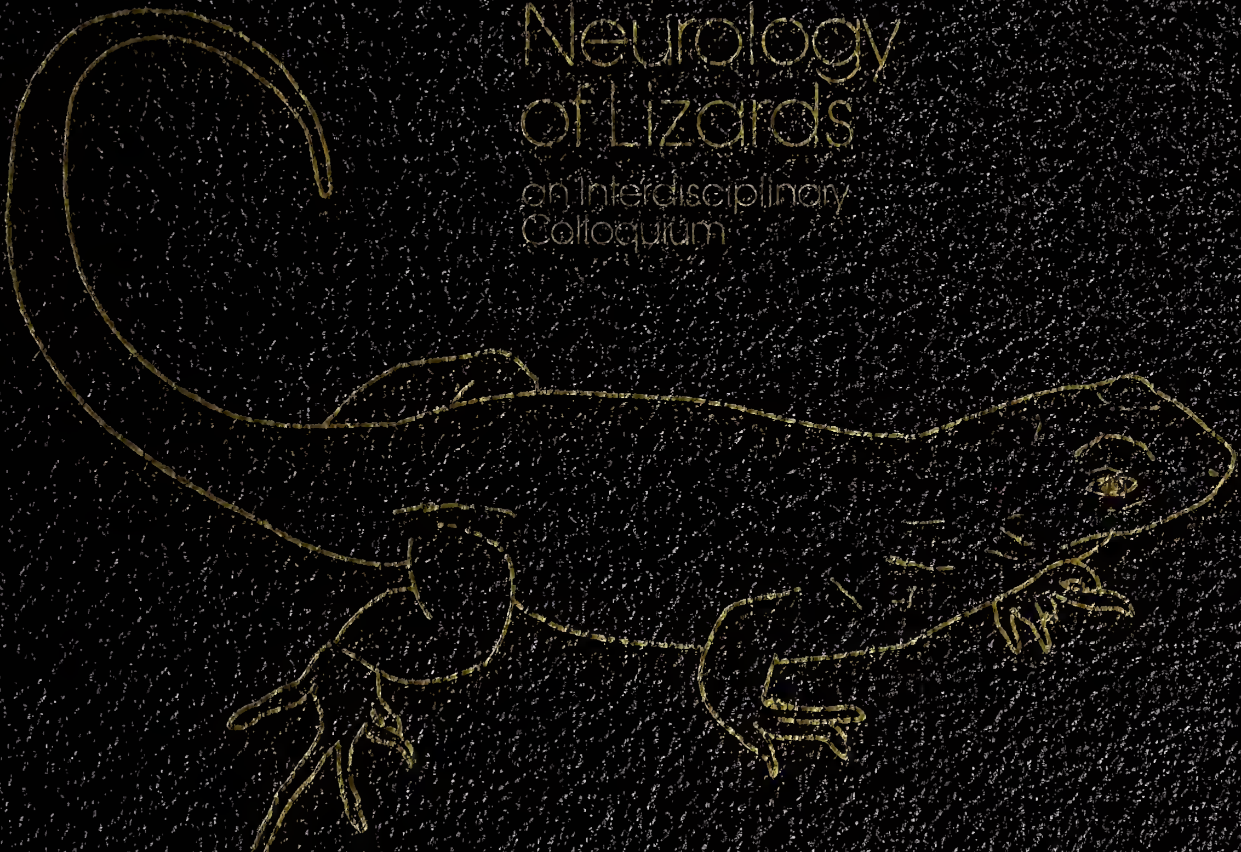
National Institute of Mental Health

Behavior and Neurology of Lizards

an Interdisciplinary Colloquium

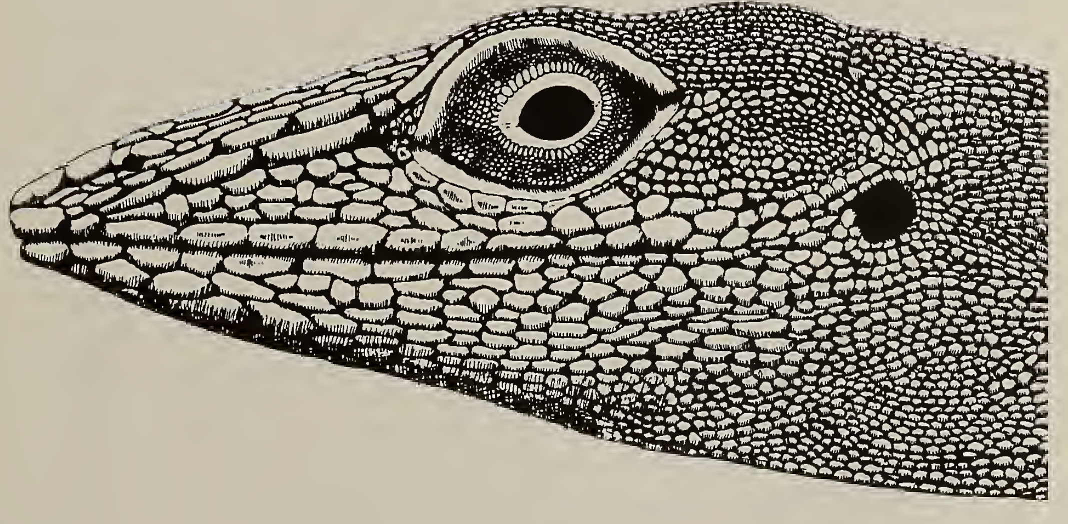


Behavior and Neurology of Lizards

an Interdisciplinary Colloquium

Edited by
Neil Greenberg and Paul D. MacLean

Laboratory of
Brain Evolution and Behavior



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Foreword

The Laboratory of Brain Evolution and Behavior was conceived 20 years ago as a place where animals could be studied in quasi-natural habitats. We wanted a facility where scientists from several biological and behavioral disciplines could collaborate in disentangling the connections between brain and action, in ways which cannot be done so well, and in some instances not done at all, in the conventional laboratory setting.

Paul MacLean developed the concept shortly after he came to the NIMH in 1957, and he and Robert Livingston, then Director of Basic Research, had it pretty well outlined by the time I returned to NIMH as Director of Intramural Research in 1961. For the next 10 years all of us worked hard to make this dream into a reality. Though progress in planning and in securing authority and funding for the new buildings was slow, we were ultimately successful, and in 1971 the new research facility was dedicated. It then consisted of 40 acres of woods and meadows, a waterfowl pond, and three laboratory buildings, and we have since added several additional habitats. It is a part of the 500 acre NIH Animal Center, which provides support and assistance of many kinds to the Laboratory.

It is a pleasure to acknowledge this symposium on The Behavior and Neurology of Lizards as the latest evidence of the importance of Dr. MacLean's concept. Since 1971 his small group of staff scientists and visiting scholars have pursued research on squirrel monkeys, dogs, rats and mice, turkeys, lizards, hamsters, and a number of more exotic species, utilizing the concepts and methods of neuroanatomy, neurophysiology, pharmacology, and psychology. From time to time they select a problem of wide interest and bring together a group of scientists to pool their knowledge, as they and the Smithsonian Institution have done in the present symposium. It is hard to overestimate the value which this very unusual, and perhaps unique, Laboratory has had in the study of brain and behavior.

Though the Laboratory has been in formal existence for only 7 years, it grew out of a neurosciences research program which is now 25 years old. That is hardly venerable, but it is a significant span of experience to be under stable leadership and with a high degree of continuity of staff membership. It has been our good fortune to have had the administrative and scientific support from NIMH and NIH to make this long record possible.

We are indebted to Drs. MacLean and Greenberg, and their colleagues from the Smithsonian Institution, Drs. Marcellini and Wimmer, for their leadership in organizing this comprehensive symposium on the lizard, a most interesting animal form. There is no question but that many other fundamental contributions will be forthcoming from this field station with its finely equipped set of laboratories set down among the meadows.

John C. Eberhart, Ph.D.
Director of Intramural Research
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Prefatory Comments

When Congress founded the National Zoological Park in 1890, it gave us the mission of the "advancement of science, education, and recreation of the people" and placed the Zoo as a bureau of the Smithsonian Institution whose mandate is the "increase and diffusion of knowledge among men." Our Zoo has a broader mission than the mere exhibition of animals. We are concerned with their study for a multitude of purposes: Better care and management, conservation and breeding of endangered species, biomedical problems, behavioral patterns; in fact, the whole gamut of inquiry about animals is covered by our various mandates.

As man's pressure on animals in the wild is increased, the role of the Zoo as a refuge for wild animals, as well as an institution of inquiry, becomes increasingly more important. We were indeed fortunate when, in 1972, we acquired the 3,000 acres of the former U.S. Cavalry Remount Station and Beef Cattle Experimental Station from the U.S. Department of Agriculture. This land, the Conservation and Research Center, is to be used primarily for the conservation and maintenance of groups of selected animals for breeding in captivity. To accomplish this, much intense study must be done on the behavior of the animals, their reproductive biology, and biomedical problems.

Among the other benefits we received with the legacy from the military and the Department of Agriculture was a conference center. It was obvious to all of our staff that these facilities provided an extraordinary opportunity for the holding of relatively small but intense conferences on specific subjects related to our interest that would both increase our knowledge and be beneficial to the welfare of future generations of animals. To date, we have had several conferences which I believe were highly productive for three reasons: (1) Subjects were confined to discrete areas of inquiry; (2) participants were invited who are knowledgeable and concerned about these areas of interest; and (3) the almost spartan existence at the Conservation and Research Center at Front Royal, Virginia had none of the distractions of a busy city, university, or museum complex, and consequently, the discussions and meetings seemed to go on far into the night. The publications resulting from these conferences have been, and will continue to be, valuable references to present to future scientists.

We are particularly happy to share this symposium on the *Behavior and Neurology of Lizards* with our long-time friends from the National Institute of Mental Health. The interest in and knowledge of lizards and reptiles concentrated these few days in the foothills of Virginia are astounding. The free exchange of information, the joyous debates, and the airing of viewpoints were stimulating and will produce results long beyond the limited time that we were gathered.

The National Zoological Park and the Smithsonian Institution are proud to be associated with such a group of dedicated scientists. We extend our thanks to Dr. Paul D. MacLean and Dr. Neil Greenberg and other members of the organizing committee, as well as to all participants for sharing with us their knowledge and ideas.

Theodore H. Reed, D.V.M.
Director, National Zoological Park
Smithsonian Institution

These proceedings of an interdisciplinary colloquium dealing with reptiles reflect major advances in the utilization of the comparative method and ethological approach that promise to be important in research on neurobehavioral problems long puzzling and troubling to researchers.

Many reptile species are highly suitable for research. Many occur in easily studied natural populations, and in the laboratory they are a clean, convenient species. Neurologically and behaviorally they are of interest as descendants of the group ancestral to birds and mammals. Like birds and mammals, they have responded to the challenges of a changing world by adapting and evolving in their own way, yet using the same basic neurological raw material.

Behaviorally, reptiles demonstrate most of the same basic patterns as so-called higher animals. That these behavioral patterns can be elicited in the lab is a testament to the value of the ethological method, with its appreciation for the ecological and evolutionary constraints on organisms.

The conference on which this volume is based was a pleasure in several ways. It grew out of a realization of the importance of interdisciplinary dialog and was markedly successful in that regard. But it also represents a collaboration with our friends and colleagues at the Smithsonian Institution. Dr. Neil Greenberg, NIMH research ethologist, and Dr. Paul D. MacLean, Chief, NIMH Laboratory of Brain Evolution and Behavior, along with Dr. Dale Marcellini, Research Curator at the National Zoological Park, and Dr. Chris Wimmer of the NZP Front Royal Research facility, identified the needed expertise and organized and hosted the 3-day meeting.

One of the mandates of the National Mental Health Act that authorized the establishment of NIMH more than 30 years ago was to conduct research in the area of mental health. Part of the excitement and enthusiasm during the days of the Conference and the preparation of this volume was due to the realization that a new group of organisms of great research potential had been brought into the fold. Scientists free of prejudice and impatience are now armed with a potent new weapon in their war on ignorance.

Bertram S. Brown, M.D.
Director
National Institute of Mental Health

Editors' Comment

This volume is based on presentations at an interdisciplinary colloquium on the Behavior and Neurology of Lizards held May 5-7, 1975, at the Laboratory of Brain Evolution and Behavior, National Institute of Mental Health, Poolesville, Maryland, and at the Research and Conservation Center of the National Zoological Park, Smithsonian Institution, Front Royal, Virginia.

After the colloquium, the transcribed presentations were sent to the participants for making corrections and including desired additions. The editors then worked with this material and assembled it. It has been possible to include only parts of the general discussion.

Fortunately, there can be no rules or regulations with respect to a person's wishes. There is the convention that a dedication is reserved for one or two individuals and that everyone else is mentioned under "acknowledgments." For this occasion we wish that we could change this convention. We wish that we could have a wide-ranging dedication that would include the pioneer investigators mentioned throughout this volume; the participants of the Conference who made this volume possible; the staff of ADAMHA who worked to produce this volume; the members of our Administration who implemented all aspects of the undertaking; the Grant Foundation which provided an NIMH Fellowship awarded to one of us (G); and finally the people of the United States and their representatives who have supported unparalleled opportunities and facilities for basic research.

Neil Greenberg
Paul D. MacLean

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Contents

Neurology

Laboratory Studies of Behavior

Field Studies of Behavior

Behavior and Neurology of Lizards
N. Greenberg and P. D. MacLean, eds.
NIMH, 1978.

Why Brain Research on Lizards?

Paul D. MacLean

Laboratory of Brain Evolution and Behavior
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Those who are familiar with lizards realize that there are more reasons for conducting research on these animals than there are investigators prepared to do the necessary work. Our own interest in lizards is easy to explain because they are distant relatives of the long-extinct mammal-like reptiles that are believed to have been the antecedents of mammals. Ordinarily, there is no apparent causal connection between a current happening and something that took place a few hundred million years ago. But it is perfectly correct to say that this Laboratory would not be here, and that this Conference would not have been held, had there not been an historical link between mammals and reptiles. When beginning to plan for the present facility 20 years ago, a primary purpose was to use new behavioral approaches in investigating the functions of a basic part of the forebrain that reflects our reptilian ancestry. The reason will be explained after defining the cerebral mass in question.

THE TRIUNE BRAIN

In its evolution the primate forebrain expands along the lines of three basic formations that can be characterized as reptilian, paleomammalian, and neomammalian. The diagram in Figure 1 depicts the hierarchic organization of the three formations. Remarkably different in chemistry and structure, and in an evolutionary sense eons apart, the three formations constitute three brains in one, or what may be called for short a *triune brain* (MacLean, 1970, 1973*b*). This neural condition suggests that psychologically we represent an amalgamation of three quite different mentalities (MacLean, 1975*a*, 1977*a*).

In mammals, the major counterpart of the reptilian forebrain is represented by the olfactostriatum, corpus striatum (caudate nucleus and putamen), the globus pallidus, and satellite collections of gray matter. Since there is no term that applies to all of these structures, I will refer to them as the striatal or R-complex (MacLean, 1973*c*).

Developments in histochemistry have been of great help in identifying the corresponding striatal structures in reptiles, birds, and mammals. The black areas in Figure 2 show how a stain for cholinesterase (originally described by George Koelle in 1954) vividly colors the R-complex in the monkey brain.

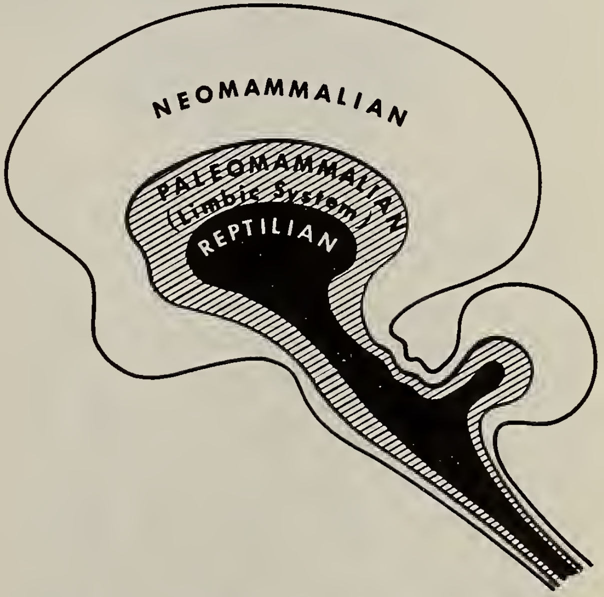

Figure 1. In its evolution, the primate forebrain expands in hierarchic fashion along the lines of three basic patterns that may be characterized as reptilian, paleomammalian, and neomammalian (from MacLean, P.D., 1967).

Figure 2. This section from the brain of a squirrel monkey shows how the greater part of the R-complex is selectively colored (black areas) by a stain for cholinesterase (from MacLean, 1972).

Figure 3 illustrates how the same stain reveals the corresponding structures in animals ranging from reptiles to primates. Using the histofluorescence technique of Falck and Hillarp described in 1959, it is striking to see the greater part of the striatal complex glow a bright green because of the presence of large amounts of dopamine, a neural sap that seems necessary for bringing into play the whole range of expressive behavior. The dopamine is transported to the olfactostriatum and the corpus striatum by nerve processes arising from cell bodies in the ventral midbrain (ventral tegmental area and compact cells of substantia nigra)*. Parts of the striatal complex are also rich in serotonin (Paasonen et al, 1957) and in opiate receptors (Pert and Snyder, 1973).

From an evolutionary standpoint, the reptilian brain is of particular interest because it allows one to visualize how developments at a critical locus in the so-called hypopallium (see Fig. 4) described by Elliot Smith (1918–1919) may have tipped the scales so

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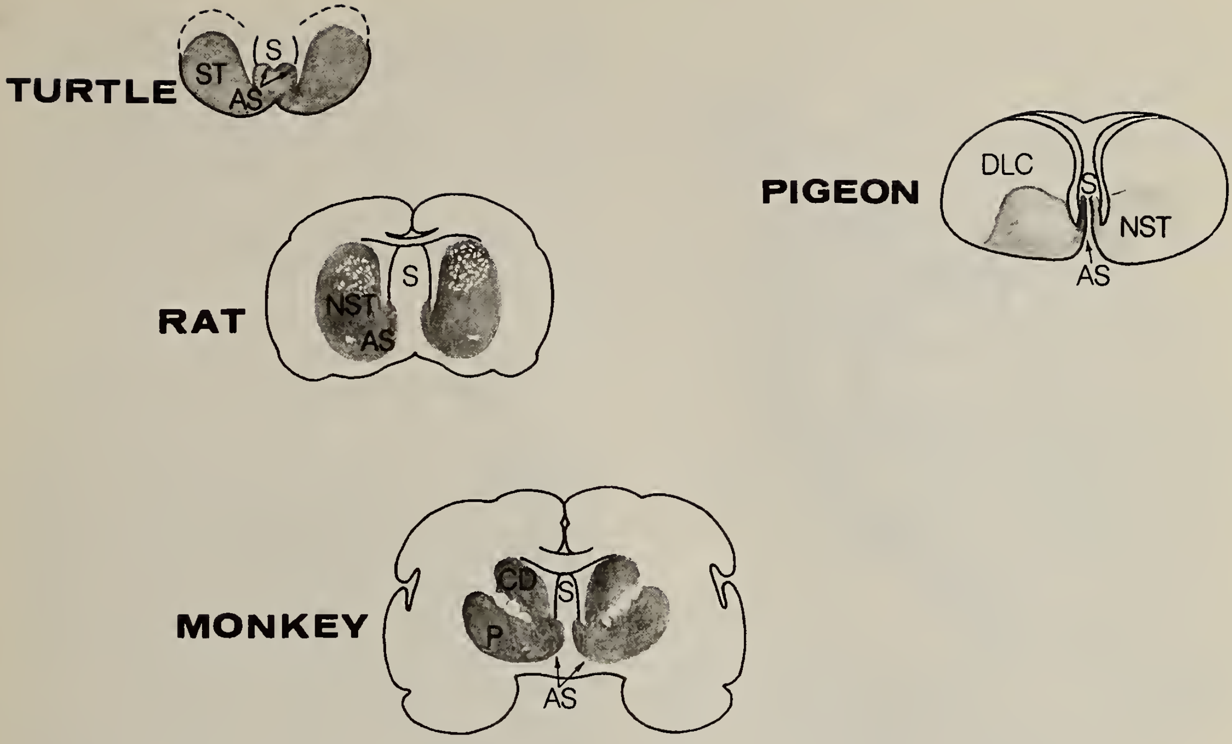
* As regards the extensive literature, see particularly the original articles by A. Dahlström and K. Fuxe (Acta Physiol. Scand., 232 Suppl., *62:* 1–53, 1964) and J. Ungerstedt (Acta Physiol. Scand., 367 Suppl., 1–48, 1971).



(After Parent & Olivier)

Figure 3. Shaded areas indicate how a stain for cholinesterase distinguishes the greater part of the R-complex in animals ranging from reptiles to primates. With the fluorescent technique of Falck and Hillarp, the same areas shown above would glow a bright green because of the high content of dopamine (Juorio and Vogt, 1967). The pallidal part of the striatal complex does not fluoresce. No existing reptiles represent the forerunners of mammals. Birds are an offshoot from the *Archosauria* ("ruling reptiles") (from MacLean, 1973*c*, and adapted from Parent and Olivier, 1970).

that some animals evolved in the direction of birds, while others went the mammalian way. The critical area lies near the ventrolateral base of what J.B. Johnston in 1916 called the dorsal ventricular ridge, presumably because it reminded him of a mountain ridge. In an extension of Johnston's analogy, the proliferating hypopallial area might be imagined as comparable to a turbulent volcanic zone. In birds, its continued eruption appears to have resulted in a piling up of ganglia upon ganglia, whereas its explosion in mammals was responsible for the mushrooming of neocortex forming the dorsolateral part of the brain. Ventromedial to the hypopallial zone is the striatal complex that continues to be firmly embedded in the brains of reptiles, birds, and mammals. The R-complex is as much the bedrock of the forebrain as the Laurentian shield is to the North American continent.

We now come to the heart of the matter regarding our special interest in the striatal complex. Twenty years ago when planning began for the present facility, almost as little was known about the functions of these structures as at the beginning of the century. In his *Text-Book of Physiology* published in 1900, E.A. Schäfer wrote: "The corpus striatum is generally believed to act as a centre for the higher reflex movements, and to be in close association with the Rolandic area, but the experimental grounds of this belief are still lacking" (p. 778). Sixty years later Crosby et al. stated: "At present . . . in spite of numerous experimental studies

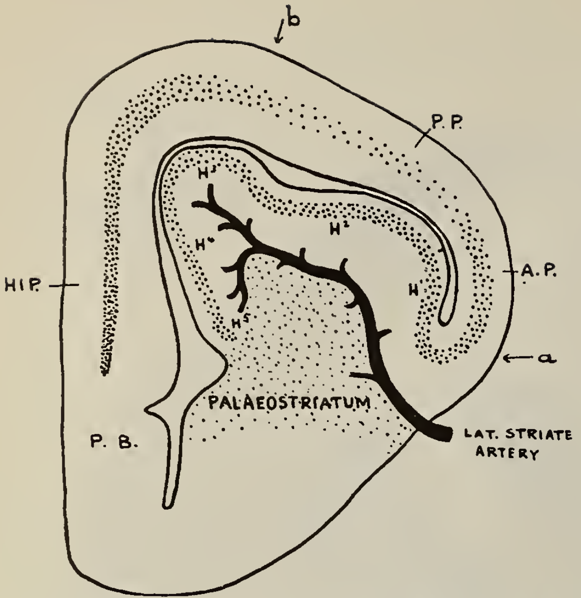


Figure 4. Reproduction of first figure of Elliot Smith's paper of 1918/1919, illustrating a frontal section through the forebrain of the tuatara (*Sphenodon punctatum*). The diagram is useful for suggesting how a proliferating area represented by the U-shaped collection of cells (arrow at a) may have been influential in determining the divergent evolution of birds and mammals. It was as though a proliferation of cells in the left limb of the U had led to a piling up of ganglia on ganglia in birds, whereas activity in the right limb resulted in a burgeoning of cortex in mammals (see text). H^1–H^5 designate areas to which Elliot Smith gave the name "hypopallium," and which J.B. Johnston had previously referred to as the "dorsal ventricular ridge." The lateral striate artery marks the boundary between the ridge and the underlying striatal complex, which is found as a constant feature in the brains of reptiles, birds, and mammals. HIP identifies the hippocampal formation, which becomes a principal site of unfolding of the limbic cortex. Other abbreviations: b, junction of Hip. and P.P., A.P., area pyriformis [sic]; P.B., paraterminal body; P.P., parahippocampal pallium.

and a wealth of clinical observations, there is no clear understanding of the precise functions of the caudate-lenticular complex *per se*, as distinct from the other brain areas with which it is in functional connection . . ." (p. 380). The traditional clinical view that the striatal complex is primarily "motor" in function is not supported by findings that large, unilateral or bilateral lesions of its various parts may result in no obvious disability (Denny-Brown, 1962; Kennard, 1944; Laursen, 1963; MacLean, 1972; Mettler, 1942; Meyers, 1942; Ranson and Berry, 1941; and Wilson, 1914).

Since the opening of the present laboratory in 1971, a primary purpose has been to conduct comparative studies on animals for testing the hypothesis that the striatal complex plays a basic role in the organized expression of species-typical, communicative behavior.

COMMUNICATIVE BEHAVIOR

Human communicative behavior can be classified as verbal and nonverbal. Like Percy W. Bridgman, the physicist-philosopher, people commonly assume that "most human communication is verbal" (1959). Contrary to the popular view, many behavioral scientists would place a greater emphasis on nonverbal communication.

Many forms of human nonverbal communication show a similarity to behavioral patterns seen in animals ranging from reptiles to primates. Since it is inappropriate to refer to nonverbal communication of animals, another term is needed to refer to such behavior. Consequently, I have used the word "prosematic," derived from the Greek (προσημα) and applying to rudimentary signaling, for referring to communication involving any kind of nonverbal signal—vocal, bodily, chemical (MacLean, 1975*a*, 1977*a*).

It has been the special contribution of ethology to provide the first systematic insights into the "semantics" and "syntax" of prosematic behavior of animals. Somewhat comparable to words, sentences, and paragraphs, prosematic behavior becomes meaningful in terms of its components, constructs, and sequences of constructs (MacLean, 1977*b*).

Since the patterns of behavior involved in self-preservation and the survival of the species are generally similar in most terrestrial vertebrates, it is not meaningful for our present purposes to refer to them in the traditional manner as species-specific behavior. But since various species perform these behaviors in their own typical ways, it is both correct and useful to refer to species-typical behavior. As ethologists have emphasized, a species can be identified as readily by its behavioral patterns as by its morphological characters.

THE MAMMAL-LIKE REPTILES

Curiously enough, in books and articles on evolution, one usually finds little emphasis placed on the mammal-like reptiles. Few people seem to be familiar with the mammal-like reptiles, and fewer still are aware that they once covered the face of the earth. Romer speaks to this point when he says, "The relatively late time at which the mammals took over the world's supremacy from the reptilian dynasties would lead one to think that the stock from which they sprang must have been one developed at a comparatively late date in reptilian history. This, however, is exactly the reverse of the true situation. The mammal-like reptiles, constituting the subclass Synapsida, were among the earliest to appear of known reptilian groups and had passed the peak of their career before the first dinosaur appeared on the earth" (1966, p. 173).

The synapsids (one temporal opening) developed from the so-called stem reptiles (Cotylosaurs) in Pennsylvanian times—roughly 250 million years ago (see Fig. 5). During Permian and early Triassic times—for a period of about 100 million years—the mammal-like reptiles populated the world in profuse numbers. Today their remains are found on every continent including Antarctica, signifying that there once may have existed one massive continent called Gondwanaland (see Colbert, 1972). Robert Broom calculated that there must be at least 800 billion skeletons of mammal-like reptiles in the Karroo beds of South Africa (1932, p. 308).

There were two main varieties of these animals—carnivores and herbivores. Reminiscent of the Serengeti Plain, some of the carnivores are believed to have preyed on herds of herbivores. What were these animals like? Some of the advanced carnivores are believed to have resembled dogs and wolves. Unlike their waddling predecessors, they had gotten up off their bellies and with legs supporting the body from underneath were able to run swiftly. The jaws and teeth were beginning to show mammalian characteristics.

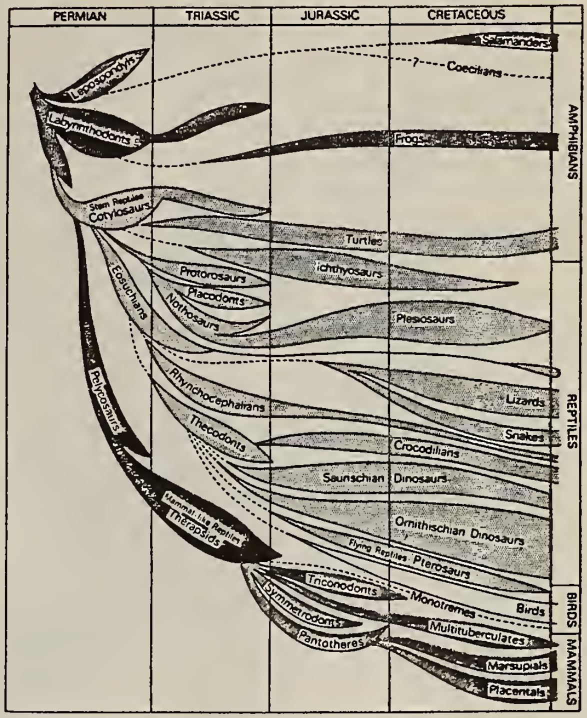


Figure 5. Family tree of reptiles (from Colbert, Figure 20, 1966).

Figure 6 shows the family tree of the Therapsids. In regard to the evolution of mammals, the two lines of main interest are shown on the left, with the Gorgonopsia leading up through the Cynodontia (dog-toothed) to the Tritylodontia, and the other line represented by Therocephalia, leading up through Bauriamorpha to the Ictidosauria (weasel-like). The latter are said to be best represented by *Diarthrognathus* discovered in South Africa. As the name implies, the jaw has dual characteristics, being a combination of the reptilian quadrate-articular joint and the mammalian squamosal-dentary joint (Colbert, 1969, p. 143). Both Romer (1966) and Colbert (1969) place this animal at the dividing line between reptiles and mammals.

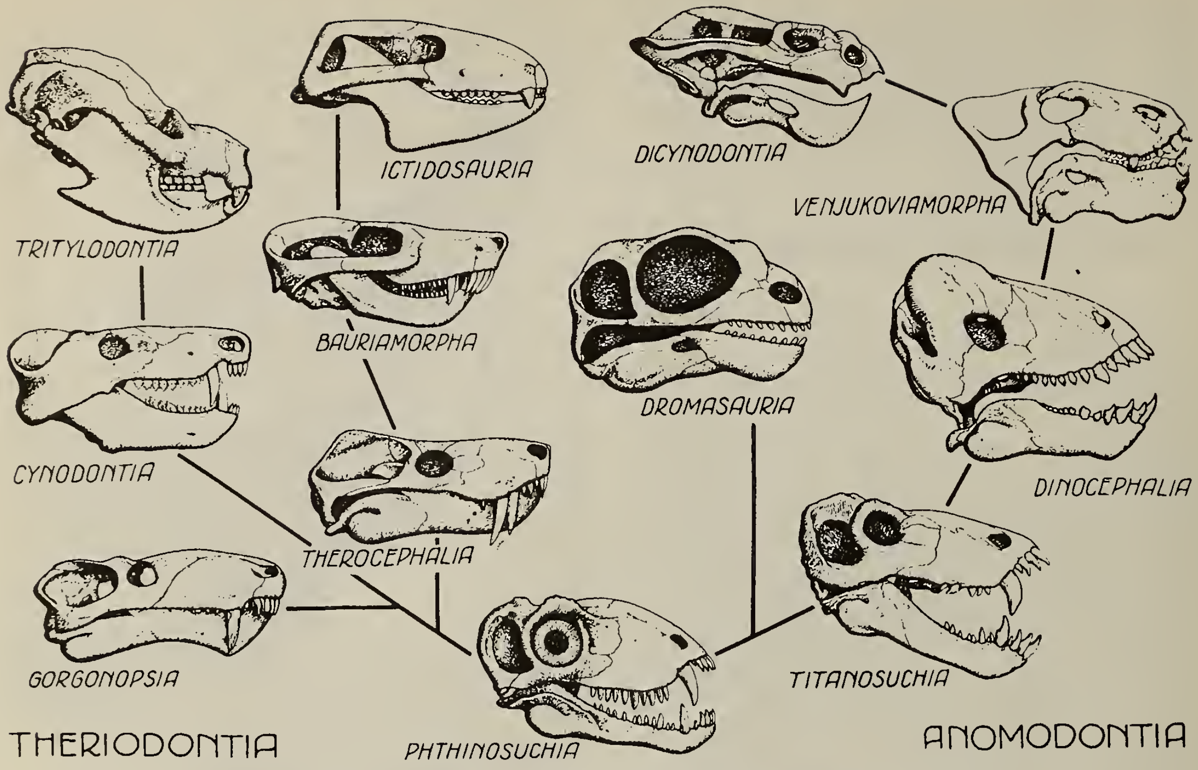


Figure 6. Family tree of therapsids (from Romer, Fig. 275, 1966).

In addition to the changes in the teeth, jaw, and posture that have been mentioned, other significant differences in the advanced reptiles include (1) a further widening of the temporal fossa, (2) the development of a secondary palate, (3) a disappearance of the pineal opening (see below), and (4) a phalangeal formula similar to mammals.

What else can be said of these animals? Did they lay eggs? Did they care for their young? Or like the contemporary Komodo lizard, did the young have to escape to the trees to avoid being cannibalized (Auffenberg, this volume)? Since the most primitive existing mammals lay eggs, it is usually assumed that the mammal-like reptiles did also. At least one case has been reported of an adult skeleton—the cynodont called *Thrinaxodon*—close to the skull of an immature animal of the same kind. This finding has suggested that some of the mammal-like reptiles may have developed parental care (Colbert, 1969, p. 140).

In the evolution of mammals, the development of vocalization and hearing became of the utmost importance for maintaining parent-offspring relationships under conditions of obfuscation. Could the mammal-like reptiles hear and vocalize, or were they essentially dumb like many of today's lizards (Marcellini, this volume)? In the advanced forms, the quadrate and articular bones were becoming smaller, but were far from being transformed, respectively, into the incus and malleus of the mammalian internal ear. Hotten has devised experiments that suggest that mammal-like reptiles had auditory perception in the low range of frequencies (Hotten, 1959). Nothing can be surmised regarding the question of vocalization.

Late in Triassic times, the mammal-like reptiles mysteriously became extinct. Ferocious, and possibly cannibalistic as they were, it is probable that they did not bring about their own destruction. Rather it is presumed that a swifter, more ferocious kind of reptiles, the thecodonts (the forerunners of dinosaurs) began to outnumber and destroy them and to steal their niches. Some of the smaller mammal-like reptiles presumably "went underground" and gradually became mammals, keeping their young nearby so that they too would not be gobbled up. Other animals derived from a different stock appear to have taken to the trees and gradually became birds, with nests for the young representing an extension of the amnion.

REPTILIAN BEHAVIOR

It is, of course, disappointing that there are no existing reptiles directly akin to the mammal-like reptiles (Fig. 5). The crocodilia are derived from the archosaurs, and the Rhynchocephalia (of which the famous tuatara is the only existing form) also betray some affinity to the archosaurs (Colbert, 1969). The turtles (Chelonia) seem to have maintained their characteristic independence since branching off from the stem reptiles. Only the lizards appear to bear any resemblance to the primitive synapsids. One of the primitive Pelycosaurs was the *Varanosaurus* which Romer has described as having proportions not unlike those of many lizards (1966, p. 174). Colbert refers to these animals as being about 5 ft. in length, with a slender body, fairly slender limbs, and a long tail. "In fact," he continues, "we might say that *Varanosaurus* was lizard like in his general aspect, though this characterization must not be taken as an indication of any close relationships with lizards." (Colbert, 1969, p. 130)

On the basis of the foregoing comments and other considerations, it would appear that lizards—and particularly the *Varanus* lizards (Auffenberg, this volume)—would bear the closest resemblance to the mammal-like reptiles. It is also to be noted that present-day lizards occupy niches similar to those of the carnivorous mammal-like reptiles.

The scientific method partly relies on the recognition of commonalities and differences in things. As described elsewhere in this volume, examination of the brains of lizards provides an excellent opportunity to identify differences in structures that appear to correlate with behavior called upon in a variety of niches. For our studies, however, we are particularly interested in identifying kinds of behavior that lizards have in common with other terrestrial vertebrates.

From an evolutionary standpoint it is curious that ethologists have paid little attention to reptiles, focusing instead on fishes and birds. Lizards and other reptiles provide illustrations of patterns of behavior commonly seen in mammals, including human beings. In Table 1, I have listed 24 types of behavior seen among reptiles that involve self-preservation and the preservation of the species. Those that primarily involve self-preservation are placed at the beginning of the list.

Five Interoperative Behaviors

There is an important pentad of prototypical forms of behavior of a general nature that may be variously operative in the activities listed in Table 1. They may be denoted as: (1) isopraxic, (2) perseverative, (3) reenactment, (4) tropistic, and (5) deceptive behavior. The word "isopraxic" refers to behavior in which two or more individuals engage in the same kind of activity (MacLean, 1975*a*, 1977a). As a purely descriptive term, isopraxic avoids preconceptions and prejudices commonly attached to such terms as "social facilitation" and "imitation" (MacLean, 1975*a*). Perseverative behavior applies to repetitious acts like those that occur in displays and would include so-called displacement or adjunctive behavior seen in conflictive situations. Reenactment behavior refers to the repetition on different occasions of behaviors seeming to represent obeisance to precedent as, for example, following familiar trails or returning year-after-year to the same breeding grounds. Tropistic behavior is characterized by positive or negative responses to partial or complete representations, whether alive

TABLE 1. COMMON PATTERNS OF BEHAVIOR*

(1) selection and preparation of homesite
(2) establishment of territory
(3) trail making
(4) marking of territory
(5) showing place preferences
(6) patrolling territory
(7) ritualistic display in defense of territory, commonly involving the use of coloration and adornments
(8) formalized intraspecific fighting in defense of territory
(9) triumphal display in successful defense
(10) assumption of distinctive postures and coloration in signalling surrender
(11) foraging
(12) hunting
(13) homing
(14) hoarding
(15) use of defecation posts
(16) formation of social groups
(17) establishment of social hierarchy by ritualistic display and other means
(18) greeting
(19) grooming
(20) courtship, with displays using coloration and adornments
(21) mating
(22) breeding and, in isolated instances, attending offspring
(23) flocking
(24) migration

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* Based on examples from Auffenberg (1972); Bellairs (1970); Ditmars (1955); Evans (1938, 1951); Eibl-Eibesfeldt (1961); Goin and Goin (1962); Greenberg (1977*a*, *b*); and Harris (1963).

or inanimate, and includes what ethologists refer to as *imprinting* and *fixed action patterns.* Deceptive behavior involves the use of artifice and deceitful tactics such as are employed in stalking a prey or evading a predator.

EXPERIMENTAL WORK IN PROGRESS

Thus far most of our experimental work on the R-complex has been conducted on squirrel monkeys. As I mentioned in the introduction, the finding that large destructions of the R-complex may result in no impairment of movement, speaks against the traditional clinical view that it is primarily involved in motor functions. Thus far, crucial findings relevant to prosematic behavior have developed from experiments on more than 100 monkeys. Squirrel monkeys perform a characteristic display of the erect phallus in a show of aggression, in courtship, and as a form of greeting. (Ploog and MacLean, 1963) Members of one species consistently display to their reflections in a mirror, providing a means of systematically testing the effects of brain ablations on the incidence and manifestations of this particular display ritual (MacLean, 1964). I have found that bilateral lesions of paleo- and neomammalian parts of the forebrain may have either no effect or only a transitory effect on the display. After bilateral lesions of the pallidal part of the R-complex (MacLean, 1973*a*; 1978), however, or interruptions of its main pathways (MacLean, 1975*b*), monkeys may no longer show an inclination to display. Without a test of the innate display behavior, one might conclude that they were unaffected by the loss of the brain tissue. These experiments provide evidence that in mammals the R-complex and its major pathways play a basic role in forms of behavior involving conspecific recognition and prosematic communication.

In the past, relatively few investigations have been conducted on reptiles in an attempt to identify specific structures of the forebrain involved in the various behaviors listed in Table 1. All that is known thus far is that the neural guiding systems for complex species-typical behavior lie forward of the midbrain. Greenberg, Ferguson, and I are conducting experiments on the effects of lesions of the striatal complex on the display behavior of the green Anolis lizard (1976). The results have been of particular interest in regard to the so-called challenge or territorial display characterized by pushups, extension of the throat fan, and profile changes, that increase the apparent size of the lizard. Because the optic nerves are almost entirely crossed, we can injure the striatal complex in one hemisphere and then test the animal's display with either eye covered. Although capable of seeing, the animal shows no interest in the rival lizard when looking with the eye projecting to the injured hemisphere. But allow him to see his rival with the intact hemisphere and the challenge display returns in full force (Greenberg, 1977*b*). Together with the experiments on monkeys, the findings indicate that in animals as widely separated as reptiles and primates, the R-complex is basically implicated in conspecific recognition and the organized expression of prosematic behavior.

CONCLUDING COMMENTS

With respect to the striatal complex, there are two other areas of research that are of timely interest. As mentioned earlier, the pineal opening disappeared with the evolution of the more advanced mammal-like reptiles. As is well known, in reptiles with a parietal eye there is a close functional relationship of this structure with the habenular nucleus and the pineal gland. The habenular-peduncular system of structures is strongly developed in terrestrial vertebrates. It not only ties in with the hypothalamus and the accessory optic system, but also receives strong projections from the pallidal part of the striatal complex and from the midbrain. In view of this extensive neural network, it is curious that so few symptoms have been detected in mammals after injury to any part of it. Such results suggest that the system may be so fundamental that, just as a flow of traffic in Paris is assured by many bridges across the Seine, so too the redundant connections of the habenula insure preservation of function in case of injury. As one would be led to expect in view of its evolutionary development, a variety of evidence is accumulating that the habenular system may be involved in thermoregulation and functions of the organism such as reproduction subject to photic influences. Apropos of research on prosematic communication, it should be noted that many of the physical manifestations of thermoregulation also find expression in social communication and in the show of emotion.

The habenular system has also been shown to be under the influence of serotonin- and norepinepherine-containing neurons located in the midbrain, pons, and medulla. As was noted earlier, parts of the striatal complex are rich in serotonin and dopamine. Parent has found that in the turtle the three recognized monoaminergic systems have essentially the same pattern of organization as in the rat (Parent, in press). In a similar study on monkeys, Jacobowitz and I found that the prototypical pattern of organization of monoaminergic systems has been preserved with remarkable fidelity in the evolution of primates (Jacobowitz and MacLean, 1978). Hopefully, the developing work on lizards will not only help to give some insight into the enigmatic functions of the striatal complex, but also of the monoaminergic systems and of the extensive habenular network.

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Forebrain and Midbrain Organization in Lizards and Its Phylogenetic Significance

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SUMMARY. The telencephalon, diencephalon, pretectum, and optic tectum are examined in representatives of all living lizard families. Two patterns of organization in the central nervous system of lizards are suggested on the basis of the observed variation in these brain areas. A *lacertid* pattern is defined, which characterizes taxa of the following families: Anguidae, Cordylidae, Dibamidae, Gekkonidae, Helodermatidae, Lacertidae, Lanthanotidae, Pygopodidae, Scincidae, Xantusiidae, and Xenosauridae. These taxa are compared to *Sphenodon* and are believed to retain more primitive characters than taxa possessing the second, or *iguanid*, pattern. The *iguanid* pattern characterizes taxa of the following families: Agamidae, Chamaeleonidae, Iguanidae, Teiidae, and Varanidae.

The major evolutionary changes in the central nervous system of lizards consist of a hypertrophy and differentiation of a multiple sensory area in the telencephalon, the dorsal ventricular ridge and its related pathways, and pretectum and central and superficial zones of the optic tectum. The functional, behavioral, and phylogenetic implications of these trends are discussed.

INTRODUCTION

Most comparative neuroanatomical studies on lizards have been stimulated by the view that these animals represent an early and simple evolutionary grade of land vertebrates leading to mammals. The assumption has been that if the "simple" brains of reptiles could be understood, then study of more "complex" mammalian brains would be greatly facilitated. Such studies usually have utilized a single species chosen by availability, experimental convenience, and speculation regarding supposed primitiveness.

While it is probably true that mammals, as an adaptive radiation, possess a more complex brain organization than do living reptiles, it is equally true that the living reptiles represent distinct and very different radiations than the reptiles that gave rise to mammals (Romer, 1966). Thus, an understanding of the neural organization and its behavioral correlates in living reptiles may tell us little, if anything, directly regarding the brain and behavior of the reptilian therapsids that gave rise to mammals.

If an examination of living reptiles will not allow us to reconstruct a model of the protomammalian brain, then why study reptiles at all? Besides the obvious answer that we may be interested in reptiles as a successful group of vertebrates occupying a variety of niches and possessing a wide variety of interesting behaviors worthy of study in their own right, the evolutionary biologist can remind us that reptiles were the first vertebrates to be truly terrestrial, and each reptilian radiation has solved many of the major obstacles to successful land invasion in a strikingly different manner (Gans, 1974).

Recognition of these different patterns of adaptation and their advantages and limitations will allow us to understand how different solutions have occurred in response to similar biological problems and, when compared to avian and mammalian solutions, will clearly tell us not only a great deal about living reptiles, but will also add new meaning to the patterns we see in birds and mammals. Thus, I believe the major task of comparative neurobiology is not to reconstruct the probable phylogenetic history of brains "from fish to man," but rather to sample the variation that exists in the brains of living taxa and to recognize common morphological patterns and their adaptive significance. Only by sampling the variation that exists can patterns of common adaptation be recognized. Once these patterns are identified, hypotheses about their biological significance can be formulated and tested.

In this paper I review studies on the organization of the forebrain and midbrain of lizards and report new observations on their morphological variability and histochemical organization. Two distinct patterns of neural organization are recognized in living lizards, and the adaptive significance of these patterns is discussed as well as their possible significance for understanding the phylogeny of lizards.

Several of the illustrations in this review are taken from a manuscript in preparation with Dr. David Senn of the Zoological Institute of the University of Basel. Many of the interpretations of tectal structure and phylogeny presented in this paper have been developed as part of our collaboration.

METHODS

Representatives of the saurian families listed in Table 1 were studied; the nomenclature follows the usage of Underwood (1971). Most of the brains were dissected from the heads, embedded in paraffin, and sectioned in the transverse plane at 15 μ. If an animal was very small, the entire head was sectioned. Sections were stained with a modification of the Bodian silver impregnation technique (Senn, 1966) or with cresyl violet.

Possible intraspecific variation in described neuroanatomical characters was checked by means of multiple brain series (N=20–20) for *Lacerta sicula, Gekko gecko,* and *Iguana iguana.* At the present level of analysis, no intraspecific variation was noted in the brain characters or features described. Many of the morphological characters de-

TABLE 1. LIZARD SPECIES EXAMINED

Dibamidae	*Anelytropsis papillosus*
	Dibamus bourreti
Gekkonidae	*Coleonyx variegatus*
	Gekko gecko
	Ptyodactylus hasselquisti
	Sphaerodactylus cinereus
	Tarentola mauritanica
Pygopodidae	*Lialis burtonis*
Xantusiidae	*Xantusia vigilis*
Iguanidae	*Anolis carolinensis*
	Basiliscus basiliscus
	Callisaurus draconoides
	Crotaphytus collaris
	C. wislizeni
	Ctenosaura hemilopha
	Dipsosaurus dorsalis
	Enyaliosaurus quinquecarinatus
	Iguana iguana
	Phrynosoma cornutum
	P. platyrhinos
	Sceloporus magister
	S. undulatus
Agamidae	*Agama pallida*
	A. stellio
	Calotes versicolor
	Draco sp.
	Physignathus lesueuri
Chamaeleonidae	
	Chamaeleo bitaeniatus
	C. chamaeleon
	C. jacksoni
Scincidae	*Ablepharus kitaibelii*
	Chalcides chalcides
	C. ocellatus
	Eumeces algeriensis
	Mabuya vittata
	Scincella laterale
	Ophiomorus latastii
Lacertidae	*Lacerta sicula*
	L. trilineata
	L. viridis
	L. vivipara
Teiidae	*Ameiva ameiva*
	Bachia intermedias
	Cnemidophorus sexlineatus
	C. tigris
	Dracaena guianensis

	Euspondylus rahmi
	Gymnophthalmus speciosus
	Leposoma parietale
	Neusticurus ecpleopus
	Ophiognomon abendrothii
	Pholidobolus montium
	Prionodactylus argulus
	Proctoporus bolivianus
	Tupinambis nigropunctatus
Gerrhosauridae	*Gerrhosaurus validus*
Cordylidae	*Cordylus cordylus*
	Platysaurus intermedius
Anguidae	*Anguis fragilis*
	Anniella pulchra
	Gerrhonotus multicarinatus
	Ophisaurus compressus
	O. ventralis
Xenosauridae	*Xenosaurus grandis*
Helodermatidae	*Heloderma horridum*
	H. suspectum
Varanidae	*Varanus bengalensis*
	V. flavescens
	V. indicus
	V. niloticus
Lanthanotidae	*Lanthanotus borneensis*

scribed in this study are genus- or family-specific and do not exhibit continuous variation across taxonomic categories.

Histochemistry

Animals were killed by decapitation under sodium pentobarbital anesthesia (20 mg/kg). Following decapitation, the brains were dissected free and then placed in plastic embedding molds containing a commercially prepared, water-soluble resin. Quick-freeze was achieved by immersing the brains in 2-methyl-butane cooled to —70° C. Twenty-five micron transverse sections were then cut on a Harris cryostat at —20°. The sections were immediately attached to slides and dried for 10 minutes in a vacuum-desiccator at room temperature. Two methods for demonstrating enzymatic activities were used: The Koelle method (Gomori, 1952) for acetylcholinesterase (AChE); and the method of Pearse (1960) for succinate dehydrogenase (SDH). Incubation periods ranged from 30 minutes to 2 hours at 30–42° C. An incubation period of 1 hour at 42° C was finally selected as optimal for both histochemical methods. As a control for the specificity of the cholinesterases demonstrated, additional sections were incubated in the reaction mixture with butyrylthiocholine rather than acetylthiocholine as the substrate. No nonspecific cholinesterases were demonstrated by this method.

The regional distribution of enzymatic reactions and their relative activities were analyzed by projecting individual sections and tracing the outline of the sections and the boundaries of the reactive zones. The optical density or absorbance (O.D.) of these zones was then measured using a Photovolt photometer (Model 502M) coupled to a Leitz Ortholux II microscope. The relative O.D. of different zones restricted to a single brain section was determined by setting the photometer to read infinite density when no light fell on the photocell and to read zero density when light was transmitted to the photocell through an area of the brain section judged to be most free of an enzymatic reaction. All measurements were made with a white light source (12v 50W tungsten halogen lamp). O.D. values less than 0.15 were not reported since these values fall within the range of background absorbance of the unstained tissue sections. The range of intensities of the histochemical reactions is reported in terms of O.D. values to avoid the more subjective terms of light, intermediate, or heavy staining reaction which have usually been reported in studies of this nature.

Autoradiography

Three specimens of *Gekko gecko* were processed for autoradiography following the injection of 50 μC of L-(4,5-^{3}H)-proline, 20 μC/μl, with a 5 μl Hamilton syringe and 26-gauge needle. The animals were allowed to survive 24, 48, and 72 hours postoperatively, after which time they were perfused with AFA (90 cc of 80% ethanol, 5 cc of formalin, and 5 cc of glacial acetic acid). The brains were removed from the skulls and stored in AFA for 1 week prior to dehydration and embedding in paraffin. The brains were cut in the transverse plane at 15 μ and defatted. Kodak NTB3 nuclear track emulsion was diluted 1:1 with distilled water at 40° C, and the slides were dipped into the emulsion and dried for approximately 1 hour. The sections were exposed for 20 days and developed in Kodak Dektol and stained with cresyl violet.

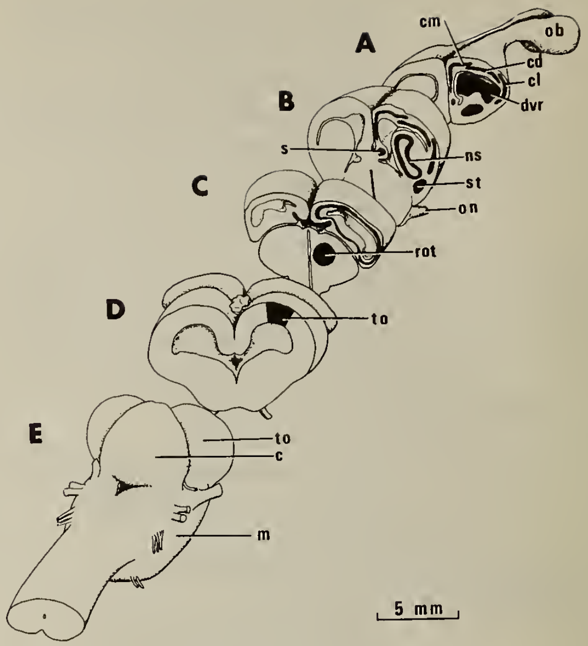

Figure 1. Exploded view of the brain of a teiid, *Tupinambis*, illustrating the relative position of major neural centers described in this work. *c*, cerebellum; *cd*, dorsal cortex; *cl*, lateral cortex; *cm*, medial cortex; *dvr*, dorsal ventricular ridge; *m*, medulla; *ns*, nucleus sphericus; *ob*, olfactory bulb; *on*, optic nerve; *rot*, nucleus rotundus; *s*, septum, *st*, striatum; *to*, optic tectum. (Figure from Northcutt and Senn, in preparation.)

RESULTS AND DISCUSSION: TELENCEPHALON

This brain division in all reptiles consists of paired cerebral hemispheres and a telencephalon medium, that portion of the telencephalon that does not evaginate. The olfactory bulbs, which are secondary evaginations from the cerebral hemispheres, form the rostral pole of the telencephalon (Fig. 1). In lizards, these bulbs may be attached to the cerebral hemispheres by very long slender peduncles, or they may attach directly to the hemispheres. Both conditions can occur within closely related genera and, thus, are unreliable taxonomic characters.

The cerebral hemispheres are divided into a roof (pallium) and a floor (subpallium). The pallium can be subdivided into three longitudinal cellular cortices: a medial cortex, a dorsal cortex, and a lateral cortex; and a large ridge of cells protruding into the lateral ventricle and termed the dorsal ventricular ridge (Figs. 1–3).

The subpallium is divided into a medial zone, including septal nuclei; a ventral zone, including nucleus accumbens and olfactory tubercle; and a lateral zone, including the striatum and amygdaloid nuclei. Rostrally the striatum can be divided into a pars dorsalis and a pars ventralis. The pars dorsalis of the striatum can be traced to the level of the lamina terminalis where it is replaced by part of the amygdaloid complex. The pars ventralis of the striatum continues more caudally and merges with the fibers of the lateral forebrain bundle where its continuation is termed the nucleus entopeduncularis.

The caudal lateral telencephalic wall is formed by a number of nuclei whose embryology is unclear. These consist of a nucleus sphericus, nucleus ventromedialis, and pars posterior of the dorsal ventricular ridge. All of these nuclei have been considered homologous to the amygdaloid nuclei of mammals, though there is no experimental evidence to support this speculation.

At present two very different theories exist regarding the origin and topographical relationships of the amygdaloid nuclei in vertebrates. Herrick (1948) argued that the amygdala of the tiger salamander was the caudal continuation of the corpus striatum and thus of basal (subpallial) origin. In contrast, Johnston (1923) argued that the amygdala consisted of pallial and basal components. Johnston believed the pallial component represented a ventral continuation of the olfactory cortices, while the basal component represented a group of nuclei situated medial to the septal nuclei and dorsal to the striatum. In Johnston's analysis the amygdaloid complex has neither embryonic nor topographical continuity with the corpus striatum. My own observations (Northcutt, 1974) support Johnston's interpretation of the amygdala, but detailed embryological, histochemical, and connectional studies of the caudal telencephalon in reptiles are required to determine which of the nuclei in this region are homologous to the amygdaloid nuclei of other vertebrates. For these reasons I have not discussed the caudal telencephalic nuclei as a single group, and no comparison with the amygdala of other vertebrates has been attempted.

The telencephalon medium consists of a nucleus interstitialis and the preoptic nucleus, as well as the lateral and medial forebrain bundles which interconnect the telencephalon with the diencephalon and medulla.

Few experimental neuroanatomical studies on lizards have been reported, and a rudimentary overview is possible only by utilizing clues provided by experimental studies on other reptiles and by examining the variation in brain structure in lizards. The organization and variation of the major telencephalic components in lizards are described beginning at the dorsomedial edge of the roof, or pallium, and moving laterally, ventrally, and then medially to end the description of the telencephalon with the septal nuclei. Each cytological area is described, its afferent and efferent connections (where known) are summarized, and the variation among taxa is noted.

Pallium

Medial cortex. The exact extent of medial cortex in lizards has been variously defined by different workers (Edinger, 1896; Goldby and Gamble, 1957; Northcutt, 1967; Lohman and Mentink, 1972; see section on dorsal cortex for a more detailed discussion of problem). However, at least two distinct cytological fields have usually been included in descriptions of the medial cortex (Figs. 2, 3): a ventral small-celled component (C2) and a dorsal large-celled component (C1). The cellular organization of these components has been described in *Chamaeleo* (P. Ramon, 1896), *Iguana* (Northcutt, 1967), and *Tupinambis* (Ebbesson and Voneida, 1969). The most common neurons forming the C2 division of the medial cortex are termed double pyramidal cells (Crosby, 1917; Northcutt, 1967). These cells are fusiform or pyramidal in shape with bipolar dendrites that extend into the medial and lateral fibrous laminae of the medial wall. Their axons arise from the cell soma and pass into the lateral (alvear) lamina where they frequently bifurcate. P. Ramon and most subsequent workers have been able to trace axons of these cells as far centrally as the septal nuclei.

The most common neurons forming the C1 division of the medial cortex can be described as small projection or pyramidal cells. These cells possess both apical and basal dendrites. The apical dendrite(s) passes dorsally and branches throughout the extent of the superficial neuropil. The basal dendrites branch in the deep neuropil, and the axons of these cells arise from the somata and pass into the deep neuropil. Their axons, like those of the C2 neurons, bifurcate, and branches can be traced ventromedially as well as laterally within the deep fibrous lamina.

At present the only data on afferents to the medial cortex in lizards relate to interhemispheric connections. Northcutt (1968), Voneida and Ebbesson (1969), Lohman and Mentink (1972), and Butler (1975) have reported that the medial cortices in *Phrynosoma*, *Tupinambis*, and *Gekko* receive reciprocal connections. Additionally these studies have also revealed medial cortical projections to the septal nuclei. This projec-

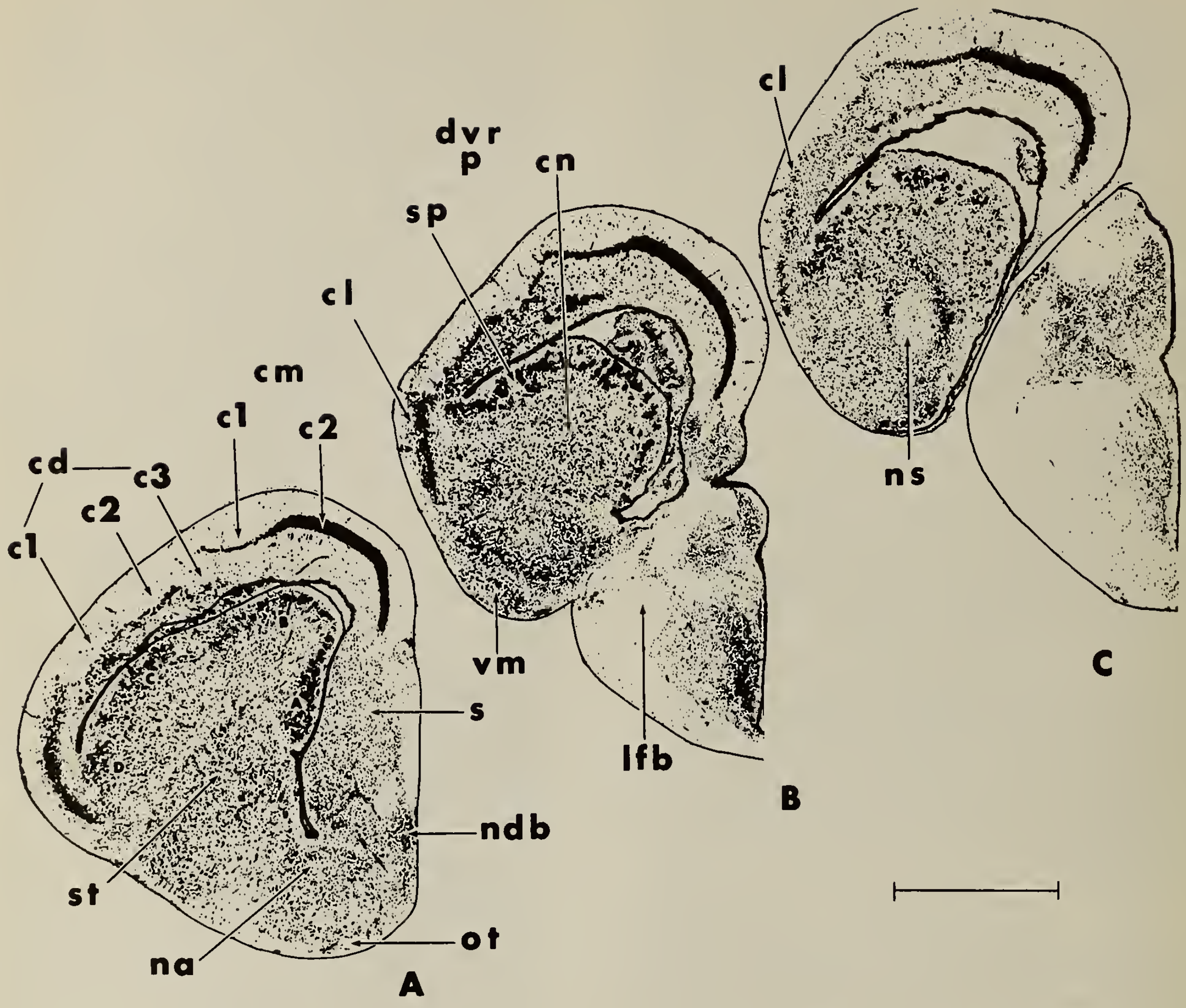

Figure 2. Transverse sections through rostral (A) to caudal (C) levels of the right telencephalic hemisphere of the tokay gecko, *Gekko gecko*, stained to demonstrate neuron cell bodies. Bar scale represents 1 mm. *A–D*, sensory zones of the anterior dorsal ventricular ridge; *cd* (C1–3), dorsal cortex and its subdivisions; *cl*, lateral cortex; *cm* (C1–2), medial cortex and its dorsal (C1) and ventral (C2) subdivisions; *cn*, central or core nucleus of dorsal ventricular ridge; *dvr,p*, posterior dorsal ventricular ridge; *lfb*, lateral forebrain bundle; *na*, nucleus accumbens; *ndb*, nucleus of the diagonal band of Broca; *ns*, nucleus sphericus; *ot*, olfactory tubercle; *s*, septal nuclei; *sp*, superficial or peripheral cellular plate of dorsal ventricular ridge; *st*, striatum; *vm*, nucleus ventromedialis.

tion pattern is strikingly similar to the hippocampo-septal projection in mammals. Added to this similarity are the topographical position of medial cortex and its histochemistry (Baker-Cohen, 1969; Kusunoki, 1971) which strongly suggest that the medial cortex of lizards is homologous to at least part of the hippocampal complex of mammals.

The only report of ascending projections to the medial cortex in lizards is that of Butler and Ebner (1972). They reported fibers from the lateral forebrain bundle coursing over the caudal pole of the telencephalon and terminating in the outer layer of the medial cortex. Their lesions were quite large, and the exact origin of the pathway or pathways was not determined. Parent (1973*a*) has reported monoamine nerve endings in the outer layer of the

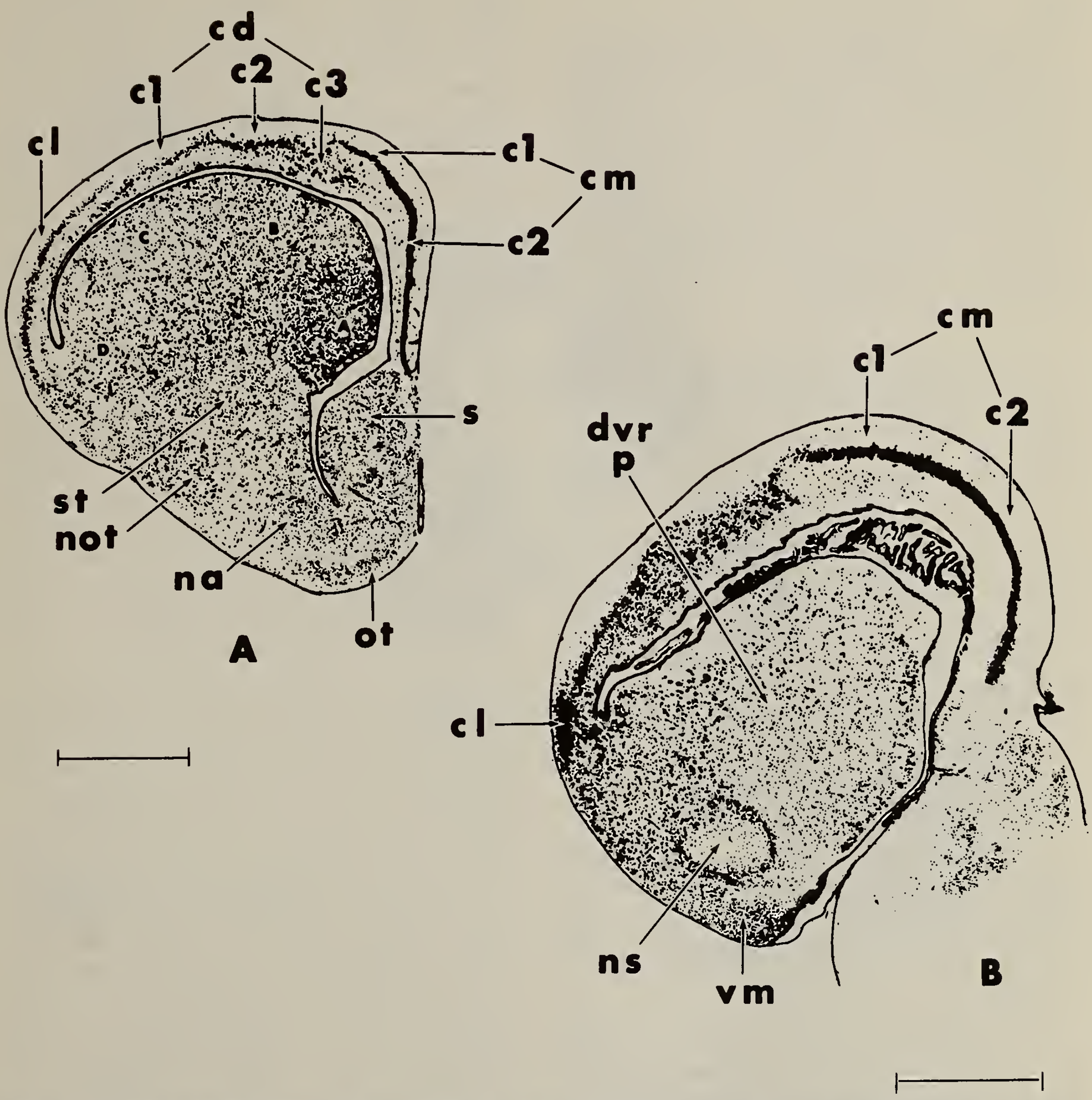

Figure 3. Transverse sections through rostral (A) and caudal (B) levels of the right telencephalic hemisphere of the green iguana, *Iguana iguana*, stained to demonstrate neuron cell bodies. Bar scale represents 1 mm. *A–D*, sensory zones of the anterior division of the dorsal ventricular ridge; *cd*, (C1–3), dorsal cortex and its subdivisions; *cl*, lateral cortex; *cm* (C1–2), medial cortex and its dorsal (C1) and ventral (C2) subdivisions; *dvr,p*, posterior division of the dorsal ventricular ridge, *na*, nucleus accumbens; *not*, nucleus of the lateral olfactory tract; *ns*, nucleus sphericus; *ot*, olfactory tubercle; *s*, septal nuclei; *st*, striatum; *vm*, nucleus ventromedialis.

medial cortex in *Chrysemys*. These fibers appear to originate in the hypothalamus and tegmentum, and similar pathways have been reported in amphibians and mammals (Hedreen, 1971; Northcutt, 1972, 1974; Kicliter and Northcutt, 1975). Thus, it appears likely that lizards also possess an ascending monoamine pathway to the medial cortex, and it is possible that large lesions of the thalamus may have interrupted such an ascending pathway in Butler and Ebner's study.

The medial cortex of gekkonids, pygopodids, and xantusiids has hypertrophied. In the gekkonids and xantusiids the medial cortex is so expanded that it forms a distinct outpocketing of cortex that overlaps the dorsal surface of the olfactory peduncles. These taxa should prove extremely useful in experimental studies directed toward understanding the organization and function of medial cortex in lizards.

Dorsal cortex. The dorsal cortex of lizards has been variably defined and subdivided by different workers (P. Ramon, 1896; Unger, 1906; de Lange, 1911; Shanklin, 1930; Frederikse, 1931; Dart, 1934; Goldby, 1934; Curwen, 1937; Goldby and Gamble, 1957; Filimonoff, 1964; Minelli, 1966; Northcutt, 1967; Ebbesson and Voneida, 1969; Platel, 1969; Lohman and Mentink, 1972; Senn and Northcutt, 1973). Opinions range from those of Minelli (1966) and Platel (1969), who claim that no dorsal cortex exists as a distinct cortical division, to those of Lohman and Mentink (1972), who recognize three subdivisions within dorsal cortex. Three distinct neural populations (Figs. 2,3) can be recognized in the dorsal roof of the telencephalon in most lizards. The nomenclatural arguments really depend on whether or not any or all of these dorsal subdivisions are homologous to isocortical (neocortex) components or to the hippocampal complex in mammals.

An examination of the AChE and SDH enzyme distributions in the dorsal cortex of *Iguana* (Figs. 4, 5) clearly reveals that this area is distinct from the medial roof components. The SDH dense regions are due to high concentrations of mitochondria and usually coincide with terminal sites of major ascending pathways (Friede, 1960; Northcutt, 1973, 1974; Kicliter and Northcutt, 1975). Butler and Ebner (1972) have reported thalamic projections to the dorsal cortex in *Iguana*, but did not specify which subdivisions were involved.

In turtles and crocodiles, electrical potentials in the dorsal cortex can be evoked by photic stimulation (Kruger and Berkowitz, 1960; Orrego, 1961; Moore and Tschirgi, 1962; Belekhova and Kosareva, 1971). Additionally, Hall and Ebner (1970) reported direct lateral geniculate projections to a portion of dorsal cortex in *Pseudemys* that is responsive to photic stimulation. These results suggest that at least part of the dorsal cortex in turtles should be considered homologous to striate isocortex (primary visual cortex) in mammals. Thus, it is likely that at least part of the dorsal cortex in lizards also receives a visual projection from the lateral geniculate nucleus of the thalamus since this pathway is widely present in other land vertebrates. However, Gusel'nikov and Supin (1964) could evoke visual responses from only the dorsal half of the medial cortex (C1) and not from the dorsal cortex in *Agama caucasica.* If this observation is corroborated by other studies, it poses a serious problem regarding the homologs of the dorsal and medial cortices among reptiles.

Northcutt (1968), Lohman and Mentink (1972), and Butler (1975) have reported on the efferent projections of the dorsal cortex in lizards. While the exact details of these studies are not in accord, projections to the medial cortex, septum, and preoptic area of the hypothalamus have been reported. There is considerable variation in the development of the dorsal cortex in lizards, and my analysis to date suggests that this character has low taxanomic value since most of the variation falls within the category of regressive changes. The most common pattern observed is that in which three subdivisions can be recognized (Figs. 2,3). In *Anniella* and *Sphaerodactylus* only two subdivisions can be recognized, and in taxa such as *Anelytropsis* and *Dibamus* the dorsal cortex is barely recognizable and is less than a quarter of the cross-sectional width of either of the other cortices. This is clearly not due to a scaling factor, as other small lizards such as *Scinella* and *Anolis* possess all three subdivisions, and in *Scinella* these are even hypertrophied with regard to the thickness of the cortical plate as seen in cross section.

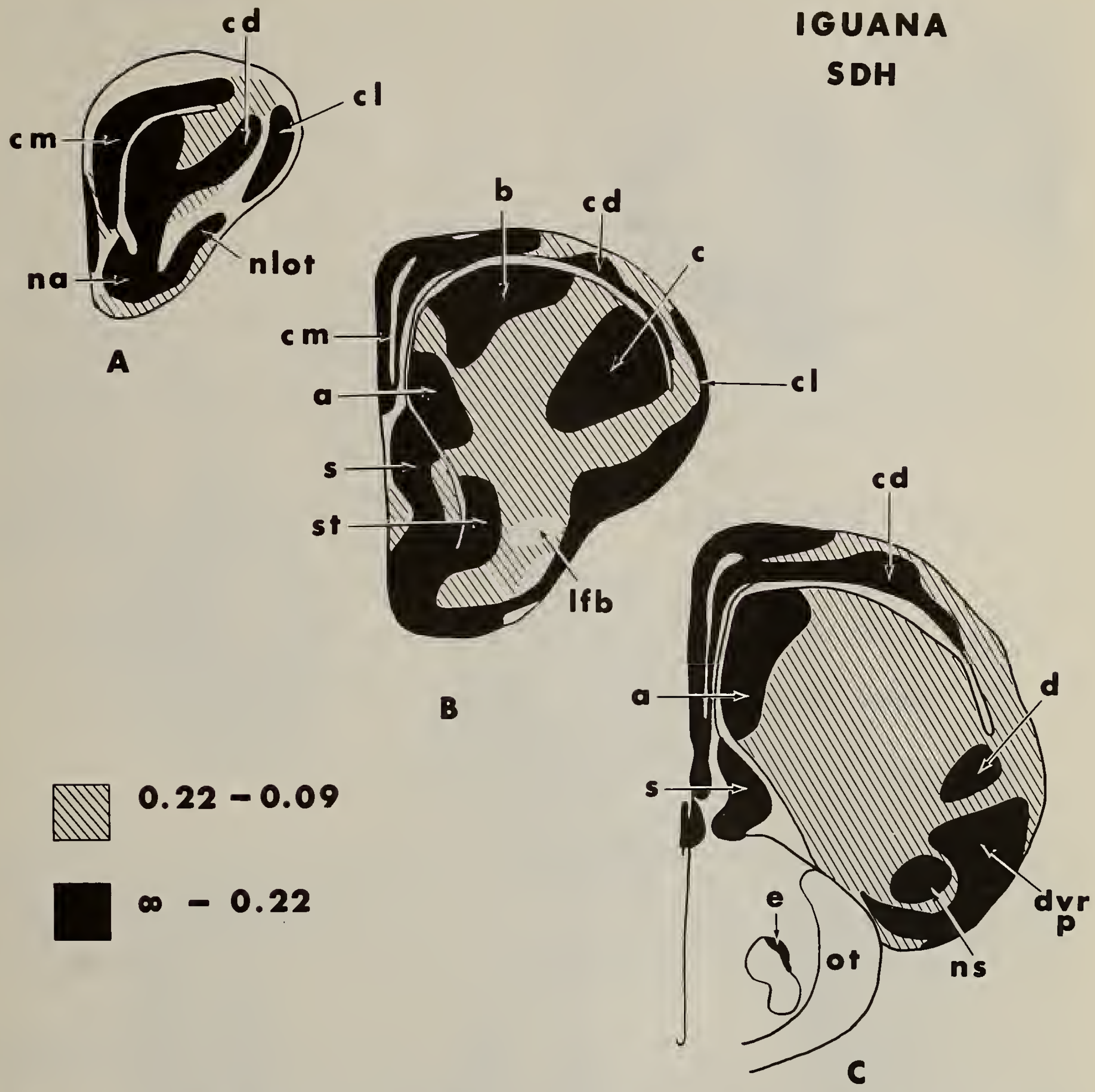

Figure 4. Plot of regional distribution and relative intensity of succinate dehydrogenase in the left telencephalic hemisphere of *Iguana iguana*. Intensity plotted as relative optical absorbance. *A–D*, sensory zones of anterior division of dorsal ventricular ridge; *cd*, dorsal cortex; *cl*, lateral cortex; *cm*, medial cortex; *dvr,p*, posterior division of the dorsal ventricular ridge; *e*, entopeduncular nucleus; *lfb*, lateral forebrain bundle; *na*, nucleus accumbens; *nlot*, nucleus of the lateral olfactory tract; *ns*, nucleus sphericus; *ot*, olfactory tubercle; *s*, septal nuclei; *st*, striatum.

Lateral cortex. The lateral cortex in lizards is the major target of the main olfactory bulb (Goldby, 1937; Gamble, 1952; Heimer, 1969). All lizards possess a pair of laterally situated main olfactory bulbs that receive axons of the olfactory nerves originating from the olfactory epithelium, and medially situated accessory olfactory bulbs that receive axons of the vomeronasal nerves originating from the vomeronasal organ. The main olfactory bulb projects to the ipsilateral anterior olfactory nucleus, olfactory tubercle, the lateral cortex, and, possibly, the rostral part of the

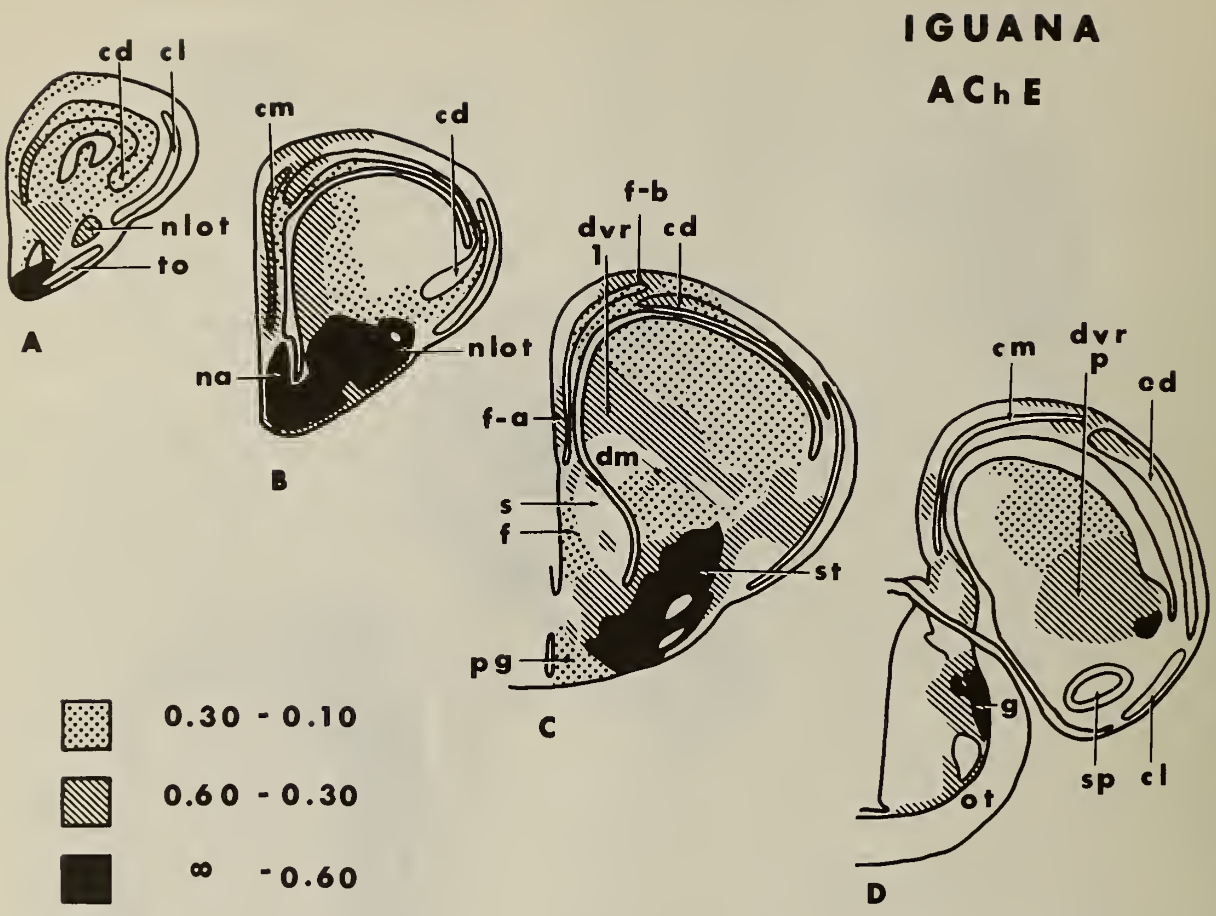

Figure 5. Plot of regional distribution and relative intensity of acetylcholinesterase in the left telencephalic hemisphere of *Iguana iguana*. Intensity plotted as relative optical absorbance. *cd*, dorsal cortex; *cl*, lateral cortex *cm*, medical cortex; *dvr 1*, medial (auditory) zone of the anterior dorsal ventricular ridge; *dvr,p*, posterior division of the dorsal ventricular ridge; *f*, fornix; *f-a,b*, areas of moderate AChE density in dorsal and ventral components of medial cortex; *g*, ventral division of lateral geniculate nucleus: *na*, nucleus accumbens; *nlot*, nucleus of the lateral olfactory tract; *ot*, optic tract; *pg*, preoptic periventricular gray; *s*, septal nuclei; *sp*, nucleus sphericus; *st*, striatum; *to*, olfactory tubercle.

septal nuclei. Contralateral projections are observed to the lateral cortex, and to the anterior olfactory nucleus after crossing in the habenular commissure and running in the contralateral stria medullaris system.

The sole target of the accessory olfactory bulb is the ipsilateral nucleus sphericus (Figs. 2, 3). Nucleus sphericus is cup-shaped with the open end directed rostrolaterally and into which the accessory olfactory tract fibers from the accessory olfactory bulb terminate. The cell bodies of nucleus sphericus thus form the walls and bottom of the cup and send their long apical dendrites toward the center of the cup (Northcutt, 1967). At present the efferent projections of the lateral cortex and nucleus sphericus are unknown in lizards.

Both the main and the accessory olfactory bulbs and their primary targets demonstrate considerable variation in lizards. In arboreal agamids such as *Calotes* and *Draco*, the lateral cortex is present only as a vestige, and the nucleus sphericus is so reduced that no cup-shaped nucleus can be identified. In *Calotes* and in the iguanid *Anolis*, extensive parts of lateral cortex are reduced to a non-neural ependymal layer—the "pallial membrane" (Armstrong, Gamble, and Goldby, 1953). This condition is most likely a case of parallelism between the agamids and iguanids since terrestrial taxa of both families possess a well-developed lateral cortex. In contrast to gekkonids, lacertids, and scincids, the agamids, chamaeleonids, and iguanids all possess a small nucleus sphericus. In some agamids and all chamaeleonids that I have examined, nucleus sphericus is so reduced that it cannot be identified with certainty and will require experimental verification. The teiids, helodermatids, and varanids possess hypertrophied accessory olfactory bulbs, and nucleus sphericus in these taxa shows a number of specializations. In *Heloderma,* this nucleus enlarges until it occupies the entire length of the dorsal ventricular ridge and actually forms a second ridge rostrally overlying the dorsal ventricular ridge (Fig. 6). In many varanids this same nucleus is again so large that the cell plate is thrown into folds giving the nucleus a laminated appearance when seen in cross section (Fig. 7). Clearly the range of variation of the vomeronasal system in lizards is so great that they are an ideal group to examine the possible role of this chemo-system in feeding, territorial, and reproductive behaviors.

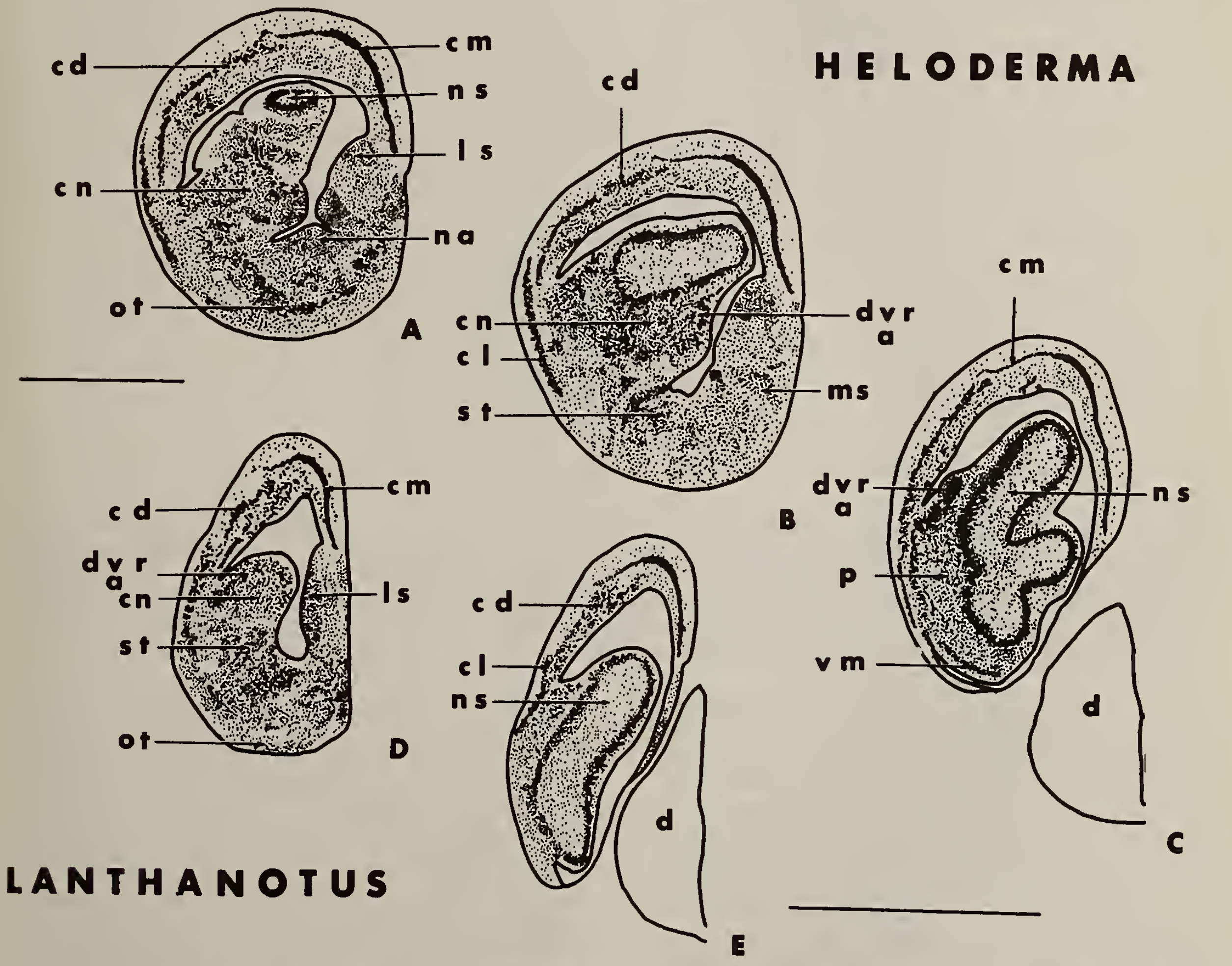

Figure 6. Camera lucida drawings of transverse sections through the right telencephalic hemisphere of *Heloderma* (A–C) and *Lanthanotus* (D–E). Bar scale represents 2 mm. *cd,* dorsal cortex; *cm,* medial cortex; *cn,* central or core nucleus of dorsal ventricular ridge; *d,* diencephalon; *dvr,a,p,* anterior and posterior divisions of the dorsal ventricular ridge; *ls,* lateral septal nucleus; *ms,* medial septal nucleus; *na,* nucleus accumbens; *ns,* nucleus sphericus; *ot,* olfactory tubercle; *st,* striatum; *vm,* nucleus ventromedialis.

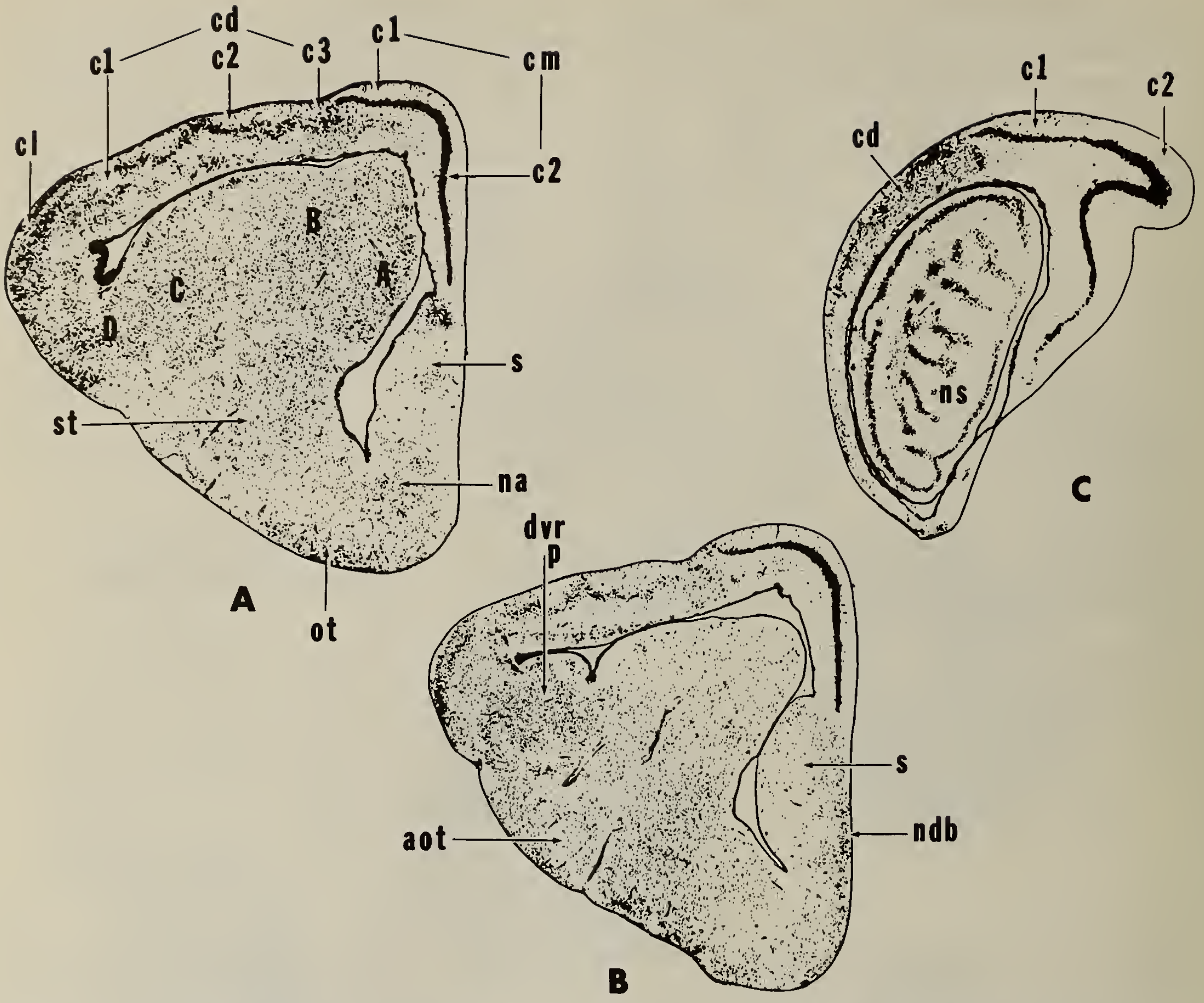

Figure 7. Transverse sections through rostral (A) to caudal (C) levels of the right telencephalic hemisphere of the Indian monitor, *Varanus bengalensis,* stained to demonstrate neuron cell bodies. *A–D,* sensory zones of the anterior dorsal ventricular ridge; *aot,* accessory olfactory tract; *cd* (*C1–3*), dorsal cortex and its subdivisions; *cl,* lateral cortex; *cm* (*C1–2*), medial cortex and its dorsal (C1) and ventral (C2) subdivisions; *dvr,p,* posterior division of the dorsal ventricular ridge; *na,* nucleus accumbens; *ndb,* nucleus of the diagonal band of Broca; *ns,* nucleus sphericus; *ot,* olfactory tubercle; *s,* septal nuclei; *st,* striatum.

Dorsal ventricular ridge. The dorsal ventricular ridge (DVR) of lizards is the single largest pallial unit, and more has been written about it than any other single brain region in reptiles. Until recently, most comparative neuroanatomists (Kappers, Huber, and Crosby, 1936; Crosby, deJonge and Schneider, 1967) regarded the dorsal ventricular ridge as homologous to the caudate and putamen nuclei of mammals. These nuclei constitute the dorsal half of the corpus striatum which occupies the ventrolateral wall of the telencephalon in mammals. The corpus striatum was believed to be the highest center for the correlation of sensory information in nonmammals, and a center mediating instinctual behavior (Herrick, 1948; Krieg, 1953). The hypertrophy of the DVR in reptiles and birds was thus correlated with their supposedly highly developed instinctual behavior, and it was concluded that reptiles possessed only a rudimentary dorsal cortex, homologous to the greatly expanded mammalian isocortex (neocortex).

In the last few years, three lines of evidence have converged to overthrow the view of the DVR as the homolog of mammalian corpus striatum.

(1) Källén (1951) examined the embryonic development of the telencephalon of a number of reptiles including the lizards *Lacerta* and *Chamaeleo.* He concluded that the DVR was of pallial, rather than subpallial, origin. Källén further noted that part of mammalian isocortex arises from the same pallial field that gives rise to the dorsal ventricular ridge in reptiles.

(2) In mammals the corpus striatum can be characterized by the highest concentrations of acetylcholinesterase and dopamine of any telencephalic region (Friede, 1966; Cooper, Bloom, and Roth, 1974). Similarly, in reptiles the ventrolateral wall—beneath the dorsal ventricular ridge, but not the ridge itself—possesses high concentrations of these chemicals (Parent and Olivier, 1970; Kusunoki, 1971; Parent, 1973*a*, 1973*b*; and see Fig. 4). The distribution of AChE is phylogenetically very stable, as the ventrolateral telencephalic wall of fish, amphibians, and birds also possesses similar distributions (Karten, 1969; Braak, 1970; Northcutt, 1973, 1974; Parent, 1975).

(3) Finally, in both birds and reptiles, the DVR has been shown to be the major target of ascending sensory projections from the dorsal thalamus (Karten, 1969; Hall and Ebner, 1970; Butler and Ebner, 1972; Pritz, 1973, 1974*a*, 1975). These same thalamic projections terminate in sensory parts of isocortex in mammals. Thus, all available embryological, histochemical, and connectional evidence argues that the DVR of reptiles should be considered homologous to parts of mammalian isocortex, rather than to mammalian corpus striatum.

The dorsal ventricular ridge of lizards has frequently been divided into anterior and posterior parts (Unger, 1906; deLange, 1911; Rose, 1923; Shanklin, 1930; Goldby, 1934; Curwen, 1938, 1939; Källén, 1951; Northcutt, 1967; Senn and Northcutt, 1973). However, there has been little consistency in recognizing the boundary between these two divisions or the cellular populations forming either division. Several authors have based their divisions on the sulcus neo-archistriaticus of Kappers (1921), a sulcus on the posterodorsal edge of the DVR that lies just rostral to the nucleus sphericus in many lizards (de Lange, 1911; Frederikse, 1931; Goldby, 1934; Filimonoff, 1963). If this boundary is used, the anterior division of the DVR includes all neural populations except nucleus sphericus and the populations immediately lateral to it, which then constitute a posterior division (e.g., Curwen, 1938, 1939). Källén (1951) argued that the cytological differentiation into anterior and posterior divisions was a late embryonic event and of minor morphological significance. Certainly many lizards do not possess a recognizable sulcus neo-archistriaticus, and the presence of this feature may be correlated with the development of the nucleus sphericus, since both are particularly pronounced in varanids and teiids.

An examination of AChE and SDH distributions in the DVR of *Iguana* (Figs. 4, 5) clearly reveals that this area is heterogenous, even excluding nucleus sphericus as a subdivision of the ridge. The ridge can be divided into anterior and posterior subdivisions based on the density and distribution of SDH (Fig. 4). The ridge rostral to the level of the anterior commissure is characterized by at least three dense areas of SDH activity (Fig. 4*B*). As noted earlier, these dense areas are due to high concentrations of mitochondria and have been correlated with terminal sites of major pathways in a number of vertebrate species. In *Iguana*, the terminal targets of ascending thalamic pathways to the anterior DVR closely match the SDH dense areas (Butler and Ebner, 1972; Butler, personal communication). While Butler and Ebner established that the thalamus does project to the anterior DVR, they did not report on discrete lesions of individual thalamic nuclei. However, a number of other reptilian taxa have been examined, and it now appears that at least three different pathways, representing three separate sensory modalities, project to the anterior DVR. In *Pseudemys* (Hall and Ebner, 1970), *Caiman* (Pritz, 1973, 1975), and *Varanus* (Distel and Ebbesson, 1975), approximately the lateral one-third (Fig. 4, area C) of DVR is the target of nucleus rotundus. This nucleus is a dorsal thalamic nucleus that receives projections from the optic tectum (Hall and Ebner, 1970; Butler and Northcutt, 1971a; Braford, 1972; Foster and Hall, 1975). Thus, the lateral anterior division of the DVR receives visual information via a retino-tecto-rotundal circuit.

The medial part of the anterior DVR (Fig. 4, area A) is the target of an ascending auditory pathway (Weisbach and Schwartzkopff, 1967; Foster, 1974; Pritz, 1974*a*, 1974*b*; Distel and Ebbesson, 1975). In *Caiman* and *Iguana,* nucleus reuniens, a dorsal thalamic nucleus, receives projections from the torus semicircularis (Foster, 1974; Pritz, 1974*a*). The torus has been shown to receive auditory information from lower brainstem nuclei by both physiological (Manley, 1971) and experimental neuroanatomical (Foster, 1974) methods, and should be considered homologous to the inferior colliculus of mammals. Nucleus reuniens projects to the medial DVR in *Caiman* (Pritz, 1974*b*), in *Iguana* (Foster and Peele, 1975), and in *Varanus* (Distel and Ebbesson, 1975). The auditory area represents the most caudal continuation of the anterior division of the DVR and can be seen to extend far caudally in the reptiles that have been examined.

A third sensory projection may be present in many reptiles. Lesions of the cervical spinal cord in *Caiman* (Northcutt and Braford, unpublished observations) and in *Tupinambis* (Ebbesson, this conference) reveal an ascending pathway that terminates, in part, in a dorsal thalamic nucleus located just caudal to nucleus rotundus. This caudal thalamic nucleus, nucleus medialis posterior of Huber and Crosby (1926), projects to the central part (Fig. 4, area B) of the anterior division of the DVR in *Caiman* (unpublished observations). At present the type of sensory information carried by this ascending spinal pathway is unknown, but it is likely of a somatic sensory nature. A similar pathway has been reported to exist in the DVR of pigeons (Delius and Bennetto, 1972). This central region of the DVR in birds is known to respond to somatosensory stimulation (Erulkar, 1955).

A fourth high density SDH region can be identified on the lateral boundary of the DVR (area D, Figs. 2,3,4). This region might be considered a part of the ridge, but, because of its dorsal continuity with the lateral edge of the dorsal cortex, it could equally be considered part of the dorsal cortex. Its high concentration of SDH suggests that this region may be the target of yet another undescribed ascending sensory pathway. In this context, it is particularly interesting to note that an ascending trigeminal pathway has yet to be described to the telencephalon of reptiles.

In birds, lesions of the main sensory trigeminal nucleus reveal a pathway that projects directly to a cell population located in the rostral basal telencephalon and termed nucleus basalis (Wallenberg, 1903; Cohen and Karten, 1974). A similar projection is observed in lizards and caimans following isthmal lesions (unpublished observations), and in these reptiles the comparable telencephalic nucleus is termed the nucleus of the lateral olfactory tract (Fig. 3). This nucleus has been clearly misnamed as it does not receive an olfactory projection, but an ascending isthmal projection, probably trigeminal in nature. In birds, nucleus basalis projects to a cell population located on the lateral edge of the dorsal ventricular ridge (Zeier and Karten, 1971), which suggests that the "lateral olfactory nucleus" of reptiles may similarly project to area D located on the lateral edge of the DVR.

The posterior division of the DVR can be characterized by lower levels of SDH, and, with the exception of the auditory ridge target which can be traced caudally into this region, does not appear to receive discrete thalamic projections in *Iguana* (Butler, personal communication) or in *Caiman* (Northcutt and Braford, unpublished observations).

In gekkonids, nucleus sphericus is restricted to the centromedial and caudal quadrant of the ridge area. In these taxa, there are a number of cytological criteria that allow subdivision of the DVR into anterior and posterior parts. The ridge can be divided into a superficial, or dorsal, cellular plate; and a central core throughout its entire rostro-caudal extent (Fig. 2). The cells of the plate are considerably larger than those of the core region and are very similar to the cells that form dorsal cortex. Rostrally, the superficial plate can be divided into at least three areas in a medial to lateral plane on the basis of cell density and differences in the cross-sectional thickness of the plate. In *Gekko,* these cytological subdivisions of the rostral superficial plate coincide with the high density SDH zones, and it is very likely that they correspond to visual, somatic, and auditory thalamic projection targets respectively. However, experimental studies are needed to confirm this hypothesis.

As the superficial plate of the DVR is traced caudal to the anterior commissure, the thickness of the plate decreases and becomes more uniform throughout its lateral to medial extent. Additionally, the cells of the plate form clusters of uniform size which are rather evenly spaced (Fig. 2). This is particularly striking in gekkonids such as *Sphaerodactylus.*

Gekkonids also possess an additional striking cytological feature in the ridge. In these taxa, giant neurons are scattered among smaller cells throughout the superficial cell plate of the dorsal ventricular ridge. In the pars posterior of the DVR there is an increased tendency for these giant cells to be located in the center of the individual cell clusters. Thus, in gekkonids at least two different neuronal populations constitute the superficial cellular plate of the DVR.

In addition to gekkonids, the DVR can be divided into a superficial cellular plate and core in all representatives that I have examined of the following saurian families: anguids, cordylids, dibamids, gerrhosaurids, helodermatids, lacertids, lanthanotids, pygopodids, scincids, xantusiids, and xenosaurids.

However, the iguanids, agamids, chamaeleonids, teiids, and varanids possess a DVR that is organized very differently (Figs. 3,7,8). In these taxa, the ridge is greatly expanded and cannot be subdivided into a superficial plate and core based on differences in either cell density or cell size. At best, a slightly higher density of cells along the extreme ventricular edge of the ridge is seen in some of these taxa and suggests a trace of the superficial cellular plate seen in other families. In lizards with this second type of ridge development, it is almost impossible to recognize anterior and posterior subdivisions on cytological criteria. As in the gekkonids, the SDH activity is much higher in the rostral half of the ridge than in the caudal half and, as in lizards with the first type of ridge development, the anterior ridge can be divided into four regions based on cell density and histochemical differences (Figs. 3,4,7,8). There are no cellular clusters to demarcate the ridge into pars anterior and pars posterior, and the only nonexperimental cytological criterion may be a lower density of cells in the pars posterior.

To date, very little is known regarding the descending projections of the DVR. Hoogland (1975) reports that lesions of the rostral DVR in *Tupinambis* reveal descending pathways that do not extend beyond the telencephalon. Projections were described to the ipsilateral striatum as well as to other parts of the DVR. When parts of the caudal ridge were invaded, an additional projection was observed to the ventromedial hypothalamus. Sligar and Voneida (1976) have reported similar results in *Tupinambis.*

Dorsal ventricular ridge as a taxonomic feature. The dorsal ventricular ridge (DVR) of lizards appears to be a useful taxonomic feature for several reasons. It possesses low intraspecific variation, is regressive in only a few taxa (such as some burrowing forms), is most likely a polygenic feature since the pars anterior is related to a number of different sensory modalities (at least three), and possesses a number of different characters or states that

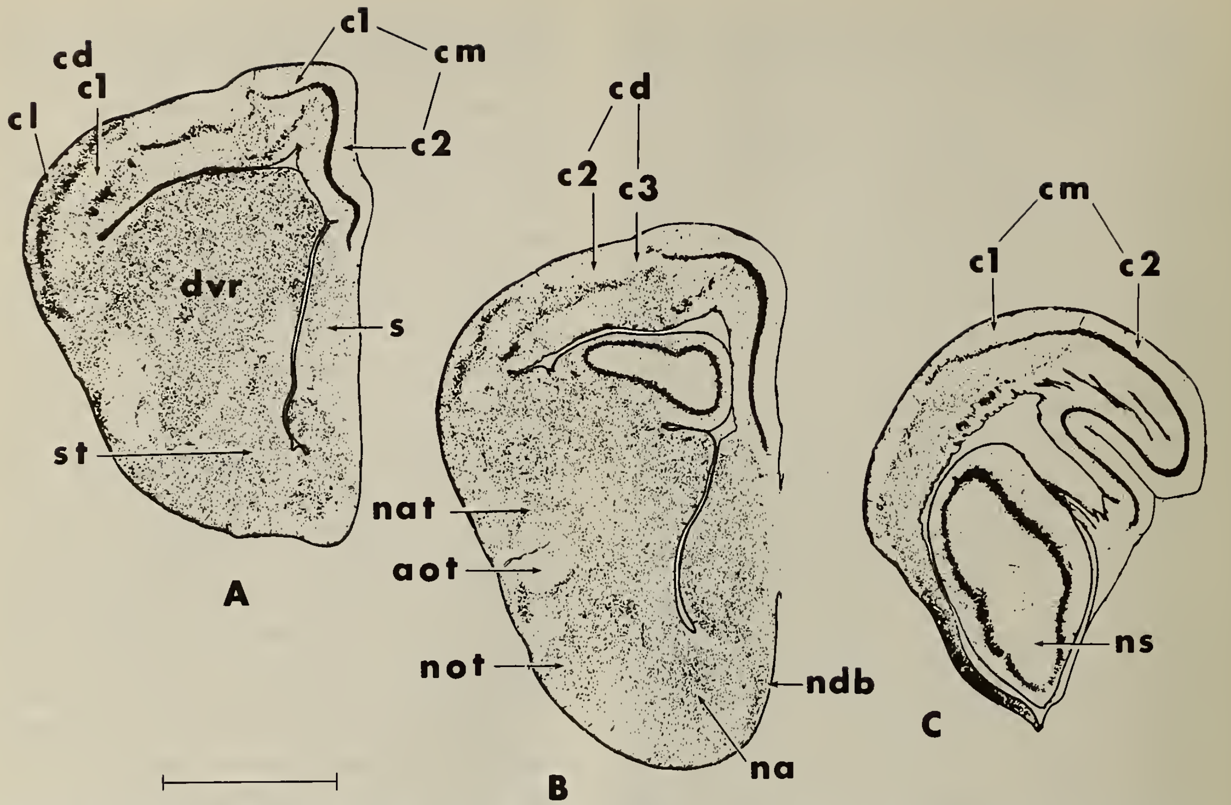

Figure 8. Transverse sections through rostral (A) to caudal (C) levels of the right telencephalic hemisphere of the teiid *Tupinambis nigropunctatus*, stained to demonstrate neuron cell bodies. Bar scale represents 2 mm.*aot*, accessory olfactory tract; *cd*, (*C1–3*), dorsal cortex and its subdivisions; *cl*, lateral cortex; *cm*, (*C1–2*), medial cortex and its dorsal (C1) and ventral (C2) subdivisions; *dvr*, dorsal ventricular ridge; *na*, nucleus accumbens; *nat*, nucleus of the accessory olfactory tract; *ndb*, nucleus of the diagonal band of Broca; *not*, nucleus of the lateral olfactory tract; *ns*, nucleus sphericus; *st*, striatum.

can be related to higher categories as presently defined on the basis of other nonneurological features.

The first type of ridge, divided into superficial cellular plate and core, is probably closer to the ancestral state than is the expanded, complex ridge seen in iguanids and other taxa of the second group. Ancestral characters are usually recognized as characters, or character states, that are scattered irregularly among a wide range of related taxa, and, in many cases, are found outside of the taxonomic category being examined (Mayr, 1969; Lynch, 1973). The rationale is that the more widely a character is distributed, the more distant the relationship indicated and the more remote the common ancestry (Hennig, 1950).

The DVR in most cryptodire turtles is also organized into a superficial cellular plate and central core (Northcutt, 1970).

Furthermore, an examination of the DVR of *Sphenodon*, the sole living rhynchocephalian and, thus, the reptilian taxon most closely related to squamates, reveals a state of development that is even more simple than the dorsal ventricular ridge of squamates or turtles (Fig. 9). The ridge in *Sphenodon* consists of a plate of cells that is continuous with the ventral border of the lateral cortex. No giant cells can be identified in this cellular plate as were seen in gekkonids. The plate cells of the ridge possess multiple apical dendrites which extend ventrally into a neuropil that contains only a few neurons. These migrated neurons may be homologous to the core neurons in the ridge of lizards. SDH preparations of the ridge in

Sphenodon reveal a single high density zone that is restricted to the outer half of the neuropil located beneath the cellular plate. This histochemical distribution suggests that most of the ascending thalamic efferents probably form synapses on the distal shafts of the apical dendrites of the plate cells, rather than on the proximal dendritic shafts or cell bodies as almost certainly is the case in most lizards.

The caudal ridge of *Sphenodon* possesses a number of similarities with the caudal ridge in gekkonids. The caudal ridge in both taxa possess low SDH concentrations and discontinuous clustering of the superficial plate neurons (Figs. 2,9). Unlike most lizards, a nucleus sphericus cannot be recognized in *Sphenodon,* even though a vomeronasal organ has been described (Parsons, 1970). Finally, the cortices in *Sphenodon* are more similar to turtles and crocodiles than to lizards, since they form a continuous plate with no cell-free breaks.

The DVR of *Lialis* and *Xantusia* are most similar to those of the gekkonids. Both *Lialis* and *Xantusia* possess a well differentiated peripheral plate with cell clusters and giant cells. The giant cells tend to be separated from the clusters, rather than located in their center as in gekkonids. The peripheral

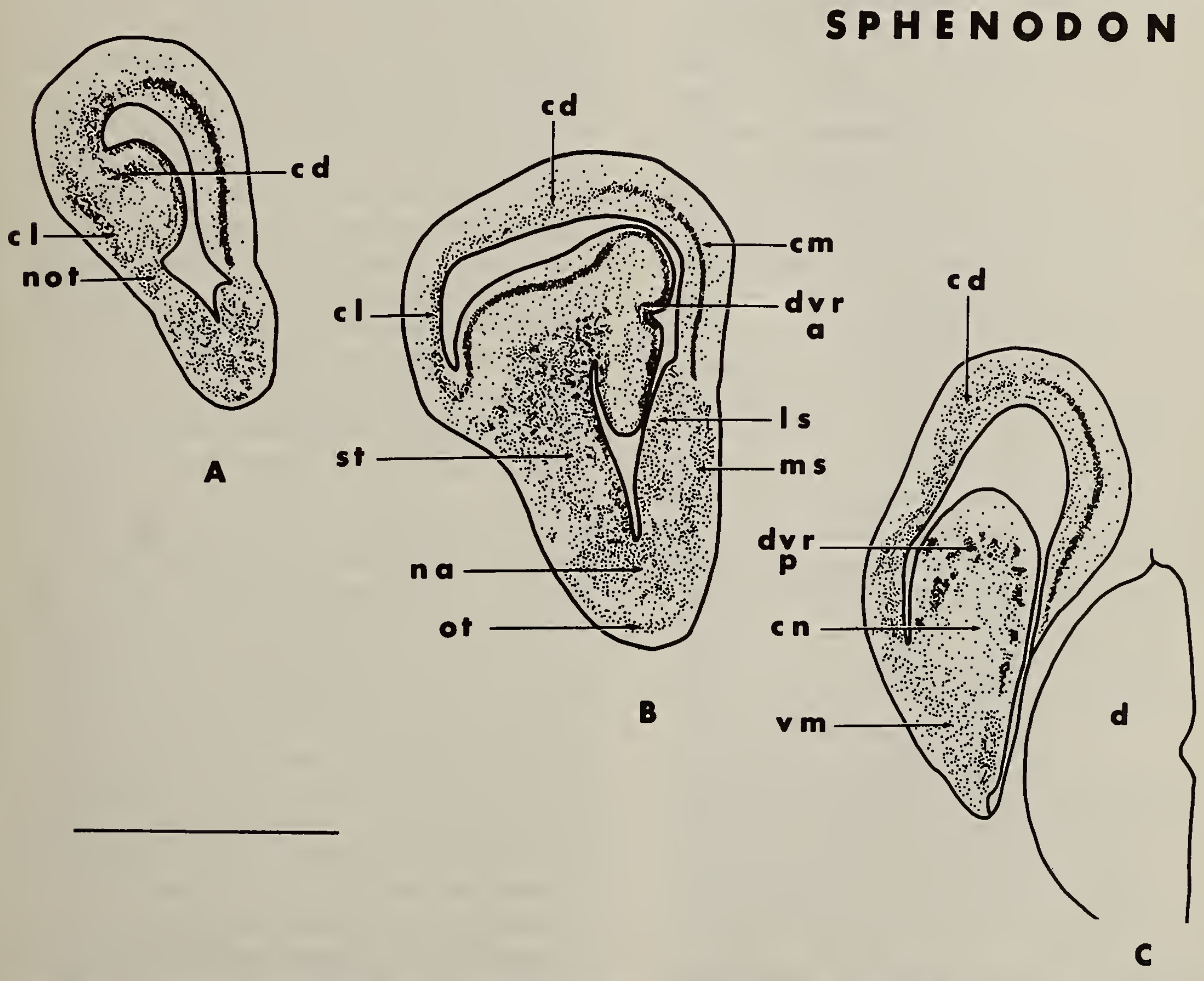

Figure 9. Camera lucida drawings of transverse sections through the right telencephalic hemisphere of the tuatara, *Sphenodon.* Bar scale represents 3 mm. *cd,* dorsal cortex; *cl,* lateral cortex; *cm,* medial cortex; *cn,* core nucleus of the dorsal ventricular ridge; *d,* diencephalon; *dvr,a,p,* anterior and posterior divisions of the dorsal ventricular ridge; *ls,* lateral septal nucleus; *ms,* medial septal nucleus; *na,* nucleus accumbens; *not,* nucleus of the lateral olfactory tract; *ot,* olfactory tubercle; *st,* striatum; *vm,* nucleus ventromedialis.

plate is asymmetrical, with the lateral edge being much thicker.

Xantusia is characterized by a medial ridge plate consisting of a solid sheet of small cells with densely staining nuclei. The medial plate is bounded laterally by a region of large cells whose density is about half that of the core. This region may be a specialized portion of the medial ridge plate and may represent a differential migration of the giant cells. *Lialis* also possesses a similar specialized ridge area, but giant cells can still be seen within the peripheral plate. Experimental studies are needed to further analyze possible ridge specializations in these taxa.

The caudal ridge of *Xantusia* is almost identical to those of gekkonids and *Sphenodon.* Distinct cell clusters are arranged in a single row or peripheral plate, and nucleus sphericus is located immediately ventral. Nucleus sphericus is moderately developed in *Xantusia* as it is in the gekkonids. However, nucleus sphericus in *Lialis* is better developed than in *Xantusia* or in gekkonids.

The DVR of lacertids and scincids are very similar. Both possess a clearly defined peripheral plate and central core. The peripheral plate is asymmetrical as seen in the transverse plane. In both families, the medial plate (area A) is at least half the thickness of the lateral plate (area C). The lateral plate is better developed in lacertids than in scincids, but in both families the cells of the lateral plate show marked clusters, and giant cells (2-3 times the diameter of the other plate cells) are scattered throughout the plate. The core cells are smaller than the plate cells, and the core is about as thick as the plate when seen in the transverse plane. The marked asymmetry in the ridge plate of both families suggests that vision is more extensively represented in the ridge than audition, and that lacertids possess a larger ridge visual area than do scincids. *Dibamus, Anelytropsis, Typhlosaurus,* and *Feylinia,* taxa closely related to scincids, all possess extremely reduced ridge areas and have been discussed in detail elsewhere (Senn and Northcutt, 1973).

The anguids (*Anguis, Anniella, Gerrhonotus,* and *Ophisaurus*) possess an even more extreme asymmetry in the DVR. In all these taxa, the rostral medial plate of the ridge (area A) consists of a plate of cells in contact with the ependymal lining of the ventricle. In these taxa, the plate of area A is 2-8 cells thick, while the core may be 18 times greater in diameter than the plate. At rostral levels, the cells of area A form a solid plate, while more caudally the cells cluster as in gekkonids. The lateral plate is usually 5 times as thick as the medial plate, its cells form the usual clusters, and giant cells are particularly obvious in the lateral plate. In anguids, the core is at least twice the thickness of the lateral plate, and giant cells are located in the core of these taxa.

Anniella exhibits an extreme case among anguids in that rostrally the entire ridge plate, as seen in transverse plane, is reduced to a periventricular layer, 3-5 cells thick. However, even in *Anniella,* giant cells are scattered among the smaller plate cells, the ridge does not appear reduced in volume, and an extensive core is present. More caudally, the plate has migrated away from the ependyma, and the cells are scattered with little tendency to form clusters.

The DVR of *Xenosaurus* closely resembles that of anguids. Rostrally, the medial plate (area A) is 2-3 cells thick and in contact with the ependyma, while the lateral plate (area C) is considerably thicker and characterized by the usual cell clusters. More caudally, the entire plate migrates centrally and forms a layer 4-5 cells thick with little tendency to form cell clusters. The core is extensive throughout and is 4-5 times as thick as the peripheral cell plate. The core cells are slightly smaller than the plate cells, but the difference in their size is not as great as in lacertids and scincids. Nucleus sphericus is not as well developed in *Xenosaurus* as in the anguids, lacertids, and scincids.

The cordylids possess large ridges with pronounced cell clusters throughout, and the cells of the plate and core are approximately the same size. The plate can be distinguished from the core primarily by a greater density of cells. The core is at least twice as thick as the plate when seen in the transverse plane. Because of the similarity in cell size, it is difficult to be certain of the exact boundaries of the plate and core in the rostral ridge. More caudally there is no difficulty in separating plate and core in these taxa as the plate assumes a packing density 2-3 times higher than the core, and the plate cells become far more clustered than the core cells.

The ridge of *Lanthanotus* (Fig. 6), while clearly differentiated into a peripheral plate and core, appears slightly reduced in volume when compared to gekkonids and lacertids. The plate is half the thickness of the core and, while some of the core cells appear as large as the plate cells, the majority are clearly smaller than the plate cells. The plate possesses a cell density twice that of the core, and giant cells are particularly pronounced in the rostral lateral plate. Nucleus sphericus is well developed in *Lanthanotus*.

Heloderma (Fig. 6) possesses a highly distorted ridge due to a greatly expanded nucleus sphericus. Yet the ridge clearly possesses a peripheral plate and a central core. The plate cells are distinctly larger, and their density is twice as high as that of the core. Both *Heloderma* and *Lanthanotus* appear to have slightly reduced ridges. However, this impression may be biased by the extensive development of nucleus sphericus in both taxa.

The DVR's of agamids, iguanids, teiids, and varanids are much enlarged and can be characterized by large cells scattered throughout the entire ridge area. The cell density, peripherally, is the same or slightly lower than the cell density centrally. No distinct cell plate and core can be recognized. All of these taxa possess some cell clustering, particularly in the medial ridge area (area A, Figs. 3,7,8), which may represent the last trace of a peripheral cell plate. It is far more difficult to recognize cytological subdivisions of the rostral ridge in these taxa than in gekkonids or lacertids. The nonexperimental criteria are poorly developed cell free zones marking the edges of areas with differential densities in cell packing. These differences are so slight that, without the observed differences in SDH activity and the experimental results of Foster (1974) and Distel and Ebbesson (1975), it would be foolhardy to recognize subdivisions in these taxa with greatly expanded ridges. Thus, more detailed comparisons among these taxa must await further experimental results.

Subpallium

The striatum. No general agreement exists in the literature regarding the extent and subdivisions of the reptilian striatum. Platel (1971) has recently summarized much of the literature on this topic. Most workers have recognized a medial division, nucleus accumbens, believed to be homologous to the same named nucleus in mammals based on its topographical position. Nucleus accumbens in lizards, as in mammals, can be characterized histochemically by high concentrations of SDH and AChE (Figs. 4,5). Distel and Ebbesson (1975, personal communication) report that nucleus accumbens receives projections from the dorsolateral thalamic nucleus, but not from nucleus rotundus nor reuniens. At present, nothing is known regarding the efferents of nucleus accumbens.

The lateral division of the striatum has been frequently subdivided into dorsal and ventral components (Crosby, 1917; Northcutt, 1967; Distel and Ebbesson, 1975, personal communication). The distribution of AChE in the striatum of *Gekko* and *Iguana* (Fig. 5) supports such a division. A dorsal component with moderate AChE concentrations and a more ventral high density component can be recognized.

However, these striatal components do not constitute homogeneous cell populations. The striatum can be separated from the dorsal ventricular ridge by the dorsal medullary lamina. This lamina consists of a dense layer of fibers with small neurons scattered throughout the fibrous plate. The lamina is easily recognized in Nissl stains, and in AChE preparations it is characterized by moderate to dense activity.

The dorsal striatal component primarily consists of medium-sized cells with little or no AChE activity. The neuropil surrounding these neurons is characterized by moderate AChE activity. A specialized neural lamina or crescent is particularly obvious in the dorsal striatal component of *Iguana*. At mid-telencephalic levels, a particularly conspicuous clustering of cells occurs within the medial half of the dorsal component characterized by high AChE activity. This high density crescent is thus sandwiched between dorsal and ventral moderate AChE zones. A similar, but more diffuse, crescent was identified in *Gekko*.

The ventral striatal component is characterized by high AChE concentrations and can be divided into dorsomedial small-celled and ventrolateral large-celled zones. The large-celled zone has been recognized by most workers (Crosby, 1917; Northcutt, 1967; Hoogland, 1975). The cells possess high concentrations of AChE and are particularly obvious as they are scattered among the fibers of the lateral forebrain bundle which demonstrates little or no AChE activity.

At present, little is known regarding the afferent and efferent connections of the striatum. Hoogland (1975) has reported extensive dorsal ventricular ridge projections to the striatum of *Tupinambis*. Distel and Ebbesson (1975, personal communication) have reported visual and auditory projections via nucleus rotundus and nucleus reuniens to the striatum of *Varanus*.

The only detailed study of the striatal efferents in a lizard is that of Hoogland (1975). He reports striatal projections to nucleus rotundus, habenula, nucleus ventromedialis, nucleus entopeduncularis, substantia nigra, mesencephalic gray, and lateral cerebellar nucleus. For the most part, these projections closely match the projections of the striatum in mammals and suggest that a fully developed ansa lenticularis is present in lizards.

The striatum of *Iguana* is better differentiated than that of *Gekko*. However, since recognition of cytological divisions of the striatum is heavily dependent on histochemical analysis, it is presently impossible to determine the range of variation among lizards. Since the dorsal ventricular ridge projects to the striatum, it is likely that hypertrophy of the ridge leads to hypertrophy of the striatum as well. In birds, the ridge projects only to the dorsal division of the striatum, which, in turn, projects to the ventral division of the striatum, which gives rise to the ansa lenticularis complex (Karten and Dubbeldam, 1973). More detailed analysis of telencephalic efferents are needed in lizards to decide if a similar pattern exists. If a similar pattern of connections does exist in lizards, it would provide strong evidence that the dorsal striatal component is homologous to the caudate and putamen nuclei of mammals, and that the ventral striatal component is homologous to part of the globus pallidus of mammals.

The septal nuclei. Most studies have recognized at least two divisions of the septum, lateral and medial septal nuclei. However, even a cursory examination of the septal complex in reptiles suggests that this region contains more than two recognizable divisions. The septal complex is particularly difficult to subdivide due to the number of fiber systems either terminating within this complex or passing through it. Reasonable subdivision will be possible only as experimental analysis reveals major terminal sites of incoming fibers and septal zones that give rise to major efferent projections.

Recently Ulinski (1975) reported on the corticoseptal projections in *Natrix* and *Thamnophis*. Medial cortex projects bilaterally to a dorsal portion of the precommissural septum with the ipsilateral projection being the more massive. A division of dorsal cortex also projects ipsilaterally to a dorsal portion of the septum caudal to the level of the anterior commissure. This terminal site shifts ventrally in the septum as it is followed rostrally. Ulinski also reported on a possible sparse projection to the ipsilateral ventral septum from the lateral cortex. Lohman and Mentink (1972) and Lohman and Van Woerden-Verkley (1976) have reported similar results in *Tupinambis*. At present, nothing is known regarding septal efferents in lizards, but it is likely that the septal nuclei project to the medial cortex and parts of the hypothalamic complex and tegmentum as in mammals.

There is considerable variation in the size and differentiation of the septal complex in lizards, but detailed cytological, histochemical, and connectional studies on taxa that show considerable septal variation, such as *Gekko* and *Iguana*, must be carried out before this variation can be described with assurance.

RESULTS AND DISCUSSION: DIENCEPHALON

Studies dealing with the organization of the reptilian diencephalon can be divided chronologically into two groups. Prior to 1926, a number of investigators began initial descriptions of many of the cell groups and fiber systems that constitute the diencephalon of reptiles (Stieda, 1875; Bellonci, 1888; C. L. Herrick, 1893*a*, 1893*b*; Meyer, 1893; Rabl-Rückhard, 1894; P. Ramon, 1896; Edinger, 1899; Gisi, 1908; C. J. Herrick, 1910; de Lange, 1913). These studies resulted in a wide range of descriptions and a bewildering array of terms which sometimes described totally different nuclei under the same name, or the same population of cells in different taxa with totally different names. In 1926, Huber and Crosby described the diencephalon of *Alligator mississipiensis* in a clear and concise manner, and subsequent studies have relied heavily on the nomenclature presented in that study.

Since 1926, a number of studies have dealt with the diencephalon of lizards (Shanklin, 1930; Frederikse, 1931; Kuhlenbeck, 1931; Senn, 1968; Butler and Northcutt, 1973; Cruce, 1974). Butler and Northcutt (1973) and Cruce (1974) have reviewed all of the earlier studies and have attempted to clarify the various earlier nomenclatures. The nomenclatures proposed by these last two studies agree, in large part, and will be utilized in the present report. Cruce's description of the hypothalamus is more detailed than that reported by Butler and Northcutt, and the overall treatment of the hypothalamus by Cruce is clearly superior.

Epithalamus, Thalamus, and Hypothalamus

The diencephalon of reptiles has been divided into epithalamus, thalamus, and hypothalamus since the studies of Edinger (1899) and C. J. Herrick (1910). The epithalamus consists of medial and lateral habenular nuclei and the habenular commissure (Fig. 12). Little is known regarding the connections of the habenular nuclei. Hoogland (1975) has suggested, on the basis of preliminary autoradiographic studies, that a portion of the striatum of *Tupinambis* projects to the habenular nuclei. Similar projections have been reported in mammals (Nauta and Mehler, 1966; Nauta, 1974). Projections from other telencephalic centers probably exit via the stria medullaris, but no experimental studies have been conducted on this pathway. As in other vertebrates, a well-developed fasciculus retroflexus exists between the habenular nuclei and the interpeduncular nucleus.

Little attention has been directed toward analysis of the reptilian hypothalamus. This brain region was first described by Edinger (1899). Crosby and Showers (1969) and Cruce (1974) presented comprehensive reviews of the literature and have extensively described the subdivisions of the hypothalamus in reptiles. The same major divisions of the hypothalamus can be recognized in reptiles as in other amniotic vertebrates, and the reader is referred to Cruce's paper for a detailed account of this region. Again, little is known regarding the connections of the reptilian hypothalamus. Our understanding of the neural substrates of reptilian behavior cannot be expected to progress very far until much more data have accumulated on the organization and function of the reptilian hypothalamus.

