Papéis Avulsos de Zoologia

PAPÉIS AVULSOS ZOOL., S. PAULO, VOL. 27 (15): 179-213 29.I.1974

FEEDING AND LOCOMOTOR MECHANISMS OF TEIID LIZARDS: FUNCTIONAL MORPHOLOGY AND EVOLUTION

WILLIAM P. MACLEAN

ABSTRACT

Macro- and microteiid lizards are distinguishable by large suites of morphological characters and are recognized as the subfamilies Teiinae and Gymnophthalminae, respectively. Large and small size are the primary adaptations of these two groups and are significant in escape or concealment from predators. Locomotor specializations in the two groups support this interpretation. Inertial feeding has been perfected in the Teiinae to rapidly ingest relatively small prey, while in the Gymnophthalminae, the feeding mechanism has been modified to handle relatively large prey.

INTRODUCTION

Ever increasing sophistication in understanding speciation and the events preceding it has monopolized evolutionary theory. Most students of evolution view the major features of life history as vast accumulations of population phenomena and, as such, as well understood as their components. The accumulations are, however, so vast that analysis at the population level is essentially impossible. Also, the microevolutionary phenomena cannot be imagined to be additive, but rather to have cause and effect relationships and degrees of importance, so that patterns arise which have theoretical interest. At present, patterns of macroevolution are poorly understood and major theoretical synthesis is not possible.

One approach is to examine a phylogenetic divergence in detail. The lizard family Teiidae is well suited to such a study. It is composed of two groups which are ecologically and morphologically quite distinct. These groups have long been informally recognized as macro- and microteiids, in reference to their size. The dichotomy has not been examined in detail. A short paper by Sinitsen (1928) notes that the groups differ in the relative positions of the nasal cavity and Jacobson's organ.

The object of this study is to find adaptively interpretable morphological variation in the Teiidae, above the species level and to correlate such variation with ecological diversity. An understanding of the ancestry of the family would certainly contribute to the interpretation of the adaptive dichotomy and radiations,

---

College of the Virgin Islands, St. Thomas, U.S. Virgin Islands, 00801.

however no progress was made in the direction. The Cretaceous fossil lizard *Polyglyphanodon* has been referred to as a primitive teiid by various authors (Hoffstetter, 1955 and 1962; Romer, 1966; Estes, 1969). An exhaustive examination of this form, including serial sectioning of a skull, indicates that it is not related to teiids and should probably be placed in the infraorder Iguania.

Great morphological variability in the Teiidae invites evolutionary analysis. This diversity is evident in size; the smallest teiids rival certain geckos for the title of smallest lizard and the largest are only exceeded by some species of *Varanus* and the largest iguanids. Preliminary anatomical studies (Camp, 1923; Sinitsen, 1928) and non-anotomical data (Gorman, 1970) indicate that the family is made up of two very distinct sub-groups, but is, nevertheless, a natural assemblage. Since size is obviously very important in the biology of an animal and because the teiids include a large and a small group which apparently have quite separate histories, a survey of the adaptations of each should prove interesting. This survey is limited to morphology due to the large number of genera and species in the family, the difficulty of obtaining live specimens of most genera and of applying techniques such as electromyography and motion analysis to the smaller forms. The results of this survey are used in framing hypotheses concerning the functional anatomy and adaptive strategies of the various groups of teiids and for making historical inferences about their evolution. The former can be tested by detailed analysis of living species and the latter by the discovery and study of additional fossil material. Also, such a survey is useful in expanding our knowledge of variability within the Teiidae, which can be applied to evolutionary analyses above the family level.

Attention has been focused on feeding and locomotor mechanisms for three reasons. Preliminary consideration revealed that there was variability in these systems, such as distinct types of tongues and body forms, which could be directly related to the way of life of the animal. These systems can be studied with little recourse to complex and time consuming techniques such as serial sectioning. Most important, feeding and locomotion are basic variables in vertebrate adaptation; many adaptive radiations are founded on shifts in one or both systems.

The basic assumption of this study is that feeding and locomotor mechanisms reflect phylogeny to some degree. The results include various hypotheses concerning the phylogeny of the teiid lizards. These can only be tested by a multiple character analysis such as that being done by Dr. William Presch. The data at hand is not suitable for such analysis because the character state phylogenies are almost all identical and thus have low resolution for distinguishing paralellism and convergence and because the data matrix is very incomplete.

Boulenger (1885) divided the Teiidae into four groups on the basis of external morphology. Group I comprises the macroteiids and groups II to IV comprise the microteiids. The macro- and microteiids are so obviously distinct that reasonable arguments could be advanced for separating them at the familial level. The three groups of microteiids are also quite distinct, however, the division is quite unequal, with group II including most of the genera and species and groups III and IV set apart due to very obvious external features. These are elongation and limb reduction in group III and skink-like features such as flattened head and body, reduction of a digit and cycloid scales in most genera for group IV. Group II could easily be divided into six to eight groups of status comparable to that of III and IV.

Peters and Donoso-Barros (1970) list 39 genera and 200 species in the family Teiidae. The validity of a few of the genera, such as *Ophiognomon* and *Cnemidophorus,* is doubtful, but this list is followed in this study. At the species level, the taxonomy of most genera is confused. Less than half of the recognized genera have been reviewed or described in this century. Many workers, including Thomas Uzzell, Thomas Fritts and James Dixon are working at this level and interesting zoogeographic patterns are resulting. The following list of genera and number of species included is taken from Peters and Donoso-Barros (1970). Readers unfamiliar with teiids should consult this work and Boulenger (1885).

Group I: *Ameiva* (15), *Callopistes* (2), *Cnemidophorus* (36), *Crocodilurus* (1), *Dicrodon* (3), *Dracaena* (2), *Kentropyx* (9), *Teius* (1), *Tupinambis* (4).

Group II: *Alopoglossus* (5), *Anadia* (11), *Argalia* (1), *Arthrosaura* (4), *Arthroseps* (2), *Cercosaura* (1), *Echinosaura* (1), *Ecpleopus* (2), *Euspondylus* (10), *Leposoma* (7), *Macropholidus* (2), *Neusticurus* (7), *Opipeuter* (1), *Pantodactylus* (2 or 3), *Pholidobolus* (2), *Placosoma* (3), *Prionodactylus* (4), *Proctoporus* (15), *Ptychoglossus* (7), *Stenolepis* (1).

Group III: *Anotosaura* (1), *Bachia* (18), *Colobodactylus* (1), *Heterodactylus* (2), *Ophiognomon* (3).

Group IV: *Colobosaura* (3), *Gymnophthalmus* (6), *Iphisa* (1), *Micrablepharus* (2), *Tretioscincus* (2).

Only two genera, *Ameiva* and *Cnemidophorus* (which are probably congeneric), have extensive distributions outside of South America. *Ameiva* is found throughout the West Indies, with many endemic species. *Cnemidophorus* extends north to the 40th parallel in Eastern United States and to the 45th in the west, where there are various species. Within South America, the genera are divisible into three quite distinct geographical groups. These correspond to the western and northern highlands, the lowlands and the eastern highlands. Only a few genera, such as *Bachia* and *Cnemidophorus* occur in more than one of these regions. About ten genera, including *Callopistes, Neusticurus, Echinosaura, Alopoglossus* and *Arthrosaura,* are restricted to the Andes from Northern Chile to Central America and the Guianian highlands. The greatest diversity of teiids in terms of numbers of genera and species in a small geographic area probably occurs in Eastern Ecuador or Northern Peru. A second large group of genera, including all the macroteiids except *Callopistes,* most of group IV and *Pantodactylus, Cercosaura* and a few others are in the Amazonian hylea and llanos and in the lowlands of Southern Brazil, Paraguay, Uruguay and Northern Argentina. A few genera, such as *Placosoma, Colobosaura* and *Heterodactylus* are restricted to the highlands of Southeastern Brazil.

The classification developed here designates the macroteiids, subfamily Teiinae and the microteiids, subfamily Gymnophthalminae (used at the family level by Wiegmann, 1834). The microteiids could further be divided into tribes, but this is not thought desirable at present. Three to five natural groups are easily recognizable within this group, but about half the genera cannot be so organized at this, time. Presch (dissertation, 1970) divides the Teiinae into two tribes, the Teiinii and Tupinambinii.

Acknowledgments

The greater part of this work formed part of a doctoral dissertation at the University of Chicago. I am grateful to Dr. Everett C. Olson for sponsoring that project and for being very helpful in all stages of its execution. Drs. Rainier Zangerl, David B. Wake, Robert F. Inger and Ernest E. Williams were all helpful in more ways than can be conveniently enumerated. For advice and information I am very grateful to Drs. Thomas Uzzell, Richard Etheridge, Thomas Frazzetta, Carl Gans, Pamela Robinson, Richard Estes, James A. Peters, and William Presch.

This project depended on the loan of specimens. For this favor I thank Drs. James A. Peters, Jay Savage, Ernest E. Williams, Robert F. Inger, Hymen Marx, Charles M. Bogert and Charles F. Walker. Howard Campbell and Dr. Albert Schwartz generously donated valuable specimens.

I am indebted to the National Science Foundation for support under a Graduate Traineeship and to the Gurley Fund of the University of Chicago for travel expenses within the United States. Travel to South America was financed by the Penrose Fund of the American Philosophical Society and by Mr. Laurence Rockefeller. The College of the Virgin Islands has supported my work through a reduction of teaching load and by the purchase of equipment and supplies.

Materials and methods

Skeletal material of the following Teiinae was examined: *Ameiva ameiva* (7), *A. alboguttata* (5), *A. aquilina* (2), *A. atrata* (3), *A. bifrontata* (2), *A. birdorum* (5), *A. crysolaema* (6), *A. corvina* (1), *A. dorsalis* (1), *A. edracantha* (7), *A. erythops* (1), *A. erythrocephala* (2), *A. exul* (3), *A. festiva* (3), *A. fuscata* (1). *A. maynardi* (9), *A. panchlora* (3), *A. pleii* (1), *A. pleurianotata* (2), *A. polops* (3), *A. quadrilineata* (4), *A. thoracica* (3), *A. undulata* (7), *A. wetinarei* (3), *Cnemidophorus communis* (1), *C. deppei* (2), *C. guttatus* (1), *C. hyperythrus* (2), *C. innotatus* (2), *C. inornatus* (1), *C. lemniscatus* (2), *C. neomexicanus* (1), *C. ocellifer* (2), *C. sacki* (3), *C. sexlineatus* (3), *C. stictogrammus* (1), *C. tessellatus* (1), *C. tigris* (10), *Callopistes flavopunctatus* (3), *C. maculatus* (2), *Crocodilurus lacertinus* (1), *Dicrodon guttulatum* (2), *D. heterolepis* (1), *D. barbouri* (1), *Dracaena guianensis* (4), *Kentropyx calcaratus* (6), *Teius teiou* (7), *Tupinambis nigropunctatus* (5), *T. rufescens* (1) and *T. teguixin* (7). For the Gymnophthalminae, skeletons studied are as follows (for each species, the first number is dry skeletons, the second cleared and stained and the third the number of specimens x-rayed): *Alopoglossus buckleyi* (2,1,5), *A. copei* (0,0,1), *A. festae* (1,1,0), *A.*

