and the dibamids retain large flap-like hind appendages (no forelimb present) which apparently serve no function in locomotion (Gasc, 1968) but may be used during courtship and mating (Steve Arnold. Univ. Chicago, pers. comm.).

Two structural patterns of limb reduction emerge. The first pattern represented by teiids (*Bachia*) and amphisbaenians and some scincids (e.g., *Lygosoma lentiginosus* and *verreauxi*) includes reduction and or loss of hindlimbs with accompanying reduction but generally only partial loss of the forelimbs. The second and more general pattern of reduction and loss of the forelimbs with corresponding reduction or possible loss of the hindlimbs appears in the pygopodids, dibamids, cordylids, some scincids (*Ophimorous* and *Brachymelus*), *Ophisaurus*, and *Anniella*. The latter group contains forms in both the fossorial (*Anguis*, *Brachymeles*, *Chamaesaura*, etc.) as well as the grass-swimming habitats (*Lialis* and *Pygopus*) (Camp, 1923). The former group contains only fossorial and subterranean forms (*Bachia* and amphisbaenians).

The remnants of a pelvic girdle have been reported in some of the primitive snakes (Infraorder. Scolecophidia and Henophidia: Underwood, 1967). Perhaps it is not unrealistic to suggest that the ancestor of snakes might be found among the limb reduced lizard groups which exhibit the second major limb reduction pattern; loss of forelimb with reduction of hindlimbs.

A second suggestion concerns the relationship of the Amphisbaenia to the lizard groups. The reduction and loss of limbs in the families Bipedidae and Trogonophidae (Gans, 1960) appear to follow the first of the major patterns described above, sharing this pattern with the teiid genus *Bachia*. Closer examination of hindlimb reduced forms may help in determining possible relationship of the Amphisbaenia to lizard groups.

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POPULATION DYNAMICS OF THE KIT FOX IN WESTERN UTAH

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Abstract: The dynamics of a kit fox, *Vulpes macrotis nevadensis*, population in western Utah was studied for four years coincidental with a population decline and initial recovery stages of the black-tailed jackrabbit, *Lepus californicus deserticola*. The study began at least one year after the rabbits began decreasing. The presence of nonbreeding adult vixens seemingly represented the initial response of the foxes to a failing food supply. This was followed by a decline in the numbers of adults and then by smaller and fewer litters. The first sign of recovery was a return to normal sized litters. Data on natality, sex ratios, age structure, and population turnover are presented. Foxes were apparently unable to sustain themselves on available secondary prey such as kangaroo rats and appeared incapable of making adjustments in their hunting habits that enabled them to take advantage of diurnal prey.

From 1952 to 1970, part of my time was devoted to field studies on the kit fox, *Vulpes macrotis nevadensis* Goldman, in western Utah. Early phases of the work dealt with methodology, life history, ecology, and ectoparasites (Egoscue, 1956, 1962, 1966). The last four and one half years were spent gathering data on the age structure, rate of attrition, fluctuations in numbers, and productivity of a relatively undisturbed fox population faced with a decline in its principal prey. Eighty-seven foxes were captured 323 times in 8541 trapnights.

METHODS

Methods and equipment employed to live-trap and tag foxes, and the biological data recorded for each animal remained unchanged from earlier studies (Egoscue, 1962). The size of the study area was enlarged from 25 to 40 square miles (10,360.1 ha), but the new boundaries contained over 90 percent of the original area and all but three den sites. The physiography, plants, animals, and climate of the area were described previously (Egoscue, 1962). I increased the number of traps from 6 to 18 and made more sets at non-den locations but continued the policy of only trapping about one fourth of the area at a time. Past experience showed that the sparse vegetation was soon destroyed and foxes were unduly disturbed by the continuous presence of traps visited daily by people in vehicles. These factors together with lack of time and the size of the area precluded use of a grid system.

The 92 den sites discovered were marked with numbered stakes and their locations plotted on a map of the largest scale available (U.S. Geological Survey Topographic Maps, 7.5 minute series). No more than eight to ten sites were occupied at any one time. Most vacant dens were in various stages of disrepair, and some remained unoccupied by foxes during the time covered by this report.

At the end of each year, adults were classified as follows: (1) resident breeders, if they whelped in the area; (2) resident nonbreeders, if they denned within the boundaries but did not breed; (3) nonresidents, if they regularly ranged into the area but denned elsewhere; (4) transients, if they were captured once and never caught again. The transient category was a potential source of error because intervals of up to 12 months elapsed between recaptures of the warier residents.

All vixens caught between February and September were examined for evidence of pregnancy or nursing. The distinctively colored fur around the nipples of lactating females facilitated recognition of these animals and left no room for error. This discoloration persisted until vixens began acquiring winter pelage in late summer.

Although kit foxes were easily live-trapped (certain trap-prone adults were retrapped 18 to 32 times), the annual censuses sometimes included untagged or tagged foxes or both that were seen but not caught and foxes whose presence was known only from tracks or other evidence. Once trapped certain foxes became difficult to recapture. One year an entire family went undetected until early August when the pups were captured; their parents were never identified.

Annual changes in rabbit numbers were monitored by 119 one-mile permanent transects se-

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lected to give geographic coverage in over 3000 square miles of black-tailed jackrabbit habitat in western Utah. A survey team of a driver and two observers ran each transect by vehicle in March, when overwintering adults reached their lowest numbers (but could be readily distinguished from young of the year), and in August when rabbit populations usually "peaked" in the area. Five of the transects were located in the kit fox study area. The transects were run between 10:00 a.m. and 4:00 p.m. during sunny weather with little or no wind. In addition to rabbits sighted, the time of day, and type and quality of habitat was recorded.

The admittedly crude index calculated from these data compared closely with results obtained during the same years in northwestern Utah and southwestern Idaho (Wagner and Stoddart, 1972) using more sophisticated census techniques.

RESULTS AND DISCUSSION

Annual Inventories: The 1966 total of 22 foxes included two tagged resident breeding females that were seen at their natal dens but never caught, and one pair known only from tracks. Three pairs and one polygamous trio produced pups; a fourth pair probably whelped in the southwest quarter of the study area, but I was unable to locate their den. My suspicions were partly confirmed by the discovery of an unmarked den site there early in in 1967 that appeared to have been used as a whelping den the previous year. Three of the four resident nonbreeders were vixens, the first such animals found in 14 years. The significance and possible explanation for this failure to breed was not recognized immediately. One adult nonbreeding female, one female pup, and one male pup were killed on the roads. No other mortality was in evidence.

Five pairs of resident breeders were found in 1967 and there was no reason to believe that any were overlooked. The seven nonbreeding residents made up one-third of the total population and included three vixens all of which were examined one or more times during the whelping season for evidence of lactation. I was unable to establish even a casual pair-bond relationship between nonbreeders. Occupancy of a den site by two or more adult animals, even when established by sight records alone, was *prima facie* evidence that pair-bonds existed. Unpaired adult foxes, especially males, never denned together; groups of twos and threes, once captured, almost invariably contained one male and one or more females. Two adults, one of each sex, were killed by vehicles.

Foxes continued to decline in 1968. Four breeding pairs were found; one of the males was not caught. Resident nonbreeders (one male and two females) accounted for 18 percent of the total population, a decrease of about half from 1967. The male apparently did not den with either of the nonbreeding vixens. There were three transients. No mortality was recorded.

In 1969, the total population dropped to a four-year low; only two breeding pairs were found and for the first time breeding residents were slightly outnumbered by nonbreeders. One breeding male was not caught. Three of the five resident nonbreeders and the only nonresident were vixens. No transients were identified, and no mortality was discovered.

In summary, the population density for adults on the 10,359.9 ha ranged from one fox per 470.9 ha in 1966 to one fox per 1035.9 ha in 1969. Excluding transients, the figures become one fox per 542.9 ha to one fox per 1035.9 ha. Hectares per breeding unit varied from 2071.9 in 1966 to 5179.8 in 1969. Unfortunately population densities recorded in this study are not strictly comparable with those obtained previously (Egoscue, 1962). The proportions of denning to nondenning habitat and suitable to nonsuitable rabbit habitat were changed by increasing the size of the area.

Natality: Six litters of puppies were born on the area in 1966, five in 1967, four in 1968 and by 1969 the number declined to an all-time low of two. For the first three years, the average litter size followed the same pattern and varied from 5.0 (range 4–6) in 1966, 3.0 (range 2–4) for 1967, and 2.75(range 2–4) for 1968. But in 1969 the average litter size increased to 5.0, the same as for 1966. This seemed to represent the initial sign that a population recovery was in progress. The litters of two found in 1967 and 1968 were the first time this litter size was recorded in 15 years.

Sex Ratios: The adult sex ratios derived from trapping results and observations of tagged foxes showed males made up 46 percent of the population in 1966; 62 percent in 1967; 56 percent in 1968; and 50 percent in 1969. About 78 percent of the transients during those four years were males.

Male puppies accounted for 57 percent of those captured in 1966; 53 percent in 1967; 67 percent in 1968; and 27 percent in 1969. Thirty puppies tagged in the mid 1950's at a time of near popula-

TABLE 1. Average ages of the total adult kit fox populations compared to the average ages of the breeding populations.

Year	Average age in years		Percentage of New Foxes in Total Population
	Total Population	Breeding Population	
1966	1.8+	1.6+	50
1967	2.0+	2.3+	42.1
1968	2.0+	2.5+	50
1969	2.2+	3.3+	33.3

TABLE 2. The average ages of breeding kit foxes compared according to sex.

Year	Ages of males (years)	Ages of females (years)
1966	1.25	1.9
1967	2.0	2.6
1968	2.0	3.0
1969*	4.0	3.0

* Only three breeders (one male and two females) identified.

tion stability were 64 percent males (Egoscue, 1962). Most puppies are easily captured, and we caught every pup in about 95 percent of the litters, so there is little reason to believe the data does not represent the puppy sex ratio. The evidence does suggest a positive correlation between kit fox puppy sex ratios and adult population density relative to its food supply. A preponderance of male pups seemingly characterize overcrowded populations or those that have reached the maximum carrying capacity of an area when food is sufficient. A reversal in favor of females such as occurred in 1969 would presumably speed population recovery.

Age Structure of Adults: Lacking reliable methods for aging live adults, I placed each year's newly tagged animals in the 1+ age class. None, however, was obviously aged or a pup of the year, and I concluded that few, if any, new or transient adults were less than one or more than five years old. Most were probably two to three years old.

There were five known age classes in the 1966 population and four age classes in the other three years. The average ages of the four adult populations ranged from 1.8+ to 2.2+ years with a mean average of 1.96+. This statistic remained remarkably constant. As might be expected, the population with the oldest average age contained the fewest newly tagged foxes.

The average maximum age attained was 5+ years (range 4+ to 6+); each population usually had one fox in its oldest age class. New foxes made up one-third to one-half of each population (average 43.1 percent) and the 1+ age class was the largest class every year except 1969. The oldest fox was 6+ year old male, the only obviously aged animal examined. He was tagged as an adult in 1961; when last trapped in 1966, he was feeble, his teeth were worn and broken, and he was at least seven years old.

Data comparing the ages of breeding foxes with the age of the total adult population are listed according to year in table 1. Breeders averaged older than the total population each year except 1966.

During the four years, the mean age of the breeding population increased by 1.7+ years while the average age of the total population increased .4+ year. The average age of the foxes caught early in 1970, when the study ended, was 1.8+ years compared with the all time high of 2.2+ recorded the previous year when a population low occurred.

The maximum age achieved by known-age breeders was 4+ years with only five of 30 (16⅔ percent) in this class. None of the 5+ or 6+ year olds were known to breed.

An interesting sex related age differential implying either a social structure under matriarchal control or a sex-specific mortality rate favorable to breeding females is illustrated by data in table 2. Females of breeding pairs averaged older than their mates from 1966 through 1968. It is also possible that females do not reach breeding age until one year later than males. Not enough known-age breeders were present in 1969 to determine if the trend continued, but two of the three foxes caught were in the 4+ class and one of these was a female.

Population Turnover: I do not know if the rate of attrition was a function of population density. A baseline for this parameter was not determined for a fox population at or near its maximum numbers. Continued "highs" in rabbit numbers combined with minimal decimating factors result in a maximum density of about 1.8–2.0 adult foxes per 258.9 ha in the optimum habitat described in my previous paper (Egoscue, 1962). Such a population had no known nonbreeding females; one to three polygamous units per 6474.9 ha; 100 percent immigration each year of the pups that survived; 100 percent recruitment for adult vacancies from adult emigrants, and a minimum of 3.2 km separating natal dens.

TABLE 3. A five year summary of the age structure, cohort size and rate of attrition for the resident adult kit fox population on a 40 square mile study area in Tooele Co, Utah. These figures include only those foxes actually captured.

Year foxes originally tagged	1966		1967		1968		1969		1970	
	No. of adults	Minimum age in years	No. of adults	Minimum age in years	No. of adults	Minimum age in years	No. of adults	Minimum age in years	No. of adults	Minimum age in years
1961	1	6+	—	—	—	—	—	—	—	—
1962	—	—	—	—	—	—	—	—	—	—
1963	1	4+	1	5+	—	—	—	—	—	—
1964	1	3	—	—	—	—	—	—	—	—
1965	5	2+	5	3+	2	4+	1	5+	—	—
1966	8	1+	5	2+	4	3+	1	4+	1	5+
1967	—	—	8	1+	2	2+	—	—	1	4+
1968	—	—	—	—	8	1+	4	2+	3	3+
1969	—	—	—	—	—	—	3	1+	4	2+
1970	—	—	—	—	—	—	—	—	6	1+
Total	16		19		16		9		15	
Avg. age (years)		1.8+		2.0+		2.0+		2.2+		1.8+

The 1966 population density was 1.7 adult foxes per 258.9 ha. There was one polygamous unit but 3 nonbreeding vixens present and the adults identified included one born and tagged in 1964 when it was a pup. From this I concluded the 1966 fox population was in an early stage of decline that was lagging behind a rabbit decline that was already in progress.

The annual rate of attrition for each cohort is apparent from the figures in table 3. For example, of eight foxes in the 1+ class of 1966, five were still present in 1967, four in 1968, and only one by 1969; the same fox was part of the 1970 population, but 87.5 percent of the new foxes caught in 1966 were gone by the end of 1969. Only two of eight foxes in the 1967 1+ cohort were in the 2+ class of 1968 representing an annual loss of 75 percent in one year. All five adults in the 2+ cohort of 1966 were still present to make up the entire 3+ group for 1967, a survival rate of 100 percent.

Of special interest was the number of 1+ animals that bred the same year they were first tagged. In 1966, three of the five males and one of three females (50 percent of the breeders) were in the 1+ cohort. But only one of each sex out of a total of 8 in this class bred in 1967 and 1968.

Puppy dispersal in late summer resulted in the complete disappearance of this class when the study area was fully occupied by a stable population. Young of the year probably lacked the capability to compete with adults for space and were forced out. Coincidental with this exodus was our failure to detect an influx into the study area of similarly displaced young from surrounding areas. Either transient pups are not susceptible to the trapping method or they do not linger in or avoid areas occupied by resident adults. When adult numbers were low during 1968 and 1969, 3 of the 21 puppies born on the area stayed and became part of the adult population.

Food Supply: Population dynamics of several canines, especially those with specialized diets or a narrow prey base, are often regulated by fluctuations in the primary prey species. Among these are the arctic fox, *Alopex lagopus* (Macpherson, 1969); and red fox, *Vulpes vulpes*, in northern Sweden (Englund, 1970); coyote, *Canis latrans* in northwestern Utah (Wagner and Stoddart, 1972; Clair, 1972); and others.

Although based largely on circumstantial evidence, the dependency of *V. macrotis* on kangaroo rats has long been accepted as axiomatic. Their similar ecological parameters, the presence of one or more species of *Dipodomys* wherever kit foxes are found, and the small size of *V. macrotis* seemingly supported this belief (Grinnell *et al.*, 1937; Baily, 1931; and others). Recent studies verified the kangaroo rat as the main prey base (80 to 90 percent) of *V. m. mutica* in parts of California (Laughrin, 1970). The foxes there also subsisted on *Lepus californicus*, but Laughrin did not compare prey availability with predation rate.

TABLE 4. Kit fox numbers and productivity (1966–1969) compared with black-tailed jackrabbit indices for 1964–1969.

Year	*Rabbit Index	Total foxes	No. breeding foxes	No. nonbreeding females	No. litters	No. pups	Avg. litter size
1964	1.7	—	—	—	—	—	—
1965	1.2	—	—	—	—	—	—
1966	0.9	22	11	3	6	30	5.0
1967	0.7	21	10	3	5	15	3.0
1968	1.1	17	8	2	4	11	2.75
1969	2.3	10	4	3	2	10	5.0

* Average number of rabbits counted per mile on 119 transects.

Black-tailed jackrabbits made up over 90 percent of the food eaten over a 64 day period in late spring by a family of *V. m. nevadensis* (Egoscue, 1962). Other evidence collected during the years convinced me that kit foxes in western Utah depend primarily on lagomorphs and secondarily on nocturnal rodents and terrestrial birds. Because rabbits of this area are subject to fluctuations in numbers (Woodbury, 1955; Wagner and Stoddart, 1972), foxes must be able to subsist on secondary resources or suffer regulatory effects imposed by food shortages.

When I began my fox population study in late 1965, *L. californicus* numbers had been declining over a wide area for at least one year and probably longer. This trend continued until 1967. The rabbits began to recoup in 1968 and were still increasing at the end of 1969.

Data presented in table 4 compare the rabbit indices obtained from transects with fox numbers and productivity for the years 1966–1969. Lacking evidence to support other hypotheses, the apparent effects of a decreasing and increasing rabbit population on the numbers and fecundity of the foxes seems unmistakable and follows the classic pattern. A similar correlation between rabbit and coyote populations occurred at the same time in northwestern Utah (Wagner and Stoddart, 1972). The implied nutritional link between food shortages and the reproductive responses of kit foxes was not evidenced by changes in weight or other obvious external symptoms such as poor fur texture. As suggested by Clark (1972) for coyotes, the influence may be more tenuous and may possibly involve a temporary breakdown of hormone controlled mechanisms that reinforce pair bonding. Kit foxes either lacked the capacity to switch to secondary prey species or the secondary prey was insufficient to make up the deficit. The home ranges of many foxes on the study area did not include or contact what little optimum kangaroo rat habitat there was, and fox dens were not concentrated near dunes supporting the highest number of *Dipodomys* and other nocturnal rodents. As rabbits became fewer, foxes did not shift their home ranges or den locations to areas where secondary prey was more plentiful. Scott and Klimstra (1955) imply that red foxes starved in the face of a food shortage rather than desert their families or change territories. Kit foxes also seemed unable to capitalize on another change that could have compensated for the decline in lagomorphs. About 1965, after being very rare for almost 30 years, the Townsend ground squirrel, *Spermophilus townsendii*, populations virtually exploded over vast sections of the Bonneville Basin. What previously had been the rarest small mammal on the kit fox study area (none to five recorded per year) suddenly became one of the most common, particularly in the greasewood-shadscale communities where most of the fox dens were found. Some occupied dens were surrounded by squirrel colonies. Previous fluctuations in rabbit numbers were not synchronized with dectectable changes in squirrel populations. Of greater significance was the apparent inability of the nocturnal predator to readjust its hunting habits. As far as the kit foxes were concerned the squirrels were about as rare as they were in 1935. Townsend ground squirrel remains were picked up at a fox den the first time in 1967. It and the scarcer antelope ground squirrel, *Ammospermophilus leucurus*, made up less than one percent of the food represented by remains at dens from 1966–1970.

Kit foxes are efficient, superbly adapted predators but the time and energy they have for hunting is limited, and adults with growing families must be increasingly successful. The whelping season when foxes make the greatest demands on their food supply coincides with the breeding season and annual peaks of abundance of rabbits and many species of rodents in western Utah. If a fox requires as much time to stalk and capture one 50 gram rodent as it does a 2000 gram rabbit, then the differential in energy balances is obvious, especially when rabbits are scarce.

Perhaps an evolved propensity for prey selection or a learned tradition based on prey brought in by the parents combined with early hunting experience in the company of adults leaves kit foxes of western Utah vulnerable to cyclic changes in black-tailed jackrabbits. Except for the usual reports of seasonal population fluctuations, I know of no studies showing that kangaroo rats are cyclic. Predators dependent upon them would not be so affected.

The data suggests that the maximum carrying capacity of the area for foxes is primarily related to their territorial requirements. Continued increases in the number of rabbits beyond what was needed to support a maximum fox population apparently does not result in further increases in foxes.

The level of predation from associated predators and raptores and its regulatory effects on fox numbers is unknown. Badgers increased after the Townsend ground squirrels became numerous, but I do not believe any foxes were displaced by badgers.

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Most of the staff of Ecology and Epizoology Research, University of Utah, Salt Lake City, contributed to the success of this project. Special thanks are due my two associates, J. G. Bittmenn and J. A. Petrovich for assistance with the field work. The rabbit transects were run by various members of the Ecology Section under the supervision of P. F. Olsen. I also recognize the encouragement given me by two former Directors, D. D. Bode and D. D. Parker. J. F. Eisenberg and D. G. Kleinman critically read the manuscript.

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SEASONAL CYCLES OF BODY WEIGHTS AND LIPIDS IN BELDING GROUND SQUIRRELS

MARTIN L. MORTON[1]

ABSTRACT: Seasonal changes in body weight, carcass composition, food habits, and general behavior were determined in *Spermophilus beldingi beldingi*, a hibernatory ground squirrel that lives at high altitude. Effects of photoperiod and constant or cycling ambient temperature on body weight regulation were tested in the laboratory. There was about a two-fold annual variation in body weight. Most of this variation was due to fluctuations in fat stores. Basic (fat-free, dry) weight was quite constant throughout the season. Carcass water content varied in that squirrels became slightly dehydrated during hibernation and total body water was inversely related to total body lipid. Prehibernatory fattening occurred over a period of about seven weeks in the population of adults at a given location and involved about a 15-fold increase in total body lipid. In individuals, the response took only about five weeks in males and three weeks in females. All individuals hibernated for about nine months. Body weights decreased during hibernation by as little as 33 percent in yearling females and as much as 43 percent in adult males. Even so, all squirrels emerged with 20 to 25 percent of total prehibernatory lipid stores intact. The schedule of prehibernatory fattening varied by as much as four weeks between individual years. This variation seemed to be related directly to snowpack. The more snow, the later fattening occurred. Following the first weeks of snow disappearance, food was plentiful. Many squirrels fattened and entered hibernation before or at the peak of vegetation abundance. Green grass was the main food item but arthropods were taken throughout the season and large quantities of seeds were eaten when they became available. A greater percentage of time above ground was spent feeding during the fattening phase than earlier in the season. Neither photoperiod nor ambient temperature affected the timing of fattening in captives. There was a seasonal change in propensity to fatten noted in captives. The abrupt inception and termination of prehibernatory fattening and the rapidity with which it occurs indicate that the response is due to hypothalamic hyperphagia and not to seasonal changes in food availability or to decreased metabolic rate. The response may be a manifestation of an annual rhythm in appetite that is phased periodically by environmental factors.

Seasonal dormancy or hibernation is a strategy commonly employed by mammals to allow them to occupy environments with pronounced annual periodicities. One such environment occurs at high altitude where trophic conditions are often favorable for only brief terms each year and temporal patterns of energy utilization in mammalian residents are affected accordingly. The periodical abandonment of endothermy in favor of dormancy is, of course, an energy conserving strategy. During hibernation metabolic rate is low but finite, and arousals occur regularly. Some hibernators may spend up to nine months per year in the dormant state and their energy requirements during this time, although low on a daily basis, are considerable when summated. The ways in which these requirements are met varies considerably among species. Many hibernatory rodents become extremely obese prior to dormancy and rely solely on fat stores (Wade, 1948; Kayser, 1950). Others do not fatten and depend on a food hoard (Lyman, 1948, 1954; Tevis, 1955; Forbes, 1966; Sheppard, 1968). Obviously a great deal of flexibility in metabolic and behavioral adjustments is possible between these two extremes. Ground squirrels of the genus *Spermophilus* occur throughout the Holarctic realm and occupy most of the major terrestrial habitats from desert valleys to high mountain meadows. Apparently some members of this group depend entirely upon the strategy of prehibernatory fattening since they do not eat in captivity during the main span of hibernation (Lyman, 1954; McKeever, 1964). Despite the importance of weight and fat cycles as indicators of hibernatory preparedness (Shubin, 1963), there are few such data for wild populations. Nor has much attention been paid to how

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the fattening response is spaced within the annual cycle with regard to the energetic demands imposed by such events as breeding, molt, lactation, or by concurrent environmental conditions.

The Belding ground squirrel (*Spermophilus beldingi beldingi*) is a hibernator that lives in the central Sierra Nevada, in particular along the eastern escarpment down to the edge of the Great Basin at altitudes between 1825 and 3650 m (Storer and Usinger, 1970). The present study was conducted on two disjunct populations living in Lee Vining canyon, Mono County, California. One population exists in the lower reaches of the canyon on Big Bend meadow where the elevation is about 2135 m (7000 ft). The other population is at the upper end of the canyon near Tioga Pass at an elevation of about 3020 m (10,000 ft). These populations are only about 10 km apart but, because of the difference in climatic conditions associated with altitude, the habitat at Big Bend is suitable for existence above ground much earlier that at Tioga Pass. As a result, events in the active season of *S. b. beldingi* at Big Bend, such as emergence, reproduction and prehibernatory fattening, occur about six calendar weeks earlier that at Tioga Pass. The major focus of this investigation was at Tioga Pass and greater emphasis will be placed on data from that population.

METHODS

Squirrels were live-trapped in Tomahawk wire mesh traps baited with peanut butter. A standard method of toe-clipping was employed using all four feet with never more than one toe clipped per foot. Body weights of live squirrels were taken by rolling them into a tarred cloth bag and weighing to the nearest 0.1 g on a Welch pan balance. Body weights increased as much as 20 percent during the day due to feeding and only weights obtained between 09:00 and 12:00 are reported.

Animals to be used for specimens were live-trapped and etherized or shot with a .22 caliber rifle. Paired fat pads and stomachs in freshly collected specimens were weighed to the nearest 0.01 g on an Ohaus analytical pan balance. Gonads were fixed in Bouin's solution and stomach contents were preserved in 10 percent formalin. Carcasses, including previously dissected portions, were kept frozen until they were analyzed for water and lipid content. Water content was determined by drying to a constant weight in a vacuum oven at 55 C. Carcasses were then homogenized and extracted with petroleum ether in a soxhlet apparatus for 24 hours to determine lipid content (Morton and Tung, 1971a). In our discussions of carcass composition we use the following terms: body weight, basic weight, body lipid, lipid index, and water index. Body weight is the total weight of the live animal. Basic weight is the weight of the carcass following extraction of water and lipid. Body lipid refers to the total amount of lipid extracted with petroleum ether. Lipid index is the weight of total body lipid divided by basic weight and the quotient multiplied by 100. Water index is the weight of total body water (live body weight minus dry body weight) divided by basic weight and the quotient multiplied by 100. Stomach contents were determined for each squirrel using the method of Gebczynska and Myrcha (1966). Briefly, ingesta were suspended in water and ten aliquots were placed on slides with coverslips. The materials on each slide were identified in terms of four simple categories: green material (I feel this was mostly grass), arthropods, seeds, and miscellaneous. The relative amount of each type of material was estimated and mean values from the ten specimens were then used as an indicator of a particular squirrel's stomach contents. A collection of reference materials from the field was used for assistance with identification.

Vegetation samples were taken along a transect every ten days in the summers of 1971 and 1972 as duplicate one m^2 cuttings of the standing crop. These samples were weighed wet, then dried, and three aliquots per sample were combusted in a Parr calorimeter.

Squirrels to be held in captivity were transported approximately 550 km from Tioga Pass to environmental rooms at the laboratory in Los Angeles within two days of capture. They were housed individually in 46 × 26 × 36 cm cages with burlap for nest material. They were fed Purina rat chow and provided with water in dropper bottles. Light was provided by daylight fluorescent tubes at an intensity of about 1000 lux. Captives were weighed during the first hour of the photoperiod.

RESULTS

Events in the Wild Population: Adult *S. b. beldingi* have a seasonal cycle in body weight above ground that can be described logically in terms of three periods: emergence, reproduction (copulation through lactation), and fattening. The first members of the population to emerge were adult

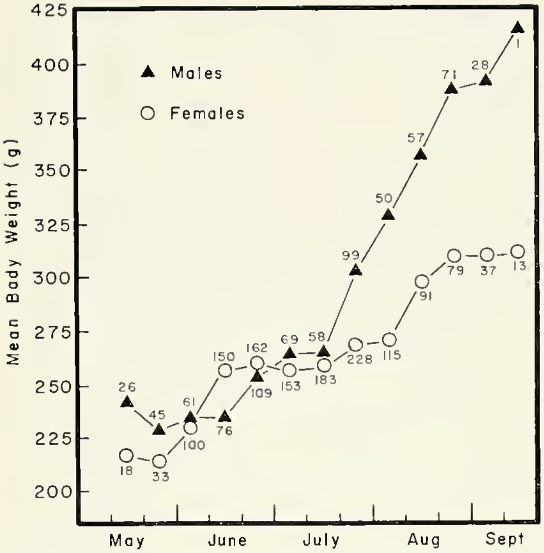

Figure 1. Seasonal changes in body weights of adult *Spermophilus beldingi beldingi* at Tioga Pass. Data collected from four years, 1969–1972. Numerals indicate sample size.

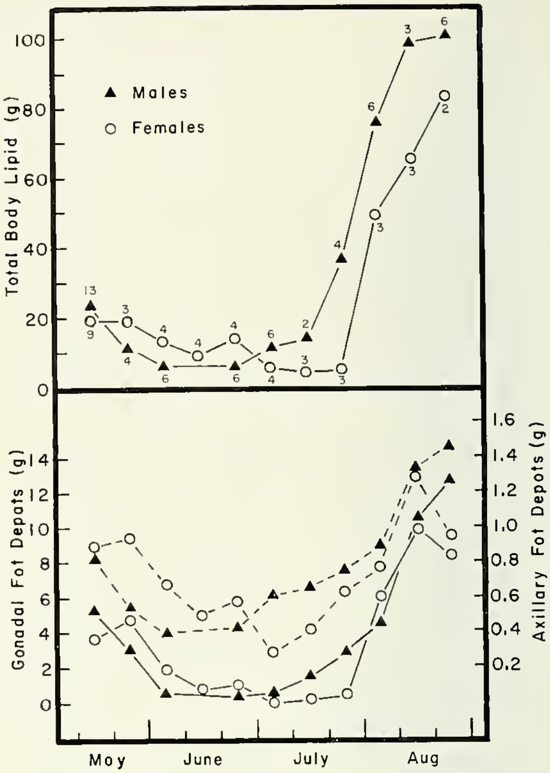

Figure 2. Seasonal changes in total body lipid (upper panel) and gonadal (solid lines) and axillary (broken lines) fat depot weights (lower panel) of adult *Spermophilus beldingi beldingi* at Tioga Pass. Data collected from three years, 1970–1972. Numerals indicate sample size in both panels.

males, but within a few days adult females and some very lean yearlings were active. Emergence at Tioga Pass occurred between the second week in May and the second or third week in June.

Adults lost a slight amount of body weight soon after emergence (Fig. 1). Both sexes then gained weight. In females, this initial gain was due primarily to intrauterine growth of embryos. Females were smaller in body size than males but for a time during pregnancy their weight exceeded that of males. In mid-July males began a period of weight gain that lasted until the onset of hibernation. Females maintained a fairly constant weight throughout the period of lactation then began a gain that was less extensive and two to three weeks later than the gain in males. These data include the general picture of body weight changes with

TABLE 1. Mean lipid indices of adult *Spermophilus beldingi beldingi* at Tioga Pass, 1970–1972.

Time Interval	Males		Females		Combined Data		
	Lipid Index	N	Lipid Index	N	Lipid Index	S.D.	N
11–20 May	40.1	14	41.3	10	40.6	24.0	24
21–31 May	19.0	4	38.0	3	27.1	17.7	7
1–10 June	10.8	6	20.8	5	15.4	8.6	11
11–20 June	10.5	2	14.4	5	13.3	6.5	7
21–30 June	9.1	6	22.0	4	14.2	10.1	10
1–10 July	18.2	6	8.8	4	14.4	10.3	10
11–20 July	19.8	2	7.6	3	12.6	11.0	5
21–31 July	46.5	4	8.5	4	27.5	30.3	8
1–10 Aug.	94.3	6	78.3	3	89.0	47.6	9
11–20 Aug.	107.2	5	94.3	3	102.4	24.3	8
21–31 Aug.	126.4	7	122.1	2	125.4	17.5	9

TABLE 2. Relationship of total body lipid to body weight and gonadal and axillary fat pad weight in adult *Spermophilus beldingi beldingi* collected throughout the active season at Tioga Pass, $N = 169$.

Y	X	Regression equation	Correlation coefficient (r)	Level of Significance (P)
Body lipid	Body weight	$Y = -98.70 + 0.460X$	0.586	< 0.001
Body lipid	Gonadal fat pad weight	$Y = 9.95 + 5.60X$	0.786	< 0.001
Body lipid	Axillary fat pad weight	$Y = 6.94 + 53.67X$	0.657	< 0.001

time but they are misleading from several perspectives. Because they are plotted as 10-day means from four separate years, they obscure annual and individual variations and they do not clearly allow accurate prediction of changes in bodily composition. For example, newly emerged individuals had, by weight, 20–25 percent of the lipid stores achieved just prior to hibernation (Fig. 2, upper). This lipid was lost during the period of reproduction then replaced very quickly in both sexes. Note that females appeared in this case to undergo a fattening response very similar to that in males.

Data that have been normalized to the form of a lipid index show that the relative magnitude of lipid stores was similar in males and females and that the proportion of lipid in newly emerged animals was about one-third of what it was at immergence (Table 1).

The seasonal oscillation in total body lipid was followed rather closely by changes in fat depot weights (Fig. 2, lower). Regressions of total body lipid on body weight and weight of paired fat pads show that they are correlated significantly and that these easily obtained measurements are good predictors of total lipid (Table 2).

To determine if relationships among body components vary seasonally, regressions of basic weight, body water, and body lipid on body weight and of lipid index on water index were calculated using data from 25 individuals collected from the central portion of each period of the active cycle (Table 3). These relationships varied somewhat with the season as shown by the slopes of the regression lines and the correlation coefficients. One notable seasonal variation was that body weight and lipid were not significantly correlated in newly emerged animals. Another interesting finding was that lipid and water were negatively correlated, particularly in the more obese animals.

I have used the equations in Table 3 as a basis for showing the continuum of seasonal changes of body components in *S. b. beldingi* (Fig. 3). This analysis shows that newly emerged animals were slightly dehydrated and had a low basic weight. Basic weight and water were added quickly, however, and remained stable during re-

TABLE 3. Regression equations for body components of adult *Spermophilus beldingi beldingi* during selected portions of their active season. $N = 25$.

Y	X	Regression equation	Correlation coefficient (r)	Level of significance (P)
Basic Weight	Body Weight			
(Emergence)		$Y = 9.09 + 0.197X$	0.692	< 0.001
(Reproduction)		$Y = 12.74 + 0.192X$	0.546	< 0.01
(Fattening)		$Y = 20.09 + 0.159X$	0.730	< 0.001
Body Water	Body Weight			
(Emergence)		$Y = 13.36 + 0.727X$	0.779	< 0.001
(Reproduction)		$Y = 5.28 + 0.706X$	0.913	< 0.001
(Fattening)		$Y = 50.60 + 0.396X$	0.845	< 0.001
Body Lipid	Body Weight			
(Emergence)		$Y = 4.29 + 0.076X$	0.131	> 0.05
(Reproduction)		$Y = 17.96 + 0.102X$	0.425	< 0.05
(Fattening)		$Y = -70.66 + 0.445X$	0.909	< 0.001
Lipid Index	Water Index			
(Emergence)		$Y = 170.2 - 0.722X$	-0.481	< 0.02
(Reproduction)		$Y = 185.2 - 0.721X$	0.224	> 0.10
(Fattening)		$Y = 141.3 - 0.564X$	0.589	< 0.01

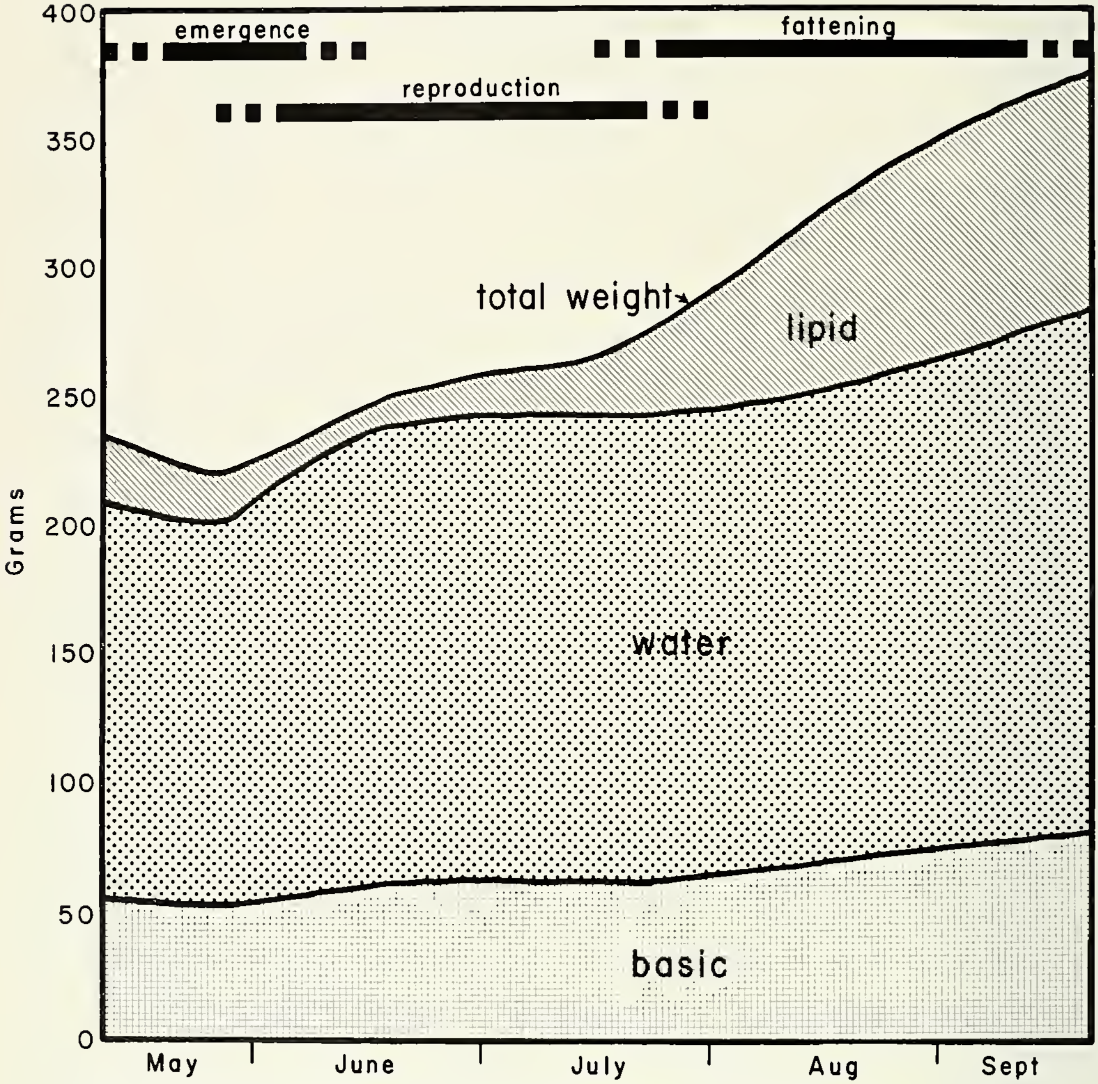

Figure 3. Model of seasonal changes in bodily composition in adult *Spermophilus beldingi beldingi.*

productive activities. As the animals fattened, water and basic weight increased but at a rate less than that predicted by the previous periods of activity. Lipid, on the other hand, was accumulated at a faster rate (see slope terms in Table 3).

Events in Wild Individuals: Data on frequently retrapped individuals show clearly that members of the Tioga Pass population were not perfectly synchronized temporally in their seasonal schedule of activities. A practical effect of this is that treating data by 10-day class intervals tends to blur the true course of weight change as it occurred in individuals. Therefore, body weights are presented of some individual, frequently retrapped squirrels of both sexes throughout the season c activity (Figs. 4, 5). Not shown adequately i figure 4 is the fact that adult males, as individual often lost 40 to 50 g of body weight in the fir weeks after emergence. Presumably this was du to the energetic cost of behavior associated wit breeding and to the scarcity of food at the tim of their emergence. Following a period of rela tively stable body weight they began prehiberna tory fattening (Fig. 4). In 20 frequently re trapped adult males, the difference between th inflection points of the weight curves at onset an at end of fattening averaged 153.2 g, a 54.0 pe cent increase in weight (Table 4). Yearling male

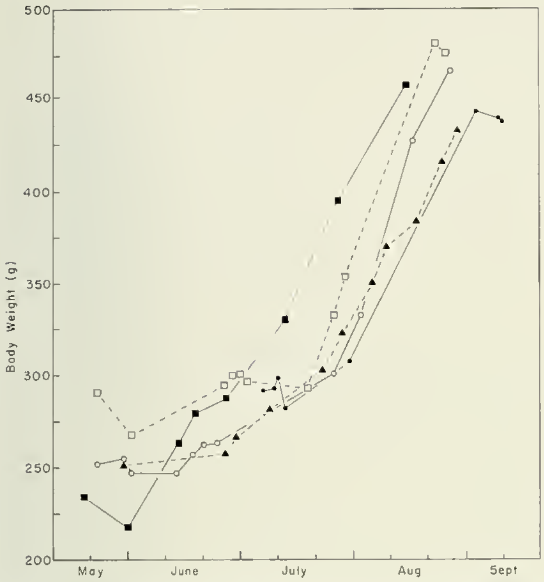

Figure 4. Seasonal changes in body weights of five individual adult male *Spermophilus beldingi beldingi* at Tioga Pass.

were smaller than adult males but their weight gain due to fattening, proportionately, was the same, 54.3 percent (Table 4).

Females had fluctuations in body weight associated with parturition early in the season and, later, abrupt weight increases due to fattening (Fig. 5). According to body weight changes, females fattened proportionately less than males; 44.0 percent in 18 adults and 41.5 percent in 14 yearlings (Table 4). The fattening response took less time in females, however, and their rate of fattening was higher (Table 4).

Using the body weight records of 20 frequently retrapped females, 8 adults and 12 yearlings,

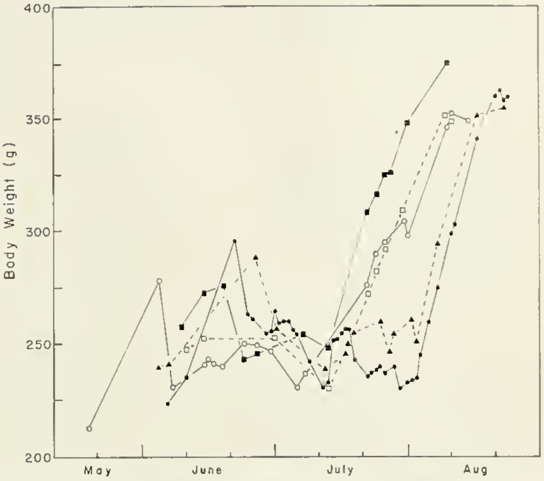

Figure 5. Seasonal changes in body weights of five individual adult female *Spermophilus beldingi beldingi* at Tioga Pass.

I calculated that prehibernatory fattening began 39.0 days (S.D. = 2.6 days) after parturition in adults and 42.0 days (S.D. = 6.9 days) in yearlings. According to a *t*-test, these means are significantly different ($P < 0.05$).

Because trapping was conducted throughout the season of activity at Tioga Pass, some quantitative statements can be made concerning the duration of hibernation and its effect on body weight in adult and yearling *S. b. beldingi.* Data from individuals judged to be captured very near the onset and subsequent termination of their whole hibernation period are shown in Table 5. When squirrels of the same group are compared, males tend to lose more weight than females during hibernation. In adult males this would seem to be a consequence of a longer hibernation period

TABLE 4. Magnitude, duration and rate of fattening in *Spermophilus beldingi beldingi* frequently retrapped at Tioga Pass, 1969–1972.

	Adults		Yearlings	
	Males (N = 20)	Females (N = 18)	Males (N = 8)	Females (N = 14)
Mean body weight at onset of fattening (g)	283.9	242.8	252.8	224.2
Mean body weight at end of fattening (g)	437.1	349.4	390.0	317.3
Increase in weight (%)	54.0	44.0	54.3	41.5
Duration of fattening response (days)	34.4	19.8	38.1	21.7
Relative rate of fattening (%/day)	1.57	2.22	1.43	1.91

TABLE 5. Body weight changes during hibernation and duration of hibernation in *Spermophilus beldingi beldingi*. Means are shown followed by standard deviations in parentheses.

	Adults		Yearlings	
	Males (N = 10)	Females (N = 15)	Males (N = 20)	Females (N = 7)
Body weight at immergence, g	418.7 (26.2)	344.9 (26.3)	375.9 (27.4)	304.5 (21.0)
Body weight at emergence, g	238.4 (31.5)	211.4 (31.8)	227.2 (26.1)	202.8 (15.6)
Body weight decrease during hibernation, %	43.2 (5.5)	38.4 (9.8)	39.5 (6.0)	33.2 (5.3)
Time in hibernation, days	280 (10)	269 (10)	262 (16)	269 (15)

but the relationship does not hold up in yearlings. Clearly, however, all animals spent about nine months in hibernation.

Climatic Conditions and Fattening Schedule: Environmental conditions varied considerably from year to year at the time squirrels emerged at Tioga Pass. I think that the most important variable, in terms of its effect on *S. b. beldingi* activities, was snow cover. The State of California has a snow survey course at Tioga Pass and their data indicate that snow depth varied greatly from year to year during our study (Table 6).

The State uses the 1 April snowpack data as a primary source for predicting annual percent runoff from Sierran watersheds. Historically these data reflect the magnitude of snowpack at near maximal seasonal accumulations. Our study area lies within the confines of the Mono Basin and runoff predicted for this basin is based on averages of measurements taken since 1931. This index to snow conditions shows that 1969 was a heavy snow year with more than double the usual runoff. In 1970, runoff was average and in 1972 and 1973 it was below average. In 1972, there was premature snowmelt runoff in nearly all Sierran basins due to a lack of precipitation and to unusually hot weather in March.

The schedule of fattening in *S. b. beldingi* seemed to be related to these fluctuations in snowpack. In 1969, an unusually heavy snow year, prehibernatory fattening, as seen in adult males, was about two weeks later than in near-normal years, 1970 and 1971 (Fig. 6). In 1972, a year when the snow melted early, fattening occurred about two weeks earlier than in 1970 and 1971. Thus, as seen in the difference between 1969 and 1972, there is as much as four weeks of flexibility in the schedule of fattening. This schedule variation was observed also in other ages and sexes of *S. b. beldingi*.

Seasonal Changes in Behavior: Activity of *S. b. beldingi* above ground was partitioned into running, digging, grooming, feeding, and picketing by Morhardt (1971). I spent about 120 hours observing these behaviors throughout the day at Tioga Pass in June and in August during the period of fattening. In the category of running are included movements of individuals as well as chase sequences involving two squirrels and I have added the category "sunning." The primary seasonal adjustment in temporal segregation of activity was a shift from agonistic actions, manifested as running-chasing, in June to feeding in August (Fig. 7).

Food Availability and Food Habits: The measurements of standing crop serve to estimate seasonal trends of food availability. At Big Bend, where squirrels emerged in late March and early April, food was minimal at emergence and was at or near peak abundance during prehibernatory fattening (Fig. 8). At Tioga Pass, maximum food availability coincided with the first part of the fattening period and declined thereafter. Vegetation on the lower altitude meadow was

TABLE 6. Snow depth at Tioga Pass and water runoff predicted for the area (Mono Basin) on 1 April. Data taken from Bulletins 120 and 129, State of California, Department of Water Resources.

	1969	1970	1971	1972
Snow depth in centimeters				
1–4 February	252	153	76	134
27–31 March	342	176	126	121
Annual percent runoff (Mono Basin)	240	100	75	60

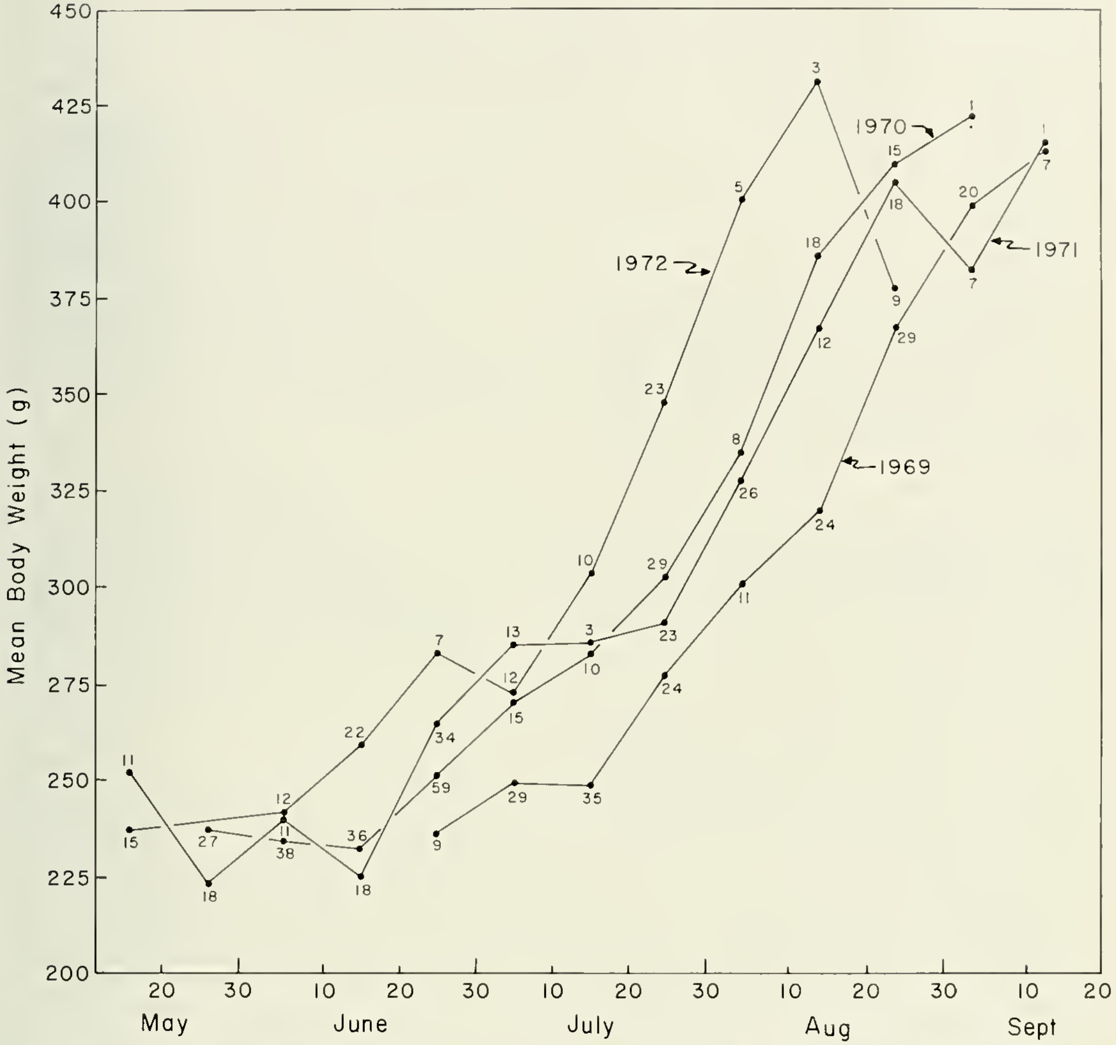

Figure 6. Annual variation in cycle of body weights in adult male *Spermophilus beldingi beldingi* at Tioga Pass. Numerals indicate sample size.

lusher than on the higher meadow, but it did not contain as many Kcal per unit weight.

The actual food selected by *S. b. beldingi*, as seen in stomach contents, indicates that they are probably opportunistic feeders. Early in the season green grass was the most important item in their diet at both study sites (Fig. 9). Seeds were more important as the season progressed and they became more available, especially at Tioga Pass. Increased seed consumption paralleled fattening at Tioga Pass but seeds were not eaten in quantity at Big Bend until the end of the season. In both cases, in my opinion, consumption was related to availability. Arthropods, particularly ants, beetles, and grasshoppers, were eaten throughout the season. Their importance as a food item may be greater than indicated in figure 9 since there were arthropod remains in 32 percent of the stomachs from Big Bend and in 45 percent of those from Tioga Pass. In the miscellaneous category were included such items as fungi, carrion, and unidentifiable materials.

Effects of Controlled Environments on Body Weights: Squirrels were brought into the laboratory from Tioga Pass at two times in relation to the annual cycle; soon after emergence and at the onset of prehibernatory fattening. In one experiment one group was held on short days (6L:18D) and another group on long days (18L:6D). Sexes were divided about evenly within

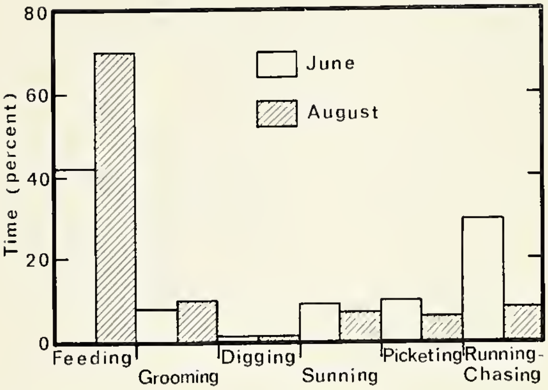

Figure 7. Relative time spent by *Spermophilus beldingi beldingi* performing various categories of above-ground behaviors.

groups but pregnant or lactating females were excluded. Ambient temperature was held constant at 20°C. Animals in both groups brought in early in the season began gaining weight on both photoperiods. Those on long days gained faster and were significantly heavier after six weeks of treatment ($P < 0.\,5$) than those on short days (Fig. 10, upper). Animals brought in later began fattening at once and the response was not different according to photoperiod treatment (Fig. 10, lower). The timing and rate of fattening in these squirrels closely resembled those of their free-living counterparts.

In another experiment, long and short days were given as before but ambient temperature was cycled with the lights such that it was 8°C during the dark period and 20°C during the light period. These temperatures realistically represented daily temperature extremes at Tioga Pass in the summer. The results obtained in this case were comparable to those obtained in the first experiment except that the long-day group brought in early was significantly heavier than the short-day group for only a brief time (Fig. 11). In both of these experiments, there was a two-to-three fold increase in food intake, as measured by feces production, once fattening began. Squirrels began exhibiting periods of torpor at about the time they achieved maximum body weight.

The rate of body weight change in four adult *S. b. beldingi* (two males, two females) on 18L:6D at 20°C, was measured during June and July. When body weight in each was 40 percent greater than initial body weight, food was withdrawn until they had lost back to initial body weight. Food was then returned. The mean rate of weight gain in the first instance was 2.12 percent/day (S.D = 0.49 percent). In the absence of food, body weights decreased at 3.40 percent/day (S.D. = 0.99 percent). Upon being refed, weight gain was 3.79 percent/day (S.D. = 0.88 percent). This rate of gain was significantly greater ($P < 0.05$) than that seen in the first period of gain.

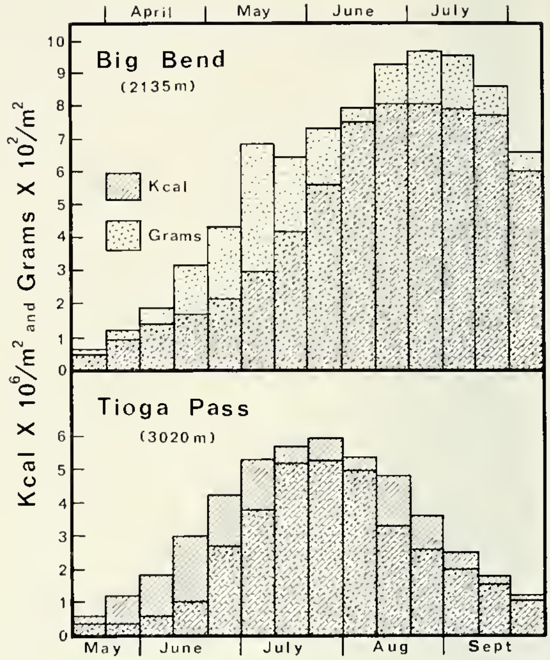

Figure 8. Seasonal change in energy content and wet weight of m^2 vegetation samples at Big Bend and Tioga Pass meadows.

DISCUSSION

Prehibernatory fattening seems to be the primary adjustment made by *S. b. beldingi* to meet the energy demands of their annual period of dormancy. Whatever the response of any hibernator to these demands, rather strict requirements must be placed on the function of the regulatory systems involved. This is true especially for a hibernator such as *S. b. beldingi* that lives in an environment with extreme annual oscillations and wherein individuals are living in a sealed hibernaculum isolated from external conditions for nine months each year.

Fattening in the adult population of *S. b. beldingi* took place over a period of seven weeks and involved about a 15-fold increase in total body lipid. This is considerably more than the increase seen in golden-mantled ground squirrels (*S. lateralis*) by Jameson and Mead (1964) but is probably not unusual for the genus according

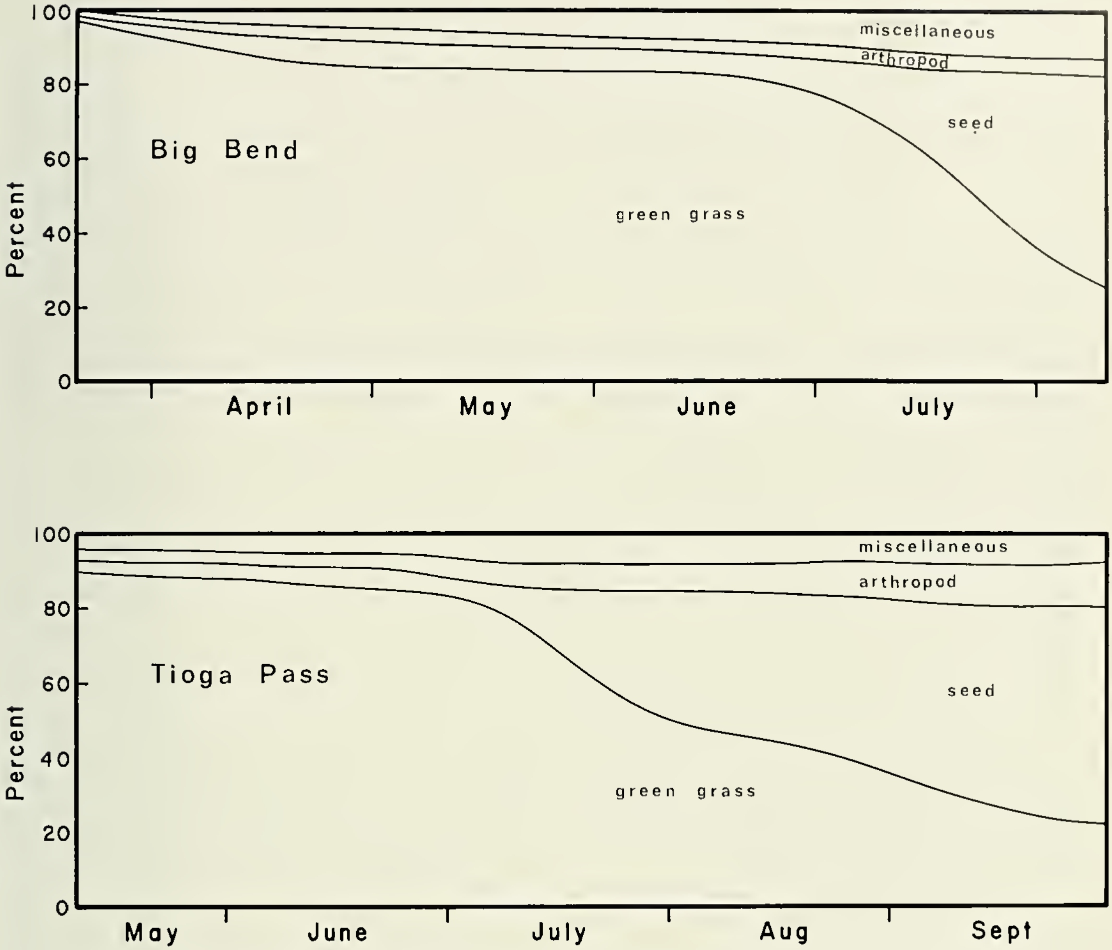

Figure 9. Seasonal trends in stomach contents of *Spermophilus beldingi beldingi.* Number of stomachs sampled was 131 at Big Bend and 134 at Tioga Pass.

to the graphic descriptions of some naturalists (Shaw, 1925; Wade, 1948; Manville, 1959; Neal 1965). At the time of immergence total body lipid equaled or exceeded basic weight in the most obese individuals. Obviously this is more than sufficient because at emergence lipid still equaled 40 percent of basic weight. This figure is slightly deceiving because basic weight did decrease somewhat during hibernation.

Emergence from hibernation with lipid stores that were depleted subsequently has been noted in a variety of sciurids (Skryja and Clark, 1970; Clark, 1970; Hock, 1960; Mayer and Roche, 1954; Snyder and Christian, 1960; Snyder *et al.*, 1961). In the case of *S. b. beldingi* these early season fat stores would seem to be useful, even essential, for survival in some cases. Many of the first squirrels to emerge each year, particularly at higher altitudes, are confronted with snow-covered terrain and food is scarce or entirely absent. We find that these first arousers may: 1) return below ground for at least several days; 2) travel, as far as 600 m, to open areas where food is available; 3) stay near the site of emergence and remain active. Even when food is available at emergence it is usually not abundant and posthibernatory fat stores may permit the normal sequence of behaviors, including hyperactivity, associated with breeding to occur earlier than otherwise. This could be critical in years of heavy snowpack given the usually abbreviated summer of high altitude.

The schedule of fat deposition varied considerably among members of the adult population but in a given year males tended to fatten about two weeks before females; the general pattern seen

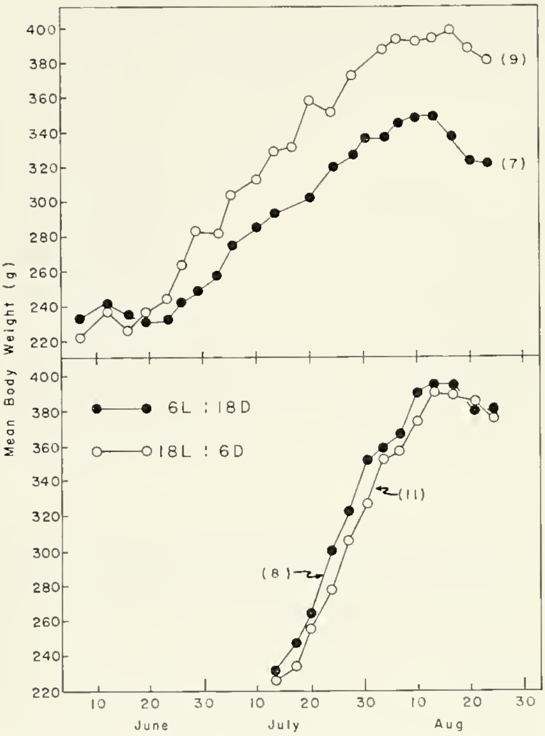

Figure 10. Body weights of *Spermophilus beldingi beldingi* held at ambient temperature of 20° C and exposed to short days (6L:18D) and to long days (18L:6D) at two different times of the season. Numerals in parentheses indicate sample size.

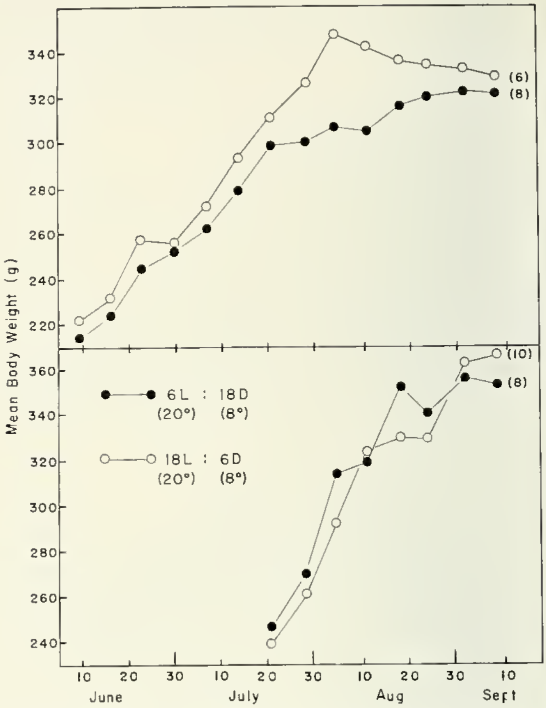

Figure 11. Body weights of *Spermophilus beldingi beldingi* held on cycling ambient temperatures of 8° C (dark period) and 20° C (light period) and exposed to short days (6L:18D) and to long days (18L:6D) at two different times of the season. Numerals in parentheses indicate sample size.

in sciurids. There was no difference, however, in the relative degree of obesity finally attained.

Weight change of both white and brown fat depots was related directly to levels of total body lipid. In the case of white fat this was expected since white fat accumulated in subcutaneous and retroperitoneal depots is the main source of energy stored in tissues of hibernators. Brown fat is known to vary quantitatively with season in hibernators and non-hibernators, but seemingly in accordance with thermogenic requirements (Didow and Hayward, 1969; Aleksiuk, 1971; Johansson and Senturia, 1972; Sealander, 1972). The good correlation of brown fat quantity to total body lipid in *S. b. beldingi* suggests, however, that seasonal fluctuations in brown fat are a direct consequence of general lipogenic activity and not the result of independent control of brown fat depot size.

Relative quantities of bodily constituents other than fat underwent seasonal fluctuations in *S. b. beldingi*. In the case of basic weight, the change was slight. In absolute terms, it increased slightly during fattening due, probably, to synthesis of nonlipid components in growing depots. But as a percentage of body weight it decreased slightly. Solving the regression equations for squirrels of the same weight at different periods of the active cycle shows that basic weight was essentially constant. If catabolism of basic components, such as bone and muscle, occurs during hibernation it is inconsequential.

The relative quantity of body water changed considerably with season. Stored lipids are dehydrated in comparison to other tissues, giving the reciprocal relationship found between body lipid and body water; a relationship observed also in fattening *S. lateralis* (Jameson and Mead, 1964). The lack of correlation between body water and lipid in our model of newly emerged animals indicates that *S. b. beldingi* becomes somewhat dehydrated during hibernation.

Fattening and Environmental Conditions: Isolated in hibernacula below the snowpack, *S. b. beldingi* cannot afford energetically to arouse frequently, dig out, test the environment, and resume dormancy if necessary. They must arouse at about the correct time each spring yet be flexible enough in their timing of activities to adjust to climatic variables. A manifestation of this flexibility is the four-week spread seen in fattening schedule between "early" and "late" years.

Usually squirrels disappeared into hibernation a few days after achieving maximum body weight. In the case of adults, the first ones entered hibernation in mid-June at Big Bend and in early August at Tioga Pass. At both locations food was not in short supply. At Big Bend, in fact, most adults had fattened before the standing crop was maximal. There are several reasons why this schedule may have survival value for *S. b. beldingi*. Direct competition for food during fattening is diminished because there is a functional segregation within the population in the timing of fattening. Adults, led by the older males, and large yearlings fattened first, followed by small yearlings. Juveniles were active for about a month after the older animals had disappeared. Thus, although members of the population were above ground for about 4.5 months each year, individuals were active for only about three months.

There is, I am convinced, another force operating to compress the seasonal cycle of activity in these squirrels. The early entry into hibernation probably prevents a considerable amount of predation. The numbers of predators such as coyotes (*Canis latrans*) and long-tailed weasels (*Mustela frenata*) undoubtedly increases toward the end of summer as their juveniles become effective hunters. There is also an autumnal migration of hawks through the Sierra. Many *S. b. beldingi* at Tioga Pass were still above ground during this migration and I have seen them taken regularly by hawks at that time. To be adaptive, the proposed advantage of early hibernation would have to more than offset the mortality accrued during hibernation. This type of mortality is difficult to measure. Pengelley and Asmundson (1970) state that it is high in *S. lateralis*, but Broadbrooks (1970) found that hibernation was the safest time of year for yellow-pine chipmunks (*Eutamias amoenus*), with nearly 100 percent survival occurring. The over-winter mortality rate of *S. b. beldingi* has not been determined, but it appears to be low. Some toe-clipped squirrels at Tioga Pass are known to be at least six years of age.

Another selective factor operating to cause early hibernation, in an ultimate sense, is the avoidance of food shortage and cold weather. This idea was favored by McKeever (1963) while studying *S. b. oregonus* in Lasson County, California. However, McKeever assumed that there was a food shortage once green grass had disappeared. This was not the case for *S. b. beldingi* because they ate quantities of insects and the seeds of dried grasses at the end of their active season.

The onset of prehibernatory fattening was often clearly defined in squirrels that were continually retrapped. Clearly, individuals began fattening on separately defined schedules related, presumably, to their metabolic status. In most cases, once fattening began it proceeded rapidly until a final stage of obesity was reached. The response appeared to be a regulated entity. This was most easily observed in males because the energetic expense of lactation beclouds the picture in females. Lactation is known to cause a two-to-three-fold increase in food intake over that of gestation in some rodents (Kaczmarski, 1966; Migula, 1969; Myrcha *et al.*, 1969). Hypothetically, fattening in female *S. b. beldingi* could occur without change in food intake if calories were diverted from milk production to lipids for storage. This is not the case, however, if our determination of lactation period is correct. We found that *S. b. beldingi* held in captivity at the study area lactated for about 24 days (Morton and Tung, 1971b). Coupling this datum with weight records of frequently retrapped wild females, I conclude that fattening begins two weeks or more beyond the end of lactation and that the two events are probably regulated independently.

There is much indirect evidence that prehibernatory fattening is due to a seasonal adjustment in appetite in *S. b. beldingi*. Our estimates of feeding activity in the wild must only approximate seasonal changes in appetite, but the data agree with those of Morhardt (1971) in that relatively more time was spent feeding during the period of fattening than before it. The sudden onset of fattening and the rate and extent of the response, as observed in retrapped individuals, point also toward a seasonal adjustment in appetite. In captives the picture was blurred somewhat because they began to fatten almost immediately after caging. It is notable, however, that the rate of fattening was greatest if they were caged at the time fattening normally began in the wild. The same relationship was obtained in starved-refed animals. Seasonal changes in regulation of appetite and lipid reserves have been observed in other hibernatory ground squirrels (Mrosovsky and Fisher, 1970; Mrosovsky, 1971).

A decrease in metabolic rate at the time of prehibernatory fattening is known to occur in some hibernators. This could contribute to fat accumulation (Bailey, 1965; Armitage and Shulenberger, 1972). In fact, this could be the fundamental energetic basis for fattening in some species (Armitage and Shulenberger, 1972), but I feel that it is more likely that pretorpor obesity is due to hyperphagia in *S. b. beldingi*. Presumably this would involve appropriate functional changes in hypothalamic centers controlling food intake (see reviews by Satinoff, 1970 and Mrosovsky, 1971).

Of considerable interest is the question of how such a functional change could be tied to environmental conditions. In recent years it has become clear that some seasonal physiological changes in various animal species may be regulated, at least in part, by endogenous rhythms with a period of approximately one year. These rhythms have been described as circannual rhythms (Pengelley and Asmundson, 1970, 1971; Gwinner, 1971). Endogenous control of annual cycles could be highly adaptive if seasonal events within the animal requiring preparation in advance were to coincide in a propitious way with annual environmental conditions (Enright, 1970). This idea seems especially applicable to hibernators at high altitude where the optimum season for reproduction and accumulation of energy is short and where the hibernator is out of direct contact with the external environment for a continuous period of about nine months each year. Indeed some of the very best information on circannual rhythms has been accumulated on hibernatory ground squirrels, especially *S. lateralis* (Pengelley and Fisher, 1963; Pengelley and Kelly, 1966; Pengelley, 1967, 1968; Pengelley and Asmundson, 1969; Heller and Poulson, 1970). There is a relationship between these rhythms and the environment in that the most rigid endogenous controls seem to have evolved in those animals inhabiting the most periodic environments. This relationship has been demonstrated or at least hypothesized for five species of *Spermophilus* (Pengelley and Kelly, 1966) and four species of *Eutamias* (Heller and Poulson, 1968, 1970).

Taking a cue from what is known about other rhythms, especially circadian rhythms, it seems reasonable to argue that if there is an endogenous annual rhythm in the regulation of energy balance, the rhythm must be synchronized periodically to environmental events. In this way, errors in timing would not accumulate and eventually render the rhythm maladaptive in an animal that lives several years. When one considers the conditions actually experienced by hibernators in the field, it seems possible that the sudden change in ambient temperature and/or photoperiod experienced upon terminal arousal and emergence could be synchronizing or phase-setting to reproductive activities and subsequently to other functions such as prehibernatory fattening (Heller and Poulson, 1970). Examination of the schedules of two *S. b. beldingi* populations exposed annually to quite different photoperiod and temperature conditions is relevant to this point. Events in the active season seem to be identical in sequence and duration at Big Bend and Tioga Pass, but because of the difference in altitude and timing of their annual cycles, *S. b. beldingi* at Big Bend fattened when average ambient temperatures were still rising and when day length (sunrise to sunset at the study areas) was near maximum or changing only slightly (Fig. 12). At Tioga Pass they fattened when temperatures were maximum or decreasing and photoperiod was decreasing. Although these populations were separated by a distance of only 10 km, gene flow between them is effectively pre-

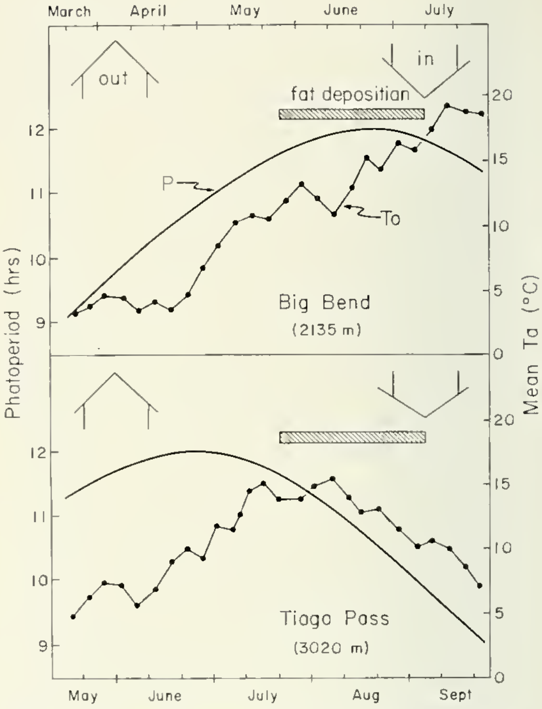

Figure 12. Relationship of end of hibernation (out), onset of hibernation (in), and prehibernatory fattening period in two populations of *Spermophilus beldingi beldingi* to seasonal trends in ambient temperature and to photoperiod.

vented by the rugged terrain and absence of intermediate colonies of *S. b. beldingi*. It seems unlikely, however, that members of the two populations independently evolved assays of thermoperiod or photoperiod that are useful for direct timing of physiological cycles. More likely, the cycles have a basic endogenous component that is reset at least once per year by sudden changes in the perceived environment.

ACKNOWLEDGMENTS

A large number of person-hours were spent collecting and analyzing the data in this study. Many of these hours were expended by a delightful group of Occidental College students. For their help, their stimulation, and their friendship, I am extremely grateful. I would particularly mention: Eric Bitterbaum, Cynthia Carey, Helen Clyatt, John Gallup, Roland Leong, Fanny Liu, Catherine Maxwell, Jorge Orejuela, Robert Parmer, Lucy Tung, Allen Tway, and Charles Wade. Financial support was provided by NFS Grant GB 29146X1.

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CALCANEA OF MEMBERS OF THE CANIDAE

Howard J. Stains[1]

Abstract: The calcanea of 25 species (14 genera) of canids are described and compared. All canids have a dual anterior surface which articulates proximally with the astragulus and distally with the scaphoid. Most canid calcanea are similar with those of *Speothos*. *Nyctereutes*, *Atelocynus*. and *Chrysocyon* being the most distinctive. Calcanea of *Canis dingo* exhibit the most variability. Those of *Vulpes vulpes* and *Vulpes fulva* are indistinguishable and those of *Canis niger* are intermediate to those of *Canis latrans* and *Canis lupus*.

Of the families of the Carnivora, the canids have a calcaneum of less variation between genera and species than any other family examined. In general the basic shape of the calcaneum of canids is like that of the felids except that the trochlear process is less distinctive and usually is not grooved. In this respect, the calcanea of the canids are intermediate to those of the hyaenas, which lack the trochlear process altogether, and the felids where it is well developed.

In most instances the anterior articular surface is small, usually dual in nature with another surface located between the anterior articular surface and the cuboid surface, and never connected broadly to the medial articular surface. The dual surface articulates with the astragulus proximally and the scaphoid (navicular) distally. An articulation with the scaphoid is found in few other carnivores.

The posterior articular surface usually is sigmoid in shape, and, except for *Speothos*, never forms the smooth curve as found in the ursids, and most felids and procyonids. The calcanea of the hyaenas are intermediate in this respect tending to be more sigmoid than forming a smooth curve.

All but one genus (*Dasycyon hagenbecki*) of the family Canidae were available for study and this genus is probably a domestic dog (see Stains in M. W. Fox, "The Wild Canids," Von Nostrand Reinhold Co., 1975). Specimens of several presumed species were not available: *Canis hallstromi*, *Dusicyon culpaeola*, *D. culpeus*, *D. fulvipes*, *D. gymnocercus*, *D. inca*, *D. sechurae*, *D. vetulus*, *D. australis*, *Urocyon littoralis*, *Vulpes bengalensis*, *V. cana*, *V. corsac*, *V. ferrilata*, and *V. ruppelli*.

The terminology of the various processes and articulations can be found in Stains (J. Mamm., 40:392–401; Syst. Zool., 11:127–130; So. California Acad. Sci. Bull. 72:137–148) and Robinette and Stains (J. Mamm., 51:527–541).

GENERA AND SPECIES OF THE FAMILY CANIDAE

Fennecus zerda—Fennec

The fennec has the smallest calcaneum of any living canid (Table 1). There is no overlap in size of the calcaneum of *Fennecus* with the calcaneum of any other species. In general, the proportions of width to length and dorso-ventral height to length, of the

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TABLE 1. Measurements of Calcanea of Members of the Canidae

		Total length (mm)		Width (mm)		D-VH (mm)		LWB (mm)	
*	No.	Range	Avg.	Range	Avg.	Range	Avg.	Range	Avg.
1	27	23.0–29.0	26.8	9.8–12.5	11.1	8.7–11.5	10.2	3.6–5.1	4.2
2	4	30.1–36.2	33.1	12.9–15.6	14.2	12.4–14.4	13.3	4.7–5.9	5.3
3	6	30.2–35.2	32.5	12.7–15.0	13.5	12.1–13.9	12.9	4.8–5.7	5.1
4	9	37.7–56.5	44.9	16.0–24.4	19.4	15.3–23.7	18.6	5.6–9.6	7.4
5	50	34.2–45.4	40.4	13.7–18.5	16.0	13.4–18.5	15.9	5.1–8.1	5.9
6	26	46.2–66.0	57.9	19.3–29.0	23.7	19.1–27.6	24.0	7.1–11.5	9.2
7	12	31.2–35.2	33.7	12.5–14.8	13.8	12.9–14.1	13.6	4.4–5.3	5.0
8	46	44.8–57.6	49.3	17.5–24.2	19.6	18.0–24.5	20.5	5.6–9.7	7.4
9	1		44.9		17.2		18.2		6.8
10	5	52.6–62.5	58.4	19.0–24.0	22.4	22.4–28.0	25.6	6.5–8.0	7.3
11	1		30.4		15.5		13.8		4.9
12	13	24.8–35.0	28.3	11.6–15.9	12.9	9.6–14.4	11.6	3.9–5.3	4.4
13	7	25.2–29.6	27.0	10.4–12.6	11.3	9.3–11.8	10.5	3.5–5.0	4.1
14	7	17.4–19.0	18.1	7.3– 8.2	7.8	6.5– 7.4	7.1	1.6–2.9	2.6
15	8	21.4–26.4	23.5	9.9–13.7	11.1	9.9–11.4	10.4	4.0–5.4	4.6
16	30	21.0–30.0	26.5	9.4–13.1	11.8	8.7–12.5	10.8	3.4–5.4	4.4
17	2	26.1–26.5	26.3	10.3–11.0	10.7	9.6–10.2	9.9	3.8–4.3	4.1
18	31	26.0–33.1	30.3	10.8–14.0	12.2	9.8–13.3	11.5	4.0–5.6	4.6
19	8	22.0–23.7	22.8	9.5–10.1	9.8	8.5– 9.0	8.8	2.7–3.5	3.1
20	14	22.9–26.4	24.7	9.1–10.6	9.9	8.6–10.2	9.4	3.2–4.2	3.5
21	3	30.4–33.7	31.9	12.4–14.4	13.3	11.8–13.2	12.4	4.3–5.6	4.9
22	5	42.3–48.3	45.7	19.1–22.1	20.2	17.7–20.2	19.3	6.8–8.3	7.3
23	11	43.6–55.6	51.3	19.0–25.2	22.1	19.8–24.8	22.7	6.3–8.0	7.4
24	8	24.5–26.5	25.2	11.3–12.4	11.8	9.8–10.9	10.4	4.3–5.0	4.7
25	8	24.4–29.8	26.4	10.1–12.9	11.5	9.8–12.1	10.7	3.6–4.8	4.1

* 1, *Alopex lagopus*, 2, *Canis adustus*, 3, *C. aureus*, 4, *C. dingo*, 5, *C. latrans*, 6, *C. lupus*, 7, *C. mesomelas*, 8, *C. niger*, 9, *C. simensis*, 10, *Chrysocyon brachyurus*, 11, *Atelocynus microtis*, 12, *Cerdocyon thous*, 13, *Dusicyon gracilis*, 14, *Fennecus zerda*, 15, *Nyctereutes procyonoides*, 16, *Urocyon cinereoargenteus*, 17, *Vulpes chama*, 18, *V. fulva*, 19, *V. macrotis*, 20, *V. velox*, 21, *V. vulpes*, 22, *Cuon alpinus*, 23, *Lycaon pictus*, 24, *Speothos venaticus*, 25, *Otocyon megalotis*. D-VH dorso-ventral height, LWB least width of body.

calcanea of *Fennecus*, are closer to those of the genus *Vulpes* than to the genus *Canis* (Table 2).

The trochlear process is small but more distinct than that in most canids (Fig. 1u). A well-developed ridge exists dorso-ventrally between the trochlear process and the sustentaculum. On each side of this ridge is a rather deep groove, wider between the ridge and the trochlear process than between the ridge and the medial articular surface. On some calcanea, the anterior and medial articular surfaces tend to be joined by a thin waist. A minute articular surface is present between the anterior surface and the cuboid surface. The body of the calcaneum extends ventrally onto the cuboid surface forming a small knob on the ventral edge of the cuboid surface.

The posterior articular surface, like those of the calcanea of most canids, is sigmoid in shape. There is a slight swelling on the body, lateral and proximal to the posterior articular surface; the body appears broader on the outer compared to the inner half when viewed from a dorsal aspect.

Specimens examined: AMNH 8, 80019, 90156, 90319; USNM 22465, 253478, 253481 (AMNH 90156 illustrated, Fig. 1u).

Urocyon cinereoargenteus—Gray Fox

The canid most closely approaching *Fennecus* in size of the calcaneum is *Urocyon*; this is in range of size, not average size. Length, width, and height proportions also are not drastically different between the two (Table 2).

The trochlear process in *Urocyon* (Fig. 1j) is even more prominent than in *Fennecus* (Fig. 1u); approached most closely by *Alopex* (Fig. 1q) in this respect. The ridge between the trochlear process and the sustentaculum is more massive at the distal (cuboid) end in *Urocyon* so that the trough or groove on each side is broader at the proximal ends rather than being slender grooves.

In no case are the anterior and medial articular surfaces joined or connected by a thin waist.

The body of the calcaneum does not extend onto the cuboid surface as in *Fennecus*; the prominent

TABLE 2. Indices for Calcanea of Members of the Canidae (for number of specimens see Table 1)

Species	W/TL*		D-VH/TL*		LWB/D-VH*	
	Range	Avg.	Range	Avg.	Range	Avg.
Alopex lagopus	38–46	42	37–46	38	35–49	41
Canis adustus	41–44	42	37–42	40	37–43	40
Canis aureus	39–46	41	38–42	40	35–45	40
Canis dingo	39–47	43	38–43	42	33–46	40
Canis latrans	37–43	40	37–44	40	32–47	36
Canis lupus	37–46	41	38–45	41	32–45	38
Canis mesomelas	39–43	41	39–42	40	32–41	37
Canis niger	36–43	40	39–45	42	31–39	36
Canis simensis		38		41		37
Chrysocyon brachyurus	36–40	38	43–45	44	26–29	28
Atelocynus microtis		51		45		36
Cerdocyon thous	43–50	46	39–43	41	34–48	38
Dusicyon gracilis	40–44	42	37–40	39	34–45	40
Fennecus zerda	42–45	43	37–41	39	25–42	37
Nyctereutes procyonoides	44–52	47	39–48	44	39–48	44
Urocyon cinereoargenteus	41–49	45	38–43	41	35–49	41
Vulpes chama	40–42	41	37–39	38	40–42	41
Vulpes fulva	37–45	40	35–41	38	36–46	40
Vulpes macrotis	42–44	43	38–41	39	30–40	35
Vulpes velox	38–42	40	36–39	38	35–45	37
Vulpes vulpes	39–45	42	37–40	39	36–48	40
Cuon alpinus	43–46	44	42–43	42	35–41	38
Lycaon pictus	41–47	43	42–46	44	30–37	33
Speothos venaticus	45–50	47	39–44	41	42–51	46
Otocyon megalotis	39–48	44	39–42	41	34–43	38

* W/TL, width divided by total length; D-VH/TL, dorso-ventral height divided by total length; LWB/D-VH, least width of body divided by dorso-ventral height (see Stains, Bull. So. California Acad. Sci., Vol. 72:138, fig. 2 for measurement procedures).

knoblike process on the cuboid surface being formed by the part of the anterior articular surface which forms an additional surface between it and the cuboid surface. Like the calcaneum of *Fennecus*, the body of *Urocyon* is broader on the outer surface of the calcaneum but unlike *Fennecus* contains a well developed pit lateral and proximal to the posterior articular surface.

Members of the genus *Canis* (Figs. 1h and c), as in *Urocyon*, usually have a small swelling instead of the obvious pit. The distinct and narrow trochlear process will separate the calcanea of *Urocyon* from those of *Canis*. In *Canis*, the trochlear process tends to be massive near the distal (cuboid) end, not more or less even as in *Urocyon*.

The calcanea of species of the genus *Vulpes* lack the pit located lateral to the posterior articular surface; in some cases there is a bump or a small swelling as in *Canis*. The sustentaculum of *Urocyon* ends proximal to the anterior articular surface. In *Vulpes* the sustentaculum continues as a ridge (sustentacular shelf) to the anterior articular surface and on to the distal end of the bone at the cuboid surface. This continuation causes the more distinctly grooved effect obtained in *Vulpes* (Fig. 1E); this is the easiest way to separate all species of *Vulpes* from *Urocyon* (Fig. 1D).

Alopex (Fig. 1q), like *Vulpes*, differs from *Urocyon* in having a distinct sustentacular shelf forming an even more pronounced groove below the sustentaculum (Fig. 1E). The anterior articular surface is small in *Alopex* and in some cases tends to continue towards the medial articular surface and the sustentacular shelf.

Nyctereutes (Fig. 1x) differs from *Urocyon* (Fig. 1j) in that the trochlear process of the calcaneum is located proximal to the cuboid surface such a distance that the greatest extension of the lip-like trochlear process is at an equal level with the distal edge of of medial articular surface. When viewed from the distal end, the cuboid surface of *Nyctereutes* tends to be round; in *Urocyon* the cuboid surface continues under the trochlear process making the surface oblong in shape. The general impression of a calcaneum of *Nyctereutes* is that it is short and stocky; *Urocyon* is more slender and elongate. The average width length index in *Nyctereutes* is 47; in *Urocyon* it is 44.

Three of nine specimens of *Speothos* (Fig. 1p) have a continuous medial and anterior articular surface; three of nine are joined by a thin waist, and three of nine have separate surfaces. These surfaces are always separate in *Urocyon*. In all specimens of *Speothos*, the shelf of the trochlear process is dis-

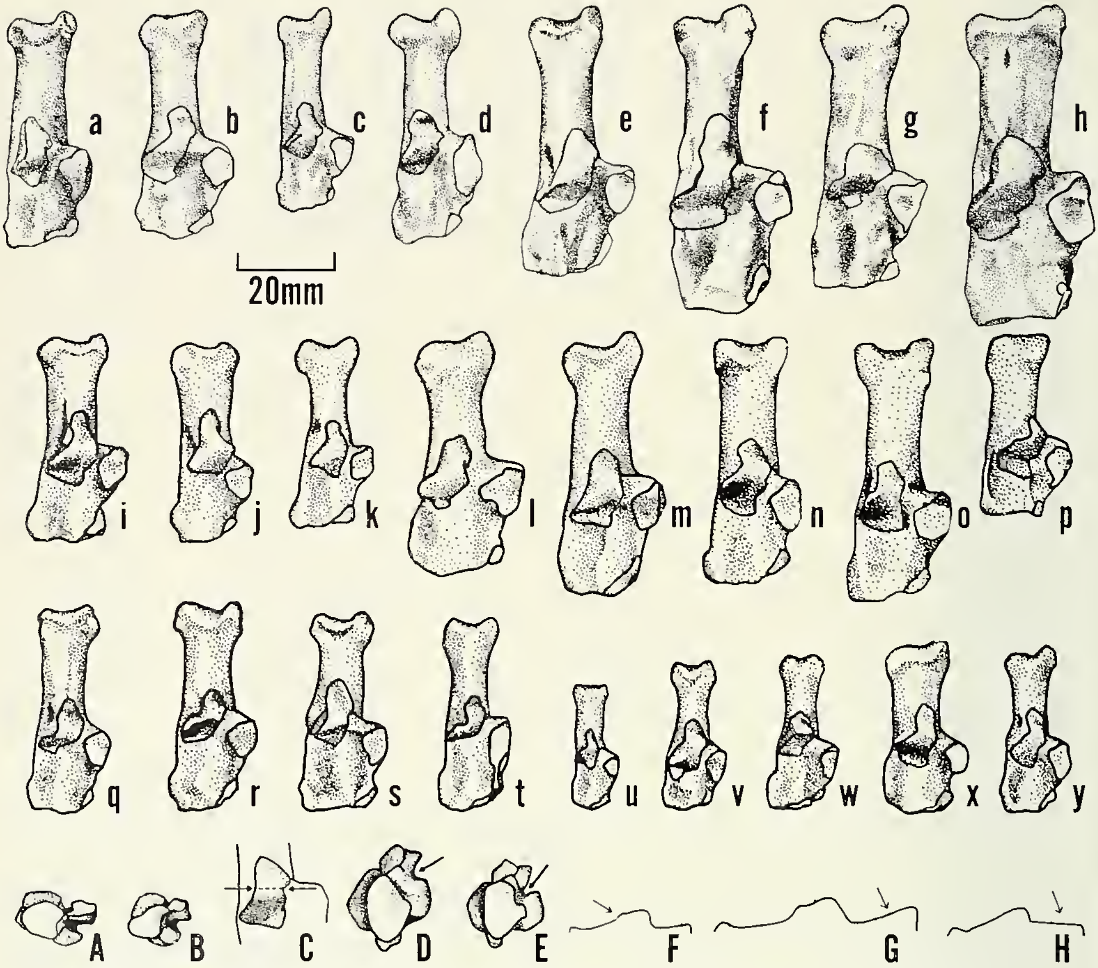

Figure 1. Right calcanea of members of the Canidae. a, *Canis simensis*; b, *Cuon alpinus*; c, *Canis latrans*; d, *Canis dingo*; e, *Lycaon pictus*; f, *Chrysocyon brachyurus*; g, *Canis niger*; h, *Canis lupus*; i, *Cerdocyon thous*; j, *Urocyon cinereoargenteus*; k, *Dusicyon gracilis*; l, *Atelocynus microtis*; m, *Canis aureus*; n, *Canis adustus*; o, *Canis mesomelas*; p, *Speothos venaticus*; q, *Alopex lagopus*; r, *Vulpes fulva*; s, *Vulpes vulpes*; t, *Vulpes chama*; u, *Fennecus zerda*; v, *Vulpes velox*; w, *Vulpes macrotis*; x, *Nyctereutes procyonoides*; y, *Otocyon megalotis*; A, cuboid surface large (*Vulpes velox*); B, cuboid surface small (*Vulpes chama*); C, width post. art. surf.; D, groove absent (*Canis*); E, groove present (*Vulpes*); F, raised post. art. surf. (*Canis*, *Cerdocyon*); G, raised distal end of dorsal table (*Canis*); H, even post. art. suf. and even dorsal table (*Dusicyon*).

tinctly separated from the posterior articular surface by a groove. No such groove occurs in *Urocyon*, the trochlear shelf being a smooth continuation from the posterior articular surface. *Speothos* is more like *Vulpes* in a continuation of the sustentaculum towards the cuboid surface but the distinct sustentacular groove is less developed or absent.

Otocyon megalotis (Fig. 1y) has a calcaneum with a slight extension of the sustentaculum, intermediate between the condition in *Urocyon* and *Vulpes*. There is a groove below the sustentaculum in *Otocyon* similar to the condition found in *Vulpes* (Fig. 1E). The anterior articular surface in *Urocyon* tends to be triangular, being broader on the end closest to the sustentaculum (Fig. 1j). There is an extremely sharp upward folding of the proximal end of the posterior articular surface making this surface extremely sigmoid in *Otocyon*. In *Urocyon* this surface has the usually sigmoid shape without the deep curvature of the proximal end of the surface. *Otocyon* like *Urocyon* has a pit located on the outer surface of the calcaneum ventral to the posterior articular surface.

The calcaneum of *Dusicyon gracilis* (Fig. 1k) falls within the size range (Table 1) and proportions (Table 2) of *Urocyon.* The trochlear process tends to be slightly more massive in *Dusicyon.* The pit ventral and lateral to the posterior articular surface is less distinctive or absent in *Dusicyon.* This pit in *Urocyon* is formed on a ledge which is a proximal extension of the trochlear process. The ledge usually causes a notch on the outer distal edge of the posterior articular surface. Such a notch is absent in the calcanea of *Dusicyon.* The dorsal table, between the posterior articulate surface and the cuboid end of the bone in *Dusicyon,* contains a narrow ridge which separates the inner side (sustentacular side) from the outer side (trochlear side). This ridge in *Urocyon* is much broader at the distal (cuboid) end than at the proximal end. The cuboid surface in *Dusicyon* tends to be more undulating than flat although in some specimens of *Urocyon* there is a tendency towards this undulating nature. This undulating appearance results from the formation of two pit-like surfaces separated by a ridge which runs dorsal-ventral near the center of the surface.

The posterior articular surface is more rounded (marble-like) in *Cerdocyon* (Fig. 1i), not as sigmoid as in *Urocyon.* The ridge on the dorsal table between the trochlear and the sustentacular processes tends to be large on *Cerdocyon* and more obviously expressed on the dorsal edge of the cuboid surface.

The width/total length and dorso-ventral height/total length indices of the one calcaneum of *Atelocynus* separate it from all specimens of *Urocyon.*

Cuon, Lycaon, and *Chrysocyon* are all much larger canids than *Urocyon. Cuon* (Fig. 1b) lacks the deep pit ventral-lateral to the posterior articular surface, *Chrysocyon* (Fig. 1f) has a swelling in this area, and *Lycaon* (Fig. 1e), like *Urocyon,* has an obvious pit. The anterior articular surface in *Lycaon* is elongate and parallel with the interior edge of the dorsal table; in *Urocyon* the anterior articular surface is triangular and parallel with the cuboid surface (Fig. 1j).

Specimens examined: AMNH 35416, 35695, 70441, 77700, 90133–4, 121498, 137994–5, 139252; USNM 771, 968, 974, 21210–3, 21215–7, 21530, 23115, 188087, 240402, 244918, 256058, 257652, 258563, 258568, 282140, 283642 (USNM 283642 illustrated, Fig. 1j).

Nyctereutes procyonoides—Raccoon-Dog

The first impression of the calcaneum of *Nyctereutes* is that it is short and stout (Fig. 1x). This impression is verified by the large width length (avg. 47) and height length (avg. 44) indices; in fact, the highest indices are obtained in specimens of this genus (Table 2).

The proximal location of the trochlear process above the cuboid surface is such that the widest part of this lip-like process is level with the distal edge of the sustentaculum; this proximal location separates the calcanea of *Nyctereutes* from those of all other canids. The position of this process is like that found in some felids and some procyonids; however, unlike those groups, the trochlear process in the raccoon-dog, like in other canids, is not grooved.

The cuboid surface also tends to be more rounded, not elliptical as in other canids.

Specimens examined: USNM 20944, 254641, 255373, 255530, 255532, 256103–4, 260687 (USNM 255530 illustrated, Fig. 1x).

Speothos venaticus—Bush Dog

Speothos venaticus is one of the few canids which has a general tendency for the anterior and medial articular surfaces to be joined which is a felid characteristic. The trochlear process on the calcanea of *Speothos* continues proximally to below the posterior articular surface and a small groove is found between this surface and the trochlear process. This groove continues distally to a rather deep pit located on the dorsal table between the posterior articular surface and the cuboid end of the bone (Fig. 1p). This characteristic of the trochlear process will separate *Speothos* from all other canids.

The posterior articular surface is smooth or weakly sigmoid. This characteristic is rather unusual as most canids have a strongly sigmoid posterior articular surface.

Specimens examined: USNM 253504, 269135 (yg), 270165, 270171, 270368–70, 307650, 314048 (USNM 270369 illustrated, Fig. 1p).

Otocyon megalotis—Big-eared Fox

The differences between the calcanea of *Urocyon* and *Otocyon megalotis* have been discussed under *Urocyon. Fennecus* has a calcaneum below the size range of *Otocyon* in both width and length. The proximal location of the trochlear process of *Nyctereutes* (Fig. 1x), and the groove between the posterior articular surface and the trochlear process of *Speothos* (Fig. 1p), distinguishes these two species from *Otocyon* (Fig. 1y).

Alopex, (Fig. 1q), like *Otocyon,* has an extreme folding of the proximal part of the posterior articular surface making this surface extremely sigmoid. *Otocyon* often has a slight groove ventral to the sustentaculum. This groove is deep on the calcanea of *Alopex* (Fig. 1E). The sustentacular shelf in *Alopex* is more developed than in *Otocyon* and obviously continues to the anterior articular surface which forms part of this shelf (one specimen of *Otocyon* approaches this condition); thus, the cuboid surface is deeply notched between the anterior articular surface and the ventral part of the body leading to the greater tuberosity in *Alopex.*

The cuboid surface extends farther under the trochlear process in *Dusicyon* than in *Otocyon* thus making the cuboid surface more of an elongate oval in *Dusicyon.* The ridge on the dorsal table between the sustentaculum and the trochlear process is narrow in *Dusicyon* (Fig. 1k); in *Otocyon* this ridge is more massive but less obvious.

Otocyon differs from *Cerdocyon* (Fig. 1i) in having a more sigmoid and less marble-like posterior articular surface. The anterior articular surface is seldom dual in *Otocyon* and obviously dual in *Cerdocyon.* The longitudinal ridge on the dorsal table of the calcanea of *Otocyon* is poorly developed; in *Cerdocyon* this ridge is massive and obvious.

The greater tuberosity of *Otocyon* is more obviously hooked when viewed from the lateral aspect than is the greater tuberosity of *Vulpes.* Most specimens of *Otocyon* have a pit located lateral and ventral to the proximal end of the posterior articular surface: this pit is absent in *Vulpes.*

The turning of the proximal end of the posterior articular surface in *Otocyon* makes this surface more strongly sigmoid than is this surface on specimens of the genus *Canis.*

Otocyon differs from *Atelocynus* in having a width/length index below 50 and a dorso-ventral height/length index below 43 (Table 2). All other canids are above the size range of *Otocyon.*

Specimens examined: AMNH 42960, 63993, 85155–6; USNM 240844, 251924, 308667, 319517 (AMNH 63993 illustrated, Fig. 1y).

Alopex lagopus—Arctic Fox

The trochlear process of *Alopex lagopus* is prominent, similar to the condition found in the calcanea of *Urocyon.* As in *Vulpes*, the calcanea of *Alopex* have a distinct sustentacular shelf which forms a prominent groove below the sustentaculum (Fig. 1E). The anterior articular surface is small in *Alopex* and in some cases tends to continue towards the medial articular surface. The posterior articular surface is strongly sigmoid.

In length of calcaneum, *Alopex* is in the size range of some species of *Vulpes, Nyctereutes, Urocyon, Speothos, Otocyon, Dusicyon, Atelocynus,* and *Cerdocyon.* The characteristics of and comparisons with *Nyctereutes, Urocyon, Otocyon,* and *Speothos* have been discussed.

The calcanea of the genera *Alopex* (Fig. 1q) and *Vulpes* (Fig. 1r, s, v, and w) are similar in most respects and difficult to differentiate. The sustentacular shelf extends towards the cuboid surface in both, forming a distinct groove below the sustentaculum. Width/length and dorso-ventral height/length indices are similar in both genera (Table 2). The formation of the longitudinal ridge on the dorsal table between the sustentaculum and trochlear process is similar. The trochlear processes in both genera are similar. The body of the calcaneum of *Alopex* tends to form grooves both below the sustentaculum and trochlear process so that when viewed from the cuboid surface, distinct notches are present between the ventral body and the more dorsal cuboid surface (Fig. 1E). The presence of the trochlear notch will separate most small specimens of *Alopex* from *Vulpes* but in larger specimens of *Vulpes fulva* and *Vulpes vulpes* the trochlear grooves may be present and in larger specimens of *Alopex* the deep distal notch below the trochlear process may be less developed. The calcanea of both *Alopex* and *Vulpes* have small knobs or swellings in the inner and outer edges of the greater tuberosity but the knob on the inner edge of the calcanea of *Alopex* tends to be more obvious (Fig. 1q) and may even be absent on some specimens of *Vulpes.* This feature is a matter of degree and one difficult to measure. The difficulty in separating members of these two genera may be an indication of their close relationship.

The calcanea of *Dusicyon* (Fig. 3k), and *Atelocynus* (Fig. 1l) lack the obvious groove below the sustentaculum and the development of a sustentacular shelf leading to the anterior articular surface. *Cerdocyon,* and especially *Atelocynus,* tend to have calcanea much wider and much higher dorso-ventrally than does *Alopex* (see Table 1). *Alopex* has a much smaller anterior articular surface (3.0–4.7 mm) than does the calcaneum of *Cerdocyon* (Fig. 1i) (4.3–5.8 mm). Only one specimen of *Cerdocyon* has an anterior articular surface below 5 mm in length. Three of 27 specimens of *Alopex* tend to have the anterior and medial articular surfaces joined.

The various species of the genus *Canis* have calcanea which are longer, lack the well developed groove below the sustentaculum (Fig. 1D) and have a posterior articular surface which is weakly sigmoid.

Specimens examined: AMNH 22809, 28114, 28116–9, 35371, 35381; USNM 1039–40, 4544, 6251, 12736, 16120, 16320 (yg), 21506, 49427, 49711, 168231 (yg), 219889, 257836–40, 275050, 291013 (USNM 275050 illustrated, Fig. 1q).

Dusicyon gracilis—South American "Fox"

The calcanea of *Dusicyon gracilis* (Fig. 1k) lack the well-developed sustentacular shelf and groove below the sustentaculum. The cuboid surface is often uneven and undulating. The posterior articular surface is weakly sigmoid. Within the same size range of calcanea examined, differences from *Nyctereutes, Urocyon, Speothos, Otocyon,* and *Alopex* have been discussed.

The extremely high width/length ratio of *Atelocyon* (Table 2) will separate the calcanea of this genus from those of *Dusicyon. Cerdocyon* also tends to have a larger width/length ratio than *Dusicyon.* When viewed from the lateral aspect, the proximal part of the posterior articular surface is raised abruptly above the body in 11 of 13 specimens of calcanea of *Cerdocyon* (Fig. 1F) while in *Dusicyon* this surface raises evenly above the body (Fig. 1H). Although the posterior articular surface of the calcanea of *Dusicyon* and *Cerdocyon* are sigmoid, this surface tends to be more strongly sigmoid in *Dusicyon*. Specimens of *Dusicyon* lack an extension of the sustentacular shelf exhibited by most specimens of *Cerdocyon* (Fig. 1i).

The calcaneum of *Dusicyon* differs from those of the genus *Vulpes* in lacking the extension of the sustentacular shelf to the anterior articular surface and the absence of the well-developed groove below this shelf (Fig. 1D and E). The posterior articular surface is weakly sigmoid in *Dusicyon* compared to that in *Vulpes*.

Most species of the genus *Canis* have larger calcanea than the genus *Dusicyon*. There is a possibility of overlap in size with the species *C. aureus*, *C. adustus*, and *C. mesomelas*. The best measurement to differentiate *Dusicyon* from all species of *Canis* is the dorso-ventral height which ranges from 9.3 to 11.8 mm in *Dusicyon* and from 12.1 to 27.6 mm in all specimens of *Canis* examined. The ridge on the dorsal table between the sustentaculum and the trochlear process is even and narrow in *Dusicyon* (Fig. 1k and H); in *Canis mesomelas* (Fig. 1o) and *C. adustus* (Fig. 1n), this ridge tends to be larger at the distal end near the cuboid surface and forms a distinct knob or raised area when viewed from the lateral aspect (Fig. 1G). The length from the proximal end of the posterior articular surface to the cuboid surface in the calcanea of *Dusicyon* ranges from 14.9 to 18.0 mm, in *C. aureus* from 18.5 to 20.2 mm, in *C. mesomelas* from 18.7 to 20.5 mm, and in *C. adustus* from 18.7 to 21.8 mm. The medial and anterior articular surfaces tend to be more massive in *Canis* than in *Dusicyon*.

Specimens examined: USNM 92139–43, 239991, 256741 (USNM 92143 illustrated, Fig. 1k).

Cerdocyon thous—Crab-eating Fox

Within the size range of the calcanea of *Cerdocyon thous*, and discussed previously, are the calcanea of *Nyctereutes*, *Urocyon*, *Speothos*, *Otocyon*, *Alopex*, and *Dusicyon*. Also within this size range are *Atelocynus*, *Vulpes*, and *Canis*.

The one specimen of *Atelocynus microtis* has a calcaneum with a dorso-ventral height/total length index above any recorded for 13 specimens of *Cerdocyon* (Table 2). The calcaneum of *Atelocynus* (Fig. 1l) lacks any distinct ridge on the dorsal table between the sustentaculum and the trochlear process. The absence of this ridge results in a smooth dorsal edge of the cuboid surface on *Atelocynus* rather than the formation of an angle along this edge of the surface as in the calcanea of *Cerdocyon*. Like many of the specimens of *Cerdocyon*, *Atelocynus* tends to have a posterior articular surface which is faintly sigmoid. Calcanea of *Cerdocyon* tend to have a slight groove below the sustentaculum; no such groove is evident in the calcaneum of *Atelocynus*.

The groove below the sustentaculum in *Cerdocyon* is not as well developed as in the calcanea of members of the genus *Vulpes*. The posterior articular surface is more definitely sigmoid in the genus *Vulpes* than in specimens of *Cerdocyon*. The calcanea of *Cerdocyon* tend to be wider and have a larger width/total length index than do those of *Vulpes* (Table 2) because of a more distinctive and more flaring trochlear process in *Cerdocyon* (Fig. 1i). There is a more obvious second articular surface between the anterior articular surface and the cuboid surface on the heelbones of *Cerdocyon* than on *Vulpes*. Most specimens of *Vulpes* have a distinct swelling lateral and proximal to the posterior articular surface; neither a swelling or pit is present in the calcanea of *Cerdocyon*.

Species of the genus *Canis* with calcanea within the size range of *Cerdocyon* are *C. aureus*, *C. adustus*, *C. mesomelas* and some specimens of *C. latrans*. Because of the greater flaring of the trochlear process, thus a more obvious process, the width length index of calcanea of *Cerdocyon* tends to be larger than in *Canis* (Table 2). The well-developed ridge on the dorsal table of the calcanea of *Cerdocyon* is reflected in the angular dorsal edge of the cuboid surface. In *Canis* this ridge is not as well developed because of the lack of a deep furrow between the ridge and the trochlear process thus the dorsal edge of the cuboid surface is a gentle curve. The only change in curvature in *Canis* is at the level of the anterior articular surface rather than at the point of interception of the ridge. *Canis* like *Cerdocyon* has a raised posterior articular surface (Fig. 1F).

Specimens examined: AMNH 10091, 14635, 23505–6, 133925, 133935, 134049; USNM 49742, 175779 (malformed), 196974, 239964–5, 253240, 270367 (AMNH 134049 illustrated, Fig. 1i).

Atelocynus microtis—Small-eared Dog

Only one specimen of *Atelocynus microtis* was available for study. This single specimen has an extremely wide calcaneum compared to total length. Six of 13 specimens of *Cerdocyon*, five of eight specimens of *Nyctereutes*, four of eight specimens of *Speothos*, one of nine specimens of *Canis dingo*, four of 30 specimens of *Urocyon*, one of seven specimens of *Otocyon*, and one of 11 specimens of *Lycaon* have W TL indices above 47. *Cerdocyon*, *Nyctereutes*, and *Speothos*, each have one specimen with an index of 50 or above. The index of the single specimen of *Atelocynus* is 51.

Of the above species only *Canis dingo* and *Lycaon* have not been discussed. Both of these have calcanea much larger than *Atelocynus*. *Atelocynus* has a minute anterior articular surface with a minute additional surface between it and the cuboid surface. Both *Lycaon* (Fig. 1e) and *C. dingo* (Fig. 1d) have large well-developed additional surfaces between the anterior articular surface and the cuboid surface. Also, in both, the anterior articular surface is well developed.

Specimen examined and illustrated: AMNH 100095 (Fig. 1l).

Vulpes macrotis—Kit Fox

General comparisons of the calcanea of the genus *Vulpes* with other genera in the same size range have been made. Most species of *Vulpes* have a weakly grooved trochlear process. The calcanea of *Vulpes macrotis* are smaller than any recorded for members of the genus *Canis*. Of the genus *Vulpes*, only the calcanea of *Vulpes velox* overlap in size with *Vulpes macrotis*. The trochlear process is more distinctly knoblike in *V. macrotis* (Fig. 1w) than in *V. velox* (Fig. 1v).

Of the genus *Vulpes*, *V. macrotis* has the smallest calcaneum. Only one of 14 specimens of *V. velox* falls within the size range of total length exhibited by the 8 specimens of *V. macrotis*. *V. macrotis* tends to have a wider calcaneum than *V. velox* so that the width/length index in *V. macrotis* is larger (see Table 2). Two specimens of *V. velox* have an index of 42 while all specimens of *V. macrotis* have indices of 42 or above. *Vulpes macrotis* tends to have calcanea with a smaller dorso-ventral height than *V. velox*. Three of 8 specimens of *V. macrotis* have a dorso-ventral height of 9 mm and 3 of 14 specimens of *V. velox* have a dorso-ventral height below 9 mm. If a specimen had either a total length of 24 mm or above, a dorso-ventral height of 9.2 mm or above, or a width/length index 41 or below, the specimen was *Vulpes velox*. In no case did any of the specimens of *V. velox* that overlapped with *V. macrotis* in size lack all three of these characteristics.

If the total length of the specimen is subtracted from the width/total length index, the calcanea of *V. macrotis* ranged from 18.7 to 21.7 and the calcanea of *V. velox* from 11.5 to 17.8.

Specimens examined: USNM 270351–2; KU 14414, 47968–71, 47988 (USNM 270351 illustrated, Fig. 1w).

Vulpes velox—Swift Fox

The differences between the calcanea of *V. velox* and *V. macrotis* are discussed under *V. macrotis*. Also within the size range of *V. velox* are the calcanea of *Vulpes chama* and *V. fulva*.

Many specimens of both *V. velox* (Fig. 1v) and *V. chama* (Fig. 1t) have calcanea in which the anterior and medial articular surfaces are joined by a thin waist or tend to be joined. In the calcanea of *V. chama*, the anterior articular surface tends to be divided by a groove so that the part joining the medial articular surface is minute and the other part above the dorsal edge of the cuboid surface is elongate and thin. In comparison with *V. velox*, which lacks this division, the articulating part of the cuboid surface of *V. chama* is small compared with the total cuboid area (Fig. 1B) while in *V. velox* the articular part of the cuboid surface is practically the entire length of the distal end of the bone (Fig. 1A). The calcanea of *V. velox* tend to be smaller than those of *V. chama*. Only three of 13 specimens of *V. velox* are as large as those of *V. chama*.

Vulpes velox has a smaller calcaneum than those of most *V. fulva*. Only one of 31 specimens of *V. fulva* fall within the range of size (total length) of the calcanea of *V. velox*. No specimens of *V. velox* (9.1–10.6 mm) were as wide as the narrowest recorded specimen of *V. fulva* (10.8–14.0 mm).

Specimens examined: AMNH 100190, 100215; USNM 21663, 22812–3; KU 65956, 68150, 68430, 72375, 72378, 81912–3, 81918, 83573 (USNM 21663 illustrated, Fig. 1v).

Vulpes chama—Cape Fox

Of the various species of *Vulpes*, the calcanea of *V. chama* have the most obvious grooved trochlear process. There is some indication of a groove in some specimens of other species of *Vulpes*. The dual nature of the anterior articular surface will separate *V. chama* (Fig. 1t) from the other species of *Vulpes* (see discussion under *V. velox* for a more detailed description of the groove between the dual anterior articular surface).

Specimens examined: USNM 253245, 253403 (USNM 253245 illustrated, Fig. 1t).

Vulpes fulva—Red Fox

Comparisons of *Vulpes fulva* with the small species of *Vulpes*, and other genera within the size range of *V. fulva*, except *V. vulpes*, have been made. The three specimens of *V. vulpes* available tend to be longer and wider than those of *V. fulva* although 13 of 31 specimens of *V. fulva* are as large as the smallest specimen of *V. vulpes* in width of the calcaneum. These two species cannot be separated with certainty and most mammalogists today consider them to be the same species.

Also falling within the size range of *V. fulva*, and not discussed previously, are *Canis aureus*, *C. adustus*, and *C. mesomelas*. Specimens of the genus *Canis* lack the well-developed groove found under the sustentaculum of *Vulpes* (Figs. 1D and E) and do not have the strongly sigmoid posterior articular surface found in specimens of the genus *Vulpes*. The anterior articular surface of specimens of *Vulpes* lack the well-developed dual nature as expressed in the genus *Canis*. Specimens of the genus *Canis* have a massive, indistinct trochlear process with no indication of a groove. In general, specimens of the genus *Vulpes* have a dorso-ventral height/total length index averaging between 38 and 39 while this index in *Canis* averages between 40 and 42 (see Table 2).

Specimens examined: AMNH 90109, 97652, 128486–8, 128490–1 (yg), 128708, 141148, 166938; USNM 678, 768, 1325, 7544–7, 21117, 21155–7, 22063, 23013, 35106, 49332, 257841, 258630, 260344, 260347, 279384, 283672 (USNM 279384 illustrated, Fig. 1r).

Vulpes vulpes—Common Red Fox

The calcanea of *V. vulpes* and *V. fulva* could not be separated with certainty thus characteristics of the calcanea of *V. fulva* can be used to identify *V. vulpes*. The three specimens of *V. vulpes* tend to be larger than those of *V. fulva*. As mentioned previously, most mammalogists today consider *V. vulpes* and *V. fulva* to be the same species; the study of calcanea support this viewpoint.

Specimens examined: AMNH 69550; USNM 1038, 253782, 254639 (yg) (USNM 253782 illustrated, Fig. 1s).

Canis sp.

The various species of *Canis* have calcanea which lack a distinct groove below the sustentaculum (Fig. 1D); also in *Canis* the posterior articular surface is weakly sigmoid. Of the species available for study, *C. aureus, C. adustus,* and *C. mesomelas* have the smallest calcanea, *C. latrans, C. simensis,* and *C. dingo* are intermediate in size, and *C. niger* and *C. lupus* are larger than any other member of the genus.

Differences between *Canis* and the smaller species have been discussed. Differences between *Cuon, Lycaon, Chrysocyon,* and *Canis* will be discussed under the species of *Canis* of similar size.

Canis aureus—Asiatic Jackal

Canis aureus is the smallest species of the genus *Canis* in terms of average length, width, and dorso-ventral height of calcaneum. Overlapping the calcanea of *Canis aureus* in size, however, are the calcanea of *C. adustus, C. mesomelas,* and *C. latrans*. The calcanea of *C. aureus* (Fig. 1m) and *C. latrans* (Fig. 1c) have a prominent ridge across the dorsal table from the inner distal edge of the posterior articular surface to the dorsal edge of the cuboid surface. In *C. adustus* (Fig. 1n) and *C. mesomelas* (Fig. 1o), this ridge is absent although there is a swelling near the cuboidal area. *Canis aureus* differs from *C. latrans* in having a large, elongate anterior articular surface (over 5 mm in greatest length); the anterior articular surface of *C. latrans* varies considerably but is much smaller (usually less than 5 mm) than that found in *C. aureus* especially when total length of the calcaneum is considered.

Specimens examined: AMNH 52049, 54516; USNM 163293, 163301–2, 164750 (AMNH 52049 illustrated, Fig. 1m).

Canis adustus—Side-striped Jackal

The calcaneum of *Canis adustus* (Fig. 1n) lacks the prominent longitudinal ridge across the dorsal table. Within the same size range and usually lacking this ridge is *Canis mesomelas* (Fig. 1o). In some specimens of *C. mesomelas* a slight angular ridge runs from between the posterior and medial articular surfaces to the central-distal edge of the dorsal table. The ridge in *C. aureus* (Fig. 1m) runs from near the center of the distal edge of the posterior articular surface to the central-distal edge of the dorsal table. Both *C. adustus* and *C. mesomelas* have a more sigmoid posterior articular surface than *C. aureus*.

Canis adustus overlaps in size of calcaneum with that of *C. latrans* although only one specimen of *C. adustus* is as long as two of the smaller specimens of *C. latrans*. There is more overlap in width and dorso-ventral height of the calcanea of these two species. The anterior articular surface of *C. adustus* (Fig. 1n) is larger than that of the calcanea of *C. latrans* (Fig. 1c) which is small and tends to be more nearly round in shape. The prominent longitudinal ridge across the dorsal table of *C. latrans* also will distinguish the two species.

Specimens examined: AMNH 27741, 33322, 34733, 82090, 83329 (yg) (AMNH 27741 illustrated, Fig. 1n).

Canis mesomelas—Black-backed Jackal

The similarities and differences between the calcanea of *C. mesomelas, C. aureus,* and *C. adustus* have been discussed. These three species are difficult to distinguish with certainty. *Canis mesomelas* (Fig. 1o), like *C. adustus*, differs from *C. latrans* (Fig. 1c) in having an elongate anterior articular surface which is seldom dual, and a less prominent longitudinal ridge of the dorsal table which, if present, tends to be at an angle across the table. There is only a slight overlap in total length of the calcanea of *C. mesomelas* and *C. latrans* with one specimen of *C. latrans* being as small as five of the specimens of *C. mesomelas*. The average dorso-ventral height and calcaneal width of *C. latrans* is larger than the largest measurement of any calcanea of *C. mesomelas*.

Specimens examined: AMNH 3770, 34734, 54209, 114228; USNM 162902, 164611, 164614, 164699, 164752–3 (yg), 241589, 251920–1 (USNM 164752 illustrated, Fig. 1o).

Canis latrans—Coyote

The calcanea of *Canis latrans* overlap those of *C. aureus, C. adustus,* and *C. mesomelas* slightly in size but on the average are much larger than any of these three species. The minor differences between these three species and *C. latrans* have been discussed under each species. The calcanea of *C. latrans* also overlap those of *C. simensis, C. dingo,* and *C. niger*, in length, width, and dorso-ventral height but on the average are much smaller than either of these species.

The calcanea of *C. dingo* (Fig. 1d) do not have a prominent longitudinal ridge on the dorsal table as exhibited by *C. latrans* (Fig. 1c). The calcanea of

C. dingo vary greatly in most characteristics but tend to average much larger than *C. latrans* with but few of them being smaller than the average calcaneum of *C. latrans.* The posterior articular surface tends to be more sigmoid and higher above the body in the calcanea of *C. dingo* and the tuberosity tends to be more flaring in *C. dingo* than *C. latrans.* The medial articular surface in *C. latrans* tends to be basin-shaped thus the lateral edge of this surface is curved while in *C. dingo* this surface is flat with no indication of a curved edge.

Some 46 specimens which may be those of *C. niger* are available and most of these have larger calcanea. The measurement of dorso-ventral height seems to be the most distinctive. There are specimens available which bridge the measurements shown in Table One of these two species but the identity of these red wolf specimens is not settled. They may be *C. niger*, *C. latrans*, coyote-dog hybrids or even *C. niger-C. latrans* crosses. Presently, the status of *C. niger* as a distinct species is even being considered. Examination of calcanea has not helped to solve the problem except to show that these are not distinct groups. Both *C. latrans* and *C. niger* have a distinct longitudinal ridge on the dorsal table.

Only one calcaneum of *C. simensis* was available for study but only two of 50 specimens of *C. latrans* were as long or longer, only four had a dorso-ventral height as high or higher, and only seven had a width as wide or wider. Except for the anterior articular surface, the calcaneum of *C. simensis* (Fig. 1a) resembles closely that of a large coyote. The anterior articular surface of *C. simensis* is 8.5 mm long and extremely narrow.

Also within the size range of *C. latrans* are the calcanea of *Cuon alpinus* and *Lycaon pictus.* The anterior articular surface is much longer (7.7–9.6 mm) in *Cuon* (Fig. 1b) than *Canis latrans* (3.2–6.5 mm). No specimens of calcanea of *C. latrans* were as wide as those of *Cuon.* The anterior articular surface of *Lycaon pictus* (Fig. 1e) tends to parallel the long axis of the calcaneum and in general is longer (5.4–9.1 mm). No calcanea of *C. latrans* were as wide or had a dorso-ventral height as great as those of *L. pictus.*

Specimens examined: AMNH 5021, 70053, 123026, 123182, 125408, 130140, 131833, 131835, 136419, 141151–64, 141166–73, 141175; USNM 1326, 1381–2 (yg), 21496, 21740–3, 22660–2, 49392, 49735, 49889–90, 49899, 270340, 291937–8 (AMNH 131833 illustrated, Fig. 1c).

Canis simensis—Abyssinian Wolf

Comparisons of the calcaneum of *Canis simensis* with those of *C. latrans* have been made. *Canis dingo*, *Canis niger*, and *C. lupus* as well as *Cuon alpinus* and *Lycaon pictus* probably are within the range of length of the calcanea of *C. simensis.*

Except for width, the size of the single specimen of *C. simensis* is near the average of the calcanea of *C. dingo.* The anterior articular surface is extremely long and narrow in *C. simensis* (Fig. 1a) while in *C. dingo* it is short and triangular (Fig. 1d). The edge of the sustentaculum is slightly grooved in *C. simensis* and *C. latrans* but is not grooved in *C. dingo.*

The 46 specimens of *C. niger* are much larger than *C. simensis* but more specimens of *C. simensis* might result in an overlap in size range. The calcaneum of *C. niger* (Fig. 1g) has a deep, broad basin between the medial and anterior articular surfaces. This basin is shallow and narrow in *C. simensis.*

All 26 specimens of *Canis lupus* have calcanea which are longer, wider, and have a greater dorso-ventral height than the one specimen of *C. simensis* but overlap also is probable in these two species. The basin or groove on the edge of the sustentaculum of *C. simensis* is faintly present in *C. lupus*, is only at the distal end of the sustentaculum in *Cuon*, and absent in *Lycaon.*

The anterior articular surface of the calcanea of *Lycaon* (Fig. 1e) tends to be parallel with the long axis of the bone not parallel to the edge of the cuboid surface as in *C. simensis* (Fig. 1a). The calcanea of *Lycaon* are much wider and have greater dorso-ventral height than those of *C. simensis.* The width of the calcanea of *Cuon* also ranges above that of *C. simensis* (Table 1).

Specimen examined and illustrated: AMNH 81001 (Fig. 1a).

Canis dingo—Dingo

The calcanea of *Canis dingo* are more varied than any other canid examined in articular surfaces as well as sizes and proportions. In total length there is a range of 18.8 mm in the nine specimens of the dingo examined; only *C. lupus*, a larger and more widespread animal geographically, with 26 specimens available, surpasses this (19.8 mm) and no other canid approaches this amount of variation. The same is true of width (*C. dingo* 8.4; *C. lupus* 9.7); width divided by total length (*C. dingo* 8; *C. lupus* 9); dorso-ventral height (*C. dingo* 8.4; *C. lupus* 8.5); and dorso-ventral height divided by total length (*C. dingo* 5; *C. lupus* 7).

In all specimens of the dingo examined, the edge of the sustentaculum is smooth without indication of a groove. The posterior articular surface varies in its sigmoid nature; in some the proximal edge is high with a pronounced dip distal to this and in others low with but a slight dip. The dorsal table lacks a distinct ridge. The anterior articular surface varies from 4.3 to 7.1 mm in length, is triangular in most cases, and usually has an additional surface between it and the cuboid surface.

The calcanea of *C. dingo* overlap in size those of *C. latrans*, *C. simensis*, *C. niger*, *C. lupus*, *Chrysocyon brachyurus*, *Cuon alpinus*, and *Lycaon pictus.* Comparisons with the first two species named have been made.

Only three specimens of *C. dingo* examined are as large as the 46 specimens of *Canis niger*. *Canis niger* (Fig. 1g) has a distinct longitudinal ridge which is absent in *C. dingo*. Only seven of 26 specimens of *C. lupus* (Fig. 1h) lack this longitudinal ridge. Two of these seven are from the Old World (Sweden and Kashmir), the only specimens examined from that part of the world. Another came from Mexico and the other three were zoo specimens. All wolves taken in the wild in Canada, Alaska, and western North America had a distinct ridge. The ridge on the three remaining zoo specimens was present but not well developed. The posterior articular surface of *C. lupus* is similar to *C. dingo*.

The calcanea of *Chrysocyon brachyurus* average longer than the largest dingo examined and average much higher in dorso-ventral height. The outer, distal edge of the calcaneum of *Chrysocyon* (Fig. 1j) slopes inward from a point opposite the distal edge of the sustentaculum thus making the bone appear compressed at the distal end. No other canid has this extreme in narrowing at the distal end. As a result, the width of the calcaneum is less compared to length which is obvious when width is divided by total length (range 36–40 as compared to *C. dingo* which ranges from 39–47). In all cases the dorso-ventral height is greater than the width of the bone in *Chrysocyon* (from 1 to 4.1 mm higher than wide); in all but two cases the width is greater than dorso-ventral height in *C. dingo* and in these two cases the difference is only 0.5 and 0.4 mm.

The calcaneum of *C. dingo* differs from that of *Cuon alpinus* (Fig. 1b) in having a much smaller anterior articular surface (*C. dingo*, 4.5–6.8 mm; *Cuon alpinus*, 7.7–9.6 mm). In addition, the distal half of the posterior articular surface does not form as steep an angle in *C. dingo* as in *Cuon*. All measurements and proportions of the calcanea of *Cuon* are within the range of measurements and proportions of *C. dingo*. This again is an indication of the variability of *C. dingo* compared with that found in other canids.

Lycaon pictus, like *Cuon*, has calcanea largely within the range of *C. dingo* but do average much larger. The anterior articular surface of the calcanea of *Lycaon* (Fig. 1e) tends to be more parallel to the long axis of the bone while that of *C. dingo* runs along the distal edge of the bone. Individuals of both species with small triangular anterior articular surfaces, however, are difficult to differentiate on the above characteristic. All specimens of *Lycaon* have one or two long, deep pits lateral and ventral to the proximal part of the posterior articular surface. Bones of *C. dingo* lack these pits.

Specimens examined: AMNH 35175, 65845, 99693 (yg), 100318; USNM 197076, 218830, 238468, 251769, 254718, 259846 (USNM 218830 illustrated, Fig. 1d).

Canis niger—Red Wolf

Comparisons with *C. dingo* and *C. simensis* have been made. Calcanea of *Canis lupus*, *Canis laterans*, *Chrysocyon brachyurus*, *Lycaon pictus* and probably *Cuon alpinus* fall within the range of *C. niger*. The 46 specimens of *Canis niger* bridge the size gap between the coyote (*Canis latrans*) and the timber wolf (*C. lupus*).

The calcanea of *C. niger* (Fig 1g) have a well developed longitudinal ridge on the dorsal table as do many specimens of *C. lupus* (Fig. 1h) and *C. latrans* (Fig. 1c). In general, it probably would be difficult to distinguish the calcanea of *C. niger* from smaller specimens of *C. lupus* or the larger specimens of *C. latrans*.

Lycaon pictus (Fig. 1e) and *Cuon alpinus* (Fig. 1b) lack a well developed longitudinal ridge on the dorsal table; *Chrysocyon* (Fig. 1f) has some indication of the ridge. The anterior articular surface is not unlike that in *C. lupus* or *Chrysocyon*. The deep groove between the medial and anterior articular surfaces of *C. niger*, separate *C. niger* from *Cuon* (Fig. 1b). The anterior articular surface is parallel with the long axis of the bone in *Lycaon* (Fig. 1e).

The elaborate sculpturing on the dorsal table of most specimens of *Chrysocyon* (Fig. 1f) and the narrowing of the distal end of the calcaneum will separate this genus from *C. niger*. In addition, the extremely narrow body of *Chrysocyon* (6.5–8.0 mm, in least width of body) should separate this species from many specimens of *C. niger* (5.6–9.7 mm) especially if this is divided by the dorso-ventral height (*Chrysocyon* 26–29, avg. 28; *C. niger* 31–39, avg. 36).

Specimens examined: USNM 267973; HJS 1551–5, 1757–1796 (HJS 1552 illustrated, Fig. 1g).

Canis lupus—Gray Wolf

Overlapping *Canis lupus* in size of calcaneum and not discussed thus far, are calcanea of *Cuon alpinus*, *Lycaon pictus*, and *Chrysocyon brachyurus*.

The posterior articular surface of *C. lupus* measured at the point of the angle of change near the center of the surface (Fig. 1C) is wider (7.1–11.2 mm) than that of the calcaneum of *Cuon* (5.3–6.8 mm). The anterior articular surface in *Cuon* (Fig. 1g) is elongate, narrow, and parallel with the distal edge of the calcaneum along the cuboid surface. The anterior articular surface in *C. lupus* varies tremendously. In some specimens, hardly any surface is present with the formation of an additional surface between the normal position of the anterior articular surface and the cuboid surface (Fig. 1h), in others the surface is triangular, and in others elongate. The additional surface (articulation with the scaphoid) is present in all specimens of *C. lupus* but in some the surface is minute. This additional surface also is present in three of the five calcanea of *Cuon* examined.

The most obvious difference between *Lycaon pictus*

TABLE 3. Summation of indices of the genera and species of the Canidae

	Total of Three Indices (W/TL, LWB/D-WH, D-VH/TL)			Total of Three Indices (W/TL, LWB/D-WH, D-VH/TL)	
Species*	Range	(avg)	Species	Range	(avg)
15	130.4–142.1	(135.8)	20	110.2–122.6	(115.6)
11		(131.9)	22	120.1–128.6	(124.0)
24	129.2–138.8	(134.1)	23	114.1–125.1	(119.9)
16	119.6–134.5	(126.6)	*Canis* sp.	109.9–134.2	(118.1)
12	118.7–130.8	(125.5)	4	111.9–134.2	(124.3)
25	116.6–132.3	(122.1)	2	121.4–123.1	(122.0)
1	113.0–129.8	(121.2)	3	117.5–123.6	(121.8)
13	113.0–128.2	(120.3)	6	113.6–130.1	(120.9)
14	102.4–124.2	(118.8)	8	110.6–124.1	(117.3)
Vulpes sp.	109.9–130.6	(117.7)	7	113.2–122.3	(117.8)
21	114.1–130.6	(120.4)	9		(116.7)
17	116.3–122.0	(119.2)	5	109.9–129.4	(115.9)
18	109.9–124.1	(118.6)	10	107.8–112.2	(110.3)
19	110.8–120.1	(116.2)			

* See Table 1.

and *C. lupus* is the presence of one or two long, deep pits lateral and ventral to the proximo-lateral edge of the posterior articular surface in *Lycaon* (Fig. 1e); *C. lupus* lacks these obvious pits. In addition, the anterior articular surface tends to be parrallel with the long axis of the calcaneum of *Lycaon*.

The high dorso-ventral height (22.4–28.0, avg. 25.6 mm) and narrow least width of the body (6.5–8.0, avg. 7.3 mm) of the calcanea of *Chrysocyon* results in a least width of body dorso-ventral height index of 26–29, avg. 28. In *C. lupus* the dorso-ventral height (19.1–27.6, avg. 24.0 mm) and least width of the body (7.0–11.5, avg. 9.2 mm) produces an index of 32–45, avg. 38. Thus, there is no overlap in these indices in the two species.

Specimens examined: AMNH 14036–7, 16138, 35553, 98225–7, 98231–2, 121086, 134940–4; USNM 977, 1035, 1308, 1384, 3497, 7154, 49978, 198458, 251794, 268194, 269140 (AMNH 98231 illustrated, Fig. 1h).

Cuon alpinus—Dhole

The calcanea of *Cuon alpinus* have been compared previously with all species within the same size range except *Lycaon pictus* and *Chrysocyon brachyurus*.

The anterior articular surface of *Lycaon* (Fig. 1e) tends to be parallel with the long axis of the calcaneum not parallel with the distal edge along the cuboid surface as in *Cuon* (Fig 1b). In addition, the calcaneum of *Lycaon* has one or two deep, longitudinal pits lateral and ventral to the proximo-lateral edge of the posterior articular surface; calcanea of *Cuon* lack these pits.

The least width of body/dorso-ventral height index of *Cuon* ranges from 35–41 (avg. 38) far above that of *Chrysocyon* (26–29, avg. 28).

Species examined: AMNH 54977, 54984; USNM 196979, 258648, 258985 (USNM 258648 illustrated, Fig. 1b).

Lycaon pictus—African Hunting Dog

The tendency for the anterior articular surface to be parallel with the long axis of the calcaneum, separates *Lycaon* (Fig. 1e) from most specimens of all other genera of the family *Canidae*. The one or two deep, longitudinal pits lateral and ventral to the proximo-lateral edge of the posterior articular surface also are found only in *Lycaon*.

Specimens examined: AMNH 35177, 35295, 70443, 120942; USNM 163291, 181508–12, 237568 (USNM 181509 illustrated, Fig. 1e).

Chrysocyon brachyurus—Maned Wolf

The easiest way to differentiate this species from all other canids of similar size is on the basis of the least width of body/dorso-ventral height index which is lower in *Chrysocyon* (Table 2). One of seven specimens of *Fennecus zerda* falls within (actually below) the above index for *Chrysocyon* but the calcaneum of *Fennecus* is much smaller in all basic measurements (Table 1). *Lycaon pictus* approaches *Chrysocyon* in the LWB/D-VH index. All species within the same size range of the maned wolf have been discussed.

Specimens examined: AMNH 133940–1; USNM 261022–3, 270371 (USNM 261022 illustrated, Fig. 1f).

CONCLUSIONS

The calcanea of the canids are similar in most respects. There are four genera that are distinct because of the unusual development of the trochlear process, shape of the posterior articular, or form of the medial and anterior articular surfaces. These four genera are *Speothos*, *Nyctereutes*, *Atelocynus*, and *Chrysocyon*. These same genera also stand out as distinctive if one but adds together the three ratios or indices taken: width/total length; dorso-ventral height/total length; and least width of body/dorso-ventral height (Table 3).

Speothos venaticus (Fig. 1c) has the most aberrant calcaneum with a smooth posterior articular surface rather than sigmoid, a tendency for the anterior and medial articular surfaces to be joined, and a groove between the outer edge of the posterior articular surface and the trochlear shelf. This genus also has a high value when the various indices are added (Table 3). The highest least width of body/dorso-ventral height index was recorded for this species as well as one of the higher width/total length indices (Table 2).

The next most aberrant calcaneum is that of *Nyctereutes procyonoides*. This calcaneum is extremely short and broad, giving large width/total length and dorso-ventral height/total length indices (Table 2). The trochlear process is located farther proximally than that of any other canid. Of the other canids, *Atelocynus* approaches *Nyctereutes* the closest in general form and also gives a large combination total of indices (Table 3).

The distal-sloping trochlear process of *Chrysocyon* produces a calcaneum with one of the lowest width/total length indices and the extremely thin body results in one of the lowest least width of body/dorso-ventral height indices (Table 2). When all three indices are combined, *Chrysocyon* has the lowest average (Table 3). Of the other canids, *Chrysocyon* is most similar to *Canis* although most species of *Canis* do not have the extreme sigmoid posterior articular surface of *Chrysocyon*. Although the trochlear process is located proximally in *Chrysocyon*, it has the massive appearance of those of *Canis*.

Canis usually has a smooth or weakly sigmoid posterior articular surface (except some specimens of *C. latrans*, *C. dingo*, *C. simensis*, and *C. adustus*). The trochlear process tends to be massive but not distinct at the distal end. Of the species, *Canis dingo* is the most variable and has one of the greatest spread of measurements (topped by the much larger *C. lupus*, Table 1) and the greatest spread of added indices (Table 3). This variability is the type obtained in domestic dogs and is, perhaps, an indication of the past history of the dingo in Australia.

The calcanea of *Lycaon* and *Cuon* are similar in many respects with a distinct distal trochlear process (like *Vulpes*) and an almost smooth posterior articular surface (like *Canis*). Thus these genera seem to be intermediate to the two major types, *Vulpes* and *Canis*.

Rather similar in most respects are the calcanea of *Vulpes*, *Fennecus*, *Alopex*, *Urocyon*, *Cerdocyon*, *Dusicyon*, and *Otocyon*. All have strongly sigmoidal posterior articular surfaces and a small but slightly expanded trochlear process located near the distal end of the bone. *Urocyon* and *Cerdocyon* appear to have slightly larger total indices than the other genera in this group (Table 3) although they are not difficult to distinguish. The trochlear process of *Vulpes*, especially *V. chama*, sometimes is faintly grooved.

Unique among the Carnivora is the dual anterior articular surface found in all members of the Canidae. This dual surface articulates proximally with the astragulus, as in all carnivores, and with the scaphoid distally, as in few other carnivores; although completely articulated feet were not examined, there are a few cases where such an additional articular relationship may be found at a later date. For example, crab eating raccoon (*Procyon cancrivorous*) and the cheetah (*Acinonyx*) appear to have dual anterior articular surfaces.

ACKNOWLEDGMENTS

Richard Van Gelder and Sydney Anderson, of the American Museum of Natural History (AMNH), and David Johnson and Henry Setzer of the U.S. National Museum (USNM), loaned the specimens which made this study possible as well as checked the identification of a few of the specimens. Frederick Knowlton and Robert Reynolds of the U.S. Fish and Wildlife Service were kind enough to make a special effort to obtain calcanea from red wolves killed on various ranches in Texas; these are now in my collection (HJS). Before this, only one specimen was available. A few specimens were examined in the collection at University of Kansas (KU), and J. Knox Jones, Jr. is acknowledged for making these available.

Miss Merl Stahlberg and Miss Billy Perkins did the completed drawings found in this work.

A grant (No. 2843, 1960) by the American Philosophical Society permitted the Author to study some fossil calcanea (not included in this study) and borrow personally the bones used in this work. Support by the Graduate School, Southern Illinois University made possible the visits to museums as well as the payments for the art work.

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EVOLUTIONARY IMPLICATIONS OF THE KARYOTYPES OF THE STENODERMINE GENERA *ARDOPS*, *ARITEUS*, *PHYLLOPS*, AND *ECTOPHYLLA*

Ira F. Greenbaum[1], Robert J. Baker[1], and Don E. Wilson[2]

Abstract: Karyotypes of representatives of four genera of the subfamily Stenoderminae (Phyllostomatidae), *Ardops*, *Ariteus*, *Phyllops*, and *Ectophylla* are presented. Karyotypic characteristics of *Ardops*, *Ariteus*, and *Phyllops* support a close relationship between these genera and the genera *Stenoderma* and *Ametrida*. The karyotype of *Ectophylla alba* does not support the conclusion that it is congeneric with the morphologically similar *Mesophylla*. Chromosomally, *Mesophylla* and *Vampyressa pusilla* are more closely related to each other than either is to *Ectophylla* or the other species of *Vampyressa* that have been karyotyped. Evolutionary, early distributional, and taxonomic aspects of the genera involved are discussed.

In 1973 when Baker constructed a phylogeny of the subfamily Stenoderminae (Phyllostomatidae) based on karyotypic characteristics, data were available from representatives of all genera except *Ardops*, *Phyllops*, *Pygoderma*, *Ariteus*, and *Ectophylla*. We report chromosomal data for all of these except *Pygoderma*.

METHODS

Specimens were collected from natural populations and standard bone marrow preparations (Patton, 1967; Baker, 1970) were made for *Ardops nichollsi*, *Ariteus flavescens*, and *Phyllops haitiensis*. Ear biopsies of a specimen of *Ectophylla alba* were collected and primary cultures were grown and karyotyped at Texas Tech University. Metacentric, submetacentric, subtelocentric, acrocentric, and fundamental number are defined by Patton (1967).

RESULTS

Ardops nichollsi, *Ariteus flavescens*, and *Phyllops haitiensis* have diploid values of $2N = 30$♀♀, 31♂♂, and a fundamental number of $FN = 56$ (Figs. 1, 2, and 3). The autosomal complement of the representatives of each genus is comprised entirely of biarmed elements with 10 pairs of metacentric or submetacentric chromosomes and four pairs of subtelocentric chromosomes. The sex-determining system in these species appears to be similar to that described for the stenodermine genus *Artibeus* where an autosome has been translocated to the X but its homologue has not been translocated to the Y (Hsu *et al.*, 1968; Becak *et al.*, 1969). In *Ariteus* and *Phyllops* (Figs. 2 and 3) the X appears to be a subtelocentric chromosome, whereas in *Ardops* (Fig. 1) the X appears to be a submetacentric chromosome. Male specimens of these three genera have two small Y chromosomes, one which shows a small second arm and one which is a small acrocentric.

The karyotype of *Ectophylla alba* has a diploid value of 30 and a fundamental value of 56 (Fig. 4). The autosomal complement is essentially identical to that described for the three genera discussed above. The sex-determining system of *Ectophylla* appears to be the classical XX/XY. The X chromosome is a medium size submetacentric chromosome and the Y is a medium acrocentric chromosome with a secondary constriction near the distal end.

DISCUSSION

Based on a shortened rostrum, a white spot on the shoulder, and geographic distribution, the genera *Ardops*, *Ariteus*, and *Phyllops* were believed to be closely related to each other and to the genera *Stenoderma* and *Ametrida* (Baker, 1973). Chromosomal data support this proposal. All five genera have $2N = 30$♀♀, 31♂♂, and a fundamental number of 56. Some minor variation in the morphology of the Y elements between the species has been observed (Figs. 1, 2, and 3) and the X chromosome in *Ardops* is apparently submetacen-

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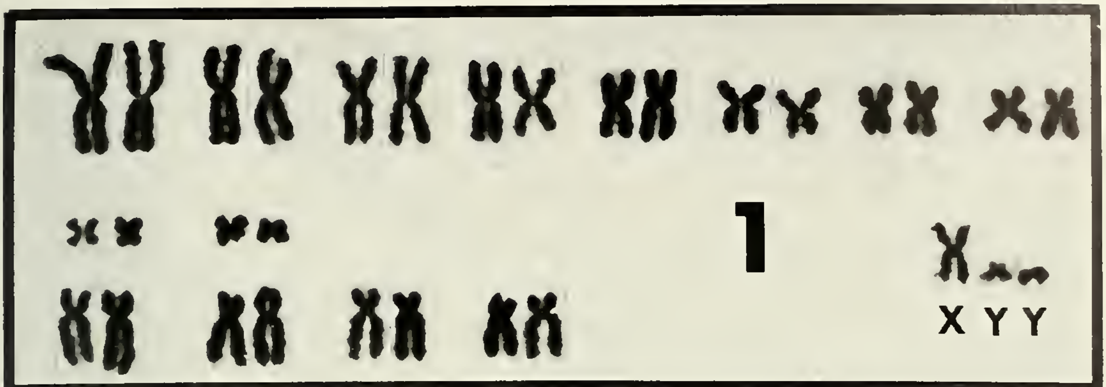

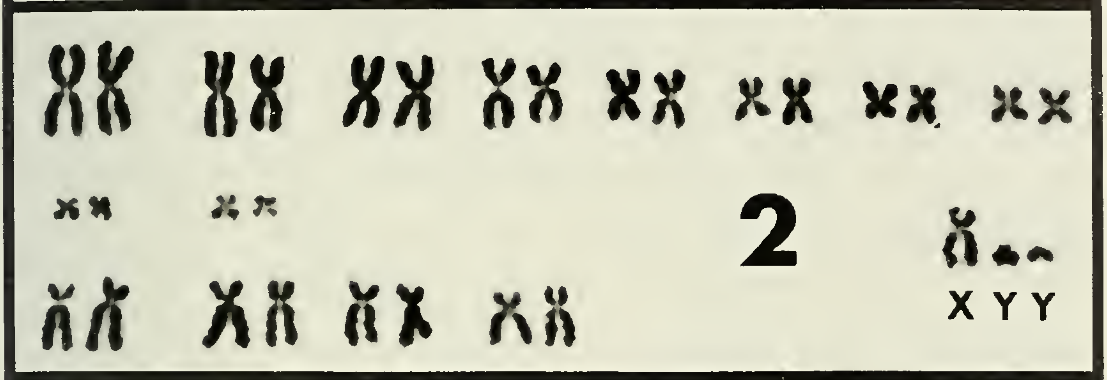

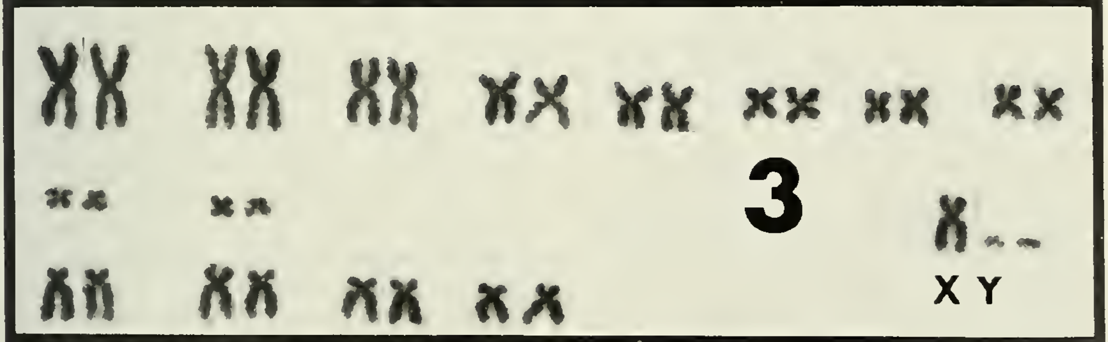

Figure 1. Karyotype of a male *Ardops nichollsi* from Guadeloupe: Basse-Terre; 1 km S. 4 km W Vernou. *Figure 2.* Karyotype of a male *Ariteus flavescens* from Jamaica: St. Ann Parrish; Queenhythe. *Figure 3.* Karyotype of a male *Phyllops haitiensis* from Haiti: Department du Sud; 1 km E Lebrun. *Figure 4.* Karyotype of a male *Ectophylla alba* from Costa Rica: Heredia; Finca "La Selva."

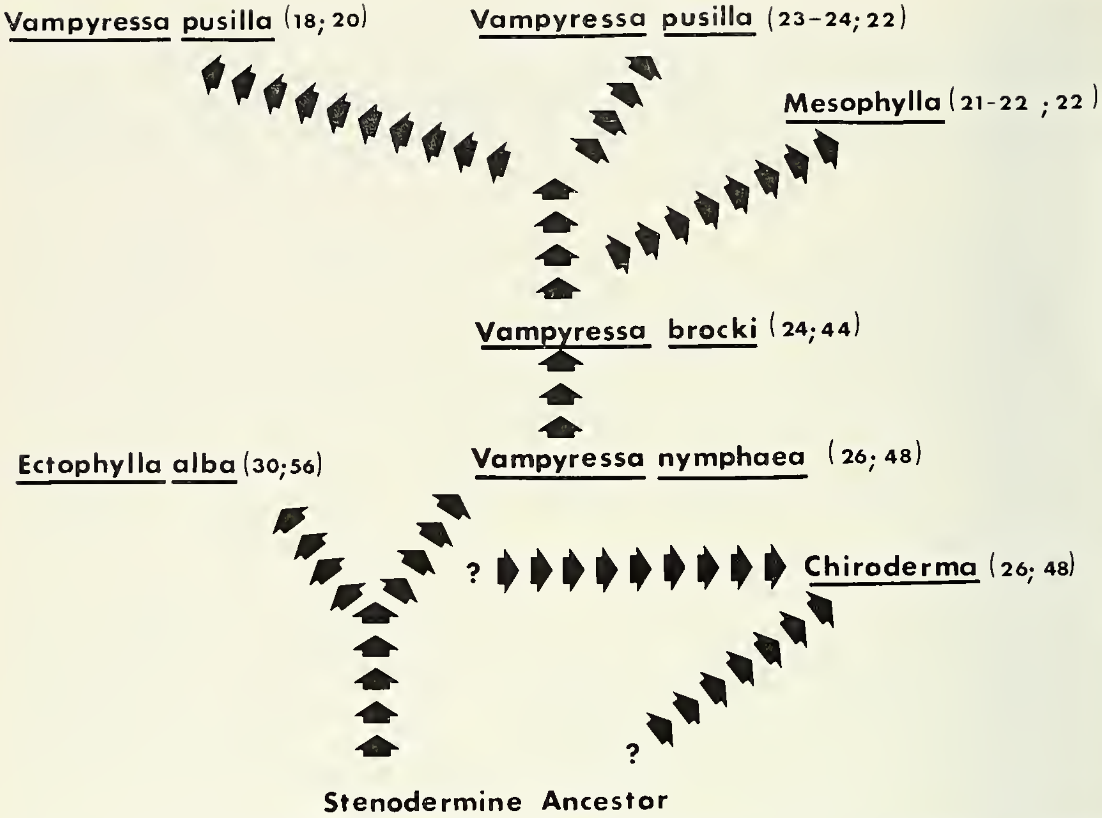

Figure 5. Proposed phylogenetic tree for the *Vampyressa, Mesophylla,* and *Ectophylla* line of evolution. Numbers in parentheses are diploid number followed by fundamental number.

tric, whereas in *Ariteus, Phyllops, Stenoderma,* and *Ametrida* the X is subtelocentric. We are under the impression that the genera *Ardops, Ariteus, Phyllops,* and *Stenoderma* represent a single invasion from the mainland of an ancestral stock which has found its way to most of the Lesser and Greater Antillian Islands with subsequent speciation. Minor changes such as extinctions and reinvasions may have occurred several times but the close morphological and karyotypic relationship of the four genera in question supports the idea of a single invasion. Varona (1974) has proposed that the genera *Ardops, Ariteus,* and *Phyllops* are congeneric with *Stenoderma.* Although Varona may be correct, we will follow the old arrangement until a proper revision accompanies the proposed change. How *Stenoderma* (as used by Varona) is distinguished from *Pygoderma* and *Ametrida* and what features serve as the basis for lumping the four Caribbean genera needs to be discussed. There are two other genera of "white-shouldered bats", *Sphaeronycteris* and *Centurio,* however these two genera are distinguished from the other "white-shouldered bats" by a diploid number of 28 and a classical XX/XY sex determining system. The white spot on the shoulder and the shortened rostrum of *Ametrida, Ardops, Ariteus, Phyllops, Centurio, Stenoderma, Sphaeronycteris,* and *Pygoderma* to us reflects a common evolutionary history that distinguishes these genera from the other stenodermines.

The relationship of *Ectophylla* to the rest of the stenodermine genera is not so clear. A close relationship between *Ectophylla alba* and *Mesophylla macconnelli* has been proposed by Laurie (1955) and Goodwin and Greenhall (1961) who suggested that the two genera were congeneric. Starrett and Casebeer (1968) concluded that *Ectophylla* and *Mesophylla* were distinct genera and that these two plus *Vampyressa* formed a distinct unit within the Stenoderminae. Further, Starrett and Casebeer (1968) concluded that *Ectophylla* was the most derived (dentally) of the species involved. From a chromosomal standpoint the genera *Vampyressa* (three species karyotyped) and *Mesophylla* formed the derived components of a proposed evolutionary line within the stenoderminae. This line was characterized by a reduced diploid and fundamental number. The genus *Chiroderma* was also included with this group (Baker, 1973). *Mesophylla* at the end of this line has the most derived karyotype, $2N = 21–22$, $FN = 22$ with the autosomal complement having all acrocentric elements. A diploid number of $2N = 30$ is assumed as primitive for the Stenoderminae (see Baker, 1973 for the theory behind this assumption). *Ectophylla alba* appears to have a karyotype that is less derived (based on Baker's hypothesis of a $2N = 30$ being primitive for the subfamily) than any of the species of *Vampyressa* and *Mesophylla* thus far karyotyped. This is in contrast to the conclusion of Starrett and Casebeer (1968) that *Ectophylla* appears to be the most highly modified dentally and cranially of the three genera. Our interpretation of the evolutionary position of *Ectophylla* (Fig. 5) is that it probably evolved from the stock that gave rise to *Mesophylla* and *Vampyressa* before there was any reduction in the diploid number. The development of the "derived" cranial and dental features then could have taken place after the *Ectophylla* line separated from the *Mesophylla-Vampyressa* line. If the above relationships are valid then *Ectophylla* must remain a genus distinct from *Mesophylla* unless the species of *Vampyressa* are also considered as congeneric with *Ectophylla* and *Mesophylla*. A close relationship of *Vampyressa pusilla* to *Mesophylla* was pointed out by Starrett and Casebeer (1968) based on cranial and dental characteristics and this relationship is reinforced by our chromosomal data (Fig. 5). If a single event resulted in the reduction in diploid number that now characterizes the evolutionary line that gave rise to *Chiroderma* and the *Vampyressa-Mesophylla* stock then *Ectophylla* is even more distantly related to this group than is the genus *Chiroderma* which is cranially and dentally very unique from *Mesophylla* and *Vampyressa*.

Specimens examined.—Voucher specimens are deposited in The Museum, Texas Tech University (*Ardops*, *Ariteus*, and *Phyllops*) or in The United States National Museum (*Ectophylla*). All microscope slides with karyotypic preparations are on deposit at Texas Tech University.

Ardops nichollsi.—Guadeloupe: Basse-Terre; 1 km W Vernou, (N = 3). 2 km E St. Claude, (N = 1). 1 km S, 4 km W Vernou, (N = 6).

Ariteus flavescens.—Jamaica: Trelawny; Duanvale, (N = 1). St. Ann Parrish; Queenhythe, (N = 1). Orange Valley, (N = 9). St. Thomas Parrish; Yallahs, (N = 1).

Phyllops haitiensis.—Haiti: Dept. du Sud; 1 km E Lebrun (N = 4). 2 km N, 2 km E Lebrun, (N = 4).

Ectophylla alba.—Costa Rica: Heredia; Finca "La Selva", (N = 1).

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RESEARCH NOTES

A NEW CHILEAN FROG OF THE EXTRA-ANDEAN ASSEMBLAGE OF *TELMATOBIUS* (AMPHIBIA: LEPTODACTYLIDAE)

While working at the British Museum (Natural History) in 1972, I had occasion to examine two specimens of a small leptodactylid collected in southern Chile in 1958. Alice G. C. Grandison thought the frogs might represent an unnamed genus related to *Eupsophus*, a genus she had revised, and urged me to describe the frogs. The characteristics she had noted immediately made it apparent that the frogs represented a new taxon but also presented a problem in that the combination of characteristics embodied in these frogs made their assignment to any currently recognized genus difficult. As Miss Grandison noted, proposing a new genus might solve the problem, but it would also leave a number of questions of intergeneric relationships of Patagonian frogs unaddressed.

The new frog is small, has appreciable webbing of the toes, nuptial asperities on the thumb and second finger, completely roofed skull (no exposed fontanelles), and has lost the middle ear and quadratojugal. This combination of traits is unique but approached by a group of Patagonian leptodactylids presently assigned to *Telmatobius* [*T. nitoi* Barrio. *T. patagonicus* (Gallardo), *T. praebasalticus* Cei and Roig, *T. reverberii* Cei, *T. solitarius* Cei, and *T. somuncurensis* Cei]. Anatomical and systematic studies of that assemblage are in progress and rather than complicate that study with the description of a new species, I will present the species description here even though the generic classification used here will be altered in a subsequent report.

In recognition of her important contribution to leptodactylid systematics and to her encouragement in naming this frog, I hereby name the new species after her.

Telmatobius grandisonae, new species

Holotype.—BM 1962.629, adult male collected on the Plateau below the south peak, Puerto Eden, Wellington Island, Magallanes, Chile, 640 m, by the Royal Society Expedition to South Chile, December 1958.

Paratype.—BM 1962.628. juvenile female taken with the holotype.

Diagnosis.—A stout-bodied frog of the extra-Andean group of *Telmatobius* differing from the six described species in having complete frontoparietals (no fontanelles exposed); and differing from all in the following combination of characteristics: toes nearly fully webbed but deeply incised (appearing less than half-webbed), full compliment of teeth (prevomerine odontophores prominent; premaxillary and maxillary teeth large, well-ankylosed to jaws), omosternum long but dilated into a broad manubrium, sternum not notched, dorsum brown without a pattern of spots or bars, venter reticulated with brown.

Description of holotype.—Snout short, round in dorsal view and in lateral profile, not greatly overhanging lower jaw; nostrils directed dorsolaterally, weakly protuberant; canthus rostralis rounded, concave; loreal region weakly concave, sloping abruptly to lip; lips not flared; eyes large, interorbital space flat, narrow relative to upper eyelid width; interorbital distance less than internarial distance; supratympanic fold thick, extending from posterior corner of eye to insertion of forearm; tympanic annulus, cavum tympanicum, and plectrum absent; choanae round, moderate-sized, not concealed by palatal shelf of maxillary arch; prevomerine odontophores prominent, oval in outline, each as large as a choana, situated between and partially posterior to choanae, nearly in contact, each bearing 3–4 teeth; tongue round, not notched posteriorly, posterior one-half not adherent to floor of mouth; no vocal slits.

Skin of dorsum, top of head, and upper flanks bearing numerous large warts; side of head, lower flanks, and limbs lacking such warts although shanks bear ill-defined warts; skin of venter smooth; weak areolations below and lateral to vent; no dorsolateral, paravertebral, or vertebral folds; forearms robust but not markedly so; no ulnar tubercles; palmar tubercle weakly bifid, larger than oval thenar tubercle; no supernumerary palmar tubercles; subarticular tubercles low, flat, rounded or slightly broader than long; digit tips without pads, weakly bulbous; no lateral fringes on fingers; thumb thicker than second finger, equal in length; nuptial asperities fine, covering medio-dorsal surface of second finger from near its tip proximally to base of finger, on thumb extending ventrally onto outer edge of thenar tubercle.

No tubercles on heel or tarsus; inner edge of tarsus bearing flap-like fold beginning at base of terminal phalanx of toe I and extending proximally on tarsus for three-fourths its length; two metatarsal tubercles, both low, flat; inner elongate (length twice width), a little smaller than round outer; no supernumerary plantar tubercles; outer metatarsals not united; subarticular tubercles smaller than those of fingers, low, non-conical, round or slightly longer than wide; digit tips not bulbous; outer edge of toe V bearing free flap from base of terminal segment to base of toe (Fig. 1); toes webbed, fringe not extending onto terminal segment of any toe; webs deeply incised so that toes appear less than one-half webbed.

Color in preservative.—Brown above and on limbs; some gray infusion on side of head and flanks; venter white with brown flecks; flanks marbled gray and brown.

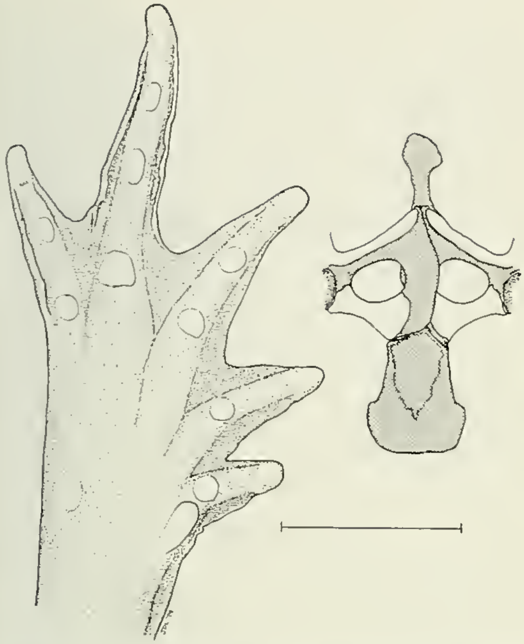

Figure 1. Foot and pectoral girdle of *Telmatobius grandisonae*, new species, (BM 1962.629). Line equals 5 mm.

Measurement of holotype in mm.—SVL 32.9; shank 14.0; head width 10.8; head length 10.6; upper eyelid width 3.2; interorbital distance 2.1; eye length 3.7; eye-nostril distance 2.5.

The paratype is an immature female, 25.7 mm SVL. The oviducts are weakly convoluted and the ovaries contain many minute nonpigmented eggs. The skin of the dorsum, head, and flanks is shagreened rather than covered with large warts.

Remarks.—The skin of the head of the holotype was cut and reflected to expose the skull bones. The frontoparietals are complete and medially extend anteriorly between the posteromedial edges of the nasal bones. The nasal bones are relatively large and narrowly separated medially. The maxillary arch is incomplete in that the quadratojugal is absent. The squamosal is unmodified with moderate length otic and zygomatic rami.

The pectoral girdle (Fig. 1) has a large omosternum with a dilated manubrial portion. The epicoracoidal cartilages are calcified in the area of overlap but the girdle is strictly arciferal. The clavicles are massive and weakly curved. The sternum is broad, non-bifurcate, posteriorly weakly expanded, and has a rather large calcified center.

Comparisons.—*Telmatobius grandisonae* differs from all other extra-Andean species except *T. somuncurensis* in having a dilated manubrial portion of the omosternum. Like all except *T. somuncurensis*, *T. grandisonae* does not have a bifurcated sternum. Both *T. grandisonae* and *T. somuncurensis* have calcified elements in the sternum but the element is single in *T. grandisonae* and paired in *T. somuncurensis*. The absence of an exposed frontoparietal fontanelle distinguishes *T. grandisonae* from the other species of the group (in the six Argentine species the fontanelle varies from small in *T. nitoi* and *T. somuncurensis* to extensive in *T. partagonicus* and *T. praebasalticus*). The toes of *T. nitoi*, *T. patagonicus*, and *T. praebasalticus* are all more fully webbed than in *T. grandisonae* which in turn has greater webbing than *T. reverberii*, *T. solitarius*, and *T. somuncurensis*. Additionally, *T. somuncurensis* has an ear (unlike all other species of the group) and *T. reverberii* and *T. solitarius* are pale frogs with large dorsal spots.

Ecology.—Both specimens were taken under stones in moorlands. The habitat was described by Grandison (Bull. British Mus. Nat. Hist., 8:120–121, 1961) from notes made by the zoologist on the expedition, Martin Holdgate. On the basis of these limited data, *T. grandisonae* must be viewed as at least a semi-terrestrial species not unlike *T. solitarius*, but quite unlike *T. patagonicus*.

Grandison (*supra cit.*) reported *Eupsophus coppingeri* (= *E. monticola*, fide Lynch, Herpetologica, 24:255–57, 1968) from Puerto Eden and although not reported, one might expect to find *Pleurodema bufonina*, *Batrachyla leptopus*, and *Bufo variegatus* at Puerto Eden as well (Cei, Batracios de Chile, Santiago, 1962). *Telmatobius grandisonae* differs from all but *E. monticola* in lacking an ear. *Pleurodema bufonina* has prominent inguinal glands and like *B. leptopus* lacks webbing and tarsal folds. *Batrachyla leptopus* has a long snout unlike *T. grandisonae*. *Bufo variegatus* lacks teeth and has parotoid glands and a distinct color pattern. *Eupsophus monticola* has pectoral nuptial asperites and enlarged forearms (in breeding males), complete maxillary arch, notched sternum, and less toe webbing (see illustration in Grandison, 1961).

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Accepted for publication March 25, 1975.

A NEW SPECIES OF *NEOTROMBICULA* (ACARINA: TROMBICULIDAE) FROM SOUTHERN CALIFORNIA

In a recent study, Spoecker (1967) reported the ectoparasites of a Mojave Desert population of side-blotched lizards *Uta stansburiana*, in Kern County, California. Examination of those chiggers listed as *Neotrombicula* species revealed that they represented a new species closely similar to described species belonging to the *microti* group.

The following description is based on the holotype and paratypes (noted in parentheses), with all measurements in microns. The types are in the chigger research collection at California State University, Long Beach, and paratypes will be distributed to appropriate institutions and individuals.

Studies upon which this paper is based were supported, in part, by the U.S. Public Health Service Research Grant AI03407 from the National Institute of Allergy and Infectious Diseases.

***Neotrombicula superciliaris*, new species**
Figure 1

Types.—Holotype and 21 paratypes from 13.7 km NNW Randsburg, el. 1100–1220 m, El Paso Mountains, Kern Co. California, all from the eyelids of 16 *Uta stansburiana* taken by Peter D. Spoecker: Holotype and one paratype (PDS 17) taken 23.II. 1964, and 20 paratypes taken from 7.XII.1963 to 19.IV.1964.

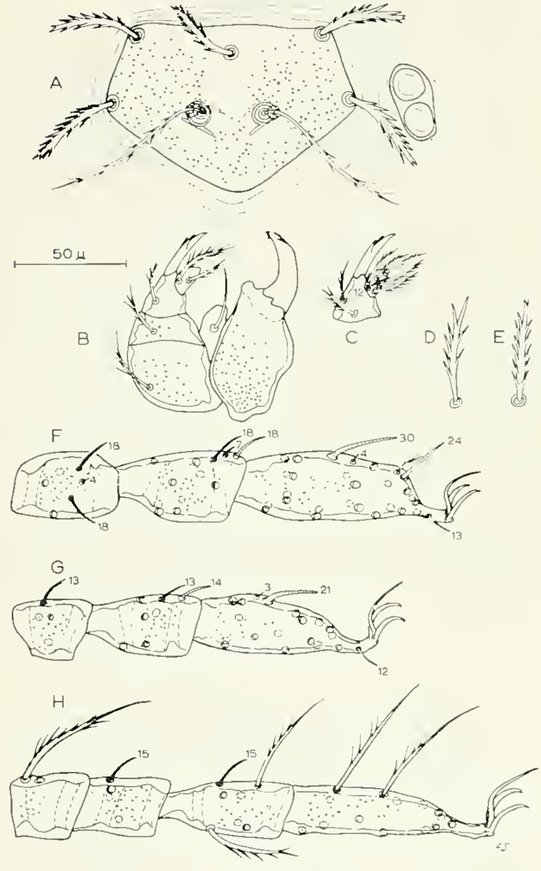

Figure 1. Larva of *Neotrombicula superciliaris*: A. Scutum and eyes; B. Gnathosoma, dorsal view; C. Palpal tibia and tarsus, ventral view; D. Posterior dorsal seta; E. Mid-dorsal body seta; F. Leg I; genu, tibia, and tarsus, with bases of branched setae, nude setae and measurements; G. Leg II; as above; H. Leg III; telofemur and as above.

Diagnosis.—Palpal setal formula B/B/BBB + 7B; galeala usually nude; tibia I with 9B; parasubterminala 1 branched; leg III with branched mastifemorala, mastitibiala, and 2 mastitarsalae; sensilla branched.

Description of holotype (with differences among paratypes in parentheses).—Body red, 396 × 549; eyes red, 2/2 on ocular plate. Dorsal setal formula 2–11–11 + 30, total 54; measurements of humeral seta 40, seta of first posthumeral row 34, posterior dorsal seta 38. Ventral setae 2–2 + 40, total 44; measurements of first sternal seta 43, second sternal seta 39, preanal seta 26, and postanal seta 37.

Scutum: Moderately punctate, SB slightly posterior to PL bases: sensilla flagelliform, branched along distal 4/5th; PL ≥ AL = AM, similar in appearance to dorsal setae. Scutal measurements of holotype (and mean and extremes of 21 paratypes, unless otherwise noted): AW 67 (70, 66–72); PW 87 (88, 85–92); SB 22 (24, 21–27), ASB 32 (33, 31–35); PSB 30 (31, 27–34); AP 26 (28, 25–31); AM 34 (32, 27–35, 19); AL 33 (33, 30–35); PL 36 (35, 33–37, 19); S 60 (61.8, 58–68, 12).

Gnathosoma: Palpal setal formula B/B/BB(N in 2)B + 7B; galeala N + IB (of 38 specimens examined, 25 (65.8%) with both N, 10 (26.32%) with N + B, 3 (7.9%) with both B); cheliceral bases and palpal coxae moderately punctate.

Legs (with B and specialized setae as follows): Leg I: coxa 1; trochanter 1; basifemur 1, telofemur 5; genu 4, 2 genualae and microgenuala; tibia 9, 2 tibialae (distal striated), microtibiala; tarsus 9 proximal, 8 medial, 6 distal (total 23), tarsala 27 (26, 25–27), anterad microtarsala, subterminala, B parasubterminala, and pretarsala. Leg II: cx 1; tr 1; bf 2; tf 4; genu 3, genuala; tibia 6, 2 tibialae (distal striated); tarsus 6 proximal, 4 medial, 6 distal (total 16), tarsala 19 (20, 19–22), posterad microtarsala, and pretarsala. Leg III: cx 1; tr 1; bf 2; tf 2 + B mastifemorala 42; genu 3, genuala; tibia 5 + B mastitibiala 44, tibiala; tarsus 3 proximal + B mastitarsala 50, 4 medial + B mastitarsala 50, 6 distal (total 15). Coxae conspicuously punctate; other leg segments with few puncta: All terminating in two claws and clawlike empodium, without onychotriches. Leg measurements of holotype (mean and extremes of 21 paratypes): I 271 (288, 225–314); II 248 (260, 233–284); III 259 (292, 265–365); total 778 (839, 772–899).

Taxonomic remarks.—In discussing the importance of leg setal formulae in leeuwenhoekiine and trombiculine larvae, Vercammen-Grandjean et al. (1973) noted that tibia I usually has 8 branched setae. However, in members of the microti group of *Neotrombicula*, tibia I has 9 branched setae. Despite the lack of a palpotarsal subterminala, and branches on the usually nude mastisetae III, *N. superciliaris* with 9B on tibia I, clearly belongs to the microti group. The microti group (Brennan and Wharton, 1950) also is represented in California by *N. brennani*, *N. californica*, *N. cavicola*, *N. dinehartae*, *N. harperi*, *N. jewetti, N. microti,* and *N. pseudoautumnalis* (Brennan and Jones, 1959 and Gould, 1956).

Loomis and Stephens (1973) reported chiggers from the upper eyelids of *Uta stansburiana* and *Sceloporus occidentalis* from Joshua Tree National Monument, California, and tentatively identified them as *Neotrombicula harperi* (Ewing), which is probably the same species listed below as *N. californica.* Among 16 larvae from San Bernardino County, tentatively identified as *N. californica* (Ewing), all had 2–4 basal branches on mastifemorala III, and one specimen had two branches on a distal mastitarsala III.

The similarity of *Hyponeocula sauricola* Tanigoshi and Loomis (1974) to *N. superciliaris* seems to be superficial as the former has only 8 branched setae on tibia I (rather than 9), 3–4 branched setae on coxae III (instead of one), and none of the branched setae on leg III resemble the branched mastisetae of *N. superciliaris.*

Specimens examined (78).—*Neotrombicula superciliaris* (55): CALIFORNIA *Kern Co:* 13.7 km NNW Randsburg, 1100–1220 m, El Paso Mountains, 7.XII.1963–19.IV.1964, 16 *Uta stansburiana* (22 types + 29). *Inyo Co*: Death Valley National Monument, 13 km SE Emigrant Jct., 1463 m, 23.III.1975, *U. stansburiana* (4).

Neotrombicula californica (23): CALIFORNIA *Los Angeles Co*: Acton, 823 m, 12.IV.1933. *Thomomys bottae* (7 types). *San Bernardino Co*: 6.4 km SE Seven Oaks (= Poopout Hill), 23.III.1969, *Sceloporus graciosus* (3); 3 km SW Seven Oaks (= Cedar Falls Camp), 23.V.1964, *S. graciosus* (3); 5 km NW Lake Arrowhead, 1463 m, 21.IV.1964, *Sceloporus occidentalis* (4); 2 km N Helendale, 765 m, 20.VII.1961, *S. occidentalis* (6).

ACKNOWLEDGMENTS

We are indebted to Dr. James M. Brennan, formerly senior research entomologist at the Rocky Mountain Laboratory, Hamilton, Montana, for the loan of pertinent type specimens, and to Peter D. Spoecker for the type series. Thanks are extended to Lee C. Spath for the illustrations.

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A CASE OF ACTIVE BROOD DEFENSE IN THE THORNBUG, *UMBONIA CRASSICORNIS* (HOMOPTERA: MEMBRACIDAE)

Although many examples of subsocial behavior have been recorded for various species of Hemiptera and Homoptera (Odhiambo, New Scientist, 8:449–451, 1960; Wilson, The insect societies, pp. 120–122. 1971), the majority of cases are limited to passive guarding of the eggs and early nymphs by an adult. Very occasionally, an adult, usually the mother, will remain close by the nymphs for a considerable portion of their development and may "shepherd" them during short excursions. Bequaert (Bull. Brooklyn Ent. Soc., 30:177–191) found that males of the African reduviid bug *Rhinocoris albopunctatus* not only stood guard over the egg masses and young nymphs, but would also impale ants with their beaks and remove them from the egg masses.

A single detailed example of passive brood defense has been recorded for the Homoptera by Beamer (Ent. News, 41:330–331). Females of the membracid bug *Platycotis vittata* were observed sitting between the early nymphs and the main stem of the food plant. These females would not fly away when touched, but were not observed to actively defend the brood.

During the last week of July, 1975, I observed three separate instances of females of the thornbug in Coral Gables, Dade Co, Florida, standing guard over clusters

Figure 1. Female *Umbonia crassicornis* preparing to kick a twig which has just been touched to the brood.

of early and half-grown nymphs on stems of *Cassia* sp. (Fig. 1). As in the case of *Platycotis* cited above, the position taken by the guarding female was always between the main stem and the nymphs, facing the brood. If a nymph was touched with a twig, the entire brood gave a convulsive shudder. The guarding female began immediately to flick its wings and then rapidly climbed the stem to the brood, whereupon it commenced carefully searching over the nymphs. When it found the tip of the probing twig, the female moved alongside it, lifted its abdomen slightly from the substrate and delivered a sharp kick to the twig with the opposite third leg. The force of this kick was enough to produce a snapping sound and was actually slightly painful to my finger. Ants and small caterpillars placed on the brood were kicked several inches away from the stem. When the disturbing stimulus was removed, the female would move back down the stem and resume its former position. This active defense of the brood was observed many times and persisted until the third or fourth instar had been reached, after which the guarding females appeared to lose much of their interest in the brood although they still remained in their guard positions.

A fairly strong stimulus was needed to elicit brood defense behavior. This stimulus could take the form of a substrate vibration produced by the stimulus itself, or by the shuddering of the stimulated brood. As very tiny insects would therefore probably escape detection, it is unlikely that the brood defense of *Umbonia* serves to protect the nymphs from parasites, as proposed for *Rhinocoris* by Odhiambo (Proc. Royal Ent. Soc., (A) 34:175–185). Instead, it appears that the defensive behavior of *Umbonia* is directed against larger insects which might eat the nymphs or compete with them for space on the twigs.

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Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus.* J. Mamm., 54: 452–458.

Brattstrom, B. H. 1969. The Condor in California. Pp. 369–382 *in* Vertebrates of California. (S. E. Payne, ed.), Univ. California Press, xii + 635 pp.

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(McWilliams, Insect mimicry, p. 216, 1970); (Holmes and Speak, J. Mamm., 54: 452–458, 1971); (Brattstrom, The Condor in California, Pp. 369–382, *in* Vertebrates of California, 1969).

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The 1976 Annual Meetings of the Southern California Academy of Sciences will be held on May 7 and 8, 1976 at the Museum of Natural History, Santa Barbara. Technical papers are solicited from the fields of natural and social sciences.

Abstracts of no more than 150 words must be typed on 3 × 5 cards and *must be received no later than March 19, 1976.* The first line of the abstract is to include author(s), student or professional, preferred section (see below), and type of projection equipment, if needed. **Send abstracts** to: *Dr. Eric Hochberg, Museum of Natural History, 2559 Puesta del Sol, Santa Barbara, California 93105.*

Technical sessions—Anthropology, Archaeology, Botany, Earth Science, Entomology, Experimental Biology, Folklore, History, Invertebrate Zoology, Marine Science, Vertebrate Zoology, Psychology, Economics, and Geography (other sections will be opened to accommodate demand). Special interest symposia will be presented.

Student awards will be presented in the Natural Science and Social Science Divisions. First award in each division will be $150.00; second award in each division $75.00.

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Banquet—The annual banquet will be held the evening of May 8; presentation of awards will be made at this time.

COVER: *A San Miguel Island Fox,* Urocyon littoralis littoralis, *on the berm of the beach on the west end of San Miguel Island, Summer 1974.*

Photography by George A. Antonelis, courtesy Marine Mammal Biological Laboratory, National Marine Fisheries Service, Seattle, Washington.

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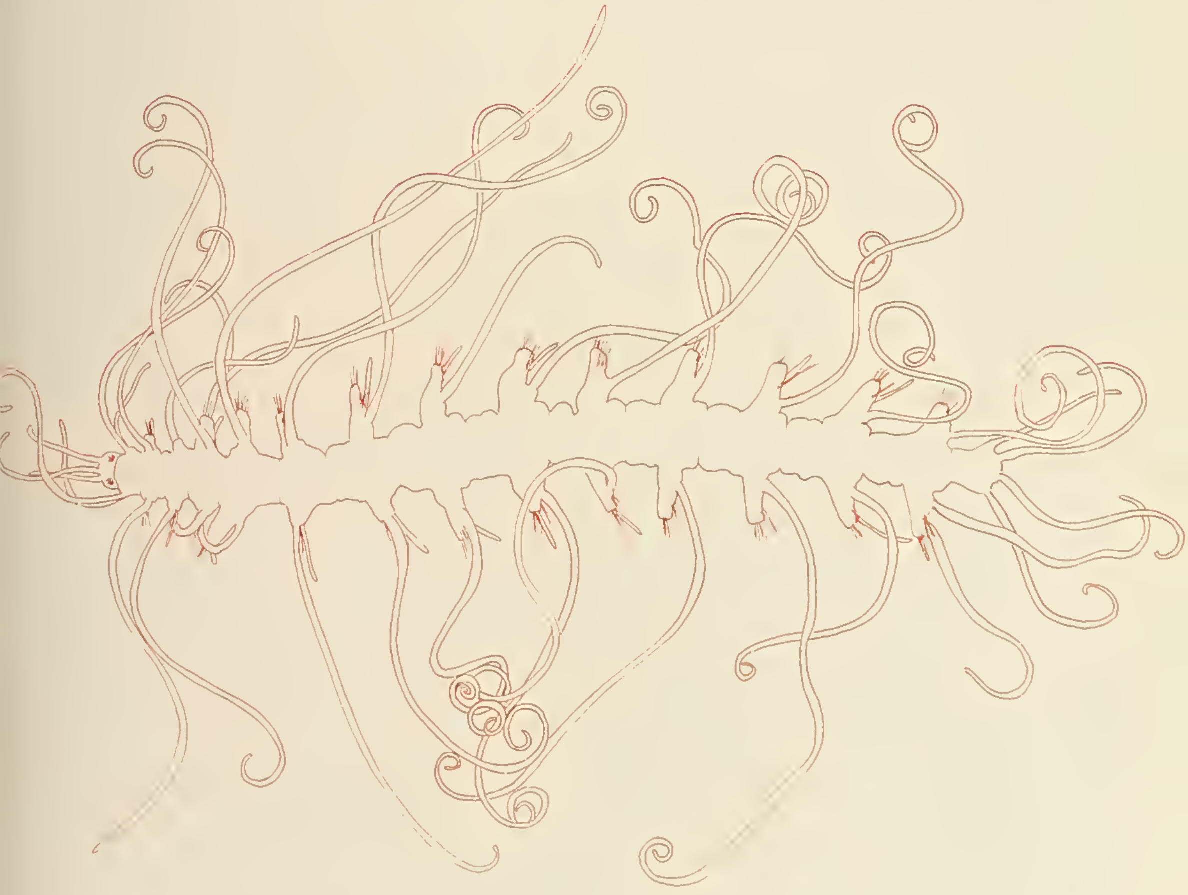

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BULLETIN OF THE SOUTHERN CALIFORNIA
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VOLUME 75 MAY 26, 1976 NUMBER 1

INVESTIGATIONS ON THE POSTANAL SAC OF THE GRAY WHALE *ESCHRICHTIUS ROBUSTUS*

FLOYD E. DURHAM[1] AND JOHN W. BEIERLE[2]

ABSTRACT: An unusual thick-walled, sac-like structure occurs embedded in the blubber of the midventral ridge of the tail posterior to the anus, and appears to be unique to the gray whale. Data on six postanal sacs are reported. Histological examination of one sac revealed a smooth-walled, striated structure with an apparent epithelial lining. Partial chemical analysis of the contents of one sac disclosed two major components consisting of relatively homogeneous types of protein-polysaccharide complexes, at least one being a glycoprotein. Inasmuch as the structure is rather consistent in shape, routinely present, and occurs in immature and adult gray whales of both sexes, it is thought to be a naturally occurring structure rather than a tumor or parasite-induced cyst. It is possible that the postanal sacs are scent glands and function in "track laying" during migration and/or to maintain group integrity.

A peculiar, thick-walled, sac-like structure is found in the gray whale (*Eschrichtius robustus*) and appears to be specific for this species. It is not known to occur on any other cetacean or other mammal. First mention appears to be that of Andrews (1914) who wrote: "A second specimen [of gray whale] had a large swelling on the ventral ridge of the peduncle, which upon being opened, proved to be a large capsular tumor about one foot in depth and of a like diameter." More recently, similar structures have been found on gray whales processed at whaling stations in Richmond, California (A. Wolman, pers. comm.; M. Spencer, pers. comm.). Similar findings have also been reported from a Russian whaling station by Zimushko (1970).

One of us (Durham) first observed a sac in March 1964 during the butchering of an immature female (9.63 m in length) at the Golden Gate Fishing Company, Richmond, California. The flensers were surprised when this football-sized object (32.5 × 25 cm) was pointed out to them. The sac was evident externally only by a slight midventral swelling of the tail, 56 cm posterior to the anus (center to center). No search was made and no sac was noted on the adult female and three adult males also butchered that spring. However, the sac has subsequently been seen by flensers and scientists on numerous occasions, particularly at the Del Monte Fishing Company, also located at Richmond. Dale W. Rice (National Marine Fisheries Service) witnessed the first sac in 1964, and Allen Wolman (also of the National Marine Fisheries Service) collected several in succeeding flensings. Rice (1967) stated that, "Most if not all individuals have a thick-walled, fluid-filled, cyst-like structure, 10 to 25 cm in diameter, on the ventral surface of the caudal peduncle between the blubber and the muscles."

Data on six sacs and the whales from which they were obtained are given in table 1. Specimen numbers are those applied by the Marine Mammal Biological Laboratory in Seattle, Washington (Rice and Wolman, 1971).

---

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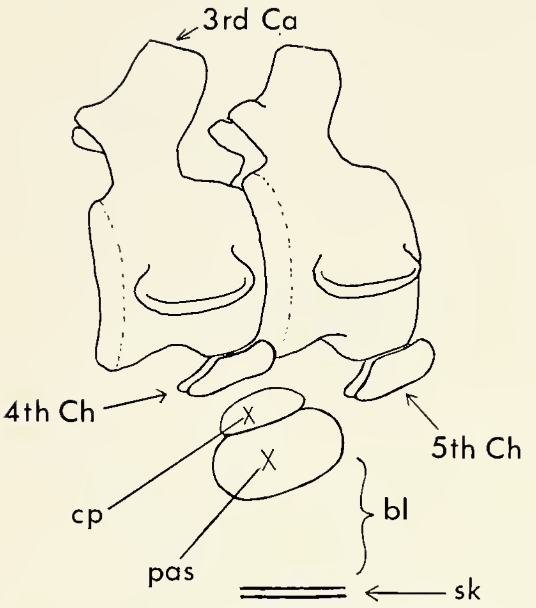

Figure 1. Schematic drawing suggesting position of the postanal sac relative to the chevron bones and ventral surface. Legend key: Ca, caudal vertebra; ch, Chevron; cp, cartilage pad; pas, postanal sac; bl, blubber; sk, skin.

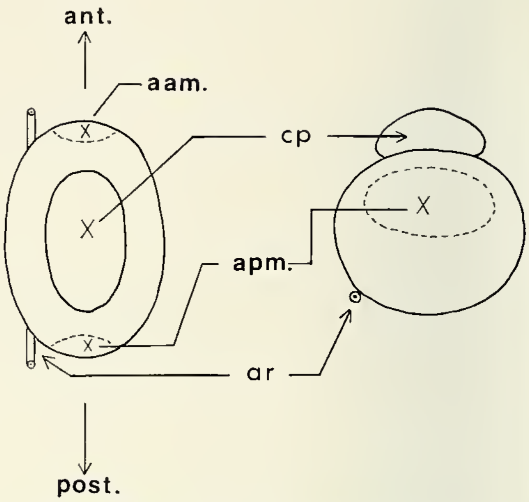

Figure 2. Schematic drawing indicating a dorsal and posterior view of the postanal sac. Legend key: post, posterior; apm, attachment of posterior muscle; cp, cartilage pad; aam, attachment of anterior muscle; ar, artery; ant, anterior.

External evidence of the sac may be conspicuous, as in Andrews' specimen, but it is usually slight or lacking, thus accounting for its being frequently overlooked. Measurements of the distance from the anus posterior to the sac of two whales ranged from 56 to 120 cm, these distances being ⅙ to ¼ the length of the tail (*i.e.,* anus to notch of flukes). Blubber invests the sac laterally and ventrally and contains long (to 15 cm), stringy, cord-like fibers. Dorsally a cartilage pad appears to be the connection between the sac and the keel of one or two chevron bones (Figs. 1 and 2). The tendons and muscles which extend anteriorly and posteriorly from the sac may regulate the size or turgor of the sac, or they may be only part of the ventral trunk musculature. A longitudinal, unbranched artery passes adjacent to the sac on the left side.

The wall of the sac has a thick, outer layer to which are attached the coarse blubber fibers (Fig. 3). The thinner, inner layer of the sac consists of a smooth-walled, striated structure (Fig. 4). Occasionally a pair of small pits and/or wrinkles appear at one or both ends of the sac but no actual pore or duct has been found in these studies, although a 5 mm diameter duct to the exterior has

TABLE 1. Distribution of the Gray Whale Postanal Sac.

Date Collected	Specimen Number[1]	Sex	Total Body Length (m)	Reproductive Condition	Length, height and width of sac (cm)	Distance from anus (cm)	Nature of contents
25 March 1964	1007	F	9.63	immature	32.5 × 25	56	—
18 January 1967	1967–60	F	12.55	mature	—	120	turbid
18 January 1967	1967–62	F	12.85	mature	20 × 18	—	—
— January 1969	—	—	—	mature	18 × 13 × 10	—	cheesy
4 January 1969	1969–10	F	12.45	mature (with fetus)	20 × 14 × 10	—	—
5 January 1969	1969–15	M	11.75	mature	20 × 14 × 10	—	cloudy[2]

[1] Rice and Wolman Reference Number, Marine Mammal Laboratory Collection Number, Seattle, Washington.
[2] Chemical analysis was performed on this specimen.

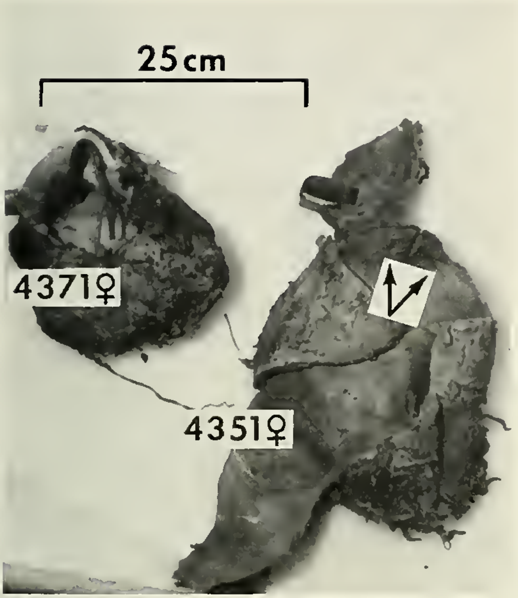

Figure 3. Photograph of two postanal sacs from female specimens revealing the smooth inner wall and the coarse exterior blubber fibers. The arrows point to the two pits in the larger sac.

been reported in two gray whales by Zimushko (1970). The pits or blind ducts noted in the sac have also been reported by Zimushko, as well. The sacs are usually turgid with fluid which varies in viscosity and opaqueness. The fluid may be nearly clear and watery, transluscent and murky, or a cheesy paste of whitish granules. Histological sections of the wall of the sac provide little clue of the nature of the sac, but the smooth lining suggests the possibility of a gland.

CHEMICAL ANALYSIS

The fluid of one sac (Table 1) was drawn out by puncturing the sac with an 18 au needle and aspirating with a 50 ml syringe. The fluid was frozen prior to chemical examination and was not exposed to any chemical fixatives. This fluid contained some precipitated materials which were removed by low speed centrifugation (1500 × g) and both the precipitate and the clarified supernatant were examined.

The precipitate was examined in a Zeiss polarizing microscope and found to contain a gelatinous mass in which was embedded many spicule-shaped crystals. They were not found in the supernatant. The addition of three volumes of saline or one volume of 1 N KOH was found to solubilize the gelatinous mass and leave the crystals intact, whereas the addition of 95% methyl alcohol dissolved the crystals and left the gelatinous mass intact. The addition of strong organic solvents (hexane, benzene) did not solubilize either the gel or the crystals. The failure of most organic solvents to either solubilize or extract substances from these isolates led us to believe that perhaps the fluid did not contain large amounts of lipid, but that the viscosity of the solution was due predominately to the presence of mucins. This was verified when the material was analyzed in the Beckman Model E analytical ultracentrifuge, 56,000 rpm, 20°, and two major peaks were revealed with Schlieren optics. Both of the peaks sedimented rapidly, and did not show buoyant patterns typical of lipids or conjugated lipids. Colorimetric analyses for sugars common to mucoprotein (Eastoe and Courts, 1963), revealed the presence of high levels of uronic acid, fucose, sialic acid, reducing sugars, as well as proteins. The pH of the fluid was 8.4 and one could precipitate the solution by lowering it to acid pH ranges (pH 4–5) or by making the solution greater than 25% in ammonium sulfate. Of great interest is the presence of essentially two molecular species in the fluid rather than numerous types. The two appear at present to be protein-polysaccharide complexes and at least one of them to be a glycoprotein, as based on colorimetric analyses of the two fractions obtained by column chromatography using Sephadex G-75 (Pharmacia Corp.).

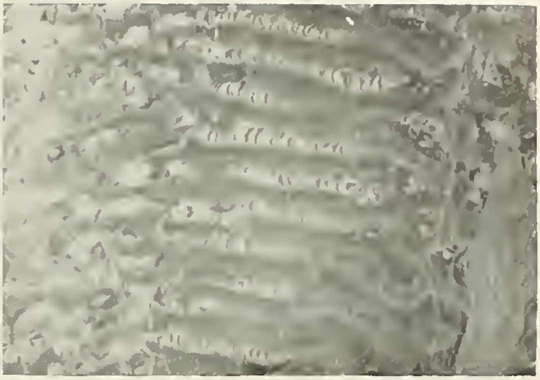

Figure 4. Histological cross section of the smooth inner wall of a sac illustrating an ordered striated structure. (Formalin fixed; embedded in Epon; methylene blue stain, × 100).

DISCUSSION

The function of the sac is currently unknown. Speculations are that it is pathological, a benign tumor (Andrews, 1914) or a cyst induced by parasites. Veterinarian John Allen (Naval Undersea Research and Development Center, Hawaii) examined a sac supplied by Allen A. Wolman, noted its resemblance to two tapeworm cysts which he found in the perianal region of a male pilot whale (genus *Globicephala*), and suggested that the gray whale is an unintentional secondary host (Richard Pierce, Univ. California, Santa Cruz, pers. comm.). We think the structure is an organ as suggested by its rather consistent location, occurrence, and morphology. This has also been suggested by Zimushko (1970) who has examined 116 whales and found 57 to contain these sacs, all in the same anatomical location, and in both immature and adult males and females. The other specimens examined by Zimushko may also have had the structure but much of the information obtained was based on the presence of an external swelling in the postanal region. His findings as to the general location, size, and structure parallel the findings presented here. Zimushko has made the suggestion that this sac is a vestigial sebaceous gland remaining only in the gray whale.

Spencer (1973) has noted seven sacs out of eleven specimens of gray whale examined at Richmond, California. He however, found no ducts or channels leading to the outer surface, and has cited the sacs as being cysts of indeterminate origin and function. Kleinenberg, Yablokov, Bel'kovich, and Tarasevich (1969) reported anal scent glands on Beluga Whales (*Delphinapterus leucas*) which may help maintain integrity of the group or may be for "tract laying," as in migration. A similar function may be served by this structure in the gray whale. Allen A. Wolman (pers. comm.) regards the structure as normal because he found the structure in the same area on all gray whales examined but two. Of those two, one animal had two sacs in line, the other had none.

Owing to our findings of the presence of a sialic acid containing glycoprotein as well as another mucinous substance it is unlikely for the fluid to be of a sebaceous nature. An alternative possibility exists however, in light of recent reports of an antifreeze glycoprotein found in Antarctic fish (Chuba *et al.*, 1973) in that this glycoprotein may act in a similar fashion. Studies on freezing point depression of our glycoprotein would have to be initiated to further clarify this possibility of function.

Although it is locally called "stink sac" by the flensers, they probably avoid it because of its assumed association with excretion. At flensing time most of the sacs were turgid with liquid which spurted out when the sac was cut. Durham found the odor to be no stronger than that of ordinary whale flesh and much less offensive than that of the contents of the digestive system. However, Wolman encountered some sacs with highly odoriferous contents. On two occasions he was sprayed and it took days to eradicate the odor from his clothing.

CONCLUSIONS

The possibility that the sac is a tumor or a cyst seems unlikely inasmuch as the sac is found in adults, postnatals and near-term fetuses of both sexes, is always found in the same general anatomical location, and is routinely found in most specimens examined. Cytological examination reveals a rather highly banded, structured wall with a smooth lining. The fluid in the sac consists primarily of only two relatively homogeneous types of protein-polysaccharide complexes. We therefore conclude that the sac is a natural structure of the gray whale and has some specific function.

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AN ANALYSIS OF THE FLUID CONTENTS IN THE POSTANAL SAC OF THE GRAY WHALE, *ESCHRICHTIUS ROBUSTUS*

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Abstract: A distinctive, thick walled, postanal sac is found midventrally on the caudal peduncle of most gray whales. The structure appears to be unique to this cetacean and is a relatively unknown organ, with no known function. This study describes partial physicochemical characterization of the fluid contents in the sac. The major chemical component is a unique glycoprotein of molecular weight greater than 150,000 daltons, as determined by gel filtration, analytical ultracentrifugation, acrylamide gel electrophoresis, and colorimetric analyses. A second component of lesser molecular weight, appears to be predominantly protein.

The postanal sac, commonly called the stink sac by flensers, appears to be unique to the gray whale. It was first described by Andrews (1914) as a large capsular tumor about 30 cm in diameter. Spencer (1973) summarized much of his work dating from a 1966 expedition on the gray whale and noted the same structure. He called the sac the tail stock cyst and noted the structure in seven out of eleven adult whales, both male and female, examined in San Francisco, as well as in one whale in Scammons Lagoon. The fluid was described as milky white, non-viscous, and containing opalescent white flakes. Spencer noted that sodium and potassium was present in the fluid and that approximately 2 grams of protein per 100 ml fluid were also present. Triglycerides averaged 58 mg percent whereas cholesterol-free lipids averaged 15 mg percent. No ducts were noted leading from the sacs to any external surfaces and the cyst was indicated to be of unknown origin and function.

This same structure was noted by Zimushko

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(1970) in the same general anatomical location, 1.2–1.3 m from the anus, on the lower edge of the tail stock. He detected the sac in 66 animals, and a surface swelling indicated the presence of the internal structure in 57 percent of all animals examined. One to three liters of fluid were found per sac. On examination, one whale exhibited an excretory duct about 5 mm in diameter leading from the cavity to the surface of the body. Several specimens demonstrated blind canals, 1 to 1.5 cm deep in the wall of the cavity. The sac was noted in females more than males, and one was even found in a 1.18 m fetus. Zimushko's histological data suggested that the structure was an anlage to sebaceous glands in land mammals and indicated that the sac might be a rudimentary sebaceous gland found only in the gray whale.

Of the specimens that we examined, the fluid contents varied in opacity and viscosity, and also contained granules which could be solubilized by several chemicals (Durham and Beierle, 1976). Our preliminary chemical assays substantiated the presence of protein (Spencer, 1973) as well as finding sugars common to glycoproteins. Our early results suggested that two main molecular components were prevalent, and at least one of them was a glycoprotein. The purpose of this study is to begin a more detailed physico-chemical characterization of the liquid contents of the sac to gain both an understanding of its chemical makeup and potential insight into its biological function.

METHODS

A sac measuring 20 × 14 × 10 cm was obtained from a mature male, 11.75 m in length. Fluid was collected by puncturing the wall with an 18 ga needle, aspirating with a 50 ml syringe, and frozen for later laboratory study. A clear aqueous fraction was separated from the particulate suspension by centifugation at 12,000 × g in a Sorval refrigerated centrifuge at 4°. It is this clarified supernatant which is described.

Column chromatography.—The fluid was fractionated by molecular sieve chromatography using a Sephadex G-150 column. The column dimensions were 3 × 38 cm with a flow rate of 0.8 ml/min. in an eluting buffer of 0.15 M NaCl, with 0.01 percent sodium azide added to prevent microbial growth. Calibration of the unit was performed with the following standards: blue dextran, 2 × 10^6 daltons; aldolase, 158,000 daltons; ovalbumen, 45,000 daltons; chymotrypsin, 25,000 daltons; and ribonuclease, 13,700 daltons (Pharmacia Corporation). Optical density readings and ultraviolet range scans were performed on a Beckman DB-G spectrophotometer.

Analytical ultracentrifugation.—Samples were analyzed in a Beckman Model E analytical ultracentrifuge using single sector, 4° cells at 59,780 rpm at 18°.

Acrylamide gel electrophoresis.—Samples were analyzed in 7 percent polyacrylamide gels (Eastman Organic at 3 milliamps/gel), using a Buchler gel electrophoresis unit. Both the top and bottom buffers were made up in Tris, pH 8.4. The runs normally took one hour. The gels were stained with the following dyes and under the following conditions:

Protein stain: 0.025 percent Coomassie blue in 12 percent Trichloracetic acid (TCA). The gels were stained overnight and destained in 12 percent TCA for five days.

Glycoprotein stain: Periodic Acid-Schiff stain (PAS). Gels were fixed for 30 minutes in 12 percent TCA, rinsed in water and then reacted with 1 percent periodic acid made up in 3 percent acetic acid for 30 minutes. After washing overnight in running tap water they were immersed in Schiff reagent for 50 minutes, then washed for 30 minutes in 0.5 percent sodium metabisulfite. Final washing to remove reagent background took a minimum of 18 hours. All gels were stored in 5 percent acetic acid.

Alcian blue stain: Alcian blue (pH 3.0) was used as a general stain to detect protein-polysaccharide complexes other than those categorized as glycoprotein per se, and specifically stained by PAS. A solution of 0.2 percent Alcian blue 8 GX in 3 percent acetic acid (pH 3.0) was used to stain gels overnight. The gels were de-stained in 3 percent acetic acid, for 2 days with changes of the acid wash, until clearing was resolved.

Colorimetric analyses.—Protein determination was after the method of Lowry; uronic acid by the carbazole method of Dische; neutral sugars by the oricinol procedure; sialic acid after the method of Warren; and amino sugars were determined by the Elson and Morgan reaction (Eastoe and Courts, 1963).

Extensive dialysis of column fractions were performed in the cold vs. water, using 3,500 dalton exclusion limit membrane tubing (National Scientific Corp.). These samples were then lyophilized to dryness and later reconstituted with water for colorimetric analyses, or in Tris buffer, pH 7.4, for analytical ultracentrifugation.

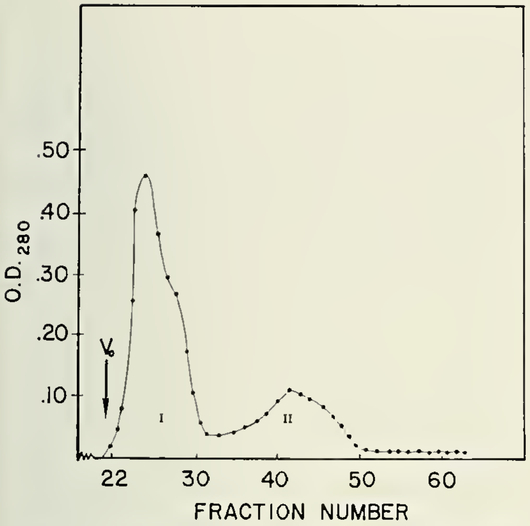

Figure 1. Sephadex G-150 column profile of adult whale postanal sac fluid; 2 ml/fraction, eluted in 0.15 M NaCl at pH 8.0, flow rate of 0.8 ml/min.

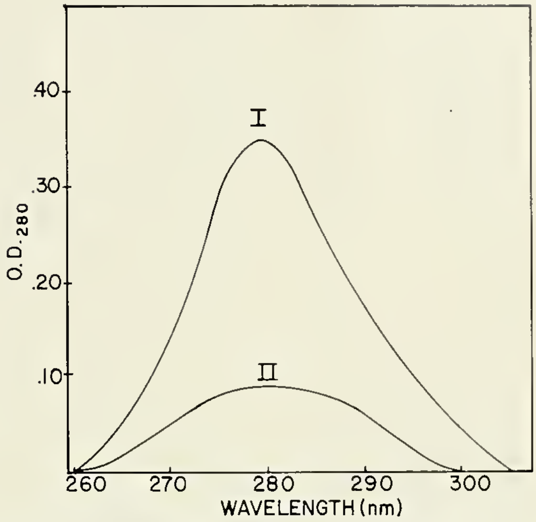

Figure 2. Ultraviolet scan of Fraction I and II isolated by Sephadex column chromatography.

RESULTS

Preliminary fractionation of the sac fluid by Sephadex G-150 column chromatography revealed two components (Fig. 1). The first component, fraction I, appeared in the void volume indicating that it was greater than 150,000 daltons. A second, broader peak (fraction II) was found in the range of 10,000–30,000 daltons, as compared with standards of known molecular weights. Ultraviolet absorption scans were performed on each fraction and revealed absorption maxima at 280 nm, indicative of the presence of protein (Fig. 2). Analytical ultracentrifugation of a diluted preparation revealed two components as well, verifying the column profile. Comparison of O.D.$_{280}$ units as well as Lowry protein analyses revealed that the concentration ratio of fraction I to fraction II was 2:1. Centrifugation of an undiluted, native solution of pH 9.4, however, revealed four components. This same native fluid, when dialyzed, or adjusted to pH 7.4 revealed only two components, similar to those found by column chromatography or in diluted native fluid (Table 1 and and Fig. 3). Although no concise explanation for this exists at present, it is indicated that a pH dependence has some effect on interactions between the molecules in this fluid. Thus ionic interactions could induce the formation of molecular aggregates, thereby generating multiple molecular species at elevated pH ranges (9.4). This is further indicated by the presence of only two components as detected by acrylamide gel electrophoresis at pH 8.6 (Fig. 4). Immunological studies in progress should aid in answering this

Table 1. Sedimentation coefficient values of the components found in various preparations of gray whale postanal sac fluid.

	Sedimentation Coefficient of each Fraction Detected			
Sample	1	2	3	4
Adult whale sac fluid, undiluted, pH 9.5 (Fig. 3a)	8.6	6.5	5.2	3.8
Adult whale sac fluid, diluted 1:5 in Tris buffer, pH 7.4 (Fig. 3b)	10.6	—	—	4.3
Fraction I (Sephadex G-150) (Fig. 3c)	8.4	—	—	—
Fraction II (Sephadex G-150) (Fig. 3d)	—	—	—	4.7
Adult whale sac fluid, undiluted, pH adjusted to 7.04 (not illustrated)	7.6	—	—	3.7

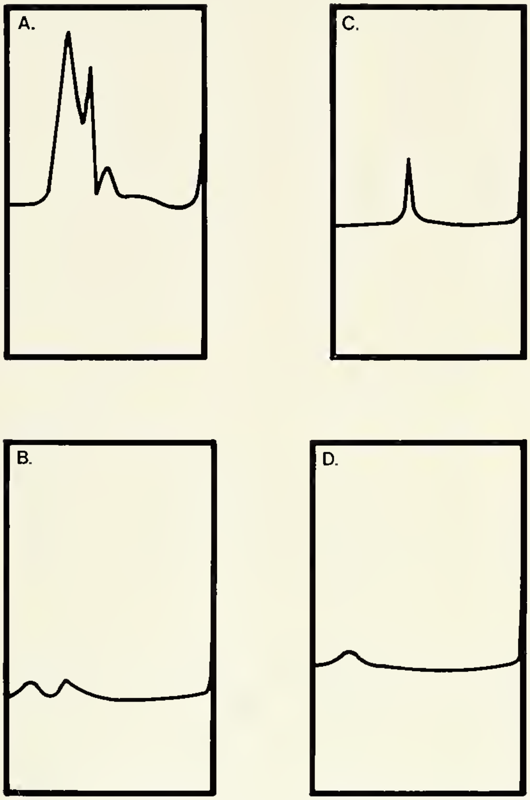

Figure 3. Analytical ultracentrifuge patterns using Schlieren optics of different preparations of adult gray whale postanal sac fluid. The centrifugation pattern is moving from left to right. A. Native, undiluted sac fluid, pH 9.5; 72 min. B, Sac fluid, diluted 1:5 in Tris buffer, pH 7.4; 26 min. C, Fraction I (Sephadex G-150), reconstituted in Tris buffer, pH 7.4; 31 min. D, Fraction II (Sephadex G-150), reconstituted in Tris buffer, pH 7.4; 39 min.

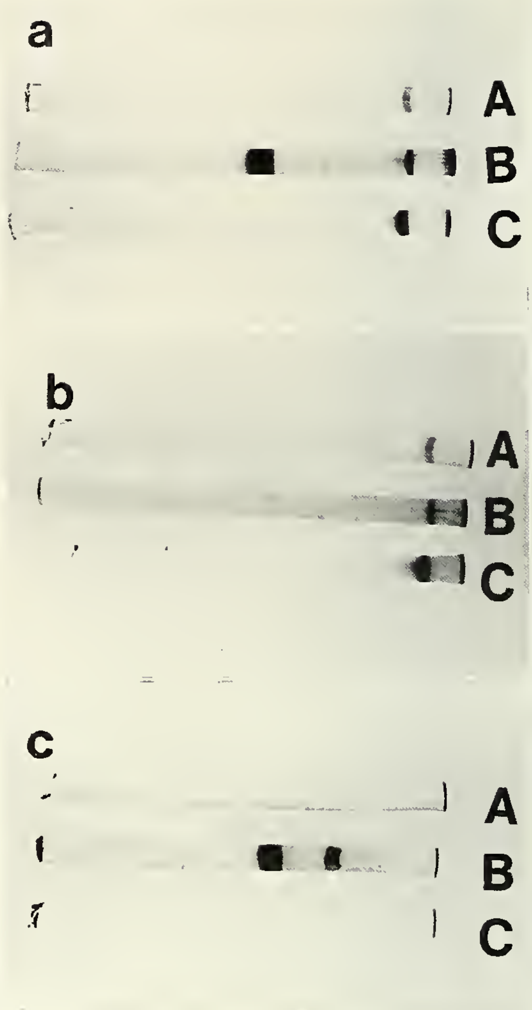

Figure 4. Acrylamide gel electrophoretic patterns of the postanal sac fluid, using differential staining. Tops of the gels are to the right; cathode to the left. a, Native sac fluid; b, Fraction I; Sephadex G-150; c, Fraction II; Sephadex G-150. A, Alcian blue; B, Coomassie blue; C, PAS.

question through the identification of specific antigenic components.

The sedimentation coefficients of these two main components show some variance dependent upon the conditions of assay. The higher molecular weight component, fraction I, averages 8.5 S whereas fraction II has an approximate sedimentation coefficient of 4.2. Fraction II however is not absolutely homogeneous, as suggested by gel electrophoresis (Fig. 4) and the peak spread one obtains on columns and gels, or in the ultracentrifuge.

Both the colorimetric analyses (Table 2) and the staining procedures used in acrylamide gel electrophoresis (Fig. 4) indicate that the higher molecular weight constituent (fraction I) is a protein-polysaccharide, and more specifically a glycoprotein. The presence of sialic acid and fucose, in the presence of uronic acid also suggest that this particular glycoprotein is unique, as these three sugars have never been reported together in a glycoprotein molecule (Schmid, 1972). Fraction II stains only with Coomassie blue and does not contain sialic or uronic acids, or amino sugars,

By lowering the pH to 4.1 one obtains a precipitate at that isoelectric point. Lyophilization of both the resultant precipitate and supernatant provided heavy powders, indicating that isoelectric

TABLE 2. Chemical composition of adult whale post anal sac fluid by colorimetric analysis.

	Adult Whale Native Fluid (in mg/ml)	Fraction I Sephadex G-150 (in μg/mg dry weight)	Fraction II Sephadex G-150 (in μg/mg dry weight)	35% Ammonium Sulfate Precipitate (in μg/mg dry weight)
Protein	35	310	187	325
Neutral Sugars	11	370	40	375
Fucose	0.16	105	410	85
Uronic Acid	0.04	14	—*	8
Sialic Acid	0.90	70	—	12
Amino Sugars	0.03	10	—	10

* undetectable

point precipitation may provide alternative ways to fractionation of the sac fluid. Ammonium sulfate precipitation revealed that two precipitates could be obtained by that method as well. One fraction precipitated at 33 percent of saturation, a second fraction at 55 percent saturation. One of these fractions was examined for chemical content (Table 2). Salting out with ammonium sulfate may eventually provide a rapid means of isolating specific moieties for the sac fluid in the future.

DISCUSSION

The common location of this organ in virtually all individuals of this species, as well as its simple, distinctive chemical makeup suggests that the structure is neither a cyst nor a tumor. The presence of only two main chemical constituents in the fluid was quite surprising. The total protein values we find are in agreement with those of Spencer (1973). Protein indeed appears to be the major constituent of the fluid. The staining patterns of acrylamide gels and chemical analysis of the two components all show that the fraction of greater molecular weight, higher sedimentation coefficient, and slower penetration through acrylamide gel was the glycoprotein moiety. The second, smaller, more rapidly migrating fraction appears to be protein, by gel staining procedures. Although a detailed chemical analysis has yet to be performed, dry weight analysis by colorimetric means revealed the presence of fucose and neutral sugars.

Zimushko (1970) had previously suggested that this organ might be a rudimentary sebaceous gland. This is unlikely as the chemical nature of these substances do not reflect the oily nature and chemical composition of sebum (Gray, 1969). We had previously raised the possibility of the organ being involved in migration tracking (Durham and Beierle, 1976), although the usual absence of a duct leading to the body surface makes this difficult to perceive at present. Other functions were also suggested, including freezing point depression by novel glycoproteins (Dunham and deVries, 1972), although at present no evidence exists which can document any such usage. It is hoped that further chemical analyses will provide some clue to the function of this organ.

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TWO NEW SPECIES OF *HELMINTHOGLYPTA* (MOLLUSCA: PULMONATA) FROM SAN DIEGO COUNTY, CALIFORNIA

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ABSTRACT: Two new species of land snails of the genus *Helminthoglypta* are described from San Diego County, California.

During the past several years there has been an accumulation of material from southern California representing several unnamed species of land snails of the genus *Helminthoglypta*. These have usually been from isolated localities, with inadequate material for anatomical study or even for a thorough study of the shell.

In the case of two such unnamed species from localities in San Diego County, we have finally accumulated a number of specimens sufficient for complete description of shell morphology and anatomy, as well as for significant comparison with other apparently related populations.

The earliest collection from one of these populations was made on 24 October 1946 by the late H. Arden Edwards, founder of the Antelope Valley Museum and former staff artist of the Southwest Museum. The second population was discovered a few miles away, on 28 March 1947, by one of us (WOG) and the late Munroe L. Walton, well-known amateur malacologist. Since then, additional collections have been made in 1953, 1954, 1957, 1959, 1961, 1963, 1970, and most recently, on 9 January 1975 by one of us (WBM) and Carl C. Christensen and Richard L. Reeder, University of Arizona graduate student malacologists. The latest collection confirmed that both populations are surviving, although the populations are subjected to pressures from encroaching human habitation, heavy recreational use, and economic management (clearing and gathering of fallen trees for firewood).

The two populations are considered to represent two very closely related but distinct species, isolated from each other not only geographically but also ecologically and, apparently, physiologically. They are described below. All measurements of shell and anatomical structures are given in millimeters.

FAMILY HELMINTHOGLYPTIDAE

Helminthoglypta waltoni, new species

Figures 1 and 3

Diagnosis.—A species of medium size, heavily papillose sculpture, and small umbilicus, characterized anatomically by a long, club-shaped, double-tubed penis, abutting distally on a short, saccular, thin-walled, hourglass-shaped preputial chamber.

Description of Holotype.—Shell helicoid, low-conic, of medium size for the genus; whorls five and one-third, convex, gradually increasing to the last whorl which is moderately expanded and descends to the aperture so that the suture lies at an angle of about 45 degrees with the axis of the shell; base rounded,

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the umbilicus contained about ten times in the greater diameter of the shell. Aperture oblique, subcircular; peristome slightly expanded and slightly thickened within, the columellar end moderately reflected over the margin of the umbilicus. A faint parietal callus connects the ends of the peristome.

Embryonic shell consists of one and one-third whorl; except on the worn embryonic shell and early neanic whorls, which are indistinctly granulose, the entire shell is heavily papillose, the papillae arranged in forwardly descending series, while under high magnification the surface between the papillae is finely wrinkly-granulose. On both upper and basal aspects of the shell, the papillae are closely spaced on the first half of the body whorl and somewhat widely spaced on the beginning of the second half of the body whorl, becoming more closely spaced behind the aperture. In addition, all whorls are conspicuously marked, both above and below, by numerous, closely spaced lines of growth.

Color light Prout's brown (Ridgway Color Standards) above and over the periphery, while the under surface is somewhat lighter in color than the upper part of the shell. Just above the periphery is a chestnut-brown band about one mm in width on the body whorl and on the last half of the penultimate whorl just above the lower suture. This band is bordered above and below by somewhat narrower bands lighter in color than the general color of the shell.

Holotype measurements: maximum diameter 23.2, minimum diameter 19.7, height 15.3, umbilicus diameter 2.3.

Anatomy.—The mantle is whitish with irregular, black pigment spots. The penis is moderately long, the epiphallus about equal in length to the penis, and the epiphallic caecum slightly longer. The penis is club-shaped, with the distal end narrow, and widening evenly toward the proximal end which narrows abruptly at its juncture with the epiphallus. In the cleared whole-mount of the genitalia, the double tube structure which is characteristic of the genus is evident; the outer wall is thick. Distal end of penis consists of a thin walled, short, saccular preputial chamber with a narrow constriction about halfway along its length, resembling an hourglass. Dart sac rather large. Spindle-shaped mucus glands attach directly to a common duct which is somewhat shorter than the dart sac. Vagina attached to the distal end of the atrium near the attachment of the penis. Lengths of reproductive structures: penis 15.4, epiphallus 15.1, epiphallic caecum 18.1, vagina 3.8, free oviduct 6.7, spermathecal duct 39.3, spermathecal diverticulum 28.0 arising 23.2 from the base of the spermathecal duct, atrial sac 7.8, dart sac 1.9 by 2.3, mucus glands 3.7, common duct of the mucus glands 0.9, spermatheca 3.3 by 5.9.

Type Locality.—Laguna Mountains, San Diego Co. California, in rockslide in small ravine on east side of Scove Canyon road (as shown on 1960 Mount Laguna topographic map, 7.5 minute series) at a point 0.8 road miles from the junction of the Laguna Mountain highway (Sunrise Highway) with the southern end of Scove Canyon road; this locality is at Lat. 32° 50.3′ N. and Long. 116° 29.3′ W. Elevation about 4500 feet. Collectors M. L. Walton and W. O. Gregg, 28 March 1947.

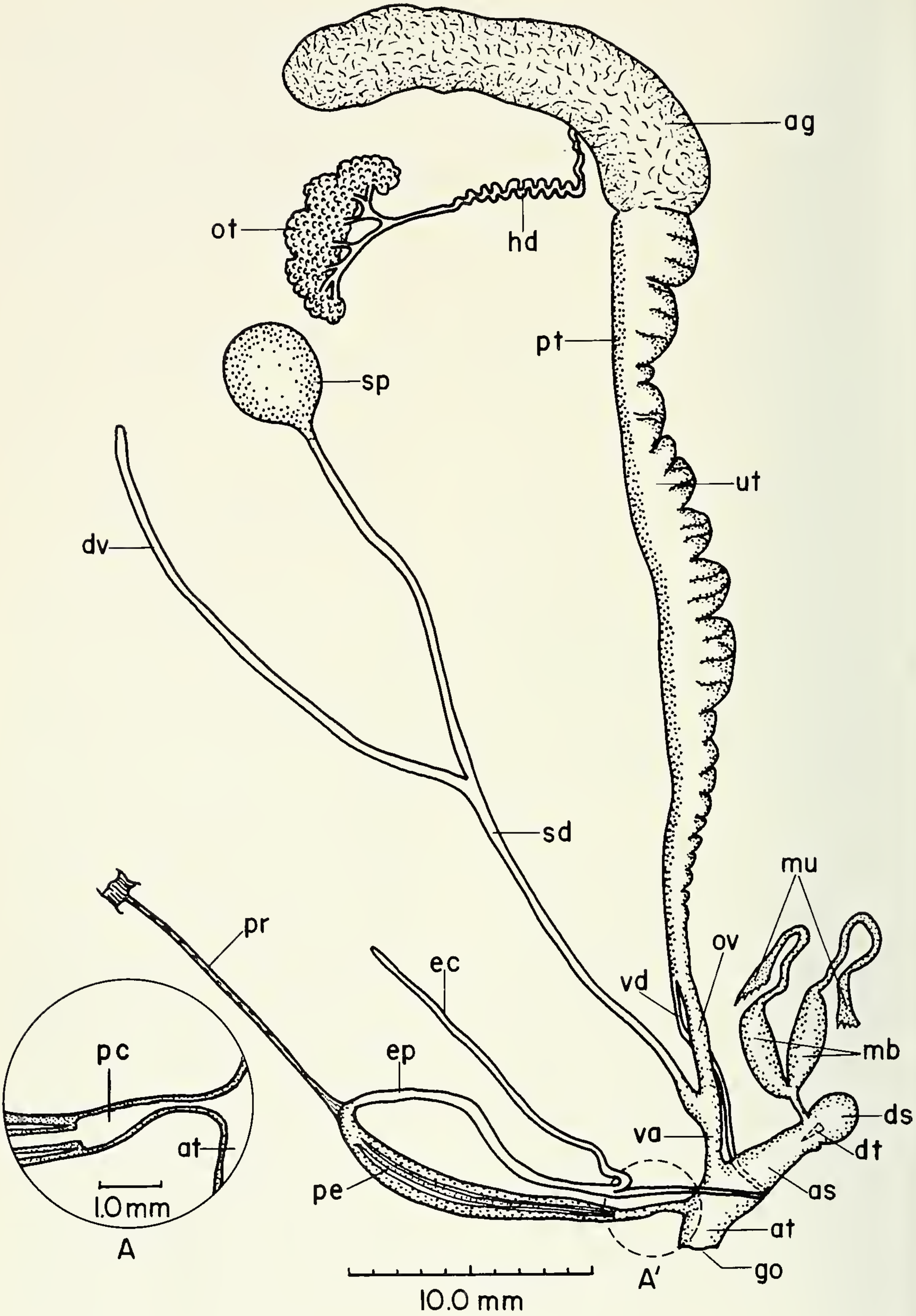
Type Material.—Holotype, Natural History Museum of Los Angeles County No. 1760. Paratypes: Natural History Museum of Los Angeles County No. 1107, Delaware Museum of Natural History (ex- M. L. Walton collection No. 6621), and private collections of S. S. Berry 19,909, W. B. Miller 2597, 4258, 4427, 6482, 6486 (ex- W. O. Gregg 3710), 6487 (ex-WOG 6292), 6488 (ex-WOG 7111), and 6489 (ex-WOG 7793), C. C. Christensen 3380, and R. L. Reeder 325.

Remarks.—In view of the fact that specimens were always scarce and found only at the type locality, many collections were made in order to obtain sufficient paratype material for adequate study. In unworn, young paratypes, the embryonic and early neanic whorls are wrinkly-granulose. The papillae first appear on the second half of the first embryonic whorl where they are widely spaced at first, becoming closely spaced on the second half of the second neanic whorl. In unworn, newly formed parts of the shell, the papillae are tipped with fine, hair-like periostracal processes. The processes, completely worn off in the holotype, are particularly conspicuous in young specimens.

Specimens killed on 28 March 1947 contained red, thread-like spermatophores. In one specimen, through the semitransparent walls of the spermathecal duct and diverticulum, fragments of spermatophores were seen, end to end as one continuous mass, from the base of the spermathecal duct well up into the diverticulum. In all specimens, the spermathecas were filled with small fragments of spermatophores, but the sections of spermathecal ducts between the diverticula and the spermathecas were empty.

The shell of *Helminthoglypta waltoni* most closely resembles that of *Helminthoglypta lowei* (Bartsch, 1918) in size, shape, and sculpture, although in the latter the papillae are less closely spaced than in *H. waltoni*. The anatomy of *H. waltoni*, however, shows it to be most closely related to *Helminthoglypta thermimontis* S. S. Berry, 1953, characterized by the same club-shaped penis and the small, hourglass-shaped preputial chamber (eversion chamber) described for *H. waltoni*. The shell of *H. waltoni* differs from that of *H. thermimontis* by its smaller umbilicus and the finer, less dense papillation of the body whorl.

The anatomy of *H. lowei* is entirely different from that of *H. waltoni* and *H. thermimontis* in that it has a large, saccular, sausage-shaped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preputial (eversion) chamber. This type of penial anatomy has been noted in other populations of snails in and around the Cuyamaca Mountains and was figured by Pilsbry (Land Mollusca of North America (north of Mexico), Acad. Nat. Sci. Philadelphia, Monograph 3, vol. 1 (1):146, fig. 73, 1939) as "genitalia of a *Helminthoglypta* of uncertain status."

This species is named for the late Munroe L. Walton, good friend and companion on countless field trips with both of us.

Helminthoglypta edwardsi, new species
Figures 2 and 3

Diagnosis.—A species of small size, heavily papillose sculpture, and small umbilicus, characterized anatomically by a long, club-shaped, double-tubed penis, abutting distally on a short, saccular, thin-walled, hourglass-shaped preputial chamber.

Description of Holotype.—Shell helicoid, flatly conic, moderately small for the genus, whorls four and three-fourths, convex, gradually increasing to the body whorl which is moderately expanded; the last quarter of the body whorl descends moderately to the aperture, with the suture lying at a 45 degree angle with the axis of the shell. Base rounded; umbilicus small, contained about ten times in the maximum diameter of the shell and one-third covered by the reflected inner lip. Aperture subcircular, oblique; basal portion of the peristome slightly reflected and slightly thickened within, while the columellar end is broadly reflected over a third of the umbilicus. A faint suggestion of parietal callus connects the ends of the peristome.

The embryonic shell consists of one and two-thirds whorl; early portion of first whorl marked with radial wrinkle-like striae, the remainder of the embryonic shell uniformly wrinkly-granulose with widely spaced, elongate papillae superimposed. These papillae, starting on the second half of the first whorl and somewhat indistinct on the worn apex of the holotype, appear in spiral and oblique series. The papillae become more closely spaced on the last third of the first neanic whorl and thus continue over the remainder of the shell, varying from elongate to evenly rounded on different parts of the shell. The underlying granulation is distinct on the penultimate and early whorls but indistinct on the body whorl. The base of the shell is uniformly papillose. Incremental striae are prominent on the body whorl. On unworn newly formed portions of the shell the papillae bear minute, hair-like periostracal processes.

Color light cinnamon-brown over the upper and peripheral aspects of the shell, lighter in color on the under surface. Above the periphery is a chestnut-brown band about one mm in width. It is bordered below by a band about the same width and somewhat lighter in color than the body of the shell, and above by a somewhat narrower light band.

Holotype measurements: maximum diameter 17.7, minimum diameter 15.9, height 11.1, umbilicus diameter 1.8.

Anatomy.—The mantle is marked with black pigment spots of varied shapes and sizes. The genitalia are similar to those of *H. waltoni*, with the spermathecal diverticulum and portion of the spermathecal duct proximal to the attachment of the duct proportionately shorter in *edwardsi*. Lengths of reproductive structures: penis 10.7, epiphallus 10.6, epiphallic caecum 13.2, vagina 1.7, free oviduct 4.2, spermathecal duct 27.3, spermathecal diverticulum 20.1 arising 12.0 from the base of the duct, spermatheca 2.0 by 2.4, atrial sac 4.5, dart sac 1.7 by 2.0, mucus glands 3.1, common duct of the mucus glands 0.8.

Type Locality.—Pine Valley, San Diego Co. California, along Manzanita Trail near Manzanita Creek, at Lat. 32° 49.7′ N. and Long. 116° 31.1′ W. Elevation about 3700 feet. Collector W. O. Gregg, 18 January 1953.

Type Material.—Holotype, Natural History Museum of Los Angeles County No. 1761. Paratypes: Natural History Museum of Los Angeles County No. 1108, Delaware Museum of Natural History (ex- M. L. Walton collection No. 6622), and private collections of S. S. Berry 19,910 and W. B. Miller 2609, 4257, 6490 (ex-WOG 3642), 6491 (ex-WOG 3698), 6492 (ex-WOG 3718), 6493 (ex-WOG 6293), and 6494 (ex-WOG 7112).

Additional Localities.—H. Arden Edwards reported finding this snail in various localities in Pine Valley, northeast of U.S. Highway 80, within a radius of one mile from the Pine Valley Post Office. Also near highway 80 along La Posta Creek (H. A. Edwards, 28 March 1947): along Pine Valley Creek and Pine Creek Road at 2.0 road miles N. of highway 80 (W. B. Miller, 4 June 1970): and along Pine Valley Creek and Pine Creek Road at 2.1 road miles N. of highway 80 (R. L. Reeder, 9 Jan. 1975).

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Figure 1. Helminthoglypta waltoni, new species. Genitalia; drawing made from projection of stained whole mount. Distal portion of penis A′ magnified in inset A to show details in sagittal section. ag. albumin gland: as, atrial sac; at, atrium; ds, dart sac; dt, dart; dv, spermathecal diverticulum; ec, epiphallic caecum; ep, epiphallus; go, genital orifice; hd, hermaphroditic duct; mb, mucus bulbs; mu, mucus gland membranes; ot, ovotestes; ov, oviduct; pc, preputial chamber; pe, penis; pr, penial retractor; pt, prostate; sd, spermathecal duct; sp, spermatheca; ut, uterus; va, vagina; vd, vas deferens.

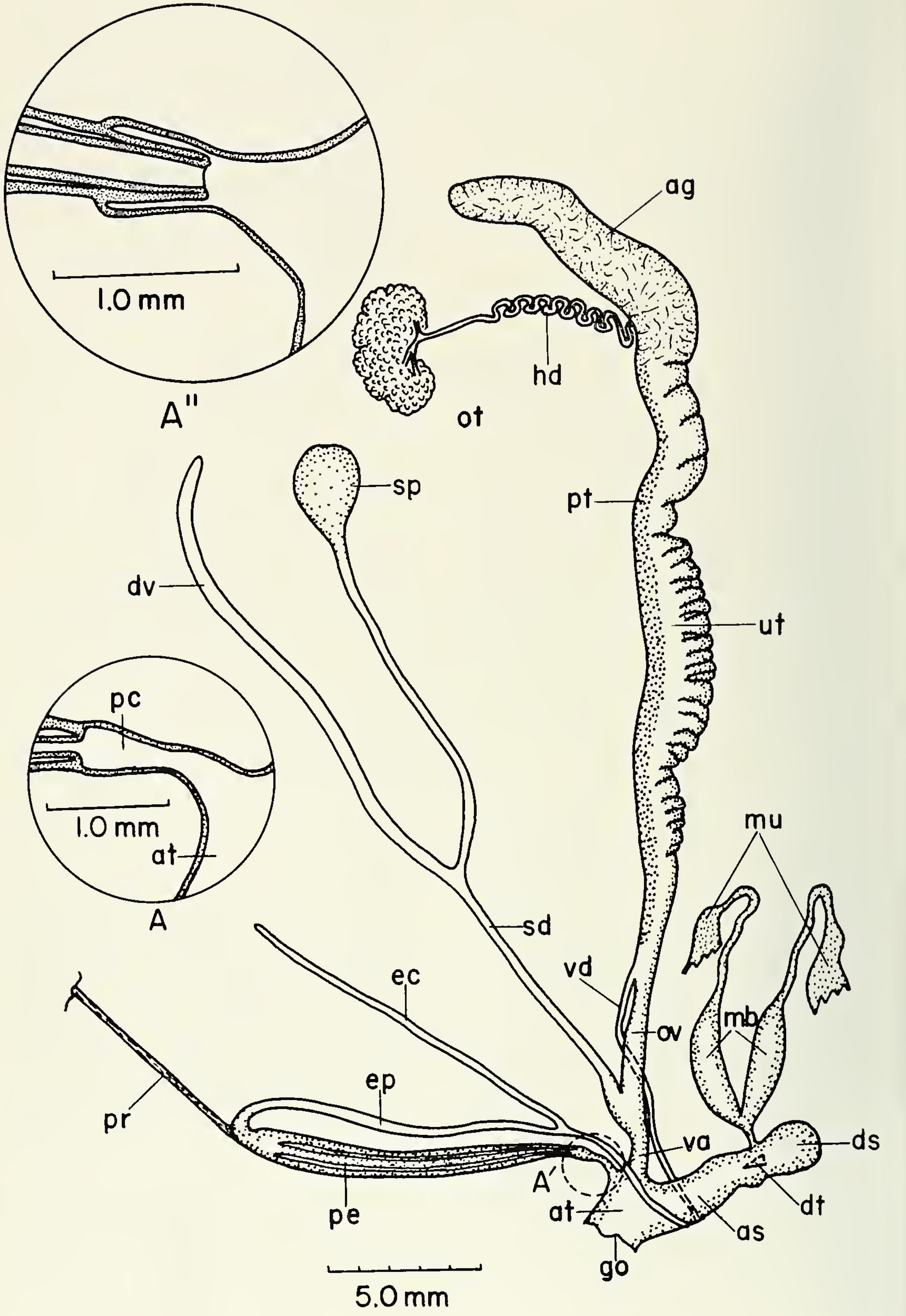
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Figure 3. A–C, *Helminthoglypta waltoni* new species; Lower figures: *Helminthoglypta edwardsi* new species.

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Figure 2. *Helminthoglypta edwardsi*, new species. Genitalia; drawing made from projection of stained whole mount. Distal portion of penis A′ magnified in inset A to show details in sagittal section. A″, sagittal section of another specimen showing partially everted penis in preputial chamber. Abbreviations same as those defined in figure 1.

Remarks.—As in the case of *H. waltoni*, specimens have always been scarce and are becoming scarcer. The type locality has been subdivided for development and is largely built up with homes. Fortunately, this snail can be found well up along Pine Valley Creek to the north wherever fallen logs can provide a suitable habitat.

Helminthoglypta edwardsi is most closely related to *H. waltoni*, differing from the latter by its less elevated, smaller shell with more closely coiled whorls, by the more widely reflected inner lip, more regularly and closely spaced papillation, and more delicate incremental striation. Anatomically, it is nearly identical to *H. waltoni*, differing from the latter by the proportionately shorter spermathecal diverticulum and portion of the spermathecal duct proximal to the attachment of the diverticulum.

In view of the fact that *H. thermimontis*, *H. waltoni*, and *H. edwardsi* have closely similar anatomies, it became necessary to decide, in our opinion, whether all three might be conspecific. *Helminthoglypta thermimontis* is a log snail living at high elevations above 5000 feet on Hot Springs Mountain (we have found it at 6100 ft) while *H. edwardsi* is a log snail living at lower elevations along Pine Valley Creek, some 35 miles south of Hot Springs Mountain, and *H. waltoni* is a rockslide inhabitant. Repeated attempts to raise *H. waltoni* in a wooden terrarium have failed, even though *H. edwardsi* has thrived in a similar terrarium; this led us to believe that *H. waltoni* has different ecological and physiological adaptations than *H. edwardsi*. Thus, in attempting to infer reproductive isolation from morphological, anatomical, ecological, and physiological differences, we concluded that it appears highly improbable that any hybrid populations (even if hybrids could be obtained) would be able to survive in any one of the three niches of the parent populations. Accordingly, *H. waltoni* and *H. edwardsi* are considered closely related but distinct species. Both are also closely related to *H. thermimontis* and all three are probably derived from an immediate common ancestor.

Helminthoglypta edwardsi is named for the late H. Arden Edwards who first brought this snail to the attention of one of us (WOG).

SOME NEPHTYIDAE (POLYCHAETA) FROM UBATUBA, BRASIL

Kristian Fauchald[1]

Abstract: Four species of nephtyid polychaetes are reported from Ubatuba, Brasil. The description of *Aglaophamus juvenalis* (Kinberg, 1866) is amplified and illustrations of median parapodia are given for all four species.

Nephtyids from Brasil have previously been reported by Kinberg (1866, p. 240; Hartman, 1948, p. 51) and Nonato and Luna (1970, p. 71). The present collection was sent to the author for identification by Edmundo Nonato of Instituto Oceanografico de Universidade de Sao Paulo. It contains four species from intertidal and shallow subtidal areas.

Station list:

A-144: Station pier, Ubatuba, under stones in black, sand mud.

A-255: Praia Dura, Ubatuba, intertidal in fine sand.

A-322: Anchieta Island, 10 m, gray, fine mud.

B-9 : Cananeia, 4 m, soft mud with organic debris.

B-63 : Cananeia, 6 m, soft mud with organic debris.

Aglaophamus juvenalis (Kinberg, 1866)
(Fig. 1a–c)

Aglaopheme juvenalis Kinberg, 1866, p. 240
Aglaophamus juvenalis, Hartman, 1948, pp. 51–52

Aglaophamus juvenalis has remained known through its original record from Rio de Janeiro only.

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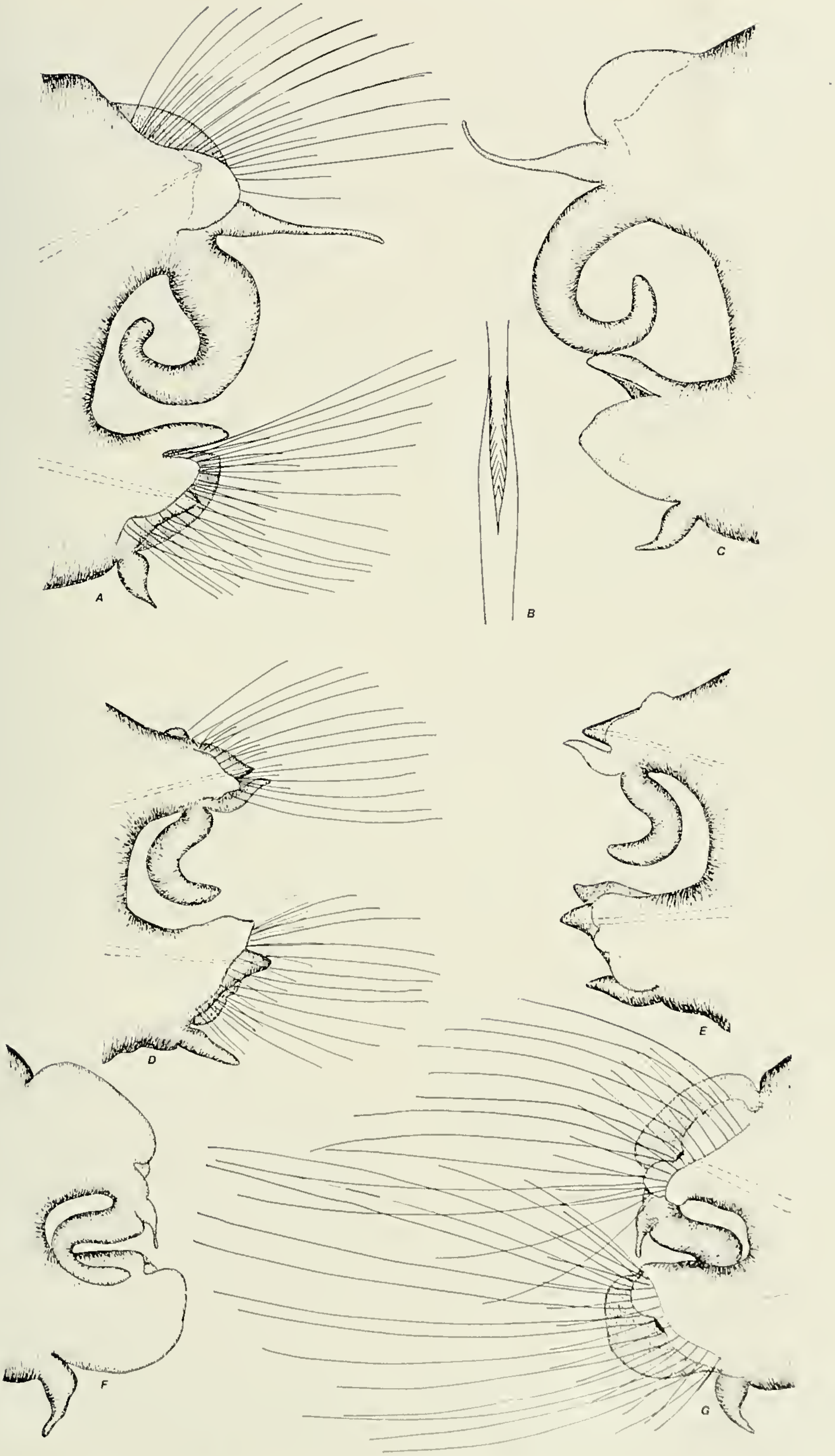

Figure 1. Aglaophamus juvenalis: A, parapodium 25, anterior view, × 34; B, furcate seta, × 257; C, parapodium 25, posterior view, × 34. *Nephtys acrochaeta*: D, parapodium 25, anterior view, × 16; E, parapodium 25, posterior view, × 16; *Nephtys magellanica*: F, parapodium 25, posterior view, × 32; G, parapodium 25, anterior view, × 32.

The species is interesting, because it is one of the few species of nephtyids which has an aberrant number of rows of subterminal papillae on the proboscis. Most species have either fourteen or twenty-two; *A. juvenalis* has sixteen rows of papillae. The original description was reviewed and amplified by Hartman (1948). The present specimen, which is incomplete with 45 setigers, fit well with Hartman's description. Some important points are reviewed below.

The proboscis has sixteen rows of subterminal papillae with five or six papillae in each row. A mid-dorsal papilla is present and is more than twice as long as all other papillae. The proximal surface of the proboscis is smooth.

Setiger I has short, button-shaped parapodia: both noto-and neurocirri are present. The acicular lobes are pointed in the fully developed parapodia (Figs. 1a, c) at setiger 20. The rounded notopodial presetal lobe covers the anterior face of the acicular lobe completely. The notopodial postsetal lobe is placed dorsal to the presetal lobe and is visible, in anterior view, above the dorsal margin of the acicular lobe. It is rounded.

A thick, folded erect lobe is on the superior margin of the neuropodia. The lobe is first present on setiger 4 and becomes reduced in setigers 35–40; it is absent posterior to setiger 40. The neuropodial presetal lobe is as high as the acicular lobe and is placed dorsal to that lobe. The postsetal lobe is triangular and is higher than all other lobes in the neuropodia, with the exception of the erect lobe. Notopodial cirri are greatly prolonged and distally filiform in median setigers; neuropodial cirri are short and tapering.

Interramal cirri are present from setiger 4 to the end of the fragment. Where fully developed, each is involute and describes approximately a semi-circle. The cirri are rapidly reduced after setiger 30; by setiger 35 each is a small, nearly straight papilla at the base of the long notopodial cirri.

Aglaophamus tabogensis Monro (1933, pp. 53–55, fig. 23) resembles *A. juvenalis* in that it has strongly prolonged notopodial cirri in median setigers. *Aglaophamus tabogensis* has rounded acicular lobes in anterior setigers; all acicular lobes are pointed in *A. juvenalis*. Interramal cirri are present from setiger 8 in *A. tabogensis* and from setiger 4 in *A. juvenalis*. The type-material of *A. tabogensis* was recently reviewed by the present author (Fauchald, in press).

Material: A-255 (1).

Nephtys acrochaeta Hartman, 1950
(Fig. 1d–e)

Nephtys acrochaeta, Hartman, 1950, pp. 114–1146, pl. 16, figs. 1–6; Hartman, 1953, p. 33.

Nephtys acrochaeta was originally described from Uruguay in 80 m depth. It is characterized primarily by the presence of spurred setae in the postacicular fascicles, but resembles *N. squamosa* Ehlers (see below) in that the dorsal body-wall is expanded to form flattened scales over the dorsum and the bases of the parapodia in a median region. This condition is also found in *N. serratifolia* Ehlers (1897, pp. 24–25, pl. 1, fig. 13; Hartman-Schröder, 1965, pp. 141–145, figs. 110–113) from Chile and southern Argentina.

Nephtys acrochaeta differs from *N. squamosa* in that it has sharply pointed, rather than bluntly rounded acicular lobes. Interramal cirri are first present from setigers 9–10 in the former and from setiger 2 in the latter (Nonato and Luna, 1970, p. 41).

Nephtys acrochaeta resembles *N. serratifolia* closely, and in fact, Hartman-Schröder (1965) suggested that the two might be synonymous. The pre- and postacicular lobes are very much higher than the acicular lobes in *N. serratifolia* and shorter than these lobes in *N. acrochaeta* both as illustrated by Hartman (1950, pl. 16, figs. 1–2) and in the present specimens. Interramal cirri are present from setiger 3 in *N. serratifolia* and from setigers 9–10 in *N. acrochaeta*.

Material: A-322 (3); B-9 (2); B-63 (4).

Nephtys magellanica (Augener, 1912)
(Fig. 1f–g)

Nephtys magellanica, Augener, 1912, pp. 208–209, figs. 27–28; Hartman, 1940, 1. 238, pl. 41, figs. 100–104; Hartman, 1950, p. 100

Nephtys magellanica has a smooth proboscis with 22 rows of subterminal papillae; a long mid-dorsal papilla is present.

Interramal cirri are present from setiger 3 and the acicular lobes (Figs. 1c–d) are broadly, but shallowly incised or excavated in the fully developed parapodia. The notopodial postsetal lobe is obliquely rounded; the neuropodial one is truncate; both are somewhat higher than the acicular lobe. The notopodial presetal lobe has an inferior free, rounded flap; the neuropodial one is continuous with the postsetal lobe around the superior margin of the neuropodial acicular lobe. Setae are very long, especially in the postacicular fascicles.

Material: A-255 (3).

Nephtys squamosa (Ehlers, 1887)

Nephtys squamosa Nonato and Luna, 1970, p. 71, figs. 27–31 and references therein.

Nephtys squamosa is well known from warmer waters on both sides of the Americas. It is distinguished from other species with the dorsal body-wall expanded as indicated above.

Material: A-255 (2).

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A NEW SPECIES OF *DIOPLOSYLLIS* (POLYCHAETA: SYLLIDAE) FROM CALIFORNIA

George J. Mueller[1] and Kristian Fauchald[2]

Abstract: A new species of *Dioplosyllis* is described. Three specimens were collected swarming at a night light. A table is presented to separate the four known species.

Dioplosyllis broadi, new species
Figures 1–6

Material Examined: Three epitokous specimens were taken at a night light located in Fishermans Cove, Santa Catalina Island, California. An anterior fragment with seven setigers was collected on 18 August 1973, and two complete specimens were collected on 19 August 1973. (Holotype No. POLY 1141, deposited in Allan Hancock Foundation; Paratype No. 740, deposited in University of Alaska Museum.)

General Description: The complete specimens are 22 and 24 mm long, 2.0 and 2.1 mm wide without parapodia and 6.0 and 6.1 mm wide with parapodia. The specimens consist of 13 setigers, a buccal segment and an asetigerous preanal segment. The outline in cross-section is ellipsoidal, strongly arched dorsally and flattened ventrally. The body in outline is tapered from the median segment to both ends. The median segment is twice the width of the anterior and posterior ends.

The body is brownish purple dorsally and lighter in color ventrally. Each segment (Fig. 1) appears regularly wrinkled with from two wrinkles on the buccal segment to 12 wrinkles on the fourth. Each wrinkle has a purple stripe with a cream colored valley in between. The parapodial wrinkles run parallel to the long axis of the body with each stripe strewn with white spots. The dorsal and ventral cirri have ten longitudinal stripes made up of rows of small purple pigment spots. The eyes in life are red-orange in color.

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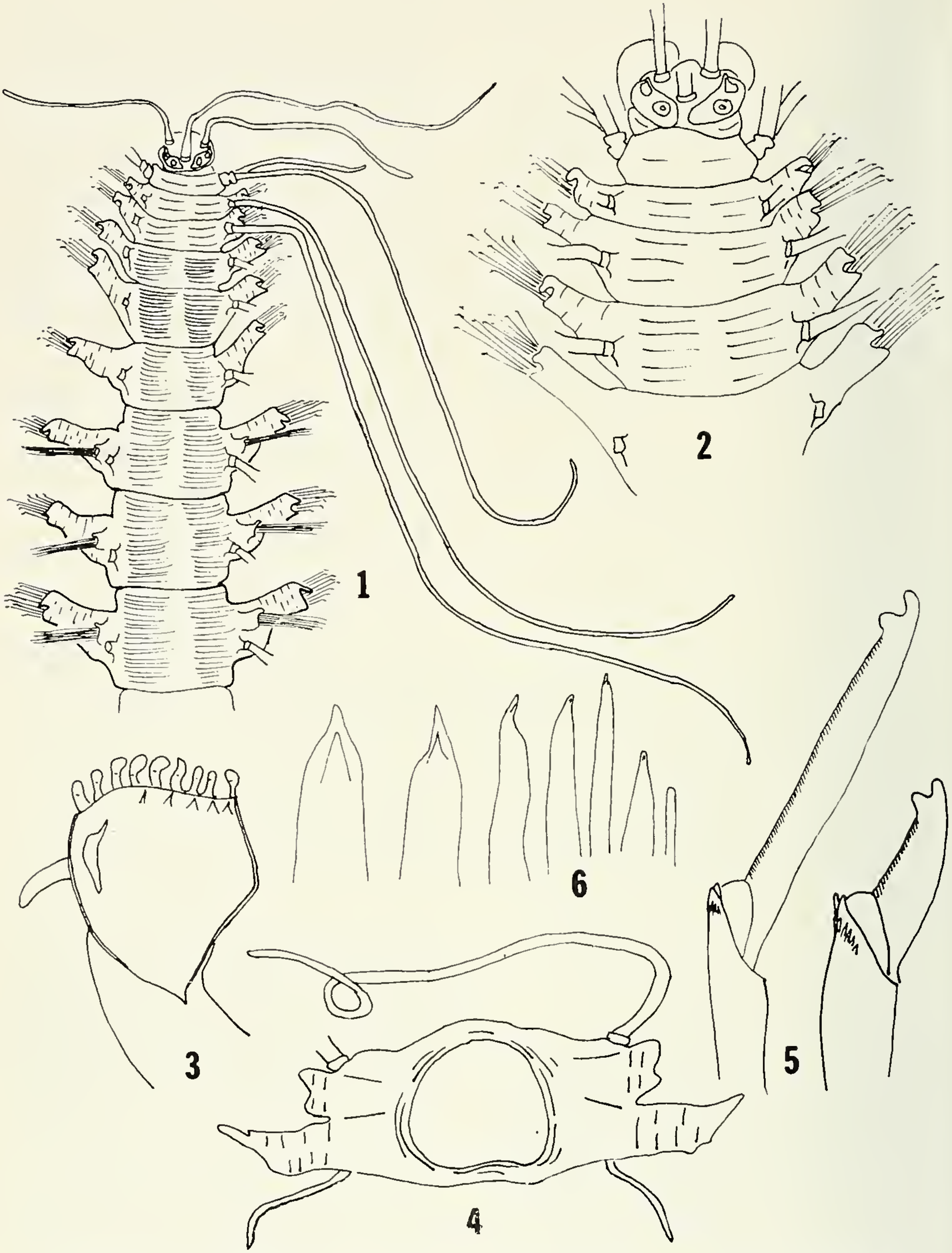

Figures 1–6. Dioplosyllis broadi, new species. *1*, Dorsal view of anterior end, × 10; *2*, Dorsal view of anterior end showing prostomial details, × 20; *3*, Distal end of pharynx showing digitiform process, ×40; *4*, Seventh setiger, anterior view; *5*, Compound falcigers from neuropodium of seventh setiger, ×500; *6*, Neuropodial acicula from seventh segment, ×500.

TABLE 1. Diagnostic characters of the species in the genus *Dioplosyllis*.

Character	*D. broadi*	*D. infuscata* (From Ehlers 1901)	*D. japonica* (From Imajima and Hartman 1964)	*D. cirrosa* (From Gidholm 1962)
Palpostyle	present	absent	present	absent
Cutting margin of falciger	minute serrations	minute serrations	smooth	distinct serrations
Nuchal ridge	present	absent	present	present
Position of proventriculus	3–6 setiger	?	4–7th setiger	12–15th setiger
Distal papillae	10	10	10	13
Pharyngal teeth of epitoke	5 small 1 large	?	6 small 1 large	5 small 1 large
Eye color	red-orange	red-brown	purple	?
Anterior eyes with tapered cone	present	absent	absent	absent
Setigers	13	13	?	63
Distal end of setal shaft	bifid	entire	entire	bifid

The prostomium (Fig. 2) is twice as wide as long with two pairs of eyes, the anterior are further apart than the posterior. The anterior eyes taper into an elevated cone and do not appear to have a pupil. The posterior eyes are raised into subelliptical elevations and each eye has a pupil. Three antennae are present with the median one inserted between the posterior pair of eyes and the lateral ones slightly antero-medial to the anterior pair of eyes. The median antenna is approximately ⅓ longer than the lateral antennae and reaches the sixth setiger. A pair of nuchal ridges is present on the posterior margin of the prostomium.

The palps are slightly more than twice as long as the prostomium. They are thick and flattened dorsoventrally with a slightly expanded proximal portion where the palps are fused at the base. Each palp has a minute style inserted laterally in a cleft approximately ⅙ of the distance from the anterior edge. The pharynx (Fig. 3) has ten soft papillae equal in size and evenly distributed around the distal margin. Five small recurved teeth are present slightly posterior to the papillae, and are evenly distributed around the lateral and ventral ¾ of the pharynx. Subdistal to the anterior margin, there is a single mid-dorsal tooth. On the inside of the pharynx, facing the coelom and opposite the mid-dorsal tooth, there is a long digitiform process (Fig. 3) approximately the same size as the tooth. The proventriculus extends from setiger 3 to setiger 6.

The peristomium is midway in width between the prostomium and the first setiger and is ½ as long as the first setiger. Two pairs of cirri are present, with the ventral ones about half as long as the dorsal cirri, which reach the eighth setiger. These cirri and all others are irregularly wrinkled.

Each parapodium of the first setiger is about ½ as long as the segment is wide. Each terminates in a superior triangular presetal lobe and a shorter truncate postsetal lobe. The long dorsal cirri reach setiger 11 and are inserted on a small elevated lobe at the base of the parapodia. The ventral cirri reach the middle of the next setiger and are inserted on the proximal third of the parapodia. A normal segment (Fig. 4) differs from the first setiger in having longer parapodia. A nephridial depression is present slightly anterior to the mid-parapodial line at the base of the parapodium on setigers 4 through 13.

The capillary setae characteristic of the epitoke vary in thickness and are first present from setiger 6. They arise from a lobe between the dorsal cirri and neuropodia. Ventral to the capillary setae is a notopodial acicular lobe containing six to seven acicular setae. The neuropodial setae (Fig. 5) are compound falcigers; the blade has a minutely serrated cutting edge and each has a short subdistal tooth and bifid tip. The end of the shaft has a subdistal row of small spines; the distal tip is bifid. The superior setae have a longer appendage than the inferior ones. Distally, the neuropodial acicula (Fig. 6) taper sharply; what appears to be longitudinal grooves are present at the tapered end.

The preanal segment is asetigerous and has reduced parapodia. Both the dorsal and ventral cirri are normal. The pygidium has two ventral cirri. The four species of *Dioplosyllis* are compared in table 1.

Etymology: This species is named after A. Carter Broad who stimulated one of the author's (Mueller) interest in polychaetes by posing a question in polychaete systematics.

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A NEW SPECIES OF CYCLOPOID COPEPOD, PARASITIC ON SHINER SURFPERCH, *CYMATOGASTER AGGREGATA* GIBBONS, IN ANAHEIM BAY AND HUNTINGTON HARBOR, CALIFORNIA, WITH NOTES ON *BOMOLOCHUS CUNEATUS* FRASER AND *ERGASILUS LIZAE* KRØYER

Doyle A. Hanan[1]

Abstract: Three species of parasitic cyclopoid copepods are reported from the Shiner Surfperch, *Cymatogaster aggregata* Gibbons, collected from Anaheim Bay and Huntington Harbor, California. One of the copepods, *Holobomolochus embiotocae,* new species, of the family Bomolochidae inhabits the nasal cavity of the shiner perch. The other two copepods, *Bomolochus cuneatus* Fraser and *Ergasilus lizae* Krøyer, are reported as new host and locality records.

The three species of cyclopoid copepods reported herein are part of a collection made by the author while examining the ectoparasites of the surfperch, Embiotocidae, in Anaheim Bay and Huntington Harbor, California. Anaheim Bay is a salt water marsh with a year-round opening to the sea and is without a fresh water inlet, other than rainwater run off. Huntington Harbor is an adjoining small boat marina. Five hundred and nineteen shiner perch from monthly collections made between 24 March 1973 to 30 March 1974 were examined. The fish were obtained by otter trawl and gill net, then individually bagged and placed on ice for later laboratory examination with the aid of a dissecting microscope.

Holobomolochus embiotocae, new species

Material examined: 603 females (395 ovigerous) and 41 males were removed from the nasal cavities of the shiner perch, *Cymatogaster aggregata* Gibbons (the type host). The incidence of infestation was 67.6 percent. The holotype USNM 151182, allotype USNM 151183, and paratypes USNM 151184 are deposited in the U.S. National Museum, Washington, D.C.

Description: *Female*. Body (Fig. 1) mean length of 26 randomly selected ovigerous females 0.938 mm with a standard deviation of 0.125 mm. Cephalon comprising about one-fourth of the total body length.

