A Phylogeny of Iguanidae

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INTRODUCTION

The family Iguanidae is the largest and most widely ranging family of lizards in the Western Hemisphere. At present about 60 genera and nearly 600 species are recognized. Iguanids extend from southern Canada southward to northern Tierra del Fuego on the mainland, and throughout the West Indies and Galápagos Archipelago; two extralimital genera occur on Madagascar and the Comoro Archipelago, and one other in the Fiji and Tonga Islands. In this century the definition and content of Iguanidae has rested upon Boulenger's (1884, 1885a) account of the family, and until recently the naturalness, or monophyly, of the group has not been in question. However, in their studies of the phylogenetic relationships of "lizard" families, Estes et al. (1988) found no convincing evidence that Iguanidae is monophyletic, and consider the family to be a metataxon. We have reached the same conclusion, and therefore our major effort has gone toward the discovery and diagnosis of monophyletic suprageneric groups within Iguanidae, and the resolution of relationships within each of these groups.

The first proposal for the formal recognition of iguanid subfamilies was that of Cope (1900). His Anolinae and Basiliscinae included only a few genera, the bulk of the family being relegated to the subfamily Iguaninae. This proposal has been largely ignored. Mittleman (1942) and Smith (1946) discussed the possible affinities of North American iguanid genera, but it was not until Savage (1958) that the next step was taken toward the recognition of specific, diagnosable, suprageneric groups. Savage (1958) introduced the term "sceloporines" for a set of North American genera, and "iguanines" for a widespread group of large herbivores. Etheridge (1959) diagnosed a small group of genera allied to *Anolis* and termed them the "anoles." Later he (Etheridge, 1964) expanded the anoles to include more distantly related South American genera, and at the same time he recognized but redefined the sceloporines and iguanines, revived Cope's (1900) "basiliscines", and proposed still another group, the South American-West Indian "tropidurines."

At about this time, some 20 years ago, one of us (RE) was asked by a colleague (E.E. Williams) to sketch out the relationships of all of the iguanid genera as he saw them at that time (Fig. 1), and although no documentation was provided, its branching lines implied certain major group relationships. We reproduce here a copy of the original diagram with the major group names added, refered to hereafter as the "Old Tree", because it has subsequently appeared, with modifications, in print (Paull et al., 1976; Peterson, 1984) and in several graduate dissertations, and finally, because the present analysis supports monophyly of many of the implied groups.

Over the past 25 years, with the aid of many colleagues and friends, a great deal more information has been accumulated on iguanid lizards, and our taxonomic coverage has expanded enormously. As a result, we have acquired a complete data set for all of the characters we employ for representatives of 58 iguanid genera, and for nearly 40 per cent of these genera our species level coverage is complete. The only iguanid genus that might reasonably be considered valid for which we have no data is *Phrynosaura* (Laurent, 1984).

