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Notes on Turtle Egg Predation by *Lampropeltis getulus* (Linnaeus) (Reptilia: Colubridae) on the Savannah River Plant, South Carolina

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ABSTRACT.— Observations on turtle egg predation by the colubrid snake *Lampropeltis getulus* on the Savannah River Plant, South Carolina, indicate that, during the turtle nesting season, some kingsnakes apparently search out and consume the contents of multiple turtle nests. This seems especially true for nests of kinosternid turtles. Future studies of predators on turtle nests within the range of *L. getulus* should take that taxon into account as a potentially prominent predator. Eggs of *Sternotherus odoratus* may hatch even after passing through the digestive tract of *L. getulus*.

Kingsnakes of the colubrid genus *Lampropeltis* have long been known to feed on a wide variety of vertebrate prey (for a review, see Wright and Wright 1957). Of particular interest is the tendency of these snakes to consume the eggs of other reptiles, especially turtles. Brown (1979) listed two turtle eggs from two *Lampropeltis getulus*, and Hamilton and Pollack (1956) listed prey items found in *L. getulus* from Fort Benning, Georgia, including the eggs of lizards and snakes. Wright and Bishop (1915) reported the eggs of *Pseudemys floridana* and *Kinosternon* spp. from stomachs of Okefenokee swamp *L. getulus* and observed that ". . . so addicted are they [*L. getulus*] to this egg diet, that the natives consider that it is a common happening to find the snake awaiting the egg deposition." They also said that, aside from "the Florida bear, there is no form in the swamp which eats turtle's eggs in such quantity as the kingsnake. It will take a whole nest of eggs at one time, as many as 14 being found in the stomach of one snake." Ernst and Barbour (1972) cite numerous turtle species whose young are eaten by various species of snakes, but relatively few turtles whose eggs are eaten.

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Recent collections and observations on two specimens of *L. getulus* from the Savannah River Plant (SRP), in Aiken, Barnwell and Allendale counties, South Carolina, shed additional light on turtle egg-eating propensities of *L. getulus* and indicate that at least a small subset of the population of *L. getulus* on the SRP may search out nesting turtles and wait for them to lay their eggs, as suggested by Wright and Bishop (1915).

On 27 May 1984, one of us (RKL) removed a *L. getulus* from a funnel snake trap along a drift fence near the northeast side of Ellenton Bay, a Carolina bay in the Aiken County portion of the SRP. This snake, a female with a snout-vent length (SVL) of 1118 mm, regurgitated 9 turtle eggs (6 ruptured, 3 intact) that, based on shape, appeared to represent several different turtle taxa. One hard-shelled egg was immediately referable to the family Kinosteridae; one was light-colored and round, apparently *Chelydra*; and the remaining 7 could have been assignable to any of several species of emydid turtles.

On 22 June 1984, one of us (JLK) collected a female *L. getulus* (1257 mm SVL) along a sandy road that courses parallel to, and averages about 50 m from, the edge of the Savannah River Swamp, ca. 2 km east-southeast of the mouth of Pen Branch Creek, in Barnwell County. The collector had stopped to capture a *Terrapene carolina* that was in the process of excavating a nest chamber (she later laid 3 eggs in the lab). When first observed, the snake was less than a meter from the turtle, with its head and neck elevated about 10 to 12 cm off the ground and directed toward the turtle. The snake was captured, placed in a collecting bag and, upon returning to the lab, was found to have regurgitated 4 hard-shelled eggs (2 intact, 1 damaged, 1 crushed). The snake was caged by itself and, after 3 days, defecated parts of, minimally, an additional 13 kinosternid eggs, 3 of them unbroken.

Three species of kinosternid turtles have been collected at SRP: *Sternotherus odoratus* and *Kinosternon subrubrum* (Gibbons and Patterson 1978), and *Kinosternon bauri* (Lamb 1983). The eggs are most likely of *S. odoratus* and/or *K. subrubrum*, as *K. bauri* is comparatively rare on the SRP, the northernmost record of occurrence for the species. Unfortunately, measurements of the intact eggs yielded no information as to their identity, for all three species lay eggs of approximately the same size.

Of particular interest was the number of turtle eggs present in the second snake. Gibbons (1983), discussing SRP *K. subrubrum*, gave a mean of 3.03 eggs/clutch, range 1-5 (N = 161). Tinkle (1961) divided a sample of adult female *S. odoratus* into two arbitrary size classes, the smaller exhibiting an average clutch size of 2.0 eggs and the larger averaging 3.2 eggs/clutch. If the snake located and devoured "average" clutches of *K. subrubrum*, then at least five or six different nests had been preyed upon, all within a fairly short period. If the same scenario is applied to "average" clutches of *S. odoratus*, the snake may have preyed on five to nine nests. Given the circumstances of its capture, it seems highly probable that the snake would have taken the contents of the *T. carolina* nest as well. Interestingly, the three intact eggs that passed through the digestive system of the snake and were then defecated were incubated in the lab and hatched after approximately 50 days, yielding three *S. odoratus*.

Imler (1945) mentioned a bullsnake, *Pituophis melanoleucus sayi*, with an "egg appetite to the extent that it will not eat anything else," and Legler (1960), citing a conversation with the late E. H. Taylor, mentioned a bullsnake that "swallowed an entire clutch of newly laid eggs [of *Terrapene ornata*] before the female turtle could cover the nest." Perhaps some individual *L. getulus* behave the same way in nature. Legler (1960) stated that nest predation may have a greater effect on populations than predation on hatchlings, juveniles, and adults. Our data suggest that *L. getulus*, particularly those in areas of extensive turtle nesting, as along the margin of the Savannah River Swamp, might contribute more than slightly to turtle egg predation totals. Any future studies of predation on turtle eggs should take this predator into account.

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Observations on the Social Behavior of the Southern Cricket Frog, *Acris gryllus* (Anura: Hylidae)

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ABSTRACT.— Southern Cricket Frogs are prolonged breeders. During the reproductive season, males occupy calling territories from which they advertise for females. Mean territory size was 0.56 m^2 (0.03-1.36 m^2), and mean nightly movement by territorial males was 52 cm (0-205 cm). Territory size was not correlated with the number of days spent calling or with mating success. Observations on courtship behavior are presented.

Anuran species are categorized as either explosive or prolonged breeders (Wells 1977a). For species composing the former group, males and females arrive synchronously at the reproductive site. In many such species, males actively search out females, and mate discrimination by the female may be limited by male assertiveness. Explosive breeders are stimulated by heavy rainfall and breed for only a fews days afterwards. Prolonged breeders often partition the reproductive site into defended calling stations. Males advertise their position by persistent vocalization, and the arrival of receptive females is typically asynchronous. In species of this type, breeding is less dependent on seasonal precipitation, and reproductive activity may continue for months.

Studies on the reproductive behavior of anuran amphibians (particularly prolonged breeding species) have greatly increased during the past 15 years (for a review see Wells 1977a,b; Arak 1983). The purpose of this investigation is to quantify the breeding and courtship behavior of the Southern Cricket Frog, *Acris gryllus*, a small, terrestrial hylid indigenous to the southeastern United States (Neill 1950). During early spring and summer, males aggregate around pools and call. Chorusing may persist throughout the summer and calling males have been reported as late as early October (Wright and Wright 1949). Females appear to arrive at breeding pools asynchronously throughout the spring and summer, with peak oviposition from late April through June (Mecham 1964), but egg clutches have been reported during early fall (Wright and Wright 1949).

Despite the fact that this species is among the most common anurans within its geographic range, little is known about its reproductive biology and social structure. Our attention shall focus on social interactions between males by testing the following hypotheses: (1) calling males occupy a territory, (2) there is a correlation between the size of a calling territory and the number of nights a male is observed at the pond, and (3) there is a correlation between territory size and mating success.

STUDY SITE

This study was conducted during June and July of 1975. The study site was a complex of three small sand pits situated in a mixed pine/deciduous flatwoods in Bryan County, Georgia. In most years the pits collect rain, and during the spring and summer are active reproductive sites for numerous amphibian species, including: the Southern Toad, *Bufo terrestris*; the Oak Toad, *Bufo quercicus*; the Eastern Narrow-mouthed Toad, *Gastrophryne carolinensis*; the Squirrel Treefrog, *Hyla squirella*; the Pine Woods Treefrog, *Hyla femoralis*; the Barking Treefrog, *Hyla gratiosa*; the Southern Cricket Frog, *Acris gryllus*; the Little Grass Frog, *Limnaoedus ocularis*; the Southern Leopard Frog, *Rana sphenocephala*; the Crawfish Frog, *Rana areolata*; the Bullfrog, *Rana catesbeiana*; the Carpenter Frog, *Rana virgatipes*; the Mole Salamander, *Ambystoma talpoideum*; the Red-spotted Newt, *Notophthalmus viridescens*; and the Striped Newt, *Notophthalmus perstriatus*.

Our study was confined to a small (D = 3.5 m) pool with gently sloping banks and a firm bottom. The margin of the pond was covered with patches of low, dense grass. This vegetation was cover for 8 to 12 calling male *A. gryllus*, and sparse enough to permit observation of the males with minimal disturbance.

METHODS

Individual Recognition.— Male cricket frogs may be distinguished individually based on their dorsal pattern (Bayless 1969). All males observed during this study had their dorsal patterns diagramed for reference. Because the breeding congress was small and never included more than eight males on any given night, individuals were easily recognized.

Calling Stations.— Male *Acris* call from land (Wright and Wright 1949), and in the present study were always within 1 m of the shoreline.

Males were located by entering the pond at a given point each night and searching the periphery from the water. When a male was located (usually by phonotaxis), a small marker was inserted into the substrate beside him. The markers were constructed from wooden dowels (D = 3 mm, L = 120 mm) to which a piece of white, waterproof tape had been attached. The identification number of the male and the observation date were printed on the tape with India ink. Calling males apparently were not disturbed by these activities.

Site Fidelity by Calling Males.— Each time the position of a calling male was marked, we recorded its spatial relationship (directional angle and distance in cm) to the most recently placed marker and to the original observation point. These measurements enabled us to plot the territories of individual males on graph paper. A Leitz planimeter (Model 3651-30) was used to calculate the area within each territory. Area values were based on an average of five separate measurements.

Statistical Analysis.— Spearman's rank correlation procedure (Zar 1974) was used to test for correlations between territory size and the number of nights a male was observed at the pond, and between territory size and mating success. The Spearman's rank procedure is a nonparametric test developed to process data obtained from a bivariate population that violates normalcy.

Operational Sex Ratio.— We calculated the operational sex ratio (OSR) for the males and females observed during this study. The OSR is defined as the average ratio of fertilizable females to sexually active males at any given time (Emlen and Oring 1977). The OSR may or may not reflect the overall sex ratio of the species, particularly for prolonged breeders in which females arrive asynchronously at the reproductive site.

RESULTS AND DISCUSSION

Site Fidelity and Size of Territory.— Individual males moved an average of 52 cm (0 to 205 cm) between nights. Table 1 compares the mean nightly movement of each male. Nine of eleven males were observed on enough nights to facilitate calculation of their calling territories. Mean territory size was 0.562 m^2 (0.028-1.362 m^2). We believe that this restricted movement and site fidelity warrant acceptance of our first hypothesis, that calling *Acris gryllus* males are territorial. We must reject our second and third hypotheses. There was no significant correlation between the size of a territory and the number of nights a male was observed at the pond (two-tailed Spearman's Rho, $r = -5.521$, $P > 0.05$). Neither was there a correlation between territory size and mating success (two-tailed Spearman's Rho, $r = 0.187$, $P > 0.05$) (see Table 2).

In our study, individuals appeared evenly spaced around the margin of the pond. On only one occasion was a calling male seen invading the calling territory of a conspecific. This occurred on 16 June, when, after 1 night at the pond, Male 10 moved into the adjacent territory of Male 1. The resident male moved 1.3 m counterclockwise and continued to call for 3 nights before disappearing from the pond. The only other example of an extensive spatial shift occurred on 13 June, when Male 5 moved 2 m counterclockwise in response to rising water, which inundated his original calling site. This shift did not cause a change in the calling territory of the adjacent male (Male 4), and Male 5 remained at his site for an additional 13 days before leaving the pond on 26 June.

Although we did not quantify intermale distance, such data are available for the species. Turner (1960) performed nearest neighbor analysis on a Louisiana population in December and April, and reported mean isolation distances of 1.94 m and 1.71 m, respectively.

Behavioral Observations.— Five of the 11 males monitored during our study (observations were made on 18 nights during a 37-night period) were observed to amplex a female. Male 4 successfully amplexed two females over a 4-night span. Five of the six amplecting pairs were observed within a 5-night period during mid-June. It is probable that additional matings occurred but went undetected, for we were unable to visit the pond every night and frequently departed while some males were still advertising.

The operational sex ratio at our study pond was skewed in favor of the males (5.6:0.3). However, it is likely that we underestimated the number of females present at the pond, and as a consequence we consider our OSR value conservative.

On three occasions during the course of our study, we had the opportunity to observe male-female interactions leading to amplexus. A summary of each follows.

(1) 13 June 1975. Male 4 was calling from his territory. With the exception of his pulsating vocal sac, he was hidden from direct view by dense grass. As we watched, a large female hopped into the circle of light. She appeared to be searching for the source of the sound. Her behavior included short, circling hops coupled with periodic cocking of her head from side to side. As the male continued to call, the female became increasingly active, crawling on the grass tussock and actually passing directly over the male on several occasions. Although the female circled eight times, the diameter of the circles never exceeded 8 cm. This sequence occupied just under 5 minutes and terminated when the male quickly emerged and amplexed the female. She neither resisted the male nor initiated contact with him.

Table 1. Linear movement of *Acris gryllus* males between consecutive nightly observations.

Male No.	Number of nights observed	Mean (cm)	Range (cm)
1	7	81.00	0-160
2	8	8.00	0-29
3	9	54.80	0-168
4	5	38.20	0-50
5	6	72.33	30-164
6	2	10.00	10-10
7	4	119.50	70-205
8	-	-	-
9	6	47.00	16-105
10	2	14.50	14-15
11	3	29.33	12-46

Table 2. Territory size, duration of calling, and mating success in a small breeding congress of *Acris gryllus*. No. nights observed = number of nights on which a male's calling position was marked. Days in residence = the span over which the male was known to be at the pond.

Male No.	Territory size (m^2)	No. nights observed	Days in residence	No. matings observed
1	0.502	9	10+	0
2	0.127	12	13+	1
3	1.373	16	37+	0
4	0.180	7	8+	2
5	1.362	11	18+	0
6	-	3	3	0
7	0.673	6	8	1
8	0.288	12	33+	1
9	-	2	4	0
10	0.028	6	8	0
11	0.545	7	23+	1
	$\bar{x} = 0.562$	$\bar{x} = 8.27$	$\bar{x} = 14.06$	

(2) 14 June 1975. Male 7 was calling in an open spot between several clumps of grass. He lowered the pulse rate of his call and became active shortly before a female became visible. As the female approached, the male began to hop in tight circles (D = 4 cm). While moving, he continued to call. After 2.5 minutes, the male ceased calling and became stationary. Immediately the female approached to within 1 cm of the male's left side, and he quickly turned and faced her, snout to snout. After a 15-second pause, the male moved behind and amplexed the female.

(3) 11 July 1975. Male 11 was calling while a female sat 3 cm away, facing the opposite direction. They remained motionless for approximately 5 minutes. Suddenly the female began what we describe as a "quiver-hop" behavior, which involved quick, nervous movement of the forelimbs and elevation of the body 1 to 2 mm in a vertical position. After the female had exhibited this behavior twice in rapid succession, the male turned, moved quickly behind the female, and initiated amplexus.

Calling male cricket frogs formed duets, trios, quartets, and occasionally quintets. The significance of this call synchrony to *Acris gryllus* was not tested, but similar behavior is reported to be important during mate selection by other hylids. In a study of the Pacific Treefrog, *Hyla regilla*, females preferred the designated bout leader during call discrimination trials involving a single male quarteting with itself (Whitney and Krebs 1975). The authors concluded that bout leadership must somehow imply greater fitness to a responding female. We doubt that bout leadership is indicative of male fitness in *A. gryllus*, for two reasons: (1) bout leadership often changed during the course of an evening, and (2) bout leadership frequently changed from one night to the next. We suggest, as an alternative hypothesis, that antiphonal calling may enhance the fitness of the participating males by reducing broadcast interference. This role has been documented for the Spring Peeper, *Hyla crucifer*, a prolonged breeder of similar size and habits (Forester and Harrison, unpubl. ms.).

Among hylids, satellite behavior and sexual parasitism by noncalling males has been well documented (Perrill et al. 1978, 1982). To employ this behavioral strategy a noncalling male positions himself near a calling male and attempts to intercept females responding to the caller. Often, calling males respond agonistically to satellites as well as to other conspecific males that violate their calling territory. During our study, in more than 70 hours of observation, we observed neither satellite behavior nor agonistic encounters between males. Our failure to document social interactions between males is more likely a reflection of low male density at our study pond, since both behaviors have been observed in dense populations of the closely related congener, *Acris crepitans*, in Indiana (S. A. Perrill, pers. comm.).

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THE SEASIDE SPARROW, ITS BIOLOGY AND MANAGEMENT

Edited by

Thomas L. Quay, John B. Funderburg, Jr., David S. Lee,
Eloise F. Potter, and Chandler S. Robbins

The proceedings of a symposium held at Raleigh, North Carolina, in October 1981, this book presents the keynote address of F. Eugene Hester, Deputy Director of the U. S. Fish and Wildlife Service, a bibliography of publications on the Seaside Sparrow, and 16 major papers on the species. Authors include Arthur W. Cooper, Oliver L. Austin, Jr., Herbert W. Kale II, William Post, Harold W. Werner, Glen E. Woolfenden, Mary Victoria McDonald, Jon S. Greenlaw, Michael F. Delany, James A. Mosher, Thomas L. Merriam, James A. Kushlan, Oron L. Bass, Jr., Dale L. Taylor, Thomas A. Webber, and George F. Gee. A full-color frontispiece by John Henry Dick illustrates the nine races of the Seaside Sparrow, and a recording prepared by J. W. Hardy supplements two papers on vocalizations.

"The Seaside Sparrow, with its extensive but exceedingly narrow breeding range in the coastal salt marshes, is a fascinating species. All the authors emphasize that the salt marsh habitat is at peril. . . . The collection is well worth reading." — *George A. Hall, Wilson Bulletin.*

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Core Temperatures of Non-nesting Western Atlantic Seabirds

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ABSTRACT.— Core body temperatures of 23 species of birds collected off the North Carolina coast did not differ with sex, weight, time of day, or season. Within the orders Procellariiformes and Charadriiformes, there seems to be no correlation of temperature with mass. Temperature data on injured birds are similar to those of ones recently killed. Results of this study compared favorably with those obtained by other researchers and indicate no significant differences between body temperatures of foraging and non-incubating procellariiform birds at the nesting colonies. Temperature differences between birds taken at sea and those studied at nesting sites amount to about 1 °C and are best attributed to the activity state of the birds.

Little uniform information is available on deep-body temperatures of seabirds away from nesting colonies. Comparing thermal information collected by different investigators, using dissimilar methods and sampling variable locations within the body, presents interpretive difficulties. The opportunity to gather temperatures from a variety of species, using uniform methods and equipment, presented itself during a long-range study into the occurrence, seasonal distribution, and food habits of seabirds off the North Carolina coast (see Lee and Booth 1979). This paper is the first extensive report of core temperatures in actively foraging seabirds. It complements the works of others who obtained most of their information from nesting colonies, and for the most part substantiates their findings and speculations.

MATERIALS AND METHODS

Information was obtained between 1977 and 1982, primarily during spring, summer, and fall. Specimens were shot from boats traveling from 30 to 60 km off North Carolina's Outer Banks. Birds were then netted from the water and a thermistor probe (#418), feeding into a calibrated telethermometer (Yellow Springs Instruments), was inserted

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through the abdominal wall near the caudal part of the sternum deep into the viscera. The maximum time between downing of the bird and the insertion of the thermistor probe was 2 minutes. Body temperature (T_b) recordings stabilized within a maximum of 30 seconds of probe insertion. In order to determine if stress and shock affected core body temperature, readings were taken from any still-living birds before death and within 1 to 3 minutes of being shot. We also monitored the rate of cooling of six specimens for 20 minutes after death. Birds were later frozen in sealed plastic bags. After thawing in the laboratory, each bird was weighed to the nearest 0.1 g and sexed while being prepared for use in other studies. Level of significance is 0.05 for correlation coefficients of regressions and sample differences (using Student's *t*-test). Data are presented as mean ± 1 standard deviation.

RESULTS

Table 1 presents deep body temperatures and body mass of 23 species of seabirds representing 4 orders, 14 genera, and 250 individuals. Mean T_b of male and female seabirds (Table 2) were not significantly different. In Audubon's Shearwater, *Puffinus lherminieri*, and Cory's Shearwater, *Calonectris diomedea*, the only species with a field collecting base spanning 6 to 9 hours, T_b did not vary with time of day. However, we made no night collections. In both of these shearwaters, as well as in the Greater Shearwater, *Puffinus gravis*, T_b did not correlate with time of year. These three species were collected during the longest calendar sequences (April-November). Additionally, intraspecific regressions of body mass versus T_b were not significant.

Cooling curves were obtained on six birds ranging in size from 39.7 to 763.5 g (Fig. 1). As expected, large birds cooled more slowly than small ones. For example, in the first 20 minutes internal temperatures dropped less than 0.8 °C on *Pterodroma*-size birds. Four of six birds showed a slight and brief increase in T_b during the first minute or two. We think this temporary increase was the result of continued cellular heat production immediately after death in the absence of convective (respiratory and circulatory) avenues of heat loss. This initial increase in temperature may mask some heat loss owing to the elapsed time between death and T_b measurements. However, temperatures of living birds and recently dead ones showed no observable differences (Table 3).

DISCUSSION

In collecting temperature information we attempted to eliminate as many biases as possible. Activity states of the birds immediately prior to temperature measurements undoubtedly accounted for some of the variation in the procellariiform birds whose body temperatures were summarized by Warham (1971). The difference between resting/incubating and active procellariiform birds amounted to about 2 °C (Farner

Table 1. Deep body temperatures and body mass of seabirds. Mean ± one standard deviation (range in parentheses).

	N	Mass (g)	Body temperature (°C)
Gaviiformes			
Gavia immer	2	3588.0 ± 58.0 (3547.0-3629.0)	39.7 ± 0.2 (39.5-39.8)
Procellariiformes			
Fulmarus glacialis	20	692.3 ± 78.5 (550.0-860.0)	39.9 ± 0.8 (38.0-42.0)
Calonectris diomedea	35	591.6 ± 81.8 (430.4-749.5)	39.6 ± 0.9 (38.2-41.0)
Puffinus gravis	25	615.1 ± 103.7 (424.3-870.0)	39.8 ± 0.7 (38.6-41.2)
Puffinus lherminieri	35	206.6 ± 20.5 (138.4-242.0)	39.5 ± 1.0 (36.5-41.2)
Puffinus griseus	1	774.0	41.0
Pterodroma hasitata	9	441.5 ± 68.8 (352.3-496.0)	39.1 ± 0.6 (38.0-40.0)
Oceanites oceanicus	25	33.5 ± 3.5 (25.9-39.4)	38.9 ± 1.3 (37.0-42.2)
Pelecaniformes			
Phaethon aethereus	2	616.4 ± 12.1 (607.8-624.9)	39.3 ± 1.1 (38.5-40.0)
Sula bassanus	4	3396.0 ± 383.0 (2898.0-3750.0)	40.7 ± 0.9 (40.0-42.0)
Phalacrocorax auritus	2	1833.9 ± 96.7 (1765.5-1902.3)	40.4 ± 0.6 (39.9-40.8)
Charadriiformes			
Phalaropus lobatus	5	37.0 ± 5.9 (31.6-46.6)	39.9 ± 1.1 (38.8-41.5)
Phalaropus fulicaria	14	55.4 ± 9.9 (38.9-73.0)	40.3 ± 1.0 (38.2-42.6)
Stercorarius pomarinus	14	743.8 ± 58.7 (660.3-849.9)	40.4 ± 1.3 (38.4-43.3)
Stercorarius parasiticus	2	522.8 ± 9.3 (516.2-529.4)	42.0 ± 0.3 (41.8-42.2)
Larus marinus	4	1641.0 ± 89.8 (1577.0-1774.0)	39.7 ± 1.0 (39.2-41.2)
Larus argentatus	6	919.5 ± 120.7 (778.0-1114.5)	40.4 ± 0.5 (39.5-41.0)
Larus atricilla	11	333.7 ± 35.8 (277.9-424.6)	40.6 ± 1.3 (37.8-42.0)
Larus philadelphia	2	211.0 ± 7.1 (206.0-216.0)	39.3 ± 0.3 (39.1-39.5)
Rissa tridactyla	10	368.0 ± 60.5 (294.7-448.4)	40.2 ± 0.6 (39.4-41.2)
Sterna hirundo	7	118.0 ± 14.4 (95.5-142.4)	40.8 ± 1.1 (39.0-42.5)
Sterna anaethetus	6	135.5 ± 15.4 (117.9-154.3)	40.4 ± 0.8 (39.2-41.8)
Sterna maxima	9	489.5 ± 29.2 (456.7-543.1)	40.1 ± 1.1 (38.0-41.1)

1956; Farner and Serventy 1959; Grant and Whittow 1983; Howell and Bartholomew 1961a,b; Warham 1971). Warham (1971) expressed doubt that the T_b of petrels flying at sea would be greatly increased, because of their energy-efficient methods of flight. Most of the temperatures presented here are from birds collected in flight, although some of the phalaropes were collected on the water. Nevertheless, most of the phalaropes were actively foraging (i.e. swimming) rather than resting on the surface. We have no way of knowing how long an individual bird had been active or how long it had been resting before collection. Avian flight (especially in birds that do not soar) typically elevates body temperatures 1 to 2 °C above the level recorded for resting birds

Table 2. Body temperatures of male and female seabirds. Means not significantly different at P > 0.05.

	Male		Female	
Species	N	°C ± 1SD	N	°C ± 1SD
Fulmarus glacialis	7	39.7 ± 1.0	13	40.0 ± 0.8
Calonectris diomedea	15	39.6 ± 0.9	15	39.7 ± 0.9
Puffinus gravis	7	39.6 ± 0.7	15	39.9 ± 0.8
Puffinus lherminieri	15	39.3 ± 1.3	15	39.6 ± 0.7
Oceanites oceanicus	9	38.6 ± 1.2	12	38.6 ± 1.2
Stercorarius pomarinus	4	40.1 ± 2.2	9	40.3 ± 1.0
Larus atricilla	4	41.3 ± 0.8	6	39.9 ± 1.4
Rissa tridactyla	4	40.3 ± 0.9	6	40.1 ± 0.4

(Berger and Hart 1974). The maximum T_b of flying birds can be seen in the upper part of the T_b range of Table 1. The T_b of seven petrel species averaged 39.7 ± 0.7 °C, which is only about 0.9 °C higher than the mean compiled for 31 species by Warham (1971). This slight and insignificant difference may result from one or more of the following: activity states of the bird, different investigator's techniques, and positioning of temperature probes (cloacal, preventricular, or visceral). We suspect, however, that it reflects the larger percentage of active birds in our samples than in samples compiled by investigators working with nesting colonies. We found no body mass, sexual, seasonal, or hourly differences in T_b within species.

McNab (1966:54) argued that the "apparent correlation between the level of body temperature and the taxonomic group is really a correlation of weight and taxonomic group. (It should be noted that within both the ratites and penguins, small species have higher body temperatures than large species)." Warham (1971) presented evidence that the mean body temperature of petrels is significantly lower than that of non-procellariiform birds. Within the order Procellariiformes, regression of T_b against body weight for our temperature (Table 1) likewise shows no correlation. Small petrels do not have higher body temperatures than do large ones, as Warham illustrated. This is true for our Charadriiformes as well. Our temperatures agree closely with the range of body temperatures reported by Dawson and Hudson (1970) for the orders Gaviiformes, Procellariiformes, Pelecaniformes, and Charadriiformes.

We found no evidence that stress and shock affected the body temperatures of still-living birds within 1 to 3 minutes after they were shot. The T_b's did not differ from those of recently expired birds (Table 3).

Table 3. Body temperatures and masses of dead and live birds.

Species	Dead			Live		
	Temperature		Mass	Temperature		Mass
	N	°C ± 1SD	g ± 1SD	N	°C ± 1SD	g ± 1SD
Calonectris diomedea	35	39.6 ± 0.9	591.6 ± 81.8	12	39.5 ± 0.7	577.5 ± 66.6
Puffinus lherminieri	35	39.5 ± 1.0	206.6 ± 20.5	16	39.9 ± 0.9	208.9 ± 22.7
Pterodroma hasitata	9	39.1 ± 0.6	441.5 ± 68.8	3	39.8 ± 0.7	491.1 ± 34.6
Oceanites oceanicus	25	38.9 ± 1.3	33.5 ± 3.5	8	38.6 ± 1.8	32.2 ± 2.6
Phalaropus lobatus	5	39.9 ± 1.1	37.0 ± 5.9	5	40.9 ± 1.2	38.9 ± 6.7
Phalaropus fulicaria	14	40.3 ± 1.0	55.4 ± 9.9	7	40.9 ± 0.9	51.8 ± 9.0
Sterna hirundo	7	40.8 ± 1.1	118.0 ± 14.4	4	41.4 ± 0.8	127.3 ± 20.1
Sterna anaethetus	6	40.4 ± 0.8	135.5 ± 15.4	3	40.6 ± 1.1	127.6 ± 5.5

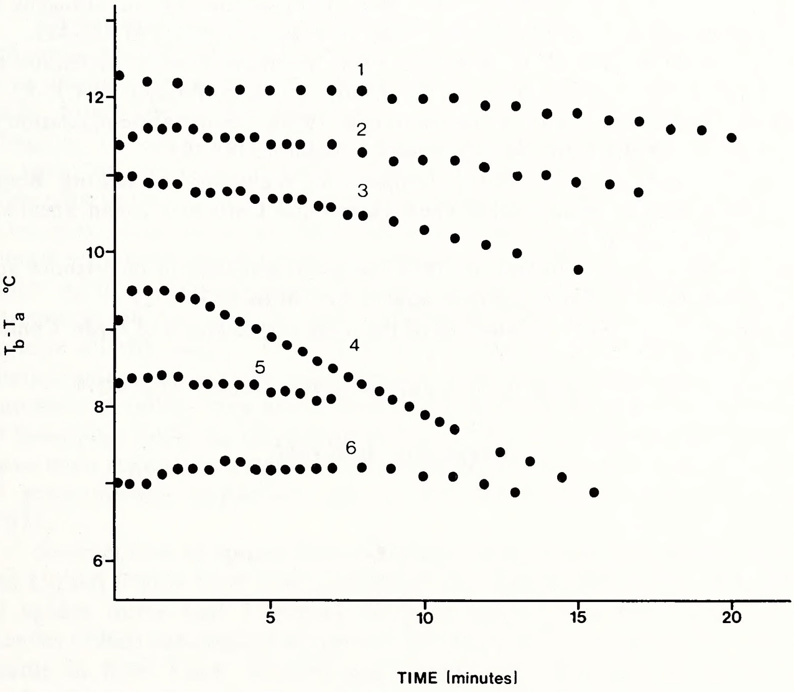

Fig. 1. Cooling curves of six seabirds of various masses. Zero time is time of death. 1. *Pterodroma*, 448.9 g. 2. *Pterodroma*, 459.0 g. 3. *Puffinus lherminieri*, 221.9 g. 4. *Oceanites oceanicus*, 39.7 g. 5. *Calonectris diomedea*, 763.5 g. 6. *Puffinus lherminieri*. 232.5 g.

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Spider Mites and False Spider Mites (Acari: Tetranychidae and Tenuipalpidae) Recorded from or Expected to Occur in North Carolina

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ABSTRACT.— Thirty-six species of spider mites have been collected from North Carolina and their host plants identified. An additional 57 species are known from the eastern United States on hosts that also occur in North Carolina. Seven species of false spider mites have also been collected in the state and their host plants identified. Twenty-nine others may occur in North Carolina, as their hosts are within the state.

Spider mites (also called spinning mites, plant mites, red mites, and red spiders) and false spider mites (also called flat mites) are phytophagous arachnids usually with a body length of less than 1 mm in the adult stage. Some species are polyphagous and others are apparently monophagous. The life cycle of egg-larva-protonymph-deutonymph-adult may be spent on the host, or some stages may leave the host to estivate or hibernate in soil litter or to search for other hosts. One or more generations may occur annually. Most species are known from both male and female specimens while others are apparently known only from females. Mites occur at characteristic locations on the host, such as leaf or fruit, depending on the species, and may usually be found in groups that include all life stages. They feed by puncturing plant cells with their chelicerae and eating the cell contents. The feeding, especially by large numbers of mites, may cause observable damage to plants in the form of bronzing, flecking, or curling of leaves. For this reason many species have been regarded as pests. More detailed accounts of the life histories of economically important species may be found in Jeppson et al. (1975).

Several lists of spider mites and false mites from the eastern half of the United States have been published. Garman (1940) listed 15 species of spider mites and 1 species of false spider mite for Connecticut. Reeves (1963) catalogued 40 species of spider mites occurring on woody plants in New York. Mellott and Connell (1965) listed 20 species of spider mites and one species of false spider mite for Delaware. Thewke and Enns (1970) listed 38 species of spider mites representing 13 genera, and 11 species of false spider mites representing 3 genera, for Missouri.

Prasad (1970) recorded 20 species of spider mites and 3 species of false spider mites from Michigan. Flechtmann and Hunter (1971) catalogued 27 species of spider mites representing 10 genera for Georgia. Ten species of Tetranychidae but no species of Tenuipalpidae were recorded for North Carolina by Brimley (1938) and Wray (1967).

Our list summarizes records for species of spider mites and false spider mites for North Carolina and provides information to collectors about additional species that might be found in the state when more extensive collecting is done. The list is based on published records and on approximately 1000 specimens, nearly all of which were collected in North Carolina, in the North Carolina State University (NCSU) Insect Collection, including Extension Entomology reference collections. An asterisk after the mite species name in Table 1 indicates specimens are in the NCSU collections and were associated with host plants also marked with an asterisk.

Since the North Carolina climate encompasses mild coastal as well as cooler mountain elements and a very diverse flora, we included species recorded in the literature from Connecticut, Delaware, District of Columbia, Florida, Georgia, Louisiana, Maryland, Michigan, Mississippi, Missouri, New York, Ohio, Pennsylvania, South Carolina, Tennessee, Texas, and Virginia on the probability that their range includes North Carolina because suitable host plants and climate are present. The collection record given is for the state geographically nearest North Carolina, although the mite may be known from several other states. The recorded hosts for each species include one or two hosts that occur in North Carolina according to Radford et al. (1968). If more than two hosts are known, they are included under "others" and may be found by consulting the reference given for the mite species. The exception is for species in NCSU collections, where all of the hosts for our specimens are given. Common names of most hosts are listed, as these are the names that appeared with collection data; however, in some cases scientific names are presented, because these were given in the literature and no common names are provided in Radford et al. (1968). Nomenclature of hosts follows Radford et al. (1968) and Bailey Hortorium Staff (1976).

Twenty-eight species of spider mites are represented by specimens in the NCSU collections, and eight more species are recorded in the literature as being from the state. Fifty-seven additional species may occur in the state. Five species of false spider mites are represented by specimens in the NCSU collections, and an additional two species are recorded in the literature as having been collected in North Carolina. Twenty-nine additional species may occur in the state.

Only 39% of the spider mites and 19% of the false spider mites recorded from the eastern half of the United States are known to be present in North Carolina. Thus, there is still a need for more thorough collections within the state. Future collectors are encouraged to record host information carefully, as correct plant species or cultivar identification is useful in identifying the mites and determining their host specificity.

Table 1. Spider mites and false spider mites recorded from or expected to occur in North Carolina.

Species	Collection record	Recorded hosts
Tetranychidae		
Aponychus spinosus (Banks) [1]	GA	American elm, linden
Beerella petiolaris Thewke [2]	MO	*Helianthus petiolaris*
Bryobia praetiosa Koch*	NC	apple leaves and bark*, grass*, Japanese holly*, horse* [accidental], indoors*, leaf litter*, orchid*, cedar stump*, vetch*, others [3]
B. rubrioculus (Scheuten)*	NC	apple leaves and bark*, grass*, others [3]
Eotetranychus carpini borealis Pritchard and Baker [2]	MO	apple [2], sugar maple [2], others [4]
E. carpini carpini (Oudemans) [3]	NY	apple, oak, others
E. caryae Reeves [3]	NY	hickory, pecan, others
E. clitus Pritchard and Baker*	NC	azalea*, blackberry*, others [4]
E. coryli (Reck) [4]	DC	red maple
E. crossleyi Flechtmann and Hunter [1]	GA	chalk maple
E. deflexus (McGregor) [5]	SC	azalea, coralberry
E. frosti (McGregor) [3]	OH	blackberry, rose, others
E. hicoriae (McGregor) [4]	NC	hickory, pecan, others
E. lewisi (McGregor) [3]	MI	citrus, clover, others
E. matthyssei Reeves [3]	NY	black locust, elm, others
E. pallidus (Garman) [3]	NY	alder, beech
E. populi (Koch) [4]	NC	poplar, weeping willow, others
E. pruni (Oudemans) [6]	DC	red maple, sugar maple, others
E. querci Reeves [6]	NY	oaks, white birch
E. sexmaculatus (Riley) [3]	FL	azalea, pyracantha, others
E. smithi Pritchard and Baker [3]	TN	cotton, rose, others
E. tiliarium (Hermann) [3]	Atlantic coast	linden, sycamore, others
E. ulmicola (Reck) [2]	MO	American elm, elm
E. uncatus Garman*	NC	apple*, pear*, rose*, others [3]
E. sp. probably *E. uncatus* Garman*	NC	willow oak*
Eurytetranychus admes Pritchard and Baker [2]	MO	incense cedar[2], juniper [2], others [4]
E. buxi (Garman)*	NC	boxwood*
Eutetranychus banksi (McGregor) [4]	FL	castor bean, citrus, others
Monoceronychus linki Pritchard and Baker [4]	FL	saw grass, others
M. mcgregori Pritchard and Baker [4]	FL	St. Augustine grass
M. scolus Pritchard and Baker [4]	NC	Bermuda grass, grass

Table 1. Continued.

