

Phylogenetic Relationships within Squamata

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INTRODUCTION

Previous analyses of Squamata or "Lacertilia" were hampered by the lack of a well-corroborated hypothesis of relationships within Lepidosauria and their fossil relatives. The present attempt at reevaluation of squamate phylogeny was prompted by several factors. One impetus grew out of the compilation of the "lizard" fossil record given by Estes (1983a) in the *Handbuch der Paläoherpetologie*. The diagnoses of the groups prepared for the *Handbuch* provided an extensive initial list of osteological characters for both fossil and Recent "lizards." Camp (1923), who we honor with the papers in this volume, made extensive use of osteological characters in his *Classification of the Lizards*. Supplementation and modification of his list of characters is therefore desirable as one means of evaluating various aspects of Camp's hypotheses of squamate relationships.

Availability of a phylogenetic systematic study of reptiles (Gauthier, 1984) and the related study on lepidosauromorph reptiles (Gauthier et al., 1988) was another factor important to the development of the present analysis. For the first time it is possible to analyze relationships within Squamata in light of a well corroborated hypothesis of relationships among squamates and their closest relatives.

Our objectives in this paper are: first, to obtain a minimum-step computer-generated cladogram of currently recognized "lizard" families based on a large number of osteological characters and characters from soft anatomy, including many of those used by Camp (1923); and second, to evaluate these results, identifying the principal problem areas, and offering a less highly resolved but better supported cladogram that can be used as an estimate of the actual phylogeny.

METHODS

CHARACTERS AND OUTGROUPS

Characters

Osteological characters are the ones most applicable to the study of fossils, and it is our eventual goal to use this data set to determine the relationships of fossil squamates to their living relatives. Most of the characters have been taken from the diagnoses of "lizard" families and suprafamilial taxa in Estes (1983a); others were offered by various colleagues or have come to our attention during the preparation of this paper. Our present list includes 130 osteological characters and 18 from soft anatomy, a total of 148. Three kinds of characters have been omitted: (1) Characters whose derived states are restricted to a single family. These derived characters may serve to diagnose that family, yet provide no information about interfamilial relationships. Although these characters are omitted from our character list, they are included in the diagnoses of our basic taxa. (2) Characters whose within-taxon variation is so great that it obscures the pattern of between-taxon variation. Such characters may be useful when working with less inclusive levels. (3) Characters that did not vary within Squamata or more inclusive groups. Such characters provide no information on relationships within Squamata; they are discussed where they exist as synapomorphies of more inclusive taxa (Gauthier et al., 1988).

The source of many of our osteological characters (Estes, 1983a) is itself largely a compilation and summary of information in numerous papers on both fossil and recent "lizards". Many of the characters used there to diagnose taxa were taken directly from the literature. Where detailed

surveys or discussions of particular characters exist, we have cited these studies in our character descriptions, and in most cases have checked these characters on specimens. For new or undescribed characters, we have examined representatives of most of the "lizard" families personally as well as checking these on published figures.

Another reason for emphasizing osteological characters in the present work is that they are readily determined in a wide variety of extant groups. Although Camp (1923) himself placed great importance on osteological characters, important aspects of his contribution lay in the analysis of characters of the soft anatomy, especially throat muscles. We have supplemented our list of osteological features with a limited number of characters from soft anatomy. This list is limited because it is more difficult to obtain a complete data set for characters of the soft anatomy than for osteological features; many workers in this area have studied only particular groups and preserved material is not always available to complete the data set. Variation in characters of the soft anatomy is less easily interpreted because of the incomplete data sets, and there is moreover a greater difficulty in making polarity decisions owing to lack of knowledge of these characters in fossil outgroups.

All of our characters are presented as linear and unidirectional transformation series. In other words, each numbered state for a given character is intended to imply direct transformation of the state designated by the next lower integer. We purposely described the characters in this way for two related reasons: (1) so that the character states of different characters would be directly comparable as derived states (e. g., state 2 is always derived from state 1, not sometimes from state 0), and (2) so that the taxon-character matrix could be analyzed using a computer algorithm without recoding any of the characters. At the time of our study, options for treating multistate characters as unordered were not available; we suggest that this option be considered in the future for similar studies.

The description of all characters as linear and unidirectional transformation series results in some unconventional characters, for example, characters 107 and 108. Because the transformation has gone in two different directions (eight cervical vertebrae is thought to be primitive; reduction and increase from this number have both occurred), the number of cervical vertebrae has been split into two characters. The result is that the plesiomorphic states of both characters contain what we believe to be derived morphologies, specifically those morphologies considered to be the derived state in the *other* member of the character pair. Because the character is thought to have transformed in two directions, we are simply focusing on one of those transformations while lumping all other morphologies as "not-such". In most cases (except reversals) this should create no problems in phylogenetic analysis, because the heterogenous state is always the primitive one and we form groups only with derived states.

Squamate Monophyly

We have used outgroup comparison (Watrous and Wheeler, 1981; Farris, 1982; Maddison et al., 1984) for inferring character polarities. In order to use this method, it is desirable that the group under study (ingroup) be monophyletic; otherwise, groups used as outgroups that are actually derived from within the ingroup can cause errors in polarity assessment. Gauthier et al. (1988) presented abundant evidence that Squamata, including "lizards," snakes, and amphisbaenians, is a monophyletic taxon. Within Squamata, however, the question arises as to whether snakes and amphisbaenians are potential outgroups of "lizards" simply because they are placed in separate taxa, or whether they arose within "lizards." Rage (1982a) listed three presumed synapomorphies favoring a monophyletic Sauria (= Lacertilia of some authors) exclusive of amphisbaenians and snakes. All three of these synapomorphies are inadequate evidence for "lacertilian" monophyly. The first, "nerf

glossopharyngien sortant du crâne par l'apertura lateralis recessus scalae tympani (état primitif chez les Lepidosauriens, le nerf glossopharyngien sort avec le nerf vague par le foramen jugulaire)," also occurs in most snakes (Rieppel, 1980b), and is variable in dibamids (Rieppel, 1984a; Greer, 1985), which are usually considered to be "lacertilians." Rage himself judged this character to be questionable because it has been checked only in a few taxa. The second presumed synapomorphy, "bord antérieur du scapulocoracoïde fenestré," is largely irrelevant to the question of "lacertilian" monophyly. The scapulocoracoid itself is absent in all snakes and is present in amphisbaenians only in *Bipes*, in which we are not convinced that fenestration (emargination) is actually lacking. Rage himself had doubts about this character as well; he indicated it with a question mark in his cladogram. Rage's third character, "pancreas rubané," is also present in amphisbaenians. Rage suggested that it is convergent in the two groups, which is to some extent supported by the compact form of the pancreas in snakes, which Underwood (1967) refers to as the primitive condition (presumably for amniotes). Nevertheless, a ribbon-like pancreas could as well be a synapomorphy of squamates that has been further modified in snakes. Rage (1982) concluded that because of the questionable nature of these three presumed synapomorphies, a "definition" of "Lacertilia" is indeed fragile; he concluded that "Les Sauriens apparaissent surtout comme le regroupement des Squamates qui n'ont pas atteint le niveau évolutif de l'ensemble Amphisbénés-Serpents." We conclude that monophyly of "Lacertilia" is doubtful. If snakes and amphisbaenians are excluded from the "Lacertilia", we know of no synapomorphies that unite the members of this group. It is therefore artificial to exclude amphisbaenians and snakes from an analysis of the relationships among all "lizards", and it is certainly unacceptable to use them as outgroups for character analysis. For the above reasons we analyze relationships within Squamata instead of within "Lacertilia" in the remainder of this paper. Because "Lacertilia" is unlikely to be monophyletic, we recommend abandonment of this term. We also recommend that the term Sauria not be used as a synonym of "Lacertilia"; Gauthier (1984) and Gauthier et al. (1988) used Sauria to include both archosauromorph and lepidosauromorph reptiles, a usage closer to the original intent of McCartney (1802), who included crocodylians in his Sauria.

Monophyly of Squamata, including "Lacertilia" (sensu Estes, 1983a), snakes, and amphisbaenians, is supported by 69 characters given by Gauthier et al. (1988) and nine more added in this paper (see Diagnoses of Taxa). Some of these synapomorphies may not occur in every squamate group, but when an apparently primitive state occurs it is clear that reversal is the simplest explanation. The monophyletic status of Squamata is thus highly corroborated, and we can now discuss real outgroups for the purpose of phylogenetic analysis.

Outgroup Analysis

We follow the recent refinement of the outgroup comparison method for establishing character polarity proposed by Maddison et al. (1984). These authors have shown that hypotheses of relationship among ingroup and outgroups can have a profound influence on hypotheses of character polarity. Fig. 1 represents an highly corroborated hypothesis of relationships among ingroup and several outgroups according to Gauthier et al. (1988); this hypothesis serves as an assumption for the assessment of character polarity in the remainder of our study. The distributions of the states of all characters among the outgroups and the polarity decisions are given in the section on the Outgroup Character Matrix.

INGROUP PHYLOGENETIC ANALYSIS

Once polarities were determined for all characters, relationships among members of the ingroup were analyzed using Hennig's (1966) method, in which only shared, derived characters are

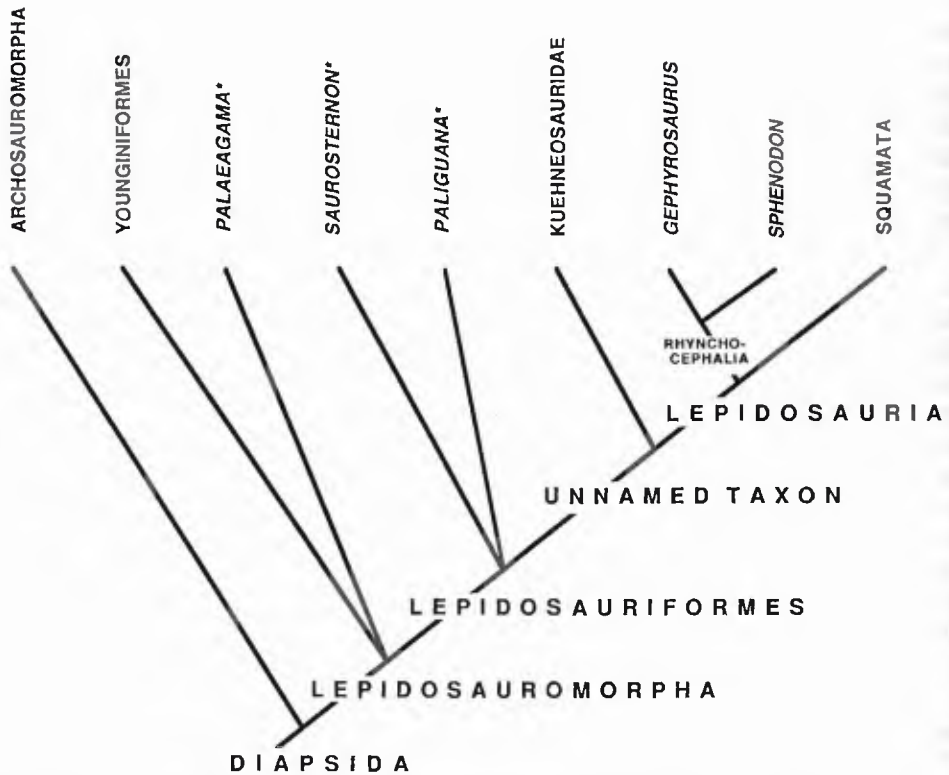


FIGURE 1. Simplified cladogram of outgroups (from Gauthier et al., 1988).

taken as evidence for close phylogenetic relationship. Because of the large size of the data matrix and the incompatibility among certain characters, we used the PHYSYS package for computer assessment of phylogenetic relationships written by J. S. Farris and installed in the California State University CYBER system. Wagner and Pimentel analyses in the PHYSYS package were utilized to assist our search for the minimum-step cladograms that account for the distribution of all of our characters within squamates. The data were also subjected to the PAUP program written by David Swofford, and run on the mainframe computer at the University of Michigan as well as on an IBM PC at San Diego State University; the results of both PAUP runs were identical.

Despite the use of such sophisticated techniques, we are not certain that we have found the best supported cladograms. The effects of the large number of basic taxa, the large size of the data matrix, the degree of character incompatibility, and missing data in some parts of the matrix cannot be determined at this time. Testing the fit of characters to all possible branching diagrams is the only possible way to insure that those of minimum length have been identified, a practical impossibility with the number of basic taxa and characters in this study. Furthermore, when within-taxon variation is considered, phylogenetic hypotheses may have to be altered to insure minimization of character state changes (see sections on Variation and Character Analysis).

Another important consideration is the meaning of the branching diagrams that result from phylogenetic analysis. If we were merely looking for the simplest internested hierarchical system to account for all of our character data, a maximally parsimonious (minimum step) cladogram would serve our purposes well. Our goals are not so limited. We are interested in *phylogenetic* relationships. Furthermore, any biogeographical analysis using the results of our study would require that the furcations in our branching diagrams be interpreted as historical events that have

yielded monophyletic groups. Some hypothesized monophyletic groups are much better supported than others. For example, the monophyly of a group the members of which are united by the unanimous possession of numerous unique, derived features is better supported than one in which the members are united by a single derived character that occurs not only in some members of that group but also in taxa outside of the group. Both kinds of groups may occur on the most parsimonious cladogram.

Although some systematists end their studies with production of minimum-step cladograms, this practice results in studies of limited usefulness. The production of a cladogram is synonymous with the inference of monophyletic groups. If these groups cannot be diagnosed adequately, then their usefulness as phylogenetic hypotheses must be seriously questioned. Diagnoses for all hypothesized monophyletic groups, whether named or not, should be a requirement of any phylogenetic study.

For the above reasons, in addition to the more highly resolved minimum-step cladograms, we present a less resolved cladogram that is intended to show what we believe are the best supported monophyletic groups, at the same time indicating the problems most in need of further research. This cladogram may also serve as the foundation for future placement of extinct taxa in larger monophyletic groups and for reevaluation of the biogeographic scenario given by Estes (1983b).

BASIC TAXA

The basic taxa in our study are the families of extant "lizards" recognized by Estes (1983a), with the addition of snakes, amphisbaenians, and *Lanthanotus*, and the use of *Varanus* rather than Varanidae. Although it would be preferable to use as basic taxa only groups (such as snakes, amphisbaenians, and chamaeleons) whose monophyly is highly corroborated, we have not done so because this information is not currently available. Indeed, one of the primary goals of this study is to identify such groups. We have used the "lizard families" as our basic taxa out of convenience. The diagnostic characters that support monophyly in these taxa appear in the section Diagnoses of Taxa.

Elsewhere (Gauthier et al., 1988) we argued against the use of Linnaean ranks such as family. We are well aware that the "lizard families" are neither equivalent to one another nor to other "families" of vertebrates. However, because these "lizard families" are widely used and because previous studies of relationships within "lizards" as a whole (Camp, 1923; Northcutt, 1978) have also used them as basic taxa, there is a greater body of character data available for evaluation of their phylogenetic status. Those taxa for which evidence of monophyly is lacking generally appear to be metataxa (Gauthier et al, 1988; indicated by an asterisk*), that is, taxa based on plesiomorphy and for which there is no character evidence indicating either monophyly, paraphyly, or polyphyly. Furthermore, if these metataxa are later identified as paraphyletic, the taxa that have been removed from monophyletic groups to render them paraphyletic are easily identified. For example, if Iguanidae* is paraphyletic, it is because the acrodont Agamidae* and Chamaeleontidae have been removed from the monophyletic Iguania, with the remaining iguanians being grouped together as the metataxon Iguanidae* because they retain the primitive pleurodont tooth implantation. Similarly, if Agamidae* is paraphyletic, it is because Chamaeleontidae has been removed from it.

VARIATION

In studies of interrelationships among higher taxa in which the basic taxa may themselves each be morphologically diverse, intrataxic variation within basic taxa is an important problem. In spite of this, methods for dealing with the problem of variation have been neglected. Numerous studies report character distributions as if virtually no variation within basic taxa exists, and simi-

larly, synapomorphies supporting particular phylogenetic hypotheses are often presented as if all members of a clade possess them as described. We suspect from our own experience that if sufficiently large samples are studied, variation will be the rule rather than the exception.

The easiest method for dealing with variation within basic taxa is simply to discard all characters that exhibit it. Unfortunately, this practice inevitably results in a concomitant loss of phylogenetic information. While it is clear that characters that vary within all of the basic taxa under consideration are not useful for analyzing relationships among these taxa, and that "ideal" characters are invariable within basic taxa, most characters fall somewhere between these two extremes. Furthermore, characters that vary within basic taxa can provide valuable phylogenetic information, especially in studies in which the monophyly of all of the basic taxa is not highly corroborated. The characters that ultimately give evidence of the paraphyletic status of a taxon are necessarily variable within that taxon. For these reasons, the systematist must exercise careful judgement before retaining or discarding variable characters.

The practice of discarding characters amounts to ignoring data -- a practice seemingly at odds with the goals of science. Characters are often said to be "bad" because they are not uniformly present in or unique to a particular group. Those who judge the characters in this way seemingly do not appreciate that the value of a character can only be assessed upon acceptance of a particular phylogenetic hypothesis. Even such "good" characters as the presence of hemipenes in male squamates are only considered to be "good" because they are concordant with our acceptance of the monophyly of Squamata. But any character would be considered "good" (unique and unreversed) if we accepted the monophyly of the group that it characterized. Therefore, it is pointless to discuss the value of a given character without clearly specifying one's assumptions concerning monophyletic groups and then considering *all* of the pertinent characters.

The fact that assessment of the phylogenetic value of characters rests on assumptions about monophyly creates a paradox for those wishing to make value judgements about characters. Before accepting an hypothesis of monophyly, the synapomorphic status of a character simply cannot be evaluated, because monophyly is the defining criterion of synapomorphy (Patterson, 1985). On the other hand, once an hypothesis of monophyly is accepted, one cannot argue against the synapomorphic status of a character, even if it occurs in other taxa or is not universal in the taxon for which it is considered a synapomorphy. The acceptance of monophyly necessitates that similar characters in different groups are not the same character *in terms of origin*. Of course, in practice such characters may be the same *in terms of morphology*. This means only that such characters *by themselves* are insufficient for diagnosing monophyletic groups. It does not invalidate these characters as synapomorphies, although it may require that what appears to be one synapomorphy is actually more than one synapomorphy.

We conclude that if one is willing to accept certain hypotheses of monophyly, then it may be reasonable to judge the value of characters not in terms of uniqueness or lack of reversal but in terms of their diagnostic effectiveness. However, in many cases in which the problematic variation occurs within basic taxa, the validity of such assumptions has not even been considered. For groups such as squamates, in which the monophyly of many currently recognized "family level" taxa has not even been evaluated, the practice of judging the value of characters is premature. The other case, in which characters are discarded because they must be interpreted as homoplastic upon the acceptance of a phylogenetic hypothesis, simply hinders scientific progress by concealing evidence against one's own preferred hypothesis.

Kluge and Farris (1969) handled variation in one character within their basic taxa by breaking each variable taxon into two, one coded invariable for one of the states, the other coded invariable for the alternative state. This method becomes increasingly impractical as the number of variable characters increases. Considering only two-state characters, a single variable character requires two

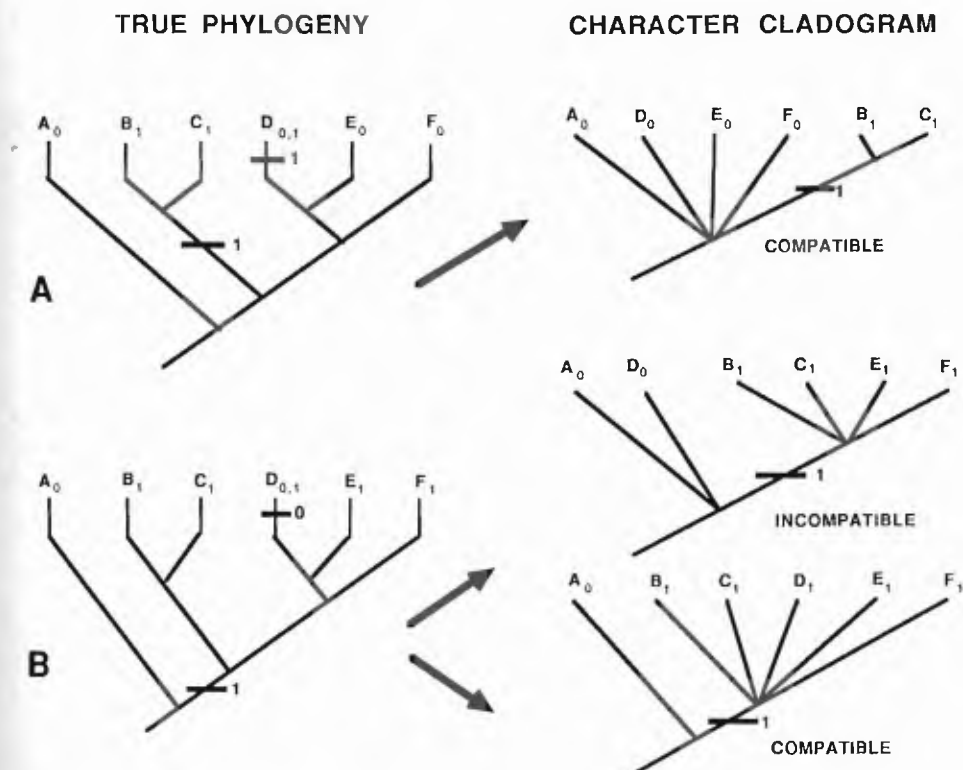


FIGURE 2. One convention for dealing with intrataxic variation. Character states on vertical lines indicate changes occurring within a terminal taxon. A, under the assumption of monophyly for each terminal taxon, the derived state (1) in some D must be nonhomologous with morphologically similar states in B and C. Because of this nonhomology, D is assigned state 0, which produces a character that is compatible with the true pattern of relationships. B, when character reversal occurs within a monophyletic terminal taxon, morphologically similar "plesiomorphous" states inside and outside the variable taxon must be nonhomologous. Therefore, assigning state 0 to D may create a character that is incompatible with the true pattern of relationships. Taxon D should really be assigned State 1, the state that is truly plesiomorphous for this taxon, but to do this requires knowledge of relationships among the terminal taxa -- the goal of the study. Thus, D must be assigned state 0 to avoid circularity.

taxa instead of one to cover all possible character combinations, two variable characters require four taxa, three such characters require nine taxa, and so forth. Most of our nineteen basic taxa have more than three variable characters out of the total of 148, making this method impractical for our study.

We have used two conventions for assigning a single character state per character to each basic taxon. The first of these relies on the assumption that the basic taxa of our analysis are strictly monophyletic, an assumption that we have noted in the section on Basic Taxa is not always well corroborated. This assumption (which we must make for the sake of practicality) permits us to assign the single most plesiomorphous character state to the taxon in question. Effectively, we are saying that if a basic taxon containing both plesiomorphous and apomorphous states for a given character is monophyletic, then derived states of that character found both within the taxon and outside of it are not true synapomorphies--they are convergent. Because we must conclude that the de-

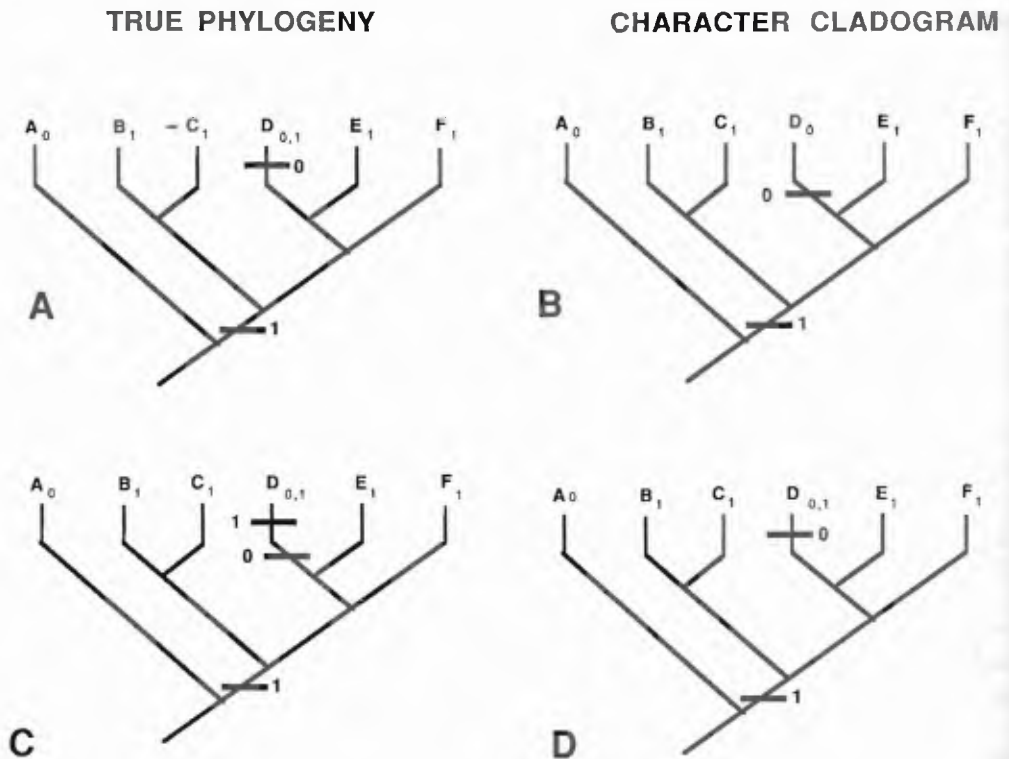


FIGURE 3. Recoding of variable characters to minimize ad hoc hypotheses of non-homology. Characters on vertical lines indicate changes occurring within taxa. A, the true phylogeny; because this is unknown, we assign state 0 to the variable taxon under our convention (see text). B, if other characters reveal the true phylogeny, reversal in the character in question will appear to be a synapomorphy of all members of the variable taxon. C, because we know that this taxon is actually variable, another reversal is required in some members of the taxon. D, the results of the phylogenetic analysis, however, make it simpler to consider state 1 to be the plesiomorphous state for the variable family, thus reducing by one (from C) the number of steps necessary to account for the observed character state distribution.

rived state inside the group is not synapomorphic with the morphologically similar state outside of it, we simply assign the most plesiomorphous state of the character to the variable taxon. This convention would work well (Fig. 2A) if character reversal did not occur. If character reversal has in fact occurred within a basic taxon (Fig. 2B), then it is actually the morphologically similar "plesiomorphous" states that are not equivalent. Because our assumption of monophyly of the basic taxa necessitates such non-equivalence, the taxon should in fact be assigned the derived state (the true plesiomorphous condition for the taxon if reversal has occurred). Knowledge of such a reversal, however, can only result from acceptance of an hypothesis of relationships among or within the basic taxa, but the former cannot be an assumption in our analysis because it is what we wish to discover. Therefore, to avoid circular reasoning, we must assign to the taxon the state that appears to be plesiomorphous on morphological grounds alone. Only after the phylogenetic analysis can we recode the character on the tree to minimize ad hoc hypotheses of homoplasy (Fig. 3).

Our second convention involves certain rare cases in which we can infer character reversal before phylogenetic analysis without resorting to circular reasoning. Such inferences require phylog-

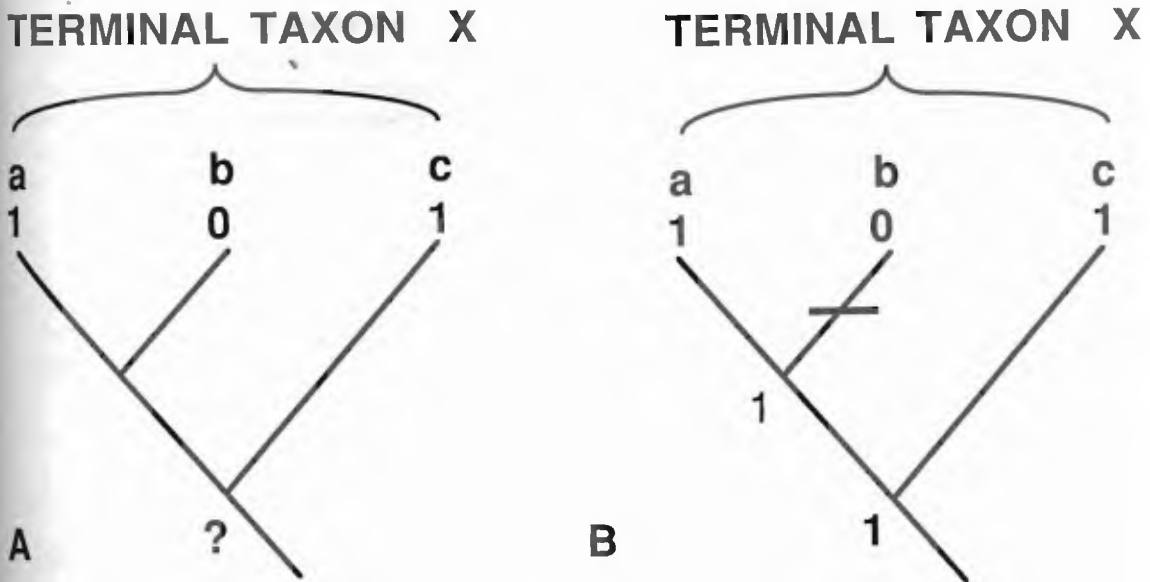


FIGURE 4. Use of phylogenetic hypotheses describing relationships within terminal taxa to infer character reversal within these units. A, character distribution and relationships. B, given the character distribution in A, it is simplest to consider the state that appears to be plesiomorphous on morphological grounds (0) to be an apomorphic reversal and to assign the alternative state (1) to the taxon.

genetic assumptions at lower hierarchical levels (Fig. 4). Given a phylogenetic hypothesis describing relationships among groups within a basic taxon, the simplest explanation of character state distributions within the taxon may necessitate that we consider a condition to be apomorphic for a family that appears to be plesiomorphous on morphological grounds alone. For example, the parietal foramen lies uniformly on the frontoparietal suture (or, more rarely, in the frontal) in iguanids*, except in some species of *Anolis* in which it is within the parietal. Although outgroup evidence suggests that a posteriorly located parietal foramen is plesiomorphous for Squamata, present hypotheses of interrelationships within Iguanidae* (Etheridge and de Queiroz, 1988) make it most reasonable to believe that the posterior location of the parietal foramen in some *Anolis* has resulted from character reversal. The alternative would be to consider the condition in these *Anolis* to be truly primitive. Such an hypothesis has unreasonable logical consequences. In one case, the relationships of *Anolis* to other iguanids* might be rejected and those *Anolis* with a posteriorly located parietal foramen might be considered to be the sister-group of all other iguanids*; this would necessitate homoplasy in numerous other characters. Alternatively the relationships within Iguanidae* might be accepted, but this would require numerous convergent acquisitions of an anteriorly located parietal foramen. Thus, the two morphologically similar "plesiomorphous" conditions that occur inside and outside the taxon (foramen occurring within the parietal in outgroups and in some *Anolis*) are most reasonably interpreted as homoplastic, and the other ("derived") state (foramen on frontoparietal suture) is assigned to the basic taxon.

Both of the above conventions used to deal with character variation within basic taxa have drawbacks. First, the assumption of familial monophyly may be unrealistic for some basic taxa. Although we assume all basic taxa to be monophyletic for the purpose of handling variation within these taxa, we note the lack of evidence for monophyly in some of our basic taxa (see the section on Diagnoses of Taxa). Secondly, both the distributions of particular morphologies within basic taxa and the absence of corroborated hypotheses of relationships within them often preclude the inference of character reversal within basic taxa prior to phylogenetic analysis. Although we have assigned only a single state for each character to all our basic taxa in our computer analyses, we indicate known variation in our Ingroup Character Matrix (Appendix Table II).

RESULTS

CHARACTER LIST FOR SQUAMATA

The following list of characters with included polarities is that used in preparing the Ingroup Character Matrix (Appendix Table II). The characters are ordered with respect to their position in the body.

Osteological Characters

I. Skull

A. Skull Roof

1. Ontogenetic fusion of premaxillae: (0) paired well into postembryonic ontogeny; (1) fused in embryo
2. Bony external naris extent: (0) opening not extended posteriorly, frontal not close to or incorporated into opening; (1) opening extended posteriorly, frontal coming close to or incorporated into opening
3. Ontogenetic fusion of nasals: (0) paired well into postembryonic ontogeny; (1) fused in embryo
4. Nasal-prefrontal contact: (0) present; (1) absent, the two bones separated by anterolateral processes of the frontals, the latter contacting the maxillae
5. Prefrontal contact with posterior orbital bones: (0) does not contact postorbital, postfrontal or fused postorbital-postfrontal above orbits; (1) contacts postorbital, postfrontal or fused postorbital-postfrontal above orbits
6. Ontogenetic fusion of frontals: (0) paired well into postembryonic ontogeny; (1) fused in embryo or early in postembryonic ontogeny
7. Lateral borders of frontals: (0) more or less parallel; (1) strongly constricted between orbits
8. Frontal shelf: (0) lacking broad shelf below nasals; (1) broad shelf underlying nasals present, frontal often exposed dorsolaterally as wedges or spikes
9. Descending processes of frontals: participation in orbitonasal fenestra: (0) weakly developed and prefrontals broadly participating in wide orbitonasal fenestra; (1) prominently developed and prefrontals narrowly or not at all in margins of narrow orbitonasal fenestra.
10. Median contact of descending processes of frontals: (0) not in contact below olfactory tracts; (1) in contact below olfactory tracts
11. Frontal tabs: (0) no tabs; (1) frontal tabs project posteriorly over dorsal surface of parietal
12. Postfrontal: (0) present, may be separate or seen to fuse at some stage of ontogeny; (1) absent (never seen as a separate element)
13. Postfrontal forking: (0) subtriangular, not forked medially; (1) semilunate, forked medially, clasping frontoparietal suture
14. Postfrontal fusion: (0) separate or absent; (1) fused to postorbital

15. Postfrontal size: (0) extensive, usually not confined to orbital rim; (1) reduced, subtriangular, confined to orbital rim
16. Postorbital: (0) present; (1) absent
17. Postorbital contribution to posterior border of orbit: (0) forms about one half of the posterior orbital border and is primarily an orbital bone with a strong ventral process; (1) forms less than one half of the posterior orbital border and is primarily a temporal bone with reduced ventral process
18. Jugal-squamosal contact on supratemporal arch: (0) no contact, bones widely separated; (1) contact present or bones approach each other very closely
19. Supratemporal fenestra restriction by postorbital: (0) open or restricted primarily by postfrontal; (1) restricted primarily by postorbital
20. Supratemporal fenestra restriction by postfrontal: (0) open or restricted primarily by postorbital; (1) restricted primarily by postfrontal
21. Ontogenetic fusion of parietals: (0) paired well into postembryonic ontogeny; (1) fused in embryo or early in postembryonic ontogeny
22. Parietal tabs: (0) absent; (1) parietal tabs present as thin, triangular structures that extend anteriorly into shallow triangular fossae on the ventral surface of the frontals
23. Parietal downgrowths: (0) absent; (1) pointed ventral downgrowths of parietal extend to (or just medial to) the epipterygoids
24. Parietal table and supratemporal process length: (0) table extensive posteriorly, largely obscuring braincase in dorsal view, supratemporal processes short; (1) braincase exposed broadly in dorsal view below and behind parietal table, supratemporal processes long
25. Parietal foramen position: (0) within parietal; (1) on frontoparietal suture; (2) within frontal
26. Parietal foramen: (0) present; (1) absent
27. Posterior extent of maxilla: (0) extends well back under orbits; (1) extends only just beyond anterior edges of orbits
28. Lacrimal: (0) present, either separate or fused to prefrontal; (1) absent
29. Lacrimal fusion: (0) separate; (1) fused to prefrontal
30. Lacrimal foramen number: (0) single; (1) double
31. Anteroventral border of orbit: (0) formed by maxilla with jugal confined to medial surface of maxilla; (1) formed by jugal
32. Jugal-postorbital bar: (0) jugal large, postorbital bar complete; (1) jugal reduced or absent, postorbital bar incomplete
33. Squamosal: (0) present; (1) absent
34. Dorsal process of squamosal: (0) present; (1) absent
35. Supratemporal: (0) present; (1) absent
36. Palpebral ossifications: (0) absent; (1) present

B. Palate

37. Pterygoid lappet of quadrate: (0) present; (1) absent
38. Vomer fusion: (0) separate well into postembryonic ontogeny; (1) fused in embryo or early postembryonic ontogeny
39. Vomer size: (0) relatively small, extends posteriorly less than half the length of the maxillary tooth row; (1) elongate posteriorly, extends one half or more the length of the maxillary tooth row and usually restricting internal naris
40. Median contact of septomaxillae: (0) separated by a gap filled by the cartilaginous internarial septum; (1) septomaxillae meet or nearly meet on midline in a raised crest

41. Dorsal expansion of septomaxilla: (0) flat or concave, Jacobson's organ small; (1) expanded and convex, reflecting large size of Jacobson's organ.

42. Posterior border of opening for Jacobson's organ: (0) not closed by bone ("paleochoanate"); (1) closed by contact of maxilla and vomer ("neochoanate")

43. Medial extensions of palatine: (0) absent; (1) medial extension from ventrolateral edge of palatine forms air passages for bony secondary palate

44. Choanal fossae of palatines: (0) small in relation to palatine size; (1) relatively prominent in relation to palatine size

45. Ectopterygoid contact with palatine: (0) fails to contact palatine anterolaterally, maxilla forms part of lateral border of suborbital fenestra; (1) contacts palatine anterolaterally, excluding maxilla from border of suborbital fenestra

46. Ectopterygoid size and restriction of suborbital fenestra: (0) ectopterygoid relatively slender, fenestra widely open; (1) ectopterygoid enlarged medially, restricting suborbital fenestra

47. Epipterygoid: (0) present; (1) absent

48. Pyriform recess width: (0) narrow throughout most of its length; (1) broad

C. Braincase

49. Alar process of prootic: (0) alar process (dorsal anterolateral edge of prootic) relatively short and primarily directed dorsally; (1) alar process elongated and anterodorsally directed (expanded upward and forward)

50. Supratrigeminal process of prootic: (0) feebly developed or absent; (1) finger-like projection above trigeminal notch

51. Opisthotic-exoccipital fusion: (0) bones remain separate or fuse to exoccipitals relatively late in postembryonic ontogeny; (1) fuse to exoccipital in embryo or in early postembryonic ontogeny, or the two bones develop from a single ossification center

52. Enclosure of lateral head vein in bony canal formed by crista prootica: (0) crista prootica may or may not extend forward onto the basiptyergoid process, but does not enclose the lateral head vein in a bony canal; (1) crista prootica extends forward onto process, enclosing lateral head vein in a bony canal

53. Posterior opening of vidian canal: (0) within basisphenoid; (1) at basisphenoid-prootic suture 2) entirely within prootic

54. Origin of jaw adductor musculature: (0) extends onto dorsal surface of parietal; (1) attaches only on ventral surface of parietal

D. Mandible

55. Meckel's canal enclosure: (0) dentary forming an open groove but not a tube around the cartilage, the latter covered partially or completely by splenial, when present; (1) variably enclosed within a bony dentary tube formed by union of upper and lower borders of dentary canal, a suture remaining lingually; (2) dentary tube closed and fused

56. Intramandibular septum of Meckel's canal: (0) subdivision of Meckel's canal occurs well anterior to the posterior end of the tooth row, with intramandibular septum poorly or moderately developed; (1) subdivision occurs near posterior end of dentary tooth row with intramandibular septum well developed

57. Meckel's canal exposure ventrally: (0) opens medially for entire length; (1) opens ventrally anterior to anterior inferior alveolar foramen

58. Subdental shelf size: (0) small or absent; (1) large

59. Subdental shelf: (0) present (large or small); (1) absent

60. Dorsal extension of coronoid process of dentary: (0) absent or with only small dorsal extension; (1) large, extends dorsally onto anterolateral surface of coronoid
61. Lateral view of disarticulated surangular: (0) tapers anteriorly, pointed distally; (1) expanded anterodorsally and nearly vertical at anterior margin; (2) as in state 1, but anterior end of surangular terminates relatively closer to level of coronoid eminence on surangular
62. Medial view of prearticular with dentary and splenial removed: (0) prearticular extends nearly to anterior end of surangular, well anterior to coronoid bone; (1) reduced, not extending well anterior to coronoid bone
63. Posterolateral dentary shape: (0) no surangular or coronoid notches present; (1) surangular and coronoid notches present; (2) coronoid and surangular notches reduced
64. Dentary-postdentary articulation: (0) extensive overlap, tongue and groove articulation present; (1) reduced overlap
65. Splenial reduction: (0) present, extends anterior to tooth row midpoint; (1) present, does not extend as far forward as tooth row midpoint; (2) splenial absent
66. Splenial posterior extent (0) extends posterior to apex of coronoid (1) does not extend posterior to apex of coronoid; (2) very limited overlap on postdentary bones
67. Splenial-dentary suture: (0) extensive bone-to-bone contact; (1) reduced, much connective tissue present
68. Coronoid lateral process as a lappet on dentary: (0) absent or covered by posterior dentary; (1) present
69. Coronoid anterior extension: (0) anterior border of coronoid curves smoothly into dentary; (1) anterior border of coronoid levels out before reaching dentary, producing a long, low, horizontally-oriented anterodorsal extension
70. Anterior end of coronoid: (0) clasps dentary, overlapping it with both lateral and medial processes; (1) anterior end of coronoid meets dentary directly, no overlapping processes present
71. Restriction of coronoid lateral process by dentary and surangular: (0) coronoid lateral process present or absent, not overlapped by dentary anteriorly; (1) lateral process overlapped anteriorly by dentary and restricted by surangular posteriorly so that lateral exposure of process is limited to a narrow wedge between dentary and surangular
72. Angular: (0) present; (1) absent (not fused)
73. Prearticular crest: (0) absent; (1) present; (2) prominent, with embedded angular process
74. Retroarticular process dorsal surface: (0) sulcus or pit present; (1) absent
75. Retroarticular process direction: (0) directed posteriorly; (1) inflected medially
76. Retroarticular process medial margin: (0) smooth medial margin; (1) tubercle or small flange on posteromedial margin of retroarticular process
77. Retroarticular process offset: (0) no offset; (1) offset medially with lateral notch forming a waist proximally
78. Retroarticular process breadth posteriorly: (0) tapered or parallel-sided; (1) broad posteriorly
79. Retroarticular process torsion: (0) not twisted posteriorly; (1) posterior border obliquely twisted
80. Finger-like angular process: (0) absent; (1) present
81. Adductor fossa size: (0) small or moderate; (1) expanded, inflated, widely open

E. Dentition

82. Palatine teeth: (0) present; (1) absent
83. Pterygoid teeth: (0) present; (1) absent
84. Marginal tooth implantation: (0) pleurodont; (1) "acrodont"
85. Marginal tooth replacement: (0) replacement tooth develops lingually, large resorption

pits present ("iguanaid" type); (1) replacement tooth develops posterolingually, small resorption pits present (intermediate type); (2) replacement tooth develops posterolingually, no resorption pits present ("varanid" type)

86. Basal infolding of marginal teeth: (0) not striated; (1) dentine infolded, producing striations

87. Step or offset in tooth margin of maxilla: (0) absent; (1) present

F. Miscellaneous skull character states

88. Scleral ossicle number I: (0) more than 14 ossicles; (1) 14 ossicles or fewer

89. Scleral ossicle number II: (0) 14 ossicles or more; (1) fewer than 14 ossicles

90. Second epibranchials: (0) present; (1) absent

91. Second ceratobranchials (0) present (1) absent

II. Axial skeleton

A. Vertebral column

92. Vertebral condyle orientation: (0) condyle and cotyle meet with no or only slight obliquity; cotyle generally not entirely visible in ventral view; (1) strong obliquity present; cotyle may or may not be entirely visible in ventral view

93. Vertebral centrum articulation: (0) amphicoelous; (1) procoelous

94. Vertebral centrum constriction: (0) not constricted anterior to condyles; (1) constricted anterior to condyles

95. Zygosphene and zygantrum development: (0) weakly developed or absent; (1) strongly developed

96. Zygosphene and zygantrum: (0) present; (1) absent

97. Cervical intercentral attachment I: (0) intervertebral or fixed under anterior part of following centrum; (1) sutured to posterior part of preceding centrum; (2) fused to posterior part of preceding centrum

98. Cervical intercentral attachment II: (0) intervertebral or fixed under posterior part of preceding centrum; (1) sutured to anterior part of following centrum; (2) fused to anterior part of following centrum

99. Posterior trunk (thoracolumbar) intercentra: (0) present; (1) absent

100. Transverse processes of caudal vertebrae I: (0) a single pair of transverse processes or two pairs of converging transverse processes; (1) two pairs of diverging transverse processes (includes presumed transformations of this pattern via loss of one pair of transverse processes)

101. Transverse processes of caudal vertebrae II: (0) a single pair of transverse processes or two pairs of diverging transverse processes; (1) two pairs of converging transverse processes (includes presumed transformations of this pattern via loss of one pair of transverse processes); (2) anterior pair of transverse processes absent

102. Location of autotomy septa in caudal vertebrae: (0) autotomy septa within a single pair of transverse processes, or between two pairs of transverse processes, or anterior to a single pair of transverse processes (includes those passing posterior to a single pair of transverse processes that are thought to be homologous with the anterior pair of processes in taxa with two pairs); (1) autotomy septa located posterior to a single pair of transverse processes

103. Autotomy septa in caudal vertebrae: (0) present; (1) absent

104. Number of presacral vertebrae I: (0) 23 or more; (1) fewer than 23

105. Number of presacral vertebrae II: (0) 25 or fewer; (1) more than 25

106. Number of presacral vertebrae III: (0) 26 or fewer; (1) more than 26

107. Number of cervical vertebrae I: (0) eight or more; (1) fewer than eight
 108. Number of cervical vertebrae II: (0) eight or fewer; (1) more than eight
 109. Number of rib attachment points on each side of sternum: (0) five; (1) four; (2) three; (3) two or fewer
- B. Ribs
 110. Postxiphisternal inscriptional ribs: (0) none continuous midventrally; (1) at least some continuous midventrally
- III. Appendicular skeleton
- A. Pectoral girdle and forelimb
 111. Scapular emargination: (0) absent; (1) present
 112. Anterior (primary) coracoid emargination; (0) absent; (1) present
 113. Posterior (secondary) coracoid emargination: (0) absent; (1) present
 114. Epicoracoid cartilage extent: (0) contacts mesoscapula and usually suprascapula; (1) fails to contact either suprascapula or mesoscapula
 115. Clavicle: (0) present throughout postembryonic ontogeny; (1) absent in postembryonic ontogeny
 116. Clavicle angulation: (0) simple curved rods, following contour of scapulocoracoids; (1) strongly angulated, curving anteriorly, away from scapulocoracoids
 117. Dorsal articulation of clavicle: (0) articulates with scapula; (1) articulates with suprascapula
 118. Interclavicle: (0) present throughout postembryonic ontogeny; (1) absent in postembryonic ontogeny
 119. Interclavicle lateral process: (0) present; (1) absent
 120. Interclavicle shape, and size of anterior process: (0) T or anchor-shaped, anterior process small or absent; (1) cruciform, large anterior process
 121. Sternal fontanelle: (0) absent; (1) present
 122. Ectepicondylar foramen: (0) ontogenetic enclosure of ectepicondylar groove to form a foramen; (1) foramen and groove absent
- B. Pelvic girdle and hindlimb
 123. Notching of distal tibial epiphysis: (0) gently convex for astragalocalcaneal articulation; (1) tibial epiphysis more or less distinctly notched, fitting onto a ridge on the astragalocalcaneum
 124. Ventral view of pubis: (0) pubis relatively short, symphyseal process short, more ventrally directed, and pubic tubercle more posterodorsally placed; (1) pubis relatively longer, symphyseal process narrower and less extensive, but remaining more or less ventrally directed, pubic tubercle more anteroventral in position; (2) as (1) except symphyseal process of pubis extremely elongated and anteriorly directed
- IV. Miscellaneous osteological character states
 125. Postcloacal bones: (0) absent; (1) present
 126. Ventral body osteoderms: (0) absent; (1) present
 127. Dorsal body osteoderms: (0) absent; (1) present
 128. Cephalic osteoderms: (0) absent; (1) present
 129. Dermal rugosities: (0) absent; (1) present, not vermiculate; (2) present, vermiculate
 130. Epiphysis fusion: (0) fuse to diaphyses at same time or after fusion of braincase elements; (1) fuse to diaphyses prior to fusion of braincase elements

Characters from Soft Anatomy

I. Adductor muscles

131. Extension of m. adductor mandibulae posterior: (0) not extending into Meckel's canal; (1) extends far into Meckel's canal

132. Origin of m. pseudotemporalis superficialis: (0) not extended posteriorly along mesial margin of temporal fossa; (1) extended posteriorly

133. Anterior head of m. pseudotemporalis profundus: (0) absent; (1) present

II. Other muscle characters

134. M. rectus abdominis lateralis: (0) absent; (1) present

135. M. extracolumellaris: (0) absent; (1) present

III. Tongue characters

136. Foretongue retractility: (0) absent; (1) retracts within posterior (hind) tongue at zone of invagination

137. Notching of free part of tongue: (0) no notching present; (1) notched less than 10%; (2) notched 10 - 20%; (3) notched 20 - 40%; (4) notched 40 - 50%; (5) notched more than 50%

138. Anterior tongue cross-section and tongue keratinization: (0) rounded, glandular papillae present throughout tongue; (1) much wider than tall, non-glandular, posterior (hind) tongue keratinized; (2) mushroom-shaped in cross-section, entire tongue keratinized and non-glandular

139. Tongue plication: (0) entire tongue scaly or papillose; (1) posterior (hind) tongue plicate; (2) entire tongue plicate

IV. Middle and inner ear characters

140. Ciliary restraint system for hair cells: (0) tectorial system (restraint imposed by tectorial membrane); (1) combined tectorial and sallet system; (2) sallet system with restraint imposed by inertial bodies (sallet or culmen)

141. Internal (quadrate) process of stapes: (0) present; (1) absent

V. Nerve characters

142. Ulnar nerve position in forelimb: (0) superficial ("lacertid") condition; (1) deep ("varanid") condition

143. Innervation of dorsal muscles of lower leg: (0) peroneal nerve; (1) interosseous nerve

VI. Miscellaneous characters

144. Femoral or preanal pores: (0) absent; (1) present

145. Course of the stapedia artery: (0) passes anterior to stapes; (1) perforates stapes; (2) passes posterior to stapes

146. Modified middorsal scale row: (0) present; (1) absent

147. Cephalic scales: (0) relatively small; (1) enlarged

148. Cycloid scales: (0) absent; (1) present

OUTGROUP CHARACTER MATRIX

A matrix of character state distributions among outgroups and an assessment of the status of each polarity decision appears in Appendix Table 1. Character numbers and character state codes correspond to those in the Character List. In the column for polarity status, 0 appears if the assessment is as we have coded it in the character list, and E is used if the polarity is equivocal, fol-

lowing the method of Maddison et al. (1984). Justifications or explanations for the use of polarities that are equivocal based on outgroup analysis are given in the Character Analysis.

The following abbreviations are used for the taxa discussed: RH = Rhynchocephalia; KU = kuehneosaurs; PI = *Paliguana**; SA = *Saurosternon**; PA = *Palaeagama**; YO = Younginiiformes; AR = Archosauromorpha.

The following symbols are used to indicate absence of data: a dash (-) indicates that data are not available (e. g. soft anatomical features or missing regions in fossil taxa, lack of availability of data on living forms); N = not applicable (e. g. limb characters in snakes); ? = data equivocal (region preserved but clear decision on state present is not possible).

INGROUP CHARACTER MATRIX

The character distribution for our basic taxa, indicating variation within each basic taxon, appears in Appendix Table 2. N indicates that the character is not applicable to that particular taxon (e. g. limb characters for snakes) because of absence or extreme modification of the region in question. A dash (-) indicates that we were unable to obtain character information for that particular taxon. A question mark indicates that for one reason or another there was some question in the scoring of the particular character. In this case the presumed state was used in our preliminary analysis and for entering in the computer matrix. For cases in which more than one state occurs in a taxon, the state listed first in the series was used in the computer analysis.

Where appropriate, we have included data from a number of fossil representatives of our basic taxa. These include polyglyphanodontine teiids, helodermatids, anguids, xenosaurs, amphisbaenians, and snakes (*Dinilysia*). These inclusions have been noted in the section on Character Analysis. References for phylogenetic hypotheses used to determine polarity of a character within one of our basic taxa are given at the beginning of that section.

CLADOGRAMS DERIVED FROM COMPUTER ANALYSIS

PHYSYS Cladogram Including Snakes, Dibamids, and Amphisbaenians

When subjected to Wagner.S analysis in the PHYSYS package for computer-assisted determination of phylogenetic relationships, one tree was obtained, with a length of 405, a Consistency Index of 41.975, and an F-ratio of 32.214. Although we give data for *Sphenodon* in the matrix, an all-plesiomorphic ancestor was used for the computer run.

This tree differs from the PAUP tree described below in the following ways: Snakes were placed as the sister group of varanoids. An amphisbaenid-dibamid sister grouping was placed as the sister group of the snake-varanoid grouping. Gekkotans were placed as the sister group of scincomorphs (Fig. 5A).

For this Wagner.S tree, we give an uninterpreted list of characters by number for each node following those used in the Character List above. All characters are state 1 unless followed by a parenthetical modification.

Node 1 - Squamata: 1, 21, 24, 37, 48, 51, 82, 88, 93, 96, 99, 112, 117, 137, 145(2).

Node 2 - Iguania: 6, 7, 8, 18, 25.

Node 3 - Acrodonta: 12, 65, 83, 84, 89, 103, 143.

Node 4 - Gekkota + Scincomorpha + Anguimorpha + Serpentes + Dibamidae + Amphisbaenia: 9, 13, 17, 34, 39, 40, 41, 44, 49, 74, 79, 105, 109, 116, 120, 123, 124, 130, 133, 134, 138, 146, 147.

Node 5 - Scincomorpha + Gekkota: 54, 58, 68, 139, 140.

Node 6 - Scincomorpha: 124(2), 129(2).

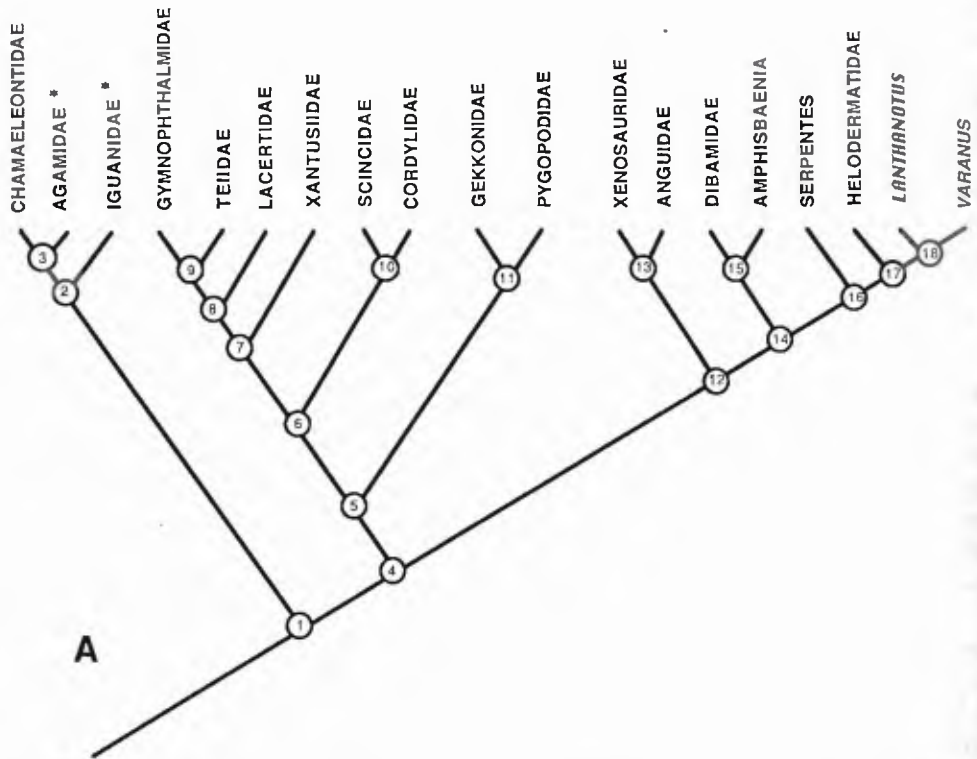
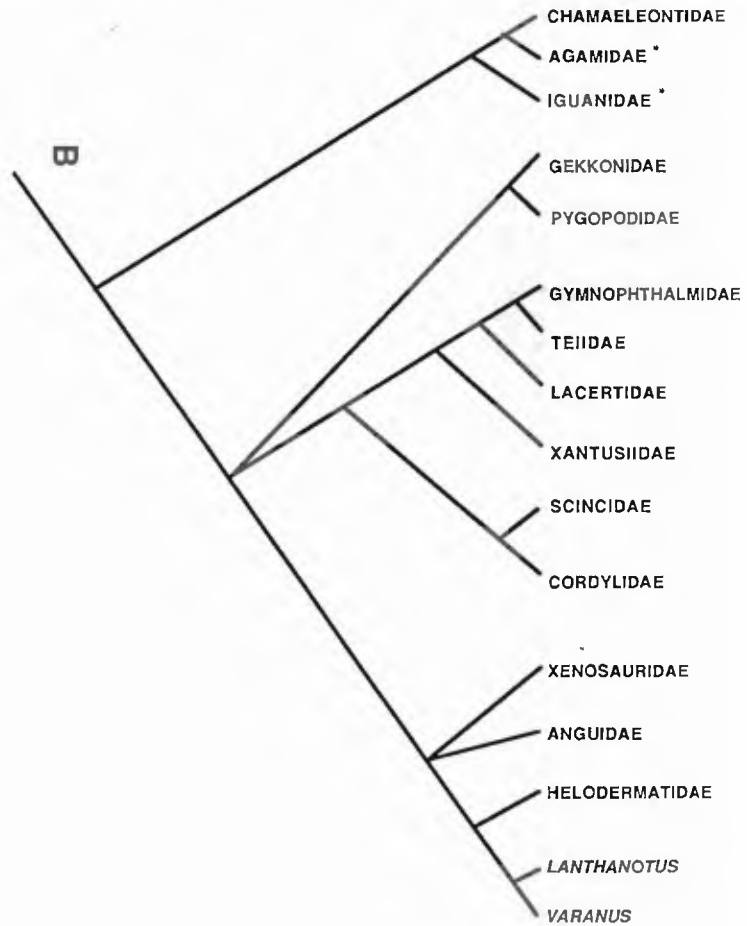
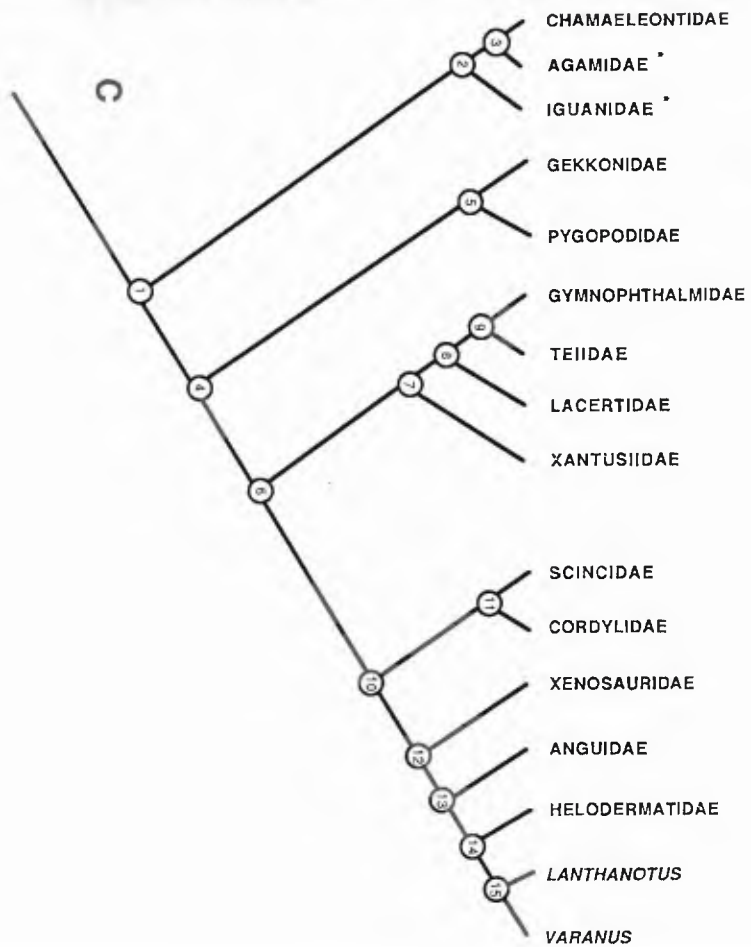


FIGURE 5. A, Wagner.S cladogram derived from the PHYSYS analysis. Snakes, dibamids, and amphisbaenians included. B, consensus cladogram based on four Wagner.S cladograms derived from the PHYSYS analysis. Snakes, amphisbaenians, and dibamids deleted. C, PAUP cladogram with snakes, dibamids, and amphisbaenians deleted. Numbers in A and C refer to nodes in the respective text sections for each cladogram, where characters used by the computer for each node are listed. Metataxa are indicated by an asterisk.

- Node 7 - Lacertoidea: 22, 73, 74(0), 79(0), 100, 131, 132, 138(2).
- Node 8 - Lacertiformes: 37(0), 48(0), 81, 87, 95, 96(0), 105(0), 121, 137(3).
- Node 9 - Teiioidea: 6, 23, 31, 54(0), 73(2), 98, 113, 122, 137(4), 142, 143.
- Node 10 - Scincoidea: 60, 71, 75, 76, 78, 96(0), 126, 127, 128, 140(2).
- Node 11 - Gekkota: 6, 10, 16, 21(0), 26, 28, 32, 52, 55(2), 65, 75, 77, 78, 83, 88(0), 102, 125, 134(0), 135, 141, 145(0).
- Node 12 - Anguimorpha + Serpentes, Dibamidae, and Amphisbaenia: 31, 85, 91, 97(2), 137(2).
- Node 13 - Xenosauridae + Anguidae: 36, 56, 57, 63, 68, 127, 128, 129, 136.
- Node 14 - Varanoidea + Serpentes, Dibamidae, and Amphisbaenia: 65, 66, 89, 90, 106, 114.
- Node 15 - Amphisbaenia + Dibamidae: 4, 35, 42, 83, 101, 109(3), 118.
- Node 16 - Varanoidea + Serpentes: 10, 26, 64, 67, 75, 82(0), 85(2), 103, 136, 137(3).
- Node 17 - Varanoidea: 27, 45, 56, 57, 59, 61, 63, 69, 86, 92, 142, 147(0).
- Node 18 - *Varanus* + *Lanthanotus* (*Varanidae* of Diagnoses of Taxa section): 2, 3, 30, 42, 61(2), 62, 63(2), 65(0), 94, 108, 109(2), 137(4).



- Agamidae*: 48(0), 50, 66, 80, 98, 117(0).
 Amphisbaenia: 5, 10, 47, 91(0), 112(0), 122, 137(4), 138(2), 141.
 Anguinae: 53, 75, 78, 101, 106, 124(2), 126, 133(0), 141.
 Chamaeleontidae: 24(0), 25(2), 38, 47, 65(2), 90, 91, 104, 107, 109(3), 110, 111, 112(0), 114, 115, 118, 122, 137(0), 142.
 Cordylidae: 19, 23, 24(0), 74(0), 105(0), 109(0), 139(2), 144.
 Dibamidae: 16, 22, 26, 27, 28, 32, 41(0), 43, 45, 49(0), 51(0), 53(2), 55(2), 58, 60, 65(2), 72, 78, 101(2), 107, 110, 115, 137(0), 139(2), 145, 148.
 Gekkonidae: 1(0), 93(0), 99(0), 111, 133(0), 147(0).
 Gymnophthalmidae: 10, 11, 26, 58(0), 90, 141, 144.
 Helodermatidae: 5, 16, 37(0), 53, 54, 68, 90(0), 112(0), 119, 127, 128, 129, 143.
 Iguanidae*: 15, 31, 37(0), 50, 80, 82(0), 96(0).
 Lacertidae: 4, 12, 20, 24(0), 36, 53, 114, 128.
Lanthanotus: 5, 16, 53, 66(2), 70, 109(3), 127, 128.
 Pygopodidae: 35, 38, 79(0), 106, 109(3), 112(0), 118.
 Scincidae: 1(0), 4, 18, 20, 36, 43, 97, 106, 138(2), 141, 148.
 Serpentes: 13(0), 17(0), 28, 33, 47, 58, 66(2), 70, 95, 96(0), 115, 118, 133(0), 137(5), 145(0).
 Teiidae: 9(0), 18, 34(0), 45, 46, 124.
Varanus: 14, 26(0), 32, 36, 82, 83, 88(0), 89(0), 113, 120(0), 124(0), 132, 137(5).
 Xantusiidae: 4, 12, 14, 19, 21(0), 23, 24(0), 27, 38, 45, 46, 52, 55(2), 60, 65, 66, 68(0), 71, 72, 83, 99(0), 140(2), 144.
 Xenosauridae: 7, 18, 24(0), 34(0), 58, 90, 120(0), 129(2), 147(0).

PAUP Cladogram Including Snakes, Dibamids, and Amphisbaenians

As a check on our Wagner tree, we also subjected the total data set to analysis in the PAUP program, developed by David Swofford (University of Illinois). A single tree with a length of 406 (one step longer than the Wagner tree) and a Consistency Index of 41.9 was obtained (Fig. 5B).

Only two differences from the PHYSYS tree were present. Snakes and amphisbaenians were placed as sister groups, and these two placed as the sister group of Gekkota + dibamids. These taxa were then collectively placed as the sister group of anguimorphs. As discussed in Diagnoses of Taxa, we do not accept this conclusion, and we do not include the character distribution from this PAUP tree. Although we give data for *Sphenodon* in the matrix, an all-plesiomorphic ancestor was used for the computer run.

PHYSYS Cladograms with Snakes, Dibamids, and Amphisbaenians Deleted

As noted above, the Wagner.S analysis including snakes, dibamids, and amphisbaenians imbedded these groups within the Anguimorpha; amphisbaenians and dibamids were placed as sister groups and together formed the sister group of snakes and varanoids. Placing snakes as the sister group of varanoids is supported by some character evidence discussed below in Diagnoses of Taxa. Clumping of the three limbless groups, however, may be the result of characters associated with limblessness. Limblessness appears to have evolved numerous times within Squamata, judging from its repeated occurrence within our basic taxa, and thus it is possible that limblessness and correlated characters swamp the analysis, linking distantly related limbless forms and causing them to be moved around as a unit on the cladogram despite the absence of characters in one or more of the limbless forms suggesting relationships to particular taxa of limbed squamates. For this rea-

son we also subjected the data to analysis with these limbless taxa excluded. Four Wagner.S trees were obtained with a length of 329, a Consistency Index of 50.760, and F-ratios of 23.389, 23.525, 23.824, and 25.048 respectively. A consensus tree of these four trees is given in Fig. 5B. We do not give character distribution for these four trees because a single, shorter tree was obtained from the PAUP analysis (see below). Although we give data for *Sphenodon* in the matrix, an all-plesiomorphic ancestor was used for the computer runs.