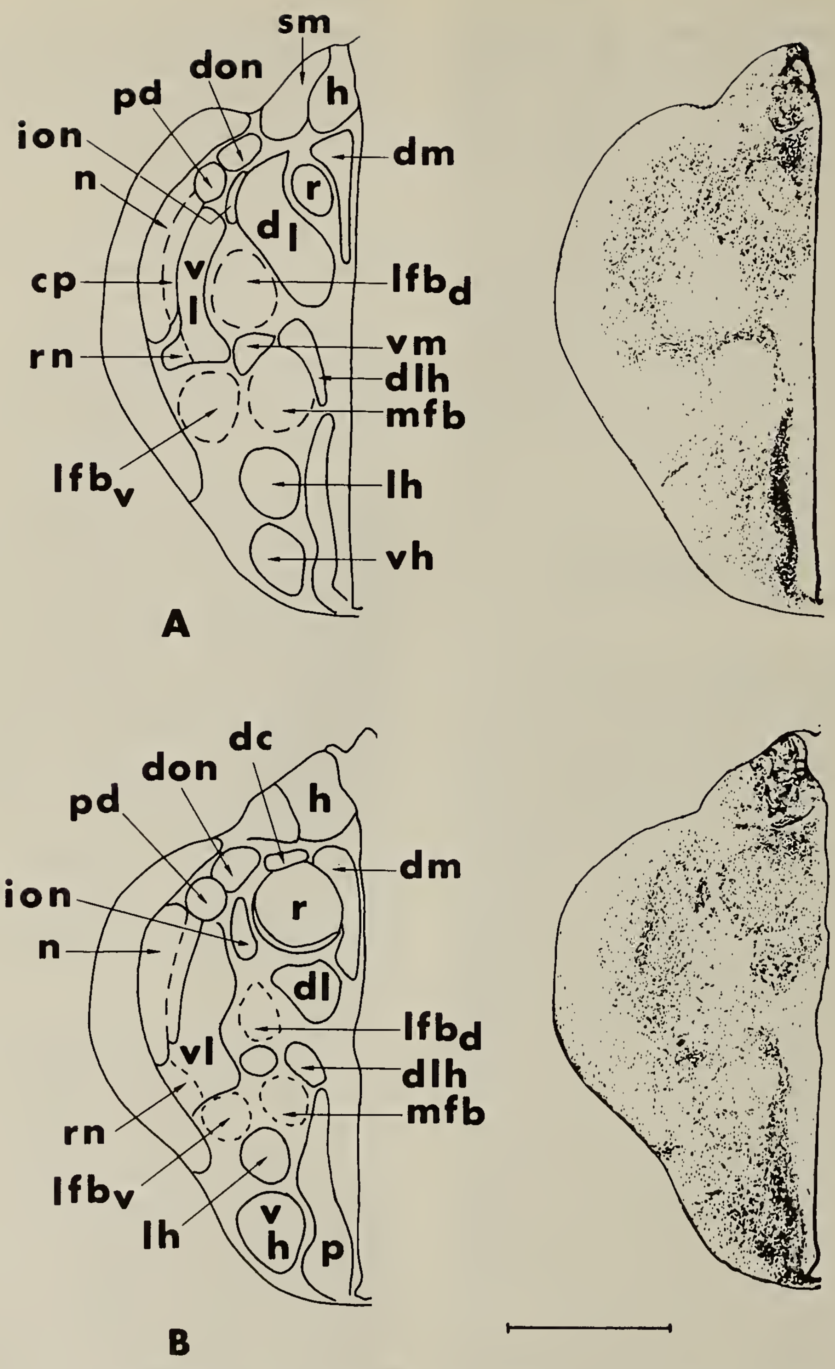

Figure 10. Transverse sections through rostral (A) and mid (B) diencephalic levels of the Tokay gecko, *Gekko gecko*. Bar scale represents 1 mm. *cp*, cell plate of pars ventralis of lateral geniculate nucleus; *dc*, dorsocentral nucleus; *dl*, dorsolateral nucleus; *dlh*, dorsolateral hypothalamic nucleus; *dm*, dorsomedial nucleus; *don*, dorsal optic nucleus; *h*, habenular nuclei; *i.o.n.*, intercalated optic nucleus; *lfb,d*, dorsal peduncle of lateral forebrain bundle; *lfb,v*, ventral peduncle of lateral forebrain bundle; *lh*, lateral hypothalamic nucleus; *mfb*, medial forebrain bundle; *n*, neuropil of pars ventralis of the lateral geniculate nucleus; *p*, periventricular hypothalmic nucleus; *pd*, pars dorsalis of the lateral geniculate nucleus; *r*, nucleus rotundus; *rn*, retinal neuropil of ventrolateral nucleus; *sm*, stria medullaris; *vh*, ventral hypothalamic nucleus; *vl*, ventrolateral nucleus; *vm*, ventromedial nucleus.

Thalamus. Most workers since the turn of the century have divided the thalamus of reptiles into dorsal and ventral divisions. These divisions have been assumed to be the homologs of the similarly named thalamic divisions in mammals. However, to date there is no experimental evidence either to support or reject this hypothesis.

The ventral thalamus of lizards can be divided into the following nuclei: area triangularis, nucleus ventrolateralis, nucleus ventromedialis, nucleus entopeduncularis, and nucleus geniculatus lateralis (Figs. 10-13). The ventral thalamus begins just caudal to the preoptic recess of the hypothalamus. At this level the ventral thalamus consists of a plate of cells (area triangularis) arching over the forebrain bundles (Fig. 12). At more caudal levels the area triangularis is split into lateral and medial divisions by the dorsal peduncle of the lateral forebrain bundle. The caudal continuation of the lateral

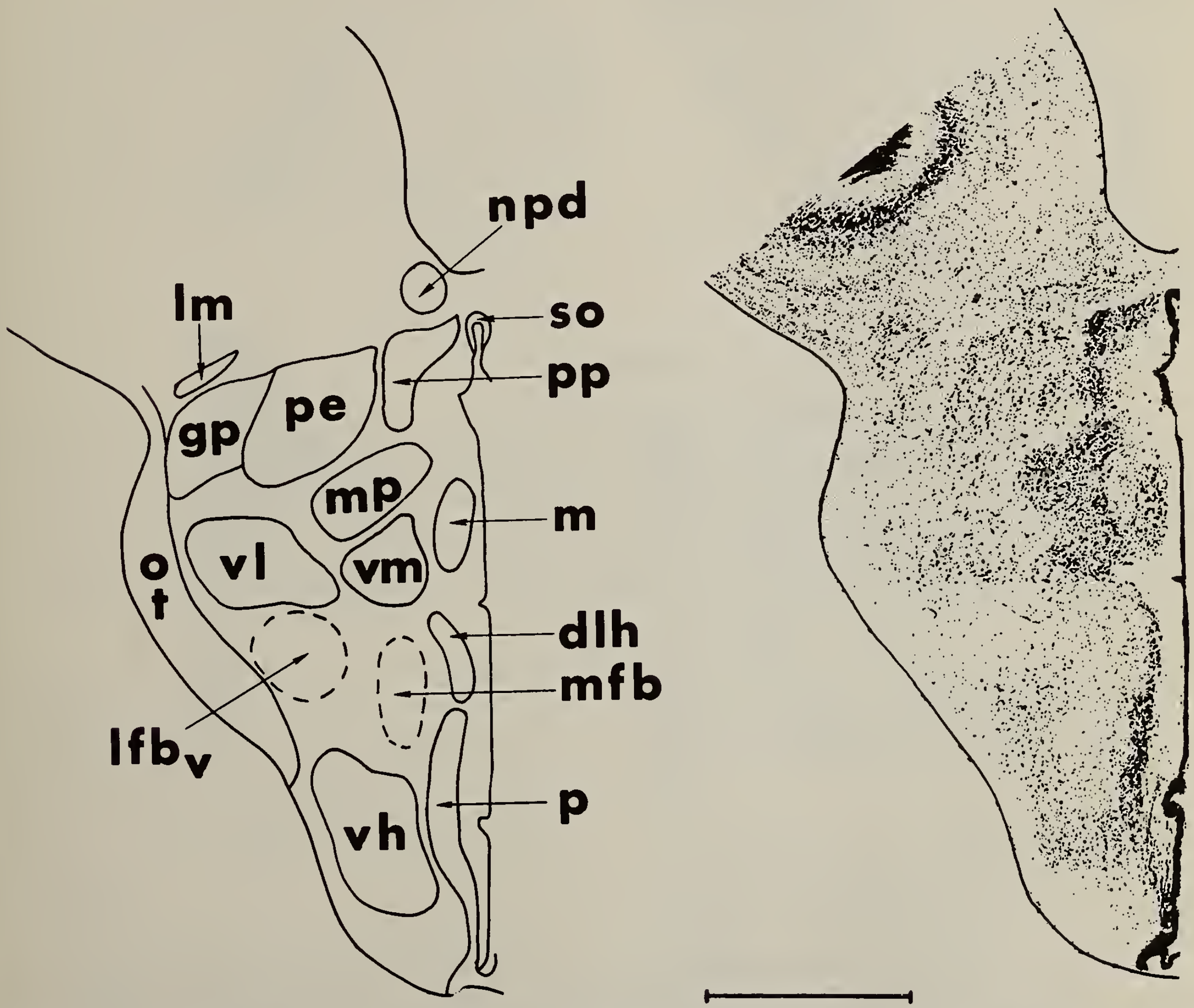

Figure 11. Transverse section through the caudal diencephalon of the Tokay gecko. Bar scale represents 1 mm. *dlh,* dorsolateral hypothalamic nucleus; *gp,* nucleus geniculatus pretectalis; *lfb,v,* ventral peduncle of the lateral forebrain bundle; *lm,* nucleus lentiformis mesencephali; *m,* nucleus medialis; *mfb,* medial forebrain bundle; *mp,* nucleus medialis posterior; *npd,* nucleus posterodorsalis; *ot,* optic tract; *p,* periventricular hypothalamic nucleus; *pe,* pars extensa of nucleus lentiformis thalami; *pp,* pars plicata of nucleus lentiformis thalami; *so,* subcommissural organ; *vh,* ventral hypothalamic nucleus; *vl,* ventrolateral nucleus; *vm,* ventromedial nucleus.

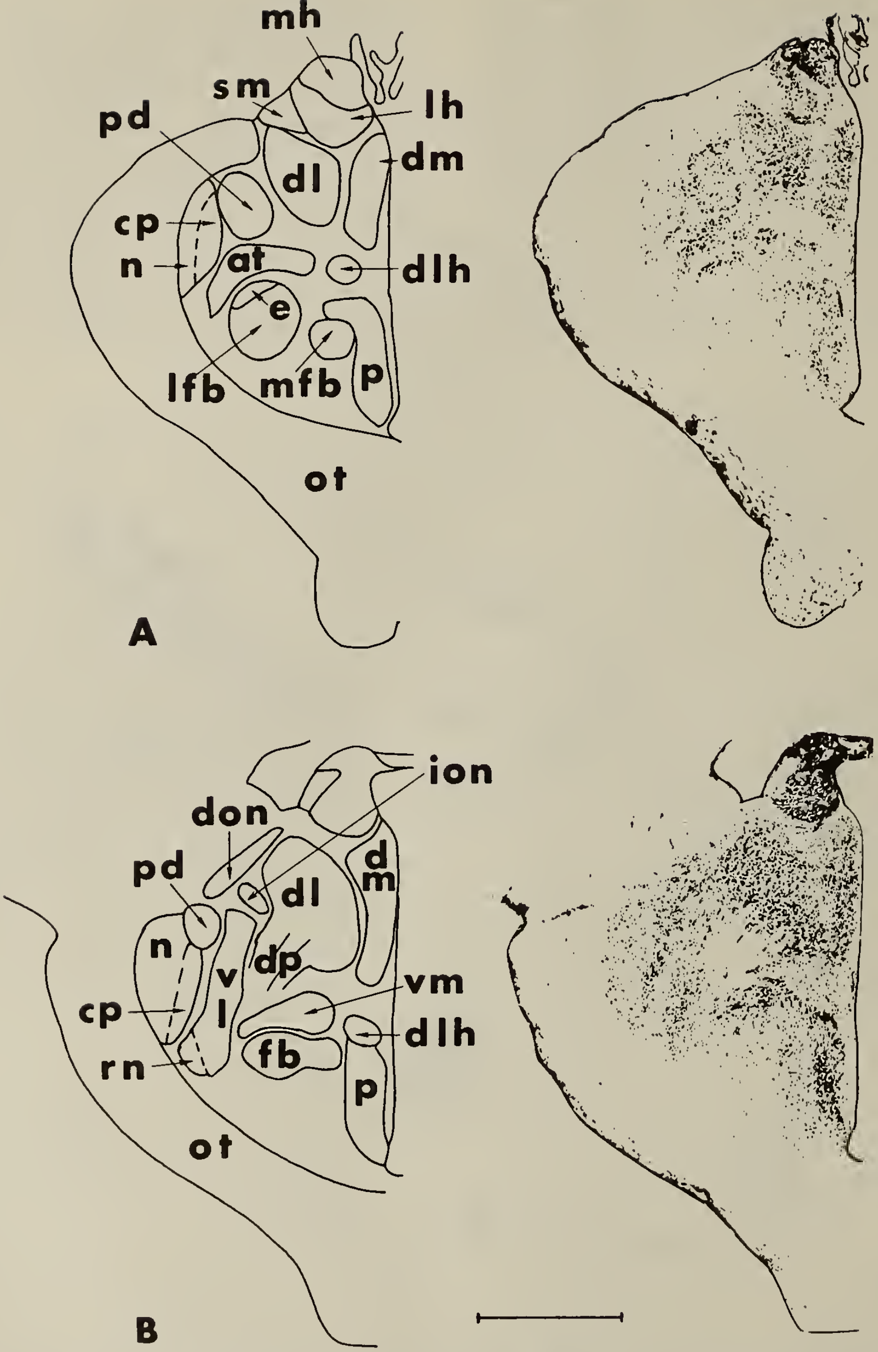

Figure 12. Transverse sections through rostral (A) and mid (B) diencephalic levels of the green iguana, *Iguana iguana*. Bar scale represents 1 mm. *at*, area triangularis; *cp*, cell plate of the pars ventralis of the lateral geniculate nucleus; *dl*, dorsolateral nucleus; *dlh*, dorsolateral hypothalamic nucleus; *dm*, dorsomedial nucleus; *don*, dorsal optic nucleus; *dp*, pars dorsalis of the lateral geniculate nucleus; *e*, nucleus entopeduncularis; *fb*, forebrain bundles; *i.o.n.*, intercalated optic nucleus; *lfb*, lateral forebrain bundle; *lh*, lateral habenular nucleus; *mh*, medial habenular nucleus; *mfb*, medial forebrain bundle; *n*, neuropil of the pars ventralis of the lateral geniculate nucleus; *ot*, optic tract; *p*, periventricular hypothalamic nucleus; *pd*, pars dorsalis of the lateral geniculate nucleus; *rn*, retinal neuropil of ventrolateral nucleus; *sm*, stria medullaris; *vl*, ventrolateral nucleus; *vm*, ventromedial nucleus.

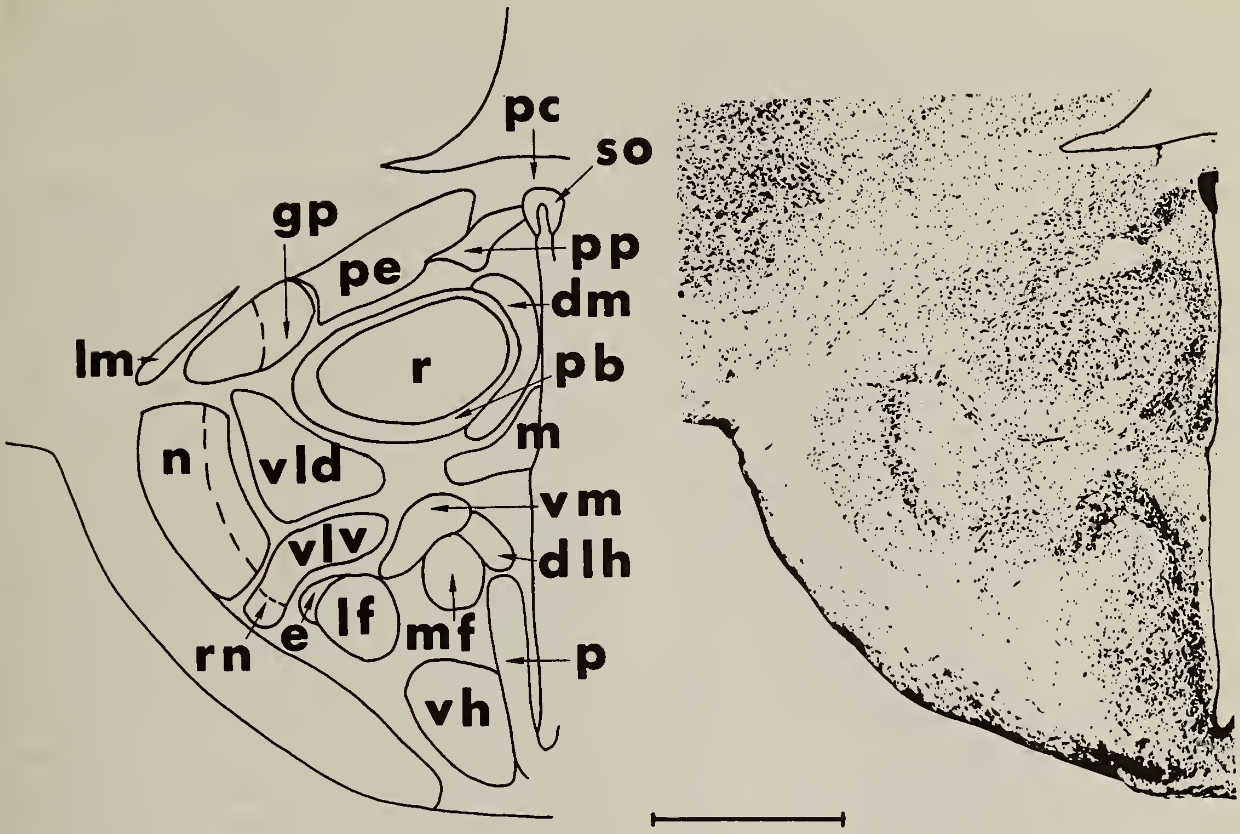

Figure 13. Transverse section through the caudal diencephalon of the green iguana. Bar scale represents 1 mm. *dlh*, dorsolateral hypothalamic nucleus; *dm*, dorsomedial nucleus; *e*, nucleus entopeduncularis; *gp*, nucleus geniculatus pretectalis; *lf*, lateral forebrain bundle; *lm*, nucleus lentiformis mesencephali; *m*, nucleus medialis; *mf*, medial forebrain bundle; *n*, neuropil of the pars ventralis of the lateral geniculate nucleus; *p*, periventricular hypothalamic nucleus; *pb*, perirotundal belt; *pc*, posterior commissure; *pe*, pars extensa of the nucleus lentiformis thalami; *pp*, pars plicata of the nucleus lentiformis thalami; *r*, nucleus rotundus; *rn*, retinal neuropil of the ventrolateral nucleus; *so*, subcommissural organ; *vh*, ventral hypothalamic nucleus; *vld*, pars dorsalis of the ventrolateral nucleus; *vlv*, pars ventralis of the ventrolateral nucleus; *vm*, ventromedial nucleus.

division of area triangularis is termed nucleus ventrolateralis, and the caudal continuation of the medial division is termed nucleus ventromedialis. These two nuclei extend throughout the entire diencephalon, reaching the level of the nucleus interstitialis which marks the beginning of the mesencephalic tegmentum.

Nucleus ventrolateralis can be divided into dorsal and ventral components. The ventral component consists of a medial cell plate and a lateral neuropil. This ventral component receives direct contralateral retinal and ipsilateral tectal projections (Butler and Northcutt, 1971*a*, 1971*b*; Ebbesson, 1972; Northcutt and Butler, 1974). Nucleus ventrolateralis also appears to receive projections from an ascending spinothalamic pathway (unpublished observations). Nothing is known regarding the efferent projections of this nucleus.

At present, the only known projection to nucleus ventromedialis arises from the medial part of the striatum (Hoogland, 1975). This pathway constitutes part of the ventral peduncle of the lateral forebrain bundle and probably is homologous to part of the ansa lenticularis complex of mammals. Nucleus entopeduncularis (Fig. 12) also receives a projection from the striatum in *Tupinambis* (Hoogland, 1975); this nucleus is a collection of cells scattered along the dorsal edge of the lateral forebrain bundle (Fig. 12). Throughout much of its rostro-caudal extent it is difficult to separate nucleus entopeduncularis from the more dorsal nucleus ventromedialis. Again, nothing is known about the efferent projections of nucleus entopeduncularis.

When the efferent projections of nucleus ventrolateralis and nucleus ventromedialis are known, it will be possible to decide whether these nuclei are homologous to parts of the dorsal or ventral thalamus of mammals. The striatum and spinal cord of mammals project to both the dorsal and ventral thalamus. Thus the afferents presently determined for the nuclei of the presumed ventral thalamus of lizards cannot resolve this problem. However, the striato-recipient dorsal thalamic nuclei (ventral anterior and ventral lateral thalamic nuclei) of mammals project to isocortex, while the striato-recipient ventral thalamus (subthalamic nuclei) projects back on the striatum. If nucleus ventromedialis projects to the dorsal ventricular ridge, this nucleus should be considered part of the dorsal thalamus of lizards and homologous to part of the dorsal thalamus of mammals. If nucleus ventromedialis projects to the striatum, it should be considered homologous to part of the ventral thalamus of mammals.

Nucleus geniculatus lateralis occupies the lateral edge of the ventral thalamus. It begins rostrally at the level of area triangularis and continues caudally under the rostral pole of the optic tectum (Figs. 10-14). Most workers have recognized a pars dorsalis and a pars ventralis. The pars dorsalis forms an oval-shaped cluster of cells dorsally and can be easily separated from the pars ventralis which is divided into a medial cell plate and a lateral neuropil (Figs. 10-14). Both the pars dorsalis and pars ventralis receive a bilateral retinal projection in *Lacerta* (Armstrong, 1950), *Iguana* and *Anolis* (Butler and Northcutt, 1971*b*), *Xantusia* (Butler, 1974), *Gekko* (Northcutt and Butler, 1974) and *Tupinambis* (Cruce and Cruce, 1975). Butler and Northcutt (1971*a*) and Foster and Hall (1975) have reported bilateral tectal projections to the pars ventralis of the lateral geniculate nucleus in *Iguana*. At present nothing is known regarding the efferent projections of the pars ventralis.

The pars dorsalis of the lateral geniculate nucleus in lizards has been assumed to be a part of the dorsal thalamus and has further been assumed to project to the dorsal cortex of the telencephalon, as does a similarly named nucleus in turtles as reported by Hall and Ebner (1970). However, this assumption must now be questioned on the basis of the discovery of four new retino-recipient nuclei in the rostral dorsal thalamus of lizards and other reptiles (Figs. 10,12; Butler and Northcutt, 1977). Most recent studies on the visual system of lizards have recognized a bilateral retinal projection to a small oval-shaped cluster of cells that caps the cell plate and neuropil of the pars ventralis of the lateral geniculate nucleus. This cell cluster has been assumed to be the most dorsal target of the optic tract in the rostral thalamus of lizards (*Lacerta*, Armstrong, 1950; *Iguana* and *Anolis*, Butler and Northcutt, 1971*b*; *Tupinambis*, Ebbesson, 1972, Cruce and Cruce, 1975; *Gekko*, Northcutt and Butler, 1974). However, in describing the retinal projections in *Gekko* (Northcutt and Butler, 1974), we were puzzled by the presence of a retinal terminal field located dorsal to the cell group that we labeled pars dorsalis of the lateral geniculate nucleus (Fig. 3, Northcutt and Butler, 1974). This terminal field was charted but not discussed. In the same year an autoradiographic study of the retinal projections in *Sphenodon* was undertaken (Northcutt, Braford and Landreth, 1974), and an equally extensive retinal target was discovered dorsal to the pars dorsalis of the lateral geniculate nucleus and was termed the dorsal optic nucleus. Subsequently, this same target has been identified in *Caretta* (Bass and Northcutt, 1975) and in *Caiman* (Braford and Northcutt, in preparation). This new target probably corresponds to the cell group identified by Knapp and Kang (1968) in *Podocnemis* as the pars dorsalis of the lateral geniculate nucleus. In

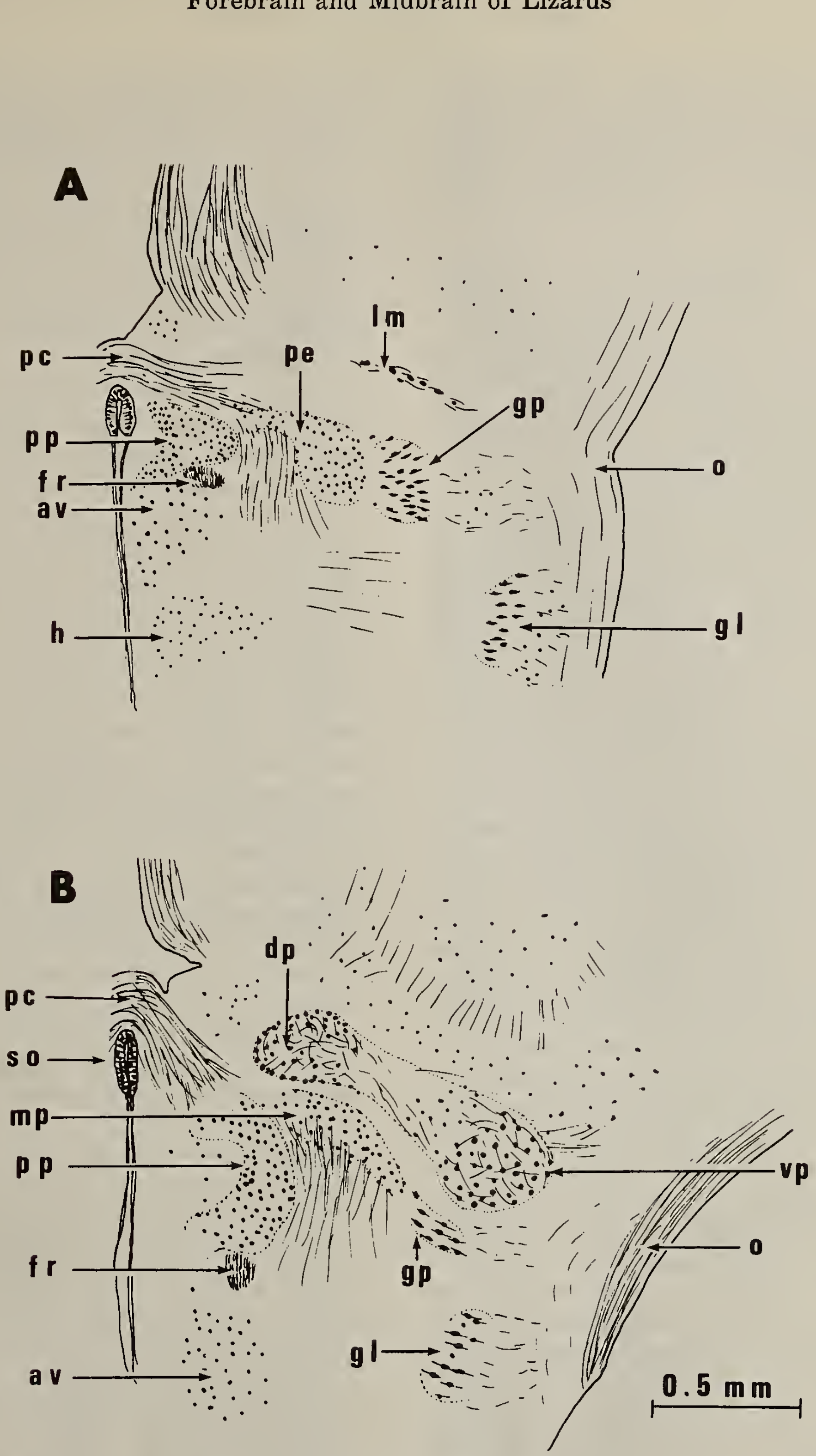

Figure 14. Camera lucida drawings of the pretectum of *Lacerta* (A) and *Iguana* (B). *av*, area ventralis; *dp*, dorsal pretectal nucleus; *fr*, fasciculus retroflexus; *gl.* pars ventralis of the lateral geniculate nucleus; *gp*, nucleus geniculatus pretectalis; *h*, hypothalamus; *lm*, nucleus lentiformis mesencephali; *mp*, medial pretectal nucleus; *o*, optic tract; *pc*, posterior commissure; *pe*, pars extensa of nucleus lentiformis thalami; *pp*, pars plicata of nucleus lentiformis thalami; *so*, subcommissural organ; *vp*, ventral pretectal nucleus. (Figure after Northcutt and Senn, in preparation.)

Podocnemis this cell group is particularly well developed, as large as the pars ventralis of the lateral geniculate nucleus, and its development appears to reach a peak in these pleurodires.

In all the reptiles I have examined, the dorsal optic nucleus lies lateral to nucleus dorsolateralis anterior, but does not appear to be a division of this nucleus. In lizards the dorsal optic nucleus begins rostrally, lateral to nucleus dorsolateralis anterior, but continues caudally to lie adjacent to nucleus rotundus, and ends just rostral to nucleus geniculatus pretectalis (Figs. 10, 12).

In reexamining the retinal projections in a number of reptiles with the new autoradiographic methods, a second new retinal target has been discovered medial to the dorsal optic nucleus. This nucleus has been termed nucleus dorsocentralis (Fig. 10). A slip of the optic tract turns medially and passes the caudal pole of nucleus dorsolateralis anterior to enter a population of cells that lie immediately dorsal to nucleus rotundus. Papez (1935) described this cell group in *Chelonia* and termed it the nucleus (centralis) lateralis (his Figs. 5, 6). This new retinal target, nucleus dorsocentralis, has also been seen in *Caretta* (Bass and Northcutt, in preparation) and in *Caiman* (Braford and Northcutt, in preparation), but not in *Sphenodon.*

A third and a fourth retinal target, not previously described to my knowledge, are also revealed in autoradiographic preparations of *Gekko* and *Iguana* (Butler and Northcutt, 1977). Both of these targets lie medial to the lateral geniculate nuclei. Optic fibers stream through the geniculate nuclei and terminate in the dorsal half of the pars dorsalis of nucleus ventrolateralis (Figs. 10*B*, 12*B*) and a previously undescribed cell group termed the intercalated optic nucleus (Fig. 11). Each of these new optic nuclei receives optic fibers via separate and distinct fascicles leaving the optic tract, and each nucleus is cytologically distinct from the adjacent geniculate nuclei. Thus, five separate and distinct cell populations (pars dorsalis of the lateral geniculate nucleus, intercalated optic nucleus, dorsal optic nucleus, nucleus dorsocentralis and pars dorsalis of nucleus ventrolateralis) exist in the rostral thalamus of many reptiles which receive direct retinal projections. The small size and close proximity of these nuclei will complicate an experimental analysis of their efferents. In an attempt to determine their efferent projections, it is probably impossible to place electrolytic lesions in these nuclei because of the problem of interrupting axons of passage. However, the newer retrograde horseradish peroxidase transport method should allow resolution of the efferents of these retino-recipient thalamic nuclei.

Ten years ago comparative neuroanatomists were wondering if nonmammalian vertebrates would possess a homolog of the mammalian pars dorsalis of the lateral geniculate. Now we are faced not with a single nucleus but with five possible candidates. A similar situation exists in birds. Five distinct cell populations located dorsal to the pars ventralis of the lateral geniculate nucleus receive direct retinal projections in birds (Repérant, 1973; Miceli, Peyrichoux and Repérant, 1975). Unlike mammals, in which only a single ipsilateral retino-thalamo-cortical projection has been reported, birds appear to possess at least two, and perhaps three, such pathways (Hunt and Webster, 1972; Karten, Hodos, Nauta and Revzin, 1973; Miceli, Peyrichoux and Repérant, 1975). Not only does the number of pathways in birds appear to be greater than in mammals, but one pathway is ipsilateral and at least one is bilateral.

The topography in lizards as well as the number of rostral thalamic nuclei that receive direct retinal projections are more similar to birds than to mammals, and it is likely that additional retino-thalamo-telencephalic projections will soon be discovered in reptiles. Until much more work has been done on the visual system of lizards and other reptiles, it is impossible to decide which, or how many, of the retino-recipient thalamic nuclei are homologous to the dorsal geniculate nucleus of mammals. Equally important, it now appears likely that lizards will be shown to possess several different visual pathways to the telencephalon and that these pathways may subserve very different visual functions.

In addition to the retino-recipient nuclei that have been described, the dorsal thalamus of lizards is formed by a number of nuclei. These nuclei are: nucleus dorsolateralis, nucleus dorsomedialis, nucleus medialis, nucleus rotundus, and nucleus medialis posterior (Figs. 10–13).

Nucleus dorsolateralis and nucleus dorsomedialis form the rostral pole of the dorsal thalamus and extend to a mid-thalamic level where nucleus rotundus first appears (Figs. 10, 12). Nucleus dorsolateralis does not extend beyond nucleus rotundus. However, nucleus dorsomedialis continues more caudally and is continuous with the pars plicata of nucleus lentiformis thalami. Nucleus dorsolateralis gives rise to the most rostral component of the dorsal peduncle of the lateral forebrain bundle (Figs. 10, 12). Recently Distel and Ebbesson (1975, and personal communication) have reported on the efferent projections of this nucleus in *Varanus*. Lesions of nucleus dorsolateralis give rise to degenerating pathways that course in both the lateral and medial forebrain bundles and enter the ipsilateral telencephalon. These pathways appear to terminate in nucleus accumbens, septum, striatum, dorsolateral cortex, and pallial thickening. Because nucleus dorsolateralis lies just medial and ventral to the retino-recipient thalamic nuclei, there is a strong possibility that one or more of the telencephalic areas believed to receive fibers from nucleus dorsolateralis may, in fact, arise from these visual nuclei whose axons were interrupted by lesions of nucleus dorsolateralis. Due to the complexity of the rostral dorsal thalamus in lizards, additional studies using horseradish peroxidase will greatly aid the analysis of this region. On the basis of horseradish peroxidase studies, Parent and Boucher (1975) have suggested that nucleus dorsolateralis and nucleus dorsomedialis project to the striatum in *Chrysemys*. At present, the afferent connections of nucleus dorsolateralis and nucleus dorsomedialis are unknown. Most workers have assumed that these nuclei in lizards are homologous to the anterior thalamic nuclei of mammals. If so, they would be expected to receive a projection from the caudal hypothalamus—another reason why hypothalamic studies in reptiles are greatly needed.

Nucleus rotundus is usually the largest single thalamic nucleus in lizards. It is capped rostrally by the dorsolateral and dorsomedial thalamic nuclei and occupies the greater part of the mid-thalamic zone, being replaced at more caudal levels by nucleus medialis posterior (Fig. 11). The optic tectum gives rise to the major afferents (both ipsilateral and contralateral pathways exist) to nucleus rotundus, which in turn projects upon the ipsilateral striatum and a dorsolateral division of the dorsal ventricular ridge (Hall and Ebner, 1970; Pritz, 1973, 1975; Distel and Ebbesson, 1975).

Recently Benowitz and Karten (1975) have reported that nucleus rotundus in birds also receives afferents from pretectal nuclei and a thalamic nucleus (nucleus reticularis thalami) as well as from the tectum. These results strongly suggest that similar pathways exist in reptiles since, to date, the majority of discovered avian neural pathways have also been found in reptiles.

In many lizards nucleus rotundus is surrounded by an annulus, or belt of neurons, called the perirotundal belt (Figs. 10, 13). At present nothing is known about the connections of these cells in lizards. However, findings with horseradish peroxidase have led Parent and Boucher (1975) to believe that these cells project upon the striatum in *Chrysemys*.

Nucleus medialis is located at mid-thalamic levels, ventral or medial to nucleus rotundus. In varanids and *Xantusia*, as well as in some turtles and crocodiles, it fuses across the midline and is then termed nucleus reuniens. Nucleus medialis is an auditory relay nucleus that receives afferents from the midbrain auditory area, torus semicircularis, and projects to the ipsilateral striatum and to a medial division of the dorsal ventricular ridge (Foster, 1974; Pritz, 1974*a*, 1974*b*; Distel and Ebbesson, 1975).

Nucleus medialis posterior is located caudal to nucleus rotundus and forms the most caudal division of the dorsal thalamus (Fig. 11). This nucleus receives an ascending spinal projection in *Caiman* and *Tupinambis* (Ebbesson, personal communication); in *Caiman*, at least, it projects to a medial component of the dorsal ventricular ridge (unpublished observations). This circuit most likely represents an ascending somatic sensory pathway found in most reptiles; a similar pathway has been reported in birds (Delius and Bennetto, 1972).

Two distinct dorsal thalamic patterns can be recognized in lizards. Agamids, chamaeleonids, iguanids, teiids, and varanids possess an expanded nucleus dorsolateralis and nucleus rotundus. The enlargement of these nuclei is correlated with a displacement of the medial dorsal thalamus. In these taxa, nucleus rotundus frequently reaches the ependymal layer; nucleus dorsomedialis is displaced dorsally, and nucleus medialis displaced ventrally. However, the density of cells forming nucleus rotundus does not appear to increase in the above taxa. Additionally, both the dorsal and ventral thalamic nuclei that receive direct retinal projections, as well as the auditory relay nucleus (nucleus medialis), are enlarged in these taxa. The remaining families of lizards possess a thalamic pattern that is very similar to that illustrated for gekkonids (Figs. 10, 11), or *Sphenodon.*

Thalamic analysis beyond this level is extremely difficult due to the extended length of most of the thalamic nuclei that complicates direct comparisons, and the probability of error in such analysis would be great without quantitative measurements. However, a few qualitative observations can be made with some confidence. *Anelytropsis*, *Anniella*, *Dibamus*, *Feylinia*, and *Typhlosaurus* show reductions or loss (i.e., an inability on the part of an observer to recognize discrete neural population) of the lateral optic nuclei. Surprisingly the microteiids, with the exception of *Bachia* and *Ophiognomon*, do not exhibit reductions in the thalamic visual nuclei, and are indistinguishable from the macroteiids. Gekkonids and *Xantusia* appear to have an enlarged nucleus dorsolateralis, but not the other dorsal thalamic nuclei. In these taxa, dorsolateralis extends far ventral and medial to nucleus rotundus (Fig. 10). In *Xantusia*, nucleus dorsolateralis actually fuses across the midline, as does nucleus medialis.

At present, there is every reason to believe that the diencephalic organization of lizards exhibits as much variation as the telencephalon or tectum. However, detailed analysis of this brain region requires further study and quantitative data.

Pretectum

The pretectum of lizards, like that of other vertebrates, occupies the dorsal and lateral walls of the caudal diencephalon. It is a transitional area bordered rostrally by the posterior commissure of the thalamus and caudally by the intertectal commissure. In lizards, as well as other reptiles, it consists of three nuclear zones extending from ventricular to pial surfaces. The most medial cell group is termed nucleus lentiformis thalami (Figs. 11, 13, 14). This nucleus is divided into a medial part, the pars plicata, and a lateral part, pars extensa, by the lateral continuation of the posterior commissure. At present nothing is known regarding the connections of pars plicata. In most lizards the pars extensa forms a lens-shaped nucleus that extends across the pretectum as seen in the transverse plane (Fig. 13). Its lateral edge is marked by a compact group of large bipolar cells which forms the cell plate of nucleus geniculatus pretectalis.

In representative taxa of many families (Gekkonidae, Dibamidae, Lacertidae, Xantusiidae, Anguidae, Xenosauridae, Cordylidae, Gerrhosauridae, Lanthanotidae, and Helodermatidae) the pars extensa is a rather uniform scattered nuclear field in which it is possible to recognize dorsolateral and ventromedial subdivisions (Fig. 14*A*). In representative taxa of other families (Teiidae, Varanidae, Iguanidae, Agamidae, and Chamaeleonidae) these subdivisions are very striking (Fig. 14*B*). There is a marked enlargement of the dorsolateral division of the pars extensa, a region that has been termed the dorsal and ventral pretectal nuclei (Butler and Northcutt, 1973). The ventromedial division has been termed the medial pretectal nucleus. These divisions of the pars extensa do not receive direct retinal projections but do receive substantial projections from the ipsilateral optic tectum (Foster and Hall, 1975). The targets of the dorsal and ventral pretectal nuclei are presently unknown, but it is likely that these nuclei are involved in an as yet undescribed visual pathway, as their hypertrophy is correlated with enlargement of the visual system. The connections of the medial pretectal nucleus are unknown.

The lateral pretectum of lizards is formed by three nuclei, all of which receive direct retinal input; nucleus geniculatus pretectalis, nucleus lentiformis mesencephali, and nucleus posterodorsalis (Figs. 11, 14). In *Gekko* these nuclei receive both contralateral and ipsilateral retinofugal projections (Northcutt and Butler, 1974). At present nothing is known regarding the efferent pathways of these retino-recipient pretectal nuclei. These lateral pretectal nuclei, like the divisions of the pars extensa, are particularly well developed in agamids, chamaeleonids, iguanids, teiids, and varanids.

The pretectum of *Sphenodon* is very similar to that of lacertid and gekkonid lizards in that pars extensa of nucleus lentiformis thalami is poorly developed. However, nucleus geniculatus pretectalis lies far more medial than in any of the lizards I have examined. Beyond this difference, the pretectum of *Sphenodon* is similar to that of lacertid or gekkonid lizards, and the same retino-recipient targets have been identified (Northcutt, Braford and Landreth, 1974).

RESULTS AND DISCUSSION: OPTIC TECTUM

The optic tectum comprises the bulk of the midbrain roof in lizards. It is a highly differentiated cortex divided into a number of alternating cellular and fibrous layers (laminae). P. Ramon (1896) divided the optic tectum of chamaeleons into 14 layers which he numbered from the ventricular to the pial surfaces. Leghissa (1962) has employed a similar numbering sequence in his analysis of tectal evolution in vertebrates. Huber and Crosby (1926, 1933) believed that many of the layers described by Ramon were subdivisions of more extensive units, and they divided the optic tectum in a different manner recognizing only six layers. Senn (1966, 1968) has reported on the tectal organization and its development in a number of lizards and believes that Ramon's subdivisions can be recognized in most lizards. Most recent studies (Butler and Northcutt, 1971*a*, 1971*b*, 1973; Butler, 1974; Northcutt and Butler, 1974; Butler and Ebbesson, 1975; Cruce and Cruce, 1975) have utilized Ramon's nomenclature as it is more useful hodologically than the nomenclature of Huber and Crosby, particularly when considering the retinal input to the optic tectum.

There is considerable morphological variation among the optic tecta of lizards, but before describing this variation it is necessary to describe the individual laminae and summarize their connections. In describing the laminae it should become obvious that these laminae can be grouped into three major zones that possess very different functions; and it is very likely that the optic tectum is not a single morphological character, or unit, under a single selective pressure, but is, in fact, part of several circuits under very different selective pressures.

The initial description of the tectal laminae will be based on the optic tectum of *Iguana* since the tectum is particularly well developed in this taxon, and the laminae can be easily recognized (Fig. 15).

Lamina 1 consists of ependymal cells lining the ventricle. These cells possess apical

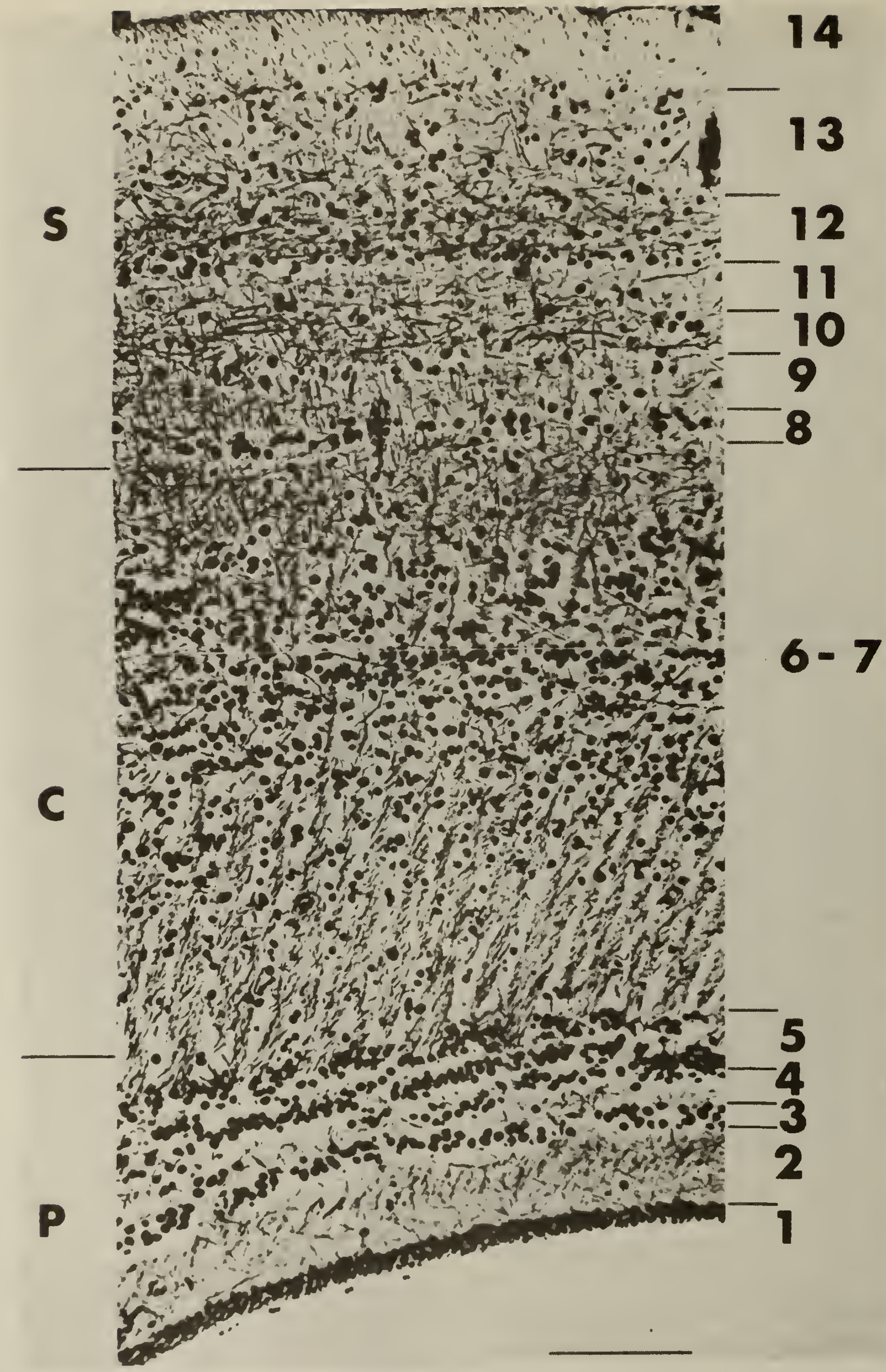

Figure 15. Photomicrograph of a transverse section through the optic tectum of the green iguana, *Iguana iguana*. Bodian preparation from a middorsal position at a rostrocaudal level similar to tectal level D in figure 1. *P*, periventricular zone; *C*, central zone; *S*, superficial zone. Numbers to right of figure identify individual laminae after the nomenclature of P. Ramón (1896) and Senn (1968). Bar scale represents 100 μ. Note reduced cellular laminae in periventricular zone, migrated neurons in upper half of central zone and thickened zone 14. These tectal features characterize the Iguania as well as teiids and varanids.

processes which pass dorsally through all of the tectal laminae and terminate as overlapping endfeet at the pial surface (Leghissa, 1962).

Laminae 2 and 4 consist of nonmyelinated and poorly myelinated axons whose origin is unknown. These laminae also contain the basal dendrites of the neurons of laminae 3 and 5 (Ramon, 1896; Leghissa, 1962; Butler and Ebbesson, 1975).

Laminae 3 and 5 are formed by the cell bodies of piriform neurons that Ramon (1896) divided into three populations: (1) cells whose apical dendrites terminate in zone 7; (2) cells whose apical dendrites extend into lamina 14, but also possess dendritic ramifications in laminae 7, 9, 10, and 13 with axons directed superficially and entering lamina 13; and (3) cells whose apical dendrites ramify in laminae 10, 12, and 14 with axons entering lamina 6. All three piriform populations possess dendrites which ramify in retinal terminal zones, with the possible exception that the first population terminates in lamina 7. It is probable that the major extent of the apical dendrites of all three piriform populations are related to nonvisual inputs or to multisynaptic visual inputs. Both telencephalic and contralateral tectal pathways are known to terminate among the dendritic processes of these piriform cells (Butler and Ebbesson, 1975).

Lamina 6 is composed primarily of myelinated axons among which a few cell bodies can be identified. The most common cell type has been termed giant fusiform or pyramidal cells by Butler and Ebbesson (1975). Such cells have been recognized in the tecta of most vertebrates (Leghissa, 1962; Potter, 1969). These neurons ramify primarily within lamina 6 with occasional dendrites directed toward the level of lamina 5. Their axons have not been described.

Lamina 7 consists primarily of cell bodies. Two basic patterns in the distribution of these cell bodies are seen in lizards. In one case there is a clear separation of laminae 6 and 7 with few, if any, cell bodies located in lamina 6, as in *Lacerta* (Fig. 16). In the second case, the cells of lamina 7 form an outer or dorsal subdivision and an inner or ventral subdivision, with some being scattered between the fibrous columns of zone 6, as in *Iguana* (Fig. 15); a distinct division into laminae 6 and 7 is impossible. Ramon (1896) recognized at least four neuronal populations in lamina 7. All of these neurons possess dendrites that ramify in the superficial tectal laminae that receive retinal terminals. In addition, many of these cells are bipolar and possess dendrites that ramify in deeper layers (laminae 6 and 5). The segregation of neurons of lamina 7 into two subdivisions may reflect differences in afferent connections. Unfortunately, little experimental data are available concerning the afferents to the central tectal region. Butler and Ebbesson (1975) have reviewed the known projections which include visual afferents to the superficial apical dendrites of cells of lamina 7, telencephalic input to the deep half of lamina 7, and intertectal projections to laminae 3 through 5. Similar intertectal projections have been reported in *Iguana* by Foster and Hall (1975). The deep dendrites of cells in lamina 7 extend into lamina 5 and perhaps form synapses with intertectal projections.

Spinal hemisections reveal few, if any, projections directly to the tectum (Ebbesson, 1967). However, the degeneration after isthmal hemisections reveals ascending projections to at least the deep and central tectal regions in *Gekko* (unpublished observations).

Laminae 8 through 14. These laminae consist primarily of layers of retinofugal fibers and their terminal neuropils. Laminae 9, 12, and 14 are composed of retinal fibers that terminate in laminae 8, 11 and 13 (Northcutt and Butler, 1974; Cruce and Cruce, 1975). The bulk of these retinal fibers issue from the contralateral eye, but ipsilateral retinotectal fibers to the rostral tectum in *Gekko*, *Tupinambis*, and *Xantusia* are now known to exist. At present considerable work remains to be done in order to characterize the cell types and dendritic ramifications of laminae 8 through 14. Leghissa's descriptions (1962) are not sufficiently detailed to

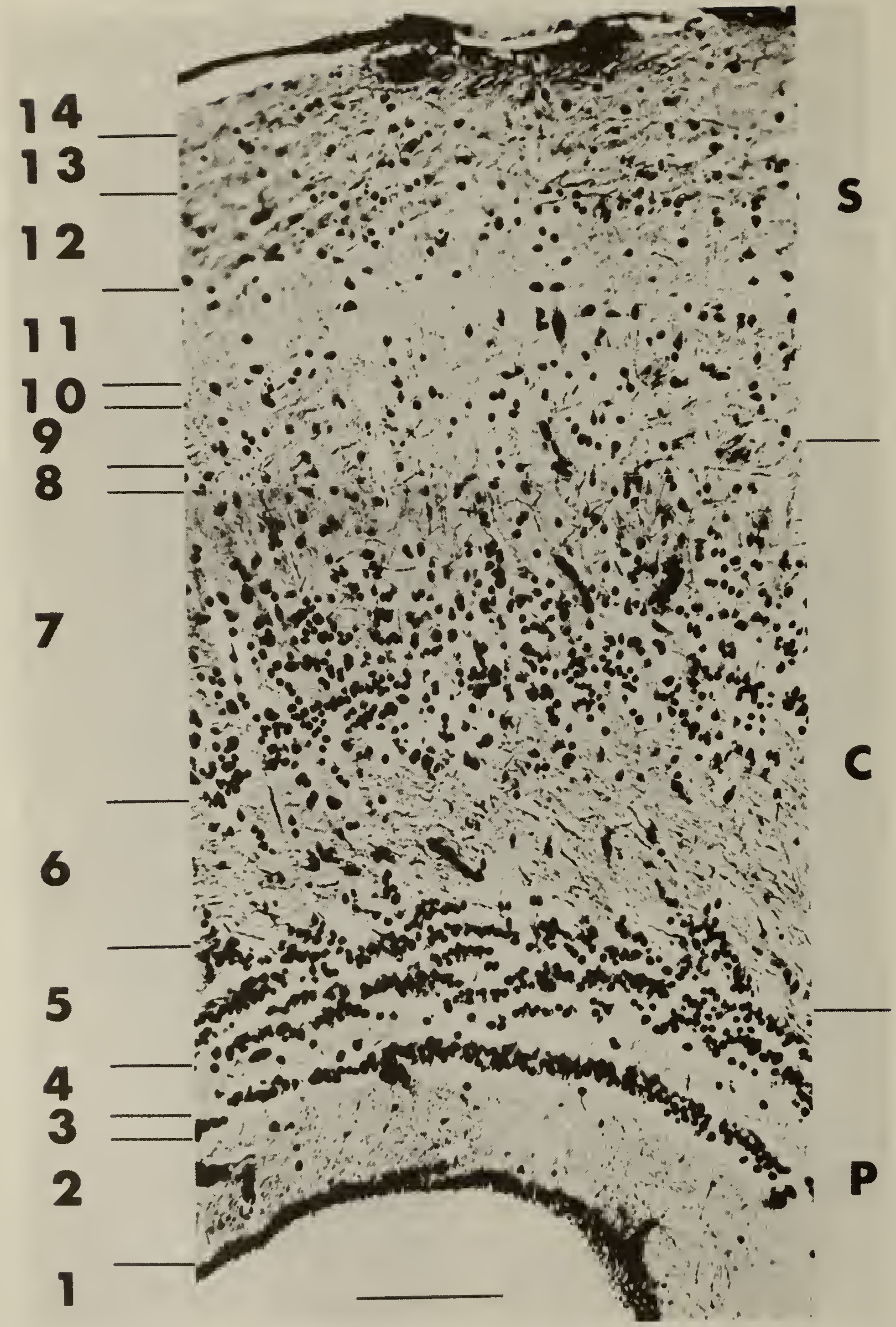

Figure 16. Photomicrograph of a transverse section through the optic tectum of *Lacerta sicula*. Abbreviations and bar scale same as Figure 15. Note increased thickness of cellular laminae in periventricular zone, clear separation of laminae 6 and 7 of the central zone and poorly developed lamina 14. These tectal features characterize most living lizards and are very similar to the tectal pattern seen in *Sphenodon* (fig. 17).

identify these laminae, and the Golgi preparations of Butler and Ebbesson (1975) suggest that this region in their material was poorly impregnated. However, both of these studies report bipolar and horizontal elements in these laminae.

Lamina 12, in addition to possessing retinal fibers, appears to contain fibers of nonretinal origin; only a fraction of the fibers of this layer degenerate following removal of the retina (Northcutt and Butler, 1974). Recently Foster and Hall (1975) have reported that in *Iguana*, tectal efferents exit in laminae 8, 12 and 14.

Senn (1968, 1970) has suggested that the tectal laminae can be grouped into three main zones based on their embryonic development. The recognition of these zones has been strengthened by recent experimental studies (Foster, Lymberis and Hall, 1973; Northcutt and Butler, 1974; Foster and Hall, 1975). Laminae 8 through 14, which primarily consist of retinofugal fibers and their terminal neuropils, have been termed the superficial zone. Laminae 6 and 7 constitute the central zone, consisting primarily of bipolar neurons whose outer dendrites ramify in the superficial retino-recipient zone and whose inner dendrites probably receive telencephalic and ascending medullar inputs. Finally, laminae 1 through 5, containing neurons that do not migrate away from the embryonic layer, constitute a periventricular zone.

Many lizards such as *Anelytropsis*, *Anniella*, *Dibamus*, *Feylinia*, and *Typhlosaurus* are characterized by extensive reductions in the visual system which are correlated with reductions in the superficial and central tectal zones. The finding that none of these species shows reductions in the periventricular tectal zone suggests that the periventricular zone is not under strong selective pressures related to vision, but may be more influenced by nonvisual parameters.

Recently Foster and Hall (1975) have demonstrated that laminar lesions of the tectum in *Iguana* reveal distinctly different outputs depending on which tectal laminae are involved in the lesion. If the superficial tectal zone is lesioned (laminae 8-14), projections are traced rostrally to the pars ventralis of the lateral geniculate nucleus and caudally to the magnocellular division of nucleus isthmi. If lesions are extended ventrally to include lamina 7, a massive projection to nucleus rotundus is observed. Only when lesions include the periventricular zone (cellular laminae 3 and 5) are the descending tecto-bulbar and tecto-spinal pathways involved. Unfortunately, Foster and Hall were unable to identify the laminae of origin of the projections to the pretectum. Their results, however, strongly support Senn's concept that the tectum is arranged in a series of zones subserving different functions mediated by distinctly different pathways. In this context, it is particularly interesting to note that the descending tectal pathways do not terminate directly on the motor nuclei of the cranial nerves, but end within the lateral and medial reticular formations of the brain stem. Whatever visual functions are mediated by the tectum are still at least one to two neurons removed from the final common motor pathway.

Two major patterns of tectal variation can be recognized in lizards (Senn, 1966). In agamids, chamaeleonids, iguanids, teiids, and varanids, lamina 14 is always the main optic fiber layer, and lamina 12 is at least half the thickness of lamina 14 as seen in the transverse plane (Fig. 15). Laminae 8 and 10 contain many cells closely packed in tight rows. Lamina 7 is never present as a single layer but is divided into inner and outer subdivisions with the neurons of the inner subdivision scattered within lamina 6. Compared to gekkonids, lacertids, and scincids, the periventricular laminae appear reduced, particularly lamina 5. This pattern is clearly seen in *Iguana*, and for purposes of brevity will be subsequently referred to as the *iguanid tectal pattern.*

Anguids, cordylids, dibamids, gekkonids, gerrhosaurids, helodermatids, lanthanotids, lacertids, pygopodids, scincids, xantusiids, and xenosaurids possess a distinctly different tectal pattern (Fig. 16) that I refer to as the *lacertid tectal pattern.* In these taxa lamina 12 is the main optic layer and is always better developed than lamina 14. Laminae 8 and 10 are not nearly as well developed as in the previously described iguanid tectal pattern, and laminae 8 and 10 are even difficult to recognize as distinctly separate laminae (Fig. 16). Lamina 7 consists of one major group of cells with little, if any, overlap with lamina 6. The periventricular laminae are much more developed, lamina 5 being twice the thickness of the comparable lamina in the iguanid tectal pattern.

The organization of the tectum in *Sphenodon* is particularly interesting when compared to the iguanid and lacertid tectal patterns. Lamina 12 is the main optic fiber layer in *Sphenodon*, while lamina 14 is barely recognizable (Fig. 17). Lamina 10 can be recognized as a poorly scattered layer of cell bodies, while the position of lamina 8 is primarily distinguished by the presence of large myelinated axons and only a few cell bodies. Lamina 7 in *Sphenodon* is less developed than lamina 7 in either lacertids or iguanids. The periventricular laminae of *Sphenodon* are very extensive, accounting for almost a third of the total thickness of the tectum. Lamina 5 is particularly well developed and consists of four to five distinct subdivisions. Clearly, the laminar arrangement in *Sphenodon* is more like the lacertid than the iguanid tectal pattern.

Consideration of the entire range of tectal variation in *Sphenodon* and lizards reveals that there are no *de novo* laminae restricted to a single taxon, but that sufficient laminar variation occurs to characterize taxa at the family level.

Gekkonids and pygopodids both possess three to five subdivisions in lamina 5 of the periventricular tectal zone. Gekkonids can be recognized from pygopodids and most other lizards by a partial fusion of laminae 7 and 8. *Xantusia* possesses a tectal lamination that appears intermediate between that of gekkonids and that of lacertids.

Both lacertids and scincids possess tecta whose organization is comparable to *Sphenodon* and many turtles, particularly *Chelydra* and *Kinosternon*. The tectum of skinks differs from that of lacertids in that it does not exhibit a distinct lamina 4, free of cell bodies, as does the lacertid tectum, and zone 5 in skinks does not exhibit distinct subdivisions.

The tecta of *Feylinia* and *Typhlosaurus* differ from those of most skinks in the reduction of the superficial tectal zone, but these taxa otherwise possess tecta that are identical to those of other skinks. The tecta of *Anelytropsis* and *Dibamus* also possess reduced superficial zones related to reduction in visual projections, but they differ from skinks in that both of these genera develop a paratorus and do not possess a recognizable lamina 4 (Senn and Northcutt, 1973).

Xenosaurus, *Anguis*, and *Anniella* possess very similar tecta, but *Xenosaurus* can be separated from the other two genera on the basis of the development of lamina 5. Lamina 5 in *Xenosaurus* consists of subdivisions one to two cells deep, while *Anguis* and *Anniella* have subdivisions two to four cells deep.

Both *Cordylus* and *Gerrhosaurus* reduce lamina 2 and increase the number of subdivisions recognized in lamina 5.

Heloderma and *Lanthanotus* possess periventricular laminae similar to the lacertids, but both genera show reductions of the superficial tectal zone. There is a reduction in lamina 13 so that distinct and separate laminae 12 and 14 cannot be recognized.

Teiids and varanids possess almost identical tecta. Both taxa possess hypertrophied laminae 14 and reduced periventricular tectal laminae. Teiids can be recognized from varanids by increased mediolateral thickness of lamina 14 and by a better developed lamina 5 than varanids. Both the macro- and microteiids exhibit identical tectal development.

Agamids, chamaeleonids, and iguanids have tecta that are so similar it is almost impossible to distinguish among them. As a group, these taxa can be separated from the teiids and varanids by clearer subdivisions of lamina 7 and by better developed periventricular zones. The superficial tectal zones of teiids and varanids are identical to

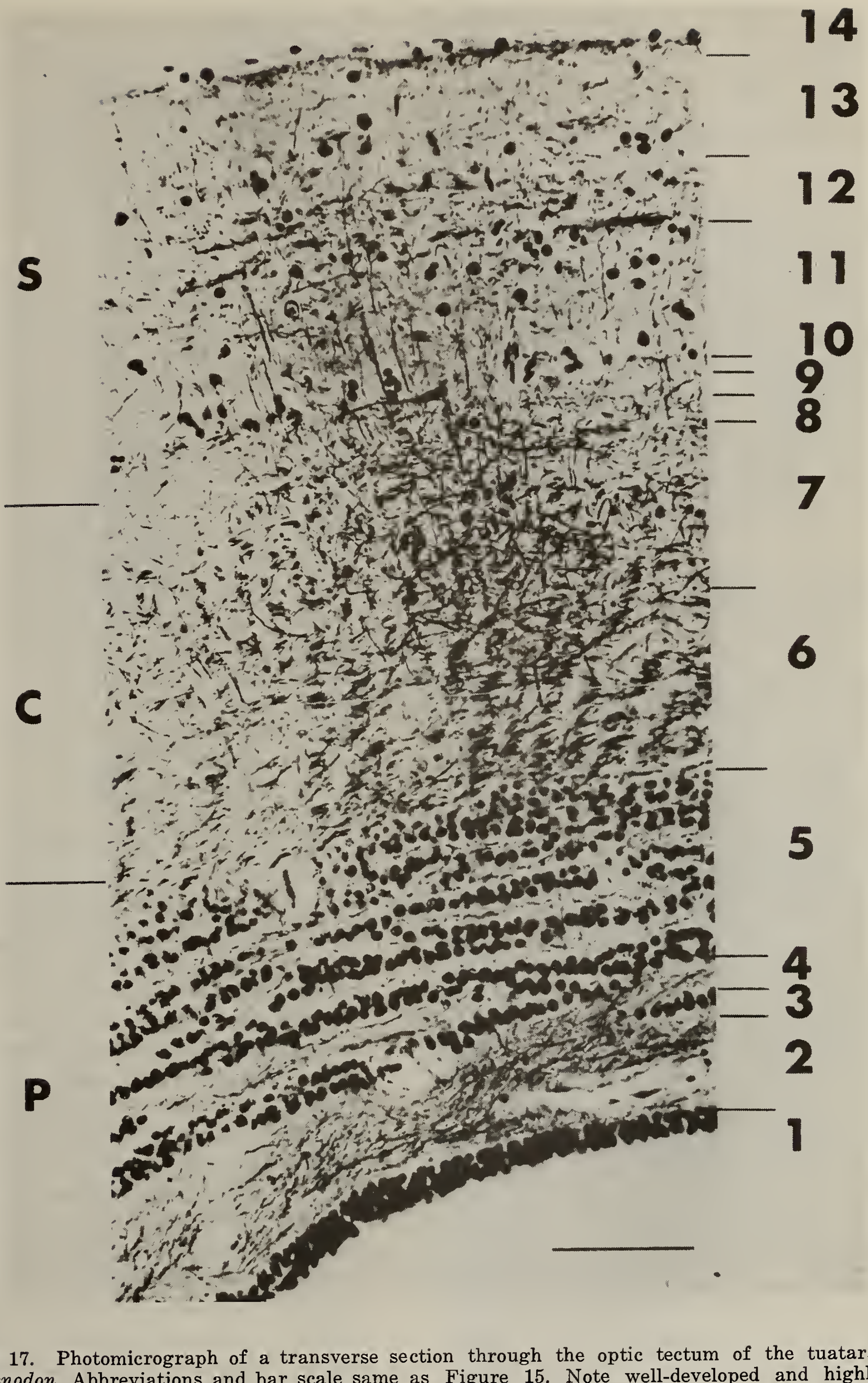

Figure 17. Photomicrograph of a transverse section through the optic tectum of the tuatara, *Sphenodon.* Abbreviations and bar scale same as Figure 15. Note well-developed and highly laminated periventricular zone, poorly developed central zone and large retinal lamina 12 in contrast to very thin retinal lamina 14.

those of agamids, chamaeleonids, and iguanids.

GENERAL DISCUSSION

Three aspects of the central nervous system of lizards will be considered, with particular emphasis given to the forebrain and midbrain. First, the neural features that differentiate reptiles from other tetrapods will be summarized. The evolution and possible functional and behavioral significance of these neural features in reptiles, particularly in lizards, will then be explored. Finally, the implications of these neural characters and their distribution is used to speculate on the phylogeny of lizards.

Comparison With Amphibians and Other Tetrapods

Generally, the brains of reptiles are twice as large as those of amphibians of the same body weight (Ebbesson and Northcutt, 1976). Most brain regions are involved in this difference rather than any single area, e.g., the optic tectum, accounting for the bulk of the increase. Substantial increase (2-4 fold) in the volume of the cerebellum occurs in most lizards and is most likely related to increased importance of the limbs in locomotion and behavior such as social signaling. Generally, most reptilian brain regions also possess more migrated neurons than do comparable regions in amphibians, and the density per unit area has probably doubled.

One of the most striking differences between amphibians and reptiles is the elaboration of a telencephalic dorsal ventricular ridge in reptiles (Fig. 18). This ridge appears to form embryonically by a proliferation of the lateral pallial wall (Johnston, 1916; Kuhlenbeck, 1938; Källén, 1962) which is also the most likely source of the ridge phylogenetically (Northcutt, 1974; Kicliter and Northcutt, 1975). The rostral half of the dorsal ventricular ridge is now understood to be the final target of multiple ascending pathways that reach the telencephalon after synapsing, for the most part, in the dorsal thalamus (Fig. 19A). Thus, as the dorsal ventricular ridge differentiates in reptiles, so does the dorsal thalamus, since they are both parts of ascending sensory systems that stretch along the entire longitudinal axis of the brain. These pathways terminate not only in the dorsal ventricular ridge, but also in the striatum. At present it is not known whether the same neurons have projections to both regions or whether separate populations located in the thalamus project to the two telencephalic targets. Amphibians clearly differ from reptiles in that the dorsal thalamic nuclei of amphibians project massively upon the striatum and only sparsely upon the pallial formations (Kicliter and Northcutt, 1975). Thus, it appears that the amphibian-reptilian transition was marked not only by an increase in the size of the entire brain, but also by the development of a lateral pallial region with a concomitant shift in the dorsal thalamic efferents from primarily subpallial to pallial targets in the telencephalon.

Birds have clearly retained this pattern of telencephalic organization (Cohen and Karten, 1974) and have increased the brain-body ratio by some seven fold (Jerison, 1973). Mammals, on the other hand, lack a dorsal ventricular ridge but have developed isocortex which is now believed to be homologous, in large part, to the dorsal ventricular ridge of reptiles and birds. It seems unlikely that the therapsid reptiles ever possessed a fully developed dorsal ventricular ridge since the telencephalon in all living birds and reptiles is approximately equal in width and length, while the endocasts of the extinct therapsids (Hopson, 1969) clearly reveal a telencephalic outline far more like that of living amphibians. It seems unlikely that theropsid reptiles would first have developed a dorsal ventricular ridge and then subsequently have migrated neurons back out onto the lateral and dorsal surface of the telencephalon to form the laminated aggregates that we recognize as isocortex in mammals. The simplest explanation is that both modern reptiles and therapsids independently devel-

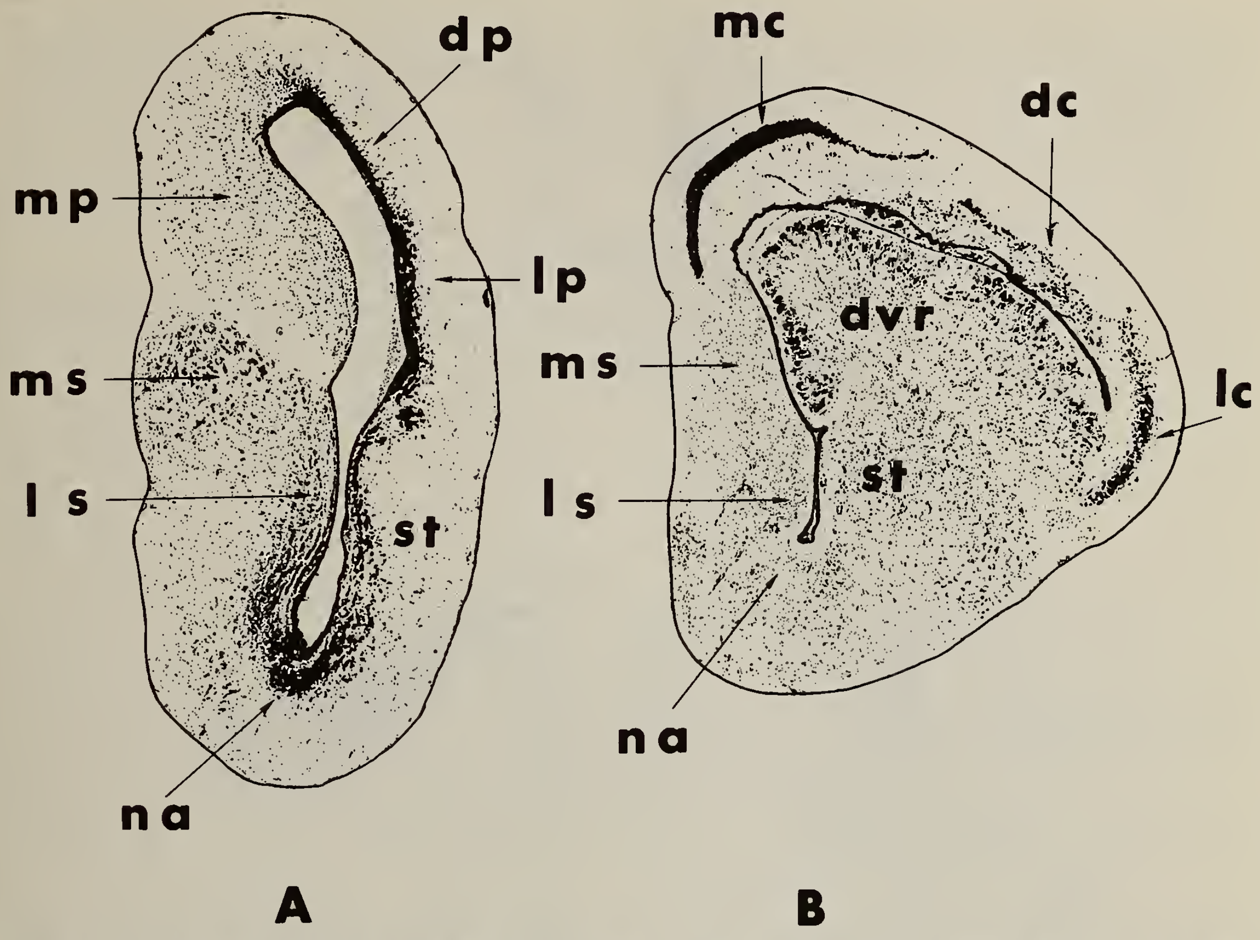

Figure 18. Representative transverse sections through the left telencephalic hemisphere of an anuran amphibian, *Rana catesbeiana,* (A) and a gekkonid lizard, *Gekko gecko,* (B) illustrating the differences in the development of the lateral hemispheric wall and the migration of neuronal populations from a periventricular position. *dc,* dorsal cortex; *dp,* dorsal pallium; *dvr,* dorsal ventricular ridge; *lc,* lateral cortex; *lp,* lateral pallium; *ls,* lateral septal nucleus; *mc,* medial cortex; *mp,* medial pallium; *ms,* medial septal nucleus, *na,* nucleus accumbens; *st,* striatum.

oped lateral pallial areas for sensory and motor processing.

A persistent riddle regarding telencephalic evolution in modern reptiles and theropsids is why both groups elaborated a lateral pallial field rather than simply expanding the striatum which already received the vast bulk of the dorsal thalamic projections. Several possibilities should be considered. First, the vomeronasal system probably arose with land vertebrates and, while clearly recognizable in amphibians, became increasingly well developed in terrestrial reptiles and most mammals. Since the sole target of the vomeronasal system is located in the caudal lateral pallial wall (Scalia, 1972; Northcutt and Royce, 1975), it is possible that, with increased importance of this chemoreceptive system in land vertebrates, additional sensory modalities were linked with this telencephalic system. This would seem particularly likely since the lateral pallium and cortical amygdala (vomeronasal target) offer a direct pathway descending out of the telencephalon to hypothalamic and tegmental centers (at least in mammals; the efferents of these telencephalic centers in reptiles have not been determined).

However, Hoogland's (1975) experimental analysis of the efferents of the rostral dorsal ventricular ridge in *Tupinambis* reveals that the striatum is the primary, if not the sole,

Figure 19. Summary of experimentally determined ascending pathways in reptiles (A) and amphibians (B). Differences are primarily related to increased differentiation of dorsal thalamus and elaboration of dorsal ventricular ridge in reptiles. *C*, cerebellum; *DL*, dorsolateral nucleus of the dorsal thalamus; *DT* dorsal thalamus; *DVR*, dorsal ventricular ridge; *H*, hypothalamus; *h*, habenular nucleus; *IT*, isthmal region of the tegmentum; *M*, medulla; *MP*, medial pallium; *OB*, olfactory bulb; *OC*, optic chiasm; *ON*, olfactory nerve; *OP*, olfactory peduncle (tracts); *OT*, optic tectum; *P*, preoptic area of the hypothalamus; *PDT*, posterior nuclear complex of dorsal thalamus; *RE*, nucleus reuniens (medialis); *RO*, nucleus rotundus; *S*, septal nuclei; ST, striatum; *T*, torus semicircularis; *VT*, ventral thalamus; *1*, spinocerebellar and spinothalamic pathways (the most rostral extent of this pathway is presently uncertain in amphibians); *2*, ascending reticular pathways; *3*, ascending auditory pathway; *4*, ascending thalamo-telencephalic pathways (in amphibians these pathways terminate primarily in the striatum; in reptiles they terminate in separate sensory zones of the dorsal ventricular ridge as well as in the striatum).

recipient of efferents from the ridge sensory areas. Similar findings have been reported in birds (Karten and Dubbledam, 1973). These results argue that, whatever the nature of the sensory function of the rostral dorsal ventricular ridge, it primarily affects lower brain centers by acting through the striatum and its descending efferents. Thus, it is likely that lesions of the rostral dorsal ventricular ridge in reptiles will not result in the outright loss of particular types of behavior. It is more likely that such lesions would result in rather subtle changes in behavior that probably cannot be measured by simple learning paradigms or by noting the presence or absence of a particular species-typical behavior pattern following such lesions.

If chemoreception did not play a decisive role in determining the position of further sensory elaboration in the telencephalon—as suggested by the close connection of rostral dorsal ventricular ridge to the striatum rather than to the lateral cortex or vomeronasal target—then what selective pressure(s) were responsible for the elaboration of the dorsal ventricular ridge? An examination of the organization and variation in ridge structure among lizards suggests possible functions from which we can deduce these selective pressures.

Possible Functional and Behavioral Implications of CNS Evolution in Lizards

Considerable morphological variation in four brain regions of lizards (dorsal ventricular ridge, dorsal thalamus, pretectum, and optic tectum) has been described earlier. The observed variation is characterized by two patterns of organization that have been termed *lacertid* or *iguanid* patterns. The *lacertid* pattern is considered the more generalized or ancestral pattern, as it is most similar to the organization of *Sphenodon* and turtles. *Sphenodon* and most lizards possess a dorsal ventricular ridge with a pronounced peripheral cellular plate and a poorly developed central core region. Those lizards possessing the *iguanid* pattern (agamids, chamaeleonids, iguanids, teiids, and varanids) have greatly expanded ridges with little trace of the peripheral cellular plate. However, the same four subdivisions of the rostral dorsal ventricular ridge can be identified in lizards with either pattern (Figs. 2, 3). Clearly the expansion of the ridge is not due to the hypertrophy of any single sensory modality, but to an increase in neurons subserving all sensory modalities that reach the dorsal ventricular ridge. In this context it is interesting to note that lizards with the *iguanid* pattern of neural organization possess the highest brain-body ratios, with the teiids and varanids being the most encephalized (Platel, 1976).

While it is now clear that the evolution of the dorsal ventricular ridge in lizards is characterized by a quantitative increase in neurons, little is known about possible neuronal evolution within the ridge itself. In *Sphenodon* the peripheral plate neurons possess long multiple apical dendrites that extend into the central core. This pattern of organization is very similar to the condition seen in turtles (Northcutt, 1970) and in the lateral pallium of amphibians (Hoffman, 1963). At present, it is impossible to characterize the neuronal types of the rostral dorsal ventricular ridge of lizards. Such a characterization would contribute greatly to our understanding of ridge evolution in lizards. Hypertrophy of the ridge could have taken place in one of two ways. There could simply have been an increase in the number of ridge cells with no change in the different types of cells present. If this were the case, then an increase in the number of neurons would probably increase the quantity of information processed per unit time, but no change in the quality of information processing would occur. However, if evolution of the ridge is characterized by the rise of new cell types with different integrative properties, as well as an increase in total cell number, those lizards with expanded ridges may process sensory information differently than other lizards.

In this context it is particularly interesting to note that much of the evolution of isocortex among mammals is related to an increase in stellate and granular (intrinsic neurons) populations (Mitra, 1953). These populations are the primary targets of the ascending thalamic sensory pathways and they in turn form connections with the so-called "motor" neurons of isocortex. The evolution of these intrinsic neurons is believed to underlie the integrative and plastic capabilities of mammalian isocortex (Jacobson, 1975). Comparable populations of granular neurons are now believed to have evolved in birds (Nauta and Karten, 1970), and their presence in reptiles would strongly suggest that the expanded ridges of lizards may be performing functions similar to mammalian isocortex or avian dorsal ventricular ridge. The complex social behavior of agamids and iguanids, and the active foraging predation of teiids and varanids, may be reflections of ridge hypertrophy.

For the most part, I have concentrated on the sensory aspects of the dorsal ventricular ridge in lizards since we know far more about this aspect of the ridge than we do about its possible motor function. However, isocortical evolution in mammals is characterized by marked changes in motor control. Most isocortical areas not only project upon the striatum, but also have considerable connections with the brainstem reticular formation, as well as having indirect influence on cranial nerve motor nuclei and spinal motor neurons. Similar descending motor populations occur in the avian dorsal ventricular ridge (Zeier and Karten, 1971; Nottebohm, Stokes and Leonard, 1976). In *Serinus*, a neuronal population located in the caudal and lateral ridge projects directly to midbrain and hypoglossal nuclear structures after receiving input from neurons adjacent to the auditory division of the dorsal ventricular ridge (Nottebohm et al., 1976). Thus, the avian dorsal ventricular ridge, like mammalian isocortex, can be characterized as consisting of a series of separate sensory areas, each analyzing a single sensory modality, and forming connections with the striatum as well as bypassing the striatum to directly influence lower brainstem centers. While Hoogland (1975) has not reported such connections from the dorsal ventricular ridge of *Tupinambis*, telencephalo-medullar and spinal pathways have been discovered in amphibians (Kokoros, 1973; Kokoros and Northcutt, 1977) as well as in birds and mammals. Such broad distribution among tetrapods suggests that reptiles almost certainly will also possess comparable cortico-bulbar pathways. One set of pathways may project from the different sensory areas of the ridge directly to the striatum, and a second pathway may project to the brainstem which arises from a distinct ridge population(s) receiving projections from adjacent ridge sensory areas.

The evolution of the dorsal thalamus and, to a lesser extent, the pretectum is closely tied to the evolution of the dorsal ventricular ridge in lizards. Since the dorsal thalamus largely consists of centers that project to the ridge and other telencephalic centers, hypertrophy of these telencephalic centers is correlated with hypertrophy of the dorsal thalamus.

As noted earlier, part of the avian pretectum projects to nucleus rotundus (Benowitz and Karten, 1975), and it is likely that at least part of the pretectal evolution in lizards is related to a retino-tecto-pretecto-rotundal pathway to the telencephalon. In other vertebrates, part of the pretectum also projects to the tectum (Trachtenberg and Ingle, 1974; Wilczynski, 1976), and it is likely that most of the variation seen in the pretectum of lizards will eventually be correlated with trends in the development of the optic tectum.

Studies by Ewert (1970) and Ingle (1973) have implicated the amphibian pretectum in various aspects of visually mediated predator-prey behavior. Lesions of the pretectum result in changes in the receptive field properties of tectal neurons, with the result that anurans attack large, inappropriate objects, as if the objects were insects, rather than responding normally by fleeing from such objects. These studies suggest a complex role for the pretectum, mediated both through the tectum and lower brainstem centers. The hypertrophy of the pretectum in lizards possessing the iguanid pattern of organization makes these animals particularly attractive for the initiation of similar functional studies in determining the role of the pretectum in lizard behavior.

The most striking changes in the optic tecta of lizards are the relative size increases, or decreases, in the various laminae (Figs. 15, 16). At present it is not possible to assign the various laminae to different functional categories with certainty, i.e. as terminal fields of specific incoming afferent systems or as the cells of origin of specific outgoing circuits. However, in reviewing our present information regarding the tectum, it is obvious that it is organized in this manner. In this context, the lamination of the superficial tectal zone is particularly interesting. It primarily consists of three laminae of incoming retinal fibers and their terminal laminae. Thus each retinal fiber lamina appears to possess a separate terminal neuropil. A similar pattern of organization is seen in bony fish and amphibians. In these taxa, each lamina consists of a distinct retinal efferent population with different receptive properties. Thus each lamina receives visual input only from stimuli of special biological significance. These ganglion cells have been selected to convey information about only a fraction of the total visual environment, primarily relating to predator and prey objects.

Comparable studies do not exist for reptiles. In geckos as in amphibians, tectal ablation or interruption of optic tract fibers projecting to the optic tectum results in a loss of visually guided predator-prey behavior (unpublished observations). Similar losses in pattern discrimination have been reported in *Podocnemis* (Bass, Pritz and Northcutt, 1973). While these studies implicate the tectum in visual pattern recognition and indicate that it is an essential pathway for predator-prey related behaviors, they do not provide information on the role of the tectum in such complex behaviors as layout of home range, defense of territories, possible intraspecific individual recognition, utilization of seasonal or spotty food resources, learned avoidance of specific predators, etc. Several of the behavioral reports presented in the present volume (for example, Jenssen and Auffenberg) clearly argue that such behaviors do exist in lizards.

While our present information regarding the neural circuitry of reptiles is far from complete, a bare skeleton of major organizational features can be assembled (Figs. 19, 20). These features of reptilian neural organization allow a number of hypotheses to be formulated regarding function and suggest many areas where much work remains to be done.

Consideration of even simple motor acts in reptiles such as orientation to potential prey, agonistic gaping, head and trunk bobbing reveals that many muscles in distinctly different parts of the body are innervated by both spinal and cranial components. Furthermore, the movements of these muscles are

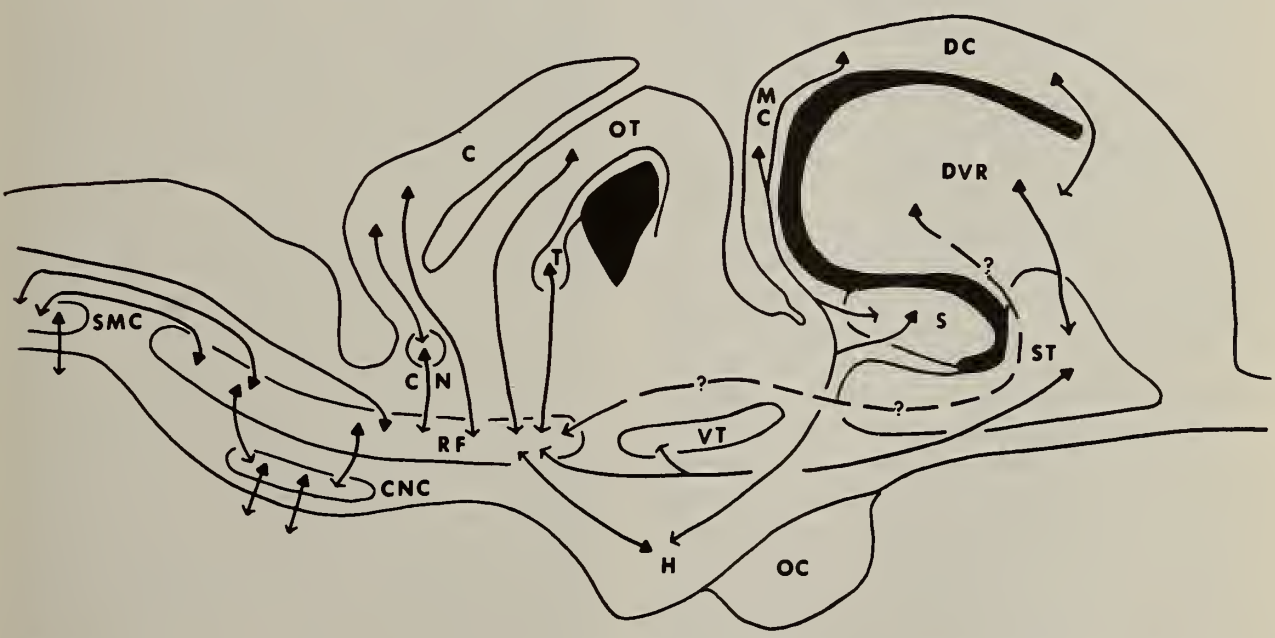

Figure 20. Summary of experimentally determined descending pathways in reptiles. Most major brain centers terminate within the reticular formation (here defined to include the red nucleus and vestibular nuclei which are usually considered derivatives of the reticular formation). Massive convergence of descending pathways onto the reticular formation suggests its possible role as a pattern generator in reptilian behavior. The descending pathways of the dorsal ventricular ridge are poorly understood at present. *C*, cerebellum; *CN*, cerebellar nuclei; *CNC*, cranial nerve motor column; *DC*, dorsal cortex; *DVR*, dorsal ventricular ridge; *H*, hypothalamus; *MC*, medial cortex; *OC*, optic chiasm; *OT*, optic tectum; *RF*, reticular formation; *S*, septal nuclei; *SMC*, somatic motor column of spinal cord; *ST*, striatum; *T*, torus semicircularis; *VT*, ventral thalamus.

obviously patterned with regard to both onset and duration of contraction.

The primary pathways, excluding the descending vestibulo-spinal paths, linking the brain to the spinal cord are the descending reticular pathways (Fig. 20). Cerebellar efferents (Senn and Goodman, 1969), tectal efferents (Foster and Hall, 1975), and telencephalic efferents (see telencephalic section for summary of studies) do not terminate on cranial nerve motor nuclei or motor neurons of the spinal cord. All of these higher neural centers funnel into the reticular formation of the brainstem. This pattern of connectivity places the reticular brainstem in an ideal position to function as a set of pattern generators. The reticular formation consists of both ipsilateral and contralateral pathways projecting to most portions of the spinal cord (Ten Donkelaar, 1975; Cruce, Newman, and Stefl, 1976). Such reticular neurons, projecting over wide segments of the spinal cord and motor nuclei of the medulla, could produce a wide range of output signals depending on the temporal and spatial nature of the arriving afferent signals from such diverse neural centers as the cerebellum, tectum, hypothalamus, and telencephalon. Such an hypothesis is consistent with electrical stimulation studies, as well as with available anatomical information. The majority of reported stimulation sites from which recognizable motor behaviors can be stimulated are found within the reticular core or its derivatives (Distel, 1973; Sugarman, 1974; Kennedy, 1975).

In mammals the cerebellum can be divided into three longitudinal zones: a medial or vermal zone, primarily related to axial muscles; an intermediate zone, coordinating whole limb movements; and a lateral zone, primarily concerned with movements involving distal appendicular muscles. It is this lateral cerebellar zone with its well-developed isocortical channels (brachium conjunctivum, cortico-olivo-cerebellar, and cortico-ponto-cerebellar pathways) that becomes greatly developed in the cerebellum of mammals.

Goodman (1964) has identified vermal and intermediate cerebellar zones in *Caiman*, but believes that lateral cerebellar zones exist only in birds and mammals. To date, neither pontine nuclei nor telencephalo-bulbo-cerebellar pathways have been identified in reptiles, suggesting that behaviors such as nest building, limb manipulation of prey, and social signaling are motor events coordinated primarily at cerebellar and reticular levels with little, if any, direct cortical control.

The nature of telencephalic involvement in motor sequences is one of the many unanswered questions regarding CNS organization in reptiles. Hoogland (1975) reported a direct pathway from the striatum to the lateral cerebellar nucleus in *Tupinambis*. At present, this pathway and the strio-bulbar pathways are the only known direct connections with the medulla. While lizards with complete telencephalic ablations do not feed, they show no obvious locomotor deficits (Goldby, 1937).

While the striatum is traditionally thought of as a motor center, it may possess a far more important role as a sensory integration center related to species-typical behaviors (Greenberg, 1977). The striatum of reptiles receives inputs from midbrain auditory and visual centers (torus and tectum) via thalamic relays, and probably receives somatic input as it does in other tetrapods. In mammals the striatal neurons are known to be multimodal (Laursen, 1963), as is likely the case in reptiles. Such multimodal units might serve as a filter to facilitate or inhibit species-typical behaviors organized at the reticular level. The possibility of such a striatal role is particularly attractive considering the midbrain afferents to the striatum and its position intermediate to the sensory areas of the dorsal ventricular ridge. The mammalian striatum may possess a similar function as suggested by the studies of MacLean (1972).

The midbrain roof areas of vertebrates possess auditory, visual, and probably somatotopic maps that are organized to perform sensory elicited orienting movements. In this sense the midbrain roof consists of a series of centers that function to tell an organism *where* stimuli exist relative to the organism. This tectal function appears common to all vertebrates. The relevant literature has recently been reviewed by Ingle (1973). Numerous studies implicate these midbrain centers in pattern recognition as well. Even in mammals, considerable color vision and pattern vision remain in the absence of isocortical sensory centers (Humphrey, 1970; Ware et al., 1972, 1974; Spear and Barbas, 1975; Cranford et al., 1976).

The ability of turtles to perform pattern discriminations in the absence of telencephalic visual centers (Bass et al., 1973), or geckos to feed on small moving insects following ablation of telencephalic visual centers (unpublished observations), indicates that the tectum of reptiles also possesses "perceptual" functions. What is not clear is whether the tectum in reptiles is sensitive to only a few sets of visual objects, or performs complex visual discriminations as well.

It is possible that the evolution of the dorsal ventricular ridge in lizards underlies complex discriminations. Increased analysis of sensory information and fine motor control characterizes the evolution of mammalian isocortex, and a similar evolutionary phenomenon may have occurred in parallel in living lizards. That lizards with the largest brain-body ratios and the most differentiated dorsal ventricular ridges also possess the most complicated behavior is probably not a coincidence, particularly if the dorsal ventricular ridge of lizards is homologous to most of mammalian isocortex. As noted earlier, the dorsal ventricular ridge receives information from many different sensory modalities and, in turn, projects massively upon the striatum. In these respects, it possesses functional similarities to mammalian isocortex and may perform complex sensory integrations and exert final control upon the functions of the striatum and other lower brain centers. The evolution of the dorsal ventricular ridge is the single most striking change in the CNS of lizards and most likely underlies much of their complex behavior.

Phylogenetic Considerations

In 1923, Charles L. Camp published his now famous study of the "Classification of Lizards." Prior to Camp's synopsis a number of widely different phylogenetic schemes had been proposed (Cope, 1864; Boulenger, 1884; Fürbringer, 1900). Nearly 50 years later, most of Camp's families and their phyletic placement remains firm, and his analysis stands as the major landmark in lizard systematics. Camp divided lizards into two major divisions, the Ascalabota and the Autarchoglossa (Fig. 21). He based this division on four characters: presence or absence of superficial rectus muscles, number of transverse rows of ventral scales, width of scale free margin, and external form of the copulatory organs or hemipenes. Camp himself noted the differences in locomotion reflected by his two divisions. It is very likely that three of his four sorting characters are tied to locomotor adaptations, and their combined occurrence may have evolved a number of times independently.

Recently it has been argued that the pygopodids and xantusiids, which possess well-developed superficial rectus muscles, are closely related to gekkonids (McDowell and Bogert, 1954; Hoffstetter, 1962). This view was supported by Romer, (1956) who suggested that the placing of the pygopodids and xantusiids near the gekkonids destroyed Camp's divisions, and that these divisions should be abandoned or redefined.

Underwood (1971), in a recent review of lizard affinities, suggested that the pygopodids and xantusiids are derivatives of the precusors of the Ascalabota and argued for the retention of Camp's divisions. He presents an updating of Camp's scheme which I have interpreted as a dendrogram in Figure 22A. The major changes in Underwood's updating of Camp's scheme, besides the transfer of the pygopodids and xantusiids to the Gekkota, relate to the placement of the cordylids and dibamids. Camp placed the Cordylidae within the anguimorphs, but noted that they possessed more ascalabotan characters than the anguimorphs. Underwood has accepted

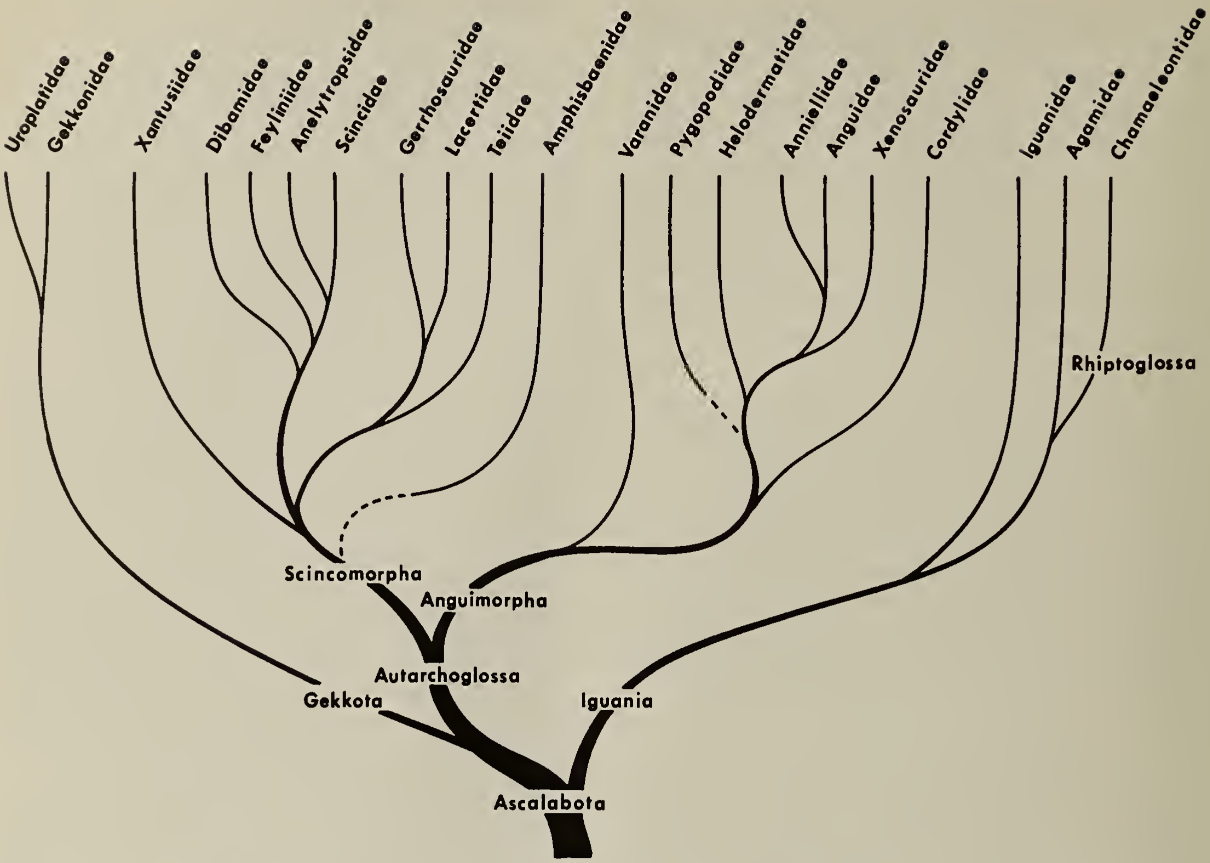

Figure 21. Dendrogram illustrating phyletic relationships of lizards as proposed by C.L. Camp (1923). Present figure redrawn from Camp's original dendrogram, deleting extinct groups and updating family names. Camp divided lizards into two divisions, the Ascalabota and Autarchoglossa, and concluded that the Ascalabota retain the largest number of primitive features.

the suggestion of McDowell and Bogert (1954) and Hoffstetter (1962) that cordylids are closely related to, if not members of, the gerrhosaurids, and has transferred the cordylids to the lacertoids.

Camp believed *Dibamus* to be a close relative of skinks, but Underwood (1957) suggested that it might be more closely related to the Gekkota. Gasc (1968) erected a separate suborder for *Dibamus* after concluding that the muscles and skeleton were convergent with both scincomorphs and gekkotans. Underwood (1971) has incorporated Gasc's suggestion in his summary.

Camp concluded that the Ascalabota retain more primitive features than do the Autarchoglossa. The distribution of derived brain characters in lizards indicates that the morphology of the central nervous system does not support Camp's contention. Two major patterns of brain variation (*lacertid* and *iguanid* patterns) have been summarized earlier, and I have argued that the *iguanid* pattern is the more derived relative to lacertids, and to *Sphenodon* and turtles. An alternate classification, based solely on brain characters, is presented in Figure 22B. The criteria on which this classification is based will be published in more detail elsewhere (Northcutt and Senn, in preparation). However, the major changes suggested by the central nervous system are the affinity of the teiids and varanids, and the erection of new major subdivisions. Camp's division of Ascalabota and Autarchoglossa is abandoned, and a new division is suggested on the basis of the *lacertid* pattern, Lacertomorpha, and the *iguanid* pattern, Dracomorpha. These

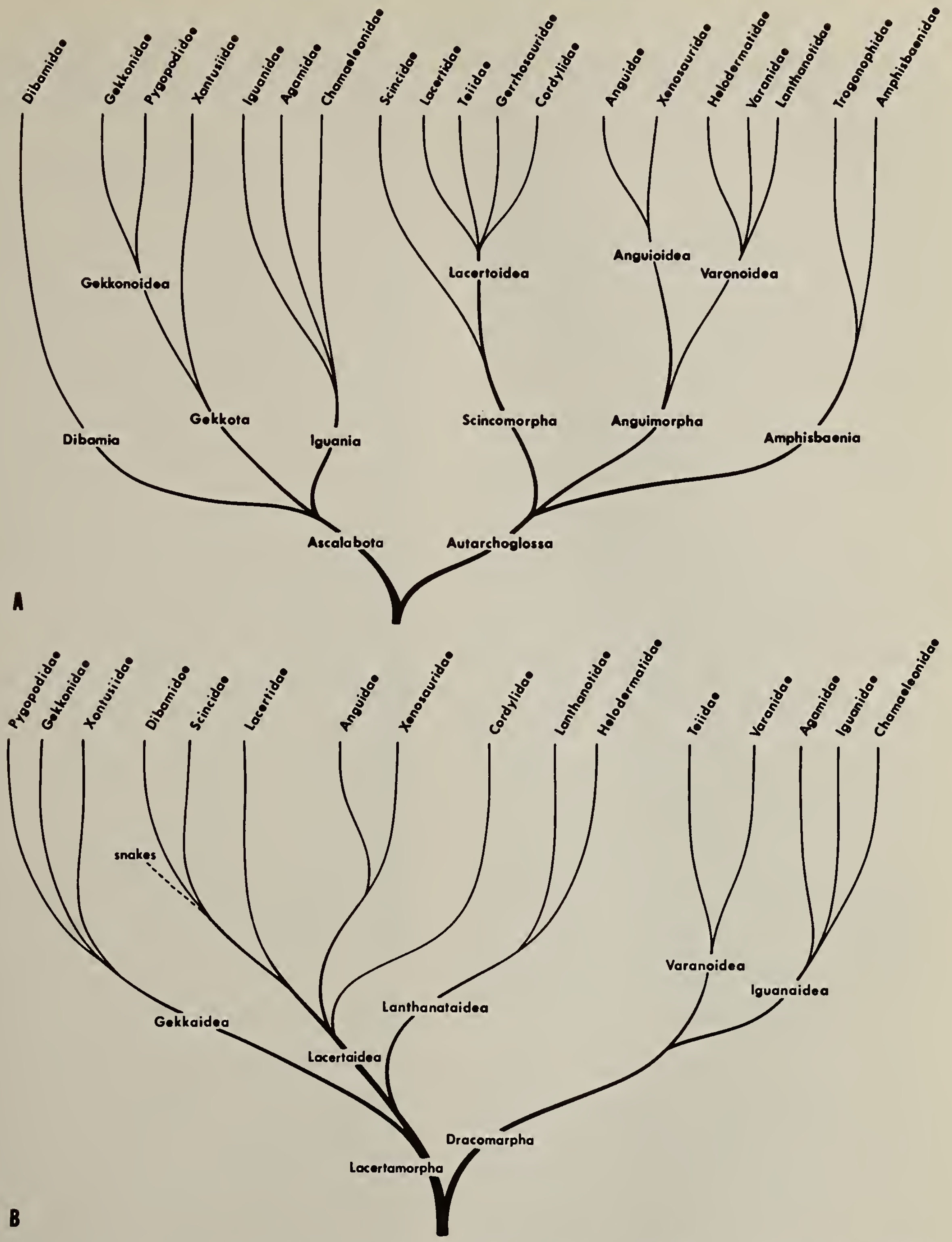

Figure 22. A. Dendrogram illustrating phyletic relationships recently summarized by Underwood (1971). Dendrogram is author's rendering of Underwood's summary classification scheme. B. Dendrogram illustrating possible phyletic relationships of lizards based on analysis of brain characters presented in present study. These new characters support the major conclusions regarding family relationships reached by Camp. The major differences relate to suggested placement of teiids and varanids, and recognition of new subdivisions, the lacertomorphs and dracomorphs. (Figure 22B after Northcutt and Senn, in preparation.)

two divisions are considered sister radiations with the dracomorphs possessing the more derived characters. These characters are: (1) elaboration of tectal lamination with specific hypertrophy of lamina 14, subdivision of lamina 7, and marked reduction of periventricular laminae; (2) hypertrophy of the pretectal nuclei with particular elaboration of the dorsal and ventral pretectal nuclei as well as nucleus geniculatus pretectalis; (3) expansion of the dorsal thalamus; and (4) complex migration and hypertrophy of the dorsal ventricular ridge of the telencephalon.

The close affinity of teiids and varanids is suggested on the basis of the remarkable similarity in their brain structure. As noted earlier (with regard to the studied brain characters) it is possible to separate teiids and varanids only by differential development of nucleus sphericus, which is laminated in varanids but not in teiids, by mediolateral differences in the thickness of lamina 14, and by a thicker tectal lamina 5 in teiids. While most taxonomic schemes have suggested close affinity between teiids and lacertids, Etheridge (1967) has suggested a close affinity between teiids and iguanids. Clearly lacertids and teiids exhibit the extreme range of brain variation seen in lizards, with the lacertids possessing characters that appear very similar to gekkonids and scincids, and the teiids and varanids possessing characters identical or most similar to the iguanoids. Thus, the morphology of the central nervous system would indicate close pylogenetic affinity among teiids, varanids, and iguanoids.

An alternate interpretation, however, must be considered. It is possible that the similarities in the assembly of taxa termed dracomorphs are due to parallelism and not to close phyletic affinity. Simpson (1961) defined parallelism as "the development of similar characters separately in two or more lineages of common ancestry and on the basis of, or channeled by, characteristics of that ancestry." It is possible, therefore, that the derived brain characters of the dracomorphs have evolved three times independently due to similar selective pressures acting on similar genomes which can reasonably be assumed to exist within a monophyletic group such as lizards.

Parallelism most frequently occurs when closely related taxa have invaded similar ecological zones so that similar selective pressures are operating. Thus, arguments accepting or rejecting suspected parallelism must include consideration of similarities in the ecological adaptations of the suspected taxa. Arguments based on the degree of similarity in characters, which are of major importance in establishing homology, are of little importance in determining parallelism since closely related taxa are expected to possess a high degree of similarity due to recent common ancestry. One additional test regarding parallelism may exist. This relates to the complexity of the character set suspected of parallelism, and the probability of its repeated independent occurrence. Mayr (1969) discusses a number of cases of parallel evolution such as structural similarities related to brachiating in primates, independent adaptation for burrowing in insectivores, soldier mandibles in termite genera, and secondary jaw articulations in birds. In each case, the adaptations involve a limited number of morphological elements and are adaptations to a specific ecological regime. These examples suggest that parallel evolution should occur most frequently in functional systems with fewer morphological features than in complex systems, and that parallel evolution most frequently occurs in response to very specific ecological adaptations.

At present the behavior and ecology of the Varanoidea and Iguanoidea are distinctly different. There is no obvious common ecological adaptation(s) that links these two groups. While both groups are primarily diurnal, so are the lacertids as well as many other taxa grouped in the Lacertomorpha. Attention has focused at this conference on two alternate types of predation—active foraging versus sit-and-wait predators. The dracomorphs clearly do not fall into one of these two categories. While many of the teiids and varanids are active foragers, many of the iguanoids are clearly sit-and-wait predators. Additionally, it should be noted that the agamids and iguanids also include the most striking examples of herbivory among lizards and the most complex social systems.

While the present iguanoid and varanoid adaptations are distinct, they do not preclude the possibility that similar selective pressures were operating at some point in their past history. This possibility can be explored only with further information regarding the fossil record of these families, information which, in the long run, is also likely to be most fruitful in determining if the dracomorphs constitute an assemblage of parallel forms.

The derived brain characters that characterize the dracomorphs do not appear to reflect adaptations to a specific ecological situation. They clearly cannot be accounted for in terms of hypertrophy of any *single* sensory modality, nor are they associated with motor specializations of any single region of the body. The brains of dracomorphs can best be described as the most complex among living lizards, with increase in both size and differentiation of most sensory modalities. The one exception is the reduction or loss of the vomeronasal system in iguanoids. The hypertrophy of this system in varanoids is the single most useful neurological sorting character in separating varanoids from iguanoids.

In summary, the dracomorphs are characterized by extensive and complex derived brain characters that do not relate to any single sensory or motor adaptation, nor do the living taxa share any obvious ecological adaptation. For these reasons, I believe the families assigned to this division share a more immediate ancestry with one another than with other lizards and are not an assemblage due to parallel evolution from a more remote common ancestor.

It is possible to recognize three major groups or superfamilies within the lacertomorphs: gekkoids, lacertoids, and lanthanotoids (Fig. 22*B*). The gekkoids include the pygopodids, gekkonids, and xantusiids. Representatives of these three families exhibit an enlarged nucleus dorsolateralis and medial cortex. Both pygopodids and xantusiids exhibit specialized medial ridge plates, and gekkonids and pygopodids possess almost identical caudal ridge plates. Finally gekkonids and pygopodids possess similar periventricular tectal laminae. These neural characters are derived with respect to *Sphenodon* with the exception of the caudal ridge plate. The close affinity of gekkonids, pygopopids, and xantusiids is also supported by considerable nonneurological data as well (McDowell and Bogert, 1954; Shute and Bellairs, 1953; Miller, 1966; and Underwood, 1957).

The lacertoids constitute a large group, six families, within which three trends can be recognized with regard to neural development. The lacertids and scincids possess very similar brain features. Both families are characterized by asymmetrical ridge plates in which the lateral division is the thickest, pronounced cell clusters of the ridge plate, and tectal laminae similar to *Sphenodon.* Skinks differ from lacertids in possessing a poorer developed lateral ridge plate and do not exhibit a distinct tectal lamina 4 or distinct subdivisions of tectal lamina 5.

Both the anguids and xenosaurids exhibit specialized medial ridge plates with little or no cell clustering and the core cells are larger than those of skinks and lacertids. Xenosaurids can be separated from anguids on the basis of a thinner tectal lamina 5.

The cordylids may be closely related to the xenosaurids. Both possess well-developed ridges and similar tectal lamination However the cordylid ridge, unlike that of *Xenosaurus*, is characterized by pronounced cell clusters. The cordylids are particularly interesting as they are diurnal insectivores exploiting a desert niche much like that of many agamids and iguanids. Thus cordylids might be expected to have developed a number of neural similarities to agamids and iguanids. At present, my analysis suggests that while the cordylids do possess well developed brains, they do not share any of the derived neural features of agamids and iguanids.

The lanthanotoids consist of only two genera: *Heloderma* and *Lanthanotus*. Both are characterized by an enlarged nucleus sphericus, reduced rostral ridge, and reduction of the superficial tectal zone. While the rostral ridge is reduced in these taxa, it is clearly divided into a peripheral plate and core. *Lanthanotus* is clearly the less specialized of the two genera.

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Forebrain Connections in Lizards and the Evolution of Sensory Systems

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SUMMARY. Recent experimental studies have contributed new insights into the organization of sensory systems in nonmammalian vertebrate brains. Many workers have discarded the classical view that the telencephalons of ancestral vertebrate species were dominated by olfactory input. The dorsal ventricular ridge of reptiles and birds, once regarded as the homolog of the mammalian basal ganglia, has been shown to be the target of ascending sensory system projections, corresponding to similar systems which project to neocortex in mammals. Ascending projections from the brainstem also terminate in the dorsomedial and dorsal cortical regions. While recent studies have supported the classical views that in reptiles the medial cortical wall corresponds to parts of the mammalian hippocampal formation and the dorsal cortex to neocortex, the relationships of these regions in reptiles to each other and their corresponding structures in mammalian brains may be more complex than previously realized. In the lizard, *Gekko,* the medial wall of the hemisphere and the entire dorsal cortex have interhemispheric commissural connections via the hippocampal commissure. The evolutionary implications of these findings regarding the mammalian neocortex and corpus callosum are discussed.

INTRODUCTION

Renewed interest in the anatomy of the neuroanatomical organization of nonmammalian vertebrate brains has resulted from recent advances in histological methods for tracing connections, particularly the development of the Nauta silver impregnation technique and its modifications, and of intra-axonal transport methods. Given these tools, and those employed in electrophysiological and behavioral studies, a number of recent findings have led to a revision of some of our basic concepts of brain evolution and have thus stimulated further inquiries into this area. It has now also been recognized that the great range of variation in the morphology of nonmammalian vertebrate brains, when studied in the light of the differences in behavior, adaptive zone, electrophysiological properties, etc., can yield a number of insights into the relationship of neuronal morphology and function. The present paper will review the anatomy of the pallial regions of the telencephalon in lizards in relation to our present understanding of the evolution of sensory systems.

ANATOMY OF THE LACERTILIAN PALLIAL REGIONS

Cross sections through the telencephalons of two lizards, *Gekko gecko* and *Iguana iguana,* are shown in Figure 1. These two species will serve to demonstrate the range of variation in the morphology of the forebrain among lizards (see Northcutt, this conference). It can be seen in both species that the cortical pallium can be divided into three major parts: medial, dorsal, and lateral. Each of these regions in turn can be subdivided. While relatively few detailed cytoarchitectonic studies have been done on reptilian telencephalons, some data regarding the distribution of cell types are available for a few species.

Lateral wall. The lateral wall can be divided into lateral cortex pars dorsalis (LCd) and lateral cortex pars ventralis (LCv) on

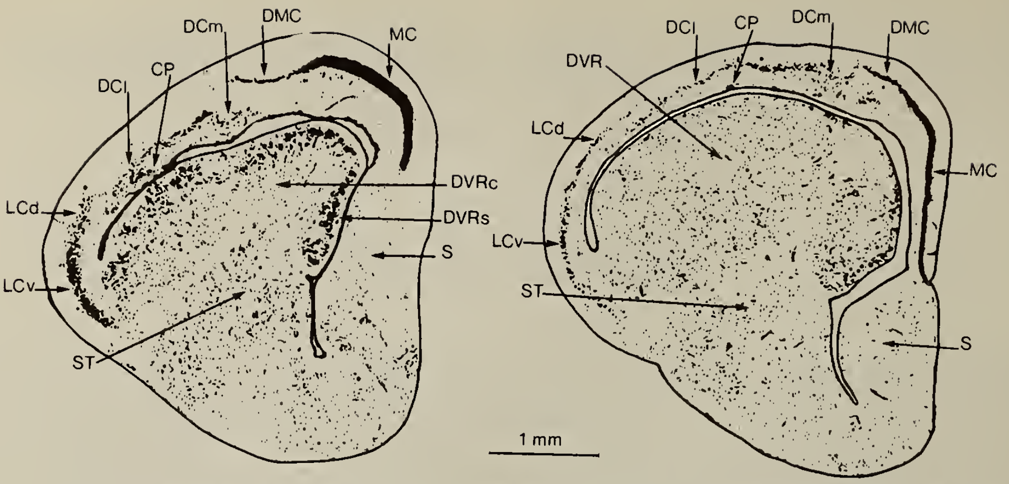


Figure 1. Photomicrographs of Nissl stained cross sections through the telencephalons of the lizards *Gekko gecko* (shown on the left) and *Iguana iguana*. Note the prominant corticoid band surrounding a core nucleus in the dorsal ventricular ridge of *Gekko*, as opposed to the presence of a number of nuclear groups and the absence of a definitive corticoid band in the DVR of *Iguana*.
AC = Anterior commissure; CP = Cell plate of dorsal cortex (Unger, '06); DC1 = Dorsal cortex pars lateralis; DCm = Dorsal cortex pars medialis; DVR = Dorsal ventricular ridge; DVRc = Core nucleus of dorsal ventricular ridge; DVRs = Surrounding corticoid band of dorsal ventricular ridge; HC = Hippocampal commissure; LCd = Lateral cortex pars dorsalis; LCv = Lateral cortex pars ventralis; MC = Medial cortex; S = Septum; ST = Striatum; V= Lateral ventricle.

the basis of cell packing density. A number of cell types have been identified in the lateral cortex of various reptilian species, including fusiform (Northcutt 1967, 1970; Voneida and Ebbesson, 1969), double pyramidal (Northcutt, 1970; Ulinski, 1974), and polygonal, multipolar, and stellate (Northcutt, 1977, 1970; Voneida and Ebbesson, 1969; Ulinski, 1974).

Medial wall. The medial wall is composed of two cortices, a small-celled medial cortex (MC) and a large-celled dorsomedial cortex (DMC). Northcutt (1967) described goblet, double pyramid, and small intrinsic cells in these cortices (his hippocampus pars dorsomedialis and hippocampus pars dorsalis) in *Iguana*. Ebbesson and Voneida (1969) found a similar variety of cells in *Tupinambis*, and Ulinski (1974) described candelabra cells in the medial cortex and a variety of cell types, including double pyramids, in the dorsomedial cortex in snakes. The medial wall of the telencephalon in turtles (Northcutt, 1970) also contains similar cell types, but the double pyramids in the dorsomedial cortex do not form the distinct layer seen in lizards.

Dorsal wall. The dorsal cortical area is usually divided into medial and lateral parts. The medial part of dorsal cortex (DCm) lies ventral to the cells of dorsomedial cortex, and the lateral part (DC1) lies medial to the dorsal part of lateral cortex. Additionally, Unger (1906), has identified a ventral cell plate which is particularly well developed in *Gekko* and is formed by clumps of cells similar to those that form the corticoid band in the dorsal ventricular ridge. Unger noted that this ventral cell plate corresponds to the corticoid band, and the continuity of these two structures can be seen in some sections.

A variety of cell types have been described in the dorsal cortex of reptiles, of which relatively large multipolar or double pyramidal cells with either spiny or nonspiny dendrites appear to be most common (Northcutt, 1967, 1970; Ebbesson and Voneida, 1969; Ulinski, 1974).

Dorsal ventricular ridge. The dorsal ventricular ridge (DVR) shows the most obvious interspecies differences in morphology. In lizards such as *Gekko*, the ridge is comprised of a core nucleus (DVR) surrounded by a corticoid band of clumped cells (DVRs);

in other lizards, such as *Iguana,* it is composed mainly of nuclear groups, having only a faint suggestion of a layer of clumped cells on the medial edge (Fig. 1). In its cytoarchitecture, the DVR in *Gekko,* a type I lizard (see Northcutt, this conference), is somewhat similar to that of snakes, turtles, and *Sphenodon,* whereas the DVR in *Iguana,* a type II lizard, is similar to that of the thecodonts—crocodiles and birds. The significance of these variations in morphology remains to be determined.

EVOLUTION OF THE VERTEBRATE FOREBRAIN

Before discussing the data on the connections and organization of the lacertilian forebrain in detail, I would like to provide a basis for a broader perspective by reviewing the history of thought on some aspects of vertebrate forebrain evolution.

The classical work of Elliot Smith (1910), Herrick (1948), and Ariëns Kappers, Huber, and Crosby (1936) developed the first coherent picture of the evolution of the forebrain. They analyzed the normal embryology and the topographical relationships of nuclei and fiber tracts in various species of nonmammalian vertebrates. In cross sections of the telencephalons of most vertebrates, several distinct regions can be recognized which appear to be fairly constant across classes. The dorsal portion, or pallium, can generally be divided into a medial and a lateral zone, between which lies a more or less developed dorsal zone. The ventral portion, or basilar region, generally contains nuclear groups and the main fiber bundles of ascending and descending systems. In reptiles and birds, a portion of the dorsal part of the telencephalon is expanded and bulges into the lateral ventricle; it is thus referred to as the dorsal ventricular ridge (Johnston 1915). Whereas the cell somas of the medial, dorsal, and lateral pallial areas in reptiles are arranged in laminae, the cell somas of the dorsal ventricular ridge have a tendency to be grouped into nuclei. Based on the latter observation and on comparisons with mammalian embryology, anatomists concluded that the dorsal ventricular ridge was homologous to the mammalian basal ganglia, terming it the "corpus striatum."

The reptilian pallial cortices were homologized with mammalian cortices on the basis of fiber connections and position, and by a complex argument involving the forebrain commissures. On the basis of its connections with the olfactory tracts, the lateral lamina of cells was identified as piriform cortex. It was more difficult, however, to argue that the medial wall was hippocampal.

In 1910, Elliot Smith reviewed the earlier views concerning the massive corpus callosum which connects the two hemispheres of the mammalian neocortex. He cited Owen as the first to recognize that there is no corpus callosum in marsupials and monotremes. Owen's view had been vigorously opposed by Huxley and others, on the grounds that *de novo* origin of the corpus callosum in eutherian mammals was untenable in terms of evolutionary theory. However, Elliot Smith supported Owen's view with his analysis of the brains of foetal monotremes. He showed that these brains have two rostral commissures which resemble the anterior and dorsal commissures of all vertebrates. While the dorsal commissure in eutherian mammals is the corpus callosum, in the foetal monotreme the dorsal commissure clearly connects the medial walls of the hemispheres, and the medial wall matures into the hippocampal cortex. By then comparing the foetal monotreme brain with that of adult reptiles, Elliot Smith concluded that the cells in the medial wall of the reptilian cerebral hemisphere, which give rise to the dorsal commissure, were also hippocampal.

Since the lateral cortex of reptiles was identified as piriform, the medial cortex as hippocampal, and the dorsal ventricular ridge as basal ganglia, the only remaining portion of the dorsal telencephalon to be dealt with was the dorsal cortex. The latter was therefore identified, as by default, as the homolog of mammalian neocortex.

The telencephalons of anamniote vertebrates were believed to be almost completely dominated by olfactory input, and these animals were thus relegated to a much less important status in terms of evolutionary theory and development. Their forebrains appeared to have less cytological differentiation than those of land vertebrates and were not thought to contain any regions homologous to neocortex. It was believed that only after vertebrates emerged onto the land were the auditory, visual, and somesthetic systems elaborated, and that these systems then invaded the telencephalon, claiming synaptic sites that had originally been olfactory.

The findings of a number of recent experimental studies have shed new light on these concepts of vertebrate forebrain evolution and have necessitated a revision of the earlier conceptions of homologies. Studies using anterograde degeneration methods have shown that the olfactory system does not dominate the telencephalon in anamniotes. In sharks (Ebbesson and Heimer, '70), actinopterygian fishes (Scalia and Ebbesson, 1971; Braford, 1973*a*; Braford and Northcutt, 1974), and amphibians (Scalia et al., 1968*a*; Scalia, 1972; Northcutt and Royce, 1975) the olfactory projections to the telencephalon are confined to relatively small and discrete areas, as they are in reptiles (Scalia, 1968; Scalia et al., 1969; Heimer, 1969) and mammals (Scalia, 1966; Heimer, 1969). Thus, it would appear that in all extant vertebrates the greater part of the telencephalon is potentially available for the reception of nonolfactory sensory system inputs, and the idea of the invasion of an olfactory-dominated telencephalon by these inputs in ancestral land vertebrates has been discarded. The question immediately raised by these findings was the nature of these olfactory-free regions in nonmammalian vertebrates. An examination of the organization of ascending sensory systems was thus initiated; and, while few species have been studied to date, it is now possible to state a number of postulates regarding the evolution of both the dorsal thalamus and the telencephalon.

Before turning to reptiles in detail, some of the relevant data on ascending sensory systems in nonmammalian vertebrates in relation to our revised concepts of forebrain evolution will be reviewed. In the visual system, retinal projections have been studied in one or more species from every extant vertebrate class. This sample, however, is not evenly distributed among classes, nor is it extensive enough to allow more than a few basic conclusions. While there is considerable variation in the presence of bilateral versus totally contralateral retinal projections (Braford, 1972*b*; Northcutt and Butler, 1976), in all nonmammalian vertebrates studied to date the retina projects to nuclei in the dorsal thalamus, ventral thalamus, and pretectum, as well as to the tectum, and, in most cases, to the basal optic nucleus in the mesencephalic tegmentum (e.g., Agnatha: Northcutt and Przybylski, 1973; Osteichthyes: Ebbesson, 1968 (teleosts); Northcutt and Butler, 1976 (holosteans); Chondrichthyes: Graeber and Ebbesson, 1972; Amphibia: Scalia et al., 1968*b*; Reptilia: Hall and Ebner, 1970*a* (turtles); Butler and Northcutt, 1971*a*; Cruce and Cruce, 1975, this conference (lizards); Northcutt and Butler, 1974a (snakes); Northcutt et al., 1974 (rhynchocephalian); Braford, 1973*b* (crocodiles); Karten and Nauta, 1968) (Aves). The tectum in turn projects to the dorsal thalamus, to a locus that in some cases overlaps topographically with the retinal target, as in amphibians (Scalia and Gregory, 1970), and in other cases does not, as in reptiles (Hall and Ebner, 1970*a*; Butler and Northcutt, 1971*b*; Braford, 1972*a*).

Auditory and somesthetic projections have been studied in fewer species, but it has been established that in reptiles and birds these systems project to the dorsal thalamus. Auditory projections are relayed from the torus semicircularis (inferior colliculus) in the midbrain to a dorsal thalamic nucleus (Karten, 1967; Pritz, 1974*a*; Foster, 1974). Somesthetic inputs have also been identified, but generally appear to be less well represented in the dorsal thalamus than the other systems (Ebbesson, 1967, this conference).

From the dorsal thalamus, ascending fibers project to the telencephalon. The dorsal lateral geniculate nucleus has been shown to project to the dorsal pallium in turtles (Hall and Ebner, 1970*b*, Foster et al., 1976) and to a portion of the Wulst (a dorsal pallial region) in birds (Karten et al., 1973). The thalamic targets of the mesencephalic optic tectum and torus semicircularis do not project to cortex but to discrete regions in the dorsal ventricular ridge (Karten, 1968; Hall and Ebner, 1970b; Karten and Hodos, 1970; Pritz, 1974*b*, 1975). These ascending pathways to the dorsal ventricular ridge appear to correspond in their organization to those of the auditory and extrastriate cortex in mammals (e.g., Graybiel, 1970, 1972; Mathers, 1971; Kaas et al., 1972; Harting et al., 1973; Harting and Casagrande, 1974; Rezak and Benevento, 1975). As the dorsal ventricular ridge (DVR) is the target of these sensory projections in reptiles and birds, it is now thought that this region of the telencephalon is homologous as a field to parts of mammalian neocortex, rather than to basal ganglia. This concept is supported by observations on the histochemistry and connections of several more basilar regions of the telencephalon (Karten, 1969; Karten and Dubbeldam, 1973) that indicate that only the latter correspond to mammalian basal ganglia.

Studies of ascending projections following unilateral transections at diencephalic, mesencephalic, and more caudal levels have been done in a wider variety of vertebrate species (Schroeder and Ebbesson, 1974; Butler and Ebner, 1972; Rubinson and Colman, 1972; Kicliter and Northcutt, 1975) and likewise demonstrate ascending systems that terminate in nonolfactory portions of the telencephalon. In the shark, it has further been shown electrophysiologically that the telencephalic target of the dorsal thalamus is a visual area (Cohen et al., 1973), and that visual deficits in pattern discrimination result from removal of this area (Ebbesson, personal communication).

Efferent projections. The efferent projections of the telencephalon have received less attention than the afferent. However, findings in amphibians and reptiles that the medial wall projects to areas which in mammals comprise parts of the limbic system (e.g., Halpern, 1972, 1974, 1976; Lohman and Mentink, 1972; Ulinski, 1975) strongly support Elliot Smith's 1910) deduction that the medial wall is homologous to the mammalian hippocampal formation.

In summary, the classical views that the medial and lateral telencephalic regions in nonmammalian vertebrates are homologous, respectively, to mammalian hippocampal and piriform cortices are supported by recent experimental evidence. The idea that the dorsal pallial region is homologous to neocortex has received some support, but, as will be discussed below, the nature of this zone may not yet be fully understood. Finally, the dorsal ventricular ridge of reptiles and birds, once thought to be homologous to basal ganglia, now appears to be homologous as a field (Campbell and Hodos, 1970) to parts of neocortex.

THALAMOTELENCEPHALIC PROJECTIONS IN REPTILES

Studies of sensory projections to the thalamus and telencephalon in reptiles have mainly been concerned with the visual system, although some data are now available on the auditory and somatosensory systems as well. As a detailed account of the visual pathways will be given elsewhere in this volume (Cruce and Cruce), I will only briefly summarize them here.

Visual System

Retinal projections to the dorsal and ventral lateral geniculate nuclei of the thalamus, to pretectal nuclei, and to the tectum have been described in a number of reptiles (e.g., Armstrong, 1950; Ebbesson, 1970*a*; Butler and Northcutt, 1971*a*; Braford, 1973*b*; Halpern and Frumin, 1973; Northcutt and Butler, 1974*a,b*; Cruce and Cruce, 1975). Tectothalamic projections to nucleus rotundus have also been demonstrated in turtles (Hall and Ebner, 1970*a*), lizards (Ebbesson, 1970*a*; Butler and Northcutt, 1971*b*), and crocodiles (Braford, 1972*a*).