Species	Collection record	Recorded hosts
Mononychellus virginiensis (McGregor)*	NC	black locust*, locust*
Oligonychus aceris (Shimer)*	NC	maple [4], sugar maple*
O. bicolor (Banks) [4]	NC	white oak, willow oak, others
O. sp. probably *O. bicolor* (Banks)*	NC	willow oak*
O. boudreauxi Pritchard and Baker [4]	MS	bald cypress
O. coffeae (Neitner) [3]	FL	camellia, grape, others
O. coniferarum (McGregor) [4]	FL	arbor vitae, juniper, others
O. cunliffei Pritchard and Baker [4]	FL	pine
O. endytus Pritchard and Baker [1]	GA	American holly [1], oleaster [1] others [4]
O. sp. near *O. endytus* Pritchard and Baker*	NC	willow oak*
O. hondoensis (Ehara) [3]	NY	Japanese cedar
O. ilicis (McGregor)*	NC	azalea*, camellia*, *Cotoneaster* sp.*, Japanese holly*, others [3]
O. indicus (Hirst) [3]	worldwide	Johnson grass, sorghum, others
O. letchworthi Reeves [6]	NY	*Ostrya virginiana*
O. milleri (McGregor)*	NC	longleaf pine*, others [6]
O. modestus (Banks) [1]	GA	bamboo, corn
O. newcomeri (McGregor) [3]	probably northeastern USA	apple, hawthorn, others
O. nielseni Reeves [6]	NY	white pine
O. platani (McGregor) [3]	NC	boxwood [3], juniper [3], others [4]
O. pratensis (Banks) [3]	GA	Johnson grass, wheat, others [3]
O. propetes Pritchard and Baker [4]	NC	hawthorn [2], oak [4], others [2]
O. stickneyi (McGregor) [3]	FL	corn, rye, others
O. ununguis (Jacobi)*	NC	Fraser's fir*, juniper*, others [3]
O. viridis (Banks) [3]	GA, SC	hickory, pecan
O. yothersi (McGregor)*	NC	azalea*, boxwood*, others [3]
Palmanychus steganus (Pritchard and Baker) [4]	FL	palmetto
Panonychus caglei (Mellott) [3]	VA	blackberry, kudzu, others
P. citri (McGregor)*	NC	citrus*, kumquat*, rose* silverberry*, others [3]
P. ulmi (Koch)*	NC	apple leaves*, elm*, *Ilex* sp.*, kumquat*, peach*, others [3]
Petrobia apicalis (Banks) [1]	GA	crimson clover [1], legumes [1], others [3]

Table 1. Continued.

Species	Collection record	Recorded hosts
P. harti (Ewing)*	NC	clover*, wood sorrel*, others [3]
P. latens (Müller)*	NC	cotton*, wheat*, others [3]
P. lupini (McGregor) [1]	GA	grass, lupines
Platytetranychus multidigituli (Ewing) [1]	NC	honey locust
P. thujae (McGregor)*	NC	arbor vitae [4], juniper*, others [4]
Schizotetranychus asparagi (Oudemans) [4]	DC	asparagus fern, *Asparagus* sp.
S. camur Pritchard and Baker [1]	GA	cane [1], reed grass [4]
S. celarius (Banks) [3]	GA	bamboo, rice, others
S. garmani Pritchard and Baker [4]	CT	willow
S. oryzae Rossi de Simons [3]	TX	rice
S. schizopus (Zacher) [4]	NY	willow
S. spireafolia Garman [4]	PA	*Spiraea alba* var. *latifolia*, others
Tenuipalpoides dorychaeta Pritchard and Baker [4]	NC	black locust, honey locust, others
Tetranychus canadensis (McGregor)*	NC	cotton*, paper mulberry*, plum*, others [4]
T. cinnabarinus (Boisduval)*	NC	*Areca* sp.*, butter bean*, butterfly weed*, cotton*, *Dracaena* sp.*, *Impatiens* sp.*, Arabian jasmine*, marigold*, passion flower*, *Schefflera* sp.*, snap bean*, kuta squash*, tomato*, others [3]
T. cocosinus Boudreaux [4]	LA	brambles, hackberry, others
T. desertorum Banks*	NC	cotton*, grass*, others [3]
T. gloveri Banks [3]	LA	cotton
T. homorus Pritchard and Baker [4]	NC	ash, hickory
T. lobosus Boudreaux*	NC	azalea*, "*Nephthytis*" sp. (probably *Syngonium* sp.)*, string bean*, wisteria*, others [7]
T. ludeni Zacher [3]	LA [4]	beans [3], cotton [3], others [3]
T. magnoliae Boudreaux*	NC	magnolia*, tulip poplar*
T. marianae McGregor [3]	FL	cotton, passion flower, others
T. mcdanieli McGregor [4]	NY	apple [3], raspberry [3], others [4]
T. merganser Boudreaux*	NC	cranberry*, privet*, others [4]
T. sp near *T. merganser* Boudreaux*	NC	European cranberry bush*
T. mexicanus (McGregor) [3]	TX	Johnson grass, magnolia

Table 1. Continued.

Species	Collection record	Recorded hosts
T. neocalidonicus Andre [4]	FL	butterfly bush, sweet potato, others
T. schoenei McGregor*	NC	apple leaves and twigs*, blackberry*, Japanese flowering cherry*, cotton*, raspberry*, weed*, others [4]
T. sinhai Baker [1]	GA	Johnson grass, wild rye grass, others
T. tumidellus Pritchard and Baker*	NC	peanut*
T. tumidus Banks*	NC	cotton*, eggplant*, *Pilea* sp.*, others [4]
T. sp. probably *T. tumidus* Banks*	NC	*Schefflera* sp.*
T. turkestani (Ugarov and Nikolski)*	NC	clover*, cotton*, green bean*, lima bean*, peanut leaves*, soybean*, strawberry*, others [3]
T. urticae Koch*	NC	apple leaves and bark*, *Areca* sp.*, Japanese aucuba*, butterfly tree*, Japanese flowering cherry*, cotton*, cucumber*, dahlia*, *Dracaena* sp.*, *Euonymous japonica**, day lily*, *Fatshedera* sp.*, gardenia*, gladiolus*, hollyhock*, *Impatiens* sp.*, locust*, peach*, peanut*, pear*, piggy-back plant*, primrose*, tomato*, water hyacinth*, wood sorrel*, others [3]
T. yusti McGregor [3]	DE	soybean, grasses, others
Tenuipalpidae		
Aegyptobia nothus Pritchard and Baker*	NC	bald cypress*, juniper*, others [8]
A. sp. probably *A. nothus* Pritchard and Baker*	NC	cedar*
Brevipalpus arcus Pritchard and Baker [8]	FL	camphor weed, weed
B. bicolpus Pritchard and Baker [8]	MD	pawpaw
B. butcheri Pritchard and Baker [8]	FL	*Amaranthus* sp.
B. californicus (Banks) [8]	MD	apple, maple, others

Table 1. Continued.

Species	Collection record	Recorded hosts
B. colpodes Pritchard and Baker [8]	FL	*Baccharis* sp.
B. columbiensis Thewke [2]	MO	sycamore
B. docimas Pritchard and Baker [8]	NC	hickory, probably walnut
B. ennsi Thewke [2]	MO	alumroot, ironweed, others
B. floridanus DeLeon [8]	FL	red bay
B. garmani Baker [8]	SC	alder [8], thoroughwort [8], others [2, 8]
B. glomeratus Pritchard and Baker [8]	VA	basswood [2], oak [8], others [2]
B. glymma Pritchard and Baker [8]	FL	lantana
B. hybus Pritchard and Baker [8]	FL	hyacinth, weed
B. lewisi McGregor [8]	NC	alder, grape, others
B. lilium Baker [8]	FL	apple, azalea, others
B. linki Baker [8]	FL	oak
B. obovatus Donnadieu*	NC	Japanese aucuba*, azalea*, dumb cane*, Japanese holly*, *Microphylla* sp.*, *Pittosporum* sp.*, rhododendron*, others [8]
B. sp. probably *B. obovatus* Donnadieu*	NC	*Dionaea* sp. leaves*, maple*
B. ogmellus Pritchard and Baker [8]	LA	oak
B. phoenicis (Geijskes)*	NC	apple*, false aralia*, goldenrod*, others [8]
B. pinicola Pritchard and Baker [8]	FL	pine
B. sayedi Baker [9]	GA	hickory, pecan
B. xystus Pritchard and Baker [8]	LA	pecan [8], pignut hickory [2], others [8]
Dolichotetranychus apaches Baker and Pritchard [8]	FL	a bromeliad
D. salinas Pritchard and Baker [8]	MD	salt grass
Pentamerismus canadensis McGregor [8]	NY	arbor vitae
P. erythreus (Ewing)*	NC	Andorra juniper*, juniper*, red cedar*, others [8]
P. oregonensis McGregor*	NC	arbor vitae*, juniper*, others [8]
P. taxi (Haller) [8]	DC	yew
Tenuipalpus argus Baker and Pritchard [8]	FL	yucca
T. bakeri McGregor [8]	FL	oak, others
T. carolinensis Baker [8]	SC	goldenrod
T. celtidis Pritchard and Baker [8]	FL	hackberry

Table 1. Continued.

Species	Collection record	Recorded hosts
T. dasples Baker and Pritchard [8]	FL	palmetto
T. pacificus Baker [3]	FL	orchids
T. rhysus Baker and Pritchard [8]	FL	*Cyrilla racemiflora*, magnolia, others

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* - mite specimens in NCSU collections and hosts associated with those specimens.

[1] Flechtmann and Hunter 1971

[2] Thewke and Enns 1970

[3] Jeppson et al. 1975

[4] Pritchard and Baker 1955

[5] McGregor 1950

[6] Reeves 1963

[7] Boudreaux 1956

[8] Pritchard and Baker 1958

[9] Flechtmann and Davis 1971

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Life History of the Wood Frog, *Rana sylvatica* LeConte (Amphibia: Ranidae), in Alabama

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ABSTRACT.— A life history study of the wood frog, *Rana sylvatica* LeConte, was conducted from February 1978 to January 1980. All populations studied were in the Blue Ridge and Piedmont physiographic provinces of Alabama, mostly in semideciduous forests along the flood plains of major streams. Breeding activity occured from mid-January to late February and coincided with the onset of warm winter rains. Most breeding occurred in semipermanent woodland pools. *Ambystoma opacum* and *A. maculatum* were consistent breeding associates. Usually present were *Notophthalmus viridescens*, *Hyla crucifer*, *Pseudacris triseriata*, *P. brachyphona*, and *Rana sphenocephala*. Mean clutch size in *R. sylvatica* was 496. Diameters of eggs and jelly envelopes are the largest reported for this species. Analysis of stomach contents indicated that adult frogs are opportunistic terrestrial feeders, but they apparently do not feed during the short, explosive breeding season.

The wood frog, *Rana sylvatica* LeConte, is a small to medium-sized ranid frog with an extensive geographic range. Martof and Humphries (1959) reported its range as extending over approximately 4,044,000 square miles (more than 10,000,000 km^2) from Alaska to Georgia. This range is exceeded in North America only by that of the *Rana pipiens* complex, which actually consists of several species. Its broad distribution and the relative abundance of *R. sylvatica* over most of its range have prompted considerable research. Most information concerning its life history appears as scattered notes in general references, in papers presenting distributional information or ecology, in studies on amphibian community structure or reproductive behavior, and in accounts in various state herpetological publications.

Rana sylvatica was first discovered in Alabama in 1974 (Mount 1975). Its presence was documented by three specimens from Mt. Cheaha, Cleburne County, in the east central part of the state. Prior to Mount's record, the southernmost locality for *R. sylvatica* was thought

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to be in northeastern Georgia, approximately 160 km northeast of the Alabama locality. The collection of additional specimens south of Mt. Cheaha and the paucity of information on Alabama populations provided the impetus for the present study. Our attention focused on features of the frog's life history, for a cohesive study of this type (especially in the southern part of the range) was lacking. Furthermore, the biology of any organism at the terminus of its range may provide insights into the adaptive significance of geographic variation in life history parameters.

MATERIALS AND METHODS

Considerable effort was devoted to locating potential breeding ponds and breeding populations. Searching was confined chiefly to the Blue Ridge physiographic province and the upper sections of the Piedmont Plateau.

Wood frogs were collected by hand in breeding ponds and on highways during warm rains. Temperatures of water, air, or both were taken with a field thermometer at the time of collection. Most specimens were killed in 20% chloretone, then positioned and fixed in 10% formalin for at least 72 hours. Formalin was injected into the body cavity to preserve food and reproductive organs. Individuals were later transferred to 70% ethanol for permanent storage in the Auburn University Vertebrate Museum.

The stomach and intestine of each frog were removed, slit longitudinally, and the contents washed into a culture dish. All food items were examined under a dissecting microscope and identified to the lowest possible taxon. The volume of food items was not determined. Ovaries or ovisacs were removed and their percentages of total body weight calculated. Ovarian or ovisacal eggs were counted, if present, and then stored in 70% ethanol.

Snout-vent lengths (SVL) were determined by measuring from the tip of the snout to the posterior edge of the urostyle. Tibiofibula lengths (TFL) were taken by measuring the maximum length of the tibiofibula when the shank was completely flexed upon the thigh (Martof and Humphries 1959), and ratios of TFL to SVL were calculated. Snout length, defined as the distance from the anterior edge of the eye to the nostril, and snout height, taken as the straight-line distance from the nostril to the edge of the upper lip (Ruibal 1957), were also measured. All measurements were made with dial calipers to the nearest 0.1 mm after specimens had been kept in alcohol for at least 3 weeks.

Information on reproduction was obtained primarily from field studies. Notes were made on calls of males, egg deposition, clutch size, egg development, egg mortality, and egg predators. Clutch size was determined by counting the number of eggs in six egg masses and by volumetric displacement of four additional egg masses. Estimates from volumetric displacement were obtained by placing an entire egg mass in a 1-l graduated cylinder containing 200 ml of water. The volume of water displaced by each egg mass was recorded and then multiplied by a standard displacement volume, obtained previously for 10 eggs, to calculate the number of eggs present in the clutch. Larval development in the field was monitored to obtain growth and mortality data. A series of 10 or more tadpoles was collected at one pond during 1979 at varying intervals until no more tadpoles could be found. All were immediately preserved in 10% formalin, then measured and staged in the manner recommended by Gosner (1960). *Rana sphenocephala* tadpoles were also collected in the same ponds at the same times so that developmental rates between the two species could be compared.

RESULTS AND DISCUSSION

Habitat and Range in Alabama

Wood frogs were collected in five counties in east central Alabama (Fig. 1). Except those on or near Mt. Cheaha, Cleburne County, all collecting localities were near mesic semideciduous forests along the flood plains of large streams. Several frogs collected on Mt. Cheaha were considerable distances from running water, but were never far from mesic sites.

All frogs were collected from localities in the Blue Ridge and Piedmont Plateau physiographic provinces. The floristic and geologic components of these areas have previously been described (Harper 1943, Hodgkins 1965, Johnson and Sellman 1975). The Blue Ridge, as used here, is synonymous with the Blue Ridge herpetofaunal province described by Mount (1975) and the Mountain Forest Habitat Region defined by Hodgkins (1965) and Johnson and Sellman (1975). From a geological standpoint, the terms "Blue Ridge" or "Mountain" may be inappropriate, for the general consensus among geologists is that the Blue Ridge province terminates in northern Georgia. However, the vegetative distribution patterns and faunal components differ sufficiently from the Ridge and Valley province and Piedmont to warrant recognition of the Blue Ridge as a separate entity in Alabama (Johnson and Sellman 1975, Mount 1975). All Piedmont localities for breeding ponds and adult frogs were in the northern subdivision known as the Ashland Plateau. To the north, this part of the Piedmont makes contact with the Blue Ridge, but the transition is gradual with a continuous gradation of the Piedmont into the uplands. The southern subdivision of the Piedmont, known as the Opelika Plateau, is geologically less complex. The different surface configurations and geological structures in the two plateaus have resulted in some differences in vegetation distribution (Johnson and Sellman 1975, Golden 1968). Mount (pers. comm.) stated that his more recent studies of the herpetofauna of this area indicate that a more distinct transition exists between the Opelika and Ashland Plateaus of the Piedmont than between the latter and the Blue Ridge, if a distinction is to be made.

The southernmost locality known for *R. sylvatica* in North America lies just south of the Tallapoosa River in Horseshoe Bend National Military Park, Tallapoosa County, Alabama. The site is near the boundary of the Ashland and Opelika plateaus in the central Piedmont. The southern boundary of the range of the wood frog in Alabama approximates the southern edge of the Ashland Plateau, although it is likely that many populations are isolates.

One wood frog has been collected in Calhoun County, Alabama (L. G. Sanford, pers. comm.), at the northern edge of the Blue Ridge, and represents the northernmost record for this species in Alabama. The known range in Alabama thus extends from the northern edge of the Blue Ridge along its contact with the Ridge and Valley province to the southern edge of the Ashland Plateau in the central Piedmont. Scattered populations probably occur in suitable habitat in that part of the Ridge and Valley province south of the Coosa Valley. Mount (1975) mentioned that wood frogs might occur in the higher elevations of the Appalachian Plateau in extreme northeastern Alabama (Jackson County). If so, they are probably derived from populations that moved southward on the Cumberland Plateau from Tennessee and not from populations in the Blue Ridge.

Known localities for *R. sylvatica* in Georgia are limited to five counties in the Blue Ridge of the northeastern part of the state (Williamson and Moulis 1979; C. W. Seyle, pers. comm.) (Fig. 2). No specimens have been collected in the 160-km-long area between the Georgia and Alabama wood frog populations, apparently because this area of Georgia has been inadequately surveyed (R. E. Daniel, C. W. Seyle, pers. comms.). Since suitable habitat does occur in this area, we feel that the Alabama wood frog populations are continuous with those in northeastern Georgia (Fig. 2). Based on our knowledge of the habitat requirements of this species in Alabama (and in the southern Appalachians), the presumed range in the intervening area is thought to be limited to the Blue Ridge (Blue Ridge, Cohuttas, Talladega Upland subdivisions), the southern part of the Great Valley, and the Upland and Gainesville Ridges subdivisions of the northern Piedmont (see Wharton 1978).

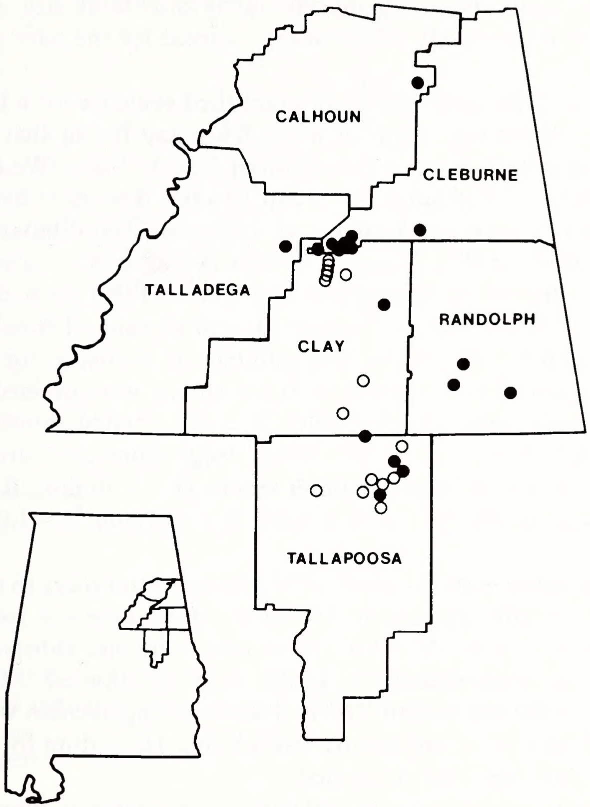

Fig. 1. Known Alabama localities for *Rana sylvatica* determined during this study. Open circles represent breeding localities; inset shows position in the state of counties from which *R. sylvatica* is recorded.

ADULT CHARACTERISTICS

Snout-vent lengths of adult male wood frogs in Alabama averaged 50.0 mm (SD = 5.5, N = 20), and adult females averaged 60.0 mm (SD = 3.16, N = 18). These values are smaller than those given by Martof and Humphries (1959) for wood frogs in northern Georgia and western North Carolina (males: $\overline{x}$ = 54.8 mm; females: $\overline{x}$ = 66.8 mm). Berven (1982a) discovered size differences along an altitudinal gradient from Maryland (lowland populations) to western Virginia (montane populations). Mountain males and females were larger (males: $\overline{x}$ = 55.3 mm; females: $\overline{x}$ = 64.4 mm) than individuals from lowland populations (males: $\overline{x}$ = 41.7 mm; females: $\overline{x}$ = 47.7 mm). Because Berven hypothesized that selection acted primarily on egg size and that selection for increased fecundity would secondarily favor large body size, comments on the size of Alabama *R. sylvatica* are reserved for the later section on egg size.

Martof and Humphries (1959) established evidence for a latitudinal gradient in relative leg length in wood frogs and found that the frogs with the longest legs occur in the southern Appalachians. We calculated TFL/SVL ratios for 19 adult males and 19 adult females to determine if this trend was evident in Alabama *R. sylvatica.* Tibiofibulas of males averaged .602 of the SVL, those of females averaged .625—a value identical to that obtained by Martof and Humphries (1959) for both sexes.

Ruibal (1957) reported a latitudinal and altitudinal clinal gradient in snout length for *R. pipiens* and pointed out evidence for a similar latitudinal gradient in *R. sylvatica.* Blunt snouts were defined as those with high height/length (H/L) values (> 1.15), pointed snouts as those with low H/L values (~ 1.00). Wood frogs from northern Canada (locality not given) possessed blunter snouts ($\bar{x}$ = 1.30 mm, R = 1.07 to 1.50, N = 14) than those from New York ($\bar{x}$ = 1.11 mm, R = 1.00 to 1.22, N = 15).

Snout lengths were measured on Alabama wood frogs to determine if this apparent cline continued. The mean H/L value was found to be 0.83 (R = 0.74 to 0.95, N = 37). These results further substantiate the evidence for a clinal increase in snout length southward. Martof and Humphries (1959) and Martof (1970) described Appalachian wood frogs as having blunt snouts, apparently a subjective description for no quantitative H/L analysis was performed.

The coloration of adult *R. sylvatica* in Alabama is typical of the Appalachian phenotype described by Martof and Humphries (1959). A color photograph resembling the Appalachian phenotype may be found in Behler and King (1979, Fig. 216).

BREEDING PONDS, BREEDING ASSOCIATES, AND BREEDING SEASON

All 14 breeding congregations of *R. sylvatica* found were in shallow (usually < 45 cm), temporary pools in or adjacent to forests. These pools fill with winter rains from December through February. Most were located in semideciduous woods along the flood plains of large streams. Three sites were found in pastures; however, these were bordered by semideciduous woods and probably had been wooded in the past.

Breeding ponds differed in the amount and type of vegetation. Ponds in open (pasture) situations received more sunlight and were generally characterized by vigorous growths of *Eleocharis* sp., *Juncus* sp., and *Carex* spp. Woodland pools generally had fewer rushes and sedges, probably because of reduced sunlight. *Peltandra virginica*, *Sagittaria*

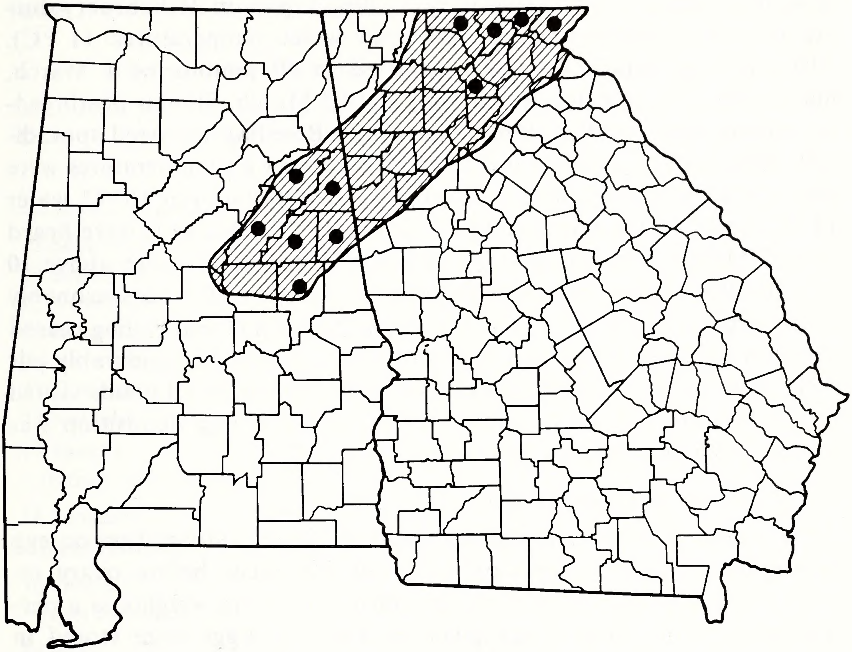

Fig. 2. Distribution of *Rana sylvatica* at the southern terminus of its range. Solid circles indicate counties (not localities) in Georgia and Alabama where specimens have been taken. Presumed range is indicated by hatching (see explanation in text).

latifolia, *Saururus cernuus*, *Sparganium americanum*, and *Ranunculus* sp. were the most common plants in these situations. *Alnus serrulata*, *Quercus* spp., and *Cornus* spp. were usually present along the edges of the pond or in shallow water.

A fairly consistent assemblage of breeding associates was present with *R. sylvatica* during the breeding season. *Ambystoma maculatum* and *A. opacum* were present at every site. *Notophthalmus viridescens*, *Hyla crucifer*, *Pseudacris triseriata*, and *P. brachyphona* were common associates. *Bufo americanus* and *Rana sphenocephala* were always present in pasture breeding ponds. Collins and Wilbur (1979) reported that, in Michigan, *R. sylvatica*, *H. crucifer*, and *P. triseriata* were breeding associates, particularly in temporary aquatic habitats.

A number of previous accounts described wood frogs as explosive breeders that generally spend only a few days in the breeding ponds (see Seale 1982), and we found this to be true of Alabama populations. Males begin calling with the onset of the first heavy, warm winter rain from mid-January to late February. Calling began on 21 February during the 1979 breeding season (air and water temperatures 11 °C). Although egg deposition was completed in all pounds by 1 March, males continued to call intermittently until 5 March. Similar postbreeding calling was noted by Waldman (1982). Breeding occurred sporadically between 21 February and 1 March whenever air temperatures were above 5 °C. Vigorous calling occurred on 22 February (air 16 °C, water 14 °C) and 24 February (air 16 °C, water 12 °C). No calls were heard after 5 March even though air and water temperatures were above 10 °C. In 1980, males began calling on 17 January after unseasonably warm weather (air 15.5 °C, water 9 °C, at 2130 CST), but calling ceased early the next morning when the temperature dropped considerably (air 4 °C, water 9 °C, at 0200). Males were in full chorus in all ponds visited on 22 January (air 9 °C, water 12 °C, at 1915). Egg deposition was completed in all ponds by 22 January.

DEVELOPMENT OF OVARIAN EGGS

Females collected throughout the year yielded information on egg development. Body weights of preserved specimens before ovary removal, ovary weights from each specimen, and ovary weights as a percentage of body weights are given in Table 1. Eggs were stored in ovisacs in one female that had completed ovulation. For this specimen, ovisacs (instead of ovaries) with ripe oocytes are expressed as a percentage of total body weight, as indicated.

Examination of females indicated that ovarian weight (expressed as a percentage of body weight) remains fairly constant from early September to late November. No preovulating females were collected immediately prior to the breeding season, but we assume that the greatest increase in size of oocytes occurs during this time (later stages of vitellogenesis). All gravid females collected in the breeding ponds had completed ovulation and mature ova were present in the ovisacs. Ovisacs in a gravid female collected in the breeding pond on 18 January composed 41.7% of the total body weight. Ovarian weight in spent females drops to 3.9 to 5.0% of total weight. The ovaries of a female collected on 14 May were macroscopically similar in appearance to those of spent females. In this female, ovaries equaled 5.3% of total body weight.

Because no females were collected between May and September, we could not determine when oocyte enlargement begins; however, based on the size and appearance of oocytes in females collected during September, we estimate that enlargement begins in July or August. Because ripe oocytes in gravid females compose such a large percentage of total

Table 1. Body and ovarian weights (g) and ovarian weight as a percentage of body weight for adult female *Rana sylvatica* collected in Alabama at different times of the year.

Date	Body weight	Ovary weight	Ovary weight as pecentage of body weight
3 September	22.4	3.3	14.7
29 September	38.4	3.7	9.6
12 November	24.9	3.1	12.4
12 November	20.4	2.9	14.2
23 November	31.3	4.3	13.7
23 November	27.4	4.0	14.6
23 November	29.1	4.8	16.5
17 January (female in breeding pond)	52.0	21.7*	41.7
18 January (spent female)	10.5	0.6	5.0
18 January (spent female)	17.6	0.7	3.9
14 May	13.2	0.7	5.3

* ovisac weight

body weight, an extended period is probably necessary for a female to reach reproductive condition. Redshaw (1972) reported that amphibian oocyte enlargement from 450μ to 1400μ required a period of 9 months.

SEXUAL DIMORPHISM, CALLING, AND AMPLEXUS

Sexual dimorphism is more pronounced during the breeding season. Males are generally much darker than females, the ground color ranging from deep brown to almost black. Howard (1980) noted that this darker color matched the dark color of the water in breeding ponds. Females are usually tan to reddish brown during the breeding season. Darker females are observed occasionally, but they are never as dark as males. The margin of the toe webbing between the digits of the hindlimb is markedly convex in males. The male thumb (first digit on the forelimb) and the musculature in the forelimb are also enlarged during this time, as in other ranid species. Noble and Farris (1929) thought that the additional surface area provided by convexity of the toe webbing allowed males more mobility in the water, a suggestion consistent with the behavior of males during the breeding season. The thumbs of male wood frogs in Alabama are slightly enlarged throughout the year, becoming more conspicuously so during the breeding season. Toe webbing in females remains concave during the breeding season, a condition found in both sexes throughout the rest of the year.

The call of male wood frogs in Alabama is similar to that described for males elsewhere (Thoreau 1881, Hinckley 1882, Dickerson 1906, Smith 1961, Martof 1970, Minton 1972). It usually consists of two high-pitched croaks or snappy clacks, and may be described as a nasal "back-up," repeated rapidly several times in succession. Solitary males call less frequently, repeating the call only once or twice at varying intervals.

Calling males float or swim at the water surface with forelimbs hanging down and hindlimbs projecting posteriorly. The digits on the hindlimbs are expanded, exposing maximum webbing surface. In large aggregations, males move and interact frequently (see Wright 1914, Noble and Farris 1929, Wright and Wright 1949, Howard 1980, Berven 1981). Calling males are extremely wary and dive below the water surface at slight disturbances, concealing themslves under leaf litter and decaying vegetation on the bottom, or hiding among roots or emergent vegetation. When calling from fairly open water, males are nearly unapproachable. If the pond is small, with emergent vegetation, one can usually approach close enough to observe floating males. Calling males can be heard continuously (though often sporadically) from dusk until dawn, but the chorusing is usually strongest immediately after sunset. Males in almost all Alabama populations call only at night; diurnal choruses were heard at only one breeding pond (W. Baker, pers. comm.). Two lethargic males were collected from the bottom vegetation and leaf litter at one pond during midday. The apparent diel restriction of calling activity is not as conspicuous in more northerly populations (Wright and Wright 1949, Howard 1980, Berven 1981, Waldman 1982). This might be a function of the extremely small population sizes in Alabama and the resultant lack of stimulation by large numbers of conspecifics.

Females in Alabama populations are less conspicuous than chorusing males and usually remain below the surface of the water. This behavior is similar to that noted by Banta (1914) and Noble and Farris (1929). Only one female was seen floating on a pond surface; all others collected in breeding ponds were taken under water while in amplexus. Amplexus is axillary (pectoral), with males clasping females just posterior to the forelimbs.

One interspecific amplexing pair was observed during this study—a male wood frog clasping a female *R. sphenocephala*. When approached, the male released his hold and swam away. The female, partly covered with vegetation, remained on the bottom of the pond. The freshly deposited *R. sphenocephala* egg mass (eggs had completely cleared the cloacal opening) was resting on the posterior surface of the female and obscured her hind limbs. Whether or not the male *R. sylvatica* had extruded sperm over the eggs is not known. The cause of the apparent breakdown in isolating mechanisms in this case is also unknown. Perhaps a breakdown in habitat isolation is a partial explanation. *Rana sylvatica* and *R. sphenocephala* were found as breeding associates only in sites where the forest had been removed. In Alabama, *R. sylvatica* usually breeds in woodland pools, whereas *R. sphenocephala* breeds in a variety of open aquatic habitats, as well as in woodland pools. Eggs of both species were found in only one woodland pool during this study. *Rana sphenocephala* has often been seen breeding in woodland pools in other areas of Alabama (R. H. Mount, pers. comm.). Some ecological separation may occur in the part of the state where the two species are sympatric.

Nelson (1971) mentioned a female *R. sylvatica* that was clasped by a male *R. pipiens*. None of the *R. sylvatica* eggs fertilized by the *R. pipiens* developed beyond gastrulation. Moore (1955) found that development did not proceed beyond gastrulation in experimental laboratory reciprocal crosses of *R. sylvatica* and *R. pipiens*. Interspecific pairing of male *R. sylvatica* with other amphibians in the laboratory was reported by Wright (1914).

OVIPOSITION

The eggs of *R. sylvatica* in Alabama are laid as submerged globular masses, usually attached to vegetation. Often, upper portions of the egg mass become emergent. Moore (1949) pointed out that the deposition of submerged egg masses by northern ranid species (those adapted to cool climates) is an adaptation that helps protect the developing embryos from freezing. The rapid drop in water level that often occurs in temporary pools in Alabama may cause exposure of the egg masses in certain situations. Desiccation then becomes an added mortality factor. The depth of water in which oviposition occurs is fairly consistent, averaging 15 to 20 cm.

Wood frogs characteristically have communal oviposition sites. The advantages of this behavior have been discussed (Wells 1977, Howard 1980, Seale 1982, Waldman 1982, Waldman and Ryan 1983). Communal oviposition sites (COS) were encountered in this study only in breeding ponds with larger populations. The largest such site was in a pond south of Mt. Cheaha where 147 egg masses, arranged in two layers, were found in an area 1.5 x 1 m square. Another COS (65 egg masses) was in a small woodland pond in northern Tallapoosa County. In both ponds all egg masses were restricted to the COS. The third largest population (60 egg masses) was in a pasture breeding pond, where communal oviposition occurred, but to a lesser extent. In this pond 31 egg masses were in a communal site, and the rest were deposited in small clumps separate from the COS. The 11 other wood frog breeding ponds discovered during this study were characterized by extremely small populations (compare Howard 1980, Berven 1981, Seale 1982, Waldman 1982). The number of egg masses found in each of these ponds varied from 4 to 28, and the tendency toward communal oviposition was less pronounced.

Clutch size varied from 350 to 709 eggs per mass ($\overline{x} = 496$). Ovarian and/or ovisac counts indicated that oviposition may occur once or twice during the breeding season. The number of ovarian eggs per female ranged from 618 to 966. When all eggs are deposited at one time, the resultant egg mass appears as two fused masses, indicating that females empty each ovisac separately. If a female moves to another site after emptying one ovisac, the resultant egg mass represents approximately one-half the ovarian complement. This probably accounts for much of the apparent variability in clutch sizes observed in the field. Even so, there is some variability in reproductive potential, as evidenced by the range in egg complements seen in gravid females. This is probably attributable to a combination of individual and ontogenetic variation. Seale (1982) found no significant difference between clutch size and ovarian egg counts in Pennsylvania wood frogs (clutch: $\overline{x} = 895$; ovarian eggs: $\overline{x} = 840$). Although there are few data available concerning ovarian egg counts, several authors have presented information on clutch size (Table 2). There is some evidence for smaller clutch size in the southern parts of the range, although this trend may be obscured by altitudinal differences (Berven 1982a). Clutch size probably varies in response to different selection pressures throughout the geographic range, creating a chaotic pattern of variation. Furthermore, variation in clutch size should be viewed with respect to differences in adult body size and egg size. At the southern terminus of the frog's range, the probability of egg mortality resulting from freezing is reduced and may be a factor in decreased clutch size. Moore (1949) pointed out that the submerged egg masses of northern species of *Rana* were poorly adapted for higher pond temperatures because diffusion of oxygen would not be rapid enough to supply the metabolic needs of embryos in the center of the egg mass. Thus, the smaller egg masses characteristic of southern populations of *R. sylvatica* would allow a more rapid diffusion of oxygen to these inner embryos. However, Savage (1961) claimed that egg masses possess intercapsular channels and that gaseous diffusion need not take place through the entire egg mass. If so, smaller clutch size resulting from selective pressures for small egg mass size would be an inappropriate hypothesis.