PAUP Cladogram with Snakes, Dibamids, and Amphisbaenians Deleted

A single tree was obtained from this analysis with a length of 323 and a Consistency Index of 50.5. This tree was six steps shorter than the four Wagner.S trees obtained in the above analysis and was identical with one of them. This tree is given in Fig. 5C. It (and one of the four PHY-SYS trees in the previous section) differs from the other computer trees in placing scincoids as the sister group of anguimorphs rather than of scincomorphs. We favor the scincomorph placement of scincoids, but this computer result reflects the rather weak basis of support for scincomorph monophyly.

For this PAUP tree, we give an uninterpreted list of characters by number for each node following those used in the Character List. All characters are state 1 unless followed by a parenthetical modification. Although we give data for *Sphenodon* in the matrix, an all-plesiomorphic ancestor was used for the computer runs.

- Node 1 - Squamata : 3, 50, 53, 93, 99, 112, 137.
- Node 2 - Iguania: 8, 9, 10, 20, 23, 27, 88, 145(2).
- Node 3 - Acrodonta : 14, 39, 65, 82, 83, 84, 89, 96, 103, 143.
- Node 4 - Scleroglossa : 11, 15, 36, 39, 41, 42, 43, 46, 51, 56, 60, 68, 82, 105, 109, 116, 117, 120, 123, 124, 130, 138, 140, 146.
- Node 5 - Gekkota : 8, 12, 18, 26, 28, 30, 34, 54, 57(2), 65, 74, 75, 77, 78, 83, 96, 102, 125, 135, 139, 141.
- Node 6 - Autarchoglossa : 19, 88, 129(2), 133, 134, 145.
- Node 7 - Lacertoidea: 24, 73, 100, 124(2), 131, 132, 138(2), 139, 147.
- Node 8 - Lacertiformes: 23, 39(0), 50(0), 81, 87, 95, 105(0), 121, 137(3).
- Node 9 - Teiioidea : 25, 26, 33, 56(0), 73(2), 98, 113, 122, 137(4), 142, 143.
- Node 10 - Anguimorpha + Scincoidea : 23, 79, 127, 128.
- Node 11 - Scincoidea : 62, 71, 75, 76, 78, 124(2), 126, 140(2), 147.
- Node 12 - Anguimorpha : 33, 56(0), 58, 59, 63, 74, 85, 91, 96, 97, 136, 137(2), 140(0).
- Node 13 - Anguidae + Varanoidea : 26, 55, 60(0), 75, 82(0), 106, 129.
- Node 14 - Varanoidea : 12, 29, 47, 61, 64, 66, 67, 69, 85(2), 86, 92, 103, 114, 137(3), 142.
- Node 15 - *Lanthanotus* + *Varanus* (Varanidae of Diagnoses of Taxa section) : 4, 5, 32, 44, 63(2), 68(0), 90, 94, 108, 109(2), 129(0), 137(4).
- Agamidae*: 26, 50(0), 52, 66, 80, 98, 131.
- Anguidae: 38, 78, 97(2), 101, 124(2), 126, 141, 147.
- Chamaeleontidae: 27(2), 40, 49, 65(2), 90, 91, 104, 107, 109(3), 110, 111, 112(0), 114, 115, 118, 122, 137(0), 142.
- Cordylidae: 21, 25, 105(0), 109(0), 144.
- Gekkonidae: 3(0), 79, 93(0), 99(0), 111.
- Gymnophthalmidae : 8, 12, 13, 28, 60(0), 90, 141.
- Helodermatidae: 7, 18, 28, 39(0), 56, 65, 89, 112(0), 119, 143.

- Iguanidae*: 17, 26, 33, 52, 80, 117.
- Lacertidae: 6, 14, 22, 38, 55, 114, 128, 139(2).
- Lanthanotus*: 7, 18, 28, 66(2), 70, 89, 109(3).
- Pygopodidae: 37, 40, 106, 109(3), 112(0), 118, 147.
- Scincidae: 3(0), 6, 20, 22, 26, 38, 45, 74, 97, 106, 138(2), 139, 141, 148.
- Teiidae: 11(0), 20, 36(0), 47, 48, 124.
- Varanus*: 16, 34, 38, 55(0), 82, 83, 88(0), 113, 120(0), 124(0), 127(0), 128(0), 132, 137(5).
- Xantusiidae: 6, 14, 21, 25, 29, 40, 47, 48, 54, 57(2), 62, 65, 66, 68(0), 71, 83, 96, 99(0), 140(2), 144.
- Xenosauridae: 9, 20, 36(0), 38, 90, 97(2), 120(0).

DISCUSSION

PREFERRED HYPOTHESIS OF SQUAMATE PHYLOGENETIC RELATIONSHIPS

We are in general agreement with many of the results of the computer analysis. The Wagner.S tree that included snakes, dibamids, and amphisbaenians (Fig. 5A), however, placed these groups in ways that our character analysis suggests may not reflect their true phylogenetic relationships (see section on Cladograms Derived from Computer Analyses). As we discuss in the section on Diagnoses of Taxa, there is some reason to believe that snakes may be more closely connected

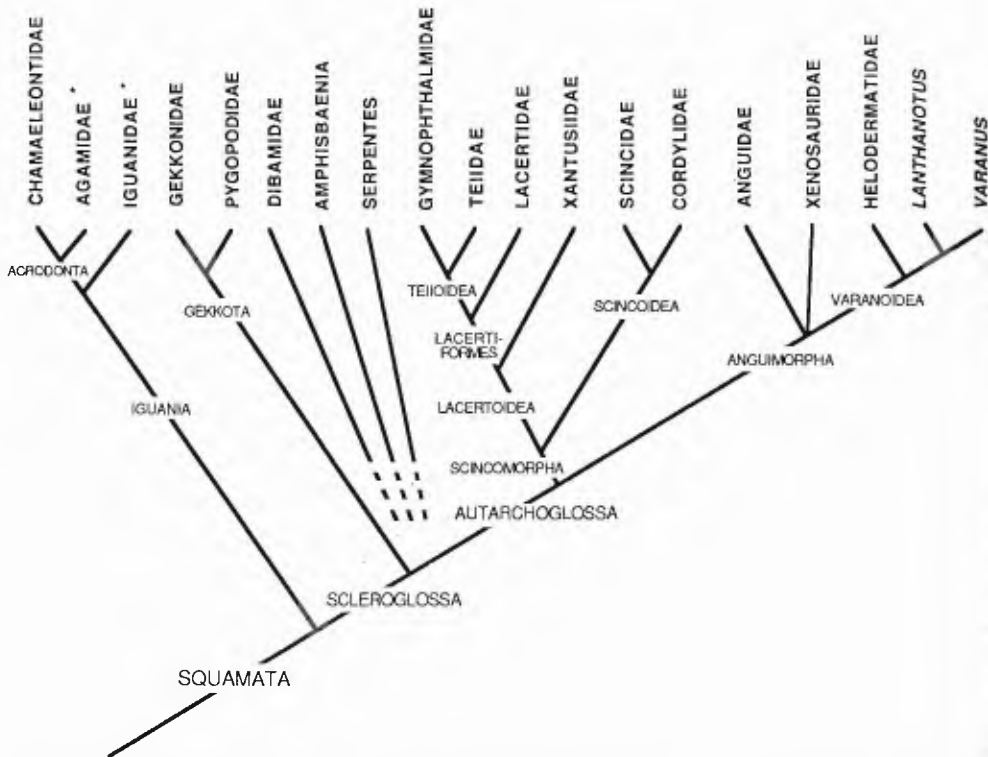


FIGURE 6. Conservative cladogram of squamate relationships derived from character analysis. Diagnostic characters for each node appear in Diagnoses of Taxa. Metataxa are indicated by an asterisk.

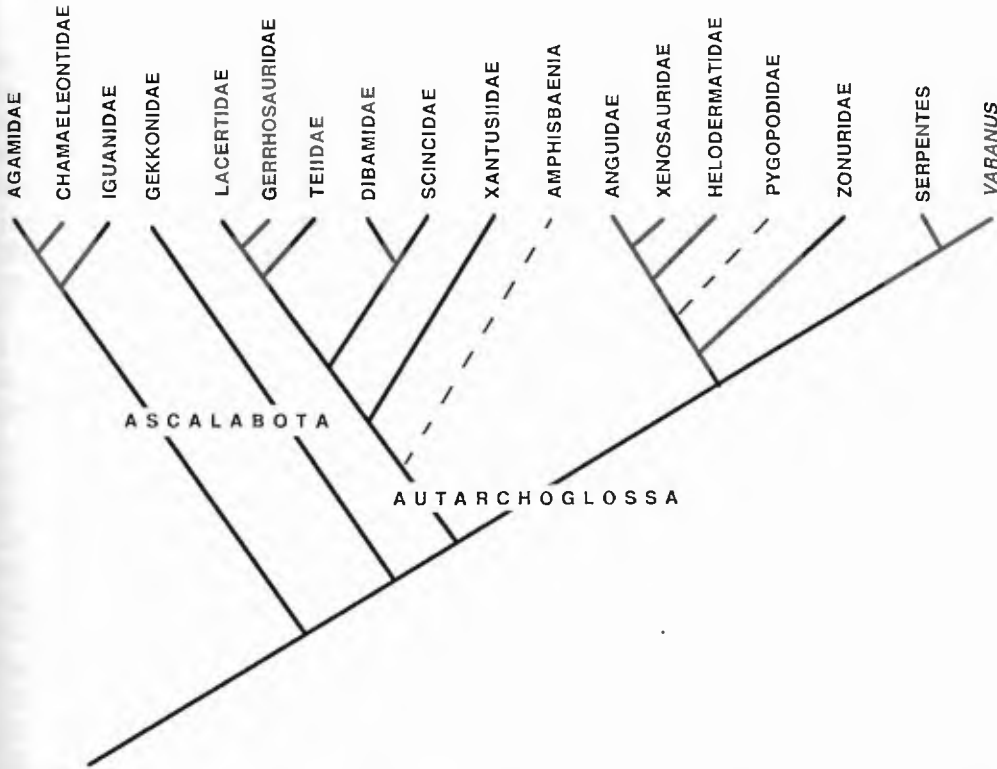


FIGURE 7. Cladogram depicting phylogenetic relationships of squamates according to Camp. Redrawn from Camp's (1923) "skiogram."

with anguimorphs (and perhaps varanoids) than with other autarchoglossans, but our analysis suggests that dibamids and amphisbaenians were drawn along with them in the computer analyses owing to the high degree of convergence in limbless forms. Most of the supposed snake-amphisbaenian synapomorphies are reductions and losses, are variable in the groups concerned, or occur widely in other of our basic taxa.

The linkage of snakes, dibamids, and amphisbaenians suggested that we perform other computer analyses excluding these groups (see text above and Figs. 5B, C). The tree topology did not change with respect to the arrangement of "lizard" groups other than placing scincoids as the sister group of anguimorphs (see above); this topology is quite close to our own conclusions. The major difference from the latter is that the Wagner tree placed Gekkota as the sister group of Scincomorpha rather than as the sister group of Autarchoglossa.

Fig. 6 depicts our conservative evaluation of relationships among squamates; it should be compared with the computer generated trees in Figs. 5A, B, C and with the section on Character Analysis. We have placed snakes, dibamids, and amphisbaenians as Scleroglossa, *incertae sedis*, the least inclusive level that is firmly supported by our analysis. In Diagnoses of Taxa, possibilities for placements in less inclusive groups are discussed.

Fig. 7 is the hypothesis of squamate relationships taken from Camp (1923), and represented as a conventional cladogram for comparison with the computer results and our own conclusions (Figs. 5, 6). Further discussion of the differences between the computer cladograms, our assessment of squamate interrelationships, and comparisons with the results of Camp (1923) is given below in Diagnoses of Taxa.

CHARACTER ANALYSIS

In the following section, we discuss each of the characters, give a summary of the distribution of the character in both ingroup and outgroups, and provide our evaluation of the level at which each character is a synapomorphy, given the phylogenetic relationships depicted in our preferred cladogram (see section on Preferred Phylogenetic Hypothesis). In some cases, our interpretation differs from that of the computer (see section on Cladograms Derived from Computer Analyses); where such difference seems to require explanation, we have provided it. Figures for most osteological characters (and some from soft anatomy) are given, either in Figs. 8-15 in this section (referred to at the beginning of appropriate character descriptions) or in the figures of relevant taxa in the section Diagnoses of Taxa. The latter figures are not referred to in this section.

In a number of cases in which variation in our basic taxa occurs, we have interpreted the derived state as plesiomorphic for that taxon (i.e., 1,0 rather than 0,1; see section on Variation) based on in-group phylogenetic analysis or data on fossils derived from various studies. We list here the analyses on which we based these decisions. Iguanidae* (Etheridge and de Queiroz, 1988); Agamidae* (Moody, 1980); Chamaeleontidae (we have made our own preliminary assessment as well as using Rieppel, 1987); Gekkonidae (Kluge, 1987); Pygopodidae (Kluge, 1976a); Xantusiidae (Rieppel, 1984b; Crother et al., 1986; Estes, 1983a for position of the extinct "*Palaeoxantusia kyrentos*"); Lacertidae (Arnold, 1973); Teiidae (Presch, 1974a; Estes, 1983a for position of extinct polyglyphanodontines); Gymnophthalmidae (Presch, 1980); Scincidae (Greer, 1976); Cordylidae (none available, we have made our own preliminary assessment, placing gerrhosaurids as the plesiomorphic sister group of cordylines); Xenosauridae (Gauthier, 1982; Estes, 1983a, both including extinct forms); Anguillidae (Meszoely, 1970; Rieppel, 1980b; Gauthier, 1982; the first and third dealing with extinct forms); Helodermatidae (Pregill et al., 1986, who also dealt with extinct forms); *Lanthanotus* (Rieppel, 1983; Borsuk-Bialynicka, 1984, on the extinct *Cherminotus*); *Varanus* (Mertens, 1942; while we have mentioned the extinct *Saniwa* it has not been included in our matrix, because further study is required to determine its relationship to *Varanus*); Dibamidae (Rieppel, 1984a; Greer, 1985a); Amphisbaenia (Gans, 1960, 1978; Estes, 1983a for extinct forms); Serpentes (Underwood, 1967; Rage, 1984; inclusion of *Dinilyisia* in snakes follows Estes et al., 1970, Rieppel, 1979a, b; Hecht, 1982, Rage, 1977, 1984b). Other than the examples given above, we have not included fossils in our analysis.

1. Ontogenetic fusion of the premaxillae.--The premaxillae of most squamates fuse in embryonic ontogeny, but remain separate in some gekkonids (Kluge, 1967), some scincids (Greer, 1970), and in fossil ardeosaurids* and bavarisaurids* (Estes, 1983a; Mateer, 1983) in which the snout is preserved. In all other lepidosauromorphs in which the condition can be determined, the premaxillae are separate, suggesting that this is the primitive condition. Both scincids and gekkonids are variable in exhibiting the seemingly primitive condition, which suggests that homoplasy is involved. Other characters indicate that scincids and gekkonids are Scleroglossa, and because Iguania, the sister group of Scleroglossa, is characterized by the condition seen not only in some scincids and gekkonids but also in all other scleroglossans (i.e. fusion of the premaxillae early in ontogeny), it is simplest to interpret ontogenetic fusion of the premaxillae as a synapomorphy of Squamata and failure to fuse them in some scincids and gekkonids as character reversals.

2. Bony external naris extent.--In *Varanus* and *Lanthanotus*, most chamaeleontids, and in colubroid snakes (sensu Rage, 1984), the bony external naris is extended posteriorly, so that the frontal closely approaches or forms part of the posterior margin of the nasal opening, unlike the condition in most other reptiles (McDowell and Bogert, 1954). In *Heloderma* the condition varies, but here it seems to be lack of suture closure rather than actual prolongation of the naris, because there is a thick pad of connective tissue filling the gap (pers. obs.). This pad is not present in *Varanus* and those chamaeleons in which narial prolongation occurs; in these groups the nasal opening is large and may be rounded posteriorly, broadly encroaching on the frontal. In *Lanthanotus* the condition

is more as in *Varanus* although not as extreme as in some species of the latter. In scolecophidians and many booids no nasal prolongation occurs; some forms may develop a narrow separation between nasal and prefrontal that appears different from the above-described conditions. No posterior extension of the naris occurs in any other lepidosauromorph. We interpret posterior extension of the nares as three synapomorphies: one for *Varanus* and *Lanthanotus*, a second within chamaeleons, and a third within snakes.

3. Ontogenetic fusion of nasals.--Nasals are almost uniformly paired in those lepidosauromorphs in which the condition is known. Among squamates, *Lanthanotus* and *Varanus* have fused nasals, and the condition occurs also in some chamaeleontids (Rieppel, 1981c), some gekkonids and pygopodids (Stephenson, 1962), some scincids (*Feylinia*; Greer, 1970), and some scolecophidians (*Liotyphlops*, some *Leptotyphlops*; List, 1966). Nasal fusion appears to be a *Varanus-Lanthanotus* synapomorphy; the other cases are synapomorphies within the variable taxa noted above.

4. Nasal-prefrontal contact.--Lack of contact between nasals and prefrontals, with anterolateral processes of frontals contacting the maxillae, occurs uniformly in dibamids, lacertids, scincids (except *Feylinia*; Greer, 1970), xantusiids (except *Xantusia henshawi* and *X. arizonae*; Rieppel, 1984b; pers. obs.), and amphisbaenians. Some cordylids, teiids, gymnophthalmids, gekkonids, pygopodids, and anguids display this condition as well (pers. obs.). All other squamates, and other lepidosauromorphs in which this character is known, have a nasal-prefrontal contact. The simplest explanation of this distribution is that lack of nasal-prefrontal contact is a scincomorph synapomorphy with independent derivation in some other basic taxa. This hypothesis requires reversals within teiids, gymnophthalmids, scincids, and cordylids. The absence of nasal-prefrontal contact in amphisbaenians and dibamids supports Camp's (1923) hypothesis that these taxa are scincomorphs, as well as the possibility of a close relationship between dibamids and amphisbaenians, one of several hypotheses of dibamid relationships suggested by Greer (1985a). If on the other hand amphisbaenians and dibamids are closer to anguimorphs than to scincomorphs, or are the sister group of these two taxa, then absence of nasal-prefrontal contact may be a synapomorphy of a more inclusive group that has reversed in most anguimorphs.

5. Prefrontal contact with orbital bones.--The prefrontal contacts the postorbital, postfrontal or fused postorbital/postfrontal above the orbits along the lateral surface of the frontal in some chamaeleontids, a few scincids (including some *Feylinia* and *Acontias*), some pygopodids, living species of *Heloderma* (fossil helodermatids lack this condition; Pregill, et al., 1986), a few anguids, some amphisbaenians, *Lanthanotus* (the bones are close but not in contact in the fossil *Cherminotus*; Borsuk-Bialynicka, 1984), and some snakes (pers. obs.). All other squamates, and other lepidosauromorphs in which this character is known, lack this contact (some agamids* and iguanids* have a different prefrontal-postorbital contact below the superciliary ridge). In the context of all of the evidence, we interpret this character as having arisen independently in each of these groups.

6. Ontogenetic fusion of the frontals.--Frontal fusion is widely present in squamates and often occurs in the embryo. Embryonic fusion of the frontals occurs uniformly in iguanians, gymnophthalmids, and (with rare exceptions) gekkonids (Kluge, 1967) and pygopodids (Stephenson, 1962; Rieppel, 1984b). The lack of frontal fusion occurs widely in cordylids, lacertids, xantusiids, scincids, and anguids, although each family includes some members in which frontals fuse either in the embryo, or, more often, postembryonically. Recent teiids have fused frontals in the embryo or shortly after hatching, but the extinct polyglyphanodontines (Sulimski, 1975) retained separate frontals well into postembryonic ontogeny. Among amphisbaenians, only a single fossil form (*Ototriton*; Estes, 1983a) shows fused frontals and they are paired in all snakes except a few colubroids (J. Cadle, pers. comm.). In the remaining squamates the frontals are paired. All other non-squamate lepidosauromorphs, except *Gephyrosaurus* (Evans, 1980) and *Planocephalosaurus* (Fraser,

1982) among the Rhynchocephalia, also have paired frontals. Embryonic fusion of the frontals is a synapomorphy of iguanians and gekkotans, groupings that are supported by numerous other derived characters. Other basic taxa have acquired it independently. In squamates, as in many other vertebrates, early ontogenetic fusion of the frontals has evolved many times.

7. Lateral borders of frontals.--The lateral borders of the frontals are strongly constricted between the orbits in all iguanians (except a few iguanids* and most chamaeleons, in which they are obviously expanded secondarily), reflecting the large eyes that are associated with the highly developed sense of vision in this group. Constriction also occurs in xenosaurs, gerrhonotine anguids, and a few gymnophthalmids and lacertids. Among other lepidosauromorphs, constricted frontals occur only in the sphenodontidan *Homoeosaurus* (Cocude-Michel, 1963), another taxon in which the orbits are relatively large. Frontal constriction is a synapomorphy of iguanians; it has arisen in parallel in some autarchoglossans.

8. Frontal shelf.--The presence of a broad shelf below the nasals, with frontals often exposed anterolaterally as prominent spikes (which may extend anteriorly as far as the maxillae), occurs only in iguanians, although some iguanids* lack it and extreme reduction of the nasals makes this character difficult to determine in many chamaeleons. It is lacking in non-squamate lepidosauromorphs in which the condition can be determined. This character is a synapomorphy of Iguania.

9. Participation in orbitonasal fenestra of descending processes of frontals (Fig. 9C-D).--Prominent descending processes of frontals that restrict the contribution of the prefrontals to the orbitonasal fenestra are uniformly present in all squamates except iguanians (the tropidurine iguanid* *Liolaemus* is an exception) and teiids. Weakly developed descending frontal processes and a broad participation of prefrontals in a large orbitonasal fenestra occur in non-squamate lepidosauromorphs. This character is a synapomorphy of Scleroglossa that has been lost in teiids.

10. Contact of descending processes of frontals.--The descending processes of the frontals are in contact below the olfactory tracts in gekkonids, pygopodids, helodermatids (including fossil forms; Pregill et al., 1986), *Varanus*, amphisbaenians, and snakes, and in some gymnophthalmids, the xantusiid *Cricosaura*, and the anguid *Anniella*. In *Lanthanotus* and the fossil *Cherminotus* (Borsuk-Bialynicka, 1984) the descending processes are large and the potential area for overlap extensive, but a narrow space separates the processes. So far as can be determined, no non-squamate lepidosauromorph has such descending processes. This character is a synapomorphy of Gekkota. We cannot determine whether reversal has taken place in *Lanthanotus*, making this character a synapomorphy of varanoids, or whether it is independent in *Varanus* and *Heloderma*. We have chosen the latter alternative in this case.

11. Frontal tab presence.--The presence of frontal tabs that project posteriorly over the dorsal surface of the frontal is a synapomorphy of gymnophthalmids that has been independently acquired by some chamaeleontids. No other squamate or non-squamate lepidosauromorph has such structures.

12. Postfrontal absence.--The postfrontal is absent in agamids* and chamaeleontids, as well as in *Dibamus* (Greer, 1985) and some iguanids* (Etheridge and de Queiroz, 1988). The postfrontal is relatively small in iguanians (see Character 15). Those iguanians that lack the postfrontal are the only squamates that do so and at the same time lack the drastic modifications of the skull seen in many limbless forms. In xantusiids and the lacertid *Lacerta* there is a single anlage in this region (pers. obs.; Rieppel, in litt., 1985); while it is not possible to determine which bone is absent, we tentatively consider it to be the postfrontal. In snakes the postfrontal is present in the Cretaceous *Dinilysia* (Estes, et al., 1970), and fused to the parietal in Aniliidae, Xenopeltidae, Uropeltidae (Rieppel, in litt., 1985). The postfrontal is absent in extant amphisbaenians (Gans, 1978), although the bone in the posterodorsal corner of the orbit in some fossil amphisbaenians has been identified as the postfrontal (e. g. Berman, 1976, in *Spathorhynchus* and *Dyticonastis*).

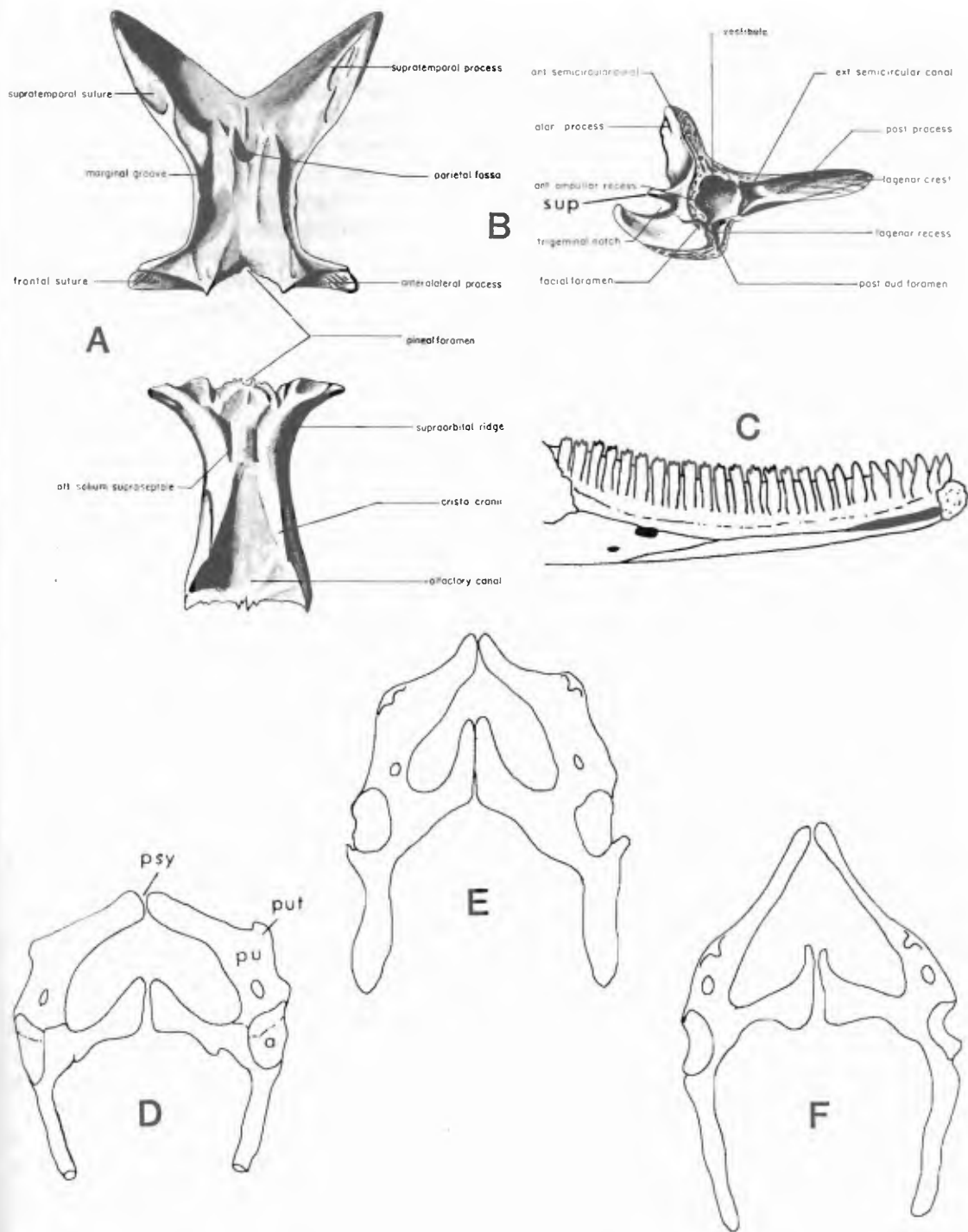


FIGURE 8. A, frontal and parietal of *Ctenosaura pectinata* (Iguanidae*) in ventral view. B, right prootic of *Ctenosaura pectinata* in medial view. C, anterior mandible of *Sceloporus magister* (REE 503; Iguanidae*). D-F, pelves in ventral view, anterior to the top. D, *Plica plica* (RE; Iguanidae); E, *Cnemidophorus sexlineatus* (RE; Teiidae); F, *Celestus cruscus* (MCZ R147434; Anguidae). A, B, from Oelrich (1956). Not to scale. See end of paper for abbreviations.

Gans (1978) considered this bone to be the postorbital. The condition in these fossil amphisbaenians is difficult to interpret. Ventral to the supposed postfrontal is a bone that meets the maxilla in a firm connection; the topographic relationships of this bone are those of a jugal. Contact of postfrontal and jugal occurs in some squamates in which the postorbital contribution to the orbit is reduced and postorbital and postfrontal are separate (e.g., the teiids *Callopietes* and *Tupinambis*), but the plesiomorphic squamate condition of the postfrontal is to be separated from the jugal. The bone in question may be a fused postfrontal and postorbital, but on the basis that the bone is narrow, lacking a posterior extension, we tentatively accept Berman's (1976, 1977) interpretation, and consider the postfrontal to be present in some amphisbaenians. We interpret absence of the postfrontal as several synapomorphies, one that diagnoses Acrodonta, and others that occur within the above variable basic taxa.

13. Postfrontal forking.--A forked postfrontal that clasps the frontoparietal suture is not present in iguanids* (absence of the bone precludes knowledge in other iguanians), in the teiid *Tupinambis*, or in snakes, but occurs in all other non-iguanian squamate taxa. Among the sphenodontidans, *Planocephalosaurus* and some individuals of *Sphenodon* show a slight widening of the frontal that has independently produced a forked postfrontal (Fraser, 1982; pers. obs.). Based on in-group phylogenetic analysis within teiids (Presch, 1974a), the absence of this forking in *Tupinambis* is a reversal. A forked postfrontal is a synapomorphy of Scleroglossa, with reversal in snakes (see p. 252).

14. Postfrontal fusion.--The postfrontal fuses to the postorbital in some anguids, some teiids, some gymnophthalmids, some lacertids, some scincids, and most xenosaurs. They are fused in all *Varanus* except some young examples (pers. obs.), and the bones are separate in the fossil *Saniwa*. The postfrontal and postorbital may be fused in xantusiids (Savage, 1963), and we have considered the postfrontal to be absent. The bone is separate in all non-squamate lepidosauromorphs. The six occurrences of postfrontal/postorbital fusion listed above are considered independent.

15. Postfrontal size.--A reduced, rodlike, or subtriangular postfrontal that is confined to the orbital rim occurs in iguanids*. In scleroglossans and non-squamate lepidosauromorphs the bone is much larger, extending into the temporal region and often contributing to the margin of the superior temporal fenestra. Absence of the postfrontal in other iguanians precludes clear resolution of this character. Nevertheless, we suggest that the reduced postfrontal in iguanids* is an intermediate state to its loss in Acrodonta, and we provisionally place it as an iguanian synapomorphy.

16. Postorbital.--The postorbital is uniformly absent in gekkonids, pygopodids, dibamids, helodermatids, and *Lanthanotus*, and is occasionally absent in some scincids (Greer, 1970). It is present in *Cherminotus*, a presumed Cretaceous relative of *Lanthanotus* from Asia (Borsuk-Bialynicka, 1984). A postorbital is present in all other lepidosauromorph taxa in which it can be determined. Postorbital loss is a synapomorphy of gekkonids and pygopodids that is supported by many other characters. The presence of a postorbital in the fossil *Cherminotus* suggests that it was lost separately in helodermatids and *Lanthanotus*.

17. Postorbital contribution to posterior border of orbit.--A postorbital that is essentially a temporal rather than an orbital bone, with the orbital portion forming less than one-half of the posterior orbital border (excluded from the orbit in some taxa) and with a reduced ventral process, occurs in all squamate taxa that have the bone except iguanians and snakes. In non-squamate lepidosauromorphs, the postorbital is broadly included in the orbit. Absence of the postorbital in some squamate families makes this character difficult to interpret. This character is indeterminate in Gekkota, in which a postorbital is absent. The extinct taxa *Eichstaettisaurus* (Estes, 1983a; labeling of postorbital and postfrontal reversed in error) and *Ardeosaurus* (Mateer, 1982) appear to have the derived condition, with a narrower orbital contribution of the postorbital. If these taxa are closely related to Gekkota, temporalization of the postorbital is a scleroglossan synapomorphy. The primitive condition is, however, present in snakes.

18. Jugal-squamosal contact on supratemporal arch.--In iguanians, scincids, teiids, xenosaurs, and the extinct ardeosaurids* (Estes, 1983a; Mateer, 1982), the jugal and squamosal are in contact or nearly in contact. These bones are well separated in cordylids, gymnophthalmids, lacertids, xantusiids, anguids, and *Varanus*. In other squamate groups, loss or reduction of the supratemporal arch makes the condition impossible to determine. In sphenodontidans, external contact of these bones does not occur in *Sphenodon* (although it is present internally) but it is present in other sphenodontidans (Gauthier et al., 1988). In kuehneosaurs, contact apparently occurs in *Icarosaurus*, but is lacking in *Kuehneosaurus* (Robinson, 1962). In other non-lepidosaurian lepidosauromorphs contact of the two bones does not occur. Although loss or reduction of the supratemporal arch in many squamates makes the character less easy to interpret, it is simplest to place the loss of contact between jugal and squamosal as an autarchoglossan synapomorphy that has reversed independently in teiids, scincids, and xenosaurs.

19. Supratemporal fenestra restriction by postorbital.--Restriction (and occasional closure) of the supratemporal fenestra primarily by the postorbital occurs in cordylids, xantusiids (if our decision that the postfrontal is absent in this group is correct; see character 12), some gymnophthalmids and anguids, and the iguanid* *Phrynosoma m'calli*. No such closure occurs in any non-squamate lepidosauromorph. This character was used as a synapomorphy of cordylids and xantusiids by Estes (1983a), but according to the present analysis it appears to be separately derived in (or within) all basic taxa in which it occurs.

20. Supratemporal fenestra restriction by postfrontal.--Restriction (and occasional closure) of the supratemporal fenestra primarily by the postfrontal occurs in lacertids, and in scincids in which a temporal arch is present. No such closure occurs in non-squamate lepidosauromorphs. It is simplest to assume that this type of closure has arisen independently in lacertids and scincids, because other characters suggest that these taxa are not sister groups.

21. Ontogenetic fusion of parietals.--Among non-squamate lepidosauromorphs, parietal fusion occurs only in the rhynchocephalians *Planocephalosaurus* (Fraser, 1982) and *Gephyrosaurus* (Evans, 1980). Separate parietals occur in most gekkonids other than eublepharines (Kluge, 1967), pygopodids other than *Lialis* (Kluge, 1967), and xantusiids except *Cricosaura* (Savage, 1963) and fully grown *Klauberina* (pers. obs.). Given the relationships proposed in this paper it is simplest to interpret ontogenetic parietal fusion as a synapomorphy of Squamata (convergent in some rhynchocephalians). Reversal occurs in Gekkonidae (eublepharines and the fossil bavarisaurids* have fused parietals) and again reverses to the fused condition in some larger gekkonids. Fusion also occurs in the pygopodid *Lialis* (see p. 206).

22. Parietal tabs (Fig. 8A).--Ventral parietal tabs that underlie the frontals are uniformly present in teiids, xantusiids, lacertids, and gymnophthalmids. Some iguanids*, agamids*, chamaeleontids, cordylids, and scincids may also show this character. *Varanus* may have parietal tabs that overlie the frontal (Rieppel, in litt., 1985). We are unable to determine the condition in amphisbaenians and the dibamid *Anelytropsis*, but *Dibamus* has parietal tabs that fit into slits in the posterior border of the frontals (Rieppel, in litt., 1985). This character is a synapomorphy of the first four families listed above (Lacertoidea), with independent origins within the remaining taxa (unless the dibamids are included within the Scincidae as suggested by Rieppel, 1984a).

23. Parietal downgrowths.--Parietal downgrowths that extend toward, to, or beyond the epityrgoids occur in cordylids, xantusiids, gymnophthalmids, teiids, and some scincids. The lower surface of the parietal in all non-squamate lepidosauromorphs in which this character can be determined lacks such downgrowths. Although this character could be interpreted in several ways, the simplest explanation for its distribution is to consider it a synapomorphy of Scincomorpha, which then requires reversal in lacertids and some scincids.

24. Parietal table and supratemporal process length.--In squamates generally, the parietal table is relatively short, exposing the braincase in dorsal view, and the supratemporal processes are relatively long and slender. In xantusiids, *Xenosaurus*, some lacertids and some cordylids, the parietal table is extensive, largely obscuring the braincase in dorsal view, and the supratemporal processes are relatively short. In small or young lacertids the condition is more like that of squamates generally. In rhynchocephalians both conditions occur, and in other non-squamate lepidosauromorphs the supratemporal processes are relatively short, and the parietal table is extensive posteriorly, covering the braincase in dorsal view. The simplest explanation for this character distribution is that the reduced parietal table and long supratemporal processes are primitive for squamates, reversing our original polarity. The condition found in xantusiids, lacertids, *Xenosaurus*, and some cordylids, while superficially similar to the condition in non-squamate lepidosauromorphs, appears to have been separately derived by the deposit of secondary dermal bone. We consider the presence of an extensive parietal table and short supratemporal processes in squamates to be four separate synapomorphies, one in lacertids, another in xantusiids, another within cordylids, and the last in *Xenosaurus*. It is an equal number of evolutionary transformations to consider this a lacertoid synapomorphy that has reversed in the Teiioidea, but because different bones are involved in closure (characters 19, 20) independent acquisition in lacertids and xantusiids is preferable.

25. Parietal foramen position.--Among recent squamates, position of the parietal foramen on the frontoparietal suture is limited to iguanians, with some chamaeleontids and iguanids* having the foramen still farther forward, within the frontal. The rare occurrence of a parietal foramen within the parietal in iguanids* is discussed in the section on Variation. Position of the foramen on the frontoparietal suture occurs in some individuals of the teiid *Teius* (Estes, 1983a) and is variable both intraspecifically and within higher taxa of the fossil polyglyphanodontine teiids (Sulimski, 1975). Among non-squamate lepidosauromorphs, the parietal foramen is within the parietal, except in kuehneosaurs, in which it occurs on the frontoparietal suture. Presence of the parietal foramen on the frontoparietal suture is most reasonably interpreted as an iguanian synapomorphy, with convergence in kuehneosaurs and some teiids.

26. Parietal foramen.--The parietal foramen is absent in gekkonids, pygopodids, dibamids, gymnophthalmids, helodermatids, *Lanthanotus*, amphisbaenians (except some species of *Monopeltis*; Gans, 1978), and snakes. The foramen is also absent in some chamaeleontids, some lacertids (*Holaspis*, *Adolfus*, *Gastropholis*, *Bedriagaia*, many *Philochortus*, and some *Nucras*; E. N. Arnold, in litt., 1985), as well as in some cordylids, iguanids*, scincids, and xantusiids (Gundy and Wurst, 1975; pers. obs.). Among extant teiids, the foramen is present only rarely in the teiine *Teius*, although it is also present in the fossil polyglyphanodontines and the extinct tupinambine *Chamops* (Estes, 1983a). The foramen is uniformly present in non-squamate lepidosauromorphs. Gundy and Wurst (1975) have shown that absence of the foramen frequently occurs in tropical and subtropical squamates. Absence of the parietal foramen is a synapomorphy of Gekkota. No pattern of loss that is consistent with results based on other characters can be discerned for the other taxa, and independent loss in all groups is the simplest explanation.

27. Posterior extent of maxilla.--Posterior extent of the maxilla that only slightly overlaps the orbit is found in *Varanus*, *Lanthanotus*, and helodermatids; it is thus a synapomorphy of the Varanoidea. It also occurs in dibamids (Greer, 1985) and xantusiids, but this is apparently independent. In the non-squamate lepidosauromorphs the maxilla extends posteriorly well under the orbit.

28. Lacrimal.--Absence of a lacrimal is uniform in dibamids, gekkonids (Rieppel, 1984b, noted a possible exception), pygopodids, and snakes, and it is also absent in some iguanids* (Etheridge and de Queiroz, 1988), agamids* (Moody, 1980), chamaeleontids (Rieppel, 1981c), cordylids (Romer, 1956), gymnophthalmids (?fused; Presch, 1980), scincids (Rieppel, 1981b), and amphisbaenians (Gans, 1978). We are unable to tell whether the lacrimal is absent or fused in

xantusiids, either in extant forms or in the extinct "*Palaeoxantusia*" *kyrentos* (contra Schatzinger, 1980). The lacrimal is present in most non-squamate lepidosauromorphs, although among rhychocephalians it is absent in sphenodontidans (Gauthier et al., 1988). This character is a synapomorphy of Gekkota; absences in our other basic squamate taxa all appear to be independent.

29. Lacrimal fusion.--The lacrimal may fuse to the prefrontal in some gymnophthalmids (Presch, 1980) and amphisbaenians (Romer, 1956). It is separate in all non-squamate lepidosauromorphs. We interpret lacrimal-prefrontal fusion in the above taxa as two separate synapomorphies.

30. Lacrimal foramen number.--A double lacrimal foramen occurs only in *Lanthanotus* and *Varanus*. In non-squamate lepidosauromorphs a double foramen is said to occur only in some Younginiformes (Currie, 1980). The character is a synapomorphy of the *Varanus-Lanthanotus* clade (character unknown for *Cherminotus*).

31. Anteroventral border of orbit.--There is considerable variation in the extent of participation of maxilla and jugal in the orbit of squamates, and this character is not easy to generalize. While individual units within our basic taxa may also show considerable variation, we have tried to describe the modal condition as follows. Formation of the anteroventral border of the orbit by the jugal occurs in iguanids*, teiids, anguids, xenosaurids, helodermatids, *Lanthanotus* (and its Cretaceous relative *Cherminotus*; Borsuk-Bialynicka, 1984), *Varanus*, and amphisbaenians. It is also the condition in some agamids*, chamaeleontids, lacertids, scincids, and cordylids. In gekkonids (e. g. *Hemitheconyx*), the jugal is elongated and excludes the maxilla from the orbit, but in others the jugal is much reduced or absent, making it difficult to assign a state. Among non-squamate lepidosauromorphs, *Paliguana**, *Palaeagama**, and younginiforms have the jugal forming the lower border of the orbit, but in kuehneosaurs and rhychocephalians the maxilla forms the lower border of the orbit, suggesting that this is the primitive condition for lepidosaurs. Although our original interpretation of this character was that formation of the lower border of the orbit by the maxilla was also primitive for squamates, it requires fewer steps (9 vs. 10) to have presence of the jugal in the orbit as a synapomorphy of Squamata, reversing our original polarity. This requires reversals in anguimorphs, xantusiids, lacertids, and within agamids*, chamaeleontids, gekkonids, pygopodids, cordylids, and scincids.

32. Jugal-postorbital bar.--In most squamates, as well as in all other lepidosauromorphs in which the postorbital and temporal regions of the skull are known, the jugal contacts either the postorbital, the postfrontal, or both of these bones posterodorsally, forming a complete postorbital bar. Reduction of the jugal, rendering the postorbital bar incomplete, occurs in dibamids (Greer, 1985a), gekkonids (Kluge, 1967), pygopodids (Stephenson, 1962), and *Varanus* (Mertens, 1942), although the jugal is not as strongly reduced in *Varanus* as in the other three taxa and may be bound by a ligament to the postorbitofrontal (Mertens, 1942). Other squamates known to possess this derived condition of the jugal-postorbital bar are the anguid *Anniella* (e. g. Coe and Kunkel, 1906), the scincids *Feylinia*, *Nessia*, and *Typhlosaurus* (Rieppel, 1981b), most amphisbaenians, and all snakes except *Dinilysia* (Estes et al., 1970). The complete postorbital bar of some extant snakes (e. g. *Python*) is formed by a modified postorbital bone (Underwood, 1957a), and the jugal is absent (Romer, 1956). The possible presence of a jugal in amphisbaenians (e. g. Vanzolini, 1951) was dismissed by Gans (1978:370) on the grounds that, "reports on this element seem to be based on the interspecifically variable position of the ectopterygoid." However, the more ventral of the two bones forming the complete postorbital bar in the fossil amphisbaenians *Hyporhina* (Gilmore, 1928; Berman, 1972), *Spathorhynchus* (Berman, 1973, 1977), and *Dyticonastis* (Berman, 1976) is incorrectly identified as the postorbital. It is clearly either a jugal, as identified by Baur (1893), or a composite jugal-postorbital. Its dorsal extension and lateral position make it very unlikely that it is an ectopterygoid. Furthermore, although the postorbital bar of *Rhineura* is

incomplete, a small jugal is present at the posterior edge of the maxilla above the ectopterygoid (Baur, 1893; Cope, 1900; Walker, 1932; figured by Zangerl, 1944, and Gans, 1967). Reduction of the jugal resulting in an incomplete postorbital bar is a synapomorphy of Gekkota and is independently derived in the other basic taxa.

33. Squamosal.--Because all non-squamate lepidosauromorphs in which the appropriate region is preserved possess a squamosal, the presence of this bone in most squamates is inferred to be a retained primitive feature. Given that the bone articulating with the dorsal end of the quadrate in snakes is correctly identified as the supratemporal (e. g., Estes et al., 1970; Rage, 1984a), then the squamosal is absent in snakes (including *Dinilysia*). This bone is also absent in a few gekkonids (Kluge, 1967), the anguid *Anniella*, and the dibamid *Dibamus* (present in *Anelytropsis*; Greer, 1985a). For pygopodids we accept the opinion of Underwood (1957) that the single bone present is the squamosal rather than the supratemporal as suggested by Stephenson (1962); in some *Aprasia* the squamosal is absent as well (Rieppel, in litt., 1985). Given the variable absence of the squamosal in gekkonids and dibamids, and the phylogenetic relationships suggested by other characters, we interpret the absence of a squamosal as a synapomorphy of snakes; the absence of this bone in some gekkonids and in *Dibamus* is considered to be convergent.

34. Dorsal process of squamosal.--Within squamates, a dorsal process of the squamosal (Robinson, 1967) is present in iguanians. In teiids, a dorsal process appears to be present in some taxa but may be variable within these taxa (*Dracaena*, *Tupinambis*). On the basis of the well-corroborated scincomorph relationship demonstrated by other characters, this appears to be an independent development. The somewhat similar structure found in *Xenosaurus* appears to be related to the closure of the superior temporal opening and is thus not a true dorsal process; this is again corroborated by the numerous other characters that support placement of this group within Anguimorpha. The dorsal process is not present in gekkonids (Gauthier, 1982; Estes, 1983a). A dorsal process is present in all non-squamate lepidosauromorphs in which it can be determined. Loss of the dorsal process is a synapomorphy of the Scleroglossa.

35. Supratemporal.--No supratemporal occurs in pygopodids (see character 33), dibamids, and amphisbaenians, as well as in most gekkonids (Kluge, 1967; 1987), some agamids* (Moody, 1980), scolecophidian snakes (McDowell and Bogert, 1954), and possibly the anguid *Anniella* (we believe the single element in this taxon to be the squamosal). Among non-squamate lepidosauromorphs, absence of the bone is widespread in rhynchocephalians (Evans, 1980; Fraser, 1982; Fraser and Walkden, 1983) and kuehneosaurs (Evans, 1980). With the possible exception of gekkotans, it seems likely that loss has occurred independently in all of our basic taxa that lack the supratemporal. Loss of the supratemporal may either be a synapomorphy of Gekkota reversed in some gekkonids, or one that places pygopodids closer to some gekkonids than to others (see p. 206). We provisionally treat the loss of the supratemporal in gekkonids and pygopodids as independent events.

36. Palpebral ossifications.--These ossifications lie in the eyelids at the anterolateral corners of the orbits, deep to the supraorbital osteoderms in those species that possess both structures. Palpebral ossifications occur in anguids (Siebenrock, 1892), lacertids (Siebenrock, 1894; Haas, 1936), *Varanus* (Mertens, 1942), xenosaurids (Barrows and Smith, 1947; McDowell and Bogert, 1954), cordylids (Siebenrock, 1892) and scincids (Siebenrock, 1892). Palpebral ossifications are said to occur in teiids (Romer, 1956), but we have not found this to be the case. They are absent in *Dibamus* (pers. obs.) and in gekkonids. Palpebrals are unknown in non-squamate lepidosauromorphs although they occur in some crocodylomorphs and in ornithischian dinosaurs (Romer, 1956; Gauthier, 1984). Given the relationships proposed in this study and the distribution of palpebral ossifications among squamate taxa, the level at which this character exists as a synapomorphy is highly problematical. For the present we interpret it as three separate synapomorphies, one for lacertids, one for scincoids (reversed in some), and one for anguimorphs reversed in *Heloderma* and *Lanthanotus*.

37. Pterygoid lappet of quadrate.--A strong lappet of the ventrolateral region of the quadrate onto the pterygoid occurs in gymnophthalmids, teiids, lacertids, and helodermatids, as well as some iguanids*. This character is present primitively in lepidosauromorphs, but based on the relationships suggested by the entire set of characters we must conclude that the most recent common ancestor of squamates had the firm primitive osseous connection reduced to a fibrous joint. This reverses our original polarity. Within squamates, the taxa noted above have reacquired a pterygoid process of the quadrate, although it is not developed to the degree of the ancestral forms and flexibility of the joint seems to be maintained. A pterygoid lappet onto the quadrate is a synapomorphy uniting the first three taxa and independently acquired in helodermatids and some iguanids*.

38. Vomer fusion.--Fusion of these bones occurs in chamaeleontids (Rieppel, 1981c), pygopodids, and xantusiids, as well as in some gekkonids (Kluge, 1967), gymnophthalmids (Estes, 1983a), and scincids (Greer, 1970). Among non-squamate lepidosauromorphs, vomers are unfused in rhynchocephalians and younginiforms, and not determinable in other taxa. Therefore, unfused vomers appear to be primitive for squamates. The distribution of this character within squamates suggests that all the basic taxa above have acquired fused vomers independently. This is another character (see p. 206) that supports an origin of pygopodids within gekkonids, as suggested by Kluge (1987).

39. Vomer size.--A large vomer that usually restricts the internal naris, extending posteriorly more than half of the maxillary tooth row, occurs in all scleroglossans except booid and colubroid snakes. In iguanians, the vomer is relatively smaller than in most scleroglossans, not extending posteriorly beyond the midpoint of the maxillary tooth row, and the choanae are relatively broad. A relatively small vomer is present in all non-squamate lepidosauromorphs in which it can be determined (except younginiforms, in which it is long, but thin, and some archosauromorphs, in which it may be long, but is never wide nor does it restrict the naris; e. g., Ornithodira, Gauthier, 1986), and thus a wider vomer with a relatively greater posterior extent, coupled with restricted internal choanae, is a synapomorphy of Scleroglossa that has reversed in booid and colubroid snakes.

40. Median contact of septomaxillae.--Meeting (or near meeting) of the septomaxillae on the midline, with formation of a raised midline crest, is characteristic of scleroglossans. In iguanians, as in *Sphenodon*, the septomaxillae do not possess a markedly raised crest. The condition cannot be determined in other non-squamate lepidosauromorphs, but in the archosauromorph *Prolacerta* (Gow, 1975) the condition is similar to that of *Sphenodon*. This character is a synapomorphy of Scleroglossa.

41. Dorsal expansion of septomaxilla.--A dorsally expanded, convex septomaxilla, reflecting an enlarged Jacobson's organ, is found in all squamates except iguanids*, agamids*, and chamaeleontids. In iguanians and in *Sphenodon*, the dorsal surface of the septomaxilla is comparatively flat and the bones are relatively small. The condition cannot be determined in other non-squamate lepidosauromorphs, but in the archosauromorph *Prolacerta* (Gow, 1975) the condition is similar to that in *Sphenodon*. This character is a scleroglossan synapomorphy.

42. Posterior border of opening for Jacobson's organ.--Closure of the posterior border of the opening for Jacobson's organ by maxilla and vomer occurs in *Lanthanotus* (Rieppel, 1983; confirmed in litt. 1985), *Varanus*, and amphisbaenians. Although published figures of *Lanthanotus* other than those of Rieppel (1983) do not show meeting of these two bones behind the opening, Rieppel showed that a dorsal flange of the vomer makes the closure. Closure of the opening by maxilla and vomer also occurs in some anguids (Gauthier, 1982), pygopodids (Stephenson, 1962; Rieppel, 1984b noted that this closure is incomplete in the few pygopodids that have it), scincids (Greer, 1970), gymnophthalmids (pers. obs.), and xantusiids (Savage, 1963). In *Dibamus* actual closure of the opening is by vomer and septomaxilla, although vomer and maxilla are firmly closed posterior to the opening. The condition in snakes is like that in *Dibamus* in that the open-

ing is closed by vomer and septomaxilla, but the maxilla is widely separated from the vomer owing to the kinetic nature of the palato-ptyergoid axis. In other squamates, *Sphenodon*, and probably in *Youngina* and the archosauromorph *Prolacerta* (Gow, 1975), the posterior border of the opening is not closed by bone. The distribution of other characters suggests that most occurrences are independent, but closure by maxilla and vomer is a synapomorphy of *Lanthanotus* and *Varanus*.

43. Medial extensions of palatines.--Medial extensions of the palatines to form a bony secondary palate are found in dibamids and scincids. In other squamates, and in non-squamate lepidosauromorphs in which this can be determined, no extensions of the palatines are present. Although the extent and detail of the palatine "tube" formed in dibamids is unique, it is a possible transformation of the scincid condition (especially that of *Feylinia*; see Greer, 1985a). Dibamids, however, possess few of the characters of scincoids or of scincids, and it is possible that both taxa acquired this character independently (but see Rieppel, 1984a and Diagnoses of Taxa).

44. Choanal fossae of palatines.--Prominent, posteriorly extensive choanal fossae are characteristic of all scleroglossans. In iguanians and in all non-squamate lepidosauromorphs in which the condition can be determined, the palatines are more or less flat, with the choanal fossae (if present) small, shallow, and far anterior. In chamaeleontids the choanal fossae are deep but are placed far anteriorly as in other iguanians, and look very different from the deep choanal fossae seen in gekkotans and (especially) autarchoglossans, snakes, dibamids, and amphisbaenians. This character is a synapomorphy of Scleroglossa.

45. Ectopterygoid contact with palatine.--Exclusion or strong reduction of the maxillary contribution to the suborbital fenestra by contact of ectopterygoid and palatine occurs in teiids, xantusiids, dibamids, helodermatids, *Lanthanotus* and *Varanus*, as well as in some anguids (*Anniella*), pygopodids, gekkonids, and amphisbaenians. The maxilla forms a significant part of the margin of the suborbital fenestra in all non-squamate lepidosauromorphs in which the character can be determined. This character is a synapomorphy of Varanoidea, a grouping supported by many other characters. It may be convergent in our other basic squamate taxa. It may also be a synapomorphy of Gekkota, but we treat its occurrence in gekkonids and pygopodids as separate for the present, because it is variable in both taxa (see p. 206).

46. Ectopterygoid size and restriction of suborbital fenestra.--Partial occlusion of suborbital fenestra by an enlarged ectopterygoid occurs in teiids and xantusiids. In other squamates and in all non-squamate lepidosauromorphs in which this condition can be determined, no such occlusion occurs. The suborbital fenestra of amphisbaenians is small or absent, but this occurs as a result of reorganization of the palate rather than enlargement of the ectopterygoid. Other characters suggest that teiids and xantusiids are not sister groups, and thus the occurrence of an enlarged ectopterygoid that occludes the suborbital fenestra appears to be convergent in these taxa.

47. Epipterygoid.--The epipterygoid is absent in all chamaeleontids and snakes, and in most amphisbaenians (Gans, 1978), the dibamid *Dibamus* (but not *Anelytropsis*; Greer, 1985a), and at least some individuals of the iguanid* *Phrynosoma solare* (Presch, 1969; but see also Axtell, 1986). In other squamates and in all non-squamate lepidosauromorphs in which this condition can be determined the epipterygoid is present. The distribution of this character in squamates suggests that all cases of epipterygoid absence among our basic taxa are independent.

48. Pyriform recess width.--A pyriform recess that is narrow throughout most of its length occurs in teiids, and some lacertids, gymnophthalmids, iguanids*, and agamids* (state 0); other squamates have a relatively broad pyriform recess (state 1). This character is difficult to describe, and is subject to some ontogenetic and size variation. The gymnophthalmid *Bachia*, for instance, has a relatively wide pyriform recess but its small size probably accounts for this condition. Similarly, lacertids that are fully grown at a small size may have to some degree the wider recess characteristic of younger animals of larger lacertid taxa. Among non-squamate lepidosauromorphs there is varia-

tion in rhynchocephalians, while kuehneosaurs and younginiforms (as restored) appear to have a narrow recess. On the basis of the outgroups, we originally polarized this character as given above. The simplest explanation of this character distribution, however, is that our original polarity should be reversed, and that a broad recess is a synapomorphy of Squamata, with reversal a synapomorphy of lacertids, gymnophthalmids, and teiids, although the presence of ontogenetic variation complicates the issue in this case. Independent occurrence is found in some iguanians.

49. Alar process of prootic.--An elongated and anterodorsally directed alar process of the prootic occurs in all non-iguanian squamates (Gauthier, 1982; Estes, 1983a; Borsuk-Bialynicka, 1983), although the condition of the alar region in snakes is difficult to assess because of the highly modified braincase. In *Dibamus* the process is short and its direction not determinable (Rieppel, 1984a); in *Anelytropsis* the process appears to be anterodorsally oriented, judging from the figures in Greer (1985a), who did not comment on this process specifically in the text. In iguanians (with some exceptions), rhynchocephalians, and non-squamate lepidosauromorphs the process is shorter and more vertical. Elongation and anterodorsal orientation of the alar process is a synapomorphy of Scleroglossa.

50. Supratrigeminal process of prootic (Fig. 8B).--A prominent supratrigeminal process of the prootic projects anteriorly, dorsal to the trigeminal notch, in most iguanids* and agamids* (Oelrich, 1956; pers. obs.). This process is lacking in other squamates and in non-squamate lepidosauromorphs in which the character can be determined. Although the computer analyses placed this character as independently acquired in iguanids* and agamids*, we interpret it as an iguanian synapomorphy that has been lost in chamaeleontids and a few iguanids* and agamids*. We prefer this interpretation because the presence of a supratrigeminal process appears to be plesiomorphic for both iguanids* and agamids*, and because the dubious monophyly of Agamidae* allows the possibility that the loss of the process within that taxon also accounts for its absence in Chamaeleontidae. Thus the hypothesis of acquisition and reversal requires three character transformations as opposed to four for the hypothesis of convergence.

51. Opisthotic-exoccipital fusion.--Fusion of these bones occurs in the embryo in all squamates except dibamids (Greer, 1985a). The bones remain separate well into postembryonic ontogeny in all non-squamate lepidosauromorphs in which the character can be determined. Although this character alone suggests that dibamids are the sister group of all other squamates (Greer, 1985a), the relationships suggested by our entire set of characters require that our original polarity be reversed, and that early ontogenetic fusion of opisthotic and exoccipital be interpreted as a squamate synapomorphy that has reversed in dibamids.

52. Enclosure of lateral head vein within bony canal formed by crista prootica.--This results from anteroventral extension of the crista prootica onto the basiptyergoid process. Pronounced anteroventral extension and formation of a fully enclosed canal occurs in xantusiids, pygopodids, most gekkonids, and some gymnophthalmids, and is one aspect of the "butterfly-shaped" basisphenoid complex believed by various authors (e.g. McDowell and Bogert, 1954) to indicate relationship of the first three groups (see Estes, 1983a:122 for discussion). Extension of the crista prootica without full enclosure of the lateral head vein occurs in other gekkonids and in some lacertids, teiids, and scincids. The only non-squamate lepidosauromorphs in which this character can be determined are the rhynchocephalians, in which it is lacking. Bony enclosure of the lateral head vein is also absent in archosauromorphs (e. g., Gow, 1975). In our opinion, its presence in gekkotans and xantusiids is convergent, because many other characters support relationship of xantusiids to other members of Lacertoidea, in which variable presence of the extension (including occasional formation of a fully enclosed canal) also occurs. The simplest explanation of the distribution of this character is that its occurrence in gekkotans and within lacertoids is independent.

53. Posterior opening of vidian canal.--The position of the posterior opening of the vidian canal in relation to the parabasisphenoid/prootic suture is subject to considerable variation. Accord-

ing to Greer (1985a) the foramen in dibamids is wholly within the prootic (state 2). On the other hand, Rieppel (1984a) figured it between the prootic and the ossified epiphysis of the sphenoccipital tubercle ("X" bone of Zangerl, 1944; not shown in Greer, 1985a) in *Dibamus*. Although there may be variation in this character, apparent absence of the "X" bone in Greer's specimens makes it difficult to make a decision; we have scored the *Dibamus* condition as N because the description given by Rieppel does not fit any of our character states. If Rieppel's interpretation is correct, *Dibamus* is derived with respect to other squamates, but, like *Anelytropsis*, the foramen position is far posterior. Anguids, *Heloderma*, *Lanthanotus*, *Shinisaurus*, and lacertids have it on the suture (state 1), and other families have it within the basisphenoid (state 0). Some cordylids, scincids, and xantusiids (pers. obs.) may also have it at the suture. Our amphisbaenian material does not permit determination of this character. In all non-squamate lepidosauromorphs in which this character can be determined the foramen is within the basisphenoid, although in these taxa the vidian canal is fully enclosed in bone for only a short distance near the anterior part of the basisphenoid, and the parasphenoid and basisphenoid remain separate well into post-embryonic ontogeny (Gauthier et al., 1988). The simplest explanation of the distribution of this character is that it is independently derived in each of the families listed above, although it may be an anguimorph synapomorphy lost in *Xenosaurus* and *Varanus* or a varanoid synapomorphy lost in *Varanus*. The far posterior position of the foramen in dibamids is a synapomorphy of that group, as is the unique position in *Dibamus*.

54. Origin of jaw adductor musculature.--Lateral expansion of the parietal is associated with attachment of the temporal musculature to the ventral surface of the parietal in lacertids, cordylids, scincids, xantusiids, gekkonids, pygopodids, and helodermatids. *Xenosaurus*, anguids (except *Anniella*; Meszoely, 1970; Gauthier, 1982), some gymnophthalmids (pers. obs.), and some iguanians (e. g. *Corythophanes*, most chamaeleontids; pers. obs.) have ventral attachment as well. In iguanians, unlike other squamates, ventral origin of the jaw adductor musculature appears to be associated with the development of casques at the back of the skull. Among non-squamate lepidosauromorphs in which this character can be determined, attachment is always dorsal (Gauthier, 1984). On the basis of extant forms, ventral attachment of temporal musculature appears to be a scinciform character with reversals in teiids and some gymnophthalmids, and a separate synapomorphy of Gekkota. Some iguanians have acquired the condition convergently. Convergence in this character may also have occurred in Anguimorpha; however, if the fossil anguimorphs *Gobiderma* and *Carusia* are considered (Borsuk-Bialynicka, 1984, 1985), ventral attachment appears more likely to be plesiomorphic for Anguimorpha. In this case, the simplest hypothesis appears to be that ventral attachment is a synapomorphy of Scleroglossa, with several reversals.

55. Meckel's canal enclosure (Fig. 8C).--Full closure and fusion of the dentary, so that Meckel's cartilage is enclosed in a tube (state 2) occurs uniformly in dibamids, pygopodids, gekkonids, and xantusiids. Such closure and fusion also occurs in some gymnophthalmids (MacLean, 1974), scincids (Greer, 1970), iguanids* (Etheridge and de Queiroz, 1988) and amphisbaenians (Gans, 1978). Closure and/or fusion does not occur in any non-squamate lepidosauromorph in which it can be determined. Other characters indicate that closure and fusion of Meckel's canal is a synapomorphy of Gekkota. Variation within other taxa suggests that they have evolved this character independently. The intermediate condition (state 1) occurs only in some cordylids (pers. obs.), scincids (Greer, 1970), teiids (Presch, 1974a) iguanids* (Etheridge and de Queiroz, 1988), and amphisbaenians (Gans, 1978). Evidence from phylogenetic analysis within the variable taxa suggests that an open Meckel's groove is primitive within these taxa, and, therefore, that state 1 is independently derived in all the variable groups. When the variation in this character discussed above is taken into account, the simplest interpretation of state 2 is that it is a synapomorphy of gekkotans, and independently derived in or within all of our other basic taxa in which it occurs.

56. Intramandibular septum of Meckel's canal (Fig. 9A).--This structure was described by Estes (1964) in anguids, and results from the reduction of overlap between postdentary and dentary bones that occurs in anguimorphs. A posteriorly placed subdivision of Meckel's canal, with a well developed intramandibular septum separating Meckel's cartilage from the lateral blood vessels and nerves, occurs in all xenosaurids, anguids, *Heloderma*, *Lanthanotus*, and *Varanus*. Pregill (1981) identified an intramandibular septum in some iguanids*. Some chamaeleontids have a similar situation that is convergent on the basis of other characters. Other squamates lack this structure (e. g., Fig. 9B) Owing to lack of disarticulated material we cannot determine the condition in amphisbaenians (except rhineurids, in which an intramandibular septum appears to be lacking), pygopodids, and dibamids. For similar reasons, this character cannot be determined with certainty in any of the non-squamate lepidosauromorphs. Nevertheless, archosauromorphs lack a well developed intramandibular septum, and we place this character as an anguimorph synapomorphy, with convergence in some iguanids* and chamaeleontids.

57. Meckel's canal exposure ventrally.--Ventral exposure of Meckel's canal anterior to the anterior inferior alveolar foramen may be caused by torsion of the jaw (Camp, 1923); it occurs in xenosaurids, anguids, helodermatids, *Lanthanotus*, *Varanus*, and some chamaeleontids. Ventral exposure of the canal is lacking in non-squamate lepidosauromorphs in which it can be determined. This character is a synapomorphy of Anguimorpha that has arisen convergently in some chamaeleontids.

58. Subdental shelf size.--A large subdental shelf occurs medial to the tooth row, forming a prominent ridge at the base of the teeth. It occurs in cordylids, scincids, dibamids, lacertids, teiids, xantusiids, gekkonids, some pygopodids, some snakes, and some gymnophthalmids (pers. obs.). The subdental shelf is small in iguanians, anguimorphs, amphisbaenians, and some gymnophthalmids, and in all non-squamate lepidomorphs in which the character can be determined. The simplest explanation for the distribution of this character is that it is a synapomorphy of Scleroglossa with secondary loss occurring in amphisbaenians, anguimorphs, and some gymnophthalmids. Alternatively, a prominent subdental shelf may exist as separate synapomorphies in scincomorphs, gekkotans, dibamids, and snakes, but this requires one more evolutionary transformation than in the previous case (if dibamids are scincomorphs, as suggested by Rieppel, 1984a, both alternatives are equally likely).

59. Subdental shelf.--A subdental shelf is absent in helodermatids, *Lanthanotus*, and *Varanus*. It is also absent in some agamids* (Moody, 1980), iguanids* (pers. obs.), chamaeleontids (pers. obs.), and amphisbaenians (Gans, 1957). In rhynchocephalians the subdental shelf is present in *Gephyrosaurus* (Evans, 1980) but it is absent in sphenodontidans. It is also present in kuehneosaurs. This character forms separate synapomorphies in varanoids and amphisbaenians, and seems to have arisen a number of times within iguanians.

60. Dorsal extension of lateral coronoid process of dentary.--A lateral process of the dentary that extends posterodorsally onto the coronoid, covering the anterior part of the coronoid projection, occurs in cordylids, xantusiids, and dibamids, and all but a few scincids. It also occurs in the anguid *Ophisaurus apodus* (Rieppel, 1980b), xenosaurids, and amphisbaenians (e. g. *Amphisbaena*, *Trogonophis*; pers. obs.). In non-squamate lepidosauromorphs there is no comparable condition because the coronoid remains small, projecting little above the dorsal margin of the mandible, unlike the prominent coronoid process that forms a derived condition in squamates (Gauthier et al., 1988). We interpret this character as a scincoid synapomorphy with independent acquisition in xantusiids and dibamids, although it requires an equal number of evolutionary transformations to have it arise in the ancestor of scincomorphs and reverse in the Lacertiformes.