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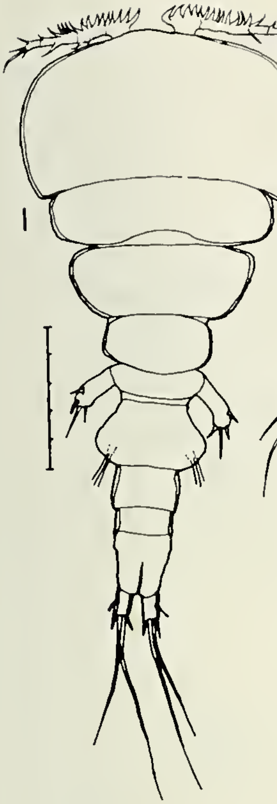
Figures 1–10. Holobomolochus embiotocae, new species, female. *1*, Body, with egg sacs removed; *2*, Genital segment and abdomen; *3*, First antenna; *4*, Rostral tines; *5*, Second maxilla. *6*, Egg sac removed; *7*, First maxilla; *8*, Second antenna; *9*, Paragnath; *10*, Mandible. Scales: Fig. 1, 0.5 mm; Figs. 6, 8, and 10, 0.05 mm; Figs. 2 and 3, 0.1 mm; Figs. 4, 5, 7, and 9, 0.01 mm.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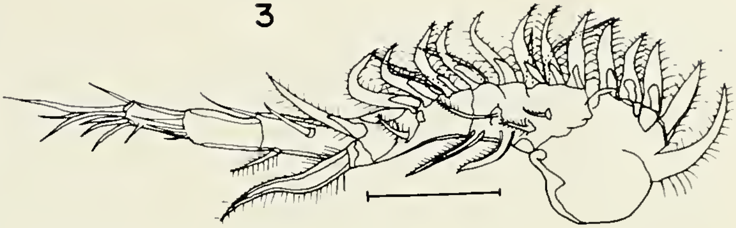
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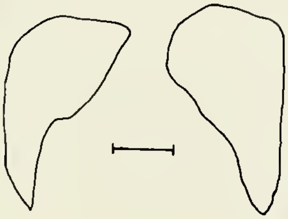
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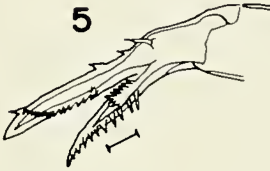
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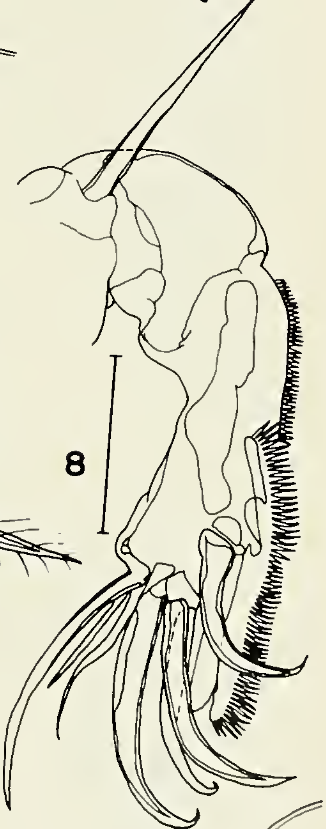
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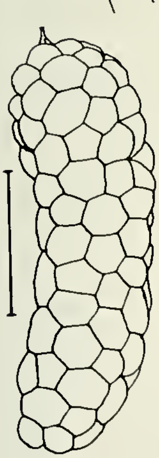
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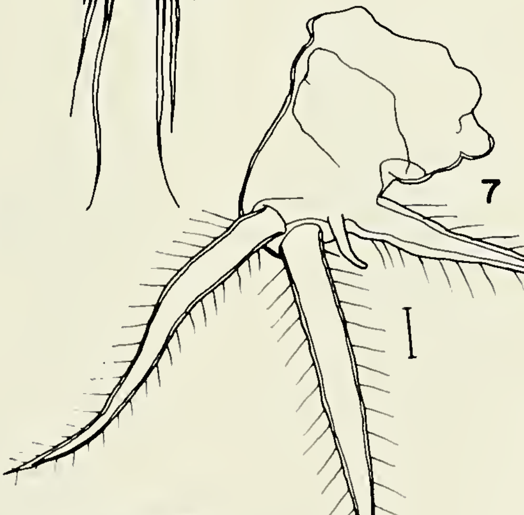
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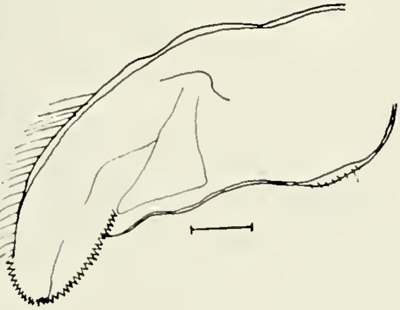
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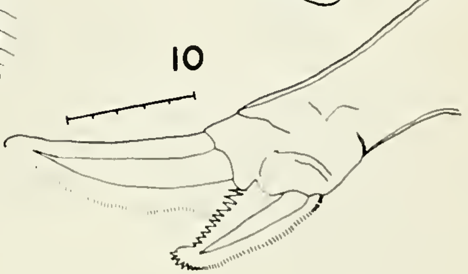
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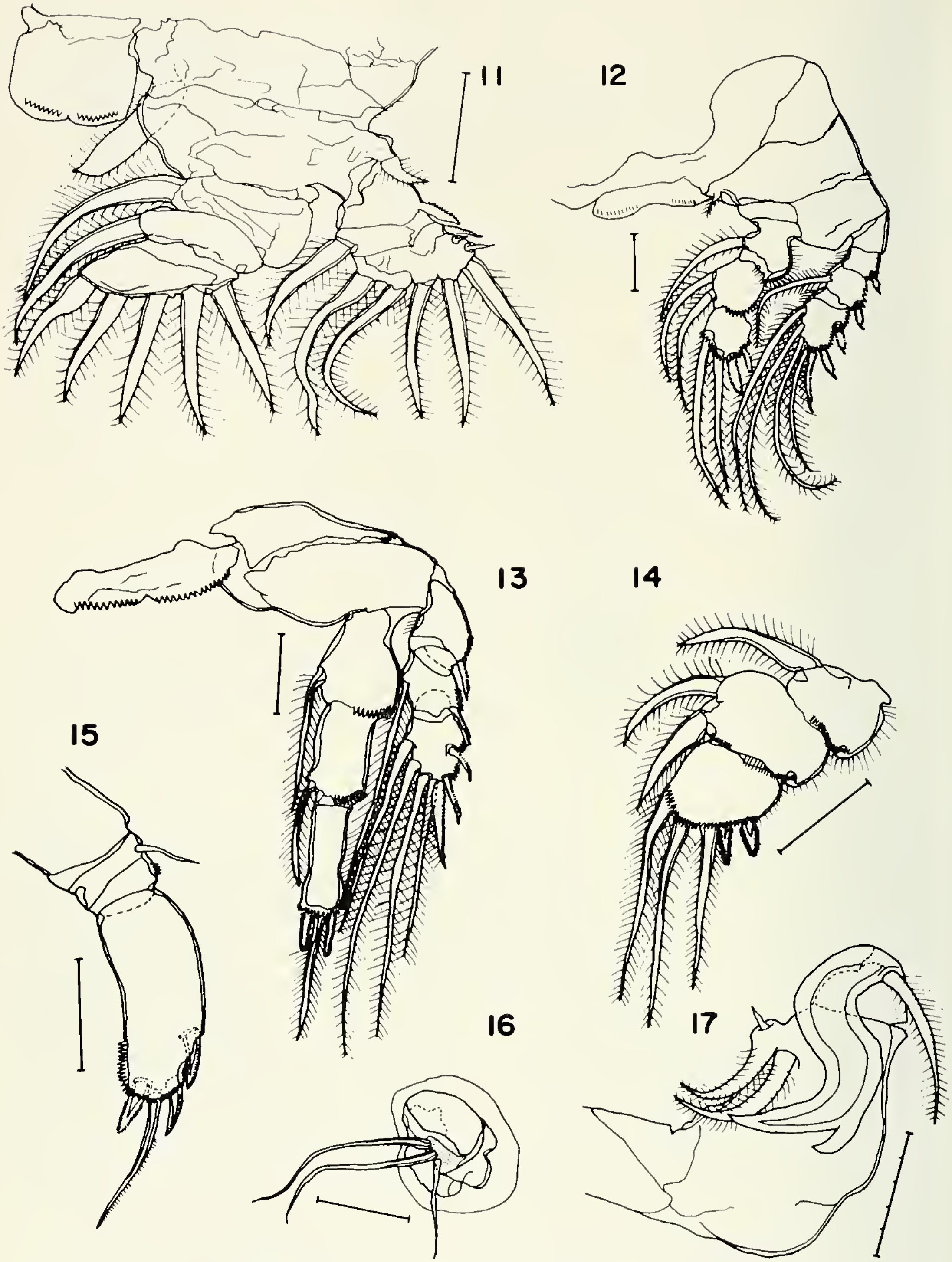
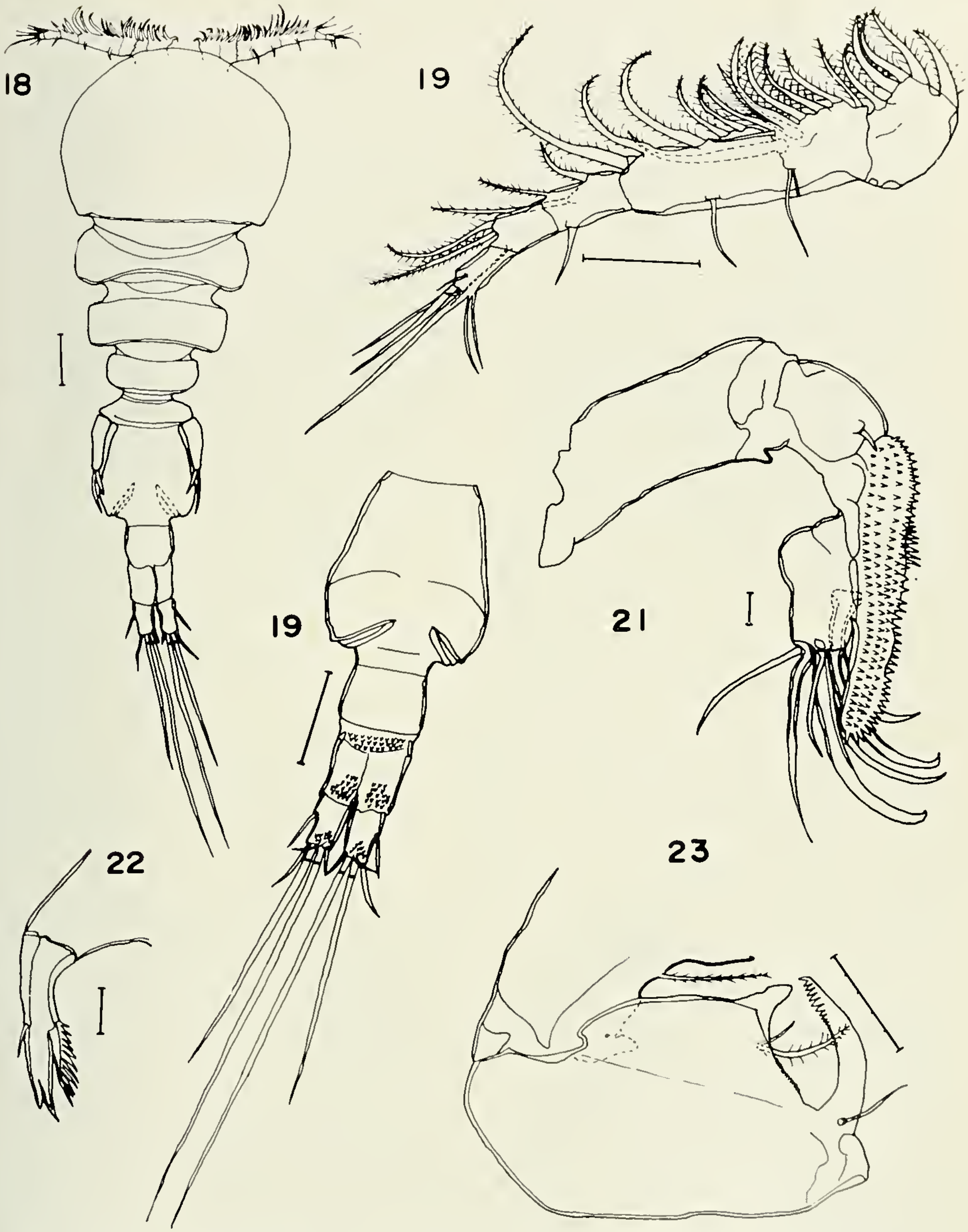
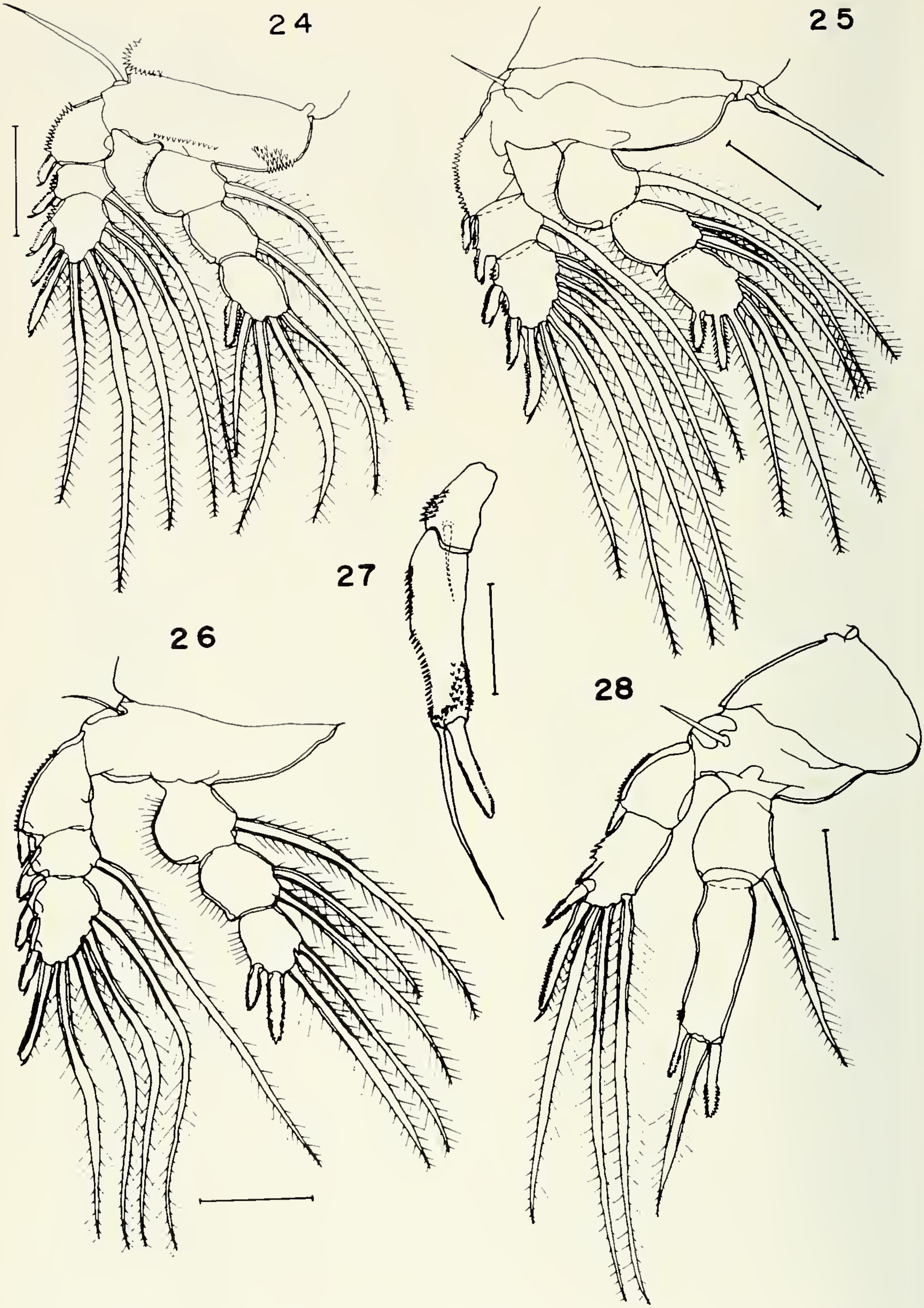


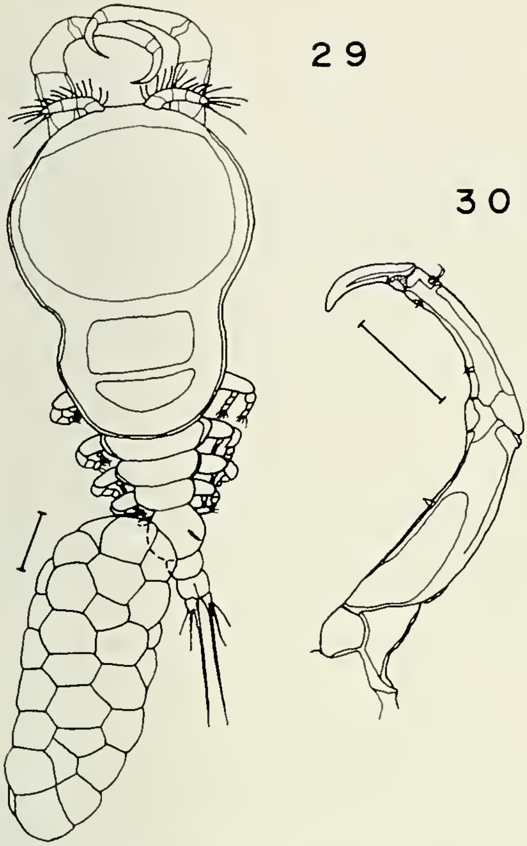
Figures 11–17. Holobomolochus embiotocae, new species, female. *11,* Leg 1; *12,* Leg 3; *13,* Leg 4; *14,* Leg 2, exopod; *15,* Leg 5, ventral; *16,* Leg 6; *17,* Maxilliped. Scales: Figs. 11–16, 0.1 mm; Fig. 17, 0.05.



Figures 18–23. Holobomolochus embiotocae, new species, male. *18*, Body; *19*, First antenna; *20*, Genital segment and abdomen; *21*, Second antenna; *22*, Second maxilla; *23*, Maxilliped. Scales: Figs. 18 and 20, 0.1 mm; Figs. 19 and 23, 0.05 mm; Figs. 21 and 22, 0.01 mm.



Figures 24–28. Holobomolochus embiotocae, new species, male. *24*, Leg 1; *25*, Leg 2; *26*, Leg 3; *27*, Leg 5, ventral; *28*, Leg 4. Scales: all figures, 0.05 mm.



Figures 29–30. Ergasilus lizae, female. *29*, Body, one egg sac removed; *30*, Second antenna. Scale: both figures, 0.01 mm.

First thoracic segment fused with head, segments 2–4 free. Genital segment (Fig. 2) one-third wider than long. Abdomen three segmented, with third segment almost as long as first two combined. Caudal rami about four-fifths as long as wide; each ramus with four terminal, one subterminal, and one lateral setae; and a patch of spinnules arranged subterminally on the ventral surface. Egg sac (Fig. 6) about two-thirds of body length.

First antenna (Fig. 3) six-segmented with terminal three segments better defined. Armature being 5, 13, 8, 3, 2, 8, with reinforcing plates over the basal one-third of setae 2–14. Rostral tines (Fig. 4) as shown in illustration. Second antenna (Fig. 8) as in other members of the genus, having terminal segment armed with four setiform claws, three setae, and rows of spinules on ventral side.

Mandible (Fig. 10) a cylindrical masticatory process tipped with two teeth, terminal tooth being about twice the length of subterminal one. Paragnath (Fig. 9) with serrated tip and fringed with setules near apex and at proximal end. First maxilla (Fig. 7) with four setae; the two largest ones nearly equal in size, the third about one-half the longest and the fourth one-tenth the longest. Second maxilla (Fig. 5) two-segmented; distal segment having two pectinate processes, ventral one armed with a small seta near its base. Maxilliped (Fig. 17) lateral to other mouth parts; three-segmented, second segment bearing two plumose setae and a small seta near base, third segment with one long plumose seta about one-half the length of the claw, which carries an auxiliary claw.

Legs 1–4 (Figs. 11–14) biramous and three-segmented. Armature of legs (leg, endopod, and exopod, respectively): leg 1, 1–0/1–0/5, 0–I/1–I/7; leg 2, 1–0/2–0/3–II, 0–I/1–I/5–I III; leg 3, 1–0/2–0/2–II, 0–I/1–I/4–III; leg 4, 1–0/1–0/I–1–I, 0–I/1–I/4–III. Terminal segment of leg 1 exopodite (Fig. 11) having five plumose setae and two small naked setae. Leg 2 (Fig. 14) differing from leg 3 (Fig. 12) only in armature of terminal segments. Leg 5 (Fig. 15) two-segmented. Leg 6 (Fig. 16) represented by three long setae on dorsal side of genital opening.

Male. Body (Fig. 18) mean length of 22 randomly selected males 0.507 mm, with a standard deviation of 0.059 mm. First thoracic segment fused as in female. Genital segment (Fig. 20) nearly as wide as long. Abdomen two-segmented; first segment unarmed, second with two groups of spinnules. Caudal rami almost as wide as long and armed as in female.

First antenna (Fig. 19) six-segmented; armature (without reinforcing plates) being 5, 13, 7, 4, 3, and 7. Second antenna (Fig. 21) as in female except for the enlarged condition of the terminal segment.

Mouth parts as in female, except second maxilla (Fig. 22) which has two strong teeth; upper tooth with a small seta at base and lined with spinnules. Maxilliped (Fig. 23) three-segmented with single plumose seta on first segment. Second segment strongly developed, with two setae and a patch of teeth. Third segment with single seta and a row of teeth on inner terminal surface.

Legs 1–4 (Figs. 24–26 and 28) with armature (leg, endopod, and exopod, respectively): leg 1, 1–0/1–0/5–I, 0–I/1–I/4–III; leg 2, 1–0/2–0/3–II, 0–I/1–I/5–III; leg 3, 1–0/2–0/2–II, 0–I/1–I/4–III, leg 4, 1–0/1–1–I, 0–I/3–I–II. Outer margin of first segment on each exopod fringed with two rows of small teeth. Exopod of leg 4 (Fig. 28) with only two segments. Leg 5 (Fig. 27) (0.1 × 0.02 mm) two-segmented, first segment with single seta and second segment tipped with two elements. One naked and nearly twice as long, but half as wide as the other armed element.

REMARKS: According to Ho (1972), there are seven species of *Holobomolochus* reported from the Pacific coast of North America. *Holobomolochus embiotocae* appears to be most closely related to *H. venustus* Kabata, 1971. The general body forms are quite similar except that *H. venustus* has more ventral flexion and greater body length. The caudal rami differ in the location of the subterminal seta. The first antennae are similar except that setae 2–10 are reinforced in *H. venustus,* while setae 2–14 are reinforced in *H. embiotocae*. The fifteenth seta is much longer in relation to the other setae of *H. venustus* than in *H. embiotocae*. The paragnath of the new species does not possess a deep notch as in *H. venustus,* nor is the serration the same. The maxillipeds differ in the lengths and number of satae as well as the lack of an auxiliary denticle in *H. venustus*. The armature differs in legs 1, 3, and 4. There also appear to be minor differences in leg 5.

Of the previously known males of *Holobomolochus,* only the description of *H. prolixus* (Ho, 1972) can be used for comparison, since the other male descriptions are inadequate. This comparison shows a great deal of variation, including the reduction of the exopod on leg 4 of *H. embiotocae* to two segments.

Eleven additional female specimens were removed from the black perch, *Embiotoca jacksoni,* white perch, *Phanerodon furcatus,* and pile perch, *Damalichthys vacca.*

Bomolochus cuneatus Fraser, 1920

Record of specimens: Numerous lots of female specimens were collected from Anaheim Bay and Huntington Harbor, California during the study mentioned in the introduction.

Hosts: *Cymatogaster aggregata* Gibbons, 1854, *Damalichthys vacca* Girrard, 1885; *Embiotoca jacksoni* Agassiz, 1853; *Phanerodon furcatus* Girrard, 1854.

As Vervoort and Arai (1966) reported, the range of this copepod seems to coincide with that of the shiner perch. This report confirms Vervoort and Arai's speculation and extends that range to a new locality and to two new host species: *E. jacksoni* and *P. furcatus.*

Ergasilus lizae Krøyer, 1863

Record of specimens: Numerous lots of female specimens were collected in Anaheim Bay and Huntington Harbor, California.

Host: *Cymatogaster aggregata,* Gibbons

The identification of this species of *Ergasilus* is based on Roberts (1970). Specimens were cleared in lactic acid and dissected. Careful comparison of the body (Fig. 29) and especially the second antenna (Fig. 30) reveals that the species is *E. lizae*. Further comparison with Johnson and Rogers (1972) confirms the identification. The significance of this record is that *E. lizae* is a new parasite on the shiner perch and yet is closely related to *E. turgidus* Fraser, 1920, which has previously been reported on the shiner in British Columbia (Vervoort and Arai, 1966; Arai, 1967). This is also a new locality record for *E. lizae.*

ACKNOWLEDGMENTS

I am indebted to William Maxwell for his assistance in obtaining the surfperch from which the copepod specimens were obtained, and to Ju Shey Ho for his advice and technical aid.

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THE CRANIAL OSTEOLOGY OF *AMPHISTICHUS ARGENTEUS* (PISCES: EMBIOTOCIDAE)

Steven L. Morris and Anthony J. Gaudin[1]

Abstract: The cranial and branchial skeleton of *Amphistichus argenteus*, a member of the embiotocid subfamily Amphistichinae, is described here for the first time and compared to that of *Damalichthys vacca*, a member of the second embiotocid subfamily, the Embiotocinae. In *A. argenteus* the circumorbital ring is composed of seven bones, and four pairs of pharyngobranchials are present; whereas in *D. vacca*, the circumorbital ring is composed of six elements and the fourth pair of pharyngobranchials is absent. The reduction in numbers of bony elements is considered to be a more derived condition and, based on this information, the Amphistichinae are here considered more primitive than the Embiotocinae.

The Surfperches (Embiotocidae) are viviparous bony fishes found in the coastal waters of the eastern Pacific. All but two of the approximately twenty-three species currently recognized are confined to the western coast of North America. The two exceptions are found off the coasts of Japan and Korea (Tarp, 1952).

The unusual method of reproduction employed by this group (viviparous development of embryos within the ovary) has drawn considerable attention, and the life history, breeding behavior, and development of various members of the family have been studied extensively (Carlisle, Shott, and Abramson, 1960; Eigenmann, 1890, 1894; Girard, 1854; Hubbs, 1921; Hubbs and Hubbs, 1954; Isaacson and Isaacson, 1966; Rechnitzer and Limbaugh, 1952; Smith, 1964; and Triplett, 1960).

The taxonomy and phylogenetic relationships of the Embiotocidae have been the subject of confusion for some time (for reviews see: Eigenmann and Ulrey, 1894; Hubbs, 1918; Tarp, 1952). Hubbs (1918) divided the Embiotocidae into three subfamilies, the Embiotocinae, the Amphisticinae, and the Micrometrinae, based on the structure of the anal fin and dentition. Tarp (1952) combined the Micrometrinae, with the Embiotocinae and recognized only two subfamilies based on anal fin structure, dentition and the morphology of the prefrontal bone. Current practice is to recognize only two subfamilies, the Embiotocinae and Amphisticinae, based primarily on the condition of the prefrontal bones. In the Amphisticinae, the prefrontals are fused medially to one another; while in the Embiotocinae, the ethmoid extends between and completely separates the prefrontals.

To date osteological information on embiotocids has been restricted largely to observation of major differences between the surfperches and other percoid fish. The presence of a suborbital shelf has been reported (Smith and Bailey, 1962), and the bones of the ethmoid region have been described (Starks, 1926). In addition, Hill (1940) described the osteology of the pile surfperch, *Damalichthys vacca*. Beyond this, little osteological data appear in the literature.

Detailed studies of the skeleton of representative members of the family would aid in clarifying the relationships with the Embiotocidae as well as to clarify their position among other teleostean fishes. The cranial and branchial elements of *Amphistichus argenteus* are described here and compared to other surfperches.

METHODS

Four specimens of *Amphistichus argenteus* ranging in standard length from 14 to 27.5 cm were obtained between September and December, 1973, approximately five miles south of Malibu, California. After fixation in 10 percent formalin for eight days, the specimens were cleared in Potassium Hydroxide, stained in Alizarine Red S, and stored in Glycerin following the procedure described by Davis and Gore (1947). The heads were dissected, and drawings were made at successive stages of dissection. Observations of both the cranial and branchial elements were made with a binocular dissecting microscope. The nomenclature for the skull bones is that of Harrington (1955) and Liem (1963).

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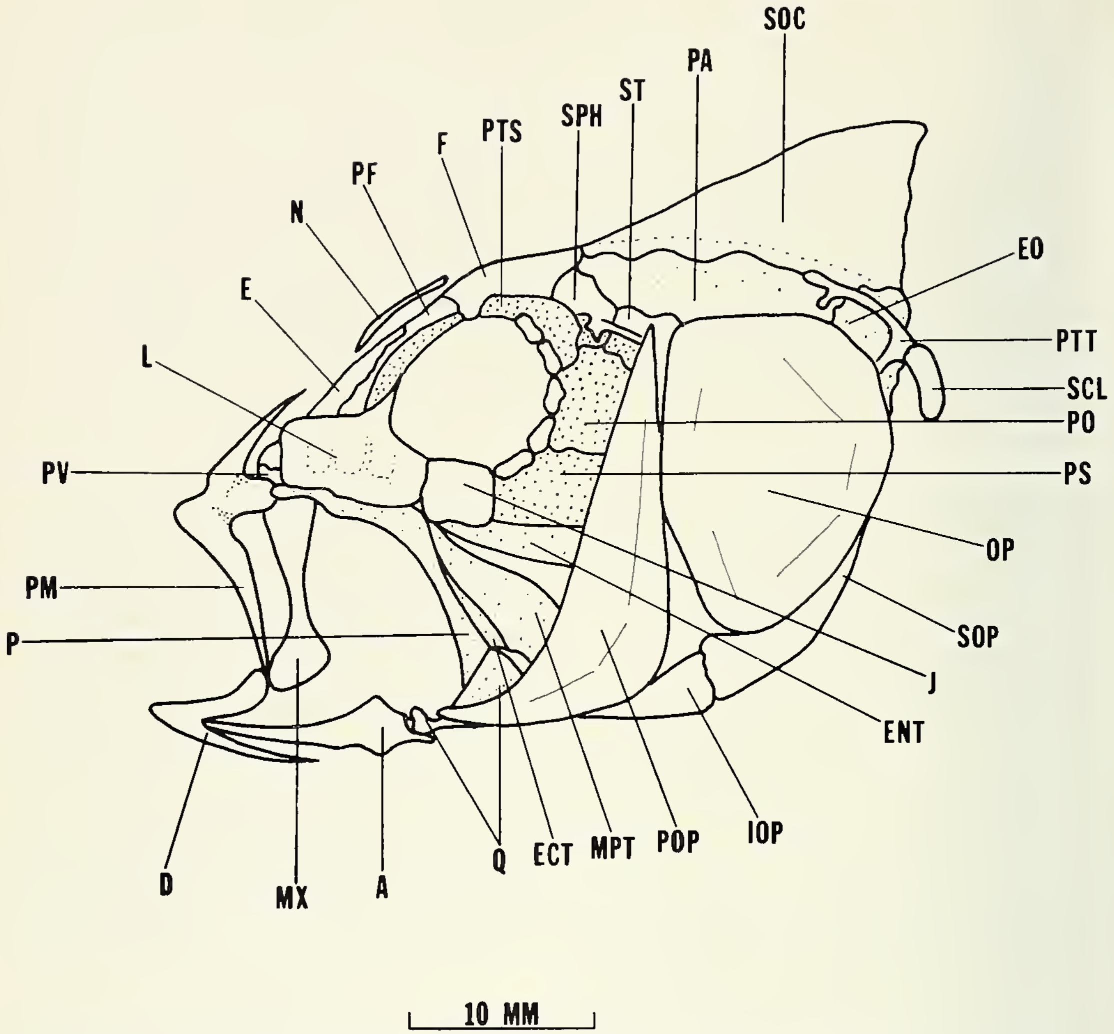

Figure 1. Lateral aspect of intact skull: A, angular; D, dentary; E, ethmoid; ECT, ectopterygoid; ENT, entopterygoid; EO, epiotic; F, frontal; IOP, interopercular; J, jugal; L, lacrymal; MPT, metapterygoid; MX, maxillary; N, nasal; OP, opercular; P, palatine; PA, parietal; PF, prefrontal; PM, premaxillary; PO, prootic; PS, parasphenoid; PV, prevomer; POP, preopercular; PTS, pterosphenoid; PTT, posttemporal; Q, quadrate; SCL, supracleithrum; SOC, supraoccipital; SOP, subopercular; SPH, sphenotic; ST, supratemporal.

CRANIAL SKELETON

Nasal region.—The nasals are flat, narrow, and rectangular, somewhat widened posteriorly and slightly convex (Fig. 1). They are separated by a fontanelle, and overlap the anterior margins of the frontals and the posterior margin of the ethmoid.

The prefrontals form the anterior margins of the orbits. Their posterior portions fuse medially behind the ethmoid, while their lateral edges are expanded into thin wing-like processes. They are bordered posteriorly by the frontals, anteromedially by the ethmoid, and anteriorly by the lateral ethmoids. Anteroventrally they rest on the parasphenoid. A well-developed olfactory foramen perforates each prefrontal near their area of fusion.

The single ethmoid is situated medially between the prefrontals posteriorly and the lateral ethmoids anteriorly. On its dorsal surface it bears a slightly raised medial ridge which slopes anteroventrally and connects with the prevomer.

The single, toothless, prevomer (Fig. 2) is covered dorsally by the ethmoid and lateral

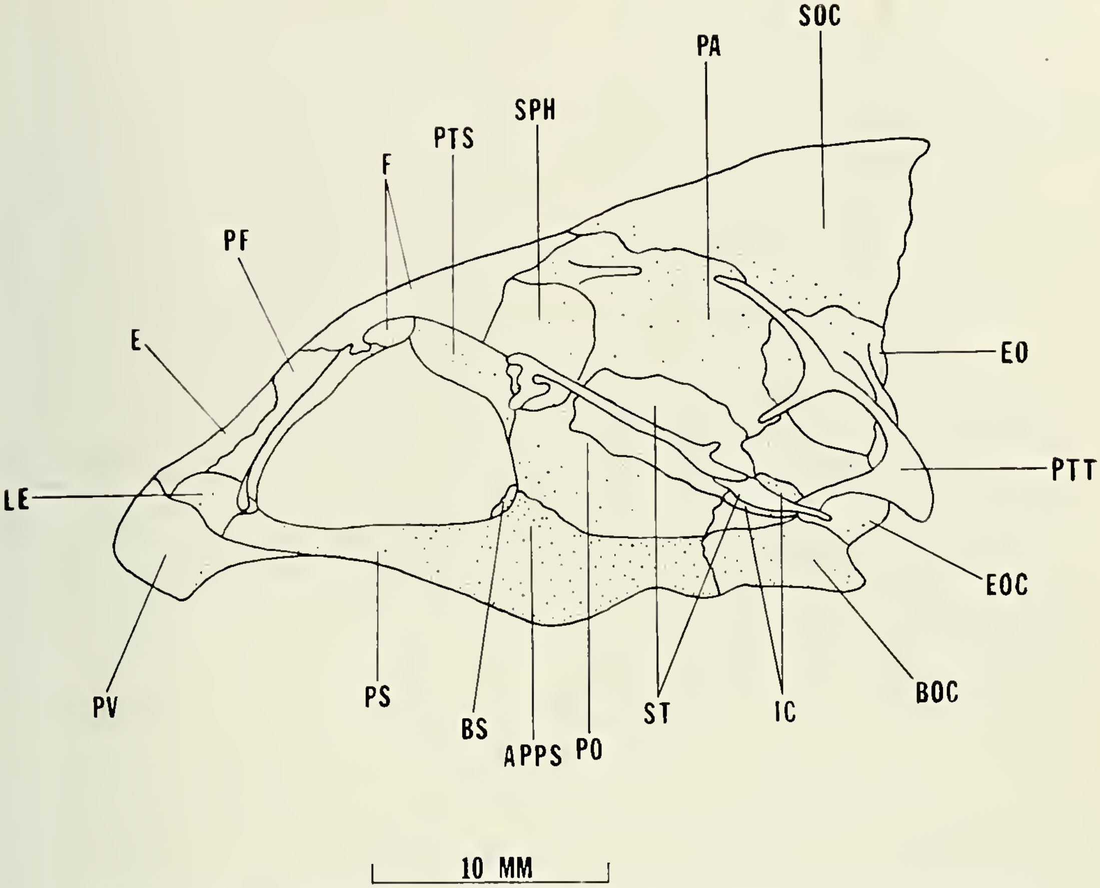

Figure 2. Lateral aspect of neurocranium. Abbreviations as for figure 1 with the following additions; APPS, ascending process of parasphenoid; BOC, basioccipital; BS, basisphenoid; EOC, exoccipital; IC, intercalary; LE, lateral ethmoid.

ethmoids as well as the anterior portion of the parasphenoid. It tapers posteriorly to a point just anterior to the midpoint of the orbit, where it enters a ventral medial groove in the parasphenoid.

Orbital region.—The paired frontals (Figs. 2 and 3) form the anterior portion of the cranial cavity roof as well as the anterior roof and margins of the orbital chambers. They overlap the pterosphenoids posteroventrally and are bordered posteriorly by the sphenotics, the parietals, and supraoccipital. Anteriorly they meet the ethmoid and the prefrontals. The lateral edges are separated from the main bones by longitudinal depressions which extend ventrally as longitudinal ridges. The two frontals are joined medially by a straight suture.

The pterosphenoids form the posterior dorsal roof of the orbital chambers. They are covered dorsally by the frontals, and are bordered posterodorsally by the sphenotics, and posteroventrally by the prootics.

The prootics, together with the basisphenoid form the posteroventral walls of the orbital chambers. They are bordered anterodorsally by the sphenotics, posterodorsally by the supratemporals, posteriorly by the exoccipitals and ventrally by the parasphenoid. On their anteroventral surface they bear a notch into which the ascending process of the parasphenoid projects. Two foramina are formed on the anterior surface of each prootic which accommodate extensions of the occulomotor nerve.

The small, triangular, basisphenoid (Fig. 2) rests on the parasphenoid medially. It bears a dorsal process that extends upward between the prootics and the pterosphenoids.

The circumorbital series (Fig. 1) consists of seven pairs of bones. The flat, rectangular, lacri-

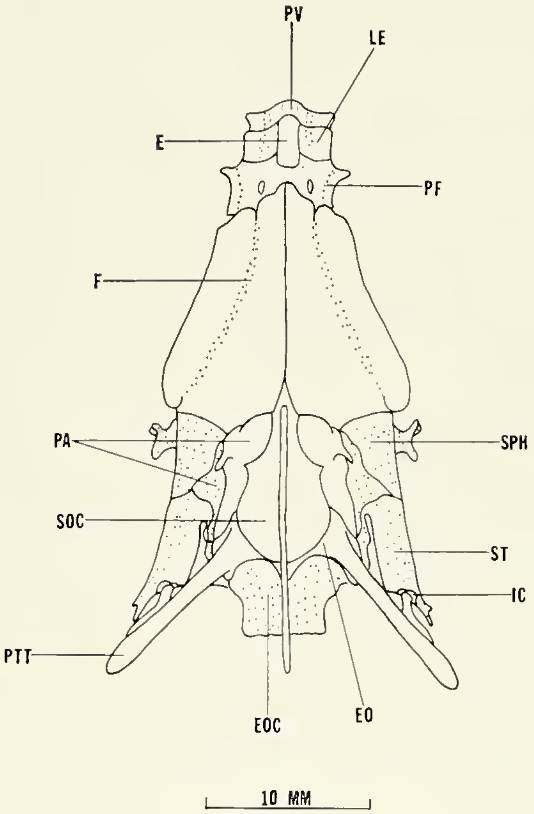

Figure 3. Dorsal aspect of neurocranium. Abbreviations as for figure 2.

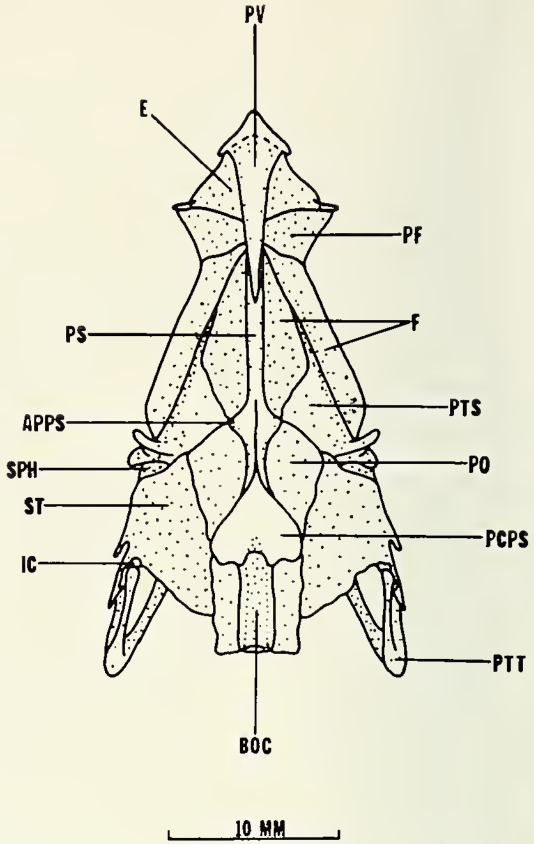

Figure 4. Ventral aspect of neurocranium. Abbreviations as for figure 2 with the following addition: PCPS, pharyngeal condyle of parasphenoid.

mals cover the anterior portion of the ethmoid and lateral ethmoids, as well as the entopterygoids and the anterior portions of the palatines. The lacrimals form the anterior margin of the orbits, and articulate with the prefrontals by a median dorsal spur. The jugals are flat square bones which form the ventral margins of the orbits. They are bordered anteriorly by the lacrimals, and overlap the central portion of the entopterygoids. The six pairs of suborbitals are small elongate bones joined end to end. Together with the second supraorbitals they form the posterior margins of the orbits. The longitudinal margins of the bones of the circumorbital series behind the jugals are projected outward to form an open groove, through which the infraorbital laterosensory canal extends. The third suborbitals are expanded medially to form a small well-defined suborbital shelf. The elements of the circumorbital series are very loosely articulated with the underlying bones of the neurocranium.

Otic region.—The sphenotics are irregularly shaped plates which form the anterior portion of the floor of the temporal groove. They are bordered anteriorly by the frontals and pterosphenoids and surrounded dorsally and posteriorly by the parietals. Ventrally they rest on the prootics. Each sphenotic bears a lateroventral projection at its anterior end which articulates with the hyomandibular.

The elongate, irregularly shaped parietals form a major portion of the dorsal roof of the cranial cavity. Medially they connect with the supraoccipital, posteriorly with the epiotics and exoccipitals, laterally with the supratemporal, and anteriorly with the sphenotics and frontals. The anterior portion of each bears a posteriorly directed ridge that communicates by means of a ligamentous connection with an anteriorly directed projection arising from the posttemporals. The shelf-like structure thus formed defines the lateral border of the supratemporal groove.

The supratemporals (Figs. 3 and 4) are elongate plates which form a major portion of the lateral walls of the cranial cavity. They are bordered medially by the parietals, posteriorly by the exoccipitals, ventrally by the prootics, and anteriorly by the sphenotics. Well-developed ridges formed by the posterior continuation of the sphenotic projections run longitudinally along the entire length of the supratemporals, forming a shelf between the temporal groove above and the dilator groove below. The lateral margin of this shelf bears a longitudinal fold for the passage of the infraorbital latero-sensory canal.

The intercalaries are small, irregular, scalelike bones located at the posterior tips of the supratemporal ridges, where they articulate with the lower arms of the posttemporals.

The cone-shaped epiotics form the posterior dorsal margin of the neurocranium. They are bordered anteriorly by the parietals, medially by the supraoccipital, and ventrally by the exoccipitals. They articulate with the upper arm of the posttemporals.

The elongate supraoccipital bears a well-developed medial crest. It forms the dorsalmost portion of the posterior cranial roof, and is bordered anteriorly by the frontals and laterally by the parietals. The supraoccipital does not reach the foramen magnum, but is bordered posteroventrally by the epiotics.

The exoccipitals are nearly rectangular. Posteriorly the two bones meet and form the upper portion of the foramen magnum. They are bordered posterodorsally by the epiotics, anterodorsally by the parietals, anteriorly by the supratemporals and prootics, and ventrally by the basioccipital. The posterior ends articulate with the first vertebra.

The crescent-shaped posttemporals articulate with the rest of the neurocranium by means of an upper arm that joins with the epiotic, and a lower arm that joins with the intercalary. In addition the posttemporals bear an anteriorly directed projection which connects by means of a ligament with the posteriorly directed projection arising from the parietals. Posteriorly the posttemporals articulate with the supracleithra, thereby providing a connection between the cranium and the pectoral girdle.

Basicranial region.—The rectangular basioccipital lies below the exoccipitals, and forms the lower portion of the foramen magnum. A deep longitudinal groove runs along its entire ventral surface. The basioccipital is bordered anteriorly by the parasphenoid, while its posterior end bears surfaces for articulation with the first vertebra.

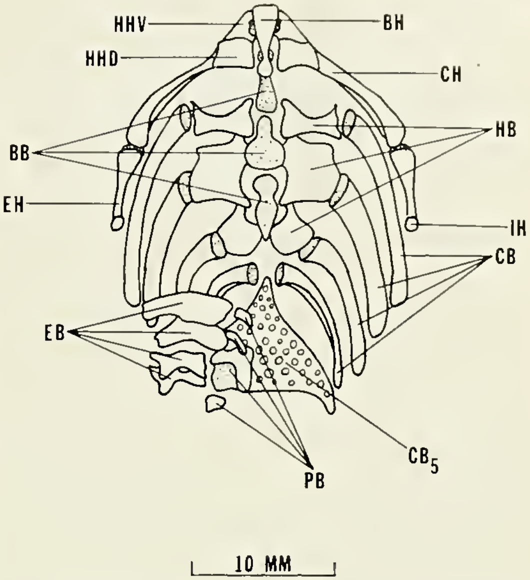

Figure 5. Dorsal aspect of hyobranchial region: BB, basibranchial; BH, basihyal; CB, ceratobranchial; CH, ceratohyal; EB, epibranchial; EH, epihyal; HB, hypobranchial; HHD, dorsal hypohyal; HHV, ventral hypohyal; IH, interhyal; PB, pharyngobranchial.

The elongate, rod-shaped, parasphenoid (Fig. 3) forms the central lower margin of the neurocranium. Anteriorly it fuses with the posterodorsal surface of the prevomer. Anterodorsally it forms the lower medial margin of the orbital chamber. Posterodorsally it is ankylosed with the prootics by means of two wing-like ascending processes. Posteriorly it connects with the basioccipital. Ventrally the expanded pharyngeal condyles (Fig. 4) provide articular surfaces for the third pair of pharyngobranchials.

BRANCHIAL APPARATUS

Hyobranchial region.—The small, rod-shaped, interhyals (Fig. 5) are borne on the dorsal posterior surface of the epihyals. The dorsal end of each interhyal articulates with the symplectic bone. The epihyals are triangular, and connect loosely with the more elongate ceratohyals. Each epihyal bears two branchiostegal rays on its lower surface, while the ceratohyals bear four. The dorsal hypohyals connect firmly with the anterodorsal surface of the ceratohyals, while the ventral hypohyals connect with the anteroventral surface of the ceratohyals

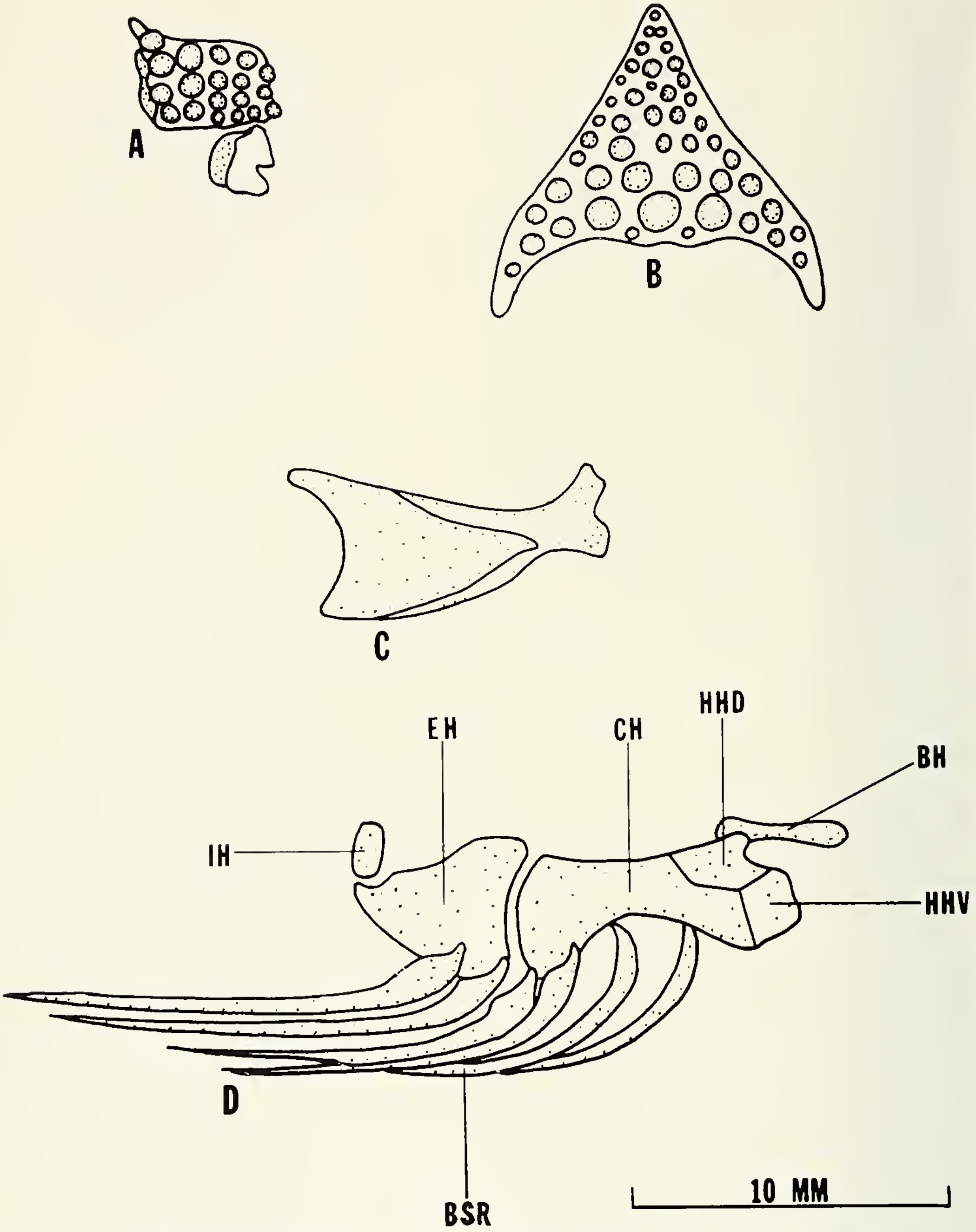

Figure 6. (A) Ventral aspect of left third and fourth pharyngobranchials. (B) Dorsal aspect of fused fifth ceratobranchials. (C) Right lateral aspect of urohyal. (D) Lateral aspect of hyoid apparatus. Abbreviations as for figure 5 with the following addition: BSR, branchiostegal ray.

(Fig. 6). The unpaired basihyal is situated between the two arms of the hyoid apparatus, and is dorsal to the hypohyals. The urohyal (Fig. 6) is a thin triangular wedge located in the midline of the hyobranchial region, ventral to the basibranchials.

A longitudinal row of three unpaired basibranchials is present (Fig. 5). The first lies under the basihyal and is narrow and elongate. The second is broadened posteriorly, and the third is hour-glass shaped.

Three pairs of hypobranchials are present as irregularly shaped flat plates. Medially the first pair arises across the suture between the first and second basibranchials; the second pair arises across the suture between the second and third basibranchials. The third pair articulates with the third basibranchial. Distally the hypobranchials articulate with the first three pairs of ceratobranchials. The fourth pair of ceratobranchials have no medial connection with the bony elements of the hyobranchial region, but are embedded in cartilage posterior to the third basibranchial. The first four pairs of ceratobranchials are elongate and project backward and upward. The left and right fifth ceratobranchials are fused medially to form a large triangular tooth-bearing bone in the floor of the pharynx.

Four pairs of epibranchials articulate with the distal ends of the ceratobranchials and curve upward to provide bony support for the branchial arches.

Four pairs of pharyngobranchials articulate with the epibranchials. The first two are small and rod-shaped. The third is enlarged and square and bears teeth on its ventral surface, forming with the fifth ceratobranchials, the pharyngeal mill characteristic of this group of fishes (Gregory, 1933). The fourth pair is small and subrectangular and is found posterior to the third pair.

Opercular Series.—The operculars (Fig. 1) have a slightly rounded anterior border and articulate with the middle portion of the posterior border of the preoperculars. The posterior borders are circular in shape. Ventrally the operculars partially overlap the suboperculars. The suboperculars are broad anteriorly and taper to a long narrow spur that connects with the ventral, posterior margin of the operculars. The interoperculars are triangular, being narrow anteriorly. Dorsally they articulate with the preoperculars. Posteriorly they slightly overlap the anterior borders of the suboperculars. The preoperculars are crescent-shaped and considerably broadened at the bend. The ventral portions extend forward to articulate with the ventral surfaces of the quadrates, while the dorsal portions articulate with the sphenotics.

Hyomandibular region.—The flat, crescent-shaped, palatines (Fig. 7) are somewhat broadened anteriorly and posteriorly. The anterodorsal surface of each bears an ethmoid process that rests against the outer surface of the articular head of the maxillaries. The dorsal edges of the palatines provide attachment surfaces for the ectopterygoids, metapterygoids and entopterygoids.

The ectopterygoids are long, slender, flat bones which taper to a point at their anterior ends. They articulate along their entire length with the palatines anteriorly and the metapterygoids posteriorly. Their ventral ends connect loosely with the quadrates.

The elongate, irregularly-shaped, metapterygoids are somewhat broadened posteriorly. They join anteriorly with the palatines, ventrally with the ectopterygoids, and posteriorly with the hyomandibulars.

The entopterygoids are elongate, broad posteriorly, and taper to a point anteriorly where they articulate with the palatines. They meet dorsomedially to form the roof of the buccal cavity.

The hyomandibulars provide the posterior points of suspension for the bones of the oromandibular region. They are roughly rectangular and slightly concave anteriorly. The thickened posterior margin ends in a head dorsally that articulates with a process on the sphenotic and with the supratemporals. Anteroventrally they overlap the metapterygoids, and posteroventrally they articulate with the symplectics.

The triangular quadrates articulate anteroventrally with the angulars. Their rounded posterior margins have a notch for the symplectics. Ventrally they articulate with the preoperculars.

The symplectics are short and rod-shaped. Posteriorly they are slightly expanded and articulate with the hyomandibulars dorsally and interhyals ventrally. Anteriorly they join the quadrates.

The premaxillaries form the anterior border of the mouth. On their dorsal surfaces they bear ascending processes which join at the midline and extend upward into a notch formed by the nasals, the ethmoid, and the ethmoid processes of the palatines. The ascending processes are approximately one-fourth the length of the body of the premaxillaries. Moderately well-developed articular processes are present lateral to the ascending processes. Postmaxillary processes are absent. The posterior ends extend under the maxillaries and over the dentaries. The premaxillaries bear a double row of conical teeth along the anterior one-half of their length.

Each maxillary shaft is narrow and expanded terminally. The anterior ends of the maxillaries form outer and inner forks. The outer fork carries the articular process of the premaxillaries,

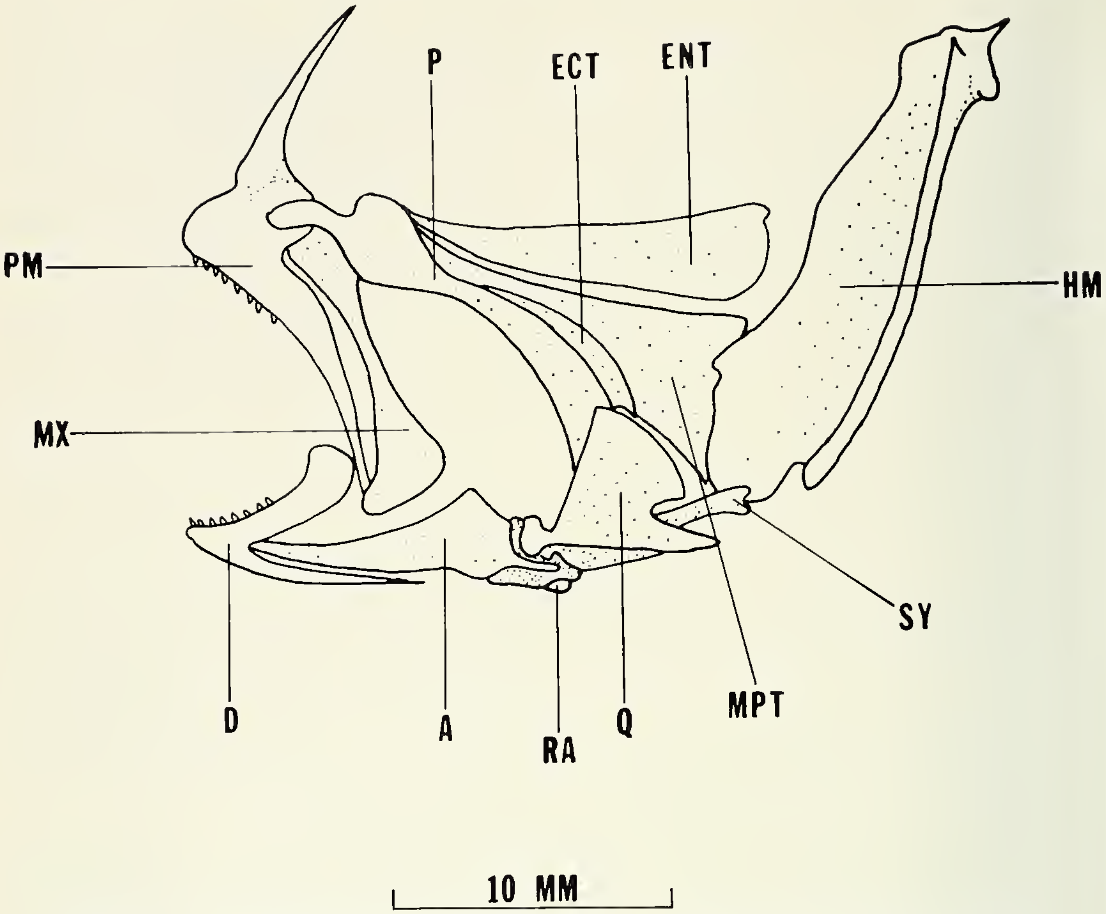

Figure 7. Lateral aspect of hyomandibular region. Abbreviations as for figure 1 with the following additions: HM, hyomandibular; RA, retroarticular; SY, symplectic.

while the inner fork articulates with the prevomer. The ventral ends of the maxillaries are connected to the lateral surfaces of the angulars by a loose fold of skin and connective tissue.

The angulars are long wedge-shaped elements, pointed anteriorly and relatively broadened posteriorly. They are lodged anteriorly into the posterior notch of the dentaries. Posteriorly they articulate with the anterior condyles of the quadrates.

The dentaries are V-shaped, and articulate posteriorly with the angulars. The dentigerous dorsal portion of the dentary bears two rows of conical teeth. The ventral arm extends posteriorly along the ventral midline.

The retroarticulars are minute irregularly shaped bones strongly ankylosed to the posteroventral corners of the angulars, ventral to the condyles of the quadrates.

DISCUSSION

Osteological data comparable in detail to that presented here are available for only one other embiotocid, *Damalichthys vacca.* Hill (1940) presented sufficient data on that species so that comparisons may be made between *D. vacca* and *A. argenteus.*

The two species have been placed in separate subfamilies; *D. vacca* in the Embiotocinae and *A. argenteus* in the Amphistichinae (Tarp, 1952). The subfamilial distinctions are made on the basis of dentition, the structure of the glandular tissue found on the anal fin of male embiotocids, and the structure of the prefrontal and ethmoid bones.

The cranial and branchial skeletons of the two species are similar in most respects, yet there are consistent differences. The subfamilial character involving the prefrontal bones is obvious. In *A.*

argenteus the prefrontals are fused at the midline, while in *D. vacca* they are separated by the ethmoid. In addition to the subfamilial characteristics, *A. argenteus* possesses seven circumorbitals while *D. vacca* has only six. The pharyngeal condyles in *A. argenteus* are fused into a shelflike ventral projection from the posteroventral region of the parasphenoid bone. In *D. vacca*, the pharyngeal condyles protrude as separate processes. In *A. argenteus* the pharyngeal condyles are more anterior than in *D. vacca* and do not overlap the basioccipital ventrally as is the case in the latter species. In *A. argenteus* the frontals are concave laterally, while they are convex in *D. vacca*. Finally, the fourth pair of pharyngobranchials are present in *A. argenteus* and absent in *D. vacca*.

Of the above skeletal differences, the most significant are probably those involving the circumorbital series and the pharyngobranchials. The trend in teleostean evolution is toward a loss or reduction of cranial skeletal structures. The presence of seven elements in the circumorbital ring represents a deviation from the typical percoid pattern of six (Gosline, 1966) and we believe that this, in conjunction with the retention of the fourth pair of pharyngobranchials indicates that the Embiotocinae, as represented by *D. vacca*, occupy a more derived position relative to the Amphistichinae.

Hill (1940) states that the Embiotocidae are most closely related to the Pomacentridae. As evidence she cites the presence in both families of a strong ridge on the ventral surface of the frontal bones, a suboccular shelf on the mesopterygoid, ventral enlargements (pharyngeal condyles) on the parasphenoid, and ankylosis of the lower pharyngeals to form a tooth-bearing plate. *Amphistichus argenteus* possesses all of the above characters, and we agree that the Embiotocidae are most closely related to the Pomacentridae. In addition, the presence in *A. argenteus* of the fourth pair of pharyngobranchials, a condition also found in the Pomacentridae, may be further evidence of this relationship.

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SPATHIPORA MAZATLANICA, A NEW SPECIES OF BURROWING BRYOZOA (CTENOSTOMATA) FROM MAZATLÁN, SINALOA, MÉXICO

JOHN D. SOULE AND DOROTHY F. SOULE[1]

ABSTRACT: A new species of burrowing Bryozoa (Ctenostomata) from México, *Spathipora mazatlanica*, is described and illustrated. The polypide anatomy of the genus *Spathipora* is determined for the first time.

Although the genus *Spathipora* was erected by Fischer in 1866 from material collected off the French Mediterranean coast, confirmation of its bryozoan ctenostomatous affinities, in general, was not made until the work of E. Marcus appeared in 1938. The specimens of *Spathipora* available to Marcus from Baia de Santos, Brazil had evidently suffered considerable cytolysis, since he was only able to show the cuticle, with the general morphology of the autozoid, and the attachment of the stolon close to the proximal (caudal) extremity of the zoid. Marcus also described the anatomical features of *Terebripora ramosa* d'Orbigny collected from the same locality, and established that the point of attachment of the stolon to the zoid was about midway between the apertural (distal) and caudal (proximal) extremities, more often closer to the apertural rather than the caudal end. Subsequent work by Soule (1950, 1963), Soule and Soule (1968, 1969a, 1969b), and Voigt and Soule (1973) has confirmed the *Terebripora* structural plan. Silén (1946, 1947) erected two new genera of burrowing bryozoans, *Immergentia* and *Penetrantia*, and described their anatomy.

In material collected at Mazatlán, México in 1973 we have found well preserved zoaria of *Spathipora*. The anatomical details of *Spathipora* are available for the first time from whole mounts and serial sections, and comparisons can be made with those burrowing bryozoans whose structure is well known.

FAMILY TEREBRIPORIDAE D'ORBIGNY 1847

Genus *Spathipora* Fischer 1866

Spathipora mazatlanica, new species

Holotype.—Allan Hancock Foundation bryozoan number 180. Allan Hancock Foundation, University of Southern California, Los Angeles, California.

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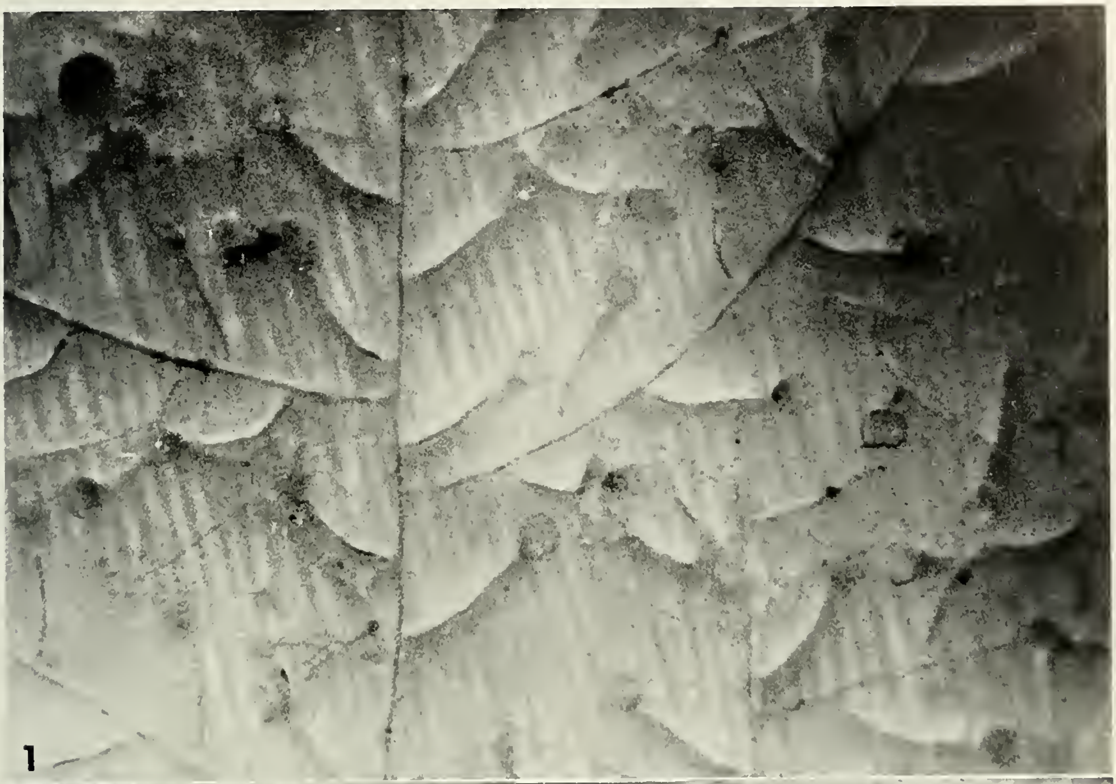

Figure 1. Photomicrograph of the tracings of *Spathipora mazatlanica*, new species, on the mollusc shell surface. Photographed × 50. *Figure 2.* Scanning electron microscope photomicrograph of an epon cast of a zoid of *Spathipora*. Photographed × 200.

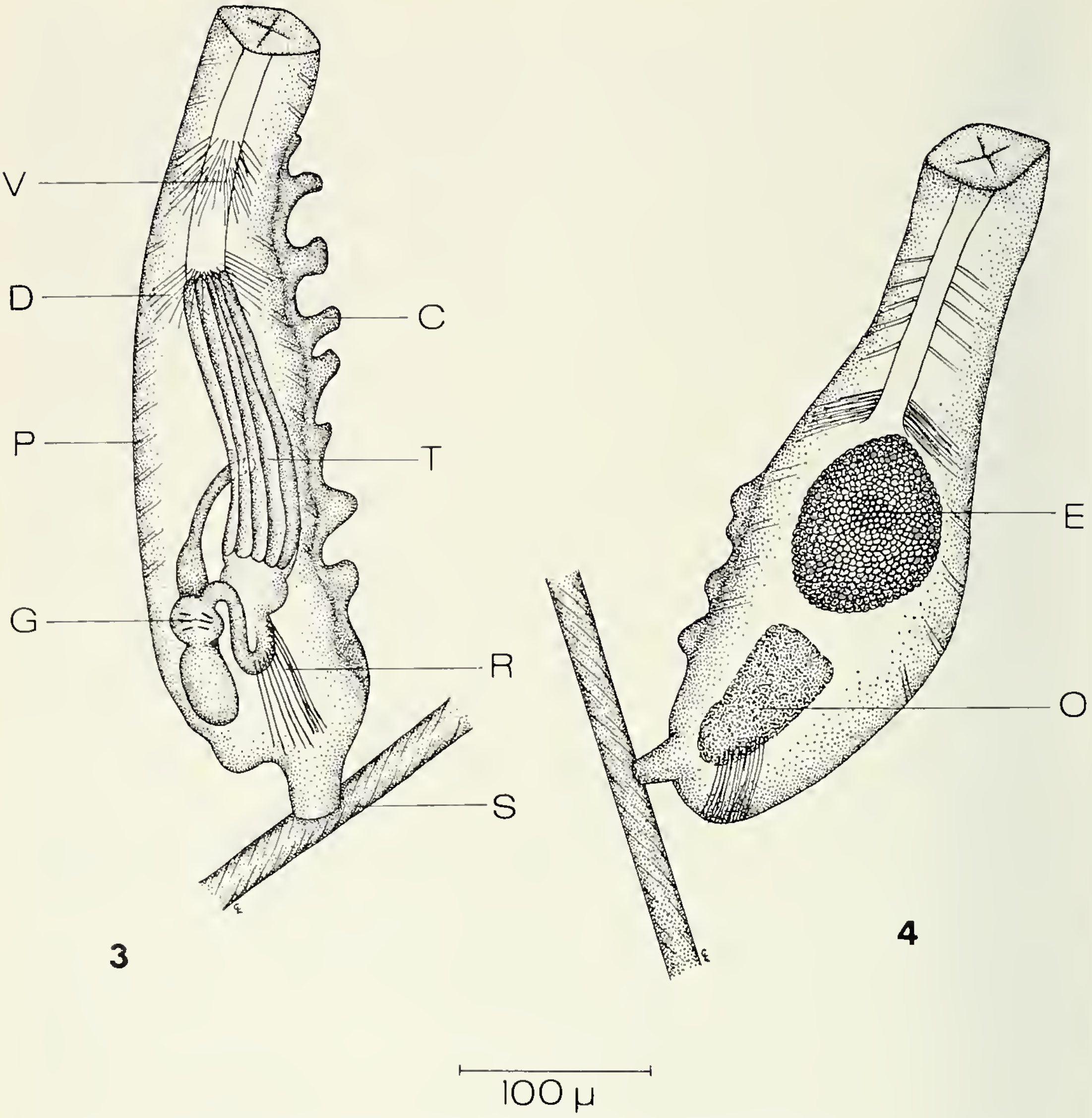

Figure 3. Drawing of a zoid of *Spathipora* showing proximal attachment, communication tubules and internal anatomy. *Figure 4.* Drawing of a reproductive zoid with embryo and degenerate polypide. C, communication tubules; D, diaphragm muscle; E, embryo; G, gizzard; O, degenerate polypide; P, parietal muscle; R, retractor muscle; S, stolon; T, tentacles; V, vestibular muscle.

Etymology.—The name is derived from the harbor at Mazatlán, Sinaloa, México, the site of the type locality.

Diagnosis.—Bryozoa, Ctenostomata, with zoaria burrowing in mollusc shells. Surface tracings are pennate, with zoid apertures alternating along both primary and secondary stolons. Apertural openings ovoid to key-hole shaped, narrowing on the side adjacent to the stolon. Zoids are elongate, weakly curved, tapered at the caudal (proximal) extremity, squared at the apertural region. Zoids attached to stolons near the caudal region. Zoids range in length from 310 μm to 510 μm, in width from 95 to 120 μm. Tentacle number is 8.

Description.—Burrowing stolonate colonies are extensive in shells of the gastropod *Strombus.* They consist of branching primary and secondary stolons, with the zoids attached by short tertiary stolons which originate near the caudal extremities. The colonies are visible on the surface of mollusc shells as regular, feather-like (pennate) tracings, with apertural openings alternating from one side to the other of the primary and secondary stolons (Fig. 1). Apertural openings are irregularly ovoid to key-hole shaped in morphology, narrowed at the edge facing the stolon. These openings are from 50 to 60 μm in diameter.

Material studied was transferred directly to formol-seawater as it was collected. Even short exposure to air causes cytolysis. Some colonies were decalcified in 5% trichloracetic acid for use in whole mounts that were stained with azocarmine, and for serial histological sections. Epon casts were made of other colonies based on the techniques of Hillmer (1968) and Pohowsky (1974) for examination by scanning electron microscopy. Zoids are moderate in size, cylindrical, slightly curved and tapering to a single, or occasionally double, knob-like proximal termination. In position, the zoids lie almost parallel to and immediately beneath the outer surface of the mollusc shell (Fig. 2). The primary and secondary stolons often have short blind extensions which reach the free surface of the mollusc shell, giving the stolons an undulating pattern.

The zoids of *Spathipora* also possess short lateral accessory tubules that extend to the surface of the mollusc shell (Fig. 3). They are found in a linear series along the abanal wall of the zoid, and range in number from a single communication tubule to as many as eight on a zoid. The stained whole mounts and serial sections show these communication tubules to be hollow, highly cellular in their basal regions, and capped by a keratinized cuticle. Their function is uncertain; possibly respiratory or excretory exchange occurs there between the zoid and the sea water.

Anatomically, the polypide consists of eight tentacles and a digestive tract of which the most distinctive feature is a prominent gizzard with chitinized denticles. The musculature consists of a set of retractor muscles located proximally, parietal muscles positioned laterally, and two pairs each of diaphragm muscles and vestibular muscles in the apertural region. The whole mounts and sections also reveal the presence of zoids with brown bodies.

Reproductive zoids (Fig. 4) were relatively rare and scattered at random throughout the colonies. The reproductive zoids ranged from 375 to 450 μm in length and 100 to 115 μm in width. Each possesses a prominent ovoid egg or embryo distally; a degenerate polypide lies proximally.

Measurements.—The smallest functional zoid was 310 μm long and 95 μm wide, the largest was 510 μm long and 120 μm wide. The length range encountered most frequently was 440 to 480 μm. The diameter of the primary and secondary stolons is 20 μm.

Type locality.—USC-Sea Grant field trip SCUBA station, off Isla Lobos, in the harbor at Mazatlán, Sinaloa, México (23°13.5′N., 106°29′W.); depth 8 meters; 28 June 1973; in eroded shells of *Strombus* (sp?); collectors, P. Pinter, J. McSweeney, P. Widdell, and M. Hooper.

Affinities.—*Spathipora* in the generic sense has many structural components that are similar to those in *Terebripora*, notably the prominent gizzard, the tapering zoid morphology and the general pattern of zoarial tracing on the molluscan shell. The tracings on the mollusc shells by *Spathipora* may be more regular and pennate than those of *Terebripora*, but they are much alike in their basic structure. The zoids of *S. mazatlanica* are smaller than those of *S. sertum* Fischer, which are 450–550 μm in length and 120–170 μm in width (Marcus 1938). There are no other anatomical details of *S. sertum* available on which a comparison can be based.

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VARIATION IN THE SOUTH AMERICAN COLUBRID SNAKE *TANTILLA SEMICINCTA* (DUMÉRIL, BIBRON, AND DUMÉRIL), WITH COMMENTS ON PATTERN DIMORPHISM

Larry David Wilson[1]

Abstract: Variation and distribution of *Tantilla semicincta* are discussed. This species exhibits pattern dimorphism. One phase has a banded dorsal pattern and the other a striped dorsal pattern. Variation in scutellation is described. This species is known to occur along the Caribbean coastal regions of Colombia and Venezuela. Purported occurrence of this snake in Panamá is discounted. Relationships of *T. semicincta* with other banded species of *Tantilla* are discussed and a key to those species is provided.

Little information is available concerning the species of *Tantilla* occurring in South America. This paper is the first in a series dealing with the taxonomy and distribution of the species of *Tantilla* known from that continent.

Tantilla semicincta (Duméril, Bibron, and Duméril) is one of the few species in the genus with a banded dorsal pattern. Only three other species, *T. annulata*, *T. shawi*, and *T. supracincta*, have such a pattern. *Scolecophis atrocinctus*, an apparent close relative of *Tantilla* (Stickel, 1943), has a pattern very similar to that of *T. semicincta*.

Tantilla semicincta is also the only species in the genus known to exhibit a pronounced pattern dimorphism. *Tantilla melanocephala* has been reported to exhibit pattern dimorphism (Roze, 1966), some individuals having a dark middorsal stripe, whereas others lack it, but it has been suggested that *T. melanocephala*, as currently conceived, may be a composite taxon (Schmidt and Walker, 1943). This problem is presently under investigation.

PATTERN DIMORPHISM AND VARIATION IN *TANTILLA SEMICINCTA*

Boulenger (1896) was the first worker to note the pattern dimorphism in *T. semicincta*, and he did so in passing by placing *Homalocranion lineatum* Fischer in the synonymy of *T. semicincta* and noting the different patterns in his description of the species.

Pattern Dimorphism.—Tantilla semicincta exhibits two basic pattern variants, one striped, and the other banded. In addition, some specimens exhibit a pattern intermediate between that of the two phases.

The striped pattern (Fig. 1) is present in two specimens examined (BMNH 86.5.15.16–17) and consists of a pale middorsal stripe occupying the middorsal scale row and adjacent halves of the paravertebral rows, flanked by dark dorsolateral

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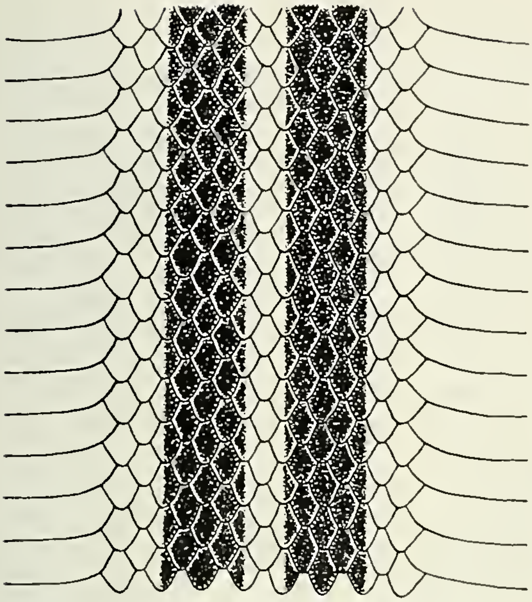

Figure 1. Dorsal color pattern of BMNH 85.5.15.16 from "Colombia."

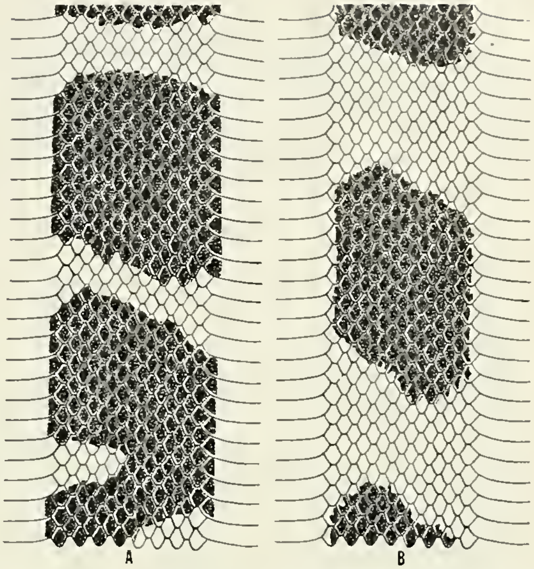

Figure 2. Dorsal color pattern of (A) BMNH 1902.5.15.11 from the Magdalena Valley, Colombia and (B) USNM 107324 from near Caracas, Distrito Federal, Venezuela.

fields extending from the lower half of the paravertebral row to the upper half of the third scale row. The remainder of the dorsum and all of the venter is pale in color. The tail is not striped in either specimen, but rather is patterned with a series of irregular spots and/or narrow crossbands. The syntypes of *Homalocranion lineatum*, which I have not seen, also exhibit this pattern (Fischer, 1883).

The banded pattern (Fig. 2) is present in 13 specimens examined. It consists of dark transverse bands on a pale groundcolor. The number of dark bands on the body ranges from 12 to 26 ($\bar{x} = 19.4$). They range from 5 to 12 scales in length ($\bar{x} = 7.8$) and extend laterally to a point ranging from the second scale row to the lateral edge of the ventrals. The pale bands range from 1 to 6 scales in length ($\bar{x} = 2.2$). Frequently, the pale bands are broken middorsally and staggered. The percentage of broken pale bands ranges from 0 to 57.7 ($\bar{x} = 37.5$). The number of tail bands ranges from 3 to 13 ($\bar{x} = 8.5$).

The intermediate pattern is characterized by a high number of short dark bands (38–47) that are most frequently divided middorsally (showing a tendency toward development of a pale middorsal stripe) and tend to be joined to one another laterally (showing a tendency toward development of a dark dorsolateral field). They also are narrow, extending to somewhere on the third scale row. This pattern is present in four specimens examined (ANSP 20831, BMNH 86.5.15.18, NMB 9154–55).

The pattern dimorphism in *Tantilla semicincta* bears a striking resemblance to that seen in the California Kingsnake (*Lampropeltis getulus californiae*—see pattern illustrations in Blanchard, 1921).

Head Pattern.—The head pattern (Fig. 3) consists of a dark head cap usually extending from the posterior half of the prefrontals to and including one-half to two-thirds of the parietals. Laterally the cap extends to the lip below the eye and at the junction of the ultimate and penultimate supralabials, thereby enclosing a postorbital pale spot.

The pale nuchal band is either complete or divided (partially divided in one specimen). If complete, it extends from the middle, posterior third, or posterior quarter of the parietals to a point from two-thirds of the first middorsal scale to one and one-half middorsal scales posterior to the parietals. The nuchal band is complete in eight specimens and divided in 10 specimens.

VENEZUELAN *TANTILLA SEMICINCTA*

Roze (1966) listed three specimens of *Tantilla semicincta* from Venezuela, one from Estado

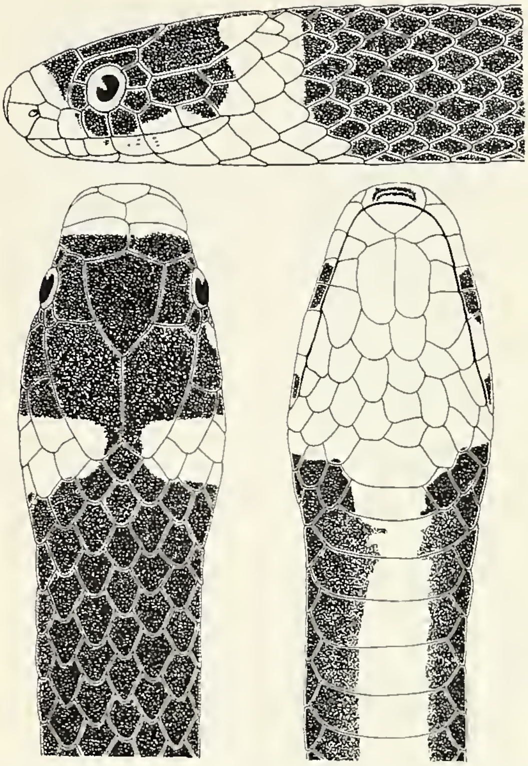

Figure 3. Lateral, dorsal, and ventral views of head of BMNH 1902.5.15.10 from the Magdalena Valley, Colombia.

Zulia and two from the Distrito Federal. In addition, the syntypes of *Homalocranion lineatum* Fischer came from Maracaibo, Est. Zulia. This name is a synonym of *T. semicincta*, according to Boulenger (1896), but I have been unable to examine the specimens. I have examined only one of these specimens (USNM 107324) from near Caracas, which differs in some respects from specimens I have examined from Colombia. In comparison with Colombian specimens, USNM 107324 has well-defined dark crossbands (Fig. 2B) that are separated by pale bands about six scales in length (1 to 3 in Colombian specimens). The number of dark tail bands is 3, which is much lower than the number in Colombian specimens (4–13, $\bar{x} = 9.1$). Also, the nuchal band is longer, occupying half of the parietals and one and one-half dorsal scales (as opposed to a maximum size of one-third of the parietals and one dorsal scale in Colombian specimens). This specimen, however, shows no scutellational distinctions compared to Colombian material.

Although USNM 107324 is distinctive in a number of features, I think it premature to consider recognizing it nomenclaturally until the other specimens from Venezuela are examined (the three syntypes of *Homalocranion lineatum* are all of the striped phase and their description by Fischer, 1883, corresponds well to that of Colombian material of the striped phase) and until additional material from the entire range of the species becomes available. Accordingly, I will consider for the present that the Caracas population is conspecific with the populations to the west and present the following taxonomic summary.

Tantilla semicincta (Duméril, Bibron, and Duméril)

Homalocranion semi-cinctum Duméril, Bibron, and Duméril, 1854: 862; Jan, 1862: 53; Jan and Sordelli, 1866, livr. 15, pl. ii, fig. 6.

Homalocranium laticeps Günther, 1860: 240 (Holotype, BMNH 1946.1.8.85; type locality: Cartagena, Depto. Bolívar, Colombia—not examined).

Tantilla semicincta: Cope, 1861: 74, 1866: 126, 1876: 145, 1900: 1111; Griffen, 1916: 209; Amaral, 1930: 222, 1931: 93; Briceño, 1934: 31; Dunn and Bailey, 1939: 19; Stickel, 1943: 110; Dunn, 1944: 208; Smith, 1958: 224; Roze, 1966: 225; Peters and Orejas-Miranda, 1970: 297.

Homalocranion lineatum Fischer, 1883: 6 (Syntypes, Naturhistorisches Museum Hamburg 1033—three specimens; type locality: Maracaibo, Est. Zulia, Venezuela—destroyed in World War II *fide* Werner Ladiges).

Homalocranium semicinctum: Boulenger, 1896: 219.

Tantilla semicinctum: Ruthven, 1922: 68.

Holotype.—MNHN 3695, adult female.

Type locality.—"Martinique," in error. Listed as "Colombia" by Peters and Orejas-Miranda, 1970.

Diagnosis.—A member of the genus *Tantilla* with a banded or striped dorsal pattern, a white venter, 161–176 ventrals, and 54–71 subcaudals.

Description.—*Tantilla semicincta* has a banded or striped dorsal pattern (Figs. 1 and 2). The banded specimens have black bands which extend to a point ranging from the second dorsal scale row to the lateral edge of the venter. The dorsal interspaces of at least some specimens are yellowish-green to reddish (Roze, 1966). These colors fade to cream in preservative. The venter is white. The striped specimens have a pale middorsal stripe flanked by broad dark dorsolateral bands. The lower portions of the dorsum are the same pale color as the venter.

A dark cap is present on the head extending from the middle of the prefrontals to the middle or posterior third to quarter of the parietals. The nose

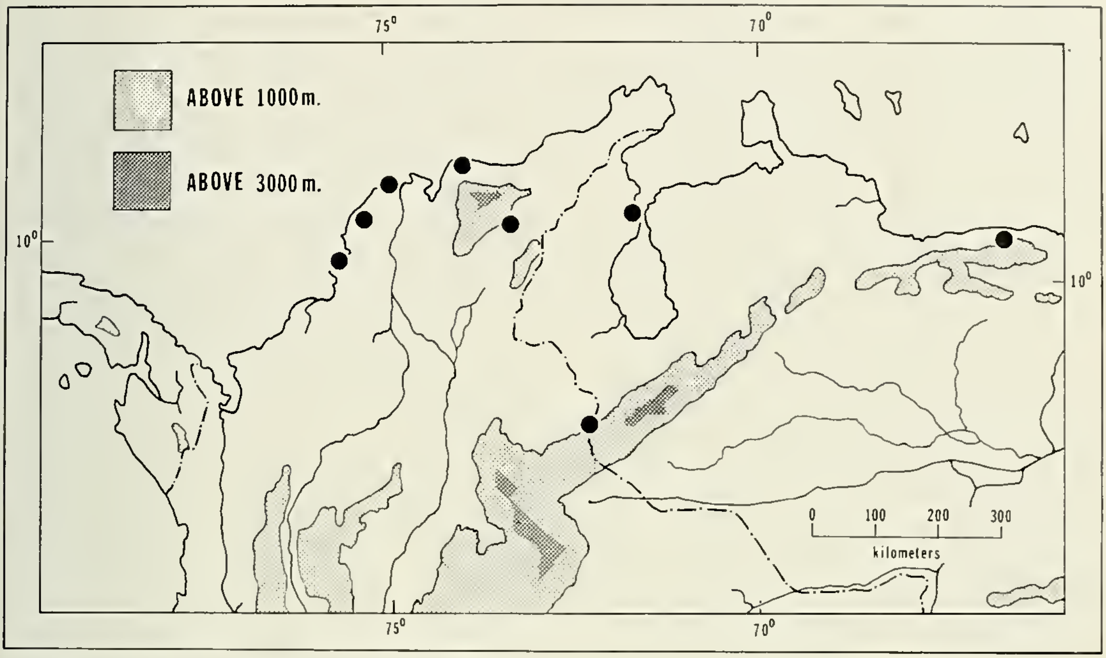

Figure 4. Distribution of *Tantilla semicincta.*

is pale in color and there is a pale postorbital spot. The dark head cap is followed by a pale nuchal band, which may be divided or not, but is always in broad lateral contact with the pale ventral coloration of the chin.

Variation in scutellation may be summarized as follows: supralabials 7-7, with 3rd and 4th entering orbit (one specimen has the fifth supralabial fused to the anterior temporal on both sides); infralabials 5 to 7, usually 6 (one specimen has 7 on one side, another has 5 on one side, and yet another has 5 on both sides); four infralabials usually are in contact with anterior chin shields when the total number is 6 and the fourth is largest (when the total number is 7, 5 are in contact, when 5, 3 or 4 are in contact); first pair of infralabials always in medial contact, separating mental and anterior chin shields; postnasal and preocular are invariably separated by contact of prefrontal and second supralabial; preoculars 1-1; postoculars 2-2; temporals 1 + 1; dorsal scales in 15 rows throughout; anal plate divided; ventrals in males 161–173 ($\bar{x} = 165.7$), in females 166–176 ($\bar{x} = 172.0$); subcaudals in males 59–71 ($\bar{x} = 65.9$), in females 54–64 ($\bar{x} = 58.3$).

Maxillary tooth counts in two specimens are 14 + 2 and 15 + 2.

Total length in snakes of all ages ranges from 171–600 mm, and tail length ranges from 37–127 mm. Relative tail length ranges from 0.222–0.257 in males and from 0.192–0.218 in females. This species grows to the greatest length of any species of *Tantilla.* Dunn and Bailey (1939) reported a specimen of *T. annulata* that measures 590 mm in total length. The largest complete specimen of *T. semicincta* I have seen (USNM 117506), a female, measures 600 mm in total length. It has a tail length of 127 mm and a relative tail length ratio of 0.212. Another female specimen (UMMZ 55033) with an incomplete tail has a snout-vent length of 479 mm. If the relative tail length ratio were the same for this specimen as for USNM 117506, then this specimen would have had a total length near 608 mm.

Range.—*Tantilla semicincta* is known to occur from near sea level to 457 m along the Caribbean coast of Colombia and Venezuela from Cartagena to Caracas (Fig. 4). Several authors (Barbour and Amaral, 1928; Amaral, 1930; Smith, 1958; Peters and Orejas-Miranda, 1970) have stated that *T. semicincta* occurs in Panamá. Apparently, this statement is based upon a report of a specimen (MCZ 24927) from Cerro Bruja identified as *T. semicincta* by Barbour and Amaral (1928). This specimen was subsequently reidentified as *T. annulata* by Dunn and Bailey (1939). Apparently, all subsequent statements about the occurrence of *T. semicincta* in Panamá are based on Barbour and Amaral's (1928) misidentification. I have examined MCZ 24927 and can verify that it is a *T. annulata.* Charles W. Myers, who is currently working on the herpetofauna of Panamá, informed me (pers. comm.) that he has seen no specimens of *T. semicincta* from that country. Accordingly, until additional information appears to the contrary, I will consider that *T. semicincta* does not occur in Panamá.

Ecological Distribution.—Little direct information is available on the ecological distribution of *T. semicincta*. Ruthven (1922) stated that a specimen from Valledupar, Depto. Magdalena, Colombia came from "dry woods." Roze (1966) considered this species characteristic of the "formación montañosa" and a species that illustrated faunal similarities between the Cordillera de la Costa Central and the Sierra de Perijá.

Most specimens of *T. semincta*, however, have come from localities that lie within xerophilic or semixerophilic vegetation. Specimens from the region of the Sierra Nevada de Santa Marta all came from low elevations in thorn scrub, characterized by the presence of acacia trees and large, columnar cacti (Ruthven, 1922). The only exceptions to the general pattern of distribution in Colombia are three specimens said to have come from Cucutá, Depto. Norte de Santander. Cucutá lies in the eastern foothills of the Cordillera Oriental at an elevation of about 310, apparently east of the broad finger of broadleaf deciduous forest bordering the Río Magdalena that passes south from the Caribbean coast to the region of Bogotá (see Fig. 14 in Uzzell, 1973).

Most specimens from Venezuela have come from areas with similar vegetation (Maracaibo) or close to areas with similar vegetation (Caracas) to that which this species inhabits in Colombia (Roze, 1966). I do not agree with Roze (1966) that *T. semicincta* is "characteristic" of the "formación montañosa" in Venezuela, but think it is more likely characteristic of the "formación costanera," covered by xerophytic and semixerophytic vegetation (Marcuzzi, 1954; Roze, 1966) and may range into the contiguous areas of the "formación montañosa."

I do not know from what portion of the Sierra de Perijá the specimen labelled "Perijá" (unnumbered specimen in the Museo de Ciencias Naturales, Los Caobos, Caracas) came but some portions of that mountain range abut the coastal areas of the northwestern portion of the Estado de Zulia.

In summary, *T. semicincta* appears to inhabit almost exclusively thorn scrub vegetation along the Caribbean coastal regions of Colombia and Venezuela.

RELATIONSHIPS

Tantilla semicincta appears to belong to a group of banded species of *Tantilla* including, perhaps, three other species, *annulata*, *shawi*, and *supracincta*. I have not examined the holotype and only known specimen of *T. supracincta* but I have examined the original description and have had the benefit of the late James A. Peters' notes on the genus *Tantilla* in Ecuador. I examined the holotype and only known specimen of *T. shawi* (LSUMZ 306) several years ago when I was a student at Louisiana State University, and I have seen a few specimens of *T. annulata*. Consequently, my comments on relationships of *T. semicincta* within the genus *Tantilla* are anything but definitive, but I hope to remedy this deficiency in subsequent studies on the members of this genus. In addition, the Central American snake *Scolecophis atrocinctus* appears to be closely related to this segment of the genus *Tantilla*.

Of the species mentioned above, *T. semicincta* is closest geographically to *T. annulata*. *Tantilla annulata* occurs in Panamá (Scott, 1969) and *T. semicincta* occurs as far west as the region around the mouth of the Río Magdalena. They resemble one another in sharing the banded dorsal pattern, and in their relative large size. They differ from one another most obviously in dorsal pattern, although the two resemble one another in head pattern. *Tantilla annulata* has a dorsal pattern consisting of alternating black-outlined pale vertical bars on a reddish-brown background (Taylor, 1951). They also differ from one another in ventral number (161–176 in *semicincta*, 148–155 in *annulata*) and the lack of consistency of postnasal-preocular separation in *annulata*.

Tantilla supracincta was described from one specimen from Guayaquil, Ecuador (Peters, 1863). It resembles *T. semicincta* in possessing a dorsal pattern of alternating dark and pale bands. The head pattern in the two appears to be virtually the same. They differ from one another most obviously in the lower number of ventrals and subcaudals in *T. supracincta* (148 and 38 in the holotype of *supracincta*, 161–176 and 54–71 in *semicincta*), which is the reason Peters (1960) recognized *T. supracincta* as a "valid lowland species on the west coast" of Ecuador (Peters' research notes).

Tantilla shawi was described on the basis of one specimen from Xilitla, San Luis Potosí, México (Taylor, 1949). It is the species most geographically distant from the ranges of the other species mentioned above. It resembles *T. semicincta* in possessing a banded dorsal pattern, a similar number of ventrals (166 in holotype of *shawi*—my count, 161–176 in *semicincta*). It differs from *T. semicincta* most obviously in dorsal color pattern. *Tantilla shawi* has a series of alternating cream vertical bars on the anterior fourth of the body. The groundcolor is black to bluish-black. The head patterns of the two are similar. *Tantilla shawi* may not be a particularly large species; the holotype measures 369 mm. *Tantilla semicincta* has a maximum known total length of 600 mm.

Scolecophis atrocinctus is an endemic Central

American snake ranging from eastern Guatemala to northwestern Costa Rica. The monotypic genus *Scolecophis* appears to differ from *Tantilla* in but a single character, viz., the presence of a loreal in the former and its absence in the latter. *S. atrocinctus* resembles *T. semicincta* most obviously in pattern. *Scolecophis atrocinctus* has a pattern of alternating dark and pale bands, but the bands completely cross the venter. The head patterns are very similar. In addition to the presence of a loreal, *S. atrocinctus* differs from *T. semicincta* in possessing a higher number of ventrals (181–198 in *S. atrocinctus*, 161–176 in *T. semicincta*) and a lower number of subcaudals (45–54 as opposed to 54–71).

Tentatively, *T. semicincta* appears to be most closely related to *T. supracincta* on the one hand and to *S. atrocinctus* on the other.

I append below a key for the identification of the banded species of *Tantilla*.

KEY TO THE SPECIES OF TANTILLA WITH A BANDED DORSAL PATTERN

1. a. Dorsum reddish-brown with pale, black-bordered transverse bands, usually extending to middorsal line and alternating with those on other side of body .... *T. annulata*
   b. Dorsal coloration not as above 2
2. a. Pale bands present only on anterior portion of body .... *T. shawi*
   b. Pale bands present the length of the body 3
3. a. Ventrals more than 160; subcaudals more than 50 .... *T. semicincta*
   b. Ventrals less than 150; subcaudals less than 50 .... *T. supracincta*

LOCALITY RECORDS

COLOMBIA: No other data (BMNH 86.5.15.16–18; MCZ 29601); Department unknown—Magdalena Valley (BMNH 1902.5.15.10–11—not mapped); Depto. Atlantico—Barranquilla (NMB 14390); Villanueva (USNM 117506); Depto. Bolívar—Cartagena (BMNH 1946.1.8.85—holotype of *Homalocranium laticeps*—not examined); Depto. Magdalena—Bonda, 46 m (CM 200, 1094; MCZ 11864); Cacagualito, 457 m (CM 2024, 2037); Sierra de Santa Marta, Valledupar (UMMZ 55033); Depto. Norte de Santander, Cucutá (ANSP 20830; NMB 9154–55). VENEZUELA: Distrito Federal—near Caracas (USNM 107324); Caracas, Alta Vista (Museo de Biología, Universidad Central de Venezuela—no number—not examined); Estado Zulia—Maracaibo (Naturhistorisches Museum Hamburg 1033—3 syntypes of *Homalocranion lineatum*—not examined); Perijá (Museo de Ciencias Naturales, Caracas—no number—not examined—not mapped).

In addition to the above-noted specimens, I have also examined the holotype of *Homalocranion semi-cinctum* Duméril, Bibron, and Duméril (MNHN 3695) purported, in error, to have come from "Martinique."

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THE COORDINATED ROLE OF THE CEREBRAL AND VISCERAL GANGLIA IN CILIARY BEATING

ANTHONY A. PAPARO[1] AND JUDITH A. MURPHY[2]

ABSTRACT: Lateral ciliary activity was studied on isolated gill preparations of the mussell *Mytilus edulis.* Electrical stimulation of the branchial nerve at 5 Hz (increased) and 50 Hz (decreased) changed the average rate of ciliary beating. These modifications in the ciliary activity were significantly altered in specimens lacking an intact cerebrovisceral connective. It appears that the cerebral and visceral ganglia exhibit a coordinated role in the control of ciliary beating.

The central nervous system of the mussel, *Mytilus edulis* consists of three symmetrically placed pairs of ganglia (the pedal, cerebropleural and visceral ganglia) connected by nerve commissures. The organization of the nervous system and specifically the innervation of the gill in *Mytilus* has been extensively reviewed (Field, 1922; Gray, 1924, 1929; Lucas, 1931a, 1931b and 1932). Briefly the cerebropleural ganglia lie ventrolateral to the esophagus. Each ganglion gives rise to a large anterior trunk to the mantle and a posterior trunk which contains the cerebrovisceral connective. The latter interconnects cerebral and visceral ganglia.

The visceral ganglia are situated on the anterior ventral surface of the posterior adductor muscle. These ganglia lie just inside the line where the gills are suspended. Each ganglion receives the cerebrovisceral connective at its anterior surface, while laterally and posteriorly several important nerves arise including the branchial nerve which distributes its axons to the gill filaments and affects ciliary beating (Aiello and Guideri, 1965 and 1966; Paparo, 1972). Aiello (1960) reported that cutting the branchial nerve caused a rapid cessation of lateral ciliary activity. Subsequently Paparo and Aiello (1970) observed, (1) low frequency electrical stimulation (5 Hz) of the branchial nerve activated the lateral cilia and (2) high frequency electrical stimulation (50 Hz) depressed ciliary beating.

Previous studies on six genera representing Filibranchiata and Eulamellibranchiata have demonstrated the coordinated function of the cerebral and visceral ganglia in cilliary motion (Drew, 1908; Woortmann, 1926; Barnes, 1955; Horridge, 1958).

The following experiments were designed to investigate the coordinated role of the cerebral and visceral ganglion on ciliary beating.

METHODS

All observations were made on the mussel, *Mytilus edulis.* The specimens were kept in "Instant Ocean" in an aquarium (temperature 16° C, pH 7.6–8.0, density 1.023). For studies of the rate of ciliary motion, gill preparations (cerebropleural ganglion/cerebrovisceral connective/visceral ganglion/branchial nerve/gill) were pinned to mats glued to the bottom of a Petri dish containing molluscan physiological solution at 21° C. Observations were made with a light microscope at a magnification of 100 ×. The field of view was centered 2 mm posterior to the visceral ganglion and contained about 50 filaments per gill preparation.

The rate of ciliary motion in beats per second (bps) was estimated by synchronization with flashes of a calibrated stroboscopic light.

When nerve stimulation was part of the experiment, the cerebrovisceral connective and branchial nerve were exposed and an electrode placed on the branchial nerve in the manner described by Paparo and Aiello (1970). In some procedures, the cerebrovisceral connective was cut at its point of emergence from the anterior surface of the visceral ganglion. The electrical pulse characteristics delivered were 10V, 2m sec pulse duration for three minutes and with either 5 Hz (low frequency) or 50 Hz (high frequency).

Specimens for scanning electron microscopy were dissected in molluscan physiological solution and prepared according to the procedure described by Paparo and Murphy (1974).

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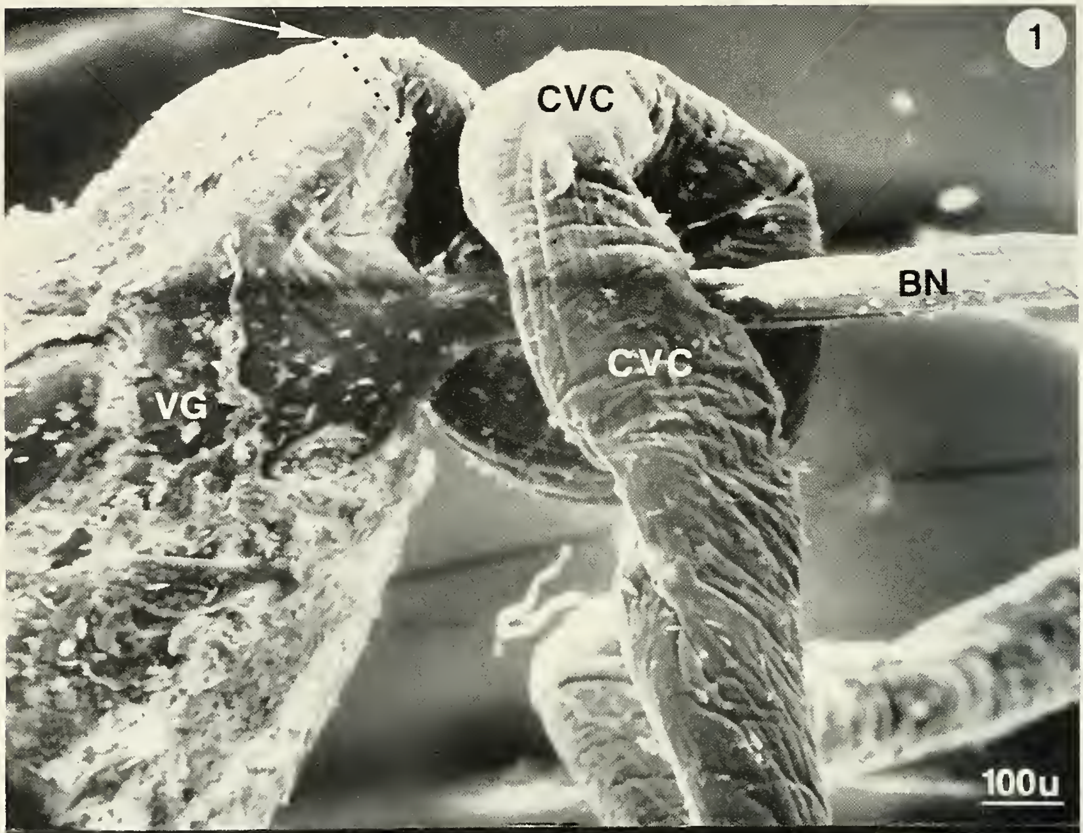
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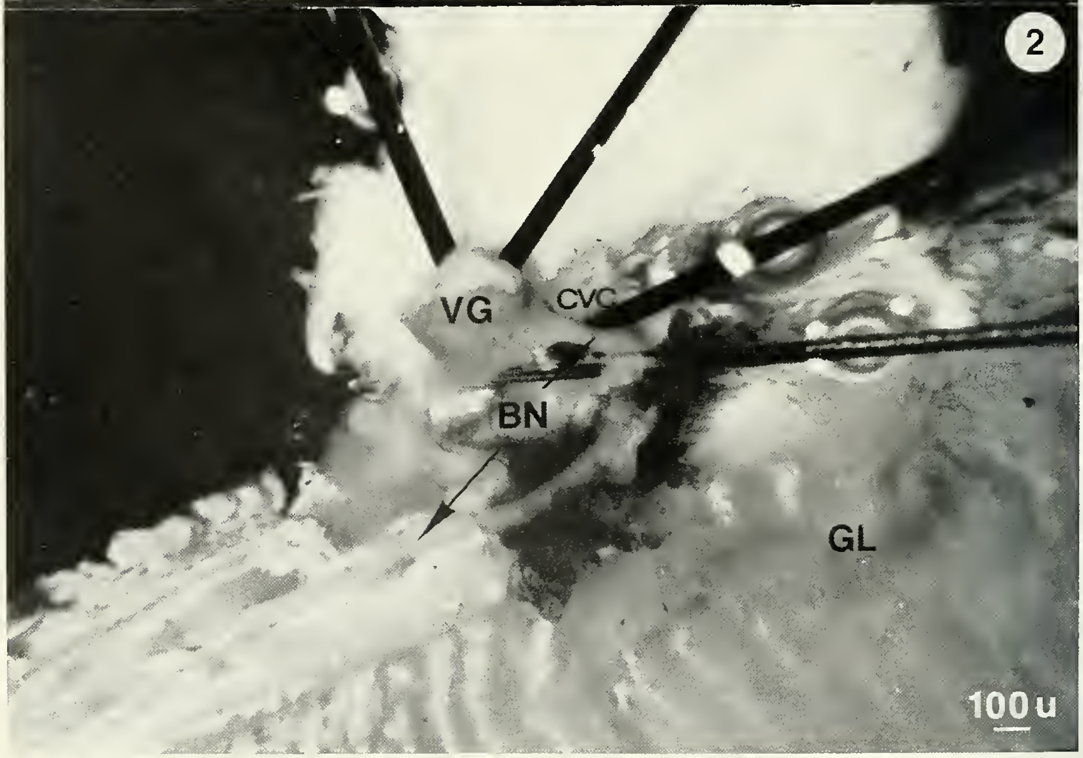
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RESULTS

General organization of nerve supply to gill.—The visceral ganglion receives the cerebrovisceral connective at its anterior surface (Fig. 1). The branchial nerve, which arises from the visceral ganglion (Fig. 1), runs obliquely downward and backward to enter the dorsal margin of the gill (Fig. 2). In its course through the gill axis it distributes its axons to the gill filaments.

The effect of stimulus frequency on the average rate of beating.—The cerebrovisceral connective was left intact and the branchial nerve was stimulated with a 2m sec, 10V pulse at a rate of 5 Hz and 50 Hz for periods of 3 minutes each (Fig. 3A). At 5 Hz stimulation the average rate of beating of the lateral cilia gradually increased compared to zero point reading ($P < 0.001$). After each period of stimulation the average rate of beating returned to about the same level observed at the onset of the experiment. The average rate of beating decreased when the 50 Hz stimulation was delivered ($P < 0.001$). Five days later the frequency of pulses were tested again (Fig. 3b). The changes in the average rates of beating produced by the 5 Hz and 50 Hz stimulation were significant (both $P < 0.001$) when compared to zero point reading (Fig. 3b). In addition, the average rates of increase produced with 5 Hz stimulation on day 1 and day 5 (Figs. 3a and 3b, respectively) compared significantly ($P > 0.85$). Similar results were obtained comparing the average rates of decrease produced by 50 Hz stimulation (Fig. 3a compared to Fig. 3b; $P > 0.80$).

The cerebrovisceral connective was cut and the branchial nerve was stimulated three days after the cerebrovisceral connective was cut (Fig. 4). At 5 Hz stimulation the average rate of lateral ciliary beat increased ($P < 0.05$) and at 50 Hz stimulation decreased ($P < 0.01$). Again, the 5 Hz and 50 Hz stimulation produced average rates which were not significantly different than average rates observed in controls (Fig. 3a and 3b; $P > 0.80$). However, the time course of recovery for the 50 Hz stimulation did differ significantly from that observed in the controls. Compare figures 3a and 3b to figure 4 (50 Hz stimulation recovery periods).

The branchial nerve was stimulated five days after the cerebrovisceral connective was cut (Fig. 5). The 5 Hz stimulation produced significant changes in the average rates of beating ($P < 0.05$). However, the changes in the rates of beating produced by the two frequency stimulations were significantly different in magnitude and period of duration from all of the previous observations (Figs. 3a, 3b, and 4).

DISCUSSION

The experiments described above indicate that the rate of beating of lateral cilia is under the control of the branchial nerve. The data support previous findings (Paparo and Aiello, 1970) that low frequency (5 Hz) stimulation is excitatory, whereas high frequency (50 Hz) stimulation is inhibitory. In addition, this study further demonstrates the coordinated role of the cerebral and visceral ganglia on ciliary activity. Cutting the cerebrovisceral connective significantly modifies the frequency electrical response of branchial nerve stimulation. Other authors have observed the complex behavioral patterns in bivalves requiring the coordination of cerebral and visceral ganglia. Lund and Powell (1957) have noted changes in the rate of water propulsion over the gills of *Crassostrea* and other species; this may be a reflex, for a shadow cast over the oyster may decrease pumping while a light stimulus has no effect. Gill filaments of *Pecten* have been observed by Setna (1930) to move closer and farther apart in a kind of concertina action, and also to flap, to shorten and to draw forward. Stimulation of the branchial nerve causes gill movements; cutting it stops them and also stops local reflex movements to solid particles passing over the gill. These facts, together with the observation of an extensive nerve supply to the gill led Setna (1930) to conclude that there must be nervous control of a coordinated respiratory and feeding mechanism. The persistence of normal reactions in isolated gills and the abundance of ganglion cells along some branchial nerve trunks (Setna, 1930;

←

Figure 1. SEM photograph of dissection of the visceral ganglion (VG), cerebrovisceral connective (CVC) and branchial nerve (BN) of *Mytilus edulis.* Arrow and dotted line indicate level at which CVC was cut in this study. × 90. *Figure 2.* Dissected specimen showing visceral ganglion (VG), branchial nerve (BN) and gill (GL). Arrow indicates level at which the cerebrovisceral connective (CVC) was cut. × 40.

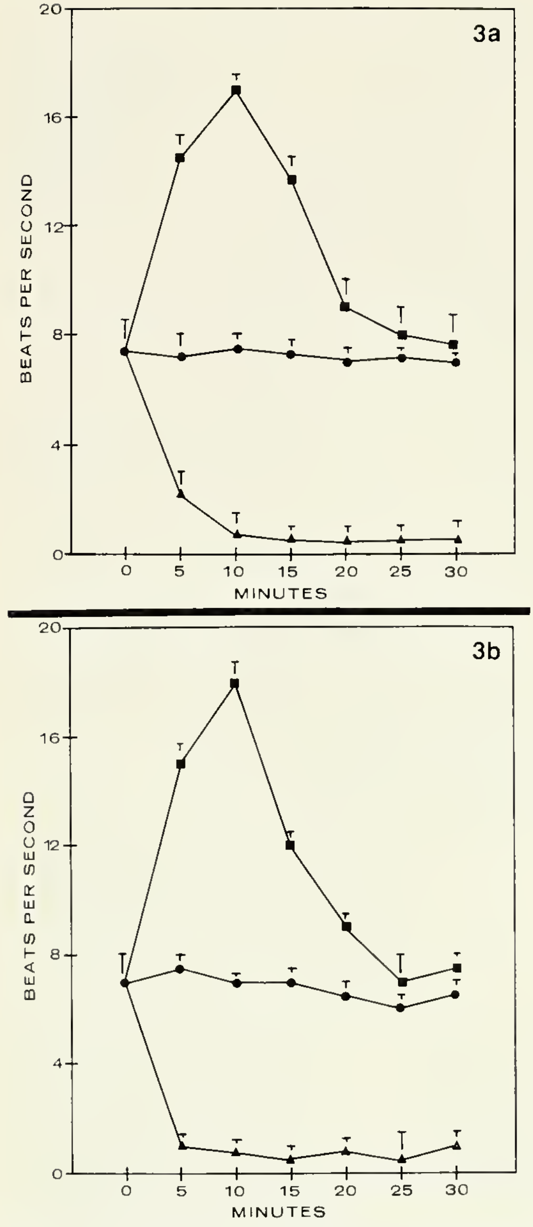
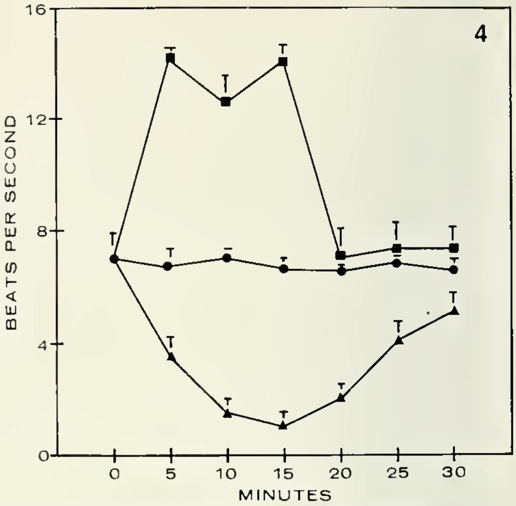
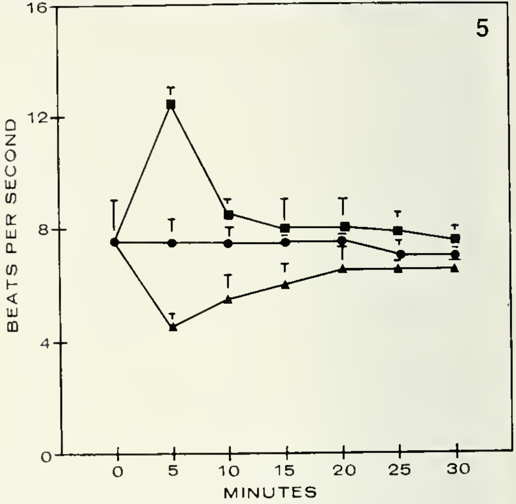


Figure 3. The effect of branchial nerve stimulation on the rate of beating of lateral cilia. Before (dots) and after [5 Hz (squares); 50 Hz (triangles)] branchial nerve stimulation. The electrical pulse characteristics were delivered on day 1 (a) and again on day 5 (b). For each curve, zero time indicates the beginning of stimulation. Each point is the average of 10 preparations, 12 readings per preparation. Standard error of the mean denoted by (T).

Paparo, 1972) may be interpreted as showing a nervous control through a peripheral mechanism such as an extended ganglion. Aiello (1960) asserted that ciliary activity in *Mytilus* depends on the integrity of the branchial nerve and to a lesser extent on that of the ipsilateral cerebrovisceral connective. Our current studies further support this hypothesis. If this view is correct, we have in the gill of pelecypods a highly developed organ with peripheral neurons, muscle cells and cilia all coordinated by an integrating nervous system. The cerebral and visceral ganglia





Figures 4 and 5. The effect of branchial nerve stimulation on the rate of beating of lateral cilia. The cerebrovisceral connective has been cut and observations were performed three (figure 4) and five (figure 5) days later. The results before (dots) and after [5 Hz (squares); 50 Hz (triangles)] branchial nerve stimulation are shown. For each curve, zero time indicates the beginning of stimulation. Each point is the average of 10 preparations, 12 readings per preparation. Standard error of the mean denoted (T).

via their connective (cerebrovisceral) could play the role of a fine controlling agent over ciliary activity, while the visceral ganglion alone serves as a coarse regulator of the ciliary mechanism.

It is not clear whether the rich supply of nerves to the gill is wholly efferent or mixed afferent and efferent or whether the ganglion cells that accompany the branchial nerve to the gill are required for the autonomous local responses involving the central nervous system. In view of the physiological data set fourth in this study along with previous histological (Aiello and Guideri, 1965; Paparo, 1972, 1973) histochemical (Aiello, 1965, 1970; Sweeney, 1963, 1968; Paparo, 1972; Stefano and Aiello, 1972; Paparo and Tate, 1973) and electrophysiological evidence (Paparo, Hamburg, and Cole, 1974; Hamburg and Paparo, 1974), it seems permissible to speculate that, in at least some species of bivalves, the gill is innervated both with afferent and efferent neurons with autonomous control of ciliary beating and also central modulation of ciliary beating.

CONCLUSION

The results of this study suggest that: (1) the visceral ganglion provides a coarse regulatory control over ciliary beating mediated via the branchial nerve; (2) a second source of ciliary activation arises from the cerebral ganglion via the cerebrovisceral connective to the visceral ganglion and (3) that the cerebral ganglion contributes (directly and/or indirectly) axons which have a fine control over ciliary activation.

ACKNOWLEDGMENTS

The Center for Electron Microscopy, So. Illinois Univ., is acknowledged for the use of its facilities including a Cambridge Mark II A Stereoscan Scanning Electron Microscope purchased with the Biomedical Sciences Support Grant No. FR-1S05 FR07118-0 and General Research Grant #00-43-2-75566.

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Accepted for publication October 15, 1975.

RESEARCH NOTES

INCIDENCE OF THE ENTONISCID PARASITE, *PORTUNION CONFORMIS* MUSCATINE (CRUSTACEA: ISOPODA) IN THE MUDCRAB *HEMIGRAPSUS OREGONENSIS* FROM SAN DIEGO COUNTY, CALIFORNIA

Menzies and Miller (*in* Light, 1975) listed parasitic bopyrid isopods, including "a genus closely related to *Portunion*," in a key to marine isopods of central California and Muscatine (1956) described a castrating isopod *Portunion conformis* found in two species of *Hemigrapsus* from the Pacific Coast. Parasitic isopods have attracted great attention as parasitic castrators, and were hypothesized by Kuris (1971) to act as a density dependent means of host population control.

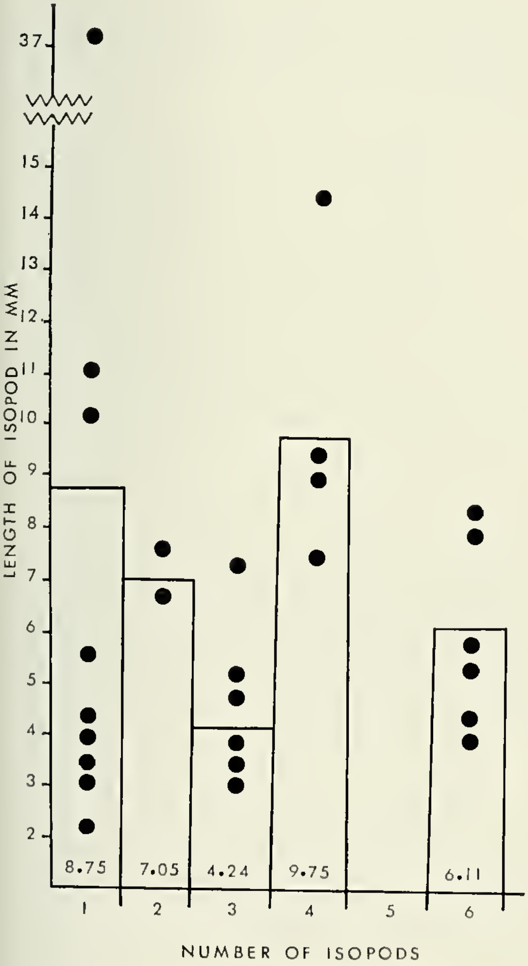

Figure 1. The average lengths of the isopod *Portunion conformis* (Muscatine), found in single and multiple infections of the mudcrab, *Hemigrapsus oregonensis*.

Portunion conformis is known to be found from Puget Sound, Washington down to Bahia San Quintin, Baja California, Mexico.

Forty nine mudcrabs, *Hemigrapsus oregonensis*, were collected periodically from June to September 1972 from the Tijuana Estuary near the city of Imperial Beach, San Diego Co. California. The crabs were collected by dip net from shallow water and transported by bucket to the laboratory at San Deigo State University. The hepato-pancreas tissue of the mudcrabs was examined to determine the incidence and intensity of infection *Portunion conformis.* Fourteen of 49 crabs collected in the Tijuana Estuary were infected with 27 parasites with a range in intensity of 1–6. Of the fourteen hosts infected, nine individuals were infected by one female isopod. The other five crabs had multiple infections with the number of female isopods ranging from 2–6. This would indicate an incidence of infection of 28.5 percent which is higher than the 4–15 percent reported by Kuris, and the 12–18 percent reported by Piltz, at Bodega Bay, California. The isopods were teased away from the surrounding hepato-pancreas tissue, then fixed in hot AFA and stored in alcohol and glycerine.

Various stages of development were encountered as evidence by the range in length of the isopods found in single and multiple infections of *Hemigrapsus oregonensis.* The length of isopods examined ranged from 2–37 mm. All measurements were made from the hood chamber to the tip of the posterior ventral ovarian process.

In one crab which was parasitized by six female isopods, all isopods showed signs of retarded development or immaturity. The pleural lamellae exhibited a lack of complexity of the marginal folds. Marsupium development was incomplete or non-existent with spheres of the cephalon demonstrating little development. In addition, the dorsal ovarian process along with the anterior and posterior ventral process normally found in adult isopods were completely absent in the examined juvenile isopods.

Their arrangement within the hemocoel was localized near the dorsal portion of the heart. Their layering structure indicated an accumulation of the isopods with probably the oldest and most mature parasite lying proximal to the heart with the newest addition positioned distal to the heart. Female isopods that were found singly showed a higher degree of development and maturity. Presence of an egg mass was used to indicate mature females.

ACKNOWLEDGMENTS

This project was carried out at San Diego State University. I am indebted to Andrew C. Olson, Jr. for his assistance.

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David Lapota, *Dept. Zoology, San Diego State Univ., San Diego, California 92182.*

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FIRST RECORD OF *ARGIS LEVIOR* (RATHBUN) FROM CALIFORNIA (DECAPODA: CRANGONIDAE)

The shrimp *Argis levior* (Rathbun, 1904) has a recorded range from Unalaska to Puget Sound, in depths of 19 to 42 fathoms (Rathbun, Harriman Alaska Exp., 10:1–210, 1904, as *Nectocrangon levoir*). On 7 August 1971, the vessel R. V. *Searcher* trawled seven individuals of this species at 20 fathoms (36 m) five miles south of Shelter Cove, Humboldt County, California. This occurrence extends the known southern limit of this species from the state of Washington to northern California.

Trawled with the specimens of *Argis levior* were the shrimps *Pandalus danae* Stimpson and *Crangon alaskensis elongata* Rathbun, and the hermit crab *Pagurus armatus* (Dana). The type of bottom was not recorded, nor was the temperature of the water.

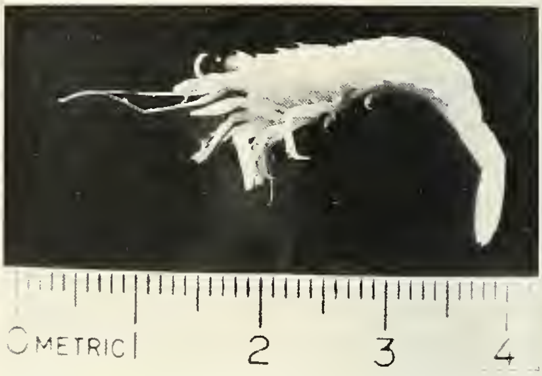

Figure 1. A specimen of *Argis levior* trawled south of Shelter Cove, California.

The only shrimp in California with which *Argis levior* might be confused is its congenor, *A. californiensis* (Rathbun), found off Santa Catalina Island and Santa Cruz Island (Rathbun, 1904). The two species can be differentiated by use of the following key (after Rathbun, 1904):

1. a. Carapace with only 2 median spines behind anterior margin, first and second abdominal segments not carinated ..... *Argis californiensis*
   b. Carapace with 3 or 4 median spines behind anterior margin, first to fourth abdominal segments not carinated .... *Argis levior*

All of the specimens of *Argis levior* taken by the R. V. *Searcher* were deposited in the collections of the Allan Hancock Foundation in Los Angeles, California. Figure 1 shows one of the best of the seven specimens taken.

ACKNOWLEDGMENTS

I thank Camm Swift, Natural History Museum of Los Angeles County, for donating the specimens taken by the R. V. *Searcher*; Fenner A. Chace, Smithsonian Institution, for identifying the specimens; John Garth and Janet Haig, Allan Hancock Foundation, for reviewing the manuscript; and John Lucas, Cabrillo Marine Museum, San Pedro, for taking the photograph.

Mary K. Wicksten, *Allan Hancock Foundation, Univ. Southern California, Los Angeles 90007.*

Accepted for publication December 15, 1975.

INSTRUCTIONS FOR AUTHORS

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It is strongly recommended that, before submitting a paper, the author ask qualified persons to review it. The author is requested to submit *at least one additional copy with the original,* on 8½ × 11 opaque, nonerasable paper, double spacing the entire manuscript. ***Do not break words at right-hand margin anywhere in the manuscript.*** Footnotes should be avoided. **Manuscripts which do not conform to the style of the BULLETIN will be returned to the author.**

An abstract summarizing in concise terms the methods, findings, and implications discussed in the paper *must* accompany a *feature article. Abstract should not exceed 100 words.*

A feature article comprises approximately five to thirty typewritten pages. Papers should usually be divided into the following sections: abstract, introduction, methods, results, discussion and conclusions, acknowledgments, and literature cited. Avoid using more than two levels of subheadings.

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The literature cited section should include six or more references; entries for books and articles should take these forms.

McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.
Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus.* J. Mamm., 54: 452–458.
Brattstrom, B. H. 1969. The Condor in California. Pp. 369–382 *in* Vertebrates of California. (S. E. Payne, ed.), Univ. California Press, xii + 635 pp.

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(McWilliams, Insect mimicry, p. 216, 1970); (Holmes and Speak, J. Mamm., 54: 452–458, 1971); (Brattstrom, The Condor in California, Pp. 369–382, *in* Vertebrates of California, 1969).

Tables and figures (line drawings, graphs, or black and white photographs) **should not repeat data contained in the text.** The author must provide *numbers* and *short legends* for tables and figures and place reference to each of them in the text. Legends should be typed on a separate sheet of paper and placed at the end of the manuscript. **Illustrations and lettering thereon should be of sufficient size and clarity to permit reduction to standard page size;** ordinarily they should be no more than twice the size of intended reduction and should not exceed 8½ by 11 inches in size. Photographs *must* be printed on glossy paper. Submit one photoduplicated copy of each illustration. All illustrations accompanying **Research Notes** will be reduced to one column width. **All half-tone illustrations will have light screen (grey) backgrounds. Special handling such as dropout half-tones, special screens, etc., must be requested by and will be charged to authors.**

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RESEARCH NOTES

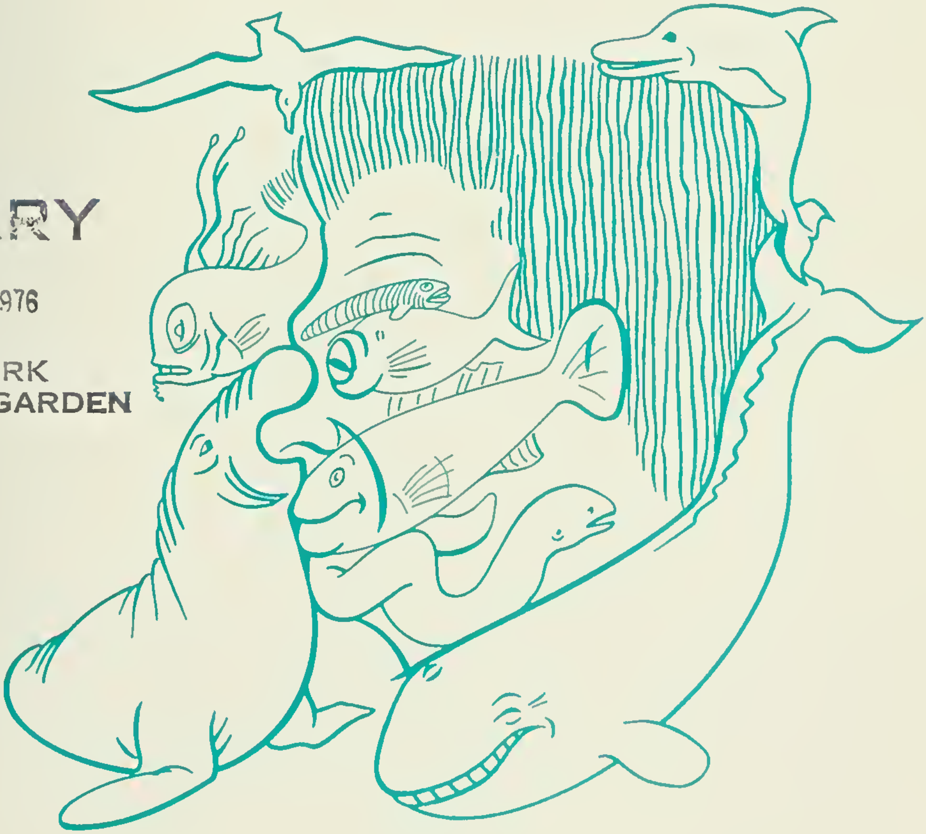
COVER: *A new species of syllid polychaete collected at a night light. Described herein by Mueller and Fauchald.*

Drawing by Kristian Fauchald, Allan Hancock Foundation.

OUTHERN CALIFORNIA ACADEMY OF SCIENCES

BULLETIN

olume 75 CARL L. HUBBS HONORARY ISSUE Number 2



BCAS-A75(2) 57–224 (1976) AUGUST 19

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BULLETIN OF THE SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

VOLUME 75 NOVEMBER 9, 1976 NUMBER 2

IN HONOR OF CARL L. HUBBS

MICHAEL H. HORN[1]

This issue of the Bulletin of the Southern California Academy of Sciences is dedicated to Carl Leavitt Hubbs whose long and productive career is a landmark in the fields of aquatic and vertebrate biology in this century. Since his first publication in 1915, Carl Hubbs has contributed a steady stream of papers on a wide variety of subjects such that his bibliography now includes about 700 titles. His range of interests perhaps can be best identified by listing here the areas of endeavor given in his biographic sketch published in the 12th edition of American Men and Women of Science: taxonomy, distribution, ecology, variation, life history and evolution of fishes; fishery biology; marine mammals; paleohydrography; oceanography; human ecology; and paleoclimatology. His principal focus over the years has been the study of fishes inhabiting both marine and freshwater environments. It is safe to say that he has been the foremost figure in North American ichthyology in the middle half of the twentieth century. He has followed in the footsteps of his mentor, David Starr Jordan, who dominated the field in the late 1800's and early 1900's. Certainly, no other person has made a greater contribution to the growth and development of ichthyology in this country than Carl Hubbs. His long commitment to and involvement with the American Society of Ichthyologists and Herpetologists (ASIH) have been shaping forces in this organization almost since its inception in 1913. The ASIH dedicated its 1974(3) issue of Copeia to Hubbs on the occasion of his 80th birthday.

While it is difficult to single out studies from the extensive list of significant contributions by Carl Hubbs, a number of particular areas of research come to my mind when considering his accomplishments. These include studies on speciation, hybridization and geographic variation in fishes; fish distributions and hydrographic history in the Great Basin region; zoogeography in the Eastern Pacific, including the relationship of temperature to coastal fish distributions; population status and related aspects of marine mammals such as the northern elephant seal, Guadalupe fur seal, and Pacific gray whale; taxonomy and distribution of lampreys; and the taxonomy, distribution and reproduction of cyprinodontid fishes. His research on the cyprinodonts included discovery of the Formosa molly (*Poecilia formosa*), an all-female species maintained by males of another species. Hubbs' interest in cyprinodontids is epitomized by his early and continuing efforts to protect the desert pupfishes. The treatise on fishes of the Great Lakes region co-authored with Karl F. Lagler has not only continued to be an important synthesis of the fish fauna of that region since the first edition in 1941, but also the standard reference on methods for making counts and measurements of fish specimens. Hubbs' concerted studies on distributional patterns of fishes and marine mammals resulted in his editorship in 1958 of a volume on zoogeography. In 1968, he co-edited, with Wheeler J. North, an important bulletin on the utilization of kelp bed resources in southern California. During his career, Carl Hubbs has written more than 140 book reviews. These evaluations have been characterized by critical analysis and have frequently contained original concepts. Elizabeth N. Shor compiled a selected bibliography of Hubbs which appears in the 1974(3) issue of Copeia and is not duplicated here.

Carl Hubbs was born 18 October 1894 in Williams, Arizona. He received his A.B. and A.M. degrees from Stanford University in 1916 and 1917, respectively, and his Ph.D. in zoology from the University of Michigan in 1927. His principal positions have been curatorial and professorial at the University of Michigan (1920–1944) and the Scripps Institution of Oceanography (1944–1969; emeritus professor 1969–present). Hubbs has been an active member of

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Carl L. Hubbs aboard the 'Orca" at Guadalupe Island June 1955 a wide variety of professional organizations and has held office in the ASIH (secretary, 1928–31, president, 1934–35, 1946–48), the American Society of Naturalists (vice-president, 1964), the Society for the Study of Evolution (vice-president, 1953, 1955) and the Society of Systematic Zoology (president, 1951). He was editor of Copeia from 1930 to 1937 and review editor of the American Naturalist from 1941 to 1947. Carl Hubbs has been a strong voice in a number of conservation groups including the Nature Conservancy, the Torrey Pines Association and the Desert Fishes Council.

Honors presented to Carl Hubbs have been many and include receipt of the Henry Russell Award at Michigan (1929–30), election to the National Academy of Sciences (1952), receipt of a Guggenheim fellowship (1952–53), the Joseph Leidy Award and Medal of the Academy of Natural Sciences, Philadelphia (1964), membership in the Linnean Society of London (1965), the Gold Medal of the San Diego Zoological Society (1970), the Shinkishi Hatai medal of Japan (1971), and the American Fisheries Society Award of Excellence (1973). According to Kenneth Norris who wrote an account of Hubbs' life in the 1974(3) issue of Copeia, five genera of fishes, one of lichens, 22 species of fishes, one bird, one whale, two molluscs, one crab, three cave arthropods, two insects, three species of algae, one species of lichen and one dry, Nevada lake have been named in honor of Hubbs.

Carl Hubbs has shared nearly 60 years of his life with a remarkable woman, his wife Laura, who throughout the years has carefully recorded field notes, meticulously organized reprints and correspondence, and frequently joined Carl on research projects. They have one daughter, Frances, and two sons, Clark and Earl. The family is biologically oriented. Earl is a biology teacher, and Clark and Robert Rush Miller (husband of Frances) are both well-known ichthyologists. Miller has collaborated with the senior Hubbs on a variety of studies of freshwater fishes.

Of perhaps equal importance to his scientific contributions, have been the encouragement and assistance Carl Hubbs has given to countless colleagues and students. His straightforward manner, dedication to solid science, and enthusiasm for the efforts of others have been significant for the continued development of the careers of many people.

Carl Hubbs' awareness and currency in the field of ichthyology was first fully appreciated by me a few years ago when I visited him at Scripps Institution soon after I had published my doctoral dissertation. I was pleased, of course, that he knew of my paper, but I was rather unprepared for his questioning of me on three small, but important, points contained well inside the covers of the article. It became obvious to me that he had read the entire paper. I was amazed—and convinced—of his attention to the field. At the end of our meeting, I received an armload of carefully selected reprints from the Hubbs stock and happily went off realizing that I had marked a kind of milestone in my ichthyological career.

Beyond this influence that Carl Hubbs has in direct exchange with colleagues and students, are the inspiration and enthusiasm that he effects simply by his presence. Many students, aware of the longevity and accomplishments of Carl Hubbs, figure they are at the "right" meeting if he also happens to be in attendance; better yet, if they present their first paper with him in the audience. What is often the best reward of all for them, however, is the informality and friendliness with which they are received when introduced to Carl and Laura after a paper session at the meeting.

Carl Hubbs has received many honors in his long career but he has never rested on them. He has no time for that. A quote attributed to him attests to his singular desire to energetically get on with the business of living. Upon receiving the 1975 Headliner Award from the San Diego Press Club, he is reported to have said apologetically, "I really don't know why I'm receiving this. All I've ever done in my life was exactly what I wanted to do." At this writing, he is preparing for an extensive trip with his family to Alaska and other parts of the United States. Descriptions of new species are waiting as are the completion of the exhaustive checklist of California fishes and other projects that I neither have space to list nor know about.

The 18 papers contained in this issue are partially representative of the multifaceted interests of Carl Hubbs. The results of systematic, ecological, behavioral, and physiological studies of both marine and freshwater fishes are included. The authors, ranging from graduate students to senior scientists, work in a diverse range of subject areas within the field of ichthyology. I trust that the papers will be of interest and value to Carl Hubbs and others in the scientific community. On behalf of the Southern California Academy of Sciences and the authors of these papers, I respectfully dedicate this issue to Carl L. Hubbs in honor of his distinguished life and scientific career.

A NEW NONPARASITIC SPECIES OF LAMPREY OF THE GENUS *ENTOSPHENUS* GILL, 1862, (PETROMYZONIDAE) FROM SOUTH CENTRAL CALIFORNIA

Vadim D. Vladykov[1] and Edward Kott[2]

Abstract: A new nonparasitic lamprey from the Friant-Kern Canal, east of Delano, California, is described and illustrated. The holotype (number CAS 35987) is deposited in the California Academy of Sciences, San Francisco, California. The species is distinguishable from all species of the genus *Entosphenus* by: 1) low number of trunk myomeres—53 in the ammocoete and between 54 and 57 (average 55.5) in transformed specimens, whereas in other species the range is 58–73; 2) reduced dentition with typical numbers of teeth—2 supraoral cusps, 1-1-1-1 inner lateral teeth on each side of the disc, 9–12 (average 10.3) posterial teeth; 3) only 3 velar tentacles, whereas in other species the number of tentacles varies from 5 to 18; 4) small size of transformed specimens, 117–142; and 5) restricted distribution. The description is based on the study of eleven newly transformed individuals and one ammocoete.

Lampreys from California of the family Petromyzonidae are represented by two genera, *Lampetra* Gray, 1851, and *Entosphenus* Gill, 1862. The first genus belongs to the subfamily Lampetrinae, whereas, the other belongs to the subfamily Entospheninae (Vladykov, 1972).

The genus *Lampetra*, as defined by Gray (1851) and accepted by several subsequent authors (Regan, 1911; Holly, 1933; Hubbs, 1967; and Vladykov and Follett, 1967), is represented in western North America by at least three species. *Lampetra ayresii* (Günther, 1870), a parasitic species recently redescribed by Vladykov and Follett (1958), and *L. pacifica* Vladykov, 1973, a nonparasitic species are found in California. Another nonparasitic species, *L. richardsoni* Vladykov and Follett, 1965, has a known distribution from Oregon to British Columbia and the possibility exists that it may be found in northern California.

The genus *Entosphenus* was established by Gill (1862) on the basis of the type species *Petromyzon tridentatus* Gairdner as described in Richardson (1836). Several authors (Berg, 1931; Holly, 1933; Vladykov and Follett, 1967; Hubbs, 1967; and McPhail and Lindsey, 1970) accepted this as a valid genus. On the other hand, some recent authors (Hubbs, 1971; Hubbs and Potter, 1971; Bond and Kan, 1973; and Kan, 1975) consider *Entosphenus* as a subgenus of *Lampetra*. The most important differences between these two genera, as pointed out by Vladykov and Follett (1967), and Vladykov and Kott (1976), are indicated in table 1.

Heretofore, in California and Oregon, three species of *Entosphenus* were known: *E. tridentatus* (Gairdner in Richardson, 1836), a large parasitic species; *E. minimus* (Bond and Kan, 1973), parasitic but small in size; and a nonparasitic species, *E. lethophagus* (Hubbs, 1971). Hubbs correctly stated that supplementary study is required for the untangling of the *Entosphenus* complex. The present description of a new nonparasitic species supports Hubbs' idea.

METHODS

In the description of the new species of *Entosphenus*, the definitions of the different body proportions follow Vladykov and Follett (1965) and the terminology of teeth is that of Vladykov and Follett (1967). The trunk myomeres were counted between the last (7th) gill-opening and the anterior tip of the cloacal slit (Hubbs and Trautman, 1937; Vladykov, 1949).

The present study is based on the examination of 11 newly transformed individuals, including the holotype, and one ammocoete received on loan from the California Academy of Sciences. Unfortunately, they are not well-preserved. All measurements are reported in millimeters unless noted otherwise.

Entosphenus hubbsi, new species

Figure 1–3

Holotype.—W336 (1 ♂, 131 mm); canal east of Delano, Kern Co., California; about 15 February

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1972; collected by D. P. Christenson; deposited in California Academy of Sciences CAS 35987.

Paratypes.—W333–335, 337–343 (7 ♂, 117–142 mm; 3 ♀, 140–141 mm), W344 (ammocoete, 160 mm): collected with the holotype; CAS 35988.

Diagnosis.—Low number of trunk myomeres, 53 in the ammocoete and between 54 and 57 in transformed specimens (average 55.5); reduced dentition; only three velar tentacles; and reduced pigmentation on its caudal fin. Other diagnostic features are summarized in tables 3–5.

Description of the holotype.—The holotype, a male 131 mm in total length, is referable to maturity stage three (early maturity: sexual products rather small; dorsal fins separated). Intestine is reduced to a threadlike thickness (0.9). Measurements (in percent of total length) are: disc length, 4.2; prebranchial length 9.2; eye length, 1.5; branchial length, 10.7; trunk length, 54.2; tail length, 28.2. Disc length, as a percentage of branchial length, is 39.3. There are 55 trunk myomeres (Fig. 2).

Since the holotype is a recently transformed individual, its disc is not fully developed and the teeth are not well-cornified. There are four inner lateral teeth on each side of the disc; the second tooth, on both sides, is bicuspid, the rest are unicuspid. There is a single row of nine unicuspid posterials. The supraoral lamina is provided with a cusp at each end, but the median cusp, as is typical for parasitic species of *Entosphenus*, is absent. The infraoral lamina has five cusps. The three lingual laminae were so poorly developed that the cusps could not be counted (Fig. 1); no enlarged median cusp was observed on the transverse lingual lamina.

The holotype is a newly transformed individual and its two dorsal fins are far apart (8) and the genital papilla is not visible. The color of the specimen, preserved in 4–5 percent formalin, is brown on the sides and back and whitish on the ventral surface. The dorsal fins are unpigmented. Pigmentation on the caudal fin is reduced to an area about the notochord and its shape is rather rounded posteriorly.

Transformed Specimens.—*Total length* (Table 2)—Lengths of eight males range from 117 to 142 (average 129.1) and of three females from 140 to 141 (average 140.3). Proportional measurements of different body regions and number of trunk myomeres are given in tables 2 and 3, respectively.

Figure 1. Enlarged disc of the holotype of *Entosphenus hubbsi*, new species, (tag W336), male, 131 mm, Friant-Kern Canal, east of Delano, California.

Dentition (Table 5)—The teeth are not fully cornified, hence, counts of some cusps are uncertain. A single row of posterials is present, which is typical for all species of the genus *Entosphenus*. The number of posterials ranges from 9 to 12 (average 10.3). These were small, weakly developed and difficult to count, all were unicuspid. The supraoral lamina has only two cusps, one at each end, except in one specimen (W338), which has a third cusp. The infraoral lamina has five cusps, blunt and weakly cornified. All specimens of *E. hubbsi* have eight inner laterals, four on each side of the disc as is characteristic of the genus *Entosphenus*. The number of cusps varies from one to three on the inner laterals; however a single cusp was most frequently observed (Table 5). The cusps on the lingual laminae were weakly developed and hence could not be counted. No enlarged median cusp was observed on the transverse lingual lamina.

TABLE 1. Principal differences between the genera *Entosphenus* and *Lampetra*.

Character	*Entosphenus*	*Lampetra*
Posterials	in one row	completely absent
Infraoral Cusps	typically 5	typically 7–8
Transverse Lingual Lamina	median cusp barely distinguishable from lateral cusps	median cusp greatly enlarged in comparison with lateral cusps
Inner Laterals	4 on each side of the disc	3 on each side of the disc
Supraoral Lamina	typically with 3 cusps	typically with 2 cusps

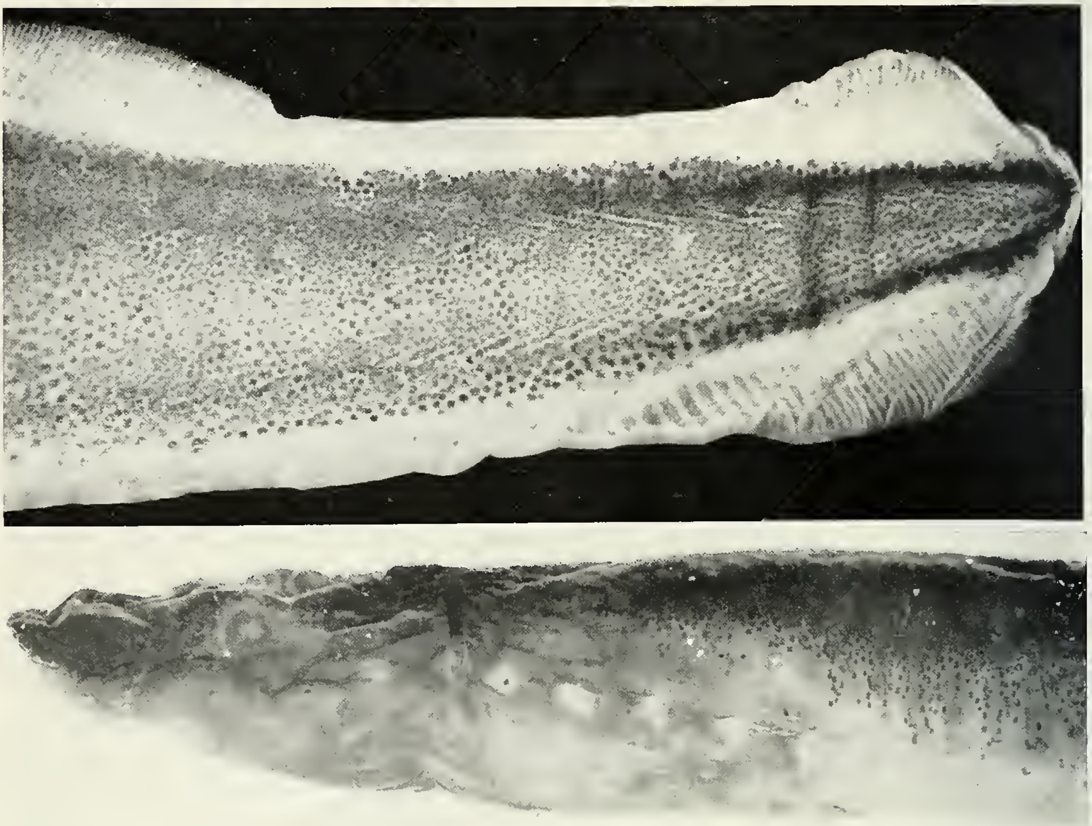

Figure 2. Enlargements of the head and tail regions of the holotype of *Entosphenus hubbsi,* new specie

Velar tentacles (Table 5)—Velar tentacles were counted in three specimens. In each only three tentacles are present, a single median, the shortest, and one lateral on each side. Length of longest tentacles was about 0.5 in all specimens.

Coloration.—The sides and back are brown and the lower surface is whitish. The dorsal fins are unpigmented. On the caudal fin black pigmentation is restricted to a narrow zone about the notochord.

Sexual dimorphism.—Secondary sexual characteristics have not yet fully developed, as the specimens had just recently transformed.

Ammocoetes.—Only one ammocoete was available for study (Table 4). It had 53 myomeres. The body proportions are shown in table 4. There is a broad nonpigmented zone above the branchial pores, and dark pigment was absent from the prebranchial region. Pigmentation of the caudal fin is similar to that of adult (Fig. 3).

This new species is dedicated to Carl Leavitt Hubbs, a distinguished friend and a keen student of lamprey taxonomy.

Comparisons.—The principal differences between *E. hubbsi* and the other three described species are as follows: 1) number of myomeres; 2) number
velar tentacles; 3) certain of the body proportions; 4
number and degree of development of different type
of teeth; and 5) pigmentation of the caudal fin. Thes
differences (other than pigmentation) are presente
in tables 3–5.

Number of myomeres.—In 11 transformed spec
mens of *E. hubbsi* there are 54–57 (mean 55.5
myomeres. This number is lower than that found i
any of the other three species. For the nonparasiti
species, *E. lethophagus,* Hubbs (1971) reported 63–6
(mean 65.6) for specimens from California, and 58–7
(mean 66.6) for those from Oregon. In the case
E. minimus, a very small, but parasitic form fro
Oregon. Bond and Kan (1973) counted 60–65 (mea
62.8). In the much larger *E. tridentatus,* we counte
66 transformed individuals with 63–70 (mean 66.3
myomeres.

Number of velar tentacles.—In the genus *Ento*
phenus, these tentacles have been counted only in
tridentatus (Mather, 1926; McPhail and Lindse
1970; and Vladykov and Pharand, 1972). Th
reported number varied from 11 to 18; however i
the present study we found that in 10 specimens th

TABLE 2. Body proportions (in percent of total length) and disc length (in percent of branchial length) of recently transformed specimens of *Entosphenus hubbsi*, new species, from Friant-Kern Canal east of Delano, Kern Co., California

Tag No.	Total Length (mm) (TL)	$\frac{d - B_1}{TL}$	$\frac{B_1 - B_7}{TL}$	$\frac{B_7 - a}{TL}$	$\frac{a - C}{TL}$	$\frac{O}{TL}$	$\frac{d}{TL}$	$\frac{d}{B_1 - B_7}$
				Males				
W334	117	9.0	9.4	51.3	30.8	1.7	4.3	45.5
W333	118	9.3	10.2	53.4	28.0	1.7	4.7	45.8
W335	121	10.7	10.7	53.7	27.3	2.1	4.5	42.3
W338	130	10.0	11.2	56.9	28.5	1.9	4.2	42.3
W336*	131	9.2	10.7	54.2	28.2	1.5	4.2	39.3
W337	135	8.8	11.1	54.1	28.9	1.9	3.7	41.7
W341	139	9.0	10.8	54.0	27.7	1.4	4.3	40.0
W342	142	9.2	9.5	54.6	28.2	1.4	4.2	44.4
Mean	129.1	9.4	10.5	54.0	28.5	1.7	4.3	42.7
Range	117–142	8.8–10.7	9.4–11.2	51.3–56.9	27.3–30.8	1.4–2.1	3.7–4.7	39.3–45.8
				Females				
W339	140	9.6	8.6	55.0	28.2	1.8	4.6	54.2
W340	140	8.9	10.7	55.0	27.5	2.1	3.9	36.2
W343	141	8.5	8.5	53.5	30.1	1.4	4.6	54.2
Mean	140.3	9.0	9.3	54.5	28.6	1.8	4.4	48.3
Range	140–141	8.5–9.6	8.5–10.7	53.5–55.0	27.5–30.1	1.4–2.1	3.9–4.6	36.6–54.2

* Holotype.

TABLE 3. Comparison between number of trunk myomeres and proportional measurements (in percent of total length) of transformed specimens of *Entosphenus hubbsi*, new species, with those of three other species of the same genus. Data refer to means and ranges for each character.

	Entosphenus hubbsi		*Entosphenus minimus*		*Entosphenus lethophagus*	*Entosphenus tridentatus*		
	Males	Females	Males	Females	Sexes combined	Males	Sexes combined	Females
Authority	Present Study		Bond and Kan (1973)		Bond and Kan (1973)	Present Study		
Number of Specimens	8	3	33	12	18	8	66	11
Myomeres	55.5	55.7	62.3	63.8	66.3[1]		66.3	
	54–57	55–57	60–64	62–65	64–70		63–70	
Total	129.1	140.3	86.4	79.8	140.8	303.1		315.3
Length (mm)	117–142	140–141	76–129	72–87	110–170	263–476		208–480
Prebranchial	9.4	9.0	15.0	14.2	12.1	14.3		13.8
Length	8.8–10.7	8.5–9.6	13.7–16.4	13.4–14.8	10.4–13.5	13.4–15.8		12.5–15.4
Branchial	10.5	9.3	9.2	9.1	10.3	10.9		10.8
Length	9.4–11.2	8.5–10.7	7.9–10.8	8.3–10.0	8.9–11.5	10.0–12.2		9.6–11.6
Trunk	54.0	54.5	44.1	48.3	46.5	45.5		46.9
Length	51.3–56.9	53.5–55.0	42.6–47.3	45.9–51.3	43.5–52.6	43.5–47.0		43.8–50.8
Tail	28.5	28.6	31.5	28.5	30.9	29.0		27.8
Length	27.3–30.8	27.5–30.1	29.0–32.9	25.9–31.0	27.1–33.5	27.8–30.5		25.2–31.3
Eye	1.7	1.8	2.4	2.5	1.6	2.4		2.4
Length	1.4–2.1	1.4–2.1	2.1–3.1	2.3–2.8	1.1–2.1	2.1–2.9		2.1–2.9
Disc	4.3	4.4	6.3	5.8	5.0	7.7		7.5
Length	3.7–4.7	3.9–4.6	5.7–7.4	5.0–7.3	3.6–6.1	7.1–9.1		6.5–9.1

[1] According to Hubbs (1971), in 83 specimens from Pit River, Sprague River, and Crooked Creek, the mean number of myomeres in *E. lethophagus* is 66.3 (range: 58–73).

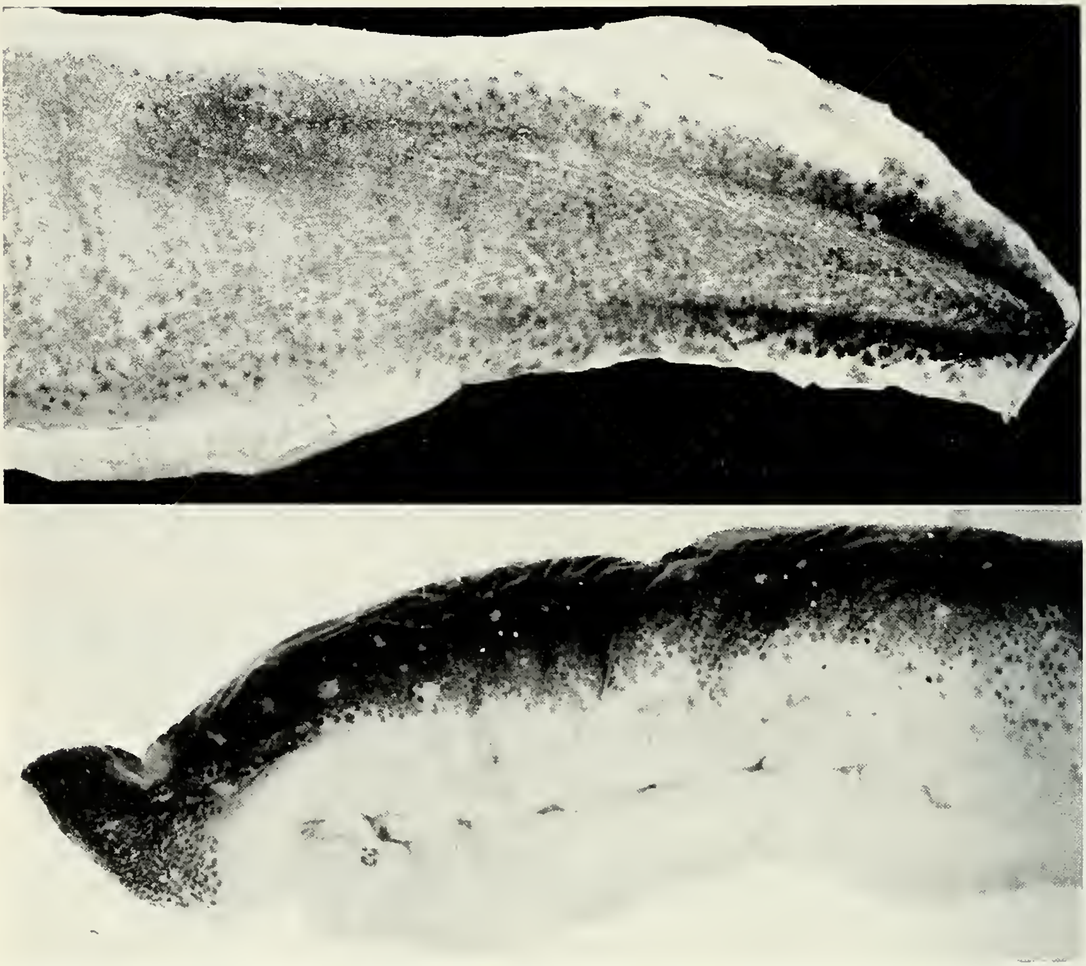

Figure 3. Enlargements of the head and tail regions of an ammocoete of *Entosphenus hubbsi*, new specie 160 mm.

number of tentacles was 9–15 (mean 12.5). In one specimen of *E. lethophagus*, and one of *E. minimus*, we counted only seven tentacles; however, in *E. minimus* the range is 5–7 according to Bond (*pers. comm.*). In three specimens of *E. hubbsi*, we found only three tentacles in each.

Body proportions in percent of total length.—In spite of the fact that our specimens of *E. hubbsi* are recently transformed individuals, they already show some specific characteristics. Their small eye length is typical for nonparasitic lampreys, in general; the average was 1.7 for males and 1.8 for females, which is very close to 1.6 for *E. lethophagus* (sexes combined). The eye length for both parasitic species, *E. minimus* and *E. tridentatus*, averages 2.4.

The disc length of *E. hubbsi* (about 4.3), as well as prebranchial length (9.4), is especially small. This can be explained partially by its nonparasitic nature and also by the fact that the specimens are only recently transformed individuals. In *E. lethophagus* (sexes combined), the disc length was 5.0; in *E minimus*, 6.3 in males and 5.8 in females; and in *E tridentatus*, 7.7 in males and 7.5 in females.

The prebranchial length in *E. lethophagus* was 10. in *E. minimus*, 9.2; and in *E. tridentatus*, almost 11. Other details are given in table 2.

The total length of *E. hubbsi* is from 117 to 14 which is intermediate between that of *E. minimu* (72–129) and *E. lethophagus* (110–170). The lengt of *E. tridentatus* is much greater, up to 690 in ou material; McPhail and Lindsey (1970) give as a max mum size 760.

Dentition.—The supraoral lamina in *E. hubbsi* typ cally has two cusps (one specimen had three). In *E lethophagus*, the number of cusps varied from tw to four (mean 2.6). In both *E. minimus* and *E tridentatus*, the number is three. In *E. hubbsi*, as in a species of *Entosphenus*, there are four inner latera teeth on each side of the disc; however the number o cusps is much lower, the typical cusp formula bein

TABLE 4. Comparison between number of trunk myomeres and proportional measurements (in percent of total length) of an ammocoete of *Entosphenus hubbsi*, new species, with those of ammocoetes of three other species of the same genus. Data refer to means and ranges for each character.

	Entosphenus hubbsi	*Entosphenus minimus*	*Entosphenus lethophagus*	*Entosphenus tridentatus*
Authority	Present Study	Bond and Kan (1973)	Bond and Kan (1973)	Present Study
Number of Specimens	1	102	52	25
Myomeres	53	61.8 59–66	65.5 63–68	68.7[1] 67–70
Total Length (mm)	160	72.8 37–111	122.9 83–190	110.3 81–132
Prebranchial Length	6.9	8.4 6.8–11.1	6.5 5.3–8.1	8.2 7.0–9.3
Branchial Length	10.6	14.1 11.7–17.5	10.8 9.8–12.7	11.8 9.0–14.1
Trunk Length	54.4	49.7 47.5–53.3	51.6 48.7–53.4	50.9 48.1–53.5
Tail Length	30.6	27.9 23.7–31.4	31.0 27.8–33.3	28.9 27.1–32.4

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[1] Number of myomeres counted in 33 specimens.

TABLE 5. Comparison between number of cusps on the various types of teeth in *Entosphenus hubbsi*, new species, with those of three other species of the same genus; and the number of velar tentacles found in these species. Data refer to means and ranges for each character. Number in parentheses is number of specimens.

	Entosphenus hubbsi	*Entosphenus lethophagus*	*Entosphenus minimus*	*Entosphenus tridentatus*
Authority	Present Study	Hubbs (1971)	Bond and Kan (1973)	Present Study
Supraoral	2.1 (11) 2–3	2.6 (28) 2–4	3 –	3.0 (18) 3
Inner Laterals				
first	1.0 (21) 1	1.9 (52) 1–3		2.0 (37) 2
second	1.3 (21) 1–2	2.4 (52) 2–4		3.0 (38) 2–3
third	1.3 (21) 1–3	2.2 (52) 2–3		3.0 (38) 3
fourth	1.1 (20) 1–2	1.8 (52) 1–3		2.0 (38) 2
typical cusp formula	1-1-1-1	2[1]-2[3]-2[3]-2[1][1]	2-3-3-2	2-3-3-2
Infraoral	5.0 (9) 5	5.1 (28) 4–7	5 –	5.06 (64) 5–6
Posterials				
total	10.3 (6) 9–12	12.1 (23) 9–15	– 13–17	17.1 (17) 12–19
bicuspids	0 –	1.9 (24) 0–12	– 2–6	2.3 (17) 0–5
Transverse Lingual Lamina	poorly developed	15.6 (11) 12–17	– 17–23	19.0 (17) 16–22
		Present Study		
Velar Tentacles	3.0 (2) 3	7 (1)	7[2] (1)	12.5 (10) 9–15

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[1] Numbers in brackets are other frequently observed counts.
[2] According to Bond (*pers. comm.*) the range is 5–7 tentacles.

1-1-1-1. In *E. lethophagus*, a typical formula is 2-2-2-2 and in the two parasitic species 2-3-3-2. The number of infraoral cusps is five in *E. hubbsi*, but it is more variable (4–7) in *E. lethophagus*. In *E. minimus*, there are five and in *E. tridentatus*, typically five and rarely six. The number of posterials is the lowest in *E. hubbsi* (mean 10.3) and all are unicuspid. In *E. lethophagus*, the mean number is 12, and these also are unicuspid. In *E. minimus*, the range of posterials is 13–17 and at least two of them are bicuspid. In *E. tridentatus*, the mean number is 17 (range 0–5) typically two to four of these are bicuspid. The transverse lingual lamina is poorly developed in *E. hubbsi*; the cusps could not be counted. In other species cusps ranged as follows: *E. lethophagus* 12–17; *E. minimus* 17–23; and *E. tridentatus* 16–22.

Pigmentation of the caudal fin.—In *E. hubbsi*, the dark pigmentation of the caudal fin is restricted to a narrow band about the notochord, leaving most of the fin membrane unpigmented. In other species of *Entosphenus*, most of the fin membrane is strongly pigmented. In *E. hubbsi*, the caudal fin is more roundish; in other species of *Entosphenus* it is more pointed.

GEOGRAPHICAL DISTRIBUTION

Our specimens of *E. hubbsi* were collected in the Friant-Kern Canal east of Delano, Kern Co, California. Because the Friant-Kern Canal is about 85 percent concrete lined with a current of at least 56.6 m^3 per second, the canal cannot be considered as the normal habitat for a small nonparasitic lamprey. Therefore, it is safe to say that *E. hubbsi* originated in the Kern River system, which before the construction of this canal was an inland system. Although the Friant-Kern Canal connects through the man-made Millerton Lake with the San Joaquin River, at present no direct connection with the sea exists. Moreover, the height (97.2 m) of the Friant Dam would make it impossible for *E. hubbsi* to ascend above this dam. Further information on the Friant-Kern Canal may be obtained from Fact Sheet U.S. Dept. Interior (1974).

The only other species of lamprey known to occur in the canal near Delano is *Lampetra pacifica*. We have four transformed specimens (119–152 mm) on loan from the California Academy of Sciences which were obtained on the west side of the canal by G. Charles Mayes on 26 January 1972.

Before the construction of the canal, the Kern River basin was an inland drainage system having no connections with rivers in which other species of *Entosphenus* occur. *Entosphenus lethophagus*, according to Hubbs (1971), has been found only in the Klamath River system of Oregon and northern tributaries of the Sacramento River in California. *Entosphenus minimus*, landlocked form, is known only from Miller Lake, southern Oregon (Bond and Kan, 1973). *Entosphenus tridentatus*, typically an anadromous species, has a very broad distribution along the western seaboard of North America, extending from Alaska to Baja California (Hubbs and Potter, 1971).

In conclusion it must be stressed that because of its restricted distribution *E. hubbsi* should be considered an endangered species in California and hence should be protected as was recommended for other lamprey species by Miller (1972) and Vladykov (1973). Delay in protection could result in extinction of *E. hubbsi* in the same way that *E. minimus* has disappeared from Miller Lake (Bond and Kan, 1973).

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FOUR NEW PUPFISHES OF THE GENUS *CYPRINODON* FROM MEXICO, WITH A KEY TO THE *C. EXIMIUS* COMPLEX

Robert Rush Miller[1]

ABSTRACT: The pupfishes (genus *Cyprinodon*) referable to the *C. eximius* complex comprise seven species that are restricted to, or had their origin in, the Chihuahuan Desert region of México and adjacent parts of Texas and New Mexico. Four are described as new; the remainder are *C. eximius*, *C. atrorus*, and *C. latifasciatus*. Most are of restricted distribution; one is extinct and another may be. Keys, diagnoses, and ranges are given for each species and all are illustrated. The distinctive morphometric characters of the new species are given. Life colors and color patterns are important in distinguishing species.

More than fifty years ago, while on the staff of the Field Museum of Natural History, Carl L. Hubbs began to gather data for an intended revision of the genus *Cyprinodon* (Hubbs, 1926: 17). He subsequently described the distinctive Yucatán pupfish, *C. variegatus artifrons* (Hubbs, 1936: 223–225, pl. 6, figs. 1–5). About this time I independently became interested in this genus and we decided to work together on it (Hubbs and Miller, 1941: 2). We did jointly describe a new species from the Bahamas (Hubbs and Miller, 1942) but in the 1950's Carl turned over to me all of his notes on *Cyprinodon*. These include helpful information on some of the species that are treated herein, including the significant observation that colors and color pattern are important specific traits.

The group of seven species (four new) included in this paper comprises those pupfishes believed to be closely related to *Cyprinodon eximius* Girard, the most widely distributed species of the complex. All are inhabitants of, or originated from ancestral stocks in, the Chihuahuan Desert region (Basin and Range Province) of northern México and adjacent parts of Texas and New Mexico (Miller, 1976b). They are distinguished in the following key.

A KEY TO THE PUPFISHES OF THE *CYPRINODON EXIMIUS* COMPLEX

1. a. Terminal black bar on caudal fin of nuptial male broad, wider than pupil, about 1.2–1.6 in orbit 2
   b. Terminal black bar on caudal fin of nuptial male of usual width for *Cyprinodon*, subequal to or less than diameter of pupil 6
2. a. Pelvic fins rather small and mandible long, the pelvic length entering mandible length more than 1.0 times .... *C. alvarezi*, n. sp. (Fig. 1D) El Potosí, Nuevo León
   b. Pelvic fins not reduced and mandible not elongated, the pelvic length entering mandible length less than 1.0 times 3
3. a. Caudal fin of nuptial male with prominent black spots or dashes on interradial membranes of basal ½ to ⅔ of fin, usually irregularly arranged but sometimes aligned in about 3 vertical rows; terminal black bar immediately preceded by a narrower light bar .... *C. eximius* (Fig. 1A) Río Conchos Basin, etc.
   b. Caudal fin of nuptial male without conspicuous black markings on interradial membranes; no light bar immediately preceding terminal black bar 4
4. a. Gill rakers 12–17; mandibular pores 0–2; scales around caudal peduncle usually 20 (uncommonly 16) .... *C. nazas*, n. sp. (Fig. 1C) Río Nazas Basin, Santiaguillo Basin
   b. Gill rakers 20–28; mandibular pores lacking; caudal peduncle scales 16 (rarely 15 or 17) 5
5. a. Ocellus on dorsal fin lacking in both sexes; lacrimal pores typically 3 (2–4); dorsal fin of nuptial male not yellow or orange; body of male with dark lateral stripe from behind eye to caudal base, set off above by a narrow silvery stripe (turquoise in life?) and below by a broad yellowish stripe .... *C. latifasciatus* (Fig. 1G) Parras Basin, Coahuila
   b. Ocellus present on dorsal fin of both sexes; lacrimal pores lacking; dorsal fin of nuptial male yellow or orange; body of male with 7–9 broad vertical bars .... *C. atrorus* (Fig. 1B) Cuatro Ciénegas Basin, Coahuila
6. a. Scales in lateral series 23 or 24; gill rakers 17–22; dorsal fin of nuptial male yellow; vertebrae usually 25 .... *C. macrolepis*, n. sp. (Fig. 1F) Ojo Hacienda Dolores, Chihuahua
   b. Scales in lateral series typically 25; gill rakers 12–15; dorsal fin of nuptial male not yellow; vertebrae 26 or 27 .... *C. meeki*, n. sp. (Fig. 1E) Río Mezquital Basin, Durango

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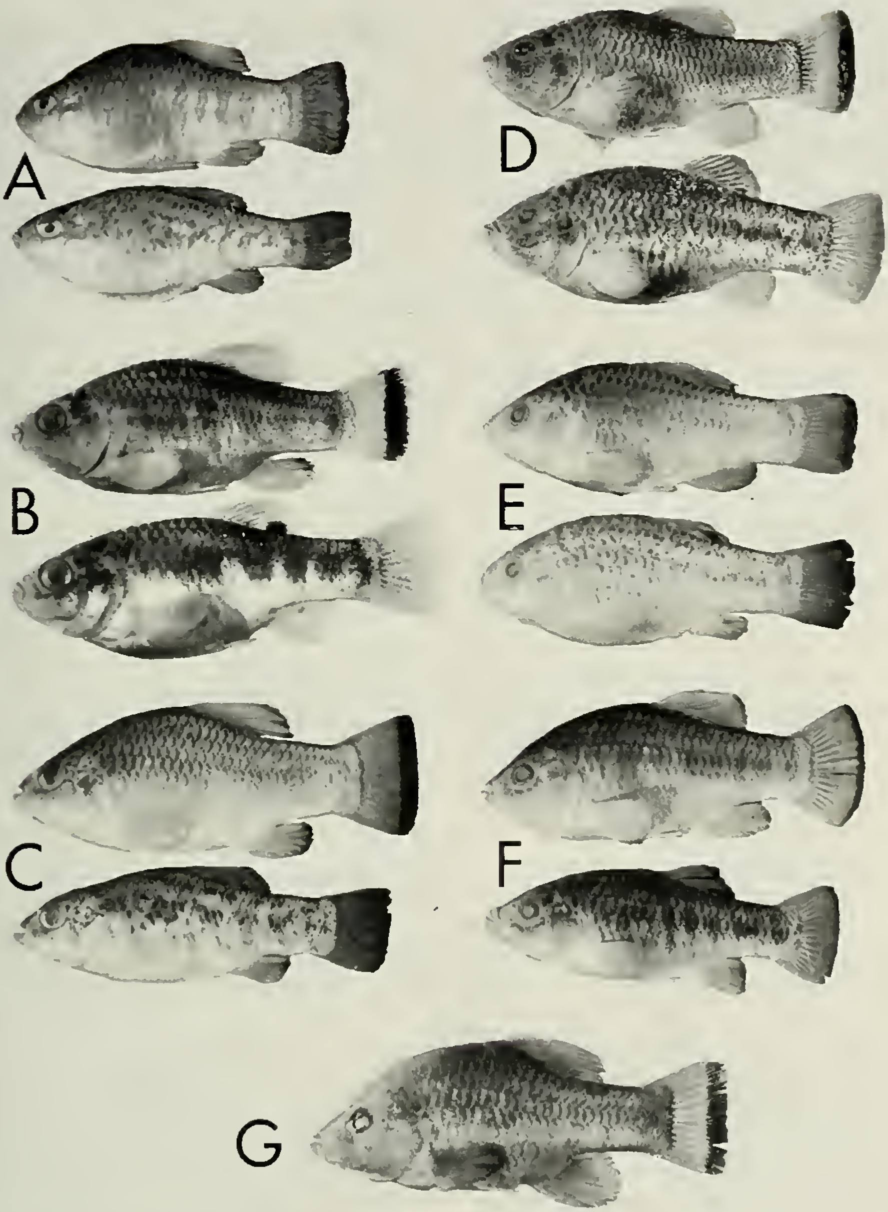

Figure 1. Seven species of *Cyprinodon* from México. A, *C. eximius*, Río Conchos at Jiménez, Chihuahua (FMNH 3556); nuptial male, 34.0, above, adult female, 34.4, below. B, *C. atrorus*, Laguna San Pablo, Cuatro Ciénegas bolsón, Coahuila (UMMZ 179846–47); nuptial male, 29.3, above, adult female, 31.8, below. C, *C. nazas*, new species, Río Nazas at San Miguel, Coahuila; male holotype (UMMZ 197419), 39.5, above, female paratopotype (UMMZ 196712), 36.3, below. D, *C. alvarezi*, new species, El Potosí, Nuevo León; male holotype (UMMZ 179638), 37.4, above, female paratopotype (UMMZ 179639), 40.3, below. E, *C. meeki*, new species, spring-fed pond near Durango City, Durango; male holotype (UMMZ 197420), 37.6, above, female paratopotype (UMMZ 166709), 37.6, below. F, *C. macrolepis*, new species, Ojo de la Hacienda Dolores, Chihuahua; male holotype (UMMZ 168982), 38.9, above, female paratopotype (UMMZ 168983), 36.4, below. G, *C. latifasciatus*, Parras, Coahuila; nuptial male lectotype (MCZ 37995), 37.3.

The members of the *Cyprinodon eximius* complex may be tentatively diagnosed by the following combination of traits: black or dark brown terminal bar on caudal fin of nuptial male broad, wider than pupil and occasionally as wide as eye (exceptions in *macrolepis* and *meeki*); gill rakers typically fewer than 20 on first gill arch, including all rudiments (*atrorus* and *latifasciatus* have 20–28, and *macrolepis* commonly has 20); dorsal fin of nuptial male yellow, orange, or amber (*latifasciatus*, *meeki*, and *alvarezi* are exceptions); mandibular pores lacking (except *alvarezi*, with 2, and *nazas*, with 0–2); cleithral process enlarged, its posterior margin extending beyond second scale of lateral series (exceptions in *atrorus*, *latifasciatus*, and *macrolepis*); pelvic fins modally with 6 rays (6 or 7 in *eximius* and *nazas*).

In addition, Liu (1970) has referred to data in his thesis indicating that there are differences in courtship behavior between this species complex and others in *Cyprinodon*. Those proportional measurements that show significant differences between the new species and *C. eximius* are given in Table 1, but to what extent these or other measurements may possibly characterize this complex has not been determined. All measurements are in millimeters.

Cyprinodon eximius Girard
Conchos pupfish
Figure 1A

Cyprinodon eximius Girard, 1859, Proc. Acad. Nat. Sci. Phila., 11: 158 (orig. descr., Chihuahua River = Río Chuviscar, at Chihuahua City, México).

Cyprinodon elegans (misidentification) Woolman, 1894, Bull. U. S. Fish Comm., 14 (1895): 59–60 (descr. of female of *eximius* separately from male, which was correctly identified as *eximius*; Río de los Conchos, Chihuahua City). Garman, 1895, Mem. Mus. Comp. Zool., 19 (1): 23–24 (Chihuahua material only). Meek, 1904, Field Colombian Mus. Publ. 93, Zool. Ser., 5: 125 (material from San Diego, Chihuahua, only). Jordan, Evermann, and Clark, 1930, Rept. U. S. Comm. Fish. for 1928, Pt. II: 181 (*eximius* wrongly synonymized with *elegans*).

Cyprinodon bovinus (misidentification) Regan, 1906–08, Biologia Centrali-Americana, 8: 84 (*eximius* wrongly synonymized with *bovinus*, which is restricted to Texas—see Echelle and Miller, 1974, Southwest. Nat., 19: 179–190, fig. 1). Fowler, 1916, Proc. Acad. Nat. Sci. Phila., 68: 429 (syntype of *eximius* listed in synonymy of *bovinus*). Buen, 1947, An. Inst. Biol. Méx., 18 (1): 277 (*eximius* synonymized with *C. b. bovinus*; records for Río Conchos and Río Sauz only).

Diagnosis.—Dorsal fin of nuptial male yellow to yellow-orange in life, the terminal black caudal-fin bar broad (much wider than pupil); basal one-half to two-thirds of caudal fin of adults with checkered pattern of prominent black spots and dashes on interradial membranes; gill rakers 12–18, usually 13–16 but 11–14 in Sauz basin; lateral scales usually 26 or 27, those around caudal peduncle 16; vertebrae usually 27 or 28; pelvic rays 6 or 7; mandibular pores consistently lacking; dorsal ocellus present in females and juveniles; cleithral process enlarged, its posterior margin extending beyond second scale in lateral series; first dorsal ray thickened, spine-like; branchiostegals 6.

Distribution.—This species inhabits the basin of Río Conchos, tributary to Rio Grande, that of the endorheic Río Sauz basin (see Minckley and Koehn, 1965), and the following Rio Grande tributaries that lie east of the mouth of Río Conchos: Alamito Creek, Presidio County, Texas; Río Alamo, Chihuahua, across from Alamito Creek (UMMZ 196768); Tornillo Creek, Brewster County, Texas (W. L. Minckley, collector); and Devil's River basin (including Dolan Creek), Val Verde County, Texas. Meek (1904, op. cit.: 125) erred in listing Jordan and Snyder's questionable record of *elegans* from Tampico lagoons as this species (it is *C. variegatus*); also, his records for San José and Ahumada pertain to an undescribed pupfish. *C. eximius* was also listed (Contreras-Balderas, 1969: 297) from Laguna de Bustillos, an endorheic basin west of Chihuahua City, but that record represents an undescribed species.

Distinctive populations occur in parts of the extensive range of this species (as in the Sauz-Encinillas basin, Rio Grande tributaries above Big Bend National Park, and Devil's River basin) but probably none of them is more than subspecifically distinct.

Cyprinodon atrorus Miller
Bolsón pupfish
Figure 1B

Cyprinodon atrorus Miller, 1968, Occas. Pap. Mus. Zool. Univ. Michigan 659: 7–12, fig. 2 (orig. descr., Cuatro Ciénegas bolsón, Coahuila, México).

Diagnosis.—Dorsal fin of nuptial male yellow to orange in life, the terminal black caudal-fin bar very broad (almost as wide as eye), the interradial membranes of rest of fin free of melanophores in both sexes; mandibular and lacrimal head pores lacking and preopercular pores usually only 3–6 (typically 4); female and juvenile with well-developed ocellus on both dorsal and anal fins; pelvic with 6 rays, fin not reaching beyond anal origin in either sex; gill rakers 20–25; branchiostegals 5, rarely 6; lateral scales 25 or 26, those around caudal peduncle 16; vertebrae 26 or 27; cleithral process moderately enlarged; first dorsal ray not notably different from second.

TABLE 1. Proportional measurements in permillage of standard length in five Mexican species of *Cyprinodon.*

Measurement	*C. eximius*[1]		*C. macrolepis*[2]		*C. alvarezi*[3]		*C. nazas*[4]		*C. meeki*[5]	
	11 ♂	10 ♀	10 ♂	10 ♀	10 ♂	10 ♀	10 ♂	10 ♀	10 ♂	10 ♀
Standard length	28.1–39.8 (34.2)	26.7–38.5 (32.1)	27.5–41.4 (33.9)	26.4–37.0 (32.2)	26.6–41.1 (35.4)	25.6–39.5 (33.5)	26.8–40.6 (34.1)	25.6–39.9 (33.4)	26.3–41.9 (33.5)	25.5–38.9 (33.5)
Predorsal length	548–601 (570)	553–590 (567)	569–625 (593)	584–616 (606)	559–596 (577)	574–598 (585)	540–583 (553)	543–576 (555)	548–578 (566)	565–602 (584)
Anal origin to caudal base	370–408 (390)	351–375 (363)	370–393 (379)	330–351 (343)	341–387 (370)	344–375 (357)	372–421 (393)	354–391 (370)	383–411 (398)	353–382 (368)
Body depth	445–500 (473)	378–481 (426)	393–456 (427)	362–440 (388)	390–474 (435)	383–445 (409)	384–461 (427)	367–406 (389)	414–480 (446)	396–457 (430)
Head depth	306–335 (327)	306–331 (320)	333–359 (345)	312–326 (319)	338–357 (348)	305–374 (330)	324–363 (343)	305–330 (320)	354–388 (368)	337–386 (362)
Caudal-peduncle length	256–274 (265)	234–262 (247)	239–257 (249)	230–249 (237)	232–271 (254)	227–254 (241)	243–271 (260)	227–270 (255)	261–288 (272)	241–262 (254)
Interorbital, bony width	116–130 (123)	113–123 (119)	137–154 (143)	137–151 (146)	111–130 (120)	112–125 (119)	108–125 (116)	106–120 (113)	120–132 (124)	116–129 (122)
Mouth width	113–126 (119)	112–124 (118)	119–137 (126)	126–143 (132)	110–124 (116)	109–134 (120)	104–121 (112)	105–120 (112)	103–128 (116)	115–137 (125)
Mandible length	98–117 (107)	99–111 (106)	85–114 (101)	87–105 (91)	107–124 (114)	109–122 (114)	95–103 (99)	93–102 (97)	85–111 (101)	97–109 (104)
Dorsal fin, basal length	192–235 (217)	189–228 (204)	191–221 (206)	170–197 (185)	185–225 (203)	158–203 (187)	203–253 (224)	181–209 (201)	167–212 (187)	144–181 (168)
Depressed length	305–370 (340)	277–310 (293)	287–342 (313)	252–289 (266)	277–320 (298)	257–284 (271)	317–379 (337)	268–291 (284)	289–346 (313)	229–273 (256)
Pectoral length	244–271 (259)	234–261 (249)	234–253 (241)	203–227 (213)	212–238 (224)	204–239 (218)	245–274 (260)	232–258 (243)	224–251 (236)	226–248 (235)
Pelvic length	121–136 (131)	113–122 (118)	91–113 (100)	72–93 (85)	90–109 (98)	86–103 (93)	116–127 (122)	98–123 (111)	106–123 (117)	103–111 (107)

[1] FMNH 3556, Jiménez, Chihuahua.
[2] UMMZ 168982, 168983.
[3] UMMZ 179638, 179639, 189021.
[4] UMMZ 197419, 196712.
[5] UMMZ 197420, 166709.

Distribution.—Restricted to the bolsón of Cuatro Ciénegas, Coahuila, México (see Minckley, 1969).

Cyprinodon latifasciatus Garman
Parras pupfish
Figure 1G

Cyprinodon latifasciatus Garman, 1881, Bull. Mus. Comp. Zool., 8 (3): 92 (orig. descr., spring near Parras, Coahuila, México). Miller, 1964, Southwest. Nat., 9 (2): 62–67 (species redescribed and figured; synonymy).

Cyprinodon bovinus latifasciatus (misidentification) Buen, 1947, An. Inst. Biol. Méx., 18 (1): 277 (synonymized with *bovinus*; Parras record only).

Diagnosis.—Dorsal fin of nuptial male dusky, probably not yellow in life (species extinct), the terminal black caudal-fin bar very broad (much wider than pupil), the interradial membranes of remainder of fin clear in both sexes; male with broad, dark lateral stripe from behind eye to base of caudal fin, set off above by a much narrower silvery band (turquoise in life?) and below by a broader yellowish stripe beneath which is a less distinct brownish stripe about same width as dorsal counterpart; female similar in body color pattern; no dorsal ocellus in either sex; pelvic fins small, 6-rayed, not reaching origin of anal fin; gill rakers 22–28; cleithral process little enlarged, not extending beyond posterior margin of second scale in lateral series; mandibular pores lacking; branchiostegals 5; first dorsal ray thickened.

Distribution.—Known only from the Parras basin, Coahuila, México, where now extinct.

Cyprinodon nazas, new species
Nazas pupfish
Figure 1C

Cyprinodon latifasciatus (misidentification) Meek, 1904, op. cit.: 126–127 (reference to Río Nazas, as part of range, only).

Diagnosis.—Dorsal fin of nuptial male yellow, yellow-orange, or amber in life, the terminal black caudal-fin bar broad (wider than pupil), the interradial membranes of remainder of fin clear in both sexes; gill rakers 12–16, rarely 17; mandibular pores irregularly developed, 0–2; scales around caudal peduncle 16–20, and around body 28–38, usually 30–36; cleithral process enlarged and thickened, its posterior margin extending beyond posterior border of second scale in lateral series; first dorsal ray thickened, spine-like; lacrimal pores typically 4; ocellus on dorsal fin of female and juvenile weak to lacking; brachiostegals 6.

Holotype.—UMMZ 197419, a nuptial male 39.5 mm in standard length (SL) from Río Nazas near its mouth at San Miguel, 7 km SSE of San Pedro de las Colonias, near edge of Laguna Mayrán, Coahuila, salinity 8.2 ppt, elev. 1,093 m; collected by R. R. and F. H. Miller, 23 March 1974. There are 207 juvenile to adult paratopotypes, UMMZ 196712, 14–46 mm SL, taken with the holotype. Additional paratypes are: UMMZ 166707, 175 young to adult, 18–37 mm, and CAS 33902, 394 from same collection, Río del Peñon del Covadonga at La Concha, 8 km SW of Peñon Blanco, Durango (elev. 1,730 m); TU 30616, 26 young to adult, 12.5–33 mm, from same stream ca. 3.2 km E of Peñon Blanco; CAS 33903, 6, 22–46 mm from Peñon Blanco; UMMZ 161674, 124 juvenile to adult, 24–45 mm, Río Trujillo (locally Río Florido), 1.6 km W of Rancho Grande, Zacatecas (trib. Río Aguanaval); USNM 132618, 5 adults, 29–38.5 mm, Río Nazas, 24 km SW of Lerdo, Durango.

Fin rays: dorsal 10–12, usually 10 or 11; anal 9–11, usually 10; pectoral 15–17, usually 16; pelvic 6–7, rarely 5; caudal 16–19, usually 16 or 17. Lateral scales 25–27, usually 26; dorsal to anal 12–14, usually 13; around caudal peduncle 16–20, usually 20 but frequently 18 or 19; around body, 28–38, usually 34–36 except in the Santiaguillo basin (see below). Gill rakers 12–17, frequently 14. Vertebrae (total, including hypural complex as one) 26–28, typically 27. Head pores: mandibular 0–2, frequently 0, usually 2; lacrimal 2–5, typically 4; preopercular 6–10, typically 7. Branchiostegals 6.

Measurements of holotype in thousandths of standard length: predorsal length 562, prepelvic length 557, preanal length 681, anal origin to caudal base 405, dorsal origin to caudal base 532, body depth 458, body width 251, head length 327, head width 251, head depth 357, caudal-peduncle length 271, caudal-peduncle depth 215, bony-interorbital width 114, snout length 101, orbit length 86, mouth width 114, mandible length 99, depressed-dorsal length 354, basal length of dorsal 233, depressed-anal length 258, basal length of anal 139, length middle caudal rays 238, pectoral length 256, basal width of pectoral 99, pelvic length 122.

Distribution.—This species occurs in the basin of Río Nazas, including that of Río Aguanaval which evidently joined the Nazas in Laguna Mayrán within historic time, and in the endorheic basin of Laguna Santiaguillo, about 75 km N of Durango City. (See Fig. 1 in Conant, 1963.)

The population of *C. nazas* inhabiting the Santiaguillo basin is probably worthy of subspecific recognition, in part on the basis of fewer scales around the caudal peduncle (usually 16) and around the body (usually 30–32).

Cyprinodon alvarezi, new species
Potosí pupfish
Figure 1D

Cyprinodon sp. Miller and Walters, 1972, Contrib. Sci. Nat. Hist. Mus. Los Angeles Co., 233 (habitat, size frequency, feeding habits, relative abundance, relationship to *C. eximius*).

Diagnosis.—Dorsal fin of nuptial male white or milky or bluish white, the terminal black caudal-fin bar broad, wider than pupil, the interradial membranes of rest of fin immaculate in both sexes; body of breeding male typically without vertical bars; mandible long, the lower jaw prominent; pelvic fin reduced; lateral scales 24–26, usually 25; gill rakers 16–20, typically 17–19; vertebrae 26–27, predominantly 26; mandibular pores consistently 2; branchiostegal rays 5 or 6; scales around caudal peduncle 14–16, typically 16, and around body 30–34, usually 32; cleithral process enlarged, its posterior margin extending beyond posterior border of second scale in lateral series; first dorsal ray not notably different from second ray; lacrimal pores 2–5, typically 4; ocellus on dorsal fin well developed in female and juvenile (small males up to at least 37 mm SL may have remnant of ocellus).

Holotype.—UMMZ 179638, an adult male 37.4 mm SL from spring-fed pond at El Potosí, Nuevo León, 18 km N of jct of highways 31 and 57 and 3.5 km E of hwy 57, 24° 51′ N lat, 100° 19′ W long, elev. 1,900 m; collected by R. R. Miller and H. L. Huddle, 23 February 1961. There are 314 young to adult paratopotypes, UMMZ 179639, 11–58 mm, taken with the holotype. An additional 244 paratypes, ENCB P. 890 (27), 13–34, and UMMZ 189021 (217), 14–59 mm, were obtained from the type locality.

Fin rays: dorsal 10–12, usually 10 or 11; anal 9–11, usually 10; pectoral 13–17, usually 15 or 16; pelvic 5–7, typically 6; caudal 16–20, usually 17–19. Lateral scales 24–26, predominately 25; dorsal to anal 10–12, usually 11 or 12; around caudal peduncle 14–16, predominantly 16; around body 30–34, typically 32. Gill rakers 16–20, usually 17–19. Vertebrae 26 or 27, predominantly 26. Head pores: mandibular invariably 2; lacrimal 2–5, usually 4, frequently 3; preopercular 6–8, predominantly 7. Branchiostegals 5 or 6, predominantly 5.

Measurements of holotype in thousandths of standard length: predorsal length 559, prepelvic length 586, preanal length 698, anal origin to caudal base 374, dorsal origin to caudal base 503, body depth 441, body width 238, head length 337, head width 243, head depth 350, caudal-peduncle length 251, caudal-peduncle depth 211, bony-interorbital width 120, snout length 104, orbit length 94, mouth width 118, mandible length 115, depressed-dorsal length 307, basal length of dorsal 211, depressed-anal length 246, basal length of anal 134, length middle caudal rays 246, pectoral length 238, basal width of pectoral 99, pelvic length 102.

Distribution.—This species is known only from the isolated spring at El Potosí, Nuevo León (see Miller and Walters, 1972: Fig. 5), where it is now rare owing to the introduction of largemouth bass in 1974.

It is a pleasure to name this pupfish for my friend José Alvarez del Villar who collected this species in 1952 and had intended to describe it but turned over the study to me. His contributions to Mexican ichthyology span a period of 30 years.

Cyprinodon meeki, new species
Mezquital pupfish
Figure 1E

Cyprinodon latifasciatus (misidentification) Meek, 1904, op. cit.: xxxvii, 126 (material from Labor and Durango, in Río Mezquital basin).

Cyprinodon bovinus (misidentification) Regan, 1906–08, op. cit.: 83–84 (material from Labor and Durango only).

Cyprinodon bovinus latifasciatus (misidentification) Buen, 1947, An. Inst. Biol. Méx., 18 (1): 277 (synonymized with *bovinus*; Río Mezquital material only).

Diagnosis.—Dorsal fin of nuptial male dark dusky (not yellow) in life, becoming blackish sometimes distally and sometimes basally, the terminal black caudal-fin bar narrow (width subequal to or less than diameter of pupil, more than 1.5 in orbit); vertical bars nowhere evident in either young or adult, the general color tone dark; body of female much spotted, the spots small and forming lengthwise rows between or along the scale rows (spots often more or less fused to form an axial stripe); ocellus of dorsal fin of adult female large and constantly present, a moderate to weak ocellus often present also on anal fin; outline of body more rounded than in the other species; gill rakers 12–15; lateral scales usually 25, those around body usually 26, and around caudal peduncle typically 16; mandibular pores consistently lacking; lacrimal pores usually lacking; cleithral process enlarged (as in *eximius* and *nazas*).

Holotype.—UMMZ 197420, a nuptial male 37.6 mm SL, from a pond fed by hot springs, tributary to Río del Tunal, about 9 km E of Durango City, Durango, México, elev. about 1,880 m; collected by S. H. Weitzman and J. D. Lattin, 3 August 1952 (pond 20.5°C, hot springs 29.5°C). There are 258 juvenile to adult paratopotypes (UMMZ 166709, 89; CAS 33901, 169), 11–44 mm, taken with the holotype. The following are designated as paratypes: UMMZ 167727 (13), UMMZ 196789 (4), and FMNH 9076 (5), 15–53 mm, Río de la Sauceda at or near Labor, 12.8 km NE of Durango City; UMMZ 179649 (1), 31, warm spring near type locality; UMMZ 192458 (96), 14–40, Río de la Sauceda, 22 km N of Durango City just below dam; FMNH 4388 (68), 23–35, Río del Tunal at Durango City; and CAS 33899 (27), 17–37, Río Canatlán, 17 km N of Durango City, Durango.

Fin rays: dorsal 8–11, usually 9 or 10; anal 9–11, usually 10; pectoral 13–16, usually 15 but frequently 14; pelvic 6 or 7, predominantly 6; caudal 15–18, usually 16. Lateral scales 24–26, typically 25; dorsal to anal 9–11, usually 10 or 11; around caudal peduncle 14–16, predominantly 16; around body 24–28, usually 26. Gill rakers 12–15, typically 14. Vertebrae 26 or 27. Head pores: mandibular consistently lacking; lacrimal 0–5, usually 0; preopercular 6–8, usually 7. Branchiostegals 6.

Measurements of holotype in thousandths of standard length: predorsal length 561, prepelvic length 566, preanal length 678, anal origin to caudal base 383, dorsal origin to caudal base 529, body depth 439, body width 245, head length 332, head width 242, head depth 383, caudal-peduncle length 261, caudal-peduncle depth 218, bony-interorbital width 122, snout length 101, orbit length 88, mouth width 120, mandible length 90, depressed-dorsal length 319, basal length of dorsal 199, depressed-anal length 253, basal length of anal 120, length middle caudal rays 226, pectoral length 242, basal width of pectoral 90, pelvic length 117.

Distribution.—This species is confined to the upper part of the Río Mezquital drainage (Río del Tunal and Río de la Sauceda—see map in Conant, 1963), a Pacific-slope stream near Durango City, Durango, México.

The Mezquital pupfish is named for Seth Eugene Meek who 75 years ago pioneered in exploring the Mexican freshwater fish fauna (Miller, 1976a).

Cyprinodon macrolepis, new species
Largescale pupfish
Figure 1F

Cyprinodon sp. ("probably new") Hubbs and Springer, 1957, Texas J. Sci., 9(3): 314 (descr. of spring and outlet).

Diagnosis.—Dorsal fin of nuptial male yellow on outer half, the terminal caudal-fin bar narrow (width less than diameter of pupil), and remainder of caudal fin without pigment on interradial membranes in both sexes; lateral scales 23 or 24 (fewer even than those of the dwarf hot-spring species, *C. diabolis*, which usually has 24 or 25), those around body 24 or 26, and around caudal peduncle 14 or 16; vertebrae typically 25; gill rakers 17–22; mandibular pores consistently lacking; lacrimal pores irregular, 0–6; cleithral process only moderately enlarged; branchiostegals 6.

Holotype.—UMMZ 168982, a nuptial male 38.9 mm SL, from El Ojo de la Hacienda Dolores, a hot spring (winter–summer temperature variation 29°–33°C) 12.5 km SSW of Jiménez, Chihuahua, México, elev. 1,405 m; collected by Clark Hubbs and Victor G. Springer, 30 June 1954; salinity 0.5 ppt. There are 135 young to adult paratopotypes, 12–43 mm, UMMZ 168983, taken with the holotype. The following are paratypes: UMMZ 168981, 40, 17–40 mm, from an irrigation ditch 1.6 km N of the type locality; and UMMZ 196736, 789, 12–40 mm, from the type locality.

Fin rays: dorsal 10 or 11, usually 10; anal 9–11, usually 10; pectoral 14–17, usually 15 or 16; pelvic 0–7, usually 6; caudal 15–19, usually 16 or 17. Lateral scales 23 or 24; dorsal to anal 9 or 10; around caudal peduncle 13–16, usually 14 or 16; around body 24–26, usually 24 or 26. Gill rakers 17–22, usually 19 or 20. Vertebrae 24–26, usually 25. Head pores: mandibular invariably 0; lacrimal 0–6, 0, 2, 4 or 5; preopercular 5–8, usually 6. Branchiostegals 6, rarely 5.

Measurements of holotype in thousandths of standard length: predorsal length 586, prepelvic length 571, preanal length 684, anal origin to caudal base 378, dorsal origin to caudal base 506, body depth 437, body width 229, head length 345, head width 242, head depth 345, caudal-peduncle length 249, caudal-peduncle depth 211, bony-interorbital width 141, snout length 118, orbit length 87, mouth width 123, mandible length 93, depressed-dorsal length 316, basal length of dorsal 206, depressed-anal length 247, basal length of anal 131, length middle caudal rays 219, pectoral length 234, basal width of pectoral 98, pelvic length 103.

Distribution.—This species is confined to the large spring-fed pool (tadpole-shaped, 50 m wide at head and ca. 80 m to where it narrows) and its outflows 12.5 km by road south-southwest of Jiménez (see Hubbs and Springer, op. cit.: Fig. 9). Although this spring outflow no doubt once connected with the adjacent Río Florido (of the Río Conchos basin), the pupfish found there (at Jiménez, Fig. 1 herein) is clearly a very different species from this one.

The name *macrolepis* refers to the large scales, so distinctive of this pupfish.

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I am grateful to Carl L. Hubbs for help and encouragement in my studies of *Cyprinodon*. José Alvarez del Villar called my attention to a locality (El Potosí) that yielded a new genus as well as the new species of *Cyprinodon* named for him. My wife, Frances, recorded and calculated all of the data and typed most of the manuscript. The following provided specimens, notes, or assisted in the field: Arthur A. and J. Ray Alcorn, Clyde D. Barbour, Martin R. Brittan, William H. Brown, James E. Böhlke, Salvador Contreras-Balderas, William N. Eschmeyer, John T. Greenbank, Clark Hubbs, Howard L. Huddle, James F. LaBounty, Robert K. Liu, Victor G. Springer, R. Kirk Strawn, R. D. Suttkus, Stanley H. Weitzman, and Loren P. Woods. Mexican officials graciously permitted me to collect fishes in their country. My field work was generously supported by the National Science Foundation (G-12904, GB-6272X, BMS72-02378) and the John Simon Guggenheim Memorial Foundation. Louis P. Martonyi, William L. Cristanelli, and David Bay took the photographs.

Abbreviations used are: CAS (California Academy of Sciences), ENCB (Escuela Nacional de Ciencias Biologicas, Mexico City), FMNH (Field Museum of Natural History), TU (Tulane University), UMMZ (University of Michigan Museum of Zoology), UNL (Universidad Autónoma de Nuevo León, Monterrey), and USNM (National Museum of Natural History).

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VERTEBRAL VARIATION IN THE EMERALD SHINER *NOTROPIS ATHERINOIDES* FROM THE OHIO RIVER: AN APPARENT CONTRADICTION TO "JORDAN'S RULE"

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Daryl E. Jennings[4], and Louis A. Krumholz[3]

Abstract: Vertebral numbers of the emerald shiner *Notropis atherinoides* collected from approximately 100-mile intervals of the Ohio River during 1957–1959 were analyzed using x-rays. Counts ranged from 36 to 42 with an overall mean of 39.58 vertebrae. There was a consistent gradual cline in numbers of vertebrae with significant differences in mean numbers. Numbers were smallest near the source and largest near the mouth of the river. This is a reversal of the usual trend of greater numbers of vertebrae at higher latitudes, but it may be consistent with Jordan's Rule in that habitats in the upper (more northerly) reaches of the river may warm more quickly, and embryonic development may proceed there at higher temperatures than in the lower reaches.

This paper is concerned with what appears to be an exception to "Jordan's Rule." The numbers of vertebrae in the emerald shiner, *Notropis atherinoides*, are consistently smaller in samples of that species taken from the upper end of the Ohio River near Pittsburgh, Pennsylvania, than in samples nearly 1,000 miles downstream near Cairo, Illinois. *Notropis atherinoides* was chosen for this study because: (1) it is the most abundant fish species in the Ohio River where it made up 57.8 percent of the total catch of 741,438 specimens in 341 collections throughout the length of the stream in 1957–1959 (Krumholz, et al., 1962); (2) it usually is present in large numbers at all locations; (3) several thousand specimens representing most areas of the river were preserved for later studies; and (4) there is a considerable body of literature on the biology of the species (Hubbs, 1922; Bailey and Allum, 1962; Flittner, 1964, unpubl. doctoral dissertation, Univ. Michigan, Ann Arbor, Michigan; Fuchs, 1967; Campbell and MacCrimmon, 1970; and others) that allows for comparison of our data with those of others.

In a paper presented to the Indiana Academy of Science in 1866 but not published, Jordan (1891:107–110) pointed out that in many families of fishes "the number of vertebrae decreases as we approach the tropics. So constant is this relation that it was thought that it might almost be termed a law." However, Jordan could not suggest "adequate cause by the operation of which such changes are brought about. . . . If the causes producing this change are still in operation, we should naturally expect that in cold water, deep water, dark water, fresh waters, and in waters of past geological epochs the process would be less complete and the numbers of vertebrae would be larger." Also, Jordan (1891:107, 109) emphasized that this generalization was first formulated by Theodore N. Gill, and that it was Gill (1864) who showed that "This generalization is applicable to the representatives of Acanthopterygian [spiny-rayed] families generally, and can be considered in connection with the predominance of true Malacopterygian [soft-rayed; here including the Anacanthine fishes] fishes in northern waters, fishes in which the increase in the number of vertebrae is a normal feature." Later, Gill (1889) claimed quite properly that the first statement of this generalization belonged to him and not to Günther (1862) who noted the phenomenon only among the Labridae (Jordan, 1891:109, 110). At the same time, Gill (1889:605) wrote "But while claiming the generalization that there is a correlation between the increase of vertebrae and the increase of latitude among fishes generally, I would not assign to it an undue value or claim for it the dignity of a law. It is simply the expression of a fact which has no cause for its being now known, if it shall ever be known. It may also be added that the generalization is true only in a general sense." Thus, what has come to be known

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as "Jordan's Rule" was formulated by Gill some quarter of a century earlier, but Gill did not consider it important enough to qualify as a law.

From those publications, it is obvious that "Jordan's Rule" applies to the increased numbers of vertebrae in cold water or northern representatives of certain groups of fishes. It should not be confused with "Jordan's Law" as proposed by Allen (1877) (see Mayr, 1963:487), that closely related forms such as species and subspecies occur in adjacent areas.

The phenomenon of variation in vertebral numbers and other meristic characters related to water temperatures and other environmental factors during the developmental stages of fishes has come under lengthy analysis and critical review by Hubbs (1922, 1926), Gabriel (1944), Tåning (1952), Seymour (1959), Barlow (1961), Fowler (1970), Lindsey and Harrington (1972), Ali and Lindsey (1974), and others. Hubbs (1922, 1926) suggested that such variations could result from the cooler, northern waters providing longer periods of embryonic development which, in turn, allowed for the creation of meristic elements in greater numbers. In his 1922 paper, Hubbs indicated a likelihood of differences in numbers of vertebrae even between year classes of the emerald shiner and the bluegill *Lepomis incisor* (= *macrochirus*) in the same populations in the Chicago, Illinois, region based on data collected in 1919. In his experiments with herring *Clupea harengus* and killifish *Fundulus heteroclitus*, Gabriel (1944) reported that mean numbers of vertebrae were higher at lower temperatures and were lower at high temperatures, and that myotome counts plotted against temperatures during development yielded a straight line with the higher counts at lower temperatures. He also stated (1944:140) that in laboratory reared killifish "taking populations as a whole, high parental vertebral numbers are associated with high numbers in the offspring, and low parental numbers are associated with low counts in the offspring, so that some degree of genetic control is indicated."

Tåning (1952), in a comprehensive study of the sea trout *Salmo trutta trutta*, reported that the numbers of vertebrae were lowest at 6 C while the value increased with both lower and higher temperatures, giving a V-shaped curve, and that the affected developmental periods may be prior to or immediately after hatching, depending on the species under study. He also reported that the plastic period for vertebral formation was early in ontogeny, long before the egg hatched, and that the number of vertebrae begins to be determined during gastrulation. He found that a change of 6 C during the "supersensitive period" produced a difference of about 1.5 vertebrae in siblings.

Lindsey (1954) found that newly hatched young of paradise fish *Macropodus opercularis* maintained at an intermediate temperature produced significantly fewer vertebrae than those maintained at either higher or lower temperatures, thus corroborating Tåning's finding of a V-shaped curve. Lindsey also reported that although the eggs hatched less than two days after fertilization, the numbers of caudal vertebrae were subject to environmental change as late as 13 days after fertilization. Bailey and Gosline (1955) reported that within any single species of American percid fish "there seems to be something of a southwest to northeast increase in vertebral number. Superimposed on this weak gradient there is a more consistent trend within any one area for the fishes at higher altitude to have more vertebrae."

Seymour (1959) pointed out some inconsistencies of findings in laboratory experiments to determine the effects of temperature on vertebral numbers, and reported V-shaped curves in numbers of vertebrae in young chinook salmon *Oncorhynchus tsawytsch* (sic) where numbers were smaller in lots reared at temperatures in the middle portion of the 39 to 62 F range than for lots at either extreme. Seymour's findings corroborated those of Tåning (1952) and Lindsey (1954). Seymour also reported that water of low oxygen content during early embryological development increased the numbers of vertebrae and that the plastic period for the formation of vertebrae begins before the midpoint of the egg stage. Barlow (1961), in his review of the causes and significance of morphological variations in fishes, suggested that different factors in the environment, such as temperature, salinity, and oxygen may control the rate of development. He also noted that "Disagreements in findings from the field and from the laboratory may result from the monotonous, uniform conditions in the laboratory, an unnatural and possibly harmful situation."

In a quite different vein, Uyeno and Miller (1962) noted that the fossil cyprinodontid fish *Empetrichthys erdisi* is distinguished readily from Recent forms of that genus by having smaller scales and more vertebrae. That confirms, to a certain extent, Jordan's (1891) suggestion that fishes of past geological ages had larger numbers of vertebrae.

Garside (1966:1544) after various experiments with salmonids and a study of the literature, re-

Figure 1. Map of the Ohio River from its origin at Pittsburgh, Pennsylvania, to its confluence with the Mississippi River at Cairo, Illinois. *0* through *10* indicate locations where fish were collected.

ported that the information available led "to the generalization that levels of constituent factors in the environment which have a retarding effect on the rate of development, thereby protracting the period of development, are associated with increased numbers of vertebrae while those factors which accelerate development are associated with reduced numbers of vertebrae as stated by Hubbs." He stated also that the generalization might be refined by determining the period of time required for differentiation of vertebrae.

MacCrimmon and Kwain (1969) reported that the "mortality, time of hatch, metabolic rate, and number of vertebrae formed correlated positively with visible light intensity but only during the pre-eyed stage of incubation" in the rainbow trout *Salmo gairdneri.* By contrast, they found that "the numbers of dorsal and anal fin rays were affected by light intensity during the posteyed incubation period, the greatest number of rays on these fins occurring in fish incubated at light intensity of 10 lux."

Fowler (1970) made a comprehensive review of factors that control meristic characters in teleosts and other vertebrates. He considered such factors as genetics, temperature, light, salinity, and dissolved oxygen in the development of fishes and reported that each factor or combinations of two or more factors may affect the formation of somites.

Lindsey and Harrington (1972), working with *Rivulus marmoratus,* noted that the "response of the 15 species studied experimentally include about equal numbers with continuous vertebral decline at higher temperatures and with U-shaped curves." Ali and Lindsey (1974:960) came to the conclusion, after carefully scrutinizing the reports given in the literature, that "distressingly few generalizations have emerged which enable one to predict, let alone explain, meristic responses to environmental stimuli. One reason is the great divergence of the species and meristic series which have been studied and the experimental protocols followed; so few aspects of published experiments have been comparable that any hypothesis must be highly speculative."

From those studies, and the many others referred to by their authors, it is quite obvious that the numbers of vertebrae and other meristic characters in a developing fish may be influenced by

TABLE 1. Locations and dates of collections of *Notropis atherinoides* (Krumholz, et al., 1962) together with the numbers of specimens in the sample used in this study, the numbers of individuals in the original collections, and the catalog numbers of the collections in the Univ. Louisville fish collection.

Location	Locality	O. R. Mile	Date	No. in sample	No. in collection	Collection No.
0	Allegheny Co, Pa.					
	Emsworth Lock and Dam	6.2	29 Jul 1958	100	255	10197
1	Ohio Co, W. Va.					
	Mouth of Wheeling Creek, W. Va.	90.7	15 Aug 1958	100	656	10940
2	Wood Co, W. Va.					
	Lock and Dam No. 20	202.5	18 Jun 1958	100	545	10172
3	Cabell Co, W. Va.					
	Lock and Dam No. 27	301.0	17 Jun 1958	100	144	10171
4	Lewis Co, Ky.					
	Lock and Dam No. 32	382.6	28 May 1957	100	562	7302
5	Boone Co, Ky.					
	Lock and Dam No. 37	483.2	29 May 1957	97	78	7331
	Lock and Dam No. 38	503.3	25 Jun 1958		89	12614
6	Jefferson Co, Ky.					
	Lock and Dam No. 41	606.8	17 Aug 1958	99	391	10654
7	Meade Co, Ky.					
	Mouth of Big Blue River, Ind.	662.9	15 Aug 1957	94	135	8755
8	Henderson Co, Ky.					
	Lock and Dam No. 1, Green River, Ky.	784.0	9 Jul 1957	72	37	7531
	Henderson Island, seining	806.0	2 Sep 1958	–	60	10429
9	Crittenden Co, Ky.					
	Backwater at Lock and Dam No. 50	876.8	26 Jun 1957	100	233	7389B
10	Ballard Co, Ky.					
	Mouth of Cache R., Ill.	974.7	25 Aug 1959	76	154	11376

a wide variety of environmental factors. It is also apparent that it is most difficult for laboratory studies to simulate in a precise manner the natural conditions under which the wild fish egg hatches and develops. Still, there is irrefutable evidence to support Hubbs' (1922) suggestion that retarded development caused by lower water temperatures gives rise to greater numbers of vertebrae.

METHODS

The specimens used in this study were collected from the Ohio River during 1957–1959 as part of an assessment of the fish population by the University of Louisville under the sponsorship of the Ohio River Valley Water Sanitation Commission (Krumholz, et al., 1962). Of the 341 collections during that study, 225 were taken with emulsifiable rotenone from navigation lock chambers, mouths of streams tributary to the Ohio River, or from backwater areas behind guide walls at lock and dam facilities. The remaining collections were made with seines, trawls, electrofishing gear, or hoopnets. The specimens used here were from 11 locations at approximate 100-mile (161-km) intervals over the entire length of the river (Fig. 1). Sample locations were numbered 0–10 consecutively from the source to the mouth of the river (Table 1). Distances between locations ranged from 56.1 to 123.3 miles (90.3–198.5 km).

Whenever possible, 100 specimens were selected from a single collection on the basis of size and quality of preservation without regard to age or sex. Since Flittner (unpubl. doctoral dissertation)

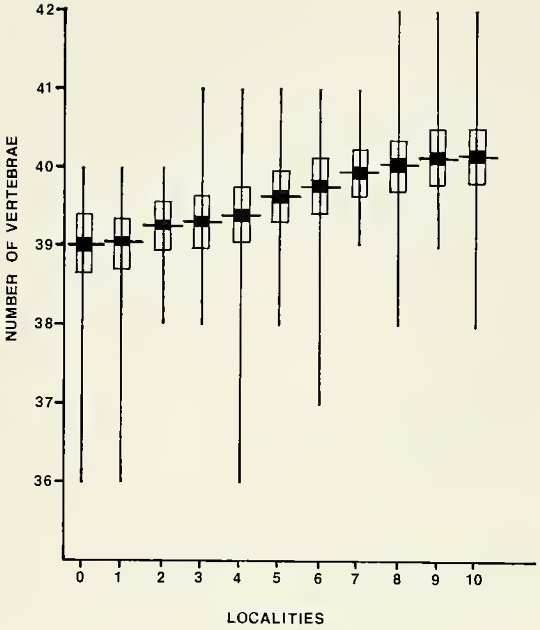

Figure 2. Numbers of vertebrae of the emerald shiner *Notropis atherinoides* at approximate 100-mile intervals in the Ohio River. Locations of collecting sites are shown in Figure 1 and described in Table 1. Vertical lines are ranges, horizontal lines are means, dark rectangles are two times the standard error of the means, and large open rectangles are one standard deviation (Modified from Hubbs and Perlmutter, 1942).

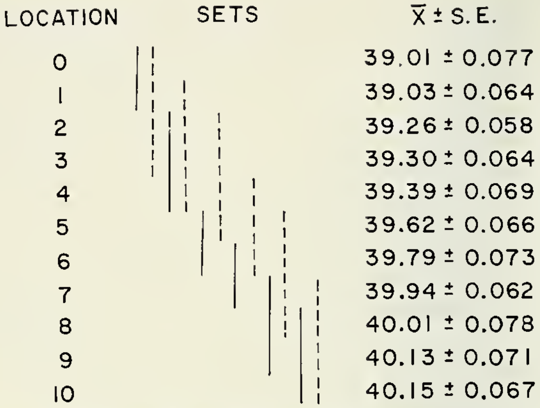

Figure 3. Mean, plus or minus the standard error of the mean, and the significance of the standard error for *Notropis atherinoides* from 11 locations in the Ohio River from its source (Location 0) to its mouth (Location 10). Collections not encompassed by the same lines are significantly different at the P = 0.05 level. Solid lines represent sets determined using Duncan's multiple range test; broken lines represent sets determined using the sum of squares simultaneous test procedure.

and Campbell and MacCrimmon (1970) reported no differences in vertebral numbers between sexes, we selected larger specimens to provide better subjects for x-ray photography. Our selection of specimens precluded any obviously deformed or poorly preserved individuals. Nine of the samples (Table 1) were from single collections and two were composed of representatives from two collections near each other.

X-ray photographs were taken using Kodak® Type A industrial x-ray film. Counts of vertebrae were made following the procedures of Bailey and Gosline (1955) with the weberian apparatus being counted as the first four vertebrae and the urostyle being included. Only 10 of the 1,038 photographed specimens were so anomalous or the pictures so unclear that accurate counts could not be made.

Statistical analyses follow Snedecor and Cochran (1967) and were compiled on an IBM 360-A computer. Means and standard deviations were calculated from the frequency distribution (Table 2). Means, ranges, standard deviations, and two times the standard error of the means were plotted (Fig. 2) using the methods of Hubbs and Perlmutter (1942) and Hubbs and Hubbs (1953). Analysis of variance, Power's (1970) modification of Gabriel's (1964) sum of squares simultaneous test procedure, and Duncan's multiple range test as modified to unequal numbers of replications (Kramer, 1956) were calculated (Fig. 3).

The Ohio River is formed by the confluence of the Allegheny and Monongahela rivers at Pittsburgh, Pennsylvania, at about 40° 25′ N latitude and flows southwesterly for 981 miles (1,580 km) and enters the Mississippi River at Cairo, Illinois, at about 36° 55′ N latitude. So far as we can determine, the Ohio River is the only river in North America in which River Mile 0 is at its source. In all other rivers, including the Allegheny and Monongahela, River Mile 0 is at the mouth. The Ohio River is typically wide, shallow, and quite turbid throughout its tortuous course, and its annual discharge is greater than that of the Mississippi and Missouri rivers combined. With its extensive series of navigation locks and dams, it more closely resembles a series of impoundments than a continuous system. The river receives runoff from extensive agricultural and forested areas together with the industrial and municipal effluents from numerous small towns and several large metropolitan areas.

TABLE 2. Mean, standard deviation, and frequency distribution of numbers of vertebrae in *Notropis atherinoides* from 11 locations in the Ohio River from its source (Location 0) to its mouth (Location 10).

		Number of vertebrae								
Location	n	36	37	38	39	40	41	42	X̄	S.D.
0	100	2	–	17	57	24	–	–	39.01	0.77
1	100	1	–	13	67	19	–	–	39.03	0.64
2	100	–	–	7	60	33	–	–	39.26	0.58
3	100	–	–	9	53	37	1	–	39.30	0.64
4	100	1	–	4	51	42	2	–	39.39	0.69
5	97	–	–	4	34	54	5	–	39.62	0.65
6	99	–	2	–	28	58	11	–	39.79	0.73
7	94	–	–	–	20	60	14	–	39.94	0.60
8	72	–	–	3	4	53	11	1	40.01	0.66
9	100	–	–	–	17	55	26	2	40.13	0.71
10	76	–	–	2	5	49	19	1	40.15	0.67
Totals	1038	4	2	59	396	484	89	4	39.58	0.53

RESULTS AND DISCUSSION

Examination of x-ray photographs of 1,038 specimens of *Notropis atherinoides* from 11 locations in the Ohio River showed a consistent, gradual cline in numbers of vertebrae over the length of the river with smallest numbers near the source and largest numbers near the mouth (Table 2). Analysis of variance showed a highly significant F-value indicating a difference between means. Duncan's multiple range test and the sum of squares simultaneous test procedure (Fig. 3) showed the locations of differences and overlaps in similarities of the mean numbers. This is an apparent reversal of the expected trend of greater numbers of vertebrae at higher latitudes and lesser numbers at lower latitudes.

Vertebral counts ranged from 36 to 42 with an overall mean of 39.58 (Table 2), a value very close to the mean for sampling Location 5 (Ohio River Miles 483.3–503.3) which brackets the midpoint of the river (Ohio River Mile 490.5). The 36 vertebrae in four individuals in the samples from Locations 0, 1, and 4 are fewer than any reported in the literature for the emerald shiner.

The first documentation of increased numbers of vertebrae in *Notropis atherinoides* in relation to lower water temperature was that of Hubbs (1922) who reported variations within one year class and also between successive year classes. His findings were based on individuals of a single population collected from an opening in the ice along shore in a lagoon in Jackson Park, Chicago, Illinois, at a latitude of about 41° 55′ N. Hubbs reported numbers of vertebrae that ranged from 39 through 44, obviously based on a different method of counting than used in more recent studies where the ranges in most instances are from 37 through 42. In addition to noting differences in vertebral numbers, Hubbs' important contribution was his statement (1922:365) "The portion of the vertebral column affected is the caudal, not the precaudal (abdominal) division . . ."

Bailey and Allum (1962:59), in referring to the emerald shiner throughout its range, noted a "clinal gradient with higher numbers in the north, whether in the Missouri basin ("*percobromus*") the Mississippi basin, or the Great Lakes ("*atherinoides*")," than in the southern part of the range that included samples from the Arkansas River and some of its tributaries in Kansas and Oklahoma (Table 3). They reported a range in vertebral numbers from 37 through 42 with mean numbers of 37.3 in Spring Creek, Kansas, at a latitude of between 37° and 38° N in the Arkansas River drainage, to a mean of 40.5 in the Big Stone Lake drainage in South Dakota at a latitude of about 45° 30′ N (Mississippi River drainage). That low mean was based on six fish, and a more likely mean for the southern part of the range is that of 38.2 to 38.8 based on 25–26 specimens from the Poteau River (Arkansas River drainage) in Oklahoma at about 35° 10′ N latitude (Table 3).

Flittner (unpubl. doctoral dissertation) reported a range of 38 to 42 vertebrae in samples of 20 specimens each from five locations from eastern Lake Erie to Siskiwit Lake on Isle Royale, Michigan. The means in those collections ranged from 40.05 in eastern Lake Erie to 41.05 in Siskiwit

TABLE 3. Comparison of mean numbers of vertebrae of *Notropis atherinoides* from the Ohio River with data from Bailey and Allum (1962) and Flittner (unpubl. doctoral dissertation) arranged by latitude from north to south.

Locality	Source	n	$\bar{X}$	S.D.
Siskiwit Lake, Isle Royale, Mich.	Flittner	20	41.05	0.38
Marias River, Mont.	Bailey and Allum	10	40.1	0.74
Missouri River, Mont.	Bailey and Allum	5	39.6	0.50
Cedar River, N.D.	Bailey and Allum	10	39.1	0.33
Big Stone Lake Drainage, S.D.	Bailey and Allum	15	40.5	0.66
James River, S.D.	Bailey and Allum	11	38.1	0.84
Fremont Lake, Mich.	Flittner	29	40.20	0.38
Lake Michigan, Mich.	Flittner	20	40.35	0.96
Eastern Lake Erie	Flittner	20	40.05	0.59
Western Lake Erie	Flittner	20	40.35	0.85
Lake Erie	Bailey and Allum	29	40.3	0.71
Clear Creek, Neb.	Bailey and Allum	20	38.2	0.56
Mile 6.2, Ohio River, Pa.	Present study	100	39.01	0.77
All Ohio River specimens	Present study	1038	39.58	0.53
Mile 974.7, Ohio River, Ky.	Present study	76	40.13	0.75
Arkansas River, Kan.	Bailey and Allum	7	37.9	0.41
Spring Creek, Kan.	Bailey and Allum	6	37.3	0.45
Arkansas River, Okla.	Bailey and Allum	20	38.2	0.69
Poteau River, Okla.	Bailey and Allum	25	38.2	0.89

Lake. None of the means was significantly different from another except that the mean for Siskiwit Lake was significantly different from all others.

Fuchs (1967), in his study of the life history of the emerald shiner in Lewis and Clark Lake, an impoundment of the Missouri River in South Dakota, did not record numbers of vertebrae.

Campbell and MacCrimmon (1970) reported a range of 37 to 41 vertebrae with an average of 40.07 in emerald shiners from Lake Simcoe, an eutrophic lake in Ontario just east of Georgian Bay of Lake Huron, at approximately 44° 30′ N latitude.

Flittner (unpubl. doctoral dissertation) and Fuchs (1967) reported a wide range of spawning times and temperatures for *Notropis atherinoides*. Unfortunately, in the present study, we are unable to correlate water temperature at the time of spawning with numbers of vertebrae in individual fish. Other physical and chemical factors (dissolved gases, pH, light, salinity) that have been reported to influence numbers of vertebral elements may be related to patterns of meristic variations, and should be examined in future analyses.

Bryan (1969) examined vertebral variation in spotted bass *Micropterus punctulatus* from nine localities in the Ohio River, and found fewer vertebrae in specimens from the lower river. He attributed the decrease in vertebral numbers to warmer water temperatures in that part of the river.

Our tentative hypothesis to explain the trend observed in emerald shiner populations, but not the spotted bass populations, is presented in the hope of stimulating further interest in this area. Certain habitats in the lower reaches of large rivers, and in particular those that now are no more than a series of impoundments, often react more slowly to changes in temperature than the upper reaches of such rivers. Much of the upper Ohio River may warm more quickly in the spring than the lower more southerly part. Emerald shiners usually spawn in the mainstem of the river and earlier in the summer than the spotted bass which usually spawn in the tributary streams. As a result, embryonic development of spotted bass may not be influenced by water temperatures in the Ohio River. Since the emerald shiner has a protracted breeding season beginning in late spring, individuals that spawn in the lower Ohio River may undergo embryonic development in water colder than that in the upper river. Also, photoperiod conditions might influence the onset of breeding activity in such a way that vertebral development in the lower river could proceed in colder water.

In future studies of meristic characters of natural fish populations, especially those in large rivers where the habitats are so diverse, it is suggested that care be taken to determine the physical and chemical conditions at the time of spawning so that reasonable deductions may be made.

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ETHOLOGICAL ISOLATING MECHANISMS IN GOODEID FISHES OF THE GENUS *XENOTOCA* (CYPRINODONTIFORMES, OSTEICHTHYES)

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ABSTRACT: Although no natural hybrids are known, fertile laboratory hybrids were readily obtained from *Xenotoca eiseni* and *X. melanosoma* in forced crosses in which a conspecific mate was not available. In choice crosses with males and females of both species, sympatric stocks never hybridized, but allopatric fishes frequently mismated. Ethological data reveal differences in courtship behavior and discriminatory ability in sympatric fishes not observed for allopatric conspecific stocks nor in fish from two populations of the congener *X. variata*. These differences, which prevent interbreeding, are offered as evidence for the perfection of premating isolating mechanisms in sympatry. Hybrid inferiority, essential for divergence in sympatry, was reflected in reduced survival and inability to compete for mates.

The Goodeidae is a family of about 35 species of cyprinodontiform freshwater fishes restricted to the Mesa Central of México. Goodeids differ from their livebearing relatives, the anablepids, jenynsiids, and poeciliids, in having true viviparity rather than ovoviviparity in which embryos develop at the expense of yolk in retained eggs and receive little or no nourishment from the mother. In all but one goodeid species, the yolk is exhausted early in embryogeny and the young receive nutrition from the female through anal rosette or ribbon-like structures analogous to the placentae of mammals. These structures, called trophotaeniae, were studied in detail by the embryologist Turner (1933, 1937). Realizing the uniqueness

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of these features among cyprinodontiform fishes, Carl Hubbs, working with Turner, used goodeid trophotaeniae and ovarian anatomy in an exhaustive family classification (Hubbs and Turner, 1939). Although a number of taxonomic papers including goodeids (deBuen, 1941, 1942; Turner, 1946; Alvarez and Navarro, 1957: Alvarez, 1959, 1963; Alvarez and Cortés, 1962; and Romero, 1967) have appeared since the Hubbs and Turner revision, only one (Miller and Fitzsimons, 1971) significantly altered their classificatory scheme. Greatly influenced by Guillermo Mendoza's study (1965) with *Xenotoca eiseni*, Robert Miller and I judged trophotaenial and ovarian anatomy of goodeids likely too variable within a species to justify broader use in a family classification. Through synonymies, we reduced the Hubbs-Turner classification by four genera and one species but in the same report managed to erect a new genus and species of uncertain phylogenetic affinity.

During a revision of the goodeid genera *Characodon* and *Xenotoca* (Fitzsimons, 1972), I learned that goodeids exhibit elaborate pair-forming rituals during courtship. Ethological data confirmed taxonomic interpretations of morphological information and, in many instances, were better indices to relationships because attention was drawn to features that the animals themselves used in distinguishing species. Although the study revealed certain elements of courtship to be generically and specifically invariable, intraspecific differences in two species of *Xenotoca* were unmistakable. This report examines these differences.

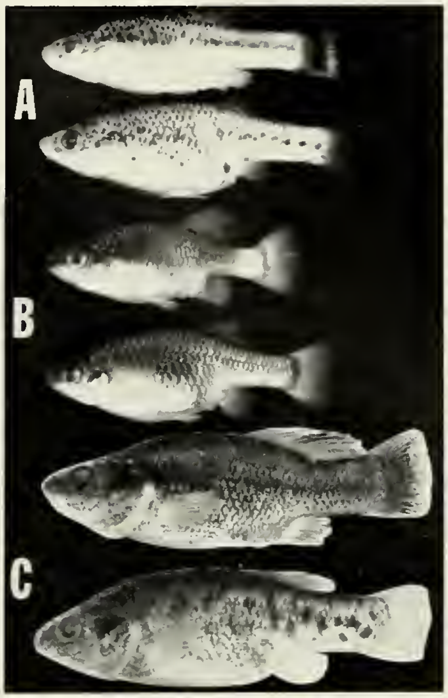

Figure 1. Males (above) and females (below) of *Xenotoca variata* (A) 41.5 and 45 mm SL, *X. eiseni* (B) 33 and 38.5, and *X. melanosoma* (C) 66.5 and 76.

The genus *Xenotoca* includes *X. variata* (Bean), *X. eiseni* (Rutter), and *X. melanosoma* Fitzsimons (Fig. 1). *Xenotoca variata*, the type species of the genus and perhaps the most widely distributed goodeid, occurs in a variety of lentic and lotic habitats associated with the drainage basins of the Ríos Verde and Aguascalientes in the state of Aguascalientes, the Río Santa María of San Luis Potosí, the Río Grande de Santiago of Jalisco and Michoacán, the Río Lerma of Guanajuato, and the Río de la Laja of Querétaro. Members of this species have not been taken sympatrically with either *X. eiseni* or *X. melanosoma*. Forced hybrid crosses (only heterospecific mates available) and artificial inseminations of *X. variata* with its congeners have been unsuccessful. The distribution of *X. eiseni* is disjunct. In Nayarit, it occurs in the Río Compostela and above 600 m in the drainage basin of the Río Grande de Santiago in which it ranges into northwestern Jalisco. The species is known from several localities along the Ríos Tamazula and Tuxpán in southern Jalisco but has never been collected in the central Jalisco basins of the Río Armería or Río Ameca which lie between its northwestern and southeastern limits. *Xenotoca melanosoma* is known only from Jalisco. Near its southern limit, the type locality is in the Río Tamazula about 16 km south by highway from the town of the same name. It ranges north into streams and ponds about 32 km south of Guadalajara, east to Lago de Chapala, and west into basins of the Río Ameca and Río Grande de Santiago. *Xenotoca eiseni* and *X. melanosoma* have been collected together at several localities in the Ríos Grande de Santiago and Tamazula. No natural hybrids are known, but in laboratory crosses fertile F_1 hybrids have been produced from all combinations of allopatric and sympatric stocks when conspecific mates were not available (Fitzsimons, 1972, 1974). In choice crosses consisting of males and females of both species, members of allopatric stocks sometimes hybridized but sympatric fishes never mismated.

The maintenance of *X. eiseni* and *X. melanosoma* as discrete species depends on the presence of one or more premating isolating mechanisms which prevent their interbreeding. For sympatric populations of these species there are two possibilities (Mayr, 1965): either potential mates do not meet (seasonal or habitat isolation) or potential mates meet but do not mate (ethological isolation). There is no evidence for seasonal or habitat isolation. Females of the two species bear young throughout the year when kept in aquaria, and pregnant females and neonates of both species are found in collections made during the same times of the year from sympatric and allopatric populations. Their ecological requirements are similar (Fitzsimons, 1972), and there is no apparent discontinuity in their distribution at a given locality—both species can be caught in the same seine haul. Thus, differences in mating behavior are likely alone responsible for preserving the integrity of these two potentially hybridizable species where they are sympatric. This paper examines the nature of ethological isolating mechanisms operative in *Xenotoca variata*, *X. eiseni*, and *X. melanosoma* and, for the latter two species, suggests how these mechanisms have evolved toward greater efficiency in sympatry.

GOODEID COURTSHIP

Internal fertilization and viviparity require that there be sexual selection and pair-forming for successful reproduction. In goodeids the male initiates pair-forming activities by orienting toward the female, approaching her, and performing one or more courtship displays. Male courtship displays range from simple broadside presentations to the female to intricate dances in which the male maximizes the exposure of sexually dimorphic features, particularly color and elongate fins. Female courtship behavior is much simpler. If the female is receptive to the male, she will respond by Head-Wagging, a rapid side-to-side swinging of the head and anterior body. Similar movements have been reported for other cyprinodontiform fishes by Foster (1967). In goodeids Head-Wagging is usually restricted to sexually receptive behavior by the female and rarely is incorporated into male courtship displays. In observations of 21 species of goodeids, the courtship movements of females were very similar and consisted of stereotyped receptive behavior (Head-Wagging) or rejection behavior (Evading, Hiding, Attacking, Pseudo-Feeding, and others). Interspecific differences in courtship were much more marked in males. Because of their complexity, variability, and species-specificity, the displays of courting males showed a greater promise for use in taxonomy (Fitzsimons, 1972; Fitzsimons and LeGrande, 1974) and in the study of ethological isolating mechanisms. The displays are assumed to be inherited and relatively unmodified by experience rather than learned characteristics because they were identical in animals with conspecific experience only, heterospecific experience only, and in those with no experience at all, i.e., ones raised in complete isolation. For at least two goodeid species underwater observations in México indicated that reproductive behavior in aquaria is the same as that which occurs naturally (Fitzsimons, 1972).

METHODS

Materials and methods included certain of those used in a recent revision of *Xenotoca* (Fitzsimons, 1972). Live stocks for behavioral studies and hybridization experiments included *X. variata*: Río Santa María, ca. 1.6 km S Villa de Reyes, San Luis Potosí, R. R. Miller and H. L. Huddle, III:26:1968; Presa El Gigante, near Santa María de Gallardo, 21 km NE (Hwy 45) on road to Loreto (at La Dichosa), Aguascalientes, R. R. Miller, H. L. Huddle, and J. Gomez, IV:1:1968; *X. eiseni*: Manantial El Sacristán, 1.3 km NW plaza Tepic, Nayarit, C. M. Bogert, 1955; *X. melanosoma*: Presa de la Vega, in Río Ameca, 32 km W jct. Hwy 15 and Hwy 70 (to Ameca), Jalisco, R. R. Miller and H. L. Huddle, V:5:1966; and *X. eiseni* and *X. melanosoma*: Río Tamazula (at Hwy 110 bridge) 5 km S Cd. Guzmán turnoff, Jalisco, R. R. Miller and H. L. Huddle, V:3:1966.

Fishes were maintained in the large aquarium facility directed by Robert R. Miller at the Univ. Michigan Mus. Zoology and in my laboratory at Louisiana State Univ.

Courtship observations and discrimination tests were conducted in a 15 or 20 gallon aquarium masked on three sides with black paper. The open side of the tank faced a black sheet with a one-way mirror mounted at its center. The mirror was tilted so that only the darkened ceiling of the room was reflected toward the aquarium. An overhead fluorescent fixture illuminated the tank, and the room was darkened. About 240 hours of courtship observations were tape-recorded. A minimum of 20 males and 20 females of each population was studied; half the pairs were individuals raised in complete isolation. Fourteen pairs of laboratory hybrids were available for mate

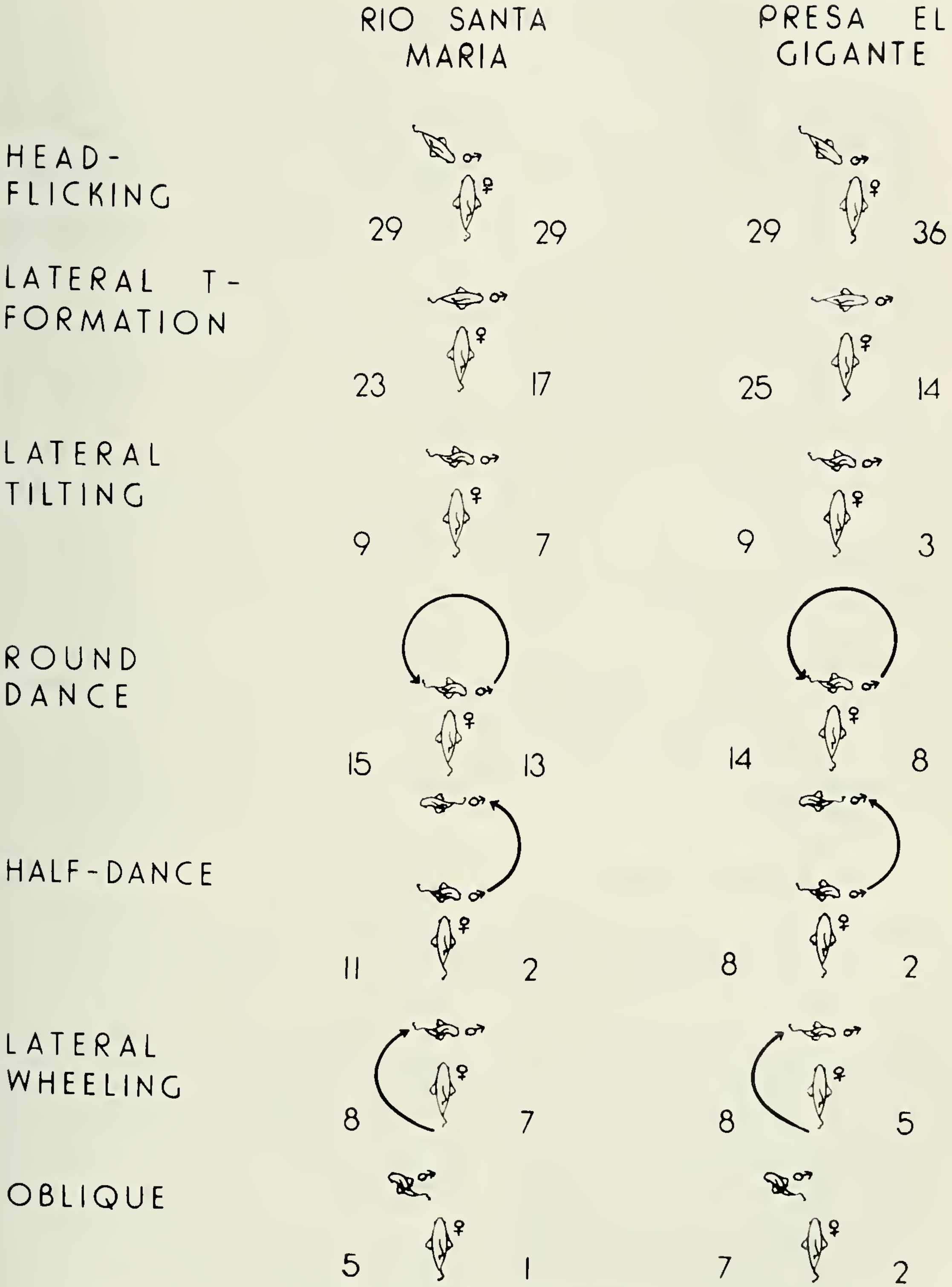

Figure 2. Male courtship display complement in two populations of *Xenotoca variata.* (The number to the left of each display indicates its percent frequency of occurrence in the total display complement; the number to the right is the percent effectiveness of the display in achieving successful copulation.)

selection experiments. In discrimination tests the aquarium was divided into three equal parts by opaque plastic partitions. The fish to be tested was placed in the center compartment and the "choice" fishes in the outer two. After fishes acclimated to new surroundings, partitions were removed and observations begun immediately. If a test male displayed to the female of his own species, a conspecific point was scored. If he displayed to the female of the other species, a heterospecific point was scored. Test points for females were based on their Head-Wagging response to male displays. To preclude the possibility that a male might select the conspecific female because the heterospecific choice was, for any number of reasons, not in equivalent reproductive condition, males of each species (and population) were tested consecutively against the same set of choice females. If one of the females was inferior, it became evident by watching her behavior in the presence of a conspecific male; when necessary, tests were repeated with another female in good reproductive condition. A parallel procedure was used in testing the discriminatory ability of females. A closed sequential test grid (Cole, 1962) was used to determine the number of animals and the number of tests per animal required to indicate differences of predetermined statistical significance ($P = 0.9$ for discrimination and $P = 0.5$ for nondiscrimination). Test animals included individuals of varying experience (exclusively conspecific, exclusively heterospecific, or no experience).

COURTSHIP MOVEMENTS

Qualitative features of courtship displays of *Xenotoca* males were used for taxonomic purposes in the generic revision (Fitzsimons, 1972); the descriptions below have been expanded to include populational differences.

Xenotoca variata.—The courtship displays of *X. variata* males included Head-Flicking, Lateral T-formation, Round Dance, Half-Dance, Lateral Tilting, Lateral Wheeling, and Oblique (Fig. 2).

Head-Flicking was the most frequent display presented to stationary or moving females; it was similar to or identical with the courtship display reported for males of many killifishes (Foster, 1967). The male rapidly twitched the anterior end of his body in a manner reminiscent of female receptive behavior (Head-Wagging), but the arc described by the right and left lateral movements was much smaller and more quickly executed than in Head-Wagging. Head-Flicking consisted of a single lateral movement, a burst of three or four at a time, or a continuous series up to six seconds duration. The male Head-Flicked while stationary in front of and broadside to the female, oblique and head-on, lateral and parallel, or while swimming actively in any of these positions.

In the Lateral T-formation display, a male approached a stationary female from her right or left, stopped broadside about one body length or less in front of her, and spread his median fins. The body was held straight and the caudal fin was flicked or jerked conspicuously.

In another type of lateral display, extreme tilting and S-curving were seen. In this Lateral Tilting display, the male also quivered his body, causing the fins, particularly the dorsal and anal, to flutter markedly.

In the Round Dance, a male briefly assumed the posture seen in the Lateral Tilting display, quickly circled in front of the female, and again resumed the lateral presentation with strong S-curving, tilting, quivering, and with the anal fin inclined toward the female. Circling was often repeated several times (two to six, usually three) but each circuit was separated by the stationary posture held briefly before the female.

In the Half-Dance display, a male postured as in the Lateral Tilting or Round Dance, immediately swam a half circle, and again postured. If the female was receptive (Head-Wagged), the male usually continued into the Round Dance.

A male performed the Lateral Wheeling display in response to an actively swimming female. He swam forward from the rear of the female, arced around in front of her from the right or left, braked with expanded pectorals, tilted, S-curved, and quivered his body and fins as in the Lateral Tilting display. This display effectively blocked the path of the swimming female.

Males performed the Oblique display by facing away from the female on an oblique angle less than one body length in front of her while tilting and S-curving; the caudal fin was brought close to her head. In this position the male quivered its body rapidly causing the semi-erected median fins, especially the dorsal and caudal, to flutter violently.

I was unable to detect individual or populational variation in the form of courtship displays in *Xenotoca variata* males from Río Santa María and Presa El Gigante; moreover, populational differences in the frequency of individual displays and their effectiveness in achieving copulation are surprisingly small ($P = 0.01$; Fig. 2).

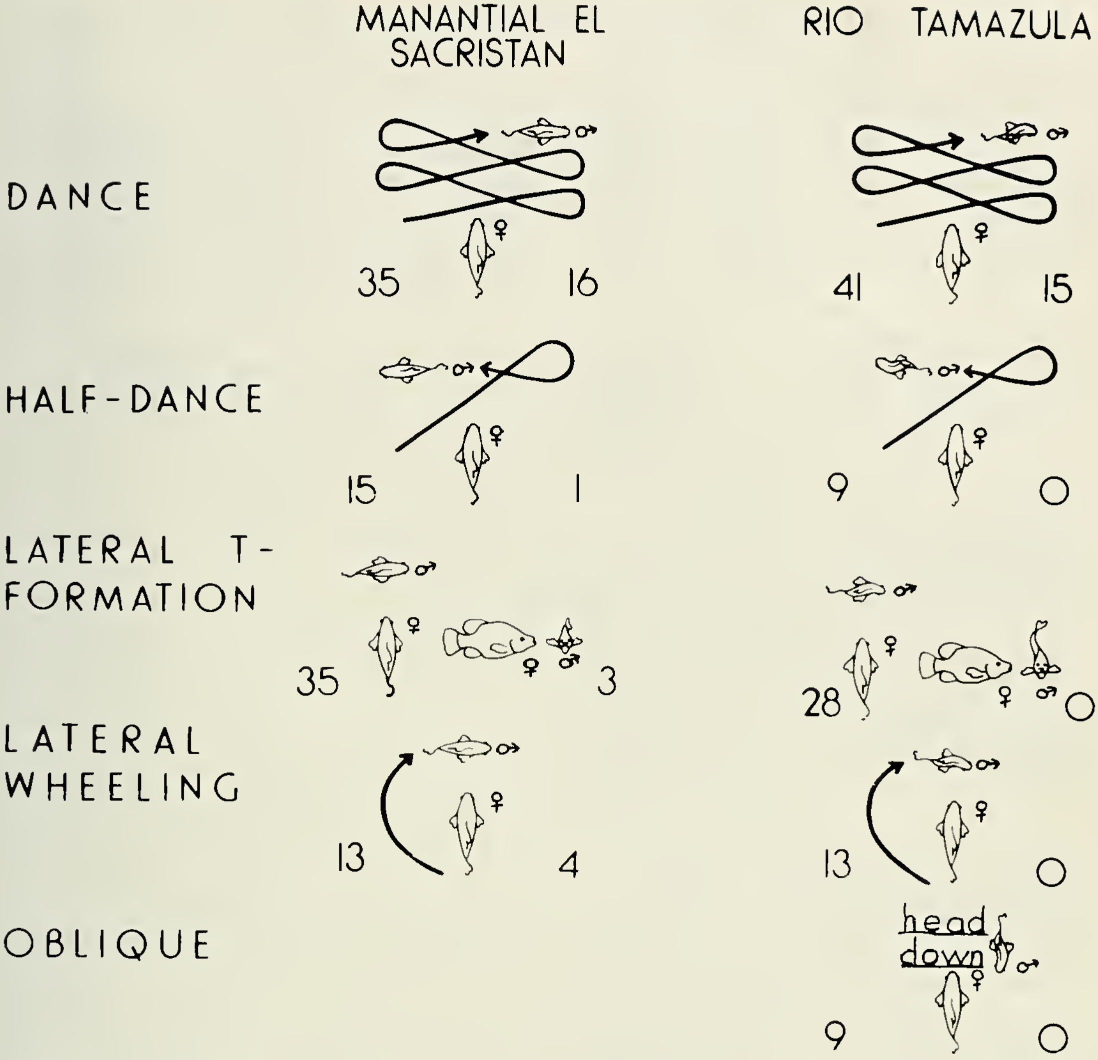

Figure 3. Male courtship repertories in two populations of *Xenotoca eiseni.* (Numbers to the left of displays indicate percent frequency; numbers to the right are percent effectiveness in achieving copulation.)

Xenotoca eiseni.—Males from the Río Tamazula exhibited five courtship displays; fish from Manantial El Sacristán had four (Fig. 3). The Loop Dance, Half-Dance, Lateral T-formation, Lateral Wheeling, and Oblique displays comprised the display repertory of Río Tamazula males; males from Manantial El Sacristán did not perform the Oblique display.

The most elaborate display was the Loop Dance, in which the male executed a series (one to six, usually four) of figure-eight movements slightly above (about half a body length) and one to two body lengths ahead of a swimming female. If the female was swimming rapidly, the forward progression of the male approximated her swimming speed so that the Dance appeared more like a series of stretched-out loops than smooth figure-eights. At the end of each leg of the Dance, the male turned back to describe a loop before continuing. During turning movements, the male strongly inclined the dorsal and especially the anal fins toward the female. When turning, a Río Tamazula male exhibited exaggerated sigmoid flexures and often tilted so much that the vertical plane of his body became nearly horizontal. A male from Manantial El Sacristán lacked sigmoid posturing throughout the display and, when turning, the fish tilted only rarely and very slightly

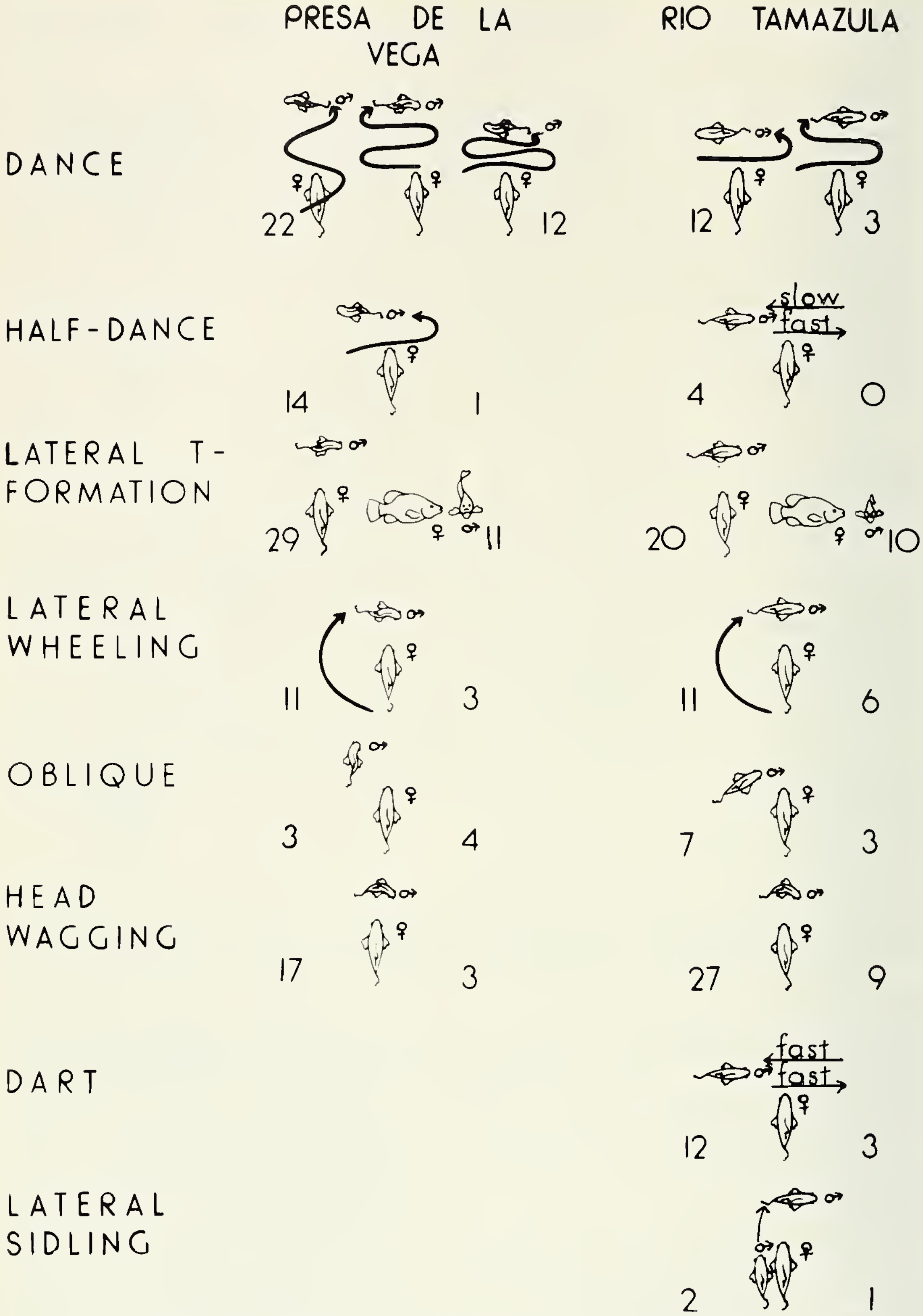

Figure 4. Elements of male courtship in two populations of *Xenotoca melanosoma.* (Numbers to the left of displays indicate percent frequency; numbers to the right are percent effectiveness in achieving copulation.)

(never more than 15° from the vertical). A Río Tamazula male quivered violently when the path of the display brought him close to the female; a male from Manantial El Sacristán never quivered.

The Half-Dance display consisted of the male swimming the first leg of the Dance, but, rather than continuing to complete a figure-eight, he stopped short in the second run. In the halted position only the male from the Río Tamazula tilted and quivered rapidly. This display was presented to a stationary or slowly swimming female.

The simplest display was the Lateral T-formation where the male swam across in front of the female, braked with expanded pectoral fins, assumed a slight sigmoid shape (Río Tamazula fish) or held the body straight (Manantial El Sacristán fish), head toward and caudal fin away from the female, dorsal and mainly anal fins conspicuously bent toward her, and the dorsum of the body tilted toward her (Río Tamazula fish). The male from the Río Tamazula also often quivered slightly. This display was presented to a stationary or very slowly swimming female.

If the female was actively swimming forward, the male approached from the rear, tilted (Río Tamazula fish), wheeled around in front of her from the right or left, stopped, and assumed the posture seen in the Lateral T-formation. This is the Lateral Wheeling display.

In the Oblique display, seen only in Río Tamazula fish, the male faced the female from an angle less than 90° on her right or left, assumed a head-down posture with the body at an approximate 45° angle to the horizontal, and bent the caudal fin and peduncle toward her. The dorsal and anal fins were strongly inclined toward the female. This display was presented only to a stationary female.

Populational variation in the form of male courtship activities was conspicuous in *Xenotoca eiseni* from the Río Tamazula and Manantial El Sacristán. Statistically significant interpopulational differences were seen in the frequency of individual displays and in the relative effectiveness of these displays in gaining copulation. These discrepancies are interpreted below with those described for the populations of *X. melanosoma*.

Xenotoca melanosoma.—Males from Presa de la Vega exhibited six courtship displays (Fig. 4): the Zig-zag Dance, Half-Dance, Lateral T-formation, Lateral Wheeling, Oblique, and Head-Wagging. In addition to these, Río Tamazula males showed the Lateral Sidling and Dart displays.

The male courtship displays of fish from the Río Tamazula lacked sigmoid posturing; Tilting was rare and never exceeded 10°.

The Zig-zag Dance of the Presa de la Vega male consisted of a series (two to six, usually three) of to-and-fro movements during which the male swam one to two body lengths in front of, and at the same swimming depth, as the female. As the male went through each turn, S-curving was extreme; in the transverse portion of the Dance, quivering and inclination of the dorsal and anal fins toward the female were marked. Restricted to the transverse legs of the dance, tilting was infrequent and never exceeded an angle of 10°. The amplitude of the lateral movements was one to two body lengths, and the pattern traced as the male moved forward appeared as a series of meanders if the female was actively swimming forward or it was compressed into sharper cornered zig-zag movements if the female was stationary or swimming very slowly. In the shortened Zig-zag Dance of Río Tamazula fish, the male swam slowly across from the right or left in front of the female, turned back to complete a second leg, stopped, and spread his median fins as in the Lateral T-formation display. The Dance rarely extended to the beginning of a third leg. The Dance was presented to stationary or very slowly swimming females.

In the Half-Dance display, the male from Presa de la Vega swam the first leg of the Dance, stopped abruptly in the second leg, and assumed a pronounced sigmoid posture while quivering and tilting (dorsum away from the female) with the dorsal and particularly the anal fins erected and bent toward the female. If the female was responsive, the male usually continued into the dance. In the Half-Dance display of Río Tamazula fish, the male approached from the rear or side of a stationary female, quickly swam in front of her, braked with pectoral fins, and backed slowly with his dorsal and anal fins fully expanded. If the female was not receptive, the male held the backed position for several (one to five) seconds, conspicuously twitching his dorsal and caudal fins before repeating the forward movement of the display. If the female was responsive, the male usually repeated the forward darting movement and continued into the short Zig-zag Dance.

In the Lateral T-formation display, a male approached the female from her right or left and paused while broadside in front of her. The male from Presa de la Vega quivered rapidly in the display, bent his body into a strong sigmoid posture, with the head toward and tail away from the female, and tilted, dorsum away from her. The

TABLE 1. Dance and Half-Dance displays in *Xenotoca* males.

	X. variata Río Santa María	*X. variata* Presa El Gigante	*X. eiseni* Río Tamazula	*X. eiseni* Manantial El Sacristán	*X. melanosoma* Río Tamazula	*X. melanosoma* Presa de la Vega
Path described by Dance	circles	circles	figure-eights or loops	figure-eights or loops	zig-zags	zig-zags
Path described by Half-Dance	half-circle	half-circle	one loop	one loop	forward and backward straight line movement	half zig-zag
Number of circles, loops, or zig-zags in Dance	3(2–6)	3(2–6)	4(1–6)	3(1–6)	2 or, rarely, 3	3(2–6)
S-Curving	strong	strong	none or slight	none	none	strong
Tilting						
extent	moderate to extreme	moderate to extreme	extreme	none or very slight	none	very slight (Dance) to extreme (Half-Dance)
direction	dorsum toward female	dorsum toward female	dorsum toward female	dorsum toward female	———	venter toward female
Quivering	strong	strong	strong	none	none	strong
Fin movements	dorsal, caudal expanded; anal inclined toward female	dorsal, caudal expanded; anal inclined toward female	median fins expanded; dorsal, anal inclined toward female	median fins expanded; dorsal, anal inclined toward female	median fins spread but not inclined toward female; dorsal and caudal also twitched in Half-Dance	median fins expanded; dorsal, anal inclined toward female

semi-erected dorsal and anal fins were strongly inclined toward her. A Río Tamazula male held its body straight, the dorsal fin erect, and the anal fin straight (usually) or slightly inclined toward the female. The lateral T-formation display was presented to stationary or slowly swimming females.

In the Lateral Wheeling display, the male approached the swimming female from the rear, wheeled around in front of her, and assumed the stationary posture described for the Lateral T-formation. At Presa de la Vega, tilting occurred throughout the male's display; it was slightest (10° or less) during wheeling and greatest (up to about 25°) during lateral presentation. The Lateral Wheeling display was presented to actively swimming females and, less often, to stationary ones.

In the Oblique display, a male took up a position at an angle less than 90° to the right or left in front of a female. In Presa de la Vega fish, the male faced away from the female and held his body in a strong sigmoid flexure, head toward and tail away from the female, while quivering rapidly with the dorsal and especially the anal fins inclined toward her. The Río Tamazula male held his body at an oblique angle to the female and presented his right or left side and median fins fully expanded but not inclined.

A male from either population sometimes approached a female from the side or front, turned broadside to her, and rapidly bent his body into a series of horizontal C-shapes. Moving through a greater arc than the rest of the body, the head was jerked erratically right and left while sculling movements of the pectoral fins offset the propulsive force of the flexing caudal peduncle and

TABLE 2. Lateral T-formation and Wheeling displays in *Xenotoca* males.

	X. variata Río Santa María	*X. variata* Presa El Gigante	*X. eiseni* Río Tamazula	*X. eiseni* Manantial El Sacristán	*X. melanosoma* Río Tamazula	*X. melanosoma* Presa de la Vega
S-Curving	none (Lat T) to strong (Wheeling)	none (Lat T) to strong (Wheeling)	slight	none	none	strong
Tilting						
extent	none (Lat T) to extreme (Wheeling)	none (Lat T) to extreme (Wheeling)	moderate	none or very slight	none	moderate to extreme
direction	dorsum toward female	dorsum toward female	dorsum toward female	dorsum toward female	———	venter toward female
Quivering	none (Lat T) to strong (Wheeling)	none (Lat T) to strong (Wheeling)	slight	slight	none	strong
Fin movements	dorsal, anal spread; caudal flicked (Lat T) or fluttered	dorsal, anal spread; caudal flicked (Lat T) or fluttered	dorsal, anal inclined toward female	dorsal, anal inclined toward female	dorsal, caudal expanded; anal slightly inclined toward female	dorsal, anal inclined toward female

fin. The dorsal fin was alternately raised and lowered (Río Tamazula males) or only slightly expanded so that the movements of the body caused it to flutter conspicuously (males from both populations). The anal fin was inclined toward the female. Except for median fin movements, this display resembled receptive behavior in the female and, accordingly, is called the Head-Wagging display. It was presented only to stationary females.

A male from the Río Tamazula stock sometimes approached the female from the front or rear, right or left, and performed the Dart display in which he quickly sprang across in front of the female with the dorsal and anal fins lowered, stopped suddenly with expanded pectorals, and sculled backward while erecting the dorsal fin and inclining the anal fin toward her. The forward movement of the Dart ceased when the trailing edge of the dorsal fin was directly in front of the female, and backing stopped when the leading edge of the fin was about in the same position. The Dart display consisted of two to six such forward and backward movements in rapid succession with the raising and lowering of the dorsal fin its most conspicuous feature. Although similar to the Half-Dance in general pattern of movements, the Dart display had a much smaller amplitude and quicker repetition of the backward and forward components so that a striking to-and-fro or see-saw-like movement was produced. The Dart display was presented to stationary females.