The results of our analysis strongly support monophyly of many of the generic groupings implied by the branching lines of the Old Tree. In particular there appears to be strong support for eight major suprageneric groups, but, the relationships of these eight groups to one another remain ambiguous. For this reason we have organized our discussions around these groups, and introduce them here.
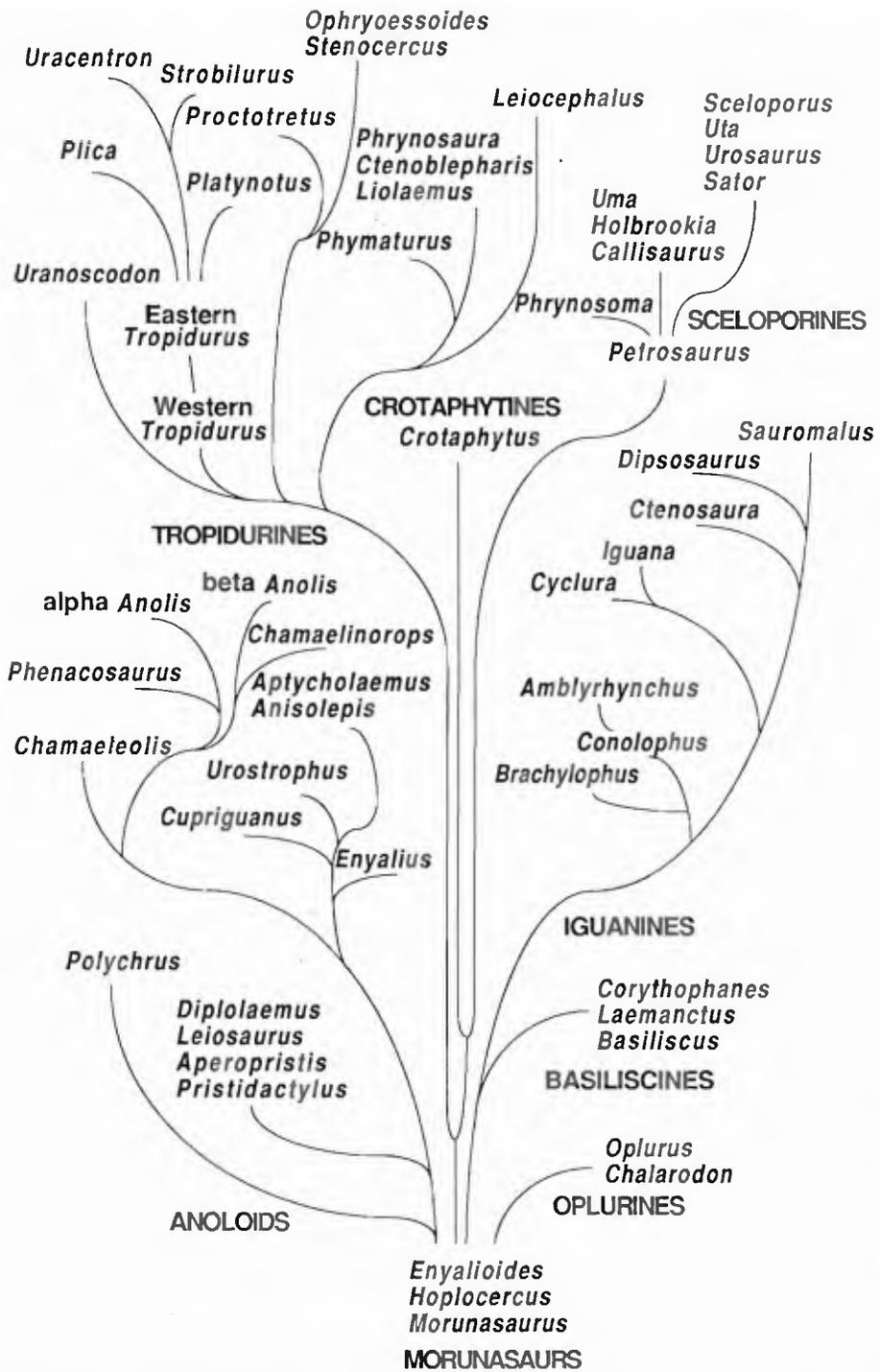
FIGURE 1. The Old Tree, prepared by R. Etheridge about 1962 and subsequently published in modified form in Paull et al. (1976) and Peterson (1984).

Morunasaurs. A small, disjunct group with three genera and 10 species in Panamá, nortwestern South America and southeastern Brazil. Some species of *Enyalioides* are arboreal; other morunasaurs are terrestrial. The group is persistently primitive in some regards and its basal placement on the "Old Tree" implies paraphyly, but the present analysis indicates that the morunasaurs form a monophyletic group.

Anoloids. A primarily South American radiation with 10 genera and about 200 species, all but 38 of which are in *Anolis*; the latter extends northward to the West Indies and southern North America. The group is primarily arboreal but with terrestrial representatives in arid austral South America.

Tropidurines. A large, South American-West Indian radiation with over 200 species in 15 genera. They live in a variety of habitats including deserts, semi-deserts, subtropical and tropical rain forest, and exhibit terrestrial, saxicolous, arenicolus and arboreal habits.

Crotaphytines. A small group of terrestrial and saxicolous lizards in western North America, with six species in one or two genera. Although the "Old Tree" indicates a sister group relationship between this group and the sceloporines, and a sister group relationship between the clade thus formed and the tropidurines, the relationships among these three groups are not resolved in our present analysis.

Sceloporines. A primarily North American group with over 100 species in eight to ten genera. Over half of the species are in *Sceloporus*, whose range encompasses that of the group as a whole and extends southward to Panamá. Sceloporines are mostly terrestrial, saxicolous and arenicolous, but *Urosaurus* and *Sceloporus* have arboreal species. Their greatest diversity is in arid and semi-arid southwestern North America.