61. Lateral view of disarticulated surangular (Fig. 10E-G).--Characters 61-65 are likely to be correlated, but each describes separate transformations in shape or reduction that form a mosaic of occurrences in our basic taxa. In lateral view, the surangular is long, tapering, and pointed anterior-

ly in most squamates and non-squamate lepidosauromorphs in which it can be determined. In *Heloderma*, however, it develops an anterodorsal expansion so that its anterior margin becomes nearly vertical (state 1). In *Lanthanotus* and *Varanus*, the configuration is the same but there is a reduction of the relative length of the anterior process of the surangular, the anterior edge of which thus terminates relatively closer to the coronoid eminence (state 2). This character was discussed by Gauthier (1982), and is related to presence of an intramandibular hinge. State 1 is a synapomorphy of Varanoidea; state 2 is a synapomorphy (by further transformation) of *Lanthanotus* and *Varanus*.

62. Medial view of prearticular with dentary and splenial removed.--The disarticulated prearticular does not extend well anterior to the coronoid in *Lanthanotus*, *Varanus*, and some snakes; the character is correlated with the development of an intramandibular hinge (Gauthier, 1982). Among non-squamate lepidosauromorphs, this character can be scored only in *Sphenodon*, in which the condition described above is present; however, in archosauromorphs, as in most squamates, the prearticular extends well anterior to the coronoid. Although the outgroup evidence for the polarity of this character is ambiguous, relationships within squamates based on other characters require that this character be interpreted as a synapomorphy of *Lanthanotus* and *Varanus* that is convergent in *Sphenodon* and some snakes.

63. Posterolateral dentary shape.--In xenosaurs, anguids, and helodermatids, a surangular notch is developed on the posterolateral border of the dentary. In *Lanthanotus* and *Varanus*, the notch is reduced, correlated with the development of an intramandibular hinge (Gauthier, 1982:53). In other squamates, and in non-squamate lepidosauromorphs in which the character can be determined, there is no surangular notch. Development of a surangular notch on the dentary is interpreted as a synapomorphy of Anguimorpha; its reduction (and occasional loss) is thus a synapomorphy of *Lanthanotus* and *Varanus*.

64. Dentary-postdentary articulation.--This character describes the overlap of dentary on the postdentary bones. In helodermatids, *Lanthanotus*, *Varanus*, and snakes the overlap is reduced compared to other squamates, in correlation with the development of an intramandibular hinge (McDowell and Bogert 1954; Gauthier, 1982). This character can only be determined for *Sphenodon* among the non-squamate lepidosauromorphs, which shows extensive overlap of dentary and postdentary bones. Reduced overlap of dentary and postdentary bones is a synapomorphy of the first three groups noted above (Varanoidea). The possible relationship of snakes with Varanoidea is discussed in Diagnoses of Taxa.

65. Splenial reduction.--The splenial does not extend anteriorly beyond the tooth row midpoint (state 1) in agamids*, xantusiids, gekkonids, helodermatids, amphisbaenians, and snakes, and in some iguanids* (Etheridge and de Queiroz, 1988), scincids (Greer, 1970), gymnophthalmids (Presch, 1980), and anguids (Meszoely, 1970; Gauthier, 1982). The splenial is absent (state 2) in dibamids and chamaeleontids, and some iguanids* (Etheridge and de Queiroz, 1988), agamids* (Moody, 1980), gekkonids (Kluge, 1967), pygopodids (Underwood, 1957b; Kluge, 1976a, see also p. 206, this paper), and amphisbaenians (Gans, 1978). Among non-squamate lepidosauromorphs a large splenial that extends anteriorly beyond the tooth row midpoint (state 0) occurs in kuehneosaurs and younginiforms, but in all rhynchocephalians the splenial has been lost. While this makes our polarity decision equivocal according to the method of Maddison et al. (1984), given our phylogenetic hypothesis it is simpler to hypothesize independent losses in rhynchocephalians and various squamate taxa rather than postulate numerous reacquisitions of the bone in squamates. Splenial reduction is a synapomorphy of both Acrodonta and Gekkota with independent reduction of the bone in some other basic taxa. Splenial loss appears to be independent in all taxa in which it occurs, with the possible exception of chamaeleontids and some agamids*.

66. Splenial posterior extent.--Reduction of the posterior extent of the splenial so that it does not reach posterior to the apex of the coronoid (state 1) occurs in agamids*, xantusiids, *Heloderma*, *Varanus*, and amphisbaenians as well as some iguanids* (Oelrich, 1956; Etheridge and de Queiroz,

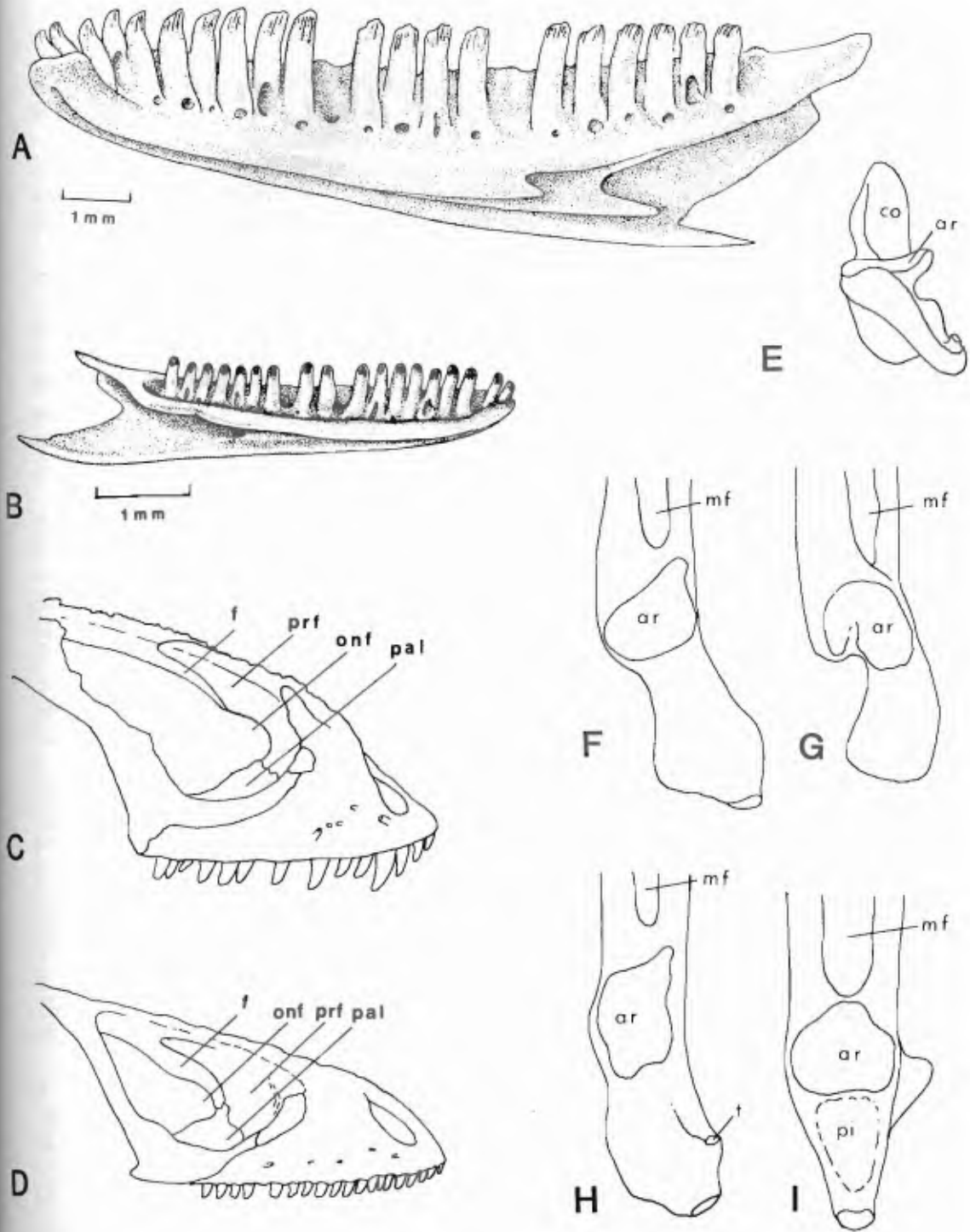


FIGURE 9. A, medial view of right dentary of *Elgaria multicarinata* (Anguidae). B, medial view of left dentary of *Eumeces skiltonianus* (Scincidae). C, oblique view of right orbit of *Crotaphytus collaris* (RE; Iguanidae*). D, same view of *Elgaria multicarinata* (RE; Anguidae). E, posterior view of jaw of *Eumeces laticeps* (REE 1331; Scincidae). F-I, dorsal view of posterior end of mandibles; F, *Diploglossus millepunctatus* (REE 1970; Anguidae); G, *Gekko gekko* (REE 616; Gekkonidae); H, *Eumeces laticeps* (REE 1331; Scincidae); I, *Leiolepis belliana* (REE 1680; Agamidae*). A-B from Gauthier (1982). C-I not to scale. See end of paper for abbreviations.

1988). Further reduction so that there is limited overlap on postdentary bones (state 2) occurs in *Lanthanotus* and snakes. This reduction is correlated with the development of an intramandibular hinge (Gauthier, 1982). This character cannot be assessed in non-squamate lepidosauromorphs, either because of lack of a coronoid or its failure to develop an apex. Archosauromorphs exhibit the entire range of variation seen in squamates. Limited overlap (state 1) is interpreted as a synapomorphy of Varanoidea, with further reduction (state 2) occurring in *Lanthanotus*. Snakes may form part of this grouping as well, or may be separately derived (see Diagnoses of Taxa).

67. Splenial-dentary suture.--A relatively loose connection of splenial and dentary, with much fibrous connective tissue present, occurs in helodermatids, *Lanthanotus*, *Varanus*, and snakes, and is correlated with the development of an intramandibular hinge (Gauthier, 1982). This character cannot be assessed in any of the non-squamate lepidosauromorphs because of splenial absence or poor preservation. A firm connection of the two bones is present primitively in archosauromorphs. This character is a synapomorphy of the first three taxa above (Varanoidea), the monophyly of which is supported by numerous other characters. If snakes are in fact related to varanoids as suggested by McDowell and Bogert (1954), this character may be a synapomorphy of a more inclusive group (see Diagnoses of Taxa).

68. Coronoid lateral process as a lappet on dentary.--A thin lateral process (or lappet) of the coronoid that overlaps the dentary is present in gekkonids, pygopodids, lacertids, gymnophthalmids, teiids, scincids, cordylids, xenosaurs, anguils, and helodermatids, as well as in some iguanids* (Etheridge and de Queiroz, 1988), some (especially rhineurid) amphisbaenians (Estes, 1983a), some snakes (Parker, 1977), and *Varanus salvator* (Rieppel, 1980b). Among non-squamate lepidosauromorphs, only rhychocephalians can be scored for this character, in which it appears in the plesiomorphic state (absence of the lateral process). Although it is simplest to interpret this character as a synapomorphy of Scleroglossa that has been lost in a few taxa, we consider the presence of a coronoid lappet on the dentary to be a synapomorphy of Squamata, a decision that reverses our original polarity. This requires additional loss in some iguanians. Treating the presence of a coronoid lappet as a synapomorphy of Squamata appears to require more evolutionary transformations (six versus five) than treating it as a scleroglossan synapomorphy, but this rests on the dubious proposition of iguanid* monophyly. Because evidence for iguanid* monophyly is lacking (see Diagnoses of Taxa) and because the coronoid lateral process is present (although sometimes small) in seven out of eight of the major groups of iguanids recognized by Etheridge and de Queiroz (1988), as well as in Late Cretaceous fossils thought to be closely related to agamids* (Borsuk-Bialynicka and Moody, 1984), we consider it to have been present in the most recent common ancestor of iguanians and thus also that of Squamata. Etheridge and de Queiroz (1988) coded the presence of the lappet as derived for iguanids* but noted that this decision was based primarily upon congruence with other characters within anoloid iguanids*. Reversal within iguanids* is required whichever interpretation is followed.

69. Coronoid anterior extension.--A long, low anterior extension of the coronoid occurs in helodermatids, *Lanthanotus*, and *Varanus*. Among non-squamate lepidosauromorphs, only rhychocephalians can be scored for this character, either because of absence of the coronoid or poor preservation; in rhychocephalians as in most squamates the coronoid ends relatively abruptly, without such an extension. Presence of an anterior extension of the coronoid is a synapomorphy of the first three taxa noted above (Varanoidea), a group whose monophyly is supported by many other characters.

70. Anterior end of coronoid.--Clasping of the dentary by medial and lateral processes of the coronoid occurs in most squamates. In *Lanthanotus*, snakes, some iguanids* (pers. obs.), and some amphisbaenians (pers. obs.), the coronoid is located more posteriorly so that it no longer clasps the dentary but meets it end-to-end. The coronoid in rhychocephalians is not displaced pos-

teriorly and this character cannot be determined in other non-squamate lepidosauromorphs. The simplest explanation of the distribution of this character is separate origin in each taxon.

71. Dentary overlap of coronoid lateral process.--Anterior covering by dentary of the lateral process of the coronoid, and posterior restriction of the lateral exposure of the coronoid by surangular, causes lateral exposure of the process to be limited to a narrow wedge between dentary and surangular. This occurs in cordylids, xantusiids, most scincids (Estes, 1969; 1983a) and some anguoids (pers. obs.). Owing to absence of the coronoid or its lack of a lateral process in non-squamate lepidosauromorphs, this character cannot be determined except in squamates. Estes (1983a) suggested this as a character allying cordylids and xantusiids. We treat overlap of the lateral process of the coronoid by the dentary as a synapomorphy of Scincomorpha that has reversed with lacertoids and some scincids. It is equally simple, however, to interpret it as separate synapomorphies of xantusiids and scincoids, with reversal in some scincids.

72. Angular.--Absence of the angular bone occurs in dibamids and some gekkonids (Kluge, 1967), pygopodids (McDowell and Bogert, 1954), scincids (Greer, 1970), and iguanids* (Etheridge and de Queiroz, 1988). An angular is absent in most extant xantusiids, but is present in some posthatchling *Xantusia vigilis* (P. Regal, pers. comm., cited by Estes, 1976) and the Eocene "*Palaeoxantusia*" *kyrentos* (Schatzinger, 1980). The simplest explanation is that absence of an angular is independently derived in or within the taxa mentioned.

73. Prearticular crest.--The presence of a crest on the prearticular (state 1) occurs in lacertids and xantusiids; a prominent crest that contains an imbedded angular process (state 2) is found in gymnophthalmids and teiids, which pass through state 1 ontogenetically. Although some iguanians have an angular process, it is not imbedded in the prearticular crest. The absence of a prearticular crest is inferred to be plesiomorphic for Squamata because it occurs in all non-squamate lepidosauromorph groups in which the character can be determined. State 1 is a synapomorphy of the lacertoids with state 2 being a further transformation in teioids.

74. Retroarticular process dorsal surface (Fig. 9G,I).--A sulcus or pit on the dorsal surface of the retroarticular process is absent in xenosaurids, anguoids, *Heloderma*, *Varanus*, *Lanthanotus*, gekkonids, pygopodids, dibamids, scincids, lacertids, and gymnophthalmids, as well as in some cordylids and iguanids*. Those snakes that have a retroarticular process (Typhlopidae, many Colubroidea sensu Rage, 1984) lack a pit. A pit is present in *Gephyrosaurus* but cannot be determined in other rhynchocephalians because the retroarticular process is absent. *Kuehneosaurus* has a dorsal depression on the retroarticular process that may or may not be equivalent to the pit (Robinson, 1962), while the condition in *Icarosaurus* is unknown. This suggests that the presence of a pit is primitive within Squamata. The simplest interpretation is to consider loss of a pit to be a synapomorphy of Scleroglossa, which requires that a pit be redeveloped in lacertoids, with independent loss of a pit in some iguanids*.

75. Retroarticular process direction (Fig. 9F-H).--Medial inflection of the retroarticular process occurs in cordylids, scincids, pygopodids, gekkonids, anguoids, *Heloderma*, *Lanthanotus*, and *Varanus*. Medial inflection also occurs in those snakes that have a retroarticular process (see character 74), although we cannot determine this with certainty in Scolecophidia. There is no inflection in any non-squamate lepidosauromorph. This character represents three separate synapomorphies of taxa that are supported by other characters: Gekkota, Scincoidea, and Varanoidea. Presence in Anguoidae may be independent, or the character may be a synapomorphy of Anguimorpha lost in Xenosauridae, or it may be a synapomorphy of a clade composed of anguoids (but not xenosaurids) and *Varanus*. Presence in snakes may be evidence for anguimorph affinity of that group.

76. Retroarticular process medial margin (Fig. 9E-H).--Presence of a small tubercle or flange on the posteromedial margin of the retroarticular process occurs in cordylids and scincids. It is not present in any other squamate or any non-squamate lepidosauromorph in which it can be determined. The character is a synapomorphy of Scincoidea.

77. Retroarticular process offset (Fig. 9G).--A retroarticular process that is offset medially, with a lateral notch forming a waist proximally, occurs in gekkonids and pygopodids. It is absent in other squamates and does not occur in any non-squamate lepidosauromorph in which it can be determined. This character is a synapomorphy of Gekkota.

78. Retroarticular process breadth posteriorly (Fig. 9F-H).--A retroarticular process that is broadened posteriorly occurs in all anguids, scincids, dibamids, pygopodids, and gekkonids, and all cordylids except some *Cordylus*. Among non-squamate lepidosauromorphs, it occurs in kuehneosaurs, is absent in *Gephyrosaurus*, and is not determinable in other rhynchocephalians owing to absence of the retroarticular process. Although the outgroup evidence is equivocal, relationships based on our entire set of characters suggest that a posteriorly broadened retroarticular process is derived within Squamata. Cordylid-scincid and gekkonid-pygopodid groupings are supported by other characters, and broadening of the retroarticular process posteriorly is interpreted as a synapomorphy of these groups, with reversal in a few cordylids.

79. Retroarticular process torsion (Fig. 9E).--An obliquely-twisted posterior border of the retroarticular process occurs in gekkonids, dibamids, amphibaenians, and autarchoglossans other than lacertoids. Snakes that possess a retroarticular process (see character 74) also show torsion, although we cannot determine this with certainty in Scolecophidia. Torsion is lacking in non-squamate lepidosauromorphs in which it can be determined. The simplest explanation for this character distribution is that retroarticular process torsion is a synapomorphy of scleroglossans that has been lost in lacertoids and pygopodids.

80. Finger-like angular process.--A discrete, finger-like angular process occurs only in agamids* and some iguanids*. A similar structure occurs in a few tupinambine teiids, in which it appears to be a modification of the prearticular flange (character 73, state 2). Rhynchocephalians lack an angular process. Among kuehneosaurs a projection of the retroarticular process is present (Robinson, 1962). It is directed posteriorly, however, and appears to be related to widening of the retroarticular process; it is quite different from the angular process of squamates. This character could be separately derived in some iguanids* and agamids*, yet this interpretation rests in part on the dubious assumption of agamid* and iguanid* monophyly, and we prefer interpretation of the presence of a finger-like angular process as an iguanian character with loss in some iguanids* and the otherwise highly modified chamaeleontids.

81. Adductor fossa size.--An inflated, widely open adductor fossa occurs in gymnophthalmids, teiids, lacertids, and some scincids. This condition results from extension of the m. adductor mandibulae posterior into Meckel's canal (see character 131). No inflation of the fossa occurs in any of the non-squamate lepidosauromorphs in which it can be determined. An inflated, widely open fossa is a synapomorphy of the Lacertiformes, with independent occurrence within scincids.

82. Palatine teeth absence.--Palatine teeth are absent in all squamates except some anguids (Meszoely, 1970), *Lanthanotus* (McDowell and Bogert, 1954; Rieppel, 1980b), some snakes (Parker, 1977), and some iguanids* (Etheridge and de Queiroz, 1988). In *Heloderma* (including the fossil *H. texana*) a few palatine teeth may be present (Rieppel, 1980b; Pregill, et al., 1986), and in *Ophisaurus apodus* and the fossil glyptosaurines (Meszoely, 1970) there are extensive palatine tooth patches. *Saniwa*, a fossil relative of *Varanus*, has a short row of palatine teeth (Gilmore, 1928). Palatine teeth are absent in scolecophidians but occur in other snakes. In iguanids* they occur in only a few genera (Etheridge and de Queiroz, 1988). Palatine teeth are present in all non-squamate lepidosauromorphs in which this character can be determined, suggesting that this is the plesiomorphic condition. However, given the distribution of palatine teeth among taxa and our conclusions about relationships among them, absence of palatine teeth appears to be a squamate synapomorphy, with reacquisition in various groups; this reverses our original polarity. The presence of palatine teeth in *Cherminotus*, a Cretaceous relative of *Lanthanotus* (Borsuk-Bialynicka, 1984) cannot be determined.

Some secondary losses are involved as well, and a great deal of homoplasy in this character occurs. Although the interpretation of reacquisition of palatine teeth differs from conventional views (e. g. Camp, 1923; Romer, 1956), the fact that potentiality for tooth formation can be retained in the oral epithelium long after teeth themselves are lost (Kollar and Fisher, 1980) suggests that teeth could be reacquired through relatively simple developmental changes. Moreover, because pterygoid teeth are present in all of the squamates with palatine teeth (possibly excepting the fossil *Heloderma texana* according to Stephens, 1977, although we are not convinced that they have not been removed in preparation), it is only a matter of extension anteriorly of the field of tooth development. Finally, vomerine teeth occur in very few squamates (only the anguids *Ophisaurus apodus* and some glyptosaurines) and have almost certainly been reacquired (cf. Rieppel, 1980b).

83. Pterygoid teeth.--Absence of pterygoid teeth occurs uniformly in agamids*, chamaeleontids, dibamids, gekkonids, pygopodids, xantusiids, *Varanus*, and amphisbaenians. Loss of pterygoid teeth also appears to have occurred within iguanids*, anguids, helodermatids, and snakes. *Saniwa* (Gilmore, 1928), *Saniwides*, and *Telmasaurus* (Borsuk-Bialynicka, 1985), fossil relatives of *Varanus*, have pterygoid teeth. In other taxa (cordylids, gymnophthalmids, lacertids, scincids, teiids, and xenosaurs) we can only say that there is variation. *Lanthanotus* retains pterygoid teeth although *Cherminotus*, its presumed Cretaceous relative, appears to lack both pterygoid and palatine teeth (Borsuk-Bialynicka, 1984). Among non-squamate lepidosauromorphs the rhynchocephalian *Gephyrosaurus* has pterygoid teeth while sphenodontidans lack them (Evans, 1980). They are also present in kuehneosaurs and younginiforms. Although the hypothesis of parallel loss of pterygoid teeth is more complex than their single loss with multiple reacquisitions (16 versus 11 steps), this situation rests on the dubious assumption of iguanid* monophyly and the inability to resolve the relationships of dibamids and amphisbaenids. In either case, a great deal of homoplasy is required. We adopt the traditional but more complex hypothesis and treat pterygoid tooth loss as separate synapomorphies occurring in Gekkota, Acrodonta, *Varanus*, xantusiids, dibamids, and amphisbaenians, with losses within several other basic taxa.

84. Marginal tooth implantation.--"Acrodont" teeth are said to be present in trogonophid amphisbaenians (Gans, 1960), agamids* and chamaeleontids (e. g. Edmund, 1969), and in snakes (Romer, 1956), but this classification is misleading. As discussed by Gauthier et al. (1988) the terms "pleurodont" and "acrodont" are not independent transformations of some more general mode of implantation, but are part of a transformation series. Kuehneosaurs may be described as subthecodont, although the teeth are set in a shallower depression or groove than those of younginiforms, in which the subthecodont teeth are at least partially socketed. In lepidosaurs, the teeth are superficially attached. Evans (1980) described the teeth of *Gephyrosaurus* as pleurodont, being attached to the medial wall of the dentary. In the majority of squamates the superficially attached teeth are also of the "classical" pleurodont type, being defined as applied to the medial surface of the jaw. So defined, however, the term pleurodont is also applicable to the supposedly "acrodont" agamids* and chamaeleontids, because the teeth are also superficially attached to the medial surface of the jaw. The "acrodont" transformation seen in the latter two groups forms a subset of the pleurodont condition in which replacement slows or ceases in much of the dentition (Robinson, 1976), and the individual teeth are heavily cemented with secondary bone, with extensive wear tending to blur their individuality. The definition of "acrodont" used by Robinson (1976:44), which indicates that such teeth are "fused", with "bone of attachment ... usually present", is equally applicable to a pleurodont dentition, because pleurodont teeth are also fused to the medial surface of the jaw by bone of attachment. The definition of apical attachment usually given to the term "acrodont" (e. g. Edmund, 1969) is misleading. Although the "acrodont" teeth of trogonophid amphisbaenians appear to be truly apical in attachment, the supposedly "acrodont" teeth of agamids* and chamaeleontids, while they may be attached closer to the apex of the jaw margin than some (but not all) pleu-

rodont teeth, are always more medial than apical. The condition seen in agamids* and chamaeleontids superficially resembles apical attachment because the spaces between the teeth are filled in by bone of attachment up to the parapet of the jaw. Thus, the "acrodont" teeth of Acrodonta and those of trogonophids are not very similar in terms of position of attachment. Similarities in the teeth of these two groups involve the lack of replacement (Edmund, 1969) and the relatively short tooth bases (also true of other amphisbaenians). We score both as "acrodont" primarily for these reasons as well as historical inertia. The condition in non-scolecophidian snakes is more readily described as apically attached, but even in this case the teeth are more medial in attachment (Romer, 1956:566 termed snakes acrodont, but on p. 451 described them as pleurodont). We consider the transformation from subthecodont to superficial attachment to separate lepidosaurs from other lepidosauromorphs. The transformation from pleurodont to "acrodont" describes parallel changes in lepidosaurs, occurring within both squamates (Acrodonta, trogonophid amphisbaenians) and rhychocephalians (Sphenodontida).

85. Marginal tooth replacement (Fig. 10A-C).--In iguanids*, gekkotans, various scincormorphs, and some anguids (Rieppel, 1978a), replacement teeth develop directly at the base of the replaced tooth, with large resorption pits developed (state 0; "iguanid" replacement of Edmund, 1969). An intermediate state, in which the teeth develop posterolingual to the replaced tooth and replacement pits are small but present (state 1; intermediate condition of Edmund, 1969) occurs uniformly in xenosaurids and dibamids, and in some gymnophthalmids (pers. obs.), teiids (Presch, 1974b), scincids (Edmund, 1960, 1969), amphisbaenians (Gans, 1978), and anguids. In snakes, helodermatids, *Lanthanotus*, and *Varanus* (Rieppel, 1978a), and occasionally in amphisbaenians (Gans, 1957), the teeth are posterolingual, and replacement pits in the replaced tooth do not occur (state 2; "varanid" replacement of Edmund, 1969). In non-squamate lepidosauromorphs in which the condition can be determined, there is direct ("iguanid") replacement (Rieppel, 1978a) except in sphenodontids, in which replacement teeth have been generally suppressed (Robinson, 1976). The intermediate state (1) is a synapomorphy of the anguimorphs with independent acquisition in dibamids, some amphisbaenians, and the other taxa noted above; the more derived state (2) is a synapomorphy of varanoids, independently derived in some amphisbaenians, and perhaps also in snakes.

86. Basal infolding of marginal teeth (Fig. 10D).--The presence of weak to well developed folds of dentine at the base of the teeth, with concomitant external striations, occurs in helodermatids, *Lanthanotus*, and *Varanus* (Rieppel, 1978a); in the latter considerable complexity of the tooth base may be produced (Bullet, 1942). Striations also occur in glyptosaurine anguids, but the folds are very superficial. Basal tooth striations and weak infolding also occur in the extinct necrosaurids*, which appear to be related to the varanoids. This character is a varanoid synapomorphy; the glyptosaurine anguids are thus convergent.

87. Step or offset in tooth margin of maxilla.--This is associated with the enlargement of the anterior maxillary teeth, which as a consequence become set at a slightly different angle than those of the posterior maxillary tooth row; it is characteristic of teiids, gymnophthalmids, and lacertids. A similar condition may occur in some iguanids* (e. g. *Ctenosaura*). This condition does not occur in any non-squamatan lepidosauromorph in which it can be determined. We consider a step in the maxillary tooth row to be a synapomorphy of Lacertiformes; it evolved independently in some iguanids*.

88 and 89. Number of scleral ossicles.--Gugg (1939) and Underwood (1970; 1984) summarized data on the number of scleral ossicles in various lepidosaurians. This number ranges from 0-40 in a single eye, with a number in the range 10-17 being most common. Fourteen scleral ossicles is widespread in squamates. More than 14 ossicles (state 0 of character 88) occurs in *Varanus*, as well as in some gekkonids and pygopodids, and *Sphenodon*; other squamates have 14 or fewer.

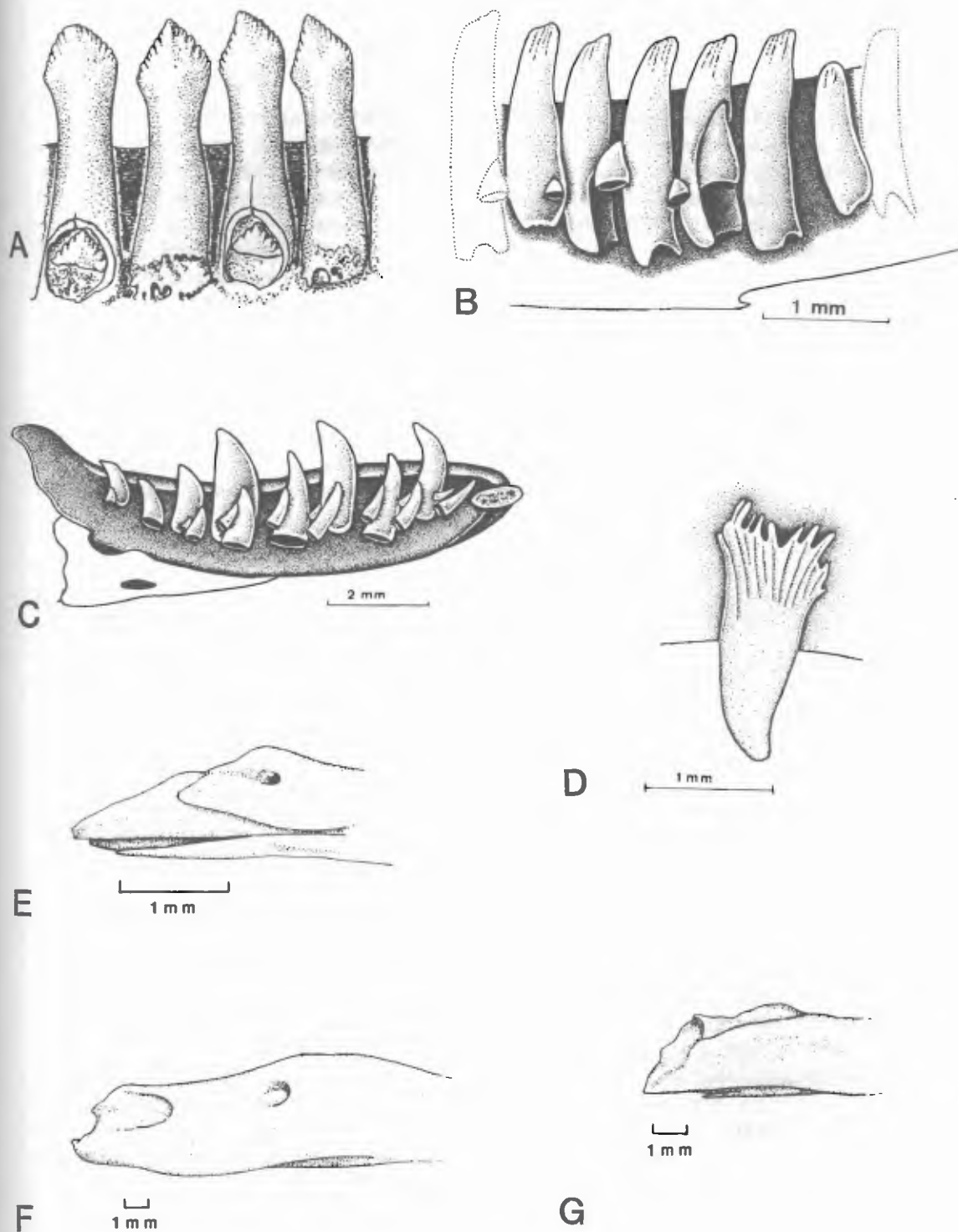


FIGURE 10. A, four teeth of *Iguana iguana* (Iguanidae*) in medial view. B, dentary teeth of *Elgaria coerulea* (Anguidae) in medial view. C, medial view of anterior left mandible of *Lanthanotus borneensis* (Varanidae). D, maxillary tooth of *Varanus salvator* (Varanidae) in medial view. E-G, lateral view of anterior end of left postdentary bones of E, *Eumeces skiltonianus* (Scincidae); F, *Heloderma suspectum* (Helodermatidae); G, *Lanthanotus borneensis* (Varanidae). A, from Edmund (1969); B-D from Rieppel (1978a); E-G from Gauthier (1982). See end of paper for abbreviations.

Fewer than 14 ossicles (character 89) are found in agamids*, chamaeleontids, *Heloderma*, *Lanthanotus*, amphisbaenians, and snakes, and some iguanids*, gekkonids, pygopodids, lacertids, gymnophthalmids, scincids, cordylids, and anguids. The ossicles are absent in dibamids, snakes, and most amphisbaenians. The distributions of these characters among squamate taxa are taken largely from Underwood (1970) with the following modifications: (1) addition of data on gymnophthalmids (Presch, 1980), (2) addition of data on the anguids *Gerrhonotus*, *Diploglossus*, and *Ophisaurus*, all of which have 14 scleral ossicles (pers. obs.), and (3) reexamination of the scleral ring of *Xenosaurus grandis*. Barrows and Smith (1947:235) reported "about 20" scleral ossicles in members of the latter species; they actually have 14 (pers. obs.).

We initially made two characters of these data based on the assumption that 14 scleral ossicles was the primitive squamate condition, and that change had proceeded in two directions, increase and decrease. This decision was based on the widespread occurrence of 14 ossicles within Squamata, although this was inconsistent with our outgroup polarity. In retrospect, the character would more appropriately have been a single one, with state 0 = more than 14, state 1 = 14, and state 2 = less than 14. To change this after the results of our study were obtained would have introduced many potential sources of error; we therefore discuss our original choice.

Because *Sphenodon* has 16 scleral ossicles, we consider more than 14 to be plesiomorphic for the outgroup node. However, the relationships within Squamata based on other characters require that 14 or fewer scleral ossicles be considered a synapomorphy for Squamata with reversals in those few taxa that have more than 14; this reverses our original polarity. This is in agreement with the assessment that 14 scleral ossicles is primitive within Squamata, based on Farris's (1982) criterion of widespread distribution. The pattern of distribution of character 88 (14 ossicles or fewer) indicates independent acquisition in all taxa, although the situation in Gekkota is complicated by uncertain monophyly of Gekkonidae (see Diagnoses of Taxa). Character 89 (fewer than 14 ossicles) is a synapomorphy of agamids* and chamaeleontids, with independent reductions in several other taxa.

90. Second epibranchials (Fig. 11).--The second epibranchials of the hyoid apparatus are present in *Heloderma*, cordylids, lacertids, teiids, xantusiids, and some agamids*, iguanids*, anguids, gekkonids, and scincids, according to Camp (1923), as well as in some pygopodids (Underwood, 1957). Camp (1923) and others cited below reported them absent in chamaeleontids, gymnophthalmids (MacLean, 1974; Presch, 1980), dibamids (Greer, 1985a), *Lanthanotus* (Rieppel, 1981), *Varanus* (Camp, 1923), xenosaurids, amphisbaenians (Gans, 1978), and snakes (Rieppel, 1981a), as well as in some iguanids*, agamids*, gekkonids, pygopodids (Underwood, 1957), scincids, and anguids. Second epibranchials are present in *Sphenodon* (Tanner and Avery, 1982) but they have not been preserved in other non-squamate lepidosauromorphs; we consider their presence to be plesiomorphic for squamates. The absence of second epibranchials is a synapomorphy of *Lanthanotus* and *Varanus*, with independent losses in the other groups.

91. Second ceratobranchials (Fig. 11).--According to Camp (1923), the second ceratobranchials of the hyoid apparatus are present in agamids* (except *Amphibolurus barbatus*; Moody, 1980), iguanids* (except some *Phrynosoma*; Presch, 1969), xantusiids, and lacertids, as well as some but not all cordylids, gekkonids, and amphisbaenians. The second ceratobranchials are present in *Bachia*, the only gymnophthalmid examined by Camp (1923), but they are absent in some other gymnophthalmids (MacLean, 1974; Presch, 1980). Second ceratobranchials are absent in *Tupinambis*, the only teiid examined by Camp (1923), but they are present in some other teiids (MacLean, 1974; Presch, 1974). Camp (1923) stated that the second ceratobranchials are absent in the pygopodids *Lialis* and *Pygopus*, but Underwood (1957) found these elements in both taxa as well as in *Delma*. Second ceratobranchials are absent in anguids (Camp, 1923), chamaeleontids (Camp, 1923), dibamids (Camp, 1923; Rieppel, 1981a; Greer, 1985a), *Lanthanotus* (Rieppel,

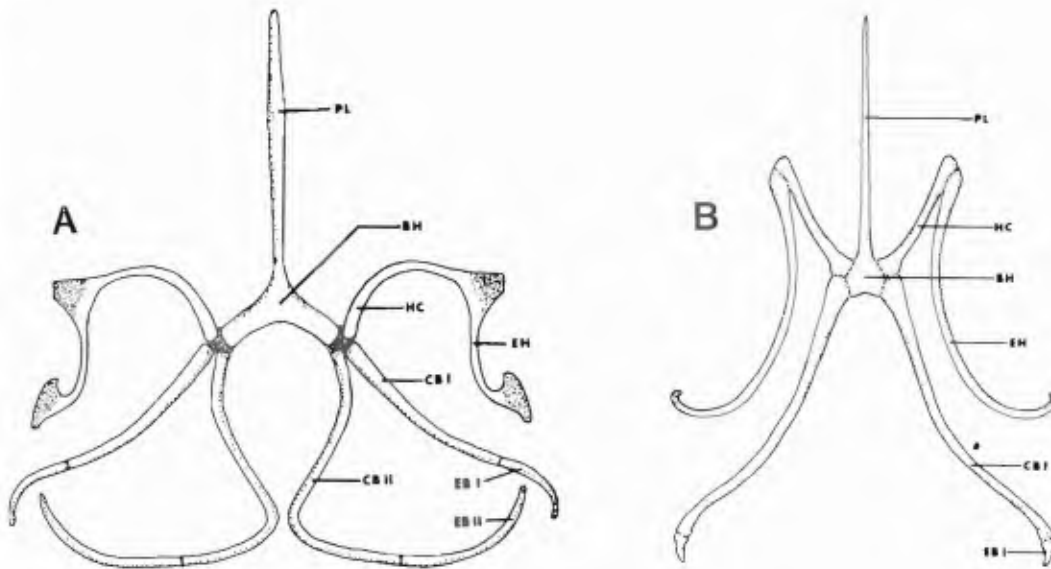


FIGURE 11. A, hyoid apparatus of *Coleonyx variegatus* (Gekkonidae) in ventral view. B, same, *Heloderma suspectum* (Helodermatidae). From Tanner and Avery (1982). See end of paper for abbreviations.

1981), *Heloderma* (Camp, 1923), *Varanus* (Camp, 1923), and xenosaurids (Camp, 1923), as well as in some amphisbaenians (Gans, 1978) and the scincid *Typhlosaurus* (Rieppel, in litt., 1985). Homologies of the parts of the snake hyoid are controversial (Rieppel, 1981). If Rieppel's homologies are accepted, then snakes lack second ceratobranchials. We take the presence of second ceratobranchials to be plesiomorphic for Squamata because this is the condition found in turtles (Romer, 1956), possibly in archosaurs (Romer, 1956), and in *Sphenodon* (Osawa, 1898). Loss of the second ceratobranchial is a synapomorphy of the Anguimorpha, with independent losses in the other groups. This character also supports the relationship of snakes and anguimorphs suggested by McDowell and Bogert (1954).

92. Vertebral condyle orientation.--A strongly oblique condyle (often but not uniformly with the entire cotyle visible in ventral view) occurs in *Heloderma*, *Lanthanotus*, and *Varanus* (McDowell and Bogert, 1954). Because all non-squamate lepidosauromorphs have amphicoelous vertebrae, the condition cannot be determined in the outgroups. This character is a synapomorphy of the varanoids.

93. Vertebral centrum articulation.--The ontogenetic development of a procoelous centrum occurs in all squamates (except some gekkonids; Kluge, 1967, 1987; Moffat, 1973) and is absent in all non-squamate lepidosauromorphs (Camp, 1923; Hoffstetter and Gasc, 1969). Relationships based on our entire set of characters require that the ontogenetic development of procoely be interpreted as a squamate synapomorphy that has been reversed in some gekkonids; this reverses our original polarity. Kluge (1987) has given the most recent evaluation of vertebral transformations within Gekkota.

94. Vertebral centrum constriction (Fig. 12A,B,D).--The presence of a constriction anterior to the condyles characterizes *Lanthanotus* and varanids, and is present in a few agamids* and teiids, as well as in most (principally booid) snakes (Hoffstetter and Gasc, 1969). The character is, however, rather subjective, and exceptions occur. All non-squamate lepidosauromorphs have amphicoelous vertebrae, and the condition thus cannot be determined with certainty in the outgroups because of the lack of condyle formation; nevertheless there is no indication in the centrum shape of the formation of such a constriction (in spite of this we have coded this character as N in the outgroup matrix). Vertebral centrum constriction is a synapomorphy of *Lanthanotus* and *Varanus*. Based on other characters, the conditions in agamids*, teiids, and some booid snakes are convergent.

95 and 96. Zygosphene and zygantrum development (Fig. 12D-E).--Strong development of the zygosphene-zygantrum articulation is uniformly present in snakes, lacertids, teiids, and gymnophthalmids, and in some (especially large) iguanids* (Etheridge, 1964) and some cordylid cordylids (Camp, 1923; pers. obs.). Only a weakly-developed zygosphene-zygantrum occurs in *Sphenodon* (Hoffstetter and Gasc, 1969) and *Gephyrosaurus* (Evans, 1981). Evans (1981) stated that they are absent in *Homoeosaurus*, although they are present in Triassic sphenodontidans (Fraser and Walkden, 1984). Kuehneosaurs lack these structures (Evans, 1981). Carroll (1975, 1977) stated that accessory articulations were present in *Saurosternon* but his figure (1977, fig. 8) does not show them, and Evans (1981) was unable to confirm his observation. Accessory articulations are present in some younginiforms but they are not homologous with zygosphenes and zygantra (Currie, 1981; contra Benton, 1985). Character 95 (strong development) is a synapomorphy of lacertids, teiids, and gymnophthalmids that has evolved independently in snakes, and in some iguanids* and cordylids.

Despite the fact that outgroup evidence is equivocal, we originally coded the presence of zygosphenes and zygantra (character 96) as primitive for squamates. The uniform absence of a zygosphene and zygantrum (as opposed to its degree of development discussed above) occurs in agamids*, chamaeleontids, dibamids, gekkonids, pygopodids, xantusiids, xenosaurs, anguids, *Heloderma*, *Lanthanotus*, *Varanus*, and amphisbaenians. They are also absent in some cordylids (pers. obs.) and some iguanids* (Camp, 1923). One possible interpretation of this character is that absence of the zygosphene and zygantrum occurs as three separate synapomorphies: one for Anguimorpha, a second for Acrodonta, and a third for Gekkota, with independent losses in the other groups. This requires eight steps, however, and it is simpler (six steps) to treat the absence of zygosphenes and zygantra as a squamate synapomorphy with reversals in various taxa, including a single acquisition of zygosphenes and zygantra in the group composed of lacertids, gymnophthalmids, and teiids (whose relationship is supported by other characters), as well as separate acquisitions in snakes, in scincids, and in some cordylids and some iguanids*. This decision reverses our original polarity (see Gauthier, et al, 1988 for an alternative view). It is equally possible that presence of zygosphenes and zygantra is a synapomorphy of scincids and cordylids and that some cordylids have lost them.

97. Cervical intercentral attachment 1 (Fig. 12G).--According to Hoffstetter and Gasc (1967), cervical intercentra may become associated with either the posterior part of the preceding centrum (this character) or the anterior part of the following centrum (character 98). For character 97 they are either sutured (1) or fused (2) to the preceding centrum. Neither of these states occurs in non-squamate lepidosauromorphs in which the condition can be determined. Sutured connection does not characterize any of our basic taxa uniformly, but may occur in some iguanids*, cordylids, and lacertids; in scincids, *Heloderma*, *Lanthanotus*, and *Varanus* they are either sutured or fused. Fusion occurs in dibamids, anguids, xenosaurs, snakes, and amphisbaenians, as well as some helodermatids, *Lanthanotus*, *Varanus*, and scincids, suggesting that association and fusion with the posterior part of the preceding centrum is an anguimorph synapomorphy. Its occurrence in dibamids, snakes, and amphisbaenians suggests possible interrelationship of these groups, and/or possible re-

relationship to anguimorphs. The sutured condition that occurs in some varanoids probably indicates that our specimens are not fully grown (rather than being a reversal), because fusion does appear to occur in full grown *Varanus* (Gauthier, 1982); ambiguity thus may result from incomplete ontogenetic information. The sutured condition in some iguanids*, some cordylids, some lacertids, and some scincids (and the further fusion in some scincids) is convergent.

98. Cervical intercentral attachment II (Fig. 12H).--In this character transformation, the cervical intercentra are associated (1) and sometimes fused (2) with the anterior part of the following centrum (Hoffstetter and Gasc, 1969). This occurs in agamids* (some show fusion), gymnophthalmids (some show fusion), teiids, and a few xantusiids and lacertids. Cordylid cordylids are variable; some have the intercentra associated (and sometimes fused) to the anterior part of the following centrum; others have the intercentra remaining in an unmodified position, neither associated nor fused with the following centrum. Association of the intercentrum with the following centrum is most simply interpreted as a synapomorphy of gymnophthalmids and teiids, with convergence in some lacertids and xantusiids. The cordylid and agamid* conditions are also independently derived. All fusions (state 2) are likewise independent. Because this transformation also occurs ontogenetically, ambiguity may result from incomplete ontogenetic sampling.

99. Posterior trunk (thoracolumbar) intercentra (Fig. 12C).--Absence of intercentra on the posterior (thoracolumbar) vertebrae is a widespread condition in squamates; they are present only in some Gekkonidae and Xantusiidae (Hoffstetter and Gasc, 1969). Intercentra are present throughout the vertebral column in all non-squamate lepidosauromorphs in which this area is known, except for kuehneosaurs and *Homoeosaurus*, which apparently lack them (Evans, 1981). Many characters place Gekkonidae and Pygopodidae as the sister group of autarchoglossans, and place Xantusiidae within autarchoglossans. It is therefore simplest to assume that absence of posterior trunk intercentra is a squamate synapomorphy, reversing our original polarity; this implies that the intercentra of gekkonids and xantusiids no longer fuse to the condyles of the vertebrae during embryonic development, as they did in the most recent common ancestor of squamates. This is one of many characters in which these families appear to be pedomorphic (Gauthier, 1982; Rieppel, 1984b).

100, 101, and 102 (fig. 12I-M). These three characters deal with the presence, number, and orientation of transverse processes on the caudal vertebrae. Etheridge (1967) described variation in the transverse processes (caudal ribs, pleurapophyses) of lizard caudal vertebrae. Many morphologies exist, not only among taxa but also within the caudal sequences of single organisms, and we refer the reader to Etheridge (1967) for detailed descriptions of these morphologies. We accept Etheridge's hypothesized character transformations, except that we consider a caudal sequence in which each autotomic vertebra bears a single pair of transverse processes through which the autotomy septum passes to be plesiomorphic for squamates. The latter vertebral morphology characterizes the autotomic portion of the caudal sequence in rhynchocephalians as well as part of this sequence in the caudal vertebrae of many squamates that also exhibit other states of these characters.

Autotomy is lacking in other non-squamate lepidosauromorphs. From the plesiomorphic condition, as seen in rhynchocephalians, we recognize three independent transformations: (1) the origin of two pairs of diverging transverse processes in that part of the sequence of caudal vertebrae bearing two pairs of transverse processes (character 100); (2) the origin of two pairs of converging transverse processes in that part of the sequence of caudal vertebrae bearing two pairs of transverse processes (character 101), and (3) a shift in the autotomy septum from within the fess to behind them (character 102). The occurrence of caudal vertebrae with two pairs of transverse processes presumably results from a splitting of the members of a single pair of caudal ribs into two parts. All three derived characters seem to have been modified further in some instances by loss of an entire caudal rib pair or of part of a split pair. However, we recognize an additional derived state (loss of the anterior pair of transverse processes) in the second transformation series only, because it is

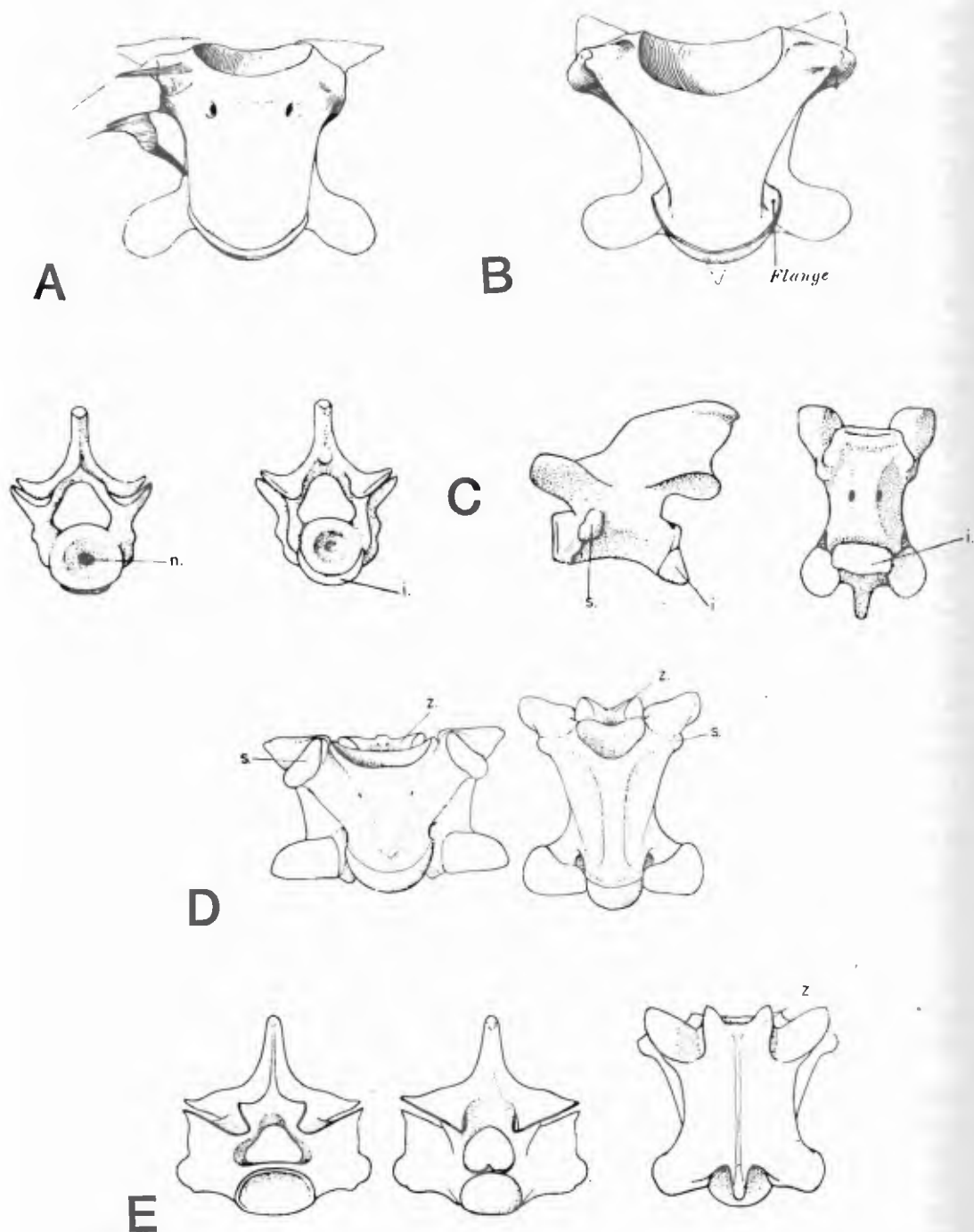


FIGURE 12. A, middorsal vertebra of *Amphisbaena alba* (Amphisbaenia) in ventral view. B, same, *Varanus niloticus* (Varanidae). C, anterior, posterior, left lateral, and ventral views of trunk vertebrae of *Gekko gekko* (Gekkonidae). D, ventral views of trunk vertebrae of *Python* sp. (Boidae) and *Iguana* sp. (Iguanidae*). E, anterior, posterior, and dorsal views of trunk vertebrae of *Tupinambis* sp. (Teiidae). F, left lateral view of anterior cervical vertebrae of *Chamaeleo chamaeleon* (Chamaeleontidae).

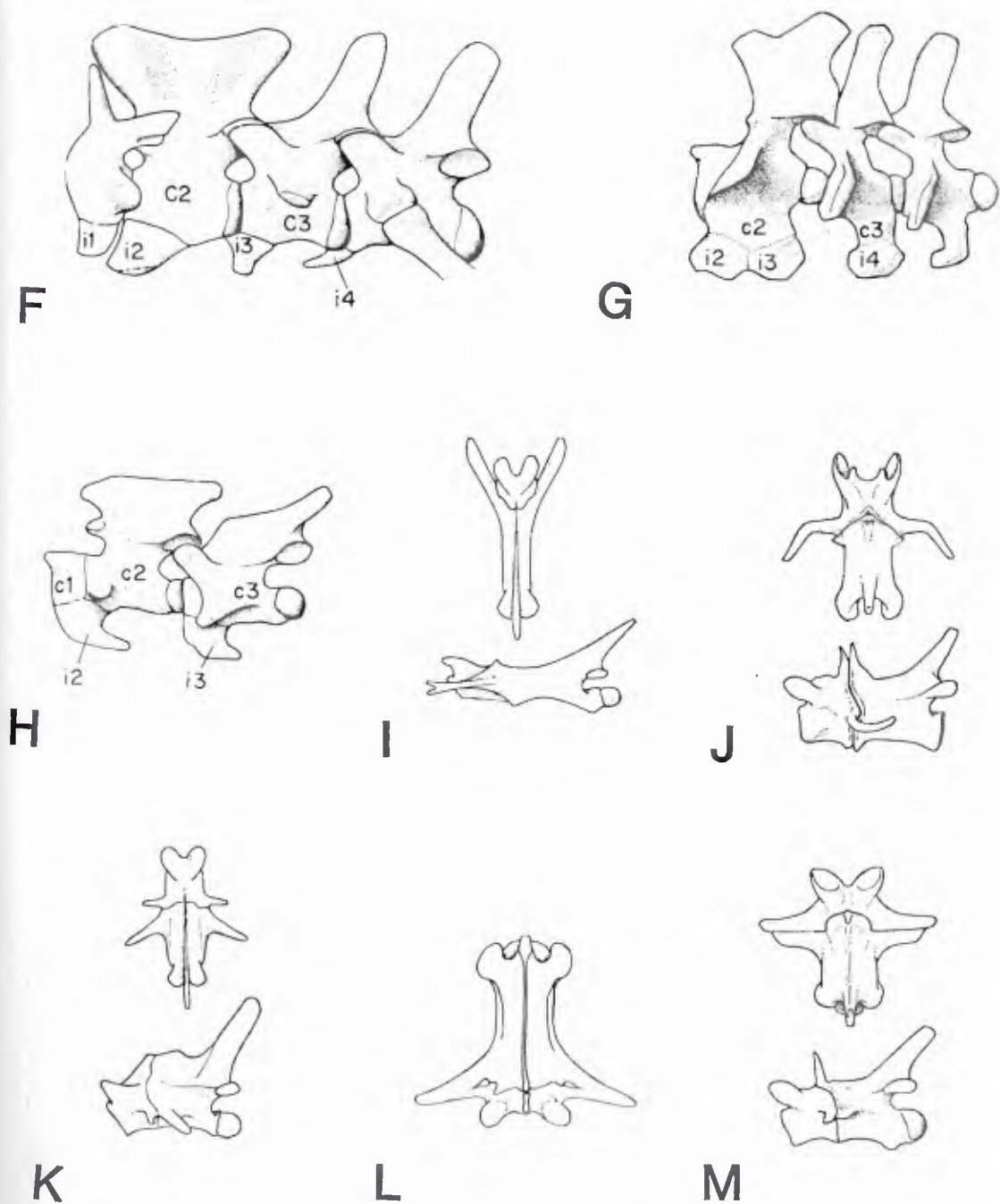


FIGURE 12, continued. G, left lateral view of anterior cervical vertebrae of *Trachydosaurus rugosus* (Scincidae). H, left lateral view of anterior cervical vertebrae of *Agama agama* (Agamidae*). I, J, K, L, M, dorsal and left lateral views of caudal vertebrae of (respectively) *Anolis sagrei* (Iguanidae*), *Gekko* sp. (Gekkonidae), *Dipsosaurus dorsalis* (Iguanidae*), *Ophisaurus ventralis* (Anguidae; dorsal view only), M, *Lacerta lepida* (Lacertidae). A, B, from Camp (1923); C-K from Hoffstetter and Gasc (1969); L after Etheridge (1967). See end of paper for abbreviations.

the only modification that characterizes more than part of one of our basic taxa. We follow Etheridge (1967) in the distribution of these characters among squamate taxa with the following exceptions or additions. (1) *Xenosaurus* lacks autotomy septa, but with the addition of data on *Shinisaurus* (Hecht and Costelli, 1969), xenosaurs are considered to exhibit the condition in which the autotomy septa pass through a single pair of transverse processes. (2) Amphisbaenians possess caudal vertebrae similar to those of dibamids and some scincids, in which a single pair of anteriorly oriented transverse processes occurs posterior to the fracture plane (Gans, 1978; Greer, 1985a). (3) Snakes possess caudal vertebrae with a single pair of transverse processes. (4) Those taxa that lack autotomy septa cannot be scored for character 102.

Divergent processes (character 100) are a synapomorphy of the group composed of teiids, gymnophthalmids, and lacertids (Lacertiformes), a grouping supported by other characters. Xantusiids with divergent processes may have acquired them independently, but this is equivocal and they may also be ancestral for lacertoids. Independent acquisition has also taken place in some iguanids* and in some cordylids.

Convergent processes (character 101), in which either one or both pairs are present, occur in both dibamid genera as well as in most anguids (some *Diploglossus* and *Sauresia* show the plesiomorphic condition) and amphisbaenians, and some scincids. The presence of convergent processes also supports a close relationship between amphisbaenians and dibamids, one of the possible hypotheses of relationship of dibamids suggested by Greer (1985a). Anguids acquired them independently, as did the few scincids that have them.

Location of the septum posterior to the pair of transverse processes (character 102) is one of many synapomorphies of Gekkota. Some iguanids* may have acquired it independently, although we favor the interpretation that it is an iguanian synapomorphy indeterminable in Acrodonta because of loss of the autotomy septa.

103. Autotomy septa in caudal vertebrae (Fig. 12).--Absence of autotomy septa is uniform in agamids* and chamaeleontids, *Heloderma*, *Lanthanotus*, and *Varanus*. In the xenosaurid *Xenosaurus* and in a few iguanids*, anguids, gekkonids, scincids, and amphisbaenians, the septum is also absent. Autotomy is rare in snakes (Hoffstetter and Gasc, 1969). Because the only snake reported to have autotomy septa actually lacks them (A. Bauer, pers. comm. 1984, contra Wilson, 1968), autotomy presumably occurs intervertebrally. Autotomy septa are present in most rhynchocephalians, but are absent in kuehneosaurs and all other non-squamate lepidosauromorphs. Absence of autotomy septa is a synapomorphy of Acrodonta, as well as of Varanoidea. Numerous other absences are independent.

104, 105, and 106. Number of presacral vertebrae.--Fewer than 23 presacral vertebrae (character 104) are found in some iguanids*, some agamids*, and (according to Hoffstetter and Gasc, 1969) some chamaeleontids. The latter reported a range of 16-23 (mode 19) in chamaeleontids, but we have never seen a chamaeleon with as many as 23 presacrals. The discrepancy may reflect intraspecific variation or sampling of different taxa. Twenty-three or more occur in all non-squamate lepidosauromorphs in which the character can be determined. This character is not useful in our phylogenetic analysis of squamate families except to indicate the possible paraphyly of agamids*, the monophyly of chamaeleontids, and to point out that the only squamate taxa that achieve this condition are iguanians.

More than 25 presacral vertebrae (character 105) occur in all xenosaurs, anguids, *Heloderma*, *Lanthanotus*, *Varanus*, dibamids, scincids, xantusiids, pygopodids, amphisbaenians, and snakes (Hoffstetter and Gasc, 1969). Some iguanids* (Etheridge and de Queiroz, 1988) and most members of the following groups show this increase as well: cordylids, gymnophthalmids, lacertids, teiids, and gekkonids. Twenty-five or fewer occur in all non-squamate lepidosauromorphs in which this character can be determined. Given the within-taxon variation, presence of more than 25 presacral vertebrae appears to be a synapomorphy of Scleroglossa.

More than 26 presacral vertebrae (character 106) occurs in at least some members of all lizard families except iguanids*, agamids*, chamaeleontids, and xantusiids, and, of course, is a natural concomitant of elongated body form. Most lacertids, teiids, gymnophthalmids, cordylids, gekkonids, and *Shinisaurus* have no more than 26 presacral vertebrae (Hoffstetter and Gasc, 1969; Hecht and Costelli, 1969). Twenty-five or fewer presacrals occur in all non-squamate lepidosauromorphs in which this character can be determined, indicating that more than 26 presacrals is derived for Squamata. Presence of more than 26 presacral vertebrae is a synapomorphy of Anguimorpha that has been reversed in *Shinisaurus*, and is convergent in a number of other taxa in which body elongation occurs.

107 and 108. Number of cervical vertebrae.--Hoffstetter and Gasc (1969:254) claimed that "Since Cuvier and especially after the work of Stannius (1894) cervical vertebrae have been defined as all those preceding that bearing the first rib united to the sternum." However, this is not true of the work of Camp (1923), among others, and for this reason, cervical vertebral counts should never be compiled from the works of different authors before differences in the method of taking these counts have been taken into consideration. According to the definition of cervical vertebrae given above, most squamates have eight cervicals, *Lanthanotus* and *Varanus* have nine, and chamaeleontids, *Dibamus*, *Ophiodes* (Anguillidae), *Chamaesaura* (Cordylidae), and *Feylinia* (Scincidae) have fewer than eight (Hoffstetter and Gasc, 1969). Amphisbaenians, snakes, and other taxa the members of which lack sternal rib connections cannot be scored for this character. *Sphenodon* has eight cervical vertebrae (Günther, 1867), and although Jurassic rhynchocephalians are said to have seven (Cocude-Michel, 1963; Hoffstetter and Gasc, 1969) this count needs confirmation. Other outgroups are less helpful. The number of cervicals cannot be determined in any non-lepidosaurian lepidosauromorph, and archosauromorphs have a range greater than, and also encompassing, that seen in squamates (Romer, 1956). We consider eight cervicals to be plesiomorphic for squamates. Even if only seven were present in the most recent common ancestor of rhynchocephalians and squamates, our analysis will not be invalidated by our calling less than eight cervicals plesiomorphic, because the only basic taxa that invariably have fewer than eight cervicals also have fewer than seven.

Fewer than eight cervical vertebrae (character 107) occurs in chamaeleontids and dibamids, as well as in a few anguillids, cordylids, and scincids. These all seem to have been independent.

More than eight cervical vertebrae (character 108) occurs only in *Lanthanotus* and *Varanus*, and is a synapomorphy of those taxa.

109. Number of rib attachment points on each side of sternum (Fig. 13).--The sternum of squamates exhibits from zero to five pairs of attachment points for sternal and xiphisternal ribs on each side (for figures of the sterna of limbed squamates see Lécure, 1968b). The presence of five pairs is considered plesiomorphic because, although *Sphenodon* has only three or four such points (Romer, 1956; Hoffstetter and Gasc, 1969), five occur in Jurassic rhynchocephalians (Cocude-Michel, 1963) and probably in younginiforms (Currie, 1981). It is not possible to determine this character in any other non-squamate lepidosauromorphs. Differences in the number of rib attachment points reflect differences in the size and form of the sternum and, for this reason, should not be confused with the number of ribs connecting to the sternum. For instance, the cartilaginous xiphisternal rods extending from the posteriormost rib attachment point may join the members of more than one pair of ribs. Therefore, a change in the number of rib pairs attaching to the sternum can occur through the failure of ribs from different body segments to unite with one another through the xiphisterna without any change in the morphology of the sternum itself. For this reason we have chosen to use the actual sternal attachment points rather than the number of ribs involved.