In the Lateral Sidling display of Río Tamazula fish, the male moved alongside the stationary or slowly swimming female with his dorsal fin inclined so that it brushed, or nearly so, the back and head of the female and, once past her, he turned in and assumed the posture seen in the other lateral displays.

In comparison to the courtship behavior observed for the two populations of *Xenotoca variata* (Fig. 2), there are noteworthy interpopulational differences between *X. eiseni* from the Río Tamazula and Manantial El Sacristán and between *X. melanosoma* from the Río Tamazula and Presa de la Vega (Figs. 3 and 4). In my opinion these differences are attributable to the reinforcement of premating isolating mechanisms where the two species are sympatric.

The most striking difference between the courtship repertories of the two populations of *X. eiseni* is that the Loop Dance was the only display which led directly to successful copulation in the Río Tamazula population, sympatric with *X. melanosoma*, but in Manantial El Sacristán fish, allopatric to *X. melanosoma*, displays other than the Loop Dance led to successful copulation in nearly one-third of the observations. Readily distinguishing

TABLE 3. Oblique displays in *Xenotoca* males.

	X. variata Río Santa María	*X. variata* Presa El Gigante	*X. eiseni* Río Tamazula	*X. eiseni* Manantial El Sacristán	*X. melanosoma* Río Tamazula	*X. melanosoma* Presa de la Vega
Position of male	facing away from female, body horizontal	facing away from female, body horizontal	facing female, head down	display not observed	broadside to female, body horizontal	facing away from female, body horizontal
C-Curving	none	none	moderate	———	none	none
S-Curving	strong	strong	none	———	none	strong
Tilting						
extent	slight	slight	none	———	none	none
direction	dorsum toward female	dorsum toward female	———	———	———	———
Quivering	strong	strong	none	———	none	strong
Fin movements	median fins semi-expanded, fluttered; caudal near female	median fins semi-expanded, fluttered; caudal near female	median fins expanded; dorsal, anal inclined, caudal bent toward female	———	median fins expanded	median fins expanded; dorsal, anal inclined toward female

X. eiseni from its congenerics, the distinctive Loop Dance has become requisite for successful mating in the Río Tamazula; its value in preventing interbreeding is unmistakable.

The shortened Zig-zag Dance and Half-Dance of *X. melanosoma* from the Río Tamazula resembled the Loop Dance and Half-Dance of *X. eiseni* much less than these displays in allopatric fish from Presa de la Vega (Figs. 3 and 4; Table 1).

The Lateral T-formation and Wheeling displays were seen in all three species (Figs. 2, 3, and 4; Table 2). These displays were identical in two populations of *X. variata*, but, because of changes in sigmoid posturing, tilting, and quivering, they were dissimilar in sympatric populations of *X. eiseni* and *X. melanosoma*.

The Oblique display was not observed in the courtship sequence of *X. eiseni* males from Manantial El Sacristán but was common in the Río Tamazula population (Fig. 3). Although this display was seen in both populations each of *X. melanosoma* (Fig. 4) and *X. variata* (Fig. 2) changes in the angle of the male relative to the horizontal and to the female, quivering, and sigmoid posturing have made the form of the Oblique display species-specific in sympatric *X. eiseni* and *X. melanosoma* (Table 3).

Intraspecific changes in the frequency of individual displays also indicate a divergence compatible with a hypothesis on the perfection of ethological isolating mechanisms in closely related, sympatric species. The Loop Dance of *X. eiseni* is about six percent more frequent in sympatry with *X. melanosoma* while the Zig-zag Dance of *X. melanosoma* is seven percent less frequent. The distinctive Head-Wagging display of *X. melanosoma* is 10 percent more frequent in sympatry and its Dart and Lateral Sidling displays, not seen in allopatry, together comprise 14 percent of the total displays of this species in the Río Tamazula. These interpopulational differences may seem slight, but they are many times the magnitude of the differences observed for the two populations of *X. variata* and are statistically significant. They may indicate a continuing selection for behavioral divergence in sympatry.

In allopatric and sympatric populations of *X. eiseni* and *X. melanosoma*, males always began courtship with one or more displays. However, after successfully copulating, males from allopatric populations resumed courtship at the copulation or copulation attempt stages without a display in 22 percent of the observations for *X. melanosoma* and in 10 percent for *X. eiseni*. In sympatry these values were reduced to nine percent for *X. melanosoma* and zero for *X. eiseni*.

I have observed the general requirement for one or more displays to precede successful pair-forming in all populations of *Xenotoca variata*, *X. eiseni*, *X. melansoma*, and in 18 other species in the family. Likely common throughout the family, male courtship displays probably have served and will continue to serve as preadaptations for the development and/or perfection of ethological isolating mechanisms in the sympatric association of two species capable of interbreeding.

The analysis of courtship displays in *Xenotoca* males indicates three major differences occur between the courtship rituals of allopatric and sympatric *X. eiseni* and *X. melanosoma*. In sympatry there is 1) an increased frequency of displays with species-specific signal function, 2) modification of movements and posturing in display types common to both species, and 3) development of fixed action patterns not seen in allopatry. I regard the first item in the list to be most important for preserving species integrity in sympatric *X. eiseni* and *X. melanosoma*. The Loop Dance of *X. eiseni* and the Head-Wagging display of *X. melanosoma* likely preadapted these goodeids for species maintenance in sympatry; the increased frequency of these displays probably occurred concomitantly with an increase in their relative importance for successful copulation where the two species live together in the Río Tamazula.

The perfection of premating isolating mechanisms from pre-existing species-specific courtship patterns requires less new genetic information and presumably is more easily evolved than new or highly modified displays. If this assumption is correct, one might predict the establishment of isolating mechanisms from preadaptive features to be a common, if not the most common, evolutionary strategy for limiting and ultimately stopping gene flow between closely related species in a zone of secondary contact. The literature is not supporting. Although Ball and Jameson (1966) concluded that mere reduction in variability rather than marked character displacement of call types accounts for reproductive isolation in the sympatric frogs *Hyla regilla* and *H. californiae*, most other studies describe conspicuous divergence in signalling behavior and often structure when two partially or completely reproductively isolated sympatric populations are compared with allopatric conspecifics (e.g., Blair, 1955a and b, 1958; Littlejohn, 1965; Littlejohn and Loftus-Hills, 1968; Smith, 1966).

DISCRIMINATION TESTS

The essential counterpart to the evolution of interspecific differences in pair-forming movements is the ability to detect conspecific distinctiveness in elements of courtship and to respond to it in a discriminatory manner. The following account attempts to measure discriminatory ability among the species of *Xenotoca* and to explain discrepancies in performance between species, populations, and sexes in terms of the differences in selective pressures they have experienced.

Xenotoca variata.—When fish from the two populations of *X. variata* were tested against *X. eiseni* and *X. melanosoma*, the conspecific partner was always chosen. Intraspecific tests between the two populations of *X. variata* indicated no discrimination; a member of one population responded to an individual of the opposite sex from the other population as readily as to one from its own.

Discrimination tests for Río Tamazula populations of *X. eiseni* and *X. melanosoma* indicated that sympatric males and females of the two species always chose the conspecific partner ($P = 0.9$). Except for heterospecifically experienced *X. melanosoma* males, a minimum number of tests (seven test fish) were required for all categories of pre-testing experience. Individuals raised in complete isolation chose their own species at first exposure as unerringly as fishes raised in large stock tanks (conspecific experience). Even fishes set up in hybrid crosses, in which they were associated since birth only with members of the other species (heterospecific experience), readily responded to the conspecific partner when a choice was available. A greater range and average number of trials per test fish were seen for heterospecifically experienced males and females of both species. The data also indicate that females discriminated more readily than males.

When sympatric *X. eiseni* and *X. melanosoma* were tested against their conspecific heterosex and F_1 hybrid, the conspecific mate was chosen but, when given the choice of the hybrid and a heterospecific mate, the hybrid was selected. However, in the latter tests 11 *X. eiseni* females and four *X. melanosoma* females responded neither to the hybrid nor the heterospecific males. Females showed greater discriminatory ability, as indicated by the fewer number of tests required for statistical significance at $P = 0.9$ and by the smaller range and mean number of trials observed for individual test fish. Hybrids showed no preference for either parental species (Fitzsimons, 1974).

Members of allopatric stocks of *X. eiseni* and *X. melanosoma* discriminated against the potential heterospecific mate, but their performance was less than that seen for sympatric stocks of the same species. Females of both species rejected F_1 hybrid males, but males of *X. eiseni* and *X. melanosoma* courted equally the females of their own species and the hybrid. Discrimination by females was greater in all test combinations. In discrimination tests between populations of *X. eiseni*, one allopatric and the other sympatric to *X. melanosoma*, fish from the sympatric population directed significantly more courtship behavior toward members of their own population. Allopatric females preferred sympatric males, but allopatric males readily displayed to females of either population.

No significant differences in discrimination were observed between the two *X. melanosoma* populations, one sympatric and the other allopatric to *X. eiseni*.

Like most behavioral processes, discrimination is the combined product of genetically fixed characteristics and individual experience. However, the performance of goodeids raised in complete isolation or allowed only heterospecific association before testing indicates that their discriminatory ability is an inherited trait requiring no specific learning for its phenotypic expression. Observations of mate discrimination in the hybrids, which showed nearly equal attention in courtship to both parental types, provide further support for a genetic basis of this behavior.

In tests between *X. eiseni*, *X. melanosoma*, and their F_1 hybrid, sympatric populations showed superior discrimination ability. I interpret this as additional evidence for the perfection of premating isolating mechanisms in sympatry. If changes in courtship movements are selected in the context of preventing interspecies matings, they can be effective only if accompanied by a concomitant evolution of relevant discriminatory ability.

Populations of *X. eiseni* sympatric to *X. melanosoma* in the Río Tamazula discriminated against their conspecifics of Manantial El Sacristán; this intraspecific discrimination is probably correlated with the differences in courtship and body color (Río Tamazula males are more extensively and brightly colored) that have arisen because of the sympatric association of the two potentially hybridizable species. However *X. melanosoma* from Río Tamazula did not discriminate against conspecific members of the Presa de la Vega population as might have been expected from observing *X. eiseni*. The lack of discrimination may have resulted from the absence of color differences between the two *X. melanosoma* populations and the manner in which discrimination test points were scored. If points had been scored in reference to the number of successful copulations, rather than being based on behavior patterns occurring early in courtship, intrapopulational preferences might have been detected.

The question of male versus female in mate selection is an old one, probably referable to all sexually reproducing animals which form breeding pairs. For fishes the debate concerning which sex makes the choice in pair-forming was renewed by the ethological studies of the stickleback by Tinbergen (1951) and of the guppy by Baerends and others (1955). In these fishes (and most goodeids) the male is very strikingly colored and otherwise sexually dimorphic, and it is the male, not the female, who must initiate courtship and successfully carry it to completion. Thus, one might argue that the male selects the female. This premise is accepted at least tentatively by a number of workers studying mate discrimination in fishes (Haskins and Haskins, 1949; Clark, et al., 1954; Hubbs and Delco, 1960, 1962; Liley, 1966; Keenlyside, 1967) even though they imply or state directly (Liley, 1966) that appropriate receptive behavior by the female is essential for successful copulation. However, a counter-argument portends that the ability to discriminate is likely to be more important for the female of any polygamous species since she would "suffer most [sic] from mistaken matings" (Bateman, 1948). In *Xenotoca* and other goodeids (Fitzsimons, 1972) both sexes effectively discriminate against heterospecific fishes but females show greater proficiency. Data 1 obtained for the preparation of ethograms show that the courtship displays of males of all species averaged only 5.6 percent (3 to 10) success in obtaining copulation with conspecific females. This indicates that females are highly discriminatory even among males of their own population. There is likely greater selective pressure for discrimination on females since, if mismated, they must carry the burden of the mistake for a full gestation period (30 to 50 days for goodeids) while males have wasted only a small amount of time and material. Nevertheless, in sympatric populations potentially capable of interbreeding, as *X. eiseni* and *X. melanosoma* in the Río Tamazula, the discriminatory ability of the male can equal that of the female.

HYBRID INFERIORITY

Offspring from forced or no choice crosses of *X. eiseni* and *X. melanosoma* in all combinations of populations (96 pairs yielding 311 broods and 2,045 young) showed less survival in the F_1 and particularly backcross and F_2 generations than in intrapopulational conspecific crosses. Sex ratios were nearly normal (1:1) in about 86 percent of the F_1 hybrids and approximated those (89 percent) obtained for a comparable number of intrapopulational conspecific crosses. However, sex ratios were judged statistically normal in only 67 percent of the F_2 and 41 percent of the backcross broods. I interpret the increased disturbance in sex ratios and decreased survival of backcross and F_2 young to indicate that any naturally produced hybrids would have less reproductive success than either parental species.

Thus, hybrid inferiority, a requirement for evolutionary divergence of actually or potentially interbreeding stocks in an area of secondary contact, was evident for *X. eiseni* and *X. melanosoma* in the inability of hybrids to compete for mates (see previous section) and in the reduced survival of hybrids.

SUMMARY AND CONCLUSIONS

The species of *Xenotoca* are members of the Mexican family Goodeidae, a geographically compact group of livebearing fishes whose males perform a variety of attracting displays during courtship.

The wide-ranging species *Xenotoca variata* is allopatric to its congeners. Conspecific males from different localities exhibited the same kind and number of courtship displays with little or no populational variation in form, frequency, and efficiency in achieving copulation. *Xenotoca variata* did not hybridize with its relatives, *X. eiseni* and *X. melanosoma*, in forced crosses and artificial inseminations. In discrimination tests males and females always chose the conspecific mate; interpopulational tests did not reveal discrimination.

Although natural hybrids of *X. eiseni* and *X. melanosoma* have not been found, fertile hybrids were produced in laboratory experiments from all combinations of sympatric and allopatric stocks when a conspecific mate was unavailable. In crosses with conspecific and heterospecific choices of mates, members of allopatric populations sometimes hybridized but sympatric fishes never mismated. Ethological data indicate that in sympatry the two species have differences in courtship movements and discriminatory ability not present in allopatric fishes. These differences effectively prevent interbreeding and are assumed to have evolved in sympatry in response to selection for perfecting premating isolating mechanisms. Sympatric changes in courtship for non-randomness in mating include an increased frequency of male displays which have species specificity, modifications in the form and frequency of displays shared by both species, and the development of new displays not observed for allopatric fishes. Discrimination tests indicate that sympatric stocks of *X. eiseni* and *X. melanosoma* more effectively discriminate against the heterospecific mate and the F_1 hybrid than do members of allopatric populations. The perfection of isolating mechanisms in sympatry requires that hybrids, if produced, must be inferior to parental species so that individuals which mismate will have less reproductive success than those that do not. Hybrid inferiority is evident for *eiseni-melanosoma* hybrids in their reduced survival, especially in the backcross and F_2 generations, and in their lack of ability to compete for mates.

The major difficulty in stating the case for the perfection of premating isolating mechanisms in sympatry is that all the evidence is retrospective and, therefore, subject to more than one interpretation. A plausible argument is that the differences in mating behavior between *X. eiseni* and *X. melanosoma* could have evolved before they became sympatric and that the differences seen in allopatric populations merely represent genetic changes which inevitably arise in geographically separated stocks of the same species. However, the close similarity in behavior between two disjunct populations of *X. variata*, at least in part, stands against this argument. Moreover, after studying mating behavior in allopatric fishes, I do not think it possible that pre-sympatric evolution in *X. eiseni* and *X. melanosoma* could have fortuitously given them just the right combination of changes in courtship displays and discriminatory ability to be 100 percent effective.

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LIFE HISTORY OF THE FRESHWATER LAMPREYS, *OKKELBERGIA AEPYPTERA* AND *LAMPETRA LAMOTTENII* (PISCES: PETROMYZONIDAE), ON THE DELMARVA PENINSULA (EAST COAST, UNITED STATES)

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Abstract: We studied the life history of the least brook lamprey, *Okkelbergia aepyptera*, and the American brook lamprey, *Lampetra lamottenii*, in Delaware. Observations of nest construction and spawning in *O. aepyptera* are presented. Mean number of eggs per female is 874. Larvae average 3.40 mm TL at hatching. Analysis of length-frequency data for ammocoetes indicates that the duration of the larval period is at least 5.4 years. Length-weight equation for ammocoetes is $\text{Log W} = -5.24 + 2.73 \text{ Log L}$. Meristic data are presented. Mean number of eggs in *L. lamottenii* is 1691. Larvae average 2.60 mm TL at hatching. Ammocoete length–weight equation is $\text{Log W} = -5.31 + 2.76 \text{ Log L}$. Comparisons are made with northern populations.

The life history of the least brook lamprey, *Okkelbergia aepyptera* (Abbott), is but poorly known and most accounts have focused on distribution (Creaser, 1939; Raney, 1941, 1952; Cook, 1952; Cooper and Hemphill, 1957; Trautman, 1957; Schwartz, 1958, 1959, 1961; Pflieger, 1971; Rohde et al., 1974, 1975). Seversmith (1953) studied life history in Maryland and Brigham (1973) considered aspects of nest construction in Tennessee. We present data on habitat, behavior, fecundity, age and growth, length, weight, and meristics based on 1976 specimens from Bright's Branch and on 234 specimens from Chapel

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Branch, both Sussex County, Delaware and tributary to the Nanticoke River, Chesapeake Bay drainage. Samples were collected in all seasons (3, 5, 17, 24 March; 7 April; 20, 30 June; 8, 14 September; 30 November 1974; and 2, 9, 23 March 1975). In addition, we present data on species-associates taken by us on 17 dates from 10 December 1970 to 23 March 1975 at all 11 *O. aepyptera* sites in Kent and Sussex counties, Delaware and in Cecil and Queen Annes counties, Maryland (see Rohde et al., 1974, 1975 for site locations).

Life history of the American brook lamprey, *Lampetra lamottenii* (Lesueur), has been studied more intensively than that of *O. aepyptera* (Young and Cole, 1900; Okkelberg, 1921; Hubbs, 1925; Vladykov, 1949, 1951; Thomas, 1962; Smith et al., 1968; Kott, 1971, 1974; Manion and Purvis, 1971; Moore and Beamish, 1973). These studies, however, refer to populations from the northern part of its range. We present data on 26 adults and 139 ammocoetes taken at six Delaware localities (Famys Branch, 2.2 km NW of Millsboro, Sussex County, Delaware and see Rohde et al., 1975) on nine dates in March 1973, March and April 1974 and March 1975. Comparisons are made with northern populations and with Delmarva Peninsula *O. aepyptera*.

METHODS

Collecting was with a 3 m × 1.2 m straight nylon seine with 3.2 mm mesh. Initial preservative was 10 percent formalin; lampreys were then washed in water and placed into 40 percent isopropanol. Each specimen was later patted dry and measured to the nearest mm and weighed to the nearest 0.01 g. Unless otherwise noted, all lengths are total (TL). No correction was made for shrinkage. Churchill (1947) and Vladykov (1960) reported about 3 percent shrinkage for ammocoetes initially preserved in formalin. Eggs and larvae were measured to the nearest 0.01 mm with an ocular micrometer. All collections are now at Iowa State University (ISU 1851–1870), the Virginia Institute of Marine Science (VIMS 03155–03164), and the University of North Carolina-Institute of Marine Sciences (UNC-IMS 10288–10302).

LIFE HISTORY OF *OKKELBERGIA AEPYPTERA*

Habitat.—We collected *O. aepyptera* only in tributaries to Chesapeake Bay. The Bright's Branch study area was 100 m long and consisted of a pool upstream of a shallow, broad meandering stream. The pool was 6 m wide and 11 m long; maximum water depth was 1.5–2.0 m depending upon season and weather. The stream was 3–4 m wide and 0.4–0.8 m deep. The current throughout was relatively slow (usually .03 m/sec or less). Water temperature ranged from 5.5–19.0 C, dissolved oxygen from 5.6–10.5 ppm, and pH from 6.0–6.6. The pool bottom was of silt and decomposing debris (leaves, twigs). Sand predominated on the stream bottom, but areas of silt, gravel and organic debris were present. The water was bordered by forest primarily of mature red maple, *Acer rubrum*, and other low, wet-tolerant species such as swamp chestnut oak, *Quercus michauxii*; willow oak, *Q. phellos;* tupelo, *Nyssa sylvatica*; American holly, *Ilex opaca*; sweetgum, *Liquidamber styraciflua*; swamp magnolia, *Magnolia virginiana*; American hornbeam, *Carpinus caroliniana*; and bitternut hickory, *Carya cordiformis.*

The Chapel Branch site was similar to Bright's Branch except that the upstream pool was slightly deeper. The vegetation was similar to that along Bright's Branch. Water temperature ranged from 6.0–13.8 C, dissolved oxygen from 9.8–13.7 ppm, and pH from 6.4–7.0. In general, the other nine sites were typical, small, slow-moving Atlantic Coastal Plain streams. Water temperature ranged from 4.0–18.5 C, dissolved oxygen from 8.9–14.0 ppm, and pH from 6.5–7.3.

We took 27 fishes with *O. aepyptera* on the Delmarva Peninsula (Table 1). All are typical of slow waters and are generally widespread on the Coastal Plain.

Spawning Behavior.—Spawning was observed in Chapel Branch for 1½ hours on 24 March 1974. Stream width in the spawning area was 4.5–6.3 m; mean water depth was 35 cm (range 25–41 cm). The substrate was primarily sand and fine gravel. Water temperature was 13.8 C, dissolved oxygen 11.6 ppm, and pH 6.6. There were six nests from the lower pool edge to some six meters downstream. Each was 15–22 cm in diameter and circular or oval in outline. Two to 15 lampreys were observed together on each. One large nest of approximately 0.8 sq m was used simultaneously by several spawning groups.

Both sexes engaged in nest construction. Stones to 2.5 cm in diameter were moved by the fish fastening the oral disc to it and then pulling by throwing the body into vigorous lateral undulations. Stone movement was mostly downstream, with occasional lateral and less frequent upstream movement and deposition. There was no ap-

TABLE 1. Fishes taken with *Okkelbergia aepyptera* and *Lampetra lamottenii* at 16 Delmarva Peninsula sites, 1974–75. The number of sites at which taken is in parentheses. A plus indicates taken with both species; an asterisk indicates taken only with *O. aepyptera*.

Petromyzon marinus (2) *
Anguilla rostrata (11) +
Umbra pygmaea (11) +
Esox americanus (5) +
Esox niger (5) +
Notemigonus crysoleucas (7) +
Notropis bifrenatus (2) +
Notropis chalybaeus (2) *
Notropis procne (1) *
Erimyzon oblongus (12) +
Ictalurus natalis (2) *
Ictalurus nebulosus (3) +
Noturus gyrinus (5) +
Aphredoderus sayanus (12) +
Fundulus heteroclitus (1) *
Gambusia affinis (1) *
Acantharchus pomotis (3) *
Enneacanthus chaetodon (1) *
Enneacanthus gloriosus (8) *
Enneacanthus obesus (2) +
Lepomis auritus (1) *
Lepomis gibbosus (10) +
Lepomis macrochirus (8) +
Micropterus salmoides (1) *
Pomoxis nigromaculatus (1) *
Etheostoma fusiforme (9) +
Etheostoma olmstedi (14) +

parent coordination of stone movement, but one group of lampreys did appear to move stones to the same general vicinity. One stone was moved by two lampreys pulling on it simultaneously. Sand was also moved from the nest in the same manner as stones. In addition, sand was moved out by vigorous body undulations as the lampreys attempted to move stones. Nest construction activity of *O. aepyptera* is similar to that reported for other Northern Hemisphere species (Hardisty and Potter, 1971b) which move the substrate with the oral disc.

Brigham (1973) reported on nest building behavior of *O. aepyptera* in Tennessee. His observations differ considerably from ours. He concluded that nest construction by *O. aepyptera*, unlike other lampreys, was by individuals rather than by groups. He also noted that an individual did not move rock or sand by fastening to it with the oral disc and pulling, but rather that material was excavated by strong lateral undulations of the body. Seversmith (1953) noted some transport of stones by use of the disc, but observed that the nests were created by the pairing lampreys as they rapidly vibrated their bodies.

We observed actual spawning in six nests. In five cases, spawning involved but one pair, and in the sixth, two males spawned with one female. During the spawning act, the female attached by her disc to a rock at the upstream side of the nest. The male then attached dorsally to her head and curved the posterior part of his body around hers. Both then vibrated vigorously for 3 to 4 sec which signified the release of gametes. Their vibration disturbed the sand and partially buried the eggs. In some cases the female continued spawning behavior with a male even after all eggs had been released. We collected a large assemblage of 14 male and 1 female spawning lampreys from one nest. The male to female ratio for all adults collected in March 1974 and 1975 was 2.7:1. Seversmith (1953) observed a male to female ratio of 1:3 in late March.

Seversmith (1953) stated that *O. aepyptera* began to spawn in the spring when the water temperature reached approximately 16 C. Trautman (1957) suggested that it began to spawn when the temperature reached 10 C. We observed spawning at a water temperature of 13.8 C.

Fecundity.—Data on fecundity were obtained from 23 adult females and three transformers. These ranged from 82–120 mm (mean 98.5) and from 0.9–3.0 g (mean 1.8). This sample contained a mean of 874 eggs (range 610–1472), and is substantially lower than the 1164 eggs reported from one specimen by Seversmith (1953). We noted a positive relationship between greater number of eggs and greater size of the female (correlation coefficient 0.7828, Fig. 1). Vladykov (1951) reported a similar relationship for four Quebec lampreys.

Egg diameter ranged from 0.75–1.14 mm (mean 0.99) as based on measurements of 10 eggs from each of the 23 females and 3 transformers. The smaller eggs were from the transformers (collected in November) and ranged from 0.75–0.82 mm (mean 0.77). Eggs from adults ranged from 0.89–1.14 mm (mean 1.02). The relative fecundity index (no. eggs/g body weight) for the 23 adults ranged from 373–687 (mean 500). Although slightly higher, these values compare well with those reported by Hardisty (1971) for other

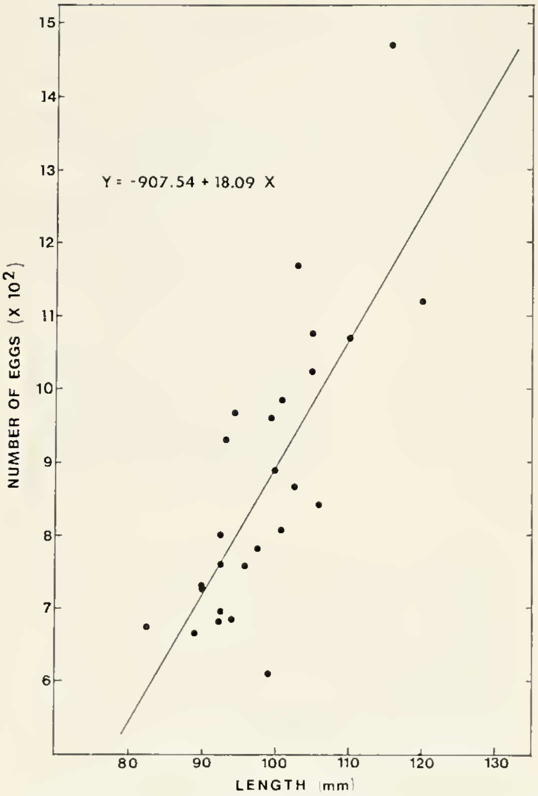

Figure 1. Relationship of egg number and total length of *Okkelbergia aepyptera* from Delaware.

nonparasitic lampreys. The maturity index (ovary weight/total weight) of the 23 adults ranged from 17.6–29.3 (mean 23.6).

We note that the eggs of nonparasitic lampreys such as *O. aepyptera* are larger than those of parasitic species. Vladykov (1951) reported a mean egg diameter of 0.89 and 1.01 mm, respectively, for the nonparasitic *L. lamottenii* and *Ichthyomyzon fossor*, and a mean of 0.73 and 0.86 mm, respectively, for the parasitic *I. unicuspis* and *Petromyzon marinus*. The relatively large mean egg size (1.02 mm) we noted in adult *O. aepyptera* conforms to this trend. Based on data for a number of species in Vladykov (1951) and Hardisty (1971) and on our data, however, we note that an increase in mean egg size is correlated with a decrease in total number of eggs produced. This relationship appears to be in agreement with Svardson (1949) who suggested that reduced fecundity in fishes might be favored by selection if such a reduction were accompanied by an increase in the size of the eggs, thus enhancing the chance of survival of the fry.

Early Life History.—*Okkelbergia aepyptera* eggs are spherical, adhesive and demersal. Several minutes after they were spawned their mean diameter was 1.53 mm (range 1.26–1.72, n = 23). The perivitelline space averaged 0.45 mm wide (range 0.27–0.64, n = 23). Egg color ranged from pale yellow to light green. Just prior to hatching, egg diameter averaged 2.16 mm (range 2.04–2.32, n = 10).

Eggs hatched in 24–26 days at water temperatures ranging from 5–16 C under aquarium conditions. At hatching the larvae averaged 3.40 mm (range 3.00–3.60, n = 8). Seversmith (1953) reported that at water temperatures ranging from 18–22 C, about 265 hours (11.04 days) were required for eggs in aquaria to hatch into 4 mm cream-colored larvae. We observed that at hatching the body was elongate, the eyespot visible, and the body bent ventrally in the caudal region. At 24 hours the larvae averaged 4.10 mm (range 3.80–4.70, n = 7) and the caudal region was straight. At about 48 hours they became active and showed lateral undulating movements of the body. However, at this stage they spent most of the time resting on their side. In nature, the young larvae later apparently move upstream from the spawning sites into the pools where they remain until they transform.

Although numerous collections were made below the spawning site throughout the year, no larvae were collected in that area, indicating an upstream movement of larvae. Several authors cited in Hardisty and Potter (1971a), however, inferred that young larvae are carried downstream and then deposited by the slower current over silt.

Age and Growth.—The length of ammocoetes, transformers, and adults from Bright's Branch was plotted for each sampling period and smoothed by use of 7 mm sliding averages. We determined that the larval period of *O. aepyptera* is usually 5.4 yrs by tracing the modes of each age group through the successive samples in figure 2. Age group 0 was first taken in June 1974 and can be easily traced (Fig. 2) through the samples to March 1975, when this group is in age group I (modal length 28 mm). Modal peaks for age group I in 1974 (age group 0 in 1973) are also evident and can be traced from a modal length of 27 mm in March 1974 to a mode of 50 mm in March 1975, when it is in age group II. Age group II in 1974 is represented by fewer specimens than is age group I but can be followed to March 1975, when it became age group III. Age group III in 1974 is more prominent and can be easily seen in the September and November 1974 samples. Good agreement is found between the younger age

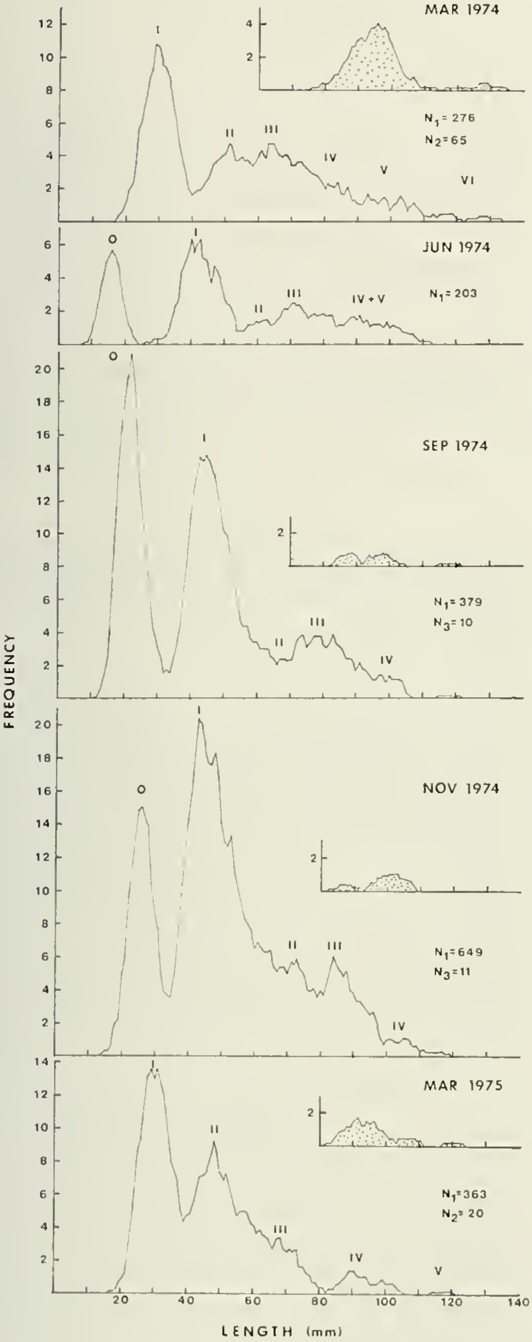

Figure 2. Length-frequency curves for ammocoetes, transformers, and adults of *Okkelbergia aepyptera* from Bright's Branch, Sussex County, Delaware. Data were smoothed by sliding averages of 7 mm. Stippled area in March 1974, 1975 represents adults; that in September, November 1974 represents transformers. N_1—Number of ammocoetes; N_2—Number of adults; N_3—Number of transformers.

group modes of the March 1974 and March 1975 samples. As Hardisty and Potter (1971a) pointed out, discerning the age groups of the older ammocoetes is difficult because growth evidently slows and the length-frequency distributions tend to merge.

We believe that there are two and possibly three additional age groups (IV–VI) present after age group III. Specimens in the first phase of transformation were first collected on 8 September 1974 and averaged 94.5 mm (range 86–114, n = 10). Simultaneously, non-transforming ammocoetes as large as 90 to 115 mm were also taken. This marked overlap in length-frequency distributions supports the view of others (Gage, 1928; Leach, 1940, 1951; Churchill, 1947; Potter, 1970; Potter and Bailey, 1972) of the existence of a rest period, or perhaps more correctly as suggested by Hardisty and Potter (1971a), of a period of arrested growth during which the metabolism is switched from growth to lipid accumulation. The large non-transforming ammocoetes we collected would then be in the arrested growth stage or in age group IV. Therefore, those ammocoetes in transformation would be in age group V. Because transformation does not occur until late summer, a larval life of at least 5.4 yrs is indicated. Some may even remain in the larval state for an additional year, as evidenced by the very large ammocoetes (longer than 125 mm) taken in March 1974. These would presumably transform the following fall. Our estimate of length of larval life is greater than the predicted one of three and four yrs, respectively, of Seversmith (1953) and Hubbs (1971). This difference may be a function of variations in the physical and biological factors in different river systems (Hardisty and Potter, 1971a). Because our series was collected from one isolated population, at successive times in one year, we feel confident of our estimate of the length of the larval stage.

Ten transforming lampreys (eight males and two females) taken in early September were in the early stages of external transformation, or in metamorphic stage 1 as defined by Manion and Stauffer (1970) for *P. marinus*. This stage is characterized by the beginning of fusion of lips, the presence of oral papillae, and the already evident eye. Hardisty and Potter (1971b) stated that most lampreys require five to six weeks to complete development of these and other external characteristics. Thus, we believe that transformation in our specimens first began in mid- to late August.

Growth of only the three younger age groups (0-II) was calculated as size limits of older groups

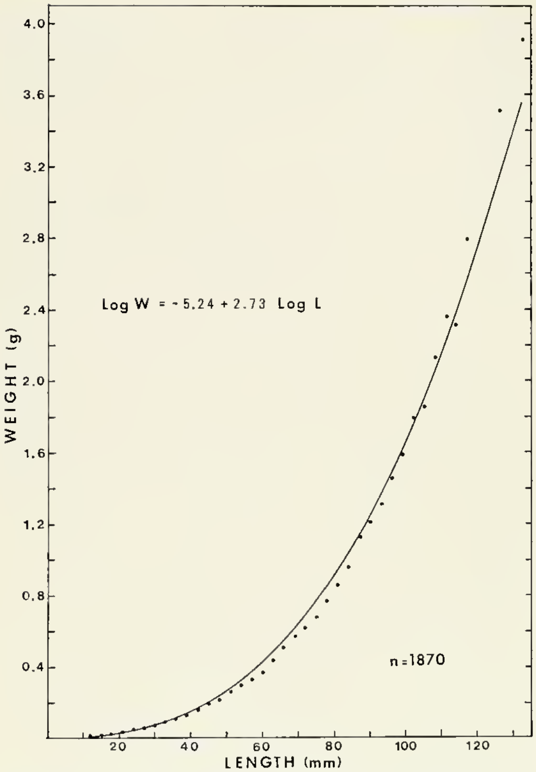

Figure 3. Length-weight relation of ammocoetes of *Okkelbergia aepyptera* from Bright's Branch, Sussex County, Delaware. Points are empirical averages by 3 mm length intervals; the curve is a plot of the length-weight equation.

were difficult to differentiate. Most growth took place from March to June (modal increase for age 0 = 12.0 mm, age I = 11.5 mm, age II = 11.5 mm). Growth then decreased from June to September (0 = 7.0 mm, I = 6.4 mm, II = 5.0 mm), and decreased further from September to November (0 = 4.0 mm, I = 0.0 mm, II = 5.0 mm). Very little growth occurred during the winter (November to March). A greater rate of growth in the spring followed by a decrease in subsequent seasons has been reported for other species by Hardisty and Potter (1971a).

Length-Weight Relationship and Condition Factor.—A total of 1870 ammocoetes was measured and weighed to determine length-weight relationships and condition factors. Empirical weights were plotted as averages for 3 mm length intervals. A linear regression was fitted to the data by least squares and was found to be Log W = –5.24 + 2.73 Log L. The weight of the ammocoetes thus increased as the 2.73 power of the length. Calculated weight was close to the observed, except in the larger ammocoetes where it was slightly less (Fig. 3). Manion and McLain (1971) noted the same in ammocoetes of *P. marinus*.

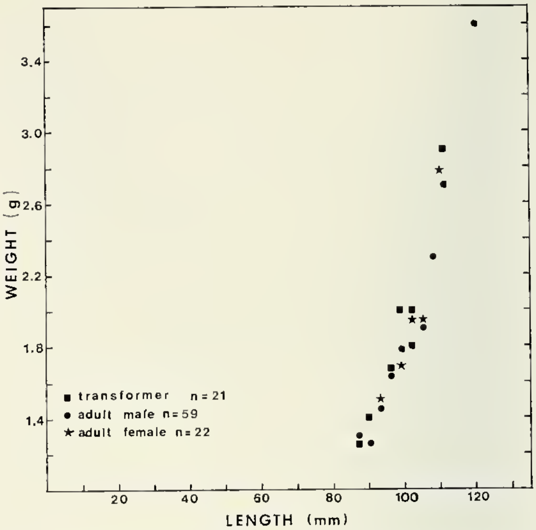

Figure 4. Length-weight relation of transformers and adults of *Okkelbergia aepyptera* from Bright's Branch, Sussex County, Delaware. Points are empirical averages by 3 mm length intervals.

We plotted length versus weight for all specimens taken in each sampling period (March, June, September, November) to determine whether there was seasonal variation in the length-weight relationship. For all samples, the length-weight relation was constant for ammocoetes up to 85 mm. However, for any given greater size, ammocoetes were heavier in March (mean weight 1.80 g) and June (mean 1.49) than in September (mean 1.27) and November (mean 1.31). Hardisty (1956, 1961) has shown that accumulation of lipids by the European *L. planeri* exhibited a marked correlation with density of phytoplankton during March, April, and May, followed by a decrease in summer. In general, the highest plankton density in the eastern United States occurs during the spring months (Welch, 1952), and these high plankton densities probably account for the greater weight per length ratios which we observed in spring.

We plotted empirical weights (in 3 mm length intervals) for 21 transformers and 81 adults (59 males, 22 females). For any given length, the heaviest were the transformers, followed by the females, and then the males (Fig. 4).

A coefficient of condition value (K), used to provide information on the relative well-being of a fish (Lagler, 1956), was determined with the

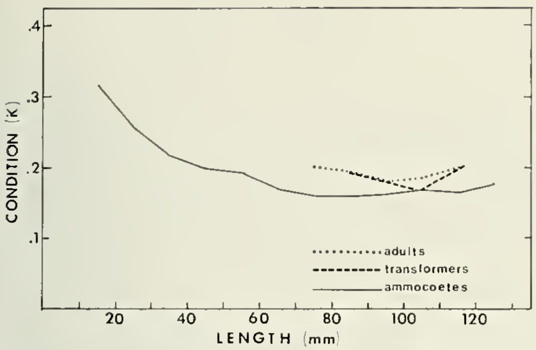

Figure 5. Length vs coefficient of condition (K) of *Okkelbergia aepyptera* from Bright's Branch, Sussex County, Delaware. Sample size of ammocoetes = 1870; transformers = 21; adults = 81.

Table 2. Mean coefficient of condition (K) values for ammocoetes of *Okkelbergia aepyptera* from Bright's Branch, Sussex County, Delaware, by 10 mm length interval groups for each sampling period (1974–75).

Length (mm)	March	June	Sept.	Nov.
11–20	–	.380	.274	.347
21–30	.279	.220	.249	.262
31–40	.246	.207	.184	.217
41–50	.208	.219	.192	.191
51–60	.176	.196	.178	.172
61–70	.180	.176	.169	.168
71–80	.160	.174	.153	.163
81–90	.171	.167	.160	.159
91–100	.173	.171	.157	.162
101–110	.171	.178	.150	.157
111–120	.173	–	.140	.155
121–130	.175	–	–	–

formula $K = W \times 10^5/L^3$ in Carlander (1969) and was plotted against length for lampreys in 10 mm length interval groups (Fig. 5). The smallest ammocoetes (11 to 20 mm group) had the maximum K value (0.32). A gradual decline in the coefficient was noted, with a low of 0.17 in the 71 to 80 mm and the 81 to 90 mm groups. It was 0.20 for the largest ammocoetes (121 to 130 mm). Values for adults were 0.18 to 0.20. Transformers had a K value of 0.17 to 0.20. For any given size, K for the transformers fell between those of the larger ammocoetes and the adults (Fig. 5). Hardisty (1944) found the same relationship in K values for the ammocoetes, transformers, and adults of *L. planeri.* As with the length-weight relationship in our specimens, we found a seasonal variation in K. Larger K values for each length group of ammocoetes were usually obtained for the March–June samples than for the September–November samples (Table 2).

Meristics and Morphology.—Little published information exists on the meristics and morphology of *O. aepyptera.* Branson (1970) gives proportional measurements and myomere counts for five adults from Kentucky while others (Raney, 1941; Vladykov, 1950; Cook, 1952; Seversmith, 1953; Trautman, 1957) present data only on myomere counts and total length.

Myomere counts on 517 specimens (all three life stages) ranged from 53–60 (mean 56.2) and agree with the data of Seversmith (1953), Blair et al., (1968), Eddy (1969), and Branson (1970). Vladykov (1955) stated that there are one or two myomeres fewer in ammocoetes than in transformers of the same species. We found no such difference in *O. aepyptera.*

Measurements (expressed in thousandths of the total length) indicate ontogenetic changes in body proportions from ammocoete to adult in our *O. aepyptera* (Table 3). Tail length increased with life history stage in males (four percent), while in females it decreased (five percent). Body depth in our sample increased (15 percent in males, 24 percent in females) and branchial length decreased (24 percent for each sex) with life history stage. Hubbs (1971) noted similar ontogenetic changes in *L. lethophaga.* The following averaged proportionally larger in the adult than in the transformer: the eye (21 percent for each sex), prebranchial length (40 percent in males, 24 percent in females), and disc length (57 percent in males, 32 percent in females). The disc length and second dorsal fin height in adult males are relatively greater than in adult females, and is characteristic of all lampreys, including *O. aepyptera.* The penis of male *O. aepyptera* is relatively long and ranges from 3–6 mm (mean 4.8, n = 10).

Adult *O. aepyptera* on the Delmarva Peninsula are relatively small. Our specimens range from 75–120 mm (mean 93.8, n = 146). The female (mean 94.6, n = 35) is not significantly longer than the male (mean 91.9, n = 111) at the 0.05 level. Seversmith (1953) noted a range of 90–120 mm TL (mean 103.7) for 22 Maryland adults. Trautman (1957) reported a range of 122–178 mm TL for Ohio specimens. Branson (1970) found that five Kentucky specimens ranged from 125–141 mm TL (mean 136.3) and Brigham (1973) observed five Tennessee individuals that ranged from 115–122 mm TL.

TABLE 3. Mean measurements in permillage of total length of *Okkelbergia aepyptera* from Bright's Branch, Sussex County, Delaware and *Lampetra lamottenii* from Delaware. Range values in parentheses.

Stage	Total length (mm)	Tail length	Trunk length	Branchial length	Pre-branchial length	Disc length	Body depth	Fin height	Eye length
					Okkelbergia aepyptera				
Ammocoetes (over 100 mm) n = 44	106 (100–130)	288 (265–308)	525 (503–562)	135 (108–154)	—	—	59 (52–65)	—	—
Transformers n = 9	95 (87–114)	298 (276–319)	529 (500–544)	109 (102–117)	80 (68–89)	28 (24–32)	67 (64–71)	—	14 (11–16)
Adults									
Male n = 29	98 (87–120)	300 (273–343)	464 (440–486)	102 (88–118)	112 (100–125)	44 (34–52)	68 (62–76)	57 (47–72)	17 (13–21)
Female n = 15	100 (89–120)	275 (253–300)	518 (501–547)	103 (91–110)	99 (90–106)	37 (32–42)	73 (52–85)	41 (32–53)	17 (12–21)
					Lampetra lamottenii				
Ammocoetes (over 100 mm) n = 19	121 (100–143)	297 (277–316)	520 (510–537)	133 (126–144)	—	—	55 (51–60)	—	—
Adults Male n = 10	128 (120–140)	306 (266–321)	475 (467–488)	101 (96–111)	123 (112–137)	53 (43–60)	65 (58–70)	51 (41–61)	21 (18–23)
Female n = 16	126 (103–149)	272 (240–298)	517 (485–535)	97 (90–106)	115 (104–126)	48 (42–53)	76 (66–87)	45 (35–59)	20 (17–26)

LIFE HISTORY OF *LAMPETRA LAMOTTENII*

Habitat.—Rohde et al., (1975) recorded *L. lamottenii* at six Delaware sites; these were given earlier. These localities range from the Piedmont well into the Coastal Plain, and all drain into Delaware and Indian River bays. *Lampetra* was collected in waters similar to those in which *O. aepyptera* was taken. At the Coastal Plain localities the water was clear and the current slow to medium; bottom type ranged from mud to sand and rooted vegetation was usually present. Water temperature ranged from 9.0–12.0 C, dissolved oxygen from 9.4–12.5 ppm, and pH from 6.7–7.0. At the Piedmont locality the water was clear, current medium to swift, and the bottom of gravel and rocks. We took 15 fishes with *L. lamottenii* in Delaware (Table 1). All are typical and generally widespread Coastal Plain species, and all were also collected with *O. aepyptera.*

Fecundity.—We obtained data on fecundity from nine adult females taken in March 1974 and 1975. Their range in length was 119–132 mm (mean 124.3), and in weight from 3.7–5.7 g (mean 4.5). Egg number ranged from 1327–2070 (mean 1691). This is considerably lower than the mean of 2339 reported by Vladykov (1951) and of 3787 given by Kott (1971). Unlike Vladykov (1951), we found no correlation between size of the specimen and the number of eggs (correlation coefficient 0.2794).

Egg diameter ranged from 0.94–1.19 mm (mean 1.06). Vladykov (1951) reported a mean of 0.89 mm for Quebec specimens. Egg diameter for Delaware specimens follows the trend already noted: that eggs of nonparasitic lampreys are larger than those of parasitic species.

Relative fecundity ranged from 297–531 (mean 381). This is lower than the mean of 450 reported by Vladykov (1951) for Quebec specimens, but close to that of 357 reported by Kott (1971) for Ontario specimens. Relative fecundity for our specimens is lower than that for *O. aepyptera* (mean 500).

The maturity index ranged from 16.2–25.4 (mean 20.8) and compares well with that of 20.0 for Quebec specimens (Vladykov, 1951). It is lower than the value we calculated for *O. aepyptera* (mean 23.6).

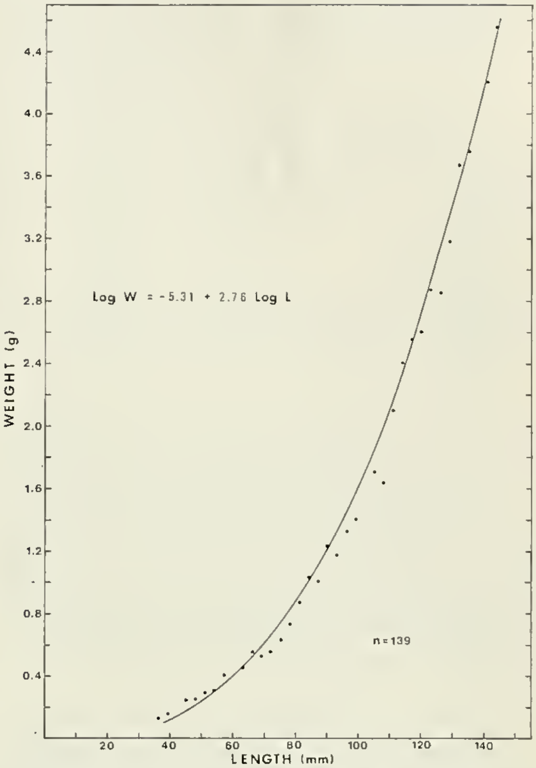

Figure 6. Length-weight relation of ammocoetes of *Lampetra lamottenii* from Delaware. Points are empirical averages by 3-mm length intervals; the curve is a plot of the length-weight equation.

Early Life History.—We observed spawning from 28 March to 4 April 1975. Water temperature ranged from 6.8–12.0 C. Nests were similar to but larger than those of *O. aepyptera.* The eggs are spherical, adhesive and demersal, and color is pale yellow to light green. Several minutes after they were spawned their mean diameter was 1.33 mm (range 1.18–1.63, n = 28). The perivitelline space averaged 0.30 mm wide (range 0.21–0.57, n = 28). Just prior to hatching, the egg averaged 1.45 mm in diameter (range 1.33–1.60, n = 19). They hatched in 20–22 days at a water temperature of 5–17 C under aquarium conditions. Larvae then averaged 2.60 mm (range 2.21–2.84, n = 6). The eyespot was visible and the body was elongate and bent ventrally in the caudal region. After 24 hours they averaged 3.40 mm (range 3.04–3.80, n = 13). They first became active at the 48-hour stage.

Age and Growth.—*Lampetra lamottenii* in Delaware attained a mean length of 38 mm (n = 6) at the end of the first year of life. This is approximately 10 mm longer than *O. aepyptera* at the corresponding age from the same geographic area.

Length-Weight Relationship.—We plotted length

TABLE 4. Comparison of morphometrics and meristics of adult *Lampetra lamottenii* from Delaware and from Big Creek, Ontario. An asterisk indicates figure expressed in permillage of total length.

	DELAWARE			ONTARIO (Kott, 1974)		
	n	x̄	range	n	x̄	range
Total length (mm)	26	125.5	103–149	457	188.0	161–217
Wt (g)	26	3.3	2.8–5.5	303	11.4	7.8–16.2
Myomere	26	68.9	66–72	303	69.1	65–74
Tail length*	26	285.3	240–321	303	294.8	262–323
Branchial length*	26	98.5	90–111	303	105.2	95–119
Disc length*	26	49.9	42–60	303	41.9	32–55
Body depth*	26	71.3	54–87	303	61.8	52–86
Second fin height*	26	47.4	35–61	303	38.6	23–53
Eye length*	26	20.1	17–26	303	15.4	12–21

and weight of 139 ammocoetes in the same manner as for *O. aepyptera* and fitted a linear regression to the data by the formula Log W = –5.31 + 2.76 Log L. Weight of ammocoetes was thus found to increase as the 2.76 power of the length. Calculated weights approximated the actual at all sizes (Fig. 6). The regression formula for *L. lamottenii* closely fits the formula for *O. aepyptera.*

Meristics and Morphology.—Considerable data on the meristics and morphology of *L. lamottenii* have recently appeared (Branson, 1970; Manion and Purvis, 1971; Kott, 1974). We found that the adult from Delaware is smaller than that of specimens from most other parts of the range of the species. Our specimens ranged from 103–149 mm (mean 126.6, n = 26). Branson (1970) reported on Kentucky individuals that ranged from 138–165 mm TL (mean 150.8, n = 6), Manion and Purvis (1971) give lengths of 111–196 mm TL (mean 154.0, n = 375) for upper Great Lakes specimens, Gage (1893) reported on New York specimens of 143–170 mm TL (mean 154.4, n =20), Vladykov (1951) gives lengths of 116–158 mm TL (mean 143.0, n = 10) for Quebec specimens, and Kott (1974) recorded lengths from 161–217 mm TL (mean 188.0, n = 457) for Ontario specimens. Only adults from New Hampshire (Sawyer, 1960) were smaller (range 106–132 mm TL, mean 115.6, n = 13) than Delaware adults. There was no significant difference in total length at the 0.01 level between Delaware adult females (mean 128.4 mm, n = 10) and males (mean 125.5 mm, n = 16).

Myomere counts could be reliably made only on those specimens (n = 101) larger than 66 mm, and they ranged from 64–72 (mean 68.0). Vladykov (1949) reported a range of 64–70 (mean 67.5, n = 154) and Kott (1974) noted a range of 65–74 (mean 69.1, n = 303).

The same ontogenetic changes in body proportions observed from ammocoete to adult *O. aepyptera* were observed in *L. lamottenii* (Table 3). Tail length increased with life history stage in the male (three percent), while in the female it decreased (8 percent), body depth increased (18 percent in the male, 38 percent in the female), and branchial length decreased (24 percent in the male, 27 percent in the female). Sexual dimorphism is marked: disc length was 10 percent greater and the second dorsal fin 13 percent higher in the male than in the female. These differences are generally similar to our observations for *O. aepyptera* and to that reported for other lampreys (Hubbs, 1971; Kott, 1974). However, noticeable differences in body proportion are evident in the adult between the Delaware population of *L. lamottenii* and the Ontario population studied by Kott (1974). Delaware specimens have a relatively longer disc, larger eye, shorter branchial length, deeper body, higher second dorsal fin, and shorter tail (Table 4). Penis size in our specimens is smaller than that of *O. aepyptera,* and ranged from 1.0–2.5 mm (mean 1.9, n = 9).

One ammocoete (89 mm) collected at Stockley Branch on 9 March 1975 had an accessory tail (9 mm long). It originated on the right side 4 mm behind the cloaca and curled ventrally. Manion (1967) reported on morphological abnormalities in this and other lampreys of the Lake Superior basin, and found only one specimen with an additional tail of 2726 specimens of *L. lamottenii* examined.

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FEEDING ECOLOGY OF THE PIT SCULPIN, *COTTUS PITENSIS*, IN ASH CREEK, CALIFORNIA

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Abstract: The diet of the Pit sculpin, *Cottus pitensis*, consists mainly of benthic invertebrates and is similar to the diet of other stream-dwelling members of the genus *Cottus*. They feed at all hours but show a peak of feeding intensity in the early morning. Electivity indices indicate that they are highly selective in their feeding but that the reasons they select particular organisms are complex. They appear to be ecologically segregated from the three species that commonly occur with them, speckled dace (*Rhinichthys osculus*), Sacramento sucker (*Catostomus occidentalis*), and rainbow trout (*Salmo gairdneri*).

Freshwater sculpins of the genus *Cottus* are important components of cold water stream ecosystems over much of North America. Consequently, as part of a much larger study of the ecology of the fishes of the great Sacramento-San Joaquin drainage system of California, we undertook an intensive study of the feeding ecology of Pit sculpin, *Cottus pitensis*. The Pit sculpin is one of the most abundant and widely distributed fishes of the Pit River and its tributaries, which drain much of the northeastern corner of California before flowing into the Sacramento River. In Oregon, the Pit sculpin is considered to be a rare, and potentially endangered, species because of its restricted distribution in the state (Bond, 1966). Little is known about the biology of this species, partly because it has been recognized only recently as being distinct from the more widely distributed riffle sculpin, *Cottus gulosus* (Bailey and Bond, 1963.) A major purpose of this paper is to report on its feeding habits. However, since the diets of most stream dwelling species of *Cottus* have been found to be similar (e.g., Bailey, 1952; Bond, 1963; Millikan, 1968; Jones, 1972; Novak and Estes, 1974; Small, 1975; Moyle, 1976), we examined the feeding chronology of the Pit sculpin, factors affecting its selection of prey organisms, and the diets of three other species of fish that commonly occur with it.

METHODS

Fish were collected from Ash Creek, Lassen and Modoc Co, one of the larger tributaries to the upper Pit River. This stream was chosen because of its moderate size (typical summer flows, 400–700 l/sec), accessibility, and substantial populations of native fishes. All fishes were collected with a Smith-Root type Va electrofisher. Daytime samples were taken on 5 May, 21 June, 24 July, and 28 October 1973, and a night time sample on October 27, 1973. On 7–8 June 1974, samples of fish were collected at four hour intervals for twenty-four hours. Most fish were taken in riffles near the middle of the stream. All fish were preserved immediately after capture in a four percent solution of buffered formalin. Although the main object of the sampling was to obtain Pit sculpins, samples of speckled dace, *Rhinichthys osculus*, juvenile Sacramento sucker, *Catostomus occidentalis*, and rainbow trout, *Salmo gairdneri* were preserved when they were taken in association with the sculpins. Sacramento squawfish, *Ptychocheilus grandis*, hardhead, *Mylopharodon conocephalus*, California roach, *Hesperoleucus*

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Table 1. Mean percent composition by weight of all bottom samples (N = 88) from Ash Creek, May 1973 to June 1974, and caloric values of invertebrates collected 21 June 1973. Number in parentheses under kilocalories per organism is the number of organisms upon which the determination was based.

Organism	Percent composition	Kcal per gm dry wt.	Kcal per organism
Ephemeroptera			
Baetis	< 1	–	–
Ephemerella	2	–	–
Isonychia	3	4.621	1.194(1)
Centroptilum	1	–	–
Ameletus	1	–	–
Heptagenia	1	6.744	0.022(2)
Iron	4		–
Plecoptera			
Acroneuria	8	5.395	0.100(26)
Isoperla	< 1	–	–
Hemiptera			
Ambrysus	2	9.664	0.218(4)
Megaloptera			
Sialis	< 1	–	–
Tricoptera*			
Hydropsyche	34	5.131	0.021(66)
Rhyacophila	6	5.792	0.055(29)
Brachycentrus	11	4.129	0.024(41)
Helicopysche	3	7.138	0.103(20)
Leptocella	< 1	–	–
Limnephilidae	5	0.893	0.737(4)
Lepidoptera			
Paragyractis	2	–	–
Coleoptera			
Eubrianax	< 1	–	–
Dystiscidae	< 1	–	–
Elmidae	< 1	–	–
Diptera			
Atherix	< 1	–	–
Limnophila	5	5.914	0.166(3)
Chrionomidae	1	–	
Gastropoda			
Physa	4	1.427	0.223(8)
Ancola	< 1	1.393	0.270(3)
Fluminicola	3	1.245	0.049(25)
Pelycepoda			
Sphaerium	2	–	–
Turbellaria	1	–	–
Hirundinea	1	–	–
Oligochaeta	1	–	–
Amphipoda	1	–	–
Dace larvae	1	–	–

* All case cadisflies were weighed without cases.

symmetricus, brown trout, *Salmo trutta*, and Pit-Klamath brook lamprey, *Lampetra lethophaga* were taken with the sculpins on occasion, but in numbers too small to be worth using for feeding habit studies. The standard length (SL) measurements of were made before the fish were used for stomach content analyses.

Invertebrates were collected using a 0.095 square meter Surber sampler. Like the fish, the invertebrates were collected mostly from the middle of riffles in order to reduce the variability between samples. The number of bottom samples taken during any day ranged from four to thirty for a total of 88. They were preserved in a two percent formalin solution. Within a week after collection, they were sorted by hand and the insects were identified using the keys in Usinger (1971). The wet weights of all individuals of each species were obtained by weighing them together on an analytical balance sensitive to 0.01 mg. On 21 June 1973 samples of benthic invertebrates were brought back to our laboratory alive, where they were weighed, dried in a drying oven, weighed again, and then their caloric content determined with a Parr Model 1341 semimacro bomb colorimeter (Table 1). A known amount of benzoic acid was added to some insect pellets in order to have a pellet of the minimum size of 0.5 gm. This was corrected for in the final calculations.

Stomach contents of the fishes were sorted and the relative importance of each item to the diet determined using the point volume estimate of Hynes (1950). Because of the difficulty of accurate determination of different genera of baetid mayflies from the fragments in the stomachs, they were lumped together under Baetidae, although the genera were determined in the bottom samples. In order to get an idea of the degree of feeding intensity of each fish species during each sample period, a stomach fullness index (Windell, 1971) was calculated:

$$100 \times \frac{\text{Average number of points per stomach}}{\text{Average standard length of fish (mm)}}.$$

An index of the average size of the organisms consumed by the fish during each sample period was obtained by dividing the total number of points assigned by the total number of organisms. The electivity index (E) of Ivlev (1961) was calculated for species in each sample period that made up more than three percent of the weight or volume of either (or both) the bottom samples or the stomach contents. This index is $R - P/R + P$ where R is the relative frequency of the prey item in the stomach, and P is the relative frequency of the prey item in the bottom samples. An organism that made up less than three percent of both bottom samples and stomach contents was considered to be too uncommon for the electivity index to be meaningful. Percentages based on weight and volume of food organisms were used interchangeably in the calculation of the electivity indices since percentages obtained by the two methods are approximately equivalent (Windell, 1971). For Ivlev's electricity index, a value of + 1.00 indicates complete positive selection by the fish for a particular organism, while a value of −1.00 indicates complete selection against the organism.

In order to test the hypotheses that size, abundance, and caloric value of the prey organisms are each characteristics of the prey that strongly influence predation on them by sculpins, the following comparisons were run, using the Spearman test for rank correlation (Langley, 1970): 1, size of prey and electivities: 2, size of prey and percent of stomach contents; 3, percent in bottom samples and electivities; 4, number in bottom samples and electivities; 5, percent in stomachs and percent in bottom samples; and 6, caloric content of prey and electivities.

RESULTS

Pit sculpins feed mostly on the benthic larvae of aquatic insects, although other aquatic organisms are taken on occasion (Table 2). Fish were not found in the stomachs of sculpin during this study. On 21 June 1973, larval speckled dace were common in Surber satmples but none were found in sculpin stomachs. However, during other studies on Ash Creek and other streams of the Pit River system, sculpins were occasionally collected and preserved that had unusually distended stomachs. These fish had usually consumed another, smaller, sculpin.

A comparison of day and night samples of sculpins taken on 27–28 October 1973, indicates that the sculpins will feed during both light and dark hours (Table 2). Examination of the diel feeding cycle of 7–8 June 1974, confirmed these findings (Table 3). Feeding activity appeared to be most intense in the early morning (0400 and 0800 samples). The June samples indicate that larger organisms, especially stonefly larvae, are taken at night that are taken during the day, although the October samples do not reflect this.

The electivity values show that Pit sculpins are highly selective in their feeding (Table 2). Some

TABLE 2. Percent composition of the stomach contents of Pit sculpins from Ash Creek, based on point-volume estimates. Numbers in parentheses are electivity values, which were calculated only if the organism exceeded three percent of either the stomach contents or the bottom samples.

Date	5/73		6/73		7/73		10/73*		10/73	6/74		Total	
Time	1000		1330		1400		1030		22	All			
Number	33		44		50		28		55	140		317	
Ave. SL (mm)	70		71		72		68		2230	61			
Ephemeroptera													
Baetidae	25	(+0.89)	15	(+0.72)	41	(+0.73)	10	(+0.29)	11	22	(+0.69)	25	(+0.56)
Heptageniidae	1		3	(−0.22)	15	(−0.13)	0		3	3	(+0.20)	2	(−0.42)
Plecoptera													
Acroneuria	21	(+0.75)	6	(+0.78)	2	(−0.61)	18	(+0.47)	1	32	(+0.39)	19	(+0.40)
Hemiptera													
Ambrysus	0	(−1.00)	2		0		13	(+1.00)	12	< 1		3	(+0.20)
Tricoptera													
Hydropsyche	12	(−0.45)	36	(+0.04)	20	(+0.11)	16	(+0.28)	12	18	(−0.47)	20	(−0.26)
Rhyacophila	0		3	(−0.69)	2	(−0.66)	0		0	0		< 1	(−0.71)
Brachycentrus	2	(−0.62)	12	(−0.42)	8	(−1.00)	10	(+0.27)	1	1	(+0.43)	5	(−0.38)
Helicopsyche	1	(−0.88)	5	(+0.16)	6	(−0.54)	4	(+0.28)	4	1	(−0.80)	3	(0.00)
Limnephilidae	0		0		0		0		0	1		< 1	
Lepidoptera													
Paragyractis	25	(+0.85)	11	(+0.80)	1		13	(+0.79)	21	10	(+0.82)	11	(+0.33)
Diptera													
Limnophila	2	(−0.56)	0		0	(−1.00)	0	(+0.07)	7	6	(+0.20)	3	(−0.25)
Chironomidae	4	(+0.66)	< 1		1		3	(+0.50)	0	3	(+0.50)	1	
Atherix	0		0		0		8	(+0.20)	4	0		1	
Miscellaneous													
Aquatic organisms	8		6		4		5		24	3		7	
Percent empty stomachs	0		11		20		3		0	6		8	
Fullness index	31		13		7		15		11	20		17	
Average number points per organism	1.6		3.5		3.4		2.4		1.7	2.4		2.6	

* Electivity values calculated from day and night samples combined.

TABLE 3. Feeding chronology of the Pit sculpin, 7–8 June 1974, as indicated by the percent composition of stomach contents by volume (point-volume estimates).

Time Number	2000 27	2400 23	0400 18	0800 22	1200 20	1500 30	Average 140
Ephemeroptera							
Baetidae	19	37	7	22	40	22	22
Heptageniidae	1	2	4	4	0	5	3
Plecoptera							
Acroneuria	29	32	59	19	8	28	32
Tricoptera							
Hydropsyche	19	10	14	18	28	28	18
Brachycentrus	1	2	1	< 1	0	1	1
Helicopsyche	0	0	2	0	< 1	0	1
Limnephilidae	6	0	0	0	0	0	1
Lepidoptera							
Paragyractis	16	2	5	20	10	4	10
Diptera							
Limnophila	1	6	7	12	2	4	6
Chironomidae	4	1	< 1	3	9	6	3
Simulidae	0	7	0	1	2	1	2
Miscellaneous aquatic organisms	4	1	1	1	0	1	1
Percent empty stomachs	7	4	22	0	5	0	6
Fullness index	14	18	36	26	18	16	20
Average points per organism	1.7	3.1	5.1	1.0	2.5	1.7	2.4

organisms showed consistently positive electives (baetid mayflies, *Paragyractis*), while the electivity values of others, including some of the most important organisms in the diet, varied from one sampling period to another. Nymphs of the stonefly *Acroneuria* were strongly selected for on all days except 24 June 1973. Larvae of the web-spinning caddisfly *Hydropsyche*, which were the most abundant organisms both in the bottom samples and in the stomachs, were either consumed roughly in proportion to their abundance in the environment or were moderately selected against. None of the Spearman rank correlation comparisons between electivity and size, abundance, or caloric value of each prey species were significant ($P > 0.05$). Similarly, the comparisons between percents of the prey species in the diet and their percents in the bottom samples, as well as with their sizes, were also not signficant.

The diet and electivity values of speckled dace from Ash Creek closely resemble those of Pit sculpin (Table 4). However, dace feed on slightly smaller organisms, show little feeding activity in the early morning when sculpins are most active, and consume algae and detritus in addition to benthic insect larvae. The feeding pattern of juvenile Sacramento sucker appears to be similar to that of speckled dace (Table 5). Their diet, however, is primarily detritus. The invertebrates they consume are mostly the early instars of baetid mayflies and the larvae of chironomid midges. Both insect groups are found in clumps of filamentous algae or associated with soft bottoms. The stomach contents of 13 rainbow trout (average SL, 86 mm), from three of the sample days, indicated they feed both on terrestrial insects (49 percent by volume) and aquatic insects (51 percent). A wide variety of aquatic insects were consumed but most abundant (13 percent) were the nymphs of baetid mayflies. This diet is similar to that of many other rainbow trout populations that have been studied more intensively (summarized in Moyle, 1976).

TABLE 4. Percent composition of the stomach contents of speckled dace from Ash Creek, based on point-volume estimates. Numbers in parentheses are electivity values, which were calculated only if the organism exceeded three percent of either the stomach contents or the bottom samples.

Date	6/73		7/73		10/73		6/74*		6/74	6/74	6/74	6/74	6/74		
Time	1330		1400		1030		2000		2400	0400	0800	1200	1500		
Number	33		30		23		16		15	9	11	11	27	159	All
Ave. SL (mm)	57		64		66		67		51	59	59	44	64	59	–
Ephemeroptera															
Baetidae	49	(+09.0)	24	(+0.30)	0	(–1.00)	26	(+0.78)	58	0	0	8	32	31	(+0.64)
Heptageniidae	1	(–0.61)	19	(+0.10)	0		3	(+0.26)	10	0	0	0	0	6	(+0.09)
Plecoptera															
Acroneuria	0		1	(–0.86)	2	(–0.80)	0	(–0.64)	2	0	0	0	8	1	(–0.78)
Tricoptera															
Hydropsyche	40	(+0.09)	22	(+0.16)	0	(–1.00)	40	(–0.37)	0	0	0	6	26	27	(–0.11)
Rhyacophila	3	(–0.71)	24	(+0.83)	0		0		0	0	0	0	0	1	(–0.71)
Brachycentrus	3	(–0.85)	0	(–1.00)	0	(–1.00)	6	(+0.47)	6	0	73	24	10	7	(–0.28)
Lepidoptera															
Paragyractis	2	(+0.18)	2		0		10	(+0.82)	0	0	27	31	9	4	(+0.33)
Diptera															
Limnophila	0		3	(–0.56)	0	(–1.00)	0	(–0.80)	0	0	0	12	1	1	(–0.66)
Chironomidae	1		1		3		1		8	0	0	0	4	2	
Simuiidae	0		0		0		3		2	0	0	0	1	1	
Miscellaneous invertebrates	1		1		26		9		7	0	0	19**	10***	8	
Algae	1		2		69		2		8	0	0	0	0	7	
Percent empty stomachs	9		3		78		0		13	100	64	18	26	31	
Fullness index	17		16		4		20		8	0	2	7	8	12	
Prey size index	1.4		2.5		–		1.5		2.0	0	2.8	2.3	1.6	2.2	

* Electivity values for entire day (n = 89).
** Includes 16 percent dace larvae.
*** Includes 8 percent dace eggs.

TABLE 5. Percent composition of the stomach contents of juvenile Sacramento sucker from Ash Creek, based on point-volume estimates.

Date Time Number Ave. SL (mm)	10/73 1030 16 89	 2400 13 75	 0400 5 114	6/74 0800 19 78	 1200 4 68	 1500 6 83	All – 63 83
Ephemeroptera							
Baetidae	0	46	45	8	9	27	12
Plecoptera							
Acroneuria	1	3	0	0	0	0	1
Tricoptera							
Hydropysche	1	0	0	0	0	5	1
Brachycentridae	4	0	0	0	0	0	1
Diptera							
Chironomidae	3	18	45	8	9	24	8
Simulidae		1	10	0	0	0	1
Algae	17	0	0	23	20	11	10
Detritus	74	32	0	61	62	32	66
Percent empty stomachs	25	8	80	79	25	17	41
Fullness index	34	11	2	1	8	8	4

DISCUSSION

The diet of the Pit sculpin is similar to that of other stream dwelling members of the genus *Cottus*. In most studies of *Cottus*, however, fish have been collected only during the day. The high intensity of nocturnal feeding found in this study, coupled with dietary differences observed at different times of the day, indicate that future ecological studies involving *Cottus* should include both day and night samples.

The electivity values show that sculpins (and speckled dace as well) are highly selective in their feeding. The factors that influence the selection of prey are complex, however, since two of the more obvious factors, size and abundance, do not appear to operate independently of other factors, or even independently of each other (Werner and Hall, 1974). However, baetid mayfly nymphs, *Acroneuria* nymphs, and *Hydropsyche* larvae, which are among the most abundant organisms in the bottom samples, are also the most abundant organisms in the stomachs, although the electivity values indicate that only the baetid mayflies and *Acroneuria* are preferred prey. Many of the abundant invertebrates are presumably not taken by the fish because they are unavailable to them (e.g., small clams and cranefly larvae that burrow into the bottom). Although we could not show in our study that the caloric value of the prey affected prey selection, it was probably nevertheless a contributing factor. Snails, for example, were rarely consumed and their caloric value was quite low because a high percentage of their body weight was indigestible shell. In general, Pit sculpins consume invertebrates that crawl actively over the bottom surfaces but that lack heavy shells or cases. However, the electivity values from this study, as well as from other studies of sculpins (Novak and Estes, 1974; Small, 1975), may be greatly influenced by the method of bottom sampling as well as by the method of fish capture. Attempts were made in this study to minimize the effects of sampling by limiting the sampling for both fish and invertebrates to the middle of the stream but sampling bias was probably not eliminated.

The apparent overlaps in the diets of the four fish species that are abundant in the riffles of Ash Creek is of interest because various species of sculpin (*Cottus*), dace (*Rhinichthys*), sucker (*Catostomus*), and trout (*Salmo*) occur together in coldwater streams throughout North America. Although the ecological interactions of these four species groups are in need of more study, observations on Ash Creek indicate that they are well segregated ecologically. Much of the diet of rainbow trout is made up of terrestrial insects and most of the aquatic insects are probably taken as drift. The opportunistic nature of trout feeding is indicated by the wide variety of invertebrates likely to be found in any one stomach (an average of 5.0 different kinds per stomach in the Ash Creek trout, as opposed to 2.6 for Pit sculpin and 2.3 for speckled dace). Sacramento suckers are bottom browsers that consume mostly algae and, detritus, and the small invertebrates associated with them. These invertebrates are largely unavailable to the other fishes. The diets and electivity values of Pit sculpin and speckled dace closely resemble each other in this study but this may be at least partially an artifact of the confinement of collections of fish to the middle of the riffles. While the fast water is the main habitat of the sculpin, the dace are much more widespread in the stream, occurring abundantly in the shallow stream edges and in pools as well as in the riffles. Even with this sampling bias, speckled dace generally were found to consume smaller organisms than sculpins and usually to show strong negative selection for *Acroneuria* nymphs, which are selected by sculpins. The two species differ in their methods and times of feeding. The dace swim about in small schools, actively picking out their prey between the rocks. Sculpin are more solitary and stationary, ambushing active prey. Dace feed mostly during the day, while sculpin feed during both the day and night, with the most activity at night. In addition, the production of benthic invertebrates in Ash Creek probably is high enough during the summer so that the insects do not constitute a limiting resource. One indication of this is that in October, when water conditions are approaching those of winter and invertebrate production is more likely to be limiting, the dace have switched to feeding mostly on algae and detritus, while the diet of the sculpins remains the same.

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HERMAPHRODITISM AND GONADAL TERATOMA-LIKE GROWTHS IN STURGEON (*ACIPENSER*)

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Abstract: Two adult sturgeon (*Acipenser oxyrhynchus* and *A. brevirostrum*) from the Hudson River exhibited ovotestes. In the former, testicular and ovarian tissues were mostly separated; in the latter, intermingled. One ovotestis of *A. brevirostrum* contained small, cyst-like structures that consisted of disorganized tissues including cartilage, bone, blood vessels, gut epithelium, and connective tissue. These teratoma-like structures may have been the result of the abnormal development of a parthenogenetic or self-fertilized egg rather than a neoplastic process. None of the abnormal growths in fishes that have been described as teratomas can be considered unequivocally as examples of a true tumor or neoplasm.

The discovery of teratomatous growths in the ovotestis of a hermaphroditic sturgeon focused our attention on the juxtaposition of these two rare conditions and raised questions about their possible interrelationship. For this reason, as well as the inherent interest in such a unique specimen, we undertook an analysis of its abnormalities.

The occasional appearance of hermaphroditic sturgeon in the Hudson River had been brought to our attention by Robert H. Boyle who obtained two specimens for our examination from Ace Lent, premier fisherman of Verplanck, New York. The lower Hudson still supports a small commercial fishery centered at Verplanck, 40 miles upstream from the Battery at the mouth of the river (Boyle, 1969). Two species of sturgeon, the Atlantic and the shortnose, enter the catch and each of these provided a single hermaphrodite.

RESULTS

The hermaphroditic Atlantic sturgeon, *Acipenser oxyrhynchus* Mitchill, weighed approximately seven pounds and was caught off Stony Point on 15 November 1965. Only its gonads were available for examination. The hermaphroditic shortnose sturgeon, *Acipenser brevirostrum* Lesueur, was caught in upper Haverstraw Bay on 19 March 1969. This fish had been skinned and the head and tail removed before it was received, but the viscera were intact and in place. Both specimens had been frozen soon after their unusual nature was recognized. In the laboratory they were thawed and fixed in 10 percent formalin. After the gonads had been described, drawn, and photographed, small pieces were removed and embedded in paraffin, sectioned at 10 microns, and stained with Masson's trichrome and with hematoxylin and eosin.

The gross configuration of the visceral organs of the hermaphroditic shortnose sturgeon, including its gonads (Fig. 1), did not differ significantly from that described in other sturgeons by Ryder (1890) and Marinelli and Strenger (1973). The ovotestes of both hermaphrodites appeared to be approaching ripeness. Large, heavily pigmented ova were present, and the testicular areas were creamy white. In neither pair were the male and female regions bilaterally symmetrical. One ovotestis of the Atlantic sturgeon was predominantly male, the ovarian tissues being confined to one end. The other was predominantly female with patches of testicular material located at either end. The demarcation between regions was definite; male and female tissues rarely intermingled (Fig. 2a).

In contrast, almost all of the ovotestes of the shortnose sturgeon consisted of eggs embedded in a matrix of testicular tissues (Fig. 1 and 2e). In this species, the membranes that line the body cavity and cover the viscera are heavily pigmented, and the nearly white testicular tissues stood out sharply against the black of the eggs and the gut. Except for a predominantly testicular area near the anterior end and in the middle of the right gonad and near both ends of the left, the ovotestes presented a more or less uniform admixture of black and white components. Only in the abnormal association of male and female elements did the ovotestes appear to differ grossly from the gonads of normal sturgeon collected at the same time.

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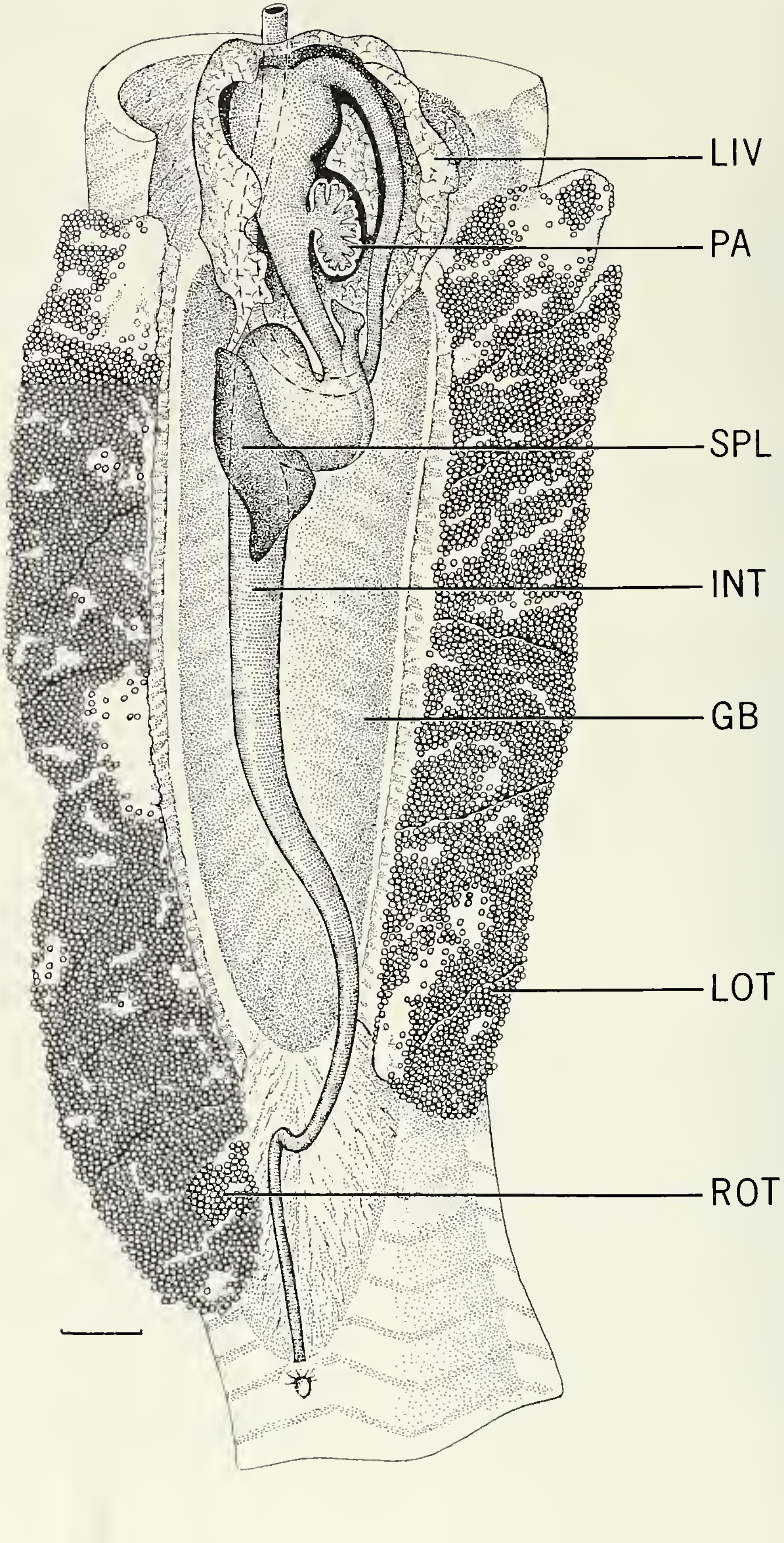
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Examination of the histological preparations revealed no sign of any inhibitory influence that the ovarian and testicular tissues may have had on each other. Developing ova and testicular elements lay in a spongy connective tissue stroma, and in the shortnose hermaphrodite, they frequently lay side by side (Fig. 2b,e). Many sperm were seen outside of the seminiferous tubules of the shortnose sturgeon, quite a few within the follicles and occasionally in the zona radiata of the more mature ova (Fig. 2f). Although rupture of testicular tubules could have occurred during the freezing and thawing of the ovotestes, the abundance of free sperm in some of the follicles appears, at least in part, not to be an artifact.

During examination of the left ovotestis of the shortnose sturgeon, two clear vesicles were found: one nearly spherical and about a centimeter in diameter, the other irregularly ovoid and slightly larger. Histological study indicated these to be teratomas. They consisted of a large central cavity and a few smaller ones surrounded by various kinds of tissue arranged in a bizarre fashion (Fig. 2b). Poor fixation and the disorganized arrangement of the tissues made their identification difficult. The cavities were lined with epithelial cells, some of which formed a stratified epithelium. A number of the epithelial cells were ciliated. Goblet cells were present, and glandular tissues occurred in what could be called a submucosa (Fig. 2b,d). Some of these formations were distinctly reminiscent of parts of a digestive tract. Much of the solid portion of the two cysts consisted of connective tissues, both dense and loose, and parts of these were vascularized (Fig. 2c). Masses of hyaline cartilage were easy to recognize (Fig. 2b). There was a little bone and nervous tissue (Fig. 2b), but no striated muscle could be identified. Subsequent investigation revealed two more vesicles; a piecemeal examination of the ovotestes might well have disclosed more, but this process would have destroyed the specimen.

DISCUSSION

When rare phenomena occur coincidentally, a causal connection between them becomes a distinct possibility. Both hermaphroditism and teratomas are rare in the sturgeons. No teratoma has been previously reported in any acipenseriform, and despite the innumerable sturgeon roes that have passed through the hands of fishermen or preparators of caviar, few instances of hermaphroditic gonads have been reported in these heavily exploited fishes.

The early accounts of hermaphroditic sturgeon by Pallas (1773) and Benecke (1886), to which Weber (1884) indirectly and somewhat inaccurately referred, were based on hearsay evidence. The species said to be involved were *Huso huso* and other unnamed European forms. There does not appear to have been a single first hand report on hermaphroditic sturgeon published until Ziemiankowski (1954). This investigator described an *Acipenser gueldenstaedti* with an ovary on the right and a testis on the left. The only other reports known to us are those of Chirkina (1957) and Nikolyukin (1964) who found a number of hermaphrodites among artificially produced hybrids between *Huso huso* and *Acipenser ruthenus*.

In the most recent comprehensive review of neoplastic diseases in fishes, Mawdesley-Thomas (1971) called attention to the rarity of teratomas in non-tetrapodous vertebrates; in fact, if we accept the restrictions of the authoritative pathologist, Rupert A. Willis, only the three cases described by Stolk (1953, 1959) in the ovary of two guppies and a platyfish and our own example from the shortnose sturgeon might qualify as true teratomas. According to Willis (1967 and earlier publications), "A teratoma is a true tumour or neoplasm composed of multiple tissues of kinds foreign to the part in which it arises." Histological examination is usually sufficient to establish the composition of whatever growth may be in question, but the criterion as to what comprises a true tumor, or neoplasm, at least in the case of the teratoma, has been a matter of controversy. Willis stated that a true tumor or neoplasm must display "some degree of progressive uncoordinated growth and is not merely a quiescent malformation" and he excluded from the teratomata all forms of abnormal twins or double monsters and particularly warned against the belief that tera-

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Figure 1. Ventral view of viscera of hermaphroditic shortnose sturgeon (semidiagrammatic). Ovotestes reflected to either side. White areas in ovotestes consist of testicular tissues. GB, gas bladder; INT, intestine; LIV, liver; LOT, left ovotestis; PA, pyloric appendage; ROT, right ovotestis; SPL, spleen. Scale line equals 2 cms.

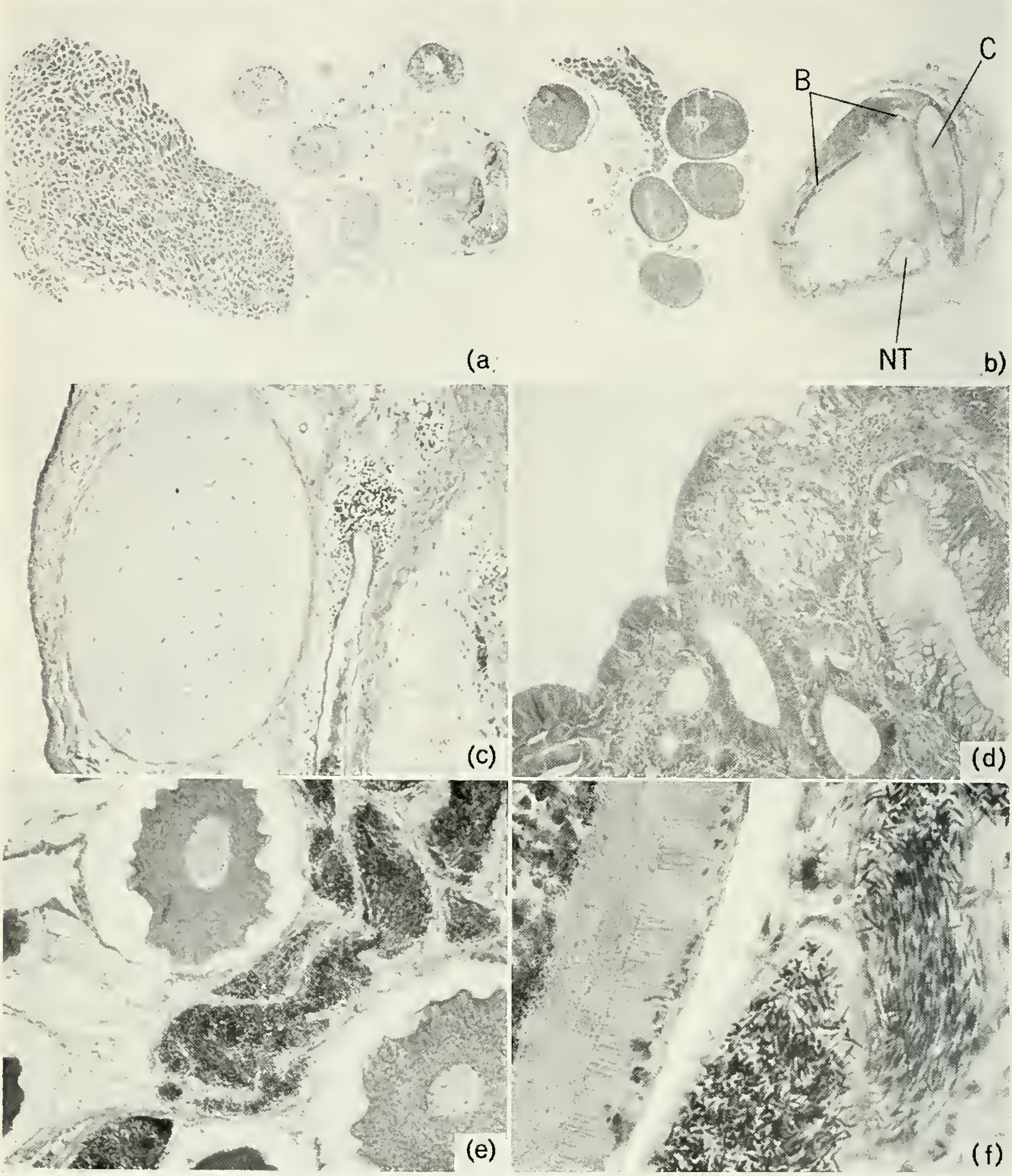

Figure 2. (a): ovotestis of Atlantic sturgeon with ovarian and testicular tissues discrete (× 7.5). (b): ovotestis of shortnose sturgeon with ovarian and testicular tissues intermingled and with teratomatous cyst on the right, its central cavity lined with epithelium, partially columnar, partially stratified. B, bone; C, cartilage; NT, nervous tissue (× 7.5). (c): wall of cyst with, left to right, oval cartilaginous mass, longitudinal section of blood vessel, and narrow band of collagenous connective tissue extending to upper right corner (× 130). (d): lining of cyst cavity with submucosa-like elements, including goblet cells, on the right and subepithelial glands at the lower left (× 130). (e): ovotestis of shortnose sturgeon with seminiferous crypts flanked by perinucleolar (Stage III) oocytes (× 130). (f): maturing ovum on the left with spermatozoa lodged in zona radiata; seminiferous crypts on the right (× 540).

tomas are included monsters or some other kind of malformed twin. Gaillard (1974) has also relegated to the category of outmoded theories the idea that teratomas originate from the inclusion of a parasite twin.

Hisaoka (1961) described as congenital teratomas 18 cases of abnormal growths which were located on the belly of the guppy, *Poecilia reticulata.* These growths ranged from small but apparent nodules of disorganized tissues, including recognizable parts of fins, to elongated formations resembling small, headless fish. The guppies and their growths were attached to each other in the same way as were four sets of siamese-twin guppies that Hisaoka also described. Stolk (1955) appears to have been the first to apply the term teratoma to such growths, and Wellings (1969), Mawdesley-Thomas (1971), Harshbarger (1972), and Huizinga (1975) seem to have followed his example in doing so. Other investigators have considered them simply as abortive twins (Schnakenbeck, 1953; Geus, 1961; Horn, 1968; Takahashi, 1974). Nearly identical growths have been described in *Xiphophorus* by Hisaoka (1963) and Cavicchioli (1971) and in *Poecilia latipinna* by Schwartz and Curtin (1954). As Hisaoka (1961) has pointed out, all these specimens can be arranged in a series that grades from fish with small abnormal growths, that could qualify histologically as teratomas of the belly skin, through various degrees of an autosite-parasite relationship in conjoined twins, to siamese twins consisting of a pair of virtually coequal partners. Among oviparous fishes, Stockard (1921) has described a very similar graduated series of abnormalities and Goetsch and Schindler (1934) a less extensive one—both of them in recently hatched trout. How should these abnormalities be interpreted? On the basis of his studies of human pathology, Willis (1967) has stressed that it would be "a mistake to suppose that a gentle series of gradations exists between double monsters and malformed twins on the one hand and teratomas on the other." Unlike some of the teratomas in human beings, the teratomatous growths of fishes show no sign of the progressive, uncoordinated growth that characterizes true tumors or neoplasms. Since the process of twinning is manifestly not a neoplastic one, the existence of the above-described series in fishes strongly indicates that the growths in question should not be considered as teratomas—a conclusion diametrically opposite from the one reached by Hisaoka (1961).

The ovary is the commonest site of teratomas in human beings (Willis, 1967), in which species these tumors have been more extensively studied than in any other. Despite their typical location, however, the ovarian teratomatous growths studied by Stolk present unusual features that raise questions about their origin and interpretation as true teratomas. In the ovaries of the playfish, *Xiphophorus maculatus*, and two guppies, *Poecilia reticulata,* to which he referred, Stolk (1953, 1959) also found good evidence for the presence of *Ichthyophonus*, a phycomycete parasite that is responsible for widespread, chronic, systemic disease in home-aquarium fishes (Reichenbach-Klinke and Elkan, 1965). Ichthyophoniasis of the poeciliid ovary (which serves as the organ of gestation, as well as egg-production, in these viviparous fishes) has been associated repeatedly with arrhenoidy, hermaphroditism, and sex reversal (Atz, 1964; Mohsen, 1965) and with the production of fatherless offspring (Stolk, 1958, 1961; Atz, 1964). Stolk (1958, 1959, 1961) attributed both the gravidity of virgin females of three species of poeciliid fishes and the development of ovarian teratomas to *pathological parthenogenesis.*

In all his fishes, Stolk attempted to rule out the possibility of fertilization by a male, in some cases more convincingly than in others, but he never seems to have ruled out the possibility that autochthonous sperm, developed in the ovary itself, could have played a role in either phenomenon. There is good evidence for abnormal but frequent and effective self-fertilization in a strain of guppies that was maintained by Spurway (1957) and, later, by Comfort (1961). In these fish, most of the "ovaries" that were examined histologically were found to contain active spermatogenic tissue, and at least some of the hermaphrodites were infested with *Ichthyophonus*. Mendelian segregation occurred among three color patterns of the fatherless offspring—patterns for which their mothers had been heterozygous (Spurway, 1957). This strongly indicates self-fertilization, rather than parthenogenesis, as the mode of reproduction in Spurway's guppies and suggests that a similar process was responsible for the "virgin births" reported by Stolk (1958, 1961). The relationship of ichthyophoniasis to the teratomatous growths, however, is more obscure. These growths may represent the abortive result of a parthenogenetic or a selfing process, or some other pathological process triggered by the presence of the parasite. Stolk (1958, 1959) and Wellings (1969) have suggested that a fungal toxin or other chemical agent was involved. Other investigators either have been unaware of the possible involvement of *Ichthyophonus* or may have had material that did not lend itself to systematic microscopical search.

The possibility of the participation of autochthonous sperm in the formation of the teratomatous growths in the ovotestis of our sturgeon is obvious, but here, too, in the absence of any more direct evidence such as chromosomal counts, less direct evidence in favor of either this or a parthenogenetic process can be adduced.

Self-fertilization is known to have occurred as a rare, abnormal event in a small number of teleosts in addition to Spurway's guppies (Atz, 1964) and it is the normal mode of reproduction of one oviparous species (Harrington, 1971). Parthenogenesis, that is, the initiation of developmental processes (either normal or abnormal) by an egg that has had no contact with any spermatozoon, has been described in a number of fishes, but viable young appear to be produced in only a few species (Rostand, 1938; Turdakov, 1961; Beatty, 1967; Kallman, 1970; Sukhanova, 1972). On the other hand, since the pioneering investigations of Carl and Laura Hubbs (1932), gynogenesis (in which sperm, typically from another species, activate the eggs but do not participate in the formation of the offspring) has been found to be the normal means of reproduction in several teleosts (Schultz, 1969, 1971; Stanley and Sneed, 1974). Many instances of abortive parthenogenetic development have been described in three species of Russian sturgeon (Ginsburg and Dettlaff, 1969; early literature reviewed by Pickford and Atz, 1957). Both ovulated and unovulated eggs were involved and these began to degenerate before they reached the gastrula stage.

Recent discoveries in mammalian embryology indicate the desirability of carrying out further investigations on the possible relationship between the tendency of sturgeon eggs to undergo parthenogenetic development and the appearance of teratoma-like growths in sturgeon gonads. A clear-cut connection between parthenogenetically developing eggs and ovarian teratomas has been described in a laboratory strain of mice by Stevens and Varnum (1974).

We may conclude that the teratomatous growths found in the ovotestis of a shortnose sturgeon meet the histological criteria for this type of abnormal growth, but that an inquiry into their possible mode of development points to the abnormal development of a parthenogenetic or self-fertilized egg rather than a neoplastic process. The same considerations apply to the three cases that Stolk has previously described in the ovary of poeciliid fishes. It remains an open question whether a true teratoma has been found yet in any fish.

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THERMAL AND RESPIRATORY STUDIES WITH REFERENCE TO TEMPERATURE AND OXYGEN TOLERANCE FOR THE UNARMORED STICKLEBACK *GASTEROSTEUS ACULEATUS WILLIAMSONI* HUBBS

C. Robert Feldmeth[1] and Jonathan N. Baskin[2]

Abstract: The tolerance to high temperature and low oxygen concentration was measured for the unarmored stickleback. These fish have a critical thermal maximum (CTM) of 30.5°C when acclimated to 8°C and a CTM of 34.6°C when acclimated to 22.7°C. Respiratory experiments indicated that the critical oxygen concentration for this species is about 2.0 ppm. Above this concentration, the respiratory rate is independent of oxygen concentration; however below 2.0 ppm, oxygen consumption rapidly declines. To maintain respiratory independence as oxygen concentration decreases, ventilatory rate rises rapidly. In an oxygen concentration of 7.4 ppm the mean ventilatory rate is 104.6 per minute. As the oxygen decreases, ventilatory rate increases to 230.7 per minute in 1.32 ppm of oxygen. In lower oxygen concentrations, gill ventilation rapidly decreases.

The unarmored stickleback *Gasterosteus aculeatus williamsoni* is an endangered fish which occurs in the headwaters of the Santa Clara River in northern Los Angeles County. The Santa Clara River in this locality is a small, intermittent shallow stream that flows through extremely arid desert scrub and coastal sage scrub terrestrial communities. The aquatic habitat consists of shallow pools and a meandering sand and silt bottomed stream bordered by emergent aquatic vegetation and willows.

Since this subspecies is restricted to an environment where shallow pools often become quite warm, and weed-chocked areas are often low in dissolved oxygen, the following study was designed to measure the tolerance of this fish to low oxygen and high temperature conditions.

Lewis, et al., (1972) found that *Gasterosteus aculeatus* in England favored open, well oxygenated waters and habitats where sand and gravel were the predominant substrate materials. Respiratory and oxygen tolerance experiments indicated that this stickleback species is probably less able to tolerate low oxygen conditions than the ninespined stickleback, *Pungitius pungitius*.

The purpose of the present study was to determine the tolerance of the unarmored stickleback both to high temperature and to low oxygen by measuring critical thermal maxima in the laboratory. Tolerance to low oxygen was measured by determining the rate of oxygen consumption and respiratory ventilation for fish in a series of dissolved oxygen concentrations. These data will be compared to field measurements of oxygen concentration and temperature.

Such information for an endangered species will allow precise habitat appraisal to be considered as a potential endangering factor. Possible refugia can also be analyzed more exactly before transplants of endangered species are made.

METHODS

Thermal Studies.—Critical thermal maximum (CTM) experiments were carried out by transporting a group of fish from the Santa Clara River to the laboratory and holding them for a period of 23 days in constant temperature rooms of 8.0, 13.0, 15.6 and 22.7°C. This period of thermal acclimation was considered to be sufficient to allow complete metabolic adjustment to each temperature (Hochachka and Somero, 1973). The fish were held in 15 gallon aquaria on a 12-12 light and dark cycle.

At the end of the acclimation period a group of 10 fish were transferred to a one gallon chamber with aeration stones and a submersible heater. The temperature of the chamber was equal to the acclimation temperature for each group and then heated at 1°C per 4 min (Fry, 1957). The critical thermal maximum (CTM) for each fish was determined as the temperature where opercular ventilatory movement ceased. Each fish was then removed and weighed.

A second CTM experiment was performed to

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determine if size was related to the maximum lethal temperature the fish could tolerate. Two groups of significantly different sized fish were held in the laboratory for three weeks at 18.6°C and subjected to CTM tests as described above. In this instance both weight and length were recorded for each fish.

O_2 tolerance studies.—To determine the effect of low oxygen upon the unarmored stickleback, fish were placed in 125 ml chambers on a substrate of sterilized sand and allowed to adjust to their surroundings for several hours. Fresh water was slowly circulated through these chambers to prevent oxygen concentrations from being lowered. A series of chambers were then filled with water of desired oxygen concentration (those used were 0.97, 1.91, 3.60, 5.25, 7.04 and 7.33 ppm), the chambers were closed and placed in the dark for approximately 30 minutes. A control chamber, containing sand and water only was also sealed. All respiratory experiments were carried out in the dark.

Oxygen consumption was measured as the difference in oxygen concentration between the control and the experimental (fish containing) chambers. Dissolved oxygen was measured for each chamber with a polarographic oxygen electrode (Southern Analytical Co.). The temperature of each chamber was recorded, and the fish were removed and weighed. Oxygen consumption for each oxygen concentration was calculated as mg of O_2 consumed per gram of fish per hour.

Gill ventilation rates in different oxygen concentrations were determined by placing five fish in separate 100 ml chambers filled with water adjusted to several oxygen concentrations (0.60, 1.32, 2.94, 4.80, 5.90, 6.40, and 7.40 ppm). After a five minute adjustment period, gill ventilations were counted visually using a hand counter and stop watch. Four counts were made for each fish and a mean was determined. At the end of each experiment the fish were weighed and returned to well oxygenated water.

RESULTS

Thermal Tolerance.—The critical thermal maximum of the unarmored stickleback is strongly influenced by acclimation temperature (Fig. 1). When acclimated to 8.0°C, the CTM is 30.5°C. When acclimated to 22.7°C, approximately the warmest temperatures they face over an extended period of time in summer, the CTM was 34.6°C.

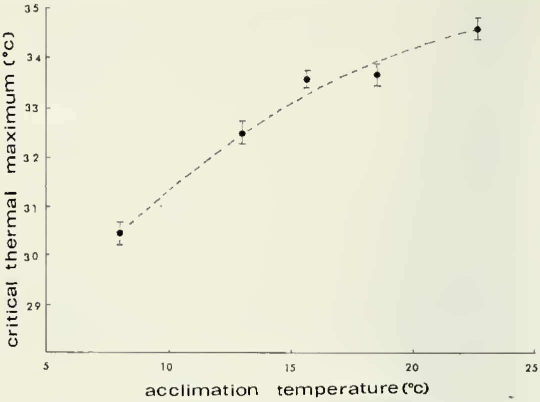

Figure 1. The effect of thermal acclimation upon critical thermal maximum. Each point represents the mean CTM for 10 fish. I-bars indicate standard errors.

When small and large fish were acclimated to a constant temperature (18.6°C) and tested to determine if size affected CTM, no significant difference was found (Table 1).

O_2 Tolerance.—The effect of oxygen concentration on the respiratory rate of the unarmored stickleback is presented in figure 2. This species shows respiratory independence over a broad range of oxygen concentrations. In oxygen concentrations below 2.0 ppm the respiratory rate begins to decline. This point of transition from respiratory independence to respiratory dependence upon oxygen concentration has been called the level of no excess activity (Fry, 1971) and it approximates the lethal oxygen level.

Gill ventilation rates in different oxygen concentrations (Fig. 3) indicate that respiratory independence requires a sizeable increase in ventilation as the oxygen concentration decreases. In 7.4 ppm O_2, the mean ventilation rate is 104.6 per minute and in 1.32 ppm ventilation increased to 230.7 per minute. In oxygen concentrations less than 1.32 ppm, ventilation rapidly decreases.

DISCUSSION

The sizeable difference in CTM's for cold versus temperate thermal acclimation for this fish indicates physiological adaptation to a rather large seasonal temperature fluctuation. In a small, shallow stream habitat in a hot, arid area where air temperature is hot in summer and relatively

TABLE 1. Critical thermal maxima (CTM) experiments: large and small fish. Acclimation temperature = 18.6.

No.	Weight (gms)	Length (mm)	CTM (°C)
	Small fish		
1.	0.265	27	33.2
2.	0.260	30	33.3
3.	0.122	24	33.3
4.	0.164	26	33.4
5.	0.245	30	33.5
6.	0.161	28	33.7
7.	0.145	26	33.7
8.	0.110	22	33.8
	$\bar{X}$ = 0.184	26.6	33.49
	S.D. = 0.063	2.77	0.223
	S.E. = 0.023	0.981	0.0789
	Large fish		
1.	1.520	53	33.4
2.	1.488	48	33.5
3.	1.592	50	33.5
4.	1.302	43	33.6
5.	1.293	41	33.7
6.	1.161	40	33.8
7.	1.538	49	33.9
8.	1.220	40	33.9
	$\bar{X}$ = 1.389	45.5	33.6
	S.D. = 0.164	5.09	0.192
	S.E. = 0.0058	1.80	0.068

cold in winter, one would expect such an adaptation.

In a survey of thermal requirements of fishes, Brett (1956) showed that of North American fishes the salmonids had the lowest CTM's with the centrarchids and cyprinids occupying an intermediate position. The highest CTM's occur among the ictalurids and a poeciliid (*Gambusia affinis*).

The CTM experiment on fish of different sizes was designed to determine if some physiological separation between adult and young fish exists. Lowe and Heath (1969) found that young desert pupfish (*Cyprinodon macularius*) often were found in the warmer, shallow waters at Quitogaguito spring in southern Arizona. Eriksen (in press) has found that a similar behavioral separation presumably established by differential temperature preference occurs in grayling (*Thymallus arcticus*) in shallow, high altitude lakes in Montana. Grayling fry had a significantly higher CTM than adults indicating a physiological adaptation to their preferred habitat. No correlation between size and CTM was found for the unarmored stickleback in the present study and no apparent separation has been reported for this species in the field.

O_2 Tolerance.—Most species of fish, over the upper part of the range of oxygen concentrations to which they are exposed, are able to maintain

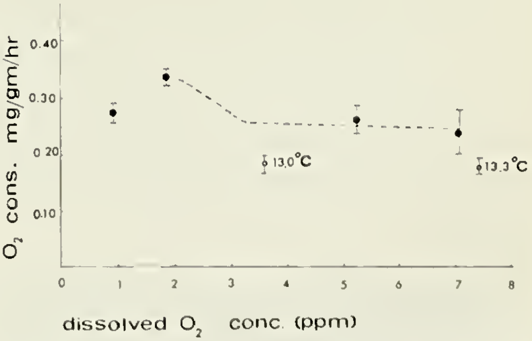

Figure 2. The effect of various oxygen concentrations on oxygen consumption. Solid circles indicate mean respiratory rates (n = 10) at 18.6°C, while the open circles are means (n = 10) for oxygen consumption at 13.0 and 13.3°C. I-bars indicate standard errors.

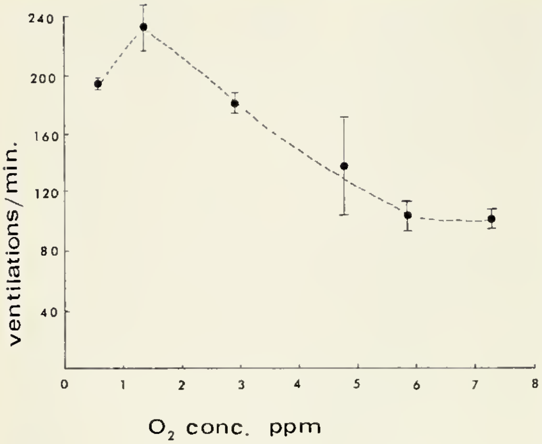

Figure 3. The effect of oxygen concentration on the rate of gill ventilation. Points are means for five fish, with 5 measurements of ventilation per minute and averaged for each fish.

fairly constant rates of oxygen consumption (Warren, 1971). The unarmored stickleback shows this homeostatic ability quite well above 2.0 ppm. In oxygen concentrations below 2.0 ppm, oxygen consumption drops rapidly.

A strong correlation exists between the level of no excess activity point, when oxygen consumption begins to rapidly decrease, and the oxygen concentration an organism is exposed to in its particular habitat (Macan, 1963). Goldfish (*Carassius auratus*) have a considerably lower incipient limiting point than do brook trout (*Salvelinus fontinalis*) (Fry and Hart, 1948; Graham, 1949; Beamish, 1964). Undoubtedly the critical dissolved oxygen concentration which causes the rate of oxygen consumption to drop can be influenced by acclimation. Similarly, the critical or lethal low oxygen concentration is also effected by acclimation. Shepard (1955) found that the survival time of brook trout in a lethal oxygen concentration of 1.06 ppm increased when fish were held for 150 hours in 3.8 ppm O_2. Fry and Hart (1948) and Graham (1949) also showed that temperature also affects the point of no excess activity.

The small increase in respiratory rate (Fig. 2) in oxygen concentrations slightly above the level of no excess activity has also been reported by Beamish (1964). This increase is believed to be caused by the large energy requirement needed for providing sufficient gill ventilation at low oxygen concentrations. Gill ventilation data for the unarmored stickleback (Fig. 3) indicates the great increase in ventilation rate required to allow respiratory independence to exist as oxygen concentration decreases. These data show that even though a field oxygen concentration of 3.0 ppm would not be lethal, a sizeable amount of energy would be required for ventilation. Such a situation would probably reduce both growth and reproductive abilities as well as general activity as energy would be diverted to maintain a sufficient metabolic rate.

Jones (1952) found that *Gasterosteus aculeatus* would avoid water with less than 2.0 ppm O_2. When a fish entered water with a dissolved oxygen concentration less than 2.0 ppm it immediately turned around or backed out of it. Data presented in this paper indicate that although the unarmored stickleback also appears to be capable of tolerating oxygen levels as low as 2.0 ppm, below this concentration death would soon occur. Hence there appears to be a good correlation between the behavioral observations of Jones and our oxygen consumption data.

The daytime oxygen concentrations in the upper Santa Clara River (mean $O_2 = 7.18$ ppm) appear to be well above this limiting level. However, in isolated stagnant pools and perhaps on warm summer nights, when photosynthetic O_2 production would be absent, lower oxygen levels might occur. The relatively high critical oxygen concentration of 2.0 ppm for this species probably indicates a preference for moving, well-oxygenated waters. Field observations show that sticklebacks have a strong preference for flowing water, and are entirely absent in ponds lacking flow.

With respect to physiological adaptations, the unarmored stickleback again appears to be intermediate between fishes such as carps, which inhabit stagnant waters and tolerate low O_2 levels, and those inhabiting cold mountain streams (salmonids).

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FISH REMAINS FROM AN ARCHAEOLOGICAL SITE AT RANCHO CARRILLO ON THE SILVER STRAND, SAN DIEGO COUNTY, CALIFORNIA

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ABSTRACT: A collection of 170 fish remains from an archaeological site on the Silver Strand, immediately west of San Diego Bay, California, represents nine species, all of which are edible: *Mustelus californicus*, *Sardinops sagax*, *Atherinopsis californiensis*, *Paralabrax* sp., *Roncador stearnsii*, *Genyonemus lineatus*, *Cynoscion parvipinnis*, *Sphyraena argentea*, and *Pneumatophorus japonicus*.

Remains of *Cynoscion parvipinnis*, a subtropical fish unknown from California in recent years, indicate the occurrence of a former warmwater fauna in this vicinity, probably during more than two centuries.

Remains of large *Sphyraena argentea* and *Pneumatophorus japonicus*, probably caught in the ocean, suggest aboriginal use of the tule balsa.

This is a report on a collection of fish remains recovered by Carl L. Hubbs and Laurence G. Jones during July 1962 from an archaeological site at Rancho Carrillo, a former Spanish ranch on the Silver Strand (Coronado Strand), San Diego Co. California. The narrow, gently curving Silver Strand is a sandspit connecting two low-terrace land masses, Coronado and Coronado Heights (about 10 km apart), and separating the moderately surf-beaten ocean beach from the extensive mud flats and open water of San Diego Bay (U.S.

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Coast and Geodetic Survey Chart 5107). The primitive topography of the Silver Strand and its vicinity is shown on a map of San Diego Bay made in 1782 by Juan Pantoja (Pourade, 1961:80). The approximate location of the site is indicated by Kroeber (1925:920, fig. 75, third site from bottom). Fish remains were recovered only at Stations B and C of this site.

Station B represents a Diegueño camp with an abundance of pottery—a culture still extant when the Spaniards arrived (Moriarty, 1961:13, 16). This station is on the light-colored, unconsolidated upper sand, among low sand dunes east of the south extension of Silver Strand State Park. It is at an elevation of 6.4 m above sea level, about 600 m from State Park Monument No. 5. A radiocarbon date of 270 ± 150 years B.P. (A.D. 1680) from material from the surface midden (LJ-210, 32°37′27″N, 117°08′09″W) was noted by Hubbs, Bien, and Suess (1962:212; 1965:104).

Station C, 0.1 km northwest from Station B, very likely represents the late stage of the La Jollan (prepottery) culture, which preceded the Diegueño; material from superficial layers of Station C is much more ancient than that from Station B. Station C is on the upper layer of the swale to the west of a sand ridge and at a much lower elevation, not much above sea level. A radiocarbon date of 3470 ± 175 years B.P. (1520 B.C.) from material from a depth of 5 to 15 cm (LJ-593) was noted by Hubbs, Bien, and Suess (1965:104). Since the material from Station C appears to represent a redeposit from the adjacent slopes to the east (Carl L. Hubbs, *pers. comm.*), the possibility cannot be excluded that the fish material at Station C was derived by surface wash from the Diegueño material of Station B.

The specimens are deposited at the Scripps Institution of Oceanography, under Accession No. 1962-VII:21.

FISHES REPRESENTED

The collection comprises 170 fish remains, most of which are incomplete or fragmentary. The stations and depths from which they were recovered are shown in Table 1. At least nine species, referable to nine genera and seven families, are represented.

Family Triakidae

Mustelus californicus Gill, 1864

The gray smoothhound (Roedel and Ripley, 1950: fig. 37) attains a total length of 163 cm and a weight of 17.2 kg, but few exceed 107 cm or 4.1 kg (Fitch, 1972:104). It was said to be the commonest shark in southern California, great numbers being taken in seines and on setlines in San Diego Bay (Starks and Morris, 1907:163).

Material: 1 vertebral centrum, diameter 5.7 mm. Identified from radiographs.

For a photograph of a vertebral centrum of this species, see Follett (1966:fig. 1a).

Records from other archaeological sites: Irvine, Ora-119B (Follett, 1966:190, 191); Ventura, Ven-3 (Fitch, 1969a:62); Diablo Cove, SLO-2 (Fitch, 1972: 104).

Family Clupeidae

Sardinops sagax (Jenyns, 1842)

The Pacific sardine (Hart, 1973:100, unnumbered fig.) has been known to attain a fork length of 41.3 cm, but usually does not exceed 33 cm (Roedel, 1953:33). A fork length of 41.3 cm would correspond to a total length of about 46 cm. At times, sardines have occurred in San Diego Bay in such abundance that bushels were left at low tide in the small puddles about piles (Eigenmann, 1892:136, 137, as *Clupea sagax*). Under such conditions, sardines could have been caught by a seine or a gill net. If the Diegueño used a seine, they might have manipulated it from balsas. By so doing, they could have avoided being stung by the round stingray, *Urolophus halleri* Cooper, which has been very common in San Diego Bay (Eigenmann, 1892:134).

Material: Articular (1), dentary (1), frontal (2), supplemental maxillary (1), opercle (3), preopercle (1), scale (4), sphenotic (1), and vertebra (10)—representing fish about 13 to 23 cm in total length.

For figures of the skeletal elements of this species, see Phillips (1942).

Records from other archaeological sites: Conejo Rock Shelter, Ven-69 (Follett, 1965:83); Tomales Bay, Marin Co (Follett, 1968a:3); Century Ranch, LAn-229 (Follett, 1968b:134); Rincon Point, SBa-1 (Fitch, 1969b:72, as *Sardinops caeruleus*); Swoape, Ven-168 (Fitch, 1969b:72, as *Sardinops caeruleus*); Diablo Cove, SLO-2 (Fitch, 1972:105, as *Sardinops caeruleus*); San Buenaventura Mission, Ven-87 (Fitch, 1975:442).

Family Atherinidae

Atherinopsis californiensis Girard, 1854

The jacksmelt (Jordan and Evermann, 1900:pl. 125 fig. 341) seldom exceeds a total length of 33 cm south of Point Conception (Cannon, 1964:234). The largest measured specimen was 44.4 cm in total length (Miller and Lea, 1972:82). Jacksmelt were abundant in San Diego Bay (Eigenmann, 1892:129, 145); they could have been caught by hook and line or by seine.

Material: Articular (1; from a fish about 23 cm in total length).

Records from other archaeological sites: Ventura, Ven-3 (Fitch, 1969a:64); Shelter Hill, 4-Mrn-14 (Follett, 1974:146); West Berkeley, CA-Ala-307 (Follett, 1975:78).

Family Serranidae
Paralabrax sp.

Three species of bass (*Paralabrax clathratus*, *P. maculatofasciatus*, and *P. nebulifer*) were abundant in the vicinity of San Diego and were known to enter San Diego Bay (Eigenmann, 1892:130, 150–151). All are food fish, readily caught by hook and line. In the skeletal elements represented in this collection, these three species are but slightly differentiated from one another. Identification is therefore to genus only.

Material: Basipterygium (1), ceratohyal (1), cleithrum (1), vertebra (1)—representing fish to perhaps 46 cm in total length.

Records from other archaeological sites: Century Ranch, LAn-227 (Follett, 1963a:302, *Paralabrax clathratus*); Arroyo Sequit, LAn-52 (Follett, 1963b: 115, *Paralabrax clathratus*); Irvine, Ora-118A and Ora-119B (Follett, 1966:191, 193, *Paralabrax maculatofasciatus*); Corona del Mar, Ora-190 (Fitch, 1967: 188, *Paralabrax* sp.).

Family Sciaenidae
Roncador stearnsii (Steindachner, 1875)

The spotfin croaker (Roedel, 1953:fig. 93) is known to attain a weight of 4.76 kg; a 673 mm specimen weighed 4.2 kg (Baxter, 1960:39). Spotfin croakers were said to be "only occasionally absent from" San Diego Bay (Eigenmann, 1892:152). They are readily caught by hook and line.

Material: Dentary (1), maxillary (1), pelvic spine (1), upper pharyngeal (1), sagitta (1), scale (24), and vertebra (3)—representing fish about 48 to 56 cm in total length.

Records from other archaeological sites: Scripps Estate, San Diego Co (Shumway, Hubbs, and Moriarty, 1961:104); San Pedro, LAn-283 (Frey, 1974:92); San Buenaventura Mission, Ven-87 (Fitch, 1975:450).

Genyonemus lineatus (Ayres, 1855)

The white croaker (Roedel, 1953:fig. 97) attains a total length of 413 mm and a weight of 1.1 kg (Fitch, 1975:450). It was abundant in San Diego Bay during December and January (Eigenmann, 1892:130, 153), but it is caught throughout the year (Baxter, 1960:38). In southern California this is one of the fishes most readily caught by hook and line from the shore.

Material: Maxillary (1), lower pharyngeal (1), sagitta (2), scale (2)—representing fish about 23 to 25 cm in total length.

Records from other archaeological sites: Scripps Estates, San Diego Co (Shumway, Hubbs, and Moriarty, 1961:104); Conejo Rock Shelter, Ven-69 (Follett, 1965:84); Ventura, Ven-3 (Fitch, 1969a:65); Rincon Point, SBa-1 (Fitch, 1969b:73); Swoape, Ven-168 (Fitch, 1969b:73); Diablo Cove, SLO-2 (Fitch, 1972:111, 120); San Pedro, LAn-283 (Frey, 1974:92); San Buenaventura Mission, Ven-87 (Fitch, 1975:449).

Cynoscion parvipinnis Ayres, 1862

The shortfin corvina (Croker, 1932:fig. 89) was said by Jordan and Gilbert (1881:48) to reach a length of about 61 cm and a weight of 3.6 kg. That appears to have been an inadvertent overstatement of the weight at that length: a specimen of normal appearance, collected by W. I. Follett and Richard S. Croker off San Felipe, Baja California, measured 59.7 cm in total length and weighed 1.8 kg. Shortfin corvinas are readily caught by hook and line. This species was common in southern California, where it now seems to have been absent for many years, though it remains abundant in central Baja California (Hubbs, 1948:466). It was originally described from the coast of Baja California at about 27°N (Ayres, 1862:156), in the vicinity of Punta San Hipólito; it was recorded from San Diego by Jordan and Gilbert (1880:28, as *Cynoscion magdalenae*), Eigenmann (1892:130, 154), Starks and Morris (1907:198).

Material: Ceratohyal (1), epibranchial (1), epihyal (1), metapterygoid (1), palatine (1; fig. 1A), and lower pharyngeal (1)—representing fish from about 43 to 51 cm in total length.

Although in certain skeletal elements this species is but slightly differentiated from the white seabass, *Cynoscion nobilis* (Ayres), which was also abundant in the region of San Diego, the identification of the present material appears satisfactory. In particular, the dorsal ridge of the palatine is more prominent than in *C. nobilis*, the lower pharyngeal is wider in proportion to its length, the epibranchial is less striate, and the ceratohyal is more deeply concave along its superior margin.

Records from other archaeological sites: I have found no published records of archaeological material of this species.

Family Sphyraenidae
Sphyraena argentea Girard, 1854

The California barracuda (Walford, 1937:colored pl. 66 fig. a) is known to attain a length of 118 cm and a weight of 8.2 kg (not the same fish) (Fitch and Lavenberg, 1971:142). Barracudas were abundant at San Diego throughout the summer, the young (about 30 cm in length), but not the adults, entering San Diego Bay in large schools (Eigenmann, 1892:147). The large individuals represented in the collection were probably caught in the ocean, presumably by hook and line trolled from a tule balsa.

Material: Cleithrum (1), hyomandibular (2),

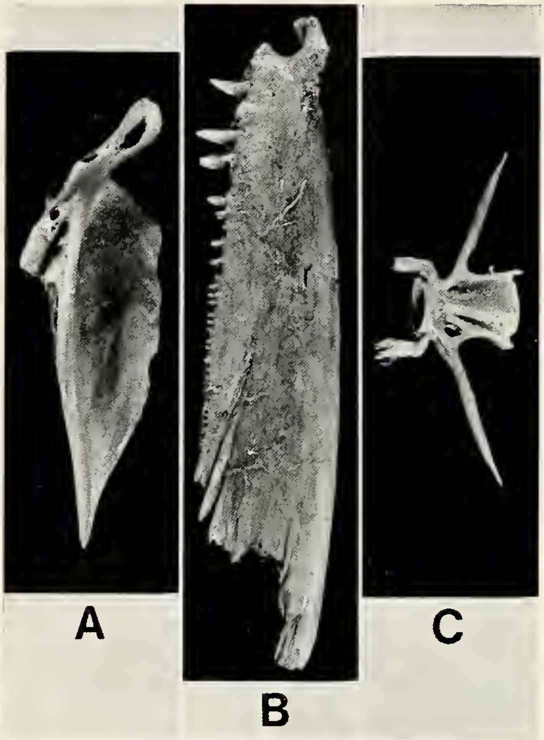

Figure 1. Fish remains from Rancho Carrillo: A, right palatine, length 39 mm, of *Cynoscion parvipinnis* (total length about 50 cm) from Station B, on slope, decimeter 2; B, right palatine (mesial aspect), length 73 mm, of *Sphyraena argentea* (total length about 92 cm) from Station B, on slope, decimeter 4; C, caudal vertebra, length 6.3 mm, of *Pneumatophorus japonicus* (total length about 28 cm) from Station B, on slope, decimeter 1.

hypural (2), maxillary (1), palatine (1; fig. 1B), vertebra (7), vomer (1)—representing fish about 86 to 110 cm in total length.

Records from other archaeological sites: Century Ranch, LAn-227 and LAn-229 (Follett, 1963a:303; 1968b:135); Arroyo Sequit, LAn-52 (Follett, 1963b:115); Conejo Rock Shelter, Ven-69 (Follett, 1965:84); Ventura, Ven-3 (Fitch, 1969a:64); San Buenaventura Mission, Ven-87 (Fitch, 1975:455); Swoape, Ven-168 (Fitch, 1975:466).

Family Scombridae
Pneumatophorus japonicus (Houttuyn, 1782)

The Pacific mackerel (Walford, 1937:colored pl. 37 fig. b) has been known to attain a total length of 63.5 cm and a weight of 2.9 kg, but usually is under 38 cm in length (Roedel, 1953:84, as *Pneumatophorus diego*). Half-grown individuals were exceedingly abundant in San Diego Bay during the autumn, but very few large ones were caught there (Eigenmann, 1892:148, as *Scomber colias*). The large individuals represented in the collection were probably caught in the ocean by hook and line from a tule balsa; the small ones, in San Diego Bay by net or possibly by hook and line.

Material: Anal spine (1), cleithrum (1), dentary (1), hyomandibular (1), interhaemal spine (1), maxillary (1), posttemporal (1), premaxillary (2), pterygoid (1), and vertebra (69; one shown in fig. 1C)—representing fish about 18 to 50 cm in total length.

Records from other archaeological sites: Century Ranch, LAn-227 and LAn-229 (Follett, 1963a:304, 1968b:135; as *Scomber japonicus diego*); Arroyo Sequit, LAn-52 (Follett, 1963b:116, as *Scomber japonicus diego*); Conejo Rock Shelter, Ven-69 (Follett, 1965:84, as *Scomber japonicus diego*); Ventura, Ven-3 (Fitch, 1969a:65, as *Scomber diego*).

DISCUSSION

Indications of Former Warmwater Faunas.—Remains of *Cynoscion parvipinnis* recovered from this site strongly corroborate the conclusions expressed by Carl L. Hubbs, some 14 years before the Rancho Carrillo collection was made, that former northward occurrences of subtropical fishes along the southern California coast did not represent merely single-season waves, but long-lasting warmwater faunas (Hubbs, 1948:465). These remains indicate that *C. parvipinnis* had persisted in the San Diego area for a considerable period of time, probably for more than two centuries. The material of this species was recovered from Station B at three distinct levels. The remains of 0–± 1 decimeter were presumably contemporaneous with the material from the surface midden that yielded a radiocarbon date of 270 ± 150 years B.P. (A.D. 1680). Presumably, the remains from decimeter 2 were older, and those from decimeter 3 were older still.

Doubtless in addition to the long-lasting warmwater periods, there has been an occasional warmwater year that may have brought *C. parvipinnis* into southern California for a short interval. Between 1927 and 1929, shortfin corvinas from 1.4 to 1.8 kg in weight were netted on several occasions in salt ponds at the southern part of San Diego Bay (John E. Fitch, *pers. comm.*). These fish may have been holdovers in this favorable habitat from a possible northward occurrence of this species in 1926—a year when other fishes are known to have strayed north of their usual range (Hubbs and Schultz, 1929). Another subtropical species, the bonefish, *Albula vulpes*

TABLE 1. Number of fish remains recovered from Rancho Carrillo site.

	Station B[1]							Station C[2]			
	On flat			On slope							
	dm 1	dm 2	0–± 1 dm	dm 1	dm 2	dm 3	dm 4	Surface misc. levels	dm 1	dm 2	dm 3
Mustelus californicus			1								
Sardinops sagax			11	1	5	1	3		2	1	
Atherinopsis californiensis			1								
Paralabrax sp.								4		1	
Roncador stearnsii			8	2	6	8	8				
Genyonemus lineatus	1	1			3	1					
Cynoscion parvipinnis			2		3	1					
Sphyraena argentea			3	2	2	3	4				1
Pneumatophorus japonicus			20	6	30	15	7			1	

[1] A radiocarbon date of 270 ± 150 years B.P. (A.D. 1680) was obtained from Pismo clam (*Tivela stultorum*) valves from Station B (Diegueño) surface midden.

[2] A radiocarbon date of 3470 ± 175 years B.P. (1520 B.C.) was obtained from Pismo clam (*Tivela stultorum*) valves from Station C (La Jollan?) at a depth of 5 to 15 cm.

(Linnaeus), is known to have occurred in some numbers in Los Angeles Co, California, during 1926. Between 25 September and 7 November 1926, while employed at the California State Fisheries Laboratory at Terminal Island, I caught three bonefish from the Terminal Island seawall, saw another, and examined two that another angler had caught. These observations, on five distinct occasions, caused me to believe, erroneously, that the bonefish was normally a member of the southern California fauna (Follett, 1928:285).

Indications of Diegueño Use of the Tule Balsa.—The presence of remains of barracudas and mackerel, of large size, indicates the use of some type of watercraft for fishing in the ocean. Large individuals of these two species were probably not caught from the shore, since they surely did not occur either on the mud flats or in the surf. According to Eigenmann (1892:147, 148), adult barracudas never or very rarely entered San Diego Bay, and very few large mackerel were caught there, although the young and half-grown of both species abounded in the bay. These remains suggest the use off San Diego, during aboriginal times, of a tule balsa such as that ascribed to the historic Diegueño by Costansó (1910:121), Menzies (1924:340), Kroeber (1925:723), and Heizer and Massey (1953:295).

Presumably, the Rancho Carrillo people were able to launch their balsas from the steep beach on the ocean side of their area of occupation. Once under way, they could have taken advantage of the local drift to reach (and to return from) an eddy in the lee of Point Loma, which may have been their most favorable fishing grounds. The dominant southeastward coastwise current, deflected by Point Loma, creates a back-set beach drift along the Silver Strand and forms a counterclockwise eddy several kilometers in extent (Davis, 1933:235). That eddy would seem to have been a feeding area for the large barracudas and large mackerel that were captured by the people of Rancho Carrillo.

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DEVELOPMENT AND DISTRIBUTION OF LARVAE AND EARLY JUVENILES OF THE COMMERCIAL LANTERNFISH, *LAMPANYCTODES HECTORIS* (GÜNTHER), OFF THE WEST COAST OF SOUTHERN AFRICA WITH A DISCUSSION OF PHYLOGENETIC RELATIONSHIPS OF THE GENUS

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Abstract: *Lampanyctodes hectoris* is a species of lanternfish which is becoming an important part of the pelagic fishery off South Africa. The Southwest Africa Pelagic Egg and Larval Survey has provided an abundance of larval specimens of this species. The larvae, transitional and early juvenile stages are described and illustrated for the first time and information on their distribution and relative abundance is provided. Larval characters are used in combination with selected adult characters to elucidate the phylogenetic affinities of this genus.

Lanternfishes of the family Myctophidae are the most ubiquitous and speciose (approximately 250 species in 30 genera) of all fishes in the oceanic mid-waters. Although their total biomass is unknown, the fact that lanternfishes, on the average, make up approximately one-half of all fish larvae taken in any oceanic plankton tow gives some impression of its immensity. Although they are small fishes, usually less than 100 mm in length, they may have the greatest biomass of any vertebrate family. Knowledge of their ecological role in the world ocean is poor, but initial studies suggest that these fishes are a major element in the oceanic food web. Among the commercially important organisms known to prey on lanternfishes are salmon (Shimada, 1948; Manzer, 1968), tunas (Alverson, 1963; Pinkas et al., 1971), rockfish (Pereyra et al., 1969), fur seals (Mead and Taylor, 1953) and cetaceans (Fitch and Brownell, 1968). Recent studies (Paxton, 1967; Holton, 1969; Legand and Rivaton, 1969; Collard, 1970; Baird et al., 1975) indicate that lanternfishes are important grazers on herbivorous zooplankton.

Historically, lanternfishes have not been commercially exploited because of their small size and relatively diffuse distribution in the water column. A growing body of observations indicates that some species of lanternfishes aggregate in large numbers at certain times during their life cycles and, at such times, may be available to a fishery. There have been several well-documented observations of lanternfish swarming at the surface in dense "balls." *Benthosema panamense* exhibits this behavior during daylight in the eastern Pacific and tuna boat skippers report that yellowfin and skipjack tuna feed exclusively on these swarms when they are observed (Alverson, 1961). Similar swarms of *Diaphus garmani* were reported at night in the central Pacific (Nakamura, 1970). Lanternfishes also aggregate in extensive shoals. Observations from submarines indicate that some species of lanternfishes, such as *Ceratoscopelus maderensis* (Backus et al., 1968) and *Benthosema panamense* (Barham, 1971), form extensive aggregations in slope waters. G. Krefft (Institut für Seefischerei, Hamburg, pers. comm.) has achieved catch rates of 1¼ metric tons/hour of *Diaphus dumerili* with a commercial herring trawl off Buenos Aires. It is well known that myctophids are often a major element in deep scattering layers of the ocean (Barham, 1966; Pearcy and Mesecar, 1971). Additional knowledge of these phenomena may lead to the commercial harvesting of lanternfishes.

Recently a fortuitous fishery for the lanternfish *Lampanyctodes hectoris* has developed incidental to the anchovy/pilchard fishery off the western coast of South Africa (Centurier-Harris, 1974). Annual landings of lanternfishes (mostly *L. hectoris*) were 1,134 metric tons or 0.3 percent of the pelagic fishery catch in this region in 1969 and increased to 42,560 metric tons or 10.45 percent of the catch in 1973. The location of the fishery is shown in figure 1. This species is particularly desirable because of its high content (20 percent by weight) of fine quality oil.

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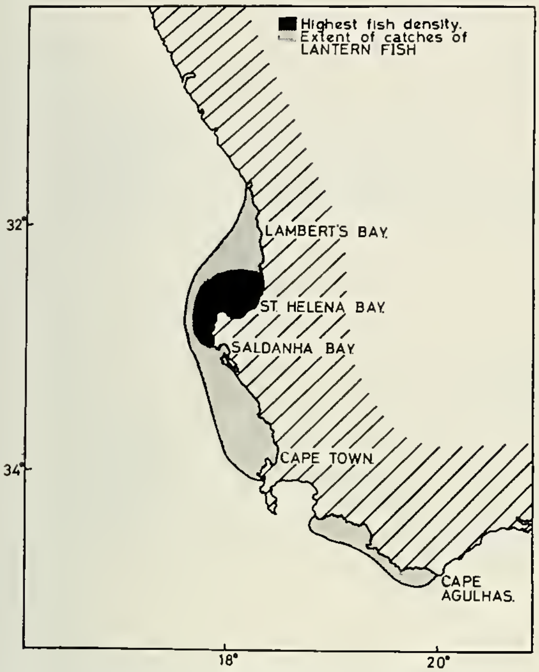

Figure 1. Region of the fishery for *Lampanyctodes hectoris* off South Africa (from Centurier-Harris, 1974).

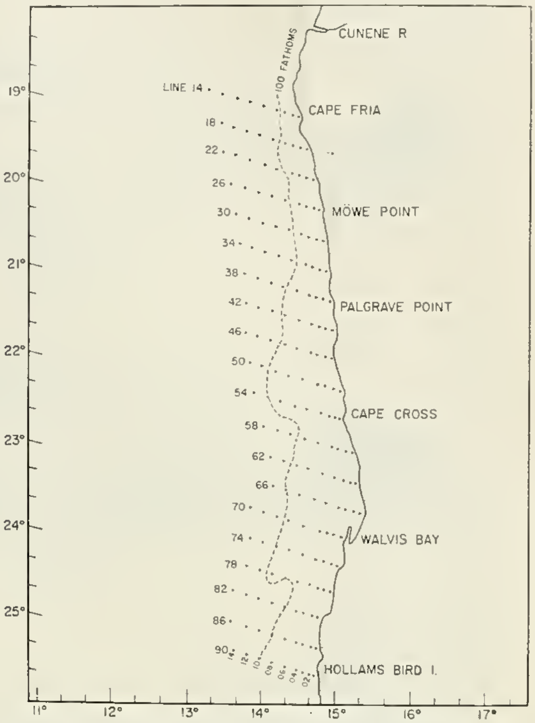

Figure 2. Station plan for Southwest African Pelagic Egg and Larval Survey (SWAPELS).

Little is known about the life history of this important species of lanternfish. However, an extensive plankton survey, the Southwest African Pelagic Egg and Larval Survey (SWAPELS), was initiated by the Sea Fisheries Branch in 1972 (O'Toole, 1974). Although the data from this survey are not completely analyzed, some information on the distribution and relative abundance of *L. hectoris* larvae will be presented in this paper, the principal purpose of which is to describe the larval, transitional, and early juvenile stages of *L. hectoris.* Previously, Moser and Ahlstrom (1972) illustrated a 9.2 mm larva of *L. hectoris* and gave a partial description of the sequence of photophore formation based on the few specimens available. Examination of the abundant larval specimens from SWAPELS has shown that Moser and Ahlstrom (1972) were in error and that their 9.2 mm larva was *Lampadena* sp. The larvae of *Lampanyctodes hectoris* have a unique generic morph, a concept discussed extensively by Moser and Ahlstrom (1970, 1972, 1974). A number of larval characters give insight into the relationships of this genus with other myctophid genera and these will be treated in the discussion section of this paper.

METHODS

Specimens for the developmental part of this study were obtained from two plankton surveys of SWAPELS (Fig. 2). Survey 1 was carried out from August 1972 to March 1973 and Survey 2 from August 1973 to April 1974. The net used on both surveys was a 57 cm bongo net: 0.940 mm and 0.940 mm mesh were paired on Survey 1 and 0.940 mm was used on the left unit and 0.500 mm on the right on Survey 2. Oblique tows were made to a depth of 50 m at all stations except where the bottom was shallower than 50 m.

Techniques used for describing the development of *L. hectoris* are outlined in Moser and Ahlstrom (1970).

Lampanyctodes hectoris (Günther)
Figures 3 and 4

Literature.—The illustration of the 9.2 mm larva of *Lampanyctodes hectoris* and the remarks on photophore formation in that species in Moser and Ahlstrom (1972) are in error and refer to a larva of *Lampadena* sp. There are no illustrations or descriptions of *L. hectoris* larvae in the literature.

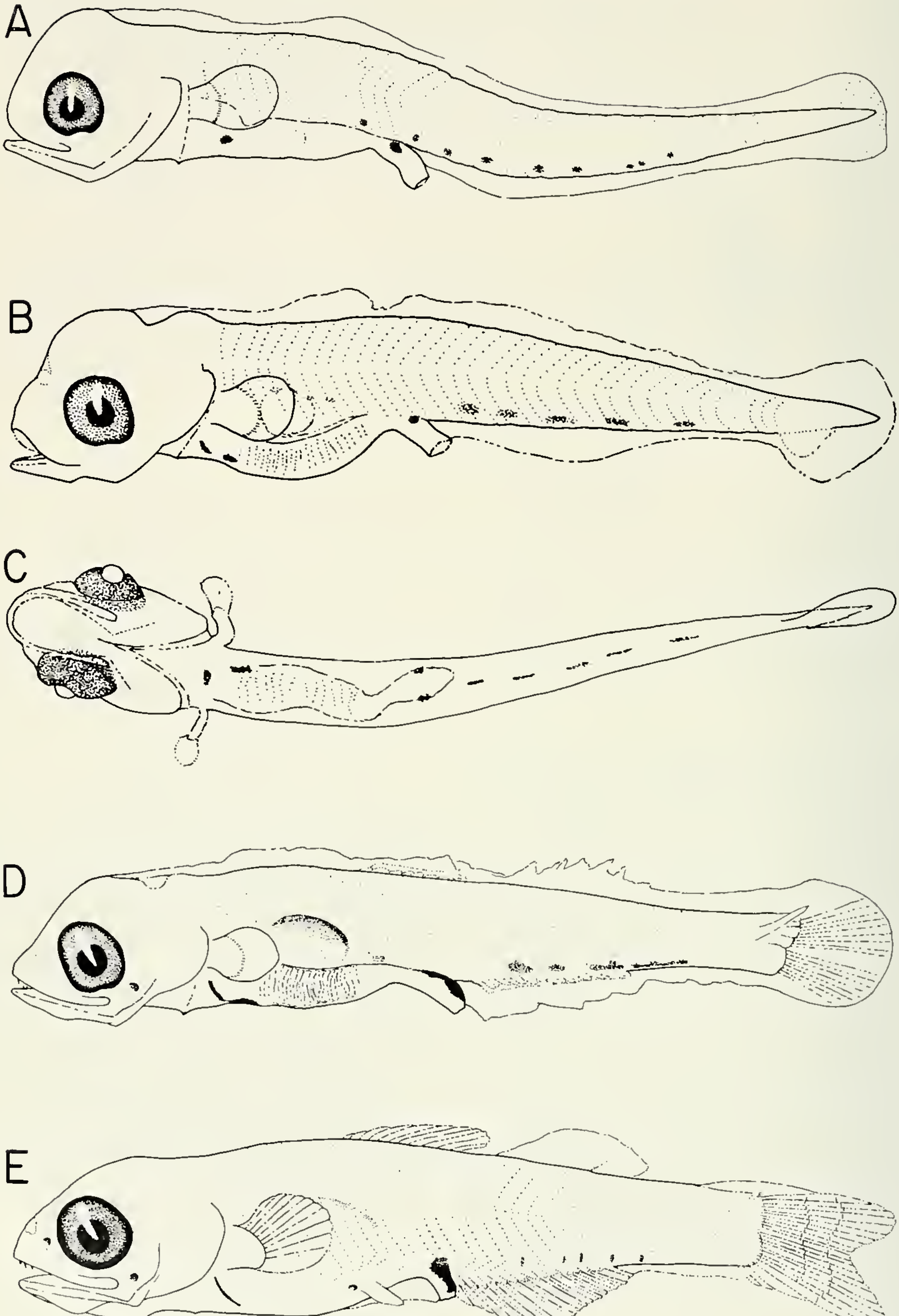

Figure 3. Larvae of *Lampanyctodes hectoris.* A. 3.8 mm; B. 5.0 mm; C. 5.0 mm, ventral view; D. 6.8 mm; E. 8.7 mm.

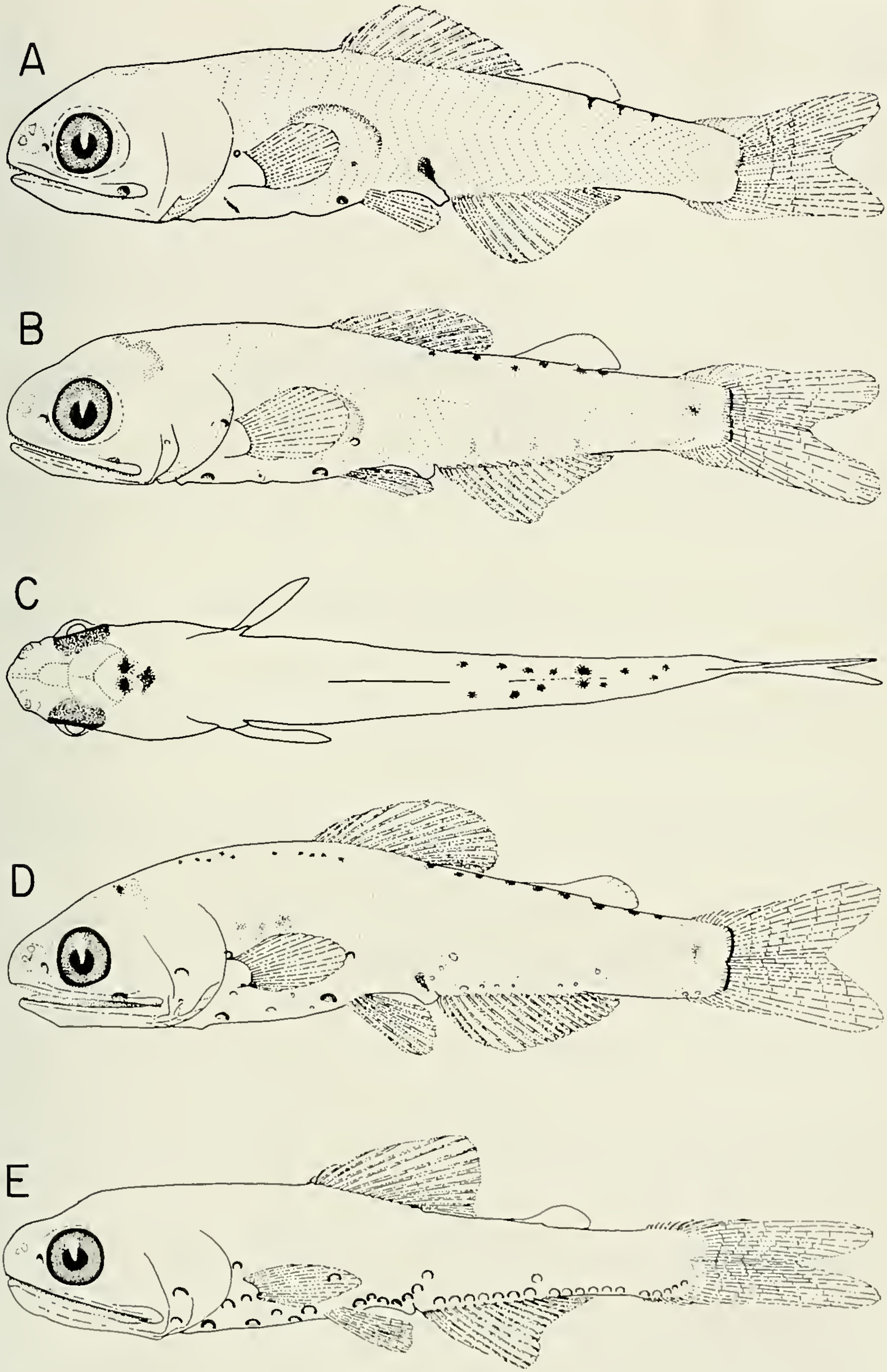

Figure 4. Developmental stages of *Lampanyctodes hectoris.* A. 11.7 mm larva; B. 13.0 mm larva; C. 13.0 mm larva, dorsal view; D. 14.9 mm transforming specimen; E. 14.2 mm juvenile.

TABLE 1. Measurements (mm) of larvae of *Lampanyctodes hectoris.* (Specimens between dashed lines are undergoing notochord flexion).

Body length	Snout to anus	Head length	Head width	Snout length	Eye width	Eye length	Length of ventral eye tissue	Body depth	Pectoral fin length	Snout to origin of pelvic fin	Snout to origin of anal fin	Snout to origin of dorsal fin
3.8	1.8	0.75	0.50	0.15	0.23	0.29	–	0.49	0.20	–	–	–
4.0	1.8	0.72	0.43	0.12	0.20	0.27	–	0.43	0.19	–	–	–
4.3	2.0	0.85	0.52	0.16	0.24	0.30	–	0.45	0.25	–	–	–
4.5	2.3	0.96	0.53	0.20	0.27	0.31	–	0.63	–	–	–	–
4.8	2.5	1.0	0.70	0.26	0.29	0.37	–	0.68	0.29	–	–	–
5.0	2.6	1.2	0.75	0.25	0.38	0.43	0.02	0.85	0.20	–	–	–
5.2	2.7	1.1	0.70	0.27	0.31	0.39	–	0.73	0.35	–	–	–
5.6	2.8	1.2	0.77	0.35	0.34	0.42	0.01	0.82	0.25	–	–	–
5.8	3.1	1.4	0.78	0.32	0.38	0.46	0.01	0.86	0.36	–	–	–
6.0	3.1	1.2	0.80	0.32	0.41	0.48	0.02	0.88	0.26	–	–	–
6.2	3.2	1.4	0.83	0.33	0.43	0.48	0.04	1.0	0.33	2.4	–	–
6.4	3.7	1.4	0.90	0.34	0.49	0.55	0.03	1.1	0.27	2.8	–	–
6.6	3.8	1.7	1.0	0.45	0.53	0.62	0.04	1.2	0.32	2.8	3.9	3.0
6.8	4.0	1.7	1.0	0.36	0.57	0.55	0.01	1.2	0.28	3.0	4.2	2.8
7.0	4.0	1.7	1.1	0.40	0.52	0.63	0.02	1.2	0.56	3.1	4.2	3.2
7.2	4.2	1.9	1.0	0.40	0.57	0.68	–	1.4	0.46	3.1	4.3	3.2
7.5	4.2	1.8	1.0	0.43	0.52	0.62	0.03	1.3	0.57	3.2	4.3	3.3
7.7	4.6	1.9	1.0	0.40	0.64	0.71	0.04	1.3	0.52	3.3	4.6	3.2
8.0	4.6	2.0	1.2	0.45	0.61	0.71	–	1.5	0.60	3.3	4.7	3.3
8.2	4.9	2.2	1.2	0.49	0.68	0.75	0.02	1.6	0.65	3.8	4.9	3.6
8.7	5.0	2.3	1.3	0.50	0.77	0.87	0.02	1.8	0.87	3.8	5.0	3.8
9.2	5.2	2.2	1.2	0.60	0.73	0.84	–	1.8	1.0	4.2	5.3	4.1
9.7	5.7	2.5	1.3	0.68	0.73	0.86	–	2.0	1.0	4.2	5.7	4.2
10.1	6.2	2.9	1.4	0.71	0.87	0.91	–	2.2	1.2	4.6	6.2	4.5
10.5	6.5	2.9	1.6	0.73	0.88	1.0	–	2.3	1.2	4.8	6.5	4.8
10.8	6.7	3.0	1.7	0.78	0.83	0.95	–	2.4	1.4	5.1	6.7	4.8
11.0	6.8	3.0	1.6	0.74	0.79	0.95	–	2.3	1.3	5.0	6.9	4.8
11.7	7.1	3.3	1.7	0.93	0.87	1.0	–	2.6	1.5	5.4	7.1	5.2
12.0	7.5	3.3	1.8	0.83	1.0	1.1	–	2.8	1.5	5.7	7.5	5.3

TABLE 1. (*Continued*)

Body length	Snout to anus	Head length	Head width	Snout length	Eye width	Eye length	Length of ventral eye tissue	Body depth	Pectoral fin length	Snout to origin of pelvic fin	Snout to origin of anal fin	Snout to origin of dorsal fin
12.3	7.4	3.4	1.8	0.80	1.0	1.0	–	2.9	1.4	5.5	7.4	5.4
13.0	7.8	3.6	2.2	0.90	1.0	1.2	–	2.9	1.7	5.8	7.8	5.8
13.8	8.3	3.7	2.0	0.96	0.98	1.0	–	3.2	1.8	6.2	8.4	6.2
14.0	8.9	4.1	1.9	0.93	1.1	1.2	–	3.2	1.6	7.0	9.1	6.1
14.9*	8.8	4.0	2.2	0.95	1.1	1.2	–	3.7	2.1	6.6	8.8	6.4
14.2**	8.6	4.6	2.0	1.0	1.2	1.2	–	3.2	1.9	6.8	8.8	6.7
16.0**	9.8	5.0	2.8	0.94	1.3	1.3	–	3.5	2.5	7.2	9.9	7.1
21.2**	13.0	6.6	3.2	1.0	2.0	2.0	–	4.9	4.0	9.8	13.0	9.5

* Transforming specimen.
** Juvenile.

TABLE 2. Meristics from cleared and stained larvae of *Lampanyctodes hectoris*.

Length (mm)	Principal caudal fin rays		Procurrent caudal fin rays		Branchiostegal rays		Pectoral fin rays		Hypural elements		Gill rakers (right arch)		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebrae
	superior	inferior	superior	inferior	left	right	left	right	superior	inferior	upper limb	lower limb			left	right	
7.5	7	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
7.7	10	9	0	1	3	3	5	5	–	–	–	–	5	–	–	–	–
8.3	10	9	–	–	3	3	4	5	–	–	–	–	7	–	–	–	–
8.7	10	9	2	3	4	4	7	7	1	3	–	–	11	7	–	–	–
9.2	10	9	3	4	5	5	9	9	2	3	–	–	13	9	4	4	–
9.6	10	9	4	5	6	6	10	9	4	3	–	–	14	12	5	5	–
10.1	10	9	5	6	7	7	12	12	4	3	–	–	15	12	7	7	–
10.5	10	9	6	7	7	7	11	11	4	3	–	–	16	13	7	7	–
11.1	10	9	7	8	8	8	11	12	4	3	–	–	16	13	7	7	26
11.8	10	9	7	8	8	8	13	13	4	3	0	12	16	14	8	8	37
12.3	10	9	–	9	7	8	–	12	4	3	5	14	15	14	8	8	37
12.7	10	9	9	11	9	9	13	13	4	3	8	17	16	14	8	8	37
13.2	10	9	9	10	9	9	12	12	4	3	4	13	16	14	8	8	37
14.4	10	9	8	9	10	10	13	12	4	3	10	17	16	14	8	8	37
15.9	10	9	10	10	9	9	13	13	4	3	10	20	16	14	8	8	37

Diagnostic features.—As for other species of lanternfishes, the pelagic eggs of *L. hectoris* are not known. The smallest larvae in our collection were 3.8 mm. Larvae obtain a moderate size in comparison with those of related genera. The largest larva in our collection is 14.4 mm and the smallest juvenile is 14.2 mm SL. A 14.9 mm specimen is undergoing transformation. Larvae of *L. hectoris* have a unique sequence of photophore development, beginning with the Br_2 in 6 mm larvae and followed by the Vn in 7 mm larvae, the PO_5 in 8 mm larvae, and the PLO and PO_1 in 11 mm larvae. Although several other genera develop this same complement of early-forming photophores, as explained in detail in a later section, none develops them in this sequence. Small larvae which have not developed photophores may be identified by their pattern of melanophores, the most characteristic of which are a persistent series of four to eight ventral tail melanophores, two melanophores in the foregut region, a bilateral pair at the divergence of the terminal region of the gut, a series of embedded spots above the mid-gut, and a melanistic shield above the developing gas bladder. In mid- and late-stage larvae, a bilateral series of melanophores develops on the posterior dorsum.

Morphology.—Larvae of *L. hectoris* have no striking morphological features. Body depth increases from a mean of 14 percent of the body length in preflexion larvae, to 18 percent in larvae undergoing flexion, to 22 percent in postflexion larvae and 23 percent in newly transformed juveniles (Table 1). Snout-anus length averages 50 percent of the body length in preflexion larvae, 58 percent during flexion and 60 percent in later developmental stages. Head size is moderate; relative head length increases gradually from a mean of 21 percent of body length in preflexion larvae to 25 percent during flexion, 27 percent in postflexion larvae and 31 percent in early juveniles. Relative head width decreases gradually during development; it averages 62, 58, and 54 percent of the head length for the three major larval stages and 49 percent in early juveniles. Snout length is moderate, averaging 24 percent of the head length over the entire larval period and shortens to 19 percent in early juveniles. The eye is moderately large; eye length averages 36 percent of the head length in larvae up to the completion of notochord flexion, is reduced to a mean of 33 percent in postflexion larvae and further to 27 percent in early juveniles. The eye is slightly elliptical in preflexion larvae; eye width averages 82 percent of eye length, but this increases to a mean of 89 percent in later larval stages and the eyes of early juveniles are round. There is a sliver of ventral choroid tissue that appears in larvae between 5.0 and 9.0 mm. It reaches a maximum relative depth of 8 percent of the eye length and is only slightly paler in color than the eye itself.

Ossification of some important larval features is as follows. Vertebrae begin to ossify at about 11.1 mm length and the full complement of 36 to 37 is ossifying in larvae 12.3 mm and larger. Branchiostegal rays begin to ossify in 7 mm larvae, but, the full complement of 11 as listed by Paxton (1972) is not achieved in larvae nor in the earliest juveniles.

The maxillary is ossifying in larvae as small as 3.9 mm but develops no teeth. The dentary is ossifying and bearing teeth by 5.9 mm, as is the premaxillary. Teeth are uniserial on the premaxillary with the anterior five or six teeth larger than the remainder; as many as 20 conical, usually straight teeth form on late-stage larvae. On the posterior two-thirds of each dentary bone a series of six to eight conspicuous hooked teeth form early in the larval period. The hooked part of each tooth projects anteriad at almost right angles to the base of the tooth. They persist to transformation. The dentary teeth anterior to these, and later between and posterior to the hooked teeth, are conical, straight and uniserial anteriorly. Late-stage larvae have more than 30 such dentary teeth. The hooked and uniserial teeth present on the jaws of larvae are shed or resorbed and replaced by the wide bands of numerous small teeth at transformation.

Fin formation.—A pectoral fin with differentiated base and blade is present in our smallest larvae (3.8 mm). The base remains small and inconspicuous throughout the larval period as does the blade, which has a rounded posterior margin. At transformation the pectorals extend posteriad to the origin of the pelvics. Rays begin to ossify in 7 mm larvae in a dorsal to ventral sequence and the full complement of 13 to 14 is present in larvae as small as 11.8 mm (Table 2).

The anlage of the caudal fin is present in larvae as small as 5.0 mm. The principal caudal rays begin to ossify in 7 mm larvae and the full complement of 10+9 rays is ossifying in a 7.7 mm specimen. Procurrent caudal rays also begin to ossify in 7 mm larvae and the full complement of 8 to 10 superior and 9 to 11 inferior rays is ossifying in 12 mm larvae. The hypural elements begin to ossify in 8 mm larvae and the full complement of four superior and three inferior elements is ossifying in 9 mm larvae. Flexion of the notochord begins when the larvae are about 6.5 mm long and is completed at about 8.0 mm length.

The anal and dorsal fin bases begin to form during notochord flexion. Anal fin rays are beginning to ossify in a 7.7 mm larva and dorsal rays are ossifying in an 8.7 mm larva. The full complements of 16 to 17 anal and 13 to 14 dorsal rays are ossifying in larvae 10.5 mm and larger. In both the anal and dorsal fins, the rays ossify posteriad and anteriad from the more central rays. In both fins the last ray to form is the short anteriormost ray.

Pelvic fin buds appear at about 6.2 mm length, but, the rays do not begin to ossify until the larvae reach about 9 mm. The full complement of 8 pelvic rays is ossifying in larvae 11.8 mm and larger.

Pigmentation.—Preflexion larvae (3.8 to ca. 6.0 mm) have two pairs of pigment dashes developed on the gut. The anterior pair is on the foregut posterior to the cleithra, while the posterior pair is on the free terminal section of the gut. The most conspicuous pigment in preflexion larvae is the series of four to eight melanistic spots or dashes on the ventral midline of the tail. By the end of the preflexion stage, melanistic pigment is developing over the gas bladder. Also the anterior foregut spots have coalesced and moved forward and dorsad to form a pigment shield over the anterior part of the liver.

Flexion larvae (6.2 to ca. 7.5 mm) have essentially the same pigment as in preflexion larvae. The ventral tail spots range from three to seven (mean of 4.4 for 27 specimens). The median ventral foregut pigment spot or patch is continuously present as are the paired patches or streaks of pigment on the free terminal section of the gut. Pigment above the gas bladder increases in amount, with sometimes a pair of internal pigment spots located between the gas bladder and the termination of the gut.

A single pigment spot develops over the hind brain in some specimens; of the 27 specimens between 6.2 to 7.5 mm, only four had this head pigment spot. Two specimens in this size range, 6.5 and 7.2 mm respectively, had a double row of small dorsal pigment spots (seven to eight spots per side) extending for most of the length of the tail portion of the body.

In postflexion larvae (7.7 to 13.9 mm) the pigment areas already described either persist or are more consistently present, and additional pigment develops on the head, back, and in the caudal region. The pigment over the gas bladder increases in extent and begins to spread laterally. Melanistic pigment is present on the cleithral margin forward of the pectoral base on most larvae 9.2 mm and larger. The ventral midline of pigment spots becomes imbedded and sometimes faint, but was absent on only four specimens. The number of pigment spots ranges between two and five (mean of 3.6 spots on 43 specimens). The imbedded pigment spot on the hind brain occurs on about ⅓ of the larvae between 7.7 and 8.7 mm, but thereafter is consistently present. By about 10 mm, two spots form over the cerebellum and are usually present on larvae larger than this. The double row of dorsal tail pigment spots is only sporadically present on larvae under 10.5 mm, but consistently present on larger larvae. The rows extend from about the termination of the dorsal fin, almost to the procurrent caudal rays; the usual count is seven or eight spots per side, but the range is from two to thirteen spots. Internal pigment forms over the hypurals, usually adjacent to the ural centrum; this pigment, first observed on a 7.7 mm specimen, is infrequently present on larvae under 10.5 mm. Pigment also forms at the hypural edge of the caudal fin. It was first observed on a 7.2 mm larva and was sporadically present until 10.5 mm. On older specimens this pigment becomes almost continuous along the hypural edge. The 14.9 mm transforming specimen added a line of dorsal pigment spots to the nape and trunk; however, a 14.2 mm juvenile had pigment over the entire body and the peritoneum was conspicuously black.

Photophore development.—A number of photophores form on larvae of *Lampanyctodes* prior to transformation. As is usual in myctophids, the Br_2 pair is the first to form; it was consistently present on specimens 6.6 mm and larger. The Vn, the second pair to form, was first observed on a 7.5 mm specimen and was consistently present by 7.8 mm. The third pair, PO_5, was present by 8.7 mm. A specimen 11.2 mm had two additional pairs, the PLO and PO_1; however, specimens 11.7 and 11.8 mm had added only the PLO pair, indicative that it forms somewhat sooner than the PO_1. Specimens 12.0 mm and larger consistently had both these pairs. A 12.7 mm specimen had three additional pairs faintly formed, the VLO, OP_2, and PO_2; however, none of these was present on a 13.7 mm specimen, and only the VLO pair was present on a 13.8 mm and a 14.4 mm specimen. A transforming specimen 14.9 mm long had the majority of photophores formed. The initial five pairs to form, the Br_2, Vn, PO_5, PLO and PO_1 became conspicuous photophores soon after their formation. This was not the case for the three other pairs

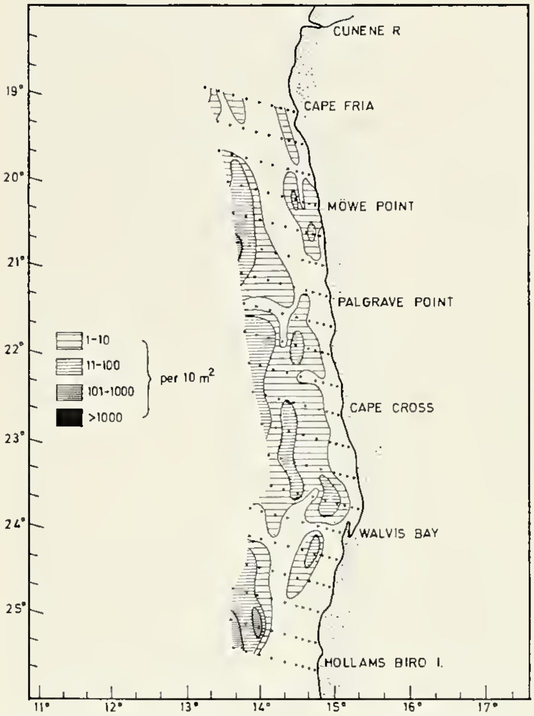

Figure 5. Distribution and abundance of larvae of *Lampanyctodes hectoris* on SWAPELS Survey 1 (August 1972 to March 1973). Numbers represent cumulative standard haul totals.

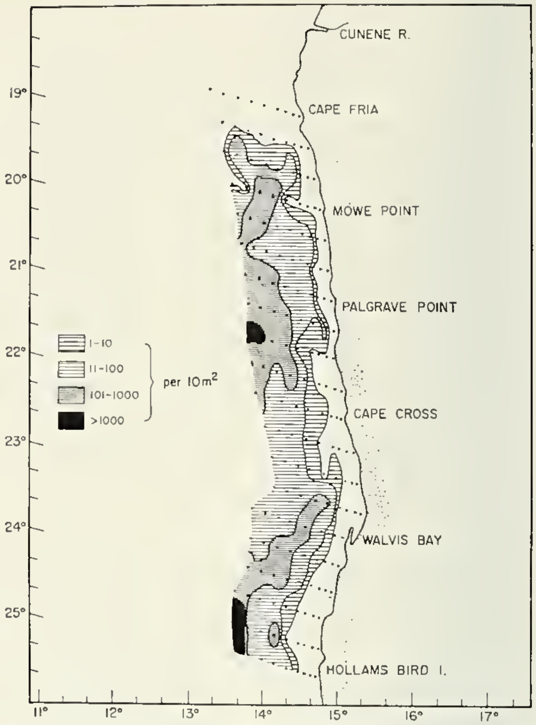

Figure 6. Distribution and abundance of larvae of *Lampanyctodes hectoris* on SWAPELS Survey 2 (August 1973 to April 1974).

mentioned above which, at best, were but faintly developed on late-stage larvae prior to transformation.

DISTRIBUTION

Lampanyctodes hectoris is a neritic species associated with land masses in the vicinity of the subtropical convergence. It is known from South Africa, New Zealand, Southern Australia, and Chile, but apparently does not occur in the western Atlantic off Argentina (McGinnis, 1974). Where it occurs, it is highly abundant, as demonstrated by the fishery off South Africa. It may occur in commercial abundance in other southern ocean areas.

There are no available data on the distribution and abundance of the larvae in the area of the fishery off South Africa, but SWAPELS provides larval data from an area just to the north of the fishery. Results from the two year survey show that larvae of the family Myctophidae formed 9.75 percent of all the fish larvae taken and larvae of *L. hectoris* comprised over 85 percent of all myctophid larvae. This species was widely distributed between latitudes 19° and 25° S (Figs. 5 and 6). Larvae were found at distances of 8 to 112 km from the coast but were most abundant in offshore waters especially between Möwe Point (20°20′ S) and Cape Cross (22° S) and between Walvis Bay (23° S) and Hollams Bird Island (25° S). Approximately 93 percent of all larvae were taken during the months of August, September, October, and November of both years. Early larval stages (those less than 5.0 mm in length) were common from August to October, but were most abundant in the plankton in August particularly in the region west of Hollams Bird Island. Over 62 percent of all early larval stages were taken during this month. The larvae of *L. hectoris* were found at surface temperatures ranging from 13.9° to 21.5° C. However, over 60 percent of all larvae occurred at mean surface temperatures of 14.0° to 15.5° C.

SYSTEMATIC RELATIONSHIPS

Although the photophores of *L. hectoris* were not mentioned in the original description of the species

(Günther, 1876), Fraser-Brunner (1949) was well aware of the unique arrangement of the light organs and, accordingly, created the genus *Lampanyctodes* for this species. He noted the marked ventral placement of the two longitudinal series of photophores, a feature which he thought was more characteristic of the "primitive" myctophine lanternfishes than of the lampanyctine genera to which it was obviously allied on the basis of morphological characters. He mentioned particularly the horizontal positioning of the two PVO photophores, an arrangement found only in the myctophine genera *Protomyctophum*, *Diogenichthys*, and *Benthosema*. His view of *Lampanyctodes* as a primitive lampanyctine genus is demonstrated by the statement, "this genus is clearly indicative of the form from which *Lampanyctus*, *Gymnoscopelus* and their allies have been derived." He did not elaborate on the relationships of *Lampanyctodes* with other lampanyctine genera nor did he construct a higher classification for lanternfishes.

It remained for Paxton (1972) to formally recognize the two subfamilies Myctophinae and Lampanyctinae and to construct a higher classification that included six tribes, two in the Myctophinae and four in the Lampanyctinae. In the latter subfamily he recognized the monotypic tribe Notolychnini, the tribe Lampanyctini consisting of eight genera, Diaphini with two genera, and Gymnoscopelini with eight genera. *Lampanyctodes* was important in his tribal arrangement as shown by his statement "the Diaphini and Gymnoscopelini are closely related, for the most primitive genus of each group, *Lobianchia* of the Diaphini and *Lampanyctodes* of the Gymnoscopelini, share a number of characters. Each form has widely ossified pubic plates, a relatively low number of ventral procurrent rays, well-developed caudal glands, one or two elevated PO photophores, and an arched or elevated series of VO photophores . . . ." He viewed *Lampanyctodes* as an essentially intermediate form that branched from the main line of gymnoscopeline evolution soon after the divergence of this tribe from the Diaphini.

Using the combination of larval and adult characters, Moser and Ahlstrom (1972) proposed a phylogenetic scheme for the subfamily Lampanyctinae that recognized the four tribes of Paxton (1972) but differed in the placement of certain genera in the Lampanyctini and Gymnoscopelini. We believe that the triad of genera, *Bolinichthys*, *Ceratoscopelus* and *Lepidophanes* belong in the Gymnoscopelini whereas Paxton placed them in the Lampanyctini. Also, we would include two other of Paxton's lampanyctine genera, *Lampadena* and *Taaningichthys*, in the Gymnoscopelini. These form a triad with the recently described *Dorsadena*. Our conception of tribal and generic relationships in the subfamily Lampanyctinae based on a combination of larval and adult characters is shown in the dendrogram (Fig. 7). Essentially the tribe Gymnoscopelini consists of the two above mentioned triads, the triad of *Lampichthys*, *Notoscopelus* and *Scopelopsis*, the well differentiated genus *Gymnoscopelus* and two monotypic isolated genera, *Hintonia* and *Lampanyctodes*. Based on Paxton's adult characters, and the larval characters given below and in Moser and Ahlstrom (1972), the genus *Gymnoscopelus* is closest to the Diaphini and in a direct line from the original tribal split. We have not yet identified the larvae of *Hintonia* and accept the view of Paxton that the genus has no distinct relationship to any member of the tribe and that this form split off early from the ancestral stock.

The genus *Lampanyctodes* is the most problematic and, phylogenetically, the most intriguing genus in the tribe. Its photophore arrangement is so unusual that it warrants a brief review. All photophores are relatively low on the body, including the PLO, VLO, 3rd SAO, POL and terminal Prc, all of which are well below the lateral line. Both a Dn and Vn pair of eye photophores are formed, although the Dn develops quite late. This feature is shared with *Lampichthys*, *Scopelopsis*, *Notoscopelus*, *Hintonia*, *Diaphus* (usually) and *Gymnoscopelus* among the Lampanyctinae and with most genera of Myctophinae.

Of particular interest is the horizontal arrangement of the two PVO photophores, an arrangement not found in any other genus of the Lampanyctinae, but present in three myctophine genera, as previously noted.

Although *Lampanyctodes* has the usual number of PO photophores, five, it is unique in having the PO_3 elevated rather than the PO_4. *Lampanyctodes* also has the usual number of VO photophores for Lampanyctinae, five, but has the series evenly arched, an unusual arrangement also found in some *Lampanyctus*. None of the AO series is elevated, the usual arrangement in most kinds of lanternfishes. The presence of a single POL is shared with all genera of *Myctophinae* except *Hygophum*, and with a half dozen genera of Lampanyctinae (*Diaphus*, *Lobianchia*, *Taaningichthys*, *Lampadena*, *Gymnoscopelus* and *Steno-*

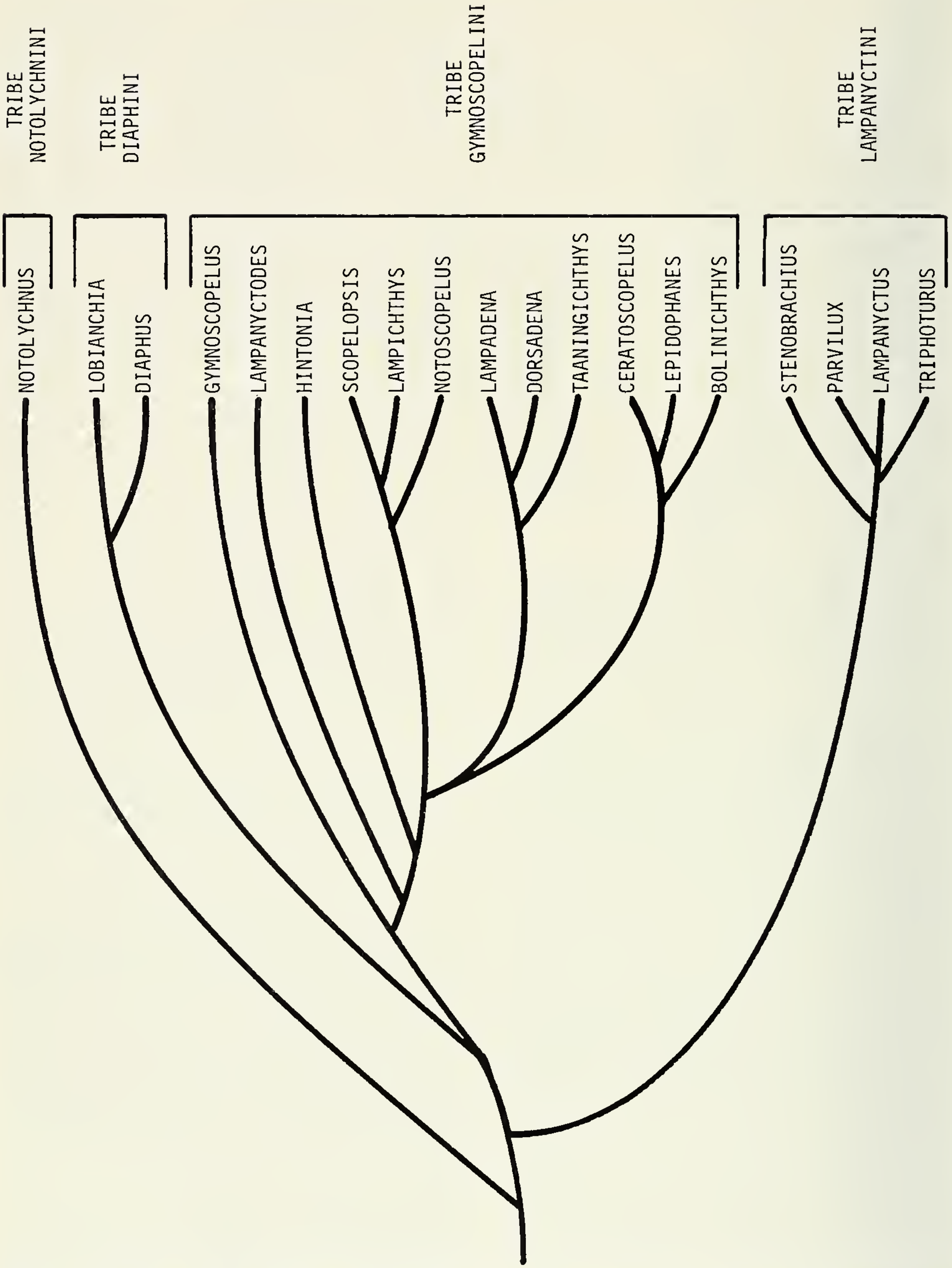

Figure 7. Dendrogram showing the generic relationships and tribal division of the subfamily Lampanyctinae based on a combination of larval and adult characters.

TABLE 3. Size at formation and sequence of early forming photophores for 10 genera of *Lampanyctinae*.

	Size at transformation (mm)	Br$_2$	Vn	PO$_5$	PLO	PO$_1$
Lampanyctodes hectoris	14–15	6.6 (1)	7.8 (2)	8.7 (3)	11.7 (4)	Ca 12.0 (5)
Ceratoscopelus townsendi	16.5–18	7.0 (1)	7.8 (2)	9.0 (4)	8.7 (3)	–
Lepidophanes guentheri	–	< 9.5	< 9.5	< 9.5	< 9.5	–
Notoscopelus resplendens	19–21	4.2 (1)	9.2 (3)	6.2 (2)	Ca 15.0 (4)	–
Lampichthys rectangularis	19–21	< 7.0 (1)	9.8 (3)	8.4 (2)	Ca 16.0 (4)	16.4 (5)
Lampadena urophaos	17–21	6.2 (1)	13.4 (4–5)	9.8 (3)	7.3 (2)	13.4 (4–5)
Scopelopsis multipunctatus	16.5–17.5	5.4 (1)	11.3 (3)	10.8 (2)	–	–
Gymnoscopelus aphya	Ca 30	< 23.5 (1)	–	< 23.5 (2–3)	–	< 23.5 (2–3)
Diaphus theta	10–11	6.0 (1)	–	6.2 (2)	–	7.6 (3)
Lobianchia gemellari	–	5.5 (1)	–	7.0 (3)	–	6.2 (2)

brachius). The possession of five Prc's is unusual, as is their arrangement in an ascending line that terminates well below the lateral line.

Lampanyctodes is among the genera that develops accessory patches of luminous tissue on the body, a character shared with most members of the tribe *Gymnoscopelini*, as we interpret it, and with *Diaphus* (most species) and *Lampanyctus* (some species). None of the myctophine genera develops accessory luminous tissue other than the supra and infracaudal glands. In *Lampanyctodes* the luminous tissue develops at the bases of the dorsal, anal, pectoral and pelvic fins, before and behind the dorsal fin, and on the dorsal surface of head; this pattern is suggestive of that developed on *Ceratoscopelus* and *Bolinichthys*. No secondary photophores are developed.

The fact that, in its arrangement of light organs, *Lampanyctodes* shares so many characters with so many other genera of Lampanytinae, and even shares a fundamental character (the horizontal PVO's) with some genera of the Myctophinae has produced an understandable confusion as to the position of this genus. We would agree with Fraser-Brunner (1949) and Paxton (1972) that the genus has had a long and independent evolution but do not consider it a primitive genus. We believe it is a highly specialized form and that the ventral and basically linear placement of photophores is related to its mode of life in shallow neritic waters. Our thesis that the arrangement of ventrally placed, well developed linear series of photophores, such as is found in most Myctophinae, is an adaptation for countershading in shallow-living lanternfishes has been stated in detail in previous papers (Moser and Ahlstrom, 1972, 1974).

The relationships of *Lampanyctodes* to other genera of Gymnoscopelini is seen more clearly from an examination of larval characters. It develops the dorsal series of pigment spots found in so many members of this tribe and, more importantly, forms several of the same photophores during the larval period (Table 3).

In an attempt to analyze the position of *Lampanyctodes* in the subfamily Lampanyctinae we selected 10 larval characters and 10 adult characters of this genus and compared them with all other genera in the subfamily. *Dorsadena* and *Hintonia* were excluded since their larvae are unknown. Two groups of larval characters were selected, those related to early forming photophores, and those related to pigment patterns. Adult characters were based mostly on photophore arrangements, presence or absence of luminous caudal glands, accessory luminous tissue, secondary photophores, sexual dimorphism, keel or ridge on fifth circumorbital bone, and a supra-

TABLE 4. Larval and adult characters of *Lampanyctodes hectoris* compared with other genera of the subfamily *Lampanyctinae*.

	Lampanyctodes	*Lampichthys*	*Scopelopsis*	*Notoscopelus*	*Ceratoscopelus*	*Lepidophanes*	*Bolinichthys*	*Lampadena*	*Taaningichthys*	*Gymnoscopelus*	*Diaphus*	*Lobianchia*	*Lampanyctus*	*Triphoturus*	*Stenobrachius*	*Parvilux*	*Notolychnus*
Larval characters																	
Early forming photophores																	
Br_2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-
Vn	+	+	+	+	+	+	-	+	-	-	-	-	-	-	-	-	-
PO_5	+	+	+	+	+	+	-	+	-	+	+	+	-	-	-	-	-
PLO	+	+	-	+	+	+	-	+	-	-	-	-	-	-	-	-	-
PO_1	+	+	-	-	-	-	-	+	-	+	+	+	-	-	-	-	-
Pigment characters																	
Series of ventral pigment spots (preflexion)	+	+	+	-	+	+	+	-	-	+	+	-	- +	+	+	?	+
Ventral series retained (postflexion)	+	+	+	-	-	-	-	-	-	+	+ -	-	-	-	-	-	-
Pigment back of head	+	+	+	+	+ -	+	+	+	+	+	- +	-	+ -	-	+ late	+	-
Dorsal body pigment	+	+	+	+	+ -	+	+ -	+	+	+	-	-	- +	+	+ late	+	-
Caudal pigment	+	+	+	+	-	-	-	-	+	+	+ -	+ -	-	-	-	-	+
Adult characters																	
Supramaxillary present	+	+	+	+	-	-	-	-	-	+	-	-	-	-	-	-	-
Circumorbital 5 keel or ridge	+	+	+	+	-	-	-	-	-	+	+ -	+	-	-	-	-	?
One or more VO's elevated	+	-	-	-	+	+	+	-	-	-	+	+	+ -	+	-	-	+
Single POL	+	-	-	-	-	-	-	+	+	-	+	+	-	-	+	-	-
Dn and Vn development	+	+	+	+	-	-	-	-	-	+	+ -	-	-	-	-	-	-
Supracaudal glands developed	+	+	+	+ -	+	+	+	+	+	-	-	+	+	+	+	+	+
Infracaudal glands developed	+	+	-	-	+	+	+	+	+	-	-	+	+	+	+	+	-
Accessory luminous tissue	+	+	+	+	+	+	+	-	-	+	+ -	-	+ -	-	-	-	-
Sexual dimorphism lacking	+	+	-	-	-	?	-	+	-	-	-	-	+	+	+	+	-
Secondary photophores lacking	+	-	-	+	+	-	-	+	+	+	+	+	+ -	+	+	+	+

maxillary. Presence of a character was rated as a "plus" and absence as a "dash". Because of variability occurring among species in some genera, some characters had to be rated both "plus" and "dash" (Table 4). In making a summation, characters rated as both "plus" and "dash" were weighted ½.

We do not assume that these 20 characters are of equal phylogenetic importance, even though none is trivial. We selected characters that are present or absent, hence had to ignore equally relevant characters that can not be so rated. Among the adult characters chosen, luminous glands on the caudal peduncle (supra and infra) probably are the most problematical, in that their presence or absence may not be as important phylogenetically as are the structural and functional differences in these glands among genera. These differences cannot be simply rated by this technique.

As noted earlier, the initial five pairs of photophores to develop on *Lampanyctodes* during the larval period are Br_2, Vn, PO_5, PLO, and PO_1. As indicated in table 4, all five pairs are also developed on *Lampichthys* and *Lampadena*, although not in the same sequence as in *Lampanyctodes*. Four of the above pairs are early forming on *Notoscopelus*, *Ceratoscopelus*, and *Lepidophanes*, three of the above pairs in *Scopelopsis*, *Gymnoscopelus*, *Diaphus* and *Lobianchia* and the remaining seven genera lack early forming photophores other than the Br_2 pair. We consider the striking similarity of these early forming pairs among genera as evidence of close relationship.

The other characters selected for larvae involve pigment patterns, including the presence or absence of a row of ventral midline pigment spots on the tail of preflexion and late-stage larvae, and the development of pigment on the back of the head, along the dorsal margin of the body, or at the base of the caudal fin of postflexion larvae.

Certain relationships emerge when the characters in the table are summed. *Lampanyctodes* is found to be most closely related to *Lampichthys* (17 points), then to *Scopelopsis* (13), *Gymnoscopelus* (13), *Notoscopelus* (12½), *Lampadena* (12), *Ceratoscopelus* (11), and *Lepidophanes* (11). These genera are among those we place in the tribe Gymnoscopelini. Although it is true that larval characters strongly influence this rating, so do several of the adult characters, such as the presence of a supramaxillary, Dn and Vn photophores, and accessory luminous tissue. *Lampanyctodes* is close to three genera that Paxton (1972) and Moser and Ahlstrom (1972) have previously shown to be closely allied (*Lampichthys*, *Scopelopsis*, and *Notoscopelus*), but also to *Gymnoscopelus*, and must have split off from the ancestral line of the triad soon after it diverged from the *Gymnoscopelus* line.

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NEW DATA ON THE RARE ALEPOCEPHALID FISH *PHOTOSTYLUS PYCNOPTERUS*

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Abstract: New data are given on the unique and infrequently reported mesopelagic alepocephalid fish *Photostylus pycnopterus*. The second figure of the species and the first figure of its distribution are presented. The new information involves, principally, the superficial structure of the stalked luminous organs and paired intermandibular flaps, numbers of gill rakers on all arches, and dentition; teeth of the premaxillary, maxillary and mandible increase in number with size of fish. All captures (17), excepting possibly two, were made within distinctly warm-water regions, and about half were made over or very near rather steeply inclined topography, the remainder over abyssal plains. Also, all captures except one are from areas of rather high productivity.

The rare, mesopelagic, alepocephalid fish *Photostylus pycnopterus* Beebe, 1933, has been reported infrequently. Goodyear (1969) provided data on six specimens, four previously unreported. Since Goodyear's study six additional specimens have been recorded: one by Kotthaus (1972) and five by Quéro (1974), who included a reproduction of the figure of the holotype provided by Beebe (1933, fig. 41). The present study presents nine additional specimens, the second figure of the species (Fig. 1), introduces new data, and reviews previous information. Of the new material, nine specimens are deposited at the Scripps Institution of Oceanography; only Scripps material has been examined for this study (Fig. 2, solid circles).

All specimens known to me are listed below, arranged by author of record, collection number, number and standard length (in mm) of specimens, locality and date of capture, and estimated depth of tow (in meters). Geographical distributions are shown in figure 2.

New Material: SIO 52–404, 1 (61.1), 01° 43.0′ N, 89° 52.0′ W, VIII:8–9:1952, 0–1000; SIO 69–20, 2 (50.5–75.6), 06° 32.5′ N, 114° 16.0′ E, IV:24:1968, 0–1120; SIO 69–330, 1 (98.2), 14° 46.0′ S, 93° 37.5′ W, III:18:1969, 0–940; SIO 72–186, 3 (96.5–101.0), 16° 50.0′ S, 75° 31.2′ W, V:8–9:1972, 0–1130; SIO 73–164, 1 (80.8), 00° 00.0′ Eq, 155° 00.0′ W, VII:14–15:1972, 0–1120; SIO 73–171, 1 (86.7), 00° 07.0′ N, 154° 56.0′ W, VII:17:1972, 0–1120.

Beebe, 1933: Holotype, USNM 170959, 1 (64.0), ca 32° 12.0′ N, 64° 36.0′ W, V:30:1929, depth of tow ?.

Grey, 1958: USNM 148472, 1 (82.5), 39° 15.3′ N, 71° 25.0′ W, VIII:?:1885, depth of tow ?.

Goodyear, 1969: USNM 200467, 1 (96.1), 05° 48.0′ N, 64° 57.0′ E, V:24–25:1964, 0–2868; USNM 202567, 1 (39.9), 01° 50.0′ N, 65° 06.0′ E, V:27:1964, 0–1250; LACM 6902–3, 1 (84.5), 32° 36.0′ N, 118° 05.0′ W, II:21:1966, 0–1260; SIO 65–611–8, 1 (93.4), 12° 03.0′ S, 78° 58.0′ W, XI:24:1965, 0–1200.

Kotthaus, 1972: St Nr 119, 1 (58.0), 29° 30.0′ N, 24° 15.0′ W, date ?, 0–400.

Quéro, 1974: "Thalassa" St X 076, 1 (45.5), 30° 45.0′ N, 14° 28.0′ W, II:10:1971, 0–1000; "Thalassa" St X 078, 1 (45.0), 36° 06.0′ N, 12° 43.0′ W, II:12:1971, 0–1000; "Thalassa" St A 131, 2 (82.5–106.5), 45° 51.0′ N, 04° 15.0′ W, 0–1200; 1 (length and capture data not given), 24° 32.0′ N, 17° 12.0′ W.

Body proportions are given below for 19 specimens (39.9–106.5 mm SL). Included are data from Goodyear (1969, table 1) and Quéro (1974) and the nine new specimens; one specimen (SIO 65–611–8), examined by Goodyear, was remeasured. As no highly significant differences between the three sets of data are apparent, the proportional data from each are combined and presented as averages and ranges (in parentheses) of milles of standard length: head length 170 (145–189); depth behind head 133 (123–148); upper-jaw length 102 (80–103); snout to bony orbit 61 (56–67); length of fleshy orbit 38 (24–44); interorbital width 36 (25–46); prepelvic length 522 (490–542); predorsal length 781 (761–796); preanal length 757 (711–781); snout to anus 613 (566–634); depth of caudal peduncle 47 (39–61).

It should be noted that a reduction in standard lengths has occurred in three specimens since the initial reports. Beebe (1933) listed 64 mm SL for the holotype (USNM 170959); Goodyear

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Figure 1. *Photostylus pycnopterus*, adult female, 98.2 mm SL, SIO 69-330, from the southeastern Pacific Ocean.

(1969:398) gave this length as 57.0 mm but listed 55.6 mm in table 1. Grey (1958) recorded 82.5 mm SL for USNM 148472, whereas Goodyear found it to be 80.5 mm. I found SIO 65–611–8 to measure 91.8 mm SL rather than 93.4 mm as stated by Goodyear.

RESULTS AND DISCUSSION

Photostylus pycnopterus is unusual in having numerous small luminous organs mounted on short pedicels that are scattered about the head and body and sparsely on the rays of all but the pectoral fins. Most of the pedicels are flattened laterally and appear to be oriented so that the thin edge of the flattened surface is presented to the flow of water. Perhaps the term photophore is a misnomer in that the luminous organ at the tip of the pedicel is variable in structure and shape, and does not appear to have any focusing mechanism such as found in "photophores" of other fishes, principally in the Myctophidae and Sternoptychidae. Some appear to be only a dorsoventrally flattened layer of reflective tissue, a portion often iridescent; most are ovoid or rounded, with a base of iridescent tissue topped by tissue that is whitish in preservative. Some of the pedicels bearing these luminous organs are dark, and the pigment often continues to the organ and covers it, except for a window over the iridescent or whitish portion. Others of these organs are sur-

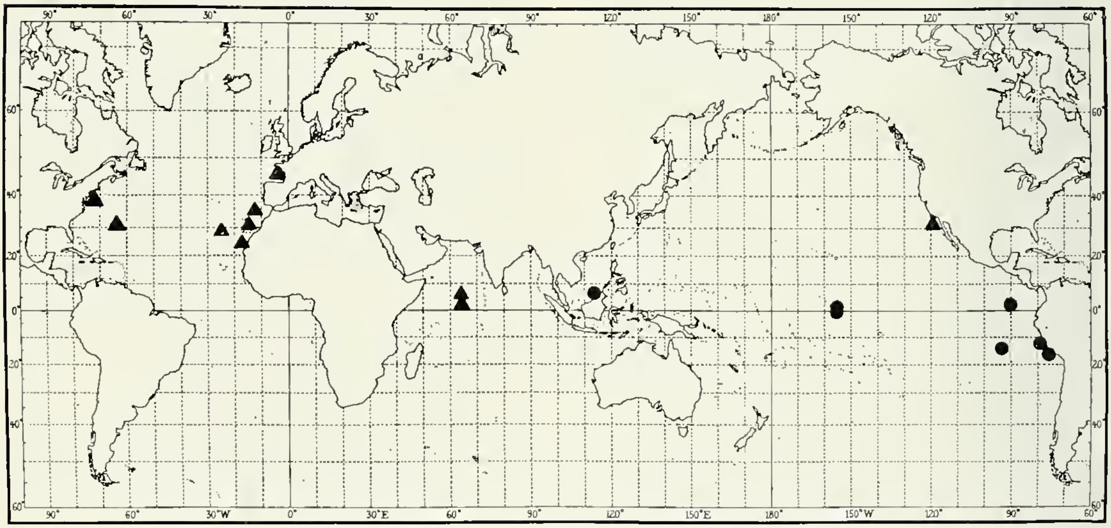

Figure 2. Capture localities for *Photostylus pycnopterus* recorded in the literature (solid triangles) and of new material (solid circles) examined in this study.

TABLE 1. Numbers of gill rakers (both sides counted) for four arches on 10 specimens of *Photostylus pycnopterus.*

	Upper rakers				Lower rakers (central raker included)				Total gill rakers						
Arches	1	2	3	4	9	10	11	12	10	11	12	13	14	15	16
First			17	3		17	3					16	2	2	
Second				20	1	8	8	3					6	11	3
Third			19	1	7	11	2				7	10	3		
Fourth	1	19			12	8			1	11	8				

rounded by iridescent tissue but have dark pigment at base and as a terminal cap.

In general, on the new material the distribution of these luminous organs is as illustrated by Beebe (1933, p. 164, fig. 41) but they are obviously fewer. Grey (1958) stated that the "papillae" of her specimen (USNM 148472) were very small, difficult to see, and apparently not as numerous as on the type specimen. Goodyear (1969) did not present a comparison of these organs on the type with those on the other specimens that he examined. Possibly the holotype was in better condition at time of examination as it was taken in a meter net (Beebe, 1931, Net 137, size of mesh not stated); USNM 148472 was taken in a large beam trawl ("Albatross" Station 2562), and all subsequent ones in Isaacs-Kidd midwater trawls. Thus, specimens other than the type may have been subjected to erosion of these organs by meshes coarser than that commonly used in meter nets, or were perhaps more crowded and abraded by forced mingling with larger catches prevalent in larger nets.

Specimens in good condition show streaks of silvery reflective tissue, which possibly are luminous but may be merely connective tissue. These streaks occur slightly in advance of bases of the dorsal and anal fins and anterior dorsal and ventral procurrent caudal rays, extending back along the rays to about the bases of the third rays in all fins. This tissue is not evident on faded or abraded specimens.

Beebe (1933) stated for the holotype: "From the intermandibular membrane arise four pairs of singular looking organs, leaf-like but rather thick and dead white. Together with several small, adjacent patches, these seem to form an illuminating organ, comparable with nothing with which I am familiar in any other Alepocephalid." Grey (1958) described the second known specimen as having fleshy, leaf-like, and relatively large organs. Goodyear (1969) stated that these leaf-like "flaps" numbered from three to five per row (four per paired row in three of his six specimens). He further stated that in Atlantic specimens the flaps appeared to be thicker than did those from the Indian and Pacific oceans. However, there is variability in the Pacific material; in the two specimens from the South China Sea these organs are substantially more robust than in the two specimens from south of Hawaii and the six from the southeastern Pacific.

Apparently these organs most often are arranged in pairs of four per side, but asymmetry was noted in the three large specimens from the southeastern Pacific (SIO 72–186): one specimen had four on the right side and three on the left; a second had five right and six left, and a third specimen had five right and four left. In these three specimens, and in all others from the southeastern Pacific, these organs are thin and weakly developed and show few traces of any possibly luminous tissue. They generally are very similar in color to and are difficult to differentiate from the intermandibular membrane. In fact, they appear to have been abraded away. But in all specimens before me the lower jaws (when undamaged) almost completely cover these organs, and there is no indication of damage to the enclosing jaw structures or to the adjacent branchiostegal rays that may have caused abrasion.

Beebe (1933) described a thick, fleshy "median fold or adipose fin" that extended from the nape to the raised fleshy base of the dorsal fin. Grey (1958) reported this feature to be distorted in her specimen (USNM 148472) and described the dorsal and ventral surfaces as misshapen and softer in texture than the sides, and intimated that they may have been rather flat in life. Goodyear (1969) stated that this long adipose fin was absent in his material, including the holotype and Grey's specimen. He suggested that it was probably of a gelatinous nature, similar to the envelope found on the Stomiatidae and Chauliodontidae, and that it covered the entire body and served to support the stalked luminous organs. In possible support of this statement, the opercular mucous gland is well developed and robust, measuring about 1.5 by 1.0 mm on a female of 98.2 mm SL. The size of this gland relative to the rather small mass of the fish (Fig. 1) would seem to be of considerable aid in secreting a mucous envelope over the body adequate to support the pedicelled luminous organs.

None of the 10 specimens examined by me show any indication of a dorsal median fold or adipose fin. Also, there is no indication that a gelatinous membrane covered the body, as suggested by Goodyear. The very excellent condition of nine specimens suggests that either the former structure was never present or that it was totally destroyed in preservation.

The excellent condition of most specimens before me strengthens Grey's suggestion that the dorsal and ventral surfaces of *P. pycnopterus* are rather flattened. In some specimens the integument in these areas appears to be quite flaccid and loosely attached to underlying musculature, or to be separated from it (Fig. 1); in places fluid seems to occupy the conspicuous intervening spaces. Slight pressure on the sides of the body causes this loose integument to separate from the body and to assume a rather flattened appearance both dorsally and ventrally, so that the body takes on a roughly rectangular form.

The numbers of dorsal fin rays (13–14, 12 twice, 15 once) and of anal rays (17–18, 19 once) are in good agreement with those listed by previous authors; in each of these fins radiographs disclosed a minute embedded first ray (not included in the counts listed). My counts of pectoral rays differ slightly from those published; Beebe (1933) gave 18 and Goodyear (1969) 18–19. Kotthaus (1972) stated: "P etwa 20." Quéro (1974) listed counts (right pectoral) of 17 (1), 18 (2), 19 (1). On nine specimens I found, counting both sides, 17 (1), 19 (7), and 20 (10). The slightly higher count may have resulted from a different counting method. I used two techniques (air jet and submergence in water) which yielded identical counts. Due to the rounded shape of the fin lobe (Beebe, 1933, fig. 41), both the upper and lower first few rays are small, short and often difficult to perceive; the rays become progressively longer and heavier toward midbase.

Beebe stated "caudal rays ca. 35"; neither Grey nor Goodyear listed counts for this fin. Radiographs of 10 specimens provided counts of 9 (7–10) procurrent rays dorsally and 6–7 (5 once) ventrally; there are 10 (11 once) principal rays in the dorsal lobe and 9 in the ventral lobe. The numbers of total caudal rays are 31 (1), 33 (1), 35 (4), and 36 (1).

All four gill arches bear well formed, smooth, closely spaced, and slender rakers. The central raker of each arch is the longest, that of the first (outer) arch about as long as the fleshy orbit. The rakers of succeeding arches become progressively shorter than those of the first arch, and decrease in number, except that those on the second arch are the highest (Table 1). On the inner face of the fourth arch are 8 (7–9) short, stout rakers, on the lower limb only, that intermesh with 8 (7–9) similar rakers on a fifth arch. The fifth arch bears no filaments.

Goodyear (1969) stated that radiographs indicated acentrous vertebrae immediately posterior to the head, and that ossification began in the caudal region and progressed anteriorly. He found four acentrous vertebrae in three adults and five in another; his smallest specimen (39.9 mm SL) had an indeterminable number, "at least 20." In my material nine are present in a 50.0 mm female (SIO 69–20). For adults, Goodyear described the anteriormost ossified centrum as short and usually ossified only ventrally, and in the succeeding four or five the ossification increased in length.

In the new material ossification is apparent only in the ventral aspect of the first ossified centrum in five of 10 specimens, and both ventral and dorsal in the other five, in which the ventral ossification is greater in three and about equal in both elements in two. In seven specimens longer than 80 mm SL the acentrous vertebrae are most often four but vary from three to five; the two shorter (61.1 and 75.6 mm) each has six. The total number of vertebrae are 41 (1), 42 (2), 43 (6), and 44 (1), following the method of Goodyear of including only the first of the two ural centra that may occur (this element is divided in seven of the 10 specimens; in the two smallest ones and in a larger one, 98.0 mm, the ural element is single). The precaudal vertebrae number 20–22 (25 once, not determinable in the 50.5 mm example).

Beebe (1933) stated that in the holotype of *P. pycnopterus* "small teeth in uniserial rows are present on the premaxillary (27), maxillary (17), mandible (24), and palatine (2); the vomer is toothless; the teeth are close-set, but besides the symphysial gaps, there are other, occasional, narrow, asymmetrical gaps and a few replacement teeth." Goodyear (1969) determined that the vomer and the palatine each bears a single tooth rather than two on the palatine only and stated that neither of these small teeth were firmly

TABLE 2. Numbers of premaxillary, maxillary, and mandibular teeth for 15 specimens of *Photostylus pycnopterus*, both sides counted, and arranged by increasing standard lengths. The number in parentheses represents counts for one side (unspecified) given by Goodyear (1969, table 1). The specimen (SIO 65-611-8), previously reported by Goodyear, was recounted for this study.

Standard Length (mm)	Premaxillary		Maxillary		Mandibular	
	Left	Right	Left	Right	Left	Right
39.9	(26)		(11)		(15)	
50.5	21	26	8	10	23	21
55.6	(27)		(17)		(24)	
61.1	32	31		8	27	19
75.6	29	26	17	20	30	26
80.5	(30)		(15)			
80.8	38	43	19	17	35	31
84.5	(31)		(21)		(27)	
86.7		37	24	22	38	36
91.8	38	40	17	20	35	35
96.1			(21)		(32)	
96.5	31	39	22	21	34	34
98.0	36	39	21	23	33	34
98.2	38	42	17	19	43	40
101.0		30		23	34	31

ankylosed and apparently were missing in some specimens. I concur with these findings. Goodyear (1969, table 1) listed counts for jaw teeth for one unspecified side only of his six specimens.

Numbers of teeth on the premaxillary, maxillary, and mandible for 15 specimens of *P. pycnopterus* are given in table 2, arranged in order of increasing standard length. The count includes alveoli where teeth are assumed to have been present but lost, perhaps by damage during capture or subsequent handling; twice loose teeth were dislodged by air jet during the count. Replacement teeth were counted if they protruded even slightly. Wholly embedded teeth, visible on several adults, were not counted.

The data in table 2 indicate a notable increase in numbers of all jaw teeth with size of fish, with very slight overlap. Averages (rounded to the nearest whole number) and ranges for the four smaller fish (39.9–61.1 mm) are appreciably lower than for the 11 larger ones (75.6–101.0 mm): premaxillary 27 (21–32) *vs* 35 (26–43), maxillary 11 (8–17) *vs* 20 (15–24), and mandible 22 (15–27) *vs* 34 (26–43).

Photostylus pycnopterus may produce rather large eggs. Goodyear (1969) reported ovarian eggs 1.4 mm in diameter in an adult female, 93.4 mm SL (now 91.8 mm) taken in November off Callao, Peru (SIO) 65–611). Goodyear also reported egg sizes of 0.1 and 0.3 mm in two other adult females, 96.1 and 84.5 mm SL, respectively.

In the new material the ovaries are in a very immature stage of development in a 61.1-mm female from the northeastern Pacific, taken in August, and in one of 80.5 mm from south of Hawaii, taken in July. A female (98.2 mm) taken off southern Peru in March has moderately well developed ovaries containing eggs of varying sizes, the largest measuring 0.7 mm in diameter.

Six of the 10 specimens examined are males, two (50.5 and 75.6 mm SL) from the South China Sea, taken in April, have only moderately developed testes, their lengths each comprising about 30 percent of SL. In three males from the southeastern Pacific Ocean (96.5, 98.0, and 101.0 mm SL), taken together in May, and in a male (86.7 mm) from south of Hawaii, taken in July, the testes appear to be in an advanced stage of development and are quite elongate, the more advanced comprising about 40 percent of SL, and extend from near the end of the fleshy peduncle of the pectoral fin to the anus.

The size of ovarian eggs at time of extrusion is not known, but the 1.4-mm eggs in the specimen from off Callao, although apparently fully developed and free in the lumen of the ovary, do not extend entirely to the genital opening and the ovarian duct is not at all expanded behind the posteriormost egg, a distance of about 7 mm. The length of the egg mass is about 29 percent of SL and the two ovaries contain a total of about 80 large eggs.

The less developed ovaries are so closely paired as to give the impression of a single ovary. Only in the more developed one, containing the 1.4-mm eggs, can the two elements be separated readily.

This same arrangment pertains to the testes of males.

Photostylus pycnopterus is widely distributed, as indicated in figure 2, but the total poulation may be small for a great many midwater trawls and other net tows have been made in all oceans without taking the species. Also, it may not be a gregarious species, as 15 of the 17 captures contained only one specimen each, two contained two each, and one three. On the basis of their weakly developed bodies these fishes probably are weak swimmers and cannot readily escape a net.

Goodyear (1969) stated that "Collection data for the four specimens indicate these fish are bathypelagic and associated with steeply inclined topography; either continental or island margin, or oceanic ridge." This appears to be true for nine of the 17 captures, the remaining half occurring in depths of between 2000 and 4000 meters and far from steeply inclined topography; possible exceptions are the two captures (one specimen each) from south of Hawaii and easterly of the Line Islands (Fig. 2), an area of confused bottom topography.

Regardless of proximity to steeply inclined topography, all collections except one appear to be from areas of rather high primary productivity, as delineated by Koblentz-Mishke, Volkovincky and Kabanova (1971, fig. 1); the exception (the holotype) was taken near Bermuda, an area of low productivity (Menzel and Ryther, 1960).

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NUMBERS OF SPECIES AND FAUNAL RESEMBLANCE OF MARINE FISHES IN CALIFORNIA BAYS AND ESTUARIES

Michael H. Horn and Larry G. Allen[1]

Abstract: Fish species numbers and surface area of 13 California bays and estuaries and the California continental shelf were positively correlated, and the slope (z) of the log–log regression was 0.21. Mouth width of bays was the only significant variable accounting for variation of species numbers in stepwise multiple regression.

Clustering based on presence or absence of fish species produced a southern and a northern group of bays. A two-way table (bay vs. species) distinguished three broad distributional categories of fish species.

Comparisons of area and species numbers of Chesapeake Bay and King Harbor (southern California) with those of California bays and estuaries supported the view that the present study has relevance for the preservation and management of bay/estuarine systems.

Bays and estuaries are widely recognized as highly productive areas that are important feeding and nursery grounds for fishes. At the same time they are natural sinks for pollutants and are becoming increasingly altered, including reduced in size, by human activities. Murdoch (1975) has called estuaries perhaps the single most endangered ecosystem in the United States. As a result of their ecological importance and threatened state, bays and estuaries are receiving increased attention including studies focused on the associated fish populations (cf. Allen and Horn, 1975).

The bays and estuaries of California generally form distinct, partially isolated bodies of water that vary in size and are irregularly positioned along the coastline (Fig. 1). More than one-half (51 percent) of the fish species of the California continental shelf (439 species) have been recorded from the 13 bays and estuaries considered in this study.

The purposes of the study were based on these attributes and were three-fold: 1), We examined the degree to which bays and estuaries function as insular habitats in the sense of MacArthur and Wilson's (1963, 1967) model of island biogeography which states that the equilibrium number of species on an island is related to the area of the island and its distance from the source region. Area-species relationships were determined for the 13 bays and estuaries as well as the California continental shelf. The shelf serves as a source region for the bays and estuaries which are partially isolated, peninsular extensions of the shelf. 2), We examined, by stepwise multiple regression, the relative importance of a series of environmental variables in accounting for the variation in species numbers in the bay/estuarine habitats. 3), We examined faunal resemblance among the bays and estuaries utilizing a coefficient of dissimilarity and cluster analysis based on presence or absence of fish species in each habitat. Because the bays and estuaries span most of the latitudinal range (32.5°N–42°N) of the California coastline and because about one-half of California coastal species occur in them, their fish faunas are appropriate for identifying new or testing established faunal regions and boundaries.

METHODS

The basic data for the study were a list of 224 coastal fish species in 78 families known to variously occur in the 13 bays and estuaries (copies of the list can be obtained upon request directly from the authors). The number of species recorded for each bay or estuary included all marine species known for the locality except midwater larval forms (three species), introduced species (three species) and freshwater forms. The number of coastal species used was that which according to Miller and Lea (1972) is comprised of fishes most frequently found in waters shallower than 400 ft (122 m).

Surface area of each bay or estuary, approximating as closely as possible that at mean tide level, was either obtained from the literature or, for Los Penasquitos Lagoon, Newport Bay, Anaheim Bay, Alamitos Bay and Elkhorn Slough, esti-

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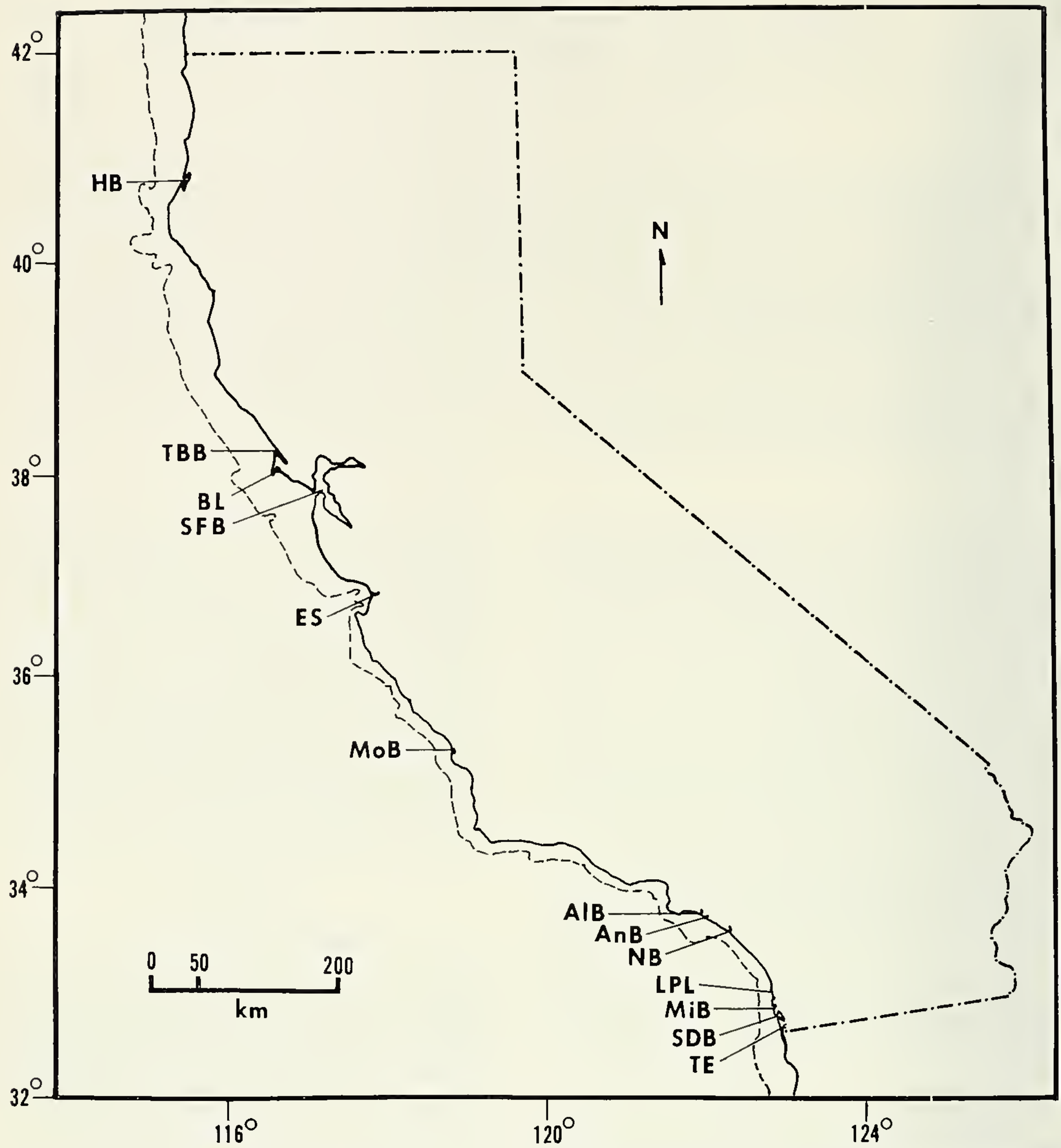


Figure 1. Map of California showing 100 fm (183 m) contour (dashed line) and locations of 13 bays and estuaries.

mated using a planimeter. Area of the California shelf to the 100 fm (183 m) contour was also determined using a planimeter. This area was considered to be sufficiently similar to that which would be estimated to the 122 m depth mentioned above. The latitude recorded was that at the midpoint of the mouth of each bay or estuary. Coastline distance from each bay ("bay" used interchangeably with "bay and estuary") to the nearest neighboring bay was determined by measuring point to point (not crossing land) along the coast on U.S. Coast and Geodetic Survey Charts. Diurnal tidal ranges (MLLW to MHHW) were obtained from National Ocean Survey Tide Tables except for the range for Tijuana Estuary which was obtained from White and Wunderlich (1976). Mouth width of each bay was determined from U.S. Coast and Geodetic Survey Charts by drawing a line across the entrance continuous with the coastline on either side and measuring the distance

TABLE 1. Numbers of fish species and values of seven environmental variables for 13 California bays and estuaries.

Bay/Estuary	Number of species	Surface area (ha)	Latitude (°N)	Distance to nearest bay (km)	Diurnal tidal range (m)	Mean annual rainfall (cm)	Mouth width (m)	Mean annual coastal temp. (°C)*	References
Tijuana Estuary (TE)	29	59	32.5	18.4	1.70	23	30	16	White and Wunderlich, 1976
San Diego Bay (SDB)	64	4287	32.6	10.6	1.80	25	620	16	Peeling, 1974
Mission Bay (MiB)	76	836	32.7	10.6	1.65	25	218	16	Chapman, 1963
Los Penasquitos Lagoon (LPL)	22	12	32.9	11.9	1.74	25	18	16	Mudie, Browning, and Speth, 1974
Newport Bay (NB)	78	433	33.6	25.0	1.62	28	282	15	Allen, 1976a
Anaheim Bay (AnB)	59	131	33.7	2.3	1.62	25	218	15	Lane and Hill, 1976
Alamitos Bay (AlB)	43	166	33.8	2.3	1.62	25	218	15	Reish, 1968; Allen, 1976b
Morro Bay (MoB)	62	526	35.4	180.0	1.59	37	300	13	Fierstine, Kline, and Garman, 1973; Gerdes, Primbs, and Browning, 1974
Elkhorn Slough (ES)	69	216	36.8	129.0	1.62	46	190	13	Browning, 1972; Kukowski, 1972; Cailliet, 1975
San Francisco Bay (SFB)	121	129555	37.8	45.0	1.74	53	1773	12	Ganssle, 1966; Aplin, 1967; Ruth, 1969; U.S. Fish and Wildlife Service, 1970; Green, 1975
Bolinas Lagoon (BL)	41	270	37.9	30.0	1.34	76	160	12	Giguere, 1970
Tomales-Bodega Bay (TBB)	103	2850	38.2	30.0	1.59	76	250	12	Bane and Bane, 1973; Hardwick, 1973
Humboldt Bay (HB)	88	6478	40.8	299.0	1.95	102	727	11	Monroe, 1973
California Continental Shelf (CCS)	439	2471978							Miller and Lea, 1972

* Calculated from data in Eber, Saur, and Sette (1968)

covered by the line. For those bays with jetties, mouth width was considered to be the distance between the jetties at their seaward end. Numbers of species and values of the seven environmental variables along with data sources for each bay are listed in table 1.

The straight line through the points of the log-log area-species plot was fitted by least mean squares and expressed as the power function $S = CA^z$ where S is the number of species, A the area, and C and z fitted constants.

The relative importance of seven independent variables in explaining the variation in numbers of species (the dependent variable) for the bays was determined by stepwise multiple regression carried out at the California State University at Fullerton Computer Center using the BMDO2R program (Dixon, 1973). In this program, the independent variable entered into the regression equation at each step is that which makes the greatest reduction in the error sum of squares, has the highest partial correlation with the dependent variable partialed on the variables which have already been added, and has the highest F value (Dixon, 1973). The minimum F value for inclusion of an independent variable in the regression equation was that at $\alpha = .10$. Linear (untransformed data) and log–log ($\log_{10}$ transformed data) models were tested. The coefficient of multiple determination (R^2) was the statistic used to estimate the cumulative proportion of variability in the number of fish species accounted for by the independent variables.

To show the degree of resemblance among the bays in terms of their fish faunas, computer-aided cluster analysis was performed. The index of association used was the Canberra-metric dissimilarity measure (Clifford and Stephenson, 1975) which is biased toward presence/absence analysis and if presented with values of 0 or 1 becomes a presence/absence coefficient according to the formula,

$$D = \frac{1}{n} \sum_{1}^{n} \frac{|X_{1j} - X_{2j}|}{(X_{1j} + X_{2j})}$$

where D = the dissimilarity between a pair of bays, summed for all species;

n = the number of species;

X_{1j} = the presence or absence of species j in bay 1;

X_{2j} = the presence or absence of species j in bay 2.

Each bay was compared to each of the remaining 12 with regard to species composition and given a rating ranging from 0.0 for complete similarity (all species in common) to 1.0 for complete dissimilarity (no species in common). The bays defined to be most similar by the index of association were joined. The resulting clusters of similar bays were then compared and grouped again according to similarity. This procedure was repeated at higher levels with the degree of similarity among the bays in groups decreasing at each higher level until distinct major groupings emerged. The sorting strategy used was group-average which conserves the distances between all points of the matrix (i.e., clusters moderately weakly) (Clifford and Stephenson, 1975), and for the similarity between two groups, is calculated as the average of all possible similarities between the two groups. Sorting results were displayed in a dendrogram and in a two-way (bays vs. species) table of occurrence according to a numerical classification program written by R. W. Smith of the Allan Hancock Foundation, University of Southern California.

RESULTS

The relationship between number of fish species and area of 13 California bays and estuaries and the California continental shelf (Fig. 2) was best described by the curve

$$S = 1.20A^{0.21}$$

which had a correlation coefficient of 0.93 ($P < .01$). Exclusion of the continental shelf resulted in a similar power function, $S = 1.28A^{0.18}$, but with a lower z value, meaning a more gradual slope of the fitted line. The correlation was slightly lower ($r = 0.86$, $P < .01$).

Linear multiple regression of numbers of species on seven independent variables (Table 2) accounted for 69 percent of the variation in the dependent variable. Mouth width explained 53 percent of the variability and was the only significant variable ($P < .005$) in the linear model. Two logarithmic multiple regressions were performed (Table 2), the first including mouth width and the second excluding mouth width as an independent variable. The first multiple regression accounted for 80 percent of the variation in species numbers. Mouth width explained 77 percent of the variability and was the only significant variable ($P < .001$) in this nonlinear analysis. The second logarithmic model accounted for 74 percent of the variability with surface area being the only significant contributor (73 percent, $P < .001$) to R^2.

Clustering of the bays (Fig. 3) based on pres-

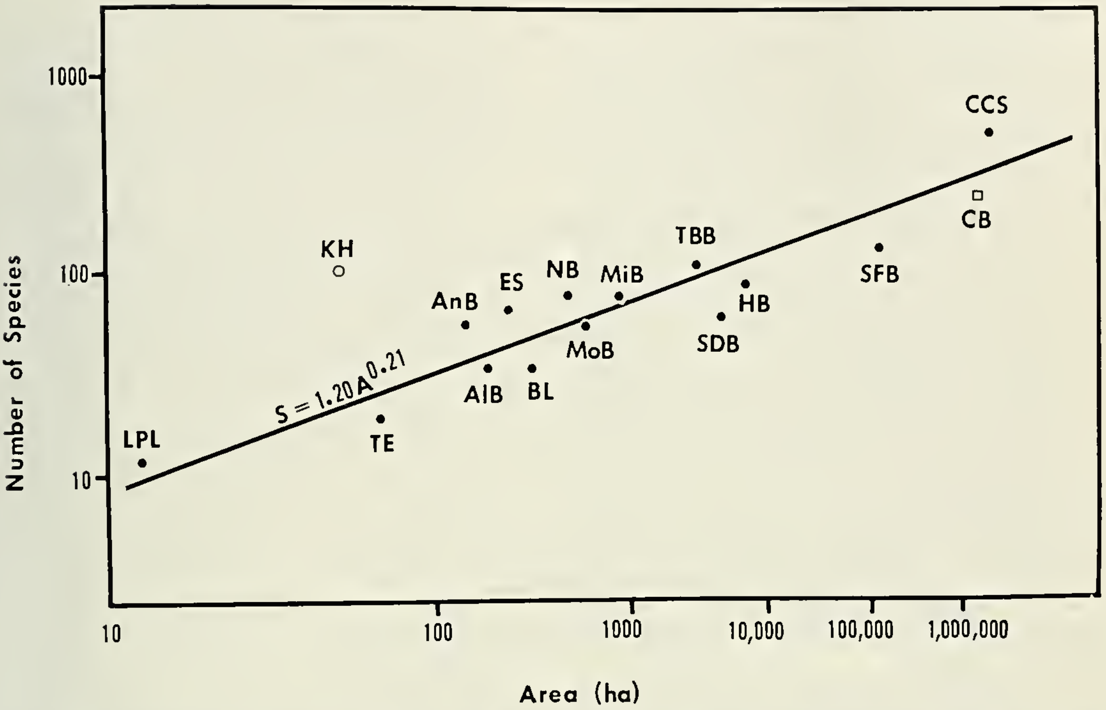


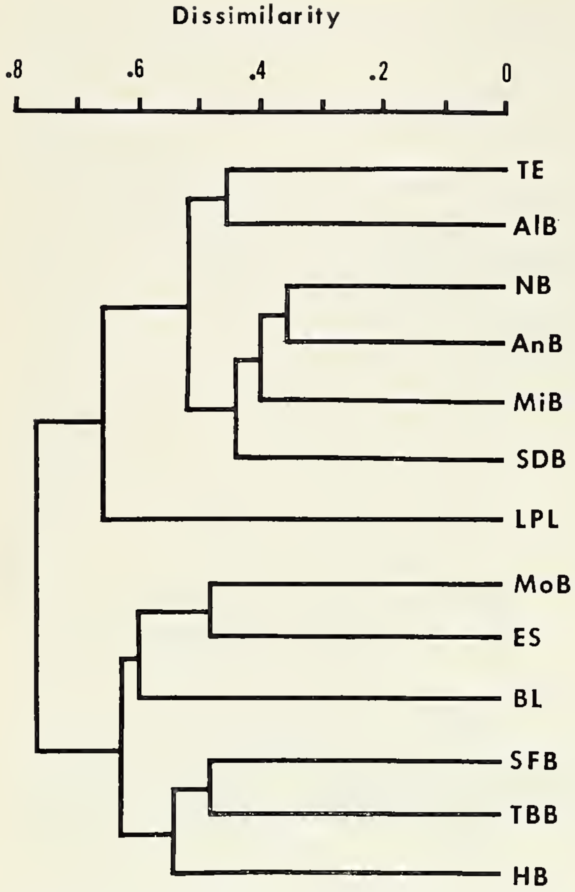
Figure 2. Relationship of numbers of species and surface area for 13 California bays and estuaries (dots), the California continental shelf (dots), King Harbor, (KH) (open circle) and Chesapeake Bay (CB) (open square). Equation based only on values for California bays, estuaries and continental shelf. $r = 0.93$ ($P < .01$). Abbreviations for California bays, estuaries and continental shelf as in table 1. (See Discussion for account of King Harbor and Chesapeake Bay).

ence or absence of species produced two distinct groups, one of seven southern (32.5°N–33.8°N) bays and one of six northern (35.4°N–40.8°N) bays. Among the southern bays, Los Penasquitos Lagoon was the most dissimilar. Tijuana Estuary and Alamitos Bay, although geographically separated, formed a related pair. Newport Bay and Anaheim Bay were the most closely associated

TABLE 2. Relative contributions of seven environmental variables to the coefficients of multiple determination (R^2) for explaining the variation in numbers of fish species of 13 California bays and estuaries.

	Linear			Logarithmic (Mouth Width Included)			Logarithmic (Mouth Width Excluded)		
Independent Variable	Contribution to R^2	F Value	Order Entered in Equation	Contribution to R^2	F Value	Order Entered in Equation	Contribution to R^2	F Value	Order Entered in Equation
Mouth Width	.5348	12.65*	1	.7687	36.55*	1	—	—	—
Mean Annual Coastal Temperature	.0772	1.99	2	—	—	—**	—	—	—**
Diurnal Tidal Range	.0236	0.45	6	.0028	0.11	4	.0090	0.34	2
Distance to Nearest Neighboring Bay	.0234	0.54	4	.0079	0.35	3	.0042	0.15	3
Surface Area	.0142	0.34	3	.0193	0.91	2	.7278	29.41*	1
Mean Annual Rainfall	.0086	0.18	5	—	—	—**	—	—	—**
Latitude	—	—	—**	—	—	—**	—	—	—**
TOTAL R^2	.6819			.7987			.7410		

* Significant at 1% level
** F value too low to be entered into regression equation



Distributional Category

	Widespread	Southern	Northern
TE	14	15	0
AlB	17	25	1
NB	30	45	3
AnB	30	28	1
MiB	29	43	4
SDB	23	39	2
LPL	10	10	2
MoB	33	8	21
ES	34	4	31
BL	20	1	20
SFB	33	5	83
TBB	28	1	74
HB	21	2	65

Figure 3. Dendrogram of the clustering of 13 California bays and estuaries based on presence/absence of fish species using the Canberra-metric index of dissimilarity and group-average sorting. The species of each bay and estuary are placed in three broad distributional categories (to right of dendrogram) based on a two-way table (bay vs. species) generated with the cluster analysis.

southern bays with Mission Bay and San Diego Bay being distinct entities near them. Among the northern bays, Morro Bay and Elkhorn Slough, the two central California localities, showed close affinity and were distantly related to Bolinas Lagoon. The larger northern bays, San Francisco, Tomales-Bodega and Humboldt, formed a distinct group with Humboldt Bay, the northernmost locality, being most dissimilar.

A two-way table showing occurrence of each species among the bays was generated in conjunction with the dendrogram and made it possible to recognize (Fig. 3) three broad distributional categories of fishes: 1), a group of 37 species having widespread occurrence in both southern and northern bays; 2), a group of 59 species occurring primarily in bays in southern California (14 of these species occur in one to three northern bays); 3), a group of 128 species occurring mainly in the northern set of bays (11 of these species variously occur in no more than one of the southern bays). These three categories are listed adjacent to the dendrogram (Fig. 3) and permit recognition of the faunal composition of each clustered bay according to these categories.

DISCUSSION

A purpose of this paper was to examine the degree to which bays function as insular habitats and meet the requirements of MacArthur and Wilson's (1967) theory of island biogeography. The MacArthur-Wilson model states that larger islands in a system will have more species than smaller islands and that islands near the source region will have more species than those farther from the source region. The number of species, S, on an island is set by or approaches an equilibrium between immigration rates and extinction rates. The S value on an island in the steady state is the number at which immigration and extinction rates become equal. The larger and less isolated the island, the higher is the species number at which it should equilibrate.

The bay system is consistent with the size component of the model. The number of fish species showed a significantly positive correlation with bay area when both were plotted logarithmically, a relationship obtaining for most insular biota (Vuilleumier, 1970). The slope (z) of the curve was 0.21 and in the lower range of z values, 0.18–0.35, found for archipelagos (Preston, 1962a; 1962b; MacArthur and Wilson, 1967). The relatively low area-species curve is probably due to a number of factors some of which are related to area. Bays are only semi-isolated habitats compared to oceanic islands or lakes and as such would tend to have a lower curve (Preston 1962a; 1962b). Also, certain of the smaller bays such as Elkhorn Slough have been more completely surveyed and/or contain all possible species whereas larger bays such as San Francisco Bay may be either inadequately sampled or could hold more species than available. Impoverishment, however, seems unlikely since San Francisco Bay has a variety of habitats and has available the large source fauna. Reduction in size and increased pollution, however, may be important factors. Lower z values (0.15–0.16) have been calculated for series of world and North American freshwater lakes by Barbour and Brown (1974) who attributed these values to the fact that while a relatively large number of species are available to colonize small lakes, larger ones are impoverished. Most of the latter lakes are recent enough such that there has not been sufficient time for endemic speciation to reach an equilibrium with extinction. The bays, likewise, are apparently too recent and also insufficiently isolated to be sites of speciation.

Distance as an isolation factor involves a special set of conditions for the bays. If the California continental shelf is considered to be the source region, as we have done, the bays are in effect peninsular extensions of the source region rather than truly insular habitats; thus, the source fauna has somewhat similar access to each bay. This fauna, however, is not homogeneous along the coastal expanse of California since both diversity (Horn, 1974) and species composition (see below) change with latitude. With regard to the equilibrium model, immigration rates are probably influenced by the so-called peninsular effect that has been described on land areas for birds (MacArthur and Wilson, 1967; Willis, 1974) and mammals (Simpson, 1964). According to MacArthur and Wilson (1967), terrestrial peninsulas reduce immigration rates by the absence of land around most of their boundaries that could serve as part of the source region. In the same sense, bays are aquatic peninsulas with an absence of water around most of their perimeters that, in combination with mouth size which influences accessibility (a distance factor), operates to determine immigration rates. Extinction rates are expected to be affected by bay area and associated parameters. Extinction here is in the local sense of a species being unable to exist in a bay.

Another distance factor considered was the distance from each bay to the nearest neighboring bay as a possible "inter-island" stepping-stone parameter. This factor, however, was found according to multiple regression analysis not to be significant in explaining variation in species numbers (see below).

Multiple regression was employed with recognition of its shortcomings in treating biogeographic data (cf. Sepkoski and Rex, 1974). Deficiencies frequently include lack of conformity of data to multivariate normal distributions, high intercorrelation of variables and inferential cause/effect relationships. We considered multiple regression to be a heuristic aid for understanding a biogeographic system and used it specifically for predicting the relative importance of independent variables in accounting for variation in species numbers.

Two logarithmic models of multiple regression both provided a better fit to the data than a linear model. In all three cases, a single variable was the only significant predictor of species numbers. Mouth width was the significant variable in the linear model and in the first logarithmic model. Surface area, with a larger standard deviation, became the significant predictor in the second logarithmic model in which mouth width, significantly correlated ($r = 0.91$, $P < .01$) with surface area, was excluded from the analysis. Latitude, mean annual rainfall and mean annual coastal temperature were also highly intercorrelated and were insignificant predictors of species numbers.

Mouth width is an interesting and possibly biologically meaningful predictor of species numbers since it is related to both area and isolation. It increases with area thus larger bays have greater access to the coastal source region and hence would be expected to have more species. Smaller bays, on the other hand, tend to have narrower mouths (i.e., less access to the coastal area) and would be expected to contain fewer species. Mouth size and configuration affect water circulation patterns and hence physico-chemical conditions in a bay and also influence the amount of rocky substrate present at entrance channels which affects the diversity of coastal fishes in a bay.

Clustering of the bays produced two groups that were separated by the greatest inter-bay distance and situated on either side of Point Conception (34.5°N), a widely recognized (Hubbs, 1948, 1960; Hedgpeth, 1957; Quast, 1968; Briggs, 1974) faunal boundary based on temperature. The cluster analysis also distinguished the smaller bays with relatively few species (especially Los Penasquitos Lagoon and Bolinas Lagoon), grouped the three northern bays together and exemplified a recently recognized (Chen, 1971; our own work in progress) central California faunal area by pairing Morro Bay and Elkhorn Slough, the two bays in that region.

Recognition of three broad distributional categories (widespread, southern and northern) of bay-occurring fishes illustrated the complex and dynamic character of the California coastal fauna that Hubbs (1974) has recently emphasized. Many species cross faunal boundaries, some as a result of local or seasonal fluctuations in environmental parameters, especially temperature. This fact serves to stress the inadequacy of a rigid delineation of marine faunal regions for California.

Hubbs (1948; 1960) noted the general tendency for primarily southern species to occur in bays in central and northern parts of California and for primarily northern species to occur in deeper (hence, cooler) waters in southern California and in cool, upwelling areas off northern Baja California. We therefore hypothesize that of the 224 bay-occurring species, southern ones would be more likely to occur in bays north of Point Conception than northern species in bays south of Point Conception. The results of the present study support this view in that of 55 primarily southern species, 25 percent occur in one to three northern bays whereas of 128 northern species only nine percent variously occur in no more than one of the southern bays. A comparison of the remaining, generally deeper dwelling, coastal fishes should show the opposite trend, i.e., Point Conception being less of a boundary to northern species than to southern ones. We have work in progress on faunal resemblance of all California coastal fishes based on species composition at each degree of latitude which corroborates this expectation.

Table 3. Number of fish species in each of 13 California bays and estuaries which occur only in that bay or estuary. Bays and estuaries listed in order of decreasing area.

Bay/Estuary	Number of Species
1. San Francisco Bay	14
2. Humboldt Bay	9
3. San Diego Bay	6
4. Tomales-Bodega Bay	19
5. Mission Bay	0
6. Morro Bay	1
7. Newport Bay	2
8. Bolinas Lagoon	1
9. Elkhorn Slough	3
10. Alamitos Bay	0
11. Anaheim Bay	0
12. Tijuana Estuary	0
13. Los Penasquitos Lagoon	0

Diamond (1975a, 1975b) has described a method of analyzing distributional patterns of birds on adequately surveyed archipelagos of the New Guinea region and southwestern Pacific which has implications for understanding assembly rules of species communities, and for predicting the probability that a species will occur on an island of a particular size. He found that certain species are found only on the largest, species-rich islands, others on only the smallest or most remote, most species-poor islands, and still others occupying a spectrum of intermediate situations. Thus, "incidence functions" can be calculated for individual species which may be applicable to fishes in bay/estuarine habitats and valuable for predicting how and to what extent species composition will change as a bay becomes increasingly altered (e.g., reduced in size). For example, analysis of distributional patterns among California bay fishes shows that of the 55 species which occur in only one of the 13 bays, 48 of these are known from one of the four largest bays and none occur in the four smallest bays (Table 3). Only five species (topsmelt, bay pipefish, staghorn sculpin, shiner surfperch and arrow goby) are known to occur in all 13 bays. These species tend to have broad environmental tolerances and/or high dispersal abilities and one or more of them frequently dominates shallow-water fish communities of differing species composition in California.

It should be recognized that the present study has limitations involving both species composition and the nature of the bays as fish habitats. In developing species lists for the bays we included with only a few exceptions (see Methods) all marine fishes with any record of occurrence in a bay. This means that some species were counted which only rarely enter bays and apparently have a limited role in bay ecology. Also, the bays differ in the degree to which they have been studied. Those such as Elkhorn Slough or Anaheim Bay have complete or nearly complete species lists whereas others such as Bolinas Lagoon or San Diego Bay probably contain more species than the lists indicate. A possibly valuable predictor of species numbers is some measure of sampling intensity although we did not attempt to establish such a measure.

A further shortcoming of a comparative study of bay fish faunas is the differing degrees of alteration to which the bays themselves have been subjected. Dredging, filling, construction of marinas and breakwaters, and dumping of pollutants all must affect bays as fish habitats in one way or another. The state of alteration among the 13 bays ranges from the relatively pristine conditions of Tijuana Estuary (White and Wunderlich, 1976) to the highly modified and diminished condition of San Francisco Bay (Pearson, Storrs and Selleck, 1970). A potentially useful predictor of species numbers might be either a combined index or a single indicator of alteration.

Despite these limitations we believe that this study provides insight for the understanding of bay/estuarine fish faunas in California and has application for the preservation and management of bays and estuaries. In support of this contention, we offer in conclusion the following statements:

1. Species number is significantly correlated with area but the relatively low area-species curve indicates that, while the bays operate to a large degree as insular habitats, they are partially isolated extensions of the continental shelf. This realization may temper the fact that the surface area of San Francisco Bay has been reduced by about 40 percent since 1850 (San Francisco Bay Conservation and Development Commission, 1969) but, nevertheless, the area-species relationship should be considered for both historical perspective and future planning for this bay. Bays falling either below or above the area-species curve can be identified and attention can be focused on bays which either may be insufficiently studied and have relatively small species lists or which may have an unusually large number of species.

2. Values for two additional semi-enclosed bodies of water, Chesapeake Bay and King Harbor, are presented on the area-species plot (Fig. 2) for comparative purposes. Chesapeake Bay, located on the middle Atlantic coast (37°N), is the largest bay in the United States. Based on a species list compiled by Musick (1972) and planimeter determination of area, the area-species value falls near the curve indicating that the area-species relationship for California bays is applicable to other regions. On the other hand, King Harbor, a small, well-studied artificial enclosure at Redondo Beach (33.8°N) in southern California, falls well above the curve and can be instructively compared with the bays.

Stephens (1972) attributed the rich fish fauna of King Harbor to the substrate heterogeneity and thermal diversity of the harbor. Both factors are partly human-induced illustrating that small artificial areas may contain a relatively large number of species and that design and location of man-made embayments are significant to their outcome as biological habitats. An implication of the King Harbor data is that structural modification of natural bays and estuaries can be carried out so that their utilization by fishes is maintained or even enhanced. It will be interesting to determine whether King Harbor is initially "oversaturated" and serving as a refuge for ecologically displaced species as Stephens (1973) has suggested and whether it will "relax" to equilibrium (cf. Diamond, 1972) with a reduced number of species. Diamond's (1975a) application of the island equilibrium model to the design of terrestrial reserves may be of relevance to the preservation of bay systems as aquatic habitats although Simberloff and Abele (1976) have recently cautioned against widespread application of the theory to conservation practices until it is more firmly validated.

A significant point in the above context is that even though the addition of certain artificial structures may enhance the environmental heterogeneity and hence the diversity of coastal marine fishes in a bay/estuarine system, truly estuarine habitats and associated species may be reduced or even obliterated.

3. Mouth width of bays was found to be the best predictor of species numbers and was significantly correlated with surface area. It is also, however, a component of isolation since its magnitude more or less separates a bay from the shelf area. This parameter may be an important habitat factor to consider in the design of breakwaters and other structural changes involving the opening of bays or estuaries.

4. Area-species relationships are consistent for

the bays in California even though species composition changes considerably along the coast (76 percent dissimilarity between bay groups north and south of Point Conception) indicating that species number is predictable among different bay faunas.

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A STUDY OF THE ORIENTATION OF SELECTED EMBIOTOCID FISHES TO DEPTH AND SHIFTING SEASONAL VERTICAL TEMPERATURE GRADIENTS

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Abstract: The effects of seasonal temperature variation on the depth distribution of five species of embiotocids in King Harbor, California were studied. Three types of depth distributions were found: *Micrometrus minimus* was restricted to the intertidal and subtidal margin: *Embiotoca jacksoni* was most abundant at middle depths and declined in abundance in both shallower and deeper water; *Hypsurus caryi*, *Rhacochilus vacca*, and *Phanerodon furcatus* formed a deeper water group. The depth distributions of all species except *M. minimus* shifted into deeper water during late summer and fall and into shallower water during winter and spring. *Micrometrus minimus* remained in the top 1.5 m throughout the year. Descent into deeper water corresponded to the period of warmest water. Deeper water species selected water colder than 16°C. *Embiotoca jacksoni* occupied a middle thermal range. The results of this study support an important role for temperature orientation in the spatial organization of this subtidal community.

The family Embiotocidae is endemic to the North Eastern Pacific except for two Western Pacific and a single freshwater species. The family's center of distribution is in the Eastern Pacific between 32° and 38°N latitude. All 20 Eastern Pacific marine species occupy this latitudinal range and 10 of the 20 are restricted to it. Tarp (1952) correlated this distribution with surface temperature conditions which vary within the latitudinal range from about 9°C to 24°C. Zoogeographically, this area includes a major faunal break at

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Point Conception, which is accepted as the northern boundary of the San Diegan Warm Temperate and the southern boundary of the Boreal Central Californian (Hedgpeth, 1957; Quast, 1968, and see Briggs, 1974; Hubbs, 1974). Waters north of Point Conception are generally cooler in the summer than those warmed by the Southern California Eddy to the south, and this temperature difference (Hubbs, 1948, 1960; Radovich, 1961) is considered the major environmental factor resulting in faunal differentiation. Fishes inhabiting the San Diegan region live in waters with greater thermal fluctuation, and, therefore, probably withstand a greater temperature range than more northern species. Several species of embiotocids have extensive latitudinal ranges and perhaps are eurythermal.

Little data have been published regarding the bathythermal distribution of embiotocids and surface water temperatures are not reliable estimators of thermal preferences. Several workers have established a relationship between field distributions and temperature for a number of intertidal species (Morris, 1961; Norris, 1963; Graham, 1970; Nakamura, 1976). Norris (1963) correlated his field work with laboratory gradient experiments.

This study examines the effect of seasonal temperature variation on the vertical distribution of five species of embiotocids inhabiting an almost vertical rock wall where thermal gradients as large as 13°C (11°–24°C) occur in 11 m of water, and where maximum depth poses no physiological or ecological restriction upon the species.

The area studied is the lee side of the outer 100 m of the breakwater at King Harbor, Redondo Beach, California. This rock wall rises from a sand floor to a vertical inside height at mean tide of 11 m. Figure 1 illustrates a typical habitat along the breakwater. The breakwater is composed of large ($\simeq$ 2–3 m) granitic blocks quarried from Catalina Island. Because of the hardness of this substrate, little infauna exists. Algal growth is present and seasonally well developed in the upper 3 m. Epifaunal growth is extensive in shallow areas but is less extensive near the breakwater base. A gorgonian region is developed along the deepest zone. The base of the breakwater is a mixture of sand, sand-mud, and shell fragments (including bryozoa). All along the breakwater at each depth are extensive crevices, caverns, and horizontal ledges formed by the granitic blocks. The breakwater bounds the entrance to King Harbor Marina and is bordered by two contrasting thermal influences. Just over 200 m from the end of the breakwater and within the entrance to the harbor is the warm water discharge from Southern California Edison's electrical generation station, while just outside the mouth of the harbor is the inshore terminus of Redondo Submarine Canyon, a source of cool upwelling water. The combination of these two influences in part produces and maintains the above described gradient.

Figure 1. Subadults of *Rhacochilus vacca* and *R. toxotes* schooling together and with *Embiotoca jacksoni* and *Hypsurus caryi* near the base of the breakwater (depth, 9 m).

Nine species of embiotocids have been observed along this breakwater: *Brachyistius frenatus*, *Cymatogaster aggregata*, *Embiotoca jacksoni*, *Hyperprosopon argenteum*, *Hypsurus caryi*, *Micrometrus minimus*, *Phanerodon furcatus*, *Rhacochilus toxotes*, and *Rhacochilus vacca*. Of these, *Brachyistius* is extremely rare and *Cymatogaster* and *Hyperprosopon* form seasonally moving schools and are absent from the breakwater for extended periods. These three species and *Rhacochilus toxotes*, for which our present data are limited, are excluded from this study. The five remaining species are present along the breakwater throughout the year. Of these five species, only *Rhacochilus vacca* and *Phanerodon furcatus* are wide ranging, the remaining three are limited to waters south of Cape Mendocino.

METHODS

Standardized transects were used in the field to measure the depth and temperature distributions of the species. In this study a transect was defined as a five minute survey during which two divers swim at a constant depth along the breakwater wall and record the numbers and approximate size class (juvenile, subadult, adult) of all fish seen between 1.5 m above and below the divers. No attempt was made to count fishes hidden deeply within crevices or caves and the data include only obvious cryptic individuals. Temperature was recorded at the beginning and end of each five minute interval. Data were recorded on plastic slates, each of which was prepared with a species list, depth gauge, and thermometer. Transects were run at 3 m depth intervals beginning at 1.5 m and extending to the maximum depth available. At each station a bathythermal profile was recorded using a Yellow Springs Instruments telethermometer from the dive boat. Tidal level, visibility, surge, and weather conditions were recorded. Transects were not run when visibility was less than eight feet. Transects were carried out monthly between August 1974 and July 1975. A total of 124 transects were completed, 2–4 per month at each depth. After transects at all depths at a station were completed, the data were summarized and recorded in a field log book. Divers' observations were compared, and for species present as either individuals or small schools, the highest counts were recorded. Counts of species present in large numbers or large schools were estimates and the observations of the two divers were averaged. In cases where a large school was overlooked completely by one diver but recorded by the other, the estimate by the latter was used and no mean calculated.

No problem was encountered distinguishing between adult and juvenile size classes in the field. The adult-subadult distinction was often unclear, however, and the subadult-juvenile distinction was occasionally difficult. It was realized that individual diver's interpretations varied, and efforts were made to minimize these differences. Though these categories are primarily based on size, field recognition of these categories largely reflects the reproductive structure of the population and both large adults and juveniles differ behaviorally from the so-called "subadult" stage.

From the transect data for each species and for each size class within each species, mean number of fish per transect at each depth interval and at each 2°C temperature range were calculated. These means were calculated monthly, seasonally, and for the whole year. Calculations were performed using a Statistical Package for the Social Sciences (SPSS) program implemented on Occidental College's IBM 370/125 DOS/VS digital computer.

Relative frequency distributions for depth were calculated by summing the means of each depth interval, then dividing each interval mean by this sum. The same procedure was followed for relative frequency distributions among the 2°C temperature ranges. The interval means for a given month were then treated as grouped data from which a mean depth, a mean temperature, and standard deviations were obtained. The same procedure was followed for mean depth calculations based on the full year's data. Maximum tidal variation during transect periods over the entire study was 1.6 m. There was no correlation noted between depth distributions and monthly tidal variation. When depth distributions are corrected for tidal variations, the significance of distributional changes was slightly enhanced. Tidal effect was, therefore, disregarded in depth analysis.

Depth distributions were tested for significant association ($p \leqslant 0.05$) using the Chi-square test for homogeneity (Simpson *et al.*, 1960). Mean depths and temperatures were tested for significant differences using t-tests (two tail, $p \leqslant 0.05$). The variances were checked for homogeneity prior to each t-test, and if significant difference between variances was shown ($p \leqslant 0.01$), t-tests were not conducted.

Preliminary laboratory temperature preference tests were run in a 198 × 55 × 36 cm horizontal gradient tank under constant illumination. A standing gradient was produced by terminal cooling and heating coils. Temperatures as low as 6°C could be obtained and gradients as large as 11°C could be maintained and shifted. Fishes were run in the shifting gradient for six to ten hours. The position of the fish within the gradient were recorded at 30 minute intervals, and the percent occurrence of fish at each available temperature was calculated. The mode was used to indicate preferred temperature.

RESULTS

Temperature Patterns: Bathythermal gradients near the tip of the King Harbor breakwater show great seasonal temperature variations. Sea surface temperature varied from 24°C in the summer to 14°C in the early spring. During the summer there was also a vertical gradient of as much as 11°C to 12°C, with surface temperature 24°C and bottom (11 m) temperature 12°C to 13°C (Fig. 2).

Summer, July through early September, was the time of greatest vertical thermal diversity. A strong thermocline was usually present. Surface water was warm, usually above 20°C, and bottom water was still cold, 13°C to 17°C. By late September the thermocline was usually broken, and

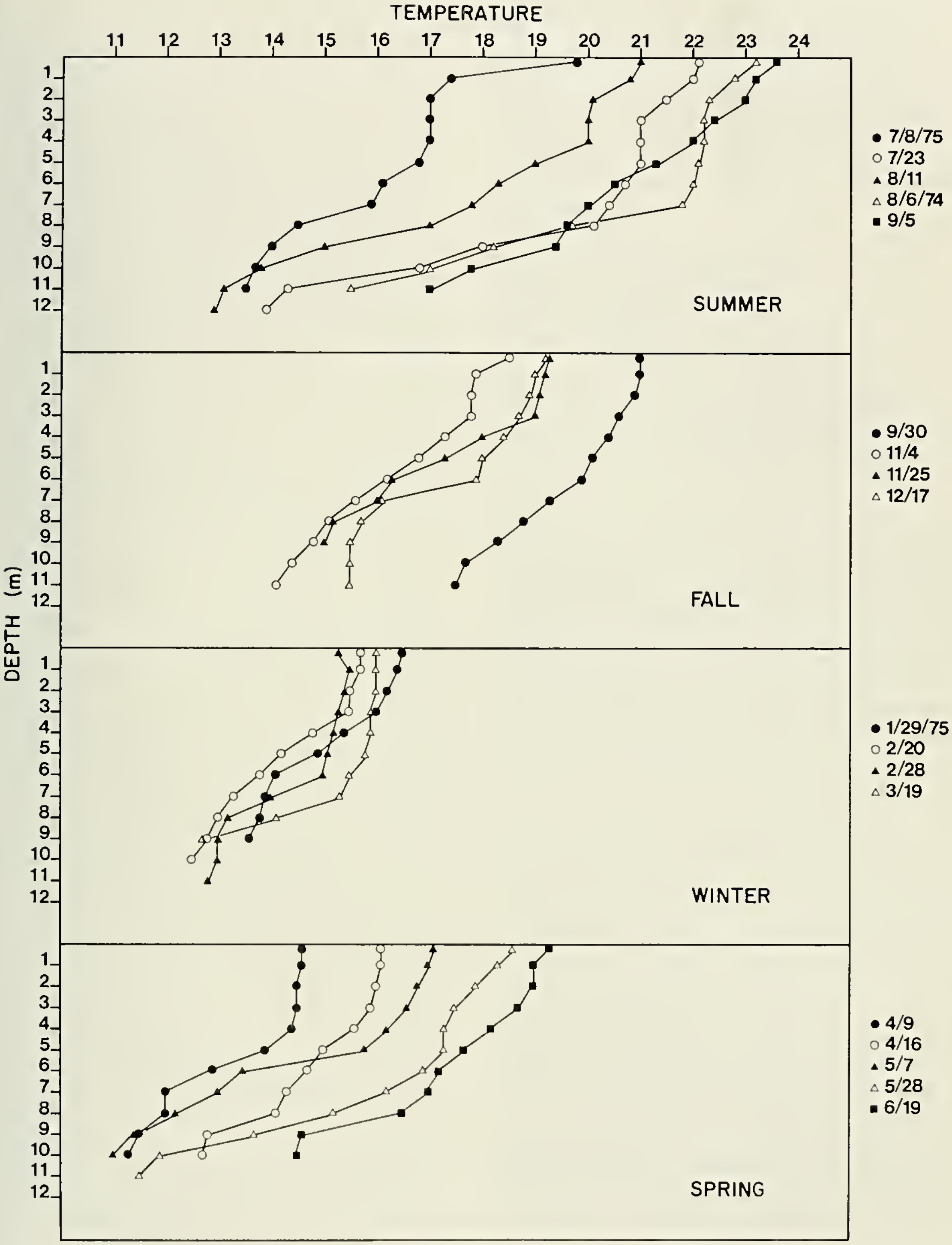

Figure 2. Seasonal changes in the temperature profile at the study site in King Harbor.

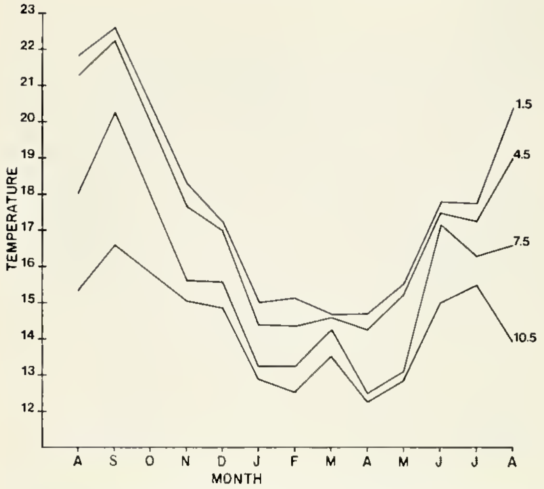

Figure 3. Monthly changes in temperature at transect depth, King Harbor (depths, 1.5–10.5 m).

bottom water was sometimes quite warm. The surface water began to cool during the fall, late September through December, then gradually the whole water column began to cool. During winter, January through March, the water was uniformly quite cold without much vertical gradient, surface water temperatures usually varying between 14°C and 16°C and bottom temperatures between 12°C and 14°C. During the spring, April through June, the surface water began to warm, a thermocline began to form, and the bottom water was often at its coldest, 11°C.

The periods of heating and cooling and of maximum and minimum thermal diversity are also clear from figure 3 which presents seasonal temperature variations at transect depths. The temperature variation was lowest for the 10.5 m transects, with means varying from 16.6°C to 12.2°C. Thermal stability was greatest for the 9.0 m to 12.5 m range, at which depth temperature variation was least in amplitude, and temperatures were stable for longer periods. The 9.0 m to 12.5 m range was warm (above 15°C) for only a short time during the fall.

Distributional Patterns: The patterns of seasonal abundance, bathymetric and thermal distributions are presented in figures 4, 5, and 6. The data below refer to these figures.

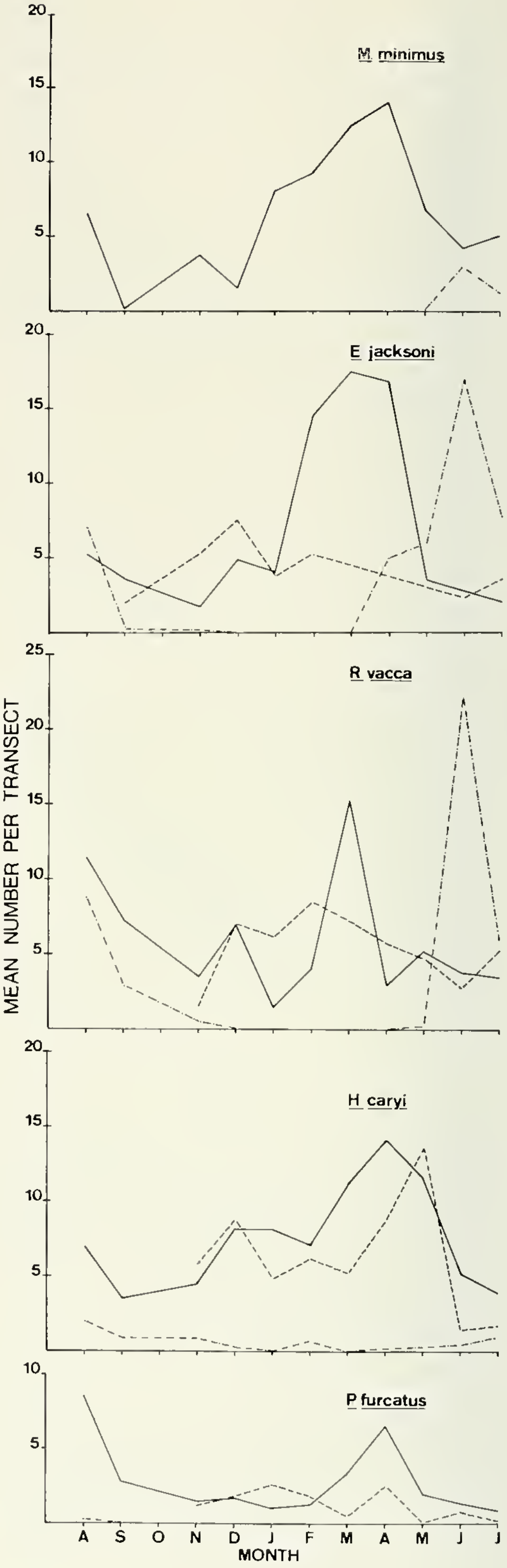

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Figure 4. Monthly changes in abundance of the five embiotocid species; adults (solid line), subadults (dotted line), juveniles (dots and dashes).

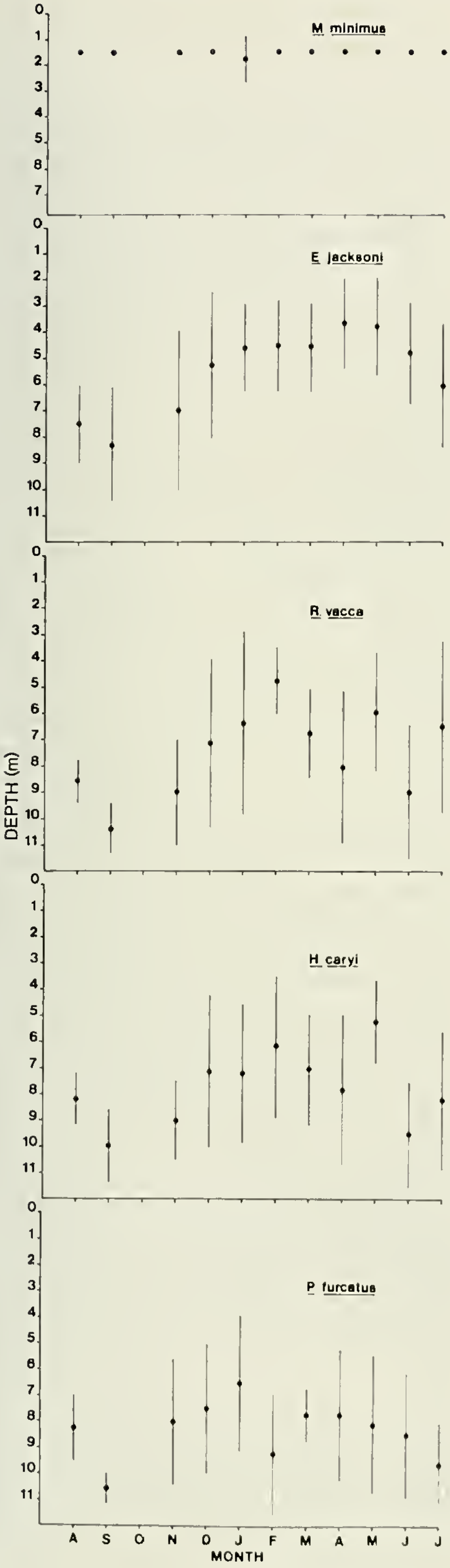

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Figure 5. Monthly variations in the depth distributions of the five embiotocid species (mean and one standard deviation above and below the mean).

Embiotoca jacksoni.—Seasonal abundance of adult fish was low from August to January ($\bar{x} \leqslant 5$/transect). Large schools of as many as 100–200 adults were present from February through April ($\bar{x} = 15$–20 transects). Abundance dropped again during May and remained low through July. Young began to be born in late March and reached their peak abundance during June.

The relative frequency at each depth for each size class varied. The adults had a distinctive distribution, most (56.3 percent) being found at 4.5 m, their abundance decreasing sharply in both shallower and deeper water. The depth distribution of the subadults was relatively even, though the curve was skewed toward shallow water. Juveniles were found primarily (64.2 percent) in shallow water, decreasing in abundance with increasing depth. Chi-square tests for homogeneity show that each of the size classes had a distribution significantly different from each of the others.

Adults showed a general pattern of movement into deeper water, 7.5 m to 8.2 m during August and September, then back into shallower water in November, staying at 3.7 m to 5.2 m from December to June. By July the mean depth of adults had moved to 6.1 m. Mean depths for August and September were significantly different from all mean depths between December and July using t-tests. The mean depth for November showed significant differences with those of April through June. By July the fish had begun to move into deeper water again, and the mean depth during July was significantly different from those of April and May, the months when the fish were shallowest. Mean depths for the subadults varied little during the year, ranging from 4.3 m to 5.9 m. T-tests comparing means for the subadults from every month with every other month show no significant differences.

The pattern of mean depth variation for the adults corresponded to the pattern of changes in water temperature. The fish were centered at 7.5 m in August and September, the period of warmest water temperature. During this time temperatures as high as 20°C extended to 9 m. The fish began to move into shallower water as the water cooled and remained around 4.5 m all winter and spring. When the water became quite warm again in July, the fish began to move into deeper water.

Figure 6 shows the distribution of adult embiotocids with regard to temperature for each month of the study. The dashed lines represent the mean temperature at 1.5 m (top line) and 10.5 m (bottom line), and thus represent the boundaries of available temperature at the study site during each month. During the winter adults were usually found in water warmer than 14°C, during the summer in water cooler than 20°C. The change in mean temperature observed for adults between August and September does not reflect a movement of fish as mean depth did not change significantly during that period. A downward movement began in June and this position was maintained into August and September. The means for these months are significantly deeper than all months from December to July. Subadult *E. jacksoni*, which showed no seasonal depth changes, also seemed not to show avoidance of warm water. They were often found in the warmer half of the available temperature range.