The eggs of Alabama wood frogs are the largest reported for any population of *R. sylvatica* ($\bar{x}$ = 2.9 mm diam., SD = .08, N = 50). Comparison of these values with previously published information indicates a general trend for egg diameter to increase southward (Table 2.). Berven (1982a) hypothesized that selection has acted primarily on egg size, and that other reproductive traits such as clutch size, body size, and age at first reproduction have evolved secondarily. Different selective pressures in different environments would confer differential selective advantages on particular sizes of eggs, clutches, and adults (see Berven 1982a,b, for discussion).

The large size of eggs in Alabama populations of *R. sylvatica* is probably a consequence of increased fitness (larger size) of larvae hatching from these eggs (see Berven 1982a,b), a phenomenon that would result in faster growth rates and shorter larval periods. In Alabama populations, selection for rapid metamorphosis would probably result from breeding exclusively in temporary ponds. An additional selective pressure for more rapid metamorphosis in *R. sylvatica* may be the concurrent breeding of *R. sphenocephala* in the same sites. This does not seem to be the case farther north. Berven's hypothesis concerning the relationship of large egg size to large body size is difficult to support with data from Alabama wood frogs. Although egg size is largest in Alabama populations, adults are somewhat smaller than those reported in other parts of the southern Appalachians (see earlier mention). Because determination of different age classes was not possible during this study, size comparisons and determinations of age and size at first (and subsequent) reproduction await further study. Larger sample sizes obtained by future workers will probably help to clarify this situation.

The diameters of egg jelly envelopes for *R. sylvatica* in Alabama are larger than values reported in other parts of the range. Diameters of inner envelopes averaged 6.6 mm (R = 5.4 to 7.2 mm, N = 50); outer envelopes averaged 14.0 mm (R = 12.4 to 17.3 mm, N = 50). Few data are available on more northerly populations (Table 2). The reasons that jelly envelopes of Alabama wood frogs are so much larger than those in northern populations are not obvious. Perhaps jelly deposition is controlled by egg size, with larger eggs receiving more jelly.

EGG FERTILITY, DEVELOPMENT, AND PREDATION

Fertility, although variable, was quite high, and several egg masses exhibited 100% fertility. Three clutches were entirely infertile, perhaps a result of oviposition in the absence of a clasping male. Early mortality of developing eggs was occasionally observed. These eggs usually were infested with fungi, which probably invaded after egg death rather than having been the cause of mortality.

Wood frog egg masses were easily recognized in breeding ponds by their characteristic shape and the large size of their jelly envelopes. Another distinguishing feature was a greenish color imparted to the jelly envelopes by a unicellular green alga. Dickerson (1906) first noted the presence of this alga and assumed that the relationship was mutualistic. Gilbert (1942) also observed this alga in jelly envelopes of wood frog eggs and identified it as *Oophila amblystomatis*, a species characteristically found in the egg jelly of *Ambystoma maculatum*. Surprisingly, there has been little inquiry into the relationship between wood frog eggs and algae by subsequent workers (see mentions by Pope 1964, Gatz 1973). Although the relationship between *A. maculatum* and *Oophila* has generally been viewed as mutualistic (Gilbert 1942, 1944; Hutchinson and Hammen 1958; Hammen and Hutchinson 1962), a higher rate of mortality has been related to the presence of the alga in some cases (Anderson et al. 1971, Gatz 1973). Further investigation concerning the relationship between the alga and *R. sylvatica* eggs is warranted.

All egg predators observed during this study were invertebrates. Mayfly naiads (Siphlonuridae, Ephemerellidae) and isopods (Asellidae) were often present between adjacent egg envelopes within egg masses. Caddisfly larvae (Phryganeidae) fed on the external surfaces of egg masses, and one leech, *Macrobdella decora*, was found feeding on an egg mass. Cory and Manion (1953) found this same leech destroying the majority of wood frog eggs in some situations in Indiana, and thought that its presence in certain populations of *R. sylvatica* might constitute a check on population size. Since only one *M. decora* was observed during our study, the effect of this species on Alabama wood frog populations is probably minimal.

Hudson (1954) reported newts, *Notophthalmus viridescens*, feeding on wood frog eggs in Pennsylvania. This salamander was a potential egg predator in Alabama wood frog breeding ponds, but predation was never observed during our study. The large diameters of egg jelly envelopes of *R. sylvatica* in Alabama populations might reduce newt predation.

Hatching, Larval Development, and Larval Mortality

The length of the period between egg deposition and hatching varies directly with water temperature. Under field conditions, wood frog tadpoles generally hatch in 7 to 9 days after eggs are deposited (water temperatures variable, 5 to 17 °C). Larvae hatch at a fairly advanced developmental stage, usually stage 20 (gill circulation, Gosner 1960) or

Table 2. Reported values for clutch size, ovarian egg count, egg diameter, and jelly envelope diameter of *R. sylvatica*.

Location	Clutch size	Ovarian egg count	Egg diameter (mm)	Jelly envelope diameter (mm)	Source
Alaska	$\bar{x}$=778		$\bar{x}$=1.6		Herreid and Kinney 1967
Manitoba			$\bar{x}$=1.6		Berven and Gill 1983
Michigan	$\bar{x}$=646		$\bar{x}$=1.82		Collins 1975
Minnesota	R=1000-3000				Bellis 1957
New York	R=2000-3000		$\bar{x}$=1.9	inner: $\bar{x}$=3.8	Wright 1914
				R=3.6-5.8	
			R=1.8-2.4	outer: $\bar{x}$=6.4	
				R=5.2-9.2	
	R=2000-3000		R=1.8-2.4	inner: R=3.6-5.8 outer: R=5.2-9.4	Wright and Wright 1949
Massachusetts	1380 (one egg mass)				Hinckley 1882
	$\bar{x}$=1019				DeGraaf and Rudis 1983
Connecticut			$\bar{x}$=1.8		Witschi 1953
Rhode Island	R=1000-3000				Dickerson 1906
Pennsylvania	$\bar{x}$=895	$\bar{x}$=840	$\bar{x}$=2.29		Seale 1982
Indiana	R=2000-3000				Minton 1972
Illinois	R=2000-3000				Smith 1961
W. Virginia			$\bar{x}$=2.0	outer (?): R=6.0-9.0	Green 1952
Virginia	$\bar{x}$=920		$\bar{x}$=2.28		Berven 1982a
Maryland	$\bar{x}$=642		$\bar{x}$=1.83		Berven 1982b
Missouri	$\bar{x}$=621				Johnson (pers. comm.)
N. Carolina			$\bar{x}$=2.25		Witschi 1953
Tennessee	$\bar{x}$=465		$\bar{x}$=2.25 R=2.1-2.4		Meeks and Nagel 1973
Alabama	$\bar{x}$=496 R=350-709	R=618-966	$\bar{x}$=2.9	inner: $\bar{x}$=6.6 outer: $\bar{x}$=14.0	This study

stage 21 (cornea transparent), and average 10.7 mm (R = 9.8 to 11.0, SD = .34, N = 10) in length. Meeks and Nagel (1973) found that hatchling size in eastern Tennessee averaged 8.0 mm, but did not indicate developmental stage at hatching. Herreid and Kinney (1967) found that hatching occurred at stage 20 in Alaskan populations.

An easily observed size difference between hatchling *R. sylvatica* and *R. sphenocephala* allowed us to monitor larval development of these two species at one pond during 1979. Leopard frog tadpoles hatch at slightly earlier stages, usually stage 19 (heartbeat) or stage 20, but are considerably smaller than *R. sylvatica* tadpoles, averaging 6.6 mm (R = 6.2 to 6.8 mm, SD = .17, N = 10) in length. The results obtained from the samples are summarized in Figure 3.

Wood frog tadpoles grew more rapidly than leopard frog tadpoles until about 15 April, at which time the tadpoles of both species were approximately the same length (*R. sylvatica*: $\overline{x}$ = 40.9 mm, N = 10; *R. sphenocephala*: $\overline{x}$ = 40.7 mm, N = 10); however, wood frog tadpoles at this time were 5 to 11 developmental stages beyond leopard frog tadpoles. Leopard frog tadpoles then continued to increase in length, whereas wood frog tadpoles began to decrease as a result of initial tail resorption with the onset of metamorphic climax. Wood frog tadpoles were last collected in the pond on 29 April, at which time most were in stage 42 (both forelimbs erupted) and averaged 40.5 mm in length. Leopard frog tadpoles averaged 53.6 mm in length at this time, with most individuals in stage 35 (toes 1 and 2 joined, others separate). Leopard frog tadpoles collected between 29 April and 5 May revealed that tadpoles of this species continue to grow. Mean length of *R. sphenocephala* tadpoles collected on 5 May (not shown on graph) was 56.0 mm, at which time larvae were in stage 38 (metatarsal tubercle formation).

It has been shown that wood frog and leopard frog tadpoles may behave as ecological equals (DeBenedictus 1974). The larger size and more advanced stage of development at hatching may give *R. sylvatica* tadpoles some initial competitive advantage over those of *R. sphenocephala*. The more rapid development of *R. sylvatica* probably represents an adaptation to breeding in temporary pools and might result in some resource partitioning on those infrequent occasions when these two species use the same breeding ponds. Alford and Crump (1982) found size class segregations in *R. sphenocephala* tadpoles, both in laboratory experiments and field situations, and felt that the negative correlation between large (and/or older) and small (and/or younger) tadpoles indicated habitat partitioning.

Since newly transformed *R. sylvatica* froglets were not collected in the field, the exact amount of time from oviposition until transformation is not known. No wood frog tadpoles were collected on 5 May,

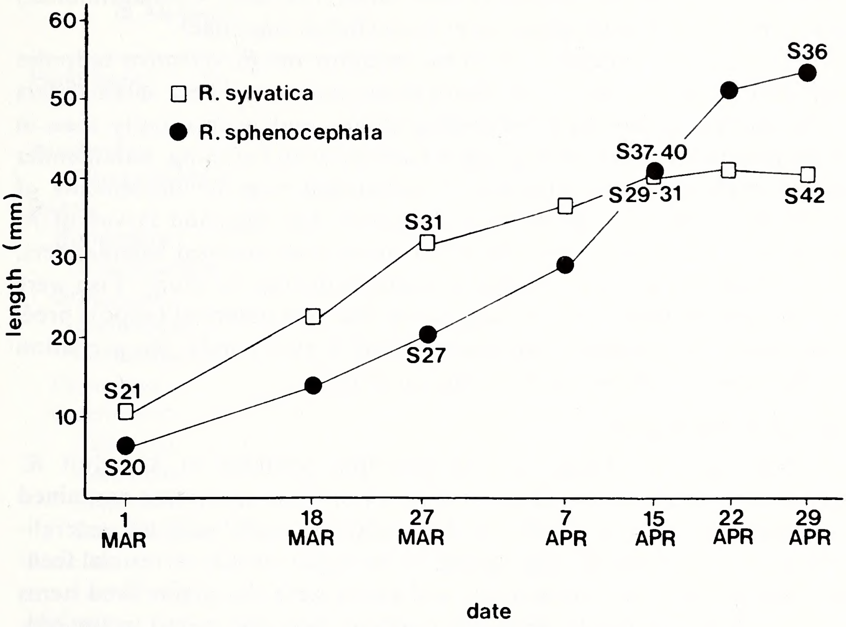

Fig. 3. Larval development of *Rana sylvatica* and *Rana sphenocephala* in Pasture Pond, Tallapoosa County, Alabama. Numerals preceded by the letter *S* indicate the developmental stage in tadpoles at the time of collection.

however, indicating that all larvae were transformed at this time. This would give a maximum transformation period of 73 days in the field. Most individuals had probably transformed by 29 April (or somewhat earlier); only four tadpoles were collected in the pond at that time. This would indicate a transformation time of about 66 days.

Various vertebrates and invertebrates preyed on wood frog larvae, though not all predators were present at each breeding pond. All invertebrate predators were insects. Adult back swimmers (Notonectidae) and predaceous diving beetles (Dytiscidae) were often seen preying on small tadpoles. Nymphal notonectids and larval dytiscids also probably preyed on wood frog larvae, as observed by Dickerson (1906). Herreid and Kinney (1966) noted extensive predation on wood frog larvae by *Dytiscus* spp. in Alaska. Formanowicz and Brodie (1982) found no survival of stage 42 and younger wood frog tadpoles when subjected to predation by larval *Dytiscus verticalis* in the laboratory. Increased survivorship in older tadpoles and froglets (stage 42 to 46) was attributed to unpalatability, a result of the development of active granular glands during later stages of metamorphosis. Other potential insect predators present were odonate naiads (Libellulidae, Lestidae, Coenagrionidae) and nymphal and adult giant water bugs (Belostomatidae).

The most significant vertebrate predator on *R. sylvatica* tadpoles appeared to be the larvae of *Ambystoma opacum*. These salamanders were always present in the breeding ponds and were usually seen in close proximity to wood frog egg masses prior to hatching. Salamander larvae probably were attracted to unhatched eggs by movements of developing embryos. Walters (1975) stated that eggs and larvae of *R. sylvatica* were readily eaten by adult newts and marbled salamanders, but neither of these was noted as a predator during our study. Fish were usually absent from the breeding ponds, but one potential tadpole predator, *Lepomis cyanellus*, was encountered in two ponds. No predation by this species was observed during our study.

ADULT FOOD HABITS

We examined stomach and intestinal contents of 42 adult *R. sylvatica* from Alabama. Because only 14 of these specimens contained identifiable food items (Table 3), this analysis is useful only for generalization. Alabama wood frogs appear to be opportunistic terrestrial feeders. Insects, spiders, earthworms, and snails were the major food items present. A scarab beetle, *Eutheola rugiceps*, was discovered in the coelom of one specimen. A large hole in the stomach indicated that the beetle had torn its way through the stomach wall after being ingested (Davis and Folkerts 1980). Neither males nor females collected in breeding ponds contained food. Since all were immediately preserved, we assume that neither sex feeds at this time. Adult wood frogs may not require food during such a short, explosive breeding period.

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Table 3. Composition of stomach contents of 14 adult *Rana sylvatica* collected in Alabama.

Food items	Percent of stomachs containing item
Arachnida	
Tetragnathidae	43
Insecta	
Homoptera	
Membracidae	7
Orthoptera	
Blattellidae	7
Gryllacrididae	29
Plecoptera	7
Coleoptera*	
Elateridae	14
Carabidae	7
Staphylinidae	14
Scarabaeidae	7
Annelida	
Lumbridae	21
Mollusca	
Gastropoda	21

* Several beetles were not identifiable.

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Notes on the Eastern Hognose Snake, *Heterodon platyrhinos* Latreille (Squamata: Colubridae), on a Virginia Barrier Island

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ABSTRACT.— An unusually high population density of the eastern hognose snake, *Heterodon platyrhinos* Latreille, is reported from a Virginia barrier island. The average snout-vent length of females in this population is significantly greater than the average SVL of males, but individuals of equal SVL do not differ in body mass. Females also differ from males in seasonal activity patterns, with males most active in early summer and females in late summer. The number of dorsal blotches of the island population differs significantly from that reported for a mainland population on the Delmarva Peninsula.

The eastern hognose snake, *Heterodon platyrhinos* Latreille, is found over much of the eastern United States (Conant 1975). Within this range it uses a great diversity of hatitats, but like other members of the genus *Heterodon* it prefers dry, relatively open, sandy areas in which it can burrow easily (Corrington 1929, Lynn 1936, Duellman and Schwartz 1958, Platt 1969). This type of habitat is abundant on Tom's Cove Hook, a fast-growing recurved spit on the southern tip of Assateague Island, Virginia, and *H. platyrhinos* is especially conspicuous at this site.

Three factors may account for the apparently high density of hognose snakes. First, Assateague hosts a depauperate snake fauna, as do many Atlantic Coast barrier islands (Gibbons and Coker 1976). Only 6 species occur on the island (Lee 1972), compared to 17 on the adjacent Delmarva Peninsula (Martof 1980). The absence of other species may promote increased numbers of *H. platyrhinos.* Second, the sparsely vegetated dunes that form the interior of the spit provide ideal foraging habitat. Fowler's toads, *Bufo woodhousei fowleri,* breed in freshwater ponds between the dune lines and are abundant on the dunes. Hognose snakes were observed several times in the act of hunting and capturing toads buried in the sand. Third, it is possible that hognose snakes on Assateague are no more abundant than on the mainland, but are simply easier to census because of the open habitat. Given the apparent abundance of *H. platyrhinos,* the objective of this paper is to present information that is ordinarily difficult to obtain for a single population.

STUDY AREA AND METHODS

I observed active hognose snakes while on a preliminary visit to Assateague Island on 18 April 1981. The vegetation of Tom's Cove Hook consists of discrete zones of sand-dune, shrub, grassland, and salt-marsh habitats. Few snakes were observed in shrub and grassland areas during preliminary sampling, and none were seen in the salt marsh. Therefore, systematic sampling was confined to the sand-dune habitat on the inland dune ridges that form a nexus on the spit. These ridges were searched two or three times per week (22 days) from 11 June to 12 September 1981. The sequence in which the dunes were searched was varied. The first five searches lasted from 0800 to 1930. No snakes were observed during midafternoon hours, and subsequent sampling was confined to morning and late afternoon. On five occasions searches were conducted for a 3-hour period after sunset.

The following data were recorded for each capture: date, time of capture, exact location on the dune lines, temperature of the substrate (52 captures only), color of snake, snout-vent length (SVL) to the nearest 0.5 cm, body mass (g), number of dorsal blotches, and number of ventral and subcaudal scales. Each individual was marked with a unique identification code (ID) by clipping two subcaudal and three ventral scales. For recaptured individuals, the linear distance traveled between captures was estimated from an aerial photograph of the site. Sex (Fig. 1) was determined by an analysis of ventral and subcaudal scale counts (Edgren 1961). Five of the snakes that were classified as males according to scale count were noted to have everted hemipenes during handling, supporting the assumption that sex can be determined by scale count.

RESULTS AND DISCUSSION

A total of 66 individuals were captured, with 6 individuals (9.1%) recaptured an average of 17.5 days after initial capture. More males (N = 38) were captured than females (N = 28), but the ratio did not differ from 1:1 ($\chi^2 = 1.52$, df = 1, $p > 0.10$). Distance moved between captures ranged from 40 to 760 m ($x = 390$ m). The recapture data were not appropriate to derive an estimate of actual population density (White et al. 1982). However, there are approximately 13.6 ha of habitat suitable for hognose snakes (excluding salt marsh and aquatic sites) on the spit. Using only the 66 individuals captured, the absolute minimum population density of *H. platyrhinos* was 4.8 snakes/ha.

Two hatchlings were found dead on the road on 15 and 19 August, and were 18.5 and 19.0 cm SVL. No hatchlings were captured during the late summer, so their growth rate could not be determined. Two juvenile males (SVL < 36.0 cm) and one adult male (62.0 cm SVL) were recaptured more than a month after initial capture. These two size classes exhibited average summer growth rates of 2.2 and 1.0 cm/month, respectively. Platt (1969) observed higher growth rates in *H. platyrhinos* juveniles (3.4 cm/month) and lower rates in large males (0.8 cm/month). Growth rates for female size classes could not be determined.

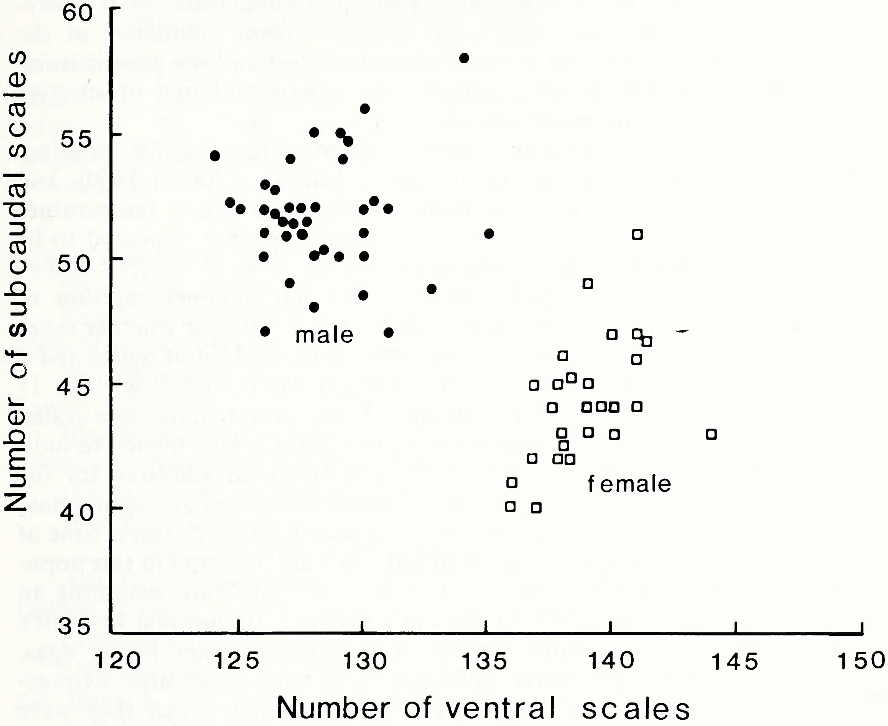

Fig. 1. Scale counts used to sex 66 *Heterodon platyrhinos* individuals found on Assateague Island, Virginia, June-September 1981.

Females were significantly longer ($t = 3.8$, $df = 64$, $p < 0.02$) and also exhibited greater body mass ($t = -2.74$, $df = 64$, $p < 0.01$) than males (Table 1). Covariance analysis was used to scale body mass for differences in snout-vent length, using SVL as the covariate. Female *H. platyrhinos* were no heavier than males of the same SVL ($F_{1,63} = 2.61$, $p > 0.10$). Sexual dimorphism in body length has been described in several populations of *Heterodon* (Edgren 1961, Platt 1969) and for other species (Fitch 1981, Gibbons 1972, Shine 1978). Platt (1969) attributed the sexual size dimorphism in *H. platyrhinos* to faster growth rates in females. Larger females of some species produce larger clutches, thereby possibly promoting selection for increased body size in females (Shine 1978, Semlitsch and Gibbons 1982).

Of the 66 individuals captured, 55 were judged to be normal in coloration, 3 were melanistic, and 8 were intermediate (very dark with some light markings). All melanistic snakes were adults. Observations on the number of dorsal blotches revealed that females have more blotches than males ($t = 4.22$, $df = 64$, $p < 0.001$; Table 1). Moreover, these means were also different (more than 2 SE) from values reported by Edgren (1961) for the Delmarva Peninsula population of *H. platyrhinos.* This difference suggests a change in gene frequency of the "blotch" allele(s), possibly owing to founder effect and the genetic isolation of the island hognose population, or perhaps a change of selective pressures in an island environment.

Most of the 72 captures were made from early to middle morning. Only five snakes were captured in late afternoon (1700 to 1930), and none were found on the five night searches. Substrate temperature ranged from 24 °C to 39 °C for 52 captures. Snakes appeared to be most active when substrate temperature was 32 °C to 35 °C ($N = 22$).

The data were grouped into early and late summer captures of adults (males $>$ 36.0 cm, females $>$ 40.0 cm SVL) to test whether sexes differed in their summer activity patterns. Seventeen adult males and 8 adult females were captured in early summer (prior to 8 July), and 11 males and 14 females in late summer. These proportions were tested using a binomial test of proportions (Lewis 1966), which tended to indicate differences in activity ($U = 1.76$, $p < 0.08$). In addition, for the period 11 June to 12 September, adult males had a median capture date of 23 June. The median for females was a month later (23 July). Nine of the 10 largest females were captured after 22 July. Females in this population probably laid their eggs in late June or early July, assuming an incubation period of 45 to 55 days (Platt 1969). In contrast to Platt's study, in which few adult females were captured after laying eggs, females on Assateague Island appeared to be most active after oviposition. Females were less active early in the summer when they were gravid, as has been reported for other species (Jackson and Franz 1981, Shine 1979).

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Table 1. Body mass, snout-vent length (SVL), and dorsal blotch number in male and female hognose snakes, *Heterodon platyrhinos* ($\overline{x}$ ± 1 SE).

Sex	N	Body mass (g)	SVL (cm)	Dorsal blotches
Male	38	94.9 ± 9.6	44.2 ± 1.8	21.8 ± 0.27
Female	28	140.6 ± 14.5	54.4 ± 2.7	23.7 ± 0.37

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A Study of Variation in Eastern Timber Rattlesnakes, *Crotalus horridus* Linnae (Serpentes: Viperidae)

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ABSTRACT.— Variation was examined in specimens of *Crotalus horridus* from the eastern United States in an attempt to investigate the status of its two described subspecies, *C. h. horridus* and *C. h. atricaudatus*, as defined by Gloyd. A particular effort was made to duplicate the results of a study by Pisani, Collins, and Edwards, who concluded that the subspecies were invalid. Maximum likelihood factor analysis and step-wise discriminant analysis on the same morphological characters, plus several others relating to adult size and pattern, produced evidence that the two subspecies of *C. horridus* are valid in the eastern portion of its range. However, standard morphological characters alone are not sufficient to discriminate between the two forms. Rather, adult size and pattern differences, in conjunction with the number of dorsal scale rows and ventral scales, best differentiate *C. h. horridus* from *C. h. atricaudatus*.

Two subspecies of the rattlesnake *Crotalus horridus* are thought to occur in the eastern United States (Conant 1975): *C. h. horridus*, the timber rattlesnake, and *C. h. atricaudatus*, the canebrake rattlesnake. Gloyd (1940) defined the former as having 23 dorsal scale rows, a lower number of ventral and caudal scales, an absent or faint postocular stripe, and less brilliant contrast between the ground color and pattern. He defined the latter as having 25 dorsal scale rows, a higher number of ventral and caudal scales, larger size, and more brilliant markings. The geographic range of the two races is shown in Figure 1.

Crotalus horridus shows considerable variation in the western portion of its range; *C. h. atricaudatus* is not known to occur in Oklahoma, yet specimens of *C. h. horridus* from southeastern Oklahoma resemble *C. h. atricaudatus* in color and pattern (Webb 1970). Anderson (1965) found that populations of *C. h. horridus* from western Missouri possessed a reddish-brown middorsal stripe like that of *C. h. atricaudatus* from southeastern Missouri. Gloyd (1940:186) also reported that "the middorsal stripe of reddish brown, although very conspicuous in typical (*C. h. atricaudatus*) specimens, is not a good definitive character because of its common occurrence in specimens of *C. h. horridus* from western localities." Smith (1961) regarded Illinois specimens from Jackson

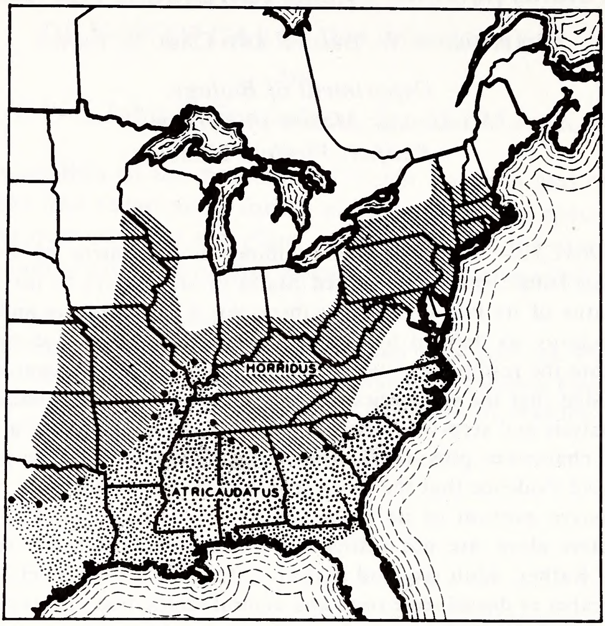


Fig. 1. Range of *Crotalus horridus* (from Klauber 1972).

County and southward as intergrades, because the specimens of *atricaudatus* from counties bordering the Mississippi River more closely resembled *horridus* in some characters.

A study by Pisani et al. (1973) concluded that, on the basis of 13 morphological characters, the recognition of subspecies in *C. horridus* could not be justified. They examined specimens from localities throughout the range, including western populations where intergradation is thought to occur.

The purpose of this study was to examine variation in pattern and adult size differences in addition to those morphological characters used by Pisani et al. (1973) in eastern *C. horridus* to determine if a more comprehensive study of the species is needed.

MATERIALS AND METHODS

Data were obtained on 337 museum specimens from New Hampshire, Vermont, Massachusetts, Connecticut, New York, New Jersey, Pennsylvania, Maryland, Virginia, North Carolina, South Carolina, Georgia, and Florida. However, only 101 specimens were suitable for the analyses used here in that they were complete in all characters examined. Twenty-one specimens were from localities of probable intergradation, and so were treated separately. Of the remaining 80, 10 were juveniles and were eliminated from some analyses. Localities of the 101 specimens used are shown in Figure 2. The characters used in this study

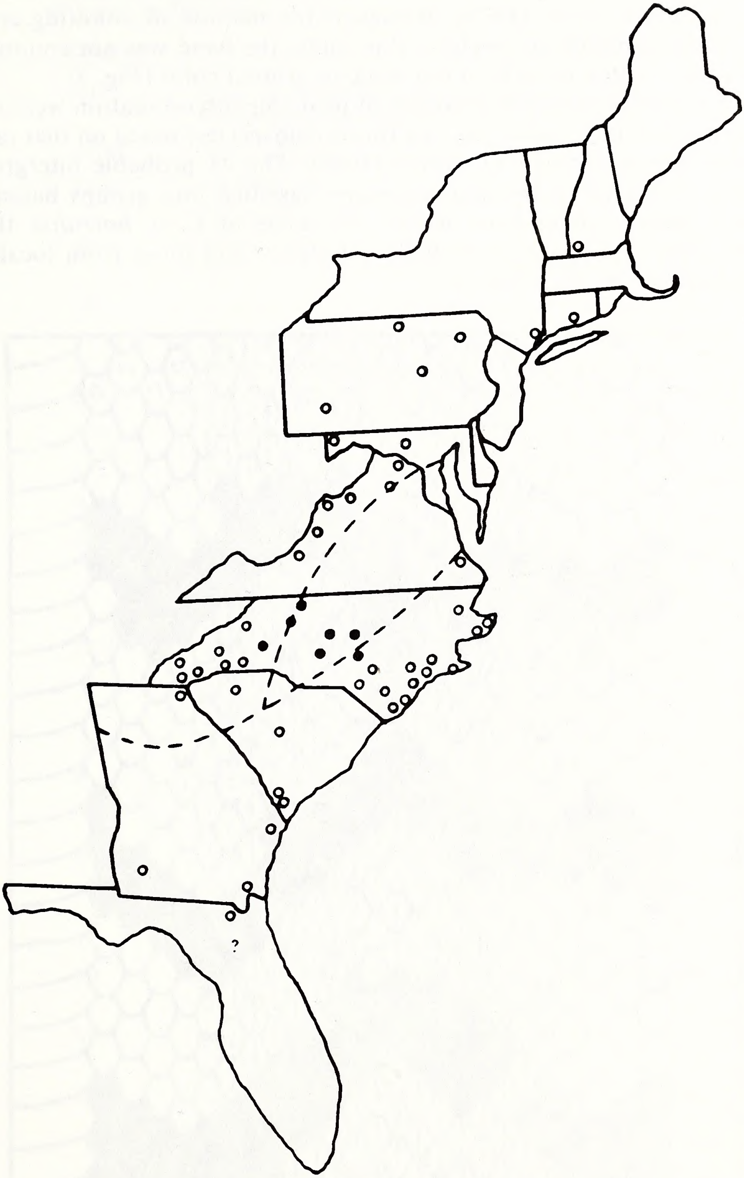


Fig. 2. Localities of specimens used in this study. Each circle represents at least one *Crotalus horridus*. Solid circles represent specimens from localities of probable intergradation. A question mark indicates an unknown locality for the state. Dashed lines are approximate range limits for each subspecies (see Fig. 1).

are listed in Table 1; the first 13 are those of Gloyd (1940) and were also used by Pisani et al. (1973). However, the method of counting crossbands was probably different in this study; the band was not counted if it was interrupted by at least one scale of ground color (Fig. 3).

Specimens not from localities of probable intergradation were classified *a priori* into one of the two forms (subspecies) based on that race's distribution as defined by Gloyd (1940). The 21 probable intergrades (Fig. 2) not used in the analyses were classified into groups based on their localities: those from within the range of *C. h. horridus*, those from within the range of *C. h. atricaudatus*, and those from localities lying between the two ranges.

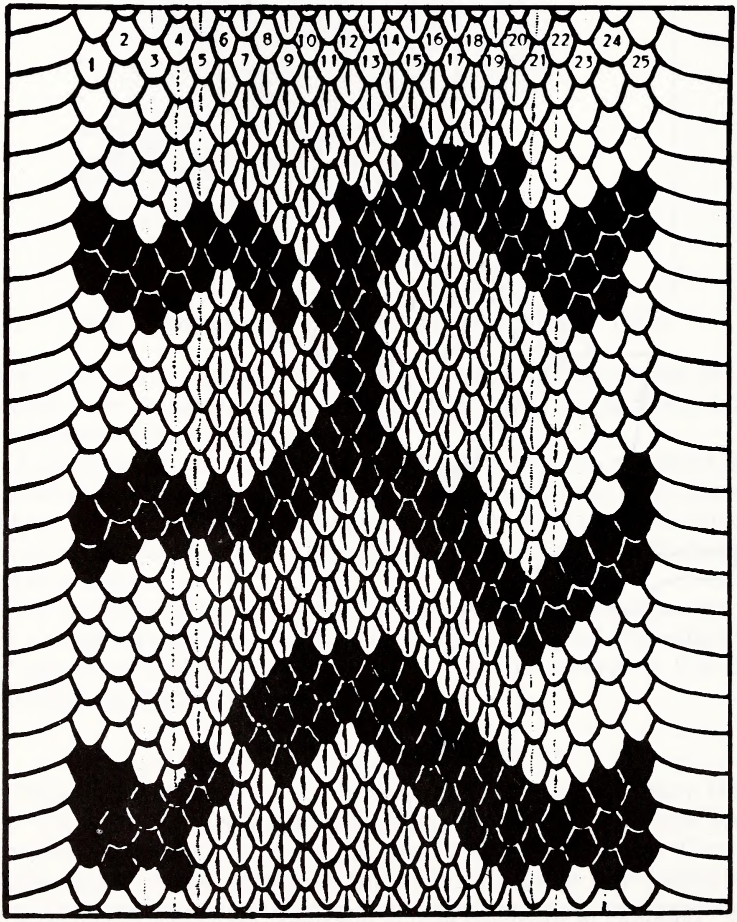


Fig. 3. Method of counting dorsal scale rows (numbered at top) and crossbands. Of the three apparent bands, only one complete crossband would be counted here, for only one is uninterrupted by any scales of ground color.

Table 1. Characters examined in this study of variation in *Crotalus horridus*. The first 13 were used by Pisani et al. (1973).

No.	Character	Description
1	ADS	Anterior dorsal scale rows, counted at one head-length posterior to the occipit (see Fig. 3).
2	DSM	Dorsal scale rows at midbody.
3	PDS	Posterior dorsal scale rows at one head-length anterior to the anal plate.
4	VS	Number of ventral scales, not including the anal plate (Dowling 1951). This method was not used by Pisani et al. (1973).
5	CS	Number of caudal scales, starting with the first complete scale posterior to the anal plate.
6	DCS	Number of divided caudal scales.
7	LSL	Left supralabials.
8	RSL	Right supralabials.
9	LIL	Left infralabials.
10	RIL	Right infralabials.
11	BCB	Number of complete body crossbands, counted between the head and anal plate (Fig. 3). This is not the method used by Pisani et al. (1973), who were not sufficiently clear on how crossbands were distinguished from blotches.
12	TCB	Number of complete tail crossbands. Although many specimens possessed tail markings that suggested banding, relatively few had tail crossbands that were clearly entire. Most specimens had a dark-colored tail with no markings, the dark color extending well anterior to the vent.
13	R	Ratio of tail length to snout-vent length. Tail length was measured from the posterior margin of the anal plate to the base of the first rattle segment.
14	SVL	Adult snout-vent length. Individuals longer than 750 mm were considered adults, but this may have failed to exclude a few sub-adults.
15	TL	Adult tail length.
16	HL	Adult head length, measured from tip of rostrum to line joining posterior tips of mandible (Peters 1964).
17	MS	Middorsal stripe, coded as zero for either faint or completely absent and as one for clearly present.
18	GC	Ground color, an attempt to measure pattern contrast. Because many museum specimens had lost some of their original color, this was coded as either zero to denote light colors, such as pale brown, tan, pinkish, yellowish, and pale gray, or as one to denote dark colors, such as plain brown, dark gray, and dark olive-greenish. Some melanistic specimens were examined, but none were used in the analyses because they lacked other essential characters.
19	POS	Postocular stripe, coded as zero for absent or faint and as one for clearly present on one or both sides of the head.

Table 2. Results of factor analyses. The first analysis was performed on the 13 morphological characters used by Pisani et al. (1973); all 19 characters were used in the second analysis.

	Factor 1		Factor 2		Factor 3		Factor 4	
	First analysis	Second analysis	First analysis	Second analysis	First analysis	Second analysis	First analysis	Second analysis
Eigenvalue	2.194	3.089	1.677	2.987	1.474	2.334	1.433	1.385
Cumulative proportion of total variance	0.15	0.20	0.24	0.36	0.40	0.42	0.52	0.52
Factor loadings (and characters)	0.922 (R) 0.866 (CS)	0.973 (SVL) 0.891 (HL) 0.572 (TL) 0.509 (POS)	0.743 (DSM) 0.734 (ADS)	0.966 (R) 0.861 (CS) 0.796 (TL)	0.977 (RIL)	0.844 (ADS) 0.609 (DSM)	0.997 (LSL) 0.557 (RSL)	0.836 (MS)

Table 3. Results of discriminant analyses. The first analysis was performed on the 13 characters used by Pisani et al. (1973); all 19 characters were used in the second analysis.