Iguanines. A widespread but highly disjunct group of mostly large, herbivorous lizards, with 31 species in eight or nine genera. They are found in Fiji and the Tonga Islands, the Galápagos Archipelago, on the American mainland from western North America southward to southern Brazil, and in the West Indies. The group is exceedingly diverse in habits, and occurs in deserts, semi-deserts, subtropical and tropical forests, and rocky marine coasts.

Basiliscines. A small group of moderately large, arboreal lizards, all with a distinctive parietal crest. Nine species in three distinct genera occur in Central America, with a few extending into México and northwestern South America. The sister group relationship between basiliscines and iguanines implied in the "Old Tree" is not well supported according to the present analysis.

Oplurines. A group widely disjunct from other iguanids, represented on Madagascar and the Comoro Archipelago by seven species placed in two genera, one monotypic. They occur in arid and semi-arid habitats where most are terrestrial and saxicolous, a few arboreal.

Prior works on the phylogenetic relationships of iguanids have dealt primarily with diagnoses and definitions of these groups, and the relationships of subsets of genera and species groups within them. We do not provide a detailed historical review of these works, but will refer to some of them in the course of our own discussions of relationships. We provide here only a guide to the literature, listed by the major generic groupings we recognize. *Anoloids*: Boulenger, 1885b, 1891; Cope, 1900; Costelli, 1973; Etheridge, 1959, 1969; Williams, 1977; Zug, 1971. *Basiliscines*: Cope, 1900; Costelli, 1973; Etheridge, 1959, 1964; McCoy, 1968; Maturana, 1962. *Crotaphytines*: Costelli, 1973; Etheridge, 1964; Mittleman, 1942; Montanucci, 1969; Montanucci et al., 1975; Robison and Tanner, 1962; Savage, 1958; Smith, 1946; Weiner and Smith, 1965; Wyles, 1980, Zug, 1971. *Iguanines*: Avery and Tanner, 1971; Boulenger, 1890; Camp, 1923; Cope, 1886, 1900; Costelli, 1973; de Queiroz, 1987; Etheridge, 1964; Gorman et al., 1971; Higgins and Rand, 1974; Iverson, 1980; Mittleman, 1942; Savage, 1958; Smith, 1946; Wyles and Sarich, 1983; Zug, 1971. *Morunasaurs*: none. *Oplurines*: Blanc et al., 1983; Costelli, 1973. *Sceloporines*: Adest, 1978; Axtell, 1958; Ballinger and Tinkle, 1972; Blackburn, 1981; Camp, 1923; Car-

penter, 1963; Clarke, 1965; Costelli, 1973; Cox and Tanner, 1977; de Queiroz, 1981, 1982; Earle, 1961, 1962; Etheridge, 1964; Fanghella et al., 1975; Hall, 1973; Larsen and Tanner, 1975; Lowe, 1955; Mittleman, 1942; Norris, 1958; Presch, 1969, 1970; Savage, 1958; Smith, 1946; Wyles, 1980; Wyles and Gorman, 1978; Zug, 1971. *Tropidurines*: Cei, 1974, 1979; Costelli, 1973; Laurent, 1984; Etheridge, 1964, 1966; Fritts, 1974; Zug, 1971.

METHODS

Because this is an attempt to reconstruct in part the evolutionary history of iguanid lizards, we have chosen analytical methods designed specifically to reveal phylogenetic relationships. We recognize suprageneric groups only when their members share what we consider to be features that have originated subsequent to the most recent common ancestor of all iguanids or are further transformations of such features.

In order to assess which features have been derived within Iguanidae, we have used the method of outgroup comparison. Unfortunately, Iguanidae is a morphotypic rather than a phylogenetic concept. Iguanids are those iguanians that possess the alternatives to the derived features of agamids and chamaeleons; for example, their marginal teeth are pleurodont rather than acrodont, they generally retain palatal teeth, the postfrontal bone is usually retained, and autotomy septa usually remain in their caudal vertebrae. Although such retained primitive features are phylogenetically uninformative concerning relationships among iguanians, they have been used as defining characters of Iguanidae. Because historically Iguanidae has been based on retained primitive features, it cannot be assumed that other iguanians, namely agamids and chamaeleons, are appropriate outgroups for an analysis of relationships within Iguanidae. The origin of Iguanidae may be identical with that of Iguania, and some iguanids may share a more recent common ancestor with Acrodonta (agamids and chamaeleons) than they do with other iguanids.