Hypsurus caryi.—The seasonal abundance pattern for all size classes of *H. caryi* was similar to that found for *E. jacksoni*. Adults were low in abundance ($\bar{x} \leqslant 7.5$ transect) from August through November, more abundant from December through May ($\bar{x} = 7.5$–15/transect). During the latter period fairly large schools of adults and subadults, often as many as 100 fish, were seen. Peak abundance was between March and May. By June the fish were less numerous and generally solitary or in small groups. The large schools common during winter and spring were gone. Subadults followed the same pattern as the adults, but were not considered a distinct size class until November. Juveniles were usually found in deep water, often over the sand, and never in very large numbers.

The adults of *H. caryi* were rather evenly distributed between 4.5 m and 10.5 m, though slightly more abundant in deeper water. The subadults' distribution was not different from the adults' according to the Chi-square test for homogeneity.

Subadult *H. caryi* did not vary in depth distri-

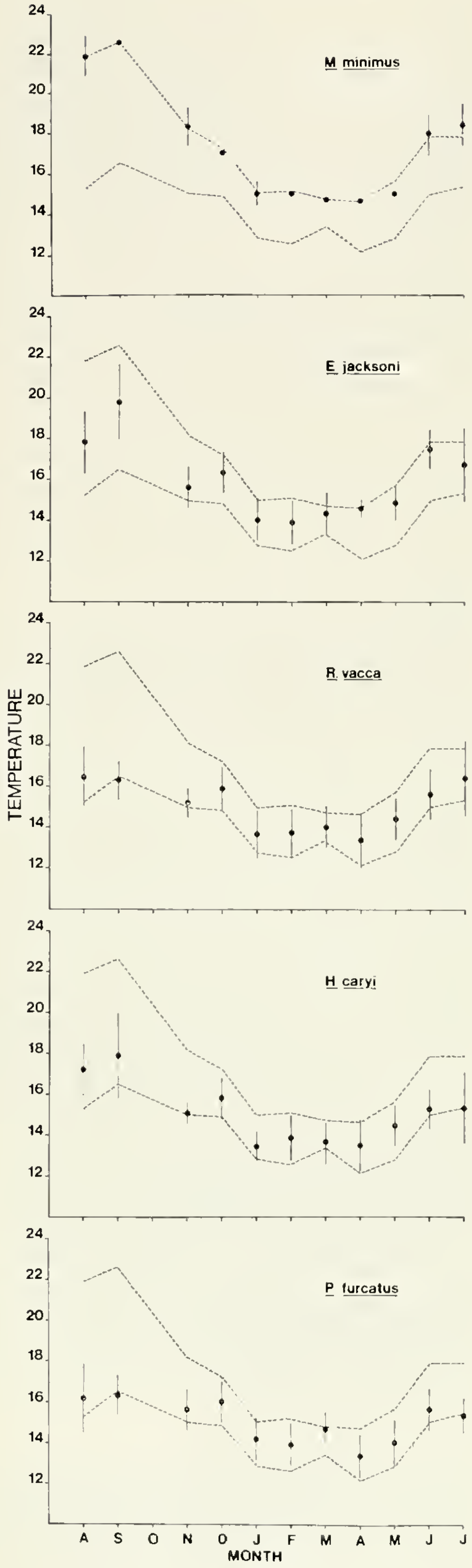

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Figure 6. Monthly variations in distribution with regard to temperature for the five embiotocid species (mean and one standard deviation). Dashed lines represent mean temperatures recorded each month at 1.5 m transects (above) and 10.5 m transects (below).

bution much during the year. The adults, however, did show major changes in depth. Adults were found in deeper water, 7.9 m to 9.0 m, between June and November, the period of warm water in the harbor. Mean depths were shallower, 5.2 m to 7.8 m, between December and May, the period of cold water. With only minor exceptions, t-tests show the significance of these depth differences.

Monthly mean temperatures for adults indicate that they were found in water colder than 16°C during most of the year and in water colder than 14°C between January and April. During August and September, the mean temperature for adults was between 17°C and 18°C, at the lower end of the temperatures available during this period. Subadults showed temperature patterns similar to the adults and were found in water colder than 16°C. Field observations have shown that during the summer, when a thermocline is present, *H. caryi* is usually found at or below this level.

Micrometrus minimus.—No subadult classification was distinguished for this species, since the males are smaller than the females and are sexually mature at birth. For the same reasons, young of the year were only considered to be identifiable juveniles for a very short period of time. In most of the analyses adults and juveniles were summed and considered one unit.

The abundance of *M. minimus* at the study site was very low from September through December ($\bar{x} \leqslant 4$/transect), but by January they were much more numerous, with peak abundance coming in April ($\bar{x} = 14$/transect). Juveniles appeared in the harbor in May and at the study site by June. During the winter and spring months, small schools of about 25 large adults were common. During the summer, fewer large adults were seen and fish were usually solitary or in small groups.

Micrometrus minimus has a unique and narrow depth preference. This species was found almost solely in the top 3.0 m of water. Of the 770 adults fish recorded in this study, only five were recorded on a transect deeper than 1.5 m. These five fish were recorded on 4.5 m transects. The juveniles were most commonly observed in the top 0.5 m, generally in the intertidal barnacle zone. Adults were seen deeper, in the shallow subtidal.

The monthly mean depths for *M. minimus* (adults and juveniles together) did not vary. Since they remained at 1.5 m all year, they must have accepted whatever water temperatures were available at this depth. The mean temperature for the fish was nearly identical to the mean available temperature at 1.5 m for each month.

Rhacochilus vacca.—The seasonal abundance data for *R. vacca* shows that adults and subadults were most abundant during the winter and spring months. This is the same pattern that was seen in *E. jacksoni*, *H. caryi*, and *M. minimus*. Juveniles of *R. vacca* began to appear in May and reached peak abundance during June.

The adults of *R. vacca* were distributed between 4.5 m and 10.5 m with very few found at 1.5 m. Depth distribution of adult *R. vacca* was nearly identical to that of adult *H. caryi*. Adults also formed large schools of 50 to 100 fish during the winter months. Subadults were nearly evenly distributed at all depths, most abundant (29.9 percent) at 4.5 m and least abundant (19.8 percent) at 1.5 m. Juveniles showed a slightly bimodal distribution, 30.8 percent at 1.5 m and 36.0 percent at 7.5 m and were least abundant at 10.5 m (12.9 percent). Chi-square tests show that the depth distributions of all size classes were significantly different from each other.

As with subadults of *E. jacksoni* and *H. caryi*, mean depths of subadult *R. vacca* did not vary significantly during the year. The adults, however, moved in a seasonal pattern very similar to adult *E. jacksoni* and *H. caryi*. During August, September, and November, mean depths for subadults were between 8.5 m and 10.4 m. During the rest of the year they were found in shallower water, usually shallower than 7.5 m. Tests of August and September with February and March show significant differences in the mean depths. Comparisons between November and all months between January and July (except April and June) show significant differences.

Mean temperatures for each month for adult *R. vacca* show that this species rarely accepted water warmer than 16°C. The subadults were seen in warmer water and did not seem to be as restricted as were the adults by water temperature.

Phanerodon furcatus.—This species is primarily a sand-schooling fish and is present along the breakwater of King Harbor in relatively low abundance. The abundance pattern of this species departed from that of all others so far described in that it did not increase in abundance during the winter and spring months. *Phanerodon furcatus* was present in the harbor at a fairly constant low level ($\bar{x} = 2$–4/transect) all year, with small peaks for the adults in August and April ($\bar{x} = 9$–10/transect). Few juveniles were seen, and these only during August and September.

The abundance of *P. furcatus* correlates positively with increasing depth at the study site. In fact, *P. furcatus* was found primarily along the base of the breakwater at the sand-rock interface.

A Chi-square test does not show significant difference in distribution between adults and subadults. For reasons of such low abundance and absence of statistical difference in distribution, the two size classes were summed for further analysis.

Monthly mean depths for *P. furcatus* showed the same movement into deeper water during September as seen in other species (except *M. minimus*). It is not possible to make t-test comparisons between September and the other months because of non-homogeneity of variances. During all months except September the mean depths were usually between 7.5 m and 9.0 m. During September, mean depth dropped to 10.6 m, giving the appearance that the fish were moving into deeper water in response to the warm water present during this month.

Monthly mean temperatures for *P. furcatus* showed that this species was found primarily in water colder than 16°C. The mean temperatures during August and September were slightly above 16°C. The coldest temperatures in the harbor during these two months were also slightly above 16°C and only available in the deepest water.

Preliminary Gradient Tank Experiments: Our present data concerning responses of the five embiotocid species in a controlled thermal gradient tank are limited, but they generally support observed field temperature distributions. *Micrometrus minimus* (adults) acclimated to 15–16°C preferred 17°C in one test and showed bimodal peaks at 16°C and 23°C in a second test. *Hypsurus caryi* (subadults) acclimated to 13–14°C preferred 11.5°C, 12.5°C, and 15.5°C in three separate tests. *Phanerodon furcatus* (subadults) acclimated to 13°C preferred 12.5°C. *Rhacochilus vacca* (subadults) acclimated to 14°C chose 10.5°C, acclimated to 18.1°C chose 14.9°C, and acclimated to 19.5°C chose 10.1°C. *Embiotoca jacksoni* (subadults) acclimated to 13–17°C consistently preferred 13.5–14.5°C water. Juvenile *E. jacksoni* preferred warmer temperatures. Four day old fish acclimated to 16°C chose 18.5°C; 15 day old fish acclimated to 16°C chose 15.5°C, acclimated to 14.7°C they chose 14.8°C.

DISCUSSION

Spatial Relationships: Space utilization can be analyzed through a comparison of mean depths for each species calculated from the 12 month data. Figure 7 shows these mean depths for adults and subadults combined. *Micrometrus minimus* was found to have a very narrow depth range and to be restricted to very shallow water. *Rhacochilus vacca*, *H. caryi*, and *P. furcatus* formed a deeper water group. *Embiotoca jacksoni* had a mean depth at the middle of the range of available depths, about 5.0 m. T-test comparisons of mean depth of *M. minimus* can not be made because of non-homogeneity of variances. T-tests show that mean depth of *E. jacksoni* was significantly different from all other species. Mean depths for *H. caryi* and *R. vacca* were not significantly different from one another. The mean depth of *P. furcatus* was not different from that of *H. caryi* but cannot be tested against that of *R. vacca* because of non-homogeneity of variances.

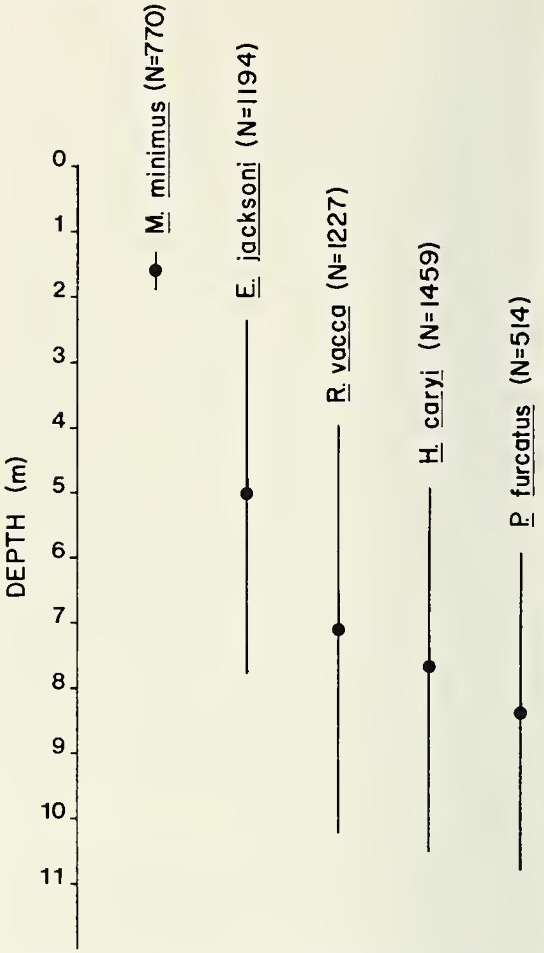

Figure 7. Depth distributions for five species of embiotocids at the study site, King Harbor. Data summed for adults and subadults and for the period from July 1974–August 1, 1975 (mean and one standard deviation).

For adults alone, three different types of dis-

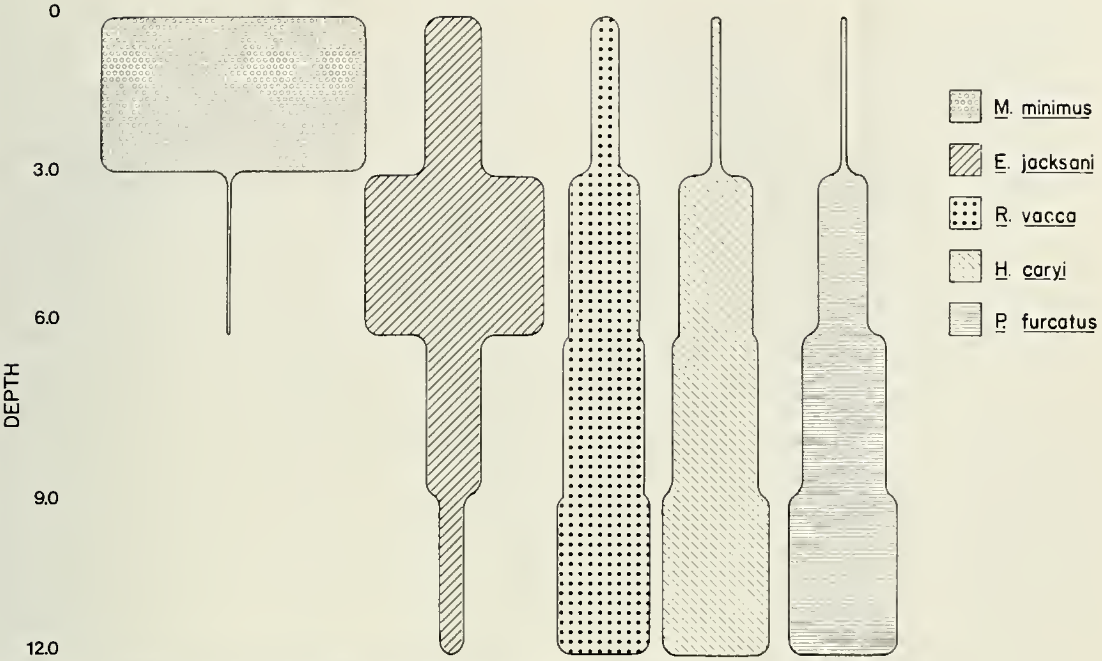

Figure 8. Changes in relative frequency distributions of the five embiotocid species with depth.

tributions can be distinguished. *Micrometrus minimus* was uniquely distributed. It was abundant in shallow water where it was also the numerically dominant surfperch, and its abundance decreased dramatically with increasing depth. *Embiotoca jacksoni* was also uniquely distributed. It was most abundant at middle depths and declined in both shallower and deeper water. At 4.5 m, *E. jacksoni* was the numerically dominant surfperch. The distributions of *H. caryi* and *R. vacca* were very similar to each other, maximum numbers occurring in deeper water, 7.5 m to 10.5 m. *Phanerodon furcatus* was distributed similarly, with its maximum numbers in deeper water. The overall abundance of this species, however, was considerably lower than either those of *R. vacca* or *H. caryi.* Chi-square tests for homogeneity of the adults indicate that both *M. minimus* and *E. jacksoni* were significantly different from each of the other species. No differences of statistical significance are found among *H. caryi, R. vacca,* and *P. furcatus.*

Subadult distributions were noticeably different from adult distributions. Subadults of each species were not greatly different in distribution from each other and were more evenly distributed at all depths than the adults. *Embiotoca jacksoni* subadults showed some decrease in abundance with increasing depth. *Rhacochilus vacca* was very evenly distributed. *Hypsurus caryi* and *P. furcatus* subadults were distributed most like the respective adults, abundances increasing with increasing depth. Chi-square tests show that the adults and subadults of *H. caryi* and *P. furcatus* did not have significantly different distributions. Adults and subadults of *E. jacksoni* and *R. vacca* do show significant differences. Juveniles were more common than adults in shallow water, especially those of *E. jacksoni* and *R. vacca.* Even juvenile *M. minimus* were shallower than the adults.

Another view of depth utilization is obtained through a diagrammatic display of relative frequency distributions of individuals within each species at each depth (Fig. 8). Regardless of species' total abundance, the species is given an area in the chart equivalent to that for each other species. This area is then apportioned at each depth according to the percentage of that species found at that depth. For each species, adults and subadults are combined in this display. The diagram confirms the impression of three different types of distributions. Note the degree of similarity among the distributions of *R. vacca, H. caryi,* and *P. furcatus* in this representation.

Temperature Orientation: Upon examination of patterns of depth and temperature distributions,

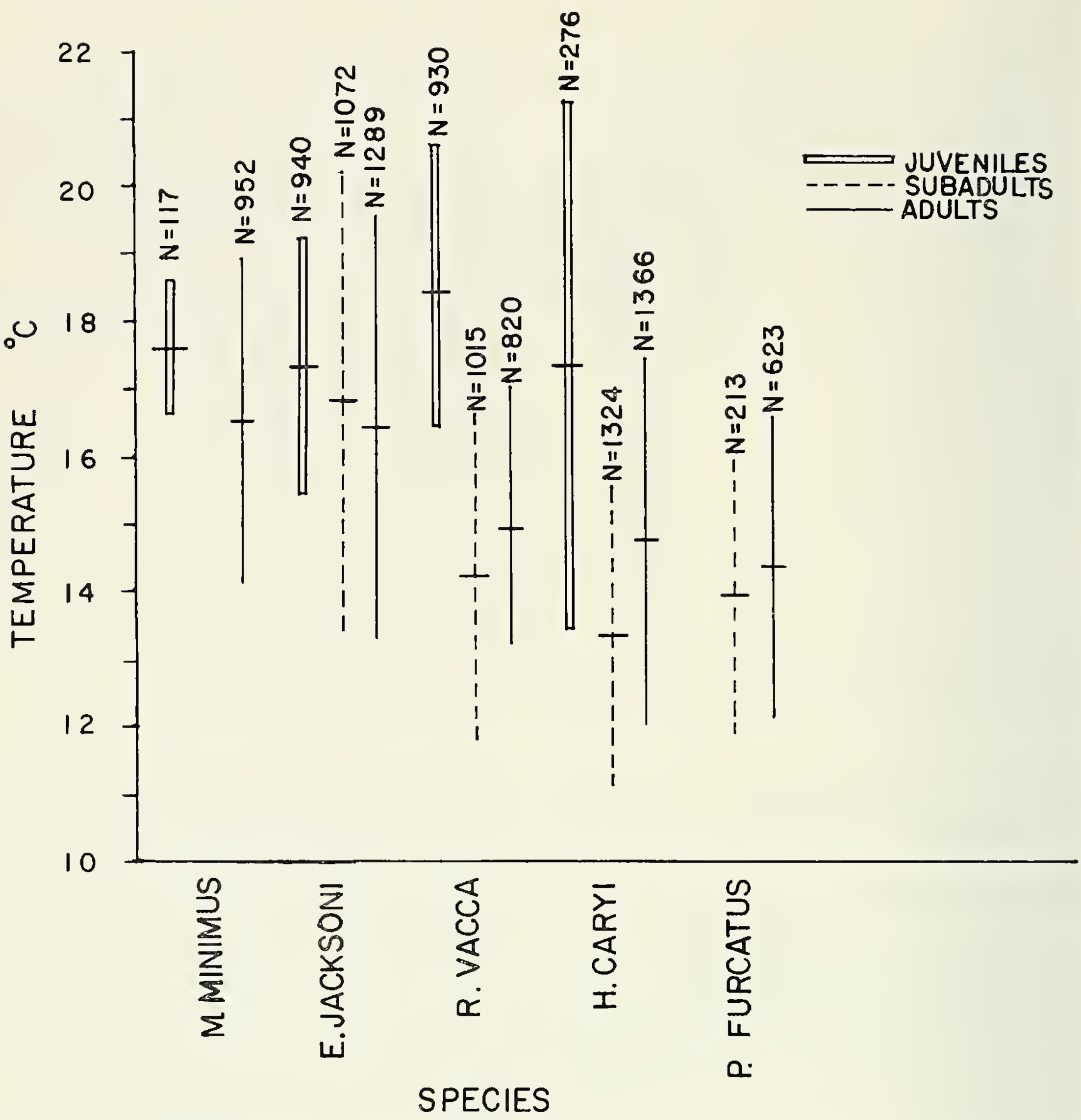

Figure 9. Thermal distributions of available life history stages of five species of embiotocids at the study site, King Harbor. Data summed from September 1974 through October 1975 (mean and one standard deviation).

it is apparent that three species, *R. vacca*, *P. furcatus*, and *H. caryi* avoid warmer water. We consider these three species to be part of the cool water element of the King Harbor fauna. We feel that temperature plays a major role in limiting their vertical distribution. Adults of these species prefer to remain in waters cooler than 16°C. This pattern is seen in both monthly distributional patterns and in the laboratory thermal gradient tank. Two of these species, *R. vacca* and *P. furcatus*, range north to Alaska, which implies successful utilization of boreal waters. In contrast to these deeper species, *M. minimus* shows no field temperature preference and remains in intertidal waters which range in temperature from 14–24°C. We consider this species to be habitat limited and since it is an intertidal species it is an obligate eurytherm. In the gradient tank, this species did not show a consistent thermal preference. *Embiotoca jacksoni*, on the other hand, appears to prefer water between 15–20°C. Juveniles of this species occupy the intertidal for several weeks but gradually move into the middle depth zone during the first few months of their existence. This change in depth correlates with an "ontogenetic" shift in temperature preference seen in the gradient tank, older fish preferring cooler water. An important facet of the seasonal distribution of *E. jacksoni* is its descent during the summer and fall months, following the pattern of the cool water species but always maintaining its center of distribution just above their distributional centers. Whereas the cooler water species stay below the thermocline, occupying the coolest available water, *E. jacksoni* does not descend below the thermocline, and its movement does not bring it into water that is much cooler than originally occupied. We suggest that *E. jacksoni* is thermally labile. This is consistent with the conclusion of Waggoner and Feldmeth (1971) who found that *E. jacksoni* was less sensitive to rising temperature than either *P. furcatus* or *R. vacca*. We believe that *E. jacksoni* is restricted from deeper water by spatial interference with the deeper species. This process of "interference" does not appear to involve overt interspecific agonistic displays and must result from more subtle processes. In our five years of fish observations within King Harbor, we have rarely observed overt interspecific behavioral responses except between occasional subadult fish. Aggregations of surfperch often include two or three species and several species are regularly observed feeding over the same substrate.

Figure 9 presents the annual mean temperatures for each recognized age class of each of the five species studied. In this presentation, differing thermal preferences are masked by seasonal temperature fluctuations. In all cases, however, the juveniles consistently occur in warmer water than adults. We feel that this response in juveniles correlates with their observed presence in very shallow water, but it also reflects the correlation of parturition with seasonal warming. Norris (1963) correlated the preference for warmer water in juvenile opaleye (*Girella nigricans*) and its resultant inshore movement with enhanced survival and growth. We feel that these conclusions are equally applicable to many embiotocids and further, that their shallow position lessens competition between juveniles and older stages.

The only species never observed to avoid warm water in the harbor, *M. minimus*, is the species that is most temperature independent, seasonally eurythermal, and has the least northern latitudinal range. This latitudinal range restriction may be due to a requirement for warm summer breeding temperature. We know that *M. minimus* has a very narrow depth range and appears to be restricted to the intertidal. Because of this habitat restriction, *M. minimus* is necessarily exposed to large seasonal temperature fluctuations. Tolerance or selection of warmer waters is probably a specialization, since the majority of the embiotocids occur in the cooler waters of the California Boreal Zone.

The three species that form part of the cool water element in the harbor, *R. vacca*, *H. caryi*, and *P. furcatus*, avoid water warmer than 16°C. This indicates a narrow thermal tolerance, possibly a thermal specialization. In contrast to the thermal specializations of both the cool water species and *M. minimus*, *E. jacksoni* appears to occupy a middle thermal position. It does not accept the warm water that *M. minimus* does, yet it is not restricted to cold water as are *H. caryi*, *R. vacca*, and *P. furcatus*. *Embiotoca jacksoni* is considered to be the most generalized species in the family by Tarp (1952). Its apparent lack of thermal specialization may be a reflection of its position as the most generalized embiotocid.

Depth and temperature are not the only ecological factors affecting the distributional patterns of embiotocids. Alevizon (1975) described the effect of substrate relief selection on distributions of some embiotocids. Bray and Ebeling (1975) recorded the presence of *Phanerodon furcatus* in all available habitats in their study area suggesting little habitat restriction. Terry (1975) and Terry and Stephens (in prep.) examined the influence of diet and interspecific interactions on the distributions of these five species. We recognize these interactions but believe that in this study, the large thermal diversity within a narrow depth range at the study site in King Harbor, provided an excellent field laboratory in which the effect of temperature on the spatial distribution of these species could be readily distinguished. Temperature or thermotaxis has previously been shown to be the most important ecological factor governing the distribution of several intertidal species (Norris, 1963; Nakamura, 1976). In this study, thermal orientation was found to play a significant role in the spatial organization of a subtidal fish community. This underscores the importance of thermal orientation in the biology of inshore fishes in general.

SUMMARY

1. Resident populations of five species of embiotocids (*Embiotoca jacksoni*, *Hypsurus caryi*, *Micrometrus minimus*, *Phanerodon furcatus*, and *Rhacochilus vacca*) were studied for one year

(August 1974–July 1975) at King Harbor, California. using diver transects.

2. The bathymetric distributions of two of the five species (*M. minimus* and *E. jacksoni*) differed significantly from the remaining three with *M. minimus* occupying the shallow intertidal and subtidal fringe, *E. jacksoni* the middle subtidal, and the *R. vacca*, *H. caryi*, and *P. furcatus* the deeper rocks and rock-sand interface.

3. Depth distribution varied seasonally (except for *M. minimus*) with adults of each species moving deeper in the late summer and fall and shallower in the winter and spring.

4. The fall descent corresponded to periods of increased surface water temperature and deepening of the thermocline. The three deeper species chose the coolest available water during this period.

5. Seasonal abundance decreased during the fall and may represent some emigration in response to warm thermal conditions.

6. Each species appears to occupy a preferred thermal range. This range is especially obvious in the deeper water species where the distributions tend to center at temperatures at or below 16°C. *Embiotoca jacksoni* appears to be more thermally tolerant. *Micrometrus minimus* appears to either select the warmest water available or more probably to tolerate whatever temperature is available in its preferred habitat.

7. Juveniles prefer warmer water than adults. Young are born from spring to late summer and generally orient to shallower, warmer water. Subadults are less depth or temperature restricted than either adults or juveniles.

8. Temperature orientation appears to play a role in controlling depth distribution and, therefore, influences spatial utilization by these surfperches.

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THE SIGNIFICANCE OF COLORATION IN FISHES OF THE GENUS *HYPSOBLENNIUS* GILL

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Abstract: The social behavior and associated colorations of five Pacific species of *Hypsoblennius* were observed under field and laboratory conditions. Behavior patterns were classified as to their functional relationship to types of behavior such as aggression and courtship. The occurrence of various color patterns was then tested for correlation to these types of behavior. This analysis indicates that coloration is of potential value as a communication signal for differentiatng between submission, aggression and courtship. Coloration was also correlated with habitat type and showed striking differences between sympatric species.

Species of the genus *Hypsoblennius* inhabit tidal pools, subtidal reefs and algae beds along the Pacific coast of North, Central and South America. Like many of the Blenniidae, they are territorial and show frequent social interactions. The behavior of some blenniid fishes has been thoroughly described (*e.g.*, Wickler, 1957, 1961, 1963, 1965; Wilson, 1969; Thompson and Bennet, 1969; Gibson, 1968; Phillips, 1971; Fishelson, 1963; Robins *et al.*, 1959; Tavolga, 1960) but fishes of the genus *Hypsoblennius* have largely escaped attention (Losey, 1968). *Hypsoblennius* species have the ability to display a variety of color patterns and can alter many features of their coloration in a matter of seconds. The signal value of coloration changes in fishes is well known in blenniids (*e.g.*, Wickler, 1957, 1963) and other fishes (*e.g.*, Barlow, 1974; Baerends and Baerends van-Roon, 1950). Hamilton and Peterman (1971) have drawn attention to the compromise between countershading as a camouflage coloration and contrasting colorations for communication in *Chaetodon lunula*. In this paper, I will describe the potential signal value of coloration in five species of *Hypsoblennius* and explore the relationships of these colorations to their taxonomic affinities and their behavioral ecology.

METHODS

All of the data presented below were drawn from laboratory observations. Field observations made in California, Mexico, and South America provided a subjective confirmation of the laboratory results. Fish were held in 150 l, 300 l, and 550 l aquariums at the Scripps Institution of Oceanography and supplied with running sea water. Aquarium heaters were used only for the tropical species. Fish were held in densities similar to those encounterd in the field and offered a variety

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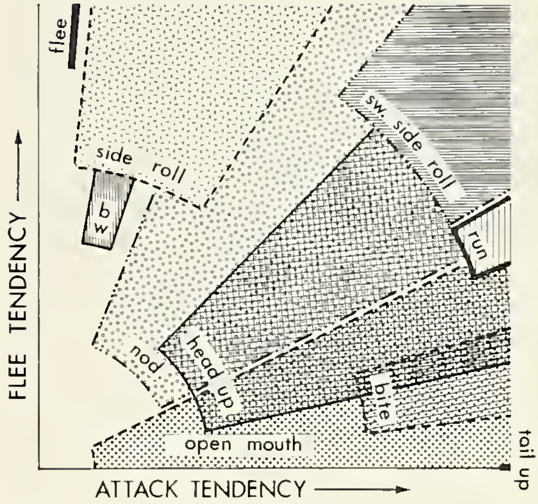

Figure 1. The agonistic action patterns of *Hypsoblennius* spp. arranged as to functional motivational context. See text for explanation.

TABLE 1. The species of *Hypsoblennius* studied with notes on zoogeography and ecology. Habitat sympatry is indicated by connecting vertical bars.

H. jenkinsi (Jordan and Everman)—California and northern Baja California. Found in barnacle tests and bore holes on shallow, subtidal reefs with disruptive background.

H. gentilis (Girard)—California and north-central Baja California. Found in a variety of habitats from grass beds to sea walls and buoys from barely subtidal depths to at least 30 m at the southern extent of its range. It has limited habitat overlap with *H. jenkinsi.*

H. brevipinnis (Gunther)—Southern Baja California to Central America and northern Peru. It inhabits barnacle tests on shallow, wave-washed rocks in barren habitats.

H. robustus (Hildebrand)—Central Peru. Habitat identical to *H. jenkinsi.*

H. sordidus (Bennet)—Central Peru to central Chile. It inhabits the same areas as *H. robustus* as well as the habitat type of *H. brevipinnis.*

of substrata: gravel bottom with cobble and broken shells, opaque plastic tubes, and *Balanus* barnacle tests resting on the bottom and mounted on vertical, artificial rock surfaces. Fish were fed an overabundance of cut frozen shrimp and living invertebrates such as brine shrimp, *Emerita* sand crabs and assorted benthic amphipods in order to encourage normal foraging behavior. Fish were held under reversed photoperiod and observed from a darkened chamber through slits in a blind. Tape recorded notes were made of essentially all of the activities of groups of fish during two to five-hour observation periods.

Two methods were used in order to approximate the motivational state of an individual as evidenced by its agonistic and sexual behavior. These methods are only intended to indicate the *functional* expression of the motivational status of a "signal sender:" that is, information that would be of major importance to another individual, the signal receiver, in forming an *impression* of the the behavioral tendencies of the signal sender. In other words, we are concerned with analysis at the level of communication and prediction of an individual's subsequent behavior rather than at the level of a causal analysis of motivation. A signal receiver can profitably form an impression of the probability that a signal sender will attack, flee or behave sexually without differentiating between the many possible causal factors of social behavior.

The first method was used to differentiate agonistic behavior according to the relative probability of attacking and fleeing. Morris (1958) introduced a diagrammatic hypothesis of the causation of agonistic behavior based on an orthogonal interaction between the tendencies to flee and attack. This has proven to be a useful tool for initial studies but Hinde (1966) has drawn attention to its limitations as an explanation of causation. I used the framework of the "attack/flee" (A/F) hypothesis in order to indicate the functional expression of agonistic action patterns according to whether they were followed by attack, flee or neutral activities. Sexually ripe individuals were omitted from this analysis. Several values were calculated for each pattern: 1) Percent followed by attack (move toward opponent or physical combat) times $90° \times 10^{-2}$ described the angle from the flee axis for the attack vector (48° for head-up display, Fig. 1); 2) percent followed by retreating (move away from opponent) times $90° \times 10^{-2}$ described the angle from the attack axis for the flee vector (12° for head-up display, Fig. 1); 3) the percent preceded by an aggressive act by the opponent (move toward, physical combat, head-up, tail-up or bite) described the distance from the origin (33% for head-up display, Fig. 1).

These three measures were used to describe an area in the A/F framework for each action pattern (Fig. 1). The area reflects both the probability of a following attack or retreat and the intensity of the behavior as indicated by the preceding behavior of the opponent which probably contributed to the causation of the display.

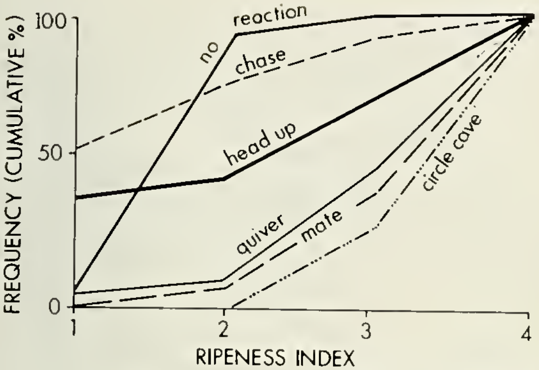

Figure 2. The distribution of the male action patterns over the ripeness of the male, expressed as cumulative percent.

For sexual behavior, the females exhibited little display other than coloration change and a submissive posture so attention was focussed on male behavior. Sexual ripeness of males was indicated by the occurrence of nest preparation behavior: 1) Not ripe, no rubbing, spitting or circle-spitting; 2) rub and spit occur but circle-spitting is lacking; 3) rub, spit and circle-spit occur but circle-spit is less common than spit; 4) same as No. 2 but circle-spit is more common than spit.

The frequency of courtship action patterns were then plotted over both the ripeness of the male (Fig. 2) and the proximity to an approaching female in order to indicate relative intensity of courtship movements.

BEHAVIORAL DESCRIPTION

The five species of *Hypsoblennius* treated below show a wide range of geographic distribution, differing degrees of sympatry with other *Hypsoblennius* species and a diversity of habitat types (Table 1). Their general behavior is, however, quite similar. All individuals are territorial except, perhaps, the females of *H. gentilis*. All except possibly *H. gentilis* show only limited movement about the habitat and may occupy the same territory for years (Stephens, *et al.*, 1970). *Hypsoblennius gentilis* appears to be far more vagile.

Pelagic prejuveniles settle out of the plankton and immediately show simple agonistic behavior and begin territorial defense within several days. They threaten nearly all congeneric intruders. Both males and females are usually polygamous but pair bonding has been observed on occasion. One female *H. jenkinsi* was observed within the territory of a male for nine days in the field. She spawned repeatedly with her partner and ignored the courtship efforts of neighboring males. The typical situation, however, is for the female to approach a courting male, deposit on the order of 1000 eggs in his refuge and leave. Males continue to court so long as they have space in their refuge for egg deposition. Courting males release a pheromone which is an attractant to other sexually ripe males (Losey, 1969). They are all carnivores and, in the field, may wander a meter or more from their refuge while foraging. Feeding patterns in an aquarium may be highly variable depending on the feeding regimen. The behavior groups and patterns that were observed and used in the analysis of coloration are briefly described below with an indication as to which species exhibit them (Table 2).

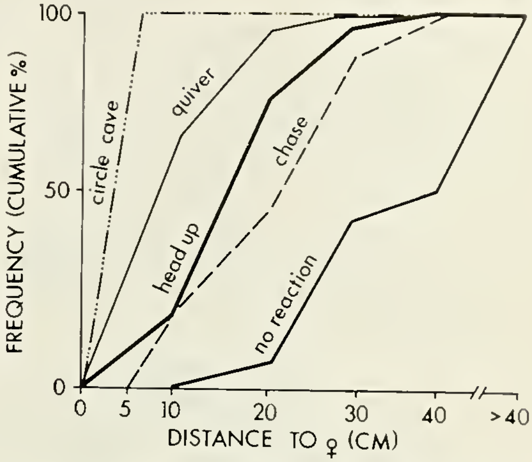

Figure 3. The distribution of the male action patterns over the proximity of a courting female to the male, expressed as cumulative percent.

Exploration.—Locomotion about the habitat without overt social interaction.

Submission.—Any action patterns with a high flee to attack ratio (Fig. 1): 1) Backwalk, the fish moves posteriorly propelled by moving the paired fins against the substrate with the head held down (Fig. 4B); 2) Flee, the actor swims away from its opponent; 3) Side-roll, the fish rolls on its side, dorsum toward the opponent with the dorsal fin erect but inclined laterally up to 90° toward the substrate and remains motionless (Fig. 4A). This is an apparent appeasement behavior that arrests the opponent's aggression. In only one of 34 occurrences was it answered by an attack. In *H. striatus*, however, it appears to serve as a threat display.

Mild Aggression.—Movement toward another individual without any overt agonistic display.

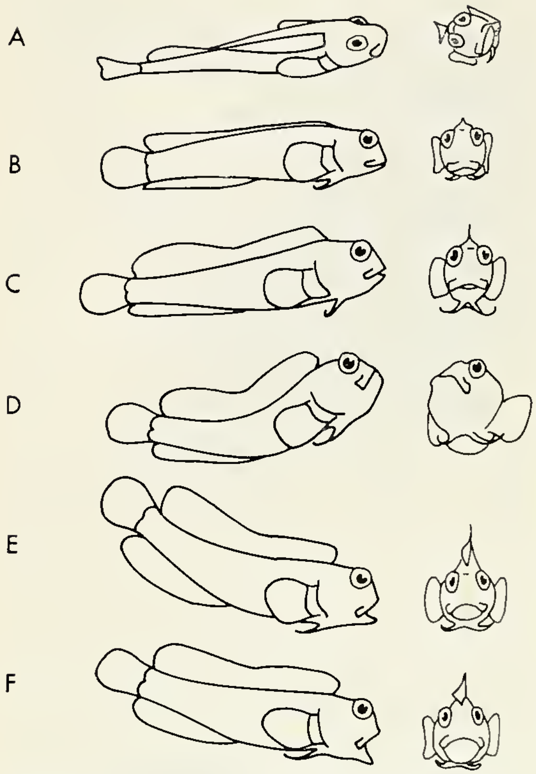

Figure 4. Display postures of *Hypsoblennius* spp. A) side-roll; B) backwalk; C) low intensity head-up; D) high intensity head-up; E) low intensity tail-up; F) high intensity tail-up.

TABLE 2. The occurrence of action patterns in species of *Hypsoblennius.* 1, indicates present but rare; 2, indicates that it is common; Dash indicates that it was not observed. No courtship was seen in *H. sordidus.*

Action Pattern	*jenkinsi*	*robustus*	*sordidus*	*brevipinnis*	*gentilis*
Backwalk	2	2	2	2	2
Flee	2	2	2	2	2
Side Roll	2	2	2	2	2
Head-up	2	2	1	2	2
Nod	1	1	1	2	–
Tail-up	1	1	2	1	–
Run	2	2	2	2	1
Carousel	2	2	2	2	1
Tail-beat	1	1	1	1	1
Open-mouth	1	1	2	1	2
Bite	2	2	2	2	2
Head-jerk	2	2	?	2	2
Quiver	2	2	?	2	2
Circle-cave	1	2	?	1	–
Rear	–	–	?	–	2
Rub	2	2	?	2	2
Spit	2	2	?	2	2
Circle-spit	1	2	?	–	–
Number of individuals sampled	46	11	2	11	19

Aggression.—Any action pattern with a low flee to attack ratio and low intensity: 1) Head up, the body is arched to raise the head which is enlarged by expansion of the oro-branchial chamber. The dorsal fin is usually erected. The actor faces the opponent at low threat intensities (Fig. 4C) but turns the head 15° to 45° to one side at higher intensities (Fig. 4D). It is usually an initial threat or challenge; 2) Nod, the head is slowly raised and lowered in repeated resumption of the head-up display. Between the species, it ranges from a rare display of irregular form to a common threat behavior with highly ritualized form in *H. brevipinnis*; 3) Open mouth, the mouth is opened, usually to the maximum extent, and held open while facing the opponent (Fig. 4F).

Strong Aggression.—Actions having a low flee to attack ratio and high intensity: 1) Tail-up, the body is arched with the head held next to the substrate, the tail is raised and the anal and soft dorsal fin erected. The head-up display slowly changes to a tail-up as the intensity of an encounter builds (Fig. 4E and F); 2) Run, this is a reciprocal "fighting" movement in which the opponents alternate between charging and withdrawing a few cm in quick succession. The body is in a high intensity head-up or a tail-up posture; 3) Carousel, the fish pivot around each other in head to tail position. This type of combat is usually fast and short lived in *Hypsoblennius* species with little tail-beating or other ritualized combat actions. It is a strong attack but there was insufficient data for A/F analysis; 4) Tail-beat, a rare behavior consisting of caudal beats toward the opponent's flank; 5) Bite, biting opponent.

Male courtship I.—Actions that were common in response to a distant female in fully ripened males or to close females in partially ripened males: 1) Head-up without quivering or head jerking (see below).

Male courtship II.—Actions common in response to a female that is close to a fully ripened male. These are usually associated with a head-up or tail-up posture: 1) Head-jerk, the head is twitched rapidly toward the female, frequently accompanied by a momentary opening of the jaws. It frequently precedes a quiver bout; 2) Quiver, lateral flexures of the body are made at ex-

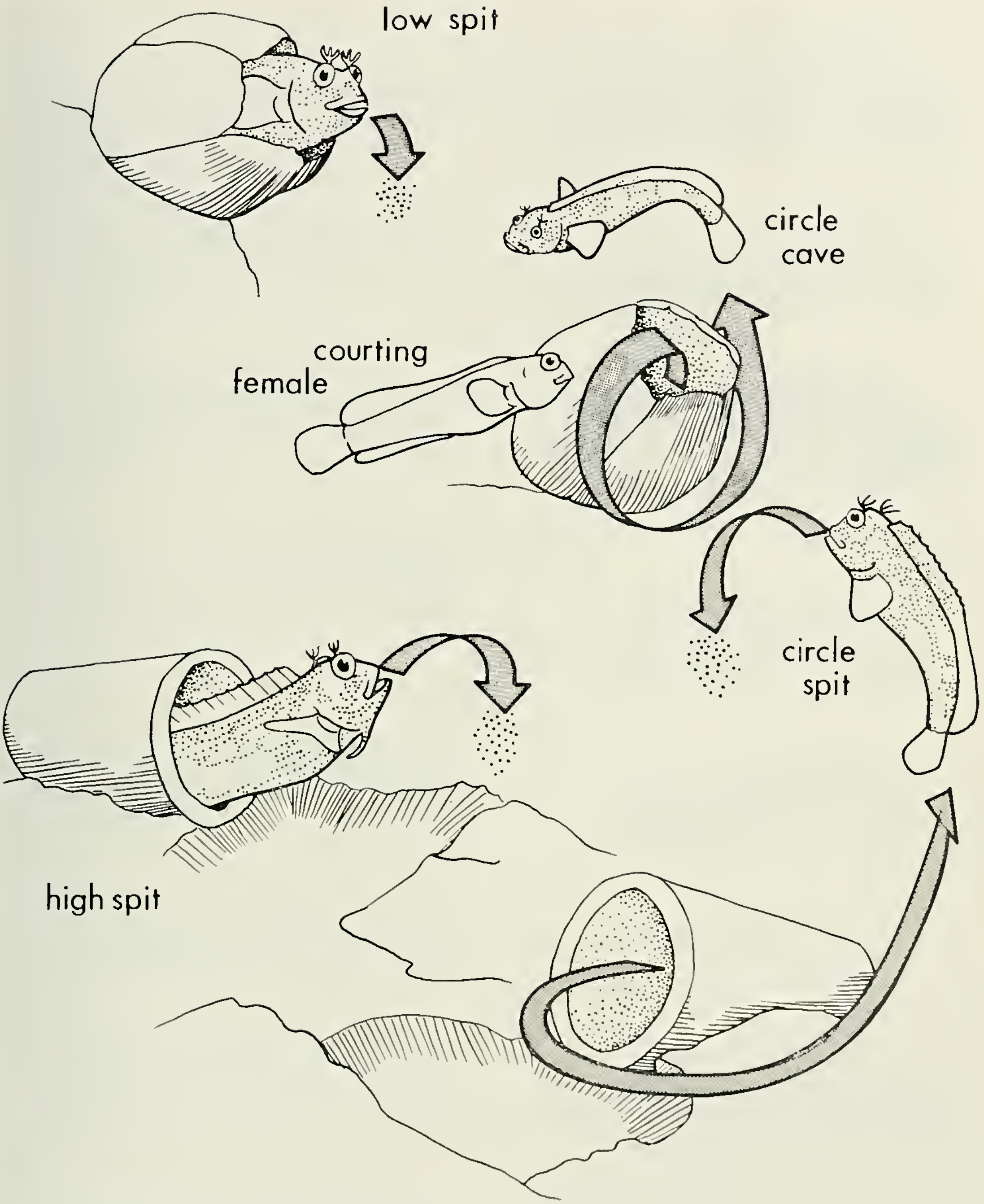

Figure 5. Some display movements of *Hypsoblennius* spp.

tremely high frequency and low amplitude. It occurs during courtship and throughout spawning; 3) Circle-cave; the male circles its refuge with jerky swimming movements. In some species, it is rare and of highly variable form while in others it is common during intense courtship and throughout spawning (Fig. 5); 4) Rearing, during the head-up display, the head is raised even further by swimming movements of the pectoral fins.

Female courtship I.—Approaching the male's refuge without agonistic display but not contacting or entering the refuge.

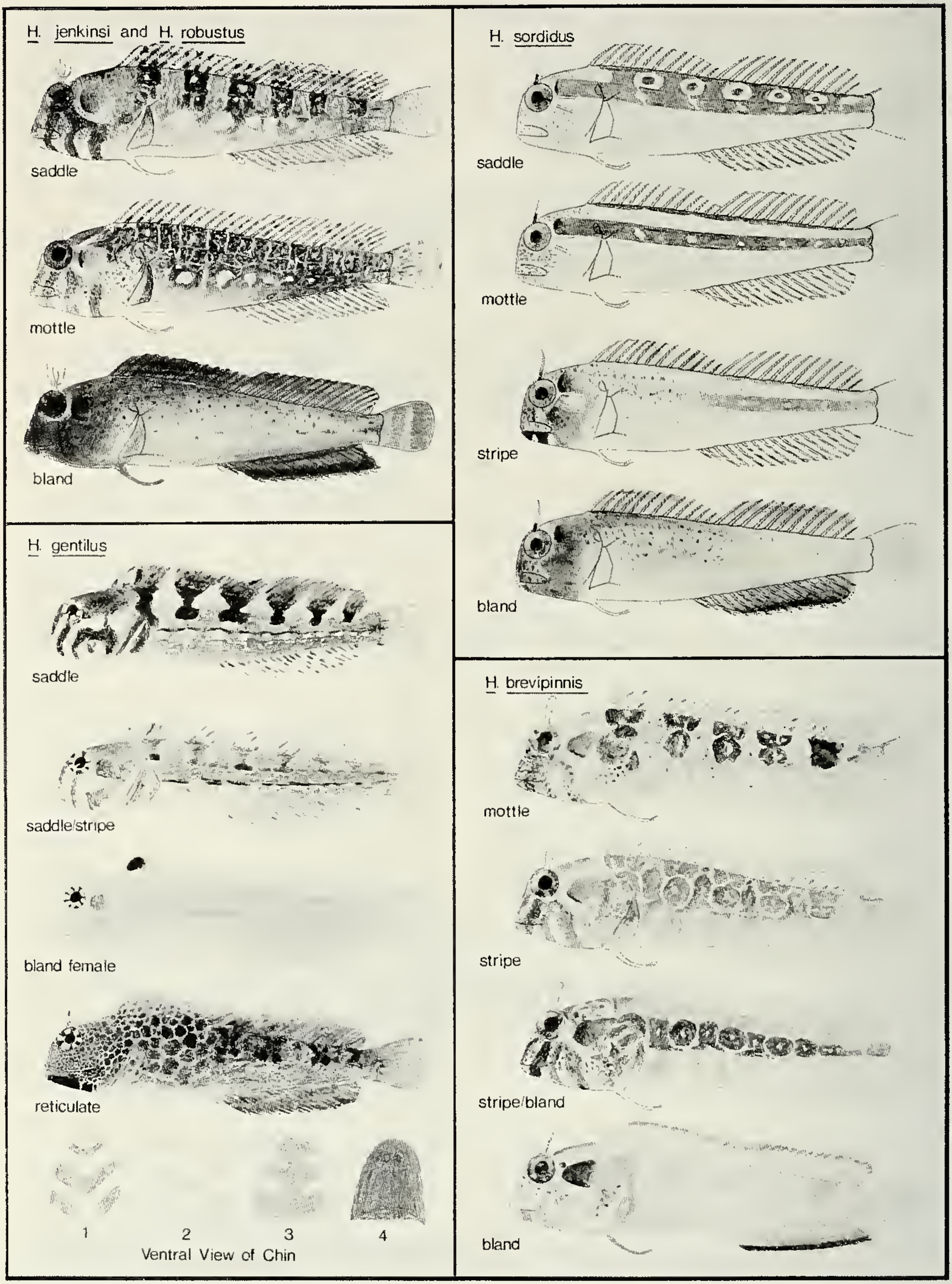

Figure 6. The major color patterns of *Hypsoblennius* species. The views of the chin of *H. gentilis* range from normal for all of the species (1.) to full reproductive ripeness (4.).

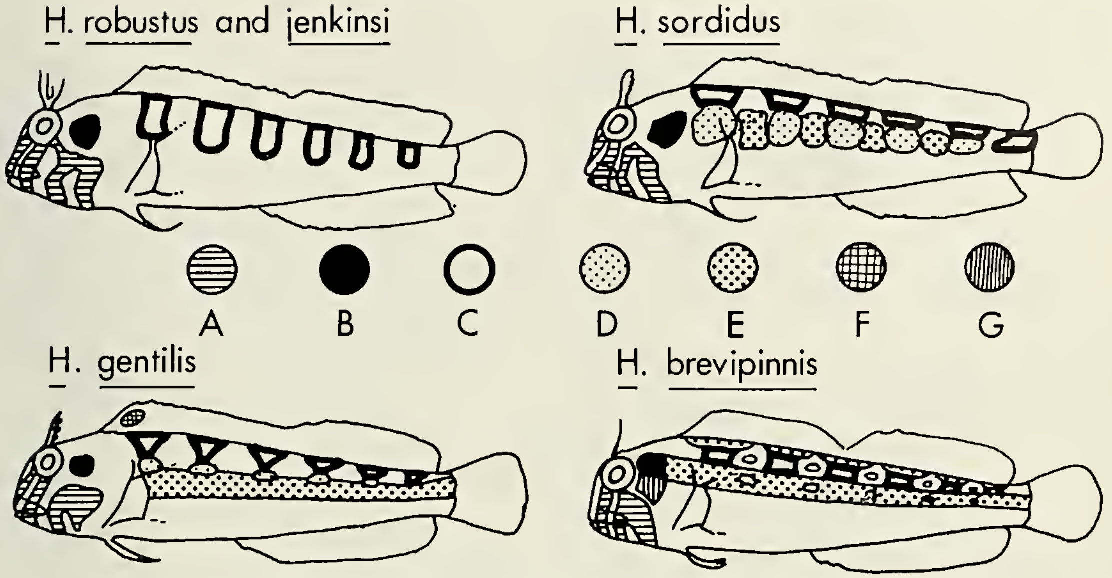

Figure 7. The major chromatophore areas for *Hypsoblennius* spp. Areas are defined by groups of melanophores that act more or less simultaneously to produce changes in pattern.

Female courtship II.—As above but contacting or entering the male's refuge (Fig. 5).

Male nesting behavior.—Behavior usually seen only in males: 1) Rub, rubbing the walls of the refuge with the anal fin pads; 2) Spit, taking gravel or detritus into the mouth and spitting it out. This display has a range of intensities (Fig. 5) and grades into: 3) Circle-spit, similar to spit except the male swims in a circle over the refuge before spitting (Fig. 5). This appears to be appetitive to courtship behavior and rarely if ever occurs when females are visible. It has not been observed in field observations.

Spawning.—The female deposits eggs on the refuge wall. The male may quiver, head-jerk, head-up and tail-up inside or outside of the refuge and/or remain inactive outside of the refuge. Sperm are deposited on the wall of the refuge during courtship that are sufficient for fertilization of the eggs.

COLORATION DESCRIPTIONS

The major color patterns and some intergrades are depicted in figure 6. Their method of formation can be compared between species by referring to fields of chromatophores that act as more or less separate units to produce various features of the coloration (Fig. 7).

Trunk pattern.—1) Saddle is a disruptive mottled coloration formed by darkening pigment areas C and D, if present. In *H. brevipinnis* adults, a true saddled coloration is never seen but the probable homology of these colorations is supported by saddle-shaped pigment areas found in prejuveniles. This is the "resting" color of all of the species except *H. brevipinnis*; 2) Mottle is a disruptive pattern seen in all species that lacks prominent saddles. This pattern was common in *H. brevipinnis*; 3) Bland is a homogeneous coloration that lacks mottling and is seen in all species: 4) Reticulate pattern extends over the head and is seen only in sexually ripe male *H. gentilis* and is acquired and lost only over a period of days: 5) Stripe is a mid-lateral darkening that lacks prominent saddles or mottling. It is the "resting" color of *H. brevipinnis* and is also prominent in *H. sordidus* when it is over a bland background. It is somewhat evident in *H. gentilis* in similar situations; 6) Darkness is a variable of all of these patterns which may range from a light tan to almost totally black; 7) Intergrades such as saddle/bland may be found in most species where only about half of the body is altered. In all species except *H. sordidus* the anterior saddles or stripe are the first to be replaced by bland or reticulate coloration. In *H. sordidus* the opposite is found: the posterior saddles and stripe are first to fade.

Head pattern.—Aside from general mottling, several special markings occur: 1) Chin bars are formed in all species by darkening pigment area A; 2) Red chin is found only in sexually ripe male *H. gentilis* in which the chin bars are slowly re-

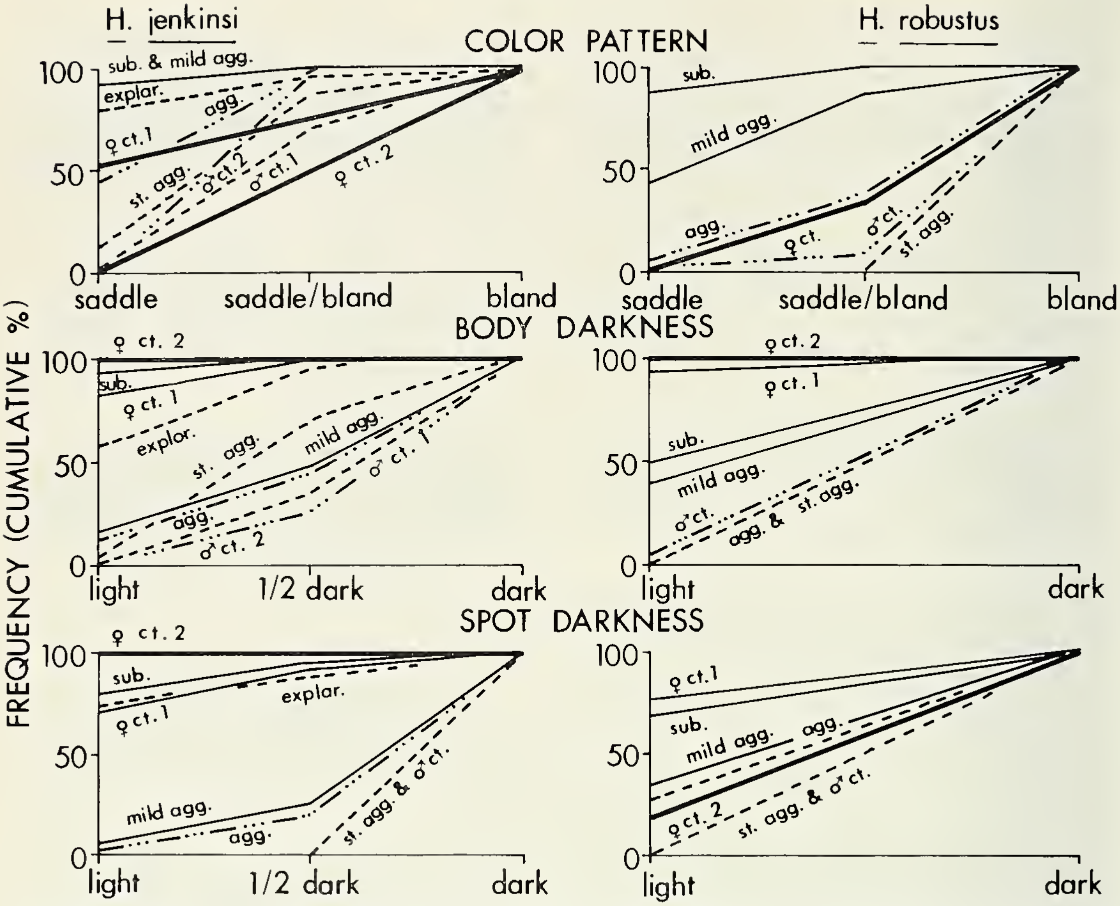

Figure 8. The occurrence of color patterns in various motivational states in *Hypsoblennius jenkinsi* and *H. robustus*. Abbreviations are: sub., submission; explor., exploration; mild agg., mild aggression; agg., aggression; st. agg., strong aggression; ♂ ct., male courtship; ♀ ct., female courtship. Due to an error in data collection, the half-dark category is lacking for *H. robustus*.

placed by a bright red to red/black field traversed by a few delicate silver streaks. This chin coloration appears and fades with the reticulate pattern; 3) Upper postorbital spot appears in all species by darkening pigment area B. It ranges from a shade that matches the rest of the head to an intense blue/black shade; 4) Lower postorbital spot appears only in *H. brevipinnis* in area F and ranges from a solid black to intense yellow outlined by paired black lines. Its color changes appeared to occur in less than one second. A hint of this spot occurs in *H. sordidus* but it is largely undifferentiated.

Fin pattern.—The fins generally track the trunk coloration and may be transparent in bland-light or stripe colorations. The dorsal spot is a small dark area in many species that does not show any differentiated function except in female *H. gentilis* in which it was large and ranged from white to a metallic blue/black.

ANALYSIS OF COLORATION

The frequency at which each element of the coloration occurred during the various categories of be-

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Figure 9. The occurrence of color patterns in various motivational states in *Hypsoblennius gentilis*. For abbreviations see figure 8.

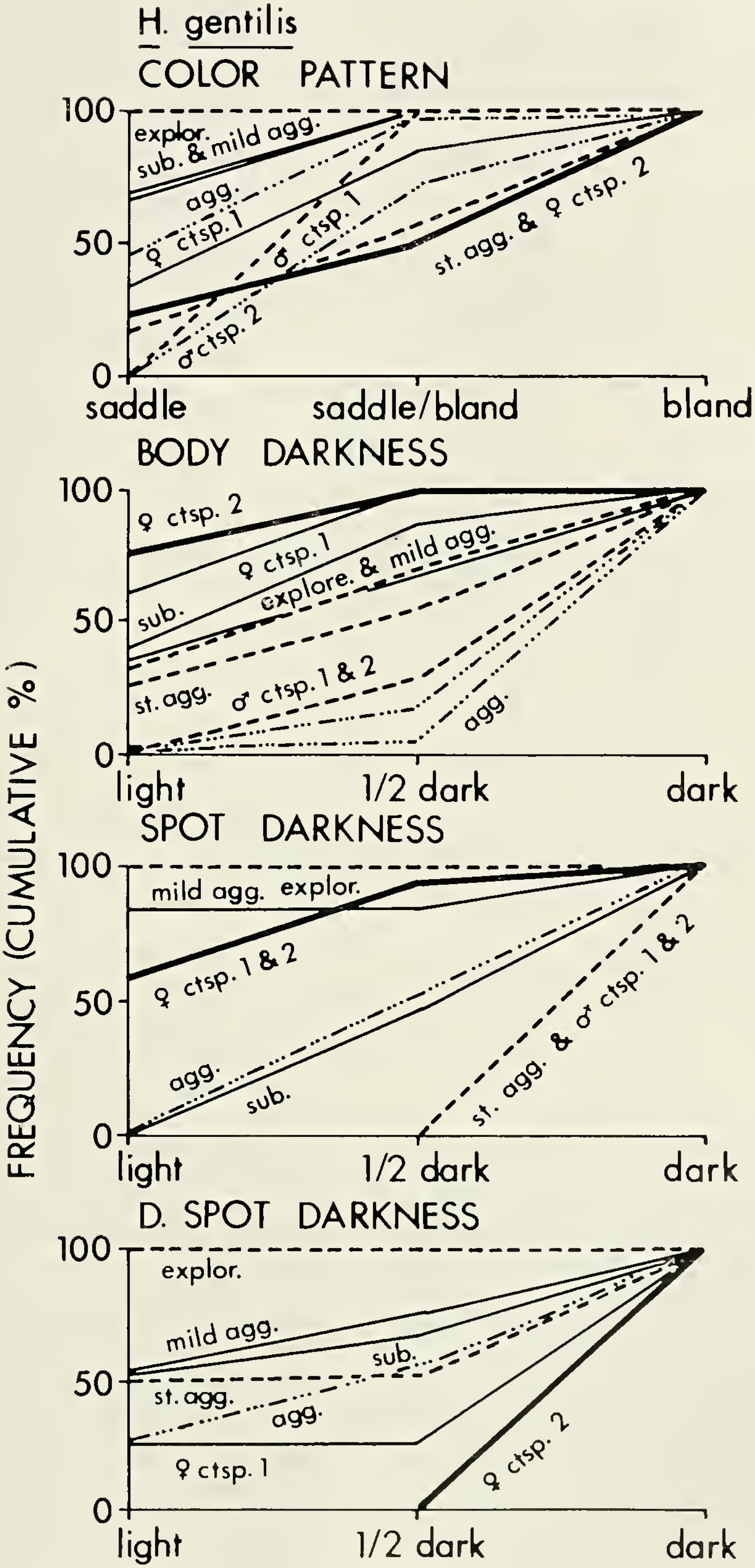
H. gentilis
COLOR PATTERN
100
50
0
explor.
sub. & mild agg.
agg.
♀ ctsp. 1
♂ ctsp. 1
♂ ctsp. 2
st. agg. & ♀ ctsp. 2
saddle
saddle/bland
bland
BODY DARKNESS
100
50
0
♀ ctsp. 2
♀ ctsp. 1
sub.
explore. & mild agg.
st. agg.
♂ ctsp. 1 & 2
agg.
light
1/2 dark
dark
SPOT DARKNESS
100
50
0
mild agg.
explor.
♀ ctsp. 1 & 2
agg.
sub.
st. agg. & ♂ ctsp. 1 & 2
light
1/2 dark
dark
D. SPOT DARKNESS
100
50
0
explor.
mild agg.
sub.
st. agg.
agg.
♀ ctsp. 1
♀ ctsp. 2
light
1/2 dark
dark
FREQUENCY (CUMULATIVE %)

TABLE 3. The relative probability of difference between the frequency distribution curves that describe the coloration in various motivational states (see Fig. 8). Due to multiple testing, the actual p level is 32 × p, so these probabilities should be used only to indicate the relative divergence of the curves. Probabilities calculated by the Kolmogorov-Smirnov method. Abbreviations are: submis. = submission, agg. = aggression, ctsp. = courtship. Bold face type indicates broader divergence.

HYPSOBLENNIUS JENKINSI

behavioral category	MOTIVATIONAL STATE OF ANIMAL					
	explore	submis.	mild agg.	agg.	strong agg.	ctsp. 1 ♂/♀
Probability of difference between frequency distributions of trunk color pattern						
submis.	0.2					
mild agg.	0.2	0.2				
agg.	0.2	**0.05**	0.1			
strong agg.	**0.02**	**0.01**	**0.01**	0.2		
ctsp. 1, ♂	**0.01**	**0.01**	**0.01**	0.2	0.2	
ctsp. 1, ♀	0.2	**0.02**	**0.02**	0.2	0.2	
ctsp. 2, ♂	**0.01**	**0.01**	**0.01**	0.2	0.2	0.2
ctsp. 2, ♀	**0.05**	**0.05**	**0.05**	0.2	0.2	0.2
Probability of difference between frequency distributions of body darkness						
submis.	0.2					
mild agg.	0.1	**0.01**				
agg.	**0.01**	**0.01**	0.2			
strong agg.	**0.01**	**0.01**	0.2	0.2		
ctsp. 1, ♂	**0.01**	**0.01**	0.2	0.2	0.2	
ctsp. 1, ♀	0.2	0.2	**0.01**	**0.01**	0.1	
ctsp. 2, ♂	**0.01**	**0.01**	0.2	0.2	0.2	0.2
ctsp. 2, ♀	0.2	0.2	**0.01**	**0.01**	**0.05**	0.2
Probability of difference between frequency distributions of darkness of postorbital spot						
submis.	0.2					
mild agg.	**0.01**	**0.01**				
agg.	**0.01**	**0.01**	0.2			
strong agg.	**0.01**	**0.01**	0.2	0.2		
ctsp. 1, ♂	**0.01**	**0.01**	0.2	0.2	0.2	
ctsp. 1, ♀	0.2	0.2	**0.01**	**0.01**	**0.01**	
ctsp. 2, ♂	**0.01**	**0.01**	0.2	0.2	0.2	0.2
ctsp. 2, ♀	0.2	0.2	**0.01**	**0.01**	**0.01**	0.2

havior was obviously nonrandom. In figures 8, 9, 10, and 11 the color patterns and common intergrades are arranged on the abscissa in order of decreasing crypticity, which was subjectively determined and coincides with the order in which coloration changes occurred. The cumulative percent of the occurrence of each pattern is plotted for each category of behavior. The probability of difference between curves is estimated by their degree of divergence (Tables 3–6). Examination of the figures indicates that coloration alone is sufficient to distinguish the following behavioral categories with a high degree of accuracy:

H. jenkinsi and *H. robustus.*—1) All aggression-all male courtship, dark saddle/bland trunk with dark upper postorbital spot; 2) Exploration-submission, light saddled trunk with light upper postorbital spot; 3) Female courtship, light saddle/bland to bland trunk with light postorbital spot.

H. gentilis.—1) All aggression-all male courtship, dark saddle/bland, bland or reticulate with saddle and bland intergrades and dark upper postorbital spot. Note that reticulate can only serve to indicate an increased probability of courtship since it is a long term reflection of gonadal ripeness; 2) Exploration-submission, as in *H. jenkinsi* but dorsal spot is dark.

H. sordidus.—Courtship was not observed but the following categories could be distinguished: 1) Exploration-submission-mild aggression, light

TABLE 4. The relative probability of difference between the frequency distribution curves that describe the coloration in various motivational states (Fig. 8). Due to multiple testing, the actual p level is 14 × p, so these probabilities should be used only to indicate the relative divergence of the curves. Abbreviations are as in Table 3.

HYPSOBLENNIUS ROBUSTUS

behavioral category	MOTIVATIONAL STATE OF ANIMAL			
	submis.	mild agg.	agg.	strong agg.
Probability of difference between frequency distributions of trunk color pattern				
submis.				
mild agg.	0.2			
agg.	**0.05**	0.2		
strong agg.	**0.01**	0.2	0.2	
ctsp. ♂	**0.01**	0.2	0.2	0.2
ctsp. ♀	**0.01**	0.2	0.2	0.2
Probability of difference between frequency distributions of body darkness				
mild agg.	0.2			
agg.	0.2	0.2		
strong agg.	0.2	0.2	0.2	
ctsp. ♂	0.2	0.2	0.2	0.2
ctsp. ♀	0.2	**0.05**	**0.01**	**0.01**

or dark stripe, mottle or more rarely saddle with a light upper postorbital spot; 2) Aggression-strong aggression, light saddle/bland or bland with dark postorbital spot. Note the reversal of the darkness of the trunk!

H. brevipinnis.—1) Exploration-submission, light mottle, mottle/stripe or stripe with light upper and lower postorbital spot; 2) Mild aggression, same as exploration except a darkened upper postorbital spot and light to dark trunk; 3) Aggression-strong aggression, dark stripe or stripe/bland with dark upper postorbital spot. The lower postorbital spot darkens only during intense aggression; 4) Male courtship, dark stripe/bland with both postorbital spots dark; 5) Female courtship, light mottle with postorbital spots dark.

Subjective examination of the families of cumulative percent curves indicates that *H. gentilis* has the least divergence between curves whereas *H. brevipinnis* has the most clear separation.

Some data are available for the response of male *H. robustus* to approaching females in different colorations. The scanty observations are not amenable to statistical analysis but examination of table 7 indicates its nonrandom nature. Males which had courted did not attack a female in courtship coloration with a light bland trunk and light postorbital spot. Note that a parental male may be nonreceptive to females if its refuge is full of eggs.

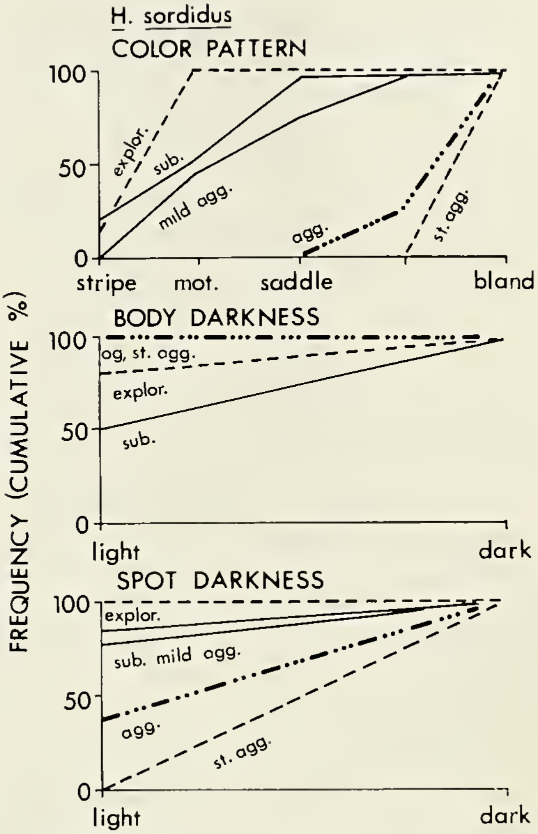

Figure 10. The occurrence of color patterns in various motivational states in *Hypsoblennius sordidus*. For abbreviations see figure 8.

DISCUSSION

Cryptic Colorations.—Species of *Hypsoblennius* show three types of coloration that appear to serve the function of crypticity: saddle, mottle and stripe. All of these colorations may be adopted by isolated fish and in nonsocial contexts but bland was only seen during social interactions. *Hypsoblennius jenkinsi* and *H. robustus* are nearly always found in saddle coloration and are restricted to disruptive habitats. *Hypsoblennius gentilis* and particularly *H. sordidus* show both saddle, stripe and mottle coloration. Saddle is usually seen when they are found over a disruptive background while mottle and stripe appear to be more common over barren backgrounds. These species have apparently analogous methods of forming the stripe

TABLE 5. The relative probability of difference between the frequency distribution curves that describe the coloration in various motivational states (see Fig. 9). Refer to Table 3 for explanation.

HYPSOBLENNIUS GENTILIS

behavioral category	MOTIVATIONAL STATE OF ANIMAL					
	explore	submis.	mild agg.	agg.	strong agg.	ctsp. 1 ♂/♀
			Probability of difference between frequency distributions of trunk color pattern			
submis.	0.2					
mild agg.	0.2	0.2				
agg.	**0.05**	0.2	0.2			
strong agg.	**0.01**	0.2	0.2	0.2		
ctsp. 1, ♂	**0.01**	**0.05**	**0.05**	0.2	0.2	
ctsp. 1, ♀	**0.01**	**0.05**	**0.05**	0.2	0.2	
ctsp. 2, ♂	**0.01**	0.1	0.1	0.2	0.2	0.2
ctsp. 2, ♀	**0.05**	0.2	0.2	0.2	0.2	0.2
			Probability of difference between frequency distributions of body darkness			
submis.	0.2					
mild agg.	0.2	0.2				
agg.	**0.02**	**0.02**	**0.02**			
strong agg.	0.2	0.2	0.2	0.2		
ctsp. 1, ♂	0.2	0.2	0.2	0.2	0.2	
ctsp. 1, ♀	0.1	0.2	0.2	**0.01**	0.2	
ctsp. 2, ♂	0.2	**0.02**	0.2	0.2	0.2	0.2
ctsp. 2, ♀	0.2	0.2	0.2	**0.05**	0.2	0.2
			Probability of difference between frequency distributions of dorsal spot darkness			
submis.	0.2					
mild agg.	0.2	0.2				
agg.	0.1	0.2	0.2			
strong agg.	0.2	0.2	0.2	0.2		
ctsp. 1, ♀	**0.05**	0.2	0.1	0.2	0.2	
ctsp. 2, ♀	**0.01**	0.2	0.1	0.2	0.2	0.2

pattern. *Hypsoblennius sordidus* includes the lower segment of each saddle in the stripe while in *H. gentilis,* the stripe is clearly separated from the pigment areas that form the saddles. Both species may be found in disruptive and barren habitats in the field. *Hypsoblennius brevipinnis* was only found in barren habitats and has stripe and, less commonly, mottle as its cryptic coloration. Only *H. brevipinnis* is found in the stripe or stripe/mottle coloration after death; all other species are saddled.

Stripe and mottle appear to function as cryptic colorations in barren habitats. They probably serve to reduce the number of light to dark interfaces that can serve as a clue of movement for visually hunting predators. Barlow (1972) has noted a correlation between body depth and coloration: He found that deep bodied fishes tended to be barred whereas long thin fishes displayed stripes. *Hypsoblennius* species, however, show both types of patterns in apparent response to their cryptic value in different habitat types.

Hypsoblennius brevipinnis appears to be additionally adapted to avoiding predation in its barren habitat through not showing displays that take it far from the substratum such as circle-spit and by showing vigorous but short duration agonistic interactions. Fighting in this species develops quickly with shorter periods of threat display (Losey, 1968).

Communication.—The pattern and darkness of the trunk and the darkness of special "signal spots" had nonrandom relationships to the behavioral state of the individual in all of the species studied. As such, they serve as an expression of the motivational status of the individual which may be perceived by other individuals. Three behavioral types are commonly discernable through patterns

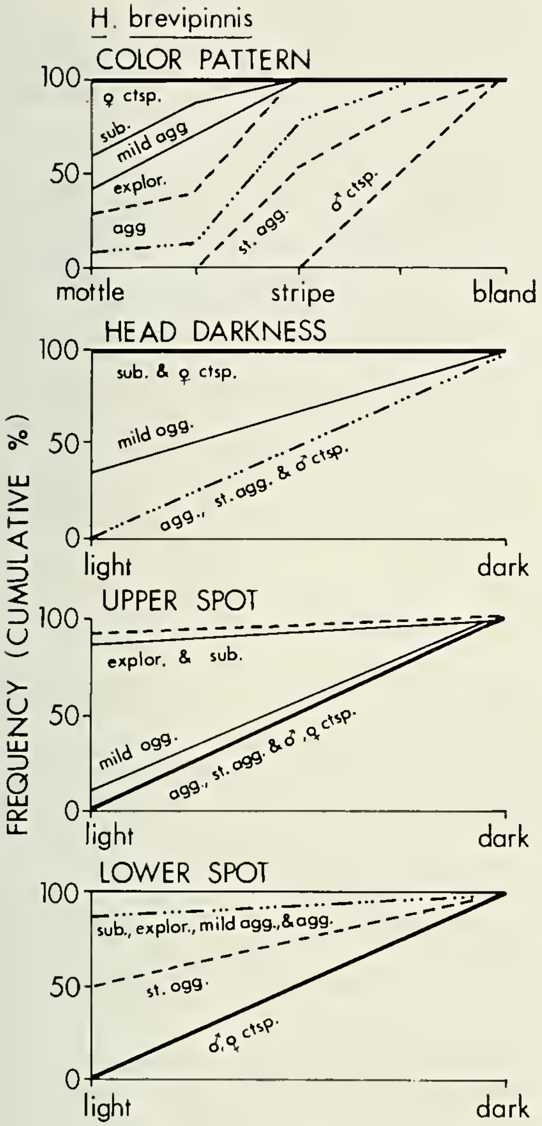

Figure 11. The occurrence of color patterns in various motivational states in *Hypsoblennius brevipinnis.* For abbreviations see figure 8.

TABLE 6. The relative probability of difference between the frequency distribution curves that describe the coloration in various motivational states (see Fig. 9). Refer to Table 3 for explanation.

HYPSOBLENNIUS BREVIPINNIS

	MOTIVATIONAL STATE OF ANIMAL				
behavioral category	explore	submis.	mild agg.	agg.	strong agg.
Probability of difference between frequency distributions of trunk color pattern					
submis.	0.2				
mild agg.	0.2	0.2			
agg.	0.2	**0.01**	**0.01**		
strong agg.	**0.01**	**0.01**	**0.01**	0.2	
ctsp., ♂	**0.01**	**0.01**	**0.01**	**0.01**	0.2
ctsp., ♀	0.2	0.2	0.2	**0.05**	**0.05**
Probability of difference between frequency distributions of head darkness					
mild agg.	0.2				
agg.	**0.05**	0.2			
strong agg.	**0.05**	0.2	0.2		
ctsp., ♂	**0.05**	0.2	0.2	0.2	
ctsp., ♀	insufficient data				
Probability of difference between frequency distributions of upper postorbital spot darkness					
submis.	0.2				
mild agg.	0.1	0.1			
agg.	**0.01**	**0.05**	0.2		
strong agg.	**0.01**	**0.05**	0.2	0.2	
ctsp., ♂	**0.01**	**0.05**	0.2	0.2	0.2
ctsp., ♀	insufficient data				
Probability of difference between frequency distributions of lower postorbital spot darkness					
submis.	0.2				
mild agg.	0.2	0.2			
agg.	0.2	0.2	0.2		
strong agg.	0.2	0.2	0.2	0.1	
ctsp., ♂	**0.01**	**0.01**	**0.01**	**0.01**	0.2
ctsp., ♀	insufficient data				

of coloration: 1) Submission and exploration, usually a light, cryptic coloration; 2) Aggression and male courtship, usually a dark, increasingly noncryptic coloration; 3) Female courtship, a light bland, and probably noncryptic pattern.

Hypsoblennius brevipinnis showed the greatest degree of divergence between the curves which describe the occurrence of coloration elements and thus the highest potential for communication. The larger number of behavioral categories that can be distinguished is partially due to the addition of the lower postorbital spot as a signal organ and my ability to distinguish more discrete types of trunk coloration and intergrades. This should enable *H. brevipinnis* to have a more efficient communication system and thus spend less time out of its refuge on the barren substratum settling territorial disputes and engaging in courtship.

It is also striking that the two pairs of sympatric species have divergent coloration codes whereas allopatric species from the same habitat have similar codes. *Hypsoblennius gentilis* shows limited sympatry with *H. jenkinsi* since they are usually found in different habitats. And yet the courtship colorations are radically different due

TABLE 7. The reaction of *H. robustus* males to an approaching female in various color patterns. The previous behavior of the male is categorized as to "parental" (guarding eggs), "quiver courtship" (having courted with *quivering*), "head-up courtship" (having courted with *head-up* but not *quiver*), and "no courtship." The response of the male to the female is categorized as to A = "attack" (*bite* or *chase*), N = no overt reaction, Q = *quiver*, M = "mate."

	FEMALE COLOR PATTERN						
BODY PATTERN	saddle		saddle/bland			bland	
BODY DARKNESS	dark	light	dark	light	dark	light	light
POSTORBITAL SPOT DARKNESS	[— — — — — — — — — — no data — — — — — — — — — — —]					dark	light
PREVIOUS MALE BEHAVIOR							
parental	—	—	—	—	—	AA	AAA
quiver courtship	N	—	—	—	—	AAA NNN QQ	N QQQQQ QQQQ MMM
head-up courtship	A	—	—	NN	N	AA NNN Q	N Q
no courtship	A	AA	A	—	—	A	A N

to the red chin and reticulate trunk of ripe male *H. gentilis* and the unique dorsal spot in courting females of this species.

Hypsoblennius robustus and *H. sordidus* show complete sympatry in Peru and have strikingly different coloration changes. Both have similar saddle patterns in this disruptive habitat but the posterior most saddle in *H. sordidus* can be darkened considerably. This saddle may or may not be darkened in preserved specimens (Victor G. Springer, pers. comm.). The possession of a stripe pattern in *H. sordidus* can probably be ascribed to its ability to occupy barren habitats. But the divergency between aggressive colorations is striking: *Hypsoblennius sordidus* lightens and loses its posterior saddles first while *H. robustus* darkens and loses its anterior saddles when becoming bland. It is frustrating that courtship was not seen in *H. sordidus* since this is a likely reason for the divergence. In all of the other species the coloration of male courtship is nearly the same as that for aggression. This suggests a link between the physiological mechanisms for producing this expression of sexual activity and that of aggression. Thus, if *H. sordidus* acquired a light courtship coloration due to selective pressure for reproductive isolation, the change in aggressive coloration might be a necessary result. It is doubtful that this change is a response to pressure for character displacement in order to reduce interspecific aggression. They show interspecific agonism that is very similar to intraspecific interactions despite having slightly different threat codes in terms of action patterns (Losey, 1968).

Hypsoblennius robustus and *H. jenkinsi* form a likely species pair. They probably speciated in allopatry after their ancestral species was split into two populations separated by a warm water barrier. They show little divergence in morphology, habitat, behavior or coloration.

Hypsoblennius brevipinnis shows highly divergent morphology and coloration. Krejsa (1960) placed this species and *H. proteus* in the genus *Blenniolus*. Three of the major characters that led to this separation were an additional pelvic ray, foreshortened body and unique coloration. Springer (1967, 1968) concluded that pelvic ray counts in this group are too variable to be used as a generic character. The foreshortened body and several related meristic counts are an obvious adaptation to living in a barren environment where the only available cover is empty barnacle tests. This study has shown that its coloration has also most probably arisen as a response to its unique habitat with similar coloration responses in *H. sordidus*. Its unique lower postorbital spot is a highly ritualized signal organ that obviously serves a communicative function. This again may be strongly favored due to the demands of its habitat for fast, efficient communication to avoid exposure to predation.

CONCLUSIONS

A study of the social behavior, habitat type and coloration of five species of *Hypsoblennius* revealed that: 1) Saddled and striped color patterns appear to be used as cryptic colorations in disruptive and barren habitats, respectively; 2) Species that inhabit both types of habitat display both types of color pattern; 3) Color pattern forms a potentially informative signal of the behavioral status of the individual in terms of agonistic and sexual tendencies; and 4) Sympatric species appear to have divergent courtship colorations.

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INFLUENCE OF TIDES AND WAVES ON THE SPAWNING BEHAVIOR OF THE GULF OF CALIFORNIA GRUNION, *LEURESTHES SARDINA* (JENKINS AND EVERMANN)

Donald A. Thomson[1] and Kevin A. Muench[2]

Abstract: A preliminary analysis of 53 spawning runs of the Gulf grunion, *Leuresthes sardina* (Jenkins and Evermann) from 1968 to 1973 in the northern Gulf of California suggests that the initiation of a spawning run is strongly dependent on tidal amplitude. Gulf grunion runs occur fortnightly from January to May following a descending series of higher high tides after the new and full moon phases. The runs begin about 3.5 days after the time of full moon and about four days after the new moon. The daytime runs of *L. sardina* result from a mid-season shift in the time of the higher high spring tides from early morning (0300 to 0500) to late afternoon (1500 to 1700).

The accelerated spawning act of the Gulf grunion appears to be an adaptation to the short period, low amplitude sea waves typical of the protected coasts of the upper Gulf of California rather than increased daytime predation of spawning fish by sea birds.

Carl L. Hubbs was the first to publish an account of grunion spawning behavior when he reported a fairly accurate description by J. P. Joplin from a letter to David Starr Jordan (Hubbs, 1916). Much later, one of Hubbs' graduate students (Walker, 1949) did the most thorough analysis of the spawning periodicity of the California grunion, *Leuresthes tenuis* (Ayres). As a tribute to Carl Hubbs' longtime interest in the grunion, this paper reports a preliminary analysis of the effect of tides and waves on the spawning behavior and periodicity of another species of grunion, the Gulf of California grunion, *Leuresthes sardina* (Jenkins and Evermann).

The only two species of grunion in the world ocean, *L. tenuis* and *L. sardina*, are geographically isolated and morphologically distinct (Moffatt, 1974; Moffatt and Thomson, 1975). Both species exhibit the unique behavior of spawning out of water, depositing their eggs under the sand of beaches following a high tide. Their spawning runs are highly predictable and coincide with the new and full moon phases which cause the fortnightly series of spring tides. The timing of the runs of both species following a moon phase is similar but the California grunion is known to spawn only at night whereas the Gulf grunion spawns in the daytime as well as at night.

Spawning runs of *L. tenuis* were believed by

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earlier workers to be controlled by tides (Thompson, 1919; Clark, 1925). After analyzing numerous grunion runs, Walker (1949) hypothesized that the timing of runs is set by the initiation of sex product maturation at the second preceding moon phase 17.9 days from the mid-point of a run series. Walker's thorough study, although never published in its entirety, led to successful predictions of California grunion runs (Walker, 1952). Since these studies, nothing has been published on the periodicity of grunion runs. Our studies on the Gulf of California grunion, *L. sardina*, began in 1968. We have attempted to elucidate some of the factors influencing the periodicity of grunion runs by comparing runs of another species in a different tidal and wave regime.

METHODS

From 1968 to 1973, *L. sardina* runs were observed along the beaches of El Golfo de Santa Clara, Sonora, Mexico, in the northern Gulf of California. Data on 53 runs were compiled and timing of each run was compared with the moon phase and the time and height of the tides before, during and after each run. [These data may be obtained from the senior author upon request]. In many instances, observers watched for runs prior to and after a predicted run series to determine the number and intensity of runs in a series. All runs in a series were used in the calculations of mean values. Since tide information was unavailable for the El Golfo de Santa Clara region, runs were compared with tide predictions for Puerto Peñasco, Sonora (Thomson, 1968–73). Observations show that the Puerto Peñasco tides are approximately synchronous with those of El Golfo although slightly less in amplitude.

Spawning behavior of Gulf grunion during night and day runs was observed, filmed with 16 mm and Super-8 mm cameras and compared with that of the California grunion. The duration of the spawning act and the period of sea waves washing on the beach were timed with stopwatches.

TIDES AND GRUNION RUNS

Spawning runs of Gulf grunion occur from January through May, whereas California grunion runs usually begin in early March and end in August. Fortnightly Gulf grunion runs occur consistently on the beaches in the vicinity of San Felipe, Baja California Norte and El Golfo de Santa Clara, Sonora, Mexico, in the northern Gulf of California. Spawning runs are also known to occur on several suitable beaches south along both coasts of the upper Gulf to Bahia Concepcion, Baja California Sur and Guaymas, Sonora. However, such runs are sporadic and do not consistently occur following each new and full moon phase. The occurrence of California grunion runs are likewise less predictable in the northern and southern margins of their range.

Figure 1. Night spawning of the Gulf grunion (*Leuresthes sardina*) on the beach of El Golfo de Santa Clara, Sonora, Mexico. Erect female in foreground is attended by five males. (Photo by D. A. Thomson.)

The most striking difference between the spawning runs of the two species of grunion is the daytime run of the Gulf grunion. However, the reason for this anomaly became clearer when the pattern of spring tides during a grunion breeding season was examined. The tides of the northern Gulf of California are of the mixed semidiurnal type. The higher high water occurs during early morning (0300–0500) in January and February which is the beginning of the Gulf grunion spawning season. Only night runs occur early in the season, closely following the early morning high tide. During mid-season there is a shift in tidal amplitude so that the two daily high tides are about equal. Daytime runs begin when the afternoon high tide approaches the height of the night high tide. When the afternoon high tide exceeds the early morning high tide only daytime runs occur. After comparing grunion runs with tide heights it appeared that *L. sardina* was timing its run with the higher high tide, regardless of when this tide occurred. During the transition of the higher high

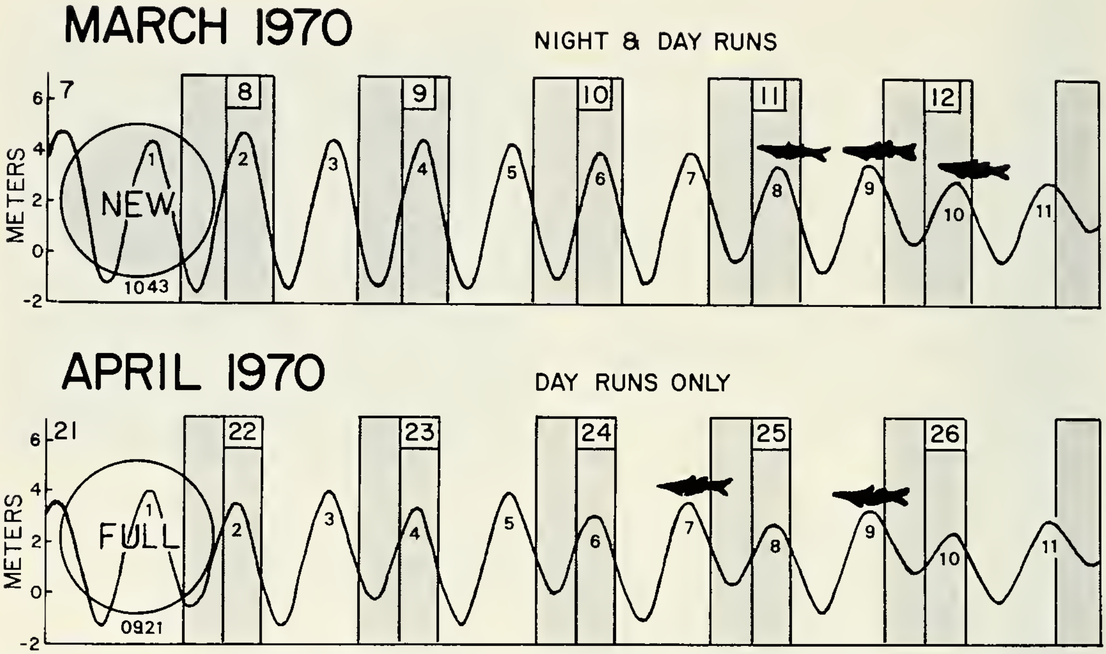

Figure 2. Gulf grunion runs at El Golfo showing transition of higher high tide to daytime and beginning of daytime runs. Shaded area denotes darkness; clear areas denote daylight; numbers under tide curves mark the number of high tides after each moon phase. Tide curves are those predicted for Puerto Peñasco, Sonora.

tide from night to day, runs were often observed on successive high tides (Fig. 2). These successive night and day runs occurred when the height difference between consecutive high tides was less than 0.5 m, indicating that the grunion were "comparing" the height of each high tide during a run series.

Walker's (1949) scheme of relating the timing of runs to the moon phases involved predicting runs beginning 2.5 days after a new moon and 4 days after a full moon. This permits a 17.9 day egg maturation period since it correlates with the short and long intervals between new and full moon (14 days) and full and new moon (15.5 days). The relationship of Gulf grunion runs to the moon phases is nearly opposite to that predicted by Walker for California grunion. After a full moon Gulf grunion runs start and reach their peak earlier than runs following a new moon. Full moon runs usually begin 2.5 days to 3.5 days after the moon phase and new moon runs begin 3.5 to 4.5 days after the moon phase. The mean difference in days between new and full moon runs is about half a day or one high tide. Although this difference is slight, it is highly consistent and statistically significant ($P < 0.001$; see Table 1). Does such a run sequence permit a uniform egg maturation period to be set by the second preceding moon phase? *L. sardina*'s runs show a mean 19.5 day interval after a full moon and 17.5 day interval after a new moon. However, the mid-point of a Gulf grunion run series occurs at about 18.5 days after either moon phase, ranging from 17.4 to 19.8 days after the new and full moon. This duration closely agrees with Walker's (1949, 1952) egg maturation period of 17.9 days for California grunion, based upon the mid-point of spawning runs.

The timing of the Gulf grunion's runs seems to be related to tide height rather than to moon phase *per se*. During our period of observation of Gulf grunion runs (January to May, 1968 to 1973) new moon tides were significantly higher than full moon tides. If grunion are selecting a tide height new moon runs might be expected to occur later after the moon phase than full moon runs. Mean tide heights at the start and end of new and full moon grunion runs were quite similar, differing only by 0.21 and 0.11 m respectively (Table 1). Comparison of tide heights between night and day runs showed no significant differences and provided even better agreement betwen the means of these tide level parameters (Table 2).

Therefore, it appears that the stimulus for initiating a grunion run is a descending high tide of the proper tidal amplitude. Runs occurred at

TABLE 1. Comparison of Gulf grunion runs following moon phases. Values include the mean ($\bar{x}$) ± one standard deviation (s). N = total number of observations. P = probability from Student's *t* test.

	NEW MOON			FULL MOON			
	N	$\bar{x}$	s	N	$\bar{x}$	s	P
HHW max. after moon phase (1970–73)*	20	5.34 m (17.52 ft)	0.28 m (0.92 ft)	20	4.86 m (15.94 ft)	0.19 m (0.62 ft)	$<.001$
No. of high tides after moon phase at start of each run	27	8.15	1.43	26	6.92	1.29	$<.01>.001$
Days after moon phase to high tide preceding each run	27	4.06	0.70	26	3.36	0.64	$<.001$
Ht. of high tide preceding each run	27	3.67 m (12.05 ft)	0.53 m (1.74 ft)	26	3.95 m (12.95 ft)	0.27 m (0.90 ft)	$<.05>.02$
Ht. of tide at start of each run	22	3.56 m (11.68 ft)	0.56 m (1.85 ft)	20	3.77 m (12.36 ft)	0.25 m (0.81 ft)	$<.1>.05$
Ht. of tide at end of each run	21	2.86 m (9.38 ft)	0.37 m (1.23 ft)	17	2.97 m (9.74 ft)	0.45 m (1.46 ft)	$<.5>.4$
Duration of run (min)	19	82.05 (1 hr 22.1 min)	33.76	17	77.41 (1 hr 17.4 min)	33.60	$<.7>.6$

* Maximum high tide heights from Estación Puerto Peñasco in Tablas de Predicción de Mareas 1970 to 1973, Apendice 1, Part B, de los Ánales del Instituto de Geofisica, U.N.A.M. Vols. 15, 16, 17, and 18. Other tide heights taken from tide curves for Puerto Peñasco (Thomson, 1968–1973).

extreme tide heights of + 4.4 to + 2.2 m, but much more frequently at heights between + 4 and + 3.4 m. These data along with the switch from night to day runs corresponding with the shift in the amplitude of the tides strongly suggest that *L. sardina* is responding to tides directly rather than the moon phase. This does not preclude the possibility that egg and sperm maturation may have a lunar rhythm, but it emphasizes that ripe grunion consistently select a proper tide level for their spawning runs.

WAVES AND SPAWNING BEHAVIOR

The spawning behavior of *L. sardina* is very similar to that of *L. tenuis* but with one important exception. The duration of the spawning act (digging in by the female, wrapping around the female's body

TABLE 2. Comparison of day and night Gulf grunion runs. Values include the mean ($\bar{x}$) ± one standard deviation (s). N = total number of grunion spawning runs observed. P = probability from Student's *t* test.

	NIGHT			DAY			
	N	$\bar{x}$	s	N	$\bar{x}$	s	P
Days after moon phase to high tide preceding each run	28	3.67	0.88	25	3.78	0.58	$<.7>.6$
Ht. of high tide* preceding each run	28	3.79 m (12.45 ft)	0.54 m (1.78 ft)	25	3.82 m (12.54 ft)	0.31 m (1.00 ft)	$<.9>.8$
Ht. of tide at start of each run	20	3.73 m (12.23 ft)	0.59 m (1.95 ft)	21	3.61 m (11.83 ft)	0.26 m (0.84 ft)	$<.4>.3$
Ht. of tide at end of each run	20	3.10 m (10.18 ft)	0.72 m (2.35 ft)	18	2.86 m (9.39 ft)	0.34 m (1.11 ft)	$<.3>.2$
Duration of run (min)	21	82.52 (1 hr 22.5 min)	34.11	17	79.65 (1 hr 19.7 min)	32.83	$<.8>.7$

* All tide heights taken from predicted tide curves for Puerto Peñasco (Thomson, 1968–73).

by the male(s), extrusion of eggs and exit of female) proceeds much more rapidly in *L. sardina.* The spawning act may last about 30 seconds in *L. tenuis* but only 3–7 seconds in *L. sardina.* The most obvious suggestion is that the faster spawning rate of *L. sardina* is an adaptation to daytime runs whereby the grunion is exposed to avian predators. Numerous observations of sea bird activity during daytime grunion runs indicate that most predation of birds on grunion occurs while the schools are moving in toward the beach. The brown pelican (*Pelicanus occidentalis*) a cormorant (*Phalacrocorax* sp.) and several species of sea gulls (*Larus delawarensis, L. atricilla, L. californicus, L. heermanni,* and *L. occidentalis*) have been observed feeding on adult grunion close to shore. Pelicans and cormorants feed on the grunion only when the schools aggregate and swim close to shore preceding a run. The sea gulls pick grunion out of the surf and from the beach. However, sea gulls feed most actively at the beginning of a run when the fish on the beach are mostly scouts (males). By the time the run reaches its peak and spawning is most intense very little predation by sea gulls is observed. The birds become satiated with grunion well before the peak of the run and predation on spawning grunion is minimal. After a run the egg pods are sought by sanderlings (*Crocethia alba*) and western sandpipers (*Ereunetes mauri*) and some egg predation occurs. However, it seems unlikely that the accelerated spawning is primarily a defense adaptation against avian predators.

An alternate hypothesis is that the spawning rate is related to the waves carrying the fish up on the beaches. The surf of the Pacific coast usually has a longer period than the sea waves of the protected northern Gulf of California. Gayman (1969) reported that sea breeze waves in the northern Gulf in the vicinities of San Felipe and El Golfo generally have periods of 2–4 seconds. The periods of waves timed with a stopwatch during Gulf grunion runs ranged from 2.9 to 4 seconds. Gulf grunion are not carried up as high on the beach by such waves as is typical of California grunion which ride the surf which strands them at a considerable distance from the water line. Gulf grunion, when interrupted by waves, completed spawning within a maximum of 7 seconds but usually in 3–4 seconds. It was noted that storm waves would sometimes prevent a run altogether when a run was expected. Therefore, it appears that the rapid spawning act of *L. sardina* is at least partially an adaptation to the short period, low amplitude waves of the Gulf of California.

DISCUSSION AND CONCLUSIONS

The switch from nighttime to daytime spawning corresponds with the shift in the higher high tide from night to day. This finding suggests that Gulf grunion spawning runs are strongly influenced by tidal amplitude. Such a shift in the daily higher high tide does not occur on the Pacific coast. Consequently, the California grunion spawns only at night following the consistent Pacific coast pattern of the higher high tide occurring only at night during the spawning season. Comparison of the heights of the high tide preceding all runs and the heights of the tide at the beginning, mid-point and end of a run showed no statistical difference between tide heights of night, day, new and full moon spawning runs. However, it is not known how the Gulf grunion is able to judge the proper tidal height as the schools approach the beach.

The striking difference in spawning behavior between *L. sardina* and *L. tenuis* probably did not evolve because of increased predation pressure on daytime spawning grunion. We feel that it is more likely that the accelerated spawning of *L. sardina* is a response to the short period waves typical of the northern Gulf of California beaches (there is no difference in the duration of the spawning act between daytime and nighttime runs). Unless the eggs are fertilized and deposited in the sand very quickly (within a few seconds) the spawning act is apt to be interrupted by an oncoming wave and any eggs laid would likely be washed out as well. These short period, low amplitude waves do not carry the grunion as far up on the beach as does the longer period surf along the unprotected Pacific coast, so spawning Gulf grunion are usually in the wave wash zone not far from the surf.

Thus, the spawning behavior of the Gulf grunion appears to be well adapted for tidal and sea wave regimes of the upper Gulf of California.

ACKNOWLEDGMENTS

We thank the numerous people who assisted us in various ways during grunion spawning runs, especially Chuck Constant and Ernie Kehl. We thank Boyd Walker for accompanying us on two Gulf grunion runs and appreciate his comments on comparisons between the two species. We also thank Stephen Russell for his identifications of sea birds. Charles Lehner, Elaine Snyder and Nancy Moffatt read the manuscript and made useful suggestions. Logistics for beginning phases of this study were supported by ONR grant NR104-897.

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A CONTRIBUTION TO THE LIFE HISTORY OF A SMALL RATTAIL FISH, *CORYPHAENOIDES CARAPINUS*

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Abstract: The North Atlantic macrourid *Coryphaenoides* (*Lionurus*) *carapinus* lives between about 1200 and 2800 m off southern New England, with greatest abundance of about 2.4 individuals/1000 m^2 in the transition zone from slope to rise. Larger individuals, mostly female, tend to live at greater depths. Winter spawning is indicated, with 50,000 to 220,000 0.5-mm eggs being produced per female. Eighty-four of 108 stomachs examined contained food. Benthic invertebrates were most important in the diet, and there was little change in food with growth. The fish feeds selectively on the ophiuroid *Ophiura ljungmani*. The subgenera *Nematonurus*, *Chalinura*, and *Lionurus* of *Coryphaenoides* seem to occupy overlapping yet distinct adaptive zones, with different prey and foraging area important considerations.

Despite the abundance and diversity of rattail fishes in the deep ocean, remarkably little is known concerning the natural history of any species, a point emphasized by Marshall (1965) in a general review of the biology of the group. Recent interest and advances in deep benthic trawling have begun to provide the material necessary for such work (e.g., Podrazhanskaya, 1967; Pechenik and Troyanovski, 1970; Okamura, 1970; Novikov, 1970; Geistdorfer, 1972, 1973; Pearcy and Ambler, 1974). Concerning the subgenus *Lionurus* of the speciose and important genus *Coryphaenoides*, the few published accounts are restricted almost entirely to distributional records. As a part of our continuing studies of the ecology of deep ocean

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communities, we report here observations on the natural history of the North Atlantic *Coryphaenoides* (*Lionurus*) *carapinus* Goode and Bean 1883. This small abyssal species occurs on the lower continental slope and continental rise at depths between about 1000 and 3000 m (Koefoed, 1927; Schroeder, 1940; Marshall and Iwamoto, 1973). It is found on both sides of the North Atlantic Ocean from the equator to about 50°N. Deep trawls in the Mediterranean (Geistdorfer and Rannou, 1972) have not taken the species. Off southern New England it is found in greatest abundance in the transition zone from slope to rise in depths near 1800–2400 m, and is numerically a dominant member of the benthic fish fauna there.

METHODS

Specimens of *Coryphaenoides carapinus* were taken in trawl collections made as a part of general studies of the distribution and ecology of the deep benthic fauna south of New England. Our primary collecting gear in deep water has been 41-ft (12.5-m) Gulf of Mexico shrimp trawls (1-inch (2.5-cm) mesh), originally fished with ordinary wooden doors but more recently with steel V-doors. A few earlier tows were made with a smaller, 16-ft (4.8-m) semiballoon trawl (Haedrich, Rowe, and Polloni, 1975). Bridles of 60 to 70 ft (18 to 20 m) led to a single towing warp. Estimated time on the bottom was approximate, from the time the winch stopped paying out to the time haulback was begun. Nets were towed at approximately 2 kn, at which speed their effective horizontal opening is some 8 m (Bullis and Cummins, 1963). Material from the trawls was preserved in 10 percent buffered formalin at sea, and was later transferred in the laboratory to 70 percent ethanol. Lengths (total and snout (Sn) to anal fin (A)) and weights were measured from whole specimens; gonads and stomachs were then removed for individual examination. Station data for collections which took *C. carapinus* are given in table 1. We have sampled in February, March, June, July, August, October, and November.

To obtain material for comparison with stomach contents, the benthic infauna was sampled from DSRV *Alvin* with an especially modified Birge-Ekman Box Corer (Rowe and Clifford, 1973) covering an area of 225 cm^2. Each sample was sieved through a 0.42 mm screen, and the material retained was preserved in 10 percent buffered formalin for final sorting and identification in the laboratory.

RESULTS

Distribution.—Coryphaenoides carapinus ranges between about 1200 and 2800 m off southern New England (Table 1, Fig. 1). The species was present in 25 (60 percent) of 42 trawls between 1270 and 2740 m and in all trawls between 1947 and 2400 m. Thirty trawls between 400 and 1100 m and nine trawls between 3000 and 3800 m took no *C. carapinus*. Observations made over measured transects from DSRV *Alvin* indicate a density of about 2.4 small individuals per 1000 m^2 (and hence 37.9 gm/1000 m^2) in the depth interval 1768–1960 m, and a density of 0.9 larger individuals (and 40.1 gm/1000 m^2) in the interval 2066–2474 m.

Larger specimens of *Coryphaenoides carapinus* are found deeper within the depth range for the species. The regression of size on depth-of-capture plotted through the points of the scattergram in figure 2 has a positive slope significantly different from 0. For data aggregated by trawl, the correlations between mean size and depth are quite respectable (for length, Sn to A, $r = 0.84$; for weight, $r = 0.81$).

Size and reproduction.—Coryphaenoides carapinus is a relatively small rattail; the largest specimen we have seen was a female 390 mm in total length and 185 gm in weight. It is very common in this species for a considerable portion of the long, thin tail to be missing. This loss cannot be laid entirely to net damage, for obvious partial regeneration, particularly of finrays, is often apparent. Since the tail is usually gone, we have used the distance from the snout to the beginning of the anal fin (Sn to A) as our length measurement. This distance is roughly 30 percent of the total length, and hence (Marshall and Iwamoto, 1973) approximately twice the head length. Figure 3 presents the length-weight relationship of all specimens examined. There was no significant difference between males and females.

Figure 3 also shows length frequencies for all specimens examined, with the fraction of immatures, males, and females indicated. No pronounced peaks, which would result from year-classes, are apparent. Females become mature at a length of about 70 mm, and grow to a larger size than the males. The eggs are rather small (maximum about 0.5 mm in diameter) and range in number from about 50,000 to 220,000 (volumetrically determined) per female. There was a weak positive correlation between egg number and weight of the fish, but little correlation between egg number and length. Figure 4 shows

TABLE 1. Station data associated with collections which took *Coryphaenoides carapinus*, including number and weight of specimens and average weight. Arranged in order of increasing depth. Times are presumed time on the bottom. SBT = semiballoon trawl; GMT = Gulf of Mexico shrimp trawl; BT = beam trawl.

Station Number	Ship	Cruise Number	Latitude	Longitude	Date	Time of Tow		Depth (m)			Gear	No. of Individuals	Total weight gm (in ETOH)	Average weight $\bar{x}$ gm/specimen (in ETOH)
						Start	End	Minimum	Maximum	Mean				
223	CHAIN	111	39°25′N	72°07′W	2/26/73	1238	1329	1250	1300	1275	16′ SBT	3	12	4
7	CHAIN	88	39°09′N	72°11′W	3/6/69	1030	1130	1280	1280	1280	40′ GMT	49	400	8
308	KNORR	35	39°24′N	72°07′W	11/14/73	1050	1150	1352	1417	1384	16′ SBT	1	2	2
311	KNORR	35	39°19′N	72°00′W	11/15/73	0015	0122	1554	1590	1572	16′ SBT	3	45	15
331	KNORR	35	39°45′N	71°07′W	11/19/73	1040	1125	1572	1645	1609	40′ GMT	16	354	22
330	KNORR	35	39°43′N	71°12′W	11/19/73	1634	1734	1645	1737	1691	40′ GMT	2	33	17
216	CHAIN	111	39°17′N	71°59′W	2/25/73	1335	1435	1500	1960	1730	40′ GMT	10	66	7
307	KNORR	35	39°19′N	72°02′W	11/14/73	0528	0625	1627	1965	1796	16′ SBT	3	24	8
511	CHAIN	124	39°44′N	70°29′W	7/8/75	0817	0930	1830	1912	1871	41′ GMT	35	717	20
201	CHAIN	110	39°45′N	70°47′W	2/1/73	2015	2105	1820	1960	1890	40′ GMT	21	339	16
521	CHAIN	124	39°45′N	70°43′W	7/10/75	0515	0615	1885	1967	1926	41′ GMT	45	880	19
325	KNORR	35	39°13′N	71°53′W	11/18/73	0850	0950	1919	1974	1947	40′ GMT	2	31	16
431	ATLANTIS II	86	38°39′N	70°25′W	3/19/70	0428	0558	2080	2155	2116	41′ GMT	8	100	13
312	KNORR	35	39°12′N	71°49′W	11/15/73	0505	0605	2081	2148	2116	16′ SBT	8	214	27
326	KNORR	35	39°12′N	71°47′W	11/18/73	1525	1625	2288	2297	2293	40′ GMT	21	338	16
429	ATLANTIS II	86	39°35′N	70°31′W	3/18/75	1935	2100	2290	2300	2295	41′ GMT	1	~65	~65
510	CHAIN	124	39°33′N	70°10′W	7/7/75	0044	0144	2306	2315	2311	41′ GMT	16	1046	65
522	CHAIN	124	39°33′N	70°44′W	7/10/75	1155	1255	2379	2416	2397	41′ GMT	21	1405	67
432	ATLANTIS II	86	39°31′N	70°20′W	3/19/75	1115	1250	2350	2450	2400	41′ GMT	3	175	58
313	KNORR	35	39°10′N	71°35′W	11/15/73	1133	1240	2468	2495	2481	40′ GMT	9	404	45
327	KNORR	35	39°20′N	71°18′W	11/19/73	0000	0110	2504	2504	2504	40′ GMT	3	341	113
424	ATLANTIS II	86	39°27′N	70°28′W	3/17/75	1330	1530	2505	2530	2518	41′ GMT	8	~480	~60
314	KNORR	35	39°09′N	71°22′W	11/15/73	1700	1800	2604	2614	2609	40′ GMT	6	555	92
509	CHAIN	124	39°12′N	70°18′W	7/7/75	1530	1700	2654	2654	2654	41′ GMT	2	144	72
415	ATLANTIS II	86	39°11′N	70°12′W	3/13/75	1825	2000	2720	2740	2730	20′ BT	5	561	112

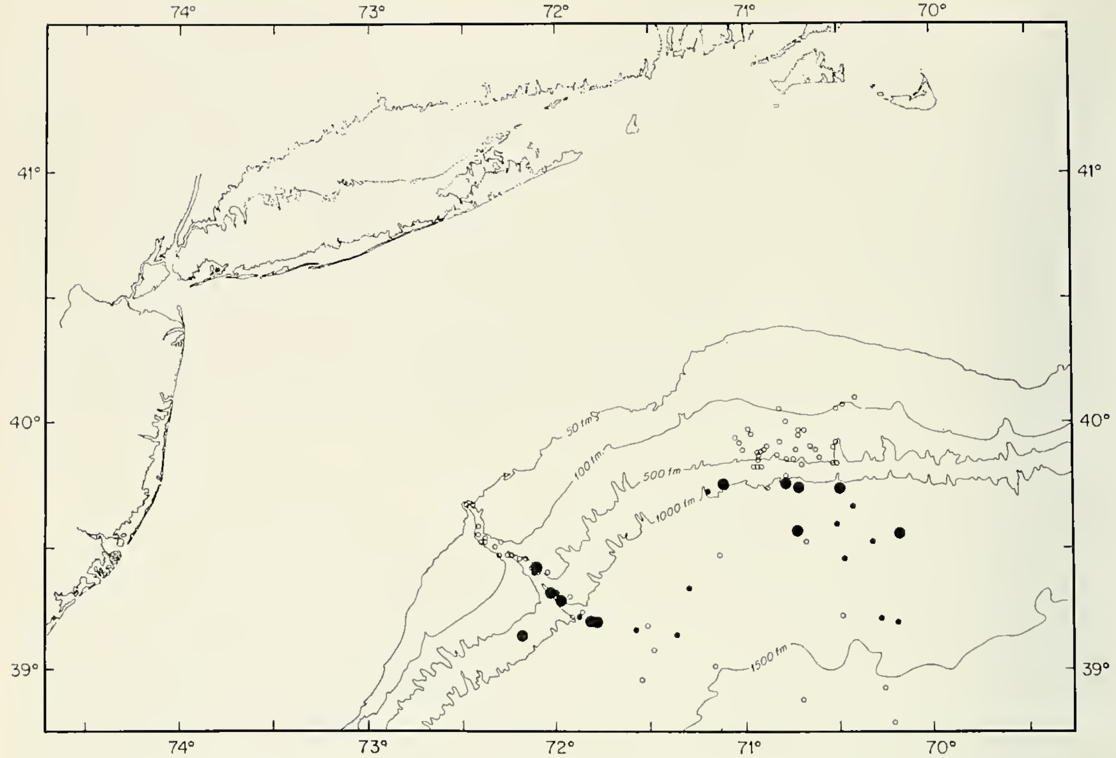

Figure 1. Positions of trawl stations south of New England. Open circles: no *Coryphaenoides carapinus*; small dots: < 9 *C. carapinus* per hour; large dots: > 9 *C. carapinus* per hour.

the relation between gonadal weight and total weight of the fish. The most obviously ripe specimens were taken in November, when the slope of the gonad weight/total weight relation was greatest. By February–March relative weight of the gonad was reduced to the lowest values observed. Weights in July were intermediate. *Coryphaenoides carapinus* is a winter spawner.

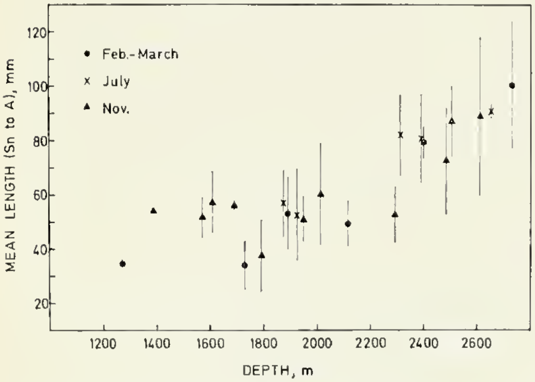

Figure 2. Size *vs.* depth of capture for *Coryphaenoides carapinus* aggregated by trawl. The symbols are at the mean value for each collection; the lines show the standard deviation.

Co-occurring species.—A number of other species were commonly taken in the same trawls which took *Coryphaenoides carapinus.* These include the fishes *Antimora rostrata, Alepocephalus agassizi, Halosauropsis macrochir,* and *Bathysaurus agassizi,* the ophiuroids *Ophiomusium lymani* and *Ophiura ljungmani,* the asteroids *Zoroaster fulgens, Benthopecten spinosus,* and *Pectinaster forcipatus,* the holothurian *Paelopatides gigantea,* and echinoids, genus *Echinus.* Preliminary analyses of our deeper trawls, following the philosophy and approach of our shallower work (Haedrich, Rowe, and Polloni, 1975), suggest that this assemblage of species is characteristic of a zone associated with the base of the continental slope and the upper continental rise.

Helminth parasites found in *Corphaenoides carapinus* include the digenetic trematodes *Glomericirrus* n. sp., *Gonocera* (probably *phycidis*), and an unidentified zoogonid, the trypanorhynch *Grillotia* (*Paragrillotia*) n. sp., and unidentified nematodes. The *Glomericirrus* and *Grillotia,* found for the first time in this material,

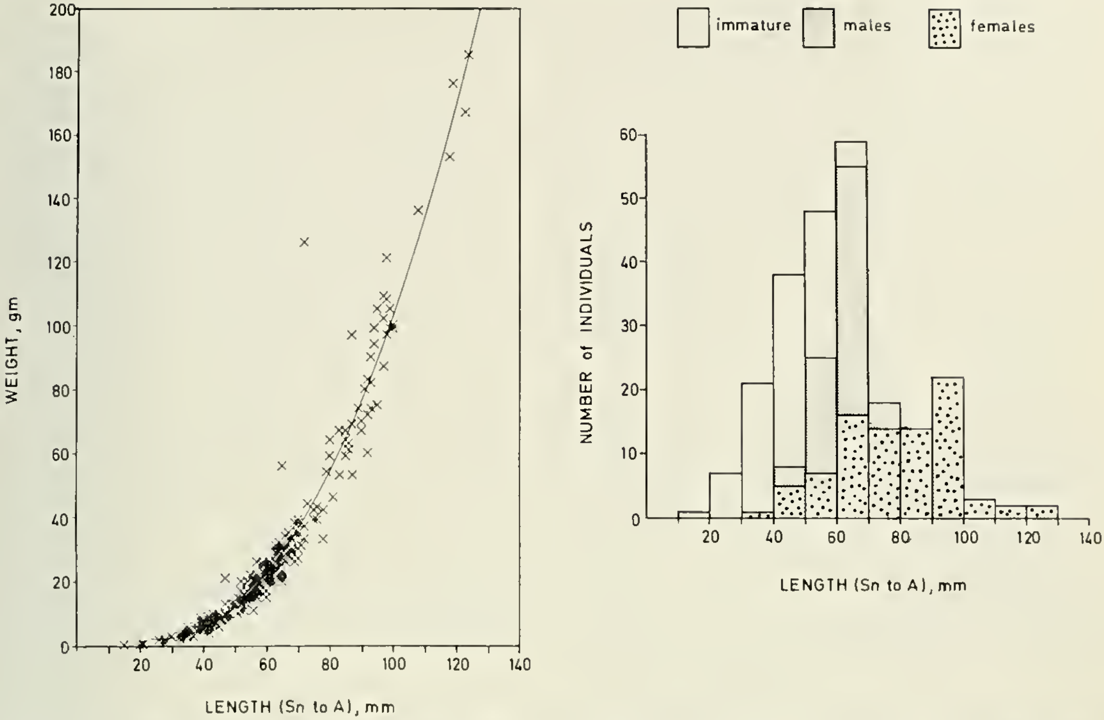

Figure 3. Length-weight relationship (left) and length frequency and sex (right) for *Coryphaenoides carapinus.*

also occur in other *Coryphaenoides* (*C. armatus* and *C. leptolepis*) from the same depths (Campbell, MS in prep). Members of the family Hemiuridae, to which the first two trematodes belong, typically utilize free-living copepods as second intermediate hosts.

Feeding habits.—Stomachs of 108 specimens were examined and their contents tabulated by size of fish (Table 2). Freshly ingested prey, possibly contaminants due to feeding in the net, were excluded. Polychaetes and crustaceans were found in more than half (57 percent and 71 percent respectively) of all 84 stomachs containing food. Ophiuroids, present in 23 percent of stomachs with food, were found only in specimens larger than 29 mm (Sn to A), but there was little other evidence of a change in food habit with increasing size or age of fish.

An Index of Electivity (Ivlev, 1961) was used to determine the extent to which selective feeding might be practiced by *Coryphaenoides carapinus.* The index is calculated by $E = (r - p)/(r + p)$, where r is the percentage a component comprises in the food ration and p is the percentage the same component comprises in the fauna. Values of the index can range from + 1, indicating that an item is strongly selected for, to −1, indicating an item is strongly selected against. Table 3 presents this information for the major taxa eaten by *C. carapinus.* Strong selection is indicated for crustaceans, particularly amphipods, and for ophiuroids. Polychaetes are eaten at a rate in keeping with their probable rate of encounter, and molluscs may be weakly selected against. Some qualification is necessary in respect to the values for amphipods: there is evidence (Wigley and Emery, 1967; Besner and Brunel, 1975, MS) that benthic grab samplers underestimate the abundance of these active animals. An underestimate of the percentage of amphipods in the fauna would result in an overestimate of the index. If, for example, amphipods comprised 5 percent of the fauna (instead of 2 percent as indicated in our grab samples), the index for this taxon would fall to + .66, a change of about 25 percent.

The animals found in *Coryphaenoides carapinus* stomachs belonged almost entirely to benthic taxa. Pelagic groups (e.g., Euphausiacea, Pteropoda) and material from the surface (terrestrial plants, *Zostera,* plastic) occurred only sparingly (Table

TABLE 2. Food items found in *Coryphaenoides carapinus* by major taxa and length (snout to anal fin) of fish. Entries are numbers of stomachs in which an item occurred.

Food Item	20–49 mm	50–79 mm	80–124 mm	Total	Frequency of Occurrence
Stomachs with food	30	34	20	84	
Stomachs empty	5	16	3	24	
Total examined	35	50	23	108	
Annelida, Polychaeta	16	24	8	48	57.1%
Arthropoda, Crustacea	22	26	12	60	71.4%
Amphipoda	15	23	8	46	54.8%
Isopoda	4	6	8	18	21.4%
Tanaidacea	2	3	3	8	9.5%
Copepoda	8	6	3	17	20.2%
Mysidacea	3	7	3	13	15.5%
Cumacea	1	1		2	2.4%
Nebaliacea		1	1	2	2.4%
Euphausiacea		1		1	1.2%
Decapoda—fragments	4	6		10	11.9%
Unidentified	8	3	3	14	16.7%
Arthropoda, Pycnogonida			1	1	1.2%
Ophiuroidea		8	11	19	22.6%
Mollusca	1	5	2	8	9.5%
Pelecypoda	1	4	2	7	8.3%
Gastropoda		2	1	3	3.6%
Priapula		1		1	1.2%
Other items					
Terrestrial plant (seeds)		1	1	2	2.4%
(*Zostera*)		1	1	2	2.4%
Spines, spicules	1		1	2	2.4%
fish cartilage?	1			1	1.2%
agglutinated forams	1	1	5	7	8.3%
planktonic foraminiferan tests	2	2	3	7	8.3%
tubes (Polychaete)		2	2	4	4.8%
(Pogonophoran?)		1	1	2	2.4%
Pteropod shells		1	1	2	2.4%
plastic sphere			1	1	1.2%

2). Polychaetes were represented by *Poecilochaetus fulgoris* (Poecilochaetidae), *Lumbrineris* spp. (Lumbrineridae), *Glycera capitata* (Glyceridae), *Praxillella* (Maldanidae), *Ammotrypane cylindricaudatus* (Opheliidae), and by species in the Polynoidae, Spionidae, and Dorvilleidae.

Amphipods present were *Harpiniopsis* (Phoxocephalidae), *Liljeborgia* (Liljeborgidae), *Rhachotropis* and *Eusirus* (Eusiridae), a probably new genus near *Bathyceradocus* in the Gammaridae, and species in the Aoridae, Corophiidae, and Oedicerotidae. Isopods were fragmented and thus difficult to identify; one of the few good specimens was in *Nannoniscus* (Desmosomatidae). Copepods were represented by benthic species of the Calanoidea in the genera *Undinella, Xanthocalanus,* and in a probably new genus near *Bradyidius.*

Almost all the ophiuroids were *Ophiura ljungmani* (Ophiuridae), an important food item. Rarely encountered were *Ophiacantha* (Ophiacanthidae) and Amphiuridae.

Molluscs were mostly clams, including *Yoldia thraciaformis* (Nuculanidae), *Nucula granulosa* (Nuculidae), *Cylichna* (Cylichnidae), and Naticidae.

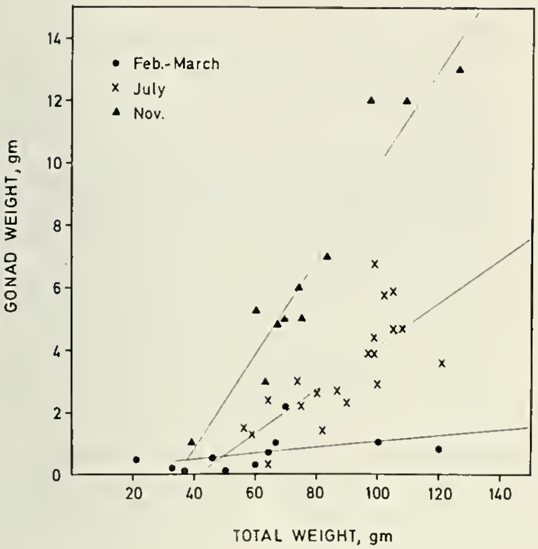

Figure 4. Gonad weight *vs.* total weight of fish by season for *Coryphaenoides carapinus.* The regression lines were determined separately for each season.

DISCUSSION

Investigations into the natural history of macrourid fishes have found them to be rather generalized in their feeding habits (Pearcy and Ambler, 1974; Haedrich and Henderson, 1974), a finding in keeping with the notion that large mobile predators in an unproductive environment should tend to be non-selective (Schoener, 1971). As Pearcy and Ambler (1974) observe, however, the distinction between "generalized" and "specialized" is difficult to apply in practice and the argument may be largely semantic. Their data do show that food overlap, using the measure C_λ of Horn (1966), is about 50 percent in three species of slope-dwelling macrourids, as compared to 5–24 percent in fishes from shallow-water, north temperate assemblages (Tyler, 1972). The deep-water macrourids are the more generalized in a relative sense, but, nonetheless, since they are not consuming the full spectrum of probably available prey, they must also be considered at least somewhat selective.

The data for *Coryphaenoides carapinus* illustrate this quandary. The list of food items (Table 2) includes representatives from virtually all important deep ocean taxa. Dominance by numbers, however, indicates that amphipods and ophiuroids are preferred prey (Table 3). The level of identification possible in the amphipods was usually only to family or genus, so the "selectivity" displayed for this group is in fact rather general. As such, the observation goes little beyond the generality that these small crustaceans are important in the diets of deep benthic fishes (Bright, 1970; Geistdorfer, 1973). The ophiuroids could be identified to species, and, with the assumption that the box core samples adequately reflect the overall abundance of this animal, it is safe to say that *C. carapinus* does feed selectively on *Ophiura ljungmani.*

Table 3. Percentages by numbers of individuals for the dominant taxa in *Coryphaenoides carapinus* stomachs in the fauna at the same depths, and an Index of Electivity.

Taxon	Percentage in: Stomachs	Fauna	Electivity
Crustacea	56.5%	6.1%	.81
Amphipoda	24.6	2.0	.85
Polychaeta	13.0	18.9	−.18
Ophiuroidea	25.7	1.3	.90
Mollusca	4.3	8.6	−.34

Coryphaenoides carapinus relies more on truly benthic animals for its food than do other *Coryphaenoides. C. rupestris,* for example, feeds almost entirely on pelagic crustaceans, with *Pasiphaea* comprising as much as 75 percent of its diet (Podrazhanskaya, 1967). *C. armatus, C. pectoralis,* and *C. filifer* depend largely on cephalopods (Pearcy and Ambler, 1974; Haedrich and Henderson, 1974), and *C. leptolepis* lives on benthic crustaceans, particularly *Crangon,* when small and shifts increasingly to pelagic shrimps and euphausiids as it grows (Pearcy and Ambler, 1974).

Originally considered genera in their own right, *Nematonurus, Chalinura,* and *Lionurus* have recently been reduced to subgenera of *Coryphaenoides* with the varying patterns of dentition important defining characters (Iwamoto and Stein, 1974). It is not surprising, therefore, to find somewhat of a dichotomy in the feeding habits along subgeneric lines. Species in *Lionurus* (*C. carapinus*) and *Chalinura* (*C. leptolepis,* Pearcy and Ambler, 1974) are more benthic in their habits, with the *Lionurus* species taking smaller animals and the *Chalinura* species larger ones. Species in *Nematonurus* (*C. armatus* and *C. pectoralis*), with large strong teeth, take even larger and often pelagic prey. One species in the subgenus *Coryphaenoides* (*C. filifer*) is quite similar to the *Nematonurus* species, but another (*C. rupestris*) feeds in the pelagial on crustaceans.

Within the subgeneric framework, other interesting observations can be made. It would appear, for example, that the subgenera which contain the large species (*Nematonurus* and *Coryphaenoides*) are the ones which seek pelagic food sources, whereas the small species (in *Lionurus*) take their food from the bottom. A large pelagic feeding species (*C. rupestris*) has drumming muscles on the swimbladder, presumably for communicating with one another, but a small benthic feeding species (*C. carapinus*) lacks them (Marshall, 1965). Clearly more data is needed, but the emerging picture of evolution in the important macrourid genus *Coryphaenoides* are one of modest radiation within overlapping yet distinct adaptive zones, with emphasis on different prey and foraging areas an important consideration.

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AQUARIUM MAINTENANCE OF MESOPELAGIC ANIMALS: A PROGRESS REPORT

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ABSTRACT: Literature and experiments in progress concerning the capture and aquarium maintenance of midwater fishes and invertebrates are discussed. The longevity and survival of mesopelagic animals captured in Monterey Bay, California, are tabulated, and those species which appear most suitable for aquarium captivity are identified. Certain mesopelagic species are insensitive to large changes in hydrostatic pressure and were maintained at ambient pressure with proper temperature and light controls.

Large public and private aquariums possess unique facilities which allow research opportunities unavailable to most universities and research laboratories. The immense water systems, water quality control and monitoring systems, and around-the-clock engineering capabilities utilized by large aquaria make them the most likely facilities at which the environment of a large aquatic ecosystem might be reproduced.

At the Steinhart Aquarium, we have attempted to investigate the behavior and natural history of animals living in the deep sea, perhaps among the most exciting of frontiers remaining in modern biology. Adaptation to life in the deep sea has resulted in fantastic and bizarre morphologies, the function of which has until recently been only inferred from preserved specimens. The development of submersibles has allowed the *in situ* observation of living deep sea animals (cf. Barham, 1966), however the goal of understanding the behavior and physiology of these creatures remains to be solved through their aquarium maintenance. The Steinhart Aquarium Midwater Maintenance Program (SAMMP), assisted by a grant from the Charline Breeden Foundation, is attempting to identify and solve the aquarium-related problems. The results of our pilot project and a review of pertinent studies relating to the aquarium maintenance of midwater animals form the basis of this report.

The Steinhart Aquarium project was conceived

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TABLE 1. Survival of deepwater fishes in captivity, various authors.

Species	Depth of Capture	Longevity	Cause of Death	Reference
Family Myctophidae				
Tarletonbeania crenularis	surface	72 hours	light leak	Robison, 1973
Myctophum nitidulum	surface	9 hours	overcrowding	Robison, 1973
Diaphus theta	surface	12 hours	net damage	Robison, 1973
Gonichthys coccoi	surface	36 hours	——	Beebe and Vander Pyl, 1944
Family Melamphaidae				
Poromitra crassiceps	>250 meters	8 hours	net damage	Robison, 1973
Family Bathylagidae				
Leuroglossus stilbius	>25 meters	24 hours	aquarium failure	Robison, 1973
Family Anoplogasteridae				
Anoplogaster cornuta	>600 meters	48 hours	net damage	Robison, 1973
	>600 meters	13 days	internal injuries	Childress and Meek, 1973
	>600 meters	23 days	internal injuries	Childress, pers. comm.
Family Berycidae				
Beryx splendens	200–800 meters	indefinite	——	Takeuchi, *et al.*, 1969
Family Himantolophidae				
Himantolophus groenlandicus	surface	8 days	thermal stress	Haneda, 1968

after discussions with Otis Barton, adventurer, engineer, developer of the Barton Midwater Trawl and accompanist of William Beebe in the 1930's bathysphere dives. Barton had prepared a film describing his experiments with a 10 m pipe-frame trawl and hyperbaric chamber of his own design. Trawling this large net at slow speed (< 3 km/hr) off the Kona Coast of Hawaii resulted in the capture of large specimens in exceptionally robust conditions, several of which were near the maximum recorded size of certain species (cf. Smith and Atz, 1973), as well as representing new capture records for the Pacific Ocean (Iwamoto, McCosker, and Barton, in press). By quickly placing the captured specimens in seawater barely above freezing, Barton has been able to maintain adult specimens of large ceratioids, whalefishes (*Barbourisia rufa*), and dragonfishes (stomiatoids), for extended periods of a day or more. Barton's dramatic results inspired us to further investigate the possibility of maintaining living specimens of deep sea animals in the Steinhart Aquarium.

Few literature references exist which discuss the survival of midwater animals in captivity. A brief review of previous studies concerning deep sea fish maintenance is found in Gordon (1970: 445–446). Summarized in table 1 are those studies which bear on our work.

Lanternfishes of the family Myctophidae are desirable candidates for aquarium maintenance because of their availability and their interesting bioluminescent organs. The universal difficulty, however, has been the tendency of lanternfishes to destroy themselves by plummeting and battering their bodies against the container walls. Certain species are more amenable to captivity, however, including those listed in table 1. Beebe and Vander Pyl (1944) maintained net-caught specimens of *Gonichthys coccoi* on shipboard for up to 36 hours. The durability of this species is evidenced by a specimen which Beebe named "Methuselah" that had survived being "subjected to all sorts of experiments, dropped on the floor twice, and placed for a moment by mistake in a bowl of formalin." Somewhat more careful treatment of myctophids has resulted in their maintenance for longer periods, particularly the work of Robison (1973) using a modified planktonkreisel (Greve, 1968) and surface-dipnetted specimens of *Tarletonbeania crenularis*, *Myctophum nitidulum*, and *Diaphus theta*. Lawry (1974) demonstrated the

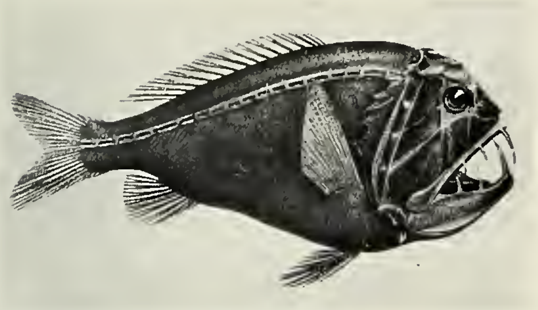

Figure 1. The bathypelagic Fangtooth *Anoplogaster cornuta*, a likely candidate for aquarium maintenance. (From Zugmayer, 1911.)

countershading function of ventral bioluminescence in live *Tarletonbeania crenularis*, however, he did not indicate their longevity in an aquarium.

Perhaps the most dramatic midwater animal that has been maintained to date is the bathypelagic Fangtooth *Anoplogaster cornuta.* This cosmopolitan species lives below 600 meters off Southern California (Berry and Perkins, 1965) and, although rare, it has been caught in approximately half of the midwater trawl runs in certain areas. Several authors have commented on its healthy condition after capture, and relate this to its lack of a gas-filled swimbladder (Fitch and Lavenberg, 1968). Childress and Meek (1973) have successfully kept living specimens aboard ship in 4 l nalgene jars at 5°C, later transferring them to 16 l cylindrical washbasins where they lived as long as 13 days. Childress (pers. comm.) has subsequently kept them in a similar manner for 23 days. Their observations of *Anoplogaster* feeding and swimming behavior made under weak red light were perhaps the first documentation of bathypelagic fish behavior. The same authors (Meek, 1973; Meek and Childress, 1973) were able to obtain oxygen consumption rates at atmospheric pressure and at 1000 psig (68 atmospheres). Their success in maintaining this species within the confines of a 16 l washbasin certainly suggests that with proper temperature controls, the midwater Fangtooth might be kept alive indefinitely in a large public aquarium.

The deepwater berycid *Beryx splendens* has been maintained for several months at Aburatsubo Marine Aquarium (Takeuchi, *et al.*, 1969). This near-benthic species, normally living at 200–800 m, adapted well to temperatures of 15–18°C and was found to prefer an illumination of 11.0 lux (within a range of 8–16 lux).

Certain ceratioid angler fishes are hardy species as evidenced by the fortuitous occurrence, capture, and study of a live *Himantolophus groenlandicus* (Haneda, 1968). Ceratioids have been kept alive for several days in shipboard aquaria (Bertelsen, pers. comm.), yet their scarcity has precluded their utilization as an experimental animal.

Many midwater fishes may be captured in near-perfect condition by taking advantage of their epipelagic distribution while juveniles. This is especially true for such desirable fishes as ceratioids and berycoids (cf. Mead, *et al.*, 1964). Robins and de Sylva (1965) described aquarium observations of juvenile *Gibberichthys pumilus* (as *Kasidoron edom*), a fascinating form with a spectacularly developed pelvic fin. Aquarium rearing of the juvenile forms through transformation could well occur and possibly aid in taxonomic studies such as the identification of disparate juvenile and adult forms.

Midwater-animal aquarium displays need not be limited to fishes. The cephalopods and crustaceans that inhabit the midwater environment are equally fascinating in their curious adaptations to existence in the deep sea, and some have proven to be more adaptable to aquarium conditions than fishes. By maintaining midwater squid (*Abraliopsis* sp.) in shipboard aquaria, Young and Roper (1976) were able to demonstrate the countershading function of squid bioluminescence. The large mysid shrimp *Gnathophausia ingens* living in the oxygen minimum layer off California, is a dramatic red crustacean that has evolved to the midwater habitat. Childress (1968, 1971) has studied the respiratory behavior of *G. ingens* under laboratory conditions and maintained them as long as 2½ years (pers. comm.). Other researchers have made use of the diurnal vertical migration of crustaceans; for example, Pearcy and Small (1968) captured and maintained *Euphausia pacifica, Thysanoessa spinifera,* and *Sergestes similis* at 100 m depth, the peak of their migration which often covers 500 m.

METHODS

The Steinhart Aquarium project, which officially began in March 1974, is at a stage where the feasibility of potential aquarium display species is being investigated. The results of our aquarium longevity studies are presented in table 2.

SAMMP animals were collected in Monterey

TABLE 2. Survival of mesopelagic and upper bathypelagic species in captivity, from SAMMP data.

Species	*n*	Temp (°C)	Depth of Capture (m)	Maximum Longevity
PISCES				
Family Scyliorhinidae				
Apristurus brunneus	2	8	500–600	2 days
Parmaturus xaniurus	3	11–15	400–500	15 days
Family Myctophidae				
Lampanyctus regalis	1	11	500–700	22 hours
Lampanyctus regalis	2	5.5	500	20 hours
Lampanyctus ritteri	3	8	500–600	6 hours
Stenobrachius leucopsarus	8	5.5	300	24 hours
Family Bathylagidae				
Bathylagus wesethi	1	5.5	400–500	20 hours
Leuroglossus stilbius	6	7	300–500	20 hours
Family Melanostomiatidae				
Bathophilus flemingi	1	7	400–500	8 hours
Tactostoma macropus	2	7	400–500	6 hours
Family Zoarcidae				
Lycodapus mandibularis	9	5.5	400–600	7.5 days
Lycodapus mandibularis	8	7	400–600	12 days
Lycodapus mandibularis	5	11	400–600	5 days
Melanostigma pammelas	21	5.5	400–600	4 months
Melanostigma pammelas	8	8	400–600	12+ months
Melanostigma pammelas	5	11	400–600	36 days
Family Liparidae				
Nectoliparis pelagicus	11	5.5	300–500	6 days
Nectoliparis pelagicus	8	8	300–400	21 days
Nectoliparis pelagicus	2	11	300–400	22 hours
Lipariscus nanus	4	7	500–600	20 hours
MOLLUSCA				
Gastropoda				
Clio pyramidata	2	8	200–300	24 hours
Pterotrachea sp.	1	7	400–500	45 hours
Cephalopoda				
Chiroteuthis calyx	1	5.5	350–500	3 days
Galiteuthis phyllura	9	7	300–500	9 days
Gonatus onyx	5	7	300–500	3 days
Histioteuthis heteropsis	1	5.5	300–500	2 days
Histioteuthis heteropsis	1	7	400–500	4 days
Japetella heathi	1	7	500–650	3 days
Octopoteuthis deletron	2	8	350–450	24 hours
Octopus sp.	2	5.5	350–400	3 days
Opisthoteuthis californiana	1	7	460–480	5 days
ARTHROPODA—CRUSTACEA				
Copepoda				
Gausia princeps	5	7	500–600	14 days
Pareuchaeta japonica	12	7	300–500	3 days
Amphipoda				
Hyperia medusarum	8	7	350–500	19 days
Lanceola sp.	2	7	200–400	7 days

TABLE 2. Continued.

Species	*n*	Temp (°C)	Depth of Capture (m)	Maximum Longevity
Orchomene obtusa	2	7	350–450	50 days
Paracallisoma coecus	1	5.5	300–550	20 days
Paraphronima crassipes	1	5.5	350–500	24 days
Phronima sedentaria	3	5.5	300–500	28 days
Scina sp.	2	5.5	350–500	19 days
Mysidacea				
Eucopia unguiculata	3	5.5	600–800	21 days
Boreomysis arctica	5	8	300	10 hours
Boreomysis california	6	7	400–600	9 hours
Gnathophausia ingens	2	7	500–600	2 days
Euphausiacea				
Euphausia pacifica	10	5.5	200–300	24 hours
Euphausia pacifica	16	8	200–300	3 days
Decapoda				
Bentheogennema burkenroadi	3	5.5	275–450	9 days
Pasiphaea pacifica	5	5.5	350–500	11 days
Pasiphaea pacifica	3	8	200–300	19 days
Sergestes similis	5	7	300–400	6 days

Bay, California. The oceanographic topography of the bay is characterized by a deep nearshore submarine canyon, providing favorable conditions for the collection and transport of midwater animals. Bimonthly collections were made from the Moss Landing Marine Laboratories (MLML) vessel R/V ST908, a 15 m converted harbor tug, utilizing a six foot (1.8 m) messenger-operated closing Tucker Trawl shortened to a length of 9 m. The flow-through, inverted-cone, canvas cod end (modified after Clarke, 1969) reduced the abrasion to captured animals. Short duration trawls also increased animal survival. Specimens removed from the net were placed in sea ice chilled, darkened plastic buckets. Experimentation with a planktonkreisel similar to that described by Robison (1973), with the expectation that it would reduce fish loss during transport, proved unproductive. Fishes were transferred to the MLML facility for study or temporary holding and kept in a 95 l darkened plastic container floated in refrigeration tanks, with maintained temperatures of 5.5, 7, or 8°C ± 0.5. The 11°C ± 1 system described in table 2 relates to the circulating system at the Steinhart Aquarium for the display of cold temperate and boreal marine fishes (Herald, 1963). The fishes were kept in a darkened 95 l tank and fed live brine shrimp (*Artemia salina*). Cephalopods were maintained in separate containers to prevent their ingestion of other animals.

RESULTS

From our data it is evident that certain species (e.g., *Melanostigma pammelas*) survive well at both 5.5°C and 11°C, while others tolerate only the colder system (e.g., *Lycodapus mandibularis* and *Nectoliparis pelagicus*). The Midwater Eelpout *Melanostigma pammelas* has thus far proven to be an exceptional display species. It is hardy, survives transport well, is not uncommon, and actively swims in the aquarium water column. Our specimens have fed heartily on live *Artemia* and, after approximately two weeks, have become "accustomed" to incandescent light. As an exhibit animal, this species is a superb example of the adaptation of a primarily benthic fish group (family Zoarcidae) to the midwater environment, exemplified by its large eyes, terminal mouth, black pigmentation, and swimming mode. Another midwater species which shows promise as an exhibit animal is the Tadpole Snailfish *Nectoliparis pelagicus*. Although small, this species is of interest in that it, like *M. pammelas*, represents a pelagic form derived from a benthic ancestor. Related deepwater zoarcids also amenable to captivity include the pelagic Pallid Eelpout *Lycodapus mandibularis* and the benthic eelpout *Maynea californica*. The Pallid Eelpout is more common than previously believed and survived for 12 days at 7°C. *M. californica*, although not a pelagic species, is an intriguing display animal and would

Figure 2. Living adult specimen of the midwater Eelpout *Melanostigma pammelas* in the Steinhart Aquarium.

be well suited for physiological research. Specimens trapped in 250 m by Richard Kliever of Moss Landing Marine Laboratories, who is presently studying the biology of *Maynea*, have fed and survived indefinitely at 11–15°C.

We have not actively pursued the maintenance of surface-dipnetted lanternfishes (family Myctophidae), but expect that through experimentation and improvement of Robison's (1973) technique, we should be able to solve the bugaboo of myctophid transport. We expect to permanently display myctophids in a rounded tank designed at the Steinhart Aquarium for the maintenance of fragile pelagic engraulids and clupeids. The problem of scale loss due to contact with the aquarium surfaces is common among these fishes and is solved by the action of a slow gyral circulation generated by the inflowing water.

The Filetail Cat Shark *Parmaturus xaniurus* has proven to be a dramatic display species. Juveniles of this species are extremely hardy and not uncommon in midwater trawl captures (Lee, 1969). Our maintenance of *Parmaturus* was incidental to the project and, in the absence of a suitable large refrigerated aquarium system, specimens were placed in an outdoor pool at MLML maintained with surface seawater. *P. xaniurus* is an instructive display species in that its large green eyes, black to brown coloration, and swimming mode are typical of the adaptations made by midwater sharks. Although uncommon, we suspect that the deep water sharks of the genera *Apristurus*, *Euprotomicrus*, and *Isistius* might also be suitable as aquarium species (Hubbs, *et al.*, 1967; Taylor, 1972).

We were successful, to a limited extent, with the maintenance of midwater cephalopods and crustacean. Midwater trawl-caught squid (*Galiteuthis phyllura*) lived as long as nine days in our 5.5°C system, finally expiring due to net damage and water circulation difficulties. Although intolerant of relatively small changes in water temperature, cephalopods were generally tolerant of exposure to subdued daylight. Mesopelagic crustaceans have survived well, as evidenced by Childress' (1968, 1971) studies on the mysid *Gnathophausia ingens*. Our specimens of *G. ingens* were infrequently captured and too damaged to allow their maintenance.

DISCUSSION

Several popular misconceptions exist concerning animals, particularly fishes, living in the deep sea. Prevalent is the belief that "fishes will 'explode' when brought up from great depths." This misconception is derived from the assumption that all fishes possess a gas or "swim" bladder which embolizes under hypobaric conditions. Nearly half of the midwater, benthic, or near-benthic fishes lack trapped air spaces (Denton and Marshall, 1958; Marshall, 1960) and are often brought up in healthy condition. The midwater environment in which our preliminary studies are directed is limited to the mesopelagic rather than the bathypelagic zone. Those fishes which do possess large gas bladders, as typified by the hatchetfishes of the genera *Sternoptyx* and *Argyropelecus*, are not suitable for live maintenance until suitable hyperbaric collecting and maintenance devices can be constructed. Certain desirable midwater species with gas bladders may be captured in healthy condition by taking advantage of their diurnal vertical migratory (DVM) behavior, particularly during the new moon (cf. Robison, 1973). Certain midwater species typically make daily vertical excursions of 1000 m, many reaching or approaching surface waters (Taylor, 1968; Marshall, 1971). Pressure effects on other physiological and anatomical systems are not obvious, although recent studies have shown that enzyme systems behave differently under hyperbaric conditions (Hochachka, *et al.*, 1970; Moon, *et al.*, 1971a, 1971b). In experimenting with the hardy bathypelagic fish *Anoplogaster cornuta*, Meek and Childress (1973) found pressure to have little effect upon oxygen consumption and suggested that some deep-living fishes are metabolically insensitive to large changes in hydrostatic pressure. Comprehensive reviews of pressure effects on living systems are provided by Knight-Jones and Morgan (1966), Morita (1967), Flügel and Schlieper (1970), Gordon (1970), Hochachka (1975), and Macdonald (1975). The problems and costs relating to maintenance of deep-living animals under hyperbaric conditions have precluded such an installation at our aquarium. The subject of high pressure aquarium systems has been discussed in a series of papers edited by R. W. Brauer (1972).

Temperature is a parameter critical to the success or failure of maintenance after capture of deep sea animals. Our preliminary data and those of others have shown that, after the initial dieoff of animals from capture-related causes, many species are able to survive at ambient pressure if their normal temperature regime is maintained. We have observed this with midwater zoarcids and liparids as have others with fishes such as *Anoplogaster* and juvenile ceratioids. Temperatures below the permanent thermocline approach levels too low to be practicably maintained using standard refrigeration units; however, we suspect that many species might become acclimated to elevated temperatures over a period of days or weeks. We have been successful in maintaining mesopelagic zoarcids at 5–6°C above the temperature of capture. Midwater collections made in higher latitudes have the advantage of passing through cold surface waters, thereby reducing the thermal stress experienced by the animals. Experiments in progress by Childress (pers. comm.) indicate that thermal stress-related mortalities can be reduced through the usage of a temperature-insulated cod end.

The intensity and quality of illumination must be carefully controlled to more nearly approach the condition of the midwater environment. Although sunlight may be measured in clear oceanic water to depths of 1000 m, the penetration through near-shelf waters is greatly reduced. Care must be taken to shield animals from bright illumination which might cause them to strike the container walls. Illumination should be weak and limited to the red hues, particularly after animals are introduced to the aquarium. Childress and Meek (1973) were able to observe and photograph *Anoplogaster cornuta* under weak red light. We have found *Melanostigma pammelas* to ignore moderate intensities of white light after being kept for several weeks.

The final parameter we have considered is oxygen. Most of the animals herein considered come from an oxygen-poor environment and all, because of the reduced temperature regime and their less active life style, have respiration rates considerably lower than related shallow water forms (Meek and Childress, 1973; Childress, 1968, 1971; Teal and Carey, 1967). For these reasons, low oxygen levels, even within a recirculating closed system, should not present a problem. Robert Meek (pers. comm.) has suggested that oxygen levels above 4 ml O_2/l may be toxic to certain mesopelagic and bathypelagic fishes. If this proves to be true, then methods such as nitrogen bubbling should be employed to reduce oxygen levels within the system.

CONCLUSIONS

The preliminary finding from SAMMP and the results of recent studies which we have outlined clearly indicate that at least some animals from mesopelagic and bathypelagic environments can be maintained in aquaria. The difficulties relating to scarcity, fragility, and light avoidance can be overcome through the development of special collecting devices and aquarium systems. The most significant finding of recent physiological studies, that temperature and not pressure is the limiting factor for many deep sea animals investigated, verifies that ambient pressure aquaria are suitable for the maintenance of these species.

In that our review of past research began with the findings of William Beebe and Otis Barton, it seems appropriate to conclude our progress report with Dr. Beebe's (1934) accounting of his observations of midwater animals made during the historic Bathysphere dives. Beebe stated that "Yet I find that I must continue to write about it, if only to prove how utterly inadequate language is to translate vividly, feeling and sensations under a condition as unique as submersion at this depth." Perhaps the time has come in which deep sea animals can be viewed and studied in aquaria.

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REPRODUCTIVE PRODUCTS IN MARINE FOOD WEBS

John D. Isaacs[1]

Abstract: The role of gametes and reproductive products such as sperm, eggs and seeds will be generally discussed as a part of the food flux in terrestrial and marine food webs. Particularly important is the opposed role of reproductive products in these two realms, constituting an "upward" flux (i.e., from the lower developed forms to the more highly developed) on land, and a "downward" flux at sea. In the sea this flux undoubtedly constrains development of higher trophic levels and mature forms. It is an important component of the homogenizing and smoothing processes affecting marine food webs, and the development of a trophic system dominated by immature creatures.

In present terrestrial food webs, reproductive products play an important nutritional role beginning at the first consumer level. There they constitute vital pathways. Indeed, in some forest, grassland, desert and island environments, seeds, nuts, and fruits constitute the major macroscopic pathway for plant material to enter into the food web. Man, of course, has capitalized and concentrated on this peculiarity of terrestrial food webs broadly to support himself and his domestic food animals on the products and their associated structures. At the subsequent consumer levels of terrestrial food webs, reproductive products must become somewhat less important, although at the second consumer level, and even at higher levels, they cannot be negligible elements. The large size of the of the clutches of some ground-nesting birds bespeaks the importance of attrition to eggs and young, and the numbers of eggs produced by most insects similarly argues for a high predatory mortality of both eggs and young. Even spiders, at some rather high level in the food web, assiduously protect their immsense clutches from a number of specialized parasitic and ovigerous predators.

At this level also, man has capitalized his food sources on the sizable eggs of seed-eating birds and the young of many species. In the remainder of the food web with which man is associated, reproductive materials continue to be of consequence. The young of most higher creatures derive most of their early food from maternal sources and, later, from the adult substrate. Undoubtedly, part of the mammalian advantage is an escape from the attrition on the adult biomass that results from predation on the eggs of oviparous forms, and instead this biomass is *added* to the adult stock.

It is the peculiarity of the marine realm that the role of reproductive products in food webs is approximately reversed from that of the terrestrial. Whereas the reproductive materials of terrestrial plants constitute a large, important and highly differentiated component of the plants' products, in marine phytoplankton they certainly constitute a virtually undifferentiated, inseparable and dominant part of the primary productivity. Throughout the remainder of the marine food web (except, of course, the marine mammals and some sharks), eggs and sperm also become an increasingly important component of the food flux.

Three aspects of reproduction by marine heterotrophic forms contribute to this importance: first, the continuing high fecundity of forms at higher positions of the food web; second, the "downward" nature of this flux; and third, the quantitative importance of such downward attrition, compounded at each step, on the form of the food web.

Thus the vital point of contrast between reproductive materials in terrestrial versus marine food webs is the reversal of the direction of flux—in the macroscopic terrestrial webs, these materials dominantly constitute an "upward" flux from plant and first consumer levels and thence to higher steps and are *added* to the adult biomass; whereas in the marine counterpart, the flux is "downward" from higher forms toward the lower components of the system and is *subtracted* from the potential growth of the adults.

Even a modest examination and quantification of this flux in the marine environment clearly would require a major research program. I will content myself with presenting some discussion, estimates, and analysis, toward showing that these products are essential and important components of marine food webs, elaborating mainly on the above points.

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There is no question that the majority of marine fishes and invertebrates find it necessary to release vast quantities of eggs and sperm, larvae, or progeny freely into the sea. Numbers of eggs most frequenty exceed hundreds of thousands and sometimes approach a half a billion per female per spawning [the average fecundity of cod and sturgeon is 9,000,000 and 200,000 respectively (Sadlier, 1973), with a range of up to 300,000,000 eggs for the ocean sunfish (McWhirter and McWhirter, 1975)]. Numbers here are, of course, important only as they relate to the small size of most of the eggs, and hence to their availability to primitive forms. The total biomass of gametes may be very large. In some fishes, the spawn depletes the adult of 70 percent of its mass. In most free-living marine creatures the mature gonads are of the order of five to 20 percent (Cushing, 1973) [up to 30 percent in the adult female capelin (Prokhorov, 1968), 5.6 percent for the adult male trout, and 10 percent for the adult female trout (Hopkins, et al., 1969; for this particular reference we found there to be no calculable difference between the marine and freshwater reservoirs)] of the adult weight and the release of the products represents from half to twice the somatic accretion. In parasitic forms, the gonads may constitute almost the entire mass [e.g., mature *Sacculina* exists merely as reproductive organs accompanied only by the necessary feeding processes (Lapage, 1951)].

There appears to be no question that the eggs and sperm are a somewhat higher quality food than is the adult somatic material. This appears particularly so for creatures that are of low food quality, such as echinoderms and salps, and less so for fatty fishes.

Clearly, also, reproduction is a heavy burden to growth. All marine creatures undergo growth discontinuity as a result of gamete production (and some expire). In almost all individuals, total weight increases rapidly with age only to sexual maturity. At that point, the general rate of growth sharply slows. Two instructive examples will suffice: One is the briefly paedogenic (dissogenous) ctenophore that displays two growth discontinuities —the first at onset of larval egg production, followed by the resumption of growth, and an ultimate flattening at onset of adult reproduction (Hirota, 1973). Another is the abalone—the extensive data of Tutschulte (1976) on abalone growth displays a decrease of growth at maturity almost precisely accounted for by gamete production.

It is not certain that gamete production results in an *increasingly* important flux in the higher forms. but it appears to be likely or at any rate important. Some of the crustacea retain their modest number and quantity of eggs and developing larvae (and hence, maintain them for a time for an "upward" flux upon predation), whereas many others as well as the pelagic fishes produce a much larger quantity of gametes and release them freely, where they are mainly available to lower forms. There seems to be some logic in having a species' reproductive products feed a range of potential prey rather than feed its unquestioned predator, although the development of specialists feeding on eggs presumably reverses this advantage (as perhaps for insects), also, the overall effect of this tactic when generally practiced by most species decreases the available food in the system, as will be indicated later.

What *does* become of the reproductive material in the sea? The sperm must be available to filter feeders of fine material (larvaceans, mussels) and to protozoa and bacteria; and the eggs to the coarser feeders (salps, small fish, copepods) and, in the case of the clupeoids, to the adults themselves.

Of course, the importance of reproductive products as food is not restricted to the sperm and eggs, but extends to the larvae for the period during which the egg material still constitutes a significant proportion of the larval mass and to asexually produced progeny also. Most of the food web of the ocean is conducted by immature creatures, and the food material of the gametes, by which they arose, undoubtedly remains of some importance for some time after hatching.

All of this flux is, in principal, a predaceous step on the adult, for the biomass otherwise could be devoted to adult growth. Hence, in effect, free-living copepods *do* eat tuna and mussels *do* eat yellowtail. It is this downward flux that typifies the reproduction in the marine food web, and is in marked contrast with the terrestrial system where rabbits undoubtedly do *not* eat young foxes.

Some quantification of this flux in marine food webs can be gleaned from various sources of data, and rough averages will suffice here. Conversion of food material into growth above first consumer level appears to be of the order of 20 percent of the intake [e.g., the adult brown trout has a conversion factor of around 18.7 percent (Cushing, 1968; again we ascertained no difference between fresh and salt water reservoirs)]. The relative gamete production (i.e., the ratio of the adult mass that is devoted to reproductive products and that converted into growth) appears to be perhaps one-quarter to two. This is in conservative agreement with adult versus juvenile growth rates. Since this gamete loss mainly flows downward in the food web, it is successively lost to higher levels and a simple expression will qualitatively demonstrate its magnitude and importance.

Consider an unstructured food web where the potential biomasses of three components can be expressed as follows:

$$(1) \quad M_p = \frac{M_0 K_1^2}{K_2}, \text{ predators;}$$

$$(2) \quad M_\mu = M_0 \frac{K_1(1-K_1)}{K_2}, \text{ particle feeders;}$$

$$(3) \quad M_d = M_0 \frac{K_1 K_3}{K_2}, \text{ detrital feeders;}$$

where M_0 is an input and K_1, K_2 and K_3 are the transfer coefficients for conversion of a substrate to living, non-recoverable, and dead recoverable material, respectively.

Now letting $K_1 \simeq 0.2$, and $K_3 \simeq 0.3$ ($K_2 = 0.5$), the effect of reproductive products equal to a value of 0.1 of the substrate conversion coefficient can be crudely approximated by allowing K_1 to have the values 0.2 ± 0.1, while K_3 takes the values of 0.3 ∓ 0.1.

The condition $K_1 = 0.3$, $K_3 = 0.2$ can be considered to represent the case where reproductive products add directly to the adult biomass and continue "up" the food web, and $K_1 = 0.1$, $K_3 = 0.4$ the condition in which reproductive products are subtracted from the adult biomass and thrown into the particulate and detrital milieu.

The effects of these conditions on the potential biomasses of the three trophic types can be seen in table 1. The potential biomass of predators is reduced by a factor of 9, while the more primitive feeders are much less affected in this treatment. In respect to predators, detrital and particle feeders are increased by factors of 3 to 6, where reproductive products are considered to become part of the particulate and detrital material rather than part of the adult biomass and higher trophic steps.

TABLE 1.

	Potential Biomass/M_0		
Trophic Type	$K_1 = 0.3$ $K_3 = 0.2$	0.2 0.3	0.1 0.4
Predator	0.18	0.08	0.02
Particle feeder	0.42	0.32	0.18
Detrital feeder	0.12	0.12	0.08
TOTALS	0.72	0.52	0.28

Another result of this exercise is evident from the table. The total potential biomass of the three forms decreases by more than half from the first to the third condition. This is the consequence of the loss and multiple reprocessing of reproductive products and the attrition involved, in contrast to the first case.

It is, of course, unrealistic to classify reproductive products merely as detritus, for they undoubtedly are much more useful food, and a more appropriate treatment will be to consider them to constitute an additional independent food pyramid with separate transfer coefficients. Such treatment is presently underway and is expected to show intensified effects in the same direction as indicated in the crude treatment above. It is also unrealistic to employ generally the level of reproductive losses of *adults* in appraising a food web that is largely conducted by immature creatures. These two imperfections are somewhat compensatory, however.

It is nevertheless evident that gamete production may constitute a successively heavy attrition and barrier to the development of higher levels and mature creatures in the marine food web. This subtracts from the adult biomass and may be a strongly leveling and homogenizing influence, superimposed on the influence of detrital production, that restricts the trophic positions of marine organisms to a narrow range.

The downward flux of high grade material in the marine food web, and the barrier to high levels of production and to adulthood in the higher forms, also, is one of the important factors in maintaining a dominant population of both small and immature creatures in the ocean. It is one of the factors in the success of the sharks and marine birds and mammals, which avoid this important loss while profiting from its importance in other forms.

The marine case, thus, is in remarkable contrast with the upward flux of reproductive products in the macroscopic terrestrial environment, where adults of the *higher* forms add directly to their biomass and profit from the losses from lower steps, often minimizing the losses themselves and where the trophic processes are dominantly conducted by adults.

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Adapted by Susan E. Smith, Fullerton, California.

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SYSTEMATICS OF THE SOUTHERN RACES OF ORD'S KANGAROO RAT, *DIPODOMYS ORDII*

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ABSTRACT: Nongeographic and geographic variation were assessed in 20 samples (224 specimens) of Ord's kangaroo rat (*Dipodomys ordii*) from southern Texas and northern Mexico. Univariate and multivariate analyses were employed in consideration of geographic variation. *Dipodomys compactus* is arranged as a separate species from *D. ordii* and four races of *D. compactus* (*compactus*, *sennetti*, *largus*, and *parvabullatus*) are recognized. Both *compactus* and *ordii* possess different karyotypes and animals with these distinct karyotypes occur in south Texas without evidence of interbreeding.

Ord's kangaroo rat, *Dipodomys ordii*, is widely distributed in the western United States and northern Mexico. The species is highly polytypic as exemplified by the recognition of 38 subspecies (Hall and Kelson, 1959) of which 14 occur in southern Texas and adjacent Mexico.

Setzer (1949) arranged the southern subspecies of *D. ordii* into three complexes. One, comprising *D. o. sennetti* and *D. o. compactus* (later expanded by Hall, 1951, to include *D. o. largus* and *D. o. parvabullatus*), includes those populations occurring in south Texas and along the barrier islands of Texas and the Mexican state of Tamaulipas. A second consists of *D. o. obscurus*, *D. o. durranti*, *D. o. idoneus*, and *D. o. palmeri* which occur in northern Mexico excluding Chihuahua. Finally, the third group consists of *D. o. ordii*, *D. o. attenuatus*, and *D. o. extractus*, all of which occur in Chihuahua or western Texas.

Dipodomys sennetti and *D. o. compactus* were originally described as distinct species by Allen (1891) and True (1889), respectively, and stood as full species until Davis (1942), on the basis of morphology (i.e., external proportions, size of mastoid bullae, width of supraoccipital, and size and shape of the interparietal), relegated them to subspecific status under *D. ordii*. Setzer (1949:516) agreed with the conclusions of Davis and noted that "in any sizable sample of *Dipodomys sennetti* there are crania closely resembling those of *Dipodomys ordii ordii* and others closely resembling those of *Dipodomys compactus*."

Recent biochemical evidence suggests kangaroo rat populations inhabiting the barrier islands of Texas may represent a separate species from *D. ordii*. Johnson and Selander (1971) found that biochemical distinctions between *D. o. compactus* and other subspecies of *ordii* were as great as the differences between many of the recognized species in the genus *Dipodomys*. According to them, "the biochemical evidence supports the . . . view that *compactus* is not merely a subspecies of *D. ordii*" and "that it is much more distinctive genically than any other populations referred to *D. ordii*." Similarily, Best and Schnell (1974) noted that in the size and shape of the baculum, *compactus* was markedly distinct from other *ordii*. Consequently, they treated *compactus* as a separate species. However, it should be noted that neither Johnson and Selander (1971) nor Best and Schnell (1974) examined *D. o. sennetti* or any of the Mexican forms of *ordii*. Rather, in both studies the island subspecies were compared only with northern races of *ordii*. Stock (1974) reported a chromosomal distinction between *D. o. compactus* and other subspecies of *ordii*, but did not consider it to indicate a wide divergence among these taxa; hence, he treated both *compactus* and *sennetti* as subspecies of *ordii*.

The purpose of this analysis is to assess, quantitatively, the geographic variation in the southern

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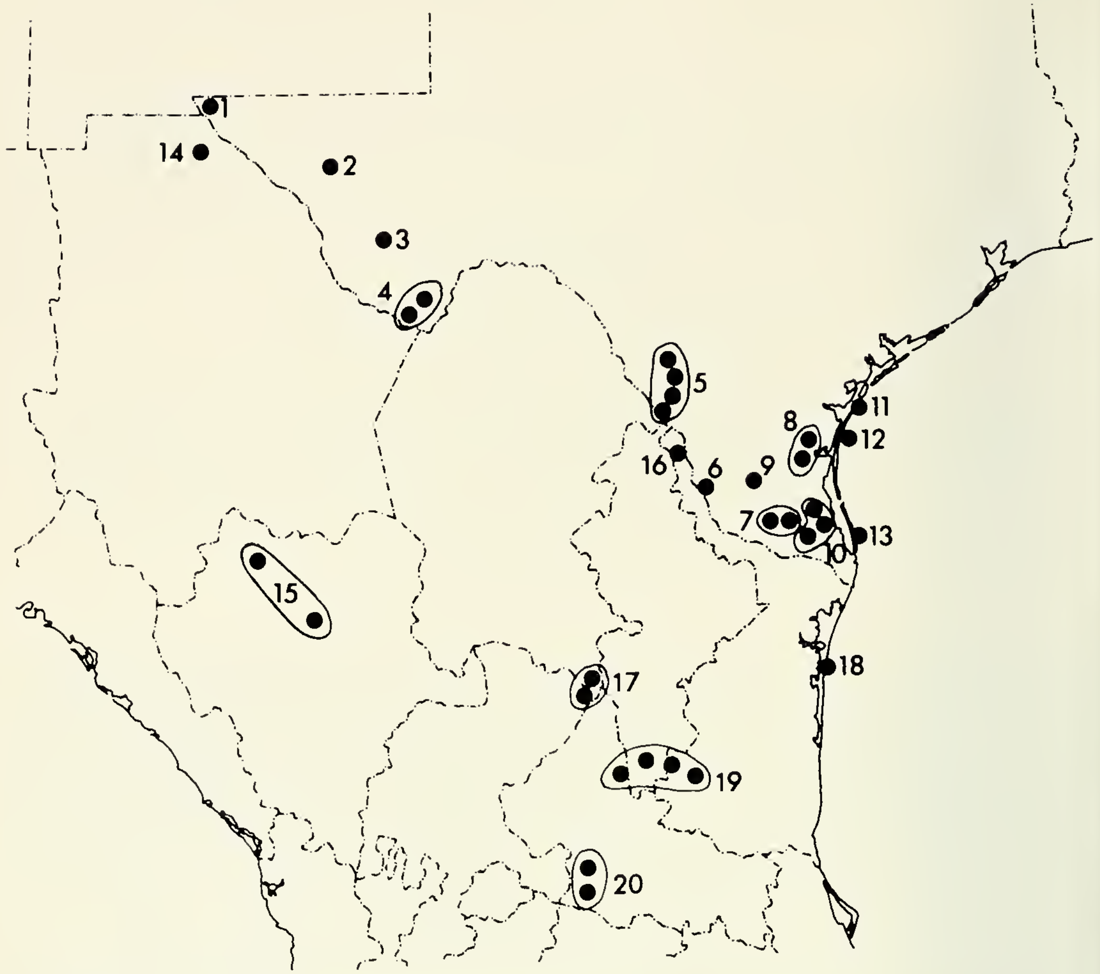

Figure 1. Sample areas used in analysis of geographic variation in *D. ordii* and *D. compactus*. See text for key to localities.

races of *D. ordii* in order to elucidate the taxonomic status of those populations occupying southern Texas and the Gulf Coast Islands of Texas and Mexico.

METHODS

In the morphological analysis, 244 specimens were examined from 45 different geographic localities. In many cases it was necessary to group specimens from several localities to obtain samples of sufficient size for statistical analysis. In so doing, we attempted to keep the sample area concerned as small as possible. We did not include specimens from more than one major physiographic region nor cross any previously recognized taxonomic boundaries. The following is a key to localities used in statistical analysis of geographic variation (sample size in parentheses): 1—El Paso, El Paso Co. (8); 2—Van Horn, Culberson Co. (16); 3—Paisano, Presidio Co. (9); 4—Big Bend, Brewster Co. (4); 5—Carrizo Springs, Dimmit Co. (6); 6—Zapata, Zapata Co. (5); 7—Willacy (10 mi NW Raymondville) and Hidalgo (Edinburg) Cos. (6); 8—Vicinity Kingsville, Kenedy Co. (13); 9—Hebbronville, Jim Hogg Co. (17); 10—Willacy (28 mi E Raymondville) and Kenedy (Rudolf) Cos. (10); 11—Mustang Island, Nueces Co. (26); 12—north Padre Island, Nueces Co. (10); 13—south Padre Island, Cameron Co. (22); 14—Samalayaca, Chihuahua (13); 15—Durango (11); 16—Nuevo Laredo, Tamaulipas (3); 17—Zacatecas and Coahuila (22); 18—Isla Boca Jesus Maria, Tamaulipas (6); 19—southern

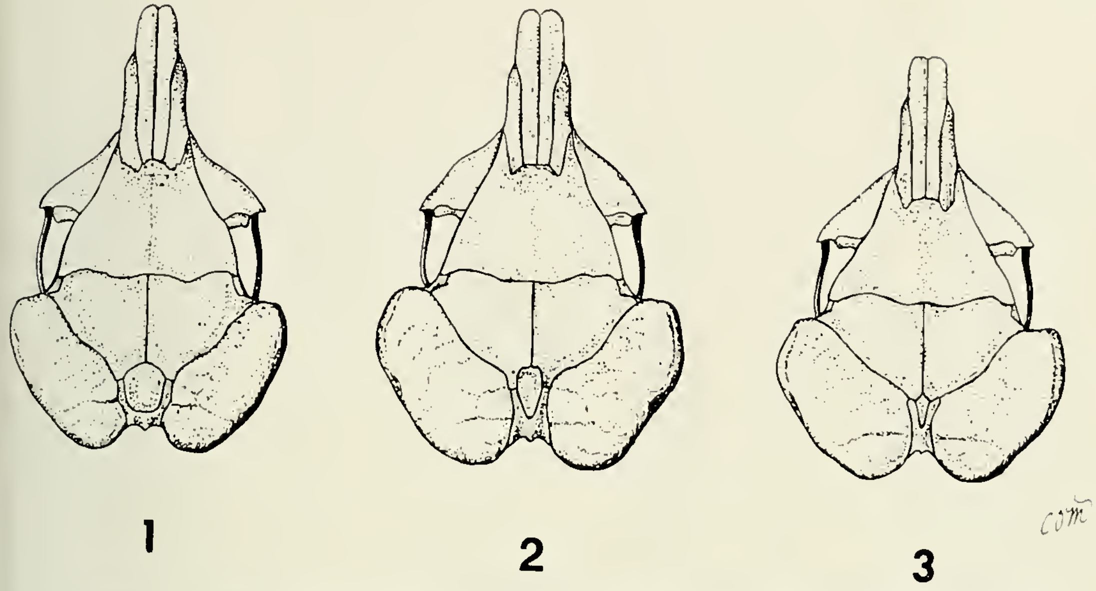

Figure 2. Dorsal view of skulls showing the degrees of inflation of the auditory bullae and the correlation of large bullae with small interparietal. Shapes of the interparietal were coded as follows: 1, wide and rectangular; 2, intermediate between condition 1 and 3; and 3, narrow and tapering. Drawing by C. O. Martin.

Tamaulipas, Nuevo Leon, and northern San Luis Potosi (17); 20—southern San Luis Potosi (20).

The following 15 characters (taken as defined by Desha, 1967) were analyzed because they could be expressed quantitatively and/or had been used to distinguish subspecies of *D. ordii* by previous workers: (the number of each measurement identifies that character at various places in the text and tables): 1) length of tail; 2) length of body; 3) length of hind foot; 4) greatest length of skull; 5) maxillary width; 6) least interorbital width; 7) greatest width of skull; 8) width of nasals; 9) length of nasals; 10) length of maxillary toothrow; 11) width of supraoccipital; 12) length of auditory bullae; 13) width of auditory bullae; 14) depth of skull; 15) shape of interparietal. All measurements are in millimeters; those recorded for the skull were taken with dial calipers in the laboratory; external dimensions are those recorded on specimen labels by field collectors. Depth of cranium was taken by using a glass microscope slide as described by Hooper (1952:10). The shape of the interparietal bone was coded as indicated in figure 2.

Univariate analyses were carried out using a computer program of the Statistical Analysis System (SAS), designed and implemented by Barr and Goodnight (Service, 1972). This program yields standard statistics (mean, range, standard deviation, standard error of the mean, variance, and coefficient of variation) and, when two or more groups are being compared, employs a single-classification analysis of variance (F-test, $p < 0.05$) to test for significant differences between or among the means of the group.

We employed several multivariate techniques to cluster samples according to phenetic affinity. The NT-SYS programs developed by Rohlf and Kishpaugh (1972) were used to generate matrices of phenetic distance and correlation coefficients from standardized character values. Cluster analyses used the UPGMA option (unweighted pair-group method using arithmetic average) on the correlation and distance matrices. Only the correlation phenogram is illustrated because it yielded a higher cophenetic correlation value than did the distance phenogram.

To assess the degree of divergence among samples, we used a multivariate analysis of variance (MANOVA) and a canonical analysis program in SAS. Canonical analysis of the data aimed at providing weighted combinations of the measurements which maximize the distinction between the groups. This program extracts characteristic roots and vectors and computes mean canonical variates for each location. New orthogonal axes, termed

TABLE 1. Sexual and individual variation in a sample of kangaroo rats from Mustang Island, Nueces Co, Texas. Significant F-values ($P \leqslant .05$) are indicated by an asterisk.

	Males				Females				
Character	*N*	*Mean*	*SD*	*CV*	*N*	*Mean*	*SD*	*CV*	*F-Value*
Total Length	12	230.42	11.09	4.82	13	223.60	8.14	3.64	1.52
Tail Length	12	118.25	6.51	5.74	13	113.00	4.15	3.67	3.82
Body Length	12	112.17	7.17	6.39	13	110.60	8.44	7.64	.15
Hind Foot Length	12	38.33	1.37	3.58	13	37.60	2.19	5.83	.71
Skull Length	12	36.55	.79	2.16	13	36.51	.72	1.98	.15
Maxillary Width	12	19.28	.55	2.85	13	19.41	.60	3.03	2.03
Interorbital Width	12	12.13	.50	4.12	13	12.41	.48	3.85	1.10
Skull Width	12	21.68	.30	1.41	13	22.09	.28	1.25	6.59*
Rostral Width	12	3.74	.21	5.66	13	3.79	.10	2.70	.23
Nasal Length	12	13.84	.45	3.25	13	13.86	.58	4.18	.01
Length Max. Toothrow	12	4.95	.26	5.20	13	4.82	.18	3.78	1.03
Supraoccipital Width	12	3.54	.35	9.99	13	3.37	.26	7.68	.99
Length Mastoid Bullae	12	13.92	.29	2.10	13	14.17	.40	2.83	2.22
Width Mastoid Bullae	12	9.45	.40	4.20	13	9.58	.43	4.50	.34
Skull Depth	12	12.69	.32	2.54	13	12.85	.30	2.37	.88

canonical variates, are constructed which extract the next best combination of characters, emphasizing those with the least within-sample and the greatest between-sample variation, hence providing the next best combination of characters to discriminate among samples. Each eigenvalue and its corresponding canonical variate (characteristic root) represents an identifiable fraction of the total variation. Sample means and individuals were plotted on those canonical variates which account for the greater fractions of total variation. The relative importance of each original variable to a particular canonical variate was computed by multiplying the vector variable coefficient by the median value of the dependent variable, summing all variable values for a particular vector, and then computing the percent of relative importance of each variable per vector.

The data were also subjected to principal components analysis (PCA) which considers data from a single universe and creates, from the original axes, new orthogonal axes corresponding to the major trends of variation in the data. The samples are then projected onto the most important of these principal components. Principal components for the data of this study were extracted using the NT-SYS programs.

In certain situations, we attempted to determine the probability of incorrectly classifying a given specimen into one or two predefined groups of kangaroo rats. To determine the probability of misclassification (PMC), we utilized an approach developed by Guseman, Peters, and Walker (1975). This procedure utilizes linear combinations of all measurements to construct a Bayes optimal or maximum likelihood classification which minimizes the PMC. Since it is difficult to compute PMC accurately in dimensions greater than one, a nonzero vector of weights (called B vectors) were derived in order to convert the problem from a multidimensional to a unidimensional situation. A non-zero B vector was selected so that the PMC was minimized. This optimal minimizing B can be used to determine the weights for the particular measurements (called b-values) and ascertain those measurements which contribute most to being able to discriminate between the two classes.

Karyotypes were prepared using the *in vivo* bone marrow technique described by Lee (1969). At least five somatic spreads were examined for each specimen. Metacentric, submetacentric, subtelocentric, acrocentric, and number of autosomal arms (NA) were used as defined by Stock (1974).

MORPHOLOGICAL VARIATION

Non-geographic variation

Age variation.—Using Desha's (1967) criteria specimens were separated according to sex and age as juveniles, subadults, or adults. Statistica analysis among populations was made only for adult kangaroo rats.

Sexual variation.—Analysis of variance was used to test each of 15 measurements in a sample from Mustang Island to determine if the means

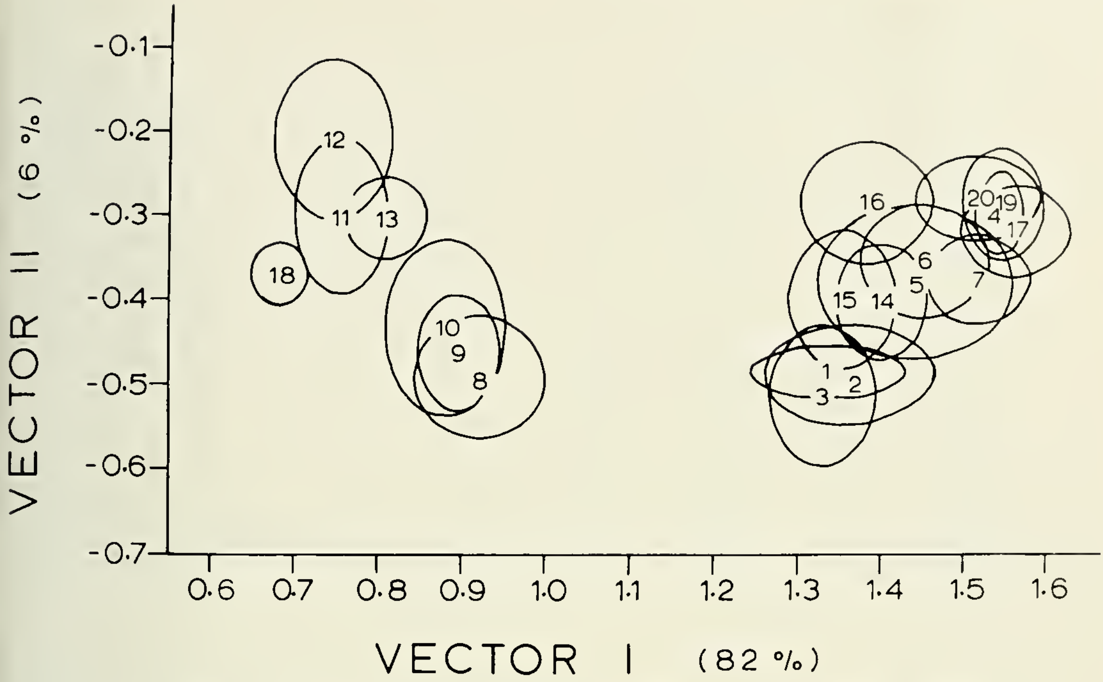

Figure 3. Projections of the first two canonical vectors illustrating the phenetic position of all samples of *Dipodomys.* Numbers are positioned at the mean value for each sample in the character space; the ellipse surrounding each number represents one standard deviation around the mean. The group of means to the left corresponds to samples of *compactus*: these to the right, to samples of *ordii*. See text for key to samples.

were significantly different between sexes (Table 1). No significant differences were found between the sexes except that females have a significantly wider skull than males at the 0.05 level. Males average slightly larger than females in all external features, whereas females were slightly larger in most cranial features.

The limited extent of sexual dimorphism in southern populations of *D. ordii* is surprising since Schmidly (1971) noted considerable sexual dimorphism in populations of this species from the Texas Panhandle. Because he also demonstrated that the degree of secondary sexual dimorphism varied from population to population in *D. ordii*, we repeated all statistical procedures for analyzing geographic variation using only male specimens and compared the results with those obtained for the sexes combined. We detected no obvious differences, hence, our tables and figures present data for males and females combined.

Individual variation.—Coefficients of variation of three external measurements used in this study in a series of adults from Mustang Island ranged from 3.58 (length of hind foot for males) to 7.64 (length of body for females); in cranial measurements they ranged from 1.41 (greatest width of skull in males) to 9.99 (supraoccipital width in females). These values are within the range of those for other samples of *D. ordii* from the northern portion of the species range (Schmidly, 1971). Males had higher coefficients of variation in nine measurements; females in six.

Geographic variation

Four different criteria (Hotelling-Lawley's Trace, Pilla's Trace, Wilks' Criterion, and Roy's Maximum Root Criterion) were used to test for the hypothesis of no overall locality effect (i.e., no significant morphological difference among samples) in the MANOVA. All four tests produced F-values that were significant at $P < .0001$; thus, significant morphological differences among samples are assumed to exist due to the effect of locality.

The first three canonical variates were computed from the variance-covariance matrix among

TABLE 2. Variable coefficients for canonical variates I and II with an estimate of the percent influence of each variable on each vector for all samples of *D. ordii* and *D. compactus*.

	Vector I		Vector II	
Character	Variable Coefficient	Percent Influence	Variable Coefficient	Percent Influence
1	0.0049	10.19	0.0076	16.26
2	–0.0022	3.68	0.0010	1.93
3	–0.0022	1.28	0.0220	13.45
4	–0.0389	22.90	–0.0151	9.34
5	–0.0003	.09	–0.0153	5.16
6	0.0109	2.23	0.0054	1.16
7	0.0436	15.82	–0.0356	13.55
8	–0.0596	3.52	0.1821	11.27
9	–0.0167	1.67	–0.0038	.85
10	–0.0603	4.63	–0.0824	6.64
11	–0.0343	1.47	0.0357	1.61
12	0.0746	17.29	–0.0148	3.59
13	0.0398	6.33	–0.0498	8.34
14	0.0135	1.35	–0.0238	5.24
15	0.1314	4.17	0.0484	1.61

the 15 characters for all 20 samples. The first canonical variate expresses 81.7 percent of the phenetic variation, the second 5.5, and the third 2.9. Two-dimensional plots of the first two canonical variates (including the mean and one standard deviation to either side of the mean for each sample) are shown in figure 3. Examination of figure 3 reveals two major groupings of kangaroo rat samples separated by a large hiatus within the character space. The group to the left, hereafter called the *compactus* group, includes samples of *D. o. compactus* (samples 12 and 13), *D. o. sennetti* (8, 9, and 10), and *D. o. parvabullatus* (18). The group to the right, hereafter called the *ordii* group, contains all samples of the Mexican and southwestern subspecies of *D. ordii* and three samples (5, 6, and 7) from south Texas which are currently assigned to the subspecies *sennetti* of the *compactus* group. Thus, members of both the *compactus* and *ordii* groups occur in south Texas. The *ordii* group (samples 5, 6, and 7) is known from Hidalgo, Webb, Willacy, Zapata, and Dimmit counties; the *compactus* group (samples 8, 9, and 10) occurs in Willacy, Kleberg, Kenedy, and Jim Hogg counties. The ranges of the two groups approach one another near Raymondville in Willacy County, where they have been found less than 15 miles apart.

The relative contributions of each character to the first two canonical variates are given in table 2. The major separation between the two main groups occurs along Vector I (Table 2, Fig. 3). Vector II primarily separates samples within each of the two main groups. Those characters having the highest percent influence on Vector I reflect size of the skull and especially the degree of inflation and size of the auditory bullae. Greatest length of skull, width of skull, and length of the auditory bullae all exert a heavy influence on this vector. The means (± one standard deviation) for all samples of the *ordii* group for these measurements are: greatest length of skull, 37.28 ± .80; width of skull, 23.98 ± .51; and length of auditory bullae, 15.76 ± .40. For the *compactus* group these same measurements, respectively, average 36.68 ± .78; 22.18 ± .53; and 14.14 ± .41. Of the external measurements, length of tail has the greatest influence on the first two vectors, whereas length of body has the least influence. Mean length of tail (± one standard deviation) for members of the *compactus* group is 118.13 ± 5.54; that of the *ordii* group, 136.38 ± 6.17.

The rationale for the use of MANOVA and projection onto canonical axes is that the variation within all of the samples is homogenous. If the within-group variation is not homogenous, then it is difficult to make use of the within-sample information and one must rely on the among-sample variation (Rohlf, 1971). The most appropriate multivariate statistic for the latter situation is principal components analysis (PCA). The first three factors in PCA accounted for 83.25 percent of the total variation (51.23 percent for Factor I; 20.63 for II; and 11.39 for III). The phenetic relationships of the sample means in the PCA analysis were similar to that for the canonical analysis and, for this reason, they have not been illustrated.

In order to compensate for some of the disadvantages of ordination techniques (for a discussion of some of these see Sneath and Sokal, 1973:251–253), another multivariate method (cluster analysis) was utilized to analyze the data. Means of each sample for the 4 external and 11 cranial measurements were used in a NT-SYS clustering analysis. A phenogram diagramming the phenetic relationships of all samples was computed by cluster analysis from correlation matrices and is presented in figure 4. The samples in this phenogram also divide into two major clusters, designated A and B in figure 4, identical to the two groups obtained using the ordination techniques. Cluster A includes all samples of the Mexican and Southwestern subspecies of *D. ordii*

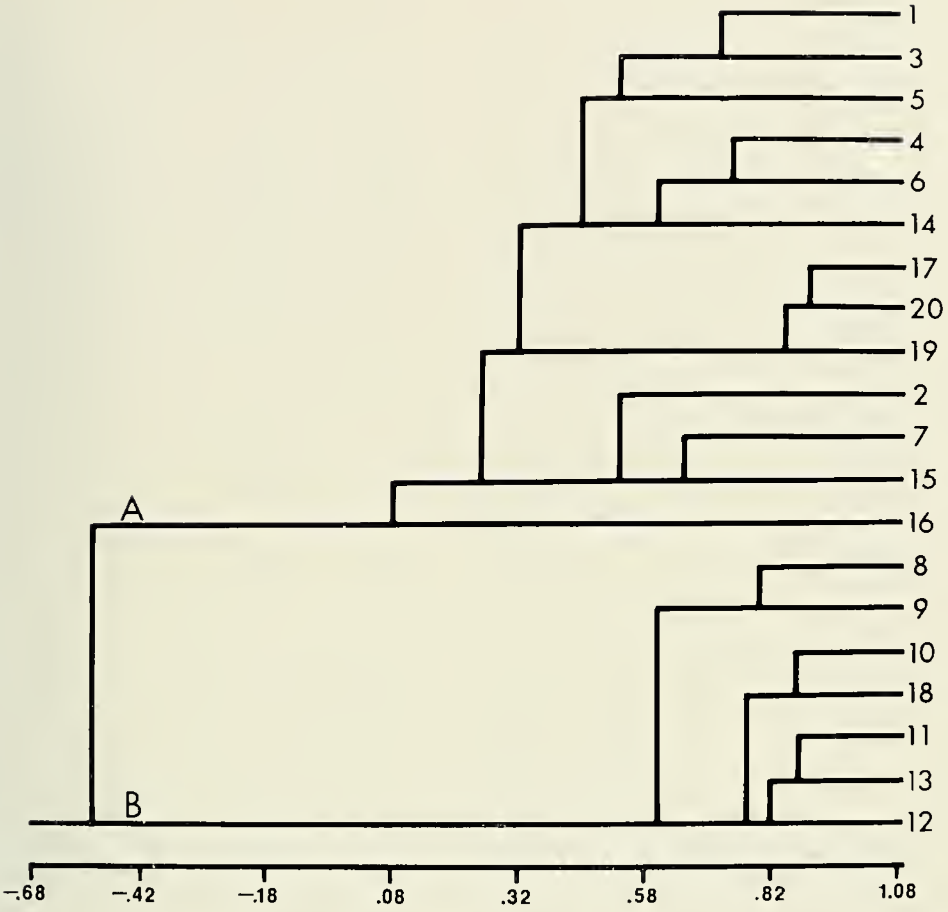

Figure 4. Correlation phenogram resulting from cluster analysis of 20 geographic samples (see Fig. 1) of *D. ordii* (branch A) and *D. compactus* (branch B).

plus samples 5, 6, and 7 from south Texas; cluster B includes all remaining south Texas samples (8, 9, and 10) plus those from the islands off Texas and Tamaulipas, Mexico. The cophenetic correlation coefficient for the phenogram is 0.938, which indicates that the phenogram accurately reflects values in its original similarity matrix.

Assuming that two morphological groups of kangaroo rats are present in the southern portion of the range of *D. ordii*, we attempted to determine the probability of misclassifying a given specimen into the wrong group. To do this, we assigned each specimen *a priori* to either the *compactus* or the *ordii* group on the basis of the results of the ordination and cluster analysis. The probability of misclassification (PMC) was calculated using Basian classification rules and is presented in table 3; the relative contribution of each character in discriminating between the two groups is indicated by the magnitude of the b-values of the table. Initially, 12 characters were used and the PMC was less than one percent (0.37 percent). In succeeding runs we eliminated the two characters with the lowest b-values, thus removing from consideration those characters having the least value in discriminating between the two groups of kangaroo rats. Theoretically, this should have increased the PMC somewhat because relevant information was discarded. In our situation, however, the PMC increased only slightly as the number of characters was reduced from 12 to 4 (Table 3); the PMC in all these cases remained less than one percent. Using only two characters, the PMC was 1.56 percent. In our opinion, these low PMC values reflect the distinctness of the two groups of kangaroo rats. In each case the characters which contribute the most to separating the two groups (as reflected by

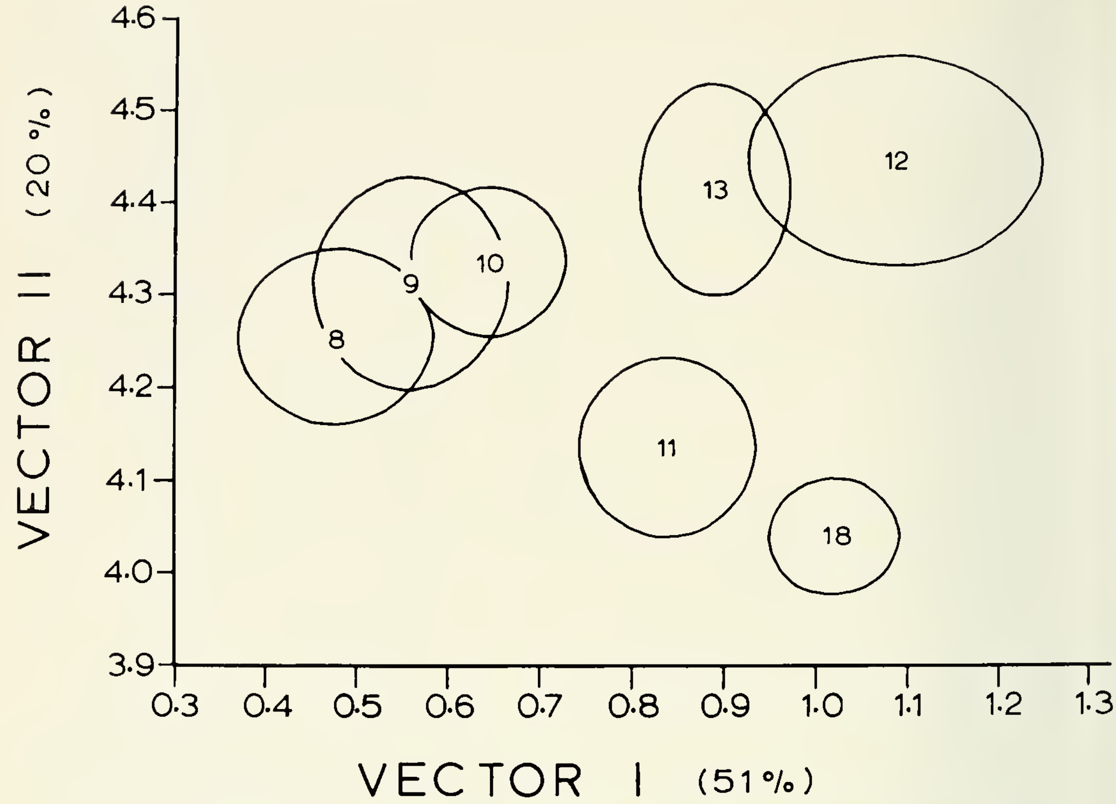

Figure 5. Projections of the first two canonical vectors illustrating the phenetic position of the seven samples of *D. compactus*. Numbers are positioned at the mean value for each sample in the character space; the ellipse surrounding each number represents one standard deviation around the mean. See text for key to samples.

higher b-values) are width of supraoccipital and length of auditory bullae. Members of the *ordii* group have a supraoccipital width that ranges from 1.0 to 2.9 mm; in the *compactus* group, from 2.5 to 4.2 mm. However, of the 140 specimens of *ordii* only five have a supraoccipital width exceeding 2.7 mm; only four of the 105 specimens of *compactus* have a supraoccipital width less than

Table 3. Six procedures (a–f) for calculating the probability of misclassification (PMC) between the *compactus* and *ordii* groups using selected morphological measurements. The numbers in the table (called b-values) reflect the discriminatory power of each character. In each successive procedure, the two characters with the lowest b-values (poorest discriminators) were eliminated.

Procedure	Tail Length	Greatest Skull Length	Maxillary Width	Least Interorbital Width	Greatest Skull Width	Rostral Width	Nasal Length	Length Maxillary Toothrow	Supraoccipital Width	Length Mastoid Bullae	Width Mastoid Bullae	Depth of Skull	PMC	
a.	.476	–.420	.137	.080	.079	.001	–.004	–.127	–.616	.401	.061	.061	.0037	(12)
b.	.475	–.422	.136	.079	.080			–.126	–.616	.400	.061	.061	.0037	(10)
c.	.479	–.412	.141	.091	.136			–.131	–.594	.428			.0038	(8)
d.	.436	–.445	.181		.134				–.602	.444			.0048	(6)
e.	.472	–.300							.600	.571			.0065	(4)
f.									–.967	.253			.0156	(2)

TABLE 4. Variable coefficients for canonical variates I and II with an estimate of the percent influence of each variable on each vector for samples of *D. compactus.*

	Vector I		Vector II	
Character	Variable Coefficient	Percent Influence	Variable Coefficient	Percent Influence
1	0.0011	1.17	0.0138	10.76
2	0.0036	3.21	–0.0001	.07
3	0.0226	6.82	–0.0184	4.45
4	0.0482	14.56	0.0755	18.27
5	0.0194	3.17	0.0207	2.70
6	0.0187	1.92	–0.0286	2.36
7	–0.0262	4.75	0.1762	25.58
8	0.1432	4.45	0.0027	.06
9	–0.0071	.80	–0.1588	14.29
10	0.2621	10.80	0.0861	2.84
11	0.0315	.90	–0.0286	.66
12	–0.2550	29.41	–0.0470	4.34
13	–0.1443	11.29	–0.1367	8.57
14	0.0606	6.43	0.0492	3.54
15	–0.0363	.32	–0.2100	1.50

2.7 mm. Length of auditory bullae ranges from 12.6 to 15.7 mm in specimens of *compactus*; from 14.6 to 16.7 mm in *ordii*. Only three specimens of *compactus* have an auditory bullae exceeding 15.1 mm in length, whereas only nine specimens of *ordii* have less than 15.1 mm. Thus, most specimens of the two groups are readily identifiable by these two cranial measurements. If taxonomic placement of a specimen is doubtful, combinations of other variables (such as width of skull and length of tail) are sufficient to discriminate between the two groups.

To ascertain patterns of geographic variation within the *compactus* and *ordii* groups, each one was separately subjected to canonical analysis. The projection of the *compactus* group is presented in figure 5 and the canonical coefficients for each vector are given in table 4. Vector I accounts for 50.9 percent of the variance and primarily separates the south Texas mainland samples (8, 9, and 10) from the island samples (11, 12, 13, and 18). The highest canonical coefficients for this vector are those for width and length of the auditory bullae, and greatest length of the skull. Vector II accounts for 20.2 percent of the variance and separates samples 11 and 18 from samples 12 and 13. The characters with the highest influence on this vector are width of skull, greatest length of skull, and length of the nasal bones.

The samples in figure 5 fall into four groups which correlate closely with currently recognized subspecies of the *compactus* group (as given in Hall and Kelson, 1959). One group includes samples 8, 9, and 10 from south Texas, which are referable to the subspecies *sennetti*. A second group consists of samples 12 and 13 from Padre Island, which are referable to the subspecies *compactus*. The third group includes a single sample (11) from Mustang Island referable to the subspecies *largus*. Group four also consists of a single sample (18) from Isla Boca Jesus Maria, Tamauli-

TABLE 5. Variable coefficients for canonical variates I, II, and III with an estimate of the percent influence of each variable on each vector for all samples of *D. ordii.*

	Vector I		Vector II		Vector III	
Character	Variable Coefficient	Percent Influence	Variable Coefficient	Percent Influence	Variable Coefficient	Percent Influence
1	0.0119	10.33	0.0034	2.66	–0.0045	4.81
2	–0.0047	3.12	–0.0010	.60	–0.0024	1.96
3	0.0366	8.41	–0.0180	3.84	0.0426	12.40
4	–0.0899	21.42	0.0518	11.17	–0.0257	7.55
5	–0.1087	14.22	0.0470	5.56	–0.0572	9.23
6	0.0522	4.33	0.0788	5.96	–0.0646	6.67
7	0.0716	10.96	–0.1567	21.77	0.1279	24.19
8	0.0599	1.33	–0.0267	.54	–0.1581	4.38
9	0.0309	2.61	–0.1162	8.98	0.0063	.66
10	–0.1894	5.80	0.1502	4.16	0.0747	2.81
11	0.0079	.12	–0.1109	1.25	–0.0826	1.27
12	0.1098	10.96	–0.1387	12.57	–0.0485	5.98
13	–0.0556	3.76	0.3287	20.09	0.1499	12.47
14	0.0229	1.97	0.0080	.61	–0.0199	2.08
15	0.0355	.57	–0.0112	.16	–0.1749	3.52

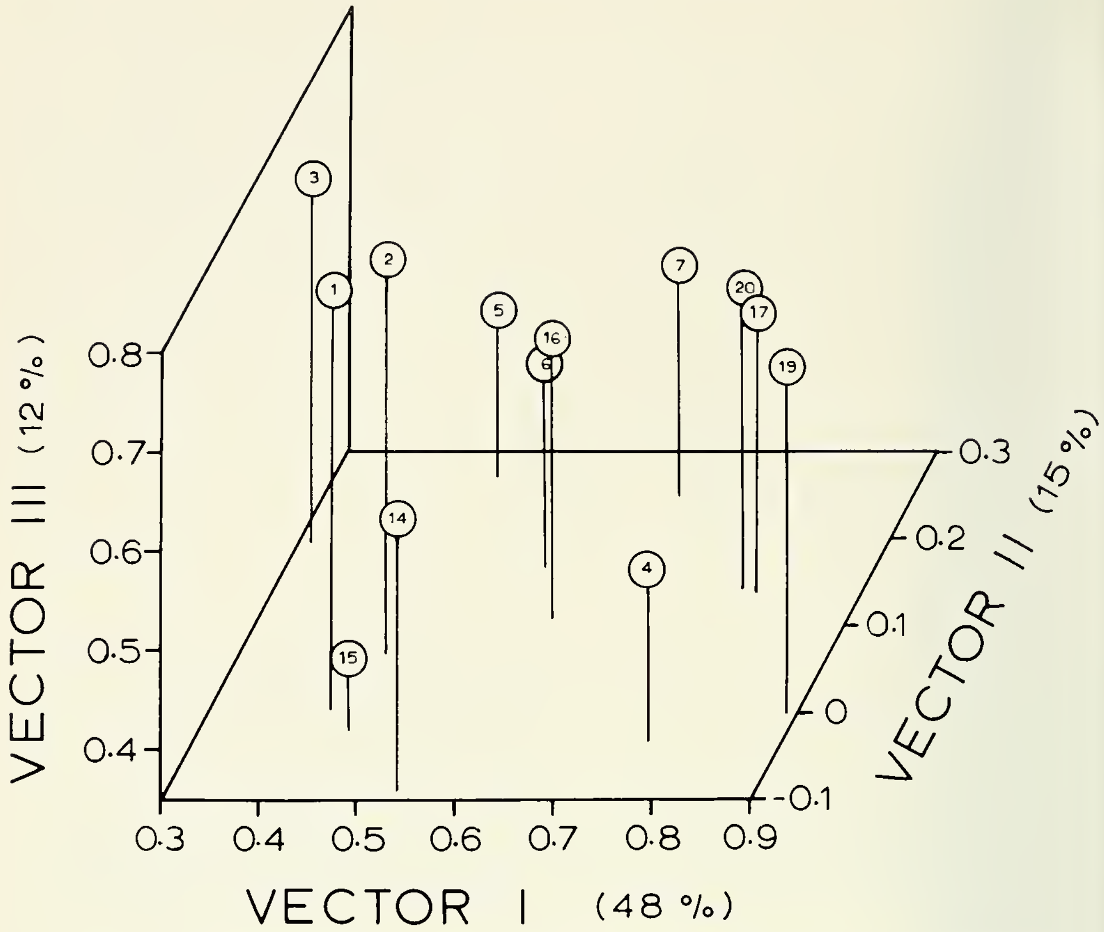

Figure 6. Three-dimensional projections of the 13 samples of *D. ordii* onto the first three canonical vectors. See text for key to samples.

pas, which is referable to the subspecies *parvabullatus*.

The pattern of geographic variation within the *ordii* group is much more complicated than that of the *compactus* group and in order to depict properly the phenetic relationships of the samples in this group it was necessary to prepare a three-dimensional stereogram of the canonical vectors. The three-dimensional projection is presented in figure 6 and the canonical coefficients for each vector are given in table 5. Vectors I, II, and III account for 48, 15, and 12 percent of the variance, respectively, in this analysis. Samples 4, 17, 19, and 20 are separated from the other samples along Vector I. Characters having considerable influence on this vector include skull length, skull width, maxillary width, and length of the auditory bullae. Vector II separates out samples 1, 2, 4, 14, 15, and 19 with skull width, length and width of the auditory bullae, and skull length having high canonical coefficients. Vector III separates out samples 5, 6, 7, and 15; characters with high canonical coefficients for this vector include width of skull, width of auditory bullae, and length of hind foot.

Six recognizable phenetic groups from the canonical analysis are evident among samples of *D. ordii*. Group one includes samples 1, 2, and 3 from Trans-Pecos Texas which are referable to the subspecies *D. o. ordii*. Group two is composed of a single sample (14) from Chihuahua which is referable to the subspecies *D. o. extractus*. A third group (sample 15 from Durango) also consists of a single sample and is referable to the subspecies *D. o. obscurus*. Group four includes samples 5, 6, and 7 from south Texas and sample 16 from Nuevo Laredo, Tamaulipas. According to Setzer (1952), sample 16 is referable to the subspecies *D. o. durranti* but the samples from south Texas are presently not referable to any subspecies of *D. ordii* since previously they were thought to belong to the *compactus* group. Group five includes samples 17, 19, and 20 from southern and northeastern Mexico. Two of the samples (nos. 17 and 19 from Nuevo Leon and Tamaulipas) are referable to *D. o. durranti*; the other (no. 20 from southern San Luis Potosi) to *D. o. palmeri*. Group six consists of a single sample (4) from the Big Bend of Texas which is referable to the subspecies *D. o. attenuatus*.

CHROMOSOMAL VARIATION

Stock (1974) examined karyotypes from six specimens of Ord's kangaroo rat from two localities (Padre Island, Cameron Co; and Benivedes, Duval Co) in south Texas. He reports the karyotypes of *compactus* and *sennetti* are identical but different from other populations of *D. ordii* in possessing an additional pair of small submetacentric chromosomes.

We have examined two specimens of *D. compactus largus* (from Mustang Island), five *D. c. sennetti* (from Kenedy and Brooks counties), and eight *D. c. compactus* (from north and south Padre Island) and find them to be karyotypically identical to specimens examined by Stock (1974: 510, fig. 2B). The diploid number (2N) is 74 and the number of autosomal arms (NA) is 144. The autosomal compliment consists of 4 metacentric chromosomes, 27 submetacentrics, and 5 subtelocentrics. Four specimens from Dimmit County in south Texas, however, differ karyotypically from *compactus* and *sennetti*. These specimens have a karyotype identical to that for the northern subspecies of *ordii* (*D. o. monoensis*, *D. o. fetosus*, *D. o. richardsoni*, and *D. o. oklahomae*) reported by Stock (1974: 510, Fig. 2A). The 2N is 72 and the NA is 140. The autosomal compliment consists of 25 pairs of size-graded biarmed chromosomes, varying in centromeric position from metacentric to subtelocentric. The X chromosome is large and metacentric; the Y, small and acrocentric.

The chromosomal differences between *compactus*, *largus*, and *sennetti* on the one hand and the subspecies of *ordii* on the other parallel the morphological distinctions between these forms. Chromosomal evidence supports the hypothesis that more than one kind of kangaroo rat is present in south Texas since both the "*compactus*" and the "*ordii*" karyotypes are known from the area.

TAXONOMIC CONCLUSIONS

We interpret the morphological data as revealing that southern populations of Ord's kangaroo rat represent more than one biological species. The morphological divergence of the island populations and of certain populations in south Texas parallels their biochemical (Johnson and Selander, 1971), chromosomal (Stock, 1974), and bacular (Best and Schnell, 1974) differences from *D. ordii* and is sufficient in our opinion to warrant their recognition as a distinct species from the other populations of *ordii*. The earliest available name for the south Texas and island populations is *Dipodomys compactus*. The fact that both *ordii* and *compactus* occur in Texas without evidence of interbreeding is further proof that they are distinct species. The ranges of the two groups come within 15 miles of one another in Willacy County and all trenchant morphological and chromosomal differences between them are maintained. The ecological and/or physical factors which separate *ordii* and *compactus* are currently unknown, although one of us (Schmidly) is investigating the distribution and ecology of the two forms in south Texas.

Within *D. compactus*, four subspecies may be recognized: *D. c. compactus* from Padre Island; *D. c. largus* from Mustang Island; *D. c. parvabulatus* from Isla Boca Jesus Maria, Tamaulipas; and *D. c. sennetti* from the south Texas mainland.

Of considerable interest at this time is the discovery of disjunct populations of *D. ordii* in south Texas from Dimmit, Zapata, Webb, and Willacy counties. Phenetically, these samples are most like specimens of *ordii* from Nuevo Laredo, Tamaulipas, which have been referred to the subspecies *durranti* by Setzer (1949, 1952). For this reason, we tentatively are referring the south Texas *ordii* samples to *D. o. durranti*. However, our analysis shows the Nuevo Laredo specimens are markedly different from topotypes of *durranti*. In our opinion, the south Texas *ordii* and the sample from Nuevo Laredo may constitute an undescribed subspecies. One of us (Schmidly) is currently investigating the genetic and taxonomic relationships of these populations.

At this time we are not recommending additional nomenclatural changes regarding the Mexican and western Texas samples because we have not seen certain critical specimens from Coahuila and Chihuahua. However, our impression is that many of the currently recognized subspecies are not sufficiently distinct to warrant recognition. For example, specimens of *D. o. palmeri* from San Luis Potosi are virtually impossible to distinguish from representatives of *D. o. durranti* from Coahuila and Tamaulipas.

SPECIMENS EXAMINED

Dipodomys compactus compactus. TEXAS. *Cameron Co*: 2 mi E, 6 mi N Port Isabel, 12 (UIMNH), 10 (TCWC). *Nueces Co*: Padre Island, 9 (USNM); 3.6 mi S Bob Hall Pier, 1 (TAI).

Dipodomys compactus largus. TEXAS. *Nueces Co* (all from Mustang Island): 5 mi SW Port Aransas, 5 (TNHC); 14 mi SW Port Aransas, 5 (KU); 15 mi SW Port Aransas, 1 (TCWC); 19 mi SW Port Aransas, 15 (TCWC); 23 mi SW Port Aransas, 1 (TCWC).

Dipodomys compactus parvabullatus. TAMAULIPAS. 88 mi S, 10 mi W Matamoros, 7 (KU); 90 mi S, 10 mi W Matamoros, 7 (KU), 1 (USNM).

Dipodomys compactus sennetti. TEXAS. *Jim Hogg Co*: 20 mi S Hebbronville, 17 (TNHC). *Kenedy Co*: 2.2 mi S Miflin, US Hwy 77, 1 (TAI); 12 mi S Sarita, 3 (TCWC); 1 mi E Rudolf, Norias Division King Ranch, 3 (TCWC). *Kleberg Co*: 2 mi S Riviera, 8 (TCWC); La Noria, 1 (TCWC). *Willacy Co*: Sauz Ranch, 2 (USNM); Red Fish Bay, 28 mi E Raymondville, 1 (TCWC); Santa Rosa, 4 (USNM).

Dipodomys ordii attenuatus. TEXAS. *Brewster Co*: Cooper's Well, 47 mi S Marathon, 3 (MVZ); mouth St. Helena Canyon, Rio Grande, 1 (MVZ), 1 (TCWC); Johnson's Ranch, Rio Grande, 1 (TCWC).

Dipodomys ordii durranti. COAHUILA. San Juan Neponuceno, 5 mi N La Ventura 4 (MVZ); La Ventura 6 (USNM). NUEVO LEON. Dr. Arroyo, 1 (USNM). SAN LUIS POTOSI. 7.6 mi S Matehuala, 2 (MVZ). TAMAULIPAS. Jaumave, 8 (USNM); Miquihuana, 6 (USNM). ZACATECAS. Lulu, 12 (MVZ). TEXAS. *Dimmit Co*: 2 mi NE Carrizo Springs, 1 (TCWC); 10 mi SW Carrizo Springs, 1 (TCWC); 2 mi SW Asherton, 2 (TCWC). *Hidalgo Co*: 17 mi NW Edinburg, 1 (TNHC). *Webb Co*: 40 mi SW Catarina, on Rio Grande, 2 (TNHC). *Willacy Co*: 10 mi NW Raymondville, 5 (TNHC). *Zapata Co*: 5 mi N Zapata, 1 (TNHC); 3½ mi NE Zapata, 4 (TNHC). TAMAULIPAS. Nuevo Laredo, 3 (USNM).

Dipodomys ordii extractus. CHIHUAHUA. 1 mi E Samalayuca, 13 (MVZ).

Dipodomys ordii obscurus. DURANGO. Rosario, 4 (AMNH); Rio de Bocas, 7 (AMNH).

Dipodomys ordii ordii. TEXAS. *Culberson Co*: 16 mi SE Van Horn, 16 (TCWC). *El Paso Co*: 3 mi NE city limits El Paso, 8 (MVZ). *Presidio Co*: 2 mi S Paisano, 9 (TCWC).

Dipodomys ordii palmeri. SAN LUIS POTOSI. 2 mi NW San Luis Potosi, 2 (MVZ); Jesus Maria, 18 (USNM).

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CALCANEA OF MEMBERS OF THE MUSTELIDAE. PART I, MUSTELINAE

Howard J. Stains[1]

Abstract: The calcanea of 20 species (7 genera) of members of the Mustelinae are described and compared. All species have a well-developed trochlear process and sustentaculum. The anterior articular surface is absent in 14 of the 20 species (all *Mustela* and most *Martes*). The genera *Martes* and *Mustela* are much alike except for size. *Galictis* is the most aberrant, approached most closely by *Poecilictis*. *Poecilogale* is close to *Mustela*; *Eira* and *Gulo* close to *Martes*.

The calcaneum of representatives of the subfamilies Mustelinae, Mellivorinae, Melinae, Mephitinae, and Lutrinae were examined. Only those of the Mustelinae will be reported here with general characteristics of the remaining subfamilies mentioned so that members of these subfamilies may be distinguished from the Mustelinae.

The shape of the calcaneum of members of the Mustelinae is what one might envision as a generalized type with a well-developed trochlear process and sustentaculum. The trochlear process usually is ungrooved or faintly grooved, lies mainly distal to the sustentaculum, and is usually

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distinct and knob-like. The posterior articular surface usually forms a smooth curve as in the bears and most cats. The medial articular surface usually is large and seldom joined to the anterior articular surface which is usually absent. The cuboid surface is often crater-like, the lowest point being the center. The greater tuberosity is often hooked and typically carnivore-like in shape (that is, it is hooked at the dorsal edge) when viewed from the side.

In the Mustelinae, unavailable for study were four genera and approximately 14 species as follows: *Grammogale africana*, *Ictonyx* (*strictus*, *zorilla*?), *Lyncodon patagonica*, *Martes* (*gwatkinsi*, *melampus*), *Mustela* (*affinis*, *kathiah*, *lutreolina*, *lutreola*, *macrodon*, *nudipes*, *strigidorsa*), and *Vormela peregusna*.

Mellivora (Mellivorinae) has a greater tuberosity with an obvious flaring towards the external (lateral) side (see Stains, 1973. Bull. So. California Acad. Sci. 72:137–148 for terminology), a massive trochlear process, and no articular surface. Members of the Melinae have a distinct anterior articular surface which is broadly joined to the medial articular surface, a posterior articular surface which is slightly sigmoid, and a bulbous greater tuberosity. The Mephitinae have a small or poorly developed trochlear process which sometimes has a groove on the dorsal surface, a width/total length ratio usually below 51, a massive and ungrooved greater tuberosity, and a small "pimple-like" swelling located distal to the outer part of the tuberosity proximal to the posterior articular surface. The Lutrinae have no anterior articular surface, and a trochlear process which often extends distal to the cuboid surface and often hooked distally.

A discussion of the features of calcanea and a comparison of the features by genus follows. The terminology and measurements of the various processes and articulations follows Stains (1973).

CALCANEA OF MEMBERS OF THE MUSTELINAE

Mustela nivalis—Least Weasel

The least weasel, *Mustela nivalis*, is the smallest representative of the order Carnivora. It also has the shortest calcaneum although specimens of *Mustela altaica*, *M. erminea*, and *M. frenata* as well as *Poecilictis lybica* are within the same size range (Table 1). These species have shorter calcanea than all other members of the Carnivora.

The posterior articular surface is rounded, not sigmoid, and rolled on the proximo-external edge. The anterior articular surface is absent or extremely minute. The trochlear process is knob-like and obviously grooved. The distal end of the dorsal table is peaked with a well-developed pit at the distal end of the posterior articular surface. Except for *Poecilictis*, the calcaneum of *M. nivalis* tends to be wider in proportion to length giving the bone a short, broad appearence (Fig. 1a). In addition, the posterior articular surface of *M. nivalis* is not distinct in outline (Fig. 1b) from a dorso-lateral view as it is in *M. altaica*, *M. erminea*, and *M. frenata* (Fig. 1c).

Mustela erminea and *M. altaica* tend to have larger calcanea. The trochlear process is seldom knob-like from a dorsal view and in *M. erminea* forms a gently sloping shelf to the disto-lateral edge of the posterior articular surface (Fig. 1d): the edge of the shelf is more parallel to the longitudinal axis in *M. altaica* (Fig. 1e). This process is slightly grooved in *M. erminea* and *M. altaica* that is, not as distinctly grooved as in *M. nivalis*. In other characteristics, *M. erminea*, *M. altaica*, and *M. nivalis* are similar.

Mustela frenata also is difficult to distinguish from *M. nivalis* although the species averages slightly larger in size than either *M. erminea* or *M. nivalis* (Table 1). The trochlear process is intermediate in shape between that of *M. nivalis* and *M. erminea*. The process is slightly knob-like, has a trochlear shelf (Fig. 1f), and does no seem to be grooved in four specimens but is obviously grooved in the other thirteen.

Extention of the trochlear process to the cuboid surface will distinguish *Poecilictis lybica* (Fig 1g) from *Mustela nivalis* (Fig. 1a).

Specimens examined: NM 1044, 233978 (NM 1044 illustrated, Fig. 1a).

Mustela erminea—American Ermine

The calcaneum of members of this species has been discussed under *Mustela nivalis*. The other species within the same size range are *Mustela* (*altaica*, *frenata* and *sibirica*) and *Poecilictis lybica*.

The trochlear shelf of *Mustela erminea* (Fig 1d) is more robust, tends to show the knob-like process less from a dorsal view, and usually starts more abruptly as well as farther from the cuboid surface than does that in *M. frenata* (Fig 1f). *M. sibirica* (Fig. 1h) has an even more distinct knob-like trochlear process starting even

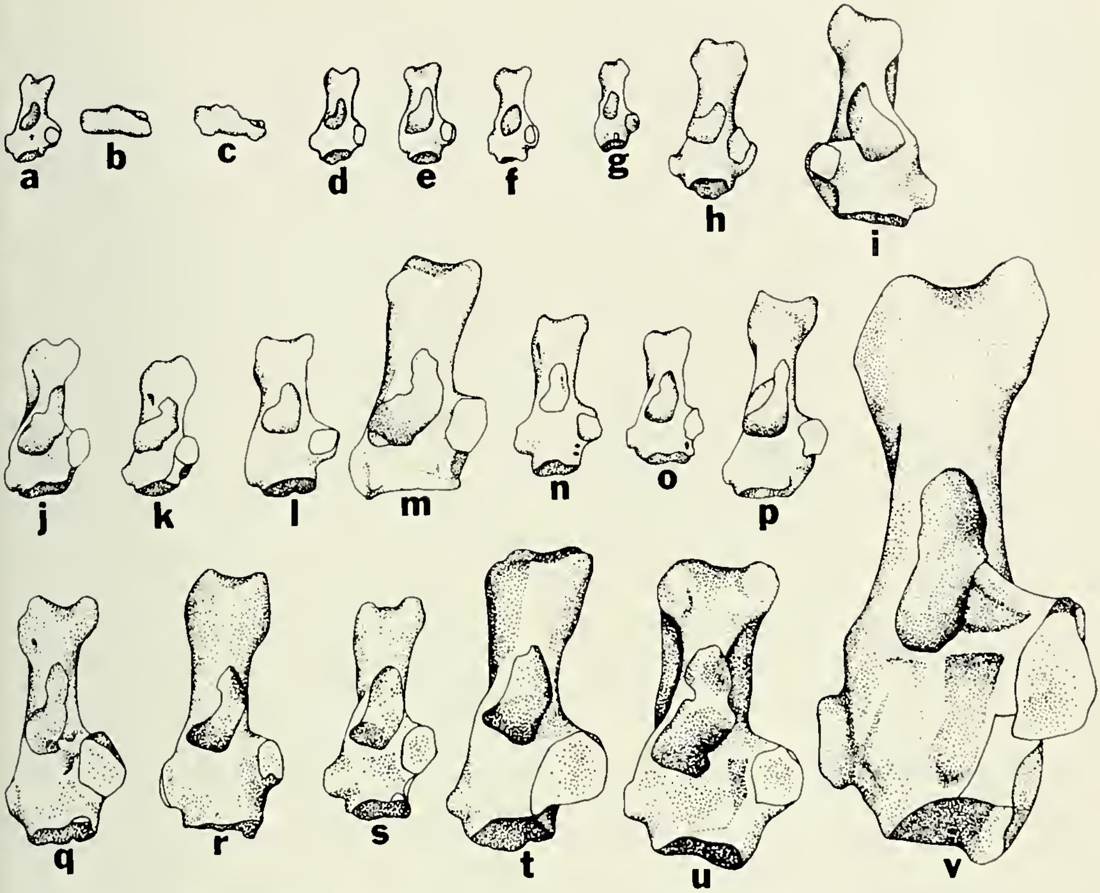

Figure 1. Right calcanea of members of the Mustelinae. a, *Mustela nivalis*; b, and c, lateral views; d, *M. erminea*; e, *M. altaica*; f, *M. frenata*; g, *Poecilictis lybica*; h, *M. nigripes*; i, *M. siberica*; j, *M. vison*; k, *Poecilogale albinucha*; l, *Galictis cuja*; m, *G. vittata*; n, *Martes americana*; o, *M. martes*; p, *Mustela putorius*; q, *Martes flavigula*; r, *M. foina*; s, *M. zibellina*; t, *Eira barbara*; u, *M. pennanti*; v, *Gulo gulo*.

more proximally. In *M. altaica* (Fig. 1e) the trochlear shelf is more parallel with the longitudinal axis of the bone than in *M. erminea* (Fig. 1d).

From the dorsal view, *Poecilictis* (Fig. 1g) is similar to *Mustela frenata* and *M. erminea*. The distinct nature of the trochlear process is similar to that of *M. frenata* but in *Poecilictis* this process tends to be more massive and more ventral in position. Viewed from a lateral aspect, the posterior articular surface is distinctly raised in both species of *Mustela* (Fig. 1c). This surface is not raised in *Poecilictis* (Fig. 1b). In specimens of *Poecilictis*, there is extreme rolling of the disto-external edge of the surface with an exaggeration of the mid area of the surface and no obvious raising of the proximal end of the posterior articular surface above the outline or the dorsal edge (Fig. 1b). Viewed from the cuboid surface, *Poecilictis* lacks the obvious groove or pit-area between the surface and the extension of the distal end of the body of the calcaneum. In essence, the body of the calcaneum of *Poecilictis* does not extend as far distally as it does in *Mustela*; as indicated by table 1, the width of the body is greater in *Poecilictis* giving the calcaneum a more massive appearance (Fig. 1g.).

Specimens examined: AM 125435, 129337; NM 1042, 188382, 219036 (NM 188382 illustrated, Fig. 1d).

Mustela frenata—Long-tailed Weasel

The calcaneum of *Mustela frenata* has been fully discussed under *Mustela nivalis* and *M. erminea*.

Calcanea of female *Mustela sibirica* and *M. altaica* may fall within the size range of *M. frenata*. The distinct knob-like trochlear process starting more proximally should differentiate *M. sibirica* (Fig. 1i) and the extension of the trochlear shelf parallel with the longitudinal axis of the bone should differentiate *M. altaica* (Fig. 1e) from *M. frenata*.

Specimens examined: AM 3862, 40028, 121543, 122393, 129338–40, 129397, 130137, 130142, 135415, 139910, 164460–1, 164856; NM 1392, 188925, 297766 (NM 297766 illustrated, Fig. 1f).

Mustela altaica—Alpine Weasel

Only one specimen of *Mustela altaica* was available for study. This specimen is a female and because of the rather large sex differences in most mustelids, the specimen probably is at the lower end of the size range for this species and falls within the size range of *Mustela erminea*, *M. frenata*, and *M. nivalis* which have been discussed. With the future availability of male alpine weasels, this species also would probably fall within the size range of *Mustela sibrica*, *M. vison*, and *Poecilictis lybica*.

The more distinct trochlear process ending abruptly on the proximal edge, distal to the posterior articular surface will distinguish *Mustela sibirica* (Fig. 1i) from *M. altaica* (Fig. 1e) in which the proximal edge of the trochlear process extends to the posterior articular surface. *M. vison* (Fig. 1j) tends to be intermediate in the expression of the proximal edge of the trochlear process between the condition found in *M. altaica* and *M. sibirica* although the process does tend to be more distinct as in *M. sibirica* but a shelf does extend to the posterior articular surface as in *M. altaica*.

The trochlear process of *Poecilictis lybica* (Fig. 1g) begins distally near the cuboid surface not more proximally as in *Mustela altica*. The index LWB/D-VH also tends to be larger in *Poecilictis* (44–47, avg 46) than in *M. altaica* (37).

Specimen examined and illustrated: NM 254587 (Fig. 1e).

Mustela nigripes—Black-footed Ferret

The calcanea of *Mustela nigripes* overlaps in size the calcanea of *Mustela* (*putorious*, *sibirica*, and *vison*), *Galictis* (*cuja* and *vittata*), and *Poecilogale albinucha* in the subfamily Mustelinae; *Melogale moschata* in the subfamily Melinae; and *Spilogale putorious* and *Mephitis mephitis* in the subfamily Mephitinae.

The calcaneum of *Mustela nigripes* has a well-developed trochlear process (Fig. 1h) which is grooved in two of three specimens. This process is located ventrally with a well-developed valley between it and the dorsal table. The cuboid surface is turned dorsally and, from the dorsal view, tends to be crater-like. The posterior articular surface is rounded, almost marble-like and smooth, not sigmoid. The width of the body is slender for a bone of this size giving a low least width of body/dorsoventral height index (Table 2); one of the smallest indices of all the mustelids.

Only one specimen of *Poecilogale albinucha* was available for study. This one specimen is slightly smaller in length and width of calcaneum than any of the three specimens of *M. nigripes* but much larger in the least width of the body so that least width of body divided by dorso-ventral height gives a value of 53 while in *M. nigripes* this index ranges from 28 to 34. In addition, *Poecilogale* (Fig. 1k) has an anterior articular surface similar to the condition found in *Melogale*. *Poecilogale* has a well-developed longitudinal pit proximo-lateral to the posterior articular surface; such a pit is absent in *Mustela nigripes*.

The calcanea of *Galictis* spp. (Fig. 1l and 1m) have a well-developed trochlear shelf, more massive that that of *M. nigripes*, without the distinct trochlear process of *Mustela nigripes* or at least a less obvious knob. Most of the measurements of the calcanea of these two animals overlap as do most of the proportions. The greatest difference seems to be the least width of the body which is much larger in *Galictis* than *Mustela nigripes* producing at least width of body/dorso-ventral height index of 28–34 (avg 30) in *Mustela nigripes* and 33–49 (avg 40) in *Galictis* spp.

Mustela nigripes has a calcaneum which differs from that of *Martes americana* (Fig. 1n) in having a posterior articular surface which is rounded and not sigmoid, a slightly narrower and slightly shorter calcaneum giving a width/total length index of 56–60 (*M. americana*, 53–54), and a trochlear process which is closer to the cuboid surface. The distal end of the trochlear process in *M. americana* is almost even with the distal end of the medial articular surface. The distal end of the trochlear process of *M. nigripes* is within one millimeter of the cuboid surface, that of *M. americana* is more than one millimeter from the cuboid surface. The calcaneum of *M. americana* tends to have a well-developed pit

TABLE 1. Measurements of Calcanea of Members of the Mustelinae.

Species	No.	Total Length (mm)		Width (mm)		D-VH		LWB	
		Range	Avg.	Range	Avg.	Range	Avg.	Range	Avg.
Eira barbara	11	22.0–31.0	25.1	11.7–17.3	13.8	9.3–13.0	10.5	3.6–4.9	4.2
Galictis vittata	6	14.4–20.8	16.3	8.6–11.4	9.6	5.7– 9.5	7.0	2.2–4.2	2.9
Galictis cuja	1		11.6		7.0		5.1		1.9
Gulo gulo	7	37.1–46.3	41.5	19.7–23.9	21.7	15.5–19.5	16.9	5.2–6.7	6.1
Martes americana	6	15.6–17.1	16.3	8.3– 9.0	8.7	6.1– 7.1	6.6	2.1–2.5	2.3
Martes flavigula	6	18.0–25.3	21.5	9.0–13.2	11.0	6.8–11.4	8.9	2.5–3.8	3.1
Martes foina	1		19.3		10.1		7.7		2.9
Martes martes	2	12.2–17.7	15.5	7.7– 9.7	8.7	5.6– 7.5	6.6	2.1–2.7	2.4
Martes pennanti	18	22.1–29.0	26.4	11.5–15.8	14.2	9.0–12.8	11.4	3.2–4.9	4.0
Martes zibellina	2	19.4–21.0	20.2	10.8–11.2	11.0	8.4– 8.9	8.7	2.6–2.7	2.7
Mustella altaica	1		7.0		3.6		2.7		1.0
Mustela erminea	5	4.6– 9.0	7.4	2.8– 5.0	4.2	2.2– 3.9	3.3	0.9–1.4	1.2
Mustela frenata	18	5.5– 9.3	7.6	2.9– 5.1	4.4	2.5– 3.9	3.2	0.9–1.5	1.3
Mustela nivalis	2	4.7– 7.8	6.3	3.0– 4.0	3.5	2.2– 2.7	2.5	0.8–1.3	1.1
Mustela nigripes	3	13.3–15.2	14.0	7.4– 8.6	8.0	6.0– 6.7	6.4	1.7–2.2	1.9
Mustela putorius	1		15.0		8.5		7.1		2.4
Mustela siberica	3	9.8–16.0	12.1	5.1– 8.4	6.5	3.6– 6.4	5.1	1.7–2.8	2.1
Mustela vison	29	10.0–16.2	12.9	5.3– 8.7	7.0	4.2– 7.1	5.6	1.3–2.6	2.0
Poecilictis lybica	2	7.7– 8.3	8.0	4.5– 5.2	4.9	3.4– 3.6	3.5	1.5–1.7	1.6
Poecilogale albinucha	1		12.2		6.5		5.3		2.8

located proximal and lateral to the posterior articular surface on the slope leading to the greater tuberosity.

The proportion of least width of body/dorsoventral height separates *Mustela nigripes* (28–34, avg 30) from *Martes martes* (36–38, avg 37). There is great overlap in most other measurements and indices although *Martes* does tend to be a little larger. As in *Martes americana*, the trochlear process is farther from the cuboid surface in

M. martes (Fig. 1o) than in *M. nigripes* (Fig. 1h): that is, more than one millimeter even though the distal end of the trochlear process is farther distally than that of *M. americana.*

The calcanea of *Mustela nigripes* and *Mustela vison* overlap in size and proportions, although the index of W/TL tends to be larger in *M. nigripes* and the index LWB/D-VH tends to be smaller thus if the second index is subtracted from the first, *M. nigripes* gives values from 25.6–28.2 (avg 27.0) and *M. vison* 12.0–23.8 (avg 18.3) with no overlap. *Mustela putorius* also probably can be separated on the same basis as the one specimen gives a value of 22.9 which is in the range exhibited by *M. vison* above. Three specimens of *Mustela sibirica* give even lower values (8.7–18.0, avg 10.5).

Specimens examined: AM 22820, 40078, 140397 (AM 22820 illustrated, Fig. 1h).

Mustela putorius—European Polecat

The calcaneum of *Mustela putorius* falls within the size range of those *Mustela nigripes* (already discussed), *Mustela* (*sibirica* and *vison*), *Galictis* (*cuja* and *vittata*), *Martes* (*americana* and *martes*), perhaps *Poecilogale albinucha*, in the subfamily Melinae, *Mephitis mephitis*, and in the subfamily Melinae perhaps *Melogale moschata.*

The index of least width of body/dorso-ventral height is much smaller (34) in *Mustela putorius* than in *Poecilogale albinucha* (53). *Poecilogale* (Fig. 1k) has the broadly joined medial and anterior articular surfaces. A well-developed longitudinal pit, proximo-lateral to the posterior articular surface, also differentiates *Poecilogale* from *Mustela putorius* (Fig. 1p) which lacks this pit.

The massive, gently rounded trochlear process of *Gilictis* spp. (Fig. 1l and m) separates this genus from *Mustela putorius.*

The relatively short calcaneum compared to dorso-ventral height gives a dorso-ventral height/total length index of 47 in *Mustela putorius* which is much larger than either *Martes americana* (39–43) or *Martes martes* (42). The trochlear process of *M. putorius* (Fig. 1p) begins more distal than either species of *Martes* (Fig. 1n and o).

Within the genus *Mustela*, differences between species are not as obvious. The one specimen of *Mustela putorius* has a dorso-ventral height which is the same as the extreme in the 29 specimens of *Mustela vison* examined (Table 1) and the dorso-ventral height/total length index is slightly larger in *M. putorius* (47) than *M. vison* (40–46) (Table 2). *Mustela sibirica* (3 specimens) tends to have a calcaneum of much lower dorso-ventral height (3.6–6.4mm) than *Mustela putorius* (7.1 mm) giving a D-VH/TL index of 39–47 (avg 40) versus 47 for the one specimen of *M. putorius.*

Specimen examined and illustrated: AM 57338, Fig. 1p.

Mustela sibirica—Siberian Weasel

The calcaneum of *Mustela sibirica* is within the size range of *Galictis* (*vittata* and *cuja*), *Martes* (*americana* and *martes*), *Mustela* (*nigripes, putorius,* and *vison*), *Poecilogale albinucha*, in the subfamily Melinae *Melogale moschata*, and in the subfamily Mephitis *Mephitis* (*mephitis* and *macroura*), and *Spilogale putorius.* Comparisons of the calcanea of *M. sibirica* with those of *M. nigripes* and *M. putorius* have been discussed under those species.

Mustela sibirica differs from *Galictis* sp. in having as distinct trochlear knob (Fig. 1i) instead of the massive, gently rounded trochlear process of *Galictis* (Fig. 1l and m); from *Poecilogale* (Fig. 1k) by the absence of an anterior articular surface joined broadly with the medial articular surface; and from *Martes americana* and *M. martes* by the least width of body/dorso-ventral height index which is smaller in *Martes* spp. (33–38, avg 35) and larger in *Mustela sibirica* (39–47, avg 40).

Mustela sibirica and *Mustela vison* are similar in proportions and measurements of the calcaneum. The three specimens of *M. sibirica* have a well-developed, flat ridge below (ventral to) the sustentaculum which tends to be a sloped area in *M. vison.* The least width of body/dorso-ventral height index of the calcanea of *M. sibirica* tends to be larger (39–47, avg 40) than that of *M. vison* (30–40, avg 36).

The calcaneum of one female *M. sibirica* is much smaller than those of the male (female 9.8 mm; male 10.6–16 mm, avg 13.3).

Specimens examined: NM 254688, 255460, 258358 (NM 254688 illustrated, Fig. 1i).

Mustela vison—Mink

The calcanea of *Mustela vison* fall within the size range of *Galictis* (*cuja* and *vittata*), *Martes* (*americana* and *martes*), *Mustela* (*nigripes, putorius,* and *sibirica*), *Poecilictis lybica, Poecilo-*

gale albinucha, in the subfamily Melinae *Melogale moschata*, and in the subfamily Mephitinae *Mephitis mephitis*, and *Spilogale putorius*.

Because of the similarity of the calcanea of *Mustela vison* and *Mustela sibirica*, the characteristics discussed under *Mustela sibirica* to differentiate that species from *Galictis vittata*, *Mustela putorius*, *Mustela nigripes*, *Poecilogale albinucha*, also will differentiate *Mustela vison*. The discussion of *Poecilictis* under *Mustela erminea* can be used to differentiate *Poecilictis* from *M. vison* if there is an overlap in size. *Poecilictis*, however, is probably below the size range of *M. vison*. *Galictis cuja* can be differentiated on the description used for *G. vittata* in the discussion under *M. sibirica*.

The more proximal position of the trochlear process in the two species of *Martes* (Fig. 1n and o) will distinguish these from *Mustela vison* (Fig. 1j).

Specimens examined: AM 35382, 98155, 120592, 128508–12, 176566; NM 14580, 21143, 34977, 132374, 155606, 188458, 199731–5, 239826, 241014, 256920, 256978, 256986, 300790–1 (NM 300791 illustrated, Fig. 1j).

Martes americana—Marten

Other species having calcanea within the size range of *Martes americana* are *Galictis vittata*, *Mustela* (*nigripes*, *putorius*, *sibirica*, and *vison*), *Martes martes*, perhaps *Martes* (*flavigula*, *foina* and *zibellina*); in the subfamily Melinae *Melogale moschata*; and in the subfamily Mephitinae *Mephitis mephitis*. Comparisons of *Martes americana* with the various species of *Mustela* are made under those species.

The massive trochlear process without an obvious grooved knob distinguishes *Galictis* (Fig. 1l and 1m) from all species of *Martes*, all of which have an obvious knob-like trochlear process which in most cases is distinctly grooved.

Of the genus *Martes*, *M. americana*, and *M. martes* exhibited the greatest overlap in size and proportions of the calcaneum. Both specimens of *M. martes* have a well-developed foramen at the sustentaculum which is obvious from the the dorsal aspect (Fig. 1o). The calcanea of *M. americana* lack this large foramen, although minute foramina may be present. *Martes americana* is slightly smaller in width/total length index (53–54, avg 53) (*M. martes* 55–58, avg 56). In general, these two species would be difficult to distinguish unless the presence of this foramen is constant in *M. martes*.

Martes flavigula, *M. foina*, and *M. zibellina* have calcanea which are larger than any calcaneum of *M. americana* measured but with more specimens there probably would be an overlap in size. *Martes flavigula* (Fig. 1q) tends to have a smooth, elongate posterior articular surface with little indication of being sigmoid. The posterior articular surface of *Martes americana* (Fig. 1n) is marble-like at its greatest height and is strongly sigmoid.

Martes foina (Fig. 1r) has a calcaneum in which the body extends prominently distal to the cuboid surface, in *M. americana* the body is but slightly distal to the cuboid surface. *Martes foina* also has a prominent raise on the dorsal table forming a ridge towards the posterior articular surface. The dorsal table of the calcaneum of *M. americana* is gently rounded. Again, however, there is considerable similarity between the calcanea of *M. americana* and *M. foina*.

The calcaneum of *Martes zibellina* also is larger than that of *M. americana* but more specimens perhaps would overlap in size. *Martes zibellina* (Fig. 1s) has a large cuboid surface causing a prominent uplift of the distal edge of the dorsal table and a rapid drop towards the posterior articular surface, such an expansion is absent in *M. americana*. A large pit is present distal to the medial articular surface at the base of the sustentaculum in *M. zibellina*; no obvious pit is present in *M. americana* but minute pits may be present. Other than these characteristics, the calcanea of these two species are similar.

Specimens examined: AM 14440, 120687; NM 7549, 9668, 270256 (NM 270256 illustrated, Fig. 1n).

Martes martes—Pine Martin

Martes martes has calcanea within the size range of *Galictis* (*cuja* and *vittata*), *Poecilogale albinucha*, *Mustela* (*nigripes*, *putorius*, *sibirica*, and *vison*), *Martes* (*americana*, *flavigula*, *foina* and perhaps *zibellina*); in the subfamily Melinae *Melogale moschata*; and in the subfamily Mephitinae *Conepatus semistriatus*, *Mephitis* (*macroura* and *mephitis*). Comparison of *Martes martes* with the various species of *Mustela* and with *Martes americana* have been made previously.

The discussions of *Galictis* sp., *Melogale moschata*, and *Mephitis mephitis* given under *Martes americana* also will separate these species from *Martes martes*.

The joined medial and anterior articular surfaces and the extremely large index of least width of body/dorso-ventral height (53) in *Poecilogale albinucha* (Fig. 1k, Table 2) will separate the calcaneum of this animal from *Martes martes* (Fig. 1o, Table 2).

The presence of a large foramen at the distal base of the sustentaculum will separate *Martes martes* (Fig. 1o) from most species of *Martes*, except *M. zibellina* (Fig. 1s). Both *M. flavigula* and *M. foina* have a smaller width/length index than does *M. martes* (Table 2).

Martes zibellina (Fig. 1s) seems to be closer to *M. martes* than the other two species and does have a foramen present at the distal base of the sustentaculum although not as large. One of the two specimens of *M. zibellina* has a well-developed anterior articular surface. The least width of body/dorso-ventral height index may distinguish the two species. In *M. martes* this index is from 36 to 38 and in *M. zibellina*, 30 to 31.

Specimens examined: AM 22898; NM 1964 (AM 22898 illustrated, Fig. 1o).

Martes flavigula—Yellow-throated Marten

The calcanea of mustelids overlapping *Martes flavigula* in size are *Eira barbara*, *Galictis vittata*, and *Martes* (*foina*, *pennanti*, *zibellina*, and perhaps *americana* and *martes* which have been discussed previously); in the subfamily Melinae *Arctonyx collaris*, *Meles meles*, and *Taxidea taxus*; and in the subfamily Mephitinae *Conepatus* (*mesoleucus* and *semistriatus*), *Mephitis* (*mephitis* and probably *macroura*); in the subfamily Lutrinae *Aonyx cinerea*, and *Lutra* (*canadensis*, *maculicollis* and *platensis*).

The trochlear process of the calcaneum of *Martes flavigula* (Fig. 1q) usually is higher (more proximal) than that of *Eira barbara* (Fig. 1t). However, this process in *E. barbara* is extremely variable in position and size and cannot always be distinguished from that of *M. flavigula*. In some cases the medial articular surface of *E. barbara* continues towards an anterior articular surface but this feature also varies from a broad continuation, to none, and to a condition where the anterior articular surface is absent. To a lesser degree the nature of the medial and anterior articular surfaces in *M. flavigula* also is extremely variable. *M. flavigula* does tend to have a smaller width/total length index and least width of body/dorso-ventral height index than found in *E. barbara*. If these two indices are added, there is a slight sparation of these two genera: *Martes flavigula* ranges from 83.5–90.7 (avg 86.1) and *E. barbara* from 91.8–103.4 (avg 95.2).

The ungrooved, massive trochlear process of *Galictis vittata* (Fig. 1m) separates this genus from *Martes flavigula*. Width/total length is greater in *Galictis* than *M. flavigula*; the greater index being due to the larger trochlear process in *Galictis*.

Martes flavigula (Fig. 1q) differs from *Martes foina* (Fig. 1r) in having a shorter distal extension of the body beyond the cuboid surface. This extension forms a notch in *M. flavigula* when the cuboid edge (distal end of the bone) is viewed from the ventral surface. In addition, the posterior articular surface of the calcaneum of *Martes flavigula* forms a smooth curve which is seldom sigmoid. The posterior articular surface of *M. foina* is abrupt at the distal end and tends to be sigmoid at the proximal end. However, the calcanea of these two species are similar and since only one specimen of *M. foina* was available for study, the differences listed may not be real ones.

The posterior articular surface of the calcaneum of *Martes pennanti* (Fig. 1u) is more obviously sigmoid than is that of *M. flavigula* (Fig. 1q). Only four of 18 specimens of *M. pennanti* have a calcaneum with a width as small as the largest *M. flavigula* examined (Table 1). Four of the six specimens of *M. flavigula* are smaller in width than the smallest of the 18 specimens of *M. pennanti*. The calcanea of *M. pennanti* (Fig. 1u) tends to have an obvious ridge leading from the medial articular surface towards the distal edge of the dorsal table. Two of the six specimens of *M. flavigula* also have this ridge. Ten of the 18 specimens of *M. pennanti* have a large, broad pit proximo-lateral to the posterior articular surface just distal to the greater tuberosity. Two of the six specimens of *M. flavigula* have a small but obvious pit at the same location. The shape of the posterior articular surface seems to be the most consistent difference in the calcanea of these two species.

Only two specimens of *Martes zibellina* (Fig. 1s) were available for study. These specimens differ from *Martes flavigula* (Fig. 1q) in having a posterior articular surface which is more abrupt at the distal end, more sigmoid, and with the medio-lateral edge rolled. In *M. flavigula* the posterior articular surface is a smooth, even curve, not obviously sigmoid, and with a sharp medio-lateral edge, not rolled. *Martes zibellina* also has a distinct pit at the base of the sustentaculum which is absent in *M. flavigula*.

Specimens examined: AM 43150, 70558

80110, 113029; NM 197238, 198053, 258429 (NM 197238 illustrated, Fig. 1q).

Martes foina—Stone Marten

Only one specimen of *Martes foina* was available for study. This specimen falls within the size range of the calcanea of *Galictis vittata*, *Martes* (*flavigula*, *pennanti*, and *zibellina*), perhaps *Eira barbara*, *Martes* (*americana*, and *martes*), *Mustela* (*nigripes*, *putorius*, *sibirica*, and *vison*), *Melogale moschata* in the subfamily Mustelinae; in the subfamily Mephitinae *Conepatus* (*mesoleucus* and *semistriatus*), *Mephitis mephitis*, and perhaps *Mephitis macroura*; in the subfamily Lutrinae *Aonyx cinerea*, and perhaps *Lutra* (*canadensis* and *platensis*). Of the above, comparisons of the calcanea of *Martes foina* with *Martes americana*, *martes*, and *flavigula* have been discussed under those species.

The massive trochlear process and wide calcaneum resulting in a large width/total length index will distinguish *Galictis vittata* (Fig. 1m) from *Martes foina* (Fig. 1r) (Table 2).

Addition of the two indices, width/total length and least width of body/dorso-ventral height, gives a combined total of 90.0 for *M. foina* which is near the upper extreme of *Martes flavigula* and below the range of *Eira barbara*. Other features of the calcaneum of *E. barbara* as discussed under *Martes flavigula* also are useful in distinguishing *M. foina*.

Martes foina has a calcaneum which is wider, longer, has a greater least width of body, and a greater dorso-ventral height than any specimen of *Mustela* spp. examined. The indices, however fall within the range of indices found in *Mustela*. In all cases the trochlear process of *Martes foina* (Fig. 1r) is farther from (more proximal) the cuboid surface than is this process in *Mustela* spp. (Fig. 1a, d, f, h, i, j, p).

There probably is no overlap in size of the calcaneum between *Martes foina* and *Martes pennanti*. All 18 specimens of *Martes pennanti* are larger in every measurement than the one specimen of *M. foina*. In all indices, however, *M. foina* falls within the range exhibited by *M. pennanti*. The trochlear process of *M. foina* (Fig. 1r) appears to be located more ventrally because of a slight ridge running longitudinally on the dorsal table from the cuboid surface to the posterior articular surface. Although the dorsal edge of the cuboid surface of *M. pennanti* (Fig. 1u) is raised, there is no ridge near the center or outer side of the dorsal table thus the trochlear process and the dorsal table are at the same level.

TABLE 2. Indices for Calcanea of Members of the Mustelinae.

Species	W/TL		D-VH/TL		LWB/D-VH	
	Range	Avg.	Range	Avg.	Range	Avg.
Eira barbara	51–59	55	38–45	40	36–46	40
Galictis vittata	55–63	59	40–46	43	33–49	41
Galictis cuja		60		44		37
Gulo gulo	51–56	52	39–43	41	32–41	36
Martes americana	53–54	53	39–43	41	33–38	35
Martes flavigula	48–53	51	36–45	41	33–38	35
Martes foina		52		40		38
Martes martes	55–58	56		42	36–38	37
Martes pennanti	51–58	54	39–45	43	32–41	36
Martes zibellina	53–56	55	42–43	43	30–31	31
Mustela altaica		54		39		37
Mustela erminea	55–65	57	42–49	44	33–41	37
Mustela frenata	52–61	57	36–46	42	32–52	40
Mustela nivalis	51–64	56	35–47	39	36–48	43
Mustela nigripes	56–60	57	44–47	46	28–34	30
Mustela putorius		57		47		34
Mustela sibirica	52–57	54	37–42	40	39–47	40
Mustela vison	51–57	54	40–46	44	30–40	36
Poecilictis lybica	58–63	61	43–44	44	44–47	46
Poecilogale albinucha		53		43		53

Martes zibellina (Fig. 1s), like *M. pennanti*, lacks the longitudinal ridge on the outer side of the dorsal table. The slightly larger least width of body and slightly smaller dorso-ventral height of the calcaneum of *M. foina* results in a large least width of body/dorso-ventral height index (38); this index in the two specimens of *M. zibellina* is small (30 and 31), in fact the smallest of all species of the genus *Martes* examined.

Specimen examined and illustrated: AM 70182, Fig. 1r.

Martes pennanti—Fisher

The largest calcanea of the genus *Martes* examined were those of *Martes pennanti.* This species is within the size range of *Eira barbara, Galictis vittata, Martes* (*flavigula, zibellina,* and perhaps *foina*); in the subfamily Mellivoriane *Mellivora capensis*; in the subfamily Melinae *Arctonyx collaris, Meles meles, Taxidea taxus*; in the subfamily Mephitinae *Conepatus* (*mesoleucus* and *semistriatus*); and in the subfamily Lutrinae *Aonyx cinerea, Lutra* (*canadensis, maculicollis, perspicillata,* and *platensis*). Comparisons of the calcanea of *Martes pennanti* with *M. flavigula* and *M. foina* have been made under those species.

Martes pennanti and *Eira barbara* have calcanea that overlap in all measurements and indices taken. The discussion of *Eira barbara* under *Martes flavigula* also is applicable to *Martes pennanti.* However, there is not a complete separation of these two species when the width/length and least width of body/dorso-ventral height indices are added since *Martes pennanti* bridges the gap found between *M. flavigula* and *E. barbara.* The added indices range from 84 to 94 (avg 89) with 5 of the 18 specimens of *M. pennanti* falling within the range of *E. barbara* and 6 of the 11 specimens of *E. barbara* falling within the range of *M. pennanti.* The calcanea of *M. pennanti* (Fig. 1u) have a posterior articular surface which is more strongly sigmoid than that of *E. barbara* (Fig. 1t) and the cuboid surface of *E. barbara* tends to be slanted more dorso-ventrally than that of *M. pennanti* thus more of the cuboid surface is in view from the dorsal aspect.

Galictis vittata (Fig. 1m) has a calcaneum with a broad trochlear process, the distal end of this process being even with the cuboid surface. The posterior articular surface of *Galictis* is almost as wide as long and tends to be rounded and smooth rather than sigmoid as in *M. pennanti.*

Martes zibellina and *Martes pennanti* probably overlap in size of calcaneum, *M. zibellina* being slightly smaller. The three specimens of *M. zibellina* do seem to have a much thinner body producing a smaller least width of body/dorso-ventral height index (*M. zibellina,* 30 to 31, avg 31; *M. pennanti,* 32–41, avg 36). *M. pennanti* (Fig. 1u) has an obvious pit at the base of the sustentaculum which is lacking in *M. zibellina* (Fig. 1s). In all other characteristics, these two species seem to have similar calcanea.

Species examined: AM 14077, 35094, 35294, 121554, 121556–7, 150094, 150260, 150302, 150303 (yg), 150304; NM 3415, 21233, 18221, 188225–7, 252773 (NM 21233 illustrated, Fig. 1u).

Martes zibellina—Sable

Only two specimens of *Martes zibellina* were available for study. These two calcanea are within or near the size range of *Eira barbara, Galictis vittata, Martes* (*flavigula* and *foina*), and perhaps *Martes martes* and *M. pennanti*; in the subfamily Mephitinae *Conepatus* (*mesoleucus* and *semistriatus*), *Mephitis mephitis*; and in the subfamily Lutinea *Aonyx cinerea,* and perhaps *Lutra platensis.*

The discussion of *Eira barbara* under *Martes flavigula* also applies to *M. zibellina.* The discussion of *Galictis vittata* under *Martes pennanti* also applies to *M. zibellina.* The distinction of *M. zibellina* from the other species of *Martes* have been discussed under those species.

Specimens examined: NM 49483–4 (NM 49484 illustrated. Fig. 1s).

Eira barbara—Tayra

The calcaneum of *Eira barbara* has been compared with the various species of *Martes* within the same size range. Also within the size range of *Eira barbara* are the calcanea of *Galictis vittata*; in the subfamily Mellivorinae *Mellivora capensis*; in the subfamily Melinae *Arctonyx collaris, Meles meles, Taxidea taxus*; in the subfamily Mephitinae *Conepatus* (*mesoleucus* and *semistriatus*) and perhaps *Mephitis mephitis*; and in the subfamily Lutrinae *Aonyx cinerea, Lutra* (*canadensis, maculicollis, perspicillata,* and *platensis*).

One of six specimens of *Galictis vittata* is slightly smaller than the eleven specimens of *Eira barbara*; the other five specimens are much smaller. All indices of these two species are similar, however. The posterior articular surface of *Galictis* is smooth, never sigmoid; those of *Eira* are smooth in five specimens and sigmoid or slightly sigmoid in six specimens. All specimens of *Galictis* (Fig. 1m) have a distinct shelf between the medial articular surface and the distal end of the calcaneum; most specimens of *Eira* lack even an indication of this shelf. All specimens of *Galictis* have a raised area on the mediodorsal edge of the cuboid surface; most specimens of *Eira* lack this small raised area. The trochlear process of the calcanea of *Galictis* always extends to, or almost to, the distal end of the calcaneum; in only one specimen of *Eira* does the trochlear process extend to the distal end. The trochlear process is seldom grooved in *Galictis* and is usually grooved in *Eira*. In all the characteristics listed above, in no case is there a complete separation of the two genera except perhaps in total length. Although there is no difference in dorsal-ventral height as usually measured, the more sigmoid nature of the posterior articular surface of *Eira* causes the proximal end of the posterior articular surface to be higher and a dorso-ventral height measured at this point will separate these two species. *Eira barbara* has a proximal posterior articular surface dorso-ventral height of 7.8–11.2 (avg 9.1 mm); *Galictis vittata* 5.1–6.9 (avg 5.7 mm).

Specimens examined: AM 389, 5937, 23487–8, 30202, 130103, 134947; NM 3839, 240886, 256177, 259003, (AM 30202 illustrated, Fig. 1t).

Galictis vittata—Large Grison

There are eight specimens of *Galictis* available for study. Six of these specimens are identified as *Galictis vittata*, one as *Galictis cuja*; and one is unidentified and intermediate in size between the two although closer to *G. vittata* and is included in *Galictis vittata* in this paper. Both species are similar except for size producing indices within the same range.

Galictis vittata falls within the size range of *Martes* (*americana*, *flavigula*, *foina*, *martes*, and *zibellina*), *Mustela* (*nigripes*, *putorius*, *sibirica*, and *vison*), *Poecilogale albinucha*, perhaps *Eira barbara* and *Martes pennanti*; in the subfamily Melinae *Melogale moschata*; in the subfamily Mephitinae *Conepatus* (*mosoleucus* and *semistriatus*), *Mephitis* (*macroura* and *mephitis*), *Spilogale putorius*; and in the subfamily Lutrinae *Aonyx cinerea*, and perhaps *Lutra platensis* in the calcaneal measurements. Various species of *Martes* and *Mustela* as well as *Eira barbara* have been discussed previously.

Both species of *Galictis* have a massive trochlear process so that width divided by total length results in a large index (*G. vittata*, 55–63, avg 59; *G. cuja*, 60).

In addition to the width/total length index, *Poecilogale albinucha* has a large least width of body producing an extremely large least width of body/dorso-ventral height index: *Poecilogale*, 53; *Galictis vittata*, 33–49, avg 41; *Galictis cuja*, 37.

There is considerable size difference between the calcanea of *Galictis vittata* and *G. cuja* although there might be some overlap since only one specimen of *G. cuja* was available for study.

Specimens examined: AM 35257, 35514, 100250 (yg), 133944; NM 35259, 115402, 307043 (NM 307043 illustrated, Fig. 1m).

Galictis cuja—Little Grison

The one specimen of *Galictis cuja* is within or near the size range of *Martes martes*, *Mustela vison*, *Poecilogale albinucha*, and in the subfamily Mephitinae *Spilogale putorius*. The Mustelinae have been compared under *Galictis vittata* as well as a comparison of the two species of *Galictis*.

Specimen examined and illustrated: AM 48094, Fig. 1l.

Gulo gulo—Wolverine

The largest mustelid calcaneum recorded was that of *Gulo gulo*. Also in the size range of the wolverine are the calcanea of *Aonyx capensis*, *Enhydra lutris*, *Pteronura brasiliensis*, and perhaps *Lutra canadensis*; all members of the Lutrinae.

Gulo has a large trochlear process, a distinctive grooved greater tuberosity, a weakly sigmoid posterior articular surface, a distal swelling of the body of the calcaneum which extends distal to the cuboid surface, and medial and anterior articular surfaces which are broadly connected.

Specimens examined: NM 1041, 3339, 21493, 174630, 189000, 257989, 269110 (NM 257989 illustrated, Fig. 1r).

Poecilictis lybica—North African Striped Weasel

Poecilictis lybica has a calcaneum similar in size to the smaller weasels, *Mustela erminea*, *M. frenata* and perhaps *M. nivalis*, *M. sibirica*, *M. altaica*, and even *M. vison*. Comparisons with *M. erminea* have been made previously. The trochlear process is relatively large in *Poecilictis* (Fig. 1g) and is located ventrally as the dorsal table is rounded or curved. The posterior articular surface is smooth, not sigmoid.

The calcaneum of *Poecilictis* (Fig. 1g) differs from *Mustela frenata* (Fig. 1f) in having a larger trochlear process that extends farther proximally. The least width of body is greater in *Poecilictis* resulting in a large (44–47, avg 46) least width of body/dorso-ventral height index. In fact, the least width of body/dorso-ventral height index separates *Poecilictis* from most individuals of the genus *Mustela* (Table 2). This index clearly separates *Mustela nigripes*, *M. altaica* and *M. vison* from *Poecilictis*. These species of *Mustela* also have a trochlear process which does not extend as far proximally as does that of *Poecilictis*.

The calcanea of *Poecilictis* also might be overlapped in size by *Galictis cuja*, *Poecilogale albinucha*, and *Spilogale putorius* although probably no overlap does occur. *Galictis cuja* (Fig. 1l), in many ways, has a calcaneum which seems to be an enlarged copy of *Poecilictis*. There is an overlap in all indices, the greatest difference being in least width of body/dorso-ventral height which is due to the proportionately greater least width of body measurement of *Poecilictis*. If least width of body is divided by width (× 100), *Poecilictis* ranges from 32.7 to 33.3 (avg 33.0) and *Galictis*, 27.1.

Poecilictis differs from *Poecilogale albinucha* in having a higher width/total length index and a lower least width of body/dorso-ventral height index. *Poecilogale* (Fig. 1k) have medial and anterior articular surfaces which are joined. *Poecilictis* have separate medial and anterior articular surfaces. The trochlear process of *Poecilogale* is smaller and located more distally than that of *Poecilictis*.

Specimens examined: AM 70083, 70093 (AM 70093 illustrated, Fig. 1g).

Poecilogale albinucha—White-naped Weasel

Only one specimen of *Poecilogale albinucha* was examined. This specimen has a small trochlear process (Fig. 1k) located at the distal end of the bone, a smooth posterior articular surface, broadly joined medial and anterior articular surfaces, and a prominent pit on the body lateral to the proximal half of the posterior articular surface and continuing proximally to the base of the greater tuberosity.

Poecilogale may be within the size range of *Galictis cuja*, *Martes* (*martes* and *americana*), *Mustela* (*erminea*, *frenata*, *nigripes*, *putorius*, *sibirica*, and *vison*), and *Poecilictis lybica* and comparisons have been made under these genera. In addition, *Poecilogale* may be within the size range of *Melogale moschata* and *Spilogale putorius* of the subfamilies Mellivorinae and Mephitinae.

Specimen examined and illustrated: AM 77699, Fig. 1k.