	First analysis	Second analysis
Number of variables in discriminant function	5	4
Eigenvalue	1.088	2.989
Wilks' lambda	0.479	0.251
Approximate F-value (P = 0.01)	16.103	48.577
Canonical correlation	0.722	0.866
Coefficients for canonical variable	-0.156 (BCB)	-0.109 (HL)
	-0.216 (VS)	-0.119 (VS)
	-0.346 (TCB)	-0.376 (ADS)
	-0.419 (DSM)	-2.217 (MS)
	-0.514 (PDS)	
Constant	57.593	35.626

A maximum likelihood factor analysis (Dixon and Brown 1979), in which all variables are evaluated simultaneously, was employed primarily to determine the existence of groups that correspond to subspecies. Two factor analyses were conducted, first on the 13 morphological characters used by Pisani et al. (1973), and then on all 19 characters. To analyze group integrity, we used stepwise discriminant analysis, which, like the factor analysis, evaluates all variables simultaneously (Dixon and Brown 1979). Again, two discriminant analyses were conducted, one on the characters used by Pisani et al. (1973) and one on all 19.

The maximum number of discriminant functions to be derived in a one discriminant analysis is either less than the number of groups or the same as the number of discriminating variables, whichever is smaller (Nie et al. 1975). Because there are only two groups in this study, there is only one discriminant function. Three criteria for evaluating this function are the eigenvalue, canonical correlation, and Wilks' lambda. The eigenvalue is a measure of the total variance explained by the discriminating characters. The canonical correlation is a second measure of the function's ability to discriminate among the groups. Wilks' lambda is an inverse measure of the discriminating power in the characters that have not been removed by the discriminant function. A smaller lambda, then, means more information is accounted for in the discriminant function. In Biomedical Computer Programs (BMDP), the Wilks' lambda is transformed into an approximate F-value.

Since there is one discriminant function, there can only be one canonical variable, which is the linear combination of variables entered that best discriminates among the groups (the largest one-way ANOVA F-value) (Dixon and Brown 1979). The canonical variable is adjusted so that the pooled within-group variance is one, and its overall mean is zero. The canonical variable is then evaluated at the group mean for each specimen, and all cases are plotted in a histogram to demonstrate separation of distinct groups. Table 3 lists the constant and canonical coefficients of the discriminating characters for each analysis. Figure 6 shows a comparison of the histogram from each discriminant analysis.

Analysis was performed at the George Mason University Computing Services on the Cyber 170-720 computer system. The P-series of the BMDP (Dixon and Brown 1979) was used, as were all default procedures, except the second factor analysis, in which four factors were requested.

Specimens Examined:

Carnegie Museum (CM): S 9130; 36497, 40186, 40187, 40192, 54721, 91446, 91447, 91482-91484, 91582, 91583, 91677, 92053, 92056, 92057, 92063, 92065

North Carolina State Museum (NCSM): 2347, 5744, 8035, 8041, 8121, 8520, 8725, 9638, 9655, 9772, 9879-9885, 9888, 10229, 10779, 10920, 11017, 11259, 11874, 11875, 12011, 12061, 12108, 12112, 12113, 12263, 12266, 12795, 12857, 12894, 12911, 13899, 14011, 14111, 14141, 15678, 15793, 15926, 16657, 16711, 17056, 17059, 17105, 17150, 19241, 19359, 19595, 19641, 21808

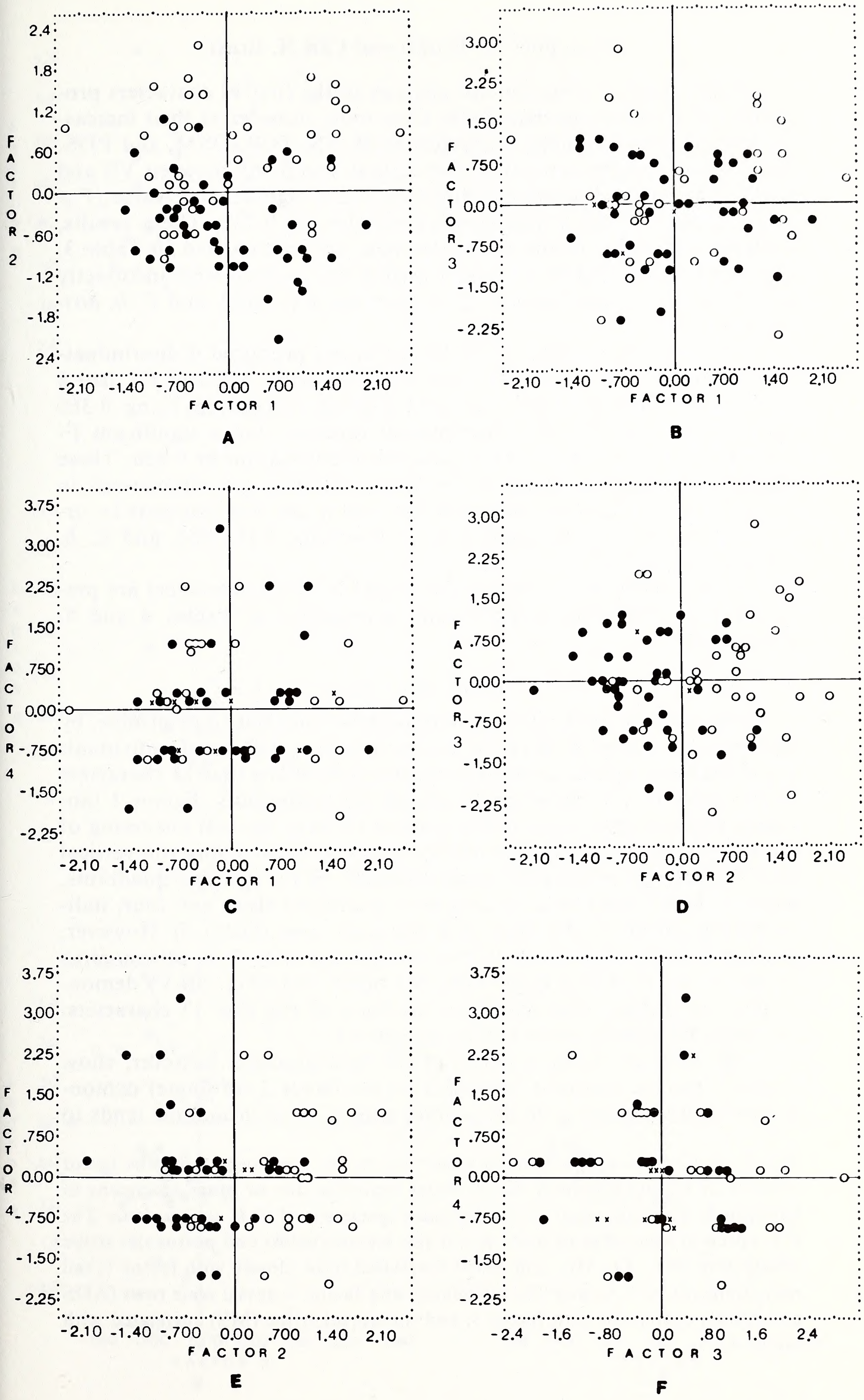
National Museum of Natural History (USNM): 8372, 9973, 10519, 14755 (2 specimens), 17959, 19970, 20651, 29362, 44313, 49958, 101858, 102714, 107879, 108687, 110487, 127601, 129094, 129759, 130167, 130168, 139618-139620, 145377, 156804, 210092, 218911.

RESULTS

Four factors accounting for 52% of the variance were produced in the factor analysis of the first 13 characters. The variation in characters CS and R correlated most closely with factor 1; ADS and DSM with factor 2; RIL with factor 3; and LSL, RSL with factor 4. Character variation that correlated less than 0.500 with any factor was not considered significant. The factor loadings and eigenvalues are summarized in Table 2, and estimated factor scores for the 80 specimens used are plotted in Figure 4.

In the factor analysis of all 19 characters, 4 factors were requested to limit the number produced. These accounted for a cumulation of 52% of the variance, but the characters SVL, TL, HL, and POS correlated most closely with factor 1; CS, R, and TL with factor 2; ADS and DSM with factor 3; and MS with factor 4. These results are summarized in Table 2. Factor scores for the 70 specimens used are plotted in Figure 5.

Fig. 4. Scatterplots of estimated factor scores for specimens from the factor analysis of the first 13 characters. Solid circles represent one or more specimens of *Crotalus h. horridus*; open circles represent specimens of *C. h. atricaudatus.* Tail measurements (characters CS and R) correlated most closely with factor 1; dorsal scale rows (ADS and DSM) correlated with factor 2; infralabials (RIL) correlated with factor 3; and supralabials (LSL and RSL) correlated with factor 4.


2.4
1.8
1.2
.60
0.0
-.60
-1.2
-1.8
-2.4
FACTOR 2
-2.10 -1.40 -.700 0.00 .700 1.40 2.10
FACTOR 1
A
3.00
2.25
1.50
.750
0.00
-.750
-1.50
-2.25
FACTOR 3
-2.10 -1.40 -.700 0.00 .700 1.40 2.10
FACTOR 1
B
3.75
3.00
2.25
1.50
.750
0.00
-.750
-1.50
-2.25
FACTOR 4
-2.10 -1.40 -.700 0.00 .700 1.40 2.10
FACTOR 1
C
3.00
2.25
1.50
.750
0.00
-.750
-1.50
-2.25
FACTOR 3
-2.10 -1.40 -.700 0.00 .700 1.40 2.10
FACTOR 2
D
3.75
3.00
2.25
1.50
.750
0.00
-.750
-1.50
-2.25
FACTOR 4
-2.10 -1.40 -.700 0.00 .700 1.40 2.10
FACTOR 2
E
3.75
3.00
2.25
1.50
.750
0.00
-.750
-1.50
-2.25
FACTOR 4
-2.4 -1.6 -.80 0.0 .80 1.6 2.4
FACTOR 3
F

Initial stepwise discriminant analysis of the first 13 characters produced 5 discriminating characters. They were, in order of their increasing ability to discriminate, characters BCB, VS, TCB, DSM, and PDS. None were strongly correlated; the highest was 0.365 between VS and DSM. The single discriminant function had a significant F-value (P = 0.01) of 16.103 and a canonical correlation of 0.722. These results, including the value of the Wilks' lambda, are summarized in Table 3. Thirteen (16%) of the 80 specimens used in this analysis were incorrectly classified into the two groups: *C. h. horridus*, 6 (13.6%), and *C. h. atricaudatus*, 7 (19.4%).

Discriminant analysis of all 19 characters produced 4 discriminating characters: MS, ADS, HL, and VS. Characters MS and HL had a weak correlation of 0.633, the next highest correlation being 0.366 between HL and VS. The discriminant function had a significant F-value (P = 0.01) of 48.577 and a canonical correlation or 0.866. These results, including the value of the Wilks' lambda, are summarized in Table 3. Five (7%) of the 70 specimens used in this analysis were incorrectly classified into the groups: *C. h. horridus*, 4 (11.1%), and *C. h. atricaudatus*, 1 (2.9%).

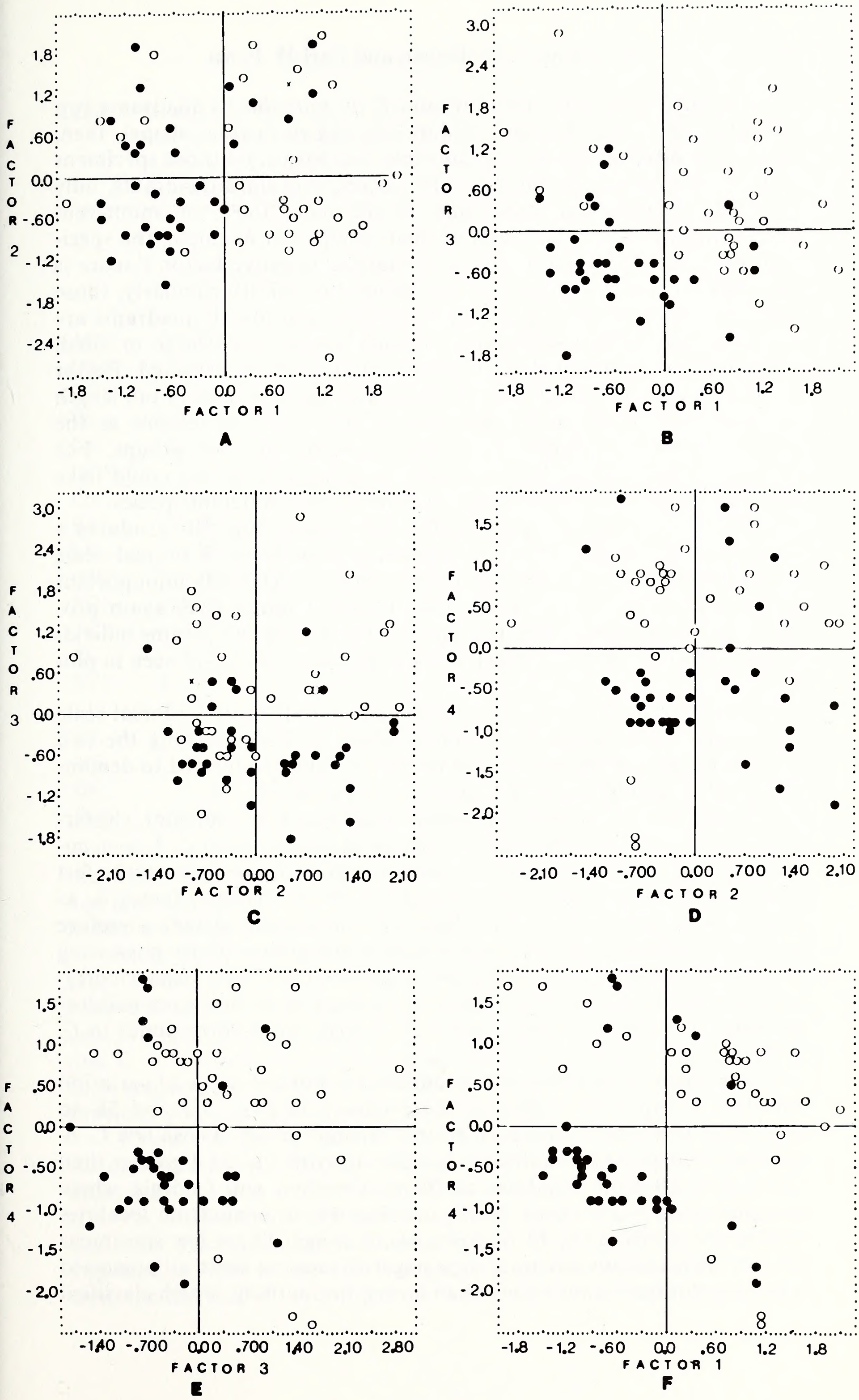
Group means and standard deviations of all 19 characters are presented for both nonintergrades and intergrades in Tables 4 and 5, respectively.

DISCUSSION

One purpose of the factor analysis performed was to determine, by inspection of the plotted factor scores, whether clusters of individuals occur that correspond to subspecies. Analysis of the first 13 characters reveals little or no clustering in any of the scatterplots. Factor 1 (abscissa) versus factor 2 (ordinate) appears to have the best clustering of the six graphs (Fig. 4A). Separation seems to occur along the vertical axis. *Crotalus h. atricaudatus* tends to cluster in the first two quadrants, while *C. h. horridus* tends to cluster in quadrants three and four, indicating separation on the basis of dorsal scale rows (factor 2). However, overlap is wide. More than 25% of the specimens of *C. h. atricaudatus* lie below the first two quadrants. No other plot (Fig. 4B-F) demonstrates any distinct clustering. On the basis of the first 13 characters, therefore, no subspeciation can be recognized.

The plots from the analysis of all 19 characters, however, show contrary results. Factor 1 (abscissa) versus factor 2 (ordinate) demonstrates clustering along the horizontal axis: *C. h. atricaudatus* tends to

Fig. 5. Scatterplots of estimated factor scores for specimens from the factor analysis of all 19 characters. Solid circles represent one or more specimens of *Crotalus h. horridus*; open circles represent specimens of *C. h. atricaudatus*. The X's represent specimens of both. Adult size measurements and postocular stripe (characters SVL, TL, HL, and POS) correlated most closely with factor 1; tail measurements (CS, R, and TL) correlated with factor 2; dorsal scale rows (ADS and DSM) correlated with factor 3; and middorsal stripe (MS) correlated with factor 4.


FACTOR 2
1.8
1.2
.60
0.0
-.60
-1.2
-1.8
-2.4
-1.8 -1.2 -.60 0.0 .60 1.2 1.8
FACTOR 1
A
FACTOR 3
3.0
2.4
1.8
1.2
.60
0.0
-.60
-1.2
-1.8
-1.8 -1.2 -.60 0.0 .60 1.2 1.8
FACTOR 1
B
FACTOR 3
3.0
2.4
1.8
1.2
.60
0.0
-.60
-1.2
-1.8
-2.10 -1.40 -.700 0.00 .700 1.40 2.10
FACTOR 2
C
FACTOR 4
1.5
1.0
.50
0.0
-.50
-1.0
-1.5
-2.0
-2.10 -1.40 -.700 0.00 .700 1.40 2.10
FACTOR 2
D
FACTOR 4
1.5
1.0
.50
0.0
-.50
-1.0
-1.5
-2.0
-1.40 -.700 0.00 .700 1.40 2.10 2.80
FACTOR 3
E
FACTOR 4
1.5
1.0
.50
0.0
-.50
-1.0
-1.5
-2.0
-1.8 -1.2 -.60 0.0 .60 1.2 1.8
FACTOR 1
F

occur in quadrants one and four, and *C. h. horridus* in quadrants two and three (Fig. 5A). Factor 1 (adult size and postocular stripe), then, appears to differentiate *C. horridus* into two forms. Of those specimens of *C. h. atricaudatus* occurring in the second and third quadrants, only one lacks a postocular stripe, and all are under 1000 mm snout-vent length, the smallest individuals of their group. For example, the specimen of *C. h. atricaudatus* having the largest negative factor 1 score is only 765 mm snout-vent length (probably a subadult). Similarly, those specimens of *C. h. horridus* lying in the first and fourth quadrants are the physically largest individuals of their group. Such large or small individuals, though not typical of their group, can be expected. Factor 2, which includes character R, demonstrates that the ratio of tail length to snout-vent length as an indicator of size is not as reliable as the lengths themselves (factor 1) in distinguishing the two groups. For instance, a large snake having a correspondingly large tail could have the same ratio as a smaller snake, or even one of a different species.

Factor 1 (abscissa) versus factor 3 (ordinate, Fig. 5B) produces a scatterplot much like plot 5A, indicating that factor 3 (dorsal scale rows), like factor 2 (adult tail measurements), is relatively unimportant in differentiating the two subspecies. Factor 1 (adult size) again produces good separation of the two groups in plot 5B with the same individuals lying far to the left or right of their respective groups as seen in plot 5A.

Since factor 2 (adult tail measurements) and factor 3 (dorsal scale rows) have been shown to be unimportant in distinguishing the two groups, the plot of factor 2 versus factor 3 would be expected to demonstrate no clustering, and this is observed in Figure 5C.

In the plot of factor 2 (abscissa) versus factor 4 (ordinate), clustering occurs along the vertical axis, with most specimens of *C. h. atricaudatus* in the first two quadrants and those of *C. h. horridus* in the last two (Fig. 5D). A similar plot occurs for factor 3 versus factor 4, as would be expected (Fig. 5E). Factor 4 (middorsal stripe) therefore appears to differentiate the specimens into two groups: those possessing a distinct middorsal stripe (factor 4 greater than zero, which corresponds to *C. h. atricaudatus*) and those possessing an indistinct middorsal stripe or none at all (factor 4 less than zero, which corresponds to *C. h. horridus*).

Specimens with factor scores outside the normal range of variation for their group were examined more closely in plots 5D and 5E to determine why they clustered with the "wrong" group. Those few *C. h. horridus* that possessed a distinct middorsal stripe (factor 4 greater than zero) were all from localities in North Carolina and Georgia where intergradation might occur. None, in other words, came from localities well to the north of the *C. h. atricaudatus* range. Those few specimens of *C. h. atricaudatus* having a large negative factor 4 score all possessed a faint middorsal stripe, rather than lacked one entirely, which classified

Table 4. Mean character values (x) and standard deviations (s) of all 19 characters for the two subspecies of *Crotalus horridus*. Numbers in parentheses are sample size. One specimen from each subspecies was not included because of unknown sex. M = male, F = female.

	C. h. horridus		*C. h. atricaudatus*	
	M (14)	F (21)	M (11)	F (22)
	x̄, s	x̄, s	x̄, s	x̄, s
ADS	25.29, 1.54	25.38, 0.97	27.54, 1.44	26.14, 1.64
DSM	23.43, 1.22	23.38, 0.80	24.46, 0.93	24.18, 1.05
PDS	18.57, 0.76	18.67, 0.73	19.27, 0.65	19.00, 0.62
VS	163.00, 2.94	166.67, 3.42	167.09, 2.34	169.54, 3.04
CS	23.64, 1.01	19.81, 1.12	25.54, 2.66	20.23, 1.90
DCS	1.50, 1.65	1.48, 1.03	3.18, 2.99	1.04, 1.13
LSL	13.86, 0.86	13.71, 1.10	13.36, 0.92	14.09, 0.92
RSL	13.86, 1.01	13.33, 0.86	13.27, 0.90	14.00, 0.98
LIL	14.50, 1.02	14.76, 0.89	15.54, 0.69	15.04, 0.95
RIL	15.21, 0.70	14.86, 1.01	15.54, 1.29	15.18, 1.14
BCB	11.14, 3.50	9.14, 3.90	12.54, 3.67	11.82, 2.58
TCB	0.57, 1.02	0.00, 0.00	1.54, 2.12	0.36, 0.95
R	0.09, 0.01	0.07, 0.00	0.09, 0.01	0.07, 0.01
SVL	939.71, 133.96	849.52, 59.77	1049.91, 128.87	1097.91, 116.14
TL	81.71, 10.62	56.95, 5.52	91.00, 13.03	72.86, 8.17
HL	42.42, 4.36	39.25, 2.98	47.52, 4.57	48.24, 4.34
MS	0.29, 0.47	0.10, 0.30	1.00, 0.00	0.86, 0.35
GC	0.36, 0.50	0.67, 0.48	0.09, 0.30	0.41, 0.50
POS	0.29, 0.47	0.14, 0.36	0.82, 0.40	0.96, 0.21

them into the *C. h. horridus* group. Of the properly classified *C. h. horridus* specimens, about 20% possessed an indistinct stripe and 90% lacked one altogether.

Since adult size and middorsal stripe appear to be the most important factors, one plotted against the other (factor 1 versus factor 4) should yield good separation of the groups along both axes, which is the case in Figure 5F. *Crotalus h. atricaudatus* clusters in the first quadrant, and *C. h. horridus* in the third quadrant. The individuals lying outside their respective clusters are a combination of aberrant individuals in the previous plots and have already been discussed.

Characters DSM, PDS, VS, BCB, and TCB were determined to be the combination of variables that best discriminated in the discriminant analysis of the first 13 characters. Pisani et al. (1973) reported characters CS, VS, DSM, and R (in decreasing order of discriminating ability) as the most discriminating in their analysis. Some differences would be expected in light of the different geographical areas sampled. In addition, the method of counting crossbands was different in this study (see

Table 5. Mean character values (x) and standard deviations (s) for each group of *Crotalus horridus* intergrades. All counties are in North Carolina. Burke, Surry, and Wilkes Counties are within the range of *C. h. horridus*; Moore County is within the range of *C. h. atricaudatus*; and Davidson, Randolph, and Stanly Counties lie between the two ranges, as defined by Gloyd (1940). Numbers in parentheses are sample size. One specimen was not included because of unknown sex. M = male, F = female.

	Burke, Surry, Wilkes Counties	Moore County	Davidson, Randolph Stanly Counties		All counties	
	F (4)	M (1)	M (5)	F (10)	M (6)	F (14)
	$\bar{x}$, s		$\bar{x}$, s	$\bar{x}$, s	$\bar{x}$, s	$\bar{x}$, s
ADS	25.00, 0.00	28.00	26.60, 0.55	26.00, 1.05	26.83, 0.75	25.71, 0.99
DSM	24.25, 0.96	25.00	24.60, 0.89	24.40, 0.97	24.67, 0.82	24.36, 0.93
PDS	19.00, 0.00	19.00	19.00, 0.00	19.20, 0.63	19.00, 0.00	19.14, 0.53
VS	167.25, 3.95	163.00	164.20, 2.28	168.20, 3.22	164.00, 2.10	167.93, 3.32
CS	19.75, 0.50	26.00	23.60, 1.14	19.20, 0.63	24.00, 1.41	19.36, 0.63
DCS	0.75, 0.50	0.00	1.40, 1.95	1.60, 2.41	1.71, 1.84	1.36, 2.06
LSL	13.75, 0.96	13.00	13.60, 0.55	14.10, 0.74	13.50, 0.55	14.00, 0.78
RSL	13.75, 0.96	14.00	14.00, 0.71	14.10, 0.88	14.00, 0.63	14.00, 0.88
LIL	15.25, 0.50	15.00	15.80, 0.84	16.00, 0.82	15.67, 0.82	15.79, 0.80
RIL	15.50, 1.00	15.00	15.40, 1.52	15.50, 1.18	15.33, 1.37	15.50, 1.09
BCB	11.50, 1.73	16.00	11.40, 2.30	10.80, 2.04	12.17, 2.79	11.00, 1.92
TCB	0.00, 0.00	1.00	0.20, 0.45	0.00, 0.00	0.33, 0.52	0.00, 0.00
R	0.07, 0.00	0.09	0.09, 0.00	0.06, 0.00	0.09, 0.00	0.06, 0.00
SVL	957.25, 46.95	983.00	1062.80, 134.64	975.00, 146.12	1049.50, 124.76	969.93, 123.93
TL	63.75, 4.11	90.00	91.20, 12.56	62.00, 8.33	91.00, 11.24	62.50, 7.25
HL	42.62, 1.16	44.60	46.90, 4.40	43.95, 4.67	46.52, 4.04	43.57, 3.98
MS	1.00, 0.00	1.00	1.00, 0.00	1.00, 0.00	1.00, 0.00	1.00, 0.00
GC	0.00, 0.00	0.00	0.20, 0.45	0.20, 0.42	0.17, 0.41	0.14, 0.36
POS	1.00, 0.00	1.00	1.00, 0.00	1.00, 0.00	1.00, 0.00	1.00, 0.00

above). For example, in their study mean body bands ranged from 23.14 to 25.05 among all groups. In our study, body crossbands averaged from only 9.14 to 12.54 (Table 4). The differences in mean tail bands is similar. In our first analysis these characteristics discriminated between the two subspecies, whereas they did not in Pisani et al. (1973); however, their method may have measured an entirely different character variable than the one they intended.

In the discriminant analysis of all 19 characters, 2 of the 6 added characters discriminated. These were HL and MS. Because head length is probably indicative of the total length of the adult snake (Klauber 1938, 1972), it appears that adult size and pattern are important in discriminating between the two subspecies. Dorsal scale rows and number of ventrals also discriminated here, as in Pisani et al. (1973), except that the discrimination was by ADS instead of DSM. Characters BCB and TCB did not discriminate in the second analysis.

In comparing the two analyses, we find that all 19 characters allowed better discrimination. This is evident in the larger eigenvalue (2.989 vs. 1.088), the larger canonical correlation (0.866 vs. 0.722), the smaller Wilks' lambda (0.251 vs. 0.479), and better classification of individuals into the two groups (7% incorrectly classified vs. 16%). In the canonical variable histograms (Fig. 6), separation of the two groups is much better in the analysis of all 19 characters, again showing the importance of size and pattern.

Comparison of the discriminating characters ADS, VS, and HL between nonintergrades and intergrades (Tables 4 and 5) shows that, as expected, the mean character values of the intergrade specimens lie between the mean character values of *C. h. horridus* and *C. h. atricaudatus*, regardless of sex. Since the remaining characters other than MS did not discriminate, their mean values for the intergrade specimens are not expected to be intermediate or even different from the mean values of either *horridus* or *atricaudatus*. Interestingly, all intergrades possessed a distinct middorsal stripe, much like intergrades reported from western localities (Gloyd 1940, Smith 1961, Webb 1970).

Of the three new pattern characters tested in this study (MS, GC, POS; Table 1), POS and, especially, MS were important. None, however, was completely free from subjectivity in measurement. In some cases, the distinction between light- and dark-colored or indistinct and clearly visible was a fine line. Use of old museum specimens, many faded by preservatives, may have induced too much subjectivity, however unintentional. Some dark-colored specimens had a middorsal stripe that had apparently faded to an almost white color, making the stripe unusually conspicuous. Had the specimens been living, the stripe may have been inconspicuous. In other specimens the ground color was faded and difficult to determine. Another problem is the inadequacy of the coding scheme for GC. Gloyd (1940) and others (Wright and Wright 1957, Conant 1975) mentioned that *C. h. horridus* has two color phases—the typical dark one, as tested for in this study, and a yellow one. There was no possible way, in certain cases, for this study to determine whether a light-colored *C. h. horridus* specimen was truly the yellow phase, as opposed to a badly faded normal dark phase, or the color of a typical *C. h. atricaudatus* specimen. Use of ground color as a discriminating character obviously requires fresh or living specimens and an improved coding scheme.

The evidence presented here suggests that, on the basis of differences in adult size and pattern, two subspecies of *Crotalus horridus* (as described by Gloyd 1940) occur east of the Appalachians. There the races are clearly more distinct than in the western populations. Standard morphological characters alone are not sufficient to separate the two taxa; rather, adult size and pattern differences, in conjunction with the number of dorsal scale rows and ventral scutes, best discriminate *C. h. horridus* from *C. h. atricaudatus*. This combination of size, pattern, and morphological differences needs to be examined in western populations, preferably on living or freshly collected specimens for accurate determination of color and pattern. We feel that the results of our study are preliminary and that a comprehensive study of variation throughout the entire range of *C. horridus* is needed.

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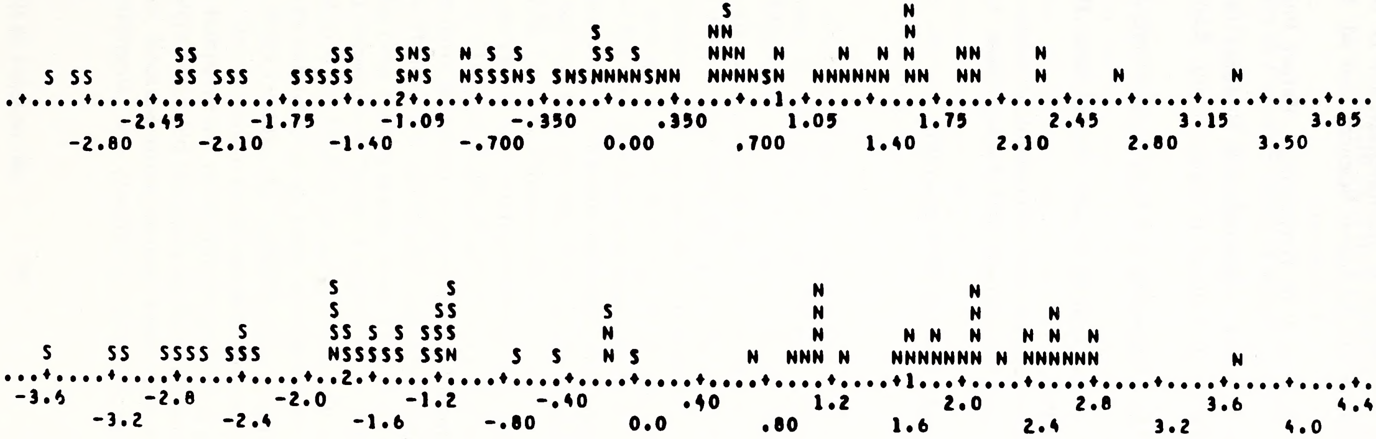

Fig. 6. Histograms of the canonical variable from discriminant analysis of the first 13 characters (top) and from analysis of all 19 characters (bottom). N = a specimen of *Crotalus h. horridus*, S = a specimen of *C. h. atricaudatus*.

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Seasonal, Thermal, and Zonal Distribution of Ocean Sunfish, *Mola mola* (Linnaeus), off the North Carolina Coast

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ABSTRACT.— Most previous information on the ocean sunfish, *Mola mola*, has been derived from beached specimens and contributed little to our understanding of typical distributional patterns of the species. More than 60 encounters with *Mola mola* in North Carolina's offshore waters reveal that this fish is an epipelagic migrant, occurring in shallow water (10 to 40 fathoms in depth) commonly in the spring between mid-March and mid-June. In the fall it has been seen less frequently (mid-October through November), and the species is essentially absent in the winter.

In spite of its cosmopolitan distribution, little information is available concerning the natural history of the ocean sunfish, *Mola mola* (Linnaeus). This is particularly true in the southeastern United States, where nearly all records are of animals found awash in the surf. Because such records may reflect atypical patterns of movement and distribution, observations on the seasonal, thermal, and zonal distribution of *Mola* at sea are of interest. Between 1977 and 1986, I conducted 126 offshore trips for the primary purpose of monitoring seasonal occurrence and abundance of marine birds and mammals. During this period, however, I also incidentally observed other pelagic organisms (see Lee and Booth 1979, Lee and Palmer 1981).

All but seven of the offshore survey trips departed from either Oregon Inlet or Hatteras Inlet, Dare County. Of the seven trips that did not, five were from Beaufort Inlet, Carteret County; one was from Wilmington, New Hanover County; and one was from Virginia Beach, Virginia. Each daylong outing lasted 10 to 11 hours and typically followed predesignated transects of 20 to 55 miles (32 to 88 km) from the point of departure and into the Gulf Stream. All of the Oregon Inlet and Hatteras Inlet surveys extended to at least the 100-fathom contour, and many went several miles beyond the 1,000-fathom contour. Trips were made at all seasons, but monthly coverage was uneven (see Table 1). Ideally, water surface temperature, directional movement, and time and location of sightings were recorded for each sunfish observed. Data are not uniform, however, because some charter boats lacked LORAN and other recording equipment, sea conditions necessitated abbreviated record

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Table 1. Seasonal and zonal occurrences of *Mola mola* compared to offshore survey dates and percentage of time spent in each zone.

Month 1977-1986	No. monthly surveys	Depth in fathoms 1-20	21-40	41-60	61-80	81-100	101-1200	Other reports	Total no. encountered in month
January	3	-	-	-	-	-	-		0
February	3	-	-	-	-	-	-		0
March	5	1	1	-	-	-	-	2	4 (5.8%)
April	11	18	15	1	1	1	-	1	37 (54.4%)
May	15	6	-	-	1	-	-	4	11 (16.1%)
June	18	1	1	-	-	2	-		4 (5.8%)
July	15	-	-	-	-	-	-		0
August	19	-	-	-	8	-	-		8 (11.7%)
September	10	-	-	-	-	-	-		0
October	10	-	-	1	-	-	-	1	2 (2.9%)
November	6	-	1	-	-	-	-		1 (1.4%)
December	11	-	-	-	-	-	1		1 (1.4%)
Approximate percent of survey time in each zone		15%	15%	10%	10%	15%	35%		
Totals	126	26 (43%)	17 (28%)	2 (1%)	10 (16%)	4 (6%)	1 (2%)	8	68

keeping, and field effort was focused on seabirds. Furthermore, surveys of ocean sunfish from boats are difficult, because surface conditions and angle of view normally limit subsurface visibility. Variations in surface conditions from one trip to another make comparisons of trip-by-trip tallies meaningless. Nevertheless, cumulative records show patterns of zones of occurrence, as well as seasonal movement and abundance.

In the North Atlantic *M. mola* ranges north to the Gulf of St. Lawrence, Newfoundland, southern Iceland, northern Norway, and the Kola Peninsula (Martin and Drewry 1978). It is not common in the tropics (Parin 1968). Information on seasonal movements is mostly conjectural, suggesting passive transport by ocean currents or foraging while following passively drifting coelenterates and ctenophores (see Martin and Drewry 1978). The species is generally regarded as pelagic and solitary, but there are reports of *M. mola* moving in pairs or small groups (Whitley 1931, Smith 1965), and there are several records of summer occurrences, both of free-swimming and surf-washed individuals, in bays such as Sandy Hook, New Jersey (Breder 1932), Isle of Wight Bay, Maryland (Schwartz 1964), and Monterey Bay, California (Myers and Wales 1930).

Records of *Mola* along the southeast coast of North America are scarce, although farther north (e.g., New Jersey; Townsend 1918) it is fairly well established that these headfish occur regularly. Most northern records are of summer encounters. Brimley (1939) documented the occurrence of *M. mola* in North Carolina, providing information on one specimen and three other records; Anderson and Cupka (1973) compiled eight records for South Carolina. The species is known from waters off other southeastern states, including the Gulf of Mexico (Dawson 1965), but generally it appears on state faunal lists with no details of occurrence (e.g., Briggs 1958).

Both *Mola mola* and *Mola* (formerly *Masturus*) *lanceolata* Lienard, the sharp-tailed mola, are found off the North Carolina coast (Brimley 1939, Funderburg and Eaton 1952). Although Dawson (1965) commented on the difficulty of identifying ocean sunfish at sea, several distinctive field characters separate these two fish. I was able to identify *M. mola* by its dull, nearly uniform color, the rounded dorsal or ventral fins, and the short blunt shape of its tail (which could be confirmed in 70% of sightings). Because nearly all fish seen were considerably greater than 1 meter total length, I assumed most were adults.