Unilateral transections at the thalamic level in the lizard, *Iguana iguana*, have been found to result in a complex pattern of degeneration in the telencephalon (Butler and Ebner, 1972). Fibers travel rostrally in the superficially lying stratum moleculare (dorsal to the dorsomedical cortex) and terminate in peridendritic fields in this layer and among the cell somas of the dorsomedial and dorsal cortices. Another group of degenerated fibers enter the dorsal ventricular ridge and terminate in several discrete fields. Other studies have shown that thalamotelencephalic fibers project (1) from the dorsal lateral geniculate nucleus to the general (dorsal) cortex in turtles (Hall and Ebner, 1970*b*; Foster et al., 1976), and (2) from nucleus rotundus to a discrete region of the dorsal ventricular ridge in turtles (Hall and Ebner, 1970*b*), crocodiles (Pritz, 1975), and lizards (Distel and Ebbesson, 1975). Thus, there appear to be two separate visual pathways to the telecephalon in reptiles, as there are in birds (Karten et al., 1973) and mammals (Schneider, 1969).

Auditory System

An auditory projection pathway to the telencephalon has also been described in reptiles. Fibers arising from the torus semicircularis (inferior colliculus) in the mesencephalon project to nucleus reuniens (medial geniculate nucleus) in the dorsal thalamus (Foster, 1974; Pritz, 1974*a*). From nucleus reuniens, projections have been traced in caiman (Pritz, 1974*b*) and in lizards (Distel and Ebbesson, 1975) to a discrete region in the DVR, medial to and distinct from the visual target of nucleus rotundus.

Somesthetic System

Of the three major ascending sensory systems, the somesthetic system has received the least study in reptiles.

Ascending spinal projections to the dorsal thalamus in *Tupinambis* (Ebbesson, 1967) have been described. Recent data on this system are discussed by Ebbesson (this conference).

It is mainly on the basis of these findings of ascending sensory projections relayed from dorsal thalamic nuclei that the dorsal ventricular ridge is now considered to correspond to parts of mammalian neocortex. While the finding in turtles of a projection of the dorsal lateral geniculate nucleus to dorsal cortex (Hall and Ebner, 1970*b*; Foster et al., 1976) strongly supports the classical idea that this pallial region is also a homolog of neocortex, other connections of this area, which will be discussed below, suggest that its nature may be more complex.

A study of telencephalic connections which was recently completed in the lizard *Gekko gecko* (Butler, 1976) will now be reviewed before returning to a discussion of the nature of the reptilian dorsal pallium and dorsal ventricular ridge.

ORGANIZATION OF TELENCEPHALON IN GEKKO

While the ascending projections from nuclei in and caudal to the dorsal thalamus have not yet been worked out in detail in *Gekko gecko* unilateral brainstem transections result in a pattern of degeneration in the telencephalon similar to that seen in the green iguana (Butler and Ebner, 1972). The dorsal and dorsomedial cortices are targets of these projections, as are the DVR and basal forebrain.

A series of ablations made by suction that variously involved part or all of the lateral, dorsal, and medial walls of the telencephalon, and the dorsal ventricular ridge was carried out in *Gekko gecko*. Survival times ranged between 14 and 32 days, after which the

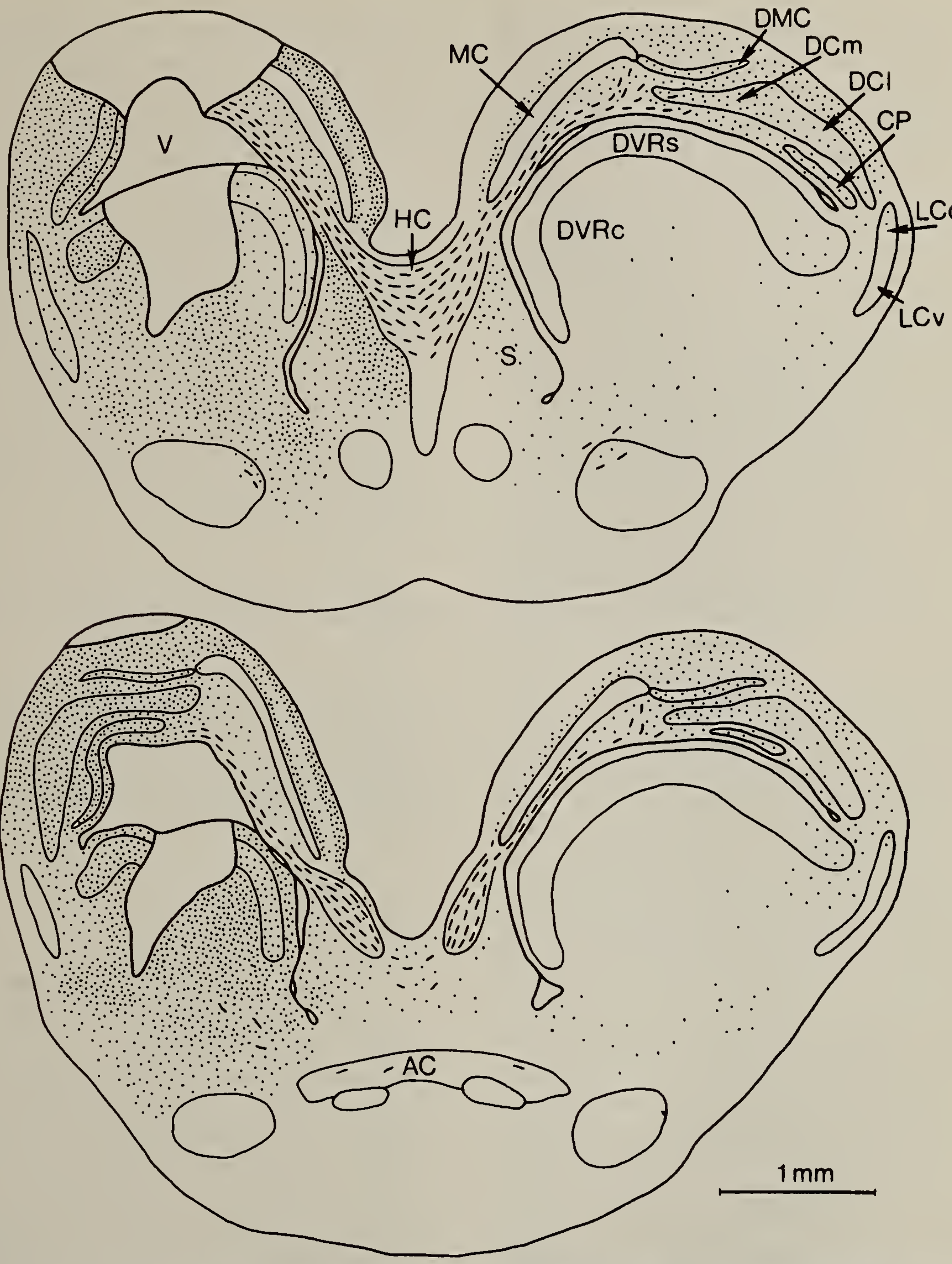


Figure 2. Chartings of anterograde degeneration seen in the telencephalon of *Gekko* **following a lesion which** involved the dorsal cortex, part of the medial wall, and the dorsal ventricular ridge. **Degenerated fibers of** passage are represented by dashes and terminal dereneration by stippling. The lesion is represented by the shaded regions on the left sides of each drawing. Most degenerated fibers cross in the **hippocampal** commissure to terminate densely in the contralateral septum (S), medial cortex MC, **dorsomedial cortex** (DMC), and dorsal cortex (DCm, DCl, and CP). Sparse terminal degeneration is present in the lateral edge of the DVR and striatal area contralaterally. Whereas ipsilaterally degeneration superficial to the cell plate of medial cortex (MC) forms three bands of different densities, contralaterally only the deepest of these bands contains degeneration. Only an occasional degenerated fiber was seen in the anterior commissure following this lesion. Modified Eager method. Survival time 16 days. See Fig. 1 for abbreviations.

animals were perfused transcardially with saline and 10 percent formalin. The brains were then embedded in egg yolk, frozen and sectioned at 30μ. Sections were processed with various modifications of the Nauta silver impregnation technique, including those of Fink and Heimer (1967), Roth (Ebbesson, 1970*b*), and Eager (1970). In *Gekko gecko,* the Eager modification produced the most successful impregnation of degenerated fibers and terminals.

The pattern of degeneration seen following one of the larger lesions, which involved dorsal cortex, parts of the medial wall, and the dorsal ventricular ridge is shown in Figure 2. Ipsilaterally degeneration extends throughout the cortices and the dorsal ventricular ridge, and into the septum and striatum. The majority of degenerated fibers traced into the contralateral hemisphere travel via the hippocampal (dorsal pallial) commissure (HC). Some fibers pass into and terminate in the contralateral septum (S), while the rest turn dorsally in the alveus, a fiber tract deep to medial cortex. Terminal degeneration associated with the medial cortex (MC) is confined to two bands on either side of the cell plate, leaving the outer portion of the stratum moleculare free of degeneration. Ventral to the dorsomedial cortex (DMC) some degenerated fibers turn dorsally and others continue laterally into the region of the ventral cell plate (CP) and medial part of dorsal cortex (DCm). Terminal debris extends throughout the dorsal cortex; in the lateral part of dorsal cortex (DCl), the degeneration is primarily concentrated in the superficial molecular layer. Sparse degeneration extends into the region of the lateral cortex (LCd) and the lateral edge of the DVR. Finally, a fairly sparse amount of degeneration is found in the contralateral basal forebrain, ventrolateral to the ventral recess of the lateral ventricle.

A series of more restricted lesions of portions of the cortex enables some dissection of this pattern of projections. A lesion which involved the lateral cortex and the lateral edges of the DVR and basal forebrain gave rise to degeneration in the contralateral hemisphere, mostly via the anterior commissure, in the striatum, lateral cortex, and more sparsely in the lateral edge of the DVR. Lesions restricted to the dorsal cortex, however, result in degenerated fibers which travel via the hippocampal commissure and alveus to terminate in the contralateral medial, dorsomedial, and dorsal cortices, and very sparsely in the lateral edge of the DVR. This distribution is similar to that seen following the more extensive lesions as described above. Further studies utilizing intra-axonal anterograde transport of tritiated amino acids and retrograde transport of horseradish peroxidase are presently being initiated to dissect further the details of these projections.

REPTILIAN DORSAL CORTEX AND DVR

Figure 3 summarizes some of the data from recent anatomical studies on the connections of the dorsal cortex and DVR in reptiles and birds. While being oversimplified for illustration, it provides an outline of current information.

Dorsal Ventricular Ridge

In turtles, lizards, and crocodiles the DVR has been found to receive an ascending visual pathway. The optic tectum projects to nucleus rotundus in the dorsal thalamus (Ebbesson, 1970*a*; Hall and Ebner, 1970*a*; Butler and Northcutt, 1971*b*; Braford, 1972*a*), and nucleus rotundus, in turn then projects to a lateral area in the anterior dorsal ventricular ridge (Hall and Ebner, 1970*b*; Pritz, 1975; Distel and Ebbesson, 1975). In lizards and crocodiles an ascending auditory pathway from the torus semicircularis (inferior colliculus), via nucleus reuniens in the dorsal thalamus (Foster, 1974; Pritz, 1974*a*), projects to a medial area in the anterior DVR (Pritz, 1974*b*); Distel and Ebbesson, 1975). As discussed above, these pathways in reptiles and similar ones in birds

(Karten, 1968; Karten et al., 1973) appear to correspond to the tecto-pulvinar-extrastriate and auditory system projections in mammals. Additionally, projections to the DVR from dorsal cortex have been described in turtles (Northcutt, 1970) and snakes (Halpern, 1976).

A recent study of the DVR in the lizard *Tupinambis* (Sligar and Voneida, 1976) demonstrated efferent projections to nucleus rotundus and to the hypothalamus. As is the case in *Gekko* (Butler 1976) and in birds (Zeier and Karten 1973), no evidence of projections to the contralateral DVR was found. Interhemispheric connections of the DVR via the anterior commissure were, however, found in turtles (Northcutt, 1970, 1974). The latter pathway may be similar to the interneocortical connection which, in monotremes and marsupials (Ebner, 1969) as well as in eutherian mammals (Ebner and Myers, 1965), travels via the anterior commissure.

On the basis of these data, particularly the findings of ascending visual and auditory pathways, the dorsal ventricular ridge appears to correspond to parts of mammalian neocortex receiving similar projections. The cell populations in the DVR which have been identified as visual and auditory occupy, however, only a small portion of the entire ridge. The circuitry of most regions of the DVR still needs to be worked out.

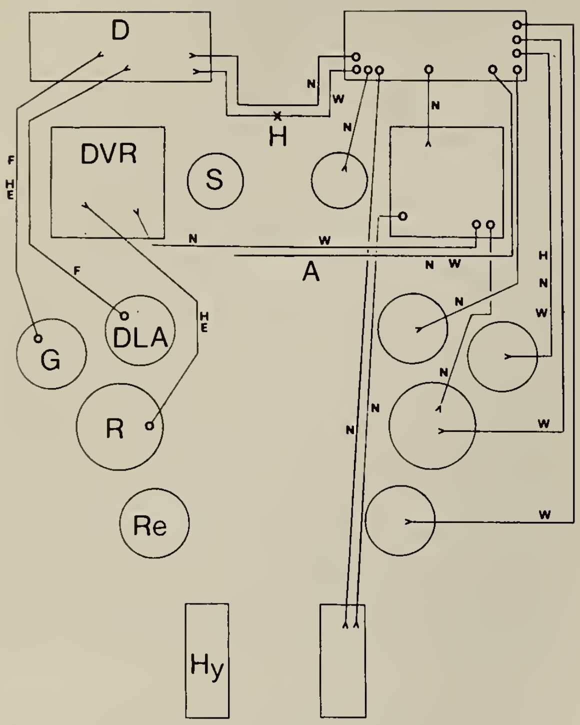
Dorsal cortex: Ascending afferent connections. As discussed above, the dorsal cortex has been found to receive ascending visual projections from the dorsal lateral geniculate nucleus in turtles (Hall and Ebner, 1970*b*; Foster et al., 1976) and birds (Karten et al., 1973). In birds this pallial telencephalic region is called the Wulst, and the projections from the dorsal geniculate (nucleus opticus principalis thalami) are confined to its lateral part. The medial part (Karten et al., 1973) receives projections from medially situated nonvisual thalamic nuclei including nucleus dorsolateralis anterior. In both turtles (Foster, et al., 1976) and lizards (Distel and Ebbesson, 1975) a projection to dorsal cortex from nucleus dorsolateralis anterior has also been found.

Dorsal cortex: Ipsilateral efferent projections. In lizards (Lohman and Mentink, 1972; Butler, 1976) and snakes (Halpern, 1974, 1976; Ulinski, 1975), lesions of the dorsal cortex result in degeneration in the molecular layer of medial cortex and in the septum. Additionally, efferent projections to the posterior part of the DVR and to nucleus anterior of Warner in the dorsal thalamus have been found in snakes (Halpern, 1976), and projections to hypothalamus in lizards (Lohman and Van Woerden-Verkley, 1976). The dorsal cortex also projects to the DVR in turtles (Northcutt, 1970) and in lizards (Lohman and Van Woerden-Verkley, 1976). In birds the lateral Wulst projects to a region of the DVR called the periectostriatal belt that surrounds the rotundal projection field (Karten et al., 1973).

Descending projections of dorsal cortex to the dorsal lateral geniculate nucleus have been reported in turtles (Hall and Ebner, 1974; Ware, 1974), as has a projection of the Wulst to nucleus opticus principalis thalami in birds (Karten et al., 1973). In turtles, projections have also been traced to nuclei rotundus and reuniens in the dorsal thalamus (Ware, 1974) and to the midbrain tegmentum (Hall and Ebner, 1974; Ware, 1974).

Dorsal cortex: Interhemispheric connections. While commissural projections of dorsal cortex were not found in the lizard *Tupinambis* (Voneida and Ebbesson, 1969; Lohman and Mentink, 1972), nor in turtles (Ware, 1974) or snakes (Ulinski, 1975; Halpern, 1976), they appear to be present in the lizard *Gekko* (Butler, 1976). Additionally, in *Gekko*, the dorsal cortex projects to part of the molecular layer of the contralateral medial cortex. These projections pass to the contralateral hemisphere in the hippocampal (dorsal pallial) commissure. A similar pathway was found in the turtle *Chrysemys* (Northcutt, 1970).

TURTLES



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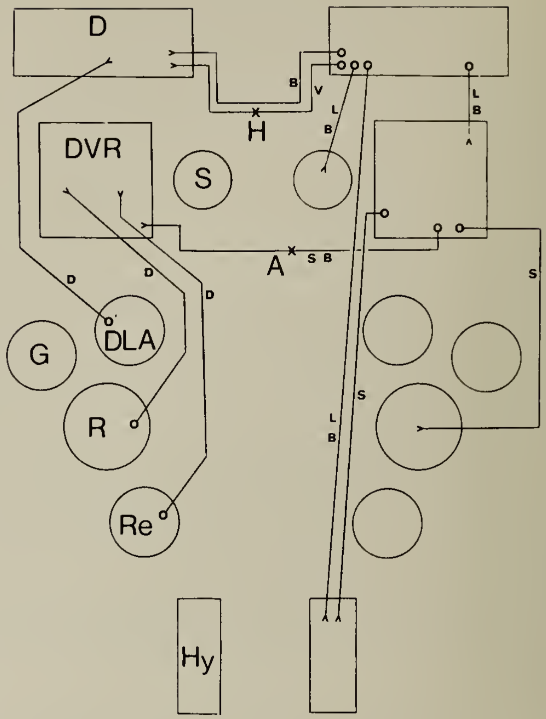

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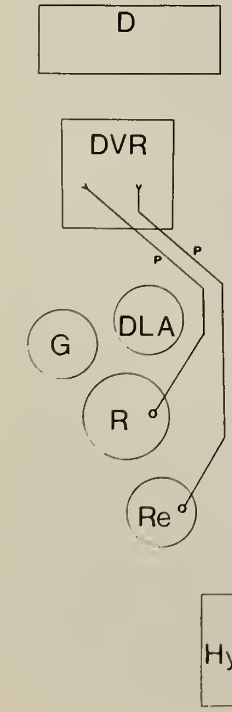

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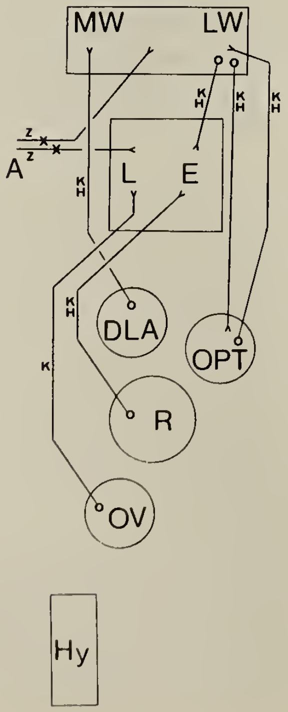
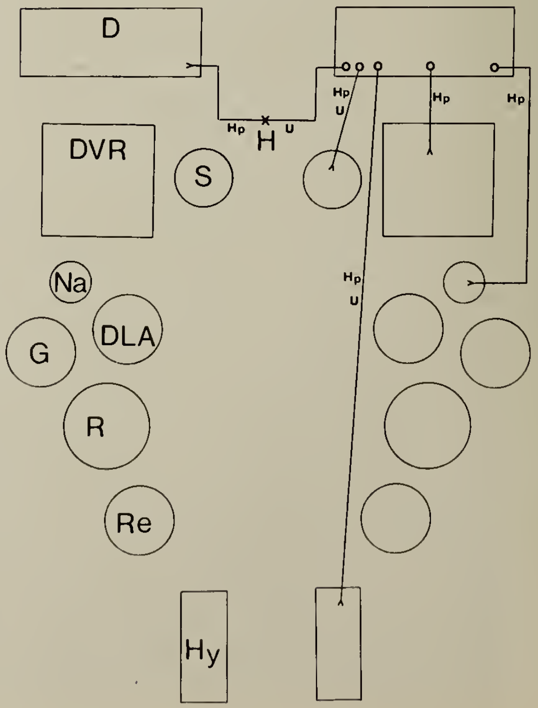


SNAKES



In summary, the reptilian dorsal cortex is the recipient of ascending projections from both the dorsal lateral geniculate nucleus and the more medially located nucleus dorsolateralis anterior of the thalamus. On the basis of its position and its apparent lack of sensory afferents, the latter nucleus may correspond to part of the anterior nuclear group in the thalamus of mammals. Efferent projections of dorsal cortex have been traced to the dorsal lateral geniculate nucleus and to an anterior nucleus in the thalamus, septum, and hypothalamus. Thus, on the one hand, the dorsal cortex appears to correspond to part of neocortex, while on the other it appears to correspond to part of the mammalian limbic system.

One possible resolution of this problem lies in noting that in lizards, for example, medial and dorsal divisions of dorsal cortex can easily be recognized. In birds, the afferent projections to the Wulst of nucleus dorsolateralis anterior and the principal optic nucleus terminate in nonoverlapping zones in the medial and lateral portions of the Wulst, respectively, and it is the lateral Wulst which projects into the DVR and reciprocally to the principal optic nucleus. The medial Wulst is juxtaposed to the medial hippocampal cortex (Karten et al., 1973), as is the medial part of dorsal cortex in reptiles. Thus the explanation of the differing results in reptiles *may* simply be that the dorsal cortex is composed of two very different parts, a medial limbic portion and a lateral portion homologous to some cell populations in the mammalian neocortex, and that these two parts are differentially developed in various species.

An alternative explanation, however, is that, while in birds the medial and lateral parts of the Wulst have evolved separate connections and functions, the entire dorsal cortex in lizards is homologous as a field to parts of both the mammalian neocortex and hippocampal formation. In either case, could the interhemispheric commissural connections of dorsal cortex found in *Gekko,* which travel in the dorsal pallial commissure, then correspond to connections of mammalian neocortex via the corpus callosum? We must consider the evidence regarding the evolution

Figure 3. Schematic representation of some of the current data on the afferent and efferent connections of the dorsal cortex and the dorsal ventricular ridge (DVR) in reptiles and birds. For turtles, lizards, and snakes, the diagrams are bilateral representations; afferent connections are shown on the left of each diagram and efferent connections on the right. For crocodiles and birds, the diagrams are unilateral. In all cases, medial cortex, dorsomedial cortex, and lateral cortex have been omitted, as have connections caudal to the level of the diencephalon. Small circles represent cell bodies; v's, axon terminals; and lines, axons. The position of cell bodies or terminals *within* structures is not necessarily anatomically precise, except in the cases of afferents to the DVR (L and E in birds) and the connections of the medial versus the lateral parts of the Wulst (MW and LW) in birds. An X placed on a line indicates that this projection has been found to be absent.

Abbreviations. Large letters indicate the structures diagramed as follows: A, anterior commissure; D, dorsal cortex; DLA, nucleus dorsolateralis anterior; DVR, dorsal ventricular ridge; E, ectostriatum; G, nucleus geniculatus lateralis pars dorsalis; H, hippocampal commissure; Hy, hypothalamus; L, fields L of Rose; LW, lateral Wulst; MW, medial Wulst; Na, a rostral extension of Warner's nucleus anterior; OPT, nucleus opticus principalis thalami; OV, nucleus ovoidalis; R, nucleus rotundus; Re, nucleus reuniens; S, septum.

Small letters placed next to lines indicate the references for the data as follows: B, Butler, 1976; D, Distel and Ebbesson, 1975; F, Foster et al., 1976; H, Hall and Ebner, 1974; HE, Hall and Ebner, 1970b; Hp, Halpern, 1974, 1976; K, Karten, 1968; KH, Karten, et al., 1973; L. Lohman and Mentink, 1972; N, Northcutt, 1970; Pritz, 1974b, 1975; S, Sligar and Voneida, 1976; U, Ulinski, 1975; V, Voneida and Ebbesson, 1969; W, Ware, 1974; Z, Zeier and Karten, 1973.

The intent of this figure is twofold. It provides a summary of current data and demonstrates the lack of information on some pathways in various groups, e.g., the connections of dorsal cortex in caiman and thalamotelencephalic connections in snakes. Secondly, and more importantly, it demonstrates the problems which arise from considering "dorsal cortex" to be a single structure. This structure has afferent and efferent connections not only both with sensory relay nuclei of the dorsal thalamus, suggesting a correspondence to neocortex, but also with other areas, such as hypothalamus and septum, indicating that it is part of the limbic system of mammals. Thus, until individual cell populations and their specific connections are identified, and until sense can be made of the variation between groups and at the species level, little additional insight can be gained.

of the corpus callosum to determine whether or not this possibility is feasible anatomically.

As was discussed above, Elliot Smith (1910) concluded that the dorsal commissure in reptiles, monotremes, and marsupials is the hippocampal commissure. Abbie (1939) working with brains from adult mammals, also presented a strong argument that the corpus callosum is a *de novo* structure in eutherian mammals, one of his points being that the corpus callosum does not develop in the lamina terminalis, but is related to it only secondarily. He believed that in development the callosal fibers "break through the subiculum" and that "the upper edge of the lamina terminalis [serves as] the necessary bridge, for the passage of fibers between the hemispheres." Streeter (1907), however, in his studies of human embryos, concluded that the corpus callosum does in fact develop within the lamina terminalis.

The mechanism of callosal development, partly obscured in the literature due to terminological differences, was finally clarified by Rakic and Yakovlev (1968). From study of human embryological material, they demonstrated that the corpus callosum and hippocampal commissure both develop in the same part of the lamina reuniens of His, a dorsal structure included descriptively by Streeter (1907) and others as part of the lamina terminalis.

Thus, were any cell groups in the reptilian dorsal cortex shown to be homologous to cell groups in the mammalian neocortex, any interhemispheric connections of these groups traveling in the dorsal pallial (hippocampal) commissure could correspond to the mammalian corpus callosum. Of course no conclusions can be drawn regarding interhemispheric connections in reptiles until the nature of the various cortices, and dorsal cortex in particular, is understood.

In addition to the questions regarding the dorsal cortex, there is a great deal of information on the organization of the dorsal ventricular ridge yet to be gained. In particular, detailed work is necessary on the organization of afferent and intrinsic projections in relation to the cytoarchitectonic arrangement of the DVR in type I and type II lizards, as well as in other reptiles and birds which have either the corticoid band-core arrangement or the nuclear arrangement of cells in the DVR. Such an analysis can provide insights into principals of neural organization in the vertebrate nervous system, by recognition of which characters are generalized, and into the relationship of morphology to evolution and function, by identification of which characters are specializations for particular adaptive zones.

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Analysis of the Visual System in a Lizard, *Tupinambis Nigropunctatus*

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SUMMARY. Retinal projections were studied in the Tegu lizard, *Tupinambis nigropunctatus*, by employing the method of autoradiographic tracing of anterograde axonal transport. In agreement with the general pattern of vertebrate visual projections as outlined by Ebbesson (1970), retinal fibers terminate in six areas of the brain of the Tegu lizard, as follows: dorsal thalamus, ventral thalamus, pretectum, tectum, hypothalamus, and nucleus of the basal optic tract. Most of these areas receive fibers from both the contralateral and ipsilateral eye with the exception of the hypothalamus and nucleus of the basal optic tract, which receive only contralateral fibers.

INTRODUCTION

The visual system plays an important role in the behavior of all vertebrates. Through the retina of the eye, visual information reaches many parts of the nervous system where the information can be analyzed, integrated, and acted upon. Visual information is received by the retinal ganglion cells and transmitted via axons traveling first as the optic nerve and then as the optic tract to the brain. In the present study, projections from retinal ganglion cells to the brain will be described in one species of lizard, the Tegu lizard, *Tupinambis nigropunctatus.* The Tegu lizard possesses large eyes, is diurnal, and, based on our informal observations of these animals in the laboratory, it appears to be very attentive to visual stimuli.

In recent years experimental analysis of the visual system has been made in a variety of different reptiles, including several species of lizards: *Lacerta vivipara* (Armstrong, 1950), *Xantusia vigilis* (Butler, 1974), *Iguana iguana* and *Anolis carolinensis* (Butler and Northcutt, 1971), *Tupinambis nigropunctatus* (Ebbesson, 1970; Cruce and Cruce, 1975), *Gekko gecko* (Northcutt and Butler, 1974*a*).

The retinofugal fiber system of lizards follows the general pattern for all vertebrates as outlined by Ebbesson (1970). The axons of retinal ganglion cells terminate in six areas of the brain as follows: dorsal thalamus, ventral thalamus, pretectum, tectum, hypothalamus, and nucleus of the accessory or basal optic tract. Some of these projections are contralateral only, while others are both contralateral and ipsilateral.

Bilateral retinal projections appear to be related to binocular vision and may allow for more complex analyses of visual information in those animals which possess them than in those animals which do not. Among the rep-

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tiles, bilateral retinofugal projections have been consistently observed in lizards and snakes, e.g., *Lacerta vivipara* (Armstrong, 1950), *Tupinambis nigropunctatus* (Ebbesson, 1970; Cruce and Cruce, 1975), *Iguana iguana* (Butler and Northcutt, 1971), *Anolis carolinesis* (Butler and Northcutt, 1971), *Vipera aspis* (Repérant, 1973), *Gekko gecko* (Northcutt and Butler, 1974*a*), *Xantusia vigilis* (Butler, 1974), *Thamnophis sirtalis* (Halpern and Frumin, 1973), *Natrix sipedon sipedon* (Northcutt and Butler, 1974*b*) but are not usually seen in turtles, e.g. *Chelydra serpentina* (Knapp and Kang, 1968*a*), *Podocnemis unifilis* (Knapp and Kang, 1968*b*), *Pseudemys scripta* (Hall and Ebner, 1970), *Caretta caretta* (Bass and Northcutt, 1975) or crocodilians, e.g., *Caiman crocodilus* (Braford, 1974), *Caiman sclerops* (Repérant, 1975) or tuatara, e.g., *Sphenodon punctatus* (Northcutt et al., 1975). In reptiles possessing bilateral retinal projections, these fibers terminate in parts of the thalamus and in some of the pretectal nuclei. Until recently, only contralateral terminals had been seen in the tectum. In lizards the first reports of bilateral retinotectal projections were those of Butler (1974) and Northcutt and Butler (1974*a*); subsequently we also saw bilateral retinotectal projections (Cruce and Cruce, 1975). Repérant (1973) reported ipsilateral retinotectal connections in the snake, *Vipera aspis*.

Many of the previous experimental studies have used the method of tracing the anterograde axonal degeneration which results from destruction of the retina; this destruction may be produced by removing the eye (i.e. enucleation) or swabbing the retina. The axons and terminals of the destroyed retinal cells then undergo a process of degeneration. After a certain time, the animal is sacrificed and its brain removed for histological procedures. The brain is cut in thin sections and stained by a reduced silver stain, usually either the Nauta-Gygax (1954) or Fink-Heimer (1967) stain which demonstrates degenerating axons.

Recently a new technique to study anterograde axonal connections (Cowan et al., 1972) has become available. This method is based on principles of active function of neurons rather than on degeneration resulting from cell destruction and death. This technique of autoradiographic tracing of anterograde axonal connections utilizes the process of transport of protein molecules along the axon from nerve cell body to its terminals. Radioactive amino acids are injected into the vicinity of nerve cell bodies. The amino acids are incorporated into protein in the somata of neurons. These radioactive protein molecules are then transported along the axon to the terminals, and their entire course may be visualized by standard autoradiographic methods. The presence of labeled molecules is indicated by the presence of developed silver grains in the emulsion overlying the brain section. Depending upon how long the animal survives after the injection, labeled protein molecules will be concentrated either in higher proportion in the nerve terminals (rapid transport with short survival times) or equally in both terminals and axons (slow transport with longer survival times).

The results presented in this paper were obtained by using the autoradiographic tracing technique to study the projections of the retina in the Tegu lizard. This technique has also recently been employed by Northcutt et al. (1974), Bass and Northcutt (1975), and Repérant (1975) to study retinal connections in other species of reptiles. In an earlier report (Cruce and Cruce, 1975), we compared the results obtained using autoradiography with those obtained using the anterograde axonal degeneration method (Nauta-Gygax and Fink-Heimer stains). We found that the autoradiographic results confirmed those derived from the degeneration method; in addition the autoradiographic technique was able to elucidate some aspects of the projection which were ambiguous with the degeneration method.

METHODS

Seven Tegu lizards (*Tupinambis nigropunctatus*) were given intra-ocular injections of either tritiated leucine (50 μCi in 50 μl) or tritiated proline (250 μCi in 25-50 μl). Survival times ranged from 1 to 13 days. The brains were cut on a freezing microtome at 25 μ. The sections were mounted on subbed slides, dipped in Kodak liquid emulsion NTB2, and stored in light-tight boxes at 5° C for times varying from 1 to 3 months. The slides were developed with D19 and stained with cresyl violet.

RESULTS

The results are illustrated in Figure 1 as a series of drawings of coronal sections through the diencephalon of the Tegu lizard taken from a description of the area by Cruce (1974). Certain parts of the brain (cortex, tectum, and part of the optic tract) have not been included in these drawings. The projections seen in Figure 1 are based on the findings in a Tegu lizard which survived 3 days after an intra-ocular injection of 250 μCi of proline. The results from the other animals were essentially the same.

In this animal the density of silver grains or label (indicating the presence of labeled protein molecules) was sparser above the fibers of the optic tract than above terminal areas (Fig. 2). Therefore we are dealing with the rapid phase of axonal transport, illustrating that the density of silver grains allows us to distinguish between areas receiving terminals of retinal axons and areas where fibers are merely passing through on their way to termination (i.e., labeled protein molecules in axons).

Retinofugal fibers project bilaterally to nuclei of the ventral thalamus, dorsal thalamus, pretectum, and tectum. The hypothalamus and nucleus of the basal optic tract receive a contralateral projection only. In all cases of bilateral projections, the density of the contralateral projection is greater than that of the ipsilateral one.

Dorsal Thalamus

Throughout the rostral-caudal extent of the dorsal lateral geniculate nucleus (GLD) retinal fibers terminate bilaterally (Figs. 1–5 to 1–7 and Fig. 2). On both sides the density of terminal labeling is not evenly distributed within the nucleus. At the level of Figure 1–6, two distinctive patches of labeling can be seen in the GLD; this configuration does not correspond to the boundaries of the nucleus as defined in a cytoarchitectonic study (Cruce 1974).

Within the contralateral dorsal thalamus a sparse but definite patch of label is located in a part of the nucleus dorsolateralis (DL) and extends beyond the limits of that nucleus (Figs. 1–6, 1–7).

Ventral Thalamus

The only cell group of the ventral thalamus which receives a projection from the retina in the Tegu lizard is the ventral lateral geniculate nucleus (GLV). The boundaries of the GLV as drawn in Figures 1–5 to 1–8 are based on a cytoarchitectonic description in nonexperimental material. In the experimental material obtained in this study patches of label were seen outside these boundaries. We consider these areas to be further subdivisions of the ventral lateral geniculate, and one of them has been labeled as pars ventralis (GLVv) in Figures 1–5 and 1–6.

At its most rostral level the contralateral GLV is completely filled with label, but only a small patch of label is present ipsilaterally in a ventral location. More caudally the GLV consists of a lateral neuropil (with few cells) which is densely labeled on the contralateral side; a medial cell plate does not contain any label. Presumably the terminals in the lateral neuropil make synaptic contact with the dendrites of neurons located in the medial cell plate. Ipsilaterally the more caudal part of the GLV contains a patch of label which is located in a dorsal position. The ipsilateral projection areas overlap those seen on the contralateral side.

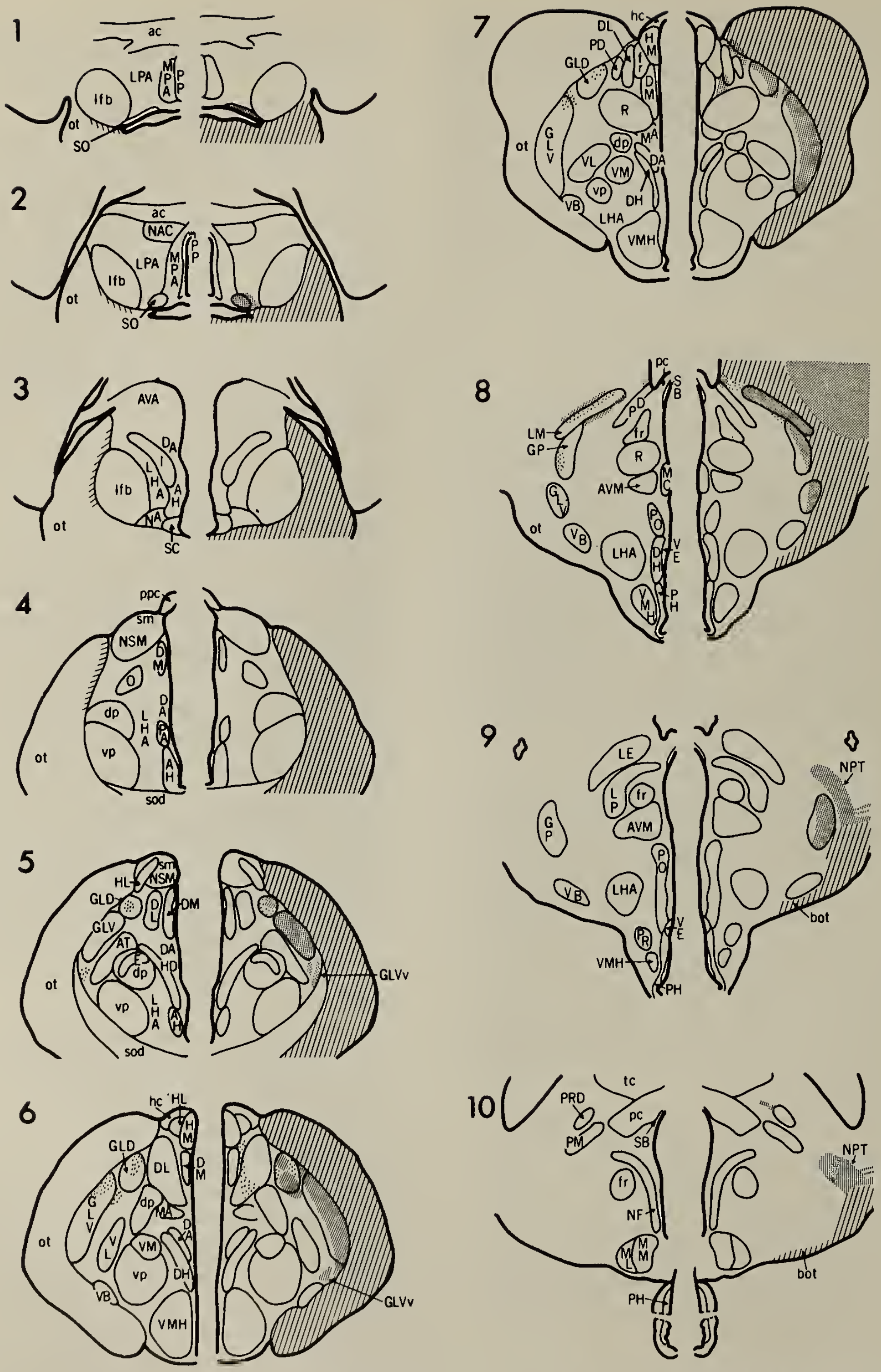

Figure 1. Line drawings of coronal sections through the brain of *Tupinambis nigropunctatus.* Figure 1-1 is the most rostral level, and Fig. 1-10 is the most caudal. The diagonal lines indicate areas of labeled fibers and the stippling indicates areas of terminal labeling. The injection of tritiated proline was into the left eye (contralateral to the side of maximum optic tract labeling). The nomenclature follows that of Cruce (1974).

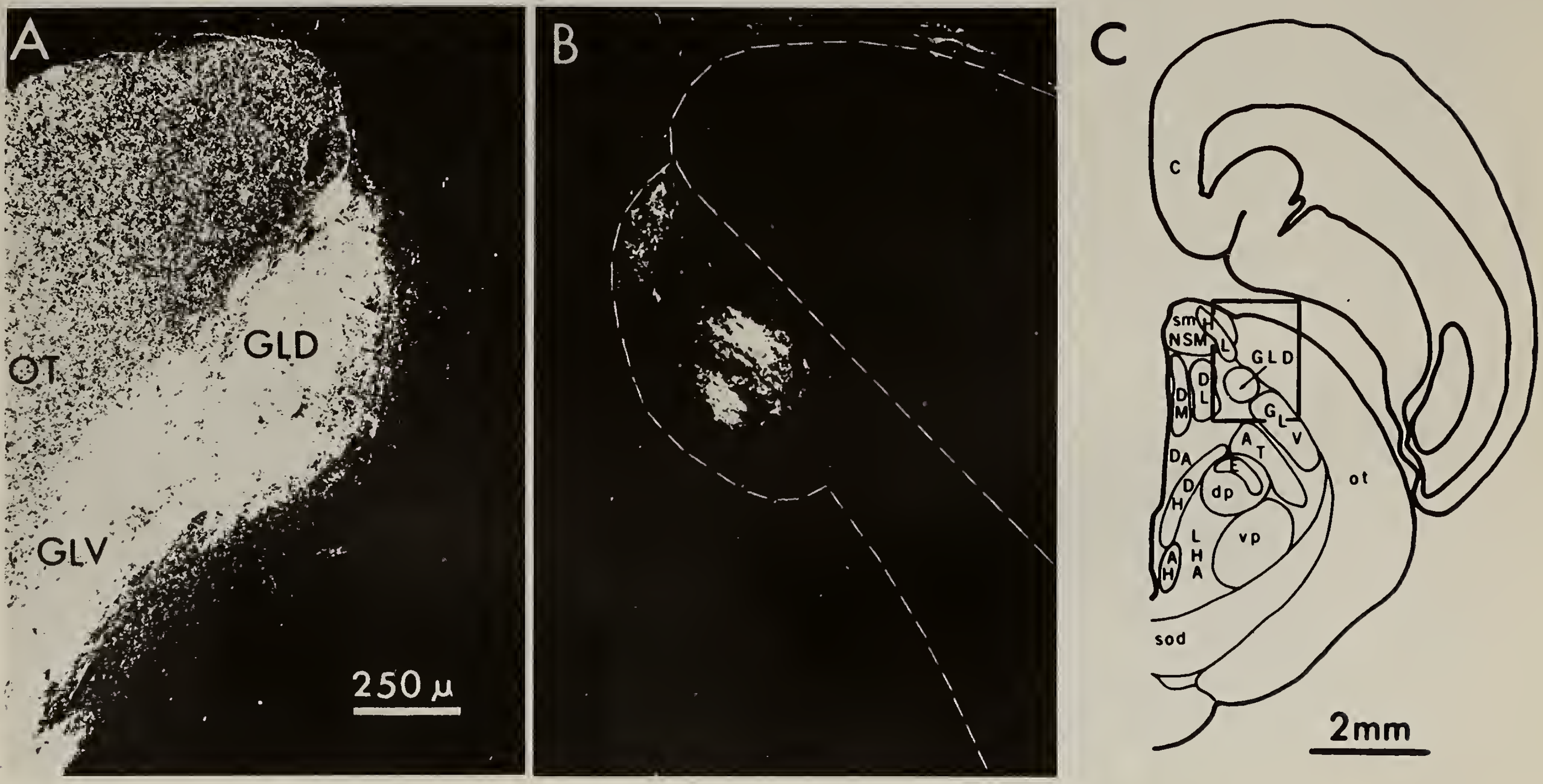

Figure 2. Dark-field photomicrographs demonstrating label in the contralateral (A) and ipsilateral (B) lateral geniculate nuclei of the Tegu lizard 3 days after injection of tritiated proline into one eye. The white dots indicate the presence of silver grains. The position of the photomicrographs is indicated by the box on a drawing (C) of a transverse section through the rostral third of the thalamus. Reprinted with permission of Elsevier Publishing Co. (*Brain Research* 85, 1975. p. 222).

Pretectum

The rostral cell groups of the pretectum are first seen in Figure 1–7. A small patch of label is associated with nucleus posterodorsalis (PD) (Figs. 1–7 and 1–8). Nucleus geniculatus pretectalis (GP) (Figs. 1–8 and 1–9) receives a bilateral projection from the retina. The ipsilateral connection is to a much more limited portion of the nucleus than the contralateral projection. Like the nucleus geniculatus lateralis ventralis, the nucleus geniculatus pretectalis consists of a lateral cell-sparse neuropil and a medial cell plate. The retinal projection is concentrated in the lateral neuropil.

A bilateral projection leads to the nucleus lentiformis mesencephali (LM) (Figs. 1–8); contralaterally the projection fills the nucleus but on the ipsilateral side the projection is outside the nuclear boundaries. The nucleus pretectalis (NPT) has not been separately described in a previous cytoarchitectonic study (Cruce 1974). In the present study, a distinctive area receiving a contralateral retinal projection has been identified and named the nucleus pretectalis (Fig. 1–9 and 1–10). Finally, in the caudal pretectum a small patch of terminal labeling appears on the contralateral side in a position dorsomedial to the cells of nucleus pretectalis dorsalis (PRD) (Figs. 1–10).

Tectum

The optic tectum is illustrated at both high and low power magnification in Figure 3. The projection of retinal ganglion cells to the tectum is bilateral. The contralateral tectum receives a heavy projection which goes primarily to layers 9, 11, and 13 (Fig. 4); these are layers which are relatively cell-free, and presumably the terminals in these layers are contacting dendrites of cells in adjacent layers. The ipsilateral retinotectal projection is much sparser than the contralateral one. Retinal fibers terminate in the rostral 300μ of the ipsilateral tectum in layer 9 only (Fig. 5).

Hypothalamus

Within the hypothalamus retinal fibers terminate in relation to the supraoptic nucleus (SO) (Figs. 1–1 and 1–2); this hypothalamic connection is to the contralateral side only.

Nucleus of the Basal Optic Tract

The cells of the nucleus of the basal optic tract are interspersed within the fibers of the basal optic tract (bot) and are located in the ventromedial part of the brain (Figs. 1–9 and 1–10). They receive contralateral optic terminations.

DISCUSSION

The pattern of connections from the retinal ganglion cells to the brain seen in the Tegu lizard conforms to the basic vertebrate plan as outlined by Ebbesson (1970). The regions of the brain that receive retinal fibers are the dorsal thalamus, ventral thalamus, pretectum, tectum, hypothalamus, and basal optic nucleus. The same pattern of organization has been seen in all reptile species studied, although there are certain variations present.

The uncrossed retinal projections seen in the present study, do not seem to be universally observed in the various reptiles studied. By the use of modern experimental techniques, ipsilateral projections have been well documented in lizards and snakes, whereas turtles and crocodiles seem to have completely crossed retinal fibers. In all the lizards and snakes which have been studied to date the thalamus seems to be the recipient of ipsilateral as well as contralateral retinal projections. In addition to the present study bilateral retinotectal projections have been reported in three other articles (Repérant, 1973; Butler, 1974; Northcutt and Butler, 1974*a*).

The findings with respect to the six major regions will now be discussed in the light of

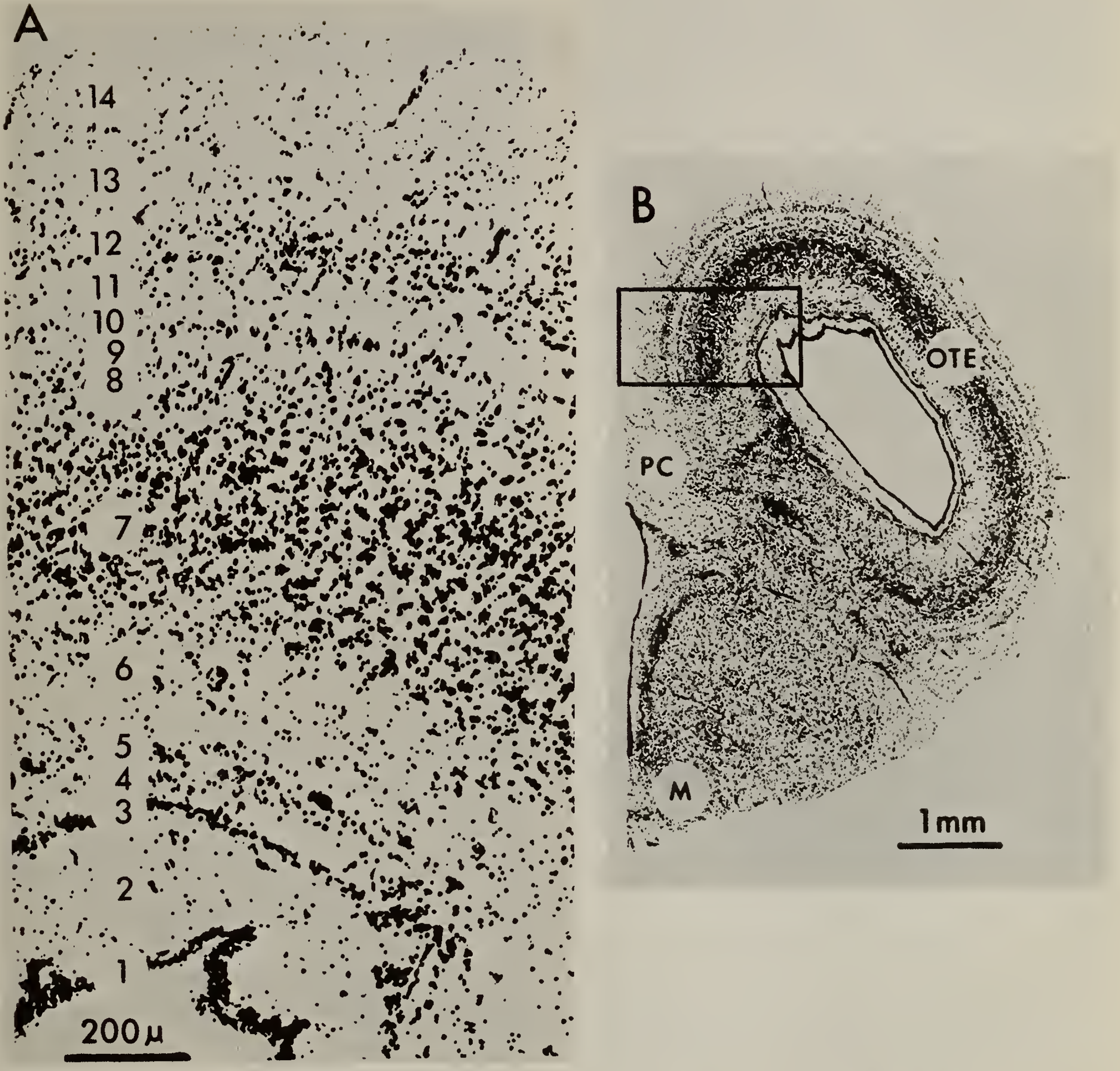

Figure 3. Layers of the mesencephalic tectum in the Tegu lizard as identified by the criteria of Ramón (1896). A high magnification view (A) is a 90° rotation of the area in the box shown at low magnification view (B). Reprinted with permission of Elsevier Publishing Co. (*Brain Research*, 85, 1975. p. 223).

comparative observations on *Lacerta vivipara* (Armstrong, 1950); *Xantusia vigilis* (Butler, 1974); *Iguana iguana* and *Anolis carolinensis* (Butler and Northcutt, 1971); *Tupinambis nigropunctatus* (Ebbesson, 1970); *Gekko gecko* (Northcutt and Butler, 1974*a*).

Dorsal Thalamus

In all lizards studied, a projection from the retina to the contralateral dorsal lateral geniculate has been observed. With the exception of *Lacerta* (Armstrong, 1950), the other lizards also have an ipsilateral projec-

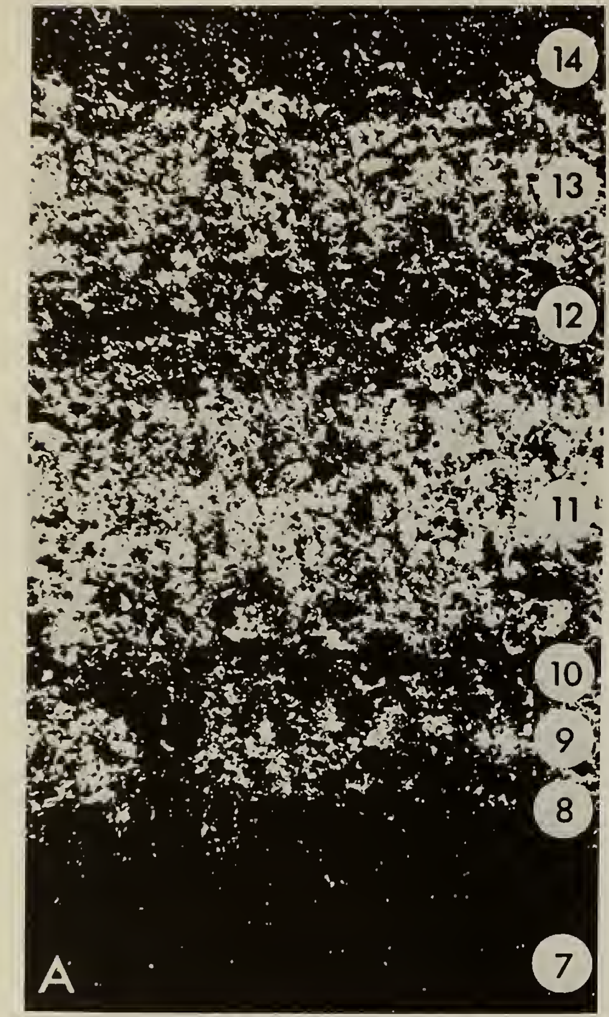

Figure 4. Dark-field photomicrograph of superficial layers of the tectum of a Tegu lizard which had been given an intraocular injection of tritiated proline in the eye contralateral to the illustrated optic tectum. The numbers are the same as Figure 3. Reprinted with permission of Elsevier Publishing Co. (*Brain Research*, 85, 1975. p. 225.)

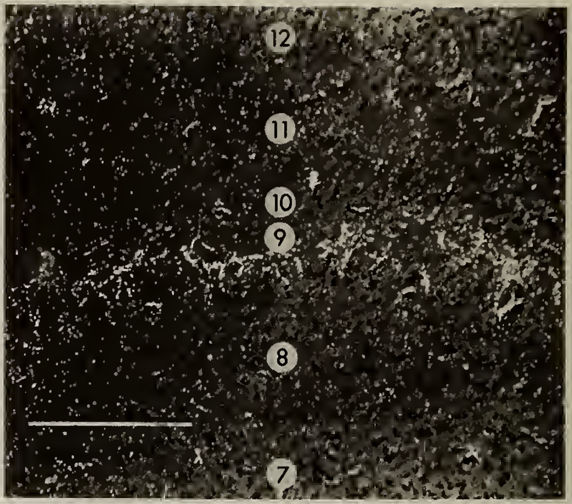

Figure 5. Superimposed dark-field and light-field illumination photomicrographs of ipsilateral retinotectal projection of Tegu lizard. The silver grains indicating terminal labeling appear as a band of white dots in layer 9 (dark-field illumination); the darker and somewhat larger structures seen in other parts of the photomicrograph are neurons (bright-field illumination). Scale bar: 200μ.

tion. In *Iguana* and *Anolis* Butler and Northcutt (1971) found that different parts of the nucleus receive differential projections, i.e., the contralateral projection was denser in the medial half of the nucleus whereas the ipsilateral projection was denser in its lateral side. In the present report such differential terminal labeling was not obtained. We found that the part of the ipsilateral nucleus receiving retinal terminals overlaps with that part of the contralateral nucleus which receives retinal fibers.

As in the case of the ventral lateral geniculate nucleus the configuration of terminals in the GLD does not exactly conform to that area labeled GLD as a result of cytoarchitectonic study. In Nissl-stained material the cells and neuropil of the GLD are not well differentiated. The terminals, however, form two non-overlapping oval areas. In view of the present experimental results a reevaluation of the boundaries of both GLD and GLV seems warranted.

In the present study, a patch of label was seen in the dorsal thalamus located between the dorsolateral and dorsomedial nuclei. This area has not been indicated as a site of terminals of retinal ganglion cells in studies on the visual system of other lizards. In their autoradiographic study in the tuatara, Northcutt, Braford, and Landreth (1975) found labeling in an area caudodorsal to nucleus dorsolateralis anterior; whether or not this projection corresponds to what we see in the Tegu lizard remains to be determined.

Ventral Thalamus

The cytoarchitectonic map of J. Cruce (1974) was used as a reference on which to place the results of our experimental study. It was found, however, that the pattern of labeling of retinal terminals did not completely correspond with the cytoarchitectonic pattern as described from normal cell stained material. In addition to the prominent ventral lateral geniculate nucleus located on the medial edge of the optic tract, two small areas ventral to that nucleus had dense terminal labeling and probably represent subdivisions of that nucleus; these same subdivisions were identified in the Tegu lizard by Ebbesson, Jane, and Schroeder (1972) as recipients of contralateral projections from the retina in the Tegu lizard. Based on an autoradiographic study in the loggerhead sea turtle *(Caretta caretta)*, Bass and Northcutt (1975) were able to distinguish dorsal and ventral components of the GLV, both of which receive retinal terminals.

In the present results, the retina was seen to project bilaterally to the GLV, with the ipsilateral GLV receiving a less dense projection. Ebbesson (1970), in his study of the Tegu lizard mentions only a contralateral projection from the retina to GLV. Butler and Northcutt (1971) saw only one animal in which an ipsilateral projection was evident. On the other hand, bilateral projections to the GLV from the retina were found in *Lacerta* (Armstrong, 1950), *Xantusia* (Butler, 1974), and *Gekko* (Northcutt and Butler, 1974*a*).

Pretectum

The pretectum is an area of the brain which shows a great deal of variation in both form and nomenclature from species to species. In all species studied some of the pretectal nuclei have been observed to be recipients of retinal ganglion cell axons. Ebbesson (1970), in his study of retinal projections in the Tegu lizard, indicated that nucleus posterodorsalis of the pretectum receives a bilateral retinal projection; our results are in agreement. According to Ebbesson (1970), nucleus geniculatus pretectalis and nucleus lentiformis mesencephali receive only contralateral fibers from the retina, whereas we found these projections to be bilateral. In addition, we found a contralateral projection to nucleus pretectalis and to the dorsal edge of nucleus pretectalis dorsalis; Ebbesson (1970) does not mention these projections.

One explanation for the discrepancy between our findings and those of Ebbesson in the same species (*Tupinambis nigropunctatus*), may be the different techniques that were employed. Ebbesson (1970) used anterograde degeneration, and we used anterograde transport. Even within the same species, we have seen what appears to be anomalous degeneration which can cause staining of pathways which were not experimentally lesioned (Cruce and Cruce, 1975). A small number of degenerating fibers might not be distinguishable from normal stained fibers whereas the silver grains of the labeled protein molecules are more easily distinguished above background levels of labeling, especially using dark-field illumination.

Contralateral retinal fibers invariably terminate in nucleus geniculatus pretectalis and nucleus lentiformis mesencephali. As in the present study, there are bilateral projections in *Gekko* and *Xantusia* (Northcutt and Butler, 1974*a*; Butler, 1974). Armstrong (1950) did not find any retinal fibers terminating in the nucleus posterodorsalis of *Lacerta*, whereas other authors did. The nucleus pretectalis as shown here has not been identified by any authors except Butler and Northcutt (1971) who, in agreement with our observations in the Tegu lizard, found that it receives contralateral retinal fibers.

Tectum

In all reptiles the contralateral optic tectum receives an input from the retina. Only two other reports in lizards (Butler 1974; Northcutt and Butler, 1974*a*) and one in a snake (Repérant, 1973) contain descriptions of the presence of ipsilateral retinotectal fibers such as we have seen in our present study of the Tegu lizard. In the Tegu lizard these terminals form a thin band in layer 9 and are limited to the rostral part of the tectum. The results of the other three studies mentioned were based on the degeneration observed after unilateral enucleation. In *Gekko* (Northcutt and Butler, 1974*a*) degenerating fibers were seen in layers 8–9 of the ipsilateral tectum, while in *Xantusia* (Butler, 1974) layers 8–14 in the rostral half of the tectum appear to be involved. In *Vipera*, Repérant (1973) saw scattered degeneration in layers 8–14 in the anteromedial part of the ipsilateral tectum. The observed variations in exact site of termination of ipsilateral retinotectal projections may reflect sensitivity of techniques (autoradiography vs. degeneration) or species differences in the predominance of type of synapse (e.g., axodendritic in the cell sparse layer 9 vs. axosomatic in layers with greater cell density).

The possibility exists that ipsilateral retinotectal fibers have been overlooked in other studies since they represent a very small number to a limited site. We feel that the autoradiographic method proved invaluable to our demonstration of these fibers, since in our anterograde degeneration material demonstration of such a projection was, at best, equivocal.

Hypothalamus

Although the presence of a retinohypothalamic connection has been mentioned in other accounts of the reptilian visual system we have been able to demonstrate the precise location of the terminals of these retinohypothalamic fibers in relation to the cells of the supraoptic nucleus. Armstrong (1950) and Butler and Northcutt (1971) found no evidence of optic fibers terminating in the hypothalamus of *Lacerta*, *Iguana*, or *Anolis*. Ebbesson (1970) lists the hypothalamus as an area which receives contralateral retinal afferents, but he does not mention any specific hypothalamic nucleus. In more recent papers, Butler (1974) and Northcutt and Butler (1974*a*) mention the possibility of fibers projecting into the hypothalamus in *Xantusia* and *Gekko* but did not see terminal areas. With the anterograde degeneration technique, one often sees fibers within the hypothalamus which may be undergoing degeneration, but with the autoradiographic labeling of terminals the existence and precise location of these fibers can be ascertained. Using autoradiography in *Caiman sclerops*, Repérant (1975) also found the supraoptic nucleus to be the site of a contralateral retinal projection.

Nucleus of the Basal Optic Tract

The nucleus of the basal optic tract has been identified as a recipient of contralateral retinal fibers in all lizard brains studied. This structure is also known as the nucleus opticus tegmenti (Armstrong, 1950; Butler, 1974; Butler and Northcutt, 1971; Northcutt and Butler, 1974*a*) or nucleus of the accessory optic tract (Ebbesson, 1970).

Conclusions

By experimental techniques of anterograde degeneration and anterograde axonal transport, used in the present study, the regions of termination of retinal ganglion cells can be identified (Fig. 6). Such identification is the first step in understanding the function which these brain nuclei play in the visual behavior of the animal.

ABBREVIATIONS

ac, Anterior commissure
AH, Anterior hypothalamic area
AT, Area triangularis
AVA, Area ventralis anterior
AVM, Area ventromedialis
DA, Dorsal hypothalamic area
DH, Nucleus dorsalis hypothalami

FIGURE 6

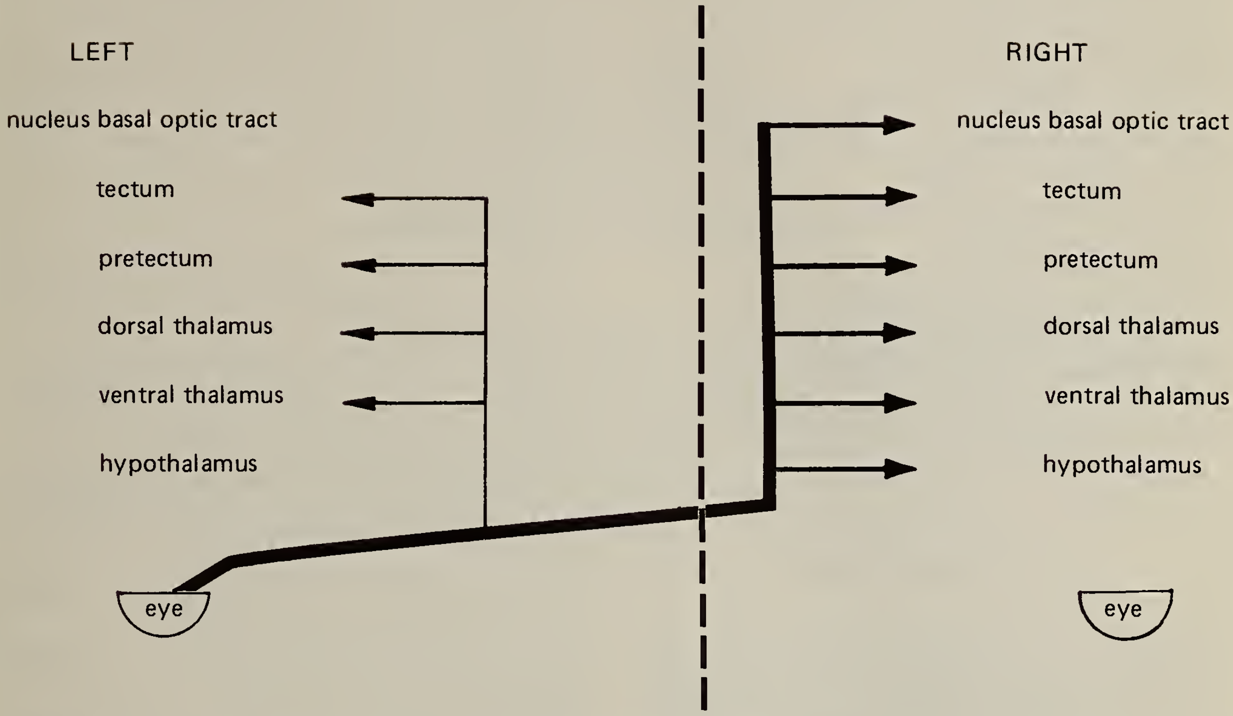

Figure 6. Schematic illustration of projections of retina of Tegu lizard, *Tupinambis nigropunctatus*. Six regions on the right side of the brain receive fibers from the left eye, while four regions on the left side of the brain receive fibers from the left eye. The contralateral projections are heavier than the ipsilateral ones.

DL, Nucleus dorsolateralis
DM, Nucleus dorsomedialis
dp, Dorsal peduncle of the lateral forebrain bundle
E, Nucleus entopeduncularis
fr, fasciculus retroflexus
GLD, Nucleus geniculatus lateralis dorsalis
GLV, Nucleus geniculatus lateralis ventralis
GLV, Nucleus geniculatus lateralis ventralis pars ventralis
GP, Nucleus geniculatus pretectalis
hc, Habenular commissure
HL, Nucleus habenularis medialis
I, Nucleus interstitialis
LE, Nucleus lentiformis thalami pars extensa
lfb, Lateral forebrain bundle
LHA, Lateral hypothalamic area
LM, Nucleus lentiformis mesencephali
LP, Nucleus lentiformis thalami pars plicata
LPA, Lateral preoptic area
M, Nuclei mammillares
MA, Nucleus medialis pars anterior
MC, Nucleus medialis pars centralis
ML, Nucleus mammillaris lateralis
MM, Nucleus mammillaris medialis
MPA, Medial preoptic area
NA, Nucleus anterior hypothalami
NAC, Nucleus of the anterior commissure
NF, Nucleus of the medial longitudinal fasciculus
NPT, Nucleus pretectalis
NSM, Nucleus of the stria medullaris
O, Nucleus ovalis
ot, Optic tract
OTE, Optic tectum
PA, Nucleus paraventricularis
pc, Posterior commissure
PD, Nucleus posterodorsalis
PH, Nucleus periventricularis hypothalami
PM, Nucleus pretectalis medialis

PO, Nucleus posterior hypothalami
PP, Nucleus periventricularis preopticus
ppc, Posterior pallial commissure
PR, Nucleus premammillaris
PRD, Nucleus pretectalis dorsalis
R, Nucleus rotundus
SB, Subcommissural organ
SC, Nucleus suprachiasmaticus
sm, Stria medullaris
SO, Nucleus supraopticus
sod, Supraoptic decussation
tc, Tectal commissure
VB, Nucleus ventrobasalis
VE, Ventricular ependymal organ
VL, Nucleus ventrolateralis
VM, Nucleus ventromedialis thalami
VMH, Nucleus ventromedialis hypothalami
vp, Ventral peduncle of the lateral forebrain bundle

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Somatosensory Pathways in Lizards: The Identification of the Medial Lemniscus and Related Structures

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SUMMARY. The sensory pathways that relay information from the spinal cord to the brain are remarkably similar in all vertebrates, including lizards. In the various taxonomic groups, the differences in ascending spinal projections relate primarily to the relative quantity of fibers in a given pathway and the degree of differentiation of the various, related nuclear groups. It is clear, for example, that the degree of limb development and the consequent increase in number and differentiation of receptors are closely correlated with the size and differentiation of the dorsal column system (Ebbesson, 1969). In addition to a review of the general organization of ascending spinal pathways in lizards, this chapter provides the first description of the projections of the dorsal column nuclei in two lizard species.

INTRODUCTION

One aspect of comparative neurology today concerns itself with the analysis of structural variation of neuronal systems in a broad spectrum of vertebrates, with the hope that such comparisons will provide insights into the evolution of systems and the significance of structural variation in the nervous system. It is significant that less than a dozen investigators in the world are currently working on reptile brain anatomy, and many of us dilute our efforts by studying other vertebrates as well. If one then considers that no one was interested in reptilian neuroanatomy 15 years ago, one realizes that much has been achieved in a short period of time. Nevertheless, only a few neuronal systems have been described, even superficially, and most of the lizard brain remains as a black box. This chapter concerns itself with one of the still obscure systems, namely the sensory pathways that relay information from the spinal cord to the brain. These pathways are often referred to as somatosensory, but they carry information from a variety of receptors ranging from visceral receptors to Golgi tendon organs. It should be pointed out from the beginning that, in reptiles, nothing is known about which receptors are related to which ascending spinal pathways. However, since such pathways in lizards are remarkably similar to mammalian pathways, it is likely that many carry information similar to that described in mammals.

The use of new experimental anatomical techniques in the last few years has radically altered our view of brain organization in poikilothermic vertebrates. The somatosensory systems in reptiles are a case in point. Contrary to earlier beliefs (Ariëns Kappers et al., 1936), it has now been shown that fibers of spinal origin reach as far as the thalamus in sharks (Ebbesson, 1972), frogs, and reptiles (Ebbesson, 1966, 1967, 1969; Ebbesson and Goodman, 1976; Pederson, 1974). Along their course through the brainstem, spinal fibers issue branches to basically the same cell aggregates that have been described in mammals (Mehler, 1957, 1969; Mehler et al., 1960; Schroeder and

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Jane, 1971), indicating that these basic systems evolved early in vertebrate evolution. The spinoreticular, spinovestibular, and spinocerebellar projections in the tegu lizard are strikingly similar to those described in mammals (Ebbesson, 1966, 1967; Ebbesson and Goodman, 1976) and will not be reviewed here. We will instead limit ourselves to the finding of a medial lemniscus in two lizard species.

The dorsal column system is an important component of ascending spinal systems, primarily reflecting the degree of limb development (Ebbesson, 1969). Although the gracile and cuneate nuclei have been described in a large number of nonmammalian species, the destination of their axons has remained a puzzle because it has not been possible to trace them for any distance in any nonmammal (Ariëns Kappers et al., 1936, 1967). Our investigations with the new, more sensitive Fink-Heimer modifications of the Nauta stain were designed to fill this void. The projections of the dorsal column nuclei in the monitor lizard described below are identical to earlier observations in the tegu lizard (Ebbesson, unpublished observations).

MATERIALS AND METHODS

Six adult specimens of the monitor lizard (*Varanus bengalensis*) were anesthetized with sodium pentobarbital (Nembutal) (25 mg/kg), and small portions of the dorsal column nuclei were removed with suction. The animals were maintained postoperatively at 30°–35° C, and sacrificed after 20–30 days by intracardial perfusion with 10 percent formalin in water. The brains were removed and stored in 10 percent formalin under refrigeration for 1–10 weeks before embedding in egg yolk (Ebbesson, 1970*a*) and sectioning transversely at 33 mμ on the freezing microtome. At least one section per 0.2 mm was processed according to a modification (Method 7 in Ebbesson, 1970*a*) of the Fink-Heimer (1967) technique for the selective silver impregnation of degenerating axons and terminals. Additional sections were processed according to a modified Nauta procedure (Method 6 in Ebbesson, 1970*a*). The degeneration pattern of each section was charted on a photomacrograph (Ebbesson and Rubinson, 1971) of the adjacent section stained with the Nissl method (Fernstrom, 1958). In the chartings (Figs. 1–10), dots and interrupted lines represent axonal degeneration, and open circles represent terminal degeneration as defined by Ebbesson (1970*a*).

RESULTS

Case 146 was chosen to illustrate the experimental material since the findings in this case were easy to define and agreed with the findings in the other cases. The animal had 24 days postoperative survival, and the lesion was restricted to the dorsal column nuclei.

Axons leaving the dorsal column nuclei collect on the contralateral side as the medial lemniscus. This fiber tract is composed of very thin axons that form a narrow band in the ventral tegmentum (Figs. 1–2). Their small size and small number probably account for the difficulty in tracing these axons when less sensitive methods are used (Ariëns Kappers et al., 1936).

At medullary levels, a few of the lateral fibers of the medial lemniscus appear to issue preterminal axons to the reticular formation (Figs. 2–3) and to the dorsal part of the facial nucleus (Fig. 2). At the level of the nucleus reticularis medius (RM), terminal degeneration is found in a poorly defined nucleus in the ventromedial tegmentum. This area is tentatively designated the inferior olive (OI? in Figs. 3–4) since such a cell group in mammals receives an input from the dorsal column nuclei. At these levels, a lateral component of the medial lemniscus separates from the main tract and, coursing in a dorsal direction, reaches the torus semicircularis and the optic tectum. A few fibers enter and terminate in (1) the stratum griseum centrale of the optic tectum, (2) the nucleus intercollicularis, (3) the ventrolateral aspect of the

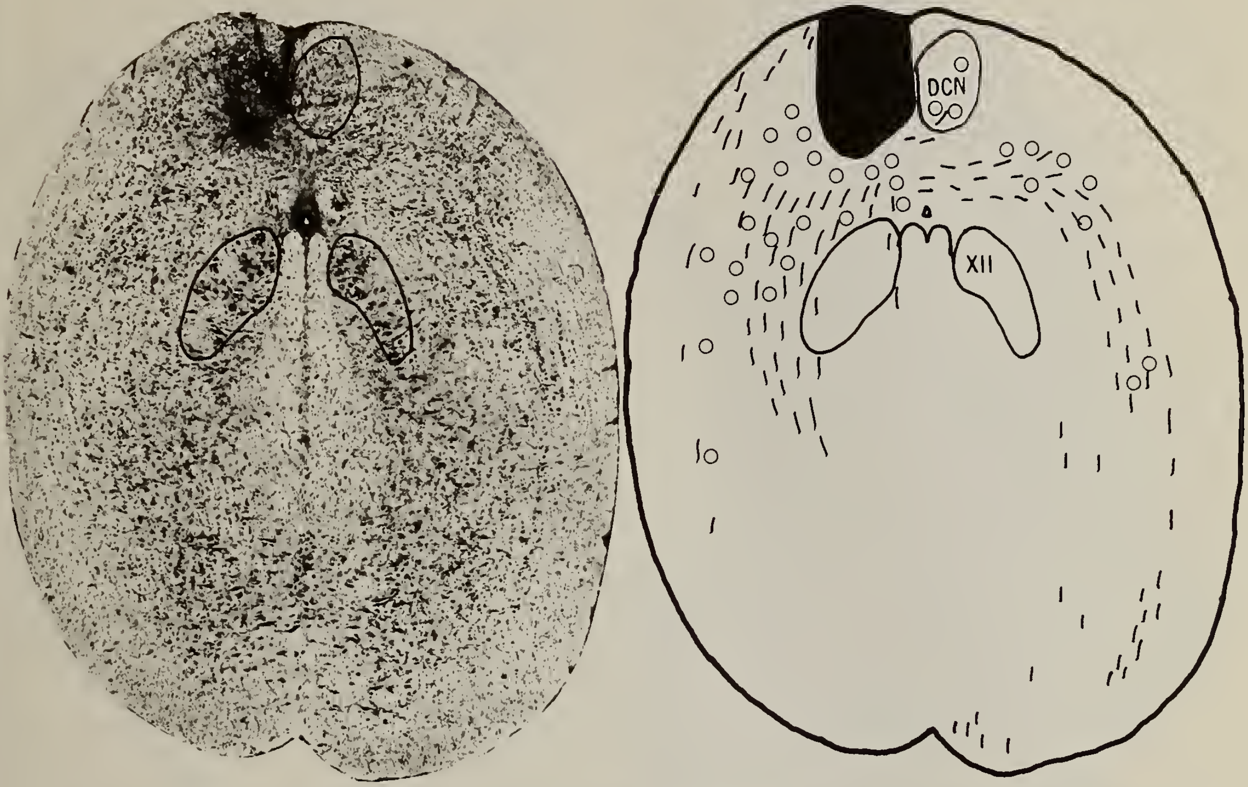

Figure 1. Site of lesion in dorsal column nuclei (left) and course of resulting degeneration (right).

central nucleus of the torus semicircularis, and (4) the central gray area (Fig. 5). Slightly further rostrally (Fig. 6), terminal degeneration is also found in the medial corner of the tectum. This zone is near the mesencephalic nucleus of the trigeminal nerve and involves all layers deep to the stratum griseum superficiale. At this level (Figs. 6–7), some terminal degeneration is found in a cell group just dorsal to the ectomammillary nucleus; this area may be homologous to the substantia nigra of mammals. The few remaining degenerating axons can be traced into the ventral thalamus where most of the degeneration observed is in the so-called ventrolateral nucleus (Figs. 7–10. This latter area is here labeled the ventrobasal complex (Vb) because of its striking similarity to the mammalian cell groups of that name.

DISCUSSION

The new findings reported here, coupled with earlier descriptions of ascending spinal projections (Ebbesson, 1966, 1967; Ebbesson and Goodman, 1976), provide clear evidence that the somatosensory pathways in lizards are very similar to those described in mammals (Mehler, 1957, 1969; Mehler et al., 1960; Schroeder and Jane, 1971; and others), amphibians (Ebbesson, 1976), elasmobranches (Ebbesson, 1972), and birds (Karten, 1963). The differences in spinal projections in the various taxonomic groups relate primarily to the relative quantity of fibers in a given pathway and the degree of differentiation of the various related nuclear groups. It is clear, for example, that the size and differentiation of the dorsal column system and the spinocerebellar systems are closely correlated with the degree of limb development (Ebbesson, 1969; Johnson, et

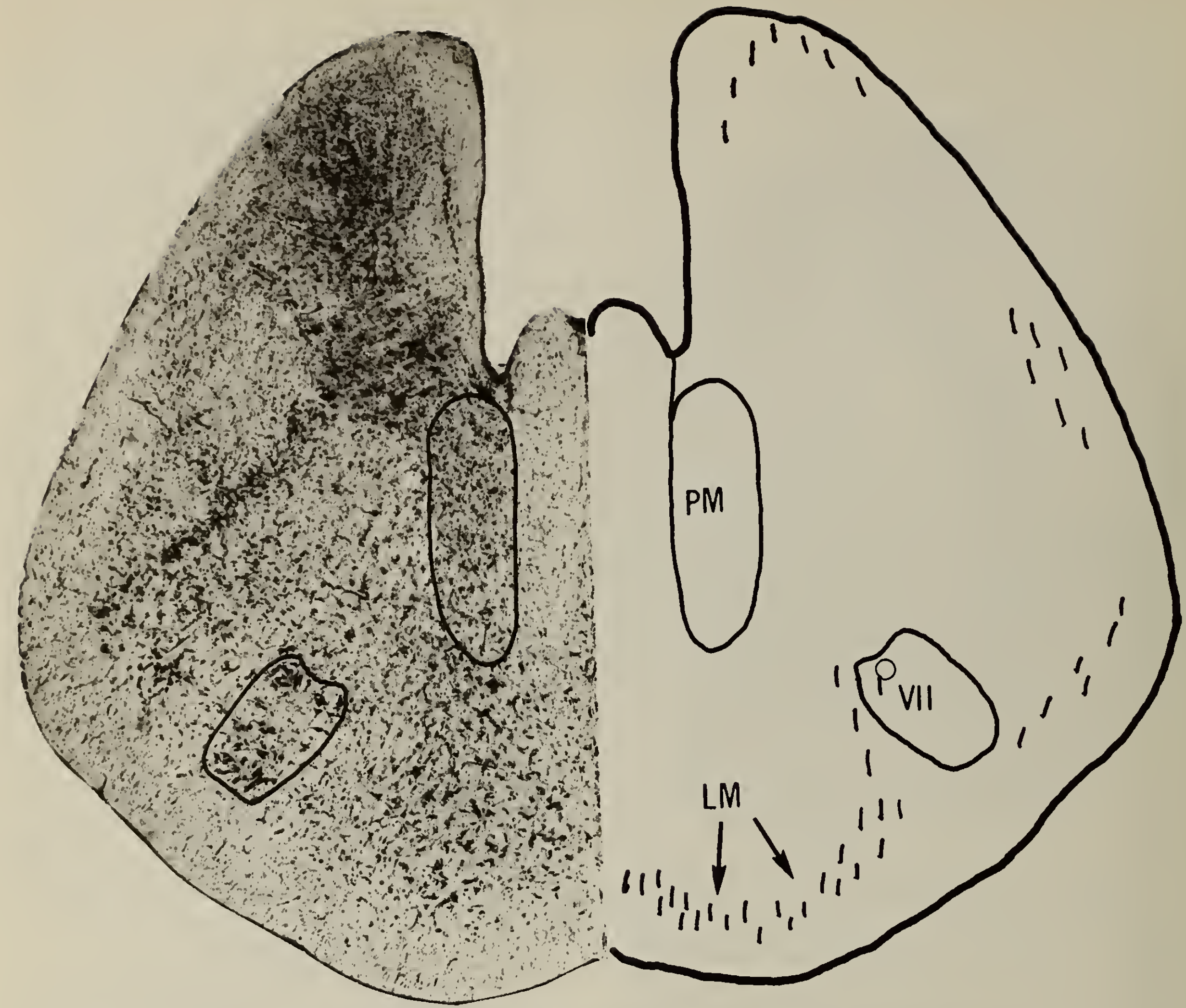

Figure 2. Nissl picture (left) and plot of degeneration (right) at level of facial nerve (VII).

al., 1968). On the other hand, little is known about what visceral afferents are represented among ascending spinal fibers. At this moment, we have no physiological data on lizards that would indicate what modalities are represented in the various ascending pathways, and which receptors are involved in each pathway.

On an anatomical basis, ascending spinal pathways in lizards can be divided into (1) the dorsal column system, (2) the spinocerebellar systems, and (3) the anterolateral systems. Only the dorsal column system is dealt with here and discussed below. For information about the last two, see Ebbesson, 1967, 1969; Ebbesson and Goodman, 1976.

The Dorsal Column Nuclei

The dorsal column system is composed of ascending dorsal funicular fibers that, in lizards, terminate in a somatotopic manner in distinct nuclei gracilis and cuneatus (Goldby and Robinson, 1962; Ebbesson, 1966, 1967, 1969). These nuclei have long been recognized in reptiles (Christensen, 1917; Zeehandelaar, 1921; Huber and Crosby, 1926; Shanklin, 1930; and others), but fibers from these nuclei have not been

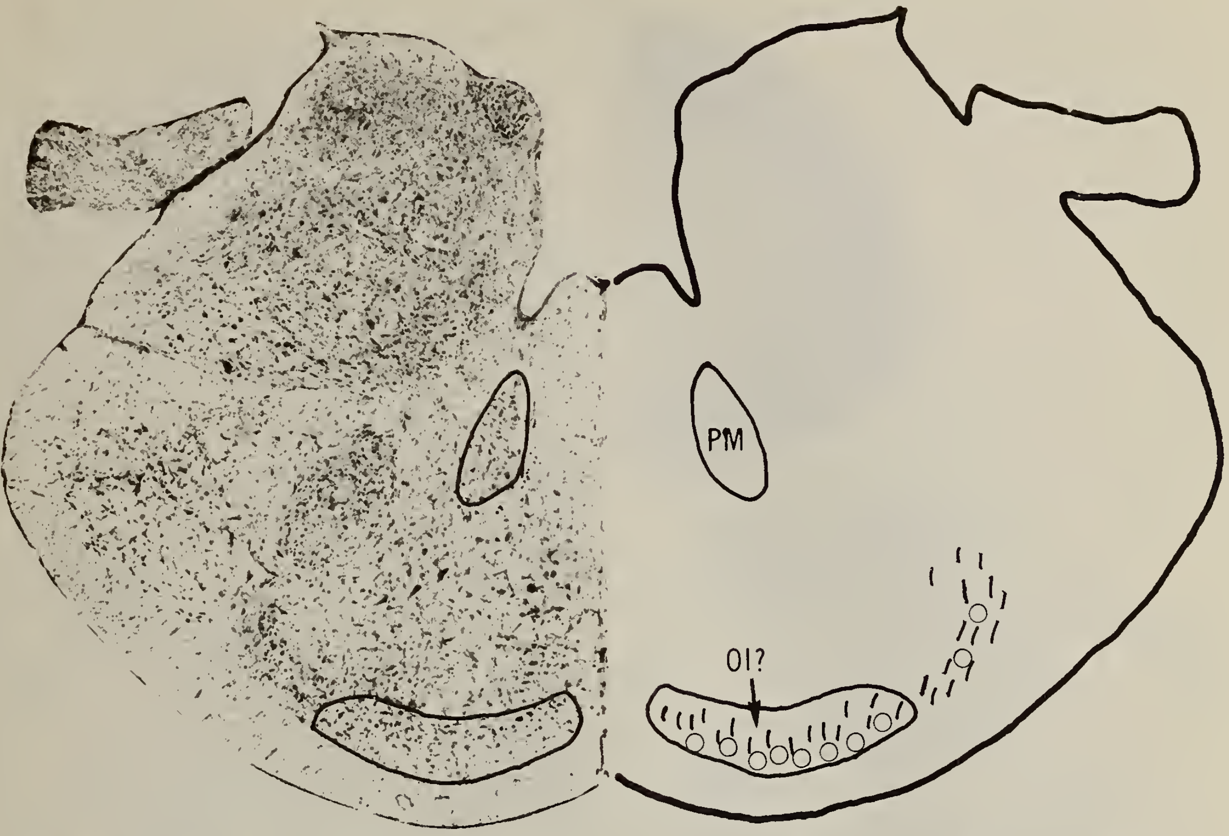

Figure 3. Nissl and locus of degeneration in nucleus tentatively designated as the inferior olive (OI–).

traced beyond the mesencephalon in any nonmammalian vertebrate (Christensen, 1917; Huber and Crosby, 1926; Shanklin, 1930). The important question of the existence of a ventral tier group of the thalamus in nonmammalian forms has thus remained unanswered. Huber and Crosby (1926), working with the alligator, were able to trace crossed fibers arising from the nucleus gracilis and nucleus cuneatus and accumulating into a bundle which appeared to turn forward. In their nonexperimental material, however, it was not possible to trace it to the thalamus, and the other projections have also remained unknown.

Although the dorsal column nuclei and the medial lemniscus were thought to be absent in amphibians (Ariëns Kappers et al., 1936, p. 190), considerable evidence for their presence has recently been reported (Ebbesson, 1976). This, together with the findings reported here, suggests that somatosensory information does indeed get to the forebrain and that paths for tactile discrimination and well-developed proprioceptive impulses are not necessarily as recent, phylogenetically, as hitherto believed (Ariëns Kappers et al., 1936).

The Inferior Olive

The major medullary target of medial lemniscal fibers in mammals is the medial and the dorsal accessory nuclei of the inferior olivary complex (Hand and Liu, 1966; Morest, 1967; Ebbesson, 1968; Boesten, 1971; Jane and Schroeder, 1971; Schroeder and Jane, 1971; Hazlett et al., 1972; Boesten and Voogd, 1975; and Groenewegen et al., 1975). Since an inferior olivary complex has not been identified in reptiles, it is not possible to say with certainty whether the poorly differentiated nucleus identified as OI? in Figs. 3–4 is indeed a homolog of its mammalian counterpart, but it appears

Figure 4. Degeneration at level of tectum.

likely, in view of the fact that direct spinal fibers also project to this cell group (Ebbesson, 1966, 1967, 1969).

Torus Semicircularis

The dorsal column nuclei were, until very recently, thought to project only to the ventrobasal complex in mammals. It is only recently that medial lemniscal fibers were also found to terminate in the inferior colliculus. In the cat, the three main divisions of this structure are known as the central, pericentral and external nucleus (Berman, 1968). Anatomical as well as electrophysiological studies have confirmed that the central nucleus serves as the main auditory area in the mesencephalon (Rose et al., 1963; Goldberg and Moore, 1967), whereas the external and pericentral nuclei, collectively usually described as intercollicular nuclei, receive direct projections from the spinal cord (Mehler et al., 1960; Jane and Schroeder, 1971; Schroeder and Jane, 1971). Dorsal column nuclei projections to

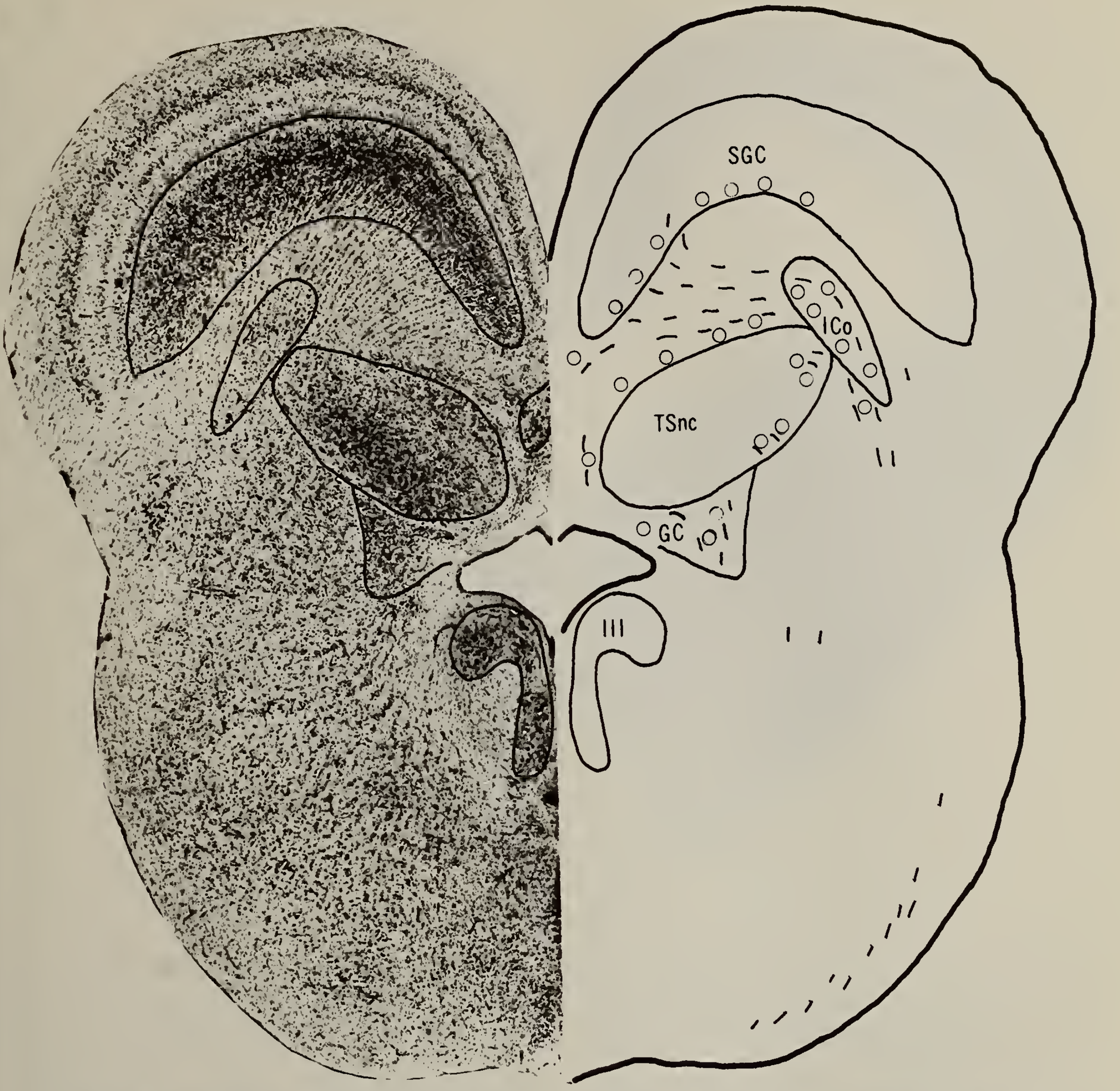

Figure 5. Degeneration in tectum at level somewhat further forward to that shown in Fig. 4.

the inferior colliculus have been demonstrated in the opossum (Hazlett, et al., 1972; Walsh and Ebner, 1970; and Robards et al., 1974), in the cat (Hand and Liu, 1966; and Van Noort, 1969), and in the hedgehog, tree shrew, African green monkey, marmoset, and slow loris (Schroeder and Jane, 1971). It is significant that, although the somatosensory input is principally to the intercollicular nucleus, a few fibers also appear to terminate in the ventrolateral region of the central nucleus.

The intercollicular nucleus in poikilothermic vertebrates was first seen in the tegu lizard (Ebbesson, 1966, 1967) during the tracing of ascending spinal projections. In this species, as well as in other reptiles (Ebbesson, 1969; Ebbesson and Goodman, 1976), the nucleus is well defined by the degenerating spinal fibers. The afferents

Figure 6. Degeneration in medial corner of tectum and bordering nucleus opticus ventromedialis (VMO).

from the dorsal column nuclei, described here for the first time, terminate profusely not only in the intercollicular nucleus, but a few axons, as in mammals, appear to reach the ventromedial corner of the central nucleus (Fig. 5).

There is presently no electrophysiological data available that provide insights into the role of the intercollicular nucleus in reptiles. However, because of the known tectal projection to it (Ebbesson, 1970*b*), multimodal integration appears likely.

The Thalamus

In lizards and other reptiles, direct spinal projections to the thalamus consist of two pathways (Ebbesson, 1966, 1967, 1969; Ebbesson and Goodman, 1975; Riss et al., 1972). The *dorsal pathway* enters the dorsal thalamus via a course through the medial optic tectum and terminates in a poorly differentiated region (labeled *nucleus intermedius dorsalis thalami* by Ebbesson, 1967) between the dorsal geniculate nucleus and the dorsolateral anterior nucleus. It has been suggested (Ebbesson, 1967; Ebbesson and Goodman, 1976), on the basis of its topographic position and neurophysiological studies by Russian workers (see Ebbesson and Goodman, 1976), that this area is homologous to the intralaminar nuclei of mammals which receive the so-called paleospinothalamic pathway (Mehler, 1957). Riss et al. (1972) have recently also suggested that

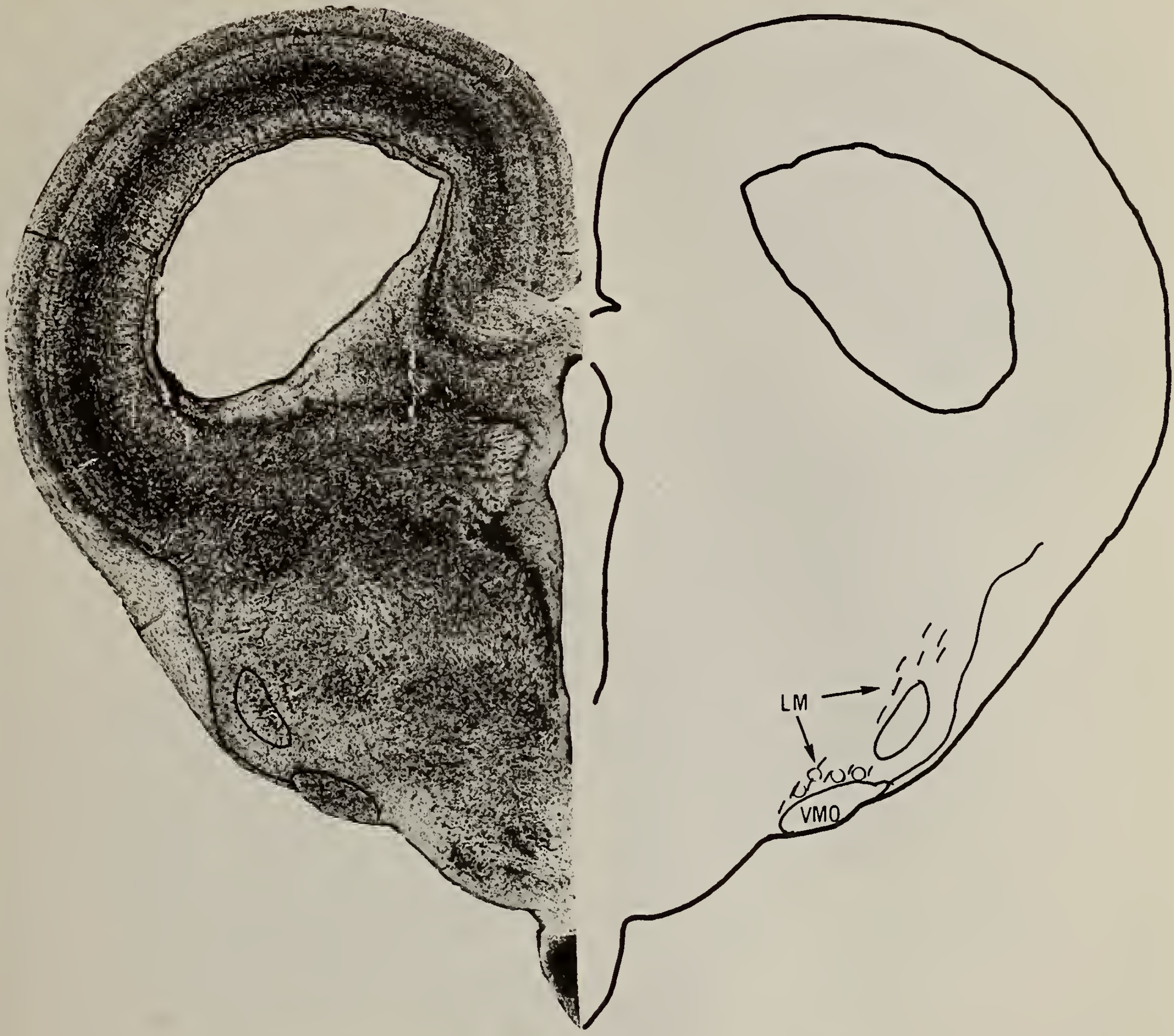

Figure 7. Degeneration seen in section somewhat rostral to that shown in Fig. 6.

this cell group may be homologous to the mammalian posterior nucleus (PO). The *ventral spinothalamic* pathway takes the same course as the medial lemniscus fibers described here and terminates in the ventrolateral area of the thalamus, here tentatively labeled as the ventrobasal complex (Vb). This projection, probably homologous to the mammalian spinal lemniscus, appears very small in all reptiles examined, except in the alligator, where the fibers were readily traced to their termination (Ebbesson and Goodman, 1976). It is from this zone (Vb) that Belekhova and Kosareva (1971) reported electrical activity following somatic sensory stimulation. The efferent projections of Vb remain unknown, but it is likely that, as in mammals, the main target is in the telencephalon (Belekhova and Kosareva, 1971).

LIST OF ABBREVIATIONS

DCN	nucleus funiculus dorsalis
GC	Grisea centralis

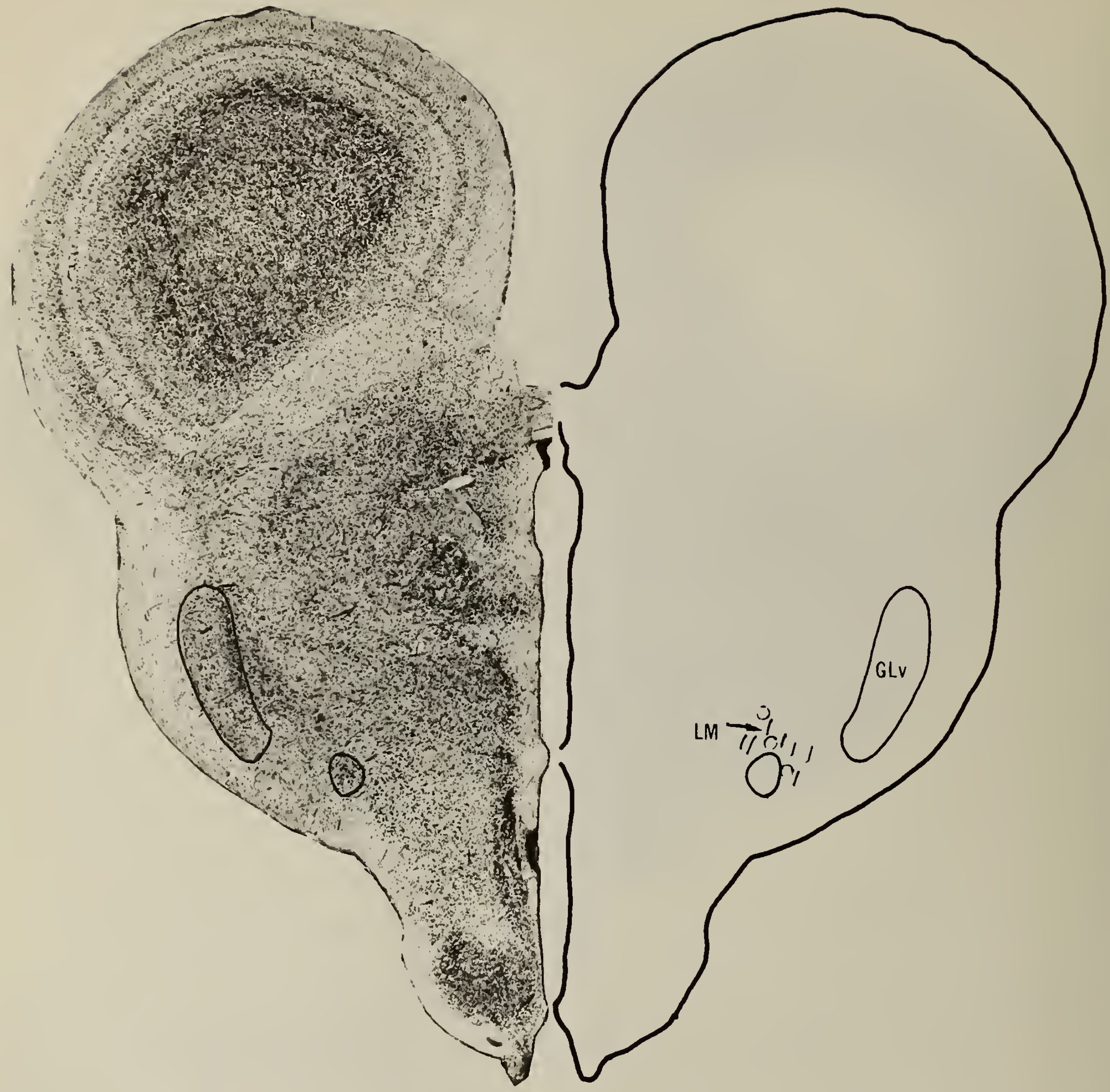

Figure 8. A few degenerating fibers were traced to the ventral thalamus in the region of the so-called ventrolateral nucleus.

GLV	nucleus geniculatus lateralis pars ventralis
ICo	nucleus intercollicularis
LM	leminscus medialis
OI	nucleus olivaris inferior
OS	nucleus olivaris superior
PM	nucleus parvocellularis medialis
RM	nucleus reticularis medius
Rot	nucleus rotundus
SGC	stratum griseum centrale
TSnc	torus semicircularis, nucleus centralis
TeO	tectum opticum
Vb	ventrobasal complex
VMO	nucleus opticus ventromedialis
III	nucleus nervi oculomotorii
VI	nucleus nervi abducentis
VII	nucleus nervi facialis
XII	nucleus nervi hypoglossi

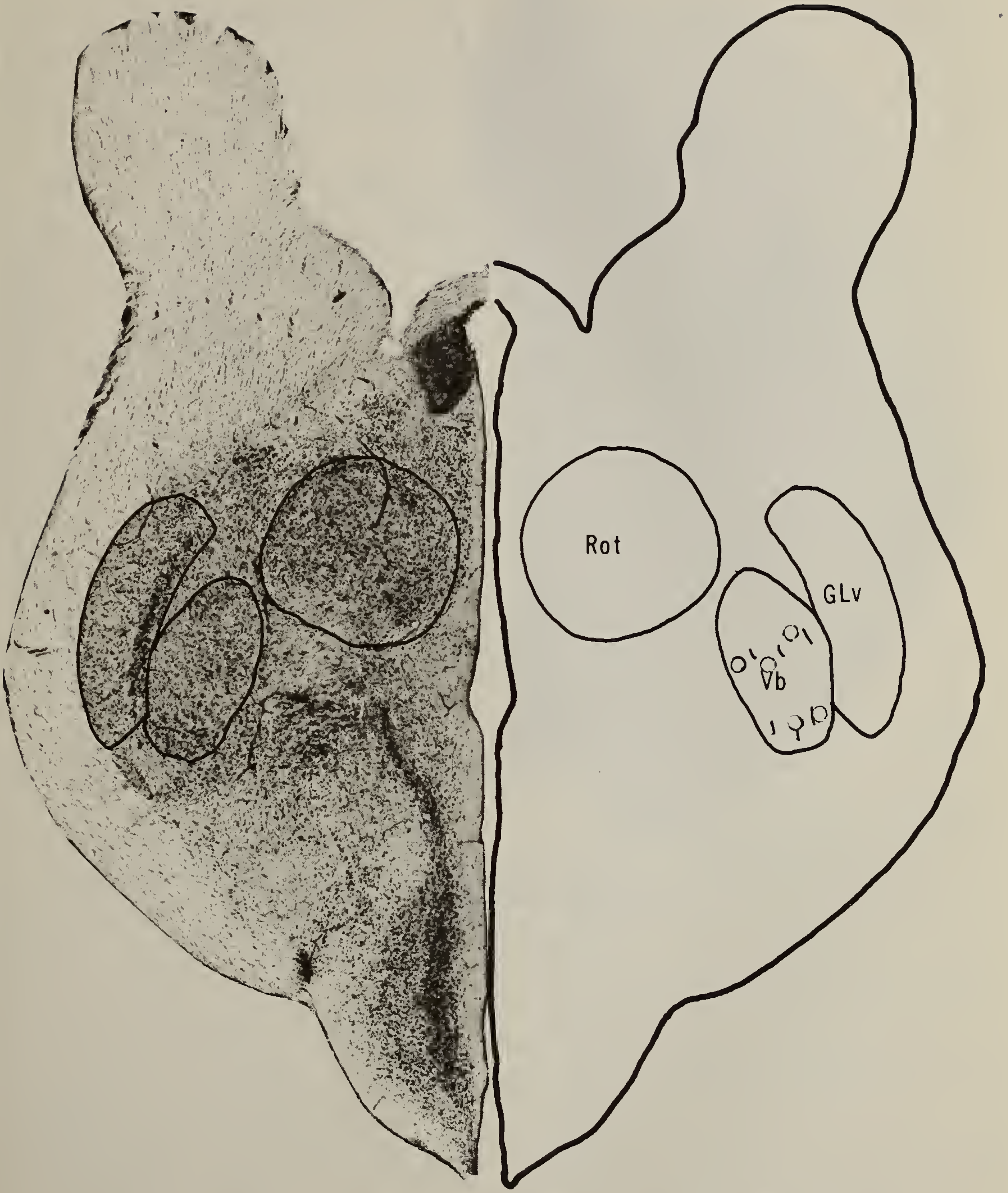

Figure 9. Degeneration in the ventrobasal complex (Vb) at level of nucleus rotundus (Rot).

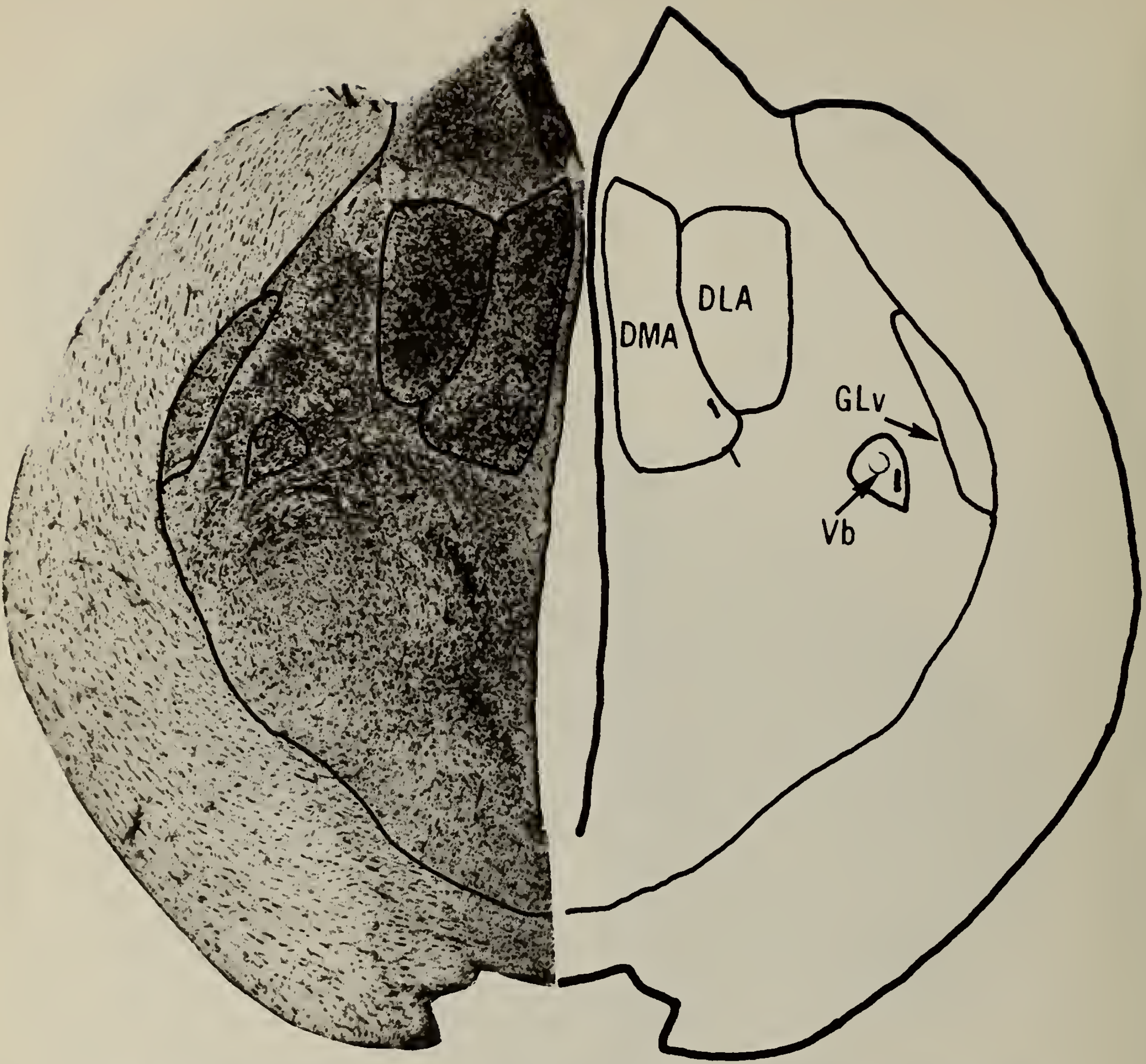

Figure 10. Degeneration in ventrobasal complex (Vb). DLA, dorsolateral anterior nucleus; DMA, dorsomedial anterior nucleus.

ACKNOWLEDGMENTS

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The Organization of Descending Pathways in the Tegu Lizard and Some Comments on the Evolution of Motor Systems

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SUMMARY. The organization of descending fiber systems was studied in the tegu lizard, *Tupinambis nigropunctatus,* using anatomical techniques and behaviorial observations. Fibers in the dorsolateral funiculus of the spinal cord which originate in the red nucleus, the metencephalic tegmentum and several myelencephalic nuclei have sparse bilateral projections to spinal laminae V, VI, and VII. Fibers in the ventromedial funiculus which originate in the interstitial nucleus, the vestibular nuclei, and the medial reticular nuclei of the metencephalon have dense bilateral projections to spinal laminae VIII and medial IX. Fibers in the ventrolateral funiculus, which originate in the metencephalic tegmentum and the myelincephalic reticular and raphe nuclei have projections into lamina VII overlapping the terminal fields of the dorsolateral and ventromedial pathways. Following high spinal hemisection, descending coordination of movement of trunk musculature is lost, while control of limb movements is only slightly affected. Comparisons are made with other species, especially mammals, and a number of common features are noted both in the organization of the descending pathways and in the organization of their target cells in the spinal cord. The data suggest that the major evolutionary changes in motor systems occurred at the level of synaptic organization of their terminals in the spinal cord.

INTRODUCTION

The spinal motoneuron is the "final common pathway" (Sherrington, 1906) for all motor acts involving musculature of the trunk or limbs. The activity of spinal motoneurons is initiated or modulated by synaptic input from spinal interneurons; both motoneurons and interneurons are, in turn, influenced by fibers descending upon them from supraspinal regions. The anatomical and functional organization of this descending input will be the subject of the present communication.

In mammals there are two major groups of descending motor pathways: those originating in the brainstem (bulbospinal pathways) and those originating in the forebrain, primarily from precentral motor cortex. Fibers originating in motor cortex may act directly upon interneurons and motoneurons of the spinal cord (corticospinal pathway) or indirectly via projections to the brainstem nuclei which give rise to the bulbospinal tracts (cortico-bulbospinal pathways).

The bulbospinal pathways in mammals may be subdivided into two groups on the basis of their patterns of termination in the spinal cord (Kuypers, 1973). One group of fibers, the lateral brainstem pathway, terminates in the lateral part of the spinal gray, unilaterally, and acts upon interneurons and motoneurons controlling distal extremity muscles, i.e., the hand and foot. The other group of fibers, the ventromedial brainstem pathway, terminates in the ventromedial part

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*Present Address: Dept. of Neurobiology, Northeastern Ohio Universities College of Medicine Rootstown, Ohio 44272 of the spinal gray, bilaterally, and acts upon interneurons and motoneurons controlling axial and proximal limb musculature.

Fibers from precentral motor cortex may overlap the spinal terminations of the brainstem pathway (Kuypers, 1973). In some primates corticospinal fibers terminate in both the lateral and medial regions of the gray, thus allowing the forebrain to have a strong direct effect upon the activity of spinal interneurons and motoneurons controlling both limb and axial musculature. In other mammals, corticospinal fibers terminate only in the lateral spinal region, as does the lateral brainstem pathway. Thus in these animals only limb musculature is under direct control of the forebrain.

Reptiles lack the corticospinal pathway and probably have no cortical efferents terminating in the brainstem (Ariëns Kappers, et al., 1936; Goldby, 1937; Goldby and Gamble, 1957; Kruger and Berkowitz, 1960). On the other hand, they possess all of the mammalian brainstem structures which project to the spinal cord (Ariëns Kappers, et al., 1936; Robinson, 1969; Cruce and Nieuwenhuys, 1974; Cruce, et al., 1976; Donkelaar, 1976*a,b*). Thus reptiles offer the possibility for studying the function and structure of supraspinal motor control in a system uncomplicated by cortical descending pathways.

The range of variation in both morphology and methods of locomotion to be found amongst the reptiles provide a number of interesting experimental models which we have only just begun to explore. While turtles have no trunk musculature and snakes (and some lizards) have no limbs, most lizards have both limb and trunk musculature which are employed in locomotion. Thus reptiles provide a number of experimental models for separating the functions of the medial and lateral brainstem pathways. Recently I have focused attention upon the Tegu lizard, a reptile which is a good example of a generalized terrestrial tetrapod and therefore a convenient species in which to begin a study of reptilian bulbospinal pathways.

A question of particular interest is whether there are any basic, ancestral mechanisms of supraspinal motor control which are common to all vertebrates. An answer to this question will be sought by looking at the organization of descending pathways in the Tegu lizard in terms of their patterns of *termination.* Additionally, the *origins* of the different descending pathways and the organization of their *target cells* in the spinal cord will be considered.

MATERIALS AND METHODS

The Tegu lizards used in this study were identified as *Tupinambis nigropunctatus* according to the key in Peters and Donoso-Barros (1970). The normal organization of the spinal cord (Cruce, 1978) was studied in animals which had not been subjected to experimental surgery. Spinal cords were sectioned in all three standard planes and stained with the Nissl method for cell bodies, the Heidenhain method for myelinated fibers, or the Golgi method for cell bodies, dendrites, and axons.

Descending fiber projections were studied (Cruce, 1975; Cruce, et al., 1976) by performing lesions at the first spinal segment and observing anterograde degeneration of the severed fibers in the spinal cord using the Nauta or Fink-Heimer reduced silver stains (Ebbesson, 1970; Heimer, 1970).

Brainstem cells giving rise to descending fiber projections were localized (Cruce, et al., 1976) by performing lesions at the first spinal segment and observing retrograde chromatolysis of cells whose fibers had been severed. These brains were from the same animals used for studying descending fiber degeneration so that terminal patterns could be accurately correlated with cell groups of origin.

RESULTS

Spinal Cord Morphology

Excellent reviews of the classical work on the reptilian spinal cord are available in the works by Ariëns Kappers et al. (1936), Nieuwenhuys (1964), and Anthony (1970); recent experimental studies on the reptilian spinal cord have been reviewed by Cruce (1978). The Tegu lizard spinal cord, like all other reptilian spinal cords, extends throughout the length of the vertebral canal and shows no evidence of foreshortening. Since lizard vertebrae are morphologically more uniform than their mammalian counterparts, spinal roots are simply numbered consecutively from the first, in a rostro-caudal sequence. However, it should be noted that there is variability in vertebral numbers in different species of lizards, therefore the numbering system used here applies only to *Tupinambis nigropunctatus*. Brachial and lumbar enlargements are present; roots 6–9 enter the brachial plexus and roots 24–28 enter the lumbar plexus.

The spinal cord can be divided into an exterior mantle of white matter, composed of fibers, and an interior core of gray matter, composed of cells. In reptiles, as in mammals, the gray matter can be subdivided into dorsal and ventral horns. In a microscopic analysis of the lizard spinal cord it was possible to delimit 10 regions of the gray matter which were similar to the "laminae" described by Rexed (1952, 1954, 1964) for the cat. Therefore, the regions were assigned the same numbers used by Rexed in his analysis (Fig. 1). Since a detailed description of these laminae is available elsewhere (Cruce, 1978), in the present paper only certain features will be pointed out which will be useful for describing the descending fiber pathways. The following description of the laminae is based primarily on Nissl-stained material (cresyl violet, thionin) and fiber-stained material (Heidenhain) except where it is specifically mentioned that Golgi-stained material was used.

As shown in Figure 1, laminae IV and V extend across the midline in all regions outside the enlargements, and lamina VI is present only in the enlargements. Laminae VII is composed of a homogenous group of scattered medium-sized, lightly staining cells. It descends into the tip of the ventral horn to surround the lateral lamina IX group only in the enlargements (Fig. 1*A*, *C*). In Golgi-stained material, cells in lamina VII appear to be either short-axon interneurons which connect with other cells in lamina VII and in lateral lamina IX (see below) or long-axon cells which give rise to ascending and propriospinal pathways.

Lamina VIII is distinguished from lamina VII by its heterogeneous cell population. Whereas lamina VIII takes a medial position in the enlargements (Fig. *1A*, *C*), outside of these regions it displaces lamina VII so as to fill the entire ventral horn (Fig. *1B*, *D*). This is consistent with its association with the medial lamina IX group, continuous throughout the cord. In Golgi-stained material, cells in lamina VIII generally fall into two classes: interneurons which connect with other cells in lamina VIII and in medial lamina IX (see below), or commissural cells which connect lamina VIII and medial lamina IX with their contralateral counterparts (Cruce, 1978).

Lamina IX is composed of large, darkly staining cells possessing abundant Nissl substance and is not at all laminar in formation. Rather, it consists of two longitudinal columns, one (present throughout the spinal cord) in a medial position and the other (present only in the enlargements) in a lateral position. The medial group is presumably composed of motoneurons innervating axial or trunk musculature and the lateral group of motoneurons innervating the limbs (Ariëns Kappers et al., 1936; Nieuwenhuys, 1964; Romanes, 1964; Cruce, 1974). In Golgi-stained material, motoneurons of the two lamina IX groups present contrasting dendritic arborizations (Fig. 2). The medial group of motoneurons tends to elaborate its dendrites within lamina VIII and in a somewhat radial pattern. On the other hand, each lateral motoneuron has two prominent dendrites; one extends into the ventral parts of lamina VIII and medial lamina IX before arborizing, and the other extends along the dorsolateral border of lamina VII to send branches radially into the lateral funiculus and into the subpial

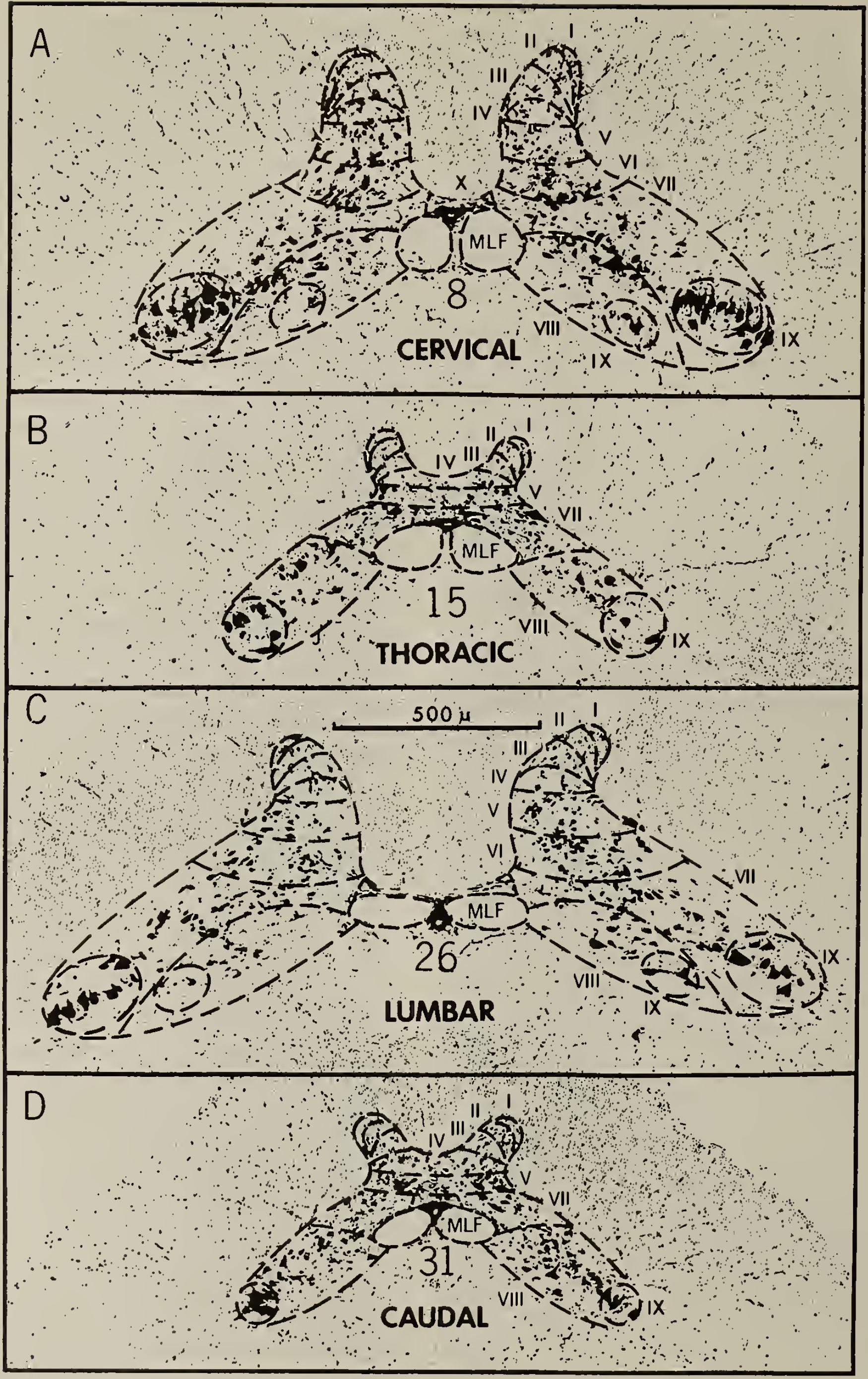

Figure 1. High contrast photographs of 30µ thick sections of lizard spinal cord stained by the Nissl method. Boundaries of different cellular regions are indicated by dashed lines. These were determined by using the criteria of Rexed and studying the sections under high magnification. Roman numerals indicate the different cellular regions or "laminae." Representative sections shown are (A) middle of brachial enlargement; (B) thoracic level; (C) middle of lumbar enlargement; (D) caudal level. The medial longitudinal fasciculus (MLF) is a spinal continuation of the brainstem pathway of that same name. Reproduced from Cruce (1975), *Brain, Behavior, and Evolution,* with permission of the publisher.

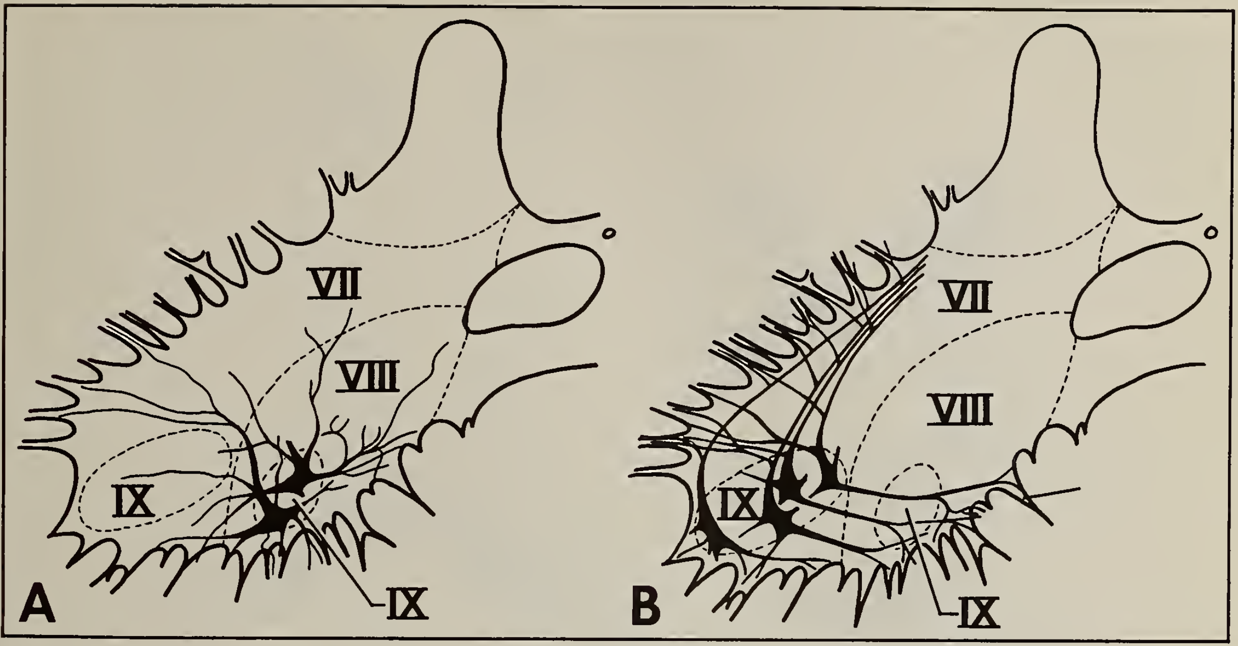

Figure 2. Camera lucida drawing prepared from Golgi-stained sections of lizard spinal cord. Different cellular regions of the ventral horn as determined in Nissl-stained sections are indicated by dashed lines. (A) Motoneurons of the medial lamina IX group. Note that dendrites of motoneurons are confined primarily to the medial lamina IX area and lamina VIII. (B) Motoneurons of the lateral lamina IX group. Note the extensive ramification of motoneuronal dendrites into laminae VII, VIII, and the medial lamina IX region. Reproduced from Cruce (1975), *Brain, Behavior, and Evolution,* with permission of the publisher.

dendritic plexus. Although the longitudinal organization of lizard motoneurons has not yet been thoroughly analyzed, some preliminary observations have been made on horizontal and sagittal sections of Golgi-stained material. Motoneuronal dendrites are seen to run in the rostro-caudal axis through the column of motoneurons. Dendritic bundles, or thickets, such as are seen in the spinal cord of mammals (Scheibel and Scheibel, 1970; Matthews, et al., 1971) and amphibians (Stensaas and Stensaas, 1971) have not been recognized, but further analysis is necessary before these can be ruled out entirely.

Descending Axon Degeneration

Following a complete hemisection at the first spinal segment (Fig. 3) degenerating fibers in the white matter were confined to the ipsilateral side in three major groups: the medial longitudinal fasciculus (MLF), the dorsolateral funiculus, and the ventromedial funiculus. In laterally placed lesions (incomplete hemisections), fiber degeneration was absent in the MLF and greatly decreased in the ventromedial funiculus (Fig. 4). Fiber degeneration in the white matter decreased in proportion to the distance below the lesion, but was still present in caudal segments.