Among squamates, the plesiomorphic condition (five attachment points) occurs only in some

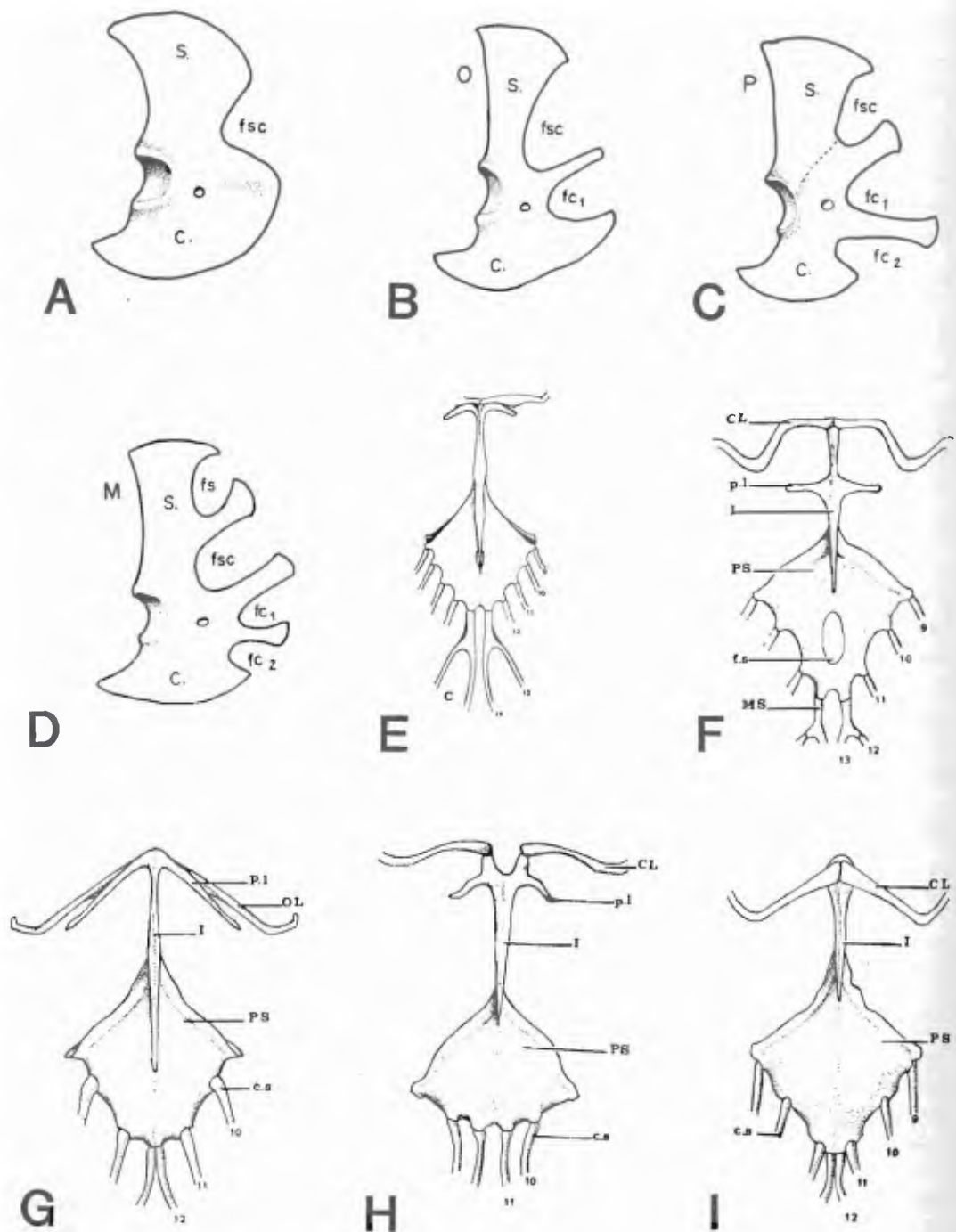


FIGURE 13. A, right scapulocoracoid of *Heloderma suspectum* (Helodermatidae). B, same, *Lacerta lepida* (Lacertidae). C, same, *Tupinambis teguixin* (Teiidae). D, *Iguana rhinolopha* (Iguanidae*). E, sternum, clavicles, and interclavicles of *Iguana iguana* (Iguanidae*). F, same, *Algyroides fitzingeri* (Lacertidae). G, same, *Varanus niloticus* (Varanidae). H, same, *Lanthanotus borneensis* (Varanidae). I, same, *Heloderma horridum* (Helodermatidae). A-D from Hoffstetter (1964); E-I from Lécuru (1968b). See end of paper for abbreviations.

iguanids*, agamids*, and cordylids. State 1 (four attachment sites) occurs in some iguanids*, agamids*, gekkonids, cordylids, lacertids, and the anguid *Gerrhonotus*. It also occurs in all scincids (except *Feylinia*), teiids, gymnophthalmids (except *Bachia*; Camp, 1923), xenosaurs, and *Heloderma*. Although Lécure (1968b) figured a *Xantusia henschawi* with three attachment sites, our specimens of xantusiids (including *X. henschawi*) all have four attachment sites. State 2 (three attachment sites) is found in some iguanids*, agamids*, gekkonids, and in all anguids (except *Gerrhonotus*, fide Lécure, 1968b, figs. 15, 16) and *Varanus*. State 3 (two or fewer attachment sites) occurs in chamaeleontids, pygopodids, the gymnophthalmid *Bachia*, the scincid *Feylinia*, *Dibamus*, *Lanthanotus*, amphisbaenians, and in some iguanids* of the genus *Phrynosoma* (Presch, 1959). Variation is thus extensive, but many iguanians (except chamaeleontids) possess state 0, while scleroglossans (except a few lacertids and cordylids) have either states 1, 2, or 3. State 1 is most simply interpreted as a synapomorphy for Scleroglossa that has appeared independently within iguanids* and agamids*. State 2 can be assigned as a synapomorphy of *Varanus* and *Lanthanotus* (the latter having the further transformation of state 3). All other occurrences of states 2 and 3 within autarchoglossans appear to be independent of one another and of the derivation of state 3 in chamaeleons.

110. Postxiphisternal inscripational ribs.--The members of one or more pairs of postxiphisternal inscripational ribs (Etheridge, 1965) unite midventrally to form continuous chevrons in chamaeleontids, dibamids (Hoffstetter and Gasc, 1969), the cordylid *Chamaesaura* (Camp, 1923), the gekkonid *Uroplatus* (Camp, 1923), the gymnophthalmid *Bachia* (Camp, 1923), some iguanids* (Camp, 1923; Etheridge, 1965; Etheridge and de Queiroz, 1988), the lacertid *Nucras* (Hoffstetter and Gasc, 1969) and some scincids (Camp, 1923). One or more pairs is thought to be derived because it does not occur in rhynchocephalians (Günther, 1867; Hoffstetter and Gasc, 1969), the only non-squamate lepidosauromorphs in which the cartilaginous inscripational ribs are known. Independent origin in all families is the simplest explanation for the distribution of this character.

111. Scapular emargination (Fig. 13).--The scapular emargination lies entirely within the anterior margin of the scapula (Lécure, 1968a). It occurs in all chamaeleontids and gekkonids, and appears in some members of the following taxa: iguanids*, scincids, teiids, and anguids (Lécure, 1968a). Scapular emarginations are absent in all non-squamate lepidosauromorphs except the sphenodontid *Planocephalosaurus* (Fraser and Walkden, 1984) and their presence thus appears to be derived for squamates. Independent origin of the scapular emargination in all squamate taxa is the simplest explanation for this distribution, although it may be a synapomorphy of Gekkota that has been lost in pygopodids as a result of shoulder girdle reduction.

112. Anterior (primary) coracoid emargination (Fig. 13).--This emargination (Lécure, 1968a) is present in all squamates except chamaeleontids, *Heloderma*, some pygopodids (Stephenson, 1962) and *Bipes*, the only amphisbaenian that can be scored for this character (Zangerl, 1945; Castañeda and Alvarez, 1968). It is absent in all non-squamate lepidosauromorphs in which it can be determined, and we therefore originally considered absence of the emargination as plesiomorphic for squamates. The simplest explanation for this distribution, however, is to consider the presence of an anterior coracoid emargination to be a synapomorphy of Squamata; the emargination has been lost independently in those squamates listed above. This decision reverses our original polarity.

113. Posterior (secondary) coracoid emargination (Fig. 13).--This structure (Lécure, 1968a) is present in all teiids, gymnophthalmids, and *Varanus* (the fossil *Saniwa* lacks it; Gilmore, 1928). It is also present in some iguanids* (Etheridge and de Queiroz, 1988), agamids* (Moody, 1980), gekkonids (Kluge, 1967), and varies from very small to absent in *Lanthanotus*, judging from the contradictory statements in Lécure (1968a) and Rieppel (1980a). It is absent in all non-squamate lepidosauromorphs. Presence of a posterior coracoid emargination is a synapomorphy of teioids, with independent origin in the other taxa noted above.

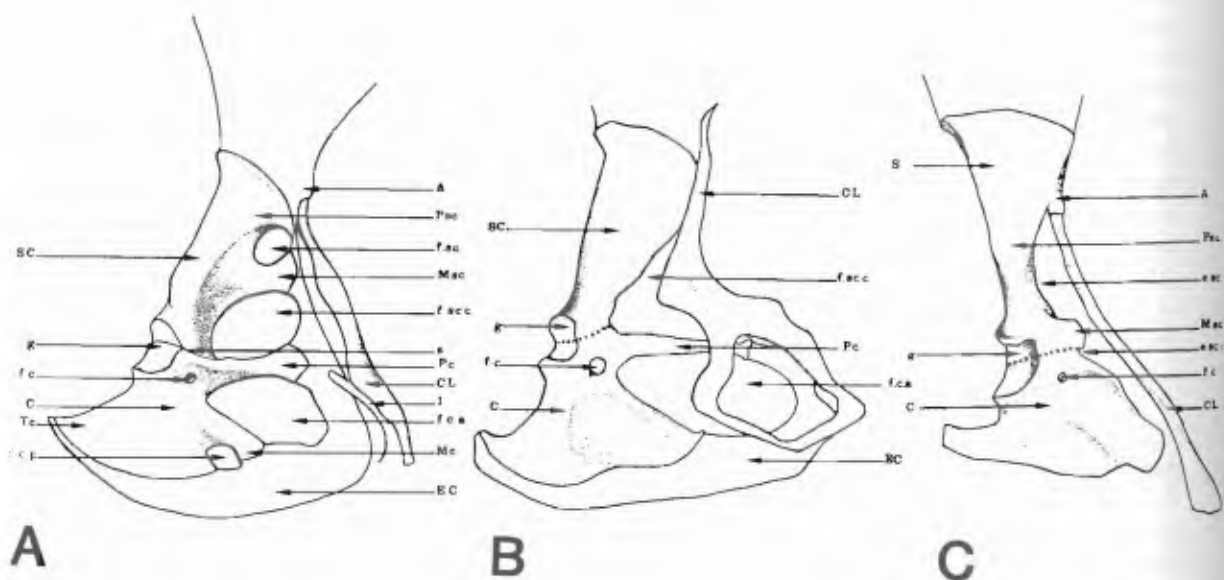


FIGURE 14. A, right scapulo-coracoid and clavicles. *Iguana iguana* (Iguanidae*). B, *Lacerta viridis* (Lacertidae). C, *Uroplatus fimbriatus* (Gekkonidae). From Lécure (1968b). See end of paper for abbreviations.

114. Epicoracoid cartilage extent.--Squamate epicoracoid cartilages lie along the ventromedial borders of the scapulo-coracoids and extend dorsolaterally along their anterior borders to varying degrees (Lécure, 1968a; Rieppel, 1980a). In most squamates the epicoracoids extend at least as far dorsally as the mesoscapulae, which lie between the scapular and scapulo-coracoid emarginations, and often contact the anteroventral corners of the suprascapulae, closing off the scapulo-coracoid emarginations anteriorly to form fenestrae. In other cases, the epicoracoid cartilages may fail to reach the mesoscapulae. This condition occurs in some iguanids* (pers. obs.), agamids* (Moody, 1980), the gekkonid *Uroplatus* (Camp, 1923), and the amphisbaenian *Bipes* (Lécure, 1968a), as well as in all chamaeleontids, lacertids, *Heloderma*, *Lanthanotus*, and *Varanus*. Although most non-squamate lepidosauromorphs lack scapulo-coracoid emarginations and concomitantly lack mesoscapulae, the epicoracoid cartilages of rhynchocephalians extend dorsally beyond the sutures between scapulae and coracoids (Günther, 1867; Cocude-Michel, 1963; but contrast with Romer, 1956), a point comparable to the location of the mesoscapula in squamates. Epicoracoid cartilages are not preserved in other fossil non-squamate lepidosauromorphs, and they are apparently absent in extant archosaurs and unknown in extinct archosauromorph taxa. Failure of the epicoracoid cartilages to contact the suprascapular cartilages is a synapomorphy of Varanoidea and independently derived in other squamate groups.

115. Clavicle.--The clavicles are present in most squamates. They are absent postembryonally in chamaeleontids (Lécure, 1968b; although they are present in embryos according to Skinner, 1959), dibamids (Greer, 1985a), snakes (Bellairs and Underwood, 1951), and amphisbaenians except *Bipes* (Zangerl, 1945; Renous 1974; Gans, 1978 calls this element a cleithrum without justification). Clavicles are present even in many taxa that either lack or have very small forelimbs, including the anguid *Anniella* (Camp, 1923), the cordylid *Tetradactylus africanus* (Berger-Dell'mour, 1983), the gymnophthalmid *Bachia* (Camp, 1923; Presch, 1975), pygopodids (Underwood, 1957; Stephenson, 1962), and the scincid *Feylinia* (Camp, 1923). Clavicles are present in all non-squamate lepidosauromorphs in which this region is adequately known, indicat-

ing that this condition is plesiomorphic for squamates. The simplest explanation of the character distribution in squamates is separate loss of the clavicle in or within all basic taxa.

116. Clavicle angulation (Fig. 14).--Strongly angulated clavicles that diverge anteroventrally from the scapulocoracoids at about the midpoint in their length occur in all squamate groups except iguanids*, agamids*, and some gekkonids (the derived condition occurs in eublepharines, while some other gekkonids have a plesiomorphic morphology). Angulated clavicles also occur in some pygopodids (the others lack clavicles), some cordylids, and some *Varanus* (Lécuru, 1968b). The clavicles do not diverge in non-squamate lepidosauromorphs in which their presence can be determined. This character appears to be a synapomorphy of Scleroglossa, with reversal in a few taxa. Absence of the clavicle in chamaeleontids, snakes, dibamids, and most amphisbaenians prevents determination of the character in these groups.

117. Dorsal articulation of clavicle (Fig. 14).--Articulation of the clavicle with the suprascapula rather than the scapula occurs in all squamate groups except some iguanids* (e. g. *Corythophanes*, pers. obs), agamids* except *Uromastix* and *Leiolepis* (Lécuru 1968a), and some gekkonids (Lécuru, 1968a). In the rhynchocephalians *Sphenodon* (Romer, 1956) and *Gephyrosaurus* (Evans, 1981), and in younginiforms (e. g., Gow, 1975; Currie, 1981) the clavicles articulate dorsally with the scapulae, indicating that this is the ancestral condition. In the case of the iguanids* and gekkonids it is clear from phylogenetic analyses within these taxa (Kluge, 1987; Etheridge and de Queiroz, 1988) that articulation with the scapula is secondarily achieved. It is therefore simplest to consider the suprascapular connection as synapomorphic for all squamates; this reverses our original polarity. In the case of agamids* only *Uromastix* and *Leiolepis* have the suprascapular connection, and reversal to a scapular articulation is probably another synapomorphy of the monophyletic group proposed by Moody (1980) consisting of all agamids* other than the two genera above. The clavicles of chamaeleons are absent postembryonically (character 115), and because they fail to articulate with the rest of the shoulder girdle in the embryo (Skinner, 1959) chamaeleontids cannot be scored for this character.

118. Interclavicle.--The interclavicle is absent postembryonically in chamaeleontids (present in the embryo; Skinner, 1959), pygopodids, dibamids, amphisbaenians, and snakes, as well as in some anguids and some scincids (Essex, 1928; Lécuru, 1968b). An interclavicle is present in all non-squamate lepidosauromorphs in which this can be determined. This character seems to be associated (independently) with girdle reduction in the remaining taxa, or with arboreality in chamaeleontids.

119. Interclavicle lateral processes (Fig. 13).--The lateral processes of the interclavicle are absent in *Heloderma*, as well as in some gekkonids and some gymnophthalmids (Lécuru, 1968b). Lateral processes are present in all non-squamate lepidosauromorphs in which this can be determined. Independent loss in all these groups is the simplest explanation of this distribution.

120. Interclavicle shape, and size of anterior process (Fig. 13).--A cruciform interclavicle, with a large anterior process, is present in all cordylids, teiids, gymnophthalmids, lacertids, and xantusiids, and in a modified form (split anterior process) in *Lanthanotus* (Lécuru, 1968b). Most gekkonids have this condition (Kluge, 1967, 1987), as do some agamids* (Moody, 1980), scincids (Greer, 1970), xenosaurids (Barrows and Smith, 1947; Costelli and Hecht, 1971), anguids (Camp, 1923), and *Varanus niloticus* (Lécuru, 1968b), *V. griseus* (pers. obs.), and the fossil *Saniwa* (Gilmore, 1928). Among iguanids*, only the tropidurine *Leiocephalus* has a well developed anterior process. An anchor-shaped interclavicle occurs in *Varanus* (except as noted above), some teiids, some agamids*, and most iguanids*. In cases in which the lateral processes are lost, the presence of an anterior process cannot be determined. Among gymnophthalmids, even the highly modified *Bachia* has at least a small anterior process and lateral processes (Camp, 1923, fig. 68). In all non-squamate lepidosauromorphs in which this can be determined, a T-shaped interclavicle is present, with at most a very small anterior process (Evans, 1981; Currie, 1981). The simplest interpreta-

tion of the cruciform interclavicle furnished with a large anterior process is that it is a synapomorphy of *Scleroglossa*, with loss of the anterior process in *Xenosaurus* and most *Varanus*, and independently acquired in some agamids* and the iguanid* *Leiocephalus*.

121. Sternal fontanelle (Fig. 13E-F).--Presence of a sternal fontanelle, an opening in the cartilaginous sternum, occurs in all gymnophthalmids and teiids. It also is found in some agamids* (Moody, 1980), some iguanids* (Etheridge and de Queiroz, 1988), some chamaeleontids (Lécuru, 1968b), some gekkonids (Kluge, 1967), some xantusiids, a few lacertids (E. N. Arnold, in litt., 1985), some scincids (Greer, 1970), and some *Varanus* (Lécuru, 1968b). A sternal fontanelle is absent in all non-squamate lepidosauromorphs in which this can be determined. Presence of a sternal fontanelle could be interpreted with equal simplicity as a synapomorphy of Teiioidea acquired convergently within xantusiids and lacertids, a synapomorphy of Lacertiformes reversed within lacertids and convergent in xantusiids, or a synapomorphy of Lacertoidea reversed within lacertids and xantusiids; all other occurrences are independent.

122. Ectepicondylar foramen.--The ontogenetic enclosure of the humeral ectepicondylar groove to form an ectepicondylar foramen is a synapomorphy of Lepidosauromorpha, and in lepidosaurs this enclosure occurs in the embryo (Gauthier et al., 1988). Thus, most postembryonic squamates (Renous, 1969), including anguids (pers. obs.; not discussed by Renous, 1969) have an ectepicondylar foramen. However, in chamaeleontids (Renous, 1969), gymnophthalmids (pers. obs. on *Echinosaurosa*, *Neusticurus*, *Proctoporus*, and *Tretioscincus*), teiids (Renous, 1969), and the only limbed amphisbaenian *Bipes* (pers. obs.), neither an ectepicondylar foramen nor an ectepicondylar groove is present postembryonically. Squamates that lack humeri cannot be scored for this character. The absence of an ectepicondylar foramen (or groove) is clearly derived for squamates, because it is present in all non-squamate lepidosauromorphs in which the ectepicondylar region is known. This character is a synapomorphy of Teiioidea; other occurrences are independent.

123. Notching of distal tibial epiphysis (Fig. 15E-F).--A notched tibial epiphysis that fits onto a ridge on the astragalocalcaneum is present in all limbed squamates except iguanians. In the latter group and in non-squamate lepidosauromorphs this notch is not present. This character is a synapomorphy of *Scleroglossa*.

124. Ventral view of pubis (Fig. 8D-F).--The pubis of squamates shows a transformation involving elongation. In iguanians and in *Varanus*, as in non-squamate lepidosauromorphs, the pubis is short, ventrally directed, and the pubic tubercle is posterodorsally placed. An intermediate condition (state 1), in which the pubis is elongate at the symphysis and the pubic tubercle is more anteroventral in position, occurs in all gekkonids, teiids, xenosaurids, *Lanthanotus*, and *Heloderma*. A greater elongation of the symphyseal process of the pubis, which becomes anteriorly rather than ventrally directed, occurs in all cordylids, scincids, lacertids, gymnophthalmids, xantusiids, and anguids. The intermediate condition (1) is a synapomorphy of *Scleroglossa*, with reversal in *Varanus*. The more derived condition (2) is an independent acquisition in scinciforms (with reversal in teiids to 1), and in anguids.

125. Postcloacal bones.--These elements occur in pygopodids and some gekkonids. Kluge (1982) argued that the similar elements in xantusiids are not homologous with the gekkotan structures, both on the basis of their structure and their topographic relationships to other hemipenial structures. No comparable structures are preserved in any non-squamate lepidosauromorph. Rieppel (1976) suggested homology of superficially similar structures in the Triassic protosauroid archosauromorph *Tanystropheus* (believed by Rieppel at the time of his study to be a lepidosaur relative), and suggested that postcloacal bones are plesiomorphic for squamates. *Tanystropheus* is more closely related to archosauromorphs than to squamates (Gow, 1975; Gauthier, 1984), and we agree with Kluge (1982:349) that the "exceptional sizes, shapes, number and orientation [of these bones] rule against their being homologous with those of xantusiids or gekkonoids". We thus consider the presence of postcloacal bones to be derived within Squamata, and interpret the post-

cloacal bones in gekkonids and pygopodids as a synapomorphy of Gekkota that has been lost in some gekkonids.

126. Ventral body osteoderms.--Ossifications in the dermis of the ventral body wall are little different from those of the dorsal surface; they are in general similar in distribution to the epidermal scales, and occur in cordylids, scincids, and anguids. Among non-squamate lepidosauromorphs no ventral body osteoderms are known in rhynchocephalians (our character excludes gastralia). Carroll (1975, fig. 6) figured ventral body osteoderms in *Saurosternon*. The position on the body of the integumentary impression in the younginiform *Hovasaurus* is unknown (Currie, 1981), and it is in any case not certain whether epidermal scale or osteoderm impressions are preserved. This character is a synapomorphy of Scincoidea, and is independently derived in anguids (Gauthier, 1982).

127. Dorsal body osteoderms.--These structures, like those in character 126, are dermal ossifications that more or less mirror the configuration of the epidermal scales. They occur in cordylids, scincids, anguids, xenosaurids, *Lanthanotus*, and *Heloderma*, and are present in a few gekkonids (Camp, 1923). Some *Varanus* also have these structures (McDowell and Bogert, 1954). A midline row of dorsal body osteoderms is known in *Youngina* (Gow, 1975) but such structures are absent as far as known in other non-squamate lepidosauromorphs. This character is a synapomorphy of Scincoidea, and of Anguimorpha, with reversal in some *Varanus*.

128. Cephalic osteoderms.--Presence of separable cephalic osteoderms occurs in cordylids, scincids, lacertids, xenosaurs, anguids, *Lanthanotus*, and helodermatids, as well as in some varanids (McDowell and Bogert, 1954) and the iguanid* *Amblyrhynchus* (de Queiroz, 1985). Separable cephalic osteoderms are not present in any non-squamate lepidosauromorph group. This character is a synapomorphy of Anguimorpha as well as of Scincoidea. The lacertid condition is separately derived; in any case only a few osteoderms on the periphery of the skull table are separable in this group. We do not include in this character the non-separable dermal sculpture seen in some iguanians, gymnophthalmids, teiids, xantusiids, and amphisbaenians. Although study of early developmental stages is necessary to determine whether the dermal sculpturing in these taxa represents separable osteoderms that fuse ontogenetically, there is no evidence known to us that indicates the presence of separable osteoderms in the latter taxa.

129. Dermal rugosities.--The presence of impressions on dermal bones of the skull that reflect the shape and number of cephalic scales can be expressed in two states. State 1 indicates the presence of such scale impressions but with vermiculate sculpture lacking. This occurs in both fossil and extant helodermatids, and in some iguanids* (some *Anolis*; see e. g. Estes, 1983a, fig. 7b for a fossil example), agamids*, and chamaeleontids. State 2 is the presence of vermiculate sculpture on these scale impressions, which occurs in cordylids, lacertids, and xenosaurids, as well as in some anguids and amphisbaenians. Such impressions are lacking in non-squamate lepidosauromorphs. The variation within basic taxa in this character makes it virtually useless for phylogenetic analysis at this level. We tentatively consider state 1 to be a synapomorphy of Autarchoglossa with numerous reversals. State 2 is a synapomorphy of scincomorphs with reversals in some gymnophthalmids, teiids, xantusiids, and scincids. The iguanian acquisitions are independent.

130. Epiphysis fusion.--Fusion of long bone epiphyses to diaphyses prior to fusion of the braincase elements is characteristic of all of our basic taxa except iguanians; no decision can be made in the case of limbless forms. In iguanians and rhynchocephalians (the only non-squamate lepidosauromorph group in which this is known) the reverse is the case. Although we have not been able to obtain a wide sampling of this character, we tentatively consider epiphysial fusion in long bones prior to that of braincase elements to be a synapomorphy of Scleroglossa.

131. Extension of m. adductor mandibulae posterior (Fig. 15D).--In most squamates and *Sphenodon* the m. adductor mandibulae posterior (MAMP) inserts around the margin of the Mecke-

lian fossa of the mandible (Rieppel, 1980c). Rieppel showed that in gymnophthalmids, teiids, lacertids, and the two agamids* examined by him, the MAMP extends deeply into the mandible, partially filling Meckel's canal and extending forward under the tooth row. In most cases, this condition is correlated with inflation of the Meckelian fossa (Character 81). In xantusiids, however, the Meckelian fossa is not inflated, although there is some MAMP extension into Meckel's canal. Although the condition of the MAMP cannot be directly determined in non-squamate lepidosauromorphs other than *Sphenodon*, the relatively small size of the Meckelian fossa in the various groups does not suggest that the muscle extends into the mandible. We interpret extension of the MAMP into the mandible as a synapomorphy of Lacertoidea; however, in xantusiids the degree of muscle involvement is intermediate between the plesiomorphic condition in which no MAMP extension occurs, and the more derived condition in lacertoids, in which there is strong muscle insertion within the mandible with the development of a median tendon. Independent development has occurred in at least some agamids*.

132. Origin of *m. pseudotemporalis superficialis* (Fig. 15).--The MPS origin in squamates is usually along the lateral and anterior margins of the temporal fossa (Rieppel, 1980c) (Fig. 15C). In xantusiids (Rieppel, pers. comm. 1982), and in gymnophthalmids, teiids, lacertids, and *Varanus* (Rieppel, 1980c), the MPS extends its origin posteriorly, along the medial margin of the temporal fenestra (Fig. 15A). *Sphenodon* has the less extensive position found in most squamates, but this cannot be determined for any other non-squamate lepidosauromorph. This character is a synapomorphy of Lacertoidea, with independent occurrence in *Varanus*.

133. Anterior head of *M. pseudotemporalis profundus* (Fig. 15B).--A separate anterior head of this muscle originating on the descending process of the parietal occurs in all squamates except iguanians, gekkonids, and snakes (Haas, 1973; Rieppel, 1980b,c; 1984a,b). The anterior head is small but present in *Heloderma* (Rieppel, 1980b,c), and is absent in some anguids (e. g. *Gerrhonotus*). We have confirmed the absence of the muscle in the gekkonids *Eublepharis* and *Coleonyx*. In the pygopodid *Delma* we found a weakly-differentiated anterior head, originating on the descending process of the parietal, in addition to the posterior head, which originates on the epipterygoid and descending process posteriorly. Rieppel (in litt., 1985) found an anterior head in *Lialis*, *Pygopus*, *Pletholax*, and *Aprasia*, and suggested that because the anterior head differentiates late in ontogeny, its absence might be a pedomorphic feature of gekkonids. The pygopodids in which the muscle occurs are spread widely through the cladogram of pygopodids given by Kluge (1976a), and we provisionally accept it as characteristic of the group. Rieppel (1981b; 1984a) was not able to determine presence or absence of the anterior head in dibamids or amphisbaenians. No anterior head is present in *Sphenodon* (Haas, 1973) and the character cannot be determined in other non-squamate lepidosauromorphs. Although it will be necessary to determine absence of this character in a broader sample of gekkotans, amphisbaenians, and dibamids, we provisionally place this character as a scleroglossan synapomorphy, with reversal in gekkonids and snakes. It is the same number of steps, however, to assume that it is an autarchoglossan synapomorphy independently derived in pygopodids.

134. *M. rectus abdominis lateralis*.--Camp (1923) described the *m. rectus abdominis lateralis* (RAL) in squamates (his *m. rectus abdominis superficialis lateralis*; terminology revised by Moody, 1983). Camp believed that this muscle was primitively present in squamates and had been lost by all iguanians (except a few agamids*) and gekkonids. The loss of a muscle that he believed to be primitively present in squamates formed part of his basis for uniting iguanians and gekkonids as the Ascalabota. Camp believed that the muscle was present in pygopodids, and placed them in Autarchoglossa. Kluge (1976b) reported that, contrary to Camp, the RAL was also absent in pygopodids, supporting the view (e. g. McDowell and Bögert, 1954) that pygopodids are closely related to gekkonids. Moody (1983) showed that the supposed RAL in the few agamids* thought by

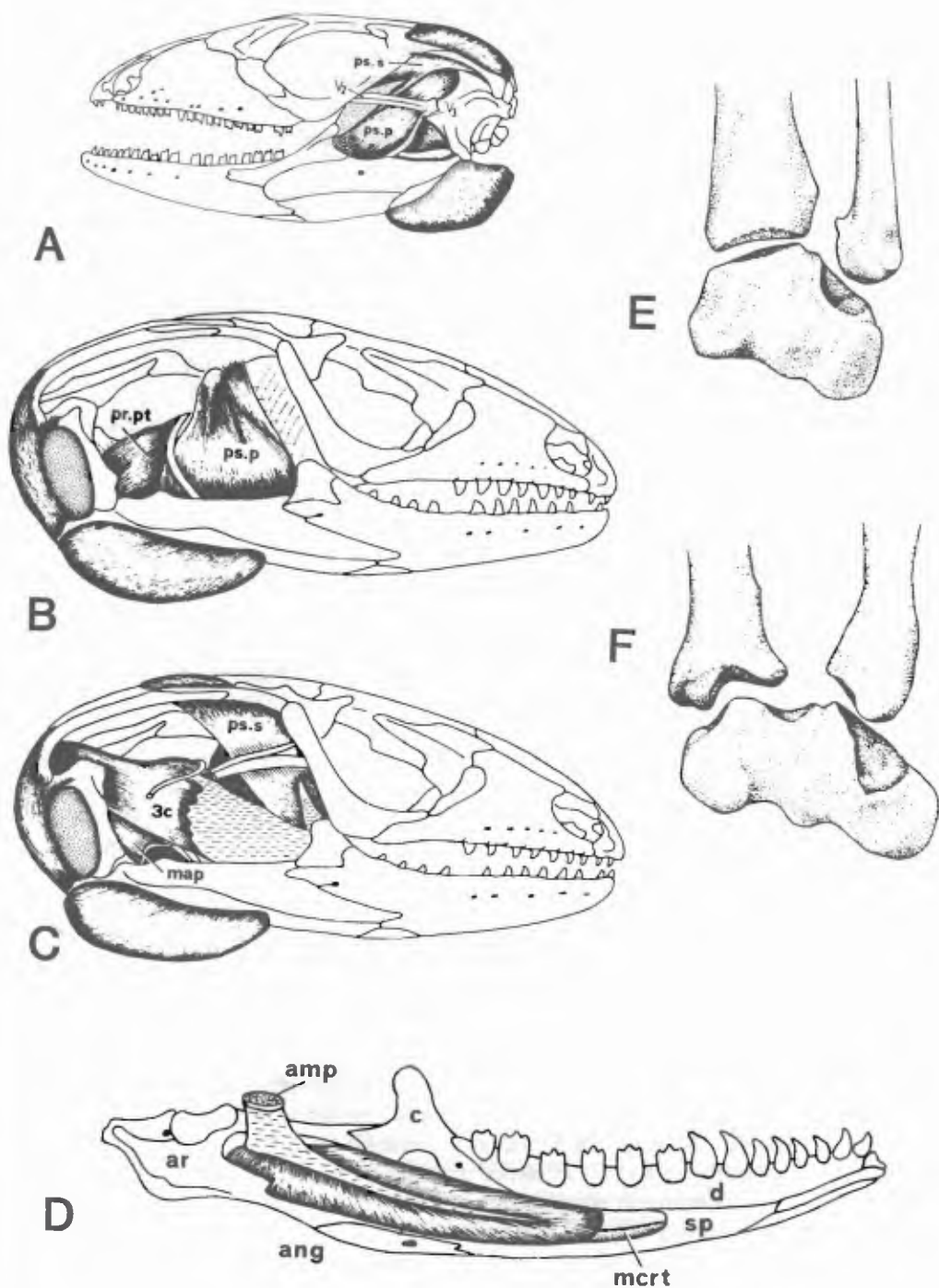


FIGURE 15. A, skull and adductor musculature of *Ameiva chrysoleama* (Teiidae). B-C, same, *Ophisaurus apodus* (Anguillidae). D, medial view of left mandible of *Tupinambis* sp. (Teiidae). E, distal tibia, fibula, and astragalocalcaneum of *Leiolepis belliana* (Agamidae*); F, *Corucia zebrata* (Scincidae). A - D from Rieppel (1980c); E from Gauthier (1984).

Camp to possess it is actually a part of the *m. pectoralis*, and Moody argued that the RAL was primitively absent in squamates. We do not know the condition in *Lanthanotus*. Among non-squamate lepidosauromorphs, *Sphenodon* (the only taxon in which the character can be determined) lacks the muscle as well (Camp, 1923). Presence of the *m. rectus abdominis lateralis* is a synapomorphy of Autarchoglossa; its presence in snakes, dibamids, and amphisbaenians suggests that they are either part of this group or are closely related to it.

Moody (1983:206-207) suggested that Camp's evaluation of polarity in the case of the RAL might have been biased by the notion of progressive evolution:

"Camp (p. 420) argued that the Autarchoglossa was primitive and that the *M. rec. abd. lateralis* would be present in primitive lizards because of their life style of terrestrial and burrowing habits, i. e., creeping, crawling, and slinking. He then argued that the Ascalabota were advanced lizards because of their life style of arboreality and saxicolity, i. e. running, jumping, and climbing. I would suggest that the prejudice of progressive evolution may have been involved unwittingly in Camp's evaluation, i. e., advanced lizards would resemble primates."

Although we accept Moody's (1983) conclusion about the level at which the presence of the RAL exists as a synapomorphy (based in part on his hypothesized muscle homologies), this argument does not provide adequate justification for his conclusion that Camp's alternative hypothesis was influenced by "the prejudice of progressive evolution."

The parallel of progress between primates and iguanians is Moody's creation; Camp made no such comparison. Furthermore, outgroup comparison with *Sphenodon* supports Camp's conclusion that arboreality (he does not mention saxicolity) is derived within Squamata. That the RAL is absent in certain terrestrial forms (e. g. *Sphenodon*, various iguanians) does not preclude an original use in crawling by autarchoglossans.

Based on Camp's interpretations of muscle homologies, his conclusion that the absence of the RAL is derived within squamates need not be based on any notion of evolutionary progress. Camp believed that the RAL was present in some members of both monophyletic groups stemming from the first dichotomy within Squamata (Iguania; Gekkota and Autarchoglossa); it was therefore reasonable for him to hypothesize that it was primitively present in squamates. Camp favored an interpretation that required more evolutionary steps, namely primitive presence and convergent loss of the RAL, but it should be noted that given Camp's hypothesis of relationships, and the distribution of what he believed to be the RAL within squamates, homoplasy is required no matter which condition, presence or absence of the RAL, is considered to be primitive. Camp may thus be accused of favoring an "unparsimonious" interpretation, but Moody's accusation that this is based on "the prejudice of progressive evolution" is unfounded.

Moody himself appears to suffer from the prejudice of progressive evolution that he ascribed to Camp, for he stated (Moody, 1983:207) "If Iguania is a relatively primitive lizard group, then they and ancestral lacertilians lacked the *M. rec. abd. lateralis*." Acceptance of the mosaic nature of evolution renders logically invalid the inference that Iguania is primitive in the condition of the RAL just because it is primitive in other characters (cf. Hennig, 1966, fig. 25). In fact, the very evidence that Iguania is monophyletic is that its members share some characters that are derived relative to other squamates. Moody simply reversed the argument that he unjustifiably attributed to Camp by calling Iguania primitive rather than Autarchoglossa. We agree with Moody (1983) in interpreting the absence of the RAL as plesiomorphic for squamates--not because it is absent in "primitive" squamates but because it is absent in non-squamate lepidosauromorphs (i.e., *Sphenodon*, as noted by Camp, 1923).

135. *M. extracolumellaris*.--The extracolumellaris muscle of the ear was described by Wever (1978:171, fig. 6-30) as extending from the pars superior of the extracolumella to an extension of

the ceratohyal process. It is present only in gekkonids and pygopodids, but the condition is not known in gymnophthalmids and *Lanthanotus*. A similar muscle in the amphisbaenian *Bipes* (Wever, 1978) has different attachments and appears to be separately derived. The so-called extracolumellar muscle in crocodylians (Wever, 1978) is unlikely to be homologous with the squamate structure because of the highly modified ear structure of crocodylians, their phylogenetic distance from squamates, and absence of the muscle in *Sphenodon* (Wever, 1978). Presence of the muscle cannot be determined in other non-squamate lepidosauromorphs. Presence of an extracolumellar muscle is a synapomorphy of Gekkota.

136. Foretongue retractility.--Retractility of the foretongue into the posterior part of the tongue at a zone of invagination has been studied in detail by McDowell (1972) and Schwenk (1988). Such retractility occurs in xenosaurids, anguids, *Heloderma*, *Lanthanotus*, *Varanus*, and snakes. Partial retractility of the hindtongue into the buccal floor beneath the larynx occurs in some teiids and chamaeleontids, but McDowell (1972) has emphasized that this situation is structurally different from the anguimorph condition. Retractility is absent in *Sphenodon* and cannot be determined in any other non-squamate lepidosauromorph. This character is a synapomorphy of Anguimorpha. The occurrence in snakes may be independently derived, although as discussed elsewhere in this paper (see Diagnoses of Taxa) it has been considered evidence of a snake/anguimorph relationship (McDowell, 1972).

137. Notching of free part of tongue.--The free part of the squamate tongue is notched to varying degree in different squamate groups (Schwenk, 1988). We have coded this as a percentage of its length, and set up six states (0-5). State 0 is found in dibamids and chamaeleontids, in which no notching of the tongue occurs. State 1, in which the tongue is notched less than 10%, occurs in iguanids*, agamids*, gekkonids, pygopodids, xantusiids, scincids, and cordylids. State 2, with notching between 10-20%, is found in anguids and xenosaurids. State 3 occurs in *Heloderma* and lacertids, with notching of 20-40%. State 4, in which between 40-50% of the tongue is notched, is found in gymnophthalmids, teiids, amphisbaenians, and *Lanthanotus*. The most derived of these states (5) occurs only in snakes and varanids, in which more than 50% of the free part of the tongue is notched. The tongue of *Sphenodon* is not notched; this character cannot be determined in other non-squamate lepidosauromorphs. Although we coded an unnotched tongue as plesiomorphic for squamates because this is the condition in *Sphenodon*, relationships based on our entire set of characters require that our original polarity be reversed, with a tongue notched less than 10% (state 1) being a squamate synapomorphy. The 0 state in dibamids and chamaeleontids is thus a reversal. A tongue notched between 10-20% (state 2) is a synapomorphy of anguimorphs, with further transformations interpretable as synapomorphies of varanoids (20-40%; state 3), the *Varanus-Lanthanotus* clade (40-50%; state 4), and finally *Varanus* (more than 50%; state 5). A similar but independent transformation is seen within lacertoids, with notching of 20-40% (state 3) being a synapomorphy of Lacertiformes and notching of 40-50% (state 4) a synapomorphy of Teiioidea. The latter condition also occurs in amphisbaenians, and is interpreted as independently derived, although it may indicate a relationship to gymnophthalmids and teiids as suggested by Schwenk (1988). That snakes and *Varanus* share a tongue notched more than 50% (state 5) has been used as evidence supporting a close relationship between them (McDowell, 1972; McDowell and Bogert, 1954); however, that degree of notching appears to be independently derived (see pp. 250-254).

138. Anterior tongue cross-section and tongue keratinization.--As discussed by Schwenk (1988), the plesiomorphic form of the squamate tongue (determined by outgroup comparison with *Sphenodon*) is rounded and glandular. Within squamates, the tongue undergoes evolutionary transformations that involve development of a keratinized posterior (hind) tongue surface and a widening (flattening) of the foretongue (state 1). In some groups, the foretongue also becomes keratinized, and further widening and flattening of the tongue results in a mushroom-shaped cross section of the foretongue (state 2). Among squamates, only iguanians have the plesiomorphic condition; sclero-

glossans (including snakes, dibamids, and amphisbaenians) are characterized by having at least state 1. State 2 appears in scincids, gymnophthalmids, teiids, lacertids, and xantusiids, and in most cordylids (*Angolosaurus*, *Cordylus*, and *Platysaurus* have a papillose foretongue although the hind tongue is keratinized), and is thus a synapomorphy of Scincomorpha.

139. Tongue plication.--The tongue of *Sphenodon* is papillose and lacks plicae (imbricate folds extending transversely across the dorsal surface of the tongue; Schwenk, 1988); the condition cannot be determined in other non-squamate lepidosauromorphs. Among squamates, the plesiomorphic non-plicate condition occurs in iguanids*, agamids*, chamaeleontids, xenosaurids, anguids, *Heloderma*, *Lanthanotus*, amphisbaenians, and some cordylids. Plications on the posterior (hind) tongue occur in gymnophthalmids, teiids, xantusiids, and some lacertids (state 1), and in a few other lacertids (E. N. Arnold, in litt., 1985) the entire tongue becomes plicate (state 2). State 1 is a synapomorphy of the Lacertoidea that has been further transformed (state 2) in some lacertids. Snakes and *Varanus* have smooth tongues (Schwenk, 1988) or may have lateral papillae (McDowell, 1972); we have scored them N because we cannot determine derivation either from a plicate or a non-plicate precursor. The ridges in dibamids may be homologous with plicae or may be separately derived; Schwenk (1988) tentatively accepted them as plicae.

140. Ciliary restraint system for hair cells.--Wever (1978) described differences in the hair cell restraint systems of squamates. The sensory hair cells of the basilar membrane of the inner ear are thought to be stimulated when their cell bodies are displaced and their ciliary tufts are restrained. Ciliary restraint systems of squamates are of two kinds. In tectorial systems, the tectorial membrane restrains the cilia of the hair cells by attaching either directly to ciliary tufts or indirectly through various kinds of fibrous structures (simple fibers, fibrous strands, finger-like processes, tectorial plates). Ciliary restraint in sallet systems is accomplished by inertial bodies known as sallets or culmens that cap the ciliary tufts. Squamates fall into three classes based on the nature of ciliary restraint: (1) those possessing tectorial systems but lacking sallet systems (state 0), (2) those in which a combination of tectorial and sallet systems provide ciliary restraint (state 1), and (3) those in which the great majority of hair cells have sallet or culmen connections (tectorial connections may be present or absent; state 2). Only the tectorial system occurs in *Sphenodon*, crocodylians, and birds, indicating that a tectorial system and the absence of sallets are plesiomorphic conditions in squamates; these conditions (state 0) also occur in iguanians, anguimorphs, amphisbaenians, and snakes. State 1 occurs in gekkonids, pygopodids, lacertids, and teiids; state 2 is found in xantusiids, cordylids, and scincids. The condition is unknown in dibamids, gymnophthalmids, and *Lanthanotus*. Two possible explanations of this distribution exist. First, state 1 is a separate synapomorphy in Gekkota and Scincomorpha (although the condition is not known for gymnophthalmids). State 2 could be a further transformation in cordylids and scincids that has been independently acquired by xantusiids. Second, it is an equal number of steps to place state 2 as a scincomorph character that has been reversed in Lacertiformes. We tentatively accept the latter interpretation.

141. Internal (quadrate) process of stapes.--The internal process of the stapedial apparatus (plesiomorphically present in tetrapods as the quadrate process) arises from the cartilaginous portion of the shaft near the junction between its cartilaginous and bony portions and extends dorsally and anteriorly to the posterior crest of the quadrate (Versluys, 1898; Wever, 1978). According to Wever (1978), an internal process is present in agamids*, iguanids*, lacertids, teiids, xantusiids except *Cricosaura* and *Lepidophyma* (pers. obs.), cordylids (including gerrhosaurids), *Anniella*, *Heloderma*, *Lanthanotus* (McDowell, 1967), and *Varanus*. Versluys (1898) recognized an internal process in chamaeleontids, but Wever (1978:328) considered the task of homologizing processes of the highly modified chamaeleontid stapedial apparatus with those of other lizards "extremely hazardous." The process is uniformly absent, so far as known, in anguids, scincids, gekkonids, pygopodids, and the xantusiids noted above. The process is absent in the limited sample of gymnoph-

thalmids checked by us (*Prionodactylus*, *Echinosaura*, *Proctoporus*). Based on the relationship of the cartilaginous portion of the stapedial apparatus to the chorda tympani, Rieppel (1980b) argued that the internal process is absent in *Anniella*, as in other anguids (contra Wever, 1978), but that it is present, although highly modified, in *Dibamus* and snakes. The stapedial apparatus of the amphisbaenians *Bipes* and *Blanus* apparently lacks any articulation with the quadrate (see figures in Wever, 1978), and in those amphisbaenians that have an association between the stapedial apparatus and the quadrate, the "extracolumellar" element associated with the quadrate is thought to be a modified epihyal rather than an internal process (Gans, 1978). To summarize, the internal process is absent in anguids, gekkonids, pygopodids, scincids, amphisbaenians, our sample of gymnophthalmids, and some xantusiids. *Sphenodon* has a process of the stapedial apparatus that, like the internal process of those squamates that have one, articulates with the quadrate, but it is not clear that the two processes are homologous (Wever, 1978). In other lepidosauromorph groups this character cannot be determined. Absence of the internal process is a synapomorphy of Gekkota. Absence in other taxa appears to be independent.

142. Ulnar nerve position in forelimb.--Jullien and Renous-Lécuru (1972a) described variations in the pathway of the ulnar nerve and their distributions among various groups of limbed squamates. They designated two alternative pathways, the "lacertid" type and the "varanid" type (Haines, 1950), both of which occur commonly in squamates. The "lacertid" pathway is the superficial position of the ulnar nerve of the forearm, with the nerve passing posterior to the elbow joint, and is presumed to be plesiomorphic for squamates because it occurs in *Sphenodon*, crocodylians, turtles, mammals, anurans, and urodeles. Among squamates, this plesiomorphic condition occurs in agamids*, gekkonids, xantusiids, scincids, cordylids, xenosaurids, and anguids, as well as in some iguanids* and lacertids. The apomorphic "varanid" pathway is the deep position of the nerve, in which it passes anterior to the elbow joint but deep to the flexor muscles; among squamates, it occurs in *Varanus*, *Lanthanotus*, *Heloderma*, gymnophthalmids, teiids, chamaeleontids, and in some iguanids* and lacertids (Renous, 1978). Jullien and Renous-Lécuru (1972a) did not examine amphisbaenians, but we have found the "lacertid" innervation pattern in *Bipes biporus* (MVZ 171489). The condition cannot be determined in snakes, pygopodids, and other limbless squamates. The deep position of the ulnar nerve forms separate synapomorphies in the Lacertiformes and in Varanoidea; phylogenetic analysis within lacertids indicates that the "varanid" condition of the nerve is primitive for this group with subsequent reversal (Estes, 1983b; E. Arnold, pers. comm. 1983). Other occurrences are independent.

143. Innervation of dorsal muscles of lower leg.--Jullien and Renous-Lécuru (1972a) also described variation in the nerves supplying the dorsal shank muscles in limbed squamates. Again, two principal conditions exist, which they designated A (peroneal nerve present) and B (peroneal nerve absent, with innervation taking place via the interosseous nerve). Innervation type A is thought to be plesiomorphic for squamates because it occurs in *Sphenodon*, crocodylians, turtles, mammals, anurans, and urodeles. Within squamates, the plesiomorphic condition occurs in gekkonids, pygopodids, xantusiids, lacertids, scincids, xenosaurids, anguids, *Lanthanotus*, and *Varanus*, as well as in some iguanids* and cordylids. In agamids*, chamaeleontids, gymnophthalmids, teiids, and *Heloderma*, however, innervation is by the interosseous nerve (Type B). Most iguanids* (opliurines, anolines, basiliscines, some sceloporines and tropidurines) also show this condition, and an incompletely derived condition is found in some cordylids (Renous, 1978). The condition cannot be determined in amphisbaenians and snakes. This character forms synapomorphies for Acrodonta (or possibly a more inclusive group because it also occurs in many iguanids*), for *Heloderma*, and for Teiioidea.

144. Femoral or preanal pores.--Femoral or preanal pores in squamates are absent in chamaeleontids, scincids, xenosaurs, anguids, *Heloderma*, *Lanthanotus*, and *Varanus* (Camp, 1923; Jullien

and Renous-Lécuru, 1972b, 1973). They are also absent in some members of the following taxa: agamids* (Moody, 1980), iguanids* (Etheridge and de Queiroz, 1988), gekkonids (Kluge, 1967), pygopodids (Kluge, 1974), amphisbaenians (Gans, 1978), gymnophthalmids (Presch, 1980), lacertids (Camp, 1923), and teiids (Presch, 1974a). Femoral and preanal pores are absent in *Sphenodon*, but their presence cannot be determined in any other non-squamate lepidosauromorph. The simplest explanation of this character distribution is that femoral and preanal pores have been gained a number of times convergently. However, we follow the traditional interpretation (which reverses our original polarity) that presence of the pores is a squamate synapomorphy with numerous independent losses. One such loss is as a synapomorphy of Anguimorpha; the others either occur as synapomorphies of our basic taxa or within basic taxa.

145. Course of the stapedial artery.--Versluys (1898), Underwood (1957b, 1971), Greer (1976), and Rieppel (1984a,b) discussed variation in the course of the stapedial artery within Squamata. In most squamates, the stapedial artery passes posterior to the stapes. In dibamids and some gekkonids it perforates the stapes, while in snakes, pygopodids, and other gekkonids it passes anterior to the stapes. The discussion by Gans (1978) of this character in amphisbaenians is ambiguous; however, Versluys (1898) stated that the stapedial artery (his facial artery) passes posterior to the stapes in *Amphisbaena fuliginosa*, and we have confirmed this observation (MVZ 174689). We have also checked squamate groups that had not been determined previously: Gymnophthalmidae (*Neusticurus ecleopus*, MVZ 174893), *Lanthanotus borneensis*, FMNH 151714), and Xenosauridae (*Xenosaurus grandis*, MVZ 146945). All three have the stapedial artery passing posterior to the stapes as in the majority of squamates. In *Sphenodon*, the stapedial artery passes anterior to the stapes in both juveniles (Wyeth, 1924, contra Gans, 1978) and adults (Versluys, 1898).

The final course of the stapedial artery is a character potentially altered by heterochronic changes, presumably because its course changes during development in at least some squamates. It passes through the stapes in juvenile *Leposternon microcephalum* (Amphisbaenia; May, 1978), but not in adults (Zangerl, 1944, fig. 17).

We coded the anterior position of the stapedial artery as plesiomorphic for squamates, because this is the position of the artery in *Sphenodon*. Our results, however, suggest that the posterior course of the artery is a synapomorphy for Squamata (reversing our original polarity), and that the perforation and/or anterior passage in snakes, dibamids, pygopodids, and some gekkonids is secondarily derived, perhaps through paedomorphosis. In this case, perforation or anterior passage is a synapomorphy of Gekkota independently achieved in snakes and dibamids. If perforation is the primitive condition for Gekkota, then anterior passage of the stapedial artery is evidence in favor of the close relationship between pygopodids and diplodactyline gekkonids suggested by Kluge (1987; see also p. 206, this paper).

146. Modified mid-dorsal scale row.--A mid-dorsal scale row is present in chamaeleontids, and in some iguanids* and agamids*, but is lacking in all other squamates. Enlargement of some dorsal scales occurs in the mosasaur *Tylosaurus* (Williston, 1898), but we cannot be certain whether the enlarged scales are mid-dorsal or parasagittal in this specimen. Absence of the middorsal scale row is considered to be derived within Squamata, because one is present in *Sphenodon* (the condition is unknown in other non-squamate lepidosauromorphs). This character is a synapomorphy of Scleroglossa, with independent loss in some agamids* and iguanids*, and possible independent acquisition in at least one mosasaur (see also Gauthier et al., 1988).

147. Cephalic scales.--The presence of a topographically homologous series of enlarged head scales is widely distributed among autarchoglossan squamates. Enlarged scales occur in cordylids, scincids, xantusiids, lacertids, teiids, gymnophthalmids, anguids, amphisbaenians, dibamids, pygopodids, and most snakes. Agamids*, chamaeleontids, many iguanids*, helodermatids, *Lanthano-*

tus, *Varanus*, and gekkonids all have granular or tessellated scales. Within iguanids*, some sceloporines and tropidurines have enlarged cephalic scales that seem in general comparable with those so common in autarchoglossans. *Sphenodon* has small granular head scales and the condition cannot be determined in other non-squamate lepidosauromorphs. We consider this character to be a synapomorphy of *Scleroglossa*, with independent acquisition in some iguanids*, and reversals in gekkonids, xenosaurids, glyptosaurine anguids, varanoids, and some snakes. If pygopodids are embedded within gekkonids as Kluge (1987) has hypothesized, they must have reacquired the enlarged head scales of *Xenosaurus* (moderately enlarged in *Shinisaurus*) are also a reversal, and suggest a relationship between xenosaurids and varanoids, but only if fossils are ignored (see Borsuk-Bialynicka, 1984). The tessellated cephalic scales of some glyptosaurine anguids, and those of varanoids, have also been reacquired, as shown by well-corroborated hypotheses of relationship within these groups (Gauthier, 1982; Pregill et al., 1986).

148. Cycloid scales.--Presence of deeply-overlapping cycloid scales is uniform in dibamids and scincids, and also occurs in gerrhosaurine cordylids, some gymnophthalmids (Presch, 1980), some gekkonids (Kluge, 1987), some pygopodids (Underwood, 1957b; Kluge, 1974), some anguids (*Anniella* and diploglossines; Hoffstetter, 1962; Strahm and Schwartz, 1977), and some snakes (Parker, 1977). Among non-squamate lepidosauromorphs *Sphenodon* has granular scalation, and this is the basis of our polarity decision that cycloid scalation is derived in squamates.

Carroll (1975, fig. 6) figured subcycloid (bony?) scutes in *Saurosternon*, and Currie (1981) indicated that overlapping oval scale or scute impressions were present in the younginiform *Hovasaurus*. The overlying scales must have reflected the cycloid shape in both cases. While this makes our polarity decision questionable, independent origin of cycloid scales in all squamate groups, and in *Hovasaurus* and *Saurosternon*, is the simplest explanation of this character distribution. It is possible, however, that this character is a synapomorphy of cordylids and scincids, with loss in cordylid cordylids. Presence of cycloid scales in dibamids is compatible with Rieppel's (1984a) hypothesis that dibamids are imbedded within scincids.

DEFINITIONS AND DIAGNOSES OF TAXA

In this section we provide diagnoses for the major taxa included in Squamata. The following taxa and their contents are diagnosed here: Squamata, Iguania, Acrodonta, *Scleroglossa* (new taxon), Gekkota, Autarchoglossa, Scincomorpha, Lacertoidea (new combination), Lacertiformes (new taxon), Teiioidea (new taxon), Scincoidea, Anguimorpha, and Varanoidea. Diagnoses are also provided for our basic taxa: the "lizard" families, amphisbaenians, and snakes.

The list of diagnostic characters is taken from our section on character analysis. In many cases this follows the computer assessment (Cladograms Derived from Computer Analyses), although additions and deletions are made based on optimization of each character individually, taking variation into account. Following each character, the number and state of the character are given for comparison with the Character List For Squamata and our evaluation of the character (Character Analysis).

Reversals are indicated by R; convergences by C; for cases in which R and C are numerous we have given only a statement such as "in and within many basic taxa"; these can be determined from the Ingroup Matrix or the Character Analysis. We have also included, from other sources, characters not part of our character list but that are diagnostic of these taxa. For these latter characters, we have not, in general, given reversals and convergences; these were not always given by the original authors and that information was not often readily available elsewhere.

Ingroup phylogenetic analyses that affect the groups included in our definitions below are listed at the beginning of the Character Analysis section.

SQUAMATA Merrem, 1820

Definition: The most recent common ancestor of Iguania and Scleroglossa (both as defined below) and all of its descendants.

Diagnosis: Gauthier et al. (1988, and addendum) gave 74 synapomorphies (listed below) that distinguish squamates from other lepidosauromorphs, and that paper should be referred to for discussion of these characters, although in many cases we have given the original references as well.

Characters varying within Squamata that our study has shown are most reasonably interpreted as squamate synapomorphies are given at the end of the list (numbers 67-84; character number in the Character List for Squamata section given in parentheses); our original polarity has been reversed in these cases for the ingroup node (Maddison et al., 1984). Character reversal (i.e. to our original 0 state) has also taken place within Squamata in numbers 67-84.

1. Reduced size of nasals, with width not as broad as the distance across the conjoined nares.
2. Frontoparietal suture more or less transverse in dorsal view and broader than nasofrontal suture.
3. Supratemporal displaced to a deep position, wrapping around the ventral surface of the parietal, and usually developed prominently on the anterior face of the supratemporal process of the parietal (Robinson, 1967).
4. Loss of ventral ramus of the squamosal.
5. Quadrate notched or fenestrate above for peg-like process of squamosal (Robinson, 1967).
6. Loss of vomerine teeth.
7. Pterygoids separated medially from one another, and from vomers, by palatines.
8. Palatine reduced posteromedially, and pterygoid broadly exposed in suborbital fenestra.
9. Septomaxilla with posteroventral projection extending towards dorsal surface of vomer to form posterior margin of duct of Jacobson's organ, and anterior and medial margins of duct formed by notch in vomer (Fuchs, 1908).
10. Septomaxilla invests enormously enlarged vestibule, roofing Jacobson's organ dorsally and flooring nasal passage ventrally (Malan, 1946; Gauthier, 1984).
11. Paroccipital process expanded distally and takes part in support of quadrate dorsally, rather than being a simple contact of the two bones (Romer, 1956).
12. Stapes very slender (Romer, 1956).
13. Columelliform epipterygoid with narrow base, not contacting quadrate (Romer, 1956).
14. Development of crista tuberalis and consequent subdivision of fissura metotica to form recessus scalae tympani anteriorly and jugular foramen posteriorly; lateral aperture of recessus scalae tympani forms "fenestra rotunda" (Kamal, 1981).
15. Vidian canal fully enclosed posterolaterally (Säve-Söderbergh, 1947).
16. Angular not reaching mandibular condyle.
17. Coronoid eminence prominent and formed only by unique, modified coronoid bone.
18. Anterior cervical and posterior trunk ribs single-headed (Hoffstetter and Gasc, 1969).
19. Cervical intercentra form prominent hypapophyses (Hoffstetter and Gasc, 1969).
20. Eight cervical vertebrae (Hoffstetter and Gasc, 1969).
21. Sacral and caudal ribs fuse to their respective centra in embryonic stages of development (Hoffstetter and Gasc, 1969).
22. Fusion of neural arches to their respective centra in embryonic stages of development (Hoffstetter and Gasc, 1969).
23. Elongate, gracile limbs.
24. Loss of entepicondylar foramen in humerus.
25. Enlarged distal epiphysis of ulna that is nearly hemispherical in profile and fits into a concomitantly enlarged depression in the ulnare.

26. "Styloid" process developed on radius that fits into a concave depression on the posteromedial surface of the proximal end of the radiale.
27. Carpal intermedium small or absent.
28. Lateral centrale in hand contacts second distal carpal, thus interrupting contact between medial centrale and third distal carpal.
29. Proximal end of first metacarpal extends into the row of distal carpals to contact the medial centrale, and the base of the element is expanded laterally to contact the second distal carpal.
30. Pubes in relatively narrow contact at symphysis, forming enlarged pelvic fenestra.
31. Modification of tibio-astragal joint by loss of ridge and trough articulation.
32. Fibulo-astragalocalcanear joint involves most of distal end of fibula.
33. Ankle joint with complex tongue-in-groove structure at the astragalocalcanear-fourth distal tarsal joint (Brinkman, 1980).
34. Squamate hooked fifth metatarsal, with angulated proximal head, prominence of medial plantar tubercle, and lateral displacement of lateral plantar tubercle (Robinson, 1975).
35. Loss of second distal tarsal.
36. Loss of gastralia.
37. Lateral division of *m. retractor bulbi* becomes *m. bursalis* (Underwood, 1970).
38. Reduced cartilaginous component of anterior braincase and interorbital septum, with membranous fenestrae in this region consequently enlarged (Bellairs and Kamal, 1981).
39. Pallets on ventral surface of tongue tip (Schwenk, 1988).
40. Paired, evertible hemepenes in males (Oppel, 1811).
41. Lacrimal duct extends far anteriorly to become associated with duct of Jacobson's organ, rather than with posterior end of choanal groove (Bellairs and Boyd, 1950).
42. Jacobson's organ completely separated from nasal capsule and with a fungiform body, rather than being a simple diverticulum of nasal capsule (Parsons, 1970).
43. Extensive development of sensory epithelium in Jacobson's organ (Pratt, 1948).
44. Jacobson's organ apparently rotated ninety degrees about its longitudinal axis, placing the paraseptal cartilage medially, with the duct of the organ opening ventrally into the oral cavity (Malan, 1946).
45. Enlarged lateral nasal gland lodged in *cavum conchale*, rather than being small and not enclosed in *cavum conchale* (Malan, 1946; Pratt, 1948).
46. Loss of caruncle; only egg tooth present (Hill and de Beer, 1949; Edmund, 1969).
47. Multiple interdigitations of *mm. intermandibularis* and *mandibulohyoideus*, rather than non-interdigitating muscles (Camp, 1923; Rieppel, 1978d).
48. Complete, rather than partial, separation of *m. depressor mandibulae* from *m. episternocleidomastoideus* (Rieppel, 1978d).
49. Facial nerve does not participate in innervation of *m. intermandibularis* (Rieppel, 1978d).
50. Fibers of *m. clavodeltoideus* extend to ventral surface of clavicles, rather than being confined to their dorsal surface only (Peterson, 1973).
51. Meniscus in knee joint a single plate pierced by cruciate ligament, rather than forming separate lateral and medial crescents on either side of cruciate ligament (Haines, 1942).
52. Prominent perilymphatic sac in *recessus scalae tympani* (Baird, 1970).
53. Cochlear duct faces laterally in adults, rather than ventrally as in amniotes ancestrally and in the embryos of squamates (Baird, 1970) (R. within snakes).
54. Loss of *pars tuberalis* of *adenohypophysis* (Wingstrand, 1951).

- 55. Interhyal either ligamentous or absent, rather than cartilaginous (de Beer, 1937).
- 56. Saccular, rather than solid, ovaries (Porter, 1972).
- 57. Tongue mediated, extra-oral chemoreception (Schwenk, 1988).
- 58. Extensive, well-organized, compound sublingual glands (Schwenk, 1988).
- 59. *M. genioglossus* comprising two parts, medial and lateral (Schwenk, 1988).
- 60. Fibers of *m. transversalis* of the tongue encircle bundles of *m. hyoglossus* and surround them completely, forming an uninterrupted loop (Schwenk, 1988).
- 61. *M. verticalis* muscle of tongue lacking fibrous median septum and muscle fiber crossover therefore occurs (Schwenk, 1988).

The following additional five characters were taken from Gauthier et al. (1988, addendum).

- 62. Parasphenoid and basisphenoid fused in embryos (R within xantusiids).
- 63. Proatlas absent.
- 64. Atlantal neural arches broadly in contact, providing extensive dorsal cover for neural canal.
- 65. Atlantal neural arches fused to intercentrum 1 at cessation of growth.
- 66. Two rows of subdigital scales.

The following additional squamate characters were identified by the present study, and our original polarity has been reversed in all of them. Most of these were included in the list given by Gauthier et al. (1988); a few additional ones were identified by this study. The character number in our Character List for Squamata section is given in parentheses, followed by an indication of taxa in which reversal occurs (R).

- 67. Premaxillae fuse in the embryo (1-1; R within scincids and gekkonids).
- 68. Parietals fuse in embryonic or early in postembryonic ontogeny (21-1; R within gekkonids, pygopodids, and xantusiids).
- 69. Braincase exposed broadly in dorsal view, supratemporal processes long (24-1; R in xantusiids, *Xenosaurus*, within lacertids and cordylids).
- 70. Anteroventral border of orbit formed by jugal (31-1; many exceptions).
- 71. Pterygoid lappet of quadrate absent (37-1; R in lacertiforms, *Heloderma*, within iguanids*).
- 72. Pyriform recess broad throughout most of its length (48-1; R in lacertiforms, also within iguanids* and agamids*).
- 73. Opisthotic fuses to exoccipital in embryo or in early postembryonic ontogeny, or the two bones form from a single ossification center (51-1; R in dibamids).
- 74. Coronoid lateral process present as a lappet on dentary (68-1; R within iguanids*).
- 75. Palatine teeth lost (82-1; R in helodermatids, *Saniwa*, within anguids).
- 76. Fourteen scleral ossicles (88-1; many exceptions).
- 77. Vertebral centrum articulation procoelous (93-1; R within gekkonids).
- 78. Zygosphenes and zygantra lost (96-1; many exceptions).
- 79. Posterior trunk (thoracolumbar) intercentra lost (99-1; R within gekkonids and xantusiids).
- 80. Anterior (primary) coracoid emargination present (112-1; R in chamaeleontids, *Heloderma*, within pygopodids and amphisbaenians).
- 81. Clavicle articulates dorsally with suprascapula (117-1; R within iguanids* and agamids*).
- 82. Tongue notched less than 10% (137-1; R in chamaeleontids and dibamids).
- 83. Femoral or preanal pores present (144-1; many exceptions).
- 84. Stapedial artery passes posterior to stapes (145-2; R in gekkotans, dibamids, snakes).

Comments: Squamate monophyly is highly corroborated (Gauthier et al., 1988). As discussed above in the section on squamate monophyly and by Gauthier et al. (1988), amphisbaenians and snakes cannot be excluded from "Lacertilia" without rendering it paraphyletic, because no de-

rived characters have been identified that unite the "lizard-like" members of this taxon. According to our analysis (and that of Camp, 1923, see Fig. 7) some "Lacertilia" are closer to Serpentes and some are closer to Amphisbaenia than they are to other "Lacertilia." This conclusion is contrary to that of Romer, (1956); Underwood (1971); Sukhanov (1976); Northcutt (1978); Rieppel (1978b) and Rage (1982a,b), who specifically excluded snakes from the "Lacertilia" (Sauria). In most of the above cases, however, the question of whether or not snakes were derived from "Lacertilia" was not explicitly addressed, and because paraphyletic taxa continue to be recognized as formal taxa by some taxonomists, it cannot be assumed that these authors considered snakes to have diverged before the existence of the most recent common ancestor of the "Lacertilia." Underwood (1957a,b; 1971) included amphisbaenians and dibamids within "lizards" but no definite statement was made regarding the position of snakes. Underwood (1970) considered snakes and "lizards" to have had a common ancestor prior to the origin of living types of "lizards" rather than being derived from within them. Our analysis, however, supports the conclusion of Camp (1923), who made clear his view that snakes, amphisbaenians, and dibamids were derived from within "lizards," although he classified snakes and "lizards" in separate suborders. If this view is correct, the terms Squamata and "Lacertilia" are identical with respect to their most recent common ancestor.

"Lacertilia" is a paraphyletic group, and we recommend that use of this taxonomic term be avoided. The informal term "lizard" is in widespread use as a synonym of "Lacertilia," and we recognize that such use is unlikely to be substantially altered by our conclusions and recommendations; indeed, if the word is used only as an informal descriptive word for squamates except amphisbaenians and snakes, no significant problem should arise. Carroll (1975, 1977, 1988), however, has used the word in a very broad sense to include a number of non-squamate lepidosauromorph groups; ill-defined usage such as this can only engender confusion.

"Sauria" has also been used more or less synonymously with "Lacertilia"; however, Gauthier (1984) and Gauthier et al. (1988) have already recommended that the name Sauria be applied to a group more in keeping with McCartney's (1802) usage (archosaurs *plus* lepidosaurs; McCartney included crocodylians in his concept of Sauria), and that it not be used as a synonym of "Lacertilia."