plicatus (0,0,1), *Anadia angusticeps* (0,0,2), *A. bogotensis* (3,0,6), *A. metallica* (1,0,1), *A. pulchella* (0,0,2), *Argalia sp.* (0,0,1), *Arthrosaura reticulata* (1,1,2), *Arthroseps fluminensis* (1,0,0), *A. werneri* (0,0,2), *Bachia sp.* (0,0,1), *B. alleni* (2,0,0), *B. barbouri* (2,1,0), *B. bicolor* (1,0,1), *B. bresslaui* (1,0,0), *B. cophias* (0,0,1), *B. d'orbignyi* (0,1,3), *B. intermedia* (4,0,0), *B. lineata* (0,1,0), *B. pallidiceps* (0,0,11), *Cercosaura ocellata* (1,0,0), *Colobosaura modesta* (0,0,1), *Colobodactylus taunayi* (1,0,0), *Echinosaura horrida* (0,1,21), *E. palmeri* (0,0,2), *E. panamensis* (1,0,0), *Ecpleopus affinis* (0,0,2), *Euspondylus bolivianus* (0,0,3), *E. brevifrontalis* (2,0,0), *E. guentheri* (0,0,2), *E. maculatus* (0,0,1), *E. ockendeni* (0,0,1), *E. simonsii* (5,0,0), *E. spinalis* (1,0,3), *Gymnophthalmus lineatus* (1,0,0), *G. speciosus* (0,1,23), *G. sumicrasti* (0,0,1), *G. underwoodi* (1,0,0), *Heterodactylus imbricatus* (1,0,1), *Iphisa elegans* (0,0,3), *Leposoma parietale* (1,1,0), *L. rugiceps* (3,0,6), *L. scincoides* (1,0,0), *L. southi* (0,0,8), *Macropholidus annectens* (1,1,0), *Microblepharus maximiliani* (0,0,2), *Neusticurus apodemus* (0,1,9), *N. bicarinatus* (0,0,1), *N. ecpleopus* (0,0,27), *N. rudis* (1,0,1), *N. strangulatus* (3,0,2), *N. tatei* (1,0,0), *Ophiognomon abendrothi* (1,0,1), *Pantodactylus schreibersii* (1,0,1), *Pholidobolus montium* (4,0,25), *Placosoma cordylinum* (1,0,2), *Prionodactylus albostrigata* (1,0,0), *P. argulus* (1,0,12), *P. manicatus* (0,0,5), *P. marianus* (2,0,0), *P. vertebralis* (1,0,4), *Proctoporus achylens* (0,0,17), *P. bogotensis* (4,0,0), *P. columbianus* (0,0,4), *P. luctuosus* (0,0,2), *P. meleagris* (0,0,6) *P. petersi* (0,2,12), *P. striatus* (0,0,12), *P. unicolor* (4,1,0), *P. ventrimaculatus* (0,0,1), *Ptychoglossus sp* (0,0,11), *P. brevifrontalis* (0,0,2), *P. festae* (0,0,39), *P. kugleri* (3,0,0), *P. plicatus* (0,0,16), *Tretioscincus agilis* (0,0,2), *T. bifasciatus* (2,1,3).

Hyoid musculature was dissected in the following Teiinae; *Ameiva bifrontata, A. festiva, Cnemidophorus sexlineatus* (2), *Callopistes flavopunctatus, C. maculatus, Crocodilurus lacertinus, Dicrodon guttulatum, D. heterolepis, D. lentiginosus, Dracaena guianensis* (2), *Kentropyx calcaratus, Teius teiou* (2), and *Tupinambis nigropunctatus* (3). And in the following Gymnophthalminae; *Alopoglossus buckleyi* (2), *A. festae, Anadia bogotensis, Arthrosaura reticulata, Bachia bicolor, B. bresslaui, B. d'orbignyi, B. lineata, Echinosaura horrida, E. palmeri, Ecpleopus affinis, Euspondylus simonsii, Gymnophthalmus speciosus* (2), *Iphisa elegans, Macropholidus annectens, Neusticurus apodemus, N. ecpleopus, N. strangulatus* (2), *Ophiognomon abendrothi, Pholidobolus montium* (2), *Prionodactylus argulus, Proctoporus petersi* and *P. unicolor.*

Feeding was observed in the following Teiinae: *Ameiva ameiva, A. exul, Cnemidophorus sexlineatus, Dracaena guianensis,* and *Tupinambis nigropunctatus* and in the following Gymnophthalminae; *Gymnophthalmus rubricauda, G. speciosus, Neusticurus ecpleopus, Pantodactylus schreibersii,* and *Proctoporus bolivianus.*

Also available were serially sectioned skulls of *Proctoporus petersi* and *Gerrhonotus multicarinatus* and dry skeletons of the following lizard families: Gekkonidae, Iguanidae, Agamidae, Chamaeleontidae, Lacertidae, Cordylidae, Xantusiidae, Scincidae, Anguidae, Varanidae, Helodermatidae, Mosasauridae, and Amphisbaenidae. All *Polyglyphanodon* and *Paraglyphanodon* material at the U. S. National Museum (listed in Gilmore 1942 and 1943) was examined and a skull of the former was serially sectioned. The fossil teiid material from the Lance formation (Estes, 1964) was briefly examined.

Most of the dry skeletons used in this study are from museum collections. Some were prepared using either trypsin or sodium hypochlorite; the former is preferred because it does not affect the bone. Clearing and staining was with trypsin and KOH, stained with alizarin red and stored in glycerine.

List of abbreviations

AMNH	American Museum of Natural History
BH	basihyal or copula
BRH	branchiohyoideus muscle
CBI	first ceratobranchial
CBII	second ceratobranchial
CH	ceratohyal
GG	genioglossus muscle
GH	geniohyoideus muscle
GHH	geniohypohyoideus muscle
HG	hyoglossus muscle
HH	hypohyal
HYH	hypohyoideus muscle
IB	Instituto Butantan
IM	intermandibularis muscle
LR	lingual rod
OH	omohyoideus muscle
SH	sternohyoideus muscle
TG	tongue
USNM	United States National Museum
WPM3rd	author's collection

ANALYSIS OF VARIATION

Skull

1. Jacobson's organ and nasal canal. — Sinitsen (1928) reported that in the Teiinae the nasal cavity is dorsal to Jacobson's organ and that in the Gymnophthalminae it is lateral to this structure. These findings are confirmed by all specimens examined in this study.

Both of these character states are considered derived from the general state in lizards. In most lizard families, the septomaxilla, which surrounds Jacobson's organ, is ventro-medial to a large nasal cavity. In all teiids, the size of the nasal cavity is greatly reduced — in the Teiinae because of the narrowness of the snout and in the Gymnophthalminae due to the relatively enormous Jacobson's organ, a result of reduction in size. Also, Jacobson's organ is relatively larger in teiids than in most other lizard families, perhaps indicating greater use of olfaction.

2. Frontal. — In all Teiinae and the genera *Arthrosaura, Gymnophthalmus, Leposoma, Tretioscincus, Bachia* and *Ophiogno-*

mon, the frontal is a flat, superficial, bone with lateral, descending ridges. In *Alopoglossus, Anadia, Cercosaura, Echinosaura, Euspondylus, Macropholidus, Neusticurus, Pantodactylus, Pholidobolus, Placosoma, Prionodactylus, Proctoporus,* and *Ptychoglossus,* the frontal is tubular, enclosing the olfactory tracts of the brain. Among other modern lizards, frontals enclosing the olfactory tracts are only known in some Platynota (McDowell and Bogert, 1954). Tubular frontals in the Gymnophthalminae is a derived state. This modification is structurally significant. With reduced size sense organs such as eyes become relatively larger. Constriction of the frontal enlarges the orbits but weakens the skull, an architectural problem which is overcome by the tubular structure. Posteriorly, the tube widens and opens near the frontal-parietal contact, but anteriorly the ventral portion of the tube contacts the prefrontals and palatines, producing a more rigid attachment of the snout than would the superficial contact of the frontal alone. The Gymnophthalminae without tubular frontals are all crepuscular litter dwellers or burrowers and have relatively smaller eyes than those with tubular frontals. In platynotans, the frontal is not tubular as it is in the Iphisinae, but the ventral portion is a narrow bridge under the olfactory tracts; it has no apparent structural significance.

3. Frontal-parietal Articulation. — The frontal-parietal contact in the Teiinae is roughly a straight line. The two bones can be weakly sutured or can form a functional joint, with the rounded posterior edge of the frontal fitting into a groove on the anterior edge of the parietal. *Teius* and *Dicrodon,* which have transversely oriented, bicuspid, occluding teeth and some of the long-snouted species of *Ameiva* and *Cnemidophorus* (such as *A. festiva*) lack a frontal-parietal joint. In these forms, precise occlusion is necessary, which would be disrupted by raising of the snout about the frontal-parietal joint. The fact that *Teius* and *Dicrodon* have relatively large pterygoid processes, which position the mandibles laterally in occlusion, supports this interpretation. Sub-adult *Tupinambis* have a functional frontal-parietal joint, which fuses in mature individuals (Hofer, 1960). The biological significance of this phenomenon is not understood, but it may be associated with the ontogenetic shift from pointed conical teeth in juveniles to blunt, molariform teeth in adults. *Dracaena,* which has extreme molariform teeth, retains a joint throughout life.

The frontal-parietal contact in the Gymnophthalminae is not a straight line; a pair of anteriorly directed tabs of the parietal overlie the frontal and a pair of posteriorly directed tabs of the frontal underlie the parietal. The frontal tabs are immediately lateral to the parietal tabs and adjacent to the postfrontal. Approximately one third of the width of the frontal-parietal contact lies between the parietal tabs. This area can be a weak, straight suture or a narrow, median fenestra.

The general pattern of the frontal-parietal contact is constant throughout the Gymnophthalminae. Variation was found in the length of the tabs. Group III has tabs far larger than those of Groups II and IV. In well sampled genera (e.g., *Neusticurus, Proctoporus*), tab length is quite variable.

Among other lizards, unstraight frontal-parietal contacts are known only in *Delma, Aprasia* and the Amphisbaenidae (all attenuate forms, with reduced limbs). The condition in the Teiinae is primitive, since it is the general condition in the Sauria. The derived state in the Gymnophthalminae is apparently a modification to suppress movement at the frontal-parietal contact. The constancy of the intricate contact pattern indicates that the feature arose only once.

4. Parietal-braincase Articulation. — In all Teiinae and most Gymnophthalminae the posterior processes of the parietal are not in contact with the braincase. This is the general condition in lizards. In *Alopoglossus, Arthrosaura, Cercosaura, Echinosaura,* some *Gymnophthalmus,* some *Leposoma,* some *Neusticurus,* some *Proctoporus,* and *Ptychoglossus* the entire posterior edge of the parietal is in contact with the braincase. The complete contact state is probably derived since it is atypical for lizards, and absent in rhynchocephalians, eosuchians, and captorhinomorphs. This feature may have some mechanical significance in consolidation of the skull, but it is probably mainly due to the relatively large size of the brain and braincase in these small forms. If accurate size distributions were available, this latter possibility could be studied.

5. Temporal Fenestra. — The temporal fenestra is roofed over in some Gymnophthalminae. This state is derived and is found in *Alopoglossus, Arthrosaura, Leposoma rugiçeps* (but not *L. parietale*), *Ptychoglossus* and *Bachia bresslaui* (but not other species). Roofing is accomplished by expansion of the squamosal and postorbital bones. Some forms have an intermediate state with the fenestra reduced to a longitudinal slit. This condition is found in *Echinosaura, Gymnophthalmus,* some *Neusticurus, Pholidobolus, Placosoma,* some *Prionodactylus* and *Tretioscincus.* Roofing of the temporal fenestra is found in a few other saurian families including most Lacertidae and Cordylidae, and some Anguimorpha. No acceptable functional interpretation of this modification can be made at present.

6. Squamosal. — All Teiinae have a dorsal process on the squamosal. This structure arises from the posterior, expanded portion of the bone, forms the rounded, posterior border of the temporal fenestra and is firmly bound to the tabular and often to the posterior process of the parietal. The squamosal bone is roughly triskelion shaped, with a long, thin anterior process, that contacts the postorbital, a short ventral process, that fits into a notch or foramen in the quadrate and the dorsal process. The Gymnophthalminae lack the dorsal process and the squamosal is of the type described by Robinson (1967) as hockey-stick shaped.