In the gray matter, degenerating axoplasm was most intense in the medial part of lamina VII, in lamina VIII, and in medial lamina IX (Figs. 3 and 4). Much of this degeneration had a disorganized random appearance suggestive of preterminal aborizations and terminals (Figs. 5*B*, *E*, *F*, and 6*D*). Sparser degeneration was present in the lateral parts of laminae V, VI, and VII (Figs. 3 and 4). Some of this sparse degeneration was organized in linear beads suggestive of axons (Figs. 5*B* and 6*E*) rather than terminal fields (but see below). Virtually no degenerating axoplasm was seen in the dorsal horn (Fig. 5*A*) or lateral lamina IX (Fig. 5*C*).

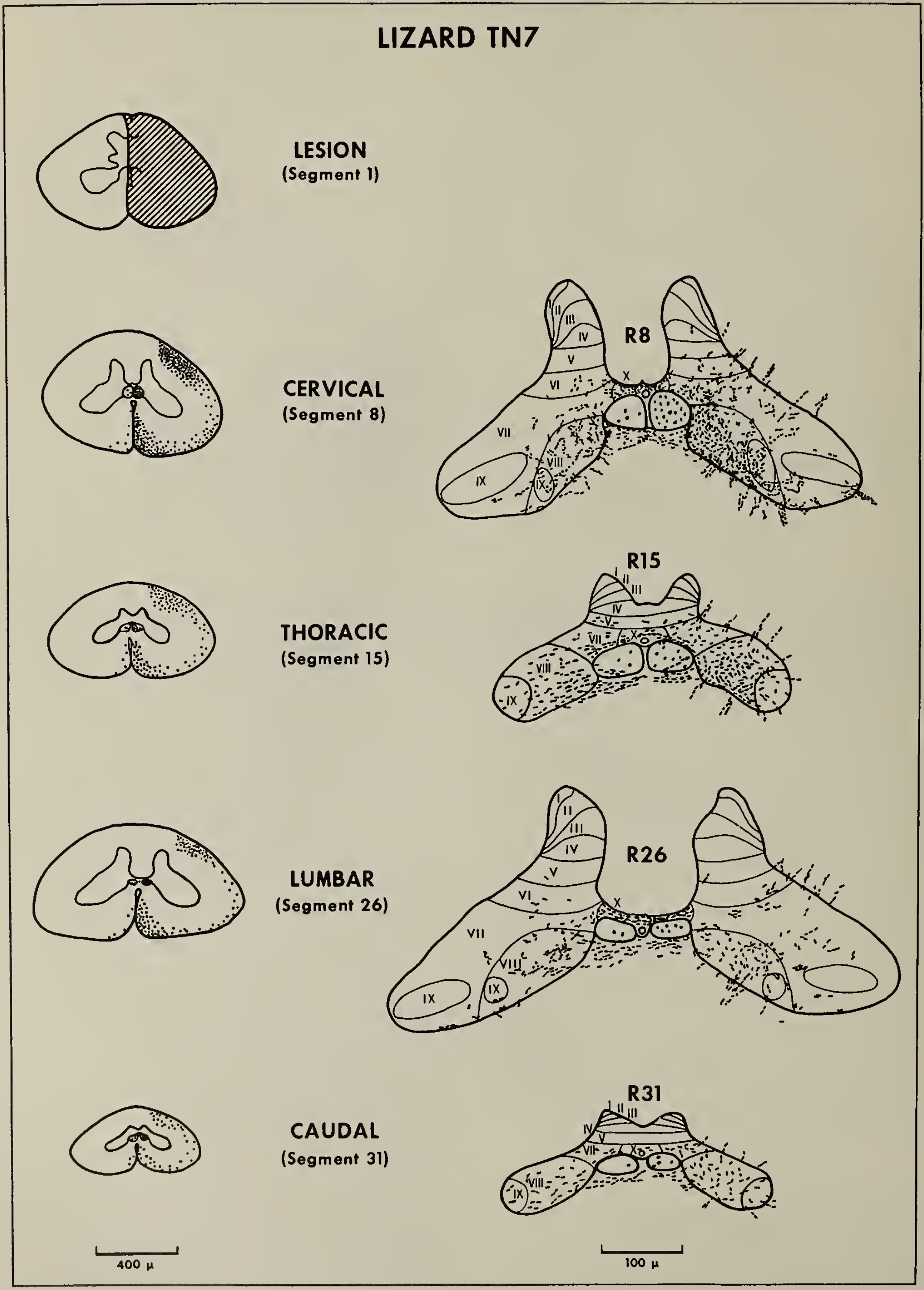

Figure 3. A plot of axonal degeneration of representative levels of the lizard spinal cord following a complete hemisection at the first cord segment. Small drawings to the left show transversely cut axonal degeneration in the white matter. The large drawings to the right depict degeneration in the gray matter. Axonal terminals are not distinguished from preterminal debris and axons-of-passage. Reproduced from Cruce (1975), *Brain, Behavior, and Evolution*, with permission of the publisher.

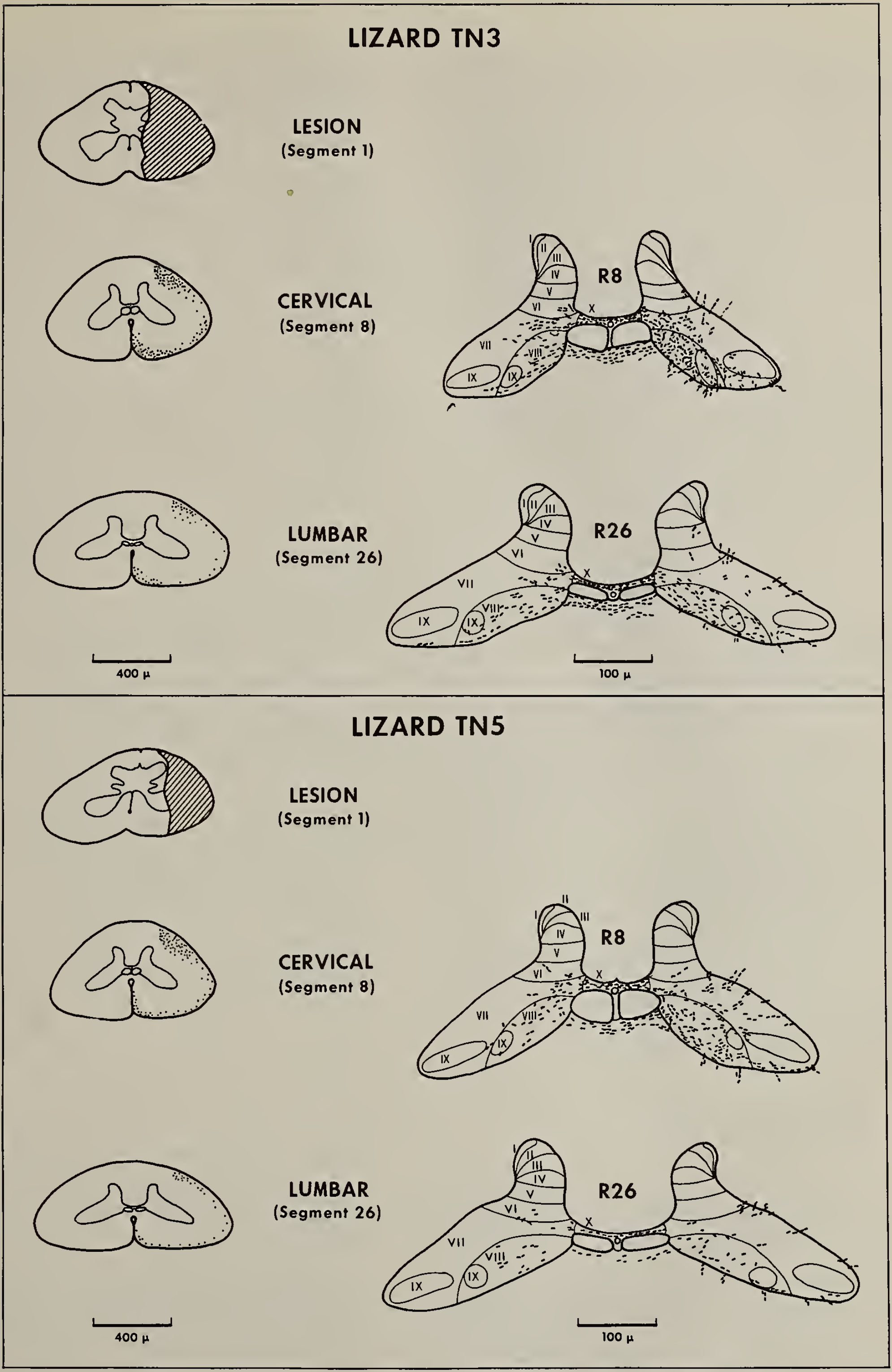

Figure 4. Plots of axonal degeneration at the brachial and lumbar enlargements of the lizard spinal cord following incomplete hemisections at the first cord segment. See legend of Figure 3 for details. Notice that the pattern of degeneration following these lesions is the same as that seen following a complete hemisection (Fig. 3), but with slightly less intensity in the medial regions of spinal gray. Reproduced from Cruce (1975), *Brain, Behavior, and Evolution,* with permission of the publisher.

Degenerating fibers were seen coursing through lamina X or the dorsal gray commissure (Figs. 3, 4, 5*E*, and 6*A*) and the ventral accessory white commissure (Fig. 6*B*) toward the contralateral side of the cord. There the degeneration took on the appearance of preterminal aborizations and terminals and was confined to the medial parts of laminae VII and VIII and medial lamina IX (Fig. 6*G*). No degeneration was present in the lateral part of the spinal gray on the contralateral side (Fig. 6*F*).

Smaller spinal lesions which avoided the MLF and the ventromedial funiculus (Fig. 4) created a similar pattern of degeneration. The density of degenerating fibers in medial regions of the ventral horn was decreased but it was still more intense than that in lateral regions. The smallest spinal lesion, confined only to the dorsolateral funiculus produced bilateral sparse degeneration, probably preterminal and terminal in nature, which was confined primarily to the lateral parts of laminae V, VI, and VII, ipsilaterally, and the medial parts of these laminae, contralaterally (Cruce et al., 1976). A similarly small lesion, confined to the ventromedial funiculus resulted in dense preterminal and terminal degeneration which was found only in lamina VIII and medial lamina IX, bilaterally (Cruce et al., 1976). A lesion which included the ventrolateral funiculus caused additional ipsilateral degeneration in the ventrolateral parts of lamina VII.

Brain Stem Chromatolysis

It is beyond the scope of this paper to describe the cytoarchitecture of the lizard brainstem. An excellent classical review is available in the work of Ariëns Kappers et al., (1936). More recent studies are covered in papers by Cruce and Nieuwenhuys (1974) and Donkelaar and Nieuwenhuys (1978). The lizard brainstem contains essentially the same cell groups as other reptiles. Most of the brainstem cell groups seen in reptiles are also seen in mammals.

Following a complete hemisection at the first spinal segment, typical retrograde changes (swelling of the cell body, clearing of the central Nissl substance, and eccentric nucleus) indicative of axonal injury were seen in cells of many brainstem nuclei (Cruce et al., 1976; Cruce and Newman, unpubl. observ.). The chief nuclei involved were the interstitial nucleus and red nucleus of the mesencephalon, the lateral tegmental nuclei of the metencephalon, the ventrolateral and dorsolateral vestibular nuclei, the medial reticular nuclei of the metencephalon and myelencephalon, the myelencephalic raphe nucleus, and the nucleus of the solitary tract.

By comparing the results from different small lesions of the funiculi at the first spinal segment, it was determined that the dorsolateral funiculus contains descending fibers contralaterally from the red nucleus, a lateral tegmental nucleus, and the solitary nucleus and ipsilaterally from a lateral tegmental nucleus and from a portion of the myelencephalic reticular formation; the ventrolateral funiculus contains fibers bilaterally from portions of the myelencephalic reticular formation and the myelencephalic raphe nucleus; and the ventromedial funiculus contains fibers ipsilaterally from the interstitial nucleus, the metencephalic medial reticular formation, and the ventrolateral vestibular nucleus and contralaterally from the dorsolateral vestibular nucleus.

Behavioral Observations

During surgery, as the lesion knife approached the midline, respiratory movements of the ribcage were abolished on the ipsilateral side. When there was no postoperative recovery of ipsilateral respiration, postmortem histological examination of the lesion revealed that the medial longitudinal fasciculus (MLF), which is located bilaterally adjacent to the midline, was transected ipsilaterally (Fig. 3).

Upon recovery from anesthesia following a complete hemisection, there was a marked curving of the animal's neck, trunk, and tail

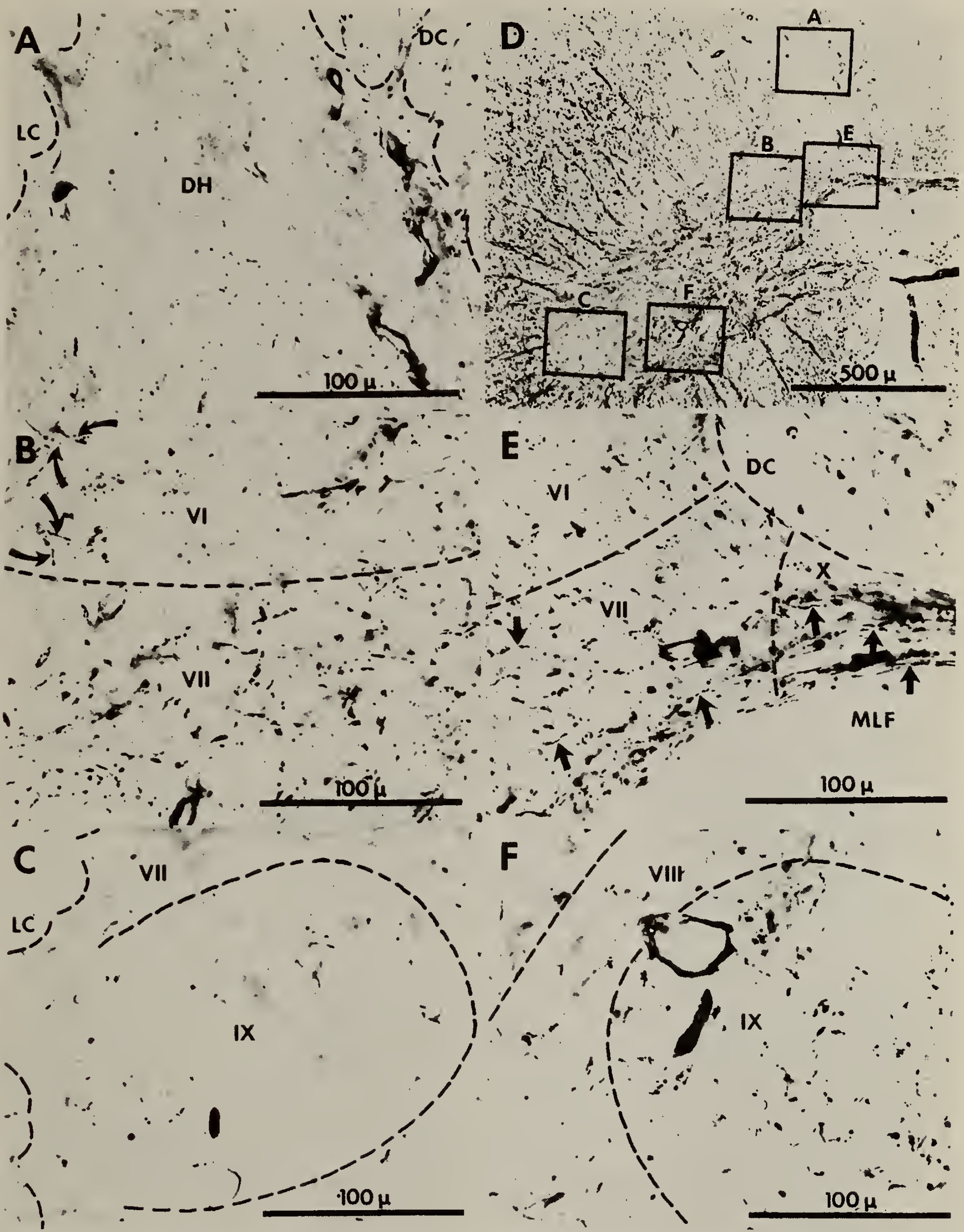

Figure 5. Photomicrographs of degeneration in the 8th segment (midbrachial) of lizard spinal cord following a complete hemisection of the first spinal segment (animal TN7; Fink-Heimer stain). (D) Low power photo of the ipsilateral spinal gray matter; squares indicate where high-power photos were taken. (A) Dorsal horn (DH): Note the absence of axonal debris. (B) The border between laminae VI and VII: Note that lamina VII is filled with axonal, preterminal, and terminal debris; lamina VI contains primarily a few degenerating axons-of-passage (arrows). (E) Preterminal and terminal debris can be seen in laminae VI and VII; axons-of-passage (arrows) can be seen coursing from lamina VII into lamina X (the dorsal gray commissure). (C) The lateral lamina IX group of motoneurons: Note the absence of axonal debris. (F) Lamina VIII and medial lamina IX: Note the preterminal and terminal debris. Abbreviations are: dorsal column (DC), dorsal horn (DH), lateral column (LC), and medial longitudinal fasciculus (MLF). Reproduced from Cruce (1975), *Brain, Behavior, and Evolution,* with permission of the publisher.

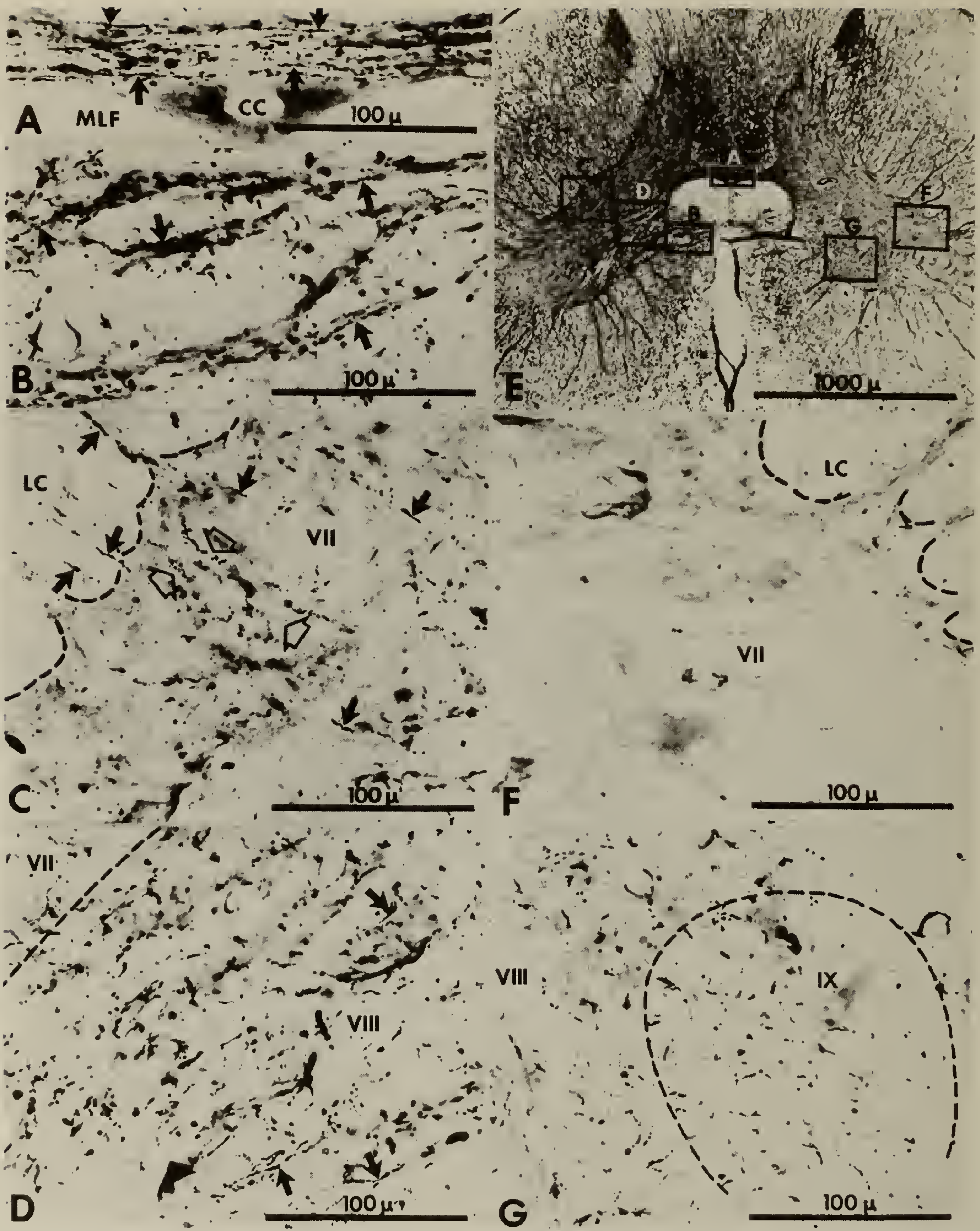

Figure 6. Photomicrographs of degeneration in the 8th segment (midbrachial) of the lizard spinal cord following a complete hemisection of the first spinal segment. The same section as pictured in Figure 5. (D) Low power photo of the spinal gray matter with the ipsilateral side on the left: squares indicate where high-power photos were taken. (A) The dorsal gray commissure (lamina X): Note that it is filled with degenerating axons-of-passage (arrows). (B) The ventral white commissure: Note the bundles of degenerating axons-of-passage (arrows). (C) The lateral border of ipsilateral lamina VII with the white matter: Note degenerating axons-of-passage (arrows) entering from the upper left and passing toward more medial regions; slight evidence of preterminal and terminal debris can also be seen (open arrow). (F) The lateral border of contralateral lamina VII with the white matter: Note the absence of axonal debris and contrast this with the ipsilateral region seen in (C). (D) Ipsilateral lamina VII: Note that it is filled with a large amount of preterminal and terminal debris as well as axons-of-passage (arrows) which are coursing into the ventral commissure. (G) Contralateral laminae VIII and medial IX: Note that the region is filled with preterminal and terminal debris and compare this with the ipsilateral region seen in Figure 5F. Abbreviations are: central canal (CC), lateral column (LC), and medial longitudinal fasciculus (MLF). Reproduced from Cruce (1975), *Brain, Behavior, and Evolution,* with permission of the publisher.

to the contralateral side. Sometimes this curvature was observed when the animal was resting. When the animal tried to run, the accentuated curvature resulted in a circling to the contralateral side, or there was a complete cessation of movement with the animal coiled contralaterally. During locomotion the normal wave of side-to-side flexion of the trunk, which travels through the body as an aid to increasing stride and leverage of the limbs (Snyder, 1952; Bellairs, 1969), was lost. The tail was also no longer used as a whip in defense. Thus, there appeared to be a loss or weakening of activity in ipsilateral trunk muscles.

Slow walking was abnormal, partly due to the loss of trunk flexion, but also due to weakness and abnormalities of movement in the limbs. The sacral trunk tended to roll to the ipsilateral side as if the ipsilateral hindlimb was unable to support the body at the hip. While the animal was able to stand on all limbs, it was unable to support its body weight on either forelimb alone, particularly when the limb was extended backwards.

There was a tendency of the resting animal to extend its ipsilateral forelimb and to fall over with the contralateral forelimb collapsed under the body. During slow walking, the ipsilateral forelimb was sometimes passively dragged in the extended position. The animal could also stand on, and locomote with, all limbs, though it appeared to tire quickly. Animals with less than complete hemisections showed losses of motor activity, except bilateral respiration (see above), though the losses were less severe than those in animals with complete hemisections. There was sometimes a slight ability to bend the neck past the midline, but strength in ipsilateral trunk muscles was greatly diminished compared to that seen contralaterally.

DISCUSSION

Spinal Cord Organization

Rexed's (1952, 1954, 1964) analysis of the cytoarchitecture of the cat spinal cord has frequently been applied to other mammalian species, e.g., tree shrew (Shriver and Noback, 1967), opossum (Martin and Dom, 1970), squirrel monkey (Harting and Noback, 1970), and chimpanzee (Noback and Simenauer, 1970). Cytoarchitectonic analyses of the avian spinal cord (Akker, 1970; Brinkman and Martin, 1973) have revealed a similarity to the mammalian structure, and recently Leonard and Cohen (1975) have shown that the organization of the gray matter in the pigeon spinal cord is quite like that described by Rexed in the cat. An organization which resembles Rexed's laminae has also been found in the lizard spinal cord (Cruce, 1978), thus suggesting that the laminar organization of the spinal cord may be a general feature of many vertebrates.

The Golgi picture of the organization of axons and dendrites of neurons intrinsic to the Tegu lizard spinal cord is similar to that seen by Ramon Y Cajal (1891, 1909–1911) in the lizard, *Lacerta,* and by Banchi (1903) in the turtle, *Emys.* In some respects it is also similar to that seen in mammals (e.g., Matsushita, 1970 *a, b*), i.e., neurons of lamina VII are related ventrally and laterally to neurons of lateral lamina IX and the lateral funiculus, while neurons of lamina VIII are related ventrally and medially to medial lamina IX, the ventral funiculus and the commissures. Since lateral lamina IX contains motoneurons innervating the limbs, and medial lamina IX contains those innervating the trunk (Cruce, 1974), it may be suggested that interneurons of lamina VII and VIII are involved in the integration of limb and trunk movement, respectively, as has been proposed to be the case in mammals (Sterling and Kuypers, 1968).

A notable difference between reptilian and mammalian spinal organization is revealed by Golgi analysis of transverse sections. Whereas mammalian spinal motoneurons exhibit a uniform multipolar dendritic pattern (Testa 1964), Tegu lizard lateral motoneurons possess two primary dendrites —a medial one and a lateral one. This dendritic configuration is reminiscent of the structure of the goldfish Mauthner cell

(Bodian, 1937) and raises the intriguing possibility that different types of synaptic input might be confined to either the medial or the lateral dendrite.

Terminal Fields of Descending Fibers

Three striking differences can be noted when the pattern of descending fiber terminations seen in this lizard is compared to that described by Nyberg-Hansen (1969) in cat: (1) the absence of terminals in the dorsal horn, (2) the prevalence of terminals in the contralateral spinal gray without any associated descending fibers in the contralateral white matter, and (3) the sparseness of terminals in the lateral regions of the spinal gray. In the following paragraphs each of these points will be considered.

The terminals in the cat dorsal horn (laminae IV, V) and a portion of those in the lateral spinal gray (V, VI, VII) are from fibers originating in cerebral cortex (Nyberg-Hansen, 1966; Petras, 1967). The absence of terminals in the lizard dorsal horn and their sparseness in the lateral gray matter is consistent with the view that a corticospinal pathway does not exist in reptiles (Ariëns Kappers, et al., 1936; Goldby, 1937; Goldby and Gamble, 1957; Kruger and Berkowitz, 1960), although it should be noted that electrophysiological and neuroanatomical techniques have not yet been used to conclusively demonstrate the presence or absence of this pathway.

Mammalian descending fibers terminate predominantly on the side of the spinal cord where they descend; most decussations are located in the brainstem. However, some fibers decussate in the spinal cord at high levels to descend for a distance in all areas of the contralateral funiculi before terminating in both lateral and medial regions of the spinal gray (Nyberg-Hansen, 1969). Other fibers appear to terminate in the segment where they decussate (Nyberg-Hansen, 1969; Martin and Dom, 1971), as in the lizard, although not with the same intensity.

Since the number of degenerated fibers in the dorsolateral funiculus is roughly equal to the number seen in the ventromedial funiculus, it is surprising that the terminal degeneration following a dorsolateral lesion is so much less than that following a ventromedial lesion. This difference is dramatic following a complete hemisection (Fig. 3) of the lizard spinal cord; degeneration in the lateral parts of the spinal gray is far less intense than that in the medial parts. Two possible explanations are: (1) The dorsolateral fibers have less extensive arborizations near their endings, and (2) the dorsolateral fibers have fewer collaterals into the spinal gray. In mammals, fibers in the dorsolateral funiculus terminate in the lateral regions of spinal gray with about the same intensity as those in the ventromedial funiculus terminate in the ventromedial regions (Nyberg-Hansen, 1966).

Mammalian rubrospinal fibers descend in the dorsolateral funiculus and project to the lateral parts of laminae V, VI, and VII (Kuypers, 1973; Petras, 1967; Nyberg-Hansen and Brodal, 1964; and Martin and Dom, 1970). The mammalian medullary reticulospinal pathway sends fibers in the lateral funiculus to project to lateral lamina VII while the pontine reticulospinal pathway descends ventromedially and projects to lamina VIII and medial lamina VII (Kuypers, 1973; Petras, 1967; Nyberg-Hansen, 1965; Martin and Dom, 1971). In lizards (Robinson, 1969; Cruce et al., 1976) rubrospinal fibers descend in the dorsolateral pathway, medullary (myelencephalic) fibers descend ventrolaterally, and "pontine" (metencephalic) fibers descend ventromedially (lizards have no true pons).

Supraspinal Effects on Motoneurons

The terminal field of fibers descending in the medial longitudinal fasciculus (MLF) to the spinal cord is probably confined to the medial part of the ventral horn (laminae VIII and medial IX). A Number of brainstem cell groups, particularly interstitial and reticular nuclei, are thought to contribute descending fibers to the MLF (Goldby and Robinson, 1961; Nieuwenhuys, 1964; Donkelaar, 1976). Behavioral observations suggest that the MLF carries fibers mediating rhythmic respiratory movements of thoracic musculature (Ebbesson, 1967; Cruce, 1975). The MLF also continues as a large bundle below thoracic levels, but the function of these fibers is unknown.

Lizard supraspinal pathways may influence medial motoneurons either through direct monosynaptic connections (since the medial lamina IX group is filled with axon terminals) or through connections to interneurons in lamina VIII which impinge on medial motoneurons. The termination of descending pathways is almost bilaterally symmetrical with respect to the medial motoneurons, although this is not to imply that the terminals on each side are functionally equal.

The behavioral effects of hemisection in the lizard are most dramatic in the trunk musculature (innervated by medial motoneurons): There is a loss of the ability to flex the trunk ipsilaterally. Thus the major net effect of fibers descending on one side of the spinal cord is to facilitate ipsilateral trunk flexion. This presumably occurs through a combination of facilitatory and inhibitory actions which reciprocally affect agonistic and antagonistic muscle groups on both sides of the body (since ipsilateral fibers project contralaterally as well as ipsilaterally).

Such a pattern of descending synaptic activity would be ideal for initiating or facilitating a horizontal wave of flexion in the trunk, exactly as has been observed during normal locomotion (Snyder, 1952; Bellairs, 1969).

Cord hemisection has little effect on limb movements; some effects which do appear (inability to support body weight) are probably due to weakness in shoulder and hip musculature, which is more related to trunk abnormalities; other effects (passive dragging of limb) might be due to sensory losses caused by cutting the ascending sensory pathways.

It has been hypothesized (Kuypers, 1973) that fibers in the dorsolateral funiculus (DLF) of mammals exert a descending control of limb musculature through synapses on interneurons in laminae V–VIII which are involved in integrating the activity in lateral motoneurons. The sparse termination of DLF fibers in the spinal gray of lizards correlates well with the minimal effects which lesions of the pathway have on coordinated limb movement.

The lateral motoneurons still may come under supraspinal influence via the medial motoneuronal dendrite which extends into lamina VIII where it might receive terminals of medial descending fibers. It is also possible that DLF pathways may influence the lateral motoneurons directly via synapses on their lateral dendrites, though these would probably be sparse. The lateral dendrite is much more likely to be influenced by dorsal root fibers which have profuse terminations in the lateral parts of laminae V, VI, and VII—exactly where the lateral motoneuronal dendrite is located (Joseph and Whitlock, 1968; Cruce, 1978). Since fibers of the DLF pathway terminate in a region overlapping with part of the terminal field of dorsal root afferents, the possibility also exists that DLF fibers exert brainstem control over incoming sensory activity at spinal levels.

Recently, Shapovalov (1975) reported that, in the turtle, stimulation of the medullary reticular formation generates EPSP's in lumbar lateral motoneurons, whereas stimulation of the red nucleus fails to generate even polysynaptic EPSS's. While this physiological evidence may not apply to the lizard, since turtles lack both trunk musculature and any significant number of medial motoneurons (Ariëns Kappers et al., 1936; Nieuwenhuys, 1964), it provides a parallel to the anatomical findings in the lizard that the medullary reticulospinal pathway could terminate on the proximal as well as distal dendrites of lateral motoneurons (laminae VII and VIII). It is far less likely that the rubrospinal pathway can influence lateral motoneurons to any great extent, both due to sparseness of terminals and to inappropriate location (laminae V and VI). In summary, it seems likely that descending control of limbs is not highly organized except in those animals, such as mammals, where the corticospinal and corticorubrospinal pathways have become highly developed.

Evolution of Motor Systems

Although only one reptilian suborder, lizards, has been studied in detail in this laboratory and although only scant information is available regarding other reptiles (Donkelaar, 1976*a, b*) and other nonmammalian vertebrate classes, there are other hypotheses regarding the evolution of motor systems worthy of investigation because of the experiments that they may generate.

(1) The location of cell bodies in the spinal cord has not changed dramatically from reptiles to mammals and may, indeed, be similar in all tetrapods. What has changed is the orientation and extent of the dendritic branching pattern of spinal motoneurons; the dendritic morphology of other spinal neurons is less understood and may not have changed much. Consistent with this hypothesis, frog motoneurons (Szekely, 1976) show a pattern of dendritic branching similar to that of lizard motoneurons, but with even more small branches in the white matter.

(2) Each vertebrate class may be characterized by one major descending motor pathway which it lacks or possesses when compared to other classes, and there may be an hierarchical sequence in which pathways were added as the classes evolved. Birds which evolved in parallel with mammals appear to possess a small projection from the forebrain to the brainstem and rostral spinal cord (Nauta and Karten, 1970) and this may be comparable to mammalian corticospinal and corticobulbar pathways. Although reptiles lack the corticospinal pathway, all of the bulbospinal pathways found in mammals are present. One of the bulbospinal pathways, the rubrospinal, is believed to exist in amphibia (Ariëns Kappers et al., 1936) and it also appears to be absent or greatly reduced in one snake species which has been studied (Donkelaar, 1976*a, b*). Less is known about other vertebrate classes, but the medullary reticulospinal and vestibulospinal pathways appear to exist in all vertebrates which have been studied (Shapovalov, 1972). Thus it may be possible to speak of "phylogenetic age" of descending pathways.

(3) While there is a certain conservatism regarding the position of particular pathways in the spinal white matter *and* their terminal fields in the spinal gray, individual pathways may "shift" even between species. These shifts in position and termination may be correlated with phylogenetic age of the pathway. The phylogenetically new corticospinal pathway is found in just about every conceivable position in the spinal white matter of mammals, including the dorsal funiculus which usually contains only ascending fibers (Verhaart, 1970) and whose terminal fields are equally variable. Such shifts in the position and terminal field might be related to shifts in the position and orientation of the dendritic fields of target neurons.

(4) Even while retaining the same position and terminal field in the spinal cord, a pathway may differ by developing more collateral branches, more elaborate preterminal arborizations, and, consequently, a greater number of synaptic boutons. Thus the rubrospinal pathway, thought to be phylogenetically new in reptiles, has, in lizards, a terminal field less dense, relative to other pathways, than in mammals. On the other hand, the phylogenetically old reticulospinal pathways have much more intense terminal fields in the contralateral relative to the ipsilateral medial spinal gray of lizards than they do in mammals. The differences in these terminal fields may be related, functionally, to the particular uses of axial rather than limb musculature in lizards and thus they may not hold for other reptilian species.

In summary, differences such as the presence or absence of a major descending pathway when comparing vertebrate classes are not as instructive as the differences in how a given species employs the motor systems which it has to use in order to cope with its environment. Fine morphological differences in the spinal cord, such as position and orientation of the dendritic tree of target neurons and the number and position of descending fiber boutons upon these dendrites, particularly when correlated with different physiological and behavioral capabilities, are likely to be fruitful avenues toward understanding how the nervous system works. Eventually such studies may lead to an understanding of how motor systems have evolved, but this understanding will require the collection of data from many more species than have currently been studied.

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A Working Concept of the Organization of the Anterior Dorsal Ventricular Ridge*

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SUMMARY. The anterior dorsal ventricular ridge (ADVR) is a large, subcortical structure which is present in the brains of all reptiles and birds. It is a major destination of ascending sensory systems (Northcutt, 1978) and is, therefore, likely to be involved in determining important aspects of the behavior of these organisms. This contribution summarizes a series of investigations which I have conducted on the ADVR of snakes with a variety of neuroanatomical techniques. Each technique provides a different piece of information about the neurons present in the structure. Together, they provide the first concept of the organization of snake ADVR.

THE NEURONS PRESENT IN SNAKE ADVR

Figure 1 shows a transverse section through the brain of a water snake (*Natrix sipedon*). The inset is a sketch of a water snake brain indicating the plane of the section which appears in the main part of the figure. The ADVR is a large structure lying inside the lateral ventricle and separated from the subjacent striatum (ST) by a thin, but distinct, cell-poor area. Neurons are distributed fairly homogeneously throughout the ADVR. This snake (and probably most snakes) thus resembles the lizards designated Type II by Northcutt (1978) on the basis of ADVR structure. Figure 2 shows a sector of ADVR depicted at a higher magnification. There are subtle, important differences in the *distribution* of these neurons which permit division of snake ADVR into four zones lying concentric with the ventricle. These zones are labeled A through D, and each contains a characteristic population of neurons.

Zone A neurons (Fig. 3) are embedded in the ependyma. Their dendrites extend through the 30μ width of the cell-poor zone A and into the subjacent zone B. Some of the cells have a fairly heavy covering of dendritic spines while others bear only a few spines. Nothing is known about the axons of zone A neurons.

Zone B neurons (Fig. 4) tend to form clusters of up to six or seven neurons which have their somatic membranes closely apposed. The areas of contact are interrupted by membrane specializations which involve a thickening of the plasma membranes for about 0.25μ and an electron lucent intercellular gap of about 50 Å (Ulinski, 1976*a*). Since the specializations generally resemble gap junctions, it is tempting to speculate that these cell clusters are multicellular units of electrotonically coupled neurons. Similar clusters are present in the ADVR in many lizards (Northcutt, 1978) and birds (Saini and Lepellsack, 1977). Zone B neurons have dendrites which extend in all directions, forming roughly spherical dendritic trees and bearing a heavy cover of dendritic spines. Their axons typically course radially into zone A where they form branches which follow the curvature of the ventricle for long distances. A few of the neurons send axons centrally into zone C.

Zone C neurons (Fig. 5) tend to occur in isolation. Although clusters of touching neurons occasionally do occur, they involve only a few neurons. They have dendritic trees

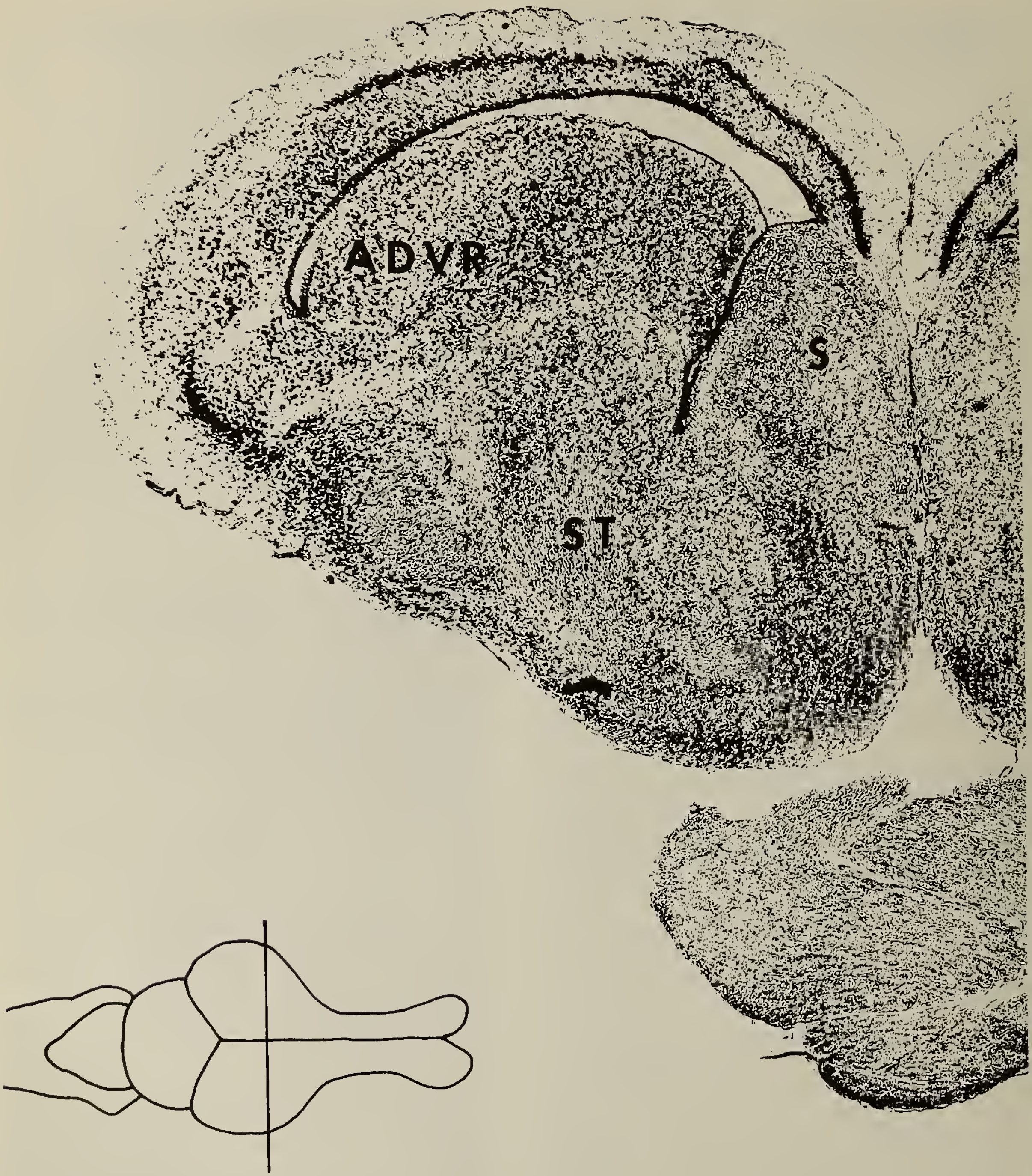

Figure 1. A transverse section through the brain of a water snake *(Natrix sipedon)* is shown in a Nissl preparation. The inset is a sketch of a water snake brain in dorsal view. The line indicates the level of the section which appears in the main part of the figure. The laminated cortex lies above the lateral ventricle. The septum (S) and anterior dorsal ventricular ridge (ADVR) lie beneath the ventricle. ADVR is separated from the subjacent striatum (ST) by a cell-poor area.

similar to those of zone B neurons; however, the dendrites bear only a few dendritic spines. Their axons extend away from the somata in all directions and ramify extensively, but they never reach more than about 300μ from the somata. The projections of neurons in zones A, B, and C, thus, are entirely intrinsic to the ADVR. Zone D neurons (Fig. 5) lie near the ventral border of ADVR. They closely resemble the neurons in zone C, except that some zone D neurons have axons which course ventrally out of ADVR and into the subjacent striatum. Zone D neurons are, thus, the only neurons in the ADVR known to have extrinsic projections.

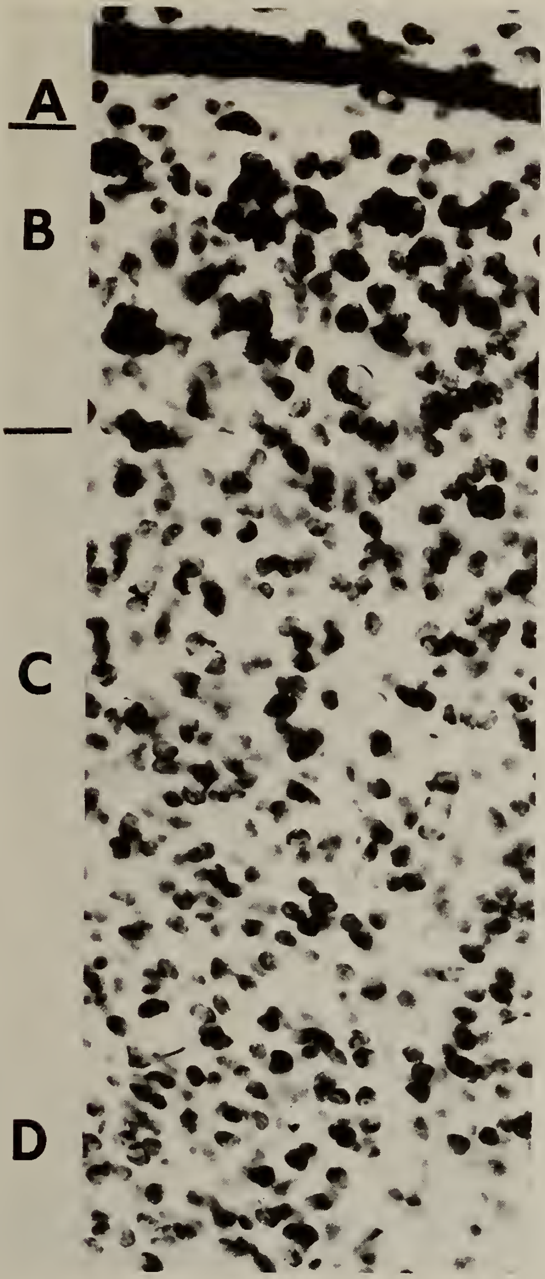

Figure 2. A higher magnification view of a sector of ADVR. The lower boundary of cortex is at the top of the figure. The ependymal surfaces of cortex and ADVR are apposed. Notice that neurons throughout ADVR are cytologically similar. However, there are differences in their distribution which permit the definition of zones A, B, C, and D. The approximate boundaries of these zones are indicated to the left of the figure. Zone A is cell poor and contains a few neurons which are embedded in the ependyma. Zone B contains clusters of touching neurons. Zones C and D contain primarily isolated neurons. The distinction between zones C and D is based on axonal morphology and cannot be made in Nissl preparations.

EFFERENT PROJECTIONS OF ADVR

It is impossible to trace the axons of zone D neurons to their terminations in Golgi preparations. Lesions were, therefore, placed in the ADVR in a number of snakes and the degeneration revealed by a Fink-Heimer stain. Selected sections through one of these cases are shown in Figure 6. Degeneration products circumscribe the lesion involving neurons in zones A, B, and C. Degenerated axons can be followed ventrally into the striatum due to the involvement of zone D neurons. Terminal degeneration is localized in three striatal structures, called the medial striatal nucleus (MS), the intrapeduncular nucleus (IP), and the perifascicular complex (PF). Degeneration products also continue caudally into the ventral part of the posterior dorsal ventricular ridge (PDVR) of Senn and Northcutt (1973). The efferent projections of snake ADVR are, thus, confined entirely to the telencephalon. Any effect that ADVR might have on the brainstem must be executed through intervening structures.

SYSTEMS AFFERENT TO ADVR

Two types of axons can be traced from the lateral forebrain bundle into the ADVR in

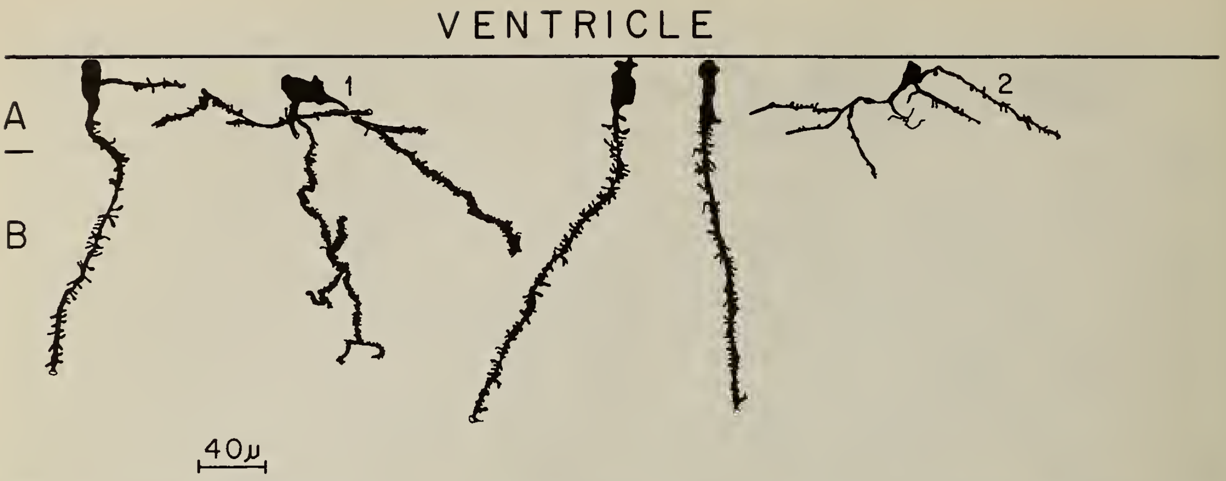

Figure 3. Zone A neurons (1 and 2) are shown as they appear in rapid Golgi preparations. Their dendrites extend down into zone B. Several ependymal cells are also shown. These bear long processes which extend radially through ADVR. Only the proximal shafts of these processes are shown.

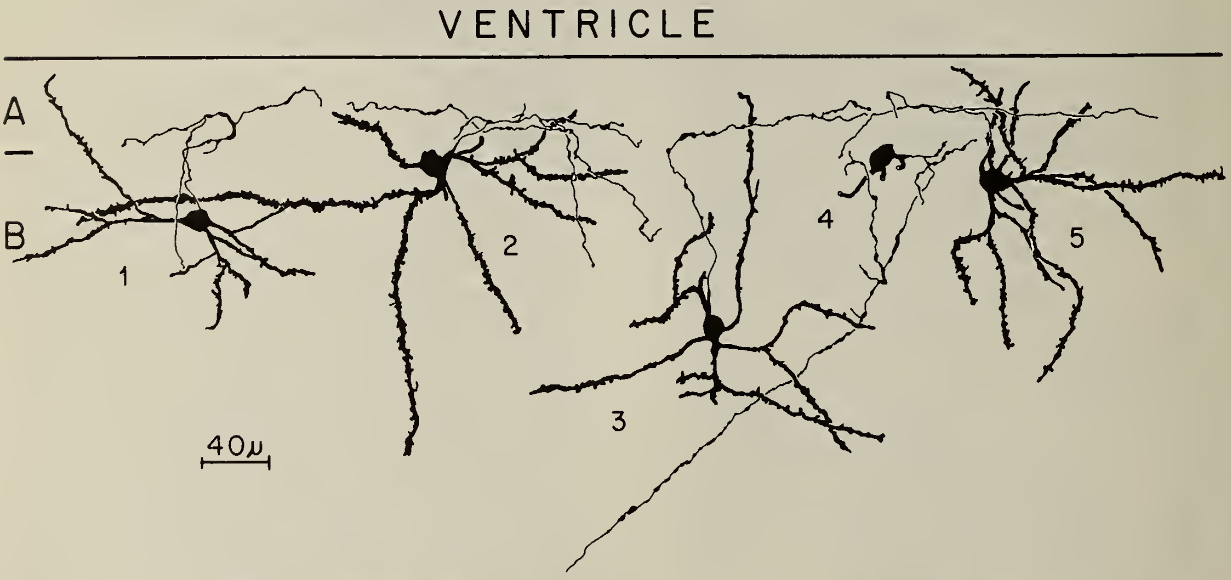

Figure 4. Zone B neurons are shown as they appear in rapid Golgi preparations. Their dendrites extend into both zones A and B bearing a high density of dendritic spines. Their axons extend primarily into zone A where they ramify concentric with the ventricle. A few zone B neurons (neuron 4) send their axons into zone C.

Golgi preparations (Fig. 7). Type 1 axons are about 2μ in caliber and proceed rectilinearly into ADVR, bearing thin collaterals which have small varicosities about 3μ long. They are confined principally to zones C and D. Type 3 axons are thin throughout their course and bear small varicosities. They extend radially through zones C and D and turn to run concentric with the ventricle in zone B. Figure 8 shows a zone B neuron intersecting the trajectories of many type 3 axons. They are positioned so that an individual fiber can contact several dendrites on the same neuron and then continue on to affect many other zone B neurons. Type 2 axons can also be defined; they are the axons of zone B neurons (Ulinski, 1976*a*).

Some information about the origins of type

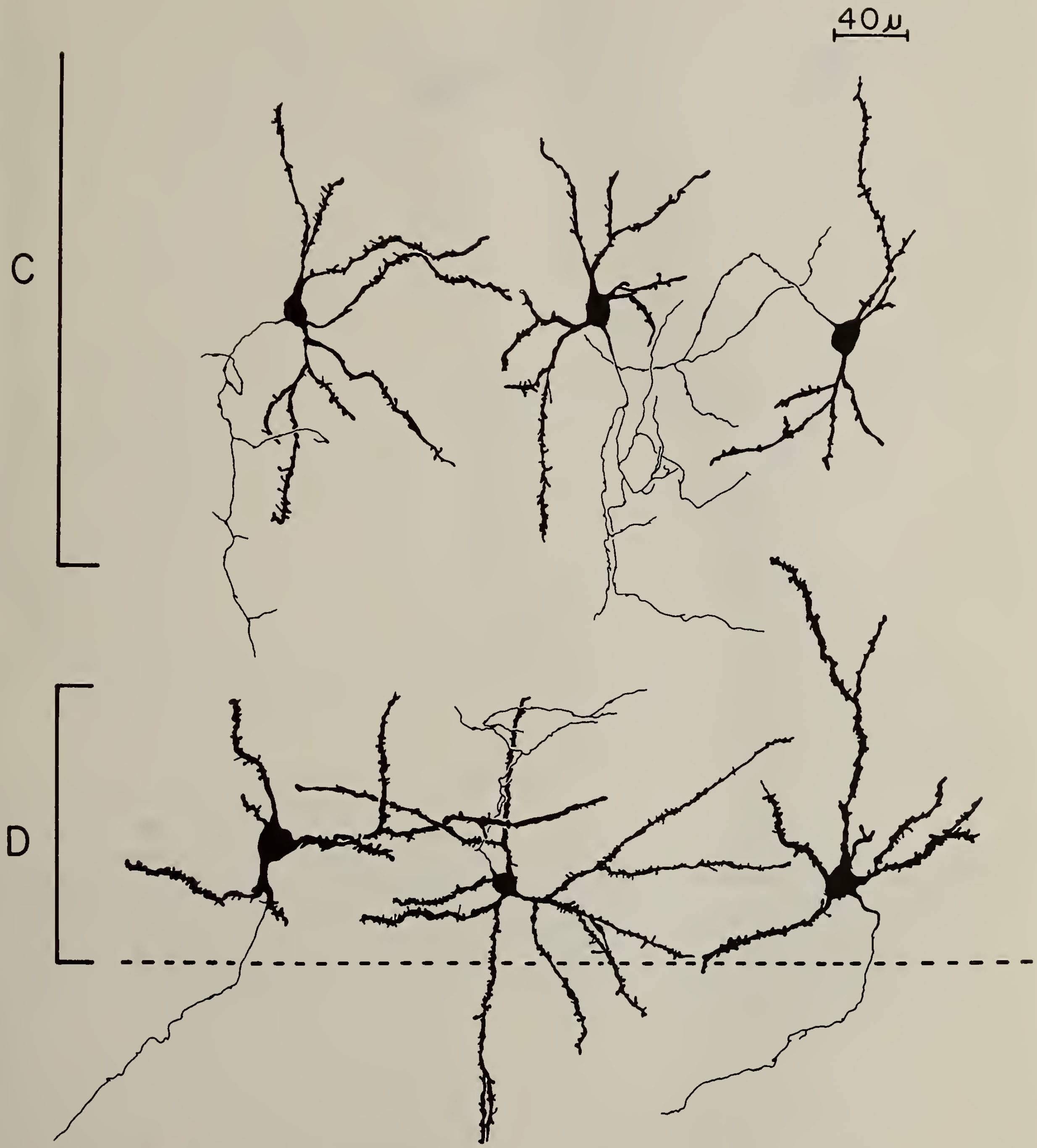

Figure 5. Zone C and zone D neurons are shown as they appear in rapid Golgi preparations. Both populations of neurons have a low density of dendritic spines. Zone C neurons have axons which ramify in all directions but remain within ADVR. Zone D neurons have axons which either proceed radially into zone C or course ventrally across the border of ADVR (dotted line) into the striatum.

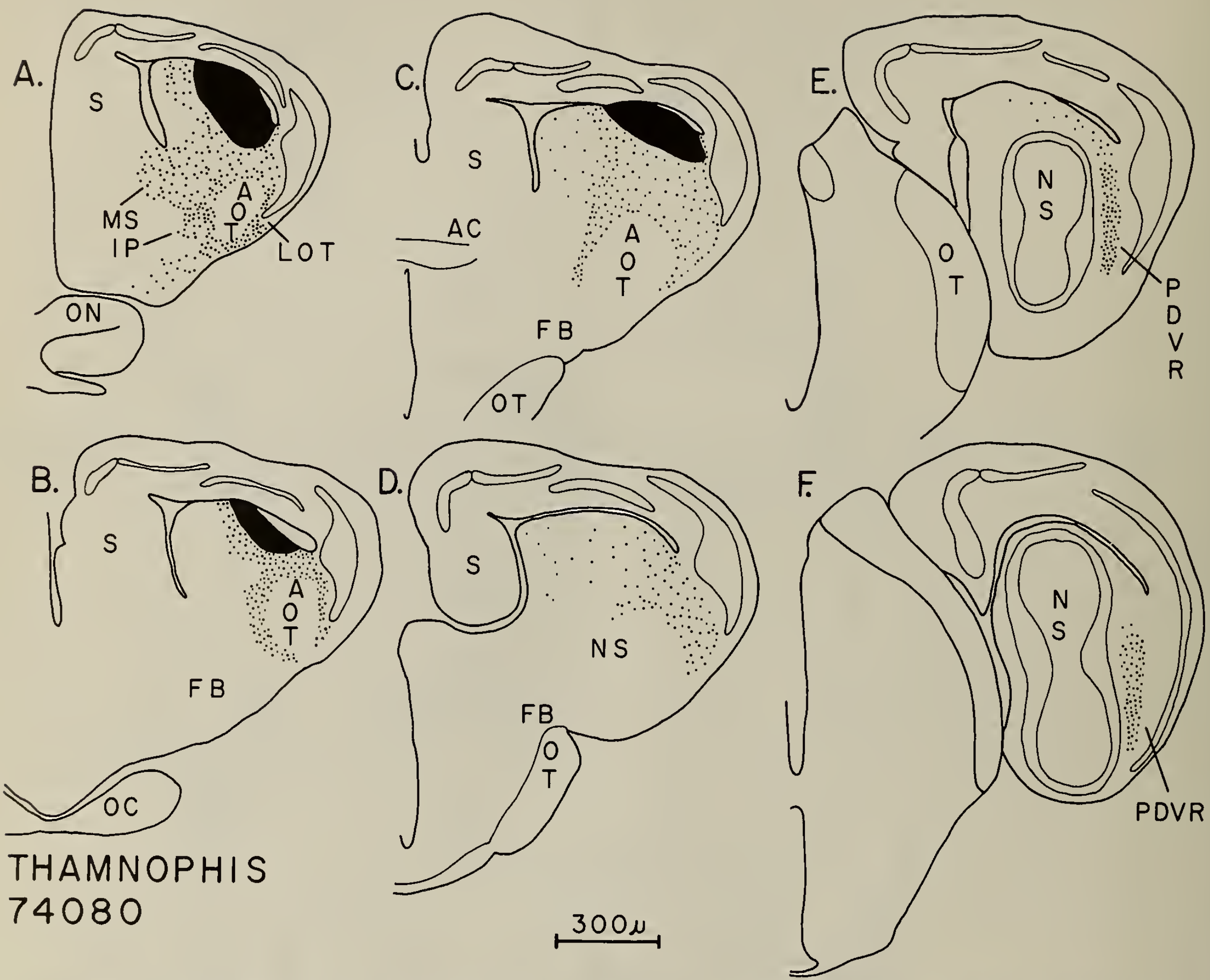

Figure 6. Sections through the forebrain of a garter snake which underwent a stereotaxic lesion of ADVR. The brain was subsequently treated by a Fink-Heimer procedure. Section A is the most rostral. Cortical damage is not shown because other studies (Ulinski, 1976*b*) indicated that cortex does not project to either ADVR or the striatum. The extent of the lesion is shown by the black area. Degeneration is shown by dots. Abbreviations: AC, anterior commissure; AOT, accessory olfactory tract; FB, forebrain bundles; IP intrapeduncular nucleus; LOT, lateral olfactory tract; MS, medial striatal nucleus; NS, nucleus sphericus; OC, optic chiasm; ON, optic nerve; OT, optic tract, PDVR, posterior dorsal ventricular ridge; S, septum.

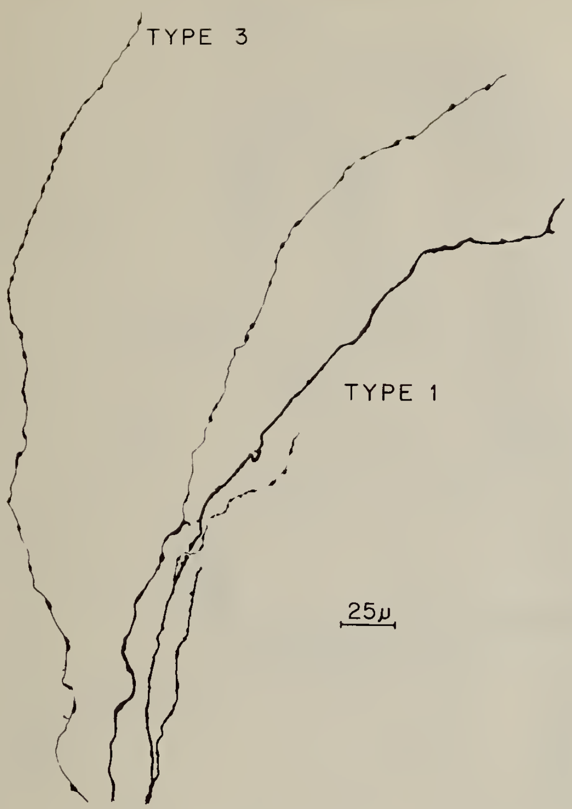

Figure 7. Two types of axons which can be traced from the lateral forebrain bundle into ADVR in rapid Golgi preparations. They are described in the text.

1 and type 3 axons can be obtained using degeneration techniques. Figure 9 shows a system of degenerated axons which runs rostrally in the forebrain bundles following a unilateral transection of the midbrain. They extend into the ADVR in two fascicles, one runs behind the anterior commissure (PCF) and one turns dorsad rostral to the commissure. These axons are about 2μ in caliber and course rectilinearly into zones C and D. Comparable but less dense projections go to ADVR contralateral to the lesion. These experiments suggest that type 1 axons originate somewhere in the brainstem caudal to the diencephalon, but their precise origin is not known.

Figure 10 shows sections from a snake which had a stereotaxic lesion of the thalamus. Lesions of this type and control lesions of surrounding structures demonstrate that cells in the caudal part of the dorsal thalmus project by way of the lateral forebrain bundle to the rostral part of the ipsilateral ADVR. The axons are of thin caliber and bear small varicosities. They are distributed throughout zones B, C, and D. The area of the thalamus involved in the lesions includes the nucleus lentiformis thalami, which receives auditory projections from the posterior colliculi (Ulinski, 1977*a*), and the central thalamus, which receives visual information from the optic tectum (Ulinski, 1977*b*). ADVR in snakes, thus, receives thalamic sensory projections comparable to those demonstrated in birds and other reptiles (Karten, 1968; Karten and Hodos, 1970; Hall and Ebner, 1970; Pritz, 1974, 1975). These thalamic afferents are type 3 axons.

ORGANIZATION OF ADVR

Figure 11 summarizes my current concept of the organization of the snake ADVR. Four populations of neurons are present, arranged in concentric zones. Each population has characteristic connections. As far as is known, zone A neurons are influenced primarily by the axons of zone B neurons. Zone B neurons form multicellular units which are strongly influenced by type 3 axons, including those of thalamic auditory and visual nuclei. These axons are arranged so that they influence neurons throughout large regions of zone B. Zone C and zone D neurons are strongly influenced by type 1 and type 3 axons coursing radially. Neurons in each zone interact with neurons in adjacent zones. Finally, zone D neurons project to the striatum and to PDVR. One virtue of this scheme is that it provides an orderly approach for conducting further experiments on the anatomy and functions of ADVR.

ACKNOWLEDGMENT

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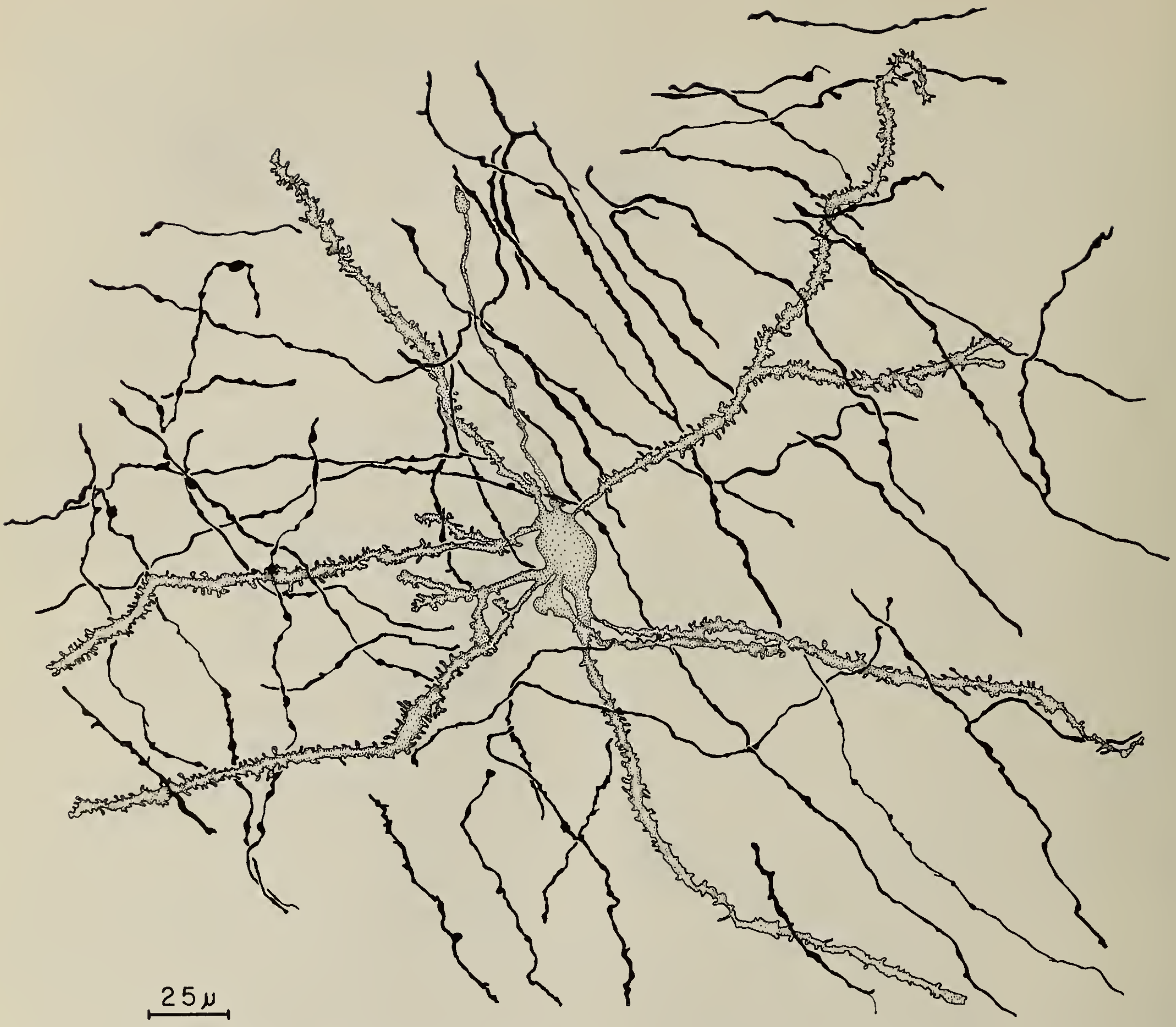

Figure 8. A zone B neuron lies embedded in type 3 axons in a rapid Golgi preparation. Notice that axons intersect the dendrites at nearly right angles. An individual axon can, therefore, intersect several dendrites of the same neuron or those of many adjacent zone B neurons.

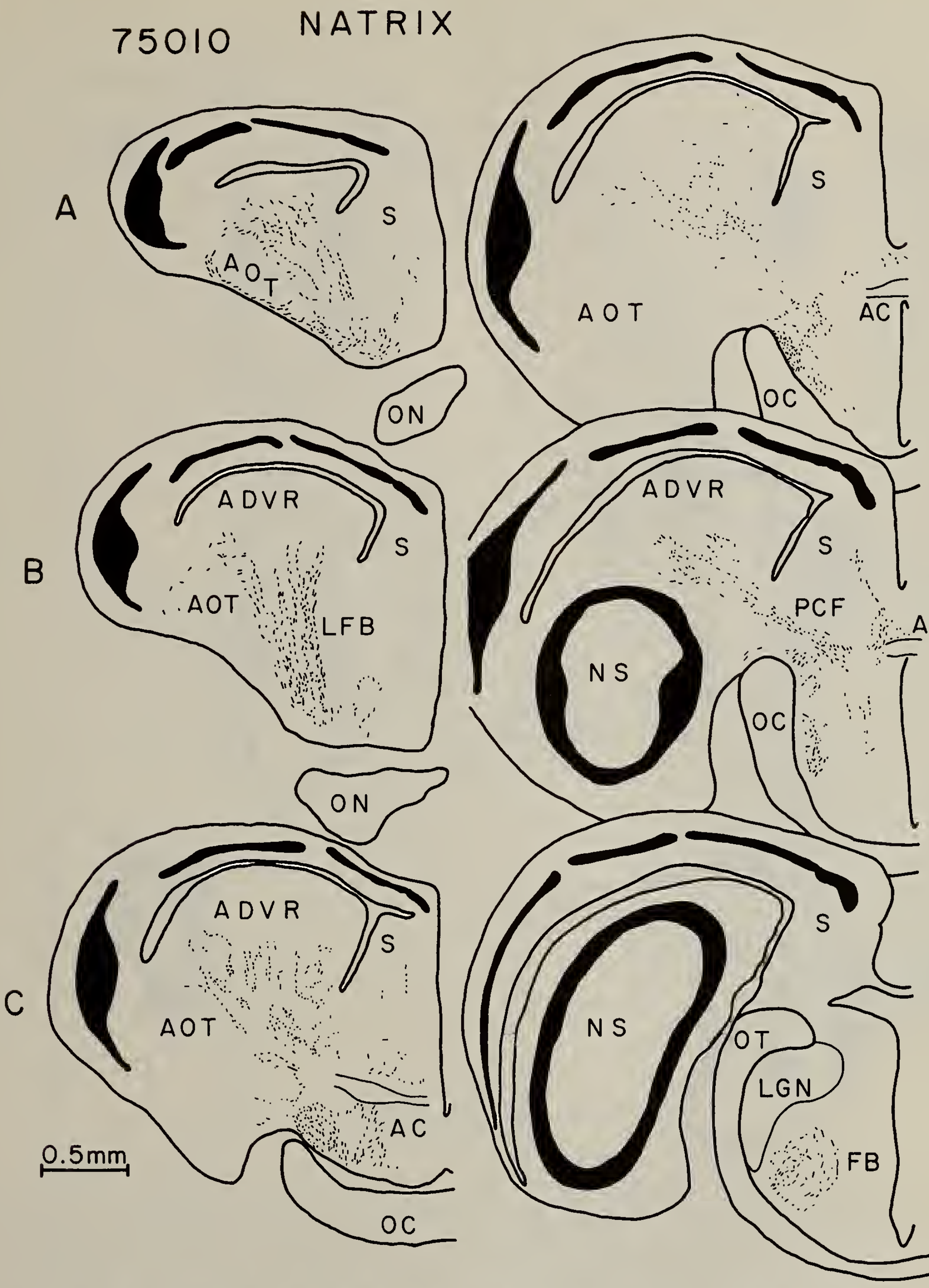

Figure 9. Sections through the brain of a water snake which underwent a unilateral transection of the midbrain. The brain was subsequently prepared by a Fink-Heimer procedure. Degenerated axons run rostrally through the forebrain bundles (FB) and extend into both caudal and rostral ADVR. A comparable but less dense projection to the contralateral side of the brain is not shown. Abbreviations: AC, anterior commissure; ADVR, anterior dorsal ventricular ridge; AOT, accessory olfactory tract; FB, forebrain bundles; LFB, lateral forebrain bundle; LGN, dorsal lateral geniculate nucleus; NS, nucleus sphericus; OC, optic chiasm; ON, optic nerve; OT, optic tract; S, septum.

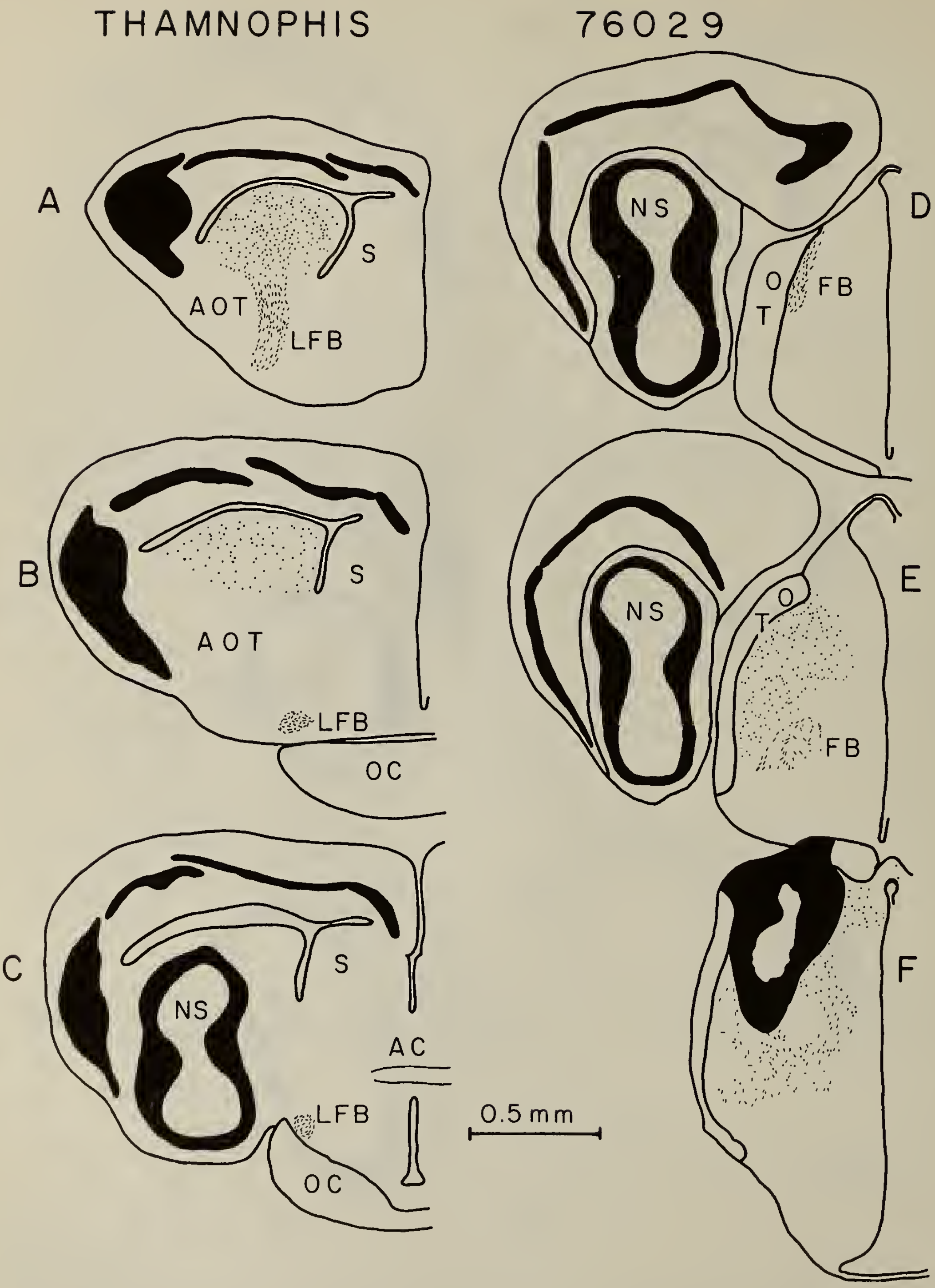

Figure 10. Sections through the brain of a garter snake which underwent a stereotaxic lesion of the dorsal thalamus. The brain was subsequently prepared by a Fink-Heimer procedure. Section A is the most rostral. The extent of the lesion is shown by black in section F. Degenerated axons can be followed rostrally through the lateral forebrain bundle (LFB) into rostral ADVR. Abbreviations: AOT, accessory olfactory tract, AC, anterior commissure; FB, forebrain bundles; LFB, lateral forebrain bundle; OC, optic chiasm; NS, nucleus sphericus; S, septum.

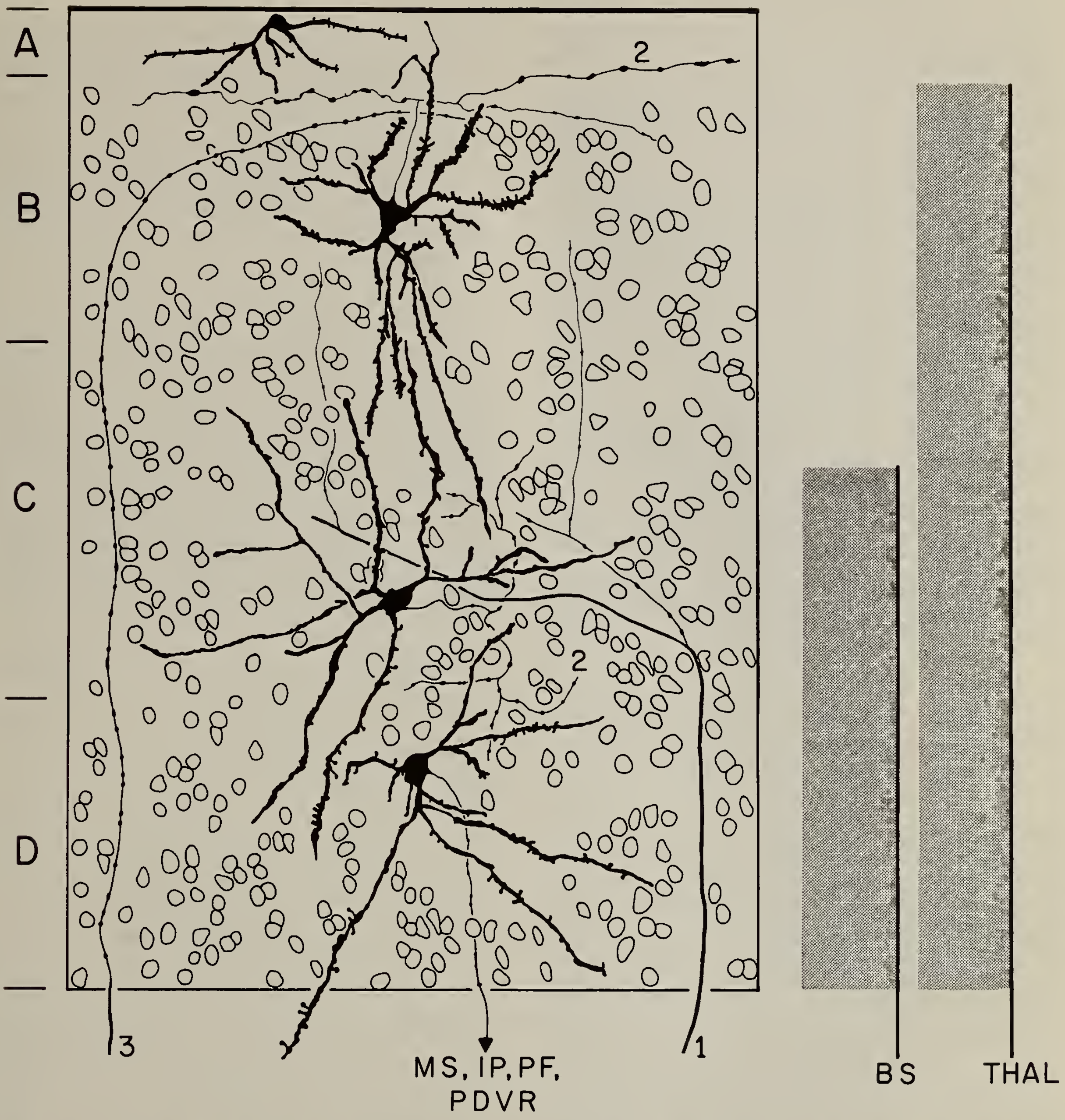

Figure 11. Current concept of the organization of snake ADVR. A sector of ADVR similar to that shown in Figure 2 is depicted diagramatically. The boundaries of ADVR zones are shown on the left. The somata of ADVR neurons as they appear in Nissl preparations are shown by open profiles. Neurons representative of those present in each zone are depicted as they appear in Golgi preparations. Type 1 and type 3 axons are shown as they appear in Golgi preparations. The axon of a zone D neuron is depicted crossing the ventral border of ADVR. Lesions which involve these neurons produce degeneration in the medial striatal nucleus (MS), intrapeduncular nucleus (IP), perifascicular complex (PF), and posterior dorsal ventricular ridge (PDVR). The distribution of degeneration following lesions of the brainstem (BS) and thalamus (THAL) are shown by the stippled bars on the right.

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*In planning the Colloquium, it was disappointing that there was no recent experimental neuroanatomical work on the projections of the dorsal ventricular ridge and the paleostriatum in the lizard. To make up in part for this deficit, we afterwards asked Philip S. Ulinski if he would write a brief account of his study on the cytoarchitecture of the anterior dorsal ventricular ridge (ADVR) in the snake and the significant finding (since borne out by P.D. Hoogland's work on the lizard, J. Morph. 152:229–246, 1977) that ADVR does not project below the level of the paleostraitum. We wish to express our thanks to him for this contribution.

DISCUSSION

PARTICIPANT to BUTLER: Since the medial portion of dorsal cortex has descending connections to the hypothalamus via the medial forebrain bundle (Lohman and Mentink, 1972), would that field not be more like cingulate cortex in mammals?

BUTLER: It does proect to the hypothalamus and certainly resembles mammalian limbic cortex in this regard. At the same time, in turtles this same topographical area has been shown to be the target of the dorsal lateral geniculate nucleus (Hall and Ebner, 1970).

MacLEAN: We have shown with microelectrode and anatomical studies that the posterior part of the parahippocampal gyrus, not the entorhinal area, receives some visual input, which appears to be direct.

PETERSON: We have animals with lesions identical to your cortical ones, which show severe behavioral deficits on successive reversals, which is a classic limbic deficit.

BUTLER: One of the problems here is whether or not the entire dorsal cortex is limbic, and it may well be. On the other hand, if the visual retino-thalamo-telencephalic pathway in reptiles is homologous to the geniculostriate system in mammals, then part of the reptilian dorsal pallium is *also* neocortical in nature. We may well be dealing with a field homology, such that the dorsal pallium in reptiles is homologous as a field to both cingulum and striate cortex in mammals. Thus, the question of the origin of the corpus callosum enters here. In the turtle *Podocnemis* (Ware, 1974), there are massive DVR–DVR connections via the anterior commissure; in contrast, these have not been found in the turtle *Pseudemys* (J. Hall, personal communication), nor in *Gekko.*

NORTHCUTT: In *Podocnemis,* however, we don't yet know which areas in the rostral telencephalon correspond to the dorsal cortex and dorsal ventricular ridge in other reptiles, due to the hypertrophy of cell groups there. We are dealing with the problem that if the two cerebral hemispheres are going to talk to each other, they must do so by means of commissural systems which can develop in the lamina terminalis embryologically, or descend to sites such as hypothalamus or tectum, cross there, and turn rostrally again. We need to know how many fiber systems there are in the lamina terminalis.

RAND: When you speak of teids, do you mean both macro and microteids?

NORTHCUTT: The micro- and macroteids are very different. The telencephalon of microteids look like that of lacertids, whereas the pretectum and tectum look like those structures in varanids. Parts of the microteid visual system are obviously well developed, but the DVR is not. It looks like the DVR in *Sphenodon* or in the gekkonids. If the CNS of microteids were primitive, then the derived condition of the CNS in macroteids would have to be considered a case of parallel evolution with varanids. However, microteid chromosomal studies suggest that microteids are advanced members of the teid radiation. Thus I suspect that the microteid DVR is secondarily simple due to their fossorial niche.

W. CRUCE: The Type I DVR of *Sphenodon* seems to be more complex in terms of having a corticoid plate. Would you comment on how you define the type II as being more complex?

NORTHCUTT: The DVR of *Sphenodon* consists of a single plate of cells with multiple apical dendrites, and what little Golgi information we possess suggests that there is a single cell type. The SDH distribution within DVR suggests that the thalamic input is restricted to the outer dendritic segments of the plate neurons. This pattern is similar to the pallial pattern in amphibians and primitive fishes such as *Polypterus*, and, therefore, I suspect it is close to the primitive pattern for reptiles. The Type II pattern can be derived from such a simple plate by migration and differentiation of the corticoid plate.

MacLEAN: Why downgrade neocortex by calling it DVR? Why not just be content with something like corticoid? That is the oddest neocortex I have ever seen!

NORTHCUTT: Homology is an issue here. If you define isocortex (neocortex) as a laminated structure, then I agree it is restricted to the mammalian grade. However, if we talk about the identity of cell populations, and we say that DVR and isocortex are homologous, then we are saying that we believe that these cell populations in reptiles and mammals can be traced back to a population or populations in ancestral reptiles or amphibians. These populations need not have identical connections or functions to be homologous.

QUESTION: What criteria do you use: what boundaries are you using to distinguish between phylogenetic similarity and convergence?

NORTHCUTT: If I thought DVR were a single modality unit—that is, a target of a single visual projection—then I would very much suspect parallelism. If what we are looking at were optic tectum to rotundus to DVR, then I could believe that the agamids, the varanids, and one group of teids independently hypertrophied the DVR, and I would argue parallel evolution. All I would have to argue is that these three groups came under similar selective pressues for that particular visual pathway—whatever it might be—independently; I have considered that as a possibility. I do not believe this happened, however, because DVR is not *just* a visual target. There is a visual target, an auditory target, a somesthetic target, and a motor area within DVR. What I am really saying is that we have two choices: Three separate radiations independently evolved complex brains with similarities in some 30 neural populations encompassing several different sensory modalities; *or* this complex pattern evolved only once.

Behavior and Neurology of Lizards
N. Greenberg and P. D. MacLean, eds.
NIMH, 1977.

Behavioral Responses to the Electrical Stimulation of the Brain in the Green Iguana.

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Max-Planck-Institut für Psychiatrie

In order to identify behavioral patterns and related brain areas amenable to more specific neurobehavioral investigations, the brains of 21 large green iguanas *(Iguana iguana* L.), 16 males and 5 females from Colombia, were explored with stimulating electrodes (Distel, 1976, in press).

The responses elicited by stimulation at 518 sites are presented in figures 1–5. The symbols in the figures indicate behavioral sequences elicited for a given range of stimulus intensities, rather than single behavioral units. Generally, the filled symbols indicate the occurrence of locomotion, whereas the open ones indicate the absence of locomotion. Two symbols were combined when responses changed and more than one sequence of responses occurred, e.g., an open diamond on top of a filled triangle means a change from a dewlap display to an escape response. Finally, circles around symbols indicate similar responses confirmed in different animals at equivalent stimulation sites.

Tongue-flicking responses were elicited fairly nonspecifically (for example after cessation of the stimulus). However, all stimulated areas which were part of the afferent olfactory system, such as the *tuberculum olfactorium* or the *nucleus sphericus,* yielded strong tongue-flicking responses, as did a region extending from the *nucleus accumbens* to the *hypothalamus,* and a more isolated area next to the *oculomotor nucleus.* Although tongue-flicking as a typical exploratory behavior is susceptible to generally arousing stimuli, its dependence on the olfactory structures is suggested by these results.

Eye-closing was generally preceded by *retreat* and *escape* responses and was, therefore, regarded as a pre-escape behavior. Eye closing and escape responses were elicited at stimulation sites throughout the brain, but eye-closing always occurred first and by lower stimulating intensities. This relationship and the simplicity of the response make eye-closing especially appropriate for further experimental study of avoidance behavior in the green iguana.

Violent flight responses developed abruptly and were preceded and followed by very little other behavior. They were elicited by stimulation at sites located in the *deep tectal layers,* throughout the *tegmentum,* and in the lateral *medulla oblongata.*

Dewlap (throat fan) *displays* were elicited by stimulation at many sites. They regularly preceded the *defensive displays* which were with few exceptions elicited only from sites in the *hypothalamus. Head-nodding displays* were seldom reliably elicited during stimulation and then only after long latencies. They occurred, however, immediately after stimulation ceased. Typically, when an aggressive animal is about to escape because of brain stimulation, and the stimulus is turned off at this moment, head-nodding display will occur. A functional relationship of the head-nodding display to displacement behavior is strongly suggested by these experiments.

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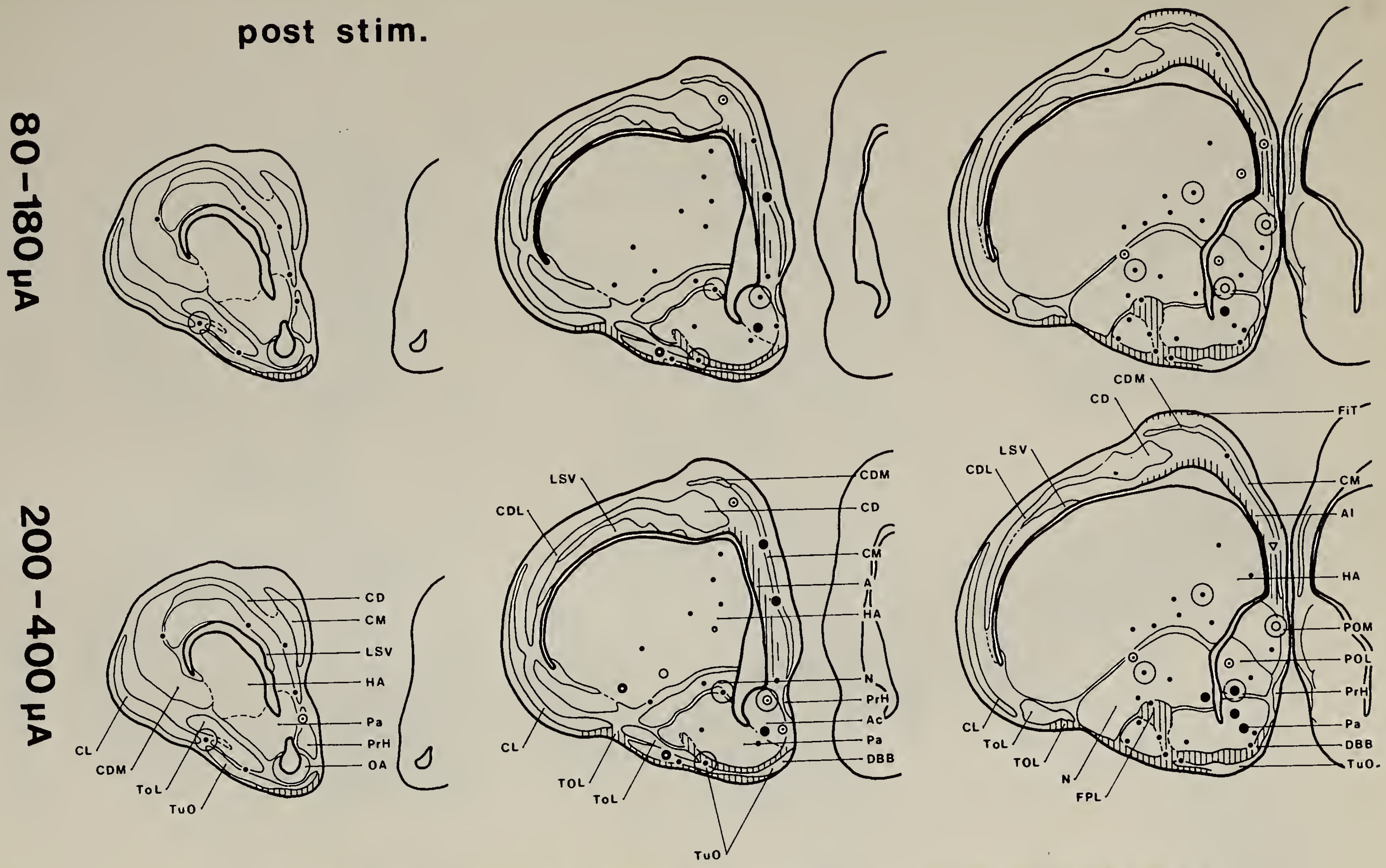
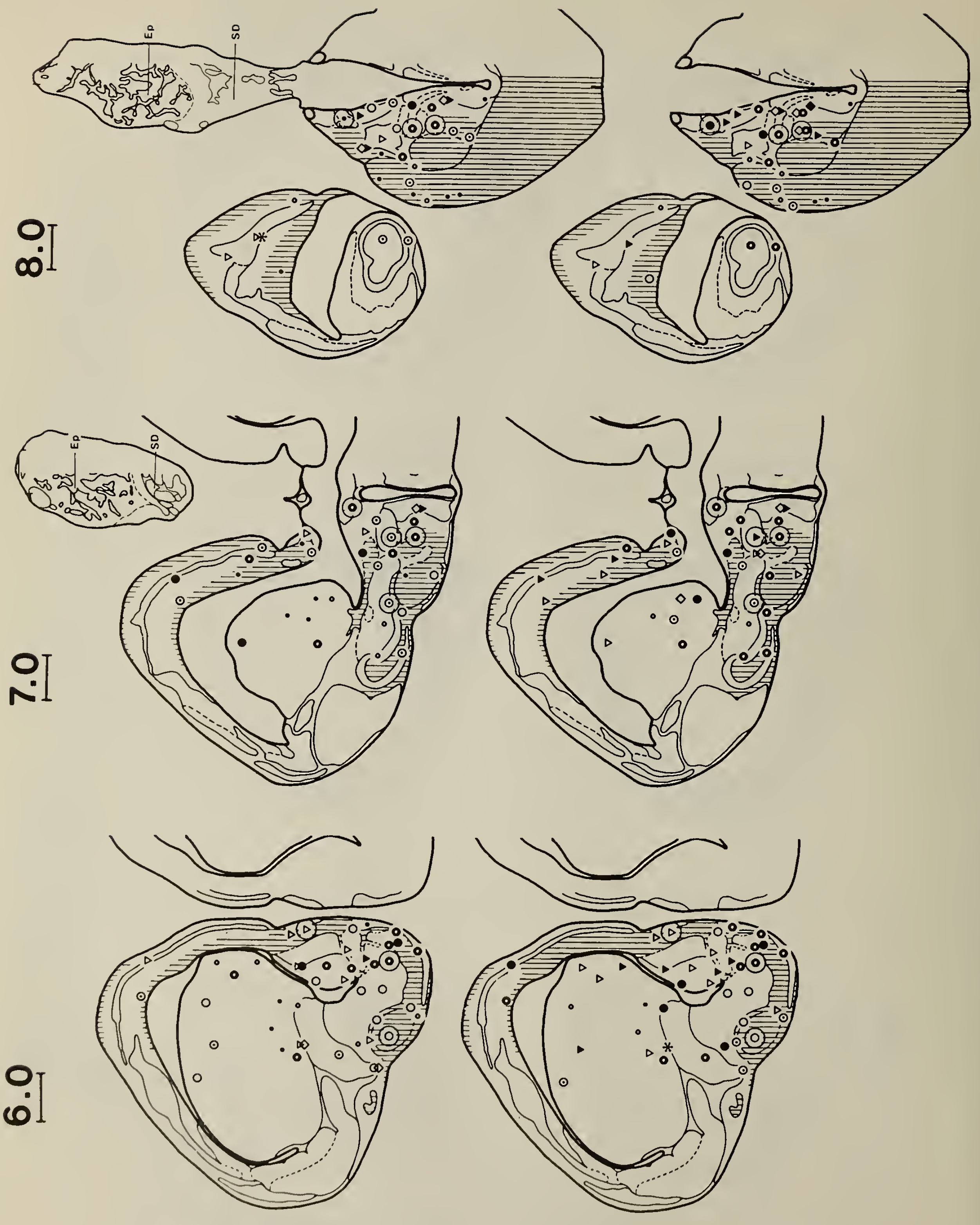
4.5
3.0
1.5
80-180 µA
200-400 µA



Figures 1–5. *Location of stimulation sites and variation of behavioral responses.* Stimulation sites are shown in schematically drawn transverse sections of the brain of iguana. Numbers underlined by a 1 mm calibration bar indicate distances in mm from the anterior tip of the brain. Ranges of stimulation intensities are given in μA. Responses during stimulation are presented on the top pages, post stimulus behavior on the bottom pages.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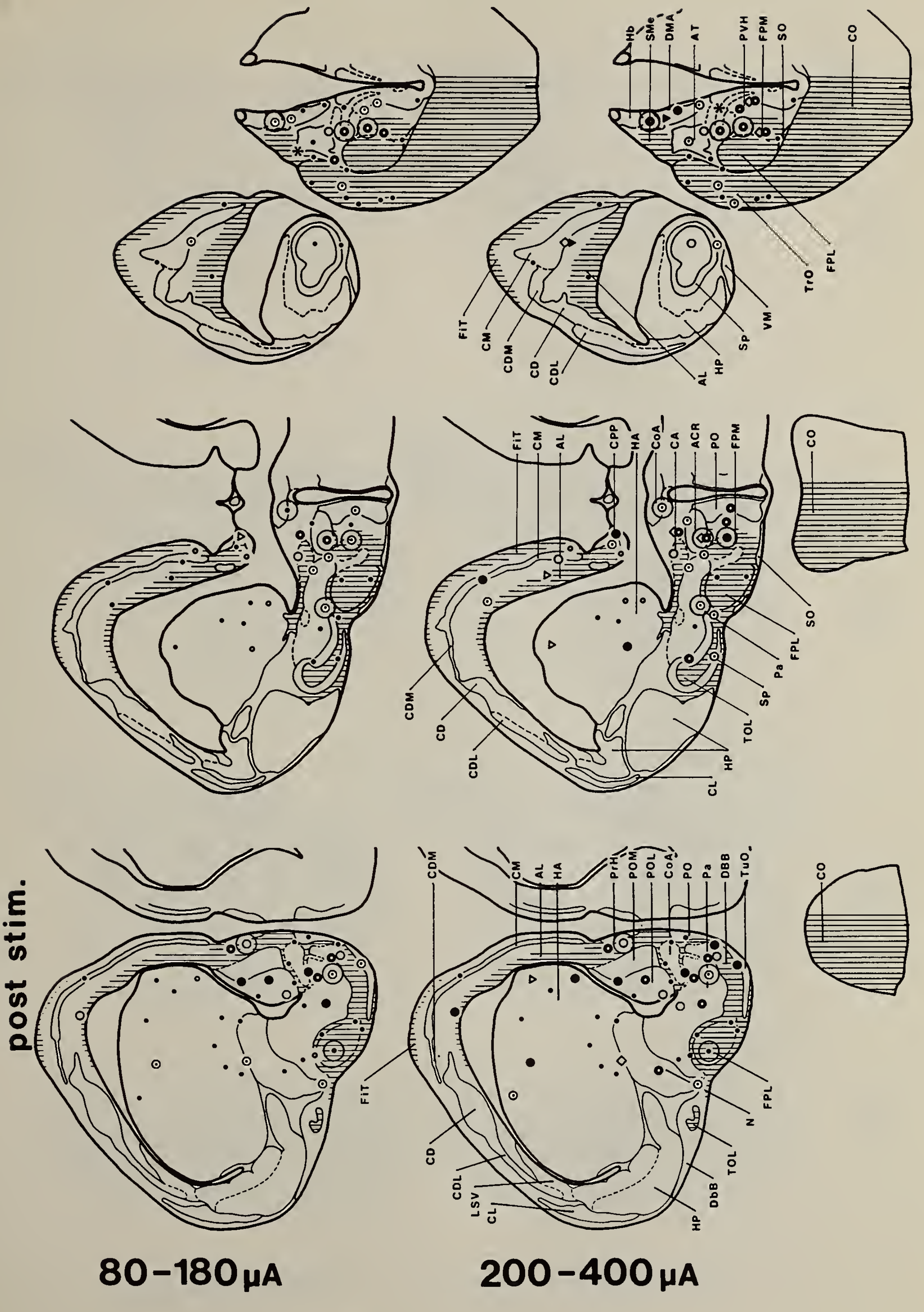
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CoA
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post stim.
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AL
HA
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POL
CoA
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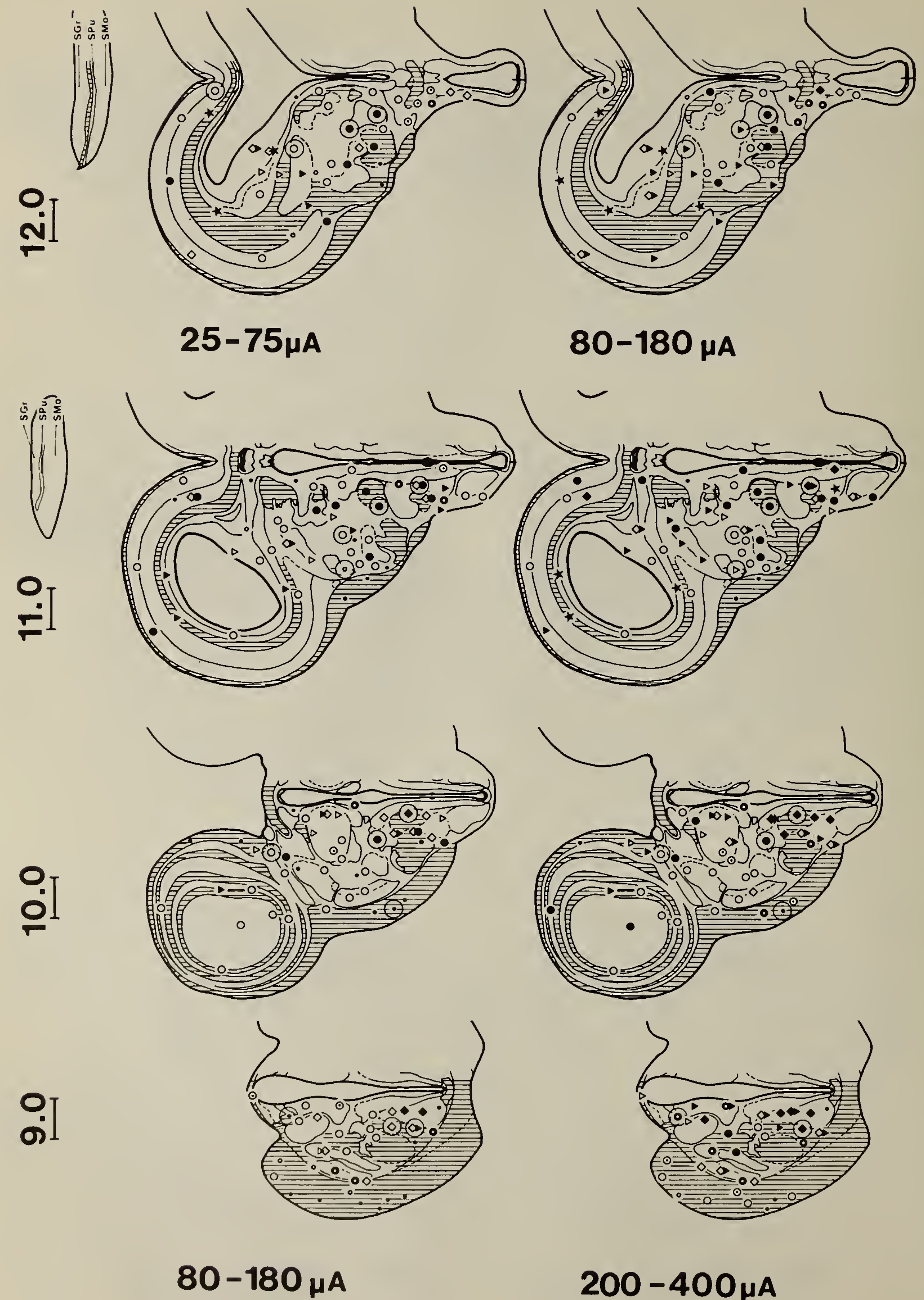
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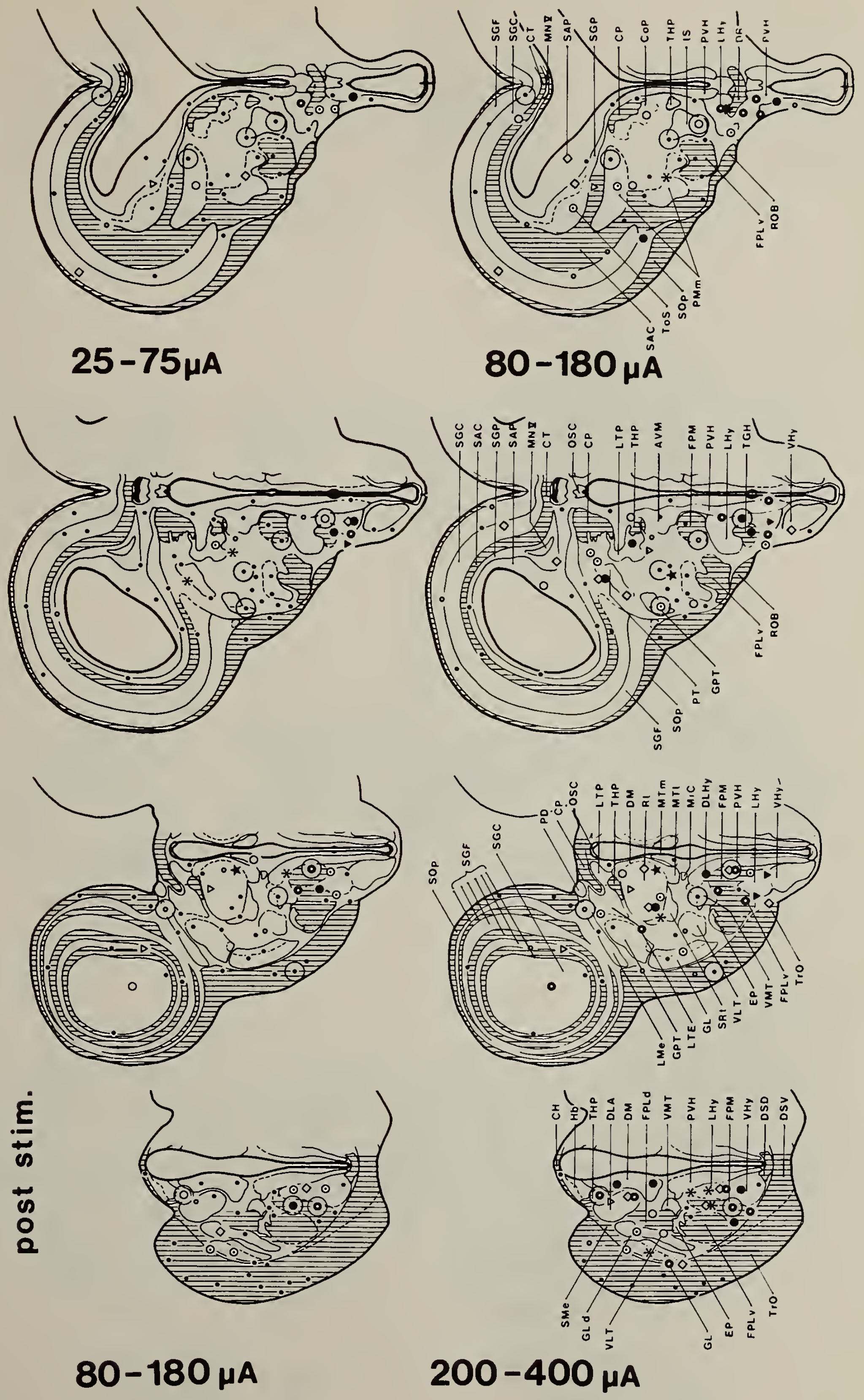
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VMT
EP
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SRI
GL
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GPT
LMe
post stim.
CH
Hb
THP
DLA
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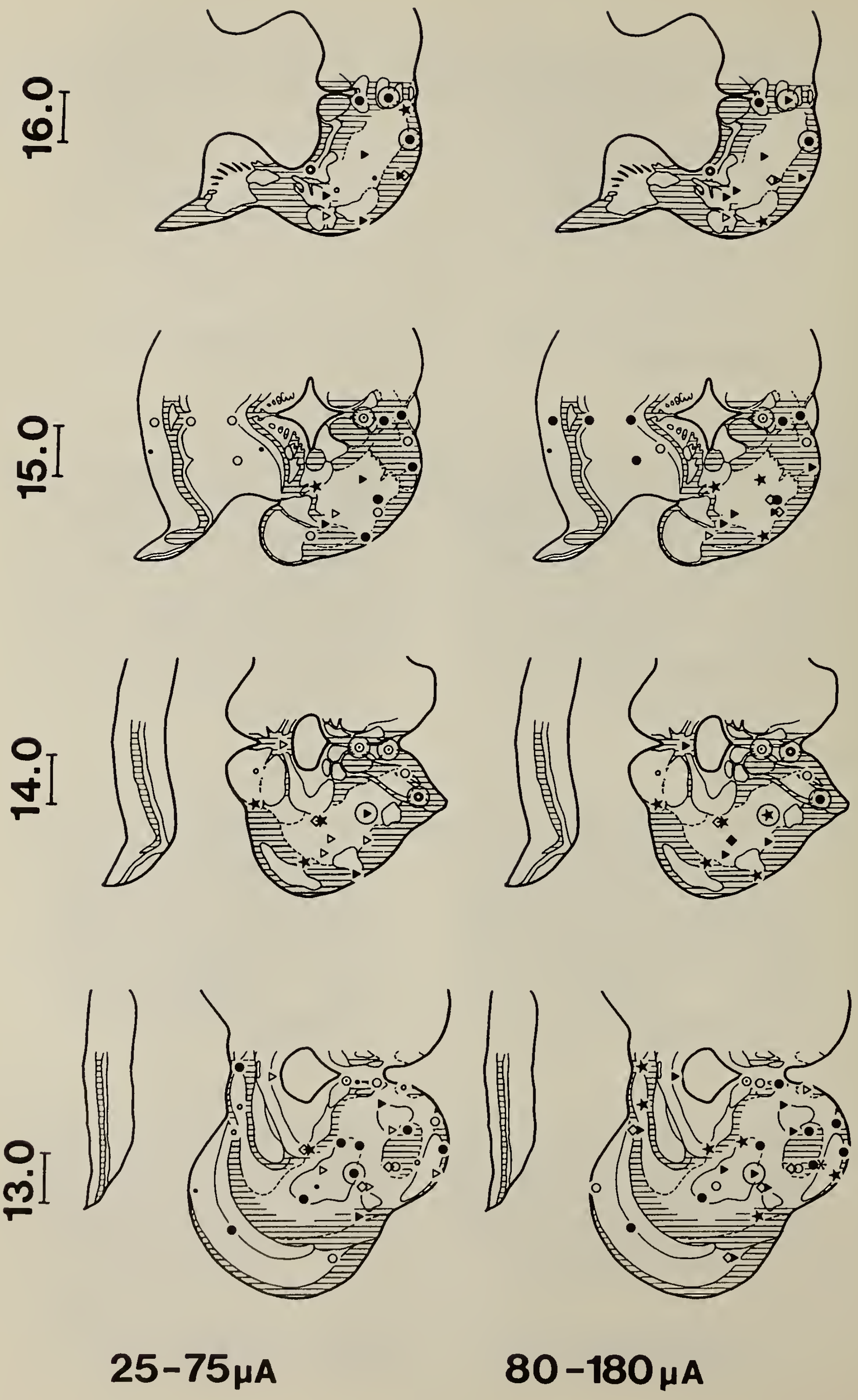
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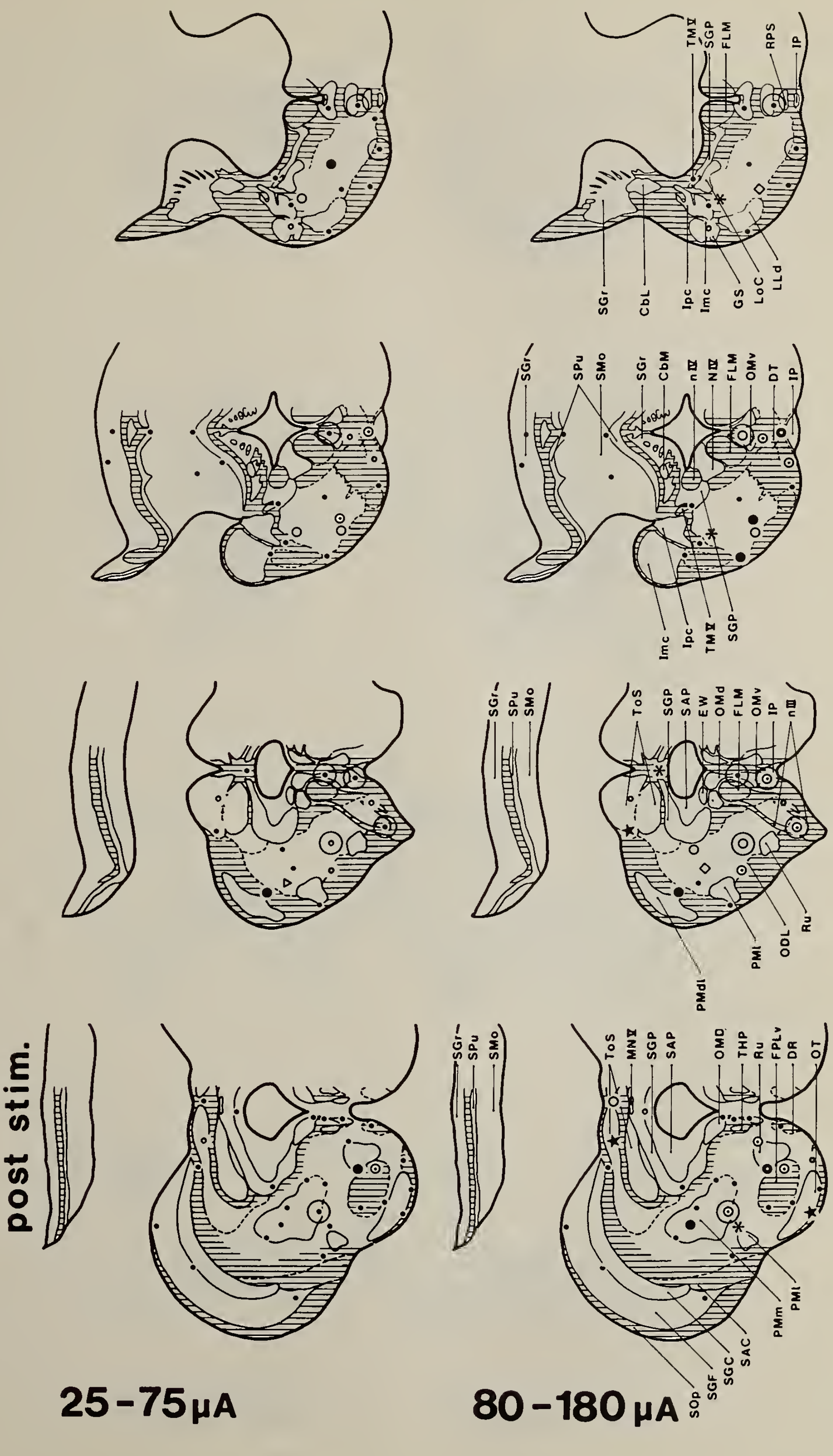
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IP
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SGr
SPu
SMo
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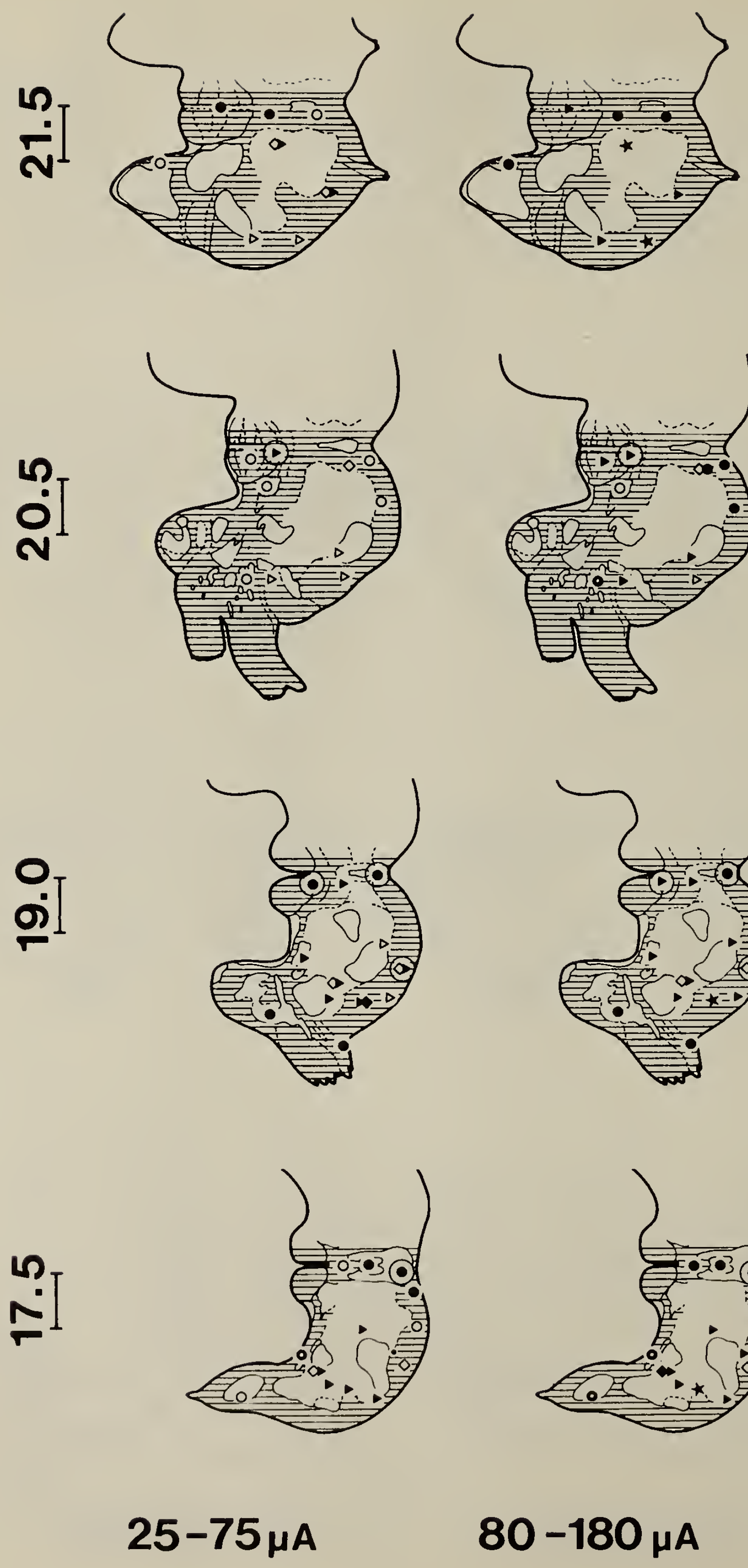
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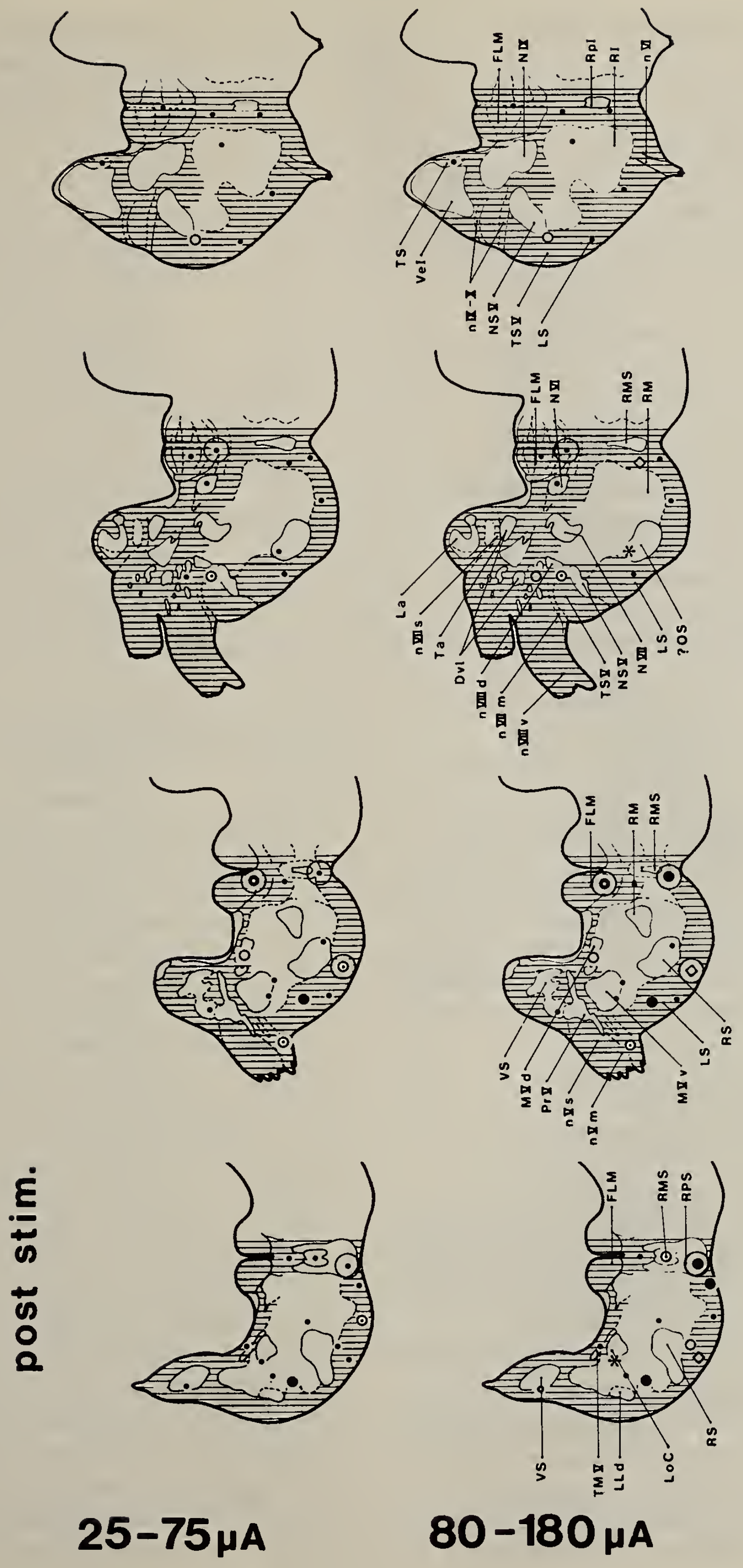

post stim.
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Dvl
nⅧd
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PrⅤ
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MⅤv
LS
RS
FLM
RM
RMS
VS
TMⅤ
LLd
LoC
RS
FLM
RMS
RPS

ABBREVIATIONS

Ac	nucleus accumbens
Al	alveus
AT	area triangularis
AVM	area ventromedialis thalami
CbM	nucleus cerebellaris medialis
CbL	nucleus cerebellaris lateralis
CD	cortex dorsalis
CDM	cortex dorsomedialis
CDL	cortex dorsolateralis
CH	commissura habenularis
CL	cortex lateralis
CM	cortex medialis
CO	chiasma opticum
CoA	nucleus commissurae anterioris
CoP	commissura posterior
CPP	commissura pallii posterior
CT	commissura tectalis
DBB	diagonal band of Broca
DbB	nucleus of the diagonal band of Broca
DLA	nucleus dorsolateralis anterior thalami
DLHy	nucleus dorsolateralis hypothalami
DM	nucleus dorsomedialis thalami
DMA	nucleus dorsomedialis anterior thalami
DR	decussatio retroinfundibularis
DSD	decussatio supraoptica dorsalis
DSV	decussatio supraoptica ventralis
Dvl	nucleus Deiters, pars ventrolateralis
DT	decussatio tegmenti
EP	nucleus entopeduncularis
GL	nucleus geniculatus
EW	nucleus Edinger-Westphal
FiT	fibrae tangentiales
FLM	fasciculus longitudinalis medialis
FPL	fasciculus prosencephali lateralis
FPLd	fasciculus prosencephali lateralis, pedunculus dorsalis
FPLv	fasciculus prosencephali lateralis, pedunculus ventralis
FPM	fasciculus prosencephali medialis
GLd	nucleus geniculatus lateralis, pars dorsalis
HA	hyperstriatum anterius (anterior dorsal ventricular ridge)
Hb	nucleus habenularis
HP	hyperstriatum posterius (posterior dorsal ventricular ridge)
Imc	nucleus isthmi, pars magnocellularis
Ipc	nucleus isthmi, pars parvocellularis
IP	nucleus interpeduncularis
IS	nucleus interstitialis fasciculi longitudinalis medialis
La	nucleus laminaris
LHy	nucleus lateralis hypothalami
LLd	nucleus lemnisci lateralis, pars dorsalis
LMe	nucleus lentiformis mesencephali
LoC	locus coeruleus
LS	lemniscus spinalis
LSV	lamina supraventricularis
LTE	nucleus lentiformis thalami, pars extensa
LTP	nucleus lentiformis thalami, pars plicata
MiC	nucleus microcellularis
MTl	nucleus medialis thalami, pars lateralis
MTm	nucleus medialis thalami, pars medialis (nucleus reuniens)
MN V	nucleus mesencephalicus trigemini
M V d	nucleus motorius dorsalis nervi trigemini
M V v	nucleus motorius ventralis nervi trigemini
N	neostriatum
N IV	nucleus nervi trochlearis
NS V	nucleus tractus spinalis nervi trigemini
N VII	nucleus nervi facialis
N IX	nucleus nervi glossopharyngei
n III	nervus oculomotorius
n IV	nervus trochlearis
n V m	nervus trigeminus, pars motoria
n V s	nervus trigeminus, pars sensoria
n VI	nervus abducens
n VII m	nervus trigeminus, pars motoria
n VII s	nervus facialis, pars sensoria
n VIII d	nervus octavus, pars dorsalis
n VIII v	nervus octavus, pars ventralis
n IX–X	nervus glossopharyngeus et vagus
OA	nucleus olfactorius anterior

ODL	nucleus oculomotorius, pars dorsolateralis
OMd	nucleus oculomotorius, pars dorsalis
OMv	nucleus oculomotorius, pars ventralis
OS	nucleus olivaris superior
OSC	organum subcommissurale
OT	nucleus opticus tegmenti
Pa	paleostriatum
PD	nucleus posterodorsalis
PO	nucleus praeopticus
POL	nucleus parolfactorius lateralis (nucleus septalis)
POM	nucleus parolfactorius medialis (nucleus septalis)
PMdl	nucleus profundus mesencephali, pars dorsalateralis
PMl	nucleus profundus mesencephali, pars lateralis
PMm	nucleus profundus mesencephali, pars medialis
PrH	primordium hippocampi
PrV	nucleus sensorius principalis nervi trigemini
PT	nucleus praetectalis
PVH	nucleus paraventricularis hypothalami
RI	nucleus reticularis inferior
RM	nucleus reticularis medius
RMS	nucleus magnocellularis superior raphes
ROB	radix optica basalis
RPS	nucleus parvocellularis superior raphes
RpI	nuclei raphes pars inferior
RS	nucleus reticularis superioris
Rt	nucleus rotundus
Ru	nucleus ruber
SAC	stratum album centrale
SAP	stratum album periventriculare
SGC	stratum griseum centrale
SGF	stratum griseum et fibrosum superficiale
SGP	stratum griseum periventriculare
SGr	stratum granulare cerebelli
SMe	stria medullaris
SMo	stratum moleculare cerebelli
SO	nucleus supraopticus
SOp	stratum opticum
Sp	nucleus sphaericus
SPu	stratum Purkinje cerebelli
SRt	nucleus subrotundus
Ta	nucleus tangentialis
TGH	tractus geniculo-hypothalamicus
THP	tractus habenulo-peduncularis
TM V	tractus mesencephalicus trigemini
TOL	tractus olfactorius lateralis
ToL	nucleus tractus olfactorius lateralis
ToS	torus semicircularis
TrO	tractus opticus
TS	tractus solitarius
TS V	tractus spinalis nervi trigemini
TuO	tuberculum olfactorium
VeI	nucleus vestibularis inferior
VHy	nucleus ventralis hypothalami
VLT	nucleus ventrolateralis thalami
VM	nucleus ventromedialis
VMT	nucleus ventromedialis thalami
VS	nucleus vestibularis superior

•	no response
∘	alerting response only
◯	similar response elicited from similar sites in different animals
combined symbols =	change or overlap in response sequence

○	motor responses e.g. head movements
●	motor responses with locomotion
⊙	head-movements with tongue flicking
o	locomotion with tongue flicking

△	pre-escape response (eye closing and crouching)
▲	escape response
★	violent flight response

◇	dewlap display
◆	defensive display
✱	head-nodding display

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N. Greenberg and P. D. MacLean, eds.
NIMH, 1978.