Most sunfish were sighted while they were swimming about 0.5 to 1.5 m below the surface. In their "sunning" behavior the fish's sides were always below the surface. Usually the dorsal fin, and occasionally the ventral fin, projected above the surface. Projecting fins were normally held at angles of 45 to 70 degrees and were constantly undulating. This allowed sunfish to be sighted from distances of more than 100 m under calm conditions. Observed fish whose fins did not project above the surface could not be detected for more than 20 to 25 meters from the boat. Normally the fish did not dive at the approach of the boat, but simply maneuvered out of its way. They sounded only if the boat was on a collision course. Boat captains say the fish are rarely if ever hit by their boats.

Sunfish were seen on calm days, days with considerable swells, and days when small white caps were prevalent, although reduced visibility made comparative counts useless. When seas were quite rough (20+ mph winds, high swells, and extensive white caps), no fish were found; but under these conditions we occasionally sighted marine turtles, sharks, and porpoises. I suspect the sunfish were then swimming deeper, and our failure to see them was not simply a result of the poor subsurface visibility.

Information pooled from 60 sightings of *Mola mola* personally obtained and other available records from the North Carolina coast suggest that the species is not randomly distributed by season or location. Although field effort was not uniform, the records obtained are informative, in that the majority are from areas and seasons having minimal opportunities for observation (see Table 1).

Season: *Mola mola* is essentially absent off the North Carolina coast during the winter (see Table 1). Although I have made few winter trips (N = 20), I have no reason to assume ocean sunfish occur regularly at this season, for boat captains and others also have not encountered them in the winter. The earliest spring record is for 16 March, and the earliest fall record is for 17 October. The species is most commonly seen in the spring. Surprisingly, the fish do not occur regularly in our waters during summer. Boat captains say they occasionally see ocean sunfish in the summer, but some of these could be the more tropical *M. lanceolata*. Interestingly, a large part of our survey time during summer was spent in the Gulf Stream, where *M. lanceolata* could be expected, but none was verified. In the summer of 1985 I personally encountered *M. mola* eight times on only 4 of 15 offshore trips, all between 17 and 29 August, a period when relatively calm water usually provides optimum subsurface visibility. No other summer records are available in spite of rather extensive offshore surveys in this season. The fact that only three *M. mola* were encountered in the fall (17 October through 20 November) suggests a different fall migration route, or perhaps a seasonal absence of surface "sunning" behavior. The three dated North Carolina records provided by Brimley (1939) are all for May. Anderson and Cupka (1973) also reported *Mola* from April (2) and May (1); but their other records were from December (2), January (1), and February (2), suggesting winter occurrence in South Carolina (see below).

Location: This fish was seldom seen in areas of deep water (> 100 fathoms); most occurred in an offshore zone between 10 and 40 fathoms deep ($\bar{x}$ = 28.19 fathoms). Most were seen more than 10 miles from shore, although one fish was seen while the survey boat was still in sight of land (19 April 1980). Only six records were in water 40 to 100 fathoms deep, and one December record is from 500 fathoms. Except for the December fish, individuals were not encountered beyond the inner edge of the continental shelf (100 fathoms), although nearly half of our survey time was spent in these deeper waters. Additionally, Charles Manooch, National Marine Fisheries Laboratory, Beaufort, informed me that all of the 15 *Mola* seen by him were between 20 and 30 miles from shore and in water 17 to 25 fathoms deep. Off South Carolina, ocean sunfish (species not determined) have been reported over water about 42 m (23 fathoms) deep (Anderson and Cupka 1973). Interestingly, Lee and Palmer (1980) documented the regular ocurrence of leatherback turtles, *Dermochelys coriacea*, another reputed coelenterate feeder, to be restricted, or nearly so, to shallow waters inshore of the 100-fathom contour.

Manooch reported an adult *M. mola* in Core Sound (Harkers Island, fall date not recorded), and the site of Brimley's (1939) Swansboro record is Bogue Sound. Although Myers and Wales (1930) noted that young individuals were of regular occurrence during the summer in Monterey Bay, California, I am not aware of any records from estuarine bays. There are no reports of *Mola*, for example, in the Chesapeake Bay. However, Steve Ross (pers. comm.) captured a single adult from near the mouth (< 20 ppt) of the Neuse River near Long Creek on 16 May 1980 in a gill net. This is the only truly estuarine occurrence of which I am aware.

Water Temperature: Ocean surface temperatures were recorded for 20 of my 60 North Carolina sightings at sea, and temperature approximations (±2 °C) are possible for 13 others based on temperatures recorded at other locations near the sighting. The coldest water in which I encountered *M. mola* was 6.8 °C on 16 March 1984, which was also the date of the earliest spring record. The warmest water was 29.4 °C on 13 June 1979, the date of the latest spring sighting. Most encounters were at temperatures between 10 and 18 °C. On all dates a surface temperature gradient was recorded, with coolest waters generally closest to land and warmest waters within the Gulf Stream. Seasonal and thermal distributions (Fig. 1) suggest that, although maximum and minimum temperatures may be critical, these fish are not simply moving into deeper, warmer waters during cool periods, or into cooler inshore waters during warm seasons. Similar findings were reported for several species of marine turtles off the North Carolina coast (Lee and Palmer 1980).

Time of Day for "Sunning": Surface "sunning" behavior was noted for most periods of the day, the earliest at 0732 EST and the latest at 1432. Additionally, several sunfish were seen in "mid- to late afternoon," but exact times were not recorded.

Miscellaneous: All sunfish observed were solitary, although on several occasions individuals were found within half a mile of each other.

Except for the one December record, none of the *Mola* I saw were known to be associated with jellyfish or other fishes, nor were any associated with sargassum beds, floating boards, or other objects. Manooch (pers. comm.), however, reported diving in water 20 to 30 miles off Beaufort and seeing one *M. mola* associated with a large number of "sea nettle type" jellyfish on 12 March 1976. Probably coelentrates are not easily seen from above the surface. At any rate, none of the coelenterates or ctenophores that could offer a prey base were seen regularly. The only jellyfish typically seen on any of the surveys was *Physalia*, and it invariably was in the Gulf Stream, offshore of the areas inhabited by *Mola*. Likewise ocean sunfish were not found along "tide lines," current edges, sites of local upwellings, or other areas where many marine organisms tend to congegrate..

Migration and Movement: In that *Mola mola* is well known north of North Carolina in summer and south of the state in winter (Anderson and Cupka 1973) and is rare or absent from North Carolina waters during these periods, most individuals seen off our coast are probably migrants. All spring individuals whose orientation was recorded (about one-half of the total) were swimming north. Their lack of apparent forward movement may be deceptive; when the boat was in motion (10 to 18 knots), the fish appeared to remain in one area. On several occasions, however, sunfish were watched moving past and out of sight of our idling boat (in one case the boat was broken down) in a short time period. As previously implied, movement was within a wide band generally over the 10- to 45-fathom contour.

The records from mid to late August 1985 are interesting in that this was the only summer in 10 years of offshore study that I have seen ocean sunfish. Although late August at first appears early for "fall" migration, I should point out that many southbound sea birds appear in North Carolina offshore waters at this time. Furthermore, various migratory sport fish locally appear or reappear in this same time period. Nevertheless, southward fall migration of *M. mola* would appear to occur primarily in October and November, with movements perhaps starting as early as late August in some years.

Most ocean sunfish were noted between mid-April and mid-May when about 80% of the total sightings were compiled. It may be that south of the Hatteras area migration occurs farther offshore. This is suggested by the few sightings made off Beaufort (5 in 175 trips made by Manooch, pers. comm.; none in 25 trips made by Wayne Irvin, pers. comm., or me). In this area, comparable water zones and the inner edge of the Gulf Stream are much farther from land than off the northern Outer Banks where most of my surveys were conducted.

DISCUSSION

The ocean sunfish, *Mola mola*, is best regarded as an epipelagic migrant in North Carolina's offshore waters. In the spring it can be

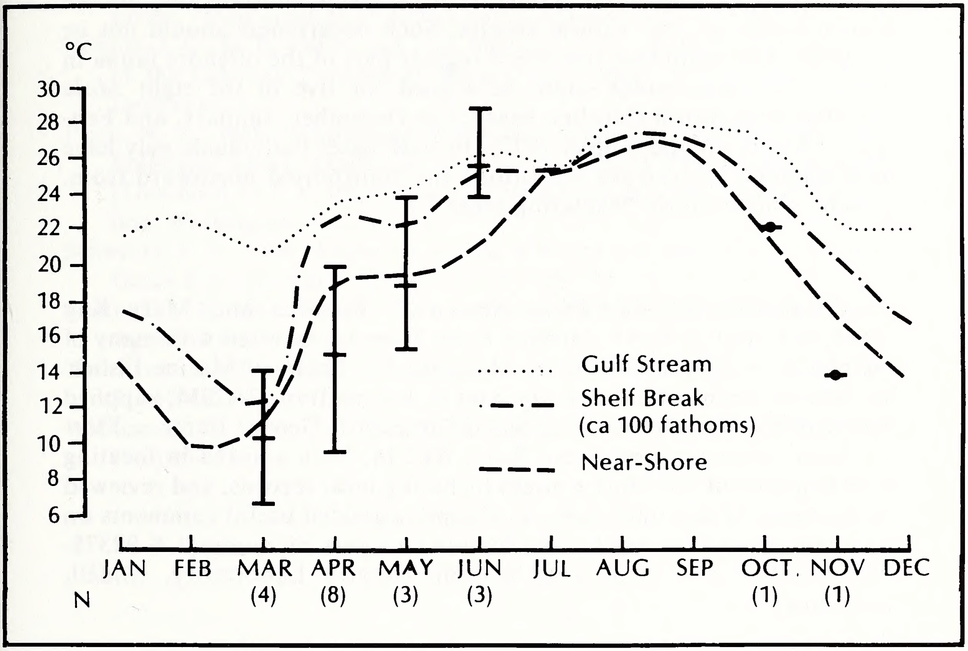

Fig. 1. Thermal distribution of *Mola mola* compared to surface temperature gradients. Ranges and means of temperatures taken in immediate vicinity of *Mola* (N = 20). Average monthly sea-surface temperatures for three areas of the North Carolina continental shelf north of Cape Hatteras (from Newton et al. 1971).

quite common. On 18 and 19 April 1980, 15 were seen each day despite sea surface conditions that offered less than maximum visibility. Five were counted on 14 May 1981, but on all other days only one or two verifiable *M. mola* were seen per trip. Sunfish actually were more common than Table 1 indicates. I often observed two to three times as many individuals as reported, but these sightings were not recorded, either because specific identity could not be confirmed or because other survey priorities were more urgent at the moment.

The dearth of *M. mola* sightings during fall is difficult to explain, especially since Anderson and Cupka (1973) stated that a boat captain reported at least 30 molas (species undetermined) in late autumn of 1970 and 1971 off South Carolina.

Local seasonality of occurrence of *Mola* based on beach stranded specimens may be misleading. Along the Atlantic coast injured, sick, or dead fish could be displaced long distances by the Labrador Current, long shore current, or Gulf Stream. The fact that six of the seven *M. lanceolata* from North Carolina (Brimley 1939, Funderburg and Eaton

1952, NCSM records) are winter records seems contradictory to the known habits of this tropical species. Such occurrences should not be interpreted to mean that they are a regular part of the offshore fauna in winter. The same point could be argued for five of the eight *Mola* reported from South Carolina beaches in December, January, and February (Anderson and Cupka 1973). In both cases individuals may have been numbed by cool sea conditions and transported northward from, to date, undetermined "wintering areas."

ACKNOWLEDGMENTS.— Steven P. Platania and Mary Kay Clark, both of the North Carolina State Museum, assisted with many of the offshore surveys. Charles S. Manooch III, National Marine Fisheries Service, Beaufort Laboratory, and E. Wayne Irvin, NCSM, supplied supplemental data from their trips off Beaufort. George Burgess, Florida State Museum, and Steve Ross, NCSM, both assisted in locating several pertinent literature sources including local records, and reviewed the contents of this note. John E. Cooper provided useful comments on the manuscript. The study was financed in part by contract # 92375-1130-621-16, U.S. Fish and Wildlife Service Laboratory, Slidell, Louisiana.

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A Late Quaternary Herpetofauna from Saltville, Virginia

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ABSTRACT.— The late Quaternary herpetofauna from Saltville, Virginia, consists of at least two salamanders, two anurans, two turtles, and four snakes; all are forms that can be found living in the area today. The fossil herpetofauna originated from three ^{14}C dated stratigraphic units. Based on the presence of all 10 taxa of the herpetofauna in Units W2 (lower) and W3, it is reasonable to conclude that this fauna has been in place for the last 13,500 to 15,000 years. Because the most northern area where all members of the Saltville herpetofauna may be found living together today is in extreme northeastern Pennsylvania, the herpetofauna is clearly not a "Boreal" one. Moreover, Boreal temperatures, as we know them today, would not provide enough warm days for the eggs of *Chelydra serpentina, Chrysemys picta*, or *Elaphe* cf. *E. obsoleta* to hatch.

The late Quaternary fluvial and lentic sediments of the Saltville Valley in Virginia have yielded the remains of large mammals for more than two centuries (Jefferson 1787, Peterson 1917, Boyd 1952, Ray et al. 1967, McDonald and Bartlett 1983). Most of these remains were found during construction activities related to agriculture or the production of salt. The first purely scientific excavation in search of late Quaternary vertebrates at this locality was conducted jointly by Virginia Polytechnic Institute (VPI) and the Smithsonian Institution (SI) in 1966 and 1967. In 1978 and 1981 Charles Bartlett, Jr., performed salvage excavations at several locations in the valley for the Town of Saltville, and in October 1980 Bartlett and J. McDonald began controlled excavations in the valley. In 1982 McDonald initiated the Saltville Project, a multidisciplinary investigation of the late Quaternary history of Saltville Valley that included the collaboration of several specialists from different institutions in eastern North America. Late Quaternary deposits in the Saltville Valley have been shown to span some 27,000 years, including a continuous record for approximately the last 15,000 years (McDonald 1984, 1985a), making this locality unusually useful for the documentation of environmental change in the middle Appalachian region through the late Wisconsin and Holocene.

The first known herptile specimen to be collected at Saltville was a partial limb bone of an anuran (fam., gen. et sp. indet.) collected on 11 August 1966, by the VPI-SI field crew (Catalog and field notes, 1966, VPI-Smithsonian Saltville Expedition). Bartlett found the second specimen—a costal bone of the Painted Turtle, *Chrysemys picta* (USNM 404721)—on 30 October 1978 (C. S. Bartlett, Jr., field notes, 30 October 1978). The 1980-1984 Radford University excavations recovered numerous herptile specimens by wet screening the finer fluvial sediments and closely examining thinly sliced lentic deposits of clay and silt. Vertical and horizontal provenience and matrix data for specimens have also been collected since 1980, which allows differentiation of faunules and inferences about faunal change (or the absence of change) over time.

Here, we describe the generically and specifically identifiable herptile material collected at Saltville through 1984, including the division of this material into three radiocarbon-dated faunules. In addition, we discuss the sampling function of the various depositional processes and comment on the paleoecological implications of these faunules. The herptile material reported here is the first to be described from the Saltville locality, and is also the first to be described from a stratified subaerial, hydraulically deposited site in the middle Appalachians. This is, therefore, a contribution to the controlled chronostratigraphy of late Quaternary herptiles in this region, a contribution free of the collecting and preservation biases characteristic of herpetofaunas from karst or karstlike features in the middle Appalachians.

STUDY AREA

Saltville Valley lies some 525 m above sea level in the Valley and Ridge Physiographic Province in southwest Virginia (Fig. 1). The floor of this small valley slopes gradually to the north, converging on a water gap that leads to the nearby North Fork of the Holston River. The valley is bordered on the northeast and southeast by foothills of Walker Mountain, and on the northwest by low limestone hills.

The herptiles described in this paper came from four sites on the valley bottom (Fig. 1). Most specimens were collected at SV-1 (the "musk ox" site: 36°52′19″N, 81°46′24″W), located near the southwest end of "The Flat" (McDonald and Bartlett 1983). Six specimens came from SV-2 (the "drug store" site: 36°52′52″N, 81°45′48″W), and one came from CSB-2A (36°52′29″N, 81°45′51″W). The anuran bone collected by VPI-SI in 1966 came from SI-1 (36°52′36″N, 81°46′01″W). SV-1 and CSB-2A are on the Glade Spring quadrangle, and SV-2 and SI-1 are on the Saltville quadrangle, USGS 7.5′ series.

Saltville Valley lies upon the Mississippian Maccrady Formation, a variable sequence of shales, siltstones, limestones, and dolomites containing substantial quantities of gypsum, anhydrite, and halite (Cooper

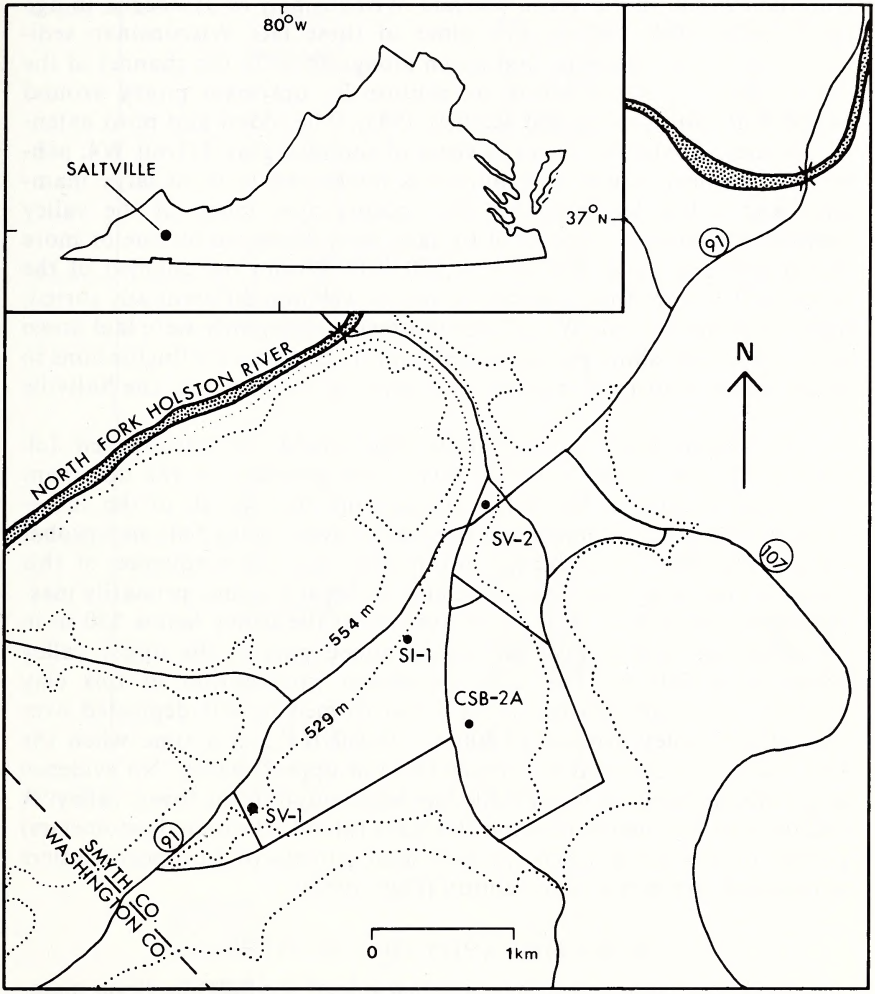

Fig. 1. The Saltville, Virginia, locality, showing location of sites within Saltville Valley that have produced herptile specimens mentioned in text.

1966). This bedrock has been scoured and incised in places by Quaternary stream action, and is now overlain by up to 3 m of late Quaternary sediments.

The Quaternary sediments result from multiple depositional episodes dating from the ?Sangamonian interglaciation through the Holocene (Fig. 2, Table 1). Terrace-like deposits above 530 m in elevation occur at several places around the edge of the valley; these are considered tentatively to date from Sangamon time. Most of the sediments lying below 530 m elevation are late Wisconsinan or Holocene in age (McDonald 1984, 1985a). The older of these late Wisconsinan sediments are fluvial deposits, laid down alongside or in the channel of the extinct Saltville River before its capture by upstream piracy around 14,000 B.P. (McDonald and Bartlett 1983). The oldest and most extensive of these fluvial deposits is a sheet of rounded gravel (Unit W4: pebbles to cobbles), containing numerous bones and teeth of large mammals and a few lag boulders, that occurs over much of the valley bottom. This unit is considered to have been deposited by one or more floods between ca. 27,000 and 14,500 B.P. Within the channel of the Saltville River are finer grained, in places well and differentially sorted, fluvial sediments (Unit W3). These sediments apparently were laid down over a relatively short period as bed load from moderate fluctuations in stream stage/transport capacity, just prior to the piracy of the Saltville River.

A shallow lake—Lake Totten (McDonald 1985b)—formed following the loss of the Saltville River, and persisted as the dominant hydrologic feature of the valley throughout most or all of the subsequent 14,000 years. Some small streams, mostly spring fed, also probably entered the valley during this period. As a consequence of this changed hydrology, fine lacustrine and marsh sediments, primarily massive clays (Units W2, H2), occur over all of the valley below 530 m in elevation and extend over an undetermined part of the upper valley lying above 530 m. The only significant interruption of this clay sequence is a mud-soil-peat mosaic that formed or was deposited over part of the valley around 10,500 to 10,000 B.P., at a time when the water table was lowered in the middle (and upper?) valley. No evidence of an equally lowered water table has been found in the lower valley. A shallow lake and marsh of some 200 acres (about 80 square hectometers) existed in the valley when the first land patents to European settlers were issued late in the 18th Century (Ogle 1981).

STRATIGRAPHY OF THE SITES

SV-1 lies directly over the southeast side of the Saltville River channel and, as a result, it contains all of the primary Wisconsinan-Holocene stratigraphic units recognized to date (Fig. 2). Since excavations began at this site in October 1980, more than 3,000 vertebrate specimens have been removed from some 200 m of excavated area. Vertebrate remains have been found in all stratigraphic units. Most fossils, however, have been found near the bottom of the lower lake clay (Unit W2: ca. 13,500 B.P.), in the sand and fine gravel deposits of the channel bottom (Unit W3: ca. 14,500 to 13,500 B.P.), and in the coarser gravel sheet (Unit W4: ca. 27,000 to 14,500 B.P.).

Most (18 of 26) of the herptile specimens described in this paper came from SV-1. Twelve specimens were recovered from the channel bottom deposits (Unit W3), which have also yielded large numbers of

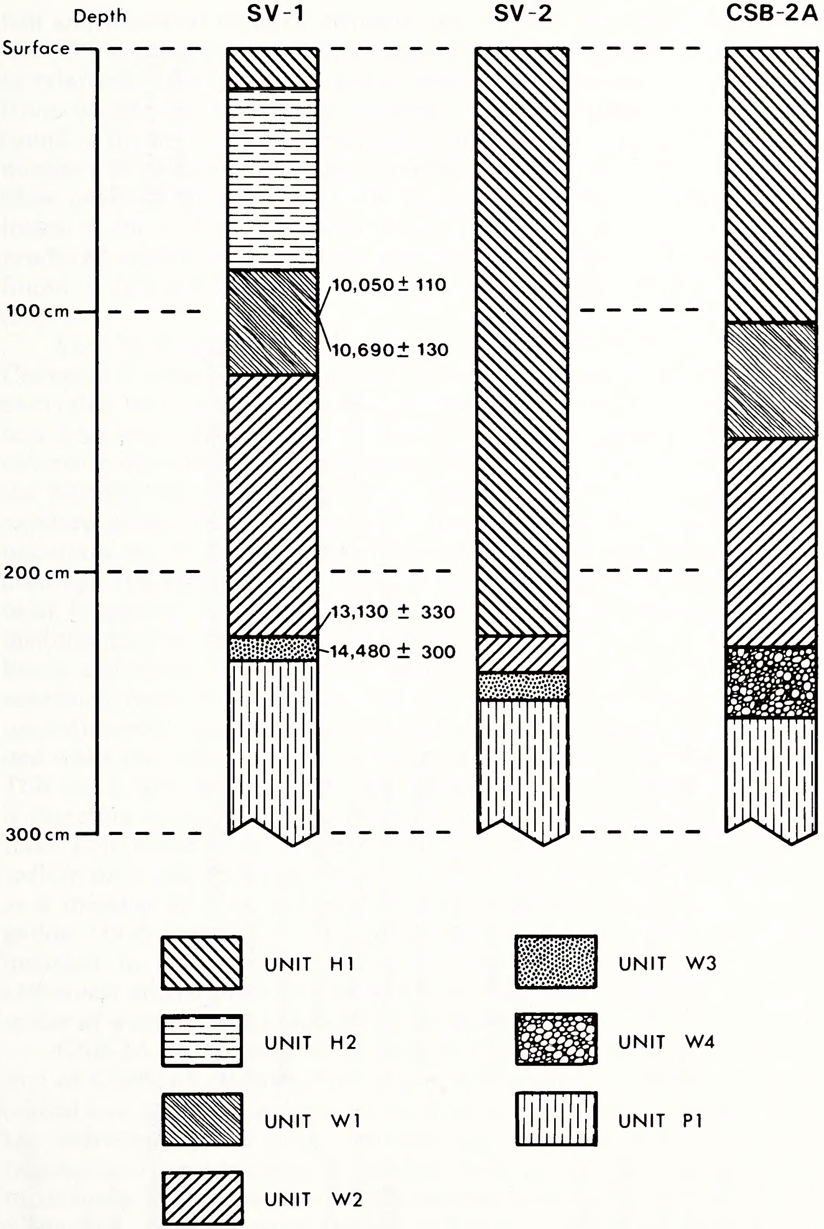

Fig. 2. Stratigraphic profiles for the three sites that have produced generically or specifically identified herptile specimens. Radiocarbon dates on Unit W1 are from samples collected near, but not at, SV-1; those on units W2 and W3 are from samples collected at SV-1.

Table 1. Distribution of herptile specimens in late Quaternary depositional units at Saltville, Virginia.

Stratigraphic Units[a]	SV-1[b]	SV-2[b]	CSB-2A[b]
H1: Historic Surface	- - - -	- - - -	- - - -
H2: Early-?Late Holocene	- - - -	- - - -	- - - -
Massive lacustrine/marsh clay			
W1: Ca. 10,500-10,000 B.P. ?Mass-wasted mud	*Bufo woodhousei fowleri* (USNM 404730) *Chelydra serpentina* (USNM 404741)	- - - -	- - - -
W2: Ca. 13,500-10,500 B.P. Massive lacustrine/marsh clay			
Upper	- - - -	- - - -	- - - -
Lower	*Cryptobranchus alleganiensis* (USNM 404722) *B. w. fowleri* (USNM 404731,-35) *Chelydra serpentina* (USNM 404740)	- - - -	?*Chrysemys picta* (USNM 404721)[c]
W3: Ca. 14,500-13,500 B.P. Channel bottom bed load and fine flood gravels.	*Notophthalmus* cf. *N. viridescens* (USNM 404723,-24,-26,-27,-29) *B. w. fowleri* (USNM 404733,-34) *Rana pipiens* group (USNM 404737,-38,-39) *Storeria* sp. (USNM 404744) *Thamnophis* sp. (USNM 404745)	*Notophthalmus* cf. *N. viridescens* (USNM 404725,-28) *B. w. fowleri* (USNM 404732) *Rana pipiens* group (USNM 404736) *Elaphe* cf. *E. obsoleta* (USNM 404742) *Nerodia sipedon* (USNM 404743)	- - - -
W4: Ca. 27,000-14,500 B.P. Flood gravel (pebble-cobble)	- - - -	- - - -	?*Chrysemys picta* (USNM 404721)[c]
P1: Mississippian bedrock (Maccrady Shale)	- - - -	- - - -	- - - -

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[a] After McDonald (1984, 1985a).

[b] Cf. Fig. 1 and 2 for location of sites and vertical dimensions.

[c] The exact stratigraphic provenience of USNM 404721 is equivocal. See text for additional comments.

fish and mammal remains. Most of the fish and herptile remains from Unit W3 are in good condition, suggesting that they have been subjected to relatively little fluvial abrasion, whereas the mammal remains range from unabraded to heavily abraded. Four herptile specimens were found in the lower several centimeters of Unit W2, associated with large numbers of mollusk, fish, and mammal remains. These remains do not show evidence of abrasion. Two herptile specimens were found in the lowest 5 cm of Unit W1, a humus-rich mud that has preserved fluid-produced whorls at its contact with Unit W2. Herptiles have not been found to date at SV-1 in units P1, W4, the upper part of W2, H2, or H1 (Fig. 2).

Late in August 1983, the foundation of the old Olin Mathieson Chemical Corporation's company store was demolished and the area excavated with heavy machinery in preparation for construction of a new drug store. This excavation (site SV-2) exposed only artificial fill or otherwise disturbed sediments around most of the periphery and across the bottom, but a small section of undisturbed natural sediment was exposed along the southeast wall. Here, 225 cm of artificial fill was underlain by 13 cm of what appeared to be natural lacustrine clay, although this stratum did contain a few very small ($\leq$ 3 mm) intrusive brick fragments. Beneath the clay was a layer of alluvium, consisting of medium sand to very fine gravel, numerous small pieces of wood, and bones and teeth. No intrusive material was found. This alluvium was separated from the overlying clay by a distinct boundary, and it lay unconformably upon well-scoured bedrock, indicating that it was deposited while the valley was still being drained by vigorously flowing water. This site is low and near the water gap leading to the Holston River; it is therefore unlikely that the alluvium could have been deposited after Lake Totten had formed unless the lake drained periodically. No radiocarbon date was obtained for this deposit, but we tentatively identify it as a member of Unit W3. Six herptile specimens were found in a 5-gallon (19-l) sample of this unit collected 3 September 1983. Also included in this sample was an abraded fragment of a mastodon (*Mammut americanum*) tooth and the unabraded crown of a superior molar of a cervid (*Sangamona* or *Odocoileus*).

CSB-2A was excavated 28 and 30 October 1978, under the direction of Charles S. Bartlett, Jr., as part of an effort to salvage paleontological and archeological resources prior to construction of bleachers at the Saltville softball park. Bartlett reported finding many rounded fragments of large mammal bones and teeth, along with one fragment of turtle bone, in a "pebble zone" that we tentatively assign to Unit W4 (C. S. Bartlett, Jr., field notes, 28 and 30 October 1978; pers. comm.). The turtle bone (USNM 404721) does not, however, show signs of abrasion. Rather, its condition is similar to other remains found in units W2 and W3. Based on the condition of USNM 404721, we suspect that it might have come from the bottom, or from near the bottom, of Unit W2 instead of from within Unit W4, which typically contains noticeably abraded remains of large mammals only. Alternatively, Bartlett's "pebble zone" might have included, or consisted entirely of, Unit W3.

SYSTEMATIC PALEONTOLOGY

The classification used here follows Dowling and Duellman (1978). The common names used follow Collins et al. (1978). Ranges and notes on modern species follow Conant (1975) or personal observations by J. A. Holman. Numbers are those of the Department of Paleobiology, Division of Vertebrate Paleontology, U.S. National Museum, Washington, D.C. (USNM). All measurements are in millimeters.

Class Amphibia

Order Caudata

Family Cryptobranchidae

Cryptobranchus alleganiensis (Daudin), Hellbender

Material. — Trunk vertebra: USNM 404722 (Fig. 3), from Unit W2.

Remarks. — This vertebra is indistinguishable from those of modern *Cryptobranchus alleganiensis.* The Saltville fossil may be separated from the extinct species *C. guildayi* Holman of the late Kansan of Trout Cave, West Virginia, on the basis of vertebral ratios. The ratio of the greatest length through the zygapophyses divided into the greatest width through the posterior zygapophyses is .65 in the Saltville *C. alleganiensis* and .56-.65, mean .602, in 18 specimens of modern *C. alleganiensis.* This ratio was .69 in the single available vertebra of *C. guildayi.*

The Hellbender occurs in the area today, and is found usually in rivers and large streams where shelter is available in the form of large rocks, snags, or debris.

Family Salamandridae

Notophthalmus cf. *N. viridescens* (Rafinesque), Eastern Newt

Material. — Five trunk vertebrae: USNM 404723, from Unit W3, SV-1; USNM 404724, from Unit W3, SV-1; USNM 404725, from Unit W3, SV-2; USNM 404726, from Unit W3, SV-1; and USNM 404727 (Fig. 4), from Unit W3, SV-1. One femur: USNM 404728, from Unit W3, SV-2. One humerus: USNM 404729, from Unit W3, SV-1.

Remarks. — The vertebrae of the genus *Notophthalmus* have a quite characteristic high, posteriorly thickened, posteriorly divided neural spine. These vertebrae appear to be identical to those of the Eastern Newt, *Notophthalmus viridescens.* The femur and the humerus also show no differences from the modern species. The Eastern Newt occurs in the area today, and the habitat of the aquatic stage is ponds, lakes, marshes, ditches, and other quiet bodies of unpolluted water. The terrestrial stage usually hides under objects in forested areas, but at times individuals may be seen walking about in the open. We are unable to tell on the basis of osteological material whether the fossils represent the aquatic or the terrestrial stage.

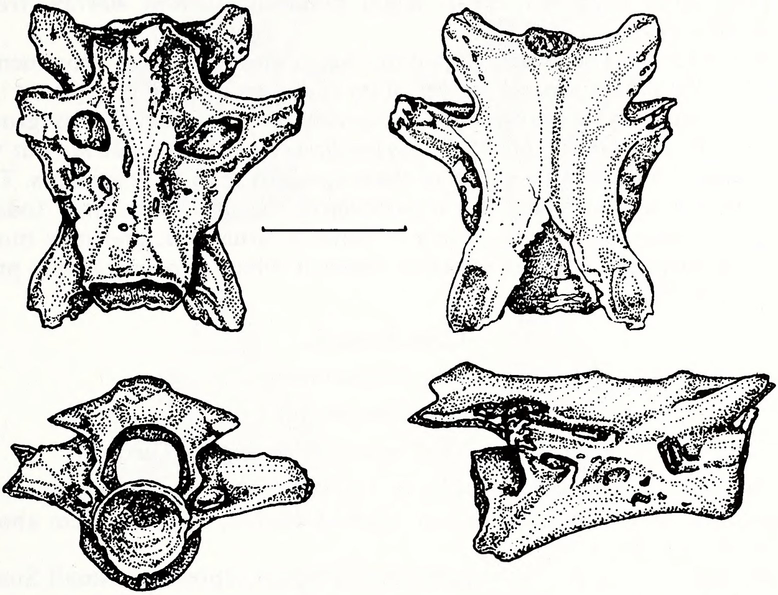

Fig. 3. Trunk vertebra of *Cryptobranchus alleganiensis* (Daudin) (USNM 404722) from Unit W2. Upper left, ventral; upper right, dorsal; lower left, posterior; lower right, lateral. Line equals 5 mm and applies to all drawings.

Order Anura

Family Bufonidae

Bufo woodhousei fowleri Hinckley, Fowler's Toad

Material. — Left ilium: USNM 404730, from near (ca. 4 cm above) base of Unit W1, SV-1. Two right ilia: USNM 404731, from Unit W2, SV-1; USNM 404732, from Unit W3, SV-2. Two tibiofibulae: USNM 404733, from Unit W3, SV-1; USNM 404734, from Unit W3, SV-1. Parasphenoid: USNM 404735, from Unit W2, SV-1.

Remarks. — Holman (1967) and Wilson (1975) discussed characters of the ilial prominence that allow separation of *Bufo woodhousei fowleri* from the morphologically similar *Bufo americanus. Bufo w. fowleri* is easily separated from its western counterpart *B. w. woodhousei* on the basis of the much higher dorsal protuberance in the latter subspecies. *Bufo w. fowleri* occurs in the area today, and occurs chiefly in sandy areas around shores of lakes, or in river valleys.

Family Ranidae

Rana pipiens group, sp. indet.

Material. — Right ilium: USNM 404736 (Fig. 5), from Unit W3, SV-2. Two left humeri: USNM 404737, from Unit W3, SV-1; USNM

404738, from Unit W3, SV-1. Right humerus: USNM 404739, from Unit W3, SV-1.

Remarks. — The small right ilium has a smooth vastus prominence and has the posterodorsal border of its ilial crest sloping gently into the dorsal acetabular expansion as in species of the *Rana pipiens* group such as *R. pipiens, R. blairi, R. berlandieri,* and *R. utricularia.* But we are unable to determine which of these species the ilium represents. The Southern Leopard Frog, *Rana utricularia,* occurs in the area today. This frog inhabits a wide variety of aquatic situations, and may move quite a distance from the water in summer where growing plants provide shade and shelter.

Class Reptilia

Order Testudines

Family Chelydridae

Chelydra serpentina (Linnaeus), Snapping Turtle

Material. — Partial nuchal bone: USNM 404740, from lowest part of Unit W2, SV-1. Scapulocoracoid: USNM 404741, from ca. 5 cm above base of Unit W1, SV-1.

Remarks. — These very characteristic bones represent a small Snapping Turtle. Preston (1979) gave some characteristics of chelydrid shell bones that allow identification of fragments. This species occurs in the area today. Snapping Turtles inhabit almost any body of water that is relatively slow moving and permanent (pers. observ.).

Family Testudinidae

Chrysemys picta Schneider, Painted Turtle

Material. — Third right costal: USNM 404721 (Fig. 6), from Unit W2 (?) or W4 (?), CSB-2A.