Robinson (1967) emphasized the taxonomic significance of the presence or absence of the dorsal process of the squamosal, using this feature to divide the Lacertilia into two major groups and establishing a third, equivalent group for her Kuehneosauridae (infraorder Eolacertilia, composed of three monospecific genera of Triassic gliding lizards). The changes in this feature between the Triassic and modern lizards lead to more streptostyly (movement of the quadrate relative to the temporal region) and she implies that loss of the dorsal process is a further stage of this trend. Although Robinson draws attention to possible different functions of quadrate mobility depending on the plane in which it moves, she suggests that the principal function of the peg and notch or hole articulation of this element with the squamosal is in preventing disarticulation. When present this articulation can be located anywhere in the quadrant, ranging from lateral to anterior to the parieto-tabular articulation with the quadrate. Since there is no actual contact between the quadrate and squamosal when the peg and notch articulation is present, the elements being bound by connective tissue fibers, a certain amount of movement is possible. The position of this articulation, relative to the other contacts of the quadrate head, directionally limits the movements of the quadrate. It is possible that when the squamosal peg is lateral to the tabular-paroccipital articulation, rotation of the quadrate about a transverse axis occurs, but not rotation about a longitudinal axis. This condition occurs in the superfamily Iguania (Camp, 1923). If the peg is anterior, then anterior rotation of the quadrate is more difficult and lateral rotation easier. This approximate condition occurs in Camp's Scincomorpha, including the teiids, and in the Anguimorpha. In the Teiidae the peg is 30° to 45° laterad from directly anterior to the tabular articulation.

Robinson presents no functional explanation for the loss of the dorsal process of the squamosal in most Scincomorpha and all Anguimorpha. If we extend our interpretation of the peg articulation of the squamosal located approximately anterior to the tabular articulation with the quadrate as permitting more rotation of the quadrate in a transverse than in a sagittal plane, then loss of the dorsal process of the squamosal permits the squamosal and quadrate to rotate in unison in the transverse plane. The hypothesized function of the peg and notch articulation in limiting sagittal rotation of the quadrate is not affected by the new freedom of the squamosal.

7. Middle Ear. — In all teiids, excepting Group III, the middle ear is of the normal lacertilian type described by Olson (1966). The tympanum is suspended from the posterior, concave edge of the quadrate. The ossified stapes is followed laterally by the cartilagenous extrastapedial. The extrastapedial is "L" shaped, with an anterior process that is in contact with the tympanum and evident from the exterior.

There is no tympanum in Group III. The stapes has a footplate of normal size and a very short process that contacts the exoccipital and quadrate bones. The extrastapedial is absent. This middle ear mechanism is convergent with those of other tympanumless squamates such as amphisbaenids (Camp, 1923) and snakes (Parker, 1878) though each group has its peculiarities. It is a derived state and probably functions principally in amplifying ground-born vibration. However, Gans and Wever (1972) have shown that the amphisbaenid ear is sensitive to airborn sound and probably not specialized to sense ground-born vibration. The adaptive significance of such ears would then be mainly protective, that is, not having a delicate tympanum at the surface.

8. Lacrimal-prefrontal. — All Teiinae have separate lacrimals and prefrontals, while these bones are fused (typical features of both are retained) in all Gymnophthalminae. The latter condition is derived. No functional intepretation can be made at present.

9. Suborbital Fenestra. — The suborbital fenestra in the Teiinae is bordered by the palatine, pterygoid, and ectopterygoid

bones. The maxilla is excluded by an anterior process of the ectopterygoid which narrows to a point between the former element and the palatine. Viewed dorsally, the ectopterygoid generally bifurcates, surrounding the foramen for the ramus maxillaris of V in the maxilla.

In the Gymnophthalminae, the ectopterygoid has no anterior process and the entire lateral border of the suborbital fenestra is formed by the maxilla. Viewed ventrally, the ectopterygoid merely abuts against the posterior tip of the maxilla and ventralmost surface of the jugal bone. On the orbital surface, the jugal and ectopterygoid have short, pointed processes that are in grooves on the maxilla. These processes are very short; neither contacts the lacrimal and the suborbital bar is formed almost entirely by the maxilla. This condition (jugal, ectopterygoid and maxilla loosely bound) is almost universal in lizards. Frazzetta (1962) considers this region an important joint in adduction of the snout complex. The teiine condition seems less flexible than that of the Gymnophthalminae. The former condition is considered derived since it is unique and the latter is general in other lizards.

10. Palate. — In all Teiinae and some Gymnophthalminae the choanae are immediately posterior to the orifice of Jacobson's organ. In these forms the breathing passages are deep lateral grooves between the maxillae and the vomers. These grooves lead to the interpterygoid vacuity, a medial groove in the soft palate. When the mouth is closed, the glottis rests in the posterior portion of the interpterygoid vacuity. Thus air is channeled to and from the glottis in grooves well above the resting position of the tongue. Many microteiids have a secondary palate, which encloses the anterior, paired grooves by joining the medial flanges of the maxilla and palatine with the lateral flange of the vomer. This state is found in *Alopoglossus, Arthroseps, Cercosaura, Colobodactylus, Echinosaura, Gymnophthalmus,* some *Leposoma, Macropholidus,* some *Neusticurus, Pholidobolus, Placosoma,* some *Prionodactylus,* some *Proctoporus, Ptychoglossus, Tretioscincus* and all members of Group III.

The secondary palate probably serves to keep food and saliva out of the breathing passages. It is absent in most lizards. Some Scincidae have secondary palates, but they differ in construction from those found in the Gymnophthalminae. The secondary palate is a derived state in the Teiidae (as it is in other groups).

11. Mandible. — One of the most frequently used criteria for identifying fossil teiids is the extension of the splenial bone to the mandibular symphysis (Estes, 1964). This is the case in all Teiinae and some Gymnophthalminae. Many Gymnophthalminae have reduced the exposure of the splenial. Examination of a sectioned head of *Proctoporus petersi* showed that, even though Meckel's groove is closed and fused, the splenial extends anteriad within the tubular dentary. This is not the case in iguanids with reduced splenials (Etheridge, personal communication). The splenial is large in Captorhinomorphs and Eosuchians (Romer, 1956) and its reduction is the derived state in teiids.

12. Dentition. — The dentition of lizards is surveyed by Edmund (1960a, 1960b, 1969). In the Gymnophthalminae tooth attachment

is pleurodont. The teeth are fused to a large labial lamina and their bases are free. The replacement series develops in the basal fossae of the teeth in service. No teiine has strictly pleurodont dental implantation. When a labial lamina is present, it is small. The teeth are fused to the jaw at the base and, when there is erosion to accommodate a replacement tooth, this seldom detaches the entire base, or when it does, the tooth is soon to be lost. Most Teiinae have acrodont implantation, with the bases of the teeth fused to a horizontal surface on the tooth bearing bone. In adult *Tupinambis, Dracaena, Teius* and *Dicrodon*, there appears to be no replacement. Replacement seems to be always present in microteiids, an apparently primitive condition.

Few dental specializations have been found in the Gymnophthalminae and none of these involve large modifications. The most extreme condition is in Group III, the three genera in this tribe lack accessory cusps, the teeth being conical and recurved. These teeth are reminiscent of those of some pleurodont amphisbaenids (Gans, 1957), being much more robust than snake teeth. *Bachia* and *Ophiognomon* have very few and relatively very large teeth. These genera have eleven or less teeth on the maxilla and a maximum of fifteen on the mandible. In Groups II and IV, only juveniles of a few species were found to have tooth counts (more accurately, the number of tooth positions) this low. The single specimen examined of *Heterodactylus imbricatus* had 18/19 maxillary teeth, 11 on the pre-maxilla and 23/24 mandibular teeth. The mandibular count is about in the middle of the range for the Groups II and IV, as are the other counts. The condition in *Heterodactylus* is considered primitive for Group III since it is the universal state in the presumed ancestral group, and since most attenuate lizards with reduced limbs (amphisbaenids, Gans, 1957, 1960; pygopodids, McDowell and Bogert, 1954; *Anguis,* Cooper, 1966)) have few teeth.

Number of tooth positions in lizards is correlated with size (Ray, 1965), so that, unless data are available to do regression analyses, trends in this feature can only be discussed in the most general terms. The only robust conclusion which can be drawn from the tooth count data for the Gymnophthalminae is that there definitely are trends involving tooth number. These data are summarized in figure 7. Due to the large ranges found in the few large samples, the ordering of genera by maxima in this graph can only be considered grossly indicative of order in the true spectrum. Frequency distributions for *Ptychoglossus* are nearly "flat", so that it would be equally misleading to order the small samples by their means. The only adequate means of analyzing this type of data is regression, but unfortunately, the vast majority of tooth counts are from x-rays and linear measurements cannot be obtained to an accuracy even 10 per cent, which is not sufficient for this purpose and samples are very small. Qualitatively, it is evident that the genera *Ptychoglossus* and *Alopoglossus* have dental adaptations involving more tooth positions than *Proctoporus* and *Pholidobolus* since the teeth of the former two are much narrower and close together.

The occurrence of secondary cusps in Groups II and IV is irregular. In an individual, the smaller anterior teeth are conical and the larger posterior teeth have one or two cusps. One species, *Gymnophthalmus underwoodi,* was found to have no secondary cusps.

The Teiinae have a wide range of dental specializations. The primitive condition is laterally compressed, bi- or tricuspid teeth, found in *Callopistes, Kentropyx, Ameiva, Cnemidophorus,* and *Crocodilurus,* as well as being the general condition in most lizard families. The specializations appear to follow two main trends. One trend involves transverse orientation of the (two) cusps, precise occlusion between upper and lower teeth (sometimes involving occlusal wear) and, in its most advanced conditions, development of a ridge linking the cusps. *Teius* and *Dicrodon* show stages of this trend. The other trend was described by Vanzolini and Valencia (1965) as molarization. The teeth in *Dracaena* (Peyer, 1929) and adult *Tupinambis* can be compared only to those of placodonts — large, flat, plate-like crushing teeth which, in the former genus, have their borders conforming to each other. In *Tupinambis* the condition is much less extreme than in *Dracaena* and is acquired only in the last stages of ontogeny. Juveniles have tricuspid, laterally compressed teeth. In young adults, sucessive tooth generations become increasingly expanded and flat-topped. There is no replacement in large adults, the flat-topped teeth becoming permanently fused to the maxilla and dentary. The premaxilla is not involved in these modifications nor are the anterior-most teeth of the dentary which are immediately below it. There are no juvenile specimens of *Dracaena* available for study, so it is impossible to say what situation pertains. From the evidence supplied by *Tupinambis,* it would appear that this type of dentition develops directly from the primitive condition, independent from the transverse expansion trend.

Edmund (1969) gives tooth counts for some Teiinae. In 1960, Edmund noted irregularities in the pattern of tooth replacement, possibly attributable to crowding out of tooth positions to accommodate development of larger teeth during growth. Pterygoid teeth occur in *Callopistes, Dicrodon,* some *Ameiva* and *Kentropyx* and in *Gymnophthalmus speciosus.*

Tongue

1. External Morphology. — Boulenger (1885) included tongue descriptions in generic diagnoses in the Teiidae, noting many variations. Most subsequent attention paid to teiid tongues has concerned the validity of Boulenger's principal character for separating *Cnemidophorus* from *Ameiva* — the condition of the posterior margin of the tongue, "more or less retractile at the base" in *Ameiva* and "not retractile" in *Cnemidophorus* (see Vanzolini and Valencia, 1965 for recent comments). Boulenger described the general condition of the tongue in teiids as "arrow headed." This consists of a narrow, bifid, smooth anterior portion and a papillate posterior part which has a bilobate rear margin.

The general external shape of the tongue in teiids is the universal condition described by Boulenger for eighteen of the twenty-one lizard families he listed. Aside from the Teiidae, the two exceptions are the Varanidae, which have long, thin, greatly extendable tongues and the Chamaeleontidae, which have a highly specialized mechanism consisting of a fleshy projectile attached to a stalk longer than the body of the lizard.

The Teiidae exhibit much more diversity in tongue morphology than does any other family of lizards. The genera *Kentropyx, Cnemidophorus, Dicrodon, Teius,* and *Crocodilurus* and all Gymnophthalminae have the "typical" tongue described above. The tongues of these Teiinae are somewhat narrower than those of microteiids, conforming to the narrower dental arcades. *Dracaena, Ameiva* (if the intermediate states between this genus and *Cnemidophorus* are ignored) and *Callopistes* lack the posterior, glandular flaps and the tongue is somewhat retractile into the floor of the mouth. These three genera have wide posterior, glandular areas, but they taper, rather than ending in lobes. *Tupinambis* has a long tongue, of nearly equal width throughout, which lacks expanded glandular areas. The tongue of *Tupinambis* is retractile into a sheath at its base and is free from the floor of the mouth anterior to the sheath (reminiscent of a varanid tongue). The tongues of other teiids examined are attached for approximately half the length of the glandular, expanded area.