Integration of Internal and External Stimuli in the Regulation of Lizard Reproduction

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Department of Biology
Department of Psychology and Social Relations

and

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Harvard University

SUMMARY. Environment, hormones, and behavior interact to regulate vertebrate reproduction. However, the integration of these factors can be fully appreciated only in an ecological context where the adaptive significance of such interaction becomes apparent.

Experiments with the lizard, *Anolis carolinensis*, indicate that internal and external factors interact to regulate different phases of the female reproductive cycle. Following female emergence from winter dormancy, environmentally induced androgen-dependent male behavior acts along with climatic aspects of the environment to modulate ovarian recrudescence; male courtship insures normal gonadotropin (GT) secretion in the female; the absence of courtship results in subnormal GT secretion, while aggression between males inhibits GT secretion. During the breeding season, females undergo cycles of sexual receptivity which depend upon hormonal conditions normally arising during follicular maturation and are restricted to the time immediately preceding ovulation. If the female mates during this period, further receptivity within that follicular cycle is inhibited. At the end of the breeding season, females are insensitive to both environmental and hormonal stimuli that would otherwise facilitate ovarian growth; this refractoriness is maintained by the atretic follicle.

These and related findings demonstrate that principles originally elaborated with inbred laboratory species can be generalized to animals in the field and shown to have clear adaptive value in the animal's natural history.

INTRODUCTION

> . . . the sexual posturing of the male produces exteroceptive stimuli which act upon the anterior pituitary of the female through the hypothalamus, and so affects the necessary synchronization between the sexual processes of the male and female . . . (F.H.A. Marshall, 1936, p. 445)

The integration of behavioral, endocrinological, and environmental factors in the regulation of vertebrate reproduction has been the subject of intensive investigation in recent years. Perhaps most notable has been the research of Robert A. Hinde and the late Daniel S. Lehrman. Due largely to their work on the canary (Hinde, 1965) and the ring dove (Lehrman, 1965), many of the fine details of the synchronization about which Marshall speculated 40 years ago have been confirmed; we can now say with some assurance that the environmentally induced endocrine-dependent courtship behavior of the male, acting along with climatic and physical aspects of the environment, stimulates pituitary gonadotropin secretion and consequent ovarian development, steroid production, and reproductive behavior in the conspecific female (Bermant and Davidson, 1974) (see Fig. 1). Changes in the female's behavior, in turn, feed back ultimately to influence the physiology and behavior of the male (Cheng, 1975). This concept of a reciprocal interaction between the animal

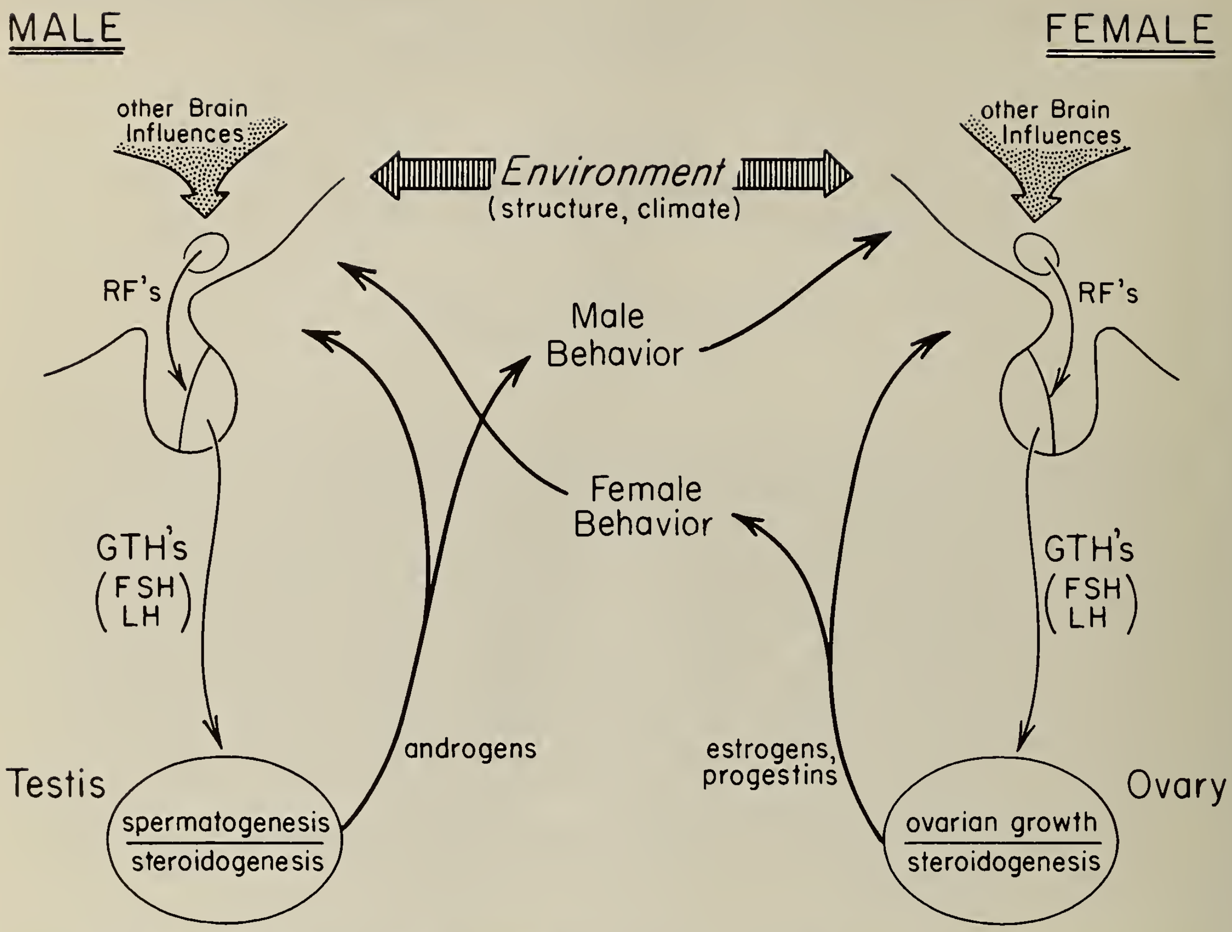

Figure 1. Interaction of environment, hormones, and behavior in the regulation of vertebrate reproduction.

and its structural and social environments has become one of the major themes in behavioral endocrinology today.

LIZARDS AS EXPERIMENTAL ANIMALS IN PSYCHOBIOLOGICAL RESEARCH

Much of my own research has been concerned with this interaction of behavior and hormones and how their interrelationship might influence another animal's behavior and reproductive physiology. Although this interest was first stimulated by Lehrman's work with the ring dove, it seemed to me that further insight into the generality and possible evolutionary and adaptive significance of principles arising from Lehrman's and others' psychobiological research would come from work with species other than the laboratory birds and mammals that are commonly used. While inbred laboratory species are useful for certain physiological studies and for elucidating complex psychoneuroendocrine relationships (e.g., the milk ejection reflex in mammals), it is necessary to study feral animals in nature or in carefully controlled, simulated habitats to understand how these interrelationships adapt animals to their particular environments.

Although present-day reptiles cannot be considered to be more primitive than extant birds or mammals, their common ancestry and similarities with the so-called "higher" vertebrates make reptiles an important vertebrate class with which to investigate the social and environmental control of reproduction. Of the reptiles, iguanid lizards are especially well suited for this type of research. Many species are small, readily available, and easily cared for in the laboratory. In addition, many species retain their full repertoire of behavior patterns and complex social systems in captivity. Finally, and more importantly from a psychobiological point of view, there is already substantial information regarding the behavior, physiology, and natural history of a number of species of two lizard genera, *Anolis* and *Sceloporus*. Perhaps the best studied of these species has been the American chameleon, *Anolis carolinensis*.

Anolis carolinensis is a small, temperate-zone lizard found throughout the southeastern United States. From late September to late January, both males and females are reproductively inactive and cluster in groups beneath the bark of dead trees, under fallen logs and rocks (Fig. 2). Beginning in late January or early February, the males emerge from this period of winter dormancy and establish breeding territories. Approximately 1 month later the females begin to be active, and by May they are laying a single-shelled egg every 10–14 days. Following the breeding season, both males and females enter a refractory phase lasting approximately 1 month during which they are insensitive to the various environmental and social stimuli responsible for inducing gonadal recrudescence in the spring.

There are three different series of experiments summarized in this paper. In the first, I illustrate how various social and environmental factors coact to control the initiation of seasonal ovarian activity in winter-dormant females. In the second, I identify some of the different internal and external stimuli to which females are exposed during the normal breeding season and how these stimuli interact to control female sexual receptivity. Finally, I describe experiments

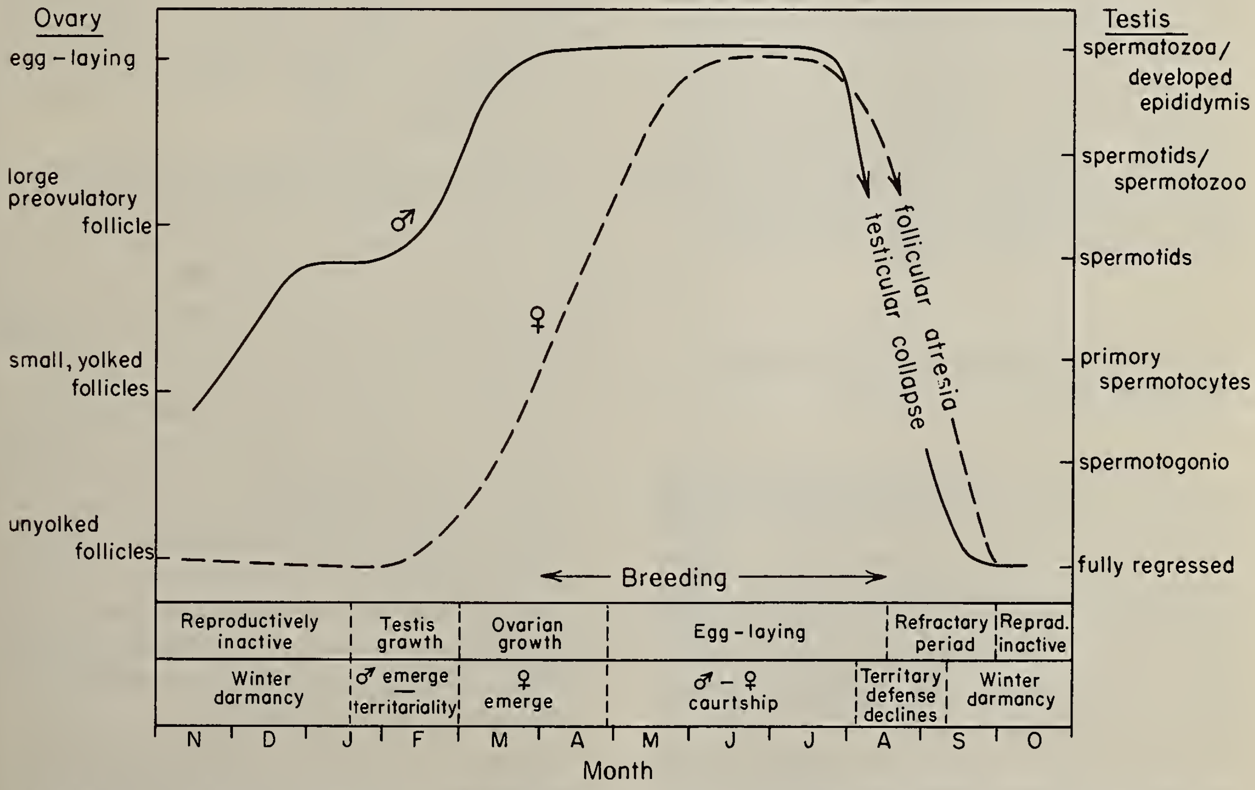

Figure 2. Schematic illustration of different behavioral and physiological events in the annual reproductive cycle of the lizard, *Anolis carolinensis* (from Crews, 1975*c*).

done with Paul Licht on the factors controlling the sexual refractory period following the breeding season.

CONTROL OF SEASONAL OVARIAN RECRUDESCENCE IN THE LIZARD, *Anolis carolinensis*

All of the experiments on the role of the male in seasonal ovarian recrudescence (OR) were conducted during the period of winter dormancy, thereby insuring an unchanging baseline measure of ovarian activity against which the effects of the various experimental manipulations could be assessed.

The same procedure applied to all of the experiments. Animals were shipped to the laboratory within a day of capture. Four days after their arrival, they were divided into groups and placed in environmental chambers. The chambers simulated the natural habitat as closely as possible and were programed to provide an environmental regime consisting of a 14:10 LD photic cycle, a daily thermal cycle of 32 C during the photoperiod and 23 C during the dark phase of the cycle, and a constant relative humidity of 70–80 percent. During each experiment, weekly samples of representative females were taken from the various groups and their reproductive condition determined.

Environmental factors regulating ovarian recrudescence

The purpose of the initial experiment was to determine first whether the environmental regime would stimulate out-of-season ovarian recrudescence in reproductively inactive winter-dormant females (Crews, et al., 1974). If ovarian activity could be stimulated in this manner, would the presence of other females or males alter the pattern of ovarian response? Finally, if the presence of conspecifics was important, was the physiological state of the conspecific critical?

In answer to the first question of whether vitellogenesis (yolk deposition) could be environmentally stimulated in winter-dormant females, I found that an increasing percentage of isolated females (as well as females in other experimental groups) had yolking follicles, whereas females in the field (Field Control) failed to show any signs of reproductive activity (Fig. 3). The presence of other females (Female Group) did not appear to be any more stimulatory than the environmental regime alone. However, the presence of intact males, whether in the Female-Male group, or in the Isolated Pairs group, significantly facilitated environmentally induced OR. Finally, the physiological state of the males was an important factor since females housed with castrated males exhibited a rate of environmentally induced ovarian activity that was not significantly different from that shown by isolated females and females in the all-female group.

In addition to a less rapid rate of OR, isolated females and females housed together or with castrated males laid only unshelled eggs. This was an important observation since Licht (1973) had demonstrated previously that the laying of shell-less eggs in *A. carolinensis* is due to subnormal pituitary gonadotropin secretion.

This experiment demonstrated therefore that, while an unseasonal environmental regime will stimulate out-of-season OR in winter-dormant females, the presence of intact males strongly facilitates OR, most likely through an effect upon gonadotropin secretion in the female.

Can this male-facilitated rate of OR be increased further? To test the hypothesis that OR would be maximally stimulated if winter-dormant females were exposed to males exhibiting environmentally induced sexual activity, freshly captured winter-dormant females were housed in cages each containing five sexually active males (Crews, 1974*a*). Results from this experiment, however, were totally unexpected.

In contrast to the gradual increase in ovarian activity by females housed with castrated males and the rapid rate of recrudes-

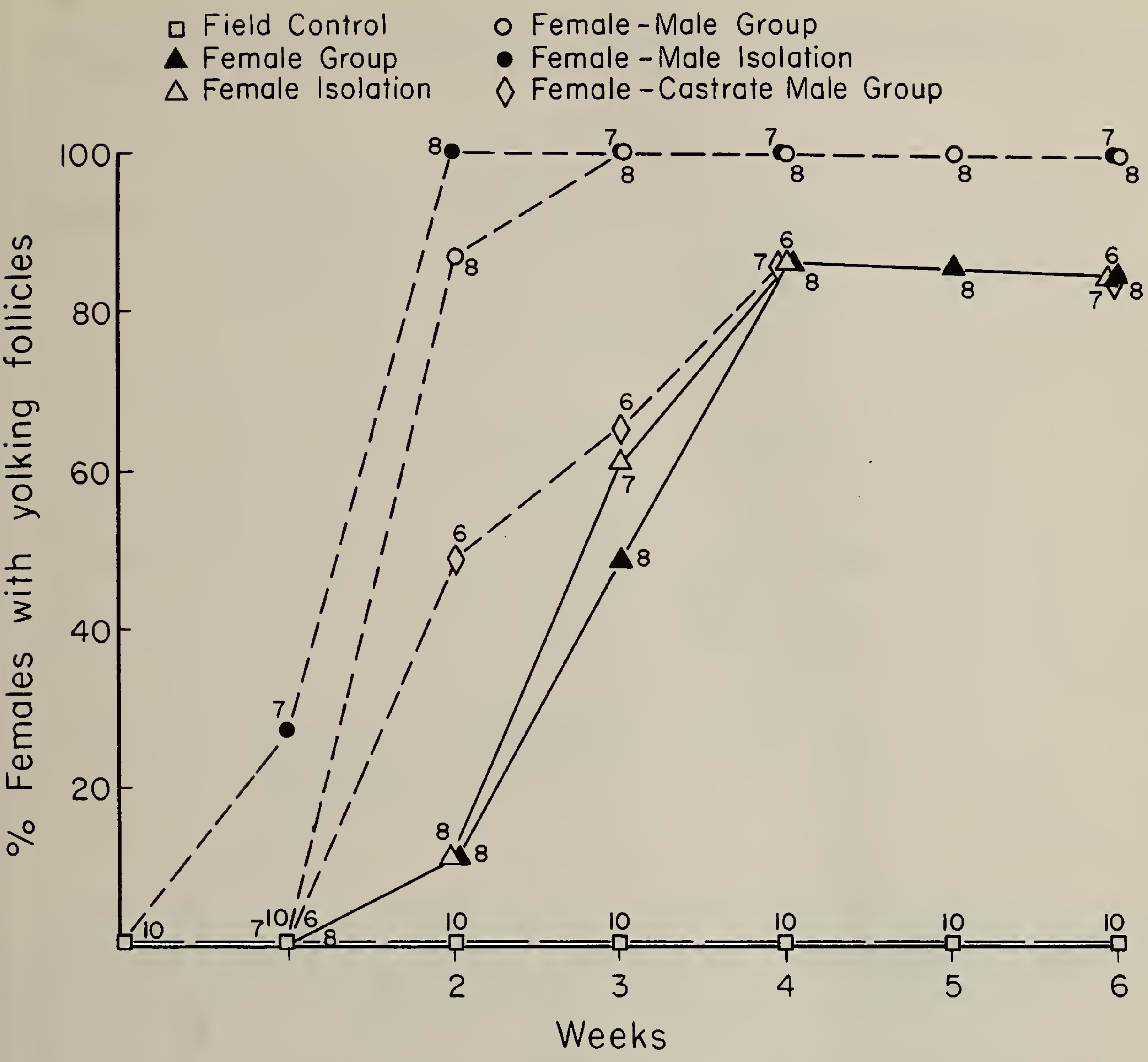

Figure 3. Patterns of ovarian recrudescence exhibited by winter-dormant *Anolis carolinensis* exposed to a stimulatory environmental regime in isolation or with conspecifics. Sample sizes shown by each point (from Crews, 1975*c*).

cence exhibited by females grouped with intact males taken from the field at the same time as the females (Stable Female-Male Group), not more than half of the females housed under these conditions (Unstable Female-Male Group) were reproductively active at any one time (Fig. 4). Equally striking were the differences in the predominant male behavior pattern and the degree of social stability between the groups (see below).

Role of male behavior in ovarian recrudescence

There are four basic display patterns in the behavioral repertoire of the laboratory populations of A. *carolinensis:* Aggression, Assertion-Challenge, Courtship, and Submission (Figure 5). These displays are distinguished easily by the patterning, context, orientation, posturing, and movement of the displaying animal (Table 1). In a previous

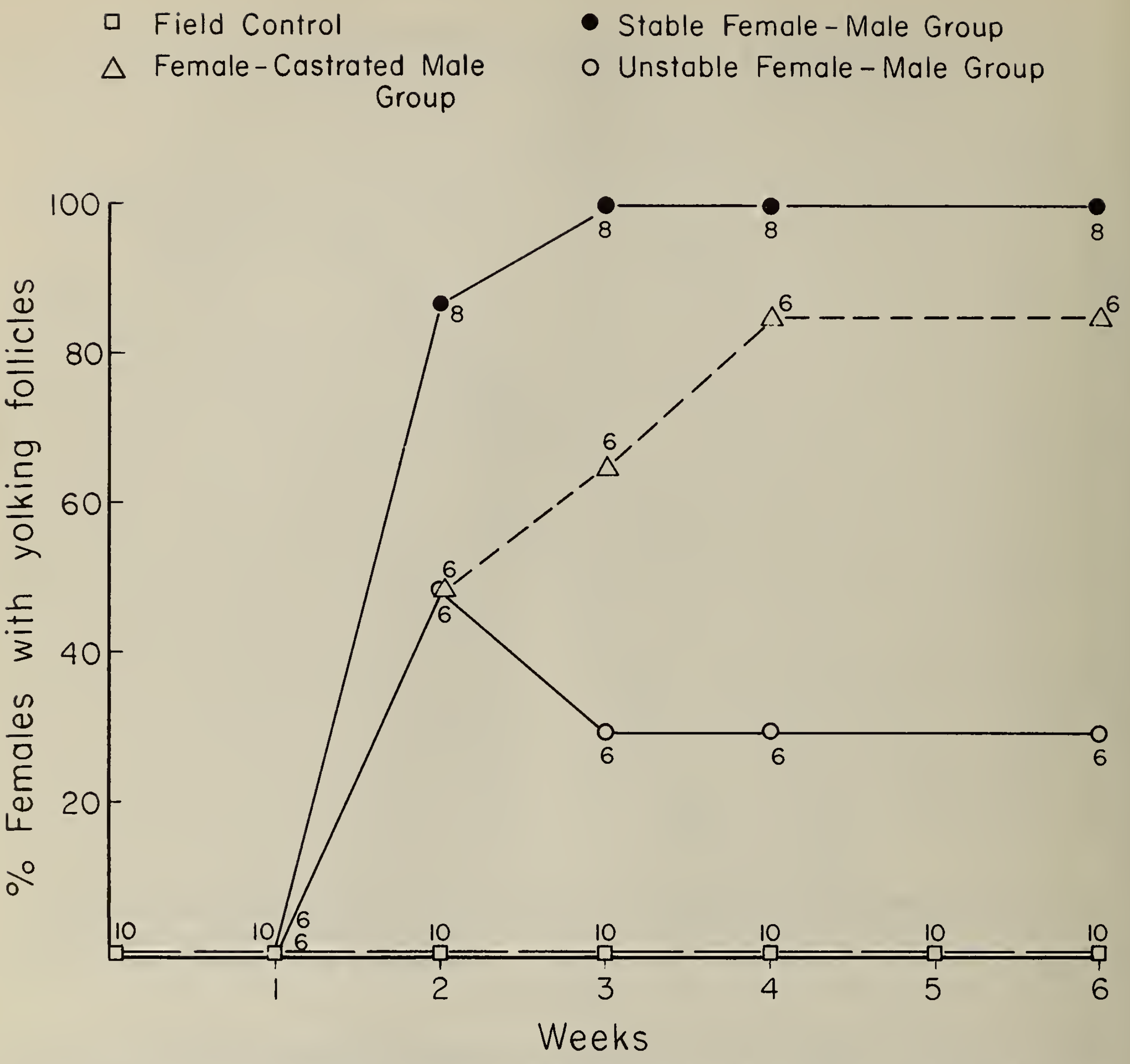

Figure 4. Patterns of environmentally induced ovarian recrudescence exhibited by winter-dormant *Anolis carolinensis* housed in stable or unstable social groups. Sample sizes shown by each point (from Crews, 1975*c*).

paper (Crews, 1975*b*), I distinguished between Challenge and Assertion displays. Upon reexamination, however, it appears that these are not separate displays, but rather a single display type possibly differing in function as a consequence of differences in context (see paper by Jenssen in this volume for discussion of the problem inherent in display analysis).

When winter-dormant males and females are taken from the field at the same time and exposed as a group to the stimulatory environmental regime described above, there is an initial high level of male-male aggressive behavior with little or no male courtship behavior (Fig. 6). By the end of the first week, however, there is a gradual change in both the nature and frequency of the predominant male behavior pattern; this change coincides with a single male becoming dominant in the group. As a single male becomes dominant, there is first a shift from male-

Table 1. Displays (Aggression, Assertion-Challenge, Courtship, and Submission) of male *Anolis carolinensis* in laboratory populations and their identifying characteristics.

	DISPLAY			
	AGGRESSION	ASSERTION-CHALLENGE	COURTSHIP	SUBMISSION
CONTEXT	performed by dominant male toward strange lizard or toward displaying male	performed by dominant male after aggressive bout or when reaching favorite perch; occasionally seen when animal alone in cage	response to female, also performed toward any lizard giving submission display	response to the approach, assertion-challenge display, or courtship display by a dominant lizard
ORIENTATION	laterally oriented towards recipient	oriented towards recipient; also performed with no apparent orientation	variable; usually 90–45° toward recipient	variable
POSTURE	laterally compressed	laterally compressed	relaxed	relaxed
PATTERN	rapid, jerking movement of whole body	rhythmical bobbing with forepart of body	rhythmical bobbing with forepart of body	rapid nodding of head only
MOVEMENT	circular	none, display stationary	approaches other lizard, stopping to display	none, display stationary
MODIFIERS	nuchal and dorsal crests erected, throat engorged, formation of black spot behind eye, jaw gaping and locking	dewlap extended, crests and eyespot diminished	dewlap extended, no crest or eyespot	none

male aggression to assertion displays by the emerging dominant followed by a general decline in their frequency. At the same time, there is an increase in the male-female courtship behavior (only the dominant male courts). By the end of the second week, the first mating usually occurs.

In the group in which females were exposed to the previously environmentally induced sexually active males (see Fig. 4), there was a constant high level of male-male aggression for the entire 6 weeks. In addition, no single male became dominant over the other males in the cage and no copulations occurred in the 6-week period of observation. In the few instances in which courtship did occur, the courting male had time to complete only one or two courtship displays before its behavior attracted other males and a male-male fight would erupt. In the castrated male group, neither male-male agression nor courtship was ever observed.

Thus, it was unclear from the results of this experiment whether the different patterns of environmentally induced ovarian activity were due to the males' performance of particular behavior patterns or attributable to a more general complex of male-related stimuli. There was the suggestion, though, from my observations, that male courtship might facilitate the environmental induction of ovarian activity while aggression between males might be responsible for the inhibition of environmentally induced OR.

Therefore, in a third experiment, winter-dormant females were exposed, in a more systematic manner, either (1) to predominantly male-male aggression for 6 weeks, (2) to 3 weeks of predominantly male-male aggression followed by 3 weeks of predominantly male courtship, or (3) to 3 weeks of predominantly male courtship followed by 3 weeks of predominantly male-male aggres-

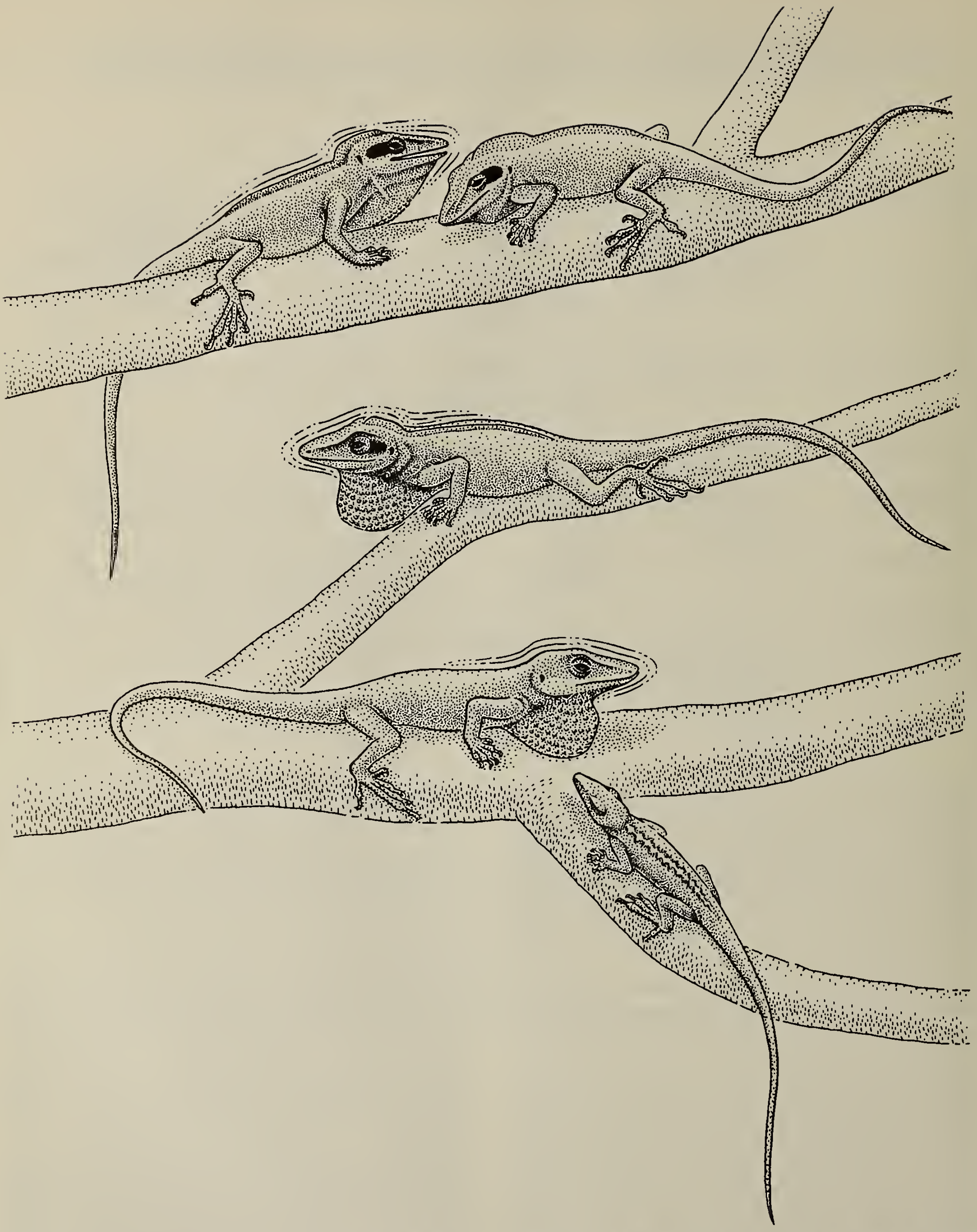

Figure 5. Displays exhibited by the male lizard, *Anolis carolinensis*. *Top:* Posturing between males during aggressive bout; note erected nuchal and dorsal crest, lateral compression of body, black spot behind eye, engorged throat, and lateral orientation. *Middle:* Assertion-Challenge display; note extended dewlap, lateral compression of body, nuchal and dorsal crest subsiding, eye-spot fading. *Bottom:* Courtship display; note extension of dewlap, relaxed body posture, crest and eye-spot absent. (See Table 1 for further details).

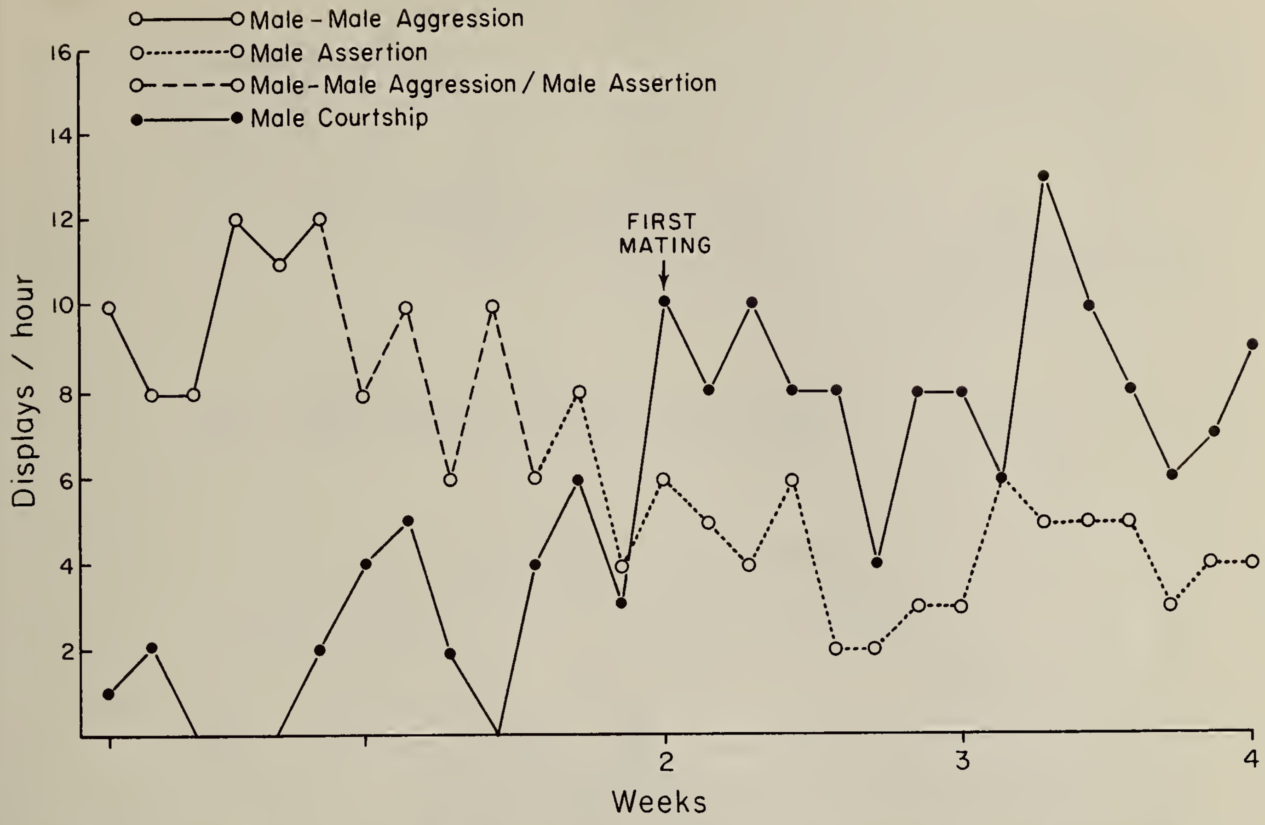

Figure 6. Transition of predominant male behavior patterns when winter-dormant males are exposed to a stimulatory environmental regime (from Crews, 1975*c*).

sion (Fig. 7). A fourth group of females exposed to 6 weeks of predominantly male courtship was not run since the previous two experiments had already demonstrated the effect of 4-to-5 weeks of predominantly male courtship; that is, facilitation of environmentally induced OR (see Fig. 4).

Results from this experiment indicated that the hypothesis that male courtship facilitated, while male-male aggression inhibited, environmentally induced OR was correct: Females exposed to male-male aggression for 6 weeks exhibited a low, unchanging level of ovarian activity. Females exposed initially to 3 weeks of male-male aggression exhibited a comparable level of ovarian activity, but, when the social stimulus was changed to male courtship, ovarian activity was dramatically stimulated (Fig. 8). Finally, females exposed first to male courtship followed by male-male aggression exhibited the facilitated rate of environmentally induced OR as in the previous experiments, but when the predominant male behavior pattern was changed to male-male aggression, ovarian activity declined.

There are several reasons for the low level of ovarian activity to be regarded as an active inhibition by male-male aggression rather than an instance of nonactivation. First, the ovarian follicles in an increasing percentage of females exposed to male-male aggression after 3 weeks exposure to male courtship became atretic, and no new follicular cycles were initiated. Secondly, female *A. carolinensis* exhibit an endogenous circannual ovarian cycle (Crews, 1973*a;* Licht, 1973). This finding, combined with the observation that females exposed to high levels of male-male aggression at a time when females in the field (Field Control) were undergoing OR, would further argue for an active inhibition of environmentally induced ovarian activity by male-male aggression.

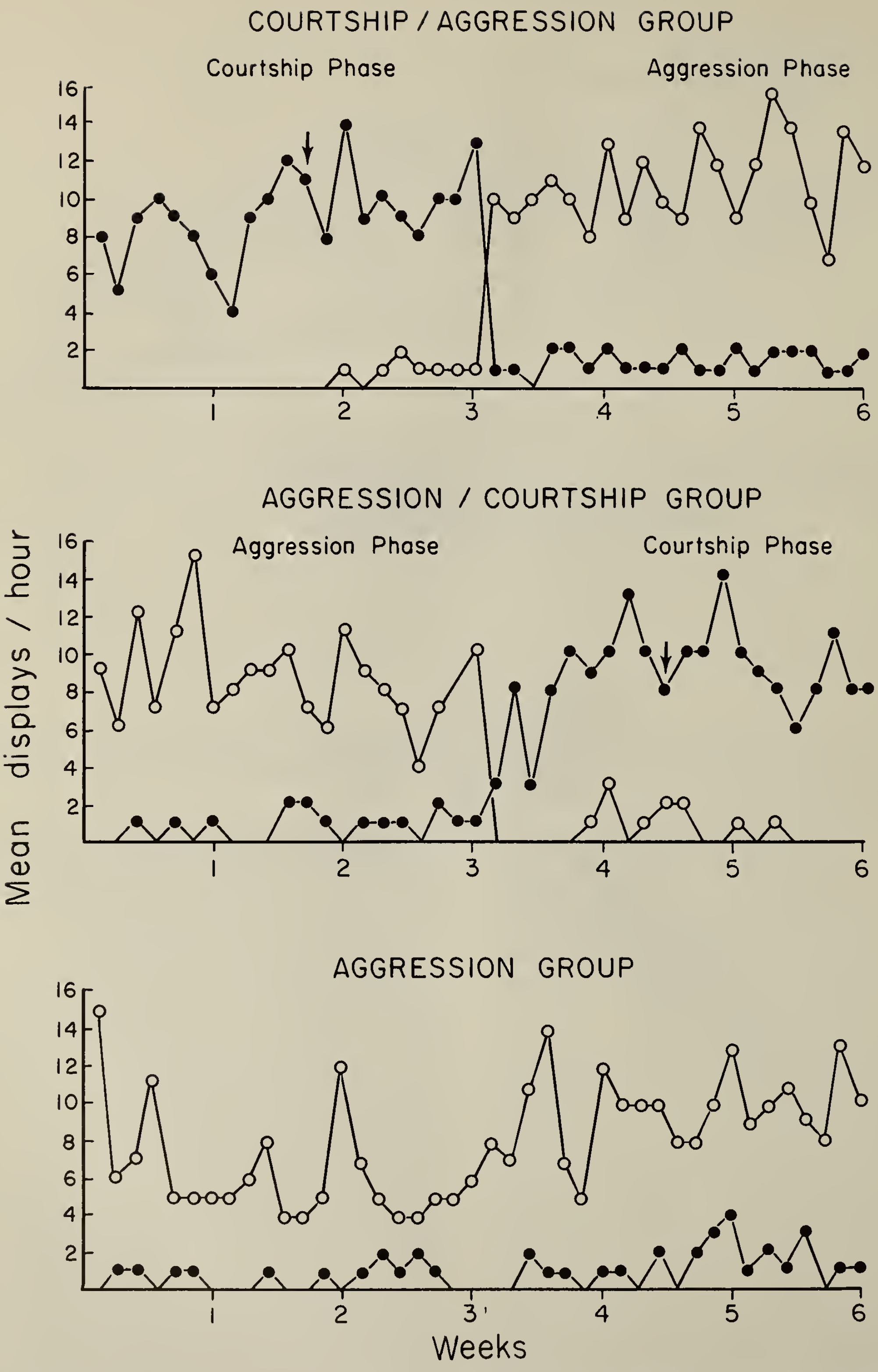

Figure 7. Level of male-male aggression and male courtship in different experimental groups (redrawn from Crews, 1974*a*).

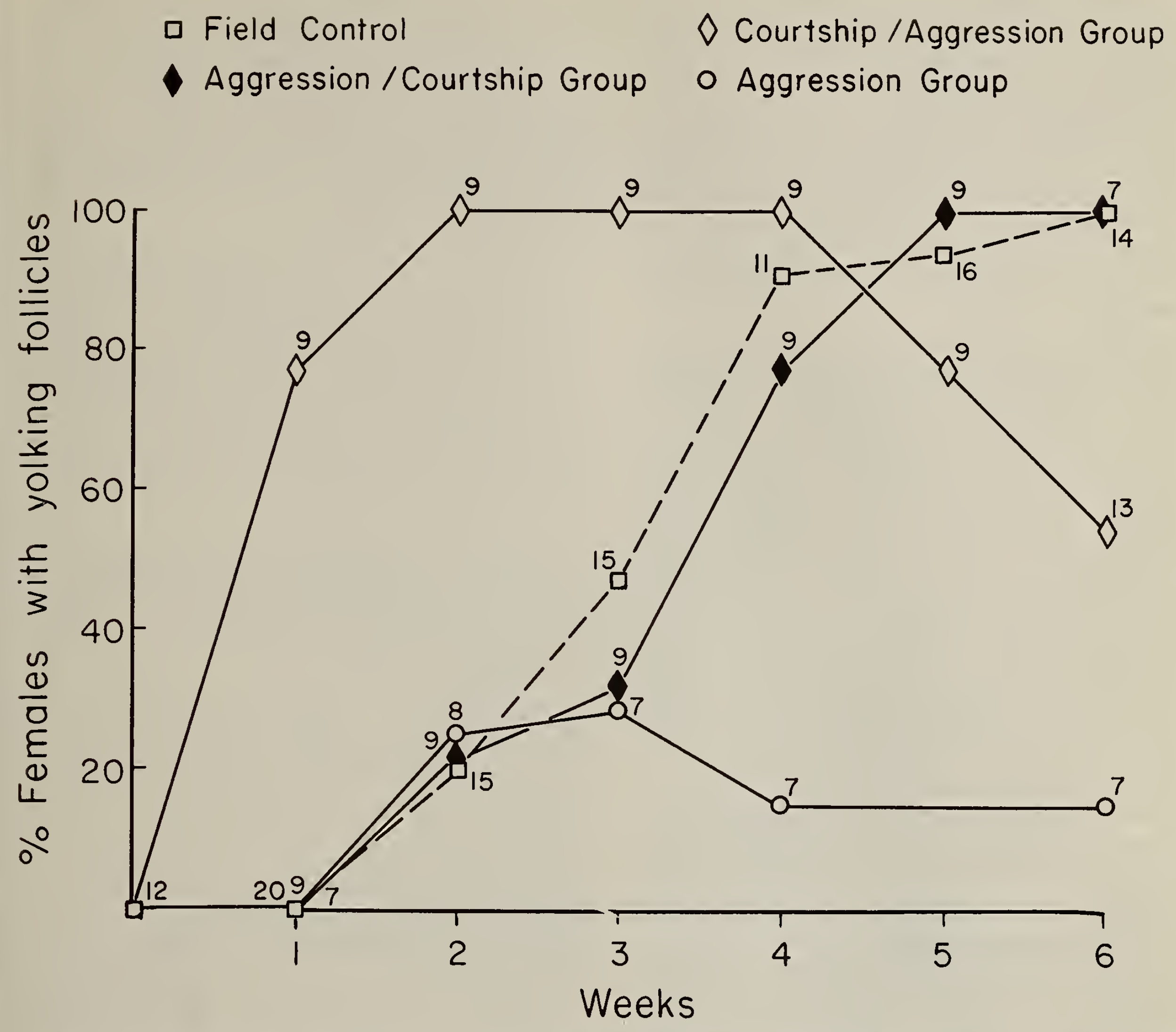

Figure 8. Patterns of environmentally induced ovarian recrudescence exhibited by winter-dormant *Anolis carolinensis* exposed to different male behavior patterns. Sample sizes shown by each point (from Crews, 1975*c*).

Thirdly, if the inhibition were due to some other stimulus, such as crowding, rather than a direct effect of aggressive behavior between males upon female reproductive physiology, then females exposed to different male behavior patterns but housed in adjoining cages under otherwise identical experimental conditions would not be expected to exhibit such strikingly different patterns of ovarian activity. Finally, in considering the argument that it was perhaps the absence of courtship, and not the presence of male-male aggression, that inhibited OR, we must recall that in the first two experiments, females exposed to castrated males that showed neither courtship nor male-male aggression exhibited gradual ovarian development, while the pattern of ovarian activity among females exposed to male-male aggression was low and unchanging or decreasing (cf., Figs. 4 and 7).

From these experiments, then, it would appear that in the lizard, *Anolis carolinensis*, male-male aggression actively inhibits the initiation of environmentally induced ovarian development, while male courtship behavior strongly facilitates the stimulatory effects of the out-of-season environmental regime. This finding also suggests that (1) in *A. carolinensis,* male courtship insures normal gonadotropin secretion, (2) the absence of male courtship results in subnormal gonadotropin secretion, as indicated by the laying of unshelled eggs, and (3) the presence of male-male aggression inhibits or greatly reduces environmentally induced gondotropin secretion.

Further experiments in which winter-dormant females were exposed to either high or low frequency courtship males indicated that gonadotropin secretion is graded in accordance with the amount of male courtship to which the female is exposed (Crews, 1974*a*). Only those females exposed to the high levels of male courtship exhibited the typical pattern of courtship facilitation of OR demonstrated in the previous experiments. Females exposed to low levels of male courtship exhibited a significantly less rapid rate of ovarian activity that was not different from that of females housed with castrated males that did not court at all.

As might be expected on the basis of previous experiments with mammals and birds (Bermant and Davidson, 1974), male courtship behavior and, in turn, courtship facilitation of environmentally induced OR in *A. carolinensis* are dependent upon testicular secretions. In another experiment, I demonstrated that castration abolished male courtship behavior and androgen replacement therapy reinstated male courtship activity to preexisting levels (Crews, 1974*b*). In addition, ovarian growth was more rapid among those females exposed to intact males and castrated males with androgen implants than among females exposed to castrated males with or without cholesterol implants (Fig. 9).

Stimulus factors in courtship facilitation of environmentally induced ovarian recrudescence

Ritualized behavior patterns, such as male courtship displays, are integrated sequences of complex motor patterns or acts. Is it necessary for the female to perceive the entire display of the male in order for the display to have its effect? What component(s) of the male's courtship display is responsible for the facilitation of environmentally induced OR?

By dissecting the stimulus configuration presented by the courting male to the female into its parts, it should be possible to examine both their individual long-term physiological or "priming" effects—that is, their relative effectiveness in facilitating environmentally induced OR—as well as their short-term behavioral or "releasing" effects—that is, their role in mate selection.

Taking this approach, I arbitrarily divided the male courtship display of *A. carolinensis* into the following components: the up-and-down bobbing movement, dewlap extension, and dewlap color.

Dewlapping in anoles is accomplished by the extension of a thin flexible part of the hyoid apparatus called the *processus retrobasilis* (Fig. 10). By surgically removing this cartilage, males were obtained which were able to perform all of the behavior patterns associated with courtship except the physical extension of the dewlap. To analyze the importance of the color of the dewlap, dewlaps of another group of males were injected with India ink; this produced males with blue dewlaps as compared with normal, red-dewlapped males (Crews, 1975a).

In the first experiment with these different-stimulus males, winter-dormant females were housed with either (1) a castrated male which was never observed to court, (2) an intact red-dewlapped male, which courted normally, (3) a hyoidectomized male which performed the bobbing and strutting advance characteristic of male courtship but, because his hyoid cartilage had been removed, could not extend the dewlap, or (4) a blue-dewlapped male which performed all the behavior patterns associated with male courtship but whose dewlap was the "wrong" color.

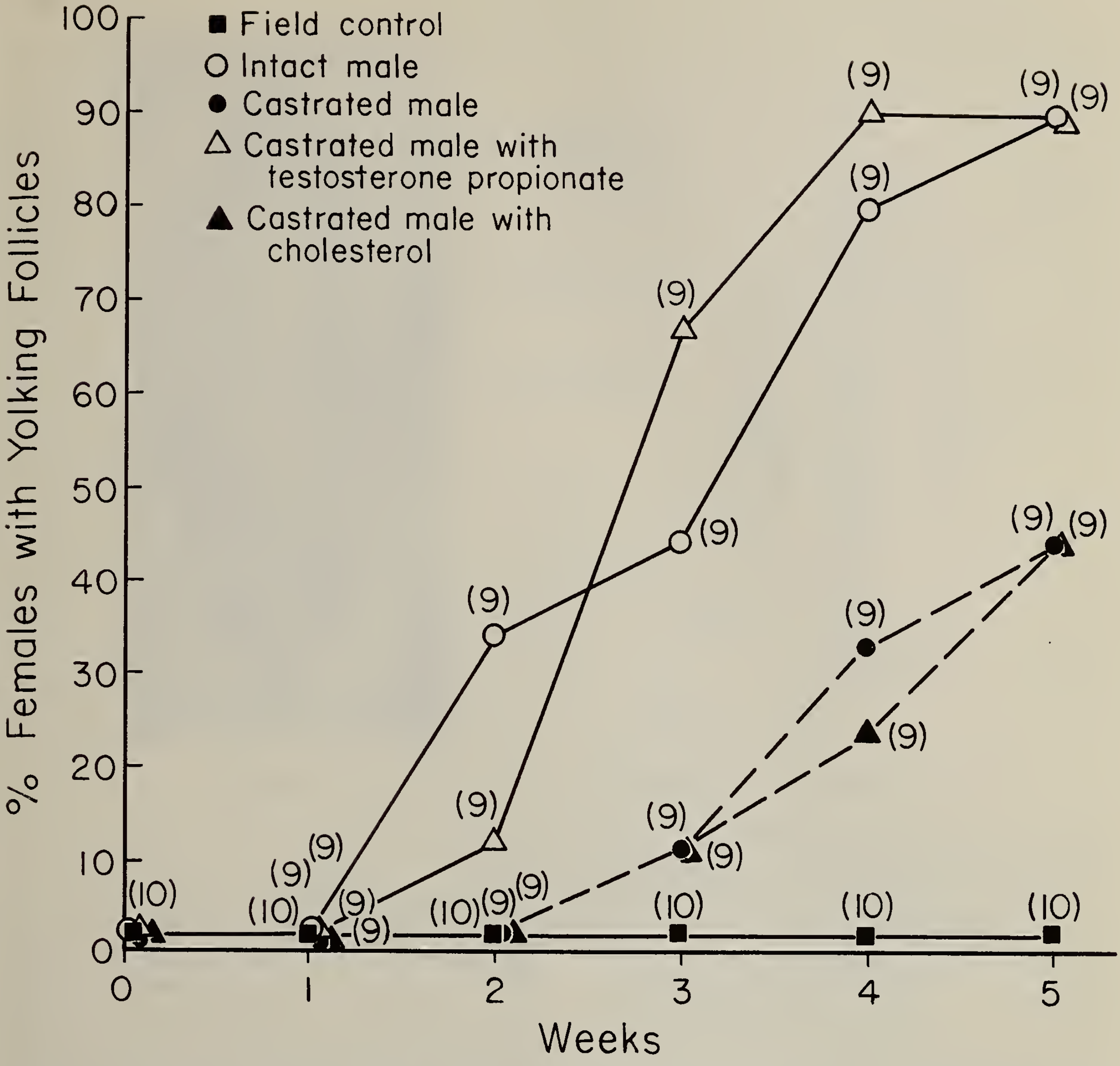

Figure 9. Patterns of environmentally induced ovarian recrudescence exhibited by winter-dormant *Anolis carolinensis* housed with castrated males implanted with testosterone propionate or cholesterol. Sample sizes shown by each Point (redrawn from Crews, 1974*b*).

Results from this study indicated that the rate of environmentally induced ovarian growth among females housed with blue-dewlapped males was comparable to that shown by females housed with normal red-dewlapped males (Fig. 11). On the other hand, females housed with hyoidectomized males exhibited a significantly less rapid rate of OR which was almost identical to that of females exposed to castrated males.

In the second experiment on the role of these various components in mate selection, females were exposed first to a courting red-dewlapped male to determine if they were receptive. Sexually receptive females were then tested with a courting hyoidectomized male followed by a similar mating test with a blue-dewlapped male. Results from these tests revealed that receptive females do not respond sexually to the courtship of hyoidec-

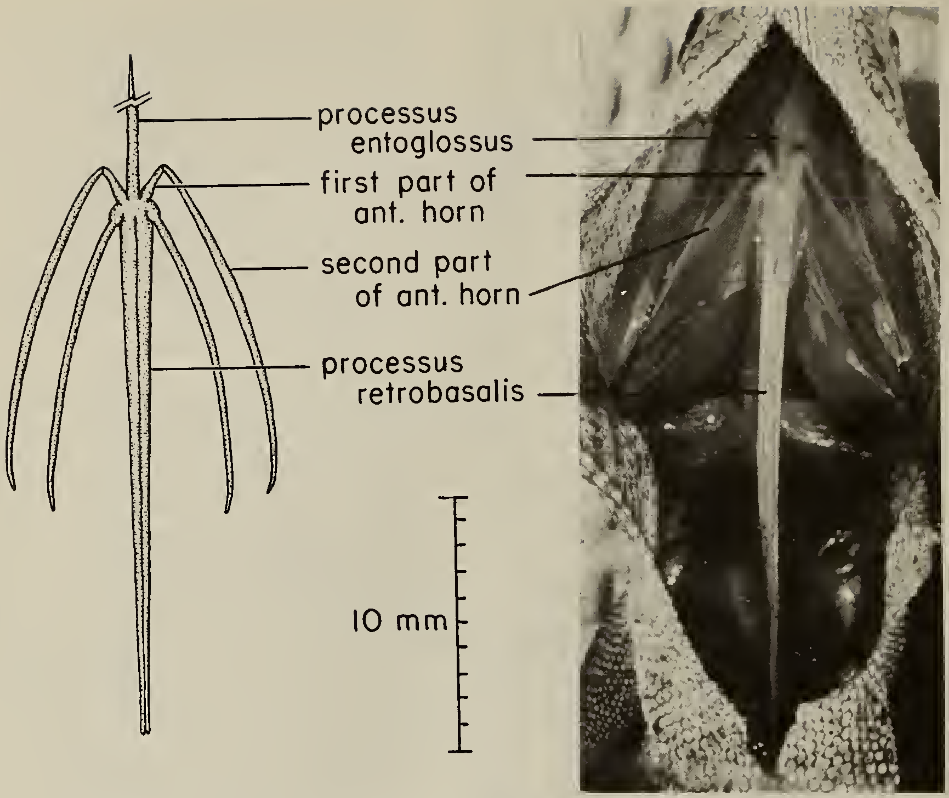

Figure 10. Hyoid apparatus of the male lizard, *Anolis carolinensis*.

Table 2 Response of sexually receptive female *Anolis carolinensis* to the courtship of hyoidectomized and blue-dewlapped males, respectively.

Test Male	Female Sexual Receptivity	
	Receptive	Nonreceptive
Hyoidectomized Male	2	10
Blue-dewlapped Male	9	3

$p<0.01$, phi coefficient

tomized males but are receptive to the courtship of blue-dewlapped males (Table 2).

These experiments suggest, therefore, that the critical factor in both courtship facilitation of environmentally induced OR and in mate selection in *A. carolineusis* is the ability of the male to extend the dewlap, thus changing his body shape, and not the color of his dewlap.

Certain limitations, however, must be placed on this interpretation. For example, we do not know if it is important for the male to change the body profile in a species-typical manner, e.g., in conjunction with the bobbing movement. Nor do we know if the lack of dewlap color per se is important for these physiological and social effects.

Adaptive significance of courtship facilitation and male-male aggression inhibition of environmentally induced ovarian recrudescence

Let me summarize this series of experiments on the factors controlling seasonal ovarian recrudescence in *A. carolinensis* by way of hypothesizing about the possible adaptive function of courtship facilitation and male-male aggression inhibition of en-

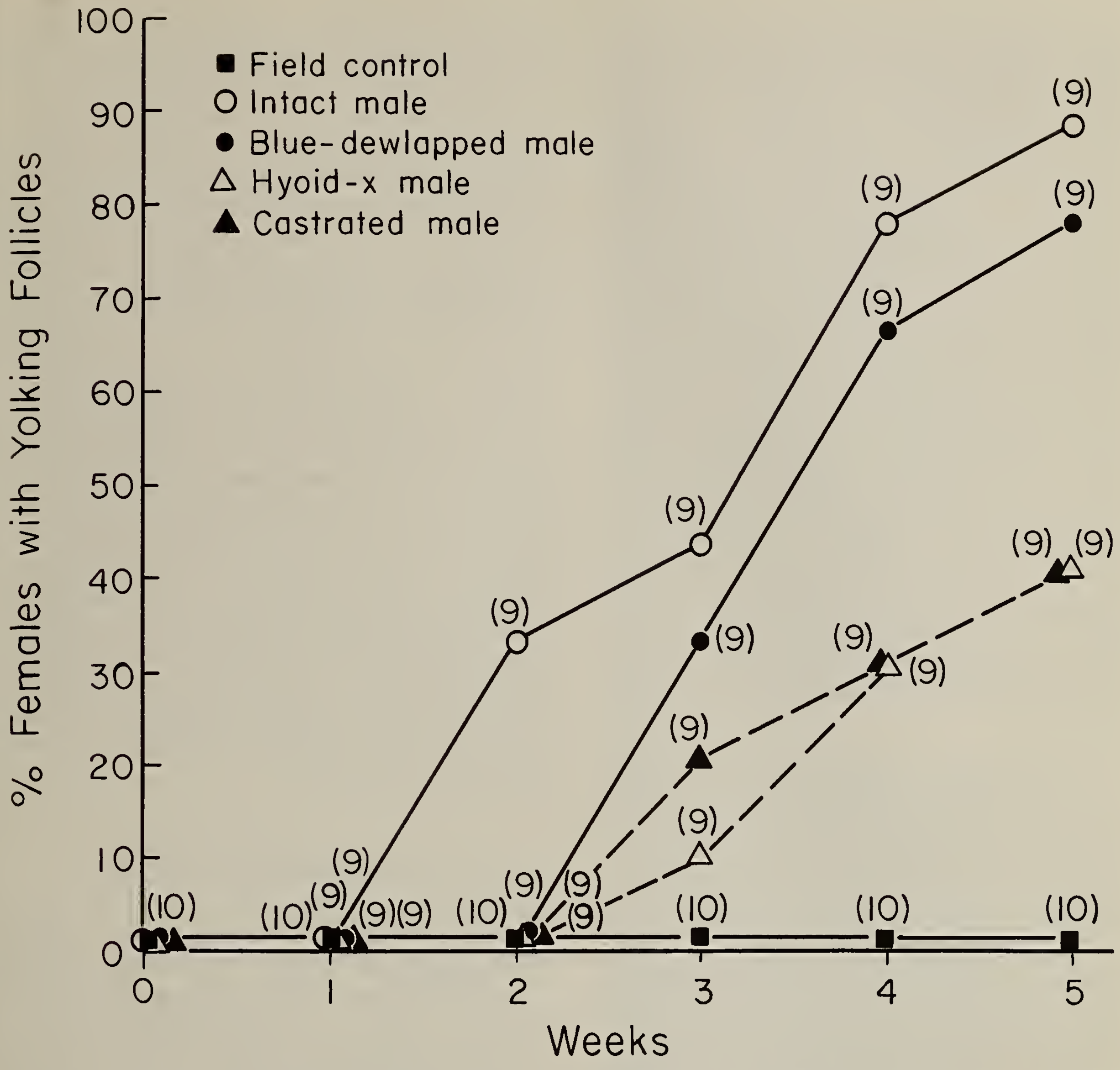

Figure 11. Patterns of environmentally induced ovarian recrudescence exhibited by winter-dormant *Anolis carolinensis* exposed to different stimulus males. Sample sizes shown by each point (redrawn from Crews, 1975*a*).

vironmentally induced OR; this hypothesis, I submit, has application to other seasonally breeding vertebrates as well.

Several herpetologists have suggested that in seasonally active reptiles, *A. carolinensis* included, the males emerge from winter dormancy, establish territories, and are in breeding condition before the females emerge. Similarly, ornithologists have long noted that in many seasonally active passerine species, the males arrive at the breeding grounds before the females and are in a more advanced reproductive state.

If we assume that these sex differences in spring emergence act to insure the presence of territory-holding, reproductively active males at a time when the females are emerging, then it is clearly adaptive for females to remain dormant while there is this high incidence of aggressive behavior among males establishing their territories. It has been reported that this aggression between males gradually declines as territorial boundaries become recognized and that the territorial males' behavior shifts to courtship with the arrival (emergence) of females (Brown, 1975). This shift from male-male aggression to male courtship, then, would act in concert with the environmental stimuli to facilitate OR. Thus, females would effectively offset their increased vulnerability to predators by rapidly attaining reproductive condition. Simultaneous male-female emergence, on the other hand, would expose females to the high frequency of male-male aggression necessary for the establishment of territories—which I have demonstrated experimentally inhibits ovarian development. Similarly, courtship facilitation and aggression inhibition of environmentally induced ovarian activity might also act to insure breeding synchrony in the population (e.g., the "Fraser Darling Effect"). For example, vitellogenesis in females which emerge early would be inhibited until the males had established their territories.

I would like to suggest, then, that while emergence from hibernation may be cued by both environmental and endogenous factors, the rate at which females respond to these environmental cues may have been influenced, through selection, to coincide with the waning of male-male aggression following the establishment of breeding territories. Thus, although these laboratory experiments do not demonstrate conclusively an adaptive significance of the facilitation and inhibition of environmentally induced ovarian activity by specific male behavior patterns in nature, they do suggest a possible function of differential emergence in temperate zone vertebrates that has not been suggested before and one that is amenable to field experimentation.

CONTROL OF FEMALE SEXUAL RECEPTIVITY IN THE LIZARD, *Anolis carolinensis*

I have also sought to identify the various factors controlling female sexual receptivity during the breeding season in *A. carolinensis*.

When a female *A. carolinensis* is introduced into a cage containing a sexually active male, the male immediately challenges the intruder (Crews, 1975*b*). If the female does not flee and/or attempt to hide from the male, the male will stop performing challenge displays and begin to court the female (see Table 1 for identifying characteristics of these display patterns). A female that remains standing for the advancing male will invariably arch her neck, enabling the male to take a neck grip. The male then straddles the female and, after pushing his tail beneath hers to oppose their cloacal regions, everts a single hemipenis. Once intromission has been achieved, the male and female cannot be separated easily, possibly as a result of hemipenile tumescence. There is no noticeable pelvic thrusting by the male during copulation. Separation occurs when the male dismounts and moves away from the female. Females often remain immobile following the male's withdrawal, sometimes for as long as 10 minutes.

Cycles of Sexual Receptivity (Estrous)

While there have been many experimental investigations relating often quite subtle ovarian changes with changes in sexual receptivity, the vast majority of these have been confined to birds and mammals (Bermant and Davidson, 1974). In one of the few such studies with reptiles, Noble and Greenberg (1941) suggested a similarity between *A. carolinensis* and mammals in that there existed a direct casual relationship between maturation of the ovarian follicle and sexual receptivity. The approach of Greenberg and Noble was to ovariectomize females and later implant crystalline hormones and note changes in genital morphology and sexual behavior. This only demonstrated that sexual receptivity was dependent upon the presence of the ovaries. I set out to test Noble and Greenberg's hypothesis more directly by comparing the changes in female sexual receptivity with the follicular changes seen during the normal ovarian cycle (Crews, 1973*b*).

For this experiment, females of unknown physiological state were introduced into test cages containing a dominant, sexually active male and two subordinate, sexually inactive males. In behavioral tests lasting a maximum of 1 hour, females were categorized as either nonreceptive or receptive depending upon whether they accepted the courting test male.

Following the behavioral test, females were removed from the test cage and their ovarian condition determined. Ovarian condition was determined in the following manner (see Table 3): First, depending upon the state of the ovarian follicles, females were classified as reproductively inactive, as indicated by the presence of previtellogenic (unyolked) follicles, or reproductively active, as indicated by the presence of yolking follicles. Reproductively active females were, in turn, categorized according to the size of the largest ovarian follicle. Finally, the reproductively active females were considered to be in their first, second, or third follicular cycles depending whether there were 0, 1, or 2 corpora lutea (CL) present, respectively. In using this procedure, therefore, neither the reproductive condition nor the sexual receptivity of the females was known prior to testing.

In three different groups of females tested in this manner—winter-dormant females environmentally stimulated in either (a) all-female or (b) male-female groups as well as (c) freshly captured breeding females—ovarian state was found to be closely correlated with sexual receptivity. None of the females later found to be reproductively inactive, as indicated by the presence of previtellogenic follicles, was receptive to the courtship of the test male. Similarly, none of the females later found to be in their first follicular cycle but with small (<3.5 mm in diameter) yolking follicles was receptive. In contrast, all of the females later found to have large preovulatory follicles—whether in their first, second, or third follicular cycles—were receptive to the courting males.

Table 3. Criteria for determining ovarian condition of female *Anolis carolinensis*.

State of Ovarian Follicles	Diameter of Largest Ovarian Follicle (mm)	Number of Corpora Lutea (follicular cycle)
Previtellogenic	1.2–1.9	
Vitellogenic	<3.5	0 (first cycle)
	3.5–6.0	1 (second cycle)
	<6.0	2 (third cycle)

Interestingly, in every group, some of the females later found to have medium-sized follicles (3.56-6.0mm) were receptive to the test male while others were not. This suggests that the transition from nonreceptivity to receptivity occurs during this phase of follicular development, but that the exact point of the switch-over varies from female to female. It is possible that these variations may be due to individual differences in neural sensitivity to levels of hormones secreted by the developing follicle.

What do these findings contribute to our knowledge of the reproductive biology of *A. carolinensis?* Female *A. carolinensis* display the typical anoline pattern of reproduction (Crews, 1975*c*). Instead of laying a number of eggs in one or more clutches as do most temperate-zone lizards, female *A. carolinensis* lay a single egg every 10 to 14 days for the duration of the breeding season (Fig. 12). This pattern of ovarian activity is generated by the development of ovulation of a single ovarian follicle alternately between ovaries. It is logical to assume that this regular pattern of follicular development, ovulation, and oviposition during the breeding season also reflects corresponding cyclic changes in the secretion patterns of gonadotropic and ovarian hormones. The demonstration of a close correlation between sexual receptivity and stage of follicular maturation further suggests that sexual receptivity in female *A. carolinensis* is dependent upon hormonal conditions which arise in the course of normal follicular development and is thus rhythmical in nature in a

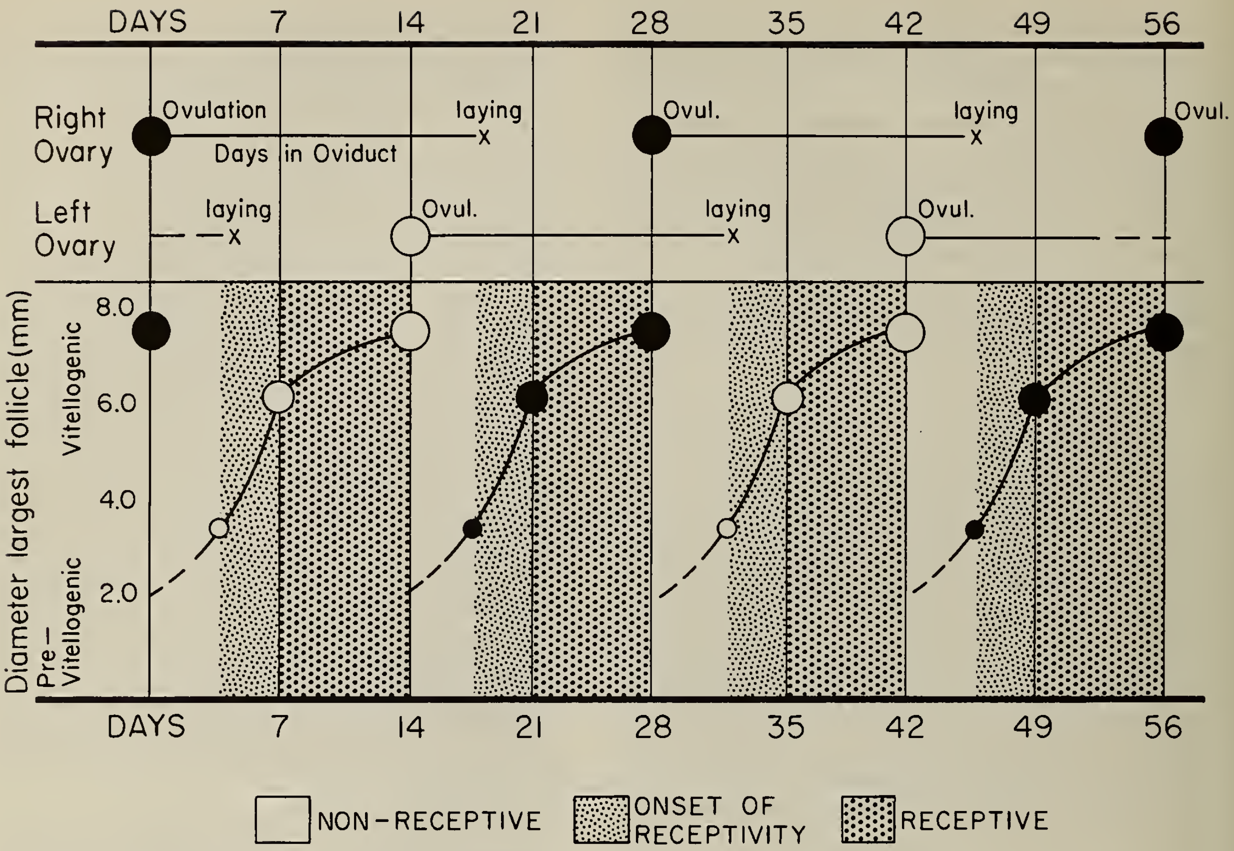

Figure 12. Schematic diagram of the relationship between maturation and ovulation of the ovarian follicle and female sexual receptivity during the breeding season in the lizard, *Anolis carolinensis* (redrawn from Crews, 1973*b*).

way that corresponds to these cyclic ovarian changes.

Coition-induced inhibition of female sexual receptivity

During the course of the above study, I discovered that, if a sexually receptive female was allowed to copulate with a sexually active male, she was no longer receptive when retested 24 hours later. However, if that female was retested several weeks later, she was found to be receptive once again. This suggested that mating might serve to inhibit further sexual receptivity within each follicular cycle, but not later sexual receptivity during subsequent cycles.

While coital inhibition of receptivity in reptiles has not been demonstrated previously, several studies have suggested its existence (Crews, 1975*c*). For example, in their classic work on the social behavior of *A. carolinensis,* Greenberg and Noble (1944) observed that one female "mated on April 13 but ran twice from the male during the same day and did not mate again until April 27" (pp. 401–402). Similarly, in a field study of *A. garmani,* R. L. Trivers (personal communication) observed that females that were allowed to copulate undisturbed were not seen to copulate again for at least another month. If, however, copulation was experimentally interrupted, the female continued to be receptive until completion of copulation. Hunsaker (1962) has also reported observations which suggest that stimuli arising from intromission terminate receptivity in lizards. He noted that reproductively active female *Sceloporus* (*torquatus* group) continued to be sexually receptive if the female's cloaca was covered with tape, thereby preventing intromission by the male.

To investigate this phenomenon experimentally, I conducted an experiment to determine (a) whether mating inhibits further sexual receptivity within each follicular cycle, (b) how rapidly the transition from sexual receptivity to nonreceptivity occurs following successful copulation, and (c) what the critical stimuli that inhibit sexual receptivity are (Crews, 1973*c*).

To answer these questions, sexually receptive female A. *carolinensis* were retested for receptivity either 24 hours, 6 hours, 3–5 minutes, or less than 1 minute following either (1) normal copulation with a sexually active male or (2) after a male was allowed to approach and mount, but not allowed to assume the copulation posture or achieve intromission. A third group of females was initially exposed to hemipenectomized males which were allowed to court and assume the copulation posture but, because their hemipenes had been removed, could not intromit.

The results were conclusive. While all the females which were just courted and mounted by the male remained receptive to male courtship, none of the females that completed copulation was sexually receptive when retested 24 hours, 6 hours, or 3–5 minutes later (Table 4). Of the 12 females retested within 1 minute following separation from the male, three were still sexually receptive. It should be noted, however, that, in these three instances, copulation was incomplete due to interruption and premature separation of the male; all three females ceased to be receptive when allowed to copulate undisturbed. Finally, all seven females tested with the hemipenectomized males were sexually receptive upon retest 3–5 minutes later.

Hemipenectomy also had an interesting effect upon the male. Although the hemipenectomized males courted normally, they copulated significantly longer, often failed to maintain cloacal contact throughout mating despite their proper orientation, and never initiated separation from the female. This suggests that sensory feedback from the hemipenis during intromission and/or ejaculation plays an important role in the maintanence and termination of copulation in the male.

Table 4. Number of female *Anolis carolinensis* still sexually receptive after varying intervals following exposure to either males that were allowed to court and mate with the female (Complete Copulation), males that were allowed to court and take the neck grip and mount, but not intromit (Courtship), or hemipenectomized males that displayed all aspects of normal mating behavior but could not intromit or ejaculate (Hemipenectomy).

Group	n	Number Receptive
Complete Copulation:		
24 hours	12	0
6 hours	6	0
3–5 minutes	12	0
<1 minute	12	3
Courtship:		
24 hours	12	12
6 hours	6	6
3–5 minutes	12	12
<1 minute	12	12
Hemipenectomy:		
3–5 minutes	7	7

There is good reason to believe that this coition-induced inhibition of female sexual receptivity may be an adaptation peculiar to the anoline mating pattern. Female *A. carolinensis* tend to mate with the male in whose territory they have their home range. In the natural habitat, mating usually occurs in exposed areas such as tree trunks, fences, and walls. During this time, the copulating pair is particularly vulnerable to predators since they can be approached and touched without immediately separating. This is presumably due to the male's inability to disengage himself rapidly from the female once intromission is achieved. In addition, copulation in this species is prolonged, often lasting more than 20 minutes.

During the breeding season, females undergo regularly recurring periods of sexual receptivity which are correlated with their cyclic pattern of ovarian activity (see above; Fig. 12). The inhibition, by mating, of further sexual receptivity during each follicular cycle, but not during subsequent cycles, could serve to minimize possible predation and maximize the probability of a female realizing her reproductive potential during a breeding season. Similarly, the specialized sperm-storage ducts that have been described in this species (Fox, 1963) probably function to insure that, following a single successful mating, a female could continue to lay fertile eggs even if the territorial male were no longer present.

CONTROL OF THE REFRACTORY PERIOD IN THE LIZARD, *Anolis carolinensis*

The annual ovarian cycle of the lizard *A. carolinensis* may be divided into three distinct periods: previtellogenesis, vitellogenesis, and regression (see Fig. 2). Previtellogenesis lasts from November to February and is characterized by inactive ovaries containing only small, translucent, unyolked follicles and atrophic oviducts. During this phase, the follicles are initially relatively uniform, ranging from 1.2–1.8 mm in diameter, but gradually increase to 1.8–2.0 mm by late February (Crews, 1973*a*). Yolk deposition (vitellogenesis) begins in March; at this time a single follicle begins to accumulate yolk and enlarges rapidly until it is ovulated at about 8.0 mm. During the ensuing breeding season, a single ovarian follicle matures and is ovulated alternately between ovaries every 10–14 days (see above). Vitellogenesis ceases in late August and the yolking follicles already present in the ovary begin to degenerate rapidly. Follicles undergoing atresia differ from normal follicles and from corpora lutea in that they are highly vascularized, discolored (orange-yellow instead of the bright yellow of a normal follicle), flaccid, and mottled in appearance (Crews and Licht, 1974). These corpora atretica (CA) are gradually absorbed and disappear completely from the ovary during October.

Experimental studies indicate that female *A. carolinensis* are sexually refactory during the early portion of the regressive phase of the annual cycle (see Fig. 2). For example, environmental (both social and climatic) stimuli that promote rapid ovarian growth in winter and spring are generally ineffective in stimulating females in September and October (Crews, 1973*a*; Licht, 1973). Females constantly maintained under stimulatory environmental conditions undergo three to four complete ovarian cycles per year (Crews, unpublished data), suggesting that seasonal ovarian growth and regression are under endogenous control. Furthermore, females appear to respond less rapidly to exogenous gonadotropic hormones in the fall than in winter and spring (Licht, 1970; unpublished data). Females exposed to a stimulatory environmental regime in late August, the beginning of the refractory period, continue to undergo follicular atresia, responding to the unseasonal environmental conditions only after the CA have been resorbed (Crews and Licht, 1974). These lines of evidence suggest, therefore, that refractoriness may be due partly to changes in ovarian hormonal sensitivity as a consequence of the presence of the atretic follicle.

To test this hypothesis, Paul Licht and I conducted an experiment in which refractory females were given daily injection of mammalian (bovine) FSH following the removal of either the CA or a normal follicle. The results were quite clearcut. Females lacking the CA were at least five times more sensitive to the exogenous gonadotropin, as indicated by ovarian and oviducal growth, than females which had had a normal follicle removed (Fig. 13); this suggested that the CA produces a substance(s) which inhibits ovarian sensitivity to gonadotropin stimulation. These results also indicate that the

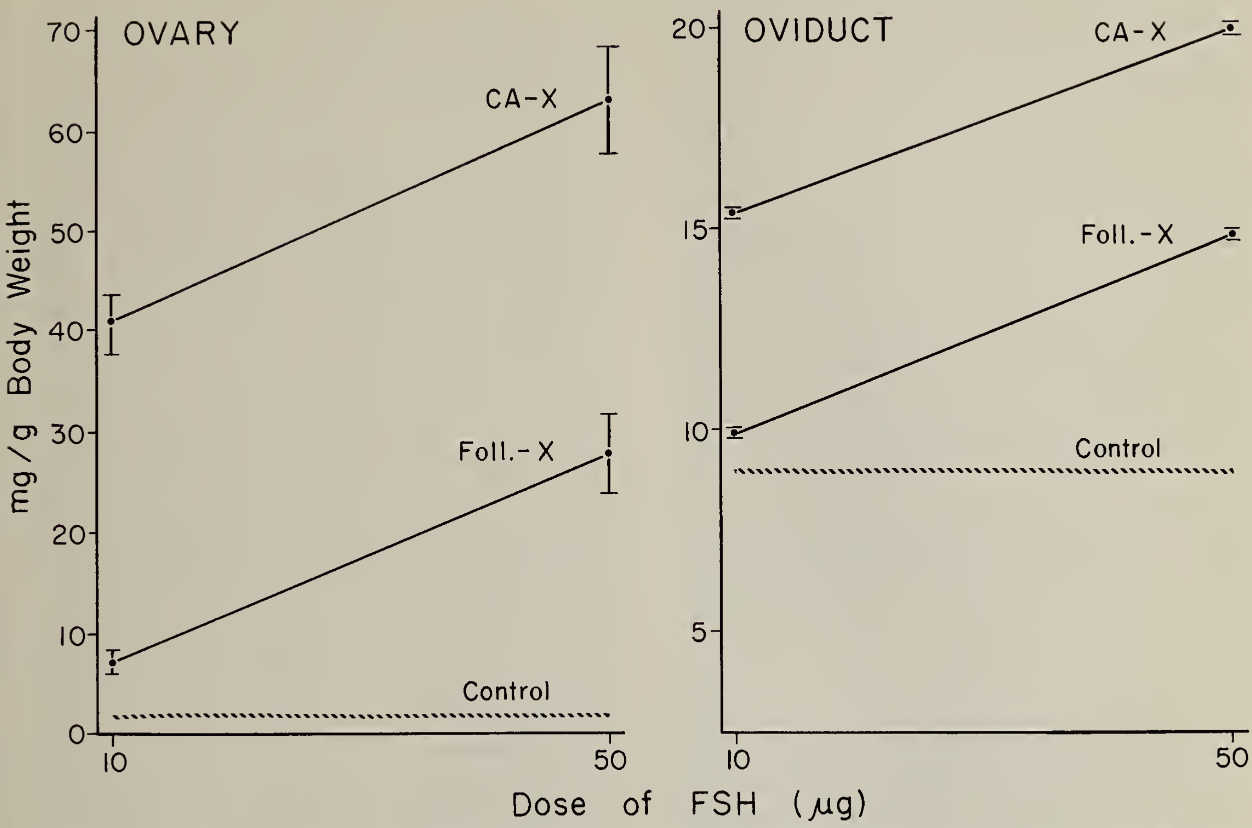

Figure 13. Effect of mammalian gonadotropin (bovine NIH–FSH–S9) on ovarian and oviduct growth in refactory *Anolis carolinensis* following removal of the atretic (CA–X) or normal (Foll–X) ovarian follicle (from Crews and Licht, 1974).

onset of sexual refractoriness in female *A. caroliensis* occurs spontaneously, independent of external factors; hence *A. carolinensis* may be regarded as an obligatory seasonal breeder.

It is generally assumed that the ultimate factors underlying the evolution of seasonal breeding in temperate species act (a) to insure that the young will not appear at a time when food resources are declining or are nonexistent, and (b) to prevent the female from investing energy into reproduction rather than the fat deposition necessary for overwintering. The correlation between the occurrence of CA and the initiation of the refactory period following the normal breeding season and the close temporal relationship between the disappearance of the CA and the onset of sexual responsiveness to environmental stimuli suggest that the CA dramatically increases ovarian responsiveness to exogenous gonadotropin further supports this hypothesis.

CONCLUSION

A number of ecological factors, including climatic (e.g., photoperiod, rainfall, humidity, temperature), structural (e.g., vegetational changes, food availability), and social (e.g., behavioral interaction, experience) stimuli, have been implicated in the control of annual sexual cycles of vertebrates. These factors, whch are believed to modify the timing of partly endogenously determined reproductive cycles and serve to coordinate breeding between individuals, interact to "fine-tune" reproductive processes. Finally, there is good evidence to suggest that, in many species, the male cycle is under strict environmental control while the female cycle is more labile and depends in part upon the performance of specific male behavior patterns and/or the social milieu of the breeding population.

These generalizations appear to be borne out by recent research on the control of seasonal ovarian growth in the lizard, *A. carolinensis*. The use of female ovarian activity as a bioassay for pituitary gonadotropin secretion experiments indicates that: (1) While an unseasonal environmental regime will stimulate out-of-season ovarian recrudescence in winter-dormant females, the presence of an intact conspecific male will cause a significantly more rapid rate of growth and is necessary for normal gonadotropin secretion; (2) The presence of a stable dominance hierarchy is necessary for this facilitation to occur (an unstable dominance hierarchy inhibits ovarian recrudescence); (3) The male behavior patterns responsible for the facilitation and inhibition of environmentally induced ovarian growth are courtship and male-male aggression, respectively; (4) Gonadotropin secretion in the female is graded in accordance with the amount of male courtship behavior to which she is exposed; (5) Both male-courtship behavior and courtship facilitation of environmentally induced ovarian development are dependent upon testicular secretions; and (6) The critical component in male-courtship facilitation of environmentally induced ovarian recrudescence is the ability of the male to extend the dewlap, thus changing his body shape in the species-typical manner.

These findings suggest that, while male courtship behavior insures normal gonadotropin secretion in the female, the absence of this courtship behavior results in subnormal gonadotropin secretion, and that aggression between males actively inhibits or greatly suppresses gonadotropin secretion. Finally, it is possible that the inhibition of environmentally induced ovarian recrudescence by male-male aggression may have been one of the selection pressures favoring the differential male-female vernal emergence that is observed in many temperate vertebrates. Females arriving simultaneously at the breeding grounds with the males would be exposed to the high levels of male-male aggression necessary for the establishment of territories which, as these experiments indicate, would prevent the female from rapidly reaching breeding condition. Females arriving after males have established breeding territories and male-male aggression has waned, however, would be exposed to both optimal environmental stimuli and male courtship and thus be maximally stimulated.

Lizards appear to be well suited for the study of behavioral adaptations associated with breeding. During the breeding season, female *A. carolinensis* undergo regular cycles of sexual receptivity which are correlated with the cyclic pattern of follicular maturation peculiar to *Anolis*. It was demonstrated experimentally that mating inhibits further sexual receptivity within each follicular cycles, but not later receptivity during subsequent cycles; the stimuli responsible for this inhibition arise from the intromission, and possibly the ejaculation, of the male. These findings, when joined with observations of the social system of this species, indicate that females mate with the territorial male once during each estrous cycle and so minimize predation pressure.

This investigation of the factors controlling different phases of the lizard reproductive cycle has also suggested, for the first time, the possible physiological basis for the sexual refractory period that typically follows the breeding season in vertebrates. Experiments indicate that the degenerating follicle secretes a substance(s) which counteracts the effects of both environmental and hormonal stimuli which, at other times of the cycle, reliably elicit ovarian growth.

I believe that the experiments discussed here demonstrate that principles originally discovered with laboratory species can be applied to feral species and shown to have clear adaptive significance in the animal's natural history.

ACKNOWLEDGMENTS

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Note Added In Proof

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Learning Studies in Lizards

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SUMMARY. Originally, learning studies on lizards were largely unsuccessful because workers either used unimportant cues and reinforcers or conducted tests at environmental temperatures too low for the lizards to become active. Recent studies have shown that learning in lizards is temperature dependent. With heat as a reinforcement, lizards quickly learn simple T-mazes, pattern discrimination, and wheel running. Given bursts of heat as reinforcement, lizards can easily learn to press a bar for additional heat. Studies have also demonstrated a lizard's capacity for discriminating noxious prey, latent learning, discriminating color, and learning refinements in thermoregulation.

INTRODUCTION

Reptiles have generally been considered to have less complex behavior than other vertebrates. This view is attributable to the early behavioral studies that were carried out at ecologically unsuitable temperatures. Under those conditions some lizards required more than 300 trials to learn simple tasks (see review in Northcutt and Heath, 1971). In these studies, ambient or radiant heat was insufficient for reptiles to reach normal efficient body temperatures. Such studies were really measuring the animal's metabolic inactivity rather than learning ability (Brattstrom, 1965, 1974). In 1968, Krekorian, Vance, and Richardson showed that learning in lizards is temperature dependent.

Recognizing that lizards assume specific orientations and postures when basking (Brattstrom, 1965, 1971; Heath, 1965), I began a series of studies on their ability to learn in order to develop new techniques for studying social or thermoregulatory behavior. About the same time, Vance and Richardson and their co-workers initiated a series of studies on learning in lizards using ecologically relevant cues and reinforcers to study brightness discrimination, temperature dependent learning, and reversal learning (Bicknell and Richardson, 1973; Garzanit and Richardson, 1974; Julian and Richardson, 1968; Krekorian, Vance, and Richardson, 1968; Richardson and Julian, 1974; Vance, Richardson, and Goodrich, 1965; and Peterson, MS). Burghardt (in press) has recently prepared an extensive review paper on learning in reptiles. I will mention here some of the key studies on learning and then describe some of the work done in my laboratory over the last 12 years that has not been previously reported.

Turtles, caimans, and the tuatara have been used in studies on reversal, spatial, discrimination, maze, and probability learning (Kirk and Bitterman, 1963, 1965; Williams, 1967*a*, 1967*b*, and 1967*c*; Williams and Albiniak, 1972; Williams and Robertson, 1970). Northcutt and Heath (1971, 1973) showed rapid learning in both caimans and tuataras using one-choice point T-maze with "return to home pen" as reinforcement. They

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Note: Instead of presenting this paper at the symposium, I presented its conclusions and then did a simulation-game of creating a lizard and its behavioral, evolutionary, genetic, anatomical, and physiological components using the participants in the symposium to play "parts" of the lizard and its environment. The task was to have the lizard awake, eat, escape from predators, and engage in aggressive behavior. The function of the players was to try to integrate their interactions. The main purpose of the game was to determine the complexity of the lizard, to recognize the portion of the lizard others were studying, and to increase the intellectual and social communication and interaction of the players.

then ran rats in the same maze using food as a reward and showed that they learned at approximately the same rate.

COLOR DISCRIMINATION

Color plays an important role in the protective coloration and displays of lizards and in the protective or aposematic color of their prey. (Rensch and Adrian-Hinsberg, 1962; Swiezawska, 1949; Wagner, 1933). Sexton (1964) showed that *Anolis carolinensis,* given a large variety of insects to choose from, learned to eat those that were the least distasteful. Later, however, Sexton, Hoger, and Ortleb (1966) found that, if the lizards were hungry, they would eat more of the distasteful insects. These lizards may have been responding to the insect's shape and pattern as well as color. Romspert, in my laboratory, exposed the whiptail lizard, *Cnemidophorus tigris,* to meal worms injected with green and red food coloring having no taste. The red worms were also injected with Angostura Bitters. After 1 to 2 trials, lizards learned to reject the red worms. This rejection continued for 7 to 11 trials (of 1 to 24 hours length). Subsequent contact (1 to 2 exposures) with bitter worms sustained the rejection behavior. The lizards may or may not have discriminated hues, rather than colors, and the aromatic effect of the bitters may have been a factor.

Benes (1969) studied color discrimination in whiptail lizards. She found that some lizards reached criterion in 6 to 10 trials, while others required 30 to 149 trials to reach criterion. Retention of discrimination ability (errorless periods) ranged from 3 to 14 weeks (13 to 74 trials).

USE OF ECOLOGICALLY RELEVANT REINFORCERS

While food is often useful as a reward in learning studies on birds and mammals, the size and energy requirements of lizards are such that satiation may develop before learning a given task. In connection with research on thermoregulation, I began a series of studies on learning, using heat as reinforcement. These studies, based on those of Weiss (1957) and Weiss and Laties (1961), utilized shuttling, bar pressing, maze learning, and other tasks (see below). Vance and Richardson and their co-workers also used ecologically relevant rewards, including heat from the substrate, radiant heat, a simulated burrow for escape for diurnal lizards, and a dark box for nocturnal lizards (Garzanit and Richardson, 1974; Julian and Richardson, 1968; Richardson and Julian, 1974; Vance, Richardson, and Goodrich, 1965). White (personal communication) had had success using dried lettuce wafers as a reinforcement for the large *Iguana iguana.*

Vance, Richardson, and Goodrich (1965) studied brightness discrimination in the collared lizard, *Crotaphytus collaris,* using meal worms and 3 minutes of substrate heat as rewards, and shock to punish incorrect responses. With five trials per day for 5 weeks, lizards reached criterion in 335 trials, whereas rats in the same maze required 105 trials. Better performance was shown by the desert iguana, *Dipsosaurus dorsalis* (Garzanit and Richardson, 1974; Peterson, MS). Krekorian, Vance, and Richardson (1968) found temperature dependent maze learning (two mazes of 2 and 4 choice points) in the desert iguana, *Dipsosaurus dorsalis,* with heat from the substrate as reinforcement. Lizards kept at substrate temperatures of 22°C between trials showed no learning at 125 trials, while those kept at 32°C did better than those at 27°C, (Mean trials to criterion for Maze I were 125 at 22°, 105 at 27°, 65 at 32°; for Maze II, 160 at 27°, 105 at 32°).

Davidson and Richardson (1970) showed that classical conditioning of autonomic and skeletal responses in *Crotaphytus collaris* took far fewer trials (150 vs. 600) when the body temperature was raised from 27–29° to 35°C. Reversal learning in *Dipsosaurus* was studied by Vance and Richardson (1966), using brightness and position cues for discrimination and reversals. Reinforcement consisted of 3 minutes of heat from the substrate and a meal worm. Experiments done at body temperatures of 43±2°C revealed an interesting age difference in learning. Young lizards reached criterion on the average of 35 trials, while older lizards reached criterion on the average of 57 trials. This result may have nothing to do with age, but may simply reflect a more rapid warming of the smaller animals. Thus the reward "magnitude" may be greater for the younger than the older lizards. Reversal learning in *Anolis carolinensis* has been investigated by Peterson (MS; Peterson, Norton, and Richardson, 1975).

Vance and Baird (MS and personal communication) studied learning behavior in the nocturnal banded gecko, *Coleonyx variegatus*, using 1 minute in a dark box as positive reinforcement, and light as negative reinforcement. Experiments were done at 15° and 30°C. The most rapid learning of brightness and pattern discrimination occurred at 30°C. The mean (and range) of trials to criterion for a brightness discrimination was 201 (40 to 300) at 15°; and 77 (16 to 110) at 30°; for pattern discrimination, no test at 15°; and 100 (40 to 160) at 30°. The lizards did not show any spatial reversal learning when tested at 30°C.

THERMAL REINFORCEMENT FOR MAZE LEARNING

Experiments in my laboratory were undertaken to learn whether or not heat would serve as a reinforcement for maze learning in lizards. In a simple T-maze an infrared heat lamp was used to supply reinforcement. If the lizard went to the wrong box, it was allowed to explore the maze until it found the reward box or until 30 minutes had elapsed. Lizards quickly learned to go to the warm end of the maze. Lizards could see the light of the infrared bulb but could not detect the differences in temperature at the choice point. Lamps were kept on at the same end (left or right) for 12 trials, switched for 7 trials, and then switched again for a total of 24 trials (12+7+6=24). Two chuckwalas, *Sauromalus obesus*, learned to go to the reward end on the first and second trials. One *Cnemidophorus tigris* learned the initial direction in two trials and switched immediately (1 trial) after the lights were reversed. After switching, all lizards had correct responses until the next switch. A single *Ctenosaura hemolopha* seemed so disturbed by the apparatus and the observer that it often refused to move from the starting position. It is not clear to me, however, whether the testing procedure reveals learning or simply rapid detection of thermal information. As a control for this possibility, Myres placed three *Dipsosaurus* in a T-maze and taught them to turn either right or left by the technique of corrected trials with 2 minutes of radiant heat as reinforcement. The heat lamp was not turned on until after the lizard reached the correct goal box. The average time to complete 5 sets of 5 trials each was reduced from 3.51 to 0.51 minutes, and the average number of incorrect responses for the 5 sets decreased from 4 to 2. This result suggests that the lizards learned the task, a finding in agreement with maze learning studies of others (Julian and Richardson, 1968; Krekorian, Vance and Richardson, 1968).

OPERANT CONDITIONING IN LIZARDS

In 1961, Anderson and I initiated a study on the use of heat as a reinforcer in learning. Western fence lizards, *Sceloporus occidentalis*, were used. They were placed in a box in which the weight of a lizard on one side activated a microswitch and turned on a 250 w infrared lamp. When the lizard left that side of the box, the lamp would turn off. Lizards placed in the box on the nonreward side would explore until by chance they entered the side containing the microswitch. When the lamp turned on they would bask up to an average body temperature of 38°C and then go to the cool side of the box. As soon as their body temperature dropped to an average of 24.5°, they would go to the reward side of the box. Minimum and maximum voluntary temperatures for these lizards in the field are 26.4° and 38.0°C respectively (Brattstrom, 1965). Hence, their behavior in the resting box appeared to represent one trial learning. As a further refinement, Harlow constructed a box in which only a small portion of the floor could drop and turn on a heat lamp, the light of which directed toward the treadle area. The experiment was conducted in a cold room (8°C). After wandering about the box and accidentally contacting the treadle and becoming warm, lizards would retreat to the cool areas of the box. After 1 to 10 minutes and a decrease in body temperature of 1 to 5°C, all lizards returned to the treadle (average body temperature leaving heat, 37°; leaving cold, 35°; mean body temperature of field animals, 35.0°C [Brattstrom, 1965]). Subsequently, shuttling behavior became more frequent and the range of body temperatures of the five tested animals was reduced (Harlow, personal communication). Thermoregulation had become more precise.

A next step was to construct a bar-pressing apparatus for operant conditioning. The animals were placed in a galvanized screen cage with a 250 w infrared lamp that is turned on when a lizard presses a small bar with his head or limbs. The heat lamp turns off at any number of fixed time periods. The time periods are changed according to the species so that there can be adequate heat gain. Body temperature is monitored by means of a thermister. In an initial study with five *Dipsosaurus,* Payne (personal communication) found that once the lizards encountered the bar, they would press the bar 1 to 17 times and raise their body temperatures from 30 to 34° to 38°C. After 15 to 40 minutes, they would leave the bar and not return. Subsequently, Stevens placed *Sceloporus occidentalis* in this apparatus and observed repeated bar pressing with return to the bar after cooling (Stevens, in press). Richardson and Brown (1975 and MS) have obtained excellent results in similar experiments with *Dipsosaurus,* although *Crotaphytus collaris,* the collared lizard is an even better subject (Richardson, personal communication).

LEARNING THE THERMAL MOSAIC OF THE ENVIRONMENT

Diurnal basking lizards (largely Iguanids and Agamids) spend a considerable amount of time in behavioral thermoregulation (Cowles and Bogert, 1944; Brattstrom, 1965, 1971; Health, 1965; and others). A minimum body temperature is required for a lizard to raise its metabolic rate to an efficient operating level. Behavioral and physiological mechanisms that allow a lizard to reduce basking time are advantageous in that they allow more time for other activities such as foraging, mating, and so forth. Efficient use of the thermal mosaic of the environment is one of the several ways lizards can reduce basking time (Brattstrom, 1965; Heath, 1965; and Templeton, 1971). Heath (1962) showed in the laboratory that morning emergence of horned lizards, *Phrynosoma,* was due to their biological clock, and that lizards that emerged prior to the turning on of heatlamps would go to patches of ground that were first struck by the light of the lamp.

DeWitt (1967*a*) carried out a series of experiments in a circular thermal gradient with *Dipsosaurus dorsalis* to show that this species becomes more precise in its behavioral regulation of body temperatures with more experience in the gradient.

For many species, laboratory-determined preferred body temperatures are characteristically lower (or higher) than field determined mean body temperatures. McGinnis and Dickson (1967) and DeWitt (1967*b*) brought the problem of the differences between behavioral thermoregulation in the field and the laboratory into question. Does the preferred body temperature of lizards determined in a thermal gradient relate to the mean body temperature in the field?

My approach to the problem was as follows: An elongated photothermal gradient, 10 x 2 x 3 ft., was constructed of wood and filled with four inches of sand and kept in a darkened room with an ambient temperature of 22±3°C. A 250 w white-bulb infrared light provided a thermal gradient of 22 to 55°C. Eleven adult male *Dipsosaurus dorsalis* and six *Sceloporus magister* with a diverse previous thermal history were the subjects. The lizards were not fed for 2 to 3 days prior to experiments and were kept at room temperature without additional light or food for the 4 or 5 days of the experiment. On consecutive days, a single male lizard was placed in the thermal gradient for *1 hour only* each day. Four to five lizards were run each day, but each individual was run at the same time in the day. Body temperatures were monitored continuously with YSI Telethermometers. The thermal gradient was monitored continuously to insure stability.

Figure 1 presents the results of a typical lizard in the gradient on 5 successive days. Initially a lizard would run around the gradient, discover the heat source, heat up, and then proceed to engage in shuttle behavior in order to maintain its preferred body temperature. On subsequent days, however, (see Fig. 1 and Table 1), they became more precise in their thermoregulation. Apparently, they had learned to use the thermal mosaic of the gradient to reduce the time needed to warm up and maintain a preferred body temperature. Table 1 presents data on mean variation in body temperature over the last 30 minutes (after initial heating) during the lizard's hour in the gradient on successive days. It is clear from these data that the variance is reduced (i.e., the lizard became more precise in its ability to behaviorally thermoregulate). The findings confirm those of DeWitt (1967*a*, *b*) and additionally show that the lizards can increase their thermoregulatory precision with only 1 hour of experience in the gradient per day. Another interesting observation was that in the process, there was a change in mean body temperature with each day. *Dipsosaurus,* while reducing variance in mean body temperature, raised its preferred body temperature on each subsequent day (mean of 1 minute readings over last 30 minutes). *Sceloporus magister*, on the contrary, lowered its preferred body temperature on each subsequent day (Table I). Acclimation effects prior to the experiment may have resulted in these changes, but animals of both species were treated similarly.

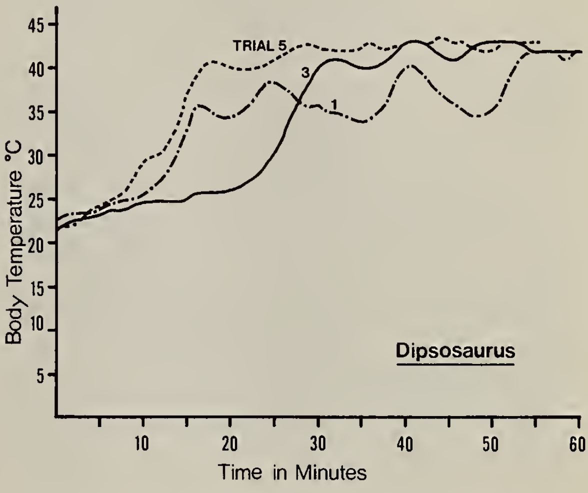

Figure 1. Precision of temperature regulation in lizards. Body temperatures of a single *Dipsosaurus dorsalis* monitored continuously when placed in a thermal gradient for one hour only a day. Data are for days 1, 3, and 5.

TABLE 1

Precision of behavioral thermoregulation in lizards. Mean variation in body temperatures (°C) of lizards for the last 30 minutes of an hour in a thermal gradient (see text). Dd.d-*Dipsosaurus dorsalis*, S.o.-*Sceloporus magister.*

Species	N	Trial				Remarks
		1	2	3	4	
D.d.	5	4.4	3.9	1.2	2.5	with means rising from 39.5–40.0.
D.d.	4	4.4	4.5	1.3	.8	with means rising from 37 to 43.
S.o.	5	4.5	2.2	2.0	1.8	with means decreasing from 38.0 to 36.8.
Average		4.5	3.4	1.5	1.7	

The present results indicate that (1) lizards can learn to use their thermal environment rapidly and efficiently; (2) lizards become more precise in their behavioral thermoregulation with increased exposure to the environment; (3) in thermal gradient studies (especially those dealing with preferred body temperatures), there must be at least a standard number of days for a lizard to be in the gradient, and a record of daily preferred body temperatures. For such experiments it would be desirable for workers to use the same size and shape thermal gradient with the same thermal parameters, but this is impractical. It is essential to state (1) the gradient size; (2) its thermal parameters including detailed descriptions of the heat source; (3) duration of time animals are in the gradient; and (4) the previous thermal and feeding history of the animals. Some workers feed their animals in the gradient, but Regal (1966) has shown that preferred body temperatures are higher after feeding. Further, it is important to have standardized photoperiods and, in view of rhythmic changes, to record temperatures at the same time each day. It is mandatory that only one lizard be in the gradient at one time as it was shown by Regal (1971, 1974) that the dominance relationship between lizards in a thermal gradiant can affect both their activity and preferred body temperatures.

WHEEL RUNNING

In an attempt to develop methods for measuring the effort and energy used in behavioral temperature regulation, I tried to get a lizard to run in a "hamster exercise wheel." Four *Cnemidophorus tigris* (numbered 1 to 4 in order of social dominance) were placed in a 110-gallon terrarium with sand, rocks, and a 250 w white-bulb infrared lamp at one end. The lamp and room lights were on from 0700 to 1900 hours. After several weeks, two hamster exercise wheels (6 inches in diameter) were placed in the cage. The lizards would not run when placed inside the wheel even when it was lined with sandpaper. Each lizard (except #2) was placed on the outside of the wheel for 1 minute. Occasionally the wheel would turn a bit while the lizard was on it. On subsequent days the lizards would spontaneously crawl on the wheel and keep it turning while facing the heat lamp, often with the tail braced against the ground. Wheel running data for the above experiment are presented in Table 2. Interestingly, the most subordinate lizard (#4) did not use the wheel. He would emerge from his burrow only when other lizards were inactive. The dominant and largest lizard often left the wheel to chase one of the subdominants or to patrol the terrarium. He, therefore, spent less time on the wheel than the subdominants, but moved the wheel faster.

This simple experiment has possibilities for investigating a variety of time/activity/energy problems with lizards. It has convinced me that lizards can be taught to do a wide variety of tasks if the tasks are related to their natural activities in the field.

"UNREWARDED" EXPLORATION AND LEARNING OF COMPLEX MAZES

Exploratory behavior occupies a considerable portion of an animal's time. While food, heat, and mates may be found in the course of this activity, much of such behavior is unrewarded. Yet, in the process, the animal learns much about its environment and may, when needed, utilize this information to ob-

TABLE 2

Wheel running in the whiptail lizard, *Cnemidophorus tigris.*

	Lizard number*			
	1	2	3	4
Av. length of time on wheel in seconds	24.6	41.3	32.3	0
Av. # revolutions/sec.	.78	.67	.65	0
Speed, inches–sec.	14.04	12.06	11.70	0

*in order of dominance, #1 highest.

tain food, warmth, or shelter. It has been shown, for example, that mice familiar with an environment were more successful in escaping from a screech owl than those without any experience in the same habitat. The experienced mice escaped into burrows that were never formerly used (Metzgar, 1967). Such "unrewarded" learning has been referred to, perhaps erroneously, by some zoologists as "latent learning." Brant and Kavanau (1964) ran both wild and laboratory mice in very complex mazes and found that most of them spent considerable time exploring. In addition to familiarizing an animal with its habitat, this activity may be self rewarding in terms of metabolic requirements.

To test for the possibility of "unrewarded" learning in lizards, Fonda and I utilized a complicated maze (Fig. 2) that had sensing devices for recording the place and times of the lizard's movements. Each of three wood-covered compartments (#1, 9, 13) had a 15 w incandescent light. The entire maze was illuminated by an overhead 100 w incandescent light bulb and the room temperature was 21±2°C. Twenty-two lizards, *Sceloporus occidentalis*, were placed, one at a time, in compartment 11 of the maze and left for 23 hours. The lizards were not observed during this period. A lizard was then removed and cooled at 10°C for 5 minutes, after which it was replaced in area 11. Lizards were removed when they reached a heat source or after 30 minutes (see Table 3). Of the 22 subjects, 87 percent went directly to a heat source (usually within 5 minutes), and of these 55 percent went the shortest way (compartments 11, 12, 13). While in the maze the first time, these animals presumably explored the maze, encountered the heat lamp, and were thus rewarded. When cooled and returned to the maze, their retention of the information about the maze allowed them to go directly to the heat source. Whatever the behavioral response is called, the significant fact is that lizards explore their environment, learn it well, and are able to use the information on subsequent occasions.

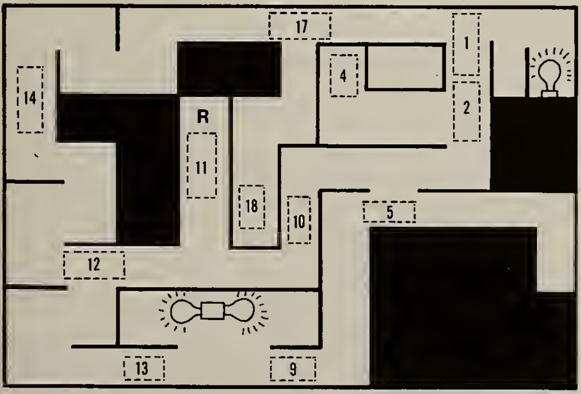

Figure 2. Diagram of the maze used to study "unrewarded" learning in the western fence lizard, *Sceloporus occidentalis*. Numbers represent treadles that monitored the lizard's movement. Lizards were released into the maze in chamber 11 at R.

CONCLUSION

It is clear that lizards can learn a variety of tasks, exhibit different types of learning, and learn most readily when provided with ecologically relevant reinforcement. The kind of experiments reported here can be useful to three types of investigators. Psychologists would find such experiments helpful in shedding light on conventional problems. Neuroanatomists and neurophysiologists will find the experimental procedures useful in investigating neurological correlates of behavior. Ecological behaviorists can utilize learning studies for gaining a further

TABLE 3

"Unrewarded" maze learning in the western fence lizard, *Sceloporus occidentalis*. Results of 22 lizards' performance after exploration of a complicated maze for 23 hr. with three heat sources, subsequently cooled at 10°C for 5 min. and returned to the maze.

	Number	Percent
Lizards going directly to heat source:	19	87
Lizards never reaching heat source in 30 min.	2	9
No movement	1	4

understanding of lizards in an ecological and evolutionary framework.

In conclusion, it is worth mentioning a few caveats. The psychologist may come up with *the* lizard (as with *the* rat and *the* monkey) for comparative studies with other classes and neglect learning studies in a diverse series of lizards. Unless the experimental neurologist is aware of the importance of ecologically relevant reinforcers, there is a danger that the findings may be irrelevant. Unless the ecological behaviorist pays attention to factors of learning, he may neglect aspects of the lizard's behavior and physiology that are perhaps equally as important as the genetic determinants of behavior.

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Behavioral Differences Between Reptiles and Mammals: An Analysis of Activity and Mental Capabilities

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SUMMARY. In the following discussion I have attempted to develop an ecological and evolutionary perspective in which behavioral capacities of reptiles can be isolated from one another and analyzed as adaptive tactics and strategies. I will discuss new information in cellular and cardiovascular physiology, as well as in behavioral and population ecology. My goal is to provide an appreciation for the difficulties and rewards one may encounter as he tries to understand the occupation of different adaptive zones by reptilesand hence the adaptive functions of their nervous systems.

ACTIVITY IN REPTILES

Foraging

Descriptive accounts of reptile activity rarely reveal the *foraging strategy,* or sequence of behaviors leading to an encounter with prey. The following accounts of foraging strategies are based on my own observations on the reptiles of the New World tropics and North American deserts, on discussions with colleagues, and on the fragmentary literature.

I wish to identify, for discussion, points within a spectrum and not to imply categories with boundaries.

Sit-and-wait Predators occupy a perch while active. Here diurnal reptiles bask and watch for prey to emerge or wander by, only occasionally rushing out to catch a passing insect, drive off an intruder, mate, or change position. Some sit-and-wait predators change perches occasionally, others frequently.

Cruising Foragers may move about their home range slowly, alert and responsive to prey but not obviously "searching for" prey. Such reptiles are more likely to find heterogeneously distributed prey species.

Intensive Foragers are characterized by the rapidity with which they move about over a relatively large home range, but they also appear to visually scan the environment with frequent jerks of the head and examine the substrate with frequent tongue flicks. Digging and poking the snout into holes and under litter are also frequent. Intensive foragers may spend much energy in hunting for food and thereby gain access to concealed and/or heterogeneously distributed food resources unavailable to the sit-and-wait predator or even the cruising forager (Schoener, 1971).

The Iguanidae, Agamidae, Chameleonidae and Gekkonidae—members of Camp's (1923) Ascalabota—provide some of the best examples of the sit-and-wait predatory strategy. As described by Cogger (1967) the agamid (*Amphibolurus inermis*) is usually seen on its perch, even in the very hottest part of a summer's day, from which it makes forays to catch passing insects (also Heatwole, 1970). Similar observations are seen in the iguanids *Uta* (Tinkle, 1967) and *Crotophytus* (Fitch, 1956). Similarly the geckos I have seen are quite active if insects are abundant; otherwise they sit-and-wait for prey. At least some of the gecko-related

Pygopodidae (Underwood, 1971) may engage in "ambush" predation (Cogger, 1967).

Many herbivorous lizards live where plant food is abundant and extensive searching is not necessary, e.g., *Sauromalus obesus* (Nagy, 1973) and *Iguana iguana* (Moberly, 1968*a*). Some *Anolis* will change position frequently and are, to that extent, "intensive foragers."

Intensive foraging is well developed in the autarchoglossan Varanidae (C. Gans, E. Pianka, personal communication; Auffenberg, this volume) and (macro) Teiidae (Hardy, 1962; Hirth, 1963; personal observations), and in certain species of Lacertidae (C. Gans, E. Pianka, R. Huey, D. Karns, personal communication), and Scincidae (Fitch, 1954).

I suspect (see below) that the primitive lizard was a cruising forager and that there was an evolutionary trend toward specialization as (1) visually oriented sit-and-wait predators among the Ascalabota and (2) "olfactory" as well as visual searchers and active foragers among the Autarchoglossa. It is interesting that *Klauberina* (Xantusiidae), which may be the most "primitive" lizard extant (Regal, 1968; Underwood, 1971), is intermediate in spontaneous locomotion between a sit-and-wait strategist and an intensive forager (Fig. 1). The presence of intermediate foraging strategies in both of the major groups is, then, best viewed as the retention of an ancestral pattern.

I made quantitative field observations on the foraging activity of an iguanid (*Leiocephalus schreibersi*) and a teiid (*Ameiva chrysolaema*) at Barahona, Dominican Republic. *Leiocephalus* basked in the sun from sunrise to sunset, and movements consisted of short rapid dashes of never more than 2 seconds in duration to catch insects or chase conspecifics. The frequency of such dashes was only 9.6/hour. Although the animals sat immobile for more than 99 percent of the day, they were usually alert and obviously capable of quick movement.

The *Ameiva* were active for only 4 to 5 hours during the middle of the day, but were moving for probably more than 70 percent of this time (except for one windy day when they were largely immobile and basking). The constant movement in and out of low thorny vegetation complicated precise estimations, but my estimation is that *Ameiva* move their length every 2 to 5 seconds while foraging and constantly probing with their snouts.

Leicephalus, *Ameiva*, and the xantusid *Klauberina* were captured and maintained in the laboratory on a 12:12 light-dark cycle in thermal gradients and fed on meal worms and ground beef. After 1 year their spontaneous activity was measured in a 1 x 1 m white open-field apparatus marked into 25 squares, with a 250 watt red-glassed heat lamp in one corner to permit thermoregulation. To avoid disturbance, observations were made by closed-circuit television. All lizards were fed.

The differences between the three lizard species in the rates at which lines were crossed were all statistically significant (Fig. 1). The rate for *Ameiva* was comparable to a laboratory mammal under the same conditions. The behavior of *Leiocephalus* and *Ameiva* appeared to reflect their activity in nature. *Klauberina* is a secretive species and its behavior in nature is unknown.

Thus, the usual image of a lizard as primitively sluggish is incorrect and misleading. Activity or its lack largely reflects foraging strategies and there is a spectrum of these among lizards.

Teiids and varanids possibly serve as a much better model for the organization of "mammalian behaviors" at a reptilian level of organization than do the more commonly studied iguanids or other less active reptiles. Detailed studies of reptilian ecology, neurology, and behavior provide useful insight into the selective factors that shaped the mammalian brain, as will be made clear in the latter sections of this paper.

INDICES OF AROUSAL

Behavior

A lizard's behavior is not a reliable indicator of its level of arousal. Immobile lizards

FIGURE 1

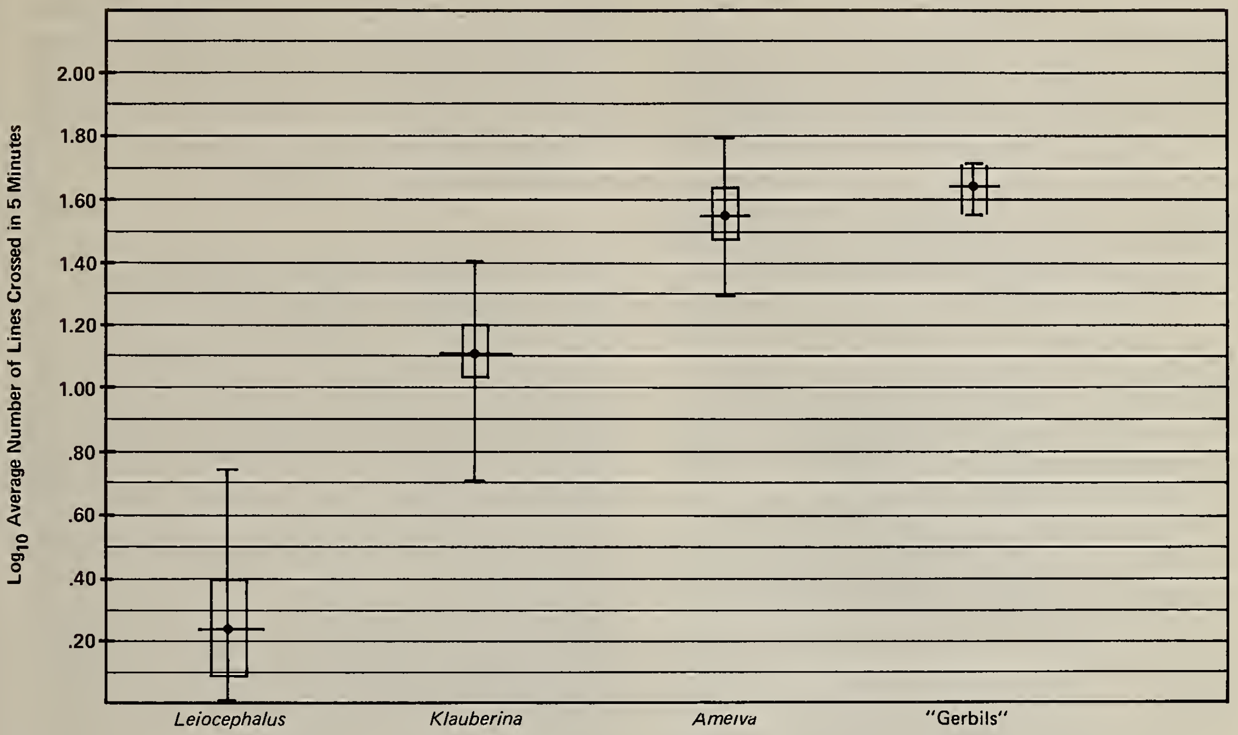

Figure 1. *Rates of spontaneous activity in three lizard species and a mammal. Leiocephalus schreibersi* (Iguanidae) is a sit-and-wait predator. The behavior in nature of the secretive *Klauberina riversiana* (Xantusidae) is poorly known. *Ameiva chrysolaema* (Teiidae) is possibly typical of the intensive forager teiids. Here in a laboratory open-field test, the rates at which *Ameiva* crosses lines are comparable to those for a "gerbil" (*Meriones unguiculatus*).

After 15 minutes in the open field, the number of lines crossed was recorded for the next 15 minutes. Each individual was studied once in the morning and once in the afternoon, and these data were pooled and reported as a 5-minute average. $n=6$(L.s.), 8(K.r.), 9(A.c.), 2(M.u.).

n=the number of individuals in each sample. The range and one standard error are indicated on each side of the mean. Analysis of variance procedures showed a highly significant species effect ($F=39.5$, Degrees of Freedom = 2, 20, $p << .001$). Further, multiple comparisons based on the F-statistic showed that means for all lizard species were significantly different at the 0.1 percent level. Statistics were performed for log-transformed data.

may be engaged in the energetic function of basking. Often, basking lizards appear alert and responsive to moderate stimuli. And, at other times, they are somewhat refractory to visual, auditory, or tactile stimuli (Greenberg, 1973). The immobility of some lizards may also result from their sit-and-wait strategy of predation. So for this reason, too, their level of arousal may not be clear from simple behavioral observations.

Electroencephalography

The literature shows that the arousal spectrum of the brains of reptiles may not be described by any simple set of criteria. Information is available on 14 species of reptiles (Table 1). The interpretation of EEGs is confusing because it is difficult to know if a reptile is "sleeping." In only a few of the studies has any attempt been made to correlate EEGs with changes in arousal thresholds.

"Behavioral arousal" may be accompanied by an increase in the amplitude of the EEG. I have observed it in *Tupinambis*. Hunsaker and Lansing (1962) reported a decrease in amplitude in *Sceloporus*.

TABLE 1

Crocodilia
  Caiman sclerops (Flanigan et al., 1973)
  C. latirostris (Peyrethon and Dusan-Peyrethon, 1969)

Snakes
  Python saebe (Peyrethon and Dusan-Peyrethon, 1969)

Lizards
  Chameleo jacksoni (Tauber et al., 1966)
  C. melleri (Tauber et al., 1966)
  Ctenosaura pectinata (Tauber et al., 1968; Flanigan, 1973)
  Iguana iguana (Peyrethon and Dusan-Peyrethon, 1969; Flanigan, 1973)
  Sceloporus olivaceus (Hunsaker and Lansing, 1962)

Turtles
  Caretta caretta (Susic, 1972)
  Emys orbicularis (Karmanova et al., 1972; Vasilescu, 1970)
  Geochelone carbonaria (Flanigan, 1974; Hartse and Rechtschaffen, 1974)
  Terrapene carolina (Flanigan et al., 1974)
  Testudo denticulata (Walker and Berger, 1973)
  Testudo marginata (Hermann et al., 1964)

Heart Rate

Cowles and Phelan (1958) could not detect any clear evidence of fear in rattlesnakes unless they were touched or could detect movement. The authors monitored heart rates as an index of the arousal caused by noxious odors and found an increase. Experience shows that heart rate might be used as an objective index of arousal for species where behavioral criteria are ambiguous or difficult to detect. Sassaman (1974) found heart rate to be a useful indicator of response in studies on social behavior in iguanid and agamid lizards. Even with this technique, however, caution is advised. Belkin (personal communication) reports that in captive green iguanas (*Iguana iguana*) there is a decrease of the heart rate as part of a "fear" response. The hog-nosed snake has a slower heart rate during death feigning (McDonald, 1974). All available information points to a need for more study of indices of arousal and caution in using those now available.

ACTIVITY RHYTHMS AND TEMPERATURE REGULATION

The classic paradigm for the regulation of motor activity levels in reptiles derives from the studies of Cowles and Bogert (1944) and Bogert (1949) on desert reptiles. Lizards emerge in the morning and orient to the sun. Their body temperatures rise through a *basking range* of temperatures until they become alert and active in an *activity range.* In this activity range, various physiological and behavioral processes are at or near an optimum (Dawson, 1975). The level of behavioral arousal is regarded as temperature dependent.

Endogenous biological rhythms are known to determine locomotor activity in reptiles under constant conditions (Barden, 1942; Brett, 1971; Bustard, 1970; Cloudsley-Thompson, 1965, 1970; Evans, 1966, 1967; Gourley, 1972; Heath, 1962; Heckrotte. 1962; Hoffman, 1960; Regal, 1968; Norris and Kavanau, 1966; Mangelsdorf and Hauty, 1972; Marx and Kayser, 1949; Mautz and Case, 1974; Underwood and Menaker, 1970). Here, the level of arousal appears to be time dependent.

To reconcile the apparent thermal and temporal inconsistency, one must envision a system in which temperature and biological rhythms interact to control activity and alertness in lizards.

We know little about control mechanisms of locomotor activity cycles in lizards. More is known about a rhythm of temperature preference (Regal, 1967, 1968, 1974; Myhre and Hammel, 1969; Gehrmann, 1971; Spellerberg, 1974; Hutchison and Kosh, 1974; Engbretson and Hutchison, 1976). Brain lesions in the posterior hypothalamus involving the mammillary bodies extended the period of voluntary hypothermia in the desert iguana, *Dipsosaurus dorsalis* (Kluger, Tarr, and Heath, 1973).

Temperature-activity relationships

Several types of reptiles may be active at night but bask at least occasionally during the day. The implications are interesting. We usually assume that central nervous system (CNS) activity in reptiles or mammals is limited at low temperatures, but in these nocturnal reptiles the greatest activity may be at low temperatures, suggesting a circadian rhythm of arousal inversely related to high body temperature.

Crocodiles, during some months of the year, bask on land for much of the day but are active primarily at night in the water (Regal, 1968; Lang, 1976), while a snake such as the sidewinder *Crotalus cerastes* regulates its body temperature by basking (Cowles and Bogert, 1944), but is largely active at night. I observed that an individual boa constrictor in a thermal gradient basked and elevated its body temperature only after feeding. It had not previously basked even in preparation for activity (Regal, 1966).

In contrast, we know comparatively little about the natural history of nocturnal lizards and other reptiles. Various nocturnal geckos (Brattstrom, 1952; Bustard, 1967) as well as the tuatara may have activity rhythms inversely related to basking behavior. Also, some diurnal turtles and the marine iguana, among others, may forage in cool water, yet bask at higher body temperatures.

Influence of the third eye on activity and thermoregulation

Many species of lizards possess a third eye that appears as a small differentially pigmented speck on the top of the head. The eye is part of the pineal system, and there is an extensive literature on the pineal system of vertebrates. A number of studies have shown that the parietal eye is biochemically highly active and electrophysiologically responsive. (See reviews by Wurtman et al., 1968; Eakin, 1973; Gundy, 1974; and Justis and Taylor, 1976.)

Most studies suggest that the third eye is involved in a negative feedback system regulating activity-temperature energetics. An interesting question is how the behavior of lizards such as the macroteiids, which lack the eye, may differ from typical lizards.

Stebbins and Eakin (1958) were the first to show behavioral effects of removal of the eye. These authors reported that in the iguanid lizards, *Sceloporus occidentalis, S. virgatus, Uta stansburiana,* and *Uma inornata,* removal of the eye resulted in an increased exposure to sunlight in the field or artificial light in the laboratory. In the parietalectomized lizards, the length of time spent in the normal activity body temperature range was extended. Compared with sham-operated animals there was a three-fold increase in displacement from previously determined home ranges. There was also less tendency to retreat when approached by an observer. Similar results were obtained by shielding the eye with foil. Subsequently, the authors themselves found it difficult to replicate these findings (Stebbins, 1963; Stebbins and Wilhoft, 1966).

In a recent study, Stebbins and Cohen (1973) parietalectomized and sham-operated *Sceloporus occidentalis* in the fall, released them, and recaptured them in the spring. Thyroid activity and reproductive condition in the females were seasonally accelerated in the experimental animals. As in an earlier study (1958), many of the experimental lizards seemed strongly attracted to bright sunlight and reluctant to take cover.

Recently, Hutchinson and Kosh (1974) monitored body temperatures of *Anolis carolinensis* over the 24-hour cycle. In parietalectomized animals, cycles were altered and the selection of temperatures below the "minimum voluntary level" in the dark was eliminated. Also, the peak of body temperature occurred somewhat later in the day. Preferred temperatures during activity were raised by parietalectomy in *Anolis carolinensis* (Roth and Ralph, 1976) and in *Sceloporus magister* (Engbretson and Hutchison, 1976).

In part, this is evidence of involvement of the parietal eye in the control of circadian rhythms. The observations may help to explain the greater exposure to sunlight reported by Stebbins and Eakin (1958). They had noted an extended exposure period for *S. occidentalis.*

Palenschat (1964) reported that parietalectomized slow worm lizards *(Anguis fragilis)* tended to desynchronize from a light cycle, showed considerably more activity than controls under equivalent illumination; the cycle's frequency increased. Further, he reported that, in normal but not in parietalectomized lizards, violet light causes an increase in activity, suggesting that the stimulatory effect of violet light is mediated by the parietal eye. [Green light had the opposite effect and stimulated experimentals but not controls.] Moehn (1974) investigated the effect of ultraviolet light on social behavior in a number of iguanid and agamid lizard species. Increases in agonistic behavior were reported in all species following UV treatment. The effects were possibly mediated via the parietal eye.

A rhythm of locomotor activity can be synchronized with a fluorescent light cycle after parietalectomy (Underwood and Menaker, 1970; Underwood, 1973). This finding does not rule out the participation of the parietal eye in normal behavior (Underwood, 1973).

The reductions or loss of the parietal eye appears correlated with vertical perching habits of some species of lizards. This finding suggests that the function of the eye is related to information about the spectral quality of the zenith sky and not simply to sunlight. At the same time, it should be pointed out that lizards with the parietal eye also tend to be restricted to low latitudes (Gundy, 1974; Gundy et al., 1975), where stress from dessication and thermal fluctuations is reduced.

The light from the zenith can, in theory, give information about time of day since the "blueness" of the sky varies with the angle of the sun to the horizon (Rozenberg, 1966; McFarland and Munz, 1975). The blue sky consists of highly polarized short wave lengths of light with a maximum intensity at a 90° angle to the sun. Although atmospheric conditions introduce some variability, the ratio of short to middle wave lengths of light at the zenith (and the characteristics of polarization) could provide a guide to the time of day. Eder et al. (1975) claim that the anatomy of the eye would allow the discrimination of polarized light.

Thus, one role of the eye could be time determination in the synchronization of rhythms or measurement of day length, when daily temperature is unpredictable.

The spectral composition of the zenith might also be useful to basking lizards under relatively stable climatic regimens. Ectotherms thermoregulate using a number of microclimatic heat sources and sinks that are changing from hour to hour. Anticipation of these changes could allow a finer adjustment to conditions than would trial and error. The available "climate space" may vary systematically throughout the year. For example, in the spring, activity temperatures may best be maintained in the middle of the day; in summer, the middle of the day may become too hot, and activity shows a bimodal pattern with morning and evening peaks (Heath, 1965). One way to anticipate changing conditions would be to link activity with the spectral quality of the zenith. Thus, for most basking lizards in hot weather, the "bluer" zenith of morning and evening would be stimulatory and the "greener," less polarized zenith of midday inhibitory. Both early and late in the year, with cooler temperatures, the "bluer" zenith might be inhibitory and the "greener" zenith of midday might be stimulatory.

This point of discussion is not to advocate a particular hypothesis but to illustrate that the eye may have a variety of effects on behavior and physiology. The reporting of damage to the eye during surgery, lighting conditions, etc., may all contribute to reproducibility of studies.