Remarks. — The smooth nature of the dorsal surface of this shell bone, and the position of the impression of the seam for the second epidermal shield, is diagnostic in *Chrysemys picta.* This turtle occurs in the area today and is an inhabitant of quiet, vegetation-choked bodies of water (pers. observ.).

Order Squamata

Family Colubridae

Elaphe cf. *E. obsoleta,* Rat Snake

Material. — Trunk vertebra: USNM 404742, from Unit W3, SV-2.

Remarks. — Auffenberg (1963) gave vertebral characters of *Elaphe obsoleta.* The above trunk vertebra is from a moderately large specimen. This snake occurs in the area today, and is a semiarboreal form that favors wooded areas and woodland edges (pers. observ.).

Nerodia sipedon (Linnaeus), Northern Water Snake

Material. — Trunk vertebra: USNM 404743, from Unit W3, SV-2.

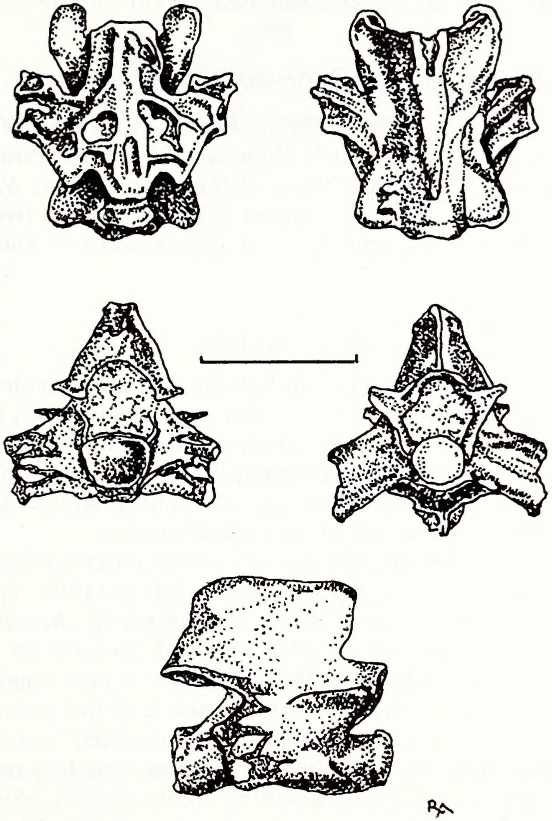

Fig. 4. Trunk vertebra of *Notophthalmus* cf. *N. viridescens* (Rafinesque) (USNM 404727) from Unit W3. Upper left, ventral; upper right, dorsal; middle left, posterior; middle right, anterior; bottom, lateral. Line equals 2 mm and applies to all drawings.

Remarks. — Holman (1967) gave vertebral characters that distinguish this species from others in the genus. The Northern Water Snake occurs in the area today and is found in many aquatic situations. Large populations are often to be found where protective shelters occur near aquatic situations (pers. observ.).

Storeria sp., Brown Snake or Red-bellied Snake

Material. — Trunk vertebra: USNM 404744,a from Unit W3, SV-1.

Remarks. — Holman and Winkler (in press) discuss the separation of isolated vertebrae of the closely related genera *Storeria* and *Virginia*. We are unable to separate the vertebrae of the two species of *Storeria*;

both *S. dekayi* and *S. occipitomaculata* occur in the Saltville area today.

Thamnophis sp., Gartersnake or Ribbonsnake

Material. — Trunk vertebra: USNM 404745, from Unit W3, SV-1.

Remarks. — Brattstrom (1967) showed that the vertebrae of *Thamnophis* are more elongate than those of the related genus *Nerodia.* It is almost impossible to separate isolated vertebrae of the two species of *Thamnophis* (*T. sauritus* and *T. sirtalis*) that occur in the vicinity of Saltville today.

DISCUSSION

The known herptile fauna from Saltville has been divided into three faunules on the basis of the depositional units from which the remains were recovered (Table 1). The taxonomic composition and chronology of these faunules can provide information about the duration of residency of the taxa, the depositional environment in which each was best sampled, and the microhabitat of the respective taxa.

Unit W3, the sorted stream channel bed load deposit found at SV-1 and SV-2, contained seven taxa including all identified specimens of *Notophthalmus* cf. *viridescens, Rana pipiens* group, *Nerodia sipedon, Thamnophis* sp., *Elaphe* cf. *E. obsoleta,* and *Storeria* sp. Only *Bufo woodhousei fowleri* is found in W3 and other depositional units. The stratigraphic nature of Unit W3—silts, sands, and fine gravels, ranging from well sorted and laminated deposits to "unsorted" masses (perhaps mixed biogenically, as by trampling by large mammals)—indicates that the member deposits were laid down by moderately to slowly moving water, perhaps through several cycles of rise and fall. Fluctuations in stream stage would have permitted periodic integration of the remains of terrestrial vertebrates into the stream bed load, especially those taxa that inhabited or periodically used the riparian zone. This might explain the presence of terrestrial taxa, including most of the snakes, in the fluvial deposits. The large amount of woody plant remains of uniform size ($\leq$ 50 mm) in Unit W3 at SV-2 strongly suggests fluvial sorting of "sediments" of terrestrial origin. Alternatively, semi-aquatic or avian predators or scavengers could have dropped the remains of terrestrial prey in or near the stream during feeding. The possibility that large mammals might have mixed units W2 and W3 at SV-1 while watering or feeding has been considered. However, in view of the fact that the composition of the herptile samples in Unit W3 at SV-1 and SV-2 is remarkably similar and that the composition of W2 and W3 at SV-1 are generally different, mixing of these two deposits must be considered unsubstantiated at present. The herptiles of Unit W3 may, therefore, be taken to represent a sampling of the Saltville Valley lotic and riparian herpetofauna as of ca. 14,500 to 14,000 B.P.

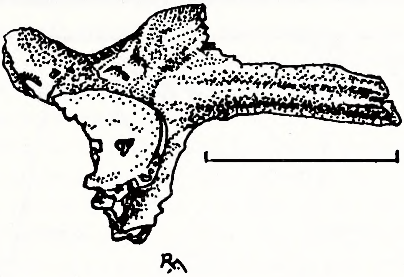

Fig. 5. Right ilium in lateral view of *Rana pipiens* group frog (USNM 404736) from Unit W3. Line equals 5 mm.

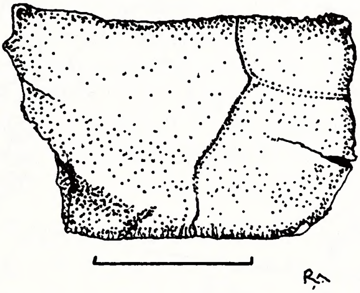

Fig. 6. Third right costal in dorsal view of *Chrysemys picta* Schneider (USNM 404721) from Unit W2 (?) or W4 (?). Line equals 10 mm.

Deposits associated with the early history of Lake Totten (ca. 14,000 to 12,000 B.P.) include ostracods, pelecypods, gastropods, fish, and mammal remains as well as those of *Cryptobranchus alleganiensis, Bufo woodhousei fowleri, Chelydra serpentina,* and (?) *Chrysemys picta.* Most of the aquatic fauna of Lake Totten probably was residual from that of the Saltville River, although the change in local hydrology caused a shift in the dominant taxa and altered the collecting bias of the depositional environment. The kinds of turtles represented are compatible with the postulated lake environment, and the remains of Fowler's Toad could easily have been deposited following death in or alongside the lake. The environmental implication of the Hellbender is more equivocal; it could have occupied a spring-fed brook entering Lake Totten near SV-1 (as does a small stream today), or it could represent feeding residue dropped by a predator or scavenger. The middle and upper parts of Unit W2 yield very few faunal remains. The reasons for this are unclear, but could include any or all of the following: change in water quality, water level fluctuation, and infilling of Lake Totten near SV-1.

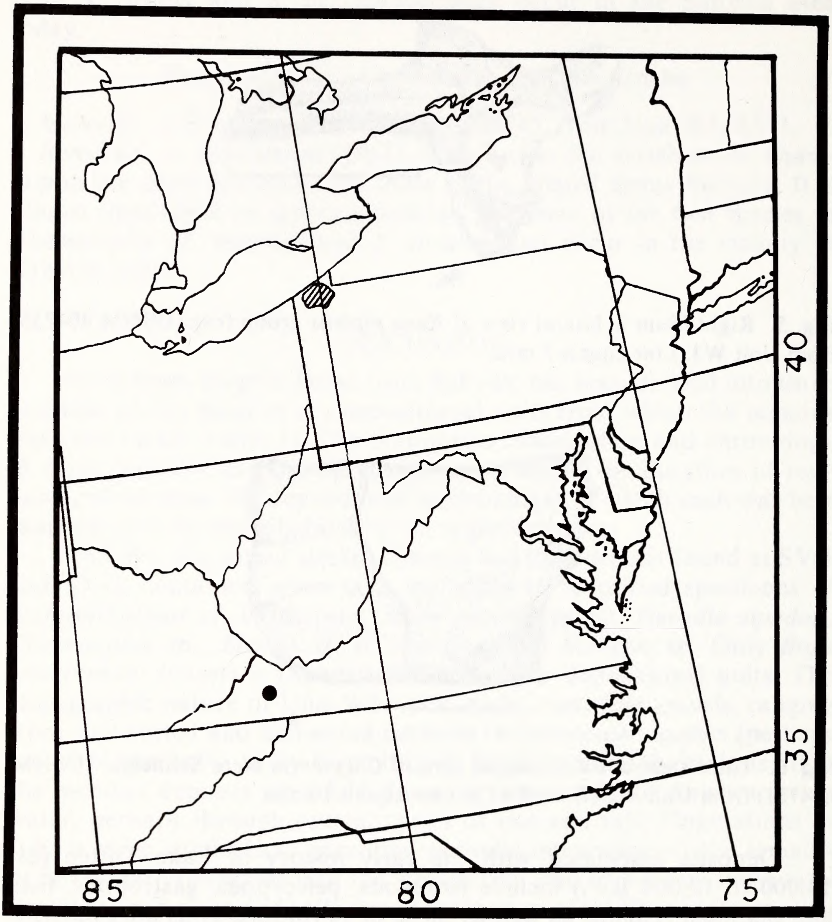

Fig. 7. Map showing the most northern area (crosshatched) where all members of the Saltville herpetofauna (dot) may be found living together today.

Unit W1, lying astride the Wisconsin-Holocene boundary (ca. 10,500 to 10,000 B.P.), consists of an organic-rich mud at SV-1 that contains remains of *Bufo woodhousei fowleri* and *Chelydra serpentina.* The boundary between W2 and W1 was distinct below where USNM 404730 and USNM 404741 were found, which suggests that these isolated remains were transported with the mud when—or deposited after—it moved, rather than being moved upward from the underlying lake deposit by bioturbation. Conceivably, the mud encompassing these specimens was a littoral deposit displaced by the downslope movement of a larger wasting mass from the adjacent hills. Because only two isolated bones were found, it is unlikely that the mud slide killed and buried the individuals from which these specimens came. Using this reasoning, both Fowler's Toad and the Snapping Turtle appear to have been present throughout the first 4,000 years of Lake Totten's history.

All of the herptile taxa present in the Saltville faunules can be found living in this area today. Based upon the presence of all 10 species in the herpetofauna in units W2 (lower) and W3, it is reasonable to conclude that this fauna has been in place for at least the last 13,500 to 15,000 years. Differences in the taxonomic composition of the faunules are probably attributable to microhabitat changes associated with hydrologic changes in the valley and to different sampling biases of the various depositional processes represented.

The most northern area where all members of the Saltville herpetofauna may be found living together today is in extreme northeastern Pennsylvania (Fig. 7) (Conant 1975: maps 3, 22, 99, 116, 119, 127, 149, 188, 198, 265, and 303). The Saltville herpetofauna, therefore, clearly is not a "Boreal" herpetofauna. Boreal temperatures as we know them today would not provide enough warm days for the eggs of *Chelydra serpentina, Chrysemys picta,* and *Elaphe* cf. *E. obsoleta* to hatch. The summers of ca. 15,000 to 14,000 B.P., and those since, must have been warm enough for the eggs of these species to hatch (cf. Stuart 1979).

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Discovery of *Noturus eleutherus, Noturus stigmosus,* and *Percina peltata* in West Virginia, with Discussions of Other Additions and Records of Fishes

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ABSTRACT.— Reports on several West Virginia fishes regarded as part of the state's ichthyofauna or known to inhabit certain drainages are ambiguous. Much of the information is unverifiable, unpublished, or erroneous, and makes preparation of state faunal and endangered species lists problematic. This paper discusses the addition of *Alosa sapidissima, Oncorhynchus nerka, Ctenopharyngodon idella, Notropis e. emiliae, Rhinichthys bowersi, Noturus eleutherus, N. stigmosus, Lepomis microlophus, Cycleptus elongatus, Percina gymnocephala, P. p. peltata, P. shumardi, Cottus cognatus,* and *C. girardi* to the state checklist. Problem data are also qualified for *Ichthyomyzon unicuspis, Lampetra appendix, Hybognathus nuchalis, Notropis dorsalis, Minytrema melanops, Noturus gyrinus, Etheostoma m. maculatum,* and *E. tippecanoe.* Verifiable or reliable records are documented for all the fishes concerned.

West Virginia waters, which include drainages from both sides of the Appalachian divide, contain a fairly unique and diverse ichthyofauna (Denoncourt et al. 1975). Although often analyzed as part of several drainages (Denoncourt et al. 1975, Jenkins et al. 1972, Stauffer et al. 1982), the fishes are most easily discussed as constituents of four distinct river systems (Miles 1971, Cincotta and Miles 1982). These are the Potomac and James rivers of the Atlantic slope, and the greater Ohio and New rivers of the Mississippi basin. The New River, technically the upper Kanawha River (Ohio River drainage), is usually regarded as a separate drainage because of its unique faunal assemblage (Addair 1944, Jenkins et al. 1972, Stauffer et al. 1982).

Historically, literature pertaining to the fishes of the state was meager and not readily available. The basis for information was dependent on the surveys of Osburn (1901), Goldsborough and Clark

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(1908), and Addair (1944). Raney (1947) and Raney and Seaman (1950, cited in Denoncourt et al. 1975) consolidated West Virginia fishery data by discussing the known and expected fauna based on the literature, numerous collections by the West Virginia Conservation Commission, personal sampling, unpublished information, and museum specimens (particularly the re-examination of Goldsborough and Clark's materials). These two checklists, which were designed as the basis for a Conservation Commission sponsorsed book dedicated to the state ichthyofauna (E. A. Seaman, pers. comm.; Anon. 1947), remained internal documents and were not widely disseminated. Unfortunately, the proposed publication was not completed.

Subsequent to E. C. Raney and E. A. Seaman's efforts and prior to 1970, numerous surveys were conducted in the state. The majority were performed by the Conservation Comission (e.g., W.Va. Wildl. Resour. Div. unpubl. records, Van Meter 1952, Menendez and Robinson 1964, Ross and Lewis 1969) and by F. J. Schwartz (e.g., *in* Core 1959; Schwartz 1958a, 1959, 1962, 1967). However, most of these data were unverifiable or unpublished. Following this period, several species were added to state faunal and drainage checklists (Miles 1971; Jenkins et al. 1972; Denoncourt et al. 1975; Stauffer et al. 1978, 1982), but were usually reported in an ambiguous manner. Although the works of Hambrick et al. (1973), Hocutt et al. (1978, 1979; in review), Stauffer et al. (1975, 1980; in press), Hardman et al. (1981), and Cincotta and Hoeft (in press) and certain systematic species reviews (e.g., Denoncourt 1969, Gilbert 1969, Jenkins 1970) clarify much data, distributional information is lacking for several species and drainages.

The purpose of this paper is to add fourteen species to the state faunal list and to clarify several ambiguous fish records. These data were compiled primarily during the preparation of Cincotta and Miles (1982, i.e., revision of Miles 1971), thus reference to this document is omitted.

MATERIALS AND METHODS

The following species accounts are based on verifiable or reliable data. Confirmation of ambiguous data for discussed species was made via literature review, personal communications with regional investigators, inspection of museum specimens, and examination of unpublished records of the West Virginia Department of Natural Resources, Wildlife Resources Division (WVWR; formerly the Conservation Commission, Fisheries Management Division). Materials from Cornell University (CU), Kentucky Department of Fish and Wildlife Resources (KFW), University of Louisville (UL), University of Michigan Museum of Zoology (UMMZ), Ohio State University (OSU), and National Museum of

Natural History (USNM) were used. Data regarding WVWR records and their deposition in the Department of Natural Resources fish museum at Elkins, are summarized in Table 1. Common and scientific names are from Robins et al. (1980).

ADDITIONS TO WEST VIRGINIA CHECKLIST

The following accounts discuss the addition of fourteen species to the West Virginia ichthyofauna, based on the checklist of Denoncourt et al. (1975). These additions are the result of recent collecting (*Noturus eleutherus, Noturus stigmosus, Lepomis microlophus, Percina peltata, Percina schumardi*), recent introduction (*Ctenopharyngodon idella*), data oversights (*Alosa sapidissima, Oncorhynchus nerka, Notropis emiliae, Cycleptus elongatus, Cottus cognatus*), description (*Percina gymnocephala*), and resurrection (*Rhinichthys bowersi, Cottus girardi*). Each species discussion is arranged in the order of listing in Robins et al. (1980), with emphasis given to those species collected by WVWR personnel (Table 1).

The data presented herein, combined with the addition of *Ammocrypta asprella* (Cincotta and Hoeft, in press) and the deletion of *Percina phoxocephala* (Hendricks et al. 1979; Thompson 1980; Stauffer et al., in press) and *Notorus gyrinus* (discussed in next section), increase the total number of West Virginia species to 164. It should be noted, however, that first West Virginia occurrence records reported by Pearson and Krumholz (1984) for *Lepisosteus platostomus, Notropis boops, N. heterolepis, Erimyzon sucetta, Fundulus notatus,* and *Etheostoma spectabile* were not treated here. These unverified data (W. D. Pearson, pers. comm.) are suspect, based on the information of Trautman (1981), Cooper (1983), and WVWR (unpubl. records). Attempts to verify much of this information by one of the authors (DAC) resulted in either redeterminations of incorrectly identified fishes or the inability to acquire voucher specimens.

Alosa sapidissima (Wilson), American shad

This anadromous clupeid is indigenous to Atlantic slope drainages of Canada and the United States (Burgess 1980). It was not reported as part of West Virginia's fauna by Goldsborough and Clark (1908), Raney (1947), Miles (1971), or Denoncourt et al. (1975). Although this shad is native to the lower Potomac River, it was introduced to the upper part (West Virginia and Maryland) of the drainage by the U.S. Fish Commission around the turn of the century (Kinney 1963). Omission of this species in past state checklists is attributed to either literature oversight or unsuccessful transplantation.

Oncorhynchus nerka (Walbaum), sockeye salmon

In North America, this species is native to Pacific slope drainages

Table 1. Summary of verifiable records for various West Virginia fish species collected by the West Virginia Department of Natural Resources, Wildlife Resources Division (WVWR).

Species	WVWR Cat. No.	Date	N	Location (Collector)
Ichthyomyzon unicuspis	113	28 Sept 1979	2	Ohio River at Gallipolis, Lock and Dam, near Henderson, Mason Co. (R. Miles, R. Preston)
	132	2 Oct 1980	1	Same as above
	153	10 Nov 1980	1	Ohio River at mouth Big Sandy River, Wayne Co. (M. Hoeft, C. Doerfer)
	228	1 Oct 1980	1	Ohio River at Racine Lock and Dam near New Haven, Mason Co. (R. Miles, R. Preston)
	390	15 Oct 1981	1	Ohio River adjacent 6th Street Bridge at Huntington, Cabell Co. (M. Hoeft, C. Doerfer)
Lampetra appendix	83	14 Apr 1977	1	Middle Island Creek at mouth Muddy Creek, Tyler Co. (R. Miles)
	388	6 Apr 1978	4	Middle Island Creek 8 km below confluence Muddy Creek, Tyler Co. (B. Dowler)
Rhinichthys bowersi	350	29 Sept 1980	2	19.3 km above confluence Monongahelia River, Mongalia/Marion Co. line (F. Jernejcic, D. Courtney).
Minytrema melanops	29	20 Sept 1976	5	Turkey Run at confluence Ohio River, Jackson Co. (B. Dowler, R. Miles)
	43	13 Sept 1977	15	Lee Creek 0.8 km above confluence Ohio River, Wood Co. (B. Dowler)
	50	3 Oct 1977	1	Tombleson Run 0.2 km above confluence Ohio River adjacent State Rt. 33, Mason Co. (S. Muth)
	87	20 Sept 1978	1	Ohio River at Hannibal Locks and Dam at New Martinsville, Wetzel Co. (R. Miles, R. Preston)

Noturus eleutherus	135	20 Apr 1979	1	Elk River at mouth King Shoals Run, Kanawha Co. (R. Miles, B. Pierce)
	278	16 Nov 1982	1	Elk River at mouth Jordan Creek near Falling Rock, Kanawha Co. (M. Hoeft, D. Cincotta, T. Oldham)
Noturus stigmosus	27	22 Sept 1976	2	Kanawha River at London Lock and Dam at London, Kanawha Co. (R. Miles, R. Preston)
	48	29 Sept 1977	1	Same as above
	336	7 Oct 1980	3	2.4 km below Matewan at railroad tunnel, Mingo Co. (M. Hoeft, F. Jernejcic, B. Dowler, D. Cincotta)
	352	5 Oct 1981	1	Kanawha River at London Lock and Dam at London, Kanawha Co. (M. Hoeft, D. Cincotta, T. Oldham)
Etheostoma m. maculatum	85	12 Oct 1978	3	Elk River 3.2 km above Bear Run, Webster Co. (R. Miles, B. Pierce)
Etheostoma tippicanoe	9	9 July 1976	28	Little Kanawha River at Newark, Wirt Co. (R. Miles)
	10	9 July 1976	12	Little Kanawha River at Sanoma low water bridge, Wirt Co. (R. Miles)
	11	9 July 1976	21	Little Kanawha River at mouth Nettle Run near Burning Spring, Wirt Co. (R. Miles)
	12	9 July 1976	18	Little Kanawha River at State Rt. 5 bridge, 1.9 km above Annamoriah, Calhoun Co. (R. Miles)
	13	6 Aug 1976	3	Little Kanawha River at Hattie, 1.5 km below Calhoun/Gilmer Co. line, Calhoun Co. (R. Miles)
	14	6 Aug 1976	9	Little Kanawha River 2.4 km above Big Bend at mouth Big Root Run, Calhoun Co. (R. Miles)
	278	16 Nov 1982	31	Elk River at mouth Jordan Creek near Falling Rock, Kanawha Co. (M. Hoeft, D. Cincotta, T. Oldham)
Percina gymnocephala	67	9 Aug 1977	2	Williams River of Gauley River 1.6 km below Webster Co. line (D. Phares)

Table 1. (Continued)

Species	WVWR Cat. No.	Date	N	Location (Collector)
	70	8 Aug 1977	1	Williams River of Gauley River, 0.2 km above State Rt. 17/4 bridge, Pocahontas Co. (D. Phares, R. Menendez)
	108	20 July 1978	3	Big Laurel Creek of Cherry River (Gauley River), 1.2 km above Jettsville, Greenbrier Co. (D. Phares, J. Reed)
	156	22 Aug 1978	1	West Fork Greenbrier River (New River) 18.8 km above mouth, Pocahontas Co. (D. Phares, T. Oldham)
Percina p. peltata	398	15 July 1977	1	Shenandoah River at Millville, 8 km above confluence Potomac River, Jefferson Co. (G. Lewis)
Percina shumardi	367	14 Oct 1980	1	Tombleson Run 0.2 km above confluence Ohio River adjacent State Rt. 33, Mason Co. (M. Hoeft, C. Doerfer)
Cottus cognatus	257	19 Aug 1975	10	Rocky Marsh Run 1.6 km N of State Rt. 45 or 4.8 km above confluence Potomac River, Berkeley/Jefferson Co. line (G. Lewis)
	256	8 June 1981	11	Turkey Run of Opequon Creek 0.2 km above Middleway, Jefferson Co. (G.Lewis)
Cottus girardi	345	18 Aug 1981	1	North Fork South Branch Potomac River 0.8 km above Grant Co. line, Pendleton Co. (D. Phares, T. Oldham, C. Heartwell)
	499	22 Aug 1983	2	Mill Creek of Patterson Creek 5 km west of Burlington at State Rt. 50 and 220 bridge, Mineral Co. (T. Oldham, D. Phares)

and has been stocked in numerous locations within the United States (Lee and Shute 1980). Although Kinney (1963) reported that "California and Pacific salmon" (species unknown) were stocked in the late 1800s in West Virginia waters (along with *Alosa sapidissima*), no salmon species have ever been included on past state ichthyofaunal checklists. Schwartz (*in* Jenkins et al. 1972), however, ambiguously indicated *O. nerka* in the Monongahela River drainage; this information is probably based on his Cheat River, West Virginia, record reported in Core (1959). During the 1950s the landlocked form of this species, the kokanee, was stocked by the WVWR in the Potomac (Stoney River Reservoir, Grant County; Cacapon Lake, Morgan County; Trout Pond, Hardy County), Monongahela (Spruce Knob Lake, Tucker County), and New (Watoga Lake, Pocahontas County) river drainages (Van Meter 1953). These records have probably been omitted from the state lists due to literature oversight or failure of the introductions.

Ctenopharyngodon idella Valenciennes, grass carp

This species, a native of China, has been introduced throughout the United States for aquatic vegetation control (Guillory 1980). Guillory gave two unconfirmed Kanawha River drainage records. WVWR Division personnel have verified the occurrence of this species in a Nicholas County pond, Gauley River drainage (B. F. Dowler, pers. comm.). Furthermore, some of the specimens from this introduction have supposedly been transferred to a pond in Wirt County, Little Kanawha River drainage. To date, there are no records of this species from lotic environments in the state.

Notropis emiliae emiliae (Hay), pugnose minnow

Gilbert and Bailey (1972) transferred this species from the monotypic genus *Oposopoeodus* to *Notropis* and recognized the subspecies *N. e. emiliae* and *N. e. peninsularis*. The latter form is endemic to the Florida peninsula, while the former is found in Lake Erie, Mississippi, and southern Atlantic slope and Gulf coast drainages. Trautman (1981) noted three lower Muskingum River records collected between 1901 and 1938 a few kilometers from the Ohio River, West Virginia (i.e., main channel). He further indicated that, since the species had not been recently collected from this area, it had been extirpated. Apparently, two records for this species have been overlooked in past reviews of the state fauna, as it is not included in previous publications. It was collected from Big Run, Wood County, in 1949 (Gilbert and Bailey 1972; CU 21054), and from Oldtown Creek, Mason County, in 1958 (UL 10523, unpubl. data of Krumholz et al. 1962; W. D. Pearson, pers. comm.). These data indicate the presence of this species in the upper Ohio River subsequent to the period discussed by Trautman (1981), and support his contention that it once was more widespread and common.

Notropis e. emiliae is either extirpated or extremely rare in the upper Ohio River, as there are no recent published records from West Virginia or Ohio.

Rhinichthys bowersi Goldsborough and Clark, Cheat minnow

This controversial form was originallly described as a species by Goldsborough and Clark (1908), but was subsequently identified as a *Nocomis micropogon* x *Rhinichthys cataractae* hybrid by Raney (1940). The distribution of this minnow appears restricted to Lake Erie and Monongahela River drainages (Hendricks et al. 1979; Stauffer et al. 1979). Although Stauffer et al. (1979) indicated that this form qualified morphometrically and meristically as a species, they could not conclusively decide its validity. Recent electrophoretic data indicate it is a true species (Goodfellow et al. 1984). In West Virginia, *R. bowersi* is rare to common in the eastern Monongahela River tributaries (Stauffer et al. 1979; Goodfellow et al. 1984). WVWR personnel recently collected two specimens from Whiteday Creek (Marion/Monongalia County; WVWR 350), which represents only the second time this minnow has been taken from western tributaries of the Monongahela River. C. H. Hocutt (pers. comm.) indicated that *R. bowersi* would be petitioned under provisions of the Endangered Species Act of 1973 as a threatened species.

Cycleptus elongatus (Lesueur), blue sucker

This sucker is usually found in the larger rivers of the Mississippi and Gulf slope drainages (Gilbert 1980a). In West Virginia, Trautman (1981) reported it in the main channel Ohio River. However, probably due to an absence of verifiable historical records (J. R. Stauffer, pers. comm.), Denoncourt et al. (1975) did not include the species on their state checklist. The authors, as did Pearson and Krumholz (1984), accepted the data of Trautman and recognize the species as part of the West Virginia ichthyofauna. Although this sucker has not been taken in numerous surveys in recent years on the West Virginia portion of the Ohio River (Trautman 1981, Preston and White 1978, WVWR unpubl. data), Trautman (1981) reported two records in Ohio near West Virginia. Additionally, a specimen may have been captured (unconfirmed) from the Ohio River adjacent to Hancock County, West Virginia, in 1981 (Pearson and Krumholz 1984). These records are possibly attributable to migrating fish from the lower river where the population is improving (W. L. Davis, pers. comm.; Pearson and Krumholz 1984).

Noturus eleutherus Jordan, mountain madtom

The mountain madtom is found sporadically in southcentral Mississippi River drainages within Oklahoma, Arkansas, and Missouri, and throughout the Ohio River to Pennsylvania (Taylor 1969, Rohde 1980b). In the vicinity of West Virginia, this madtom is known from the Levisa Fork of the Big Sandy River in Kentucky (Jenkins et al. 1972, Rohde

1980b, Stauffer et al. 1982, and from tributaries immediately adjacent the main channel Ohio River in Ohio (Trautman 1981). The mountain madtom may have been collected by Krumholz et al. (1962) from the main channel Ohio River of West Virginia, but the specimens assigned UL 11461 and 11617 are missing (W. D. Pearson, pers. comm.). On 20 April 1978 and 16 November 1982, the species was collected from two locations in lower Elk River (Kanawha River drainage) during seining surveys (WVWR 135 verified by Hocutt, 278 by Jenkins). These WVWR records represent the first verifiable evidence of *N. eleutherus* in the state, and a distributional record for the lower Kanawha River.

On each occasion, the mountain madtom was taken in swift riffles (ca. 50 cm depth) containing medium to large rubble. The river was ca. 30 m wide at both sites. Species associates common to both localities were: *Etheostoma blennioides, E. camurum, E. tippecanoe, E. variatum, E. zonale, Percina copelandi,* and *P. macrocephala.* Absence of *N. eleutherus* in past surveys is attributed to a lack of sampling in large rivers and their major tributaries.

Noturus stigmosus Taylor, northern madtom

Rohde (1980a) gave this madtom's range as tributaries of the Mississippi River from the western margin of Tennessee, northeastward throughout much of the Ohio River basin to the western edge of Pennsylvania; it also occurs within the western Lake Erie drainages in Ohio, Indiana, and Missouri. Relative to West Virginia, Clay (1975; KFW 1221) and Burr (1980) reported this species from the Levisa Fork of the Big Sandy River in Kentucky, Trautman (1981) reported it from the lower Muskingum River and a minor tributary near the main channel Ohio River in Ohio, and Cooper (1983) reported it from certain tributaries of the Allegheny River drainage in Pennsylvania. Denoncourt et al. (1975) expected it to occur within West Virginia waters. The following data represent the first verfication of the species in West Virginia (C. H. Hocutt, pers. comm.; Stauffer et al. 1982). Paucity of surveys from large rivers probably explains its exclusion from previous collections.

In 1976, 1977, and 1981 *N. stigmosus* was taken from the Kanawha River at London, West Virginia, during lock rotenone surveys (WVWR 27, 48, 352; first two verified by Hocutt). In addition, two specimens were collected from the same area in 1977 by Virginia Polytechnic Institute personnel (C. H. Hocutt, pers. comm.). On 7 October 1980 the fifth collection of this species occurred in Tug Fork River (Big Sandy drainage) during a rotenone survey near Matewan, Mingo County, West Virginia (WVWR 361). Species common to all WVWR samples were: *Notropis volucellus, Moxostoma anisurum, M. macrolepidotum, Ictalurus punctatus, Noturus flavus, Pylodictis olivaris, Micropterus punctulatus,* and *Percina caprodes.*

Taylor (1969) and Rohde (1980a) reported that in the Ohio River drainage *N. stigmosus* prefers large creeks and rivers with bottoms of shifting sand and mud, and water varying from clear to turbid with moderate current. The 0.85 hahabitat sampled in the Tug Fork consisted primarily of riffles with boulders (30%) and rubble (70%) and a long pool of primarily sand bottom. The water was turbid, and flows in the 30.48-m-wide channel were 4.8 to 5.9 cm/second. Water quality parameters recorded with a Hach kit at the time of the sampling were: pH (7.6), Fe (.18 mg/1), alkalinity (160 mg/1 as $CaCo_3$), conductivity (68 micromhos/cm), and water temperature (14.4 °C). This area of the river is known to experience repeated load violations regarding organic suspended solids (i.e., domestic sewage) and iron (Steele and McCoy 1980).

Lepomis microlophus (Günther), redear sunfish

Lee (1980) considered this species native to the Mississippi, southern Atlantic slope, and Gulf slope drainages from Florida to Texas. In the immediate vicinity of West Virginia, the redear sunfish was collected from the main channel Ohio River and the Big Sandy River in Kentucky (Clay 1975, Burr 1980, Lee 1980), and the Monongahela River in Pennsylvania (Jenkins et al. 1972, Lee 1980, Stauffer et al. 1982). Denoncourt et al. (1975) listed the redear sunfish as expected, but Miles (1971) regarded it as present in West Virginia based on WVWR records (Anon. 1950, Menendez and Robinson 1964). Other evidence supporting its existence in the state comes from the Ohio River sampling summary of Preston and White (1978; some *L. microlophus* specimens verified by M. L. Trautman, pers. comm.) and Trautman (1981). These authors found the species generally infrequent in its introduced range in the upper Ohio River.

Percina gymnocephala Beckham, Appalachia darter

This endemic upper Kanawha River species was recently described by Beckham (1980). He discussed its relationship to *P. maculata* and *P. peltata.* The Appalachia darter appears to be more closely aligned with *P. peltata*, which is confined to Atlantic slope drainages. *Percina gymnocephala* has been recently collected in West Virginia by Hocutt et al. (1978, 1979; in review), Stauffer et al. (1975, 1980), and WVWR (67, 70, 108, 156). These data indicate the species is widely distributed throughout the upper Kanawha River system in West Virginia, but is usually not abundant.

Percina peltata peltata (Stauffer), shield darter

This darter is known to inhabit streams of the Atlantic slope from New York to North Carolina (Malick 1980). Geographic variation in the species was reported in Raney and Suttkus (1948) as *P. p. peltata* from the James River, Virginia, to Hudson River, New York; as *P. peltata nevisense* from the Neuse and Tar rivers, North Carolina; and as *P. p.* subspp. from the upper Roanoke River. This percid was expected to occur in the West Virginia part of the Potomac and James rivers by Raney (1947) and Denoncourt et al. (1975). Stauffer et al. (1978) indicated that it was not known in the upper Potomac River west of the Blue Ridge divide. On 15 July 1977 a single specimen of the shield darter was collected from the Shenandoah River, West Virginia, during a boat electrofishing survey (WVWR 398, verified by Jenkins). This capture represents an upstream distribution record, and an addition to the Shenandoah River (R. E. Jenkins, pers. comm.) and West Virginia fauna. Other species taken concurrently were: *Anguilla rostrata, Cyprinus carpio, Catostomus commersoni, Hypentelium nigricans, Moxostoma* sp., *Ictalurus punctatus, Lepomis auritus, L. gibbosus, L. macrochirus, Micropterus dolomieui,* and *M. salmoides.* The inability of past investigators to collect *P. p. peltata* in the Potomac River, West Virginia, suggests that it is either extremely rare or restricted to large-river habitat.

Percina shumardi (Girard), river darter

Gilbert (1980b) indicated that the river darter is broadly distributed throughout the Gulf slope, Mississippi basin, Lake Huron, Lake Erie, and Hudson Bay drainages of North America. It is sporadically distributed and rare in the Ohio River basin, especially in the middle and upper reaches of the main channel (Trautman 1981, Clay 1975, Smith 1979, Burr 1980). Trautman (1957) reported it from only a few Ohio localities in the Ohio River drainage. He indicated it was definitely known from the Ohio River proper before 1900, and depicted three records (two in West Virginia) from this period. No new records in West Virginia were noted by Trautman (1981). Although Miles (1971) listed the species as known in the state, Raney (1947) and Denoncourt et al. (1975) reported it as an expected species (probably due to the absence of verifiable specimens). On 14 October 1980, one specimen of the river darter was found in a rotenone sample of an Ohio River backwater area (WVWR 367, verified by R. M. Bailey). This record represents the first report in over 80 years of *P. shumardi* in the Ohio River, West Virginia. In 1981 another individual was collected from the Ohio River adjacent to Mason County, West Virginia, by personnel of Geo-Marine Inc. (J. A. Pfeiffer, pers. comm.; specimen verified by Pearson).