2. Hyoid Skeleton. — Zavattari (1908) and Fürbringer (1922) surveyed the hyoid skeleton of lizards. The medial portion of the hyoid skeleton is beneath the glottis, which is immediately posterior to the tongue. This is the copula or basihyal, a triradiate bone with a thin anterior process, which usually terminates in the base of the tongue, and paired postero-lateral processes, which are much more robust. A thin rod of calcified cartilage lies between the hyoglossus muscles in the body of the tongue and is embedded in the intrinsic musculature. This rod terminates near the tip of the anterior or lingual process of the copula and extends anteriad, almost to the bifurcation of the tongue. Jollie (1960) called it a detached anterior process of the basihyal. *Callopistes* differs from other teiids in the position of the basihyal, which is much farther posterior. The lingual process of the basihyal is very long in this genus and its tip lies beneath the glottis. The postero-lateral processes in the Gymnophthalminae are distinctly more laterally oriented than are those of the Teiinae (Fig. 12).

Two long rod-shaped bones are attached to the lateral terminus of the basihyal on either side. The antero-laterally directed rod is the hypohyal and the postero-laterally directed bone is the first cerato-branchial. The hypohyal terminates near the lingual surface of the mandible, just beneath the floor of the mouth. This element is relatively longer in microteiids than in macroteiids. The ceratohyal, another rod shaped bone, is attached to the posterior edge of the hypohyal and is posteriorly directed, anterior and parallel to the first ceratobranchial. Both the hypohyal and the first ceratobranchial curve upwards, separated from the throat skin by thin sheets of muscle and terminating just posterior to the tympanum. The first ceratobranchial in the Teiinae is an approximately straight rod, except for its upward curvature, following the roundness of the throat. In the Gymnophthalminae, this element is almost longitudinally oriented medially and laterally oriented distally (Fig. 12). Attached to the termini of the ceratohyal and first ceratobranchial are thin, cartilagenous epi-elements, which in some forms (e.g., *Cnemidophorus sexlineatus*) are attached to the posterior surface of the braincase (exoccipital). Many Gymnophthalminae have disjunct epi-elements, one portion attached to the cerato-element and the other to the braincase. Second ceratobranchials are thin, tapered, posteriorlly directed cartilage rods which are attached to the posterior edge of the basihyal. The second ceratobranchials in *Callopistes* are relatively about four times longer than those of any other teiid (Fig. 9). This element is vestigial in all teiids and little significance can be attached to its large size in this genus. Many microteiids and a few macroteiids lack second ceratobranchials.

A teiid hyoid is distinguishable from that of all other lizards except amphisbaenids by its large hypohyals, which extend far beyond the base of the ceratohyal. The hyoid skeleton in the Amphisbaenidae (Camp, 1923; Fürbringer, 1922; Richter, 1933; Jollie, 1960; Gans, 1960) is very similar to that of teiids, but it is about half its size relative to skull length. The Iguania (Iguanidae, Agamidae, Chamaeleontidae differ in hyoid structure from all other lizards in their large, apposed second ceratobranchials, which are associated with gular fans. The presence of a large hypohyal in only one highly derived family besides teiids, indicates that this may be a derived feature in the Teiidae. Large hypohyals have not been found in embryonic lizards or *Sphenodon* (DeBeer, 1937) which supports the view that it is a derived structure.

3. Hyoid Musculature. — The hyoid musculature of lizards has been surveyed by Richter (1933), Zavattari (1910, 1911) and Edgeworth (1935). Oelrich (1956) gives an excellent description for *Ctenosaura*. The hyoglossi muscles of teiids, which have been mentioned above as forming the core of and terminating in the tips of the tongue, run posteriorly, ventral to the hypohyal, to insert on the first ceratobranchials in all squamates (MacLean, 1968). In Iguanids and agamids, which have fleshier and less extensible tongues than teiids, the hyoglossi are robust and insert on the proximal portion of the first ceratobranchial (Gandolfi, 1908). In the Gymnophthalminae the hyoglossi are somewhat less robust, closer to fusiliform than flat, and insert on the first ceratobranchial immediately lateral to its inflection (Figs. 10, 11, 12). In all Teiinae except *Callopistes* the hyoglossi are narrow and fusiliform, running posteriorly in a groove formed by a curved medial portion of the hypohyal and the parallel edges of the ceratohyal and first ceratobranchial, to insert on the tip of the ceratobranchial (Figs. 8, 12). This state is derived, since the microteiid state is almost universal in other lizards. The hyoglossi retract the tongue by contracting and greater length would permit greater extensibility. The tongue is extended by the genioglossus muscles, which originate on the mandible near the symphysis and insert on the hyoglossus muscles anterior to the basihyal.

In both species of *Callopistes*, the hyoglossus muscle inserts on the medial half of the first ceratobranchial (Fig. 17) as it does in the Gymnophthalminae. *Tretioscincus bifasciatus* approaches the teiine condition in having the insertion of the hyoglossus on the distal quarter of the ceratobranchial. Genioglossus muscles are lacking in Group III; it appears that their tongues are either not capable of protraction or are protracted slightly by muscles which can move the hyoid forward (Fig. 21).

Two muscles connect the hyoid apparatus to the shoulder girdle. The omohyoideus muscle has its origin on the anterior edge of the clavicle and inserts on the ventral surface of the basihyal and on the posterior edge of the first ceratobranchial. These paired muscles are always apposed along the midline. Deep to the omohyoideus is the sternohyoideus muscle, which originates on the sternum and inserts on the posterior edges of the basihyal and first ceratobranchial. The second ceratobranchials, when present, are between the sterno- and omohyoideus. In *Callopistes* and most Gymnophthalminae the sternohyoidei do not insert on the basihyal and are not apposed, as they are in other Teiinae. The sternohyoideus muscles are absent in Group III.

The hyoid skeleton is attached to the mandible on either side by two muscles. The larger of these is the geniohyoideus, a large, flat sheet which runs from the ventro-medial edge of the coronoid region of the ramus to the anterior facing edges of the first ceratobranchial and basihyal. In teiids, the medial borders of the geniohyoideus muscles diverge, but in *Callopistes* and *Dicrodon lentiginosus* they are apposed for their entire length, their origin reaching the mandibular symphysis. In *Crocodilurus*, *Dracaena* and *Dicrodon lentiginosus* there is interdigitation of the geniohyoideus and the anterior portion of the intermandibularis (a thin transverse band connecting the rami), but in all other teiids examined, the anterior slip of the intermandibularis is immediately deep to the geniohyoideus. Interdigitation of these muscles is widespread in other families of lizards. The posterior portion of the intermandibularis is a thin sheet of muscle, superficial to all of the hyoid muscles, which runs between the posterior halves of the mandibles. Posterior and more or less continuous with this muscle is the constrictor colli musculature, which wraps around the neck.

The second muscle running from the mandible to the hyoid is the geniohypohyoideus. The anterior portion of the origin of this muscle on the mandible is deep to the insertion of the anterior intermandibularis. The posterior extent of the origin of the geniohypohyoideus is variable and depends on its width, which ranges from a thin ribbon (*Proctoporus*, Fig. 10) to a substantial sheet (*Cnemidophorus sexlineatus*, Fig. 8). The geniohypohyoideus inserts on the hypohyal or the ceratohyal, or splits and inserts on both.

Two muscles are confined to the hyoid. The hypohyoideus runs between the hypohyal and the ceratohyal. It varies from a ribbon connecting the distal ends of these elements to a sheet attached to the entire anterior edge of the ceratohyal and most of the posterior edge of the hypohyal. The branchiohyoideus muscles connect the ceratohyal to the first cerotobranchial. In *Macropholidus annectens* the branchiohyoideus lies lateral and deep to the hyoglossus, due to the unique condition of the latter muscle discussed above. The branchiohyoideus muscle is absent in Group III. In other Gymnophthalminae examined and *Callopistes* the branchiohyoideus is lateral to the hyoglossus. In other macroteiids, the branchiohyoideus is deep to the genioglossus, the insertion of the latter muscle lying distal to the former.

The condition of the hyoglossus muscle in the Teiinae, excepting *Callopistes*, is a derived state and a specialization which increases the extensibility of the tongue. *Callopistes* and the Gymnophthalminae are primitive in this regard.

Group III, which has derived states of many features not related to the tongue, has lost the sternohyoideus, branchiohyoideus and genioglossus muscles. The other muscles retain a typical microteiid arrangement (Fig. 11). but without genioglossus muscles, only very limited protraction of the tongue seems possible.

The impasse to better understanding of the functioning of teiid hyoid apparatuses is the lack of knowledge concerning the movements and deformations of the hyoid skeleton. Langebartel (1966) considers the hyoids of snakes and a few lizards as immobile, with all of the muscles not directly associated with the tongue functioning only to stabilize the hyoid. Observation of live *Dracaena* and *Tupinambis* clearly shows that this is not the case in teiids. The outlines of the ceratohyal and first ceratobranchial on the throat move forward when the tongue is protracted. It also seems that elements become more horizontal, but little confidence can be placed in this kind of observation. Without more detailed information on these movements, it is impossible to associate variations in structure with different functions.

Trunk and Limbs

1. Number of Presacral Vertebrae. — All Teiinae examined have 24 or 25 presacral vertebrae. Presacral counts in the Gymnophthalminae range from 24 to 50 (Fig. 13). Number of body vertebrae is directly related to relative body length in the Gymnophthalminae, the individual vertebrae being of approximately the same proportions in all species. Group II and IV have 24 to 34 presacrals. Eight genera have only 24 or 25 presacral vertebrae: *Arthrosaura, Leposoma, Pholidobolus, Placosoma, Arthroseps, Ecpleopus, Macropholidus,* and *Pantodactylus.* Seven genera have representatives in this low range, and others which ranged higher: *Echinosaura, Neusticurus, Prionodactylus, Euspondylus, Proctoporus, Alopoglossus* and *Ptychoglossus.* The remaining nine genera examined (including one undescribed genus) ranged higher than 25 presacrals: *Argalia, Tretioscincus, Anadia, Calliscincopus, Microblepharus, Iphisa, Colobosaura* and *Gymnophthalmus.*

Group III has between 34 and 50 presacral vertebrae, the entire range being encompassed by the ten species of *Bachia* examined. The single count for *Heterodactylus* was 36 and single count for *Ophiognomon,* 46.

It is likely that 24-25 presacral vertebrae is the primitive state in teiids. This range is associated with typical lizard ("lacertiform") body form in teiids. Hoffstetter and Gasc (1969) refer to 24 presacral vertebrae as a fundamental number in lizards and their discussion indicates that they think it is the primitive state. Eosuchians, rhyncocephalians and Captorhinomorpha approximate this value.

In *Anadia,* which has a wide range of presacral counts, there is some indication that longer bodied forms occur at lower altitudes (Dunn, 1944).

2. Dermal-vertebral Correlation. — In all Gymnophthalminae with more than 25 presacral vertebrae and in a portion of those with this count, there are either one or two dermal segments (usually annuli) per vertebra. These correlations are arrived at by examining x-rays in which both vertebrae and scutulation are evident. Precise correlation means that the border of each or of alternate dermal segments corresponds to a given position on a vertebra. If this was

not the case, then counts were made of the number of dermal segments corresponding to the number of dorsal vertebrae. Those Gymnophthalminae with 24 and some of those with 25 body vertebrae have their body scales arranged seemingly at random relative to the metameric segmentation (about 1 1/2 dermal segments per vertebra). In the few specimens which were examined with this situation in mind, those with precise dermal-vertebral correlation had heavy sub-dermal musculature and slips of the rectus abdominis attached to the posterior edge of each dermal segment. The forms without precise correlation have much less sub-dermal musculature and no dermal association with the trunk muscles. Precise dermal-vertebral correlation is problably a derived state in teiids, since it is associated with elongation. The distribution of this character in other squamates is confused. Alexander and Gans (1966) clarified the situation in snakes and amphisbaenids, finding that these groups, excepting the Typhlopidae, have precise correlation, be it 1 to 1 or 1 to 2. It is impossible to use Camp's (1923) and Stehli's (1910) information here, since both of these workers seem to have counted dermal segments and vertebrae separately and, assuming that the correlation is always a whole number ratio, assigned the closest ratio, ascribing discrepancies to method. Their conflicting arguments about the primitiveness of one or the other ratio must be rejected and new data collected and analyzed.