Other iguanians are not necessarily suitable outgroups, and therefore we have compared iguanids with more distantly related taxa at two or more successively removed levels of relationship, depending on the character under consideration. These levels are (1) non-iguanian squamates (= Scleroglossa of Estes et al., 1988), (2) rhynchocephalians (*sensu* Gauthier et al., 1988), and (3) all other lepidosauromorphans (Gauthier et al., 1988), which actually represent more than one outgroup. Justifications for this order of outgroups are presented by Gauthier et al. (1988) and Estes et al. (1988). Because only the first two of these outgroups have living representatives, they are the only ones suitable for the many characters that are not generally preserved in fossils. In a few cases more distantly related outgroups are also used.

Outgroup comparison does not always yield unambiguous results, especially in this case where the first and most significant outgroup (Maddison et al., 1984) is the enormous, morphologically diverse taxon that includes all other squamates. Therefore, although we have relied primarily on outgroup comparisons for determining the evolutionary polarities of characters, we have not limited ourselves to such comparisons. Our decisions have also been influenced by other sources of information including developmental pathways and congruence with other characters. We have attempted to state explicity the bases for all of our polarity decisions.

We have analyzed an initial set of 49 characters for phylogenetic information relevant to the question of relationships within Iguanidae. These characters are ones that we have been able to score in all iguanid genera except *Phrynosaura*, and they serve as the basis for a preliminary analysis of relationships within Iguanidae as a whole. We have analyzed these data first with the Wagner program (characters unweighted, 100 branch swappings specified) of the PHYSYS package installed by J. S. Farris on the California State University CYBER system. The same data were also evaluated without the aid of a computer program, attempting to minimize homoplasy but this time weighting characters. Our basis for weighting is neither completely subjective nor complete-

ly objective. Certain characters require extensive homoplasy no matter which "reasonable" phylogeny is considered. On the other hand, when these characters are considered to be uniquely evolved, even more extensive homoplasy is required in other characters. For such characters our perceptions of morphological similarities and differences can only be weakly related to actual evolutionary character transformations. Therefore, we grant these characters less significance as evidence for the monophyletic status of groups, especially when these groups are very inclusive and are incongruent with seemingly less plastic characters. The characters have not been assigned actual numerical weights; instead, we have reduced resolution by eliminating particular groupings that we feel are not well supported by the character data.

Basic Taxa

Ideally, the base level taxa in a phylogenetic study should be monophyletic. This simplifies analysis in that it facilitates the identification of variation within basic taxa that must be homoplastic and that which is potentially synapomorphic. However, this study is the first explicit attempt to delimit monophyletic groups, in the modern sense, within Iguanidae as a whole. Thus, the monophyletic subgroups of iguanids are largely unknown. In such cases it is common practice to pick currently recognized taxa at a single level in the taxonomic hierarchy as basic taxa. We have chosen the iguanid genera as our basic taxa, keeping in mind that they may not all be monophyletic. Furthermore, we have used a highly split generic classification. This should ultimately provide us with more information about the monophyly of more groups than would a less split classification. In the interest of nomenclatorial stability we make no recommendations for the formal synonymy of those genera which, according to this analysis, are derived from more inclusive groups that are also given generic status (i.e., are paraphyletic). We hope that others will refrain from adopting this study as the basis for formal nomenclatorial changes until questionable groups have been studied in more detail.

CHARACTER ANALYSIS

Our initial character list (Appendix 1) consists of 49 characters representing what we hypothesize to be 57 transformation series and a minimum of 86 synapomorphies (evolutionary transformations), provided that no characters exhibit homoplastic similarity among our basic taxa. This initial list includes those characters that could be scored for all genera of iguanids save *Phrynosaura*. In the following character discussions we present the logic, or at least explicitly state the biases, behind our polarity decisions. For each character, we give descriptions of the variation seen within Iguanidae as well as the conditions in agamids and chamaeleons. We then compare these variations with the conditions seen in various outgroups and explain the basis for our decisions about the numbers of transformation series involved and about the sequence of evolutionary transformation within each series.