Cottus cognatus Richardson, slimy sculpin

This sculpin is broadly distributed in Canada and the northern United States. It is found in certain drainages west of the Rocky Mountains, the Great Lakes basin, and the north and central Atlantic slope

(Wallace et al. 1980). Its southeastern range limit is the Potomac-Shenandoah drainage (R. E. Jenkins, pers. comm.), and the taxonomic status of this Potomac River population is uncertain. Strauss (1980) said that the Potomac River population represents an undescribed endemic species, genetically similar to *Cottus girardi* but morphometrically similar to *C. bairdi.* However, Jenkins (pers. comm.) indicates it may only be a subspecies of *cognatus.* For the purpose of this paper, the Potomac River population is recognized as *Cottus cognatus.*

Until 1975, the slimy sculpin was regarded as part of the West Virginia fauna by Raney (1947), Hubbs and Lagler (1958), and Miles (1971). Denoncourt et al. (1975) altered the occurrence status to anticipated because of the absence of verifiable specimens (J. R. Stauffer, pers. comm.). The only published West Virginia record of this cottid was recently reported ambiguously by Wallace et al. (1980). This information, which may be in error (R. L. Wallace, pers. comm.), is probably based on a missing UMMZ collection (75426) taken from South Branch Potomac River in 1939. Apparently the first records of this species in West Virginia were overlooked, as in 1909 E. L. Goldsborough collected it from two locations in the Opequon Creek drainage of the Potomac River, Berkeley County (USNM 64591, 64593; R. E. Strauss, pers. comm.). The only other records of this fish in the state were taken in 1975 and 1981 by WVWR personnel from two streams in Jefferson County, West Virginia (WVWR 256, 257, verified by Jenkins). Species common to both locations were *Rhinichthys atratulus, Semotilus margarita,* and *Catostomus commersoni.* Absence of *C. cognatus* from numerous past collections in the West Virginia part of the Potomac River suggests a sparse distribution or confusion with *Cottus bairdi* or *C. girardi.*

Cottus girardi Robins, Potomac sculpin

This species is currently known only from the Potomac, James, and Susquehanna river drainages of the Atlantic slope (Strauss 1977). Although originally described and aligned to the *carolinae* species group by Robins (1961), Savage (1962) considered it synonymous with *Cottus bairdi.* Its taxonomic status remained controversial (Jenkins et al. 1972, Mathews et al. 1978, Stauffer et al. 1978) until resurrected by Strauss (1977) and Mathews (1980). It may be fairly common in the upper Potomac River tributaries as suggested by data of Mathews et al. (1978), Jenkins et al. (1980), Goodfellow and Lebo (1981), and Cincotta et al. (ms.). The WVWR has only two verifiable records of this species to date (WVWR 345, 499, former verified by Jenkins).

AMBIGUOUS RECORDS

The first attempt to document fishes of West Virginia was made by Goldsborough and Clark (1908), but most of their data were collected from small waters. It was not until the extensive Kanawha River work of Addair (1944) and the annotated checklist of Raney (1947) that the occurrence and distribution of many species was generally understood. Although the recent drainage surveys by Hocutt et al. (1978, 1979; in review), Stauffer et al. (1975, 1980; in press), and Hardman et al. (1981) resulted in significant contributions in this regard, information relative to several species is lacking. Investigators have encountered difficulty in preparing state nongame or "endangered species" documents because much information relative to West Virginia's ichthyofauna is ambiguous, unverifiable, and/or unpublished. This section discusses the status of several species that are uncommon either statewide or in a particular drainage. New information collected by WVWR is noted (Table 1).

Ichthyomyzon unicuspis Hubbs and Trautman, silver lamprey

This parasitic lamprey is found in the Mississippi basin, primarily from Tennessee northward to the Great Lakes, St. Lawrence and Hudson Bay drainages (Rohde and Lanteigne-Courchene 1980). It was not reported from West Virginia drainages by Raney (1947), Schwartz (1958b), Jenkins et al. (1972), or Stauffer et al. (1982); but Miles (1971), Denoncourt et al. (1975), and Stauffer (pers. comm.) considered it native on the basis of unpublished WVWR records. The earliest West Virginia record for the silver lamprey was that reported from the main channel Ohio River by Trautman (1957, OSU 11657). This record appears to have been overlooked by past investigators, probably due to the nearness of the site to the boundaries of Kentucky, Ohio, and West Virginia. Verifiable specimens have since been taken from four Ohio River locations (WVWR 113, 132, 153, 228, 390). These data suggest that the silver lamprey population in the upper Ohio River is increasing, rather than decreasing as theorized by Trautman (1981).

Lampetra appendix (DeKay), American brook lamprey

Lampetra appendix (= *lamottei*) is a nonparasitic lamprey of the subgenus *Lethenteron.* It is known from the Great Lakes and Atlantic slope drainages from Minnesota to Virginia, and throughout the middle and upper sections of the Mississippi River basin (Rohde 1980c). Raney (1947) reported this species in the state on the basis of the Monongahela River record of Gribble (1939). Rohde (1980c) did not show the American brook lamprey in West Virginia, but indicated occurrence in the Ohio River drainage of Kentucky, Ohio, Pennsylvania, and New York. The species was noted as native to only the Little Kanawha River by Jenkins et al. (1972) and Stauffer et al. (1982). Stauffer (pers. comm.) indicated that there are no confirmable specimens from state waters. WVWR personnel recently collected *L. appendix* from Middle Island Creek of the Ohio River drainage (WVWR 83, 388). The WVWR vouchers and an uncatalogued Little Kanawha River specimen at the

USNM (F. C. Rohde, pers. comm.) are the only verifiable records of this lamprey from West Virginia.

Hybognathus nuchalis Agassiz, Mississippi silvery minnow

Pflieger (1980) indicated that *H. nuchalis* contains three nominal subspecies of uncertain relationships that probably qualify for specific designations due to their morphological distinctiveness and allopatric ranges. The two forms whose ranges encompass West Virginia are *H. n. nuchalis,* of the Mississippi River and Mobile Bay drainages, and *H. n. regius,* of the Lake Ontario, St. Lawrence, and Atlantic slope drainages south to Altamaha River, Georgia (Pflieger 1980). Lee et al. (1980) and Robins et al. (1980) recognized the specific distinctiveness of *H. regius* (see Hubbs and Lagler 1958 for characters). To date, there are no published records of *Hybognathus regius* from West Virginia (C. H. Hocutt, pers. comm.; Pflieger 1980). *Hybognathus nuchalis* was apparently first collected from the state in 1888 from the mouth of the Big Sandy River, Wayne County (Everman 1918). Raney (1947) confirmed the only other silvery minnow record from the Monongahela River drainage, based on a specimen misidentified as *Notropis whipplei* by Goldsborough and Clark (1908). The exclusion of these records in Jenkins et al. (1972), Pflieger (1980), and Stauffer et al. (1978, 1982) is attributed to either oversight or absence of verifiable materials. Absence of *H. nuchalis* from recent collections from the upper Ohio River drainages (Preston and White 1978, Trautman 1981) and *H. regius* from the upper Potomac River drainages (Mathews et al. 1978; Stauffer et al. 1978; Goodfellow and Lebo 1981; Cincotta et al., in ms.) suggests that both are either rare in or extirpated from these waters. Trautman (1957) attributed the silvery minnow's extirpation from Ohio to turbidity and siltation.

Notropis dorsalis (Agassiz), bigmouth shiner

The bigmouth shiner is found primarily in the upper Mississippi and Great Lakes (excluding Lake Huron) drainages (Gilbert and Burgess 1980a). It is discontinuously distributed in the eastern part of its range. Prior to Gilbert and Burgess (1980a), only Schwartz (*in* Jenkins et al. 1972) and Denoncourt et al. (1975) indicated its presence in West Virginia. Schwartz regarded the species native to the Little Kanawha River, but a lack of verifiable specimens led C. R. Gilbert (pers. comm.) and Stauffer et al. (1982) to doubt this assumption. Gilbert and Burgess (1980a) indicated a single Monongahela River drainage record for West Virginia (UMMZ 198279, Tygart River, collected and identified by C. L. Hubbs and M. B. Trautman). Omission of this shiner from past literature on the Monongahela River is attributed to the obscurity of the record. *Notropis dorsalis* is probably extirpated from the state, as it has not been collected since 1932.

Minytrema melanops (Rafinesque), spotted sucker

This sucker is known from the lower Great Lakes (Erie, Huron and Michigan), throughout the Mississippi, and from the Gulf slope and southern Atlantic coastal basins (Gilbert and Burgess 1980b). Jenkins et al. (1972), Stauffer et al. (1978), and Hendricks et al. (1979) originally considered this species native to the Monogahela River drainage based on the Youghiogheny River record of Schwartz (1964), but the validity of this record is now questioned since no verifiable specimens exist (Gilbert and Burgess 1980b, Stauffer et al. 1982). The spotted sucker was confirmed in the West Virginia section of this basin by Raney (1947), based on a specimen misidentified as *Moxostoma macrolepidotum* by Goldsborough and Clark (1908). Although these data support the record of Schwartz (1964), *M. melanops* has not been recently collected from the Monongahela River drainage. This sucker is still common in other Ohio River drainages of West Virginia (e.g., WVWR 29, 43, 50, 87).

Noturus gyrinus (Mitchell), tadpole madtom

The tadpole madtom is found throughout the Mississippi, Gulf coast, and Atlantic slope (including Great Lakes) drainages of North America (Rohde 1980d). Although it is widely distributed in Ohio (Trautman 1981) and is reported in the lower Potomac and James rivers (Stauffer et al. 1982), this species has never been verified from West Virginia waters. Raney (1947) anticipated its occurrence in West Virginia, but Miles (1971) and Denoncourt et al. (1975) listed the species as part of the fauna. This madtom may have been collected from the main channel Ohio River of West Virginia by Krumholz et al. (1962), but no specimens are extant (W. D. Pearson, pers. comm.). The closest records of this species to West Virginia are those of Trautman (1981), only a few kilometers from the state border. Owing to the absence of confirmable records, C. H. Hocutt (pers. comm.) presently regards these species as expected to occur in the state.

Etheostoma maculatum maculatum Kirtland, spotted darter

Zorach and Raney (1967) reviewed the systematics and distribution of the three recognized subspecies that are restricted to the Ohio River drainage: *E. m. maculatum*, *E. m. sanguifluum*, and *E. m. vulneratum* Etnier (1980) noted that the nominate form exhibited a disjunct distribution pattern in the Ohio River basin from New York to Kentucky. Schwartz (*in* Jenkins et al. 1972) reported *E. m. maculatum* from lower Kanawha River (below Kanawha Falls), but did not substantiate the record. Based on these unverifiable data the species was listed as part of West Virginia's fauna (Miles 1971, Denoncourt et al. 1975). In 1978, WVWR personnel collected three spotted darters in a rotenone sample on the Elk River (Kanawha River drainage; WVWR 85). These specimens represent the only verifiable occurrence of this species from West Virginia (J. R. Stauffer, pers. comm.), and this record is depicted in the distributional review of Etnier (1980).

Etheostoma tippecanoe Jordan and Everman, Tippecanoe darter

This species is restricted to the Ohio River basin, where it is broadly but discontinuously distributed (Zorach 1969). It was first collected in West Virginia by WVWR personnel (unpubl. data, verified by Schwartz) in 1966 from Little Kanawha River and later in the same year by Schwartz from Elk River. Although these two unpublished records were overlooked by Zorach (1969), Schwartz ambiguously reported both in Jenkins et al. (1972). Hocutt (1980) depicted records for this percid in the state, but did not include detailed data. WVWR data (WVWR 9, 10, 11, 12, 13, 14, 278) suggest that the species, which is considered generally rare within its range (Kuehne and Barbour 1983), is common in the Little Kanawha and lower Elk rivers.

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The Pre-Pliocene Tennessee River and Its Bearing on Crawfish Distribution (Decapoda: Cambaridae)

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ABSTRACT.— Recent demand for fossil fuels has provided opportunities for extensive and detailed examination of surface and subsurface unfossiliferous clastic deposits of the Coastal Plain of the Gulf of Mexico. Among the new discoveries is an ancient outlet directly into the Gulf for the upper Tennessee River more than once during mid- and late Tertiary times. Also discovered is evidence that the intrusion of the Mississippi Embayment apparently occurred much later than implied by surface outcrops in Mississippi and Alabama. Many Cambaridae distribution patterns show close associations with these Tertiary deposits; included are *Cambarellus*, *Fallicambarus*, *Faxonella*, *Hobbseus*, *Procambarus* (*Acucauda*), *P.* (*Girardiella*), *P.* (*Leconticambarus*), *P.* (*Pennides*), and *P.* (*Scapulicambarus*). Some possible interpretations relating to these distributions are discussed, as is the pattern of *Orconectes* and *Cambarus* invasion. Much detailed study is badly needed, and potentially fruitful areas for investigation are indicated.

The earliest attempts to explain the population of North America by cambarid crawfishes were based on the assumption of a Mexican epicenter, from which the major groups radiated to invade the United States and Canada, east of the continental divide. This was probably best articulated by Ortmann (1905). Subsequently, however, Hobbs has presented a cogent and compelling series of arguments in favor of an origin in the southeastern United States (1958, 1962a, 1967, 1969, 1981, 1984; Hobbs and Barr 1972). Probably his best statements appeared in his treatment of the Pictus Group of *Procambarus* (1958) and his masterly analysis of *Cambarus* (1969). He continued his strong contentions in a monograph of Georgia species (1981) and an analysis of the distribution of *Procambarus* (1984).

Although a detailed analysis of phylogenetic relationships is inappropriate here, it does seem worthwhile to review some of the major trends. Most of these are based on Hobbs. A *Procambarus*-like ancestor is generally accepted, and indeed no one has taken issue with Hobbs's contention that the Pictus Group of the subgenus *Ortmannicus*, of all extant species, is most like the ancestral form (1958). He has, however, recently (1981, 1984) added that certain members of the subgenus *Pennides* are among the most primitive. Although he has somewhat revised his concepts of relationships (1972, 1981, 1984), Hobbs has retained

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much of the phylogeny of *Procambarus* that he expressed in his review of the Blandingii Section (1962a). Two of his "Groups" in that paper were elevated to subgenera in 1972, with the remaining species of the Section being assigned to the subgenus *Ortmannicus*. It is important to reemphasize in this paper that certain members of the subgenus *Pennides* (formerly the Spiculifer Group of the Blandingii Section) possess many of the "primitive" characters assigned to the "ancestral procambarid" (multiple cervical spines; short, broad areola; strongly acuminate rostrum; "striped saddle" pattern of coloration; male first pleopod with full complement of terminal elements, those elements relatively simply constructed; etc.). One must likewise keep in mind that in the Cambaridae the male and female organs associated with sperm transfer are the most—and sometimes only—reliable taxonomic characters; one can develop good concepts of initial (i.e., early) plesiomorphies in other characters/structures, but they are all subject to considerable convergence or modification in response to environmental habits, making determination of synapomorphies nearly impossible.

Considerable data are accumulating to indicate that the "upper Tennessee" river had independent access to the Gulf of Mexico at least as recently as the early Pliocene. This new interpretation does not refute the phylogeny of the Cambaridae accepted by the more recent workers, but it does require reexamination of temporal assignments for events. Certain zoogeographic confusions are partially resolved. Alternate explanations to those currently accepted are proposed to (1) account for the distribution of the early-emerging Cambarellinae, (2) elucidate the existence of "primitive forms" of the subgenera *Pennides* and *Ortmannicus* of *Procambarus* in their present geographic distribution, (3) suggest the origin of the subgenus *Scapulicambarus* as being in lower Georgia in pre-Miocene times, (4) propose that the spread of the genus *Fallicambarus* east of the Mississippi River is post-Miocene, (5) place the origin of the genus *Faxonella* in central Louisiana during the Eocene, (6) identify the origin of the genus *Hobbseus* as eastcentral Mississippi during the Eocene, and (7) suggest pre-Eocene origins for the genera *Orconectes* and *Cambarus*, with their spread into the area of the Mississippi Embayment occurring only relatively late in geologic time.

PHYLETIC AND ZOOGEOGRAPHIC OVERVIEW

The genera *Barbicambarus*, *Cambarus*, *Distocambarus*, *Fallicambarus*, *Faxonella*, *Hobbseus*, *Orconectes*, and *Troglocambarus* have been demonstrated to be derivatives of the ancestral procambarid (Hobbs 1967, 1969, 1981). Hobbs, however, did not visualize a more or less lineal descent with a simple cladistic dichotomy. Instead, he postulated radiate evolution in which some *Procambarus*, principally eastern species, arose at one level of the tree and diversified, and a second, somewhat later in time, series of diversifications in one of the stem stocks organized around an adorconectoid stock. (Mexican diversity, especially interesting to a zoogeographer, is outside the realm of this treatment.) From the former (earlier) populations we see today members of the subgenera *Capillicambarus*, *Hagenides*, *Lonnbergius*, *Ortmannicus*, *Pennides*, *Scapulicambarus*, *Tenuicambarus*, and *Villalobosus*, plus the genus *Troglocambarus*.

From the adorconectoid line (later temporally), stocks developed that culminate in the procambarid subgenera *Acucauda*, *Austrocambarus*, *Girardiella*, *Leconticambarus*, *Mexicambarus*, *Paracambarus*, *Procambarus*, and *Remoticambarus*, plus the genera *Barbicambarus*, *Cambarus*, *Distocambarus*, *Fallicambarus*, *Faxonella*, *Hobbseus*, and *Orconectes*. One of the more striking features of the latter assembly is that, except for *Cambarus* and *Distocambarus*, geographically they are more or less western (in relation to the proposed center of origin of the cambarines). Although not a complete "family tree" for the Cambaridae, Figure 11 of Hobbs's Georgia monograph (1981) is adequate to demonstrate his ideas. He does not visualize polyphyletic origins; instead, he sees the non-procambarid genera as widely divergent stocks that originated from divers stocks of *Procambarus*. (The groupings as I have made them fundamentally rest on Hobbs, as I have cited him; but if they prove to be non-congruent to his concepts, the fault is entirely misinterpretation on my part.) This latter adorconectoid line seemed to be the less conservative of the two main *Procambarus* stocks, as evidenced by the extremes—recognized as genera—of apomorphies developing in it.

Another early divergence from the cambarine-procambarid stock resulted in the monogeneric Cambarellinae. Hobbs' last lengthy discussion of this phylogeny (1969) was concerned with establishing the relationships between the Cambarinae and the Cambaroidinae, taking for granted an understanding of the close association of the former and the Cambarellinae. More recently, Fitzpatrick (1983) addressed the infrageneric relationships of the members of *Cambarellus* and tried to establish their phylogenetic affinities with other Cambaridae. The dwarf crawfishes are also basically western in distribution.

The determination of these lineages did not, however, afford non-moot concepts and explanations of current distributions. Indeed there are many enigmas and paradoxes. Among these are the geographic ranges of those *Cambarellus* most like the ancestral form, and an explanation of why the culminations of an early offshoot of cambarine evolution would be excluded from the proposed ancestral home. Yet they seem to be highly competitive and successful against advanced (and therefore, competitively selected) members of groups that emerged at a later date (Penn and Fitzpatrick 1962, 1963).

Members of the subgenus *Pennides* have many characters attributable to the "ancestral procambarid": a full complement of simple terminal elements on the male pleopod; multiple carapace spines; a short, broad areola; the shape of the rostrum, chela, carapace and pereiopodal coxae; and color pattern. In the subgenus there are two principal assemblages, not formally recognized by Hobbs (1972). In one group, a full complement of terminal elements is present on the gonopod; in the other (*gibbus*, *raneyi*, *spiculifer*) the cephalic process is absent; in *P.* (*Pe.*) *ouachitae* Penn the cephalic process is also sometimes absent.

I am not sure that Hobbs would still believe that *P.* (*Pe.*) *vioscai* Penn is the most "primitive" extant species of the subgenus, but there is no doubt that a reduction in terminal elements is apomorphic. Of the three species so disposed, all are found in the most eastern part of the range of the subgenus, while species with a full complement of terminal elements also found in that part of the range have quite specialized pleopods and annuli ventrales (Fig. 1). The more generalized species are found from Mississippi westward.

Populations of *P.* (*Pe.*) *ouachitae* (or siblings) occur allopatrically in Arkansas and Mississippi. This species seems to be morphologically intermediate between species with the full-complement of terminal elements and those with a short-complement. Further, the populations of *P.* (*Pe.*) *vioscai* that occur east of the Mississippi River have a much more modified cephalic process than those west of the river. They are sufficiently different that work I have in progress will probably result in my proposing subspecies categories for the two forms. The siblings, *P.* (*Pe.*) *penni* Hobbs and *P.* (*Pe.*) *clemmeri* Hobbs, are so distributed that the more eastern form is also the more remote (from the ancestral type) form (Fitzpatrick 1977a). The entire picture suggests an invasion of the lower Gulf Coastal Plain by an early offshoot of *Procambarus* stock, and subsequent reinvasion of the southeastern United States along corridors located near the present coastline (Fig. 2).

Except for the nearly unique subgenus *Lacunicambarus*, which Hobbs (1969:163) believed to have been "one of the earliest branching stocks," *Cambarus* is represented in the central Gulf area only by *C.* (*Depressicambarus*) *striatus* Hay. Bouchard (1978) assigned this species to the superspecific assemblage he considered the more advanced, yet one must remember that Hobbs (1969) believed *Depressicambarus* to represent a moderately early digression in cambarid evolution. Hobbs (1969:169) conceded that his proposed dispersal corridors to this region, especially for *Lacunicambarus*, are tenuous.

The representatives of *Orconectes* in the area are all members of specialized and advanced Virilis and Palmeri Groups. Except for *Fallicambarus fodiens* (Cottle) and *F. uhleri* (Faxon), all members of that genus occur on the Gulf Coastal Plain or in reasonable proximity to its central and western parts. Further, the most primitive species lie in southwestern Louisiana and southwestern Arkansas, "probably not far from the ancestral home of the genus" (Hobbs 1969:124). The most "primitive" *Faxonella*, *Fx. creaseri* Walls, is found in northcentral Louisiana, while *Hobbseus* is confined to the middle and upper Tombigbee

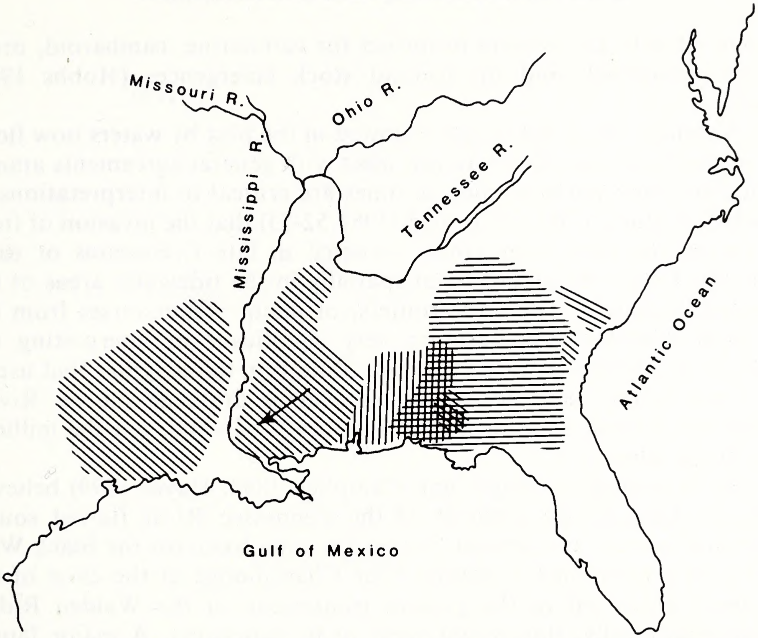

Fig. 1. Distribution of *Procambarus* (*Pennides*). Arrow designates route of proposed "Miocene Tennessee River." Diagonal rulings = cephalic process present; horizontal rulings = cephalic process absent; vertical rulings = *P.* (*Pe.*) *versutus*.

River drainage (proper) and the upper part of the Pearl River drainage (Fitzpatrick 1977b). Clearly, then, considerable diversity of cambarine crawfishes seems to have originated in a secondary center associated with the lower reaches of the Mississippi River and its environs, markedly distant from the "southeastern" primary center envisioned by Hobbs (loc. cit.). An enigma of how the several populations became established there presents itself. Since this is not a taxonomic paper, it seems improper to continue a discussion of detailed relationships; besides, Hobbs (1967, 1969, 1981, 1984) has explained well our current knowledge of phylogenies. Instead, I propose to examine geographic and geologic information, particularly some recently collected data, which could assist in resolving some of the apparent paradoxes of crawfish distribution.

GEOLOGIC CONSIDERATIONS

Classical thinking by crawfish workers (and many others) establishes a thesis that, during some pre-Pleistocene period, the upper and lower portions of the Tennessee River were separate. Faunal comparisons certainly seem to indicate this. The upper basin is more intimately associated with the centers proposed for cambarine, cambaroid, orconectoid, graciloid, and mexicanoid stock emergences (Hobbs 1981, 1984).

Although the exact routes followed in the past by waters now flowing in the Tennessee River do not meet with general agreements among geologists, their paths at specific times are critical to interpretations of crawfish evolution. Hobbs argued (1981:52-53) that the invasion of fresh waters by the cambarine stock occurred in late Cretaceous or early Cenozoic times. He placed them spatially in the tidewater areas of the extreme Southeast. Thus, the route(s) of major watercourses from the southern Appalachians becomes very significant in interpreting the invasion of North America. It is important, too, to recognize that use of the word "river" here designates a basin or drainage source. Rivers themselves have lives measured in thousands of years, not the millions of geologic times.

Some geologists (Hayes and Campbell 1894, Hayes 1899) believed that the Appalachian segment of the Tennessee River flowed southwestward through the present Coosa-Alabama basin (or the Black Warrior). They envisioned a capture near Chattanooga at the close of the Tertiary, which led to the present transection of the Walden Ridge. Zoogeographically, this would seem to be supported. A major faunal break seems to be associated with the Walden Gorge.

Some geologists (Johnson 1905, Wright 1936) believed otherwise. They insisted that the present route of the Tennessee River has existed at least since the Schooley (dissection of the peneplain ending probably in the Miocene). The geological evidence to support this thesis is of equal strength as that supporting the one of Hayes and some subsequent authors. The Tennessee remains a difficult problem. A good review is in Thornbury (1965:124-126).

Sedimentary analysis of Mississippi "Eocene" deposits by Grim (1936), however, provided compelling data to indicate the delta of a sizeable river in eastcentral Mississippi. The Midway alluvial deposits (Paleocene) (Fig. 3) indicate that a significant river had a delta in the vicinity of the Chickasaw-Clay counties area near the juncture of the Porter's Creek and Clayton formations. The succeeding Wilcox deposits (early Eocene) (Fig. 4) demonstrate the continuance of this river into the Choctaw-Montgomery-Webster counties area. Grim (p. 208) attributed both the Midway and Wilcox deposits to a "complex of ancient rocks located in the present Piedmont Plateau." The Claiborne deposits (mid-Eocene), in contrast, suggest that "many streams" (p. 214) rather than one contributed to them. Similarly, the post-Claiborne Jackson Formation (late Eocene) indicates the major "Appalachian [= Tennessee] River" was not a controlling depositional factor in Mississippi.

Brown (1967) was concerned over an apparent inconsistency of the major streams of southern Mississippi. Contrary to other Recent drainage patterns, they flow at a decided angle to the dip and strike of the

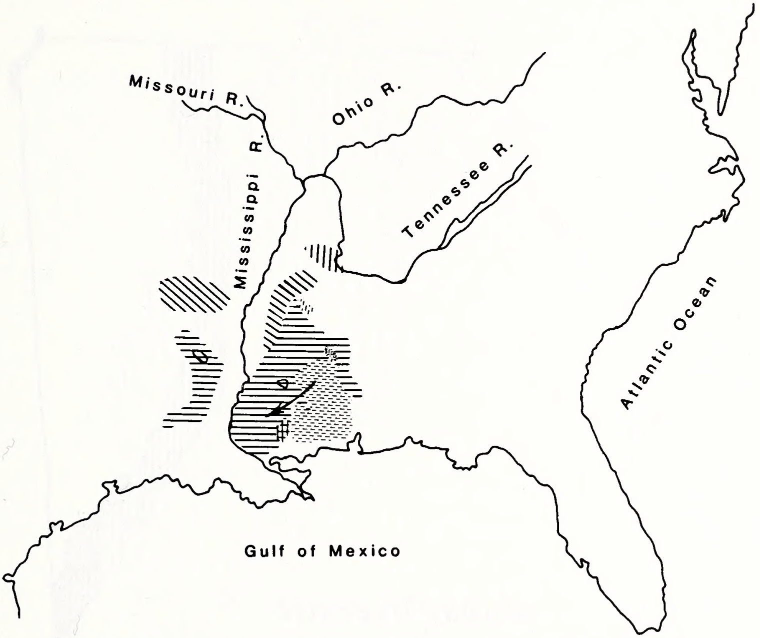

Fig. 2. Distribution of western species of *Procambarus* (*Pennides*). Arrow as in Figure 1. Solid vertical rulings = *P.* (*Pe.*) *ablusus*; broken vertical rulings = *P.* (*Pe.*) *lylei*; solid horizontal rulings = *P.* (*Pe.*) *ouachitae*; broken horizontal rulings = *P.* (*Pe.*) *clemmeri*; cross-hatching = *P.* (*Pe.*) *penni*; stippling = *P.* (*Pe.*) *lagniappe*; enclosed by open circles (2) = *P.* (*Pe.*) *elegans*.

"Miocene" belt. Northeast trending fluvial ridges, which form a drainage divide, readily explain the disparity (Fig. 5). The underlying deposits that defend the ridges are mapped as Citronelle Formation (Pliocene-Pleistocene). (It should be noted that many geologists question the accuracy of equating the Mississippi-Alabama Citronelle with the formation of the same name farther to the east in Florida and to the west in Louisiana.) Brown's analysis of the gravels led him to postulate the existence of a "very large river flowing southwestward" (p. 82), the gravels forming a part of that river's bed.

New studies, using different and more modern techniques, have helped resolve some of these problems. An important aspect of contemporary geology, especially along the Gulf Coastal Plain, is the greatly expanded search for fossil fuels. Geologists are no longer confined to outcrops as sources of stratigraphic data. Indeed, the economic considerations of the petroleum industry have mandated an intensive study of subsurface formations and expanded drilling activities. The masses of new information have transformed the study of the Coastal Plain into a rapidly evolving, incessantly refined activity. Along with this have come many reevaluations of the relationships between stratigraphic series,

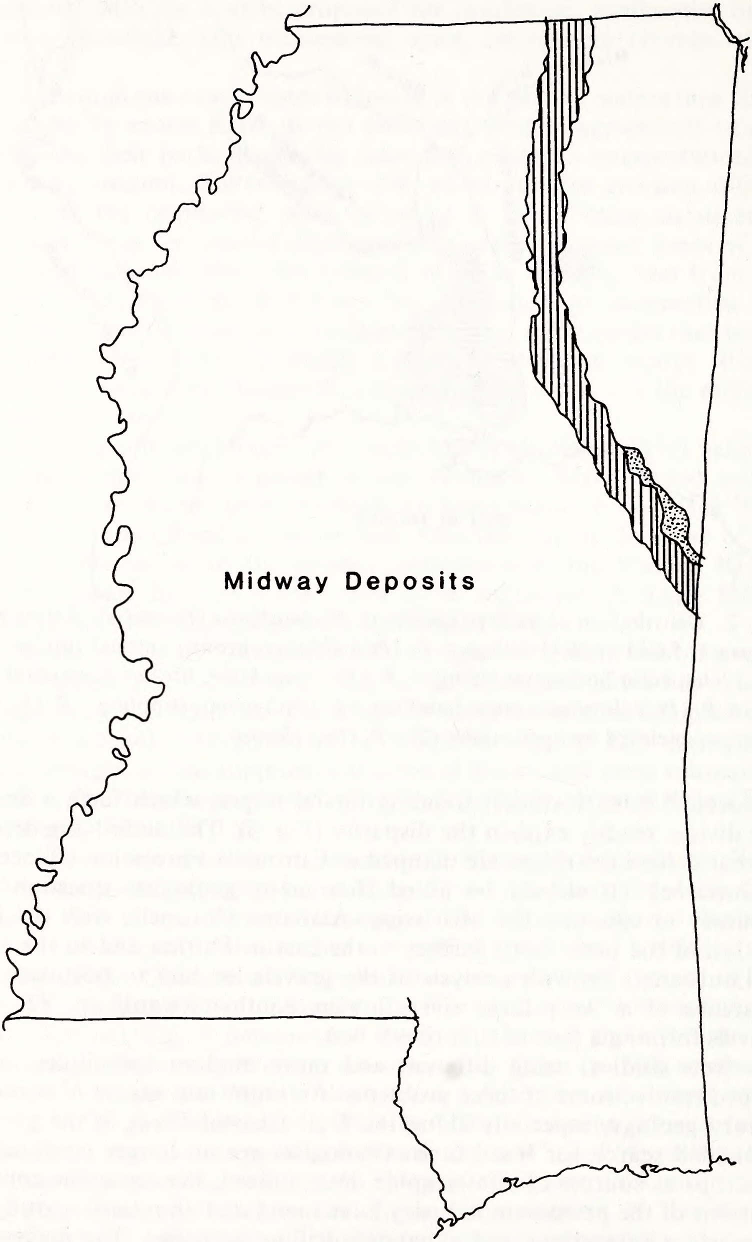

Fig. 3. Midway deposits in Mississippi. (Redrawn from Grim 1936.) Vertical rulings = Porter's Creek Formation; stippling = Clayton Formation.

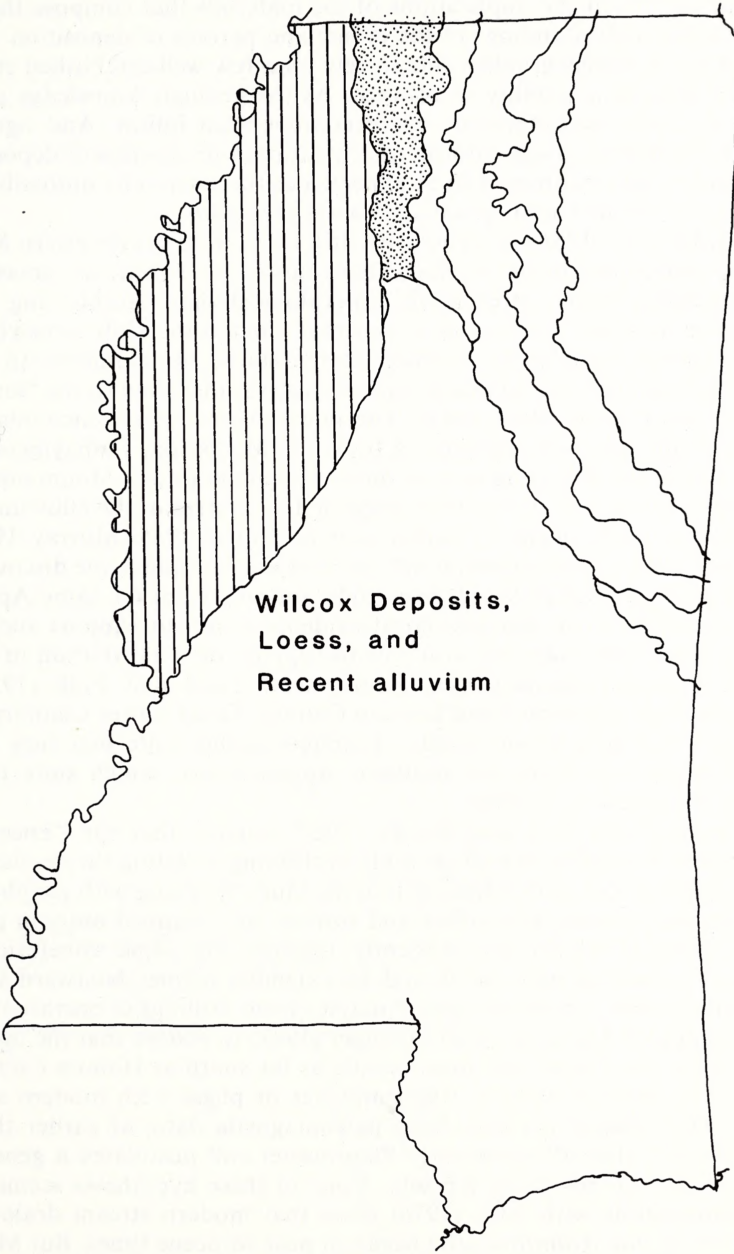

Fig. 4. Wilcox, loess, and river alluvium in Mississippi. (Redrawn from Grim 1936). Vertical rulings = recent river alluvium; stippling = loess, loam, gravel, etc.; other lines delimit the several formations of the Wilcox deposit.

interpretations of the implications of the materials that compose them, and clearer understandings of the events and periods of deposition. No longer is the zoogeographer able to rely on a few well-established studies and assume a stability of concept. As the geologic knowledge progresses, so the zoogeographic interpretations must follow. And significant modification of age, stratigraphic relationships, sources of deposits, and biological responses is to be expected as the essentially unfossiliferous clastics of the Gulf Coastal alluvia are examined.

Isphording (1981), working with drill cores from southwestern Mississippi and especially in the Hattiesburg Formation (Miocene), amassed considerable, nearly irrefutable mineralogical data establishing the existence in Miocene times of a river that entered the Gulf somewhere near Hattiesburg (Fig. 6). Further, these data tie the sediments to the eastern Piedmont and southern Appalachians rather than to the "local" source areas (Isphording 1983). The mineralogical suites encountered are incompatible with weathering from the Mississippi Embayment to the north of the collecting sites or the more remote Rocky Mountains or Central Interior, which had been suggested as sources of the alluvium of the central Embayment by earlier writers (Storm 1945, Murray 1955, MacNeil 1966). Such a river, if not the Tennessee, requires the discovery of yet another river of equal magnitude draining from the same Appalachian source area. No geological evidence exists to support such a thesis. Even more data are available to support the contribution of the southern Appalachians to the Embayment. Todd and Folk (1957), working with sediments from Bastrop County, Texas (lower Claiborne), reported that they encountered a kyanite-saurolite suite that they felt could come only from the southern Appalachians, which suite they called "diagnostic" (p. 2560).