The dermal-vertebral correlation in the autotomizing portion of the tail of teiids is always 2 to 1. An annulus corresponds to the anterior half and another to the posterior half of each autotomizing vertebra. The first three to seven caudal vertebrae do not autotomize and the dermal-vertebral correlation is the same here as on the body. Dermal-vertebral correlation in the caudal region is known only in the Amphisbaenidae, among other families of lizards, where it is 2 to 1 except in *Blanus,* where it is 1 to 1, as it is in snakes (Alexander & Gans, 1966).

3. Abdominal Skeleton. — The Teiinae have a xiphisternal arrangement similar to that found in the Iguanidae (Etheridge, 1965). The two abdominal ribs posterior to the last sternal rib meet a xiphisternal rod on each side, which is attached to the sternal plate anteriorally. In the Gymnophthalminae, there is a medial xiphisternal rod, to which attach two or three pairs of inscriptional ribs. The inscriptional ribs posterior to the xiphisternal ribs do not meet or contact any skeletal element medially in these forms.

In Group III the abdominal skeleton is highly modified, as it frequently is in elongate lizards (Camp, 1923). In the three cleared and stained specimens I have examined, there was a median xiphisternal rod to which one pair of inscriptional ribs was attached. Thus the asymmetrical conditions in Camp's illustration is probably anomalous. The eleven to fifteen pairs of inscriptional ribs posterior to the pair of xiphisternal ribs are attached to medial, ventral elements. Etheridge (1965) prefers not to call these elements parasternae, since they are cartilaginous and not homologous with the bony parasternalia of *Sphenodon* and archosaurs, which are of dermal origin. Similar median elements have been developed independently in burrowing forms in other families (Camp, 1923) and are probably not homologous with any elements of forms which lack post-xiphisternal, median, abdominal, skeletal structures.

The teiine condition, paired xiphisternal rods, which is found in the Iguania and many other lizards as well, is probably the primitive state in teiids. The condition found in Groups III and IV can be considered derived from the teiine states; median xiphisternal rods are not known outside the Gymnophthalminae. Due to its median xiphisternal rod, the arrangement found in Group III may be considered derived from that found in Groups II and IV.

4. Limbs. — All Group IV microteiids examined show some phalangeal reduction in the manus. In all forms, except *Macropholidus annectens,* the first digit is reduced: this ranges from very short first two phalanges (of three), as in *Tretioscincus bifasciatus* and *Micrablepharus,* to a single phalanx in all species examined of *Gymnophthalmus. Macropholidus annectens* is unique in having three short phalanges in the first digit and five in the fourth, as opposed to the usual six. No phalangeal reduction was found in any species of Group II.

Only *Dicrodon* and *Teius* among macroteiids exhibit any phalangeal reduction. In *Dicrodon* the first digit of the pes has two short phalanges, in place of the usual three. This digit is lacking in *Teius.* The manus and pes are degenerate in Group III. Not more than three short digits occur on the former and two on the latter. Boulenger (1885), Camp (1923) and Fübringer (1870) adequately document the reduction of the extremities, in these forms.

DISCUSSION

Feeding Mechanisms

The Teiinae are specialized for inertial feeding. The frontal-parietal joint serves to raise the snout segment relative to the occipital segment (Frazzetta, 1962), thus quickly disengaging the teeth from the prey. The tongue has little function in ingestion and can become specialized for olfaction as in varanids and snakes. In *Tupinambis,* the long narrow tongue often hangs limply out of the angle of the mouth during feeding. *Dracaena* is an exception. This lizard has been observed to carefully manipulate food with the tongue, when feeding on snails, but it can also feed inertilly on other prey. The ectopterygoid-maxila contact in the Teiinae is strengthened to increase the rigidity of the snout segment. The dental arcades are narrowed, resulting in a rearrangement of the nasal cavities and Jacobson's organs. The teeth are fused to the jaws at their bases, to withstand increased shocks.

The Gymnophthalminae, because their primary adaptation is being small, ingest relatively larger prey than the Teiinae. Thus, the quadrates are more freely suspended from the occipital segment, so that they can swing laterally and increase the gape. The tongue functions to manipulate the prey in the mouth. The frontal-parietal joint is lost, but the maxila is loosely attached to neighboring elements, so that the upper dental arcade can widen. These anatomical conclusions have been confirmed by extensive laboratory observations of feeding in *Neusticurus ecpleopus.* In the semi-aquatic microteiids the tongue protrudes only very slightly in olfaction (a small fraction of the head length, as contrasted with close to twice the head length in *Tupinambis*). During feeding, the tongue is active in manipulating food .in the mouth. This is especially evident when large morsels are being ingested. Rocking of the quadrates and advance of the mandibles, independent of the skull, were easily observed. When eating smaller items, *Neusticurus* occasionally uses inertial feeding.

Locomotion

In one meristic character, presacral vertebral count, many genera and some species of Gymnophthalminae are more variable than all Teiinae combined. Stability of this character and of general body-limb proportions in the Teiinae indicates adaptive stability of the locomotion system. "High performance" locomotion is a central adaption of the Teiinae, while it is much less so in the microteiids. Preliminary support comes from Urban's (1965) "quantitative study of locomotion in teiid lizards". Motion analysis of running in five teiine genera (*Ameiva, Cnemidophorus, Teius, Tupinambis,* and *Crocodilurus*) and one gymnophthalmine (*Pholidobolus*) showed that the microteiid was by far the poorest performer in size independent measurements. An integration study (Olson and Miller, 1958), would probably show that this system is more highly integrated in the Teiinae than in the Gymnophthalminae.

CONCLUSION

Phylogeny and Adaptation

The macro-microteiid dichotomy is the major feature of the descent of modern teiid lizards. Morphology and ecology clearly indicate that the Teiinae and Gymnophthalminae are natural groups.

Size and feeding mechanisms are the key morphological differences between subfamilies. The Teiinae have frontal-parietal joints, squamosal with dorsal processes, rigid maxilla-ectopterygoid contacts, acrodont or sub-acrodont tooth implantation and extendable tongues. The Gymnophthalminae have suppressed the frontal-parietal joint, have lost the dorsal process of the squamosal, have flexible contact between maxillae and ectopterygoids, retain pleurodont tooth attachment and fleshy tongues which are only slightly extendable.

Gymnophthalminae are specialized primarily in their shape. The advantage of small size for an insectivorous lizard is in escape from the notice of predators. They produce two eggs per clutch, one from each oviduct. Dybas (1966) reports the same adaptation in the smallest beetles. This reproductive limitation can be compensated for by laying various clutches in a single year. Indirect evidence for this phenomenon in *Euspondylus brevifrontalis* is given by Fouquette (1968). The prey are much larger relative to Gymnophthalminae than to Teiinae. The feeding mechanism is modified in the former to increase gape and the frontal-parietal joint, which in the larger forms functions in inertial feeding, is discarded. The maxilla-ectopterygoid flexibility and presumed associated loosenings allow the upper dental arcade to widen, while loss of the dorsal process of the squamosals permits lateral swing of the quadrates and wider separation of the mandibular rami. The tongue is broad and muscular and functions in food manipulation, besides olfaction.

Inertial feeding may be, in general, a mechanism for rapidly ingesting moderate to small sized food particles. In the Teiinae this speed would be an advantage, since a conspicuous animal is vulnerable while feeding. Although no motion analysis have been done on teiid feeding, some Teiinae with extremely narrow dental arcades, appear to have the most highly developed inertial feeding mechanisms among lizards.

Whereas the Gymnophthalminae rely on secretiveness and have thus been able to experiment widely with body and limb proportions, the Teiinae escape from, rather than escape the notice of predators and their body and limb proportions are relatively constant.

Taxonomy

Among the twenty odd families of lizards, there are relatively few pairs which are indisputably closely related. Examples of such pairs are the Agamidae — Chamaeleontidae, Iguanidae — Agamidae, Varanidae — Mosasauridae, Gekkonidae — Pygodidae, and Lacertidae — Gerrhosauridae. The dichotomy in the Teiidae is not comparable to the taxonomic distances between these most closely related pairs of lizard families, although an unequivocal statement will have to be based on quantitative analysis. In addition, division of the Teiidae into two families would not result in clarification for students who are not intimately familiar with the classification of lizards. Thus the decision was made to divide the Teiidae into two subfamilies. Diagnoses for the family and subfamilies are presented below. It is noteworthy that all previous anatomical diagnoses of the family (i. e., Camp, 1923; Romer, 1956) exclude the microteiids.

Family Teiidae

Skull arches present, the temporal fenestra generally open, the parietal not expanded laterally over the fenestra. Frontals and parietals unpaired. Postfrontal small or fused with postorbital which is well developed. Supra-temporal generally well developed, extending forward along lateral margin of parietal process. Parietal foramen generally absent. Supraorbital absent. Descending flange of pterygoid weakly developed. Vomers elongate; interpterygoid vacuity narrow, the palatines meeting anteriorly. Dentition generally heterodont. Teeth large. Replacement teeth developed in sockets at tooth bases. Second ceratobranchials and hypohyals present. Zygosphenezygantrum articulations present. Scapulocoracoid and both coracoid fenestrae present. "Parasternum" generally absent. No osteoderms on head or body.

Subfamily Teiinae, New Subfamily
(Macroteids, Boulenger's Group I)

Temporal fenestra open. Postfrontal and postorbital frequently fused; when separate, jugal and postfrontal in contact, excluding postorbital from orbit. Functional joint generally present at frontal-parietal contact. Dorsal process of squamosal prominent. Lacrimal present. Ectopterygoid excludes maxilla from suborbital fossa. Dentition strongly heterodont. Teeth acrodont or sub-acrodont. Replacement frequently suppressed in adults. Teeth conical, blunt bi- or tricuspid. Pterygoid teeth present in a few genera. Descending flanges of frontal weakly developed. Splenial large, continuous to symphysis. Hyoglossus muscle incerts on distal tip of first ceratobranquial except in *Callopistes*. Two caudal annuli per vertebra. Large, active, diurnal lizards common throughout tropical and temperate North, South and Middle America and Antilles.

Subfamily Gymnophthalminae, New Subfamily

(Microteiids, Including Boulenger's Groups II, III and IV)

Temporal fenestra frequently roofed over by postorbital and squamosal. Postfrontal and postorbital not fused. Jugal and postfrontal not in contact; postorbital included in orbital margin. Frontal and parietal strongly sutured by median, superficial frontal tabs and lateral, deep parietal tabs. Dorsal process of squamosal absent or, if present, a secondary development associated with roofing over of temporal fenestra. Lacrimal absent. Maxilla forms entire lateral border of suborbital fossa. Dentition weakly heterodont. Teeth strongly pleurodont, conical, bi- or tricuspid. Replacement not suppressed in adults. Pterygoid teeth absent. Descending flanges of frontal generally well developed and frequently fused ventrally to form a tube. Splenial small, frequently extending anteriorly only to alveolar foramen. Hyoglossus muscle inserts medially on first ceratobranchial. Small, generally secretive lizards which are most diverse on the Amazonian slopes of the Andes. Moderately diverse in the Guiana highlands and the slopes of the Brazilian Plateau. Range includes most of the American tropics, the western slopes of the northern Andes and the southernmost Antilles.

REFERENCES

ALEXANDER, A. A. & C. GANS

1966. The pattern of dermal-vertebral correlation in snakes and amphisbaenids. *Zool. Med. Leiden 41* (11): 171-190.

BOULENGER, G. A.

1885. *Catalogue of the lizards in the British Museum (Natural History)*, vol. 2. 497 pp. London.

CAMP, C. L.

1923. Classification of the lizards. *Bull. Amer. Mus. Nat. Hist. 48:* 289-481.

COOPER, J. S.

1966. Tooth replacement in the slow worm (*Anguis fragilis*). *Jour. Zool. 150*: 235-248.

DEBEER, G. R.

1937. *The development of the vertebrate skull.* XVIII + 552 pp. Oxford: Clarendon Press.