CONCLUSIONS

The calcanea of the Mustelinae are typical carnivore calcanea with a smooth and large posterior articular surface, a well-developed medial articular surface and an anterior articular surface which is seldom present and usually minute when present.

The trochlear process is knob-like, distinct and proximal to the cuboid surface in *Mustela*, *Martes*, *Eira*, *Poecilogale*, and *Gulo*; less distinct and reaching the cuboid surface in *Galictis* and *Poecilictis*. For this reason, the first seven genera mentioned are regarded as most closely related with the last two being more distinct. Having similar trochlear processes are *Mellivora*, *Conepatus mesoleucus*, *Spilogale*, and *Melogale* but other subfamily characteristics of the calcanea will distinguish these forms: the flaring greater tuberosity in the Mellivorinae, the "pimple-like" swelling on the body the greater tuberosity in the Mephitinae, and the large joined medial and anterior articular surfaces in the Melinae.

The greater tuberosity in the Mustelinae tends to be grooved as in the Lutrinae, Canidae and Felidae and unlike that in most of the Mellivorinae, Melinae, Mephitinae, Ursidae, Procyonidae, Hyaenidae, and Viverridae.

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CALCANEA OF MEMBERS OF THE MUSTELIDAE. PART II, MELLIVORINAE, MELINAE, MEPHITINAE, AND LUTRINAE

Howard J. Stains[1]

Abstract: Calcanea of one species of the Mellivorinae, four (four genera) of the Melinae, five (three genera) of the Mephitinae and eight (four genera) of the Lutrinae are described and compared. Members of the Mellivorinae lack or have a minute anterior articular surface; those of the Melinae have a distinct anterior surface, broadly joined to the medial articular surface. Calcanea of the Mephitinae are similar to each other, more so than the calcanea of members of other subfamilies in the Mustelidae. In the Lutrinae, the trochlear process is often hooked distally.

The calcanea of the Mustelinae have been reported (Stains, 1976) together with papers on terminology (Stains, 1973, 1975). Unavailable for study were specimens of *Melogale* (*everetti* and *personata*), *Mydaus javanensis*, and *Suillotaxus* (*Mydaus*) *marchei* of the Melinae; *Conepatus* (*castaneus*, *chinga*, *humboldtii*, *leuconotus*, and *rex*), and *Spilogale pygmaea* of the Mephitinae; and *Lutra* (*annectens*, *enudris*, *felina*, *incarum*, *lutra mira*, *provocax*, and *sumatrana*) of the Lutrinae. A total of 12 genera and 18 species were studied in the four subfamilies reported in this paper.

CALCANEA OF MEMBERS OF THE MELLIVORINAE

Mellivora capensis—Honey Badger

The subfamily Mellivorinae contains a single species *Mellivora capensis*. The calcaneum of this animal has an inward flaring greater tuberosity and a peaked dorsal table (Fig. 1A). Of the various other subfamilies, *Mellivora* resembles most closely members of the Melinae. There is considerable variation in the three specimens of *Mellivora* examined; two come from different parts of Africa and one from India.

Within the size range of *Mellivora capensis* (Table 1) are the calcanea of *Eira barbara* and *Martes pennanti* of the Mustelinae; *Arctonyx collaris*, *Meles meles* and *Taxidea taxus* of the Melinae; and *Aonyx capensis*, and *Lutra* (*canadensis*, *maculicollis*, and *perspicillata*) of the Lutrinae.

Both *Arctonyx collaris* (Fig. 1B) and *Mellivora capensis* (Fig. 1A) have calcanea with smooth posterior articular surfaces. Most specimens of *Arctonyx* have a longitudinal ridge on the dorsal table although some have a raised mid-central distal area as does *Mellivora*. More of the cuboid surface is in view from the dorsal aspect in *Mellivora* (Fig. 1A) than in *Arctonyx* (Fig. 1B). All specimens of *Arctonyx* have joined medial and anterior articular surfaces; *Mellivora* lacks the anterior articular surface in two of the three specimens. The dorso-ventral height is about the same in the two species but since the calcaneum of *Mellivora* is slightly longer than *Arctonyx*, the dorsal-ventral height/total length index in *Mellivora* is slightly smaller (41 to 42, avg. 41) than that of *Arctonyx* (42 to 46, avg. 44) (Table 2). The greater tuberosity tends to flare towards the inner side in *Mellivora* while *Arctonyx* tends to be straight giving the calcaneum a stouter appearance.

Meles meles (Fig. 1C) has a calcaneum in which the posterior articular surface is sigmoid, the proximal end of the surface being especially turned upward so that this half of the process is most dorsal. In *Mellivora*, the posterior articular surface is smooth with the midpoint of the surface being the most dorsal. The trochlear process of *Meles* is more distinct and larger than that of *Mellivora*. The medial and anterior surfaces usually are broadly joined in *Meles*. *Meles* tends to have a broader body producing a least width of body/dorso-ventral height index of 50 to 52 (avg. 51) compared to 40 to 48 (avg. 43) in *Mellivora* (Table 2). *Meles* also has a well-developed pit or groove located lateral and ventral to the proximal end of the posterior articular surface. Such a groove is absent in *Mellivora*.

Taxidea taxus (Fig. 1E) has a massive trochlear process, medial and anterior articular surfaces which are broadly joined, a broad flat area

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TABLE 1. Measurements of calcanea of members of the Mellivorinae, Melinae, Mephitinae, and Lutrinae.

		Total Length (mm)		Width (mm)		D-VH		LWB	
Species	No.	Range	Avg.	Range	Avg.	Range	Avg.	Range	Avg.
MELLIVORINAE									
Mellivora capensis	3	28.8–32.1	30.5	16.1–17.5	17.0	11.7–13.2	12.6	4.9–6.3	5.4
MELINAE									
Arctonyx collaris	4	25.5–27.4	26.5	14.3–15.2	14.7	11.4–12.4	11.7	4.8–5.8	5.3
Meles meles	2	28.0–31.3	29.7	16.5–17.9	17.2	12.6–13.5	13.1	6.3–7.0	6.7
Melogale moschata	9	13.7–16.2	15.0	6.8– 9.2	8.0	5.2– 6.9	6.0	2.3–2.8	2.5
Taxidea taxus	9	24.9–30.2	27.4	13.5–16.4	15.2	10.3–12.4	11.3	5.2–6.2	5.5
MEPHITINAE									
Conepatus mesoleucus	1		19.2		9.8		6.5		3.6
Conepatus semistriatus	3	17.7–22.1	19.6	8.6–10.2	9.3	6.4– 7.8	7.0	3.5–4.4	4.0
Mephitis macroura	1		15.8		7.4		6.6		2.5
Mephitis mephitis	22	15.1–20.9	18.2	7.5–10.5	9.0	5.5– 8.8	7.1	2.4–3.7	3.0
Spilogale putorius	5	11.2–12.2	11.8	5.3– 6.2	5.8	4.0– 4.5	4.3	1.9–2.1	2.0
LUTRINAE									
Aonyx cinerea	3	19.4–22.0	21.0	10.4–12.0	11.4	8.7–10.9	9.8	3.0–3.3	3.2
Aonyx capensis	2	35.5–36.9	36.2	21.4–21.5	21.5	17.1–18.9	18.0	5.3–6.0	5.7
Enhydra lutris	9	37.3–45.5	41.8	23.6–25.8	24.6	15.8–17.8	16.9	8.3–10.4	9.3
Lutra perspicillata	1		32.5		17.2		15.1		5.3
Lutra canadensis	17	23.5–34.9	27.7	13.1–21.4	15.9	11.2–17.4	13.1	4.3–6.6	5.4
Lutra platensis	1		23.2		13.2		11.3		4.4
Lutra maculicollis	1		25.9		14.5		12.9		4.9
Pteronura brasiliensis	3	43.2–45.8	44.4	24.3–27.7	25.8	19.0–20.5	19.7	7.7–8.7	8.1

on the inner side of the greater tuberosity, and a least width of body/dorso-ventral height index that is slightly larger (*Taxidea*, 45–52, avg. 49; *Mellivora*, 40–48, avg. 43) (Table 2).

Aonyx capensis (Fig. 1L) has a hooked, distinct trochlear process, a slightly sigmoid posterior articular surface, and a narrow greater tuberosity when viewed from the dorsal aspect. The proportionately greater dorso-ventral height results in a much greater dorso-ventral height/total length index in *Aonyx* (*Aonyx*, 48–51, avg. 50; *Mellivora*, 41–42, avg. 41) and a smaller least width of body/dorso-ventral height index in *Aonyx* (*Aonyx*, 31–32, avg. 31; *Mellivora*, 40–48, avg. 43) (Table 2).

Lutra canadensis, *L. maculicollis*, and *L. perspicillata* have calcanea which in most cases have distinct hooked, trochlear processes. The dorso-ventral height tends to be proportionately greater resulting in a larger dorso-ventral height/total length index (*L. canadensis*, 44–52, avg. 47; *L. maculicollis*, 50; *L. perspicillata*, 47: *Mellivora*, 41–42, avg. 41) (Table 2). The greater tuberosity of *Lutra* is twisted toward the inner side of the calcaneum so that the dorsal outline of the outer edge of the body slopes inward (or towards the midline) at the level of the greater tuberosity (Fig. 1N and O) not outward as in *Mellivora* (Fig. 1A).

Specimens examined: AM 83450, 89011; NM 164700 (AM 89011 illustrated, Fig. 1A).

Arctonyx collaris—Hog-badger

The calcaneum of *Arctonyx collaris* (Table 1) is near or within the size range of the calcanea of *Eira barbara*, *Martes* (*flavigula* and *pennanti*), *Mellivora capensis*, *Meles meles*, *Taxidea taxus*, and *Lutra* (*canadensis*, *maculicollis*, *perspicillata*, and *platensis*).

The posterior articular surface of *Arctonyx* (Fig. 1B) is smooth, not sigmoid. The trochlear process is large, runs from the distal end of the bone to the distal edge of the posterior articular surface, and is ventrally located. The medial and anterior articular surfaces are broadly connected and the greater tuberosity is bulbous.

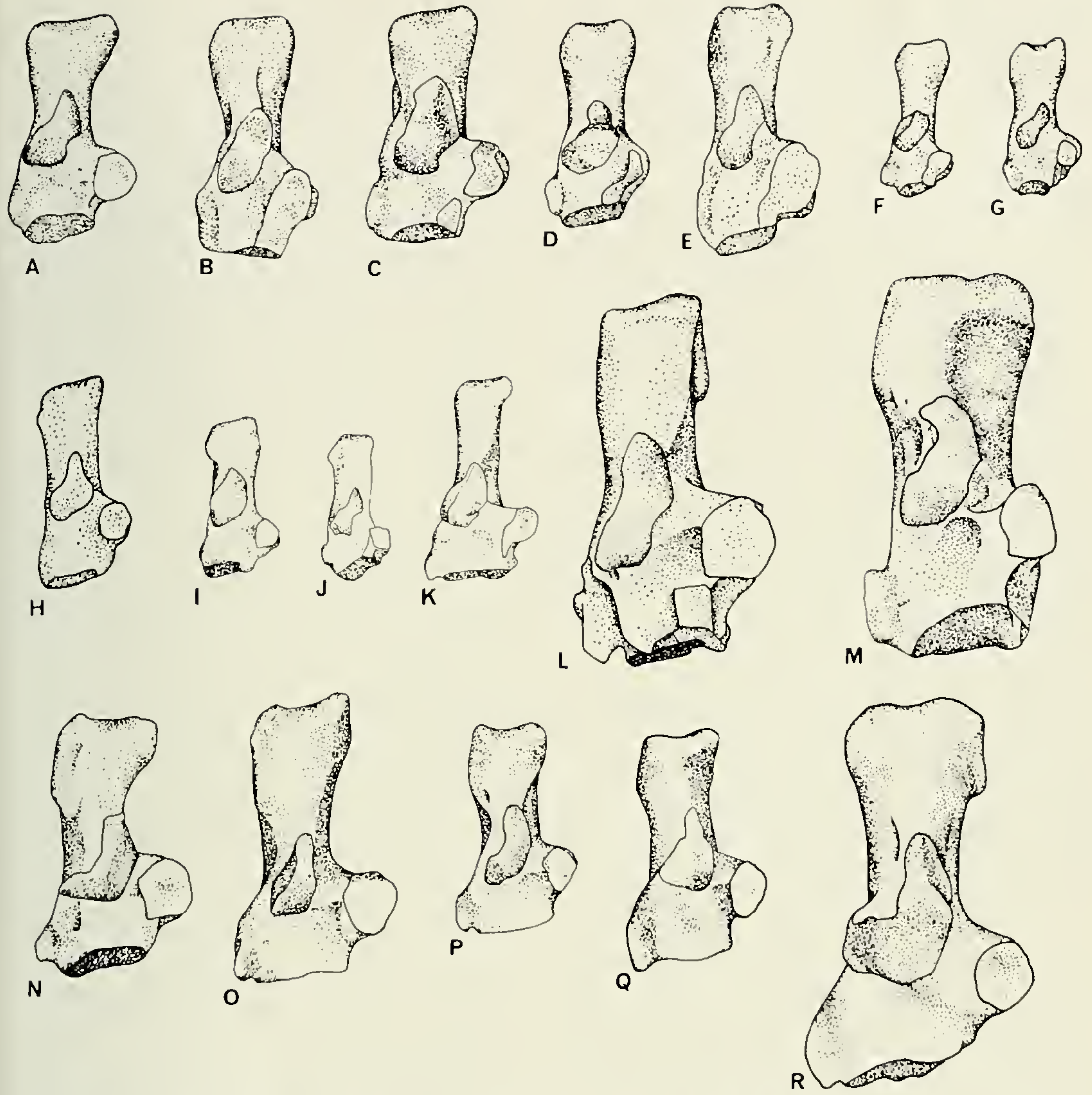

Figure 1. Right calcanea of members of the Mellivorinae, Melinae, Mephitinae and Lutrinae. A. *Mellivora capensis*; B. *Arctonyx collaris*; C. *Meles meles*; D. *Melogale moschata*; E. *Taxidea taxus*; F. *Conepatus mesoleucus*; G. *Conepatus semistriatus*; H. *Mephitis macroura*; I. *Mephitis mephitis*; J. *Spilogale putorius*; K. *Aonyx cinerea*; L. *Aonyx capensis*; M. *Enhydra lutris*; N. *Lutra canadensis*; O. *Lutra perspicillata*; P. *Lutra platensis*; Q. *Lutra maculicollis*; R. *Pteronura brasiliensis*.

Meles meles (Fig. 1C) has a sigmoid posterior articular surface with the proximal edge raised dorsally such that it is the most dorsal part of the calcaneum. Most indices of *Meles* and *Arctonyx* are the same (Table 2), the greatest difference being that of the least width of body/dorsoventral height which tends to be slightly larger in *Meles* largely because of the greater least width of body. The bulbous nature of the greater tuberosity of *Arctonyx* is most obvious from a lateral view producing a curved outline for the ventral surface not straight as in *Meles*.

Taxidea taxus is like *Arctonyx* in having a curved outline of the ventral surface of the body but differs from *Arctonyx* having a flattened area on the inner side of the greater tuberosity (Fig. 1E). There is an overlap in all indices and measurements in these two species (Tables 1 and 2)

TABLE 2. Indices for calcanea of members of the Mellivorinae, Melinae, Mephitinae, and Lutrinae.

	W/TL		D-VH/TL		LWB/D-VH	
Species	Range	Avg.	Range	Avg.	Range	Avg.
MELLIVORINAE						
Mellivora capensis	55–57	56	41–42	41	40–48	43
MELINAE						
Arctonyx collaris	53–60	56	42–46	44	42–51	45
Meles meles	57–59	58	43–45	44	50–52	51
Melogale moschata	49–57	53	38–43	40	40–46	42
Taxidea taxus	52–59	56	40–43	41	45–52	49
MEPHITINAE						
Conepatus mesoleucus		51		34		55
Conepatus semistriatus	46–49	47	34–38	36	56–58	57
Mephitis macroura		47		39		41
Mephitis mephitis	46–53	49	35–43	39	37–48	42
Spilogale putorius	45–52	49	36–38	37	44–48	47
LUTRINAE						
Aonyx cinerea	54–55	55	45–50	47	30–35	33
Aonyx capensis	58–60	59	48–51	50	31–32	31
Enhydra lutris	56–64	59	38–43	41	48–62	55
Lutra perspicillata		53		47		35
Lutra canadensis	50–66	57	44–52	47	37–47	41
Lutra platensis		57		49		39
Lutra maculicollis		56		50		38
Pteronura brasiliensis	55–61	58	44–45	44	39–42	41

and the bones are, in general, similar. The dorsal table of *Taxidea* does tend to be slightly flatter. The sustentaculum of *Taxidea* is broader than *Arctonyx* and extends almost to the cuboid surface.

The calcanea of *Lutra canadensis*, *L. maculicollis*, *L. perspicillata* and *L. platensis* tend to have smaller, hooked trochlear processes (except slight in *L. perspicillata*, Fig. 10) and smaller least width of body/dorso-ventral height indices although there is some overlap of this index with *L. canadensis* and probably *L. platensis* (Table 2). The straight, non-expanded nature of the greater tuberosity of *L. perspicillata*, and the inward curving of the greater tuberosity of *L. canadensis*, *L. maculicollis* and *L. perspicillata* will separate these species from the bulbous tuberosity of *Arctonyx*. The prominent longitudinal ridge from the disto-lateral edge of the posterior articular surface to the cuboid surface of *Arctonyx* (Fig. 1B) will separate the hog-badger from all the lutrines.

Specimens examined: NM 255957, 256670, 259014–5, 276638 (NM 276638 illustrated, Fig. 1B).

Meles meles—Old World Badger

The calcaneum of *Meles meles* has a posterior articular surface with the proximal edge turned sharply dorsal resulting in this part of the calcaneum being the most dorsal part. The anterior and medial articular surfaces usually are broadly joined (Fig. 1C). Within the size range (Table 1) are the calcanea of *Eira barbara*, perhaps *Martes* (*flavigula* and *pennanti*), *Mellivora capensis*, *Arctonyx collaris*, *Taxidea taxus*, and *Lutra* (*canadensis*, *maculicollis* and *perspicillata*).

Taxidea taxus (Fig. 1E) has a smooth posterior articular surface, not sigmoid, and a large, flattened area on the outer side of the greater tuberosity. The trochlear process also tends to be broader in *Taxidea*, extending a greater distance laterally from the base of the posterior articular surface. The sustentaculum is broader and extends closer to the cuboid end of the bone in *Taxidea*.

Lutra canadensis, *L. maculicollis*, and *L. perspicillata* also have smooth posterior articular surfaces but have greater tuberosities that are turned inwardly not straight as in *Meles*. The least width of body tends to be smaller in *Lutra* again resulting in a smaller least width of body/dorso-ventral height index (*L. canadensis*, 37–47, avg. 41; *L. maculicollis*, 38; *L. perspicillata*, 35; *Meles*, 50–52, avg. 51) (Table 2).

Specimens examined: AM 70603; NM 22253, 239585 (yg) (NM 22253 illustrated, Fig. 1C).

Melogale moschata—Chinese Ferret-badger

Melogale moschata has the smallest calcanea of the members of the Melinae examined. The anterior and medial articular surfaces tend to be joined (Fig. 1D) as in the other representatives of the Melinae. The posterior articular surface is slightly sigmoid and, of the Melinae, is more similar to *Meles* (Fig. 1C) than *Arctonyx* (Fig. 1B) or *Taxidea* (Fig. 1E). Of the other genera of mustelids, *Melogale* is most like *Martes*. Within or near the size range of *Melogale* (Table 1) are the calcanea of *Galictis vittata*, *Martes* (*americana*, *martes*, and perhaps *flavigula* and *foina*), *Mustela* (*nigripes*, *putorius*, *sibirica*, and *vison*), perhaps *Poecilogale albinucha*, *Conepatus semistriatus*, *Mephitis* (*macroura* and *mephitis*) and perhaps *Spilogale putorius*.

Of the various indices, the width/total length index of *Melogale* tends to show the greatest difference (49–57, avg. 53) from all the skunks (*Conepatus semistriatus*, 46–49, avg. 47; *Mephitis macroura*, 47; *M. mephitis*, 46–53, avg. 49; *Spilogale putorius*, 45–52, avg. 49) (Table 2). This index difference is due mostly to the proportionately smaller width of the calcaneum in the skunks, most of which have poorly formed trochlear processes (Fig. 1G, H, I, and J). The bulbous, club-like greater tuberosity of the skunks also will separate the calcanea of these animals from *Melogale*. In addition, all of the skunks have a smooth posterior articular surface, not sigmoid as in *Melogale*.

Specimens examined: AM 43167; NM 239586, 240996, 254588, 254917–8, 255528, 258014–5 (NM 258014 illustrated, Fig. 1D).

Taxidea taxus—American Badger

The calcaneum of *Taxidea taxus* has a large trochlear process (Fig. 1E) which extends from the cuboid surface to a point slightly proximal to the distal edge of the posterior articular surface. Probably the most distinctive characteristic of the calcaneum of *Taxidea* is the flattened area on the outer side of the greater tuberosity. This flattened area gives the greater tuberosity a triangular shape when viewed from the proximal end of the bone and the attachment of the tendon of Achilles is more on the inner dorsal region of this greater tuberosity. *Arctonyx* (Fig. 1B) has a calcaneum more similar to *Taxidea* than does *Meles* (Fig. 1C).

Other calcanea within the size range of *Taxidea* (Table 1) are those of *Eira barbara*, *Martes* (*flavigula*, *pennanti*, and perhaps *foina* and *zibellina*), *Mellivora capensis*, *Arctonyx collaris*, *Meles meles*, *Aonyx cinerea* and *Lutra* (*canadensis*, *maculicollis*, and perhaps *perspicillata* and *platensis*).

Aonyx cinerea (Fig. 1K) has a calcaneum with a straight, narrow body leading to a narrow tuberosity; lacks the flattened area on the outer side of the greater tuberosity; and has a much lower least width of body/dorso-ventral height index (*Aonyx cinerea*, 30–35, avg. 33; *Taxidea*, 45–52, avg. 49) (Table 2).

Lutra canadensis has a smaller least width of body/dorso-ventral height index (37–47, avg. 41), as does *L. maculicollis* (38), *L. perspicillata* (35), and *L. platensis* (39) (Table 2). A prominent inward twisting of the greater tuberosity of *Lutra* will distinguish this genus from *Taxidea* as well as the characteristics of *Taxidea* listed above.

Specimens examined: AM 35178, 35878, 70423, 120577; NM 1389, 188995, 259041, 264140, 300299 (NM 300299 illustrated, Fig. 1E).

Conepatus mesoleucus—Hog-nosed Skunk

One specimen of *Conepatus mesoleucus* was available for study. Members of this genus have the typical bulbous greater tuberosity characteristic of the Mephitinae. Both *C. mesoleucus* (Fig. 1F) and *C. semistriatus* (Fig. 1G) have a reduced trochlear process, a smooth posterior articular surface, and a cuboid surface which is at a dorso-ventral angle to the main axis of the calcaneum (not perpendicular as in most species). The anterior articular surface may be present, absent, or joined to the medial articular surface.

Within the size range of *Conepatus* (Table 1) are the calcanea of *Eira barbara*, *Galictis vittata*, *Martes* (*americana*, *flavigula*, *foina*, *martes*, *pennanti* and *zibellina*), *Mustela* (*nigripes*, and perhaps *putorius*, *sibirica* and *vison*), perhaps *Melogale moschata*, *Mephitis* (*macroura* and *mephitis*), *Aonyx cinerea*, and perhaps *Lutra* (*canadensis* and *platensis*).

Mephitis and *Conepatus* tend to be close in general appearance but in measurements *Conepatus* averages larger in least width of body and this measurement divided by dorso-ventral height gives indices of 55 for *C. mesoleucus*, 56–58 (avg. 57) for *C. semistriatus*, 37–48 (avg. 42) for *M. mephitis*, and 41 for the one specimen of *M. macroura* (Table 2).

Aonyx cinerea (Fig. 1K), *Lutra canadensis* (Fig. 1N) and *L. platensis* (Fig. 1P) have more prominent trochlear processes than *Conepatus* thus usually a wider calcaneum and greater width/total length index (*Aonyx cinerea*, 54–55, avg. 55; *Lutra canadensis*, 50–66, avg. 57; *L. platensis*, 57; *Conepatus mesoleucus*, 51; *C. semistriatus*, 46–49, avg. 47) (Table 2). But an even greater difference is noted in the indices dorsal-ventral height/total length (*Aonyx cinerea*, 45–50, avg. 47; *Lutra canadensis*, 44–52, avg. 47; *L. platensis*, 49; *Conepatus mesoleucus*, 34; *C. semistriatus*, 34–38, avg. 36) and least width of body/dorso-ventral height (*Aonyx cinerea*, 30–35, avg. 33; *Lutra canadensis*, 37–47, avg. 41; *L. platensis*, 39; *Conepatus mesoleucus*, 55; *C. semistriatus*, 56–58, avg. 57) (Table 2).

The two species of *Conepatus* are similar in shape and indices. The one specimen of *C. mesoleucus* does have a large, more obvious trochlear process producing a large width/total length index (Table 2) and continuous medial and anterior articular surfaces but these features may overlap when more specimens are examined.

Specimen examined and illustrated: AM 136415, Fig. 1F.

Conepatus semistriatus—Striped Hog-nosed Skunk

Conepatus semistriatus (Fig. 1G) has been discussed in detail and compared with other species within the same size range under *Conepatus mesoleucus*. The three specimens of *C. semistriatus* are variable in expression of the anterior articular surface while that of *C. mesoleucus* is obvious and broadly joined with the anterior articular surface. The trochlear process of one specimen appears absent, slightly expressed as a small knob in one, and small but obvious in the other. The trochlear process of *C. mesoleucus*, by comparison, is large and obvious.

Specimens examined: AM 69609, 133946, 133948 (AM 133946 illustrated, Fig. 1G).

Mephitis macroura—Hooded Skunk

Only one specimen of *Mephitis macroura* was examined and this one specimen is within the size and index range of *Mephitis mephitis*. This specimen (Fig. 1H) has an obvious pimple-like knob on the outer surface at the base of the greater tuberosity. *Mephitis mephitis* (Fig. 1I) also has this knob usually slightly larger but not as distinct. *Mephitis mephitis* has a shallow pit in the outer side of the body near the proximal end of the posterior articular surface which *M. macroura* lacks. Characteristics of this type often vary so that this perhaps would not always separate the two species. *Mephitis macroura* also has an obvious dish-shaped greater tuberosity with the inner edge being much higher. The greater tuberosity of *M. mephitis* usually is flat or sometimes even rounded.

Other species within the size range of *Mephitis macroura* (Table 1) are *Galictis vittata*, *Martes* (*americana*, *martes*, and perhaps *flavigula*), *Mustela* (*sibirica*, *vison*, and perhaps *nigripes* and *putorius*), *Melogale moschata*, and *Conepatus* (*mesoleucus* and *semistriatus*).

Specimen examined and illustrated: AM 137007, Fig. 1H.

Mephitis mephitis—Striped Skunk

The species within the size range of *Mephitis macroura* also fall within the size range of *Mephitis mephitis* (Table 1). In addition, *Eira barbara*, *Martes* (*pennanti* and *zibellina*), and *Aonyx cinerea*, fall near or within the size range of *M. mephitis*.

The discussion of *Mephitis macroura* aptly describes the calcaneum of *M. mephitis*. *Aonyx cinerea* has a prominent trochlear process (Fig. 1K) and a narrow tuberosity not bulbous as in *Mephitis* (Fig. 1I). All indices tabulated in Table 2 clearly separate these two species.

Specimens examined: AM 15905, 120581, 121199, 124213, 131836; NM 670, 917, 15670, 20973, 35230, 188597, 188997, 199730, 239114–5, 240473–4, 240911, 255390, 260920–1 (AM 121199 illustrated, Fig. 1I).

Spilogale putorius—Spotted Skunk

Like the other skunks, *Spilogale* (Fig. 1J) has a bulbous tuberosity and a small trochlear process. The anterior articular surface, if present, is minute and in one case there is a continuation or joining of the medial and anterior articular surfaces. The trochlear process is not as far distally as in the other skunks and is more obvious. The swelling on the outer side of the base of the greater tuberosity is present in all specimens, as it is in the other skunks, but is not as distinct. The sustentaculum extends almost to the cuboid surface, closer to this surface than that in either *Conepatus* (Figs. 1F and G) or *Mephitis* (Figs. 1H and 1); *Conepatus* being intermediate in this respect.

Other Mustelids within the size range of *Spilogale* are *Eira barbara*, *Gulo gulo*, *Mustela* (*nigripes*, *frenata*, *nivalis*, *sibirica*, and *vison*), *Martes* (*flavigula*, *foina*, and *pennanti*), *Melogale*, *Conepatus*, *Mephitis*, and *Lutra canadensis*.

Specimens examined: AM 131840, 135961, 136421, 137373; NM 49811 (AM 136421 illustrated, Fig. 1J).

Aonyx cinerea—Oriental Small-clawed Otter

Both species of *Aonyx* have an extremely thin greater tuberosity so that, from a dorsal view, both inner and outer edges form almost a straight line proximally from the dorsal table. The trochlear process of *Aonyx cinerea* (Fig. 1K) is located at the distal end of the calcaneum and extends distally beyond the cuboid surface. The posterior articular surface is smooth. The medial articular surface tends to extend toward a minute anterior articular surface.

Within, or perhaps within, the size range of

Aonyx cinerea (Table 1) are the calcanea of *Eira barbara, Galictis vittata, Martes* (*americana, flavigula, foina, martes, pennanti,* and *zibellina*), *Mustela* (*nigripes, putorius, sibirica,* and *vison*), *Arctonyx collaris, Melogale moschata, Taxidea taxus, Conepatus* (*mesoleucus* and *semistriatus*), and *Mephitis mephitis. Lutra canadensis* and *L. platensis* may also overlap *Aonyx cinerea* in size.

The straight body and greater tuberosity of *Aonyx* (Fig. 1K) separates this genus from *Lutra canadensis* (Fig. 1N) and *L. platensis* (Fig. 1P) in which the tuberosity is twisted inward.

There probably is no overlap in size between *Aonyx cinerea* and *Aonyx capensis. Aonyx capensis* (Fig. 1L) tends to have a greater extension of the trochlear process producing a greater width in proportion to length and giving an index of 58 to 60 (avg. 59) compared to 54 to 55 avg. 55) for *A. cinerea* (Table 2). In some cases, however, the two species may be difficult to distinguish if there is a size overlap. Some authors (Simpson, 1945: Walker, 1964:1218) regard *Aonyx cinerea* to be a different genus, *Amblonyx.*

Specimens examined: NM 49929, 155324, 198054, (NM 155324 illustrated, Fig. 1K).

Aonyx capensis—Cape Clawless Otter

The characteristics of *Aonyx capensis* are similar to those of *Aonyx cinerea* discussed above. Also within the size range of *Aonyx capensis* (Table 1) are *Gulo gulo, Mellivora capensis, Meles meles, Enhydra lutris, Lutra canadensis, L. perspicillata* and perhaps *Pteronura brasiliensis.*

The entire ventral surface of the calcaneum of *Enhydra lutris* is shifted to the inner side of the calcaneum (Fig. 1M). The body and tuberosity of *Aonyx* are straight (Fig. 1L). *Lutra canadensis* tends to have an obvious twisting of the greater tuberosity towards the inner side of the bone (Fig. 1N). *Lutra perspicillata* (Fig. 10) is intermediate between *L. canadensis* and *Aonyx* in this regard. The trochlear process of *Aonyx capensis* is situated on a massive shelf, that of *Lutra canadensis* is knoblike. The trochlear process of *Lutra perspicillata* is massive but with little development of a shelf. The trochlear process of *Aonyx* is located more ventral to the rounded dorsal table than that of *Lutra perspicillata* which has a more-or-less flat dorsal table, otherwise the calcanea of these two species are similar.

There is probably no overlap in size between the calcanea of adult *Aonyx* and *Pteronura, Pteronura* being much larger (Table 1). *Pteronura* (Fig. 1R) has the typical v-shaped body—greater tuberosity relationship rather than the straight or parallel relationship of *Aonyx. Pteronura* also has a broader, flatter and slightly sigmoid posterior articular surface which is reflected in the smaller dorso-ventral height/total length index (*Pteronura,* 44–45, avg. 44; *Aonyx capensis,* 48–51, avg. 50) and in the least width of body/dorso-ventral height index (*Pteronura,* 39–42, avg. 41; *Aonyx capensis,* 31–32, avg. 31) (Table 2) so that if the last index is subtracted from the first, a rather obvious difference exists (*Pteronura,* 1.9–4.9, avg. 3.1; *Aonyx,* 17.2–19.4, avg. 18.3).

Specimens examined: AM 51837, 51853 (AM 51853 illustrated, Fig. 1L).

Enhydra lutris—Sea Otter

Enhydra lutris differs from all mustelids examined by the shifting of the entire ventral surface internally (Fig. 1M). The posterior articular surface is quite flat, smooth, largely facing dorsally, located near the center of the calcaneum rather than more towards the outer side, and comparatively small for the size of the bone.

Within or near the size range of *Enhydra* (Table 1) are the calcanea of *Gulo gulo, Aonyx capensis, Lutra canadensis, L. perspicillata* and *Pteronura brasiliensis.*

The characteristics listed above for *Enhydra* will distinguish the calcanea of this animal from other mustelids of the same size. *Lutra* sp. tends to have a higher, more curved and typical posterior articular surface which faces more inwardly than dorsally.

The posterior articular surface of *Pteronura* (Fig. 1R) is positioned much like that of *Enhydra* but is much larger and wider. The greater tuberosity of *Pteronura* is similar to most mustelids, in being v-shaped with no twisting or shifting of position as in *Enhydra.*

Specimens examined: AM 28226, 100394 (broken); NM 3423, 7383, 11794, 13304, 21336, 22067, 49459, 49492 (NM 49459 illustrated, Fig. 1M).

Lutra canadensis—River Otter

An inward twisting of the greater tuberosity is the most distinctive characteristic of *Lutra canadensis* (Fig. 1N). The posterior articular surface is smooth and the anterior articular surface is absent. A twisting of the greater tuberosity is accompanied by the presence of an elongate ridge running parallel with the main axis of the bone on the outer side of the tuberosity. The trochlear process is located near the distal end of the calcaneum and usually is small and knob-like.

Mustelids with calcanea within or perhaps within the size range of *Lutra canadensis* (Table 1) are *Eira barbara*, *Gulo gulo*, *Galictis vittata*, *Martes* (*flavigula*, *foina*, *pennanti*, and *zibellina*), *Mellivora capensis*, *Arctonyx collaris*, *Meles meles*, *Taxidea taxus*, *Conepatus* (*mesoleucus* and *semistriatus*), *Aonyx cinerea*, *Mephitis mephitis*, *Aonyx capensis*, and *Enhydra lutris*.

Three other species of *Lutra*, one specimen of each, were available for study. *Lutra platensis* is at the lower end of the size range of *L. canadensis* and is similar to *L. canadensis* in most respects. All measurements and indices of *L. canadensis*, except total length, include the one specimen of *L. platensis*. The two species would be difficult to tell apart (Tables 1 and 2). *L. platensis* (Fig. 1P) does have a small medial articular surface compared to the specimens of *L. canadensis* available. This surface is less than 4mm in width; the smallest surface found in *L. canadensis* was more than 5mm in width. The greater tuberosity tends to be less twisted internally or perhaps not as obvious because of a large swelling on the outer dorsal edge of the greater tuberosity of this specimen of *L. platensis*. The swelling may not be natural. Calcanea of both *L. platensis* and *L. maculicollis* have a distinct groove between the trochlear process and the dorsal table; in *L. canadensis* this area is broad and curved.

Lutra maculicollis (Fig. 1Q) is close to *L. canadensis* in averages and indices (Tables 1 and 2). The greater tuberosity has an obvious dorsal attachment in *L. maculicollis*.

Lutra perspicillata (Fig. 1O) lacks the twisting of the greater tuberosity (present in *L. canadensis*), the sides of the main body and the tuberosity tend to be paralled as in *Aonyx* (Fig. 1K and L). The measurements and indices of *L. canadensis* and *L. perspicillata* are similar (Tables 1 and 2). *Lutra perspicillata* have calcanea near the upper end of the size range of *L. canadensis*.

Specimens examined: AM 77746, 125566, 165762; NM 3142, 3459, 4446, 21232, 49506, 49578, 49902, 144553, 152236, 188618, 199562, 256976, 259464, 267303, 301947 (NM 267303 illustrated, Fig. 1N).

Lutra perspicillata—Smooth-coated Indian Otter

The one specimen of *Lutra perspicillata* is near or within the size range of *Eira barbara*, *Mellivora capensis*, *Arctonyx collaris*, *Meles meles*, *Taxidea taxus*, *Martes pennanti*, *Aonyx capensis*, and *Lutra canadensis*. See in particular the discussions under *L. canadensis* and *Aonyx capensis*.

Specimen examined and illustrated: AM 99610, Fig. 1O.

Lutra platensis—Silver Otter

This one specimen of *Lutra platensis* is near or within the size range of *Eira barbara*, *Galictis vittata* *Martes* (*flavigula*, *foina*, *pennanti*, and *zibellina*), *Arctonyx collaris*, *Taxidea taxus*, *Conepatus* (*mesoleucus* and *semistriatus*), *Aonyx cinerea*, and *Lutra* (*canadensis* and *maculicollis*). See in particular the discussion under *L. canadensis*.

Specimen examined and illustrated: AM 133950, Fig. 6P.

Lutra maculicollis—Spotted-necked Otter

The one specimen of *Lutra maculicollis* is similar to those of *L. canadensis*. This specimen differs from those of *L. canadensis* in having a distinct groove between the trochlear process and the dorsal table and a distinct attachment area on the dorsal edge of the greater tuberosity (Fig. 1Q). Indices and measurements fall within the range and near the average for the 17 specimens of *Lutra canadensis* (Tables 1 and 2).

Other species near the size range of *L. maculicollis* are *Eira barbara*, *Martes* (*flavigula*, and *pennanti*), *Mellivora capensis*, *Arctonyx collaris*, *Meles meles*, *Taxidea taxus*, *Aonyx cinerea*, and *Lutra* (*canadensis* and *platensis*).

Specimen examined and illustrated: AM 51827, Fig. 1Q.

Pteronura brasiliensis—Giant Otter

Only *Gulo gulo*, *Enhydra lutris* and possibly *Aonyx capensis* have calcanea as large as those of *Pteronura brasiliensis*.

Pteronura (Fig. 1R) differs from all the Lutrinae in having a greater tuberosity which is typical v-shaped (as found in most mustelids) rather than being twisted internally (*Lutra canadensis*, *Enhydra*) or parallel with the body (*Aonyx*, *Lutra perspicillata*). *Lutra platensis* (Fig. 1P) of the Lutrinae, is perhaps the closest to *Pteronura* in this general shape of the greater tuberosity. The rather flat, broad posterior articular surface is often sigmoid at both the proximal and distal halves in *Pteronura* (Fig. 1R). The anterior articular surface is absent. The trochlear process is wedge-shaped, flat and located near the distal end of the calcaneum.

Specimens examined: AM 30190–1, 77735 (AM 77735 illustrated, Fig. 1R).

CONCLUSIONS

The various members of subfamilies of the Mustelidae have features which will separate them from other subfamilies. The Mustelinae have a large posterior articular surface which is smooth, a well-developed medial articular surface, and an anterior articular surface which usually is absent or minute when present (see Stains, 1976). The greater tuberosity of most members of the Mustelinae and Lutrinae tends to be grooved while in the Mellivorinae, Melinae and Mephitinae the groove is absent. In addition, members of the Mustelinae, with calcanea of the same size, can be distinguished from the Mellivorinae and Mephitinae by the larger least width of body measurements producing a higher LWB/DVH ratio; and from the Melinae which have a larger, more distally located trochlear process and continuous, or nearly continuous, medial and anterior articular surfaces. The Lutrinae have a thin greater tuberosity which tends to curve inward and a hooked trochlear process located distally. Members of the Mephitinae have a pimple-like swelling on the body distal to the greater tuberosity on the medial surface; the massive tuberosity does not curve inward and the small indistinct grooved trochlear process produces a small width/length index. Mellivora of the Mellivorinae has a flaring greater tuberosity. Members of the Melinae have large joined medial and anterior surfaces, a large trochlear process and a bulbous greater tuberosity.

Perhaps the most distinctive mustelid is the aquatic sea otter (*Enhydra lutris* of the Lutrinae). There is an inward shifting of the entire surface of the calcaneum. The posterior articular surface is flat, smooth, and largely facing dorsally near the center of the calcaneum rather than towards the lateral side; this surface is comparatively small for the size of the bone.

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SEASONAL CHANGES IN WING LOADING, BODY COMPOSITION, AND ORGAN WEIGHTS IN *MYOTIS THYSANODES* AND *M. LUCIFUGUS* (CHIROPTERA: VESPERTILIONIDAE)

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Abstract: Embryo-free, fat-free live body weight and lean dry body weight showed significant differences in all reproductive seasons (prepregnant, pregnant, lactating, post lactating) for *Myotis thysanodes* while only prepregnant *M. lucifugus* had significantly lower fat-free live and lean dry body weight than at other reproductive states. Prepregnant and post lactation wing loadings in *M. thysanodes* were significantly lower than during pregnancy and lactation whereas wing loadings for *M. lucifugus* followed the pattern for body weight. Also, maximum wing loading was significantly greater than minimum during all reproductive seasons for *M. thysanodes* but only for prepregnant and pregnant *M. lucifugus*, thus indicating significant daily decreases in wing loading at these times. Fat indices for both species were consistently low until fall at which time a significant increase occurred. Water index and gross body composition (percent water, percent non-fat organic, and percent mineral) followed the same pattern as body weight for each species. The left adrenal was significantly heavier than the right in *M. thysanodes* and both were significantly heavier during lactation than at any other time. A significant increase in spleen weight from prepregnant to post lactating *M. thysanodes* occurred, thus indicating an increase in erythropoietic activity at this time. No significant changes were observed for organ weight in *M. lucifugus*. Thus, the two species examined showed a number of differences which may relate to differences in their physiological-ecological strategies.

The functional morphology of North American insectivorous bats has been investigated in detail with respect to ecological considerations (Vaughan 1959, Findley *et al.*, 1972). In addition, Farney and Fleharty (1969) have given values for wing loading and aspect ratio for 22 species of bats. Davis (1969), however, has pointed out that seasonal changes in wing loading must be considered due to seasonal fluctuations in body weight.

Fat and water indices of several species of bats have been examined and presented primarily to document the fall accumulation of fat (Baker *et al.*, 1968; Weber and Findley, 1970). The annual cycle has been described for only one bat species (*Myotis grisescens*) (Krulin and Sealander, 1972). As noted by Ewing *et al.*, (1970), gross body composition studies of bats have been neglected. In addition, the examination of various organ weights in relation to physiological demands in bats has received little attention, but variations in adrenal size associated with reproductive status (Christian, 1956; Short, 1961; Rudd and Beck, 1969), and population states (Christian, 1956) have been described for some bats. Furthermore, fluctuations in splenic weight have been attributed to hibernation (Lidicker and Davis, 1955).

For the past several years, we have conducted an intensive study on the biology of *Myotis thysanodes* and *M. lucifugus occultus*. This report describes some seasonal changes in wing loading, body composition, and organ weights and the factors which influence these.

METHODS

The fringe-tailed bat, *Myotis thysanodes*, and the little brown bat, *M. lucifugus occultus* (*M. occultus*, Findley and Jones, 1967), were the two species examined in this study. A sample of six adult females of each species usually was collected at Montezuma Seminary, Montezuma, San Miguel Co, New Mexico, at weekly intervals from 19 April to 25 September 1970 for *M. thysanodes* and 1 May to 6 September 1970 for *M. lucifugus*. For a detailed description of the maternity roost see O'Farrell and Studier (1973). These animals were assigned a relative age as

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described by O'Farrell and Studier (1975), and were used in other studies (Studier and O'Farrell, 1972; O'Farrell and Studier, 1973).

Various measures were taken to determine the seasonal variation of wing loading and aspect ratio. Individual maximum and minimum wing loading were determined by the method of O'Farrell and Studier (1973). Maximum wing loading was based on body weight of each bat upon return to the roost in the morning, whereas, minimum wing loading was based on body weight of each bat just prior to the evening emergence. Aspect ratio is presented as wing span^2/area of wings.

After obtaining physiological measurements, all bats were dissected and spleen and adrenals were removed and weighed separately. Bats were dried to constant weight under reduced pressure at 40°C and fats were extracted with petroleum ether following the procedure of Ewing *et al.*, (1970). All fat-free residues were dried to constant weight and ashed at 620°C for 12 hours. From these data, fat index (g fat/g lean dry weight), water index (g water/g lean dry weight), and gross body composition (percent water, percent non-fat organic and percent mineral based on fat-free, embryo-free live weight) were calculated. Since thermoregulatory experiments prior to sacrificing were designed to simulate roost conditions, we feel that undue stress was eliminated and that the values obtained are representative of the populations.

Two 3 × 4 factorial analyses of variance (ANOVA) were performed on the following parameters: body weight; lean dry weight; aspect ratio; maximum, minimum, and mean wing loading; fat and water indices; percent water; percent mineral and percent non-fat organic; and weights of left and right adrenals and spleen. These were examined for each species separately; one analysis was of age and reproductive season, respectively, the other of thermoregulatory state and reproductive season, respectively. Prepregnant refers to late spring (April to early May); pregnant and lactating refers to early and mid-summer (May through late June and July), respectively; and post lactating refers to late summer and early fall (August through September). Thermoregulatory states were defined as regulators, conformers, and shifters as described by Studier and O'Farrell (1972). Significance levels, unless otherwise stated, were $P < 0.05$. All percentages for body composition were subjected to an arc sine transformation and all significant F values were examined by the Roy-Scheffe' multiple range test (Scheffe', 1959).

RESULTS

Flight Characters.—Variations in maximum and minimum wing loading and embryo-free live body weight for both species are shown in figure 1; reproductive season and chronological season coincide and therefore cannot be separated for analysis. F values for embryo-free live body weight and wing loadings were significant for reproductive season for both species, and for thermoregulatory state with respect to wing loading in *M. thysanodes*. Mean values of body weight for *M. thysanodes* were significantly different between all reproductive seasons. Wing loading values (based on embryo-free live body weight) for prepregnant and post lactating bats were significantly lower than those for pregnant and lactating individuals except for minimum loading where pregnant bats were not significantly differ-

TABLE 1. Mean values for fat and water indices and lean dry body weight by reproductive season in *Myotis thysanodes* (upper values) and *M. lucifugus* (lower values). 2 $SE_{\bar{x}}$ are given in parentheses. See text for discussion of significance of comparison.

	N	Fat Index	Water Index	Lean Dry Weight
Prepregnant	21	0.134 (0.027)	1.983 (0.050)	2.429 (0.081)
	13	0.137 (0.043)	2.013 (0.059)	2.146 (0.079)
Pregnant	31	0.133 (0.020)	2.233 (0.054)	2.639 (0.073)
	37	0.114 (0.018)	2.346 (0.069)	2.458 (0.060)
Lactating	10	0.119 (0.016)	2.496 (0.123)	2.699 (0.075)
	18	0.111 (0.027)	2.295 (0.092)	2.400 (0.112)
Post Lactating	53	0.362 (0.058)	2.126 (0.048)	2.500 (0.048)
	15	0.397 (0.145)	2.275 (0.067)	2.390 (0.091)

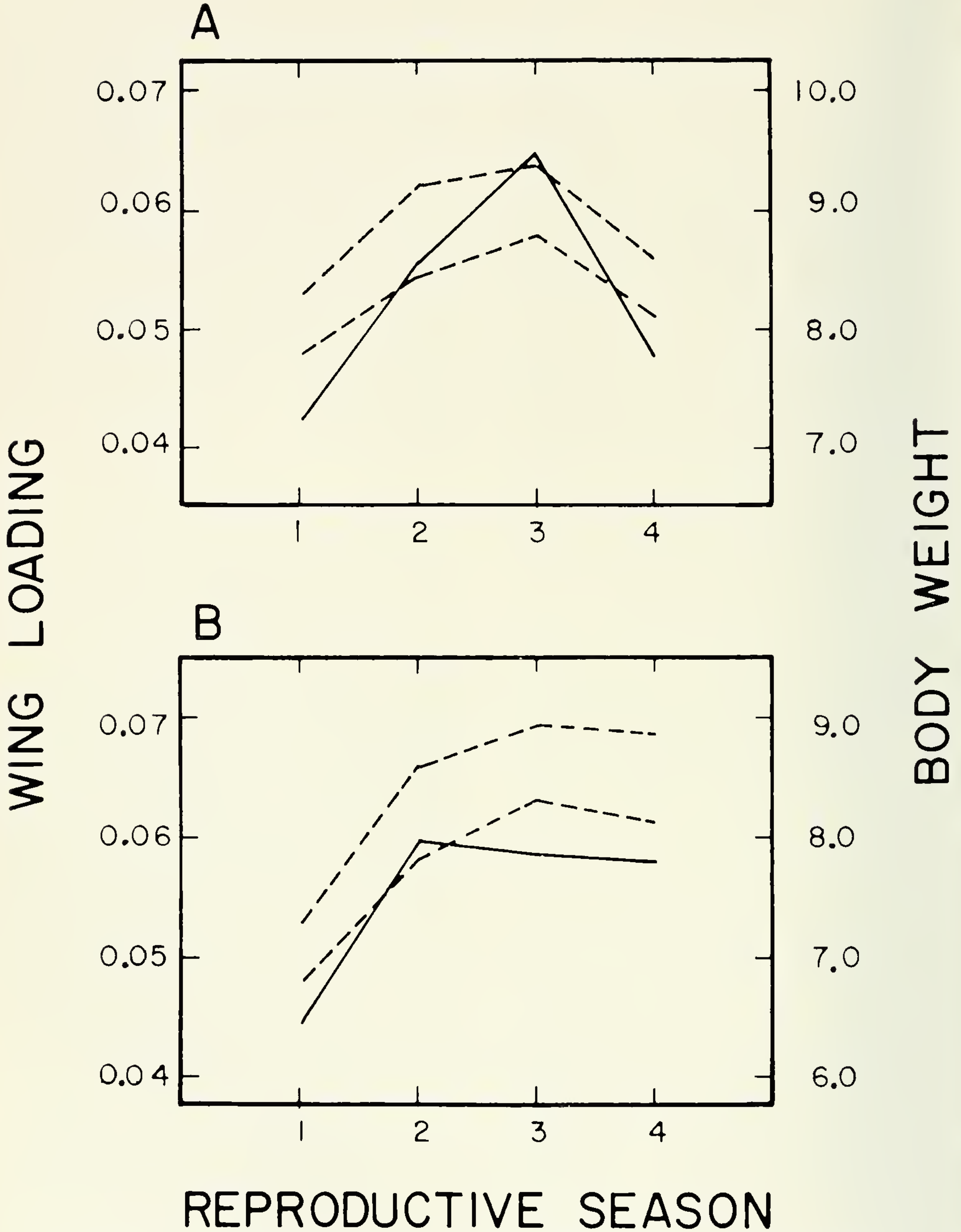


Figure 1. Mean values for embryo-free live body weight (solid lines) and maximum and minimum wing loading (upper and lower dashed lines, respectively) for *Myotis thysanodes* (A) and *M. lucifugus* (B) in relation to reproductive season. 1 = prepregnant; 2 = pregnant; 3 = lactation; 4 = post lactation.

TABLE 2. Mean values for gross body composition by reproductive season in *Myotis thysanodes* (upper values) and *M. lucifugus* (lower values). 2 $SE_{\bar{x}}$ are given in parentheses. See text for discussion of significance of comparison.

	N	% Water	% Organic	% Mineral
Prepregnant	21	66.17 (0.77)	28.14 (0.66)	5.69 (0.16)
	13	66.67 (0.64)	27.55 (0.25)	5.79 (0.54)
Pregnant	30	69.02 (0.51)	25.89 (0.44)	5.09 (0.11)
	38	69.64 (0.58)	24.49 (0.50)	4.88 (0.11)
Lactating	9	71.40 (1.08)	23.87 (0.94)	4.73 (0.23)
	18	69.94 (1.11)	25.34 (0.94)	4.73 (0.24)
Post Lactating	51	67.79 (0.45)	26.76 (0.39)	5.45 (0.09)
	15	69.31 (0.65)	25.85 (0.57)	4.84 (0.17)

ent from those in post lactation (Fig. 1). Additionally, in relation to thermoregulatory state, wing loadings of conformers were significantly lighter than for regulators. In contrast, *F* values for body weight and wing loadings of prepregnant individuals of *M. lucifugus* were significantly lower than for all other reproductive seasons.

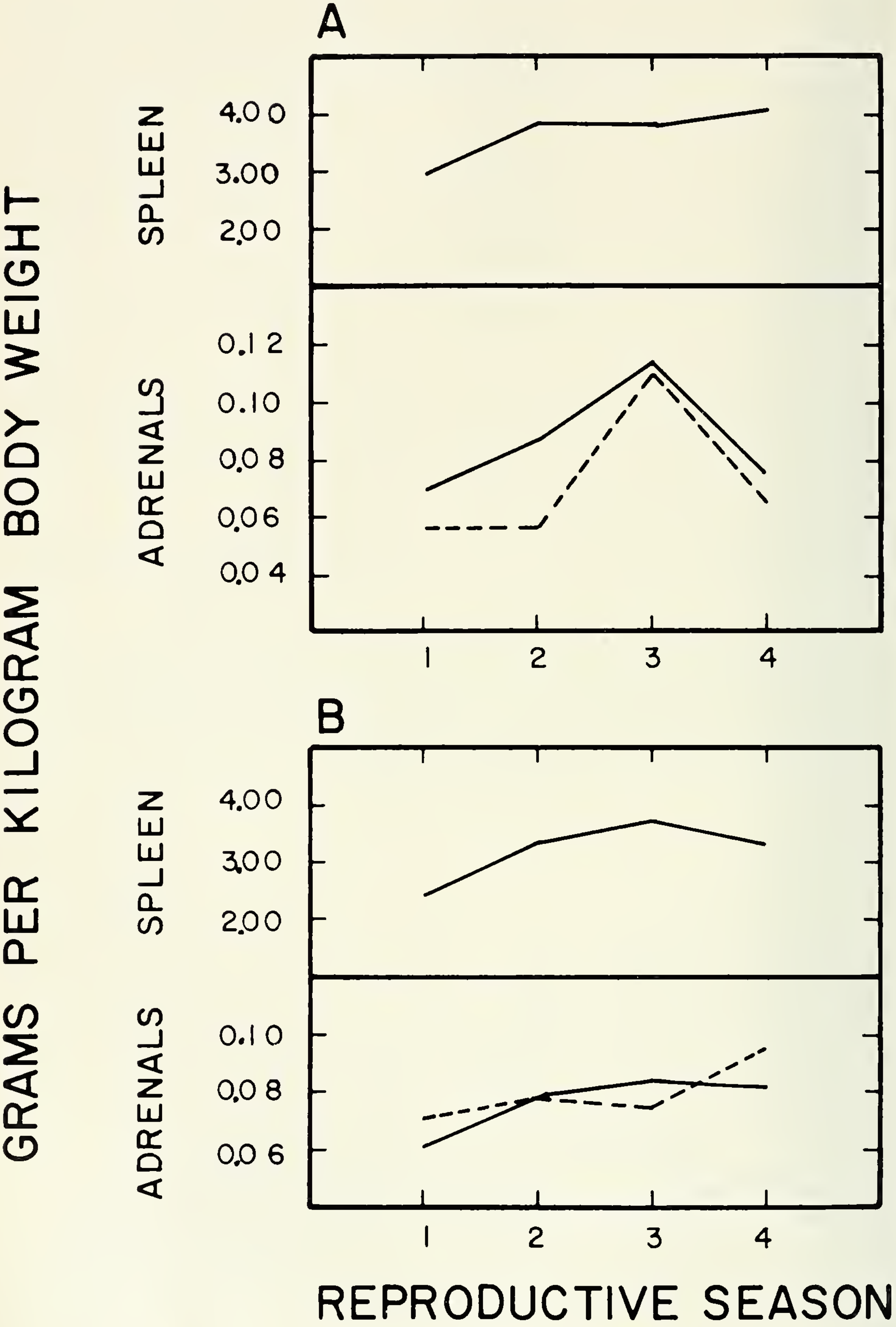
F values for aspect ratio of both species showed no significant differences among any of the variables examined. Mean aspect ratio ± 2 S.E. for each species were: *M. thysanodes* (6.002 ± 0.062, N = 100) and *M. lucifugus* (6.180 ± 0.066, N = 117). *Myotis thysanodes* had a significantly lower aspect ratio than *M. lucifugus*.

Body Composition.—Mean values for fat and water indices and lean dry body weight by reproductive season are given in table 1; *F* values for

TABLE 3. Partial correlation coefficients of various body parameters with main effects and interactions of reproductive season and age removed. Upper values for *Myotis thysanodes* and lower for *M. lucifugus*. BW = Body weight; LDW = Lean dry body weight; AR = Aspect ratio; MAX = Maximum wing loading; MIN = Minimum wing loading; MEAN = mean wing loading; FI = Fat index; WI = Water index; ASW = Arc sine water; ASO = Arc sine organic; ASM = Arc sine mineral.

	BW	LDW	AR	MAX	MIN	MEAN	FI	WI	ASW	ASO	ASM
BW											
LDW	**0.88**										
	0.66										
AR	0.08	0.02									
	–0.10	0.07									
MAX	**0.53**	**0.42**	**0.64**								
	0.69	**0.67**	*0.32*								
MIN	**0.59**	**0.50**	**0.55**	**0.95**							
	0.66	**0.68**	*0.30*	**0.93**							
MEAN	**0.56**	**0.46**	**0.61**	**0.99**	**0.98**						
	0.69	**0.68**	*0.31*	**0.98**	**0.98**						
FI	0.09	0.14	0.10	**0.38**	**0.40**	**0.39**					
	0.25	0.23	–0.17	*0.33*	*0.37*	*0.37*					
WI	**0.41**	–0.07	0.16	**0.36**	*0.33*	**0.36**	–0.03				
	0.65	–0.03	–0.06	**0.40**	**0.39**	**0.43**	–0.04				
ASW	**0.35**	–0.07	0.11	0.22	0.14	0.19	–0.13	**0.89**			
	0.68	0.02	–0.07	**0.42**	**0.43**	**0.45**	0.00	**0.93**			
ASO	*–0.33*	0.09	–0.15	–0.23	–0.15	–0.20	0.07	**–0.86**	**0.98**		
	–0.64	0.03	0.07	*–0.38*	*–0.38*	**–0.41**	0.03	**–0.93**	**–0.99**		
ASM	*–0.03*	–0.02	0.08	–0.08	–0.05	–0.07	0.27	**–0.61**	0.67	**0.49**	
	–0.70	–0.22	0.03	**–0.54**	**–0.53**	**–0.56**	–0.16	**–0.73**	**–0.82**	**0.75**	

Note—Italicized values indicate significance at $P < 0.05$ and boldfaced values indicate significance at $P < 0.01$.


A
GRAMS PER KILOGRAM BODY WEIGHT
SPLEEN
4.00
3.00
2.00
ADRENALS
0.12
0.10
0.08
0.06
0.04
1
2
3
4
B
SPLEEN
4.00
3.00
2.00
ADRENALS
0.10
0.08
0.06
1
2
3
4
REPRODUCTIVE SEASON

both species were significant for reproductive season. The fat index of post lactating individuals of *M. thysanodes* was significantly higher than that of individuals from all other reproductive seasons. Likewise, the water indices also were significantly different at all reproductive states. Lean dry weight of prepregnant and post lactating individuals was significantly lower than for pregnant and lactating bats. *Myotis lucifugus* showed an identical pattern with respect to fat index with a significant increase in post lactating individuals. However, prepregnant water index and lean dry weight were significantly lower than for other reproductive states.

Mean values for gross body composition by reproductive season for both species are given in table 2; *F* values were significant for reproductive season. Mean percent water of *M. thysanodes* was significantly different for all seasons, whereas, mean percent organic was significantly different for all seasons except between pregnant and post lactating individuals. The pattern for percent mineral in relation to reproductive season was identical to that of percent organic; yet, there was also a significant increase with age except in the oldest category. Although these trends were apparent for percent mineral, a significant age-reproduction interaction was exhibited. Mean values for percent water, organic, and mineral of *M. lucifugus* showed a different pattern than did *M. thysanodes*. Percent organic and mineral was significantly higher and percent water was significantly lower in prepregnant *M. lucifugus*.

Organ Weights and Correlations.—Mean changes in spleen and adrenal weights for both species are shown by reproductive season in figure 2; *F* values for the various organ weights were significant for reproductive season only in *M. thysanodes*. Mean adrenal size in lactating individuals was significantly larger than at other times and splenic weights of post lactating bats were significantly higher than prepregnant bats. In addition, the left adrenal was significantly larger than the right adrenal in *M. thysanodes*, whereas, no such difference was observed for those of *M. lucifugus*.

Correlation coefficients between different body parameters are given in table 3. General trends for *M. lucifugus* indicate that parameters such as percent water, organic and ash, which reflect body weight, are correlated with wing loadings. This does not hold for *M. thysanodes*; fat and water indices are positively correlated with wing loading. No correlation exists when body composition is considered.

DISCUSSION

Examination of aspect ratio and wing loading aid in describing certain aspects of the biology of bats. Aspect ratio may be used as an index of flight speed and foraging habits (Fenton, 1972; Findley *et al.*, 1972). Wings of high aspect ratio are usually indicative of high speed flight, whereas, wings of low aspect may characterize low speed flight or perhaps hovering. Our aspect ratios for *M. thysanodes* and *M. lucifugus* are relatively low and are comparable with values given by Farney and Fleharty (1969). The aspect ratio for *M. thysanodes* was significantly lower than that of *M. lucifugus*, which supports the findings of Findley *et al.*, (1972) that the former is capable of precision, low speed flight not exhibited by the latter.

Davis (1969) has argued against the use of an average wing loading value. Since wing loading is a function of body weight, it is reasonable to expect significant changes in wing loading concomitant with changes in body weight. Wing loading of female *Antrozous pallidus* follows such a pattern with a low in the spring; a significant increase during pregnancy, a significant decrease during lactation, and another increase in the fall (Davis, 1969). This pattern does not fit that of the two species which we have examined (Fig. 1), primarily because we utilized embryo-free live weight. No significant differences occurred from pregnancy to lactation, although there is a general trend toward a slight increase during lactation. Wing loading seems to follow a general pattern for embryo-free live weight, thereby indicating absolute embryo weight does not account for the total increase in wing loading. Also, the decrease in wing loading in post lactational *M. thysanodes* does not reflect the deposition of fat in the fall.

If one should examine seasonal changes in wing

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Figure 2. Mean values for spleen and adrenal weights (solid line = left adrenal; dashed line = right adrenal) by reproductive season for *Myotis thysanodes* (A) and *M. lucifugus* (B). See figure 1 for explanation of reproductive season.

loading due to significant changes in body weight, then it follows that daily changes should also be examined. We assume for this study that upon return to the roost in the morning, a bat will be near peak wing loading due to recent ingestion of food and water. Likewise, at evening emergence a bat should be at its minimum wing loading. Kunz (1974) has demonstrated that, at certain times of the year, maximum weight of *Myotis velifer* is reached after the first foraging period and that weight upon return to the diurnal roost may not reach maximal levels. Therefore maximum values reported by us should not be considered as true maximal values; but any significant daily change from maximum to minimum wing loading is real, and would only be further accentuated in light of true peak weights as reported by Kunz (1974). Studier *et al.*, (1970) reported that *M. lucifugus* loses an average of 10.5 percent of its body weight and *M. thysanodes* an average of 15.8 percent body weight in 12 hours of normal roosting. These values for post lactational bats are higher than for pregnant females (Procter and Studier, 1970). The daily weight loss of *M. thysanodes* results in a significant decrease in wing loading for all reproductive seasons ($P < 0.01$; Fig. 1), whereas, the daily weight loss in *M. lucifugus* results in a significant decrease in wing loading only in prepregnant and pregnant individuals ($P < 0.01$; Fig. 1). In light of the significant daytime decrease in wing loading, it would seem to be advantageous for a bat to do most of its evening flying at a reduced wing loading, particularly during pregnancy. There is, in fact, evidence of short, intermittent foraging flights at this time (Kunz, 1974).

Fat cycles have been followed in two species of hibernating bats, *Eptesicus fuscus* (Weber and Findley, 1970) and *Myotis grisescens* (Krulin and Sealander, 1972), and for a possible migrator, *Nycticeius humeralis* (Baker *et al.*, 1968). All three species exhibited similar trends with a low fat index (between 0.10 to 0.50) in late spring, relatively stable levels through June and July, and a marked rise in late summer or early fall to high fat indices (between 1.4 to 2.7). Fat deposits decrease through winter and spring in hibernators (Krulin and Sealander, 1972), but a second, late winter to early spring increase may occur in migrators (Weber and Findley, 1970). Water indices for these three species also followed a similar pattern with peak values during pregnancy and lactation and a decrease with fat deposition.

The trends observed in the present study for fat and water indices (Table 1) are similar to those observed in other bat species. However, the magnitude of fat deposition reported in other studies is not reflected in table 1. Maximum values prior to fall emigration from Montezuma Seminary were 0.496 for *M. thysanodes* and 1.067 for *M. lucifugus*. These values are lower than those reported by Ewing *et al.*, (1970) for *M. thysanodes* and *M. lucifugus*. Both species spend the roosting period in torpor prior to the fall emigration (Studier and O'Farrell, 1972). This strategy of feeding and torpor definitely facilitates the rapid deposition of fat. Utilizing the formulae of Ewing *et al.*, (1970), we determined that *M. thysanodes* contains insufficient fat stores for migration or hibernation, whereas, *M. lucifugus* is capable of prolonged hibernation, particularly if a short period of feeding takes place upon reaching the hibernaculum. The fat values obtained in this study further support our earlier contention (Studier and O'Farrell, 1972) that *M. lucifugus* behaves as a classic hibernator, whereas, *M. thysanodes* is physiologically incapable of prolonged hibernation and must remain periodically active throughout the winter as does *Pipistrellus hesperus* (Bradley and O'Farrell, 1969).

Seasonal changes in body composition in rodents are not presented in terms that are readily comparable to our results (e.g., Hayward, 1965; Fleharty *et al.*, 1973). However, these studies do indicate a relative constancy in protein and ash, respectively, and an inverse relationship between percent water and fat. Likewise, Ewing *et al.*, (1970) reported a constancy over the month prior to autumn exodus for *M. lucifugus* and *M. thysanodes*; however, *M. yumanensis* showed a significant increase in non-fat organic and a significant decrease in percent water during this same period.

The dynamic nature of gross body composition (Table 2), particularly for *M. thysanodes*, aids in the interpretation of the fall study conducted by Ewing *et al.*, (1970). Apparently, *M. thysanodes* had already finished the transition from the period of lactation to autumnal exodus, whereas, *M. yumanensis* was in the transition process. The changes in ratio between percent water and non-fat organic by reproductive season not only reflect the demands of pregnancy and lactation, but also exhibit the established pattern of fat deposition with a concomitant decrease in water content (Hayward, 1965; Fleharty *et al.*, 1973). Krulin and Sealander (1972) found no significant seasonal change in fat-free dry weight in *M. griseseens.* However, our findings of the dynamic nature of body composition (Table 1) appears to refute their findings.

Rudd and Beck (1969) documented a trend, in North American bats, for an increase in right adrenal weights during pregnancy which corresponds with the consistent implantation in the right uterine horn. In our study *M. lucifugus* did not exhibit this trend and *Myotis thysanodes* appears to show the reverse (Fig. 2). In this species, although the significant increase occurred in the left adrenal, implantation occurred consistently in the right uterine horn.

In bats there is a recognized relationship between adrenal weight and reproductive state (Christian, 1956; Short, 1961; Rudd and Beck, 1969). Adrenal weight increases throughout pregnancy, reaches a peak in late pregnancy, then declining to an annual low in mid-winter. The increase during pregnancy has been associated with the production of sex steroids (Christian, 1956). We observed a significant relation between adrenal weight and reproductive season in *M. thysanodes*, but the highest weights were reached during lactation. This may be due to the high energetic demands and concomitant stress during lactation (Studier *et al.*, 1973). Conversely, *M. lucifugus* did not exhibit changes in adrenal weight. However, adrenal weights were consistently higher than those for *M. thysanodes* which may indicate an additional stress imposed by differences in population structure and behavior (O'Farrell and Studier, 1975).

Specific differences are also apparent with respect to spleen weight (Fig. 2) with a significant increase occurring in the fall for *M. thysanodes.* Splenic hypertrophy in bats has been associated with erythrocyte storage during hibernation (Lidicker and Davis, 1955), whereas, in rodents, there is evidence to indicate a relation to erythropoietic function (Sealander and Bickerstaff, 1967). The bats in the present study were sacrificed after thermoregulatory experiments (Studier and O'Farrell, 1972); all were exposed to the equivalent of high, afternoon attic temperatures and would not be expected to store erythrocytes under these conditions.

The general increase in spleen weight for both species during pregnancy and lactation (Fig. 2) may be associated with increased erythropoiesis in response to increased physiological demands. The trend towards decreased splenic weights for *M. lucifugus* in the fall may reflect a general decrease in erythropoiesis prior to hibernation. However, the significant hypertrophy in autumn *M. thysanodes* may reflect the ability of this species to fly at reduced body temperature (Studier and O'Farrell, 1972) and associated physiological stress. Periodic winter activity may produce sufficient physiological demands to warrant a high degree of erythrocyte production.

When the various body measures are considered (Table 3) it becomes apparent that some flight characteristics are highly correlated with parameters that are a function of weight. Both species exhibit this tendency, but *M. thysanodes* deviates slightly when gross body components are considered. The differences between the two species are probably due to the fact that all body parameters examined for *M. lucifugus* tended to be consistent from season to season, whereas *M. thysanodes* exhibited significant changes between most seasons.

Both species of *Myotis* examined, exhibited a surprising number of differences throughout the study. Although they inhabit the same maternity roost structure, they utilize different microclimates (O'Farrell and Studier, 1973), employ different thermoregulatory strategies (Studier and O'Farrell, 1972) and probably overwinter in different ways. These differences in the physiological ecology of the two species of *Myotis* are undoubtedly responsible for the differences observed herein.

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SYSTEMATICS AND THE STATUS OF SEA OTTERS, *ENHYDRA LUTRIS*

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Abstract: A recent criticism of a study of sea otter subspecies is reviewed and found deficient. Subspecific recognition is not necessary to protect the sea otters of California, and protection is inappropriate as a reason for subspecies designation.

The growing population of sea otters (*Enhydra lutris*) which inhabits the coast of central California has been the subject of considerable public interest and concern during recent years. One aspect of this interest has been the taxonomic status of the population, since it has been felt that it might have a bearing on the protection given to sea otters. In the light of recent controversy on this subject, a brief review of the taxonomic status of sea otters seems appropriate.

Merriam (1904) first described Californian sea otters as a distinct subspecies, *E. l. nereis*, on the basis of a single skull. The validity of *nereis* was strongly challenged by Scheffer and Wilke (1950), who examined additional specimens from California, Oregon, and Washington. They found that individual variations in skull features made it impossible to separate Californian skulls from those of Alaskan animals, and therefore synonymized *nereis* with *E. l. lutris*. However, their paper was ignored by later authors, and *E. l. nereis* continued to be recognized in the literature (Miller and Kellogg, 1955; Hall and Kelson, 1959).

In 1965 the California Department of Fish and Game began salvaging dead sea otter carcasses that were found along the California coast. As a result, a large number of skulls finally became available for study. Such a study was made, using discriminant analysis to compare 50 Californian skulls with 156 skulls from the Aleutian Islands (Adak and Amchitka). Differences were found between these two populations, and the validity of *E. l. nereis* seemed reestablished (Roest, 1971). Subsequently however, additional skulls from southern Alaska became available, and when these were analyzed it was found that they represented an intermediate population (see Fig. 1). As a result of this analysis, as well as other factors, the Californian population was considered to represent one end of a cline in otter form, extending along the entire Pacific coast of North America, through the Aleutian Islands, and to the Commander Islands. Sea otters throughout this range represented a single subspecies, *E. l. lutris*. A second subspecies, *E. l. gracilis* of the Kurile Islands, was also recognized (Roest, 1973).

Davis and Lidicker (1975) recently published a criticism of Roest's (1973) paper, in which they attempted to point out deficiencies in the analyses and interpretations. Their stated purpose for the criticism was ". . . the possible importance of the taxonomy of the California sea otter to this animal's rare and endangered status, and to future management decisions. . .". They concluded by considering *E. l. nereis* a valid subspecies. Although their criticism appeared superficially sound, it was actually deficient in several ways, and a clarification seems necessary to avoid further confusion in the literature.

One of the points made by Davis and Lidicker (1975) was that *E. l. gracilis* is ". . . of comparable distinctiveness to *E. l. nereis* . . .". This is simply not the case. *E. l. gracilis* is immediately distinguishable from all other sea otters, with 100% accuracy, using *any one* of four different skull features, and in addition has a differently colored underfur. In contrast, otters from California can be distinguished from those of the Aleutian Islands only when discriminant analysis is used to analyze four skull variables together, with only 90 percent accuracy. Individually, *none* of these four variables is effective in distinguishing between the two populations, and when comparison includes specimens from southern Alaska the differences become even less clear. Further, the underfur color of otters from Alaska and California is identical.

Davis and Lidicker (1975) also stated that recognition of a southern subspecies of sea otter would more accurately reflect the "existing natural situation." The existing situation is *not* natural however, but is an artifact of human activities. The 1700 mile gap in distribution, between Prince

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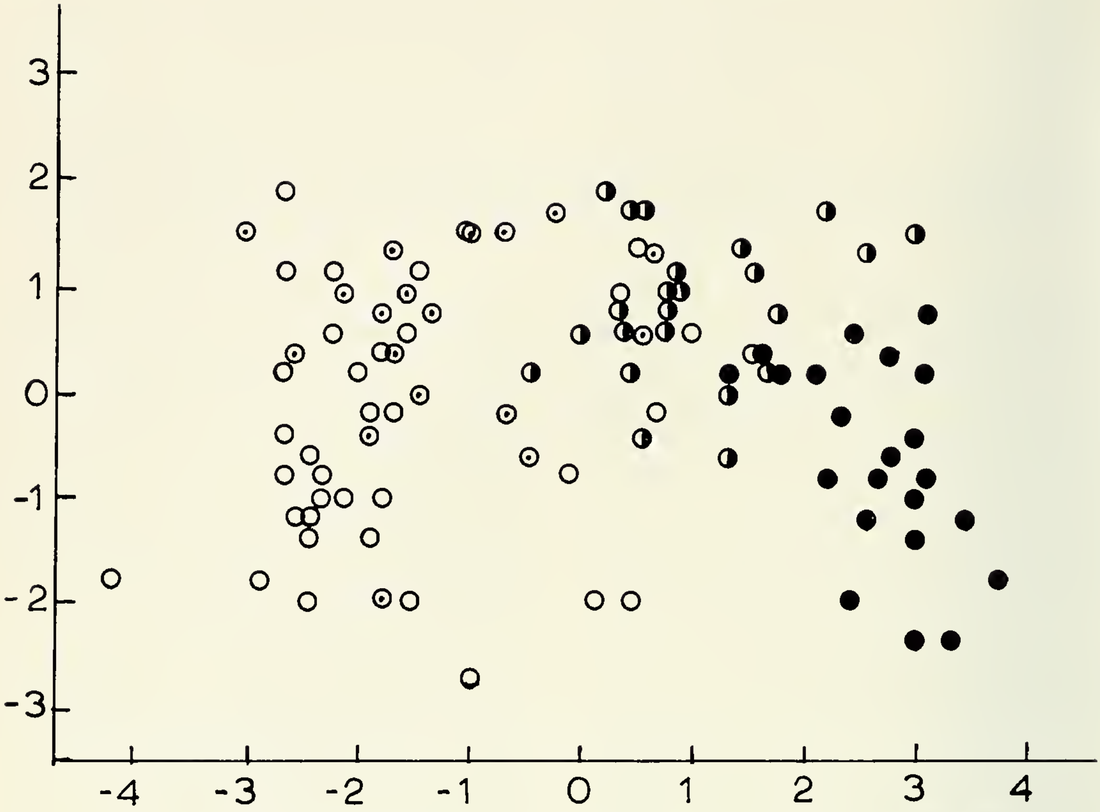

Figure 1. Canonical graph from BMDO7M Program (Dixon, 1970), illustrating relationships between male sea otters, as determined by discriminant analysis of 4 skull variables. Specimens from Amchitka are indicated by open circles, from Adak by dotted circles, from southern Alaska by half black circles, and from California by solid black circles. Corresponding graph for females is similar. For complete discussion see Roest, 1973.

William Sound and California, is the result of extermination brought about by hunters engaged in the fur trade during the nineteenth century. By implication, Davis and Lidicker's statement suggests that it should be possible to create subspecies at will, simply by exterminating the central populations of any widely distributed species, which is of course absurd.

Although Roest (1973) did not examine specimens from the 1700 miles between Prince William Sound and California, Davis and Lidicker (1975) are in error when they state that the nature of variation in this area is therefore unknown. Scheffer and Wilke (1950) *did* examine the few specimens known from this region, and reached a conclusion similar to that of Roest (1973): that only one form of sea otter exists along the North American coast.

The presence of a step, or change in slope, in the cline which relates the Aleutian and Californian sea otter populations was also suggested by Davis and Lidicker (1975). They attempted to prove its existence by a breakdown of the data from the southern Alaskan otter sample. In doing so they stated that the great circle distance between Port Heiden and Prince William Sound is only 435 miles. A glance at a map of the area shows that, as the sea otter swims, the distance is actually over 1100 miles, measured around the coast. Sea otters cannot travel great circle routes overland! The step in the cline suggested by Davis and Lidicker disappears completely when the variation observed in southern Alaskan specimens is spread over the greater distance.

Only brief comments need be made regarding some of the other errors or misinterpretations in Davis and Lidicker's (1975) paper: their naive use of statistics (Student's *t* test and Chi-squared analysis to reevaluate the results of the BMDO7M discriminant analysis program) (Dixon, 1970);

their inappropriate size comparisons (already fully discussed and correctly interpreted by Roest, 1973); and their use of behavioral differences as a taxonomic feature (each passing year of observations reduces any differences which might exist—see, for example, Calkins and Lent, 1975). In short, the criticisms they make are inappropriate, or in error.

Lidicker (1962) previously has commented that ". . . the ability to prove that two populations are statistically different in one or several characters is only a measure of the persistence and patience of the systematist. To base formal subspecific descriptions on this kind of evidence seems . . . almost meaningless." Davis and Lidicker (1975) appear to be attempting just that!

What is certainly more important than the differences between Californian and Aleutian sea otters are the great similarities between them. What is remarkable is how *little* difference there is between these populations from such widely separated areas. A highly sophisticated analysis was necessary to emphasize the differences in four skull features, while 20 other features were *not* particularly different. It seems clear that *E. l. nereis* is not a recognizable form; the proper designation for all sea otters from any North American locality is *E. l. lutris.*

As mentioned earlier, Davis and Lidicker (1975) indicated that the taxonomy of the sea otter in California might be important to the "rare and endangered" status of the population. The Department of the Interior, through the Fish and Wildlife Service, does not recognize a "rare" category of wildlife. The Department has established criteria to be used to determine whether a species is endangered or threatened (Greenwalt, 1975). A species may be determined to be either endangered or threatened because of any of the following factors:

1. The present or threatened destruction, modification, or curtailment of its habitat or range. [The range of the sea otter in California is not threatened with destruction or modification.
2. Overutilization for commercial, sporting, scientific, or educational purposes. [Sea otters are not currently used in any destructive way; in California they are subjects of interest for visitors to the central coast region.]
3. Disease or predation. [There is no evidence that these factors are seriously affecting the California population.]
4. Inadequacy of existing regulatory mechanisms. [Existing regulations are well enforced, as evidenced by the continuous growth of the population; mortality from any cause does not constitute a threat.]
5. Other natural or manmade factors affecting its continued existence. [Possible threats of this type include oil spills or water pollution; neither can be considered as more than a partial threat over the 150 mile range of Californian otters, and then only if they should occur.]

Each of the above criteria is of importance only if there has been a decline in numbers in a species which can be attributed to them. In contrast, the sea otters in California have continued to increase since they were first rediscovered in 1938. At that time it was estimated that 150 to 300 otter constituted the surviving population, and this number has now grown to at least 1700 (Miller, 1974). Population growth, and a corresponding range expansion, have continued each year, in spite of apparently normal mortality. The animals have been legally protected in California since 1913 (Miller, 1974), and law enforcement has obviously been successful. Recently sea otters have expanded their range into areas which are intensively used by humans (Monterey Bay, for example). Although they are probably subject to the water pollution present in such areas, there have been no deaths which could be attributed directly to pollution.

In conclusion, the sea otters of California are not a distinct subspecies. They are of course the only naturally occurring population of the species which can be found in the contiguous United States, and should be protected for their considerable interest, both historically and behaviorally. Protection does not depend on their taxonomic status however, as Davis and Lidicker (1975) suggest; many species are protected without special subspecies status. Nor do they need to be considered rare or endangered in order to be extended protection, and especially when they do not meet Federal criteria for an endangered form. A species can be protected by passing appropriate laws or regulations concerning its use by or interaction with man, whatever its status. To try to develop protective legislation by falsely recognizing a population as a subspecies is a dangerous misuse of the whole concept of subspecies and subspeciation.

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NOTES ON MYCOPLASMA-LIKE ORGANISMS IN SKIN TUMORS OF DOVER SOLE, *MICROSTOMUS PACIFICUS*, TAKEN NEAR SEWAGE OUTFALLS

Hitoshi Matsudo[1] and Dilworth W. Chamberlain[2]

Abstract: Electron microscopical observations of skin tumors of Dover sole, *Microstomus pacificus*, taken near sewage outfalls at Santa Monica Bay, Newport Beach, and Port Hueneme, California reveal mycoplasma-like organisms in all tumors (nine) of the five specimens. Since a mycoplasma, *Acholeplasma laidlawii*, has been isolated from sewage, the presence of mycoplasma-like organisms (if indeed they are mycoplasmas) in the skin tumors of *M. pacificus* suggests that sewer effluent may be a possible source.

The occurrence of skin tumors on flatfish appears to be widespread and has been reported in various species (McArn, Chuinard, Miller, Brooks, and Wellings, 1968; Kimura, Sugiyama, and Ito, 1967; Young, 1964; Thomas, 1926; Johnstone, 1925). The tumors may be found on any part of the flatfish (Fig. 1) but are usually restricted to the pigmented surface. Virus and virus-like particles (Brooks, McArn, and Wellings, 1969; McArn *et al.*, 1968; Wellings, Chuinard, Gourley, and Cooper, 1964; Wellings, Chuinard, and Bens, 1965; Nigrelli, Ketchen, and Ruggieri, 1965)

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have been reported as etiologic agents and sewer effluent or pollution has been suggested as the source (Wellings *et al.*, 1965; Carlisle, 1969; Young, 1964; Russell and Kotin, 1957; Turner and Strachan, 1969). An unidentified cell type (altered fish cell or unicellular parasite having nucleus and mitochondria) labeled "X-cell" has been observed in tumors of various species of flounder (Brooks *et al.*, 1969) and also in tumors of Dover sole (Mearns and Sherwood, 1974a).

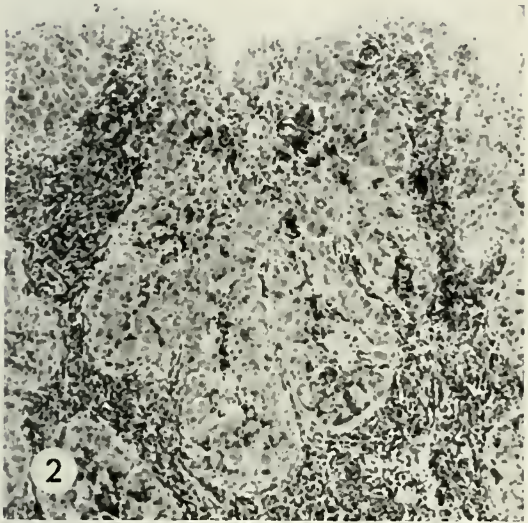
On several occasions *Microstomus pacificus* were collected near sewage outfalls in Santa Monica Bay, Newport Beach, and Port Hueneme, California. All of the five specimens examined were small, 82 to 122 mm standard length and weighed 6.5 to 21.5 g. Skin tumors occur on the eyes, mouth, fins, and body. They are roughly circular, 2.2 to 10 mm in diameter. The mass of the tumor is raised above the level of the surrounding normal tissue and extends slightly into the epidermis (Fig. 2). The surface of the tumor is furrowed; on some tumors the furrows radiate outward. Mycoplasma-like organisms were found in all tumors (nine) of the five specimens.

For electron microscopy, tissues were fixed in sodium cacodylate buffered glutaraldehyde and postfixed in osmium tetroxide also buffered with sodium cacodylate. Tissues were dehydrated in graded series of ethanol and embedded in Epon 812. Sections were stained with aqueous uranyl acetate and lead citrate.

Electron microscopical observations of the epidermal papillomas from *M. pacificus* reveal organisms (Figs. 3–4) having the morphological characteristics of mycoplasmas—that is, absence of a cell wall, plasticity of body form, a triple layered membrane surrounding the organism, no apparent nuclear membrane, no membranous organelle, and size range of 0.33 to 1.0 μm in diameter but variable with species (Anderson, 1969; Horne, 1972; Maniloff, 1972; Boatman, 1973). The mycoplasma-like organisms in the tumors of *M. pacificus* are 0.25 to 0.9 μm in greatest dimension.

Mycoplasmas have not previously been found


1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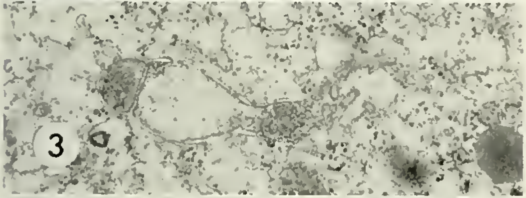
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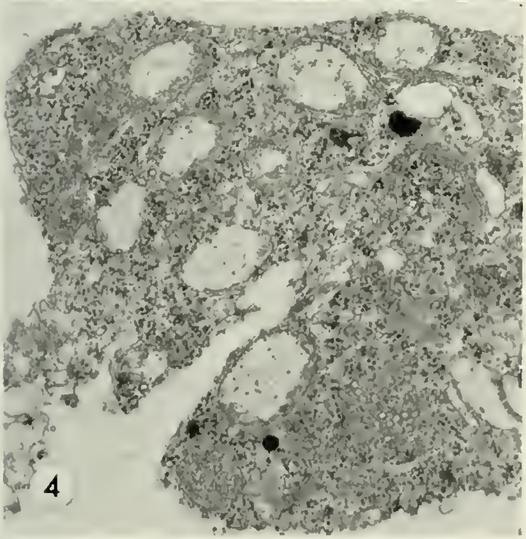
4

Figure 1. Dover sole with skin tumors (arrows) on pectoral and caudal fins and abdomen. *Figure 2.* Photomicrograph of a section through an epidermal papilloma on the eye of a Dover sole. Mycoplasma-like organisms are found in the large, round tumor cells which appear lighter. Haematoxylin and eosin stain. × 194. *Figures 3 and 4.* Electron micrographs of portions of tumor cells showing mycoplasma-like organisms. × 25,000.

in either fish or in piscine tumors. They have, however been isolated from human malignant tumors but their oncogenic potential has not been proven (Hayflick, 1972). Whether these organisms in the skin tumors of *M. pacificus* are indeed mycoplasmas, and whether they are the etiologic agents or whether they represent a secondary infection remains to be determined.

Furthermore, a mycoplasma, *Acholeplasma laidlawii*, has been isolated from sewage (Laidlaw and Elford, 1936). Although studies (Mearns and Sherwood, 1974a, 1974b) of the distribution of Dover sole in Southern California coastal waters with fin erosion and those with tumors suggests that fin erosion is brought on by contact with sediments around sewage outfalls and that skin tumors are not initiated by and thus not related to wastewater discharge, the presence of mycoplasma-like organisms in tumors of *M. pacificus*, a bottom dwelling flatfish taken near sewage outfalls, suggests that sewer effluent may be a possible source.

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NEST STRUCTURE AND MICRO-CLIMATE OF THE DESERT COCKROACH, *ARENIVAGA APACHA* (POLYPHAGIDAE, DICTYOPTERA)

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Abstract: Eighteen rodent mounds were analyzed for specific locations of cockroach nests, temperatures, and relative humidities. This study indicates that the cockroaches cooperate to to build nests from the material taken from rodent caches. The nests insulate the cockroaches from the extreme changes in the desert environment and from the less extreme changes in the microclimate of the rodent burrows.

The banner-tailed kangaroo rat, *Dipodomys spectabilis*, is known to create large mounds atop their extensive burrowing systems (Burt and Grossenheider, 1964). These mounds contain a large diversity of organisms, some permanent inhabitants of the mounds, some staying only temporarily for part of a season or part of their life cycle. One of the permanent inhabitants is the desert cockroach, *Arenivaga apacha* (Saussere).

Pradhan (1957) points out that little is known about the ecology of arid-zone insects, and Roth and Willis (1960) emphasize that ecological information concerning desert cockroaches is very scarce. Edney (1967) describes the sub-sand wandering habits of *A. invesigata* during their activity period. The former authors suggest that through their association with rodents, desert cockroaches can avoid the extreme temperatures and aridity characteristic of desert habitats. The present study is concerned with the nature of *Arenivaga* nests found extensively in the large mounds of the banner-tailed kangaroo rat in the mesquite-grassland community near Portal, Cochise Co, Arizona.

METHODS

Eighteen kangaroo rat mounds were dug over a two-week period before, during, and following heavy summer rains (from 15 August through 28 August 1972). For each mound a trench the length of the mound and three feet deep was dug on the level ground on the east side of the mound. Then each mound was carefully taken apart by a continuous stripping away of the soil and nesting material. Nesting material, an accumulation of grasses, *Yucca* seeds, *Ephedra* seeds, and grass seeds, as well as seeds from *Atriplex elegans*, and associated soil were carefully sifted with soil screens to locate cockroaches and other organisms associated with the nests. Position and structure of the nests and the locations of the organisms were recorded.

Soil temperatures and relative humidities were measured with a Weston dial thermometer and a

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Table 1. Air temperatures (A.T.) and relative humidities (R.H.) of 16 Banner-tailed Kangaroo Rat Mounds. Temperatures are in °C and relative humidities are in percent.

Mound Number	Surface		1 foot		2 feet		3 feet		Nest	
	A.T.	R.H.	A.T.	R.H.	A.T.	R.H.	A.T.	R.H.	Temp.	R.H.
1	23.5	69	24	69	24	71	23	71	17.0	95
2	23.5	70	24	75	23	80	23	80	16.5	98
3	22.0	70	23	71	22	78	22	78	17.0	97
4	23.4	82	23	82	—	—	—	—	17.5	97
5	31.0	79	30	83	30	83	—	—	17.0	93
6	32.0	50	34	62	33	54	—	—	17.0	97
7	33.0	48	33	50	34	51	—	—	18.0	96
8	32.0	52	31	51	32	54	—	—	17.5	97
9	27.2	57	28	56	27	76	—	—	17.5	98
10	45.0	44	32	75	34	37	35	40	16.0	98
11	29.6	45	28	35	28	65	—	—	19.0	92
12	28.0	48	28	48	27	48	—	—	17.0	98
13	25.3	77	24	80	24	80	—	—	17.5	95
14	27.0	89	28	85	28	85	—	—	17.0	92
15	20.2	45	25	42	—	—	—	—	17.0	91
16	22.3	48	27	48	20	47	20	47	18.0	93

Yellow Springs telethermometer and an Atkins gun psychrometer and humidity papers (Solomon, 1957). Prior to disturbing the mounds, measurements were made at the surface of burrow openings, one, two, and three feet into burrows. Soil temperatures were taken extensively throughout the mounds, especially at the sites of the nesting material (Table 1). Temperature and humidity probes were inserted 10 cm deep to reduce influences of outside air. This procedure was repeated continuously as the mounds were stripped. Telethermometer probes and humidity papers were inserted at various depths prior to digging, and temperatures were recorded and correlated with maps of the mound structure determined after digging.

Nesting material and soil were collected and placed in jars and aquaria with 142 collected cockroaches so that they could be observed manipulating these materials. The containers were kept in a darkened chamber at 22° ± 5°C. The cockroaches were fed *Atriplex* seeds, sesame seeds (a food for which they showed a marked preference), and ground Purina dog chow (dried). No water was given the animals as it was found that water caused the food to mold.

RESULTS

No cockroaches were found in burrows that were not connected with chambers packed with nesting material. Only three cockroaches out of 142 were found outside the nesting material or away from the shelves built by the cockroaches. The three animals found outside the nest seem to be individuals disturbed from a nearby nest.

In the laboratory we observed the cockroaches digging shelves and lining them with nesting material. Evidently, the nesting material originally brought into the mounds by the rodents is used by the cockroaches to line the shelves that they dig extensively through the rodent mound. Often the grass-lined shelves and cockroach-stored caches of seeds articulate two or more large sized rodent caches. In other words, the cockroaches build a microenvironment of burrows within the main rodent burrow.

In the nests built by the cockroaches, we observed several small caches of seeds—mainly *Atriplex*. Our suspicion that the cockroaches gather and hoard provisions was confirmed when we saw the cockroaches carry dried dog food and and sesame seeds that were sprinkled over the top of the aquaria soil through the shelves and into small caches underground. In the rodent mounds the type of seed in the cockroach caches corresponded with the type of seed in the nearby rodent cache.

The soil closely associated with the shelves, especially that immediately below the shelves, was frequently found to be of extremely fine texure. In the laboratory it was observed that the cockroaches worked the soil with their mouth parts and reduced large gravel-sized lumps to fine sand and silt-textured soil. The ease with which the

Figure 1. (Top) The mounds made by *Dipodomys spectabilis*. *Figure 2.* (Bottom) A cut into the mound. The pen is pointing to the "shelf" dug by the cockroaches, lined with nesting material, and articulating between two kangaroo rat tunnels.

cockroaches move through the fine material when approached suggests at least one function of crumbling the soil—a quick avenue of escape from predators.

While many cockroach nests (shelf systems) were found between two and five feet deep, only one of these was found to contain *Arenivaga.* The cockroaches were found almost entirely at the upper levels, between one and one and one-half feet deep. While burrow temperatures were as high as 48°C (not less than 30°C, as mentioned by Roth and Willis, 1960) and soil surface temperatures were as high as 60°C, the temperature of the shelves range from 14.5°C to 18.0°C ($\bar{x} =$ 16.5°C). It should be noted that the nest conditions described here refer also to the soil immediately associated with the nest. While the humidity of the burrows was as low as 20 percent, the shelves remained saturated or nearly saturated (91 percent being the lowest reading) at all times.

The mounds examined after heavy rain (2.7 inches in 23 hours) revealed that the nesting material close to the surface (less than one foot) seemed to become soaked, though two cockroaches were found in this wet material. However, the nesting material deeper than one foot remained very dry (Fig. 2), while the soil above the material and below it remained soaked. There were large numbers of cockroaches found in the drier material. It was also interesting to note that among the cockroaches found after the rain were three adult (winged) males—a phenomenon not previously recorded according to Roth and Willis. (1960).

DISCUSSION

The nature of the cockroach nests within the mounds of banner-tailed kangaroo rats or *Dipodomys spectabilis* is interesting for a number of reasons. The severe conditions (extreme aridity, extreme temperatures, and heavy rains) would prohibit delicate organisms such as *Arenivaga apacha* from living in this environment. The kangaroo rat mounds seem to be a refuge from these extreme conditions. However, the conditions in the rodent mounds are also extreme, certainly more harsh than predicted by Roth and Willis (1960) and were it not for the alterations in the microenvironment made by the cockroaches, existence in the mounds would be nearly as difficult as in the open desert. The networks or shelves built by the cockroaches present a very stable microclimate where the cockroaches can flourish.

Edney (1966) has shown that *Arenivaga* (now identified as *A. investigata*) that live in the California sand dunes can absorb moisture from unsaturated air (82 percent relative humidity). Although it has not been demonstrated that the present species has such a water absorption ability, since they rarely leave an area that is less than 92 percent relative humidity, it seems clear that they are probably never in danger of excessive water loss. This would not be the case if the animals were subject to the unaltered burrow conditions with relative humidities of 20 percent or lower.

Although no data are available concerning the critical thermal maximum of these cockroaches, animals that were subjected to temperatures exceeding 40°C died within a three to five minute period even when there was adequate water available. So it seems that they are very temperature sensitive. However, since they have such a stable temperature situation in the kangaroo-rat mound shelves, they do not seem to be in danger of overheating.

As soil becomes too water soaked the cockroaches cannot move through it freely as they can in drier soil. Also there is danger of the interstitial air being replaced by interstitial water. However, the danger of suffocation is obviated by the nests' resistance to soaking. Eventually, as the bulk of the water passes to lower levels or is evaporated, the nesting material absorbs some of the moisture and probably retains it long after the surrounding soil has become too dry for the cockroaches' tolerance. Therefore, the effect of having shelves lined with tightly packed grasses is one of great temperature and moisture inertia, a condition that gives a greater environmental stability in a habitat characterized by radical changes.

Another problem in the mesquite-grassland community is the sporadic nature of food availability. This problem is solved by the storage of food by the kangaroo-rats and the concentration of seeds from the kangaroo-rat caches by the cockroaches. With this stored food available through the year and with the very stable environmental conditions, the cockroaches have an ideal kind of oasis in the midst of a harsh desert environment.

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We wish to thank Ashley Gurney for identifying the species of cockroach described here, E. B. Edney for kindly reading this manuscript and for making many helpful suggestions, Lonnie McClanahan for originally suggesting this project. We also thank Vincent Roth for allowing us use of the facilities of the American Museum Southwestern Research Station.

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RESEARCH NOTES

TWO NEW SPECIES OF THE GENUS *PSEUDOSCHOENGASTIA* (ACARINA, TROMBICULIDAE) FROM MEXICO

Chiggers of the genus *Pseudoschoengastia* Lipovsky (1951) occur throughout North America, from Kansas and Nevada southward into Venezuela (Brennan and Reed, 1975). They are common in Costa Rica where 13 species are known (Geest and Loomis, 1968) and in Mexico where 14 species are reported, including the new species described below.

Each description of the larval stage is based on the holotype and paratypes (noted in parentheses) with all measurements in microns. The types are in the chigger research collection, Californa State University, Long Beach, and paratypes wll be distributed to appropriate institutions and individuals.

Studies upon which this paper is based were supported by the U.S. Public Health Service Research Grant AI03407 from the National Institute of Allergy and Infectious Diseases, and by a Faculty Research Grant from the California State University Long Beach Foundation.

Pseudoschoengastia bisetosa, new species
Figure 1

Types.—Holotype and 121 paratypes from La Laguna, Baja California Sur, Mexico, 1670 m, July 9, 1967, from 11 *Peromyscus truei lagunae* Osgood (Piñon Mouse), taken by R. M. Davis, E. M. Fisher and L. M. Robbins: holotype and 12 paratypes with original number RMD670709-37.

Diagnosis.—Larva, in subgenus *Pseudoschoengastia*, with PLs off scutum, and in *farneri* group with 2 genualae I, short ALs, and short legs; but differing from all other species in having at least 2 branched setae on coxa II and III.

Description of holotype (with differences among paratypes listed in parentheses).—Idiosoma whitish, elongate, engorged 450 × 300; eyes red, 1/1 on ocular plate. Dorsal setal formula 4 (humerals)–6 (lateral humerals)–12(12–14)–8–10–12–10+20, total 80 (80–84); humerals 37, 1st posthumeral 26, posterior dorsal seta measuring 28. Ventral setal formula 2–2 (sternals) –4 (lateral sternals) +50 (preanals) +30 (postanals), total 90 (88–92); 1st sternals 33, posterior ventral seta measuring 27. Total idiosomal setae 160 (158–166).

Scutum: rectangular with posterior margin rounded, PLs off scutum; few scattered puncta; sensilla expanded (see fig. 1). Scutal measurements (in parentheses, mean and range of 10 types); AW 47 (46.1, 44–48), PW 68 (69, 64–76), SB 17 (17.9, 17–19), ASB 20 (19.7, 18–21), PSB 18 (17.7, 16–19), AP 33 (31.9, 30–35), AM 28 (27.1, 26–28), AL 22 (21.9, 20–32), PL 38 (37, 36–39), S 31 (32.2, 31–35) × 13 (12.5, 12–13).

Gnathosoma: chela with tricuspid cap and ventral tooth; chelobase and capitular sternum sparsely punctate. Galeala B. Palpal setal formula B/B/BBB; palpal tarsus 5B, T (8μ), palpotibial claw trifurcate.

Legs: I, 2, genualae, tarsala 17 (16.8, 16–18), sub- and parasubterminala; II, coxa 2B, genuala, 2 tibialae, tarsala 15 (14.9, 14–16), pretarsala; III, coxa 2–3B (2–2 in 93 percent of 122 types), genuala, tibiala, no mastisetae. All legs short: I 222, II 186, III 216, total index 624; segments 7–6–6 (femora fused, with 3 internal bars, and suture distinct) terminating in 2 claws and clawlike empodium without onychotriches.

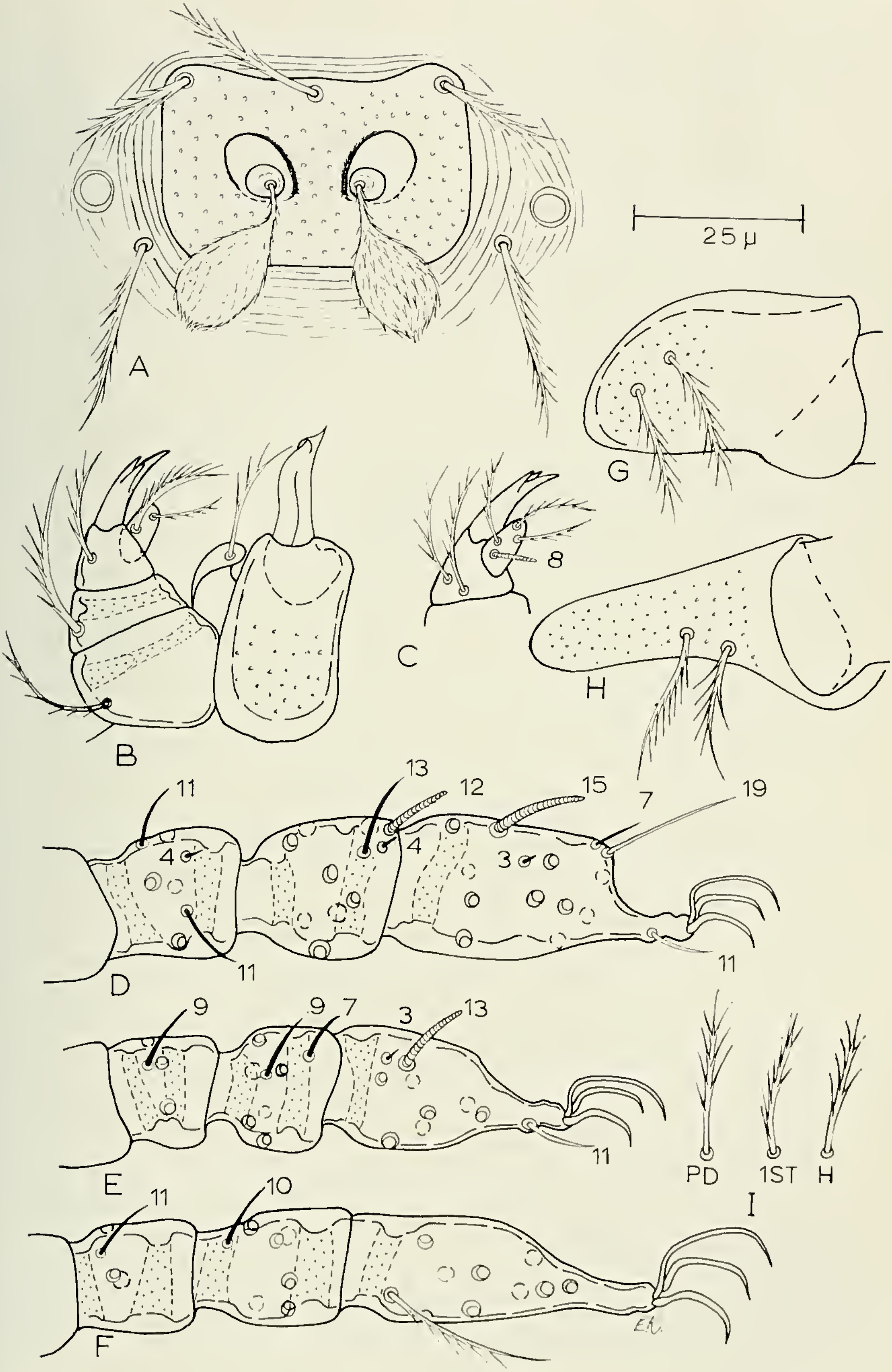
Taxonomic remarks.—This species belongs to the *farneri* group and seems most closely similar to *P. aeci* Brennan (1965) of Nevada (and California), *P. occidentalis* Brennan (1952) of California, and *P. pedregalensis* (Hoffmann) of the Mexican plateau. They share most characteristics and in addition, the first two species have additional sternal setae (more than 2–2) which seem to be correlated with the extra coxal setae of *P. bisetosa.*

Ecological notes.—With one exception, all larvae were found deep within the ears (external auditory meatus) of two species of cricetine mice, *Peromyscus eva* and *P. truei.* More than half of the described species of *Pseudoschoengastia* are closely associated with one or several species of *Peromyscus.* This new species seems restricted to the Cape region of Baja California as it was absent from numerous collections of chiggers from *Peromyscus* and other rodents taken in central and northern parts of the peninsula.

Specimens examined (139).—*MEXICO.* BAJA CALIFORNIA SUR. El Chorro, *Peromyscus eva,* 29.X.1968 (2); 11 km W Santiago, *P. eva,* 31.X.1968 (2); La Burrera, 2 *P. eva,* 6.VII.1967 (6); La Laguna, 11 *Peromyscus truei,* 9.VII.1967 (122); 3.2 km S San Antonio, 29.VI.1967, *P. eva* (4), *Perognathus spinatus* (1).

→

Figure 1. Larva of *Pseudoschoengastia bisetosa.* A. Scutum and eyes; B. Gnathosoma, dorsal aspect; C. Palpal tibia and tarsus, ventral view; D. Leg I, genu, tibia, and tarsus, with nude setae and measurements; E. Leg II, as above; F. Leg III, as above; G. Coxa III; H. Coxa II; I. Idiosomal setae, PD, posterior dorsal, 1st, first sternal, and H, humeral.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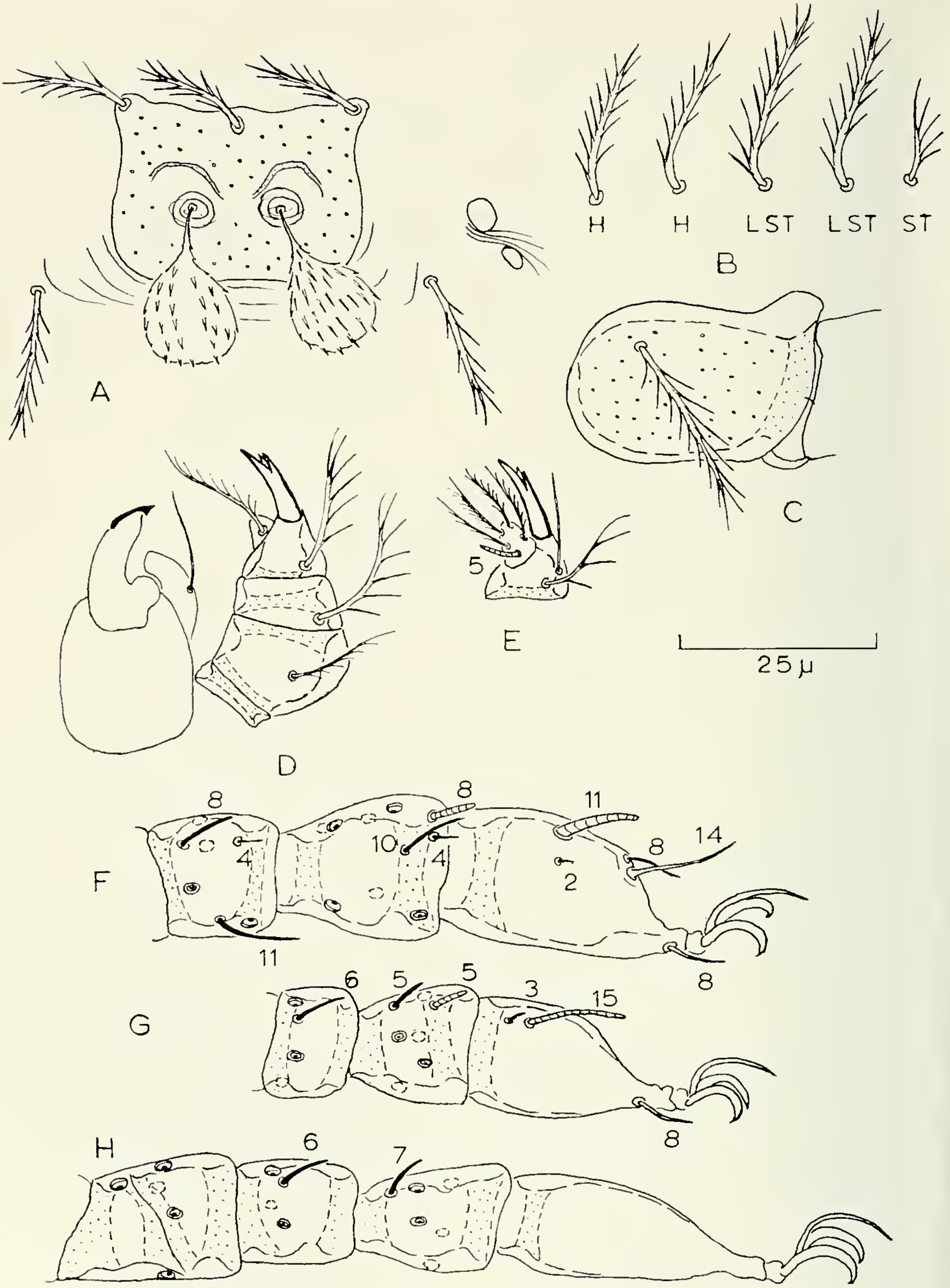

Figure 2. Larva of *Pseudoschoengastia smithi.* A. Scutum and eyes; B. Selected idiosomal setae, H, humerals, LST. lateral sternals, and ST, sternals; C. Coxa III; D. Gnathosoma, dorsal aspect; E. Palpal tibia and tarsus, ventral view; F. Leg I, genu, tibia and tarsus, with nude setae and measurements; G. Leg II, as above; H. Leg III, femur (fused), genu, tibia, and tarsus.

Pseudoschoengastia smithi, new species
Figure 2

Types.—Holotype and 69 paratypes from 13 km SSE Alamos, Rio Cuchujaqui, 274 m, Sonora, Mexico, from 16 *Peromyscus eremicus sinaloensis* Anderson (Cactus Mouse), original number of holotype and 1 paratype, WLH650718-13, taken July 18, 1965 by W. Leon Hunter; and 68 paratypes taken March 27, 1961 (5), April 17, 1962 (6), April 9–11, 1963 (21), July 18, 1965 (30) and Dec. 20, 1966 (6).

Diagnosis.—Larva, in subgenus *Pseudoschoengastia*, with PLs off scutum, and in *farneri* group with 2 genualae, short ALs, and short legs; similar to *P. farneri* Lipovsky in having galeala N, palpal setal formula B/–/BNB, and $AL \leqslant AM < PL$; and differing from it in having palpal genual seta B.

Description of holotype (with differences among paratypes listed in parentheses).—Idiosoma whitish, elongate, partially engorged 312 × 143; eyes red, 2/2, anterior larger, ocular plate obscure. Dorsal setal formula 4 (humerals) –4 (lateral humerals) –8–10–11–10–10–8–4+33, total 102; humerals 25, lateral humerals 28, 1st posthumerals 15, posterior setae measuring 19. Ventral setal formula 2–2 (sternals) –4 (lateral sternals) –8–8–6–4–2, total 36; 1st sternal 25, 2nd sternal 14, lateral sternal 29, posterior ventral measuring 11. Total idiosomal setae 138.

Scutum: rectangular with posterior margin slightly concave, PLs off scutum; sensilla capitate with barbules of 2 types. Scutal measurements (in parentheses, mean and range of 24 types); AW 31 (33, 31–36), PW 55 (64, 49–83), SB 12 (12, 11–14), ASB 17 (18, 16–20), PSB 12 (13, 11–15), AM 18 (19, 16–22), AL 16 (18, 14–22), PL 22 (24, 22–26), S 23 (23, 20–26, 11).

Gnathosoma: chela with tricuspid cap and ventral tooth; chelobase and capitular sternum punctate; galeala N; palpal setal formula B/B/BNB; palpal tarsus 5B, T (5μ); palpotibial claw trifurcate.

Legs: I, 2 genualae, tarsala 11, sub- and parasubterminala; II, coxa 1B, genuala, 2 tibialae, tarsala 15, pretarsala; III, coxa 1B, genuala, tibiala, no mastisetae. All legs short, segments 7–6–6; I 166, II 143, III 161, total index 470 (481, 442–503 in 23), all legs terminating in 2 claws and clawlike empodium without onychotriches.

Taxonomic remarks.—This is another species of the *farneri* group which is much closer to *P. farneri* Lipovsky (1951) than to the other western North American species such as *P. aeci*, *P. bisetosa*, *P. occidentalis* and *P. pedregalensis*.

Ecological notes.—All larvae were found deep within the external auditory meatus of the ears of *Peromyscus eremicus*. Additional studies should uncover more than the two localities listed below.

Comments.—This species is named for Dr. James Dale Smith, California State University, Fullerton, who has provided us with many chiggers, while at the University of Kansas and since his arrival in California. It also acknowledges his professional editorship of this publication.

Specimens examined (71).—*MEXICO.* SONORA. Type series (70); 16 km E Navojoa, *Peromyscus eremicus*, 19.IV.1962 (1).

ACKNOWLEDGMENTS

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SECONDARY PALATE FORMATION IN MICROTEIID LIZARDS (TEIIDAE: LACERTILIA)

A secondary palate is well developed in mammals, birds and some reptiles. Many fossil reptiles have a

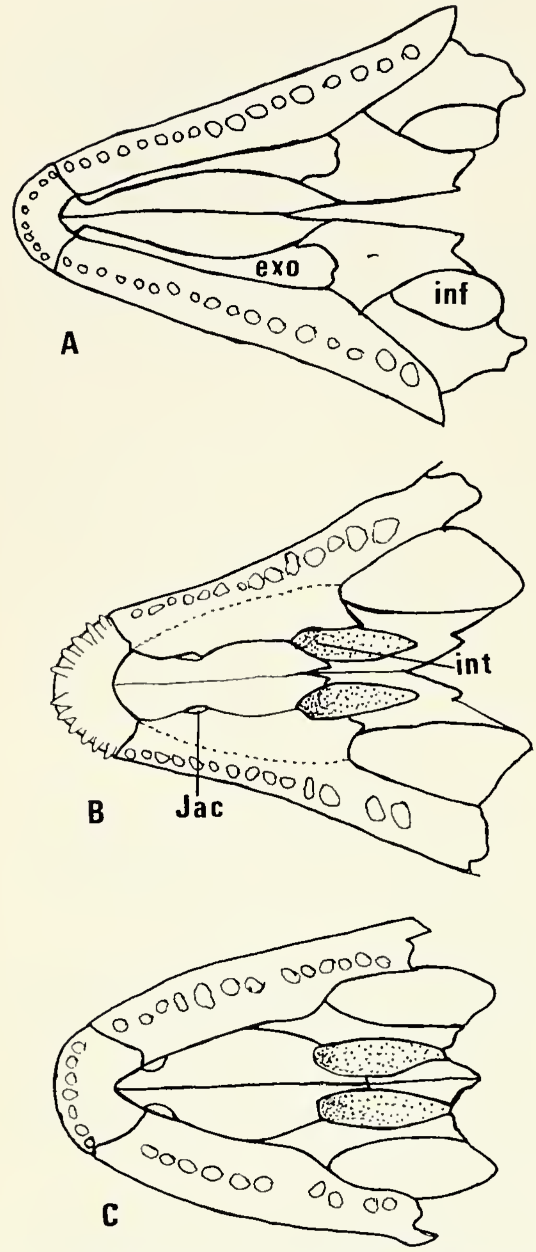

Figure 1. Ventral view of the maxillary segment of the teiid lizard skull A) *Kentropyx,* B) *Neusticurus,* and C) *Bachia.* Not drawn to scale; exo, *fenestra exochoanalis*; int, *internal nares*; Jac, *opening of Jacobson's organ*; inf, *inferior orbital foramen.*

well developed secondary palate (Romer, 1956) but among living forms only the crocodilians and some turtles and lizards possess such a structure. Camp (1923) commented on the contact of the pterygoids in the midline of the palate in scincids and agamids. Goodrich (1930) referred to the secondary palate as a false palate when describing the structure in crocodilians. Jollie (1960) described the elements associated with the palate in lizards but failed to mention the presence or absence of a secondary palate in the groups he examined. Greer (1970) described the secondary palate in scincids and stated that this character was a diagnostic feature of the family. The shape and arrangement of the palatines and pterygoids which are involved in the formation, are useful in recognizing subfamilies and taxa of lower rank among the scincids (Greer, 1967a, 1967b; Greer and Parker, 1968). MacLean (1974) reported on the presence of a secondary palate among many genera of the subfamily Gymnophthalminae (Family Teiidae), but did not describe, in detail, the structure or form that it takes in those genera.

In lizards the elements which may contribute to the secondary palate are the vomers, maxillae, pterygoids and the palatines. The vomers are paired, flat plates that articulate with the medial palatal process of the maxillae and the premaxillary anteriorly and with the palatines posteriorly. The vomers do not contact the pterygoids. Among the majority of lizard genera there is an elongated fenestra, the *fenestra exochoanalis,* between the medially positioned vomers and the lingual shelf of the maxillae (Fig. 1A). This long fenestra, forms posteriorly, the opening of the internal nares into the mouth cavity and, anteriorly, provides a foramen for an entrance to Jacobson's organ.

The structural elements involved in the formation of the secondary palate in microteiids, based on my observations, include the maxillae and vomers. The palatines form a posteriorly oriented groove dorsal and lateral to the internal nares. The pterygoids do not play a role in the formation of the structure as in scincids.

Within the microteiid genera two structural conditions of the secondary palate can be recognized. MacLean (1974) reported that *Alopoglossus Cercosaura, Colobodactylus, Echinosaura* and *Gymnophthalmus* possessed a secondary palate. To that list I am adding *Ecpleopus,* and *Heterodactylus.* In these genera maxillae form a complete lingual shelf that contacts the slight expanded vomers medially, eliminating the *fenestra exochoanalis.* The vomer extends anteriorly, contacting the premaxillary. The presence of an anterior foramen in the maxillae-vomer suture leads to Jacobson's organ (Fig. 1B).

The internal nares exit in the posterior portion of the mouth cavity medially to the position found in nonsecondary palate forms. The vomers are anteroventral to the external nares. A groove on the ventral surface is formed by the ventral surface of the palatine bones. The internal nares are bordered by the vomers, anteromedially and anteroventrally and by the palatine bones dorsally and dorsolaterally.

In *Bachia* (Fig. 1C) the maxillae do not contribute an expanded flange to the lingual shelf. The shelf is formed by an anterolateral process of the palatines which contacts the ventrolateral edge of the expanded vomers, and the ventromedial process of the maxillae eliminating the *fenestra exochoanalis.*

The secondary palate may be complete or incomplete depending on the degree of development of the maxillae and or palatine processes. MacLean (1974) reported on the variability of the secondary palate in *Leposoma, Macropholidus, Neusticurus, Pholidobolus, Placosoma, Prionodactylus, Proctoporus, Ptychoglossus,* and *Tretioscincus.* In *Anadia, Arthrosaura, Euspondylus* and *Iphisa* the secondary palate is intermediate. The palatal process of the maxillae contacts and may overlap but does not form a suture with the vomers. The *fenestra exochoanalis* may be present in the form of a vertical slit between the overlapping bones, or as a fenestra posterior to the maxillary palatal process.

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A PLEISTOCENE HERPETOFAUNA FROM SMITH CREEK CAVE, NEVADA

Smith Creek Cave, located approximately 34 miles north of Baker, White Pine Co., Nevada, contains a fauna that is Late Pleistocene to Recent in age. Early excavations by M. R. Harrington of the Southwestern Museum were followed up by a field party from the Natural History Museum of Los Angeles County. During October 1955, T. Downs, R. M. Ariss, and L. Bessom collected a quantity of vertebrates by carefully screening the site. This collection included a number of amphibians and reptiles and these are reported on here.

The fauna of the cave includes the spectacular Incredible Condor, *Teratornis incredibilis* Howard, typical Late Rancho LaBrean forms as: *Equus, Camelops, Canis dirus, Gymnogyps, Breagyps, Coragyps, Neogyps,* and a northern, Rocky Mountain element of Mountain Goat (described as a distinct species, *Oreamnos harringtoni* by Stock, 1936), *Ovis, Marmota, Lynx, Martes, Microtus,* as well as such desert forms as: *Dipodomys, Neotoma, Thomomys, Lepus, Taxidea.* Scorpions, *Stenopelmatus* crickets, scarab beetles, and other insects have also been found (Howard, 1952; Harrington, 1934).

The cave (LACM, VP Locality 1138 = CIT Locality 251) is located at 6200 feet, 1500 feet above Smith Creek stream channel, about 6 miles W of the Utah-Nevada State Line, North of U.S. Hy. 6. Downs' field notes indicate that there was little or no stratification within the cave, except in sections 34-37 SW. Horse remains were found 24 and 12" deep and *Oreamnos* were found 6–12" deep. The section and depth data are from the collector's field notes. Vertebrates were also collected in "dump" and "fill" deposits. The upper layer of the cave shows indian occupation of the cave. Numbers are LACM VP specimen numbers and are preceded in the LACM catalogue by the locality number, LACM (CIT) 251.

AMPHIBIANS

Numerous amphibian vertebrae and limb elements were recovered from the cave. Many are fragments, so only a few of these can be identified.

Bufo sp.—Vertebrae (Sec. 12, 12–18") and two tibia-fibula (Sec. 25, 0–6" and Sec. 8, 18–24") are of this genus but are too fragmentary for further identification.

Rana?—One illium (Sec. 36, 6–12") may be of this genus.

Scaphiopus cf. *hammondi.*—A parasphenoid with a length of 9.8 mm from (Sec. 11, 6–12") is similar enough to the Western Spadefoot to be referred to that species.

REPTILES

Numerous unidentifiable fragments of lizard and snake vertebrae and jaws were found in the excavation; the following forms have been identified.

Uta stansburiana.—A small jaw from (Sec. 11, 12–18″) is of this species.

Sceloporus graciosus.—A mummified skeleton from (Sec. 36, 6–12″; 72777) appears to be of this species.

Sceloporus magister.—A frontal, 6.8 mm L, from (Sec. 11, 12–18″) is clearly of this species.

Phrynosoma platyrhinos.—A parietal bone with posterior horns from (Sec. 8, 0–6″; 72778) is clearly of this species.

Crotaphytus sp.—A dentary from (Sec. 11, 30–36″; 72776) measures 14.1 mm and another from "old dump" near (Sec. 6 and 13; 72775) is 18.3 mm long. The latter has four mental foramen, the first of which is the largest. A fragment of a frontal, 8.7 mm long, from section 8, 18–24″ is badly worn, but is probably of this genus. I am reluctant to make specific identifications of this material due to its limited nature and the current changes taking place in the systematics of this genus.

Pituophis melanoleucus.—Four sections of vertebrae of gopher snakes come from the earlier Harrington collections and 17 vertebrae from the later Downs collection. The latter come from sections 12 (12–18″), 11 (0–6″, surface hearth contents), 8 (12–18″) and various fill piles and dumps (4824-28).

Coluber constrictor.—Five vertebrae of racers come from sections 12 (12–18″), 8 (18–24″) and 12 (hearth area) and from the dump (4816-20, 4823). Two of these vertebrae measure 5.5 and 5.6 mm in centrum length.

Masticophis flagellum.—One section of 9 vertebrae of a whipsnake comes from cut 2, 48–60″ (72774) of the earlier Harrington excavations.

Lampropeltis getulus.—Kingsnakes are the most common snake found in these deposits coming from almost every section (especially 8, 11, and 12) and from all depths (from 24–30″ to hearth areas; 4829-50). Centra lengths range from 2.1 to 5.6 mm.

Hypsiglena torquata.—One small vertebra from (Sec. 12 6–12″; 4814) and another from section 8 (12–18″; 4815) are both similar to, but slightly larger than modern *Hypsiglena t. deserticola* (compared to BHB #881). The centrum length of the latter is 2.1 mm. The fossil vertebrae are referred to this genus on the basis of size, shape of the subcentrum keel, and the shape of the prezygapophysis. These characters are not like that found in *Chionactis*, *Sonora*, or *Tantilla* with which it might be confused. The vertebrae are referred to this species on geographical grounds. This is the first fossil record of this genus.

Crotalus viridis.—This rattlesnake is the second most common snake in the collections. The specimens, isolated vertebrae, come from all depths from surface hearth areas to 30 inches (4807-13, 4800-6, 4821-2).

DISCUSSION

All the amphibians and reptiles identified from these deposits are found in the area of the cave today. *Sceloporus magister* reaches the northernmost limits of its range here, and *Coluber constrictor* does not occur south of here (except far to the east and along the west coast). *Masticophis flagellum* and *Lampropeltis getulus*, though they occur farther north in western Nevada, stop their northern distribution in eastern Nevada just south of the cave.

It would be tempting to speculate that the *Coluber* occurred in the cave in cooler times (12–24″) and that the *Sceloporus magister*, *Phrynosoma platyrhinos*, *Lampropeltis*, and *Masticophis* were present in warmer times. However, the *Coluber* also occurs in the hearth area (though it could have been brought in by indians) and the *Lampropeltis* occurs at all depths. Since the cave is poorly or not stratified and the role of the indians bringing in food items is not known, all such speculations are probably not warranted. However, it is interesting to note that the fauna of the lower depths (18–60″) includes: *Bufo*, *Coluber*, *Crotaphytus*, *Lampropeltis*, *Pituophis*, *Masticophis*, and *Crotalus*; that the fauna of 6–18″ consists of *Bufo*, *Rana*, *Scaphiopus*, *Uta*, *Sceloporus magister* and *graciosus*, *Crotaphytus*, *Pituophis*, *Hypsiglena Lampropeltis*, and *Crotalus*; and the fauna of the top 6″ and hearth area includes: *Bufo*, *Phrynosoma*, *Pituophis*, *Coluber*, *Lampropeltis*, and *Crotalus*. Further careful excavation in this and other nearby caves may indicate shifts in the fauna in this area between northern, cool faunal elements and warmer, semi-desert elements, and this may be correlated with changes in the mammalian fauna.

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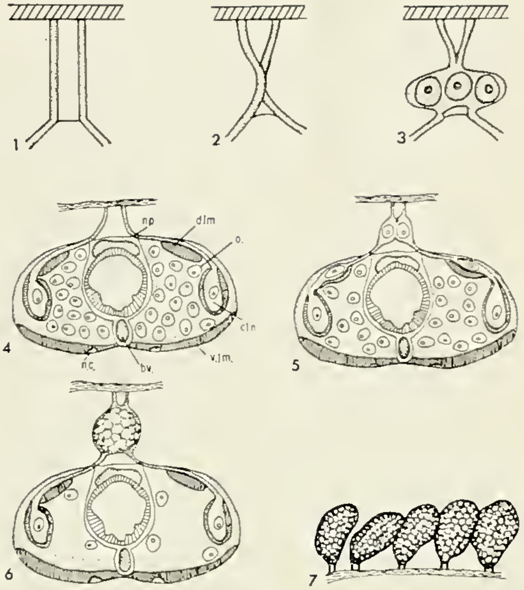
EGG CAPSULE FORMATION IN THE POLYCHAETE *POLYDORA LIGNI*: CONFIRMATION OF AN HYPOTHESIS

The deposition of eggs in segmental mucoid sacs, known as egg capsules (Fig. 1g), attached inside the tube of the female worm is known to occur in the polychaete family Spionidae. Egg capsule formation and brood protection are common among members of the subfamily Spioninae which includes the genus *Polydora*. Even though the formation of egg capsules has been known since the late 19th century, direct observation of the process of capsule formation had had not been observed. The occurrence of egg capsules and its implications regarding sperm transfer, fertilization, and protection of developing young is of particular interest since egg capsules represent a specialized and probably more advanced reproductive system than is found in many other polychaetes.



Figures 1–3. Postulated sequence of events leading to egg capsule formation in *P. ligni.* Redrawn from Söderström (1920) p. 187. *Figures 4–7.* Cross section of observed sequence of events in egg capsule formation. *4*, initial mucus filaments contact wall of tube; *5*, first two eggs emerge; *6*, complete egg capsule ready to be detached from female, *7*. portion of egg capsule string inside tube. np., nephridiopore; d.l.m., dorsal longitudinal muscle; o., oocyte; c.l.n., central lumen of nephridium (nephrostome not shown; v.l.m., ventral longitudinal muscle; b.v., blood vessle; n.c., nerve cord; g., gut.

Whitelegge (1890) suggested that the capsules were formed inside the body of the female and were released through a rupture in the cuticle of the adult and subsequently attached to the inside wall of the tube. No evidence was presented to support this theory. Mesnil and Caullery (1917) proposed that the egg capsules were formed from secretions of the segmental "glandular pouches" formed in many spionids, but their theory did not account for such characteristics as the number of connecting filaments on each capsule or the method of egg placement in the capsules. Söderström (1920) noted that the female worms survived spawning without signs of cuticle rupture associated with capsule formation and postulated that the capsules were formed by secretions of the paired nephridia found in each egg-bearing segment. He noted that the egg capsules were attached inside the tube by two mucus filaments in species having paired nephridial openings (*Polydora ciliata, Polydora ligni*) and by a single filament in species with one common nephridiopore per segment (*Pygospio elegans*). He theorized that capsule formation began when the worm pressed her dorsum against the inside of the tube and gradually pulled away leaving, attached to the wall of the tube, a filament of mucus from each nephridiopore. In *P. ligni* he proposed that the two filaments came in contact and joined together due to movement of the adult before egg deposition (Fig. 1 a–e). The eggs inside the female then entered the nephridia through the nephrostome (ciliated funnel), moved along the ciliated nephridial canals, and out the nephridiopores. At this point, the eggs were surrounded by the mucus secretion of the nephridial cells. Since the two original mucus filaments had merged into one along part of their length, the eggs formed a single capsule for each egg-bearing segment and were attached to the tube by two filaments. This theory accounted for the main characteristics of the egg capsules and was generally accepted. Söderström (1920) and Dorsett (1961) made unsuccessful attempts to observe the method of egg capsule deposition. In a recent study of the reproductive biology of *P. ligni* the actual the actual formation of egg capsules was observed in a female worm living in a glass capillary tube and is described below.

Adult specimens of *P. ligni* were collected from a local estuary and kept in the laboratory in glass petri dish (100 × 20 mm) cultures. The adult worms normally built tubes of debris on the bottom of the dish and could be observed inside their tubes through the glass bottom. In addition, many adults were placed inside glass capillary tubes with an inside diameter of 1.1 to 1.2 mm and were observed under both the dissecting and compound microscopes. Egg capsule formation by a female worm inside a glass capillary tube was observed under the dissecting microscope.

At the beginning of egg laying, the female worm remained very still within the tube with her palps extended posteriorly over the dorsum. The nephridial canals on the dorsum of each egg-bearing segment appeared milky white. These canals terminate in a nephridiopore on either side of the mid-dorsal line. A thin stream of nephridial mucus was forced out of each nephridiopore and contacted the wall of the tube above the dorsal surface of the worm (Fig. 4). Shortly after this, eggs began to move up the nephridial canals toward the nephridiopores. The eggs were squeezed into an oblong shape as they passed in in single file along the canal. The distance between the two nephridiopores was small enough that when the first two eggs passed through the pores the mucus tubules were stretched and came in contact with one another (Fig. 5). The mucus tubules surrounding the eggs merged, like adjacent soap bubbles, producing a single chamber into the rest of the eggs from that segment were deposited. When all the eggs had passed into the capsule, the female moved to and fro a short distance within the tube and freed the capsules from her body with her palps. The capsule-forming mucus remained sticky for a sufficient period of time for adjacent capsules to adhere to one another; however, free capsules were not uncommon within a string of egg capsules. The mucus seemed to harden gradually upon contact with sea water. The entire process took about five minutes and 25 egg capsules were produced by the female possessing 70 setigers. Cleavage of the eggs began about two hours after egg laying.

To our knowledge this is the first time that the formation of these egg capsules has been directly observed and described. Söderström's hypothesis has been confirmed. With regard to *P. ligni*, the only point where Söderström's hypothesis differed from the present observations was when the two initial mucus filaments from each segment merge to form a single capsule. Söderström (1920) believed that the coalescence of the two filaments occurred before the first eggs were deposited, whereas actually the first two eggs that left the nephridial canal caused the filaments to merge. Söderström had difficulty explaining how the capsules were freed from the female, but it appears from our observations that the palps, which are normally employed in food gathering, are used in this capacity. Further studies of this system are needed to determine the stimulus that initiates egg laying and also the exact point when fertilization occurs.

This research was supported in part by research grant R-800962 from the U.S. Environmental Protection Agency to Dr. Donald J. Reish, California State University, Long Beach.

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Brattstrom, B. H. 1969. The Condor in California. Pp. 369–382 *in* Vertebrates of California. (S. E. Payne, ed.), Univ. California Press, xii + 635 pp.

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RESEARCH NOTES

COVER: *Killer whales; adapted from a mural in the Natur-Museum Senckenberg, Frankfurt am Main, West Germany.*

Adapted by Susan E. Smith, Fullerton, California.

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Date of this issue 18 October 1977

A New Species of *Rhynchospio* (Polychaeta: Spionidae) from San Clemente Island, California

John H. Dorsey

Abstract.—A new species of *Rhynchospio* is described from shallow subtidal rocky areas at San Clemente Island. Comparisons are made with related *Rhynchospio* species.

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During investigations at the Wilson Cove sewage outfall, San Clemente Island, California, specimens of a new species belonging to the genus *Rhynchospio* Hartman, 1936, were collected from coralline algal mats at low water and shallow subtidal depths. The specimens could not be identified to any known species of *Rhynchospio* and were determined to represent an undescribed species.

Rhynchospio microcera, n. sp.

Figs. 1, 2

Material examined.—Wilson Cove, San Clemente Island, California, from collections made in February, June, September and December 1973; taken from coralline algal mats, intertidally to approximately 3 m in depth; 1 holotype, 15 paratypes (holotype and paratypes collected in June 1973), and 10 additional specimens deposited in the collections of the Allan Hancock Foundation, University of Southern California, and 15 paratypes and 10 additional specimens deposited in the National Museum of Natural History, Washington.

Diagnosis.—Anterior body region inflated, beginning behind prostomial horns; prostomial horns minute, connected basally, and directed anteriorly or obliquely forward; prostomium extending to setiger 2 as a caruncle bearing three or four small eyes; peristomium reduced; branchiae beginning on setiger 2, curled over dorsum but not overlapping; tridentate neuropodial hooded hooks beginning on setiger 9 with up to five hooks per fascicle.

Description.—Entire individuals with 31 to 42 setigerous segments; holotype with 42 setigers, measuring 8.0 mm in length and 0.5 mm in width; anterior segments wider than those further back, thus giving worm an inflated appearance when viewed dorsally.

Prostomium terminating as two small prostomial horns which project anteriorly or obliquely forward (Fig. 1A, B); shallow cleft beginning at the inside base of horns, extending posteriorly to a point in line with anterior pair of eyes, giving prostomium a bifid appearance; prostomium terminating posteriorly at setiger 2 in form of a caruncle or small keel; two pairs of dark eyes in trapezoidal arrangement on prostomium (examination of the paratypes, however, indicated that eyes varied from three to four per individual); peristomium reduced, limited to small lateral extensions located ventral to mouth region.

Branchiae first present at setiger 2, extending posteriorly to last setiger, curled forward over the dorsum anteriorly, but not overlapping.

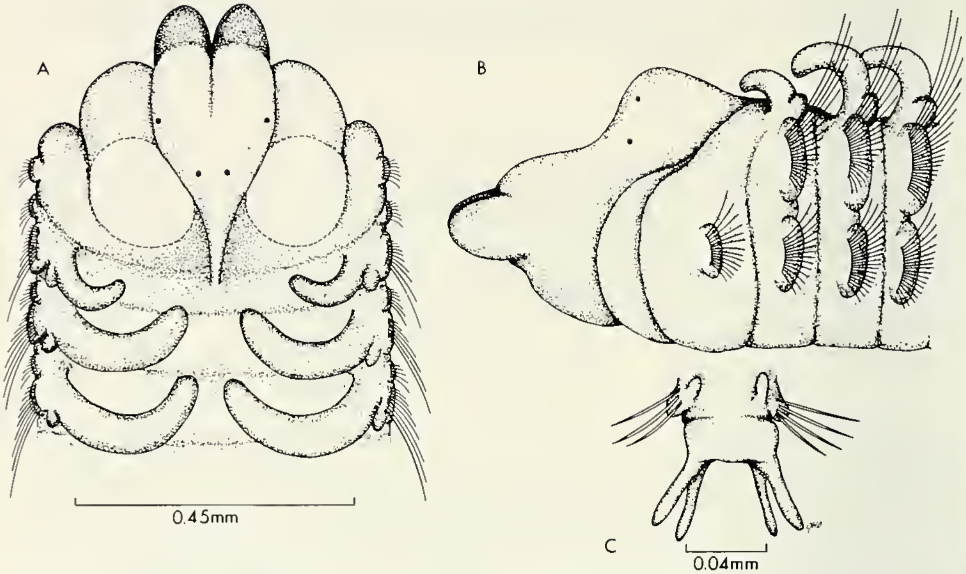

Fig. 1. *Rhnchospio microcera*, n. sp.: A. Anterior end, dorsal view (palpi removed); B. Anterior end, lateral view (palpi removed); C. Pygidium, dorsal view.

First setiger with only a neuropodial lobe, remaining segments supporting neuropodial and notopodial lamellae (Fig. 2A–C); anterior postsetal notopodial lamellae generally subquadrate in shape, becoming more acute toward middle region, and finally reduced to small, rounded lobes in posterior segments; dorsal cirri minute; anterior postsetal neuropodial lamellae subquadrate in shape, reduced to rounded lobes in posterior segments.

Setae of two kinds: granular capillaries and tridentate hooded-hooks; neuropodial and notopodial simple setae long, thin and faintly granular; superior simple setae of notopodium longer than inferior; those of neuropodium equal in length; tridentate, neuropodial hooded-hooks (Fig. 2D) first appearing at setiger 9, averaging five to a fascicle, each accompanied by similar number of long, thin setae; notopodial hooks absent.

Table 1. Characters distinguishing California species of *Rhynchospio*.

Character	*R. microcera*	*R. arenincola*
Prostomial horns	anterior to oblique in direction, joined at base	lateral in direction, separated at base
Caruncle	thin, extending to setiger 2	low truncate, extending to setiger 2
Neuropodial hooded-hooks	tridentate, beginning on setiger 9	tridentate, beginning on setiger 18
Pigment	small, blackish-brown speckles on anterior dorsum, a spot may be present at base of first branchiae	absent

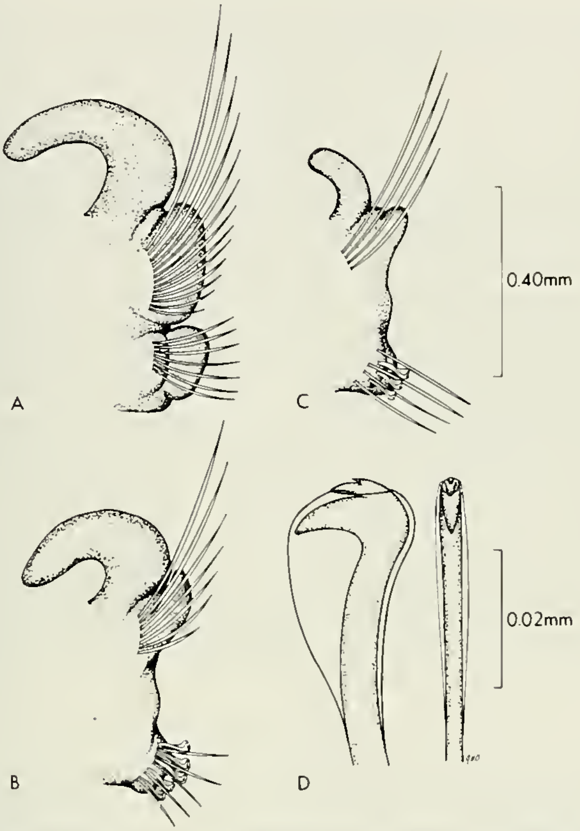

Fig. 2. *Rhynchospio microcera*, n. sp.: A. Parapodium of setiger 3; B. Parapodium of setiger 25; C. Parapodium of setiger 38; D. Tridentate hooded-hook from neuropodium of setiger 25.

Pygidium of holotype (Fig. 1C) terminating in 4 cirri of equal size (of 30 individuals examined, only 5 specimens possessed pygidia, and of these, the number of cirri varied from three to four per individual).

Anterior dorsum speckled with black pigment; a blackish-brown spot present at base of first pair of branchiae of holotype (only half of the specimens examined possessed this pigment spot but all have black speckles over their dorsal surface).

Habitat.—This species was found living in a tight-fitting tube constructed of sand grains, shell and coralline algal debris.

Distribution.—Specimens were taken in the vicinity of Wilson Cove, San Clemente Island, California, from low water to subtidal depths of approximately seven meters. The substratum consisted of coralline algal mat (mostly *Lithothrix aspergillum* J. E. Gray) in which sand and shell debris had accumulated.

Etymology.—The specific name *microcera* (feminine; *micro*, Greek = small; *cera*, Greek = horn) refers to the minute frontal horns of the prostomium.

Discussion.—Excluding *R. microcera*, three species and one subspecies of *Rhynchospio* have been described to date: *R. arenincola* Hartman, 1936; *R. arenincola asiatica* Chlebovitsch, 1959; *R. inflatus* Foster, 1971 (described as *Malacoceros* (*Rhynchospio*) *inflatus*); and *R. glutaea* (Ehlers, 1897). *Rhynchospio* *microcera* differs considerably from *R. arenincola* (Table 1). The latter occurs from Washington (Banse, 1963) to southern California (Hartman, 1936) where it inhabits sand and muddy sand from intertidal to shelf depths.

Rhynchospio arenincola asiatica was described from the Kurile Islands, north of Japan, where it was found from upper sublittoral to littoral in *Laminaria* holdfasts, muddy sand, sponge and under encrusting ice (Chlebovitsch, 1959). This subspecies is distinguished from *R. arenincola* by its larger anterior eyes; thus, the differences between it and *R. microcera* are essentially the same as those found between *R. arenincola* and *R. microcera*.

On a global basis, *R. microcera* is morphologically similar to *R. inflatus* from the west coast of Bimini, West Indies. Both species possess inflated anterior ends and a pigmented dorsum. Bidentate, tridentate, and quadridentate neuropodial hooded-hooks are all present in *R. inflatus* and all begin on setiger 37; *R. microcera*, however, possesses only tridentate hooks which begin on setiger 9. *Rhynchospio inflatus* also differs from *R. microcera* in that the prostomium of *R. inflatus* ends abruptly at setiger 1, whereas, it extends to setiger 2 as a caruncle in *R. microcera*.

Rhynchospio microcera differs from *R. glutaea* in having pigment on its anterior dorsum (absent in *R. glutaea*). The neuropodial hooded-hooks first appear on setiger 16 in *R. glutaea*, but begin on setiger 9 in *R. microcera*.

All described species of this genus inhabit low intertidal and shallow subtidal regions, and are usually found in algal mats, holdfasts, sand or muddy sand areas.

Acknowledgments

I thank P. Kenis and M. Salazar of the Naval Undersea Research Center, San Diego, for their assistance in arranging transportation and living accommodations on San Clemente Island. I am also indebted to D. J. Reish, California State University, Long Beach, and K. Fauchauld and T. Kauwling, both of the Allan Hancock Foundation, University of Southern California, for their advice and criticism of the manuscript. Most of all I wish to acknowledge R. Rowe who assisted with all field collections.

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Morphology of *Sorella* in Natural Habitats and under Laboratory Conditions

Joan G. Stewart

Abstract.—Although thalli attributable to the genus *Sorella* (Delesseriaceae, Rhodophyceae) can be easily recognized, determination of species is difficult. The characters described for differentiating the type species are found to vary and overlap when numerous specimens are examined. Attempts to correlate morphological aspects with environmental variables (e.g., depth, substrate, light, temperature, or season) were unsuccessful. When plants typical of each of the California species were grown in the laboratory under a series of different light and temperature regimes each maintained its distinctiveness. Development of reproductive structures, vegetative growth rates, and a *Polysiphonia*-type life history are described from cultured plants. It is suggested that non-pinnate variants, whether broad or narrow, be referred to *S. delicatula*; all specimens of this species were of the size described for var. *californica*. Pinnately branched, often but not always relatively broad, thalli with either paired or median spermatangial sori are treated as *S. pinnata*.

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Variation among populations of certain taxa of marine benthic red algae is difficult to interpret for taxonomic purposes where experimental data are lacking on how the environment may modify thallus form. For a few species of red algae, correlations of different phenotypes with field gradients of light, temperature, or exposure (Abbott, 1972; Burns and Mathieson, 1972; Edelstein et al., 1969; Lamb and Zimmermann, 1964; Neushul, 1972; Stewart, 1968) have permitted the inclusion in resultant circumscriptions of a defined range of variation in certain characters. *Sorella* (Delesseriaceae) is a genus with three species presently assigned to it, one in Japan (*S. repens*), and two whose distributions include California and both sides of the Baja California peninsula (*S. delicatula* and *S. pinnata*). The combinations of characters originally described for the two California species have proved inadequate for separation of recently collected specimens from southern California where they are rather common in certain subtidal habitats and abundant material is now available for study.

A drift specimen, 9 cm high (Johnston No. 139, UC 94715) from southern California, was first described by Gardner (1926) as the type specimen of *Erythroglossum delicatula*, which subsequently became the type species of *Sorella* (Hollenberg, 1943). The presence of median tetrasporangial sori was considered to distinguish *Sorella* from *Erythroglossum* where the sori lie near margins. In the same paper, Hollenberg (1943) described the much smaller but otherwise similar plants collected from low intertidal habitats in Orange County as a variety of the same species. He additionally described *S. pinnata* from intertidal sites, "often along with *S. delicatula* var. *californica*" but with broader, pinnately-branched thalli possessing paired spermatangial sori. Dawson (1962) recognized both species in his collections from Mexican shores. He included in *S. delicatula* the small specimens he found of non-pinnate plants, placing Hollenberg's variety in synonymy on the stated assumption that the size of the large type specimen described originally by Gardner (1926) as *Erythroglossum delicatula* was related to an environmental effect, and that similarly large plants would be found in deep water as Hollenberg (1943) had earlier suggested.

Sorella divaricata, based on *Erythroglossum divaricatum* (Gardner, 1926) from northern California, was also recognized in Hollenberg's (1943) treatment of the new genus. He suspected that the material described by Gardner might prove to be identical with *S. delicatula* var. *californica* from southern California, but nonetheless made the transfer as *S. divaricata*. Collections by G. M. Smith of *Sorella* (*Erythroglossum*) *divaricata* now in the Dudley Herbarium (UC) cannot be distinguished from the southern species and the synonymy has been included in *Marine Algae of California* (Abbott and Hollenberg, 1976). The Japanese species, *Erythroglossum repens* (Okamura, 1929), transferred to *Sorella* by Hollenberg (1943), was later studied by Yamada (1971).

The work described in the present paper combines field studies and laboratory experiments in an effort to determine relationships between thallus morphology and environmental factors, and to assess the applicability of such information to delimit species of the genus.

Methods

Naturally growing *Sorella* specimens were collected throughout the year from intertidal and subtidal (to 33-m depth) sites off the coast of San Diego County for several years. This area is central in the presently known eastern Pacific range of *S. delicatula* and *S. pinnata*. Water temperatures on the surface range from about 13°C in late December through March, to 20°C or somewhat higher in August–October (UC-SIO pier water temperatures). A summer thermocline lies about 10 m down in the subtidal sites most often sampled. Below this discontinuity the temperature seldom, if ever, rises to the surface maxima, ranging instead between 11–15°C, rarely to 16 or 17°C (Clarke, 1968). Light levels at the 15-m depth were generally below 70 ft-c, as measured by a Weston photoelectric cell (Model 703-67). Intertidal specimens were collected from an exposed reef site where the population persists throughout the year, and from within the Mission Bay channel where the thalli grow in very shallow water but are probably never exposed.

Collected thalli were preserved either in 2–4% formaldehyde-sea water or dried on herbarium sheets. Semi-permanent glycerin-jelly mounts were prepared for microscopic observation and served as material for photographs and camera lucida drawings. Clonal cultures derived from freshly collected thalli were grown in an enriched natural sea water medium (Murray et al., 1972) in 80 × 100 mm deep culture dishes. In Percival growth chambers, comparative growth studies were successful at 10°C with light periods of 20L-4D, 16L-8D, 12L-12D, 8L-16D; at 16°C, with 8L-16D, 16L-8D, and 24L-0D. Growth measurements were made at 16°C with 16L-8D. Light levels above 50 ft-c were not satisfactory. Treatments with germanium dioxide (~10 ppm) and penicillin G (250 units/ml) were utilized to eliminate or partially control growth of contaminant diatoms and blue-green algae, respectively. Herbaria cited are: University of California, Berkeley (UC), J. Stewart collections (JS).

Results

Field observations.—Small size (less than 2.5 cm) and delicate structure cause thalli of *Sorella* to be inconspicuous in the field. The lack of lateral venation, linear shape of thallus parts, and the divergent branches of the same size and shape as main axes, contrast with the more generally leaf-like blades of related species (e.g., *Branchioglossum undulatum*, *Membranoptera weeksiae*, and *Phycodrys profunda*) that grow in the same habitats and often are collected with *Sorella*. Specimens are found associated with several benthic organisms, rather than being restricted to a particular substrate. Beneath overhanging edges of rock where light is very dim, *Sorella* thalli have been found with turf-forming algae such as *Murrayellopsis dawsonii*, *Pterosiphonia dendroidea*, and other small filamentous species (Foster, 1971; Stewart, unpublished data). Outside such cave-like habitats, thalli frequently are epiphytic on genicula of articulated coralline algae or other larger red algae, or epizooic on sponge masses, bryozoan clumps, worm tubes, mollusk shells, or tunicate stalks (*Styela* sp.). The basal parts of *Sorella* thalli also may be embedded in encrusting coralline algae on rocks. Plants epizooic on sponge and bryozoan tissue often develop marginal rhizoids or proliferations which provide secondary attachment to the substrate. When the alga is epiphytic, short peg-like haptera can grow from blade surfaces and keep *Sorella* axes adherent and attached to the larger basiphyte. Sand plus surge, grazing, and rapid succession of vegetative and reproductive growth possibly explain the ragged specimens common in collections. In the laboratory apices often appear damaged when reproductive structures were shed. No correlations between thallus morphology and substrate, depth, site, or time of year could be shown by study of over 49 collections from 12 areas over a period of several years.

Vegetative morphology.—Field-collected thalli (Fig. 1) consisted of marginally-branched, erect blades with smooth margins above stipes that develop from attached basal discs or haptera. Prostrate axes dissimilar to the erect blade axes were not observed. The lower part of the main stipe bears one or several branch stipes. Blades are one-layered outside the midline and veins are not formed from secondary cell rows.

A conspicuous primary apical cell divides transversely; cells of the primary cell row divide to form one, then two (Fig. 2A, B) lateral pericentral cells, as is typical for the family. Apparently random intercalary divisions occur in some central cells close to the apex, while others elongate and do not divide in this way. After such divisions in a central cell the resultant short cells cannot be distinguished from adjacent blade cells. The lateral pericentral cells divide obliquely or in a plane almost perpendicular to that of the preceding division in the central cell by which they were formed, to produce secondary apical cells (Fig. 2C). Each lateral pericentral cell divides a second time, more or less at right angles to the preceding division, to form an abaxial tertiary apical cell (Fig. 2D). Subsequent development of primary, secondary, tertiary and higher cell rows may or may not be precisely ordered; a pattern beyond the first few segments cannot be recognized in the final arrangement of cells. From the apex, the blade widens slightly into a linear region

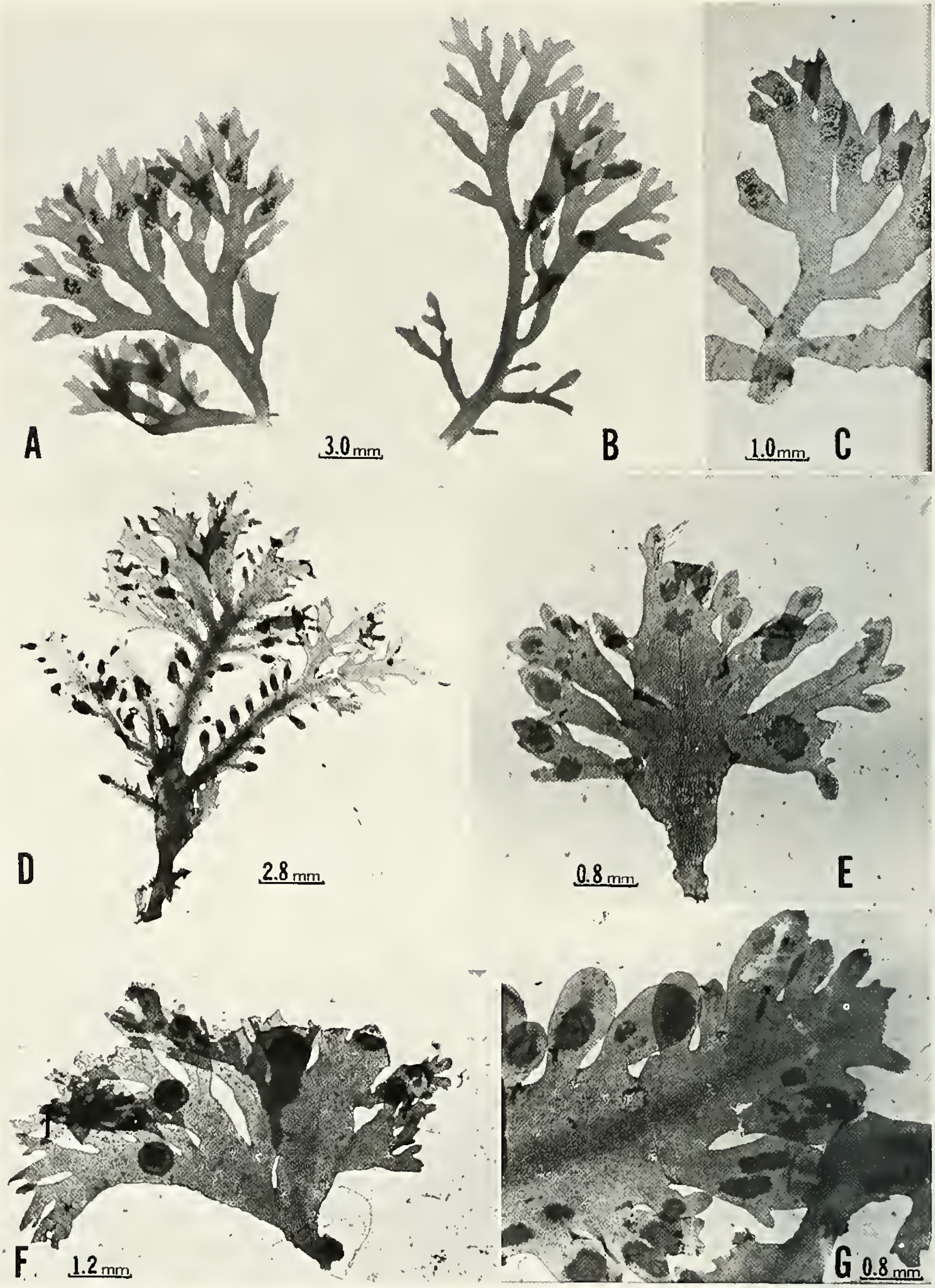

Fig. 1. Representative *Sorella* specimens collected from coast of San Diego County: A. Tetrasporangial thallus, typical *S. delicatula* var. *californica*; B. Cystocarpic thallus, typical *S. delicatula* var. *californica*; C. Broad tetrasporangial thallus, with faint midline, intermediate branching pattern; D. Narrow tetrasporangial *S. pinnata* thallus, with broad midrib; E. Broad spermatangial thallus, primary branching rather pinnate, but with more developed secondary axes, with faint midline; F. Broad cystocarpic thallus, flabellately branched *S. delicatula* var. *californica*; G. Portion of a broad spermatangial *S. pinnata* thallus.

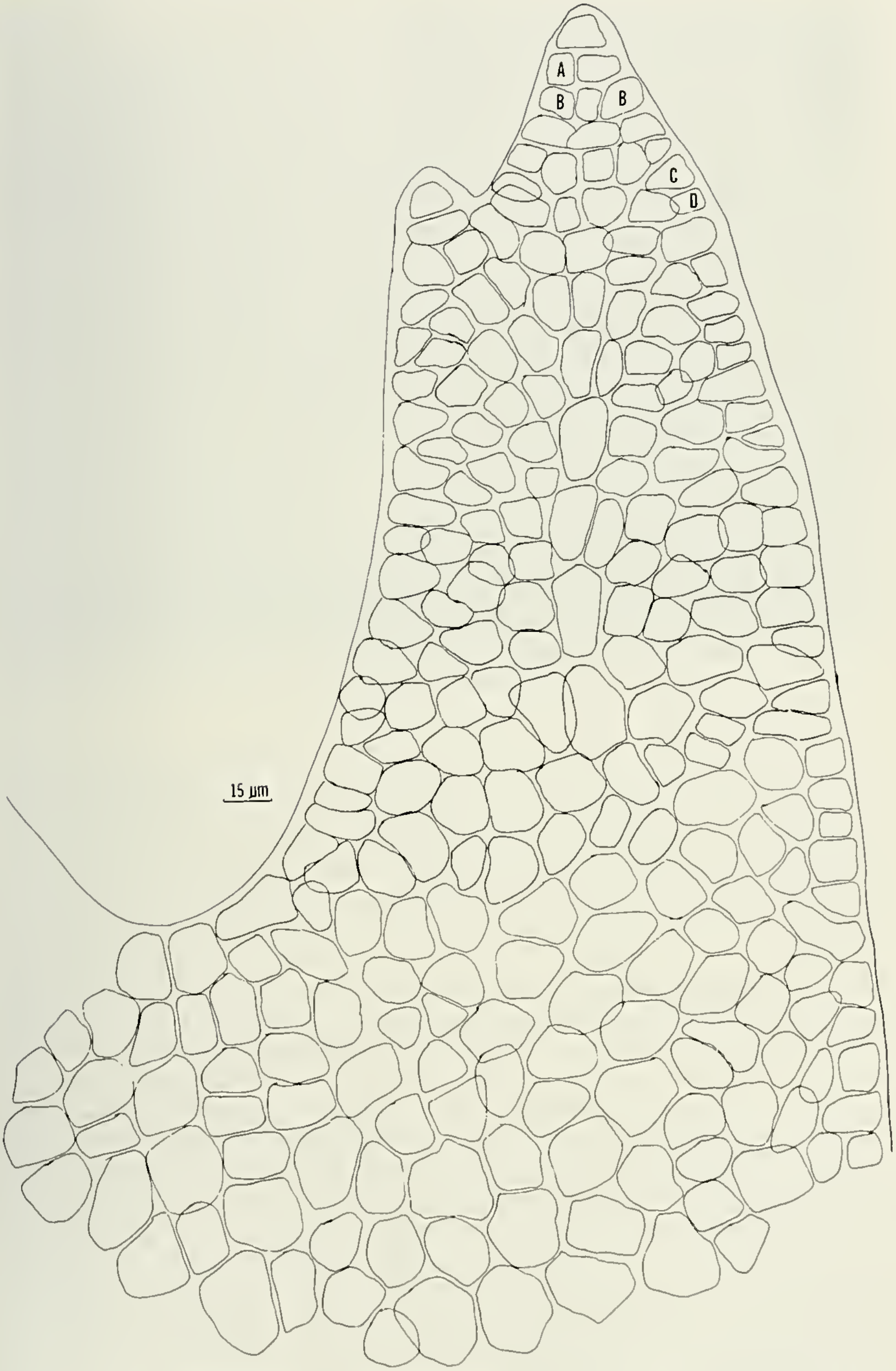

Fig. 2. Apex of *Sorella* blade. A = single lateral pericentral cell; B = two lateral pericentral cells in segment; C = secondary apical cell; D = tertiary apical cell.

where segments tend to consist of approximately the same number of uniformly enlarged cells.

The characteristic faint midline mentioned by Hollenberg (1943) consists of the central cell row with over- and underlying pericentral cells. When, additionally, cells are formed dorsoventrally from cells to the sides of this single row, the midline area appears broader and can be considered a midnerve, or midrib. Thalli with very narrow indistinct midlines predominated in all collections. On pinnate axes, arrangement of lateral branches was irregular, neither consistently alternate nor opposite.

In culture, development of thalli from tetraspore germlings followed the same sequences of cell division described above from static observations on field-collected apices. Lateral branches develop from divisions in a marginal apical cell close to the main apex (Fig. 2) and thallus margins lacked dentations other than these distal branch initials. Adventitious branches occasionally developed on more proximal margins of older cultured thalli, but were not noted on collected plants.

Clones of *S. delicatula* var. *californica*, established from cystocarpic and tetrasporangial plants collected from 30 m off La Jolla (JS #2034, 2043), were used for laboratory studies. Under all conditions of light and temperature tested, the thalli were similar both to other experimental thalli and to the original collected thalli. Clones of *S. pinnata* (JS #2417) likewise did not vary in vegetative growth under the same set of culture conditions. Continuing experiments with additional clones generally confirm that morphological changes do not follow changes in the conditions under which thalli are grown in the laboratory.

Field-collected *Sorella* thalli revealed that cells anywhere on distal damaged edges can function as apical cells. All regenerated apices from erect blades and stipes showed the same pattern of cell divisions seen in primary blade apices, branch initials, and germlings. In general, secondary blades do not grow from midrib or blade surfaces. On one occasion a blade was observed which bore a branch-blade from the blade surface, rather than the margin; this was perhaps related to an apparent infection by another organism. Thalli that secondarily come into contact with the substrate in the field may form uni- or multiseriate attachment structures along blade margins, or in cases of epiphytic *Sorella* specimens, from blade surfaces. Such structures, in contrast with the regular development of marginal attachment structures in laboratory-grown thalli of related genera (Stewart, 1976), never formed on laboratory-grown thalli of *Sorella*.

In all cases, increase in length of axes initiated by germinating spores or from small apical portions was rapid at first, but the maximum thallus length attained under any conditions was always close to 20 mm. To obtain a more precise understanding of how growth proceeded, a 4 mm apex was cut from an actively growing *S. delicatula* var. *californica* thallus and moved to a separate culture dish. Little growth occurred the first week; then length increased steadily until the ninth week. Branches were initiated after the third week, and tetraspores were present at the end of the fifth week on proximal branches. Between the ninth and 13th weeks growth of the primary axis increased by only 3 mm, but secondary axes (branches) grew and became branched. As was common for reproductive thalli, apical areas at this time became colorless and further divisions of the apical cell were not observed.

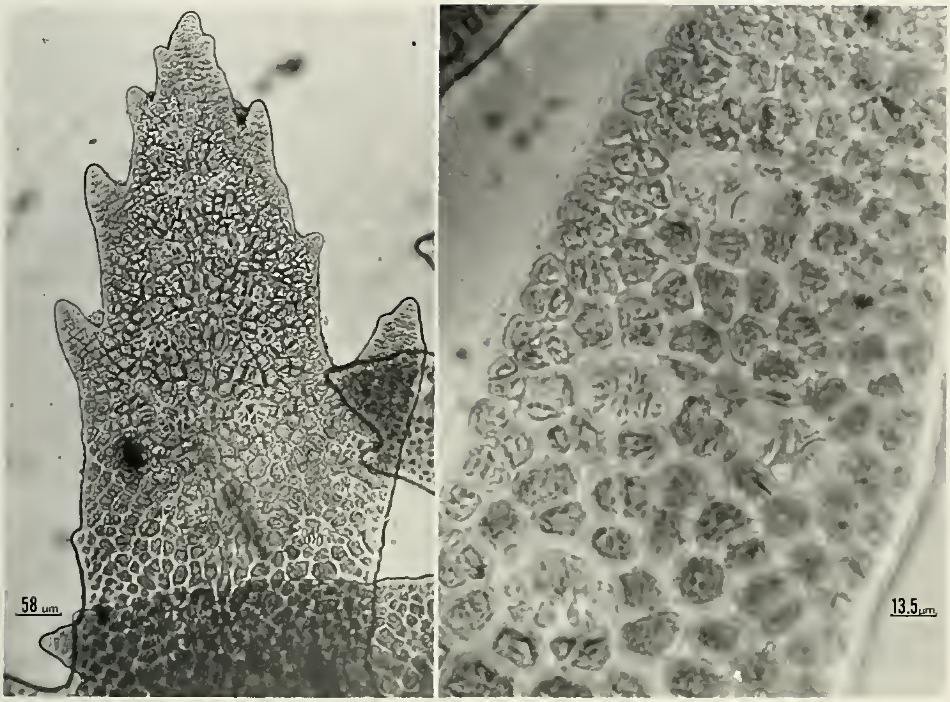

Fig. 3. Carpogonial development (JS #1773).

Life history and reproductive structures.—In culture, discharged carpospores germinated and grew into thalli which bore and shed tetraspores. Germlings from these tetraspores grew into thalli on which male and female gametangia developed, on separate plants, indicating the presence of a *Polysiphonia*-type life history. The cycle, under laboratory conditions approximating ambient light and temperature, could be completed within a six to eight week period. All plants were vegetatively similar.

In a clump of presumably young, very small unbranched thalli collected in the field, one blade, 3.6 mm high, bore a spermatangial sorus which implies that rapid development of a germling to reproductive maturity can occur in the ocean as well as in the laboratory.

Most collections made throughout the year included blades with apparently mature tetrasporangia, cystocarps, and male sori. Tetrasporangial sori were median on blades, covering the midline, and were often large and thick, protruding from both surfaces. No sori were positioned in any other way, substantiating the use of this criterion to separate *Sorella* from *Erythroglossum* (Hollenberg, 1943). Initially, tetrasporangial mother cells develop from cells close to the apex to either side of the central cell row on both surfaces of the blade. A layer of very small (3–4 μm) cells overlies the enlarging sporangia and small cells appear scattered in the sori from which spores have been shed. Division into tetrahedrally arranged spores occurs when the sporangial mother cell is about 22 μm in diameter. As cell walls and cytoplasm enlarge, undivided sporangia come to lie over the central line, the sori appearing eventually single and median (Fig. 1A, C, D). Shed spores

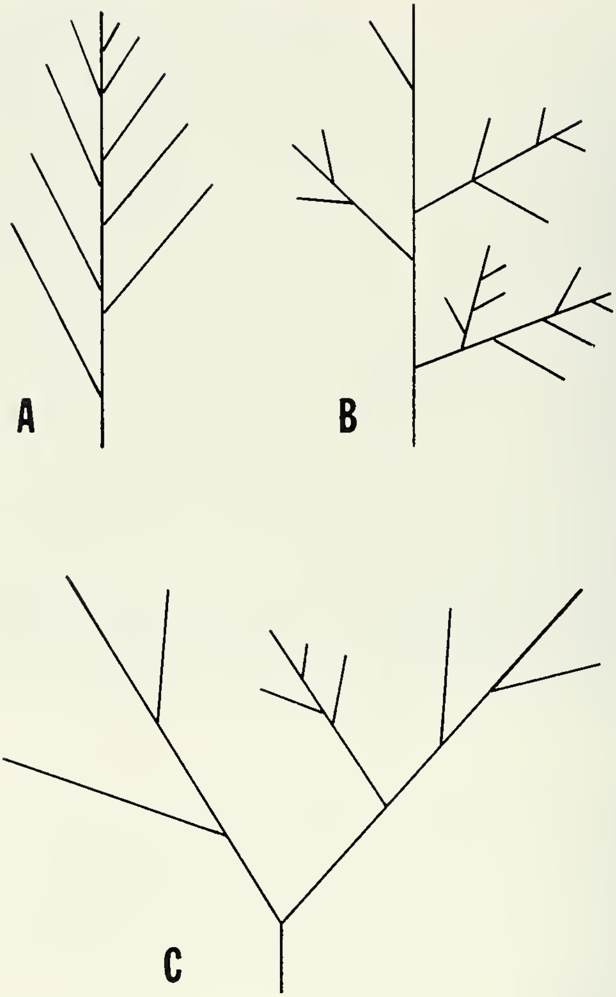

Fig. 4. Diagram of branching patterns of selected field-grown specimens. See text for explanation.

measure up to 50 μm in diameter. A non-fertile margin always remains around the sorus.

Regular close spacing of procarps on either side of the midline aids recognition of female gametangial blades (Fig. 3). Typically the vegetative cells which gave rise to carpogonial branches are more than one cell to the side of the central cell row, and about five cells apart on each side. The simplest stage showed two small cells overlying an apparently undifferentiated blade cell. Later arrangements appeared similar to those described for *S. repens* (Yamada, 1971). One to several cystocarps can be found on one or both surfaces of the same blade (Fig. 1B, F). Carpospores cannot be described as single and terminal, but were of graduated sizes with several shapes in short chains.

Spermatangial mother cells also are recognized initially to either side of the central cell row. No reproductive cells, therefore were derived directly from cells of the primary cell row. Spermatangia were 2–5 μm broad, colorless, and overlay vegetative cells in monostromatic regions, generally in median sori (Fig. 1E, G). In some cases paired sori in basal parts of a blade were separated by broad midnerves while sori more distal on the same axis were single and median. Paired sori also occurred lateral to very indistinct narrow midlines.

Criteria for discrimination of species.—Three types of branching patterns observed in collected *Sorella* thalli are diagrammed in Fig. 4: A) strictly pinnate, with simple branches of graduated length along a percurrent axis; B) a percurrent axis displaying less regular and more complex orders of branches; C) flabellate or dichotomously branched thalli lacking a percurrent axis. Each of these arrangements can be recognized in plants with broad or narrow axes, with narrow or broader midline development. Narrow (300–500 μm wide) dichotomous-flabellate variants with inconspicuous midlines (Fig. 1A, B) are most often found and represent thalli described as *S. delicatula* var. *californica*. Broad (800–1,200 μm wide) pinnate plants (Fig. 1G) with broad midribs and paired spermatangial sori are as Hollenberg (1943) described *S. pinnata*, but note the additional presence of single median sori on the same blade in Fig. 1G. Other specimens show broad/narrow blades combined in various ways with different branching patterns and with thin, faint or broader midlines (Fig. 1C, D, E, F).

Paired spermatangial sori are not obligately developed on broad pinnate plants; i.e., single median sori are not restricted to narrow-dichotomous thalli (Fig. 1E, G). Median, single sori on spermatangial blades are more frequently found, whatever the branching pattern of the thallus.

Discussion

Extensive sampling of California *Sorella* from a variety of habitats documents that specimens with the typical characteristics described for *S. pinnata* are uncommon. In the same locations narrow thalli (to 500 μm wide) that are dichotomously or flagellately branched with indistinct central lines are more commonly found and can be attributed to *S. delicatula* var. *californica*. Thalli intermediate in breadth (500–800 μm), branched in less typical ways, or that combine the breadth described for one species with the branching pattern of the other are less easily classified. Developmental morphology of neither vegetative apices nor reproductive structures provided distinctions between the two species. Attempts to correlate any one morphological character with another (e.g., branching pattern with width, midrib development, height) or any of these characters with an environmental factor, have failed to demonstrate interrelationships. Efforts to induce variation in these characters under varying culture conditions have provided no positive evidence that light or temperature affect their appearance. Finding typical *S. pinnata* and *S. delicatula* var. *californica* thalli together in the field indicates that environmental control of form, if operative in these species, is indirect or complex. Mature reproductive structures are similar on all vegetative forms and cannot be used for species discrimination.

Careful subtidal collecting with SCUBA showed all *Sorella* specimens are ±2 cm high, offering no support for suggestions that the large 9-cm high specimen on which Gardner established *Erythroglossum delicatula* represents deep-water forms of the species. Herbaria were searched for properly identified specimens larger than those found in San Diego collections but none were found. The source and relationships of the type specimen therefore remain enigmatical.

To combine several intergrading morphological forms of California specimens into a single variable species, although perhaps convenient, does not emphasize the distinctiveness of the several morphologies which at present are unexplained by associations with particular habitats, or by light and temperature effects as tested in the laboratory.

An alternate solution to the taxonomic question is to distinguish the two species as originally typified regarding vegetative morphology, relying on branch arrangement as the most useful criterion. In this way most dichotomous thalli with blades of varied widths can be treated as *S. delicatula* var. *californica*, reserving *S. pinnata* for plants that are pinnately branched, and often but not necessarily relatively broad. It is suggested that var. *californica* be maintained for the small specimens despite the lack of thalli corresponding to the large var. *delicatula*.

The short period of time needed to complete the life history for this alga in the laboratory, the presence in natural habitats of reproductive structures on very small, presumably young plants, and the fact that fertile thalli are found in most collections, suggest that rapid and continual growth and reproduction are factors in the successful maintenance and dispersal of *Sorella* populations.

Acknowledgments

Conversations with G. J. Hollenberg concerning how best to identify the specimens found off San Diego were a valuable impetus to continue the study of *Sorella* species. P. C. Silva and I. A. Abbott offered help in the use of herbaria at the University of California, Berkeley and Hopkins Marine Station, Stanford University. A large portion of the work was supported by an NSF fellowship and represents a portion of a dissertation submitted to the University of California, Irvine, prepared under the guidance of P. S. Dixon whose assistance and advice is gratefully acknowledged.

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A Small Herpetofauna from the Late Pleistocene of Newport Beach Mesa, Orange County, California

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Abstract.—A Late Pleistocene herpetofauna consisting of *Hyla regilla*, *Bufo boreas*, *Rana aurora*, *Aneides lugubris*, *Thamnophis*, *Lampropeltis getulus*, *Masticophis flagellum*, and *Crotalus viridis* has been identified from Newport Beach Mesa, Orange County, California. *Aneides lugubris* is reported as a fossil for the first time. Corrections and further identifications have been made on fossil herpetofaunas from two other Orange County localities. These faunas suggest post-LaBrean changes in the coastal Orange County vegetation from chaparral and live-oak woodland with riparian woodlands to that of coastal sage scrub with sycamore woodlands. Subsequently the sycamore riparian community receded into the nearby Santa Ana Mountains leaving coastal sage scrub and intermittent grasslands in coastal Orange County. These communities have subsequently been reduced by increased agriculture and urbanization.

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Late Pleistocene assemblages of amphibians and reptiles are known from only a few locations in California. These include a few caves (Brattstrom, 1953a) and the asphalt deposits at La Brea, McKittrick, and Carpenteria (Brattstrom, 1953a, b, 1955; Miller, 1942). We report here a small herpetofauna from Orange County, California that comes from a stream deposit. We further make comments and identifications on recently discovered fossil amphibians and reptiles found in other Orange County localities.

The locality (LACM 3877, old number 1067; Newport Bay Mesa Locality; Miller, 1971) is a Late Pleistocene Rancho LaBrean deposit from a road cut (no longer in existance) located east of MacArthur Blvd. about two miles west of the Irvine campus of the University of California, Orange County, California (Miller, 1971). The fossils were imbedded in a water soluble, clay-like matrix apparently the result of stream deposition. The abundance and clumping of the material suggests that it may have been the results of erosion of an owl pellet cache (Miller, 1971) but the microfauna is much more diverse than usually found in owl pellet caches found today.

The material, collected by Dr. Ted Downs (TD Loc. 295), is deposited in the Natural History Museum of Los Angeles County (LACM). It has been catalogued by Paul Langewalter (LACM) as including numbers 56821 to 56972. The fossil material, consisting of over 100 bones and representing four species of amphibians and four species of reptiles, has been compared with extant skeletons and fossil bones in the collections of California State University, Fullerton (CSUF) and the LACM.

This paper is dedicated to Dr. Carl L. Hubbs because of his interest in changes in the climate along the California coast as well as for his long-term support and encouragement of one of us (BHB) as a scientist and as a friend.

Class Amphibia

Aneides lugubris—Arboreal Salamander

Material.—Three complete left dentary bones and one left dentary fragment (LACM 56864-7). The robust size of the pedicels and the triangular elevation arising from the dorsal surface just posterior to the midpoint of the dentary serve to characterize *A. lugubris* (Wake, 1966). The complete bones all have nine pedicels which occupy less than one half of the ramus length, also characteristic of *A. lugubris* (Wake, 1966). The above material is identical to two fossil bones previously described in the literature as *Taricha* sp. by Miller (1971) from Costeau Pit (LACM Loc. 65129, 18930) and from the Newport Mesa Locality (LACM Loc. 1067, 20563). The well-developed pedicels borne mediad on the dorsal ramus unmistakably characterize these as being from *A. lugubris*.

Three left and two right maxillary fragments (#56857–61). The pars distalis is 50-60% edentate and bears six or seven robust pedicels per bone.

Twenty-five presacral and two atlas vertebrae. The trunk vertebrae are amphicoelous, constricted ventrally, without a ventral spine; neural spine is reduced but present throughout; parapophyses are supported by a dorsoventrally compressed plate-like shelf that arises from ventrolateral surfaces of anterior and posterior margins of the centrum and extends to the distal tip of the parapophyses. The shelf results in a diamond-shape appearance of the vertebra when viewed ventrally (Wake, 1966). The atlas vertebrae posses a boss, rounded anteriorly, becoming broader posteriorly and terminating at the posterior margin of the neural arch. Over 100 other salamander fossils, including caudal vertebrae and various girdle fragments, were examined but could not be positively identified. *Aneides lugubris* has apparently not been previously reported from the fossil record (Gehlback, 1965). This species occurs in Orange County today, although not near the deposition site.

Bufo boreas—Western Toad

Material.—One sacral vertebra, one each of the 4th, 5th, and 6th presacral vertebrae, one radio-ulna (#56821–25). The sacral vertebra is procoelous, with two posterior condyles; sacrum free from urostyle, its diapophyses moderately expanded as characteristic of *Bufo* (Holman, 1962). The vertebrae and radio-ulna are indistinguishable for extant *B. boreas* in the collections and do not resemble other medium-sized bufonids (such as *cognatus* and *woodhousei*) ranging anywhere near Orange County today. *Bufo boreas* is a common Pleistocene fossil and occurs in the area today.

Rana aurora—Red-legged Frog

Material.—One sacral and one presacral vertebrae, eight radio-ulnas, one humerus fragment (#56826–7, 56968–72). The sacral vertebra has one anterior and two posterior condyles and has non-expanded diapophyses. According to the criterion of Chantell (1970) the fossils can be ascribed to extant members of the western *Rana* group including *R. aurora*, *boylei*, *muscosa*, and *cascadae*. The latter three are montane forms and the fossils most resemble the extant *R. aurora* when compared to skeletons of all these species. We therefore refer this material to *R. aurora*. This species has been found in the La Brea deposits and occurs near the deposition site today.

Hyla regilla—Pacific Treefrog

Material.—Three presacral vertebrae, four humeri, four radio-ulnae, one femur, 13 tibio-fibula, three left and three right ilia. The ilia have a well-developed dorsal protuberance with its anterior edge slightly anteriad to the anterior edge of the acetabulum; subacetabular expansion wide and forming a relatively sharp angle with the ilial shaft. There is no ilial crest and the supra-acetabular expansion is short, straight, and directed dorsoposteriad (Chantell, 1970). The material is indistinguishable from *Hyla regilla* in our reference collection. A few of the larger tibio-fibulas may be indicative of a larger morph. *Hyla regilla* occurs in Orange County near the deposit today.

Class Reptilia

Although intercolumnar, ontogenetic, and individual variations present an array of problems in the identification of snake vertebrae (Holman, 1962, 1965) several authors have been able to assign well-preserved thoracic vertebrae to the generic and specific level (Holman, 1963; Brattstrom, 1954, 1964, 1967; Auffenberg, 1963), but those identifications must rely ultimately upon direct comparison with recent specimens or with other fossil specimens of known identity (Brattstrom, 1967).

Crotalus viridis—Western Rattlesnake

Material.—Four thoracic vertebrae (#56899–902). The fossil vertebrae are those of a medium sized adult and are indistinguishable from both extant and Pleistocene specimens of *C. viridis* in the reference collections. Fossils of *C. viridis* are common in western North American Pleistocene and have been taken from several sites in California. The species occurs in Orange County today.

Lampropeltis getulus—Common Kingsnake

Material.—Eight thoracic vertebrae (#56903–10). All vertebrae are apparently from young adults and represent at least two individuals. The species is a common Pleistocene fossil and is found in the area of the deposit today.

Masticophis flagellum—Coachwhip Snake

Material.—Four complete and five thoracic vertebral fragments (#56828–36). Based on comparison with recent material these specimens are referred to *M. flagellum*. Many workers, however, refuse to make distinctions between the various species of fossil *Masticophis* (Holman, 1965). The species occurs in the area of the deposit today and in many Pleistocene deposits.

Thamnophis sp.—Garter Snake

Material.—Seventeen thoracic vertebrae (#56843–56). Species of *Thamnophis* are difficult to distinguish when alive and almost impossible to differentiate on the basis of vertebrae alone. We have therefore suspended specific identification. *Thamnophis* is a common Pleistocene fossil; two species occur in the Los Angeles–Orange County basin today.

Other Orange County Pleistocene Herpetofaunas

Miller (1971) reported on Late Pleistocene (Rancho LaBrean ±40,000 pp) amphibians and reptiles from Costeau Pit (LACM Loc. 65129) that is some 14 km to the southeast of the Newport Mesa locality and near the city of El Toro. We have confirmed and further identified his specimens and changed his identification of *Taricha* to *Aneides lugubris* (see above). The Costeau Pit herpetofauna now consists of: *Aneides lugubris, Bufo boreas, Rana aurora, Sceloporus, Cnemidophorus, Clemmys marmorata, Gopherus, Crotalis viridis*, and *Pituophis melanoleucas*. The pond turtle, *Clemmys*, does not occur in coastal Orange County today, but probably did in historic times. *Gopherus* had not previously been reported from the Pleistocene of the Los Angeles–Orange County basin before Miller (1971).

Newport Mesa Locality (LACM Loc.) 1066 is a mixed marine and terrestrial deposit. The only herpetological remains from this site consists of portions of the carapace of a large marine turtle (Miller, 1971). We find that it most closely compares with the Green Sea Turtle, *Chelonia mydas*, and have identified the material as of that species.

Discussion

The plethodontid material reported herein constitutes the first occurrence of *Aneides lugubris* in the fossil record. Although other plethodontids are fairly common in the fossil record (Gehlback, 1965), the genus *Aneides* is rarely represented, probably in part due to the arboreal and secretive habits of these salamanders.

All of the species from the Newport Beach Mesa Locality (3877-1067) represent forms living today. Furthermore, all of these species can be found within the Orange County area today, however not all occur near or at the deposition site. The members of this assemblage are either semi- or fully aquatic, or are known to frequent riparian habitats. All can be found in and around permanent or semi-permanent water courses in the Santa Ana Mountains to the northeast.

Coastal Orange County in the vicinity of the fossil locality consisted (before the advent of agriculture and urbanization) of primarily low coastal sage scrub with intermittent grasslands. Low chaparral occurs on hills 8–16 km to the south and 32 km to the east. East of the deposit, the Santa Ana Mountains rise to an elevation of 1,734 m. While occasional patches of pine and big cone spruce occur near the top, the vegetation is largely chaparral, live-oak woodland, and alder-sycamore riparian vegetation. Sycamores occur along the streams as they emerge from the mountains and may occur along these streams to the ocean (as at San Onofre to the south and near the Costeau Pit Locality). Sycamores do not, however, follow the course of the San Diego Creek through central Orange County toward the Newport Beach Mesa deposit area and Upper Newport Bay. *Bufo boreas, Hyla regilla, Lampropeltis getulus* and *Masticophis flagellum* are common about the area of the deposit today. *Thamnophis* is rare here; *Crotalus* occurs only a few miles south, and *Rana aurora* is found only closer to the mountains; but these are clearly the result of recent historical changes in the area associated with agriculture and urbanization. The Arboreal Salamander, *Aneides lugubris*, is common in the alder-sycamore riparian zone in the Santa Ana Mountains to the east. It occasionally follows the sycamores along water courses for a short way as they emerge from the mountains. They do not occur near the area of the Costeau Pit nor the Newport Beach Mesa localities today. This would suggest that post-Pleistocene changes in coastal Orange County include the recession of the riparian woodland towards the mountains.

The fossil fauna of the Newport Beach Mesa Locality includes ducks, quail, crow, red-winged blackbirds, shrews, rabbits and rodents characteristic of the area today, but also extinct mastodon, horse, and camel. The presumedly, slightly older, other Newport Mesa Locality (1066) contains extant species and extinct sloths (*Megalonyx* and *Nothrotherium*), horse, tapir, camel, and bison. The Costeau Pit Locality (± or >40,000 yr BP) to the southeast is similar, but its extinct megafauna includes sloth (*Paramylodon*), dire wolf, saber-tooth cat, mammoth, horse, camel, dwarf pronghorns (*Capromeryx*), and bison (both *B. antiquus* and *latifrons*) according to Miller (1971).

These faunal assemblages, including the herpetofaunas, suggest that coastal Orange County in the Late Pleistocene was slightly wetter, similar to the environment of Rancho La Brea in Los Angeles County (Brattstrom, 1953a, 1956). Associated with or following the extinction of the mammalian megafauna, the oak woodland, chaparral, and lastly the alder-sycamore riparian plant associations probably receded from coastal Orange County (and elsewhere in the Los Angeles-Orange County basin; except for patches of chaparral in the Palos Verdes and San Joaquin-Laguna Hills). Left in their place was the more open, low coastal sage scrub and intermittent grasslands. The latter two plant communities have become subsequently destroyed in the central part of Orange County by agriculture and urbanization over the last 100 years.

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Surface Air Flow in Coastal Southern California

Gerald Hannes

Abstract.—Resultant winds are presented at hourly values for each month in 1972 at three sampling sites located in coastal southern California. The end point of the onshore flow vector during certain afternoon hours describes either a clockwise or counterclockwise rotation. The counterclockwise movements are not likely related to topographic restraints but are probably caused by other factors. The land breeze has two distinct offshore flow regimes at each individual site, especially during the month of December. These two flow regimes generally display opposite vector rotational characteristics through time. During the summer months, the land breeze is not present in the mean, but is replaced by a flow that generally parallels the coast.

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In recent years numerous studies describing air flow in a coastal area have been conducted. Many of these research papers have dwelled upon the study of the land-sea breeze circulation. Haurwitz's (1947) study theoretically described the effect of the Earth's rotation and frictional effects on the change in air flow direction throughout the diurnal heating and cooling cycle. Since this paper was written, numerous other works have been published (Defant, 1951; Pearce, 1955; Dexter, 1958; Edinger, 1959; Schroeder et al., 1967; Halpern, 1974).

An interesting aspect of many of these studies is the question of which physical factors are responsible for the variations of the diurnal period surface winds. Oscillations in flow can be produced by either gravitational potential or by solar radiational effects. Oscillations can also be caused by tidal influences (Chapman and Lindzen, 1970) which in turn are produced by both gravitational and thermal effects. In most instances, however, tidal effects can be quite small (Harris, 1963; Roden, 1965; Pearce, 1955). Furthermore, thermotidal winds as described by Lettau (1967) have not been studied as extensively as the thermally driven land-sea breeze system.

In general, sea breeze motion is produced mainly by land-water thermal contrasts. The winds blow onshore at nearly right angles to the isotherms and isobars with surface speeds between 5 to 7 mps (Defant, 1951). The maximum surface flow occurs between 1100 and 1400 h followed by a period of decline in the flow from 1400 to 2000 h. Concerning the vertical development, the sea breeze system does not usually extend over 800 m in depth.

The onshore surface flow vector exhibits a clockwise rotation through time in the northern hemisphere. Haurwitz (1947) found that Coriolis, horizontal pressure gradient, frictional, and inertial forces were responsible for the vector rotation through time. Dexter (1958), Staley (1957), and Frenzel (1962) have described the various different shapes of hodograph ellipses produced by a sea breeze flow. These differences are thought to be related to either topographic restraints or superimposed geostrophic wind influences on the surface air motion.

In comparison to the sea breeze, the land breeze is usually much weaker in magnitude. The summertime land breeze, especially on the west coast of the United States, is quite weak because the general horizontal pressure gradient favors a diurnal onshore motion, thus impeding any strong offshore flow (Neiburger et al., 1973). In addition, the monsoonal effects of the Pacific High pressure cell also restrict a strong offshore flow from late spring to early fall (Schroeder et al., 1967) in the California coastal areas.

Study Area and Objectives

The study area is located in coastal, southern California. This area was chosen because of a potentially strong ocean-air interaction resulting from the presence of cool, seasonally upwelled waters offshore (Stevenson and Gorsline, 1956; Reid, 1960). Also, the Los Angeles Basin is nearly flat and thus should not strongly impede the motion of the basic horizontal air flow as would be the case in a more topographically complex area. Because of the seasonal change in location and magnitude of the Pacific High pressure area in conjunction with seasonal variations in insolation, the surface air flow in the study area should alter seasonally and diurnally in both direction and magnitude (Stevenson, 1960; Edinger, 1963).

The three sampling sites are Costa Mesa (33°39′N, 117°54′W), Anaheim (33°50′N, 117°55′W), and La Habra (33°56′N, 117°57′W). The geographical position of the three cities is such that they form a rough north-south transect. Costa Mesa is nearest to the Pacific Ocean, while La Habra is farthest inland. Their elevations above mean sea level do not exceed 120 m. Therefore, all three sites could conceivably be affected by a land and/or sea-breeze circulation.

This paper has two main objectives: first, to describe the seasonal variation in the monthly diurnal resultant winds at each site; and second, to identify the monthly periods of maximum onshore and offshore flow at each location.

Data Analysis and Format

In order to properly evaluate both wind speed and directional values, the two variables must be analyzed vectorially. Vectors can be reduced to their appropriate vector components and then averaged. The mathematical basis for the calculation of a resultant wind is described by Pant (1968).

The hourly wind data were organized into twelve monthly blocks for each of the three stations. Resultant surface winds were calculated by averaging the hourly values each day of each month for each site during the 1972 study period. Once this was completed, vector diagrams for each month at the three stations were constructed. With the data organized into monthly time periods, the basic shape of the wind hodographs can be ascertained. Furthermore, any clockwise and counterclockwise vector rotations of the onshore flow can readily be seen in this type of data display.

In this study, an onshore flow will be considered as any air flow coming form the S, SSW, SW, WSW, or W, while an offshore flow will be identified as motion from the N, NNE, NE, ENE, or E directions of the compass.

Results by Station

The monthly diurnal resultant winds are organized by station and will be discussed in the following order: a) Costa Mesa (coastal), b) Anaheim (intermediate), and c) La Habra (inland). The characteristics of the land breeze will be presented first and then followed by a description of the onshore flow system for each individual sampling site. Lastly, the monthly maximum resultant winds for both the onshore and offshore flow at each station for the entire year will be presented.

Costa Mesa.—The offshore flow has the greatest frequency of occurrence in the winter months (winds for the month of January were not analyzed because of insufficient observations). December records the greatest number of hours with an offshore flow, followed by November and October respectively (Fig. 1). The largest magnitude of the surface offshore flow also occurs in December. This finding is in general agreement with the research of Neiburger et al. (1973). It was found that the land breeze in December has two distinct periods of build up: a) from 0400 through 0600 h, and b) from 2100 through 2300 h. During both periods of speed increase, a clockwise rotation of the vectors occurs. This rotation probably reflects the influence of Coriolis force on the general air motion.

On the other hand, an offshore flow does not take place during May, June, July, and August. As noted by Schroeder et al. (1967), the monsoonal effect is most pronounced during this general time period. However, one must remember that because of the averaging process used in this study, the infrequent occurrence of an offshore flow does not appear in the resultant wind data. Hannes (1972) found through a frequency analysis of the 1972 July and August wind data that the percentage of occurrence of the offshore wind was very small.

Concerning the sea breeze air flow at Costa Mesa, all months examined have a general onshore wind. The strongest flow, as one might expect, occurs in August, while the months of June and July have the next largest resultant winds. However, with regard to the duration of the onshore flow, the months of June and July have a greater total number of hours than does August.

With respect to the clockwise rotation of the vectors, several of the months exhibit this feature. For example, during August from 1000 through 1500 h, there is a period of clockwise movement followed by a normal decline period (1600 through 2000 h; Fig. 1). However during the month of December, this orderly clockwise rotation does not exist. December, which has the weakest onshore flow, is the only month that has an extensive period of backing winds prior to the hour of maximum flow (from 1200 to 1400 h).

Another curious period of counterclockwise vector motion occurs in the month of October from 0800 to 1100 h. Somewhat like December's backing period, this month has several hours of predominately the same type of rotation between the time of the offshore and onshore flow (0800 to 0900 h). Furthermore, this time period coincides with the equilibrium time span or the stagnation period as described by Staley (1959). After this brief interval of counter motion, the onshore flow is established (1100 h) and the normal clockwise vector rotation begins.

Anaheim.—The intermediate station in the coastal transect, records the strongest offshore flow during the month of December (Fig. 2). The hour at which this occurs (0800 h) is not what one would expect. The offshore maximum should take place around sunrise; however, the offshore flow at Anaheim occurs later in the day and even continues until 1100 h. Also during December, the land breeze duration is

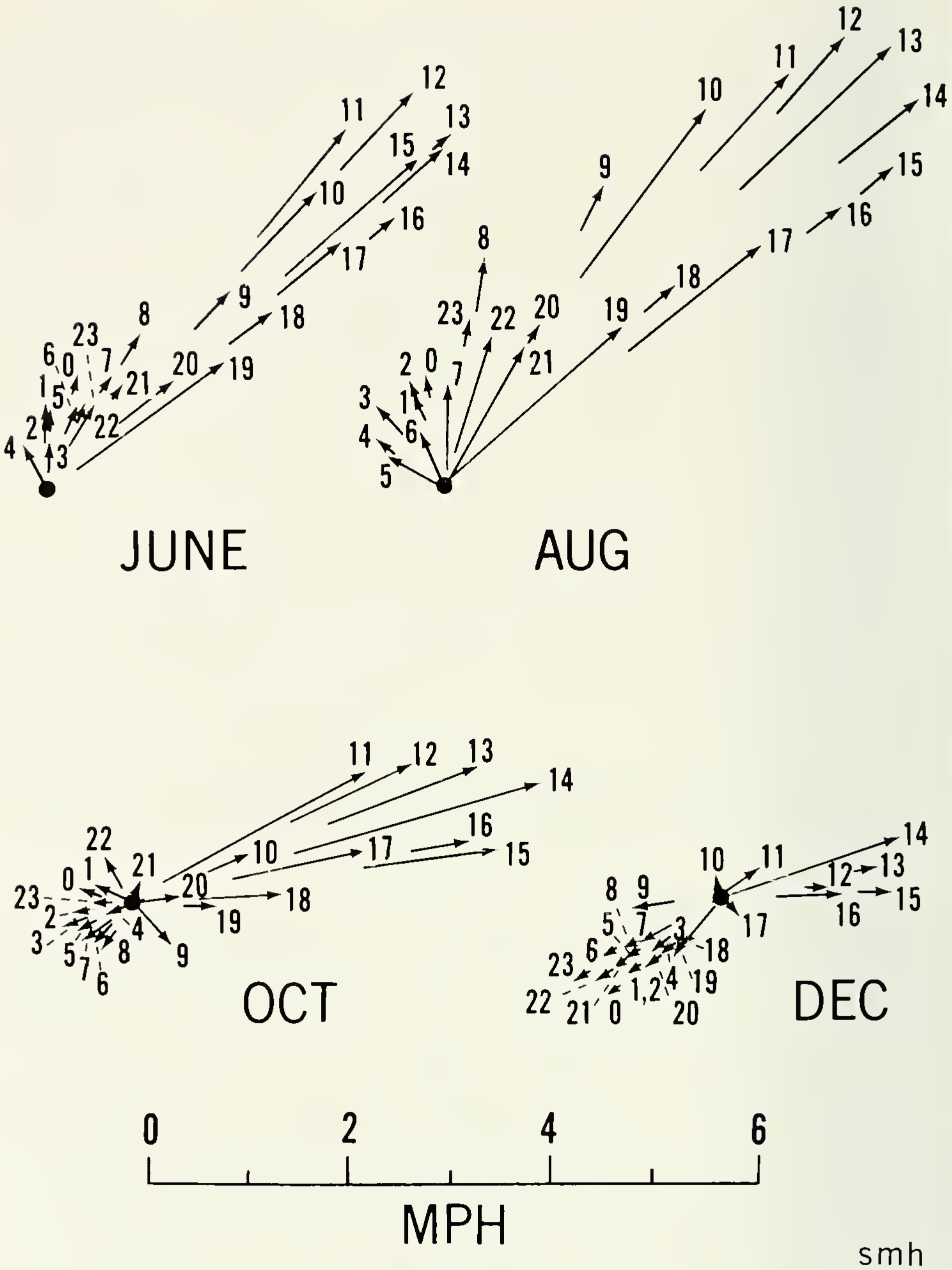

Fig. 1. Resultant Winds: Costa Mesa.

greater than that of the sea breeze. This is mainly attributed to the seasonal insolational cycle and its effect on land-water thermal contrasts. Furthermore, it was also found that the months of January and November have strong land breezes; however, they are still less than the December maximum speed.

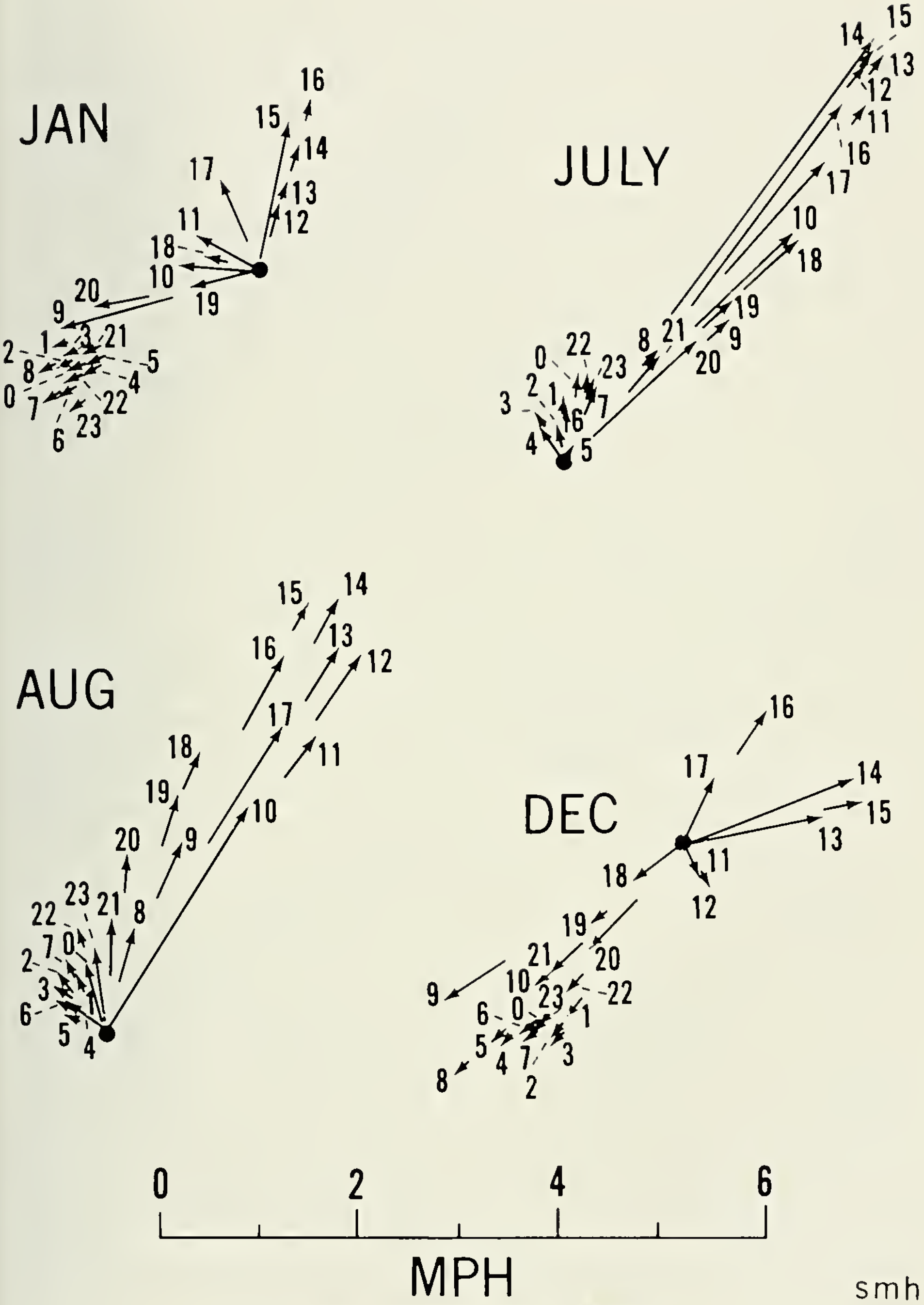

Fig. 2. Resultant Winds: Anaheim.

If one were to construct land breeze ellipses for the months of November, December, January, and February, one would find them to be quite narrow and elongated. This narrowness could be attributed to the seasonal heating cycle and not necessarily to topographic constraints as described by Staley (1959). Moreover, during the spring with the increased solar heating of the land and atmosphere, the ellipses would become smaller in length than those for the winter months.

With regard to vector rotation, the land breeze does exhibit a normal pattern in December. For example, from 0100 to 0500 h there is a general increase in speed and an attendant clockwise rotation. However, around sunrise (0600 and 0700 h), the speed decreases and backing prevails until the time of the maximum motion at 0800 h. On the other hand, considering January, the strongest offshore flow from 0200 to 0700 h experiences both counterclockwise and clockwise motion prior to the maximum at 0700 h. In addition, January also has another period of strong surface flow during the late evening hours (2000 to 2300 h). However, these hourly winds indicate a definite backing motion before the greatest value at 2300 h.

Following the winter months of maximum land breeze, the spring months are characterized by surface winds that parallel the coast. Moreover, during late spring the offshore winds decline in frequency, while the summer months are altogether devoid of a land breeze in the mean. The summer months have a dominant onshore flow; however, this frequent onshore air motion is associated with a weak secondary flow that parallels the coast (e.g., Fig. 2; July at 0300 and 0400 h). Again, this dominance in the onshore surface winds suggests a reinforcement by a larger scale regional onshore pressure gradient.

The sea breeze has its greatest frequencies in May (17 h), June (20 h), July (21 h), and August (14 h). Nevertheless, the strongest hourly wind occurs in April. The reason for April's larger magnitude might possibly be related to either the effects of increased thermal turbulence in late summer which would slow down the winds (Yu and Wagner, 1970), or to a greater enhancement of April's surface flow by a stronger regional circulation. This difference in monthly speeds can only be properly explained after a detailed study of the vertical energy transfers and wind field in and around the Los Angeles Basin is made.

The clockwise rotation of the sea breeze flow at Anaheim is not typical, especially in July and August (Fig. 2). During July (1000 to 1200 h and from 1300 to 1400 h) and August (1100 to 1400 h), there is a counterclockwise vector rotation predominately associated with speed increases. It appears that the horizontal pressure gradient force outweighs the effects of Coriolis force and that the winds respond with a backing motion. Other considerations that have never been fully ascertained in the Los Angeles Basin include the thermal effects of the surrounding mountains, the diurnal movement of the heat low, and urban effects on the local wind field. Although Fosberg (1969) did study the August airflow over the Santa Ana Mountains as well as a thermally unstable boundary layer, his results might not be applicable to the other summer months examined in this study. However, his research did identify three diurnal changes in the flow field and vorticity field which might account for some of the resultant wind turnings in the basin air motion.

La Habra.—This station is farthest inland and thus should be least affected by unmodified marine air. As marine air penetrates from the coast during the daytime, it will likely be modified through convectional activity and mechanical mixing. Therefore, the surface air temperature regimes at La Habra should be different

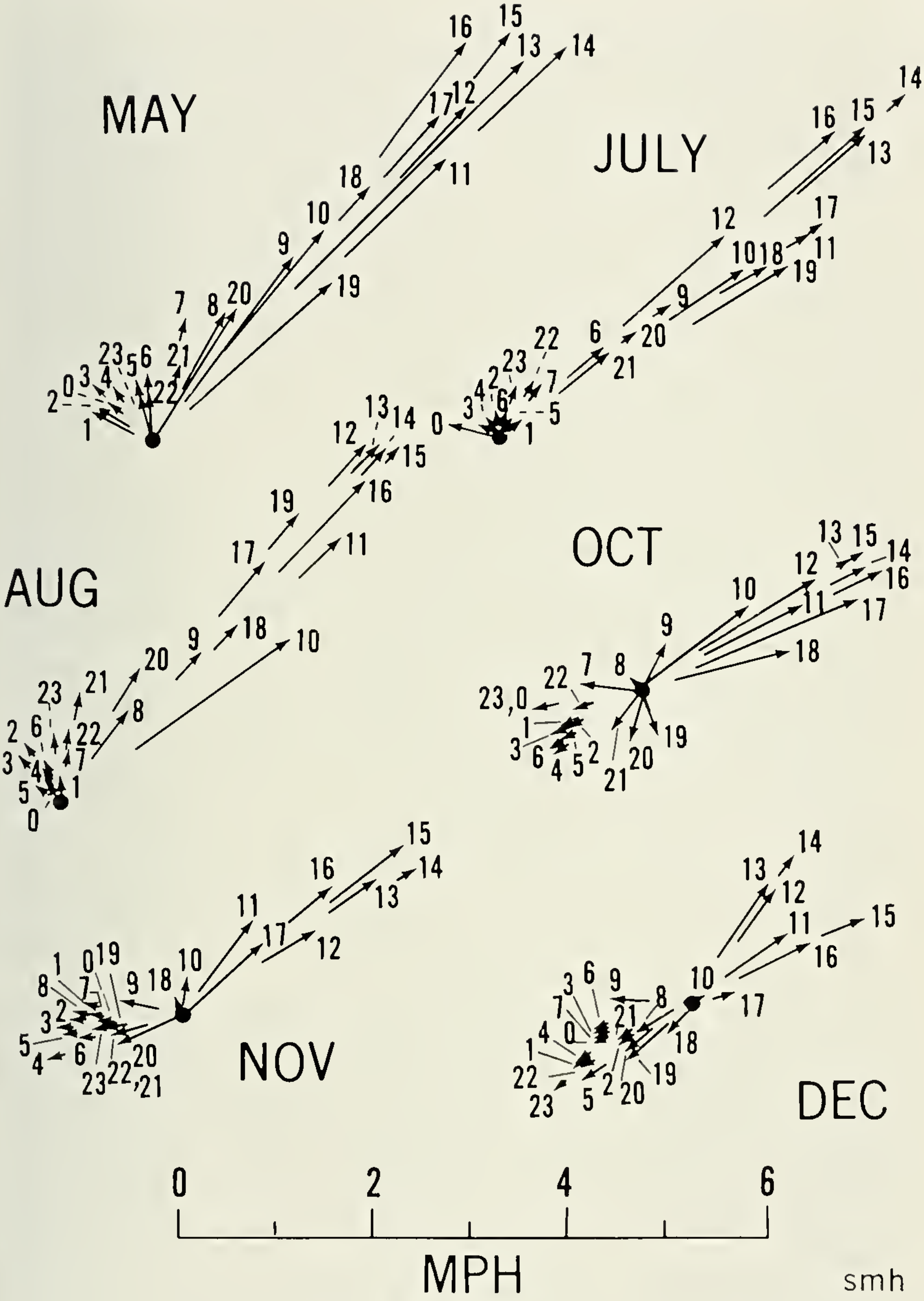

Fig. 3. Resultant Winds: La Habra.

from those recorded at the other sites. Hence, the land and sea breeze flow structure will differ from the more coastal locations.

The first aspect of the surface air flow at La Habra examined is the land breeze (Fig. 3). The greatest duration, as one might expect, occurs during the winter months: a) October (11 h), b) November (13 h), c) December (15 h), d) January (13 h). Similar to the other stations discussed previously, December records the strongest hourly resultant wind (2300 h). In addition, the individual monthly hourly resultant winds for each of the winter months are strongly clustered about one another (e.g., November; Fig. 3). This suggests the presence of a weak but persistent offshore horizontal pressure gradient in the study area.

The hours at which each individual monthly maximum speed occurs seem to be the end product of a two to five hour buildup period. The time span over which the speed increases is associated with either a backing or a veering motion. October, for example, has a general clockwise vector rotation in the late evening hours (1900 to 2300 h). On the other hand, the strongest offshore flow increases from 0100 to 0600 h (Fig. 3), but it is not dominated by one particular type of rotation. Thus La Habra, especially in October, maintains a dual land breeze system of nearly opposite rotational characteristics.

This double land breeze system is also found during the months of November and December. However, in each of these two months the twofold land breeze regime is not as easily identified as in the October regime. November exhibits a build up of a weaker flow in the late evening hours (from 2000 to 2300 h; generally clockwise), while the early morning winds are stronger but associated with a counterclockwise flow (0100 to 0400 h). In addition to this, December also has two distinct offshore flow periods: a) the late evening (1800 to 2300 h; generally clockwise), and b) the early morning (0300 to 0500 h; counterclockwise). Thus, the individual monthly land breeze maxima are usually situated at the end of a speed increase period that is associated with either type of rotary motion.

The second aspect of La Habra's wind data examined is that of the seasonal sea breeze variations. The summer months of May (15 h), June (18 h), July (20 h), and August (16 h) have the greatest frequencies of the onshore flow, while an offshore wind is totally lacking during these same time periods. The strongest resultant wind occurs in May at 1400 h (Fig. 3). Again, one might expect the strongest onshore flow to take place in either July or August, but these lesser monthly magnitudes might be partially attributed to the results of the averaging of winds from various directions employed in this study.

La Habra, like Anaheim, also exhibits certain anomalous counterclockwise rotational characteristics in the afternoon resultant wind vectors. For example, during the month of July, there is a general backing of the wind vectors between the following time intervals: a) 1300 to 1400 h, and b) 1500 to 1600 h. Furthermore, between 1300 and 1400 h the counterclockwise vector rotation is accompanied by a speed increase. Contrary to this type of backing motion, August displays a normal sea breeze pattern from 1200 to 1500 h (Fig. 3). Furthermore, during both months, the hourly resultant winds tend to cluster about the monthly maximum value.

Lastly, the fall months have a general decrease in the duration and magnitude of the onshore flow, but they nevertheless maintain a general clockwise vector rotation which resembles that of the summer months. For example, in October the clockwise movement starts at 0800 and continues veering in this direction until 1800. The only exception to this sea breeze motion takes place between 1100 and 1200. Coriolis force is obviously responsible for this steady veering in the onshore motion.

Table 1. Costa Mesa: maximum velocity of monthly periods of air flow.

	Offshore			Onshore		
Month	Vel.	Azimuth	Time	Vel.	Azimuth	Time
J	—	—	—	—	—	—
F	1.0 mph	57°	0700PST	3.1 mph	227°	1300PST
M	0.4	87°	0600	5.1	230°	1400
A	0.6	78°	0500	5.5	242°	1400
M	—	—	—	5.2	228°	1300
J	—	—	—	5.6	222°	1200
J	—	—	—	5.5	215°	1300
A	—	—	—	6.3	226°	1300
S	0.4	62°	0600	4.9	259°	1300
O	0.7	70°	0300	4.3	253°	1400
N	1.3	57°	0300	4.1	236°	1300
D	1.7	55°	2300	1.8	247°	1400

Table 2. Anaheim: maximum velocity of monthly periods of air flow.

	Offshore			Onshore		
Month	Vel.	Azimuth	Time	Vel.	Azimuth	Time
J	2.5 mph	57°	0700PST	1.8 mph	196°	1600PST
F	1.7	67°	0800	3.4	218°	1400
M	1.0	80°	0700	4.4	221°	1400
A	1.0	64°	0600	6.1	226°	1400
M	—	—	—	6.1	223°	1400
J	—	—	—	5.0	221°	1300
J	—	—	—	5.4	220°	1400
A	—	—	—	5.1	210°	1400
S	0.5	57°	0600	4.4	212°	1400
O	1.4	34°	0700	3.2	241°	1500
N	2.3	50°	0800	2.9	230°	1400
D	3.3	44°	0800	1.9	257°	1500

Table 3. La Habra: maximum velocity of monthly periods of air flow.

	Offshore			Onshore		
Month	Vel.	Azimuth	Time	Vel.	Azimuth	Time
J	1.5 mph	81°	2200PST	1.9 mph	223°	1500PST
F	1.1	79°	0400	3.7	228°	1500
M	0.4	83°	0000	4.9	229°	1400
A	0.9	82°	0200	5.4	233°	1400
M	—	—	—	5.9	225°	1400
J	—	—	—	5.1	220°	1300
J	—	—	—	5.4	221°	1400
A	—	—	—	5.1	223°	1500
S	0.2	48°	0300	4.7	234°	1400
O	1.1	66°	0600	2.8	244°	1600
N	1.5	72°	0400	2.9	238°	1400
D	1.6	58°	2300	1.9	243°	1500

Maximum Offshore and Onshore Resultant Winds

Tables 1, 2, and 3 contain the monthly periods of offshore and onshore air flow for each site during 1972. The azimuths give the direction from which the winds are coming. From an examination of all three tables, the lack of an offshore flow during May, June, July, and August can clearly be seen. During this time interval the offshore movement is usually replaced by a weak air current which parallels the coast. However, the hour at which the maximum offshore flow does occur at each site throughout the year seems to be a function of geographic position. Anaheim's largest monthly maximum winds are found in the early morning hours at either 0600, 0700, or 0800 h, but the other two locations also record some monthly maximums at earlier hours. Thus, at Costa Mesa and La Habra there is no simple discernible pattern to the times that maximum offshore flow occurs.

On the other hand, the onshore flow exists in all the months examined at each of the sampling locations. The largest monthly maximums are found mainly during the summer months of May, June, July, and August. These maximum values occur between the hours of 1200 and 1600 h, although the highest frequency is generally recorded between the hours of 1300 and 1500 h.

Another unique characteristic of the individual monthly onshore wind maximum is that from January through April there is a speed increase associated with a clockwise vector rotation. For example, at Anaheim (Table 2) the directions for the monthly maximums are as follows: a) 196° (January), b) 218° (February), c) 221° (March), d) 226° (April). However, from April to May this clockwise motion ceases and a prevailing backing movement is noted at all locations. Also, the summertime monthly maximum sea breeze values at each particular site do not exhibit a great deal of variation in their flow orientation.

Summary

A description of the seasonality of the onshore-offshore flow in coastal southern California has been presented in this study. Generally, the land breeze is strongest in the winter months, while in the summer the land breeze effect merely reduces the night time velocity without reversing the direction. In winter the offshore flow is further characterized by two distinct flow patterns which usually have counter rotational characteristics through time (e.g. in December). These contrary flow systems are likely the end product of various forcing functions affecting coastal air flow. The stagnation point between these two wintertime land breeze systems at each particular site occurs in the late evening or early morning hours (e.g., 0100 and 0200 h). As mentioned by Staley (1957), these stagnation points might represent changes in the inertial oscillation which is related to alterations in frictional force.

In essence, then, the backing of the onshore hourly resultant winds (e.g. La Habra; July) could result from several possible factors including: a) the effects of the general flow; b) the diurnal changes in air stability; c) the modification and interactions caused by the slope winds of the nearby mountains (e.g., San Gabriel, San Bernardino, and Santa Ana); and d) the alterations brought about by pressure fluctuations. The modification by each of these possible factors can only be ascertained by a more detailed study of the climatology-meteorology of the Los Angeles Basin and its environs.

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DOPA Decarboxylase Activities and Potassium Stimulation of Lateral Cilia on the Gill of *Mytilus edulis*

I. A Response to DOPA Decarboxylase Inhibitors and Chemical Sympathectomy

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Abstract.—DOPA decarboxylase and potassium stimulation of ciliary activity was measured in the gill of *Mytilus edulis*. DOPA decarboxylase inhibitors (STH, and α-methyl-DOPA) decreased the decarboxylase activity in extracts of gill with subsequent enhancement of potassium stimulation of ciliary activity. Intramuscular injection of STH and α-methyl-DOPA caused a gradual decrease in the DOPA decarboxylase and green-fluorphore activities with an increase in lateral ciliary activity in response to potassium stimulation. Recovery was observed ten days after a single dose of α-methyl-DOPA. Intramuscular injection of 6-OH-DOPA caused a rapid decrease in the DOPA decarboyxlase and green-fluorophore activities with a rapid increase in lateral ciliary activity in response to potassium stimulation. However, there was a decrease in all three parameters to near zero activity within 10 days.

This study shows that potassium enhancement of lateral ciliary activity is correlated with and may depend on the amount of DOPA decarboxylase in the gill. A decrease in this enzyme results in a potentiation of the potassium effect on lateral ciliary activity.

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Among the many physiologic substances that can be extracted from ciliated cells, none has been shown to have more profound or more diverse effect on ciliary activity than the simple inorganic cations (Gosselin, 1966). Potassium effects on cilia are especially ubiquitous (Aiello, 1960). Furthermore, addition of this cation to the perfusates alters the daily pattern of mussels (Koshtoyants and Salanki, 1958). Catecholamines are present in the gill. Gills were found to metabolize L-[^{3}H] tyrosine and L-[^{3}H]DOPA to [^{3}H]DA (Paparo and Finch, 1973; Paparo and Tate, 1973). The purpose of this study is to examine the relationship between DOPA decarboxylase activity and potassium stimulation of ciliary beating.

Materials and Methods

All experiments were performed on the marine mussel *Mytilus edulis*. Gill preparations were dissected using the technique of Aiello (1960). DOPA decarboxylase activity assays were performed in 5-ml test tubes on extracts of visceral ganglion or gill tissue. For the visceral ganglia assays 0.05 ml of homogenate (20–25 visceral ganglia, average weight 105 mg), 0.85 ml of phosphate buffer, and 0.1 ml of 0.01 M DL-[1-^{14}C] DOPA (total radioactivity, 1.6×10^6 c.p.m.) were added to the test tube. For gill tissue assays 0.1 ml of gill homogenate (5–10 gill pieces, average weight 1.0 mg), 0.80 ml of phosphate buffer, and 0.1 ml M DL-[1-

Table 1. Effect of in vivo administration of STH on the average rate of lateral ciliary beating in response to potassium stimulation and on the DOPA decarboxylase activities in the gills.

Day after administration		Lateral ciliary beating (beats per second)		DOPA decarboxylase (units per g tissue)	Green fluorophore (μ amperes)
Control and experimental		Before potassium stimulation	After potassium stimulation	Gills	Gills
0	Control	5.1 ± 0.8	16.3 ± 1.1	172 ± 3	18.1 ± 1.2
	Experimental	6.4 ± 1.3	14.9 ± 1.7	170 ± 6	15.6 ± 0.9
1	Control	4.8 ± 0.7	17.2 ± 1.8	169 ± 5	16.3 ± 0.4
	Experimental	6.9 ± 0.9	15.6 ± 0.9	169 ± 8	16.8 ± 1.3
2	Control	4.9 ± 1.2	18.1 ± 0.9	168 ± 4	17.1 ± 1.6
	Experimental	7.0 ± 1.1	27.3 ± 1.0	162 ± 11	18.1 ± 0.9
3	Control	5.2 ± 0.6	18.9 ± 1.6	175 ± 8	14.9 ± 1.3
	Experimental	7.2 ± 0.9	27.3 ± 1.0	141 ± 6	12.2 ± 0.8
4	Control	5.9 ± 1.0	16.7 ± 1.9	164 ± 9	14.3 ± 1.3
	Experimental	6.9 ± 0.6	38.4 ± 1.3	132 ± 5	12.0 ± 0.2
5	Control	6.1 ± 0.9	16.3 ± 0.8	173 ± 3	18.9 ± 1.6
	Experimental	6.5 ± 1.0	47.6 ± 0.6	115 ± 4	8.9 ± 1.2
6	Control	5.3 ± 0.3	20.1 ± 1.9	173 ± 9	15.6 ± 0.5
	Experimental	6.7 ± 0.8	58.1 ± 0.8	71 ± 6	6.7 ± 0.3
7	Control	5.8 ± 0.5	19.13 ± 1.4	175 ± 5	17.9 ± 0.6
	Experimental	7.4 ± 0.3	61.1 ± 1.3	49 ± 2	5.2 ± 0.2
8	Control	4.7 ± 0.3	16.9 ± 1.0	176 ± 7	16.8 ± 0.9
	Experimental	7.8 ± 0.8	71.8 ± 2.1	51 ± 8	4.8 ± 0.6
9	Control	5.3 ± 0.7	17.3 ± 0.6	166 ± 8	19.1 ± 0.4
	Experimental	7.3 ± 0.9	76.3 ± 1.8	52 ± 4	4.9 ± 0.1
10	Control	6.3 ± 0.7	16.9 ± 1.2	169 ± 5	16.3 ± 1.2
	Experimental	7.4 ± 0.4	75.1 ± 1.1	47 ± 3	4.8 ± 0.2

^{14}C]DOPA were added to the test tube. The test tubes were stoppered with rubber covers, from each of which was suspended a well containing 0.1 ml of 1 M KOH as a CO_2 trap. The extracts were incubated at 37°C for 15 minutes. The reaction was terminated by injecting 0.2 ml of 1 M H_2SO_4 solution through the rubber cover to release CO_2 from the main solution. The test tubes were placed on a reciprocating shaker for 45 minutes. The well containing the trapped $^{14}CO_2$ was then dipped in 10 ml of liquid scintillation medium and the radioactivity was determined in a liquid scintillation counter. Counts on heat-inactivated extracts were performed simultaneously.

Additional decarboxylase assays were run in the presence of aromatic amino-acid decarboxylase inhibitors: α-methyl-DOPA (DL-α-methyl-3, 4-dihydroxy-phenylalanine) $10^{-3}M$; STH (N'(DL-seryl)-N^2-(2,3,4 trihydroxybenzl)hydrasine) $10^{-4}M$; 6-OH-DOPA (6-OH-methyl-3,4-dihydroxyphenylalanine) $10^{-3}M$.

The isolation of gill preparations and subsequent measurement of average rate of beating in beats/sec. by calibrated stroboscopic light follow the procedure of Paparo and Aiello (1970). The localization of the green-fluorophore in the gill was accomplished by means of the fluorescence-histochemical method. Relative measurement of the green fluorophore in μ amperes were made with a Leitz MPV11

Table 2. Effect of in vivo administration of α-methyl-DOPA on the average rate of lateral ciliary beating in response to potassium stimulation and on the DOPA decarboxylase activities in the gills.

Day after administration		Lateral ciliary beating (beats per second)		DOPA decarboxylase (units per g tissue)	Green fluorophore (μ amperes)
Control experimental		Before potassium stimulation	After potassium stimulation	Gills	Gills
0	Control	8.6 ± 1.2	19.5 ± 0.9	169 ± 1	15.2 ± 0.9
	Experimental	7.0 ± 0.3	17.9 ± 1.3	159 ± 6	21.3 ± 0.8
1	Control	7.7 ± 0.9	21.2 ± 0.8	180 ± 2	16.3 ± 1.2
	Experimental	6.9 ± 0.8	18.3 ± 1.0	164 ± 4	20.4 ± 0.3
2	Control	8.1 ± 0.7	18.9 ± 0.7	171 ± 3	16.0 ± 1.1
	Experimental	6.8 ± 1.0	17.1 ± 0.8	158 ± 5	19.1 ± 0.8
3	Control	7.1 ± 1.2	19.2 ± 1.1	171 ± 1	17.3 ± 0.9
	Experimental	6.1 ± 0.9	35.3 ± 0.9	131 ± 2	17.2 ± 0.8
4	Control	6.9 ± 0.9	17.6 ± 0.9	168 ± 2	21.0 ± 2.1
	Experimental	5.9 ± 1.0	49.1 ± 0.8	129 ± 6	15.1 ± 1.2
5	Control	6.3 ± 1.3	18.9 ± 1.2	161 ± 3	17.3 ± 1.3
	Experimental	6.2 ± 0.8	78.2 ± 0.9	101 ± 4	10.2 ± 0.3
6	Control	7.9 ± 0.9	22.3 ± 0.7	164 ± 2	17.2 ± 1.4
	Experimental	5.8 ± 0.9	81.9 ± 2.1	72 ± 1	8.2 ± 1.0
7	Control	7.6 ± 1.1	19.2 ± 0.8	166 ± 1	17.0 ± 0.9
	Experimental	5.7 ± 0.7	69.1 ± 1.8	98 ± 2	10.2 ± 0.8
8	Control	8.2 ± 1.3	18.9 ± 1.1	167 ± 1	16.9 ± 0.7
	Experimental	6.9 ± 0.9	42.1 ± 1.4	119 ± 3	15.8 ± 0.7
9	Control	9.1 ± 1.2	19.2 ± 1.0	177 ± 3	17.3 ± 1.1
	Experimental	6.8 ± 0.5	29.3 ± 1.3	127 ± 3	22.1 ± 0.9
10	Control	8.4 ± 0.7	20.9 ± 0.9	180 ± 4	17.9 ± 1.3
	Experimental	7.2 ± 0.7	21.1 ± 2.3	145 ± 2	25.1 ± 0.8

system equipped with a photomultiplier and digital print-out apparatus (Paparo and Murphy, 1975). Potassium chloride (160 mM) was added to the isolated gill preparation.

Results

Intramuscular injection of STH significantly reduced the DOPA decarboxylase in the gill from 170 ± 6 (mean ± standard error) to 47 ± 3 within 10 days after administration ($P < 0.001$). Catecholamine levels within the gill measured by relative amounts of the green-fluorophore in μ amperes also were significantly reduced from 15.6 ± 0.9 to 4.8 ± 0.2 ($P < 0.01$). After 10 days administration of STH, potassium increased the basal rate of beating by about ten times. There was no significant change in the basal rate of beating during the ten day observation period ($P > 0.85$; Table 1).

In vivo administration of α-methyl-DOPA produced maximal potassium enhancement of ciliary activity at 6 days postinjection. At this time, the DOPA decarboxylase and green-fluorophore activities were at their lowest levels in the gill. There was subsequently a gradual increase in both the DOPA decarboxylase and fluorophore activities. This also marked a decrease in the cilioexcitatory effect

Table 3. Effect of in vivo administration 6-OH-DOPA on the average rate of ciliary beating in response to potassium stimulation and the DOPA decarboxylase activities in the gills.

Day after administration		Lateral ciliary beating (beats per second)		DOPA decarboxylase (units per g tissue)	Green fluorophore (μ amperes)
Control experimental		Before potassium stimulation	After potassium stimulation	Gills	Gills
0	Control	8.1 ± 0.3	19.9 ± 0.8	189 ± 2	20.1 ± 0.3
	Experimental	9.9 ± 0.9	26.4 ± 1.1	179 ± 3	22.2 ± 0.9
1	Control	7.5 ± 0.8	18.2 ± 0.9	181 ± 5	19.2 ± 1.1
	Experimental	8.9 ± 0.9	45.1 ± 0.7	132 ± 1	14.1 ± 0.6
2	Control	7.9 ± 0.5	18.8 ± 0.9	188 ± 4	18.8 ± 1.4
	Experimental	7.8 ± 1.2	89.8 ± 1.2	73 ± 6	9.2 ± 0.8
3	Control	7.5 ± 0.7	20.5 ± 0.5	169 ± 1	17.2 ± 1.5
	Experimental	6.9 ± 0.8	19.2 ± 0.9	36 ± 8	5.1 ± 0.3
4	Control	6.8 ± 0.8	18.9 ± 0.5	158 ± 2	18.1 ± 0.9
	Experimental	6.8 ± 0.9	11.2 ± 0.9	19 ± 1	3.1 ± 0.2
5	Control	7.1 ± 0.6	21.9 ± 0.8	168 ± 1	17.1 ± 0.8
	Experimental	6.8 ± 0.9	6.3 ± 0.6	12 ± 1	2.2 ± 0.1
6	Control	5.9 ± 0.5	18.9 ± 0.6	172 ± 3	16.9 ± 1.2
	Experimental	3.9 ± 0.7	3.1 ± 0.9	6 ± 1	1.0 ± 0.3
7	Control	6.3 ± 1.3	22.3 ± 0.9	157 ± 5	16.8 ± 1.3
	Experimental	2.1 ± 0.5	1.9 ± 0.5	1 ± 0	0.6 ± 0.2
8	Control	6.5 ± 0.9	21.9 ± 0.3	162 ± 6	17.1 ± 1.7
	Experimental	2.0 ± 0.3	1.8 ± 0.1	1 ± 0	0.2 ± 0.2
9	Control	6.9 ± 1.2	23.1 ± 0.5	168 ± 4	17.9 ± 1.3
	Experimental	1.0 ± 0.2	0.9 ± 0.2	0 ± 0	0.1 ± 0
10	Control	7.5 ± 0.9	21.7 ± 0.8	173 ± 5	18.1 ± 0.9
	Experimental	0.9 ± 0.1	0.7 ± 0.3	0 ± 0	0.0 ± 0

of potassium to levels previously observed at zero time after injection of α-methyl-DOPA. There was no significant alteration in the basal rate of beating during the course of the experiment ($P > 0.80$; Table 2).

Injection of 6-OH-DOPA, produced a rapid maximal potassium enhancement of ciliary activity in only 2 days with a significant decrease in DOPA decarboxylase and green-fluorophore activities ($P < 0.001$ and $P < 0.01$ respectively). After 2 days there was a rapid decrease in the basal rate of beating, potassium effect decarboxylase and green-fluorophore to near zero readings. This indicates a complete chemical sympathectomy (Table 3).

Discussion

The properties of the DOPA decarboxylase present in the gill of *Mytilus* are in some respects similar to those observed in mammalian tissues (Sourkeo, 1966). The lamellibranch enzyme is inhibited by the aromatic amino-acid decarboxylase inhibitors, STH and α-methyl-DOPA. The enzyme remains inhibited even on the tenth day postinjection with STH. However, this enzyme recovers after 6 days postinjection with α-methyl-DOPA. The potentiation of the cilioexcitatory effect with potassium in the presence of reduced decarboxylase activity is probably related to a decrease in the dopamine levels in the gill. This is indicated by a decrease in the green-fluorophore in the gills treated for fluorescence-histochemistry. Chemical sympathectomy by administration of 6-OH-DOPA (DeChamplain and Nadeau, 1971) results in an even greater decrease in the decarboxylase activity of the affected gills, which suggests that decarboxylase activity is associated primarily with the catecholamine-containing nerve fibers. Investigation has shown that the ratio of DOPA decarboxylations to 5-HTP decarboxylations is about 6:1 (Paparo and Tate, 1973). This is a similar ratio observed for the partially purified enzyme from hog kidney (Christenson, Dairnan, and Udenfriend, 1970). It must be pointed out, however, that since our studies were done with crude soluble extracts of the tissues, there is a possibility that separate enzymes, geared for the decarboxylation of DOPA and 5-HTP, may be present in lamellibranchs.

The decarboxylase studies are in agreement with the studies on the localization, metabolism, and content of catecholamines in this mollusc (Paparo and Finch, 1972), which showed natural green fluorescent varicose nerve fasicles in *Mytilus*. This mollusc was shown to metabolize L-[^{3}H]tyrosine to [^{3}H]DA. DA has also been found by Dahl, Falck, von Mecklenberg, Myhrberg, and Rosengren (1966) in the ganglia of *Mytilus* and other lamellibranchs. The inhibitory effects of DA have been observed in *Mytilus* (Paparo and Aiello, 1970). DA also has been shown to have inhibitory effects on the brain of the snail, *Helix aspersa* (Kerkut and Walker, 1961; Walker, Ralph, Woodruff and Kerkut, 1970). Recent studies in our laboratory indicate that DA has an inhibitory effect on neuronal activity in the visceral ganglion of *Mytilus* (Paparo and Hamburg, 1973).

Summary

This study shows that the enhancement of the cilioexcitatory effect with potassium depends on the decarboxylase activity in the gill. Since DOPA decarboxylations to 5-HTP decarboxylations are about 6:1 in the gill, the potentiation of the potassium effect is probably caused by decrease in DA stores in this tissue.

Acknowledgments

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Interbreeding Members of the *Sphyrapicus varius* Group (Aves: Picidae) in Oregon

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Abstract.—Evidence from specimens collected in south-central Oregon provides further support for considering *Sphyrapicus nuchalis* and *S. ruber* as distinct species of the *S. varius* group.

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The different forms of the *Sphyrapicus varius* group of sapsuckers have been variously treated as races by Grinnell (1901, 1937) and Howell (1952). *Sphyrapicus varius* and *S. ruber* have been treated as distinct species by Ridgway (1914) and Dickinson (1953). The American Ornithologists' Union Check-list (1957) considered the forms of the *S. varius* group as races. More recently, Short (1969) recognized the forms *S. varius, S. nuchalis*, and *S. ruber* (includes *S. r. daggetti*) as three distinct species since hybrids and parental forms are known to occur in zones of overlap. Devillers (1970), following Short (1969), discussed the interbreeding of the different forms and offered further reasons for regarding the forms as distinct species, based on additional information on specimens collected in California.

Browning (1973) reserved opinion on the taxonomic status of the *S. varius* group and followed the A.O.U. Check-list (1957) in maintaining the different forms as races. However, based on reconsideration of the status of the group and examination of additional specimens, I prefer to follow Short (1969) in considering the different forms as distinct species. The following summarizes the distribution of *S. ruber* and *S. nuchalis* in south-central Oregon.

Two species of the *S. varius* group breed in Oregon, *S. ruber* and *S. nuchalis*. The former breeds from the east slope of the Cascade Mountains west to the Coast Range and is represented by two races. *Sphyrapicus ruber ruber*, a dark-backed race, breeds in the Cascades from northern Oregon to southern Douglas County in the southern part of the state (Fig. 1). The nominate race also breeds in the Coast Range and is reported from every county along the coast of Oregon (Gabrielson and Jewett, 1940). The pale-backed race, *S. r. daggetti*, breeds in the mountains of the southern part of the state from Josephine County on the west side of the Cascades (Howell, 1952) east to western Klamath County (Fig. 1). The second species found breeding in Oregon, *S. nuchalis*, breeds in the mountains of the eastern part of the state west to the east slope of the Cascades (Howell, 1952) south to parts of central Oregon (Fig. 1). The range of *S. nuchalis* overlaps that of *S. ruber ruber* on the eastern slope of the Cascades in northwestern Deschutes County, and that of *S. r. daggetti* in Klamath County (Fig. 1). Hybridization occurs in both these regions.

Hybridization between *S. ruber ruber* and *S. nuchalis* has been discussed by Howell (1952). He reported specimens collected west of Sisters in Deschutes County (Fig. 1) that had varying characteristics of hybrids, as well as specimens with typical phenotypes of the two species. In addition to the specimens reported by Howell (1952) there are two specimens (AW 1042 and 3238) collected at Sisters

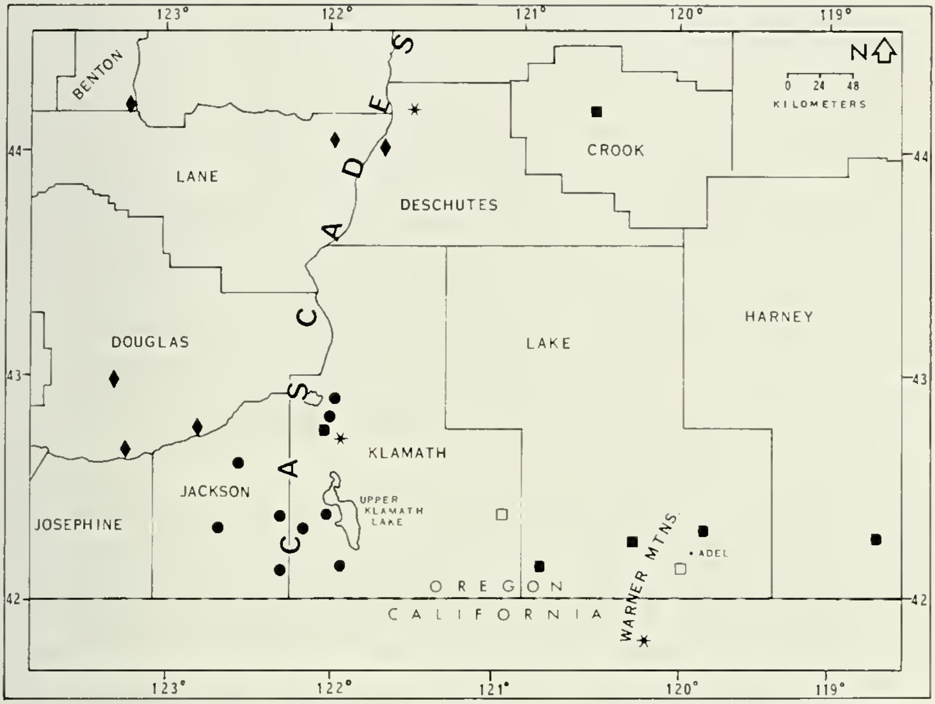

Fig. 1. Distribution of members of the *Sphyrapicus varius* group in south-central Oregon and northern California: ★ = collecting localities of specimens of hybrids and parental phenotypes of *S. ruber* and *S. nuchalis*, ◆ = *S. r. ruber*, ● = *S. r. daggetti*, ■ = *S. nuchalis*, and □ = hybrids between *S. ruber* and *S. nuchalis* but closer to the latter species.

that are intermediate between *S. r. ruber* and *S. nuchalis* (Howell's 1952, hybrid type 4). Other specimens that I examined from western Deschutes County are either typical *S. ruber* or *S. nuchalis*.

Hybridization between *S. r. daggetti* and *S. nuchalis* in northern California has been reported by Howell (1952) and Johnson (1970). A critical examination of specimens reveals that the two forms also interbreed in south-central Oregon.

Hybridization between *S. r. daggetti* and *S. nuchalis* occurs in the Ft. Klamath region (Fig. 1) on the east slope of the Cascades in Klamath County. A male (AW 1063) has a well-delineated hood that does not blend into the white breast feathers as in typical *S. r. daggetti*. Compared to other specimens from Ft. Klamath, AW 1063 appears somewhat intermediate between *S. nuchalis* and *S. r. daggetti*, but closer to the latter form. A female (CM 127466) has a greater amount of white in the rectrices that is usual in typical *S. r. daggetti* and is also similar to *S. nuchalis* in the white of the facial stripes. Although it is possible that CM 127466 is an extreme example of the range of individual variation in *S. r. daggetti*, I tentatively consider the specimen to be a hybrid equivalent to Howell's (1952) type 6. All other specimens from Ft. Klamath are typical *S. r. daggetti* except for an unreported specimen (CM 127429) of *S. nuchalis* collected 10 km northwest of Ft. Klamath on 28 June 1941. *Sphyrapicus nuchalis* is apparently rare near Ft. Klamath. Farner (1952) saw two near Ft. Klamath. An adult, an immature, and a set of eggs identified as belonging to this species were collected there by Bendire

Table 1. Examined specimens of *Sphyrapicus ruber*, *S. nuchalis*, and their hybrids from south-central Oregon.

n	Locality	*S. r. daggetti*	*S. r. daggetti* × *S. nuchalis*	*S. nuchalis* × *S. r. ruber*	*S. r. ruber*	*S. nuchalis*
3	Benton County				3	
7	Douglas County				7	
1	Lake County				1	
9	Jackson County	9				
6	Sisters, Deschutes Co.			2	2	2
3	14 km W Sisters				3	
6	11 km NW Sisters			1		5
1	Three Sisters				1	
14	Ft. Klamath, Klamath Co.	10	2			2
5	10 km NW Ft. Klamath	4				1
1	Rocky Point, Klamath Co.	1				
2	8 km W Keno, Klamath Co.	2				
3	13 km SE Bly, Klamath Co.		1			2
2	Howard, Crook Co.					2
1	Drews Creek, Lake Co.					1
6	Warner Mountains, Lake Co.					6
2	32 km NE Adel, Lake Co.					2
14	23 km SE Adel, Lake Co.		4			10
1	Steens Mountains, Harney Co.					1

(Browning, 1973). Bendire (1888) considered *S. nuchalis* to be rare in the Ft. Klamath region, but stated that it breeds in sympatry with *S. r. daggetti* without observable interbreeding.

Most specimens from south-central Oregon in eastern Klamath County and in southern Lake County are typical *S. nuchalis* (Fig. 1, Table 1). A male (CM 127411) collected 13 km southeast of Bly in eastern Klamath County (Fig. 1) has reduced white back markings and the amount of white in the rectrices is reduced like that of typical *S. r. daggetti*. Howell (1952) stated that the amount of white on the back and in the rectrices is similar in *S. r. daggetti* and *S. nuchalis*; although, he added that the extent of white areas may be reduced in *S. r. daggetti*. In Oregon specimens of *S. r. daggetti* at least, the reduction of the amount of white appears to be a character of geographic variation with the white becoming reduced from east to west. Other specimens collected at the same locality are typical *S. nuchalis*.

Four of the series of 14 specimens (CMNH) from 23 km southeast of Adel in Lake County also depart from the average of individual variation found in *S. nuchalis*. These four specimens exhibit a greater amount of red into and beyond the black upper breast band and two of the four have red feathers in the face. Three specimens in the Adel series have the white of the back reduced as in typical *S. r. daggetti* from Oregon. One of the three specimens also has extensive amounts of red feathers in the black breast band. All other specimens examined from Lake County are typical *S. nuchalis*.

The characters of some of the specimens from near Bly and near Adel suggest either individual variation of *S. nuchalis* or possibly introgression of characters of

S. nuchalis and *S. r. daggetti*. Neither condition is here considered to be conclusive evidence of interbreeding of the two forms.

Other specimens from eastern Oregon, including the Warner Mountains, are typical *S. nuchalis*. Johnson (1970) collected one *S. nuchalis*, one *S. r. daggetti*, and a mated pair of hybrids (male, type 4; female, type 6) at Pine Canyon in the Warner Mountains, California, near the Oregon line (Fig. 1). Howell (1952) also found mated mixed pairs and hybrids in the Warner Mountain region of California.

Partial isolating mechanisms restricting gene exchange between parental phenotypes, and hybrids in a zone of overlap are criteria for considering members of the *S. varius* group as distinct species (Short, 1969). Zones of overlap and hybridization have been reported in California by Howell (1952), Johnson (1970), and Devillers (1970). Zones of overlap and hybridization in central Oregon (Howell, 1952) and in west-central Klamath County also suggest that the forms *S. nuchalis* and *S. ruber* should be considered distinct species.

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A New Species of Autolytus (Polychaeta: Syllidae) Commensal on a California Hydrocoral

John D. Wright and Keith H. Woodwick

Abstract.—A new species of polychaete of the genus *Autolytus* is described from the hydrocoral *Allopora californica*. The atokous stage lives on the surface of the hydrocoral within a blister of host origin. This type of host association was not previously known in the genus *Autolytus*.

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A new species of *Autolytus*, a syllid polychaete of the subfamily Autolytinae, was found in the hydrocoral *Allopora californica* Verrill. Only two other species of *Autolytus*, *A. ?cornutus* Agassiz and *A. varius* Treadwell, have been reported from California (Hartman, 1968). Hartman (1955) also reported an *Autolytus* sp.

The subfamily Autolytinae has been extensively studied by two workers: Imajima (1964, with O. Hartman, 1966) wrote two descriptive papers on Japanese autolytins; Gidholm (1963, 1965, 1967a, 1967b, and 1969) published on the taxonomy and biology of Scandanavian forms.

Materials and Methods

Specimens utilized in this study occurred in separate collections of hydrocoral from Farnsworth Bank off Santa Catalina Island and Gull Island off Santa Cruz Island, California. The Farnsworth Bank specimens were taken at a depth of over 18.4 m while the Gull Island material was from about 6.1 m.

All of the material examined for the descriptive portion of the present study was collected by the senior author at Gull Island and fixed in formaldehyde at the collecting site. Following fixation the material was transferred to 70% ethanol for examination and storage. Portions of hydrocoral with polychaete blisters were decalcified in dilute HNO_3, washed, post-fixed in osmium tetroxide, and then dehydrated by an ethanol series followed by propylene oxide. The material was then embedded in Spurr's epoxy-resin (Spurr, 1969). Sections (0.75 μm) were cut with glass knives on an LKB Ultratome III, transferred in a drop of water to a microscope slide, dried down on a hotplate, and hot-stained with Paragon epoxy tissue stain (Spurlock et al. 1966). A few thin sections were also cut from the same specimens, section-stained with uranyl acetate followed by lead citrate and examined with a Philips EM 300. Scanning electron microscopy was performed on specimens which had been dehydrated in ethanol, critical-point dried, shadowed with carbon followed by gold or gold-paladium, and examined with a Cambridge Stereoscan SEM.

Illustrations of setae are composites based on both phase-contrast and scanning electron microscopy. The trepan illustration is a composite from a through-focus series of light micrographs of an excised pharynx.

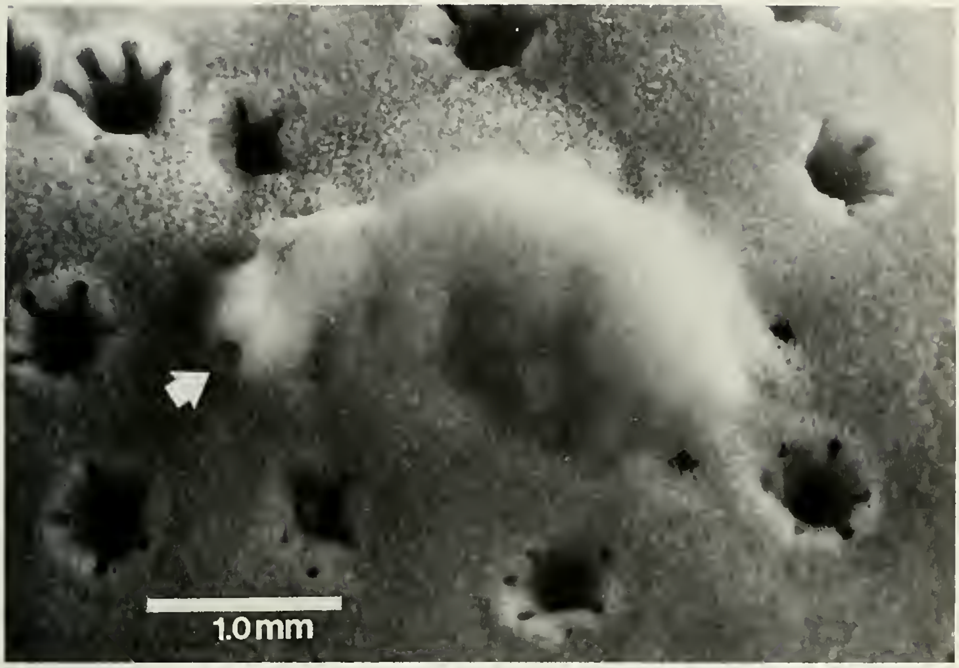

Fig. 1. Photomicrograph of the vermiform mound or blister of *Autolytus penetrans* on *Allopora californica*. Arrow indicates entrance to blister.

Autolytus (Regulatus) penetrans, n. sp.

Type material.—Holotype (Poly 1176), complete atokous specimen along with coral sample from which it came; Paratype (Poly 1241), male epitoke described below. Both deposited in the collections of the Allan Hancock Foundation, University of Southern California, Los Angeles.

Diagnosis.—*Autolytus penetrans* can be separated from other species by the following combination of characteristics: (1) trepan with nine regular teeth, (2) S-shaped pharynx, (3) generally smaller size (less than 3.0 mm), and (4) association with *Allopora californica*.

Description of atokous stage.—Atokous stage forming a blister on surface of hydrocoral; blister vermiform in exterior appearance with average length 3.0–4.0 mm, width 0.8 mm (Fig. 1); blister provided with pore or opening through which (it is assumed) worm feeds and releases stolonic buds (Fig. 1, arrow). Prostomium broader than long, possessing two pairs of red lenticular eyes, trapezoidally arranged, with anterior pair slightly larger and farther apart; size and length of antennae, tentacles, and cirri variable due to preservation (but some generalizations are appropriate): median antenna, located just forward of and between anterior pair of eyes, longer than lateral antennae; lateral antennae arising from anterior margin of prostomium; antennae irregularly annulate (Fig. 2).

Two pairs of anteriorly directed, tentacular cirri arising from anterolateral margin of peristomium; dorsal tentacular cirrus slightly shorter than lateral antennae, not annulate; ventral tentacular cirrus as long as or longer than median antenna, irregularly annulate (Fig. 2); ventral segmental cirri absent; dorsal segmental cirri

Fig. 2. Scanning electron micrograph of anterior view of *Autolytus penetrans*.

short, generally not articulated, and showing tendency for reduction in size in posterior region of body; nuchal epaulettes not observed in preserved material (even after otherwise obscurring antennae or cirri had been removed); S-shaped pharynx leading to proventriculus of about four segments long, normally located within setigers 4–8 (in one specimen the proventriculus had about 26 rows of muscle bands, and a cross section of another had 25 radially arranged muscle bundles); pharynx terminating distally in a ring of five rather blunt papillae (in several preserved specimens the trepan was located at the posterior edge of the first setiger, but in others at the posterior margin of the peristomium or within the second setiger); dorsal epidermal gland of Gidholm's (1967a) sphaerulate A-type observed in peristomium.

Each setigerous segment with pair of dorsoventrally aligned setal fasicles consisting of 4–9 setae per side; single dorsalmost bayonet-type setae (of the thick type following terminology of Gidholm, 1967a) often present in each bundle (Fig. 3B); remainder of setae compound bidentate (Fig. 3D).

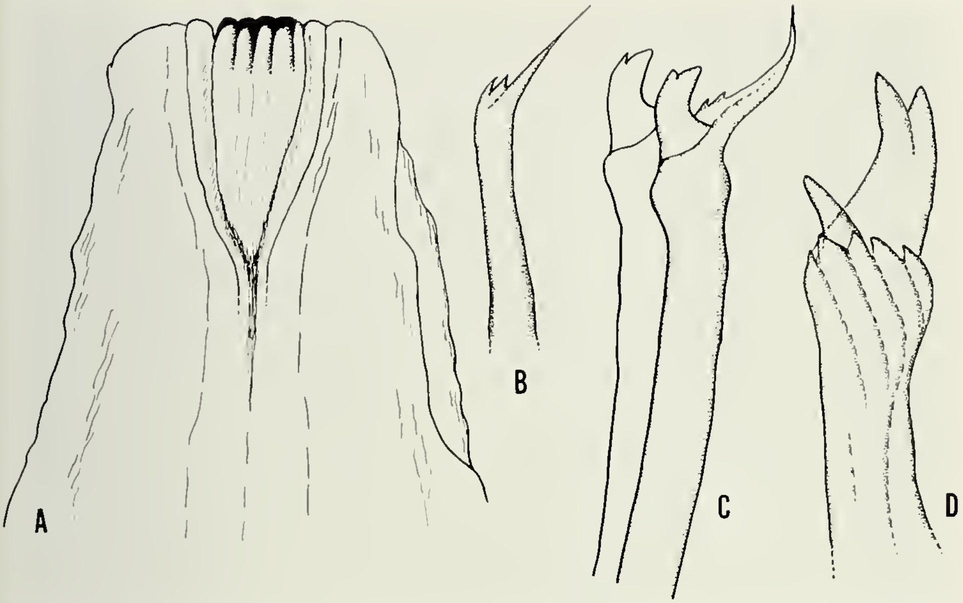

Fig. 3. *Autolytus penetrans*: A. Trepan, B. Bayonet seta, C. Progenitor seta, D. Compound bidentate seta.

A complete non-stolonic atokous specimen measured 2.5 mm long by about 0.5 mm wide and consisted of 38 setigerous followed by 5 non-setigerous segments. The color of the specimens preserved in formaldehyde and stored in 70% alcohol is white, but the eyes retain a reddish pigmentation.

Description of epitokous stage.—Several apparently immature epitokes of *Autolytus penetrans* were found within coral blisters. One of these possessed swimming setae. Except for enlargement of the anterior pair of eyes, the presence of swimming setae, no obvious proventriculus, and sperm duct glands in segments two through five, they differed little in general appearance from the atokous form. A more mature male or "Polybostrichus" stolon obtained from a blister which also contained an atokous individual is described as follows: specimen about 2.0 mm in length, consisting of prostomium, peristomium, and 36 setigerous segments, plus terminal non-setigerous segment; prostomium with 2 bifid antennae arising from anterior ventrolateral angles and 2 enlarged anterior eyes; other dorsal prostomial appendages broken off or absent; tentacular cirri of peristomium of undetermined length; setiger 1 with fasicle of compound setae including bayonet seta similar to atokous variety; setigers 2–5 with same setal arrangement but also containing sperm duct glands; setigers 7–25 with larger but normally-shaped atokous seta on neuropodia and long swimming setae on enlarged notopodia; setigers 26–35 distinctly smaller, bearing only normal atokous fasicles; worm terminating in a nonsetigerous segment with two blunt ovoid appendages.

Discussion

Autolytus sp. (Hartman, 1955) was dredged from fine mud material at a depth of 732 m and from mud and sand at 31 m in the San Pedro Basin, California. *Autolytus cornutus* and *A. varius* were collected intertidally as epitokes. Pettibone

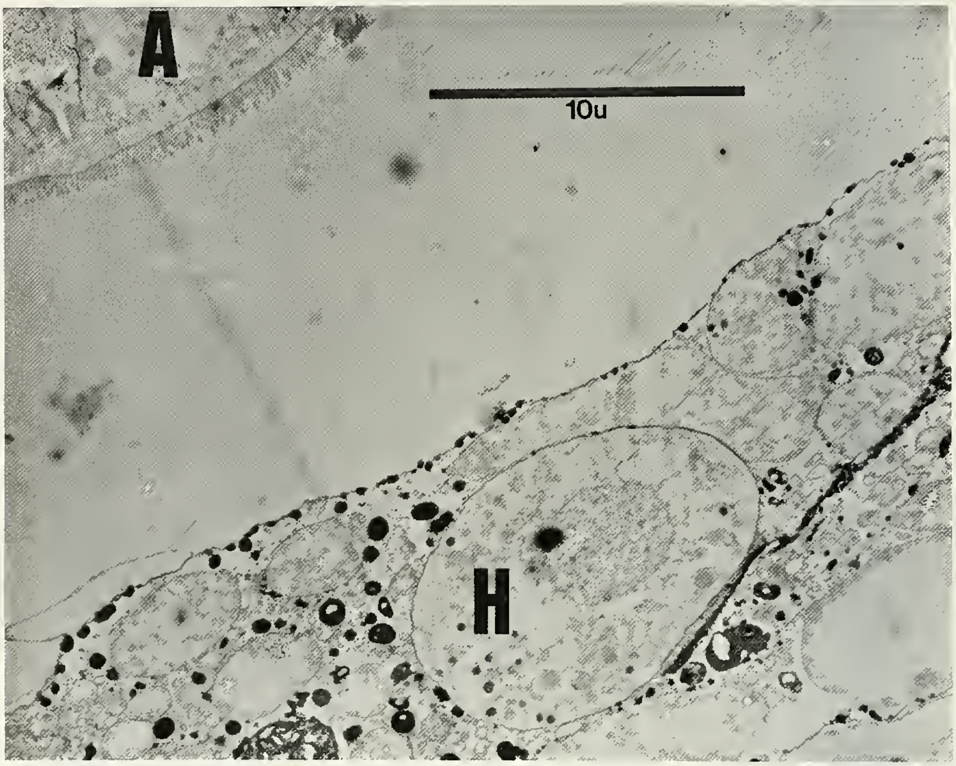

Fig. 4. Transmission electronmicrograph of the inner lining of the coral blister demonstrating its cellular make-up. A = *Autolytus penetrans*, H = hydrocoral.

(1963) reported that *Autolytus cornutus* constructs cylindrical tubes attached to algae and branches of hydroids, but she mentioned no species of *Autolytus* associated with hydrocorals. Hartman (1954) reported *Autolytus* sp. from the lagoon side of Rigili Island, Eniwetok Atoll from blocks on the reef flat close to the beach rock belt. The type of association with living coral, if any, was not mentioned.

The present species forms a blister on the hydrocoral. Although this habitat is unusual for *Autolytus* forms, blister forming polychaetes are not unique. Some polydorids and other polychaetes actually drill the shell. Blake and Evans (1973) reported on the burrowing activities on polydorid worms (Spionidae) and have described what they call polydorid "mud-blisters" on the surface of mollusks to which the mollusk reacts by secreting over the mud a roof of conchiolin and later a layer of nacreous material. The worms live within the mud-filled blister which communicates with the surface. The burrow eventually becomes U-shaped or modified U-shaped. Blake and Evans (1973) also stated that the method of burrow formation is independent of setal structure or position in *Polydora*. They suggested that chemical methods are most likely involved. While they mentioned the boring or blistering activities of *Polydora* and related forms into corals and hydrocorals, they also stated that there has been no research on the biology of coral infesting polydorids.

Ostarello (1973), in her study of the natural history of the hydrocoral *Allopora californica*, listed three obligate commensals including the following: *Balanus* *nefrens* Zullo, a barnacle; *Polydora alloporis* Light, a spionid polychaete; and *Pedicularia californica* Newcomb, an ovulid snail. The first two commensals were also found in material collected for the present study. The minute size of the blister of *Autolytus penetrans* and of the worm itself has probably led to this commensal form going unnoticed until this time.

The worm apparently penetrates the surface of the hydrocoral resulting in a hyperplasia of cellular and calcareous material to produce the characteristic vermiform mound. An electron micrograph (Fig. 4) reveals the cellular makeup of the blister lining in spite of the formaldehyde fixation and acid decalcification. Light microscopy reveals that the mound is also lined by a layer of mucus, presumably the worms, but there is no evidence of a mucus tube such as described by Pettibone (1963) for *A. cornutus*. The blister may be located almost anywhere on the living hydrocoral with no specific association with the coral polyps. Occasionally a blister is encountered with the lumen oriented directly perpendicular to the surface of the hydrocoral. It could not be determined if this was the result of expanding the depression left by a polyp or entirely the result of the worm's activities.