IGUANIA Cuvier, 1817

Definition: The most recent common ancestor of Iguanidae*, Agamidae* and Chamaeleontidae, and all of its descendants.

Diagnosis: The following characters are synapomorphies of Iguania.

1. Frontals fuse in embryo (6-1; C in gekkotans, gymnophthalmids, and xenosaurs, within many other groups).

2. Frontals strongly constricted between orbits giving them the shape of an hourglass (7-1; secondarily expanded in most chamaeleons; C in some autarchoglossans).

3. Broad frontal shelf underlying nasals with frontals often exposed dorsolaterally as wedges or spikes between nasals and prefrontals (modified in chamaeleons) (8-1; R in some).

4. Prefrontal bosses present (Gauthier, 1984).

5. Postfrontal reduced or lost; when present, subtriangular and confined to orbital rim (15-1).

6. Parietal foramen displaced anteriorly; on frontoparietal suture or within frontal (25-1, further transformed to 2 in some taxa; R within *Anolis*; C within teiids).

7. Prominent supratrigeminal process above trigeminal notch (50-1; R in chamaeleontids, within iguanids* and agamids*).

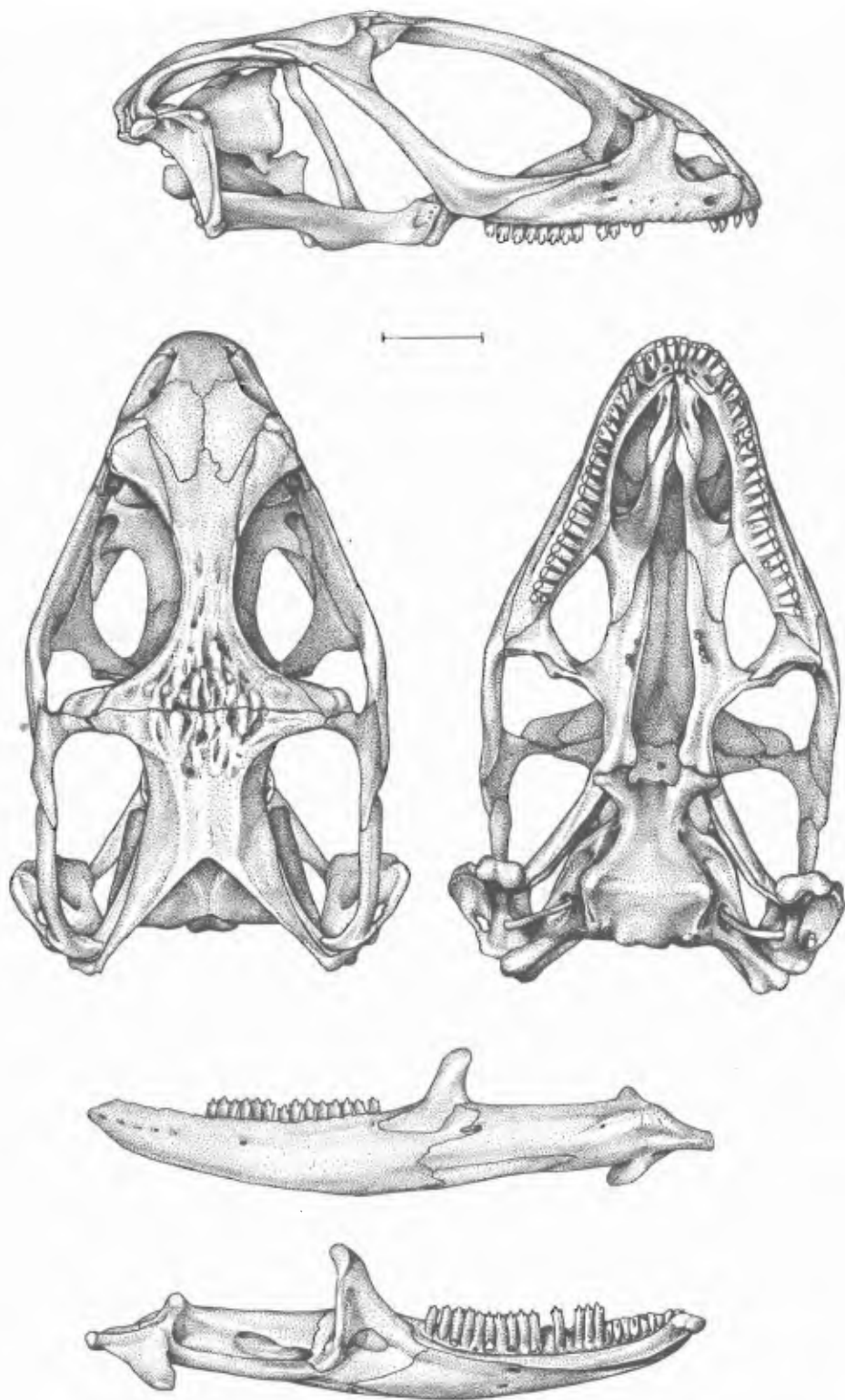


FIGURE 16. Skull of *Morunasaurus annularis* (REE 1956; Iguanidae*) in dorsal, lateral, and ventral views; mandible in medial and lateral views. Scale = 5 mm. See end of paper for abbreviations.

8. Finger-like angular process on retroarticular process (80-1; R in chamaeleons, within iguanids* and agamids*).

9. Caudal autotomic septa posterior to transverse processes (102-1; polarity questionable, may be iguanid* character but cannot be scored in Acrodonta).

10. Metachromatism (Etheridge pers. comm., 1985).

11. Dracomorph brain (Northcutt, 1978).

12. Loss of *m. intercostalis ventralis* (Camp, 1923).

13. Tongue mucocytes mostly serous and sero-mucous (Schwenk, 1988).

14. Enlarged conical papillae present on posterior limbs of the tongue (Schwenk, 1988). R in chamaeleontids, within iguanids*.

Comments: As defined here, Iguania is approximately equivalent to Iguania (*Pachyglossa*) plus chamaeleons (*Rhoptoglossa*) of earlier authors (e. g. Cuvier, 1817; Latreille, 1825; Cope, 1900; Camp, 1923), and to Iguania of more recent authors (e. g. McDowell and Bogert, 1954; Romer, 1956; Underwood, 1971; Moody, 1980; Estes, 1983a). Chamaeleons were originally separated from Iguania because of their numerous distinctive morphological features (see diagnosis of Chamaeleontidae). However, both Cope (1900) and Camp (1923) recognized that these were derived characters of chamaeleons, and hypothesized a close phylogenetic relationship between chamaeleontids and agamids*. This relationship is now widely accepted (for evidence see diagnosis of Acrodonta), making the separation of *Rhoptoglossa* from Iguania untenable on phylogenetic grounds.

IGUANIDAE* Gray, 1827

Definition: Iguanidae* is a metataxon. Therefore, it can only be defined in terms of a common ancestor and all of its descendants if it is considered a potential synonym of Iguania. If Iguanidae* excludes Agamidae* and Chamaeleontidae, it must either be defined in terms of a morphotype composed of a combination of ancestral and derived characters or in terms of its included taxa. We prefer the latter. Iguanidae* is defined as the metataxon composed of all those Iguania except Acrodonta. Currently, this includes anoloids, basiliscines, crotaphytines, iguanines, morunasaur, oplurines, sceloporines, and tropidurines (all sensu Etheridge and de Queiroz, 1988).

Diagnosis: Because Iguanidae* is a metataxon, it cannot be diagnosed by synapomorphies that apply to members of this taxon alone. Iguanids* possess the diagnostic synapomorphies of Iguania but lack either some or all of the diagnostic synapomorphies of Acrodonta (Fig. 16).

Comments: Moody (1980) provided a list of 24 diagnostic iguanid* features that he implied were "principally apomorphic character states" (Moody, 1980:342). The existence of apparent iguanid* synapomorphies would refute our claim that Iguanidae* is a metataxon. However, none of Moody's characters can reasonably be interpreted as an iguanid* synapomorphy. Each of these supposedly diagnostic features corresponds to an alternative character in similar lists that he provided for agamids* and chamaeleontids (e. g. interclavicle present in iguanids* and agamids*; interclavicle absent in chamaeleontids). In each case the iguanid* condition falls into one or more of three categories that are uninformative concerning iguanid* monophyly. (1) The iguanid* condition is plesiomorphic within Iguania (Moody's characters 1 in part, 2, 6, 7, 8, 10, 13, 14 in part, 15?, 16? 17, 18, 19, 21?, 22, 23). (2) Both plesiomorphic and apomorphic states occur in iguanids* (characters 1 in part, 3?, 4, 5, 9, 11, 12, 14 in part, 15, 17, 19, 20, 23, 24). (3) The information is incorrect (characters 1, 4, 5, 24). One possible iguanid* synapomorphy is the presence of the *m. mandibulohyoideus* III (McDowell, 1972), but more extensive data is needed for this character. Renous (1973) stated that the carpal intermedium is absent in iguanids*, but even if this were known to be uniform in the group, its absence in some other squamate groups suggests that

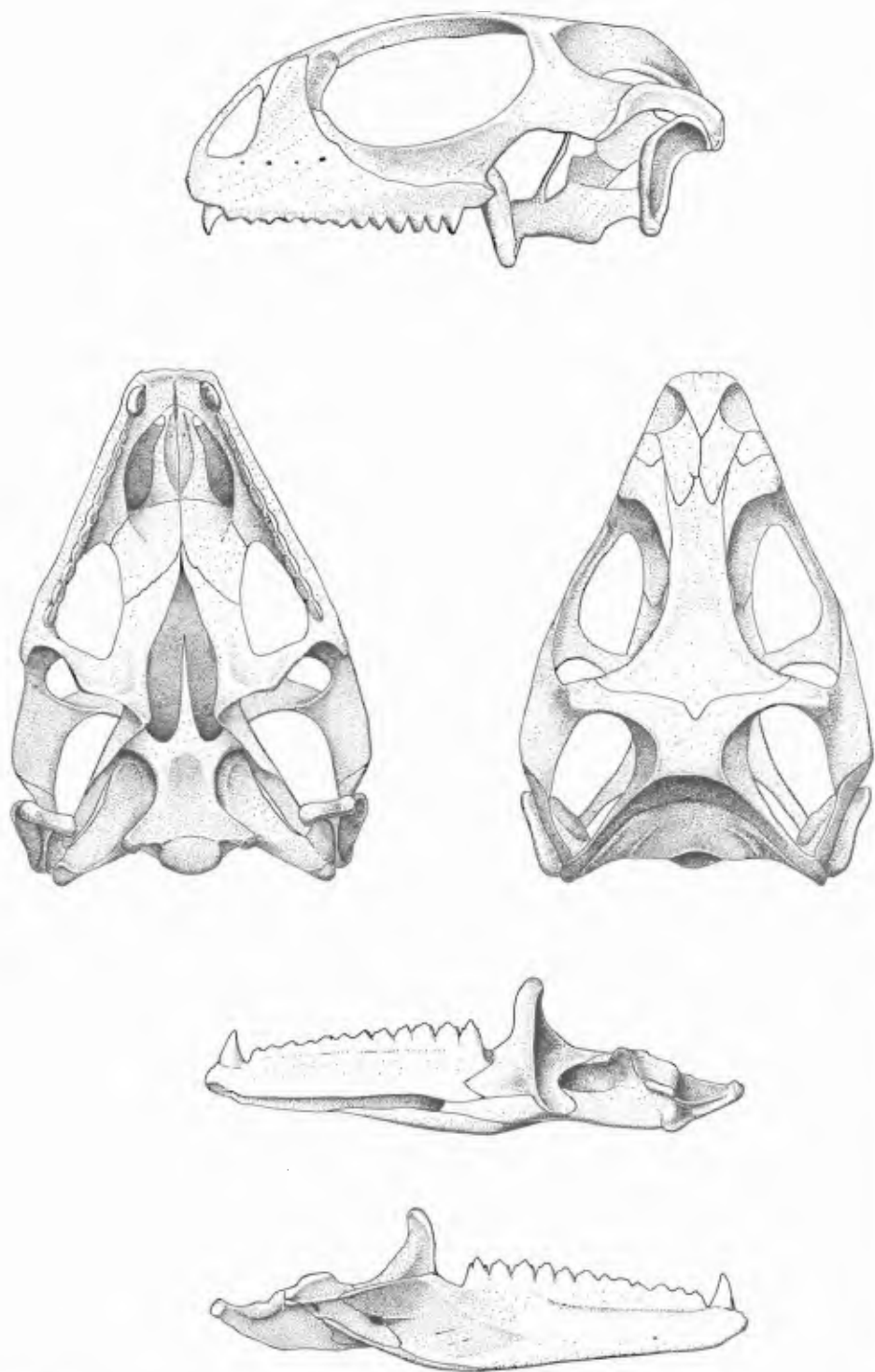


FIGURE 17. Skull of *Leiolepis belliana guttata* (REE 1993; Agamidae*) in dorsal, lateral, and ventral views; mandible in medial and lateral views. Scale = 5 mm. See end of paper for abbreviations.

this feature is not in itself useful in demonstrating iguanid* monophyly. Furthermore, the sharing of several derived characters by acrodontans, and some but not all iguanids*, necessitates that the case for iguanid* monophyly be supported by more than one derived character.

The recognition of oplurines as a family separate from other iguanids* (e. g., by Moody, cited in Blanc et al., 1983) serves no useful purpose in a phylogenetic system, because it merely changes the content of Iguanidae* without changing its uncertain phylogenetic status. Alternatively, one could abandon the taxon Iguanidae*, recognizing only subgroups of iguanids* that appear to be monophyletic; however, this would do nothing to clarify the relationships among these monophyletic groups and their relationships to Acrodonta. Therefore, we provisionally retain Iguanidae*, but call attention to its uncertain phylogenetic status by designating it a metataxon. This is meant to indicate that the monophyly of Iguanidae*, and thus the early history of Iguania, are areas in need of further study.

ACRODONTA Cope, 1864

Definition: The most recent common ancestor of extant Agamidae* and Chamaeleontidae and all of its descendants.

Diagnosis: The following characters are potential synapomorphies of Acrodonta (but see comments below).

1. Postfrontal lost (12-1; C in *Dibamus*, xantusiids, *Lacerta*, within iguanids* and amphisbaenians).
2. Splenial reduced or lost (65-1; C in many scleroglossan groups).
3. Maxillae meet anteromedially below palatal portion of premaxilla (Cope, 1864; Rieppel, 1984b:310 noted variation in agamids*; C in some gekkonids).
4. Enlarged lacrimal foramen (except in *Uromastix* and *Leiolepis*; Moody, 1980; Etheridge and de Queiroz, 1988).
5. Coronoid lateral process as a lappet on dentary lost (68-0; R of squamate synapomorphy, also R in xantusiids, dibamids, *Lanthanotus*, within iguanids*, *Varanus*, amphisbaenians, and snakes).
6. Pterygoid teeth lost (83-1; C in many scleroglossan groups).
7. Posterior maxillary and dentary teeth "acrodont", not replaced (84-1).
8. Number of ossicles in scleral ring reduced to 12 or 11 (89-1; C in many squamate groups).
9. Caudal autotomy septa lost (103-1; C in varanoids, within iguanids*, gekkonids, scincids, anguils, snakes, and amphisbaenians).
10. Dorsal muscles of lower leg innervated by interosseous nerve (143-1; C in teioids, *Heloderma*, within iguanids*).
11. M. mylohyoideus anterior in two layers, superficial (principal) layer transverse or anteriorly oblique, profound layer directed transversely and obliquely backward (Camp, 1923; polarity of this character needs confirmation).
12. Reticular papillae present on fore and hind tongue (Schwenk, 1988).
13. Extension of entire tongue, including posterior limbs, beyond the mandibular symphysis during feeding bouts (Schwenk, 1988). Needs additional coverage for Agamidae*.

Comments: Close relationship of Agamidae* and Chamaeleontidae has often been suggested and is generally accepted. Camp (1923:417) stated it explicitly: "The chamaeleons are offshoots of agamid stock." Of the above listed synapomorphies, only the anteromedial contact of the maxillae below the premaxilla, the "acrodont" dentition, and the pattern of reduction in the number of scleral ossicles is unique to Acrodonta within Iguania. Twelve scleral ossicles also occur in some sceloporine iguanids* (Underwood, 1970; de Queiroz, 1982); however, the pattern of overlap suggests that this reduction has been reached independently of the attainment of 12 or fewer scleral ossicles

in Acrodonta (cf., Underwood, 1984). The remaining characters occur in some iguanids* as well as in Acrodonta, indicating that either convergence is involved or the characters are synapomorphies that diagnose a monophyletic group more inclusive than Acrodonta but less inclusive than Iguania.

The discovery of an acrodont Cretaceous iguanian (*Priscagama*; Borsuk-Bialynicka and Moody, 1985) that retains primitive features not seen in any agamid* or chamaeleon helps to clarify some of these transformations. In the above list, numbers 1, 3, and 7 occur in *Priscagama* and thus may apply at a more inclusive level; numbers 2, 4, 5, and 6 do not occur in *Priscagama* and are therefore interpreted as synapomorphies of Acrodonta or convergent in some iguanids*.

AGAMIDAE* Gray 1827

Definition: Agamidae* is a metataxon composed of all Acrodonta except chamaeleontids.

Diagnosis: Agamids* possess the diagnostic synapomorphies of Acrodonta but lack either some or all of the diagnostic synapomorphies of chamaeleontids (Fig. 17).

Comments: Moody (1980) listed 24 agamid* characters that he implied were "principally apomorphic character states" (Moody, 1980:342). While many of these characters are apomorphic within Squamata and even within Iguania, few if any are apomorphic within Acrodonta (i.e., relative to the condition seen in chamaeleontids). Instead, most of these characters can be placed in one or both of two categories that are uninformative concerning agamid* monophyly. (1) They are plesiomorphic within Acrodonta (characters 1 in part, 2, 3, 5, 6, 8, 9, 10 in part, 12, 13, 14 in part, 17, 18, 19, 20, 21). (2) Both plesiomorphic and apomorphic conditions occur in agamids* (characters 1 in part, 3, 4, 5, 7, 11, 14 in part, 15, 22, 23, 24).

From Moody's (1980) character list and our own, we have been able to identify three potential agamid* synapomorphies: (1) Caniniform teeth at anterior ends of maxillae and dentaries; (2) cervical intercentra sutured to anterior parts of following centra; and (3) presence of 12 (or 11) scleral ossicles with only a single plus ossicle on the dorsal side of the ring (Underwood, in litt. 1985). The first of these characters provides only weak evidence supporting agamid* monophyly exclusive of chamaeleons, because not all agamids* have caniniform teeth. The second and third characters are insufficient evidence for agamid* monophyly because various derived characters shared by chamaeleontids and some agamids* (e.g., narrow premaxilla, splenial absent, femoral and preanal glands absent) suggest that Agamidae* is paraphyletic. Resolution of the problem of agamid* monophyly awaits a detailed analysis of relationships within Acrodonta. Recognition of a family Uromastycidae (e.g., Moody, 1983) does not clarify the situation, because the relationships of chamaeleontids remain uncertain.

CHAMAELEONTIDAE Gray, 1825

Definition: The most recent common ancestor of extant *Bradypodion* (including *Lophosaura* and *Microsaura*), *Brookesia*, *Chamaeleo*, and *Rhampholeon*, and all of its descendants.

Diagnosis: The following characters are potential synapomorphies of chamaeleontids (but see comments, below) (Fig. 18):

1. Premaxilla narrow, rostral body not much wider than nasal process (also present in some agamids*, Moody, 1980).

2. Except in *Brookesia* (Siebenrock, 1893) and *Bradypodion*, which is intermediate (Engelbrecht, 1951; Rieppel, 1981c), and some *Rhampholeon* (Rieppel, 1987), nasals reduced, bony external nares extended posteriorly so that frontal comes close to or is incorporated into either narial border or border of "prefrontal fontanelle" in those chamaeleons in which bony external nares are divided by prefrontal-maxillary bar (character 4) (2-1; C in *Lanthanotus* and *Varanus*, within snakes).

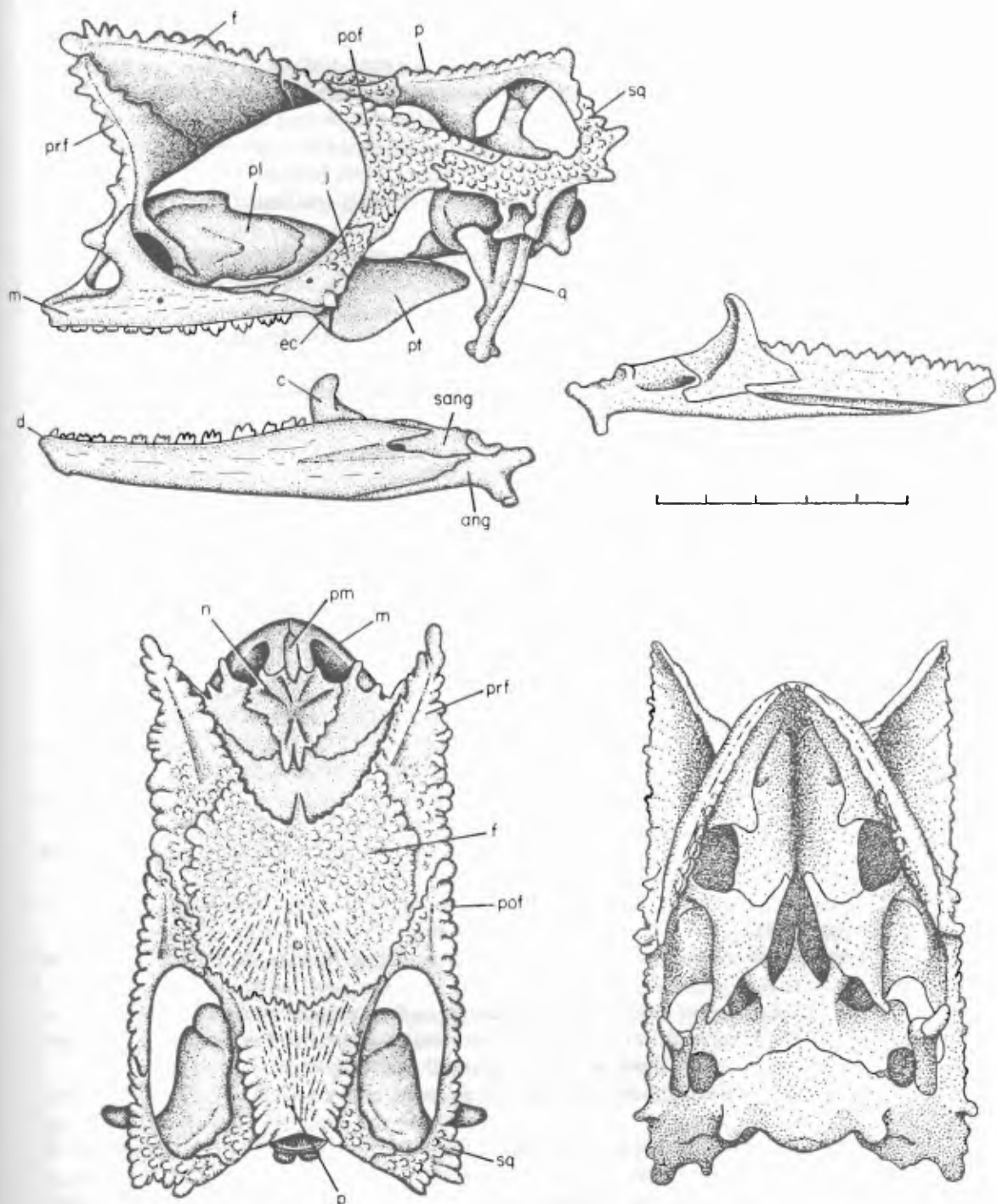


FIGURE 18. Skull of *Brookesia* (Chamaeleontidae) in dorsal, ventral, and lateral views; mandible in medial and lateral views. Ventral view of skull and medial view of mandible are of *B. stumpffii* (REE 1911); other views from Rieppel (1987) are of *B. superciliaris*. Scale = 2 mm. For abbreviations see end of paper.

3. Nasals fuse in embryo (3-1; C in *Lanthanotus* and *Varanus*, within gekkotans, scincids, and snakes). Nasal fusion occurs in *Brookesia* (Siebenrock, 1893; Rieppel, 1987), *Bradypodion* (Rieppel, 1987), some but not most *Chamaeleo* (contra Rieppel, 1987), and not in *Rhampholeon* (Rieppel, 1987). Its status as a chamaeleontid synapomorphy is therefore questionable.

4. Prefrontal with anterior process on canthal ridge that, except in *Brookesia* and some *Rhampholeon* (Rieppel, 1987), contacts maxilla dividing external naris into two parts, the posterior one of which is called the "prefrontal fontanelle" (Romer, 1956; Rieppel, 1981c).

5. Frontal expanded laterally so that it roofs orbit dorsally (prefrontal and postorbital also contribute to expansion) (pers. obs.).

6. Postorbital extended ventrally on medial side of postorbital bar to contact ectopterygoid (Rieppel, 1981c; also in some agamids* fide Siebenrock, 1895).

7. Parietal foramen within frontal (25-2; foramen lost in some; C within iguanids*).

8. Except in *Brookesia* (Siebenrock, 1893) parietal with dorsal midsagittal crest extended posteriorly to form a skull casque (e.g., Rieppel, 1981c, figs. 1,2).

9. Supratemporal process of parietal reduced (*Brookesia*, *Bradypodion* [= *Microsaura*], some *Rhampholeon*), or absent (*Chamaeleo*, other *Rhampholeon*) with concomitant enlargement of dorsal process of squamosal and loss of contact between supratemporal and parietal; supratemporal lies wholly along medial surface of squamosal rather than lateral surface of supratemporal process of parietal (modified from Rieppel, 1981c; 1987).

10. Maxillae extended posteriorly along anteromedial borders of external nares to contact nasals, excluding premaxilla from narial border (e.g., Siebenrock, 1893, fig. 5; maxillary extensions that fail to contact nasal occur in some agamids* fide Moody, 1980).

11. Ventral border of upper temporal arch lies well above dorsal head of quadrate; elongated ventral process of squamosal forms articulation with cephalic condyle (= lateral head of Rieppel, 1981c) of quadrate (Bellairs and Kamal, 1981). *Brookesia*, *Rhampholeon*, and *Bradypodion* seem to be less modified than *Chamaeleo* (pers. obs.).

12. Septomaxillae lost (Parker, 1885; Siebenrock, 1893; Malan, 1946; Visser, 1972).

13. Vomers reduced and fuse before maximum size (38-1; C in pygopodids and xantusiids, within gekkonids, gymnophthalmids, and scincids).

14. Vomer and vomerine process of palatine elevated relative to remainder of palate, and thus separated from maxillary and pterygoid process of palatine by distinct step formed by edge of internal naris; results in dorsoventral compression of nasal capsule and very low nasal septum (Bellairs and Kamal, 1981).

15. Quadrate ramus of pterygoid greatly expanded to form wing-shaped structure (Romer, 1956; Rieppel, 1981c).

16. Loss of bony connection between pterygoid and quadrate (Boulenger, 1887; Romer, 1956; Rieppel, 1981c).

17. Ascending process of embryonic palatoquadrate cartilage reduced or absent (Bellairs and Kamal, 1981) and epipterygoid absent (47-1; reduced in some agamids* fide Moody, 1980; C in *Dibamus* and snakes, within amphisbaenians and the iguanid* *Phrynosoma*).

18. Quadrate columnar with lateral conch and tympanic crest greatly reduced or absent (pers. obs.).

19. Dorsal tubercle of medial crest of quadrate forms distinct medial head that articulates with crista prootica (Rieppel 1981c; approached by some agamids*, e.g., *Lyriocephalus*, pers. obs.).

20. Parasphenoid rostrum lost (Bellairs and Kamal, 1981. Also in some agamids*, e.g. *Lyriocephalus*, pers. obs.).

21. Loss of supratrigeminal process of prootic (50-0; R of iguanian synapomorphy. Also in some agamids, e.g. *Lyriocephalus*, pers. obs.).

22. Fenestra "rotunda" closed, and system for mobilization of endolymphatic fluid concomitantly modified (Wever, 1978).

23. Trabecular cartilages fuse over entire length ontogenetically rather than remaining separated posteriorly, crista trabecularis of basisphenoid single rather than paired (e.g., Visser, 1972, figs. 44, 48. Approached in some agamids*, e.g. *Lyriocephalus*, pers. obs.).

24. Basioccipital portion of occipital condyle reduced, often excluded from border of foramen magnum.

25. Dorsal midsagittal crest of supraoccipital meets ventral midsagittal crest of parietal (Rieppel, 1981c).

26. Except in *Brookesia* (Siebenrock, 1893) and *Rhampholeon* (pers. obs.), marginal processes of ossified chondrocranium formed entirely by supraoccipital (rather than supraoccipital and prootic), and drawn out into thin stalks that fail to contact the parietal.

27. Splenial lost (65-2; C in dibamids, within iguanids*, agamids* fide Siebenrock, 1895, gekkotans, and amphisbaenians). According to Rieppel (1987) a splenial is present in *Bradypodion*, *Chamaeleo*, and in some *Brookesia* and *Rhampholeon*. These observations need to be confirmed. We have not observed a splenial in any chamaeleon, and other authors report its absence in *Bradypodion* (Engelbrecht, 1951), *Brookesia* (Siebenrock, 1893), and *Rhampholeon platyceps* (Frank, 1951), one of the species reported by Rieppel (1987) to possess the bone. Judging from the figures in Parker (1885) and Fineman (1941), the splenial is absent in *Chamaeleo*, although these authors misidentified part of the dentary and the angular, respectively, as the splenial.

28. Retroarticular process reduced (Camp, 1923; Romer, 1956; Rieppel, 1981c).

29. Finger-like angular process reduced or lost (80-0; R of iguanian synapomorphy).

30. Premaxillary teeth greatly reduced in size and number, but not lost (Rieppel, 1981c; also in some agamids*; Moody, 1980).

31. Scleral ossicles reduced to 11; 1,5,7 positive, 4,6,8 negative (89-1). The agamid* *Phrynocephalus* also has 11 scleral plates (Gugg, 1939), but the pattern of overlap suggests nonhomology.

32. Second epibranchials lost (90-1; C within agamids* and iguanids*).

33. Second ceratobranchials lost (91-1; C in dibamids, anguimorphs, and snakes, within scincids and amphisbaenians).

34. Elongated lingual process of hyoid serves as support for highly protrusible tongue (Boulenger, 1887; Gnanamuthu, 1930).

35. When tongue retracted, first ceratobranchials directed anterodorsally rather than posterodorsally (e.g., Gnanamuthu, 1930, fig. 2).

36. Centra of presacral vertebrae elongate and cylindrical (Camp, 1923; Hoffstetter and Gasc, 1969; Moody, 1980).

37. Except in *Brookesia* (pers. obs.) anterodorsal surfaces of neural arches of thoracic vertebrae flattened and lacking midsagittal crest.

38. Except in *Brookesia* (pers. obs.) neural canal visible between neural arches in dorsal view.

39. Atlantal intercentrum truncated posteriorly, does not extend ventral to axial intercentrum (e.g., Hoffstetter and Gasc, 1969, fig. 44).

40. Dorsal part of atlantal neural arch very narrow (e.g., Hoffstetter and Gasc, 1969, fig. 44).

41. Except in *Brookesia* (pers. obs.) transverse processes of caudal vertebrae oriented ventrolaterally, forming acute angle between them.

42. Number of presacral vertebrae reduced to 23 or fewer (104-1; C within iguanids* and agamids*).

43. Number of cervical vertebrae reduced to 5 (107-1; also reduced in dibamids and within scincids, cordylids, and anguids, but reduction number not necessarily similar).

44. Pairs of rib attachment points on sternum reduced to two (109-3; C in pygopodids, *Dibamus*, the scincid *Feylinia*, *Lanthanotus*, and amphisbaenians).

45. Numerous postxiphisternal inscriptional ribs form continuous chevrons midventrally (110-1; C in dibamids, and within gekkonids, gymnophthalmids, lacertids, cordylids, and scincids).
46. Posteriormost presacral ribs fused to corresponding vertebrae (also in some agamids*; Moody, 1980).
47. Scapular emargination present (111-1; C in gekkonids, and within iguanids*, teiids, scincids, and anguids).
48. Anterior coracoid emargination lost (112-0; R of squamate synapomorphy).
49. Scapula extremely tall and narrow, suprascapular cartilage relatively small (e.g., Skinner, 1959, fig. 19).
50. Epicoracoid cartilages greatly reduced, fail to contact suprascapula or mesoscapula dorsally (114-1; C in lacertids, varanoids, and within iguanids*, agamids*, gekkonids, and amphisbaenians).
51. Clavicles extremely small and lost ontogenetically (Skinner, 1959), fail to articulate with remainder of pectoral girdle while present (115-1; C in dibamids, snakes, and amphisbaenians).
52. Interclavicle lost ontogenetically (118-1; C in pygopodids, dibamids, amphisbaenians, and snakes, and within scincids and anguids). Interclavicle lacking lateral processes also applies but is redundant (119-1; C in gymnophthalmids and *Heloderma*).
53. Ectepicondylar foramen and groove lost (122-1; C in teioids and the amphisbaenian *Bipes*).
54. Olecranon process of ulna relatively short (pers. obs.).
55. Ball and socket intercarpal joint, with ball formed by large central carpal (either distal carpal 1, 2, or 3, or lateral centrale, or some combination of these elements) and socket formed by radiale, ulnare, and pisiform (Romer, 1956; Renous, 1973).
56. Metacarpals relatively short and flat, shorter than proximal phalanges (Romer, 1956; Renous, 1973).
57. Manus modified for grasping with digits 1,2,3 opposing digits 4,5, and extensive proximal articulation between metacarpals 3 and 4 (Renous, 1973); opposing groups of phalanges united by skin.
58. Phalanx lost from digit IV of manus; phalangeal formula 2,3,4,4,3 (Romer, 1956; Renous, 1973). Further reduced to 2,3,3,3,3 in *Brookesia* (pers. obs.). Phalanges are also lost from the manus of certain agamids* (Moody, 1980).
59. Carpal intermedium lost (Renous-Lécuru, 1973; C in iguanids*, gekkotans and *Varanus*, within teiids and scincids).
60. Ventral portion of pelvic girdle tilted backwards resulting in more vertical orientation of girdle as a whole (pers. obs.).
61. Anterior iliac process lost (pers. obs.).
62. Dorsal ends of ilial blades compressed laterally, ilial epiphyses expanded into triangular plates that converge dorsomedially (pers. obs.).
63. Ischial tubercle lost or continuous with hypoischial cartilage (pers. obs.).
64. Pubis reduced (except in *Brookesia*, pers. obs.) not markedly outturned dorsally; acetabulum formed primarily by ilium and ischium (pers. obs.).
65. Prepubic tubercle (pectineal process) displaced anteromedially towards symphysis (pers. obs.).
66. Internal trochanter of femur reduced, not set off as distinct head (pers. obs.).
67. Ball and socket intertarsal (mesotarsal) joint formed by distal tarsal 4 (ball) and astragalocalcaneum (socket); distal tarsal 3 lost or fused to distal tarsal 4 (e.g., Romer, 1956, fig. 190).
68. Pes modified for grasping with digits 1,2 opposing digits 3,4,5, and extensive proximal articulation between metatarsals 2 and 3 (e.g., Romer, 1956, fig. 190); opposing groups of phalanges united by skin.

69. Metatarsals relatively short and flat, shorter than proximal phalanges (e.g., Romer, 1956; fig. 190).

70. One phalanx lost from digits 4 and 5 of pes; phalangeal formula 2,3,4,4,3 (Romer, 1956). Further reduced in *Brookesia* to 2,3,3,3,3 (pers. obs.). Phalanges are also lost from the pedal digits of certain agamids* (Moody, 1980).

71. Free part of tongue not notched (137-0; C in dibamids).

72. Loss of enlarged, conical papillae on the posterior limbs of the tongue (Schwenk, 1988). C within iguanids*.

73. Ulnar nerve of varanid type, does not separate from main brachial trunk until reaching elbow region (142-1; C in teioids and varanoids, and within iguanids* and lacertids).

74. Femoral and inguinal pores lost (144-0; R of squamate synapomorphy; C in anguimorphs and within numerous other groups).

75. Body strongly compressed laterally (Boulenger, 1887); manifested in compression of girdles (pers. obs.).

76. Eyes relatively large and capable of independent movement, covered by a thick granular lid except for small opening for pupil (Boulenger, 1887).

77. M. levator bulbi ventralis lost (Underwood, 1970; Haas, 1973).

78. Nictitating membrane lost (Underwood, 1970).

79. External ear opening and tympanic membrane lost (Wever, 1978). Similar modifications of the ear also present in some agamids* (Smith, 1938).

80. Sphenethmoid commissures lost (Bellairs and Kamal, 1981).

81. Lungs with caecal outgrowths (diverticula) on ventral and caudal margins (Klaver, 1973, 1977, 1981).

82. Carotid duct lost (Underwood, 1957b).

83. Prehensile tail (Boulenger, 1887; C within agamids*; Moody, 1980).

84. Dermal rugosities usually present, sometimes underlying horns or other processes (pers. obs.).

85. Subdigital scales in multiple rows (Etheridge and de Queiroz, 1988).

Comments: Chamaeleontids are a very distinctive group of squamates, and like other distinctive groups, such as amphisbaenians and snakes, they have sometimes been placed in their own higher taxon separate from all other "lizards" (e.g., Boulenger, 1884, 1885). However, in a phylogenetic system it is clear that chamaeleontids are not only squamates but also iguanians and, in particular, acrodontans.

The list of diagnostic chamaeleontid synapomorphies presented above results from only a cursory survey of chamaeleon anatomy, primarily osteology. Although some of these characters are probably correlated with others in the list, the list of chamaeleontid synapomorphies is long, and other diagnostic chamaeleontid synapomorphies undoubtedly exist. Not all of the characters presented above are necessarily synapomorphies of Chamaeleontidae as defined above, because some also occur in some agamids* and some do not occur in all chamaeleons. Nevertheless, all are potential synapomorphies at some level: those characters occurring also in some agamids* are potentially useful for determining relationships of chamaeleons within Acrodonta, and those characters present only in some chamaeleons may be useful for identifying monophyletic groups within Chamaeleontidae. Relationships within Chamaeleontidae have recently been studied by Rieppel (1987) and Klaver and Böhme (1986).

SCLEROGLOSSA, new taxon

Definition: The most recent common ancestor of Gekkota and Autarchoglossa (Scincomorpha, Anguimorpha), and all of its descendants.

Etymology: Greek, scleros, tough, hard; glossa, tongue. Refers to the flattening and keratinization of at least the posterior part of the tongue (character 138-1).

Diagnosis: Scleroglossans differ from all other lepidosaurs, including Iguania, in possessing the following synapomorphies.

1. Descending processes of frontals prominently developed and prefrontals narrowly or not at all in margins of narrow orbitonasal fenestra (9-1; R in teiids and C within iguanids*).
2. Postfrontal semilunate, forked medially, clasping frontoparietal suture (13-1; R in snakes, and within teiids).
3. Postorbital forms less than one-half of the posterior orbital border, and is primarily a temporal bone with a reduced ventral process (17-1; many basic taxa not determinable owing to absence of supratemporal arch).
4. Dorsal process of squamosal lost (34-1; R within teiids and xenosaurs).
5. Vomers extend posteriorly less than half the length of the maxillary tooth row (39-1; R within snakes).
6. Septomaxillae meet on midline in a raised crest (40-1).
7. Dorsal surface of septomaxillae expanded and convex, reflecting large size of Jacobson's organ (41-1).
8. Choanal fossae of palatines relatively prominent in relation to palatine size (44-1).
9. Alar process of prootic elongated and anterodorsally directed (expanded upward and forward) (49-1; ?R in dibamids, C within iguanids*).
10. Adductor musculature attaches only on ventral surface of parietal (54-1; R in teiids, dibamids, *Lanthanotus*, *Varanus*, amphisbaenians, snakes, within gymnophthalmids, xenosaurs, and anguids; C within iguanids*, agamids*, and chamaeleontids).
11. Subdental shelf large (58-1; R in anguimorphs, amphisbaenians, and within gymnophthalmids).
12. No pit on dorsal surface of retroarticular process (74-1; R in lacertoids, C within iguanids*).
13. Posterior border of retroarticular process obliquely twisted (79-1; R in pygopodids and lacertoids).
14. More than 25 presacral vertebrae (105-1; R within gekkonids, gymnophthalmids, lacertids, teiids, and cordylids, C within iguanids*).
15. Not more than four rib attachment points on sternum (109-1; R within lacertids and cordylids, C within agamids* and iguanids*).
16. Clavicles strongly angulated, curving anteriorly, away from scapulocoracoids (116-1; R within xantusiids, scincids, and anguids).
17. Interclavicle cruciform, with large anterior process (120-1; R within xenosaurids and *Varanus*, C within iguanids* and agamids*).
18. Distal tibial epiphysis more or less distinctly notched, fitting onto a ridge on the astragalocalcaneum (123-1).
19. In ventral view, pubis relatively long, symphyseal process narrow and extensive, pubic tubercle relatively proximal in position (124-1; R in *Varanus*; further transformed in Scincomorpha and Anguinae).
20. Epiphyses fuse to diaphyses prior to fusion of braincase elements (130-1).
21. Anterior head of m. pseudotemporalis profundus present (133-1; R in gekkonids and snakes).
22. Foretongue flattened and tongue keratinized at least posteriorly (138-1).
23. Prey prehension exclusively mediated by jaws rather than tongue (Schwenk, 1988).
24. Glandular epithelium of foretongue lost (Schwenk, 1988). R in scincoids.

25. Oscillatory chemosensory tongue protrusion (Schwenk, 1988; R in gekkonids, condition not known for xantusiids, xenosaurs, and dibamids). This character also occurs in snakes and amphisbaenians. It is an equal number of steps for this character to be a synapomorphy of Autarchoglossa that is convergent in pygopodids.

26. Modified mid-dorsal scale row lost (146-1).

27. Cephalic scales enlarged (147-1; R in varanoids, and within snakes, gekkonids, and anguids).

Comments: Since Camp (1923), "lizards" have often been divided into two main groups, Ascalabota and Autarchoglossa. Camp (1923) chose Wagler's (1830) term Autarchoglossa for all lizards except iguanians and gekkonids (Camp placed pygopodids with anguimorphs), and he placed Gekkonidae with the Iguania in the taxon Ascalabota. Camp's "skiogram," which appears here as Fig. 7, makes it clear that his ideas regarding phylogenetic relationships of squamates did not differ from our own so far as the position of Gekkonidae is concerned, i. e., that the latter (and pygopodids, as subsequent work has shown) form the sister group of all other non-iguanian squamates (including snakes and amphisbaenians), even if his taxonomy did not reflect this (Camp himself, 1923:336, noted that "the agreement between classification and phylogeny is seldom exact and allowances must be made for artificiality on both sides.").

Our analysis supports that of McDowell and Bogert (1954), as well as the more recent studies by Kluge (1974, 1976a,b; 1987), that ally pygopodids with gekkonids, rather than with anguimorphs as Cope (1900) and Camp (1923) suggested. Sukhanov (1962, 1976) presented data that supported a relationship of gekkotans and scincomorphs based on locomotor adaptations, but because he did not include anguimorphs in his study the phylogenetic relationships of gekkotans were not resolved. His study is important, however, in emphasizing a closer relationship between gekkotans and scincomorphs than between gekkotans and iguanians. More recently, placement of Gekkota (gekkonids and pygopodids) as the sister group of autarchoglossans (Gauthier, 1982, 1984; Estes, 1983a) has been advocated. Aside from accepting the transfer of Pygopodidae to Gekkota, we retain Autarchoglossa as it was constituted by Camp (1923), and here name a new taxon, Scleroglossa, to include the two sister groups Gekkota and Autarchoglossa, with snakes, amphisbaenians, and dibamids placed as *Scleroglossa incertae sedis*. Recognition of Scleroglossa, with consequent abandonment of Camp's (1923) paraphyletic taxon Ascalabota, makes squamate taxonomy congruent with Camp's "skiogram" (represented in our cladogram of Fig. 7; see also discussion at beginning of this section).

We are not certain if character 133 (anterior head of *m. pseudotemporalis profundus* present) is a synapomorphy at this level. Rieppel (in litt., 1985) suggested that loss of the muscle in gekkonids could be one manifestation of pedomorphosis in this group. Given the apparent wide distribution of the muscle within pygopodids, we have provisionally placed it as a scleroglossan rather than an autarchoglossan synapomorphy.

GEKKOTA Cuvier, 1817

Definition: The most recent common ancestor of Gekkonidae and Pygopodidae, and all of its descendants.

Diagnosis: The following are potential synapomorphies of gekkotans.

1. Ontogenetic fusion of frontals (6-1; C in iguanians, gymnophthalmids, teiids, and xenosaurs, within many other basic taxa).

2. Descending processes of frontals in contact below olfactory tract (10-1; C in *Heloderma*, *Varanus*, amphisbaenians, and snakes, within gymnophthalmids, xantusiids, and anguids).

3. Absence of postorbital (16-1) and supratemporal arch (Romer, 1956). C in dibamids, *Heloderma*, *Lanthanotus*, within scincids and amphisbaenians.

4. Parietal foramen lost (26-1; C within many other basic taxa).
5. Lacrimal lost (28-1; possibly present in some eublepharines; Rieppel, 1984b; C in xantusiids, snakes, within many other basic taxa).
6. Jugal reduced or lost, postorbital bar incomplete (32-1; C in dibamids, *Varanus*, and snakes, within anguids, scincids, amphisbaenians).
7. Epipterygoid abuts directly against ventral surface of alar process of prootic rather than lying lateral (other Scleroglossa) or anterior (Iguania) to it (Bellairs and Kamal, 1981).
8. Crista prootica extends forward onto basiptyergoid process, forming bony canal for the lateral head vein (52-1; C in xantusiids, within gymnophthalmids, R? in some gekkonids. Extension without full enclosure occurs in some teiids, lacertids, and scincids).
9. Bipartite occipital condyle present, owing to projection of exoccipitals posterior to basioccipital (Rieppel, 1984b).
10. Quadrate articulates loosely with facet on paroccipital process of opisthotic ("paroccipital abutting" of Rieppel, 1984A), owing to absence of supratemporal in most forms.
11. Processus ascendens tecti synotici lost (Bellairs and Kamal, 1981). C in snakes.
12. Anterior shelf of maxilla separates premaxilla and vomer (Rieppel, 1984b; R within pygopodids).
13. Meckel's canal in closed and fused dentary tube (55-2; C in dibamids and xantusiids, within iguanids*, gymnophthalmids, scincids, and amphisbaenians).
14. Splenial does not extend anteriorly beyond tooth row midpoint or lost (65-1; in and within many squamate taxa).
15. Retroarticular process inflected medially (75-1; C in scincoids, anguids, varanoids, ?within snakes).
16. Retroarticular process offset medially with lateral notch forming a waist proximally (77-1; unique).
17. Retroarticular process broadened posteriorly (78-1; C in scincids, dibamids, cordylids, and anguids, R within cordylids).
18. Pterygoid teeth lost (83-1; C in many other basic taxa).
19. Paired, dentinal egg-teeth present (Kluge, 1987). Unique.
20. Large, wing-like hyoid cornu present (Kluge, 1987). Unique.
21. Persistent notochordal canal in adults, regardless of whether amphicoely or procoely prevails (Holder, 1960).
22. Autotomy septa in caudal vertebrae located posterior to a single pair of transverse processes (102-1; C within iguanids*).
23. Postcloacal bones present (125-1; R within gekkonids).
24. Carpal intermedium lost (Renous-Lécuru, 1973; C in iguanids*, chamaeleontids, and *Varanus*, within teiids and scincids).
25. *M. extracolumellaris* present (135-1; unique).
26. Ciliary restraint system for hair cells with combined tectorial and sallet system (140-1; C in lacertids and teiids).
27. Spindle body present on tectorial membrane (Wever, 1978; unique).
28. Elongated cochlear duct and basilar membrane (Wever, 1978; unique).
29. Medial aperture of recessus scalae tympani divided into two foramina (Rieppel, 1984).
30. Meatal closure muscle present and well-developed (Wever, 1978; R within gekkonids).
31. Internal (quadrate) process of stapes lost (141-1; gekkotans, gymnophthalmids, scincids, anguids, within xantusiids).
32. Stapedial artery passes anterior to stapes (145-0; R of squamate synapomorphy; C in snakes; may perforate stapes in some taxa, so that 145-1 may be plesiomorphic for gekkotans).

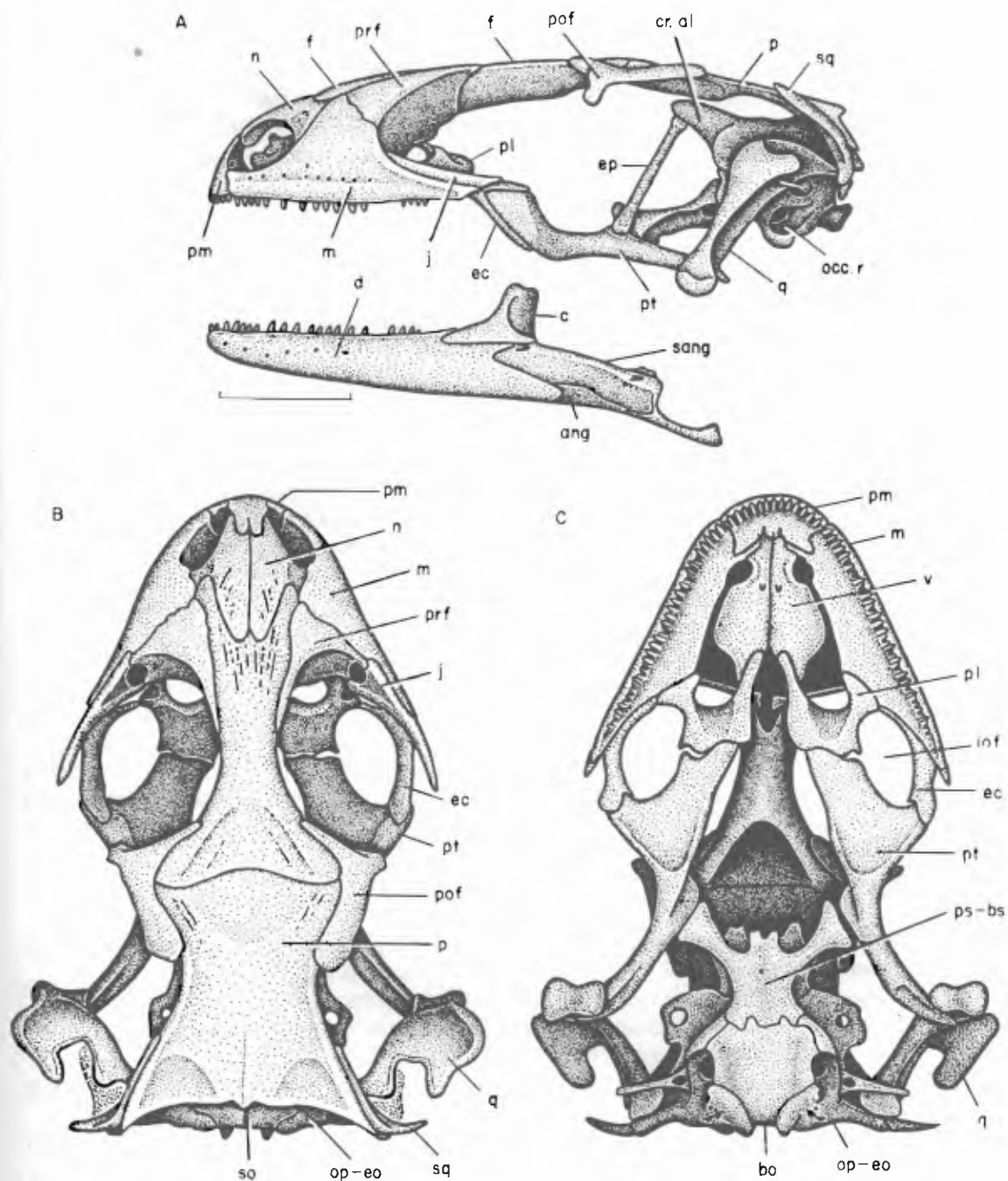


FIGURE 19. Skull and mandible of *Hemitheconyx caudicinctus* (Gekkonidae) in left lateral, dorsal, and ventral views. Scale = 5 mm. From Rieppel (1984b). See end of paper for abbreviations.

33. Cochlear limbus extremely large (Wever, 1978; unique).
34. Facial tongue-wiping behavior present (Moffat, 1973). C in xantusiids (Greer, 1985b).
35. Sublingual glands diffusely scattered across floor of mouth (Schwenk, 1988). Unique.
36. Very thin, flat foretongue, with broad and untapered tip (Schwenk, 1988, believes this may be correlated with facial tongue-wiping; C in xantusiids).
37. Short, flat-topped peg-like papillae of foretongue (Schwenk, 1988; C in xantusiids).
38. Multiple longitudinal bundles of hyoglossus muscle (Schwenk, 1988). Unique.
39. Double visual cells in straight horizontal rows with alternation of orientation of the members along the row (Underwood, in litt., 1985).
40. Periventricular tectal laminae present in the brain (Northcutt, 1978).
41. *M. levator anguli oris* poorly defined (Rieppel, 1984b).
42. *M. pseudotemporalis superficialis* lost (Rieppel, 1984b).
43. Bodenaponeurosis forms tendinous gutter on coronoid bone (Rieppel, 1984b). Unique.
44. *M. adductor mandibulae posterior* poorly defined or lost (Rieppel, 1984b).
45. Graded series of acrocentric chromosomes without distinct break between macro- and microchromosomes (Pauli, et al., 1976).
46. Clutch size reduced; modally two eggs or less (Fitch, 1970; occasionally four eggs present).

Comments: Rieppel (1984b) and Kluge (1987) have provided recent summaries of gekkotans. Kluge's arrangement within Gekkota differs from ours in that he recognized eublepharines as a separate taxon from Gekkonioidea (the latter containing gekkonids and pygopodids). His only synapomorphy for eublepharine monophyly is procoely, because he accepts amphicoely as the plesiomorphic gekkotan condition, contrary to our results. Grismer (1988) has discussed additional evidence that supports eublepharine monophyly; his paper should be referred to for discussion of this problem, which is beyond the scope of our study.

Kluge (1987) also expanded the Pygopodidae to include the diplodactylines (formerly gekkonids), because of an hypothesized sister group relationship between Pygopodidae of other authors and diplodactylines. Kluge gave a single synapomorphy for a clade including diplodactyline geckos and pygopodids, the O-shaped meatal closure muscle, but the characters at his node III support his hypothesis. The evidence for pygopodid-diplodactyline relationships, however, is contradicted by other characters, and for this reason we retain for the present the traditional arrangement that has eublepharines and diplodactylines as parts of Gekkonidae, and pygopodids as a separate taxon (for further discussion see comments on Gekkonidae and Pygopodidae).

GEKKONIDAE Gray, 1825

Definition: The most recent common ancestor of eublepharines, diplodactylines, gekkonines, and sphaerodactylines (sensu Kluge, 1967) and all of its descendants.

Diagnosis: The following characters are potential synapomorphies of this taxon (Fig. 19).

1. Contact between pterygoids and palatines, and between palatines and vomers, reduced (Rieppel, 1984b; character may not be uniformly developed in taxon).
2. Trigeminal notch enclosed anteriorly by bone to form a foramen (pers. obs.; reversed in some taxa, e. g. *Gekko gekko*).
3. Anteromesial processes of maxillae extending between premaxilla and vomer, occasionally separating these bones (Rieppel, 1984b; C in Acrodonta).
4. Quadrate broad, flaring (Rieppel, 1984b).
5. Crista alaris of prootic extended ventrolaterally into crista prootica to form a three-crested process (pers. obs.).
6. Type C double cells present in retina (Underwood, 1957b).

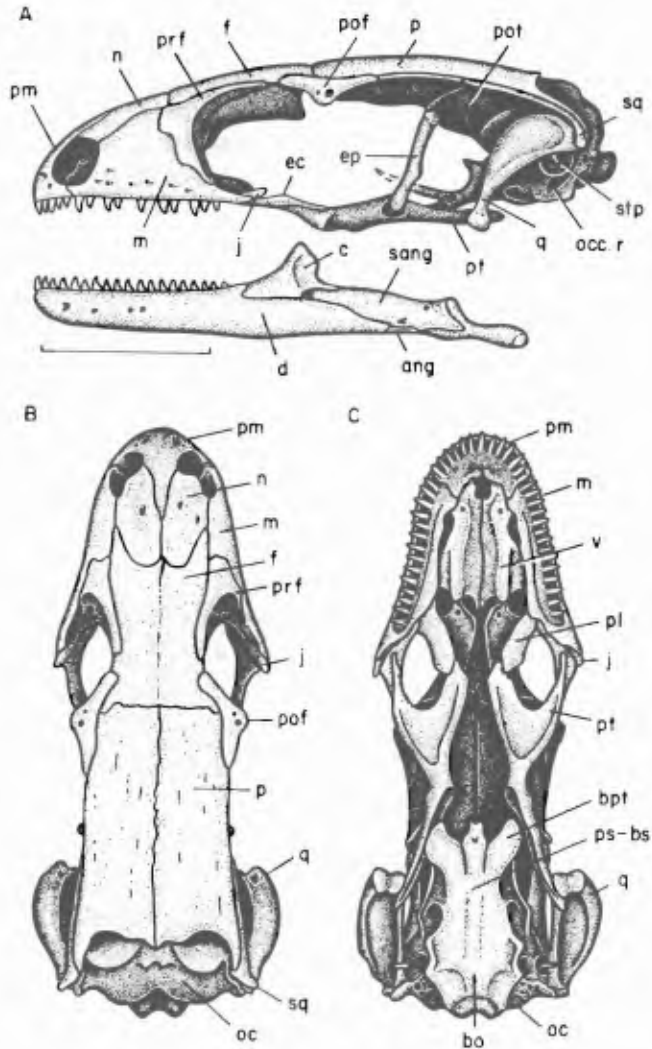


FIGURE 20. Skull and mandible of *Pygopus lepidopus* (Pygopodidae) in left lateral, dorsal, and ventral views. Scale = 5 mm. From Rieppel (1984b). See end of paper for abbreviations.

- 7. Quadrate aponeurosis of m. adductor mandibulae posterior lost (Rieppel, 1984b).
- 8. Single ventral scleral ossicle reduced at orbital margin (Underwood, 1970).
- 9. Posterior trunk intercentra present (99-0; R of squamate synapomorphy).
- 10. Scapular emargination present (111-1; C in chamaeleontids, within iguanids*, scincids, teiids, and anguids).
- 11. Cephalic scales relatively small (147-0; R of scleroglossan synapomorphy).

Comments: Kluge (1987) has given the most recent summary of this taxon. If his hypothesis that pygopodids are nested within what we call gekkonids is accepted, changes in the level at which some of the above characters exist as synapomorphies will need to be made (see comments on Pygopodidae below). Given the rather extensive character conflict, it is possible that Gekkonidae should be considered a metataxon. We provisionally accept Gekkonidae as monophyletic because we have been able to find more derived characters supporting gekkonid monophyly than those sup-

porting a sister-group relationship between pygopodids and some gekkonids. This is an area requiring further study.

PYGOPODIDAE Gray, 1845

Definition: The most recent common ancestor of extant pygopodids (see Kluge, 1974) and all of its descendants.

Diagnosis: The following synapomorphies identified in this study apply to this taxon (Fig. 20).

1. Supratemporal lost (35-1; C in dibamids, amphisbaenians; within agamids*, gekkonids, anguids, and snakes).
2. Vomer fused (38-1; C in chamaeleontids, xantusiids, within gekkonids, gymnophthalmids, and scincids).
3. Retroarticular process not twisted posteriorly (79-0; R of scleroglossan synapomorphy; C in lacertoids).
4. Harder's gland discharges directly into lacrimal duct (Underwood, 1957b).
5. Lacrimal duct does not open into choanal groove (Underwood, 1957b).
6. More than twenty-six presacral vertebrae (106-1; up to 100 or more vertebrae, according to Kluge, 1987; C within many basic taxa).
7. Two or fewer rib attachment points on sternum (109-3; C in chamaeleontids, *Lanthanotus*, and amphisbaenians, within iguanids*, gymnophthalmids, scincids).
8. Interclavicle lost (118-1; C in chamaeleontids, dibamids, amphisbaenians, and snakes, within anguids and scincids).
9. Serpentine habitus, forelimb remnants (if present) not protruding beyond body surface; hind limbs paddle-like or reduced to a single scale area (Kluge, 1974).
10. Ribs with long muscular processes near the rib head (Romer, 1956).
11. Uniformly two eggs per clutch (Kluge, 1987; C within gekkonids).
12. Ocular spectacle present (Kluge, 1974). C in xantusiids, within gekkonids, and numerous other scleroglossans.

Comments: Boulenger (1885) placed this taxon with the gekkonids, but Camp (1923) placed it in the Anguimorpha. Studies by McDowell and Bogert (1954), Underwood (1957b), and Kluge (1974; 1976a,b; 1987) have agreed with Boulenger's assessment, and our study also supports these results. Kluge (1987) presented a case for placing pygopods as the sister group of diplodactyline gekkonids. A number of our characters support nesting of pygopodids within gekkonids (characters 35-1, 38-1, 145-0; possibly also 21-0, 45-1, 65-2; in addition, clutch with two eggs, and presence of spectacle). We have treated the two taxa as separate because there are other characters in which pygopodids appear to retain a primitive condition not seen in gekkonids (see diagnosis and comments for Gekkonidae), and there is thus no compelling reason to change the traditional arrangement. If Kluge's conclusion is accepted, Gekkonidae as we have defined it here is a synonym of Gekkota, and Gekkonidae excluding Pygopodidae is paraphyletic. This is a problem requiring further study.

AUTARCHOGLOSSA Wagler, 1830

Definition: The most recent common ancestor of Scincomorpha and Anguimorpha, and all of its descendants.

Diagnosis: Autarchoglossans differ from other squamates in having the following synapomorphies.

1. Loss of jugal-squamosal contact on supratemporal arch (1801; R in teiids, scincids, and xenosaurids). This character cannot be determined in snakes, amphisbaenians, and dibamids.

2. Dermal rugosities present (129-1; C within iguanids*, agamids*, chamaeleontids, anguids, and *Varanus*). This character is of doubtful significance and may not apply here.

3. *M. rectus abdominis lateralis* present (134-1). This character also occurs in snakes, dibamids, and amphisbaenians, and may be a synapomorphy of a more inclusive group.

Comments: Autarchoglossa here is as Camp (1923) originally constituted it, except that pygopodids are removed. The basic taxa, however, have been arranged in a somewhat different way. Included here are Scincomorpha and Anguimorpha. Dibamidae, Amphisbaenia, and Serpentes may also be autarchoglossans, or at least they may be closer to the latter than are gekkotans (see comments on the former three taxa). Autarchoglossa, long regarded as a well-supported taxon, can be diagnosed by only a few characters. Note that one of these (2) is of doubtful significance, and that another (1) cannot be determined in snakes, dibamids, and amphisbaenians. The third character, presence of a *m. rectus abdominis lateralis*, may diagnose Autarchoglossa, but only if snakes, dibamids, and amphisbaenians are imbedded within that group. If they are not, then this character may apply to a more inclusive group.

SCINCOMORPHA Camp, 1923

Definition: The most recent common ancestor of Scincidae, Cordylidae, Xantusiidae, Lacertidae, Teiidae, and Gymnophthalmidae, and all of its descendants.

Diagnosis: This taxon is diagnosed by presence of the following synapomorphies.

1. Nasal-prefrontal contact lost, the two bones separated by anterolateral processes of the frontals, the latter contacting the maxillae (4-1; R within teiids, gymnophthalmids, scincids, cordylids, C within gekkonids, pygopodids, and anguids).

2. Pointed ventral downgrowths of the parietal extend to (or just medial to) the epipterygoids (23-1; R in lacertids, within scincids).

3. Lateral process of coronoid overlapped anteriorly by dentary so that lateral exposure of process is limited to a narrow wedge between dentary and surangular (71-1; R in lacertids, teiids, gymnophthalmids, within scincids, C within anguids). It is an equal number of steps for this character to be interpreted as separate synapomorphies of Scincoidea and Xantusiidae.

4. In ventral view, pubis relatively long, symphyseal process extremely elongated and anteriorly directed (124-2; R in teiids, C in anguids).

5. Vermiculate dermal rugosities present (129-2; R within teiids, xantusiids, gymnophthalmids, and scincids, C within iguanids*, xenosaurids, and amphisbaenians).

6. Anterior tongue mushroom-shaped in cross section, entire foretongue keratinized and non-glandular (138-2; R within cordylids, C in amphisbaenians).

7. Flattened, imbricate, lingual scales present (Schwenk, 1988). R in xantusiids. C in amphisbaenians.

8. Ciliary restraint system for hair cells includes a combined tectorial and sallet system (140-2; R in lacertiforms). It is an equal number of steps for 140-1 to be a scincomorphan synapomorphy with C in gekkotans, further transformed to 2 in scincoids and xantusiids).

9. Bodenaponeurosis with tapering posterior expansion that extends toward the post-temporal fossa within the 3b head of the *m. adductor mandibulae externus profundus* (Rieppel, 1980c).

Comments: Except for the cordylid cordylids, which Camp (1923) placed in Anguimorpha, all of the taxa included here in Scincomorpha were also included in Camp's taxon of the same name. In addition, Camp included Amphisbaenia and Dibamidae in his Scincomorpha. Our analysis does not preclude the possibility that the latter two taxa are scincomorphs, but we consider their relationships uncertain.

Although the content of our Scincomorpha is similar to that of Camp (1923), our diagnosis is considerably different. Most of the derived characters or trends cited for this group by Estes (1983a) have been assigned to more or less inclusive taxa by the present study.

Presch (1988) discussed the phylogenetic relationships of Scincomorpha. His results differ from ours in some respects, and he gave some reasons why our hypotheses differ. He placed Scincidae and Xantusiidae as sister groups, with cordylids, lacertids, and the teiid/gymnophthalmid clade successively as sister groups. Only one of the five characters he gave in support of scincomorph monophyly also appears in our diagnosis of this group (tapering of the posterior expansion of the quadrate bodenaponeurosis). We place three of the remaining four as synapomorphies at different levels (133-1, anterior head of the m. pseudotemporalis profundus; 96-0, presence of zygosphenes and zygantra, our original polarity being reversed by our study, and 6-1, fused frontals), and consider his fifth character, autotomy septa anterior to transverse process, to be plesiomorphic for squamates.

Although xantusiids possess a seemingly plesiomorphic tongue morphology, we consider the presence of imbricate scales on the foretongue to be a scincomorph synapomorphy. This implies reversal in the tongue of xantusiids (perhaps by paedomorphosis), but it is equally simple to interpret the xantusiid condition as plesiomorphic for scincomorphs, with convergence in Lacertiformes and Scincoidea.

LACERTOIDEA Camp, 1923

Definition: The most recent common ancestor of Xantusiidae, Lacertidae, Teiidae, and Gymnophthalmidae and all of its descendants.

Diagnosis: The following synapomorphies unite the members of this taxon.

1. Parietal tabs present as thin, triangular structures that extend anteriorly into shallow triangular fossae on the ventral surface of the frontals (22-1; C in dibamids, and within iguanids*, agamids*, chamaeleontids, cordylids, and scincids).

2. Prearticular crest present (73-1; further transformed in gymnophthalmids and teiids).

3. Pit or sulcus present on dorsal surface of retroarticular process (74-0; R of scleroglossan synapomorphy, C within iguanids*).