DUNN, E. R.

1944. The lizard genera *Anadia* and *Ptychoglossus* in Colombia. *Caldasia* 3: 63-68.

DYBAS, H. S.

1966. Evidence for parthenogenesis in the featherwing beetles, with a taxonomic review of a new genus and eight new species (*Coleoptera: Ptiliidae*). *Fieldiana* (*Zool.*) *51*: 11-52.

EDGEWORTH, F. H.

1935. *The cranial muscles of vertebrates.* 493 pp. London: Cambridge University Press.

EDMUND, A. G.

1960a. Evolution of dental patterns in the lower vertebrates. In "Evolution. Its science and doctrine." *R. Soc. Can. Studia Varia Ser.* 1960 (4): 45-62.

1960b. Tooth replacement phenomena in the lower vertebrates. *Contr. Roy. Ontario Mus., Life Sciences Div. 52*: 1-190.

1969. Dentition. In *"Biology of the Reptilia"*, Gans *et al.* ed., pp. 117-200. Academic Press.

ESTES, R.

1964. Fossil vertebrates from the late Cretaceous Lance Formation, Eastern Wyoming. *Univ. Cal. Publ. Geol. Sci. 49*: 1-180.

1969. Relationships of two Cretaceous lizards (Sauria, Teiidae). *Breviora 317*: 1-8.

ETHERIDGE, R.

1965. The abdominal skeleton of lizards in the family Iguanidae. *Herpetologica 21*: 161-168.

FOUQUETTE, M. J. JR.

1968. Observations on the natural history of microteiid lizards from the Venezuelan Andes. *Copeia 1968*: 881-884.

FRAZZETTA, T. H.

1962. A functional consideration of cranial kinesis in lizards. *Journ. Morph. 3*: 287-320.

FÜRBRINGER, M.

1870. *Die Knochen und Muskeln der Extremitäten bei den Schlangenähnlichen Sauriern.* 135 pp. Leipzig.

1922. Das Zungenbein der Wirbeltiere insbesondere der Reptilien und Vögel. *Ab. Heidelberger Ak. Wiss. B.* (11): 1-164.

GANDOLFI, H.

1908. Die Zunge der Agamidae und Iguanidae. *Zool. Anz. 32*: 569-580.

GANS, C.

1957. "Anguimorph" tooth replacement in *Amphisbaena alba* Linnaeus, 1758, and *A. fuliginosa* Linnaeus, 1758 (Reptilia: Amphisbaenidae).

1960. Studies on the amphisbaenids (Amphisbaenia: Reptilia). 1. A taxonomic revision of the Trogonophinae and a functional interpretation of the amphisbaenid adaptive pattern. *Bull. Amer. Mus. Nat. Hist. 119* (3): 129-204.

GANS, C. & E. G. WEVER

1972. The ear and hearing in Amphisbaenia (Reptilia). *J. Exp. Zool. 179* (1): 17-34.

GORMAN, G. C.

1970. Chromosomes and the systematics of the Family Teiidae (Sauria, Reptilia). *Copeia* 1970: 230-245.

HOFER, H.

1960. Vergleichende Untersuchungen am Schädel von Tupinambis und Varanus mit besonderer Berücksichtigung ihrer Kinetik. *Morph. Jahbr. 100* (4): 706-746.

HOFSTETTER, R.

1955. Squamates de type moderne. In *"Traité de Paléontologie V"*, J. Piveteau ed., pp. 606-662. Paris: Masson.

1962. Révue des recentes acquisitions concernant l'histoire et la systématique des squamates. Prob. Actuels Paleon. (Evolution des Vertebres), *Coll. Internat. Centre Nat. Recher. Sci. 104*: 243-279.

HOFFSTETTER, R. & J.-P. GASC

1969. Vertebrae and ribs of modern reptiles. In *"Biology of the Reptilia"*, Gans *et al.* ed., pp. 201-310. Academic Press.

JOLLIE, M. T.

1960. The head skeleton of the lizard. *Acta Zool. 41*: 1-64.

LANGEBARTEL, D. A.

1968. The hyoid and its associated muscles in snakes. *Ill. Bio. Mono. 38*: 1-156.

MACLEAN, W. P. 3RD.

1968. Review of Langebartel's "The hyoid and its associated muscles in snakes." *Copeia 1968*: 654-655.

MCDOWELL, S. B. & C. M. BOGERT

1954. The systematic position of *Lanthanotus* and the affinities of the anguinomorphan lizards. *Bull. Amer. Mus. Nat. Hist. 105* (1): 1-142.

OELRICH, T. M.

1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). *Misc. Publ. Mus. Zool., Univ. Michigan 94*: 1-22.

OLSON, E. C.

1966. The middle ear — morphological types in amphibians and reptiles. *Amer. Zool.* 6: 399-419.

OLSON, E. C. & R. A. MILLER

1958. *Morphological integration.* 317 pp. Univ. of Chicago Press.

PARKER, W. K.

1878. On the structure and development of the skull in the common snake (Tropidonotus natrix). *Phil. Trans. Roy. Soc.* (London) *169*: 385-418.

PETFRS, J. A. & R. DONOSO-BARROS

1970. Catalogue of the Neotropical Squamata: Part II. Lizards and Amphisbaenians. *Bull. U. S. Nat. Mus. 297*: VIII + 293 pp.

PRESCH, W. F. JR.

1970. *The Evolution of Macroteiid Lizards: An Osteological Interpretation.* 266 pp. Univ. of S. Cal. Ph. D. diss.

RAY, C. E.

1965. Variation in the number of marginal tooth position in three species of iguanid lizards. *Breviora 236*: 1-15.

RICHTER, H.

1933. Das Zungenbein und seine Musculatur bei den Lacertilia vera. *Jena. Z. Naturw. 66* (3): 395-480.

ROBINSON, P. L.

1967. The evolution of the Lacertilia. *Prob. Actuels Paleon. 163*: 395-407.

ROMER, A. S.

1956. *Osteology of the reptiles.* XXI + 772 pp. Univ. of Chicago Press.

1966. *Vertebrate paleontology.* 468 pp. Univ. of Chicago Press.

SINITSEN, D. T.

1928. The types of the skull in the family Teiidae. *Zool. Anz. 76*: 232-236.

STEHLI, G.

1910. Über die Beschuppung der Reptilien. *Jena Zeitschr. Natur. 46*: 737-800.

URBAN, E. K.

1965. Quantitative study of locomotion in teiid lizards. *Animal Behaviour 13*: 513-529.

VANZOLINI, P. E. & J. VALENCIA

1965. The genus *Dracaena*, with a brief consideration of macroteiid relationships (Sauria, Teiidae). *Arq. Zool. Est. S. Paulo 13*: 7-35.

WIEGMANN, A. F. A.

1834. *Herpetologia Mexicana seu descriptio amphibiorum Novae Hispanniae. Pars prima. Saurorum species.* VI + 54 pp., 10 pls. Berlin: C. G. Luderitz.

ZAVATTARI, E.

1908. Materiali per lo studieo dell'osso ioide dei Sauri. *Atti R. Accademia Scienze Torino 43*: 706-713.

1910. I muscoli ioidei dei sauri in rapporto con i muscoli ioidei degli altri vertebrati. Prima parte. *Memorie R. Accademia Scienze Torino, serie seconda 60*: 351-392.

1911. I muscoli ioidei dei sauri in rapporto con i muscoli ioidei degli altri vertebrati. Parte seconda. *Memorie R. Accademia Scienze Torino, serie seconda 61*: 55-134.

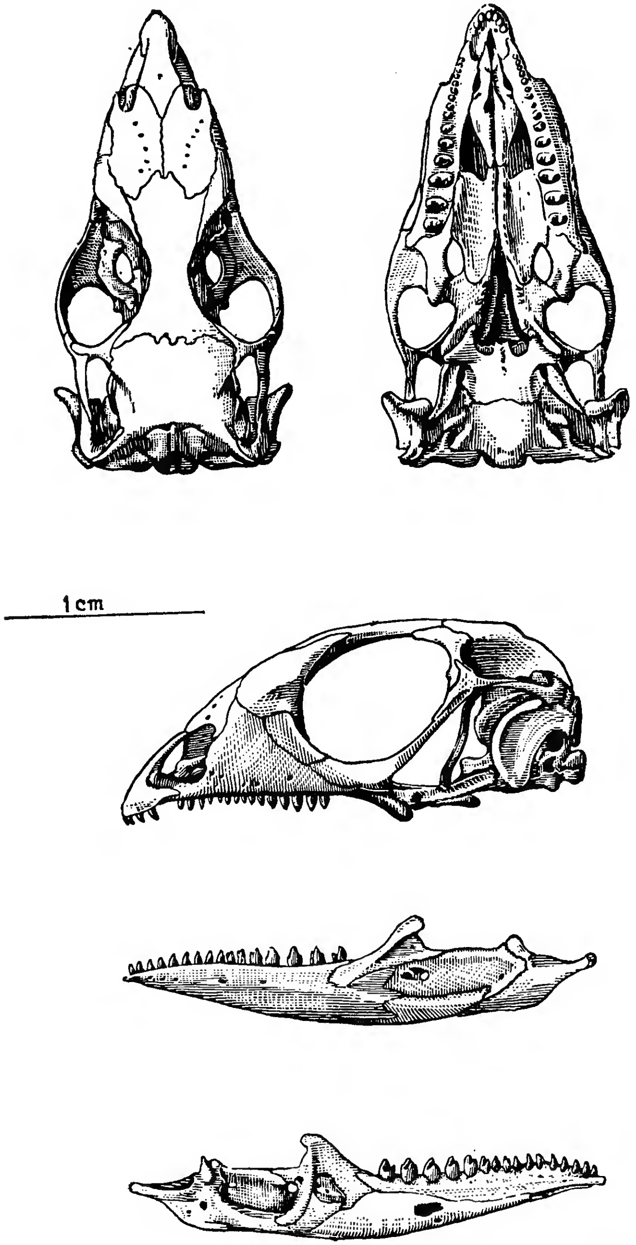


FIG. 1. Skull of *Teius teyou* (AMNH 21094). Drawing by S. B. McDowell.

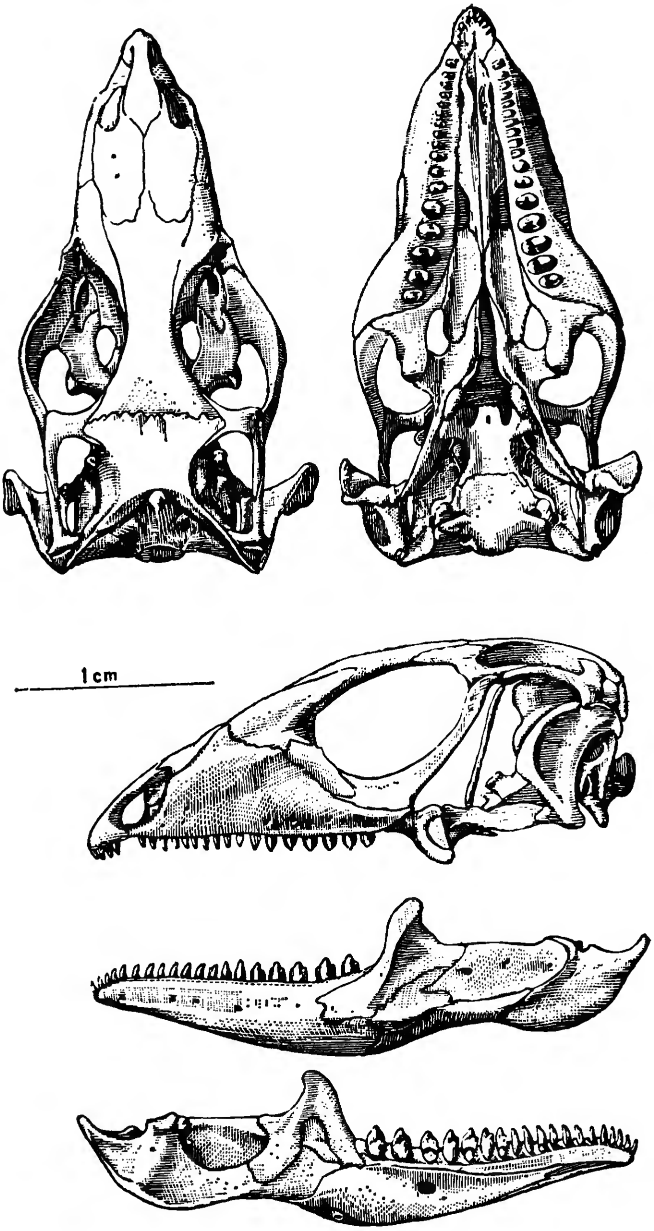


FIG. 2. Skull of *Dicrodon lentigenosus* (AMNH 21871). Drawing by S. B. McDowell.