Imajima (1966) made extensive use of trepan teeth in *Autolytus* taxonomy. Following the pattern suggested by Imajima (1966) *Autolytus penetrans* has been assigned to the subgenus *Regulatus* on the basis of a trepan of nine regular teeth (Fig. 3A). *Autolytus (R.) convolutus* is the only other species in which only nine regular teeth are known. *Autolytus penetrans* differs in pharyngeal configuration having an S-shaped pharynx in contrast to the irregularly coiled pharynx of *A. convolutus.*

Because of its repeated collection from the hydrocoral *Allopora californica* from more than one locale and in different years, it is suggested that *Autolytus penetrans* is a well established species in this one habitat in California waters.

One additional general note is suggested by the appearance of the main seta in Fig. 3C. This seta could serve as the progenitor of the bayonet seta by loss of the distal, bidentate compound portion and of the compound bidentate by erosion of the bayonet portion. It would be interesting to determine if this is the actual pattern in *Autolytus penetrans* and, if so, whether it is characteristic of other more inclusive taxonomic groups.

Acknowledgments

The authors wish to thank Mr. Lance Hollister of Reseda, California who collected the original material, and Dr. Kristian Fauchald, Allan Hancock Foundation, University of Southern California, Los Angeles who provided advice on preparation of this paper.

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Taxonomic Notes on *Tantilla* (Serpentes: Colubridae) from Tropical America

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Abstract.—Distributional and taxonomic notes are given for eight species of the colubrid snake genus *Tantilla* from México, Guatemala, Costa Rica, Colombia, and Ecuador.

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In the course of ongoing studies on the systematics of the genus *Tantilla* from México, and Central and South America, we have accumulated noteworthy data on a number of species, most of which have been recently reviewed. We here take this opportunity to present these data.

We are indebted to the following curators for the loan of specimens in their care: William E. Duellman, Museum of Natural History, University of Kansas (KU); Olivier Reippel, Naturhistorisches Museum Basel, Switzerland (NMB); Douglas A. Rossman, Museum of Zoology, Louisiana State University (LSUMZ); John W. Wright, Los Angeles County Museum of Natural History (LACM); George R. Zug and Ronald I. Crombie, National Museum of Natural History, Washington, D.C. (USNM). We would also like to thank Donald E. Hahn, Cottonwood, Arizona, for the loan of a specimen from his personal collection and Norman J. Scott, Jr. for depositing a specimen from his personal collection in a permanent one.

Tantilla alticola (Boulenger)

During the course of studies on the *Tantilla melanocephala* group, we were sent some material of *Tantilla* from Costa Rica by Norman J. Scott, Jr., among which is a single specimen of *Tantilla alticola* (LACM 125561). This species was described from Colombia (Boulenger, 1903) and has been recorded only from that country (Niceforo Maria, 1942; Peters and Orejas-Miranda, 1970). The specimen reported upon herein thus constitutes not only a new record for Costa Rica, but for Central America as well.

The specimen from Costa Rica was collected 4 km SSW San Vito, Prov. Puntarenas at an elevation of 1,200 m on 29 July 1970 by Norman J. Scott. The snake is a male with the following scutellational characteristics: supralabials 6–7 (6th and 7th supralabials fused on left side of head), with the 3rd and 4th entering orbit; infralabials 6–6, four touching anterior chin shields, 4th largest, first pair broadly separated by contact of mental with anterior chin shields; preocular single, in narrow contact with postnasal; postoculars 2–2; temporals 1 + 1, both elongate; ventrals 133; anal plate divided; subcaudals 52+ (a few scales are missing from the end of the tail); dorsal scales in 15 rows throughout. The total length (minus the tip of the tail) is 298+ mm, the tail length is 71+ mm.

The dorsal coloration in alcohol is as follows: dorsum brown on the neck region grading to dark brown at midbody to almost black on the posterior body region, each scale outlined with darker pigment; dorsal coloration extends onto lateral edges of ventrals an increasing amount toward the posterior until on the posterior body region there are scatterings of darker pigment along the posterior edges of the ventrals on an otherwise cream-colored venter; underside of tail marked with narrow, broken line of dark pigment along the posterior edges of the subcaudals against a cream background; dorsum of head very dark brown with creamy tan pigment on the snout covering most of the internasals and prefrontals; a creamy tan complete collar occupies the posterior tips of the parietals and extends one dorsal scale length posterior to the parietals, the collar expands slightly laterally to merge with the cream color of the chin and is bounded posteriorly by a series of black spots, each occupying most of a dorsal scale, barely distinguishable from the groundcolor of the dorsum of the body; a pale preocular spot occupies the postnasal and most of supralabials 1 and 2; a dark subocular blotch present on supralabials 3 and 4; a postocular pale spot occupies supralabial 5 and the anterior third of supralabial 6, the posterior two thirds of the postoculars with a small extension onto the parietals posterior to the supraoculars.

The only other known specimens of *Tantilla alticola* are the three specimens that form the syntype series of *Homalocranium alticola* (Boulenger, 1903) and the two specimens that make up the syntype series of *Homalocranium coralliventre* (Boulenger, 1913). Amaral (1929) demonstrated the conspecificity of the two. The name *Tantilla alticola* is based on specimens from Santa Rita, north of Medellín, Colombia at an approximate elevation of 2,743 m, while the name *Homalocranium coralliventre* is based on material from Pena Lisa, near Condoto, Depto. Chocó, Colombia at an approximate elevation of 91 m. Although I have not examined this material, the descriptions given by Boulenger (1903, 1913) agree in all important particulars of scutellation and color pattern with that of the Costa Rican specimen.

Tantilla alticola, thus, is now known from low to intermediate elevations of southern Costa Rica and northwestern Colombia. Scutellational variation may be summarized as follows: prefrontals and second supralabials separated from one another by contact of postnasal and single preocular; postoculars 2; temporals 1 + 1; supralabials 6 to 7 (usually 7), with the 3rd and 4th entering orbit; first pair of infralabials separated by contact of mental and anterior chin shields; ventrals 133–149 (133–135 in two known males, 141 in one known female); anal plate divided; subcaudals 55–64 (59 in one known male, 56 in one known female). Maximum known total length is 330 mm.

Only three other species, *T. reticulata* (Niceforo Maria, 1942; Wilson and Meyer, 1971), *T. melanocephala* (Wilson and Mena, ms.), and *T. annulata* (see below), are known to occur in both Central and South America. *Tantilla reticulata* has a distribution reminiscent of the known distribution of *T. alticola*.

Tantilla annulata Boettger

Recently, through the courtesy of Ronald I. Crombie and Fran I. McCullough of the National Museum of Natural History, we had the opportunity to examine a specimen of *Tantilla annulata* (USNM 198714) from Ecuador. *Tantilla annulata* has been recorded previously only from the Central American countries of Nicaragua, Costa Rica, and Panamá, so the USNM specimen constitutes not only a new record for Ecuador but for the continent of South America as well.

Tantilla annulata was originally described from an unspecified locality in Nicaragua (Boettger, 1892) and, as noted by Wilson and Villa (1973), has not been rediscovered in that country. The Costa Rican distribution has been summarized by Scott (1969), who stated that *T. annulata* occurs from sea level to 850 m in the wet uplands and lowlands on both versants of the country. The known distribution in Panamá is based on three specimens reported by Dunn and Bailey (1939) from Cerro Bruja and Cana in the uplands of the Canal Zone and Darien, respectively, and by Dunn (1940) from Panama City. It should be noted that Peters and Orejas-Miranda (1970) erred in giving the distribution of *T. annulata* as "Nicaragua to Costa Rica." *Tantilla annulata* is now known to occur from low to moderate elevations of both versants from Nicaragua to Panamá and on the Pacific versant of northwestern Ecuador.

The specimen from Ecuador was collected at San Lorenzo, Prov. Esmeraldas, Ecuador, by M. Olalla in May 1959. It is a male with the following scutellational characteristics: supralabials 7–7, with the 3rd and 4th entering orbit; infralabials 6–6, four touching anterior chin shields; 4th largest, first pair separated by contact of mental and anterior chin shields; preocular single, in narrow contact with postnasal on left and barely separated on right; postoculars 2–2; temporals 1 + 1, both elongate; ventrals 140; anal plate divided; subcaudals 59; dorsal scales in 15 rows throughout. The total length is 224 mm, the tail length is 50 mm, and the tail length/total length ratio is 0.223.

The dorsal coloration in alcohol is as follows: dorsum pale orange with 12 black-bordered white bands on body and 4 on tail (counted on left side of body), all but first two bands on body and first on tail interrupted medially, the two halves longitudinally offset from one another; pale portion of each dorsal band about one-half to one scale long, the black portion at each end one to one and one-half scales long; each scale in orange groundcolor with a posteriorly placed black dot; venter immaculate cream except where black pigment of dorsum encroaches on lateral portion of ventrals to enclose ventrally the pale portion of each diad; dorsum of head black except for pale band across snout covering most of the internasals and anterior one-third of prefrontals, and extending laterally to the labial line; postocular pale spot present, covering anteroventral corner of anterior temporal, posterior portion of lower postocular, posterior quarter of supralabial 4, supralabial 5, and anterior quarter of supralabial 6; black head cap partially bounded posteriorly by short pale band about one-half scale in length, divided medially, the two halves separated by almost three dorsal scales; area between pale nape band and first diad on body paler than head cap but darker than dorsal orange body band.

Descriptional information on *Tantilla annulata* is limited. We are able to find in the literature data on only ten additional specimens (Dunn and Bailey, 1939; Dunn, 1940; Taylor, 1951, 1954). These data indicate a ventral range of 147–155 and a subcaudal range of 54–65. Available data on numbers of supralabials, infralabials, preoculars, postoculars, and temporals show agreement with the data for the Ecuadoran specimen. The first pair of infralabials may be in contact or not as are the preocular and postnasal. Maximum known total length is 590 mm. Body rings range from 11 to 14 and may cover the entire body or only a portion thereof.

The only notable distinction between the Ecuadoran specimen of *T. annulata* and those from Central America is in the number of ventrals (140 as opposed to

147–155). Such a difference is not surprising in view of the approximate distance of 760 airline km between the locality in Ecuador and the nearest locality in Panamá.

Tantilla canula Cope

Few specimens of this small *Tantilla* are available from the Yucatán Peninsula. Duellman (1965) reported one from Champotón, Campeche, which he stated was the third known specimen from the peninsula. The other two came from Chichén-Itzá and Libre Unión, Yucatán. During a trip in June 1974 to the Yucatán Peninsula, we secured two additional specimens of *Tantilla canula*, one of which (LSUMZ 28597) is from Centenario (near Silvituc), Quintana Roo and constitutes a new record for that state. The other specimen (LSUMZ 28598) came from Pisté, Yucatán.

Color notes in life are available for the specimen from Pisté and are summarized as follows: dorsum pale orange-brown grading to pale yellowish-brown laterally; a peppery effect is produced by the presence of dark brown reticulations on each dorsal scale; pale orange middorsal stripe present the length of body and tail (produced by a lack of dark reticulations on the middorsal scale row); venter white; dorsum of head brown with heavy dark brown reticulations, slightly paler on snout and posterior portions of parietals; side of head, except for supralabials, brown; supralabials gray with a frosting of white punctations; chin white, except for most of infralabials, which are pale gray with a frosting of white punctations.

The scutellation of this specimen falls within the range for the species. The other specimen is too badly damaged to make scale counts.

Tantilla cuniculator Smith

Tantilla cuniculator is a poorly known species from the Yucatán Peninsula. It was originally described as a subspecies of *Tantilla moesta* (Smith, 1939), an apparently unrelated species from the Yucatán Peninsula and El Petén region of Guatemala (Stuart, 1963), but was later raised to species level (Smith, 1942). Thus far, only four specimens have been reported (Smith, 1939; Duellman, 1965); all are females and are from the state of Yucatán.

We here report upon a fifth specimen (LSUMZ 28599), also a female, from the state of Quintana Roo, which represents a new record for that state. The specimen came from the vicinity of Pueblo Nuevo X-Can, a village near the common border of the state of Yucatán and Quintana Roo (Duellman, 1965, fig. 1). It was collected on 19 July 1974 by a local inhabitant.

Colors in life have not been described for this species and are here presented in detail, as follows: dorsum dark brown grading to slightly paler brown on first two dorsal scale rows, color of dorsum produced by black reticulations and tan and cream punctations on a brown background (visible only under scope), first two scale rows appear paler because of combined effect of a slightly paler groundcolor, slightly paler reticulations (dark brown), and more pale punctations; barely discernible pale lateral stripe on adjacent halves of rows 3 and 4, about as pale in color as first two scale rows but discernible because it is bounded below by dark brown stripe occupying lower half of scale row 3; lateral stripe most evident on neck, becoming progressively less evident posteriorly, but still barely evident at end of body, also barely evident the length of the tail; no evidence of a pale middorsal stripe; venter reddish-orange almost entire length of belly and tail, color becomes paler toward anterior end of body to a point where on the neck the color is pink with a frosting of white punctations; color of venter invades the dorsum on about the posterior third of body, especially evident on first four dorsal scale rows but also slightly tinging all dorsals in that area; dorsum of head a shade darker than dorsum of body, very dark brown with a few pale brown punctations; pale spot on snout, ocher (pale yellow-orange) in color, occupying upper half of rostral, most of internasals, except for the lateral vertex, and anterior half of prefrontals; middle portion of prefrontals pale orange-brown and lateral and posterior edges very dark brown; collar complete and beginning on posterior third of parietals and continuing 2½ scales posterior to parietals, crossing last supralabial; most of portion of parietals covered by collar pale orange-brown, which color also extends onto middle of posterior temporal; remainder of collar ocher, this color fading on lateral side of head into color of chin; preocular spot not evident as such, first three supralabials white anteriorly and dark brown posteriorly; fourth supralabial with triangular dark brown blotch (apex pointing ventrally) in middle of otherwise white scale; postocular pale spot on posterior half of 4th supralabial, all of 5th, anterior half of 6th, all of lower postocular, and anteroventral corner of anterior temporal; chin flesh-colored with white frosting; brown pigment present along labial edge of all supralabials, decreasing in amount posteriorly; iris reddish-orange dorsally grading to black (indistinguishable from color of pupil) ventrally; tongue gray, darker toward tips.

Scutellation for this specimen is as follows: supralabials 7–7, with 3rd and 4th entering orbit; infralabials 6–6, four touching anterior chin shields; preocular single, in broad contact with postnasal; postoculars 2–2; temporals 1 + 1; ventrals 153; anal plate divided; subcaudals 48; dorsal scales in 15 rows throughout. The total length is 193 mm, tail length is 38 mm, and the tail length/total length ratio is 0.197.

Tantilla cuniculator is known from five female specimens. In view of its scarcity, it appears useful to provide a summary of scutellational data: prefrontals and second supralabial separated from one another by contact of postnasal and single preocular; postoculars 2; temporals 1 + 1; supralabials 7, with 3rd and 4th entering orbit; infralabials 6–7, four in contact with anterior chin shields, first pair separated by contact of mental and anterior chin shields; ventrals 140–154 ($\bar{x}$ = 146.8) in females; and plate divided; subcaudals 48–53 ($\bar{x}$ = 49.8) in females. Maximum known total length is 193 mm.

Tantilla cuniculator is now known from three localities: Mérida and Pisté, Yucatán and Pueblo Nuevo X-Can, Quintana Roo.

The affinities of *T. cuniculator* have been poorly detailed. Originally described as a subspecies of *T. moesta*, to which it is only distantly related, it was later allied with *T. phrenetica* (=*T. schistosa phrenetica*) by Smith (1942). That association was made because both supposedly have a collar, a standard *Tantilla* habitus, no stripes on the dorsum, an elongate secondary temporal, and a dark dorsal coloration separated sharply from the ventral color. Smith (1962), however, placed *T. phrenetica* as a subspecies of *T. schistosa*. Thus, the relationships of *T. cuniculator* are still open to question.

It is evident from a survey of the groups of *Tantilla* that *T. cuniculator* bears most resemblance to the members of the *T. taeniata* group, an opinion shared by its describer, Hobart M. Smith (pers. comm.). This group has recently been revised (Wilson and Meyer, 1971). At the time of that revision, the *T. taeniata* group was characterized as *Tantilla* "having a light middorsal stripe and variable light markings on the nape." Since that time, however, an additional species belonging to the *T. taeniata* group has been described (Savitzky and Smith, 1971). This species, *T. briggsi,* lacks a pale middorsal stripe, as does *T. cuniculator.*

It appears that *T. cuniculator* belongs to the subgroup of the *T. taeniata* group which is characterized by having the pale lateral stripe located on the adjacent halves of dorsal rows 3 and 4 (Wilson and Meyer, 1971), as is also the case with *T. briggsi* (Savitzky and Smith, 1971). That subgroup also contains *T. jani, T. striata,* and *T. taeniata. Tantilla striata* does not appear to be closely related to *T. cuniculator* because of great differences in pattern (collar reduced to two nuchal spots) and subcaudal number (48–53, $\bar{x}$ = 4,918 in *T. cuniculator*, ♀♀, 31–34, $\bar{x}$ = 33.1 in *T. striata*, ♀♀). *Tantilla jani* also appears not to be a close relative because of differences in pattern (each scale of rows 5 through 7 has a diffuse median stripe; anterior and posterior edges of collar not clearly defined) and numbers of subcaudals (38–47, $\bar{x}$ = 42.3 in *T. jani*, ♀♀). *Tantilla jani* usually has the first pair of infralabials in contact, whereas *T. cuniculator* does not. But there are resemblances in numbers of ventrals (140–154, $\bar{x}$ = 146.8 in *T. cuniculator*, ♀♀; 141–153, $\bar{x}$ = 148.5 in *T. jani*, ♀♀). *Tantilla briggsi*, although exhibiting resemblances in pattern (lack of a middorsal pale stripe, poorly-defined pale lateral stripe) appears distantly related because of the very high number of ventrals. The male holotype of *T. briggsi* has 172 ventrals and since females generally have greater numbers of ventrals, *T. briggsi* females probably have 30 to 40 more ventrals than do *T. cuniculator* females. The subcaudal count (68) is also high in *T. briggsi,* similar to those in male *T. taeniata* (63–67), but female *T. taeniata* have 58–64 subcaudals, which does not overlap the range of *T. cuniculator.* Thus, *T. briggsi* females probably have more subcaudals than do female *T. cuniculator.*

Tantilla taeniata appears to be the most likely candidate for close relationship with *T. cuniculator* (Savitzky and Smith, 1971, also concluded that *T. taeniata* is the closest known form to *T. briggsi*). There are important differences, however, as *T. taeniata* has more ventrals (158–178, $\bar{x}$ = 165.4 in *T. taeniata*, ♀♀) and subcaudals (58–65, $\bar{x}$ = 62.0, in *T. taeniata*, ♀♀). Also *T. taeniata* has the paraventral dorsal scale row divided into a dark upper and a pale lower half, a character not shared with *T. cuniculator.* Nonetheless, on the basis of reasoning similar to that used by Savitzky and Smith (1971) to defend their position that *T. taeniata* is the closest known relative of *T. briggsi,* we are of the opinion that *T. taeniata* is also the closest known form to *T. cuniculator.*

The above disposition also makes reasonable zoogeographic sense. *Tantilla taeniata* is a wide-ranging form that appears to be close to the stem from which *jani* and *striata* (as well as *T. briggsi*) developed (Wilson and Meyer, 1971). It seems reasonable to envision *T. cuniculator* becoming adapted to and isolated within the subhumid vegetational assemblage that developed on the northern end of the Yucatán Peninsula with the close of the Pleistocene (Duellman, 1966; Savage, 1966).

Tantilla deppei (Bocourt)

Until the specimen (KU 140078) reported here came to light, *T. deppei* was thought to be confined to the Mexican state of Morelos (Wilson and Meyer, ms.).

This specimen, which was collected 5 mi (by road) N of turnoff to Tlaxiaco on Mexico Hwy. 190, Oaxaca, México, represents a range extension of approximately 233 km to the southeast.

The scutellational data agree with that for specimens from Morelos. The coloration agrees with that of other specimens except that the pale border of the spatulate anterior extension of the dark middorsal stripe onto the head is not present.

Tantilla flavilineata Smith and Burger

Wilson and Meyer (1971) recently reviewed the *T. taeniata* group to which *T. flavilineata* belongs. They examined a total of 11 specimens, and since that time an additional specimen (DEH 9882) has come to light. The specimen is from 16.4 km N Mexico Hwy. 190 (Ciudad Oaxaca) on Mexico Hwy. 175, Oaxaca, a locality intermediate to the other known localities (vicinity of Nochixtlán and Mitla). The scutellational data for DEH 9882 fit within the ranges given by Wilson and Meyer (1971).

Tantilla jani (Gunther)

This species was also recently reviewed by Wilson and Meyer (1971). They examined specimens from two localities in Guatemala. Three additional specimens (NMB 2114–16) from Guatemala have been found. These specimens are from the vicinity of Mazatenango, Depto. Suchitepequez, approximately 9 km from a locality (Finca El Cipres) from which Slevin (1939) reported a number of specimens. All data on these specimens are in accord with that published by Wilson and Meyer (1971), with the exception of one female specimen (NMB 2116), which has 155 ventrals, 2 scales outside the range given in their paper. In addition, this same specimen has the prefrontal and supralabials in contact on both sides of the head, an unusual condition in *T. jani*.

Tantilla reticulata Cope

In their revision of the *Tantilla taeniata* group, Wilson and Meyer (1971) gave the range of *T. reticulata* as "low and moderate elevations of the Atlantic versant from southeastern Nicaragua to Panamá." At that time they were unaware of the occurrence of *T. reticulata* in Colombia (Niceforo Maria, 1942). Niceforo Maria (1942) reported *T. reticulata* from Quibdó, Depto. Chocó and the Río San Juan, which runs through the departments of Caldas and Chocó and between those of Chocó and Valle. We have not examined these specimens but until evidence to the contrary is forthcoming we assume the identification to be correct and amend the statement of distribution for *T. reticulata* to read "Low and moderate elevations of the Atlantic versant of Central America from southeastern Nicaragua to Panamá and the Atlantic and Pacific versants of northwestern Colombia."

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Research Notes

A New Genus and Species of Polychaete (Family Capitellidae) from Southern California

This addition to the thirty genera of Capitellidae (Hartman, 1947, 1959, 1965) is based upon specimens collected in a study of southern California sandy beaches (Patterson, 1974) funded by the Sea Grant Office of the Department of Commerce Grant #2-35227. The author wishes to express thanks for permission to use the material. Dr. Dale Straughan provided funds for the study. All specimens are deposited in collections of the Allan Hancock Foundation (AHF), University of Southern California.

Amastigos, n. gen.

Type species *Amastigos acutus*, n. sp.

Diagnosis.—Neuropodial and notopodial hooded hooks present in both thorax and abdomen; capillary setae entirely absent; prostomium followed by a short peristomium; thorax consisting of eight setigers with an abrupt transition from thorax to abdomen at setiger nine; no visible branchia or nephridial papillae; posterior end terminating in a short conical pygidium.

Amastigos is most closely related to *Bucherta* Rullier (1965) in lacking capillary setae in both thorax and abdomen. *Amastigos* differs from *Bucherta* in the abrupt and distinct change from the thorax to abdomen, lack of visible branchial structures or nephridial papillae, structure of the hood covering the setae, and general shape of the body.

Etymology.—The generic name derives from the lack of capillary setae.

Amastigos acutus, n. sp.
Figs. 1,2

Material.—Holotype, AHF Poly 1239; paratype, AHF Poly 1240; Hope Ranch, near Carpinteria, California, on sandy beach; 35 additional, small individuals.

Description.—Length of holotype 38.0 mm, maximum width 0.5 mm, total number of segments in holotype 131; color white in preservative; surface epithelium smooth except for segmental grooves which are more pronounced toward posterior end of animal; abrupt transition from thorax to abdomen at setiger nine marked by change from narrow thoracic segments to wider abdominal segments, an increase in number of setae per fascicle and increase in length of hooded hook shafts.

Thorax consisting of peristomium and eight setigers (Fig. 1a); prostomium acute, approximately two and one-half times long as wide; no obvious palpode or eyes present and nuchal slits not discernible on any specimen examined; two eyespots located beneath epithelium on opposite sides of body toward anterolateral margin of peristomium; thoracic setigers eight, first two indistinctly separated from peristomium and from each other, each three times longer and much broader than remaining, distinctly separated setigers; four hooded hooks (Fig. 2a, b) present in both notopodial and neuropodial fascicles of setiger 1; number of hooks

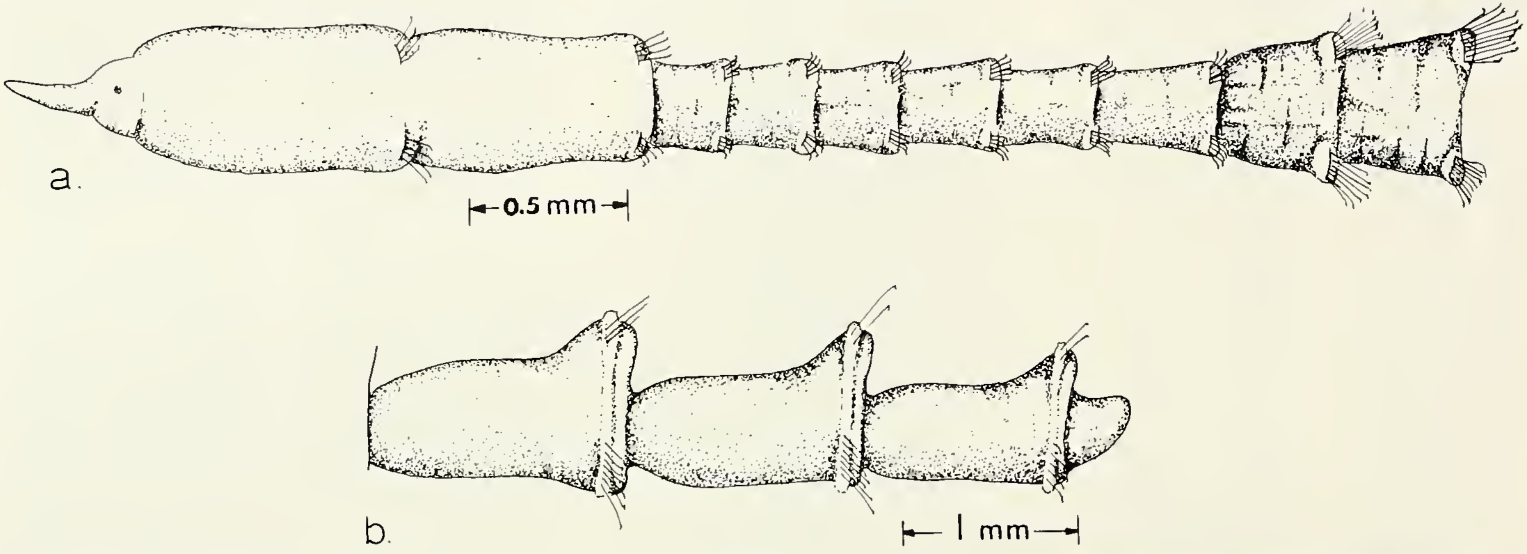

Fig. 1. *Amastigos acutus*, holotype AHF Poly 1239. a. Lateral view of thorax and first two abdominal setigers; b. Pygidium and last three abdominal setigers.

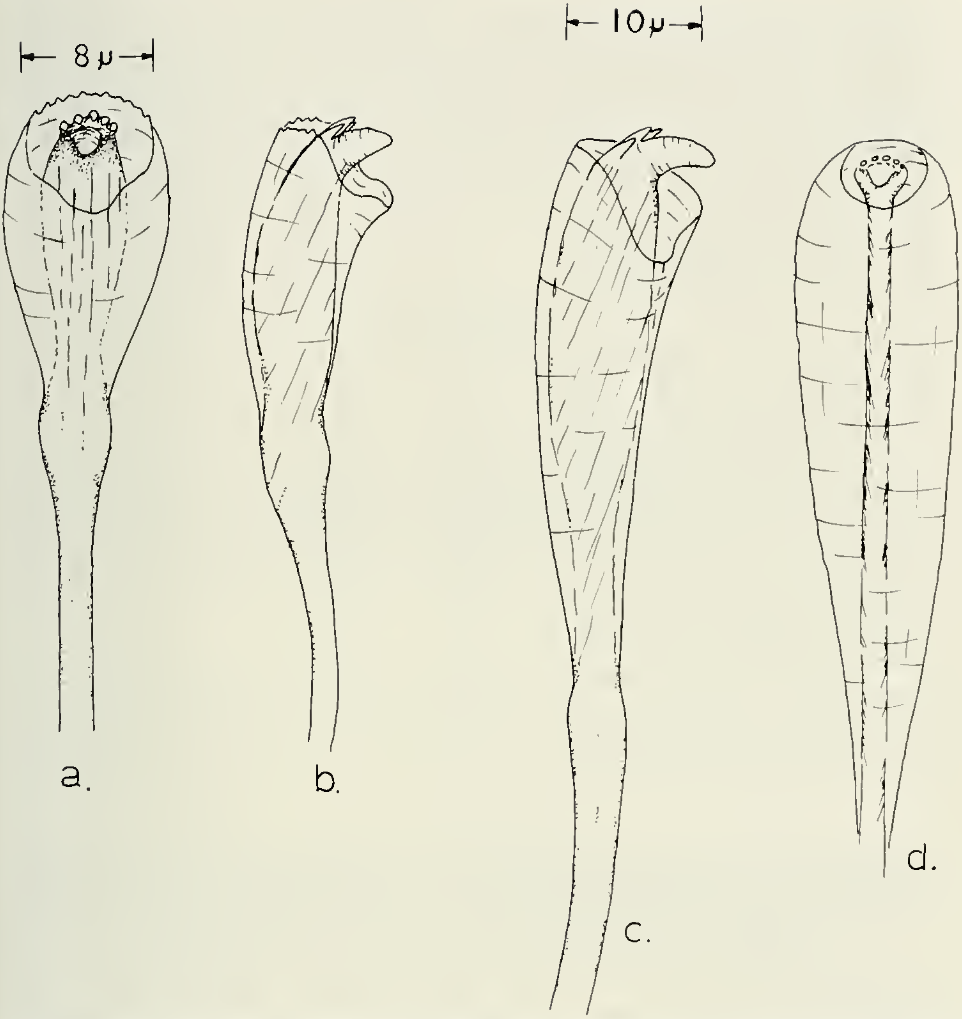

Fig. 2. *Amastigos acutus*, holotype AHF Poly 1239: a. Frontal view of notopodial hooded hook from setiger number 3; b. Lateral view of notopodial hooded hook from setiger number 3; c. Lateral view of neuropodial hooded hook from setiger number 34; d. Frontal view of notopodial hooded hook from setiger number 12.

increasing to six per fascicle by eighth thoracic setiger; setal fascicles marked by slightly raised ridge in thoracic setigers 3–8.

Abdomen consisting of 123 segments in holotype, terminating in a small conical pygidium with anal opening marked by slight dorsal depression; posterior abdominal segments about one and one-half length of anterior abdominal segments; ridges marking notosetae more pronounced in posterior abdominal setigers than anterior (Fig. 1b); branchia and nephridial papillae not observed; setae in form of hooded hooks with long shafts occurring 12 to 20 per fascicle in both notopodia and neuropodia (Fig. 2c, d); number of setae per fascicle decreasing posteriorly, but present in all segments up to pygidium.

Hooded hooks (Fig. 2a–d) long handled, terminating in a large fang surmounted by five smaller teeth in a single row; hood expanded with large opening in thoracic setae and abdominal neurosetae, with smaller opening in abdominal notosetae; notosetae differing from other hooks on body in being longer, thinner, with less indication of node on shaft; slight crenulation appearing at upper margin of hood in thoracic setae.

Etymology.—The specific name derives from the acutely pointed prostomium.

Distribution.—*Amastigos acutus* inhabits fine-grained, sandy beaches in southern California, intertidal regions.

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Response of *Cerithidea californica* (Haldeman) to Lowered Salinities and its Paleoecological Implications

Cerithidea californica (Haldeman) is the most common mollusc inhabiting the intertidal mudflats in coastal lagoons of southern California and Mexico (MacLean, 1969). Hence this species is an important paleoecological indicator for interpreting the Holocene history of these lagoons. Several investigations have used this mollusc to designate intertidal marine depositional environments (Phleger and Ewing, 1962; MacDonald, 1969; Cromwell, 1975); however, little is known concerning the response of this organism to environmental changes.

Presently, the influence of civilization appears to cause some abnormal conditions to occur within the coastal lagoons of southern California. The construction of highways and railroads across the tidal marshes and near the mouths of the lagoons restricts flow between the ocean and the lagoon (Mudie et al., 1974). The resulting reduced tidal prism allows a temporary sand barrier to be built at the mouth which then completely stops tidal flow into the lagoon. During periods of high freshwater runoff, the freshwater may be impounded behind these lagoon mouth barriers, creating a fresh to brackish water condition. It is known that these conditions occur now, but there is only limited evidence that suggests these

Table 1. Behavior of *Cerithidea californica* in water of different salinities. Numbers indicate the number of specimens in each jar. Numbers decrease in low salinity jars because specimens were removed during experiment.

	Salinity				
Dates of observation and water temperatures (°C)	0.	6.	16.	29.	33.
3/6/74 20.0	20W*	20W	2A 18W	20A	20A
3/7/74 20.0	20W	20W	10A 10W	20A	20A
3/8/74 16.5	18W	18W	20A	20A	20A
3/11/74 17.3	16W	1A 15W	20A	20A	20A
3/12/74 22.0	2D 12W	2A 12W	20A	20A	20A
3/13/74 22.0	3D 9W	3A 8W	20A	20A	20A
3/15/74 22.0	3D 5W	5A 7W	20A	20A	20A
3/18/74 22.0	8D	4A 1D 7W	20A	20A	20A

* A = active.
W = withdraw.
D = dead.

freshwater conditions existed before civilization arrived in southern California (Scott, 1976). By examining the response of *C. californica* to lowered salinities it is possible to determine whether or not the absence of this species will be indicative of an extended freshwater impoundment in subsurface sediments.

Cerithidea californica is generally an intertidal invertebrate; therefore, the animal is normally exposed subaerially at least twice daily during low tides. However, the abnormal conditions described above will preclude any tidal action and will often cause the intertidal mudflats to be submerged for several days (Mudie et al., 1974). Often the freshwater is replaced by normal seawater in less than 10 days (Bradshaw and Mudie, 1972) when the barrier is breached by overflowing runoff and the tidal conditions are restored. It may also be possible for the freshwater to remain trapped longer than 10 days if the amount of runoff is not sufficient to breach the barrier.

We devised a short experiment that would give some indications of the response of *C. californica* under the abnormal conditions of total submergence in fresh or brackish water. One hundred living specimens of *C. californica* were collected from a nearby lagoon in San Diego and allowed to acclimate overnight in normal sea water (33‰). Different amounts of freshwater were placed in five, one-gallon, aerated jars. These jars were then filled with normal sea water (33‰) so that salinities of 0‰, 6‰, 16‰, 29‰, and a control of pure sea water (33‰) were obtained. This range of salinities was observed by the authors (also Carpelan, 1969) in investigations of several lagoons during and after periods of high runoff.

Twenty live specimens of *C. california* were placed in each jar. The jars were then covered with a nylon screen and a piece of glass to keep the specimens in the water at all times. The specimens in each jar were observed for a total of 12 days. At daily intervals two non-active specimens were removed from the lower salinity jars and placed in normal sea water. If the specimens removed were alive, they would emerge in normal sea water and become active; these specimens were not returned to the jars.

The first observation (3/6/74) showed that all specimens in the lower salinity solutions (0‰, 6‰, 16‰) were withdrawn while all specimens in the higher salinity solutions were actively moving (Table 1). All specimens in the 16‰ solution became active after one day, some specimens in the 6‰ showed activity after 5 days and more specimens in the 6‰ solution showed activity by the end of 12 days. In the 0‰ solution, however, no specimens were ever active although tests showed individuals to be living up to 9 days after immersion in the solution. This experiment was only allowed to run for 12 days because first, it was shown that all specimens in the 0‰ had died by the end of 12 days and second, in the natural environment the animals in higher salinities could have escaped submersion within this time period.

A decrease in the ability of *C. californica* to become active can be seen to correlate with a decrease in salinity, however, the animal appears to be able to acclimate to all but the lowest salinities. Even if the salinity where the animal is living remains at 0‰ for a few days, this mollusc has the ability to withdraw to his shell and wait for the water to recede, which it usually does within 10 days. However, in rare cases where salinities remain extremely low for more than 10 days, our experiment indicates that a large decrease in the living population of *C. californica* will occur. There is evidence that lagoons were subjected to brackish conditions over extended periods of time in the past (Scott, 1976) and the absence of *C. californica* in short intervals of subsurface cores may reflect a freshwater time interval.

Unfortunately, the calcareous shell of *C. californica* may also be removed from some intertidal deposits by solution after death in anoxic (low pH) marsh and mudflat sediments. Therefore, before any environmental interpretation can be made for a certain subsurface time interval, the investigator must examine the sediment for any indication that solution of the carbonates has taken place.

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Carotid Arteries in the Rodent Genera Pappogeomys, Geomys and Thomomys (Family Geomyidae)

In a survey of the carotid circulation in the Rodentia, Guthrie (1963) found no internal carotid artery in the one preserved specimen of *Geomys* that he injected with latex and dissected. As no evidence of a carotid canal in any skull belonging to members of the Geomyidae was found, it was assumed that this family lacked the internal carotid artery. However, Hill (1935) found an internal carotid artery in *Thomomys*, entering the skull near the front of the bulla. This apparent descrepancy within the geomyids was unexpected and led to the present study of fresh, latex injected specimens of *Thomomys* (five individuals), *Geomys* (two individuals) and *Pappogeomys* (two individuals), in an attempt to determine the exact nature of the carotid pattern within this family.

The carotid arterial pattern found within the three genera dissected (Fig. 1) is quite uniform with variation only in the position of minor arteries and some variation in the Circle of Willis.

The common carotid artery, after giving rise to the superior thyroid and ascending pharyngeal arteries divides into the external and internal carotid arteries at the level of the occipital condyle. The internal carotid passes forward along the medial margin of the bulla and enters the skull through an opening between the bulla and the basisphenoid near the anterior margin of the bulla. Within the skull the internal carotid connects with the Circle of Willis. The external carotid also passes forward at the anterior end of the bulla giving rise to the external maxillary and lingual arteries either separately or by a common trunk that soon branches. Immediately anterior to this branching the external carotid gives rise to the internal maxillary artery. This artery almost immediately gives rise to its pterygoid and mandibular branches, the latter represented by the inferior alveolar artery. The remaining orbital portion of the internal maxillary enters the alisphenoid canal, emerging in the orbit where it gives rise to the usual branches of this artery including the ophthalmic artery. The external carotid continues laterally after

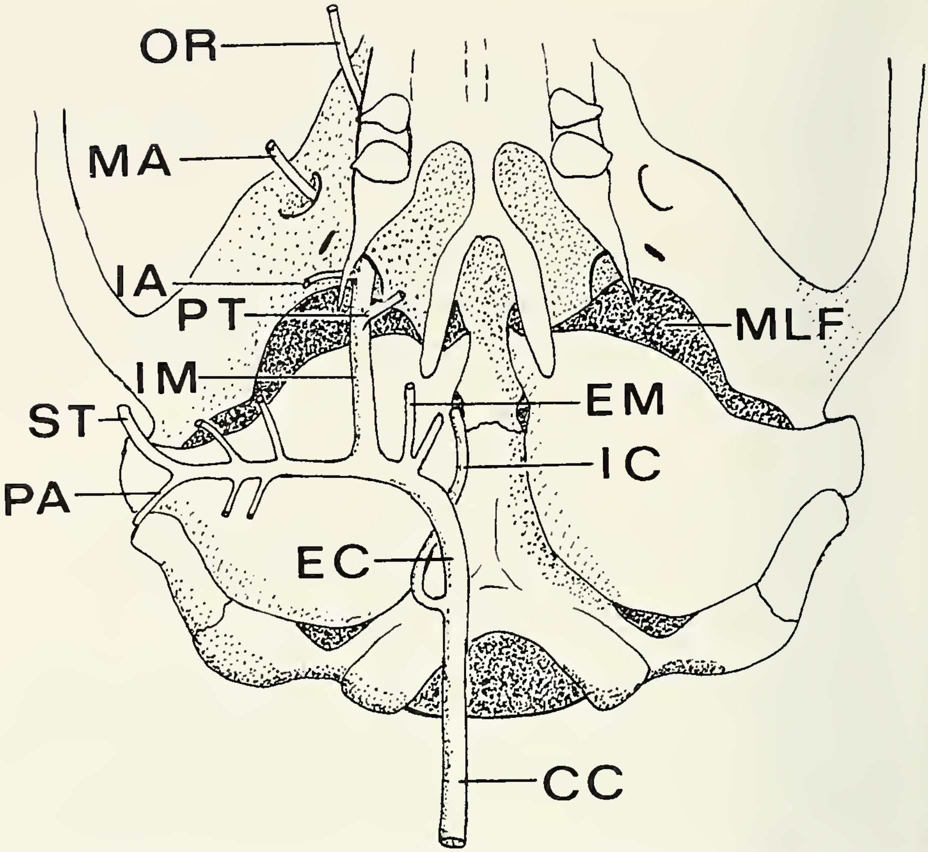

Fig. 1. Geomyid carotid arteries based on *Thomomys*, ventral view. CC = common carotid, EC = external carotid, EM = external maxillary, IA = inferior alveolar, IC = internal carotid, IM = internal maxillary, MA = masseteric artery, MLF = middle lacerate foramen, OR = orbital portion of the internal maxillary, PA = posterior auricular, PT = pterygoid portion of the internal maxillary, ST = superficial temporal.

giving rise to the internal maxillary, giving off small nutritive branches to the masseter musculature and the glands and muscles of the throat. In the region of the ear the external carotid divides into its usual terminal branches, the anterior and posterior auricular arteries and the superficial temporal artery.

The Circle of Willis differs slightly between the three genera dissected (Fig. 2). In *Pappogeomys* the internal carotid receives no connection from the basilar artery through the superior cerebral artery. In both *Geomys* and *Thomomys* a posterior communicating artery is present, connecting directly to the internal carotid in *Geomys* and to the posterior cerebral artery in *Thomomys*. In both cases, however, the posterior communicating artery is very small and unimportant in cranial circulation.

During embryonic development in rodents the internal carotid artery enters the skull through the posterior lacerate foramen, a slit-like opening on the medial side of the bulla, between the basioccipital and basisphenoid bones. With further ossification this foramen may close, with opening remaining only where vessels or nerves pass through this fissure. The opening for the jugular foramen, when

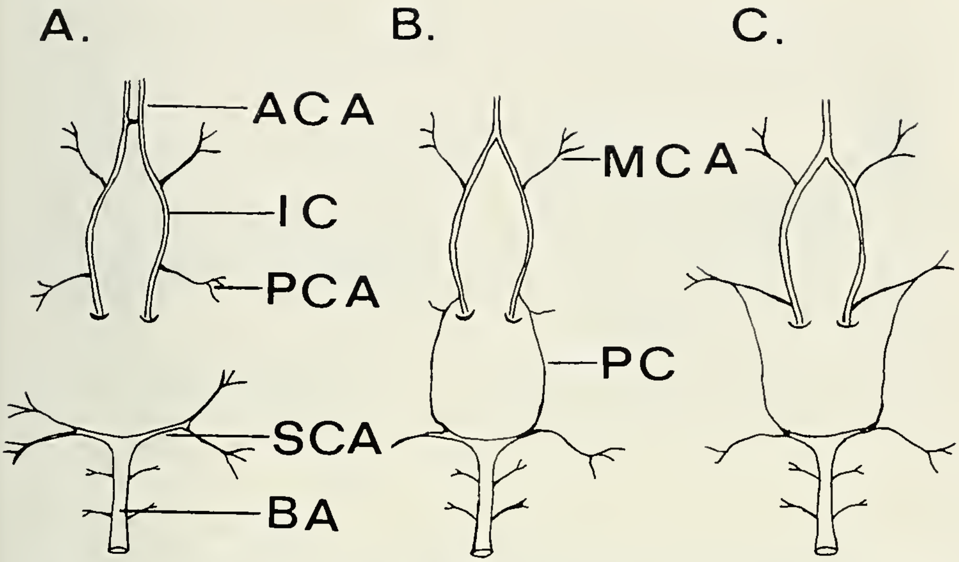

Fig. 2. Geomyid arteries in the Circle of Willis: A. *Pappogeomys*; B. *Geomys*; C. *Thomomys*. ACA = anterior cerebral, BA = basilar, IC = internal carotid, MCA = middle cerebral, PC = posterior communicating, PCA = posterior cerebral, SCA = superior cerebral.

present, is usually at the posterior margin of the bulla, and the opening for the internal carotid artery is usually just in front of this, between the bulla and the basioccipital bone. The more anterior positioning of the internal carotid artery, as found in the geomyids, is unique among rodents, and as far as we can tell, among mammals. Despite the odd position of the internal carotid in geomyids, there can be no question as to its identity. There are no other segments of the embryologic aortic arch pattern (from which the adult carotid pattern is derived) that could have been retained to account for this change in position. Although, the carotid canal is usually defined as an opening between the basioccipital and the perotic and tympanic bones just anterior to the jugular foramen or posterior lacerate foramen (see Hill, 1935; Wahlert, 1974), we also favor use of this name for the opening by which the internal carotid enters the skull in geomyids. Despite the anterior position of this opening, its homologies are with the carotid canal.

The arterial pattern found in the Geomyidae is the same as that found in the Castoridae and similar (except for the origin of the internal maxillary artery) to the pattern in the heteromyids. The original finding by Guthrie (1963) that the internal carotid artery was missing in *Geomys* was in error, due most likely to poor dissection material. Elimination of this apparent variation among the geomyids brings their arterial pattern more closely in line with that found in their closest relatives and strengthens the finding that while much variation in the carotid artery pattern occurs between rodent families, these patterns are usually uniform within families.

Acknowledgments

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Larvae of *Onthophagus p. polyphemi* Hubbard and *Onthophagus tuberculifrons* Harold (Coleoptera: Scarabaeidae)

Despite the relative abundance of dung beetles of the genus *Onthophagus* Latreille and the ease with which most species can be reared, the larvae of the majority of North American species remain undescribed.

Onthophagus p. polyphemi Hubbard is an obligate commensal of the gopher tortoise, *Gopherus polyphemus* Daudin, and is restricted to the Florida peninsula and the adjacent southeastern coastal plain along with its host. The beetles rarely occur outside of the tortoise burrows, and are best collected by excavation or by scraping the burrow walls 1 or 2 m inside the entrance during the spring (Howden and Cartwright, 1963). *Onthophagus tuberculifrons* Harold is a general dung feeder found over much of the eastern United States. It is especially common in pastures on fresh cow dung, although it has been collected from practically every type of dung as well as from rotten vegetables and carrion (Woodruff, 1973).

The following descriptions employ the terminology of Ritcher (1966).

Onthophagus p. polyphemi Hubbard, third-stage larva (description based on three, third-stage larvae reared from gopher tortoise dung brood cells which were constructed in the laboratory by adults collected by excavation of an old tortoise burrow at Hicoria, Highlands Co., Florida in October 1975; Fig. 1): maximum width of head capsule, 1.66–1.68 mm; maxillary stridulatory area with a row of six to seven conical teeth; gibbosity on dorsum of third abdominal segment with two patches of 45–50 weakly curved setae; venter of last abdominal segment with two subcircular patches of 49–56 caudally directed setae; teeth of epipharyngeal phoba relatively long and coarse; mandibular cusps especially prominent and heavily sclerotized.

Brood cells of *O. p. polyphemi* constructed in the laboratory were cylindrical (approximately 8 by 20 mm) and placed at the ends of tunnels against the glass of

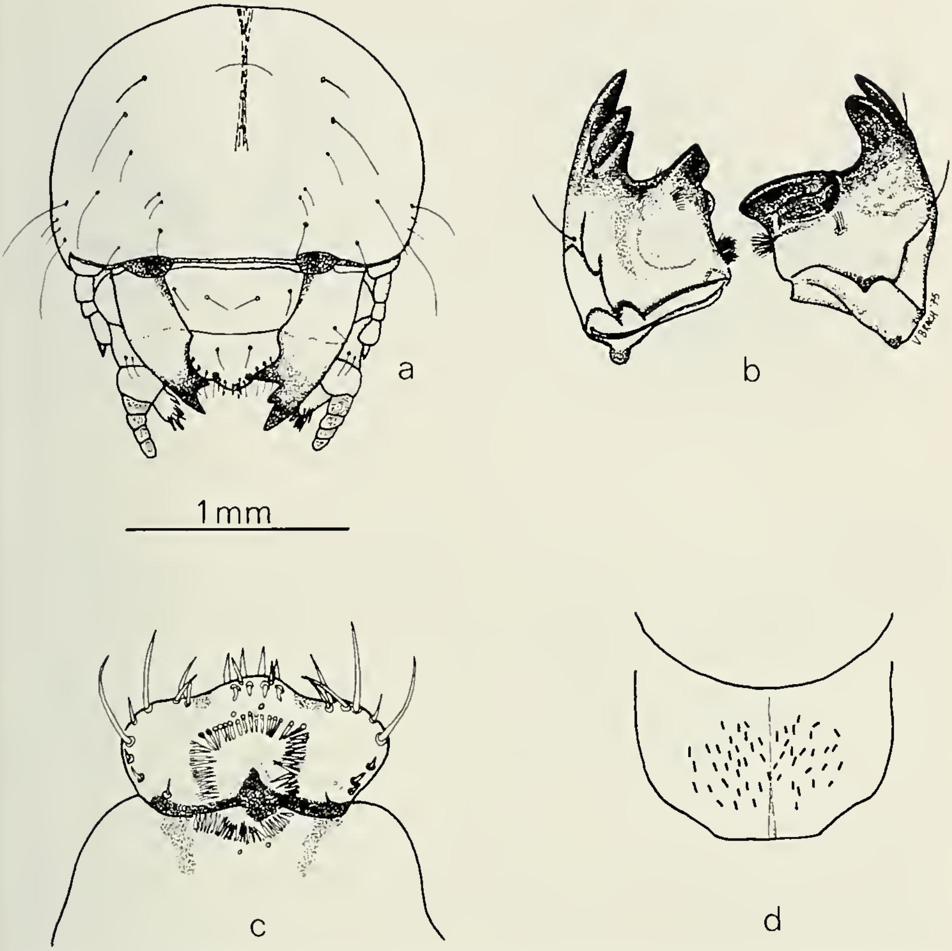

Fig. 1. Third-stage larva of *Onthophagus p. polyphemi* Hubbard: a. Head capsule; b. Mandibles; c. Epipharynx; d. Arrangement of setae on venter of last abdominal segment (diagrammatic).

the rearing jar, 10 cm or more beneath the surface of the soil. Only pasty, finely worked dung was used in the manufacture of the cells.

Onthophagus tuberculifrons Harold, third-stage larva (description based on six third-stage larvae reared from cow dung brood cells constructed by adults collected at the Archbold Biological Station, Highlands Co., Florida in December 1975; Fig. 2): maximum width of head capsule 1.33–1.42 mm; epicranial stem deeply forked basally on frons; maxillary stridulatory area with a row of five to seven short, conical teeth; gibbosity on dorsum of third abdominal segment with two patches of 45–52 weakly curved to straight, finely-pointed setae; venter of last abdominal segment with two sparsely-set, irregular patches of 30 to 39 caudally directed setae; teeth of epipharyngeal phoba small and conical; anterior and lateral borders of epipharyngeal paria weakly, but distinctly marginate; mandibular cusps and scissorial areas only moderately sclerotized.

Brood cells of *O. tuberculifrons* constructed in the laboratory were subspherical

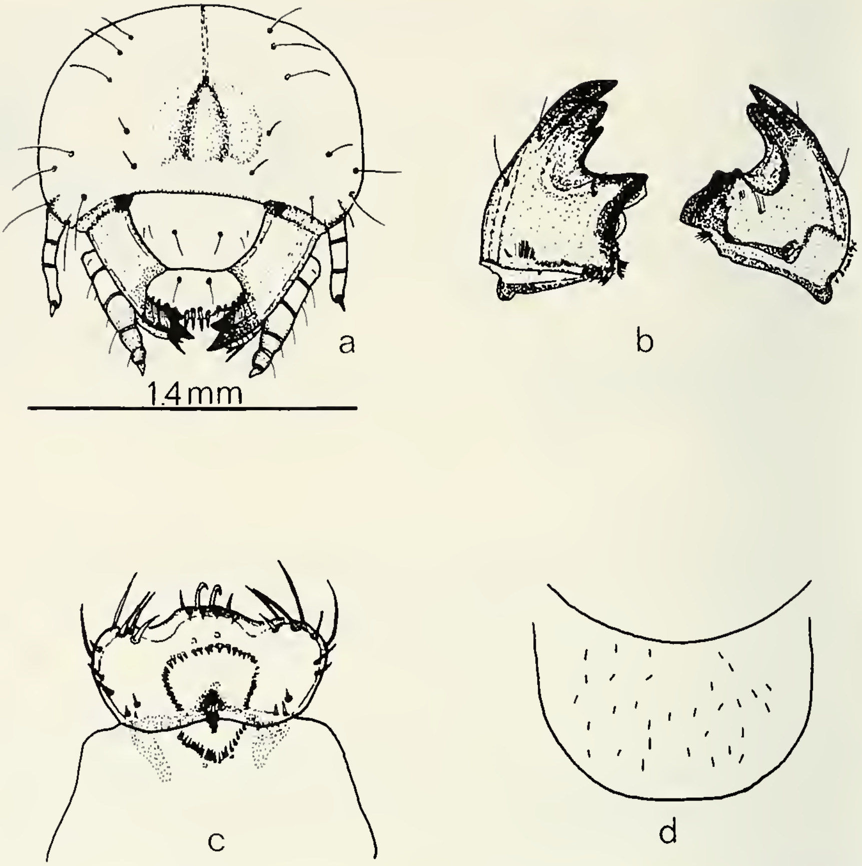

Fig. 2. Third-stage larva of *Onthophagus tuberculifrons* Harold: a. Head capsule; b. Mandibles; c. Epipharyx; d. Arrangement of setae on venter of last abdominal segment (diagrammatic).

(approximately 12 by 13 mm) and made at the ends of tunnels dug 10 cm or more beneath the surface of the soil.

Acknowledgments

I thank Mitch Masters, Chester Winegarner, David Worley, and John Douglass for assistance in the collection of the *Onthophagus* adults.

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A New Species of *Eutrombicula* (Acarina: Trombiculidae) from Lizards of Nevado de Colima, Jalisco, Mexico

There are approximately 85 genera and subgenera, and more than 450 species of chiggers known from the Western Hemisphere. The second largest genus is *Eutrombicula* Ewing, which has more than 26 species, including 16 new species recently described by Brennan and Reed (1974).

A study of *Eutrombicula* larvae taken from lizards found above 2,012 m on Nevado de Colima in the Mexican state of Jalisco has revealed another new species, for which we propose the following name.

Eutrombicula bitarsala, n. sp.

Fig. 1

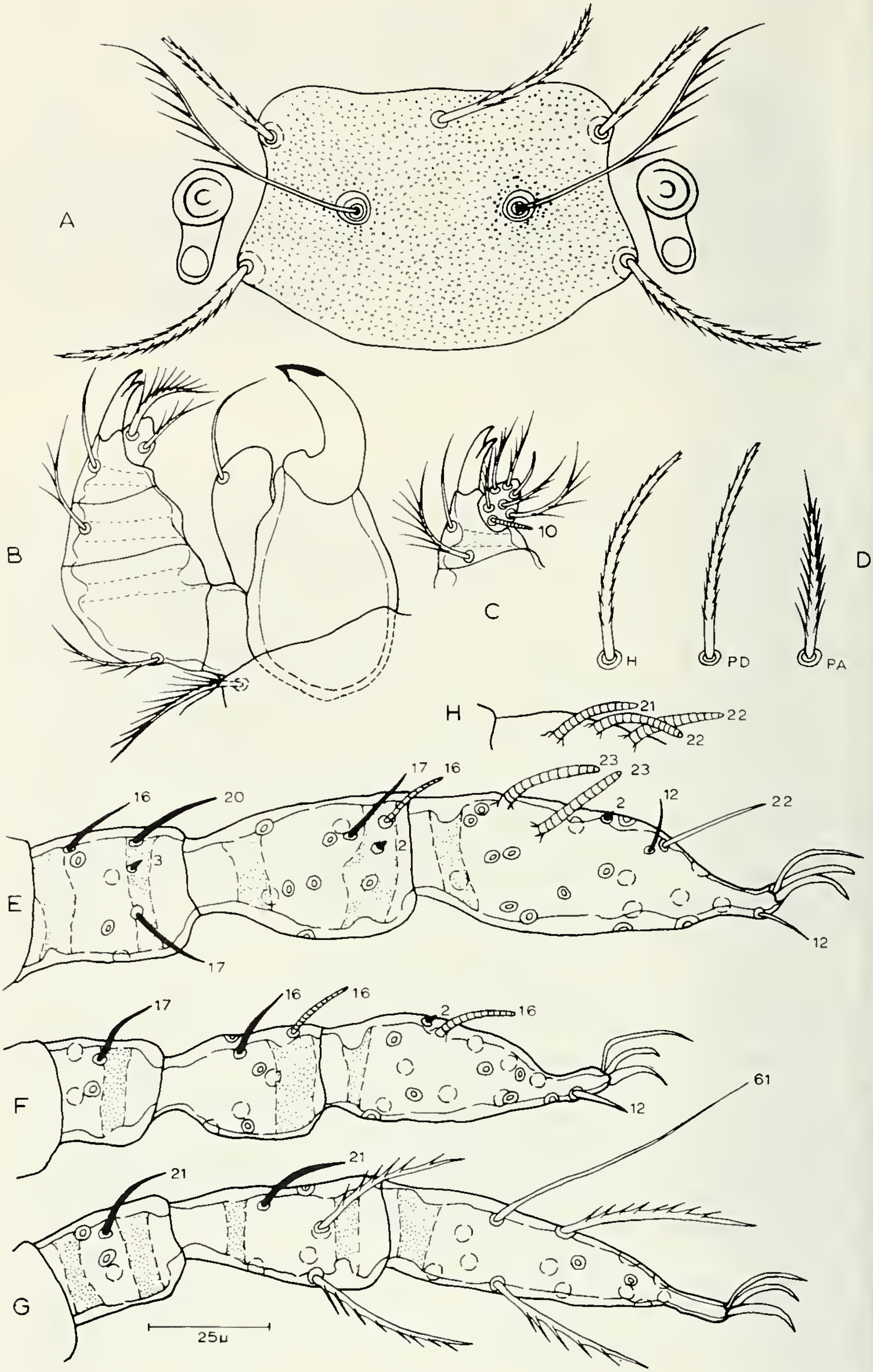
Types.—One hundred fourteen larvae, all from Jalisco, Mexico; holotype and 23 paratypes from Nevado de Colima, 2,440 m, taken by Eric M. Fisher on June 30, 1965 off *Barisia imbricata* (alligator lizard), original number EMF650630-1; and 1 paratype, same locality, 2,135 m, taken by L. M. Williams on June 26, 1967 off *Eumeces brevirostris* (skink), LMW670626-1; Volcan del Fuego, 2,988 m, July 7, 1966, *Barisia imbricata*, PLC 11026, by P. L. Clifton (8 paratypes); 14.5 km W Atenquique, 2,012 m, July 16–17, 1966, 2 *Eumeces brevirostris*, JRD 10439 (4), JRD 10495 (1); 5 *Sceloporus bulleri* (spiny lizard), JRD 10448 (4), JRD 10470 (3), JRD 10474 (1), JRD 10478 (8), JRD 10479 (8); 21 km W Atenquique, 2,440 m, July 15, 1966, *Barisia imbricata*, JRD 10347 (9); 3 *Sceloporus bulleri*, JRD 10385 (1), JRD 10387 (4), JRD 10388 (8); 3 *Sceloporus grammicus* (mesquite lizard), JRD 10315 (4), JRD 10377 (8), JRD 10379 (1); 24 km W Atenquique, 2,440 m, July 12, 1966, *Sceloporus bulleri*, JRD 10273 (8); 27 km W Atenquique, 2,866 m, July 12, 1966, 2 *Sceloporus grammicus*, JRD 10271 (7), JRD 10272 (2), all taken by J. R. Dixon. All types are in the chigger research collection, California State University, Long Beach.

Diagnosis.—Larva, with 2 tarsalae on tarsus I.

Description of holotype (unless otherwise noted, all measurements are in microns, with means and extremes of type series in parentheses).—Body partially engorged, 280 × 430; eyes 2/2, anterior eye larger, on ocular plate; 22 dorsal setae, similar to scutal setae, arranged 2-6-6-4-2-2; 2-2 sternal setae; 8 preanal setae; 2 postanal setae; sternals and preanals with longer branches than on dorsals and postanals; total body setae 36. Gnathosoma: Palpal setal formula B/B/NNB; palpotibial claw bifurcate and deeply cleft; chela curved with apical dorsal tooth and subapical ventral tooth; cheliceral base triangular, longer than wide, basal half punctate; galeala nude. Scutum: Rectangular and punctate with broadly curved posterior margin; all setae branched; sensilla flagelliform; sensillary bases equidistant between anterior and posterior margins.

Scutal measurements (114 larvae): AW 77 (75, 69–82), PW 87 (88, 70–93), SB 38 (37, 35–42), ASB 28 (28, 24–31), PSB 34 (32, 29–35), AP 31 (30, 25–33), AM 40 (39, 32–48), AL 34 (34, 30–40), PL 53 (49, 43–62), S — (62, 56–71, 21 specimens).

Legs: All legs 7 segmented; claws and empodia without onychotriches; coxa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each with 1B seta. Leg I with 3 genualae, microgenuala; 2 tibialae, microtibiala; 2 tarsalae (3 on left tarsus of holotype), subequal, 23 (23, 20–26), microtarsala, subterminala, parasubterminala, and pretarsala. Leg II with genuala; 2 tibialae; tarsala 16 (16, 15–19), microtarsala, and pretarsala. Leg III with genuala; tibiala; and long, nude, whiplike mastitarsala.

Taxonomic remarks.—Two tarsalae I are unique. All other described species of the genus, and virtually all described species of the family, possess a single tarsala I. *Eutrombicula bitarsala*, *E. alfreddugesi*, *E. lipovskyana*, *E. jenkinsi*, and *E. splendens* have a long nude mastitarsala III and no mastisetae on tibia III. However, *E. alfreddugesi* has shorter scutal setae (means of 28 for AM, 29 for AL, and 40 for PL), *E. lipovskyana* has a larger scutum (means of 86 for AW, 100 for PW, and 44 for SB), *E. jenkinsi* has more than 6 setae in the first posthumeral row, and *E. splendens* has 24–28 dorsal setae. For more characteristics the reader should refer to Brennan and Reed (1974), Jenkins (1949), and Wolfenbarger (1953).

Ecological notes.—The following description of Nevado de Colima is taken largely from Baker and Phillips (1965). El Nevado de Colima, at an elevation of 4,340 m, rises at the western border of the Mexican interior basin in the state of Jalisco and dominates the westernmost part of the Transverse Volcanic Belt of central Mexico. The boreal and alpine environments of the upper slopes of this mountain are isolated from those of other nearby mountains. The base of El Nevado de Colima, at least to the southeast, consists of semiarid, subtropical country, mostly cleared for cultivation and pasturage, with field borders of thorn shrub. Pines, oaks, and broadleaf understory appear at approximately 1,661 m. Larvae of *E. bitarsala* from lizards were taken no lower than 2,012 m. In addition to *E. bitarsala*, larvae of *E. alfreddugesi* were taken from three *Sceloporus bulleri* at 2,012 m and one *Barisia imbricata* at 2,440 m. Firs appear first at 2,378 m and become the major forest species at approximately 2,683 m; whereas, the highest record for *E. bitarsala* is at 2,988 m. An open alpine zone begins at about 3,810 m.

The above information suggests that *E. bitarsala* is an isolated high mountain species of Nevado de Colima which overlaps with, but is separate from, *E. alfreddugesi*.

Specimens examined.—*Eutrombicula bitarsala* (114 larvae of the type series). *Eutrombicula alfreddugesi* (18): MEXICO, Jalisco: Nevado de Colima, 14.5 km W Atenquique, 2,012 m, July 16–17, 1966, 3 *Sceloporus bulleri* (17); 21 km W Atenquique, 2,440 m, July 15, 1966, *Barisia imbricata* (1).

Acknowledgments

We thank Eric M. Fisher, Linda M. Williams, Percy L. Clifton, and Dr. James R. Dixon for collecting the lizards and/or chiggers, and Lee C. Spath for the illustrations. This study was supported in part by the U.S.P.H.S. Research Grant A103407 from the National Institute of Allergy and Infectious Diseases to California State University, Long Beach.

←

Fig. 1. Larva of *Eutrombicula bitarsala*: A. Scutum and eyes; B. Gnathosoma, dorsal view; C. Palpal tibia and tarsus, ventral view; D. Body setae: H, humeral; PD, posterior dorsal; PA, preanal; E. Leg I; genu, tibia, and tarsus, with bases of branched setae, nude setae, and measurements; F. Leg II; as above; G. Leg III; as above; H. Tarsus I and tarsalae of left leg of holotype showing variation.

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ANNOUNCEMENT

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It is strongly recommended that, before submitting a paper, the author ask qualified persons to review it. ıe author is requested to submit *at least one additional copy with the original*, on 8½ × 11 opaque, non- asable paper, double spacing the entire manuscript. ***Do not break words at right-hand margin anywhere in the ınuscript.*** Footnotes should be avoided. **Manuscripts which do not conform to the style of the BULLETIN ill be returned to the author.**

An abstract summarizing in concise terms the methods, findings, and implications discussed in the paper *ust* accompany a *feature article. Abstract should not exceed 100 words.*

A feature article comprises approximately five to thirty typewritten pages. Papers should usually be di- ded into the following sections: abstract, introduction, methods, results, discussion and conclusions, acknowl- lgments, and literature cited. Avoid using more than two levels of subheadings.

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Abbreviations: Use of abbreviations and symbols can be determined by inspection of a recent issue of the ULLETIN. **Omit periods after standard abbreviations:** 1.2 mm, 2 km, 30 cm, but Figs. 1–2. Use numerals *fore* units of measurements: 5 ml, but nine spines (10 or numbers above, such as 13 spines). The metric stem of weights and measurements should be used wherever possible.

Taxonomic procedures: Authors are advised to adhere to the taxonomic procedures as outlined in the ternational Code of Botanical Nomenclature (Lawjouw *et al.*, 1956), the International Code of Nomencla- re of Bacteria and Viruses (Buchanan *et al.*, 1958), and the International Code of Zoological Nomenclature toll, *et al.*, 1961). Special attention should be given to the description of new taxa, designation of holo- pe, etc. Reference to new taxa in titles and abstract should be avoided.

The literature cited: Entries for books and articles should take these forms.

McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.

Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus*. J. Mamm., 54: 452–458.

Brattstrom, B. H. 1969. The Condor in California. Pp. 369–382 *in* Vertebrates of California. (S. E. Payne, ed.), Univ. California Press, xii + 635 pp.

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COVER: Pterois volitans; *submitted by Robert R. Johnson, Department of Biology, California State University, Long Beach.*

SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

BULLETIN

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AUGUST 1977

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Date of this issue 25 November 1977

Diagnostic Characters and Color Convergence of the Garter Snakes *Thamnophis elegans terrestris* and *Thamnophis couchii atratus* along the Central California Coast

Jeanne M. Bellemin and Glenn R. Stewart

Abstract.—Along the central California coast, the closely related garter snakes *Thamnophis elegans terrestris* and *T. couchii atratus* have very similar color patterns. Both are characterized by a dark dorsum with three yellow stripes, no red markings, and yellowish throats. Plasma samples from 38 live specimens were subjected to electrophoresis and autoradiography to establish identity on the basis of transferrin mobility. Fourteen morphological characters were studied in the same specimens and correlated with the transferrin types by a stepwise discriminant analysis program. Discriminant functions derived from these specimens were tested on an additional 101 live and preserved specimens.

The results indicate that the most important diagnostic characters are the amount of internasal-rostral contact, internasal width versus length, number of dorsal scale rows, and vertebral stripe width. Counts of posterior scale rows and ventral scales, and estimation of relative pupil size, may aid in identification. Further observations have shown that coastal populations of *T. elegans terrestris* and *T. couchii atratus* can be distinguished reliably by ventral coloration. However, geographic variation in color patterns is evident, and we suggest that dorsal color patterns of these snakes are strongly convergent in San Luis Obispo and Monterey counties primarily in response to predator selection pressure.

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The *Thamnophis elegans* complex of garter snakes has provided systematists with numerous and vexing problems. Currently, two polytypic species are recognized: *T. elegans*, which is primarily terrestrial, and *T. couchii*, primarily aquatic (Fitch, 1940; Fox, 1951; Rossman, 1964; Fox and Dessauer, 1965). Dessauer et al. (1962) and Fox and Dessauer (1965) demonstrated that the two species could be consistently and unambiguously separated on the basis of electrophoretic mobility of the transferrin blood protein.

Between Monterey Bay and Point Conception in coastal California, *T. elegans terrestris*, *T. couchii atratus*, and *T. c. hammondii* are sympatric (Fig. 1). *Thamnophis e. terrestris* occurs from just north of the California-Oregon border, south to Point Conception, *T. c. atratus* occurs from San Francisco Bay south to Point Conception, and *T. c. hammondii* ranges from Monterey Bay south to northwestern Baja California, Mexico. Although the ecology of these snakes needs further study, their sympatry in this area apparently is possible because of differences in food and microhabitat selection. *Thamnophis e. terrestris* is clearly terrestrial and prefers slugs, plethodontid salamanders, and rodents. *Thamnophis c. atratus* seems more terrestrial than aquatic and feeds on tadpoles, juvenile *Rana aurora*,

Fig. 1. Distribution of *Thamnophis elegans terrestris* (diagonal lines), *T. couchii atratus* (horizontal lines), and *T. c. hammondii* (vertical lines) in California. Collection sites are indicated for *T. e. terrestris* and *T. c. atratus*.

and *Hyla regilla*. *Thamnophis c. hammondii* is the most aquatic in its habits and food preference, eating fish, fish eggs, and *H. regilla* (Fitch, 1940; Fox, 1951).

Thamnophis elegans terrestris, as currently recognized, usually is easily separable from *T. couchii* north of Monterey Bay on the basis of its red markings and other color characteristics (Fox, 1951; Stebbins, 1966). South of Monterey Bay, however, *T. e. terrestris* and *T. c. atratus* are extremely similar and easily confused in the field. Both can be described as having an *atratus* color pattern, i.e., three yellow stripes, a throat ranging from lemon yellow to pale yellow, a very dark dorsum, and no red color (see Stebbins, 1966, pl. 37). *Thamnophis c. hammondii*, in the sympatric area, is readily distinguished by the lack of a vertebral stripe and melanism (Stewart, 1971). The California red-sided garter snake (*T. sirtalis infernalis*), ranging along most of the California coast, is sympatric with all of the above species and can be identified by its color pattern and scutellation (Stebbins, 1966).

The populations of *T. elegans terrestris* and *T. couchii atratus* occurring between the Little Sur River in Monterey County and the Santa Maria River at the southern edge of San Luis Obispo County have not been described by previous investigators. A majority of the non-red, three striped snakes we have encountered here exhibit terrestrial tendencies, such as escaping into brushy cover on approach and feeding on terrestrial prey. The objectives of this study were to identify a sample of these snakes by electrophoresis of transferrin protein, to determine which external features are useful in distinguishing *terrestris* and *atratus*, and to supplement previous descriptions of geographic variation in these subspecies.

Methods and Materials

Thirty-eight live specimens of *T. elegans terrestris* and *T. couchii atratus* were collected for blood samples at 16 localities in coastal California, from San Luis Obispo County north to Mendocino County (Fig. 1). A few days after collection, the tip of the tail was severed from each specimen and a blood sample taken in several heparinized microhematocrit tubes. The sample tubes were centrifuged for 5 min at 3,400 rpm and placed in a freezer for storage at $-12°C$. Prior to electrophoresis, a blood sample was thawed, the red blood cells were discarded, and the plasma sample of approximately 50 μl was placed on a sheet of Parafilm. To this large droplet was added 2 μl of radioactive iron (Fe^{59} or Fe^{55}) solution (Dessauer et al., 1962). The mixture was applied to a Beckman electrophoresis membrane of cellulose polyacetate (Kohn, 1968) and electrophoresis was conducted using a Beckman Microzone Cell (Model R-101). This apparatus permitted eight samples to be run simultaneously. All samples were run at 240 volts for 45 min.

Membranes that were to be autoradiographed were taken out of the electrophoresis chamber and immediately applied to a glass plate to dry. When dry they were taped against a 5 × 7-inch sheet of Kodak No-screen medical X-ray film (NS2T), placed in a Picker X-ray cassette, and left for 5 or 6 days to expose the film. When the film was developed, the membranes that had been affixed to the film were stained, rinsed, dehydrated, and cleared. The position of the autoradiographed band on the exposed film permitted identification of the transferrin protein band on the membrane, after correction was made for expansion of the

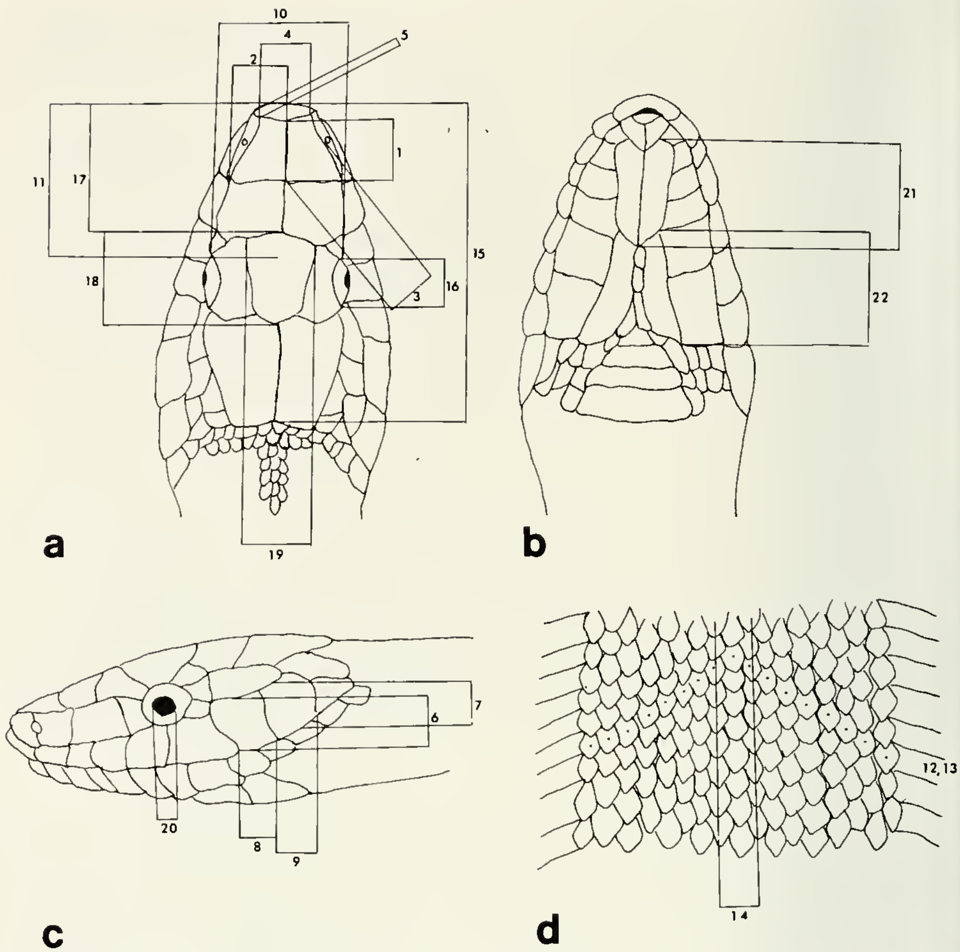

Fig. 2. Mensural and meristic features used for the morphological analysis of *Thamnophis elegans terrestris* and *T. couchii atratus*. a. Dorsal view of head; b. Ventral view of head; c. Lateral view of head; d. Dorsal view of flattened body skin. (Numerals refer to features described in Table 1.)

membrane during the staining process. The migration distance of the transferrin band from the application site was measured to the nearest tenth of a millimeter. The distance of migration of the albumin band was also measured. As the latter distance was identical in both species, it was used to standardize different runs. Results were expressed in terms of transferrin migration distance as a percent of albumin migration distance ("percentage of migration").

A total of 22 mensural and meristic features were studied on the specimens sampled (Fig. 2). Measurements were taken with a divider, then transferred to Vernier calipers and recorded to the nearest tenth of a millimeter. All linear measurements were paired and handled as ratios to eliminate the problem of comparing snakes of various sizes (Table 1). The mensural and meristic data, describing 14 characters, were separated into two groups ("*terrestris*" and "*atratus*") based on the electrophoretic data. These morphological data were evaluated in a stepwise discriminant analysis program (BMDO7M; Dixon, 1970). The

Table 1. Characters used in discriminant analysis program. Numbers in parentheses refer to features shown in Fig. 2.

1. Ratio: internasal width/internasal length (2/1)
2. Ratio: internasal median length/internasal width (3/2)
3. Ratio: internasal-rostral contact/nasal-rostral contact (4/5)
4. Ratio: sixth supralabial height/ventral margin width (6/8)
5. Ratio: seventh supralabial height/ventral margin width (7/9)
6. Ratio: snout length from rostral to orbit/head width between orbits (11/10)
7. Thoracic scale row count taken slightly anterior to mid-body (12)
8. Posterior scale row count taken two to three head lengths anterior to vent (13)
9. Vertebral stripe width taken near mid-body (14)
10. Ratio: pupil diameter/eye diameter (20/16)
11. Ratio: eye diameter/head length (16/15)
12. Ratio: snout length/frontal length (17/18)
13. Ratio: frontal width/frontal length (19/18)
14. Ratio: anterior genial length/posterior genial length (21/22)

results of the program weighted each character according to the amount of separation it indicated between the two species, listed the characters in order of value, presented a canonical graph depicting spatial relationships among the snakes, and derived a set of 14 discriminant functions for both *atratus* and *terrestris*. These discriminant functions enable one to classify any snake suspected of being either *atratus* or *terrestris* by using the same 14 characters (Roest, 1973).

With another computer program, the discriminant functions were tested on 94 preserved and 45 live specimens, including the 38 originally identified by electrophoresis. This larger sample also was used to further evaluate characteristics that may distinguish *T. couchii atratus* and *T. elegans terrestris*. The means of various samples described in this paper were compared statistically with Student's *t*-test.

Results

Dessauer et al. (1962) showed that the transferrin of *T. couchii atratus* has a slower electrophoretic migration rate than that of *T. elegans terrestris*. The electrophoresis of plasma samples from the 38 snakes used in this study showed that 11 of the snakes possessed the *atratus* transferrin and 27 possessed the *terrestris* transferrin. Electrophoresis of samples from several *T. c. hammondii* also showed the transferrin of the aquatic group. The average percentage of migration for *atratus* transferrin was 42% and that of *terrestris* was 52%, when compared with albumin migration on the same runs. This difference is significant to the 0.01 level.

The discriminant analysis program for the 38 specimens indicated that the seven top ranked characters, out of the 14 studied, may be useful for identification (Table 2). Characters #3 (internasal-rostral contact/nasal-rostral contact) and #1 (internasal width/internasal length) contribute the most to distinguishing between *T. elegans terrestris* and *T. couchii atratus*. Character #7 (thoracic scale row count) is about one-third as important as either of these. Character #10 (pupil diameter/eye diameter) and #9 (vertebral stripe width) are similar in weight, and when combined, are about equal to #7. The next two characters (#2, internasal median length/internasal width and #8, posterior scale row count) carry slightly less weight than the vertebral stripe width and are nearly identical to each other.

Table 2. Summary of data derived for 14 mensural and meristic characters in 11 *Thamnophis couchii atratus* and 27 *T. elegans terrestris* identified by electrophoresis of plasma transferrins.

Character	Relative numerical value	*T. c. atratus* (n = 11) $\bar{x}$, range, SE	*T. e. terrestris* (n = 27) $\bar{x}$, range, SE
3. Internasal-rostral contact/nasal-rostral contact	49.87	$0.80^{++} \pm 0.04$ 0.61–1.11	$1.24^{++} \pm 0.04$ 0.64–1.76
1. Internasal width/internasal length	42.48	$0.94^{++} \pm 0.03$ 0.80–1.10	$1.19^{++} \pm 0.02$ 1.00–1.43
7. Thoracic scale row count	16.78	$19.36^{++} \pm 0.24$ 19.00–21.00	$20.57^{++} \pm 0.16$ 19.00–21.00
10. Pupil diameter/eye diameter	8.40	$0.53^{++} \pm 0.02$ 0.42–0.65	$0.60^{++} \pm 0.01$ 0.50–0.71
9. Vertebral stripe width in scale rows	6.14	$2.34^{+} \pm 0.17$ 1.50–3.25	$2.00^{+} \pm 0.06$ 1.50–2.50
2. Internasal median length/internasal width	5.24	$1.06^{+} \pm 0.04$ 0.85–1.25	$0.98^{+} \pm 0.02$ 0.70–1.10
8. Posterior scale row count	5.22	$16.46^{+} \pm 0.28$ 15.00–17.00	$16.93^{+} \pm 0.07$ 15.00–17.00
11. Eye diameter/head length	3.42	0.22 ± 0.005 0.19–0.25	0.23 ± 0.003 0.20–0.26
14. Anterior genial length/posterior genial length	3.28	0.84 ± 0.02 0.70–0.94	0.92 ± 0.03 0.68–1.45
5. Seventh supralabial height/ventral margin width	2.79	1.29 ± 0.05 1.00–1.52	1.39 ± 0.03 1.06–1.83
4. Sixth supralabial height/ventral margin width	1.70	1.02 ± 0.03 0.83–1.15	1.06 ± 0.02 0.87–1.54
12. Snout length/frontal length	1.41	0.91 ± 0.04 0.73–1.10	0.94 ± 0.01 0.83–1.07
13. Frontal width/frontal length	1.17	0.60 ± 0.02 0.53–0.71	0.63 ± 0.02 0.44–0.88
6. Snout length from nostral to orbit/head width between orbits	0.61	0.92 ± 0.03 0.75–1.04	0.90 ± 0.02 0.77–1.13

$^{+}$ Difference between means significant at 0.05 level.
$^{++}$ Difference between means significant at 0.01 level.

In practice, however, these internasal measurements are difficult to make and character #2 is not considered further in this report. Differences between the means of *atratus* and *terrestris* for the first four characters (Table 2) are significant at the .01 level; those for the next three characters (Table 2) at the .05 level. The means of the seven remaining characters (Table 2) are not significantly different.

In the canonical graph (Fig. 3), each of the 38 snakes is represented as either "T" (*T. e. terrestris*) or "A" (*T. c. atratus*), depending on their electrophoretic classification. The small stars, one on either side of the graph, mark the mean for each subspecies. Clearly the snakes are clustered on the graph around the means of their respective subspecies. However, if a boundary is constructed by drawing a vertical line equidistant from each star down the center of the graph, one specimen of *terrestris* remains on the *atratus* side of line. This specimen was classified

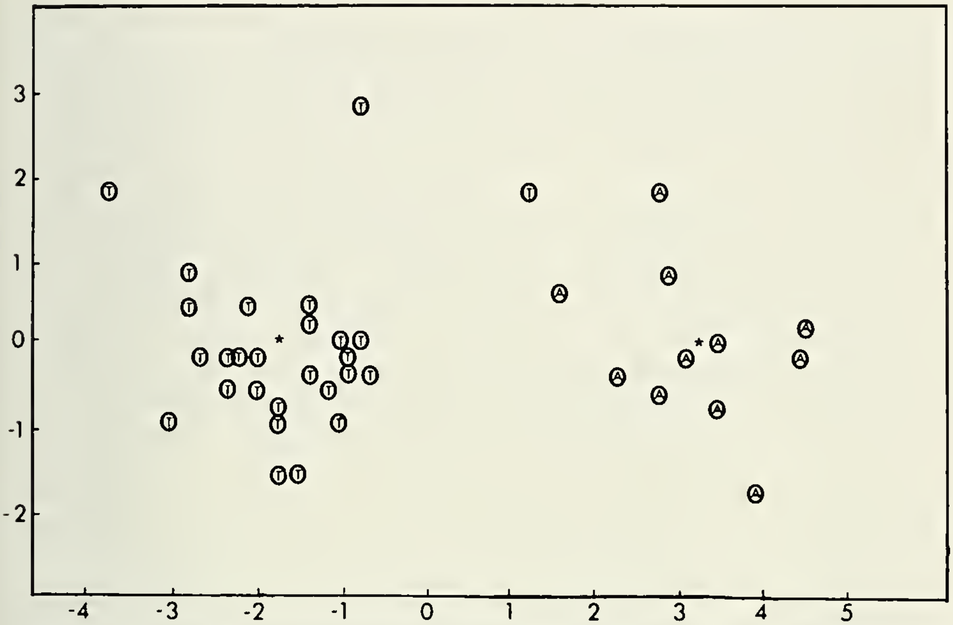

Fig. 3. Canonical graph showing spatial relationships among 38 snakes as determined by discriminant analysis of 14 mensural and meristic characters. Ⓐ indicates *Thamnophis couchii atratus* and Ⓣ indicates *T. elegans terrestris*.

as *terrestris* on the basis of electrophoretic results and color pattern. Remeasuring showed the original morphological data to be accurate, and the snake was found to have a rather narrow pointed snout as well as 19 thoracic scale rows, both of which are more characteristic of *atratus* than *terrestris* (Tables 2 and 3). Situations of this kind remind one of the very close morphological similarity between the terrestrial and aquatic snakes, and suggest that as much information as possible be used in determining identity.

Each of the 139 snakes used in the computer classification test was carefully examined by the authors to verify identity based on general appearance, color pattern, scale counts, locality of collection, and electrophoretic data, if any. This inspection led to the conclusion that 87% of the specimens, including 36 of the 38 electrophoretically identified snakes, were classified correctly by the computer using the 14 discriminant functions. Lack of complete agreement here can be attributed primarily to distortion caused by preservation and to geographic variation in the sample (Table 3).

Discussion

Thamnophis couchii, being a semiaquatic species, has been considered more slender and streamlined in head and body shape than *T. elegans* (Fox, 1951). Therefore, most of the measurements, ratios, and counts used in this study were selected to reveal such differences. The results of this analysis (Tables 2 and 3) agree with Fox's (1951) results. Though he did not rank them relative to each other, Fox (1951) believed that the ratio of internasal-rostral contact/nasal-rostral contact, and the shape of the internasals, were the most important characters

Table 3. Geographic variation of seven important mensural and meristic characters in 50 *Thamnophis couchii atratus* and 89 *T. elegans terrestris*.

	T. c. atratus			*T. e. terrestris*			
Character	All *atratus* (n = 50) $\bar{x}$, range, SE	South of Monterey Bay (n = 43) $\bar{x}$, range, SE	Monterey Bay to San Francisco (n = 7) $\bar{x}$, range, SE	All *terrestris* (n = 89) $\bar{x}$, range, SE	South of Monterey Bay (n = 51) $\bar{x}$, range, SE	Monterey Bay to Mendocino County (n = 24) $\bar{x}$, range, SE	Humboldt and Del Norte Counties (n = 14) $\bar{x}$, range, SE
3. Internasal-rostral contact/nasal-rostral contact	0.94^{++} ± 0.03 0.61–1.60	0.95^{++} ± 0.03 0.61–1.60	0.82^{++} ± 0.04 0.66–1.00	1.20^{++} ± 0.02 0.64–1.76	1.19^{++} ± 0.02 0.76–1.50	1.19^{++} ± 0.05 0.64–1.76	1.25 ± 0.05 1.00–1.64
1. Internasal width/internasal length	0.98^{++} ± 0.01 0.67–1.23	0.99^{++} ± 0.02 0.67–1.23	0.96^{++} ± 0.02 0.85–1.00	1.18^{++} ± 0.01 0.76–1.50	1.16^{++} ± 0.02 1.00–1.70	1.22^{++} ± 0.03 1.00–1.43	1.17 ± 0.03 1.00–1.37
7. Thoracic scale row count	19.32^{++} ± 0.10 19.00–21.00	19.33^{++} ± 0.11 19.00–21.00	19.29^{+} ± 0.26 19.00–21.00	20.51^{++} ± 0.09 19.00–21.00	20.96^{++} ± 0.04 19.00–21.00	20.33^{+} ± 0.19 19.00–21.00	19.14 ± 0.14 19.00–21.00
10. Pupil diameter/eye diameter	0.48^{+} ± 0.02 0.25–0.90	0.48 ± 0.02 0.28–0.90	0.50 ± 0.05 0.25–0.65	0.52^{+} ± 0.01 0.31–0.68	0.52 ± 0.01 0.35–0.68	0.57 ± 0.02 0.32–0.67	0.46 ± 0.02 0.31–0.60
9. Vertebral stripe width in scale rows	2.06^{++} ± 0.06 1.00–3.25	1.95^{+} ± 0.04 1.00–3.00	2.68^{++} ± 0.18 2.00–3.25	1.88^{++} ± 0.04 1.00–2.50	1.78^{+} ± 0.05 1.00–2.50	2.02^{++} ± 0.06 2.00–2.50	1.97 ± 0.05 1.50–2.15
8. Posterior scale row count	16.60^{++} ± 0.11 15.00–17.00	16.67^{++} ± 0.11 15.00–17.00	16.14^{++} ± 0.37 15.00–17.00	17.00^{++} ± 0.03 15.00–18.00	17.04^{++} ± 0.03 17.00–18.00	16.92^{++} ± 0.08 15.00–17.00	17.00 ± 0.00 17.00
* Ventral scale count	151.72^{++} ± 0.81 139.00–167.00 (n = 47)	151.61^{++} ± 0.85 139.00–167.00 (n = 41)	152.50 ± 0.45 149.00–158.00 (n = 6)	156.20^{++} ± 0.68 137.00–169.00 (n = 79)	157.48^{++} ± 0.72 137.00–169.00 (n = 44)	156.00 ± 0.47 146.00–162.00 (n = 22)	152.23 ± 0.65 141.00–161.00 (n = 13)

* This character not used in discriminant analysis program; sample size smaller due to unavailability of 13 specimens.

$^{+}$ Difference between means of *T. c. atratus* and *T. e. terrestris* in same geographic area significant at 0.05 level.

$^{++}$ Difference between means of *T. c. atratus* and *T. e. terrestris* in same geographic area significant at 0.01 level.

distinguishing the two species. Our results (Table 2) indicate that these characters each are more than twice as important as the next ranked character (number of thoracic scale rows). Based mostly on specimens collected north of Monterey Bay, Fox (1951) found that *T. c. atratus* almost always had 19 thoracic scale rows and *T. e. terrestris* usually had 21, except that 19 was the usual count in the most northern *terrestris* (from Humboldt and Del Norte counties). Our data on 139 specimens (Table 3) show that *atratus* and *terrestris* are most reliably distinguished by thoracic scale row counts south of Monterey Bay, where the identification problem is most acute. While 16% of the *atratus* we examined here had an atypical count of 21 thoracic scale rows, only 2% of the *terrestris* had an atypical count of 19. In the area from Monterey Bay to Mendocino County, 33% of the *terrestris* had 19 thoracic scale rows, whereas 93% of our specimens had this lower count in Humboldt and Del Norte counties. This northward decrease in scale row counts may be a result of exposure to low temperatures during gestation (Fox et al., 1961).

Fox's (1951) data suggest that five other characters (number of posterior scale rows, width of the vertebral stripe, number of ventral scales, ratio of gape/head length, and ratio of interorbital width/head length) are useful in distinguishing *T. couchii atratus* from *T. elegans terrestris*. Only the first two of these were evaluated in our computer program, though ventral counts were recorded on 126 specimens. Except for ventral scale counts, the data for these three characters (Table 3) show statistically significant differences between *atratus* and *terrestris* in all geographically matched samples. Posterior scale row counts in our study were made two to three head lengths (rather than the customary one head length) anterior to the vent. Examination of 11 randomly selected specimens of each subspecies found that five *atratus* (but no *terrestris*) had fewer scale rows at the usual counting position. Thus, posterior scale row counts should provide a better separation of *atratus* and *terrestris* than our data indicate. The contrast in vertebral stripe width is greatest in the Monterey Bay to San Francisco area (Table 3). South of Monterey Bay, both *atratus* and *terrestris* exhibit a narrower vertebral stripe, though that of *terrestris* remains the narrowest. Ventral scale counts (Table 3) may aid in distinguishing *atratus* from *terrestris*, but they are tedious and sexually dimorphic. The low counts obtained in our small sample of northern *terrestris* are not in line with Fox's (1951) data and are not due to a sex bias. They may be due to chance and/or low incubation temperatures (Fox et al., 1961). Pupil diameter/eye diameter ratio, a character suggested by Stevan J. Arnold (pers. comm.), is useful when working with live specimens (Table 2). The relatively small pupils of *atratus* often are quite noticeable upon casual inspection. However, this character becomes unreliable in preserved material.

The color patterns of *Thamnophis elegans terrestris* and *T. couchii atratus* have always been considered among the most useful characters for field identification. Fox (1951) described these patterns in some detail, but did not recognize the distinctiveness of the *terrestris* pattern south of Monterey Bay nor its similarity to that of *atratus* in this region. However, Fox (1951) did report that *terrestris* from the more eastern canyons of the Coast Ranges east of San Francisco Bay are "very dark, almost black." The rather terrestrial non-red, three-striped snake that we have found to be most common along stream margins and in marshy areas associated with ponds and river mouths in northern Santa Barbara, San Luis

Obispo, and Monterey counties also is a dark phase of *terrestris*. This dark phase is characterized by three bright yellow stripes on a dark grey-brown to black background, often marked with two rows of paired dark spots on each side of the vertebral stripe. Light colored flecks are scattered on scale edges and the skin between the scales. A black ground color, lacking dark spots and having reduced light flecks, is characteristic of specimens in the area from Point Buchon to San Simeon, San Luis Obispo County. The throat color usually is lemon yellow and blends into an unmarked pale yellow-green or olive venter.

From Santa Cruz County north into Mendocino County, *T. elegans terrestris* is represented by a red color phase, as described by Fox (1951) and illustrated by Stebbins (1966, pl. 37). The red coloration ranges from wine red or blood red to a light orange-red, and may vary in extent from a few flecks to a suffusion of red pigment that blends evenly with the ground color. Specimens representing both the dark and prominently red phases can be found near the mouth of the Pajaro River astride the Monterey-Santa Cruz county line.

The semiaquatic, non-red, three-striped snake that apparently is less common along stream margins and in marshy areas in San Luis Obispo and Monterey counties is *T. couchii atratus*. In these southern portions of its range, *atratus* is characterized by three yellow stripes on a black background marked with blue or turquoise flecks on the edges of and between the dorsal scales. The ventral scales are pale yellow-green to deep blue and blotched centrally with various shades of orange that blend into the pale yellow or lemon yellow of the throat region. In contrast, *atratus* from the more northern coastal counties of its range usually has an orange or yellow-orange vertebral stripe (see Stebbins, 1966, pl. 37), and blue-black specimens from the northern Santa Cruz Mountains and San Francisco Peninsula generally lack lateral stripes (Fox, 1951).

Throughout the area of sympatry along the coast, we have found that ventral coloration provides a reliable means of separating *T. couchii atratus* from *T. elegans terrestris*. While all live *atratus* specimens collected along the coast south of San Francisco had large and essentially continuous orangish blotches on their venters, the venters of *terrestris* specimens usually had just an irregular sprinkling of orange or red flecks. Such flecks were lacking in *terrestris* from south of Monterey Bay. These differences in ventral coloration may be recognized even in faded preserved specimens.

Perhaps some of the variation in the dorsal color pattern of *T. elegans terrestris* can be explained in relation to climatic variation along the coast of California. Climatic data (U.S. Dept. of Commerce, 1974) show that the average annual precipitation in San Francisco is 61% higher than in Santa Maria, which lies near the southern end of the ranges of *T. e. terrestris* and *T. couchii atratus*. Color character divergence (or displacement) between *terrestris* and *atratus* may have been possible in the San Francisco Bay area because higher precipitation, a more humid climate and lush vegetation permit *terrestris* to occupy habitats farther away from water. To the south (and probably the east), where the climate is more arid, *terrestris* is confined more closely to the very limited and discontinuous riparian habitats occupied by *atratus*. In San Luis Obispo County, especially, there is color convergence in these snakes, *terrestris* becoming very dark, probably to meet camouflage requirements in the dark riparian environment. Similarly, the dorsal stripe of both subspecies becomes narrower. Color convergence also is observed here in melanistic *T. c. hammondii* (Stewart, 1971) and *T. sirtalis infernalis*. The latter snake near San Francisco displays a red head and a regular bright red pattern dorsally (see Stebbins, 1966, pl. 37). The same subspecies collected near Oceano, San Luis Obispo County has a black head and a black dorsum with very faint red blotches. All of these dark snakes in San Luis Obispo County probably are responding to the same selection pressure. We believe this is primarily predation, though dark snakes also may have a slight thermoregulatory advantage.

Live specimens examined.—Thamnophis couchii atratus: Contra Costa Co., Kellogg Creek (2); *San Mateo Co.*, Pescadero Creek (1); *Santa Cruz Co.*, Scott Creek (2); *San Luis Obispo Co.*, Pico Creek (4), San Simeon Creek (1), San Luisto Creek (1), Coon Creek (1).

Thamnophis elegans terrestris: Mendocino Co., Navarro River (4); *Marin Co.*, (1); *San Mateo Co.*, San Bruno (1), Laguna Salada (6), Crystal Springs Reservoir (2); *Santa Cruz Co.*, Scott Creek (3); *Monterey Co.*, Pajaro River (5), Little Sur River (1); *San Luis Obispo Co.*, San Simeon Creek (1), Coon Creek (3), Dune Lakes (1); *Santa Barbara Co.*, Santa Maria River (6).

Preserved specimens examined.—Thamnophis couchii atratus: Santa Clara Co., (LACM2844); *Monterey Co.*, Big Sur (LACM21287), Nacimiento River (CPP01189), Salmon Creek (CPSH248); *San Luis Obispo Co.*, Arroyo del Corral (CPP01176-7), Pico Creek (CPP01165, 01195-6), San Simeon Creek (CPP01174), Upper Salinas River (CPP01183, 01185, CPSH120), Cayucos (CPS2428), Morro Bay (CAS43372), Reservoir Canyon (CPS3220, 3227-8), Coon Creek (CPP01181, 01190), Islay Creek (CPP00453), Brizziolari Creek (MVZ31730), Perfumo Canyon (CPS2413, 2426, 3218-9, H188-9), Price Canyon (CPS3223-4), San Luis Creek (CPSH191), San Luis Obispo (CPS2436), Lopez Canyon (CPS2437, 3216, 3225), Oceano (CAS43367); *Santa Barbara Co.*, 40 mi S Santa Maria (CPSH94).

Thamnophis elegans terrestris: Del Norte Co., Fort Dick (CPS2342-3, 2345-7), Smith River (CPS2348); *Humboldt Co.* (LACM27952, 27954-6, 27958-61); *Santa Clara Co.* (LACM2843, 2845); *San Luis Obispo Co.*, 4 mi S Monterey Co. (CPSH363), Arroyo del Corral (CPP01175), San Simeon Creek (CPP01173, 01178, 01184), Pico Creek (CPP01166, 01179, 01187, 01194), Cambria (CPS2424, 3200, 3221, H246), Cayucus (CPSH192), Morro Bay (CPSH190, H355, CPP01182, 01186, MVZ7158, 36322), Baywood Park (CPSH116, H122), Islay Creek (CPP00454, 00460-1, 01180), Coon Creek (CPP01191-3), San Luis Obispo (CPS3190), Oceano (CAS43366), Oso Flaco Lake (CPP01188); *Santa Barbara Co.*, Santa Maria River (CPP01167-71), 40 mi S Santa Maria (CPSH93), Santa Ynez River (MVZ4317).

Abbreviations used.—CPP = California State Polytechnic University, Pomona; CPS and CPSH = California Polytechnic State University, San Luis Obispo; LACM = Natural History Museum of Los Angeles County; MVZ = Museum of Vertebrate Zoology, Berkeley; and CAS = California Academy of Sciences.

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Brooding Behavior and Protandry in *Hipponoe gaudichaudi* (Polychaeta: Amphinomidae)

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Abstract.—Analysis of two extensive museum samples of *Hipponoe gaudichaudi* Audouin & Milne-Edwards indicates that this amphinomid polychaete broods its juveniles in intersegmental grooves. Juveniles undoubtedly migrate from the ventrum to the dorsum of juveniferous worms as they increase in size. Analysis of oocyte diameters and spermatocyte densities in relation to the number of body segments indicates that this species is a protandric hermaphrodite. The spermatozoa are primitive (Franzén, 1956).

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Hipponoe gaudichaudi Audouin and Milne-Edwards is a cosmopolitan amphinomid polychaete that inhabits the mantle cavity of pelagic barnacles of the genus *Lepas* (Pettibone, 1963). Nicol (1964) classifies this species as an inquilinistic commensal. Augener (1910, 1922) investigated some adult-juvenile relationships and confirmed that the juveniles of this species are not parasitic. The purpose of this paper is to re-examine adult-juvenile relationships, and report on the reproductive system of this amphinomid.

Methods

Two samples containing over a total of 300 specimens, stored in alcohol, were obtained from the Allan Hancock Foundation, University of Southern California, Los Angeles, California, and the Australian Museum, Sydney. Body measurements were made with an ocular micrometer. Twenty-one specimens were serially sectioned at 10 μm and stained with Haemotoxylin, Eosin B and Alcian Blue. Gametes were measured from tissue sections of anterior, middle and posterior body segments. Estimates of 25 oocyte diameters for each of 13 worms were taken only from those oocytes in which the nucleolus was visible. Spermatocyte concentrations were measured in the same 13 worms with a calibrated ocular grid and 25 randomly paired coordinates. It is assumed that all sections were of uniform thickness.

Results

Juvenile-adult Relationships.—Juvenile worms were invariably found in the intersegmental grooves of juveniferous worms; their heads were directed towards the midventrum. The largest juveniles, firmly attached to the dorsum, had similar orientations (Fig. 1). Juveniles were attached to both functional males and females. In one case, a 12-setiger juvenile had a 5-setiger worm firmly attached to its lateral surface. Although some juveniles were detached from adult worms, the most juveniles recorded from an adult was 44. Juvenile

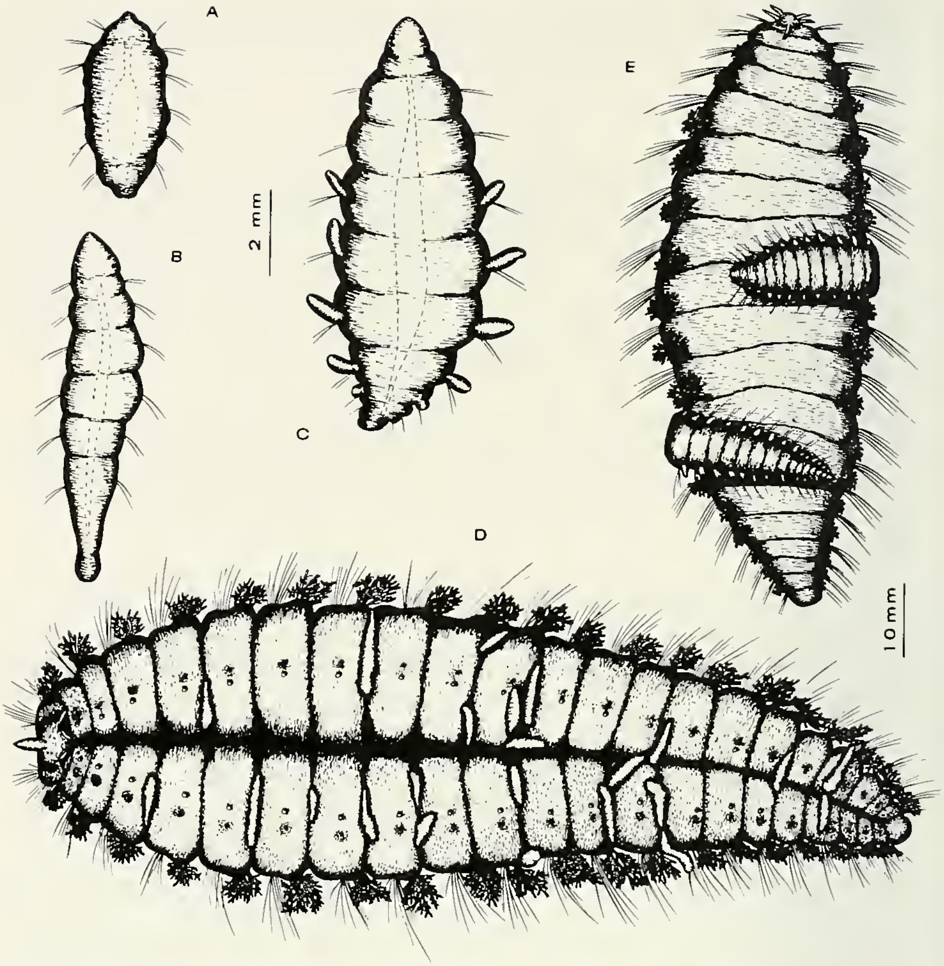

Fig. 1. *Hipponoe gaudichaudi*: A–C, Juvenile specimens from the ventral and lateral surfaces of a juveniferous specimen; D–E, Ventral and dorsal aspects of adults with juveniles.

activities on adult worms do not result in tissue damage to the latter because their neurosetal hooks penetrate only the outer half of the adult's cuticle.

Juveniles ranged in length from 0.3 to 3.6 mm, although most were less than 1.3 mm. Mean body lengths and segment numbers of juveniles were 0.66 ± .03 mm and 6.16 ± .14 segments from the ventral surface; 1.06 ± .04 and 7.91 ± .21 from the lateral surface; and 2.21 ± .24 and 13.00 ± .85 from the dorsal surface. The differences observed between the juvenile body measurements from each adult region are significant ($P < .05$ for all cases). Considerable growth in *H. gaudichaudi* occurs during the period when the last few segments are added.

Histology.—*Hipponoe gaudichaudi* has segmentally arranged coelomic "pockets" formed by the parapodial musculature and intersegmental grooves; septa and botryoidal tissue are absent. All gametes develop next to one another throughout the coelom.

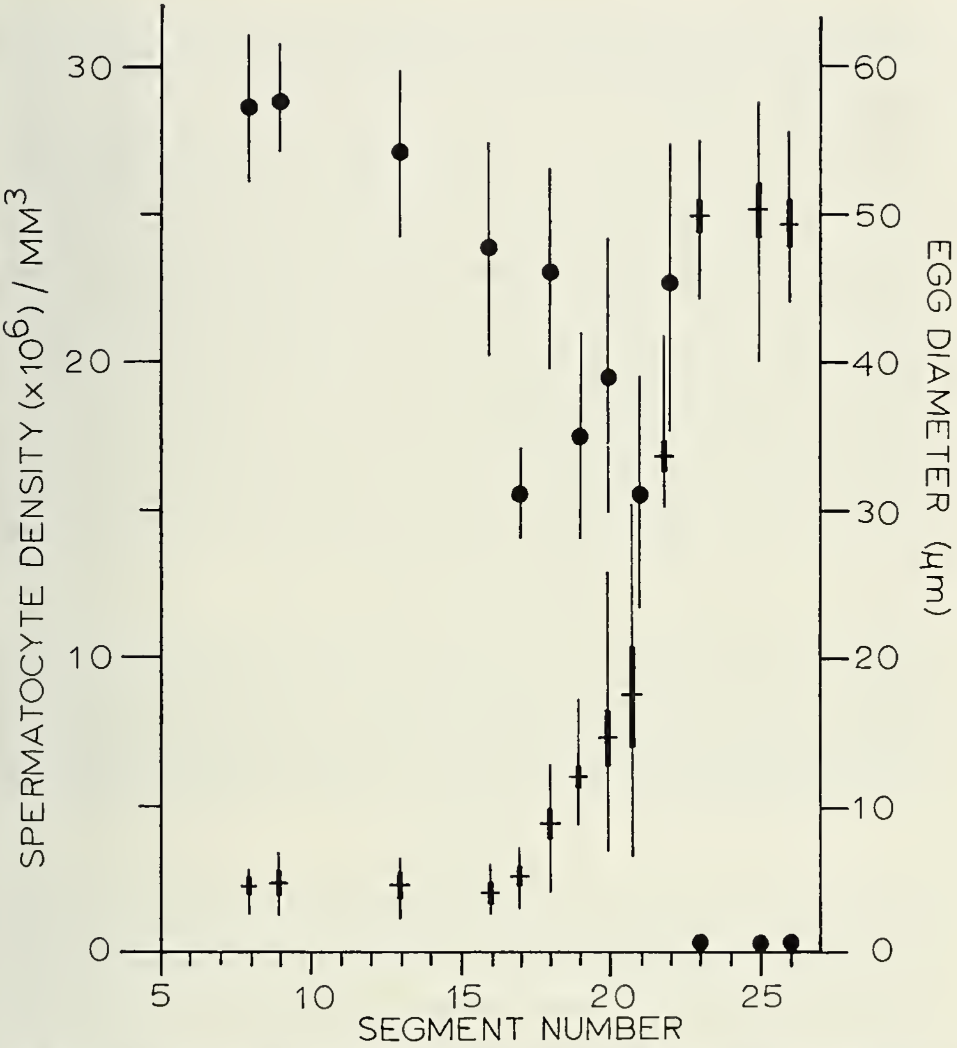

Fig. 2. Spermatocyte densities and oocyte concentrations *vs.* the total number of body segments for each of 13 *H. gaudichaudi*. Thin vertical lines represent sample ranges; dots and horizontal bars are sample means for spermatocytes and oocytes, respectively. The thick vertical bars are the 95% confidence intervals of the means for oocytes.

Worms with 5–9 setigers contain two kinds of gametogonia. One type occurs in sparse grape-like clusters which are 5–10 μm in diameter; the cells within these packets measure 3–7 μm wide. The other gonial cell type occurs singly, is 3–5 μm in diameter, and practically fills the coelom. Both cell types exhibit strong affinities for haemotoxylin. I interpret the cell packets to be oogonia, and the solitary cells to be spermatogonia. The site of gametogenesis is unknown, and stem cells were not observed. Flat, dense staining cell clusters, however, were observed in the coelomic cavity.

Juveniles with 13 setigers resemble closely those with 5–9 setigers, except that the oogonial packets are more prevalent and larger (10–15 μm in diameter). The number of oogonia observed within various packets form sequences described by the equation, $y = 2^n$ (where y = number of oogonia from numerical packet, and $n = 1, 2, 3$, or 4). Most of the cells in these packets dissociate in the coelom where vitellogenesis occurs.

Specimens with 16–18 setigers have many spermatocytes and many small oocytes that have begun vitellogenesis. Spermatocytes are ellipsoidal and measure 5 μm long and 4.5 μm wide. Oocytes are generally less than 10 μm in diameter, and numerous oogonial packets are still present.

Individuals with 20 setigers contain mature spermatozoa with blunt heads that are 4 μm in diameter, and tails approximately 40 μm long. The nephridia of these and other stages are similar to those described for other amphinomids (Gustafson, 1930). They may function in the removal of spermatozoa from the coelom because their coelomoducts were filled with sperm. The oocytes in these specimens averaged 15 μm in diameter, and had distinct germinal vesicles and nucleoli.

Worms with 23 or more segments are functional females that generally lack spermatozoa. The primary oocytes are around 50 μm in diameter. The coelom is filled with oocytes, and the body wall is highly distended. The nephridia become elongate and the nephrostomia highly constricted. Oocytes were not observed in coelomoducts. The gut and body wall musculature appears to have been lysed.

Quantitative Relationships.—As expected with a protandric hermaphrodite, spermatocyte densities are initially high, but decrease as the number of segments increase (Fig. 2). The lower and upper limits, for functional males range from 18–22 segments. Oocyte diameters in worms with 5–17 setigers are initially small, enter a growth phase in worms with 18 setigers, and a stationary phase in those with 23 or more (Fig. 2).

Discussion

This study confirms the observations of Augener (1910, 1922). The juveniles of his samples were of a similar size range, location and orientation on juveniferous worms; adults carried similar numbers of juveniles on their bodies. I found that juveniles migrate from the ventrum to the dorsum, and speculate that the purpose of this movement is to avoid mechanical interference.

The gametes of *H. gaudichaudi* may be proliferated from the peritoneum of parapodial muscles; they are produced from the peritoneum of botryoidal blood vessels and the gut wall in *Eurythoe complanata* (Pallas) and *Pareurythoe californica* (Johnson) (Kudenov, 1974; for review, see Clark and Olive, 1973). Sperm platelets and morulae that are typical of other polychaetes were not observed in *H. gaudichaudi* (Clark, 1965). Oogonial packets similar to those described by Olive (1975) for *Eulalia viridis* (Müller) were present.

The metanephridia of functional male *H. gaudichaudi* probably function to remove coelomic spermatozoa, as they do for two *Euphrosyne* spp. (Schroeder and Hermans, 1975). Gametes are removed from the coelom through the pygidium in other examined amphinomids (Kudenov, 1974).

Brooding behavior of the kind reported for *H. gaudichaudi* also occurs in *Amphinome pulchra* Horst, another amphinomid inhabitant of floatsum communities (Horst, 1912) and probably a chrysopetalid, *Bhawania goodei* Webster (Kudenov, 1975). It is not known whether *A. pulchra* is hermaphroditic. Brooding behavior in polychaetes is well known (Schroeder and Hermans, 1975). The brooding of oocytes, larvae and juveniles in specialized receptacles or in tubes occurs, for example, in spirorbids, autolytids, exogonids, polynoids, spionids, capitellids and onuphids. Some phyllodocids tend to egg masses deposited on rocky substrata (Olive, 1975). The brooding of juveniles on the body surface, however, is not common amongst polychaetes.

The control of gametogenesis in *H. gaudichaudi* may resemble that described for the protandric hermaphrodite, *Ophryotrocha puerilis* Claparede and Metschnikow (Pfannenstiel, 1973). Pfannenstiel hypothesized that a gonadotropic hormone directly controls the differentiation of gonial cells towards oogenesis; spermatogenesis is not influenced by this hormone. However, both spermatogenesis and vitellogenesis occur simultaneously in *H. gaudichaudi*, suggesting that another substance may be operating in addition to a gonadotropic hormone. It is possible that a metabolic by-product from spermatogenesis inhibits oogenesis. Such feedback systems from coelomic gametes operate in some dioecious polychaetes (see Clark and Olive, 1973). Whether they operate in protandric hermaphrodites like *H. gaudichaudi* remains conjectural.

Acknowledgments

I thank Jabe B. Wills, University of Houston, Kristian Fauchald and the late Olga Hartman, University of Southern California, James A. Blake, Pacific Marine Station, Paul C. Schroeder, Washington State University, and Walter B. Miller, University of Arizona, for their assistance and criticism of this paper. P. Hutchings, Australian Museum, Sydney, loaned specimens for examination. This paper is a contribution from the Marine Biology Program of the University of Arizona.

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Reconnaissance Geology of Cedros Island, Baja California, Mexico

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Abstract.—Cedros Island is composed of late Jurassic melange of Franciscan aspect (herein designated Cedros Formation) which nearly everywhere is in tectonic contact with ophiolite and a superjacent sedimentary sequence of middle Jurassic to late Cenozoic age. Analogy with structural relationships in California suggests that the Cedros Formation was subducted beneath the ophiolite as oceanic and continental plates converged. Subduction was initiated during latest Jurassic time and concluded during the early Cretaceous. The San Carlos fault, presumably the subduction surface, may be a southern extension of the Coast Range thrust. During late Cenozoic time, three bodies of Cedros Formation were uplifted along faults which truncated ophiolite, superjacent rocks through Pliocene age, the San Carlos fault, and the San Agustín shear zone.

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Cedros Island, which lies off the Pacific Coast of Baja California (Fig. 1), reveals an extensive Mesozoic and Cenozoic record of the peninsular borderland. Previous, but essentially fragmentary reports of the island geology, have been made by Veatch (1869), Hanna (1925, 1927), Tafall (1948), Hutchins (1950), Mina (1957), van West (1958), Kilmer (1972) and Jones et al., (1976). This paper, based upon reconnaissance mapping (1963–74), presents a graphic summary of the island geology (Figs. 2, 3, and 4) and a brief discussion of Cedros Island ophiolite, late Mesozoic subduction history and Cenozoic structural development. Nine formational units were mapped, five of which are new, including the Cedros, Choyal, Gran Cañon, Coloradito and Morro Redondo formations; formal descriptions will appear in a future paper.

Basement Rocks, Ophiolite and Their Relations

Cedros Formation.—This melange-structured unit, which includes graywacke, shale, chert, volcanics, limestone, serpentinite, amphibolite, and glaucophane schist, is reminiscent of the Franciscan assemblage of California. A new name—Cedros Formation—is provisionally designated because (1) detailed comparative lithologic studies of the two formations have not been made, (2) geographic continuity with undoubted Franciscan of southern California, 600 km northwest, has not been demonstrated, and (3) some lithologic differences exist, though slight, in that limestones are more abundant in the Cedros, and bedded black cherts, rare or non-existent in the Franciscan, are relatively common. Radiolarians from one chert indicate a late Jurassic age (Jones, pers. comm., 1976); those from another chert have a late Jurassic-early Cretaceous range (Riedel, pers. comm., 1974). This fossil evidence coupled with the recognition of Cedros detritus in the superjacent Coloradito Formation of probable latest Jurassic age suggests that the Cedros age is latest Jurassic and (?) older. Other occurrences of Cedros Formation in Baja Cali-

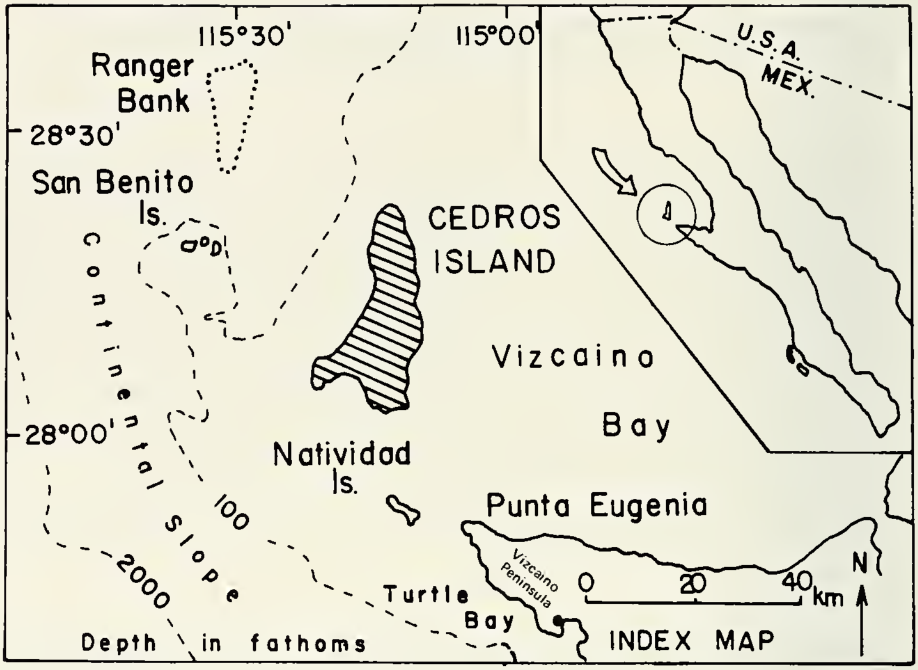
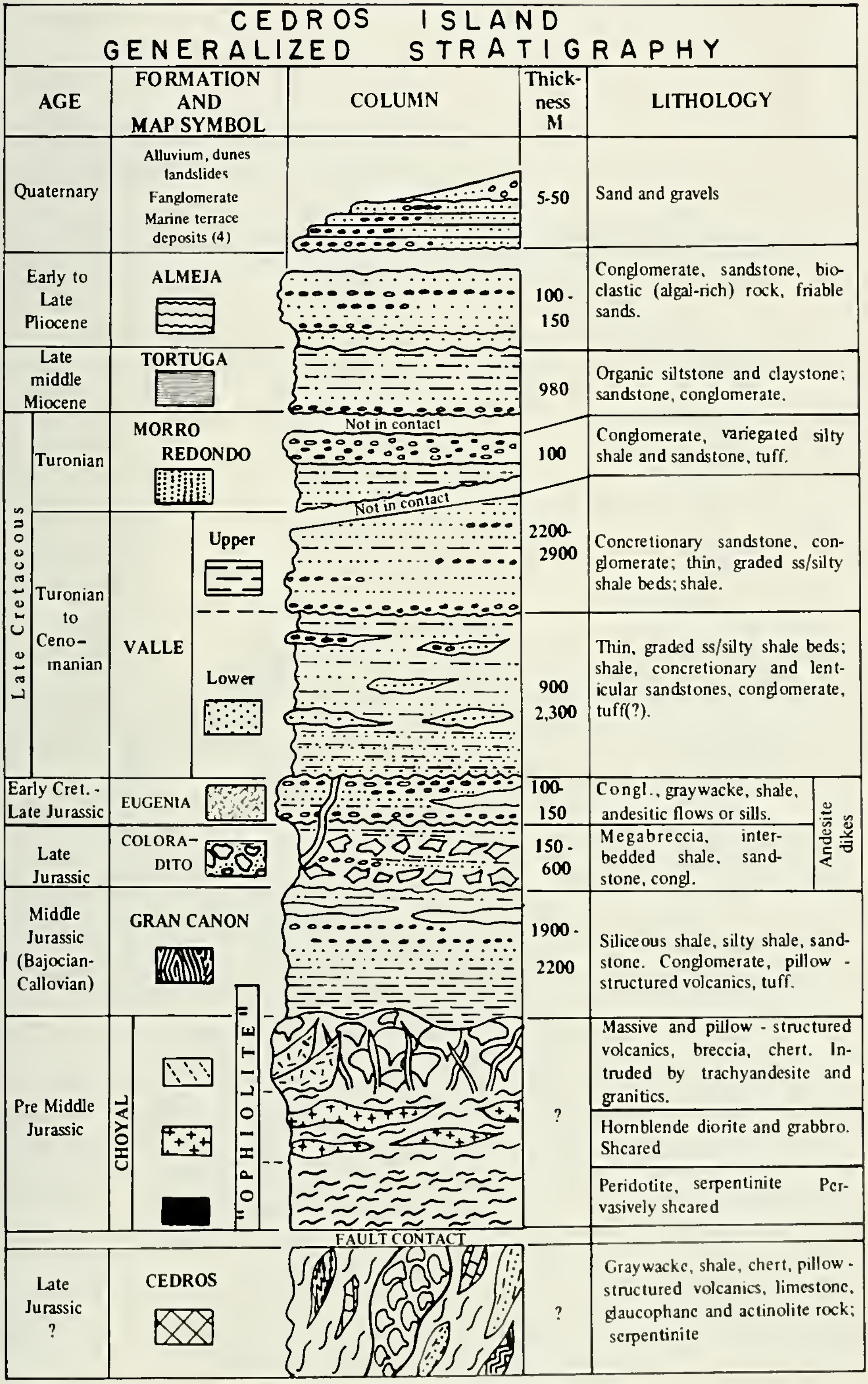


Fig. 1. Index Map.

fornia, apparently include Ranger Bank (Emery, 1948), and the San Benitos Islands, where Cohen et al., (1963) referred it to "Franciscan Group."

Choyal Formation.—This formation consists of three steeply dipping units which, along the north and northwest slopes of Monte Cedros, are in fault contact with the Cedros Formation along the San Carlos fault. The belts, in order of superposition are (1) 150- to 350-m wide belt of sheared peridotite and serpentinite, which is separated from the Cedros Formation by the San Carlos fault, (2) an intermediate, 500-m wide belt of sheared, hornblende gabbro and diorite and (3) a belt of pillow-structured greenstones intruded by trachyandesite dikes. At Punta Norte, the greenstones are also intruded by eight small plutonic bodies composed of granodiorite, quartz diorite, and gabbro. The granitic intrusions apparently are younger than the trachyandesite dikes. Suppe and Armstrong (1972) dated two quartz diorite cobbles from Punta Norte at 142 ± 13 my and 148 ± 6 my, indicating late Jurassic plutonism. The Choyal is interpreted as an oceanic crust/mantle remnant because of its similarity to rock sequences in California which Bailey et al., (1970), concluded were fragments of ancient oceanic crust.

Gran Cañon Formation.—The lower third of this unit is radiolarian siliceous shale which rests depositionally upon Choyal greenstones. The siliceous shales grade upward into a clastic section including hornblende-rich sandstones, siltstones, andesitic conglomerate, and minor volcanics. *Bositra buchi* (Roemer), a small marine bivalve from near the middle of the formation, indicates a middle



CEDROS ISLAND GENERALIZED STRATIGRAPHY

AGE	FORMATION AND MAP SYMBOL	COLUMN	Thickness M	LITHOLOGY	
Quaternary	Alluvium, dunes landslides Fanglomerate Marine terrace deposits (4)		5-50	Sand and gravels	
Early to Late Pliocene	ALMEJA		100-150	Conglomerate, sandstone, bioclastic (algal-rich) rock, friable sands.	
Late middle Miocene	TORTUGA	Not in contact	980	Organic siltstone and claystone; sandstone, conglomerate.	
Late Cretaceous: Turonian	MORRO REDONDO	Not in contact	100	Conglomerate, variegated silty shale and sandstone, tuff.	
Late Cretaceous: Turonian to Cenomanian	VALLE: Upper		2200-2900	Concretionary sandstone, conglomerate; thin, graded ss/silty shale beds; shale.	
	VALLE: Lower		900 2,300	Thin, graded ss/silty shale beds; shale, concretionary and lenticular sandstones, conglomerate, tuff(?).	
Early Cret.-Late Jurassic	EUGENIA		100-150	Congl., graywacke, shale, andesitic flows or sills.	Andesite dikes
Late Jurassic	COLORADITO		150-600	Megabreccia, interbedded shale, sandstone, congl.	
Middle Jurassic (Bajocian-Callovian)	GRAN CANON		1900-2200	Siliceous shale, silty shale, sandstone. Conglomerate, pillow-structured volcanics, tuff.	
Pre Middle Jurassic	CHOYAL "OPHIOLITE"		?	Massive and pillow-structured volcanics, breccia, chert. Intruded by trachyandesite and granitics. Hornblende diorite and grabbro. Sheared Peridotite, serpentinite Pervasively sheared	
		FAULT CONTACT			
Late Jurassic ?	CEDROS		?	Graywacke, shale, chert, pillow-structured volcanics, limestone, glaucophane and actinolite rock; serpentinite	

Fig. 2. Generalized Stratigraphy of Cedros Island.

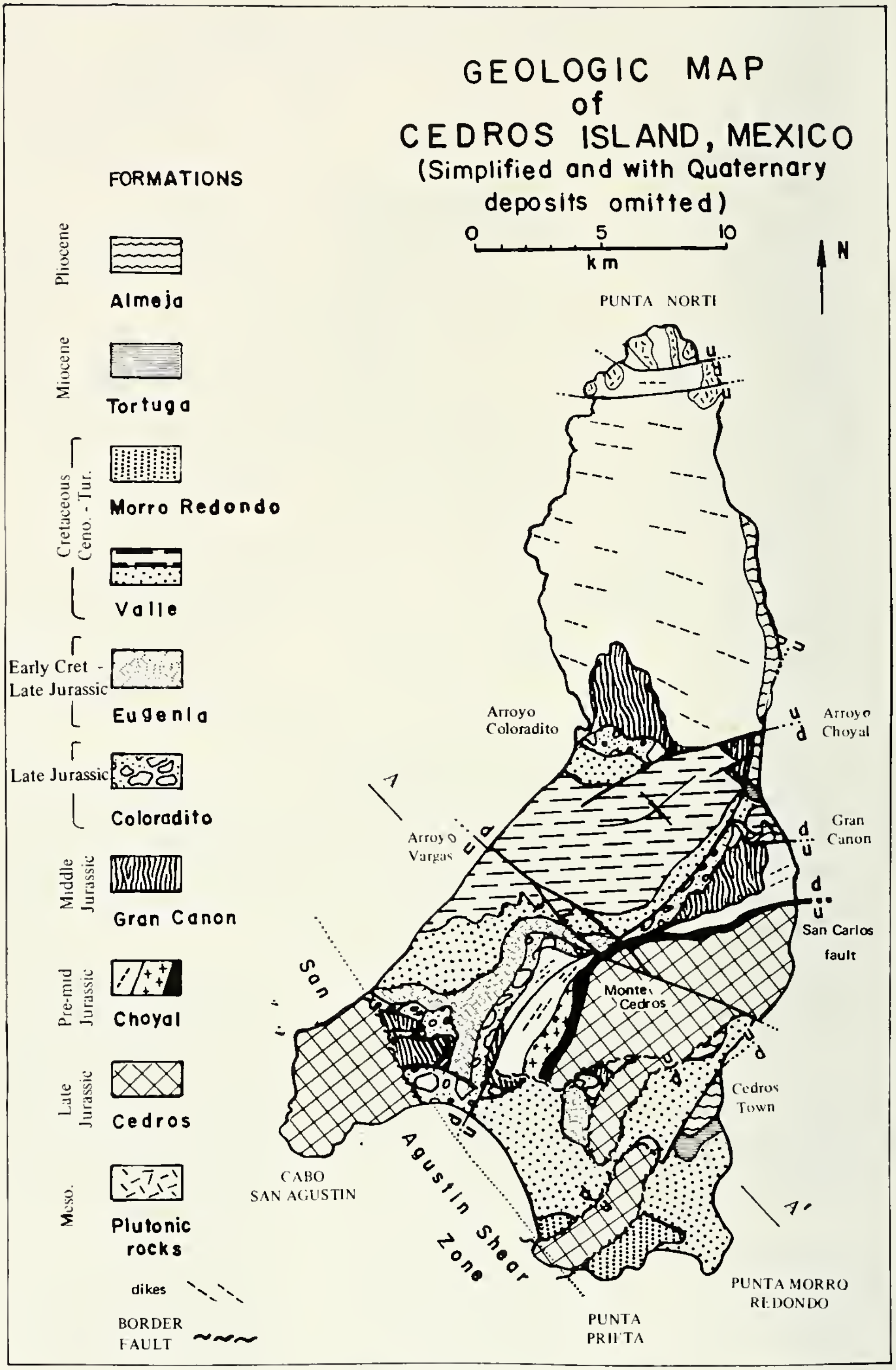


Fig. 3. Generalized Geologic Map of Cedros Island.

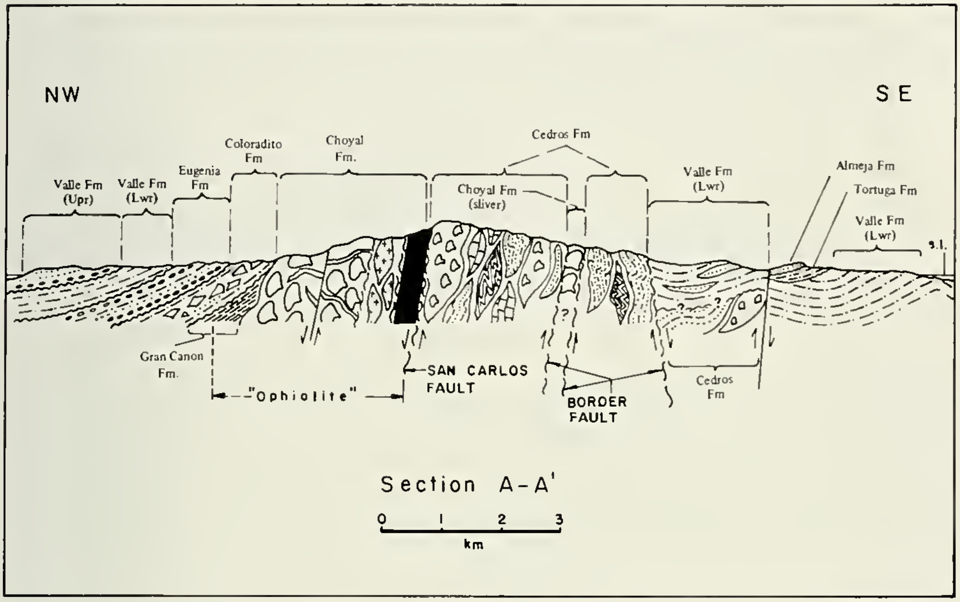


Fig. 4. Geological Section A-A'.

Jurassic (Bajocian-Callovian) age (Imlay, pers. comm., 1968). Similar lithologic sequences, which rest depositionally upon oceanic crust, are reported from the Coast Ranges (Bailey et al., 1970; Page, 1972), but these appear younger (i.e., late Jurassic-early Cretaceous) than the Gran Cañon. Gran Cañon correlatives may occur in the Sierra Nevada or Peninsular Ranges which include middle-late Jurassic sedimentary sequences (Schweikert and Cowan, 1975; Imlay, 1964).

Cedros Island Ophiolite.—If the Choyal is correctly interpreted as an oceanic lithosphere remnant, then siliceous shale of the Gran Cañon and the Choyal constitute an ophiolite. The ophiolite is not completely exposed at any one place because of faulting and overlap by younger beds. The Choyal peridotite/serpentinite and gabbro/diorite belts are exposed 5 km west of Cedros town, while Choyal greenstones and Gran Cañon siliceous shale are revealed in Gran Cañon.

The San Carlos Fault and Subduction

The San Carlos fault is a steeply dipping, northeasterly trending fault which separates Cedros and Choyal formations along the western and northern slopes of Monte Cedros. Along it, Cedros rocks are locally foliated and altered to glaucophane schist, while the adjacent Choyal serpentinite/peridotite belt is pervasively sheared. The arcuate pattern of the Choyal, dipping steeply away from a Cedros "core," suggests that the Cedros Formation structurally underlies the Choyal. The absence of dikes in the Cedros, so widespread in the overlying Choyal, coupled with melange development within the Cedros Formation itself, suggests that the Cedros was tectonically emplaced beneath the Choyal, either by subduction of Cedros or obduction of Choyal. Given substantial evidence favoring Mesozoic subduction in California, (Schweikert and Cowan, 1975; and others), Cedros emplacement is explained by subduction along the San Carlos fault, beneath a westerly-moving continent which had earlier incorporated an ophiolite (Choyal-Gran Cañon) along its western margin.

Duration of Subduction

Detritus of probable Cedros origin occurs in two formations which lie depositionally immediately above the Gran Cañon, including the Coloradito (late Jurassic) and Eugenia, (latest Jurassic-early Cretaceous). The Coloradito is composed of megabreccia and interbedded units of thinly bedded sandstone and shale. The megabreccia includes blocks of (1) abundant black chert, green chert, graywacke and greenstone of Cedros aspect, (2) occasional limestones, some of which contain Paleozoic fossils (Jones, pers. comm., 1976) and (3) rare Gran Cañon sandstone. These blocks "float" in a dark gray, shaly matrix of probable Cedros origin. In the Eugenia conglomerate, rare glaucophane schist occurs at one place.

To account for Cedros detritus in the Coloradito, it is postulated that subduction began in latest Jurassic time with Cedros rocks being, in part, uplifted along the converging continental/oceanic plate margin so that elevated blocks and masses of sheared shale could slide eastward and accumulate on the Gran Cañon. Blocks of Paleozoic limestone and Gran Cañon sandstone may have been derived directly from the continent during Coloradito deposition or were deposited earlier in the Cedros "geosyncline" and later redeposited along with chert, graywacke and greenstone. Periods of megabreccia deposition alternated with deposition of sands and muds. The rarity of glaucophane schist suggests that only a relatively small amount of this rock type was being revealed at the surface during Eugenia deposition.

Termination of subduction is suggested by the contact separating Cedros and Valle formations, 4 km southwest of Cedros town where Cedros rocks are "overlain" by Valle sandstone and shale along a gently north-dipping contact. Valle strata show little structural disturbance or alteration adjacent to the contact except for being "blackened" adjacent to thin seams of serpentinite which occupy it locally. In one place, Valle strata completely surround a knoll of Cedros rocks; the orientation of the strata surrounding the knoll is essentially constant with no signs of major faulting, diapiric deformation or landsliding. This contact is interpreted as an unconformity along which serpentinite was squeezed, causing minor shearing and blackening of adjacent Valle strata. If the Cedros/Valle contact is correctly interpreted, then Cedros subduction probably terminated during the early Cretaceous (pre-Cenomanian), well in advance of the termination of Franciscan subduction in California (Page, 1970). It is not clear when Franciscan subduction along the Coast Range thrust (Barbat, 1971) began in California. Barbat (1971) proposes a late Cretaceous beginning, while Schweikert and Cowan (1975) and Dickinson (1975) suggest a late Jurassic start. If the latter age is correct, then the San Carlos fault may be an extension of the Coast Range thrust.

Other Major Structural Features

San Agustín Shear Zone.—This northwest trending structure underlies the 5 km-wide Cabo San Agustín peninsula and a limited area at Punta Prieta (Fig. 3). It consists of an extensively sheared Cedros assemblage with predominant structural trend of N50°W. The zone appears to be a southern extension of the San Benito fault

(Cohen, et al., 1963) and probably extends southeast onto the Baja California peninsula. It may represent a zone of late Cretaceous-early Tertiary strike-slip motion between oceanic and continental plates following Cedros subduction.

Border Faults.—During post-Pliocene time, three discrete Cedros blocks were uplifted along sinuous, steeply-dipping faults, herein referred to as Border faults. Fault contacts are generally marked by a band of sheared serpentinite, including gabbro and diorite blocks. The Border faults truncate all Mesozoic and Tertiary formations as well as the San Agustín shear zone and the San Carlos fault.

Summary

Structural and stratigraphic relationships on Cedros Island indicate a late Jurassic-early Cretaceous subduction interval, wherein rocks of eugeosynclinal aspect, herein named Cedros Formation, were driven beneath middle Jurassic or older ophiolite attached to the western margin of the North American plate. The San Carlos fault, which separates the ophiolite from the Cedros Formation, probably represents the subduction plane; it may represent a southern extension of the Coast Range thrust. During subduction, Cedros debris, blocks of Paleozoic limestone and middle Jurassic sandstones, were deposited as megabreccia on the ophiolite and immediately overlying beds (Gran Cañon Formation); Cedros debris may have been derived by landsliding from Cedros masses locally uplifted along the boundary of converging oceanic and continental plates. Following subduction, it is speculated that during late Cretaceous-early Tertiary time the San Agustín shear zone was developed, possibly as a result of strike-slip movement between the plates. Uplift of three major structural blocks occurred during late Pliocene time along a new set of faults, herein called Border faults, which truncated all previous formations and major structures. General uplift during latest Pliocene and Pleistocene time, accompanied by development of marine terraces, essentially brought the island mass to its present elevation.

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Five New Morphotypes of *Phyllobothrium delphini* (Cestoda: Tetraphyllidea), Their Relationship to Existing Morphotypes, and Their Zoogeography

Jacqueline Testa and Murray D. Dailey

Abstract.—*Phyllobothrium delphini* (Bosc, 1802) was recovered from 25 marine mammals representing 12 species in two orders from four geographical localities. Five new cyst morphotypes are described. Comparison of mean measurements of each morphotype with the others suggests that *P. delphini* may represent more than one species. New host records for *P. delphini* are reported for *Tursiops gilli* Dall, *Pontoporia blainvillei* Gervais, and *Lagenodelphis hosei* Fraser. An apical sucker is noted for the first time on *Monorygma grimaldii*.

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Since its discovery in the early 1800's, large numbers of a larval cestode have been recovered from the blubber of numerous marine mammals throughout the world. First described by Bosc (1802) under the name of *Hydatis delphini*, this worm has since been the subject of many publications.

It has generally been accepted that there are at least two kinds of phyllobothriid cysts found in marine mammals, namely *Phyllobothrium delphini* (Bosc, 1802) from the blubber, and *Monorygma grimaldii* (Moniez, 1889) from the mesenteries of the body cavity. Baer (1932) recognized two groups of phyllobothriid larvae in marine mammals which he named "delphinii" and "grimaldii." Scolices of the "delphinii" group were at the ends of short (12–15 mm) invaginations while those of the "grimaldii" group were at the ends of long (12–100 cm) filament-like invaginations. Baylis (1932) listed five species of *Phyllobothrium* larvae with a total of ten synonyms, three species of *Monorygma* with seven synonyms, and *Scolex delphini* Stossich 1898 from cetaceans. Literature reviews have been published by Dollfus (1964a) and Guiart (1935).

In his discussion of *P. delphini*, Guiart (1935) described four cyst types, emphasizing that he was not trying to determine whether the larvae were different stages of the same species or different species of worms. Delyamure (1955) accepted Guiart's types and described two additional ones.

There still remains some confusion as to the relationship of *M. grimaldii* to *P. delphini*. Williams (1968) discussed the former under the name of *P. chamissonii* (Linton, 1905).

The present study was conducted to determine the systematic position of *M. grimaldii* in relation to *P. delphini* and to compare the morphology of the latter according to morphotype, different host individuals, and different host species from four geographical locations. The possibility of the existence of more than one cosmopolitan species was also examined.

Table 1. Zoogeography of *Phyllobothrium delphini* morphotypes. Parentheses indicate number of host individuals examined.

	Types											Total larvae examined per locality
	1	2	3	4	5	6	7	8	9	10	11	
Southern California												
Delphinus delphis (8)			1	14			4		1		4	
Lagenorhynchus obliquidens (4)		1	1	10	2		1	1				
Lissodelphis borealis (4)				8			4			2		
Phocoenoides dalli dalli (1)				2								
Tursiops gilli (1)							1				1	
No. of each type examined		1	2	34	2		10	1	1	2	5	58
Africa												
Arctocephalus pusillus (1)										2		
Lagenodelphis hosei (1)			1	1	4			1				
Lagenorhynchus obscurus (1)									2			
Stenella graffmani (1)		1			2							
No. of each type examined		1	1	1	6			1	2	2		14
Florida												
Kogia breviceps (1)			2	1						1	1	
Stenella caeruleoalba (1)				2			1					
No. of each type examined			2	3			1			1	1	8
Hawaii												
Stenella longirostris (1)								1				
No. of each type examined								1				
Total number examined	–	2	5	38	8	–	11	3	3	5	6	81

Materials and Methods

Phyllobothrium delphini cysts were obtained from 25 host individuals, representing 12 species of marine mammals in two orders from four geographical localities (Table 1). Host taxonomy follows that of Rice and Scheffer (1968).

With the exception of one sample collected by the junior author, all southern California samples were collected by Mr. William Walker while Curator at Marineland of the Pacific. Of these, three were from captured animals that died in captivity; the remainder from beach strandings. Cysts were received fixed *in situ* in 10% formalin or alive in the blubber. Live larvae were excised and fixed in AFA or Bouin's solution.

Hawaiian, Floridian and African samples were fixed *in situ* or free from the blubber in formalin. A single larva from *Pontoporia blainvillei* from South America was dehydrated upon arrival and unsuitable for further examination.

Cysts from *Kogia breviceps* and *Arctocephalus pusillus* were sectioned at 15 mμ, those from remaining hosts at 25 mμ. All were stained in Delafield's hematoxylin and counterstained in eosin.

Gross measurements of length and width of longitudinal sections of bladder were made with a centimeter ruler, all others by ocular micrometer. All measurements are in millimeters unless otherwise stated. Measurements considered

Table 2. Measurements of previously described morphotypes of *Phyllobothrium delphini.*

	Type			
Character	2	3	4	5
Bladder				
Long	2.8–3.5 (3.1)	5.4–9.0 (7.5)	3.5–9.5 (6.3)	4.0–6.5 (5.0)
Wide	1.5–1.7 (1.6)	4.0–4.5 (4.1)	2.0–6.5 (3.4)	2.5–6.0 (4.0)
Wall Thick	0.102–0.326 (0.214)	0.468–0.958 (0.705)	0.048–1.428 (0.827)	0.286–0.652 (0.471)
Neck				
Long	1.26–1.43 (1.35)	3.77–7.75 (6.09)	2.86–8.16 (4.72)	2.14–3.98 (2.93)
Wide	—	0.550–0.958 (0.802)	0.714–1.530 (1.077)	0.673–1.530 (1.151)
Ratio Bladder				
L to Neck L	1.9–2.7 (2.3)	—	1.01–1.80 (1.35)	1.26–2.12 (1.59)
Scolex				
Long	0.714–0.913 (0.814)	0.714–1.124 (0.898)	0.612–1.326 (1.032)	0.612–1.122 (0.887)
Wide	0.469–0.673 (0.571)	0.918–1.183 (1.122)	0.685–1.570 (1.172)	0.673–1.040 (0.856)
Acc. Sucker				
Diameter	0.113–0.162 (0.133)	0.162–0.218 (0.190)	0.145–0.284 (0.196)	0.145–0.218 (0.181)
Apical Sucker				
Long	0.046–0.065 (0.056)	0.051–0.085 (0.065)	0.036–0.091 (0.059)	0.055–0.081 (0.066)
Wide	0.046–0.065 (0.056)	0.040–0.091 (0.069)	0.042–0.111 (0.070)	0.051–0.087 (0.066)
Ex. Tubules				
Diameter	0.014–0.038	—	—	0.010–0.063
No. Examined	2	5	38	8

include length and width of bladder (as measured from the outer surface), thickness of bladder wall, length and width of neck and scolex, diameter of accessory suckers, length and width of apical sucker, and diameter of excretory tubules within the bladder wall.

Eighty-one larvae were sectioned and measured. Numbers of larvae examined from each host species and locality are listed in Table 1.

For comparison, several scolices of *Monorygma grimaldii* were embedded in paraffin, sectioned at 15 mμ, stained in Delafield's hematoxylin and counterstained in eosin. Other scolices were teased out of the invaginated neck, stained in acetocarmine, and mounted in piccolyte.

Results

All scolices of larvae recovered from the blubber were typical for *P. delphini*, being composed of four ruffled bothridia each bearing an anterior accessory sucker. A fifth (apical) sucker was present on the myzorhynchus. During this study, four of the six existing cyst morphotypes were encountered (Figs. 1a–f). As previous descriptions are incomplete, their measurements (taken from this study) are given in Table 2. Five new types were also found (Figs. 1g–k). Their measurements are given in Table 3.

Remarks.—There were similarities observed between two of the existing morphotypes as listed by Guiart (1935) and Delyamure (1955) and four of those found during this study. Type 7 (Fig. 1g) is similar to their Type 4 (Fig. 1d), in that the in-

Table 3. Measurements of previously undescribed morphotypes of *Phyllobothrium delphini*.

Character	Type 7	Type 8	Type 9	Type 10	Type 11
Bladder					
Long	3.2–6.5 (5.0)	8.0	5.0–8.5 (6.7)	3.5–11.0 (6.7)	5.0–9.5 (6.5)
Wide	3.0–5.5 (3.5)	3.5–4.5 (3.8)	5.0–6.0 (5.5)	2.5–4.5 (3.4)	3.0–4.0 (3.6)
Wall Thick	0.408–0.877 (0.765)	0.469–0.673 (0.598)	0.612–0.918 (0.734)	0.408–0.551 (0.462)	0.571–0.979 (0.773)
Neck					
Long	4.28–8.97 (5.62)	6.12–7.65 (6.66)	6.32–9.59 (8.36)	2.24–5.04 (3.59)	3.89–7.96 (4.23)
Wide	0.714–1.224 (0.982)	0.612–0.918 (0.775)	0.816–1.305 (1.074)	0.979–1.632 (1.278)	1.122–1.693 (1.377)
Ratio Bladder					
L to Neck L	0.68–0.98 (0.83)	1.05–1.31 (1.21)	0.71–0.89 (0.80)	1.56–2.25 (1.84)	1.20–1.63 (1.34)
Scolex					
Long	0.612–1.224 (0.863)	0.816–1.326 (1.020)	1.122–1.428 (1.265)	0.673–1.428 (1.152)	0.775–1.428 (0.989)
Wide	0.816–1.428 (1.124)	0.775–1.693 (1.244)	0.979–1.305 (1.189)	0.551–1.385 (0.944)	0.857–1.224 (1.047)
Acc. Suckers					
Diameter	0.145–0.243 (0.186)	0.162–0.218 (0.198)	0.203–0.267 (0.239)	0.146–0.267 (0.198)	0.170–0.218 (0.192)
Apical Sucker					
Long	0.040–0.065 (0.058)	0.063–0.067 (0.065)	0.057–0.085 (0.071)	0.050–0.107 (0.086)	0.048–0.077 (0.067)
Wide	0.050–0.081 (0.066)	0.069	0.071–0.097 (0.084)	0.068–0.123 (0.104)	0.055–0.085 (0.067)
Ex. Tubules					
Diameter	0.010–0.095	0.030–0.061	0.019–0.076	0.012–0.036	0.016–0.051
No. Examined	11	3	3	5	6

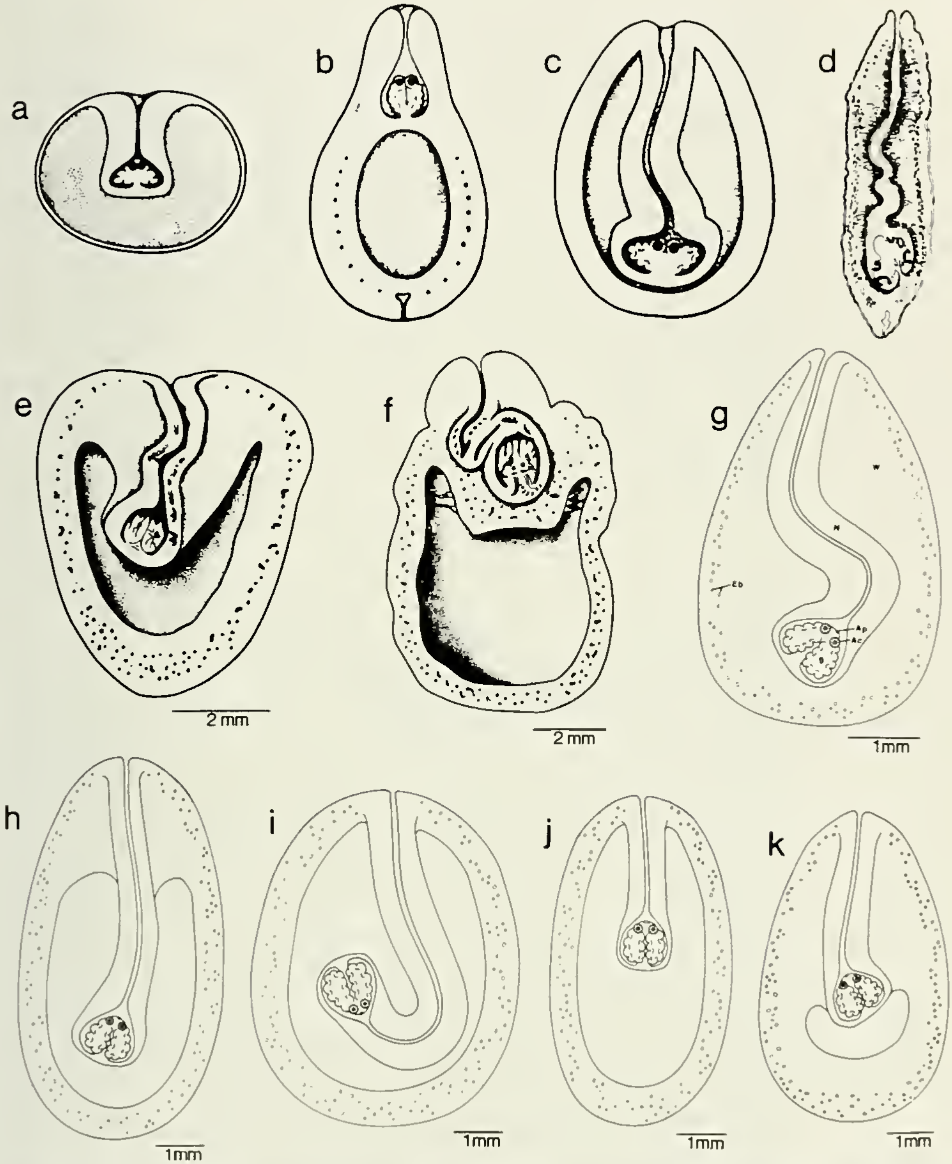


Fig. 1. Morphotypes of *Phyllobothrium delphini*: a–c, morphotypes 1–3 (Guiart, 1935); d, morphotype 4 (Baer, 1932); e–f, morphotypes 5–6 (Delyamure, 1955); g–k, morphotypes 7–11 (original). Ac, accessory sucker; Ap, apical sucker; B, bothridium; Eb, excretory tubules of bladder wall; N, invaginated neck; W, bladder wall. (No size scales available for Figs. 1a–d.)

vaginated neck and scolex are in contact with the bladder wall. However, it differs from Type 4 (as figured by Baer [1932] and described by Guiart [1935]) in ratio of bladder length to neck length (greater than one in Type 4). Type 8 (Fig. 1h) differs from the previously described Type 3 (Fig. 1c) in its thickness at the point of invagination. Types 9 and 10 (Figs. 1i and 1j), also similar to Type 3 (Fig. 1c), vary

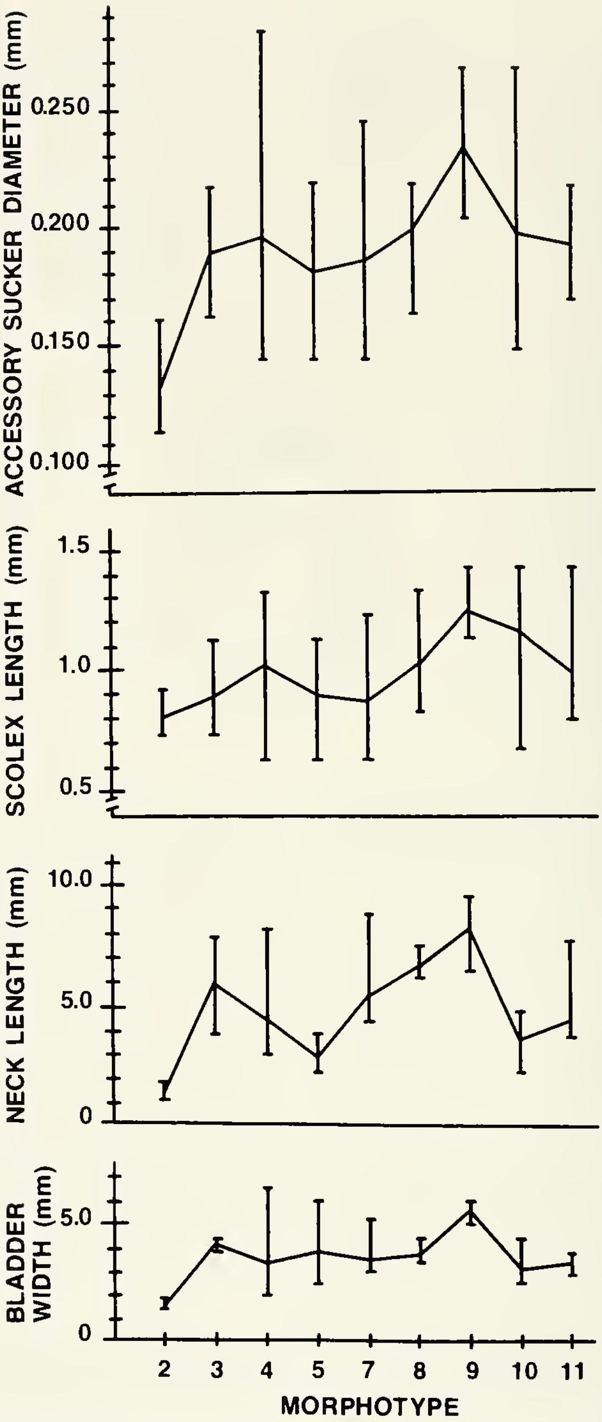


Fig. 2. Relationships of mean measurements for diameter of accessory sucker, length of scolex, length of neck, and width of bladder for each morphotype.

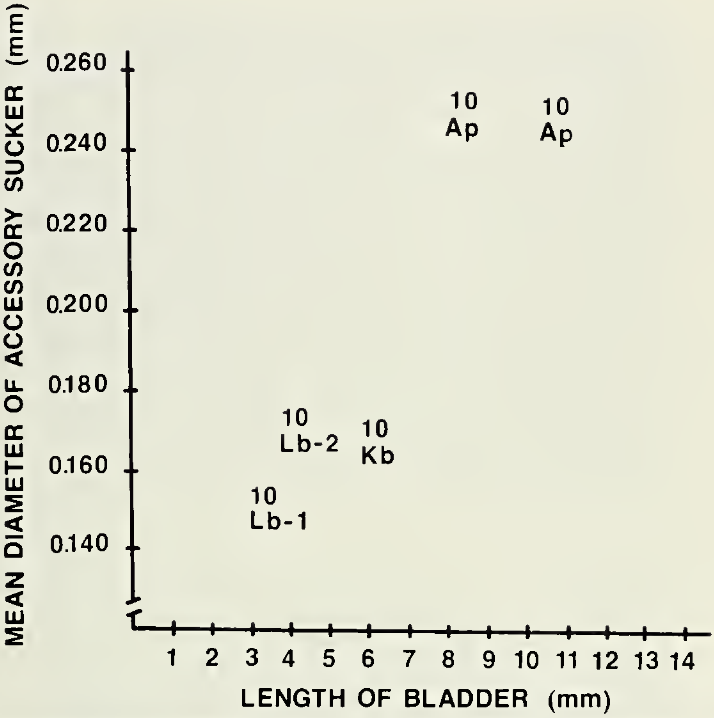


Fig. 3. Comparison of mean diameter of accessory sucker against length of bladder of morphotype 10 by host individual. Ap = *Arctocephalus pusillus*; Kb = *Kogia breviceps*; Lb 1 and 2 = *Lissodelphis borealis* 1 and 2.

in neck length–bladder length ratio (neck longer than bladder in Type 9 and reaching only to near center of bladder in Type 10).

No cysts of Types 1 or 6 were seen during this study. Delyamure (1955) described Type 6 as having accessory suckers at the "bottom" of the bothridia. The accessory suckers of all larvae examined were situated anteriorly.

New host records are noted for *Tursiops gilli* from southern California, *Pontoporia blainvillei* from South America, and *Lagenodelphis hosei* from Africa.

Scolices of *M. grimaldii* were typical for that genus. The bothridia were sessile and oval with smooth margins, and each bore an anterior accessory sucker. An apical sucker on the myzorhynchus is reported for the first time.

Discussion

A comparison of *P. delphini* and *M. grimaldii* scolices indicates that they both should maintain separate generic status. Scolices of all *P. delphini* from this study were composed of four folded bothridia, each with an anterior accessory sucker and a fifth (apical) sucker on the myzorhynchus. The four bothridia of *M. grimaldii* are oval and smooth, each bearing an anterior accessory sucker in addition to an apical sucker on a relatively large myzorhynchus. This is the first report of a fifth sucker. It is possible that this structure was overlooked by previous authors, as it had been in *P. delphini*.

Neither Guiart (1935) nor Delyamure (1955) attempted to separate the larvae of *P. delphini* taxonomically by morphotype. For the purposes of this study their

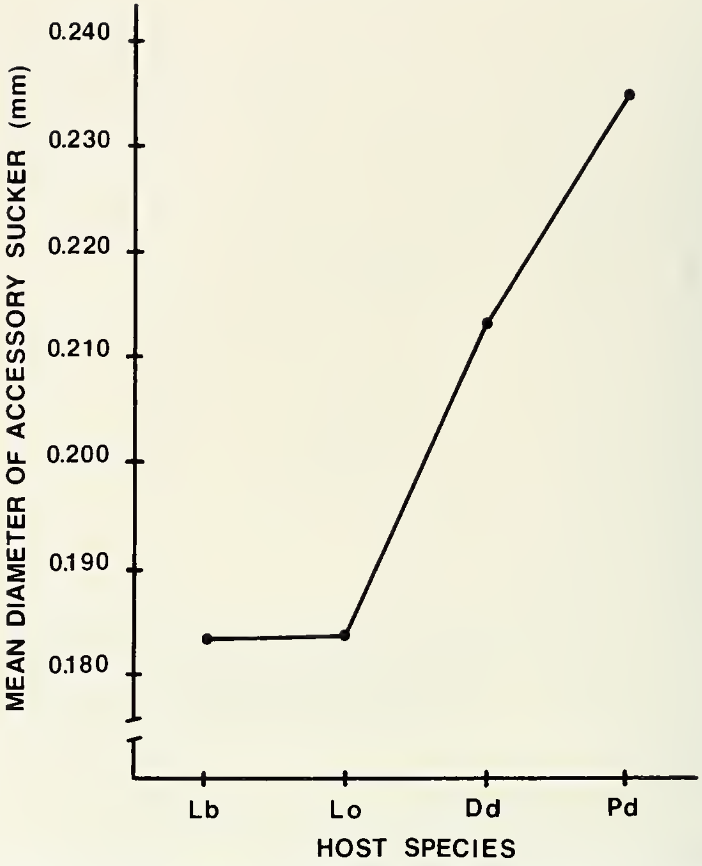
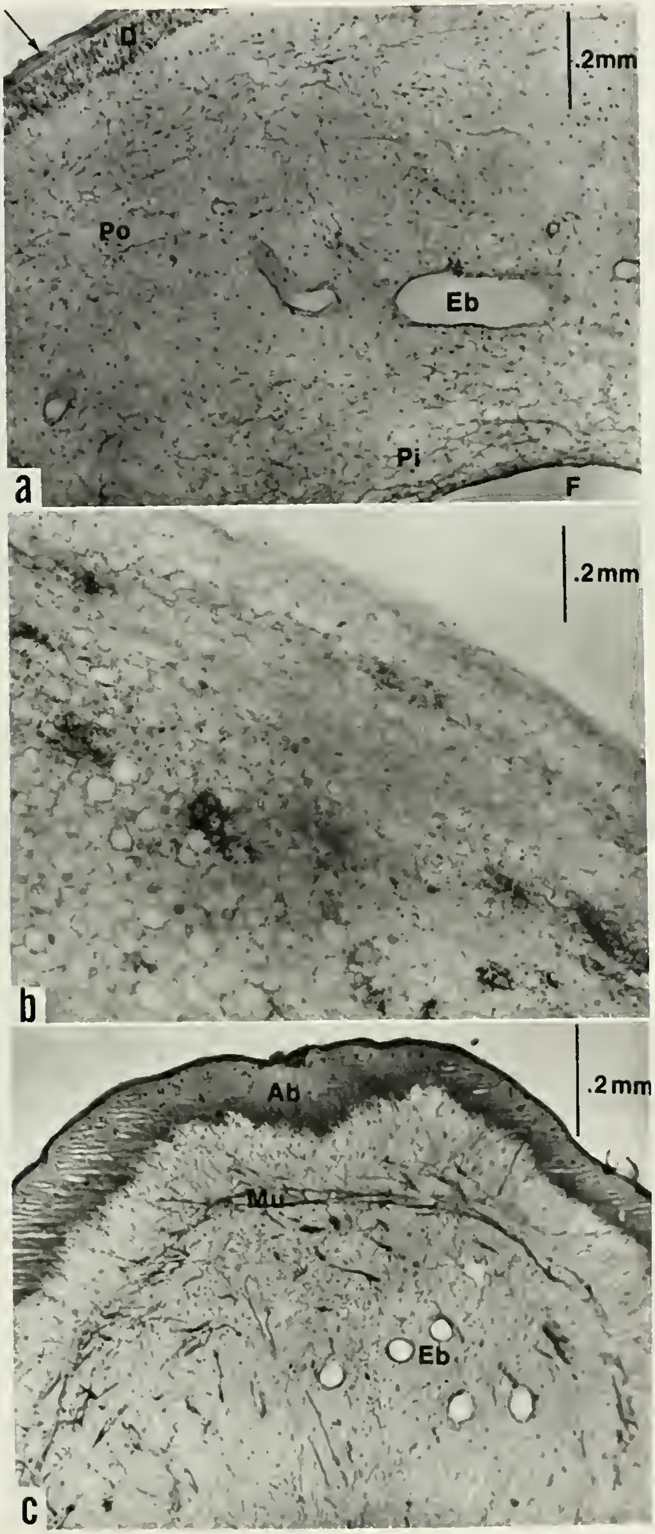


Fig. 4. Comparison of mean diameter of accessory suckers of morphotype 4 from different host species. Dd = *Delphinus delphis*; Lb = *Lissodelphis borealis*; Lo = *Lagenorhynchus obliquidens*; Pd = *Phocoenoides dalli dalli*.

types were accepted as valid morphological variants. New types encountered were grouped according to gross morphological appearance during the initial phase of our investigation. Mean body measurements of worms of a given morphotype, from a single host individual, or from a single host species were then compared with one another. Only when values for length of scolex and neck, width of bladder and diameter of accessory sucker were considered according to morphotype does a pattern emerge (Fig. 2). That is, for a given morphotype, body dimensions fell into a somewhat predictable range. This represents the possibility that each morphotype or group of related morphotypes may indeed represent separate species.

→

Fig. 5. Longitudinal sections of *Phyllobothrium delphini* bladder wall: a. Section through normal bladder wall; b. Section of abnormal bladder wall of a cyst recovered from *Delphinus delphis* (normal histology is absent from all parts of the bladder); c. Section through abnormal bladder wall of a cyst recovered from *Phocoenoides dalli dalli*. Ab = abnormal outer layer; D = dense layer of dark staining cells; Eb = excretory tubules of bladder wall; F = fluid filled portion of bladder; Mu = muscle fibers; Pi = inner layer of loose bladder parenchyma; Po = outer layer of parenchyma with muscle fibers; arrow indicates clear outer layer.


D
.2mm
Po
Eb
Pi
F
a
.2mm
b
Ab
.2mm
Mu
Eb
c

Numbers of individuals of each morphotype are listed in Table 1 according to locality and host species. It is apparent that members of a type class can be found in different localities, host species and even different orders. There is also a variation in the distribution of morphotypes. Type 4 was the most commonly encountered larva in southern California, while Type 5 was most frequent in Africa. This, in all probability, reflects the distribution of adult worms.

There is some indication of host influence on the larvae (Fig. 3). The number of cysts is too small to be able to draw any firm conclusions, but the suggestion is that at least different orders of marine mammals may play a role in determining the overall size of the cysts. Data shown in Fig. 4 supports this idea, showing differences in accessory sucker diameter for a large number of worms of the same morphotype taken from different host species. Further evidence comes from the fact that, regardless of morphotype, the bladder walls of all larvae recovered from a particular host individual were histologically alike, whether normal (Fig. 5a) or not (Figs. 5b and 5c). Abnormal appearances could not be attributed to post-mortum degradation.

Just how the marine mammal becomes infected with *P. delphini* is still a matter of conjecture. Skrjabin (1972) eliminated krill as the possible primary intermediate host, due to the fact that odontocete and baleen whales which had fed on fish were heavily infected, while those baleen whales which had fed on krill were rarely infected. He found that *Phyllobothrium* larvae from squids were digested in the whale's stomach while *Scolex pleuronectis* larvae entered the mucous membranes of the gut. From this Skrjabin (1972) concluded that *S. pleuronectis*, taken with a fish meal, burrowed through the gut wall and entered the circulatory or lymphatic system. From there they settled in the blubber and through a series of transformations came to look like *P. delphini*. He and Euzet (1959) reported having seen all phases of this transformation, but Dollfus (1964b) did not.

Partial argument against this idea is given by Skrjabin (1972) in his statement that dolphins of the Black Sea are not parasitized by *P. delphini* even though the local fish are infected with *S. pleuronectis*.

The recent work of Hamilton and Byram (1974) provides additional insight into this problem. They induced in vitro transformation of a plerocercoid with quadriloculate bothridia taken from the gastropod *Fasciolaria tulipa* to a larva with triloculate bothridia, one pair of bifurcated hooks, an accessory sucker and muscular pad. These changes placed the worm in the genus *Acanthobothrium* van Beneden, 1849. Their (Hamilton and Byram, 1974) figure of the untreated larval scolex is like that of *Scolex polymorphus trilocularis* illustrated by Dollfus (1964b, fig. 16). This raises the possibility that the *Scolex* larvae are onchobothriids as adults, introducing once again the problem of an elasmobranch cestode infecting marine mammals.

If Skrjabin's (1972) observation that *Phyllobothrium* larvae in squid are digested in the whale's stomach is typical, one would expect the same fate for those larvae in teleosts. There must then be another mode of infection, possibly through the procercoid taken with a fish or squid that had recently fed on an infected crustacean. If "activation" (i.e. stimulation of the larva to begin the next stage of development) of the procercoid in the fish or squid has taken place, the stimulus may be sufficient to allow development of the larva into a plerocercoid in the marine mammal. This idea is consistent with Skrjabin's (1972) statement that the

Fig. 6. *Phyllobothrium delphini* in blubber of *Delphinus delphis*.

krill-eating baleen whales, which accidentally ingest an occasional fish, are only rarely infected with *P. delphini*.

It appears possible that sharks become infected with *P. delphini* by eating the flesh of marine mammals, since these larvae are such common parasites of the blubber (Fig. 6). Southwell and Walker (1936) note that "cysticerci found in seals are capable of retaining their viability for at least 11 days after death of the host." During the present study, larvae in the blubber were viable after being stored at 4°C for one month.

Shark attacks on cetaceans have been previously reported (Wood et al., 1970). Ridgway and Dailey (1972) show evidence of an attack on a common dolphin (*Delphinus delphis*) by a mako shark (*Isurus oxyrhynchus*, according to tooth pattern) that occurred along the southern California coast. The Greenland shark, *Somniosus microcephalus*, is known to bite off the flesh of living whales (Johnston, 1937, according to Williams, 1968).

Additional work is underway using experimental infections and *in vitro* cultivation to answer the remaining questions on the transmission, distribution and speciation of *P. delphini*.

Acknowledgments

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The Effect of Endogenous 5-HT on K Ion Enhancement of Ciliary Activity in the Mussel *Mytilus edulis*

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Abstract.—The cilioexcitatory effect of 5-HT (serotonin) on lateral cilia has been observed in *Mytilus*. In the presence of exogenous 5-HT, K ions enhanced the cilioexcitatory effect of 5-HT after a 3 s lag period. Addition of BOL (bromolysergic acid; 5-HT inhibitor decreased the cilioexcitatory effect of 5-HT. An increase in the lag period was also observed. Addition of PCPA (p-chlorophenylalanine; tryptophan hydroxylase inhibitor) decreased endogenous stores of 5-HT and the cilioexcitatory effect of K ions. An increase in the lag period was also observed. The present investigation shows that K ions have a cilioexcitatory effect on lateral cilia after producing a momentary lag period. Furthermore, the presence of 5-HT is required to bring about the cilioexcitatory effect of K ions.

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The cilioexcitatory effect of 5-HT (serotonin) has been observed in *Mytilus* (Aiello and Guideri, 1965). Its presence has been demonstrated by photofluorometry, bioassay and paper chromatography (Gosselin, Moore and Milton, 1962; Aiello, 1962). Enzymes have been proved to exist not only for the biosynthesis of 5-HT, but also for its oxidation (Aiello, 1965; Blaschko and Milton, 1960). The evidence thus far indicates that 5-HT is the principal endogenous cilioexcitatory substance involved in the nervous control of ciliary activity in the gill of *Mytilus*.

Potassium (K) ion effects on cilia are especially ubiquitous (Aiello, 1960). K ions activate or increase the average rate of beating of lateral cilia (Gray, 1922). This ion has also caused momentary abrupt stoppage of cilia referred to as the lag effect (Takahashi, 1971). The purpose of this investigation was to study the relationship of endogenous stores of 5-HT and the K enhancement of ciliary activity.

Methods and Material

All experiments were performed on the mussel, *Mytilus edulis*. Before each experiment, mussels were placed in a container of sea water. The posterior adductors were cut, each gill was isolated with its branchial nerve, visceral ganglion and a piece of adductor muscle for support. The rate of beating of lateral cilia was measured with a calibrated stroboscopic light source. Drugs were added by replacing the contents of a perfusion dish with the desired concentration of the drug in sea water at 21°C and continuing to perfuse with the drug solution. The following drugs were used: bromolysergic acid diethylamine (BOL; 10^{-6}M); 5-hydroxytryptamine (5-HT, serotonin; 10^{-6}M) as creatinine sulphate; p-chlorophenylamine (PCPA; 10^{-7}M) as a methyl ester; hydrochloride and potassium (K^+; 30–400 mM) as a chloride.

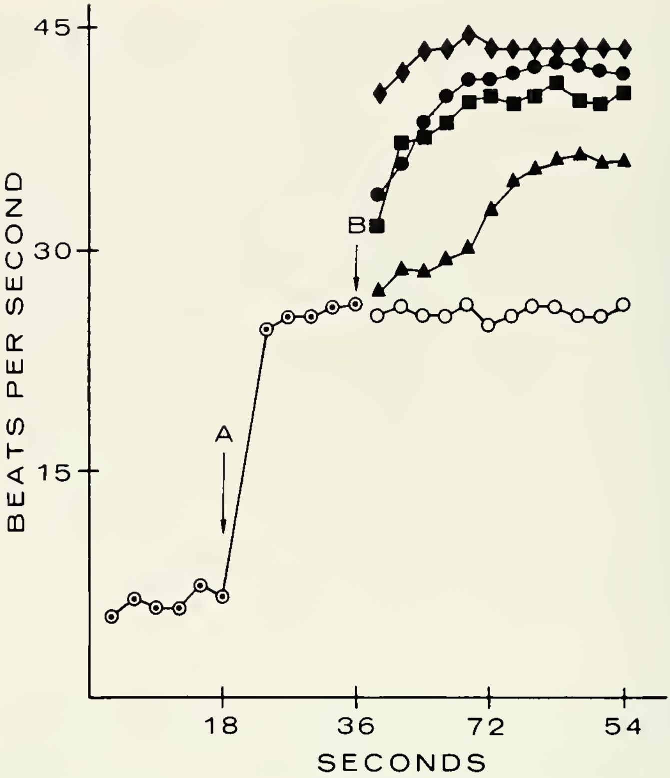


Fig. 1. The effect of 5-HT and K^+ on the average rate of beating of lateral cilia. Addition of 10^{-6}M 5-HT is indicated (letter A). Letter B indicates subsequent perfusion with 30 mM K^+ (○—○), 80 mM K^+ (▲—▲), 120 mM K^+ (■—■), 160 mM K^+ (●—●) and 400 mM K^+ (◆—◆).

The localization of 5-HT in the branchial nerve was accomplished by means of the fluorescence histochemical method and the relative measurement of the 5-HT fluorophore was made with a Leitz MPVII system equipped with a photomultiplier.

Results

In the presence of 10^{-6}M 5-HT, K^+ produced significant increases in the average rate of beating of lateral cilia. However, there was a lag period lasting three seconds before a significant increase in average rate of beating was observed. The 30 mM K^+ maintained the basal rate of beating of lateral cilia in the presence of 5-HT. Concentrations of $K^+ > 30$ mM produced significant increases in the average rate of beating (Fig. 1). The addition of 10^{-6}M BOL significantly altered the cilioexcitatory effect of K^+. The 30 mM K^+ did not maintain a basal average rate of beating. Furthermore, there were periods of about twelve seconds delay when lateral ciliary activity stopped. However, increasing amount of K^+ added to the perfusate decreased the lag period. K^+ could not enhance ciliary activity for long periods of time when BOL was present (Fig. 2). Intramuscular injection of PCPA decreased the intensity of the 5-HT fluorophore within the gill (Fig. 3). Specimens were removed subsequent to 5-HT fluorophore measurement on days one, four,

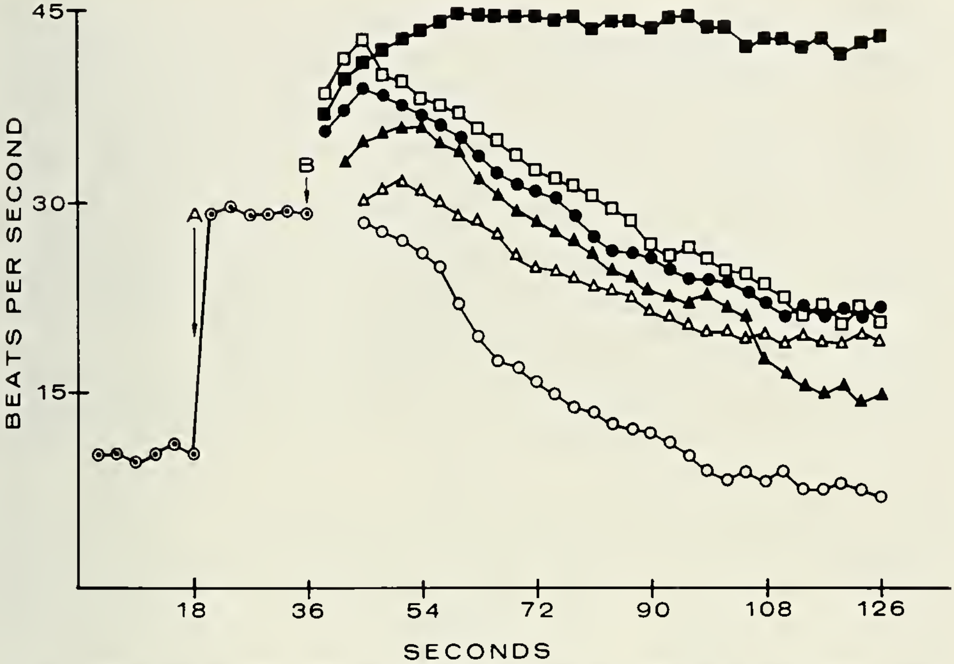
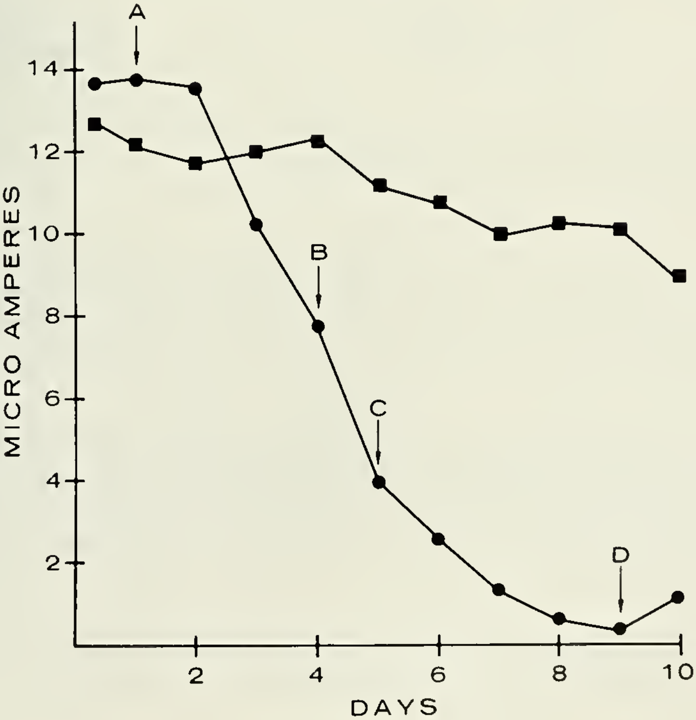


Fig. 2. The effect of 5-HT, BOL and K^+ on the average rate of beating of lateral cilia. Letter A indicates addition of 10^{-6}M 5-HT. Letter B indicates subsequent addition of 10^{-6}MBOL plus 30 mM K^+ (○—○), 80 mM K^+ (△—△), 120 mM K^+ (▲—▲), 160 mM K^+ (●—●) and 400 mM K^+ (□—□). Note 400 mM K^+ was added with subsequent removal of BOL (■—■).



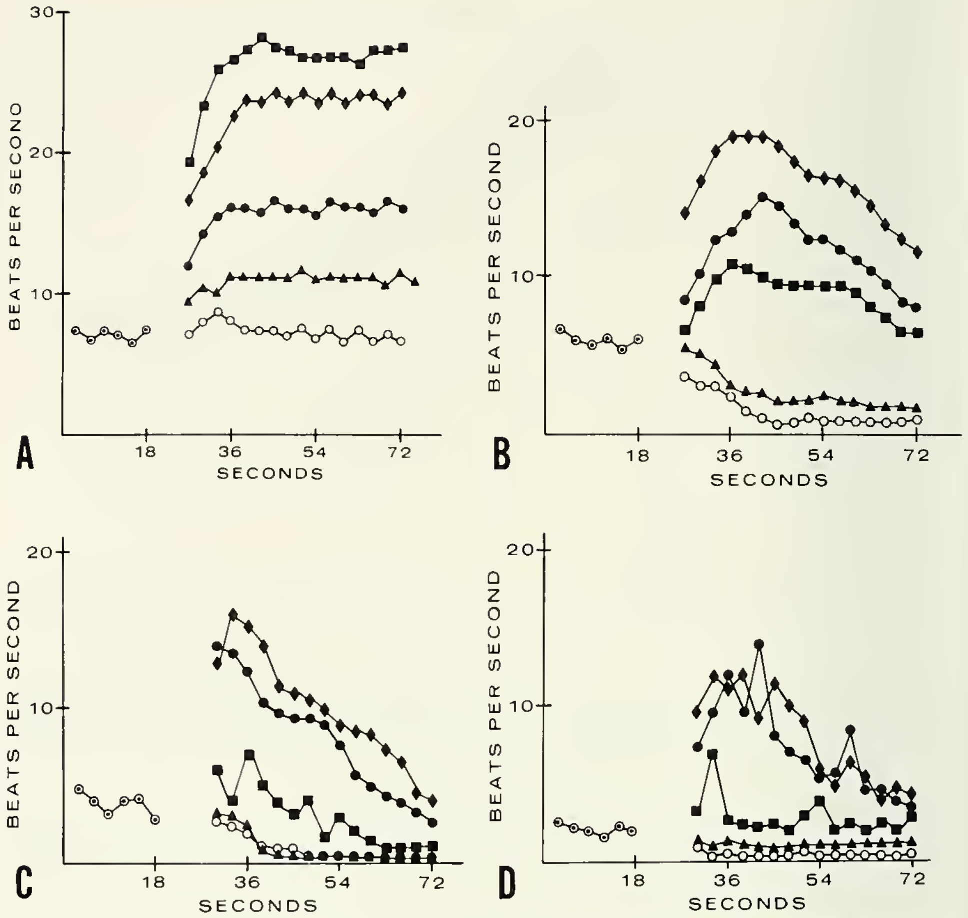


Fig. 4. The effect of K$^+$ on ciliary activity: A–D represent samples specified by the same letters appearing in Fig. 3. The gills were perfused with 30 mM K$^+$ (○—○), 80 mM K$^+$ (▲—▲), 120 mM K$^+$ (●—●), 160 mM K$^+$ (◆—◆) and 400 mM K$^+$ (■—■).

five and nine (Fig. 4A–D, respectively). The cilioexcitatory effect of increasing amounts of K decreased with time. There was also a gradual increase in the lag period produced by K$^+$. A dosage of 400 mM K$^+$ which was previously maximally cilioexcitatory was virtually ineffectual at the end of the time period.

Discussion

The above experiments show that increasing amounts of K$^+$ in the perfusate enhance the average rate of beating of lateral cilia. A momentary lag period of 3 s is first observed before cilioexcitation is initiated. The lag effect of K$^+$ supports the view that the response is related to the excitable properties of the lateral

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Fig. 3. Relative measurement of 5-HT yellow fluorophore in normal (■—■) and PCPA (10^{-7}M) treated (●—●) specimens. Letters indicate times at which specimens were removed for stroboscopic examination.

ciliated cell membrane (Takahashi, 1971). Although the transmembrane electrical potential has not been recorded from these cells, the effects of direct current (Murakami, 1968) and of K^+ ions indicate that these agents probably exert their action by depolarizing the ciliated membrane.

PCPA is believed to bind to tryptophan hydroxylase (rate limiting enzyme for 5-HT formation) at or near the active site (Sanders-Bush, Gallager and Sulser, 1974). In this study PCPA caused a decrease in the 5-HT fluorophore with a concomitant decrease in the enhancement of cilioexcitation, and an increase in the lag effect produced by K^+. These results suggest that the short lag effect of K^+ requires the presence of 5-HT and might be indicative of an effect on the transmembrane potential of the ciliated lateral cell. While the long lag effect observed in the absence of 5-HT might imply that changes in the intracellular concentration of K^+ within the cilia lateral cell are required to produce an effect on ciliary activity.

Conclusion

The present study shows that the cilioexcitatory effect produced by K^+ ions requires the presence of endogenous 5-HT. Removal of endogenous 5-HT significantly modifies the response of lateral cilia to K^+.

Acknowledgments

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A New Species of *Rhinebothrium* (Cestoda: Tetraphyllidea) and Redescription of Three Rhinebothriate Species from the Round Stingray, *Urolophus halleri* Cooper in Southern California

Ralph Appy and Murray D. Dailey

Abstract.—A new species of *Rhinebothrium* (Tetraphyllidea: Phyllobothriidae) is described from the spiral valve of three round stingrays, *Urolophus halleri* Cooper, collected in Anaheim Bay, Seal Beach, California. Redescriptions of *R. urobatidium* (Young, 1955) n. comb., *R. bilobatum* (Young, 1955) n. comb. and *Caulobothrium multorchidum* (Young, 1954) n. comb. are made from material available in the USNM Helminthological Collection and new material from the type host. The validity of generic characteristics is discussed and generic evaluations of *Rhinebothrium* Linton, 1890, *Caulobothrium* Baer, 1948, and *Rhabdotobothrium* Euzet, 1953, are emended.

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Young (1954, 1955), reported and described several species of *echeneibothrium* Beneden, 1849, from *Urolophus halleri* Cooper (=*Urobatis halleri*) in Southern California. Williams (1966) noted some of Young's species as erroneously allocated to *Echeneibothrium*, and both Campbell (1970) and Cornford (1974) indicated confusion in their generic allocations. This report is aimed at substantiating the taxonomic status of some of these species, and emending the generic evaluations of *Rhinebothrium* (Linton, 1890) Baer, 1948, *Caulobothrium* Baer, 1948, and *Rhabdotobothrium* Euzet, 1953, to include recently described generic variability.

During August and September, 1973, four round stingrays, *Urolophus halleri* Cooper, collected in Anaheim Bay, Seal Beach, California were found to be infected with two previously described and one new species of rhinebothriate cestodes. Specimens were removed from the spiral valves, observed, then fixed in hot AFA. Whole mounts were stained in celestine blue B or Semichron's carmine, dehydrated in ethanol, cleared in xylene and mounted in Permount. Paraffin sections were cut at 8 and 10μ and stained in Delafield's hematoxylin and eosin. All figures were drawn with the aid of a drawing tube and represent material collected in this study. Average measurements and standard deviations of measured items are given with ranges and sample size (N=), in parentheses. Redescriptions of *R. urobatidium* (Young, 1955) n. comb., *R. bilobatum* (Young, 1955) n. comb. and *Caulobothrium multorchidum* (Young, 1954) n. comb., were made from type material available in the USNM Helminthological Collection and specimens found in the present study. All measurements are in microns unless otherwise stated.

Rhinebothrium urobatidium (Young, 1955) n. comb.
(*Echeneibothrium urobatidium* Young, 1955)
Fig. 1

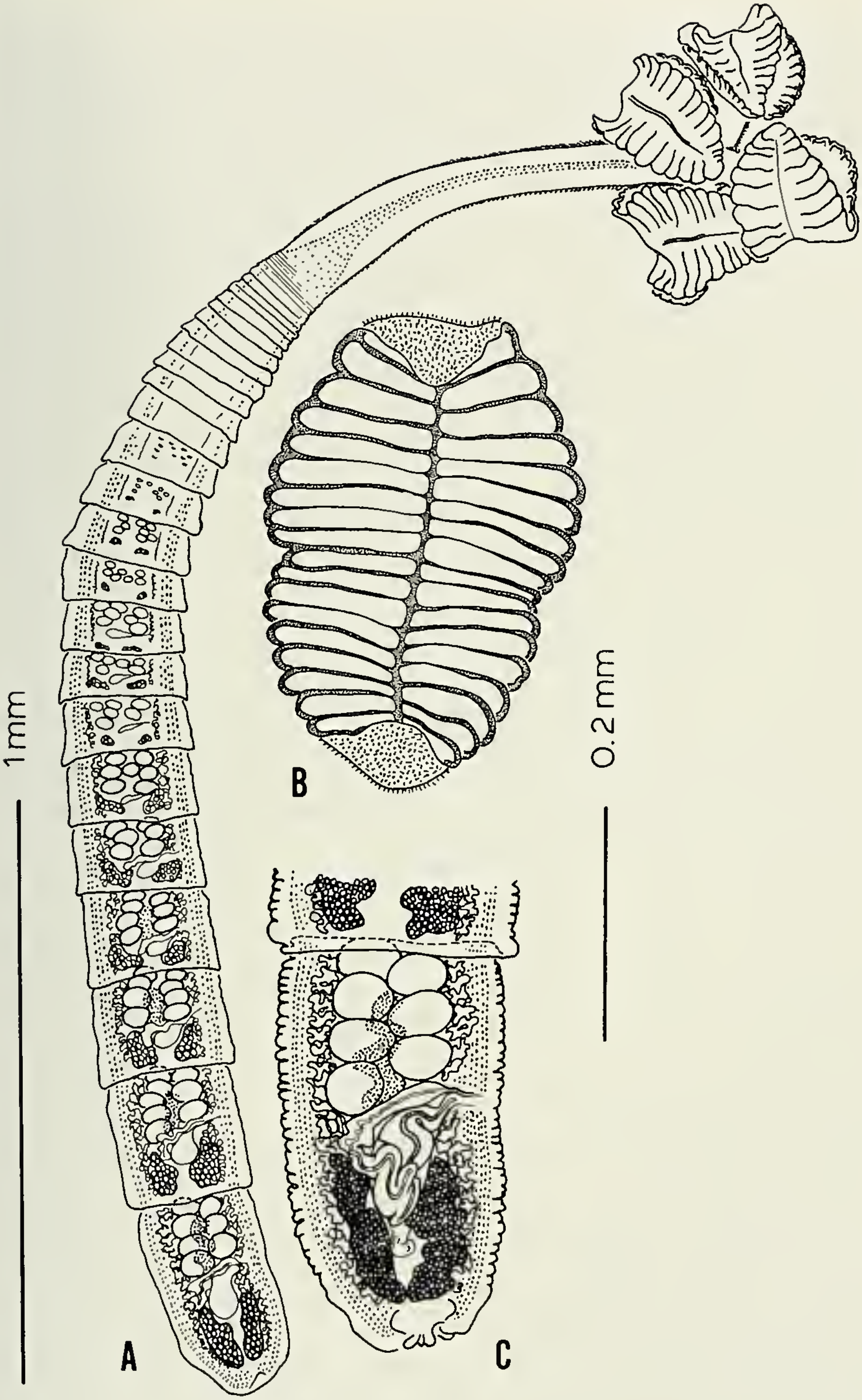

Fig. 1. *Rhinebothrium urobatidium* (Young, 1955) n. comb.: A. Entire worm; B. Bothridium; C. Terminal mature proglottid.

The following description is based on ten specimens: one, of two specimens present on Young's (1955) type slide, and nine complete specimens (three mature, six immature) found in three type host individuals from Anaheim Bay. Since neither specimen on Young's type slide is designated as the holotype, the larger and more mature of these is hereby designated as lectotype.

Phyllobothriidae: Mature individuals, small craspedote worms, (N = 3) 3.3 (3.1 to 3.4) mm long by 256 (242 to 283) wide (lectotype 7.5 mm by 296); number of segments 30 to 41 (N = 3) (lectotype 58); four bothridia borne on pedicels, 91 (67 to 128) long by 68 (47 to 81) wide (N = 7) (lectotype 117 to 167 by 61 to 74); bothridial margin slightly lobulated; peduncle 550 (478 to 660) long by 101 (87 to 114) wide (N = 3) (lectotype 996 by 141); bothridia 401 (363 to 451) long by 195 (188 to 215) wide (N = 5) (lectotype 243 to 301 by 227 to 291), and divided by one longitudinal and 19 to 21 (lectotype 22) transverse septa (N = 5) into 38 to 42 (3 worms, N = 5) (lectotype 44) weak loculi; rostellum absent; terminal segment longer than wide, 435 (357 to 573) long by 219 (210 to 227) wide (N = 3) (lectotype 267 to 428 by 207 to 448); cirrus pouch lateral, extending posteriorly into medullary region in more mature proglottids, 87 (58 to 129) long by 56 (43 to 77) wide (N = 7) (lectotype 70 to 150 by 24 to 60); testes subspherical, 6 to 12 in number (N = 26) (6 to 9 in lectotype), located anterior to cirrus pouch and measuring 48 (37 to 67) long by 49 (27 to 80) wide (N = 9) (lectotype 25 to 62 by 32 to 79); Cirrus spined; genital pore in posterior half of segment in mature proglottids; genital atrium absent; ovary restricted to posterior one-third of proglottid, lobes 108 (60 to 247) long by 51 (35 to 75) wide (N = 16) (lectotype 25 to 62 by 32 to 79); ovary X-shaped in transverse section (tetralobate); vitellaria compact, extending in lateral bands entire length of proglottid; spines present on peduncle and pedicels; peduncle spines 5 long, diminishing in size at area of strobilization; pedicel spines approximately 3 long.

Immature worms (those showing only some testis development), are 1.9 (1.2 to 2.5) mm long by 146 (121 to 175) wide (N = 6); number of segments 22 (16 to 24) (N = 6); peduncle 339 (87 to 606) long by 82 (74 to 101) wide (N = 6), spined; bothridia 437 (337 to 538) long by 190 (155 to 276) wide (N = 13), and divided by one longitudinal and 19 to 23 transverse septa into 38 to 46 weak loculi (N = 15); rostellum absent; testes subspherical, varying in number from 7 to 12 (N = 33), located anterior to cirrus pouch and measuring 16 (10 to 23) long by 27 (13 to 45) (N = 7) wide.

One mature and one immature specimen have been deposited in the USNM Helminthological Collection.

Type host: *Urolophus halleri* Cooper (=*Urobatis halleri*).

Location: Spiral valve.

Locality: San Diego Bay, California; Anaheim Bay, California.

Type specimens: Lectotype and paralectotype USNM Coll. No. 49097 and referred specimens No. 74599.

Remarks.—Young's original description (1955) of five individuals of *R. urobatidium* neglected to include measurements of the length and width of the total worm, pedicels, bothridia, cirrus pouch, testes and ovary. Young also described 10 to 12 testes while his figure depicts only seven. Measurements of mature proglottids do not fit measurements taken from the type material and, in addition, spines present on the peduncle and pedicels were not mentioned.

While the mature specimens examined in this study were similar to the type material, several discrepancies were noted: total length (3.1 to 3.4 vs. 7.5 mm), number of proglottids (30 to 41 vs. 58), number of testes (6 to 12 vs. 6 to 9), and number of loculi in each bothridium (38 to 42 vs. 44). The present material appears less mature than the type specimen which may explain the smaller size and fewer segments. The range in number of loculi in each bothridium is more likely due to an error in counting than to natural variation as septa are weak and bothridia usually somewhat crumpled. The range in the number of testes, while greater than the type specimen, corresponds to Young's (1955) original description (10 to 12). Immature specimens, while proportionately smaller in most respects, show bothridial measurements and loculi counts that are similar to those of the more mature worms. Spines present on the peduncle and pedicels, and the craspedote nature of proglottids of all individuals help distinguish this species. The validity of *E. urobatidium* is not questioned; however, its placement in the genus *Echeneibothrium* warrants change since all members of the genus possess a rostellum. The authors therefore designate the type specimen as *Rhinebothrium urobatidium* (Young, 1955) n. comb. in keeping with its nonrostellate nature, and absence of testes between the cirrus pouch and the ovary on the poral side of the proglottid.

Rhinebothrium bilobatum (Young, 1955) n. comb.
(*Echeneibothrium bilobatum* Young, 1955)

The following description is based on a single, badly fractured holotype (only specimen) in the USNM Helminthological Collection.

Phyllobothriidae: Small worm, 2.7 mm (measurement taken from Young's, 1955, figure) in total length; bilobed bothridia borne on pedicels; pedicels 131 and 139 long by 60 and 70 wide; peduncle 153 long by 99 wide; both pedicels and peduncle without spines; rostellum absent; genital atrium not visible.

Type host: *Urolophus halleri* Cooper (=*Urobatis halleri*).

Location: Spiral valve.

Locality: San Diego Bay, San Diego, California.

Type specimen: Holotype USNM Helm. Coll. No. 45976.

Remarks.—Young's description (1955), based on a single immature worm, appears valid. The description neglects, however, the presence or absence of spines. In addition, the lack of a definitive "neck" (=peduncle), noted by Young (1955), is difficult to confirm due to overstaining of the holotype. It appears that a short peduncle may be present. The absence of a rostellum in this species warrants the new generic designation *Rhinebothrium bilobatum* (Young, 1955) n. comb. Euzet and Carvajal (1973) previously regarded this species as belonging to the genus *Rhinebothrium*.

Caulobothrium multorchidum (Young, 1954) n. comb.
(*Echeneibothrium multorchidum* Young, 1954)
Fig. 2

The following description is based on material available in USNM Helminthological Collection, and one additional specimen found in *U. halleri* from Anaheim Bay. Two specimens are present on Young's (1955) type slide; the larger was designated by him as holotype and is used in this description.

Phyllobothriidae: Small acraspedote worm, 2.6 mm long by 162 wide (holotype

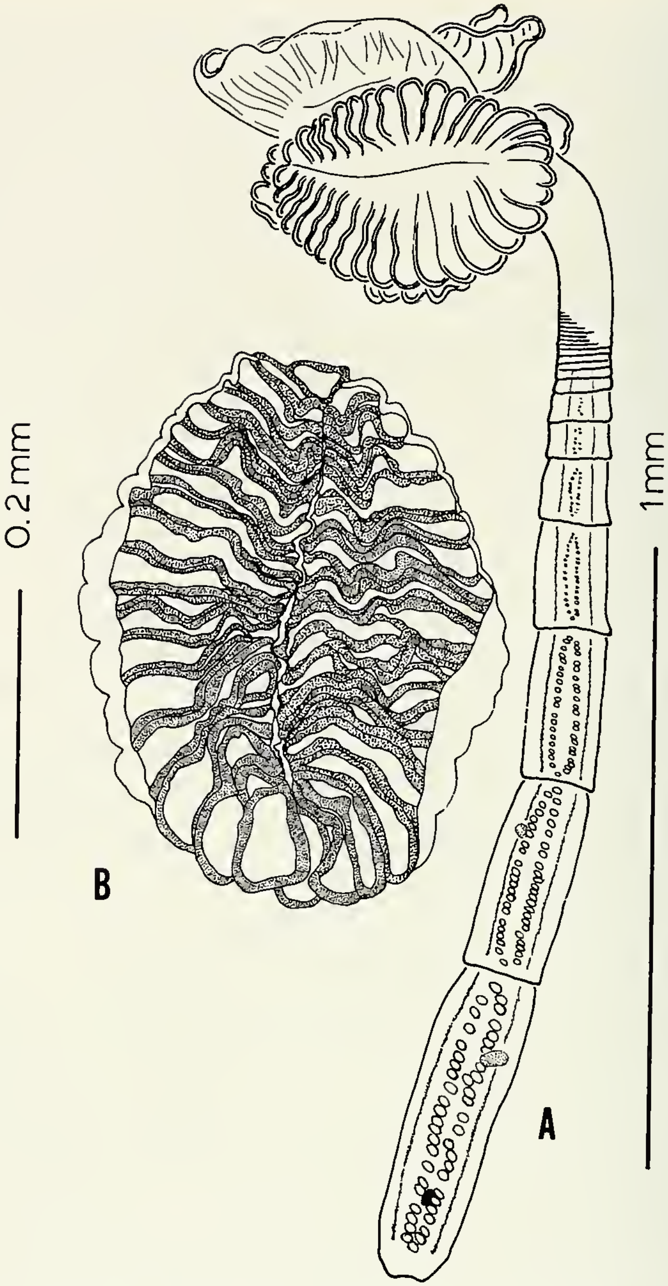

Fig. 2. *Caulobothrium multorchidum* (Young, 1955) n. comb.: A. Entire worm; B. Bothridium.

3.9 mm by 215); number of segments 11 (holotype 18); scolex with four pedicellated bothridia; pedicels approximately 81 long by 121 wide (holotype 170 by 97); peduncle aspinose, 404 long by 94 wide (holotype 578 by 114); bothridia 513 (485 to 565) long by 370 wide (holotype 518 to 591 by 237 to 324); each bothridium divided longitudinally by a single median septum and transversely by 19 (holotype 20) septa forming 2 parallel rows of 18 loculi (holotype 19) with a single unpaired loculus at both ends of each bothridium; total number of loculi per bothridium 38 (holotype 40); rostellum absent; mature segments longer than wide, 534 long by 160 wide (holotype 234 to 418 by 207 to 217); cirrus pouch lateral, poorly visible; genital pore in anterior half of segment, alternating irregularly; genital atrium (?); testes located in lateral fields from anterior to posterior margins of proglottid, 42 to 48 in number (holotype 51 to 62); testes oblong to subspherical in shape 20 (17 to 23) long by 31 (22 to 38) wide (holotype 12 to 42 by 17 to 50); ovary faintly visible; vitellaria in indistinct lateral bands extending total length of proglottid.

Type host: *Urolophus halleri* Cooper (= *Urobatis halleri*).

Location: Spiral valve.

Locality: San Diego Bay, San Diego, California.

Type specimen: Holotype USNM Helm. Coll. No. 45976, referred specimen No. 74598.

Remarks.—Young's (1954) original description of *E. multorchidum* failed to include the total length of the worm, and the presence or absence of a rostellum; testes are enumerated ambiguously as 30 to 45 while 58 are depicted in the figure (a single mature worm from this study shows 48 and 42 testes in the two terminal proglottids). The absence of a rostellum and the presence of testes between the ovary and the cirrus pouch on the poral side in these specimens dictates their placement in the genus *Caulobothrium*. The form is therefore redescribed as *C. multorchidum* (Young, 1954) n. comb. Cornford (1974) listed *E. multorchidum* Young, 1954, as a possible species of *Rhinebothrium*. This suggestion was no doubt based on Young's (1954) description rather than the type material. *Caulobothrium multorchidum* resembles *C. opisthorchis* Riser, 1955, and *C. myliobatidis* Carvajal, 1977, in having testes distributed posterior to the ovary. It differs from *C. myliobatidis* in having a fewer number of loculi (38 to 40 vs. 54 to 58), and smaller bothridia (485 to 565 vs. 760 to 1,100). It differs from *C. opisthorchis* only in being smaller (2.6 to 3.9 mm vs. less than 15 mm), having fewer testes (42 to 62 vs. 78 to 90) and a shorter peduncle (404 to 578 vs. 1,120). Dissimilarities between *C. multorchidum* and *C. opisthorchis* may be due to total size, and further study may dictate their synonomy. In describing *C. opisthorchis*, Riser (1955) noted its dissimilarity to other members of the genus in having testes posterior to the ovary, suggesting the possibility of erecting a new genus. He evidently did not recognize Young's (1954) description of *E. multorchidum* as having a similar testicular distribution.

Rhinebothrium ditesticulum n. sp.

Fig. 3

The following description is based on 18 specimens from two hosts (17 from one; one, non-strobilate individual from another).

Phyllobothriidae: Craspedote, apolytic, medium sized worms, 20.7 ± 5.5 (9.6 to 28.7) mm long (N = 17), by 812 ± 130 (577 to 1,143) wide (N = 17); strobila cylindrical, number of segments 229 ± 35 (160 to 276) (N = 17); scolex with four, pedicellated, bilobed bothridia; peduncle long, terminating abruptly at area of strobilization; neck absent; pedicels 693 ± 218 (155 to 1,030) long (N = 63); peduncle 9.4 ± 2.0 (4.9 to 12.6) mm long (N = 17), by 312 ± 58 (237 to 443) wide (N = 17); bothridia 1.8 ± 0.2 (1.4 to 2.2) mm long (N = 49); bothridial lobes of unequal size, completely separate, hinged at pedicel, distal lobe 1,043 ± 92 (793 to

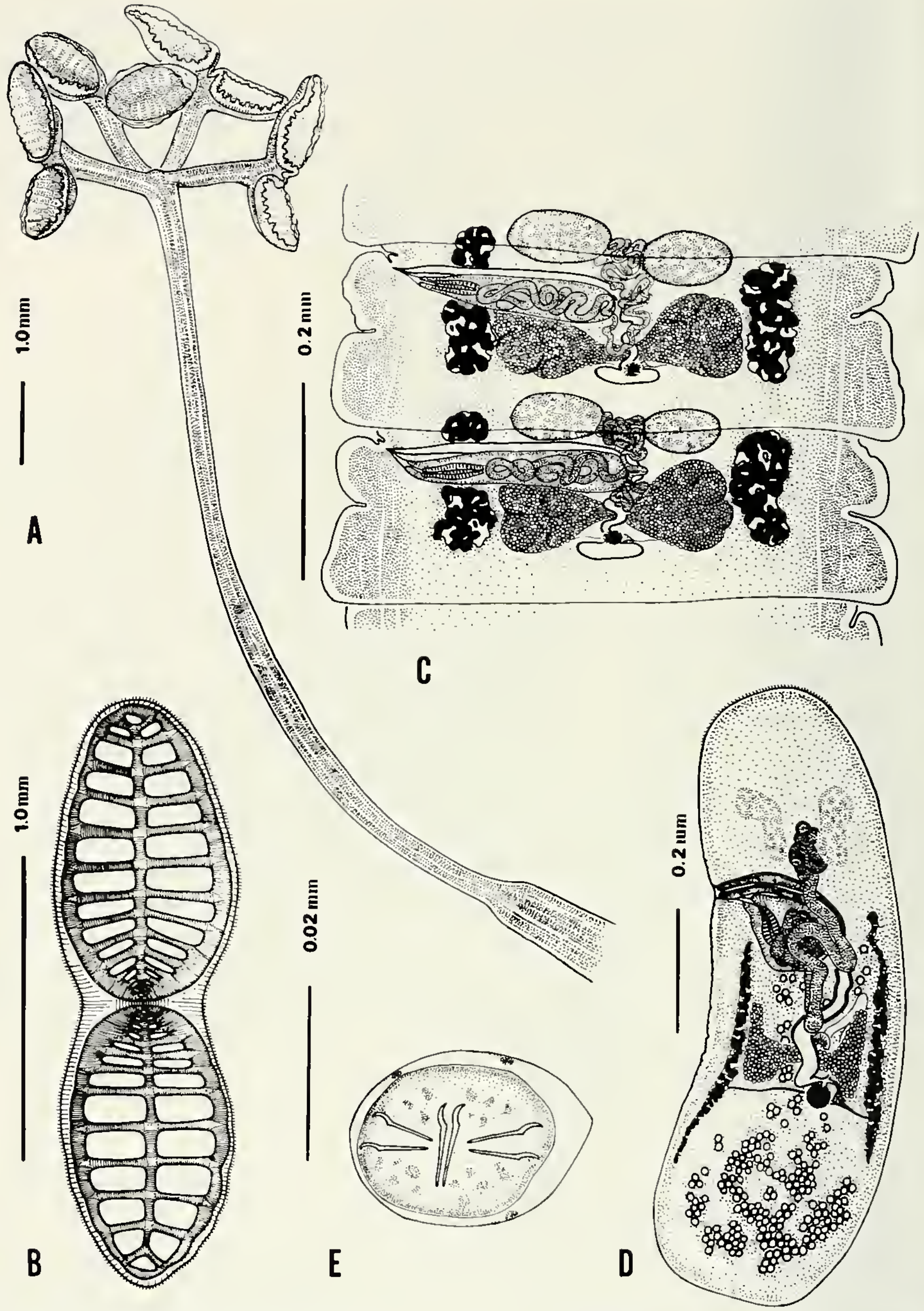

Fig. 3. *Rhinebothrium ditesticulum* n. sp.: A. Scolex; B. Bothridium (diagrammatic); C. Mature proglottids; D. Gravid proglottid; E. Egg.

1,308) long (N = 59), by 578 ± 85 (433 to 731) wide (N = 23); proximal lobe 854 ± 78 (690 to 1,020) long (N = 55), by 496 ± 64 (422 to 639) wide (N = 17); lobes divided longitudinally by a single median septum and transversely by 12 to 14 septa in distal lobes (N = 34), and 12 to 13 septa in proximal lobes (N = 32), forming 2 parallel rows of 11 to 13 and 11 to 12 loculi respectively; a single unpaired loculus at each of both lobes (in slightly curled lobes terminal loculi are difficult to see); total number of loculi per bothridium (17 worms, 30 bothridia) 50 (48 to 54); rostellum absent; pedicels, peduncle and back surfaces of bothridia spinose; spines approximately 3 long; mature segments, except terminal proglottid, wider than long, 222 ± 62 (80 to 347) long (N = 40), by 502 ± 105 (344 to 691) wide (N = 40); terminal proglottids longer than wide, 415 ± 127 (273 to 640) long (N = 14), by 377 ± 82 (239 to 507) wide (N = 14); cirrus pouch lateral, extending to middle of proglottid, oblong in mature and terminal segments, 163 ± 28 (104 to 204) long (N = 18), by 64 ± 20 (32 to 95) wide (N = 18); cirrus armed, spines approximately 4 long; genital atrium absent; genital pore in anterior half of segment, alternating irregularly; testes large oblong to subspherical 68 ± 6 (39 to 94) long (N = 22), by 117 ± 25 (65 to 169) wide (N = 22), 2 per segment, opposite, located anterior to or slightly overlapping cirrus pouch, atrophied in terminal gravid proglottids; ovarian lobes equal, extending to middle or posterior border of cirrus pouch; lobes club-shaped in mature segments becoming more elongate in terminal proglottids, X-shaped in transverse section (tetralobate) 125 ± 57 (29 to 226) long (N = 24), by 93 ± 32 (42 to 124) wide (N = 24); vitellaria in dense lateral bands 148 ± 73 (47 to 312) long (N = 22) by 52 ± 22 (18 to 86) wide (N = 22); vitellaria does not encroach laterally on medullary parenchyma; longitudinal musculature of parenchyma well-developed.

Gravid free segments 988 ± 80 (905 to 1,089) long (N = 6) by 394 ± 70 (338 to 533) wide (N = 6); cirrus pouch lateral, anterior to ovary, 156 ± 14 (130 to 177) long (N = 6) by 109 ± 18 (88 to 140) wide (N = 6); ovarian lobes elongate 234 ± 85 (114 to 291) long (N = 6) by 85 ± 16 (62 to 96) wide (N = 6); uterus distended into oblong sac from posterior of proglottid to just anterior of genital pore; anterior margin of proglottid covered with minute spines; eggs subspherical to spherical 27 ± 1 (25 to 29) long (N = 20) by 21 ± 1 (20 to 23) wide (N = 20), without filaments (eggs measured in-utero only); onchosphere hooks approximately 9 long by 1 wide, handle and blade measured 6 and 3 long, respectively.

A single immature individual from a second host measured 6.6 mm long (unsegmented strobila 3.5 mm long by 446 wide). Other features as in adult.

Type host: *Urolophus halleri* Cooper, round stingray.

Location: Spiral valve.

Locality: Anaheim Bay, Seal Beach, California.

Holotype and paratype: USNM Helm. Coll. No. 73100. 73101.

Remarks.—Six echeneibothriate species have been reported by Young (1954, 1955) from *U. halleri* in southern California: *E. flexile* (Linton, 1890) = *Rhinebothrium flexile* Baer, 1948; *E. tumidulum* (Rudolphi, 1819) = *R. tumidulum* Euzet, 1956; *E. minimum* (Beneden, 1850) = *R. minimum* Euzet, 1956; *E. multorchidum* (Young, 1954) = *Caulobothrium multorchidium* n. comb.; *E. urobatidium* (Young, 1955) = *R. urobatidium* n. comb.; *E. bilobatum* (Young, 1955) = *R. bilobatum* n. comb. *Rhinebothrium ditesticulum* closely resembles *R. flexile* in the separation of bothridial lobes and the long, distinct peduncle; it can be distinguished, however, by the number of testes (2 vs. 14 to 18) and the number of loculi per bothridium (50 vs. 46). *Rhinebothrium tumidulum*, *R. minimum*, *R. urobatidium* n. comb., and *C. multorchidum* n. comb. lack distinct bothridia present in *R. ditesticulum* n. sp.; while *R. bilobatum* n. comb. is much smaller (2.7 vs. 20.7 mm), and has a greater number of testes (6 vs. 2). In comparing those rhinebothriate species not from the type locality, *R. ditesticulum* n. sp. closely resembles the larval form of *E. bifidum* Yamaguti, 1952, from *Trachurus trachurus* in Japan, and *R. hawaiiensis* Cornford, 1974, in possessing completely bilobed bothridia; but is distinguished from the former by the number of longitudinal septa per bothridium (1 vs. 2), and, from the latter, in size (20.7 mm vs. 2.1 mm) and number of testes (2 vs. 11 to 13). *Rhinebothrium ditesticulum* can be distinguished from all species of *Rhinebothrium*, except *R. spinicephalum* Campbell, 1970, *R. rhinobati* Dailey and Carvajal, 1976, and *R. tetralobatum* Brooks, 1977, in having only two testes. It differs from *R. spinicephalum* and *R. rhinobati* in greater size (20.7 mm vs. 3.9 and 2.4 mm long), greater number of locules (48 to 54 vs. 32 to 34 and 23), completely distinct bothridial lobes and number of proglottids (229 vs. 44 and 24). In addition, *R. rhinobati* has unequal ovarian lobes, a large genital atrium, is acraspedote and has a very short peduncle. *Rhinebothrium ditesticulum* can be distinguished from *R. tetralobatum* in having a greater number of segments (299 vs. 82 to 100), a long spinose peduncle (9.4 mm vs. 0.96 to 0.144 mm), and in having only a single, paired ovarian lobe visible in dorsoventral view.

Rhinebothrium ditesticulum is very similar to *Caulobothrium tetrascaphium* Riser, 1955, in bothridial morphology, the long peduncle and the developed, longitudinal musculature of the parenchyma. It differs in lacking testes between the ovary and the cirrus pouch on the poral side.

Discussion

The validity of *Rhinebothrium* has been disputed since Linton's description in 1890. Wardle and McLeod (1952), Young (1956), Yamaguti (1959) and Alexander (1963) considered this genus a synonym of *Echeneibothrium* Beneden, 1850. In contrast, Williams (1958, 1966), Euzet (1953, 1954, 1956), Baer (1961), Campbell (1970, 1975), Euzet and Carvajal (1973), Cornford (1974), Dailey and Carvajal (1976), Brooks and Thorson (1976) and Brooks (1977) presented *Rhinebothrium* as distinct from *Echeneibothrium* in lacking a rostellum. The finding of three populations, totalling 53 scoleces, all lacking rostella, even in a non-strobiliated individual, appears to substantiate the stability of the character.

Since species of *Echeneibothrium* are restricted to hosts of the superfamily Rajoidea (skates), and, at least in the Northern Hemisphere (Euzet and Carvajal, 1973; Dailey and Carvajal, 1976, have found *Rhinebothrium* from Rajoidea and Rhinobatoidea respectively in Chilean waters), *Rhinebothrium* is restricted to Myliobatoidea (stingrays) (Williams, 1966, Campbell, 1970, 1975), it seems possible that all the species reported by Young (1954, 1955) from *U. halleri* (Myliobatoidea) are probably either *Rhinebothrium* or *Caulobothrium*. This possibility becomes more evident with the knowledge that Young (1954, 1955) did not recognize either of these genera at the time he described the three new species of *Echeneibothrium* here redescribed as species of *Rhinebothrium* and *Caulobothrium*. In addition, *E. minimum, E. tumidulum* and *E. flexile*, reported by Young (1954, 1955), have all been established as species of *Rhinebothrium* (Baer, 1948, Euzet, 1959), though none of these species were found in this study. Riser's (1955) descriptions of three new species of *Echeneibothrium* from skates in the eastern Pacific help to confirm the local host group specificity of these genera.

Recent descriptions of species of *Rhinebothrium* (Linton, 1890, Baer, 1948), *Caulobothrium* (Baer, 1948, Euzet, 1953) and *Rhabdotobothrium* (Euzet, 1953) have neglected to or erroneously emended generic evaluations. Campbell (1970) emended the generic description of *Rhinebothrium* by stating "Posterior portion of scolex modified into a peduncle. . . ." This is in contrast with earlier evaluations which indicated a peduncle may be present or absent (Baer, 1948, Euzet, 1953, 1956). *Rhinebothrium minimum* (VanBeneden, 1850) Euzet, 1954, *R. tumidulum* (Rudolphi, 1819) Euzet, 1953, and *R. moralaraii* Brooks and Thorson, 1976, would not be included in Campbell's evaluation. Descriptions of new *Caulobothrium* species by Carvajal (1977) and Brooks (1977), also indicated departures from the original generic description in having short peduncles, being acraspedote and having an inconspicuous genital atrium (Brooks, 1977). Similarly, *Rhabdotobothrium anterophyllum* Campbell, 1975, is described as being acraspedote and having a well-developed genital atrium, contrary to Euzet's (1953) generic description.

Due to variability described in this paper and noted by other workers the following generic emendations are made.

Genus Rhinebothrium *Linton, 1890, Baer, 1948, emended.*—Phyllobothriidae: Scolex with 4 pedicellated bothridia, their adherent surfaces divided by muscular septa, either many transverse septa, or 1 or 2 longitudinal septa in addition to transverse septa, forming locculi; bothridial margin lobulated or entire in form, hinged or not; rostellum absent; peduncle present or absent, spined or not; neck present or absent; scolex may be covered with short spines; strobila craspedote or acraspedote, segments well defined, apolytic; genital pores marginal, irregularly alternating; genital atrium present or absent; vitellaria in lateral bands; testes few to numerous, distributed in median field anterior to cirrus pouch, none between cirrus pouch and ovary on poral side; cirrus pouch conspicuous, cirrus armed; ovary having 2, 4, 6 or 8 lobes in dorsoventral view, X-shaped in cross section; uterus simple, median, tubular; vagina passes immediately anterior to cirrus pouch and opens into genital atrium or genital pore; seminal receptacle present or absent; parasitic in rays (Myliobatoidea) and infrequently in skates (Rajoidea).

Type species: *R. flexile* Linton, 1890.

Genus Caulobothrium *Baer, 1948, emended.*—Phyllobothriidae: Scolex with 4 pedicellated bothridia their adherent surfaces divided by muscular septa, or 1 longitudinal septa in addition to transverse septa, forming loculi; bothridial margins lobulated or entire in form, hinged or not; rostellum absent; posterior portion of scolex always modified into a peduncle; strobila craspedote or acraspedote, apolytic; longitudinal musculature of parenchyma developed or not; genital pores marginal, irregularly alternating; genital atrium present or absent; vitellaria in lateral bands, may connect behind ovary; vitellaria may encroach laterally on medullary parenchyma; testes numerous, distributed in median field sometimes posterior to ovary and always present between cirrus pouch and ovary; cirrus pouch present, cirrus armed or not; ovary X-shaped in cross section; uterus simple, median, tubular; vagina passes immediately anterior to cirrus pouch and opens into genital atrium or genital pore; parasitic in rays (Myliobatoidea).

Type species: *C. longicolle* (Linton, 1890) Baer, 1948.

Genus Rhabdotobothrium *Euzet, 1953, emended.*—Phyllobothriidae: Scolex with 4 pedicellated bothridia, their adherent surfaces divided by muscular septa, either many transverse septa, or 1 longitudinal septa in addition to transverse septa, forming loculi; bothridial margin lobulated or entire in form; rostellum absent; peduncle always absent; neck present or absent; strobila craspedote or acraspedote, apolytic; genital pores marginal, irregularly alternating; genital atrium present or absent; vitellaria in lateral bands; testes numerous, distributed in median field anterior to ovary, and always present between cirrus pouch and ovary; cirrus pouch conspicuous, cirrus armed; ovary bilobed in dorsoventral view, X-shaped in cross section; uterus simple, median, tubular; vagina passes immediately anterior to cirrus pouch and opens into genital atrium or genital pore; parasitic in rays (Myliobatoidea).

Type species: *R. dollfusi* Euzet, 1953.

Recent finding of *Caulobothrium* species with short peduncles (Brooks, 1977, Carvajal, 1977) foreshadows problems in distinguishing this genus from *Rhabdotobothrium*. This possibility becomes more credible in comparing the related genus *Rhinebothrium* where a peduncle can be present or absent, and where, in *R. rhinobati* Dailey and Carvajal, 1976, the peduncle is very short (0.06 mm). It is even disputable whether or not the major distinguishing character of testes distribution between *Rhinebothrium* and *Caulobothrium* compensates for morphological heterogeneity found intragenerically (e.g. *R. ditesticulum* n. sp. vs. *R. urobatidium* n. comb.), and homogeneity found intergenerically (e.g. *R. ditesticulum* n. sp. vs. *C. tetrascaphium* Riser, 1955). While Euzet's (1953) scheme has been useful in temporarily categorizing these three rhinebothriate groups (see also Campbell, 1975), it is possible that future study will not confirm these as natural groupings. It is necessary, therefore, that new descriptions be complete and that generic emendations be made apparent. It is erroneous to state "with characters of the genus" if the species being described differs from the generic evaluation. Whether *Rhinebothrium*, *Caulobothrium* and *Rhabdotobothrium* are actually synonymous or distinct, it is evident that they are in need of revision. It is only through careful descriptions that this task will be made easier.

Acknowledgments

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Research Notes

Range Extensions and New Host Records of Cymothoid Isopods (Isopoda: Cymothoidae) in the Eastern Pacific Ocean

For the past few years the author has been studying isopod fish symbionts of the family Cymothoidae, as well as a number of other isopod families from the eastern Pacific region. From these studies, several significant range extensions and new host records have been established. The material upon which these data are based, with the exception of *Nerocila californica*, are deposited in the Crustacea collections of the Allan Hancock Foundation, University of Southern California. Specimens of *N. californica* are deposited at the National Museum of Natural History, Smithsonian Institution. I have attempted to present accurate specific as well as common names for all host fishes mentioned. In this regard I have considered the following three documents as sources of spellings and vernacular names: Thomson and McKibbin (1974), Miller and Lea (1972) and Shiino (1972). Sincere appreciation is extended to Dr. Thomas Bowman (Smithsonian Institution) for the loan of specimens of *N. californica* and for reviewing the manuscript. This research was supported, in part, by grants from Sigma Xi, the National Science Foundation (Alpha Helix Research Program), and the University of Southern California.

Lironeca panamensis Schioedte and Meinert, 1884

Former known range.—Mazatlán, Sinaloa, Mexico to Panama.

New records.—Numerous locations in the Gulf of California and the west coast of Baja California. Northernmost records are the delta of the Colorado River and Bahía San Quintin, Baja California Norte; ovigerous females collected in January, February and May. Considerable morphological overlap occurs between *L. panamensis* and the temperate species *L. vulgaris* Stimpson 1857 and the two may eventually be shown to be synonymous.

Host records.—No positive association has been made between this isopod and its host fish(es). For nearly 100 years now, the identity of the host(s) of *L. panamensis* has eluded scientists. The reason for this is unknown but perhaps the simplest explanations would be that the adults are (1) very short lived, or (2) have a tendency to abandon their host fish under the least amount of stress. Of the two, the latter seems most likely. Since these isopods are nearly always captured in trawling gear it may be that the simple cessation of swimming activity by the host fish is enough to stimulate its symbiont to detach itself and begin "wandering." This phenomonon has been witnessed numerous times by this author, in other species of cymothoids. It may well be that the isopod is highly sensitive to dissolved oxygen availability and the lack of proper water flow across its pleopods triggers an immediate release reaction. This behavioral pattern of abandoning the stressed (captured or immobilized) host is quite likely a major reason for such questionable host records for various cymothoids (in the literature) as squid or some of the more unlikely fishes. One should use caution when attempting to determine the proper host fish amongst a full trawl of fishes and wandering or "fugitive" isopods. Two host criteria recommended are: the presence of actual tissue damage suspected to be attributable to the isopod, and repeated occurrences of the isopods on the same species of fish.

Lironeca convexa Richardson, 1905b

Former known range.—Hondurus to the Gulf of Guayaquil, Ecuador.

New records.—Bahía Juanico, west coast of Baja California Norte, Mexico, from a pompano (*Trachinotus* sp.); and, Santa Catalina Island, California; ovigerous females collected in February.

Nerocila californica Schioedte and Meinert, 1881

Former known range.—San Diego, California to Panama, excluding the Gulf of California. Richardson (1905a) listed Pt. Sur (*sic*) as a northernmost record.

New records.—Numerous records from the Gulf of California, Baja California and southern California, north to Los Angeles. One record from La Lagunilla, Peru. Ovigerous females collected in April, May, June and July.

New records of "host fishes."—*Cetengraulis mysticetis* (anchovy). Extensive tissue damage evident; throughout upper Gulf of California.

Syacium ovale (pleuronectid flounder). Extensive tissue damage evident; upper Gulf of California.

Micrometrus minimus (dwarf surfperch). Tissue damage present; San Diego, California.

Oligoplites mundus (leather jack). Tissue damage present; upper Gulf of California.

Mugil cephalus (striped mullet). Extensive tissue damage present; throughout the Gulf of California.

Sphoeroides annulatus (bullseye puffer). No tissue damage; upper Gulf of California.

Paralabrax clathratus (kelp bass). No tissue damage; San Diego, California.

Umbrina roncador (yellowfin croaker). No tissue damage; San Diego, California.

Embiotoca jacksoni (black surfperch). No tissue damage; San Diego, California.

Atherinopsis californiensis (jacksmelt). No tissue damage; King Harbor, Los Angeles, California.

Stereolepis gigas (giant sea bass). Fish not included with specimen; Cape San Lucas, Baja California Sur, Mexico.

Istiophorus platypterus (sailfish). Fish or notes not included with specimen; Mazatlán, Sinaloa, Mexico.

Cynoscion macdonaldi (totuava). Fish or notes not included with specimen; upper Gulf of California.

Mycteroperca xenarcha (broomtail grouper). Fish or notes not included with specimen; Magdalena Bay, Baja California Sur, Mexico.

Atherinops affinis (topsmelt). Fish or notes not included with specimens; Long Beach, California.

As will be noted above, I have put the heading of this section in quotation marks, the reason being that most of these records are suspect for one reason or another. The only fishes fitting the two host criteria discussed above (under *Lironeca panamensis*) are: *Cetengraulis mysticetis, Syacium ovale, Micrometrus minimus, Oligoplites mundus* and *Mugil cephalus*. All others remain speculative or questionable. It is to be regretted that collectors finding parasitic associations often do not take the time to keep better notes on their observations. Most of these records are from trawl or seine collections, where fugitive isopods are a common occurrence.

Codonophilus gilberti (Richardson, 1904)

Former known range.—Known only from the type locality of Mazatlán, Sinaloa, Mexico (as *Meinertia gilberti*).

New records.—Puerto Penasco, Sonora, Mexico, from the mullet *Mugil hospes*; and, Estero de Punta Banda, Baja California Norte (west coast), from the striped mullet *Mugil cephalus*. Ovigerous females have been collected in December.

Codonophilus gaudichaudii (Milne-Edwards, 1840)

Former known range.—Mazatlán, Sinaloa, Mexico to Chile, including the Galapagos Islands and a single dubious record from New Guinea (Richardson, 1905a).

New records.—Bahía San Juanico, Baja California Sur (west coast), Mexico; from a pompano (*Trachinotus* sp.).

Cymothoa exigua Schioedte and Meinert, 1884

Former known range.—Panama and the Galapagos Islands.

New Records.—Throughout the upper Gulf of California, from El Golfo de Santa Clara, Sonora, to Huatobampito, near Yavaros, Sonora, Mexico. Ovigerous females collected in April, May, July, August and November.

New records of host fishes.—Commonly found associated with the grunt *Orthopristis reddingi*, in the upper Gulf of California; a single record associates this isopod with the flatfish *Etropus* sp., at Puerto Penasco, Sonora (tissue damage present).

This note extends the ranges of *Nerocila californica* northward and into the Gulf of California and south to Peru (approximately 1,600 miles); *Lironeca convexa* northward approximately 2,420 miles; *Lironeca panamensis* northward about 600 miles; *Codonophilus gaudichaudii* northward about 300 miles; and, *Cymothoa exigua* northward approximately 2,650 miles.

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The Striped Dolphin, *Stenella coeruleoalba,* in the Gulf of California

Though known from many locations in both the Atlantic and Pacific Basins, the Striped Dolphin, *Stenella coeruleoalba* Mayen, had only rarely been observed or collected prior to 1970 in the eastern Pacific above 30°N latitude (Sampson, 1970). In 1973, Hubbs et al. reported on a series of observations and collections of this species, establishing their presence in the southwestern tropical Pacific from an area near the tip of the Baja California Peninsula, at 22°20′N, 108°04′W to the then southernmost record for the species at 9°36′N, 89°29′W. Since 1970 at least 36 additional records have further extended the known range of *S. coeruleoalba* to the equator (Perrin, 1975). The purpose of this note is to report upon the collection of a specimen of the Striped Dolphin in the Gulf of California and to thereby further extend the known range of this species.

On January 15, 1975, a group of biology students and faculty from the University of San Francisco collected the remains of a 159-cm dolphin from a beach midway between Dispensa and Lupona Points at the southernmost end of Espiritu Santo Island (24°24′28″N, 110°19′47″W) in the Gulf of California. The nearly complete skeleton had been cleaned of most flesh by scavengers and insects. The vertebral column remained articulated, however, and the skull was in excellent condition with all of the teeth in place. After recording a series of measurements, the bones were labeled and collected for transport to the university for preparation and further study.

Initially the specimen was believed to be that of a Pacific White-sided Dolphin, *Lagenorhynchus obliquidens* Gill, a common resident of the Gulf. After careful cleaning, however, the number of vertebrae (80) and small, acute teeth (41–49 in each tooth row) as well as skull measurements, indicated that the skeleton was that of a small *S. coeruleoalba*. Comparison with skeletal material at the Southwest Fisheries Center, La Jolla, California, confirmed this identification. The skull and skeleton (lacking several ribs and the pelvic bones) have been deposited in the California Academy of Sciences, San Francisco, California (CAS 16720).

Collection of this specimen confirms the presence of *S. coeruleoalba* in the Gulf of California and extends the range of this species more than 150 miles to the northwest and into a body of water in which it had been previously unknown. It is not likely that the carcass drifted to the collection site from any great distance and it can be assumed that more than this single individual of a normally gregarious species (Nishiwaki, 1972) was in the Gulf when the animal died. Indeed, the similarity in appearance and behavior between *S. coeruleoalba*, the White-bellied Porpoise *Delphinus delphis* Linnaeus, and *L. obliquidens* (Leatherwood et al., 1972) may have long permitted relatively fewer numbers of the first mentioned species to go undetected as regular visitants or even residents of the Gulf of California. This collection coupled with other reports of whales and dolphins beached in the Gulf (Brownell, 1969; Gilmore, 1957) indicate that a richer marine mammal fauna exists in the Gulf than that listed by Huey (1964). It is suggested that a systematic program of observations on the Gulf waters could provide more meaningful estimates of the marine mammal fauna of the Gulf of California than those presently available.

Acknowledgments

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A New Species of *Cymatoceras* (Nautilida: Cymatoceratidae) from West Texas

While investigating the herpetofauna of Pecos County, Texas, in June 1975, we collected a specimen of *Cymatoceras* from an unknown horizon of the Duck Creek Formation (Washita Group, Lower Cretaceous). This specimen represents a new species of *Cymatoceras* described below.

Cymatoceras pecosense, n. sp.

Material.—Holotype and only specimen (essentially complete) deposited in the Field Museum of Natural History, Chicago, PE 28358, Pecos Co., Texas, 8 air km W of Iraan (=2.3 km SW jct. Tex. Hwy. 29 and Tex. Hwy. 349), 30°55′N, 101°59′W. The specimen was weathered out of an abandoned road cut and since there were several fossiliferous horizons its exact position in the Duck Creek Formation is unknown. The ammonite genus *Mortoniceras* was very abundantly represented at the type locality.

Diagnosis.—A species of *Cymatoceras* with shell about as high as wide; ornamentation only on adoral end on internal mold of mature shell; sutures essentially straight.

Description.—Moderately large nautiliconic shell (diameter at least 115 mm), slightly distorted, left side partially eroded (Fig. 1A); umbilicus small, diameter about 5 mm; umbilical callus not determined (since holotype is an internal mold); shell 48 × 52 mm at 180° adapicad of oral margin; shell 63 × 98 mm at adoral end (which may be somewhat crushed in a dorso-ventral direction); adoral half whorl consisting of living chamber while remainder is phragmocone; venter more narrowly rounded than lateral areas, forming slight sulcus on adoral portion of living chamber; umbilical shoulders rounded, more or less indefinite; mold widest ventrad of umbilical shoulders; only adoral quarter of specimen bearing ribs (Fig. 1B); low rounded ribs forming broad lateral salients and prominent, deep, narrowly-rounded, almost V-shaped, ventral sinus; ribs separated by rounded depressions, best developed ventrally, and on ventral half of sides becoming obsolete on dorsal half of sides; growth lines fairly coarse, present only on small portion of sides bordering umbilicus; sutures almost transverse to longitudinal axis of shell with only shallow lateral lobe and shallow umbilical saddle; internal suture and position of siphuncle unknown.

The specimen may represent a mature individual as the adoral portion of the living chamber is slightly modified (Fig. 1C). The modification consists of a transverse groove at the adoral margin of the shell similar to the one reported for *C. loeblichi* by Miller and Harris (1945).

Etymology.—Named for Pecos County, Texas, from which the holotype was collected.

Comparison.—Of the previously described species of *Cymatoceras*, *C. pecosense* is most similar to *C. hilli* (Shattuck, 1903) and *C. loeblichi* Miller and Harris (1945). Both *C. hilli* and *C. loeblichi* are more compressed and expand at a slower rate than *C. pecosense*. *Cymatoceras hilli* has sinuous sutures whereas *C. pecosense* has nearly straight sutures similar to those of *C. loeblichi* (Miller and

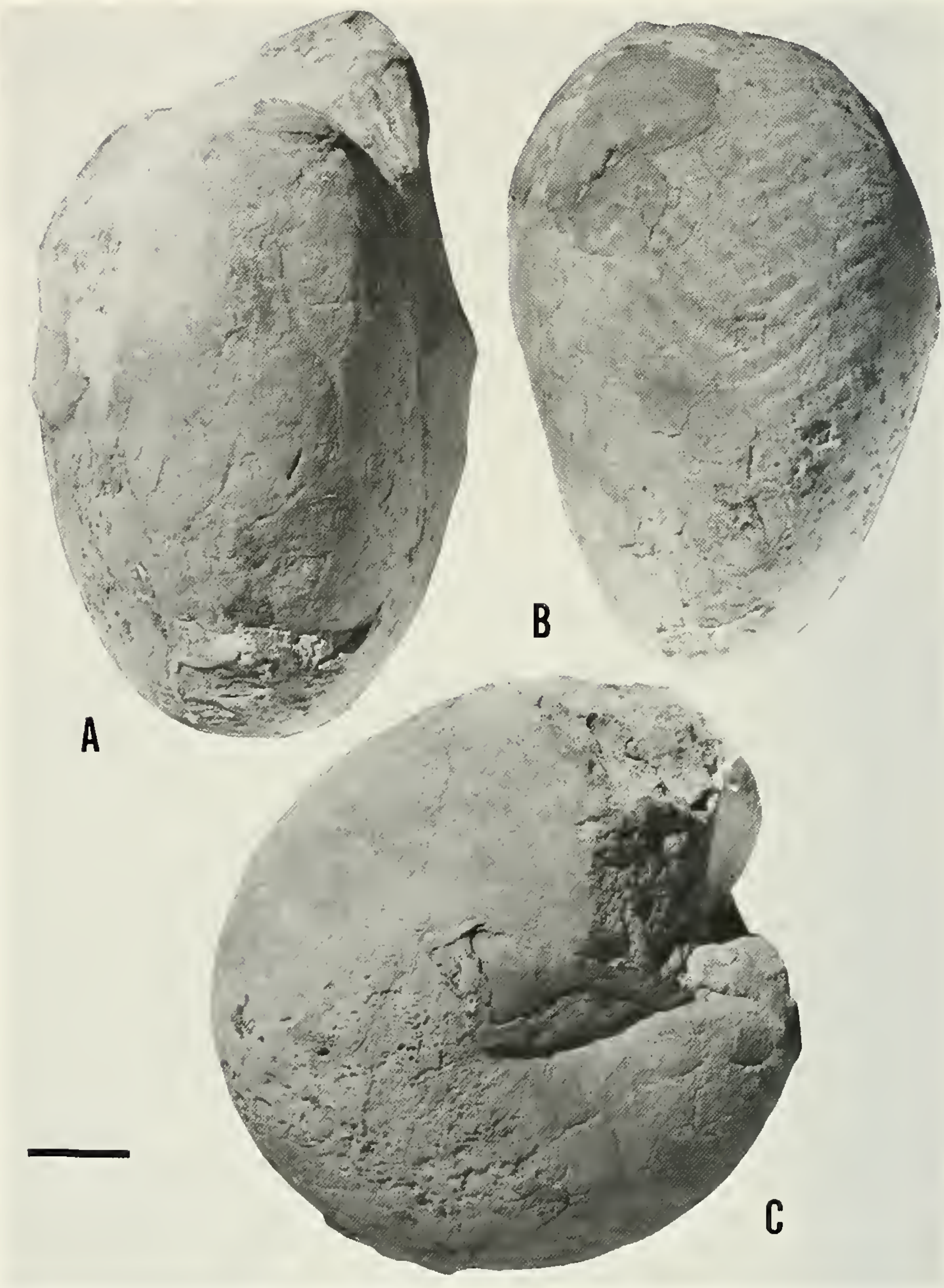

Fig. 1. *Cymatoceras pecosense*, holotype, Field Museum of Natural History, PE 28358: A. dorsal view; B. Ventral view; C. lateral view. Bar equals 2 cm.

Harris, 1945, Fig. 2). Also, *C. loeblichi* has ribs that reach well past the junction of the phragmocone and living chamber, whereas the ribs of *C. pecosense* do not reach the phragmocone.

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Notes on the Biology of *Ceuthothrombium cavaticum* (Acari: Trombidiidae), a Parasite of Cave Crickets (Rhaphidophoridae: *Ceuthophilus*)

Recently, *Ceuthothrombium cavaticum* Robaux et al. (1976) was described from larvae removed from several species of preserved *Ceuthophilus* collected from caves in Texas, New Mexico, and Mexico. Subsequent acquisition of living larvae from crickets obtained from Spider Cave, Eddy Co., New Mexico, gave the opportunity to rear this species through its post-larval stages. The systematic placement of trombidiid mites is based primarily on nymphal and adult specimens, therefore the establishment and study of correlated life-stage series, including the larva, is important to the taxonomic stability of this species.

Twenty larvae were obtained from five crickets that had been killed and placed over a pan of water to which a drop or two of detergent had been added. The larvae dropped off within two days and were recovered from the water and placed individually in 5-dram plastic vials. The vials had been filled to near the top with a 9:1 mixture of plaster-of-Paris and charcoal liquified with distilled water, a procedure adapted from Lipovsky (1953). This substrate allowed the maintenance of a high humidity (nearly 100%) by a weekly addition of several drops of distilled water. The mites were kept in the laboratory where the temperature ranged from 23–25°C. No attempt was made to control light intensity or photoperiod, although, by virtue of the culture vial and its lid, light was of low intensity. Active post-larval stages (deutonymphs and adults) were fed regularly with newly deposited eggs from a laboratory culture of collembolan insects (family Entomobryidae) that in turn were fed Fleischmann's dry yeast. The mite cultures were checked on an average of 3 to 5 days and 10 eggs were placed in each deutonymph's vial as soon as it emerged. When the eggs were consumed, five to 10 more were added to the vial. Numbers of eggs put into the culture vials were recorded and, in most instances, eggs were available to the mites as their needs required. On several occasions, crushed, early-instar collembolans were offered to certain mites but were not fed upon. During the course of rearing, selected individual protonymphs (nymphochrysalises; calyptostases), deutonymphs, tritonymphs (imagochrystalises; calyptostases), adults, and all observed cast exuvia (shed skins) were recovered and preserved separately in 75% ethanol or mounted on microscope slides in polyvinyl alcohol-lactic acid. In a number of cases when adults were reared, a series of correlated slides was made of the larval and nymphal exuvia and the adult mite.

An accounting of the 20 cultured larval *C. cavaticum* is as follows: 1) 19 larvae became immobile, i.e., entered the quiescent protonymphal stage, 1 to 10 days ($\bar{Y}$ = 4.1) after culturing (one larva was lost); 2) two protonymphs were preserved, one 10 days and the other 15 days after immobilization; 3) active deutonymphs emerged from the 17 remaining protonymphs 14–21 days ($\bar{Y}$ = 16.0) after becoming immobile; 4) 10 deutonymphs entered the quiescent tritonymphal stage, 37–74 days ($\bar{Y}$ = 54.6) after emergence; 5) seven deutonymphs did not enter the tritonymphal stage because two were preserved in ethanol, one was mounted in PVA-L on a slide, two were lost, and two remained in the active stage throughout the course of observations; 6) nine adults emerged from the 10 tritonymphs 14–21 days ($\bar{Y}$ = 17.3) after immobilization; 7) two adults were mounted in PVA-L; 8) one tritonymph was preserved 10 days after becoming quiescent. Attempts to breed the seven adults and obtain eggs were unsuccessful.

All life stages of *C. cavaticum* were white and translucent, even in engorged larvae, although in one case it was noticed that one partially engorged larva had a reddish color that was also the color of the host cricket's intersegmental membrane.

A comparison of the rearing data of *C. cavaticum* with those of *Allothrombium fuliginosum* discussed by Robaux (1974) showed that *C. cavaticum* fit well in the range of stadial duration times and in general with the developmental cycle of this trombidiid species.

All active post-larval stages became locomotory when the lid was removed from the culture vial for observation and feeding and may have been due to the mites' photo-sensitivity or response to the change in humidity. Several nymphs and adults were seen in grooming behavior which consisted of a mite leaning to one side or the other and "combing" the opisthosomal setae with the first and second legs. Nymphs and adults also tested the environs of the vial by alternate and repeated touching of the substrate with the front pair of legs. Sensory organs are obviously situated in these appendages.

Whether or not *C. cavaticum* is a true cave-dweller is uncertain even though the larvae were found attached to crickets recovered in Spider Cave. Post-larval stages are known only from laboratory-reared specimens and the larvae were removed from cricket hosts that exhibit regular circadian migration into and out of the cave (Campbell, 1974). Berlesed samples of cave floor detritus yielded only one specimen each of a mesostigmate and a cryptostigmate mite. Furthermore, according to Campbell (1974), the soil on the floor of Spider Cave was sandy and contained little organic material. The appearance of *C. cavaticum,* however, suggests a cavernicolous habit because of the lack of eyes and pigmentation, and the presence of long slender legs characteristic of a number of cave-adapted arachnids.

We express our gratitude to James R. Reddell of the Department of Biological Sciences and The Museum, Texas Tech University, Lubbock for his aid and criticisms of the manuscript.

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MANUSCRIPT PREPARATION

It is strongly recommended that, before submitting a paper, the author ask qualified persons to review it. ıe author is requested to submit *at least one additional copy with the original*, on 8½ × 11 opaque, non- asable paper, double spacing the entire manuscript. ***Do not break words at right-hand margin anywhere in the ınuscript.*** Footnotes should be avoided. **Manuscripts which do not conform to the style of the BULLETIN ll be returned to the author.**

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The literature cited: Entries for books and articles should take these forms.

McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.
Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus*. J. Mamm., 54: 452–458.
Brattstrom, B. H. 1969. The Condor in California. Pp. 369–382 *in* Vertebrates of California. (S. E. Payne. ed.), Univ. California Press, xii + 635 pp.

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Research Notes

COVER: Ancient mexican bird motiff from a flat stamp found near Guerrero, Mexico.

SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

BULLETIN

Volume 76 Number 3

Der Löwe. Felis Leo Lin.

BCAS-A76(1) 139–212 (1977) OCTOBER 1977

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Date of this issue 31 December 1977

The Effect of Potassium Ions on the Rate of Ciliary Activity in *Sphaerium transversum*
I. A Different Response in Small and Large Clam Preparations

Anthony A. Paparo, Richard E. Sparks, Judith A. Murphy, and
Kathleen J. Cunningham-Paparo

Abstract.—The presence of potassium in the bathing solution is necessary to maintain a basal rate of beating in *Sphaerium transversum*. There is a significant difference in the response of small and large specimens to: (1) short- and long-term responses to various concentrations of potassium; (2) removal and subsequent addition of potassium; (3) variation of maintenance dosage of potassium in the washing solution; (4) lag period of response to a specific dose. The results suggest that an intracellular transmembrane potential change (surface effect) is necessary to activate ciliated cells of small clams. This latter change in small clams would account for the relatively short lag period for potassium activation.

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Among the many physiologic substances that can be extracted from ciliated cells, none has been shown to have more profound or more diverse effect on ciliary activity than the simple inorganic cations (Gosselin, 1966). Potassium effects on cilia are especially ubiquitous (Aiello, 1960). Potassium activates, or increases the rate of movement of cilia (Gray, 1922), and also causes momentary abrupt stoppage of the same cilia (Takahashi, 1971). One interpretation of the results above is that potassium acts on two possibly independent mechanisms which control different parameters of ciliary movement. Furthermore, addition of this cation to the perfusates alters the daily pattern of freshwater mussels (Koshtoyants and Salanki, 1958). Takahashi and Tsuchiya (1971) have observed effects with potassium that they have divided into three major phases: (1) abrupt stoppage, (2) initial activation, and (3) delayed activation.

The purpose of this investigation is to study the effect of potassium on the rate of beating of cilia on the gill of *Sphaerium*. Furthermore, this research illustrates a rapid laboratory method that can be used to determine the effects of other drugs on bivalve ciliary activity.

Methods

All experiments were performed on the freshwater clam, *Sphaerium transversum* which was kept for one to two days in an aquarium (temperature 21°C, pH 7.2–7.5). Before each experiment clams were measured and then placed into small (1–4 mm) or large (5–9 mm) categories. The adductor muscles were cut and the gill and adductor muscles (gill preparation) were isolated. The gill preparation was pinned to rubber mats glued in the bottom of a Petri dish containing molluscan Ringers. The dish was then placed in a movable stainless steel platform which was

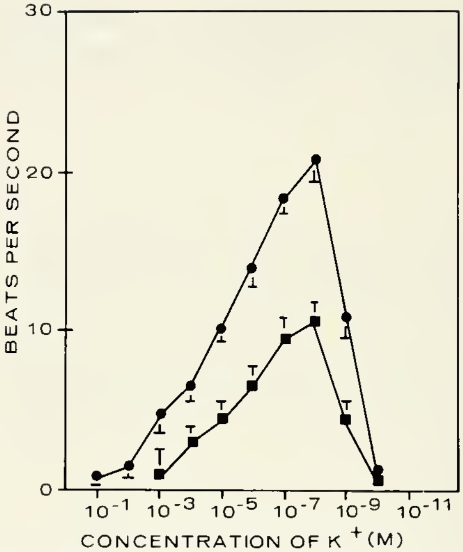
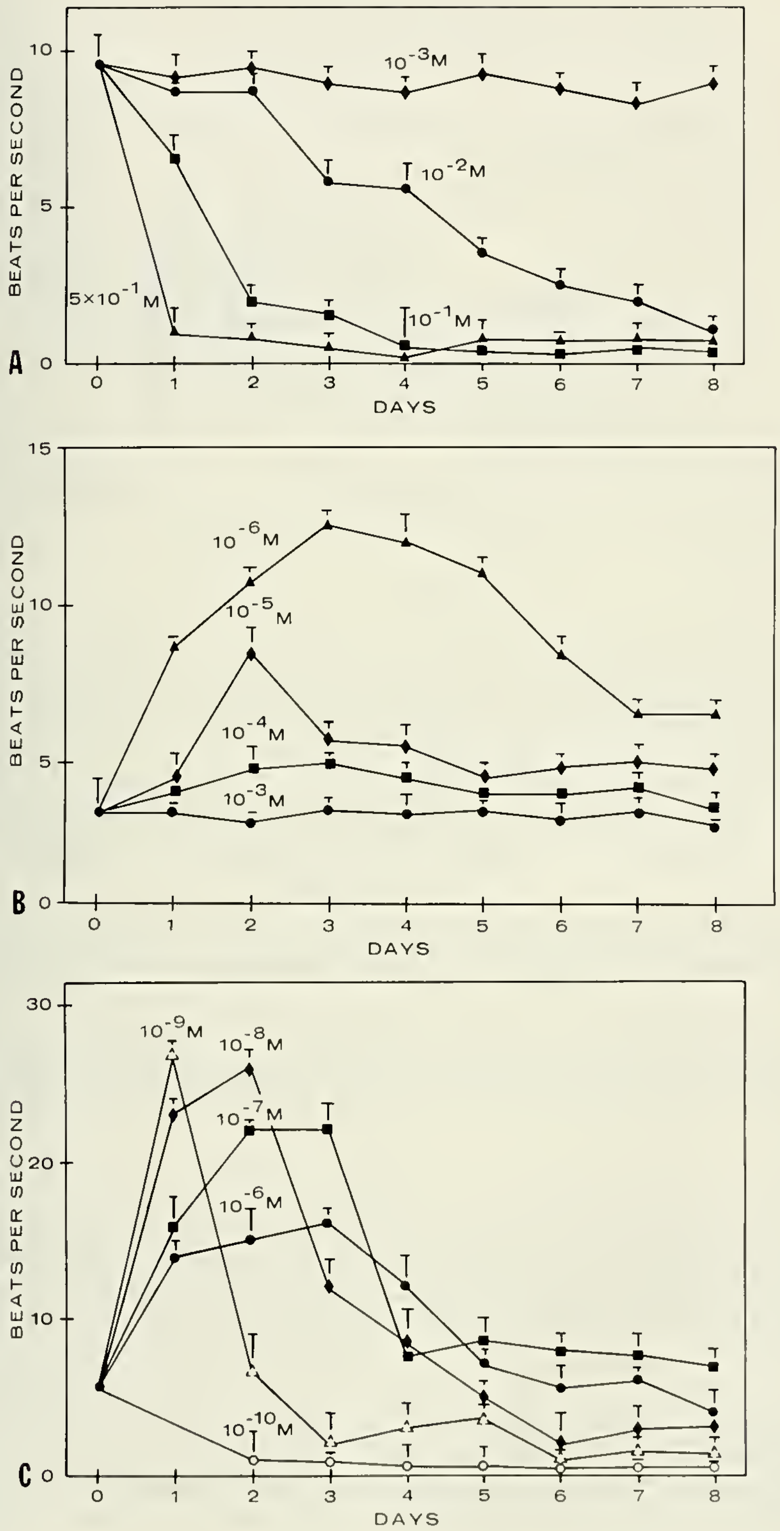


Fig. 1. Dose response curves for potassium in small (●—●) and large (■—■) clams based on 1 min exposure times for each dose.

fitted to the adjustable stage of a microscope. The incorporated gear mechanism o the platform permitted accurate location of designated areas in a gill preparation A field was selected for observation which contained 50 gill filaments grouped fo ease of observation into three vertical columns. By moving the stage each filamen could be followed from its dorsal attachment at the axis to its free vertical end Each column was subdivided into four horizontal rows, demarcated by fixe number of interfilamentary junctions, from dorsal to ventral end. The rate o ciliary beating in beats per second was estimated by synchronizing the rate o flashing of a calibrated, stroboscopic light, used in place of the substage lamp with the rate of beating of the cilia. Synchronization was achieved when th metachronal wave appeared to stand still. Measurements were made from left t right across the field, giving twelve sets of measurements.

The Petri dish was perfused with molluscan Ringers (standard solution) or molluscan Ringers to which potassium (as a chloride) was added (test solution) via four channel variable speed pump with a flow rate of ~0.5ml/min. The planetar gear mechanism of this pump ensured minimum pulsing and stable drift-free flo permitting accurate measurement of ciliary movement. A positive displacemen piston metering pump with micrometric adjustment permits rapid removal of solution from the Petri dish. A continuous flow of solution can be maintained acros the dish. Constant temperature is maintained by means of a stainless steel tubin which cools down the movable platform (~1.0°C/0.5 min) using circulating wate from a cooling system.

Fig. 2. Dose response curves for potassium in small clams based on 8-day exposure times for eac dose: A. Potassium concentrations 5 × 10^{-1} to 10^{-3} M; B. Potassium concentrations 10^{-3} to 10^{-6} M; Potassium concentrations 10^{-6} to 10^{-10} M.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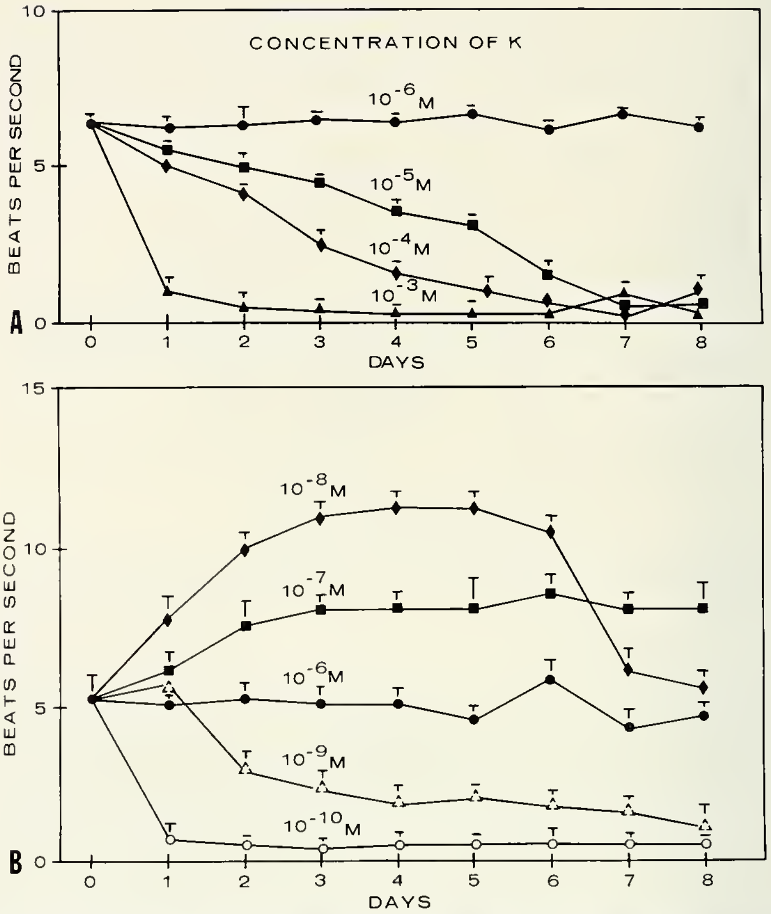

Fig. 3. Dose response curves for potassium in large clams based on 8-day exposure times for each dose: A. Potassium concentrations 10^{-3} to 10^{-6} M; B. Potassium concentrations 10^{-6} to 10^{-10} M.

The data (standard errors of the average rates of beating plotted against time) are based on averages of five gill preparations, 12 readings per gill preparation.

Results

Short-term Responses to Various Dosages of Potassium.—The small and large size categories of clams were compared as to their sensitivity to various concentrations of potassium. The experimental results show that there is a significant difference in the responses of cilia in small and large clams (Fig. 1).

Long-term Responses to Various Dosages of Potassium.—The cilia of the small size category of clams were inhibited with concentrations of potassium $>10^{-3}$ M. Concentrations of potassium equal to 10^{-3} M were sufficient to sustain a basal rate of beating for periods up to eight days (Fig. 2A, B). Concentrations of potassium $<10^{-3}$ M were cilioexcitatory. 10^{-6} M potassium proved to be the most effective

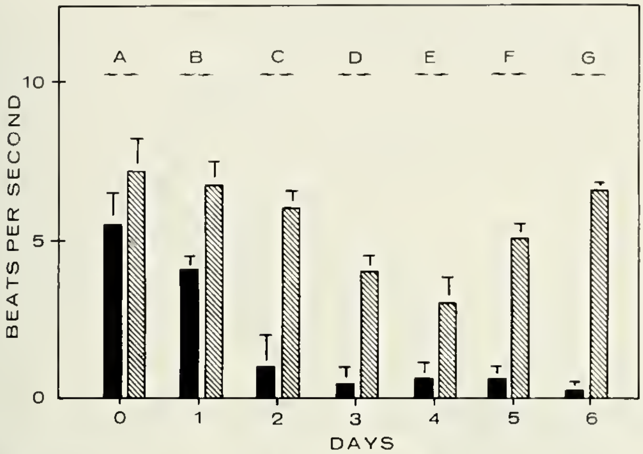

Fig. 4. Effect of addition and removal of 10^{-6} M and 10^{-3} M potassium on basal beating rate of large (■) and small (▧) clams, respectively: A. Addition; B. B–E. Subsequent removal; F–G. Subsequent addition.

and readily sustaining concentration of potassium for this group (Fig. 2B, C). However, maximal cilioexcitatory effect was achieved with potassium concentrations of 10^{-9} M. Less than this, did not sustain a basal rate of beating (Fig. 2C).

The rate of beating of cilia in the large size category of clams were inhibited with potassium concentrations $>10^{-6}$ M (Fig. 3A). 10^{-6} M potassium was needed to sustain a basal rate of beating (Fig. 3A, B). Concentrations of potassium $>10^{-6}$ M but $\leq 10^{-8}$ M were cilioexcitatory (Fig. 3B). However, concentrations $\leq 10^{-9}$ M were insufficient to sustain basal rate (Fig. 3).

The Effect of Removal/Addition of Potassium on the Basal Rate of Beating.—The minimal amount of potassium to maintain a basal rate of beating was introduced into the perfusate of large and small clams (Fig. 4A; 10^{-6} M and 10^{-3} M, respectively). Subsequent removal of potassium from the perfusate resulted in a decrease in the basal rate in both groups (Fig. 4B–E). Readdition of potassium to the perfusate resulted in a recovery of the basal rate in small clams only (Fig. 4F–G).

Variation in the Maintenance Concentration of Potassium in the Washing Solution.—A series of experimental runs involving the use of 10^{-3} M (Fig. 5A) and 10^{-6} M (Fig. 5B) in the washing solution were performed. These experiments confirm above results that 10^{-3} M and 10^{-6} M potassium are the maintenance dosage for basal rate of beating in small and large clams. The hypothesis that there is a physiological difference in the responses of ciliated cells in these animals will be mentioned in the discussion.

Lag Period of Response to a Specific Dose of Potassium Over a Long Period of Time.—Both small and large clams were exposed to 10^{-8} M potassium. This dose proved in the above experiments to be cilioexcitatory for both groups of clams.