4. Retroarticular process posterior border not twisted obliquely (79-0; R of scleroglossan synapomorphy, C in pygopodids).

5. M. adductor mandibulae posterior extends well into Meckel's canal (131-1; C within agamids*).

6. Origin of m. pseudotemporalis superficialis extended posteriorly (132-1; C in *Varanus*).

7. Posterior (hind) tongue plicate (139-1; C in dibamids (?) and within cordylids and lacertids, further transformed in both the latter).

Comments: Camp (1923) placed teiids (including gymnophthalmids), lacertids, and gerrhosaurs in this taxon; we remove the latter and add xantusiids.

XANTUSIIDAE Baird, 1859

Definition: The most recent common ancestor of the extant genera *Cricosaura*, *Klauberina*, *Lepidophyma*, and *Xantusia* (sensu Savage, 1963) and all of its descendants.

Diagnosis: The following synapomorphies characterize this taxon (Fig. 21).

1. Postfrontal lost (12-1; C in acrodontans, lacertids?, within iguanids*, dibamids, amphisbaenians, and snakes).

2. Supratemporal fenestra closed primarily by postorbital (19-1; C in cordylids, within gymnophthalmids and anguids).

3. Parietals paired well into postembryonic ontogeny (21-0; R of squamate synapomorphy, fused in *Cricosaura* and adult *Klauberina*; C within Gekkota).

4. Parietal table extensive posteriorly, largely obscuring braincase in dorsal view, supratem-

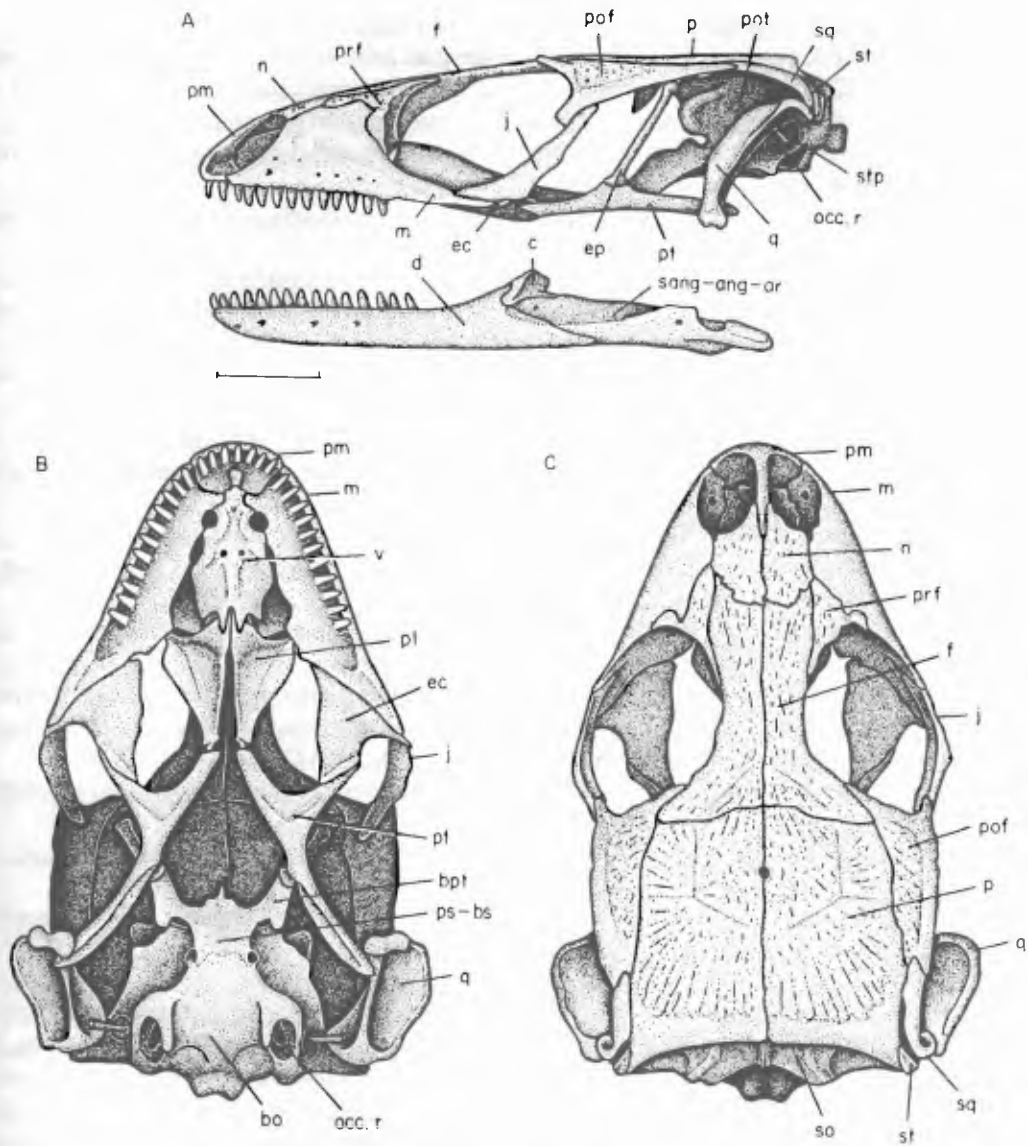


FIGURE 21. Skull and mandible of *Xantusia henshawi* (Xantusiidae) in left lateral, dorsal, and ventral views. Scale = 5 mm. From Rieppel (1984b). See end of paper for abbreviations.

poral processes short (24-0; apparent R of squamate synapomorphy, but derived by posterior growth of skull table).

5. Maxillae extend posteriorly only just beyond anterior edge of orbits (27-1; C in varanoids and dibamids).

6. Vomers fused (38-1; C in chamaeleontids and pygopodids, within gekkonids, gymnophthalmids, and scincids).

7. Ectopterygoid contacts palatine anterolaterally, excluding maxilla from suborbital fenestra (45-1; C in teiids, dibamids, varanoids, within anguids, pygopodids, gekkonids, and amphisbaenians).

8. Ectopterygoid enlarged medially, restricting suborbital fenestra (46-1; C in teiids).
9. Crista prootica extends forward onto basiptyergoid process, forming bony canal for lateral head vein (52-1; C in pygopodids, within gekkonids and gymnophthalmids, anterior extension of crista prootica without complete enclosure of vein may occur within other lacertoid taxa).
10. Dentary tube closed and fused (55-2; C in gekkonoids, dibamids, within iguanids*, gymnophthalmids, scincids, and amphisbaenians).
11. Lateral coronoid process of dentary large (60-1; C in cordylids, dibamids, within scincids, xenosaurs, anguids, and amphisbaenians).
12. Splenial tiny, not extending as far forward as tooth row midpoint (65-1; may fuse to dentary; C in *Heloderma* and snakes, within iguanids*, agamids, gekkonids, pygopodids, gymnophthalmids, scincids, anguids, amphisbaenians).
13. Splenial does not extend posterior to apex of coronoid (66-1; C in agamids*, *Heloderma*, *Varanus*, and amphisbaenians, and within iguanids*, gymnophthalmids).
14. No coronoid lateral process as a lappet on dentary (68-0; R of squamate synapomorphy, C in agamids*, chamaeleontids, dibamids, and *Lanthanotus*, within iguanids*, *Varanus*, and amphisbaenians).
15. Dentary overlap of coronoid lateral process and restriction by surangular so that lateral exposure of process is limited to a narrow wedge between dentary and surangular (71-1; C in cordylids, within scincids and anguids).
16. Pterygoid teeth lost (83-1; C in gekkotans, acrodontans, dibamids, amphisbaenians, *Varanus*, within many basic taxa).
17. Ciliary restraint system for hair cells by inertial bodies (sallet or culmen) (140-2; convergent in scincoids).
18. Facial tongue-wiping behavior present (Greer, 1985b). C in Gekkota.
19. Short, flat-topped, peglike papillae present on foretongue (Schwenk, 1988). C in gekkotans.
20. Foretongue significantly wider than bundles of m. hyoglossus (Schwenk, 1988). C in scincoids.
21. Thin, flat foretongue that is particularly broad and untapered (Schwenk, 1988). C in gekkotans.
22. Unique, circular, depressed scale organs (Peterson and Bezy, 1985).

Comments: Xantusiids have often been placed with scincomorphs (e. g. Camp, 1923; Romer, 1956; Moffat, 1973; Estes, 1983a), but other studies have suggested gekkotan affinities (e. g. McDowell and Bogert, 1954; Savage, 1963; Northcutt, 1978). Presence of supposed postcloacal bones in the taxon has certainly played a part in generating suggestions of gekkotan affinity, but Kluge (1982) interpreted these structures in the two taxa as not homologous; in any case they are present only in some xantusiids. Peterson and Bezy (1985:520), in their study of scale microstructure, noted that xantusiids lack "derived characters found in the Gekkonidae." Estes (1983a) summarized evidence that supported scincomorph relationship of xantusiids, and placed them as the sister group of scincids and cordylids, but we find (as did Gauthier, 1984) that xantusiids share a greater number of derived characters with lacertids, teiids, and gymnophthalmids. Many of the xantusiid synapomorphies cited by Estes (1983a) are placed in this study at more or less inclusive levels.

LACERTIFORMES, new taxon

Definition: The most recent common ancestor of lacertids, teiids, and gymnophthalmids and all of its descendants.

Etymology: Latin, lacerta, lizard, referring here specifically to lacertids; forma, shape.

Diagnosis: Monophyly of this taxon is supported by the following synapomorphies.

1. Pterygoid lappet of quadrate present (37-0; R of squamate synapomorphy, C in *Heloderma*, within iguanids*).
2. Pyriform recess narrow throughout most of its length (48-0; R of squamate synapomorphy, R again within lacertids, gymnophthalmids, C in snakes, within iguanids* and agamids*).
3. Coronoid lateral process present or lost, not overlapped by dentary anteriorly (71-0; R of scincomorph synapomorphy, also R within scincids). May also be interpreted as a retained primitive feature, see Character Analysis).
4. Adductor fossa expanded, inflated, widely open (81-1; C within scincids).
5. Step or offset in maxillary tooth margin present (87-1; C within iguanids*).
6. Frontoparietal suture more or less strongly interdigitating between prominent parietal tabs (Gauthier, 1984).
7. Heterodont dentition including unicuspid and at least some bicuspid teeth (Gauthier, 1984).
8. Facial region elongated and snout region laterally compressed (Estes, 1964, 1983a; Gauthier, 1984).
9. Strong development of zygosphenes and zygantra (95-1; R within gymnophthalmids, C in snakes, within iguanids* and cordylids). Character 96-0 is also a reversal at this node, but because presence of zygosphenes is subsumed in character 95 inclusion here would be redundant.
10. Two pairs of diverging transverse processes in some caudal vertebrae (includes presumed transformations of this pattern via loss of one pair of transverse processes) (100-1; C within iguanids*, xantusiids, and cordylids).
11. Sternal fontanelle present (121-1; R within lacertids, C within iguanids*, agamids*, chamaeleontids, gekkonids, xantusiids, scincids, and *Varanus*).
12. Notching of free part of tongue between 20-40% (137-3; further transformed in teiids and gymnophthalmids, C in varanoids).
13. Ulnar nerve in deep (varanid) position (142-1; R within lacertids, C in chamaeleontids and varanoids, within iguanids*).
14. Well differentiated posterior section of the hemipenial m. transversus perinei present (Arnold, 1984).
15. In spinal cord, nucleus reticularis ventrolateralis of reticulospinal system present (Cruce and Newman, 1984; C in dibamids and snakes, possibly present in scincids and varanids). If the RVL is found to occur in cordylids this character may be a scincomorph synapomorphy lost in xantusiids.

Comments: This clade is supported by many characters, and appears to be one of the most stable within squamates. It has consistently been identified as monophyletic by all of the many computer runs made throughout the course of this study. Recognition of the relationship between lacertids and teiids (including gymnophthalmids) was also accepted by Camp (1923) and has been supported by many other authors.

LACERTIDAE Gray, 1825

Definition: The most recent common ancestor of extant taxa currently assigned to Lacertidae (e. g. Romer, 1956) and all of its descendants.

Diagnosis: We have identified the following lacertid synapomorphies (Fig. 22).

1. Supratemporal fenestra closed primarily by postfrontal (20-1; C in scincids).
2. Loss of parietal downgrowths (23-0; R of scincomorph synapomorphy, C within scincids).
3. Parietal table extended posteriorly and supratemporal processes short (24-0; R of squamate synapomorphy, C in xantusiids, within chamaeleontida, cordylids, and xenosaurids).

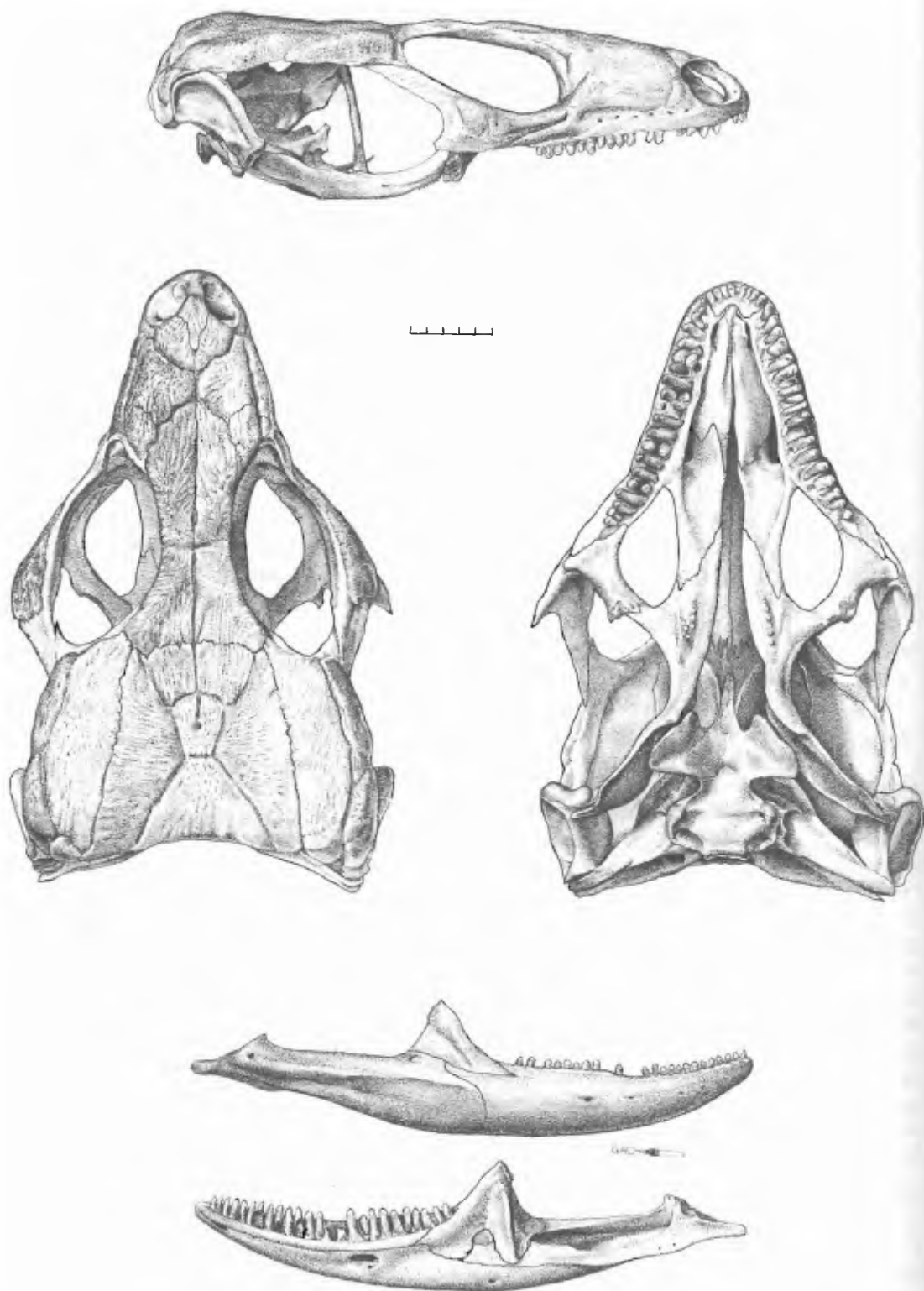


FIGURE 22. Skull and mandible of *Lacerta lepida* (REE 2270; Lacertidae). Skull in left lateral, dorsal, and ventral views; mandible in medial and lateral views. Scale = 5 mm. See end of paper for abbreviations.

4. Palpebral ossifications present (36-1; C in scincoids, anguimorphs).
5. Posterior opening of vidian canal at basisphenoid-prootic suture (53-1; C in anguids, *Heloderma*, and *Lanthanotus*, within xantusiids and scincoids).
6. Epicoracoid cartilage fails to contact either suprascapula or mesoscapula (114-1; C in chamaeleontids and varanoids, within iguanids*, agamids*, gekkonids, and amphisbaenians).
7. Cephalic osteoderms present (128-1; C in scincoids and anguimorphs, within iguanids*).
8. Entire tongue plicate (139-2; C within cordylids).
9. Laryngochoyoid ligament gives off two small, dense dorsolateral branches that extend independently into the loose connective tissue ventral to the laryngeal cartilage (Schwenk, 1988). C in scincoids.
10. Quadrate aponeurosis with parasagittal vertical sheet connecting to temporal fascia (Rieppel, 1980c).

Comments: Lacertid-teiid affinity has long been suggested (e.g., Camp, 1923), but absence of a comprehensive systematic treatment of the lacertids has hampered development of unambiguous evidence for this relationship. Studies by Arnold (1973, 1984) are beginning to provide better understanding of the interrelationships of lacertids.

TEIIOIDEA, new taxon

Definition: The most recent common ancestor of gymnophthalmids and teiids and all of its descendants.

Etymology: Greek, eides, like, referring to teiid-like groups.

Diagnosis: Monophyly of this taxon is supported by the following synapomorphies.

1. Prearticular crest prominent, with angular process imbedded in it (73-2).
2. Prominent surangular fossa extends ventrally to angular (Gauthier, 1984).
3. Jacobson's organ relatively large (MacLean, 1974).
4. Cervical intercentra sutured to anterior part of following centrum (98-1; C in agamids*, within xantusiids, lacertids, and cordylids).
5. Posterior coracoid emargination present (113-1; C within iguanids*, agamids*, gekkonids, and *Lanthanotus*).
6. Ectepicondylar foramen and groove lost (122-1; C in chamaeleontids, the amphisbaenian *Bipes*).
7. Free part of tongue notched 40-50% (137-4; C in amphisbaenians).
8. Infralingual plicae present on the tongue (Harris, 1985).
9. Lingual scales of tongue extremely flattened, arranged in regular diagonal rows (Schwenk, 1988). C in amphisbaenians.
10. Hypohyals large relative to those of other squamates (MacLean, 1974; C in amphisbaenians).
11. Separate lingual segment (process) of basihyal (Harris, 1985; = entoglossal process of Schwenk, 1988).
12. Bodenaponeurosis lacks lateral septum and is divided caudally into two lobes. Rieppel (1980c) stated that this character also is characteristic of lacertids, but E. N. Arnold (in litt., 1985) indicates that most lacertid species do have the lateral septum, and that Rieppel's sample unfortunately included the few that lack it; therefore, this character is either a teioid synapomorphy that is C in some lacertids, or it is a lacertiform synapomorphy reversed in some lacertids.
13. Dorsal leg muscles innervated by interosseous nerve (143-1; C in acrodontans and *Heloderma*).
14. Dracomorph brain present (Northcutt, 1978). C in iguanians and *Varanus*.

Comments: The close relationship of these two taxa has long been recognized (but see Presch, 1983), and they have usually been included in a single family Teiidae. More recently, Estes

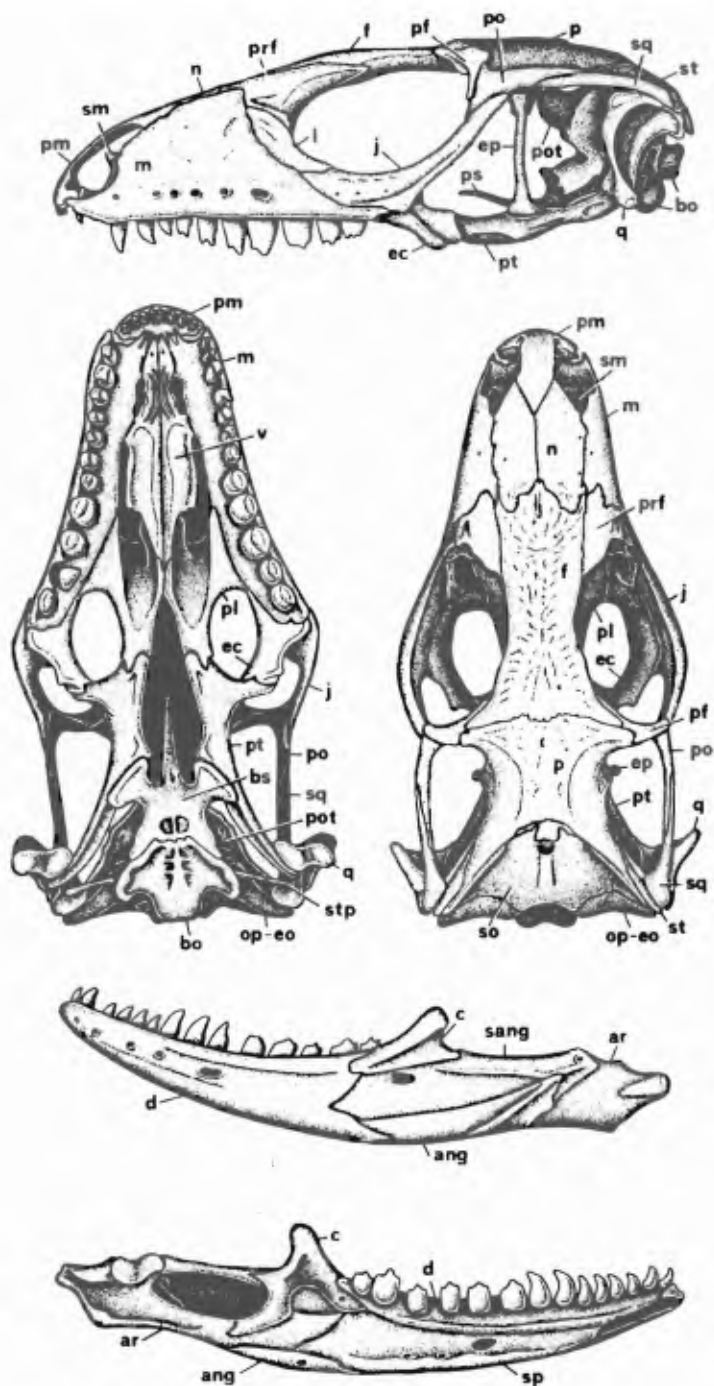


FIGURE 23. Skull and mandible of *Tupinambis nigropunctatus* (Teiidae). Skull in left lateral, dorsal, and ventral views; mandible in lateral and medial views. Scale = 5 mm. From Rieppel (1980c). See end of paper for abbreviations.

(1983a) and Presch (1983) independently separated gymnophthalmids ("microteiids") from other teiids ("macroteiids") at the family level, a separation previously recognized at the subfamily level by MacLean (1974). Harris (1985) stated that the evidence does not yet support monophyly for the "microteiids". The present study, however, has identified characters that support both the relationship of the two taxa as well as characters that support the monophyly of each of them.

TEIIDAE Gray, 1827

Definition: The most recent common ancestor of the Teiinae and Tupinambinae (see Estes, 1983a), and all organisms sharing a more recent common ancestor with these taxa than with any other extant organisms.

Diagnosis: We have identified the following synapomorphies for this taxon (Fig. 23).

1. Frontals fuse in embryonic or early postembryonic ontogeny (6-1; C in *Iguania*, *Gekkota*, within many other groups). Extant gymnophthalmids also have fused frontals. Extinct polyglyphanodontine teiids may have either paired or fused frontals. We tentatively consider this character to have evolved independently in gymnophthalmids and teiids. It may, however, have reversed within polyglyphanodontines.

2. Descending processes of frontals weakly developed and prefrontals broadly participating in wide orbitonasal fenestra (9-0; R of scleroglossan synapomorphy).

3. Jugal-squamosal contact on supratemporal arch present or close (18-1; C in iguanians, scincids, and xenosaurids).

4. Ectopterygoid contacts palatine anterolaterally, excluding maxilla from suborbital fenestra (45-1; C in and within many basic taxa).

5. Ectopterygoid restricts suborbital fenestra (46-1; C in xantusiids).

6. Origin of jaw adductor musculature extends onto dorsal surface of parietal (54-0; R of scleroglossan synapomorphy).

7. Replacement teeth develop in deep subcircular cavities at tooth bases (Romer, 1956).

8. Extensive deposit of cementum on tooth bases (Presch, 1974b).

9. Vomers elongate, approaching pterygoids (Romer, 1956).

10. Dentary reduced posteriorly during ontogeny, because of hypertrophy of temporal musculature (Gauthier, 1984).

11. Splenial hypertrophied relative to plesiomorphic squamate condition, continuous to symphysis with only a small symphyseal foramen (MacLean, 1974).

12. *M. hyoglossus* narrow, fusiform, extending posteriorly in a groove formed by a curved medial portion of the hypohyal and the parallel edges of the ceratohyal and first ceratobranchial, inserting on the tip of the ceratobranchial (MacLean, 1974).

13. Scapular emargination present (111-1; varies in the group and may not be a synapomorphy at this level; C in chamaeleontids and gekkonids, within iguanids*, scincids, and anguids).

14. Pubis relatively longer in ventral view, symphyseal process narrow and more extensive, but remaining more or less ventrally directed, pubic tubercle more anteroventral in position (124-1; this state is a scleroglossan synapomorphy, R of scincomorph synapomorphy (hence a double R), C in anguids).

Comments: As defined here, Teiidae contains only the so-called "Group I" (Boulenger, 1885) or "macroteiid" genera (Ruibal, 1952; Presch, 1974) among living squamates, although the extinct Polyglyphanodontinae (Estes, 1983a) also appear to be teiids. The so-called "Group II" or "microteiid" genera are placed in the following taxon.

GYMNOPHTHALMIDAE Merrem, 1820

Definition: The most recent common ancestor of the "microteiid" genera (sensu Presch, 1980) and all of its descendants.

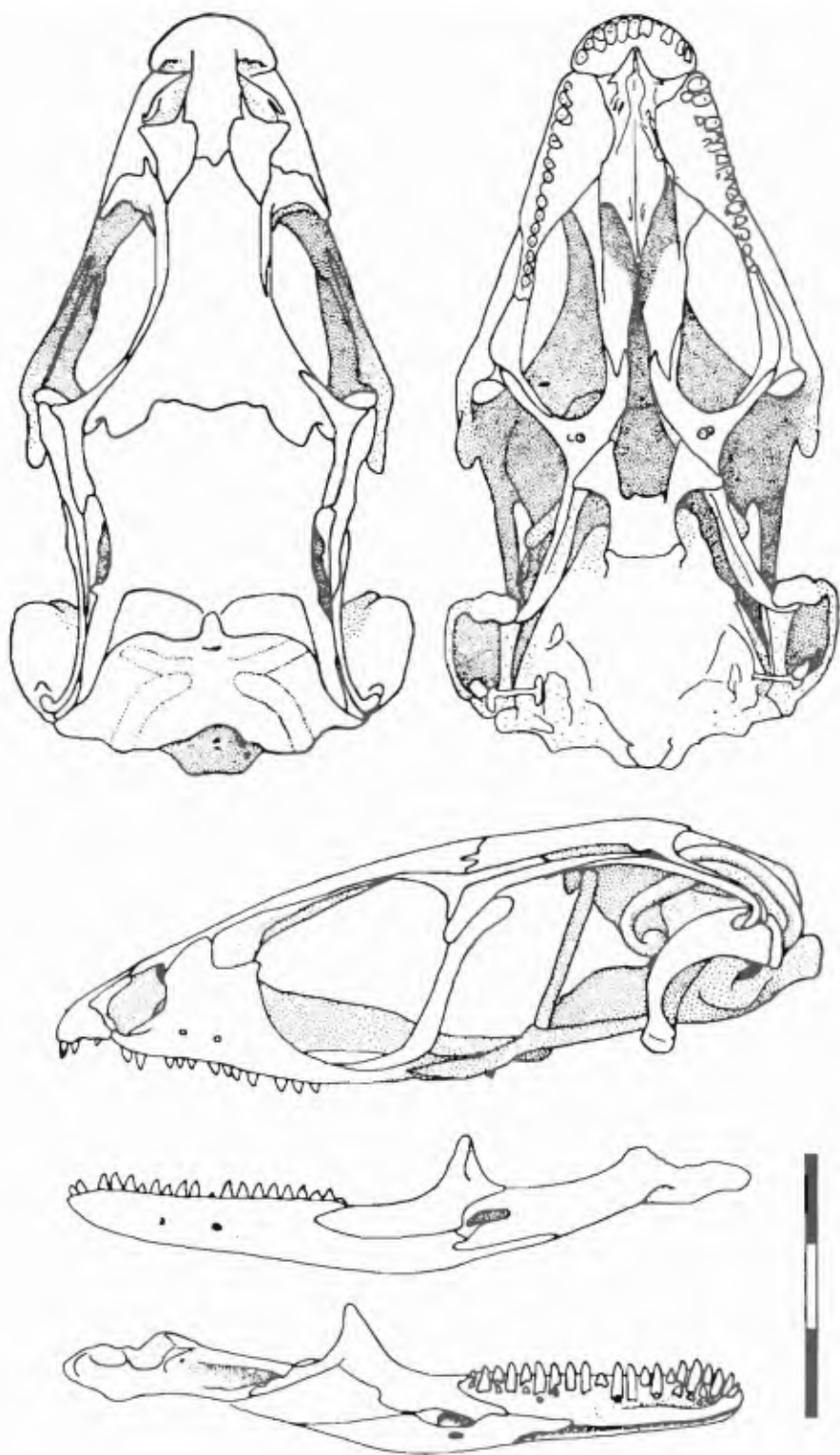


FIGURE 24. Skull and mandible of *Gymnophthalmus speciosus* (Gymnophthalmidae). Left lateral, dorsal, and ventral views of skull; lateral and medial views of mandible. Scale = 3 mm. From MacLean (1974). See end of paper for abbreviations.

Diagnosis: The following synapomorphies characterize this taxon (Fig. 24).

1. Frontals fuse in embryonic or early postembryonic ontogeny (6-1; C in Iguania, Gekkota, within many other groups). Extant teiids also have fused frontals, but this character is variable in the extinct polyglyphanodontines.
2. Descending processes of frontals in contact below olfactory tracts (10-1; R within group; C in gekkotans, helodermatids, and *Varanus*, within anguids and xantusiids).
3. Frontal tabs project posteriorly over dorsal surface of parietal (11-1; C within chamaeleontids).
4. Parietal foramen lost (26-1; C in and within many basic taxa, including teiids).
5. Second epibranchial lost (90-1; C in chamaeleontids, dibamids, xenosaurids, *Varanus*, amphibaenians, and snakes, and within many other basic taxa).
6. Anterior nasal scales separated by one or two frontonasal scales (Boulenger, 1885).
7. Nasal cavity lateral to Jacobson's organ (MacLean, 1974).
8. Posterolateral processes of basihyal laterally oriented (MacLean, 1974).
9. First ceratobranchial with strong lateral angulation (D. Harris, pers. comm. 1985, who notes that this character should be critically examined).
10. Quadrate process of stapes lost (141-1; we have checked only *Echinosaura*, *Proctoporus*, and *Prionodactylus*; C in gekkotans, scincids, and anguids, and within xantusiids).
11. Xiphisternum fused to sternum (D. Harris, pers. comm. 1985).
12. Calcified spines embedded in hemipenial flounces (D. Harris, pers. comm. 1985, who notes that these may be lacking in some taxa, and that this character needs examination).

Comments: Constitution of this taxon follows Presch (1980). Synapomorphies given for gymnophthalmids by Estes (1983a) were for the most part variable characters.

SCINCOIDEA Oppel, 1811

Definition: The most recent common ancestor of Scincidae and Cordylidae and all of its descendants.

Diagnosis: Scincoids have the following synapomorphies.

1. Palpebral ossifications present (36-1; rare exceptions occur; C in lacertids and anguimorphs with some reversals within the latter).
2. Lateral coronoid process of dentary large, extending dorsally onto anterolateral surface of coronoid (60-1; C in xantusiids and dibamids).
3. Retroarticular process inflected medially (75-1; C in gekkotans, anguids, and varanoids).
4. Retroarticular process medial margin with tubercle or small flange (76-1).
5. Retroarticular process broadened posteriorly (78-1; some exceptions within *Cordylus*; C in gekkotans and anguids).
6. Body osteoderms present dorsally (126-1; C in anguimorphs).
7. Body osteoderms present ventrally (127-1; C in anguids).
8. Cephalic osteoderms present (128-1; C in lacertids and anguimorphs).
9. Osteoderms compound (Camp, 1923).
10. Ciliary restraint system for hair cells imposed by inertial bodies (sallet or culmen) (140-2; C in xantusiids).
11. Fibers of the 3b head of the profundus layer of the m. adductor mandibulae externus invade the mesial margin of the upper temporal fossa (Rieppel, 1980c).
12. Tongue tip arrowhead-shaped, formed by convex margins of tip and extension of ventral pallets laterally at tongue base (Schwenk, 1988).
13. The laryngochoyoid ligament, just anterior to its insertion into the larynx, gives off two

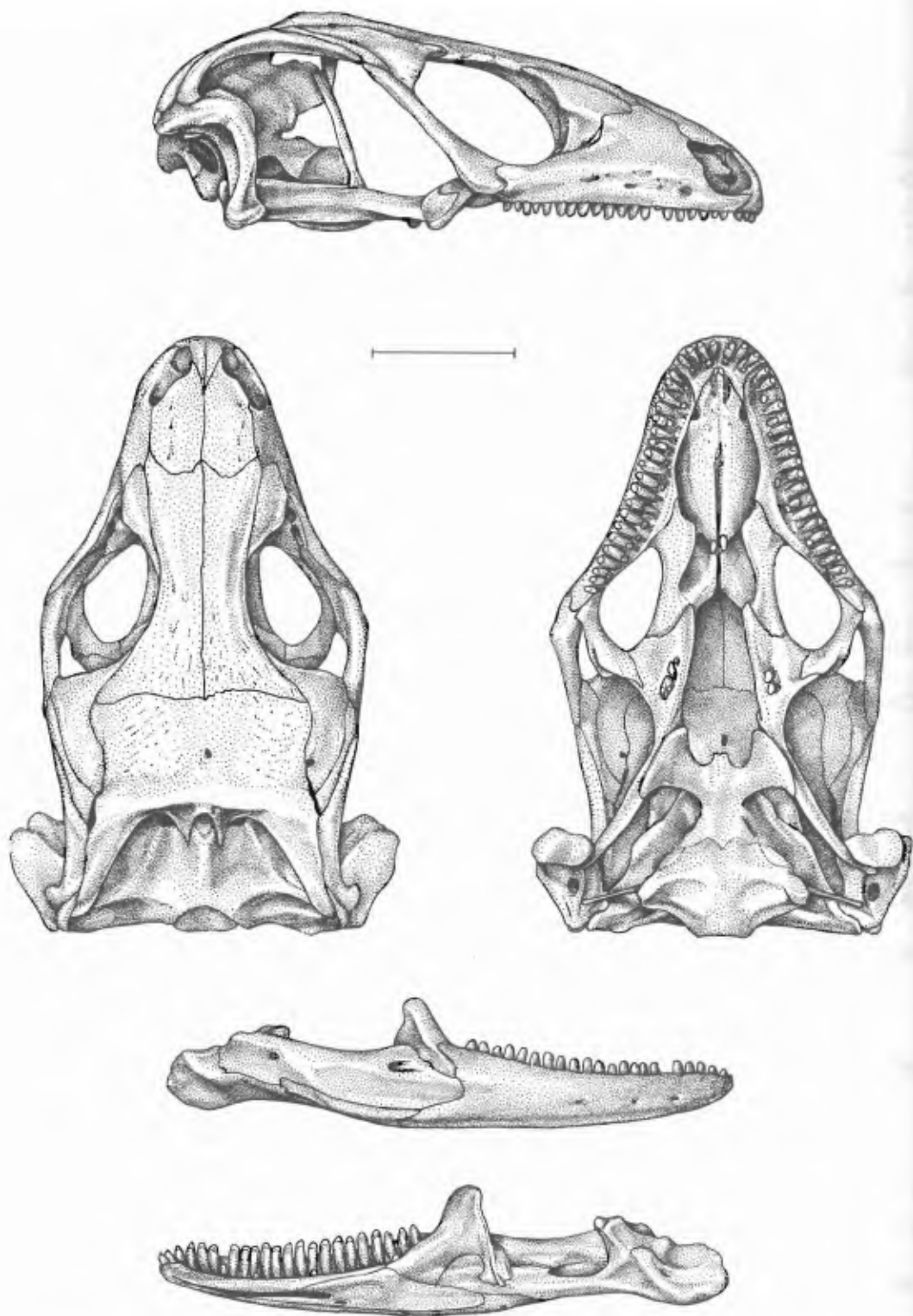


FIGURE 25. Skull and mandible of *Eumeces obsoletus* (CAS 71603; Scincidae). Skull in left lateral, dorsal, and ventral views; mandible in lateral and medial views. Scale = 5 mm. See end of paper for abbreviations.

small, dense dorsolateral branches that extend independently into the loose connective tissue ventral to the laryngeal cartilage (Schwenk, 1988; C in lacertids).

14. Tongue scales with irregular trailing edge (Schwenk, 1988).

15. Foretongue significantly wider than bundles of *m. hyoglossus* (Schwenk, 1988). C in xantusiids.

16. Glossopharyngeal nerve enters medial wall of braincase through separate foramen rather than through the medial aperture of the recessus scalae tympani. Bellairs and Kamal (1981) reported that this occurs in most scincids examined and that the nerve often passes through the cochlear portion of the otic capsule. They noted that in *Mabuya capensis* the nerve is extracapsular, but according to Skinner (1973) it still enters the braincase through a separate foramen. We have observed a foramen in a similar position in *Gerrhosaurus* and *Cordylus*, but not in *Tupinambis*, *Varanus*, *Cyclura*, *Uromastyx*, *Lacerta*, or *Gekko*. We consider the separate foramen for the glossopharyngeal nerve to be a synapomorphy of Scincoidea, although it occurs also in *Anniella* (Rieppel, 1978c) and *Dibamus* (fig. 3 in Rieppel, 1985). A more extensive taxonomic survey is desirable.

Comments: We include here Scincidae (as did Camp, 1923) but add to it the Cordylidae (which Camp divided between Lacertoidea and Anguimorpha). Camp also included the Dibamidae in this taxon. Rieppel (1984a) provided additional synapomorphies that support this placement, but as noted below in the section on dibamids, allocation of dibamids to Scincidae requires loss in dibamids of most of the diagnostic characters of scincoids and scincomorphs. Rieppel's (1984a) list is impressive, but is weakened (as he realized) by the absence of scincoid and scincomorph characters in dibamids.

Camp (1923), Rieppel (1980c), and Gauthier (1984) have all provided data that suggest monophyly of Scincoidea. The synapomorphies identified in the present study corroborate the results of the latter studies.

SCINCIDAE Gray, 1825

Definition: The most recent common ancestor of Scincinae*, Acontinae, Lygosominae, and Feylininae (sensu Greer, 1970) and all of its descendants.

Diagnosis: The following combination of synapomorphies characterizes this taxon (Fig. 25).

1. Jugal-squamosal contact on supratemporal arch present or close (18-1; C in teiids and xenosaurs).

2. Supratemporal fenestra closed primarily by postfrontal (20-1; C in lacertids).

3. Medial extensions from ventrolateral edges of palatines form air passages for bony secondary palate (43-1; C in dibamids).

4. Zygosphenes and zygantra present (96-0; R of squamate synapomorphy, C in lacertiforms, scincids, and snakes, and within iguanids* and cordylids).

5. Cervical intercentra sutured to posterior part of preceding centrum (97-1; may be further transformed in some; C in varanoids, and within iguanids*, cordylids, and lacertids).

6. Internal (quadrate) process of stapes lost (141-1; C in gekkotans, gymnophthalmids, and anguids, and within xantusiids).

7. Femoral and preanal pores lost (144-0; R of squamate synapomorphy, C in and within many basic taxa).

8. Cycloid scales present (148-1; C in dibamids, within gekkotans, gymnophthalmids, anguids, cordylids, and snakes).

9. Compound osteoderms present both dorsally and ventrally (Camp, 1923).

10. Tongue scales serrated (Schwenk, 1988).

11. Nucleus reticularis ventrolateralis of the spinal cord present (Cruce and Newman, 1984, who indicated that their observation of presence is uncertain). C in lacertids, gymnophthalmids, teiids, snakes, and dibamids.

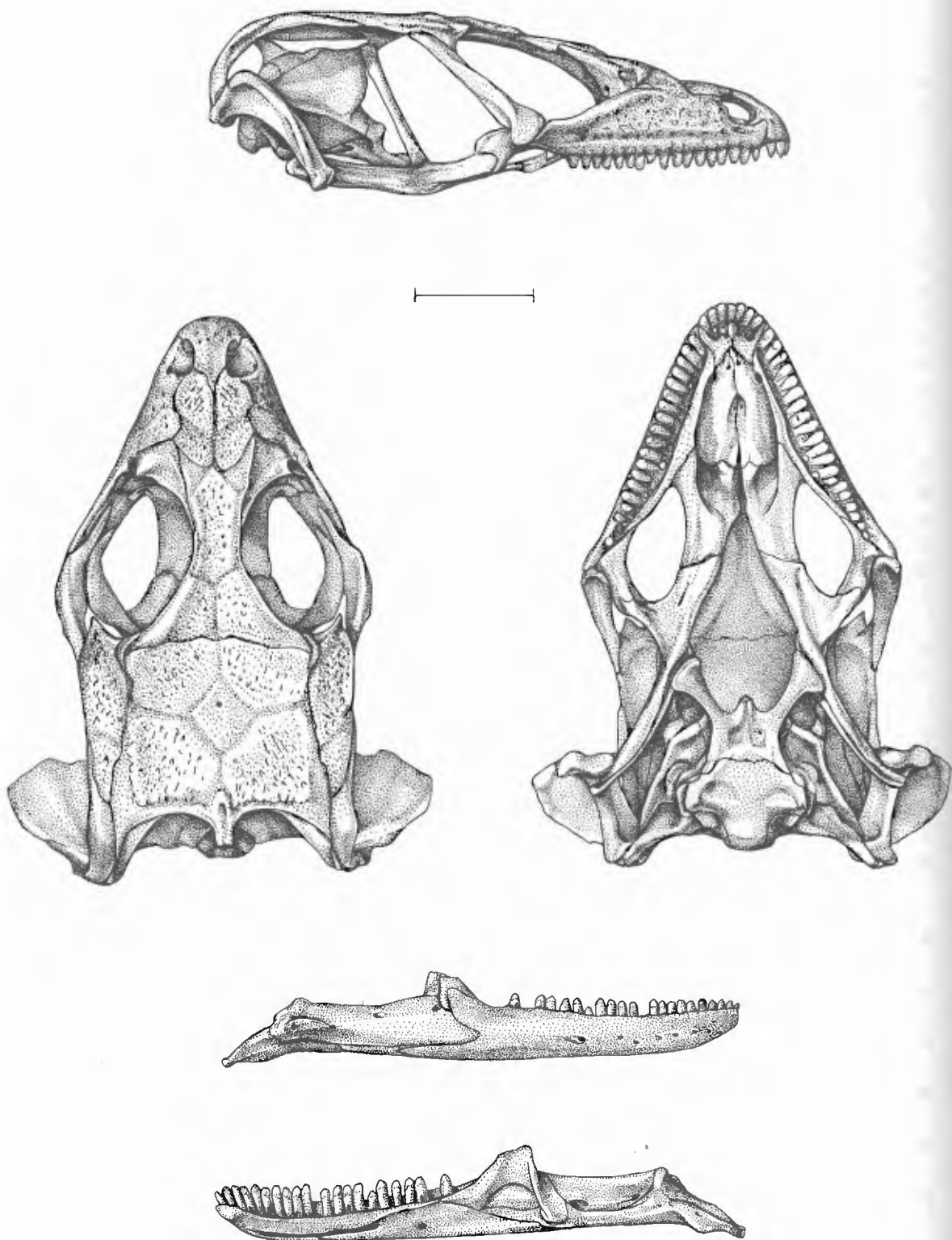


FIGURE 26. Skull and mandible of *Cordylus polyzonus* (REE 201; Cordylidae). Left lateral, dorsal, and ventral views of skull; lateral and medial views of right mandible. Scale = 5 mm. See end of paper for abbreviations.

Comments: Most of the scincid synapomorphies given by Estes (1983a) apply to more or less inclusive groups in the present study, or else they are variable within scincids. Rieppel (1980c; 1984a) suggested that scincids are paraphyletic, in that acontines may be more closely related to dibamids than to other scincids. Relationships within *Eumeces** are unresolved, which makes it impossible to decide whether Scincinae* is monophyletic or paraphyletic, but the monophyly of the other subfamilies can be accepted for the present (Greer, 1970; 1986). Nevertheless, if dibamids are most closely related to acontine scincids as Rieppel (1984a) suggested (see also section below on Dibamidae), they must be included within Scincidae to avoid paraphyly. Dibamids have only four of the seven scincomorph synapomorphies from our character list, and share six of our twelve scincid synapomorphies. *Dibamus* nevertheless share a number of derived characters with acontines, as listed by Rieppel (1984a), some of which are also present in *Anelytropsis* (Greer, 1984a). Resolution of the phylogenetic relationships of scincids and dibamids is an important phylogenetic problem, but it is beyond the scope of this paper.

CORDYLIDAE Gray, 1837

Definition: The most recent common ancestor of Cordylinae and Gerrhosaurinae (sensu Romer, 1956, who treated these as families) and all of its descendants.

Diagnosis: The following synapomorphies characterize this taxon (Fig. 26).

1. Supratemporal fenestra closed primarily by postorbital (19-1; C in xantusiids, within gymnophthalmids and anguids).
2. Symmetrical pattern of posterior skull epidermal scales surrounding a small central interparietal (Estes, 1983a).
3. Coracoid relatively large and expanded (Estes, 1983a).
4. Origin of 3b head of the profundus layer of the m. adductor mandibulae externus from the lateral edge of parietal and supratemporal (Rieppel, 1980c).
5. Some fibers of the 3c head of the profundus layer of the m. adductor mandibulae externus attach posteroventrally on the lateral surface of the bodenaponeurosis (Rieppel, 1980c).
6. Compound osteoderms present only ventrally (Camp, 1923).
7. Five attachment points for ribs on each side of sternum (109-0; R of autarchoglossan synapomorphy, C within iguanids* and agamids*).

Comments: Camp (1923) placed cordylines with anguimorphs but included gerrhosaurines in the Scincomorpha. Cordylids as defined here are an extremely variable group that seems to be monophyletic (McDowell and Bogert, 1954; Rieppel, 1980c; Estes, 1983a). In retrospect, however, we might have evaluated the monophyletic status of this group more adequately if we had scored cordylines and gerrhosaurines separately. The group is in need of more detailed treatment than it has received to date.

ANGUIMORPHA Fürbringer, 1900

Definition: The most recent common ancestor of Xenosauridae, Anguidae, *Heloderma*, *Lanthanotus*, and *Varanus*, and all of its descendants.

Diagnosis: Anguimorphs are diagnosed by the following synapomorphies.

1. Palpebral ossifications present (36-1; C in lacertids and scincoids, R in *Heloderma* and *Lanthanotus*, and within scincoids).
2. Meckel's canal subdivided near posterior end of dentary tooth row with intramandibular septum well developed (56-1; C? within iguanids*).
3. Meckel's canal opens ventrally anterior to anterior inferior alveolar foramen (57-1; C within chamaeleontids).
4. Posterolateral dentary with surangular notch (63-1; further transformed in *Lanthanotus* and *Varanus*).

5. Replacement teeth develop posterolingually, small resorption pits present (intermediate type) (85-1; C in dibamids, and within gymnophthalmids, teiids, scincids, and amphisbaenians; further transformed in varanoids).
6. Second ceratobranchial lost (91-1; C in chamaeleontids, dibamids, and snakes, within teiids, gymnophthalmids, scincids, amphisbaenians).
7. Cervical intercentra sutured to posterior part of preceding centrum (97-1). Fusion (97-2) may also be an anguimorph synapomorphy, but this is uncertain given the ontogenetic nature of the fusion and incomplete ontogenetic sampling (see Character Analysis).
8. More than 26 presacral vertebrae (106-1; R in *Shinisaurus*, C in all other long-bodied squamates).
9. Dorsal body osteoderms present (127-1; R within *Varanus*, C in scincoids); a single osteoderm present in each epidermal scale (Gauthier, 1982).
10. Cephalic osteoderms present (128-1; C in lacertids and scincoids, R within *Varanus*).
11. Foretongue retracts within hind tongue at zone of invagination (136-1; further transformed in *Varanus*; C in snakes, within teiids).
12. Free part of tongue notched 10-20% (137-2; further transformed in varanoids).
13. Asymmetrically pointed epithelial apices of filamentous tongue papillae (Schwenk, 1988; R in *Varanus*)
14. Cochlear duct with much thickened neural limbus (Miller, 1966).
15. Urinary and genital canals open on ventrolateral or ventral face of urodaeum (Saint-Girons, 1976).
16. Sero-mucous cells present, deep in the inferior labial glands (Saint-Girons, 1976).
17. Acini of fundic glands of stomach composed of serous cells only, with histologically differentiated mucous neck cells (Saint-Girons, 1976).
18. Characteristic long, pointed cells in the suprarenal glands (Saint-Girons, 1976).
19. Femoral pores lost (144-0; R of squamate synapomorphy).
20. Dorsum with longitudinal rows of enlarged scales, separated by broad areas of granular scutellation (Gauthier, 1982).
21. General color pattern consisting of dark cross-bars and black nuchal mark, and a dark line extending along temporal arch to back of eye (Gauthier, 1982).
22. M. geniomyoideus present (Camp, 1923).

Comments: Anguimorpha is diagnosed by many synapomorphies ranging from histological through gross anatomical levels, and is one of the best supported squamate groups. Gauthier (1982) found no evidence, however, to support the monophyly of McDowell and Bogert's (1954) taxon Anguioidea*. Although we have identified some characters that do support a sister group relationship between Xenosauridae and Anguidae, we have also identified characters that support alternative views, namely that either anguids or xenosaurs are more closely related to varanoids. Given this lack of clear resolution, an unresolved tritomy among Varanoidea, Anguidae, and Xenosauridae expresses the state of our knowledge regarding the interrelationships of these taxa most adequately (Fig. 6).

Our computer analysis that included snakes, dibamids, and amphisbaenians placed snakes as the sister group of varanoids, while dibamids and amphisbaenians were placed as the sister group of varanoids and snakes. Rieppel (1984a) gave characters that place dibamids as the sister group of acontine scincids. We consider this hypothesis (see comments for Scincidae), and one that places snakes with anguimorphs, to be the best supported hypotheses of relationships for dibamids and snakes within Scleroglossa, but we have no defensible hypothesis for the relationships of amphisbaenians within Scleroglossa. For the present we prefer to place all three taxa as Scleroglossa, incertae sedis (see discussion below under the taxa in question).

XENOSAURIDAE Cope, 1886

Definition: the most recent common ancestor of *Xenosaurus* and *Shinisaurus* and all of its descendants.

Diagnosis: Monophyly of this taxon is supported by the following synapomorphies (Fig. 27).

1. Lateral border of frontals strongly constricted between orbits (7-1; C in agamids* and chamaeleontids, within iguanids*, lacertids, and anguids).
2. Jugal-squamosal contact on supratemporal arch (18-1; C in teiids and scincids).
3. Frontals fuse in the embryo (6-1; C in Iguania, Gekkota, Gymnophthalmidae, within many other groups). Extinct relatives of xenosaurids underwent frontal fusion in postembryonic ontogeny (Gauthier, 1982).
4. Second epibranchials lost (90-1; C in chamaeleontids, gymnophthalmids, dibamids, *Lanthanotus*, *Varanus*, amphisbaenians, and snakes, and within iguanids*, agamids*, pygopodids, gekkonids, scincids, and anguids).
5. Dermal rugosities with vermiculate sculpture present (129-2; C in cordylids and lacertids, and within anguids and amphisbaenians).
6. Cephalic scales relatively small (147-0; R of scleroglossan synapomorphy; this reversal occurs also in varanoids and may be a synapomorphy of xenosaurids and varanoids).
7. Rectangular cross-section of skull owing to presence of canthal crest on temporal arch (Gauthier, 1982; Estes, 1983a).
8. Widened and sculptured postorbital branch of jugal (Gauthier, 1982).
9. Ectopterygoid exposed laterally on skull (McDowell and Bogert, 1954).
10. Cervical intercentra fused to posterior part of preceding centrum (97-2; C in dibamids, anguids, snakes, and amphisbaenians, and within scincids, *Varanus*, *Lanthanotus*, and *Heloderma*). This is a possible synapomorphy for Anguioidea, although there are problems with sampling and ontogenetic variation (see Character Analysis).
11. Carotid fossa reduced (Costelli and Hecht, 1971).
12. Scaly tympanic covering (McDowell and Bogert, 1954).

Comments: As Gauthier (1982) noted, *Shinisaurus* and *Xenosaurus* are very different in their general adaptation. Nevertheless, we accept here the hypothesis of relationships suggested by McDowell and Bogert (1954) because the above synapomorphies support it.

ANGUIDAE Gray, 1825

Definition: The most recent common ancestor of Anguinae, Anniellinae, Diploglossinae, and Gerrhonotinae, and all of its descendants.

Diagnosis: Monophyly of this taxon is supported by the following synapomorphies (Fig. 28).

1. Posterior opening of vidian canal at basisphenoid-prootic suture (53-1; C in lacertids, *Heloderma*, *Shinisaurus*, and *Lanthanotus*; within xantusiids and scincoids).
2. Reduced supratemporal arch and narrowed supratemporal fenestra (Gauthier, 1982).
3. Dentary forms dorsal and anterior border of anterior inferior alveolar foramen (Estes, 1964).
4. Retroarticular process deflected medially (75-1; C in gekkotans, scincoids, and varanoids, within snakes). This character may be a synapomorphy of anguids and varanoids together.
5. Retroarticular process broadened posteriorly (78-1; C in gekkotans, scincoids, dibamids).
6. In occlusal view, cutting edge of posterior teeth forming an inwardly-pointing V, crown apex lies slightly posterior and lingual to center of long axis of tooth; crown often rotated about the long axis of tooth and apex tipped posteriorly, so that in profile the leading edge is

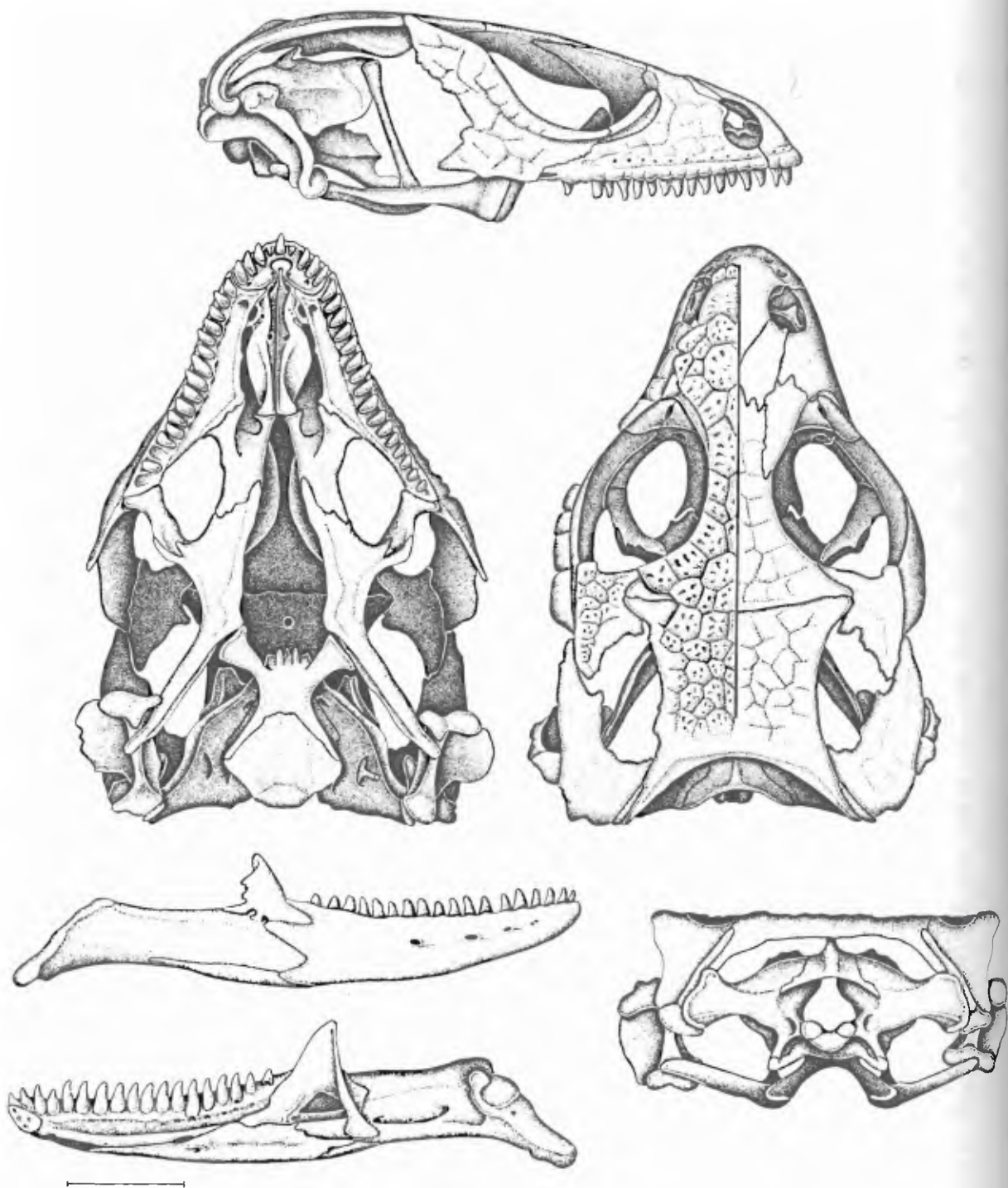


FIGURE 27. Skull and mandible of *Xenosaurus grandis* (Xenosauridae). Right lateral, dorsal, ventral, and occipital views of skull; lateral and medial views of mandible. Scale = 5 mm. From Rieppel (1980b). See end of paper for abbreviations.

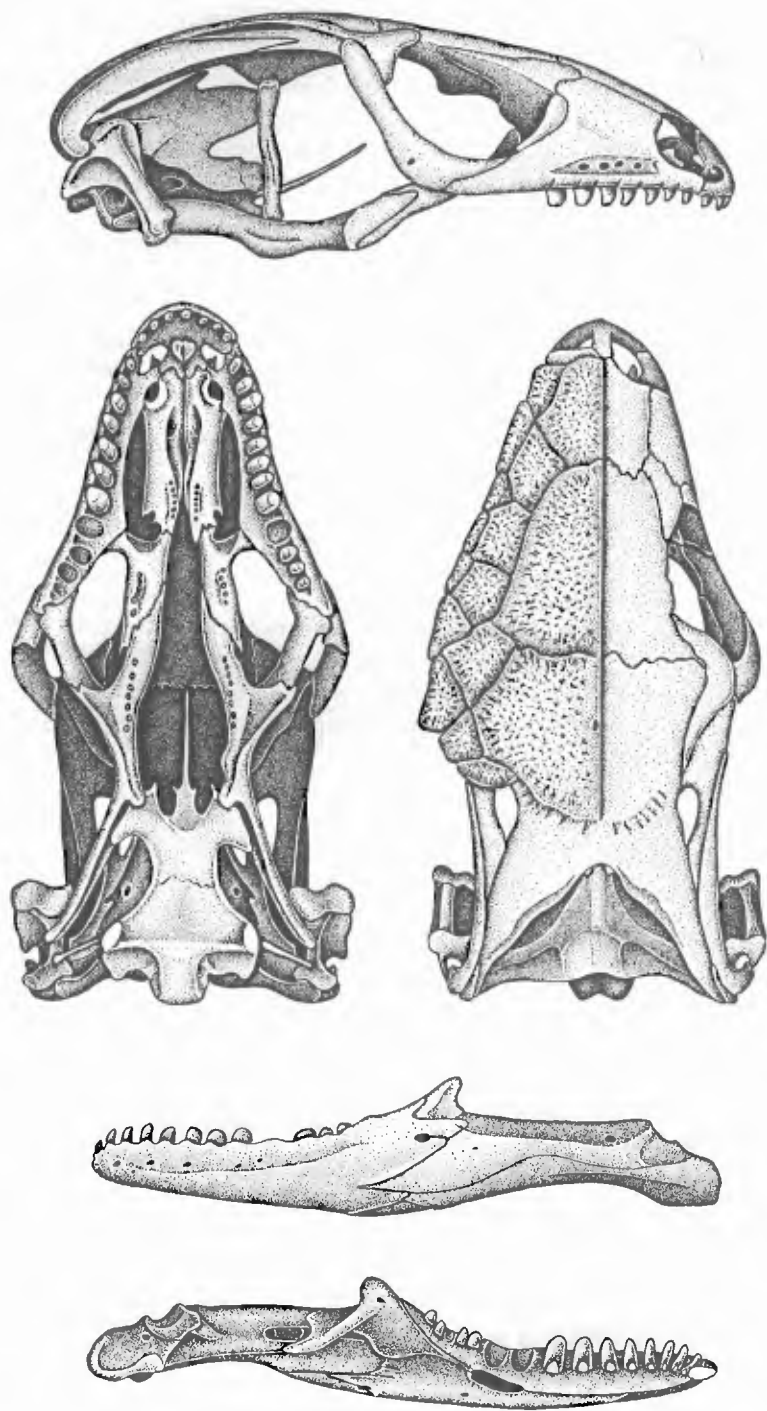


FIGURE 28. Skull and mandible of *Ophisaurus apodus* (Anguillidae). Right lateral, dorsal, and ventral views of skull; lateral and medial views of mandible. Scale = 5 mm. From Rieppel (1980b). See end of paper for abbreviations.

prominently convex and extends back to the apex, giving a recurved, chisel-shape to the crown (Estes, 1964).

7. Tooth crowns striated on medial and, less often, lateral faces (Gauthier, 1982).

8. Cervical intercentra fused to posterior part of preceding centrum (97-2; C in dibamids, xenosaurs, amphisbaenians, and snakes, and within *Heloderma*, *Lanthanotus*, and *Varanus*). This is a possible synapomorphy for Anguioidea, although there are problems with sampling and ontogenetic variation (see Character Analysis).

9. Caudal vertebrae with two pairs of converging transverse processes (includes presumed transformations of this pattern via loss of one pair of transverse processes) (101-1; R within group, C in dibamids, within amphisbaenians and scincids).

10. Three rib attachment points on sternum (109-2; R within *Diploglossus monotropis*, some species of *Celestus*, and *Sauresia sepsoides* according to Etheridge, 1967; C in *Varanus*, and within iguanids*, agamids*, and gekkonids).

11. Pubis relatively long in ventral view, symphyseal process extremely elongated and anteriorly directed (124-2; C in scincomorphs).

12. Ventral body osteoderms present (126-1; C in scincoids).

13. Presence of lateral fold in body squamation (McDowell and Bogert, 1954). R in *Anniella*, diploglossines.

14. Reduced size of frontoparietal scales, and increased size of frontal and parietal scales, resulting in a narrow contact on the midline between the latter two scales (Meszoely, 1970).

15. An odd number of interparietal scales, usually one (Meszoely, 1970).

16. Rectangular, imbricate scales and osteoderms enclose body and tail except for lateral fold and some areas on the limbs and neck, osteoderms deeply imbricate anteroposteriorly but only moderately imbricate laterally (Gauthier, 1982).

17. Internal (quadrate) process of stapes lost (141-1; C in gekkotans, gymnophthalmids, scincids, and amphisbaenians, and within xantusiids).

18. Small, inset tympanum (McDowell and Bogert, 1954).

Comments: Meszoely (1970), Sullivan (1979), Rieppel (1980b), Gauthier (1982), and Estes (1983a) have discussed this taxon and the interrelationships of the included taxa; we note only that monophyly of the group is highly corroborated.

McDowell and Bogert (1954) pointed out the close affinity of the fossil glyptosauroids to anguids, and Meszoely (1970) placed the extinct group in the Anguidae as a subfamily. Gauthier (1982) made more explicit the relationship of the group to the other anguids. We have treated the glyptosaurines as anguids, accepting his hypothesis that they are descended from the most recent common ancestor of the extant subfamilies.

VARANOIDEA Camp, 1923

Definition: The most recent common ancestor of Helodermatidae, *Lanthanotus*, and *Varanus* and all of its descendants.

Diagnosis: Monophyly of this taxon is supported by the following synapomorphies.

1. Descending processes of frontals well developed, approaching each other on midline ventrally below olfactory tracts (McDowell and Bogert, 1954). Contact of the processes occurs anteromedially in *Heloderma* and posteromedially in *Varanus*, but the posteromedially-directed extensions do not meet in *Lanthanotus*.

2. Supratemporal reaches level of parietal notch (apex of angle formed by supratemporal processes of parietal; Pregill et al., 1986).