Isphording (1981) and Brown (1967) implied that the "Eocene" deposits of Grim (1936) were possibly misleading in dating the demise of the last Tennessee outlet directly into the Gulf. Working with geophysical logs and clastics, subsurface and surface, and mapped outcrop patterns, May (1981:29) independently reached the same conclusions: "Miocene outcrop patterns should be extended further landward into the Embayment," in Mississippi. Analyses from drillings in northcentral Mississippi led Murphey and Grissinger (1981) to believe that the materials under the Pleistocene loess mantle as far south as Holmes County suggest an erosion surface, frequently out of phase with modern surfaces. They placed the age, from paleomagnetic data, at earlier than 700,000 B.P. (late Pliocene-early Pleistocene) and postulated a general "Citronelle" age for these deposits. None of these hypotheses seems to be incompatible with Alt's (1974) ideas that modern stream drainage patterns (*on the Atlantic coast*) began in post-Miocene times. But Murphey and Grissinger's (1981) conclusions indicated clearly that modern drainage patterns in the upper Embayment are unreliable indicators of history before the late Pleistocene.

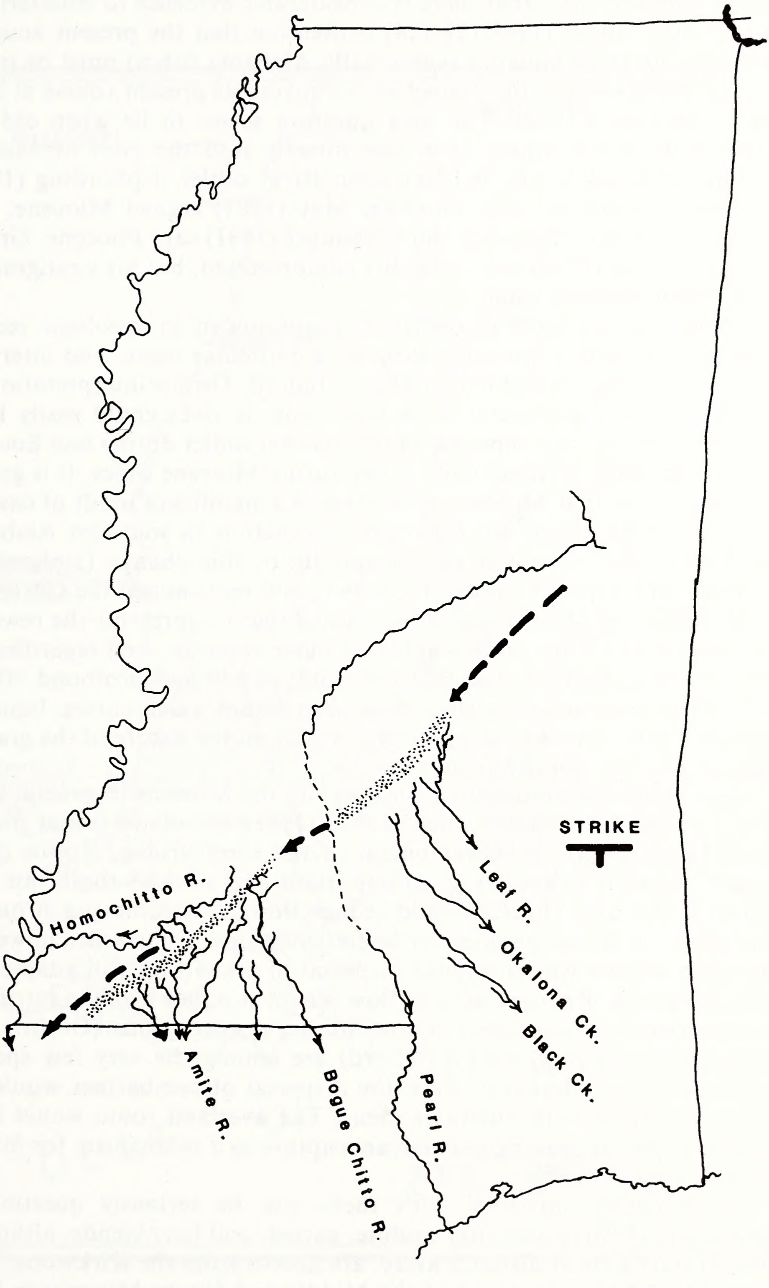

Fig. 5. Proposed Miocene "Tennessee River." (After Brown 1967.) Stippling = gravel-defended ridges; broken arrows = proposed route of river.

It appears, then, that there is considerable evidence to counterindicate Smith-Vaniz's (1968:122-124) contention that the present zoogeographic pattern of aquatics (specifically Alabama fishes) must be interpreted on the basis of the Tennessee occupying its present course at least since Cretaceous times. The only question seems to be when did the connection of the upper Tennessee directly into the Gulf of Mexico become replaced by the indirect Ohio River outlet. Isphording (1981) claimed Miocene or early Pliocene; May (1981) argued Miocene; and Brown (1967) and Murphey and Grissinger (1981) said Pliocene. Grim's Eocene datings (1936) seem possibly compromised, but his stratigraphic relationships remain valid.

Equally, one must recognize that nothing in the geologic record requires continuous discharge through a particular basin, and intermittent flow remains a viable hypothesis. Indeed, Grim's interpretation of Claiborne sediments seems to indicate this. A river could easily have accounted for Grim's deposits, found another outlet during late Eocene, and reestablished a direct Gulf outlet during Miocene times. It is generally recognized that Miocene is the date of a significant uplift of eastern North America. Even the Citronelle Formation in southern Alabama exhibits a "tilt" to reflect the magnitude of this change (Isphording, pers. comm.). Isphording and Flowers (1980) reexamined the Citronelle in Alabama and Mississippi and suggested that it represents the reworking, largely as a result of this uplift, of older deposits. And regardless of precise interpretations, the Miocene uplift surely had profound effects on the directions and flow rates of the then-extant watercourses. Equally, the uplift would have had significant impact on the nature of the gravels and patterns of their deposition.

Alt's (1974) opinions on drainages and the Miocene in general were given considerable weight when Hobbs (1981) speculated about phylogeny. In reviewing the development of the Cambaridae, Hobbs overlooked, possibly deliberately, an important part of Alt's thesis: an arid Miocene. An arid climate would reduce flow of streams and promote emergence of forms adapted to lentic situations. Contrarily, however, the same climate would impede dispersal of crawfishes still adapted to lotic situations. Reduced stream flow would produce a saline intrusion into estuaries. *Procambarus* (*Ortmannicus*) *acutus acutus* (Girard) and *P.* (*Scapulicambarus*) *clarkii* (Girard) are among the very few species with any saline tolerances; thus, the dispersal of cambarines would be effectively blocked in tidewater areas. The overland route would likewise be impaired, leaving only stream capture as a mechanism for invading new river systems.

Fortunately, however, Alt's thesis can be seriously questioned. Isphording (1970) noted that epidote, garnet, and hornblende, although present only a short distance away, are absent from the Kirkwood Formation and Cohansey Sand of the Middle and Upper Miocene in New Jersey. Otherwise, he found that the remaining heavy mineral species,

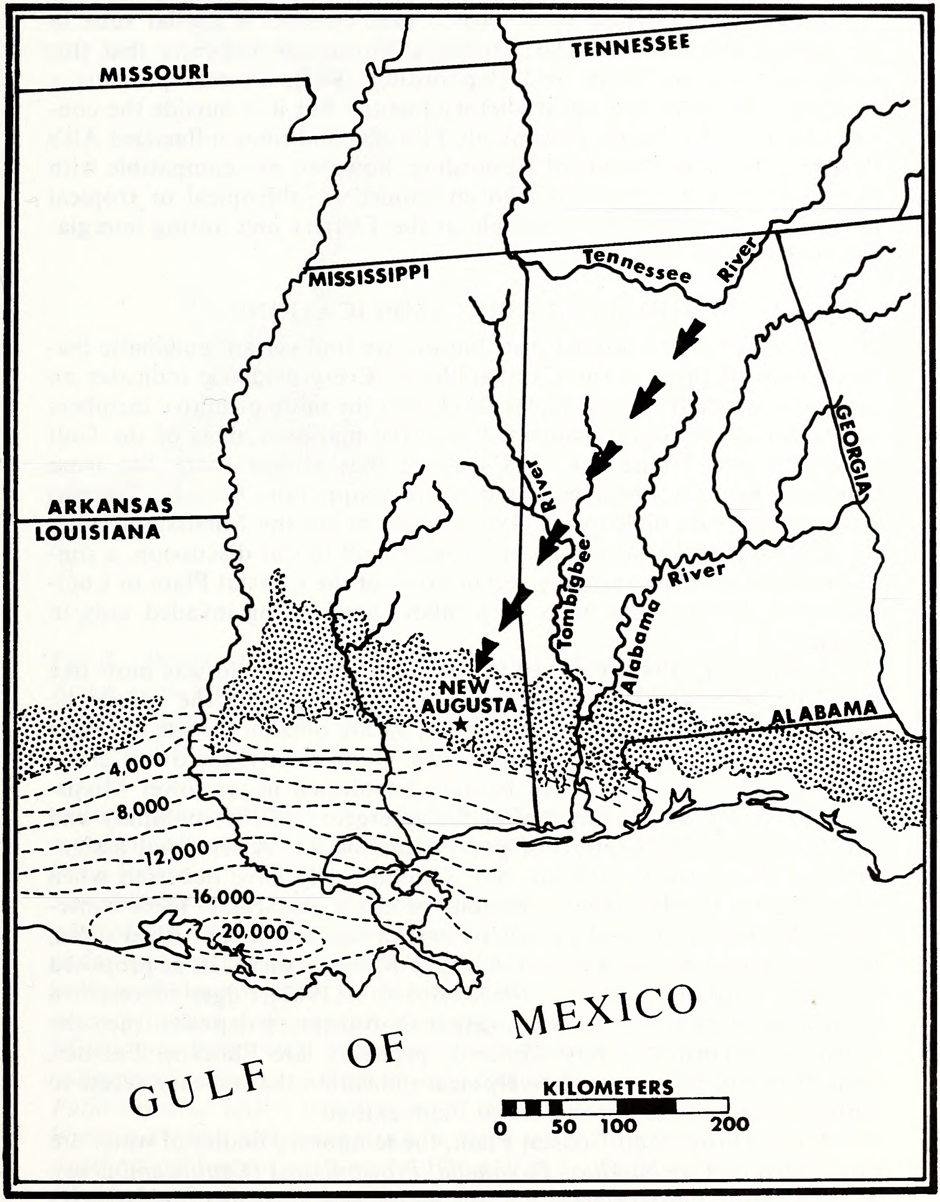

Fig. 6. " 'Ancestral' Tennessee River" (arrows) of Isphording (1983). (Reproduction of his Fig. 10, p. 303.) Stippling delimits Miocene outcrop.

less susceptible to weathering, were present in expected amounts. This, plus other mineralogical considerations, led to an hypothesis that the period was characterized by a warm, moist climate. A similar suite in the comparable Pascagoula-Hattiesburg Formation indicates that this area, too, was far from arid (Isphording 1983). Florida presents a somewhat different and contradictory picture, but it is outside the considerations of this paper; presumably Florida conditions influenced Alt's thinking. The conclusions of Isphording, however, are compatible with the position of Dorf (1960) who envisioned a subtropical or tropical climate on the Gulf Coast throughout the Tertiary and during interglacial stages of the Pleistocene.

ZOOGEOGRAPHIC IMPLICATIONS

Turning now to animal distribution, we find certain enigmatic features. One of these is the Cambarellinae. Every evidence indicates an early divergence from cambarine stock. Yet the more primitive members of the genus are found associated with the marginal areas of the Gulf Coastal Plain. Fitzpatrick (1983) noted that almost every site from which the genus has been collected in Mississippi (and Florida/Georgia) is south and east of Brown's (1967) ridges or on the Mississippi River flood plain (Fig. 7). Although not as pertinent to this discussion, a similar restriction to geologically recent areas of the Coastal Plain in Louisiana and Texas exists, with deep inland areas being invaded only in Mexico.

Fitzpatrick (1983) believed the ancestral cambarellid was most like *Cambarellus puer* Hobbs and its relatives; but among the species he considered as candidates for this status, all are outside the site of origin for the Cambaridae proposed by Hobbs. Quite clearly, the dwarf crawfishes arose from a stock that became established in the lower Mississippi River lowlands shortly after the emergence of the subfamily and before much diversification of populations began. A temporal assignment of this event is difficult, but it could easily have occurred when proposed by Hobbs (late Cretaceous or early Cenozoic). Their subsequent diversification and expansion east of the Mississippi River delta, however, could not have occurred before Miocene times. If, as proposed by Isphording and Flowers (1983), Brown's (1967) ridges represent a reworking of Miocene deposits, rather than primary deposits, then the eastward expansion is post-Miocene, probably late Pliocene. Further, their distributions give a relatively clear indication that no easy access to lentic habitats of the upper Coastal Plain existed.

On the lower Gulf Coastal Plain, the temporary bodies of water are dominated by *Cambarellus*, *Faxonella*, *Procambarus* (*Capillicambarus*), *P.* (*Scapulicambarus*) *clarkii*, and the ubiquitous, probably multi-species taxon, *P.* (*Ortmannicus*) *acutus acutus*. All are tertiary burrowers. They are complemented, often sympatrically, by primary burrowers of *Fallicambarus*, *Cambarus* (*Lacunicambarus*), *Procambarus* (*Acucauda*), and *P.* (*Hagenides*). The upper Coastal Plain and inland areas have an

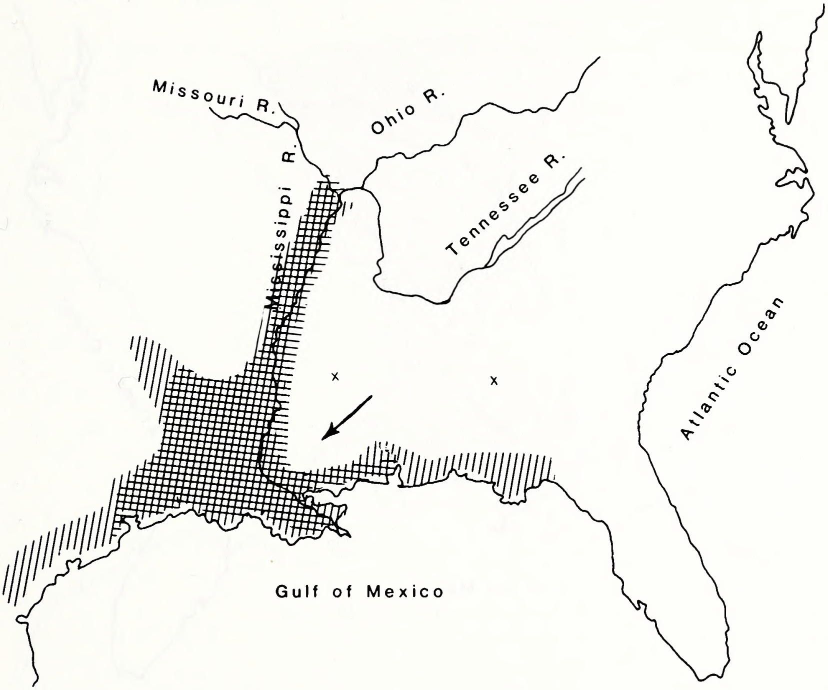

Fig. 7. Distribution of non-Mexican *Cambarellus*. (After Fitzpatrick 1983.) Arrow as in Figure 1. Horizontal ruling = subgenus *Dirigicambarus*; vertical rulings = subgenus *Pandicambarus*; crosses indicate small allopatric, probably introduced, populations of *Cs.* (*D.*) *shufeldtii*.

entirely different fauna in these habitats, and the latter two faunae are more closely related to each other than either is to the lower Coastal Plain species.

Procambarus (*Capillicambarus*) and most of *Fallicambarus* are west of the area in question. *Procambarus* (*C.*) *hinei* (Ortmann) occurs as far east as the Florida Parishes of Louisiana, but most of the distribution of the subgenus is in Louisiana and Texas. The range of the more primitive *Fallicambarus* suggests origin of the genus west of the Mississippi River with expansion from there. *Fallicambarus fodiens* is widespread, occurring from lower Ontario to Arkansas and Alabama. *Fallicambarus uhleri* is a species of the Atlantic Coastal Plain, and *F. hortoni* Hobbs and Fitzpatrick is apparently of restricted distribution north of the lower Gulf Coastal Plain (Fig. 8). *Fallicambarus hedgpethi* (Hobbs) scarcely crosses to the east bank of the Mississippi River above the delta region, but it can be found in relatively recent deposits all the way to southwestern Georgia. The latter species and *F. fodiens* require thorough taxonomic study before firm conclusions about their distributions can be made.

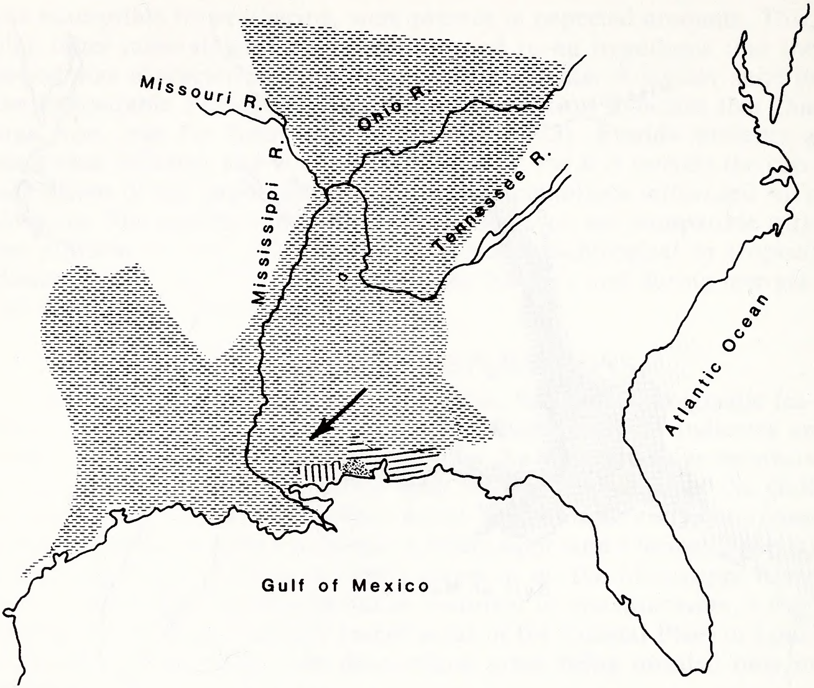

Fig. 8. Distribution of *Fallicambarus* (excluding *F. uhleri*). Arrow as in Figure 1. Horizontal rulings = *F. byersi*; vertical rulings = *F. oryktes*; stippling = *F. danielae*; enclosed by open circle = *F. hortoni*.

Fallicambarus oryktes (Penn and Marlow) is found in the Florida Parishes of Louisiana and along the Mississippi coast. Its eastern limits abut the western limits of the morphologically and ecologically distinctive *F. byersi* (Hobbs). The latter taxon probably represents more than one species, but this does not interfere with the geographic interpretations; the populations occur as far east as the Yellow River basin in Florida. As does *F. oryktes*, it (they) occurs in the immediate vicinity of the coast, rarely penetrating more than 100 km inland. *Fallicambarus danielae* Hobbs is similarly distributed, but apparently it is geographically sympatric with the respective extremes of the two earlier-mentioned species in the central part of the coast. Thus, the spread of these taxa seems to be an event of the late Pliocene or early Pleistocene (Fig. 8). I am not prepared here to discuss the factors that led to establishment of other species of the genus, except to note that the genus and at least some species probably are the result of pre-Pliocene events.

Faxonella probably began in the environs of central Louisiana, where one finds the greatest diversity and the apparently most primitive forms. Indeed, only *Fx. clypeata* (Hay) is widely distributed, and it is found restricted to post-Eocene areas of Alabama and Mississippi in

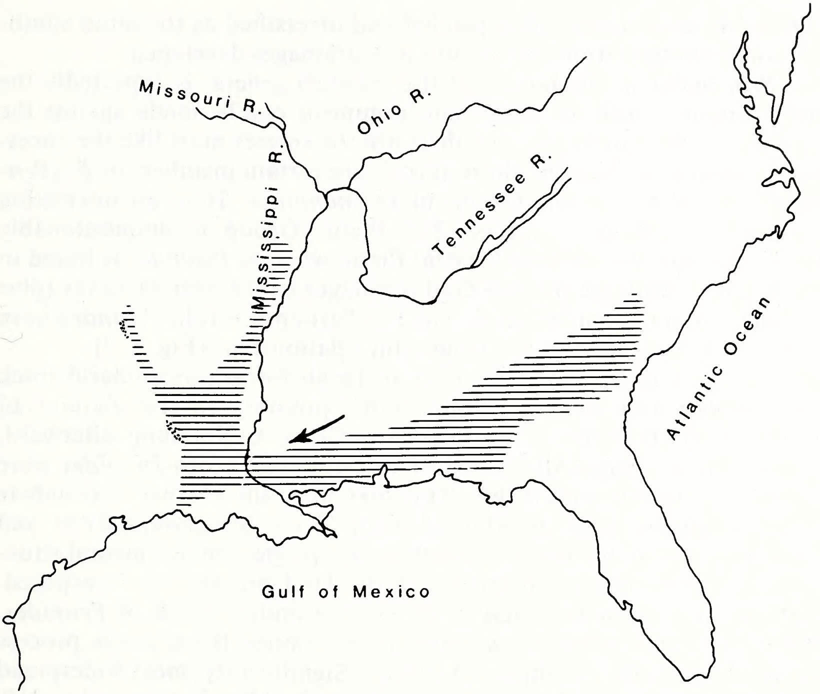

Fig. 9. Distribution of *Faxonella*. Arrow as in Figure 1. Horizontal rulings = *Fx. clypeata*.

that part of its range (Fig. 9). Other, apparently later-differentiating species of other taxa, which have similar environmental habits and cohabit successfully with *Faxonella* elsewhere, are not so widely distributed. Thus, such a distribution as exhibited by *Fx. clypeata*, a relatively advanced member of the genus, argues for an Eocene origin for the genus.

Hobbseus orconectoides Fitzpatrick and Payne, the most primitive member of that genus, occurs in streams associated with Midway (Paleocene) deposits (Fig. 10). The other species occur up and down the Tombigbee drainage, except for one just across the divide in the headwaters of the Pearl drainage. As May (1981) and Murphey and Grissinger (1981) suggested that surface materials analyzed by Grim (1936) represent post-Eocene alluvium rather than primary deposits, the above areas could easily be considerably younger than proposed. One cannot escape the close relationship between *H. orconectoides* habitat and the delta of Grim's (1936) "river of considerable size" or "late Eocene" (probably Miocene). The intimate association of the genus with the Tombigbee drainage makes one suspect that some members of the archiorconectoid stock became isolated in the lower reaches of the river during Miocene times and expanded and diversified as the more southern lands emerged from the sea and new drainages developed.

Procambarus, the largest of the crawfish genera, is expectedly the most complex. And no significiant argument can be made against the supposition that among its members are the species most like the ancestral Cambarinae. Equally, those species are certain members of *P.* (*Pennides*) and of the Pictus Group of *Ortmannicus*. Here an interesting geographic dichotomy occurs. The Pictus Group is unquestionably associated with the Atlantic Coastal Plain, whereas *Pennides* is found in the Atlantic drainage *and* the Gulf drainages as far west as Texas (plus an isolate in northern Mexico). The two "groups" within *Pennides* have been noted, as have been the geographic relationships (Fig. 1, 2).

I suggest a very early isolation of the ancestral procambarid stock into eastern and western populations, possibly in the vicinity of northeastern Alabama or northwestern Georgia. Not long afterward, possibly by the large Midway river of Grim, the proto-*Pennides* were divided. Fitzpatrick and Hobbs III (1968) noted the absence of members of the subgenus from the alluvial plain of the Mississippi River and suggested that such a feature, which denies proper environmental situations, is as effective a barrier as if a dry-land bridge were interposed. Perhaps such a barrier acted to isolate a primitive stock of *Pennides*. During Miocene times the western stock retained the cephalic process but diversified into a complex of species. Significantly, most widespread members are west of the Mississippi River, but *P.* (*Pe.*) *vioscai* and *P.* (*Pe.*) *ouachitae* have variants on the east side. Recently, Hobbs, Jr., and I have discovered what appears to be a population of *P.* (*Pe.*) *elegans* Hobbs on the east side, but that species seems to be of limited distribution on both sides of the river. *Procambarus* (*Pe.*) *ablusus* Penn is essentially isolated in western Tennessee. The siblings, *P.* (*Pe.*) *clemmeri* and *P.* (*Pe.*) *penni,* are found south of the "river" of Brown (1967), indicating their divergence and spread occurred no earlier than the Pliocene. The other Mississippi species, *P.* (*Pe.*) *lagniappe* Black and *P.* (*Pe.*) *lylei* Fitzpatrick and Hobbs, seem to be very restricted, regional isolates.

Farther eastward are the species of *Pennides* that lack a cephalic process. For these, Hobbs's (1981:36-38, 53-54) arguments seem valid. The two enigmas to me are *P.* (*Pe.*) *petersi* Hobbs and *P.* (*Pe.*) *versutus* (Hagen), both of which have a cephalic process. Otherwise, *P.* (*Pe.*) *petersi* is close to *P.* (*Pe.*) *raneyi* Hobbs, morphologically and geographically. Perhaps this is indicative that the eastern proto-*Pennides* retained for a short while the cephalic process, but most populations lost it early. Surely the most difficult to interpret is *P.* (*Pe.*) *versutus.* Hobbs (1981:38) said, "Considering the Georgia representatives of *Pennides* alone, clearly the most disjunct of the five is *Procambarus versutus* . . . ." I concur, but add that it is different from all other *Pennides*, too. It shares many characteristics with the highly restricted *P.* (*Pe.*) *lylei*. Both have a distinct shoulder on the cephalic surface of the male

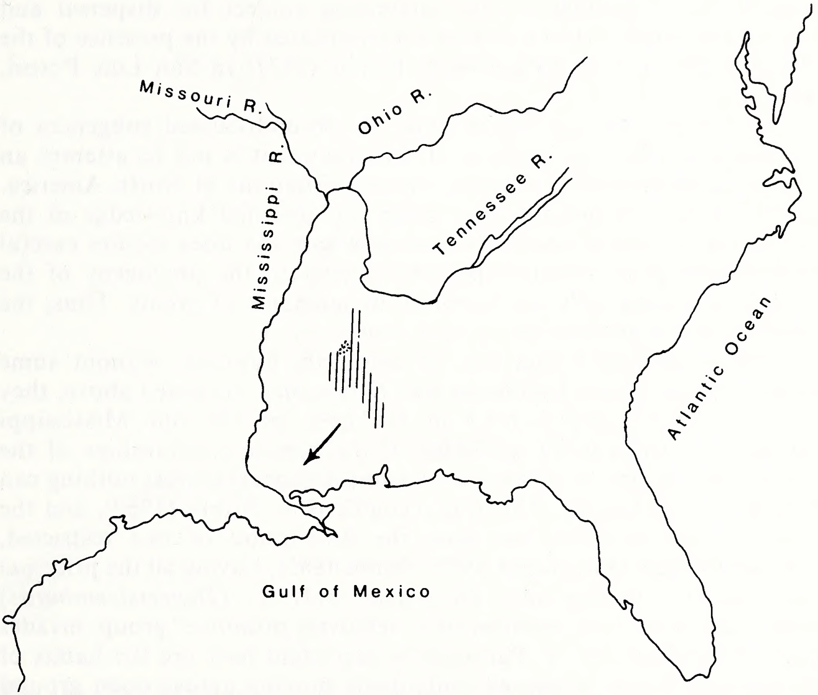

Fig. 10. Distribution of *Hobbseus*. Arrow as in Figure 1. Stippling = *H. orconectoides*.

pleopod; the appendage in each has an attenuated tip; and both have a carinate rostrum. Several western species have caudal projections of the sternite just anterior to the annulus, which partially obscure the receptacle, but none is developed in the same way or to the degree as is the case in *P.* (*Pe.*) *versutus*. It is unique in the subgenus in retaining a strong spine on the basis of the cheliped. Despite considerable geographic variation, the species stands alone. It is confined to areas younger than Grim's (1936) "Eocene." Does it represent a third line of proto-*Pennides* descendants, is it a Miocene phenomenon, or is it both of the preceding?

Moving to a second subgenus of *Procambarus*, *Scapulicambarus*, another pattern related to post-Miocene development can be seen. Only *P.* (*S.*) *clarkii* (and one other, below) is found significantly outside the southern Atlantic Coastal Plain or the Flint-Chattahoochie basin (Fig. 11). The easternmost limit of this species is in Escambia County, Florida, and where it traverses the coast it is in post-Miocene areas. Again, its dispersal seems to be a post-Miocene event. As its relatives are all in the extreme southeastern United States, an origin in that area is not unreasonable. Equally, a post-Miocene origin is feasible. But since the species has spread as far as Mexico (Hobbs 1962b) in such a short time, it becomes a very interesting subject for dispersal and competition studies. The question is complicated by the presence of the relatively primitive *P.* (*S.*) *strenthi* Hobbs (1977) in San Luis Potosí, Mexico.

Numerous other problems exist in the undiscussed subgenera of *Procambarus*. But the purpose of this treatment is not to attempt an exhaustive resolution of zoogeographical situations of North America. Instead, it is to emphasize that more sophisticated knowledge of the geology of an evolutionarily critical area can and does require careful reflection on prior conclusions with respect to the phylogeny of the animals, and especially the temporal assignments of events. Thus, the specific answers are best left to other studies.

The discussion would not be complete, however, without some mention of the genera *Cambarus* and *Orconectes*. As noted above, they both are poorly represented in the area of the old Mississippi Embayment. Until more is known of the precise relationships of the several populations of *Cambarus* (*Lacunicambarus*) almost nothing can be said of their history. This was recognized by Hobbs (1969), and the only progress thus far has been the description of two restricted, peripheral species (Fitzpatrick 1978, Hobbs 1981), leaving all the principal questions still unanswered. Otherwise, only *C.* (*Depressicambarus*) *striatus*, an "advanced" member of a "relatively primitive" group, invades to the Mississippi River. Particularly important here are the habits of this species. I have observed individuals moving across open ground when the humidity is only moderately high, and I have found their burrows on hillsides somewhat removed from flowing or standing surface water. Surely, this species is not as restricted in its dispersal as are many others.

Orconectes is represented by no relatively primitive species. Although the exact relationships of the taxa are presently undetermined, I am sufficiently progressed in a monographic study of the genus to be comfortable with the concept that the area in question is populated by relatively advanced forms. Many are members of the Palmeri Group; they probably represent an invasion from the west. Most of the remainder are Virilis Section species, which probably represent an eastern assemblage expansion. The striking feature is the absence of simple, less advanced forms.

Hobbs's (1967, 1981, 1983) arguments in favor of an early divergence of procambarid-like stocks are quite sound. Equally, his ideas of the emergence of proto-*Cambarus* and proto-*Orconectes* cannot be faulted. The paradox exists in the geologic data that suggest a large Midway-time river from the southern Appalachians, entering the Mississippi Embayment in the area near the headwaters of the present Pearl River (Grim 1936). Another strong river reworked the "Citronelle" deposits and emptied just north of Lake Pontchartrain (Brown 1967). Current dating would place these events in late Miocene or early Pliocene.

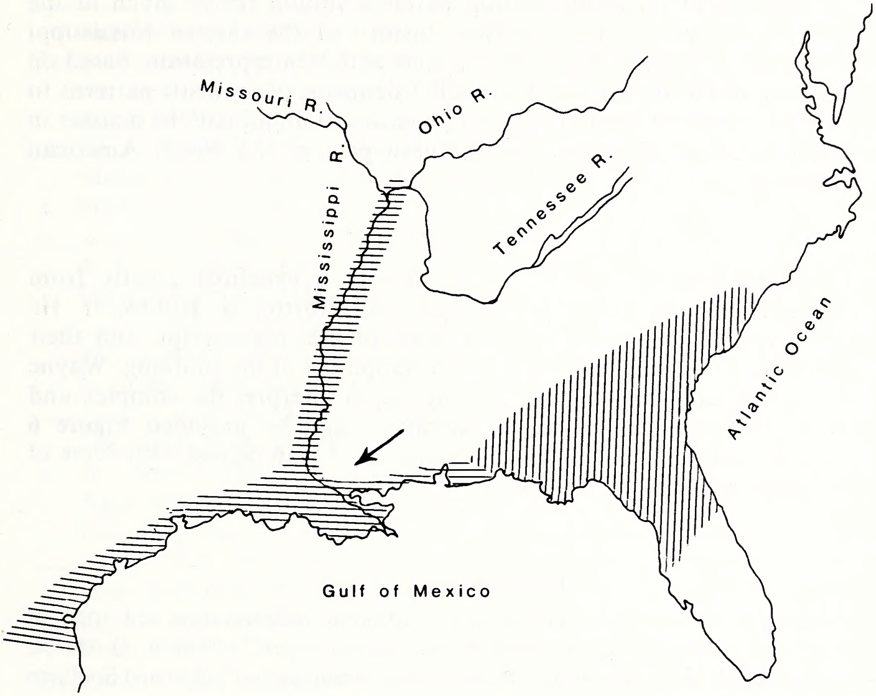

Fig. 11. Distribution of *Procambarus* (*Scapulicambarus*). Arrow as in Figure 1. Horizontal rulings = *P.* (*S.*) *clarkii.*

Mineralogic data argue strongly that the southern Appalachian highlands had a significant role in contributing to sediments of the central Gulf Coastal Plain, probably via a major river—the "upper" Tennessee—until late Pliocene times (Isphording 1983).

It is difficult to imagine that a vigorous *Cambarus* and *Orconectes* stock established in the southern Appalachians or on the Cumberland Plateau would not exploit this route (or routes) for the invasion of the newly emerging habitats. Thus, either the two genera were well established and diversified by the end of the Miocene or they did not emerge until Pliocene times. Logic favors the former thesis. Otherwise, crawfishes would be undergoing speciation at a rate not supported by any other evidence.

A Miocene intrusion in Mississippi to within 50 km of the Tennessee boundary (May 1981, Murphey and Grissinger 1981) is a significantly different situation than previously assumed. As Murphey and Grissinger (1981) indicated, the Eocene (and probably subsequent) drainage patterns have been buried. Surely, the influential Miocene uplift had profound effects on the freshwater drainage. A very fruitful area for study exists in Alabama and Mississippi. Detailed analysis of the specifics of microdistribution patterns should reveal much of the geologic, as well as the faunistic, history of the eastern Mississippi Embayment. Correlation of these results with reinterpretation, based on the more recent datings of "Citronelle" deposits, of faunistic patterns to the east or west of the Embayment promises to illuminate the manner in which aquatics populated the southern part of the North American continent.

ACKNOWLEDGMENTS.— As always, I benefited greatly from conversations and exchanges of ideas with Horton H. Hobbs, Jr. He and Perry C. Holt read an early draft of this manuscript, and their criticisms contributed much to the development of my thinking. Wayne C. Isphording is thanked for helping me to interpret the complex and often very technical geological literature, and he provided Figure 6 (from Isphording 1983, Fig. 10); George M. Lamb helped with some of the geomorphological concepts.

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To John E. Cooper, with Appreciation

In August 1985, John E. Cooper resigned from the staff of the North Carolina State Museum of Natural History and from the editorship of *Brimleyana*. His accomplishments during his 11 years here are many.

Dr. Cooper nourished *Brimleyana* from an idea to 11 thick issues published between March 1979 and October 1985. Because of his voluminous correspondence with colleagues throughout the country, his broad background as a museum curator and population ecologist, and his special skills as a writer and scientific illustrator, John was unusually well qualified to found and edit an interdisciplinary journal devoted to the zoology and ecology of the Southeast.

A native of Maryland, Cooper graduated from Johns Hopkins University and obtained M.S. and Ph.D. degrees from the University of Kentucky at Lexington. Prior to joining the staff of the North Carolina State Museum in September 1974, he lived and taught in Baltimore, where he was a strong, constructive force in the Maryland Natural History Society and the principal editor of *Maryland Naturalist*. His particular interests are herpetology, crayfish biology, and cave life. At the N.C. State Museum, John organized the Research and Collections Section and was for a time the assistant director in addition to his service as editor of the journal.

Although biologists are supposed to remain detached and analytical in regard to the organisms they study, most of us develop a strong sense of stewardship for them. John is no exception. Well known for his expertise in the biology of cave systems, he deserves credit for the development of the biological and conservation ethics of the National Speleological Society. During his tenure at the museum, he organized the 1975 Symposium on the Endangered and Threatened Plants and Animals of North Carolina, edited the proceedings, and participated in similar symposia in other states. One example is his keynote presentation at the Symposium on Threatened and Endangered Plants and Animals of Maryland. Entitled "Vanishing Species: The Dilemma of Resources Without Price Tags," this is one of the most recent in a long series of scientific contributions dating back to a boyhood interest in biology.

John Cooper served this museum well, and when he resigned, he did so in typical Cooper style. He departed just as *Brimleyana* 11 was going to press and after copy for the present issue was ready for typesetting. He did everything possible to ensure a smooth transition of responsibility to the managing editor, and now acting editor of the journal, Eloise F. Potter.

"Coop," we who worked with you at the museum and the contributors to *Brimleyana* wish you well in your future endeavors. We will do our best to maintain the high standards you set.

JOHN B. FUNDERBURG
Director, N.C. State Museum
Editor-in-Chief, *Brimleyana*

MANUSCRIPT REVIEWERS

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