PHYSIOLOGICAL AND ECOLOGICAL CONSTRAINTS ON REPTILE ACTIVITY

Tetrapod Hearts

When tetrapod vertebrates invaded the land, a variety of systems for the separation of oxygenated and deoxygenated blood evolved in the hearts of animals in the major phyletic lines. Contemporary lizards, snakes, and turtles possess complex hearts that apparently lack the potential to evolve a complete double pump for the pulmonary and greater circulation. Birds and mammals evolved from groups in which the interventricular septum was apparently aligned so as to allow the eventual evolution of the double pump. A complete double pump "encouraged and allowed" the full development of energetically advantageous aerobic metabolic pathways, and I will argue that this and other considerations in turn allowed mammals to develop fully, active-foraging food-gathering strategies and endothermy.

Functional Anatomy of the Lizard Heart

An understanding of the function and evolution of the heart in vertebrates is only now developing (Foxon et. al., 1956; Johansen, 1959; Tucker, 1966; White, 1956, 1959, 1968, 1970; Webb, 1972; Baker, 1974, Baker and White 1970).

The "three-chambered heart," consisting of two auricles and a ventricle, is, in lizards, snakes, and turtles, actually a five-chambered heart because the ventricle is functionally divided into three compartments (Fig. 2).

Recent studies show that this five-chambered heart is capable of maintaining a relatively complete separation between oxygenated and nonoxygenated blood (Foxen et. al., 1956; White, 1956, 1959, 1968, 1970; Tucker, 1966; Steggerda and Essex, 1957; Baker and White, 1970; Johansen, 1959; Baker, 1974), but these as well as other studies (Praskash, 1952; Khalil and Zaki, 1964) indicate that separation of the bloodstreams is *not always* present. Separation is possible largely because of (1) the "septa" which divide the ventricle into "pockets" (trabeculation), (2) pressure gradients within the chambers that facilitate laminar (nonturbulent) flow of the blood, and (3) a timesharing of certain spaces within the ventricle by the two bloodstreams. (In particular, during ventricular filling, the CV is in part a pathway for blood between the right atrium and the CP. Then, during late ventricular systole, the CV becomes a pathway for the oxygenated blood flowing between the CA and the two aortic arches).

It should be noted that there is relatively good separation of the blood streams even in some lungfish, amphibia, and the tuatara where division of the ventricle into separate chambers is not so advanced as in the lizards, snakes, and turtles (Johansen and Hol, 1968; Johansen and Hanson, 1968; Grigg and Simons, 1972). [Separation within the heart is complete in the crocodilians. However, the left systemic arch originates in the right ventricle along with the pulmonary arch. Deoxygenated blood is pumped back into the systemic circulation except when oxygenated blood from the left ventricle flushes the left systemic arch through the foramen of Panizzae which connects the left and right arches. This separation of the pulmonary and systemic circulations is documented in anesthetized *Caiman* (White, 1956, 1968, 1970). The complicated dynamics of this heart probably relates to diving.]

The vascular pump of lizards appears awkward when compared with the double pump in birds and mammals, yet it may have certain advantages. The pulmonary circulation can be bypassed, and this may have advantages because the flow of blood to the skin can be increased to pick up heat during basking without the energetic expense of forcing this blood through the lungs (Tucker, 1966; Baker and White, 1970; Baker, 1974; Webb, 1972). Bypass of the lungs also has been shown to take place when turtles (and alligators using a different system) dive, and preferential distribution of blood *to* the lungs can occur with emergence from the water

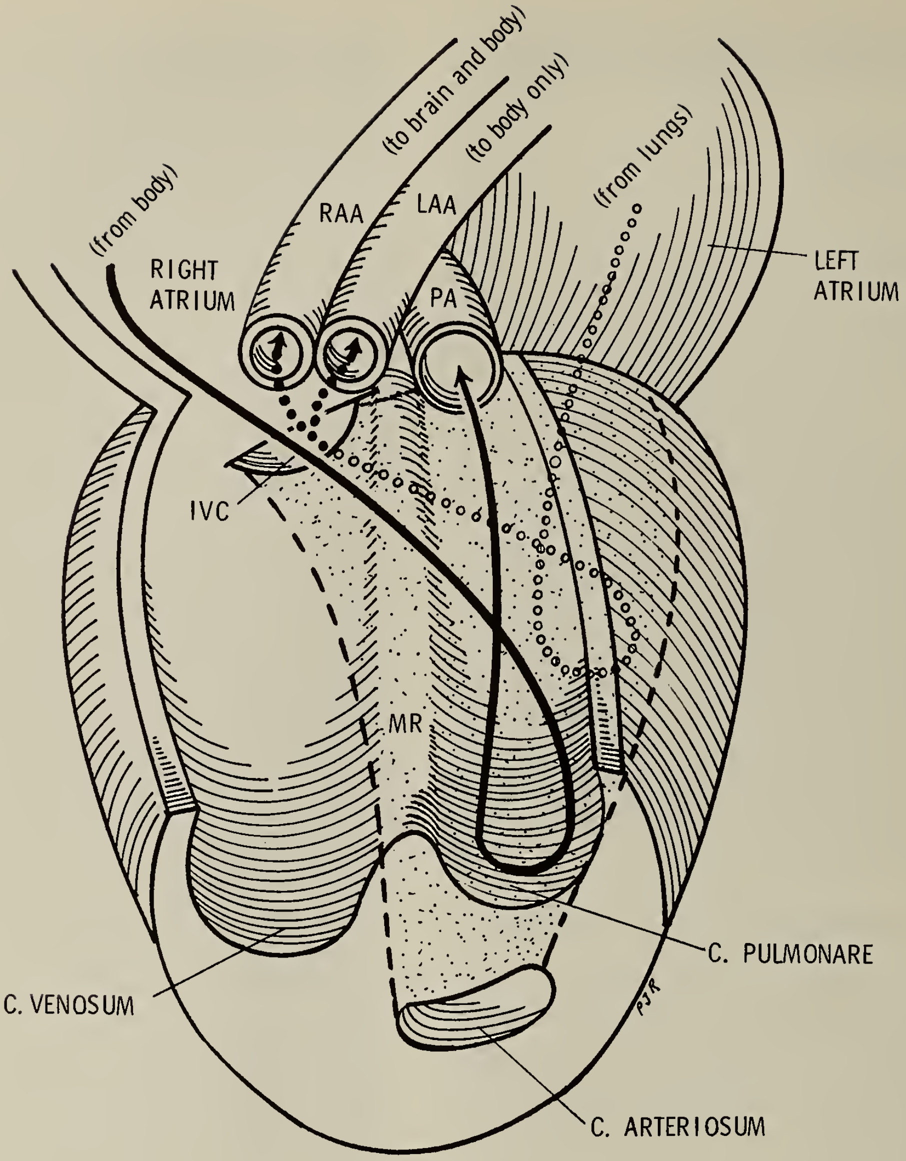

Figure 2. MODEL OF BLOOD FLOW THROUGH A LIZARD HEART (after White, 1959). The ventral and posterior portions of the ventricle are cut away.

The heart fills during ventricular diastole with deoxygenated blood from the body crossing the muscular ridge (MR) and pooling in the cavum venosum (CV) and cavum plumonare (CP); at the same time oxygenated blood from the lungs pools in the cavum arteriosum (CA). Mixing between the dorsal chamber (CA) and the ventral chambers (CP and CV) via the interventricular canal (IVC) is prevented by the atrioventricular valves which are not shown here.

During ventricular systole the deoxygenated blood exits from the ventricle into the pulmonary artery (PA) prior to any ejection into the aortae (owing to the relatively low resistance of the pulmonary circuit); then the oxygenated blood in the CA is forced through the IVC and into the right and left aortic arches (RAA and LAA). (Mixing between the CP and CV is restricted when the muscular ridge presses against the ventral wall of the ventricle which is cut away here. Thus the muscular ridge prevents oxygenated blood from the CA from entering the low-resistance pulmonary circuit, and this blood is directed immediately to the systemic aortic arches. The atrioventricular valves are shifted away from the IVC and seal off the atria from the ventricular chambers during this phase.)

The degree of equality of the distribution of cardiac output between systemic and pulmonary circuits is dependent upon the relative resistances of the circuits. High pulmonary vascular resistance during the apneic phase of respiration (turtles) or during diving produces a shunt. Such a shunt around the pulmonary circuit may also be effective during basking (see text).

(White, 1970). Hence, there may be distinct advantages of hearts that traditionally have been regarded as incomplete stages in the evolution of the four-chambered heart.

The temporal duality in function of the CV, the apparently critical alignment of septa within the pulsating heart muscle, and the delicate balance of pressures apparently necessary to maintain laminar flow within the heart—all lead to the prediction that effectiveness in separating the blood streams will vary as function of heart rate and possibly also of stroke volume. Thus, while we do not know with certainty the precise effects of any of these factors upon the efficiency of separation, it is probable that the squamate heart does not function both at rest and at work or at high pressures with the same efficiency as the mammalian heart consisting of two separate pumps. This conclusion is based on a study of the heart's structure and its flow patterns in restrained and anesthetized animals. Direct experimental evidence is limited at this time, consisting only of the observation that oxygen content is not always equal in the two systemic arches. There is an increase in arterial-venous differences in oxygen saturation at higher metabolic rates, but this is caused by increased oxygen use by the tissues, not an improvement in the separation of the two flows (Tucker, 1966).

The squamate heart is probably too highly specialized to evolve into a complete double pump through a series of small morphological changes. Because of this and the *advantages* of the squamate system for ectothermy lizards are locked into a relatively inefficient cardiovascular system (from the standpoint of a complete separation of bloodstreams at high pressures and heart rates [though see Holmes, 1975.].)

Hearts in Competition

Characteristic activity patterns and behaviors of mammals and of reptiles reflect their foraging strategies. Hence, an evolutionary and comparative perspective must consider the adaptive zones (*sensu* Simpson, 1953) occupied by each group and the structural, physiological, and energetic constraints that have determined the evolution of their present situation.

All other things being equal, a squamate should not be able to compete effectively with a mammal in situations requiring sustained, intense muscular effort. If two hypothetical species make equivalent evolutionary advances in lung structure, oxygen transport systems, and cellular metabolic machinery, a species with a five-chambered heart would still be at a disadvantage relative to a species with a double pump for reasons discussed in the next section.

Hence, due to competition we might have predicted the general evolutionary bias among lizards, snakes, and turtles toward more passive feeding strategies: sit-and-wait feeders, slow cruisers, and sluggish browsers. Animals with four-chambered hearts could, on the other hand, effectively radiate into niches open to actively hunting carnivores, browsers, grazers, and omnivores.

Aerobic and Anaerobic Metabolic Capacities of Reptiles

Aside from the newborn and hibernating species, mammals die after about 5 minutes in pure nitrogen. Most reptiles are, however, quite tolerant of anoxia. Belkin (1963) reported that 43 species of lizards, snakes, and crocodilians would live for 20 to 118 minutes breathing pure nitrogen. The turtles in Belkin's study were all remarkably tolerant and survived 114 to 1,980 minutes. Belkin (1968) argued that, in turtles at least, the prolonged maintenance of CNS functions is related to anaerobic glycolysis. Also, he showed that circulation of the blood is essential to prolonged anoxic brain function, at least in turtles.

Recent studies show a considerable dependence in reptiles on glycolysis for strenuous activity, and most species rapidly accumulate lactic acid and quickly become fatigued. Subsequent repayment of the oxygen debt and removal of the lactic acid burden are slow. The rate at which energy is aerobically generated seems to be independent of body temperature in *Iguana* but not in *Sauromalus*. However, in those species studied, there is certainly an optimum temperature at which each can repay its oxygen debt and and at which the "aerobic scope" is greatest. Consequently, a lizard may become fatigued more quickly when its body temperature is below this optimum (Berkson, 1966; Moberly, 1968*a*, 1968*b*; Bennett, 1972*a*, 1972*b*; Bennett and Dawson, 1972; Bennett and Licht, 1972; Bennett et al., 1975; Gatten, 1975; Ruben, 1976*a*, 1976*b*).

An active predatory life is correlated with a relatively increased aerobic capacity and the ability to pay back quickly an oxygen debt in some species. Bennett (1972*b*) found that "*Varanus* recovers from activity more than three times as rapidly as *Sauromalus*. Its total oxygen debt is only two thirds that of the iguanid." Depending on how one calculates the data, the resting, largely aerobic, metabolic rates of reptiles are about 13 to 20 percent of those for a resting mammal. Yet the oxygen consumption of a vigorously active *Varanus* may exceed that of a resting mammal. Varanids have highly developed lungs with a large surface area, unusual for lizards. Ruben (1976*a*, 1976*b*) reported relatively high aerobic scope correlated with specializations in lung structure and high axial muscle myoglobin content in the species of active snakes he studied.

In short, reptiles generally have limited aerobic capacities probably correlated with their simple lungs and an incomplete double pump for the blood. Accordingly their dependence on anaerobic glycolysis during activity is great. The circumstances under which oxygen debts are accumulated and repayed will be seen to have important consequences for their biology. Complex lungs have evolved in some snakes and turtles, varanid lizards, and crocodilians. These and advances in cellular physiology may result in an improved capacity for oxygen consumption and oxygen debt repayment in a relatively few species.

Metabolic Costs and Foraging Strategies in Reptiles and Mammals

Air and the Ecological Cost of Energy

Air is rich in oxygen, and therefore metabolic energy is ecologically cheap for terrestrial and surface-water animals. In aerobic metabolism of glucose, some 36 high energy phosphates (ATP) are formed as compared with only 2 in anaerobic glycolysis. This means that an anaerobic organism must find and eat 18 times as much food to do the same job as a comparable aerobic individual. In an oxygen-rich habitat an aerobic species would always win in direct ecological competition with an anaerobe since the former would require only one-eighteenth as much food or it would spend one-eighteenth the time searching for food, and could theoretically divert the surplus time and energy to rapid growth, shortened generation time, care of young, hiding from predators, territorial defense, etc. Likewise any degree of anaerobic metabolism where lactic acid is not reconverted to glucose or glycogen would be expensive to an individual in terms of the time required simply to obtain food even in a rich habitat.

During activity most terrestrial vertebrates build up lactic acid, as part of the oxygen debt, which they later reconvert to glucose or glycogen when oxygen is available. The "toxic" products of glycolysis are handled by storage, tolerance of lactic acid, and reconversion. Hence, the price paid for less than maximal efficiency of aerobiosis is usually not a loss of energy, but one of *time and efficiency* as fatigue sets in and the individual slows or stops ongoing activity to repay the oxygen debt.

Evolutionary Options

Primitive terrestrial vertebrates may have had simple lungs, incomplete double circulation, and a high dependence on glycolysis, as do most modern amphibians and reptiles that we know of. The early reptiles might have had in glycolysis a "reserve capacity" (or metabolic scope) for bursts of activity but would be expected to have had a strategy of usually slow behaviors in order to maintain this reserve (as do many modern reptiles).

Conservation of reserve capacity could explain why many reptiles are relatively motionless sit-and-wait predators. This feeding strategy has long been an efficient pattern in the context of primitive oxygen support systems. Note, too, that with such foraging strategies as sitting and waiting and cruising there are relatively small demands on the oxygen support systems and so their evolution would tend to be (and has been) conservative.

Still other primitive reptiles with the same physiological limitations might have abandoned their metabolic reserve and foraged intensively near the limits of exhaustion. Such foraging patterns would have provided the selective basis for the subsequent evolution of improved oxygen delivery systems since the maintenance of some reserve would usually be of advantage in escaping predators, winning mates, or dashing after fast prey. The evolution of more efficient lungs, cardiovascular and cellular metabolic systems would each improve the cost/benefit ratio of active foraging: By increasing the amount of intensive foraging vs. time recuperating, the food benefits accruing from a given length of exposure would be increased. Physiological advances would result in increased net benefits in terms of the ecological effectiveness of an active forager. Advancement to this next level of organization would only be possible in the absence of more efficient competitors.

The Synapsida, mammal-like reptiles, were present in the Pennsylvanian and this makes them among the earliest of reptile groups. Their mammal-like posture and dentition suggest that in the absence of competition some of these early forms were active animals. This radiation, and subsequently that of the true mammals, may have filled the niches for small active animals for the last 300 million years. This would have reduced lepidosaurian evolutionary options so that lizards retain many primitive aspects in their locomotor and oxygen support systems.

It is interesting to speculate as to why a few lizards such as some teiids and varanids have evolved relatively advanced active-foraging abilities. Several *Cnemidophorus*, *Ameiva*, and *Varanus* forage during the day in desert or dry habitats, whereas a mammal with similar habits would expose itself to dehydration because of its higher metabolic rate. Also, seasonal scarcity of food would present many types of small mammalian carnivores or insectivores with energy-budget problems. Water monitors occupy specialized niches, and possibly the ability to make long dives in part allows them to minimize competition with mammals. Interestingly, varanids are most diverse in Australia which has been essentially free of larger-brained, advanced, placental carnivores.

Studies on niche separation and competition (particularly in humid forests) between such active reptiles and mammals, which take into account their respective metabolic demands and capabilities, are needed and would be of considerable interest not only for the evolution of brain functions.

Strategies in Reptiles and Mammals Metabolic Costs and Thermoregulatory

The resting metabolic rate and food requirements of mammals are several times those of reptiles. Basking reptiles may obviously have advantages in ecological situations where solar energy is abundant and food is scarce, while mammals can be active in habitats where adequate food can be found but where the climate would be unfavorable for ectothermy. Other considerations may have also been involved in the evolution of endothermy among mammals and in the retention of ectothermy among reptiles.

The Evolution of Endothermy

Endothermy among reptiles is known only in the large Indian rock python during incubation and in the leatherback turtle (Hutchinson et al., 1966; Friar et al., 1972). Perhaps it is rare among reptiles because, for an animal with a five-chambered heart, a 3- to 8-fold increase in the standard metabolic rate would result in an animal with little if any metabolic scope. When modern reptiles are forced to vigorous "maximal" activity, 58 percent to 90 percent of the ATP production is anaerobic (Bennett and Dawson, 1972; Bennett and Licht, 1972). A struggling lizard quickly builds up an oxygen debt and lactic acid burden and fatigues, then rests and pays back the debt. An endothermic lizard, with a constant high resting metabolic rate would retain little or no metabolic scope (or would have very great food requirements).

Endothermy may be relatively more economical for animals with complete double pumps and advanced lungs, but why should it have evolved at the expense of absolute increases of 3- to 8-fold over reptilian metabolic rates?

One obvious possibility, often argued, is that endothermy is an adaptation for cold at high latitudes, altitudes, in a cooling climate, or at night. There is, however, another set of selection pressures that is independent of paleoclimatic arguments. For example, as birds became more active in the air, increased convective heat loss gave advantages to the conservation of heat generated in activity and to an increase in basal metabolic rate, insofar as they damped out body temperature fluctuations (Jerison, 1971; Regal, 1975). Processes such as the repayment of an oxygen debt take place most efficiently at particular temperature optima (Moberly, 1968*a;* 1968*b*; see also Hochachka and Somero, 1973); and in such facts may be the advantage of temperature stability for very active animals.

Similarly, a small terrestrial ectothermic protomammal actively "poking" about in search of food and moving in and out of shade would either suffer a decrement in efficiency (e.g. fluctuations in sensitivity to fatigue) by allowing its body temperature to fluctuate or might need to budget time for basking if diurnal.

The same problem would have faced a semiaquatic animal with active habits. This is significant because some authors have argued aquatic associations for the early mammals (Olson, 1966; Smith, 1972).

Basking is a thermoregulatory strategy that is particularly compatible with "sit-and-wait" predation. In many lizard species, basking orientations can take place in the sunny but cool desert mornings and afternoons or in cool clear climates while the lizard sits and waits for prey to approach. Perhaps this consideration helps to explain why many teiids actively forage for a restricted time period during the hot hours of the day when high body temperatures can be maintained with a minimal time investment in basking. The ecological conditions that allow such behavior may be limited and are in need of elucidation.

Active ways of life could have provided the behavioral substrate for more efficient locomotor systems and erect and bipedal postures in mammals, birds, and extinct reptiles. One possible factor in the abandonment of the primitive sinusoidal undulations of the trunk is that the efficiency of sinusoidal locomotion may be constrained by the natural resonant frequency of the trunk. Some modern lizards running at top speed on level ground may become bipedal with the front legs held off the ground.

These and other advantages of erect postures would apply to *either* endothermic or ectothermic animals. It is not correct to reason that an erect posture necessarily indicates endothermy (or even *necessarily* active foraging) as has been argued for dinosaurs. Similarly, not all fusiform-shaped fish are warmblooded.

Yet, once endothermy based on a high metabolic rate is established in a lineage, it becomes increasingly probable that selection will tend to perfect mechanisms for rapid energy assimilation because tachymetabolism increases the cost of living. Endothermy combined with active foraging habits in a group with a complete double pump would be one powerful set of conditions favoring evolutionary "advances" in anatomy and behavior. Hence, it could have been that endothermy accelerated the (often parallel) evolution of the various neurological, locomotory, and masticatory specializations associated with "intelligence," agility, and speed in various mammalian groups.

Selection pressures for endothermy based on a high resting metabolic rate may have been most intense in small animals. The thermal inertia of large bodies damps out temperature fluctuations and also facilitates the retention of heat generated in muscular activity. This recycling of the heat of activity (as in insects and likely also in the leatherback turtle) can provide a degree of independence from thermal fluctuation during activity to reduce the selection pressures for an increase in resting metabolic rate among large animals. This line of thought suggests that large mammals have a high resting metabolic rate primarily because this became fixed in the physiology of their small ancestors. Also, minimizing selection for a great increase in the basal metabolic rate of animals approaching the size of giant dinosaurs is that high metabolism could compound heat overloading problems because the low surface to mass ratios may present a difficulty in dumping heat.

FORAGING MENTALITIES AND BRAIN EVOLUTION

What differences might we expect in mental functions between active foragers and sit-and-wait predator lizards? This question is of interest for understanding factors leading to diversification of lizards' brains, and its answer may also give insight into the evolution of the mammalian nervous system inasmuch as a typical mammal is a more active forager than a typical reptile.

Since large brains are found in warm-blooded birds and mammals, some are tempted to assume that such nervous systems are somehow dependent upon endothermy (e.g., Young, 1962). Jerison (1973) has argued, rather, that the relationship was caused by separate factors in the history of each group: flight in birds, and nocturnality in mammals. Heath (1968) argued that mammalian brain specializations may have begun in response to the locomotor shifts from a sprawling to an erect gait. I suggest that development of a four-chambered heart allowed extreme specialization in active foraging and that, for this way of food gathering, there are great selective advantages to be derived from the development of enlarged memory capacities and enlarged and advanced information-processing capacities and systems, especially for terrestrial animals. Endothermy is simply another adaptation for this same way of life and is related to brain enlargement only because, once it became established in the physiology of any species, for reasons discussed above, endothermy would lock individuals into high food requirements and hence bias future evolution toward progressively refined active forager adaptations, including behaviors and mental capacities. Sitting and waiting may be expensive (in terms of time wasted) for many mammals with their high energetic demands.

Some Operational Assumptions

Brain Size and "Intelligence"

There is general agreement that large-brained vertebrates are more "intelligent" than those with smaller brains, yet the specific adaptive significance of brain size has not yet been identified (Holloway, 1974; Jerison et. al., 1975; Miller and Tallarico, 1974; Radinsky, 1975). To avoid speculating on the significance of brain size or on the meaning of "intelligence," I propose *a set of deductions about specific mental qualities* which may be useful in generating verifiable predictions about the adaptive functions, ecological correlates, and phylogenetic distributions of behaviors and of patterns of brain organization.

Foraging vs. Predation

Predation need not include extensive foraging and vice versa. Lizards that prey on insects may simply sit and wait for the prey to reveal itself.

This often misunderstood point is critical. Perhaps it can be best understood by reference to bats where the neocortex and total brain are enlarged in fruit eaters relative to insect eaters (Pirlot and Stephan 1970); Stephan and Pirlot 1970; Stephan, Pirlot, and Schneider 1974). This may make no sense in terms of the skill and agility required to capture the two food types. But, it makes good sense in terms of foraging skills, since tropical flowering and fruiting trees are widely and heterogeneously distributed and their efficient exploitation by bats or monkeys over the year requires familiarity with an extensive area and plant community.

Environmental Grain

My use of the term intensive forager implies much more than simply high activity levels or carnivory. It indicates the capacity to exploit environments with rare and patchily distributed prey.

In the last 15 years, ecologists have made important contributions to our understanding of environmental complexity and its consequences for the organism. One useful concept is of environmental "grain" (figuratively the perceived "size" of each resource particle). All things being equal, as a habitat becomes more complex, the grain becomes more fine. However, animals may evolve that make *coarse-grain responses* and utilize a class of resources from the environment as though each particle was large and easier to detect or *select* in a nonrandom fashion. Such animals may exploit rare resources and complex environments more effectively than does a species with fine-grain responses (Wiens, 1976). In the development of this concept, the emphasis has been upon understanding community structure (e.g., How many species can a given class of resources support? What determines species diversity in a given area?). I propose here that we focus upon the physiological and mental traits required of animals making fine-grain, in contrast to coarse-grain, responses and that these traits are relevant to an understanding of the organization and evolution of the nervous system in vertebrates. I envision the physiological and mental qualities associated with active foraging in lizards and mammals as representing one system for allowing coarse-grain responses—utilizing large spaces and retaining flexibility in feeding and relative generality in diet at the same time.

Spontaneous Exploration

The sit-and-wait predator primarily needs to occupy a suitable perch until a stimulus appears (Askew et. al., 1970), to focus upon the stimulus (Ewart, 1974; Ingle, 1975), and then to leave its perch to approach and seize food objects of appropriate size, shape, and speed (for example, an insect within a particular size range and of a particular velocity; or an herbivorous lizard orienting itself to a young leaf, flower, or fruit of a particular shape, color, or smell).

The foraging strategies of cruising and intensive-foragers may require the "endogenous" generation of most locomotor activity. Food rewards may eventually result from simple patrolling of an area or from curious searching, but even searching need not be stimulated by the sensing of food. Hence, there are advantages to mechanisms that will sustain (first) spontaneous locomotion and (second) actual searching behavior over long periods of time in the absence of the ultimate biological reinforcers. Apparently, in mammals there is a rearrangement of the logic of the nervous system so that movement, and "purposeful" familiarization with the environment (curiosity, exploration), occur without extrinsic reward (Kavanau, 1967; Neuringer, 1969).

Intelligence is not a useful concept in discussing such behavior. Sitting and waiting may be an "intelligent" foraging strategy for most lizards, considering their limitations, yet the behavior should not be credited to "brain power." Spontaneous exploration may, however, be a prerequisite for the acquisition of large amounts of complex data and the development of information-retrieval strategies and hence provide the basis for higher order decisions, associations, and responses.

A question that emerges from this discussion: Will some degree of curiosity and exploration be found among the intensive-foraging lizards?

Frequent tongue flicking and apparent visual scanning accompanied the high rates of movement in recently fed *Ameiva* (Fig. 1). [Chisar et al., 1976, regarded tongue flicking as a valid index of investigatory behavior.]. In additional tests, *Ameiva* frequently approached, "explored," and often entered small 3 x 5 cm canisters placed in the open field. Even the most active individuals of *Leiocephalus* ignored the canisters. While it appeared that recently fed *Ameiva* were purposefully exploring the open field, I regard the study as preliminary. Tests controlling for alternative possibilities are indicated.

Searching, Stalking and Capture Strategies

We would predict that a sophisticated active forager will not simply move about. It will adopt different behaviors for different sorts of prey living in different microhabits within its range.

So doing would require not only an enlarged memory, but the ability to make associations between the sights, sounds, or smells of particular species, as well as their microhabits and occurrence in time; and beyond this, associations between particular species and *one's own motor patterns* that will optimize the chances of securing particular types of foods.

The concept of the search image (Croze, 1970; Murton, 1971; Krebs, 1973; Mueller, 1975) is useful here, but it is incomplete to think simply of "learning to see" certain prey items against a complex configurational background. Our idealized active forager will form a *search strategy* as well as a search image and we may expect a variety of search images and strategies.

On this basis, one would expect such "mammalian" behaviors to be at least partially developed among some of the intensive-forager lizards. Auffenberg's detailed report of the Komodo dragon's predatory behaviors is of considerable interest in this connection.

Cooperation

There may be advantages for active foragers to cooperate in feeding and also in cultural transmission between and within generations ("transfer of search images," Turner, 1964; Davis, 1973, for a recent review), particularly where the prey is rare or patchy in distribution, has evolved effective concealment or escape mechanisms, or is large and dangerous.

By contrast, more passive reptilian feeding strategies largely demand only the toleration of other individuals. "Companions" are relatively unimportant to sit-and-wait foragers. Greenberg (1976) describes social feeding in two species of iguanids in the laboratory. However, this may be social facilitation rather than advanced cooperation.

Among the intensive-foraging teiids and varanids, rare instances of group foraging have been noted in *Cnemidophorus inornatus* and *C. tessellatus* (Milstead, 1961). Auffenberg (this volume) has also noted gregarious foraging in young Komodo dragons, and Cott (1961) summaries the evidence for cooperation between pairs of *Varanus niloticus*. One varanid will draw a female crocodile away from its nest while another excavates the eggs. The first then returns to join in eating the eggs.

Predictive Ability

Ideally, the intensive forager has an advantage if it has information not only about its own location but of its limitations and capacities. The "awareness" of itself would be important in "selecting" appropriate behaviors for obtaining different kinds of prey.

This is clear from our own experience, but we can reach the same conclusion from mathematics (game theory). Knowledge of one's own "position" together with that of other players in a game allows a "game of perfect information," and "in such games there is always a 'best way to play,' which can be specified without mentioning chance" (Rapoport, 1966).

There are obvious advantages to capacities such as "reason" that would allow the individual to predict events in novel or complex situations, where simple conditioning would be inadequate to allow predictions that might prevent escape of prey or injury to self.

Any improvement in perceived predictability is, of course, likely to fall short of absolute predictability. Even in literate adult humans there is a considerable gap. Mathematics and science have great power precisely because they can narrow the gap.

This discussion emphasizes again the particular character of the behaviors which I suggest allow coarse-grain responses. It also leads to the specific prediction that if the rudiments of "reason" or "self-awareness" are to be found among any lizards, it is likely to be among varanids or teiids.

CONCLUSIONS

The Paleozoic-Mesozoic adaptive radiations of diapsid and mammal-like reptiles took place in plant communities that were considerably more simple than those of the late Cretaceous-Tertiary in which modern mammal and lizard groups have evolved. Throughout the (late) Cretaceous and Tertiary there has been a dramatic increase in the numbers of plant species, and ecosystems have grown much more complex (Dorf, 1955; Axelrod, 1974; Regal, 1977; Hickey and Doyle, 1977).

I see "intelligence" as reflecting a loose "federation" of mental traits—each has a role in reducing the perceived randomness of encounters with, and captures of, rare or patchily distributed resources in complex environments. Perhaps, then, it is no surprise that the large brains of modern mammals apparently did not evolve among the mammal-like reptiles in their 100-plus million years on an earth with relatively simple ecosystems.

Some lizards have penetrated active forager "adaptive zones" but not to the extent that mammals have. Perhaps their five-chambered hearts would not support both continuous activity and endothermy and still allow competition with mammals which have their complete double circulations.

Whatever the exact evolutionary causes for the relative differences between the behavior of reptiles and mammals, a major point to stress is that reptiles include forms with a diversity of mental strategies for foraging. Modern reptiles may provide good models not only of the primitive "Reptile brain" upon which the Paleomammalian and Neomammalian brains were layered in evolution (MacLean, 1973, this volume), but of *transitional stages* in the development of higher processes.

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Ethological Considerations in the Experimental Study of Lizard Behavior

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SUMMARY. The importance of an ethological approach to the experimental study of an unfamiliar species is described and several of its problems discussed. The selection of units of behavior is a crucial first step in the development of a behavior inventory. The correlation of a behavioral unit with a particular context is necessary to ascribe function to that unit and to develop an ethogram. Methods of studying lizards under controlled conditions are described and discussed. Constraints on behavior that must be considered in an experimental study include the microclimate and its thermal qualities, food and water, shelter utilization, and social behavior. Ritualized display patterns are proposed as sources of hypotheses about the neurophysiological control of social communications.

INTRODUCTION

This report will first discuss some issues in an ethological approach to the study of an unfamiliar species and will then describe some observations that bear on the development of an experimental design for the study of lizard behavior in the laboratory.

The observations described, both my own and those gleaned from the literature, are presented to indicate the complexity of the environmental constraints on lizard behavior. They constitute something of a guide for researchers—be they students of reptiles devoted to a favorite group or those who see lizards as a possible model for experimentally testing hypotheses about the causation and function of behavior.

THE ETHOGRAM AND UNITS OF BEHAVIOR

Naturalistic observation is the essence of ethology and the fountainhead of hypotheses about the causation and function of behavior as well as the foundation on which experimental tests of these hypotheses must be built.

The importance of the ethogram in the interpretation of an experimental study of a species is stressed by most ethologists (e.g., Lorenz, 1935, trans. 1970:111; Tinbergen, 1951; Thorpe, 1973). Failure to consider all aspects of normal behavior has diminished the usefulness of many experimental studies (Adams, 1973; Eibl-Eibesfeldt, 1970; Thorpe, 1973).

Units of Behavior

A problem in developing ethograms has proven to be the objective delineation of separate units in what is a continuum of behavioral patterns. To minimize the arbitrary nature of behavioral classification, the investigator attempts to identify reliable, easily recognizable diagnostic features. Ideally, behavioral units should be of the type that a neurophysiologist could deal with. Barlow (1968) asserts that, in this regard, only quantifiable behavior is of interest because the behavior must be mathematically modeled if it is to be considered in neurophysiological terms. But preoccupation with quantification can be hazardous, interfering with the Gestalt perception of a phenomenon

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that is crucial to generating creative hypotheses (Lorenz, 1971). For example, time sampling can often be misleading unless the environmental or social context is considered, and that is not always possible (Driver, 1968). As Vowles (1975) points out, a preoccupation with quantification may be an understandable response to the subjective and introspective approach of early psychology.

The selection of units of behavior must be suitable to the questions being asked. The hard decisions of "lumping" and "splitting," familiar to taxonomists, must also be made when behavior patterns are to be organized into manageable groups. This is true at the level of individual units in a coordinated sequence as well as in more complex behavioral categories. It is often helpful to begin with a broad overview of general activity patterns and then subdivide them until the appropriate "resolution" is achieved (Fig. 1). A neurophysiologist may profitably deal with units as fine as a muscle group and its associated actions (e.g., the "functional unit" of Liem, 1967, cited by Barlow, 1968: 217), while a population biologist may be concerned with a complete communicative act and its consequences.

While too fine a preliminary analysis can obscure a behavioral pattern with trivial details, if the units of behavior utilized in the study of a species are too broad, difficulties may emerge that could not have been anticipated until the comparative perspective was brought to bear on a problem. For example, details of behavior that might suggest a physiological mechanism or the evolutionary sources of signal behavior can be overlooked. This can be a problem in studies of display behavior where the individual components of the display and/or their time course are often not as clearly delineated as the general form of the display. A notable exception is the comparative study of the vertical "bobbing" movements of displaying males of the genus *Sceloporus* by Purdue and Carpenter (1972). Such analysis is useful because the body movements in the ubiquitous bobbing displays of iguanid lizards have generally been treated as a single unit, when they may, in fact, represent multiple behavioral patterns which have coalesced; neck and limb movements may represent two alternative mechanisms which have become combined to effect a display. Some species have several bobbing movements for different displays which utilize limb and neck movement to different degrees or even dispense with one type of movement.

Another difficulty in defining units of behavior is that motor patterns and sequences are too easily defined in functional terms which combine explanation and description. This can interfere with comparative interpretations and replications of the original study.

The Evolutionary Perspective

One goal of comparative studies is the development of the evolutionary perspective that leads to an appreciation of the genetic (and to that extent "innate") contribution to behavior (Brown, 1969). Comparative studies are also useful to investigators in suggesting hypotheses and in analyzing the adaptive aspects of natural units of behavior. Both analogy and homology are important considerations in thinking comparatively about behavior.

In evolutionary biology, Mayr (1969) asserts that only homologous characters are of taxonomic importance. Homology originally referred to an anatomical correspondence between structures in two animals sharing a similar body plan, but, in current use, the evolutionary explanation for homology has usurped the original meaning of the term (Beer, 1974).

Two characters under consideration by a biologist may differ markedly in form or function and yet be related through derivation from a common ancestral precursor. Such relatedness may provide valuable insights into the causation of dissimilar behavioral patterns and the manner in which animals evolve.

The idea of behavioral homology, however, is a continuing source of confusion. The con-

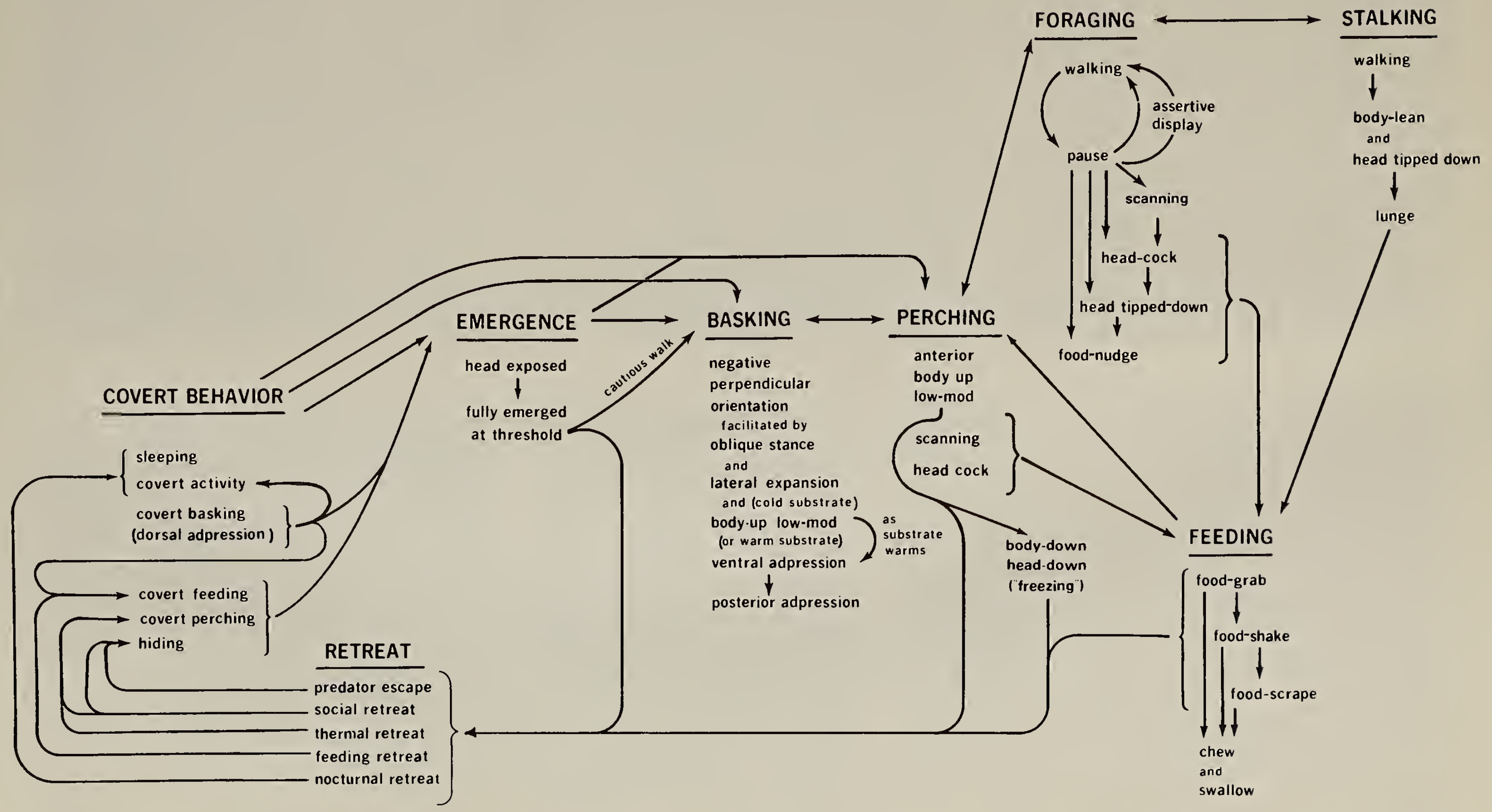

Figure 1. A preliminary ethogram of the blue spiny lizard, *Sceloporus cyanogenys*. Such a broad overview of daily maintenance patterns may be used as a baseline against which subsequent manipulations may be contrasted to indicate distortions in behavior induced by experimental or maintenance regimens.

cept resists attempts at rigorous definition and yet is of obvious use. Atz (1970) examined the criteria used to recognize homologous behavior and argued that only morphologically defined behavioral patterns could be properly homologized.

Hodos (1977) extended Atz's ideas and concluded that behavior patterns may be regarded as homologous only to the extent that their morphological substrates can be traced back to a common ancestral precursor. He proposes a morphocentric definition of behavioral homology:

> Behaviors are considered homologous to the extent that they can be related to specific structures that could, in principle, be traced back through a genealogical series to a stipulated ancestral precursor irrespective of morphological similarity.

According to this definition, two behavioral patterns would be homologous if they are associated with homologous structures, no matter how different the functions of the behavioral patterns might be. Such morphocentric definitions of behavioral homology rightly regard behavioral patterns as evanescent extensions of anatomical structures into evolutionary time. But, it is the very disjunction of behavior and morphology that Atz regards as the crucial problem in considering behavioral homology.

Strictly applied, a morphocentric definition creates a difficulty if two different behavioral patterns associated with homologous structures have arisen independently. To avoid using the term in a misleading sense, perhaps the definition should be amended to include a stipulated ancestral behavioral pattern. Such a condition would also satisfy the definitions of behavioral homology ventured by Baerends (1958) among many others (Atz, 1970). Of course, "stipulated ancestral" behavioral patterns are derived from the comparative study of closely related extant species, and thus all proposed homologies must be regarded as hypotheses that ultimately are untestable (but see Evans, 1959*a*, 1959*b*, 1959*c*). The heuristic value of such considerations, however, is uncontested.

Hodos also suggests that any statement about homology must specify the basis on which it is adduced, that is, precisely what the ancestral precursor structure might be. The level of analysis depends on the detail of anatomical structures considered, and their specification is a necessary part of a statement of a homology or proposed homology.

To further clarify the issue, Hodos recommends the use of the terms "homoplasy," referring to similar behavioral patterns, associated with nonhomologous structures, and "analogy" to refer to behavioral patterns which are functionally similar.

Analogy is important to many researchers, particularly comparative psychologists who are searching for simplified models for human behavior. This anthropocentric selection of research problems has been criticized by Beach (1960), but, nevertheless, functionally analagous behavioral patterns in different species are useful for suggesting causal mechanisms (Zeigler, 1973). Wickler's (1973) analyses of convergent behavioral adaptation provide excellent examples of particular behavioral functions which are the outcome of different internal mechanisms in distantly related animals. Under such circumstances we may be more confident that similarities in the behavioral patterns of species that are not evolutionarily related are necessary to the solving of a particular ecological problem. Indeed, Lorenz (1971, 1974) regards the study of analogy crucial to an understanding of the survival function of a behavioral pattern.

Regardless of the more useful perspective for approaching a specific problem, an excellent case can be made for the presentation of behavioral data in two complementary forms: a *behavior inventory,* in which behavioral patterns are defined in morphological terms with minimal, if any, regard for function, and an *ethogram,* in which the context and apparent functions of behavioral patterns are described.

Laboratory and Field Studies

For contextual information and confirmation of the "naturalness" of behavior, field studies are valuable but present certain problems. Field conditions may vary considerably from area to area and from year to year, necessitating many years of observation before an investigator might be confident that he has inventoried the complete range of behavior. Further, field studies may be prejudiced by the presence of the observer (Cowles and Bogert, 1944; Schneirla, 1950), partly because the observer may be perceived as a potential predator (Edson and Gallup, 1972).

Laboratory studies, on the other hand, generally rely on a specific behavior performed out of context by animals in an ecologically impoverished environment. Deprivation of outlets for some activities may profoundly influence other behavioral patterns in unexpected ways (Hediger, 1955; Morris, 1964; Kavanau, 1964, 1967). For example, general activity may increase, depending upon the nature of the opportunities (Hinde, 1970). Compulsory regimes and the constraints of small habitats may also lead to distortions of behavior that cause contradictory or paradoxical results (Kavanau, 1964, 1967).

Giving the animal some control over its habitat or initiative in environmental manipulation may be illuminating in some respects, but there is the danger that the search for "good performers" or tractable animals may find only subjects that demonstrate principles peculiar to themselves (Breland and Breland, 1961). When an animal is required to make arbitrary associations, the principles explicated may be peculiar to those associations and not necessarily applicable to the animal in nature (Morris, 1964; Seligman, 1970).

Ideally, the experimental ethologist dealing with an unfamiliar species would have a thorough knowledge of the habitat in which the animal's behavioral patterns were forged. Indeed, without such knowledge, Hediger points out, there may be contradictory impressions of the abilities of an animal (1950: 84). Furthermore, without the intimate and continuing experience with a species that the development of an ethogram requires, there may be contradictory interpretations of function (Hediger, 1955:140).

Lorenz (1935, trans. 1970:111–112) has pointed out the difficulties of objective communication of "pure" observations as opposed to experimental results. In a recent review of observational sampling methods, Altmann (1974) has contrasted internal and external validity, corresponding in each case to the consistency of laboratory research and the generalizability of field studies. A critical aspect of any experiment is the presence of controls. These, of course are not absent in the field, but are nonmanipulative. According to Altmann, it is the observer's sampling decision that influences the relative internal validity of the observations.

According to Seligman (1970), the premise of equipotentiality that underlies much psychological investigation (general learning theory) is limited in its usefulness because of its emphasis on arbitrary associations, events, and its avoidance of "contamination" by an animal's biology or experience (Seligman and Hager, 1972). He proposes a "preparedness continuum" that is recognized, for example, by the ease with which an animal can make an association (acquisition). The point along the continuum at which an animal functions in a given situation is significantly influenced by its evolutionary and developmental history. This suggests that a behavioral pattern readily demonstrated or easily elicited in the laboratory is a response that an animal is "prepared" to make, and that its causation and function are probably not significantly different from that found in nature (Jenssen, 1970*a*). As Hediger points out, however, a captive animal that is no longer subject to the constraints of its natural environment may behave in unpredictable, even unprecedented ways (Hediger, 1950:91).

The ability of lizards to learn is attracting considerable attention (Brattstrom, this volume; Peterson, discussion). As Lorenz and others have observed, some things are more easily learned than other by a particular species. Mayr (1974) regards this as a situation reflecting the ease with which a genetic program manifesting itself in behavior may be modified and refers to more or less "open" or "closed" genetic programs. An "open" program is highly susceptible to ontogenetic experiential influences, whereas one which is "closed" is not subject to subsequent modification—it is "fixed."

Laboratory and Field Perspectives Combined

From the ethological perspective, experiments are regarded as most useful when animals are unencumbered by apparatus, unaffected by handling, not subject to unnatural constraints, and free to interact with their environment and with each other. A satisfactory research method is one that provides a simulation of a field habitat under laboratory control. The use of ecologically relevant cues in learning paradigms has been effectively utilized by Brattstrom (1974) and others (Brattstrom, this volume).

For conducting neuroethological experiments on display behavior in lizards (Greenberg et al, 1976; Greenberg, 1977*b*), my first concern has been to obtain behavior inventories and ethograms for lizards that are likely subjects for laboratory experiments. To do this, I have tried to create as complex a habitat as possible to provide lizards with a variety of natural stimuli and behavioral options. Such habitats are adjusted until benchmark aspects of the animal's behavior estimated from field observations and the literature are approximated. Then, types of behavior that are less amenable to field study can be monitored (Figs. 2, 3).

In this way, I have developed preliminary behavior inventories and ethograms of the blue spiny lizard, *Sceloporus cyanogenys* (1973*a*, 1977*a*); the rainbow lizard, *Agama agama;* and the green anole, *Anolis carolinensis*.

Once contextual constraints on behavioral patterns are revealed from observations made on subjects in complex habitats, different kinds of behavior may be teased out by providing the relevant stimuli in relatively restricted habitats which are more appropriate for tests on experimentaly treated animals.

An effective way of doing this is to obtain a preliminary ethogram (Fig. 1) and then to concentrate on a specific portion of it.

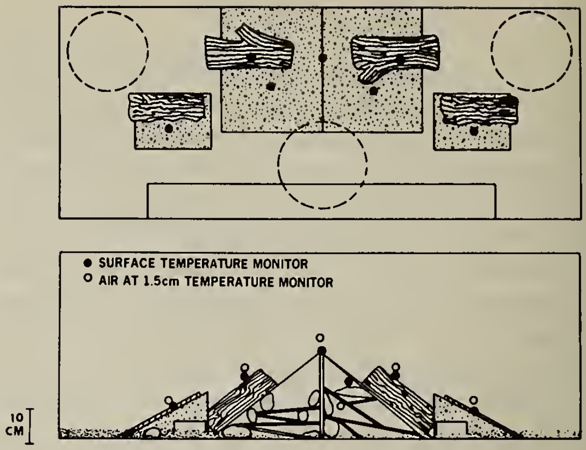

Figure 2. A complex laboratory habitat and its microhabitats. In an attempt to elicit natural behavorial patterns, a variety of perches and substrates, crevices, and feeding sites are provided. Diverse prey forms are provided on an irregular schedule in order to compel lizards to maintain a natural level of alertness.

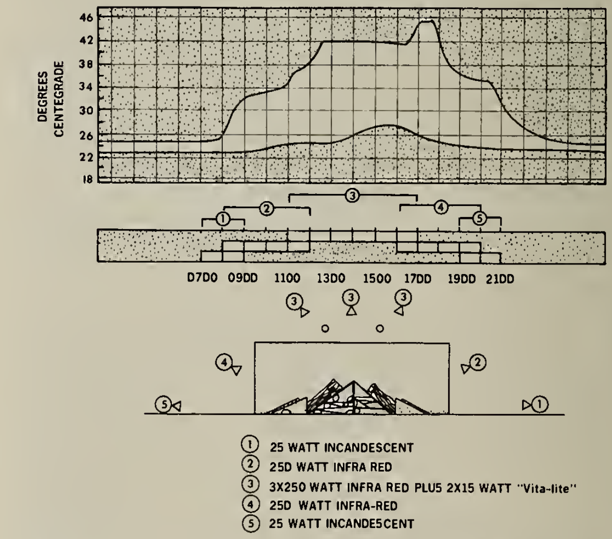

Figure 3. A complex laboratory habitat and its photothermal regimen. The diversity of thermal levels simultaneously available is indicated above.

Such preliminary work contributes to one's confidence in the "normality" of behavior when a laboratory habitat is modified to emphasize behavioral patterns or to facilitate observations of behavioral patterns of special interest.

Observations

The techniques employed in making behavioral observations must be adapted for each species of lizard in their experimental habitats. *Anolis carolinensis* seems less subject than many other lizards to the observer effect, and it is possible to record their activity while seated a few meters away in a darkened room. Blue spiny and rainbow lizards are another matter. There is no one ideal way to observe them, but a balanced use of direct observations through a blind fitted with a one-way window and closed circuit television is effective.

The video monitoring system I employ consists of two monitors attached to a zoom lens capable of very close focus (e.g., Dage model RGS–50) and a third monitor attached to a wide angle camera so that an animal can be quickly located and peripheral activity followed (Fig. 4). The use of a time-lapse videotape recorder (e.g., GYYR model VTL 300) also allows relatively straightforward analysis with resolution of up to 60 frames per second in replay. The tongue touching of the substrate commonly associated with the *Agama's* display may be revealed clearly in only one frame. By recording in the time-lapse mode, up to 99 hours may be compressed onto a 1-hour tape.

The Esterline-Angus pen-writing event recorder controlled by on-off-momentary switches continues to provide a reliable means for the recording of continuous states (e.g., postures, color, territorial sites) as well as momentary events (e.g., motor acts).

For extended observation of large numbers of delineated behavioral units, Dr. Richard Radna and I are developing a system that converts any conventional communications terminal into an event recorder by the use of a system of FORTRAN programs called CABER (programs and user's guide available). CABER permits us to enter any two-digit alpha-numeric code as one would type. The internal clock of an IBM 370 is accessed, and the time, to whatever precision desired (up to one-hundredths of a second) is entered whenever the return key is hit (Fig. 6).

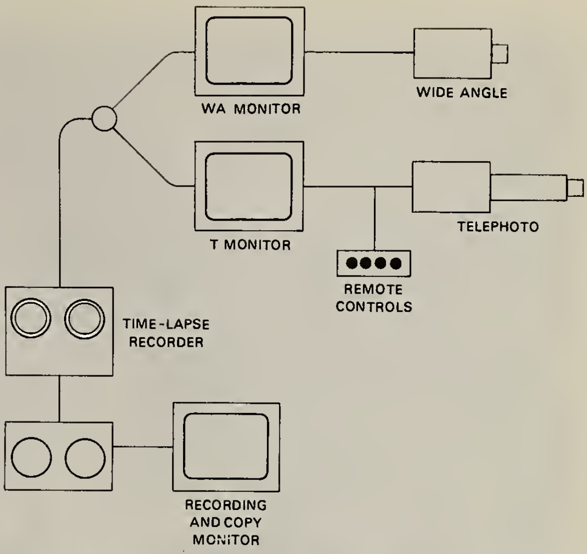

Figure 4. Separate closed-circuit television monitors are connected to (1) a zoom camera capable of extreme closeups and (2) a wide-angle camera so that peripheral action can be followed or an animal quickly located. The picture on either monitor can be recorded and events of interest can be quickly copied onto an adjacent recorder.

CONSTRAINTS ON BEHAVIOR

Microclimate

The quality and quantity of light are not only of importance for thermoregulation in ectothermic lizards, but influence behavior in other ways. Photoperiod length has been associated with gonadal regulation (Fox and Dessauer, 1958), appetite and growth (Fox and Dessauer, 1957). Species differences in response are apparent (Mayhew, 1964), and the response to photoperiod may be substantially altered by the ambient temperature (Licht, 1973), humidity (Crews et al., 1974), and possibly population density. In my study

Figure 5. Closed-circuit television closeup. The CCTV system has a timebase generator to record the date and time to one hundreths of a second on each frame.

of blue spiny lizards (1973*a*), individuals maintained in a large habitat (Fig. 2) spontaneously resumed a seasonal pattern of social activity after more than a year under constant conditions. Those in much smaller habitats did not.

Dim light is of little thermal significance, but simulated twilight transitions have been shown to have a potent effect in normalizing the activity patterns of animals in the laboratory (Kavanau, 1962, with mice; Regal, 1967, with lizards). Dim light may cue a lizard's shelter seeking so that it will not be caught far from its shelter when night falls (Regal, 1967). In the morning, some lizards may be cued by light to emerge (Greenberg, 1976*a*), while others apparently rely on the penetration of morning warmth into their shelters (McGinnis and Falkenstein, 1971; Bradshaw and Main, 1968).

An endogenous circadian rhythm was posited by Heath (1962) to account for the emergence of *Phrynosoma* in apparent "anticipation" of the onset of laboratory heatlamps, but McGinnis (1965) has argued that such a rhythm could be an artifact of the consistency of the laboratory habitat.

The importance of ultraviolet light for some species is apparent both with respect to metabolic needs (Reichenbach-Klinke and Elkan, 1965) and the expression of normal behavior (Moehn, 1974). Licht (1973) has