3. Maxillae extend posteriorly only just beyond anterior edges of orbits (27-1; C in dibamids and xantusiids).

4. Moderate retraction of naris, with nasal and maxilla not (or very little) in contact (Pregill et al., 1986). This is less derived than in our character 2.
5. Vomers more than twice the length of palatines, palatines approximately as wide as long (Pregill et al., 1986). This character may apply to a more inclusive group, depending on the phylogenetic position of some Cretaceous forms (Borsuk-Bialynicka, 1984).
6. Ectopterygoid contacts palatine anterolaterally, excluding maxilla from suborbital fenestra (45-1; C in teiids, xantusiids, and dibamids, and within gekkotans, anguids, and amphisbaenians).
7. Reduced palatal shelving through reduction of vomers (Pregill et al., 1986; also in *Cherminotus*, a Cretaceous relative of *Lanthanotus*, although the latter has reversed this condition).
8. Subdental shelf lost (59-1; C within all three iguanian groups and amphisbaenians).
9. In lateral view, disarticulated surangular is expanded anterodorsally and is nearly vertical at anterior margin (61-1; further transformed in *Lanthanotus* and *Varanus*).
10. Reduced overlap of dentary and postdentary bones (64-1; C in snakes).
11. Intramandibular septum notched posteriorly (Pregill et al., 1986).
12. Splenial does not extend posterior to apex of coronoid (66-1; C in agamids*, xantusiids, and amphisbaenians, and within iguanids*; further transformed in *Lanthanotus*).
13. Splenial-dentary suture reduced, much connective tissue present (67-1; C in snakes).
14. A long, low, horizontally-oriented anterior extension of coronoid present (69-1).
15. Retroarticular process inflected medially (75-1; C in gekkotans, scincoids, and anguids, within? snakes). This character may be a synapomorphy of anguids and varanoids together.
16. Replacement teeth develop posteriorly, no resorption pits present (varanid type) (85-2; C in snakes, and within amphisbaenians).
17. Bases of marginal teeth with infolded dentine (plicidentine), producing striations (86-1). Striations, but little if any infolding, may occur in glyptosaurine anguids and necrosaurids; this character may apply to a more inclusive group, but the strong infolding seen in varanoids appears to be appropriately placed at this level.
18. Teeth unicuspid, trenchant, recurved, and widely spaced (McDowell and Bogert, 1954).
19. Premaxillary teeth much smaller than maxillary teeth (Pregill et al., 1986). C in various taxa, e. g. *Tupinambis*.
20. Less than 13 maxillary teeth (Pregill et al., 1986).
21. Vertebral condyle with strong obliquity present (92-1).
22. Autotomy septa in caudal vertebrae lost (103-1; C in acrodontans and snakes, and within iguanids*, gekkonids, scincids, anguids, and amphisbaenians).
23. Epicoracoid cartilage fails to contact either suprascapula or mesoscapula (114-1; C in chamaeleontids and lacertids, within iguanids*, agamids*, gekkonids, and amphisbaenians).
24. Only a single pair of ribs attaching to the xiphisternum (Lécuru, 1968a, b).
25. Clavicles gracile, not expanded (Lécuru, 1968a, b).
26. Ulnar nerve in forearm in deep (varanid) position (142-1; C in chamaeleontids, gymnophthalmids, and teiids, and within iguanids* and lacertids).
27. Cephalic scales relatively small (147-0; R of scleroglossan synapomorphy).
28. Cochlear duct robust and broad, limbus elongate and heavy (Miller, 1966).
29. Insertion of m. episternocleidomastoideus reaches supratemporal process of parietal (Rieppel, 1980a, b).
30. M. adductor mandibulae externus profundus (3b layer) originates from supratemporal only (Pregill et al., 1986).
31. Insertion of m. geniomyoideus at least partly deep to m. genioglossus medialis (Rieppel, 1980a, b).
32. Narrow-based bodenaponeurosis attaching to caudomesial edge of coronoid process

(Rieppel, 1980a, b; not present in *Lanthanotus* and may be separately derived in *Heloderma* and *Varanus*; Pregill et al., 1986).

33. Insertion of *m. levator pterygoidii* extends posteriorly beyond columellar fossa of pterygoid (Rieppel, 1980a,b). This character may be separately derived in *Varanus* and *Heloderma* (Pregill et al., 1986).

34. Free part of tongue notched 20-40% (137-3; C in lacertids, further transformed in *Lanthanotus* and *Varanus*).

35. Large, anatomically differentiated sero-mucus gland on lower jaw (Gland of Gabe; Kochva, 1974).

36. Calyciform duodenal cells of muco-serous rather than mucus type (St. Girons, 1976).

37. Carotid duct lost (Underwood, 1957b for *Varanus*, *Heloderma*; and snakes; McDowell, 1972 for *Lanthanotus*).

Comments: Monophyly of Varanoidea is supported by many synapomorphies; it has been recognized in its present form, including Helodermatidae, *Lanthanotus*, and *Varanus*, since the study by McDowell and Bogert (1954). Rieppel (1980b), Gauthier (1982), Estes (1983a), and Pregill et al. (1986) have discussed the interrelationships within the taxon most recently.

Characters 8-12 above are correlated with the formation of a "mandibular hinge" (see McDowell and Bogert, 1954; Gauthier, 1982).

HELODERMATIDAE Gray, 1837

Definition: *Heloderma*, and all organisms sharing a more recent common ancestor with this taxon than with any other extant organisms.

Diagnosis: Monophyly of this taxon is supported by the following synapomorphies (Fig. 29).

1. Steep nasal process of maxilla, contributing to a rounded muzzle and short face (McDowell and Bogert, 1954).

2. Prefrontal and postfrontal approach each other but are not in contact above orbits (This is a more plesiomorphic state of our character 5-1; the latter is C in *Heloderma* and *Lanthanotus*).

3. Subolfactory processes of frontals in contact below olfactory tract (10-1; C in gekkotans, *Varanus*, amphisbaenians, and snakes, within xantusiids, gymnophthalmids, and anguids).

4. Postorbital bone and upper temporal arch lost (16-1; C in *Lanthanotus*).

5. Parietal foramen lost (26-1; C in *Lanthanotus*, and in and within many basic taxa).

6. Palpebral ossifications lost (36-0; R of anguimorph synapomorphy, C in lacertids and scincoids, anguids, and *Lanthanotus*).

7. Pterygoid lappet of quadrate present (37-0; R of squamate synapomorphy, C in gymnophthalmids, teiids, lacertids, within iguanids*).

8. Posterior opening of vidian canal at basisphenoid-prootic suture (53-1; C in lacertids, anguids, *Shinisaurus*, and *Lanthanotus*, within xantusiids and scincoids).

9. Maxillary dental shelf curved medially (Pregill et al., 1986).

10. Splenial not extending anteriorly beyond tooth row midpoint (65-1; C in agamids*, xantusiids, gekkonids, amphisbaenians, and snakes, within iguanids*, scincoids, gymnophthalmids, and anguids).

11. Fewer than fourteen scleral ossicles (89-1; C in acrodontans and *Lanthanotus*).

12. Skull robust, short, and broad (Romer, 1956).

13. Teeth with venom channels (Bogert and del Campo, 1956).

14. Reduction of hypapophyses on posterior cervicals (Hoffstetter and Gasc, 1967).

15. Vertebral neural spines narrow and tall, rising at an acute angle (Pregill et al., 1986).

16. Body long, with 32-36 presacral vertebrae (Pregill et al., 1986); this character is a more

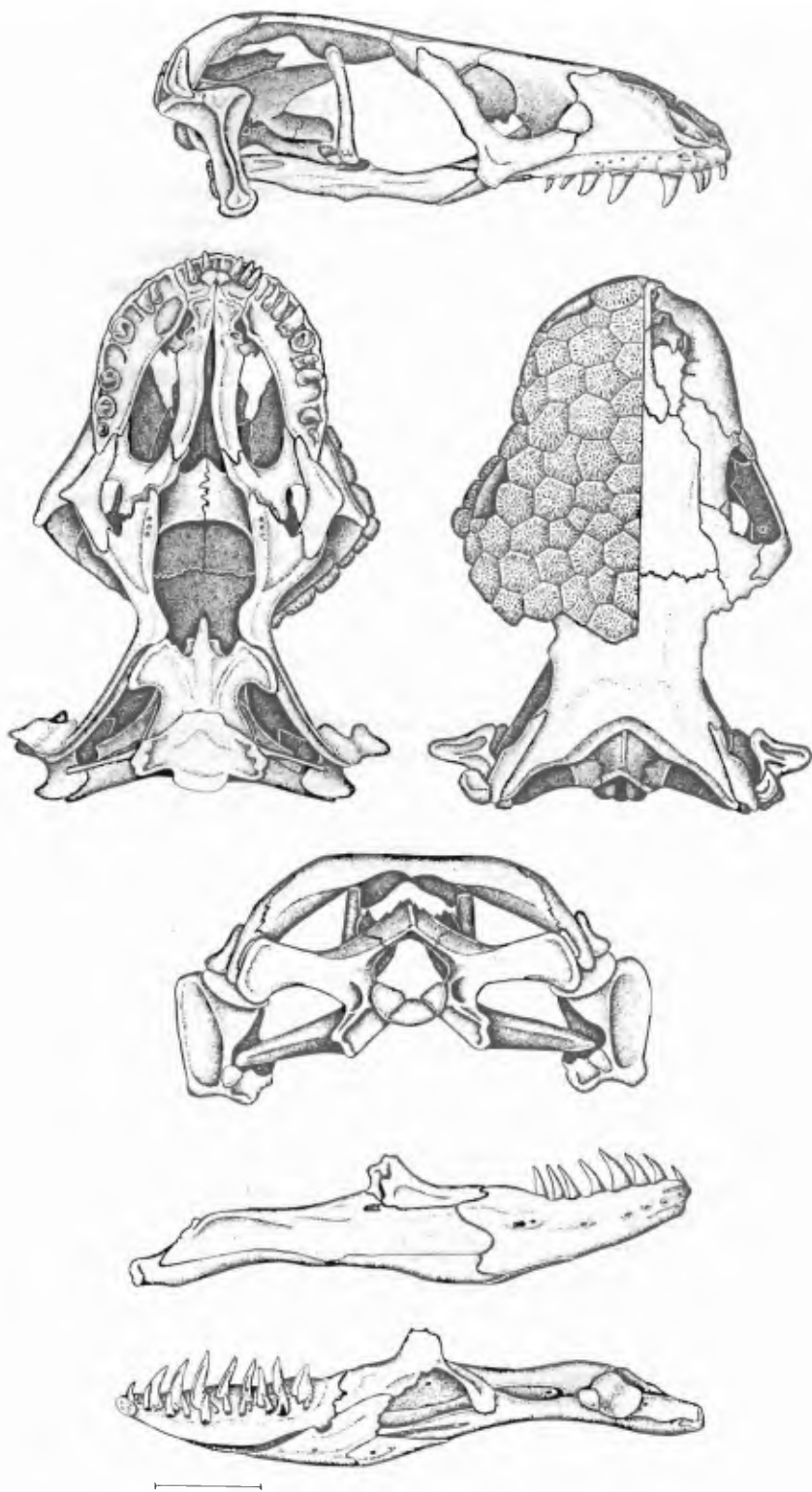


FIGURE 29. Skull and mandible of *Heloderma s. suspectum* (Helodermatidae). Right lateral, dorsal, occipital, and ventral views of skull; lateral and medial views of mandible. Scale = 5 mm. From Rieppel (1980b). See end of paper for abbreviations.

specific state than our character 105, which specifies only more than 26 and is thus a synapomorphy at a more inclusive (scleroglossan) level.

17. Tail short, with 25-40 caudal vertebrae (Pregill et al., 1986).

18. Anterior (primary) coracoid emargination lost (112-0; R of squamate synapomorphy, C in chamaeleontids, within pygopodids and amphisbaenians).

19. Lateral arms of the interclavicle lost (119-1; C within gekkonids and gymnophthalmids).

20. Osteoscutes thick, subconical, polygonal, covering body (McDowell and Bogert, 1954).

21. Innervation of dorsal leg muscles by interosseous nerve (143-1; C in acrodontans, gymnophthalmids, and teiids, within iguanids* and possibly cordylids).

22. Gland of Gabe a venom-producing organ (Bogert and del Campo, 1956).

23. Diet includes unusually large prey items (Pregill, et al., 1986).

Comments: Pregill et al. (1986) discussed the relationships within this taxon, including an evaluation of fossil taxa.

McDowell and Bogert (1954) and Rieppel (1980a) both reported a pedal phalangeal formula of 2,3,4,5,3 in *Heloderma*, but Pregill et al. (1986) demonstrated that this is only found in some individuals of *H. horridum*.

VARANIDAE Gray, 1827

Definition: The most recent common ancestor of *Lanthanotus* and *Varanus* and all of its descendants (see comments below).

Diagnosis: The members of this taxon possess the following synapomorphies.

1. Bony external naris opening extended posteriorly, frontal coming close to or incorporated into opening (2-1); this is correlated with nasal and prefrontal bones that have little or no contact, and nasals and maxillae that are not in contact (Pregill et al., 1986).

2. Nasals fused in embryo (3-1; C within chamaeleontids, gekkotans, scincids, and snakes).

3. Nasal process of maxilla rises from posterior position on the bone (McDowell and Bogert, 1954; Pregill et al., 1986).

4. Lacrimal foramen double on orbital margin (Pregill et al., 1986).

5. Posterior border of opening for Jacobson's organ closed by maxilla and vomer (42-1; C within pygopodids, xantusiids, gymnophthalmids, scincids, *Dibamus*, and anguids).

6. Jaw adductor musculature attaches on dorsal surface of parietal (54-0; R of scleroglossan synapomorphy).

7. Supraoccipital makes broad contact with parietal (McDowell and Bogert, 1954; Pregill et al., 1986).

8. Osteoderms do not fuse to skull (McDowell and Bogert, 1954).

9. Supratemporal processes of parietal narrow (Pregill et al., 1986).

10. Well-developed descending (subolfactory) processes of the frontal, directed posteromedially, and in contact or nearly so (McDowell and Bogert, 1954).

11. Reduction of outer conch of quadrate (McDowell and Bogert, 1954; Pregill et al., 1986).

12. Hypoglossal foramen enlarged, confluent with vagal foramen (McDowell and Bogert, 1954; Pregill et al., 1986).

13. In lateral view, disarticulated surangular expanded anterodorsally and nearly vertical at anterior margin, termination of bone relatively closer to anterior end of postdentary bones (61-2).

14. With dentary removed, medial view of prearticular reduced, not extending well anterior to coronoid bone (62-1; C within snakes).

15. Coronoid and surangular processes reduced on posterolateral dentary (63-2).

16. Splenial moves with dentary in intramandibular kinesis (Pregill et al., 1986).

17. Loss of tongue papillae, foretongue covered by a smooth, keratinized, even layer of stratified squamous epithelium (Schwenk, 1988; C in snakes).

18. Sublingual glands dense, compact, and round in transverse section (Schwenk, 1988; C in snakes).
19. Anterior head of *m. pseudotemporalis* enlarged (Rieppel, 1980b).
20. *M. genioglossus lateralis* subdivided into separate bundles (Rieppel, 1980b).
21. *M. constrictor colli* extends anteriorly, covering first ceratobranchials (Rieppel, 1980b).
22. Second epibranchial lost (90-1; C in chamaeleontids, gymnophthalmids, and dibamids, and within pygopodids, xenosaurids, amphisbaenians, and snakes).
23. Nine cervical vertebrae (108-1).
24. Precondylar constriction in vertebrae (94-1; C within agamids*, teiids, and snakes).
25. Caudal chevrons and cervical hypapophyses attach on centrum only (Pregill et al., 1986).
26. Peduncles on cervical and caudal vertebrae long (Pregill et al., 1986).
27. Three pairs of rib attachment points on sternum (109-2; further transformed in *Lanthanotus* to two; C within iguanids*, agamids*, gekkonids, cordylids, lacertids, and anguids).
28. Free part of tongue notched between 40-50% (137-4; C in gymnophthalmids, teiids, and amphisbaenians; further transformed in *Varanus* to state 5).
29. Paired horns in the apical regions of the hemipenes (Branch, 1982).

Comments: *Lanthanotus* shares at least six derived characters with *Heloderma* that do not occur in *Varanus*: contact of prefrontal and postorbital above orbits (5-1), absence of postorbital bone with concomitant interruption of upper temporal bar (16-1), absence of a parietal foramen (26-1), absence of ossified palpebrals (36-0), posterior opening of vidian canal at basisphenoid-prootic suture (53-1), and a reduction in the number of scleral ossicles (89-1). Nevertheless, we consider these shared derived features to be convergent because the number of derived characters shared by *Lanthanotus* and *Varanus* but not *Heloderma* is even greater. This conclusion is strengthened when *Cherminotus* (Borsuk-Bialynicka, 1984), a Cretaceous relative of *Lanthanotus*, is considered (although most of the above characters are not known for *Cherminotus*). Pregill et al. (1986) also provided a discussion of this convergence.

We follow Pregill et al. (1986) in placing *Lanthanotus* within Varanidae. We accept relationship of *Cherminotus* and *Lanthanotus*, and relationship of the Eocene *Saniwa* (Gilmore, 1928) and the Cretaceous *Sanivides* and *Telmasaurus* (Borsuk-Bialynicka, 1984) to *Varanus*, as proposed by Pregill et al. (1986), but for the present have not included them in our definitions above and below. This is not only because they were not included in our character matrix, but because we believe that further analysis of these taxa is needed that is beyond the scope of this paper. Pregill et al. (1986:169), for instance, pointed out for the Cretaceous forms that "These new varanoids ... [are] ... difficult to place unambiguously ..."

Numbers 13-16 in the list above are correlated with the formation of an intramandibular hinge (Gauthier, 1982).

Lanthanotus Steindachner, 1878

Definition: Given the monospecific nature of *Lanthanotus*, we leave it undefined. The name should eventually be applied to one of the monophyletic groups containing the species *Lanthanotus borneensis*. In this paper we treat *Lanthanotus* as if it is synonymous with *L. borneensis*.

Diagnosis: *Lanthanotus* is characterized by the following synapomorphies (Fig. 30).

1. Prefrontal contacts postfrontal above orbits (5-1; C in *Heloderma*, within chamaeleontids, pygopodids, scincids, anguids, amphisbaenians, and snakes; contact not present in *Cherminotus*).
2. Postorbital and upper temporal arch lost (16-1; C in gekkotans, *Heloderma*, and dibamids, within scincids; postorbital present in *Cherminotus*).
3. Loss of parietal foramen (26-1; C in and within many basic taxa, including *Heloderma*; foramen present in *Cherminotus*).

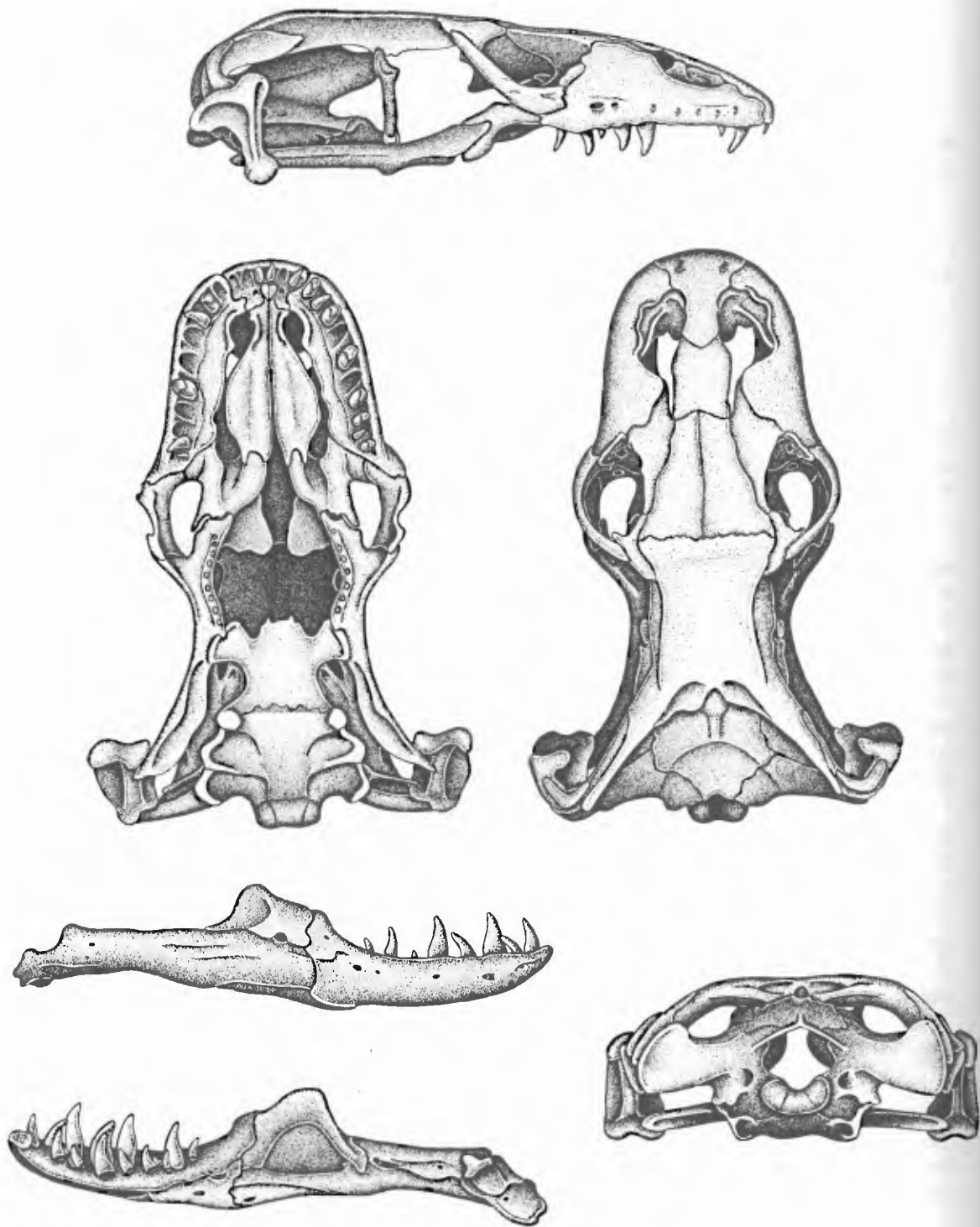


FIGURE 30. Skull and mandible of *Lanthanotus borneensis* (Varanidae). Right lateral, dorsal, occipital, and ventral views of skull; lateral and medial views of mandible. Scale = 5 mm. From Rieppel (1980b). See end of paper for abbreviations.

4. Loss of palpebral (36-0; R of anguimorph synapomorphy, C in *Heloderma*, within scincoids).
5. Posterior opening of vidian canal at basisphenoid-prootic suture (53-1; C in lacertids, anguids, *Shinisaurus*, and *Heloderma*, within scincoids and xantusiids).
6. Splenial with very limited overlap on postdentary bones (66-2; C in snakes).
7. Anterior end of coronoid meets dentary directly (70-1; C in snakes, within iguanids* and amphisbaenians).
8. Vertical suture between angular and splenial on medial side of jaw (McDowell and Bogert, 1954).
9. Broad palatal shelves (Pregill et al., 1986; not present in *Cherminotus*).
10. Presence of palatine teeth (82-0; R of squamate synapomorphy, C within iguanids*, anguids, and snakes).
11. Six scleral ossicles (89-1).
12. Prominent ascending lateral pillar on septomaxilla (McDowell and Bogert, 1954).
13. 3-c layer of m. adductor mandibulae externus profundus double layered, second layer originating from the crista prootica (Rieppel, 1980b).
14. Sternum with two or fewer pairs of rib attachment points (109-3; C in chamaeleontids, pygopodids, and amphisbaenians).
15. Dermal rugosities lost (129-0; R of autarchoglossan synapomorphy, C in many groups).
16. Only four phalanges on the fourth digit of manus and pes; only three phalanges on digit five of pes (McDowell and Bogert, 1954; Rieppel, 1980a).

Comments: Although in our original arrangement of basic taxa we scored *Lanthanotus* and *Varanus* separately, we have included them here in Varanidae, following Pregill et al. (1986).

Rieppel (1982) found no evidence of special similarity of *Lanthanotus* and snakes, nor has our study identified further similarities. We therefore follow most previous authors in not accepting the hypothesis of close relationship between the two taxa suggested by McDowell and Bogert (1954) and McDowell (1972). Evidence for a relationship between snakes and varanoids as a whole is discussed in the comments on snakes below.

Varanus Merrem, 1820

Definition: The most recent common ancestor of the extant species of *Varanus* (sensu Mertens, 1942) and all of its descendants.

Diagnosis: Monophyly of this taxon is supported by the following synapomorphies.

1. Descending processes of frontals in contact below olfactory tracts (10-1; C in gekkotans, *Heloderma*, amphisbaenians, and snakes, within xantusiids, gymnophthalmids, and anguids).
2. Postfrontal fused to postorbital in postembryonic ontogeny (14-1; C within lacertids, gymnophthalmids, scincids, and xenosaurs; bones separate in the fossil *Saniwa*, may be separate occasionally in young *Varanus*).
3. Jugal reduced, postorbital bar incomplete, but may be bound by ligament to postorbitofrontal (32-1; C in gekkotans, dibamids, and snakes, within scincids and anguids).
4. Double lacrimal duct remains double internally, as well as externally (duct single in the fossil *Saniwa*; pers. obs.).
5. Pterygoid teeth lost (83-1; C in acrodontans, gekkotans, xantusiids, dibamids, and amphisbaenians, within many basic taxa).
6. Tooth bases highly expanded, with labyrinthine infolding forming a honeycomb-like sponge (Bullet, 1942).
7. Elongated, fork-shaped premaxilla (Rieppel, 1980b).
8. Fifteen scleral ossicles (88-0; R of squamate synapomorphy).

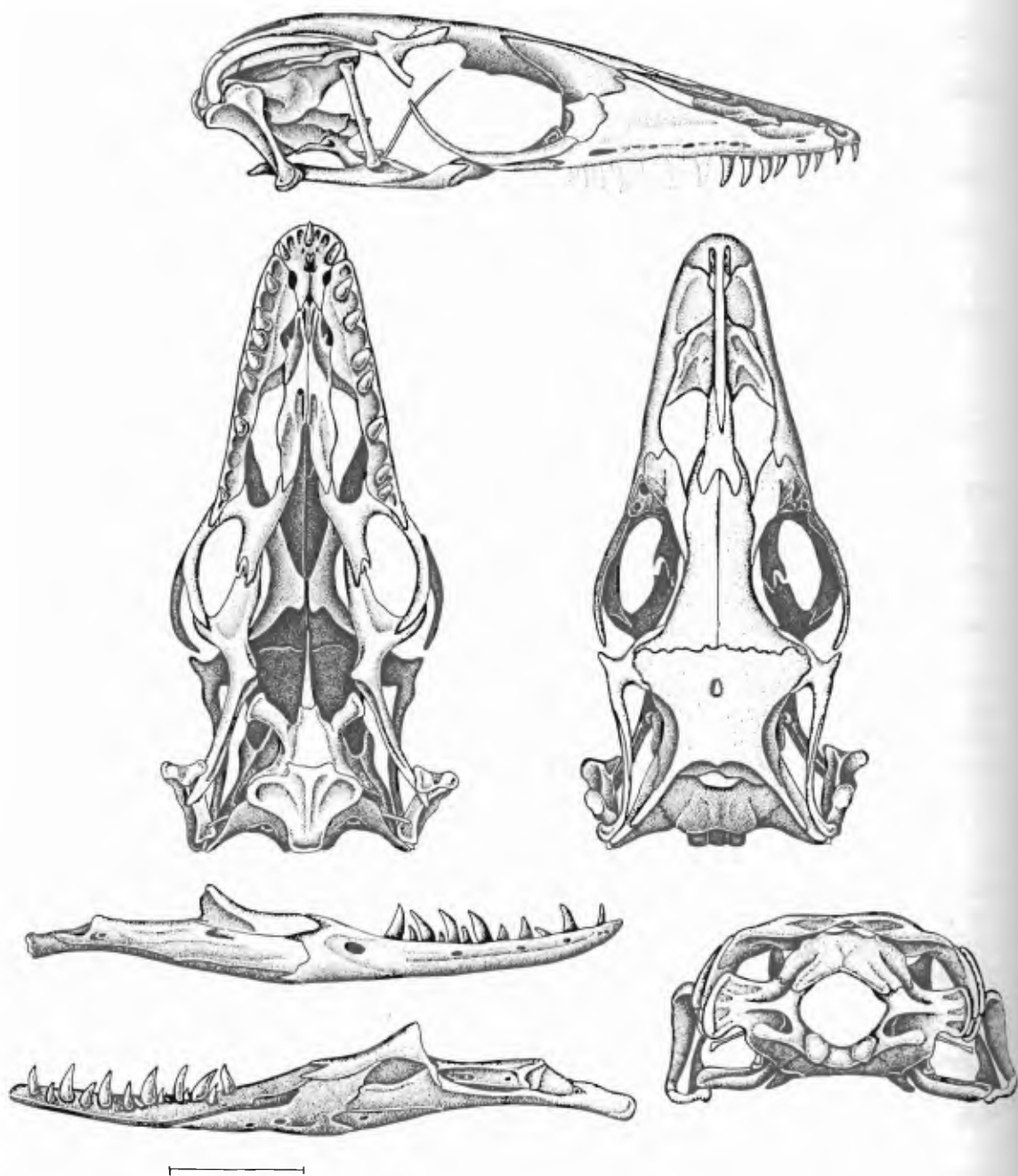


FIGURE 31. Skull and mandible of *Varanus salvator* (Varanidae). Right lateral, dorsal, occipital, and ventral views of skull; lateral and medial views of mandible. Scale = 5 mm. From Rieppel (1980b). See end of paper for abbreviations.

9. No cervical ribs on fourth cervical vertebra (Hoffstetter and Gasc, 1967).
 10. Cervical vertebrae elongated (Hoffstetter and Gasc, 1969).
 11. Posterior coracoid emargination present (113-1; C in teiids and gymnophthalmids, within iguanids*, agamids*, and gekkonids; also present in some *Lanthanotus*, and it is possible that this is a *Varanus-Lanthanotus* synapomorphy).
 12. Pubis relatively short, symphyseal process short, more ventrally directed, and pubic tubercle more distally placed (124-0; R of scleroglossan synapomorphy).
 13. Carpal intermedium lost (Renous-Lécuru, 1973).
 14. Reduced proximal articulations of fifth metatarsal (Robinson, 1975).
 15. Origin of *m. pseudotemporalis superficialis* extended posteriorly (132-1; C in lacertoids).
 16. Many specializations of the head musculature (see Rieppel, 1980b).
 17. Free part of tongue notched more than 50% (137-5; C in snakes).
 18. Lingual tongue sheath comprising inner and outer sheathing folds (McDowell, 1972; Schwenk, 1988; C in snakes).
 19. Unique configuration of pituitary and other gland histology (Saint-Girons, 1970, 1976; Gabe and Saint-Girons, 1976).
 20. Nucleus reticularis ventrolateralis of spinal cord present (Cruce and Newman, 1984, indicated some uncertainty regarding their identification of this structure in *Varanus*). C in lacertids, teiids, gymnophthalmids, dibamids, and snakes, and possibly scincids.
 21. Dracomorph brain (Northcutt, 1978). C in iguanians, teioids.
- Comments:* Identification of monophyletic groups within *Varanus* is possible (e. g., at least some of the subgenera of Mertens, 1942); demonstration of the relationships between these taxa and the fossil taxa *Saniwa*, *Sanivides*, and *Telmasaurus* (Gilmore, 1928; Borsuk-Bialynicka, 1984) is an area deserving of future work (see also Pregill et al., 1986).

SCLEROGLOSSA incertae sedis

We discuss below the reasons for our placement of dibamids, snakes, and amphisbaenians as Scleroglossa. Table 1 lists characters that diagnose both Scleroglossa and Autarchoglossa, and gives the condition of these characters for snakes, dibamids, and amphisbaenians.

As seen in Table 1, snakes, dibamids, and amphisbaenians possess the great majority of the diagnostic scleroglossan characters for which they can be scored. Absence or extreme reduction of limbs and limb girdle accounts for our inability to score for one or the other (or both) of the remaining characters (109-130). Although dibamids and amphisbaenians are each plesiomorphic for two of the diagnostic scleroglossan characters, and snakes for three, the fact that in each case one or two of the characters are different suggests that homoplasy is involved.

At the level of Autarchoglossa the picture is much less clear (Table 1). State 1 of characters 17, 129, and 134 diagnoses autarchoglossans, and of these, dibamids, amphisbaenians, and snakes have only 134 (presence of the *m. rectus abdominis lateralis*). Because snakes, dibamids, and amphisbaenians possess one (but lack others) of the autarchoglossan synapomorphies, they may be outside of Autarchoglossa, yet more closely related to autarchoglossans than are gekkotans. However, we also consider it possible that all three taxa are nested within Autarchoglossa. Dibamids may be most closely related to acontine scincids (Rieppel, 1984a). Amphisbaenians may be more closely related to scincomorphs than to other squamates (Schwenk, 1988), or more specifically to Lacertoidea (Gauthier, 1984). Snakes, on the other hand, are more likely to be anguimorph than scincomorph relatives. We have discussed these possibilities more fully below, but unfortunately, we cannot document them with much confidence at present.

We discuss below, for each of the three groups, the characters of other scleroglossan taxa that each possesses. The synapomorphies for dibamids, amphisbaenians, and snakes given in the list

come from three sources: (1) Those from our character list that were identified as convergent with *Autarchoglossa* or one of its subgroups. (2) Squamatan and scleroglossan reversals possessed by dibamids, amphisbaenians, and snakes, because our evidence indicates that they are squamates, and *Scleroglossa* is the least inclusive group to which we can refer them. (3) Characters from the literature. Indication is given of the taxa with which each of these three limbless groups shares the characters in question. A more robust hypothesis of relationships within scleroglossans may ultimately show that some of the characters are synapomorphies of more inclusive groups or represent multiple synapomorphies.

DIBAMIDAE Boulenger, 1884

Definition: The most recent common ancestor of *Dibamus* and *Anelytropsis* and all of its descendants.

Diagnosis: The following synapomorphies characterize dibamids (Fig. 32).

1. Nasals and prefrontals separated by anterolateral processes of the frontals, the latter contacting the maxillae (4-1). Scincomorphs, amphisbaenians.
2. Postorbital lost (16-1). *Heloderma*, *Lanthanotus*, gekkotans; within scincids, amphisbaenians.
3. Parietal tabs present as thin, triangular structures that extend anteriorly into shallow triangular fossae on the ventral surface of the frontals (22-1; determined only in *Dibamus*). Lacertoids; within iguanians and scincoids.
4. Parietal foramen lost (26-1). Gekkotans, gymnophthalmids, helodermatids, *Lanthanotus*, snakes; within iguanids*, lacertids, scincids, xantusiids, cordylids, chamaeleontids.
5. Posterior extension of maxillae reaches only just beyond anterior edge of orbits (27-1). Xantusiids, varanoids; within anguids.
6. Lacrimal lost (28-1). Gekkotans, xantusiids, snakes; within iguanids*, lacertids, scincids, amphisbaenians.
7. Jugal reduced or lost, postorbital bar incomplete (32-1). Gekkotans, varanids; within snakes, anguids, scincids, amphisbaenians.
8. Posterior border of opening for Jacobson's organ closed by contact of maxilla and vomer (42-1). The opening is actually finished by septomaxilla in *Dibamus* (Rieppel, 1984a), and is thus more derived than the vomer-maxilla contact seen in *Anelytropsis* (fide Greer, 1985a) and many other squamates.
9. Medial extensions from ventrolateral edges of palatines form air passages for bony secondary palate (43-1). Scincids.
10. Ectopterygoid contacts palatine anterolaterally, excluding maxilla from suborbital fenestra (45-1). Xantusiids, teiids, varanoids; within anguids, gekkotans, amphisbaenians.
11. Opisthotic and exoccipital bones remain separate or fuse relatively late in ontogeny (51-0). R of squamate synapomorphy.
12. Posterior opening of vidian canal lies entirely within prootic (53-2). This condition occurs in *Anelytropsis*; in *Dibamus* it is also far posterior, either at anteroventral margin of the fenestra ovalis (Greer, 1985a), or between prootic and the ossified epiphysis of the sphenoccipital tubercle (Rieppel, 1984a). In both genera, the foramen is in a far posterior position, and the canal is open dorsally over its anterior course through the basisphenoid.
13. Large, laterally placed fenestra ovalis (Rieppel, 1984c; Greer, 1985a). Amphisbaenians, other squamates with miniaturized skulls and/or burrowing adaptations.
14. Closure of lateral aperture of recessus scalae tympani (Rieppel, 1984a; Greer, 1985). Chamaeleontids, amphisbaenians.

15. Absence of cartilaginous interorbital septum (Rieppel, 1984a). Amphisbaenians, snakes.
16. Absence of cartilaginous processus ascendens tecti synotici (Rieppel, 1984a). Gekkotans, snakes.
17. Dentary tube closed and fused (55-2). Xantusiids, gekkotans; within iguanids*, gymnophthalmids, scincids, amphisbaenians.
18. Lateral coronoid process of dentary large (60-1). Xantusiids, scincoids; within anguids, xenosaurs, amphisbaenians.
19. Splenial lost (65-2). Chamaeleontids; within iguanids*, agamids*, gekkotans, amphisbaenians.
20. No coronoid lappet on lateral surface of dentary (68-0). Acrodonta; within iguanids*, varanids, snakes.
21. Angular lost (not fused) (72-1). Within xantusiids, gekkotans, scincids, iguanids*, amphisbaenians, snakes.
22. Retroarticular process broadened posteriorly (78-1). Gekkotans, scincoids, anguids.
23. Marginal replacement teeth develop posterolingually, small resorption pits present (intermediate type) (85-1). Anguimorphs; within gymnophthalmids, teiids, scincids, amphisbaenians.
24. Scleral ossicles lacking (89-1). Snakes, most amphisbaenians.
25. Second epibranchials lost (90-1). Chamaeleontids, gymnophthalmids, varanids, amphisbaenians, snakes; within iguanids*, agamids*, gekkotans, anguids.
26. Second ceratobranchials lost (91-1). Chamaeleontids, anguimorphs, snakes; within iguanids*, agamids*, cordylids, gymnophthalmids, scincids, gekkonids, teiids, amphisbaenians.
27. Cervical intercentra fused to posterior part of preceding centrum (97-2). Anguids; variable in *Heloderma*, *Lanthanotus*, *Varanus*, scincids.
28. Anterior pair of transverse processes of caudal vertebrae lost (101-2). Amphisbaenians; variable in scincids, anguids.
29. More than 26 presacral vertebrae (106-1). Anguimorphs, within many other basic taxa.
30. Less than eight cervical vertebrae (107-1). Chamaeleontids; variable in anguids, cordylids, scincids.
31. One pair of rib attachment points on each side of sternum (109-3). Within iguanids*, gymnophthalmids, scincids, amphisbaenians; further transformation of scleroglossan synapomorphy (109-1).
32. At least some postxiphisternal inscriptional ribs continuous midventrally (110-1). Chamaeleontids, *Uroplatus* (gekkonid), *Chamaesaura* (cordylid), *Bachia* (gymnophthalmid), *Nucras* (lacertid); within iguanids* and scincids.
33. Clavicle lost (115-1). Chamaeleontids, snakes; within amphisbaenians.
34. Interclavicle lost (118-1). Chamaeleontids, pygopodids, amphisbaenians, snakes; variable in anguids, scincids.
35. *M. rectus abdominis lateralis* present (134-1). Autarchoglossans.
36. Anterior tip of tongue not notched (137-0). R of squamate synapomorphy. Chamaeleontids.
37. Stapedial artery perforates stapes (145-1). Some gekkonids.
38. *M. geniomyoideus* present (Groombridge, 1979). Anguimorphs.
39. Cycloid scales present (148-1). Scincids; variable in gekkonids, pygopodids, gymnophthalmids, cordylids, snakes.
40. Interdigitation of the periventricular gray zones of the optic tectum and enlargement of lamina 7 of the posterior colliculus (Senn and Northcutt, 1973). Feyliniine scincids, snakes.

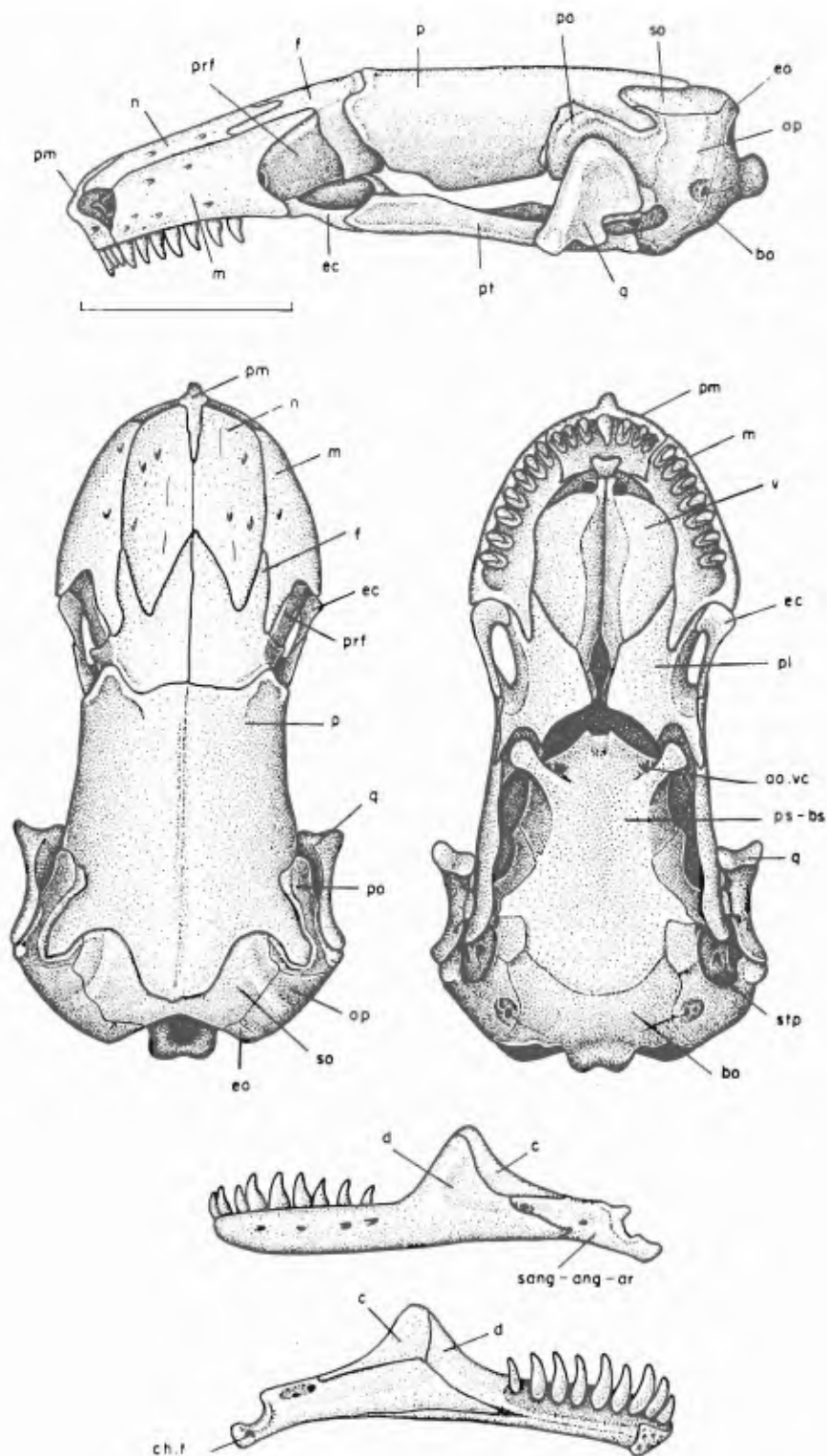


FIGURE 32. Skull and mandible of *Dibamus novaeguineae* (Dibamidae). Left lateral, dorsal, and ventral views of skull; lateral and medial views of mandible. Scale = 2 mm. From Rieppel (1984a), by permission of the Zoological Society of London. See end of paper for abbreviations.

TABLE 1. Diagnostic characters of Scleroglossa and Autarchoglossa, and their distribution in dibamids, amphisbaenians, and snakes. Bold italicized entries indicate plesiomorphies.

SCLEROGLOSSA	DIBAMIDAE	AMPHISBAENIA	SERPENTES
9 - 1	1	1	1
13 - 1	1, N	1, N	0
17 - 1	N	N	0
34 - 1	1, N	1	N
39 - 1	1?	1	1, N
40 - 1	1	1	1
41 - 1	1	1	1
44 - 1	1	1	1
49 - 1	0?	1, 0	N?
54 - 1	0	0	0
58 - 1	1	0	1
74 - 1	1	1	1, N
79 - 1	1	1	1, N
105 - 1	1	1	1
109 - 1	3	3, N	N
116 - 1	N	N	N
120 - 1	N	N	N
123 - 1	N	N	N
124 - 1	N	N	N
130 - 1	N	1	N
133 - 1	-	-	0
138 - 1	1	2	1
146 - 1	1	1	1
147 - 1	1	1	1, 0
Prey Grasping by Jaws	?	1	1
Oscill. Tongue Protrus.	?	1	1
No Foretongue Gl. Epith.	1	1	1
AUTARCHOGLOSSA	DIBAMIDAE	AMPHISBAENIA	SERPENTES
18 - 1	N	N	N
129 - 1	0	0, 2	0
134 - 1	1	1	1

41. Nucleus reticularis ventrolateralis of spinal cord present (Cruce and Newman, 1984). Lacertiforms, possibly varanids and scincids.

42. Kidneys precloacal (Underwood, in litt., 1985). R of squamate or lepidosaur synapomorphy. Snakes (see comments in section on Serpentes).

Comments: Studies by Rieppel (1984a) and Greer (1985) have greatly increased our knowledge of dibamids. Greer identified five taxa to which dibamids might be related, and gave percentages of his 49 assessable derived characters that each of these taxa shared with dibamids: amphisbaenians (64%), snakes (58%), *Anniella* (53%), scincids (49% with feyliniines; 43% with acontines), and pygopodids (37%). He also identified some characters suggesting that dibamids are the sister-group of all other squamates, but realized that these characters might be reversals. In Table 1 above, dibamids, amphisbaenians, and snakes are compared with Scleroglossa and Autarchoglossa.

Dibamids have most of the scleroglossan characters for which they can be scored (16 of 27; Table 1). They lack two: alar process elongated and anterodorsally directed (49-1) and origin of jaw adductor musculature attaches only on ventral surface of parietal (54-1). In both cases, modification of the braincase associated with miniaturization and burrowing adaptations (Rieppel, 1984a) have almost certainly modified these characters. The five scleroglossan limb characters, of course, cannot be determined for dibamids. We have no information for three characters: presence of anterior head of *m. pseudotemporalis profundus* (133-1), prey grasping by jaws, and oscillatory tongue protrusion. This tabulation gives rather strong support for scleroglossan affinities of dibamids, although as we detail below, a more resolved interpretation cannot be offered.

Dibamids have nine of 45 gekkotan synapomorphies: postorbital lost (16-1), parietal foramen lost (26-1), lacrimal lost (28-1), jugal reduced or lost, postorbital bar incomplete (32-1), dentary tube closed and fused around Meckel's canal (55-2), splenial lost (65-2, a further transformation of the gekkonid state 1, does not extend as far forward as tooth row midpoint), retroarticular process broadened posteriorly (78-1), and pterygoid teeth lost (83-1). Also as in gekkotans, they lack the processus ascendens tecti synotici. The majority of these are characters associated with reduction or loss of various structures or are shared with many other taxa, and we agree with Rieppel (1984a) that relationship of dibamids to gekkotans is not well supported.

One autarchoglossan synapomorphy occurs in dibamids: presence of *m. rectus abdominis lateralis* (134-1). They cannot be scored for 17-1 and 18-1 because of absence of the postorbital and supratemporal arches. They lack dermal rugosities (129-1). Although, as noted above, dibamids have nine gekkotan characters, six of these are loss characters that occur frequently in various squamate basic taxa, and the other two (55-2 and 78-1) also occur in or within scincids, the group suggested by Rieppel, 1984a to include the most likely sister group of dibamids. In view of the above, and the presence in dibamids of the *m. rectus abdominis lateralis*, it seems reasonable to suggest that dibamids are closer to autarchoglossans than to gekkotans.

Dibamids have one of the nine scincomorph synapomorphies, nasal-prefrontal contact lost, the two bones separated by anterolateral processes of the frontals, the latter contacting the maxillae (4-1). They have one of the seven lacertoid synapomorphies, parietal tabs present (22-1), and share two of our thirteen scincoid synapomorphies, lateral coronoid process of dentary large, extends dorsally onto lateral surface of coronoid (60-1) and retroarticular process broadened posteriorly (78-1). They have three of our list of eleven scincid synapomorphies: the unique and complex folding of palatine bones (43-1), cycloid scales present (148-1), and presence of the nucleus reticularis ventrolateralis of the spinal cord. Their low representation of other characters that diagnose scincomorphs (or taxa within scincomorphs) allows only a weak hypothesis of relationship to that taxon based on our study. Rieppel (1984a) concluded, however, that *Dibamus* is most likely to be the sister group of the acontine scincids, a conclusion similar to that reached by Camp (1923), who considered *Dibamus*, *Anelytropsis*, and *Feylinia* to be derived from scincids. The derived characters that acontine scincids and *Dibamus* share for the most part also occur in *Anelytropsis* (Greer, 1984a).

Dibamids share only four of the 22 anguimorph synapomorphies: marginal replacement teeth develop posterolingually, small resorption pits present (85-1), second ceratobranchials lost (91-1), cervical intercentra fused to posterior part of preceding centrum (97-2), and presence of more than 26 presacral vertebrae (106-1). Only seven of our 42 amphisbaenian synapomorphies occur in dibamids. Lack of contact between nasals and prefrontals, with anterolateral processes of frontals contacting the maxillae (4-1), second epibranchials lost (90-1), interclavicle lost (118-1), far lateral position of the fenestra ovalis, closure of the lateral opening of the recessus scalae tympani, and lack of an interorbital septum. Rieppel (1984a) discussed characters that are possible synapomorphies of amphisbaenians and *Dibamus*. Many of these occur only in a few amphisbaenian taxa, a

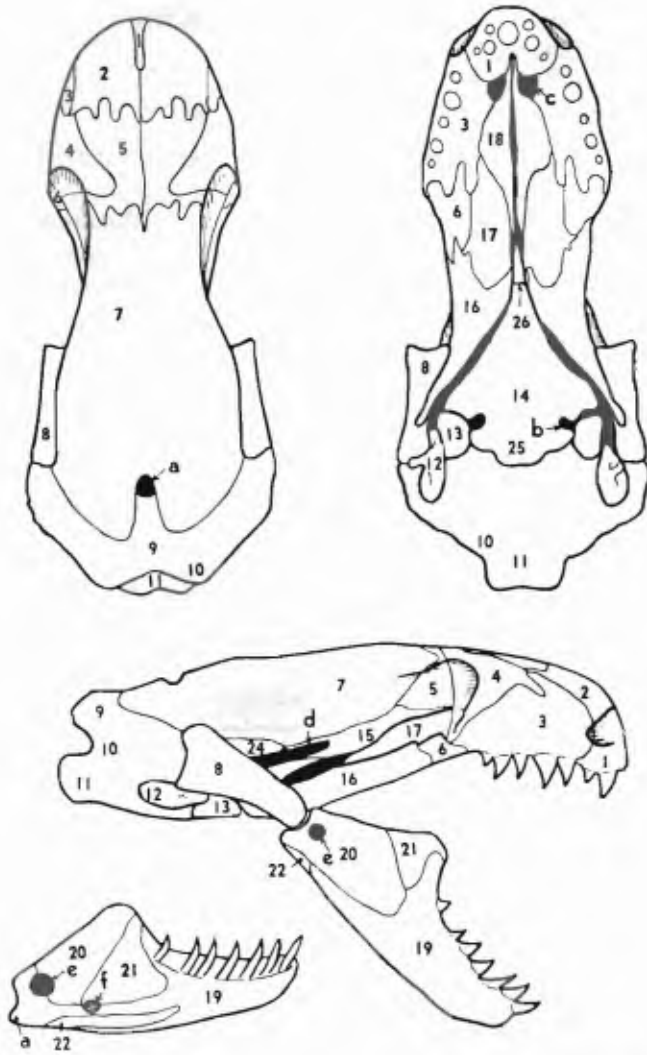


FIGURE 33. Skull and mandible of *Amphisbaena fuliginosa* (Amphisbaenia). Dorsal, right lateral, and ventral views of skull; medial view of mandible. Scale = 2 mm. From Zangeri (1944). See end of paper for abbreviations.

number of characters involve loss, and others are shared with various squamate taxa. Nevertheless (as Greer, 1985a, also noted), there are some remarkable similarities shared by dibamids and amphisbaenians. As in dibamids, amphisbaenians (at least some) have a posterodorsal process of the maxilla that enters the orbit (this is not present in *Anelytropsis*, judging from the figure in Greer, 1985a), and posterior position of the posterior opening of the vidian canal.

Dibamids share few characters with snakes, as Rieppel (1984a) pointed out, and the few characters held in common must be weighed against the much greater number of similarities with other groups of squamates.

Although we agree with Rieppel (1984a) that relationship of dibamids to acontine scincids may be the best documented hypothesis of dibamid relationships within Scleroglossa, our own study only permits placement of dibamids as Scleroglossa incertae sedis. Resolution of relation-

ships within scincids and additional study of *Dibamus*, and especially *Anelytropsis*, may help resolve the relationships of dibamids within Scleroglossa.

AMPHISBAENIA Gray, 1844

Definition: The most recent common ancestor of *Rhineura*, Amphisbaenidae*, *Bipes*, and Trogonophidae, and all of its descendants.

Diagnosis: The following synapomorphies characterize amphisbaenians (Fig. 33).

1. Lack of contact between nasals and prefrontals, with anterolateral processes of frontals contacting the maxillae (4-1). Scincomorphs, dibamids; within gekkotans, anguids.
2. Prefrontal contacts postfrontal (or fused postorbital-postfrontal?) above orbits (5-1). *Heloderma*, *Lanthanotus*; within chamaeleontids, scincids, pygopodids, anguids, snakes.
3. Descending processes of frontals in contact below olfactory tracts (10-1). Gekkotans, helodermatids, *Varanus*, snakes; within gymnophthalmids, xantusiids, anguids.
4. Supratemporal lost (35-1). Pygopodids, dibamids; within gekkonids, agamids*, snakes; possibly lost in the anguid *Anniella*.
5. Posterior opening of Jacobson's organ closed by maxilla and vomer (42-1). *Anelytropsis*, *Varanus*; within anguids, pygopodids, scincids, gymnophthalmids, xantusiids.
6. Epityrgoid lost, or minute in a few taxa (47-1). Chamaeleontids, snakes, *Dibamus*; within iguanids*.
7. Orbitosphenoid a membrane bone rather than a cartilage ossification (May, 1978; Bellairs and Gans, 1983). Unique, but determined only in *Leposternon*. Rieppel (1981b) posited that this bone (his pleurosphenoid) is equivalent to the crista alaris of the prootic of lizards.
8. Skull extremely solid, anterior bones with complex interdigitations (Gans, 1978). Unique.
9. Median enlarged premaxillary tooth (Gans, 1978). Unique.
10. Anterior braincase closed by bone (Gans, 1978). Snakes.
11. Large, lateroventrally placed fenestra ovalis (Rieppel, 1984a; Greer, 1985a). Dibamids; other fossorial forms in various taxa.
12. Closure of lateral aperture of recessus scalae tympani (Rieppel, 1984a; Greer, 1985a). Dibamids, chamaeleontids.
13. Subdental shelf small or lost (58-0). Iguanians, anguids, varanoids; within gymnophthalmids.
14. Splenial reduction and loss (65-1,2). Many squamate taxa.
15. Splenial does not extend posteriorly to apex of coronoid (66-1). Agamids*, xantusiids, *Heloderma*, varanids; within iguanids*, gymnophthalmids.
16. Pterygoid teeth lost (83-1). Many squamate taxa.
17. Marginal teeth replaced posteromedially, small replacements pits present (intermediate type) (85-1). Anguids, xenosaurs, dibamids; within gymnophthalmids, teiids, scincids. Varanoids and snakes, and some amphisbaenians, are further transformed.
18. Scleral ossicles highly reduced (89-1). Reduction takes place in a number of taxa, but only snakes and dibamids, in which they are lacking entirely, exhibit as great or greater reduction than amphisbaenians.
19. Second epibranchials lost (90-1). Chamaeleontids, gymnophthalmids, dibamids, *Lanthanotus*, *Varanus*, xenosaurs, snakes; within iguanids*, agamids*, gekkonids, pygopodids, scincids, anguids.
20. Hypohyals large relative to other squamates (MacLean, 1974). Teioids.
21. Cervical intercentra fused to preceding centrum (97-2). Anguimorphs, dibamids, snakes; within scincids.

22. Caudal vertebrae with two pairs of convergent processes, either pair being present (101-1). Anguids, and within scincids.
23. More than 26 presacral vertebrae (106-1). Anguimorpha, within many other basic taxa.
24. Caudal autotomy at a single vertebral site (autotomy annulus) (Gans, 1978). Unique.
25. One or no pairs of rib attachment points on sternum (109-3). Chamaeleontids, *Lanthanotus*, pygopodids.
26. Anterior coracoid emargination lost (112-0; R of squamate synapomorphy). Chamaeleontids; within pygopodids and *Heloderma*.
27. Epicoracoid cartilages fail to contact either suprascapula or mesoscapula (114-1). Chamaeleontids, lacertids, varanoids; within iguanids*, agamids*, gekkonids.
28. Interclavicle absence (118-1). Chamaeleontids, pygopodids, dibamids, snakes; within anguids, scincids.
29. Ectepicondylar foramen and groove lost (122-1). Chamaeleontids, teioids.
30. *M. rectus abdominis lateralis* present (134-1). Autarchoglossans.
31. Free part of tongue notched between 40-50% (137-4). Teioids, *Lanthanotus*.
32. Anterior tongue mushroom-shaped in cross section, entire tongue keratinized and non-glandular (138-2). Scinciforms.
33. Lingual glands entirely lost (Schwenk, 1988). Unique.
34. Imbricating lingual scales present (Schwenk, 1988). Teioids.
35. Choanal folds and ectochoanal cartilage reduced (Pratt, 1948). Within autarchoglossans and iguanians.
36. Internal process of stapes lost (141-1). Anguids, scincids, gekkotans; within xantusiids.
37. *M. vertebrocutaneous* present (Gans, 1978). Unique.
38. Left lung dominant (Gans, 1978). Unique.
39. Kidneys essentially unconnected to mesentery in the coelomic cavity (Gans, 1978; Crook and Parsons, 1980). Unique.
40. Islets of Langerhans with 70% beta and 30% alpha cells (Gans, 1978; the reverse frequency is shown by other squamates, but we are not certain of the polarity of this character). Unique.
41. Left aortic arch dominant (Gans, 1978). Unique.
42. Carotid duct lost (Underwood, 1957b). Chamaeleontids, varanoids, snakes.

Comments: Our analysis has been unsatisfactory in terms of fully resolving the phylogenetic position of amphisbaenians. Gans (1978:402) stated "The Amphisbaenia are clearly more similar to lizards than to snakes. When there is a departure from the general squamate condition, it rarely appears to be in 'the direction' of snakes; hence, amphisbaenians cannot be considered intermediate between snakes and lizards." In contrast, Rage (1982a,b) argued for a sister-group relationship between snakes and amphisbaenians (discussed below under *Serpentes*). We do not support Rage's hypothesis here, but we have come to no more well supported conclusion.

Amphisbaenians have all of the scleroglossan characters for which they can be scored (19 of 27), except adductor musculature attaches only on ventral surface of parietal (54-1), and subdental shelf large (58-1). Except for *Bipes*, they cannot be scored for most limb characters. The adductor musculature character can be explained as a reversal resulting from skull modification concomitant on their burrowing habitus, but we have no explanation for the lack of a large subdental shelf. Although this seems to suggest that Amphisbaenia is outside of Scleroglossa, the sharing of derived characters by amphisbaenians and several subgroups of Scleroglossa contradicts such placement. For this reason, we place Amphisbaenia as Scleroglossa, *incertae sedis*.

Amphisbaenians have four of 46 gekkotan synapomorphies: descending processes of frontals in contact below olfactory tracts (10-1), splenial reduction (65-1), pterygoid teeth lost (83-1), and internal process of stapes lost (141-1). Other gekkotan characters present in amphisbaenians are variable within the latter taxon.

Amphisbaenians share only one of the three autarchoglossan synapomorphies: presence of the *m. rectus abdominis lateralis* (134-1). They lack dermal rugosities (129-1), except for some rhineurids, which have a more derived state (129-2), and cannot be scored for a further character, jugal and squamosal in contact on supratemporal arch, because of doubt regarding homology of the jugal and absence of the supratemporal arch. Presence of this single autarchoglossan synapomorphy in Amphisbaenia suggests that amphisbaenians are closer to that group than to gekkotans, and other characters (discussed below) indicate that they may be nested within Autarchoglossa.

Amphisbaenians have two of nine scincomorph synapomorphies: nasal-prefrontal contact lost, the two bones separated by anterolateral processes of frontals, the latter contacting the maxillae (4-1) and anterior tongue mushroom-shaped in cross section, entire tongue keratinized (138-2). Within scincomorphs, they have none of the synapomorphies of lacertoids or scincoids. Amphisbaenians have three of 14 teioid synapomorphies: ectepicondylar foramen and groove lost (122-1), free part of tongue notched between 40 and 50% (137-4), and imbricating lingual scales. Other workers have suggested possible scincomorph or within-scincomorph relationships for amphisbaenians. Boulenger (1884), Bogert (1964), and Böhme (1981) suggested a relationship to teiids (our Teiioidea). More recently Schwenk (1988), on the basis of tongue structure, found more support for a sister group relationship between amphisbaenians and scincomorphs than for placement within scincomorphs as the sister group of Teiioidea. Investigation of synapomorphies that link amphisbaenians with particular scincomorph clades may ultimately lead to resolution of amphisbaenian relationships.

Amphisbaenians have four of 22 anguimorph synapomorphies: replacement teeth develop posterolingually with small resorption pits (85-1), cervical intercentra fused to posterior part of preceding centrum (97-2), more than 26 presacral vertebrae (106-1), and tongue notched between 40-50% (137-4, a further transformation of the anguimorph state 1, and also found in some scincomorphs). Amphisbaenians share only three of 37 synapomorphies of varanoids: subdental shelf small or lost (58-0, reversal of scleroglossan synapomorphy), epicoracoid cartilages fail to contact suprascapular cartilages (114-1), and absence of the carotid duct.

Snakes and dibamids share four amphisbaenian synapomorphies: epipterygoid lost (47-1), fewer than 14 scleral ossicles (89-1; lost entirely in snakes and dibamids), second epibranchials lost (90-1), and interclavicle lost (118-1). In addition, dibamids have the following amphisbaenian synapomorphies: absence of supratemporal (35-1), far lateral position of the fenestra ovalis, and closure of the lateral aperture of the recessus scalae tympani. Further derived characters shared by snakes and amphisbaenians include: replacement teeth develop posterolingually, no resorption pits present (85-1), and anterior braincase closed by bone. In total, amphisbaenians have seven of 42 dibamid synapomorphies and six of 51 snake synapomorphies.

Amphisbaenian relationships are a problem in need of further attention. Lacking a well supported hypothesis, we place amphisbaenians as Scleroglossa, incertae sedis.

SERPENTES Linnaeus, 1766

Definition: Scolecophidia, Alethinophidia, and all organisms sharing a more recent common ancestor with these taxa than with any other extant organisms.

Diagnosis: Snakes have the following synapomorphies (Figs. 34, 35, 36).

1. Descending processes of frontals in contact below olfactory tracts (10-1). Gekkotans, *Heloderma*, *Varanus*, amphisbaenians; within gymnophthalmids, xantusiids, anguils.
2. Postfrontal subtriangular, not forked medially (13-0). Possible R of scleroglossan synapomorphy; see pp. 146, 252.
3. Parietal foramen lost (26-1). Gekkota, dibamids, gymnophthalmids, *Heloderma*, *Lanthanotus*; within iguanids*, chamaeleontids, cordylids, scincids, xantusiids, amphisbaenians.

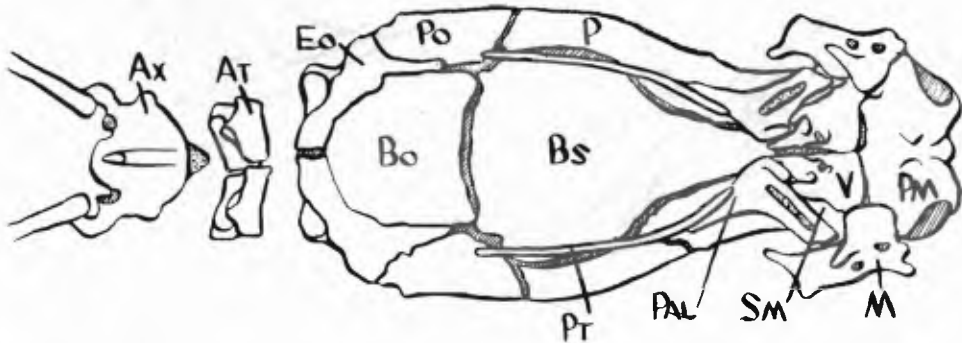
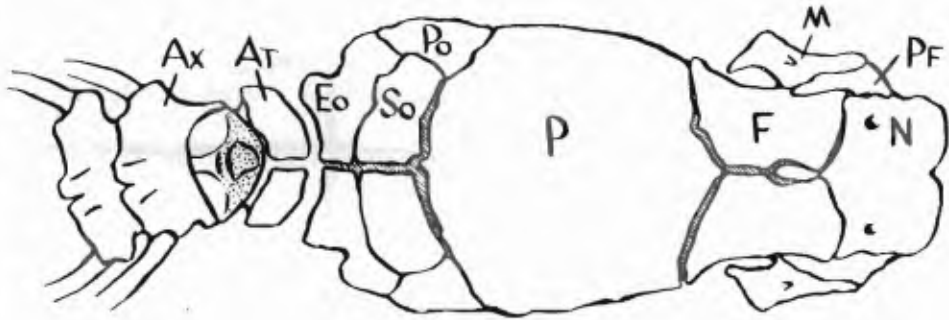
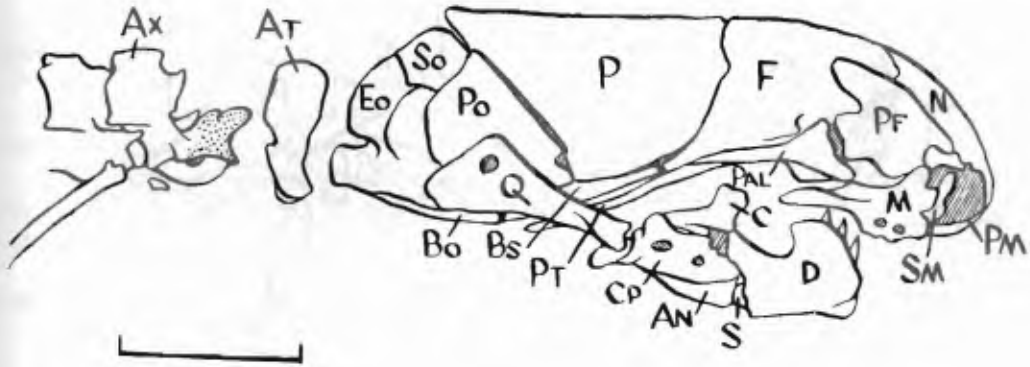


FIGURE 34 (A-C). Skull and mandible of Typhlopidae and Leptotyphlopidae. Right lateral, dorsal, and ventral views of *Leptotyphlops bakewelli* (Leptotyphlopidae).