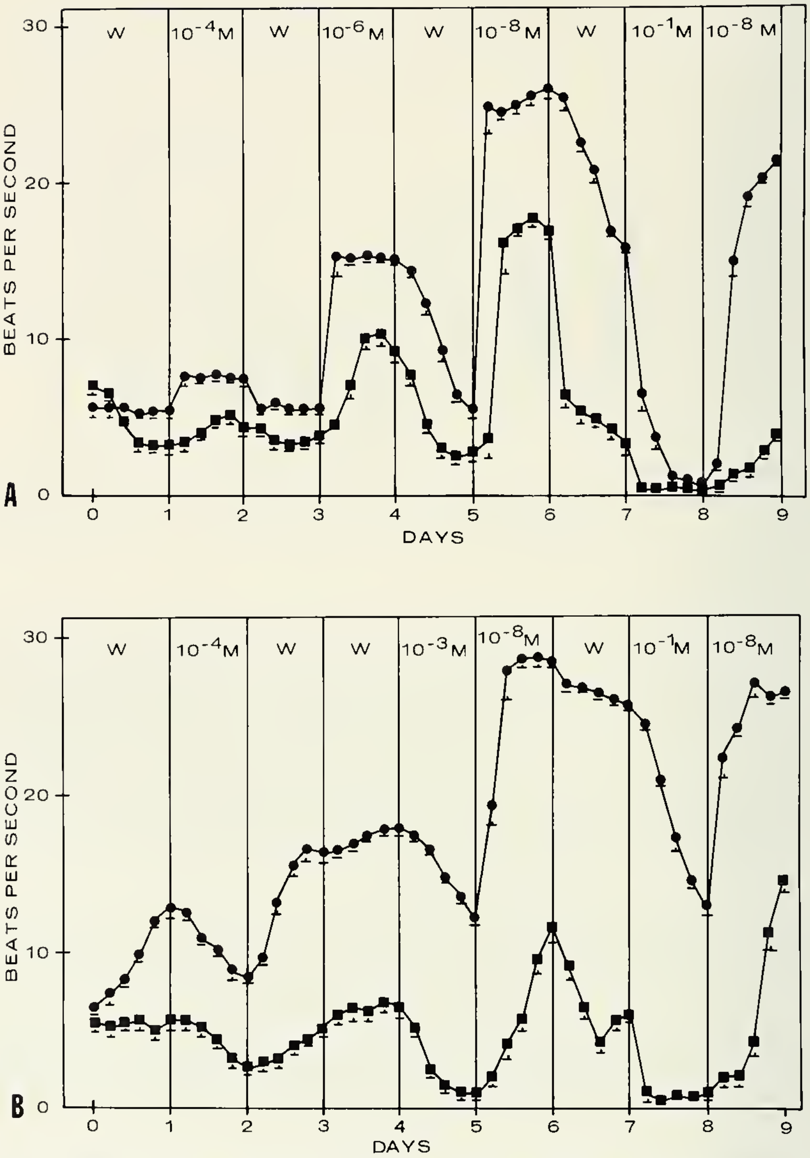

Fig. 5. Variation in maintenance dose of potassium in washing solution (W) of small (●—●) and large (■—■) clams: A. Potassium doses 10^{-3} M; B. Potassium doses 10^{-6} M.

Results here show that incubations of one hour or more with 10^{-8} M potassium demonstrate unequivocal stimulation by potassium in the large clams. In contrast, the cilia of small clams are activated after a lag period of less than 15 min (Fig. 6).

Discussion

The above experiments show that potassium is required to maintain a basal rate of isolated beating cilia in *Sphaerium*. The dose of potassium necessary to sustain a basal rate of beating differs in small clam preparations (10^{-3} M) and large (10^{-6}

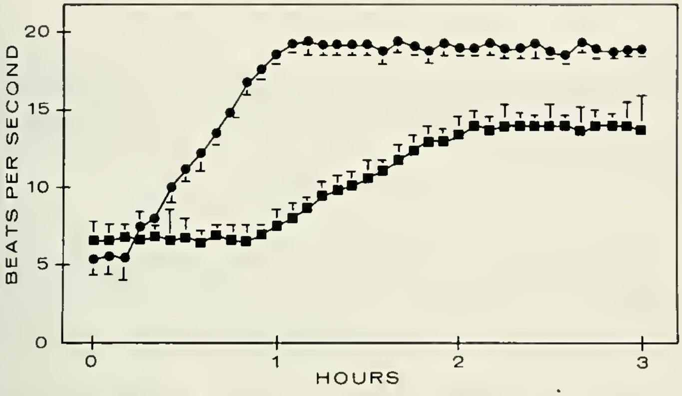

Fig. 6. Response of lateral cilia to 10^{-8} M potassium in small (●—●) and large (■—■) clams.

M). Removal of potassium from the bathing solution of large clam preparations produces irreversible damage to the ciliated cells. The lag period of response to a specific dose of potassium differs. This suggests that the short lag period of small clams may be indicative of a surface effect on the transmembrane potential of ciliated cells, while the long lag period for large clams might imply that changes in the intracellular concentrations of potassium within the ciliated cell are required to produce an effect on ciliary activity. The lag effect of potassium ions supports the view that the response is related to the excitable properties of the ciliated cell membrane (Takahashi, 1971). Although the transmembrane electrical potential has not been recorded from these cells, the effects of the direct current (Murakami, 1968) and of potassium ions indicate that these agents could exert their action by depolarizing the ciliated membrane.

Acknowledgments

This study was supported by a Special Research and Project Grant (Southern Illinois University) and a grant from the Office of Water Research and Technology (Department of Interior #14-31-0001-6072).

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Accepted for publication November 1, 1976.

A Survey of the Family Caprellidae (Crustacea, Amphipoda) from Selected Sites Along the Northern California Coast

Donald M. Martin

Abstract.—Nineteen species of caprellid amphipods representing six genera are described for the northern California coast. The study area extended from the Oregon-California border south to Fort Bragg. Twenty-one collecting sites were established and classified as to habitat type. The ranges for the following six species have been extended: *Caprella brevirostris*, *C. greenleyi*, *C. pustulata*, *C. alaskana*, *C. acanthogaster*, and *Cercops compactus*. The latter five species are new to California, and one of these, a new subspecies of *Caprella acanthogaster*, is described. A key is presented, and correlations between the types of coastal habitat and observed caprellid distribution patterns are discussed.

Division of Environment, Department of Health and Welfare, Statehouse, Boise, Idaho 83720.

The family Caprellidae was surveyed along the northern California coast between latitudes 39°N and 42°N. Nineteen species of caprellids are treated here. The ranges for six species have been extended, five of which have not been previously recorded from the California coast, thereby increasing the total number of species found on the California coast to twenty-four.

There are relatively few published accounts from the nineteenth century of caprellid amphipods occurring in the northeastern Pacific (Stimpson, 1857; Boeck, 1872; Mayer, 1882, 1890, 1903). Major investigations of the Caprellidae of the California coast during this century have been almost as limited. Dougherty and Steinberg (1953) published an account of the caprellids of California between latitudes 36°N and 38°N, although they made collections in only three localities, Dillon Beach, Moss Beach, and Monterey Bay. They described a new genus and two new species and recorded sixteen species previously described. They published a key to those species in Light et al. (1954).

Laubitz (1970) was the first since Mayer to reveal the diverse nature of the Caprellidae of the northeastern Pacific. She published an account of twenty-six species from the North American Pacific between latitudes 44°N and 60°N, including six new species and one new genus. In all, forty-one species of caprellids have been recorded from the Pacific Coast of North America prior to this work. Of these, twenty have been found along the California coast.

This paper discusses systematically all the species recorded, includes a key for their identification, and evaluates certain ecological factors which may affect the distribution of these organisms.

Materials and Methods

Specimens were collected from twenty-one selected sites between Fort Bragg, California, and the Oregon-California border between January 1971, and August

1972 (Figs. 1, 2). Collections were made at two locations at the Fort Bragg site (Point Cabrillo), one of which was subtidal and designated as Fort Bragg (1), and the other, intertidal, as Fort Bragg (2).

Intertidal collections were made during low tide periods. Samples of substrate suspected of housing caprellids were taken at each of the selected sites. These samples included bryozoans, hydroids, algae, sponges, ascidians, and asteroids. Some material was supplied by other collectors.

Subtidal specimens were obtained using scuba apparatus at Fort Bragg (1) and at an artificial reef in Humboldt Bay. An otter trawl, Smith-McIntyre bottom grab, and rock trawl were used to sample the nearshore benthos of Humboldt Bay. A complete reference collection of caprellids from this study has been deposited in the Invertebrate Museum, Department of Biology, Humboldt State University.

The recorded lengths for each species are of the largest male, the largest female, and the smallest ovigerous female.

An attempt was made to provide complete synonyms for each species, but where they became too lengthy, reference is made to an author which provides them in depth for that particular species.

Systematics

Family Caprellidae Dana, 1852

Diagnosis.—Head often partially fused with 1st segment of pereon; palp of maxilliped 1- to 4-jointed; pereon often with fewer than 7 pairs of legs, rarely 3 segments of pereon with brachial vescicles, 2 segments in female with marsupial plates, 1st joint of gnathopods and pereopods reduced; pleon and its legs rudimentary; eyes small, 1 pair; hepatopancreatic tubes 2, rectal glands none; heart with 3 pairs of ostia; posterior ganglia on nerve-chain very small, none situated in pleon (Laubitz, 1970).

Comments.—Mayer (1882, 1890, 1903) utilized eleven characters to differentiate genera within the Caprellidae. These were the number of articles in the flagellum of antenna 2, the number of articles in the mandibular palp and the setal formula for the terminal article, the presence or absence of swimming setae on antenna 2, the number of gill pairs, the number of appendage pairs on both the male and female abdomens, the number of articles in pereopods 3–5, and the length ratio of the inner and outer lobes of the maxilliped. McCain (1968) has since added to the list of generic characters the presence or absence of a molar and the position of the insertion of pereopod 5.

Laubitz (1970) has suggested that the setation of the female brood plates appears to be stable within each genus, and may serve as a generic character.

Several of Mayer's characters, such as the number of articles in pereopods 3–5 and the number of appendage pairs on both the male and female abdomens, appear to be quite unstable for the purpose of delineating caprellid genera. Both of these characters seem to be undergoing reduction, especially the abdomens, and therefore their continued use for delineating genera does not seem reliable.

The key below is based upon stable traits, and characteristics refer to both sexes unless otherwise stated. All tables used to compare species utilize adult male characteristics only.

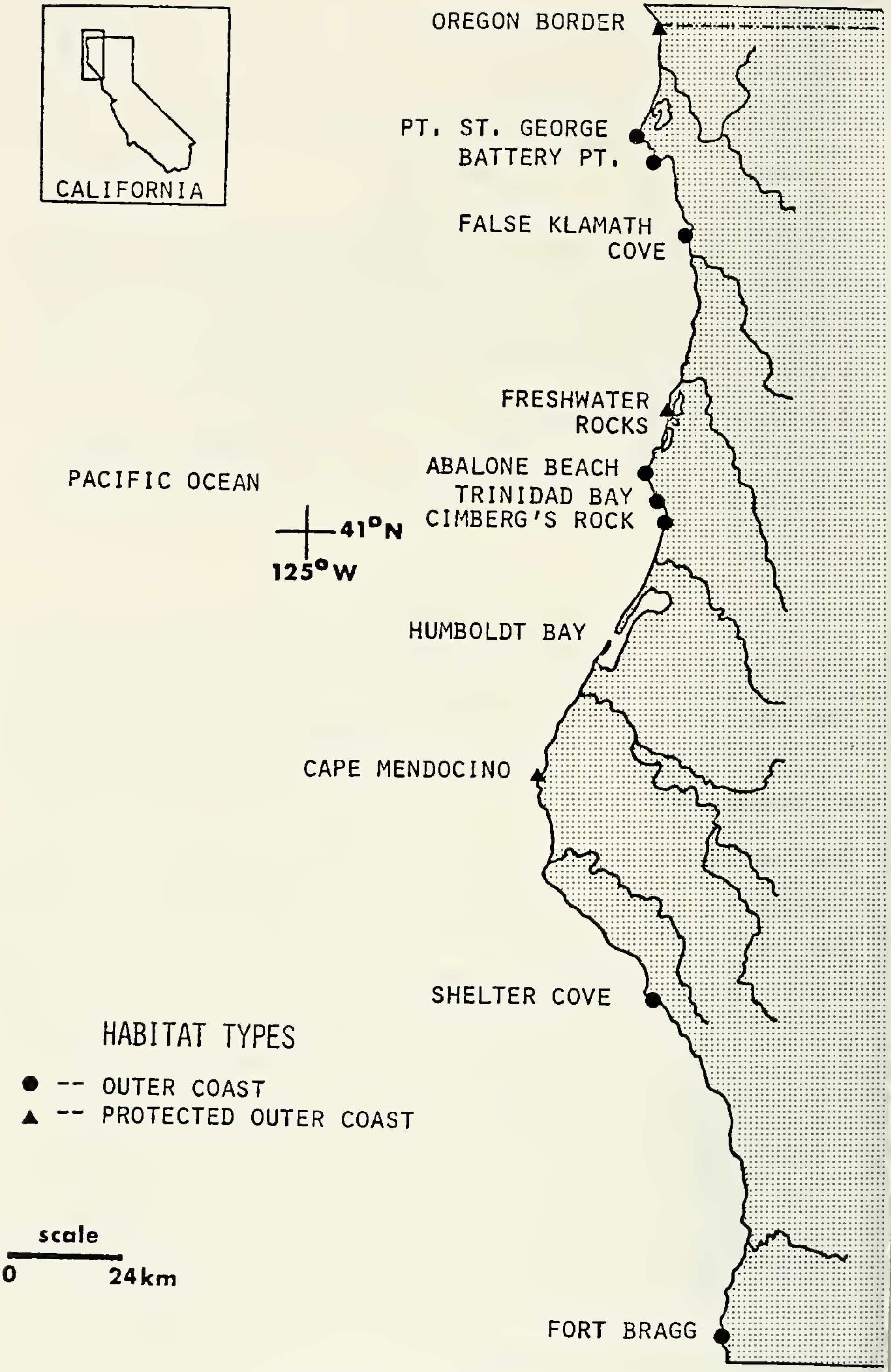

Fig. 1. Map of study area with collection sites indicated.

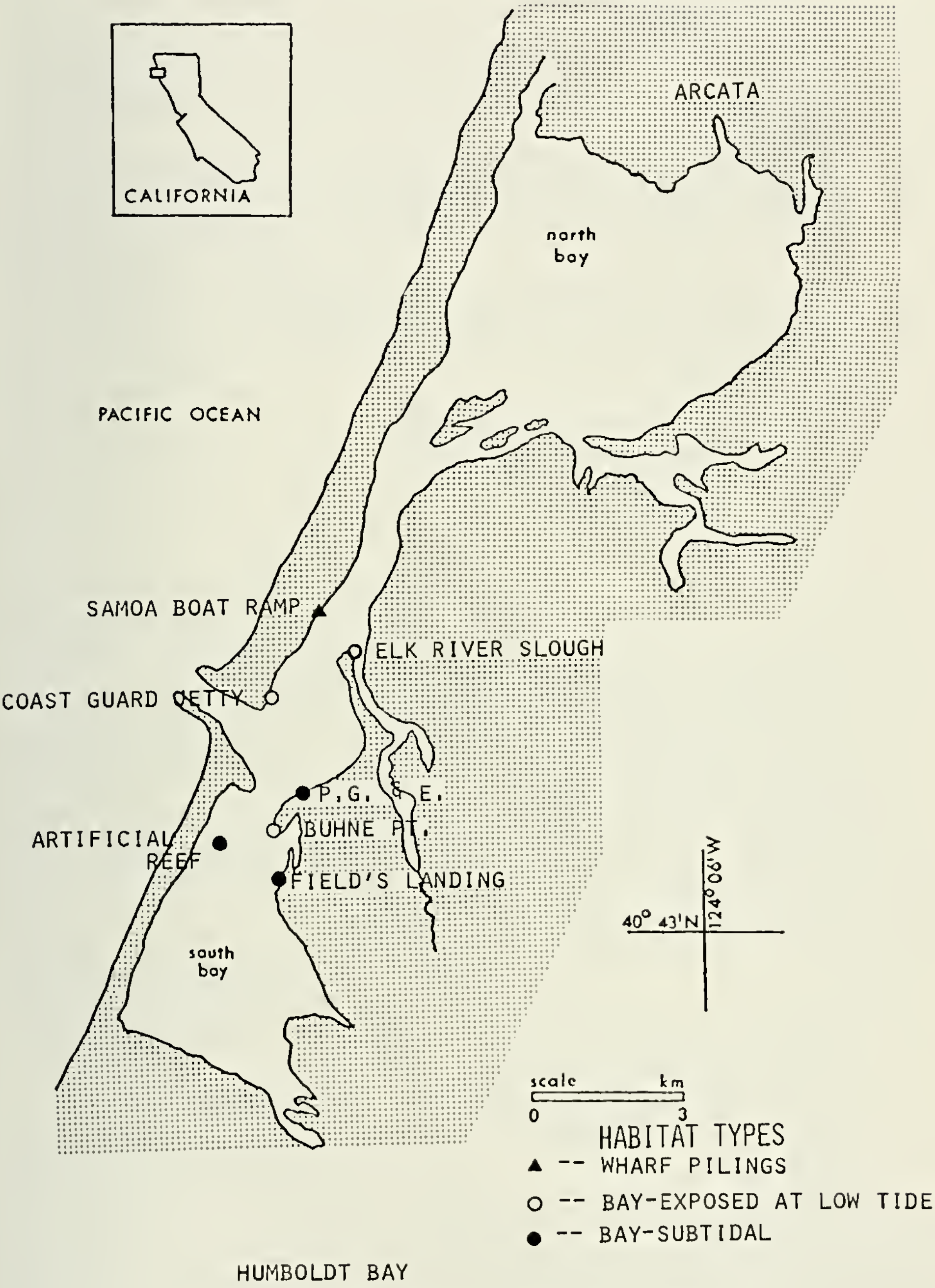

Fig. 2. Map of Humboldt Bay with collection sites indicated.

Key to the Caprellidae of the Northern California Coast

1A. Rudimentary pereopods present on pereonites 3 and 4; mandible with palp 2
1B. Rudimentary pereopods not present on pereonites 3 and 4; mandible without palp 6
2A. Gill pairs present on pereonites 3 and 4 3
2B. Gill pairs present on pereonites 2, 3, and 4 5
3A. Antenna 2 without swimming setae; cephalon with spine or knob .... *Deutella californica*, p. 152
3B. Antenna 2 with swimming setae; cephalon smooth 4
4A. Pereonites 3 and 4 with median lateral projections over the gills; antenna 2 flagellum slender with long swimming setae; pereopods 5–7 articles slender .... *Tritella pilimana*, p. 152
4B. Pereonites 3 and 4 without median lateral projections over the gills; antenna 2 flagellum stout with short setae; pereopods 5–7 articles stout .... *Tritella laevis*, p. 152
5A. Abdomen five-segmented and with uropods; pereonites 5 and 6 short and stout .... *Cercops compactus*, p. 151
5B. Abdomen minute; pereonites 5 and 6 long and slender .... *Perotripus brevis*, p. 151
6A. Ventral spine present between insertions of gnathopods 2 7
6B. Ventral spine absent between insertions of gnathopods 2 9
7A. Cephalon with long, slender anteriorly directed projection; pereonite 5 with single median dorsal spine .... *Caprella californica*, p. 158
7B. Cephalon flattened anteriorly and/or smooth; pereonite 5 without single median dorsal spine 8
8A. Pereonites 3–5 with antero-lateral projections . *Caprella equilibra*, p. 159
8B. Pereonites 3–5 without antero-lateral projections *Caprella mendax*, p. 162
9A. Palm of propodus of pereopods 5–7 straight or convex 10
9B. Palm of propodus of pereopods 5–7 concave 12
10A. Propodus of pereopods 5–7 with distinct tufts of long setae .... *Caprella brevirostris*, p. 156
10B. Propodus of pereopods 5–7 without distinct tufts of long setae 11
11A. Propodus of gnathopod 2 massive, width two-thirds the length; antenna 1 flagellum uniarticulate .... *Caprella greenleyi*, p. 159
11B. Propodus of gnathopod 2 length at least twice the width; antenna 1 flagellum with 16 articles in males and at least 18 articles in females .... *Caprella alaskana*, p. 156
12A. Cephalon smooth or with paired spines or tubercles 13
12B. Cephalon with one spine or tubercle 16
13A. Pereon entirely smooth dorsally .... *Caprella laeviuscula*, p. 162
13B. Pereon not entirely smooth dorsally 14
14A. Pereonite 5 with five pairs of spines dorsally .... *Caprella acanthogaster humboldtiensis*, p. 154
14B. Pereonite 5 with three pairs of spines dorsally 15
15A. Pereonite 4 with paired spines postero-dorsally ... *Caprella ferrea*, p. 159
15B. Pereonite 4 with unpaired spines postero-dorsally .... *Metacaprella kennerlyi*, p. 153

16A. Cephalon with dorsally directed single blunt projection .... *Caprella pustulata*, p. 163
16B. Cephalon with anteriorly directed triangular projection 17
17A. Pleura absent; body spines never on pereonite 1 .... *Caprella natalensis*, p. 163
17B. Pleura present; body spines always present on pereonite 1 18
18A. Pereon covered with large, blunt spines dorsally and laterally; antenna 1 flagellum with 9 articles in males and 7 articles in females .... *Caprella verrucosa*, p. 164
18B. Pereon covered with small to medium-sized spines dorsally; antenna 1 flagellum with 11 articles in males and 9 articles in females .... *Caprella incisa*, p. 161

Species Accounts

Genus *Cercops* Krøyer, 1842–43

Cercops compactus Laubitz, 1970

Cercops compactus Laubitz, 1970.

Material examined.—Battery Point, 1 female; False Klamath Cove, 2 males; Abalone Beach, 2 males; Shelter Cove, 1 male.

Remarks.—Four out of the six specimens of *C. compactus* examined possessed a small median dorsal tubercle on pereonite 6, and one specimen also possessed three very small tubercles on pereonite 5. The two specimens which lacked the tubercle on pereonite 6 were immature, measuring 1.6 mm; therefore the tubercle could be an adult characteristic. According to Laubitz (1970), her type specimens of *C. compactus* lack any kind of body spination. Until more specimens can be inspected, the significance of this variation in the spination of the posterior pereonites remains unclear.

Specimens were found on bryozoans, hydroids, and coralline algae. Length of largest male 3.0 mm and largest female 3.0 mm.

Distribution.—Type locality: Puffin Bay, Baranof Island, Alaska. Other localities: Cape Arago and Cape Blanco, Oregon.

Genus *Perotripus* Dougherty and Steinberg, 1953

Perotripus brevis (La Follette, 1915)

Paedaridium breve La Follette, 1915.

Perotripus brevis Dougherty and Steinberg, 1953, 1954; Laubitz, 1970.

Material examined.—Trinidad Bay, 1 female and 2 males.

Remarks.—Both Laubitz (1970) and I have found the outer lobe of maxilla 1 of *P. brevis* with four serrate spines instead of six as indicated by Dougherty and Steinberg (1953). Although the number of spines on maxilla 1 has been used as a taxonomic character, the reliability of this character is doubtful. Length of largest male 2.7 mm and largest female 2.2 mm.

Distribution.—Type locality: Laguna Beach, California. Other localities: Southern Prince William Sound, Alaska; Pacific coasts of Alexander Archipelago, Alaska, and Vancouver Island, British Columbia; British Columbia mainland coast from Banks Island to Rivers Inlet; San Juan area, Washington.

Genus *Deutella* Mayer, 1890

Deutella californica Mayer, 1890

Deutella californica Mayer, 1890, 1903; Dougherty and Steinberg, 1953, 1954; Steinberg and Dougherty, 1957; Gardella, 1962; McCain, 1968; Laubitz, 1970.

Material examined.—Abalone Beach, 1 female; Trinidad Bay, 7 males, 4 females, and 1 juvenile; Samoa Boat Ramp, 7 males, 9 females, and 7 juveniles; Coast Guard Jetty, 4 males and 2 females; Elk River Slough, 16 males and 4 females; Humboldt Bay, 7 males and 7 females; Artificial Reef, 152 specimens; Fort Bragg (2), 1 female; Field's Landing, 39 males and 22 females.

Remarks.—Specimens were found on algae, bryozoans, hydroids, eelgrass, compound ascidians, and the tentacular radioles of the sabellid worm, *Eudistylia polymorpha*. Length of largest male 9.5 mm, largest female 6.0 mm, and smallest ovigerous female 2.5 mm.

Distribution.—Type locality: Cape Mendocino, California. Other localities: Southern Prince William Sound, Alaska; Juan de Fuca Strait, British Columbia; San Juan area, Washington; Pacific coasts of Vancouver Island, Washington and Oregon; "probably Port Aransas, Texas" (Steinberg and Dougherty, 1957); Monterey Bay and Mussel Point, California.

Genus *Tritella* Mayer, 1890

Tritella laevis Mayer, 1903

Tritella laevis Mayer, 1903; Dougherty and Steinberg, 1953, 1954; McCain, 1968; Laubitz, 1970.

Material examined.—Point Saint George, 4 males, 4 females, and 1 juvenile; Battery Point, 14 males, 2 females, and 53 juveniles; Abalone Beach, 4 males, 3 females, 26 juveniles; Shelter Cove, 3 males, 6 females, and 4 juveniles; Fort Bragg (2), 3 males, 4 females, and 2 juveniles.

Remarks.—Specimens were found on hydroids, algae, bryozoans, coralline algae, and sponges. Length of largest male 6.5 mm, largest female 5.7 mm, and smallest ovigerous female 3.2 mm.

Distribution.—Type locality: Santa Catalina Island, California. Other localities: Mainland coast of Queen Charlotte Sound and Queen Charlotte Strait, British Columbia; Washington and British Columbia coasts of Juan de Fuca Strait; Pacific coasts of Queen Charlotte Islands, Vancouver Island and Oregon; Pacific Grove, Dillon Beach, Moss Beach and Monterey Bay, California.

Tritella pilimana Mayer, 1890

Tritella pilimana Mayer, 1890, 1903; Dougherty and Steinberg, 1953, 1954; McCain, 1968; Laubitz, 1970.
Aeginella hirsuta La Follette, 1915.

Material examined.—Oregon Border, 190 males, 136 females, and 95 juveniles; False Klamath Cove, 2 males, 1 female, and 7 juveniles; Freshwater Rocks, 10 males and 9 females; Trinidad Bay, 30 males, 31 females, and 17 juveniles; Cimberg's Rock, 2 males and 1 female; Samoa Boat Ramp, 24 males, 17 females, and 16 juveniles; Coast Guard Jetty, 4 males and 1 female; Elk River Slough, 4 males, 1 female, and 6 juveniles; Cape Mendocino, 1 male; Field's Landing, 1 male and 1 female; Humboldt Bay, 6 males, and 15 females; Artificial Reef, 1,094 specimens.

Remarks.—One 'female' intersex specimen of *Tritella pilimana* was found among the 1,094 specimens collected from the Artificial Reef in South Humboldt Bay. This intersex specimen possessed male gnathopod 2, an abdomen with penes, female brood plates, and genital openings on the posterior ventral surface of pereonite 5.

The published accounts of caprellid intersexes are limited. Mayer (1903) made record of two "Hermaphite" specimens of *Caprella bispinosa* Mayer (1890), Laubitz (1970) reported two intersex specimens of *Tritella laevis* Mayer (1903) and Laubitz and Mills (1972) have noted that all the type specimens of *Thorina spinosa* Stephensen (1944) were intersexes. Laubitz (1972) also found intersex specimens of *Aeginia longicornis* Krøyer, 1842–43 and recently noted (Laubitz, pers. comm.) intersexes in one species of *Dulichia* (Gammaridea; Podoceridae). Kevin C. Myers (pers. comm.) of San Francisco State University has reported intersexes of *Caprella equilibra* Say (1818) collected in San Francisco Bay. I have also found intersexes in *Caprella incisa* Mayer (1903) and *Caprella laeviuscula* Mayer (1903) which are discussed below.

Specimens were found on hydroids, bryozoans, coralline algae, algae, eelgrass, compound ascidians, and the tubes of sabellid worms. Length of largest male 8.3 mm, largest female 5.2 mm, and smallest ovigerous female 3.0 mm.

Distribution.—Type locality: Mendocino, California. Other localities: Southern Prince William Sound, Alaska; Dixon Entrance and mainland coast south to Johnstone Passage, British Columbia; Washington coast of Juan de Fuca Strait; San Juan area, Washington; Pacific coasts of Queen Charlotte Islands, Vancouver Island and Oregon; Humboldt Bay, Laguna Beach, Dillon Beach, and Moss Beach, California.

Genus *Metacaprella* Mayer, 1903

Metacaprella kennerlyi (Stimpson, 1864)

Caprella kennerlyi Stimpson, 1864; Mayer, 1882, 1903; Holmes, 1904; Johnson and Snook, 1927; Wailes, 1931; Light, 1941; Ricketts and Calvin, 1952.

Metacaprella kennerlyi Dougherty and Steinberg, 1953, 1954; Gardella, 1962; Saunders, 1966; Laubitz, 1970.

Material examined.—Freshwater Rocks, 2 females; Trinidad Bay, 8 males and 5 females; Cimberg's Rock, 2 males and 1 female; Samoa Boat Ramp, 1 female; Artificial Reef, 1 specimen; Fort Bragg (1), 2 males and 7 females; Nearshore Benthos off Humboldt Bay, 42 males and 34 females.

Remarks.—Specimens were found on hydroids, bryozoans, the exterior shell surface of an abalone, and the tentacular radioles of the sabellid worm, *Eudistylia polymorpha*. Length of largest male 22.0 mm, largest female 9.0 mm, and smallest ovigerous female 7.0 mm.

Distribution.—Type locality: Puget Sound, Washington. Other localities: Popof Bay, Yadutat, Dutch Harbour and Kodiak Harbour, Alaska; Washington and British Columbia coasts of Strait of Georgia and Juan de Fuca Strait; Pacific coasts of British Columbia, Vancouver Island, Washington and Oregon; Queen Charlotte Islands; off Washington and Oregon; Friday Harbor, Washington; California coast south to Santa Barbara.

Genus *Caprella* Lamarck, 1801

Caprella acanthogaster humboldtiensis, new subspecies

Figure 3

Material examined.—Field's Landing, 71 males and 55 females; holotype and paratypes deposited in the Invertebrate Museum, Department of Biology, Humboldt State University, Arcata, California; paratypes deposited in the National Museum of Natural Science in Canada, Ottawa, Canada.

Description.—Body spination of male as follows: Cephalon and pereonite 1 smooth dorsally, pereonite 2 with one to three pairs of small spines posteriorly, pereonite 3 with seven spine pairs along its length, pereonite 4 with eight pairs along its length, pereonite 5 with five spine pairs, pereonites 6 and 7 with paired spines medially and posteriorly; laterally, spines at the base of second gnathopod, posterior spines on pereonite 2, seven spines marginally on pereonites 3 and 4, and two spines anteriorly on pereonite 5. Cephalon, pereonites 1 and 2, and gnathopod 2 set with long setae, quite dense in older males; males also exhibit elongation of pereonites 1 and 2. In females, cephalon usually smooth but may have one pair of spines, pereonite 1 always bearing one pair of spines postero-dorsally pereonites 2–5 with variable spination both laterally and dorsally, pereonites 6 and 7 similar to that of the male; in both sexes, occasional unpaired spines dorsally or laterally on the pereon; pleura slightly developed. Length of largest male found 18.0 mm, largest female 11.0 mm, and smallest ovigerous female 6.0 mm.

Antenna 1 of male almost as long as cephalon plus pereonites 1–3, female antenna 1 longer than cephalon plus pereonites 1–4, flagellum with twenty-five articles in males and nineteen articles in females. Peduncle article 3 of antenna 1 produced into a small projection antero-dorsally. Antenna 2 shorter than the two basal articles of antenna 1 in males; in females, antenna 2 shorter than peduncle articles 1–3 of antenna 1, flagellum with swimming setae.

Mouthparts typical of genus; lacinia mobilis of right mandible denticulate but not five-toothed.

Propodus of gnathopod 1 with 2 proximal grasping spines, grasping margin of dactylus and propodus serrate. In males, gnathopod 2 propodus almost three times as long as wide, and only slightly longer than basis, palm with large projection proximo-medially with grasping spine, also poison tooth between proximomedial projection and a distal triangular projection; dactylus heavy and scimitar-shaped; basis having an antero-lateral projection distally, and attached posteriorly on pereonite 2. Female gnathopod 2 propodus longer than basis, palm with proximal grasping spine and two accessory spines, distal minute poison tooth and more distal rounded projection, basis attached anteriorly on pereonite 2.

Gills ovate to elliptical in both sexes.

Pereopods 5–7 increasing in length posteriorly, propodus with 2 proximo-medial grasping spines, palm expanded near grasping spines.

Abdomen of male and female typical of genus.

Brood plates of female typical of genus.

Remarks.—*Caprella acanthogaster* Mayer (1890) was originally described from

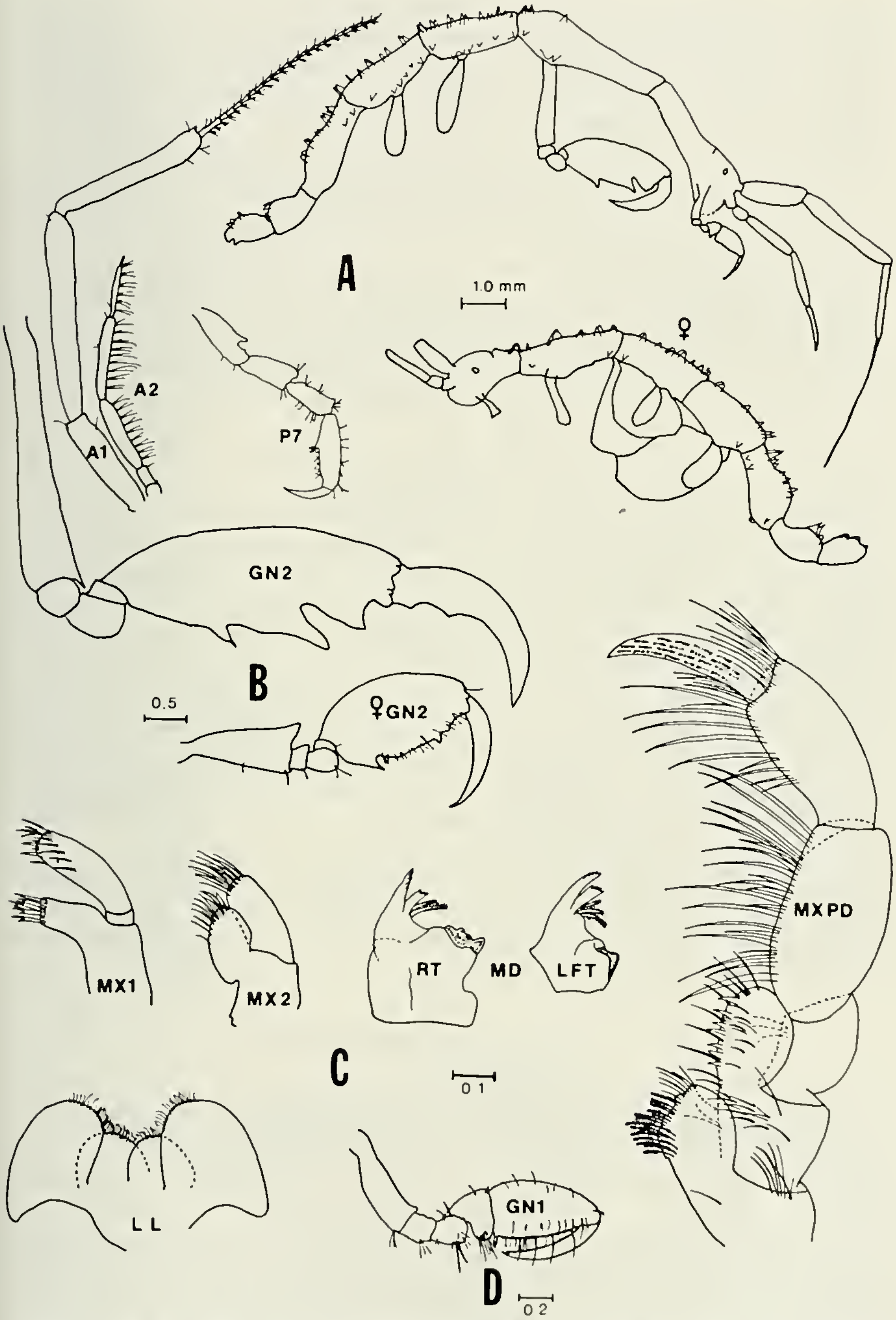

Fig. 3. *Caprella acanthogaster humboldtiensis*: A. Male and female, lateral view; appendages, antenna 1, antenna 2, and pereopod 7; B. Male gnathopod 2 and female gnathopod 2; C. Male mouthparts; D. Male gnathopod 1; measurements are in millimeters. Key to figure symbols: A = antenna; GN = gnathopod; LFT = left; LL = lower lip; MD = mandible; MX = maxilla; MXPD = maxilliped; P = pereopod; and RT = right.

along the coast of China, and from that description and the description in Mayer's (1903) monograph there appear to be certain differences between the species he described and my specimens (Table 1). These morphological distinctions plus the geographical distance between the populations are my basis for assigning the specimens to a new subspecies.

Specimens of *C. acanthogaster humboldtiensis* were found on the hydroids *Obelia borealis* and *Plumularia corrugata*. One specimen of *C. acanthogaster humboldtiensis* was observed with a polyp of the hydroid *Obelia* sp. attached to the dorsal surface of pereonite 2.

Caprella acanthogaster humboldtiensis at Field's Landing in Humboldt Bay comprised forty percent of the caprellid collection at that location and was associated with five other species of caprellids common to the Bay. It is suspected that this species was introduced into the Bay by the fouling on ships or with oyster spat *Crassostrea gigas* which were imported from Japan.

Caprella alaskana Mayer, 1903

Caprella alaskana Mayer, 1903; Laubitz, 1970.

Material examined.—Trinidad Bay, 2 males; Samoa Boat Ramp, 1 female.

Remarks.—This species shows great variation in the degree of spination on the cephalon and pereon. Specimens described by Mayer (1903) were quite spiny in comparison to those examined by Laubitz (1970), which were almost spineless. According to Laubitz (1970), "The differences are, in fact, so great that they create a doubt that these are members of the same species." Laubitz (pers. comm.) has since emphasized that, in species where the body spination is highly variable, this character is not reliable. The specimens found within my study area were moderately spiny, and the spination of males and female was quite similar.

Specimens were found on bryozoans and the tubes of sabellid worms. Length of largest male 9.2 mm and largest female 8.5 mm.

Distribution.—Type locality: Not known, probably Alaska. Other localities: Aleutian Islands, Kodiak Island, Prince William Sound, and Alexander Archipelago, Alaska; Fort Rupert, Queen Charlotte Islands, Queen Charlotte Strait, and Vancouver Island, British Columbia.

Caprella brevirostris Mayer, 1903

Figure 4

Caprella brevirostris Mayer, 1903; Dougherty and Steinberg, 1953, 1954.
Caprella septentrionalis La Follette, 1914 (*non* Krøyer, 1842–43.)

Material examined.—Fort Bragg (1), 1 male; Fort Bragg (2), 5 males and 5 females.

Description.—Cephalon with small anteriorly directed triangular projection, pereonites 1–5 smooth, pereonite 6 with paired spines postero-laterally, pereonite 7 with paired spines postero-laterally and one postero-medial spine; pereonites 1 and 2 are elongated in males with posterior pereonites shortening quickly.

Antenna 1 in males longer than cephalon plus pereonites 1 + 2; in females, antenna 1 longer than cephalon plus pereonites 1–3; flagellum with twelve articles in males and eight articles in females. Antenna 2 of male as long as peduncle

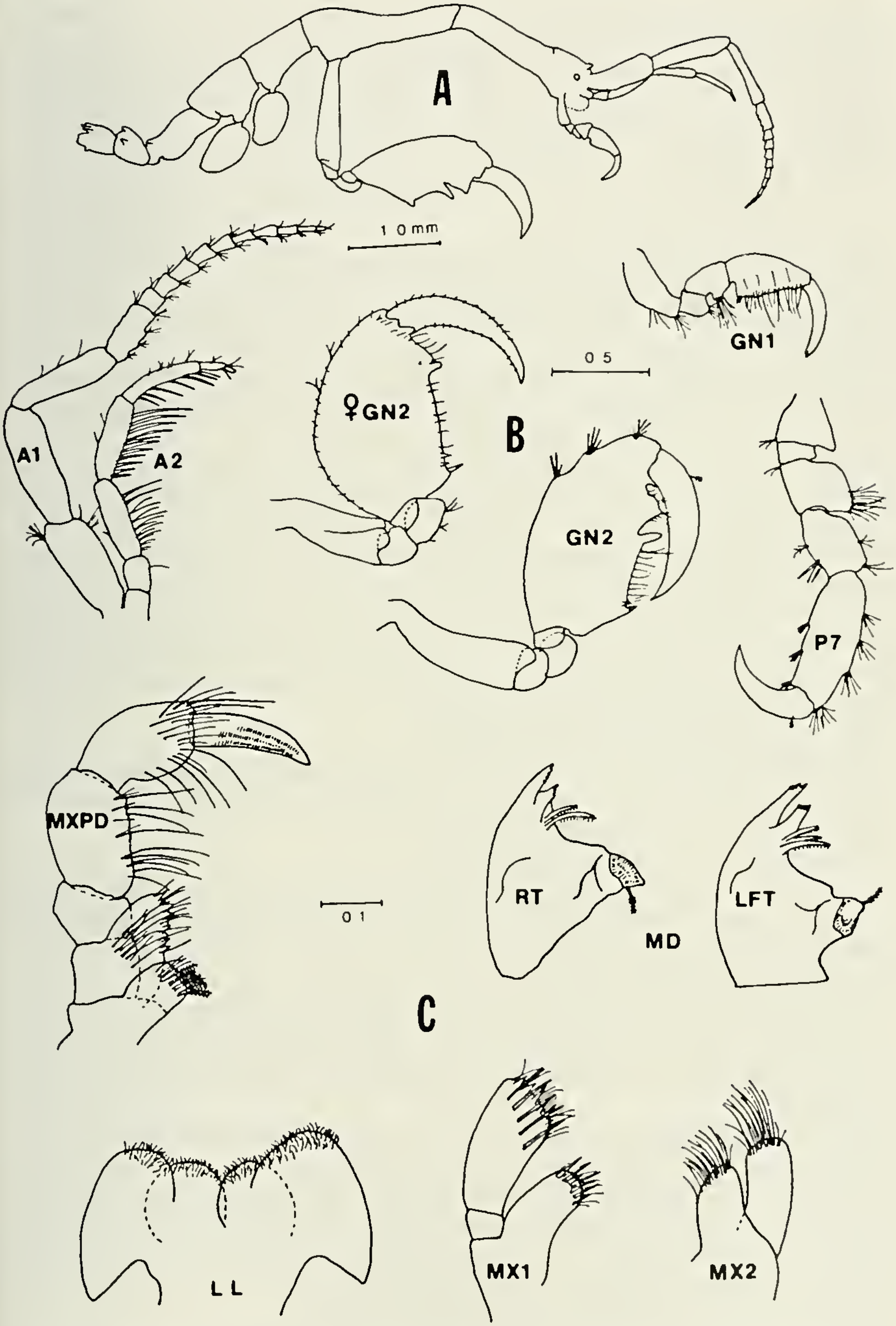

Fig. 4. *Caprella brevirostris*: A. Male, lateral view; B. Female gnathopod 2; and male antenna 1, antenna 2, gnathopod 1, gnathopod 2, and pereopod 7; C. Male mouthparts; measurements are in millimeters. Symbols as in Figure 3.

Table 1. Morphological distinctions between *Caprella acanthogaster acanthogaster* and *C. a. humboldtiensis*.

	C. a. acanthogaster	*C. a. humboldtiensis*
Size (largest)	42 mm	18 mm
Gills	long, slender	ovate to elliptical
Spination of pereonite 5	approximately 10 pairs of spines	5 pairs of spines

articles 1 + 2 of antenna 1; in females, antenna 2 longer than entire peduncle of antenna 1, flagellum with swimming setae.

Mouthparts typical of genus; lacinia mobilis of right mandible toothed but not five-toothed.

Propodus of gnathopod 1 with 2 proximal grasping spines, grasping margin of dactylus and propodus serrate. Gnathopod 2 propodus of males almost twice as long as broad, and with tufts of setae antero-dorsally and on the sides of palmar projections, palm with proximo-medial projection with grasping spine and accessory spine, palm also with distal acute poison tooth and more distal triangular projection; dactylus somewhat scimitar-shaped with serrate grasping margin; ischium with antero-lateral rounded projection; basis curved at distal end, attached posteriorly on pereonite 2, and having two small antero-dorsal ridges. Female gnathopod 2 propodus longer than basis, palm with proximal grasping spine and two accessory spines, also small acute poison tooth distally and more distal rounded projection; basis attached anteriorly on pereonite 2, and having antero-distal ridge with terminal rounded projection.

Gills oval to oblong in males and females.

Pereopods 5–7 increasing in length posteriorly, propodus with three tufts of truncated spines on palm, convex surface with tufts of long setae.

Abdomen in both sexes typical of genus.

Brood plates of female typical of genus.

Remarks.—In his 1903 monograph, Mayer devoted one paragraph and four figures to the actual description of *C. brevirostris*. Since that time subsequent authors have given mere mention of this species, therefore, I have given a complete redescription and set of figures.

My specimens varied from Mayer's (1903) descriptions only in size. His largest male and female specimens measured 12.0 mm and 5.0 mm, respectively, whereas my largest male measured 7.5 mm and the largest and smallest ovigerous female measured 3.0 mm.

Specimens were found on a hydroid, an alga, and the exterior shell surface of an abalone.

Distribution.—Type locality: Straits of Korea. Other localities: Pacific coasts of Korea and China; Pacific Grove and Tomales Point, California.

Caprella californica Stimpson, 1857

Refer to Laubitz (1970); *see also* Keith, 1969, 1971.

Material examined.—Abalone Beach, 1 female; Trinidad Bay, 1 male and 1 female; Samoa Boat Ramp, 4 males, 4 females, and 1 juvenile; Elk River Slough, 2 males and 1 female; Artificial Reef, 436 specimens; Field's Landing, 55 males and 56 females; Humboldt Bay, 19 males and 25 females.

Remarks.—Mayer (1903) separated the three varieties of *Caprella scaura* on the basis of the spination of pereonite 5. Laubitz (1970) assigned two of the varieties, *spinorostris* and *scauroides*, to the third, *C. californica*, because of the high degree of variability in body spination seen in *C. californica*. Considering the variations seen in my specimens, Laubitz' decision appears justified.

Specimens were found on algae, eelgrass, hydroids, and the tubes of sabellid worms. Length of largest male 19.5 mm, largest female 14.1 mm, and smallest ovigerous female 6.5 mm.

Distribution.—Type locality: San Francisco Bay, California. Other localities: South China Sea and Formosa Strait; Korea Strait and off Korea; Tsugaru Strait and off southwestern Japan; Queen Charlotte Islands, Hecate Strait, Queen Charlotte Sound, and Strait of Georgia, British Columbia; Pacific coasts of Vancouver Island and Washington; Juan de Fuca Strait and San Juan area, Washington; California from San Diego to Humboldt Bay; Caldera, Chile.

Caprella equilibra Say, 1818

Refer to McCain, 1968; *see also* Light, 1941; Laubitz, 1970; Keith, 1969, 1971.

Material examined.—Field's Landing, 1 female; Pacific Gas and Electric Company Nuclear Power Plant Outflow Canal, 19 males and 23 females; Artificial Reef, 257 specimens.

Remarks.—Specimens were found on hydroids and bryozoans. Length of largest male 15.0 mm, largest female 7.0 mm, and smallest ovigerous female 5.0 mm.

Distribution.—Type locality: South Carolina. Other localities: *See* McCain, 1968; also San Juan area, Washington; Vancouver Island, Queen Charlotte Sound, and Hecate Strait, British Columbia.

Caprella ferrea Mayer, 1903

Caprella ferrea Mayer, 1903; Laubitz, 1970.
Metacaprella ferrea Dougherty and Steinberg, 1953, 1954.

Material examined.—Freshwater Rocks, 3 males and 4 females; Trinidad Bay, 22 males and 20 females; Samoa Boat Ramp, 2 males and 3 females; Fort Bragg (1), 1 male; Fort Bragg (2), 1 female.

Remarks.—Specimens of *C. ferrea* collected at Freshwater Rocks differed from Laubitz' (1970) description in that peduncular segments 2 and 3 of antenna 1 were heavily setose.

Specimens were found on hydroids, bryozoans, the tubes of sabellid worms, and the exterior shell surface of an abalone. Length of largest male 9.0 mm, largest female 6.5 mm, and smallest ovigerous female 4.5 mm.

Distribution.—Type locality: Humboldt Bay, California. Other localities: Moss Beach and Monterey Bay, California; Pacific coasts of Vancouver Island and Queen Charlotte Islands, British Columbia; Alexander Archipelago, Alaska.

Caprella greenleyi McCain, 1969
Figure 5

Caprella greenleyi McCain, 1969.

Material examined.—Abalone Beach, 2 males; Cimberg's Rock, 1 female.

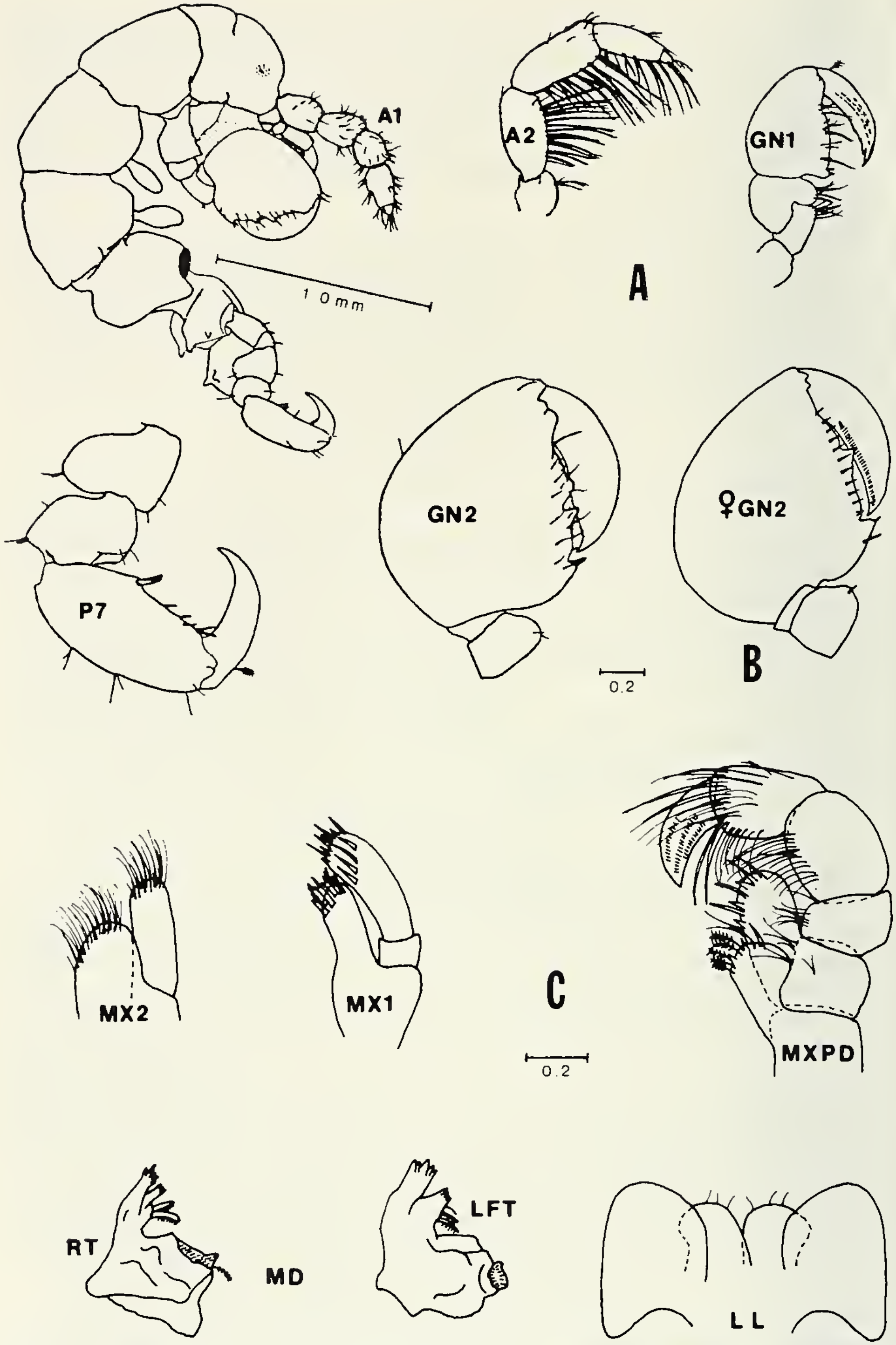

Fig. 5. *Caprella greenleyi*. A. Male, lateral view, antenna 1, antenna 2, gnathopod 1, gnathopod 2, and pereopod 7, not to scale (from McCain, 1969); B. Female gnathopod 2; C. Female mouthparts; measurements are in millimeters. Symbols as in Figure 3.

Description.—Cephalon, body, and appendages robust and covered with microtubercles, small median dorsal paired tubercles on pereonite 5, large median dorsal paired tubercles on pereonites 6 and 7, anteriorly directed pleural projections on pereonites 3 and 4.

Antenna 1 approximately equal to pereonites 1 + 2, flagellum uniarticulate. Antenna 2 shorter than antenna 1, flagellum uniarticulate, with swimming setae.

Mouthparts typical of genus; lacinia mobilis of right mandible toothed but not five-toothed.

Propodus of gnathopod 1 with 2 proximal grasping spines, grasping margin of dactylus and propodus serrate. In males, propodus of gnathopod 2 approximately two-thirds as broad as long, palm with 2 proximal grasping spines and medial notch; in females, propodus of gnathopod 2 palm with single medial projection; dactylus in both sexes massive and scimitar-shaped with slightly serrate grasping margin; basis attached medially on pereonite 2 in males and females and having antero-lateral ridge.

Gills oval in males and females.

Pereopods 5–7 stout, slightly increasing in length posteriorly, propodus with 2 proximal grasping spines.

Abdomen of both sexes typical of genus.

Remarks.—*Caprella greenleyi* is an unusually small caprellid species, the original description was based on specimens ranging from 2.7 mm to 3.6 mm. My recorded lengths were: largest male 1.5 mm, largest female 2.3 mm, and no ovigerous female was found. This species was first found clinging to the sea star *Henrica leviscula* (Stimpson, 1857); McCain (1968) suspected it of having a direct association with that particular sea star. Inspection of over 300 specimens of *H. leviscula* in this study failed to produce any specimens of *Caprella greenleyi*.

My specimens of *C. greenleyi* possess enough variation from the original description (McCain, 1968) to warrant the supplemental redescription and figures which are presented.

Specimens were found on a coralline alga and bryozoans.

Distribution.—Type locality: Boiler Bay, Oregon. New records: Abalone Beach and Cimberg's Rock, California.

Caprella incisa Mayer 1903

Caprella acutifrons var. *incisa* Mayer 1903.

Caprella incisa Dougherty and Steinberg 1953, 1954; McCain 1968; Laubitz 1970.

Material examined.—Point Saint George, 5 males and 1 female; Battery Point, 18 males and 13 females; False Klamath Cove, 1 male; Trinidad Bay, 3 males and 3 females; Buhne Point, 35 males and 42 females; Artificial Reef, 14 specimens; Fort Bragg (1), 3 males; Fort Bragg (2), 178 males, 209 females, and 1 intersex.

Remarks.—Specimens of *C. incisa* examined in this study included two distinct size classes and one intersex specimen. Adult specimens found north of Trinidad Bay were unusually small (approximately 5.0 mm), but I have included them with *C. incisa* on the basis of the type of spination, some pleural development, distal palmar development on gnathopod 2, and general body proportions. The adult specimens found south of Trinidad Bay were of 'normal' size.

The so-called ‘female’ intersex specimen of *Caprella incisa* possessed male gnathopod 2 and abdomen with penes, and female brood plates and genital openings on the posterior ventral surface of pereonite 5.

Specimens were found on hydroids, bryozoans, coralline algae, and algae. Length of largest male 11.0 mm, largest female 7.5 mm, and smallest ovigerous female 3.0 mm.

Distribution.—Type locality: California, precise locality not known. Other localities: Pacific coasts of Oregon, Washington, Vancouver Island, and Alexander Archipelago; Washington coast of Juan de Fuca Strait; Queen Charlotte Sound, British Columbia; Pacific Grove, Santa Catalina Island, Point Reyes, Dillon Beach, and Moss Beach, California.

Caprella laeviuscula Mayer, 1903

Refer to Laubitz, 1970.

Material examined.—Abalone Beach, 2 males and 3 females; Trinidad Bay, 118 males, 42 females, and 23 juveniles; Samoa Boat Ramp, 21 males, 31 females, and 12 juveniles; Elk River Slough, 2 males; Artificial Reef, 1,825 specimens; Field's Landing, 4 males and 12 females; Humboldt Bay, 297 males, 493 females, and 440 juveniles.

Remarks.—The 1,825 individuals of *C. laeviuscula* collected from the Artificial Reef included five intersex specimens. Four of these specimens possessed male second gnathopods, penes, female brood plates, and female genital openings on the posterior ventral surface of pereonite 5. The fifth specimen possessed only secondary sex characteristics of both sexes and male genitalia; there was no sign of female genitalia on pereonite 5 of this specimen.

Several individuals of *C. laeviuscula* were inspected which had the epiphytic diatom *Isthmia nervosa* attached to the dorsal surface of the pereon. Caprellids are often found covered with detritus, but rarely with living material. On one occasion prior to the initiation of this study, I found large numbers of the hydroid *Clytia* sp. attached to the dorsal surface of the pereon of several active, apparently healthy caprellids. The presence of detritus or living material may serve as camouflage.

Specimens were found on hydroids, bryozoans, compound ascidians, alga, eelgrass, and the tubes of sabellid worms. Length of largest male 15.2 mm, largest female 7.0 mm, and smallest ovigerous female 3.0 mm.

Distribution.—Type locality: Pacific coast of North America, precise locality not known. Other localities: Akkesni Bay, Japan; Kodiak, Adakh, Prince William Sound, and Alexander Archipelago, Alaska; Queen Charlotte Islands, Queen Charlotte Sound, Queen Charlotte Strait, Strait of Georgia, Juan de Fuca Strait, Victoria Harbor, and Fort Rupert, Vancouver Island, and the Pacific Coast of Vancouver Island, British Columbia; Puget Sound, Washington; Pacific coast of Oregon; Humboldt Bay and (?) Monterey Bay, California.

Caprella mendax Mayer, 1903

Caprella mendax Mayer, 1903; Laubitz, 1970.
Caprella equilibra Dougherty and Steinberg, 1953.

Material examined.—Benthos off Humboldt Bay, 1 female, 7.9 mm.

Table 2. Comparison of morphological characteristics between *Caprella scabra*, *C. pustulata* and *C. pilipalma*.

	C. scabra	*C. pustulata*	*C. pilipalma*
Cephalic spine	pointed, stout	blunt, stout	pointed, slim
Antenna 1 length	scarcely ⅓ body length	⅓ body length	⅓ body length
setation	none	dense	none
Gnathopod 2 attachment	median	posterior	posterior to median
poison tooth	present	present	absent
setation	none	dense	dense
grasping spine	none	one, small proximal	none
Spination (body)	small, low anteriorly; larger posteriorly	raised and large	low and small

Remarks.—The single specimen was collected in a Smith-McIntyre bottom grab at a depth of 80 meters off Humboldt Bay.

Distribution.—Type locality: California, precise locality not known. Other localities: Pacific Grove, Santa Barbara, and San Diego, California; Vancouver Island and Hecate Strait, British Columbia; San Juan Islands, Washington.

Caprella natalensis Mayer, 1903

Refer to Laubitz, 1972.

Material examined.—Battery Point, 3 males and 1 female; Trinidad Bay, 1 male; Cimberg's Rock, 3 males and 3 juveniles; Buhne Point, 16 males and 39 females; Humboldt Bay, 13 females; Fort Bragg (1), 4 males and 7 females; Fort Bragg (2), 13 males and 15 females.

Remarks.—Laubitz (1972) presented an excellent discussion of a portion of the *Caprella acutifrons* group, in which she gave *C. acutifrons* var. *natalensis* specific status. McCain (1968) has presented a thorough treatment of the group as a whole and also discussed the current taxonomic standing of the remaining varieties.

Specimens were found on bryozoans, hydroids, algae, and the exterior shell surface of an abalone. Length of largest male 9.6 mm, largest female 7.5 mm, and smallest ovigerous female 4.0 mm.

Distribution.—Type locality: Port Natal, Indian Ocean. Other localities: Durban, Cape Town, and Cape Peninsula, South Africa; South West Africa; Tristan da Cunha; Queen Charlotte Islands, British Columbia south to Oregon; Pacific Grove and Santa Cruz, California.

Caprella pustulata Laubitz, 1970

Caprella pustulata Laubitz, 1970.

Material examined.—Oregon border, 5 males, 1 female, and 13 juveniles; Freshwater Rocks, 3 males and 3 females; Abalone Beach, 3 males and 1 female; Samoa Boat Ramp, 1 male; Elk River Slough, 2 males and 3 females.

Remarks.—Those adult specimens of *C. pustulata* collected in the northern portion of the study area were unusually small (approximately 4.0 mm). The occurrence of these small-sized adults in this species and *C. incisa* suggests that the populations sampled were young at the time of collection (winter), or their adult size is limited by some environmental factor.

Since *C. pustulata* is quite similar in structure and distribution to *C. scabra* Holmes (1904) and *C. pilipalma* Dougherty and Steinberg (1953), Table 2 is made from the original descriptions for reference.

Specimens were found on hydroids, bryozoans, and the tubes of sabellid worms. Length of largest male 9.0 mm, largest female 4.5 mm, and smallest ovigerous female 3.5 mm.

Distribution.—Type locality: Gudal Bay, Graham Island, Queen Charlotte Islands, British Columbia. Other localities: Baranof Island, Prince William Sound, and Canoe Bay, Alaska; Vancouver Island, Koeye Estuary, and Queen Charlotte Islands, British Columbia; Washington and Oregon.

Caprella verrucosa Boeck, 1872

Refer to Laubitz, 1970.

Material examined.—Point Saint George, 1 male; Battery Point, 1 male and 3 females; False Klamath Cove, 2 males, 1 female, and 2 juveniles; Trinidad Bay, 1 female and 2 juveniles; Fort Bragg (2), 2 males, 1 female, and 1 juvenile; Cimberg's Rock, 15 males, 10 females, and 4 juveniles.

Remarks.—Specimens were found on hydroids, bryozoans, and coralline algae. Length of largest male 5.5 mm, largest female 4.5 mm, and smallest ovigerous female 2.7 mm.

Distribution.—Type locality: California, probably near San Francisco. Other localities: Misaki, Yokohama. Tateyama Bay, and Onagawa Bay, Japan; Pacific coasts of Queen Charlotte Islands, Vancouver Island and Washington; Dillon Beach, Pacific Grove, Santa Catalina Island, Point Reyes, and Laguna Beach, California.

Discussion

Nineteen species of caprellid amphipods representing six genera were found in this study. Five other species have been recorded previously from the California coast: *Tritella tenuissima*, *Caprella gracilior*, *C. uniforma*, *C. pilipalma*, and *Metacaprella anomala*. The first two are typically deepwater organisms and are rarely found intertidally; in addition, *T. tenuissima* has not been recorded north of Carmel Bay, while *C. gracilior* has been recorded both north and south of the study area. *Caprella uniforma* and *C. pilipalma* are intertidal species which have not been recorded north of Pacific Grove, California. *Metacaprella anomala* is an intertidal species which is occasionally found in deep water and has been recorded north and south of the study area.

Table 3 lists the caprellid species and the coastal habitat types in which the specimens were collected. The nineteen collecting sites were classified as outer coast, protected outer coast, bay and wharf piling, using the system of Ricketts and Calvin (1968) and nearshore benthos (Figs. 1 and 2). The bay habitat was divided into two sub-types: (1) those exposed at low tide and (2) those subtidal. Those exposed at low tide included mudflats, sandflats, and jetties, while subtidal

Table 3. Distribution data for the Caprellidae of the northern California coast. Numbers indicate specimens collected.

	Oregon border	Freshwater rocks	Cape Mendocino	Pt. St. George	Battery Pt.	False Klamath Cove	Abalone Beach	Trinidad Bay	Cimberg's Rock	Shelter Cove	Fort Bragg (1)	Fort Bragg (2)	Samoa Boat ramp	Coast Guard jetty	Buhne Pt.	Elk River slough	Artificial reef	Field's Landing	P. G. & E.
Habitat type	OC →	→	→ →	POC →	→	→	→ →	→	→ →	→	→ →	→ →	WP	BAY	(1) →	→ →	(2) →	→ →	→
# of samplings	1	1	1	1	1	1	4	8	3	1	1	1	4	1	1	1	9	2	1
Species																			
Perotripus brevis								3											
Caprella brevirostris											1	10							
C. greenleyi							2		1										
Cercops compactus					1	2	2			1									
Tritella laevis				9	56		33			13		8							
Caprella verrucosa				1	4	5		3	29			4							
C. alaskana								2					1						
C. natalensis					4			1	6		11	28			55				
C. incisa				6	31	1		6			3	389			77		14		
Deutella californica							1	12				1	23	6		20	152	61	
Caprella laeviuscula							5	183					64			2	1,825	16	
C. californica							1	2					9			3	436	111	
Metacaprella kennerlyi		2						13	3		9		1				1		
Tritella pilimana	421	19	1			9		73	3				57	5		11	1,094	2	
Caprella ferrea		7						42			1	1	5						
C. pustulata	19	6					4						1			5			
C. equilibra																	257	1	42
C. acanthogaster humboldtiensis																		126	

locations were floating docks, an artificial reef in South Humboldt Bay, and floating debris.

There were three outer coastal (OC) habitat sites, nine protected outer coastal (POC) habitat sites, one wharf piling (WP) habitat site, and seven bay (BAY) habitat sites. An attempt was made to correlate the distribution of the listed caprellid species with the type of coastal habitat in which they were found.

The outer coast was characterized by four species and all these were present on the protected outer coast, which possessed the most diverse caprellid fauna of all the coastal habitat types. Sixteen species of caprellids characterized this habitat.

The wharf piling habitat was characterized by seven species, and appears to be quite similar in its species composition to that of the bay habitat in which eleven species were found. *Tritella pilimana* was the most cosmopolitan species found throughout the study area. *Caprella equilibra* and *C. acanthogaster humboldtiensis* were found only in subtidal situations. *Caprella equilibra* was the only species present in the outflow canal of the Pacific Gas and Electric Company Nuclear Power Plant, where the water temperature was 21C as compared to the normal temperature range of Humboldt Bay of 9–13C.

It is suspected that the distribution of the listed caprellid species within the study area is influenced by the amount of wave action in the specific habitat type. Keith (1971) speculated that temperature and the amount of wave action are the primary factors affecting caprellid distributions. Other investigations have shown that temperature and salinity are the primary factors affecting the distribution of these organisms (McCain, 1968; Laubitz, 1970). Another potential factor is the duration of exposure at low tide.

The nearshore benthos off Humboldt Bay yielded *Caprella mendax, Metacaprella kennerlyi* and a third species of questionable identification. The questionable species is thought to be *Caprella ciliata* G. O. Sars (1882); a single specimen was obtained in a rock trawl at 100 m. This caprellid has previously been recorded in deep water off Alaska. Its poor condition made positive identification impossible. Laubitz (pers. comm.) has agreed that this is probably *C. ciliata*. Future collections within the study area should yield an even more diverse caprellid fauna than that reported here.

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The Diet of Large and Small Individuals of the Sea Anemone *Metridium senile*

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Abstract.—Microscopic examination of waste pellets of *Metridium senile* on wharf pilings in Monterey, California, revealed that the same foods were utilized by both large and small anemones. Zooplankters, including copepods, polychaete larvae, bivalve and gastropod veligers, copepod nauplii, and barnacle nauplii and cyprids constituted nearly all of the available planktonic animals and identifiable animals in waste pellets. Zooplankters were eaten roughly in proportion to their availability. Pieces of flesh, scraped from fish or squid by fishermen, were available in the water, and commonly occurred in waste pellets. Both large and small specimens of *M. senile* appear to feed non-selectively on small waterborne animal foods.

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Metridium senile is an abundant anemone species of circumpolar distribution, occurring in protected bays and harbors in cold to temperate waters (Hand, 1955). Much of the earlier work on *M. senile* is summarized in Stephenson (1935). The numerous papers of Batham and Pantin (e.g., 1950, 1951) cover many aspects of its structure and function.

Previous studies include some work on the feeding behavior in *Metridium senile*. Parker (1896, 1905, 1917) described reactions to food, ciliary currents and their reversal on the lips and pharynx, and fatigue in the feeding response due to repeated stimuli, but made no investigation of the natural diet. Hand (1955) stated from laboratory observations: "Small specimens readily accept pieces of macrofood such as clam or fish. What is interesting is that large specimens respond sluggishly or not at all to solid food and seem to accept it only when quite hungry. Even such small macrofood as copepods is not readily taken by large specimens of *Metridium*, which suggests these anemones may be almost exclusively microplankton feeders. These observations are original and agree in general with those of Elmhirst (1925), Pax (1928), and Stephenson (1935)."

No studies have yet been conducted to determine the natural diet of *Metridium senile* of any size, or to determine whether the reported feeding preferences of small and large animals are reflected by the food selected in nature. This study was undertaken to discover the natural diet of large and small individuals of *M. senile*.

Methods

The research was conducted at the Hopkins Marine Station of Stanford University in Pacific Grove, California from September through November 1975. Animals were collected from Monterey Municipal Wharf #2. In this study, small individuals were those specimens less than 10 cm in expanded column height, large individuals were 20 to 35 cm in expanded column height. Dense aggregations of small individuals occur from the intertidal level on the pilings to the bottom. The very large specimens of *M. senile* occur as solitary individuals within 2 m of the bottom. The collections made in this study were from areas where both sizes occurred.

In order to determine foods consumed by *Metridium senile* in nature, waste pellets were collected from small individuals in the field. Within the tremendous population of small individuals, numerous individuals had waste pellets extruded which remained inside the ring of tentacles prior to removal by water action. These were easily collected using a medicine dropper. The pellets were then squirted into one of two bottles, thereby separating pellets from anemones at the edges of aggregations from those located at the centers of aggregations. The plankton in the water taken into the dropper and bottle along with the waste pellets was the only source of contamination. To eliminate this, samples were examined immediately after return to the laboratory and live zooplankters removed. Large specimens of *M. senile* (much less common) were collected in the field, returned to the laboratory, and settled in clean aquaria provided with running seawater. Batham and Pantin (1950) stated that specimens of *M. senile* produce waste pellets within 48 h after feeding. In the present study, large anemones freshly brought from the field produced waste pellets in 24 to 48 h. Contamination of the samples by benthic organisms was minimized by thoroughly cleaning the pedal disc of the anemones prior to settling. Again, pellets were examined soon after extrusion and live zooplankters removed.

Waste pellets from 50 large individuals of *Metridium senile*, and approximately 150 small individuals each from center and edge areas, were examined under a dissecting microscope. The pellets contained detritus and food animals in various stages of digestion. Recognizable remains of organisms were separated from the unidentifiable detritus. When necessary for identification, the remains were examined under a compound microscope. Relative abundances of the different species or taxa were determined from counts and from estimates of their percentage of the total biomass. To determine what foods were available to the animals from which waste pellets were collected, material was scraped from the pilings near the collection site, and plankton tows were taken by swimming at the same depth close to the pilings at that site. Living or dead algae, sponge, hydroids, bryozoans, and tunicates scraped from the pilings were placed in 95% ethanol and shaken vigorously to remove the small invertebrate fauna. Plankton samples were killed in 95% ethanol. The relative abundances of organisms in the piling scrapings and plankton samples were estimated as above.

Eight collections were made during the study. Each collection included a plankton tow, a scraping from the pilings, acquisition of several large specimens of *M. senile* and the removal of waste pellets from numerous small individuals. Altogether, the waste pellets from 50 large and approximately 300 small anemones were examined. Phytoplankton, unrecognizable detritus, and sand, abundant in the water, were not included as food sources as their nutrient contributions and that of the associated bacteria could not be determined.

Results

The relative abundances (from counts and estimated percentages of total biomass) encountered in the environment and in the waste pellets of large and

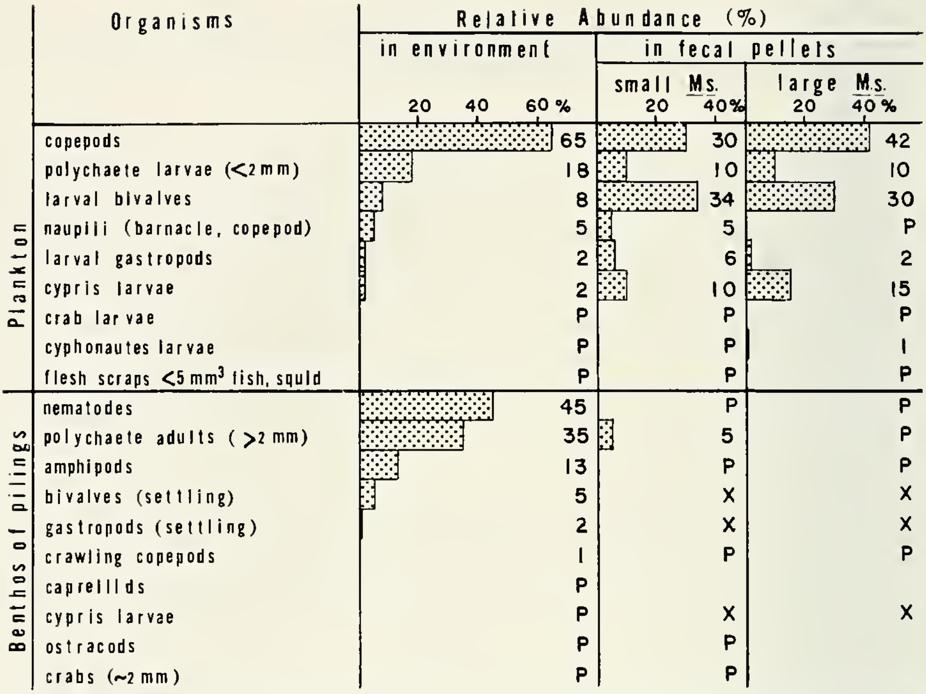

Fig. 1. Relative abundance of organisms in the environment, and in waste pellets of small and large individuals of *Metridium senile*. P = frequently present, but in small numbers or impossible to quantify; X = percentages included with planktonic forms.

small specimens of *Metridium senile* are compared in Figure 1. The percentages listed are averages of data obtained from all eight collections. Relative amounts of the zooplankters and detritus varied considerably between collections. The results obtained for small individuals were nearly identical regardless of the positions of the anemones within the colony, and are combined in Figure 1.

The diets of both large and small specimens of *M. senile* consist almost exclusively of planktonic organisms. The proportions of the remains of planktonic foods in waste pellets coincide well with proportions in the environment, indicating that zooplankters are consumed more or less in proportion to their availability. Larval bivalve and cypris larva remains appear in somewhat greater proportions than their availability would predict, and copepods somewhat less. In marked contrast, benthic organisms were rarely eaten. Perhaps they are less available than their proximity to the tentacles of small anemones might suggest. Values for large and small individuals of *M. senile* are nearly identical, though small individuals consumed a slightly greater proportion of the benthic forms.

Additional organisms whose remains occurred in waste pellets but are not listed in Figure 1 due to their rare occurrance, include caridean larvae, and echinoderm larvae in the plankton, fecal pellets of other organisms, and tiny opisthobranchs, sipunculids, and flatworms from the benthos. Waste pellets from individuals of both sizes of *M. senile* include sponge fragments and spicules, crustacean fecal pellets (from the water or possibly from the guts of digested prey), and barnacle exoskeletons (probably consumed as floating exuvia).

Scraps of flesh a few cubic millimeters in volume, presumed to be remnants of the cleaned catches of fishermen, were sometimes visible in the water near the pilings. Larger chunks and even whole fish and squid occasionally littered the bottom. Pieces of flesh were seen caught in the tentacles of small specimens of *M. senile* several times. Whole dead fish and squid, when washed against the pilings, are caught by numerous adjacent small individuals. Frequently pieces of partially digested flesh, either squid or fish, were present in waste pellets from both large and small *m. senile*. Twenty percent of the large animals regurgitated sizeable amounts of flesh, and numerous fish scales (up to 150) coated with mucus. The eyes and beak of a squid were recovered from one large individual, indicating the ingestion of a sizeable piece.

Discussion

Large and small individuals of the sea anemone *Metridium senile* from Monterey Wharf #2 utilize mainly the same foods: microscopic zooplankters, and waterborne fish and squid scraps. The slightly larger proportion of benthic fauna consumed by small individuals is probably related to the closer proximity of their tentacles to the substratum. Benthic organisms, swimming briefly, or swept from the pilings, are likely to be nearer to the tentacles of small individuals (approximately 3 cm from the pilings) than to those of large individuals (usually at least 15 cm distant).

The differences between relative availability and relative amount consumed, as judged from recognizable remains of the various food organisms in waste pellets, are attributable to the integrity of the digested remains of the prey. Copepods, nauplii, and polychaete larvae are usually thoroughly broken during digestion. They may very well be consumed in proportion to their availability, but their remains are not always recognizable after digestion. In contrast, the shells of larval molluscs and cypris larvae are easily recognizable.

Hand (1955) suggested that large individuals of *M. senile* may consume foods of different sizes than do small individuals. The present study does not support this idea. The two size classes of anemones appear to feed on the waterborne organisms most readily available for capture. Where debris from human fishing activities is available, fish and squid fragments also commonly constitute part of their diet, including sizeable pieces taken by both large and small individuals.

Large specimens of *M. senile* have numerous short tentacles that join the oral disc 1–15 cm from the mouth. These anemones may be unable to transport "big" or "heavy" food (size undetermined) in towards the mouth from distal areas of the oral disc. "Big" food pieces (e.g., the squid head) in relation to the small zooplankton foods, could probably be injested if the pieces fell on or near the mouth of the anemone.

The tentacles of small specimens of *M. senile* join the oral disc within 2 cm of the mouth. All tentacles can deliver food directly to the mouth. The upper size limit for food particles may be determined by food size relative to the area of the oral disc and to the open mouth. The responses of small and large individuals of *M. senile* to graded food sizes are currently being studied.

The possibility exists that the diet of *Metridium senile* living in the artificially enriched environment of the wharf pilings is not representative of the diet in more natural locations. To determine whether such a dietary difference occurs, two populations of *M. senile* were examined in the same manner as previously stated: 1) small individuals at the pilings along side of the Coast Guard breakwater, Monterey Harbor, and 2) large individuals from a rock reef 15 to 25 m deep off Hopkins Marine Station. The two sizes of anemones did not co-occur at either site.

One collection was made at each location, including a plankton and a benthos sample. Comparison of animal remains in waste pellets from 30 small specimens of *M. senile* and 10 large individuals with organisms available in their environment suggests that here, too, both populations feed upon microscopic planktonic organisms in proportion to their abundance in the environment. The fragments of flesh often included in the waste pellets of wharf anemones were not found in those from the other habitats, nor were pieces visible in the water.

The enriched food supply in the wharf environment is accompanied by large populations and high population densities of anemones. The outer wharf pilings, where fishing boats clean their catches, bear aggregations of over 1,000 per square meter (Phillips and Borie, unpublished report). Individuals are so densely packed that the pedal discs of each individual usually contacts those of neighboring anemones on all sides. Populations of small specimens of *M. senile* on similar substrata at the breakwater consist of many fewer anemones (aggregations rarely exceeded 100 individuals) and individual anemones are seldom in contact with others on all sides.

The size of the specimens of *M. senile* dominant in a particular environment may depend upon the type of food available. Small animals may require an artificially enriched food supply to maintain extensive clones which virtually cover the available substratum. This is further suggested by the solid cover of only small specimens of *M. senile* surrounding the Monterey sewer outlet. The large individuals, in contrast, may have the advantage where solely planktonic food is available.

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Selective Pressure on Predator and Prey When an Age Class Becomes a Refuge from Predation

Harrington Wells

Abstract.—A Lotka-Volterra predator-prey model, in which a sexually immature and a sexually mature age class exists, is studied in order to discover the effects on the system of an age class refuge from predation. Prey density-dependent effects are also considered. This refuge situation was found to be advantageous, in terms of group selection for predator and prey, but individually disadvantageous for predators. Prey density dependence reduces the likelihood of an equilibrium between predator and prey populations, but also reduces the necessary criteria for local stability when an equilibrium point exists. A method for the initial occurrence of group selection is suggested.

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Organisms which are preyed upon may have a state (age, density, etc.) in which predation is low or nonexistent. In such cases, one state or stage in the life cycle becomes a refuge from predation. This type of predator-prey interaction can change the dynamics of model systems dramatically, and correspondingly, also seems to be a very important factor in nature. The most notable mathematical works to date on stability in predator-prey systems are by Gause (1934, 1935), Crombie (1946), Leslie and Gower (1960), Rosenzweig and MacArthur (1963), May (1974), Smith and Mead (1974), and Murdoch and Oaten (1975). These theoretical studies have shown that stability is added to the models considered when the species is predation-free below a threshold density. Similarly, in some systems, age structure can enhance stability. An age-class division is an important model which needs consideration in terms of density dependence and varying refuge effectiveness because many organisms undergo a size, form, behavioral, or other characteristic change with the development of sexual maturity. It is important to note that prey age in itself is not important, but the change in size or form which accompanies aging may greatly influence predator efficiency. Since an age (time) dependent escape from predation is potentially available to all organisms, I will consider only that one type of model. The model I consider is a modification of the Lotka-Volterra predator-prey equations (Lotka, 1925; Volterra, 1926) in which a sexually immature and a sexually mature age class of prey exists.

One example of age dependent predation is that of wolves (*Canis lupus*) on Isle Royale (Lake Superior) which prey upon moose (*Alces americana*) which are less than one or over six years old, with age class 2–6 providing a temporary refuge. Usually only 40% of the moose that are less than one year old survive to see their first birthday. The exact effect of wolf predation on moose over six years old is harder to estimate, but the older animals are clearly more vulnerable than the refuge class (Mech, 1966, 1970). It has been suggested that this situation may be typical of carnivore-ungulate ecosystems in general (Pimlott, 1967).

Smaller organisms also have been shown to have age dependent havens from predation. Calef (1973), studying mortality in a population of *Rana aurora*, demonstrated that most mortality occurred because of predation by salamanders on the sexually immature (tadpole) age class. In Calef's study site nearly 300,000 tadpoles hatched, but only 15,000 survived to reach sexual maturity. Furthermore, mortality decreased as the tadpoles became larger. Laboratory studies demonstrated that less than 6% die from starvation alone and that up to 100 times the maximum observed field density of tadpoles could survive to metamorphosis in the absence of predators. Enclosures in the field, designed to eliminate predators, showed 60% tadpole mortality, while no tadpoles survived in enclosures containing both salamanders and tadpoles. Salamanders captured in the field often had tadpole remains in their stomachs, confirming their predator role. Mortality of the adults was not studied, but it is expected that size would eliminate the frog stage as prey for salamanders.

Evidence that size (which is related to age) plays a significant role in predation of the California blennies *Hypsoblennius gilberti*, *H. jenkinsi*, and *H. gentilis* has been gathered by Stephens et al. (1970). Once a fish outgrows the largest available crevice in which it lives, it is eliminated from the blenny population by predators (which at Stephens' study sites were spotted sand bass, *Paralabrax maculatofasciatus*; giant kelpfish, *Heterostichus rostratus*; kelp bass, *Paralabrax clathratus*; and cabezon, *Scorpaenichthys marmoratus*). The number of crevices available for a particular blenny in a habitat is inversely related to fish size. In transplant experiments with tagged fish, none of the larger (greater than 35 mm), introduced fish survived, compared to 33% survival among the larger, indigenous individuals. Smaller, introduced fish were not eliminated. As the results of the introduction experiments predict, size distribution of blennies and crevices correspond closely in all environments studied by Stephens et al. (1970).

Data indicating that size is an important factor in planktonic predation has been gathered by Brooks and Dodson (1965), and Brooks (1968). *Chaoborus* (Sprules, 1972) and *Diaptomus* (Dodson, 1974), predators on various species of *Daphnia*, have been shown to prefer larger prey individuals. Werner and Hall (1974) found sunfish (*Lepomis macrochirus*) to be size-selective when feeding on *Daphnia magna*, and Connell (1972, 1975) has provided evidence that age, as it relates to size, plays an important part in escape from snail predation by *Balanus cariousus*. The latter case is so extreme that predation is close to 100% on the young, and nearly 0% on the mature individuals. Population age structure in species of *Mytilus* (Kitching et al., 1959), *Thais* (Connell, 1966), *Pisaster* (Landenberger, 1967), *Strongylocentrotus* (Ebert, 1968), *Lottia* (Stimson, 1970), and *Ocenebra* (Fotheringham, 1971) suggest that similar situations exist for these genera.

Methods

The following modification of the Lotka-Volterra predator-prey equations will be used to explore the effects on individual and group fitness of a change in age class vulnerability to predation.

$$\frac{dH_1}{dt} = c_1H_2 - k_1H_1P - c_2H_1 \qquad (1)$$

$$\frac{dH_2}{dt} = c_3H_1 - k_2H_2P - c_4H_2$$

$$\frac{dP}{dt} = -c_5P + k_3H_1P + k_4H_2P$$

where: H_1 = the number of sexually immature prey, H_2 = the number of sexually mature prey, P = the number of predators; c_1, c_2, c_3, c_4, c_5, k_1, k_2, k_3, and k_4 are positive constants related to net birth, death, and predation rates, and where t represents time. Specifically: c_1 = prey birth rate; c_2 = rate at which prey leave the sexually immature age class either becoming sexually mature or due to death other than from predation; c_3 = rate at which prey enter the sexually mature age class; c_4 = death rate of sexually mature prey other than from predation; c_5 = predator death rate; k_1 and k_2 = predation rates of sexually immature and mature age classes, respectively, and; k_3 and k_4 = predator birth rates for predators feeding on immature and mature prey, respectively.

Various types of density dependent population ceilings will be explored later for their effects on the conclusion reached from the initial model. Figures 1, and 3 through 6 depict three dimensions with axes P, H_1, and H_2 by showing four planes of the space. Each plane has the curves labeled where a class of organisms (i.e. P, H_1, or H_2) is neither increasing nor decreasing in number of individuals (i.e. isoclines: $dH_1/dt = 0$, $dH_2/dt = 0$, $dP/dt = 0$). Note that the isoclines refer to one dimensional spaces in the planes (e.g., lines in Fig. 1) rather than two dimensional spaces. The arrows show the direction of movement of H_1 and H_2 within the planes depicted. Note that each arrow is the sum of two vectors (see Fig. 1, dotted arrows). The shaded region of these graphs is the area where P is decreasing in number, and the unshaded portion is the region where P is increasing in number of individuals. Stability refers to the ability of the model to return to a point of equilibrium when small perturbations are made to the system at equilibrium (see May, 1971, for a complete discussion of stability).

Analysis

The isocline of dH_1/dt is a line whose slope increases as P increases, while the isocline of dH_2/dt is a line whose slope decreases as P increases. The isocline of dP/dt is a line whose slope is $-k_3/k_4$. In non-degenerate situations (i.e., $P \neq 0$) if $c_2c_4 < c_1c_3$, then a real positive equilibrium point exists $(\hat{H}_1, \hat{H}_2, \hat{P})$. As the difference increases, so does $\hat{P}$. The equilibrium point ($\hat{P}_*$ in Fig. 1) is:

$$\hat{H}_1 = \frac{c_1c_5}{k_4k_1\hat{P} + c_2k_4 + k_3c_1} \tag{2}$$

$$\hat{H}_2 = \frac{c_3c_5}{k_2k_3\hat{P} + c_4k_3 + k_4c_3}$$

$$\hat{P} = \frac{-(k_1c_4 + k_2c_2) + ((k_1c_4 + k_2c_2)^2 - 4k_1k_2(c_2c_4 - c_3c_1))^{1/2}}{2k_1k_2}.$$

The criterion $c_2c_4 < c_1c_3$ is the ability of the prey to increase in number when predators are absent. When a linearised stability analysis was performed (see May 1971) it showed that the equations are characterized by damped oscillations for positive parameter values when $c_2c_4 < c_1c_3$ and $(k_1 - k_2)\,[k_3(k_1\hat{P} + c_2) - c_3k_4] > 0$. The only requirement for the special cases of this model ($k_2 = k_4 = 0$ or $k_1 = k_3 = 0$) is that $c_2c_4 < c_1c_3$; this is also the only criterion necessary for a real positive equilibrium point for these cases (the equations for the special cases were solved by Smith and Mead, 1974, who, however, failed to note the restriction that $c_2c_4 < c_1c_3$).

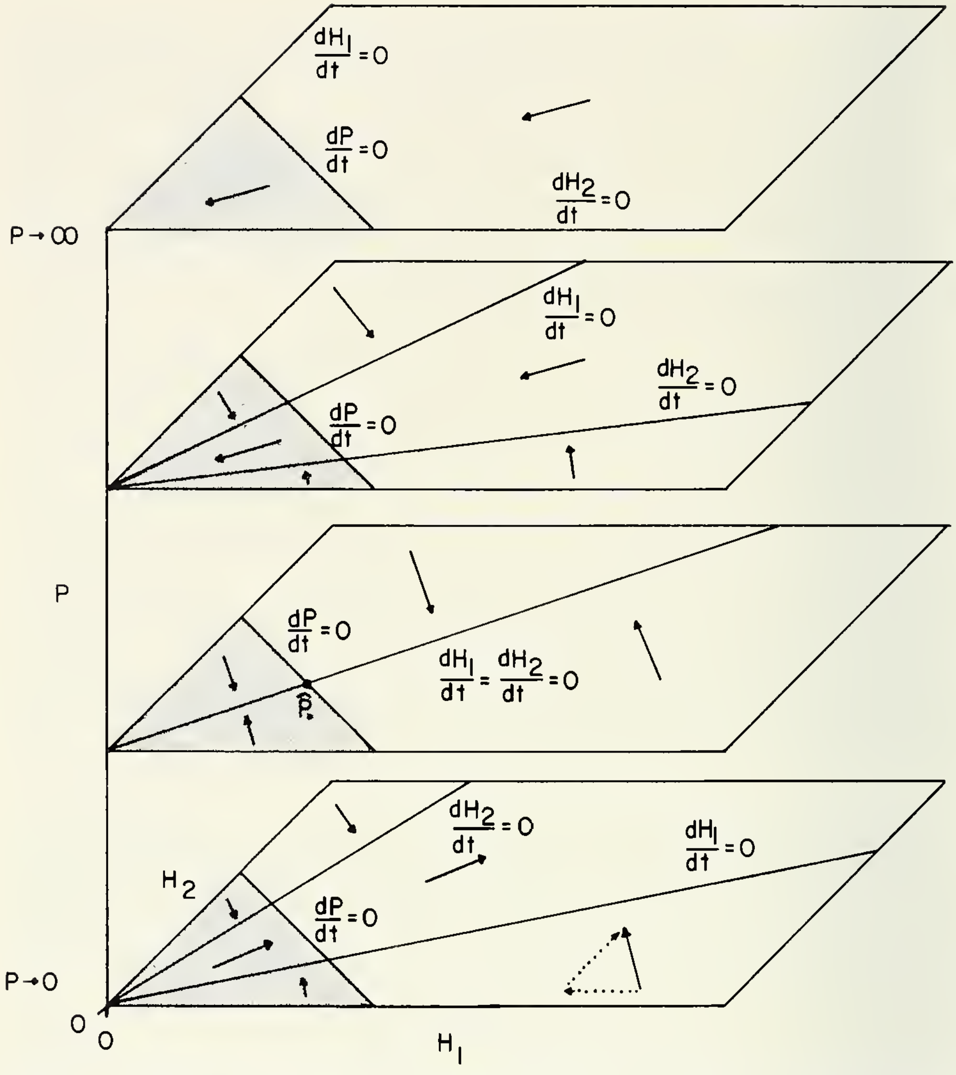

Fig. 1. Density-independent model. $\hat{P}*$ = equilibrium point ($\hat{H}_1$, $\hat{H}_2$, $\hat{P}$); arrows show movement of H_1 and H_2 in the planes; P decreases in the shaded region and increases in the unshaded area.

Consider now what happens when the sexually mature age class, H_2, becomes invulnerable to predation. When $k_2 = k_4 = 0$, the equilibrium point is:

$$\hat{H}_1 = \frac{c_5}{k_3}, \quad \hat{H}_2 = \frac{c_3 c_5}{c_4 k_3}, \quad \hat{P} = \frac{(c_1 c_3 - c_2 c_4)}{k_1 c_4}. \tag{3}$$

Obviously $\hat{H}_1$ is greater than before. In non-degenerate situations, if $c_2 c_4 < c_1 c_3$, then $\hat{P}$ can be seen to be greater by substituting for P $(c_1 c_3 - c_2 c_4)/(k_1 c_4)$ in the equation used to find $\hat{P}$ when no refuge exists (see Fig. 2). $\hat{H}_2$ is also obviously greater than in the general case where k_2, k_4 or $k_1, k_3 \neq 0$. The overall result is that both predator and prey benefit because there are fewer criteria necessary for local stability, and since stability is maintained when larger perturbations from equilib-

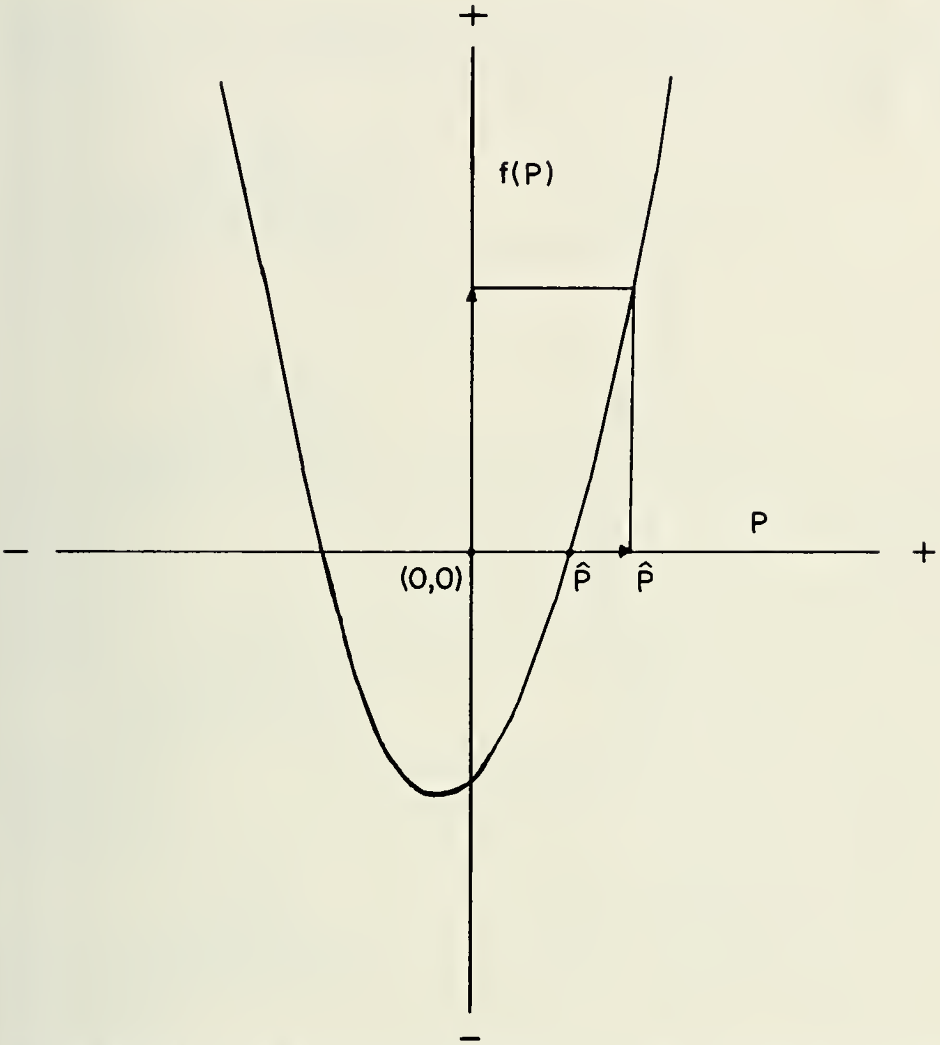

Fig. 2. Plot of $f(P) = k_1k_2P^2 + (k_1c_4 + k_2c_2) + (c_2c_4 - c_3c_1)$. Using $\hat{P}$ for refuge and non-refuge cases to solve for $f(P)$ shows that refuge $\hat{P} >$ non-refuge $\hat{P}$.

rium occur. Thus, the probability of extinction of predator-prey groups is lessened when an age class refuge from predation is added. Therefore a net increase in the fitness of these groups has occurred (group fitness). Stability under larger perturbations can be seen to occur when $\hat{H}_1$, $\hat{H}_2$, and $\hat{P}$ are increased by observing what happens to the population size at equilibrium, S, when it is perturbed to $S(1 - \delta)$ since the method used (May, 1971) is only dependent on picking a sufficiently small δ compared to unity, but not on the actual perturbation size, $T = \delta S$. Thus, if $S_1 > S_2$ then $\delta S_1 > \delta S_2$ so $T_1 > T_2$. Now if $\hat{\delta}$ is the largest δ possible for stability, $T_1 = T_2$, $S_1 > S_2$, and $T_1 = \hat{\delta} S_1$ then stability will not hold for S_2 whereas it will for S_1.

Assume now that some individuals of the predator population evolve or develop the capability of preying on age class H_2 in addition to H_1. This results in two types of predator, P_1 which is restricted by prey age, and P_2 which is not. Letting birth, death, and predation rate constants remain unchanged from those constants described for the original model the new system can be described by the following set of equations.

$$\frac{dP_1}{dt} = -c_5P_1 + k_3H_1P_1 \tag{4}$$

$$\frac{dP_2}{dt} = -c_5P_2 + k_3H_1P_2 + k_4H_2P_2$$

$$\frac{dH_1}{dt} = c_1H_2 - c_2H_1 - k_1H_1(P_1 + P_2)$$

$$\frac{dH_2}{dt} = c_3H_1 - c_4H_2 - k_2H_2P_2.$$

There are two real positive stable equilibrium points for this set of equations (characterized by damped oscillation). They are: $\hat{P}_1 = 0$, $\hat{P}_2$, $\hat{H}_1$, and $\hat{H}_2$ equal to the solution for k_2, $k_4 \neq 0$, and $\hat{P}_2 = 0$, $\hat{P}_1$, $\hat{H}_1$, and $\hat{H}_2$ equal to the solution for $k_2 = k_4 = 0$. Note also that the individual fitness (defined by the rate of reproduction of an individual) of a member of P_2 is greater than that of a member of P_1. The group fitness (at equilibrium) where $P_1 \neq 0$ as shown, however, is greater than that of P_2. Finally, when stochastic behavior is considered in computer models, age structure prey refuges add stability when compared to models with a single type of prey (Smith and Mead, 1974).

Altering the model such that the immature prey age class, H_1, becomes invulnerable to predation and the sexually mature age class, H_2, is vulnerable to predation does not change the results of this model system. The ability to reach an equilibrium point for $\hat{P}, \hat{H}_1, \hat{H}_2 > 0$, and the criteria necessary for stability if such an equilibrium point can be reached, is changed by density dependent terms and will now be explored in some models.

Density dependence of the form: $dH_2/dt = c_3H_1 - c_4H_2 - k_2H_2P - eH_2^2$ (i.e. only sexually mature prey are affected by the density of organisms, and then, only by the number of sexually mature prey) makes it more difficult to obtain a real positive stable equilibrium point. The H_2^2 term changes the H_2 isocline from a line into a parabola (Fig. 3). A real positive equilibrium point exists if: $(c_3c_1 - c_4c_2)/(ec_2) > (c_2c_5)/(k_3c_1 + c_2k_4)$. It becomes more difficult to obtain a real positive equilibrium point when $k_4 = k_2 = 0$; however, if one exists, it is stable. Notice also that as e becomes smaller the criterion becomes easier to meet. Stability criteria for the case where k_2, $k_4 \neq 0$ are the same as for the density-independent model except for the addition of a variable which is always positive to the left hand side of the criterion equation. Similar results are obtained when only dH_1/dt is density dependent (upon H_1).

Next, consider density dependence of the type:

$$\frac{dH_1}{dt} = c_1H_2 - k_1H_1P - c_2H_1 - fH_2^2 \tag{5}$$

$$\frac{dH_2}{dt} = c_3H_1 - k_2H_2P - c_4H_2 - eH_2^2$$

(i.e. both prey age classes are affected by the density of organisms, but only by the

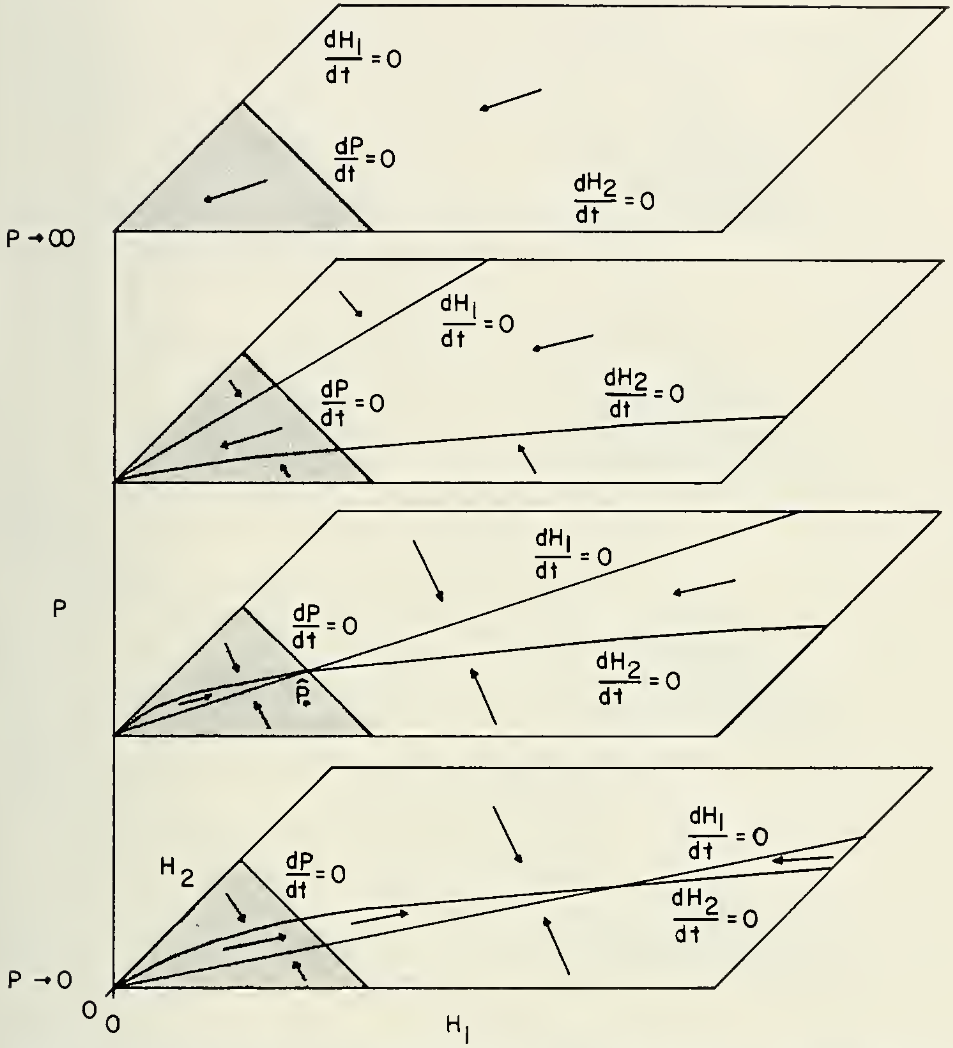

Fig. 3. Density-dependent model where dH_2/dt is dependent on H_2^2. $\hat{P}_*$ = equilibrium point; arrows show movement of H_1 and H_2 in the planes; P decreases in the shaded region and increases in the unshaded area.

number of sexually mature prey). Both equations represent parabolas (Fig. 4). A real positive equilibrium point

$$\text{exists if:}\quad \left[c_3\frac{(ec_1 + fc_4)}{(ec_2 + fc_3)} - c_4\right]\left[\frac{(ec_1 + fc_4)}{(ec_2 + fc_3)} + k_4\right] > \frac{c_5 e}{k_3}.$$

It can be seen that when $k_2 = k_4 = 0$, conditions for the existence of a real positive equilibrium point are more stringent; however, local stability about that point occurs if it exists. When $k_2, k_4 > 0$, the stability criteria are similar to those of the density-independent case except that an extra variable which is always positive is added to the left hand side of the equation, and the criterion: $x + k_1\hat{H}_1\hat{P} + c_2\hat{H}_1 > f\hat{H}_2^2$ must be met (x is a variable which is always positive, and composed of terms of the original equations). Thus, in cases where decrease in individuals

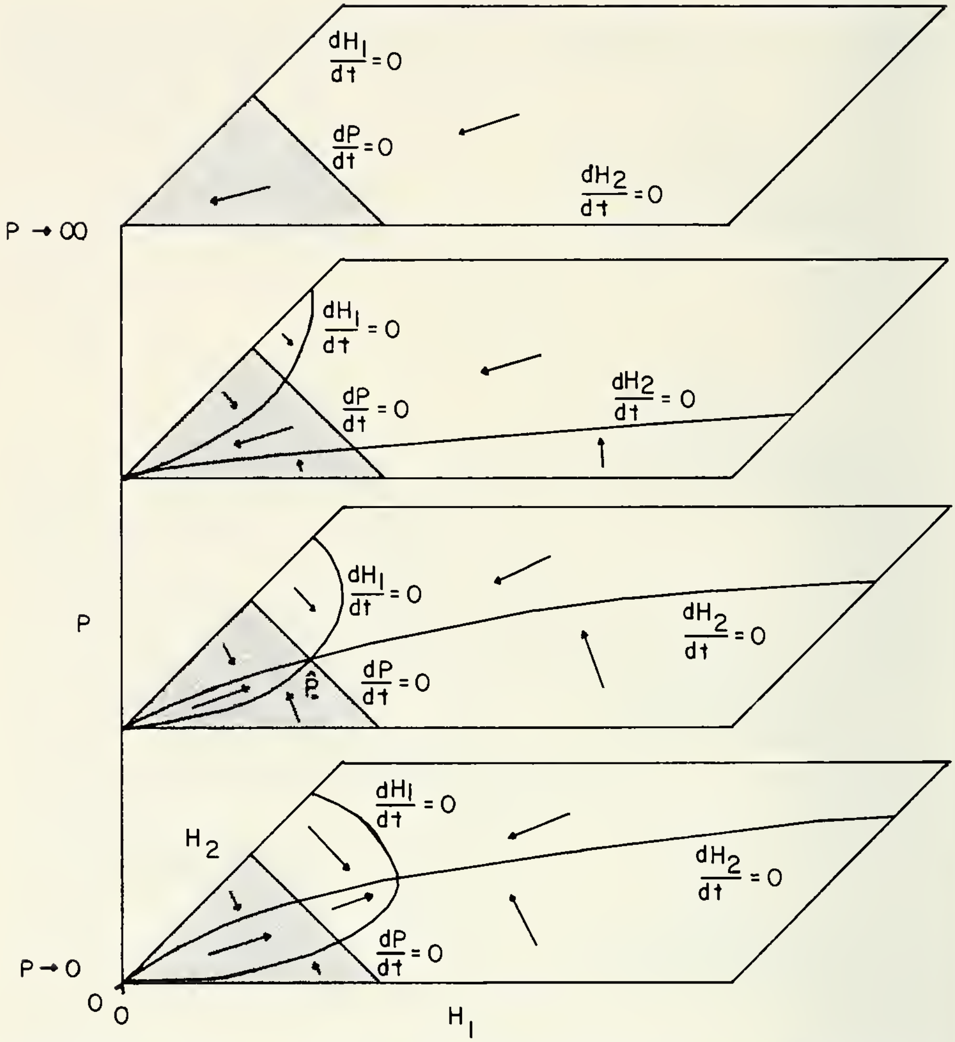

Fig. 4. Density-dependent model where both dH_1/dt and dH_2/dt are dependent on H_2^2. $\hat{P}*$ = equilibrium point; arrows show movement of H_1 and H_2 in the planes; P decreases in the shaded region and increases in the unshaded area.

due to the density-dependent term is less than the decrease in individuals due to other causes in the equation dH_1/dt, stability is easier to obtain than in the density-independent case. Large values of f relative to the other constants in the equation dH_1/dt will however unstabilize the predator prey model. Similar results occur when both age classes are dependent on H_1.

Density dependence where H_1 is density dependent on the density of H_1, and H_2 on the density of H_2 results in the two parabolic equations:

$$\frac{dH_1}{dt} = c_1H_2 - k_1H_1P - c_2H_1 - fH_1^2 \tag{6}$$

$$\frac{dH_2}{dt} = c_3H_1 - k_2H_2P - c_4H_2 - eH_2^2.$$

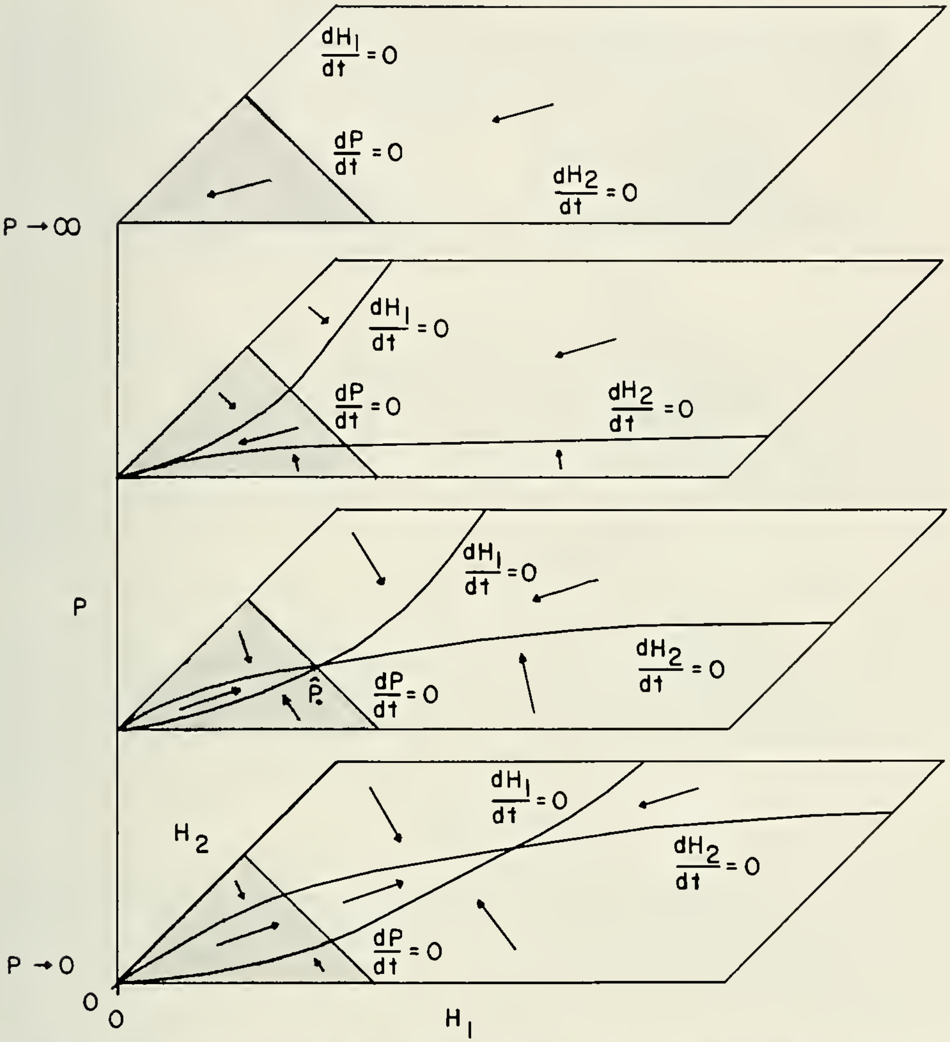

Fig. 5. Density-dependent model where dH_1/dt is dependent on H_1^2, and dH_2/dt is dependent on H_2^2. $\hat{P}_*$ = equilibrium point; arrows show movement of H_1 and H_2 in the planes; P decrease in the shaded region and increases in the unshaded area.

The parabolic isocline of H_1 opens parallel to the H_2 axis, while the isocline of H_2 opens parallel to the H_1 axis. The parabolas always cross at $H_1 = H_2 = 0$ (Fig. 5). A real positive equilibrium point occurs when $k_2 = k_4 = 0$ if:

$$\frac{-c_4 + (c_4^2 + (4ec_3c_5/k_3))^{1/2}}{2e} > \frac{(c_2k_3 + fc_3)}{c_1k_3} \tag{7}$$

or when k_2, $k_4 > 0$ if:

$$\frac{-(c_4k_3 + c_3k_4) + ((c_4k_3 + c_3k_4)^2 + 4ec_3c_5k_3)^{1/2}}{2ek_3}$$

$$\geqslant \frac{(2fk_4c_5 + c_1 + c_2k_4k_3) - ((2fk_4c_5 + c_1 + c_2k_4k_3)^2 - 4fk_4^2(k_3c_2c_5 - fc_5))}{2fk_4^2}.$$

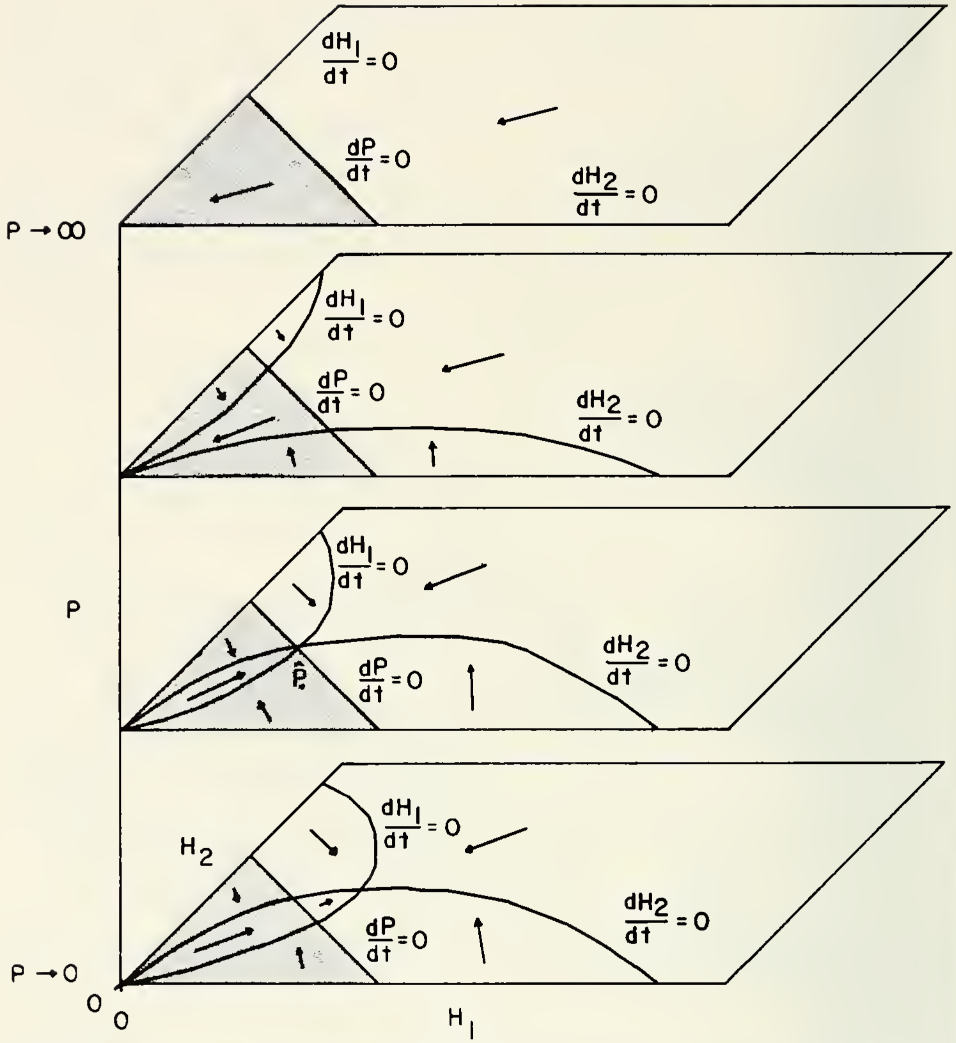

Fig. 6. Density-dependent model where both dH_1/dt and dH_2/dt are dependent on H_1^2 and H_2^2. $\hat{P}* =$ equilibrium point; arrows show movement of H_1 and H_2 in the planes; P decreases in the shaded region and increases in the unshaded area.

Through graph analysis it can easily be shown that in the non-refuge situation it is easier to obtain a real positive equilibrium point. The stability criterion when $k_2 = k_4 = 0$ is the same as for the density-independent case. When $k_2, k_4 > 0$ stability occurs when: $x + (k_1 - k_2)[k_3(k_1\hat{P} + c_2 + f\hat{H}_1) - k_4c_3] > 0$ where x is a variable which is always positive composed of terms from the original equations. Depending upon the value of $k_1 - k_2$ density dependence in this case may either add to or subtract from stability in the non-refuge situation.

Finally, density dependence of the following form will be considered:

$$\frac{dH_1}{dt} = c_1H_2 - k_1PH_1 - c_2H_1 - eH_2^2 - fH_1^2 \tag{8}$$
$$\frac{dH_2}{dt} = c_3\mathrm{H}_1 - k_2PH_2 - c_4H_2 - gH_2^2 - iH_1^2$$

(i.e. both prey age classes are density dependent upon both age classes of prey). These ellipse equations always cross at $H_1 = H_2 = 0$ when $dH_1/dt = dH_2/dt = 0$. Furthermore, when $dH_1/dt = 0$ the isocline of dH_1/dt crosses the H_2 axis at $H_2 = c_1/e$, and when $dH_2/dt = 0$ the isocline of dH_2/dt always crosses the H_1 axis at $H_1 = c_3/i$ (Fig. 6). If $k_2 = k_4 = 0$ then a real positive equilibrium point exists if:

$$\frac{c_1 + \left(c_1^2 + \frac{4e}{k_3^2}(c_2c_5k_3 + fc_5^2)\right)^{1/2}}{2e} \leqslant \frac{c_4 - \left(c_4^2 - \frac{4g}{k_3^2}(ic_5^2 - c_3c_5k_3)\right)^{1/2}}{2g}. \tag{9}$$

If k_2, $k_4 > 0$ then an equilibrium point for $P > 0$ exists if the smallest value of H_2 when $H_1 = (-k_4H_2 + c_5)/k_3$ is substituted into the equation $0 = c_1H_2 - c_2H_1 - eH_2^2 - fH_1^2$ is real and less than the greatest value of H_2 when the substitution is made for the equation $0 = c_3H_1 - c_4H_2 - gH_2^2 - iH_1^2$ and H_2 is again real. When $k_2 = k_4 = 0$ the equilibrium point is always stable locally if the equilibrium point is real and positive. If k_2, $k_4 > 0$ local stability for a real positive equilibrium point occurs when:

$$x + (k_1 - k_2)(k_3(k_1\hat{P} + c_2 + f\hat{H}_1) + k_4i\hat{H}_1 - k_4c_3) > 0, \quad \text{and} \tag{10}$$

$$y + k_3k_2(k_1\hat{P}\hat{H}_1 + c_2\hat{H}_1 + f\hat{H}_1^2 - e\hat{H}_2^2) + k_4k_1(k_2\hat{P}\hat{H}_2 + c_3\hat{H}_2 + g\hat{H}_2^2 - i\hat{H}_1^2) > 0$$

where x and y are variables which are composed of terms from the original equations and which are always positive. These criteria have much the same effect as the criteria in the last two density-dependent models examined, although more complex and thus even more difficult to completely interpret.

Discussion

Therefore, the overall effect on predator-prey numbers when an age class refuge from predation for prey is added to density-dependent situations is the same as for the density-independent model. This can easily be seen to be true since a prey refuge (e.g. $k_2 = k_4 = 0$) still makes one of the prey isocline curves (e.g. $dH_2/dt = 0$) independent of P, and leaves the other isocline unchanged. Thus, the H_1 and H_2 isoclines cross at the P isocline at a greater value of P. Similarly, by graphical analysis, H_2 and H_1 can be seen to be greater.

Summary

1) An age class refuge from predation in the prey population increases the number of predators and prey (both H_1 and H_2 age classes) at equilibrium in the model considered.
2) Predators which prey upon both age classes of prey are individually more fit than those predators which prey only upon one age class of prey. A group of predators which preys on only one age class of prey are more fit, however, than a group of predators which preys on both age classes of prey. Thus, a mechanism for the initial occurrence of a group whose individuals are less fit, but as a group are more fit, than the individuals of another group (group selection) is suggested.
3) Density-dependent population ceilings for the prey do not change the results if an equilibrium point (real positive) exists and it is locally stable.

4) Density-dependent population ceilings for the prey tend to make it more difficult to have an equilibrium point which is real and positive. However, if such a point exists, stability criteria may be made easier to meet in some models (stability = characterized by damped oscillations in the region surrounding the equilibrium point).

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I wish to thank Dr. Allan Oaten, and Dr. William W. Murdoch for reading and making suggestions for improvement of this paper.

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Extraction of a Phytoecdysone, Ponasterone A, from *Podocarpus gracilior* Pilger, and Its Effect on *Paramyelois transitella* (Walker) (Lepidoptera: Pyralidae)

Victoria Y. Yokoyama

Abstract.—A compound with insect-molting hormone activity extracted from *Podocarpus gracilior* Pilger was identified as ponasterone A by thin layer chromatography. Topical applications had no effect on the eggs or larvae of the navel orangeworm, *Paramyelois transitella* (Walker). Premolt sclerotization was induced in sixth instar larvae by intrahemocoele injection and 0.5 μg produced the greatest response. A larval-pupal intermediate was the most common type of premature development induced by the compound. Isolated abdomens from larvae with thoracic ligatures were highly sensitive to the phytoecdysone and were used to detect molting hormone activity. Ponasterone A applied to the larval stage by injected and oral dosages reduced the fecundity of the female survivors. The phytoecdysone had no effect when incorporated in the larval diet.

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Ponasterone A was discovered in *Podocarpus nakaii* Hay when the plant was screened for potential cancer chemotherapeutic activity (Nakanishi, 1969). The chemical structure of ponasterone A (Fig. 1) was elucidated and found to be similar to the insect molting hormone, α-ecdysone; it was observed that ponasterone A could also produce molting hormone-like effects in insects (Nakanishi, et al., 1966). Ponasterone A was isolated from a number of plant sources and further studies revealed the existence of many other active molting hormone-like compounds collectively known as phytoecdysones (Horn, 1971; Imai et al., 1969; Siddall, 1970; Williams, 1970).

In the plant kingdom phytoecdysones occur in a number of Pteridophyta, Gymnospermae, and Angiospermae species. The presence of these compounds does not indicate phylogenetic relationships because closely related species may produce either different types of compounds or none at all. Although it has not been demonstrated, phytoecdysones may possibly function in insect-plant interactions by providing plants that produce the compounds with resistance to insect attack. At present phytoecdysones are considered to be secondary plant chemicals (Klun, 1974).

Soon after the discovery of the phytoecdysones it was proposed that hormones could be used to control insect pests (Ellis, 1968). This suggested a new selective type of control agent that could be used to regulate insect growth and development without causing deleterious effects in higher animals and the environment.

The Podocarpaceae has been the largest group of plants from which ponasterone A has been extracted. Most of these plants are Asiatic in origin. In this study *Podocarpus gracilior* Pilger, endemic to Africa, was examined for ponasterone A as a potential new geographic source of the phytoecdysone. In addition, Acala SJ-2 cotton, *Gossypium hirsutum* L. (Malvaceae), a plant of agricultural

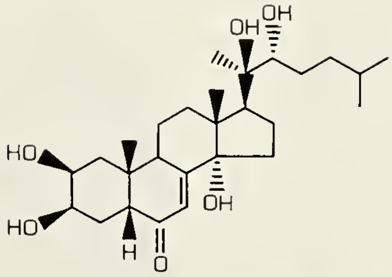

Fig. 1. Structure for ponasterone A.

importance, was also examined for the phytoecdysone in the search for compounds that may protect cotton from insect attack. Finally, the molting hormone-like effects of ponasterone A was tested on the navel orangeworm, *Paramyelois transitella* (Walker), a pest of the California walnut and almond industry. The compound was investigated as a possible control agent for this economically important insect.

Methods

Leaf extraction.—Leaves from *P. gracilior* were obtained from the Botanical Garden, University of California, Berkeley, and from the Los Angeles State and County Arboretum, Arcadia, California. Acala SJ-2 cotton leaf samples were taken from the United States Cotton Research Station, Shafter, California.

Approximately 500 g of fresh *P. gracilior* leaves from the Berkeley Botanical Garden or 6 mg of dried cotton leaves were macerated and extracted with methanol and acetone. Cellular debris was removed by filtration and the filtrate evaporated. The concentrate was diluted with water and extracted with chloroform. An aliquot of the chloroform extract was applied as a band on a silica gel F-254 (EM Laboratories, Elmsford, New York) thin-layer chromatography (TLC) plate of 0.25 mm gel thickness adjacent to a ponasterone A reference standard. The plate was developed in solvent system A (Table 1). Ponasterone A was detected by fluorescence upon exposure to ultraviolet light or by a red chromogenic response produced when sprayed with 20% sulfuric acid and heated at 100°C for 5 min. The band from the plant extract having the same Rf value as the standard compound was scraped from the plate and eluted with chloroform. A concentration series of the supernate was spotted against known quantities of ponasterone A and developed in solvent system A. Spot size comparisons were used to derive an approximate estimate of the ponasterone A concentration in the extract.

Bioassay.—A navel orangeworm colony was reared by a method similar to one described by Finney and Brinkman (1967). Ponasterone A (Calbiochem, San Diego, California) in methanol was applied to the insects by topical and injected dosages with a 10 μl Hamilton syringe and repeating dispenser. Control groups were treated with solvent alone.

Three to four replicates of approximately 200 navel orangeworm eggs each were treated topically with 0.05, 0.1, 0.5, 1.0, 1.5, and 2.0 μg ponasterone A 6 hr after oviposition. The treated eggs were placed on dampened filter paper in sealed petri dishes and held at 27°C. The percent hatch was determined after four days.

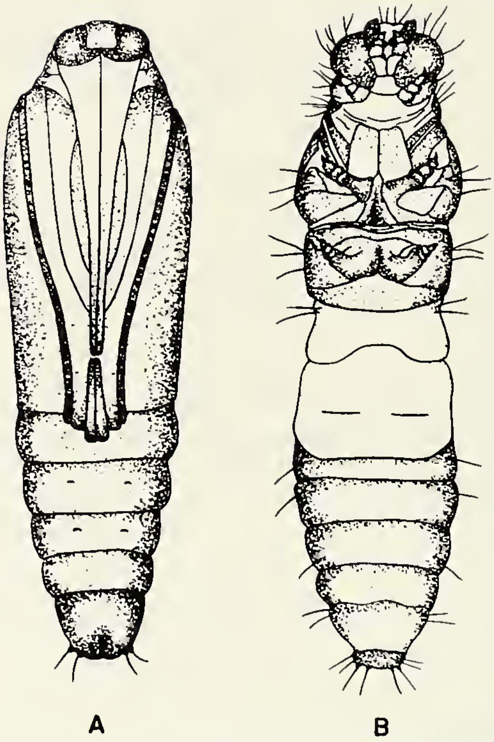

Fig. 2. *Paramyelois transitella*: A. Normal pupa; B. Larval-pupal intermediate induced by ponasterone A.

Larvae in the sixth instar prior to pupation were treated topically on the dorsum of the abdomen or injected laterally between the intersegmental membrane of the third and fourth abdominal segments. Isolated abdomens were prepared from larvae ligated behind the second thoracic legs. The abdominal fragments were treated after the portion anterior to the ligature had shown metamorphic development. The effects of 0.25, 0.5, 1.0, 2.0, and 3.0 μg of ponasterone A on growth and development in three replicates of 10–20 larvae were evaluated within a seven day period.

Larvae that survived ponasterone A treatments and pupated normally were placed in 500 ml glass jars. Two strips of masking tape, 10 cm long and 2.5 cm wide, were placed on opposite sides of the jars. Moths that emerged from these pupae mated and oviposited on the tape until they died. The fecundity of the adults was evaluated by a comparison of the mean number of eggs laid by each female per 25 cm^2 of tape.

Table 1. Solvent systems (Imai et al., 1967) and Rf values for ponasterone A.

A	B	C	D	E
6 $CHCl_3$ 2 C_2H_5OH 1 $CH_3C(O)CH_3$	6 $CHCl_3$ 2 CH_3OH 1 $CH_3C(O)CH_3$	5 $CHCl_3$ 1 CH_3OH	25 CH_2Cl_2 5 CH_3OH 3 C_6H_6	16 CH_2Cl_2 1 C_2H_5OH 4 $CH_3C(O)CH_3$
Rf 0.61	0.70	0.86	0.94	0.27

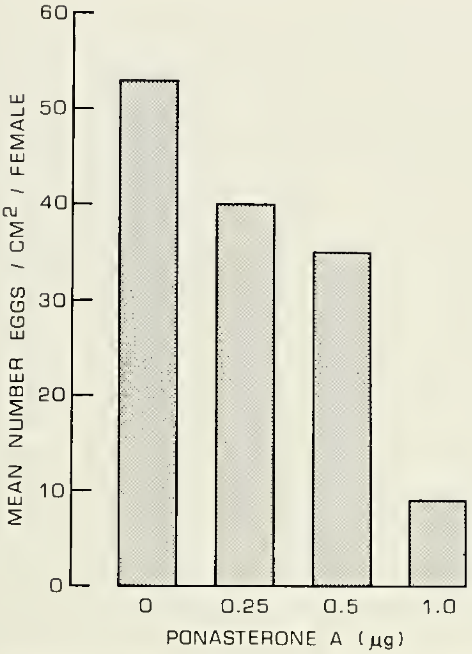

Fig. 3. Fecundity of adults treated with ponasterone A in the larval stage.

Ponasterone A was incorporated into 1 g of the larval food media. The treated diet was replicated in concentrations of 50, 100, and 200 ppm. Each replicate was placed in a 20 ml plastic cup with ten newly hatched larvae. After the larvae pupated, the cup was placed in a 500 ml jar. The total number of eggs laid per emerged female was determined after the death of the adults.

The sixth instar larvae were force-fed ponasterone A by injecting various dosages past the mouthparts into the lumen of the foregut with a 30 gauge blunt-tipped needle.

Results

Ponasterone A-like compound from P. gracilior.—A compound extracted from *P. gracilior* was shown to have the same Rf values as ponasterone A reference standard in solvent systems A to E (Table 1). Both the extracted compound and ponasterone A co-chromatographed two-dimensionally in solvent systems B and E and in C and D without separation. A small amount of the extract was assayed by injection of navel orangeworm larvae. Molting hormone activity was evident based on the response of a few insects. No quantitative assays were made. The estimated yield of ponasterone A or equivalent ultraviolet absorbing material of the same Rf values was 125 ppm. Ponasterone A was not detected by TLC in Acala SJ-2 cotton leaf extracts.

Effect on P. transitella.—Topical applications of ponasterone A on navel orangeworm eggs had no apparent effect on egg hatch. The mean hatch in untreated control groups was 69% and 68% in solvent treated controls. Although the hatch was lowest in the 1.0 μg egg treatments (53% SD ± 5), there was no difference between the control groups and the survivors of 1.0 μg treatments in relation to the numbers that reached maturity (51%) or in the sex ratios of the moths (47%).

Topical applications of ponasterone A had no effect on the larvae of the navel orangeworm. However, injection of the phytoecdysone initiated various degrees of premolt sclerotization. These abnormalities were characterized by four types of structural variations: Type 1) larvae with cuticular darkening and hardening around the site of injection; Type 2) larvae with minor tanning of the dorsal sclerites; Type 3) larvae with extensive tanning of both the dorsal and ventral sclerites; and Type 4) shortened larval-pupal intermediates with pupal cuticle beneath the larval skin in some areas, but with many immature traits. These intermediates represented the most extreme effect of ponasterone A on normal chronological growth (Fig. 2).

Intrahemocoele injections of 0.5 μg ponasterone A produced the greatest morphological response in sixth instar larvae. Premature development was induced in 64% of the treated insects. Two percent of these larvae showed Type 2 precocious development, 26% represented Type 3, and 36% were larval-pupal intermediates. There was no response to 0.25 μg applications of ponasterone A, and 1.0, 2.0, and 3.0 μg caused premature development in only 41, 28, and 27% of the treated insects, respectively. Type 4, larval-pupal intermediates, was the prevalent type of development elicited by ponasterone A injections at all dosages.

Cuticular darkening and hardening was induced in 61, 72, and 78% of the 74-day old isolated abdomens of ligated larvae by 1.0, 2.0, and 3.0 μg ponasterone A.

Adult moths that survived injections of ponasterone A in the larval stage showed a decrease in egg production (Fig. 3).

Ponasterone A added to the larval diet did not affect the development of the immature stages or the fertility of the adults. Egg laying was suppressed in adults that were given oral dosages of the phytoecdysone in the sixth larval instar. Females surviving 1.0 μg treatments laid a mean of 19 eggs/25 cm^2 while females in the control group laid 71/25 cm^2.

Discussion

The ineffectiveness of topical applications of ponasterone A has been observed in insects other than the navel orangeworm. The outer wax layer of the insect cuticle constitutes a barrier against the penetration of polar toxicants such as ponasterone A. Therefore, it is unlikely that the phytoecdysone could readily penetrate either the cuticle or the chorion of the insect egg.

A linear dose-response relationship for intrahemocoele injections of ponasterone A was not observed. In fact, higher concentrations were less effective in initiating premature development. This observation may result from problems associated with solubility, or suggests a physiological response.

The sixth instar larvae treated with ponasterone A were not in the same phase of developmental responsiveness. Ponasterone A augmented the existing hormone titer in each insect. Differences in morphological response to the phytoecdysone reflected the random molting hormone titer of individuals in the sample population. Thus larval-pupal intermediates were induced in insects during a phase of high-molting hormone production while lesser morphological changes were induced in insects treated at a time of low hormone production.

The standard technique for detecting molting hormone activity with ligated insects was used successfully with ponasterone A. In this method the abdomen of the larva is separated from the natural source of molting hormone, the prothoracic glands. Only hormone-active materials could initiate further development in the isolated abdomen. Ponasterone A induced a larval-pupal type of metamorphosis but did not induce pupation, the next stage of normal development. This observation implies that the phytoecdysone cannot be substituted for the natural hormone, α-ecdysone, at the dosage levels studied.

Female moths that survived injections of ponasterone A in the larval stage laid fewer eggs. There was also a decrease in egg production of adults that were force fed the phytoecdysone in the sixth instar. The observed reduction in fecundity suggests that ponasterone A may have a chemosterilant effect. Ponasterone A incorporated in the diet had no effect on growth and development. However, it is possible that the compound may have been degraded in the medium.

Ponasterone A is not a prospective insect control agent for the navel orangeworm because the larvae are insensitive to topical applications of the compound. The presence of low levels of ponasterone A in certain plants such as ornamental *Podocarpus* may be more important in regulating insect populations. Insects feeding on the foliage may not show immediate toxic effects from the phytoecdysone, but experience deleterious long range effects on growth, development, and reproduction similar to that observed in the navel orangeworm. This would provide these plant with a type of insect resistance that would ultimately reduce pest populations. It may be a possible reason why the Podocarpaceae have few insect pests. There is potential for such resistance factors to be bred into agricultural plants like cotton. The development of insect resistant varieties would help alleviate the amount of insecticides used in pest control.

Acknowledgments

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A Telemetric Study of the Behavior of Free-Swimming Pacific Angel Sharks, *Squatina californica*

Edward A. Standora and Donald R. Nelson

Abstract.—Nine Pacific angel sharks were tagged near Santa Catalina Island, California, with single-channel or multichannel ultrasonic transmitters incorporating various combinations of sensors to measure swimming speed, depth, light, and temperature. The sharks were tracked for periods of 13 to 25 h and were found to be basically nocturnal, apparently cuing on decreased light intensity averaging 7 lux (range, 1–16) to begin swimming activity which peaked at dusk and midnight. Mean of maximum rate of movement for each shark was 490 m/h. The tagged sharks moved an average of 4 km (range, 2–9) during the trackings and collectively occupied a home area of approximately 150 ha. The sharks swam at depths ranging from 27 to 100 m and readily crossed thermoclines. The number and size of individuals seen at the tagging site changed with season.

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A pilot behavioral study utilizing a multichannel, ultrasonic telemetry system was conducted between 26 November 1971 and 2 July 1972 on Pacific angel sharks, *Squatina californica*. This inshore species, common in southern California, occurs in cooler waters from the Gulf of California to southern Alaska (Kato et al., 1967; Miller and Lea, 1972). It is a sluggish shark, typically found partially buried in sandy or muddy bottoms, usually adjacent to rocky areas. According to Limbaugh (1963) and Feder et al. (1974), stomach contents have included fishes such as corbina, *Menticirrhus undulatus*, queenfish, *Seriphus politus*, and California halibut, *Paralichthys californicus*. These authors also report some general underwater observations, but detailed studies of the life history, ecology, and behavior of this shark are lacking. That very little was known about the behavior of *S. californica*, and that it was readily accessible, made it a perfect candidate for both testing the telemetry system and obtaining biological data. This paper contributes some basic behavioral information on this understudied species.

Materials and Methods

Prior to this work, only two other research groups had applied sonic telemetry to the tracking of sharks (Bass and Rascovich, 1965; Thorson, 1971). Almost all of the earlier fish-tracking studies utilized transmitters containing no sensors, which acted only as acoustic beacons. More recently, researchers have employed sensors in their transmitting packages in order to telemeter parameters such as temperature or pressure (Carey et al., 1971; Luke et al., 1973; Rochelle and Coutant, 1974). The transmitters used in the present study, and in that of Sciarrotta and Nelson (1977), were multiplexed, multichannel units and were the first of this type to be used to monitor fish behavior (Standora et al., 1972; Nelson, 1974).

The transmitters measured about 15 cm in length, 3.5 cm in diameter, emitted 10

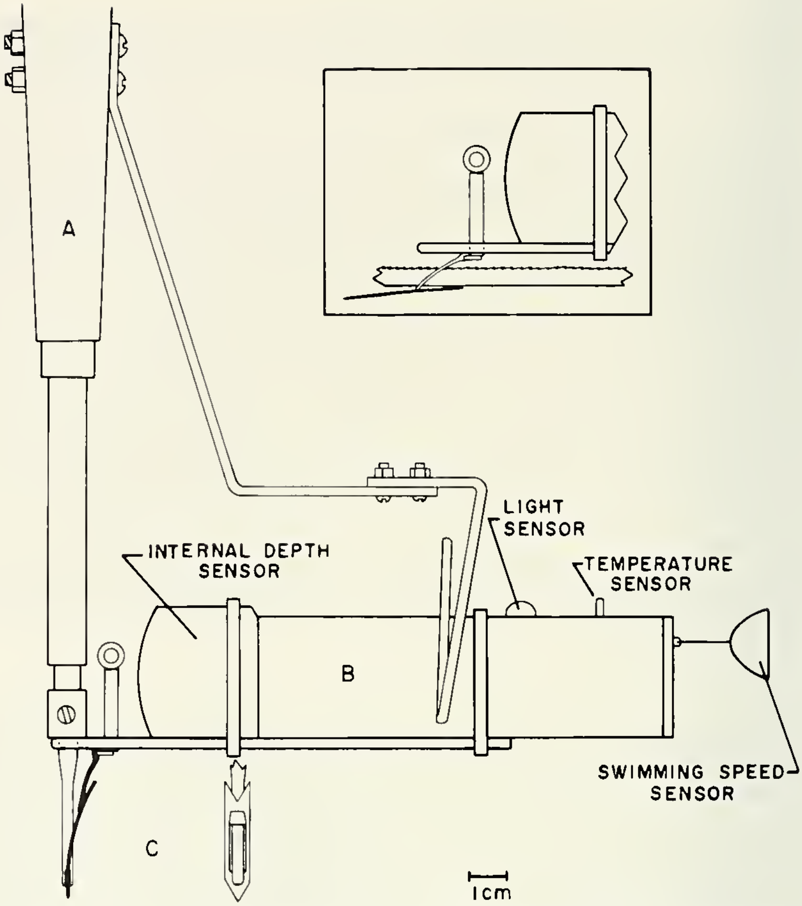

Fig. 1. Apparatus for attaching transmitters to sharks. A, applicator pole; B, transmitter, held in place by support; C, side and front view of attachment dart; Inset shows position of dart and magnesium break-away link after implantation under skin.

msec sonic pulses (tone bursts) at 40 kHz, had a life of up to one week, and a maximum range of 5 km. These units could be used to transmit up to eight channels of information, with multiplexed data encoded as pulse rate (pulse interval) which varied with the value of resistive sensors. The present study employed sensors for measuring swimming speed, depth, ambient light, and water temperature. Further details on transmitter circuitry and sensors are given by Ferrel et al., 1974.

The units were attached to the sharks by a stainless-steel dart (modified Floy FH69 dart tag) thrust beneath the skin via a diver-held applicator pole (Fig. 1). The tagging procedure involved two scuba divers descending with transmitter, applicator pole, and measuring tape. Once a resting shark was located (nearly all were at rest during the day), it was cautiously approached, measured, sexed (presence of claspers noted), and then tagged lateral to the mid-dorsal line with the transmitter. Tagging was usually done in the early afternoon so that both dusk and dawn transitions would be included in the tracking.

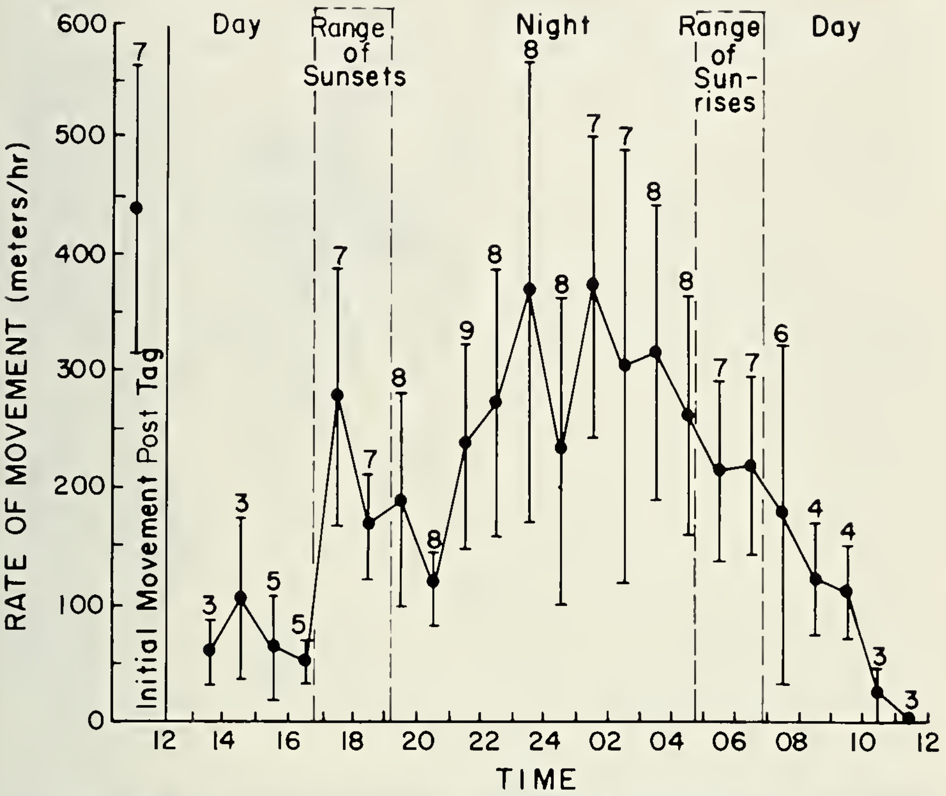

Fig. 2. Mean rate of movement for telemetered sharks. Initial movement post tag indicates movement during first hour after tagging and includes artifactual burst of swimming caused by tag application. All tagging occurred between 1130 and 1500 h. Vertical bars represent two standard errors of the mean.

The sharks were tracked from a 7-m powerboat. Sensor-data recordings were made every half-hour, and locations plotted every hour when possible. The signals were detected using a tuneable, ultrasonic receiver (DuKane N15A235) equipped with a directional hydrophone. Incoming data pulses were recorded on magnetic tape, then later converted to paper oscillograms. Sensor data were manually decoded by measurement of distances between pulses on the oscillograph records.

Transmitters were recovered either directly by receiver-equipped scuba divers or by providing the transmitter package with a syntactic-foam float and magnesium break-away link which corroded through after a predetermined time in sea water, allowing the unit to float to the surface.

The study area was the waters surrounding Ship Rock, a 23-m high pinnacle of rock located about 2.3 km north of the isthmus of Santa Catalina Island, California. The submerged rocky, kelp-covered portion of Ship Rock drops off steeply to a depth of about 30 m where a more gradually sloping sandy bottom begins. The angel sharks which were tagged were found in this sandy area, just beyond the rocks, at depths between 29 and 37 m.

Five male and four female sharks were successfully tagged and tracked for periods of from 13 to 25 h. Four individuals carried single-channel transmitters

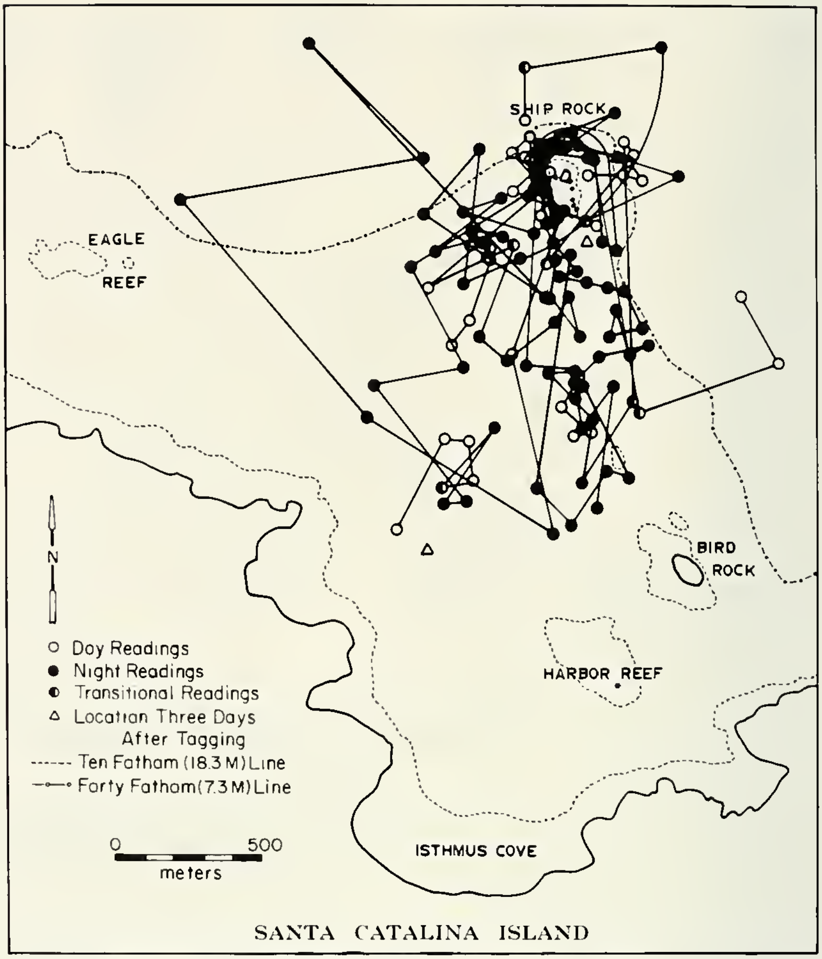

Fig. 3. Hourly positions of all sharks tracked. The sharks remained almost exclusively in an area of about 150 ha.

(three with depth sensors, one with speed sensor) and the remaining five carried multichannel transmitters, each with swimming-speed, depth, light, and temperature sensors.

Results and Discussion

Activity.—Rate of movement was the primary index used to determine the diel activity pattern of the tagged sharks. This value was obtained by measuring the distance between two successive location points and dividing by the elapsed time. The mean rate of movement of all tagged sharks (Fig. 2) showed a distinctly nocturnal pattern, with an abrupt increase in activity at dusk, maximum activity during the middle of the night, and much less movement during the day. Five of the sharks had their maximum mean rate of movement in the dusk transition (1 h prior to 1 h after sunset), two during the night (sunset to sunrise), and two during the dawn transition (1 h prior to 1 h after sunrise). One of the latter two sharks, however, was exposed to an unusual feeding opportunity (see later section on

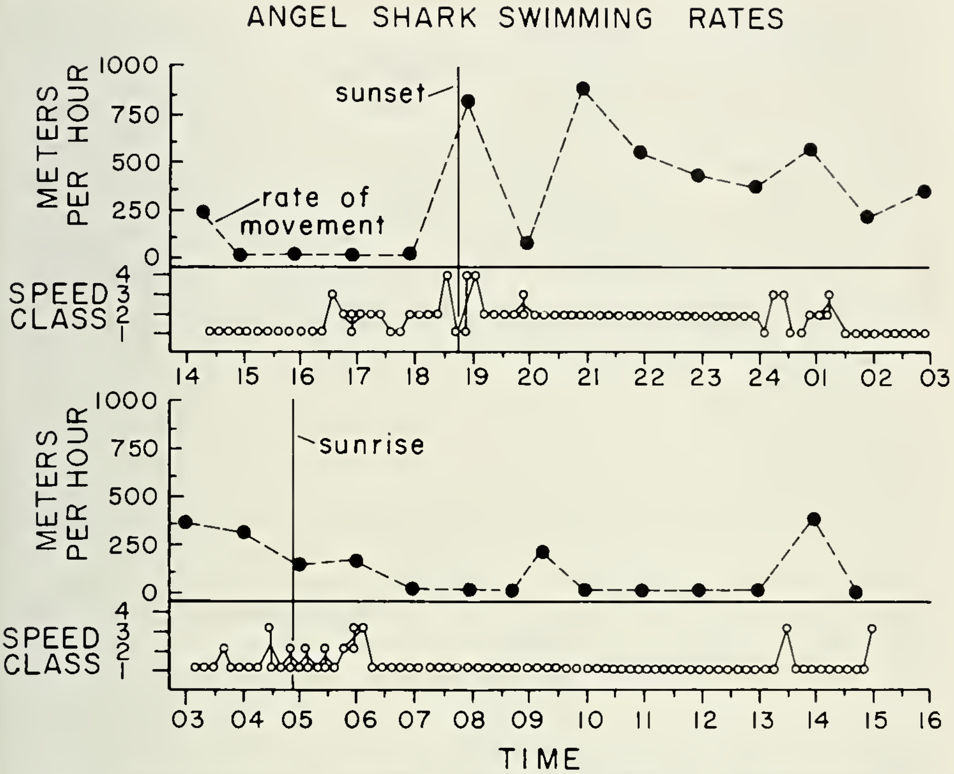

Fig. 4. Swimming speed data obtained at 10-min intervals from one *S. californica* tagged with a single-channel transmitter. Speed class 1, 0–15 cm/sec; 2, 15–50 cm/sec; 3, 50–75 cm/sec; 4, >75 cm/sec. When two points are plotted they represent maximum and minimum speeds during the one minute sampling period.

"Atypical Behavior"). None of the sharks showed maximum mean rate of movement during the day (sunrise to sunset).

There was no indication that a properly-placed transmitter affected the movement of the sharks, except for a brief burst of swimming immediately after tag application. One shark, however, was tagged improperly, too far posteriorly, resulting in the unit actually trailing beyond the body. This probably impaired the shark's swimming ability, as this individual moved the least of any of the tagged sharks (less than 600 m during the 20-h tracking session).

Home range.—One significant finding of this study was that the angel sharks at Ship Rock appeared to confine their movements to a distinct, limited area (Fig. 3). Although the durations of the individual trackings were not sufficient for accurate determinations of individual home ranges, the data collectively indicated a common area preference. The telemetered sharks, excluding the improperly tagged one, moved an average of 4 km (range, 2–9 km) during the tracking sessions, but nearly all movements were in an area of approximately 150 ha (1.0 by 1.5 km). This area includes a narrow circular region around Ship Rock itself, and the waters generally south of it for a maximum distance of 1.3 km. Within this area water depths are about 33 to 73 m. Although water of greater depth is readily accessible on the north, east, and west sides of Ship Rock, the sharks only in-

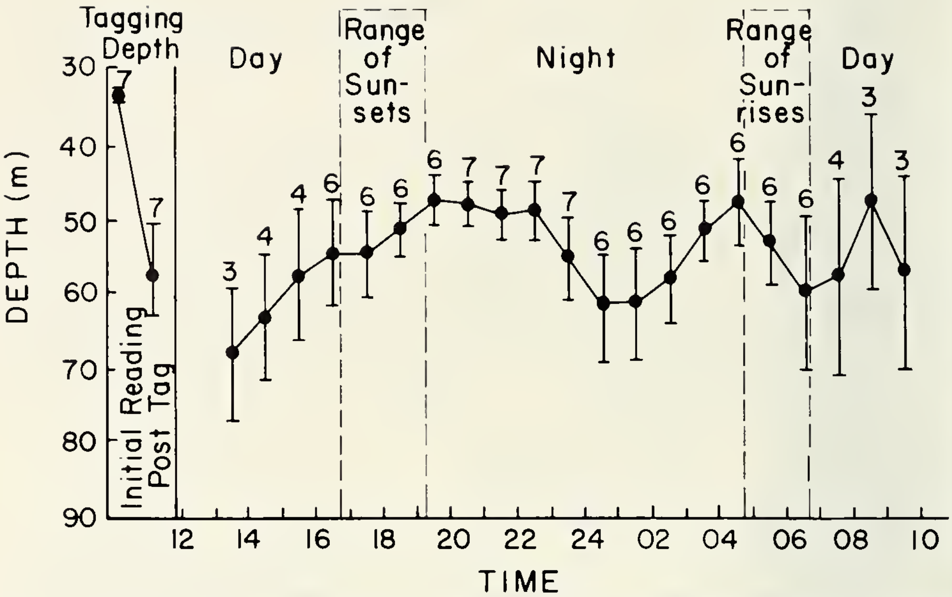

Fig. 5. Mean depths for all sharks tracked. Tagging occurred between 1130 and 1500 h. Vertical bars represent two standard errors of the mean.

frequently moved into these regions. They never moved into the shallower water closer inshore towards the island shoreline.

Further evidence of a limited home range for the Ship Rock angel sharks is provided by two trackings in which the transmitter was not recovered at the end of the initial tracking period. When these sharks were acoustically relocated 3 days later, they were still within the home area described above.

Two of the monitored sharks returned to the near vicinity of Ship Rock for the next daytime inactive period. These sharks had moved about 9 and 4 km during the night, but were located the next morning less than 400 and 200 m respectively from the locations where they were tagged. Although these two trackings could be considered evidence that the sharks had returned to a relatively specific resting site (the sandy base of Ship Rock), they must be considered in view of the other seven tagged sharks which did not return. The question of specific resting sites for the angel shark, although unresolved by the present study, should remain open, as such behavior has been shown in another shark species, the reef whitetip, *Triaenodon obesus*, which does return to specific home caves over many successive days (Nelson and Johnson, In Press).

Telemetered data from sensors.—In contrast to the above findings on rate of movement and home range (as determined from shark-location data), the following information on swimming speed, depth, light, and temperature came from measurements made on the shark by sensors in the transmitter package. Although in this initial study only a small percentage of the available telemetered data could be utilized, the results did establish the feasibility of using multichannel telemetry as a tool for studying shark behavior at sea. In the present study, due to the prohibitive slowness of manual data decoding, it would have been superfluous to make continuous recordings of multichannel data; therefore, only brief recordings were made at half-hour intervals throughout the trackings. This limitation reduced the usefulness of the data as the shark's behavior during these brief readings was not always representative of its overall behavior.

The most complete data on instantaneous swimming speed were obtained from a shark tagged with a single-channel transmitter (Fig. 4). Because it was a single-channel unit, stop-watch decoding could be performed in the field and more frequent data readings obtained (every 10 min). Swimming speed was at or near zero during the middle of the day, except for a few brief periods. During dusk and most of the night, speeds increased to approximately 15–50 cm/sec, with occasional bursts to 50–75 cm/sec or to over 75 cm/sec. Due to the frequency of readings, and because the shark was apparently not deviating much from straight-line movement, the swimming-speed data corresponded well to the rate-of-movement data.

The mean depth for all the tagged sharks showed an abrupt increase immediately after tag application (Fig. 5). This post-tagging response seems at least partly due to the bottom topography around Ship Rock, where the most available direction for escape is down slope. Data indicated that the sharks moved to shallower depths at dusk, but this was probably an artifact due to the abnormally deep positions occupied prior to dusk (i.e., if the sharks did not swim away after tag implantation, but remained at the tagging site until dusk, then they probably would have moved deeper at dusk). Data also indicated that the sharks moved to deeper levels at dawn. This result was unexpected, as each one of the tagged sharks had, on the previous day, moved shallower in order to reach the site at which they were tagged.

In most instances, the sharks swam relatively close to the bottom, but there were occasions when they were apparently quite far (15, 91 m) above the bottom. During the trackings, sharks were monitored at depths ranging from 27 to 100 m. There was no evidence of depth variation with season.

The extrapolation of surface light level to that found at depth is difficult because of the problems of water clarity and critical angles of acceptance. By having the light sensor on the shark it was possible to determine the illumination actually reaching the individual being monitored. It appeared that the angel sharks were using light intensity as a cue to beginning nighttime activity. Data indicated that such increases in activity occurred at ambient light levels between 1 and 16 lux. In comparison, horn sharks, *Heterodontus francisci*, a nocturnal species also studied at Ship Rock, were found to begin nightime activity at the much lower mean light level of .03 lux (Finstad and Nelson, 1975).

In general, telemetered water temperature decreased with increasing depth, but in some instances there were unexpectedly high or low readings for short periods of time possibly due to isolated pockets of water from the shallows of the island shoreline, or from the depths of the San Pedro Channel. Thermoclines were evident as the sharks changed depths, but no reluctance to cross them was noted. Throughout the study, sharks were tracked in waters ranging from 9.0° to 16.5°C.

Atypical behavior.—One angel shark, tracked on July 1–2, exhibited an activity pattern basically opposite to that observed in the other tagged individuals. This shark showed quiescent, nocturnal behavior with a sudden increase in activity at dawn. This tracking was unusual, however, in that it occurred during the annual, post-spawning mortality of blacksmith, *Chromis punctipinnis* (Turner and Ebert, 1962). Immediately prior to entering the water for this tagging, the divers noted numerous dead blacksmith on the surface. During the dive, blacksmiths were seen with necrotic white patches on portions of their lateral and dorsal surfaces. These fish were not swimming normally and could be easily approached. Others were observed flipping erratically and swimming on their sides just above the bottom, a seemingly ideal feeding opportunity for angel sharks or other large predators. Several blue sharks, *Prionace glauca*, a basically pelagic species not often seen at Ship Rock, were also observed during this dive.

At the tagging site, the divers observed two angel sharks which were lying on top of the sand in an apparently alert posture, not settled into the sand and well-camouflaged as was typical for this species. One of these individuals was tagged with the transmitter and the other was speared for examination of stomach contents. The speared shark contained four blacksmith (11–15 cm total length) which were nearly intact and apparently recently ingested. The above facts suggest that, despite the angel shark's normally nocturnal behavior, they are sufficiently plastic in their behavior to take advantage of unusual feeding opportunities, even if this necessitates diurnal activity.

Population observations.—In addition to the behavioral findings of this study, some definite fluctuations in population characteristics were noted. During the winter months, there was a sharp decrease in the number of sharks at the tagging site. The number of sharks available for tagging decreased from November to December, and on 22 January a search of the area at the base of Ship Rock produced only one shark. By March the number of individuals was increasing, and most, but not all, were smaller in size (60 to 90 cm TL) than the average fall size (90 to 120 cm TL). It was not determined if this winter decrease in numbers was due to a major migration or to a more limited movement away from the base of Ship Rock. During June and July, sharks were again very numerous; e.g., with good visibility (20 m) up to 20 sharks could be seen by a diver from a single location within the tagging area, and most appeared to be of adult size.

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Research Notes

Notes on the Behavior of Elasmobranch Fishes Exposed to Magnetic Fields

Agalides (1969) and Kalmijn (1974) demonstrated that at least four species of elasmobranchs, *Scyliorhinus canicula, Triakis semifasciata, Negaprion brevirostris*, and *Raja clavata*, are sensitive to minute electric fields in seawater. Kalmijn (1973, 1974) advanced an hypothesis to explain the mechanism by which an elasmobranch might use this extreme electrical sensitivity to detect and utilize the earth's magnetic field for purposes of orientation. Non-uniform magnetic fields, approximating the earth's magnetic field strength (.5 gauss), have been shown to elicit behavioral responses in *Triakis semifasciata* (Kalmijn, 1973; Zahuranec, 1975) and *Urolophus halleri* (Kalmijn, 1975). However, while Kalmijn's hypothesis and the above mentioned literature suggest that this electromagnetic sensory capability is common to all elasmobranchs, there is limited published evidence to substantiate this conclusion. Therefore, we decided to examine three species of elasmobranchs for evidence of sensitivity and behavioral response to magnetic fields of varying magnitude and direction.

Two shark species, *Cephaloscyllium ventriosum* (swell shark) and *Heterodontus francisci* (horn shark), and one species of ray, *Urolophus halleri* (round stingray), were collected in shallow water at Santa Catalina Island, California, and were maintained in .5 × 1 × 1-m plexiglass, flowing-seawater tanks at the Catalina Marine Science Center of the University of Southern California. In these preliminary experiments, two *Heterodontus*, one *Cephaloscyllium*, and one *Urolophus* were studied. They all averaged 25–30 cm in total length. Each animal was exposed to continuous and randomly-pulsed, uniform (non-uniform with respect to the earth's magnetic field) magnetic fields of two magnitudes, low and high. Both types of field were generated with electromagnets; the low strength magnet consisted of 700 turns of 30 gauge enameled copper wire on a 7.5-cm × 1.5-cm diameter hardened steel core (current flow at 12 Vdc = .25 A, flux density at 2 m from the magnet = 1.1 gauss); the high strength magnet consisted of 250 turns of 20 gauge enameled copper wire on a 7.5-cm × 1.5-cm diameter hardened steel core (current flow at 12 Vdc = 24 A, flux density at 2 m from magnet = 49 gauss). A randomly-pulsed field refered to the lack of a repetitive pattern in either the amplitude, duration or rate of the pulsed dc power supplied to the magnets. A moving field indicated that the magnet itself was moving with respect to the test animal. Tests, conducted both at night and during the day, were arranged so that the magnets and the investigators were hidden from the animal's view during test runs.

Each species responded in a unique manner to magnetic stimulation. In *Heterodontus*, a pulsed, high-strength field produced only a very slight full body twitch (with magnet 20–50 cm from animal). Habituation was very rapid (less than 2 s) and multiple responses of this type were hard to elicit. The continuous and pulsed low strength fields, as well as the continuous high strength field, caused no observable behavioral responses, regardless of the distance from magnet to animal. By monitoring the breathing rate of the animals through the use of implanted electrodes, we noted an increase in the number of breathing arhythmias (from an average of seven per minute to an average of 35 per minute) when the animal was exposed to a moving, continuous low strength field from a distance of approximately 75 cm. Repetition of these tests, with a load between the electrodes electrically equivalent to that of the animal's body, showed that these changes were not due to any direct influence of the magnetic field on the electronic equipment. We also noted a latency in onset of response as well as a post-stimulus persistence of response.

In *Cephaloscyllium,* exposure to a pulsed high strength field (magnet 10 cm from animal) elicited an intense eyelid contraction as well as a full body twitch. Habituation, however, was rapid and after approximately 15 s of exposure, all responsiveness ceased. After a rest period of 30 to 60 s, the animal was again responsive to the field. With the magnet placed more than 10 cm from the animal, no responses were elicited. We also noted a sustained eyelid contraction when the animal was exposed to a continuous high strength field, regardless of whether the magnet was moving or not. With no other sensory input (hitting the tank, dropping objects into the tank, moving objects into the animal's visual field, etc.) were we able to produce this sustained eyelid contraction. Regardless of the distance from magnet to animal, the animal showed no discernible response to the low strength field, whether continuous or pulsed. These results suggested that the response to the high strength field was not mediated by specific receptors but was caused by the field acting directly on nerves and muscles.

In *Urolophus,* we noted a wide range of behavioral responses to the magnetic fields that were subtle and difficult to interpret objectively. When exposed to a stationary, continuous low strength field at night, the animal became aroused and would often swim back and forth along a line at right angles to the long axis of the electromagnet, moving from a meter to within a few centimeters of the magnet and then away again. However, it was not necessarily attracted or repelled by the field. Twice we noted a full body twitch reaction to the pulsed high strength field (magnet about 50 cm from the animal) but this type of response was too sporadic to be considered a fixed action pattern and may have been due to direction stimulation of the nerves. Latency, both in onset and termination of response, was again apparent but there was no marked habituation. During the day, pulsed low and high strength fields (from any distance less than a meter) usually initiated a "burial" response in the test animal; a response that, in its natural environment, would result in its being covered with sand and thereby hidden from view. Thus, during the day, non-uniform magnetic fields appear to elicit a fixed-action pattern, "withdrawl" response.

These preliminary findings suggested the following tentative conclusions: 1) *Heterodontus francisci* displayed what could be electroreceptor-mediated responses, while those of *Cephaloscyllium ventriosum* are possibly a result of direct stimulation of nerves and muscles by the magnetic field. 2) The responses of *Urolophus halleri* suggest orientation along a magnetic axis. Such findings are in accord with those of Kalmijn (1975). 3) The magnetic field strengths that elicited responses were greater than the earth's magnetic field strength. Kalmijn's (1973, 1974) hypothesis suggested an explanation for this by showing that sensitivity to magnetic fields is partly a function of body size. Thus in smaller individuals, such as the ones used here, a greater flux density will be required to produce a signal that could elicit a response. 4) The sensitivity of the electroreceptor organs, and the use to which the information they supply is put, could vary as a function of the ecology of the species in question. Thus, free-ranging, epipelagic sharks may use their electromagnetic reception capabilities for fixed-space orientation, while more sedentary, near-shore species may use them to locate live food sources or not use them at all (Kalmijn, 1971, 1974). Experiments investigating these possibilities are currently in progress.

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Unseasonable Occurrences of Gray Whales

Two sightings of California gray whales, *Eschrichtius robustus* (Lilljeborg, 1861) in Mexican waters during May were related to us and prompted a search of the literature for other unseasonable occurrences. The migrations of this stock of gray whales between their summer range in the Bering and Chukchi seas and their winter grounds in more southern latitudes have been summarized by Rice and Wolman (1971). Exact migration dates for southern California, central California (Monterey Bay area) and the Washington-British Columbia regions have been summarized more recently by Leatherwood (1974), Sund and O'Connor (1974) and Pike and MacAskie (1969), respectively.

As a result of their aerial censuses, Gilmore and Ewing (1954:30) raised the possibility that some gray whales may reside in the vicinity of Crescent City, northern California and in the northern portion of the Gulf of California throughout the summer months, as do many finback whales. Gilmore (1960:1) subsequently reported specific summer sightings of grays in northern California and southern Oregon. Pike and MacAskie (1969:30) concluded that some grays probably reside throughout the summer and fall along the coasts of Washington and British Columbia. Rice and Wolman (1971:12) state that "Not all gray whales migrate to the Arctic in the summer." They reported additional summer sightings at Washington, Oregon, central California and Baja California. Brownell (1971) listed several unseasonable sightings in northern and southern California. His gray whale record (1971:275) on 14 September 1965 at the Nuclear Power Plant, San Onofre, Orange County, is in error, however, as this specimen (LACM 27059) is the partial cranium of a minke whale, *Balaenoptera acutorostrata* found on the beach.

All the unseasonable occurrences of gray whales known to us are presented in Table 1. Any records of gray whales from British Columbia southward between late May and late September were considered unseasonable occurrences for the purposes of this study. Included are two previously unpublished sightings, a year apart, of large aggregations of gray whales at times and places when, by all conventional knowledge, they should have been elsewhere.

A large number of whales was observed on 27 May 1972 in the Canal de los Ballenas between Isla Angel de la Guarda and Isla San Lorenzo in the northwestern portion of the Gulf of California. The sighting was made from the fish charter boat *Poseidon* out of San Felipe, Mexico, by Mr. Hank Lackman of Venice, California. Mr. Lackman relayed the information to the U.S. agent for the *Poseidon*, Mr. Charles Rucker, who in turn communicated with us. Mr. Lackman described the animals as large whales lacking dorsal fins with rather narrow, triangular heads (encrusted with ectoparasites) and having an overall gray appearance with white blotches or mottling.

In addition to its being an unseasonable occurrence, this sighting is one of only a few that have been reported from the northern extremities of the Gulf of California. Ten gray whales were reported by Gilmore (1960:9) during the winter "In the Gulf, north of the regularly used La Paz and Yavaros areas . . . ."

The second sighting was made by Mr. and Mrs. Peter Leupold of Alameda,

Table 1. Unseasonable occurrences of California gray whales in the southern migratory range of western North America.

Locality	Date	Remarks	Source
CANADA:			
British Columbia:			
Langara lighthouse, Queen Charlotte Islands	late August and early September, 1959 and 1960	"several" sighted	Pike & MacAskie (1969)
Near Ucluelet, Vancouver Island	16 August 1966	Stranded young male	Pike & MacAskie (1969)
UNITED STATES:			
Washington:			
Near Lapush	June–July 1961 and July 1967	"some" sighted	Rice & Wolman (1971, *ex.* C. Munson & A. Wolman)
Near Kalaloch	July 1968	"few" sighted	Rice & Wolman (1971, *ex* A. M. Johnson)
Oregon:			
Near Cannon Beach	July 1969	"one" sighted	Rice & Wolman (1971, *ex.* C. Fiscus)
Southern Oregon-northern California:			
Pelican Bay	September 1947 and June 1948	12–15 grays sighted	Gilmore (1960)
Vicinity of Pelican Bay, St. George Reef & Crescent City	summers of 1940's	"small herds" sighted	Gilmore (1960)
Near Crescent City	6 August 1963	"33′ 8″ gray" (10.3 m)	Brownell (1971)
Central California:			
Farallon Islands	throughout summer of 1964 (to late September–early October)	"few" sighted	Rice & Wolman (1971, *ex.* L. Newton)
Pigeon Point	Throughout summers of 1951 and 1952	"one" sighted	Rice (1963)

Table 1. Continued.

Locality	Date	Remarks	Source
Southern California:			
Los Angeles County, Portuguese Bend	August 1963	Stranded after caught in net	Brownell (1971, *ex.* J. Prescott)
Cabrillo Beach	May 1963	Stranded gray	Brownell (1971, *ex.* J. Olguin)
Presumably in the vicinity of Los Angeles	13 July 1962	6.7–7.0 m, caught in fishing net and shot	Brownell (1971, *ex.* J. Prescott)
San Diego County, La Jolla	15 June 1963	8.3 m male, caught in fishing net & shot	Brownell (1971)
Terminal Island, California	1 May 1976	Stranded yearling male	Samaras & Patten, WFS-1033, L.A.C.M.
MEXICO:			
Baja California (west coast):			
South of Punta San Jose	25–30 May 1973	Numerous groups of adults with calves, heading south	This paper (*ex.* P. Leupold)
Bahia Magdalena	11 June 1965	"small gray whale" sighted	Rice & Wolman (1971, *ex.* K. Balcomb)
Gulf of California:			
Canal de las Ballenas	27 May 1972	"very large group"	This paper (*ex.* C. Rucker)

California, while sailing their 33 ft sloop, *Santa Maria*. north along the west coast of Baja California. From 25–30 May 1973 they observed numerous groups of gray whales swimming south below Punta San Jose. Most of the whales observed during the five days were large and presumably adult; many were thought to be sexually mature females inasmuch as at least 25 calves were observed within the groups encountered. The only other unseasonable sighting along the west coast of Baja known to us is that by Ken Balcomb at Bahia Magdalena on 11 June 1965 (Rice and Wolman, 1971).

These sightings, as well as those cited in the literature, suggest that some individuals of groups of gray whales do not participate in the established pattern of migration. Populations appear to reside throughout the year in the Gulf of California, off the Farallon Islands west of San Francisco and in the vicinity of Vancouver Island, British Columbia. The few unseasonable strandings from British Columbia and California were sexually immature animals. This raises the possibility that some immature gray whales may terminate their northbound migration prematurely in these waters.

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The Natal Pterylosis of the House Finch

The avian order Passeriformes includes about 60 percent of the living species of birds. The relationships within this group have so far eluded the continuing efforts of many workers utilizing diverse techniques. One additional source of information, natal pterylosis, provides limited information on passerine relationships (Markus, 1972; Collins and Kemp, 1976). Wetherbee (1957, 1958) summarized the natal pterylosis of North American passerine birds and presented typical patterns for each family. Notably absent from this summary was quantified information on any member of the genus *Carpodacus*.

This paper provides detailed information on the natal pterylosis of the House Finch, *Carpodacus mexicanus*, a widespread species of the western United States and a recent colonizer of many eastern states. Previous workers, cited by Wetherbee (1957:392), noted only that the neossoptiles of the House Finch are 4 to 10 mm long and whitish in color.

The eight specimens of newly hatched House Finches (Stage A of Wetherbee, 1957:356) used in this study were collected from 2 nests found in Bell Canyon, Orange Co., California on 5 May 1974. Except for the abdominal and crural tracts, variability within any one tract was relatively low. The total number of neossop-

Table 1. Counts of neossoptiles of *Carpodacus mexicanus*.

	Number of neossoptiles		
Tract	Minimum	Typical	Maximum
Ocular	7	9	12
Coronal	12	13	16
Occipital	8	9	11
Mid-dorsal	5	8	13
Pelvic (lateral)	6	8	9
Pelvic (medial)*	6	7	9
Scapular	5	10	10
Tertiary	0	0	1
Femoral	9	12	15
Abdominal	4	9	13
Crural	10	15	22
Rectrix	5	6	6
Upper rectrix covert	0	1	4
Under rectrix covert	0	0	1
Primary	1	6	10
Secondary	0	2	5
Greater primary covert	0	5	8
Greater secondary covert	8	10	10
Middle secondary covert	7	8	9
Lesser secondary covert	0	0	3
Carpel remex covert	0	1	1
Alular covert	0	0	2
Patagial covert	0	0	1

* Unpaired row on midline; all others bilaterally paired.

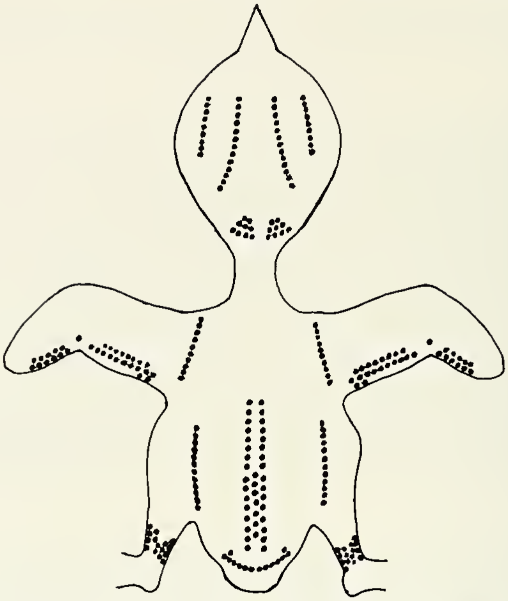

Fig. 1. Typical natal pterylosis of the House Finch. Each dot represents a single neossoptile.

tiles varied from 228 to 314 per bird. The typical number of neossoptiles for the species is 271. This number closely approximates the average total number of neossoptiles, 273, recorded for the eight nestlings. The typical number was determined by summing the modal number of neossoptiles noted for each tract, or the median number in cases where there was great variation and/or a nearly bimodal distribution. The typical number of neossoptiles and the range of variation for each tract are presented in Table 1. Neossoptiles on the tracts for the lower rectrix coverts and the patagial coverts were present in only one individual. This nestling also had exceptionally high counts of neossoptiles on the abdominal and crural tracts and the highest total count (314) of the eight specimens examined. Another individual, having the second highest total count of neossoptiles (286), was the only one to have downs on the alular coverts. These observations are in agreement with the findings of Clark (1967). He noted in his study of Red-winged Blackbirds, *Agelaius phoeniceus*, that nestlings with the greatest total amount of natal down were also the ones most likely to have extra downs present on additional tracts or other parts of the body.

The total number of neossoptiles in the House Finch greatly exceeds the average total number (161) recorded by Wetherbee (1957, 1958) for the two other species in the Carduelinae that he examined. The pattern of neossoptile distribution in the House Finch (Fig. 1) also shows substantial departures from the basic pattern presented for the Fringillidae (including the Carduelinae) by Wetherbee (1957:Fig. 13). Among the most notable differences in pattern were: 1) the presence of three, rather than two, rows of downs in the occipital tract, 2) the presence of two rows of downs rather than one, in the femoral tract, 3) the dense patch of downs in four or five rows, rather than two, in the crural tract, and 4) the presence of three nearly equal rows of downs in the pelvic region, rather than the more usual one. Of these differences, those noted in the pelvic region are perhaps the most unusual. In the House Finch, the downs in this region occur in two paired lateral and an unpaired medial row. Those of the medial row are slightly offset anteriorly from the corresponding ones in the adjacent lateral rows. The lateral pelvic rows were aligned with the paired rows of the immediately anterior mid-dorsal region. Sometimes the break between them was not distinct. In most of the species we have examined, the lateral pelvic rows, if present, are confined to 1–3 neossoptiles adjoining the posterior portion of the medial row. It is most unusual for the lateral rows to be as long as those of the House Finch. This condition is approached by only one other ossine passerine we have examined; the Red-capped Cardinal, *Paroaria gularis* (Collins and Bender, MS).

The natal pterylosis of the House Finch shows substantial departures from the typical number and pattern of neossoptile distribution recorded for other species of the Carduelinae. The full interpretation of these differences will have to await further information on intraspecific variation in the House Finch as well as data on the natal pterylosis of more species of the Carduelinae, particularly congenors. The abundance and availability of the House Finch would seem to make it a particularly suitable species for further studies giving attention to intraspecific and interpopulational variation.

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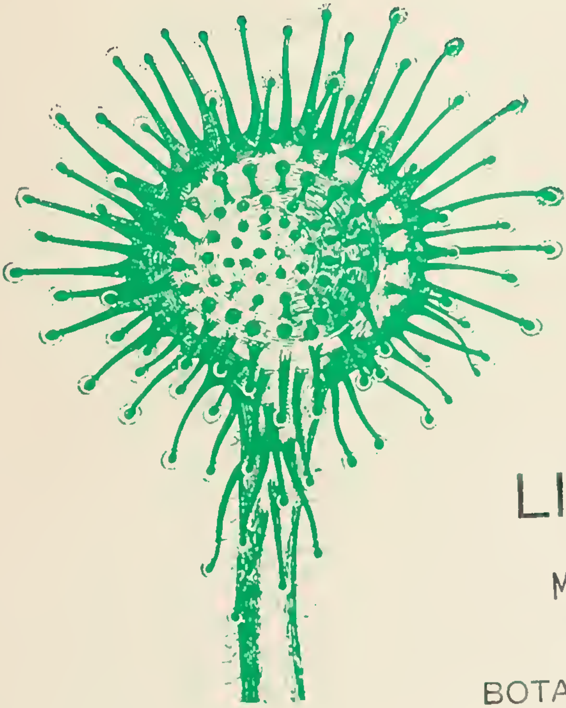
Volume 77 Number 1



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A Resurvey of E. Yale Dawson's 42 Intertidal Algal Transects on the Southern California Mainland after 15 Years

Ronald M. Thom and Thomas B. Widdowson

Abstract.—The 42 intertidal transects established by E. Y. Dawson on the southern California mainland from 1956–1959 were resurveyed for their algal flora during 1973–1974. Although there were no losses of conspicuous species, the relative abundances of various forms had changed over the time period. The shift in the flora has been toward the turf and crustose species and away from the massive species. The Orange County flora showed the greatest change and the Los Angeles flora the least. In the Santa Barbara, Ventura, and San Diego areas the flora was modified to an intermediate extent.

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As part of an oceanographic and biological study of coastal waters for the California State Water Pollution Control Board, Dawson (1959a, 1959b, 1965a, 1965b) surveyed the algae of 44 localities representative of rocky shores in southern California. Forty-two of his stations were on the mainland, and two others were situated on two of the Channel Islands. Dawson (1959a) was unable to find at least 50% of the species collected before 1912 by University of California phycologists Setchell and Gardner at White's Point and Sunset Boulevard Beach located in the Los Angeles area. He concluded that, although major changes in algal populations were possibly related to water pollution of human origin, the most striking fluctuations resulted from non-human influenced physical factors such as sand movement and drying winds. He suggested that his stations be resurveyed during 1971–1974.

Widdowson (1971) revisited 15 of Dawson's transects in the vicinity of Los Angeles during 1968–1970. He found that general and widespread declines in numbers of algal species had taken place and that these declines were caused mainly by human usage of intertidal areas, air pollution and water pollution.

In the Santa Barbara area, a number of Dawson's transects were studied shortly after the 1969–1970 Santa Barbara oil spill (Foster et al., 1971; Nicholson and Cimberg, 1971; Cimberg et al., 1973). These studies showed that the number of algal species had declined at many stations since Dawson's surveys. Although the oil did have a varying amount of impact, the most notable influence on the algal populations was thought to be sand movement.

The purpose of the present study is to resurvey all of Dawson's 42 mainland transects to contrast the current (i.e. 1973–74) status of the algal flora with that reported by Dawson approximately 15 years earlier.

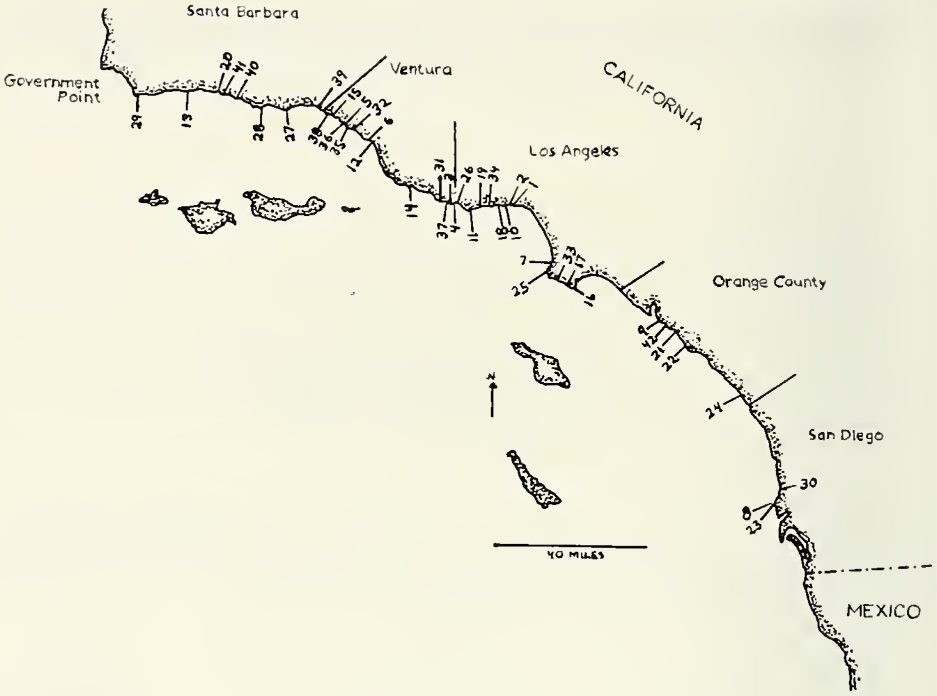

Fig. 1. Positions of Dawson's (1959a) 42 mainland stations. See Table 1 for station names.

Methods

Dawson's data is qualitative in nature, but he did assign abundance estimates to the species he encountered during his station visits. He organized these values into a table which included data taken from November 1956 through March 1958 (Dawson, 1959a). Dawson's surveys continued well into the year 1959, but he never published a subsequent listing of algal abundances for this final period. Therefore, we thought it best to compare the 1973–74 flora with Dawson's 1956–58 data.

From February 1973 through February 1974, each of the 42 stations were surveyed during the month(s) it was sampled by Dawson (Fig. 1, Table 1). During a station visit, Dawson's shore base point (SBP) and transect were located. His field procedure was followed for all surveys. This consisted of making a thorough search for the algal species that occurred within a few feet of the transect line. The abundance of each species was estimated as being high, medium or low, corresponding to Dawson's values of 10, 3 and 1, respectively. Voucher specimens were collected to help confirm identifications made in the field. These specimens were placed on file in the herbarium of the California State University, Long Beach. Algal nomenclature follows that of Abbott and Hollenberg (1977).

The species found at each station (multiple visits to a station were combined) during 1973–74 were compared to those of 1956–58 using the Czekanowski coefficient (C) of similarity (Clifford and Stephenson, 1975):

Table 1. Summary of species list and species abundance comparisons between 1956–58 data and 1973–74 data at Dawson's 42 stations (see text for explanation of C and Cw).

Station Number	Station Name	Number of Species		Similarity		Difference
		1956–58	1973–74	C	Cw	(|C-Cw|)
Santa Barbara						
29	Government Pt.	49	70	55%	44%	11%
13	Gaviota Beach	55	63	63	39	24
20	Lento	65	45	50	44	6
41	Refugio Beach	43	63	65	51	14
40	El Capitan Beach	35	35	54	40	14
28	Goleta Pt.	45	49	45	34	11
27	Santa Barbara Pt.	64	54	60	49	11
39	Monteceito	50	37	69	41	28
Ventura						
38	Loon Pt.	47	36	34	27	7
15	Carpenteria	57	65	58	40	18
36	Rincon Del Mar	33	48	56	53	3
5	Mussel Shoals	50	57	65	46	19
35	Rincon Park No. 4	41	53	57	45	12
32	Pitas Pt.	32	33	62	45	17
6	Two miles west of Ventura	38	48	43	33	10
12	Palm Street, Ventura	39	33	54	45	9
14	Port Hueneme	28	24	69	40	29
31	Pt. Mugu	29	29	49	35	14
37	Bass Rock	24	25	48	35	13
3	Yerba Buena Road	69	56	67	58	9
4	Arroyo Sequit	64	55	58	58	0
Los Angeles						
26	Lechuza Pt.	63	39	51	43	8
11	Pt. Dume Bay	58	64	60	57	3
19	Latigo Shore Road	52	58	70	58	12
34	Malibu Road	28	46	57	50	7
18	Malibu Beach	44	42	49	47	2
10	Big Rock Beach	41	50	61	48	13
2	Topanga Canyon Road	35	38	63	57	6
1	Sunset Boulevard Beach	39	54	56	44	12
7	Flat Rock Pt.	33	53	64	46	18
25	Lunada Bay	44	47	64	46	18
33	Portuguese Pt.	18	24	41	29	12
17	White's Pt.	36	43	56	47	9
16	Pt. Fermin	45	42	51	44	7
Orange County						
9	Corona Del Mar	40	61	53	39	14
42	Crystal Cove	26	39	41	38	3
21	Laguna Beach	32	65	42	36	6
22	North of Dana Pt.	55	60	59	53	6
24	Camp Pendleton	18	20	40	36	4
San Diego						
30	Scripps Institution Reef	63	43	65	53	12
8	Neptune Place	76	70	64	42	22
23	Bird Rock	51	66	63	42	21

$$C = \frac{2a}{2a + b + c} \times 100\%$$

where a = the number of species in common between the 1956–58 and 1973–74 accounts; b = the number of species exclusive to the 1956–58 account; and c = the number of species exclusive to the 1973–74 account.

The abundances of the species were also used to compare floral records by employing a weighted Czekanowski coefficient (Cw) (Prentice and Kain, 1976). With this measure, the sum of the percent abundance (i.e. the abundance divided by the total abundance of all species and multiplied by 100%) of the species was substituted for the number of species in the above equation. The range of both C and Cw is 0% (no similarity) to 100% (identical). Comparison of the weighted coefficient with the unweighted coefficient indicates how the flora differs between the two accounts. For example, a relatively high unweighted C coupled with a relatively low weighted C would indicate that the species present have changed little but that the abundance of each has been modified.

Dawson filed specimens from his collections in the Herbarium of the Allan Hancock Foundation of the University of Southern California, Los Angeles. A search for this material revealed that he had, in a few cases, failed to include some species into his species abundance list. These species were assigned an abundance value of one and incorporated into the data.

Results

One hundred and thirty-one of Dawson's 163 species were found during 1973–74 (Table 2). Of these, a higher proportion of the species of green algae (89%) than brown (78%) and red (78%) algae were noted in 1973–74. No species that was found more than a few times (considered rare) during Dawson's study was absent in 1973–74. Similarly, most species exclusive to the 1973–74 flora were either inconspicuous (due to small size) or of rare occurrence. An exception to this is the brown kelp *Sargassum muticum* (eight occurrences). Detailed species-station information is presented elsewhere (Thom, 1976).

Figure 2 is a graphic representation of the percent change in the number of species since 1956–58. In general, the stations in the Los Angeles and Orange County areas showed the greatest increase. Additionally, geographically adjacent stations tended to exhibit similar changes. At some stations, particularly those in the Orange County area (stations 9, 21, 42), where there were relatively large increases in the number of species, there was a corresponding low similarity (C) (Table 1). Conversely, in the Santa Barbara and Ventura areas (stations 6, 28, 38) the low C values did not correspond to large increases in species.

Weighted similarities tended to be highest at the stations in the Los Angeles area (Table 1). Furthermore, the largest differences between the weighted and unweighted similarities were generally found at the Santa Barbara, Ventura and San Diego area stations. Notable among these were Gaviota (station 13) and Monteceito (station 39) in the Santa Barbara area; Carpinteria (station 15), Mussel Shoals (station 5), Pitas Point (station 32) and Port Hueneme (station 14) in the Ventura area; and Neptune Place (station 8) and Bird Rock (station 23) in the San Diego area. Major differences in the similarity measures were also seen at Flat

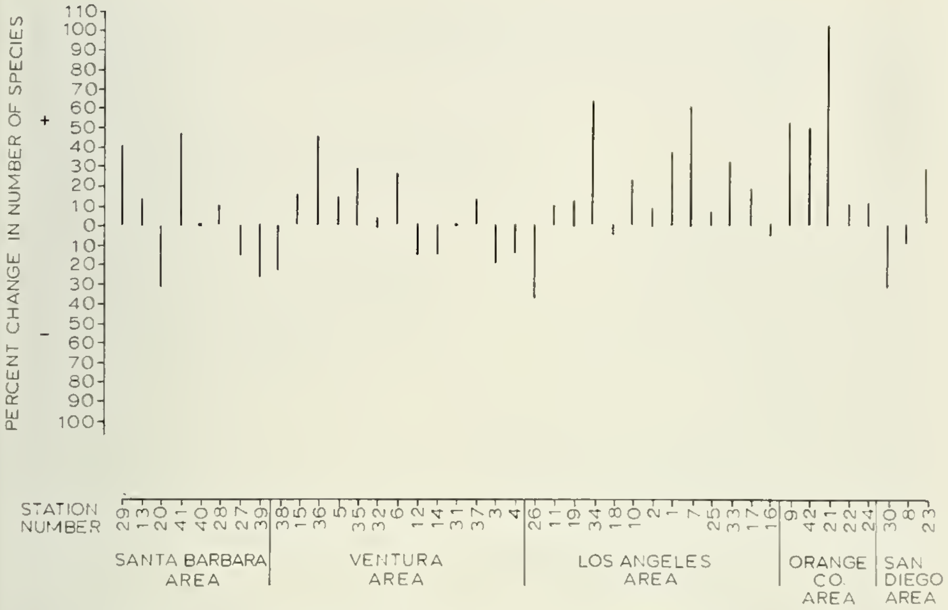

Fig. 2. The percentage change in the number of species at Dawson's stations (1956–58 versus 1973–74).

Rock Point (station 7) and Lunada Bay (station 25), located next to one another and near the city of Los Angeles.

Species were classified by habit type following the criteria of Widdowson (1971). Abundance values for each habit type within each of the five geographic areas were then summed up for both the 1956–58 and 1973–74 data. The grouping of stations by geographic area was carried out because Dawson tended to select stations that formed clusters within these areas and changes appeared to be similar at stations that were adjacent (Fig. 2 and Table 1).

Changes in the contribution of each habit type within each area are presented in Figure 3. The abundance of articulated corallines exhibited a large decline in the Ventura, Orange and San Diego areas, but remained relatively unchanged in the other two areas. Crustose species generally increased in abundance in the Santa Barbara, Ventura and San Diego areas. Leafy species declined in the Santa Barbara area, but increased in abundance in the Los Angeles, Orange County and San Diego areas. Massive species (mostly kelps) declined in the Los Angeles and Orange County areas. In Orange County, there was a substantial increase in the occurrence of turf-like species. The value for Cw between the 1956–58 and 1973–74 floras based upon their habit types was highest at Los Angeles stations (92%) and lowest at Orange County stations (79%). The values for Cw in the Santa Barbara, Ventura and San Diego area stations were 86%, 90% and 84%, respectively.

Discussion

Although there were no losses of conspicuous species (Table 2), the invasive, low-intertidal kelp, *Sargassum muticum*, appeared in rather high frequency (eight

Table 2. The species encountered during 1956–58 and 1973–74 at Dawson's 42 stations.

Species	Occurrence 1956–58	1973–74
Seagrass		
Phyllospadix spp.	x	x
Chlorophyta		
Bryopsis corticulans Setchell	x	x
B. hypnoides Lamouroux	x	x
Chaetomorpha californica Collins		x
C. linum (Mueller) Kuetzing	x	x
C. spiralis Okamura	x	
Cladophora albida (Huds.) Kuetzing		x
C. columbiana Collins	x	x
C. graminea Collins	x	
C. microcladioides Collins	x	x
Cladophoropsis fasciculatus (Kjellm.) Okamura	x	x
Codium fragile (Suringer) Hariot	x	x
C. setchellii Gardner	x	x
Derbesia marina (Lyngbye) Kjellman		x
Enteromorpha compressa (Linnaeus) Grounow	x	x
E. clathrata var. *crinita* (Roth) Hauck	x	x
E. flexuosa (Roth) J. Agardh		x
E. intestinalis (L.) Link	x	x
E. linza (Linnaeus) J. Agardh	x	x
E. prolifera (Mueller) J. Agardh		x
Lola lubrica (Setchell & Gardner) A. & G. Hamel		x
Rhizoclonium riparium (Roth) Harvey		x
Ulva angusta Setchell & Gardner/*U. taeniata* (S.) Setchell & Gardner	x	x
U. californica Wille	x	x
U. costata (Howe) Hollenberg		x
U. dactylifera Setchell & Gardner		x
U. expansa (S.) Setchell & Gardner		x
U. lactuca Linnaeus	x	x
U. lobata (Kuetzing) Setchell & Gardner	x	x
U. rigida C. Agardh	x	x
U. vexata Setchell & Gardner		x
Urospora sp.		x
Phaeophyta		
Coilodesme rigida Setchell & Gardner	x	
Colpomenia sinuosa (Roth) Derbes & Solier	x	x
Cylindrocarpus rugosus Okamura	x	x
Cystoseira spp.	x	x
Desmarestia spp.	x	x
Dictyopteris undulata Holmes	x	x
Dictyota flabellata (Collins) Setchell & Gardner	x	x
Ectocarpus simulans Setchell & Gardner		x
Egregia menziesii (Turner) Areshoug	x	x
Eisenia arborea Areschoug	x	x
Endarachne binghamiae J. Agardh	x	x
Feldmannia cylindrica (Saunders) Hollenberg & Abbott		x
F. hemispherica (Saunders) Hollenberg		x
F. irregularis (Kuetzing) Hamel	x	
Fucus distichus subsp. *endentatus* (de la Pyl.) Powell	x	x
Giffordia granulosa (J. E. Smith) Hamel	x	x
G. mitchelliae (Harvey) Hamel	x	
G. saundersii (Setchell & Gardner) Hollenberg & Abbott		x

Table 2. Continued.

Species	Occurrence	
	1956–58	1973–74
Halidrys dioica Gardner	x	x
Hapterophycus canaliculatus Setchell & Gardner	x	
Hesperophycus harveyanus (Decaisne) Setchell & Gardner	x	
Laminaria dentigera Kjellman		x
L. farlowii Setchell	x	
L. sinclarii Harvey	x	x
Macrocystis pyrifera (Linnaeus) C. Agardh	x	x
Pachydictyon coriaceum (Holmes) Okamura	x	x
Pelvetia fastigiata (J. Agardh)	x	x
Petalonia fascia (Mueller) Kuntze		x
Ralfsia spp.	x	x
Sargassum agardhianum Farlow	x	x
S. muticum (Yendo) Fensholt		x
S. palmeri Grounow		x
Scytosiphon lomentaria (Lyngbye) Link	x	x
Sphacelaria furcigera Kuetzing		x
Taonia lennebackerae Farlow	x	x
Zonaria farlowii Setchell & Gardner	x	x
Rhodophyta		
Acrochaetium microscopicum (N.) Naegeli		x
A. rhizoideum (Drew) Jao		x
Acrosorium uncinatum (Turner) Kylin	x	x
Ahnfeltia spp.	x	x
Amphiroa zonata Yendo	x	x
Anisocladella pacifica Kylin	x	x
Antithamnion defectum Kylin		x
Bangia fusco-purpurea (Dillwyn) Lyngbye	x	x
Bossiella californica subsp. californica (Decaisne) Silva		x
B. chiloensis (Decaisne) Johansen	x	x
B. orbigniana subsp. *dichotoma* (Manza) Silva	x	x
B. orbigniana subsp. *orbigniana* (Decaisne) Silva	x	x
B. plumosa (Manza) Silva	x	
Botryoglossum farlowianum (J. Agardh) J. DeToni	x	x
Calliarthron chielosporioides Manza	x	x
Callithamnium pikeanum Harvey	x	x
Callophyllis linearis (Kylin) Abbott & Norris		x
C. obtusifolia J. Agardh	x	x
C. violacea J. Agardh	x	
Carpopeltis bushiae (Farlow) Kylin	x	x
Centroceros clavulatum (C. Agardh) Montagne	x	x
Ceramium californicum J. Agardh	x	x
C. codicola J. Agardh		x
C. eatonianum (Farlow) J. DeToni	x	x
C. pacificum (Collins) Kylin	x	x
Chondria californica (Collins) Kylin	x	x
C. decipiens Kylin	x	x
C. nidifica Harvey	x	x
Choreonema thuretii (Bornet) Schmitz		x
Coeloseira compressa Hollenberg		x
C. parva Hollenberg		x
Corallina officinalis var. *chilensis* (Harvey) Kuetzing	x	x
C. pinnatifolia (Manza) Dawson	x	x
C. polysticha Dawson	x	

Table 2. Continued.

	Occurrence	
Species	1956–58	1973–74
C. vancouveriensis Yendo	x	x
Cruoria profunda Dawson	x	
Cryptonemia obovata J. Agardh	x	x
Cryptopleura corallinara (Nott) Gardner	x	x
C. crispa Kylin	x	x
C. lobulifera (J. Agardh) Kylin	x	x
C. violacea (J. Agardh) Kylin	x	x
Cryptosiphonia woodii (J. Ag.) Agardh	x	x
Cumagloia andersonii (Farlow) Setchell & Gardner		x
Endocladia muricata (Postels & Ruprecht) J. Agardh	x	x
Erythrocystis saccata (J. Agardh) Silva		x
Erythroglossum californicum (J. Ag.) Agardh		x
Erythrotrichia carnea (Dillwyn) J. Agardh		x
Farlowia mollis (Harvey & Bailey) Farlow & Setchell	x	
Fosliella paschalis (Lemoine) Setchell & Gardner		x
Gastroclonium coulteri (Harvey) Kylin	x	x
Gelidium coulteri Harvey/*G. pusillum* (Stackhouse) LeJolis	x	x
G. nudifrons Gardner		x
G. purpurascens Gardner	x	x
G. robustum (Gardner) Hollenberg & Abbott	x	x
Gigartina canaliculata Harvey	x	x
G. corymbifera (Kuetzing)		x
G. harveyana (Kuetzing) Setchell & Gardner	x	x
G. leptorhynchos J. Agardh	x	x
G. papillata (C. Agardh) J. Agardh	x	x
G. spinosa (Kuetzing) Harvey/*G. volans* (C. Agardh) J. Agardh	x	x
Gloiosiphonia capillaris (Hudson) Carmichael		x
Graciliaria andersonii (Grounow) Kylin	x	x
G. sjoestedtii Kylin	x	x
G. textorii (Suringer) J. Agardh	x	x
G. turgida Dawson		x
G. verrucosa (Hudson) Papenfuss	x	x
Grateloupia doryphora (Montagne) Howe	x	x
G. prolongata J. Agardh	x	x
Gymnogongrus leptophyllus J. Agardh	x	x
G. platyphyllus Gardner	x	x
Haliptylon gracile (Lamouroux) Johansen	x	x
Halymenia schizymenioides Hollenberg & Abbott		x
Herposiphonia tenella f. *secunda* (C. Agardh) Hollenberg	x	
H. verticillata (Harvey) Kylin	x	x
Heteroderma nicholsii Setchell & Mason		x
Hildenbrandia spp.	x	x
Hydrolithon decipiens (Foslie) Adey	x	
Hypnea johnstonii Setchell & Gardner		x
H. valentiae (Turner) Montagne	x	x
H. variabilis Okamura		x
Iridaea cordata var. *splendens* (Setchell & Gardner) Abbott	x	
I. flaccida (Setchell & Gardner) Silva	x	x
I. heterocarpa Postel & Ruprecht	x	
I. lineare (Setchell & Gardner) Kylin	x	
Janczewskia lappacea Setchell		x
Jania adhaerens Lamouroux		x
J. crassa Lamouroux	x	x

Table 2. Continued.

Species	Occurrence 1956–58	1973–74
J. tenella Kuetzing	x	x
Laurencia lajolla Dawson		x
L. pacifica Kylin	x	x
L. spectabilis var. *diegoensis* Dawson	x	x
L. spectabilis var. *spectabilis* Postel & Ruprecht	x	x
L. splendens Hollenberg	x	x
L. subopposita (J. Agardh) Setchell	x	x
Lithothamnium californicum Foslie	x	x
L. crassiusculum (Foslie) Mason	x	x
Lithothrix aspergillum J. E. Grey	x	x
Lomentaria casea Dawson		x
L. hakodatensis Yendo		x
Melobesia marginata Setchell & Foslie	x	x
M. mediocris (Foslie) Setchell & Mason	x	x
Microcladia californica Farlow		x
M. coulteri Harvey	x	x
Nemalion helminthoides (Velley) Batters	x	x
Neoagardhiella baileyi (Harvey *ex* Kuetzing) Wynne & Taylor	x	x
Neogoniolithon setchellii (Foslie) Adey		x
Neoptilota densa (C. Agardh) Kylin		x
Ozophora clevelandii (Farlow) Abbott	x	
Petroglossum parvum Hollenberg	x	
Petrocelis franciscana Setchell & Gardner	x	x
Phycodrys setchellii Skottsberg	x	
Pleonosporium squarrulosum Kylin	x	x
Plocamium cartilagineum (L.) Dixon	x	x
P. violaceum Farlow	x	x
Pogonophorella californica (J. Agardh) Silva	x	
Polyneura latissima (Harvey) Kylin	x	x
Polysiphonia confusa Hollenberg	x	
P. hendryi var. *compacta* (H.) Hollenberg		x
P. hendryi var. *gardneri* (Kylin) Hollenberg	x	x
P. hendryi var. *hendryi* Gardner		x
P. indigena Hollenberg		x
P. mollis Hooker & Harvey	x	
P. nathaniellii Hollenberg		x
P. pacifica var. *delicatula* Hollenberg		x
P. pacifica var. *pacifica* Hollenberg	x	x
P. paniculata Montagne	x	
P. scopulorum var. *villum* (J. Agardh) Hollenberg	x	x
P. simplex Hollenberg	x	
Porphyra perforata J. Agardh	x	x
P. thuretii Setchell & Gardner	x	x
Prionitis australis J. Agardh		x
P. cornea (Okamura) Dawson	x	x
P. lanceolata (H.) Harvey	x	x
P. lyallii Harvey	x	x
Pseudogloiophloea confusa (Setchell) Levring	x	x
Pterocladia capillacea (Gmelin) Kuetzing	x	x
P. media Dawson	x	
Pterosiphonia baileyi (Harvey) Falkenberg	x	x
P. bipinnata (Postels & Ruprecht) Falkenberg		x
P. dendroidea (Montagne) Falkenberg	x	x

Table 2. Continued.

Species	Occurrence 1956–58	Occurrence 1973–74
P. pennata (Roth) Falkenberg		x
Ptilota filicina J. Agardh	x	
Rhodochorton purpureum (Lightfoot) Rosenvinge		x
Rhodoglossum affine (Harvey) Kylin	x	x
R. californicum (J. Agardh) Abbott	x	x
R. roseum (Kylin) Smith	x	
Rhodomela larix (Turner) C. Agardh	x	x
Rhodymenia arborescens Dawson		x
R. californica var. *californica* Kylin	x	x
R. californica var. *attenuata* (Dawson) Dawson		x
R. pacifica Kylin	x	x
R. rhizoides Dawson	x	
Schizymenia pacifica (K.) Kylin	x	
Smithora naiadum (Anderson) Hellenberg	x	x
Stenogramme interrupta (C. Agardh) Montagne	x	
Tenarea spp.	x	x
Tiffaniella snyderiae (Farlow) Abbott	x	x

occurrences). This species is reported to be rapidly extending its distribution southward since its introduction into the coastal waters of western Canada approximately 30 years ago (Norton, 1977). It apparently had not reached southern California, or was of such restricted occurrence by the time of Dawson's study that it was not noted by him.

Changes in the algal flora have taken place and are manifested as modifications of species abundances and possibly species replacements (Fig. 2, Table 1). It is beyond the purpose of this paper to document the reasons for these changes. However, certain observations can be made based upon Widdowson's (1971) conclusion that human usage, air pollution, and water pollution (in that order) were effective in modifying the floral composition at 15 stations in the Los Angeles area. In the Orange County area there has been a relative large increase in the number of species since 1958. This has been coupled with a low degree of similarity between the 1973–74 and 1956–58 flora, which indicates a change in the species composition by the predominance of algal species either not present 15 years ago or present in low relative abundance. Along these lines there has been a substantial increase in the number of turf-like species and a decrease in articulated coralline and massive forms. Orange County has undergone the most rapid increase in human population since about 1960 and the flora has correspondingly shown the most rapid change compared to the Santa Barbara, Ventura, Los Angeles and San Diego areas.

The flora in the Santa Barbara, Ventura and San Diego areas has changed less. It appears that since Dawson's study, relative abundance has changed, but not the species involved. Crustose species have been increasing in abundance, while sand-dwelling species have been decreasing in all three areas. The stations that have shown the greatest modifications in algal abundances (i.e., 13, 15, 39, 5, 32, 14, 8, 23) are all either located in heavily populated metropolitan areas or are public parks with heavy recreational use. Conversely, the stations exhibiting the

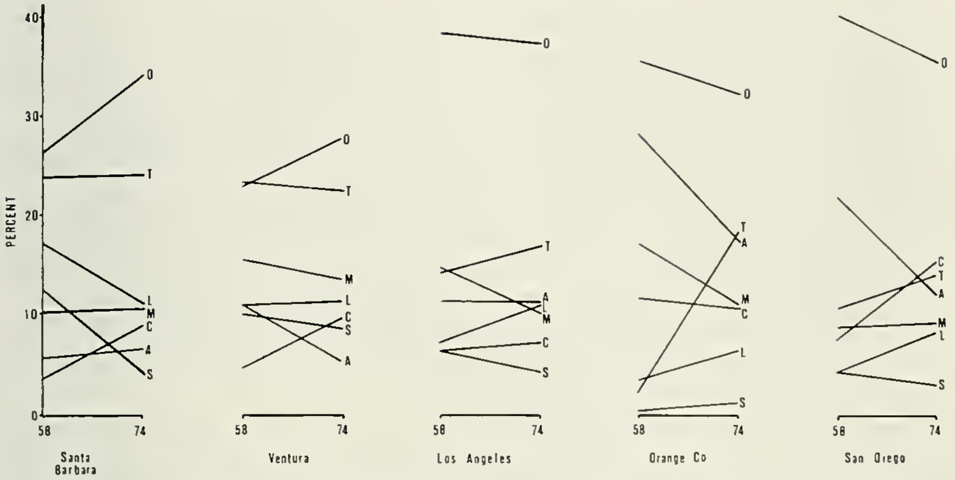

Fig. 3. Change in percentage contribution of the seven algal habit types between 1956–58 and 1973–74 in the five areas. A = articulated corallines; C = crusts; L = leafy; M = massive; O = other; T = turf; 58 = Dawson's 1956–58 data; 74 = the 1973–74 data.

least change in algal abundance (e.g., stations 20, 38, 36, 11, 18, 42, 24) are located on beaches with little use and are relatively far from water and air borne pollutants.

The algal flora in the Los Angeles area has changed the least (Cw = 92%) of all areas since 1958 (Table 1, Figs. 2, 3). This suggests that the intertidal algae in this area had reached an equilibrium by or near 1956 with the polluted and trampled conditions that have existed in the Los Angeles area for a long time prior to 1956. Recent restrictions on the collection of marine organisms may also have slowed the amount of change in the algae of this area.

There are, however, a number of Los Angeles stations where the flora still appears to be undergoing alteration. White's Point (17) and Point Fermin (16) are both heavily used and very near the sewage outfall of the County of Los Angeles (located approximately 2 km off White's Point). The number of species decreased at Point Fermin and increased only slightly at White's Point since 1958 (Fig. 2). The similarities (C and Cw) were very low relative to other stations near Los Angeles (Table 1). Furthermore, the flora at these beaches has been declining at least since the collections made before 1912 by Setchell and Gardner (Dawson 1959a).

Portuguese Point (station 33), located near White's Point, is probably little used due to difficulties in access. The number of species increased by greater than 30% since 1958 (Fig. 2). Dawson (1959a) reported that the flora here was quite depauperate both intertidally and subtidally. Although the similarities are very low, the increase in species may account for this, as suggested for the Orange County Stations. Unlike the Orange County flora, however, which was in a relatively undistributed condition during Dawson's study, this information at station 33 possibly indicates some degree of recovery.

Widdowson (1971) found that the flora in the Los Angeles area had shifted in the direction of turf-forming species and away from leafy and massive forms. He also noted that the articulated corallines were decreasing. The present study bears out these conclusions except that the articulated corallines remained essentially unchanged. The most pronounced shift toward turf algae and away from massive species was seen at stations in the Orange County area.

Dawson (1959a) reported that articulated corallines were increasing in southern California. He based this conclusion mainly on observations he had made during the early 1940's in the San Diego area and upon the records of Setchell and Gardner at White's Point and Point Fermin. Although no area showed an increase in articulated corallines in the present study, the rank by frequency of individual articulated coralline species has been shown to be higher now than before Dawson's survey (Thom, 1976). This phenomenon could be the result of the decline in frequency of occurrence of massive forms, which may open space for the apparently hardier articulated corallines.

The results of this study concerning changes in numbers of species coincide fairly well with those of similar studies (Foster et al., 1971; Nicholson and Cimberg, 1971; Widdowson, 1971). Foster et al. recorded declines (ranging from one to 16 species) at seven of the nine Dawson stations they resurveyed in the Santa Barbara area. At no time, however, were the declines noted in 1973–74 as great as those found by Nicholson and Cimberg.

On a smaller scale, Littler and Murray (1975) found a situation similar to ours while studying the effects of raw sewage on intertidal communities. The area directly influenced by the outfall is characterized by the elimination of massive and leafy species (e.g., *Egregia menziezii*) and an increase in the percent cover and productivity of turf algae (e.g., blue-greens and *Ulva californica*), creating a monotonous flora of low species number.

Conclusion

The intertidal algae of southern California have undergone measurable changes over the past 15 years. Dawson's data from 42 mainland stations represent important baseline information that can be used to document these changes. It appears that coastal areas having rapid increases in human population (such as Orange County) also have a rapid change in their algal flora. This change progresses as a modification of algal abundances favoring turf-forming and crustose algae, and disfavoring massive forms as reported by other workers (Widdowson, 1971; Littler and Murray, 1975).

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The Natal Pterylosis of Hummingbirds

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Abstract.—Of the hummingbirds examined, most have a common pattern of natal down distribution: a single paired row of filamentous mid-dorsal neossoptiles. One exception, *Glaucis hirsuta*, typically has 50 short conglomerate downs on eight tracts, including the dorsal cervical region. The taxonomic usefulness of natal pterylosis seems to be at the intrafamilial level in the Apodiformes.

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The natal pterylosis of birds has received considerable attention in recent years. In some cases the color and pattern of the downy plumage of precocial species have proven to be of considerable taxonomic importance (Jehl, 1968). The number and distribution of natal downs or neossoptiles in altricial species, particularly passerines, have been considered by several workers (Burkhardt, 1954; Wetherbee, 1957, 1958; Collins, 1963a, 1973; Clark, 1967; Markus, 1970, 1972) and in some cases have proven to be of limited taxonomic usefulness (Markus, 1972; Collins and Kemp, 1976). To date there is still a paucity of information on most non-passerine species. Despite many reports to the contrary (Dwight, 1902; Ridgway, 1911; Landsborough Thompson, 1964) it is now clear that most, if not all, hummingbirds have at least a sparse covering of natal down. This paper summarizes the available information on the natal pterylosis of the hummingbirds (Apodiformes, Trochilidae). This family appears to possess one basic pattern with at least one notable exception.

Wetherbee's observations (1958) on the Ruby-throated Hummingbird, *Archilochus colubris*, provided the first detailed data on natal downs in a hummingbird where the distribution, number and length of the neossoptiles were presented. This species has 12 pairs of tawny filamentous downs in a single row on the mid-dorsal region of the spinal tract (Fig. 1). The numerous other descriptions of natal downs in hummingbirds, usually part of life history studies, are summarized in Table 1. Although the accounts vary substantially in detail, they all can be interpreted as being in agreement with Wetherbee's basic pattern (allowing for some variation in the number of pairs of downs). My field observations and data from detailed examination of preserved specimens are mostly in agreement with this basic pattern. However, there is also evidence that in at least some species of hummingbirds there may be either a different pattern or a total absence of downs. These exceptions are of interest and would be of great value if they in any way helped to clarify the intra-familial relationships of this bewildering array of tiny birds: 331 species in 123 genera (Storer, 1971).

Most descriptions of naked hummingbird chicks are probably in error due to workers overlooking the sparse mid-dorsal downs. Skutch (1967), who has studied many species of hummingbirds, reports that the nest of the Black-bellied Hummingbird, *Eupherusa nigriventris*, contained "two naked nestlings." This account is the only recent one that seems clearly to describe a young hummingbird as

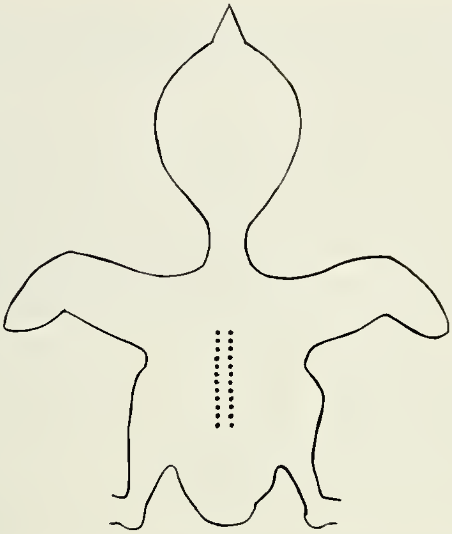

Fig. 1. Typical distribution of neossoptiles in most hummingbirds examined. Each dot represents a single feather. The number of paried neossoptiles varied from 8 to 12.

lacking downs. Skutch (1972) also reports that two-week-old nestlings of the Long-billed Starthroat, *Heliomaster longirostris*, had "their upper parts, throat, and breast . . . covered with short, whitish down, more abundant than that on any other hummingbird." It seems unlikely that this refers to true natal downs; it may well represent an early appearing portion of the first teleoptile plumage. Such down-like coverings have been noted for many swifts (Collins, 1963b, 1965, and unpubl.) and at least one passerine (Collins, unpubl.), but are presently unknown for hummingbirds.

In addition to the paired mid-dorsal downs, I observed a single advantitious down, probably representing the coronal tract, on the head of one of two nestlings of the Ruby-topaz Hummingbird, *Chrysolampis mosquitus*. The only other report of capital region downs is that of Haverschmidt (1952) for the Glittering-throated Emerald, *Amazilia fimbriata*. However, if the head were bent back against the interscapular region, the typical posture of nestling hummingbirds, it would have been easy to mistake some of the filamentous mid-dorsal downs as originating on the crown.

A further exception to the general pattern of a single mid-dorsal row of neossoptiles is found in the Rufous-breasted Hermit, *Glaucis hirsuta*. My data (Table 2) from nine living nestlings examined in the field and three preserved specimens, all from Arima Valley, Trinidad, indicate that this species has an average of 53 neossoptiles per bird (range 25–76) distributed on eight or nine tracts. The typical number (based on the modal number present on each individual tract) (Fig. 2) for the 12 individuals examined was 50 neossoptiles on eight tracts. Except for the femoral tract, variability within any one tract was generally low. Crural neossoptiles were noted on only one individual.

Table 1. Number and distribution of neossoptiles of hummingbirds. English and scientific names are from Meyer de Schauensee (1966) and Eisenmann (1965). "Number of Downs" indicates number of neossoptiles (left/right) on mid-dorsal region of spinal tract.

Species	Number of Downs	Source
Green Hermit *Phaethornis guy*	?	"chesnut-fawn on its back" (Snow, 1974)
Long-tailed Hermit *Phaethornis superciliosus*	?	"the nestlings hatch with the dark skin, sparse down . . . typical of newborn hummingbirds" (Skutch, 1964a)
Reddish Hermit *Phaethornis ruber*	?	"some light brown down on their backs" (Oniki, 1970)
Little Hermit *Phaethornis longuemaris*	12/12, 11/11	Counts from 2 specimens (Trinidad); this study
Scaly-breasted Hummingbird *Phaeochroa cuvierii*	8/8 (?)	"along the middle of the back are two parallel rows of pale grey down-feathers, about eight in each" (Skutch, 1964b)
Green Violetear *Colibri thalassinus*	10/10	"a few tufts of tawny down along the middle of the back" (Skutch, 1967:35); counts from diagrams (Wagner, 1945, 1967)
Sparkling Violetear *Colibri coruscans*	?	row of paired downs on dorsum (pers. comm., J. W. Hardy re. specimens Moore Lab. Ornith., Occidental College)
Ruby-topaz Hummingbird *Chrysolampis mosquitus*	12/12, 9/11	counts from 2 nestlings in field (Trinidad); this study. One adventitious coronal down on one nestling (see text)
Fork-tailed Emerald *Chlorostilbon canivetti*	?	"two rows of brownish down along the back behind the interscapular region" (Wolf, 1964)
Broad-billed Hummingbird *Cyanthus latirostris*	?	row of paired downs on dorsum (Pers. Comm., J. W. Hardy, re. specimens, Moore Lab. Ornith., Occidental College)
White-eared Hummingbird *Hylocharis leucotis*	9/9 (?)	counts from diagram (Wagner, 1967:230)
Glittering-throated Emerald *Amazilia fimbriata*	?	"golden-colored down on its back and head" (Haverschmidt, 1952)
Copper-rumped Hummingbird *Amazilia tobaci*	12/12	dorsal downs obs. in photograph (Schwartz, 1963); counts from a specimen (Trinidad): this study
Rufous-tailed Hummingbird *Amazilia tzactl*	?	"naked except for two lines of short tawny down extending the length of the back on either side of the middle line" (Skutch, 1931)
Blue-throated Hummingbird *Lampornis clemenciae*	10/10 (?)	counts from diagram (Wagner, 1967)
Crimson Topaz *Topaza pella*	?	"a thin dorsal tuft of ochraceous down" (Nicholson, 1931)
Andean Hillstar *Oreotrochilus estella*	?	"the body is naked except for a large tuft of down in the middle of the spinal tract" (translation mine) (Dorst, 1962:115, Fig. 6)
Black-tailed Trainbearer *Lesbia victoriae*	?	mid-dorsal downs obs. in photograph (Greenewalt, 1960: 674)
Ruby-throated Hummingbird *Archilochus colubris*	12/12, 12/12	a row of paired mid-dorsal downs: counts from 2 specimens (Wetherbee, 1958)

Table 1. Continued.

Species	Number of Downs	Source
Black-chinned Hummingbird *Archilochus alexandri*	?	a row of paired mid-dorsal downs (field obs. of nestlings by S. Wells)
Anna's Hummingbird *Calypte anna*	11/11	a row of paired mid-dorsal downs (field obs. of nestlings by S. Wells and C. T. Collins); count from one specimen (California): this study
Costa's Hummingbird *Calypte costae*	12/12	a row of paired mid-dorsal downs (field obs. of 2 nestlings, this study); count from 1 specimen (California) this study
Rufous Hummingbird *Selasphorus rufus*	?	"two slight tracts of greyish down extending longitudinally along the back" (DuBois, 1938)
Allen's Hummingbird *Selasphorus sasin*	12/12	"down . . . present in small quantities along parts of the spinal tract" (Orr, 1939); row of paired downs on dorsum (field obs. of nestlings by S. Wells); count from one specimen (California): this study
Broad-tailed Hummingbird *Selasphorus platycercus*	?	dorsal downs obs. in photograph (Ratcliffe, 1964)

In six of the individuals examined there was a pair of downs present in the dorsal cervical region. One individual had only a single unpaired down present and the remaining five had no downs present in this region. This is the first record of any neossoptiles being present in the dorsal cervical region of an altricial species. Similar downs recently have been found in one Neotropical passerine species (Collins and Bender, ms). Ventral cervical neossoptiles have been recorded for two species of African passerines (Markus, 1970, 1972) but not as yet for any North American or Neotropical species.

The natal down feathers of *Glaucis* are appreciably different in texture and appearance (Fig. 3) from the typically long filamentous downs of other hummingbirds. These distinctive feathers were examined by Dr. Kenneth C. Parkes as part of a review of avian natal downs. He states (Parkes and Clarke, ms.) that "their gross appearance in the day-old bird is rather thick and club-like. They are seen under magnification to consist of densely bundled, more or less parallel barbs and barbules, seemingly held together as if in an invisible sheath. Later this coherence of the barbs gives way, and the structure of the down feather can be seen. In two almost fully grown feathers of this species the downs are attached only to the tips of the two central barbs of the juvenal pennaceous feather. They appear under magnification like dense bundles of more-or-less parallel straws. There is no appearance of 'downiness,' fluffiness or laxity. Less than 10 individual barbs meet at the base of the down feather; the dense, almost bushy appearance is caused by long, relatively rigid, apparently somewhat twisted barbules of irregular thickness, lying almost parallel to the barbs." He also felt that these were "exceptions to the generalization that most prepennae have barbs whose tips are free of barbules."

The downs of *Glaucis hirsuta* were shorter than in those of most other hummingbirds, being only 1–2 mm long on the head and body with a few on the lower back as long as 3 mm. The mid-dorsal downs of *Archilochus colubris* measured

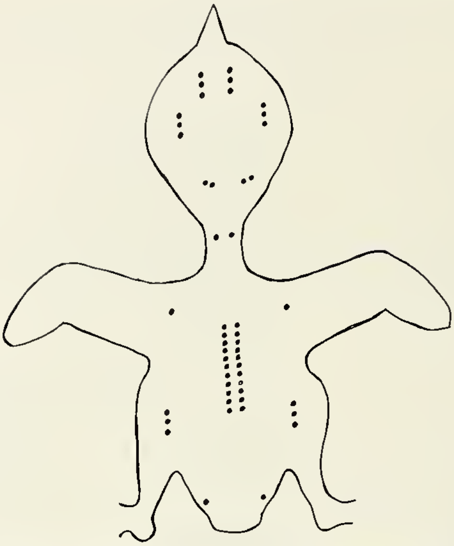

Fig. 2. Typical distribution of neossoptiles in *Glaucis hirsuta*. Each dot represents a single feather.

by Wetherbee (1958) were 4 mm long, and they appeared to be at least that long or longer in most of the other species I have examined.

None of the several suggested functions of natal downs (Wetherbee, 1957:353; Markus, 1970:13) offers any ready explanation for the unique natal pterylosis of *Glaucis hirsuta*. The natal pterylosis of relatively few of the many genera and species in this diverse family having been examined to date, there is always hope that future data on additional species may clarify the functional significance of the number and distribution of natal downs for nestling hummingbirds.

Comments on the Natal Pterylosis of the Apodiformes

Most currently used classifications place the hummingbirds (Trochilidae) in a distinct suborder, Trochili, within the Apodiformes. This order also includes the swifts (Apodidae) and the crested swifts (Hemiprocnidae) in the suborder Apodi

Table 2. Natal Pterylosis of *Glaucis hirsuta* (based on observations of 12 nestlings).

Tract	Number of downs present		
	Minimum	Typical	Maximum
Coronal	0	3	3
Orbital	1	3	6
Occipital	1	2	5
Cervical (Dorsal)	0	1	1
Scapular	1	1	2
Spinal	5	11	14
Femoral	0	3	8
Crural	0	0	1
Rectrix	1	1	5

Fig. 3. Developing contour feather of *Glaucis hirsuta* with attached neossoptile.

(Storer, 1971). The relationship of these groups, argued at great length by past workers, has been reviewed by Cohn (1968) who supported the ordinal separation of the hummingbirds from the swifts and crested swifts. Natal pterylosis adds little helpful information to this analysis. As noted above, all or nearly all hummingbirds have natal downs, but usually on only one tract. The crested swifts have natal downs on many tracts (Whistler, 1930; Collins, unpubl.) although no quantified data are presently available. All swifts in the Apodidae however, appear to lack natal downs entirely. I have verified the occurrence of naked nestlings for 18 species of swifts from eight genera in all three subfamilies. In all cases where downs or downy plumage has been described for nestling swifts it appears to be a part of the first teleoptile generation of feathers (Collins, 1963b, 1965, and unpubl.). Natal pterylosis thus seems taxonomically useful only at the intrafamilial level in the Apodiformes.

Acknowledgments

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A New Species of *Syllides* (Polychaeta: Syllidae) with Notes on *Amblyosyllis speciosa* Izuka from San Clemente Island, California

John H. Dorsey

Abstract.—A new species of *Syllides* is described and *Amblyosyllis speciosa* is recorded for the first time from California. Both species were taken from shallow rocky areas at San Clemente Island.

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During studies at San Clemente Island (Dorsey, 1975) two species of polychaetes belonging to family Syllidae were collected and determined to be either new or unreported from California. An undescribed species of *Syllides* and *Amblyosyllis speciosa* Izuka, 1912, were taken at Wilson Cove, San Clemente Island, where they were living within coralline algal mats (mostly *Lithotrix aspergillum* G. E. Gray) in which sand and shell debris had accumulated. Specimens of these species are deposited in the collections of the Allan Hancock Foundation, University of Southern California.

Amblyosyllis speciosa Izuka, 1912
Figures 1a–c

Amblyosyllis speciosa Izuka, 1912:183–184, pl. 20, fig. 1; Imajima and Hartman, 1964:106–108, pl. 23, figs. a–i; Imajima, 1966:86–88, text-fig. 27.
Amblyosyllis nigrolineata Okuda, 1934:317–320, text-figs. 1, 2.

Material examined.—Twenty-eight specimens from Wilson Cove, San Clemente Island, 1–4 m depth, among coralline algal debris and mats.

Remarks.—These specimens agree with the description given by Izuka (1912), Imajima and Hartman (1964) and Imajima (1966) as follows. The body has 16 segments, of which the first and last two are asetigerous (Fig. 1a). Nearly all segments are wider than long; the fifth and last two are square. The prostomium is subglobular with two pairs of lenticulated red eyes. A pair of nuchal appendages is inserted posteriorly on the prostomium and extends to setiger 2. The pharynx is armed with circlet of six pentacuspid teeth (Fig. 1b). Prostomial, peristomial and dorsal cirri are long, annulated. Ventral cirri are spindle-shaped and do not project beyond the parapodia. Parapodia are conical and extend laterally.

Setal fascicles have around eight composite bidentate falcigers. Appendages of superiormost setae are longer than inferiormost.

These specimens differ from previous descriptions as follows. Specimens from Wilson Cove are smaller in size than those described from Japan. The holotype (Izuka, 1912) measured 10.0 mm in length and 1.6 mm in width. Imajima (1966) found individuals up to 15.0 mm in length and 3.7 mm wide. The largest individual from Wilson Cove was a female with swimming setae and eggs which measured 4.8 mm long and 1.0 mm wide.

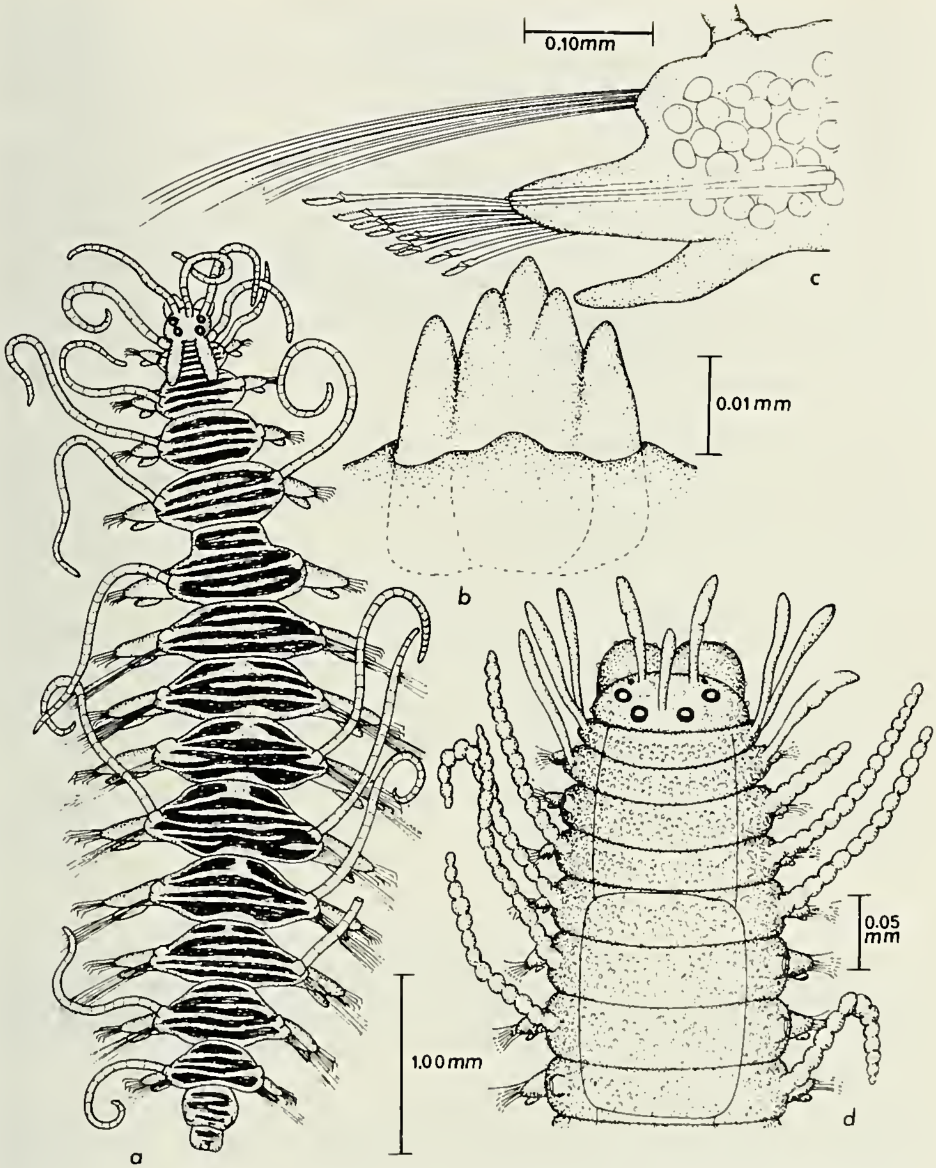

Fig. 1. a–c. *Amblyosyllis speciosa*: a. Entire specimen, dorsal view; b. Pentacuspid tooth; c. Parapodium 7 with swimming setae and oocytes, posterior view. d. Holotype, AHF POLY 1215, *Syllides reishi*, anterior end, dorsal view.

Wilson Cove specimens had four to six anastomosing dusky black transverse bands on the dorsum of each segment. The prostomium, ventral and dorsal cirri lack pigmentation. This color pattern differs from any of the five color patterns present in the Japanese material. All Japanese patterns consist of transverse bands.

The proventriculus extends from setigers 3 to 5 in the Wilson Cove specimens, but from setigers 5 to 6 in Japanese species.

Parapodia are supported by 4 acicula in Wilson Cove specimens, whereas in Japanese material acicula number 8 per parapodium. Parapodia of individuals with swimming setae (from Wilson Cove) have small notopodial lobes present on setigers 6 to 14 (Fig. 1c). This lobe and specialized setae are absent from immature specimens.

Wilson Cove specimens have been assigned to *A. speciosa* primarily due to the number and structure of pentacuspid teeth and the square shape of the fifth segment. Although the color pattern differs from Japanese material, this characteristic appears to be variable. Imajima (1966) demonstrated that dorsal coloration in *A. speciosa* changes from different areas, even within the same locality. Color variation on the specific level also occurs in other amblyosyllid species, as noted by Fauvel (1923) for *A. formosa*. Therefore, dorsal pigmentation patterns can be variable within these species and taxonomically should be used with caution.

This genus was first recorded from the west coast of North America by Berkeley (1923) who described *A. lineata alba* from Western Canada. Hartman (1944) placed several syllid fragments collected from Tomales Point, central California, in the genus *Pterosyllis* Claparède, 1863, but later (Hartman, 1961, 1968) decided that they approached *A. lineata alba*. Hartman (1968) made no mention of color patterns, but stated that the specimens possessed a pharynx armed with six bi- or tricuspid teeth. *Amblyosyllis lineata alba* lacks coloration (Berkeley, 1923) and has a pharynx armed with six tricuspid teeth (Berkeley and Berkeley, 1948). *Amblyosyllis speciosa* differs from *A. lineata alba* by the presence of a characteristic dorsal pigmentation and the possession of a distally armed pharynx with a circle of six pentacuspid teeth.

Distribution.—*Amblyosyllis speciosa* has been recorded from northern to southern Japan. This is the first report of this species on the west coast of North America.

Syllides reishi, n. sp.
Figures 1d, 2a–f

Material examined.—Wilson Cove, San Clemente Island, California, from collections made in February, June, December 1973; taken from coralline algal mats, intertidally to approximately 3 m depth; one holotype (A.H.F. POLY 1215) and nine paratypes (A.H.F. POLY 1216).

Diagnosis.—A *Syllides* species with papillated epidermis, composite setae with bidentate appendages which are serrated on the cutting margins, and shaft tips with minute teeth on cutting margins.

Description.—Holotype measures 1.8 mm long, 0.3 mm wide (without parapodia), 0.4 mm wide (with parapodia); 27 setigerous segments. Largest specimen 2.0 mm long, 0.4 mm wide (without parapodia); 30 setigers. Smallest specimen 1.4 mm long, 0.2 mm wide (without parapodia); 26 setigers. Body golden-brown with dark brown papillae; many dorsal cirri golden or yellow. Small, multi-lobed, irregularly shaped papillae distributed over entire body, except inter-segmental regions; more abundant dorsally than ventrally, sparse on prostomium, palps and parapodia. Prostomium oval when proboscis inverted; sub-pentagonal when everted. Holotype prostomium is 0.1 mm long and 0.2 mm wide (Fig. 1d). Two pairs reddish-brown eyes in trapezoidal arrangement; one pair small anterior

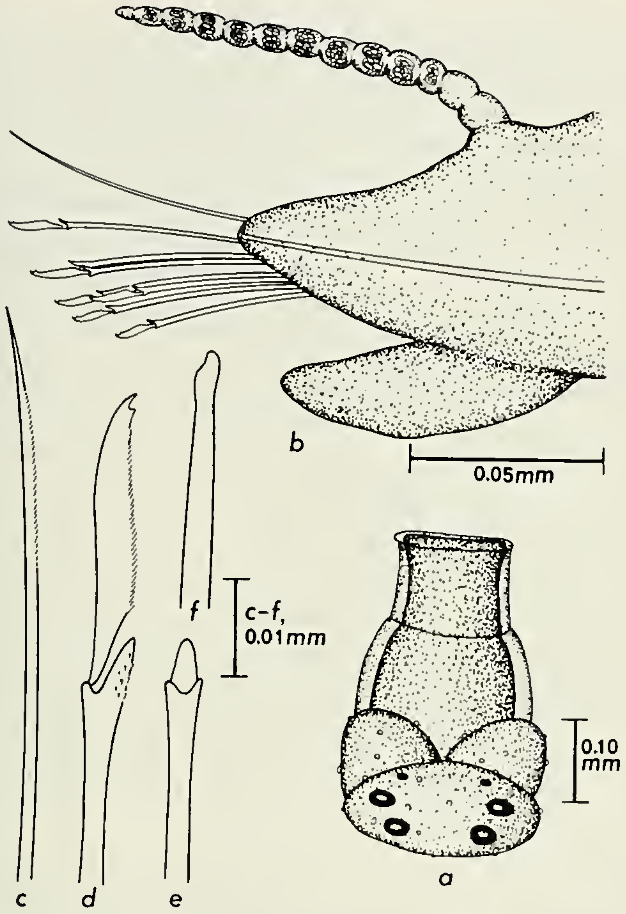

Fig. 2. a. Paratype, AHF POLY 1216, *Syllides reishi*, proboscis, dorsal view. b–f. Holotype, AHF POLY 1215, *Syllides reishi*: b. Parapodium 16, posterior view; c. Superior simple seta, parapodium 10; d. Composite seta, parapodium 10; e. Shaft of composite seta, rotated 90°; f. aciculum, parapodium 10.

ocular spots near anterior prostomial margin. Palpi twice wide as long, nearly long as prostomium. They are directed ventrally, basally fused. Prostomial antennae smooth, clavate. Median antenna arises between posterior eyes, approximately 1–1.5 times longer than the prostomium. Lateral antennae, inserted anteromedial to anterior pair of eyes; are nearly three times length of prostomium, twice length of median antenna. Pharynx (Fig. 2a) unarmed, lacks distal papillae, trepan or teeth. Proventriculus, inverted, extends through setigers 4 to 7. Two pairs tentacular cirri on peristomium; resembling prostomial antennae in shape, approximately 1.2 times as long. Parapodia short, conical (Fig. 2b). Parapodia of setiger 1 with dorsal cirrus distally inflated, wrinkled throughout. Dorsal cirri of remaining setigers strongly articulated; anterior cirri have 15–20 articles decreasing to around 10 articles in posterior parapodia. Golden-yellow color of dorsal cirri due to presence of one or two fluid-filled vesicles within each article (Fig.

2b). Distribution of vesicles irregular within cirrus; many cirri lack them. Ventral cirri short, non-articulated, conical, extend to tip of parapodia. Parapodial setal fascicles with one superior simple seta, six to nine inferior compound falcigers. Eight to 10 setae per anterior fascicle; three to five per fascicle posteriorly. Simple setae begin on setiger 1; slightly serrated along one edge (Fig. 2c). Compound setal appendages distally bifid, inconspicuously serrated cutting margin (Fig. 2d). Distal end of shaft has minutely rounded teeth; prongs of shaft far apart (Fig. 2e). Superior compound appendages two times longer than inferior ones. Acicula occur singly; enlarged tips (Fig. 2f). Pygidium with three equally sized spherical cirri.

Etymology.—This species is named after Donald J. Reish who first introduced me to polychaetes and greatly stimulated my interest.

Remarks.—Banse (1971) presented a key to all known species of *Syllides*. Only one species, *S. papillosa* Hartmann-Schroeder, 1960, possessed a papillated epithelium. This species has been recorded only from the Red Sea. *Syllides reishi* and *S. papillosa* are similar in that they are papillated and are yellowish-brown in color. Inspection of *S. papillosa* paratypes revealed several characters which distinguish these as separate species. Dorsal papillae are larger and regularly spaced in *S. papillosa*; they are smaller, more dense and irregularly distributed in *S. reishi*. *Syllides papillosa* has 10 pharyngeal papillae while *S. reishi* has none. The distal shaft of compound setae is distinctly serrated in *S. papillosa; S. reishi* possesses minutely rounded teeth which are almost indistinguishable, even at 1,000× magnification. Appendages of compound setae lack a serrated cutting margin in *S. papillosa*; they are minutely serrated in *S. reishi*.

Distribution.—All specimens of *S. reishi* were taken from Wilson Cove, San Clemente Island, California.

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I would like to thank Richard Rowe (Allan Hancock Foundation) who assisted with all field collections at San Clemente Island, and Dr. G. Hartmann-Schroeder for loan of *Syllides papillosa* paratypes. Marine Biological Consultants, Inc., kindly provided facilities and support during the initial part of this study. Most of all, I would like to especially thank Jerry D. Kudenov (Marine Pollution Studies Group, Ministry for Conservation, Victoria, Australia) and Donald J. Reish (California State University, Long Beach) for their advice, taxonomic discussions and criticism of the manuscript. I would like to thank the U.S. Navy Underseas Laboratory, San Diego, for providing transportation to and from San Clemente Island and use of facilities while on the island.

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Phycological Notes VIII.
Two Brown Algae (Phaeophyta) New to California

George J. Hollenberg

Abstract.—Two brown algae, *Cutleria cylindrica* Okamura and *Myriactula rivulariae* (Suhr in Areschoug) J. Feldmann from Santa Catalina Island are reported as new to California. Neither genus has been previously reported from the eastern north Pacific Ocean. Comparisons with related taxa are not wholly conclusive because of anomalous features shown by the California plants.

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Two species of brown algae, collected on Santa Catalina Island off southern California by Nancy L. Nicholson (recently of the Allan Hancock Foundation, University of Southern California) and given to me for identification and study, are both new to the eastern north Pacific Ocean. These collections, deposited in the Herbarium of the Allan Hancock Foundation, University of Southern California, Los Angeles, form the basis for the following note.

Cutleria cylindrica Okamura

Material.—Nicholson No. 1003, from rocks at a depth of approximately 3 m, Pebbly Beach, Avalon, Santa Catalina Island, 4 May 1973 (largest specimen shown in Fig. 1A).

Description.—California specimens erect from discoid holdfast; branches dichotomously branched with slender apices, 120–200 μm in diameter; growth in length trichothallic, involving meristematic activity at uniseriate base of numerous terminal, simple, colored filaments (Figs. 1B–D, 2C); filaments cylindrical, up to 1 mm long and 12–18–(20) μm in diameter, quickly becoming multiseriate by longitudinal divisions of cells (these filaments are soon shed); cells cut off from base of assimilatory filaments (branchlets) directly forming pseudoparenchymatous branch apex with cells more or less cuboidal, in distinct longitudinal rows (Fig. 2A); older branches with medullary cells cuboidal to slightly elongate (branches soon becoming fistulose); cells around small central cavity elongated parallel with cavity and relatively loosely associated; cortical cells progressively smaller outward; deciduous assimilatory branchlets soon partially replaced by numerous protuberant soral tufts of unbranched fertile filaments (Figs. 1A, 2B); sori not confluent, occurring from near base of plant to within 5–6 cm from branch apices; fertile filaments (Fig. 2D) 0.8–1.2 mm long, about 8 μm in diameter near base of unbranched fertile part, 12–15 μm in diameter in widest parts and attenuate to about 6 μm at rounded apex; cells of fertile filaments basically uniseriate (but some cells are divided longitudinally, and infrequently they are multiseriate throughout the sterile terminal part), mostly about one-half as long as diameter in sterile pigmented portion, but longer in less pigmented fertile region near base; fertile filaments bearing one to six plurangia (plurilocular reproductive structures) per filament (Fig. 2D); plurangia multiseriate, 98–120 μm long and 15–24 μm in diameter, cylindrical to slightly fusiform with about four longitudinal rows of

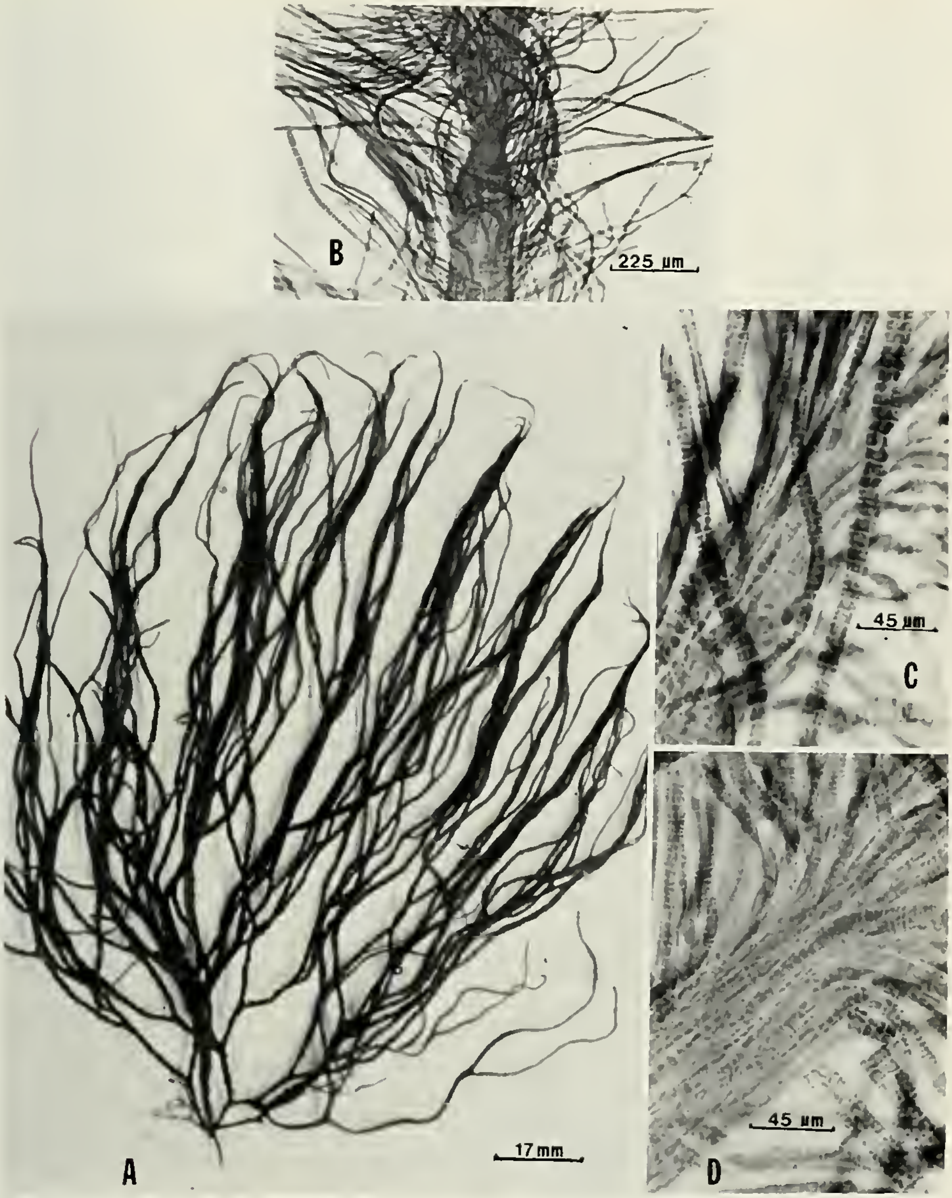

Fig. 1. *Cutleria cylindrica* Okamura from Santa Catalina Island: A. Photograph of large specimen taken underwater showing dichotomous branching and soral tufts (by Nancy L. Nicholson); B–D. Photomicrographs of branch apices showing central terminal assimilatory filaments in the meristematic region.

locules; plurangia borne on one to five-celled pedicels; unangia unknown; phaeophycean hairs absent.

Discussion.—The identity of the Santa Catalina specimens was much in doubt until Michael Wynne of the Department of Botany of the University of Michigan, suggested that they probably should be identified with *Cutleria cylindrica*. This species, illustrated and later originally described by Okamura (1900, pl. 28; 1936), has been reported from several localities in Japan but not elsewhere. Through the kindness of Professor M. Kurogi of Hokkaido University, I was able to examine in detail a specimen of *C. cylindrica* collected at Sagami Bay, Japan, by Yukio Yamada in May 1932. The Japanese specimen corresponded closely in most respects with the California algae, namely: 1) cylindrical branches with dichotomous branching, 2) apical growth by intercalary cell division at the base of a terminal tuft of initially uniseriate unbranched filaments, 3) the deciduous nature of the laterally oriented filaments, 4) the multiseriate mature parts of the assimilatory filaments, 5) plurangia developed on fertile filaments in surface tufts, and 6) the multiseriate nature of the plurangia, one to several arising at the base of the fertile filaments.

Okamura (1936) described the cells of the assimilatory filaments as being only "here and there divided by longitudinal walls," whereas all cells of the mature parts of the assimilatory filaments are longitudinally divided in the California alga. Okamura does not mention longitudinal divisions of the cells of the fertile filaments that are frequently present in the California alga. Also, judging by Okamura's (1900, pl. 28) figure, the fertile filaments of the Japanese alga are shorter than those of the California specimens. Despite these slight differences, I believe that the California alga should be identified with the Japanese species. However, certain features of this taxon raise questions concerning its placement in the Cutleriales.

The chief features justifying placing *C. cylindrica* in the Cutleriales seem to be as follows: (1) trichothallic growth by cell division at the base of unbranched colored filaments; (2) soral grouping of the fertile filaments and (3) multiseriate plurangia borne at the base of the fertile filaments. However all of these features are found in one or more genera in the Chordariales.

Features which seem to exclude *C. cylindrica* from the Cutleriales are: (1) the cylindrical nature of the branches; (2) the multiseriate assimilatory filaments and (3) the promptly deciduous nature of the assimilatory filaments. According to Fritsch (1945), the marginal assimilatory filaments of *Cutleria* are in two superimposed series; there is no suggestion of this feature in *C. cylindrica*.

Since the central axis of this alga is formed as a result of trichothallic growth near the uniseriate base of numerous terminal and subterminal assimilatory branchlets, it seems logical to consider the possibility that it is a member of the order Chordariales as characterized by Kylin (1940). The grouping of the fertile filaments in soral tufts is similar to that found in several genera of the Spermatochnaceae. However, in that family, phaeophycean hairs are present, and growth in length occurs by means of apical cells of the central filaments, whereas neither of these features are characteristic of the California alga. In the Chordaria-Group of the Chordariaceae (as delimited by Kylin, 1940), the central axis arises from

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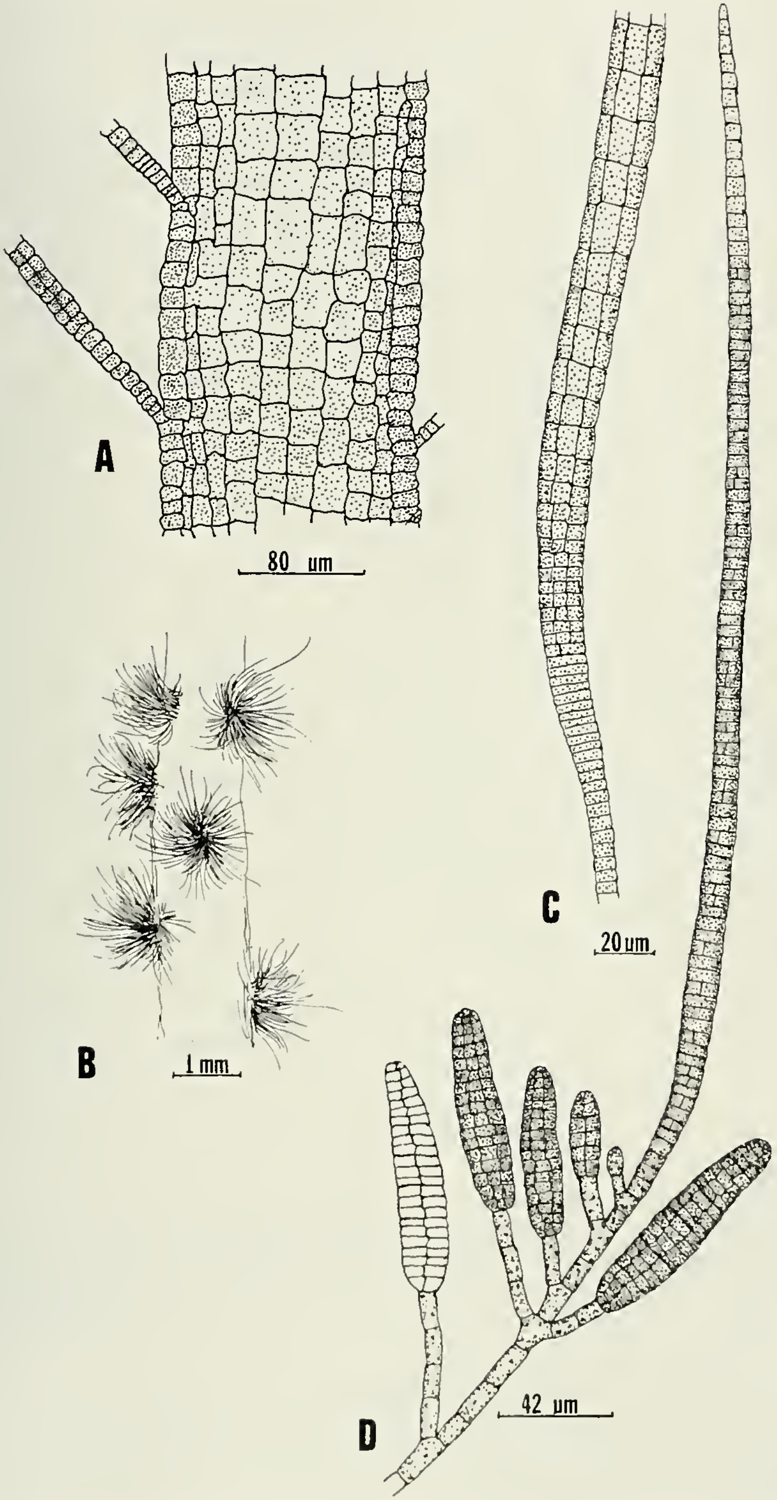
Fig. 2. *Cutleria cylindrica*: (fig. 2A) near median longitudinal section close to branch apex, showing longitudinal rows of cell derivatives of central assimilatory filaments; (Fig. 2B) sketch of portion of branch with soral tufts; (Fig. 2C) basal portion of an assimilatory filament, showing the uniseriate meristematic base and polysiphonous mature portion; (Fig. 2D) fertile filament with Durangia.


A
80 um
B
1 mm
C
20 um
D
42 um

intercalary growth at the base of unbranched central filaments, but phaeophycean hairs are present, and the assimilatory filaments are relatively short and uniseriate. Furthermore, in the Chordaria-Group, plurangia, as far as is known, arise by transformation of cells of the assimilatory filaments.

The Splachnidiaceae are represented by a single genus, *Splachnidium*, which is very different from the California alga: (1) although growth in *Splachnidium* occurs at the base of a group of apical filaments, the filaments are very short, uniseriate and branched, and end in numerous short clavate assimilators; (2) the cortex of *Splachnidium* is likewise very specialized, becoming uniquely cavernous and traversed by numerous branched hyphae; (3) unangia of *Splachnidium* arise in pitlike sori or conceptacles accompanied by numerous phaeophycean hairs. None of these features are characteristic of the California alga.

The California alga seems closer to the Myriogloia-Group of the Chordariaceae, as described by Kylin (1940). In that group, growth in length involves intercalary cell divisions near the base of numerous monopodial monosiphonous central filaments; descending rhizoidal filaments are not present in the cortex, and phaeophycean hairs are lacking (although the latter are present in other groups within the family). *Levringia* seems to be the only genus in the Myriogloia-Group that has multiseriate plurangia borne near the base of fertile filaments, similar to those of the California alga. (Levring, 1939, fig. 1d.)

The California alga differs from *Levringia* in the soral grouping of the fertile filaments of the former (Figs. 1A, 2B), and in certain features of these filaments, including the presence of frequent longitudinal divisions of the cells (Fig. 2D). Furthermore, the multiseriate nature of the main parts of the assimilatory filaments (Figs. 1C, D, 2C) is a very distinctive feature, unlike that of any previously described genus in the order Chordariales. Finally, rhizoidal filaments, present in *Levringia*, are lacking in the outer cortical layers of the California alga.

If placed in the Chordariales, the California alga appears to be most similar to *Myriogloia* as described by Kuckuck (1929) and Levring (1939). However, it differs from *Myriogloia* in a number of important respects: (1) the central filaments are unbranched and multiseriate in the California alga, whereas in *Myriogloia* they are branched and uniseriate; (2) in the California alga the central filaments appear fused below the meristematic zone (forming a pseudo-parenchyma [Fig. 2A] as described by Parke, 1933, for *Myriogloia* species), and are not readily separated by pressure as they are in the more gelatinous *Myriogloia* species; (3) assimilatory filaments (branchlets) are soon shed in the California alga, whereas in *Myriogloia* they form a more or less permanent covering over the branches; (4) unlike *Myriogloia*, plurangia arise in sori in the California alga; (5) rhizoidal filaments are absent in the outer cortex of the California alga, whereas numerous such filaments occur in the outer cortex of species of *Myriogloia*.

The chief, and perhaps the only feature which seems to exclude *C. cylindrica* from the Chordariales (as delimited by Kylin, 1940) is the multiseriate nature of mature parts of the assimilatory filaments. Other characteristic features of this alga are represented in one or more genera of the order as treated by Kylin. This raises a question concerning the statement by Kylin (1940) that true parenchyma never occurs in the Chordariales. Obviously, this is an area of study in which clarification is needed to better understand this poorly defined order. Culture studies of *Cutleria cylindrica* would probably help in determining the true relationship of this remarkable alga.