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20:  8:26  79 ES 53 OD BD HL FD RB YO DB
20:  9:20  73 22 OD BD HM FD RE YO BN
20:  9:34  99 ES 23 OU BD HD FD RC YO DB
20: 10:22  79 ES PA
20: 10:36  79 ES 53 OD BD HD FD RC YO DB
20: 10:41  73 NC
20: 11:42  99 ES 23 OU BD HD FD RC HP DB YO
20: 11:46  99 ES MV PA
20: 11:58  99 ES 23 OD BD HL SC FD RE YO DB
20: 12:  3  73 SC
20: 12:  5  99 ES TT
20: 12:  9  79 ES NC
20: 12:32  73 HA HC
20: 13:36  73 HA PA
20: 13:52  73 22 OD BD HD FD RC YO BN
20: 14:24  99 ES 23 OD BD HD FA RE YO DB
20: 14:35  79 ES 53 OD BD HD FD RC YO DB
20: 15:20  NC
20: 16:  1  NC
20: 16:58  73 HA HL
20: 17:  3  79 ES
20: 17:  6  99 ES
20: 17:21  73 22 OD BD HL FD RC YO BN
20: 17:31  79 ES 53 OD BD HD FD RC YO DB
20: 18:52  99 23 OD BD HD FA RE YO DB ES
20: 19:44  79 PA
20: 19:47  99 PA
20: 20:21  73 22 OD BD HL FD RB YO GB
20: 20:52  99 HA SN
20: 20:58  79 NC
20: 21:  8  99 PA MV 23 OD
20: 21:23  73 PA MV 23 OU
20: 21:38  99 PA MV 23 OD SN
20: 21:41  99 AD
20: 21:52  73 HA HM AD
20: 21:54  99 AD
20: 22:  2  73 TT
20: 22:11  99 23 OD BD HD FD RE DB ES
20: 22:43  73 22 OU DB FD RB YO GN
20: 22:45  79 HA
20: 22:55  79 53 OD BD HD FD RB YO DB ES
20: 22:58  99 -- ES
20: 23:  7  99 23 OD BD HD FD RE YO DB
20: 23:22  73 22 OU BD HD FD RB YO GN
20: 23:25  99 HA HC
20: 23:31  99 PA MV
20: 23:42  99 23 OU BD HA AD
```

Figure 6: Examples of data as stored and formatted by CABER. On a data line, the first six numbers are the time, the next two represent an animal, and subsequent entries represent behavioral patterns. The computer indicates the time whenever the carriage-return is depressed.

found evidence of an influence of the spectral quality of light on testicular recrudesence in *Anolis carolinensis*. Other possible influences of the spectral quality of visual light are discussed by Regal (this volume).

The influence of wind gusts on the activity of *Sceloporus* was observed by Jackson (1974). He suggests that these lizards change perching sites to increase their predatory surveillance area and that they make these site changes during gusts of wind when they may be less subject to predation because their movements would be less conspicuous.

Thermoregulation

Since the landmark study of Cowles and Bogert (1944), reptilian thermoregulation has been intensively studied. It is clear now that most lizards, given an environment with some thermal diversity, are capable of regulating their body temperatures at levels appropriate to their individual physiological or ecological circumstances. Few biologists today would ignore this aspect of an experimental setting. Nevertheless, there are studies which have mistaken metabolic inactivity for an inability to learn (Brattstrom, 1974; this volume). A similar potential source of error may be encountered in neurobehavioral investigations. Damage to the parietal eye, an often-used surface landmark overlying the forebrain of many lizards, may cause aberrations in behavioral thermoregulation (Roth and Ralph, 1976). Berk and Heath (1975) have cautioned investigators that, since there is an elaborate central neural network involved in thermoregulation, lesion studies might confound behavioral deficits with thermal torpidity.

The thermal requirements of lizards are not simply satisfied by keeping them at any "ideal" temperature. As Regal (1968) has observed, keeping some lizards cool for extended periods does not necessarily compromise their health. Given a diversity of thermal gradients, they will demonstrate circadian thermophilic tendencies. Wilhoft (1958), however, has demonstrated that housing lizards at their "preferred" temperatures may lead to thyroid hypertrophy and eventually death.

The thermal biology of lizards is sufficiently understood to allow the laboratory maintenance of many species. There are, however still serious deficits in our knowledge about the differential effects of heat and light, time sharing of thermal resources, and the relationship of heat seeking to energy budgets, arousal and activity (see Regal, this volume). In *Lacerta* freshly received from the field and in those kept at low temperatures in the laboratory, Boycott and Guillery (1959) have observed cerebral changes that resemble those noted by Cajal in the brains of hibernating reptiles. These changes take 1 to 4 weeks to develop and are reversible, and it is not certain that the cytological effects of cold can be dissociated from the effect of cold on activity (Boycott, Gray, and Guillery, 1961). Daily variations in low temperature tolerance (indicated by a loss of the righting reflex) were described by Spellerberg and Hoffmann (1972), who attributed the changes to short-term acclimation during the cold night hours as well as an endogenous daily rhythm.

Cabanac (1971) observed that body temperature and arousal are so intimately related as to require a knowledge of the animal's internal state when considering its responses to various stimuli. He has ventured the term "alliesthesia" for the phenomenon of changing stimulus value with variations in the animal's internal state. For example, Garrick (1974) has observed that the selection of body temperature by two species of lizard is affected by the animals' reproductive and hormonal state. Other species respond to bacterial infection by selecting warmer microhabitats and effectively developing a "fever" (Kluger, Ringler, and Anver, 1975) which may be important to survival (Bernheim and Kluger, 1976).

In a study of blue spiny lizards, thermal radio transmitters were used to monitor the lizards' body temperatures during various activities (Greenberg, 1976*a*). It was of interest that these lizards basked until their body temperatures attained the maximum voluntary level, after which they were relatively passive in regard to the thermal qualities of their microhabitats (Fig. 7). This suggested that after an initial "warming up," behavioral thermoregulation would not compete with or complicate an interpretation of subsequent activities. Such a eurythermic species seemed at first to be an ideal laboratory subject, until the body temperature correlates of feeding and foraging were analyzed (Fig. 8).

Feeding occurred across a wide range of body temperatures, but foraging occurred in a relatively narrow range of elevated body temperature. It is reasonable to assume that a lizard would be both a better predator, as well as a less vulnerable prey, if it limited forays to times at which body temperatures are elevated to levels conducive to both maximum alertness and action.

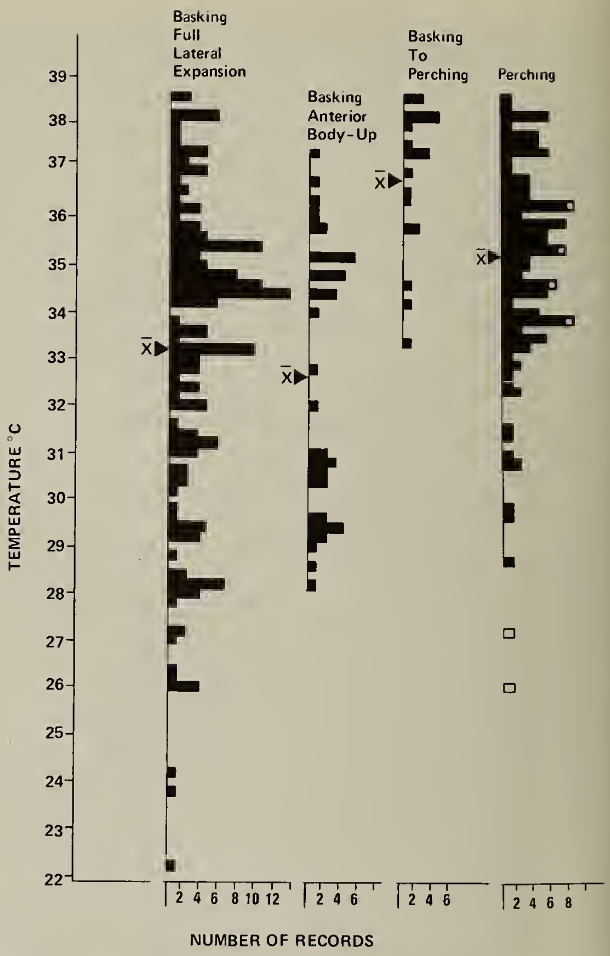

Figure 7. The body temperatures associated with two basking postures, the transition from basking to perching, and the perching "range." Most basking and all other temperatures were obtained by use of temperature sensitive miniature radio transmitters implanted in three lizards. (Adapted from Greenberg, 1976*a*).

These observations suggest that if one provided only the minimum conditions necessary to keep a lizard feeding well and apparently healthy, one might be misled in an interpretation of spontaneous activity.

Basking and Perching

Basking is a commonly employed thermoregulatory behavior among diurnal lizards. It can be defined as an activity in which

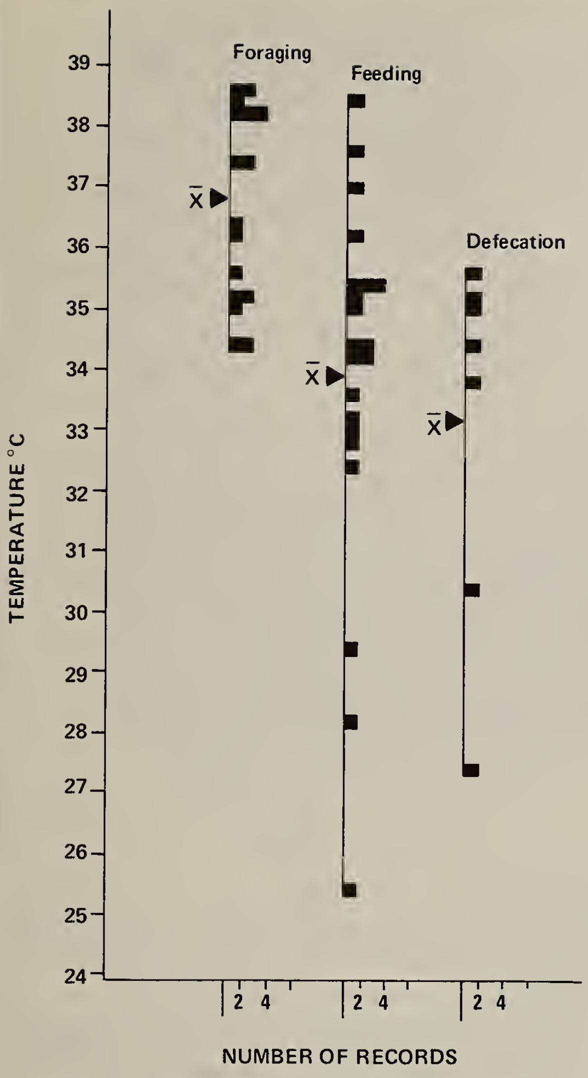

Figure 8. The body temperature correlates of sit-and wait feeding (predation from the perch) and foraging.

lizards expose themselves to the sun (heliothermy) or some other thermal source and assume postures or orientations which maximize the rate of heat gain. Since basking behavior can vary with the habitat and with the lizard's physiological requirements, it is unlikely that all lizards must necessarily bask in order to become active (Regal, this volume).

The blue spiny lizard and rainbow lizard use distinctive postures when they find sources of thermal reinforcement (Figs. 9, 10). They sometimes get into awkward postures when orienting to a photothermal source—clinging, for example, to rock prominences or shelves to expose their dorsum to the light.

The postures employed when perching are more suggestive of readiness for rapid action than those of basking. A relative insensitivity to stimuli in basking lizards was noted by Rand (1964) for *Ameiva*, Bartholomew (1966) for the Galapogos marine iguana, *Amblyrhynchus*, and Anderson (personal communication) for two species of *Sceloporus*. That lizards respond to stimuli more readily when in the perching posture is indicated by an analysis of the feeding and foraging episodes that occurred during basking or perching (Table 1) (Greenberg, 1973*b*), During basking, relative immobility would make exposed lizards less attractive to predators.

The postural distinction between basking and perching may vary considerably among species, but familiarity with the differences may be useful in making observations on levels of arousal, activity, and alertness.

Food and Water

Most knowledge of lizard feeding habits is derived from gastric or scat analyses (for example, Fitch, 1954; Knowlton, 1938; Blair, 1960) and occasional observations of predatory encounters. There is only scant information about the drinking habits of lizards. One suspects that these aspects of a lizard's life are among the most sensitive to the "observer effect." The cues that may draw a lizard into a drinking or feeding situation are not understood, but prey movement, sound, odor, or the feeding activity of congeners are probably important. *Anolis carolinensis* typically requires a dew-like coating from which water may be licked, while *Sceloporus cyanogenys* may learn of available water only by moving drops or ripples.

Freedom from the need to search for food has been implicated as a factor contributing to abnormal behavior in some small captive

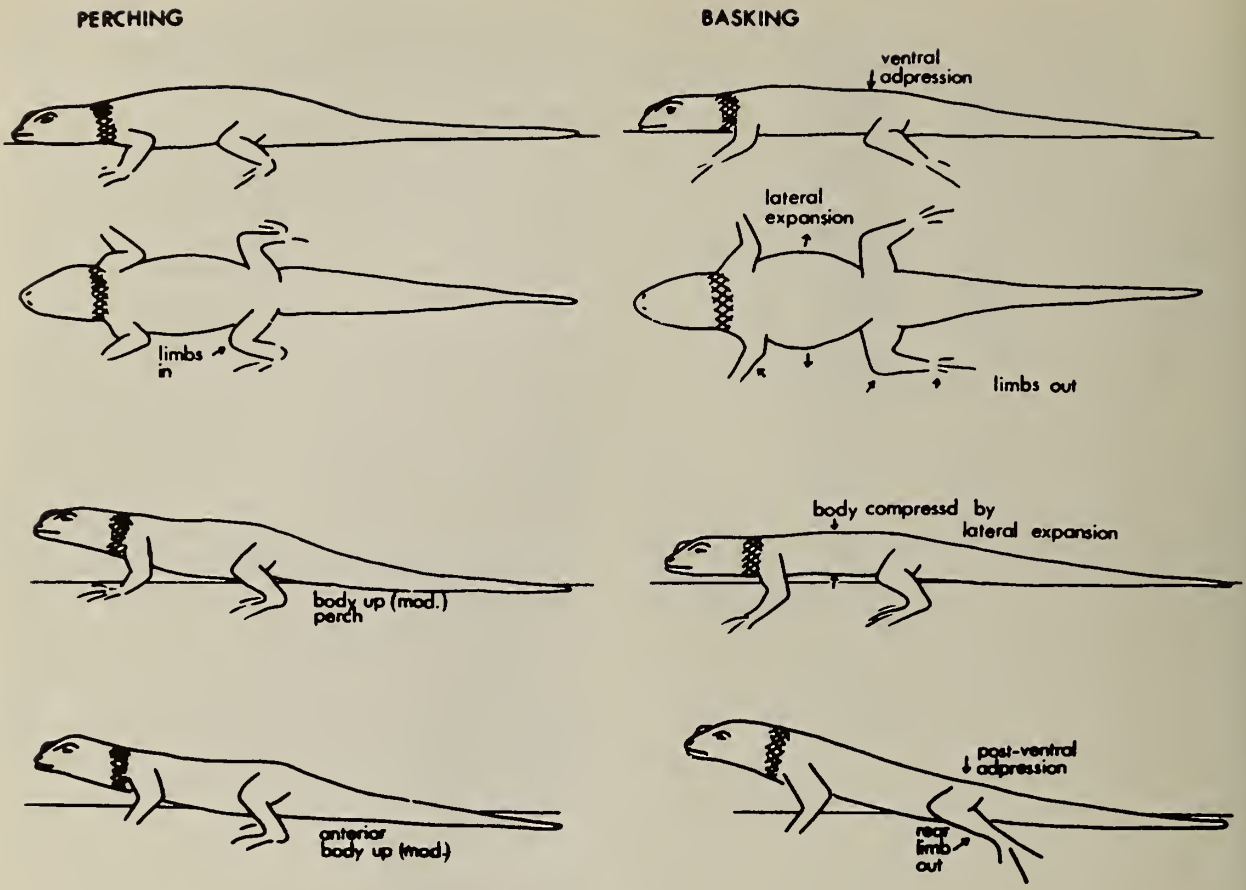

Figure 9. Basking and perching postures in the blue spiny lizard have been operationally defined. When basking, the profile of the body is expanded and the legs are out; in perching, the limbs are closer to the body in a way that suggests readiness for rapid action.

animals (Kavanau, 1967). in my present studies, lizards in colonies are initially fed a variety of prey. *Tenebrio* larvae, pupae, and adults, crickets, sweep-net contents, and an occasional neonatal mouse are provided on an irregular schedule in order to provide a variety of prey types (and prey behaviors) to induce lizards to explore their habitats in a natural way.

Sceloporus cyanogenys are more likely to feed or forage during perching than basking (Greenberg, 1973*b*, 1976*a*). Feeding episodes that are initiated from the perch occur when a lizard perceives prey (or another lizard) moving in its surveillance area. At times, in the absence of moving prey, a blue spiny lizard will spontaneously begin a foray, alerting it to prey that would otherwise be ignored. For example, nonmoving *Tenebrio* pupae would be nudged until they twitched, and then quickly eaten (Greenberg, 1977*a*). A foraging lizard will always attack prey.

Another consideration in the interpretation of predatory aggression is social feeding (Greenberg, 1976*b*). In some situations, perching lizards, watching each other as well as looking for prey, will be guided to a feeding site by the activity of congeners, or be stimulated to search their habitual feeding sites by the sight of a feeding congener. Food stealing is a common social interaction at feeding sites and may be a source of information about novel prey. Large prey will be shared when attempted stealing results in a pulling contest that rends the prey.

Deference to dominants at a feeding site, or an apparent reluctance to be active near a dominant, can compromise the activity of

Figure 10. Photo of CCTV frame of the legs-out component of the basking posture in *Agama*.

some lizards. Juveniles, however, rarely show such reluctance and may in fact be the initiators of a feeding episode.

Dietary supplements are often employed to compensate for the deficiencies inherent in diets of limited prey types. Of these supplements, calcium may be the most important. Changes in activity may occur because of inadvertant dietary deficiencies. For example, there is an increase in activity observed in fowl deprived of calcium and sodium (Hughes and Wood-Gush, 1973).

Use of Shelters

The shelter appears to be more than a mere site of sequestered rest, a hiding place from potential predators or aggressive conspecifics, or protection from environmental extremes. The availability of shelter has been shown to have a function in the normal expression of circadian thermal activity (Regal, 1968). At certain times, the crevice-dwelling blue spiny lizard will defend a crevice as a territory. Excluded individuals have been observed burying themselves in loose substrate (Greenberg, 1973*a*).

Blue spiny lizards will occasionally bask inside their shelter, sometimes orienting to a thin shaft of light and at other times pressing their backs to a warm overlying rock shelf. Such "covert basking" is not uncommon; it has also been observed in *Gehyra* (Bustard, 1967), *Dipsosaurus dorsalis* (DeWitt, 1971), and even in the usually arboreal *Anolis nebulosis* (Jenssen, 1970*a*). Perching just inside the threshold of a shelter, alert for prey or social activity, was often observed. The pattern of shelter utilization seemed to reflect the social organization of the population. Some lizards were consistently more exposed than others.

These data indicated that observations of activity within a shelter would be of value. To make such observations of the blue spiny lizard, the "shelter column" enclosure was developed. This habitat was constructed to

Table 1: The context in which blue spiny lizards fed, foraged, or were aware of prey but made no move to feed. Based on 238 observations of a four lizard population in a large complex habitat. The ratio of daily time spent in basking versus perching is about 1:3, but the ratio of feeding episodes initiated during basking versus perching is about 1:5, and for foraging the ratio is about 1:10

	BASKING full-body	BASKING anterior body up	COVERT PERCHING	PERCHING	FORAGING	OTHER	(n)
DOMINANT MALE							
FEEDING	6.5	4.3	19.6	56.5	13.1	0	(46)
FORAGING	6.2	3.2	25.0	62.5		3.1	(32)
AWARE OF PREY	25.0	0	0	75.0	0	0	(4)
SUBORDINATE MALE							
FEEDING	16.7	12.5	0	54.2	16.7	0	(24)
FORAGING	0	9.4	3.1	84.4		3.1	(32)
AWARE OF PREY	11.1	11.1	11.1	55.6	0	11.1	(9)
FEMALE							
FEEDING	9.5	9.5	9.5	42.9	28.6	0	(21)
FORAGING	0	9.4	3.1	84.4		3.1	(14)
AWARE OF PREY	22.2	0	22.2	55.6	0	0	(9)
FEMALE							
FEEDING	0	11.1	5.5	72.2	11.1	0	(18)
FORAGING	8.3	4.2	16.7	62.5		8.3	(24)
AWARE OF PREY	20.0	40.0	0	40.0	0	0	(5)
CUMULATIVE							
FEEDING	8.3	8.3	11.0	55.9	16.6	0	(109)
FORAGING	3.9	4.9	14.7	71.6		4.9	(102)
AWARE OF PREY	14.8	14.8	11.1	55.5	0	3.7	(27)

reveal in an ant-nest fashion the inner recesses of a saurian shelter (Fig. 11).

The findings depicted in Figure 12 suggests that only the dominant male conforms to the often reported—almost classic—activity profile for diurnal lizards; the subordinate male and female were more variable in their behavior. It is also important to note that there were no overt agonistic social interactions that led to this pattern, and the environmental temperatures never reached aversive levels.

Lizards typically "slept" with their heads wedged tightly into the angles of the crevices (Greenberg, 1971). Animals were generally more alert on the wider parts of shelves. This apparent alertness seemed to follow a diurnal pattern suggesting a circadian variation in thigmotaxic tendency (Fig. 13).

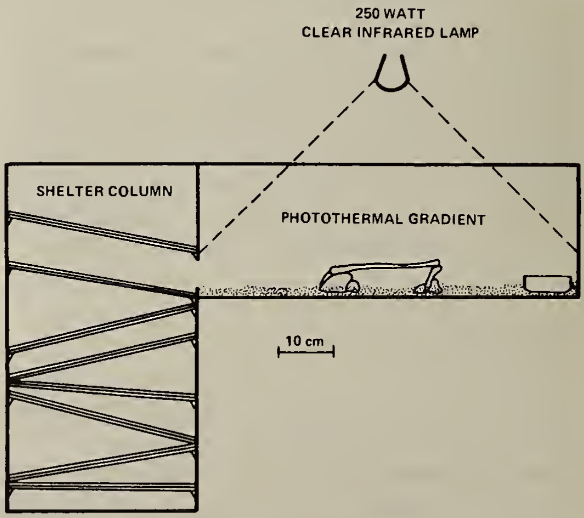

Figure 11. This habitat reveals in bee-hive fashion the inner recesses of a shelter. Observations suggested important differences in the way different members of the population utilized their space.

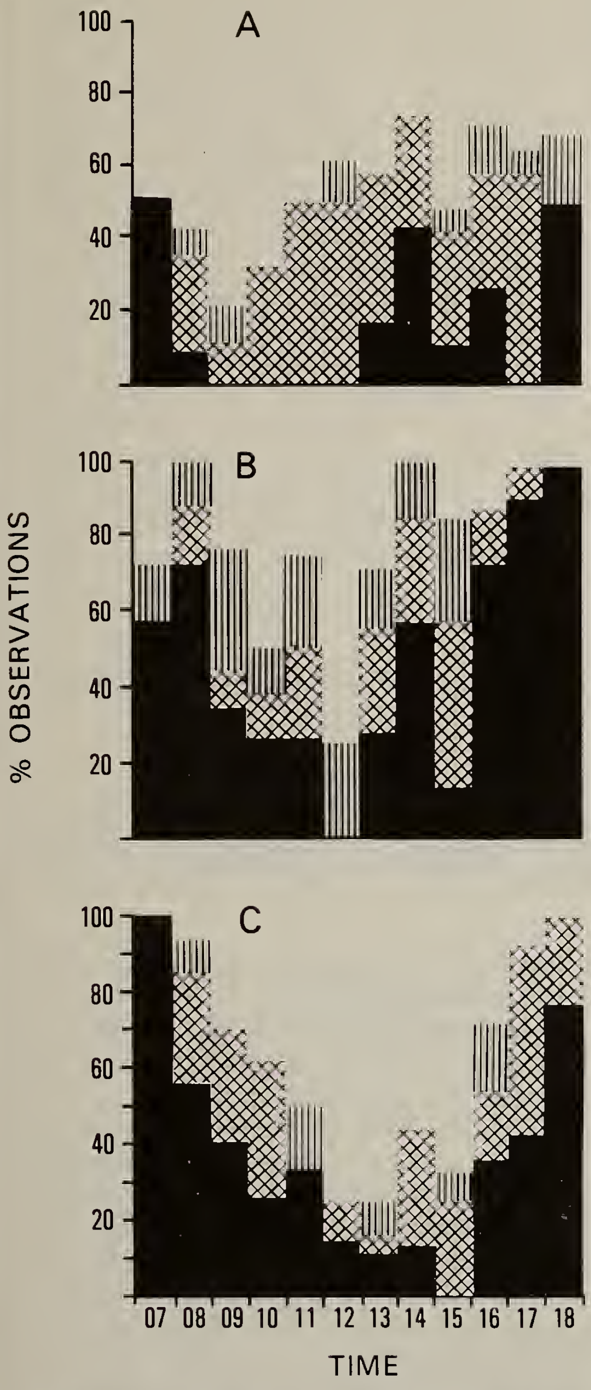

Figure 12. The proportions of the kinds of activities observed within the shelter for subjects A (female), B (subordinate male), and C (dominant male). The dark portion of each bar = sleeping or quiescent animals; the hatched portion = animals are active on or between shelves; the striped portion = time spent surveying the habitat from within the shelter ("covert perching").

These observations make it clear that, in an experimental design concerned with activity levels, one must also consider activity that may occur in microhabitats normally concealed from the observer.

Social Behavior

In his study of *Anolis nebulosus* ethoecology, Jenssen (1970*a*) used crowded conditions to "catalyze" social interactions. He was confident that the motor patterns exhibited under these conditions were essentially the same as those seen in nature, although the frequency of displays was probably abnormal.

The behavioral or perceptual space of a laboratory habitat can affect some lizards in unexpected ways. In some cases small enclosures in which lizards are continually exposed to one another will diminish interactions. Mayhew (1963*a*) observed that a large and a small *Amphibolorus pictus* cohabited peacefully in a small enclosure, but when both were transferred to a larger vivarium, the large male vigorously pursued the smaller animal. Mayhew proposed that the small enclosure inhibited the normal expression of territoriality.

I have observed the same phenomenon in a colony of *Agama agamas.* Harris (1964) observed that some *Agama* males are "repressed" by the presence of a dominant male, made conspicuous by its bright red head. Perhaps such a "repression" exists in small laboratory habitats where lizards are continually exposed to dominants. Repression may then abate under less restrictive conditions in which the smaller lizard may develop territorial habits that elicit aggressive responses in the dominant.

In nature, environmental influences on aggression in lizard populations are not uncommon. Many lizards that are mutually intolerant under normal conditions will aggregate during adverse weather or at night (Evans, 1967, in *Coleonyx;* Curry-Lindahl, 1957, in *Agama cyanogaster;* and Regal, 1968; in *Klauberina*), or at sites hav-

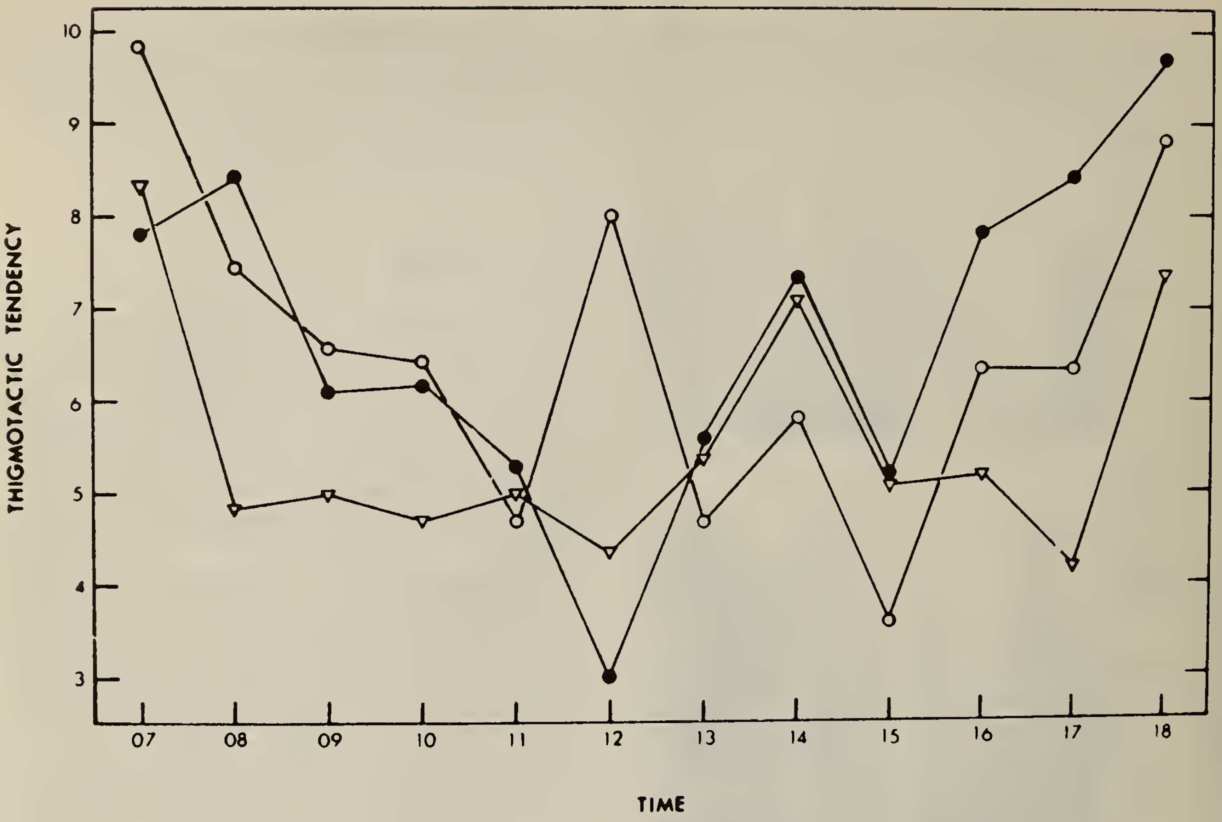

Figure 13. The curves for three lizards suggest a diurnally varying thigmotactic tendency. Lizards were scored on the basis of posture and activity—with the highest score going to sleeping animals with their heads wedged into crevices. Triangle = female, closed circle = subordinate male, and open circle = dominant male.

ing an abundance of prey (Evans, 1951; Fitch, 1940; Norris, 1953).

Social behavior has received much attention by students of saurian behavior—possibly because of the early attention drawn to the work of Noble and Bradley (1933) by Lorenz (1935). Since Carpenter's (1962) introduction of the "display action pattern" analysis display activity has been subject to intense research (Jenssen, this volume).

Context is of importance in an interpretation of either arousal (operationally defined by postures and activities) or the communicative significance of a display. W.J. Smith (1969) points out that since there are more functions served by displaying than there are displays, recipients of displays must rely heavily on contextual information. The possibility of a discontinuity in the physiological causation of superficially similar displays that appear in various contexts must be considered.

A prevalent view is that the bobbing displays of iguanids include two types which represent a continuum of "intensity" (Carpenter, 1967). These displays are designated "assertive" and "challenge"; the former is performed in social and nonsocial situations and may be elicited by a broad range of stimuli; the latter is performed as part of ritualized territorial defense. The possibility of a gradient between these displays recalls Moruzzi's suggestion that different responses are possible at different arousal levels (cited by Andrew, 1974). Stamps and Barlow (1973) have analyzed the display behavior of *Anolis aeneus* and observed that while some components may indicate a gradient of "intensity" between displays, in general, no smooth continuum exists between the "challenge" display (Gorman, 1968) and the lower intensity "fanbob" that they observed.

In my observations of blue spiny lizards, a discontinuity of display "motivation" was suggested by the finding that assertive displays varied greatly in intensity and were often performed with much more vigor than many challenge displays.

An analysis of the conditions in which assertive displays occur suggests that the only thing that they all have in common is a clearly elevated level of arousal—at least in terms of sensitivity to peripheral stimuli (Table 2).

The appearance of an assertive display during foraging illustrates the importance of the experimental habitat for the eliciting and subsequent functional interpretation of social displays.

SOCIAL CLUES ABOUT THE CAUSATION OF BEHAVIOR

Manning (1967) regards the species differences in the head-bobbing patterns of *Sceloporus* described by Hunsaker (1962) as an elegant example of gene control of changes affecting thresholds within the nervous system. An analysis of display behavior may be of value in suggesting hypotheses about the neurophysiology of displays if sufficient information about different species is obtained to suggest how displays have evolved.

Display is often the most dramatic behavioral pattern with which ethologists deal. It is probably at the end of a continuum of homologous behavioral patterns that begins with less striking behavior, such as locomotor intention movements (Daanje, 1950) or somatic or autonomic responses (Morris, 1956). We may ask with Barlow (1968:227) —do shared effectors mean shared central nervous system mechanisms? If we think that they might, ideas about the different functions of homologous behavioral patterns might yield important clues about the neural aspects of ritualized behavior.

Consider the head nodding of an iguanid in terms of conflicting components of autonomic stimulation. I have observed an exchange of signals in blue spiny lizards (Greenberg, 1973*a*, 1977*a*) that suggests that the nod may represent an alternating pattern of fear and aggression: Every time a dominant

Table 2: The contexts in which the "assertive" display of the blue spiny lizard is observed. About 75 percent of the display were in nonsocial contexts.

	Female	Male	% of Total Assertive Displays	(n)
NON-SOCIAL				
SPONTANEOUS	100.	00.0	09.0	(7)
AFTER MOVEMENT DURING FORAGING	52.6	47.4	25.3	(19)
AFTER ATTAINING PERCH	14.8	85.2	36.0	(27)
DURING EMERGENCE	00.0	100.	02.6	(2)
SOCIAL				
RESPONSE TO ACTION OR APPEARANCE OF ANOTHER LIZARD	80.0	20.0	20.0	(15)
IMMEDIATELY AFTER SOCIAL INTERACTION	00.0	100.	06.7	(5)

raised its head, revealing its signal blue color, the subordinate lowered its head in apparent submission. In other species also, dominant lizards characteristically elevate their heads when aroused, and subordinate lizards lower their heads to the substrate (Carpenter 1967:99). These are the same patterns seen in lizards when exploring or when making themselves inconspicuous.

Or consider the origin of the profile changes of an aggressive lizard in terms of thermoregulation—the expansion of the surface area of the body and hence the solar interface. *Phrynosoma* (Milne and Milne, 1950), *Uma* (Carpenter, 1963), *Amphibolorus barbatus* (Brattstrom, 1971), and *Leiolepus belli* (Regal, personal communication) use a similar kind of posture in thermoregulation as in a show of aggression.

The tail-lashing "attention-getting" of the female blue spiny lizard is remarkably like that of the tail-to-side reflex in mating (Fig. 14). It recalls the "rejection" movements of *Sceloporus undulatus* (Carpenter, 1962), the tail lashing of "excited" *Amphibolorus* (Mayhew, 1963*a*), and the stalking of *Anolis* lizards (Ruibal, 1967; Jenssen, 1970*a*). How are such motor patterns brought under more and more specific stimulus control?

Might the tail-in-the-mouth minuet of the blue spiny lizard (Fig. 15) be related to the

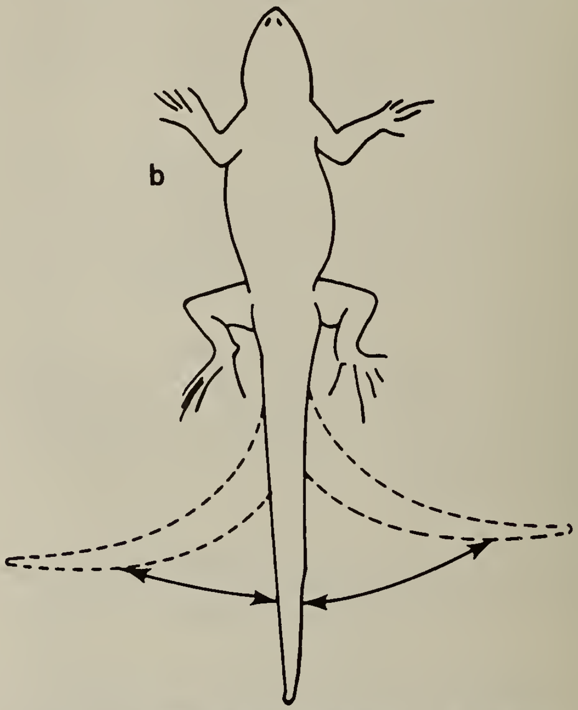

Figure 14. The tail-lash pattern of the female blue spiny lizard.

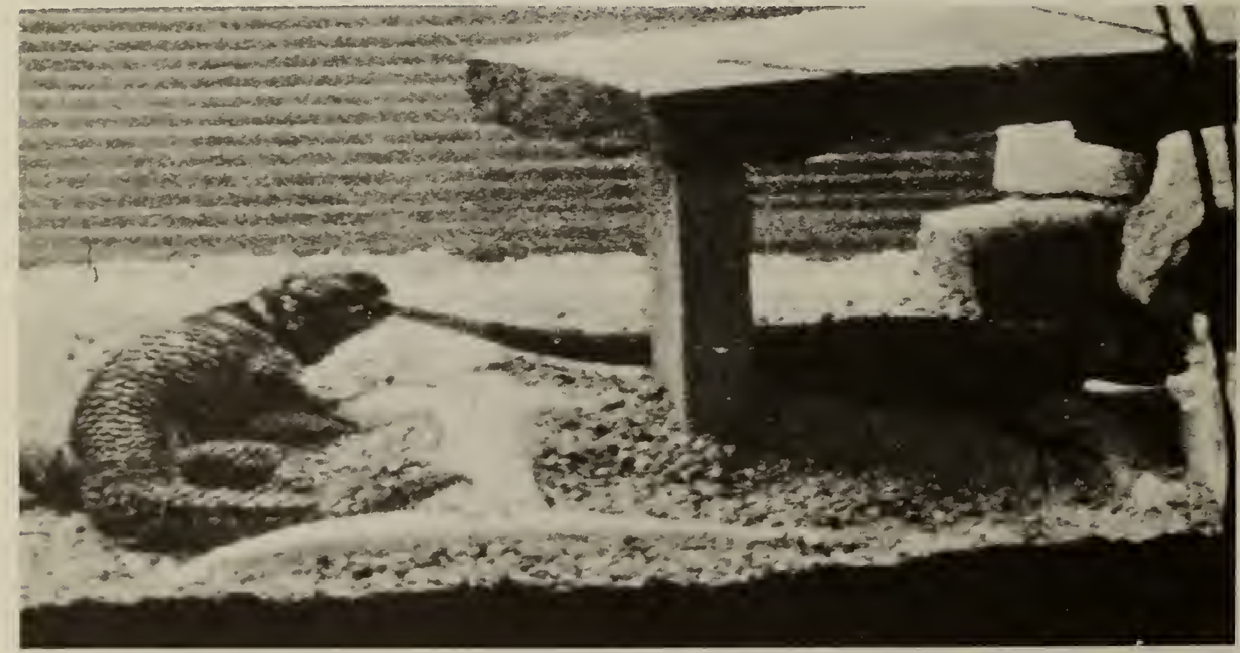

Figure 15. The tail-grip courtship ritual of the blue spiny lizard.

tail-biting aggression so familiar to observers of iguanids, or to the tail-tasting form of sexual discrimination employed by *Coleonyx* (Greenberg, 1943)?

I have observed an increase in the frequency of "exploratory" tongue-touching of *Anolis carolinensis* when in a new habitat. This is much like the tongue-touching of the substrate by *Sceloporus iarrovi* in novel situations (DeFazio et al., 1976). Might the tongue-touching seen in other species under other conditions be a "displacement" derivative of such behavior—for example, the tongue-touching used in the reinforcement of social status by the *Amphibolorus barbatus* (Brattstrom, 1972) or the tongue-touching that I have seen during the aggressive display of *Agama agama?*

Anolis carolinensis are occasionally observed engaging in social grooming during shedding (Fig. 16). Might this behavioral pattern be comparable to the ectoparasite "grooming" of young *Iguana* (Burghardt, 1975) or to the food-stealing so often observed during social feeding of blue spiny lizards (Fig. 17) and green anoles (Greenberg, 1976b)?

Although these suggested relationships are hypothetical, they may be of value in providing clues about the underlying organization of behavior. Particularly, the mechanisms by which autonomic reflexes and fragments of motor patterns become elaborated and progressively brought under the control

Figure 16. *Anolis carolinensis* allogrooming.

Figure 17. Blue spiny lizard hatchlings tug-of-war with mealworm.

of higher neural structures and more specific external stimuli. They also illustrate the diversity and complexity of the behavioral patterns of lizards that make these animals such fascinating subjects for ethological investigations. A researcher need only shed his preconceptions to appreciate the uniqueness of each species and its exquisitely tuned eco-evolutionary adaptations.

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DISCUSSION

PETERSON to GREENBERG: Regarding naturalistic settings, it is important to realize that there are some problems that only a simplified laboratory setting can deal with. For example, natural settings exaggerate the possibility that an experimental effect may be overlooked. This is because in a complex environment the brain can compensate for some kinds of deficits, but in an unnatural laboratory setting the animal may be compelled to live in a certain way and this can be very revealing. For example, Schneider's tectal lesioned hamsters looked normal in some environments but an important deficit showed up in others. There is also the possibility of misinterpreting a deficit. For example, in 1970 Humphrey (BBE 3:320–337) dispelled the old belief that primates with striate cortex lesions are blind. In an unnatural setting he was able to show that the deficit is really one of recognition.

GREENBERG: your point is good about the difficulty of interpreting behavior in complex settings. The main thing is to have a reasonable idea of the normal behavior of the animal. Without such an idea you may find yourself investing considerable effort in investigating a laboratory-induced pathology of relatively limited interest. Once a naturalistic overview is obtained one could successively simplify experimental habitats until an appropriate one for the experiment is obtained. Also, naturalistic observation may reveal behavioral patterns that you might otherwise be totally ignorant of.

REGAL to CREWS: This research contributes to our understanding of the process of sexual selection. I think the difference between emergence of males and females might relate to the fact that it is to the female's advantage to let the subordinate males get "weeded out" so that, when the female finally selects a male, it is a male with a superior genetic constitution (a territory-holding male) who has possibly selected a better habitat. In any event, the chosen male has won out in some sort of competition and presumably would give her superior male offspring, etc.

CREWS: I believe females are presented with two different types of choices in terms of sexual selection. First, when the female emerges from winter dormancy, she must establish a home range; this choice is probably determined by a combination of habitat preferences and some aspect of the male in whose territory she will reside. Second, male choice is perhaps more important for the transient female who moves about the habitat. This would be especially important when the female has a large, preovulatory ovarian follicle—which male does she choose to mate with?

MacLEAN to CREWS: Can you keep animals cycling year round with the environmental conditions you have described?

CREWS: Female *Anolis carolinensis* will go through at least three complete ovarian cycles (ovarian quiescence, recrudescence, breeding, and regression) under this environmental regimen in a one-year period. Within each reproductive phase, females will usually go through at least ten estrous cycles and sometimes lay up to 15 eggs before the ovaries regress.

MACLEAN: What other lizards have this sort of an estrous cycle?

CREWS: Most temperate species that I am aware of are single or multiple-clutch layers; that is, they only exhibit one or two estrous cycles, after each of which they lay a clutch of eggs. All anoline lizards, however, exhibit the pattern of ovarian activity I have described here.

GARRICK to CREWS: Is there any evidence for hormone-brain interactions in some of these behaviors that you observed?

CREWS: We have recently begun an investigation of the neural and hormonal determinants of sexual behavior in reptiles.

PETERSON: I would like to expand on a point raised by Dr. Brattstrom, namely, that learning may play a more important role in the normal behavior of lizards than has heretofore been suspected. One gets the impression, both from remarks made at this conference and from an examination of the behavioral literature, that data on lizards gathered from the learning laboratory are somehow irrelevant to the behavior of these animals in the wild. I believe that such an attitude may be misguided. Over the last 10 years, a body of literature has emerged from the learning laboratory which indicates quite clearly that lizards are capable of a wide variety of learned behaviors. It is difficult for me to understand just how the ability could have evolved in the first place were it not exhibited by animals in the wild.

In this connection, it is important to understand that the paradigms studied by comparative psychologists are not simply laboratory curiosities but are, at least in many cases, representative of situations encountered routinely by animals in their normal habitats. For example, the paradigm known as passive avoidance learning refers to a situation in which an animal learns to withhold a response—under certain stimulus conditions—which otherwise has a high probability of occurring. This is precisely the kind of behavior which underlies the putative success of the Batesian mimic. Another example would be the capacity for "latent learning" as discussed by Dr. Brattstrom. Recently, Philabosian has suggested that this type of behavior may occur in *Anolis cristatellus*. The point is that one cannot safely ignore the implications of these laboratory studies on lizards—that is, that learning may play a significant and unsuspected role in the naturally occurring behavior of this very successful vertebrate group.

I would also like to suggest that it may be productive to think of learning ability (or, more properly, abilities—since there are many different types of learning) as an evolutionary strategy which may affect the survival of a species just as, for example, the tendency to develop digital lamallae or species-specific displays. Like any character, certain lineages should exhibit more highly developed learning capabilities than others—and it may be possible to relate this differential distribution of learning ability to either taxonomic status or type of niche utilization. For example, large predatory lizards, especially opportunistic hunters such as *Varanus komodoensis* described by Dr. Auffenberg might be expected to rely more heavily on learned behaviors than lizards which occupy a highly structured, relatively invariant, behavioral niche. Whatever the distribution of learning ability across lizard species, it is reasonable to expect that such a capability will play a role in the naturally occurring behavior of lizards and in the adaptive success of certain Saurian taxa.

HEATH to REGAL: Why couldn't a reptile just develop an unusually large heart for its size? Reptiles are generally small-hearted. This is a path that they could follow. Increased perfusion of the tissues can be accomplished by increasing capillary diameters as well.

REGAL: Increasing size will not increase efficiency, and efficiency is what might count in competition between two or more otherwise comparable species. I would have to have data on what the benefits would be of enlarging an "inefficient" heart relative to the costs. We lack the data to answer your question.

GANS: At an equivalent temperature, reptiles have a lower metabolic rate than birds or mammals. So one could raise a larger herd of dinosaurs on a pasture of land than a herd of cows. Ectotherms can maintain more mass on an equivalent energy input.

REGAL: Yes, I agree that there are distinct advantages to ectothermy just as there are to endothermy and I believe that we should spell these out.

GANS: Crocodilians have essentially four-chambered hearts, and yet their metabolic rates are still low. This illustrates that there are advantages to ectothermy. Reptiles can maintain a larger biomass than mammals on an equivalent amount of food as long as it is possible for them to get away with paying the price, which may be resigning themselves to basking or sit-and-wait predation, or whatever.

REGAL: Yes. I see no reason why endothermy should *automatically* be selected for because of a four-chambered heart. The heart simply *allows* selection for intense activity strategies to proceed and the species may be superior in competition of the appropriate sort.

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Demographic Analysis: A Tool for the Study of Natural Selection of Behavioral Traits

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SUMMARY. While there has been considerable literature on lizard displays and social behavior, few investigators have realized the potential of iguanid lizards for the quantitative study of the effects of natural selection on variations of behavior traits. The combined ease of mark and recapture analysis, of behavioral observation and cinematography in the laboratory and field, and of experimental manipulation, render lizards ideally suited for such a study.

The studies of prairie swifts (*Sceloporus undulatus garmani*) described here indicate how varying egg size, hatchling size, and degree of aggressiveness in juveniles may influence fitness. As food supplies for hatchlings dwindle in late summer and lizard densities increase, resource competition increases. The increased competition manifests itself as an increase in dispersion and density dependent mortality toward the end of the hatching season. As an adaptive response to greater late seasonal competition of hatchlings, females apportion more of their available energy into each egg. They produce larger eggs which hatch into larger and more aggressive hatchlings. Survival of larger late hatchlings to the next breeding season (fitness) is significantly greater than that of smaller late hatchlings. Among early hatchlings, survival of larger hatchlings is not significantly different from that of smaller hatchlings.

Signature displays of lizards have been shown to vary geographically. The adaptive significance of this variation has been the source of considerable speculation. Signature display complexity in the side-blotched lizard (*Uta stansburiana*) has been shown to be positively correlated with vegetation density. This phenomenon is the basis of a model that generates predictions testable using observational and demographic techniques and relates the display complexity to the conspicuousness of displaying lizards to predators, and their conspicuousness to conspecific lizards.

INTRODUCTION

Within the past two decades, the description of reptilian display behavior has advanced from the anecdotal qualitative level to a relatively sophisticated level of quantitative analysis of variation within and between populations (Carpenter, in press; Ferguson, in press, for reviews; Jenssen, this volume). Also, nondisplay aspects of lizard social behavior such as territoriality, dominance, and aggressiveness have been extensively studied (Fox, 1973; Brattstrom, 1974; Ruibal and Philibosian, 1974; Simon, 1975; Vinegar, 1975*b*).

While a number of investigators have focused on the evolution of social behavior, few have realized the potential of monitoring behavioral variation or variation of traits with some signal value in lizards to reveal natural selection within populations. Studies that show how individual "fitness" [1] is correlated with trait variants and how environmental variable are likely to influence fitness

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[1] Fitness is defined as the ability of an individual to contribute to the next breeding generation.

promise to provide insight into the workings of natural selection. Kettlewell's (1961) studies on the evolution of industrial melanism consider these factors and may serve as a model for students of evolutionary biology. It is our purpose to illustrate how studies on lizard social behavior are particularly suitable for throwing light on the processes of natural selection.

There are four main attributes of lizards (particularly many species of iguanids and agamids) that make them excellent subjects for such studies: (1) Many lizards, particularly diurnal heliothermic species, are conspicuous in their habitat. They can be easily discovered by an investigator and observed for long periods of time. (2) Individuals often have restricted lifetime movements so that they can be repeatedly discovered, observed and photographed for over a period of days, weeks, months, or years. (3) Individuals often can be easily caught or trapped for marking; and (4) Restricted removal of toes renders individuals easily identified by an investigator for the life of the animal. Small distinctive paint markings render individuals easily identified by an investigator from a distance and without recapturing the animal. Such markings, however, are only retained until the animal undergoes ecdysis (usually to a few weeks).

Due to these factors, the number of studies on the life history and demography of lizard populations has steadily increased since the original work by Fitch on *Sceloporus occidentalis* and Stebbins on *Sceloporus graciousus* (Fitch, 1940; Stebbins, 1948; Stebbins and Robinson, 1946; see also Blair, 1960; Harris, 1964; Tinkle, 1967, 1969; Tinkle et. al., 1970; Turner et. al., 1970; Jenssen, 1970*b*; Tinkle and Ballinger 1972; Vinegar, 1975*a*, 1975*c*). Accurate schedules of age-specific mortality and fecundity are now known for a number of populations of a number of species. Mortality and fecundity, so easily observed in these populations by mark and recapture techniques, are the major measures of fitness (Williams, 1966).

In addition to demographic studies, studies of quantitative variations of both display and nondisplay behavior have been conducted in recent years in both a natural and laboratory setting (Ferguson, 1970, 1971, 1973; Jenssen, 1971, 1975, this volume, for studies on variation of stereotyped displays; Harris, 1964; Tinkle, 1967; Rand, 1967; Yedlin and Ferguson, 1973; Fox, 1973; Ruibal and Philibosian, 1974; Philibosian, 1975; Simon, 1975; Vinegar, 1975*b*, for studies of variations in aggressiveness or territorial behavior.) These studies reveal the existence of easily quantifiable variations of social behavioral traits within a population. Thus, since the fitness of individuals can be determined through monitoring of survival and reproductive success, the fitness of individuals bearing variants of behavioral traits can also be recorded. In short, a means exists for observing the outcome of natural selection.

There remains the difficulty of identifying what environmental factors are responsible for the differences in fitness between individuals bearing different variants or degrees of a trait and how these factors operate. An established ecological method of dealing with this problem is the manipulation in a natural setting of the variables considered most likely to affect fitness and/or the close observation of the interactions between organisms and specific environmental factors. Thus, for example, Connell (1961) demonstrated the effect of competition on survival of a barnacle species by removing another closely related species; Paine (1971) demonstrated the effect of predatory starfish on the competition between prey species in a coral reef community by removing starfish. In the side-blotched lizard *Uta stansburiana*, Turner et. al. (1973), demonstrated an effect of winter rainfall and predators on reproduction and survival by watering the environment in experimental field plots in winter and by removing predatory leopard lizards in an enclosed natural plot. In the same species, Fox (1973) determined through mark and recapture analysis and careful observation that certain patterns of activity, as well as the consumption of poorer quality food, were correlated with lower survival of smaller juveniles. An hypothesis consistent with his data is that smaller juveniles, forced by larger juveniles into territories containing lower quality food, would be obliged to forage at times of the day (early and late) and on types of days (cloudy and cool) when known predators were likely to be actively feeding. Manipulation of predator density and supplementary feeding of lizards on "poorer" territories would provide a test of this hypothesis. In short, mark and recapture analysis, careful behavioral monitoring of individuals, and manipulation of important environmental variables are likely to provide insight into the workings of natural selection.

In the present article we illustrate an alternative approach to a study of the effects of natural selection on the evolution of behavioral or phenotypic traits related to social behavior. Finally, we present a model for display behavior variability relative to the performer's visibility to conspecifics and predators.

HATCHLING SIZE, AGGRESSIVENESS, RESOURCE COMPETITION, AND FITNESS: SEASONAL CHANGES

A number of studies of lizard life histories suggest that clutch size and egg size (relative to female body size) differ between closely related species and between populations within a species (Tinkle, 1969; Tinkle et. al., 1970; Ballinger and Schrank, 1972). Although these and other investigators have tried to relate these variations to natural selection, the adaptive significance of these differences is unknown (Tinkle et. al., 1970). Pianka (1970, 1972) suggested that larger egg size might increase the chances of hatchling survivorship, but he did not discuss how this advantage might occur, nor did he explicitly suggest that hatchling size and aggressiveness might be intimately involved in this adaptation.

In a number of temperate multibrooded lizards, there is a seasonal decrease in the size of successive clutches (Table 1). In several populations a seasonal decrease in clutch size has been shown to accompany an increase in egg size (Tinkle, 1967; Turner et. al., 1970; Ballinger and Schrank, 1972; Tinkle, 1972; Ballinger et. al., 1972; Derickson, 1976). In only the last study were data sufficient to show that egg size correlates with hatchling size. This phenomenon poses an excellent opportunity to gain insight into the adaptive explanation for the observed clutch size and egg size differences between populations and species.

Research on the ecology, reproduction, and behavior of a population of the prairie swift lizard *Sceloporus undulatus garmani* conducted during the past 4 years has led to the following hypothesis: Seasonal decreases in availability of food during the hatching season accompanied by increases in hatchling density causes increased resource competition. The production by females late in the season of fewer but larger eggs that hatch into larger, more aggressive juveniles is adaptive because these juveniles are better able to aggressively defend the few optimal territories available at the time. Production of larger, more aggressive hatchlings early in the season when resources are relatively abundant, fails to result in higher juvenile survivorship and sacrifices offspring number. The adaptive response is more but smaller eggs. In this section we will discuss the data from our studies that support the hypothesis.

MATERIALS AND METHODS

The prairie swift *Sceloporus undulatus garmani* is a small lizard of the family Iguanidae. Adults measure about 55 mm from the tip of the snout to the cloacal opening. They inhabit a variety of habitats in Kansas, ranging from sandy river bottoms in the south and central part of the State to sandstone and limestone outcroppings in the western prairies. This race of lizard is part of a geographically widespread species that occurs from New Jersey to Florida in the eastern United States, where it is primarily a forest-edge tree dweller, and to southern

Table 1. Multibrooded lizard species showing seasonal decreases in clutch size, increases in egg size, increases in hatchling size.

Species	Decreased Clutch Size	Increased Egg Size	Increased Hatchling Size	Authority
Sceloporus undulatus	Yes, at least 7 populations	Yes, at least 1 population	Yes, at least 1 population	Ballinger and Tinkle (1972); Derickson (1976); Tinkle (1972)
Sceloporus occidentalis	Yes	No data	No data	Goldberg (1973)
Sceloporus graciosus	Yes	No data	No data	Goldberg (1975)
Cophosaurus texanum	Yes	Yes	No data	Ballinger et. al. (1972)
Uta stansburiana	Yes, at least 2 populations	Yes, at least 2 populations	No data	Tinkle (1967); Hoddenbach and Turner (1968); Turner et. al. (1970)
Uma inornata	Yes	No data	No data	Mayhew (1965)
Uma scoparia	Yes	No data	No data	Mayhew (1966)
Amphibolurus isolepis	No	No data	No data	Pianka (1971)
Tachydromus tachydromoides	Yes	No data	No data	Telford (1969)
Cnemidophorus sexlineatus	Yes	No data	No data	Hoddenbach (1966)
Cnemidophorus gularis	Yes	No data	No data	Ballinger and Schrank (1972)
Ameiva festiva	No	No data	No data	Smith (1968)
Ameiva quadrilineata	No	No data	No data	Smith (1968)
Lygosoma laterale	Yes, several populations	No data	No data	Anderson (1965); Brooks (1967); Fitch and Greene (1965)
Gerrhonotus liocephalus	Maybe	No data	No data	Burkett (1962)

Utah in the west, where it is primarily a canyon-rock dweller. The demographic patterns have been well studied by Tinkle and Ballinger (1972) in Ohio, Georgia, Texas, Colorado, and South Carolina, by Tinkle (1972) in Utah, by Vinegar (1975*a*, 1975*c*) in New Mexico and Arizona.

In the spring of 1971, an isolated population was located in the Kansas River bottom near Belvue, Pottowattomie County, Kansas. An area including about four acres was selected and divided into 40-foot quadrats so as to facilitate the recording of locations and movements of individual lizards.

The habitat of the area included a loose sand and gravel substrate, sparsely vegetated with grasses and other annual weeds. Small cottonwood, mulberry, and elm trees were distributed across the area, occasionally forming small groves. The study area was bordered on the north by a pond, on the south by a riparian forest and ditch, and on the east and west by plastic drift fences. Thus the population was relatively confined.

Several other vertebrates inhabited the area. Some of these that are potential lizard predators were: birds (bluejays, brown thrashers, catbirds, shrikes, cuckoos, sparrow hawks, kingbirds); mammals (deermice, shrews, moles, raccoons, opossums, skunks, badgers, and coyotes); amphibians (western toads, bullfrogs, leopard frogs); and lizards (racerunners, prairie skinks, and plains skinks). No snakes known to prey on lizards were observed in the area.

We began a census of the population in May 1971 and, for the purposes of this report, terminated it October 1972. The census methods were similar to those reported by Tinkle (1967). Processing of individual lizards included capturing; measuring and recording snout-vent length; clipping toes of individuals and recording the toe-clip patterns for future identification; recording location and recording habitat; painting tail base; and then releasing individuals at the location of their capture. The area was searched systematically. On the first search all lizards seen were captured and processed. On subsequent searches all lizards lacking a paint mark were captured and processed, while those with a paint mark were merely tallied. After six to eight sweeps, the proportion of "new" lizards was usually less than 10 percent, and the census was considered complete. Population sizes were estimated by use of the Haynes index (Hayne, 1949). Due to the high rate of hatching in the period from July 23, 1971 through September 7, 1971, and the low manpower available during that time, that entire 47-day period was considered a single census. Subsequent census periods were shorter and included for purposes of this report: September 27 through October 10, 1971; July 10 through July 17, 1972; July 31 through August 8, 1972; August 21 through August 23, 1972; and September 26 through October 11, 1972.

Data from these census periods analyzed in this report included density change for each of the 24 sectors. Each sector was a square composed of four adjacent quadrats. The total area was considered large enough (6400 square feet) to include the home range of a large number of juvenile lizards and small enough to generate a number of individual sectors for analysis of the effect of population density on survivorship. A few sectors were not included in the analysis because they contained marginally suitable habitats and did not support juveniles for more than a few days. In order to assess density change for a given sector over a time interval, the number of juveniles registered during a census period "t_0" at the beginning of the interval was compared to that registered on the same sector during a later census period "t_1" at the end of the interval. A ratio t_1/t_0 of less than one indicated a decrease in population density in the sector between the two census periods; a ratio greater than one, indicated an increase in density.

Survivorship of marked lizards was also analyzed for each sector by noting the proportion of individuals marked on a sector at "t_0" and still alive somewhere on the total study area at "t_1". The effect of density on both density change and survivorship was analyzed by comparing the 24 sectors, which had variable "t_0" densities.

Insect food available to lizards on the study area was estimated during the summer of 1972. An 8½ x 11 inch sheet of paper was affixed to a wooden clipboard and coated with "stickum special," a commercially available petroleum compound. These "insect traps" were placed on the ground throughout the study area in microhabitat regions suitable for lizards. Traps were set in place for 2 hours and after removal were immediately replaced with a fresh trap. On each "insect census day" traps were in place from 0700 to 1900 hours. After removal of a clipboard, the insects trapped on it were identified to Order, classified according to length and width and counted.

Observations indicated that ants avoided the clipboard traps. Because ants were suspected to be important food sources, their density was assessed by enclosing a 10 cm^2 area with a wire square and counting the number of them entering the area in a given period of time. There were four "insect census days" a month from June 1 to August 11. As a further means of assessing dietary habits, a sample of 5 to 10 lizards was periodically removed from the habitat adjacent to the study area and the contents of their stomachs examined.

The social behavior of juvenile lizards previously marked on this study area was observed for 26 fifteen-minute periods from August 8 to September 15, 1972. Periods of observation were concentrated in midmorning and early afternoon. The number of social encounters, individual lizards involved in each encounter, and the nature of each encounter were recorded on audio tape and later transcribed to summary sheets. After the final observation period, each lizard was recaptured and remeasured. Lizards were recaptured again between these dates only if their paint mark was lost.

Finally, crowding tolerance tests were conducted on juvenile prairie swifts hatched from eggs laid by females from Reno County, Kansas. A complete description of the technique is given in Tubbs and Ferguson (1976). Briefly, eggs were harvested in outdoor enclosures and incubated in small jars. The hatchlings were measured, weighed, marked by toe clipping, and introduced either singly or in groups of 5 to 10 into 2 x 5-feet metal enclosures. The metal sides of the tanks prevented escape of the lizards and 2-inch wire mesh covering the top prevented the entry of bird predators. The behavior of the juveniles in isolated and group environments was observed each day, and growth and survival rates were recorded. Care was taken in each case to make the crowded and group environments as similar as possible in regard to sun exposure, substrate temperature, food availability per lizard, cage accessories, substrate type, and natural plant growth within the enclosures. Thus, the major difference between the environments of lizards during experiment was social density. Two experiments were conducted: one early in the hatching season with early clutch hatchlings (July 24 to August 18, 1972), and the other later in the season with late clutch hatchlings (August 8 to October 10, 1970; and August 31 to October 19, 1971). The design and schedules of the experiments are given in Table 2.

Lizards were fed "standard net sweeps" of insects according to the schedule in Table 2. A "standard net sweep" was obtained by driving a car through a grassy field at 20 m.p.h. with the insect net out of the window and dragged in the grass for approximately 1 minute. Large insects and spiders which could potentially harm lizards were removed. Catches from net sweeps were introduced just after behavioral observation periods.

The "standard net sweep" feeding schedule seemed to provide sufficient food. Although the number of palatable insects available to each lizard was not assessed quantitatively for a "standard net sweep," small insects such as small black ants and lepidopteran larvae (known from stomach analysis to be eaten by this species in the field in Kansas, Table 6) were often eaten during the observation periods just prior to an introduction of net sweep catches.

RESULTS AND DISCUSSION

Aggression in the Field

During the 26 observation periods, 12 natural encounters were observed (Table 3). Eleven encounters were between two juveniles of different sizes, while one involved an encounter between a juvenile and an adult. All encounters resulted in an aggressive interaction of varying intensity, and in all interactions the larger lizard was clearly dominant, i.e., caused the other lizard to

Table 2. Distribution of hatchling spiny lizards in three crowding tolerance experiments conducted in enclosures near Manhattan, Kansas.

Enclosure	# of Minutes Behavior Observed	# of Hatchlings Per Tub (# males/ # females)	Feeding Schedule SNS*	Date Lizards Introduced	Date Experiment Terminated
Experiment 1—late clutch hatchlings:					
A	315	7 (4/3)	7 SNS 1–3 times/week	9/1/71	10/19/71
B	90	7 (2/5)	"	8/17, 18/70	10/10/70
C	105	6 (2/4)	"	8/13–15, 17/70	10/10/70
D	45	9 (4/5)	"	8/15, 17, 29–70	10/10/70
E	135	7 (2/5)	"	8/8, 9, 14, 17/70	10/10/70
F	240	1 (1/0)	1 SNS 1–3 times/week	8/31/71	10/19/71
G	60	1 (0/1)	"	9/ 1/71	10/10/71
H	75	1 (1/0)	"	8/13/70	10/10/70
I	75	1 (1/0)	"	8/ 9/70	10/10/70
J	90	1 (1/0)	"	8/11/70	10/10/70
K	90	1 (1/0)	"	8/13/70	10/10/70
L	90	1 (1/0)	"	8/14/70	10/10/70
Experiment 2—early clutch hatchlings:					
A	0	10 (2/8)	10 SNS 2 times/week	7/29; 8/1–2/72	9/ 7/72
B	0	7 (3/4)	7 SNS 2 times/week	7/29–8/2/72	"
C	0	5 (2/3)	5 SNS 2 times/week	7/29–30/72	"
D	0	5 (1/4)	5 SNS 2 times/week	7/30–8/2/72	"
E	0	1 (1/0)	1 SNS 2 times/week	7/24/72	"
F	0	1 (0/1)	"	7/29/72	"
G	0	1 (0/1)	"	7/29/72	"
H	0	1 (1/0)	"	7/29/72	"
I	0	1 (0/1)	"	7/29/72	"
J	0	1 (0/1)	"	7/29/72	"
K	0	1 (0/1)	"	7/30/72	"
L	0	1 (0/1)	"	7/24/72	"
M	0	1 (0/1)	"	7/29/72	"

* SNS—Standard Net Sweeps (see text).

flee, hide, or assume a submissive posture (Carpenter, 1967).

There seemed to be a correlation between the intensity of the interaction and the similarity of size of the interacting lizards (Table 3). Thus, the most vigorous interaction which included several chases and several attacks was between the two combatant lizards most similar in size. The four most vigorous interactions, which included at least two chases and resulted in the subordinate being chased from the view of the

Table 3. Summary of social interactions of juvenile spiny lizards on Pottowattomee Co., Kansas, study area.

Number of hours observed	5.8
Dates observed	8/10–9/15/1972
Number of interactions	12
Percent of interactions aggressive	100
Percent of interactions in which the larger lizard dominated	100
Mean snout to vent length of combatants (range)	34.5 mm (26–55)
Mean percent size difference of combatants (range)	22.8 (7–40)
Mean percent size differences of combatants in most vigorous encounters	14.7
Mean percent size difference of combatants in least vigorous encounters	26.8
Probability that difference between mean percent size differences of combatants in more and less aggressive encounters is due to chance (Mann Whitney U-test)	0.055

dominant, were between lizards significantly more similar in size than those involved in the eight less vigorous encounters (p=.055). The less vigorous encounters involved only a single chase by the dominant and did not result in the subordinate's being chased from the view of the dominant.

Another observation of interest was that, while a number of juvenile lizards of all sizes were present in the sector where observations were conducted, the mean size difference between interacting lizards was 23 percent (Table 3). Thus, the stronger aggression between size peers seemed to cause the size peers to disperse and reduce their probability of encounter. Interactions between juveniles of different sizes had less of a dispersal effect. Rand (1967) demonstrated similar size peer territories in juvenile *Anolis lineotopus* lizards, in Jamaica.

Effect of Density on Dispersal

The effect of density and presumably higher rates of aggressive interaction on dispersal was assessed by comparing the density change on "more crowded" sectors with those "less crowded" (Table 4). The criterion for a more or less crowded sector was arbitrary, and it differed in 1971 and 1972. We reasoned that, if aggression between lizards was causing dispersal, more crowded sectors with higher rates of aggressive interaction should show more dispersal (or a greater lowering of density) than less crowded sectors, which might increase in density due to immigration. In both 1971 and 1972, early in the hatching season, the difference between crowded and noncrowded sectors in density change was in the predicted direction but was not significant. Later in the hatching season the difference was highly significant and in the predicted direction, suggesting that dispersion was greater later in the hatching season than it was earlier.

Effect of Density on Survival

The effect of density and presumably higher rates of aggressive interaction on survival was assessed by comparing the survival of lizards beginning on more crowded sectors with that of lizards beginning on less crowded sectors (Table 5). As in density change, survival was affected more by high initial density that occurred later in the hatching season, but only in 1972 was there a significant trend.

Comment on Field Study

The seasonal increase in population and its effect on both density change and sur-

Table 4. Ratios of final density to initial density of juvenile spiny lizards on "crowded" versus "noncrowded" sectors of a 4-acre study area in Pottowattomee Co., Kansas. Significant differences between density changes of crowded and noncrowded sectors indicated as follows: **$p<.01$, ***$p<.001$ (Chi squared test).

	# of Lizards at Beginning of Interval "t_0"		# of Lizards at End of Interval "t_1"	$\#t_1/\#t_0$
1971 A. Late July to Late August Interval:				
# of crowded sectors (>12 lizards/6400 ft.^{2})				
9	152		147	0.97
# of non-crowded sectors (<12 lizards/6400 ft.^{2})				
15	77		92	1.19
1971 B. Late August to Late September Interval:				
# of crowded sectors (>12 lizards/6400 ft.^{2})				
7	140		88	0.63
# of noncrowded sectors (<12 lizards–6400 ft.^{2})		**		
17	105		187	1.78
1972 A. Late July to Late August Interval:				
# of crowded sectors (>3 lizards/6400 ft.^{2})				
8	39		33	.85
# of noncrowded sectors (<3 lizards/6400 ft.^{2})				
12	24		24	1.00
1972 B. Late August to Late September Interval:				
# of Crowded Sectors (>3 lizards/6400 ft.^{2})				
7	41		29	.71
# of crowded sectors (<3 lizards/6400 ft.^{2})		***		
11	20		61	3.05

vival can be attributed to an increase in competition for limited resources. However, because we feel that the most important source of mortality was predation (Ferguson and Bohlen, 1972) and some predators are known to influence their prey species in a density dependent fashion (Tinbergen, 1960), we cannot rule out the possibility that the above effects are due to a shift in the importance of different predator species. Thus, high predation by toads early in the season would not show a density-dependent effect. Toads are largely nocturnal predators, but in August they concentrated around the shadier parts of the study area in the daytime in numbers that seemed sufficient to affect the lizard population density. On several occasions a toad readily devoured a tethered lizard offered to it on the end of string. Later in the season, a possible increase in the abundance of birds preparing for fall migration could increase the density-dependent effect that birds are known to exert on their prey.

Table 5. Survivorship of juvenile spiny lizards on "crowded" versus "noncrowded" sectors of a 4-acre study area in Pottowattomee Co., Kansas. Significant differences between survivorships on crowded and noncrowded sectors are indicated as follows: *$p<.05$ (Chi squared test).

		# of Lizards at Beginning of Interval Not Surviving to End of Interval	# of Lizards at Beginning of Interval Surviving to End of Interval	Proportion Surviving to End of Interval
1971 A. Late July to Late August Interval:				
# of crowded sectors (>12 lizards/6400 ft.^{2})	5	45	59	.57
# of noncrowded sectors (<12 lizards/6400 ft.^{2})	14	43	72	.63
1971 B. Late August to Late September Interval:				
# of crowded sectors (>13 lizards/6400 ft.^{2})	6	40	87	.69
# of noncrowded sectors (<13 lizards/6400 ft.^{2})	14	35	74	.68
1972 A. Late July to Late August Interval:				
# of crowded sectors (>4 lizards/6400 ft.^{2})	8	18	21	.54
# of noncrowded sectors (<4 lizards/6400 ft.^{2})	12	14	10	.42
1972 B. Late August to Late September Interval:				
# of crowded sectors (>3 lizards/6400 ft.^{2})	8	23	14	.38
# of noncrowded sectors (<3 lizards/6400 ft.^{2})	12	6 *	13	.68

However, additional circumstantial evidence suggested that there was a possible seasonal increase in resource competition. Food availability per lizard clearly was decreasing during the hatching season (Table 6). Thus, while lizard numbers increased from 60 to 90 from early August to October, 1972, the density in the habitat of those insect species also found in the intestinal tract of lizards decreased during September to 44 percent of the level of early August. While this does not prove that resource competition was increasing, such a change in availability would certainly accompany an increase in competition. While predation is probably an important source of mortality, we suspect that an interaction between predation and competition similar to that suggested by the data of Fox (1973) on *Uta stansburiana* may be causing the observed pattern of mortality and density change.

Table 6. Estimated density of those insects most important in the diets of juvenile spiny lizards on the study area in Pottawattomee Co,. Kansas.

Insect Order	Percent of Volume of Lizard Gut Contents	Insect Density (mm^3 of insect/ cm^2 of trap/hour	Period 2 Insect Density/Period 1 Insect Density
A. Period 1—4 July to 11 August, 1972:			
Hymenoptera (ants)	40.8	0.0014	
Hymenoptera (others)	11.1	0.0089	
Homoptera	14.3	0.0002	
Orthoptera	11.1	0.0223	
TOTALS	77.3	0.0328	0.436
B. Period 2—11 August to 4 October, 1972:			
Lepidoptera (adults)	29.7	0.0084	
Lepidoptera (larvae)	22.2	0.0030	
Arachnida	19.7	0.0017	
Hymenoptera (ants)	12.4	0.0012	
TOTALS	84.0	0.0143	

Hatchling Size and Fitness

If seasonal increase in competition did cause greater density dependent mortality, was the mortality biased toward individuals of a smaller size? More importantly, did this bias result in a lower fitness? Of those lizards hatching early in the season, the larger hatchlings did not survive to the next breeding season at a rate significantly higher than that of the smaller hatchlings (Table 7). However, of those lizards hatching later in the season, when competition presumably was greater, the larger hatchlings survived at twice the rate of the smaller hatchlings. Aggressive dominance by larger hatchlings seemed to be resulting in a higher fitness later in the season when resource competition was likely to be more severe.

Table 7. Survivorship of small and large hatchling spiny lizards on the study area in Pottawattomee Co., Kansas. Significance value designations same as in Table 4 and 5.

Survivorship of Late July Hatchlings until the Following Spring Breeding Season:

hatchling length (snout to vent in mm)	20–23	24–26
# survivors	12	5
# nonsurvivors	39	12
proportion surviving	0.24	0.29

Survivorship of Late August Hatchlings until the Followng Spring Breeding Season:

hatchling length (snout to vent in mm)	22–24	25–26
# survivors	13	15
		*
# nonsurvivors	48	20
proportion surviving	0.21	0.43

Clutch Size, Egg Size, and Hatchling Size

Has this seasonal increase in fitness of larger hatchlings occurred with sufficient predictability to result in the evolution of any adaptive mechanisms in the adult, egg-producing females? W. Kenneth Derickson, as part of his comparison of lipid cycling in two species of *Sceloporus* (1976) demonstrated that females of a given body length (55 mm) contain roughly the same amount of energy in an early and a late clutch of eggs (Table 8). However, females sampled late in the egg-laying season produced significantly fewer but larger eggs than females sampled early in the egg-laying season. The larger eggs resulted in significantly larger hatchlings. Thus, there seems to be an adaptive shift in energy allocation as the egg-laying season progresses. Early in the season, females divided their energy into more but smaller packages which produce more but smaller offspring early in the hatching season when hatchling size does not correlate with fitness significantly. Later in the season, females divide their energy into fewer but larger packages which produce larger offspring later in the hatching season when larger hatching size does correlate with a fitness advantage.

Table 8. Reproductive energetics of adult female and juvenile spiny lizards. Data are adapted from those of Derickson (1976). The first three parameters were taken from regression line equations of the parameters versus snout-vent length and are for females 55 mm in length. Significance value designations same as in previous tables and are those given by Derickson for the probability of differences due to chance of the regression lines.

	Early Clutches		Late Clutches
Calories/ clutch	4335		4707
Clutch size	6.5 eggs	*	5.5 eggs
Calories/egg	667	**	854
Mean hatchling size (mm)	22.8	**	24.1

Aggressiveness

If dominance is responsible for a higher fitness, all predictors of dominance, such as size, should be correlated with fitness. Aggressiveness is also a predictor of dominance (Guhl, 1956). Although the quantitative assessment of degree of aggressiveness has proven elusive, ethologists generally agree that the tendency to behave aggressively toward a conspecific varies. Eisenberg (1967) and Philibosian (1975) have employed crowding intolerance as a comparative measure of aggressiveness of different species of rodents and *Anolis* lizards, respectively. In spiny lizards the difference in survivorship between crowded and isolated hatchling lizards was not significant at the .05 level in the experiment using early hatchlings; but the grouped lizards survived significantly less in the experiment using later hatchlings (Table 9). Also, the survival of grouped early hatchlings was significantly greater than that of grouped late hatchlings.

In summary, a decreasingly plentiful food supply for later emerging hatchlings has resulted in the evolution of a variable energy allocation mechanism in females. This mechanism results in fewer but larger, more aggressive hatchlings late in the season when the competitive environment of juveniles is more severe.

VISIBILITY, PREDATOR DETECTION, CONSPECIFIC COMMUNICATION, AND GEOGRAPHIC VARIATION OF SIGNATURE DISPLAYS

Introduction

The signature display (Stamps and Barlow, 1973) was originally described by Carpenter and Grubitz (1961). It is a stereotyped species- or population-typical display performed by iguanid and agamid lizards of many species. The most common features of the display include pushup, nodding, and or dewlap extension movements. While seen

Table 9. Survivorship of hatchlings maintained in outdoor enclosures at different densities (see Table 2 for experimental treatments). + = p <.1. Other significance value designations as in Tables 4 and 5 (Chi square or Fisher exact probability tests).

	# Surviving First 3 Weeks of Experiment		# Not Surviving	Proportion Surviving
A. Isolated Hatchlings				
early hatchlings (experiment 2)	6		3	.67
late hatchlings (experiment 1)	6		1	.86
B. Grouped Hatchlings				
early hatchlings (experiment 2)	25	***	2	.93
late hatchlings (experiment 1)	15		21	.42
C. Early Hatchlings (experiment 2)				
isolated hatchlings	6	+	3	.67
grouped hatchlings	25		2	.93
D. Late Hatchlings (experiment 1)				
isolated hatchlings	6	*	1	.86
grouped hatchlings	15		21	.42

in both social and nonsocial contexts, the displays are considered by most observers to be primarily involved in adaptive conspecific communication. Experimental evidence of their communicative functions is available (Hunsaker, 1962; Jenssen, 1970).

The signature display of the side-blotched lizard *Uta stansburiana* is geographically variable (Ferguson, 1971). One possible explanation for this variability might be character displacement (Ferguson, 1971; Brown and Wilson, 1956). Thus, in each "zone of pushup similarity" (Table 10) side-blotched lizards were sympatric with different species of iguanid lizards. In each zone a different direction of evolutionary change might have resulted to render side-blotched lizards (1) distinct from those species most likely to be encountered, and (2) less likely to be involved in nonadaptive hybridization.

Another possible explanation for geographic variation of the signature display was the effect of plant density on the visibility of *Uta* to predators and to each other (Aubert, 1966; Ferguson, 1971). Thus, in the deserts in which the lizards occupied sparsely vegetated habitats (e.g., Lahonton Basin and Mohave Desert), the display included only one or two brief pushup units. In those regions in which the lizards were more closely associated with heavier vegetation (e.g., Chihuahuan—desert grassland, Chaparral), the display included four or more pushup units (Table 11). This suggested an alternative model relating the evolution of display complexity to predator avoidance and communication efficiency.

The Model

Two consequences of a lizard display are conspecific communication and predator detection. In the sparsely vegetated habitat, where visibility is good, a simple display will be as likely to catch the attention of a nearby resident conspecific as a more complex display. However, the simple display will be more likely to escape the notice of a searching predator than a complex display for the

Table 10
Overlap of iguanid fauna:
A. Iguanid lizard species sympatric with *Uta* in each of seven zones of push-up similarity. Plus in a column indicates presence of a given species in that geographic zone.

Small iguanid species sympatric with *Uta*	Geographic zones of push-up similarity in *Uta* 1	2	3	4	5	6	7
Urosaurus graciosus	+		+				
Urosaurus ornatus	+						
Urosaurus microscutatus				+			
Sceloporus magister	+	+	+	+			
Sceloporus undulatus	+						
Sceloporus graciosus	+	+	+				
Sceloporus occidentalis		+	+	+			
Sceloporus clarki	+						
Sceloporus orcutti				+			+
Sceloporus linestulus						+	
Callisaurus dracionoides	+	+	+				
Holbrookia maculata	+						
Holbrookia texana	+						
Uma	+		+				
Streptosaurus mearnsi				+			

B. Percent overlap of iguanid fauna between zones. $P = 100[c/(a+b)]$, where P = percent overlap, a = number of species inhabiting zone a, b = number of species inhabiting zone b, c = number of species inhabiting both zones a and b.

Zones

1	2	3	4	5	6	7	*Zones*
	27	45	7	0	0	0	1
		67	43	0	0	0	2
			22	0	0	0	3
				0	0	0	4
					0	0	5
						0	6

following reasons: If the predator is a bird, it will be searching a larger area than that of the conspecific lizard and will probably be farther away from the displaying lizard than the conspecific lizard. If the predator is a snake, it will also be searching a larger area, but at the same ground level, being alert for lizards, other snakes, and small mammals as potential food items.

In a more heavily vegetated habitat, both simple and complex displays would be less likely to be detected by the wandering type of predators described above. Lizards performing simple displays with a background of moving grass or foliage might be harder for conspecifics to detect than lizards performing more complex displays that are distinct from random movements of vegetation. In sum-

Table 11. Signature display complexity (number of units) and subjectively assessed vegetation density in several populations of the side-blotched lizard *Uta stansburiana*.

Locality	# of Units in the Display	Vegetation Density
Lahonton Basin, Nevada	1	low
Mojave Desert, California	2	low
Bonneville Basin, Utah	2	low-medium
Colorado River Basin, Colorado	4	medium
Chihuahuan Desert-grassland	4	medium-high
Chaparral, California coast	7	high

mary, in the sparsely vegetated habitat, the balance of selection would favor a simple display that would avoid detection by searching predators. In more heavily vegetated habitats, the balance of selection would favor a more complex display to facilitate adaptive conspecific communication. A similar model was proposed by Rand and Williams (1970) to explain complexity of *Anolis* lizard displays.

A Potential Test of the Model through Observation and Mark and Recapture Analysis

With each generation, genetic recombination should reconstitute less adapted genotypes so that the variance of a character with a high heritability should be greater in offspring than in adults. Signature displays have a high heritability (Ferguson, in press). They are performed by lizards of all ages. Thus, one can observe changes in population variance of display characters throughout the life history. Because the mortality of side-blotched lizards is probably due to predation (Tinkle, 1967; Fox, 1973; Turner et. al., 1973), a greater loss of particular display types during ontogeny would be due to predation. Since an identified lizard's home range and overlap of territory is easy to measure in the field, the exclusiveness of a male's mating rights to one or more females can be determined.

If the above model is correct, one would predict: (1) In the sparsely vegetated habitat, juvenile lizards with simple displays would disappear during their maturation period at a lower rate than lizards with complex displays. In the more heavily vegetated habitat, the difference in the rate of disappearance would be less; (2) In the heavily vegetated habitat, males with simple displays would be less likely to prevent invasion of their mating territories and/or would fail to attract as many females into their territories as males with complex displays.

An ideal location to perform such a study would be in the intergrade zone between simple and complex displaying populations of *Uta* (McKinney, 1971). In such zones combining sparsely and densely vegetated habitats, one finds large populations of side-blotched lizards with a wide variety of signature displays.

Conclusion

The types of studies that have been dealt with in this paper are illustrative of how it may be possible in the future to show how environment variability may affect individual fitness and natural selection.

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Display and Dispute Settlement in Nesting Iguanas

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SUMMARY. In this paper we describe a study that resulted from combined research interests in (1) the ecology and behavior of a specific lizard, *Iguana iguana;* (2) the overall pattern and outcome of disputes between animals, and (3) the general stochastic modeling of behavior situations.

We describe the nesting behavior of female iguanas in Panama to illustrate the disputes that occur over nest burrows in a communal nesting site (Rand, 1968); then we discuss the process involved in settling these disputes, including the role of display and the importance of energy factors.

INTRODUCTION

In our approach it is assumed that a dispute occurs when two animals meeting in a conflict situation "disagree" about its outcome. In most social situations one sees little serious disputing; one animal is recognized as dominant and is deferred to rather than challenged. Animals fight only when they differ about which is going to dominate. Thus each conflict situation essentially involves the value of what is sought after; the cost of contesting for it, and the probability of winning. We attempt to apply these ideas, derived from Game and Decision Theory, to the behavior of nesting iguanas.

When one tries to fit any kind of model to the real world, the first problem is that of identifying the various factors—in this case those factors which should affect the animal's behavior. The probability of winning can be evaluated by going into the field and counting frequencies of wins and losses in different situations. This is a standard approach, and we think it is a reasonably valid one. Evaluating the worth of the prize and the cost of winning is more difficult. We argue that, in the "iguana" situation, we can reasonably evaluate both in terms of energy: the energy available to and the energy expended by an individual iguana.

In terms of evolutionary time we subscribe to the view that costs and benefits are to be evaluated on the basis of fitness; it is on fitness that selection acts. But fitness in animals as long lived as iguanas is not easy to measure during the time available to a biologist. The "decisions" an animal must make in specific situations affect its fitness; selection, it may be supposed, acts to maximize fitness and determines the animal's strategies. A species which is well adapted will "make decisions" that, on the average, optimize its fitness. The assumption of adaptation is essential since it allows one to say that what one observes is the animal maximizing its fitness.

In the situation of iguanas it appears that energy considerations are among the most important factors and that these are used in their "decisions." An approach using energy to evaluate evolutionary strategies is familiar to ecologists in the form of energy budgets (Gates, 1965, and others) and in feeding strategy models (Schoener, 1971, and others). We have encountered no approaches quite comparable to ours in behavioral analyses.

We choose energy over two other important variables of any situation, time and risk, primarily because how energy is used explains much of the observed situation. Intuitively we feel that, for any animal that spends much of its time motionless as an iguana does, time is less important than risk. For practical and heuristic reasons we have concentrated on energy and invoke risk only when energy factors do not seem adequate to explain what we see.

One of the virtues about using "energy" in building a model is that it can be measured. Although the techniques developed by Bennett and Dawson, 1972, and Bennett and Licht, 1973, for measuring metabolism in active iguanas could, with some modification, have been applied in our studies, we did not use them. Instead, we ranked or ordered the various acts, particularly the displays, in terms of energy costs. This was done (Tables 1 and 2) by watching the animals, classifying the acts, and applying some simple rules. Acts that were performed more vigorously than others were considered to take more energy. In assessing similar acts, the one which took longer or moved the animal further was considered to take more energy, and a combination of two acts was considered to take more energy than either act alone.

COMMUNAL NESTING OF IGUANAS

Iguanas are large, herbivorous, arboreal lizards that are widespread in the neotropics. Usually iguanas nest singly, but occasionally (presumably when a site is particularly favorable) they may nest communally. Slothia, a tiny islet off Barro Colorado Island (the Smithsonian Tropical Research Institute preserve in the Panama Canal), is such a communal nest site (Rand, 1968). Here most nesting occurs in a 5 × 10 meter clearing next to which we built a blind. From here the action was watched and photographed.

During the nesting season, one commonly saw 10 to 12 iguanas in the clearing, and as many as 30 may be in sight at one time. We estimated that perhaps 150 to 200 females nest on Slothia every year during the dry season. No iguanas live on Slothia permanently. Females come here only to nest, but we do not know from how far. We radiotracked one female which traveled about three miles after finishing her nesting (Montgomery et al., 1973).

A newly arrived female must explore the island. On the ground and particularly in the open, she is very nervous at first and does much bobbing and tonguing. Females

Table 1. Initial Approach by "Intruder," Number of Times Observed (Expected), % Effective

	Slow approach Low energy investment			Quick approach High energy investment			X^2(df)
Hole depth							3.66
Shallow	121	(113)		23	(31)		
Deep	263	(271)		82	(74)		
Resident's position							23.30
Out of hole	200	(221)	23.5%	81	(60)	59.3%	
Head in	75	(66)	12.0%	9	(18)	22.2%	
Body in/head out	39	(38)	2.6%	9	(10)	0	
All in	70	(60)	0	6	(16)	0	
Resident's occupation							12.59
Waiting	149	(163)	23.5%	65	(51)	50.8%	
Digging	110	(96)	8.2%	17	(31)	31.3%	

frequently follow one another. They spend much time resting and sunning.

The females maintain short individual distances and show only occasional aggression. In selection of a site for the nest, a depression is desirable and a partially completed burrow even better. The female digs by scratching the dirt out with several strokes of a front foot and then kicking it back with the hind foot on the same side. She alternates digging with the left and right legs. Digging is a precarious occupation, particularly in the early stages; since the female must put her head down into the hole, she cannot watch for an approaching predator, whereas her body, outside, is fully exposed to any attack. Once the hole is deep enough, she turns around inside and emerges head first, pushing dirt before her.

The iguanas, by their digging, help maintain the clearing from year to year. The soil, because it has been burrowed into repeatedly, is relatively free of roots and surface vegetation. Even so, digging the nest burrow is probably the hardest work that an iguana ever does. It usually takes several days to complete a nest. A female rests many times between her bouts of digging. Presumably she builds up an oxygen debt as she digs and defends herself and then pays it back as she rests. The level of oxygen debt she will tolerate determines how long she can work and, as we shall see later, how vigorously she defends her burrow. When she is ready to resume digging, she may find the burrow occupied by another iguana actively digging and defending it. She must then either displace this new resident or build a nest elsewhere. Sometimes an impatient female attempts to force her way into an occupied burrow, but she is seldom successful. She may have difficulty in getting out again when the resident bites and holds on.

Although iguana bites are obviously unpleasant, it is unlikely that they produce the serious kinds of injury inflicted by predators. One female observed in 2 successive years was missing her left front leg; her injury was probably from a predator. Iguanas, particularly young ones, are sought after by many kinds of predators. One of the most conspicuous is the crocodile, which also nests on Slothia and is frequently around during the nesting season. One observer saw a crocodile catch and eat an adult iguana in the water just off Slothia. Predation on adult iguanas, however, is relatively low, and many females survive for more than one breeding season.

Once the female has completed her burrow, she lays her eggs in a chamber at the end. Iguanas lay large clutches; the precise number of eggs varies with the size of the female. In our study, the number ranged from two dozen eggs for a 31 cm female to five dozen for a 44 cm female Iguanas lay one clutch a year. Hatchlings mature in two or, perhaps more commonly, in 3 years.

In the course of digging her own nest, an iguana may encounter one made earlier, and, when she does, she kicks out the eggs as if they were pebbles. Eggs on the surface are quickly eaten by vultures. The digging-up of earlier nests seems to be a major way in which nesting iguanas on Slothia interfere with one another. After the eggs have been laid, the female emerges from the nest and fills the burrow. She pushes and kicks dirt into the nest with her feet and tamps it down with her snout. Because of the large excavation, she must scratch dirt toward the nest from a considerable distance.

After passage of the eggs, the shrunken sides of the spent female are conspicuous. There are also hollows at the tail base and the temples. Iguanas do not feed during nesting. When they reach the nest site, there is little, if any, food in the gut and very small fat deposits. During the laying operation an iguana expends a considerable fraction of the energy available to her. This is one of the energy constraints on a nesting female and one of the reasons why we conclude that energy limitations are important. The energy content of the eggs themselves is only a part of the cost of reproduction.

The limb movements used in filling a burrow look identical to those used in digging. Only the reverse orientation of the body is different. Once the hole has been filled, the female works out from it, surface filling. She scratches at the surface, shifts debris, and fills any other holes or depressions in the area.

For a solitary female, the surface filling conceals the precise location of her nest from any predator in the general area. In the dense aggregation on Slothia, such surface filling causes complications. When females interfere with one another, one occasionally sees quite unusual displays such as tail lashing. (This is much more common in an antipredator situation in which it can be quite effective. The "filling" female usually seems to win out, without, however, preventing the other one from completing her digging.

At the height of the season, the clearing on Slothia is full of iguanas. They gather to nest, presumably because the advantages of doing so outweigh the disadvantages (Sexton, 1975). We have identified some of the advantages: easier digging, sunlight for spotting predators, and, perhaps most important, the location on a small island and fewer egg predators (Rand and Robinson, 1969). The costs of nesting on Slothia include: a greater distance to travel, the need to defend the burrow against other iguanas, the conspicuousness of the site to predators, and, perhaps most significantly, the loss of eggs dug up by other iguanas.

IGUANA DISPUTES AND THEIR ENERGETICS

We have outlined the nesting behavior of female iguanas on Slothia and the advantages and disadvantages of nesting in this reptile rookery. We describe next the kinds of disputes that occur between females and the displays involved. We feel that the key to understanding this situation is the iguanas' "concern" with conserving energy. The importance that we place on energy is consistent with what is known about lizard energetics from the work of Bartholomew and Tucker (1964), Moberly (1968*a*, *b*), Bennett and Dawson (1972), and Bennett and Licht (1973). As mentioned during the film, energy available to a fasting iguana is limited at two levels. First, the energy available to a female for the whole nesting season is the energy that she has stored in her body at the beginning of the season and must use to move to the breeding site, dig and defend a burrow, lay eggs, fill the hole, move back to a feeding area, and still retain a reserve to escape the attack of a predator. Energy is limited because of: (1) the small fat reserves of the females examined on their way to the nest site; (2) the inability of the iguanas to replenish energy by feeding during the nesting; and (3) the emaciation of the female after nesting. It is this energy limitation that puts a premium on a female's gaining a partially completed burrow and defending it once she has it. Energy is also limited at a second level by the amount available during a single bout of activity. Lizards (except monitors) do not sustain activity by aerobic metabolism. Instead they build up an oxygen debt during activity

Table 2 Energy and Effectiveness of Displays

Displays in order of increasing energy	Times observed	% times displayer wins immediately	% times displayer wins dispute, immediately or eventually
Mouth open	24	29.2	62.5
Head swing	59	57.6	78.0
Huff	146	62.3	93.8
Head swing/huff	57	63.2	96.5
Lunge	79	79.7	91.1
Lunge/huff	30	93.3	100.0
Bite	35	17.1	100.0

bouts that they discharge during rest periods (Bennett and Dawson, 1972; Bennett and Licht, 1973). High levels of lactate can be tolerated, but an oxygen debt must eventually be paid for either aerobically during a rest period or possibly anaerobically at a much higher energy cost. It is this energy restraint that we suggest forces a female to periodically interrupt her digging and rest.

An additional point about energy must be made. Ectotherms such as lizards have a very low resting or basal metabolism. Any act, even one using a small absolute amount of energy, involves a much larger relative increase in energy expenditure for a reptile than it does for an endothermic bird or mammal with its much higher basal metabolism. For an endotherm, at least some of the energetic cost of activity can be charged against the metabolic activity required to maintain body temperature. We believe that a display that might be a trivial energetic cost to a mammal or bird would be significant to a reptile operating on a much lower energy budget.

These considerations suggest to us that the iguanas are "making their decisions" to dispute on the basis of three aspects of the situation: The value of the nest hole in terms of energy invested in its digging, the probability of winning or retaining it, and the cost of the dispute in terms of energy expended. From our rankings of displays in order of energy cost, we are at the very least able to evaluate the cost of a dispute point by noting which acts are more or less expensive in terms of energy; from the depth of the nest burrowed we are able to gauge the worth of the prize; and from examination of some 580 encounters, we are able to estimate the probabilities of winning and losing associated with different situations and courses of action. (For an extensive presentation of these data, see Rand and Rand, 1976.) We will present several aspects of these analyses to illustrate how energy considerations help to explain the observed situation.

First, we would predict that a female looking for a place to dig would invest more energy in winning a deep hole than in winning a shallow one. Also she is likely to invest more energy in disputing for a hole that she will probably win (i.e., one to which the resident seems less than fully committed). On the basis of the data given in Table 1, it is evident that both the position of the resident at the hole and what the resident is doing influence the outcome. This table also shows correlations between the types of approach used with respect to both the resident's position and nature of activity at the hole. An iguana is more likely to make the high energy approach under conditions indicating that a resident is likely to be displaced. The correlation between approach and depth of hole, though in the predicted direction, is not nearly as strong as expected. A possible explanation is that the approaching iguana frequently cannot tell from outside how deep the hole actually is.

Let us consider next the resident's response to an intruder. We contend that whether a resident leaves the hole, relinquishes it, or defends it, depends on the energy immediately available to her. If she has very little energy (i.e., already has a fairly high oxygen debt) or at least not enough energy both to defend and dig further, she leaves. If sufficient energy is available for both activities, she stays, defends, and continues to dig. Sometimes she miscalculates, defends and wins, and then leaves presumably because not enough energy remains to dig further.

Even if she had not been challenged, she eventually would have had to interrupt her digging to depart and rest awhile. In one sense we are saying that a resident's response to a challenge depends on how close she is to the required moment to rest.

As we have described, when a resident is approached she may respond with one of the displays listed in Table 2. Displays differ both in the amount of energy expended in their execution and in their effectiveness in driving off the intruder. The correlation between these two aspects of the display is very high. The more energy an iguana puts into a

Table 3. Escalation of Displays
Successive Displays by an Iguana Irrespective of the
Intervening Act of Her Opponent

	Second Display						
First Display	Mouth open	Head swing	Huff	Head swing/ huff	Lunge	Lunge/ huff	Bite
Mouth open	1			1	1		
Head swing		2	1		4		
Huff		1	9	2	9	3	2
Head swing/huff		3		2	2		1
Lunge			1		2		3
Lunge/huff							2
Bite			1				1

display, the more likely it is to be effective. Only in the ultimate display involving the bite does the one lizard touch the other.

Why, then, does an iguana use any display other than the most effective one? We suggest that part of the explanation revolves around the energetic cost of giving the display; and the energy expended in a display is a "statement" by the displaying lizard of how much energy she is willing to invest in defense of the hole. This inference is supported by the agreement found when one compares the ranking of displays by energetic cost and the ranking by the eventual outcome of the dispute. Iguanas that used a low intensity display lost the encounter more frequently than did those that used high energy displays.

If the energy cost of displays is important, one might expect that the tactic of using a low energy display whenever it was likely to succeed would be part of the strategy and that occasionally an iguana might be expected to use a low energy display even when fully capable of expending more energy. We find that this appears to be the case when we compare the sequences of displays given by the same individual in a single dispute shown in Table 3. The data indicate that, during a dispute, energy expended in displays tends to escalate; if a low energy display does not work, the lizard often next tries one that is more emphatic.

In conclusion, we have tried to summarize here a very complex situation in which we have attempted to show that nesting female iguanas in dispute situations behave as if they were evaluating probabilities and energy costs and that such considerations "decide" their actions.

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Ritualistic Social Behaviors in Lizards

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SUMMARY. The social behavior of lizards falls into three main categories: (1) agonistic, (2) courtship and mating, and (3) parental care. Agonistic behaviors relate to aggression and submission, territoriality, hierarchies, display, threat, fighting, and vocalizations. Courtship and mating behaviors include action sequences (both sexes) leading to copulation.

A significant feature of lizard social interactions is their ritualistic nature. Ritualistic behaviors appear to be more highly developed in those lizard families which exhibit social systems based on territoriality (Iguanidae, Agamidae, Chameleontidae, Gekkonidae). In less "territorial" lizards (Lacertidae, Teiidae, Scincidae, Varanidae, and Xantusiidae) there appears to be correspondingly less ritual. Little is known of the social interactions in other lizard families.

DISPLAY BEHAVIOR

Display behaviors may involve a variety of different types of movements (often time-specific), postural changes, color changes, and pattern accentuations, or the morphological elaboration of special structures. The interplay between male and female during courtship may relate to specific signals based on movements, postures, and other actions that are often different from agonistic behaviors only in their social context.

Representative examples of the above, primarily from iguanid and agamid lizards, exhibit the diversity of such actions and indicate the species-characteristic nature (ritualization) of these behaviors. Such behaviors offer bases for investigations of neural substrates of ritualized activity.

For the present discussion, I shall define social behavior as those behaviors performed by an individual lizard which may be elicited by another individual or may have some effect on another individual(s), usually of the same species, but sometimes of another species.

The social behaviors of lizards fall into three main categories— (1) agonistic, (2) courtship and mating, and (3) parental care. The approach to the study of social behavior of lizards, can be either through field or laboratory studies and not only involves observations on the natural attributes of social structures, but also the experimental analysis of social interactions, the physiological bases of social status and actions, and the ritualistic characteristics of the behavior patterns performed.

Parental care is little known in lizards and most of my remarks will deal with agonistic and courtship behavior.

Agonistic behaviors include action involved in aggression, submission, territoriality, and hierarchy formation, and entail displays, threats, fighting, and certain vocalizations. Courtship and mating behaviors include those action sequences by one or both sexes which prepare for or lead to copulation.

The lizard social systems for which adequate information is available range from those characterized by territoriality and/or hierarchies to those with incipient territorial development, to those showing intolerance between individuals that do not defend a particular area.

Those lizard families which have been shown by field and laboratory studies to establish and protect territories (Table 1) are the Iguanidae (Berry, 1974; Carpenter, 1962, 1966, 1967*a*, 1967*b*; Evans, 1951; Fitch, 1940; Hunsaker, 1962; Jenssen, 1970; Milstead, 1970; Noble and Bradley, 1933; Rand,

Table 1. Various social behaviors and associated actions recognized for families of lizards.

FAMILY	TERRITORIAL	THREAT	DISPLAY	SUBMISSION	COURTSHIP	COPULATION HOLD
Iguanidae	Well developed Widespread	Gape, Bite Some posture and color change Accessories*	Exaggerated posturing, dewlap Head butting, Pushups, Head bobs Orientation Some inflation	Flatten	Head nodding Circling Nudging Some ♀ rejection display	Neck or shoulder bite hold
Agamidae	Well developed Widespread	Gape, bite Posturing with color change Accessories*	Exaggerated posturing, some dewlap, some butting Pushups, Head bobs, Circumduction Orientation Tail movements and postures.	Circumduction Flatten Bow	Head nodding Circling Nudging Some ♀ rejection display	Neck or shoulder bite hold
Chameleontidae	Present	Gape, Bite Posture Inflate Color change Accessories*	Some posturing, Head butting Head sway, Body rock Inflate Color change		Head wagging Color change Rocking	Straddle hold
Gekkonidae	Present	Posture Vocalize Gape	Some posturing Vocalizations Tail waving	Flatten	Head nod Vocalize	Neck or shoulder bite hold
Teiidae	Poorly developed	Slight posturing Bite	Slight posturing	Flatten	Cloacal rubbing	Flank or Groin bite hold
Lacertidae	Poorly developed	Slight posturing Bite	Slight posturing Head nodding Orientation		Foot movements	Flank or Groin bite hold
Scincidae	Poorly developed	Slight posturing Bite	Slight posturing Head jerking		Leg stroking	Flank or Neck bite hold
Varanidae	Probable	Slight posturing Inflation Bite	Ritualistic embracing			Neck bite hold
Anguidae		Slight posturing			Foot tap Leg stroke	Head or Neck bite hold
Other families	Unknown or very little known. Pygopodids may mimic snake postures, Helodermatids may show slight posturing with inflation and nudging.					

* Accessories—Erectible skin flaps, ridges, crests as well as permanent skin flaps and rigid protruberances.

1967; Stamps, 1973; Tinkle, 1967); Agamidae (Blanc and Carpenter, 1969; Brattstrom, 1971; Carpenter, Badham and Kimble, 1970; Harris, 1964; John, 1970; Pfeffer, 1962); Chameleontidae (Brain, 1961; Bustard, 1966; Parcher, 1974); and the Gekkonidae (Greer, 1967; Kastle, 1964). Those families with some species showing some degree of territorial behavior are the Teiidae (Carpenter, 1962; Hirth, 1963; Mueller, 1971); Lacertidae (Boag, 1973; Steward, 1965; Weber, 1957); Scincidae (Fitch, 1954; Noble and Bradley, 1933); Varanidae (Pfeffer, 1959); and Xantusiidae (Lowe, 1948).

The families for which little information is available on agonistic interactions or territoriality are the Anguidae, Cordvlidae, Aniellidae, Dibamidae, Gerrhosauridae, Helodermatidae, Lanthanotidae, Pygopodidae, and Xenosauridae. The dearth of information appears to be due to the secretive nature of the species in these families or to the lack of adequate studies.

The territorial male performs some type of display to declare himself present to other males, to challenge and intimidate neighbors, or invading males. It demonstrates agonistic contact behavior such as biting, head butting, tail slapping, and chasing to assert its determination to defend an area, its territory. In some species females may exhibit territorial defense behavior, e.g., *Uta stansburiana,* (Tinkle, 1967). *Uma exsul* defend nesting burrows (Carpenter, 1967*b*), as do *Amblyrhynchus cristatus* (Carpenter, 1966). The intensity of territorial actions may vary with the onset and waning of the breeding season.

Among teiids, lacertids, the skinks, as well as the less known varanids and xantusiids, very few examples of defended areas have been recorded, although there is frequent overlapping of activity ranges.

The relationships of females, juveniles, and hatchlings to the territorial and nonterritorial systems are less understood. Monogamous male-female associations within a territory (Tinkle, 1967), as well as harems of females associated with one male, are recorded for iguanids (Carpenter, 1967). The relationships of mating systems to social structure, as dealt with by Noble and Bradley (1933), Tinkle (1969), Milstead (1970), and Hunsaker and Burrage (1969), need much more study before generalizations can be stated.

RITUALISTIC ASPECTS OF BEHAVIOR

The remainder of my remarks will be directed to the ritualistic nature of lizard behaviors. Each of these behaviors is made up of acts and/or act systems which involve specific motor patterns in their performance. An act is the most basic movement produced by a particular set of muscular actions (e.g., raising the head and lowering the head are separate acts). An act system is a series of acts performed in a particular sequence, either simultaneously and/or in a series (e.g., head bobbing, tail waving, striking, or biting). Some acts may contribute to more than one act systems (See Russel, Mead, and Hayes, 1954, and Dilger, 1960, for further discussion of acts and act systems).

In discussing these behaviors, I arbitrarily separate categories for the sake of examination, but with the knowledge that some of these behaviors appear in a variety of contexts and sequences. My remarks pertain primarily to iguanid and agamid lizards because I am most familiar with them and because their behavior is best known.

Agonistic Behavior

Threat

Perhaps the simplest type of agonistic behavior, as a type of aggression, is threat behavior. Threat generally involves some type of postural change on the part of the performer which in some way increases its apparent size and may present a new pattern or color to an adversary. Some examples of threat which appear quite spectacular are as follows:

Chlamydosaurus kingi (frilled lizard of Australia) is an agamid which, in aggressive encounters, erects a large colorful flap of skin in the neck region. Directing this frill forward toward the adversary, it gapes, rises on its front legs, and sometimes lunging forward, creates a startling effect (Fig. 1). The toad-headed agamid (*Phrynocephalus mystaceus*), a small agamid of Central Asia, erects lateral flaps in the neck region, while gaping toward its adversary. The bearded dragon (*Amphibolurus barbatus*) of Australia erects and laterally expands a ventral beard-like gular flap while gaping (Fig. 2).

An iguanid with fixed ornamentation which enhances its threat posture is *Corythophanes hernandezi* of Central America. While it threatens with mouth agape, there are color changes which result in vivid patterning that enhances its "aggressive appearance." And at the same time it compresses its body, thus increasing its laterally viewed size (Fig. 3). Many other lizards will gape as a threat, but have no ornamentation to enhance this threat. The anguid lizard *Abronia deppei* lowers its head and presents the top of its head adorned with large armor-like scales to its adversary (Fig. 4). The gila

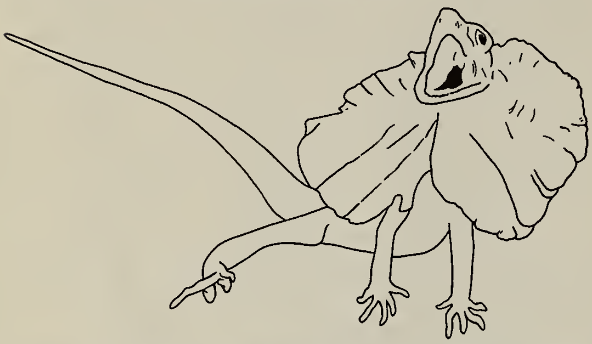

Figure 1. The threat posture of the adult male Frilled Lizard (*Chlamydosaurus kingi*—Agamidae) of Australia. The accessory skin flaps are erected, the mouth is gaped as he rises high on all four legs and orients toward his adversary. He may rise on the hindlegs alone and sway back and forth.

Figure 2. The threat posture of the Bearded Dragon (*Amphibolurus barbatus*—Agamidae) of Australia. The gular area expands forward and laterally as the mouth is gaped and he orients toward his adversary.

Figure 3. The threat posture of the Helmeted Lizard (*Corythophanes hernandezii*—Iguanidae) from Mexico. Besides gaping, a very dark pattern of black appears on the dewlap, head, and shoulder region.

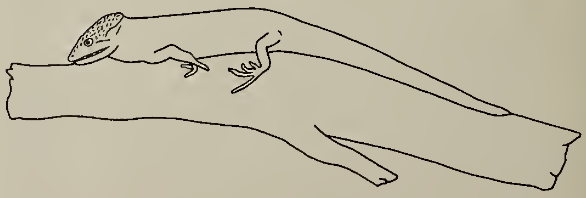

Figure 4. When threatening, *Abronia deppei* (Anguidae) lowers its head, which is provided dorsally with knobbed scales, and moves toward its adversary with mouth slightly agape.

monster (*Heloderma suspectum*) inflates its body, lowers its head, and thrusts or butts at its adversary.

The marine iguana (*Amblyrhynchus cristatus)* of the Galapagos Islands characteristically attempts to drive off another male encroaching on its territory by attacking with lowered head which is crowned with large conical scales. The adversary counters with the head directed in a like manner (Fig. 5). The result is a head-butting contest. The significance of this performance has been demonstrated experimentally by holding a male in the territory of another male and observing the attack and counter reactions. A male has been observed to butt the severed head and shoulders of another male from its territory. Females of this species also exhibit head butting in defense of nest burrows on the nesting beaches (Carpenter, 1966).

The little anole from western Mexico, *Anolis nebulosus,* when threatening another, may initially stand on its hind legs while extending the dewlap. The other male often responds in the same manner (Jenssen, 1970). This behavior appears only under high intensity aggression and at the start of displaying.

Color change may serve to enhance the intimidating appearance of an aggressive male. This is most highly developed in certain agamid lizards and in the Chameleontidae. Color change in the dominance-subordinate social context is most pronounced in the rainbow lizard (*Agama agama agama*) of Ghana. A subordinate male is light brown in color, but, with changes in dominance, may show gradations of a very contrasting color pattern of orange head, cyanine blue legs and trunk, and banded orange and blue tail (Harris, 1964). The small agamid from North Africa (*Agama savignyi*) demonstrates only partial color changes. When this lizard is subordinate or in a nonsocial context, its throat region is much the same color of light brown as the rest of the body. When the animal is dominant, the throat becomes a deep blue color and develops a pouch-like dewlap that contrasts greatly with the rest of the body (Fig. 6).

Territoriality

Central to the development of aggressive behaviors in the iguanids and agamids is the defense of a territory (Carpenter, 1967). The territory and its defense are evidently related to the visual sense. This is suggested by the behavior of the marine iguana (*Amblyrhynchus cristatus)*. The male will defend the top surface of a large boulder on the reef or shore area, while another male—out of sight—may defend a territory below this boulder (Carpenter, 1966) (Fig. 7). Most iguanids and agamids display from elevated sites in their territories where they are most likely to be seen by their congeners.

Display

The greatest degree of ritualism, stereotypy or rigidity of behavior appears in the display. Although my colleagues have shown there is geographical variation in these display rituals, the basic pattern within most iguanid species appears to represent an evolved, genetically programed performance (Ferguson, 1971; Jenssen, 1971).

The study of these aggressive displays has advanced considerably from the original time-motion studies using a stopwatch (Carpenter and Grubitz, 1961; Hunsaker, 1962). It was apparent in my early studies that the display involved more than movement, and a series of categories was established for recording all elements of the display: display site; position (orientation) on this site during an encounter; the postural changes that took place; and the types of movement and temporal sequences of the body movements (Carpenter, 1962). By using these categories, it was possible to compare the displays of various genera, species, subspecies, and populations. The use of motion pictures (at specific speeds) and single frame analysis projectors has greatly increased the accuracy of measurements of the time-motion elements of the display, providing more precise quantification of which to base statistical analysis.

Figure 5. Two male Marine Iguana (*Amblyrhynchus cristatus*—Iguanidae) from the Galapagos Islands contest a territorial boundary by butting heads and pushing. The top of the head has many enlarged knobbed scales.

Figure 6. The expanded throat region (dewlap) of the displaying dominant male Savigny's Agama (Agamidae) of North Africa turns very dark blue.

The time-motion characteristics (that is movements through time) of each species were called the display-action-patterns (DAPs) and, when plotted graphically as graphs (DAP graphs), served to illustrate the species-specific patterns for various species. The variability of the display-action-patterns which I studied early in my program was not great. By averaging the data on the individual units of a display, and the total sequence, a representative DAP graph could be produced (Fig. 8). More recent studies on other species have indicated greater degrees of variability and have led to more sophisticated statistical treatment demonstrating variations in the displays within a population (Jenssen, 1971; Stamps and Barlow, 1972), between populations

Figure 7. The sketch depicts three high-crested male Marine Iguana (*Amblyrhynchus cristatus*—Iguanidae) on their territories consisting of separate large boulders at the base of an oceanside cliff on Hood Island, Galapagos Islands. Eight females move throughout the territories.

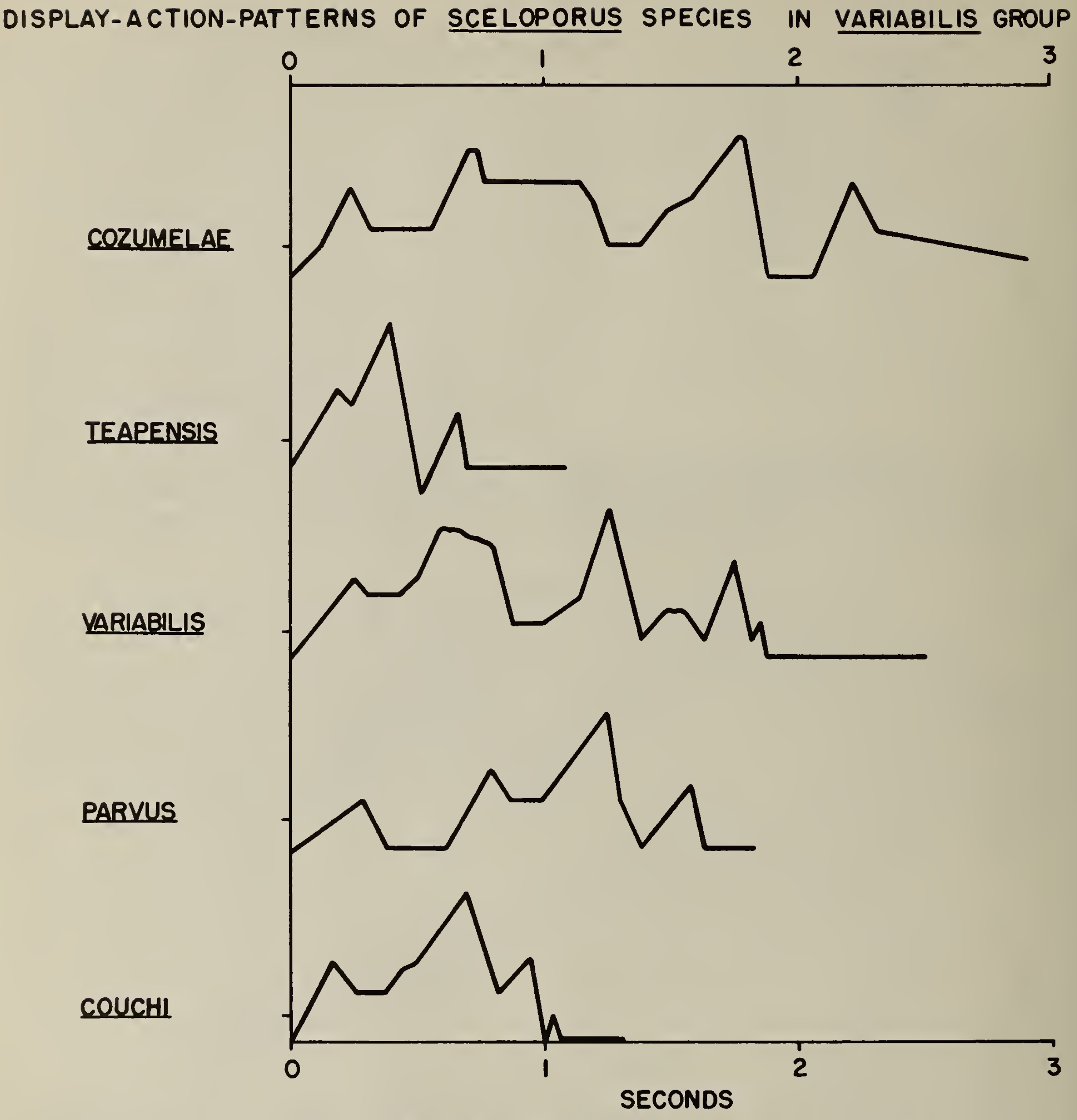

Figure 8. Representative display-action-pattern graphs of the five species of the *variabilis* group of the iguanid genus *Sceloporus* from Mexico. These graphs indicate the time-motion sequences of the front-leg pushups performed by the displaying males of these species.

(Ferguson, 1971), as well as certain species exhibiting more than one type of aggressive display (Jenssen, 1975).

Generally, small sceloporine lizards, displaying from elevated sites such as high boulders, brush, and trees exhibit more color and exaggerated movements than ground dwellers which only infrequently utilize higher sites. Ground dwellers also show less color and less exaggerated movements and generally appear to be less adapted to communicating over longer distances.

It is quite characteristic of iguanid and agamid lizards when displaying at close range during an encounter with a conspecific male to assume a position of lateral presentation toward their adversary, usually facing in the opposite direction (Fig. 9). I call this the faceoff (a term borrowed from ice hockey). The aggressive, challenging male postures by compressing his trunk laterally (lateral compression) and extending his dewlap. In many iguanids (i.e., most sceloporine genera—*Sceloporus, Uma, Holbrookia, Urosaurus*) this postural change enhances the appearance of usually sexually dimorphic colors or patterns present ventrolaterally and on the dewlap of the male. The total effect is to increase the laterally viewed size, color, and pattern of the male. In some species (*Anolis*) a roach or crest may also be erected along the mid-dorsal line, enhancing the laterally viewed size. The crest may also show contrasting color (*Amblyrhynchus cristatus* from Hood Island in the Galapagos Islands). Size increases may also be effected by inflating the trunk region (*Conolophus*, some *Tropidurus*) or by arching the back (*Crotaphytus*) (Fig. 10). The manner or degree of posturing may in some way relate to the ecological niche or the display site used by a species.

The type of movements and the parts which are moved may at first seem to be the same, but in light of what I shall describe below, considering them in more detail may be very useful.

Some movements may involve no more than the head and neck while others bring the whole or the entire body into play, including the tail. The most common type of movement in small- to medium-sized iguanids and agamids is the pushup effected by leg extension and flexion (Fig. 11). This type of movement is seen in the many species of the iguanid genera *Sceloporus* and *Tropidurus*. In the genus *Sceloporus* there are forms which perform the pushup display primarily with the front legs only—two-legged pushups e.g., *Sceloporus undulatus* and *S. occidentalis*), whereas others engage in four-legged pushups (e.g., *Sceloporus jalapae, Sceloporus merriami)*. Purdue and Carpenter (1972) showed that there is a general relationship between size and leg

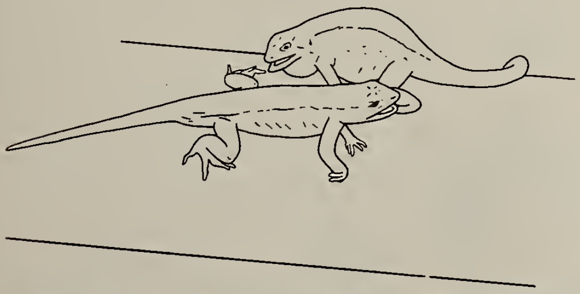

Figure 9. An encounter between two challenging male *Sceloporus siniferus* (Iguanidae) from Mexico. Posturing, they present laterally toward one another (face-off) while intermittently displaying and charging, biting or tail-lashing one another.

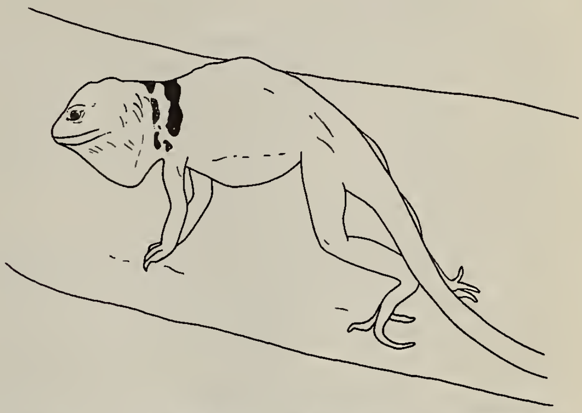

Figure 10. The male Collared Lizard (*Crotaphytus collaris*—Iguanidae) from Oklahoma arches his back and bounces on his front feet while posturing during his aggressive display.

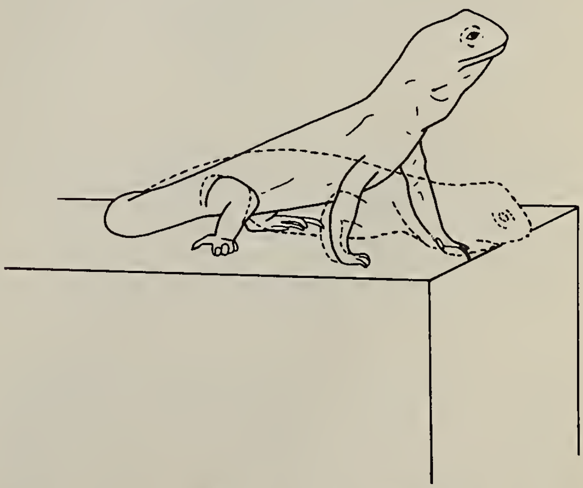

Figure 11. A diagramatic representation indicating the change in amplitude during the front-leg pushup of a displaying male Netted Dragon (*Amphibolurus reticulatus*—Agamidae) from Australia.

use—i.e., four-legged pushups are performed by the smaller species of *Sceloporus*, while the larger species use only the front legs. In other genera, those species performing four-legged pushups are small species (all species of *Urosaurus*). Some agamid forms may perform pushups in such a way as to appear as bowing (head raised up and down, *Amphibolurus barbatus*, Carpenter, Badham and Kimble, 1970) and may do this while walking forward (*Uromastix aegyptius*). The collared lizard (*Crotaphytus collaris collaris*) appears to bounce on its front legs while displaying.

The genera of larger iguanids and agamids may perform only head nods or bobs (*Conolophus, Amblyrhynchus, Cyclura, Physignathus, Brachylophus*). The same is true for some medium sized genera (*Oplurus sebae* from Madagascar), and even smaller forms (*Phrynosoma*, Lynn, 1965).

In the large genus *Anolis*, although pushups and head nodding occur, it seems that the signaling movement has mainly been transferred to the very extensible dewlap which is often pulsed at species-specific cadences (Fig. 12). Among anoline species, dewlaps vary in color and patterns of color contrasts (Gorman, 1968; Ruibal, 1967).

In the genera of sand lizards such as *Uma, Holbrookia, Callisaurus, Cophosaurus* (Clarke, 1965), and *Leiocephalus* (curl-tailed lizards) the tail may be curled up and forward over the body (Fig. 13) to varying degrees as a signaling device (Evans, 1953).

Figure 12. During the display of the Cocos Island Anole (*Anolis townsendi*—Iguanidae) the large dewlap is expanded and pulsed twice while the head nods.

Figure 13. The displaying male Bimini Curl Tail Lizard (*Leiocephalus carinatus*—Iguanidae) raises the tail forward over its back.

In certain species of the agamid genus *Amphibolurus* (reportedly also in *Physignathus)* the legs are very rapidly raised and lowered in a circumduction action (Fig. 14) during or just preceding display, and this action appears to be associated with dominance (*Amphibolurus reticulatus* and *A. muricatus*) (Carpenter, Badham and Kimble, 1970). Such circumduction also appears in the context of submissive behavior, but the action is much slower (*Amphibolurus barbatus*), may be accompanied by bowing (*Amphibolurus muricatus)*, and is seen more commonly in females. Similar movements have also been observed in the Egyptian agamid *Uromastix aegyptius*.

Courtship and Mating Behavior

Let us now consider courtship and mating behaviors primarily of iguanids and agamids. Courtship can be defined as those actions, performed primarily by the male and, to a lesser extent, by the female, that bring the two sexes together to permit copulation. Generally, in iguanid lizards, the courting male approaches a female with its head nodding rapidly up and down in a shallow manner (Carpenter, 1967*a*). This pattern is

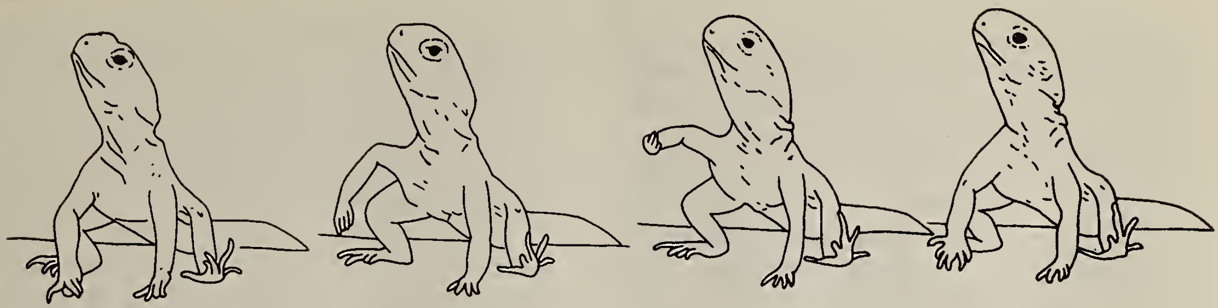

Figure 14. The displaying male Netted Dragon (*Amphibolurus reticulatus*—Agamidae) of Australia often preceeds his pushup movements with rapid circumduction actions of a front leg, bringing the leg rapidly back, up and down. Similar movements, but much slower, are seen in subordinate individuals.

similar for most species and is different from the aggressive species-specific display-action-pattern. In those species whose DAPs are head nods, the difference, if present, may be difficult to discern. In the iguanid genus *Uma*, the rapid headnodding during courtship is accompanied by alternate leg shaking that appears quite comical (Carpenter, 1963). I have observed a courting male *Basiliscus vittatus* hip wagging as it approached the female. The courting male of some species circles about the female (i.e., *Uta stansburiana*) (Ferguson, 1970).

The iguanids and agamids, like the teiids and lacertids, have a characteristic hold during copulation that differs strikingly from the teiids and lacertids (Carpenter, 1967*a*). Iguanids and agamids obtain and maintain bite holds on the skin of the neck or shoulder region of the female whether in the large forms such as *Amblyrhynchus cristatus*, medium sized *Basiliscus vittatus*, or small forms such as *Sceloporus scalaris* (Fig. 15) and *Urosaurus bicarinatus*. All forms use a hindleg across the female pelvic region to help hold her.

Figure 15. The characteristic copulation position for iguanid and agamid lizards is shown here by a pair of Bunch Grass Lizards (*Sceloporus scalaris*—Iguanidae) from Mexico. Notice the bite-hold on the skin of the shoulder region by the male as he holds the female with legs wrapped about her body.

In the genus *Cnemidophorus* (Teiidae) a behavior I have called cloacal rubbing is commonly observed. The male rapidly shakes or rubs his pelvic region back and forth laterally, especially in the presence of a female, but also when in the vicinity of a burrow where a female may be present. I have observed a male *Cnemidophorus tigris* which persistently courted a male *Uma exsul* with pelvic rubbing and attempts to obtain a mating bitehold. After some time, it appeared that the sexual excitement of the *Cnemidophorus* increased and, having failed to mount and hold the *Uma* successfully, it moved away and, in vacuuo, assumed for a few seconds the arched position of a *Cnemidophorus* male during copulation. In the typical hold obtained by a copulating teiid or lacertid, the male moves across the trunk or flank of the female and obtains a biting hold on this region while arching its body across the female and bringing its cloacal region into juxtaposition with hers before inserting a hemipenis (Fig. 16). A hindleg may be thrown across the base of the tail of the female as a holding mechanism. This hold is usually maintained throughout copulation in *Cnemidophorus,* but in the lacertid *Acanthadactylus bosquianus* once insertion is obtained the male may release his bite hold on the female.

Another type of behavior that I believe to be ritualistic is the response of iguanid females which appear to be nonreceptive to courting males. This response has been seen in a number of iguanid genera, and I have called it female rejection behavior (Carpenter, 1962). The features of female rejection behavior are: caudal orientation toward the aproaching male, arched back, raised tail with tip pointing dorsally, and often a lowering of the head and inflated trunk, (Fig. 17). In this posture some species may sidlehop in a half circle about the male (*Sceloporus undulatus, Tropidurus albemarlensis).* In *Holbrookia maculata,* such rejection behavior is further enhanced by exposure of the thigh which in this species has a contrasting yellowish color (Clarke, 1965).

A most unusual type of ritualistic encounter between males occurs in *Varanus gilleni,* a small monitor (Varanidae) from Australia (Murphy and Mitchell, 1973; Carpenter, et al., 1976). Two males, when placed together, proceed to move along side of one another and with their legs flaying attempt to embrace each other. Once they begin to embrace with belly to belly contact, they immediately flex their trunks laterally away from the substratum, and with simultaneous lateral flexion of the neck and tail, still embracing, rise from the substratum to form a tetrapod arch, the two snouts and the posterior tail regions forming the posts of the tetrapod (Fig. 18). Such actions are repeated many times.

What I have presented here is a variety of behaviors in lizards related to social organization which exhibit various degrees of ritualization. There are, of course, other aspects of social behavior and ritualistic actions which I have not discussed. We are just beginning to understand many aspects of lizard behavior.

To gain some perspective on "where we have gone and where we might go" I have included a model (Fig. 19) that I made up a number of years ago that is centered around the ritualistic display-action-patterns exhibited by iguanid and agamid lizards. Without getting involved in all of the possible relationships suggested by this model, I would like to point to some critical areas requiring investigation. Looking at the right upper part of this diagram we may first

Figure 16. The characteristic copulatory position of teiid and lacertid lizards involves the male's biting and holding the flank or groin region of the female as he arches across her trunk—as here seen in a pair of the Six-lined Racerunner (*Cnemidophorus sexlineatus*—Teiidae) from Oklahoma.

Figure 17. A female Lesser Earless Lizard (*Holbrookia maculata*—Iguanidae) may reject the courtship actions of the male by rising high on all four legs, arching her back, presenting caudally toward the male. This action presents a yellow mark on the posterior thigh region to the male.

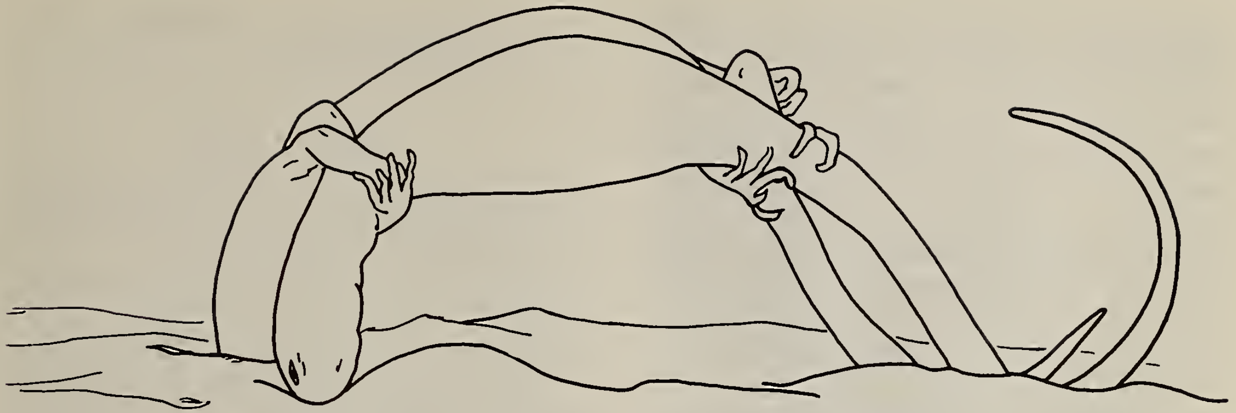

Figure 18. Two male Pygmy Mulga Monitors (*Varanus gilleni*—Varanidae) of Australia embrace one another and rise to a four-posted stance during a combat ritual.

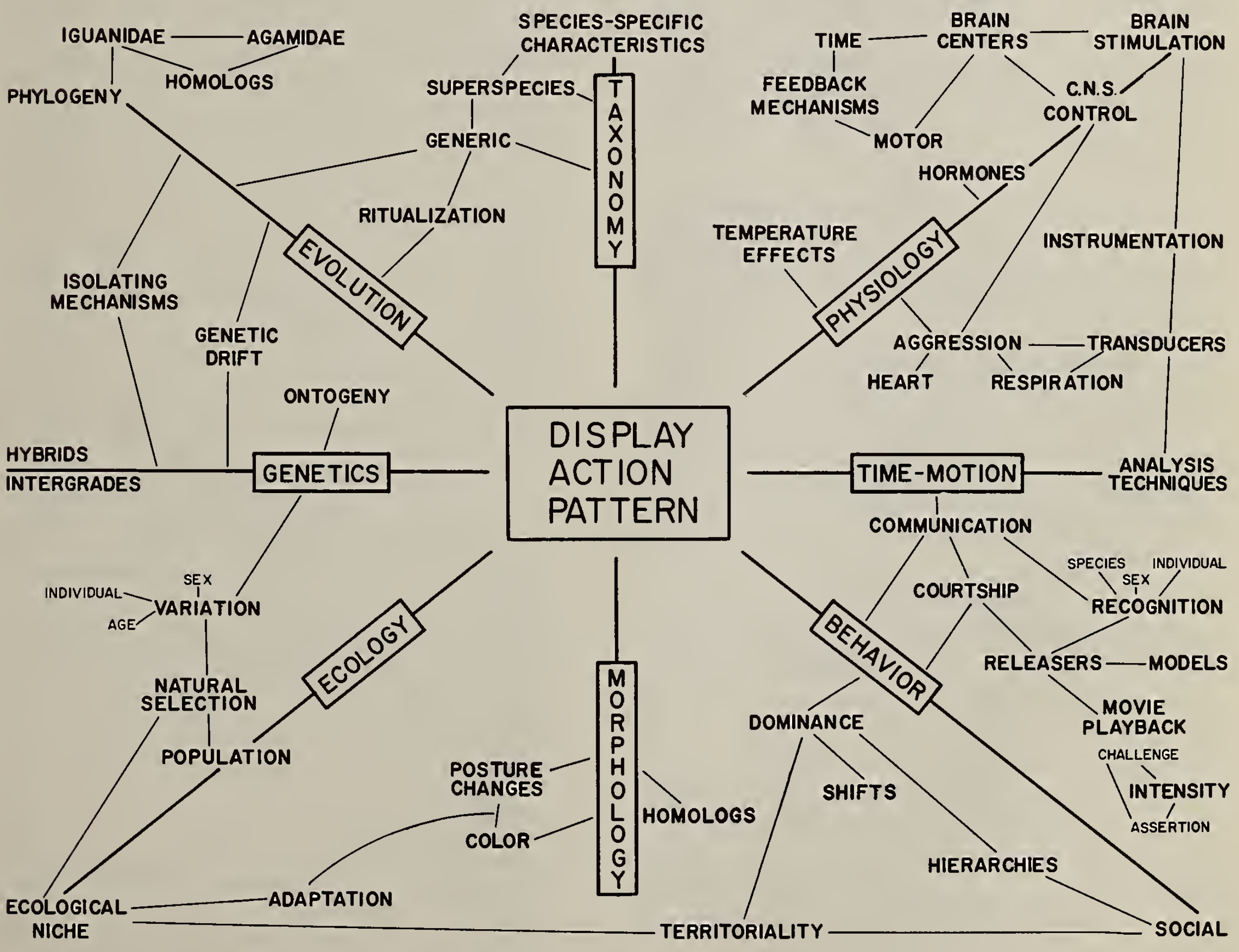

Figure 19. A model, with the ritualistic display-action-pattern as central and indicating potential relationships, areas, and approaches to the study of this behavior in iguanid and agamid lizards.

ask, what is the relationship between the display-action-pattern (a time-motion phenomenon) and the central nervous system control, or how is this behavior programed in the brain? Experimental neurologists are beginning to delve into this problem. With respect to physiological measures, we have used a polygraph to record changes in heart rate of displaying lizards (Sassaman, 1974) and have shown that temperature does not have a strong effect on the display performance (McCardell, 1971).

The significance of differences or similiarities in display-action-patterns of closely related forms to allopatry and sympatry and their function as an isolating mechanism need further study.

With the evidence indicating that the displays are genetically determined, is it possible to produce hybrid or intergrade individuals with intermediate displays? This will take perseverance and time because raising newly hatched or newly born lizards to maturity is a difficult task.

A fascinating possibility for understanding the relationship between the social behavior patterns of a species and its ecological niche requirements lies in the study of ecological homologs and equivalents. When I examined the book by Donoso-Barros (1966) on the reptiles of Chile, I was impressed by the frequent similarities in appearance between certain species of the South American iguanid genus *Liolaemus* and some of our North American iguanid species in the genus *Sceloporus*.

Do these similarities relate to particular ecological adaptations, and, if so, are the social structures and the agressive displays also similar? Likewise, there are species of agamids in Australia that appear to be ecological equivalents of certain North American iguanids, the most striking being the ant-eating *Moloch* and *Phrynosoma*. How similar are their social behaviors, including their displays? Perhaps the agamid *Physignathus* has social behaviors quite similar to those of the iguanid genus *Iguana*.

The question is: How did these ritualistic, species-specific display-action- patterns originate with the early progenitors of the iguanids and agamids?

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Display Diversity in Anoline Lizards and Problems of Interpretation

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SUMMARY. Anoline display characteristics have been found to vary considerably among species. Examples are provided to contrast: (1) degree of stereotypy in displays, (2) degree of display complexity, and (3) size of display repertoire. Behavioral methods are described.

A classification scheme is suggested to differentiate display types and deal with display variability: (1) *Intra-population stereotypy* refers to display elements having population-wide stereotypy; these characterize a display's pattern and help define a display type. (2) *Intra-individual stereotypy* refers to display elements that are typical for an individual, vary among population members, and make individual recognition possible. (3) *Intra-population variability* refers to display elements that vary population-wide, may vary in a like manner and extent for all population members, and reflect the displayer's relative level of arousal. (4) *Pattern variability* refers to display elements which vary so much that no stereotypy is evident.

A survey of display diversity among anoline lizards is presented along with a discussion of display analysis.

I then speculate on factors affecting display evolution, such as social organization and features of the habitat.

INTRODUCTION

Anoline social displays exhibit broad behavioral diversity. For iguanid lizards, these social signals are basically comprised of stereotyped body and head movements. For *Anolis,* an added measure of display versatility is provided by the extensible and colorful dewlap (throat fan), a hallmark of the genus. It provides an added dimension to visual signaling and is used in conjunction with head bobbing, body pushups, tail movements, and various posturings to communicate social intent and relative motivation. Display repertoires of anoles appear to be more extensive than those of any other studied iguanid genus. However, within *Anolis,* there exist considerable interspecific differences with respect to body parts used in displays, temporal patterning of body movements, total number of displays within a species' repertoire, and degree of stereotypy of the displays.

These differences are not suprising in view of the great ecological and social diversity exhibited in this genus. For example, more than any other group of iguanid lizards, anoline species exhibit extensive ecological radiation. Anoles have adapted to a wide range of niche dimensions as exemplified by the following comparisons. *Anolis onca* of Venezuela survives in a notably xeric habitat, while *Anolis townsendi* has adapted to the almost perpetual precipitation of Cocos Island. *Anolis poncensis* inhabits bright open areas of Puerto Rico, as contrasted to the deep shade environs of the forest and cave dwelling *Anolis lucius* of Cuba. The small size of *Anolis semilineatus* of Haiti is adaptive for living in the species' grass habitat, while the giant *Anolis cuvieri* of Puerto Rico is found high in the crowns of trees. *Anolis sagrei,* a successful colonizing species, appears to have broad ecological tolerances, while the opposite applies to *Anolis reconditus,* which has a very restricted distribution in Jamaica's Blue Mountains.

Besides the diversity in morphology and physiology that accompanies the adaptation to diverse habitats, anoles also demonstrate diverse behavioral characteristics. Researchers are discovering that anoline social structure can take many forms. *Anolis agassizi* has a nonterritorial organization based on loose dominance hierarchies (Rand et al., 1975) that may be related to its habitat on Isla Malpelo, a small rocky outcropping in the Pacific, where food resources are localized and unpredictable. As regards Jamaica's *Anolis valencienni,* while the females are free-ranging and nonterritorial, the males are weakly territorial (Trivers, MS). In the Lesser Antilles, male *A. aeneus* can defend areas large enough to accommodate as many as 12 females; these females are territorial toward members of their own sex, but when their densities increase within a male's territory, the females form dominance hierarchies (Stamps, 1973). In the Mexican *A. nebulosus,* whose adult sex ratio is more nearly equal than that of *A. aeneus,* male territories are small and contain no more than two territorial females (Jenssen, 1970). There is evidence that large adult *A. limifrons* females in Panama may be solitary and occupy territories which are exclusive of permanent male residents (Jenssen, in press).

METHODS

Observations and Documentation

I usually begin a study by working with lab-held animals, since the highest quality films or videotape recordings of displaying lizards are achieved in the laboratory.

In maintaining laboratory populations, I keep low densities of animals in relatively large holding cages. These enclosures contain a reasonable facsimile of the species' natural micro-habitat (e.g. grass and twigs for grass anoles; stumps, horizontal branches, and foliage for arboreal species). I find a dense habitat is valuable as it shortens line of sight and decreases interactions between dominant and subordinate lizards. Several food and water dishes are placed on elevated sites around the enclosure to counter the reluctance of subordinate lizards to seek food and water.

In recording displays, I work from a blind because many of the anoline species are shy and their behavior is affected by the presence of an observer. The filming enclosure is large, contains simulated natural habitat, and is fitted with a slanting glass front to decrease the chance that the lizard will react to its own reflection. Heat-filtered floodlights are used not only for photographic purposes, but for stimulating increased activity in the lizards. Various combinations of conspecifics are placed in the enclosure so as to evoke different types of displays.

To elicit aggressive encounters between males or between females, I allow a lizard to establish residency of several days in the enclosure. Then I release another lizard of the same size and sex into the enclosure. The ensuing response is usually short-lived, with the resident the victor. Another technique which more closely simulates natural conditions utilizes a long, partitioned enclosure (Fig. 1) with similar habitats in each of its far ends. With the partition in place, I release male and female pairs into each half of the enclosure. Recordings are made of the kinds of displays and their frequency of occurrence. After a day or more the partition

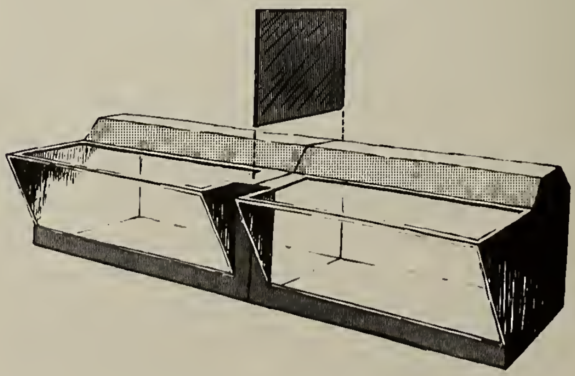

Figure 1. Enclosure used in partition experiments.

is removed. Now there are two potential male combatants which are both "residents" and are initially at long range to each other. Observations are made on the effect of distance upon the characteristics of the displays and on the effect of displays of one lizard on the subsequent behavior of the other animal with similar territorial status.

In the field, lizards can be manipulated in several ways to obtain displays performed in different contexts. For recording male-female interaction, I use a camera with a strong telephoto lens (e.g. Nizo S80) and follow the male's movements. As he patrols his territory, he frequently will give nondirected displays upon changing his perch site and will interact with resident females. I also may release an intruder into a resident's territory. To elicit aggressive displays, for instance, I use a male as large or larger than the territorial male under observation. The release takes place out of sight of the resident male, allowing the intruder to recover from being handled before he encounters the resident. The same method can be employed when releasing a female. Another procedure is to take a small aquarium containing a conspecific and place it within the territory of the observed lizard. In this experimental situation, the resident male should be attracted to the confined conspecific. Knowing where the encounter will take place allows me to prepare the camera position.

Cinema film and videotape are used to record display behavior. The television format has several advantages over film. The video tape has 60 continuous minutes of recording capability, so all antecedent behavior is known and all displays are captured from the beginning. The 60 frame/sec resolution of the videotape also permits accurate analysis of extremely fast movements. Tape decks are available to permit frame-by-frame advancement of videotaped images. The main disadvantage is that the picture on a TV monitor is not as sharp as that of film. Trying to detect changes in body position from one frame to the next with a transparent grid overlay is almost impossible; the reference lines of the overlay becomes lost in the sweep lines of the monitor. However, a digitizer (e.g., Numonics Model 234) can easily record the X-Y coordinates of the body parts by touching the monitor screen in successive frames with a hand-held stylus. These data can be manually recorded, or fed into a table top computer for processing.

Lightweight Super 8 equipment is good for recording displays in the field. Filmed displays can be analyzed accurately by relatively low-cost techniques. For example, frame-by-frame analysis of Super 8 films is performed using a Kodak Ektagraphic MSF-8 projector, support box, mirror, clipboard, and clipboard guide (Fig. 2). Each sequentially viewed frame is projected off the mirror onto graph paper mounted on a clipboard. Head and dewlap positions are plotted for each frame, and the clipboard is progressively moved along a guide to receive each sequential frame of the movie. The rubber-backed clipboard guide is adjusted before each display so that the projected head movement of the lizard is parallel with the Y-axis of the graph paper. The movable clipboard guide also allows compensation during occasional display sequences when the camera moved slightly or the lizard's perch moved (i.e., leaf or twig).

Terminology

A lizard display is typically composed of up and down head movements (usually aug-

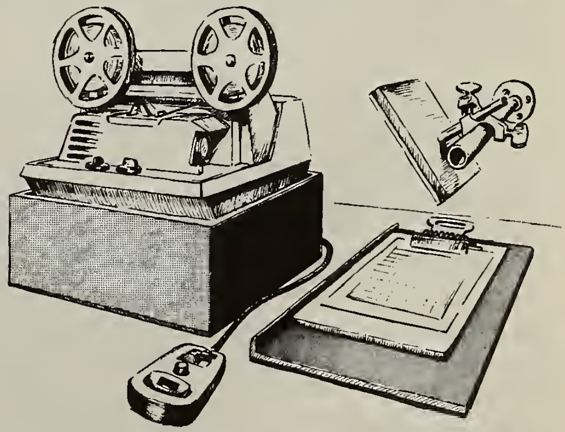

Figure 2. Equipment set up of frame-by-frame analysis technique.

mented by limb flexion and extension) which are at times interspersed with periods of no amplitude change. Variables which can create different appearing displays are: direction of head movement (up or down), rate of head movement (constant or changing), relative amplitude of the movement, and elapsed time between movements. With anoles, dewlap movement can be coordinated with head movements. The physical and functional aspects of displays are referred to by the terms "display pattern" and "display type."

Display Pattern

Display pattern is a descriptive term used to refer to the change in amplitude through time of a lizard's head and dewlap as the lizard performs a head bob display. As a rule, the pattern is reoccurring for a species which indicates it is stereotyped. It is basically the same as Carpenter's (1967: 96) "display-action-pattern" (DAP). A display pattern can be analyzed according to its "units" (subdivisions of a display's movements), "sequence" (the ordering of units), and "cadence" (relative unit durations). Plotting head and dewlap amplitude changes (Y-axis) through time (X-axis) from films or videotapes results in a display-action-pattern graph (DAP graph).

Display Type

Display type is a primary category. It encompasses: (1) the stereotyped head and/or dewlap movement pattern (i.e., stereotyped *display pattern*), (2) any consistently associated stereotyped movements by other body parts (e.g., tail lift), (3) any other postures and movements which less consistently accompany the stereotyped display pattern, and (4) the functional significance.

It is assumed each display type has a unique function, although a single display type may appear in more than one social context, suggesting that it has more than one function. In contrast, more than one display type may be performed by an individual within the same social context.

Display Modifier

Display modifier is a posture or body movement which is not always present with a particular stereotyped display pattern, but at times is added to the pattern. The concept is useful in classifying the variability found between displays by helping to distingush what different display types are and what variations of the same display type are. A modifier may be static (a posture) or dynamic (body movement) which is not always associated with a particular display type, but can be added to the permanent elements of a display type as an option employed by the entire population (Jenssen, 1977*b;* Jenssen and Hover, 1976). *Static modifiers* are such postures as raised nuchal crest, lateral compression of sides, open mouth, and a sustained posture during a display such as elevated on all four legs. Although not strictly a posture, color change might also be considered a static modifier.

A *dynamic modifier* can be (1) optional head and/or dewlap movements added just prior to the stereotyped core display, (e.g., introductory rolling movement of head preceding the *A* display of *A. limifrons;* see Fig. 8; (2) optional head and/or dewlap movements occurring at the end of the stereotyped core display (e.g., repetitious bobs following first seven head bobs of *A. limifrons* signature display, see Fig. 8); or (3) any occasionally incorporated movement of the body part besides the head or dewlap which is concurrent with the display (e.g., tail lifts during signature display of *Anolis brevirostris;* pers. observ.

Assertion, Challenge, and Signature Displays

Carpenter (1962, 1967) coined the terms "assertion" and "challenge" to describe a single, head bobbing display pattern in nonanoline iguanid lizards according to the social context in which it appeared. The display can be performed with or without a conspecific present. Under the latter condition, the display pattern shows slight head movement amplitude with few or no modifiers, e.g., throat lowered, body sides compressed. The species-typical display pattern given under these low-conflict or motivational situations was labeled the "assertion display." The same display pattern performed under high conflict or motivational situations, e.g., male-male confrontations, is produced with maximum head amplitude movements, i.e., via full extension of the legs, and is accompanied by many modifiers. This form of the display was called the "challenge display." Bussjaeger (1971:35-36) has thoroughly described the distinction between these two terms in his display analysis of sceloporine lizards. Stamps and Barlow (1973: 69-70) first suggested the term "signature bob" to indicate the stereotyped head bobbing display pattern unique to *Anolis aeneus*. For species with more than one stereotyped display pattern, the signature display would be defined as that display type performed in a context in which there is little or no social interaction (the "assertion" context). Displays within this context may be nondirected. In my experience, the signature display is used in courtship and challenge as well as in assertion contexts; however, display types other than the signature display are not observed in the assertion context.

A SURVEY OF DISPLAY DIVERSITY

I have found marked interspecific differences in many features of anoline display behavior in the eight species I have examined. Since the genus contains over 250 species, more differences will doubtless be found as more species are systematically studied.

To provide an appreciation for the breadth of display diversity in *Anolis*, contrasts between species are provided for three display characteristics: (1) degree of display stereotypy, (2) degree of display complexity, and (3) size of display repertoire.

Degree of Display Stereotypy

Phenacosaurus heterodermus, a near relative of anoles (Etheridge, 1960) living in Colombia, is a good example of strong display stereotypy. Jenssen (1975) found that a male performed its signature display (Fig. 3) with almost no temporary variability. The coefficient of variation $\left(\text{C.V.} = \frac{\text{standard deviation}}{\text{mean}} \times 100\right)$ for the units which comprise the signature display ranged from 2.9 to 5.8 percent, and the C.V. for the total duration of the signature display was 3.9 percent. Such consistent temporal stereotypy is relatively rare in the ritualized signals of animals as indicated by Barlow's (in press) review of modal action patterns.

In contrast to the consistent displays of *P. heterodermus*, the displays of *Anolis opalinus* do not have a single stereotyped pattern (Jenssen, in press). From an analysis of 639 displays by 51 males, no discrete pattern or patterns emerged for either the species or any one individual. The *opalinus* displays consist of four to eleven head bobs followed either by none or up to eight pulses of the dewlap. The bobs within a display are qualitatively similar, being produced by a simple up-and-down motion of the head. It is the interbob

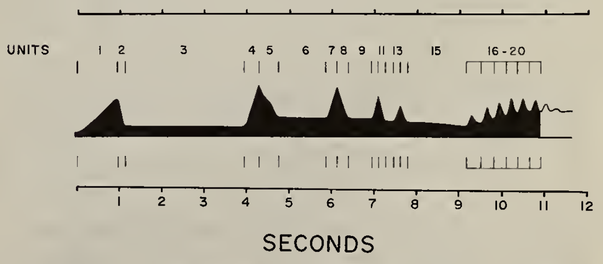

Figure 3. Display-action-pattern (*DAP*) graph of the signature display from a male *Phenacosaurus heterodermus*. Upper edge of the blackened area represents head amplitude movement through time.

pauses which determine the bob cadence and serve as the major pattern-producing factor.

As a case in point, the data from 33 filmed displays of a typical male *opalinus* show the displays varying from five to eight bobs (Fig. 4), with a range of head-bob durations of 1.7 to 4.3 s, and a C.V. of 23.3 percent.

Degree of Display Complexity

Anolis lineatopus neckeri from Mandeville, Jamaica, has a very short and stereotyped signature display (Fig. 5). The pattern, derived from 93 filmed displays by four males, consists of a short series of continuous sine wave bobs (Jenssen, 1977*a*). The total duration of the display is just over one second.

In contrast to *A. l. neckeri,* the signature display of *Anolis sericeus* from Vera Cruz, Mexico, is usually long, averaging almost 30 s, and is quite complex. Closely coordinated dewlap pulses are integrated with a complex head bobbing pattern (Fig. 6). Based on 21 filmed displays of five males, the pattern is quite predictable except for some introductory head movements and a terminal dewlap pulse (nondarkened areas in Fig. 6). This display is about 30 times the duration of the signature display of *A. l. neckeri.* The greater variety of muscular movements and their nonrhythmic coordination are in marked contrast to *A. l. neckeri's* cyclic and continuous sine wave bobs.

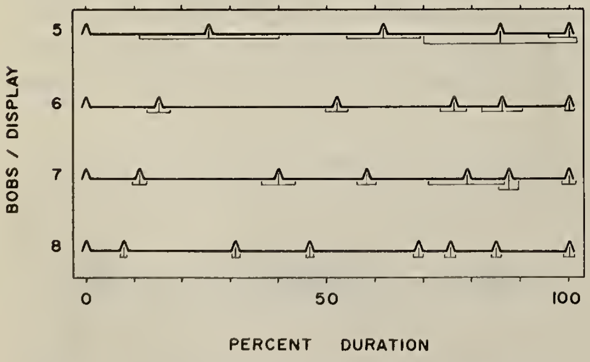

Figure 4. Distribution of bobs within displays having the same number of bobs/display (5-bob to 8-bob displays) by a male *Anolis opalinus.* Head-bob amplitude is stylized, with the interbob pauses expressed as a percentage of the total display duration. The thin horizontal lines denote one standard deviation on either side of the mean inter-bob pause values (medial vertical lines).

Size of Display Repertoire

In analyzing displays, I treat a species' repertoire size conservatively, restricting the count of different display types to only those body movement patterns which are stereotyped and species-unique (Jenssen, 1977*b*).

According to such criteria, *Anolis nebulosus* from Nayarit, Mexico, has only one display type (Fig. 7a). I originally called this stereotyped pattern the "assertion" display (1970; 1971) but, keeping with more recent terminology, it is more appropriately labeled as the species' signature display.

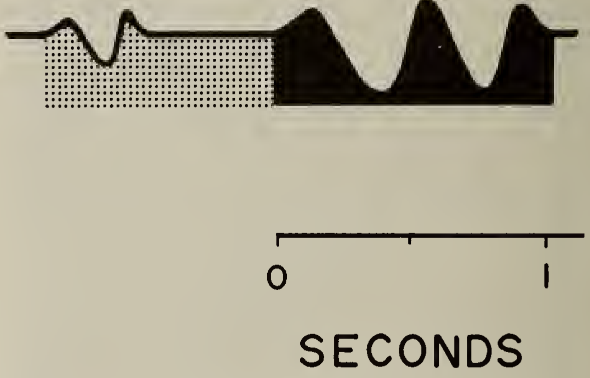

Figure 5. *DAP* graph of the signature display of *Anolis lineatopus neckeri.* Upper edges of the blackened area depicts head amplitude movement through time. Stippled area represents a different bob pattern sometimes associated with the signature display.

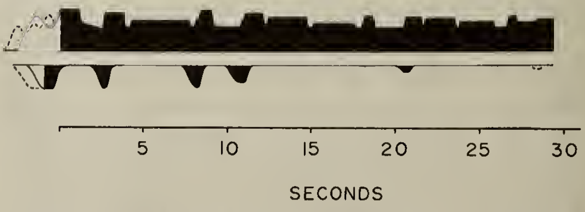

Figure 6. *DAP* graph of the signature display of *Anolis sericeus.* Upper block depicts head amplitude movement, and lower block represents dewlap extension. Blackened areas are stereotyped portions of the display, and white areas are examples of variable portions of the pattern.

Figure 7. *DAP* graphs of the *Anolis nebulosus* signature display (A) and an agonistic related signature display prefaced with an introductory movement (B). Upper block represents head amplitude movement through time, and lower block represents dewlap extension through time.

Male *A. nebulosus* also perform shallow rapid head bobs during courtship and frequently expand and contract their dewlaps under various conditions (Jenssen, 1970). These behaviors, however, are not considered in my analysis of repertoire size because they are common to many anoles (not species-typical) and are not particularly stereotyped.

In addition to the usual "dewlapping" and courtship-related rapid head bobs, the repertoire of male *Anolis limifrons* from Panama includes five main display types (Fig. 8) (Jenssen and Hover, 1976, Hover and Jenssen, 1976). These five types have been designated *A-E*. Type *A* functions as the signature display (analogous to the *nebulosus* assertion display) and is performed in several contexts ranging from assertion, to challenge, to courtship. Types *B* to *E* almost always involve male-male interactions.

ANALYSIS OF DISPLAY BEHAVIOR

Display analysis is not always straightforward. A species may have several different stereotyped display patterns in its repertoire, with some patterns being similar. Furthermore, each stereotyped display pattern may appear in conjunction with many display modifiers to produce a graded signal of varying elaboration. Therefore, one is faced with dissecting out elements of stereotypy in order to distinguish one reoccurring display pattern from another, and evaluating the residue of display variability for its contribution to signal function. I suggest the following perspective for a display analysis.