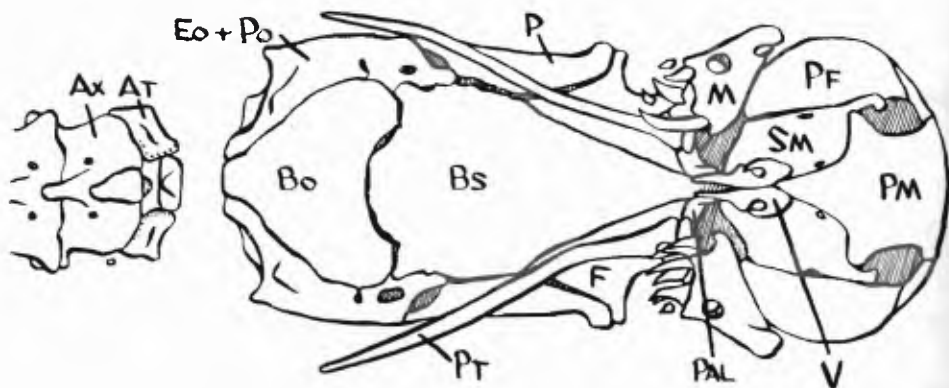
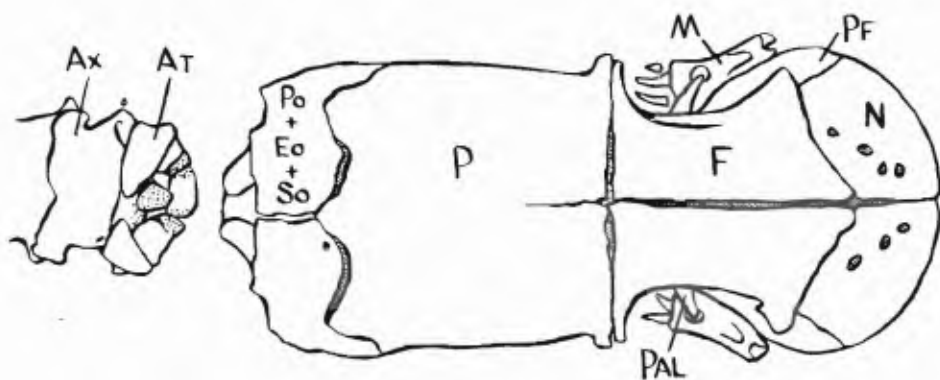
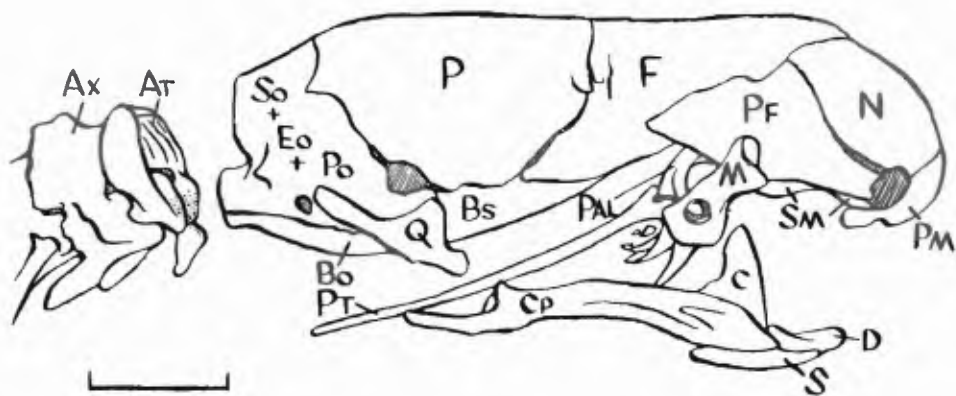


FIGURE 34 continued (D-F). Same views of *Typhlops lineatus* (Typhlopidae). Scale = 1 mm. All from List (1966), by permission of the Board of Trustees of the University of Illinois. See end of paper for abbreviations.

4. Lacrimal lost (28-1). Gekkotans, dibamids; within iguanids*, agamids*, chamaeleontids, gymnophthalmids, scincids, amphisbaenians.
5. Squamosal lost (33-1). *Dibamus*; within pygopodids, gekkonids.
- ✓6. Supraoccipital excluded from the margin of the foramen magnum by the exoccipitals (rare exceptions; Rage, 1984). Unique.
7. Close sutural contact between lateral edge of vomer and mesial edge of septomaxilla, the two bones forming a closed capsule for Jacobson's organ (Underwood, 1957a; Rieppel, 1984a). *Dibamus*.
8. Epipterygoid lost (47-1). *Dibamus*, chamaeleontids, most amphisbaenians; within iguanids*.
9. Crista circumfenestralis present, surrounding fenestra ovalis (Estes et al., 1970). Unique.
10. Vidian canal open over its anterior course through basisphenoid (Rieppel, 1978c; Greer, 1985a). *Anniella*, dibamids.
11. Overlap between dentary and postdentary bones reduced (64-1). Varanoids.
12. Dentaries loosely united at symphysis (Rage, 1984). Unique.
13. Splenial does not extend anterior to tooth row midpoint (65-1). Dibamids, *Heloderma*, xantusiids, amphisbaenians, gekkotans, agamids*; within iguanids*, gymnophthalmids, scincids, anguids.
14. Splenial with very limited overlap on postdentary bones (66-2). *Lanthanotus*.
15. Splenial-dentary suture reduced, much connective tissue present (67-1). Varanoids.
16. Anterior end of coronoid meets dentary directly (70-1). *Lanthanotus*; within iguanids*, amphisbaenians.
17. Marginal replacement teeth develop posterolingually, no replacement pits present (varanid type) (85-2). Varanoids; within amphisbaenians.
18. Scleral ossicles lost (89-1). Only amphisbaenians and dibamids, which also have the ossicles extremely reduced or lacking, are similar (Walls, 1940; Underwood, 1957b, in litt., 1985).
19. Skull platytrabic, interorbital septum lost (Rage, 1984). Rieppel (1984a) noted that the intermediate condition in scolecophidians suggests that this character may have arisen within snakes. *Lanthanotus* is possibly platytrabic (Rieppel, 1983).
20. Second epibranchials lost (90-1). Chamaeleontids, gymnophthalmids, dibamids, varanids, xenosaurids, amphisbaenians; within agamids*, iguanids*, gekkonids, pygopodids, scincids, anguids.
21. Second ceratobranchials lost (91-1). Anguimorphs, chamaeleontids, dibamids; within iguanids*, gekkonids, gymnophthalmids, scincids, teiids, cordylids, amphisbaenians.
22. Zygosphenes and zygantra strongly developed (95-1; R of squamate synapomorphy). Character 96-0, which indicates presence or absence of these structures, is redundant with character 95). Lacertids, teiids; within iguanids*, gymnophthalmids, cordylids.
23. Cervical intercentra fused to posterior part of the preceding centrum (97-2). Anguimorphs (but see Character Analysis), dibamids, amphisbaenians, within scincids.
24. Autotomy septa lost in caudal vertebrae (103-1). Acrodonta, varanoids; within anguids, xenosaurids, iguanids*, gekkonids, scincids, amphisbaenians.
25. More than 26 presacral vertebrae (106-1). Anguimorphs, within many other basic taxa. Snakes are unique in having more than 120 precloacal vertebrae (Hoffstetter and Gasc, 1969).
26. Clavicle lost (115-1). Chamaeleontids, dibamids; most amphisbaenians.
27. Interclavicle lost (118-1). Chamaeleontids, pygopodids, amphisbaenians, dibamids; within anguids, scincids.
28. Scapula, sternum, and postxiphisternal inscriptional ribs lost (Rage, 1984). Most amphisbaenians.

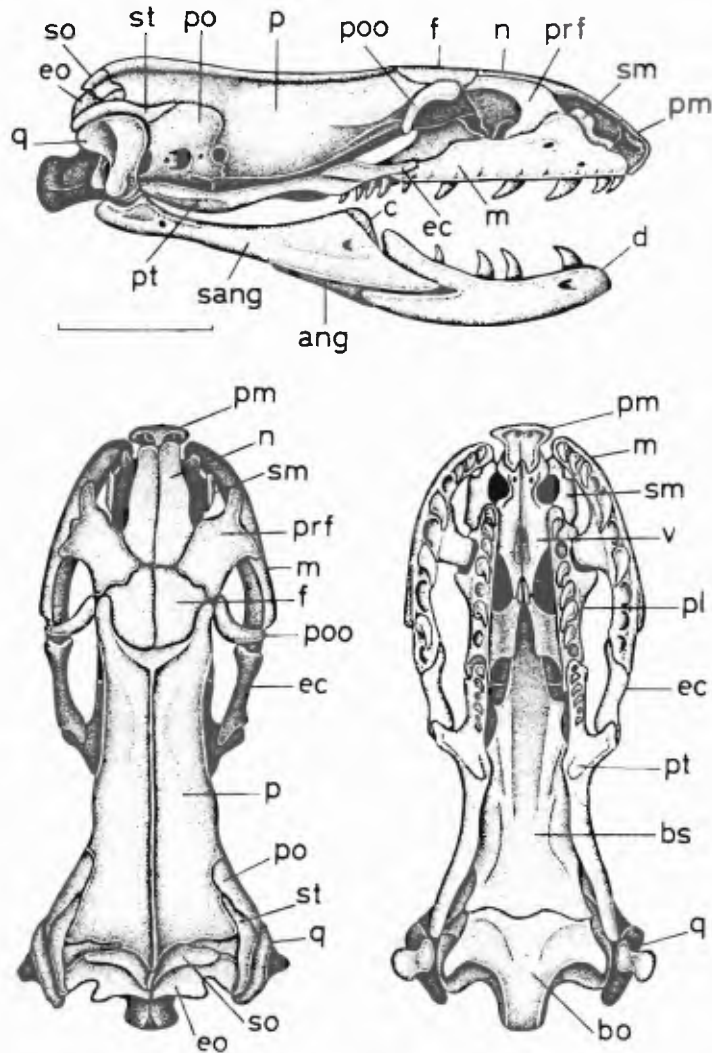


FIGURE 35. Skull and mandible of *Cyindrophis rufus* (Serpentes, Aniliidae). Right lateral, dorsal, occipital, and ventral views. Scale = 5 mm. From Rieppel (1983), by permission of Paul Parey, Hamburg. See end of paper for abbreviations.

29. Forelimbs lost. Pygopodids, dibamids; within scincids, cordylids, anguids, amphisbaenians other than *Bipes*.

30. Hind limbs lost or minute (Romer, 1956). Amphisbaenians, dibamids, pygopodids; within gymnophthalmids, scincids, cordylids, anguids.

31. *M. rectus abdominis lateralis* present (134-1). Autarchoglossans.

32. Foretongue retracts within hindtongue at a zone of invagination (136-1). Anguimorphs; within teiids.

33. Free part of tongue notched more than 50% (137-5). Varanids.

34. Foretongue surface covered by a smooth, keratinized, even layer of stratified squamous epithelium (Schwenk, 1988). *Varanus*.

35. Sublingual glands remarkably dense, compact, and round in transverse section (Schwenk, 1988). *Varanus*.

36. No femoral or preanal pores (144-0; R of squamate synapomorphy). Many squamate taxa.
37. Stapedial artery passes anterior to stapes (145-0; R of squamate synapomorphy). Gekkotans.
38. Left lung reduced or lacking, right lung dominant (Rage, 1984). Occurs in all other elongate squamates in which lung reduction takes place, except amphisbaenians, in which the right lung is reduced (Gans, 1978).
39. Tympanic membranes and Eustachian tubes lost (Rage, 1984). Within iguanians and scincids (Etheridge and de Queiroz, 1988; Greer, 1970).
40. Ophthalmic branch of trigeminal nerve enclosed within braincase by lateral downgrowths of parietal, usually entering orbit through optic foramen (Bellairs and Kamal, 1981). Unique.
41. Transparent spectacle covers eye (Rage, 1984). Xantusiids, pygopodids; within gekkonids, scincids, lacertids, gymnophthalmids.
42. Visual cells of retina lacking oil droplets (Underwood, 1957b). Most gekkotans.
43. No muscles in ciliary body (Walls, 1940). Unique.
44. Standard type vertebrate rods present (Walls, 1940; Underwood, 1970). R of lepidosaur synapomorphy (rods few and modified in *Sphenodon*, lost in all squamates except snakes, not known for amphisbaenians according to Underwood, in litt., 1985).
45. Interdigitation of the periventricular gray zones of the optic tectum and enlargement of lamina 7 of the posterior colliculus (Senn and Northcutt, 1973). Dibamids, feyliniine scincids.
46. Nucleus reticularis ventrolateralis of spinal cord present (Cruce and Newman, 1984). Dibamids, amphisbaenians.
47. Ramus communicans externus n. facialis cum glossopharyngeo passes in front of stapes (Rieppel, 1980d). R of squamate synapomorphy.
48. Kidneys precloacal (Underwood, in litt., 1985). R of squamate (lepidosaur?) synapomorphy. Dibamids; see comments below.
49. Left systemic arch larger than the right (Underwood, in litt., 1985; some exceptions). Unique.
50. Carotid duct lost (Underwood, 1957b). Chamaeleontids, varanoids, amphisbaenians.

Comments: Rage (1984) has given the most recent compilation of snake characters, but unfortunately he did not designate those that are derived. We have included here those from his study and from other sources that we were able to polarize.

Rieppel (1983, 1985) gave seven snake characters that suggested to him that snakes and "lizards" originated from a basal dichotomy within Squamata. We have added others to Rieppel's seven, and list all below.

These are: (1) structure of the retina, including the presence of characteristic vertebrate rods, (2) structure and development of oral glands, (3) course of the ramus communicans externus n. facialis cum n. glossopharyngeo in front of the stapes, (4) absence of a straight frontoparietal suture in *Dinilysia*, (5) structure of the basicranium in scolecophidians, (6) mode of subdivision of the metotic fissure to form the recessus scalae tympani, and (7) position of the perilymphatic foramen. To these we add: (8) course of the stapedial artery in front of the stapes (145-0), (9) lack of a ribbon-like pancreas, and (10) precloacal position of the kidney.

We do not propose to discuss these characters in depth here, but we comment briefly on them.

(1) According to Underwood (1970), "lizards" are derived relative to snakes in that the former have lost rods and thus have a simplex retina (only cones present), while the latter retain a duplex retina (both rods and cones present). Although the retina of *Sphenodon* is said to be structurally duplex, the structures hypothesized to be rods are rare and functionally insignificant (Underwood, 1970). Thus, if the functionally and structurally duplex retina of snakes is a retained primitive feature rather than a reversal, then *Sphenodon* and "lizards" must have reduced their rods convergently.

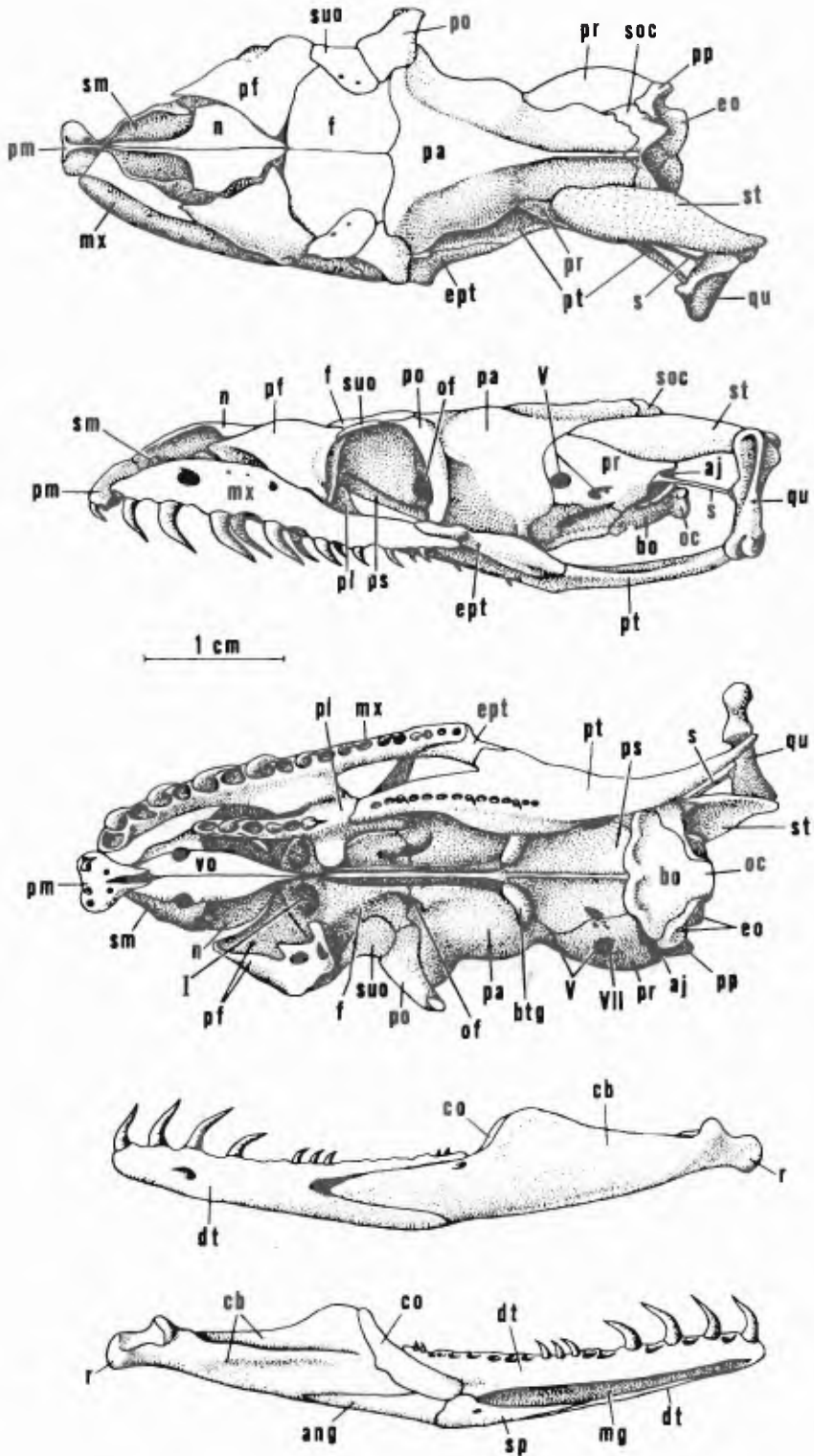


FIGURE 36. Skull and mandible of *Python regius* (Serpentes, Boidae). Dorsal, left lateral, and ventral views of skull. Lateral and medial views of mandible. From Rage (1984), by permission of Gustav Fischer Verlag, Stuttgart. Scale 10 mm. See end of paper for abbreviations.

In other words, taken alone, this character actually suggests that snakes diverged from "lizards" before the divergence of *Sphenodon*.

(2) Rieppel (1983) was not specific about the structure and development of the oral glands, but only referenced Kochva (1978), who diagrammed an evolutionary dichotomy between snakes and all other squamates. Kochva, however, gave no oral gland character in which snakes are plesiomorphic relative to all other squamates. Snakes retain what is thought to be the primitive squamate condition of having both supra- and infralabial glands, but this condition is retained also by amphisbaenians and iguanians.

(3) According to Rieppel (1980d), the ramus communicans externus of snakes and *Sphenodon* passes in front of and ventral to the stapes. In "lizards", it passes behind the stapes. Thus "lizards" appear to be derived relative to snakes.

(4) Snakes generally (not only in *Dinilysia*) lack the transverse frontoparietal suture seen in most "lizards." This character, however, is misleading in that it is stated negatively. Although snakes lack a transverse frontoparietal suture, the curvature of the suture in snakes is more or less the inverse of the plesiomorphic lepidosaur condition retained in rhynchocephalians (Gauthier et al., 1988). Thus, the condition seen in snakes can be interpreted as a further modification of that seen in most "lizards," and does not, therefore, suggest that snakes are the sister group of all other Squamata.

(5) In "lizards" the parasphenoid has lateral wings that underlie the palatine nerve and artery, enclosing these structures in a bony Vidian canal when the parasphenoid fuses to the overlying basisphenoid. In scolecophidian snakes, as in *Sphenodon*, the lateral wings are small or lost, and the Vidian canal is represented by an open groove in the marginal zone of the basisphenoid (Rieppel, 1979). Although Rieppel (1983) cited this as possible evidence for an early divergence of snakes within Squamata, he correctly noted in an earlier paper (Rieppel, 1979) that because the derived condition occurs in all other snakes, the scolecophidian condition could also be interpreted as a secondary loss.

(6) In all squamates, the metotic fissure, a gap between the otic capsule and the basal-occipital portions of the skull, is subdivided ontogenetically to form the recessus scalae tympani anteriorly and the jugular foramen posteriorly (Rieppel, 1985). In *Sphenodon*, subdivision of the metotic fissure does not occur. The mode of subdivision differs between "lizards" and snakes, occurring by apposition of part of the otic capsule to the margin of the basal plate in the former, and by the development of a downward strut of cartilage from the medial wall of the otic capsule or by a upgrowth from the basal plate in the latter. This difference led Rieppel to conclude that subdivision of the metotic fissure must have been derived independently in "lizards" and in snakes from a common ancestor with an undivided metotic fissure. This argument, however, is based on the assumption that the mode of development of a structure is always conserved in phylogeny. The validity of this assumption is dubious (de Queiroz, 1985b).

(7) Rieppel (1985) noted that the perilymphatic foramen of the otic capsule in *Typhlops* resembles that of *Sphenodon* in having a mesial position relative to that of "lizards." All other snakes, however, exhibit a lateral position of the foramen. Therefore, the seemingly primitive position of the perilymphatic foramen in *Typhlops* can just as reasonably be interpreted as secondary.

(8) The stapedial artery (our character 145) of most "lizards" passes posterior to the stapes, but in snakes and in *Sphenodon* it passes anterior to the stapes. There are some "lizards" in which the artery perforates the stapes, and in pygopodids and some gekkonids it passes anterior to the stapes as in snakes and *Sphenodon*. Therefore, although snakes retain the seemingly primitive condition, this condition is also seen in some "lizards."

(9) According to Rage (1982) "lizards" and amphisbaenians have a ribbon-like pancreas, while snakes retain a compact pancreas similar to that seen in *Sphenodon*.

10) Underwood (in litt., 1985) noted that the kidneys of most "lizards" are derived relative to the ancestral tetrapod condition in being posteriorly placed, in contact with the caudal end of the body wall, or in a postcloacal extension of the peritoneal cavity. The kidneys of snakes and dibamids are similar to those of most other tetrapods in being located anterior to the cloaca. *Sphenodon*, however, has the postcloacal position, and it seems possible that this is a lepidosaur synapomorphy lost in snakes and dibamids.

Of the ten characters identified as possible evidence that snakes are not descended from the most recent common ancestor of extant "lizards," one (2) seems to be incorrect, another (6) is based on a dubious assumption, and five (1,4,5,7,10) involve dubious polarities (1 and 10, because *Sphenodon* possesses the condition seen in "lizards," 4, because it is stated as an absence and snakes do not possess the plesiomorphic condition, 5 and 7, because they occur only in some snakes, with other snakes exhibiting the condition seen in "lizards."). One other character (8) occurs in some "lizards," but we have interpreted this as a reversal, and because we do not consider snakes to be closely related to the group in which it occurs (Gekkota), it can still be argued that snakes retain the primitive condition. The last two characters (3, 9) appear to be legitimate but they must be weighed against the characters suggesting that snakes are scleroglossans, as well as those that suggest placement of snakes within subgroups of Scleroglossa (e. g. the varanoid resemblances).

In light of Rieppel's conclusion that snakes arose from a basal position within squamates, it is of interest to determine the characters used in our study that snakes share with various groups of squamates.

Snakes have 15 of our 27 scleroglossan synapomorphies and cannot be scored for eight of the others (Table 1). They lack four: postfrontal semilunate, forked medially, clasping frontoparietal suture (13-1), postorbital forms half or less of orbital border (17-1), origin of the adductor musculature on the ventral surface of the parietal (54-1), and absence of the anterior head of the m. pseudotemporalis profundus (133-0). The plesiomorphic state of the adductor muscle character in snakes (origin of the musculature on the dorsal surface) is a necessary consequence of the enclosure of the braincase by bone, whatever the original condition may have been, and does not in our view form a significant exception to placement of snakes as scleroglossans. The lack of postfrontal forking and the plesiomorphic form of the postorbital are not easy to dismiss. There is variation within snakes in one of the scleroglossan characters, cephalic scales large (147-1), but presence of small scales is an infrequent within-group reversal and thus does not affect the similarity to scleroglossans. Thus, although the postfrontal and postorbital characters suggest that snakes are outside Scleroglossa, given the derived characters shared by snakes and certain subgroups of Scleroglossa noted below, it seems reasonable to place them within Scleroglossa.

Gekkotan synapomorphies present in snakes include five of the 46 from our list. These include: descending processes of frontals in contact below olfactory tracts (10-1), parietal foramen lost (26-1), lacrimal lost (28-1), jugal reduced or lost, splenial does not extend as far forward as tooth row midpoint (65-1), stapedia artery passes anterior to stapes (145-0, in gekkonids it may also perforate the stapes, 145-1). Except for the anterior course of the stapedia artery, the above characters are widely distributed in squamates and do not speak very strongly for a close relationship between snakes and gekkotans.

Snakes have one of our three autarchoglossan characters (Table 1): presence of the m. rectus abdominis lateralis (134-1). This character suggests that snakes are closer to autarchoglossans than to gekkotans.

Snakes share none of the scincomorph synapomorphies from our character list. Similarly, there is little evidence that snakes are closely related to any subgroup of scincomorphs: snakes share none of the lacertoid synapomorphies, have two of 15 lacertiform characters, including strong

zygosphene and zygantum (95-1) and a tongue notched more than 50% (137-5, a further transformation of the lacertiform 137-3). Of the 15 teioid synapomorphies, snakes have only one: a tongue notched more than 50% (137-5), which is a further transformation of the teioid condition (137-4). Some alethinophidian snakes have a medially inflected retroarticular process (75-1), the only one of the 17 scincoid characters seen in snakes.

Snake characters that are the same as anguimorph synapomorphies include seven of the 22 from our list. These are: replacement teeth developing posterolingually with no resorption pits present (85-2, a further transformation of the anguimorph 85-1), second ceratobranchials lost (91-1), cervical intercentra fused to posterior part of preceding centrum (97-2, a further transformation of the anguimorph 97-1), more than 26 presacral vertebrae (106-1), foretongue retracts within posterior (hind) tongue at zone of invagination (136-1), tongue notched more than 50% (137-5, a further transformation of the anguimorph 137-1), and preanal pores lost (144-0).

Of the 37 varanoid synapomorphies in our list, snakes have six: reduced overlap of postdentary and dentary bones (64-1), splenial with very limited overlap on postdentary bones (66-2, a further transformation of the varanoid 66-1, also found in *Lanthanotus*), spleniodyntary suture reduced with much connective tissue present (67-1), retroarticular process inflected medially (75-1, but known only for those few snakes that possess a process), replacement teeth develop posterolingually, no resorption pits present (85-2), tongue notched more than 50% (137-5, a further transformation of the varanoid 137-3). Evidence for the varanoid hypothesis of snake relationships was first documented extensively by McDowell and Bogert (1954), who proposed that *Lanthanotus* in particular showed special relationship to snakes. This hypothesis has been developed further by McDowell (1972) but has not been supported by other workers (e. g. Underwood, 1957a; Rieppel, 1980b, 1982, 1985). Rieppel (1983) in particular has shown that there is no special similarity between *Lanthanotus* and snakes.

Snakes have two of 29 of our list of varanid synapomorphies. These are: second epibranchials lost (90-1) and tongue notched more than 50% (137-5), the latter a further transformation forming a specific similarity to *Varanus*.

An hypothesis of anguimorph (perhaps even varanoid) relationship for snakes is thus more strongly supported than one allying them with scincomorphs, although we agree with Rieppel (1983) that *Lanthanotus* in particular is not implicated. Three of the varanoid similarities to snakes (64-1, 66-2, and 67-1) are correlated with the development of an intramandibular hinge, as argued by Gauthier (1982). Moreover, because snakes do not have all of the scleroglossan and autarchoglossan synapomorphies, it can be argued that the similarities to anguimorphs are convergent. It may be a simpler hypothesis, given the numbers of anguimorph and varanoid similarities to snakes, that the single remaining autarchoglossan synapomorphy (129-1), and four scleroglossan synapomorphies (13-1, 17-1, 54-1, 133-1) have been reversed in snakes.

Rage (1982, 1984) argued that snakes may be the sister group of amphisbaenians. The case for snake-amphisbaenian relationship is not easily resolved. From our list, snakes have ten of 42 amphisbaenian synapomorphies. These are: median contact of descending processes of frontals below olfactory tracts (10-1), absence of epipterygoid (47-1), splenial does not extend forward as far as the tooth row midpoint (65-1), posterior end of splenial with very little overlap on postdentary bones (66-2, a further transformation of the amphisbaenid 66-1), replacement teeth develop posterolingually, no resorption pits present (85-2, a further transformation of the amphisbaenian 85-1), scleral ossicles lost (89-1), second epibranchials lost (90-1), cervical intercentra fused to posterior part of preceding centrum (97-2), interclavicle lost (118-1), and tongue notched more than 50% (137-5, a further transformation of the amphisbaenid 137-4). Many of these characters are associated with reductions and compaction of the skull seen commonly in serpentine or semi-burrowing forms. Because these characters also occur in many other scleroglossan taxa, none speak strongly for a close relationship between snakes and amphisbaenians within Scleroglossa.

Given the problems with most of the characters purportedly indicating that snakes represent one branch of the basal dichotomy within Squamata, and given that they possess most of the synapomorphies of Scleroglossa for which they can be scored, as well as one of the three synapomorphies of Autarchoglossa, we consider snakes to be scleroglossans. Snakes share derived characters with various subgroups of Scleroglossa, but although the anguimorph relationship of snakes suggested by several previous authors is reasonably well supported, it is not clearly superior to alternative placements, and it requires several reversals of scleroglossan and autarchoglossan synapomorphies. For these reasons we place Serpentes as Scleroglossa, incertae sedis.

PHYLOGENETIC TAXONOMY OF SQUAMATA

We present here a phylogenetic taxonomy of squamates derived from this study (Table 2). The conventions used in this taxonomy follow those used by Gauthier et al. (1988). For reasons given more fully there we give only an indented taxonomy and do not recognize formal categorical ranks.

One of our reasons for doing this is that taxa given the same rank such as Class, Order, and Family are not equivalent from one group to another because the concepts of such ranks lack uniformity in the minds of systematists. Their information content is thus minimal. Lack of Linnaean ranks does not, however, hinder discussions of the phylogenetic properties of the identified monophyletic groups.

Three new taxa are named, and we have placed *Lanthanotus* and *Varanus* in the Varanidae, following Pregill et al. (1986).

We have used the category incertae sedis for taxa that can be placed within a particular clade but whose position within that clade is uncertain. We are relatively confident that Dibamidae, for instance, is referable to Scleroglossa, but its precise relationships within Scleroglossa are not yet clearly understood.

As indicated earlier in this paper, we follow Gauthier et al. (1988) in identifying as metataxa (indicated by an asterisk) groups, often based on plesiomorphy, the status of which is uncertain because neither monophyly or paraphyly can be demonstrated (see, e.g., section on Basic Taxa).

SUMMARY AND CONCLUSIONS

The classic study of squamate relationships by Camp (1923) has been a major focus for many students of these fascinating animals. As Underwood (1971) has already pointed out, the freshness of approach that Camp's work still maintains after more than fifty years is remarkable. This derives not only from the careful and detailed work that he accomplished, but also from the ease with which a phylogenetic systematist can make use of those data. The opportunity to extend Camp's work in the present study has been rewarding not only because of the above, but because our results, based on many characters derived from Camp's study, in great part corroborate his conclusions.

Osteological characters were used because of their potential use in paleontology and because they can be readily determined in a large number of groups, but we have also evaluated a number of characters from soft anatomy for which we could obtain adequate data. We included as many of the characters used by Camp (1923) as possible.

Character polarities were determined by outgroup comparison (Watrous and Wheeler, 1981; Maddison et al., 1984).

Relationships among the basic taxa were analyzed using Hennig's (1966) method. The PHYSIS package for computer assessment of phylogenetic relationships (including Wagner and Pimental analyses) was used to provide initial minimum-step cladograms. The characters used were reanalyzed in light of known variation in order to present a diagnosis for each monophyletic group; we consider such diagnoses to be an essential part of any phylogenetic hypothesis. Later in the

course of our study, we analyzed the data using the PAUP program, when it became available. Differences between the PAUP and PHYSYS results were minimal.

We present both the minimum-step cladograms (Fig. 5) as well as a less resolved cladogram (Fig. 6). The latter indicates what to us are the best supported monophyletic groups, and identifies the problem areas deserving of further research.

Snakes, dibamids, and amphisbaenians are all limbless, and we are not certain what effect absence of limb data had on the computer cladograms. In any event, the placement of these groups by the computer varied more widely than for our other basic taxa. Limblessness has evolved numerous times within Squamata, and it is possible that limblessness and correlated characters cause these groups to be moved around on the cladogram despite the absence of characters suggesting relationships to particular taxa of limbed squamates in one or more of the limbless forms. For this reason we performed another analysis in which these taxa were removed, and used this and our character analysis to prepare a less resolved cladogram (given in Fig. 6) that contained only well supported groups.

Monophyly of Squamata was supported by Gauthier et al. (1988) on the basis of 74 synapomorphies, to which we have added others that were reversed by the present study; this list of 84 sy-

TABLE 2. Phylogenetic taxonomy of squamates as determined by this study.

SQUAMATA
Iguania
Iguanidae*
Acrodonta
Agamidae*
Chamaeleontidae
Scleroglossa, new taxon
Incertae sedis: Dibamidae, Amphisbaenia, Serpentes
Gekkota
Gekkonidae
Pygopodidae
Autarchoglossa
Scincomorpha
Lacertoidea
Xantusiidae
Lacertiformes, new taxon
Lacertidae
Teiioidea, new taxon
Teiidae
Gymnophthalmidae
Scincoidea
Scincidae
Cordylidae
Anguimorpha
Anguinae
Xenosauridae
Varanoidea
Helodermatidae
Varanidae
<i>Lanthanotus</i>
<i>Varanus</i>

napomorphies is given. The polarity based on outgroup criteria of 18 of our characters was reversed by acceptance of our preferred phylogenetic hypothesis. Monophyly of "Lacertilia" exclusive of amphisbaenians and snakes, however, cannot be demonstrated, and we were thus unable to use the latter two taxa as outgroups. The results of our study suggest that both amphisbaenians and snakes are descended from the most recent common ancestor of "Lacertilia." We therefore recommend that the paraphyletic taxon "Lacertilia" be abandoned in preference to Squamata. We also recommend that Sauria not be used as a synonym of Lacertilia, because Gauthier et al. (1988) used this term in a more inclusive sense to encompass both archosauromorph and lepidosauromorph reptiles, a usage closer to the original content of McCartney's (1802) group.

A monophyletic Iguania is diagnosed by 14 synapomorphies. Iguanidae* is designated a metataxon because it is based on plesiomorphy, but cannot yet be demonstrated to be paraphyletic. Acrodonta is a monophyletic taxon that includes Agamidae* and Chamaeleontidae and is diagnosed by 13 synapomorphies. Agamidae* is also a metataxon, although we were able to identify three potential synapomorphies for the group. Monophyly of Chamaeleontidae is highly corroborated. This taxon is diagnosed by 85 synapomorphies, although some of these may apply to more or less inclusive groups. Determination of their precise level awaits a detailed analysis of relationships within Acrodonta and Chamaeleontidae.

Scleroglossa, new taxon, includes Gekkota (Gekkonidae and Pygopodidae) and Autarchoglossa. The latter includes the remaining non-iguanian squamates with the possible exception of snakes, dibamids, and amphisbaenians, which are placed incertae sedis in Scleroglossa. This is an highly supported taxon, diagnosed by 27 synapomorphies. Recognition of Scleroglossa forms our major difference from the taxonomy of Camp (1923), who divided squamates into Ascalabota (iguanians and gekkotans) and Autarchoglossa. Camp recognized that the phylogenetic relationships of gekkotans were closer to autarchoglossans than to iguanians (see Fig. 7), but his taxonomy does not reflect this.

Gekkota is diagnosed by 46 synapomorphies. Although monophyly of Pygopodidae is well supported (12 synapomorphies), that of Gekkonidae is problematic. We have identified 11 potential synapomorphies that support a monophyletic Gekkonidae; a smaller number of characters used in our study (see p. 206) supports the conclusion of Kluge (1987) that Pygopodidae is nested within Gekkonidae. If Kluge's results are accepted, Gekkonidae as we have constituted it is paraphyletic. While we provisionally accept a monophyletic Gekkonidae, it might be treated as a metataxon.

Autarchoglossa includes Scincomorpha and Anguimorpha. It is diagnosed by three synapomorphies. At present, we consider this taxon to be well supported by presence of the *m. rectus abdominis lateralis* (which formed part of the original diagnosis of Camp, 1923); this character shows relatively little homoplasy.

Scincomorpha is diagnosed by nine synapomorphies; it includes Lacertoidea (including Xantusiidae, Lacertidae, Teiidae, and Gymnophthalmidae) and Scincoidea (including Cordylidae and Scincidae). Lacertoidea is diagnosed by seven synapomorphies. Within Lacertoidea, Xantusiidae (22 synapomorphies), Lacertidae (10 synapomorphies), and Teiidae (14 synapomorphies) are groups the monophyly of which is highly corroborated. Gymnophthalmidae is diagnosed by 12 synapomorphies and appears to be monophyletic, although additional study of this taxon is needed. Lacertidae, Teiidae, and Gymnophthalmidae form a monophyletic group that we refer to as *Lacertiformes*, new taxon (15 synapomorphies); another monophyletic group is represented by Teiidae and Gymnophthalmidae, to which we give the name *Teiioidea*, new taxon (14 synapomorphies).

Scincoidea is monophyletic, and supported by 16 synapomorphies. Scincidae is diagnosed by 11 synapomorphies, and Cordylidae by seven. If the suggestion by Rieppel (1984a) that dibamids are nested within scincids is accepted, Scincidae as we have constituted it here is paraphyletic.

Anguimorpha is diagnosed by 22 synapomorphies. It includes Xenosauridae (12 synapomorphies), Anguidae (18 synapomorphies), and Varanoidea (37 synapomorphies). Anguioidea* is a metataxon, because Xenosauridae and Anguidae cannot be demonstrated to be more closely related to each other than either is to varanoids. Anguioidea* is not nearly as widely used as are other metaxa recognized in this study, and we see little reason to recognize it formally. Therefore, we have placed xenosaurs, anguids, and varanoids in an unresolved tritomy.

Varanoidea includes Helodermatidae (23 synapomorphies), *Lanthanotus* (16 synapomorphies), and *Varanus* (21 synapomorphies). The two latter taxa are placed together in the Varanidae, following Pregill et al. (1986), a taxon that is diagnosed by 29 synapomorphies.

Dibamidae and Amphisbaenia are each diagnosed by 42 synapomorphies, and Serpentes by 50 synapomorphies. Although these three taxa can reasonably be considered to be scleroglossans, within Scleroglossa their relationships are problematic. They have what we consider to be the only significant synapomorphy of autarchoglossans, presence of the m. rectus abdominis lateralis, suggesting that they are closer to Autarchoglossa than to Gekkota. Rieppel (1984a) documented synapomorphies of *Dibamus* and acontine scincids, most of which are also present in *Anelytropsis* (Greer, 1985a). In our opinion, it is possible that Dibamidae is a scincid relative, but because dibamids have few scincomorph and scincoid characters, we have not formally accepted Rieppel's conclusions, but rather place Dibamidae as Scleroglossa, incertae sedis.

Amphisbaenia has few anguimorph or scincomorph synapomorphies, and possesses one synapomorphy of Lacertiformes. On the basis of the tongue characters studied by Schwenk (1988), Amphisbaenia shows closest relationship to Scincomorpha, and it may be a member of that group. However, we prefer to place it as Scleroglossa, incertae sedis. We find no compelling support for a sister group relationship of amphisbaenians and snakes, nor for one between amphisbaenians and dibamids.

Serpentes shares several derived characters with *Varanus*, others with *Lanthanotus*, others with varanoids, and others with anguimorphs as a whole, but also lacks several of the synapomorphies of each of these taxa. It shares few characters with scincomorphs. The hypothesis that snakes are anguimorphs or their sister group is better supported than any of the other possibilities, but we prefer to place the taxon as Scleroglossa, incertae sedis. We find no compelling evidence for the hypothesis of McDowell and Bogert (1954) that *Lanthanotus* has a special relationship to snakes, nor for the hypothesis of Rage (1982) that snakes and amphisbaenians are sister groups, nor can we support a conclusion that snakes are the sister group of the "Lacertilia."

We present both definitions (based on ancestry) and diagnoses (based on characters) for Squamata and all monophyletic taxa within it, down to the level of our basic taxa.

SPECIMENS USED IN THIS STUDY

Although we relied on a number of previous studies (listed below) in determination of character states present in a given lizard group, in every possible case the characters were confirmed on actual specimens in the private collections of Richard Estes, Kevin de Queiroz, Mark Norell, and Richard Etheridge (REE), as well as specimens in the collection of the Museum of Comparative Zoology (MCZ, Harvard University), the Museums of Vertebrate Zoology and Paleontology (MVZ, UMMP, University of California, Berkeley), the San Diego Natural History Museum (SDSNH), the California Academy of Sciences, San Francisco (CAS), the American Museum of Natural History, New York (AMNH), and the University of Michigan Museum of Zoology, Ann Arbor (UMMZ). A few specimens on loan to us from a number of other museums were also used. While we recognize the advantages of tabulating specimens examined, in this case they are too numerous to list.

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ABBREVIATIONS

a = acetabulum	C. = coracoid
A = acromial process	cb = compound bone
aj = lateral aperture of juxtastapedial fossa	C1 = centrum of atlas
amp = M. adductor mandibulae posterior	C2 = centrum of axis
an = angular	C3 = centrum of third vertebra
ang = angular	CB I = first ceratobranchial
ao.vc = anterior opening of vidian canal	CB II = second ceratobranchial
ar = articular	ch.t = foramen for chorda tympani
BH = body of hyoid (basihyoid)	CL = clavicle
bo = basioccipital	co = coronoid or coronoid process
bpt = basipterygoid process	cp = compound bone
bs = basisphenoid	cr.al = crista alaris
btg = basipterygoid process	c.s. = sternal ribs
c = coronoid	d = dentary

- dt = dentary
 EB I = first epibranchial
 EB II = second epibranchial
 ec = ectopterygoid
 EC = epicoracoid cartilage
 EH = epihyal
 eo = exoccipital
 eo + po = fused exoccipital and prootic
 ep = epipterygoid
 ept = ectopterygoid
 e.sc.c = scapulocoracoid emargination
 f = frontal
 f.c. = coracoid foramen
 fca = anterior coracoid emargination
 f.c.a. = clavicular fenestra
 fcp, f.c.p = posterior coracoid emargination
 fc1 = anterior coracoid emargination
 fc2 = posterior coracoid emargination
 Flange = condylar flange demarking precondylar constriction
 fsc = scapulocoracoid emargination
 f.sc.c = scapulocoracoid emargination
 fs = scapular emargination
 f.s. = sternal fontanelle
 g = glenoid cavity
 HC = hyoid cornu
 i. = intercentrum
 i1 = intercentrum of atlas
 i2 = intercentrum of axis
 i3 = intercentrum of third vertebra
 i4 = intercentrum of fourth vertebra
 I = foramen for olfactory tract
 IC = interclavicle
 iof = infraorbital fenestra
 j = jugal
 l = lacrimal
 m = maxilla
 map = m. adductor mandibulae posterior
 mcrt = Meckel's cartilage
 Mc = mesocoracoid process
 mf = Meckelian fossa
 mg = Meckel's groove
 MS = mesosternum
 Msc = mesoscapula
 mx = maxilla
 n = nasal
 n. = notochordal canal
 oc = occipital condyle
 occ.r = occipital recess
 of = optic foramen
 op-eo = fused opisthotic and exoccipital
 onf = orbitonasal fenestra
 p = parietal
 pa = parietal
 pal = palatine
 Pc = procoracoid process
 pf = prefrontal
 pi = pit on dorsal surface of articular
 pl = palatine
 p.l. = processus lateralis of interclavicle
 PL = processus lingualis of hyoid
 pm = premaxilla
 po = prootic
 pof = postfrontal
 poo = postorbital
 pot = prootic
 pp = paroccipital process
 pr = prootic
 prf = prefrontal
 pr.pt = m. protractor pterygoidei
 ps = parasphenoid
 ps.p = m. pseudotemporalis profundus
 ps.s = m. pseudotemporalis superficialis
 PS = presternum
 Psc = proscapula
 ps-bs = fused basioccipital and parasphenoid
 pt = pterygoid
 pu = pubis
 put = pubic tubercle
 q = quadrate
 s = stapes
 s. = synapophysis
 S. = scapula
 sang = surangular
 sang-ang-ar = fused surangular, angular, and articular
 SC = scapulocoracoid
 sm = septomaxilla
 so = supraoccipital
 soc = supraoccipital
 sp = splenial
 sq = squamosal
 SSC = suprascapular cartilage
 st = supratemporal
 stp = stapes
 suo = supraorbital
 sup = supratrigeminal process
 t = tubercle
 tb = supratemporal
 Tc = metacoracoid process
 v = vomer
 vo = vomer
 V = foramen for trigeminal nerve
 VII = foramen for facial nerve
 z = zygosphene
 3C = m. adductor mandibulae externus profundus, head 3C

APPENDIX TABLE 1

OUTGROUP MATRIX

Abbreviations: RH = Rhynchocephalia; KU = kuehneosaurs; PI = *Paliguana**; SA = *Saurosternon**; PA = *Palaeagama**; YO = Younginiformes; AR = Archosauromorpha. Dash (-) = data not available; N = not applicable; ? = data equivocal. For polarity decisions: 0 = polarity as given in Character List; E = polarity equivocal (see pp.134-135).

CHARACTER	OUTGROUPS							POLARITY
	RH	KU	PI	SA	PA	YO	AR	
1	0	0	-	-	-	0	0, 1	0
2	0	0	-	-	-	0	0, 1	0
3	0	0	0?	-	0	0	0, 1	0
4	0	0	0	-	0	0	0	0
5	0	0	0	-	0	0	0, 1	0
6	0, 1	0	0	-	0	0	0, 1	0
7	0, 1	0	0	-	0	0	0, 1	0
8	0	0	-	-	-	0	0	0
9	0	0	0?	-	0?	0	0	0
10	0	0	0?	-	0?	0	0	0
11	0	0	0	-	0?	0	0	0
12	0	0	0	-	0	0	0, 1	0
13	0, 1	0	0	-	0	0	0, N	0
14	0	0	0	-	0	0	0, N	0
15	0	0	0	-	0	0	0, 1	0
16	0	0	0	-	0	0	0	0
17	0	0	0	-	0	0	0	0
18	0, 1	0, 1?	0	-	0?	0	0	0
19	0	0	0	-	0	0	0, 1	0
20	0	0	0	-	0	0	0, N	0
21	0, 1	0	0	-	0	0	0, 1	0
22	0	-	-	-	-	-	0	0
23	0	0	-	-	-	0?	0, N	0
24	0, 1	0	0	-	0	0	N?	0
25	0	1	0	-	0	0	0, N	0
26	0	0, 1?	0	-	0	0	0, 1	0
27	0	0	0	-	-	0	0, 1	0
28	0, 1	0	0	-	0	0	0	0
29	0, N	0	0	-	0	0	0	0
30	0	-	-	-	-	1	0, 1	E
31	0	0	1	-	1	1	1	0
32	0	0	0	-	0	0	0, 1	0
33	0	0	0	-	0	0	0	0
34	0	0	0	-	0?	0	0, 1	0
35	0, 1	1	0?	-	0?	0	0, 1	E

CHARACTER	OUTGROUPS							POLARITY
	RH	KU	PI	SA	PA	YO	AR	
36	0	0?	0?	-	0?	0?	0, 1	0
37	0	0	-	-	-	0	0	0
38	0	-	-	-	-	0	0, 1	0
39	0	0?	-	-	-	1	0	0
40	0	-	-	-	-	-	0, N	0
41	0	-	-	-	-	-	0, N	0
42	0	-	-	-	-	0, ?	0, N	0
43	0	0	-	-	-	0	0, 1	0
44	0	-	-	-	-	0	0	0
45	0	0	-	-	-	0	0, N	0
46	0	0	-	-	-	0	0, N	0
47	0	-	-	-	-	0	0, 1	0
48	0, 1	0?	-	-	-	0	0, 1	0
49	0	-	-	-	-	0	0	0
50	0	-	-	-	-	0?	0	0
51	0	0	0	-	-	0	0, 1	0
52	0	-	-	-	-	-	0, N	0
53	0	0	-	-	-	0	0	0
54	0	0	0	-	0	0	0	0
55	0, 1	-	-	-	-	-	0	0?
56	0?	-	-	-	-	-	0	0
57	0	0	-	-	-	-	0	0
58	0	0	-	-	-	-	N, 1?	0
59	0, 1	0	-	-	-	-	N	0
60	N	N	-	-	-	N	N	?
61	0	0	-	-	-	-	0	0
62	1	-	-	-	-	-	0	E
63	0	0?	-	-	-	-	0	0
64	0	-	-	-	-	-	0, 1	0
65	2	0	-	-	-	0	0, 1, 2	E
66	N	-	-	-	-	-	0, 1, 2	E
67	N	-	-	-	-	-	0	0?
68	0	N	-	-	-	-	0, N	0
69	0	N	-	-	-	-	0, N	0
70	0	-	-	-	-	-	0, N	0

CHARACTER	OUTGROUPS							POLARITY
	RH	KU	PI	SA	PA	YO	AR	
71	N	N	-	-	-	-	N	?
72	0	0	-	-	-	-	0	0
73	0	0?	-	-	-	-	0	0
74	0, N	0?	-	-	-	-	N	0
75	0, N	0	0	-	-	-	N	0
76	0, N	0?	-	-	-	-	N	0
77	0, N	0	-	-	-	-	N	0
78	0, N	1	-	-	-	-	N	E
79	0, N	0?	-	-	-	-	N	0
80	0, N	0?	-	-	-	-	N	0
81	0	0	-	-	-	-	0, 1	0
82	0	0	-	-	-	0	0, 1	0
83	0, 1	0	-	-	-	0	0, 1	0
84	0, 1	0	-	-	-	N	N	0
85	0, N	0	-	-	-	-	0, N	0
86	0	0?	-	-	0?	-	0	0
87	0	0	-	-	-	0	0, 1, N	0
88	0	-	-	-	-	-	0, 1	0
89	0	-	-	-	-	-	0, 1	0
90	0	-	-	-	-	-	0?, 1	0
91	0	-	-	-	-	-	0?, 1	0?
92	N	N	-	N	N	N	N, 0	?
93	0	0	-	0	0	0	0, 1, N	0
94	N	N	-	N	N	N	0, N	?
95	0	0	-	-	-	0	0	0
96	0, 1	1	-	-	-	1	0	E
97	0	N	-	-	-	0	0, N	0
98	0	N	-	-	-	0	0, N	0
99	0	1	-	0	0	0	0, 1	0
100	0	0	-	0	0	0	0	0
101	0	0	-	0	0	0	0	0
102	0	N	-	N	-	N	N	0
103	0	1	-	1	-	1	1	E
104	0	0	-	-	0?	0	0	0
105	0	0	-	-	0?	0	0, 1	0

CHARACTER	OUTGROUPS							POLARITY
	RH	KU	PI	SA	PA	YO	AR	
106	0	0	-	-	0?	0	0, 1	0
107	0, 1?	-	-	-	-	-	0	0
108	0	-	-	-	-	-	0, 1	0
109	0, 1, 2-	-	-	-	-	0?	0	0?
110	0	-	-	-	-	-	N	0?
111	0	0	-	0	-	0	0, 1	0
112	0	0	-	0	-	0	0, 1?, N	0
113	0	0	-	0	-	0	0	0
114	N	N?	-	N?	N?	N?	N	?
115	0	-	-	0	-	0	0, 1	0
116	0	-	-	0	-	0	0, N	0
117	0	-	-	-	-	0	0, N	0
118	0	-	-	0	-	0	0, 1	0
119	0	-	-	0	-	0	0, 1, N	0
120	0	-	-	0	-	0	0, N	0
121	0	-	-	0?	-	0	0, N	0
122	0	0	-	0	-	0	0, 1	0
123	0	0	-	-	-	0	0	0
124	0	0	-	0?	0?	0	0, N	0
125	0	0?	-	0?	0?	0?	0?	0
126	0	0	-	1	0	0	0, 1	0
127	0	0	-	0?	0	0, 1	0, 1	0
128	0	0	0	-	0?	0	0, 1	0
129	0	0	0	-	0	0	0, 1	0
130	0	-	-	-	-	N	N	0
131	0	-	-	-	-	-	0	0
132	0	-	-	-	-	-	-	0?
133	0	-	-	-	-	-	0	0
134	0	-	-	-	-	-	0	0
135	0	-	-	-	-	-	0	0
136	0	-	-	-	-	-	0	0
137	0	-	-	-	-	-	0, 1?	0
138	0	-	-	-	-	-	0, 1?	0
139	0	-	-	-	-	-	0	0
140	0	-	-	-	-	-	0	0

TAXON	CHARACTER									
	11	12	13	14	15	16	17	18	19	20
Agamidae*	0	1	N	0	N	0	0	1	0	0
Anguidae	0	0	1	0,1	0	0	1	0	0,1	0
Chamaeleontidae	0,1	1	N	0	N	0	0	1	0	0
Cordylidae	0	0	1?	0	0	0	1	0	1	0
Dibamidae	0	0,1	1,N	0	0,N	1	N	N	N	N
Gekkonidae	0	0	1	0	0	1	N	N	N	N
Gymnophthalmidae	1	0	1	0,1	0	0	1	0	0,1	0
Helodermatidae	0	0	1	0	0	1	N	N	N	1,N
Iguanidae*	0	0,1	0	0	1,N	0	0	1	0	0
Lacertidae	0	1?	1	0,1	0	0	1	0	0	1
<i>Lanthanotus</i>	0	0	1	0	0	1	N	N	N	N
Pygopodidae	0	0	1	0?,1	0	1	N	N	N	N
Scincidae	0	0	1	0,1	0	0,1	1	1	0,N	1,N
Teiidae	0	0	1,0	0,1	0	0	1	1	0	0
<i>Varanus</i>	0	0	1	1	0	0	1	0	0	0
Xantusiidae	0	1?	1	0	-	0	1	0	1	0
Xenosauridae	0	0	1	0,1	0	0	1	1	0	0
Amphisbaenia	0	0?,1	1,N	0	0,N	0?,1	?,N	N	N	N
Serpentes	0	0,1	0	0	0,N	0	0	N	N	N
<i>Sphenodon</i>	0	0	1,N?	0	0	0	0	0,1	0	0

	21	22	23	24	25	26	27	28	29	30
Agamidae*	1	0,1	0	1	1	0	0	0,1	0,N	0
Anguidae	1	0	0	1	0	0	0,1	0	0	0
Chamaeleontidae	1	0,1	0	0,1	2,N	0,1	0	0,1	0,N	0
Cordylidae	1	0,1	1	0,1	0,N	0,1	0	0,1	0,N	0
Dibamidae	1	1	N	1	N	1	1	1	N	N
Gekkonidae	0,1	0	0	1	N	1	0	1	N	N
Gymnophthalmidae	1	1	1	1	N	1	0	0,1	0,1	0
Helodermatidae	1	0	0	1	N	1	1	0	0	0
Iguanidae*	1	0,1	0	1	1,0,2	0,1	0	0,1	0,N	0
Lacertidae	1	1	0	0	0	0,1	0	0	0	0
<i>Lanthanotus</i>	1	0	0	1	N	1	1	0	0	1
Pygopodidae	0,1	0	0	1	N	1	0	1?	N	0
Scincidae	1	0,1	0,1	1	0,N	0,1	0	0,1	0,N	0
Teiidae	1	1	1	1	N,0,1	0,1	0	0	0	0
<i>Varanus</i>	1	0	0	1	0	0	1	0	0	1
Xantusiidae	0,1	1	1	0	0,N	0,1	1	N	N	0
Xenosauridae	1	0	0	0,1	0	0	0	0	0	0
Amphisbaenia	1	-	N	1	0,N	0,1	0	0,1	0,1,N	0
Serpentes	1	0	N	1	N	1	0	1	N	0
<i>Sphenodon</i>	0	0	0	1	0	0	0	1	N	0

TAXON	CHARACTER									
	31	32	33	34	35	36	37	38	39	40
Agamidae*	0,1	0	0	0	0,1	0	1	0	0	0
Anguidae	1	0,1	0,1	1	0,1?	1	1	0	1	1
Chamaeleontidae	0,1	0	0	0	0	0	1	1	0	N
Cordylidae	0,1	0	0	1	0	0,1	1	0	1	1
Dibamidae	N	1	0,1	1,N	1	0	1	0	1?	1
Gekkonidae	0,1,N	1	0,1	1	0,1	0	1	0,1	1	1
Gymnophthalmidae	1	0	0	1	0	0	0	0,1	1	1
Helodermatidae	1	0	0	1	0	0	0	0	1	1
Iguanidae*	1	0	0	0	0	0	0,1	0	0	0
Lacertidae	0,1	0	0	1	0	1	0	0	1	1
<i>Lanthanotus</i>	1	0	0	1	0	0	1	0	1	1
Pygopodidae	0,N	1	0,1	1	1?	0	1	1	1	1
Scincidae	0,1,N	0,1	0	1	0	1,0	1	0,1	1	1
Teiidae	1	0	0	0,1	0	0	0	0	1	1
<i>Varanus</i>	1	1	0	1	0	1	1	0	1	1
Xantusiidae	0	0	0	1	0	0	1	1	1	1
Xenosauridae	1	0	0	0,1	0	1	1	0	1,0	1
Amphisbaenia	1	0,1	0	1	1?	0	1	0	1	1
Serpentes	N	0,1	1	N	0,1	0	1	0	1,N	1
<i>Sphenodon</i>	0	0	0	0	1	0	0	0	0	0

	41	42	43	44	45	46	47	48	49	50
Agamidae*	0	0	0	0	0	0	0	0,1	0	1,0
Anguidae	1	0,1	0	1	0,1	0	0	1	1	0
Chamaeleontidae	N	0	0	0	0	0	1	1	0	0
Cordylidae	1	0	0	1	0	0	0	1	1	0
Dibamidae	1	1,N	1	1	1	0	0,1	1	0?	0
Gekkonidae	1	0	0	1	0,1	0	0	1	1	0
Gymnophthalmidae	1	0,1	0	1	0	0	0	0,1	1	0
Helodermatidae	1	0	0	1	1	0	0	1	1	0
Iguanidae*	0	0	0	0	0	0	0,1	1,0	0,1	1,0
Lacertidae	1	0	0	1	0	0	0	0,1	1	0
<i>Lanthanotus</i>	1	1	0	1	1	0	0	1	1	0
Pygopodidae	1	0,1	0	1	0,1	0	0	1	1	0
Scincidae	1	0,1	1	1	0	0	0	1	1	0
Teiidae	1	0	0	1	1	1	0	0	1	0
<i>Varanus</i>	1	1	0	1	1	0	0	1	1	0
Xantusiidae	1	0,1	0	1	1	1	0	1	1	0
Xenosauridae	1	0	0	1	0	0	0	1	1	0
Amphisbaenia	1	1	0	1	0,1	0	1,0	1	1	0
Serpentes	1	N	0	1	0	0	1	1,N	N?	0
<i>Sphenodon</i>	0	0	0	0	0	0	0	1	0	0

TAXON	CHARACTER									
	51	52	53	54	55	56	57	58	59	60
Agamidae*	1	0	0	0,1	0	0	0	0	0,1	0
Anguidae	1	0	1	0,1	0	1	1	0	0	0,1
Chamaeleontidae	1	0	0	0,1	0	0,1	0,1	0	0,1	0
Cordylidae	1	0	0,1	1	0,1	0	0	1	0	1
Dibamidae	0	0	2,N	0	2	-	N	1	0	1
Gekkonidae	1	1,0	0	1	2	0	N	1	0	0
Gymnophthalmidae	1	0,1	0	0,1	0,2	0	0	0,1	0	0
Helodermatidae	1	0	1	1	0	1	1	0	1	0
Iguanidae*	1	0	0	0,1	0,1,2	0	0	0	0,1	0
Lacertidae	1	0	1	1	0	0	0	1	0	0
<i>Lanthanotus</i>	1	0	1	0	0	1	1	0	1	0
Pygopodidae	1	1	0	1	2	-	N	1	0	0
Scincidae	1	0	0,1	1	0,1,2	0	0	1	0	1,0
Teiidae	1	0	0	0	0,1	0	0	1	0	0
<i>Varanus</i>	1	0	0	0	0	1	1	0	1	0
Xantusiidae	1	1	0,1	1	2	0	N	1	0	1
Xenosauridae	1	0	0,1	0,1	0	1	1	0	0	0,1
Amphisbaenia	1	0	-	0	0,1,2	-	N	0	0,1	0,1
Serpentes	1	0	0	0	0	0	0	1	0	0
<i>Sphenodon</i>	0	0	0	0	0	-	0	0	1	0

	61	62	63	64	65	66	67	68	69	70
Agamidae*	0	0	0	0	1,2	1	0	0	0	0
Anguidae	0	0	1	0	0,1	0	0	1	0	0,N
Chamaeleontidae	0	0	0	0	2	N	N	0	0	0
Cordylidae	0	0	0	0	0	0	0	1	0	N
Dibamidae	0	0	0	0	2	N	N	0	0	N
Gekkonidae	0	0	0	0	1,2	0	0	1	0	0
Gymnophthalmidae	0	0	0	0	0,1	0,1?	0	1	0	0
Helodermatidae	1	0	1	1	1	1	1	1	1	0
Iguanidae*	0	0	0	0	0,1,2	0,1	0	0,1	0	0,1
Lacertidae	0	0	0	0	0	0	0	1	0	0
<i>Lanthanotus</i>	2	1	2	1	0	2	1	0	1	1
Pygopodidae	0	0	0	0	1,2	0	0	1	0	0
Scincidae	0	0	0	0	0,1	0	0	1	0	N
Teiidae	0	0	0	0	0	0	0	1	0	0
<i>Varanus</i>	2	1	2	1	0	1	1	0,1	1	0
Xantusiidae	0	0	0	0	1	1	N	0	0	N
Xenosauridae	0	0	1	0	0	0	0	1	0	0
Amphisbaenia	0	N	0	0	1,2	1	0	0,1	0	0,1
Serpentes	0	0,1	0	1	1	2	1	0,1,N	0,N	1
<i>Sphenodon</i>	0	1	0	0	2	N	N	0	0	0

TAXON	CHARACTER									
	71	72	73	74	75	76	77	78	79	80
Agamidae*	0	0	0	0	0	0	0	0	0	1
Anguidae	0,1	0	0	1	1	0	0	1	1	0
Chamaeleontidae	0	0	0	N	0	0	0	0	0	0
Cordylidae	1	0	0	0,1	1	1	0	1,0	1	0
Dibamidae	0	1?	0	1	0	0	0	1	1	0
Gekkonidae	0	0,1	0	1	1	0	1	1	1	0
Gymnophthalmidae	0	0	2	0,1	0	0	0	0	0	0
Helodermatidae	0	0	0	1	1	0	0	0	1	0
Iguanidae*	0	0,1	0	0,1	0	0	0	0	0	1,0
Lacertidae	0	0	1	0	0	0	0	0	0	0
<i>Lanthanotus</i>	0	0	0	1	1	0	0	0	1	0
Pygopodidae	0	0,1	0	1	1	0	1	1	0	0
Scincidae	1,0	0,1	0	1	1	1	0	1	1	0
Teiidae	0	0	2	0	0	0	0	0	0	0,1
<i>Varanus</i>	0	0	0	1	1	0	0	0	1	0
Xantusiidae	1	1	1	0	0	0	0	0	0	0
Xenosauridae	0	0	0	1	0	0	0	0	1	0
Amphisbaenia	0	0,1	0	1	0	0	0	0	1	0
Serpentes	N,0	0,1	0	1,N	1,N	0,N	0,N	0,N	1,N	0
<i>Sphenodon</i>	N,0	0	0	N	N	N	N	N	N	0

	81	82	83	84	85	86	87	88	89	90
Agamidae*	0	1	1	1	N	0	0	1	1	0,1
Anguidae	0	0,1	0,1	0	1	0,1?	0	1	0,1	0,1
Chamaeleontidae	0	1	1	1	N	0	0	1	1	1
Cordylidae	0	1	0,1	0	0	0	0	1	0,1	0
Dibamidae	0	1	1	0	1	0	0	1	1	1
Gekkonidae	0	1	1	0	0	0	0	0,1	0,1	0,1
Gymnophthalmidae	1	1	0,1	0	0,1	0	1	1	0,1	1
Helodermatidae	0	0,1	0	0	2	1	0	1	1	0
Iguanidae*	0	0,1	0,1	0	0	0	0,1	1	0,1	0,1
Lacertidae	1	1	0,1	0	0	0	1	1	0,1	0
<i>Lanthanotus</i>	0	0	0	0	2	1	0	1	1	1
Pygopodidae	0	1	1	0	0	0	0	0,1	0,1	0,1
Scincidae	0,1	1	0,1	0	0,1	0	0	1	0,1	0,1
Teiidae	1	1	0,1	0	0,1	0	1	1	0	0
<i>Varanus</i>	0	1	1	0	2	1	0	0	0	1
Xantusiidae	0	1	1	0	0	0	0	1	0	0
Xenosauridae	0	1	0,1	0	1	0	0	1	0	1
Amphisbaenia	0	1	1	0,1	1,2,N	0	0	1	1	1
Serpentes	0	0,1	0,1	0	2	0	0	1	1	1
<i>Sphenodon</i>	0	0	1	1	N	0	0	0	0	0

TAXON	CHARACTER									
	131	132	133	134	135	136	137	138	139	140
Agamidae*	0,1	0	0	0	0	0	1	0	0	0
Anguidae	0	0	0,1	1	0	1	2	1	0	0
Chamaeleontidae	0	0	0	0	0	0	0	0	0	0
Cordylidae	0	0	1	1	0	0	1	1,2	0,2	2
Dibamidae	0	0	-	1	0	0	0	1	2?	-
Gekkonidae	0	0	0	0	1	0	1	1	1	1
Gymnophthalmidae	1	1	1	1	-	0	4	2	1	-
Helodermatidae	0	0	1	1	0	1	3	1	0	0
Iguanidae*	0	0	0	0	0	0	1	0	0	0
Lacertidae	1	1	1	1	0	0	3	2	2	1
<i>Lanthanotus</i>	0	0	1	-	-	1	4	1	0	-
Pygopodidae	0	0	1	0	1	0	1	1	1	1
Scincidae	0	0	1	1	0	0	1	2	1	2
Teiidae	1	1	1	1	0	0,1	4	2	1	1
<i>Varanus</i>	0	1	1	1	0	1	5	1	N	0
Xantusiidae	1	1	1	1	0	0	1	2	1	2
Xenosauridae	0	0	1	1	0	1	2	1	0	0
Amphisbaenia	0	0	-	1	0	0	4	2	0	0
Serpentes	0	0	0	1	0	1	5	1	N	0
<i>Sphenodon</i>	0	0	0	0	0	0	0	0	0	0

	141	142	143	144	145	146	147	148
Agamidae*	0	0	1	0,1	2	0,1	0	0
Anguidae	1,0	0	0	0	2	1	1	0,1
Chamaeleontidae	N	1	1	0	2	0	0	0
Cordylidae	0	0	0,1	1	2	1	1	0,1
Dibamidae	0	N	N	0	1	1	1	1
Gekkonidae	1	0	0	0,1	0,1	1	0	0,1
Gymnophthalmidae	1	1	1	0,1	2	1	1	0,1
Helodermatidae	0	1	1	0	2	1	0	0
Iguanidae*	0	0,1	0,1	0,1	2	0,1	0,1	0
Lacertidae	0	0,1	0	0,1	2	1	1	0
<i>Lanthanotus</i>	0	1	0	0	2	1	0	0
Pygopodidae	1	N	0	0,1	0	1	1	0,1
Scincidae	1	0	0	0	2	1	1	1
Teiidae	0	1	1	0,1	2	1	1	0
<i>Varanus</i>	0	1	0	0	2	1	0	0
Xantusiidae	0,1	0	0	1	2	1	1	0
Xenosauridae	0	0	0	0	2	1	0	0
Amphisbaenia	1	0,N	N	0,1	2	1	1	0
Serpentes	0	N	N	0	0	1	1,0	0,1
<i>Sphenodon</i>	0?	0	0	0	0	0	0	0