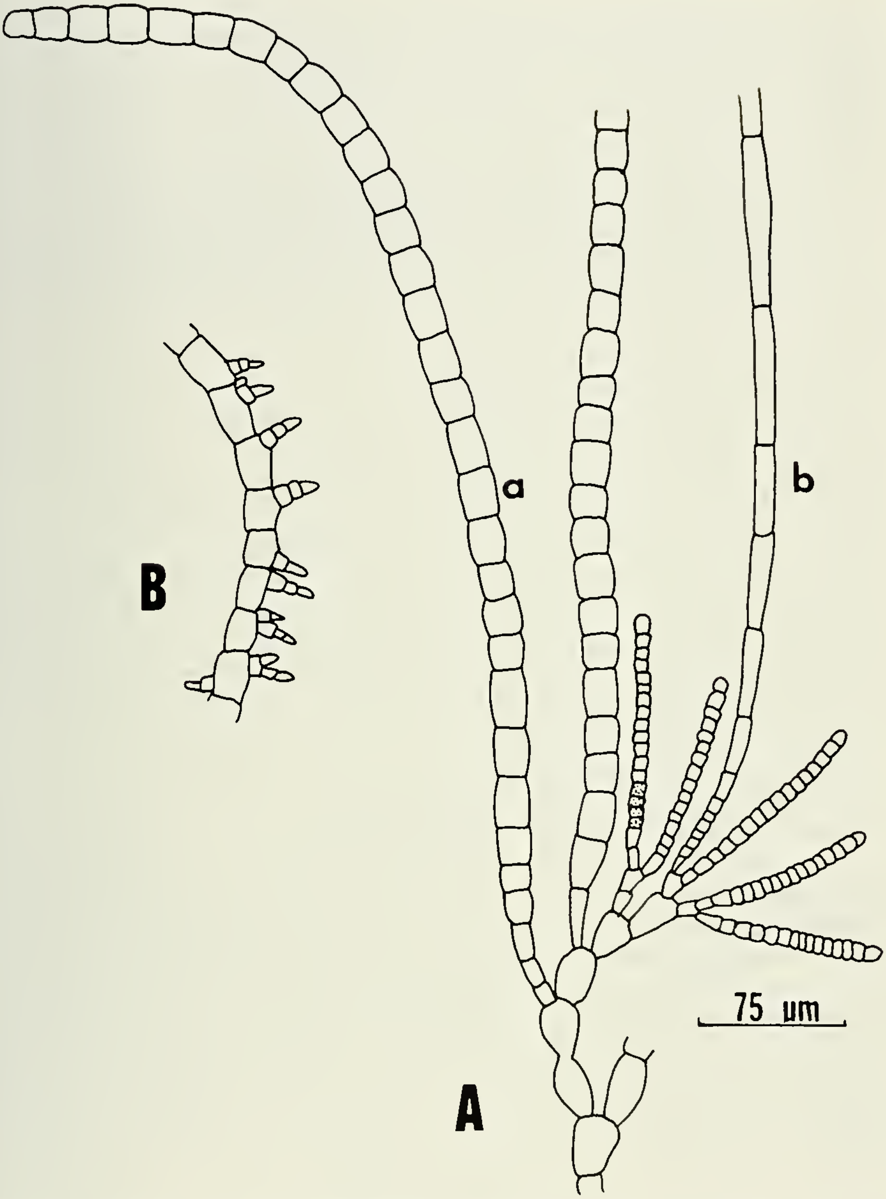


Fig. 3. *Myriactula rivulariae* (Suhr in Areschoug) J. Feldmann (?) from Santa Catalina Island: A. Assimilatory filaments and associated plurangia (a = assimilatory filament, b = colorless hair, presumed "paraphyses" not shown); B. Presumed plurangia borne laterally on apical portion of frequent assimilatory filaments.

Myriactula rivulariae (Suhr in Areschoug) J. Feldmann

Material.—Nicholson No. 900, a single collection of numerous thalli growing on *Sargassum palmeri* Grunow at Big Fisherman Cove, Santa Catalina Island, 5 April 1973.

Description.—This alga is a pulvinate partial endophyte, with basal cushion of irregular colorless cells penetrating host and bearing numerous free radiating assimilatory filaments (Fig. 3A,a), to 960 μm long and composed of up to 52 cells (mostly less than 40); filaments straight or somewhat curved, with abruptly narrowed base of relatively colorless cells, above which cells are pigmented; assimilatory filaments 14–18 μm in diameter, with cells about as long as diameter or slightly longer; filaments taper slightly toward rounded apex; similar but shorter and more slender pigmented filaments (which some authors designate as "paraphyses," not shown in Fig. 3) often present; colorless hairs (b) usually present; hairs considerably longer than assimilatory filaments, about 8 μm in diameter, composed of cells 3–6 times as long as wide; hairs may arise in place of plurangial branches or among pigmented filaments.

Plurangia uniseriate, very numerous, mostly 60–90 μm long, and composed of 10–15–(24) locules; plurangia arising in fasciculate clusters on short branching stalks from basal cushion; much shorter plurangia (?) (Fig. 3B) frequently arise separately as laterals on upper portions of assimilatory filaments (such structures are known for several species of *Myriactula*); unangia not observed.

At least 25 species of *Myriactula* have been described as epiphytes or endophytes, mostly on larger species of brown algae. A number of these are very poorly distinguished. The southern California specimens are tentatively identified with *M. rivulariae*. The southern California specimens differ from *M. rivulariae* in a number of respects, having longer assimilatory filaments, with mostly longer cells and relatively little upward tapering. Comparison with figures of *M. rivulariae* provided by Hamel (1935, fig. 31) indicate such differences.

Discussion.—*Myriactula johnstonii* and *M. marchantae* were described as *Gonodia johnstonii* and *G. marchantae*, respectively (Setchell and Gardner, 1924) from material collected in the Gulf of California. A portion of the type material of *M. johnstonii* was examined. The assimilatory filaments are much shorter than those of the California specimens. They are mostly less than 200 μm long and either clavate or distinctly tapering above the center. Plurangia are composed of usually less than 12 locules. As stated by Setchell and Gardner (1924), the apparent lack of hairs in these two algae raises a question as to their identity. In any case, they do not appear to be closely related to the southern California specimens.

More extensive study of the genus *Myriactula* is needed before the tentative assignment of the southern California specimens to *M. rivulariae* can be confirmed.

Acknowledgments

I am grateful to Isabella A. Abbott of Stanford University and Peter S. Dixon of the University of California at Irvine for valuable comments and suggestions concerning the manuscript and for loan of pertinent reference material. The assistance of Susan Manchester in preparation of the line drawings is also gratefully acknowledged. Photomicrographs were prepared with the assistance of Charles D. Howell of the University of Redlands.

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Accepted for Publication December 1, 1977.

ANNOUNCEMENT

The Joint Science Department of the Claremont Colleges has many incomplete sets of the *Pomona Journal of Zoology and Entomology*, including volumes 7, 8, 11, 13, 15, 29. These volumes include much work in the 1940's and earlier on marine and fresh water invertebrates and insects. These sets are being given away for the cost of mailing. Contact Professor Daniel A. Guthrie, Joint Science Department, Joint Science Building, 11th and Dartmouth Avenues, Claremont, Ca. 91711.

Bull. Southern California Acad. Sci.
77(1), 1978, pp. 36–39

Research Notes

A New Species of Chiton (Neoloricata: Ischnochitonidae) from the Galápagos Islands

A study of the chiton collections of the Allan Hancock Foundation (AHF), now in the care of the Los Angeles County Museum of Natural History (LACM), has resulted in the finding of an undescribed species of the family Ischnochitonidae from the Galápagos Islands.

Ischnochiton macleani, n. sp.
Figs. 1 and 2

Type material.—The holotype and 14 paratypes were collected at Tagus Cove (0°16′38″S, 91°22′44″W), Albemarle Island (Isla Isabela), Galápagos Islands, Ecuador, at a depth of 55 m, on rock and coral, on 13 January 1934 (AHF Station 147-34). The holotype, consisting of disarticulated valves, mounted girdle, and mounted radula, is deposited at the Natural History Museum of Los Angeles County (LACM-AHF 1853). Paratypes have been deposited at the California Academy of Sciences CASIZ Type Series 699, United States National Museum of Natural History (USNM 771232), American Museum of Natural History (AMNH 183856), Academy of Natural Sciences, Philadelphia (ANSP A7213), San Diego Natural History Museum (SDNH 69305), and the Los Angeles County Museum of Natural History (LACM-AHF 1854).

Color slides of the holotype and paratypes are filed in the California Academy of Sciences, Department of Invertebrate Zoology (CASIZ Color Slides Series 3335–3337).

Other material.—A single specimen of *Ischnochiton macleani* was collected at a depth of 91–128 m, on rock and shell bottom, between Albany and James Islands (0°10′45″S, 90°52′08″W), Galápagos Islands, Ecuador, on 24 January 1934 (AHF Station 183-34). The specimen, light brown in color, preserved in alcohol, is damaged; the posterior four valves are missing, and only fragments of the anterior valves are present. Nevertheless, the tegmental sculpture and girdle characteristics are sufficient to permit firm identification. Estimated length of the specimen is 4.5 mm.

Diagnosis.—Very small chitons, high arched, moderately carinated, light brown in color; end valves and lateral areas bearing well-formed, round tubercles; central areas with small granules, crowded together in the jugal areas, but, in the pleural areas, arranged in longitudinal ribs bent inwardly as they converge anteriorly; mucro anterior; sutural laminae sharp, semiquadrate, separated by a well-formed sinus; insertion teeth somewhat thickened at edges; slit formula of holotype 8-1-8; girdle covered with small, oval, striated, imbricated scales.

Description of holotype.—Oval in outline with high arch, moderately carinated; valves slightly beaked and mucronated; specimen, considerably curled, preserved in ethyl alcohol; estimated dimensions (including girdle) 5 mm in length, 3 mm in width, 1 mm in height; jugal angle about 90°.

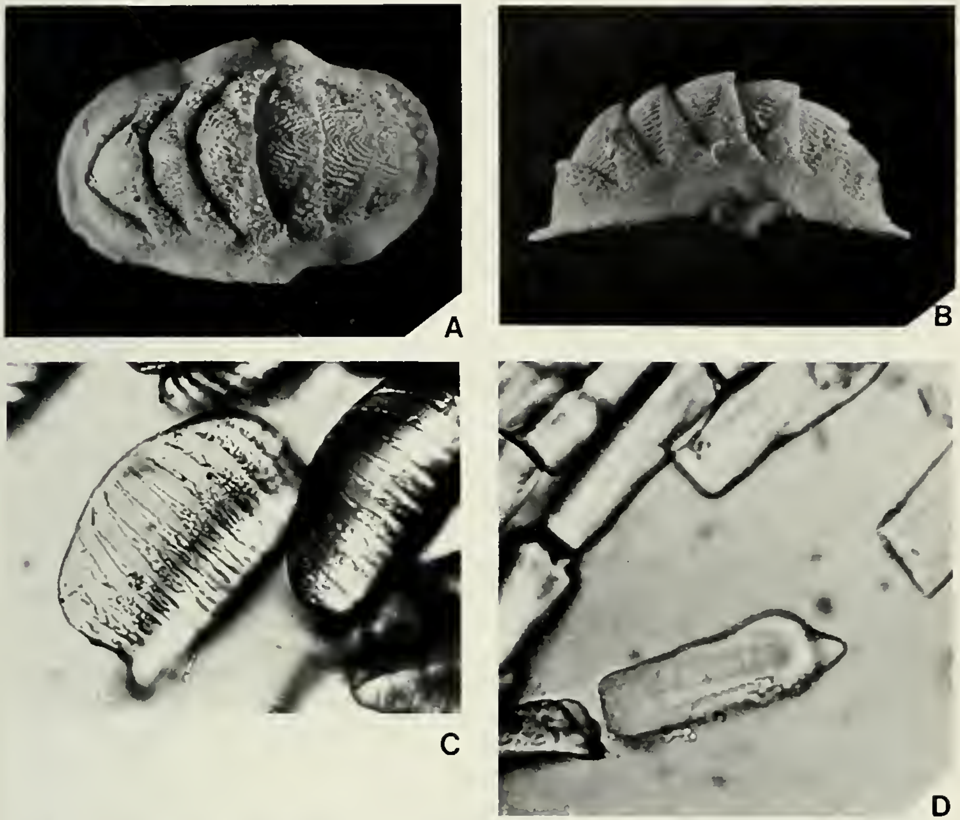

Fig. 1. *Ischnochiton macleani*, n. sp. A. Paratype, 6.2 mm long, LACM-AHF 1854, dorsal view; B. Same paratype, lateral view; C. Girdle scales of holotype, LACM-AHF 1853; D. Scales on underside of girdle of holotype.

Tegmentum a light brown color throughout; lateral areas of intermediate valves well-defined, but only moderately raised, bearing round tubercles, about 80 μm in diameter and height, which seem to be disposed in four or five radial series; tubercles separated by a distance greater than twice their diameter; spaces apparently left by dislodged, broken tubercles produce a seemingly disordered distribution of tubercles on lateral areas, in anterior valve, and in postmucro portion of posterior valve; central areas of intermediate valves covered with well-formed, round, somewhat flat-topped granules, measuring about 40 μm in diameter; in jugal areas, these granules are crowded mostly in quincunx, but in pleural areas are arranged in neatly defined longitudinal ribs, about 10 per side, which curve inwardly as they converge anteriorly; in posterior valve, mucro is discrete and definitely anterior; postmucro area is moderately concave.

Girdle lightly banded in two tones of brown, covered with imbricated, oval scales up to 100 μm in length, and with 8–10 well-cut striations (Fig. 1C); a fringe of fine spicules (about 15 μm in diameter) at outer margin of girdle, mostly short except for an occasional very long one (up to 300 μm); underside of girdle covered with very thin rectangular scales, 50 × 20 μm in size, many bearing a pointed mammilla pointing towards periphery (Fig. 1D).

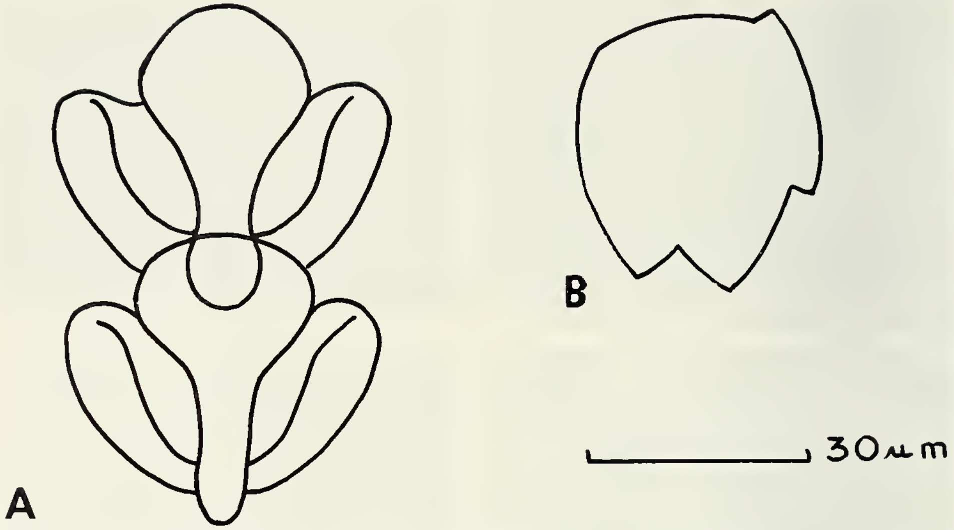

Fig. 2. *Ischnochiton macleani*, n. sp. Holotype. Radula: median, and first lateral teeth, and cusp of second (major) lateral tooth. (×1000).

Articulamentum white; sutural laminae sharp, short, subquadrate, separated by well-formed sinus; insertion teeth neatly cut, somewhat thickened at edges, and followed by slit-rays; slit formula 8-1-8.

Radula measures 1.90 mm in length and 0.35 mm in width, with 36 rows of mature teeth; median tooth (Fig. 2), wide anteriorly (30 μm), narrows medially (to 13 μm) but becomes somewhat globose at posterior end; first lateral tooth quadrangular with a thickened outer edge; second (major) lateral tooth has a tricuspid head on a thick (about 100 × 50 μm) shaft; marginal (outermost) teeth are slightly longer (45 μm) than wide (38 μm).

Remarks.—Judging from the observed specimens, *Ischnochiton macleani* does not show much variation in tegmental sculpture. Most specimens have no spiculose fringe, but that may be due to the fragility of the longer spicules. Color varies from a uniform light brown or tan to two tones of brown, with the darker brown tones usually in the pleural areas. Banding of the girdle is present in only eight of 16 specimens. All specimens are small, but apparently mature. The largest specimen (Figs. 1A, 1B) measures 6.2 mm in length, including the relatively wide (0.8 mm) girdle; the smallest specimen in the type lot measures 2.8 mm in length.

The tegmental sculpture of *Ischnochiton macleani* is remarkably similar to that found in members of the genus *Chaetopleura* Shuttleworth, 1853. However, the ischnoid articulamentum and the scaly girdle with no hairs or spicules (except for the marginal fringe) indicate that it belongs to the genus *Ischnochiton* Gray, 1847; the tegmental similarity to *Chaetopleura* may be regarded as an example of evolutionary convergence.

Ischnochiton macleani shows no obvious phylogenetic relationship to any one species of the genus. The lack of a sound subgeneric scheme in *Ischnochiton* (Ferreira, 1977) prohibits a subgeneric assignment at this time.

A recent list of chitons of the Galápagos Islands (Smith and Ferreira, 1977) included 11 species, of which seven (64%) appeared to be endemic. The finding of *Ischnochiton macleani* adds another probable endemic species to the list, raising the number of known chiton species in the Galápagos Islands to 12, of which eight (75%) can be considered endemic.

Etymology.—The new species is called *macleani* after Dr. James H. McLean, Curator of Malacology, Natural History Museum of Los Angeles County, who has generously contributed much of his time and knowledge to stimulate and encourage my interest in the study of chitons.

Acknowledgments

I wish to express my appreciation to Dr. James H. McLean, Curator of Malacology, Los Angeles County Museum of Natural History for trusting the chiton collection to my study, and for critically reading the manuscript.

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Bull. Southern California Acad. Sci.
77(1), 1978, pp. 40–43

A New Genus and Species of Capitellidae (Polychaeta) from California

A new genus and species of Capitellidae has been found off the coast of southern California. This genus differs from the other genera in the family by having 11 thoracic setigers and one abdominal setiger with capillary setae. In reference to the number of setigers bearing capillary setae, the new form may be known as:

Dodecaseta n. gen.

Diagnosis.—Thorax with 11 segments; peristomium asetigerous, following 11 segments bear capillary setae in both rami; first abdominal notopodium with capillary setae; neuropodium bearing all capillary setae, all rostrate uncini, or mixture of both; rest of abdominal setigers with rostrate uncini in both rami; abdominal branchiae present.

Dodecaseta most closely resembles *Notadasus* in the number of thoracic segments and setigers, but differs in having a biramous first thoracic setiger and capillary setae in the first abdominal segment. *Dodecaseta* differs from *Notamastus* in having capillary setae on the first abdominal segment. *Rashgua* lacks abdominal notouncini, and *Mastobranchus* has two setigers with mixed rostrate and capillary setae. *Dodecaseta* has 11 thoracic setigers; *Leiochrides* has 12. *Scyphoproctus* has 12 to 14 thoracic setigers, and has an asetigerous segment following the peristomium (Fauchald, 1977).

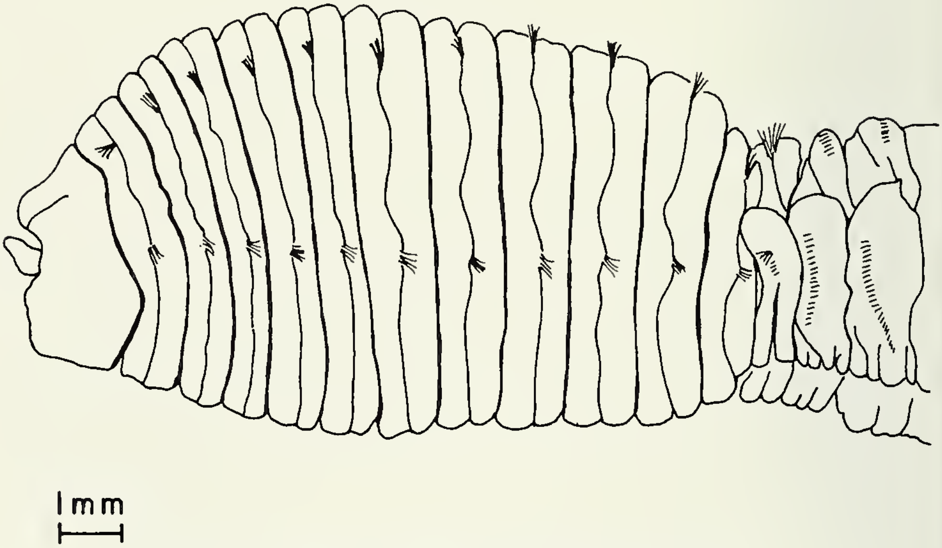

Fig. 1. Lateral view of anterior end. *Dodecaseta oraria*, n. sp.

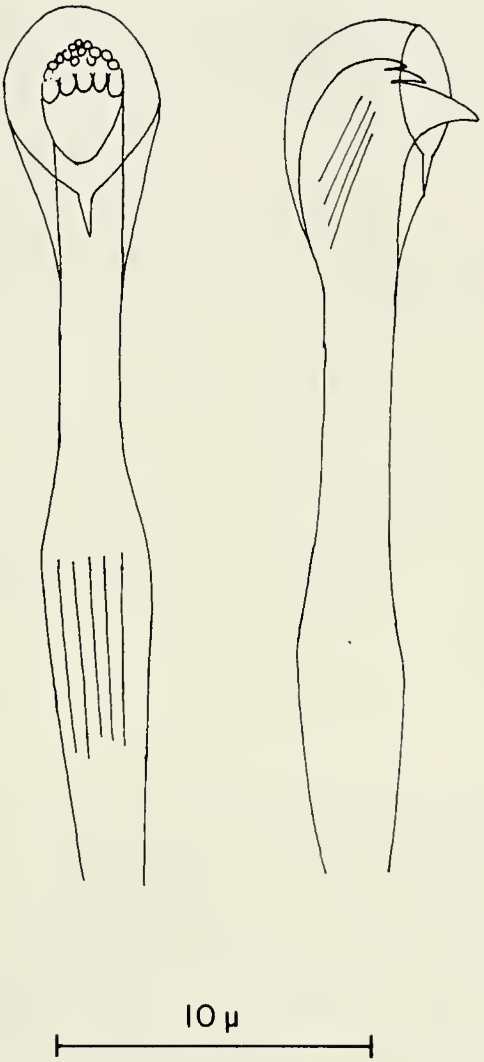

Fig. 2. Ventrolateral view of branchiate, posterior abdominal segments. *Dodecaseta oraria*, n. sp.

Dodecaseta oraria, n. sp.

Material examined.—Twelve specimens from 30 to 180 m off Palos Verdes, California. The holotype and two paratypes are deposited in the collections of the Allan Hancock Foundation.

Description of holotype.—Specimen incomplete with about 85 setigers, 15 mm long and 1.4 mm wide in anterior thoracic region; thoracic region smooth, segments closely biannulate (Fig. 1); anterior abdominal segments longer and annulation becoming less distinct posteriorly.

Triangular prostomium small with pair of faint, lateral eyes and short, digitate terminal palpode; prostomium almost concealed by collar-like peristomium; peristomium asetigerous, clearly separated from first setiger.

Fig. 3. Frontal and lateral views of abdominal hooded uncinus.

Thoracic setigers all biramous and strongly biannulate, with deep intrasegmental furrows from which pointed, bilimbate setae emerge; thorax blunt, broadest about setiger 5; setigers 10 and 11 tapering abruptly to narrow waist (Fig. 1).

First abdominal setiger biannulate, wider than last thoracic setiger; notopodial fascicle slightly more dorsal than thoracic notopodia; notosetae all pointed and bilimbate; neurosetae mixed, dorsal setae in fascicle bilimbate, ventral setae hooded rostrate uncini; each uncinus with slender subdistally expanded shaft; large fang surmounted by crest of four to five subapical teeth in a row, and about 10 small apical teeth in variable arrangement; hood short with smooth edge (Fig. 2).

Dorsal wall of median and posterior abdominal segments thin; gut contents readily visible; ventrum of each abdominal segment muscular, bearing large neuropodial torus on its posterio-lateral half; small notosetal fascicle seated on indistinct torus, separated from neuropodium by projecting nephridial pore; notopodia well separated medially; all abdominal setae rostrate uncini, except for first abdominal setiger.

Eversible branchiae complexly palmate, occurring in posterior abdominal setigers only; branchiae inserted at posterio-dorsal corners of neuropodial tori (Fig. 3).

The pygidium is missing from the holotype.

Remarks.—The first abdominal neuropodium of *D. oraria* may bear all capillary setae, all rostrate uncini, or a mixture of both. A single specimen bears capillary setae in the second abdominal notopodium also. The last thoracic capillary setae usually point posteriad, those of the first abdominal setiger usually are directed anteriad; the setae may meet or cross each other. Branchiae may be retractile, as they are often not observed or appear to be digitate.

Distribution.—*Dodecaseta oraria* has been collected in olive silts and sandy silts at depths of 30 to 180 m off the Palos Verdes Peninsula, Los Angeles, California.

Etymology.—The name *oraria* means belonging to the coast.

Acknowledgments

We are grateful for the assistance and encouragement provided by Kristian Fauchald of the Allan Hancock Foundation of the University of Southern California, Los Angeles.

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James A. McCammon and Janet K. Stull. *County Sanitation Districts of Los Angeles County, Whittier, California 90601.*

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It is strongly recommended that, before submitting a paper, the author ask qualified persons to review it. The author is requested to submit *at least one additional copy with the original*, on 8½ × 11 opaque, nonerasable paper, double spacing the entire manuscript. ***Do not break words at right-hand margin anywhere in the manuscript.*** Footnotes should be avoided. **Manuscripts which do not conform to the style of the BULLETIN will be returned to the author.**

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McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.

Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus*. J. Mamm., 54: 452–458.

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Research Notes

COVER: Sundew Leaf (*Drosera rotundifolia*) with tentacles extended, from Charles Darwin's *Insectivorous Plants*, 1875. Courtesy of Theodore W. Pietsch.

SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

BULLETIN

Volume 77 Number 2

BCAS-A77(2) 45–87 (1978) AUGUST 1978

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Date of this issue 30 November 1978

Bull. Southern California Acad. Sci.
77(2), 1978, pp. 45–51

Survivorship Patterns in Captive Killer Whales (*Orcinus orca*)

Clifford A. Hui and Sam H. Ridgway

Abstract.—Captive killer whales have an overall mortality rate of 4.7% per year. Females have a significantly higher (7.0%) rate than males (2.1%). Larger females have a shorter captive life span than the smaller females. The ability to cope with the psychological dislocation caused by capture may be greater in younger females. The captive state may also possibly reduce intrasexual stress normal to wild males. Less stressful capture procedures may possibly increase captive longevity.

Biosciences Department, Naval Ocean Systems Center, San Diego, California 92152.

Introduction

Killer whales (*Orcinus orca*) have been used as show animals in oceanaria only since 1965 (Bigg and Wolman, 1975). Since that time, over 30 animals have been captured for public display in North America. These institutions have served the public by increasing general awareness and knowledge of the animals and by providing opportunities for research that could not otherwise be conducted.

A total of 50 killer whales from the waters of the state of Washington and British Columbia have been placed in oceanaria around the world. Some of these whales went to facilities in Japan, Australia and Europe. We were not able to judge the standards of care in most of these places, but we know that the majority of the exported whales have died. Some whales which were placed in smaller North American oceanaria where the facilities were simply not adequate also have died. We know of 31 killer whales in North American oceanaria that have been kept under standards considered acceptable today. Such standards have been promulgated by the U.S. Marine Mammal Commission established by the Marine Mammal Protection Act of 1972 and are employed in issuing permits under the Act. The standards include minimum requirements for pool size, water quality, nutrition and health care.

A continuing question regarding captive animals, however, is whether or not captivity is more of a detriment to the animals than it is a benefit to the public. This examination of captive killer whale mortality was undertaken to describe the patterns of captive survival and compare them to information on natural populations of other odontocete cetaceans. In addition, we have compiled data on the disease conditions causing deaths in these extremely valuable display animals.

Materials and Methods

From inquiries sent to oceanaria where killer whales are kept, information was obtained on each animal's sex, date of capture or acquisition, length and weight at acquisition, date of death, length and weight at death or the nearest recorded figures as of May 1976, and cause of death. The data were tabulated and double-checked with telephone calls to the oceanaria, as well as to Mr. Bob Wright of Victoria, B.C., Canada, or Mr. Don Goldsberry of the Seattle Marine Aquarium, Seattle, Washington, who were associated with most of the killer whale captures and kept records of the capture and disposition of each whale.

The data available for this study are summarized in Table 1. Of these animals maintained at various oceanaria in North America starting in 1965, 19 were females, 12 were males. 14 of the 31 have died; 3 males and 11 females.

In standard life tables, annual mortality is calculated as the percent of the cohort at time t_0 which died during the ensuing year. The cohort at t_0 is the sum of the number of deaths plus the number of end-of-year survivors. The relationship is expressed in Eq. 1:

$$C_{t_0} = D + C_{t_1} \tag{1}$$

where C_{t_0} is the cohort of individuals at the beginning of the study period, D is the number of individuals that died during the study period, and C_{t_1} is the number of individuals alive at the end of one year.

The data for the present study cannot be adapted easily to Eq. (1) since the animals were acquired throughout a span of 12 years. Also, the small sample size would greatly amplify the effects of rounding off the dates to the nearest whole year. In order that the computations be compatible with standard life tables, the unit of "animal-year" was utilized.

An animal-year is here defined as one animal living in captivity for one year. By using the unit of an animal-year, fractions can be readily utilized. Animals collected in the middle of the calendar year would therefore account for ½ animal year in the calculations. The life table data can then be calculated using a slightly modified version of Eq. (1):

$$P_{t_0} = D - Y_{t_1} \tag{2}$$

where P_{t_0} is the total potential animal years, D is the mortality dividend which is the fraction of the year the deceased lived before it died, and Y_{t_1} is the sum of animal years credited from those surviving to time t_1. This equation is true even for animals which were collected and died within the same calendar year.

Mortality rates for each sex were calculated for each calendar year using

$$M = 100(D/P) \tag{3}$$

where M is the annual mortality in percent, D is the number of deaths, and P is as defined in Eq. (2). The annual mortality rate was also calculated for males and females combined.This computation was not a function of the rates for the individuals sexes but was the result of applying Eq. (2) to all the data for each year. The overall mortality for each sex and for both sexes combined was also determined by submitting the appropriate groups of data to Eq. (2).

The annual mortality rates between males and females were compared using the non-parametric Wilcoxon two-sample test (Sokal and Rohlf, 1969). This test compares two groups of values (annual mortality rates in this case) and estimates the probability that they were sampled from a single group. The mortality data 1969–1976 were used in this comparison since they all had P values greater than

Table 1. Captive killer whale data.

						At May 1976 or at Death		
	Sex	Date Acquired or Captured	Length (m)	Weight (kg)	Date Died	Length (m)	Weight (kg)	Diagnosis
1	♀	Oct 65	4.1		23 Aug 71			Pyometra-Septicemia
2	♀	Feb 67	4.3			5.8		
3	♂	Feb 67	2.9			5.3		
4	♂	Feb 67	4.1			6.1		
5	♂	Jul 67	4.3		22 Jul 69			Influenza
6	♂	Feb 68	4.0	900		6.8	4091	
7	♂	Mar 68	2.9			5.4		
8	♀	Apr 68	4.0		Dec 70	5.0		Mediastinal Abscess
9	♂	Apr 68	5.1			7.2		
10	♀	May 68	5.4		Jul 68			Stillbirth
11	♀	May 68	5.4	3182–3636		6.1		
12	♂	Oct 68	4.3			6.1		
13	♀	Dec 69	4.1		22 May 72	4.8		Pneumonia
14	♀	Dec 69	3.7			5.9		
15	♀	Dec 69	2.9		4 Aug 71			Salmonellosis
16	♀	Feb 67	3.1		16 Jun 71	4.4		Liver Necrosis & Pneumonia
17	♀	Dec 69	3.2	682		4.3	1364–1818	
18	♂	Dec 69	3.7	1136		4.9	1818–2727	
19	♀	Mar 70	3.5		21 Nov 72	4.3		Chediak-Higashi Syndrome
20	♀	Mar 70	4.1			6.1		
21	♀	Aug 70	4.3	909		5.9	2955	
22	♀	Aug 71	3.2	864	15 Jun 75	5.1		Uremia-Nephritis
23	♀	Aug 71	4.3			5.4		
24	♂	Nov 71	4.0	818		5.4	2045	
25	♂	Mar 72	2.9		1 Dec 74	4.2		Anemia & Fungus (*Candida*) Infection
26	♀	Aug 73	5.8		May 74	5.8		Ruptured Aorta
27	♂	Oct 73	5.9		29 Jan 74	5.9		Influenza
28	♀	Oct 73	5.4		16 Nov 73			Pneumonia
29	♀	Mar 73	4.8			5.6		
30	♀	Aug 75	3.8		Jun 76	3.9	1040	Perforated Post-Pyloric Ulcer
31	♂	Sep 75	4.3	1364		4.3		

5.00. The years with low potential animal years (see Eq. 2) would produce extreme and perhaps misleading mortality values.

In order to determine if there is a relationship between longevity in captivity and the size of an animal, the data for the females were examined. The eleven female deaths were divided into two groups according to size at sexual maturity (Jönsgard and Lyshoel, 1970): less than 4.9 m long, and equal to or greater than 4.9 m. These two groups were compared using the non-parametric Wilcoxon test. The male data were inadequate for this analysis.

Table 2. Captive killer whale mortality as calculated using Eqs. (2) and (3).

	MALES			FEMALES			
Year	Mortality Dividend	Potential Anim—Yrs	Mortality %	Mortality Dividend	Potential Anim—Yrs	Mortality %	Overall Mort. o + o
65		0.0		0	0.21	0.0	0.0
66		0.0			1.00	0.0	0.0
67	0	2.17	0.0	0	2.75	0.0	0.0
68	0	5.50	0.0	0.17	4.50	3.8	1.7
69	0.54	6.58	8.2	0	5.17	0.0	4.6
70	0	7.00	0.0	0.96	10.96	8.7	5.3
71	0	7.17	0.0	1.71	10.46	16.3	9.7
72	0	8.79	0.0	1.29	9.29	13.9	7.1
73	0	9.17	0.0	0.08	8.45	1.0	0.4
74	1.0	9.00	11.1	0.38	9.38	4.0	7.5
75	0	8.29	0.0	0.46	8.83	5.2	4.4
76	0	9.00	0.0	0.50	8.50	5.9	2.9
Summary	1.54	72.67	2.1*	5.55	79.50	7.0*	4.7**

* Computed by applying Eq. 3 to the Summary data.

** Computed by applying Eq. 3 to the Summary data for males and females combined.

Results

The morality rates are summarized in Table 2. The overall annual mortality for males was 2.1%, for females 7.0%, and for all the animals 4.7%. Male mortalities occurred in only two of the eight study years while female mortalities occurred in seven.

The female mortality was significantly ($P \leq .01$) higher than that of the males. The larger females also had a significantly ($P \leq .05$) shorter life span in captivity than the smaller females (see Figure 1).

Discussion

Three of the 11 females that died were diagnosed as having disorders that related to the urogenital system. One whale was apparently pregnant at capture and died after a stillbirth. Two of the three males were diagnosed as having influenza that resulted in death. To our knowledge, no viruses were isolated. Atherosclerosis has been reported from wild killer whales (Roberts *et al.*, 1965) and it is not surprising that one of the larger, and probably older, females died from a ruptured aorta associated with atherosclerotic lesions.

A "white" killer whale kept at a Canadian oceanarium was observed to have the faint ghost of the usual markings or body coloration which is seen in some species with Chediak-Higashi syndrome, an inherited autosomal recessive trait. A blood smear was taken and found to be positive for the syndrome (Taylor and Farrell, 1973). Humans and animals with this trait are highly susceptible to infection (Padgett *et al.*, 1968) and usually die at an early age. This whale died not long after the diagnosis. Although white whales might make attractive display specimens, any such animals should have blood smears examined for the presence of the disease.

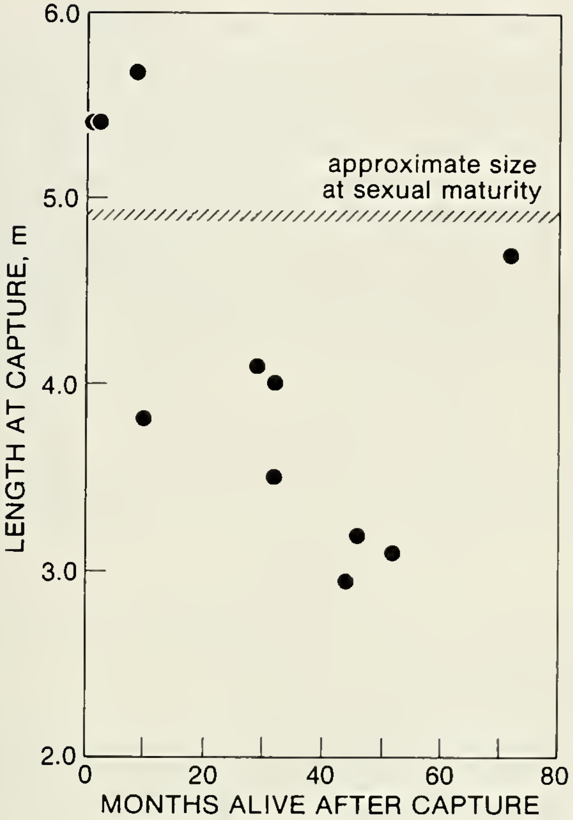

Fig. 1. General relationship between the length of female killer whales when captured and their captive longevity. Except for the unusually long post-captive life span of the 4.7 m animal, the trend is for smaller females to live longer after capture. The longest-lived female believed to be sexually mature did not live as long as the shortest-lived female believed to be sexually immature.

An accurate estimate of mortality for captive killer whales is difficult to obtain because of the small sample size. It has been only since 1965, when a netting technique to capture live specimens was developed (Bigg and Wolman, 1975), that maintaining captive killer whales has become a major interest of oceanaria. Also, the captive conditions, transportion, and maintenance and ages of the animals have varied. The results of this short study, therefore, must be considered to be only tentative.

The available data indicate that there is a significant difference in the susceptibility of females over males to terminal illness, resulting in a lower female survivorship. A disparity in mortality rates between sexes is indicated in wild populations of pilot whales also and is believed to be related to the uneven sex ratio in the population (Sergeant, 1962). Uneven sex ratios in wild stocks have been reported for *Stenella longirostris* (Perrin *et al.*, 1977) and *S. attenuata* (Perrin *et al.*, 1976). Although the sex ratio in killer whale stocks has not been determined, it does not seem unreasonable to expect an uneven relationship.

thereby suggesting an uneven mortality rate. It is possible that the captive animal mortality rate ratios reflect natural ratios.

The disparity in survivorship between larger and smaller females is probably related to factors of maturity. Examining data from males and females combined, Bigg and Wolman (1975) have concluded that the maturity of a killer whale is clearly related to its captive survival; the immature animals surviving longer. The analysis in the present study is more conservative but confirms their findings.

It is possible that survival in captivity is related to the psychological stress caused by the captive condition. Major illness episodes have been shown to occur after major life-change events in humans (Rahe *et al.*, 1967). This does not necessarily apply to other species. Younger animals are still experiencing many things for the first time; perhaps captivity is less traumatic for them than for the older animals.

No information is available on the maximum life span of killer whales. However, if the mortality rates derived in this study are assumed to represent mortality from all causes, the general range of the maximum expected life span can be calculated from:

$$S^x = B$$

$$\bar{x} = (\log B)/(\log S) \tag{4}$$

where S is the annual survivorship, x is the years, and B is the fraction of the original population surviving after x years.

The value of 0.10 was arbitrarily selected as the value for B, while the value for S was calculated as $1 - M$ for each sex and for both sexes combined. For an overall annual survivorship of 0.953, the expected maximum longevity is 47.8 years. The female survivorship of 0.930 indicates 31.7 years for maximum expected longevity. The high male survivorship of 0.979 produces an unreasonably high longevity of 108.5 years.

The female and combined-sex maximum expected longevity values are reasonably close to those for other cetacean species: *Delphinapterus leucas*, 26 years (Sergeant, 1973); *Globicephala melaena*, more than 22 years (Sergeant, 1962); and *Stenella caeruleoalba*, 40 years (Kasuya, 1976). The males, however, have an unreasonably large calculated longevity, partially accounted for by the small size and short time period of the data sample used in this study. However, the low mortality rate may possibly be related also to the easing of the normal intrasexual aggression and competition in the social hierarchies. Captivity for young males may actually reduce physical and psychological stress and result in a longer median life span. It is possible that removal of some young aggressive males may not be detrimental to the wild population.

Capture techniques and maintenance conditions may be major factors in maximizing longevity for captive animals. Collection techniques which minimize psychological dislocation and minimize the potential for physical injury have been used for collecting zoo animals which have set longevity records (Stott, 1977). Similar collection techniques can be adapted easily for coastal cetaceans such as *Orcinus* and *Tursiops*. However, these techniques require extensive prior knowlege of local populations and behavior so animals can be acclimated to special areas designed for collecting. This should greatly reduce stress when capture occurs. This type of collection requires a longer time over which investment capital must be expended before a return is realized. However, every aspect of collection (technique, number of animals, sex, size, time of year, general health, standing in the social hierarchy, etc.) could be monitored as prime candidates are selected from among all the acclimated animals.

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Sympatry in *Bufo boreas* and *Bufo canorus* and Additional Evidence of Natural Hybridization

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Abstract.—The second case of sympatry and hybridization between *Bufo boreas* and *B. canorus* in the Sierra Nevada Mountains is reported. The location of contact is Frog Lakes, a group of tarns at 3,170 m elevation in Mono County, California. Specimens of both species were collected in late summer of 1976. General appearance, amount of ventral pigmentation, and particularly measurements of parotoid gland width and of hind foot web length indicate that several of the specimens are actually hybrids.

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Both the Western toad, *Bufo boreas,* and the Yosemite toad, *B. canorus,* occur in the Sierra Nevada Mountains of California. *Bufo canorus* is seldom found below 2,134 m and occupies a strip of the central Sierra Nevada that generally experiences heavy snowfall. *Bufo boreas* is found throughout much of the western United States including many high altitude areas, but, in the Sierra Nevada, it is rarely found above 2,438 m and its range tends to encircle that of *B. canorus* (Karlstrom, 1962).

Although there are noticeable differences between these species in size, coloration, vocalizations, habitat preferences, and in eggs and larvae (Karlstrom and Livezey, 1955; Mullally, 1956; Savage and Schuierer, 1961), *B. canorus* probably evolved from *B. boreas* during the early Pleistocene (Stebbins, 1951; Karlstrom, 1958, 1962).

Despite their close phylogenetic relationship and proximity of distribution, secondary contact between these species is rare. Sympatry has been reported previously only in the northern Sierra Nevada at Upper Blue Lake, Alpine County (Karlstrom, 1958). No hybrids were found at this site. One possible natural hybrid was found in Alpine County (Mullally and Powell, 1958) but Karlstrom (1962) suggests that the specimen is an immature *B. boreas.* Karlstrom (1962) was able to cross *B. boreas* and *B. canorus* in the laboratory and rear about a dozen hybrid individuals through transformation.

Herein we report a second area of sympatry for *B. boreas* and *B. canorus* in the central Sierra Nevada and evidence for natural hybridization at that location.

While surveying central Sierran areas for *B. canorus* in 1976, we discovered a population of toads at Frog Lakes, Mono County. Frog Lakes is a cluster of three shallow tarns at 3,170 m elevation due west of Virginia Lakes, near the western boundary of northern Mono County. On our first visit through the area, 10 to 13 July, we toe-clipped and released 70 individuals at Frog Lakes, all were recorded as *B. canorus.* On 25 July Sokolski visited the area and collected a male *B. boreas.* Frog Lakes was visited again on 3, 9, and 23 August. Of 81 toads

Table 1. Collection site, sample size, sex distribution, and snout–vent length of toad specimens used in this report.

	Bufo boreas	*Bufo canorus*	Frog Lakes Specimens
County of Collection			
Alpine	13	7	0
Fresno	0	5	0
Inyo	9	2	0
Madera	0	8	0
Mono	12	13	29
Plumas	10	0	0
Tehama	1	0	0
Tulare	5	0	0
Tuolumne	1	2	0
Total Sample Size	51	37	29
Sex Distribution			
Males	28	24	21
Females	23	13	8
Snout–vent Length, mm			
Mean	79.9	52.2	57.1
S.D.	14.3	3.6	7.4
Range	48.0–111.4	45.5–58.8	47.5–79.0

gathered in August, 52 were marked and released and 29 were retained and preserved. The collected toads were subsequently catalogued into the Moore Laboratory of Zoology collection at Occidental College. Most of the August specimens resembled *B. canorus* from other study sites but several were noted to be like *B. boreas* or intermediate between *B. boreas* and *B. canorus* in appearance.

Frog Lakes specimens were compared eventually with known members of each species borrowed from the Museum of Vertebrate Zoology, University of California, Berkeley, and from the Los Angeles County Museum. The latter collection includes the specimen reported by Mullally and Powell (1958) as a possible hybrid (Table 1).

Eleven of the 29 Frog Lakes specimens were judged to be pigmented over 40% or more of the pelvic region. This was typical of the *B. boreas* we examined whereas *B. canorus* were unmarked or only lightly pigmented in this area. Analysis of color patterns for comparative purposes was difficult and inconclusive. Decisive information was provided by our measurements of parotoid gland width and of web length. Both were measured to nearest 0.1 mm with calipers. Web length was measured between the third and fourth toes of the left hind foot from proximal point of origin to distal margin midway between the toes.

A plot of ratios generated by dividing parotoid width and web length by snout-vent length separates *B. boreas* and *B. canorus* into two groups (Fig. 1). Measurements of the Frog Lakes toads scatter across and between the *B. boreas* and *B. canorus* groupings. This suggests that *B. boreas* as well as hybrids between *boreas* and *canorus* exist together at Frog Lakes. The specimen of Mullally and Powell (1958) is also a hybrid according to our criteria (see Fig. 1).

The existence of *B. boreas* at Frog Lakes is surprising since this location is

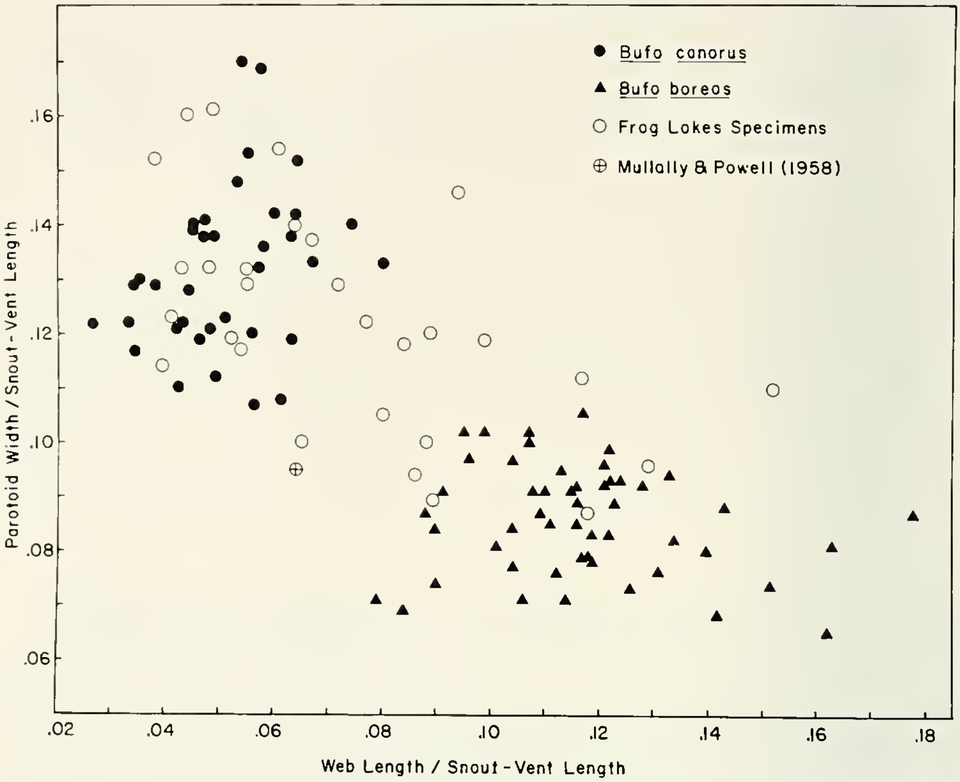

Fig. 1. Ratio of parotoid gland width/snout-vent length plotted against ratio of web length/snout-vent length in specimens of *Bufo* from museum collections (filled symbols) and from Frog Lakes, Mono County, California (open symbols).

about 610 m higher than this species usually occurs in the Sierra Nevada. Two factors may be mentioned that seem relevant to the occurrence of *B. boreas* at Frog Lakes. First, the area is at the head of a glaciated canyon with relatively smooth contours that is easily accessible from lower basins to the east. These basins are known to harbor breeding populations of *B. boreas*. Second, neither *B. boreas* nor hybrids were noticed at Frog Lakes until late July or August. It may be that these toads appeared only briefly in late summer to hydrate. Obviously the interactions of toads during the breeding season at Frog Lakes should be studied in the future.

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The genus *Calloplax* Thiele, 1909 (Mollusca: Polyplacophora) in the Americas

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Thiele (1909:19, 20) erected the genus *Calloplax* to accommodate the Caribbean species *Chiton janeirensis* Gray, 1828, on noticing that it did not belong in the genus *Chaetopleura* Shuttleworth, 1853, to which it had been assigned by Pilsbry (1892:37, 38). Until recently, *Calloplax* was regarded as a monotypic genus for which placement in the Family Chaetopleuridae, as suggested by the spicular girdle and *Chaetopleura*-like tegmental sculpture of *Calloplax janeirensis*, had been generally accepted (A. G. Smith, 1960:60–62). The realization that a Galapagan species, *Callistochiton duncanus* Dall, 1919, was also a member of *Calloplax* led to a better definition of the genus, and its likely allocation in the Family Callistoplacidae Pilsbry, 1893, instead (A. G. Smith & Ferreira, 1977:86, 87).

The study of two lots of *Callistochiton viviparus* Plate, 1902, collected in Chile by Dr. James H. McLean, Curator of Malacology, Natural History Museum of Los Angeles County (LACM), revealed that this species also belongs in the genus *Calloplax* for which membership in the Family Callistoplacidae is now established. Further understanding of the genus was obtained through the examination of other chiton material graciously made available by the British Museum (Natural History) (BMNH), the Museu Oceanográfico do Rio Grande, Brasil (MORG), and the California Academy of Sciences (CAS).

As presently understood, the genus *Calloplax* seems to be confined to American waters with three species known, *C. janeirensis* in the tropical Caribbean, *C. duncanus* in the Galápagos Islands, and *C. viviparus* in the warm-temperate region of Chile.

Class POLYPLACOPHORA de Blainville, 1816
Order NEOLORICATA Bergenhayn, 1955
Suborder Ischnochitonina Bergenhayn, 1930
Family Callistoplacidae Pilsbry, 1893

Family diagnosis.—Small to medium in size, with strongly sculptured tegmentum of heavy radial ribs on end valves and lateral areas of intermediate valves; insertion plates cut by teeth that tend to be thickened at the edges of slits and festooned at the free edges, and correspond in number and position to the radial ribs (A. G. Smith, 1960:59).

Genus *Calloplax* Thiele, 1909

Generic diagnosis.—Central areas sculptured with longitudinal riblets; mucro central, elevated, with convex, steeply sloping postmucro; girdle with spicules interspersed amidst small, striated scales.

Type species.—*Chiton janeirensis* Gray, 1828, by monotypy.

Fig. 1. *Calloplax janeirensis* (Gray, 1828), lectotype, Rio de Janeiro, Brazil (BMNH 197741). Length, 16.2 mm.

Fig. 2. *Calloplax viviparus* (Plate, 1902) [="*Chiton janeirensis* (var.?)" Gray, 1828], Valparaiso, Chile (BMNH 197742). Length, 13.2 mm.

Calloplax janeirensis (Gray, 1828)

Figures 1 and 3

Chiton janeirensis Gray, 1828:6 [reference is made, erroneously, to pl. 6, instead of plt. 3, both unpublished but on file at BMNH, *teste* A. Blake *in litt.*, May 16, 1977].

Calloplax janeirensis Thiele, 1909:19, pl. 2, figs. 57–65—Kaas, 1972:60–65, text figs. 117–123, pl. 4, figs. 1, 2 [with synonymy]—Rios, 1970:142; 1975:267, pl. 88, fig. 1288.

Type material.—Lectotype and paralectotype, BMNH 197741.

Type locality.—Rio de Janeiro, Brazil [22°54′S, 43°15′W]. Thanks to the courtesy of Aileen Blake, Mollusca Section, Department of Zoology, British Museum (Natural History), I had the opportunity of examining the type lot which consists of two specimens preserved dry and fully extended. Both specimens, light tan in color, are in fair condition and show indications of having been glued to cardboard. The larger specimen (Fig. 1), here designated as lectotype, measures 16.2 mm in length, 7.8 mm in width, including girdle. The smaller specimen, a paralectotype, measures 13.2 mm in length. The lectotype has 12 strong granose radial ribs on the anterior valve; the posterior valve has a central mucro, and 15 granose radial ribs in the postmucro area; the intermediate valves have well defined lateral areas with 3 or 4 coarsely granose radial ribs, and central areas with about 12 somewhat beaded longitudinal riblets per side, which tend to converge anteriorly and become obsolete at the jugum. The girdle features, obliterated by dust and decay, are difficult to ascertain except for the presence of small imbricated scales and the probable remnant of an occasional spicule. In all respects, the specimens correspond to the current interpretation of *Calloplax janeirensis*.

A second lot of "*Chiton janeirensis*" (BMNH 197742), contains a single specimen with the Museum label, "*Chiton janeirensis* Gray/Syntype/Reg. No. 197742/Valparaiso/1 spec."; a second label reads "Valparaiso/W. H. Hennah." and a third label, in pencil, adds faintly "*Chiton janeirensis* from Gray Spic. Zool./Blainville [?] Proc. Zool. Soc. 1832 [?] fig . . . 69 [?] *Callistochiton pulchellus*." From the evidence this seems to be the specimen referred to by Gray in Spicilegia

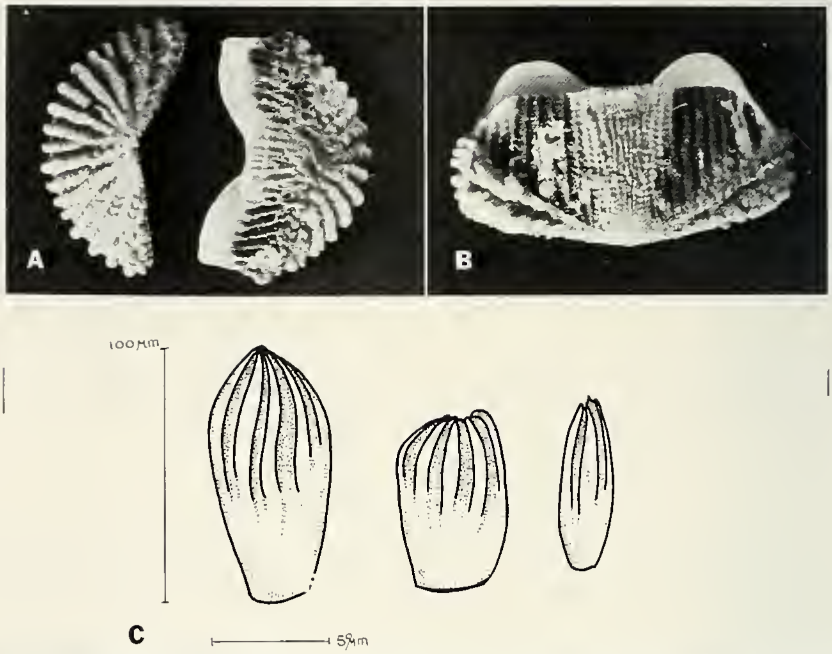

Fig. 3. *Calloplax janeirensis* (Gray, 1828), Virgin Gorda, British Virgin Islands (AJF 294). Disarticulated specimen, original length, 17.0 mm. *A*. Anterior and posterior valves. *B*. Intermediate valve. *C*. Girdle scales.

Zoologica (1828:6, sp. no. 9) as "Var.?" of "*Chiton janeirensis*," for which he had already admitted to be "probably a distinct species." My examination of the specimen revealed that it is, indeed, of a species different from the Caribbean *Calloplax janeirensis*: In fact, the specimen (Fig. 2) is conspecific with the later described *Callistochiton viviparus* Plate, 1902.

The Caribbean *Calloplax janeirensis* is discussed in detail and illustrated by Kaas (1972). It differs from the two other species of *Calloplax* in the Pacific not only in details of the tegmental sculpture (Fig. 3*A*, *B*), but in the girdle scales, which tend to be somewhat polymorphic with irregular and coarse striations (Fig. 3*C*), and in the spicules which tend to be longer in the specimens examined. An interesting feature of the species is the presence of very long (up to 200 μm) and closely packed spicules in the cuticular bridges that stand between the valves as tenuous continuations of the girdle. It is also worth noting that in *Calloplax janeirensis* the apices of the valves iv to vii are often turned upwards, as if "upswept," a feature first described in *Callistochiton elenensis* (Sowerby, 1832) by Thorpe (*in* Keen, 1971:875).

In size, *Calloplax janeirensis* rarely attains 2 cm; the largest specimen I have examined measures 20.8 mm in length (St. Thomas Bay, Virgin Gorda Is., British Virgin Islands, in 3–5 m, *leg*. A. J. Ferreira, May 10–13, 1976, AJF sta. 294). As reported in the literature (Kaas, 1972), *C. janeirensis* is present in most of the tropical Caribbean Province, having been collected from both coasts of Florida, Florida Keys to Dry Tortuga, Puerto Rico, Virgin Islands, San Martin, Saba, Dominica, Trinidad, and Brazil. In addition, I have collected the species in Ven-

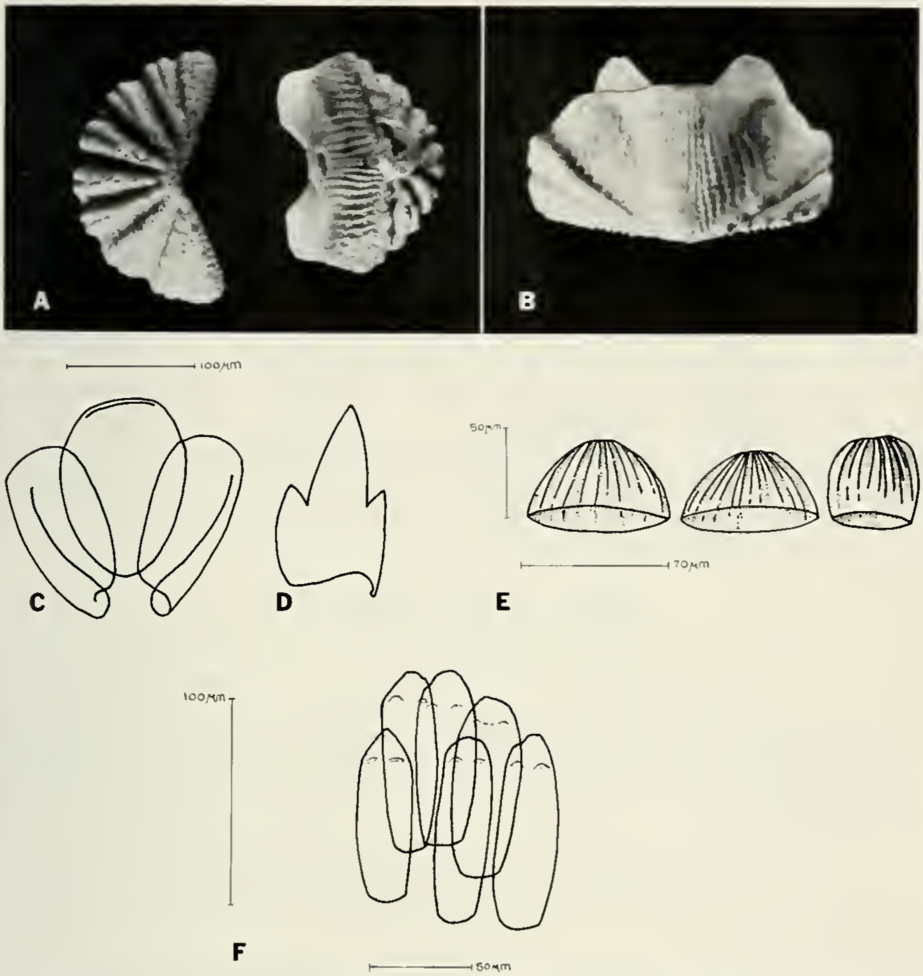

Fig. 4. *Calloplax duncanus* (Dall, 1919). Charles Island, Galápagos Archipelago, Ecuador (LACM-AHF 806-38). Disarticulated specimen, length, 12.0 mm. *A*. Anterior and posterior valves. *B*. Intermediate valve. *C*. Radula: median and first lateral teeth. *D*. Radula: head of second (major) lateral tooth. *E*. Girdle scales. *F*. Scales of the underside of girdle.

ezuela (at Puerto Mara, Quetepec, Guiria, Carupano, and Santa Fé, depth 1–5 m, August, 1977), and have examined specimens from Cozumel Is., Mexico (LACM 70-61), Bonita Springs, Florida (LACM 2114), and from the Brazilian coast at San Sebastião (MORG 17174), São Sebastião (MORG 18772), and Porto Belo, Santa Catarina (MORG 16529) [27°10′S, 48°39′W], its southernmost record.

Calloplax duncanus (Dall, 1919)
Figure 4

Callistochiton duncanus Dall, 1919:512–513—Thorpe *in* Keen, 1971:873
Calloplax duncanus A. G. Smith and Ferreira, 1977:86–87, figs. 8–9.

Type material.—Holotype, USNM 218772.

Type locality.—Duncan Island (Isla Pinzón) Galápagos Islands, Ecuador [0°35′ S, 90°40′W].

Endemic to the Galápagos Islands, *Calloplax duncanus* hardly attains 13 mm in length; the largest specimen I have examined is 13.3 mm long. A specimen of *C. duncanus* (LACM AHF 806-38: Charles Island, Galápagos Islands, Ecuador), 12.0 mm in length (Fig. 4*A*, *B*), was disarticulated: Slit formula 7-1-8. The radula measures 4.2 mm in length, i.e. 35% of the length of the specimen, and 0.8 mm in width; it has 40 rows of mature teeth. The median tooth (Fig. 4*C*) is oval shaped and it bears a thin blade on its anterior end that measures about 90 μm in width; the major lateral teeth are tricuspid (Fig. 4*D*) the head measuring about 90 μm in width, and 120 μm in the length of the middle (longest) cusp. The outer-marginal teeth measure 100 μm in length, and 50 μm in width. The girdle scales (Fig. 4*E*) are closely packed, somewhat conical, about 65 μm in length, and 50 μm in height, with some 8 to 10 coarse striations that tend to converge at the apex. Spicules, interspersed throughout the girdle, are easily rubbed off, and measure up to 100 μm in length. The underside of the girdle is paved with rectangular scales (Fig. 4*F*) measuring about 60 × 25 μm, often vaguely striated and ending in a point directed outwardly.

Calloplax viviparus (Plate, 1902)
Figures 2 and 5

Callistochiton viviparus Plate, 1902:154–163, pl. 9, figs. 267–281—Dall, 1909:246—Gigoux, 1934:281—Boudet, 1945:134—Leloup, 1956: 46—Stuardo, 1959:144, 146—A. G. Smith, 1966:436, 437, 441, 442.

"*Chiton janeirensis*, Var.?" Gray, 1828:6—Sowerby, 1840:6, sp. no. 78 (spelled "*janierensis*").

"*Callistochiton pulchellus* Gray, 1828," d'Orbigny, 1841:489; 1854:55.

Type material.—Syntypes, one dried specimen and one set of plates, Zoologisches Museum, Humboldt University, Berlin (Dr. R. Kilias, *in litt*., 6 Sept., 1978.)

Type locality.—Isla Pacharos, near Coquimbo, Chile [29°58′S, 71°21′W].

Plate's excellent description and illustrations (1902) left no doubt of the validity of the species. Yet, until now, no further collection record has been cited in the literature. Dall (1909), Gigoux (1934), Boudet (1945), and Stuardo (1959) listed but did not collect or examine the species. Leloup (1956) found no specimens of *Callistochiton viviparus* in the abundant chiton material collected by the Lund University Chile Expedition, 1948–1949. Marincovich (1973) in a report on intertidal mollusks collected at Iquique, Chile, found no representatives of the species. Thus, it was with surprise and excitement that I recognized the species in the specimen described by Gray (1828) as "*Callistochiton janeirensis*, Var.?" from Valparaiso, Chile [33°02′S, 71°38′W] (BMNH 197742), and in two lots of chitons collected in Chile by Dr. James H. McLean, who generously entrusted them to me for study.

Gray's single specimen from Valparaiso (Fig. 2) is dry, fully extended, fairly well preserved, light tan in color, and measures 13.2 mm in length and 6.2 mm in width, including girdle. The soft parts had been removed, revealing a white articulamentum. The anterior valve has 9 strong, well-defined radial ribs. The posterior valve is elevated at the central mucro, and has a steeply convex postmucro area with 9 well defined radial ribs. The intermediate valves have clearly

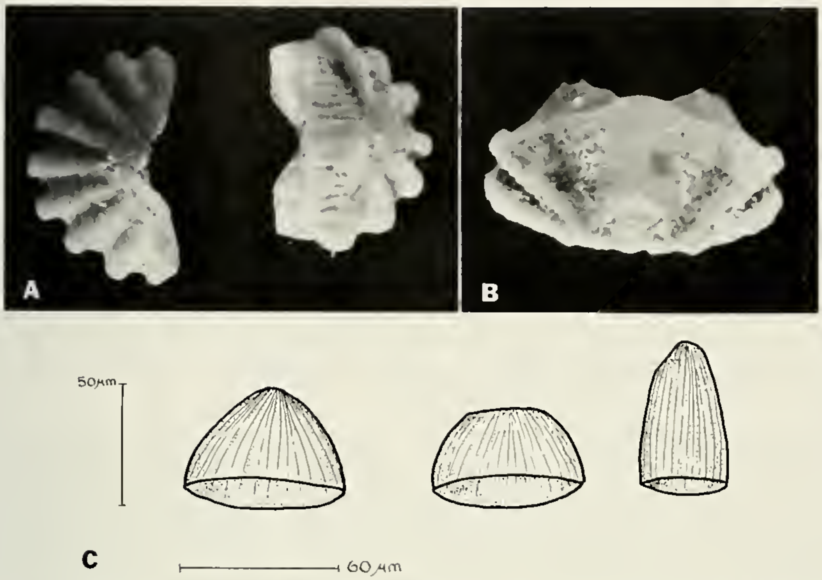

Fig. 5. *Calloplax viviparus* (Plate, 1902), Antofagasta, Chile (LACM 75-17). Disarticulated specimen, length ca. 8 mm. *A*. Anterior and posterior valves. *B*. Intermediate valve. *C*. Girdle scales.

defined lateral areas with two strong radial ribs; the central areas have about 8 longitudinal riblets per side, well marked in the pleural areas but becoming obsolete at the jugum. The riblets tend to converge anteriorly and are not latticed. The girdle is covered with very small scales, the features (? striations) of which are unclear; occasional spicules are seen interspersed among the scales. Gray's specimen conforms well to Plate's description and illustrations of *Callistochiton viviparus*.

The two lots of chitons collected in Chile by Dr. J. H. McLean, mentioned above, were also found to be conspecific with *C. viviparus*. The first lot (LACM 75-10; "Intertidal, Pozo Toyo (S of Iquique), Tarapaca Prov., Chile (20°25′S, 70°10.5′W), *leg*. J. H. McLean, sta. 1, 29 Sept., 1 Oct., 1975") consists of a single specimen, preserved in alcohol, discovered in a lot of 26 specimens of *Callistochiton pulchellus* (Gray, 1828) [not "*Callistochiton pulchellus*" of Pilsbry and other authors =*Callistochiton periconis* Dall, [1908], which it greatly resembles in color, size, and shape. The specimen measures 6.8 mm in length; it has 11 radial ribs in the anterior valve, and 8 in the posterior valve. The girdle shows a conspicuous fringe of spicules in addition to occasional spicules amidst the girdle scales.

The second lot (LACM 75-17: "Intertidal, mainland E of Isla Santa Maria, N of Antofagasta, Antofagasta Prov., Chile (23°25′S, 70°36′W), *leg*. J. H. McLean & Jorge Tomicic, sta. 8, 7 Oct., 1975"), also in alcohol, consists of 16 specimens preserved fully extended. In length, including girdle, the largest of the specimens measures 14.3 mm, the smallest 6.5 mm; six other specimens measure over 10 mm. All specimens are a uniform yellowish cream in color; large specimens tend to be somewhat eroded and encrusted. Tegmental sculpture (Fig. 5*A*, *B*) as described by Plate (1902); longitudinal riblets in the central area become obsolete at the jugum which is mostly smooth; articulamentum white. Slit formula 7-1-10;

insertion teeth *Callistochiton*-like, with festooned free edges, thickened at the slits which correspond in number and position with the radial ribs of the tegmentum. The girdle scales are close packed, with occasional interspersed fine spicules; the scales are mostly conical, about 55 μm in diameter, and 45 μm in height.

As in *Calloplax duncanus*, the scales are striated, only here the striations are much finer, more clear-cut, and number about 20 per scale (Fig. 5*C*). The radula (of a specimen 8.0 mm long) measures 3.0 mm in length, i.e. 38% of the length of the specimen, and has 45 rows of mature teeth. The radular median tooth is oval shaped, with maximum width of 65 μm at its middle; anteriorly, it bears a blade about 45 μm wide. The major (second lateral) tooth has a tricuspid head, with the middle cusp longer than the others; the cusps, in the specimens examined, seem to be slightly more deeply cut than in *C. duncanus*. The outer-marginal teeth measure about 70 × 35 μm.

Calloplax viviparus is rather similar to *C. duncanus* in size, color, articulamentum, and tegmental sculpture. The two species are unquestionably very closely related. However, *C. viviparus* differs from *C. duncanus* in some consistent features: (1) a rounded back (which is very definitely subcarinated in *C. duncanus*), (2) the sculptureless jugum and adjacent central area with fewer longitudinal riblets confined to the pleural areas, (3) the absence of latticing between the longitudinal riblets (latticing often present, even conspicuous, in *C. duncanus*), and (4) girdle scales with much finer and more numerous striations. Also, *C. duncanus* show radial ribs with a tendency to bifurcate towards the margin of the valve, a feature not seen in *C. viviparus*.

At the present, *Calloplax viviparus* is known only from four localities, the intertidal zone of Valparaiso, Isla Pacharo (Coquimbo), Antofagasta, and Iquique, that is between the parallels 20° and 33°S.

Discussion

The presence of *Calloplax* on both sides of the South American continent reveals that the genus predated the separation of the Pacific and Atlantic oceans by the emergence of the isthmus of Panama in the mid-Pliocene. The geographically isolated populations are still similar enough to have led Gray (1828), faced with specimens of what are now known as *Calloplax janeirensis* and *C. viviparus*, into believing he might have been dealing with a single species. However, it is easy to see, now, that *C. janeirensis* differs from *C. viviparus* and *C. duncanus* by several important characters: (1) much larger size, (2) greater number of radial ribs in anterior and posterior valves, (3) the frequent presence of more than 2 radial ribs in the lateral areas of the intermediate valves, (4) the much more granose appearance of the radial ribs, and (5) the granular, often beaded appearance of the longitudinal riblets in the central areas (also seen, but not so distinctly, in *C. duncanus*), which induced early authors into assigning the species to the genus *Chaetopleura*. Also, the girdle scales in *C. janeirensis*, well illustrated by Kaas (1972), are irregular in shape, from flat to elongated or spicular, bearing 6–8 coarse striations, and without the conical appearance usually seen in the girdle scales of *C. viviparus* and *C. duncanus*.

As illustrated here, the radula (Figs. 4*C*, *D*) and the scales that pave the underside of the girdle (Fig. 4*F*) in *Calloplax duncanus* appear identical to

Table 1. Comparison of meristic characters in the three known species of the genus *Calloplax* Thiele, 1909.

				Radula					
							radular teeth		
	Specm. length mm	Slits formula	Girdle scales length × height μm	length		rows no.	median length × width μm	major lat. blade length × width μm	outer marginal length × width μm
				μm	%				
C. janeirensis	17.0	7-1-11	45 × 90	6.5	38	40	130 × 100	110 × 100	130 × 75
C. viviparus	8.0	7-1-10	55 × 45	3.0	37	45	75 × 65	55 × 40	70 × 35
C. duncanus	12.0	7-1-8	65 × 50	4.2	35	40	125 × 100	120 × 90	100 × 50

those of *C. viviparus* and *C. janeirensis*. Other characteristics of the three species of *Calloplax* are compared in Table 1.

The close relationship between the genera *Calloplax* and *Callistochiton* seems unquestionable. The general characteristics of the valves, both in tegmenta and articulamenta, are very similar in the two genera. However, the two groups are distinct enough in their girdle elements—oval, strongly imbricated scales covering the girdle of *Callistochiton;* conical to elongated, only loosely imbricated scales, together with interspersed spicules in *Calloplax*—to warrant their separation into two genera. The separation is further supported by radular distinctions, particularly the rather wide, oval shaped median tooth, and the elongated (twice as long as wide) outer marginal teeth, uncommon in *Callistochiton*, but found in all three species of *Calloplax*.

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I would like to thank Aileen Blake, Mollusca Section, Department of Zoology, British Museum (Natural History); Dr. R. Kilias, Zoologisches Museum, Humboldt University, Berlin; Dr. Eliézer de Carvalho Rios, Director, Museu Oceanográfico de Rio Grande, Rio Grande do Sul, Brazil; Dr. James H. McLean, Curator of Malacology, Natural History Museum of Los Angeles County, California; Dr. Peter U. Rodda, Chairman and Curator, Department of Geology, and Dr. Welton L. Lee, Chairman and Curator, and Dustin Chivers, Senior Scientific Assistant, Department of Invertebrate Zoology, California Academy of Sciences, San Francisco, who made their collections and other information generously available to me. I am particularly thankful to Barry Roth, Curatorial Assistant, Geology Department, California Academy of Sciences, for his most valuable help in several phases of this work, and in the critical reading of the manuscript.

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On the Taxonomic Affinities of *Collisella edmitchelli* (Lipps) (Gastropoda: Acmaeidae) a Late Pleistocene Limpet from San Nicolas Island, California

David R. Lindberg

Abstract.—The taxonomic affinities between the extinct acmaeid *Collisella edmitchelli* (Lipps, 1966) and Recent California species has been previously studied using highly variable exterior shell characters. I use shell structure, a character I believe to be more conservative than either shell or radular morphology, to determine the taxonomic and phylogenetic relationships of this species. The shell structure of *C. edmitchelli* is identical to that of *C. scabra* (Gould, 1846). This shell structure group is not known to occur in any other acmaeid species. Although closely related to *C. scabra*, *C. edmitchelli* is morphologically distinct and is retained as a valid, extinct species known only from Late Pleistocene deposits on San Nicolas Island, California.

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Collisella edmitchelli (Lipps, 1966) is an extinct acmaeid limpet from late Pleistocene deposits on San Nicolas Island, California (33°16′N, 119°30′W). It was originally described as *Acmaea mitchelli* Lipps, 1963, but renamed because the name was preoccupied by *Acmaea striata mitchelli* Oldroyd, 1933. Taxonomic affinities between *C. edmitchelli* and Recent California species have been questioned several times. Lipps (1963) considered *C. edmitchelli* to be closely related to *Collisella limatula* (Carpenter, 1864) based on similarity of shell sculpture, including the presence of imbricated primary and secondary ribbing. McLean (1966) considered *C. edmitchelli* to be only superficially similar to other California acmaeids, based on shell morphology. He compared the ribbing of *C. edmitchelli* to the Japanese species *Collisella dorsuosa* (Gould, 1859) and noted the similarity in width of the interior margin to that of *Collisella scabra* (Gould, 1846). More recently, Marincovich (1976) has used shell sculpture to synonymize *C. edmitchelli* with *C. scabra*, based on apparent intergrades between the two species in Pleistocene deposits from the southern California mainland. Lipps (1963) commented that one of the best characters for inferring acmaeid phylogenetic relationships, the radula (a structure seldom preserved in the fossil record), was not available for study. Therefore, the suggested taxonomic relationships of these authors have been based on less reliable characters of shell morphology, which in many species is environmentally controlled. In the present study, shell structure is considered to be a more conservative character in acmaeid systematics than either shell or radular morphology. Thus, taxonomic and phylogenetic relationships inferred from shell structure are thought to be most accurate.

Theim (1917) was the first to recognize differences in the shell structure of acmaeids. Bøggild (1930) further expanded this work, describing eight patelloid shell structure groups. However, the use of shell structure was not applied to

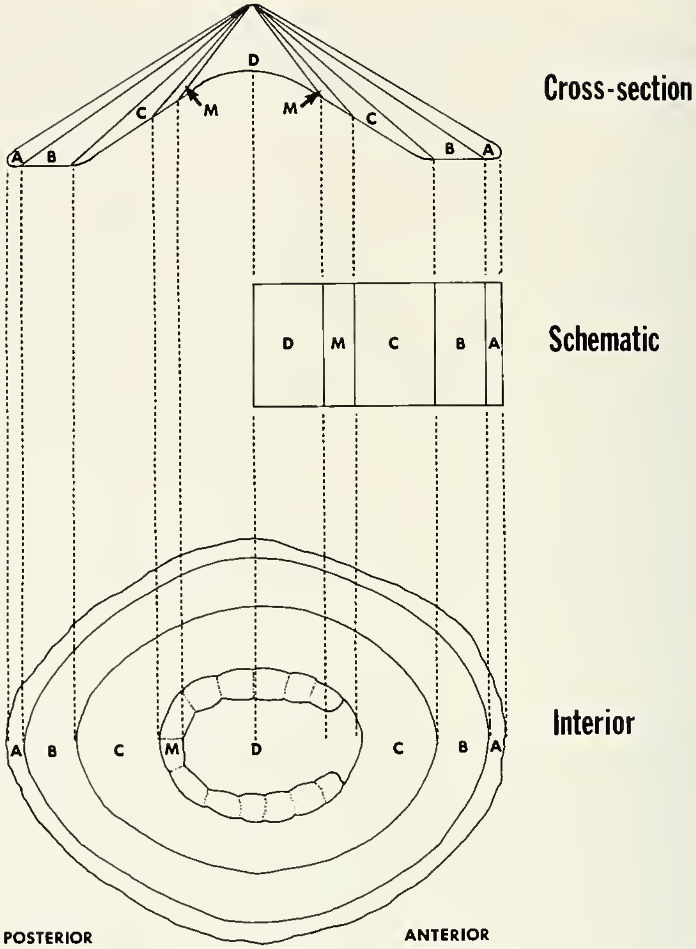


Fig. 1. Relationship of internal shell structure to interior bands or layers, also showing derivation of the schematic representation of shell structure. A–D = structural elements, M = myostracum (= muscle scar). (Modified after MacClintock, 1967.)

patellacean systematics until the work of MacClintock (1963), in which the genus *Proscutum* was reclassified based on its shell structure and muscle scar position. MacClintock (1967) later published an atlas of patelloid shell structures, in which he recognized seven acmaeid and 10 patellid shell structure groups. Because acmaeid shell structure has remained stable (or conservative) during the late Cenozoic it may be used to infer the taxonomic affinities of *C. edmitchelli* with other species.

Dr. Edward Wilson, Department of Invertebrate Paleontology, Natural History Museum of Los Angeles County (LACMIP), made available to me on loan topotypes of *C. edmitchelli* (LACMIP Locality No. 4658). In addition, I examined both the primary type material of *C. edmitchelli* and the specimens reported by Marincovich (1976) from the upper terraces of the Palos Verdes Hills.

The topotypes were examined intact, except for a single specimen which was radially sectioned and fractured by rapid alternation of heating (Bunsen burner)

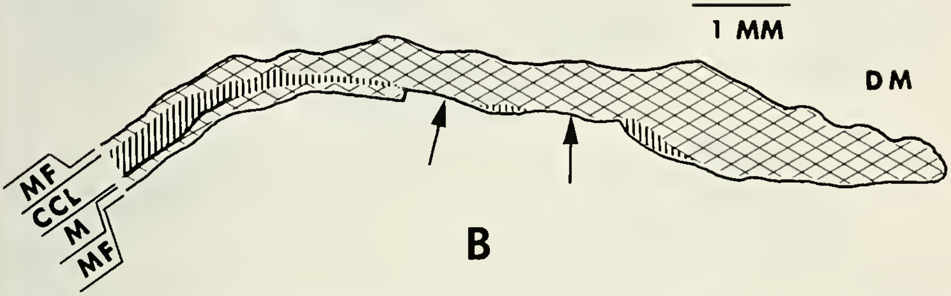


Fig. 2A. Cross-sectional view of *Collisella edmitchelli* (Lipps) (LACMIP Locality No. 4658). Shaded area indicates section illustrated in Fig. 2B.

Fig. 2B. Cross-sectional view showing structural elements. Arrows indicate areas from which the inner elements have exfoliated. MF = modified foliate structure, CCL = concentric crossed-lamellar structure, and M = myostracum; DM = dorsal margin. *Camera lucida* drawing.

and cooling (ice water) (MacClintock, 1967:110). This technique bakes the conchioline matrix, which then induces fractures to form around the structural elements. Specimens of other species exemplifying specific shell structure groups were also prepared by this method for comparison with the *C. edmitchelli* section.

The shell of *C. edmitchelli* contains four structural elements, which are expressed as visible concentric bands on the interior shell surface. The first structural element is visible as a wide dark interior margin and as the outer surface of the shell. The second element is considerably narrower and is present between the dark margin and the myostracum (= muscle scar). The third element is the myostracum, and the fourth is the large white apical area inside of the myostracum. These visible concentric bands are also found in the shell of *C. scabra*. The relationship of the shell structural elements to the concentric bands in a generalized acmaeid with five structural elements is shown in Fig. 1.

The structural elements in the shell of *C. edmitchelli* (Fig. 2) are identical to those in the shell of *C. scabra* (Fig. 3) in structure, position, and relative thickness. The shell structure of *C. scabra* was stated to be unique among California acmaeids by MacClintock (1967). The present study shows that this shell structure is shared with *C. edmitchelli*, but remains distinctive among California acmaeids.

Discussion

Based on shell morphology, I consider the specimens of *C. edmitchelli* reported by Marincovich (1976) from Late Pleistocene of the Palos Verdes Hills to be specimens of *C. scabra*. Marincovich's report of intergrades involves specimens only of the latter species. Thus, *C. edmitchelli* remains a valid species, as yet unknown from the California mainland.

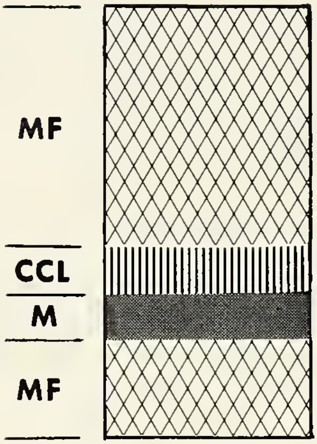
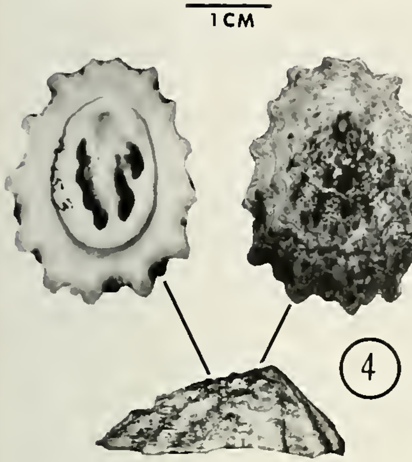


Fig. 3. Schematic representation (*cf.* Fig. 1) of the shell structure of *Collisella scabra* (Gould). See Fig. 2B for legend. Dorsal shell surface at top of figure. (After MacClintock, 1967.)

Both *C. scabra* and *C. edmitchelli* have primary and secondary ribbing and crenulate apertures, but the species are otherwise dissimilar in appearance. The primary ribs of *C. scabra* (Fig. 4) typically range between 10 and 20, and they are approximately twice as wide as the secondary ribs. Some of the ribs may bear nodes or spines, but they are not imbricated. The primary ribs are triangular in section and project strongly at the shell edge, producing a heavily crenulate aperture. The anterior, posterior, and lateral slopes tend to be straight giving the species an angular appearance in profile. In *C. edmitchelli* (Fig. 5) the number of primary ribs ranges between 20 and 30, although some specimens may have as few as 18. Differences in size between the primary and secondary ribs are not as distinct as in *C. scabra*, and the ribs of *C. edmitchelli* are rounded in section rather than triangular. In contrast with *C. scabra* the ribs are imbricated and projection of the ribs at the shell edge produces only a slightly crenulate aperture. The anterior, posterior, and lateral slopes are convex, giving the shell a rounded appearance in profile.

The interiors of the two species differ markedly. The shell edge of *C. scabra* typically has fine digitations between the projecting primary ribs. These digitations are lacking in *C. edmitchelli;* instead these interspaces are smooth. The apical area of *C. scabra* is typically overlain with a thick white callus that is streaked with irregular brown markings. *Collisella edmitchelli* lacks a callus and the apical area is entirely white.

Thus, *C. edmitchelli* is retained as a valid, extinct species, closely related to and sympatric with *C. scabra* on San Nicolas Island during the late Pleistocene. As pointed out by McLean (1966) the reasons for the limited geographical and geological occurence of *C. edmitchelli* are not known. Perhaps the oscillating thermal conditions of the Pleistocene coupled with the insular environment of San Nicolas Island produced this offshoot of *C. scabra*. Because *C. scabra* is a predominately warm-temperate species, species differentiation may have occurred during a cold period, so the ancestral stock of *C. edmitchelli* was a cryophilic variant of *C. scabra*. Subsequent warming may have been adverse to



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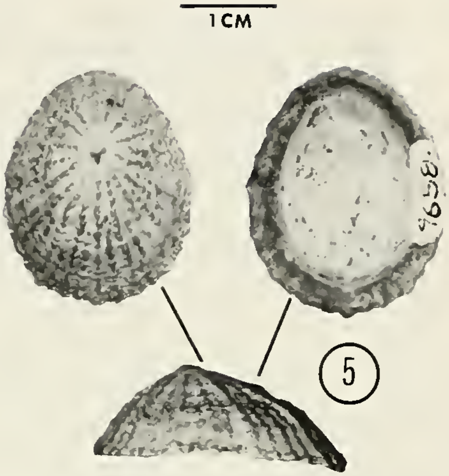

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Fig. 4. *Collisella scabra* (Gould). CALIFORNIA: San Francisco County, Southeast Farallon Island. (LACM Malacology Section Catalog No. 29858.)

Fig. 5. *Collisella edmitchelli* (Lipps). CALIFORNIA: Ventura County, San Nicolas Island. (LACMIP Locality No. 4658.)

C. edmitchelli and favored *C. scabra* which then repopulated the former cool areas. For a short period of time *C. scabra* occurred together with *C. edmitchelli* on San Nicolas Island. Extinction of *C. edmitchelli*, possibly due to thermal mortality, may have been hastened by competition or hybridization with *C. scabra*. *Collisella edmitchelli* is not known to have populated the adjacent mainland.

Collisella edmitchelli and *Notoacmaea lepisma* (Berry, 1940) are the only acmaeids from the California Pleistocene not known in the Recent fauna.

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I wish to thank Edward Wilson, Los Angeles County Museum of Natural History, for the loan of specimens and the courtesy extended to me on my visits. I also wish to acknowledge John S. Pearse, University of California Santa Cruz, Louie Marincovich, U.S. Geological Survey, Menlo Park, California, and James H. McLean, Los Angeles County Museum of Natural History, for their reading of the manuscript and helpful suggestions.

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This paper is dedicated to the memory of George E. Radwin, San Diego Museum of Natural History, a fine malacologist and friend.

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Some Estimates of the Distribution of Benefits from Los Angeles City Government Activity

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Abstract.—Analysis of the distribution of benefits generated by Los Angeles city government activity suggests that Los Angeles expenditure patterns may not be pro-poor. Benefits from nine program areas of service delivery are estimated and distributed to various income classes. For each program area a wide range of incidence assumptions is made. Results suggest that for the entire range of assumptions the lowest class does not benefit more than other classes. Furthermore for some assumptions the lowest class is significantly worse off. If the lowest class is ignored in the analysis, the remaining classes are treated identically under all assumptions. Because other studies have found such pro-poor expenditure patterns, these results may imply that Los Angeles is atypical of large U.S. cities. One reason for this difference may be that Los Angeles does not provide the education, welfare or health services that some large cities provide. In Los Angeles these services are provided by county or district level governments so benefits from these pro-poor services are not at all due to Los Angeles city government activity.

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The concept of taxation incidence is not new in public finance for the question of who bears the burden of national, state or local taxation has been exhaustively covered in the literature. However, much less attention has been paid to the question of distribution of benefits, particularly for local government activity.

According to folklore, the poor get most of the benefits of local government activity. The proverbial welfare mother is viewed as the head of a matriarchal clan adept at appropriating benefits from municipal, county and state governments. Many students of public finance seem to confirm this folk wisdom. Musgrave (1973) argues that the overall benefit rates decline as we move up the income scale. Netzer (1974) suggests income redistribution is the net result of local government supplying public goods; providing merit goods like education and health, free of user charges; and political compromises in state and local tax policies. Indeed most studies of expenditure incidence find this pro-poor pattern (Brownlee, 1960; Gillespie, 1965; Netzer, 1966; Donheiser, 1966). The results of this analysis suggests that Los Angeles City may be atypical, for the lowest income class consistently received the fewest benefits under a wide range of assumptions.

This paper attempts to analyze the distribution of benefits from the operation of Los Angeles City Government. Specifically excluded from this analysis are the following:

1. Spacial incidence effects on the residents of other Southern California jurisdictions.
2. Benefits generated from enterprise and proprietary agencies of Los Angeles

City Government. These agencies, LAX (Airport), Department of Water and Power and the Harbor Department, are not included in the annual operating budget presentation and are therefore not included in this analysis.
3. Revenue side taxation incidence effects.

Benefit from government expenditure has been viewed in basically two ways—one theoretical, the other applied. The theoretical approach suggests that the utility of a nonrival/nonexcludable social good is constrained only by preferences or tastes for the good in question. Because the utility for social goods is not subject to an income constraint, total benefits are dependent only upon consumer taste for the good in question. In fact, this theoretical approach suggests that consumer utility is likely to be constrained by crowding diseconomies due to over exploitation of the good rather than by any income constraint.

A second view of benefits is applied rather than theoretical and is based on cost-benefit analysis. Cost-benefit analysis is a decision tool that allows for the rational organization of timing, cost and benefit data. The cost-benefit criterion utilizes a discount rate to explicitly consider the timing of costs and benefits under the assumption that one dollar today is worth more than one dollar in the future. Benefit side analysis of cost-benefit analysis would estimate net present benefits to society by discounting future benefits at various discount rates. Usually no attempt is made to distribute the benefits to various subgroups within the society—i.e., the level of analysis is aggregate benefit to the total society.

The approach utilized in this paper examined nine (9) categories of program service provided by the city of Los Angeles. Program benefits are directly related to the size of the program budget. Total benefits increase monotonically with budget size. The paper assumes full employment. The full employment assumption forces us to recognize an opportunity cost because public expenditures employ resources from alternative uses. The effect is to net out the salaries of Los Angeles employees from the benefits to be allocated to the various income classes. Relaxation of the full employment assumption would mean that public expenditures employ idle resources, implying no opportunity cost. The effect of relaxation would increase benefits to those income classes represented in the Los Angeles City Government work force. Unfortunately, the Los Angeles budget does not contain a comprehensive salary and position schedule so that it is difficult to be exact in describing the effect of the relaxation of the full employment assumption. However, to the extent that Los Angeles City workers are not members of the \$0–\$5,000 income class, the effect of relaxation will tend to be regressive—i.e., only higher income classes will benefit from the relaxation.

The program areas examined are:

1. Police Services
2. Traffic Services
3. Fire Services
4. Housing and Community Development Services
5. Library Services
6. Recreation Services
7. Capital Improvement Program Services
8. Pension Program Services
9. General Governmental Services

For each program service area, alternative benefit incidence assumptions will be made. Because little progress has been made in reaching agreement about the incidence of benefits, a range of assumptions is proposed to facilitate analysis.

Generally, Assumption One will be the assumption we expect to give the lowest income class the most favorable allocation. Assumption Two will treat the lowest class second best and Assumption Three will give the lowest class the least favorable distribution. The reader will note that occasionally Assumption Two outperforms Assumption One in benefits allocated to the lowest income class. This may be due to a senior citizen effect caused by some persons in the lowest income class with low current income by relatively high wealth holdings—for example, real estate.

In the General Government category, benefits are assumed to provide support for all the functions of government. Benefits from this category are distributed in the same proportion as the aggregate distribution of program areas one through eight.

The income distribution used for Los Angeles is a modification of 1970 Census data. Census data is aggregated into four income classes: $0–$4,999; $5,000–$9,999; $10,000–$14,999, and over $15,000. Household income is the amount of money income received by each person 14 years of age or older in a household from the following sources: (1) Money wages or salary, (2) net income from non-farm self-employment, (3) net income from farm self-employment, (4) Social Security, (5) interest on bonds or savings, dividends, and income from annuities, estates or trusts, (6) net income from boarders or lodgers, or from renting property to others, and (7) all other regular sources of income such as unemployment benefits, public assistance, alimony, etc. Irregular sources of income due to capital gains are not included.

Allocators for distributing benefits to the various income classes will be the following:

1. Percent of total income by income class—developed from Census data for Los Angeles City.

Income Class	% of Total Income
1 ($0–$4,999)	4.23
2 ($5,000–$9,999)	16.42
3 ($10,000–$14,999)	23.69
4 ($15,000+)	55.66

2. Percent of real estate ownership by income class—national data developed by the Survey Research Center, Institute for Social Research, University of Michigan.

Income Class	% Real Estate Ownership	% Real Estate ($35,000+) Ownership
1	8.3	3.6
2	20.2	12.6
3	25.2	8.6
4	46.3	75.2

3. Percent of purchases of new and used automobiles by income class—national data developed by the Survey Research Center, Institute for Social Research, the University of Michigan.

Income Class	% of Purchase of New & Used Cars
1	11.5
2	37.0
3	30.5
4	21.0

4. Percent of purchases of household durables by income class—national data developed by the Survey Research Center, Institute for Social Research, University of Michigan.

Income Class	% Purchase of Household Durables
1	11.2
2	27.9
3	27.2
4	33.7

5. Percent of purchases of hobby items by income class—national data developed by the Survey Research Center, Institute for Social Research, University of Michigan.

Income Class	% Purchase of Hobby Items
1	6.3
2	23.7
3	35.9
4	34.1

6. Per Household allocations are based on number of households by income class.

Income Class	Number of Households
1	130,289
2	196,428
3	172,857
4	195,509

The results of this analysis are interesting not only because of the differences in class benefits but also because of the similarities.

Usually incidence studies involve regression analysis of benefits or tax rates—i.e., benefit over income or tax over income. The analysis focuses on the B statistic. If $B > 0$, then taxes are progressive. If $B = 0$, then taxes are proportional. If $B < 0$, the taxes are regressive. In benefit studies $B > 0$ implies anti-poor expenditures; $B = 0$ implies neutral expenditures; and $B < 0$ implies pro-poor expenditures.

This approach was not taken here. First we are concerned with distribution of aggregate benefits rather than ratios of benefit over income. Second, because our data is divided into only four income classes, regression results would be based upon only four observations.

For these reasons we conduct a statistical test of variance on class aggregate benefit profiles. We do not use the standard ANOVA F test because of the highly dependent way benefits have been allocated. Instead, we selected the Kruskall-Wallis one way analysis of variance. This test is an extension of the Wilcox two-sample rank-sum test and does not require a normal distribution as does the ANOVA test. In our case the procedure will assign ranks, one through 36 for each program by class. The result is a 4 × 9 matrix of unique rank assignments. The null hypothesis is that the rank assigned to any particular observation has an equal chance of being any number one through 36, regardless of the sample group to which it belongs. The test calculates a K score. If $K < \chi^2$, accept H_0. If $K > \chi^2$, reject H_0 (H_0 : all classes treated equally).

Results When All Four Income Classes Are Considered

		χ^2 (3 df)			
Assumption	K Score	$\alpha = .05$	$\alpha = .1$	$\alpha = .25$	$\alpha = .5$
1	2.959	7.815 (A)	6.25 (A)	4.108 (A)	2.36 (R)
2	4.11	7.815 (A)	6.25 (A)	4.108 (R)	2.36 (R)
3	8.43	7.815 (R)	6.25 (R)	4.108 (R)	2.36 (R)

Under Assumption One, alpha must increase to .5 before we can reject the null hypothesis that equity exists between the four income classes. Under Assumption Two, alpha increases to .25 before reject occurs; and under Assumption Three, rejection occurs at alpha equal .05. We conclude that though the lowest income class is worse off under all assumptions it is only significantly worse off under Assumption Three.

This result does not at all suggest the pro-poor pattern found in other studies. One possible reason is that Los Angeles does not provide the education, welfare or health services that many large cities provide. In Los Angeles these services are provided by either county government or district government.

Perhaps the most interesting result is the similarity of benefit distribution when the lowest class is ignored.

Results When Lowest Income Class Is Ignored

			χ^2 (2 df)		
Assumption	K Score	$\alpha = .05$	$\alpha = .5$	$\alpha = .75$	$\alpha = .995$
1	.0740	5.991 (A)	1.386 (A)	.575 (A)	.010 (R)
2	.0035	5.991 (A)	1.386 (A)	.575 (A)	.010 (A)
3	1.8449	5.991 (A)	1.386 (R)	.575 (R)	.010 (R)

When the lowest class is excluded under Assumption One, alpha must be forced to .975 before rejection occurs. Under Assumption Two, rejection never occurs— $(\alpha = .995) = .0100251 > .0035$. Under Assumption Three, rejection occurs at alpha equals .5.

These results suggest extremely little variation between classes two, three, and four. We conclude that they are treated identically under all assumptions.

Police Services

Police services are provided by the police department, which has the duty and power to enforce the penal provisions of the City Charter, the ordinances of the city and the laws of the state and nation. The Police Department engages in patrol, prevention of crime, investigation of reported crime, apprehension of suspects, gathering and preservation of evidence and various other staff activities for the purpose of protecting persons and property and preserving the peace of the community. The FY76 Police Budget was $196,961,922, of which $187,827,819 was salary and wage.

In the past, studies have often employed identical assumptions to redistribute benefits from fire and police. The allocator is usually income or value of property holdings. However, Greene, Neenan and Scott (1974) assume that the principal benefit of police services is a heightened feeling of safety. They therefore distribute benefits on the basis of hours spent in the jurisdiction. This technique has calculated benefits to non-residents, attempting to address the spacial incidence issue excluded from this analysis. Their study, which attempted to determine Washington, D.C., benefits accrued to Maryland and Virginia residents, used DMV state registration data to estimate spacial incidence.

The technique here assigns benefits based upon the three alternative incidence assumptions:

Assumption One: Protection of Persons

Police benefit is the foregone loss of income due to death, recuperation, etc., in the absence of police protection. The allocator is income.

Assumption Two: Protection of Property

Police benefit is the foregone cost of property loss. The allocator is real estate ownership. Note that value of holdings is ignored here. All real estate holders are viewed as equal beneficiaries.

Assumption Three: Protection of Property Valued at $35,000+

Here the allocator is ownership of real estate valued at $35,000+.

	Assumption		
Class	1	2	3
1	2.9	5.8	2.3
2	7.6	9.3	5.8
3	12.5	13.3	4.6
4	26.0	21.6	35.1

Under each set of assumptions, the benefits of police services are accrued to principally the highest income classes. It is interesting to note that greater benefits accrue to the lowest class under the real estate allocation than under the income allocation. Perhaps this counter intuitive result is due to the senior citizen effect mentioned previously. That is, senior citizens may have real estate holdings even though their current income is quite low. Note that mean benefits per household for the lowest income class under the real estate assumption is twice the benefits under the income assumption.

Traffic Services

Traffic Services are provided by three agencies of Los Angeles City Government: the Traffic Department, the Off-Street Parking Agency, Department of Public Works (Bureau of Right-of-Way and Land), and Department of Public Works (Street Maintenance). The Traffic Department analyzes the effect of proposed developments on the parking and traffic needs of the city and also provides for the installation and maintenance of traffic control and safety devices. The FY76 Traffic Department Budget was $11,317,974 of which $8,818,883 was salary and wages.

The Off-Street Parking agency coordinates off-street parking. The FY76 budget was $117,709 of which $115,587 was salary and wages.

The Department of Public Works (Bureau of Right-of-Way and Land) acquires right of way for city streets. The FY76 budget was $6,680,452 of which $2,846,024 is salary and wages.

The Department of Public Works (Street Maintenance) repairs, cleans and maintains streets, sidewalks, bridges, etc. The FY76 budget was $36,993,370, of which $27,196,288 was salary and wages.

Benefits of traffic services are assumed to accrue to the users of the road. The allocator of benefits is the purchase of new and used cars. This is the only incidence assumption for traffic services. Note that to the extent that commercial enterprises benefit from road improvement regressivity has been understated.

	Assumption		
Class	1	2	3
1	5.5	Same as 1	Same as 1
2	11.9	Same as 1	Same as 1
3	11.1	Same as 1	Same as 1
4	6.8	Same as 1	Same as 1

Table of Mean Benefits Per household ($)

Note that the greatest benefit from traffic services accrue to the middle two income classes. These classes receive more than two thirds (2/3) of the total traffic service benefits.

Fire Services

Fire services are provided by the fire department, which controls and extinguishes fires. The fire department inspects buildings, enforces laws relating to fire prevention, conducts fire prevention education programs, investigates cases of arson, and provides rescue and emergency ambulance service. The FY76 fire budget was $84,947,615 of which $80,702,316 was salary.

As noted under the police service discussion, fire incidence assumptions have in the past been the same as those for police service—income or property allocators. Greene, Neenan, and Scott assign 90% of fire benefits to property and 10% to individuals.

The assumptions here are:

Assumption One: Protection of Household Furnishings and Durable Goods

The benefit of fire services is the foregone cost of lost furnishings and durable goods. Benefit allocator is the purchase of household durables.

Assumption Two: Real Estate

The benefit of fire service is the foregone cost of lost property. Benefit allocator is real estate holding.

Assumption Three: Major Real Estate ($35,000+)

Benefits only accrue to holders of real estate valued at $35,000 or more.

	Assumption		
Class	1	2	3
1	3.6	2.7	1.0
2	6.0	4.3	2.7
3	6.6	6.1	2.1
4	7.3	10.0	16.3

Table of Mean Benefits Per Household ($)

Note that under each assumption the lowest income class is considerably worse off, and the highest income class is most well off.

Housing and Community Development Services

Housing and Community Development Services are provided by a $96,002 low income housing fund and a $28,838,880 community development trust fund. Budget data does not indicate the portion of these funds for salary. The project activity breakdown leads on to believe that salary is a considerable element of the funding. We assume a salary component of 89%. Alternative incidence assumptions are:

Assumption One: War on Poverty

Benefits from Housing and Community Development services accrue to the lowest income classes—75% to the lowest and 25% to the next to lowest.

Assumption Two: Inverse Income

Benefits are distributed inversely to the percentage of total income by class. For example, the highest income class has 55.66% of income; therefore, 55.66% of the benefits of housing and community development is assigned to the lowest income class. The second highest income class has 23.69% of income; therefore, 23.69% of benefits go to the second lowest class, etc.

Assumption Three: Real Estate

Benefits in the long run accrue to the owners of real estate.

	Assumption		
Class	1	2	3
1	33.3	24.7	3.6
2	7.3	6.9	5.9
3	0.	5.4	8.4
4	0	1.2	13.7

Table of Mean Benefits Per Household ($)

Note that under Assumptions One and Two benefits are highly progressive but that under Assumption Three there is regressiveness.

Library Services

The Library Department operates a central library, 54 branch libraries and five mobile libraries. In FY76 $14,278,068 was allocated to the library fund, of which $12,370,155 was salary. The ideal allocator would be book purchase by the income class. Because this data could not be found, we use hobby expenditure by income class as a proxy. This is the only assumption for library.

	Assumption		
Class	1	2	3
1	0.9	Same as 1	Same as 1
2	2.3	Same as 1	Same as 1
3	3.9	Same as 1	Same as 1
4	3.3	Same as 1	Same as 1

Table of Mean Benefits Per Household ($)

Recreation Services

Recreation Services are provided by Recreation and Parks. In FY76 $24,977,234 was allocated to the Recreation and Parks Fund. Budget data does not indicate the percent for salary and wages. We assume 80%. We assign equal benefits to each income class.

	Assumption		
Class	1	2	3
1	9.5	Same as 1	Same as 1
2	6.3	Same as 1	Same as 1
3	7.2	Same as 1	Same as 1
4	6.3	Same as 1	Same as 1

Table of Benefits Per Household ($)

Capital Improvement Program

For simplicity we treat CIP as though Los Angeles had a no debt policy for capital projects. Since this is almost the case, this simplification introduces very little bias. Alternative incidence assumptions are:

Assumption One:

All classes benefit from CIP equally.

Assumption Two:

Principal beneficiaries of CIP are users of the road.

Assumption Three:

Principal beneficiaries are real estate owners.

	Assumption		
Class	1	2	3
1	86.6	39.8	28.7
2	57.4	85.0	46.4
3	65.3	79.7	65.8
4	57.7	48.5	106.9

Table of Benefits Per Household ($)

Pension Programs

Pensions are viewed as transfer payments to former municipal employees. FY76 Pensions allocations were $143,758,217. This is viewed as a present value of future transfer payments caused by FY76 Los Angeles government activity. The ideal allocation would be the distribution of Los Angeles City government employees by income class. Because the budget does not provide a schedule of salary and positions, we have assigned 0% to the lowest income class and equally divided pensions through class two, three, and four.

	Assumption		
Class	1	2	3
1	0.0	Same as 1	Same as 1
2	243.0	Same as 1	Same as 1
3	277.2	Same as 1	Same as 1
4	245.0	Same as 1	Same as 1

Table of Mean Benefits Per Household ($)

General Government; All Other Benefits

General government expenditures are assumed to provide support for the other eight categories of service. Therefore, benefits from general government are distributed in the same proportion as the aggregate distribution for service categories one through eight.

	Total Benefit Effect		
	Assumption		
Class	1	2	3
1	250.2	151.3	93.1
2	586.7	633.0	553.9
3	655.7	690.8	649.2
4	603.0	591.4	746.5

Table of Mean Benefits Per Household ($)

Our results suggest that:

1. The lowest income class is worse off under all assumptions (a regressive distribution) and significantly worse off under assumption three.
2. Classes 2, 3, and 4 are equitably treated (a proportional distribution).

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Research Notes

A First Report of *Heteropodarke heteromorpha* Hartmann-Schröder, 1962 (Polychaeta: Hesionidae) from California

Specimens of *Heteropodarke heteromorpha* Hartmann-Schröder, 1962, were taken during the course of several benthic studies throughout southern California. This is the first record of the genus from the northeastern Pacific Ocean; it is known also from Peru and New Caledonia. All material has been deposited in the Allan Hancock Foundation.

Heteropodarke Hartmann-Schröder, 1962
Emended

Type.—*H. heteromorpha* Hartmann-Schröder, 1962. Body small and threadlike. Prostomium rounded, with 4 eyes, 1 median and 2 lateral pseudoannulated to annulated antennae. Palpi smooth to pseudoannulated. Pharynx with distal papillae; no jaws. Number of tentacular cirri vary with size; up to 8 pairs. Parapodia sub-biramous; 1–2 thin notoaciculae at dorsal cirrophoral base. Dorsal cirri longer than parapodia, pseudoannulated to annulated. Ventral cirrus similar to dorsal cirrus. Anterior setae as thick composite falcigers with bidentate appendages accompanied by a single thin composite spiniger or capillary seta. Setae of median and posterior segments as composite falcigers with unidentate appendages.

Remarks.—With the addition of the subspecies, *H. heteromorpha africana* Hartmann-Schröder, 1974, and collection of Californian specimens, the original generic definition has been emended. Details include variation in structure of cephalic appendages, tentacular cirri number, and a more detailed account of setal morphology and distribution.

Heteropodarke heteromorpha Hartmann-Schröder, 1962
Figure 1, a–c

Heteropodarke heteromorpha Hartmann-Schröder, 1962:117–120, pl. 5, fig. 30; pl. 6, figs. 31–34. Laubier, 1967:95–97, fig. 1a–f.

Material examined.—Isla Santa, Peru, April, 1956, 2 paratypes; Huntington Beach, MBC Sta 1D, 8/75 (2) 9/72 (2); Los Angeles Harbor, MBC Sta 27a, 8-75 (2); Ormand Beach, MBC Sta C3, 1-76 (2); Velero Stations on Tanner Bank 24130, 1-76 (2); 24134, 1-72 (1); 24372, 2-76 (1); 24140, 1-76 (9). Velero Station 23189, 11-76 (1) on Santa Rosa Island and 24380, 2-76 (1) on Cortez Bank.

Diagnosis.—Body small, threadlike, up to 6 tentacular cirri; setal fascicles of anterior segments with five thick composite falcigers having bidentate appendages, plus a single very thin composite spiniger; median and posterior setae all unidentate composite falcigers.

Habitat.—All Californian specimens were taken from fine to coarse sand at depths of 3–98 m.

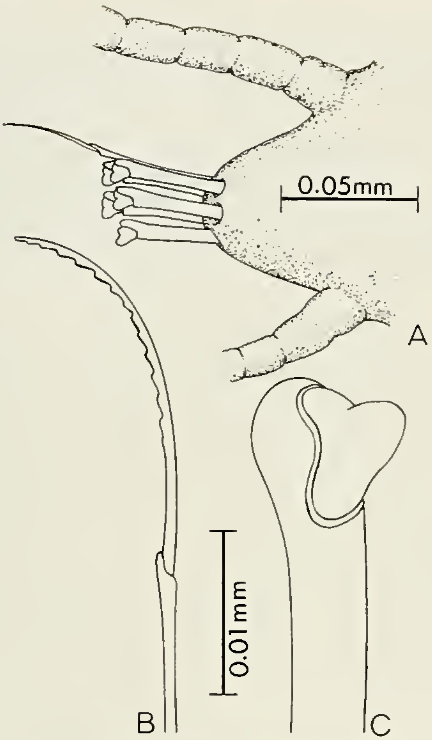

Fig. 1. *Heteropodarke heteromorpha:* a. Parapodium from setiger 18, lateral view; b. composite spiniger; c. composite falciger.

Remarks.—These specimens closely fit descriptions given by Hartmann-Schröder (1962) and Laubier (1967), especially in regard to the number, length and position of cephalic and tentacular structures, parapodial structure and general setal morphology and distribution.

Palps of the holotype were described as smooth, but those of Californian specimens are pseudoannulated, as were palpi of New Caledonia individuals (Laubier, 1967). Palps were missing from Peruvian paratypes.

A very thin composite spiniger accompanies each anterior fascicle of thick composite falcigers (Fig. 1a–c). Hartmann-Schröder mentioned the occasional appearance of very fine bristles among anterior segments which corresponds to this seta. Examination of paratypes showed that this seta was distributed as in Californian specimens.

The number of tentacular cirri is dependent on individual size and this variability has been discussed by Hartmann-Schröder (1962, 1974) and Laubier (1967). Large specimens of *H. heteromorpha* have up to 6 pairs of tentacular cirri, and *Heteropodarke heteromorpha africana* has up to 8 pairs. Variability of this character has been noted in other hesionid genera; Blake (1975) found juveniles of *Gyptis brevipalpa* to have 6 pairs of tentacular cirri whereas adults possess 8. This information suggests that keys to hesionids should be used carefully in regard to this character.

Acknowledgements

I sincerely wish to thank Gesa Hartmann-Schröder (University of Hamburg) for loan of paratypes, Tom Gerlinger (Marine Biological Consultants Inc.) and John Pilger (Allan Hancock Foundation) for additional Southern California specimens. Specimens from all VELERO stations were collected during the Southern California Baseline Studies and Analysis (FY 1975–1976) funded by the Bureau of Land Management (U.S. Department of Interior), Contract Number 08550-CT5-52. James A. Blake, Jerry D. Kudenov and Kristian Fauchald kindly reviewed the manuscript.

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The Species of *Plesionika* from California and Western Mexico (Natantia: Pandalidae)

Three genera of pandalid shrimp are known from offshore waters of southern California, U.S.A. and Baja California, Mexico: *Pandalopsis*, *Pandalus*, and *Plesionika*. Of these three, only *Plesionika* is characterized by possession of exopods on the third maxillipeds.

During sorting, cataloguing, and identification of shrimp in the collections of the Allan Hancock Foundation, specimens of *Plesionika beebei*, *Plesionika mexicana*, and *Plesionika martia semilaevis* were found. Extensions of the ranges of all three species are presented in this paper. *Plesionika mexicana* is reported for the first time from California. A key to the species in the eastern Pacific Ocean is provided.

Plesionika beebei Chace 1937

Plesionika beebei Chace 1937:114–115, fig. 2.

Previous records.—23 miles east by south of Tortuga Island, 13–20 miles northeast of San Ildefonso Island, Gorda Banks, Mexico; between 74 and 923 m (Chace, 1937).

Material.—34 miles southeast of Punta Tosca, Baja California, 528–738 m, 24 January 1954, R.V. *Velero IV* station 2586-53, one broken specimen. Southeast of Salina Cruz, Gulf of Tehuantepec, Mexico, 410 m, 20 November 1958, Wisner and Parker, one specimen.

Plesionika martia semilaevis Bate 1888

Plesionika semilaevis Bate 1888:644, pl. 113, fig. 3.
Plesionika martia semilaevis: de Man, 1920:116–121, pl. 10, figs. 24–24b.
Plesionika sp.: Ebeling, Ibara, Lavenberg, and Rohlf, 1970:12.

Previous records.—Philippines, Borneo, Sydney Harbor, Kermadec Islands, Fiji, South Africa, Japan, and Hawaiian Islands; 262–2215 m, on green mud, coral mud, and volcanic mud (Bate, 1888; de Man, 1920). San Pedro Basin, California, lower mesopelagic (Ebeling et al. 1970).

Material.—Twenty-seven specimens from 38 stations, from 18½ miles off Santa Barbara Island, California to 51 miles from Cabo Punta Banda, Baja California; 812–3046 m, Isaacs-Kidd midwater trawl, 1952–1969, R.V. *Velero IV*.

Remarks.—As mentioned by de Man (1920), *P. martia* is a most variable species. The specimens examined possess two small spines or spinules on the dorsal surface of the rostrum instead of six dorsal teeth, which de Man (op. cit.) found to be the most common number in his specimens. The ventral armature of the rostrum varies from pronounced fine teeth (from five to 12 in the specimens examined) to teeth almost obscured by a thick fringe of setae. A carina along the dorsal midline of the carapace, characteristic of the species, is present in specimens from California and Baja California.

The specimens trawled by the R.V. *Velero IV* usually were broken badly. The walking legs were torn either at the base or below the carpus, preventing the accurate counting of their meral spines or measurement of the proportions of the segments of the walking legs relative to each other. In the least damaged specimens these legs are extremely long and delicate relative to the carapace.

Scales occur on the carapaces of undamaged specimens. These scales, similar to those figured by Mauchline et al. (1977, figs. 2–5) for acanthephyrid and systellaspid shrimp, may have a sensory function.

The specimens from California were colored red in life (Yaldwyn, 1963, unpublished key). Ovigerous females were taken on 26 July 1967 and 19 September 1963.

Plesionika mexicana Chace 1937

Plesionika mexicana Chace 1937:112–114, fig. 1.

Previous records.—Arena Bank, Gorda Banks, and three miles east of Cabo Falso, Baja California, Mexico; 55–138 m. muddy, sandy, shelly and hard substrates (Chace, 1937).

Material.—Off Redondo Beach, California; 90–258 m, 5 May 1940, R. V. *Velero IV* station 1034-40, numerous specimens, many of them ovigerous. 1¼ mile southwest of Cabeza Ballena, Mexico; 55 m. 11 March 1949, R.V. *Velero IV* station 1726-49, 13 specimens. Off Pacora Island, off Bahia Honda, Panama, 28–46 m, *Velero III* station 245-34, 21 February 1934, four specimens, one of them ovigerous. Off Medidor Island, Bahia Honda, Panama, 55–65 m, rock and mud.

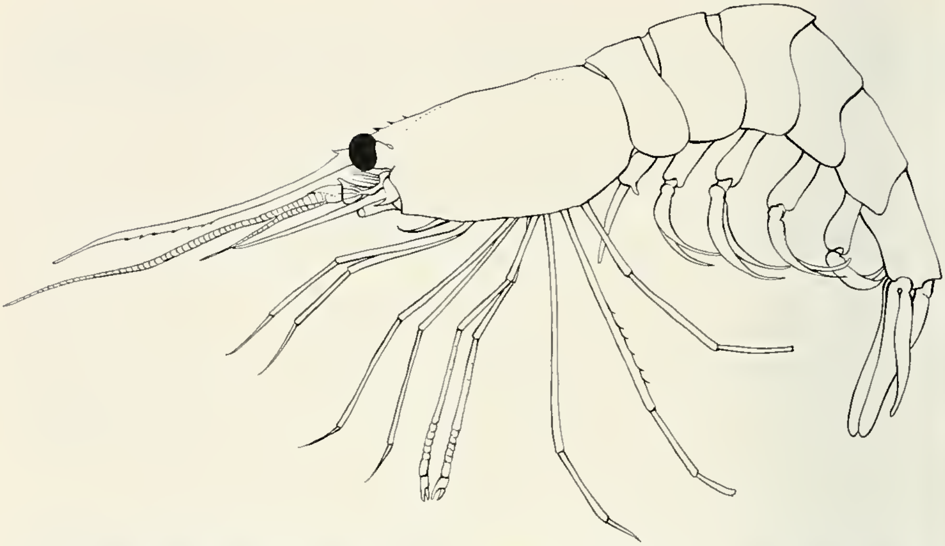

Fig. 1. *Plesionika martia semilaevis.* Female, total length 49.5 mm. 5.7 miles, 43½° true from Ship Rock, Santa Catalina Island, California, 846–864 m, 24 February 1961. R. V. *Velero IV* station 7299-61.

28 March 1939, *Velero III* station 948-39, numerous specimens, many of them ovigerous. Off La Plata Island, Ecuador; 83–102 m, rock and mud bottom, 10 February 1934, *Velero III* station 212-34, two specimens, one of them ovigerous.

Remarks.—Despite extensive collecting by the R.V. *Velero III* and *Velero IV*, other ships and collectors, no specimens of *P. mexicana* have been reported from California since 1940. These animals may have strayed into northern waters during a particularly warm year but were unable to maintain a population in the area.

Key to the Eastern Pacific Species of *Plesionika*

1. Second pereiopods markedly unequal in length .... *P. mexicana.*
   Second pereiopods equal or subequal in length 2
2. Rostrum moderately upcurved, with 2–8 dorsal spines ....
   .... *P. martia semilaevis.*
   Rostrum straight or strongly upcurved, with 11 or more dorsal spines 3
3. Carpus of second pereiopod with 8 segments, rostrum nearly straight
   .... *P. beebei.*
   Carpus of second pereiopod with 14–17 segments, rostrum strongly upcurved ....
   ...... *P. trispinus* (Pacific coast of Colombia, Squires and Barragan, 1976).

Acknowledgments

I thank Fenner A. Chace, Jr., National Museum of Natural History, for the loan of specimens of *P. trispinus*. The specimens of *P. martia semilaevis* in the collections of the Allan Hancock Foundation were sorted by John Yaldwyn and Manuel Murillo. The drawing was done by Ginny Mickelson.

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Iolmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus*. J. Mamm., 54: 452–458.

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Research Notes

COVER: *Anisolabis maritima* Géné (Dermaptera: Labiduridae) sharing the carcass of a spider with two of its brood, submitted by Vincent Brach, Dept. of Biology, Texas Eastern University, Tyler, TX 75701.

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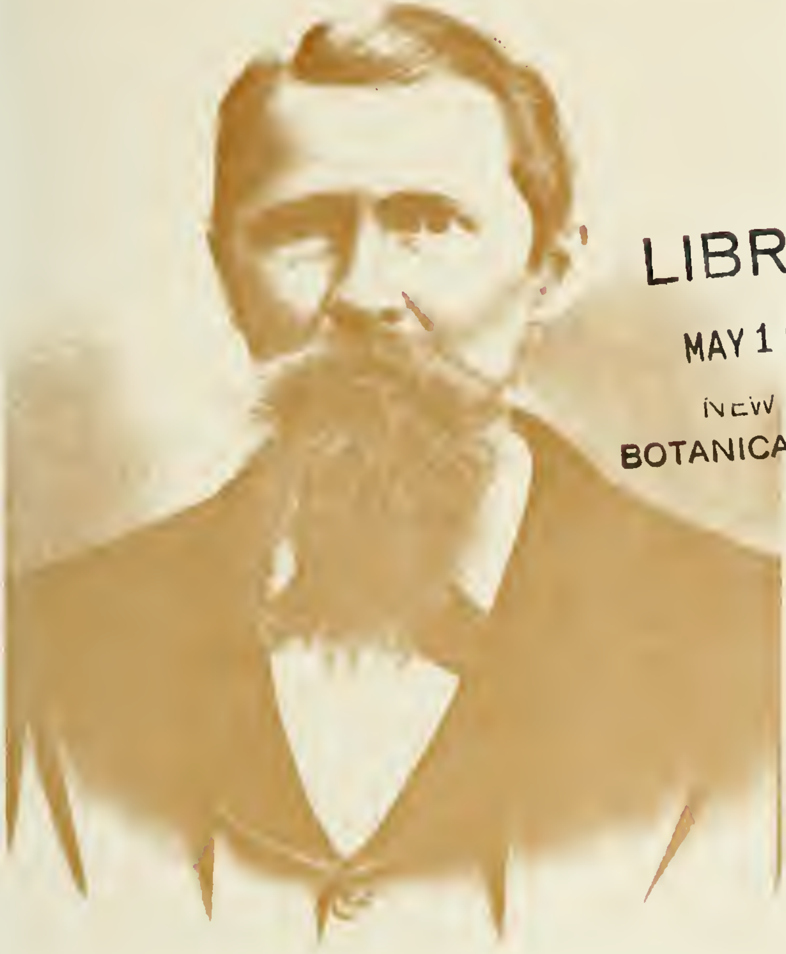

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'Peter Left Because . . .': A Comparative Study of Family Oral Histories

Nancy Thym

Abstract.—In 1854, Peter Oest left the small, northern German town of Otterndorf for America. He left behind a productive farm and high social position for the life of an unlucky gold miner in the California foothills. In Otterndorf the descendants of Peter's brother give one reason for Peter's seemingly irrational behavior, while Peter's descendants in California give quite another reason: the former, that he left for marital reasons, the latter, that he left for military reasons. The truth in these disparate accounts is no longer possible to determine and is perhaps not as important as the exploration of the motivations behind each family's account and the insights the accounts give us into the way in which narratives are generated.

On the River Elbe in northern Germany, between Hamburg and Cuxhaven, lies the small hamlet of Lüdingworth. Nearby stands a red brick farmhouse with thatched roof and white trim. In the very middle of the house is a tiny room with no windows. Here, in 1831, Peter Oest was born, the fourth of thirteen children born of Christian and Catharine-Margrethe Oest. Peter attended the local school and, after his confirmation in 1847, helped his family on the farm.

In 1854, at the age of 23, Peter left the farm in Lüdingworth to help his grandparents build a larger farm in nearby Otterndorf. While working on the farm Peter met Maria Dorothea Martens, a serving maid employed by his grandparents. A relationship soon developed between the two and Peter asked permission to marry the girl. But Maria Dorothea was not only a serving maid, but had been born out of wedlock. At that time a marriage between a man of his station and a serving maid, particularly an illegitimate one, was impossible and his parents forbad it.

But Peter was not to be discouraged. Without his parents' knowledge he travelled to Bremerhaven, a nearby port, and shipped aboard a cargo ship as a sailor. For over a year his parents had no idea of Peter's whereabouts. His mother, Catharine, would sit by the window and say, "Wo wird mein Sohn sein? Wo wird mein Sohn sein?" ('Where will my son be? Where will my son be?') Finally, a year and a half later, in 1856, a letter arrived from New York via a returning cargo ship and a farmer travelling from Bremerhaven to Lüdingworth. The letter was from Peter.

In 1857 Peter returned to Otterndorf and on April 22, despite his parents objections, he married his illegitimate serving maid. In Autumn he returned to New York taking his bride with him. Their first son, Heinrich, was born in December.

There was little work to be had in New York, however, and wanderlust and stories of gold eventually led Peter and Maria to the California gold fields, again against the wishes of his parents. The means of travel to California by the young family is not known but part of the journey was by land. They arrived in California with one cow and one son, ten years too late for the Gold Rush. Their cow died shortly thereafter.

mate serving maid, Peter's mother waiting at the window for her son's return, and both parents' love for their son as expressed in the letter wishing his return. This sensitivity may also reflect the narrator's concern for his audience: in this case, an American descended from German emigrants.

In Calvin's account Peter's arrival in California represents a new beginning. Peter is the patriarch of the new world clan. Calvin spends little time recounting Peter's military reasons for leaving Germany. He dwells instead on Peter's ordeals in reaching the California gold fields and his life in Auburn. Here, the story takes on some of the traditional elements of an origin legend: Peter is elevated to the status of a culture hero exhibiting superhuman powers. He walks from San Diego to Auburn, a distance of some 600 to 700 miles, depending upon the route. If he averaged 40 miles a day he would have had to walk at a speed of four miles per hour, ten hours a day; or three and a half miles per hour for twelve hours a day. Peter also walks across the Isthmus of Panama but finds a wagon for his wife and son. In later years he exhibits the wisdom of a judge.

As a member of an old family in a gold mining area, Calvin's sense of pride and belonging is probably strengthened by the knowledge that he is descended from a gold miner, one of Auburn's original settlers. Despite Peter's lack of success in discovering gold, his descendants needed a reason for Peter's presence in California. I suggest that this need is the underlying motivation for the adjustment of the date of Peter's arrival from 1857 (which can be confirmed through letters) to 1851. 1857 is simply too late for a proper Gold Rush story. Because of this need to justify his presence in Auburn, Calvin's choice of narrative elements may reflect similar elements in other stories of gold miners and pioneers: the date, the long trek on foot, the need for a judge in a lawless area, etc. Only after Calvin stresses the Gold Rush as Peter's reason for coming to California, does he mention Peter's success as a farmer.

In California scandal is not a part of the story of Peter Oest. Of course one does not normally tend to tell one's own children when one is illegitimate; but a family wishing for respect in a new land would especially avoid and suppress any intimation of scandal. Witness, for example, Calvin's reaction to the suggestion that his grandmother might be illegitimate.

There is no scandal involved in Peter's reason for leaving Germany. As Calvin explained, Peter did not run away from military service; he left because he disapproved of the military regime in power in Germany. The idea of avoidance of military service is perhaps too distasteful and scandalous for a patriotic American, so Calvin stresses the German political situation rather than the military. In America, where many early immigrants left their homelands for political reasons, this justification would be understood and respected. Albert Oest also stresses that Peter's reason for not serving in the military was perfectly legal, illegitimacy being perhaps less scandalous than avoidance of military service!

Another of Peter's American grandsons, when asked about Peter's reasons for leaving Germany, boomed in reply: "The only reason I know of was adventure. There was no trouble! His family sent him money two or three times. He went back to Germany once or twice. His family sent him money." The money somehow symbolizes for him the lack of scandal. Albert also tells of money being sent to California. On both sides of the family there seems to be a concern that father and son remained on good terms. Albert's narrative choice may, in this case, again reflect his concern for his audience.

While Albert, in his accounts, stresses the emotions of Peter's family, Calvin emphasizes Peter's ambition, self determination, and courage: his strength in walking from San Diego to Auburn; and his wisdom in acting as a judge in later years. These character traits as well as being those which Calvin himself admires and displays, are often the traits stressed and praised in stories of those first pioneers who built America. This narrative choice may again reflect the need of Calvin's family to feel they were part of the building of a new state in a new country.

Calvin stresses Peter's ambition, self determination, courage, strength, wisdom, and the romantic, adventurous nature of the Gold Rush, even changing the date of Peter's arrival to correspond with the Gold Rush period. But Calvin also expresses bitterness at his grandfather's stubborn persistence in continuing a hopeless search for gold while his family starved. He says: "Even after he was a successful farmer, he never gave up looking for gold. And he'd force the children to help him search when they should have been working the farm. My father never could understand why he just didn't give up. I feel sort of sorry for him. That he never found any gold." I suggest that these seemingly contradictory attitudes can be explained by the pride of Calvin's family and their need to feel a part of local history, while, at the same time, being aware of the reality of the situation.

The examination of these two differing accounts told on two different continents involves two distinct problems: The first, explicated above: what factors have led these two men to tell their history of the family in the distinct way in which they do? The second problem: what factors have led each of these two particular individuals to assume the role of family historian? The first problem involves striking differences in needs and concerns; the second problem, precise parallels.

Both Albert and Calvin Oest are story tellers. I have heard them tell these stories several times, and they enjoy recounting Peter's adventures to those who show an interest. Albert learned the stories from his father, who was also interested in the family history and visited his cousins in California in the early 1920s. Albert tells the stories primarily when American relatives come to visit. He shows them the pictures of family members and the old buildings and tells the stories at the same time. Calvin learned the stories as a child while listening to his father and his aunts talking among themselves. He says: "I tell 'em to the family and perhaps to others if the occasion happens to come up to mention it. I don't advertise it." His wife often urges him to "tell that one." Each narrator tends to tell the story in the same way with each narration: the events in the stories occur in the same order and are described in the same way, as if the stories have become fairly fixed through frequent narration.

What is it about these two men which makes them the family story tellers? Aside from a natural talent for telling the stories themselves, both men are concerned with other aspects of the history of the family. Both treasure old photographs and paintings of early family members and display them prominently in their homes. Both attempt to preserve family heirlooms and possessions. While other descendants have moved to other parts of Germany and California, both Albert and Calvin continue to live and work on the farms which they inherited from their grandparents through their fathers. For these men, living on the original family property, the family history is a more immediate concern than for family members living elsewhere. Although differing needs and concerns within the families of Albert and Calvin Oest have led them to tell very different accounts of the same event, their parallel circumstances as farmers living on the original family property, their shared concern for preserving the family heirlooms and stories, and their shared ability as story tellers, have led them to the identical roles of family historian and story teller within their branch of the family.

The generation of two strikingly different accounts based on the same historic events has profound implications for the study of history, particularly the interpretation of oral history. Witness, for example, the public furor when the extent of Alex Haley's poetic license in *Roots,* a book based on the oral history of a Black American family, was suggested. Haley's audience was concerned that what they had read was "not true."

What they read was "true" but perhaps not "factual." It is my suggestion that the "facts" upon which a narration is based are, in the case of oral history, not as revealing as the factors influencing the process of narration itself. The question which needs to be asked is not, "What do these stories tell us about Peter Oest, German, and Californian history?" but rather, "What do these stories tell us about their narrators?"

Here, a folkloristic approach can contribute significantly to the field of oral history, whose aim is to distill and present historic fact from oral accounts. Narrators of oral history, such as Albert and Calvin Oest, believe that the stories they tell of their ancestors are "true." But as has been demonstrated in the case of these two differing accounts of the same event, although narrators of oral history may wish to give a factual account of their family's history, their perceptions of historic fact are colored by what they want to believe about their ancestors, by their own and their audience's concerns, and by their need to justify their present existence. These social, economic, and psychological concerns have shaped the process of their selection of narrative elements until the narration of history has become an artistic, legend making process leading to two diverging accounts. The oral historian must be aware of this legend making process before a true interpretation of oral history can be reached.

In Germany, a need to justify his own family's decision not to emigrate and an ambiguous attitude towards emigrants seems to have led Albert Oest to emphasize the negative aspects, the scandal, involved in Peter's departure. In California, based on a need to explain their presence in a new land, the story of Peter Oest has become a family's origin legend, accruing elements from similar accounts of pioneers and gold miners. A desire for respect in this new life may have led Calvin's family to suppress elements of scandal and to emphasize Peter's fierce individualism, his desire for gold and adventure, and the personality traits which have "built America."

Ultimately these two divergent accounts represent not so much a historical picture of Peter's real motivations for leaving Germany, but rather a valuable means of gaining insights into the factors influencing the legend making process and the needs, concerns, and motivations of the men who tell the stories.

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Residual Effects of Summer Irrigation on Mojave Desert Annuals

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Abstract.—The response of summer and winter annuals to early summer irrigation and/or natural precipitation was determined for a rocky slope and a sandy bajada near East Ord Mountain in the Mojave Desert, California. Irrigation stimulated the germination of summer annuals on the rocky slope but not on the bajada, where a thundershower later in the summer caused a profusion of annuals. The following season, winter annuals showed markedly reduced densities on both irrigation plots and on the area receiving summer rain. These surprising results suggest that summer precipitation may have a much greater influence on vegetation response than had been previously supposed. Annuals comprised over 80% of the plant species on the two sites. Native winter annuals appear as components of highly integrated stable communities. The spatial heterogeneity of annual communities is greater than for perennial communities.

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Introduction

A survey of plant life forms compiled by Cain and Castro (1959) shows annuals (therophytes) making up 17 to 58 percent of the local flora in 12 different desert regions of the world. Death Valley and the Salton Sink, representing California deserts, have values of 42 and 47 percent respectively. In contrast the annual flora of most forests falls below 10 percent and in local stands may be zero. This distribution pattern suggests that the annual habit has special evolutionary significance in the vegetation of hot, arid regions. A selective advantage may be afforded by the capacity for completing the entire life cycle (from seed to seed) during relatively short intervals of moisture availability. New seeds thus produced during these intervals lie quiescent or dormant through subsequent drought periods until germination requirements are again satisfied.

The natural progression of events leading to the conditions needed for the germination and development of annuals has been of great interest to desert botanists through the years (Went, 1948, 1949; Tevis, 1958a, 1958b; Beatley, 1974). It is clear that native species must experience rather specific soil temperature and moisture conditions before germination will take place. Two distinct groups of annuals appear to have evolved in the deserts of southwestern North America. Those that germinate in response to sufficient precipitation during periods of high temperature, the summer annuals, and those that germinate in response to sufficient precipitation during periods of low temperature, the winter annuals (Shreve, 1951). The two groups are further distinguished on the basis of their modes of photosynthesis. Summer annuals predominately exhibit the C-4

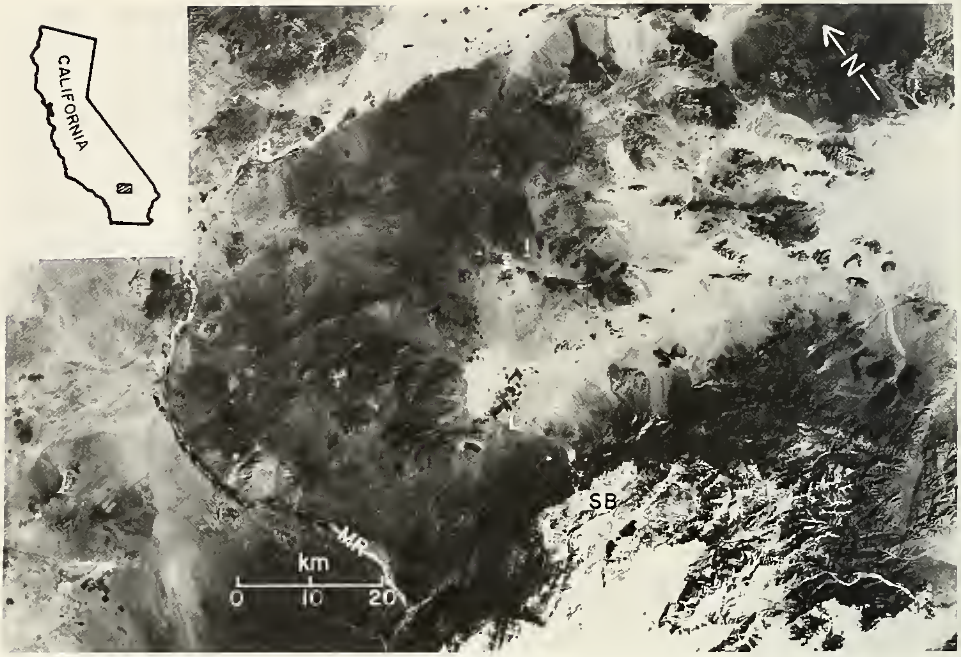

Fig. 1. Southern Mojave Desert region. Sky Lab IV. Feb. 7, 1974. NASA photo 081 RL 78. The general Lucerne Valley area occupies the central portion of the photo. L, Lucerne Valley; B, Barstow; MR, Mojave River; SB, San Bernardino Mountains (snow covered); 1, rocky slope irrigation site; 2, sandy bajada irrigation site; 3, sandy wash reference site, Lower Lucerne Valley; 4, sandy bajada reference site, Lower Johnson Valley; 5, sandy bajada reference site, Upper Johnson Valley. Tonal variations represent different substrates which may be associated with distinctive types of annual vegetation.

carbon pathway while the winter annuals have the C-3 (Johnson, 1975; Johnson, 1976; Mulroy and Rundel, 1977).

A model describing the phenology of desert plants in relation to temperature and precipitation has been proposed by Beatley (1974) for the Mojave Desert. She ascribes particular significance to single, heavy, late autumn rains (greater than 25 mm) for initiating the developmental cycle in winter annuals. She further concludes that summer storms have little immediate significance for the native biota. Other workers (Went, 1948; Tevis, 1958) have reported apparent cumulative effects resulting from light sequential showers. They observed that storms which by themselves would be too light to trigger germination have done so when preceded by other appropriately spaced nontriggering showers.

Droughts in parts of the Mojave Desert, severe enough to preclude the germination of many desert annual seeds stored in the soil, occur with a high frequency and may embrace several years at a time. Precipitation is particularly unpredictable during the summer season in the Mojave. Characterization of the annual flora during extended dry spells is virtually impossible since many of the species present are represented only in the soil seed reserve. This study was initiated to obtain an inventory of summer annuals by substituting sprinkler irrigation for natural precipitation in hopes of inducing seed germination. The study

Table 1. Properties of Lucerne Valley well water used for irrigating study plots.*

Element	μg/ml	Element	μg/ml
Aluminum	<0.3	Phosphorus	<1
Barium	0.03	Potassium	<1
Boron	0.10	Silicon	1.2
Cadmium	<0.009	Silver	<0.0004
Calcium	66	Sodium	24
Chromium	<0.1	Vanadium	0.002
Cobalt	<0.009	Zinc	0.63
Copper	0.014		
**Fluorine	0.40	**Compounds	m.e./l.
Iron	0.019	Bicarbonates	239
Lead	0.02	Chlorides	96
Magnesium	22	Sulfates	57
Manganese	<0.003	Nitrates	1.8
Molybdenum	0.007		
Nickel	0.003		

pH = 7.7; E.C. × 10^3 = 0.75 millimhos or approximately 480 ppm dissolved solids

* Water analysis contributed through the courtesy of G. Bradford, Department of Soils, Univ. of Calif., Riverside. A direct reading spectrograph was used for making the measurements.

** Supplementary data from Western Ag Lab, Redlands, Calif., for a nearby well whose elemental analyses corresponded closely with the data presented.

area, which had been subjected to intense drought prior to this investigation, received scattered thundershowers during the early part of the experiment and unusually heavy general storms during the following winter (1972–1973). The combination of summer irrigation and natural precipitation thus provided a variety of experimental conditions affecting plant growth. The purpose of this paper is to describe the response of desert annuals to these conditions and to discuss the highly unexpected results in terms of their possible significance to understanding the structure and function of desert plant communities.

Procedures and Physical Setting

Two sites representing different phases of the Creosote Bush Scrub Community (Munz and Keck, 1959) in the Mojave Desert of California were selected for irrigation. The first was located on a gentle, south facing rocky slope and the second on an east facing alluvial fan (bajada) composed of coarse sand. Both sites are in the Lucerne Valley Region near East Ord Mountain, at elevations of approximately 1100 m (Fig. 1). The entire area is shielded from coastal storms by the San Bernardino Mountains to the south.

Water for irrigation was transported to the site in a 450 gallon tank mounted on a trailer. The tank was filled from a well at the Lucerne Valley fire station. A detailed analysis of the water (Table 1) showed it to be of high quality and free of excessive mineral concentrations that might render it detrimental to plant growth. Well water from this area is generally considered to be of outstanding quality for both crop irrigation and human consumption. Water from the tank was applied through a sprinkler head driven by pressure from a pump powered by a 2½ horse power engine mounted on a trailer. The sprinkler when in operation irrigated a circular plot about 10 meters in diameter. The sprinkler was subjectively located to cover a plot representative of the immediate surroundings, particularly in terms of perennial plant composition and the conditions of the substrate. The rate of application was approximately 1 cm/hr which was slow enough to preclude runoff. Each site was irrigated twice in early summer, the rocky slope on 10 and 28 June, and the sandy bajada on 23 June and 11 July, for two hours at a time to give a total of 4 cm of water applied. Water penetrated rather uniformly on the fan and reached a depth of approximately 30 cm. Infiltration on the rocky site was irregular due to the small scale drainage and concentration effects associated with the many exposed stone surfaces. The actual depth of water penetration was not determined here because of the excessive site disturbance that would have been required in making the assessment.

Two summer storms passed through the study area. The first, in early June, dropped a small amount of precipitation (judged to be less than 1 cm) on the rocky slope where the irrigation plot #1 was subsequently located. The second, a high intensity storm on the 28th of August, struck the northern half of the bajada (fan) where irrigation plot #2 was established, wetting the soil to a depth of 35 to 50 cm (judged to be greater than 3 cm of rain). The southern part of the bajada received no rain on either occasion. The combination of irrigation and natural precipitation thus provides the following series of moisture treatments.

Rocky Slope.
  A. Light summer showers plus irrigation (Irrigation Plot 1)
  B. Light Summer showers only (area surrounding Irrigation Plot 1)
Alluvial Fan.
  C. Irrigation plus summer rain (Irrigation Plot 2)
  D. Summer rain only (area surrounding Irrigation Plot 2)
  E. No summer water (South part of alluvial fan)

A sixth possible combination namely irrigation and no summer rain, is absent because of our inability to plan the time and place of summer thundershowers. The general winter storms started in November and were spaced rather evenly as judged from records at the Lucerne Valley Weather Station, about 10 miles from the study area, and from the general response of plant growth throughout the Mojave Desert.

The density of winter annuals was determined on 0.1 m² circular subplots located at intervals along several 50 m line transects extending from the center of the irrigated plots into the surrounding nonirrigated areas. Subplots were located at 0.5 m intervals within the marked irrigated area and at 1.0 m intervals in nonirrigated areas. The irrigated areas were not quite circular, owing to wind effects at the time of irrigation. Actual radii varied from 5 to 8 m, thus the number of treatment subplots varied from one transect to another. In addition, occasional subplots had full, dense shrub cover and were not scored for annuals. Winter annual plants were inventoried by species at the end of the growing season. This approach was feasible because the dry skeletons of individuals persisted for several months after senescence; many plants were still visible and recognizable even a year later. The perennial vegetation for the general Lucerne Valley area

Table 2. Density of summer annuals per m^2 in the summer of 1972 on the 10 m diameter irrigation plots and comparable adjoining areas.

	Rocky slope		Sandy bajada		
	A After irrigation	B Not irrigated	C After irrigation & before rain	C' Irrigation, and rain	D Rain only
SPECIES					
Pectis papposa	60	0	0	39	87
Aristida adscensionis	p*	0	0	0	0
Boerhaavia erecta	p	0	0	0	p
Bouteloua barbata	0	0	0	p	p
Bouteloua aristidoides	0	0	0	0	0
Euphorbia micromera	0	0	0	0	p
Euphorbia setiloba	0	0	0	54	22
Mollugo cerviana	0	0	0	0	p
Amaranthus fimbriatus	0	0	0	0	p

* p indicates the species presence on the irrigated site but not in sample plots.

has been described in other reports (Vasek et al., 1975a, 1975b). The data on perennial species given in this paper were obtained using 2 meter wide belt transects, permanent plot inventories and photographs taken at appropriate intervals of time. Taxonomic nomenclature follows Munz (1974).

Results

The response of annual and perennial plants to artificial and natural precipitation as observed in this study can be best analyzed in terms of: 1) the immediate or short term responses evident soon after watering took place and 2) the delayed or residual effects that persisted into subsequent growth periods.

Rocky slope.—The immediate result of irrigation on the rocky slope site (plot #1) on June 19th was to stimulate a pulse of growth in all the perennial species on the plot whereas plants in the surrounding area remained in summer dormancy. Two succulents, *Echinocactus polycephalus* and *Echinocereus engelmannii*, were the first to respond and underwent an obvious greening and swelling of the stems within 4 days. Two shrubs, *Larrea tridentata* and *Ambrosia dumosa*, responded more slowly. *Larrea* was observed to be actively growing and producing new leaves within ten days whereas *Ambrosia*, which was initially without any leaves, was fully foliated by 11 July (22 days). In all, 3 *Larrea*, 10 *Ambrosia*, and 6 succulent plants were stimulated to grow by two trailer tank loads of water.

In the case of annuals, three species, *Pectis papposa*, *Boerhaavia erecta*, and *Aristida adscensionis* were in full flower on the irrigated site on 11 July, 22 days after the first irrigation. *Pectis* was by far the most abundant and had a density of approximately 60 plants/m^2 (Table 2). The other species were represented by only one or two individuals. By 3 August *Pectis* had completed its life cycle and had withered away.

Bajada.—The perennial species on the sandy bajada site responded similarly to those on the rocky slope but their timing was different. *Larrea* plants on the study plot had developed noticeably denser foliage 18 days after the first irrigation had taken place. *Ambrosia dumosa* and *Cassia armata* were not obviously affected until after the second irrigation on 11 July. By 3 August *Cassia* was green and flowering and the *Ambrosia* had developed a few leaves. The net results of the irrigations was the activation of all perennial plants on the irrigation plot, namely 3 *Larrea,* 3 *Ambrosia*, and 2 *Cassia* bushes. The perennial plants in the surroundings persisted through this period in a state of slow decline.

No annuals were stimulated to grow on the bajada irrigation plot and in this respect there was a marked distinction between the two study sites. The failure of summer annuals to respond to irrigation in this instance cannot be ascribed to the absence of seed in the soil since the rain on 28 August, a month and one-half later, stimulated an abundance of annual production all across the northern part of the bajada including the study plot itself (Table 2). Plants of *Pectis papposa* and *Euphorbia setiloba* that germinated at this time were characteristically distributed uniformly in the spaces among the larger shrubs, a pattern that stands in contradistinction with that of winter annuals which will be noted later.

Residual effects.—Long term residual effects of the irrigation became surprisingly evident during the following year. Perennials on the plots of both sites showed greater vigor than those in the immediate surroundings during the summer of 1973. This was surprising since the north bajada area received a torrential downpour in late August 1972 and the entire study area received abundant winter moisture through the latter part of 1972 and early 1973. The sustained stimulation was most evident for *Larrea tridentata* which showed denser foliage and greater flower and fruit production on the watered plots (photographic record). The enhancement as judged visually was still somewhat apparent in the spring of 1974. The succulents on the rocky slope plot also appeared especially robust in the summer of 1974 when compared to other succulents nearby. The most astounding residual effects of all, however, concerns the winter spring annuals.

A profusion of annuals all across the Mojave Desert followed the abundant and evenly distributed moisture falling during the fall, winter, and spring 1972–73. However, the irrigation plots showed a marked reduction in annual plants (Table 3). The reductions were readily visible and appeared as a rather abrupt change in the vigor and density of annuals at the border marking the beginning of the sprinkled plots. The density of winter spring annuals in the spring of 1973 was inversely related to the summer moisture of 1972.

On the sandy bajada, the highest density ($64/m^2$) was found on the part of the bajada that did not receive summer moisture of any kind, the next highest density was on the part that received summer rain alone ($52/m^2$) and the lowest density ($40/m^2$) on the plot that received both summer irrigation and summer precipitations (Table 3). Similarly on the rocky slope, a low density ($24/m^2$) of winter annuals occurred on the plot that received summer irrigation, whereas a higher density ($43/m^2$) occurred in the surrounding area (Table 3). These data indicate that summer moisture in the form of artificial sprinkling, natural rain, or both may reduce annual density the following spring by up to about one half, and that the amount of reduction appears to be proportional to the amount of summer moisture received.

Reductions in density may take place through the development of patchiness

Table 3. Density of winter annuals per m² in the spring of 1973 on two summer irrigation plots and adjoining areas. A and C were irrigated, A and B received light early summer showers, C and D received summer rain, and E received no moisture at all during summer of 1972.

	Rocky slope		Sandy bajada		
	A	B	C	D	E
Introduced annuals					
Erodium cicutarium	.10	.80	9.90	15.79	43.56
Schismus barbatus	.31	.09	7.55	9.24	3.66
Subtotal	(.41	.89)	(17.45	25.03	47.22)
Intershrub native annuals					
Eriastrum eremicum	—	.13	3.06	3.57	.74
Eschscholzia parishii	10.52	24.35	.71	1.08	.15
Gilia latiflora	9.79	12.76	—	—	—
Gilia scopulorum	—	—	6.12	11.17	6.68
Others*	2.40	2.78	2.65	3.71	6.29
Subtotal	(22.71	40.02)	(12.54	19.53)	(13.86)
Shrub-associated annuals					
Phacelia fremontii	—	.33	9.59	6.37	2.23
Descurainia pinnata	.10	.16	—	.26	.59
Others**	.63	.88	.20	.76	.05
Subtotal	(.73	1.37)	(9.79	7.39)	(2.87)
Total density/m²	23.85	42.28	39.78	51.95	63.95
Number of subplots (0.1 m²)	96	453	98	342	202
Total plants observed	229	1915	390	1777	1252
% of subplots without plants	16.7	8.6	15.3	6.7	0.7
No. species observed	11	19	12	21	19

* Others on rocky slope: Chorizanthe rigida, Cryptantha circumscissa, Cryptantha micrantha, Eriogonum pusillum, Nama demissum, Phacelia crenulata, Salvia columbariae. Others on sandy bajada: Anisocoma acaulis, Camissonia brevipes, Chorizanthe thurberi, Eriogonum angulosum, Eriophyllum wallacei, Langlosia punctata, Lepidium sp., Malacothrix californica, Nemacladus rubescens; Others on both rocky slope and sandy bajada: Camissonia claviformis, Chorizanthe brevicornu, Cryptantha barbigera, Lupinus concinnus, Pectocarya heterocarpa.

** Others on rocky slope: Eucrypta chrysanthemifolia, Caulanthus cooperi; Others on sandy bajada: Linanthus parviflorus; Others on both rocky and sandy areas: Amsinckia tesellata, Chaenactis carphoclinia, Mentzelia affinis, Phacelia distans.

with large intervening bare areas or by a general thinning of the populations. Both responses are evident in the data.

The annual species observed may be considered according to the functional categories: introduced, intershrub native, and shrub associated native as outlined in Table 3. Introduced species, which appear less differentiated with regard to positive and negative shrub associations showed a significant reduction with summer moisture on the sandy bajada but not on the rocky slope (Table 4). Intershrub natives were significantly reduced at both study sites in response to summer moisture, and shrub associated annuals were not significantly different on either site (Table 4). These responses tended toward creating a patchiness in the overall annual community.

The development of patchiness in winter annuals is of common occurrence and

Table 4. Summary of mean plant density of winter annuals on two summer irrigated plots and adjoining areas; group data and notations taken from Table 3; S.E. = standard error of the mean; significance of comparison between irrigated and nonirrigated plots: NS = not significant; ** and *** = significant respectively at p = 0.01 and 0.001.

	Rocky slope				
	A—irrigated		B—not irrigated		
Annual type	mean	S.E.	mean	S.E.	Sig.
Introduced	0.41	0.25	0.89	0.16	NS
Intershrub	22.71	2.16	40.02	1.50	***
Shrub assoc.	0.73	0.16	1.37	0.27	NS
Total	23.85	2.62	42.28	2.52	***
	Sandy bajada				
	C—irrigated		D—not irrigated		Sig.
Introduced	17.45	2.40	25.03	1.41	**
Intershrub	12.54	1.87	19.53	1.59	**
Shrub. assoc.	9.79	2.13	7.39	0.90	NS
Total	39.78	3.56	51.95	2.15	**

is particularly evident in their frequent concentration around the bases of long lived shrubs (Went, 1942; Muller, 1953). Although the development of an annual halo around the base of shrubs is a general phenomenon that can be observed throughout the desert in years of good annual growth, the pattern is not always consistent from one place to another even when areas being compared are strikingly similar in physical characteristics. When the halo is apparent it is likely to be comprised of the plant species indicated in Table 3. In fact, some of these species show an almost complete restriction to the canopy of shrubs. The tendency for patchiness was especially pronounced on the irrigation plots where much of the intershrub space failed to produce plants (Tables 3 and 4). General observations showed that the pattern was much less evident on the adjacent part of the bajada that did not receive summer moisture. Here, the spaces between the shrubs were rather densely occupied by annuals.

At the species composition level of consideration differences between the two study sites were apparent. Altogether, 36 species were encountered. Fifteen of these were common to both sites and 21 were not common (Table 3). The contrasting rocky and sandy substrates are thought to be largely responsible for the differences in annual species composition although the perennial plant cover is very similar for the two sites.

Differences in the annual species richness within treatments on the sites, i.e. on the irrigated or nonirrigated plots, are rather pronounced in the recorded data but these differences in part represent differences in the number of plots sampled in the treatment areas (Table 4). All the species on the small irrigated plots on both sites were encountered in the more extensive samples taken in the immediate surroundings. However, the larger samples from the nonirrigated areas showed 8 additional species in the case of the rocky slope and 9 in the case of the bajada. Some of this difference in richness may be due to some kind of species specific inhibitory effect of summer moisture but is more likely a reflection of sample size since the number of species encountered per plot is essentially the same (.062 vs. .063) for the treatments.

Discussion

The foregoing observations on desert plant response to irrigation and natural precipitation pose several questions that merit further consideration. The first concerns the paradoxical results on whether summer annuals can be induced to grow with artificial moisture. The reason for the failure of irrigation to stimulate the growth of summer annuals on the bajada as it did on the rocky slope is not known but two factors are probably involved. First, the specific sites of germination (soil pockets between bare rock surfaces) on the rocky slope received considerably more water from the irrigation on a per unit area basis than did germination sites on the bajada, even though the same procedure was followed in both places. Runoff from the many uneven stone surfaces would result in the local concentration of water in the intervening soil pockets. Moisture penetration was more uniform on the bajada even though water repellant layers under the shrubs may have caused some channeling of the water entering the soil (Adams et al., 1970 and unpublished data). The amount of water infiltrating the soil is a significant factor with respect to seed germination and was evidently insufficient on the bajada but not on the rocky slope. The second factor that might be involved is the possibility of a positive preconditioning effect resulting from a light shower on the rocky slope in early June (Juhren et al., 1956).

The second major question posed by the irrigation experiments concerns the negative residual effect of summer moisture on winter annuals the following season. To our knowledge this effect has not been previously reported in the literature although a corollary is suggested by the observations that summer showers were less effective in producing summer annual growth when they followed seasons of good spring growth (Martin and Cable, 1974). In the case of our observations on winter annuals, we suggest three general working hypotheses as possible explanations: 1) the actual presence of good seeds in the soil seed reserve was altered; 2) the environment of the seeds was so changed that germination was inhibited; or, 3) survival after germination was reduced.

In the first case seeds could have been removed or destroyed by granivores and/or parasites. In this connection we did observe an increase in animal activity on the irrigation plots. *Larrea* bushes that were stimulated to produce new leaves by the irrigation were pruned rather heavily, presumably by jack rabbits, around 3 August. Perhaps more importantly, fresh digging around the bases of the perennial shrubs gave evidence of increased rodent activity in the area. Rodents utilize seeds of annuals as a primary food source (Soholt, 1973) and it appears plausible that their foraging intensity may have become more concentrated on these small 10 m diameter areas. The possible role of seed parasites, microbes, and invertebrates, in reducing the germinable seed population under such conditions is poorly understood. It seems safe to presume, however, that summer moisture would have stimulated the growth activity of both consumer and decomposer organisms that would have an impact on the seeds in the soil (Coleman, 1973).

We doubt, however, that the action of granivores and seed parasites would be sufficient to account for the reductions noted over such a short period of time. High soil seed reserves are known to persist for many years without replenishment as evidenced by the experiments of Epling et al. (1960) and the observations of Shreve (1951). Epling et al. were unable to detect a reduction in the population density of the desert annual *Linanthus parryae* over a period of 6 years even though each year throughout their study they removed all plants from their study plots before seed set. Shreve has routinely found abundant germination of annuals after extended drought periods of a decade and longer. Furthermore the recent studies reported by Nelson and Chew (1977) indicate that the soil seed reserve should remain adequate for full stand establishment much longer than one year.

A second general hypothesis, that summer moisture reduces winter annuals as a consequence of the action of inhibitors on germination and survival, has a number of facets that could involve both physical and biotic factors. Tevis (1958) suggested that water from wells and other commercial sources may be much less effective than natural precipitation in causing annual germination. The implication seems to be that something in tap water may have an inhibiting effect. Our studies are ambiguous on this point, since irrigation water from the same source produced an abundance of summer annuals on the rocky slope but none on the bajada. Furthermore, it is difficult to conceive of a mechanism by which the water applied could have had such drastic consequences by itself. The total amount of mineral added through the water was on the order of grams per 100 m^2 and was made up of constituents already abundant in the soil (Table 1). Salt redistribution in the soil profile due to capillary movement should also be expected to be slight because of coarse texture soils on the study plots. A triggering of biotic interactions by summer moisture are thus thought to provide the most likely explanation for the observed reduction in annual production. In view of the recent advances that have been made in studies on allelopathy (Whittaker and Feeny, 1971; Putman and Duke, 1974) it would be naive to suppose that such factors are not operative in the natural plant communities under consideration.

The contrasting distribution pattern of summer and winter annuals described above suggests that the summer annuals may produce materials that can inhibit the growth of the winter annuals later on. The reduction in the densities of winter annuals were always most pronounced in plots where summer annuals had flourished (Tables 2 and 3). Furthermore, the intensified halo effect on the plots receiving summer moisture was primarily the result of density reductions in the intershrub spaces that were formerly densely occupied by summer annuals. The accumulative effect of irrigation plus natural precipitation however, does not permit complete acceptance of the argument that summer annuals alone cause all the inhibition noted in the following generation of winter annuals. Recall that the early irrigations did stimulate perennial activity and any inhibitory materials or competitive advantages that might have been devloped by the *Larrea* and *Ambrosia* could contribute to the observed results.

Another likely facet of an inhibitory regime might involve the microflora and fauna which because of their abundance and general distribution, are in an ideal position to exercise a considerable influence on the biochemical environment of all soil seeds. These organisms would be, in all likelihood, stimulated into activity by moisture as evidenced by soil respiration studies (Wiant, 1967; Coleman,

Table 5. The contribution of annuals to plant species richness in geographical units of varying size.

Geographical unit	# Sp	% Annuals	Source
California Deserts	1084	39	Johnson (1968)
Deep Canyon Drainage	334	47	Floristic list for Deep Canyon watershed (1973)
Johnson Valley	87	60	Vasek et al. (1974) Plant list from combined study plots & transects
Rocky slope (Lucerne Valley)	28	82	This study
Bajada (Lucerne Valley)	25	88	This study

1973). The residual consequences from brief periods of growth activity by soil microbes on seed germination can at this point only be conjectural.

Finally, moisture falling at the "wrong" time of year may stimulate the seeds themselves to produce inhibitory substances which keep them from germinating in the "wrong" season. Such inhibitory substances thus produced might tend to persist throughout the following favorable season. The demarcation in germination between summer and winter annuals is rather sharp. The former do not germinate in the winter even though abundant moisture is available and the latter do not germinate in the middle of the summer regardless of how much rain falls.

The reduced vigor of the annuals occurring on the irrigation plot also suggests that growing conditions were unfavorable even after germination did occur.

The last question of significance posed by this study relates to the place of annuals in desert plant communities in general. Floristically, the contribution of annuals on the bajada and rocky slope is much greater than would be expected from the life form spectra usually ascribed to deserts (Table 5). The generalization that approximately half of the plant species found in deserts are annuals (Cain and Castro, 1959) does not hold when looking at specific habitats or community types. The dramatic increase in the percentage of annuals in scaling down from the whole California desert area to the sandy bajada and rocky slope study sites (Table 5) tends to emphasize the significance of annuals in particular segments of desert vegetation. The recent recognition that in favorable years the production of annuals may exceed that of perennials (Norton, 1974) underscores our contention that the community ecology of deserts is deeply involved with ephemeral plants.

Changes in annual species composition from one locality to another without corresponding changes in the perennials, as is evident on the bajada and rocky slope study sites (Table 3), suggests that winter annuals may act as plant communities themselves somewhat independent of the longer lived shrubs. To illustrate this point further, a matrix of similarity coefficients was prepared (Table 6) from vegetation inventories of the bajada and rocky slope and three additional reference sites chosen from Vasek et al. (1974), in order to provide a general representation of the greater Lucerne Valley area (Fig. 1). The similarity among the sites on the basis of perennial plant cover ranged from 0.48 to 0.86 but fell to values between 0.01 and 0.23 when based on the density of annual plants. The

Table 6. Similarity coefficient matrix based on perennial plant cover (upper right hand portion) and annual plant density (lower left hand portion) for 5 study areas in the general Lucerne Valley region (see Fig. 1). * Similarily coefficients were calculated after Jacard, $C = 2W/(a + b)$ (Phillips, 1959).

Study areas	(C based on perennials)				
	1	2	3	4	5
1	—	.85	.71	.60	.70
2	.06	—	.58	.48	.58
3	.01	.02	—	.86	.82
4	.03	.04	.13	—	.77
5	.05	.23	.05	.05	—

similarity between the rocky slope (1) and the bajada (2) of 0.86 in the first instance and 0.06 in the second illustrates how similar and yet how different two neighboring areas can be (Table 6). The low similarity indicated in relation to annuals reflects variations in the substrate of the different areas to a large extent, and suggests the possiblity of genetic evolutionary units fine tuned to specific edaphic conditions. Annuals are seldom recognized as being part of such highly integrated plant communities but are more often regarded as an opportunistic life form charactierizing early successional stages of disturbed vegetation (see Vasek, 1978).

It might be argued that differences in the amount and timing of rainfall may account for some of the spatial variability in annuals noted here since species specific germination patterns have been reported in relation to different temperature and moisture regimes (Went, 1949; Tevis, 1958b; Beatley, 1974). In the cases reported however, such effects are though to be minimal since all plots were located in the general Lucerne Valley region where the winter precipitation appears to have been rather uniform over large areas.

The shift in species composition in going from one locality to another is most apparent with regard to the kinds of annuals that grow in the winter and spring as contrasted with those that grow in the summer. Species that grow in response to summer precipitation are comparatively few in number and are generally distributed in all available habitats (Table 1). They have the particular distinction of possessing the C-4 photosynthetic pathway (Johnson, 1975) which places them in a physiological group that has been regarded as having an unusual potential for weediness (Black et al., 1969). The winter annuals on the other hand, appear to be rather closely attuned to specific conditions. Their greatest richness occurs in the areas showing high stability in terms of both plant cover and surface characteristics (Vasek, 1978). The species composition shifts rather dramatically from one surface type to another (Table 4). This differentiation on the local scale presents an interesting contrast to Shreve's (1964) observation that ". . . the ephemeral vegetation on the Sonoron Desert falls into a smaller number of regional categories than does the perennial vegetation." On the local scale the annual communities clearly show the greatest diversity.

Acknowledgments

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Relict Survival of the Sea Otter in Central California and Evidence of Its Recent Redispersal South of Point Conception

Stephen Leatherwood, Linda J. Harrington-Coulombe, and Carl L. Hubbs

Abstract.—Historically the sea otter abounded around the North Pacific Rim from northern Japan to central Baja California, Mexico. But the population south of Alaska was so heavily hunted in the 18th and 19th centuries for its valuable fur that by very early in the 20th century it generally was assumed to have been extirpated there. In 1938, a remnant population was reported along the nearly inaccessible coast of southern Monterey County, California. Extensive exploration of the reefs from northern Washington to northern Baja California between 1913 and 1926, resulting in sightings only at Bixby Creek, supports the contention that the species persisted nowhere else in that area. The population has since markedly increased in central California, resulting in expansion of the species' range. Twenty four recent records south of Point Conception provide increasing evidence of limited redispersal there.

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The biology and status of the sea otter, *Enhydra lutris,* have been summarized by Kenyon (1969) and Miller (1974). Historically the species was distributed from northern Japan to central Kamchatka, north to the Commander and Pribilof Islands, throughout the Aleutian Chain, and along the North American mainland from the Alaskan Peninsula south to Morro Hermoso, Baja California (27°32′N) (Figure 1). The well known reduction of the species' numbers due to hunting in the 18th and 19th centuries nearly exterminated the stocks throughout its range (Kenyon, 1969). That the California stock still survived, however, was evidenced by a report of sea otters at Point Sur (Bryant, 1915) and the "rediscovery" of its population at Bixby Creek in Monterey County, California, in 1938 (Bolin, 1938). In reporting 150 sea otters off the mouth of Bixby Creek and additional smaller herds somewhat farther south, Bolin (1938) wisely assumed that this remnant population had probably been residing in the vicinity for years. He also implied that with the full protection initiated in 1913 by the California Department of Fish and Game (CFG) an increase in the population could be anticipated.

This rugged coast was virtually inaccessible until the coast highway was opened in 1937. When Hubbs visited Gorda in southern Monterey County in mid-May of 1916 he clearly observed a sea otter at close range. Later it was learned that Dr. Joseph Grinnell, Director of the University of California Museum of Vertebrate Zoology, had known of a small relict population in this area prior to 1916. Grinnell and local ranchers and CFG personnel, who also knew of this population, suppressed the information for fear someone might collect the last remnant.

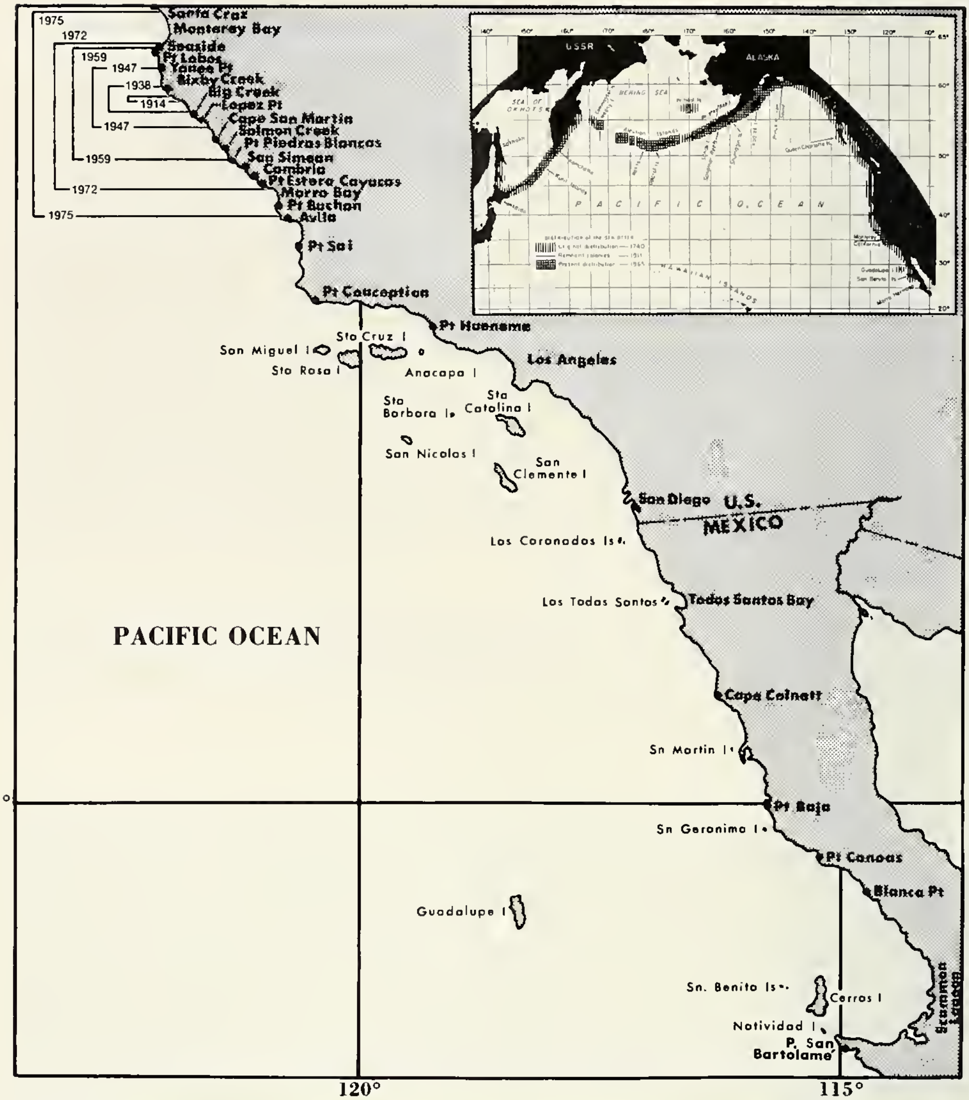

Fig. 1. Historical distribution of the sea otter in the North Pacific (from Kenyon, 1969) and current reported limits of the established southern stock (courtesy Daniel J. Miller).

Oyer (1917) reported two sea otters at Monterey in 1916, and Farnsworth (1917) reported 31 sea otters "off Catalina Island."

The Farnsworth record has been ignored by Kenyon (1969) and others as of questionable validity. If there were, indeed, otters at Santa Catalina Island as late as 1917, it may safely be assumed that this relict aggregate was harrassed into extinction, as enforcement in the insular area was difficult at that time. Kenyon (1969) reported that a remnant population at San Benito Islands, Baja California, was hunted to extinction in 1919, and that a small population at Queen Charlotte Islands, British Columbia, was extirpated by hunters in 1920. Thus the remnant population at Point Sur, California was very probably the only viable aggregation that survived beyond 1920 south of Prince William Sound, Alaska. No wanderers were reported in Baja California or Caifornia outside Monterey County from 1917 to 1940.

The questionable 1926 observation of a sea otter at Guadalupe Island, reported in this paper, if valid, was most probably also an isolated remnant. In exploring most of the intertidal reefs from northern Washington to northern Baja California, from 1913 through 1926, Hubbs observed only 2 otters, the individual at Gorda in 1916 reported above and another at Cape San Martin in 1915. Hubbs did not survey the Point Sur area during this period.

By 1976 the California stock of sea otters was established from Santa Cruz (39°00′N) to Pecho Rock approximately (34°30′N) (Daniel J. Miller CFG, personal communication, 1976).[2] One or two individuals were sighted in 1973 and 1974 off Shell Beach, San Luis Obispo County, during routine aerial censuses. Inasmuch as control of the expansion of the sea otter population into historically occupied areas has been considered (Wild and Ames, 1974) records concerning dispersal of this artificially isolated population are of particular interest.

Since the extirpation of the San Benito Islands stock in 1919, sightings of only 15 (possibly only 13) sea otters south of the current established range have been published (Figure 2). These are: A. one in the kelp off Santa Barbara Island in 1940 (von Bloeker, 1967); B. one on the northwestern side of Santa Barbara Island in 1940 and two at Anacapa Island in 1943 (Kenyon, 1969); C. two on the south side of Bat Rock, San Miguel Island (≈34°00′N) in 1954 (Allanson, 1955); D. three at Point Conception (34°00′N) in 1957 (Boolootian, 1961); E. and F. one each from Santa Barbara (34°24′N) and Malibu Point, Santa Monica Bay (34°02′N) during a one-month period in 1967 (perhaps the same individual at both locations) (Bissell and Hubbard, 1968); G. one from inside Los Angeles Harbor, near the 22nd Street Landing (Daugherty, 1972); H. one from the kelp bed off Point Loma, San Diego, California (approximately 32°40′N, 117°51′W) in 1969 (Anonymous, 1970, Gilmore, 1976); I. one from Imperial Beach, San Diego County, California in 1976; (Gilmore, 1976); J. one possible sighting from San Clemente Island, an unverified report to the CFG reported by Hubbs (1954). With the exception of this last, which was an acknowledged rumor unconfirmed, we have no particular doubts about the credibility of any of these records, though they are reported in highly varying detail and several might be accepted with some reservations.

This paper reports 15 additional records, of varying certainty, of sea otters south of Point Conception. Details of each sighting, numbered to correspond with the locations shown on Figure 2, are as follows:

1. Robert F. Dill informed Conrad Limbaugh, Scripps Institution of Oceanography (SIO), that several abalone fishermen had reported frequently seeing otters in Santa Barbara County as far south as Point Conception: although the reports were unconfirmed, Dr. Dill felt sure that the fishermen's concern about the sea otters assured the reliability of the observations (from Hubbs' records 21 September 1954).

2. During a 1953 flight on a U.S. Coast Guard reconnaissance plane, Hubbs observed a single sea otter in the kelp off the south side of San Miguel Island.

3. In April 1971, Henry Hoover found a sea otter on the west end of San Miguel

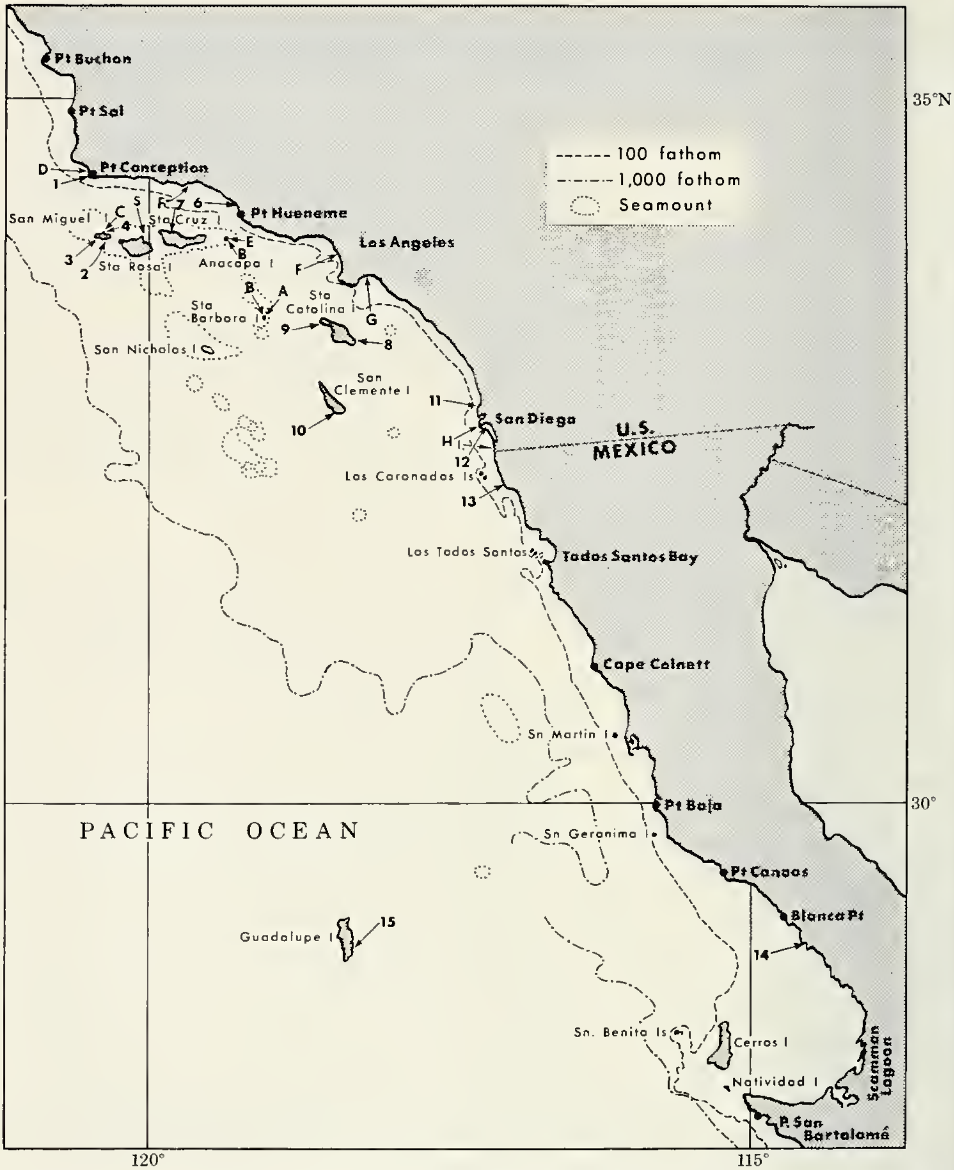

Fig. 2. Locations of sea otter sightings. (The letters correspond to published records. The numbers correspond to numbered details of each sighting in the text.)

Island near Symington Cove, Point Bennett (H. Hoover, CFG, personal communication to C. L. Hubbs, 19 November 1974).

4. C. Carr Tuthill, a former employee of SIO, and familiar with sea otters, reported seeing sea otters in the northwest end of Cuyler's Harbor on San Miguel Island on 9 August 1954, perhaps the same animals reported by Allanson (1955). Other fishermen also reported having seen otters at this location (from Hubbs' notes, 26 August 1954).

5. On 15 December 1973, Laurence Hall reported to the CFG that while fishing from a party boat he had observed a single sea otter off the northeast tip of Santa Rosa Island, one mile from shore; no confirmation was obtained by CFG personnel (Daniel J. Miller, personal communication, 12 November 1974).

6. The CFG confirmed a sighting of a sea otter inside the harbor at Ventura Marina (34°09'N) on 24 August 1974. This otter, which was apparently in the marina during most of July and August 1974, patrolled the region daily, coming into boat docks, and was frequently observed feeding on shellfish. An article pertaining to this sighting appeared in the *Star Free Press*, Ventura County, on 29 July 1974 (Daniel J. Miller, personal communication, 1974).

7. The CFG also reports a sighting by Fred Clogston and others of California State Polytechnic University, San Luis Obispo of an otter at Diablo Point, Santa Cruz Island, on 14 December 1974 (Jack A. Ames, personal communication, 3 January 1975).

8. Paul Streate informed Conrad Limbaugh that two young sea otters had been observed east of Avalon, Catalina Island, by an abalone diver (Hubb's notes, 19 September 1954). The observation was not confirmed by Limbaugh or Streate.

9. On 10 December 1972, Morris F. Wintermantel, of the Naval Ocean Systems Center, observed two sea otters off the west end of Santa Catalina Island. The animals approached to within 20 yards of the vessel and were clearly visible and identifiable (Leatherwood notes, April 1974).

10. On 21 June 1972, a member of the security patrol on San Clemente Island, returning from the south end of the island, reported having seen a sea otter off China Point. Leatherwood (field notes, 1972) drove to the area and because of failing light, only briefly observed a sea otter traveling south through the kelp. It was not present in that area the following day.

11. In June of 1969, the same year in which a confirmed sighting of an otter was made in the Point Loma kelp bed in December (Anonymous, 1970, Gilmore, 1976), Louis H. Zinn, an SIO student and part-time commercial fisherman, reported having seen a single sea otter close to a minor kelp bed near shore in La Jolla Bay (between "the Cove" and "the Caves," off a point known locally as "The Clam") (Hubbs' notes, 23 March 1975). Zinn observed the animal for 10–15 minutes approaching as near as ten feet.

12. On 8 May 1951, Captain William Miller of the F/V SILVERGATE reported having seen a pair of sea otters outside Ballast Point on Point Loma. He said that he had seen them about six times and suspects they may be residing in the area (Hubbs' notes, 9 May 1951).

13. Richard J. Beck, a student, reported (via Professor Keith W. Radford) having seen three otters on 5 April 1965 inside the kelp just north of El Sauzal school, Baja California. The otters, estimated to be nearly 4 feet long, remained in the area all day, and were reported to be feeding on purple urchins, *Strongylocentrotus purpuratus* (from Hubbs' notes, 8 April 1965). From the detailed notes accompanying the observation, the identification appears reliable.

14. The late Dennis Bostic, then of Palomar College (personal communication, November 1974) reported having seen a single sea otter off Point Falsa on the northeast side of Bahia Sebastian Vizcaino on 9 April 1971. Because the single individual was observed only briefly, the reliability of the identification is subject to some question.

15. In 1928, Harry Fisher, one of those who had collected two bull fur seals from Isla Guadalupe in 1928 for the San Diego Zoo, volunteered that he saw a sea otter on 1 January 1926 in the "kelp" immediately north of a pinnacle rock about 4 miles north of the south end of the island. He said that the otter was about 3 feet long and swam along at the surface so close that he could have reached it with an oar. He had no question on the identification (Hubbs' notes, 9 January 1950). Although there are no other acknowledged records of sea otters at Isla Guadalupe, and although there are no beds of kelp of the species preferred by otters, Scammon (1874, p. 69) listed the island among the "choice" places to pursue otters during the active days of otter hunting in Baja California and there are newspaper accounts of ships arriving from this island with sea otter pelts (e.g. MacMullen, 1968). These data lend some credibility to the somewhat questionable observation in 1926.

These observations are presented to document that sea otters have occasionally wandered south of Point Conception for over 30 years and to suggest that their continued dispersal can be expected.

The agency primarily responsible for monitoring movements and status of the sea otter in California is the CFG. Photographic verification is also highly desirable.

Sea otter sightings and strandings should be reported to that office in as much detail as possible, including such data as date, time, precise location, number and size of individuals, behavior and basis for identification.

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Footnotes

[1] Current address: Hubbs/Sea World Research Institute, 1700 So. Shores Rd. San Diego, California 92109.

[2] The past distribution of the species and established populations by 1976 are presented in Figure 1.

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The Subspecific Status of *Onychomys torridus clarus* Hollister 1913 (Rodentia: Cricetidae)

John O. Matson and Richard D. Friesen

Abstract.—The subspecific status of various populations of the southern grasshopper mouse (*Onychomys torridus*) was examined using univariate and multivariate procedures. Sex, age and individual variation were assessed for the two populations with the largest sample sizes. Twenty four populations were analyzed for patterns of geographic variation corresponding to currently recognized subspecific boundaries of *Onychomys torridus clarus*, *O. t. longicaudus*, and *O. t. pulcher*.

The Museum, Michigan State University, East Lansing, Michigan 48824, and Natural History Museum of Los Angeles County, Los Angeles, California 90007.

During the course of a study of the distribution of rodents from the southern Owens Valley of California, Matson (1972, 1976) collected specimens of the southern grasshopper mouse (*Onychomys torridus*) from within the published geographic range of the subspecies *O. t. clarus* Hollister 1913. These specimens proved difficult to identify to subspecies on the basis of the morphological characters given by Hollister (1914). At that time, Matson (1972) did not have available a sufficiently large series of *O. t. clarus* or its two contiguous subspecies (*O. t. longicaudus* Merriam 1889 and *O. t. pulcher* Elliot 1904) to make definite subspecific determination. These specimens were simply identified on the basis of geographic locality as given by Hollister (1914) as subsequently modified by Grinnell (1933) and Hall and Kelson (1959).

Recently, the Natural History Museum of Los Angeles County (LACM) acquired a large series of *Onychomys torridus* from within the ranges of the above mentioned subspecies. These, along with specimens in the Museum of Vertebrate Zoology, University of California at Berkeley (MVZ) and the mammal collections, California State University, Long Beach (CSULB), have provided a sufficient number of specimens to evaluate the subspecific status of *O. t. clarus*. We have not examined type specimens; however, topotypes of all three subspecies were examined.

According to Hollister (1914:465), *O. t. clarus* differs from *O. t. longicaudus* by being ". . . clearer and brighter colored . . . . Skull as in *longicaudus*, but with anterior palatine foramina averaging longer, reaching backward fully to line of fronts of first molars." It differs from *O. t. pulcher* by being ". . . much more intensely pinkish-cinnamon." Van Cura and Hoffmeister (1966) question the use of color and length of the palatine (incisive) foramen in identifying specimens from Arizona. As reviewed by Matson (1972), rodents from the southern Owens Valley of Inyo County, California, tend to show a distinct, bright reddish or pinkish color. Matson (1972) concluded that the distinct color is correlated with the presence of borates in the soil which "bleach" the pelage.

The objective of this study is to assess the taxonomic status of *O. t. clarus* based upon 20 body and cranial characters.

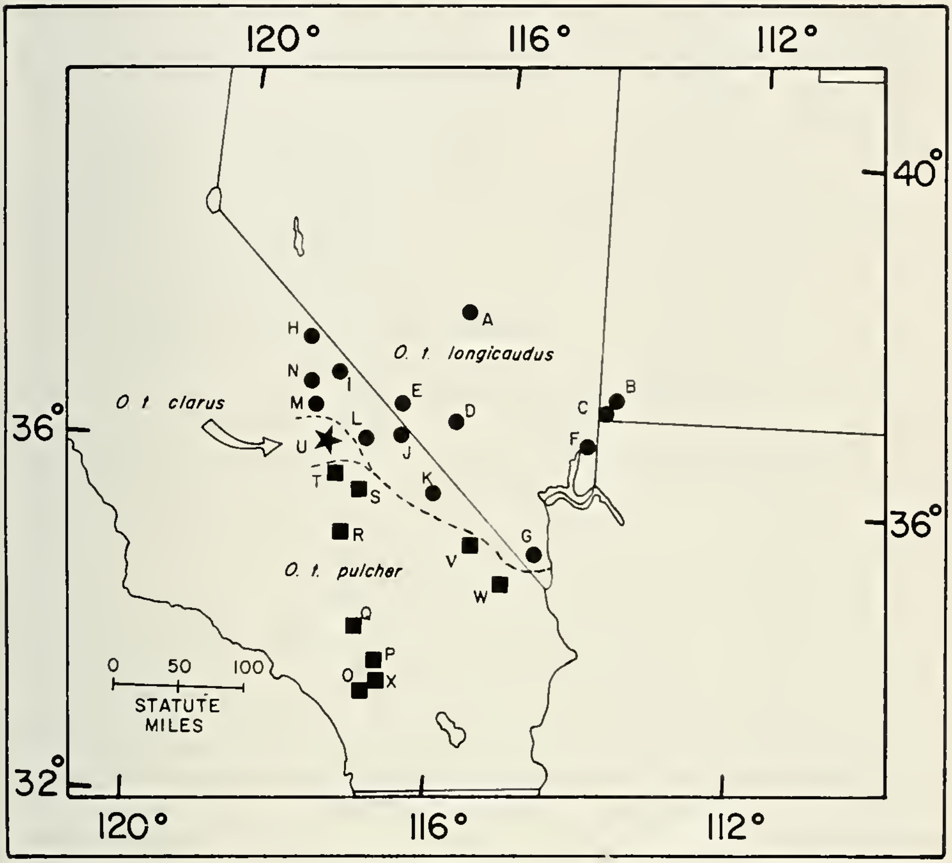

Fig. 1. Map showing sample populations used in this study. Dotted lines indicate currently recognized boundaries of subspecies as given in Hall and Kelson (1959). See text for further explanation.

Methods and Materials

Characters.—External measurements were taken from specimen labels. Cranial measurements were taken, in millimeters, by Matson using a measuring microscope similar to that described by Anderson (1968). Depth of the braincase was taken as described by Hooper (1952). The remaining cranial measurements are as described in Cockrum (1962).

Two qualitative characters of the skull were examined. The development of a spine on the posterior margin of the bony palate was scored as described by Van Cura and Hoffmeister (1966), as follows: (1) prominent spine; (2) a well developed convexity; (3) a slight convexity; (4) no spine or even concave. The other qualitative character is the extension of the incisive foramen relative to a plane at the front of the first molars. Scoring was done as follows: incisive foramen ends (1) in front of molars, (2) on line with molars, (3) behind molars.

Sample populations.—Specimens of *Onychomys torridus* (n = 304) were examined from 78 localities within the ranges of *O. t. clarus*, *O. t. longicaudus*, and *O. t. pulcher*. In most cases, because of small sample sizes, we pooled specimens from nearby localities as shown in Figure 1. These pooled localities correspond to the letter designations and subspecies (sample size in parentheses), as follows: *O. t. longicaudus*—A, Railroad Valley, Nye Co., Nevada (7); B, near Saint George, Washington Co., Utah, type locality (9); C, Beaverdam Slope, Washington Co., Utah (4); D, Nevada Test Site, Nye Co., Nevada (53); E, Grape Vine Peak, Nye Co., Nevada (7); F, Virgin Mtns., Clark Co., Nevada (4); G, Searchlight, Clark Co., Nevada (2); H, near Benton, Mono Co., California (7); J, Death Valley, Inyo Co., California (12); K, Shoshone, Inyo Co., California (1); I, Deep Springs, Inyo Co., California (1); L, Emigrant Springs, Inyo Co., California (9); M, Independence, Inyo Co., California (5); N, Goodale Creek, Inyo Co., California (2). *O. t. pulcher*—V, Kingston Mtns., San Bernardino Co., California (6); W, Providence Mtns., San Bernardino Co., California (29); X, Joshua Tree Natl. Mon., Riverside Co., California (11); O, near Cabazon, Riverside Co., California (21); P, near Morongo Pass, San Bernardino and Riverside Co's., California, type locality (4); O, Victorville, San Bernardino Co., California (26); R, near Randsburg, Kern and San Bernardino Co's., California (58); S, Argus Mtns., Inyo Co., California (6); T, Little Lake, Inyo Co., California (1). *O. t. clarus*—U, southern Owens Valley, Inyo Co., California, type locality (19). A detailed list of specimens examined can be obtained from Matson.

Statistical analysis.—For each character, standard statistics (mean, range, standard deviation, and standard error) were computed for each age and sex at each pooled locality, using Biomedical program BMDP3D (Dixon, 1970). This program also performed Students t-test between selected groups. To assess geographic variation, a stepwise discriminant function analysis and a canonical variate analysis which optimizes separation between groups (BMDO7M) were performed. All computations were run on IBM 360 computers at the University of Southern California Computer Center and the University of Connecticut Computer Center.

Non-geographic Variation

Age variation.—Each specimen was assigned to one of the six age classes described by Van Cura and Hoffmeister (1966). Only specimens of age class III and above were measured in this study since these were considered to be adults by Van Cura and Hoffmeister (1966). In two of our largest series (population D, n = 53, population R, n = 58), age class III showed marked differences from age class IV. Using Students t-test, we tested for differences between these two age classes for each character independently. Similar results for non-geographic variation were found for both populations D (Nevada Test Site) and R (Randsburg). Results of the analysis for population R are given in Table 1. Nine of the 20 characters show significant differences (two at $p < .05$ and seven at $p < .01$). Consequently, age class III was not grouped with the remaining age classes. No significant differences were found between age class IV and VI, so these were lumped to form one "adult" age sample.

Secondary Sexual Variation.—There was no evidence that any differences existed between the sexes for the characters studied ($p > .1$ for all comparisons). Therefore we combined sexes in subsequent analyses.

Individual Variation.—External body (skin) measurements generally have higher coefficients of variation (CV) than cranial measurements. The CV's reported here for cranial measurements (Table 1) are in the range of those expected

Table 1. Comparison of age classes III and IV from a single pooled locality at Randsburg (Population R in Figure 1). Significant differences determined by Students t-test (* P < .05; ** P < .01).

	Age III				Age IV				
Character	N	Mean (range)	SD	CV	N	Mean (range)	SD	CV	t-value
Total length	24	128.04 (121–141)	4.66	3.64	20	132.10 (127–138)	3.45	2.60	3.22**
Tail length	24	43.46 (35–49)	2.78	6.40	20	42.95 (36–48)	3.05	7.10	0.58 ns
Hind foot length	24	19.04 (17–20)	0.86	4.52	20	19.10 (17–21)	1.02	5.34	0.21 ns
Ear length	24	16.38 (14–18)	1.06	6.47	20	16.55 (15–20)	1.15	6.94	0.53 ns
Development of spine	26	3.58 (3–4)	0.50	13.97	21	3.62 (3–4)	0.49	13.54	0.29 ns
Extension of incisive foramen	26	2.12 (1–3)	0.86	40.57	21	1.76 (1–3)	0.83	47.16	1.42 ns
Basilar length	26	18.70 (17.7–19.8)	0.53	2.83	21	19.25 (18.7–19.7)	0.29	1.51	4.25 **
Postpalatal length	26	8.63 (8.1–9.2)	0.27	3.13	21	8.98 (8.7–9.3)	0.16	1.78	5.02 **
Length of palatal bridge	25	4.33 (4.0–4.7)	0.18	4.16	21	4.45 (4.1–5.0)	0.18	4.04	2.22 *
Palatilar length	26	10.06 (9.6–10.8)	0.30	2.98	21	10.23 (9.9–10.7)	0.19	1.86	2.73 **
Length of maxillary toothrow	26	3.73 (3.5–4.0)	0.12	3.22	21	3.75 (3.5–4.0)	0.12	3.20	0.57 ns
Diastemal length	26	5.72 (5.4–6.1)	0.22	3.85	21	5.86 (5.6–6.1)	0.15	2.56	2.57 *
Length of incisive foramen	25	4.27 (4.0–4.7)	0.20	4.68	21	4.33 (4.1–4.6)	0.15	3.46	1.15 ns
Postnasal length	26	15.54 (14.9–16.5)	0.40	2.57	21	15.90 (15.5–16.7)	0.32	2.01	3.40 **
Greatest length of skull	26	24.44 (23.2–25.7)	0.58	2.37	20	24.86 (24.1–25.6)	0.37	1.49	2.84 **
Nasal length	26	8.90 (8.3–9.5)	0.30	3.37	20	8.98 (8.4–9.3)	0.20	2.23	1.09 ns
Zygomatic breadth	26	12.67 (11.6–13.6)	0.42	3.30	21	13.18 (12.7–14.0)	0.32	2.40	4.48 **
Breadth of braincase	26	10.86 (10.3–11.3)	0.25	2.30	21	10.97 (10.6–11.5)	0.24	2.19	1.49 ns
Least interorbital constriction	26	4.77 (4.6–5.0)	0.14	2.29	21	4.81 (4.6–5.1)	0.11	2.29	1.25 ns
Depth of braincase	26	8.96 (8.6–9.3)	0.18	2.01	21	8.98 (8.7–9.3)	0.17	1.89	0.40 ns

Table 2. Ranked order of variables as determined by the stepwise discriminant analysis. An * indicates F-values significant at $P < .05$.

Variable	F to remove
Diastemal length	2.82*
Maxillary toothrow	2.25*
Interorbital constriction	1.97*
Length of palatal bridge	1.78*
Palatilar length	1.89*
Length of incisive foramen	1.69*
Nasal length	1.29
Breadth of braincase	1.22
Development of spine	1.23
Postpalatal length	1.06
Postnasal length	1.21
Depth of braincase	1.27
Extension of incisive foramen	0.60

for small rodents. The two qualitative characters have high CV's which would tend to question their utility in assessing geographic variation.

Geographic Variation

Univariate comparisons of the characters did not exhibit any discernable pattern of geographic variation. Thus, in order to assess the relationships between populations we relied upon the multivariate analyses. Since the multivariate analyses require complete data for each specimen, external measurements were excluded from analysis because a number of localities were represented by skulls only. In addition, zygomatic breadth was excluded as a character because many zygoma were broken on skulls. Because of the age restriction to classes IV through VI, the number of pooled localities was reduced to 20 and the number of specimens reduced to 147.

The results of the stepwise discriminant analysis are given in Table 2. The characters are ranked in order of their discriminatory ability. Of the 15 original characters, 13 were entered by the stepwise procedure; although only the first six had significant F-values. In separating the three subspecies, the two characters that Hollister (1914) believed to be important (spine and incisive foramen) ranked 9th and 13th, respectively, indicating that they are not significantly useful in classifying populations to subspecies. The program also assigns each specimen into a classification matrix based upon degrees of phenetic overlap (see Bogan, 1975). Table 3 shows the results of this classification procedure. As can be seen, the classification matrix does not correspond well to our *a priori* assignments. This is especially evident in the larger samples, in which there is a more or less even spread of individuals across the supposed subspecific boundaries.

Results of the canonical variate analysis are given in Figure 2. Each group mean for the canonical variables is surrounded by a 95 per cent conifidence radius as discussed by Seal (1964) and Bogan (1975). This radius would optimize the separation of groups. The first two canonical variates account for only 43.78 per cent of the total dispersion. Six canonical variates are required to account for 82.76 per cent of the variation. Thus, it is apparent that the characters we used

Table 3. A classification matrix for adult *Onychomys torridus* based upon discriminant analysis. Localities are by letter designation as in Figure 1. Numbers to the far left refer to the *a priori* groupings (see text for explanation of sample sizes). For each sample, the n of which is listed on the left, the number correctly classified appears on the diagonal. Numbers of specimens to the right or left of the diagonal represent misclassifications.

	A	B	C	D	E	F	G	H	J	V	W	X	O	Q	R	S	U	L	M	N
2 A	1									1										
2 B		2																		
4 C			4																	
19 D	2			3	1		1	1	4		1				2		1	3		
5 E					4										1					
1 F						1														
1 G							1													
4 H								2	1					1						
5 J	1								4											
4 V	1	1								2										
14 W		1		1	1			1			6	1		1	1		1			
7 X	1			1								4							1	
8 O								1			2		5							
21 Q	1								1	2	3	1		10	1			1	1	
30 R	1	2		3	2	1		2	1	2	3	2	1	2	6			1	1	
3 S								1								2				
9 U			1												1		6	1		
5 L				1					1			1		1				1		
2 M														1					1	
1 N																				1

do not adequately separate the subspecies as currently recognized. Certain trends, however, can be detected. Inspection of Figure 2 reveals two major clusterings when the group means of the first two canonical variates are plotted. One cluster is composed of samples C, H, O, U, E, and J, which (except for sample O) would correspond to *Onychomys torridus longicaudus* and *O. t. clarus*. In other words, *O. t. clarus* cannot be adequately separated from *O. t. longicaudus*. Sample O, which groups with *longicaudus*, is geographically at the western margin of *O. t. pulcher* and may show more affinity to the coastal subspecies *O. t. ramona* which was not examined. The second cluster includes samples currently recognized as *O. t. pulcher*, with the exception of sample L (Emigrant Springs, n = 5) which is *O. t. longicaudus* in Hall and Kelson (1959). In addition, the small sample (n = 2) from the type locality of *O. t. longicaudus* (locality B in Figure 1) and other small samples (n = 1–2) from within the supposed range of *O. t. longicaudus* (i.e., samples A, F, G, M, N in Figure 1) show greater affinity with *O. t. pulcher*. It is interesting to note that population D lies almost directly between the two major clusters. This might indicate an area of extensive intergradation between the two groups.

We conclude from this study that the population of *Onychomys torridus* from the southern Owens Valley does not warrant separate subspecific status. It seems best for now to include it with *O. t. longicaudus*. One problem that remains is determining the status of the other two subspecies, *longicaudus* and *pulcher*, which show considerable overlap. Evaluation of their status must await a more thorough study of *Onychomys torridus* from throughout its range.

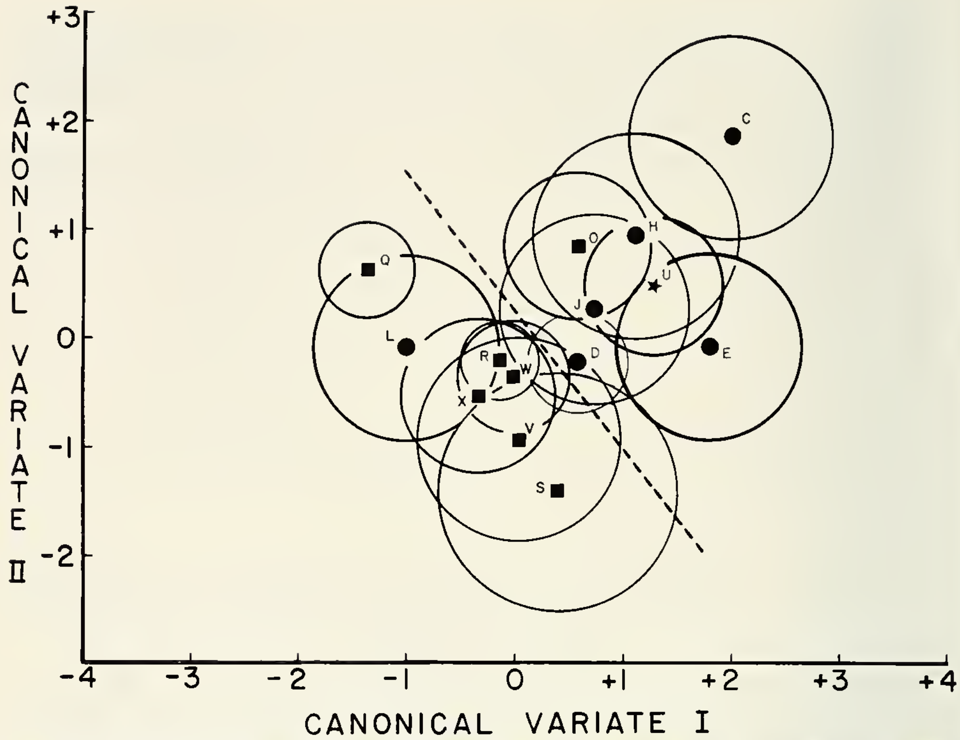

Fig. 2. Projection of sample population means (for N > 2) onto the first two canonical variates surrounded by 95 per cent confidence radii (see text).

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Pollination Ecology of *Chlorogalum pomeridianum* (D.C.) Kunth. (Liliaceae)

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Abstract.—The pollination ecology of *Chlorogalum pomeridianum* was studied. This lily is a member of the Southern California coastal scrub community. Flower opening occurs at dusk and happens in a few seconds. The flowers deliquesce later the same evening. Large native bees appear to be the only effective pollinators. Self compatibility and the ability to self pollinate were studied.

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Introduction

Plant reproduction and the survival of plant pollinators are frequently interdependent (Powell and Mackie, 1966; Levin, 1971; Macior, 1971; Cruden, 1972). Although co-adaptation of pollinator behavior, plant morphology and physiology has perhaps been best documented in the tropical orchids (Kullenberg, 1956, 1961; Dodson, 1962; Dodson et al., 1969), numerous papers on less specialized, but significant plant and pollinator relationships have recently been published (for instance, Thein, 1969; Duffield, 1972; Kiang, 1972; Cruden, 1973). A previously unstudied plant pollinator association exists between *Chlorogalum pomeridianum* (D.C.) Kunth., a component of the coastal scrub community of Southern California, and large native bees.

Chlorogalum pomeridianum is the most abundant member of its genus. It occurs below 5000 feet chiefly in the dry valley grassland, coastal scrub and foothill woodland communities in California (Munz and Keck, 1970). From seed, it takes 5 to 7 years to reach reproductive age (Hoover, 1940). Flowering occurs from May to August in its various habitats. The inflorescence is a large panicle of up to 200 flowers of which only a few are open each evening. Although open only a few hours, they are visited by numerous potential pollinators. The ovary of the flower is composed of three locules, each locule having two ovules. Vegetative reproduction can also occur when plants are mature by longitudinal splitting of the bulb (Hoover, 1940).

We investigated the pollination ecology of *C. pomeridianum*, and specifically studied its pollen vectors, its nutritive rewards and the dependence of the plant's fecundity on its pollinators. We also studied the mechanism that causes its flowers to pop or burst open.

Methods

Intensive studies were conducted of populations of *C. pomeridianum* on the Occidental College Campus, Los Angeles (June 1974) and along Painted Cave

Table 1. Percentage of ovaries developing on selfed and open pollinated plants of *C. pomeridianum*.

Plant	Means of pollination	Ovaries developing	Ovaries not developing	% ovaries developing
A	hand self pollinated	9	2	82
B	hand self pollinated	4	0	100
C	isolated, not pollinated	0	10	0
D	open pollinated	152	131	53
E	open pollinated	64	100	39
F	open pollinated	149	63	71
G	open pollinated	107	25	81

Road (San Marcos Pass) near Santa Barbara (July 1974), with additional observations in subsequent years. The dominant vegetation of both areas is chaparral.

The time of flower opening and anther dehiscence, the time at which potential pollinators appeared, the types of pollinators present and the effectiveness of the various potential pollen vectors were observed and recorded.

Nectar production was studied by covering inflorescences with plastic bags to exclude all visitors. Five microliter pipets were used to measure nectar volumes. Nectar was measured at the time the flowers opened and periodically thereafter. Sugar concentration was measured with a Bausch and Lomb low range refractometer.

Compatibility was determined by experimentally hand selfing flowers of several plants, covering them with plastic bags, and collecting the styles the following mornings. Styles were squashed and stained with potassium iodide to test for pollen germination and pollen tube growth. Plants were determined to be self compatible, however, self compatiblity does not necessarily result in self fertilization since floral morphology may inhibit pollen transfer from a flower's anthers to its stigma. A plant was potted, isolated from the population, and subsequently observed for fruit maturation.

Flower buds were sectioned to study anatomical features relating to flower opening. Buds were fixed in Craf-Navashin's fixative approximately 1 hour before the time at which they were expected to open. They were subsequently dehydrated using a TBA series and imbedded in paraffin following the procedure outlined by Jensen (1962). Longitudinal and cross sections (9 microns) were cut with a rotary microtome. After mounting the sections they were stained using a safranin and fast green series.

Results and Discussion

Chlorogalum pomeridianum was determined to be self compatible. Pollen tubes developed normally in both experimentally selfed and outcrossed plants. Most ovaries of the hand self pollinated flowers developed (Table 1). Fruit set on the open pollinated control plants ranged from 39 to 81 percent, somewhat less than those which we hand pollinated. Fertilization was found to be dependent upon pollinators even though the plants are self compatible. Flowers which developed normally on a potted plant which had set fruit the year it was collected, set no

Table 2. Phenology of six plants of *C. pomeridianum* on June 23, 1974. First number refers to number of flowers open; second to flowers which have dehisced anthers; () to microliters of nectar per flower when first opened.

	Plant number					
Time	1	2	3	4	5	6
6:30 p.m.	—	—	—	10/0(2.0)	—	—
6:37	—	—	—	12/9	—	—
6:42	—	2/0(2.0)	—	12/9	—	—
6:45	—	6/0	—	12/9	—	—
6:50	—	6/0	—	12/9	5/0(7.4)	—
7:00	—	6/0	—	12/9	5/0	7/0(2.5)
7:05	2/0(0)	6/0	2/0(2.1)	12/9	9/0	7/0
7:07	2/0	6/2	2/0	12/12	9/0	7/0
7:10	9/0	6/6	5/0		10/6	8/3
7:20	10/2		15/1		10/10	10/8
7:30	10/9		15/7			10/8
7:37	10/10		15/10			10/10

seed when we isolated it from all pollinators. This illustrates the dependence of *C. pomeridianum* on animal vectors for pollination.

Floral development on a typical plant was found to proceed in the following manner. In the early evening (4:30–5:30 p.m., PDT) those flowers which were to open began to swell and appeared slightly inflated in comparison with other buds. By 6:30 p.m., some of the flowers had sepals which had separated at the base but remained attached to one another at the top. Flowers began to burst open shortly thereafter and by 7:30 p.m. all but a few had opened (Table 2). Bud sections revealed the presence of small trichomes at the apex of each sepal that are entangled and that cell division is not occurring in the flowers the evening they will open. Thus, it appears that turgor pressure in the sepals finally overcomes the resistance created by these hairs and the flowers suddenly pop open. Often one sepal would pull away first and then 4 to 60 seconds later the remaining attached sepals would suddenly pull apart. The time required for most buds to open ranged from 10 to 30 seconds. Each flower then remained open for several hours after which time the sepals twisted together and began to deliquesce.

The anther sacs remained turgid and pollen was usually not available for pollen gathering bees for 10 to 30 minutes after the flowers had opened (Table 2). During this time the flower could easily be outcrossed by nectar foragers that had come in contact with pollen at other flowers which had already shed their pollen (Table 2). Flowers from different plants and flowers of the same plant often opened in a continuum from about 6:30 to 7:30 p.m. Even though the plants are self compatible, flowers initially could only be outcrossed because their own anthers were not yet dehisced. For example, on 23 June (Table 2) at 7:05 there were 38 flowers open from six plants but the only pollen available for pollination was that of plant number four, or that which was brought in from other parts of the population. Therefore, plants 1, 2, 3, 5, and 6 could only be outcrossed at that time.

The amount of nectar present in flowers of *C. pomeridianum* was found to be highly variable between plants (Table 3). The mean amount present per plant when the flowers first opened ranged fromm 0.0 to 8.50 microliters. A one way

Table 3. Amount of nectar available when flowers first open and its rate of flow (24 June 1974: same plants as Table 2, different day and sample size).

	Initial amount of nectar removed					
Plant #	Mean (microliters)	S.D.	N	Lapsed time before recollection (min)	Ave. amount of nectar per flower (microliters)	Ave. rate of production (microliters/min.)
1	0.0	0.0	7	20	0.0	0.0
2	2.25	0.075	6	23	1.2	0.052
3	2.06	0.67	8	—	—	—
4	1.75	0.375	6	15	1.0	0.067
5	8.50	2.20	6	20	1.3	0.065
6	1.85	0.058	10	—	—	—

ANOVA on initial amount of nectar removed.

Source of variation	df	SS	MS	F
Among group (plants)	5	269.13	53.83	175.04**
Within group (plants)	37	11.38	.31	
Total	42	280.51		

** $P \leqslant .01$.

ANOVA was performed to test for a significant difference between plants (Table 3). The statistic showed that there is a significant ($P \leqslant .001$) added variance component among plants for initial amount of nectar. Thus, the reward obtained by pollinators visiting newly opened flowers is not only very variable, but is plant dependent. We observed no obvious difference in the frequency of visitation by pollinators to the different plants studied. Therefore, it appears that some plants are expending little energy in nectar production, but are being visited due to their association with nectar producers. The rate of nectar production for the first 20 minutes after opening was high and appeared to be fairly constant for those plants sampled (Table 3). Sugar concentration of the nectar ranged from 15.5 to 19.5 per cent.

The flowers of *Chlorogalum pomeridianum* were visited by seven potential pollinators (Table 4). Yellow jackets (*Vespula pennsylvanica* Sanss.), *Lasioglossum sisymbrii* Ckll., and Allen's hummingbirds (*Selasphoras sasin*) were rare or infrequent visitors at the flowers. *Vespula* and *Lasioglossum* were occasional nectar foragers and *Lasioglossum* was observed collecting pollen but neither came in contact with the stigma. *Selasphoras* also was observed as a nectar forager and may have been a potential pollinator. However, due to its low frequency and the fact that few anthers had dehisced at the time of its presence, it is probably of little importance as a pollinator.

Apis mellifera was an important visitor at both study areas. As early as 5 p.m. honey bees visited flowers which would open later in the evening. They often inserted their probosces between the sepals and removed much of the nectar. This activity was very common and undoubtedly caused a wide range in the amounts of nectar available in the flowers when they opened. If the sepals re-

Table 4. Flower visitors of *Chlorogalum pomeridianum.*

Species	Frequency Los Angeles	Frequency Santa Barbara
Apis mellifera	numerous	numerous
Bombus sonorus	numerous	rare
Bombus vosnesenskii	numerous	rare
Lasioglossum sisymbrii	infrequent	rare
Vespula pennsylvanica	infrequent	rare
Xylocopa tabaniformis	infrequent	numerous
Selasphoras sasin	not seen	infrequent

mained tightly closed at their base, honey bees were unable to gain access to the nectar.

Xylocopa tabaniformis orpifex F. Sm. (carpenter bee), *Bombus sonorus* Say and *B. vosnesenskii* Rad. (bumblebees) are large native bees. Their behavior at the flowers of *C. pomeridianum* was similar and constant. Prior to flower opening (approximately 5:30–6:00 p.m.) these bees began visiting the site. The bees flew systematically from plant to plant and between sites separated by 20 to 40 meters apparently searching for open flowers. They appeared ready to swarm over the flowers as they opened. *Bombus sonorus* was occasionally observed inserting its proboscis into the base of unopened flowers and robbing them of nectar; *Xylocopa* and *B. vosnesenskii* were never observed robbing nectar.

By 6:30 p.m. many flowers were usually open and the large bees were abundant and gathering nectar and also pollen from dehisced anthers. As nectar levels decreased and more anthers began to dehisce, pollen collecting became the more important activity. However, a nectar search was usually the initial activity upon visiting a flower.

In contrast to the honey bees, which entered the flowers at the base of the sepals, the larger native bees foraged over the entire flower. Frequently they contacted the stigma, often using it as a part of a landing platform or crawling over it in search of nectar and/or pollen. The large native bees are apparently responsible for most of the pollination which occurs.

It appears that *Chlorogalum pomeridianum* capitalizes on the fact that at a specific time each evening, for a period of approximately two months, it presents nectar and pollen resources which are regularly present at that time of day. Large native bees anticipate availability of these resources, swarm over the flowers when they open, and effectively pollinate them. *Chlorogalum pomeridianum,* which does not set seed in the absence of an animal pollen vector, is assured of a high frequency of pollination by this system. Since diurnal temperature is high and water availability low in the Southern California chaparral during June, July, and August, these plants may also benefit by expending less energy than they would if they flowered throughout the day. Bee pollinators also may benefit by expending less energy than they would if they foraged throughout the hot dry day. The pollinators may, in fact, have been one of the forces selecting for dusk flowering in *Chlorogalum pomeridianum.*

Acknowledgments

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Research Notes

Additional Notes on the Western Conenose, *Triatoma p. protracta* (Insecta: Hemiptera: Reduviidae), as a Carrier of Chagas' Trypanosome

From August 1974 to December 1977, 175 *Triatoma protracta protracta* (Uhler) were collected from Wildwood Park wood rat houses (24 adults, 126 nymphs), nearby homes in Thousand Oaks (3 adults) and under street lights of the Wildwood Parkside Tract (22 adults) since the discovery by Wood (1975) of natural infection with *Trypanosoma cruzi* Chagas in Wildwood Park, Thousand Oaks, Ventura County, California. Yearly totals were 8—1974, 2—1975, 148—1976 and 17—1977. Of these, 28 were males, 21 females, 41 fifth, 24 fourth, 24 third, 23 second and 14 first instar nymphs. Three males, 7 females and 4 fifth instar nymphs (8 percent) were positive for *T. cruzi*. Evidence of home invasions in Thousand Oaks included 1 negative male (3.VIII.1975), 1 infected female (8.VIII.1975) and 1 infected male (3.VIII.1976) from Wildwood Parkside Tract residences. Three adults not examined nor included in the above tally were taken in another Parkside home on 23 August 1977, 2 being found in the bedroom. Young collectors working under street lights brought us 8 males and 4 females in summer 1976, with 2 males (8.VII.1976) being positive; and 5 males and 5 females in summer 1977, with 2 females (27.VII. and 4.VIII.1977) positive. This indicates that a reservoir of *T. p. protracta* exists in Wildwood Park and that they are disseminated during periods of high summer temperatures to nearby homes in Thousand Oaks. These dispersal flights of adult triatomes are similar to those reported from Griffith Park, Los Angeles, by Wood and Wood (1967).

In 1976, 21 rodents (2 males and 2 females of *Neotoma fuscipes*, 1 female *Peromyscus maniculatus* and 7 males and 9 females of *P. truei*) were live-trapped in Wildwood Park in August and September. Xenodiagnosis of these rodents using 1 fifth instar nymph of *T. p. protracta* and 27 fifth and 4 fourth instar nymphs of *Triatoma protracta navajoensis* Ryckman was negative.

As noted in Table 1, of 883 *T. p. protracta* collected from wood rat houses, 136 (15.4 percent) were naturally infected with *T. cruzi*. Table 1 reveals that the best time of year to search wood rat houses for naturally infected *Triatoma* is in the winter quarter when the infection rate with *T. cruzi* was 34.2 percent. In spring the infection rate for bugs was 3.3 percent, summer 6 percent and fall 14.7 percent. Although the highest infection rate was in winter, more bugs were captured in fall in most wood rat houses (Wood, 1978). The higher infection rate of winter is probably due to the stress of low temperature on the rodents, resulting in a greater hunger drive and consumption of more triatomes as food by the *Peromyscus* and *Neotoma* in wood rat houses. Rodents can be infected experimentally when fed infected triatomes (Kofoid and Donat, 1933). The cold stress also stimulates higher parasitaemias in the infected rodents, causing more nymphal and adult triatomes in wood rat houses to become infected (Wood and Wood, 1967). The fewer adult triatomes in wood rat houses during spring may indicate

Table 1. Wood Rat House Populations of *Triatoma protracta protracta* in Arizona (44), California (511), New Mexico (318) and Utah (10).

Yearly quarter*	Number of triatomes								Infected with *Tryp. cruzi*		No. of wood rat houses		No. of triatomes per wood rat house	
	Adults		Nymphal instars											
	♂♂	♀♀	5	4	3	2	1	Total	No.	Percent	Total searched	With bugs	All houses	Houses with bugs
Spring	8	13	38	42	30	13	4	148	5	3.3	57	24	2.5	6.1
Summer	30	35	66	58	22	4	1	216	13	6.0	67	48	3.2	4.2
Fall	56	71	51	51	33	35	8	305	45	14.7	30	24	10.1	12.7
Winter	31	39	57	26	42	16	3	214	73	34.2	46	22	4.6	9.7

* Spring: March, April, May; Summer: June, July, August; Fall: September, October, November; Winter: December, January, February.

either the beginning of the active dispersal period of adult bugs or predation of imagos by *Neotoma* in the preceding winter. There is probably more predation from spiders and assassin bugs in wood rat houses in spring and summer due to rising environmental temperatures. Also there are more deaths from overheating and from enforced fasting when the host rodents are destroyed. There is more rapid metamorphosis of fourth and fifth instar nymphs during the hot spells of summer and fall. Thus, the ratio of adults to nymphs in Table 1 indicates 6 times more nymphs in wood rat houses in the spring, approximately 2 times as many in summer and winter and 1.4 times as many in the fall quarter.

By combining the numbers of larger nymphs (fifth and fourth) and smaller nymphs (second and first) in Table 1 and comparing ratios, the fourth and fifth instar nymphs were 24.8 times more numerous than first and second instars in summer in wood rat houses, 4.7 times in spring, 4.3 times in winter and 2.3 times in fall. This reduction in number of nymphs in summer is due to more frequent feedings, regulation of metamorphosis and change of fifth instar nymphs to adults, under the rising environmental temperatures. Likewise, more fourth instars become fifth instar nymphs, and some become adults in early fall. The fall populations of small nymphs are largely from eggs left by adults during the summer before their forced evacuation (death or migration of host) or natural dispersal in search of other food sources.

Of 939 *T. p. protracta* collected from homes of man from 21 July 1939 to December 1977 in Arizona, California, New Mexico and Utah, 720 were examined and 153 (21.2 percent) were positive for *Trypanosoma cruzi*. Of 4,881 *T. p. protracta* collected from all habitats in southwestern United States, 4,217 have been examined, of which 993 (23.5 percent) were found naturally infected. An apparent low virulence of the trypanosomes may protect man from Chagas' disease in the southwestern United States.

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Branchiate Dorvilleidae (*Polychaeta*) from the North Pacific

Bathyal collections off Southern California and intertidal collections in Puget Sound, Washington, have produced two new forms of dorvilleids. They are unusual in possessing branchiae or branchialike (vascular loop not apparent) structures. The presence of branchiae in dorvilleids widens the generally accepted definition of Dorvilleidae (Fauchald, 1977) and places the familial status of Iphitimidae in doubt. These problems will be discussed after a description of the two new species.

The first new species described herein was collected intertidally at several Puget Sound, Washington, beaches (as described in Armstrong et al., 1976). Specimens were obtained from 1.0 mm-sieved samples. The second species was collected with a box corer (0.42 mm screened) at 1140 m depth in Santa Catalina Basin, Southern California continental borderland (Jumars, 1976).

Jaws were dissected from several individuals. The terminology of the parts is discussed in Jumars (1974). Drawings and measurements were made with a camera lucida attachment for a Wild M20 microscope.

Protodorvillea pugettensis sp. nov.
(Fig. 1)

Material examined.—The holotype (AHF Poly 1259) and 14 additional specimens were externally examined. The holotype is from Carkeek Park, Seattle, Washington. The paratypes are from Carkeek Park (4, AHF Poly 1260), Lincoln Park (7, AHF Poly 1261), Point Wells (2, AHF Poly 1262) and West Point (1, AHF Poly 1263). All of these collection locations are in or near Seattle. Jaws are dissected from two of the paratypes.

Description.—The holotype measures about 4.6 mm long and is widest (0.3 mm) at the 4th setiger. The holotype, though broken into two pieces, is complete and consists of 48 setigers plus prostomium, peristomium, and pygidium. The sizes of the paratypes are comparable. The prostomium in all specimens is roughly pear shaped but is slightly compressed dorsoventrally (Fig. 1A). A pair of clavate antennae insert dorsally near the midpoint of the prostomium. A pair of biarticulate palps insert ventral to the shorter antennae. Two eyespots are present: one is located between each antenna and palp. The eyespots often fade in preservative. The peristomium is composed of two rings which are fused dorsally. A single branchialike structure (Fig. 1C) inserts dorsally on parapodia 3 through 10 to 14, greater numbers being found on larger specimens. The branchialike structures arise fully developed on parapodium 3 and remain fully developed through all the parapodia on which they occur. Dorsal cirri are absent. A short, digitate ventral cirrus is present and fully developed on all parapodia (Fig. 1C). A second cirruslike protuberance is weakly present ventrally on most parapodia. Parapodia are uniramous. The setae above the aciculum include one denticulate capillary and one furcate seta (Figs. 1D and 1E, respectively). The setae below the aciculum are all compound: one with an elongate, tapering, denticulate blade (Fig. 1G) and

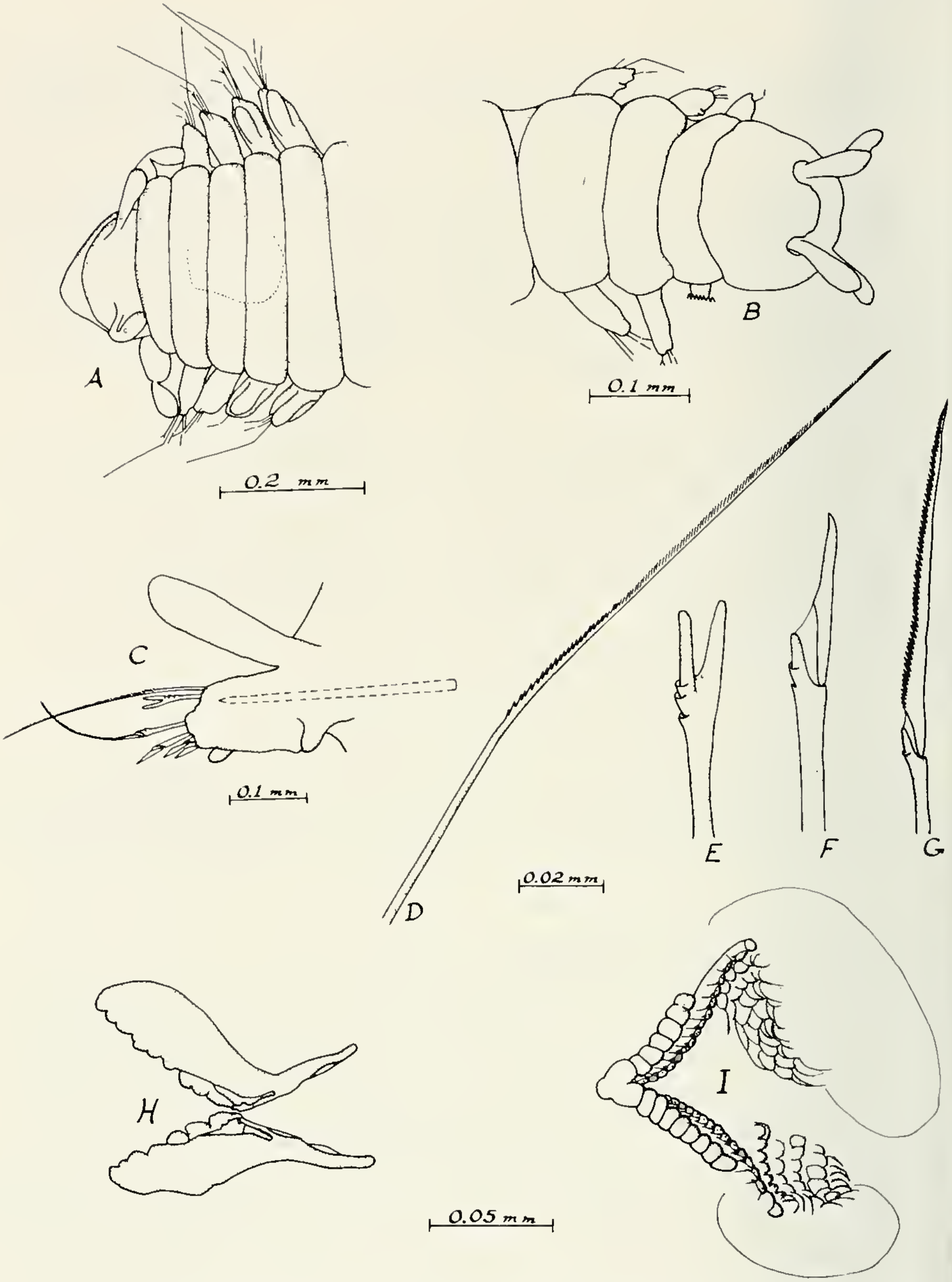

Fig. 1. *Protodorvillea pugettensis* sp. nov.: A, anterior in dorsal view (dashed lines indicate position of jaws); B, posterior of same specimen in dorsal view; C, parapodium 7; D, simple seta of parapodium 42; E, furcate seta of parapodium 19; F, short compound seta of parapodium 19; G, elongate compound seta of parapodium 42; H, mandibles in dorsal view; I, maxillae in dorsal view. A and B are drawn from the holotype while C–I are from paratypes.

three with short blades (Fig. 1F). One to four ridges are present on the distal ends of the shafts of the compound and furcate setae. The pygidium is rounded and bears four clavate cirri of approximately equal length (Fig. 1B). A dorsal, shelflike anal flap covers the terminal anus.

The jaws are not apparent through the body wall because they are surrounded by a dense muscular mass. The mandibles are butterfly shaped, anteriorly rounded and medially denticulate (Fig. 1H). The maxillae consist basically of four rows of denticles, two on each side (Fig. 1I). Additionally, there are several rows of accessory denticles anterior and inferior to the four principal rows. The carriers appear fused with each other and with the basal plates of the superior rows of denticles, and these in turn appear fused with the basal plates of the inferior rows. All the denticles have minute teeth distributed uniformly over their dorsal surfaces. In addition, denticles of the inferior rows have a larger main fang posterodorsally, followed by one, two, or rarely three, smaller fangs and several minute teeth.

The gut is apparently empty in all available specimens.

Differential diagnosis.—Comparisons between the above species and the only known dorvilleid with branchialike structures, *Protodorvillea parva*, are difficult because the description of *P. parva* is based upon a single, possibly juvenile specimen (Rullier, 1974). *P. pugettensis* differs from *P. parva* in the following ways: its antennae insert posterior to the midpoint of the prostomium rather than anterior to the midpoint; the two peristomial rings are fused dorsally; four pygidial cirri are present rather than two; the branchialike structures begin on the third rather than the first parapodium; the globular, cirruslike protuberance located on the proximal end of most parapodia appears to be lacking in *P. parva*; and minor differences appear to exist between the shorter compound and capillary setae of the two species. Comparisons of the maxillae were not possible because no specimens of *P. parva* were available for dissection.

Distribution.—*P. pugettensis* is known only from eastern central Puget Sound, Washington. It was collected in the intertidal zone in mixed sand, gravel and cobble substrates between mean lower low water (MLLW) and 1.8 m above MLLW.

Protodorvillea dibranchiata sp. nov.

(Fig. 2)

Material examined.—The holotype (AHF Poly 1264) and one paratype (AHF Poly 1265) were externally examined. The former came from a core at 32°57.7′N, 118°22.2′W and the latter was similarly collected at 32°58.3′N, 118°22.2′W. The anterior end of the paratype was mounted whole. Jaws were dissected from the paratype.

Description.—The holotype is comprised of two fragments. The anterior fragment consists of the prostomium, peristomium and 30 setigers. This fragment is 3.4 mm long and is widest (0.4 mm) at the third setiger. The posterior fragment is 2.4 mm long and consists of 17 setigers and the pygidium. The posterior end of the paratype is lacking. The prostomium of both specimens is rounded and slighlty compressed dorsoventrally (Fig. 2A). A pair of clavate antennae insert dorsally on the prostomium. In both specimens, the right antenna is nearly bi-

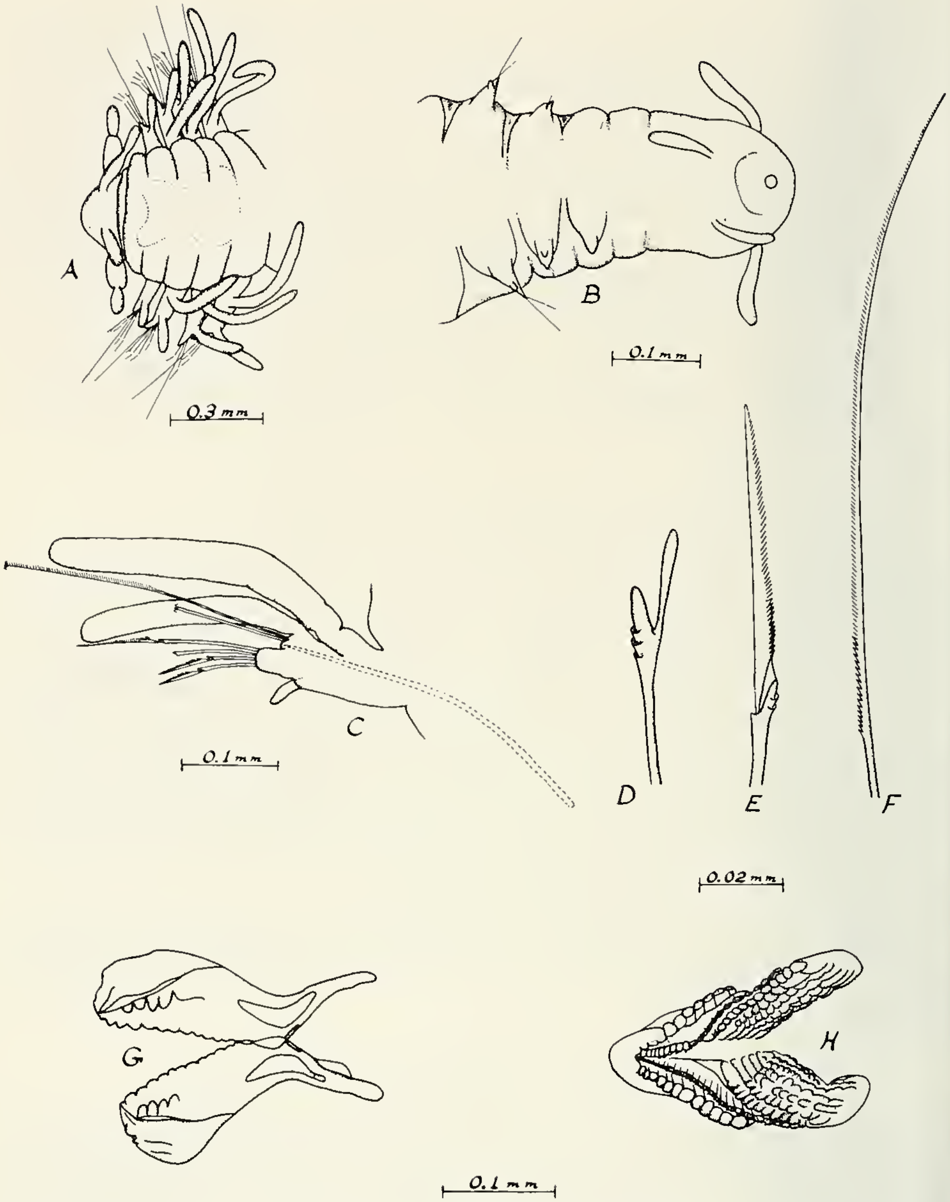

Fig. 2. *Protodorvillea dibranchiata* sp. nov.: A, anterior in dorsal view (dashed lines indicate position of jaws); B, posterior in ventral view; C, parapodium 10; D, furcate seta; E, compound seta; F, simple seta; G, mandibles in dorsal view; H, maxillae in dorsal view. B is drawn from the holotype while A and C–H are from the paratype.

articulate, and the left antenna is shorter and shows less distinct articulation. A pair of biarticulate palps insert ventral to the antennae. Eyes appear to be absent. The peristomium is composed of two rings, the first narrower than the second. Branchiae are present on the first 13 to 17 parapodia. The first parapodium has one branchia which inserts dorsally at the distal end of the parapodium. The second parapodium also has a dorsal proximal branchia as well as the distal. These two branchiae are present and increase in size on successive parapodia, being fully developed by parapodium five (Fig. 2C). Both branchiae gradually decrease in size from about the 14th through the 17th parapodia in the holotype and from the 11th through the 13th parapodia in the paratype. The proximal branchia is absent by parapodium 18 in the holotype and parapodium 14 in the paratype. The distal branchia persists as a globular "dorsal cirrus" on all remaining posterior parapodia. A digitate ventral cirrus (Fig. 2C) is present and fully developed on all but the first parapodium. The setae above the aciculum include one denticulate capillary and one furcate seta (Figs. 2F and 2D, respectively). There are three to four compound setae with elongate, denticulate blades below the aciculum (Fig. 2E). Two to three ridges are present on the distal ends of the shafts of the compound and furcate setae. All of these setae are present on each parapodium. The pygidium (Fig. 2B) is rounded and bears four elongate, clavate cirri, the two dorsal cirri being longer then the ventral ones. A conical depression surrounds the anus.

The mandibles are butterfly shaped, anteriorly rounded and medially denticulate (Fig. 2G). The maxillae consist of four rows of denticles, two on each side (Fig. 2H). There are several rows of accessory denticles anterior and inferior to the four principal rows. The carriers appear fused with each other and with the basal plates of the superior rows of denticles, and these in turn appear fused with the basal plates of the inferior row. All the denticles bear minute teeth distributed uniformly over their dorsal surfaces. In addition, denticles of the inferior rows have a large posteriodorsal main fang, followed by three to four smaller fangs and several minute teeth.

The gut is apparently empty in both specimens.

Differential diagnosis.—P. dibranchiata differs from all previously described dorvilleids by the presence of paired branchiae on each parapodium, beginning on the second and persisting through the 13th to 17th parapodia.

Distribution.—P. dibranchiata is known only from the Santa Catalina Basin at bathyal depths.

Discussion

The two descriptions above widen the range of jaw morphologies found in Dorvilleidae. The several accessory rows of denticles have not been described before. On the basis of Jumars' (1974) description we suspect, however, that the jaw structure of *P. gaspeensis* may be similar. Unfortunately, insufficient material was available to perform additonal dissections on this species.

The finding of branchiae in Dorvilleidae, in *P. parva* first by Rullier (1974) and now in two additional species, also forces a widening of the definition of Dorvilleidae. At the same time, the finding of a new species of *Iphitime* (*I. hartmanae* Kirkegaard 1977) which is not limited to crab branchial cavities broadens the concept of Iphitimidae and makes the family less distinct from Dorvilleidae. Although *Iphitime* remains distinct as a genus, we can no longer find reasonable criteria for excluding it from Dorvilleidae. *Iphitime's* jaw morphologies, setae, presence of branchiae, and number of prostomial appendages, when considered separately, all fall within the known range of Dorvilleidae as described by Jumars (1974) and herein.

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Additions to the Cerambycidae of the Revilla Gigedo Islands (Coleoptera)

Four species of Cerambycidae have been previously reported from the Revilla Gigedo Islands (Linsley and Chemsak, 1966). Although this oceanic island group consists of four islands, Cerambycidae are known to occur on only two: *Stenodontes dasytomus socorrensis* Linsley and Chemsak and *Acanthoderes socorrensis* Linsley on Socorro Island and *Nesodes insularis* Linsley and *Acanthoderes peritapnoides* Linsley on Clarion Island.

This report is based upon material collected by C. Hogue and A. Evans on Socorro Island during the Steele Expedition of 1977. The specimens of Cerambycidae were made available for study by C. Hogue through the Los Angeles County Museum of Natural History. Types will be deposited at that institution.

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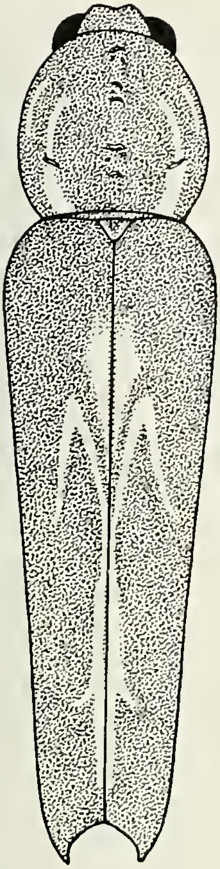
Permission to carry out scientific studies in the area were kindly authorized by Dr. Antonio Landázuri, Dirección General de la Fauna Silvestre, Secretaria de Agricultura y Recursos Hidraulicos, México.



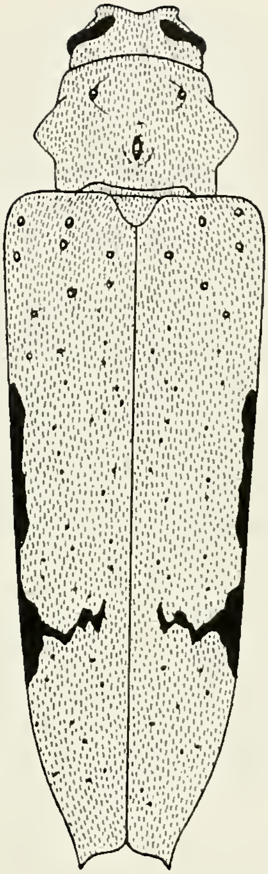


Fig. 1. Left. *Neoclytus steelei* Chemsak and Linsley, ♂.
Fig. 2. Right. *Oreodera glauca pacifica* Chemsak and Linsley, ♂.

Stenodontes dasytomus socorrensis Linsley and Chemsak

One male and one female were taken under bark of dead *Ficus* on 6 June. There is a good probability that this plant is the host of this subspecies.

Neoclytus steelei, new species
(Fig. 1)

Male.—Form moderate sized, tapering posteriorly; integument reddish brown, pubescence fine, appressed. Head densely, shallowly punctate, sparsely pubescent, eye emarginations with a dense patch of pale yellow pubescence; antennae slender, extending over basal ⅓ of elytra, basal segments sparsely pubescent, segments from fourth finely, densely pubescent, segments two to five fringed beneath. Pronotum as long as broad, sides rounded; disk with a longitudinal row of transverse carinae, each side behind middle with a single carina; punctures dense, subopaque appearing; pubescence fine, dense, appressed, sides of middle with longitudinal lines of yellowish appressed pubescence which extend to base and across to coxal cavities, sides with a yellow patch of pubescence often extending toward apex; prosternum shining, transversely rugulose, pubescence sparse, appressed, with numerous long, erect, pale hairs interspersed; meso- and metasternum with condensed patches of yellowish pubescence at posterior margins of episternum. Elytra more than 2½ times as long as basal width, sides tapering posteriorly; punctures fine, dense, shallow; pubescence fine, appressed, lying transversely behind middle, condensed yellowish patches consisting of a narrow M shaped median band extending back along suture to about apical $\frac{1}{6}$ where it expands slightly and forms a vague, narrow, curved band which does not extend to margins, basal ½ with a sutural, elongate diamond shaped patch extending back very near to median band; apices obliquely truncate, angles dentate, outer more prominently. Legs robust, middle and hind pairs elongate; middle and hind femora bispinose at apices, spines short; hind tibiae arcuate. Abdomen sparsely pubescent; last sternite shallowly emarginate at apex. Length, 10–14 mm.

Female.—Form less tapering. Antennae extending to basal ¼ of elytra, segments from fifth slightly enlarged. Pronotum with an irregular row of small carinae each side of median row. Legs shorter. Abdomen with last sternite narrowly rounded. Length, 11–15 mm.

Holotype male, allotype and 10 paratypes (6 males, 4 females) from Socorro Island, 6 June 1977.

The pubescent pattern of this species is unlike that of any other *Neoclytus* known to us. The median band of the elytra occasionally extends forward laterally to form a "W." Even rubbed specimens may be distinguished by the pattern of carinae on the pronotum and broadly spinose to dentate apices of the middle and hind femora and elytra.

Neoptychodes trilineatus (Linnaeus)

This widespread species has not previously been recorded from these islands. Forty-five males and 28 females were taken on 6 and 8 June, on branches and trunks of *Ficus,* many *en copula.*

These individuals are similar to mainland forms except that the white sutural band of the elytra occupies only about the basal one fourth. *Ficus* is a common host elsewhere and these collections indicate that it is at least one of the hosts on Socorro Island.

Oreodera glauca pacifica, new subspecies

(Fig. 2)

Form moderately large; integument reddish brown; pubescence dense, appressed, grayish to dark brown. Antennae uniformly pale reddish brown, very finely grayish pubescent. Elytra with 2–3 small, elevated calluses on each side at base; surface finely, sparsely punctate, nonasperate; lateral brownish patches small, mostly pale brownish, transverse band at apical ⅓ slightly arcuate up to suture. Legs with tibiae vaguely infuscated at apices, tarsi except claws reddish brown. Length, 17–24 mm.

Holotype male, allotype and 14 paratypes (8 males, 5 females) from Socorro Island, 6–8 June 1977.

This population differs at once from all mainland material examined by us in the absence of large, glabrous asperites down the elytra. Additionally, the antennae are not black annulate, the tibiae and tarsi only vaguely infuscated and the overall pubescence appears less thick, creating a somewhat shining aspect.

Acanthoderes socorrensis Linsley

This species, originally described from Socorro Island, is represented by 7 males and 1 female collected on 6–8 June 1977.

The host plant is *Hippomane mancinella*.

Trichastylopsis hoguei, new species

Female.—Form small to moderate sized; integument light to dark reddish brown; pubescence dense, appressed, mottled pale brownish, gray and black, long, pale, erect hairs numerous. Head with front shallowly convex, subquadrate, deeply impressed between antennal tubercles, densely gray-brown pubescent; antennal tubercles elevated, divergent; eyes coarsely faceted, deeply emarginate, separated above by about diameter of antennal scape; mouthparts, genae and vertex with a few long, erect hairs; antennae a little longer than body, basal segments mottled with dark brown, segments with numerous long erect hairs beneath to ninth, scape with a few erect hairs dorsally, third segment subequal to scape, fourth shorter than third; vertex with a black spot at middle behind eyes. Pronotum broader than long, sides tuberculate behind middle; base broadly impressed, apex narrowly, not deeply impressed; disk with two rounded tubercles on each side of middle just behind apical margin; punctures rather uniform, fine; pubescence grayish with pale brown spots at sides and over lateral tubercles, basal margin with a black median patch and a small dark patch on each side, sides near base with several long, erect hairs; prosternum very narrow, excavated, sparsely pubescent, intercoxal process medially impressed; meso- and metasternum finely, densely pubescent, pubescence much coarser at sides. Scutellum broader than long, broadly rounded at apex. Elytra slightly more than 1½ times as long as broad, apical ⅓ tapering, broader than pronotum; disk with two rather prominent black tufts of pubescence near base, small seta bearing tufts linearly arranged down suture and along three discal costae; pubescence appressed, mottled grayish and pale brownish, costae pale brownish, two black tufts present at apical ⅓ and small black spots sparsely interspersed, especially along suture, long, pale erect hairs numerous; basal punctures coarse at middle, becoming finer toward apex; apices rounded. Legs robust, femora clavate; pubescence dense, gray brown, long flying hairs numerous. Abdomen moderately densely pubescent; last sternite rounded at apex. Length, 7–9 mm.

Male.—Form similar. Antennae extending about two segments beyond body. Abdomen with last sternite narrow at apex, truncate. Length, 8 mm.

Holotype female and two paratypes (1 male, 1 female) from Socorro Island, 6 June 1977.

The pronotum often appears to have two dark longitudinal vittae on the disk and the black spots at the apical ⅓ of the elytra give an impression of short, oblique vittae to the naked eye.

This species is closely related to *T. albidus* (LeConte) but differs by the shorter, more convex form, rounded apices of the elytra and different pubescent pattern.

T. albidus has the apical one third of the elytra dark and dark lateral spots behind the humeri. Two of the available specimens of *hoguei* are badly rubbed, making it impossible to ascertain any variation in the pubescent pattern.

We dedicated this species to C. L. Hogue for kindly providing the material for study.

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First Report of Brooding in *Syllides japonica* Imajima (Syllidae: Polychaeta)

We have recently had the opportunity to examine reproductive specimens of *Syllides japonica* Imajima (Eusyllinae). In this paper additions are made to the description of sexually mature individuals and the exogonine like brooding is described.

Specimens of *Syllides japonica* were obtained within the root masses of the marine angiosperm *Phyllospadix*. *Phyllospadix* roots were taken from the lower intertidal near the Slip Point Coast Guard Station at Clallam Bay Washington, on the Strait of Juan de Fuca, and sorted in the laboratory. The syllids were identified using Banse and Hobson (1974), and were checked against the descriptions of Imajima (1966) and Banse (1971).

Several specimens of *Syllides japonica* were collected, including a mature male, two mature unspawned females, and a female which was brooding embryos. All mature animals were approximately 5 mm long, consisting of 45 or 46 setigers. Although none of the animals was swimming, these epigamous individuals had bundles of long capillary setae on all segments from setiger 10. Banse (1971) described a mature pelagic specimen from Cape Cod which had long capillary setae beginning on setiger 10. No capillary setae were present on the brooding animal; they were probably lost after spawning. Unspawned animals had coelomic gametes present from setiger 11 and in all subsequent segments except the last two. The eggs were white, yolky and about 130 μm in diameter.

The brooding female was an anterior fragment consisting of 23 setigers (Fig. 1A). Beginning with setiger 11, each segment had 4 embryos attached in a row across the ventral surface. One embryo of each pair was attached to the body near the base of the parapodium while the other was attached to the body approximately half way between the first and the ventral midline (Fig. 1B). Each

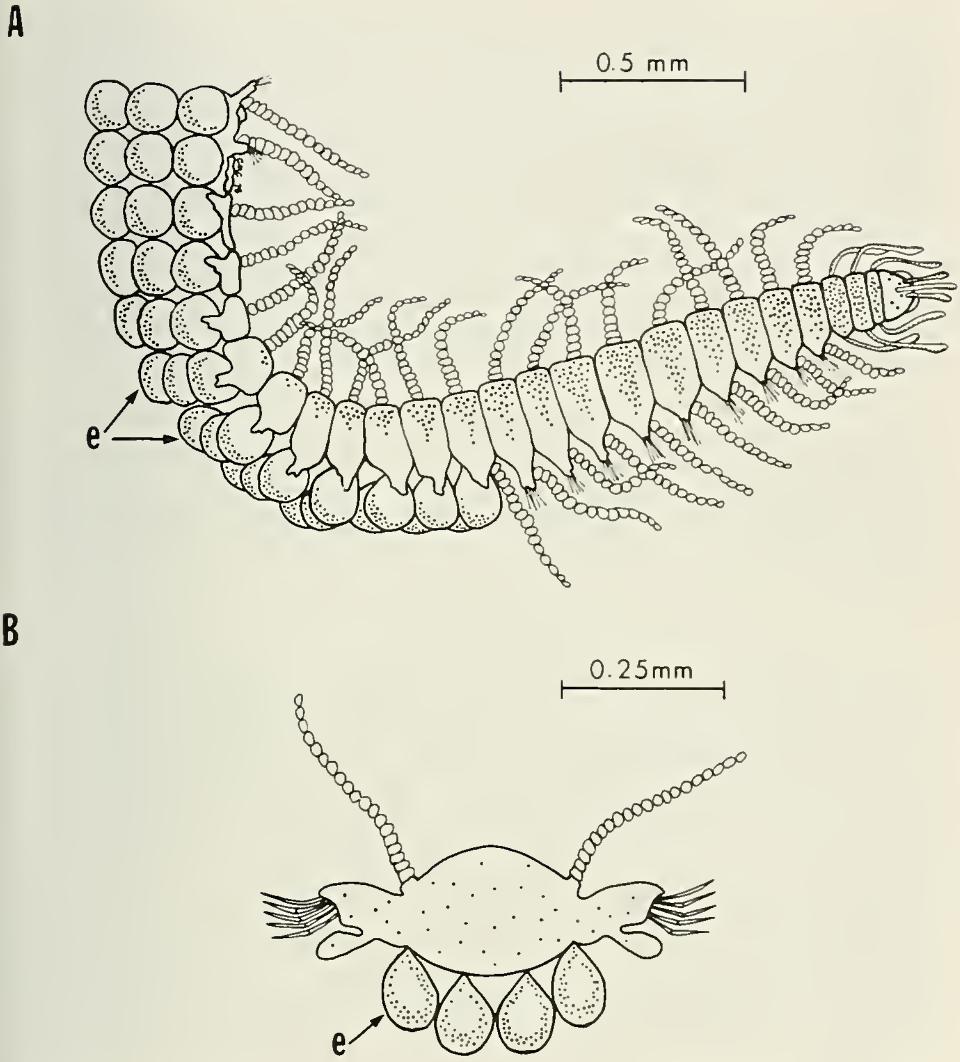

Fig. 1. *Syllides japonica*. A. Brooding female (setae and dorsal parapodial cirri not shown on all segments); B. Diagrammatic cross section showing the segmental arrangement of the developing embryos. Letter e indicates developing embryos.

light colored embryo was rather oblong and tapered toward the proximal attachment point. The developing embryos, which were enclosed within a transparent extraembryonic membrane, measured 150 μm long by 130 μm in diamter at the widest part. The developing embryos were thought to be trochophores, but they were not critically examined.

A number of polychaete species afford their young some degree of protection by various brooding methods (see Schroeder and Hermans, 1975 for review). Within the family Syllidae two primary methods of brooding have been described. The stolon forming Autolytinae, as a group, brood their young in a specialized cavity in the reproductive stolon; in the epigamous Exogoninae, developing embryos (1 to 4 per segment) are attached externally to the dorsal or ventral body wall. In addition, two species in the epigamous subfamily Eusyllinae, *Pionosyllis pulligera* (Viguier, 1884; Cognetti, 1957) and *Pionosyllis neapolitana* (Goodrich, 1930), brood their young in a manner similar to that exhibited by the exogonines. In the eusylline genus *Syllides, S. edentula* is known to lay its eggs in a gelatinous mass where they are attended by both parental animals (Cognetti-Varriale, 1971).

Brooding, however, has not been previously recorded for this genus. In his description of *S. japonica,* Imajima (1966) made no reference to reproductive forms. Banse (1971) did examine an anterior fragment of a mature female but did not describe brooding, which is here described for the first time.

Acknowledgments

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Notes on the Biology of *Lithurgus gibbosus* Smith in Florida (Hymenoptera: Megachilidae)

The tribe Lithurgini, which contains the single widely distributed genus *Lithurgus* Latreille, consists of primitive, long tongued megachilid bees which ex cavate nest tunnels in decayed wood (Lieftinck, 1939; Parker and Potter, 1973). Floral records and analysis of pollen from nests of *L. apicalis* Cresson (Parker and Potter, 1973) and *L. gibbosus* Smith (Mitchell, 1962) suggest that *Opuntia* flowers provide the major pollen source for these two species. The study of Parker and Potter (1973) on *L. apicalis* in Utah represents the only detailed account of the biology of any North American *Lithurgus*. In the present paper, the nest of *L. gibbosus* in Florida is described and notes on its general biology are given.

Nesting site.—Archbold Biological Station, Highlands Co., Florida, in a weathered 150 × 150 mm thick weathered softwood post supporting the lintel of a tractor shed. The door of the shed faced east; bees were seen excavating holes in the south, north and west wides of the post.

Nest construction.—Observations were made on the original nest site (the shed post) and on two trap nests made in a 100 × 100 × 250 mm seasoned fir block in which several 6.4 mm holes of varying depths were drilled. The block was wired to the original nest post and was colonized within a few days after attachment. After the trap nests were completed by the bees, the block was removed and split along the grain to expose the nests.

The original nest post was extensively mined by the bees and showed evidence of use during prior seasons. By blowing smoke into holes known to be in use, it was determined that considerable intercommunication existed between the tunnels, and bees which entered nests through one hole would occasionally exit through another. By marking holes and bees, it was determined that at least 45 holes were in use by as many different *L. gibbosus* females during the study period (29 March to 5 April 1976).

In almost all respects, the two trap nests recovered from the fir block resembled those described for *L. apicalis* (Parker and Potter, 1973). The bees excavated two tunnels diverging away from the axis of the "starter" holes in both trap nests (Fig. 1a, b). The diameters of the nest tunnels excavated by the bees averaged 6.5 mm (range 6.0–7.0 mm), while the lengths of the brood cells averaged 12.4 mm (range 9.0–18.0 mm). The longest nest tunnel held three brood cells. Partitions between the cells consisted of thin layers of scraped wood fibers. There were no vestibular cells, empty spaces, or preliminary plugs (terminology of Krombein, 1967), but a large wood fiber closing plug averaging 14.0 mm in length (range 7.0–20 mm) was constructed in each branch of the nest tunnels (Fig. 1a, b). One of the trap nests contained two blind side tunnels extending approximately 20 mm downward and upward into the wood; neither contained provisioned cells (Fig. 1a, b).

Nest provisions.—The pollen used in the trap nests was exclusively that of *Opuntia rigida* and contained little or no nectar. As in *L. apicalis*, the egg chamber was located in the middle of the provision (Fig. 1a) (Parker and Potter, 1973).

Mating.—A single mating was observed on 29 March 1976. The female faced upward on the nest post while the male landed on her back, curving his abdomen down and slightly underneath hers while she curved her abdomen slightly upward into the bend of the underside of the male's curved abdomen. The entire mating episode lasted only a few seconds.

Development.—The combined egg and larval stages of *L. gibbosus* last approximately seven weeks from the time the nest is plugged. One of the trap nests

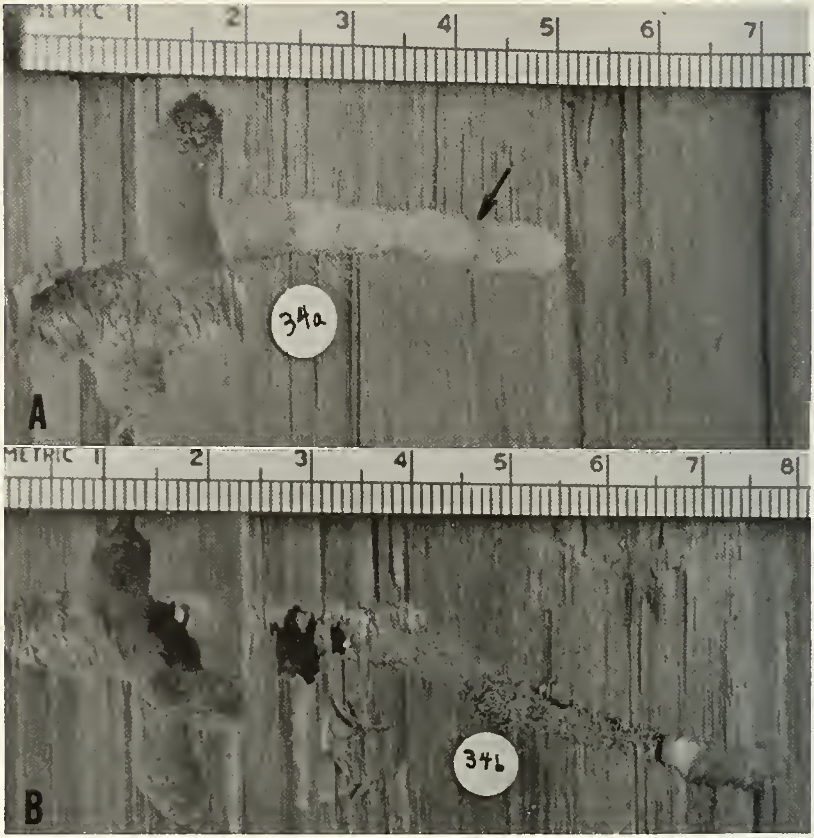

Fig. 1a. Portion of trap nest of *Lithurgus gibbosus* Smith. The arrow indicates the thin portion of wood fibers separating the penultimate from the terminal cell. A young larva may be seen through the small hole in the pollen provision of the last cell. Fig. 1b. Same as above, but showing a different portion of the nest. This photograph was taken after all but the larva in the terminal cell had made cocoons; the larva, shown here, has started to spin.

was sealed 4 April 1976; by 21 May three of the four larvae had formed cocoons and the fourth was beginning to spin (Fig. 1b). This last larva was removed and placed in a 7.0 mm I.D. shell vial, where it completed its spinning and was cocooned in eight days. The other cocoons were removed from the trap nest afte measurement for rearing in separate vials. The appearance and form of the co- coons were identical to those of *L. apicalis* (Parker and Potter, 1973). Cocoo lengths of two sizes were made, reflecting the sex of the bee. Of those measured the smaller cocoons were 11.0, 12.0, 12.0 and 12.0 mm long, whereas the large measured 15.0 and 18.0 mm respectively. One of the larger cocoons was para sitized by *Melittobia* wasps and did not mature; most of the others emerged the following spring. The first to emerge were males, three of which emerged betwee April 12 and 13, 1977. A single female emerged from one of the larger cocoon (cell with larva visible, Fig. 1b) on May 2, 1977. The placement of the sexes i the nests showed that in one case a male cell was made first. However, the singl female reared to maturity came from the terminal cell shown in Fig. 1b.

Nest associates.—The post containing the nests of *L. gibbosus* was utilized by large numbers of the smaller megachilid bee *Megachile brevis pseudobrevis* Mitchell. No aggressive interactions between *M. brevis* and *L. gibbosus* were ever observed. The *M. brevis* frequently used much smaller holes than those used by *L. gibbosus* and may not have come into physical contact with them at any time. No *M. brevis* colonized the trap nest block, possibly because of the large size of the "starter" holes. Also seen using the post and the trap nest block was a small eumenid wasp, *Stenodynerus fulvipes rufovestis* Bohart, a common trap nesting species at the Archbold Station (Krombein, 1967). *Melittobia* wasps, probably *M. chalybia* Ashmead, infested the majority of nests provisioned by *S. fulvipes* and may have infested many of the megachilid nests in the post, although only one trap nest cell was infested. Occasional specimens of chrysidid and leucospid wasps (*Chrysis* sp. and *Leucospis* sp.) were seen investigating nest entrances on the post, but no data on depredations by these parasites were obtained.

Acknowledgments

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COVER: Charcoal and pastel drawing of Peter Oest which hangs in the living room of Calvin Oest. Submitted by Nancy Thym, University of California, Los Angeles.