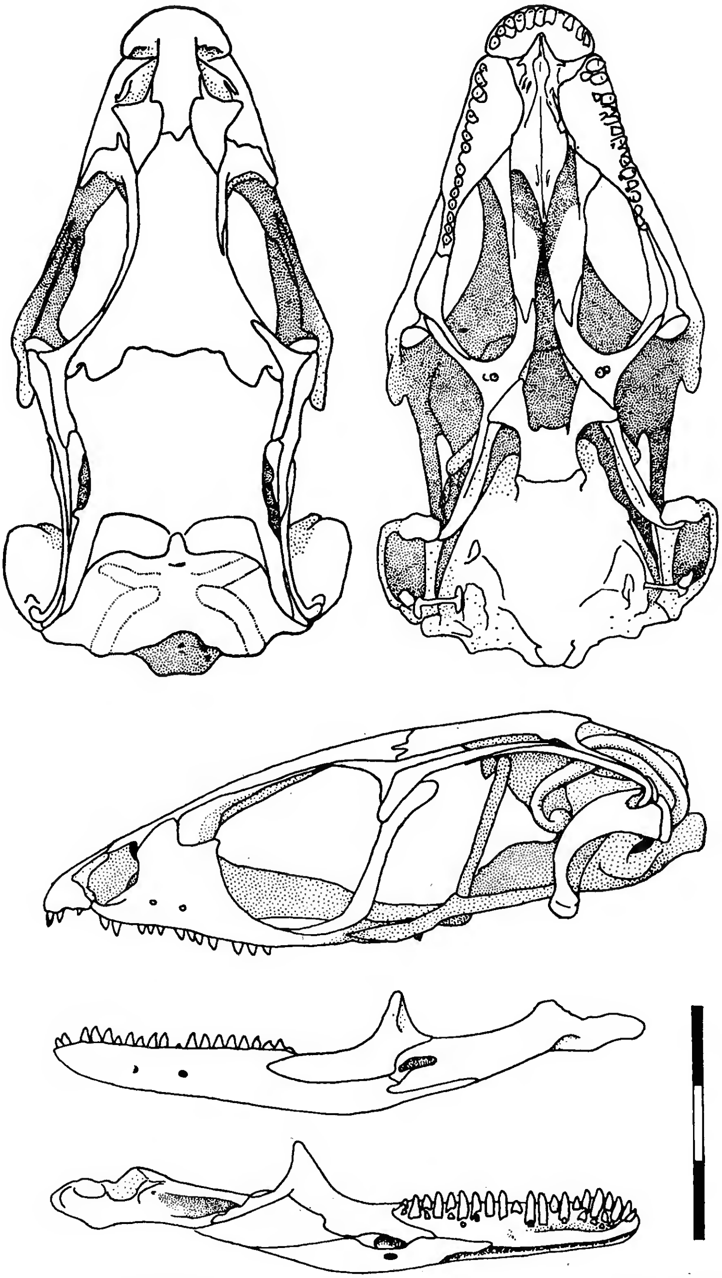


FIG. 3. Skull of *Gymnophthalmus speciosus* (WPM3rd 1531). Scale is 3mm.

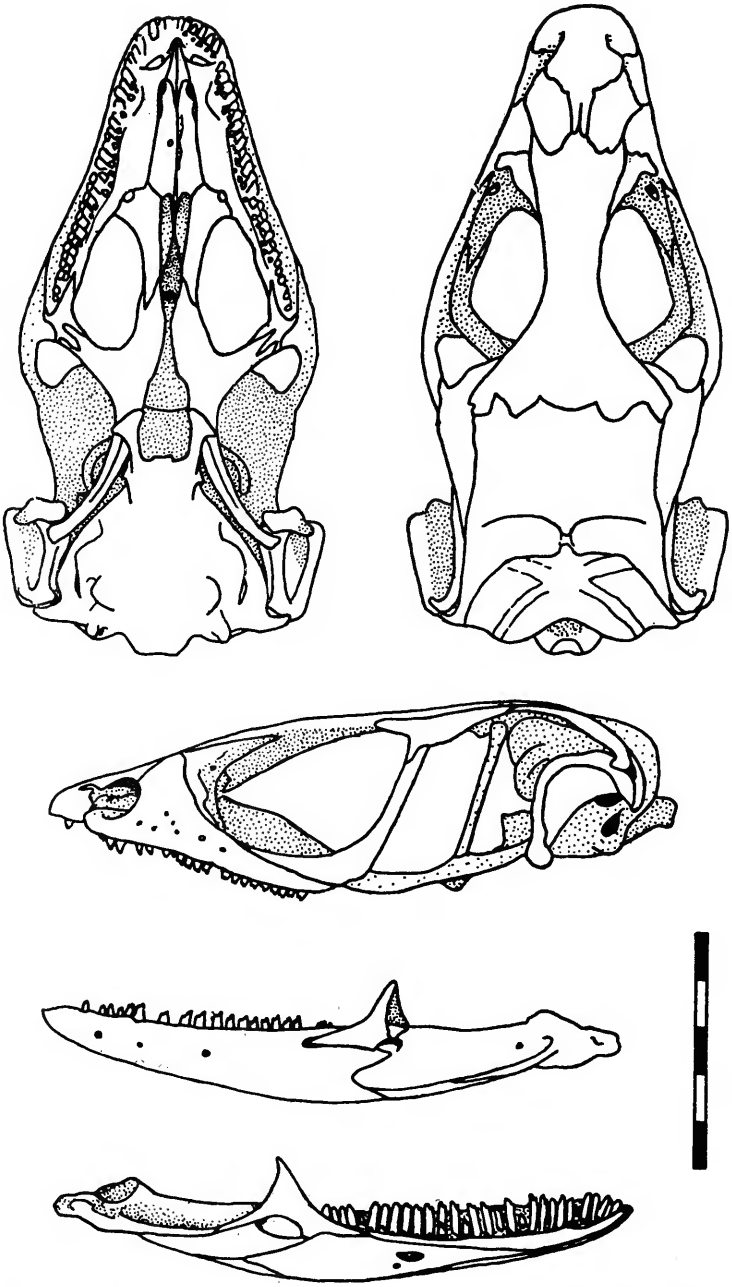


FIG. 4. Skull of *Alopoglossus buckleyi* (USNM 163438). Scale is 5mm.

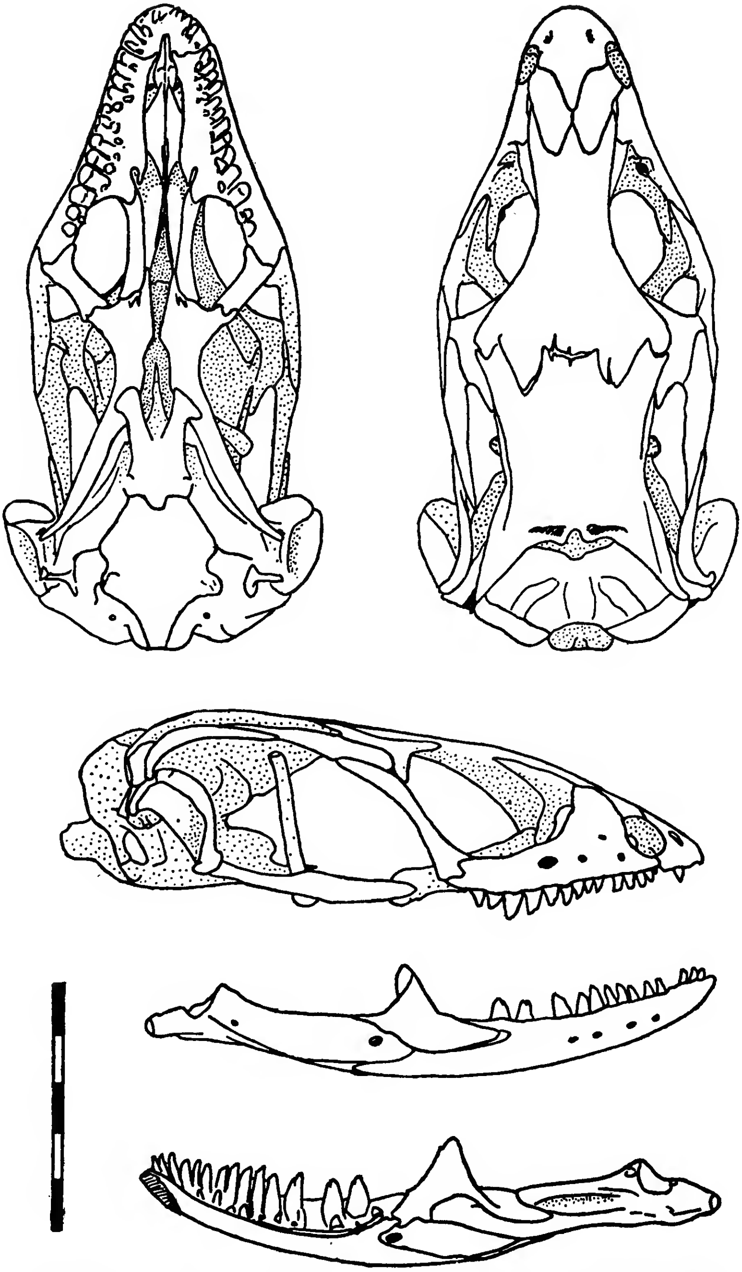


Fig. 5. Skull of *Proctoporus unicolor* (USMN 163428) Scale is 5mm.

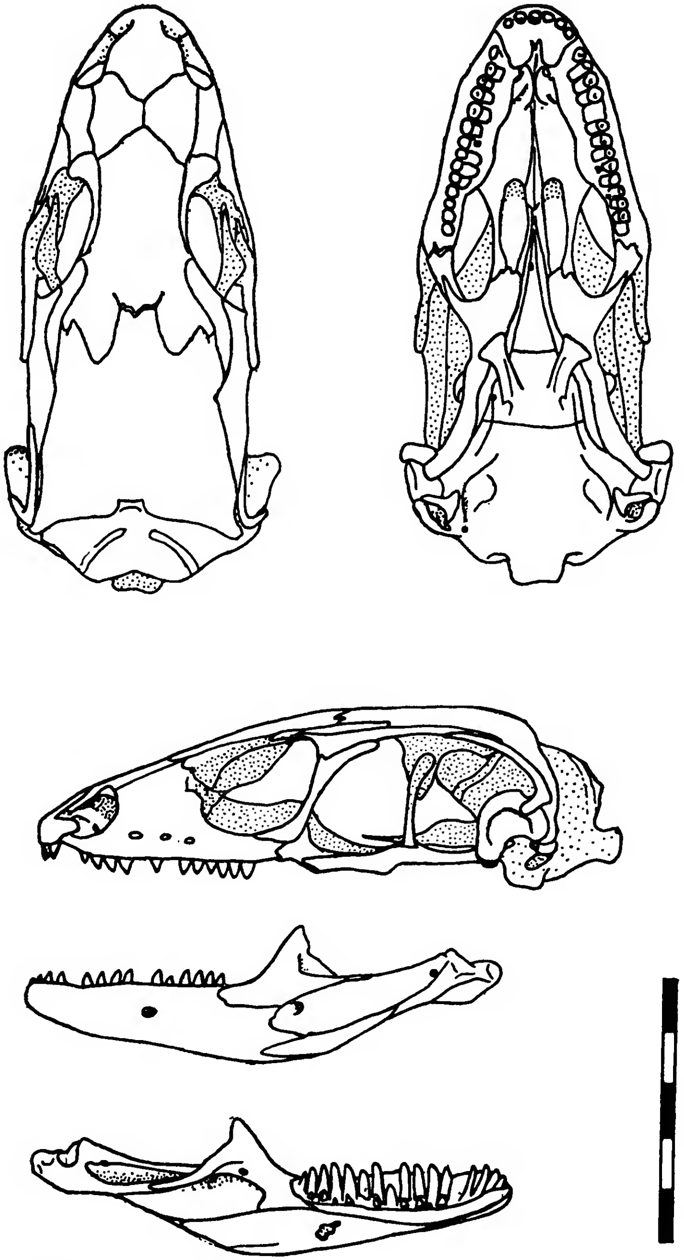


FIG. 6. Skull of *Bachia bresslaui* (IB 216). Scale is 5mm.