A display is a gestalt of postures and movements. From each display performance, one can quantify the presence or absence of body movements, (e.g., head nods, dewlap pulses) and postures (e.g., erected nuchal crest, lateral compression of body sides, mouth open, tongue out). One notes what is moved, how far it is moved, along what spatial coordinates it is moved, the rate of movement, the number of times a movement is repeated, and the coordination of all the moved parts through time.

Having quantified the passive and active elements, one can now compare display performances to verify what is constant and what is variable. At this point of analysis there is a set of fundamental questions: (1) What passive and active elements are always present; (2) of those elements always present, how much variability exists in their expression from one display performance to the next; (3) does the change in magnitude of a variable element correlate with a change in expression of some other element in the same display or to a change in social events; (4) of those elements not always present, are their appearances correlated with a change in expression of a permanent display element or to a change in social events; and (5) are the permanent and optional elements of a lizard's displays similar to those of other conspecifics, or do some lizards have individual differences to their displays?

By answering questions like the ones above, one can differentiate between different expressions of the same display type and between different display types, and have the descriptive data necessary for assessing communication potential of the display behavior.

I will now narrow the behavior under consideration. Because an anole's stereotyped display pattern primarily incorporates vertical movements (Jenssen, 1977*b*), dewlap

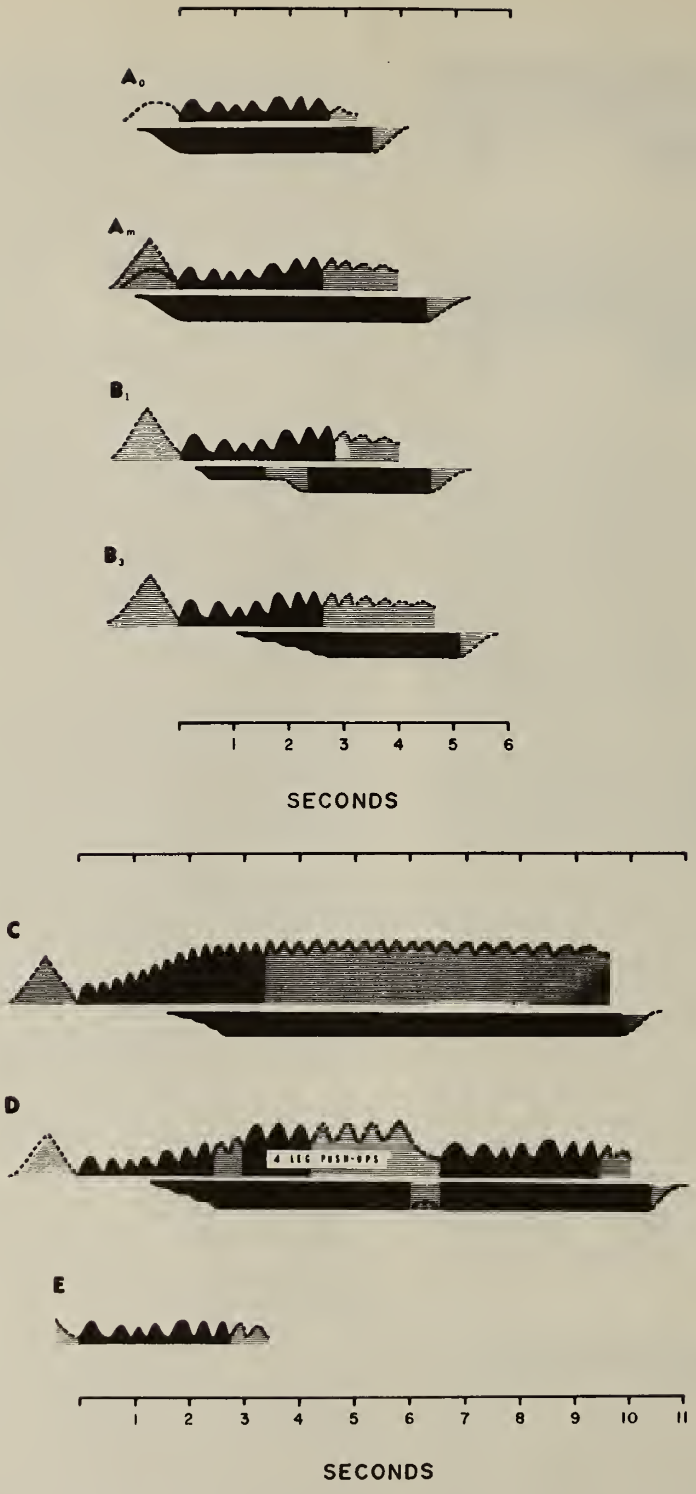

Figure 8. *DAP* graphs for the signature display (A) and agonistic related display types (B–E) of *Anolis limifrons*. Stereotyped portions of the displays are blackened, and variable portions are shaded. Upper block represents head amplitude movement through time, and lower block represents dewlap extension through time.

movement and head amplitude changes through time are important considerations for defining a display. The head amplitude is the best single criterion of vertical body movement, whether it is effected by the neck muscles, forelimbs, and/or hindlimbs; ideally, however, each group of effectors should be monitored for its contribution.

My objective in a descriptive analysis is to isolate display elements that are stereotyped in order to distinguish display types, and to place elements of display variability into recognizable categories. To formally categorize display stereotypy and variability, I suggest the following four concepts (Table 1): Intra-population stereotypy, intra-individual stereotypy, intra-population variability, and pattern variability

Intra-population stereotypy refers to the permanent elements of a display behavior as performed by a population. These permanent elements form the core of a predictable and recurring pattern of movements and postures which define a display type. These elements may be used to distinguish one display type from others of a species' repertoire. Display elements characterized by intra-population stereotypy promote species recognition.

Intra-individual stereotypy refers to those elements of a display (especially the permanent elements) which are consistent for an individual, but are absent or show wide variability between members of a population. Consistent, individual-unique elements promote individual recognition.

The following examples demonstrate the concept of intra-individual stereotypy. Even though all observed *A. nebulosus* performed an identical signature display pattern (Fig. 7A), each individual performed its display with a consistent duration which tended to be different from the display durations of the other lizards (Fig. 9). An analysis of variance showed that only 2 percent of the variability in display duration existed within groups and 98 percent between groups (Jenssen, 1971). Each lizard tended to have its own particular display duration.

Stamps and Barlow (1973) also found a very stereotyped bob pattern for the signature display of *A. aeneus*. The duration of each display unit for the overall *aeneus* pattern was fairly constant within individuals, but varied much more from one individual to another.

Table 1. Proposed classification for partitioning stereotypy and variability in lizard behavior.

Term	Defining Characteristic	Possible Function
Intra-population Stereotypy	Any element of a display which reflects population-wide stereotypy, is species unique, and helps define the core display.	Can facilitate species recognition.
Intra-individual Stereotypy	Any element of a display which exhibits little intra-individual variability and much interindividual variability.	Can facilitate individual recognition.
Intra-population Variability	Any element of a display which exhibits much intra-individual variability and little interindividual variability.	Can provide information on relative level of arousal.
Pattern Variability	Variation in the stereotyped portion of the population's display sufficient to disrupt that pattern, as produced by (a) a few population members on occasion, or (b) all population members consistently.	Function of variability not apparent; may denote (a) anomalous behavior or (b) relaxed selection pressure for stereotypy.

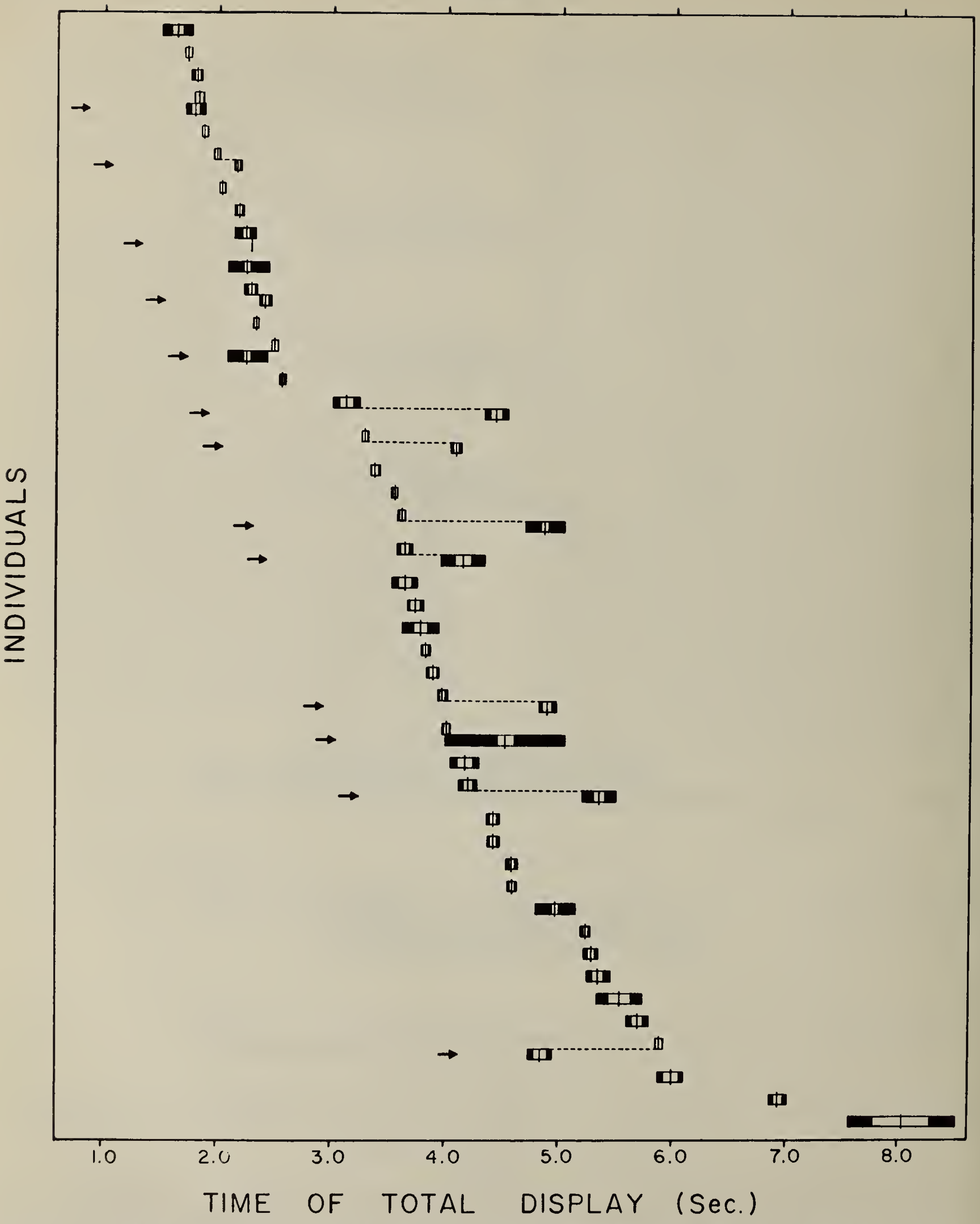

Figure 9. Elapsed time of total display durations from 43 *Anolis nebulosus* performing signature displays. Arrows indicate individuals whose displays were reanalyzed after a year. Ends of the outer black bars give 95 percent confidence limits of the means, medial vertical lines indicate means, ends of inner white bars represent the standard error of the means.

In a nonanoline species, Berry (1974) found a population-wide head-bobbing pattern in *Sauromalus obesus* consisting of a single fast bob, two bobs of longer duration, and then one or more single fast bobs. The pattern was quite stereotyped in individuals (Berry, 1974) but showed interindividual variations in the cadence and bob amplitudes.

Intra-population variability refers to display elements (especially modifiers) having a wide range of expression which can vary to a similar extent in the displays of all population members. These display elements can function as indicators of relative arousal.

For example, the signature display of *A. limifrons* has display components which are a source of variability shared by the entire population (Jenssen and Hover, 1976). The stereotyped portion of the signature display consists of seven head bobs having a cadence within the first five bobs of one long, three short, one long (Figs. 10 and 11). However, the addition of dynamic modifiers can alter the overall pattern. Many of the seven-bob signature displays are performed with a preceding introductory head roll and two additional bobs at the end of the display (Fig. $8A_o$); however, the stereotyped seven-bob pattern can be elaborated to an even greater extent (Fig. $8A_m$). The optional introductory movements can vary in amplitude, and the optional terminal head bobs can vary in number from none to ten. The addition of the dynamic modifiers to the seven-bob core display was not specific for individuals; it was an option performed to a similar extent by all the observed males.

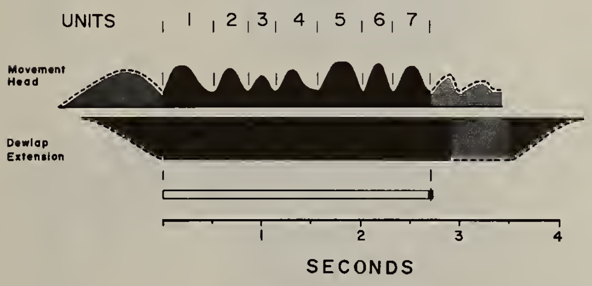

Figure 10. *DAP* graph of the signature display of *Anolis limifrons*. Stippled areas indicate display portions not always present. Bar below *DAP* graph gives mean total duration of the first seven head bobs (vertical line), the standard error of the mean (outer ends of small white boxes), and 95 percent confidence limits of the mean (outer ends of small black boxes).

In his review, Carpenter (1967) describes many species of lizards as being able to vary the relative bob amplitude between display performances. As the lizards become more aroused, head amplitude grades from being primarily effected by neck muscles, to displays having head bobs produced with forelimb extension and flexion, and finally to displays in which all four limbs are creating the bob pattern. Thus, the optional use of the limbs to produce vertical body movement can be classified as a dynamic modifier. The ability to use this optional display element and the range of expression is shared by a population, making the modifier an example of intra-population variability.

Pattern variability refers to aspects of the core display which are expected to be consistent for the displays of a population, but which are altered to the extent that the display pattern is changed.

Pattern variability can occur on the individual level when a few individuals of a population may, for instance, occasionally drop a bob or add an extra dewlap pulse to the stereotyped portion of their display.

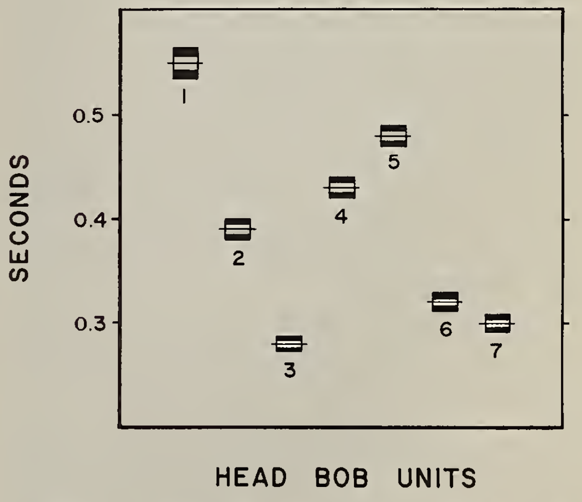

Figure 11. Mean duration for each of the first seven head-bob units of 316 *Anolis limifrons* signature displays. Horizontal line indicates unit mean, outer white bars denote standard error of the mean, and outer black bars provide 95 percent confidence limits of the mean.

The result is infrequent anomalous display performances.

Pattern variability can also occur at the population level in two forms. First, a species may not have enough permanent display elements to produce a consistent display pattern. This situation is expected to be rare and could result if selection pressure for stereotypy has become relaxed, resulting in unexplained variability in the display behavior. Second, members of a population may have many permanent elements of their displays not interindividually shared, so that there is no single core display pattern held in common by the population. The latter situation is an extreme case of intra-individual stereotypy.

As an example of pattern variability at the individual level, Jenssen (1971) found that approximately 7 percent of a population of *A. nebulosus* would occasionally vary the pattern of their signature display by deleting the first dewlap pulse or sandwiching a third pulse between the usual two (Fig. 12). This is an instance of pattern variability since these same animals would also perform the species-typical signature display pattern.

The altered signature display pattern was in no way shared by the population as a whole and thus was not a case of intra-population variability or another display type. It is considered anomalous behavior.

Another example of occasional pattern variability by a minority of population members is provided by Stamps and Barlow (1973). The normal *A. aeneus* signature display pattern of a male was altered by unit deletion.

An example of pattern variability at the population level is provided by *A. opalinus* which shows population-wide disruption of display patterning (Jenssen, in press). Figure 4 illustrates some displays by a male. *A. opalinus*; these inconsistent patterns are normal for the species. Not one discrete stereotyped bob pattern was found for the species after analyzing 639 filmed displays. Bobs per display were quite variable. This in itself does not preclude a stereotyped display pattern. For instance, Jenssen and Hover (1976) found *A. limifrons* had a predictable seven-bob display cadence to which optional numbers of bobs can be added (dynamic modifier). However, no such core of stereotyped cadence or patterns was detected for *A. opalinus*. For example, in one eight-bob display, a male distributed the bobs in a double-single-double-triple pattern. In another eight-bob display he performed a single-triple-quadruple cadence. The interbob pauses do not maintain any consistent proportionality between displays for this species.

To this point I have stressed a descriptive approach for separating the display behavior of anoles. This is the first step of any taxo-

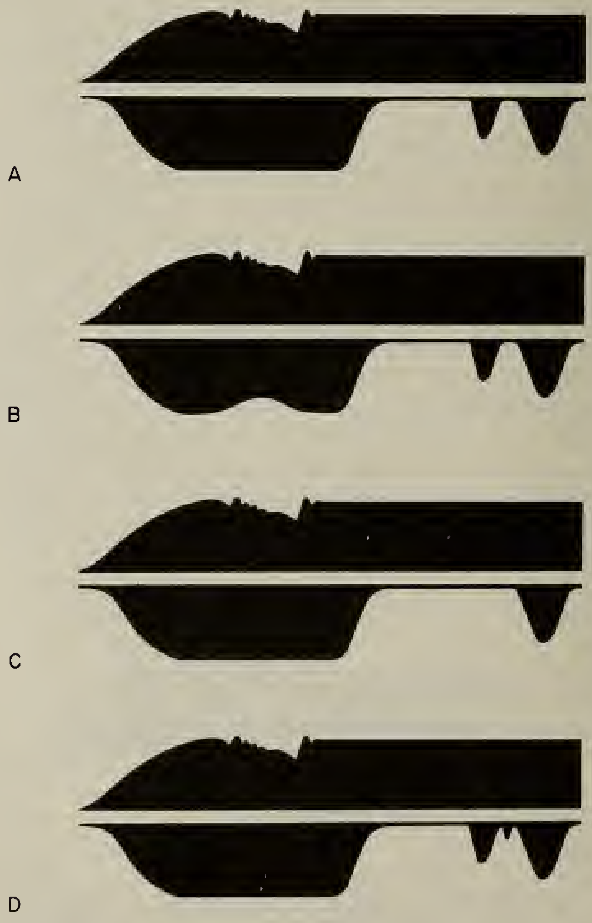

Figure 12. Four signature display patterns observed in *Anolis nebulosus*. Upper block represents head amplitude movement through time, and lower block represents dewlap extension through time. Normal signature display pattern (A). Deviations from the normal signature display pattern (B, C, and D).

nomic endeavor. However, the function of a behavior must be understood to ultimately classify the displays of a species' repertoire. Unfortunately, this understanding is obtained by inference. While the descriptive approach to display analysis can be quantified to give a detailed statistical description of the physical signals, one assigns function to a display type by correlating the display type with the social contexts in which it appears. This is still a relatively unrefined means of evaluating the information content of the displays. Nevertheless, this technique must be employed to verify the classification of descriptively derived display types.

Context can be a criterion for determining display types. Display variability can make it difficult to distinguish between what might be two distinct but similarly appearing display types and what might be a single display type with much variation. Specifically, the signature display (*A* display) and the *B* display of *A. limifrons* are differentiated by the appearance of the dewlap in relation to the head-bob pattern (Fig. 8). During the signature display, the dewlap appears before the first head bob, and in the *B* display the dewlap appears during the first bob or as late as the fifth bob (Hover and Jenssen, 1976). Such a division of display types might seem arbitrary were it not that the signature display and the *B* displays appear in different contexts.

To quantify the difference of display usage by *A. limifrons*, a cage 3 meters long was divided in half by a sliding partition (Fig. 1), and a male and female were paired in each end. After a day, observations were made for an hour with the partition in place. Dewlapping and signature displays composed 98 percent of the displays during male-female association; *B* displays were rare. The partition was then removed, and displays were recorded for an equal length of time. The frequency of *B* displays rose seven-fold during male-male interactions. This observation and the fact that in almost 700 observed displays the signature display (*A* display) appeared eight times more frequently than the most common *B* display variant indicates to me that there is no functional continuum. Dividing the behavior into two display types was suggested by the animals' own use of these display patterns.

Distinctions between different display types within a species' repertoire and actual socially significant variations of a particular display type may be complex and open to interpretation. This interpretation will reflect the investigator's conceptual orientation. For this reason, a framework is needed in which to categorize not only the stereotyped portions of display behavior, but also the seemingly less predictable elements. By being able to analyze and evaluate the entire behavior, we will make greater progress in unraveling the enigmas of display function and evolution. See Table 2 for selected examples.

SPECULATION: FACTORS AFFECTING THE EVOLUTION OF DISPLAY CHARACTERISTICS

Because anoline lizards are easily studied in the field and have undergone extensive ecological radiation, *Anolis* investigations have generated notable advances in ecological theory (Lister, 1976*a*, *b*; Rand, 1969; Roughgarden, 1972; Schoener, 1967, 1968, 1969, 1970*a*, 1970*b*, 1971; Williams, 1969, 1973). This same genus is a potential fountainhead for understanding factors influencing behavioral evolution.

Some immediate questions and speculations which come to mind regarding the evolution of anoline visual signals are the relationship between display characteristics and the following:

Types of Social Organization

Large-bodied species with relatively expansive territories might be expected to have simple repertoires containing few display types, with most ritualized disputes being settled while the conspecifics are still widely separated. The display type for declaring

Table 2. Summary of display characteristics for a few species of *Anolis*.

Species Studied and Authorities	Size of Display Repertoire	Signature Display Complexity	Signature Display Characteristics			
			Elements of Intra-population Stereotypy	Elements of Intra-individual Stereotypy	Elements of Intra-population Variability	Pattern Variability Present
aeneus (Stamps & Barlow, 1973)	Perhaps two ('bob' and 'fanbob')	Moderate	Evident	Present	Present	A few lizards, on occasion
limifrons (Jenssen & Hover, 1976, Hover & Jenssen, 1976)	Five	Moderate	Evident	Not observed	Present	Not observed
lineatopus neckeri (Jenssen 1977*a*)	Complete repertoire not known	Low	Evident	Not observed	Present	Not observed
nebulosus (Jenssen 1970, 1971)	One	Moderate	Evident	Present	Present	A few lizards, on occasion
opalinus (Jenssen, In press)	Impossible to confirm	Not applicable	Not evident	Not observed	Present	Population-wide, consistently
sericeus (Jenssen, Unpubl. Data)	Complete repertoire not known	Very high	Evident	Not observed insufficient data to confirm	Present	Not observed, insufficient data to confirm
townsendi (Jenssen & Rothblum, 1977)	At least four	High	Evident	Not observed, insufficient data to confirm	Present	A few lizards, on occasion

territorial occupancy to the nearest neighbor would function over long distances. This display would most likely lack subtlety, being composed of movements of relatively large amplitude. A large dewlap would also enhance such signals.

In contrast, nonterritorial species or those having large home ranges with little defense of discrete boundaries might possess aggressive signals that are exchanged at close range when individual distances are violated. These displays could effectively incorporate subtle, complex movements, temporally compressed bob patterns, and numerous modifiers.

Life History Characteristics

Species forming stable territories and remaining territorial and sexually active most or all of the year would benefit by decreasing aggressive interactions with their nearest neighbors. This could be facilitated by individuals having displays containing individual-unique characteristics. Intra-individual stereotypy of obvious display features would be even more expected if the species were long lived.

Species which are territorial and sexually active throughout most of the year, but are short lived, would tend to experience a rapid turnover in nearest neighbors, especially if population densities are high. The frequent territorial interactions with unfamiliar conspecifics would be more tenable if the species' agonistic repertoire contained a number of display types. This would permit ritualized escalation and place a greater reliance on bluff than on fighting to maintain territories. Risk of injury should be decreased with a large display repertoire.

Species which are short lived, maintain breeding territories over a limited season, and live in low population densities would least likely have unusual or elaborate display characteristics. Expected would be a small repertoire having a signature display of strong intra-population stereotypy and the usual display modifiers.

Presence of Syntopic Congeners

In mixed anole communities, especially where syntopic congeners have like ecologies, character divergence could have influenced displays and signaling structures. Where species of similar appearance could potentially hybridize, selection might favor interspecific divergence of dewlap color, body color, body proportions, and/or display patterning to facilitate species recognition.

Kind and Intensity of Predation

If a species were under potentially heavy predation pressure, the evolution of its signals would reflect compromise. While one aspect of selection would favor cryptic morphology, body color, and behavior, there are certain social benefits in having conspicuous signals. An optimal trade-off would probably occur where displays are performed less frequently, are of shorter duration, and utilize dewlaps of smaller size and less conspicuous coloration than might be true if the species lived in areas with few predators. Only diurnal, visual predators would affect these displays.

Physical Characteristics of the Habitat

Ideally, a signal should stand out against the sender's background. Contrast can be obtained by coloration (e.g., anoles in shaded understories might have white or light-colored dewlaps) or by movement (e.g., display movements might be asynchronous with any rhythmically swaying vegetation in the habitat). In open habitat, where displays can be seen at great distances, gross head movements and sweeping extensions of a large dewlap would be more easily discerned by conspecifics with less chance of signal loss. On the other hand, a species in a dense habitat having a restricted line of sight would be displaying over short distances. Their displays would use subtle as well as gross display characteristics.

Social Function of the Display Type

When confronting syntopic congeners, shared signals for interspecific communication would be advantageous. Therefore, it seems reasonable that some modifiers and other elements of agonistic displays appearing interspecifically might be phylogenetically more conservative than signals involved in social encounters requiring species' recognition.

Male display types functioning in courtship would require a pattern for species recognition which contains strong, stereotyped elements unique to the species or population. The same requirement for species recognition would also be found in displays used for declaring territorial occupancy to conspecifics.

Some anoles use more than one display type during extended intraspecific aggressive encounters. These display types probably evolved from a single ancestral display pattern (e.g., a signature display pattern). By altering or adding elements to this pattern, a more extensive repertoire evolved. For species with extensive agonistic display repertoires, it would be expected that each display type would not be completely different from the others; a display type would share many permanent display elements with one or more of the other display types.

Based on observations of naturally occurring aggressive encounters of anoles, I would expect species with multiple agonistic display repertoires to perform these displays in a progressive fashion. Each successive display type would be more elaborate in the ritualized interaction than the previous type, except for that display type performed in closest proximity to the antagonist (within biting distance). This short-distance display would be the least elaborate type within the agonistic repertoire, being of brief duration, having little or no dewlap extension, and involving postures ready to receive or deliver an attack. In species with only one or two display types, ritualized jaw sparring might substitute for a formal short-distance display type.

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An annotated minimal list of references to guide the reader to bibliographies, terminology, techniques, descriptive information, and functional analyses dealing with lizard display behavior.

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The Acoustic Behavior of Lizards

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SUMMARY. The acoustic behavior of lizards is reviewed with emphasis on geckos. Many lizards emit sounds, but some geckos produce calls that have a consistent form and pattern and carry an intraspecific message. In the geckos, the subfamily *Gekkoninae* is the most vocal and emits calls in three basic categories: multiple chirps (MC), churrs, and squeaks. In general, hearing in lizards is less well developed than in a typical mammal, but within a restricted frequency range the acoustic sense may be as sensitive as that of mammals. The lizards with the most sensitive hearing are the geckos. The acoustic behavior of *Hemidactylus frenatus* is reviewed and compared to that of other gecko species. Similarities are found in (1) Type of calls produced; (2) contexts in which calls are emitted; (3) calling periodicity; and (4) structure of calls. The species specificity of the multiple chirp (MC) call of geckos is discussed and found to be population specific. Experiments on the functional significance of the MC call of *H. frenatus* indicate that it is implicated in territorial behavior.

The contexts and functions of visual displays of iguanid lizards and the acoustic displays of geckos are compared and significant similarities between the two are described.

INTRODUCTION

Bioacoustics has made remarkable strides during the last decade. Work has been done on a wide variety of animal types, principally arthropods and vertebrates. The majority of the vertebrate investigations have dealt with four groups: fish, amphibians, birds, and mammals. The acoustic behavior of reptiles had been little studied until the last few years when work was undertaken with crocodilians (Campbell, 1973; Garrick, 1975) and turtles (Campbell and Evans, 1972). Lizard vocal behavior, even that of the very vocal geckos, has been largely ignored until recently.

After a brief review of sound production and hearing in lizards and particularly geckos, I will describe some of my work on the acoustic behavior of *Hemidactylus frenatus*, including experiments on the functions of gecko calls. In conclusion, I will compare the vocal behavior of geckos with the visual displays of diurnal lizards.

LIZARD SOUND PRODUCTION

Sound production in reptiles has been recently reviewed by Gans and Maderson (1973). Sounds produced by lizards will be divided here into "vocalizations" and "other sounds." A "vocalization" will be defined as an oral explusion that can be modulated, reproduced consistently in form and pattern, and carries some intraspecific message. "Other sounds" will apply to any sounds that do not fit the above definition. Included in this category are hissing, roaring, integumentary sounds, and some forms of squeaks. Geckos are apparently unique among lizards in possessing vocal cords (Gans and Maderson, 1973).

Many species of lizards in a number of families produce sounds other than true vocalizations. Chameleons are reported to hiss when approached by a predator and to bark during intraspecific encounters (Rosen, 1950; Bustard, 1967*a*). Monitors hiss and squeal in similar contexts (Pianka, 1970; NZP Keepers, personal communications) and lacertids also squeal and hiss in response to predators (Falck, 1953; Simms, 1970; Klemmer, 1971; Vogel, 1973). Glass snakes have been reported to produce mewing sounds (Simmons, 1877) and day geckos (*Phelsuma*) have been heard to "purr like a kitten" (Demeter, personal communication). *Cnemidophorus tigris*, a teiid, can produce squeaks when handled (Campbell, 1966). Iguanids are also known to squeal and hiss in response to predators and during intraspecific interactions. *Gambelia w. wislizenii* (Weaver et al., 1966) and 13 species of *Anolis* (Milton, 1974) produce vocal sounds.

Until the recent work on *Anolis grahami* by Milton (1974), little or no quantitative or experimental work had been done on the structure, contexts, and functions of the sounds of iguanid lizards. Milton's work demonstrates that *Anolis grahami* can produce more than one type of sound, but the sounds are apparently an antipredation device and are incidental on the rare occasions when they occur during intraspecific interactions. In the terminology of the present paper, the sounds produced by *A. grahami* would be considered in the category "other sounds."

Integumentary sound production in lizards is known to occur in geckos of the genus *Teratoscincus*. These animals produce a hissing noise by rubbing caudal scales against one another. Werner (1967) has studied the morphology and regeneration of the caudal scales. The functional significance of the sound itself is not known.

In lizards, true vocalizations are probably found only in the family Gekkonidae. These animals have long been renowned for their vocal abilities (Smith, 1849; Evans, 1936; Mertens, 1946; Loveridge, 1947), and many have both common and scientific names that reflect these abilities. The generic name *Gekko* is intended to resemble the sound produced by these animals. Tokay, the common name for *Gekko gecko*, refers in Malay to the sound produced when the animal calls. The specific epithet in *Ptenopus garrulus*, also emphasizes the *vocal* nature of these animals.

Many species of geckos have been reported to produce sounds. Table 1 provides a partial list, with comments on the types of sounds produced. It has been suggested that all geckos vocalize (Werner, personal communication), and many more species could, no doubt, be added to the list. Species in the Eublepharinae are not very vocal, and animals such as *Coleonyx* and *Eublepharis* produce only squeaks and are not known to vocalize in the manner defined in this paper. *Phelsuma* and other diurnal geckos are also largely lacking in true vocalizations. The sounds produced by the members of the Eublepharinae and those of diurnal geckos are not known to fulfill any social function. True vocalizations are produced in only one subfamily of geckos. The Gekkoninae produce a variety of types of calls in three basic categories: multiple chirps, churrs, and squeaks. Some of these calls appear to be involved in intraspecific communication and meet all the criteria for true vocalizations.

As mentioned earlier, geckos are apparently unique among the lizards in possessing vocal cords (Gans and Maderson, 1973). Only one study has been done on the mechanism of sound production. Paulsen (1967) studied sound production in the distress call (churr) of the tokay gecko and noted that the sound was produced by passing air between tensed vocal cords that vibrate at right angles to the air stream. Dominant frequencies of the calls are between 40 and 200 Hz, with changes in frequency determined by the length of time the vocal cords lie in contact with each other.

Sound Reception in Lizards

Hearing in lizards has received a great deal of attention by Wever and his coworkers at Princeton (Peterson, 1966; Wever and Hepp-Reymond, 1967; Wever and Werner, 1970). A brief summary of the results of these investigations follows.

The work by Wever using cochlear potentials has shown that the acoustic apparatus in lizards is generally less sensitive than that

Table 1. Some geckos known to produce sounds with comments on the types of sounds produced.

Subfamily	Species	Sounds Produced	Authority
Eublepharinae	*Coleonyx variegatus*	Squeaks when handled	Greenberg, 1943
	Eublepharis macularis	" " "	Pers. Obs.
Diplodactylinae	*Nephrurus asper*	Churr when threatened	Bustard, 1967b
	Phyllurus platyurus	" " "	Mebs, 1973
Gekkoninae	*Artistelliger praesignis*	Multiple chirps + squeak	R. Crombie, Pers. Comm.
	A. nelsoni	" " "	" " " "
	A. lar	" " "	" " " "
	Cyrtodactylus kotschyi	Squeaks when handled	Y. Werner, Pers, Comm.
	Gymnodactylus kotschyi	Multiple chirps	Evans, 1936
	Gekko geko	Multiple chirps + churr	Many investigators
	Gekko chinensis	Multiple chirps	R. Crombie, Pers. Comm.
	Hemidactylus brooki	Multiple chirps + squeak	" " " "
	H. flaviviridis	" " "	Mahendra, 1936
	H. frenatus	" " squeak + churr	Marcellini, 1974
	H. mabouia	" " + squeak	R. Crombie, Pers. Comm.
	H. turcicus	" " "	Pers. Obs
	Phelsuma madagascarensis	Purring sounds + squeak	Keepers, NZP
	Phyllodactylus tuberculosus	Multiple chirps + squeak	Pers, Obs.
	Ptenopus garrulus	Multiple chirps	Haacke, 1969
	P. carpi	" "	" "
	P. kochi	" "	" "
	Ptychozoon kuhli	" " + squeak	Pers. Obs.
	Ptyodactylus hasselquistii	" " "	Frankenberg, 1974
	Stenodactylus sthenodactylus	Squeaks when handled	Y. Wener, Pers. Comm.
	Thecadactylus rapicauda	Multiple chirps + squeak	Pers. Obs.
	Tropiocolotes steudneri	Squeaks when handled	Y. Werner, Pers. Comm.
Sphaerodactylinae	*Sphaerodactylus sp.*	Squeaks when handled	R. Crombie, Pers. Comm.

of a typical mammalian ear, but within a restricted frequency range some species of lizards are comparable to many mammals. The range of sensitivity in lizards is from approximately 100 Hz to 10,000 Hz, and the greatest sensitivity is between 100 Hz to 3000 Hz. Of the lizards studied, the geckos *Coleonyx* and *Ptyodactylus* were found to have the most sensitive hearing. It is important to note that some members of other families of lizards have ears that are as sensitive as some geckos. *Crotaphytus collaris* and *Gerrhonotus multicarinatus* are two such nongekkonid lizards. One of the geckos, *Colenoyx variegatus*, with the most sensitive hearing is not very vocal, while the unusually vocal tokay gecko (*Gekko gecko*) has an acoustic sensitivity less than half that of *Coleonyx*. Factors other than the reception of intraspecific signals are obviously involved. For example, sensitive hearing might be valuable in *Coleonyx* as a mechanism of escaping predators in its desert environment.

Acoustic Behavior of *Hemidactylus frenatus*

The data concerning the acoustic behavior of *H. frenatus* have been published in detail (Marcellini, 1974). *Hemidactylus frenatus* has a vocal repertory of three functionally and physically distinct calls. The multiple-chirp call is the most common and is closely associated with agonistic behavior and territoriality (Fig. 1). The multiple-chirp has a consistent temporal pattern of chirps (Fig. 2), and the call rate varies directly with air temperature. When diel calling periodicity was investigated, the calls were observed to increase in frequency from dusk to the early morning hours (Fig. 3). Increasing call

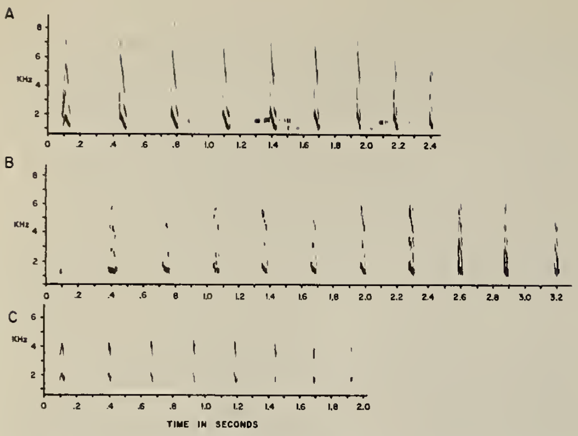

Figure 1. Sonagrams of the multiple chirp (MC) call of three adult male *Hemidactylus frenatus* recorded in Ciudad Vales, San Luis Potosi Mexico, March-May 1969. Fig. 1B is a recording of a captive animal and is completely free of background noise while Fig. 1A and C are sonagrams of calls of free-living geckos and show attendant background noise between the chirps.

counts were positively correlated with the number of active geckos. The churr call (Fig. 4) is an infrequently heard sound occurring only during aggressive encounters between males, and may function as a threat. The single chirp call is frequently heard, closely associated with distress, and may facilitate escape from predators (Fig. 4).

Types of Call Produced

Most calls mentioned in the early literature appear similar to the multiple chirp call of *H. frenatus* (Beebe, 1944; Schmidt and Inger, 1957; Brain, 1962; Petzold, 1965). The authors variously describe a series of chirps, barks, and clicks. Frankenberg (1974) and Haacke (1969), in their quanti-

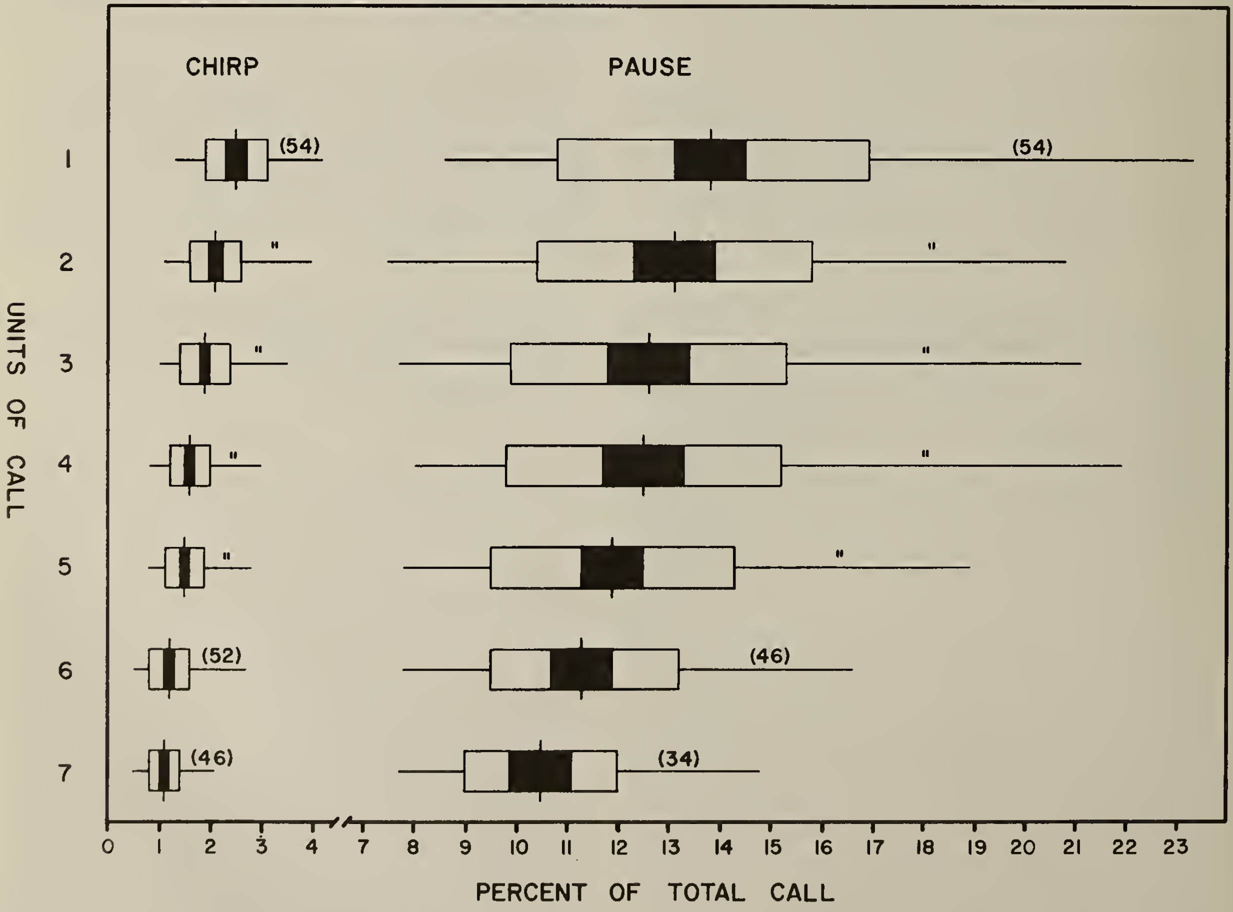

Figure 2. Duration of chirps and pauses of the multiple chirp call of *Hemidactylus frenatus* expressed as a percent of total call. Horizontal lines show observed ranges; rectangles mark standard deviation with solid black indicating 95 percent confidence intervals for the means. Mean values are indicated by vertical lines, and the number of records for each chirp and pause is shown in parentheses.

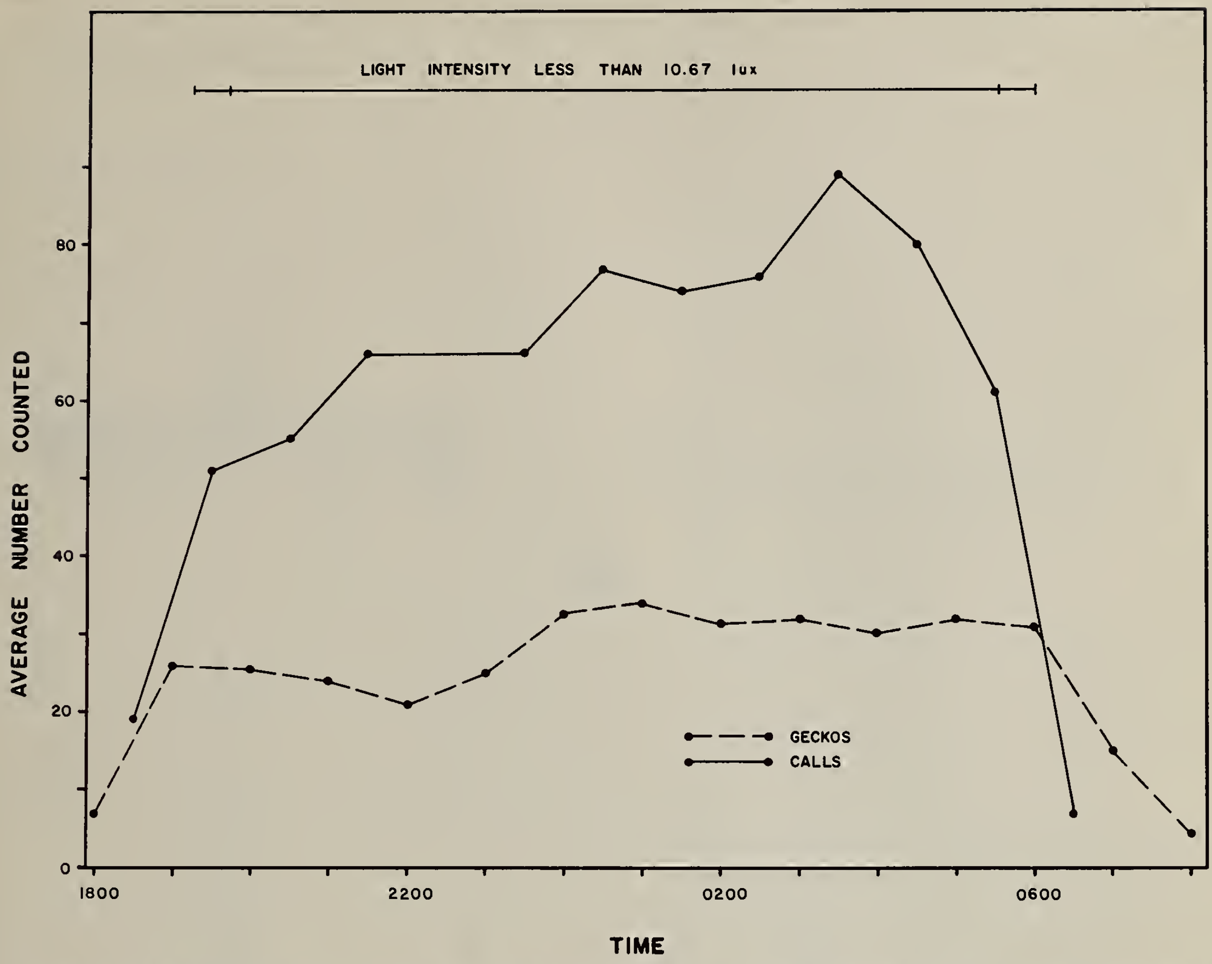

Figure 3. Mean number of multiple chirp calls of *Hemidactylus frenatus* per hour, mean hourly gecko census, and hours of light intensity less than 10.67 lux for 5 nights. Vertical lines on light intensity line indicate variation in time of sunset and sunrise.

tative studies, also discuss calls consisting of a series of clicks or chirps. Several of the authors cited above have also mentioned squeaks (single chirps), generally in response to rough handling. The churr call, or something akin to it, has been reported in *Gekko gecko* (Wever et al., 1963) and in *Nephrurus asper* (Bustard, 1967*b*). The churr has not been reported in other geckos, although this may be due to its low intensity and infrequent occurrence.

Contexts of Calls

The contexts of the multiple chirps are seldom mentioned in the literature. Haacke (1969) states that calls are produced when animals emerge from diurnal retreats. Frankenberg (1974) mentions that geckos may call in response to another animal's call. Curry-Lindahl (1961) states that *H. mabouia* call upon seeing their mates. Such statements and my own observations indicate that multiple chirp calls have varied contexts and are often associated with social behavior.

Single chirps occur in fewer contexts. Single chirps have been reported in response to rough handling (Mahendra, 1936; Greenberg, 1943; Frankenberg, 1974) or when an animal is bitten by a conspecific (Marcellini, 1974).

Published observations of churr calls indicate that they always occur as response to a

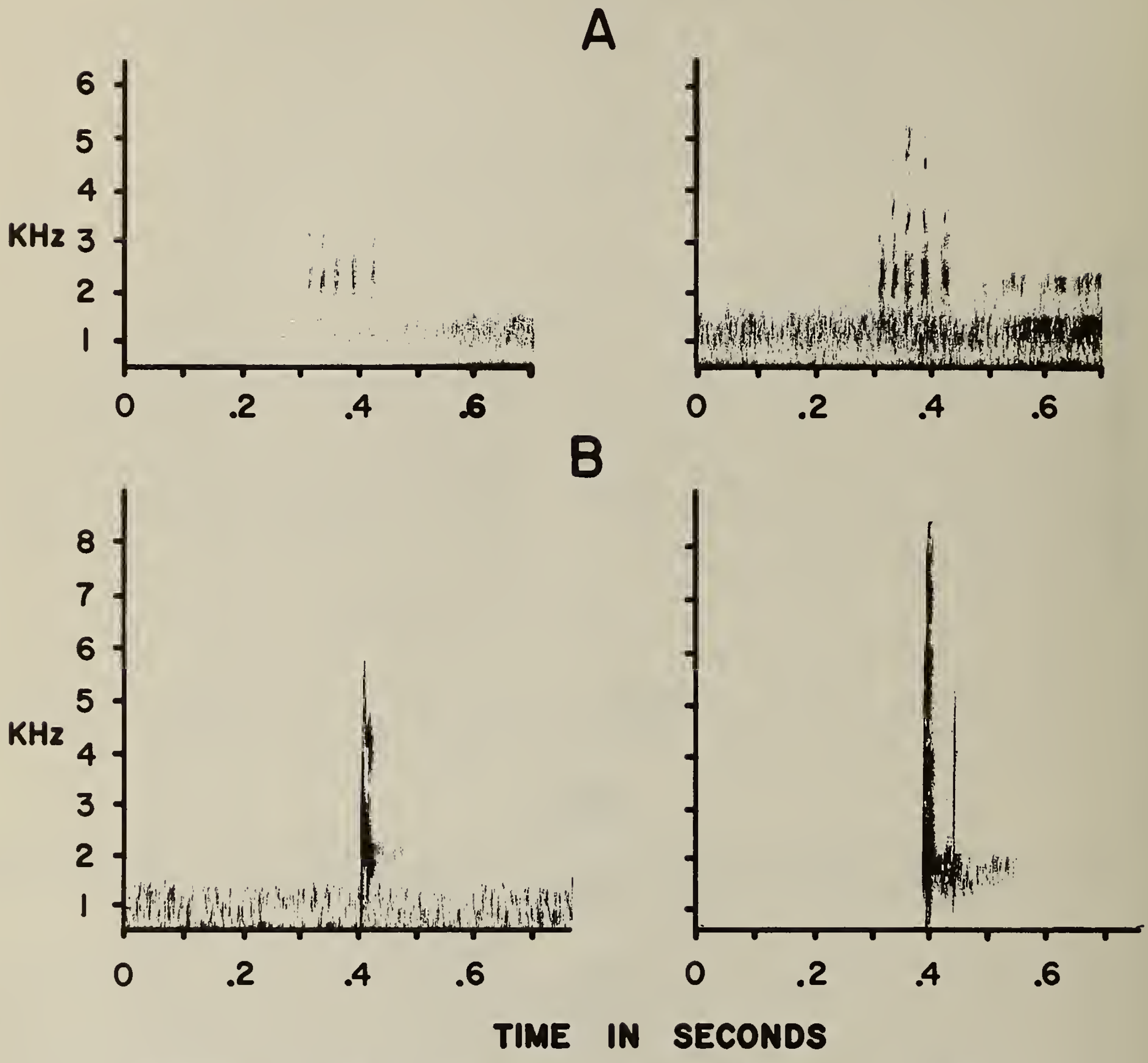

Figure 4. Sonagrams of churr calls (A) and single chirp calls (B) of *Hemidactylus frenatus.*

human "predator" (Wever, et al., 1963; Bustard, 1967*b*). I have observed that both *H. frenatus* and *Gekko gecko* use churrs during intraspecific aggressive interactions.

Age and Sexual Factors

The single chirp call has been reported to be produced by adults and juveniles of both sexes, but much more commonly by adults (Table 1). Churr calls have only been heard from adults. Although males are more prone to use this call, females can also produce them (Wever, et al., 1963; Bustard, 1967*b*; personal observation). Reports of multiple chirp calls in the literature have mentioned only adult male vocalizations (Haacke, 1969; Frankenberg, 1974). In *H. frenatus,* I have observed both adult male and female geckos making this call; it is produced more frequently by males. In summary, all three calls appear to be largely restricted to adults, with males being more vocal.

Calling Periodicity

In the remaining analysis of the vocalization of geckos, I shall deal only with multiple chirps. There are many references to gecko diel calling periodicity in the literature. Brain (1962) states that *Ptenopus garrulus* produces calls in the late afternoon that increase in frequency until sundown and then decrease during the night. Haacke (1969) agrees with Brain, but mentions that on some days occasional calls may be heard all day long. Evans (1936) described an increase in calling by *Gymnodactylus kotschyi* in the evening as the animals fed. Calling in *H. frenatus* is restricted during high winds and rain (Marcellini, 1974), whereas calling in *Ptenopus* is said to be stimulated by rain (Haacke, 1969). From the above, it is apparent that geckos call most commonly when light intensities are low, especially at dusk.

Description of Calls

Comparative information about multiple chirp calls have been largely provided by three investigators (Haacke, 1969; Frankenberg, 1974; Marcellini, 1974). The loudness of multiple chirp calls ranges from the very low intensity sounds of *Phyllodactylus tuberculosus* that can only be heard from a few meters to those of *Gekko gecko* that can be heard from 200 m and more (personal observations). The loudness of the calls of some small species is impressive, the calls of *Ptyodactylus hasselquistii* and *H. frenatus* being discernible from 50 to 100 m (Frankenberg, 1974; Marcellini, 1974).

The frequency range of multiple chirp calls ranges from 500 to 10,000 Hz; dominant frequencies are usually between 500 to 6000 Hz. The lowest dominant frequency has been recorded from *Gekko gecko* (personal observations), the highest from *Ptyodactylus*.

The number of chirps per call is variable within individuals (Marcellini, 1974), between subspecies (Frankenberg, 1974) and between species (Haacke, 1969). The call rate is also highly variable, ranging from a low of 0.5 chirps per second for *Gekko gecko* to nearly 9.0 per second for *Ptenopus* (Haacke, 1969). The number of chirps and call rate appears to be dependent on the animal's "emotional" state, and may also be affected by the environmental temperature (Marcellini, 1974). Haacke (1969) demonstrated that midnight and morning were slower than those of the evening when temperatures were higher. Frankenberg (1974) found no direct correlation between the rate of calls and fluctuating temperature and observed an overall increase in call rate with a rise in temperature. An effect of temperature on call rate might be expected in view of findings on insects and anurans (review by Frings and Frings, 1962; Blair, 1963).

Temporal patterns with respect to clicks and pauses of gecko calls have been reported. Haacke (1969) recognizes a consistent pattern in the calls of *Ptenopus garrulus*. Frankenberg (1974) has also shown pattern consistency in *Ptyodactylus*. These data and the findings on *H. frenatus* (Marcellini, 1974) indicate that geckos have consistent, reproducible, temporal patterns in their multiple chirp calls.

Species Specificity of Gecko Multiple Chirp Calls

Calls produced by an individual may vary in number of chirps but are remarkably uniform in structure (Frankenberg, 1974; Marcellini, 1974). Frankenberg has reported change in individual call structure of *Ptyodactylus* in different contexts. Male-male calls differ from male-female calls in being more protracted, although chirps are similar in structure and frequency. Haacke (1969) describes two distinct calls in one population of *Ptenopus garrulus* that may also be contextually related.

Haacke (1969) shows two types of calls differing in number of chirps and temporal pattern, within the *Ptenopus garrulus maculatus* subspecies. Haacke also describes differences in number of chirps per call in animals on opposite sides of a 150 m wide sand dune. Frankenberg (1974), on the other hand, found calls within a subspecies to be remarkably consistent and distinctive for that subspecies.

Variation of calls between species has been mentioned by Haacke (1969) who states that each species of *Ptenopus* has a different call that can be recognized by differing call rates and number of chirps per call. Werner (1965), in his study of *Ptyodactylus* in Israel, states that the males of two species produce different calls.

Figure 5 shows sonograms of male *Hemidactylus frenatus. H. turcicus*, and *Phyllodactylus tuberculosus* recorded at approximately the same temperature. In the sonogram of *H. turcicus*, the calls of two individuals are superimposed; only the stronger five-chirp call should be focused on. Species differences in duration of pauses and chirps, intensity pattern of chirps, and physical characteristics of the chirps are apparent. The call of *H. turcicus* has longer pauses and a concomitant lower call rate than those of the other two species. In *H. frenatus* and *H. turcicus*, the individual chirps appear to decrease in intensity from first to last. The dominant frequency of the calls is approximately the same, but harmonics for *H. turcicus* are much closer together than those for *H. frenatus*.

Table 2 gives the call parameters for 9 species and subspecies of geckos. Although the sample sizes are small, there are evident differences between species and subspecies in all three parameters of the call. *Ptenopus kochi* and *P. hasselquistii guttatus* and *P. h. puiseuxi* differ in dominant frequency and call rate. *Gekko gecko* appears to have a lower dominant frequency and slower call rate than the other geckos.

Although the calls of many species and subspecies of geckos differ in many respects, it would be premature to postulate taxon-specific calls on the basis of the limited observations. More data are needed in order to determine quantitatively the degree of variation within individuals, between populations, subspecies, and species. When such data are available, we may be able to utilize acoustic behavior in conjunction with other evidence to solve taxonomic problems.

Functional Significance of the Multiple Chirp Call of *Hemidactylus frenatus*

I have made observations on the functional significance of the multiple chirp call of *H. frenatus* utilizing an experimental procedure in which individual females and males were exposed to the male multiple chirp in a choice situation (Marcellini, 1977). Females made no directed response to the male multiple chirp call, and seemed weakly stimulated to move (Table 3). Males gave a significant negative response to the call and were more active (Table 4), indicating that the call might function to establish and maintain territories.

Comparison of Visual and Acoustic Displays

Adaptation to a nocturnal existence by gekkonid lizards required a number of changes in their behavior and ecology. One important change involved display behavior. Lizards ancestral to geckos, were, no doubt, diurnal (Underwood, 1954; Kluge, 1967) and, like modern iguanids and agamids, probably utilized visual channels for intraspecific communication. Residual parts of these displays can still be seen even in nocturnal geckos. *Hemidactylus frenatus* postures during close-range encounters between individuals.

Males in high intensity aggressive encounters hold their head low and their back arched as they approach an antagonist. Other nocturnal geckos such as *Phyllurus platurus*, *Teratoscincus scincus*, and *Nephrurus asper* are known to have visual components in their threat displays (Mebs, 1966, 1973; Bustard, 1967*b*). The limited usefulness of visual displays for distance communication

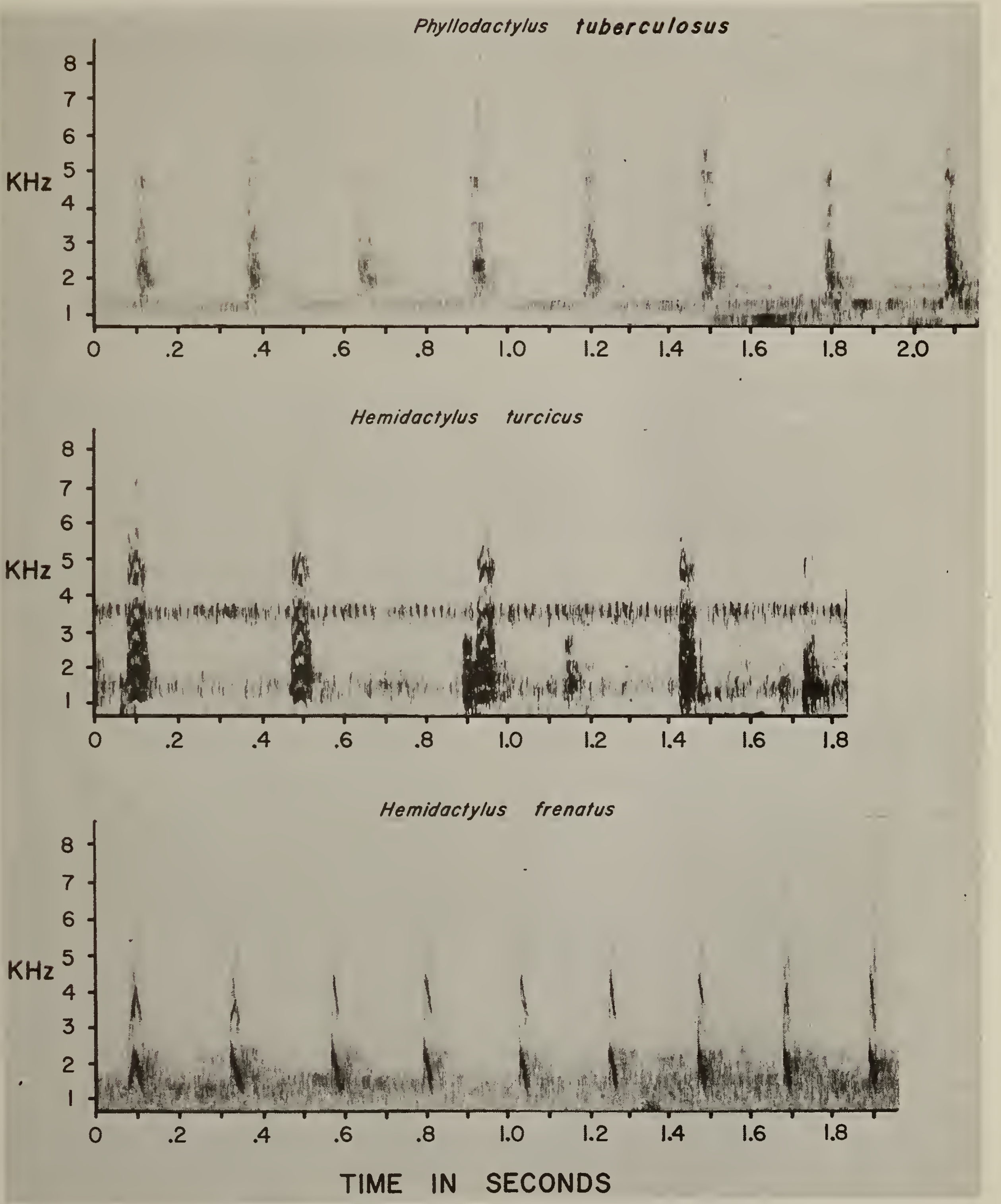

Figure 5. Sonagrams of the multiple chirp call of the Mexican geckos *Phyllodactylus tuberculosus*, *Hemidactylus turcicus*, and *Hemidactylus frenatus*.

Table 2. Comparison of call parameters for 9 species and subspecies of geckos.

Species and Subspecies* (Number of vocalizations)	Number of Chirps Mean (Range)	Dominant Frequency From Sonagrams Hz	Mean Call Rate Chirps Per Second
Hemidactylus frenatus (143)	9 (5–15)	1000–2000	4.51
H. turcicus (7)	13 (7–17)	1500–2000	approx. 3
Phyllodactylus tuberculosus (10)	7 (5–9)	2000–2500	3.5
Ptenopus garrulus (262)	6 (3–9)	3000–4000	5.5
P. kochi (27)	11 (9–16)	3000–4000	8.9
Ptyodactylus hasselquistii guttatus ♂ + ♂ (13)	12 (11–14)	3000–4000	1.2
P. hasselquistii guttatus ♂ + ♀ (5)	9	4000–6000	slower than ♂ + ♂
P. hasselquistii puiseuxi ♂ + ♀ (7)	5 (2–9)	4000–6000	1.5
Gekko gecko (3)	(9–10)	500–2000	0.5

* *Hemidactylus*, *Gekko* and *Phyllodactylus* data from author, *Ptenopus* data from Haacke, 1969 and *Ptyodactylus* data from Frankenberg, 1974.

Table 3. Responses of female *Hemidactylus frenatus* to a recorded male call with statistical evaluation of results.

Trial	Responses		
	Toward	Away	No Choice
1	7	4	8
2	4	8	6
1 + 2	11	12	14

Table 4. Responses of male *Hemidactylus frenatus* to a recorded male call and to white noise with statistical evaluation of results.

Experiment	Responses		
Male Call	Toward	Away	No Choice
Trial 1	4	12*	2
Trial 2	6	12	
1 + 2	10	24**	2
White Noise	Toward	Away	No Choice
Trial 1	6	8	3
Trial 2	6	7	2
1 + 2	12	15	5

* Significant deviation from expected; $P<0.05$
** Significant deviation from expected; $P<0.25$

in nocturnal lizards has resulted in a dependence on acoustic displays in many species of geckos. Diurnal geckos are believed to have evolved from nocturnal forms (Underwood, 1954; Kluge, 1967) and have secondarily reverted to visual displays, including posturing and head movements (Kastle, 1964).

Table 5 compares visual displays of the iguanid lizards, *Anolis nebulosis* and *Uta stansburiana*, and the vocal displays of a gecko, *Hemidactylus frenatus*. The two iguanids were chosen because their display behavior is well known and they appear to represent extremes in complexity of iguanid lizard display behavior.

It is my supposition that the behaviors of the two iguanids are contextually similar and that some of the same things are being accomplished by the displays, the difference being that *Anolis* seems to exercise more variety and utilizes an additional part of its body (dewlap) in its displays. Allowing for such disparities, we may compare the contextual and functional similarities between visual and acoustic displays.

The single chirp has no apparent analog in visual displays, but, as discussed previously, nongekkonid lizards are known to produce squeaks when threatened or handled roughly, demonstrating a similarity with geckos in this behavior.

The churr call of *H. frenatus* has been shown to be associated with high-intensity aggressive encounters. At first, it might appear to function as a challenge display, but it is only used when an attack is occurring and not at a distance. The churr may function as an acoustic component of the aggres-

Table 5. Comparison between visual display behavior of two species of iguanid lizard with the vocal display behavior of a gecko.

*Anolis nebulosus**	*Uta stansburiana*	*Hemidactylus frenatus*
Assertion Performed by: Males, Females, Subadults Juveniles and hatchlings. Contexts: Males; when stopping at new perch sites, upon sighting another male, upon sighting a female, before and during courtship, after courtship. Females; when approached by another female, when approached by a male, when approached by a courting male. Suggested Functions: Warning to other lizards that area occupied. Attract females Specificity: Population specific.	Assertion Performed by: Males, Females, Hatchlings, Juveniles, Subadults. Contexts: Males; when stopping at new perch sites, when sighting another male, when sighting a female, before and during courtship, after feeding. Females; when approached by another female, when approached by a courting male, after feeding. Suggested Functions: Warning to other lizards that area occupied. Attract females Specificity: Population specific.	Multiple Chirp Performed by: Males, Females Contexts: Males; when emerging from diurnal retreats, during movements, when sighting another male, when sighting a female, before courtship, after courtship, after feeding, after defication. Females; when sighting another female, when emerging from diurnal retreats, after courtship. Suggested Functions: Warning to other lizards that area occupied. Attract females Specificity: Population specific.
Challenge Display Performed by: Males, Occasionally adult females. Contexts: During close range aggressive encounters. Suggested Functions: Intimidation. Specificity: Highly variable.	Challenge Display Performed by: Males Contexts: During close range aggressive encounters between males. Suggested Functions: Intimidation. Specificity: Population specific.	Churr Performed by: Males. Contexts: During high intensity aggressive encounters. Suggested Functions: Intimidation Specificity: Probably not specific.
Flagging Performed by: Males and Females. Contexts: Males; when sighting another male, when seeing a female display, when approached by a female. Females; when approached by another female, when displayed at by a courting male, when being mounted by a male. Suggested Functions: Advertise presence. Specificity: Color of dewlap specific but display variable.	Courtship Nods Performed by: Males Contexts: During close approach to female prior to copulation. Suggested Functions: Calm female. Recognition that it is a courting male. Specificity: Not specific.	Single Chirp Performed by: Males, Females and large Juveniles. Contexts: During rough handling, when bitten by another lizard. Suggested Functions: Startle predator aiding escape. Release call? Specificity: Probably not specific.
Flagging Plus Assertion Performed by: Males and Females. Contexts: Males when approached by females. Females; when courted by males, during copulation. Suggested Functions: Combination of above.		
Courtship Nods Performed by: Males Contexts: During close approach to female prior to copulation. Suggested Functions: Calm female. Recognition that it is a courting male. Specificity: Not specific.		

* *Anolis nebulosus* data from Jenssen, 1969; *Uta* data from Ferguson, 1971 and personal observations; *Hemidactylus* data from authors work.

Table 6. Some significant contributions to the literature on gekkonid acoustic behavior.

Author and Year	Taxon	Findings
Frankenberg, E. 1974	*Ptyodactylus* sp.	Calls of 3 forms of *Ptyodactylus* analyzed. Calls consisted of a series of clicks. Male to male calls differed from male to female calls.
Gans, C. & Manderson, P.F.A. 1973	Many reptiles	Review of literature on reptilia sound production with comments on gecko sound producing mechanisms.
Haacke, W.D. 1969	*Ptenopus* sp.	Calls of 3 species of *Ptenopus* analyzed and each has a different call. Calls consist of a series of clicks. Certain populations of some species may have more than one type of call.
Marcellini, D.L. 1974	*Hemidactylus frenatus*	*H. Frenatus* has three types of calls. Multiple chirp, single chirp and churr. These calls appear to perform different functions. Call rate varies directly with temperature.
Peterson, E.A. 1966	Many species both gekkonid and non-gekkonid	Hearing sensitivity of 13 species analyzed. The lizards with the most sensitive ears were generally the geckos, but some other lizards have ears that are as sensitive as some geckos.
Werner, Y.L. 1965	*Ptyodactylus* sp.	The call of *Ptyodactylus* consists of a series of barks. Some subspecies have differing calls.

sive face-off posture, signaling that attack is imminent. But, it does not appear to have a direct analog in visual display behavior.

Milton (1974) has pointed out that *Anolis grahami* produces sounds during intraspecific conflicts. These sounds are contextually and structurally similar to churr calls of *H. frenatus.*

The multiple chirp call appears to be similar in function to much of the display behavior of the two iguanid species. As in most visual displays, it is emitted predominantly by males in situations associated with the visual assertion and challenge displays of iguanids.

Hemidactylus frenatus and other nocturnal geckos have not been shown to possess anything comparable to the courtship needs of iguanid lizards. Diurnal geckos, such as *Phelsuma,* however, perform head movements when courting a female at close range (Kastle, 1964). In the diurnal species, the visual display seems to have the effect of keeping the female from running away. In nocturnal lizards, on the contrary, the male can approach closely without being seen, rush the female, and mate with her. In *H. frenatus* no close-range courtship behavior was seen. Males approached to within a few feet, then rushed the female, obtained a neck grip, and copulated.

That acoustic and visual displays of lizards show analogies is not surprising. The two groups presumably had a common ancestry, and they have similarities in their population ecology that is reflected in comparable social systems in which similar messages are conveyed.

Social messages can apparently be transmitted equally well by visual or acoustic systems. Both systems allow a great diversity of messages, one providing variations in color, pattern and movement, the other, differences in frequency, intensity, and pattern. The systems have the capacity for producing stereotyped, reproducible messages. Both channels can function well as directional systems and both afford rapid transmission over considerable distances. The major difference is that the visual system is dependent on light and the absence of intervening barriers.

The common aspects of visual and acoustic displays of lizards indicate that a knowledge of the literature concerning both types of displays is important to a researcher in either area of lizard behavior.

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Social and Feeding Behavior in *Varanus Komodoensis*

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SUMMARY. The social and feeding behavior of the Komodo monitor (*Varanus komodoensis*) is described and shown to differ significantly from that of iguanid and agamid lizards. Scent plays a major role in individual and sexual recognition and carrion location, as well as in prey ambush and stalking. Population density, activity ranges, and territoriality are discussed with respect to intraspecies interactions. Communicative and display behavior related to spacing and social hierarchy phenomena are influenced by visual, olfactory, tactile, and auditory factors. Territorial behavior is related to the size and sex of the animals and ranges from exclusive use by large, resident, sexually mature males to complete lack of established ranges among the smaller members of the population.

Komodo monitors are opportunistic carnivores, the adults feeding on live prey or carrion ranging in size from insects to water buffalos. The species is behaviorally and morphologically adapted to ingest as much food as possible in the shortest time. Adults are highly successful predators of live animals, either from ambush or by stalking, and feed largely on deer.

Evidence is presented that there is pair bonding of some large mature monitors. Activity ranges of male and female pair members overlap broadly; that the individuals recognize one another seems assured. Ritualized courtship behavior occurs at every meeting. Most courtship and mating takes place at carrion feeding sites.

INTRODUCTION

Most of what we know about lizard behavior is limited to species of the families Iguanidae and Agamidae. Consequently the behavioral patterns of these two groups are often taken as representative of lizards in general.

The present account focuses on the social and feeding behavior of the Komodo monitor or ora (*Varanus komodoensis*), based on a 13-month field study conducted on the islands of Komodo and Padar (July, 1969-June, 1970 and August, 1972) and Flores (June-July, 1971), Lesser Sunda Group, Republic of Indonesia.

The species is believed to be near the evolutionary base of the family Varanidae (Mertens, 1942). None of the species comprising the family is well known behaviorally, mainly because (1) most varanid species attain large size and are difficult to maintain under laboratory conditions, and (2) population densities tend to be low in the wild.

HABITAT

The behavioral repertoire of poikilothermic animals depends on the limitations and opportunities of the habitat, as well as on the morphologic and physiological characteristics of the species.

The most important environmental influence on *V. komodoensis* is the open, savanna type habitat. Thus, insolation is high, and *V. komodoensis* is normally subjected to great heat loads. Forests at the lower elevations are deciduous, monsoon types. The major problem faced by larger specimens, and perhaps also by the smaller animals, is ridding the body of excess heat (McNab and Auffenberg, 1976). This physiological problem continually interferes with daily behavioral patterns unrelated to thermoregulation (Auffenberg, 1970, 1974). Typically, individuals are awake from approximately 4:30 to as late as 23:30 hours. However, the pattern is *bimodal,* with activity peaks at about 9:30 and 15:30 hours.

The annual precipitation pattern is seasonal, and the total amount of rain is small. These are very important features with respect to both shelter and prey.

THE ANIMAL

Perhaps the most significant physical factor affecting the behavior of the adult Komodo monitor is its great size. The average total length of 49 cm for hatchlings is considerably longer than the adult length of most lizards. Adults reach a length of slightly over 3 m and a weight of 60 kg in the wild; in captivity, they are sometimes unnaturally obese. The teeth are highly adapted for cutting flesh, being large, compressed laterally, and provided with serrations on the posterior edge. The claws are large, strong, recurved, and sharp. As in most monitor species, the tail is heavy and long, provided with effective muscular control, and often used as a defensive weapon. Combined, these physical characteristics enhance the potential for inflicting serious injury during intraspecific coaction and for killing large prey.

Komodo monitors are capable of running quadrupedally at speeds approaching 30 km/hr and are able to sustain such locomotion for distances of nearly 1 km. On occasion, individuals move bipedally, although they do not move far or fast by this means. They are effective climbers, reaching heights of 20 m (particularly the young); are strong swimmers, having been observed as far as 4 km from shore; are reasonably effective divers, having been found as much as 2 m below the surface; and are capable of excavating burrows of up to 10 m in length.

The accessory olfactory and visual systems are quite well developed in Varanids (Northcutt, this volume). Age and sex recognition seem to be based more on chemical cues than on color, form, or movement. The skin colors and patterns of this species are largely cryptic and thus important in predatory behavior and hiding.

Studies by Bartholomew and Tucker (1964) have shown that a closely related varanid species (*V. varius*) has a remarkably high metabolic rate for a reptile. Core temperatures of *V. komodoensis* are also high (37–39.5 C, McNab and Auffenberg, 1976). The heart has a more complete ventricular septum than any other lizard studied so far (Meinertz, 1952; Vorstman, 1933), which assures less mixing of oxygenated and unoxygenated blood. Such physical and physiological characteristics provide *V. komodoensis* with the potential for complex behavioral patterns.

TERRITORIES

Behavioral data to be described are based largely on observations made from blinds erected in different parts of the study areas. One hundred and ten animals were captured and marked with numbered plastic tags attached to the skin, and the same identification number was painted in large size on one side of the body for identification from a distance. Sex, weight, general condition, and other data were obtained during initial and subsequent processing.

Population Density

Results of marking-resighting studies suggest that in all habitats there is an average of 8.8 Komodo monitors/km^2. Densities vary with habitat and geography (Table 1).

There are varieties of area tenure patterns in the Komodo monitor which appear to be largely size and sex dependent. These patterns range from exclusive use of a territory (core area) by large, sexually mature males, to complete lack of established ranges, particularly in the smaller members of the population.

Table 1. Population parameters of adult *Varanus komodoensis* (Komodo only)

Habitat type	Approximate Area (Km^2)	Approximate Monitor Population/ Km^2
Tropical deciduous forest	57	14
Forest—savanna ecotone	10	16
Savanna	103	9
Tropical steppe	60	6

Table 2. Size and sex of transient and resident *V. komodoensis* in the southern part of Loho Liang, Komodo, 1969–1970.

Sizes Classes (Total length in mm)	Residents (freq. and sex)		Transients (freq. and sex)
1.1–1.5	M	1	12
	F	0	5
1.6–2.0	M	1	14
	F	2	2
2.1–2.25	M	1	4
	F	1	1
2.6–3.0	M	1	0
	F	0	0
Totals		7	38

Core Areas

Most studies of carnivorous lizards show that individuals spend approximately half their time in a fairly small core area (Rand, 1967), compared to the total area visited during the course of a day. The core area is that part of the total range most heavily used and has the least overlap with ranges of other individuals of the same species.

The core area for a mature Komodo monitor is where it spends most of its time and in which it is concerned with predation on live animals and maintenance of the pair bond. Often included within the core area are one or more knolls or hills extensively used by the resident. Collectively these sites constitute the activity center of the individual's core area and are important in thermoregulatory behavior and surveillance.

Few individuals (described below) were found to have activity patterns fitting the definition of core area, at least when applied to a time period of several months. The Komodo Island population is comprised of many transient and relatively few resident individuals. Only a few of the 300 individuals observed in our Komodo study area were regularly seen during the study period. Most remained in the area from only a few days to a few weeks. All residents were large adults, while transients included the whole range, from hatchlings to unusually large animals (Table 2). Almost none of the transients were adult females. Thus, the transients (including many mature males) represented a dynamic faction in the local population, with new individuals constantly entering new areas and interacting with residents and other transients.

The core areas of resident male and female adults often broadly overlapped. In such cases there is believed to be a pair bond (see below). Core area overlap of presumably pair-bonded individuals was estimated as nearly 80 percent in the two cases for which sufficient data were available. Overlap between nonpair-bonded individuals ($n=27$) is 5.7 percent.

Although adult male oras generally stay within their mutually exclusive core areas, they are often seen in one another's scavenging ranges (see below). The fact that carrion occurs within the core area of a resident adult male does not discourage intrusion of the core by nonresidents of any sex or size.

Because all long-term residents of established core areas are adults, it can be presumed that residency does not normally occur until the individuals are at least 7 years old. Evidence suggests that some large *V. komodoensis* may live around one core area for periods as long as 25 to 40 years (Auffenberg, MS). Unfortunately, it is not known how residency is established or lost, or what behavioral and physical characteristics enable certain individuals to become residents. Presumably aggression plays a major role.

Residency confers certain advantages. Long residency enables the individuals to learn shelter locations (often difficult to find for individuals this size), waterholes, sentinal sites, and the location and activity cycles of prey animals. The overlapping core areas of adult males and females certainly confer reproductive advantages.

Activity Range

Tracking studies on Komodo show that adults may move as much as 10 km/day, although the mean is 1.8 km/day.

The activity (foraging) range (mean area=4.2 km^2) extends from 2 to 4 km in several directions from this central area, over which the resident tends to move fairly regularly, but not on a daily basis (Fig. 2). Such a large area makes the definition of an activity range difficult.

In most species studied so far the shape of the activity range appears determined by the distribution of prey (or sites from which it can be monitored) and the interrelationship of territorial boundaries established by individuals comprising the population (Fig. 3). Typically, most lizards patrol all the principal perches or monitoring sites at least once a day.

The activity range of both transient and resident individuals includes a core area, with some type of shelter such as a burrow, rock pile, or hollow tree. The size of the daily activity range reflects the extent of a feeding foray (Figs. 1, 2). Its size and shape depend upon the type of prey sought, the local topography, and the size of the foraging individual (see Table 3).

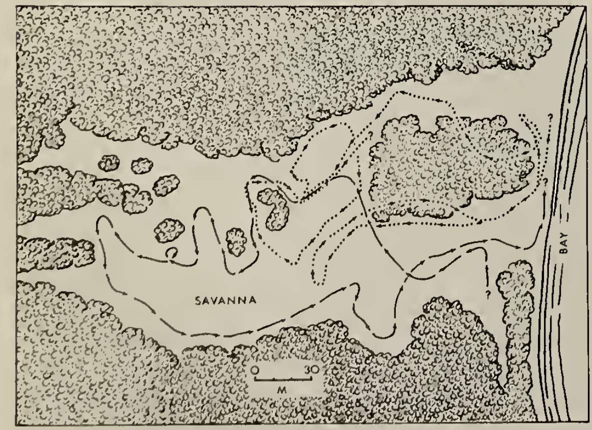


Figure 1. Typical diel foraging pattern of 1 m long *Varanus komodoensis*, Nov. 20 (dashes) and Nov. 23 (dots) in Loho Liang savanna, Komodo.

Scavenging Range

The scavenging range is superimposed on the activity ranges of many resident and transient oras. When carrion is available, the typical foraging patterns are abandoned and resident monitors may leave their regular core areas for distances as great as 8 km. Along with transients, they may pass through foraging ranges and even core areas of other oras. Aggregations of monitors at carrion are thus composed of individuals unfamiliar to one another, having experienced no encounters in overlapping hunting ranges. Since meeting of strangers is the rule, there is a high level of social interaction (see below). When the carrion meal is completed, the larger residents return to their core areas while transients continue to wander.

TERRITORIAL BEHAVIOR

It is not known to what extent, if at all, *Varanus komodoensis* is territorial. No aggressive behavior was seen at the edges or within core areas. The distribution of in-

Table 3. Monitor size forage area (in M^2) and proportionate forage area.

Monitor Size Classes (Total l. in m)	Forage Area (in m^2)	Forage Area/ Body Area*
1.1–1.5	1,863 ± 148	7,165
1.6–2.0	58,900 ± 1330	109,074
2.1–2.5	336,040 ± 8677	292,209
2.6–3.0	1,008,000 ± 3,400	514,285

* Total length X greatest width

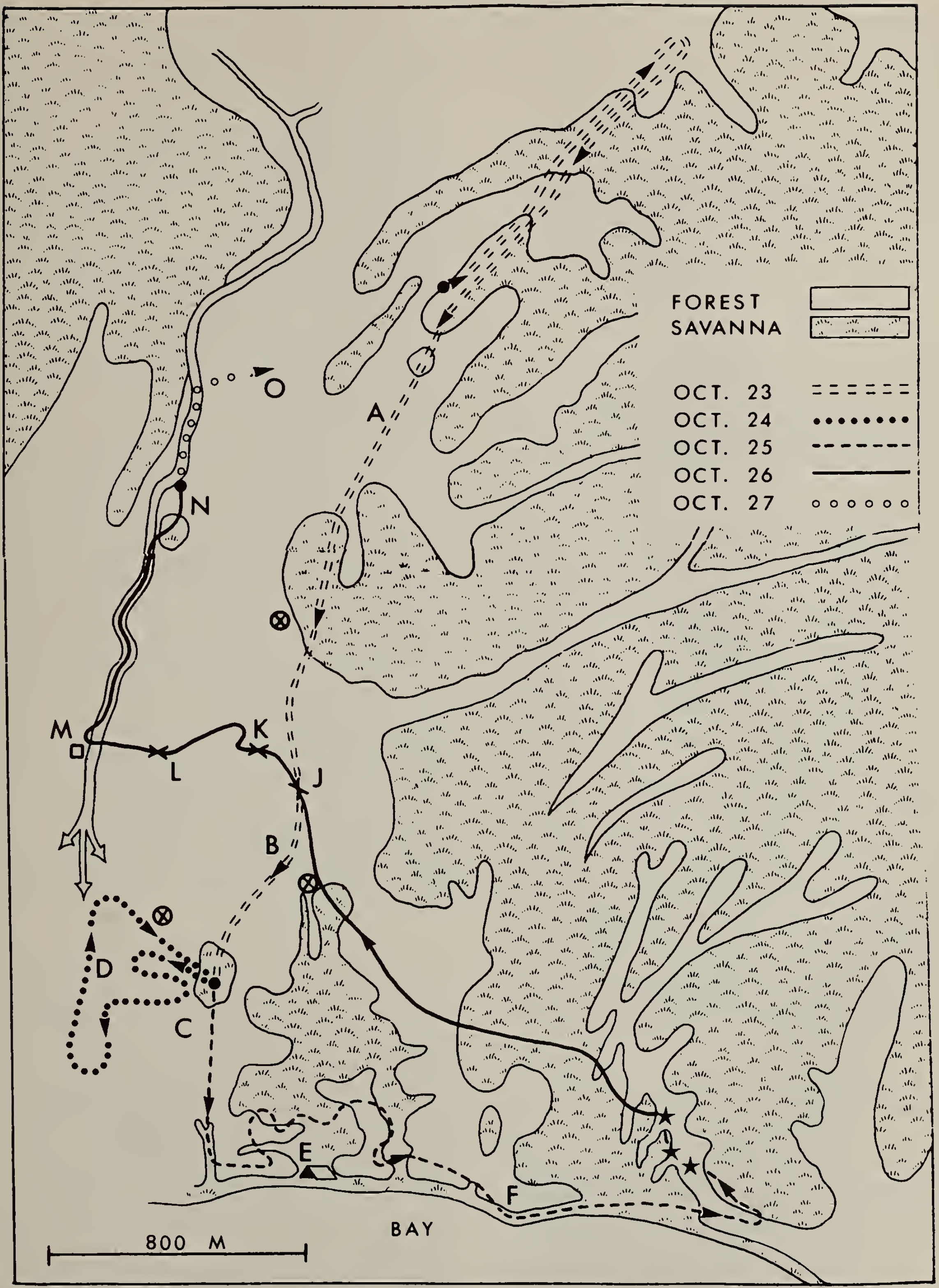


Figure 2. Typical foraging pattern of 2½ m *V. komodoensis* during a period of 5 days, Loho Liang forest and savanna, Komodo.

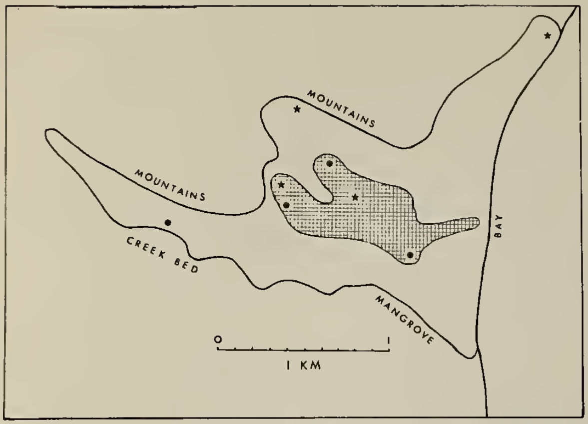


Figure 3. Core (cross-hatched) and foraging (clear) ranges for 19W, a 2.8 m resident male *V. komodoensis*, Loho Liang, Komodo. Stars show location of thermoregulatory sites, dots are commonly used shelters. Boundary features indicated.

dividuals suggests that the core areas are infrequently trespassed. If there is a territorial system, it is probably less rigid than that observed in the iguanids. The activity areas are large and defense of the entire boundary would be difficult.

The fact that the region around the core area is heavily forested and hilly in some places suggests that vision compared with scent plays a minor role in monitoring the presence of intruders. In all our encounters (n=415) with walking Komodo monitors, none was seen in pairs or aggregations, except at food. Hunting is apparently a solitary activity. Meetings between hunting monitors are probably rare, due to low density. In fact, meetings may be avoided so as not to provoke aggression. In the Komodo monitor, spacing is regulated by auditory, olfactory, tactile, and visual communication.

Olfactory and Related Communication

Some chemical cues used by Komodo monitors (such as those providing sexual identification during courtship) are immediate. But others (such as fecal pellets) may indicate a past event (that is, the passage of an individual in that area). It may also indicate a future encounter (possible aggression from another individual in the same area).

Accumulations of fecal pellets are often found near the sentinal sites, where residents regularly spend the night in very specific areas (see below). Early morning basking normally occurs close to these sleeping areas. The fecal pellets of residents are usually deposited just after they have attained optimal core temperature and before they begin their search for food. Thus most pellets are deposited at the basking area (Fig. 4). The few rains that fall on Komodo ensure that the fecal material at these dunging sites remains for many months. Fecal pellets are also often deposited along game trails and dry creek beds where monitors go daily in search of food (Fig. 5).

A fecal pellet in the path of an individual usually elicits much investigative behavior. There is frequent tongue flicking and circling around the pellet. At such times juveniles often present an appeasement display (see below). There is, in fact, so much interest in the pellets that I am led to the conclusion that they constitute an important source of information regarding the sex, age, and breeding condition of another lizard.

Olfactory cues have a quality of persistence. Olfacients associated with the fecal pellets deposited on the ground have a chance for surviving a longer time than odors released into the air. I believe that in the scent-oriented Komodo monitor, social integration is accomplished largely by fecal

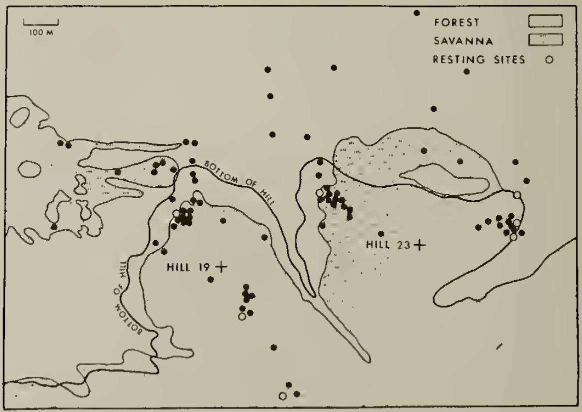


Figure 4. Fecal pellet distribution on Hills 19 and 23, Loho Liang, Komodo, showing concentration near thermoregulatory sites. (hollow circles).

Table 4. Communication types important in social and feeding behavior of Komodo monitors.

Sensory type	Stimulus	Response	Probable Communicatory Function
Chemical	Fecal odor	Investigatory behavior	Sexual maturity, individual identification, density, dominance odors, territorial, and home-range markers.
	Body surface olfacients	Investigatory behavior which may lead to avoidance, courtship, or other behavior	Sexual maturity and individual identification.
Tactile	Casual bodily contact	Remaining close, nonaggressive contact, or alarm behavior (stress or flight)	
	Body scratching (by male)	Nil, aggression, or alarm behavior	May serve to quiet the female by indicating the male's intent to breed rather than fight.
	Mounting	Nil, aggression, or alarm behavior	May serve to quiet the female by indicating the male's intent to breed rather than fight.
	Tail invitational movements	Attempts to insert hemipenis	Communicates female's intent to mate rather than flee or fight.
	Neck biting	Restrains female movement	Perhaps no communication except indirectly to indicate male's readiness to mate.
Visual	Stress reaction	Usually nil if not combined with other cues	Introduction to an important, perhaps aggressive, display.
	Weaponry exhibition or low level threat	Usually avoidance behavior, sometimes threat or flight	Prelude to potential territorial conflict.
	Appeasement display	Usually avoidance behavior, sometimes threat or flight	Nonaggression.
Auditory	Hiss	Usually nil if not combined with other cues	Often part of threat display.

olfacients. Perhaps the single most important fact regarding the fecal pellet is that it is *not* hidden, but deposited conspicuously along trails and other open areas. Such pellets probably aid in preventing unnecessary encounters among monitors. Leyhausen (1956) suggests that olfactory marks of cats communicate such information as "this section closed," "proceed with caution," "go ahead."

Fecal material on hilltop sites is conspicuous by its location and white color. There can be no doubt that on ascending practically any major hill, a newly arrived transient monitor quickly learns of the presence and sex of other monitors in the area. As in wolves (Seton, 1909), the major "news items" essential to their survival may be obtained largely by this system. Most individuals comprising a local monitor population probably do not recognize one another. At the same time, their rights as residents need constant reinforcement—not only through social interaction at carrion (see below), but by means of fecal scent signals. The use of this kind of signaling system is quite common in mammals and snakes. Such signals may prevent the intrusion of nonresidents.

Other important chemical cues are those associated with the discharge of cloacal and gastric contents. Cloacal emptying as a

Table 5. Major Display categories in *Varanus komodoensis.*

Category	Directed to:	Sensory Type	Behavioral Display	Remarks
I. *Intraspecific* Social: appeasement	Usually larger individuals of same species	Visual	*body:* "Schragstellung," slightly flattened laterally, body raised with arched vertebral column; *head:* held straight out, down or up; held stiff, usually off ground; *locomotion:* slow, stiff, deliberate, often parallel to or an an angle with percipient (see Fig. 6).	Easily and quickly shifted to warning display if necessary
General Information	All individuals	Olfactory	Scents associated with droppings and other spoor.	
Threat	Predators and assailants	Visual	*body:* "Schragstellung," body sometimes slightly compressed laterally, bowed away from assailant; *head:* low, dorsal surface sometimes directed to assailant—in stronger reaction with mouth open, rarely with slight foam production; *neck:* hyoid expanded; *locomotion:* none; *tail:* bowed away from assailant, ready for sweeping tail blow. Tail sometimes switched back and forth, or vibrated.	Sometimes difficult to distinguish from above (graded series)
		Auditory	Hissing	
Sexual: courtship	Other sex	Tactile	Males scratch females on neck and back with claws of one front foot.	
		Olfactory	"Tonguing" of scales of head and body.	
II. *Intraspecific* Passive predator deterrent	Predators	Chemical	Emptying cloaca and stomach	

fright reaction is common in many lizards. We have observed it many times during handling of smaller Komodo monitors. It occurs also when monitors are attacked, suggesting a protective function. Disgorging the gastric contents is also common, particularly during the first several days following a large meal. It occurs most often before an impending attack and seems to be either a preparation for action or a deterrent against attack.

The loose organization in a feeding group of Komodo monitors presupposes that each of the members is able to recognize one another at least temporarily.

The importance of scent in sex and species identification is clearly related to the highly developed olfactory sense of Komodo dragons. Olfactory sexual differences are apparently easily recognized. Prior to, and during courtship, adult males touch their tongues to the body and head of the prospective mate, particularly around the sides of the head, between the eye and nostril, and at the junctions of the hind leg with the body.

Figure 5. Fecal pellet of large adult monitor (19W) placed on open sand of dry creek bed.

Visual Communication

Visual cues include color, pattern, position, and form. Colors and patterns of potential communicative importance include the vivid juvenile body pattern, bright eyelid yellow of adults, and the bright yellow tongue in specimens of all sizes. Generally, however, color cues are probably not as important in this species as they are in others of the genus.

Form and posture also play a role in communication. Components of possible importance are: raising the roach (crest); tail position (e.g., held straight and stiff, as opposed to lashing it or bowing it to one side); head posture (at angle to ground, sometimes also turned to side); and *Schragstellung* (the positioning of the body so that the greatest surface area is shown, lateral body compression, hyoid expansion, mouth open, and body raised high on legs).

The *Schragstellung* is associated with defensive tactics and part of the threat display. It is common in several species of *Varanus* (Mertens, 1946; Murphy and Mitchell, 1974; Honegger and Heusser, 1969). Preceding and during an attack, the head and anterior parts of the body are usually lowered. A lateral sigmoid curve in the neck is often associated with an impending attack, as in snakes.

During a threat display, many *Varanus* species, including *V. komodoensis*, commonly lower the head and arch the back (Mertens, 1946). Typically, the head is turned slightly to one side so that the dorsal surface is presented to the offending object. The eyes peer out from beneath their protruding brow and a defensive or offensive attack is usually imminent. The arching of the back and tail is a conspicuous visual cue used particularly by smaller individuals when approaching other monitors, or by large individuals when approaching or being approached by humans. It is often accompanied by a stereotyped, slow, stiff-legged walk in which the body is slowly thrown from side to side in exaggerated lateral undulations (Fig. 6).

Often accompanying such movements, but sometimes independent of them, is a display in which the throat is visibly enlarged (Fig. 8). This is accomplished by an anterior, lateral, and posterior movement of the hyoid apparatus so that the bottom of the throat looks like a slightly inflated balloon. It has been described in many *Varanus* species (e.g., Mertens, 1946; Cowles, 1930). It is often associated with lateral body compression. To make the body appear even larger, the roach is often raised along the vertebral line of the neck and anterior half of the body.

The multiplicity of contexts in which the roach is raised, hyoid expanded, and head held at an angle suggest that these manifestations represent a *stress reaction.* This reaction does not appear to communicate a specific message but, rather, represents a general state of being to which other cues may be added. Together the entire complex constitutes a specific display. (see Table 5 and Fig. 7).

Visual display in particular provides several examples of behavioral scaling (varia-

Figure 6. Appearement display in young monitor approaching carrion where a larger specimen is feeding (top right). Head position and raised roach are part of display, but by themselves constitute a stress reaction (see text).

tions in the magnitude or qualitative state of a behavior). One example is the rate of display with respect to population density. As another example, the average number of stress reactions/hour among individuals of 1.5 m or less at carrion was 1.6 when aggregations consisted to 2 to 5 individuals; 2.8 for aggregations of from 6 to 9; and 4.1 at aggregations of more than 10. Similarly, the number of tongue flicks vary according to aggregation densities around carrion. (X= 8.2 flicks/minute for aggregations of from 2 to 5, 12.1 for aggregations of 6 to 9, and 19.6 for more than 10). Fighting itself probably falls into the same category, but the differences for the three density classes of the present study are statistically insignificant.

Scaling can also be related to the intensity of the communicative cue or display. For example, in the threat display the tail bow and open mouth are presented when the displayer cannot, or seems unwilling to move. Together with other cues they constitute the highest level of threat display prior to attack. Tail bow and open mouth are not part of the stress reaction but enter into a scaled threat display ranging from low levels without weaponry shown to high levels in which teeth and tail are used. On an ascending scale of intensity, the first step is probably the simple stress reaction, followed by lateral body compression and back arching. Hissing may occur as an additional component at this stage, followed by tail movements and finally varying degrees of mouth opening (Fig. 8).

Auditory Communications

Sounds produced largely by the respiratory apparatus are infrequently used by reptiles in communicating information to each other

Figure 7. Warning display of hatchling *V. komodoensis*. Weaponry emphasized by tail lashing prior to tail sweep. Head position, "inflated" hyoid and raised roach are part of display, but by themselves constitute a stress reaction (see text).

or to other organisms in the vicinity. The most common sound is hissing which has been reported in almost all species of *Varanus* (Mertens, 1946; Grijs, 1899; Faussek, 1906; Stirling, 1912; and many others). It is usually associated with defensive tactics and as part of the threat display. During hissing, the mouth is held partly closed. Individuals of V. *komodoensis* hiss at one another during feeding, when approaching one another while moving around carrion, and when attacking one another. Females often hiss at males during courtship and particularly during mount attempts. Nearly all trapped individuals hiss when approached by humans or if closely pressed along game trails.

Tactile Communication and Contact Behavior

Pushing with the body, tail, head, or even with a wide open mouth (jaw fencing) is common in many species of lizards (Mertens, 1946). None of these was observed in interactions among Komodo monitors.

A common defensive tactic of many species of *Varanus*, including *V. komodoensis*, is the "tail blow." In the threat display preceding it, the tail is bowed away from the stimulus. When the stimulus comes within striking distance, the lizard lashes laterally with its tail (Fig. 8). The force of the blow is often exaggerated in popular literature.

Biting is common in both offense and defense, producing severe wounds that often lead to the death of one of the individuals.

To summarize, reference should be made again to Table 4. The listed categories are not rigidly separated. While scent may be the most important cue in the core areas, this is not the case in the feeding aggrega-

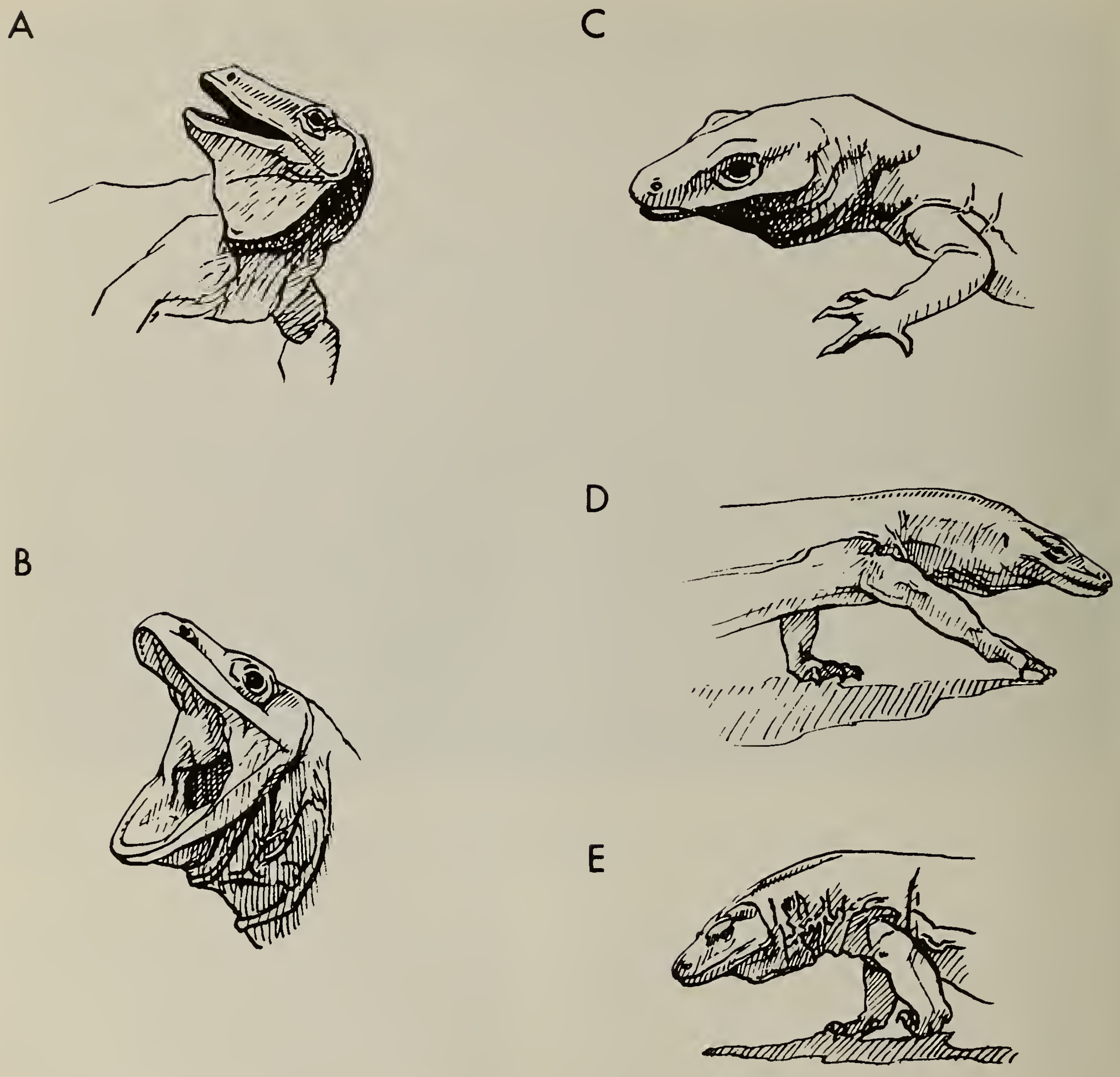


Figure 8. Head positions in overt, high level threat (left) and in stress reaction (right) associated in several display contexts. (A) Hatchling—threat, with teeth shown as potential weapon. (B) Adult—higher level threat, involving wide gape to display teeth. (C) Hatchling—stress reaction, in this case part of threat display involving tail lashing. (D) Subadult—stress reaction, in this case as part of appeasement display. (E) Adult—stress reaction, in this case part of threat display following its attack on another individual. All photo tracings.

tion where visual cues are more important. In this situation communication depends more on the general appearance of the monitors moving around carrion than on any particular marks or patterns. Movement in itself appears to be the chief component in social communications. The movement of the larger Komodo monitors around carrion apparently provides the entire group with frequent opportunities for recognition which results in repositioning of the smaller individuals.

Only around large carrion can this recognition and response be maintained visually.

Tactile and chemical signals, although they are important in certain behavioral patterns, such as mating, play no significant part in group behavior.

Spacing and the Maintenance of Hierarchies

Varanus komodoensis possesses a strong hierarchial system maintained by frequent aggression. Included in their aggresive, agonistic behavior are threats, attacks, and displacement in space or in rank (Table 6). Submissive behavior includes flight and appeasement reactions. Submissive monitors may also accede to homosexual mounting or courtship behavior, such as back scratching.

For purposes of analysis, an attack was considered any aggressive encounter involving physical contact. Attacks were not common and usually amounted to one individual's biting or attempting to bite another. I have no evidence that attacks were ever redirected to smaller individuals lower in the hierarchical system. Most attacks were precipitated by the close approach of a subdominant individual to a dominant one, rarely the reverse, and then only in courtship.

Displacements in space and rank at a carrion feeding site were the most common social interactions observed. Active displacement in which one monitor's presenting a threat display caused another to move was uncommon compared with passive displacement in which no overt threat was involved. In general, smaller individuals simply avoided or moved out of the way of an approaching larger one (Table 7). There was no correlation between displacement behavior and sex (Table 8). Specimens of equal size and of either sex tended to ignore one another unless

Table 6. Aggressive behavioral categories in *Varanus komodoensis*.

Type	Function	Remarks
Territorial or Dominance	Repulse potential users of resources claimed by one individual. Most commonly the resource is carrion prey.	It is not clear whether *V. komodoensis* exhibits aggressive behavior to repulse trespassers. Appeasement displays are used by largely females, subadults, juveniles, and most transients to transmute aggressive displays into conciliation.
Sexual	Males threaten and attack females for mating purposes. This includes scratching, biting, chasing, and mounting.	Males sometimes engage in homosexual back scratching, neck biting, chasing, and mounting in connection with dominance aggression.
Predator aggression	Large specimens sometimes attack and kill smaller ones, apparently to feed on them.	

Table 7. Percent of spacial displacement per interacting size classes (in m) (n=167).

Size Classes Displaced	Size Classes Not Displaced			
	1.1–1.5	1.6–2.0	2.1–2.5	2.6–3.0
1.1–1.5	52(48)	61(38)	78(22)	93(7)
1.6–2.0	1(38)	54(46)	65(21)	73(24)
2.1–2.5	0(22)	14(21)	49(51)	51(37)
2.6–3.0	0(7)	3(24)	12(37)	46(54)

* Percent of no displacement in either member of pair shown in parentheses.

Table 8. Percent of spacial displacement per interacting monitor pairs (n=167).

Sex Displaced	Sex Not Displaced	
	Males	Females
Males	29(40)	18(27)
Females	23(27)	30(33)

overtly threatened. Threat was normally communicated at fairly close distances (X=2.2 m).

Displacements were highly reliable indicators of rank. There were no alterations of dominance in at least the resident monitors during the entire study period. However, the hierarchial structure around carrion changed constantly as new individuals entered the area and earlier arriving individuals left (Table 9).

Appeasement displays were never performed by large individuals (dominant or not). Such displays were performed by animals 1 to 1.5 m in length. Appeasement behavior occurred most commonly as a displaying individual approached carrion around which other individuals had already gathered. It frequently occurred at distances of 3 to 10 m (Table 10) as the displayer moved back and forth beyond the attack range of larger individuals. That the displaying animals were under stress is suggested by the fact they were easily frightened by nonagonistic movements of the monitors nearby, by the human observers, by boughs moving with the wind, or even by leaves blowing across the ground. When disturbed, these individuals dashed headlong into the surrounding underbrush. Displacements of low-ranking individuals around carrion always occurred when high-ranking individuals moved (Fig. 9).

Table 9. Percent displacement of transient and resident *V. komodoensis* at carrion during any interactions in which a displacement occurred (n=103).

Displaced Size Classes	Displacements in	
(in m)	Residents	Transients
1.1–1.5	72	98
1.6–2.0	13	71
2.1–2.5	7	32
2.6–3.0	2	10

Table 10. Distance over which appeasement displays are presented by small to large *V. komodensis.*

Display Distance (Approx., in m)	Frequency per monitor Size Class (in m)				
	1.1–1.5	1.6–2.0	2.1–2.5	2.6–3.0	Total
1.0–1.9	8	8	6	3	25
2.0–2.9	15	11	9	1	36
3.0–3.9	38	18	15	0	71
4.0 +	16	3	0	0	19
Totals	77	40	30	4	151

Table 11. Frequency of agonistic behavior demonstrated by resident (=R) and transient (=T) monitors.

Size Classes (in m)	Status	Number of Agonistic Displays (n=355)
1.1–1.5	R	40
	T	103
1.6–2.0	R	32
	T	69
2.1–2.5	R	26
	T	47
2.6–3.0	R	13
	T	25

Within the hierarchy established at carrion sites, agonistic behavior was more commonly seen in monitors of lower rank and smaller size. Agonistic behavior was least often demonstrated by the dominant residents (Table 11). Aggressive display was no indication of social rank, since high-ranking monitors at feeding sites generally ignored those of lower rank. However, the reverse was not true; appeasement display was often directed toward animals of higher rank. This display was more reliable in determining social hierarchy than any other.

Figure 9. A 1.2 m *V. komodoensis* (right) reacts stressfully (roach raised, head tilted downward and hyoid "inflated") showing a startled alarm movement when larger feeding monitor in background moves carcass.

The appeasement display of small monitors when near a group of larger individuals is clearly related to submission, since it fails to elicit aggressive behavior by the adults. Carpenter (1961) has reported similar displays in juvenile desert iguanas when approaching adults.

The function of the monitor's appeasement display is apparently to block aggression and may be regarded as a type of formalized nonaggression in which all functional movements of threat or defense are avoided. Carpenter (1961) similarly concluded that such "actions probably work to protect the juveniles."

With few exceptions, large monitors around carrion are within 3 m of each other and seldom are within the 3 to 6 m range; smaller individuals tend to be distributed around the periphery of these larger specimens. Thus, there is a definite correlation between rank and social spacing around carrion (Table 12), but none with respect to sex (Table 13). When resting between feeding periods, there is a tendency for large higher-ranking specimens to remain separated from other individuals.

Table 12. Size and social spacing of monitors around carrion

Size Classes (in m)	Distance from carrion (in m)		
	0–2.0	2.1–4.0	4.1+
1.1–1.5	39	89	154
1.6–2.0	51	94	127
2.1–2.5	86	41	39
2.9–3.0	119	67	28

Kaufmann (1962) has shown that there is no strong hierarchical system in the loosely organized mammalian social group of coatis, *Nasua narica,* apparently because they have a limited repertoire of social displays. Thus intraband disputes are commonly settled by fighting. The behavior of individuals within a feeding aggregation of Komodo monitors more closely approximates this situation than that reported for other lizards. However, because *V. komodoensis* is cannibalistic, there is utility in maintaining spacing, at least as far as the smaller individuals are

Table 13. Sex and social spacing around carrion when equal or larger monitors were feeding.*

Sex	Distance from carrion (in m)		
	0–2.0	2.1–4.0	4.1+
Males	216	205	275
Females	79	86	71
Totals	295	291	346

* Sex ratio is normally 3.5:1 (Auffenberg, MS).

concerned. They are sometimes pursued, and they try desperately to escape. In the desert iguana, Carpenter (1961) noted that chased individuals often assumed a submissive pose, but this was never observed in Komodo monitors. If a small monitor stopped running, the larger, chasing individual undoubtedly would have attacked it. During the present study, two smaller monitors (1.44 m and 1.54 m total length) were attacked and killed without provocation by a resident male 2.5 m long. A 2.3 m female severely lacereated a 1.8 m nonresident male that had tried to mount her. I noted many instances in which smaller individuals were bitten on the hindlegs, tail, and back. Escape plays an important social role for small Komodo monitors.

The less antagonistic the higher-ranking individuals are, the more active the feeding of the lower-ranking ones. The high-ranking monitor of a feeding group is normally tolerant of the movement of lower-ranking ones toward the food itself. The dominant normally fails to display its superiority, except passively by means of its large mass. The mere presence of a large individual at a feeding site elicits signs of social stress and submissive appeasement behavior in smaller ones. Large size confers special site and feeding privileges to certain individuals, and these are accepted and remain unchallenged by smaller ones. This situation is somewhat similar to that described in dogs and wolves (Schenkel, 1967).

The open associations around carrion are thus based on a type of social situation in which individuals (particularly smaller ones) are anonymous as individuals, but regarded on the basis of their size as low-ranking individuals. Large, high-ranking individuals are also probably anonymous to the smaller ones. Large residents are not anonymous to one another, since they apparently recognize individuals on the basis of both physical and chemical characteristics. This leads to a kind of relationship between resident individuals that is lacking between residents and nonresidents.

FEEDING BEHAVIOR

Most medium to large monitor species are known to feed on both live and dead prey. The degree to which they are predators or scavengers depends on the species, age of the individual, hunger level, and the opportunities presented. The same is true of the Komodo monitor, which may be characterized as a scavenger-predator type of carnivore.

Scavenging

During the first day after death, the volatile oils produced by the decomposition of a carcass are not produced in sufficient amount to attract any but the very closest lizards. In 48 hours, however, the decay is sufficiently advanced that considerable scent is produced, and many monitors from over a large area begin to move toward the carcass.

One important characteristic of the scent tracked by a monitor to a rotting carcass is that, while the chemical stimuli may vary in intensity, they lack directional properties. Also, regardless of its distance from a carcass, a monitor cannot detect a scent unless there is an actual diffusion of volatile oils through the air. Thus, it is clear that the location of the carcass, its size, and the direction of the wind are critical factors (Fig. 10). The greatest distance from which we have attracted lizards to a bait is approximately 8 km. Under most natural circumstances this distance would not be greatly exceeded, because a carcass produces only a finite quantity of volatile substances.

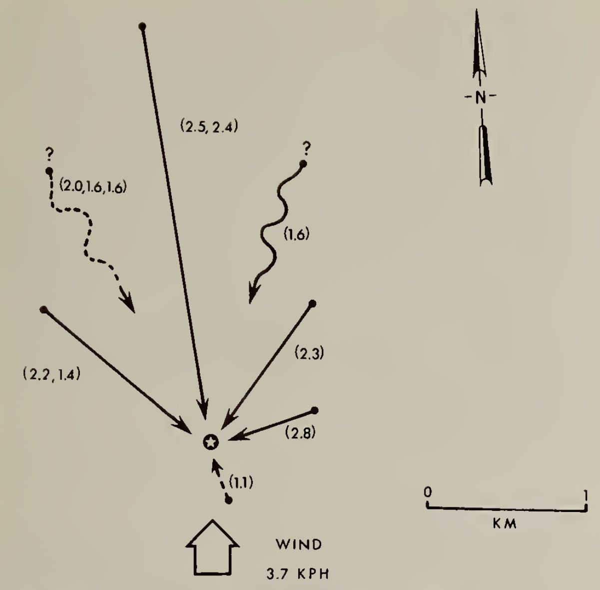


Figure 10. Wind direction and velocity, Loho Liang, Komodo, showing direction, distance and size (in m) of resident (solid lines) and transient monitors (dashed lines) that came to carrion on Nov. 21–23, 1969. Wavy lines represent monitors that came from unknown distances or directions.

Because topographic and vegetational features modify wind patterns, some locations are more favorable than others as sentinel areas from which windborne odors may be detected. Because of the generally prevailing southern, inshore, daytime winds, these favorable areas tend to be the higher, exposed knolls and ridges above forested valley floors.

Ordinarily, simple airstreams have no influence on the direction of the motion of a monitor, but when that same airstream carries the scent of carrion the monitor turns into the air current and moves toward the source of the odor, usually in the valleys where the winds are more variable. The monitor's search pattern is such that directional turns occur irregularly, to either the right or left at certain junctures with other trails. Trailing studies have shown that more directional changes occur when the monitor moves into a weaker scent field than into a stronger one (Table 14). The sum total of its maneuvers gives the impression of a drift-like movement toward the bait that seems obvious to an observer in the field, but is difficult to document. Thus the movement of oras towards a carcass represents a typical case of klinokinesis, similar to that described by Fraenkel and Gunn (1961) for other lower vertebrates.

Table 14. Number of directional changes with distance from carrion.

Distance From Carrion (in m)	Number of Directional Changes per 100 m
1–100	12
101–200	31
201–300	46
301–400	108
401 +	201

Feeding Techniques and Adaptations

Feeding on large carrion begins by the monitor's ripping open the body wall and pulling out the intestines. Sometimes the body wall is eaten first. The stomach and intestines are usually violently slung from side to side in order to free them of their contents that are not intentionally eaten. Next the ora's head is thrust deep within the body cavity, and the diaphragm, lungs, and heart are pulled out and eaten. The remaining body wall is then cut away, followed by the muscles of the axial skeleton and girdles (for details, see Burden, 1928; Pfeffer, 1959; Auffenberg, 1972).

Varanids are the only living reptiles, other than turtles, that *cut* their food into sections before swallowing it. Of all the species described, *V. komodoensis* is the most adept at this process. Burden (1928) and others have shown that the compressed, serrated teeth, large mass, and jerking body movements are largely responsible for this efficiency.

Due to skull specializations conferring great mobility to the head (Auffenberg, MS), the size of the pieces swallowed and the amounts eaten are sometimes astonishing (Burden, 1928; Hoogerwerf, 1954; Auffenberg, 1972, MS). Feeding is very rapid, with carrion intake rates as high as 2.5 kg/min. However, an average of only 6.9 min/day is spent in actual feeding; the remaining time is devoted to social and thermoregulatory activity.

With the exception of the large snakes, waste is lower for the Komodo monitor than in any other large carnivorous vertebrate. Bones, hooves—almost everything is devoured. Minimum nonutilized amounts of carrion are about 12 percent. Their prodigeous appetite, high feeding rate and low waste are undoubtedly all important factors in niche utilization efficiency. These are undoubtedly the most important factors in reducing interspecific competition for carrion. Oras probably share less carrion with other species than any other large scavenger (Auffenberg, 1972; MS).

Feeding Aggregations

Because of their wide-ranging activity and the efficiency with which Komodo monitors locate either a fresh kill or carrion, groups of hungry individuals quickly gather around a localized food source. As already mentioned, the scent of decomposing flesh is a source of attraction; in the case of a fresh kill, it is the scent of the intestinal contents slung out of the viscera by the initial predatory individual. Within a few hours after a fresh kill, one commonly finds three or four monitors feeding. As many as 17 individuals (Mean=3.9) may feed from a carcass in 1 day, with smaller groups (Mean/day=1.7) found at fresh kills than at carrion (Mean=4.6/day). An aggregation of monitors is seldom seen for more than 2 days, by which time even large carcasses are usually completely consumed.

Normally, an aggregation is "fluid," with some individuals leaving and others arriving. Not all individuals feed at the same time; they are frequently spread over several hundred square meters, alternately feeding and walking about, or resting under vegetation. Individuals in an aggregation range in length from approximately 1 to 3 m, and include, both residents and transients. As already noted, such gatherings lead to a great deal of interaction, with agonistic behavior predominating (Burden, 1928; Broughton, 1936; Hoogerwerf, 1954; Oesman, 1970, and others). The fact that the monitors are cannibalistic doubtless has a shaping influence on the relationship of the feeding group.

Aggregations at carcasses apparently facilitate mating in Komodo monitors. However, gregariousness is obviously not vital for successful mating in varanids. Fighting is important to the attainment of social standing in the temporary hierarchy and thereby to certain rights to food or to a mature female.

Active Predation

There is much confusion in the literature regarding the extent to which this species attacks and kills living prey. That young monitors probably capture and eat small animals is undoubted, although little data are available. The feeding of large individuals, however, has generated controversy. The earlier literature (Burden, 1928; Lallemont, 1929, and de Jong, 1937) is rather specific in its emphasis on the utilization of large prey. My work indicates that the earlier workers were correct when they stated that large, live prey are often attacked, killed, and eaten (Auffenberg, MS).

It is now clear that the predatory activities of *V. komodoensis* fall into three main categories reflecting predator sizes: (1) hatchlings that feed exclusively on small animals, such as insects and lizards found under bark, in crevices of stumps, logs, trunks of trees, and in the grass; (2) small to medium-sized monitors that feed largely on rodents and birds normally obtained on or under the ground (in burrows, rock piles, etc.); and (3) large monitors that *may* feed on animals as large, or larger, than themselves. As shown below, these are located by both sight and scent and obtained through both stealth and surprise along established game trails and in thickets. Detailed analysis of the prey species and their age, etc., eaten by various size *V. komodoensis*, are provided in Auffenberg (MS). I would like to emphasize the behavioral patterns that place the Komodo monitor in a unique niche among lizards—that is, the ability for large mature individuals to successfully attack prey animals up to 20 times the lizard's own mass.

In order to observe and document stalking and killing techniques, several live, tethered goats were offered as prey near a hanging decomposed bait (to attract monitors into the immediate area as an economy of time). Abbreviated notes of March 14, 1970 (excerpted from Auffenberg, MS) illustrate the behavioral sequences involved. The attacking monitor (number 19W) was 2.5 m total length and weighed 42 kg. A live goat of 25 kg was tethered to a ground anchor with a 10 m lead. A decaying 21 kg goat was pulled 5 m into a nearby tree. The major steps in the attack sequence are illustrated in Fig. 11.

9:10 A.M. 19W approached bait area from downwind. It had seen the grazing goat almost immediately after stepping out of the thicket. It was then 15 m from the live goat with its head held so it could peer over the grass, watching the goat alternately out of one eye and then the other.

9:21 19W moved forward 1.2 m, stopped and continued to watch the goat. The latter now saw the lizard for the first time and would have bolted off had it not been tethered.

9:24 19W moved forward 0.5 m and stopped.

9:25 19W moved forward 0.5 m and stopped.

9:27 Moved up to 3 m from goat, flicking out tongue occasionally. The head was now held low and the neck slightly bowed to the side. The neck was then slowly moved into a horizontal S-shape, with head held a little to one side.

9:27:4 19W lunged at goat, catching the thigh with several teeth of the lower jaw, producing a bleeding wound about 1 cm deep and 10 cm long.

9:27:34 19W approached goat to within 1.2 m, bowed neck and lunged but missed.

9:27:39 Spun around and again stepped to within 1.2 m of goat. Bowing its neck into an S-shape, and with its head slightly to one side, it stared at goat, which was now facing monitor.

9:28:00 Lunged when goat turned to side, grasping it over the ilial projections of the hip with the upper part of goat held down against ground, while goat struggled to get to its feet.

9:28:45 Released goat, but immediately bit it again in lumbar region. The monitor is now better able to hold the struggling animal against the ground with its neck arched vertically.

9:29:45 Goat tried to struggle to its feet and was almost successful, but lizard quickly released goat, grabbing left front leg and jerking prey back to the ground.

9:30:00 19W changed hold to back of neck, but goat then tried to raise on to hindlegs.

9:30:10 19W changed hold to lumbar region again and jerked goat posteriorly to throw it back to the ground. Goat stopped struggling; apparently in shock.

9:30:20 Goat bleating feebly; no movement other than sporadic breathing.

9:30:30 Released goat and flicked it with tongue. Bit out section of abdominal wall and then pulled out most of intestines, shaking out their contents and swallowthem. Goat dies from massive abdominal hemorrhage.

9:38:00 19W bit into goat's back, then easily lifting and carrying it to

9:40:00 All goat muscular motion ceases. Monitor still eating viscera.

tether end, where it is placed on the ground and resumed eating viscera.

In all cases it was obvious that an adult monitor was quite capable of killing an animal approximately half its own weight. The goats were easily held down, dragged, and even carried. These prey were killed within 2½ to 4 minutes after the initial attack. Though the goats tried to remain on their feet (and were surprisingly quiet), they were thrown and held down, making it difficult for them to push or pull away with their feet. In some sequences the goat was violently shaken both laterally and vertically. This part of the attack pattern is evidently most important in immobilizing the prey. Death usually occurred as the result of massive hemorrhage associated with evisceration.

A similar pattern occurs with prey as large as *Bos bubalis,* the Asian water buffalo. Individuals weighing as much as 750 kg are known to have been attacked and killed, although most buffalo prey are much smaller. The technique first involves injuring the lower limbs. Severe lacerations often sever the tendons (including the Achilles tendon) and immobilize the prey (Fig. 12). This stage is followed by evisceration. Successful attacks against such large prey may last 20 minutes or more.

Another interesting facet of this monitor's behavioral pattern is the manner in which wild, free-ranging deer (their most common large prey) are taken. Two different tactics are used: either stalking deer when asleep or, more commonly, lying in ambush.

The local deer species (*Rusa timorensis*) is most closely related to the Asian sambar, with large stags weighing about 170 kg. Small herds of about one dozen individuals often feed on the open savanas during the predawn period. With the first light they begin to move toward nearby grassy hillsides. At this time of the morning, the monitors are not yet active and the deer move unmolested up the slopes. Here they usually remain on relatively flat-topped spurs above the forested valley floor, lying in the tall grass until some time between 0900 and 1100 hours. Then they move single file back down the slopes, following well-defined game trails into the wooded valleys below. The resident monitors apparently know the location of these major trails and often have trails of their own that lead to them. The adult monitors will lie in ambush, their heads within about 1 m of the trail. Sometimes they select places where several trails converge (Fig. 13).

It is under these conditions that most deer are attacked and brought down. Figure 14 illustrates typical, successful deer hunts. Excerpts from my field notebook for October 31, 1969 provide information to accompany the figure:

9:30 A.M. While going to the 'second grass patch' members of our group heard a dog barking and a crow calling from just inside the forest edge. On investigating the disturbance we found three monitors tearing flesh from the thorax of an adult doe deer approximately 45 kg, killed so recently that the carcass was still bleeding. . . . From signs nearby, the entire sequence was easily reconstructed. Five deer were known to remain on either the north or south spurs of Hill 23 every morning. Prior to 9:30, the small herd moved down the slope to the small savanna and crossed it on a well-established deer trail. They then entered the forest near the junction of 'Sugito's path' and the 'North-South trail.' The ora must have lain in grass about 0.5 m high along the game trail (near the hollow dots of Fig. 14) for here we found much fresh blood and crushed grass. Prey and predator must have continued the

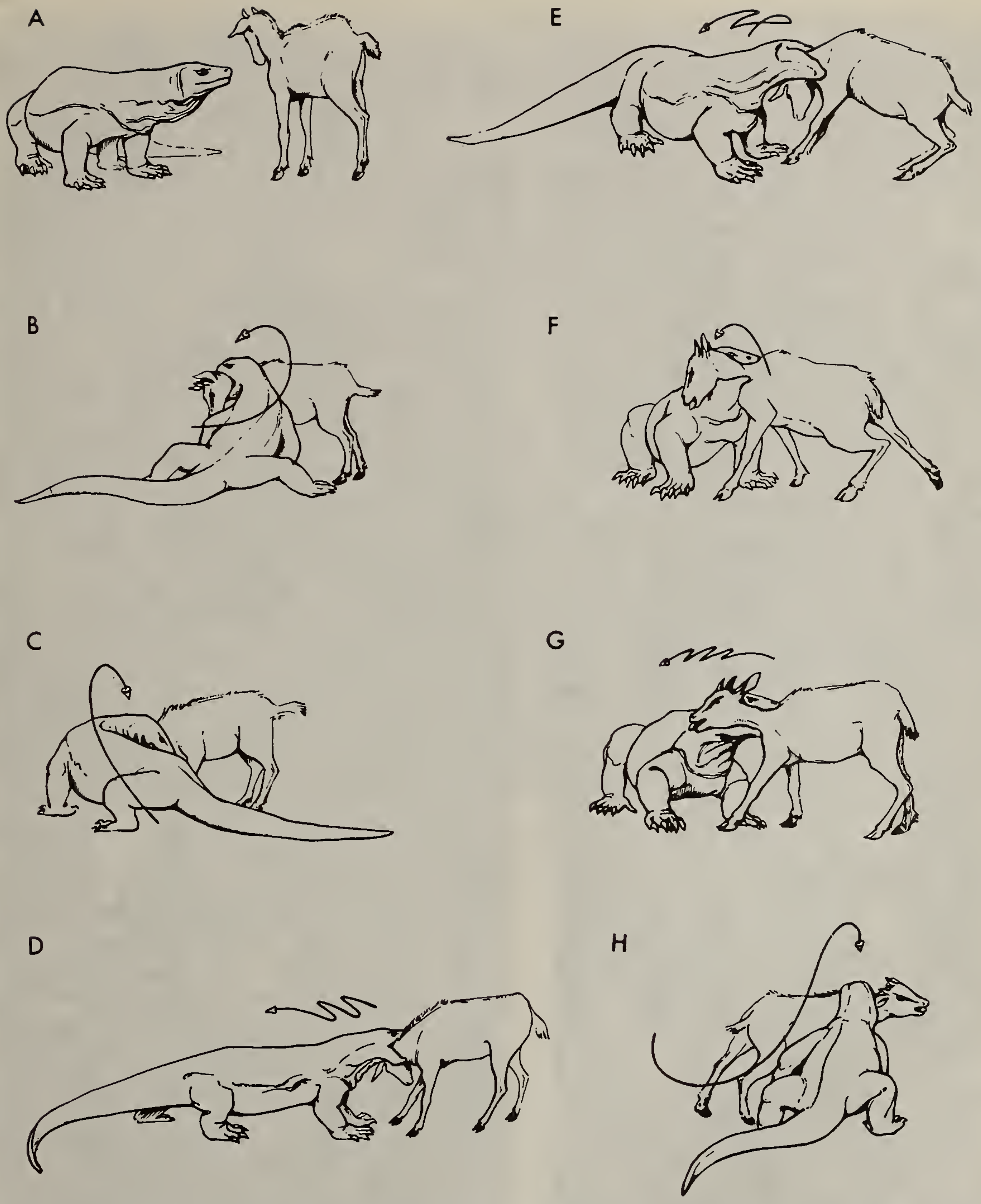


Figure 11. Transparency tracings of attack sequence of 42 kg monitor on 27 kg goat, photographed in Loho Liang, Komodo, April, 1970. (A) Instant before attack from a distance of less than 1 m. (B) First contact, goat grasped by neck (arrows show direction of lizard's head movements). (C) Head of goat forced downward. (D) Goat violently jerked from side to side, then yanked toward monitor. (E) Goat pushed down onto haunches, then violently jerked back and forth in opposite directions. (F) Goat pulled laterally towards monitor and starting to go into shock. (G) Violent lateral jerking with posterior movement by monitor, apparently intended to throw goat to ground. (H) Sudden change of tactic by moving counterclockwise and then pushing goat to ground with downward movement.

Figure 12. Phalangeal area of left hindfoot of 320 kg domestic water buffalo attacked by a 2.8 m monitor (killed by villagers during attack) near Nggoer, Flores. Wounds of the upper jaw appear above the base of the hooves on the anterior surface (left) and of the lower jaw on the posterior surface (right). An infection has already begun in the latter (see Auffenberg, 1973, for importance of septic wounds caused by *V. komodoensis*).

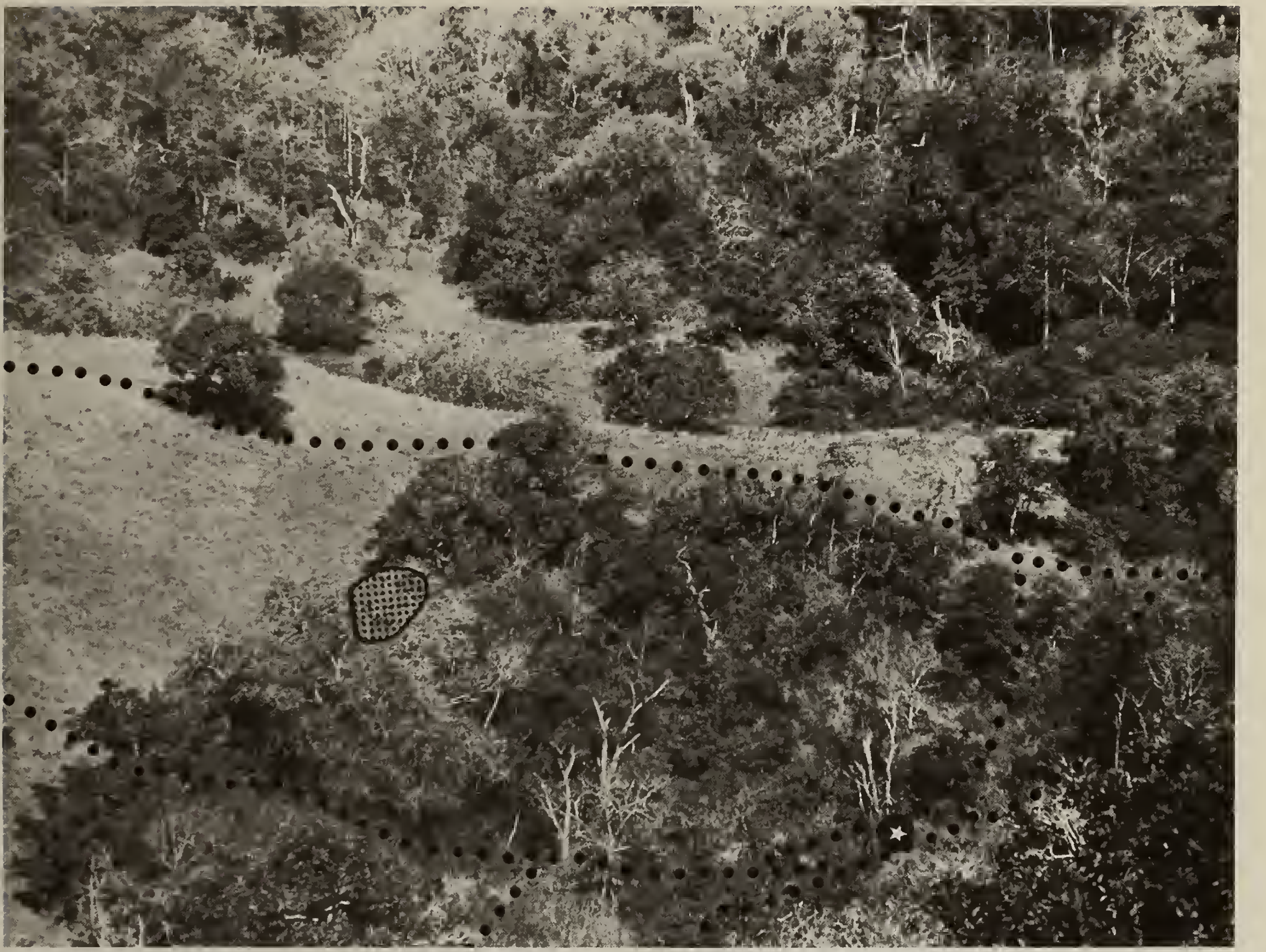
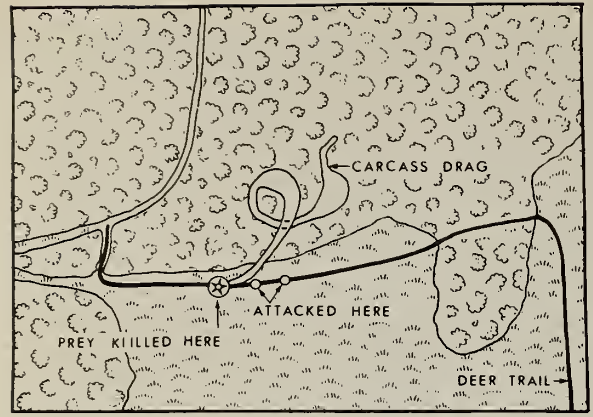


Figure 13. Ambush sites are often located near a concentration of game trails. The large black dot with enclosed star shows the ambush location of a large monitor (23W) at Hill 23, Loho Liang, Komodo, May 24, 1970. Small dots trace the game trails near the base of the hill. The stippled area was frequently used by the same adult as a thermoregulatory site.

struggle a few feet farther along the trail, where we found more blood and another area of crushed grass. The struggle then moved farther down the trail, where the doe fell or was pulled down. Here it certainly died, because intestinal contents were scattered over an area of packed-down and torn-up grass 1.2 m in diameter; 2 m from the forest edge there was evidence of massive bleeding. After the intestines were eaten the carcass was dragged about 15 m into the forest, where more of it was eaten. By this time, two smaller monitors, a dog, and a crow had arrived, probably attracted by the scent of the fresh intestinal contents. The remaining part of the carcass was later dragged another 15 m and consumed.

During the afternoon, most deer herds bed down in thickets and adult monitors often attempt to find and attack them there. The sleeping animal is usually grasped by the legs or back. According to the reports of local inhabitants, the deer that are killed are usually those unable to stand. The path of a Komodo dragon hunting for sleeping deer is



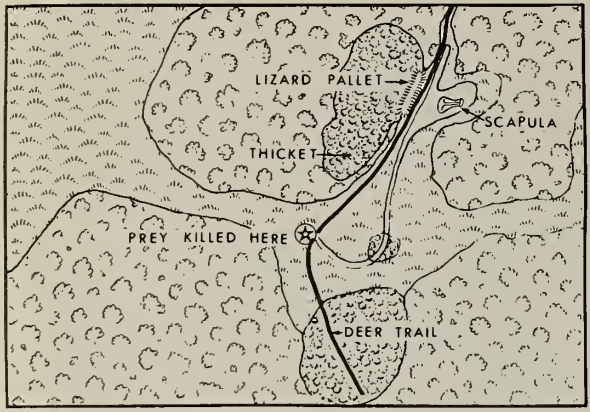


Figure 14. Top, schematic of successful attack by a 42 kg monitor (19W) upon a 45 kg(ca) doe deer, described in text. Bottom, conditions of successful attack on 27 kg (ca) deer by a large monitor, May 24, 1970. Lizard pallet—area scratched free of ground litter in which the monitor lay in ambush adjacent and parallel to the game trail. After it was killed, the deer was dragged by the monitor back to the attack site, where the entire carcass, was eventually consumed.

shown in Fig. 15. Its path of travel makes it obvious that all the potential sleeping sites were known to the monitors. Resident animals know the location of game trails, watering holes, and other topographic features important in their feeding strategy. The importance of such information is obvious—those individuals possessing it are more successful predators than those that lack it. Detailed knowledge of the large activity ranges of adult monitors demands a depth of experience obtainable only after long residence. Indeed, this is probably the major benefit of

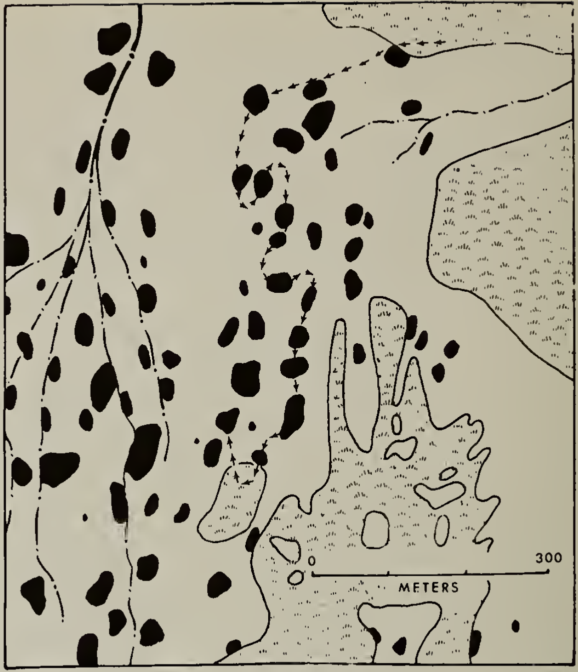


Figure 15. Afternoon foraging behavior of 19W within its core area. Its path suggests it is familiar with the location of thickets (black areas) in the monsoon forest (white areas). See text for discussion.

permanent residency. Some adult monitors, known by their peculiar markings, have lived in relatively small areas for periods as long as 15 years.

Though we do not know to what extent experience is important in determining the proportion of certain prey eaten by Komodo dragons, it is quite likely that inexperience or former successes and failures of an individual affect not only the area in which it hunts, but the prey hunted and even the technique utilized. Elsewhere (Auffenberg, 1973, MS), I have commented on the variation in attacks of adult monitors on livestock in different savannas. The proportion of different types of livestock taken in these savannas is believed largely due to the behavioral peculiarities of resident Komodo monitors and not to the proportion of domestic species available. The physical and psychological characteristics of individual large mammalian predators (such as man-eating lions) are recognized as extremely important. Except for crocodilians, the same factors in reptilian predators remain largely unappreciated, probably because most predatory reptiles studied have been small, common, and relatively short-lived. Small size makes it more difficult to recognize slight behavioral differences; their abundance tends to mask individual differences, and the short life span limits the number of experiences to which they might be exposed.

COURTSHIP

Since the early studies of Noble and Bradley (1933), courtship and mating have been described and studied in many families of lizards. Falk (1921) reports pairing in *V. exanthematius* and Werner (1893) in *V. griseus*, but important details are not given. A photograph of a breeding pair of *V. komodoensis* is shown in Stadt (1939) but undescribed. Tanzer and van Heurn (1938) simply state that a captive male Komodo monitor "in the course of copulation . . . lies over the female, in the usual manner." During the present study *V. komodoensis* sexual behavior was observed on 10 different occasions. These data, plus those available on breeding in zoological gardens, constitute our present knowledge of courtship and mating in this species.

Courtship was observed nearly all year (January 19 through October 1); however, the time for successful coition is more limited, extending from June 28 to early October. Lengthy courtship periods are often associated with multiple egg clutches during a long reproductive season (Tinkle, 1969). However, in the Komodo monitor the short period of actual copulation results in a strongly peaked annual reproductive pattern. The frequent sexual behavior of at least certain adult male and female oras during most of the year raises the question of the purpose of this nonconsummated courtship activity. Though the relationship between courtship activity and successful breeding is not clear, it appears that in the Komodo monitor the repetition of courtship behavior is related to pair-bond formation.

It is significant that the courtship and mating of oras often occur in the presence of aggregations, unlike the situation in most other lizard species where the mating pair is usually alone. The frequency of sex activity in or near aggregations is due to the fact that courtship and breeding often take place near carrion. The number of individuals in an aggregation, including the courting pair, varied from two to six and consisted of individuals of both sexes and of various sizes. It is particularly interesting that the dominant male in one study area (19W) courted female 23W most consistently, even though other mature females were occasionally present.

All courtship observed between 19W and 23W occurred within the broadly overlapping portion of their activity ranges, (Auffenberg, MS). The sharing of activity ranges between a male and one or more females is of course very common among vertebrates, including lizards (Rand, 1967).

19W courted only two other individuals other than 23W in the 10 sequences observed; while 23W had only two other males court her. Both these males were transients, young and apparently inexperienced. One was severely bitten by 23W during his attempts to mount her. No courtship resulting in copulation was successful except with 19W. The frequency and smoothness of courtship between them, as well as the infrequency of sexual behavior with other individuals and the confusion often attending these attempts, lead me to conclude that 19W and 23W probably recognized one another as individuals. Rand (1967) came to the same conclusion in his behavioral studies of the iguanid *Anolis lineatopis*, and, because of this, he and others (e.g., Milstead, 1961; Fitch, 1956) have suggested the possibility of pair bonding in some species of iguanid lizards. I believe that the frequency of unconsummated courtship in coactions between both 19W and 23W and other individuals, as well as the near nonexistence of precopulatory displays, serve to maintain a pair bond through the year. Pair bonding is probably important in organisms not only capable of killing one another, but often cannibalistic. Such pair bonding as a function of territorial display is well established in the bird literature.

Homosexual courtship and even mounting attempts were witnessed on several occasions. All the attempts were by young, relatively inexperienced individuals and were completely ignored by large males, such as 19W. Rand (1967) reports similar homosexual behavior in the iguanid genus *Anolis*. The only difference in homo- and heterosexual courtship behavior was that males always ran away, whereas females ran away only when the male was not accepted.

The following courtship sequence taken from field notes of March 2, 1970 illustrates the typical pattern:

10:55 A.M. 19W moves out of brush, approaches 23W, attempts to bite her back, and is then unsuccessful in his rapid attempt to mount her. 23W presents appeasement display to 19W and then moves to shade. 19W eats carrion.

11:05 19W, still eating, threatens 23W as she approaches carrion, and 23W retreats to shade. 19W still eating. 23W approaches carrion, and both eat side by side. 19W stops feeding and scratches 23W on on her side and her face with the claws of his right front foot. 23W moves in circle and returns, with weak appeasement display. They again eat side by side. 23W moves into shade, then back to carrion, where they again feed side by side.

11:15 19W suddenly mounts 23W, slides off, and retires to brush. 23W continues to eat. 19W presents appeasement display to 23W several times as he moves to carrion, though he quickly returns to shade.

11:20 With no prior movement on the part of either individual, 19W dashes out of shade and chases 23W, who runs 15 m into brush. He returns to carrion, eats, and suddenly spins around and chases 23W for 8 m. When she stops, 19W threatens her, and she immediately runs away, stopping only when 19W returns to food.

11:40 19W feeding and 23W again approaching carrion.

11:45 19W retires to shade as 23W comes close to carrion, but is then chased by 19W. She is quickly mounted, though 19W slides off in a few seconds. As she rests with belly and tail on the ground and head in an attentive pose, he rubs her entire back with the sides of his face. 19W again mounts 23W, but immediately slides off. He scratches her back with the claws of his right front foot, then stops, and moves slightly anteriorly, again scratching her with his right foot (Fig. 16). He then mounts her completely, with his front legs clasped around her body just behind her front legs and his hindlegs on either side of the base of her tail (Fig. 17). 23W remains completely passive. After few moments he slides off and scratches her over her hip and back, suddenly again mounting her completely. After a few seconds he slides off, nudging and licking her side at the insertion of the hind limb with her body, and rubbing the sides of his face in the same area. He then scratches her back anterior to the hips. She remains very still, and he again mounts her completely, slides off imme-

Figure 16. During courtship one of the most obvious displays is scratching the back of the female (23W) by the male (19W).

diately, and rubs his face on her side just before momentarily mounting her again. When he slides off after several seconds, she moves a few feet forward. He again scratches her back with his right front foot. She walks forward, and he follows her into the brush, where she begins to run. He follows very closely at the same pace, trying to place his right foot on her back.

13:14 19W returns to carrion.

14:08 13W presents appeasement display to 19W as the former approaches from downwind.

14:25 13W runs away as 23W approaches carrion from downwind. 19W immediately walks to 23W and mounts her without any preliminaries. She presents a stress reaction and moves a few feet as he slides off her back and begins to feed on the carrion.

14:52 23W returns to carrion and both eat together. 19W seems to be trying to crawl underneath 23W, forcing his head, neck, and anterior part of the

Figure 17. Male (19W) mounting female (23W) as part of the ritualized courtship sequence apparently intended to reinforce the pair bond (see text).

> body between her body and the ground surface.
>
> *15:02* 19W scratches 23W on the back so hard with his left front foot that he pulls her to him. He clambers over her back, and they both feed on the carcass. He scratches her on her hip with his snout, tries to stick his head underneath her belly again, scratches her on the side of her face with his right foot, licks the side of her face a number of times and then both eat together. . . .

Successful copulation in these two specimens during late June to early October was preceded by similar courtship behavior. However, on one of the frequent mountings, copulation occurred when the female raised the base of her tail. This was followed by a rapid tail twist by the male, who placed his cloaca in contact with hers and began a short period of feeble thrusting. They remained in this posture approximately 12 minutes.

The feeding territorial behavior of a dominant male ora, such as 19W, may complicate the process of pairing and mating by introducing an element of hostility. The first reaction of such a male to a female is usually aggressive, since in the usual territorial context she is an intruder into an ill-defined territory around the carcass, and, since oras are not obviously sexually dimorphic, she possesses essentially all the morphologic characteristics of males. Hence, large males may be ambivalent in their approaches to a female and may threaten her, obviously interfering with successful courtship.

When two or more lizards meet near a carcass, the smaller individuals behave in a characteristic way: They may be restless; they change rapidly from one activity to another; and their movements may be incomplete or distorted. In the case of courtship, males may on one occasion court a a female intently and on another ignore her completely, as is shown above to be a typical pattern between 19W and 23W. The variation in this sexually directed responses, and in their duration and intensity all are probably reflections of competing responses.

Cues in Courtship

Included in Table 4 are cues important in courtship behavior. The typical sequence above illustrates the point that stress reactions occur only in the early phases of courtship and are associated with conflict. Hyoid inflation is not necessarily related to dominance as it is in iguanids, nor are visual displays a significant factor in the courtship of monitors, as in agamid and iguanid lizards. There are no systematic variations of stereotyped movements, such as the rhythmic repetition of head bobbing, often involved in the

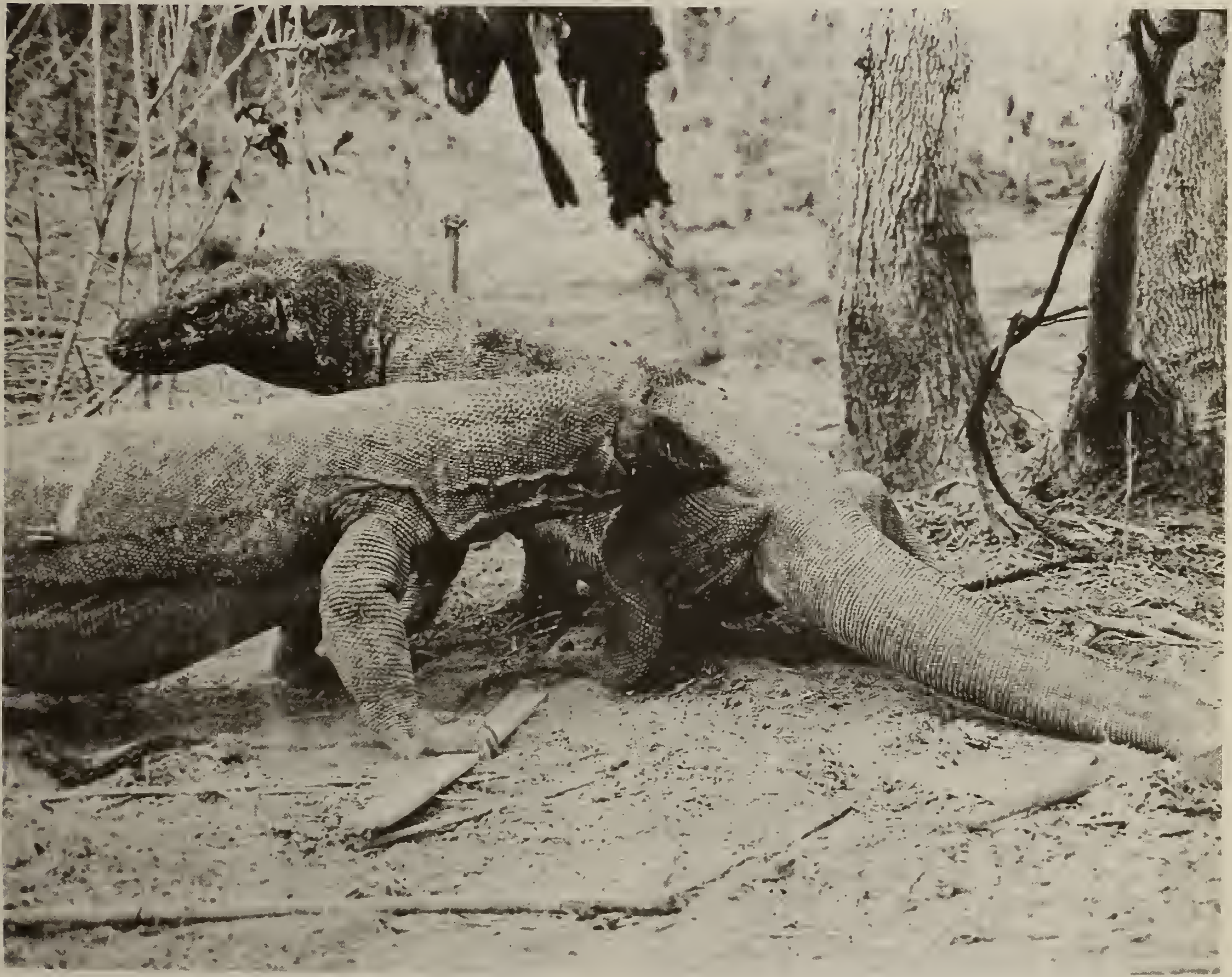


Figure 18. Male (19W) touching female (23W) with tongue and tip of snout during courtship behavior.

visual displays of other lizards. However, courtship in Komodo monitors does include many tactile cues. There is much touching by the tongue tips or pushing of the snout around the sides and top of the female (Fig. 18). Detailed anatomical study of these areas is currently underway to clarify the functions of this behavior. It may have a chemical, as well as a tactile, basis. Hard scratches with the claws administered on the back of the female by the male are obviously important tactile cues that may serve to quiet the female. Neck and shoulder biting may serve to immobilize the female as well as to anchor the male and place him slightly posterior, where cloacal correspondence is more likely.

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DISCUSSION

RUIBAL to RAND: You will have a hard time defending the position that a lunge and a huff take less energy than a single bite.

RAND: Yes, if by bite you mean a single nip and release. But an iguana usually bites and holds on despite the struggles of the bitten individual and this appears to take a lot of energy. Still, I would like very much to have real measurements of the costs of these activities.

RUIBAL: If 99 percent of the energy is in digging the hole, then the energy involved in display is meaningless in the economy of the animal anyway.

RAND: That is possible, but we are suggesting the contrary. We suggest that the energy used in display is important to these animals. The close correlation between energy and effectiveness of displays, for example, argues that energy costs are important. In this lizards differ from birds and mammals. The much lower maintenance energy budget of an ectotherm means that any action, even a fairly simple one, costs a much larger fraction of the energy the animal will use in the course of its day than would be the case of a homeotherm with its much higher maintenance energy budget.

CREWS to MARCELLINI: Did you ever follow one or several animals through the night to determine calling periodicity?

MARCELLINI: No, I didn't, but in captivity animals tend to call more females in the evening and morning hours.

CREWS: Did courting males call from near females or distantly; and did females stand for males after calling or did they move away?

MARCELLINI: Calls varied in distance from a few centimeters to as much as several meters. Females frequently moved away from calling males but males pursued them. There was little, if any, courtship; males simply rushed females, took a neck grip, and copulated.

JENSSEN: Before man built habitable buildings for dense populations of geckos to live in, how do you think the calls functioned in sparse natural populations of geckos?

MARCELLINI: Many populations of geckos are naturally dense, even in habitats such as trees or rock cliffs. The calls function in these situations just as in my study.

JENSSEN to FERGUSON: Did you run your density dependence analysis between years as well as between sectors within a year?

G. FERGUSON: Yes, and we did not detect density dependence. The densities between the 2 years were quite different, yet "apparent" competition was greater in the low-density year. Variation between years in carrying capacity was probably masking density dependent effects.

CREWS: Could you compare growth rates of early and late clutch hatchlings and relate differences to differences in food availability?

G. FERGUSON: Later hatchlings did grow slower. However, the temperature was lower and cloud cover was greater later in the hatching season. So, even if food were equally available to early and late hatchlings, the later ones might have grown slower due to fewer favorable growth periods per unit time.

BRATTSTROM: Have the first clutch hatchlings attained a larger size by the next spring?

G. FERGUSON: Yes, and we did not detect may have a fitness advantage over younger siblings due to dominance advantage or larger clutches, but within a size-peer group of younger (hatched later) lizards there is a definite fitness advantage of the larger ones.

RAND: In your proposed test of the predator avoidance model for the evolution of *Uta* displays, how are you going to distinguish between a lizard that gives a long display less frequently and one that gives a short display more frequently so that the total time of display for the two lizards is the same?

G. FERGUSON: One must measure frequency of display. The model assumes that display frequency is not different, but only the display complexity.

GREENBERG: The real selection in such a system is for being cryptic and displaying at the same time.

G. FERGUSON: Yes, one needs to consider other aspects of crypticity and factor these out, if possible.

RAND: Are there the same number of predators in the two types of areas?

G. FERGUSON: Probably not.

RAND: That will need to be factored out too.

G. FERGUSON: If one works in the intergrade zones of *Uta* where there are patches of high and low visibility habitat fairly close to each other, the number of predators might be roughly equivalent for the two areas and the same ones might be searching both types of habitat.

CREWS: Let me see if I understand your idea. You got a correlation between visibility in the habitat and complexity of the display, right? Because redundancy insures recognition of the conspecific, it follows that the animal has to see only part of the display to recognize a conspecific, recognize an individual, or be aroused to a certain "motivational state." Why would an animal use a complex display? Why not just do a series of very simple displays?

G. FERGUSON: In low visibility a lizard is unlikely to see an entire display.

RAND: As Gary alluded to originally, in an area with a lot of vegetation, there is a lot of leaf movement, stick movement, much of which is oscillatory, O.K.? If you want a display that can be picked out easily by a conspecific but at the same time you don't want a predator to recognize it, you want the display to be within the range of movements of the vegetation so that you are not recognized as something else. This is the argument put forth for stick insects, etc. But you want to be recognized by a conspecific so you pick a display that is stereotyped and in which the movements are somehow different. A simple display won't do it, because you are more likely to duplicate something that a leaf is doing. With a more complex display you are more likely to be doing something unique.

GANS: If another animal sees only part of a display, it can move around to see the whole display next time. But the thing that Rand mentioned is quite important to me because I have been watching tree snakes and they move only when the branches are moving. If a little wind comes up, here goes the *Ahaetulla* through the branches. As soon as the wind stops, the *Ahaetulla* stops and the next time the wind picks up you get another curious weaving movement. During every movement of the forepart of the body, a loop forms behind the head and it just moves another few inches. Then, the head stops as the wind stops. That kind of blending into the background must be exceedingly critical in recognition so what you want to do is to put some kind of a specific code into the middle. But, I'm not concerned about the conspecific not seeing the whole signal because he can move around and orient to get the rest of it.

CREWS: Has anyone figured out what the probability is of a lizard displaying a second time after it has displayed once?

JENSSEN. *Anolis limifrons* lives in the deeper forest and has a long, complex, often repeated display. *Anolis nebulosus* lives in deciduous oak where there is more of an open habitat. The display is shorter and not repeated as often.

RUIBAL: A number of times in the discussion the implication has been that this display is used for recognition of a conspecific. In the case of *Uta* they must have terrible vision if they need a display to distinguish another *Uta* from other lizards. It seems that there is a very low probability that a *Uta* would ever confuse another lizard with a *Uta* because they are so different in other characteristics.

G. FERGUSON: You are talking about distance, too. At close range there would be no problem, but further away there might be.

RAND: I have suggested that the display is not used to distinguish a conspecific from other species but from other movements in the environment. There is much more in an assertion display than species recognition information. There is sex recognition, reproductive condition, territorial ownership, etc.

RUIBAL: I agree, a great deal of information is being sent. It is clear that solitary anoles have as complex a display repertoire as those living with other congeneric forms. Therefore, the phrase that was being used, "the display is for the identification of a conspecific," may not be valid. I'm not sure that any display is necessary for identification of a conspecific. I think that conspecifics are identified much easier than that. I suggest a little restraint in the hypothetical conditions that were set up. You have some very good methods of detailed analysis to show the differences between displays, but I gather that at this point there has been very little analysis of what these movements mean to another lizard.

G. FERGUSON: Correct.

PETERSON: An important point from my perspective is that the perceived conspicuousness of a display within any given context will depend on the visual system of the observer, whether congener or predator. In cases where information is exchanged between individuals via visual signals, we can expect that the characteristics of those visual signals will have evolved together with the responses to them, as demonstrated (for auditory signals) by Roeder in his study of moths and bats, and by Straughan in his analysis of species recognition in *Hyla*. The visual system properties of those species which *respond* to a visual signal, such as a display, are as much a part of the context of that behavior as is the displaying animal's morphology or structural niche. Thus there is a real need to understand the visual system physiology of the species involved in these social or predator-prey systems if we are to fully appreciate the adaptive strategies that have evolved.

GREENBERG to JENSSEN: Have you ever seen the tongue being used to lick the substrate during a display in the manner of the *Agamas* I had described?

JENSSEN: I have seen substrate licks performed by all the anoline species I have observed. However, the substrate lick does not appear to be a part of any display. It usually occurs while a male is patrolling his territory and he is just about to move or has just moved; this is also the most frequent time to expect a signature display. Substrate licks are also frequently observed when a male is placed in a novel situation, for instance in a new cage.

QUESTION: Were your observed *nebulosus* from a single population?

JENSSEN: Yes. All were collected from Tepic, Nayarit, Mexico.

QUESTION: Is there a correlation in the Tepic population of *nebulosus* between duration of display and age or size?

JENSSEN: I tried to correlate display duration versus snout-vent length. No correlations emerged. There was only a slight tendency as animals got older for their displays to get longer.

REGAL: If one plotted the lizards' display durations it would not be a Gaussian (normal) distribution; it would be linear. It looks as if they were almost deliberately splitting the available information. If differences between the lizards' display durations were genetic variability then you would expect a Gaussian distribution.

JENSSEN: That is a good point; it would agree with my suggestion that intraindividual stereotype functions as individual recognition signals.

QUESTION: Did you ever observe a correlation between duration of display and temperature for *nebulosus?*

JENSSEN: No, however, an individual's displays were filmed under many temperature conditions, such as in the morning when the lab was cool and then progressing through the filming session it would get bloody hot under the flood lamps. The lizards never got to the point that they were panting, but they were exposed to a wide range of temperatures and still I found narrow confidence limits. If the lizards are going to separate themselves out for, say, individual recognition on the basis of display duration, they will have to maintain consistent durations under a wide range of temperatures in their natural habitat.

QUESTION: Does your classification system of the type *A limifrons* display mean that there is no difference between courtship and aggressive display?

JENSSEN: That is true inasmuch as the basic physical signal is the same. However, the recipient of the signal is different in the two social contexts. The *A* display appears in many contexts such as assertion, courtship, and challenge. Therefore, its meaning is probably determined by the characteristics of its social context, its modifiers, and its recipient.

DISTEL: In species having several display types in their repertoires, do different display types have different effects on the receiving animal? Do different signals mean something?

JENSSEN: There is no direct way of knowing how the signal is perceived and interpreted. One can only look for correlations.

REGAL: Neil Greenberg showed us how certain patterns would change throughout the day. Have you seen an indication of daily variability or a rhythm in social activity?

JENSSEN: To detect any circadian rhythm in displaying would require much field data. This I do not have for *limifrons*, but for *nebulosus*, activity generally was suppressed during the warm hours of the spring days. From about 1130 to 1430 the ambient temperature was above the preferred body temperature and displaying was rare. Moving about and socially interacting at these hours was also infrequent.

GANS: I am a little unhappy with the analysis of complex movements of this kind based entirely on the position of the head. There may be all kinds of things happening here which are not critical to the way in which the animal gets its head up and down. If that is all it is, then it does not matter for the signal whether the animals gets its head up and down by moving the arm and neck or by pushing with the shoulders. But if the receiver is looking at the shoulder movement rather than just the head movement, then it becomes very critical.

JENSSEN: I agree. The display-action-pattern graphs only depict how the head moves through time. The next thing to do is what you suggest. In my descriptive scheme, the contribution by various effectors to the production of the bob pattern should be quantified. The variations in movement of these body parts would most likely be considered modifiers. However, from a functional standpoint, how the extent to which the body parts are moved actually affects the information content of the display is a much more difficult question to find answers for.

GARRICK: I have a few observations about lizard signaling systems. Examination of three papers reporting displays of diurnal lizards showed that they combine and use signals in varied ways. Consider the following: (1) Composite displays are common among iguanid lizards that employ head nods, bobbing of the body or push ups, and extension of the throat fan. Separate displays are linked together temporally to form various combinations, e.g., the signature bob of *Anolis aeneus* (Stamps and Barlow, 1973, Behaviour, 47:67–94); (2) Graded displays employing the common Iguanid components were described for a series of male displays by chuckwallas (Berry, 1974, UC Publ. Zool. 101:1–60), and Carpenter (1967, W.W. Milstead, ed., *Lizard Ecology*, Univ. Mo. Press) observed a grading of intensity between assertion and challenge displays; (3) Individual recognition based on bob pattern were noted for *Anolis aeneus* and *Sauromalis obesus* by those workers mentioned previously; (4) The same display may be used in many different situations, e.g., flagging display of *Anolis nebulosus* (Jenssen, 1970, J. Herp. 4(1–2):1–38), and different displays may be used in the same social situations, e.g., the use of flagging and flagging-assertion displays by dominant males approached by females (Jenssen, 1790); and (5) It is also obvious that the entire problem of syntax, or order of a particular display or group of displays in the individual's sequence or its position in the complex signaling dialog between two lizards, should be examined very closely.

These examples point up that many of the ways of handling information common to other vertebrate groups also occur among the lizards and that the problem of understanding communication between lizards is open to new approaches.

MacLEAN and GREENBERG: With the thought of new approaches in mind, we would like to say how disappointed we are that Llewellyn Evans was unable to participate in the symposium and we would like to draw attention particularly to his fine study on the black lizard (1951. Am. Mus. Nov. No. 1493. pp 1-26).

Behavior and Neurology of Lizards
N. Greenberg and P. D. MacLean, eds.
NIMH. 1978.

Appendix:
Taxonomy of Lizards

Taxonomy involves the formulation and assignment of names to groups of animals. When named animals are classified, taxonomy grades into systematics, the science of describing relationships between groups of animals. Taxonomy and systematics are the bases on which meaningful conclusions may be drawn about the unity and the diversity of biological phenomena, and they are valuable heuristic and didactic tools. Indeed, first approximations of the generalizability of observational or experimental studies are founded in taxonomy and systematics and take much of their impetus from hypotheses suggested by these sciences. For convenience, three "levels" of taxonomy are often distinguished: "alpha taxonomy" (description and preliminary arrangement); "beta taxonomy" (classification developed); and "gamma taxonomy" (attempts at causal interpretations of diversity).

An excellent brief guide to the literature of reptilian classification has been provided by Gans and Parsons (1970), and many of the methodological difficulties have been reviewed and discussed by Mayr (1969). It is the intention of this list to contribute to a practical appreciation of the diversity within the taxon that includes lizards and to familiarize the student with unfamiliar species often discussed in specialized literature. This understanding is important, particularly now that the value of reptiles as research subjects is attracting the attention of researchers that may not be familiar with the herpetological literature.

There is little agreement among herpetologists on a "best" taxonomy. Using Bellairs' (1970)· criterion of convenience and utility, The taxonomy presented here is adapted from the Bellairs (1970) elaboration of Romer (1956) and is annotated with the guidance of Goin and Goin (1971), Porter (1972), Mertens (1960), Bellairs (1970), and Klemmer (ed., 1971).

SYNOPSIS

CLASS: **Reptilia**

SUBCLASS: **Anapsida**

ORDER: **Chelonia (Testudinata)**

SUBCLASS: **Lepidosauria**

ORDER: **Rhyncocephalia**

ORDER: **Squamata**

SUBORDER: **Sauria (Lacertilia)***

SUBORDER: **Serpentes (Ophidia)**

SUBCLASS: **Archosauria**

ORDER: **Crocodilia**

*SUBORDER: Sauria (Lacertilia)

The lizards; about 360 living genera and 3000 species.

INFRAORDER: **Iguania**

Family Iguanidae (iguanids)

A predominantly New World family of active, four-legged diurnal lizards, desert-living, arboreal or amphibious in habits.

Some iguanids grow up to two meters in length. Vision is the predominant sense, as in other Iguania, and many species have bright colors, and appendages such as crests and throat-fans; some can change color. Difference in appearance between male and female sometimes marked. Palate sometimes toothed. Osteoderms usually absent. Tongue broad, scarcely or not at all notched. Nearly all oviparous.

Family Agamidae (agamids)

Old World counterparts of the Iguanidae, but distinguished from the latter by acrodont teeth (except often at front of jaw); palate toothless. No limbless forms. Tongue broad, with or without slight notch. Oviparous. Known as "dragons" in Austalia where there are many genera.

Family Chamaeleonidae (true chameleons)

Mostly arboreal Old World lizards, probably of agamid descent. Skull usually adorned with casque; horns and other appendages sometimes present. Teeth acrodont. Palate toothless. Osteoderms usually absent. Feet with opposible digits. Organ of Jacobson rudimentary or absent. Tongue modified for capture of prey. Tail prehensile, no autotomy. Marked power of color change. Mostly oviparous.

INFRAORDER: Gekkota

Family Gekkonidae (geckos)

A very large family of small lizards found in warm countries throughout the world, prone to introduction in ships, fruit cargoes, etc. Head and body usually flattened. Palate toothless. Digits often modified for climbing, sometimes for movement over sand. Eyelids generally fused to form spectacle. Tongue broad, with very slight notch. Almost all oviparous, laying hard-shelled eggs.

Family Pygopodidae (snake lizards)

A small Australasian group of snake-like lizards, surface-dwellers or burrowers. Palate toothless. Osteoderms absent. Spectacle covering eye. Tongue notched. Oviparous.

INFRAORDER: Scincomorpha (Leptoglossa)

Family Xantusiidae (night lizards)

A small New World family of secretive, superficially gecko-like forms with normal limbs. Palate toothless. Osteoderms probably absent. Spectacle over eye. Tongue short, barely notched. One genus *(Xantusia)* is viviparous with well-developed placenta.

Family Teiidae (teids, whiptails)

A New World family containing some very large as well as some very small forms. In some genera the body is snake-like and the limbs reduced. No osteoderms. Palate usually toothless. Tongue forked, and long and protrusible in *Tupinambis*. Mostly oviparous; several parthenogenetic species.

Family Scincidae (skinks)

A large and cosmopolitan family, mostly living on or beneath the ground. Numerous genera have reduced limbs. Well-developed osteoderms on head and body. Palatal teeth sometimes present. Eyelids fused to form spectacle in some cases. Tongue fairly broad, slightly notched. Oviparous and many viviparous species, some with well-developed placentation.

Family Dibamidae (dibamids)

One burrowing limbless form. Systematic position doubtful; differs from burrowing skinks in lacking osteoderms. No external openings for eyes or ears.

Family Lacertidae (lacertids, true lizards)

Generalised Old World family paralleling the Teiidae in some respects but without limbless forms. Palate often with teeth. Osteoderms often present on head only. Tongue fairly long, forked at tip. Nearly all oviparous.

Family Cordylidae (girdle-tailed lizards)

African lizards, previously placed in two distinct families but probably related. Palatal teeth present in one group. Osteoderms on head, often on body. Some forms with reduced limbs. Tongue short, hardly notched. One subfamily mostly viviparous.

INFRAORDER: Diploglossa
SUPERFAMILY: Anguidae

Family Anguidae (lateral fold lizards)

A small family of Old and New World lizards, with and without limbs. Upper temporal arch and postorbital arch usually present. Palatal teeth present or absent. Osteoderms usually present. Tongue fairly long, forked tip. Oviparous or viviparous.

Family Xenosauridae (xenosaurids)

Incompletely known form with well-developed limbs; probably related to Anguidae, but with reduced osteoderms. One genus has palatal teeth. Some viviparous.

SUPERFAMILY: Platynota (Varanoidea)

Family Helodermatidea (beaded lizards)

Two North American species, both with poison fangs in lower jaw. Palatal teeth present. Osteoderms on head and body. Tongue fairly long, forked and protrusible. Oviparous.

Family Lanthanotidae (earless monitors)

A single form, *Lanathanotus borneensis*, the earless monitor of Borneo, a burrowing platynotid with a long body and short limbs. Upper Palatal teeth present. Osteoderms present. Tongue quite long with forked tip. Tiny eyes, no external ear openings.

Family Varanidae (monitors)

A single genus of Old World and Australasian lizards, some very large, with predatory habits. Palate toothless. Osteoderms generally reduced or absent. Tongue long, forked, highly protrusible. Oviparous.

INFRAORDER: Amphisbaenia (Annulata)

Family Amphisbaenidae (worm lizards)

A successful group of worm-like burrowers with reduced eyes found mainly in the warmer parts of America and Africa. The skull is massive; palate toothless. Middle ear highly modified. Well-developed median premaxillary tooth. Limbs usually absent. No osteoderms. Scales arranged in rings around the body. Oviparous and viviparous.

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Index

Note: Page numbers appearing in bold face type indicate major discussions.

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