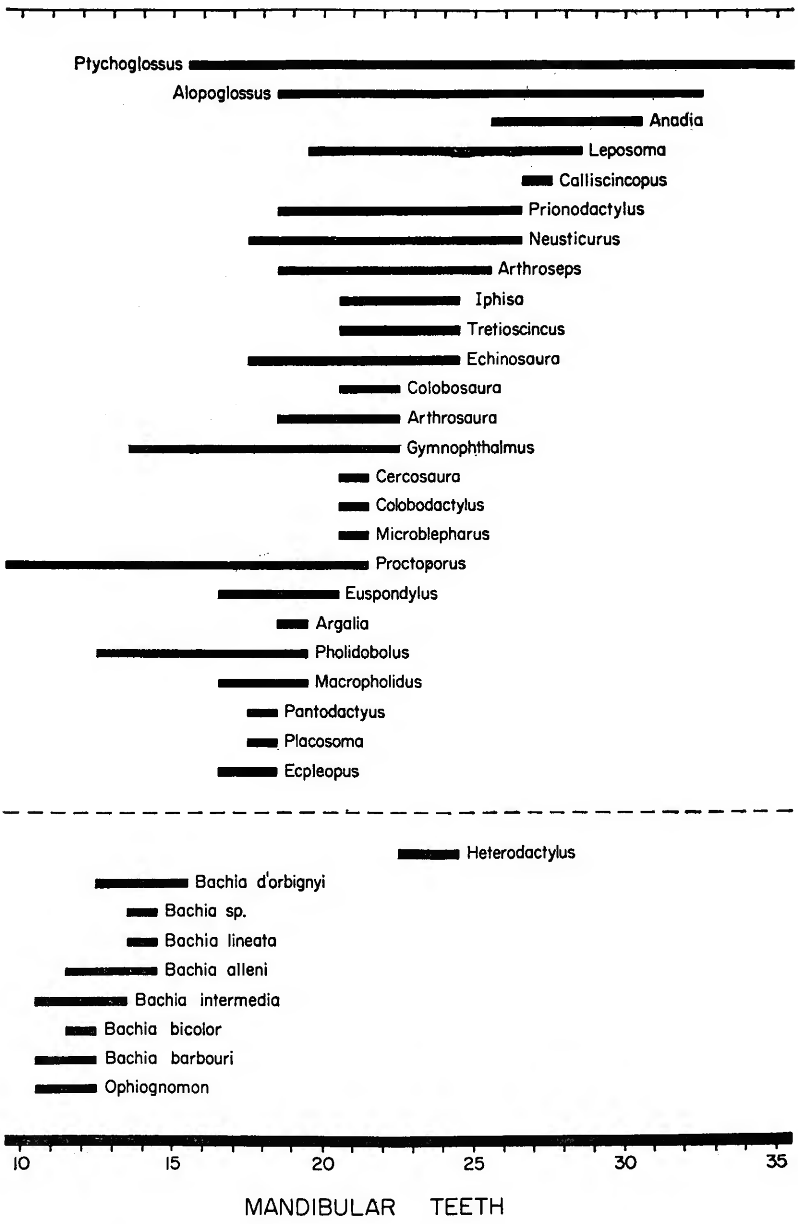


FIG. 7. Microteiid mandibular tooth counts.

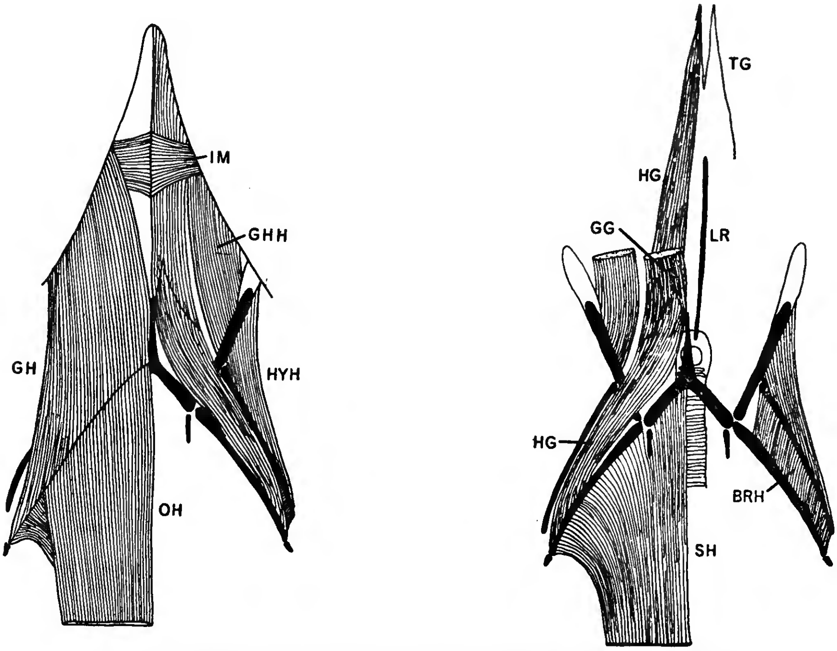
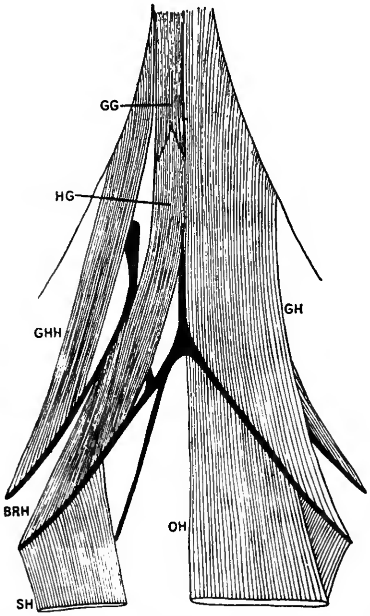


FIG. 8. Hyoid musculature of *Cnemidophorus sexlineatus*.



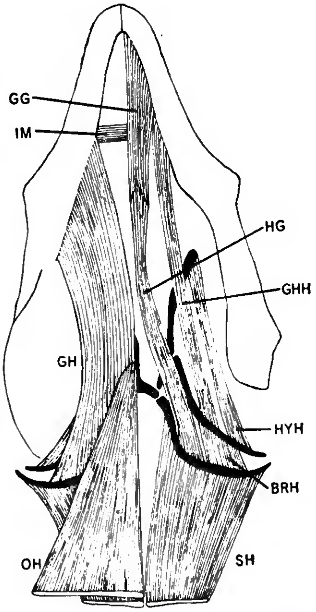


FIG. 9 (left). Hyoid musculature of *Callopistes flavopunctatus*. FIG. 10 (right). Hyoid musculature of *Proctoporus petersi*.

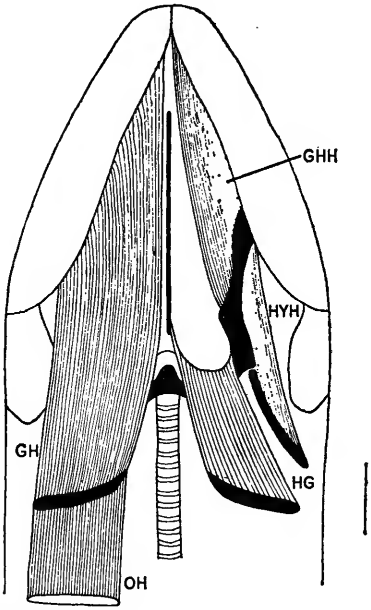


Fig. 11. Hyoid musculature of *Ophiognomon abendrothi.*

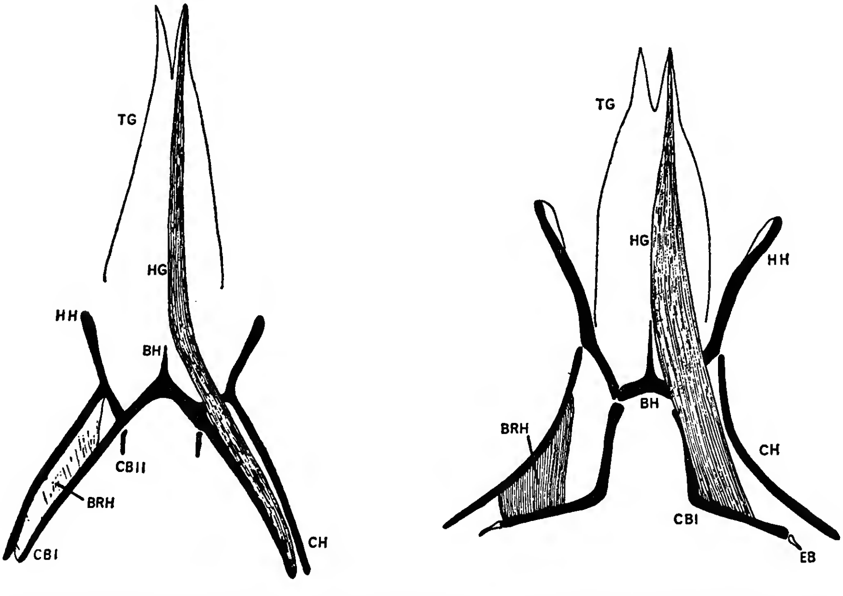


Fig. 12. Macro- (left) and microteiid (right) hyoglossi and branchohyoidei.

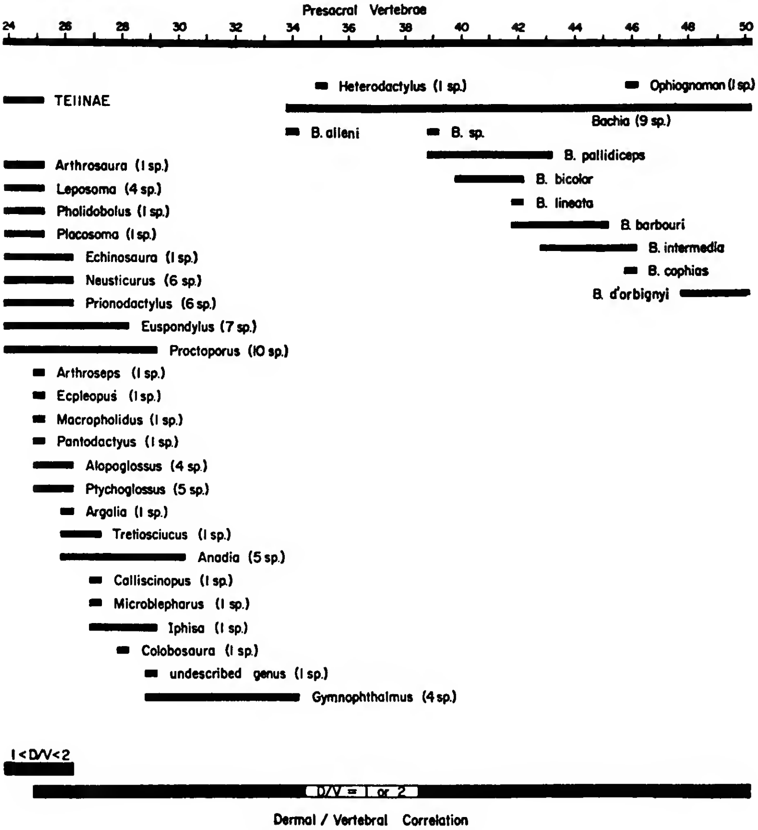


FIG. 13. Teiid presacral vertebral counts.