Premaxilla-nasal relationship (1). In most iguanids the nasal process of the premaxilla lies entirely dorsal to the nasal bones, but in some the medial borders of the nasals completely or partly overlap the nasal process (Etheridge, 1966, fig. 3). In chamaeleons and in most agamids the nasal proceess of the premaxilla is entirely dorsal to the nasals, but its posterior part is partly overlapped by the nasals in some agamids. Among non-iguanian lizards we have found the nasal process of the premaxilla overlapped by the nasals only in the xantusiid *Lepidophyma flavimaculatum* and some species of *Varanus*. The process is entirely dorsal to the nasal bones in *Sphenodon*. Since the nasal process of the premaxilla is entirely dorsal to the nasal bones in *Sphenodon* and the great majority of lizards we conclude that this condition is primitive, and that overlap of the nasal process of the premaxilla by the nasal bones is derived.

Parietal Foramen (2). In most iguanids the parietal foramen pierces the dermal skull roof along the midline at the frontoparietal suture. In a few iguanids the parietal foramen lies more anteriorly, entirely within the frontal bone. More rarely (some *Anolis*) the foramen is positioned more posteriorly, lying entirely within the parietal. In still other iguanids, the parietal foramen is absent. Like that of most iguanids, the agamid parietal foramen lies within the frontoparietal suture (Moody, 1980). In chamaeleontids the foramen lies entirely within the frontal or is absent.

The parietal foramen is commonly absent in non-iguanian squamates (Estes et al., 1988). When present it invariably lies entirely within the parietal. In lepidosauromorphs other than squamates the parietal foramen is invariably present and, except for kuehneosaurs in which it is located at the frontoparietal suture, the parietal foramen lies within the parietal (Gauthier et al., 1988). Thus, although it is not unequivocal, the evidence from outgroup comparisons suggests that the presence of a parietal foramen located within the parietal is primitive for iguanids. Nevertheless, in this analysis we consider the primitive location of the parietal foramen to be on the frontoparietal suture. Within iguanians, the parietal foramen lies within the parietal only in some of the anoles. We will present evidence below that the anoles are a monophyletic group and that they are also members of several more inclusive monophyletic groups, all of whose other members have the parietal foramen located at the frontoparietal suture. Thus, the interpretation that a parietal foramen located within the parietal is a retained primitive feature in the few anoles that possess it is incongruent with a large number of other characters. For this reason we favor the more congruent interpretation that the primitive location of the parietal foramen in iguanids is on the frontoparietal suture and that derived conditions have evolved independently by anterior and posterior displacements of the foramen. Because the loss of the parietal foramen can conceivably be derived from a foramen at any location, we treat the presence or absence of a parietal foramen as a separate character and consider its location in taxa in which it is absent to be indeterminable.

Adult parietal roof shape (3). The parietal roof of most neonatal lizards forms a flat table, trapezoidal in outline, with the lateral margins slightly converging posteriorly and forming obtuse or nearly right angles with the posterior margin. This shape is maintained with slight modification during growth in most iguanids, but in some the lateral margins converge with age and ultimately contact posteriorly at the midline to form a "V" (Etheridge, 1966, fig. 4). In some of these the sides of the parietal continue to converge posteriorly, forming a sharp median crest where they meet in a Y-shape with the lateral margins (Etheridge, 1959, fig. 9). In most agamids the trapezoidal outline of the parietal roof is maintained throughout life, although in a few the roof becomes triangular. The peculiar vaulted parietal of chamaeleons appears to be unique to that group. Most scleroglossans also maintain the trapezoidal outline, but we have seen a triangular outline in some large teiids. The parietal of adult *Sphenodon* differs considerably from that of lizards; it is paired, with no definable roofing part except immediately around the parietal foramen, the two elements meeting posterior to the foramen to form a pair of steeply sloping shelves that meet at the dorsal midline to form a grooved crest. A similar condition is found in sapheosaurs but not in other sphenodontidans.

Because most iguanids and other lizards retain the trapezoidal outline of the parietal roof as adults, we consider this form to be primitive within iguanids, and that triangular and Y-shaped roofs represent progressively derived conditions.

Lacrimal (4) and *Lacrimal Foramen* (5) (Fig. 2). The lacrimal of most iguanids, like that of squamates generally, is a small bone confined to the anterior orbital margin. In a few iguanids, however, no separate lacrimal is present, and judging from the lack of bone in the lacrimal region it appears to have been lost rather than fused to a neighboring bone. In *Morunasaurus* the lacrimal may be present or absent. When present it is but a tiny sliver of bone, again suggesting loss rather than fusion at least in this genus. Both agamids and chamaeleontids are also variable in the presence of a lacrimal.
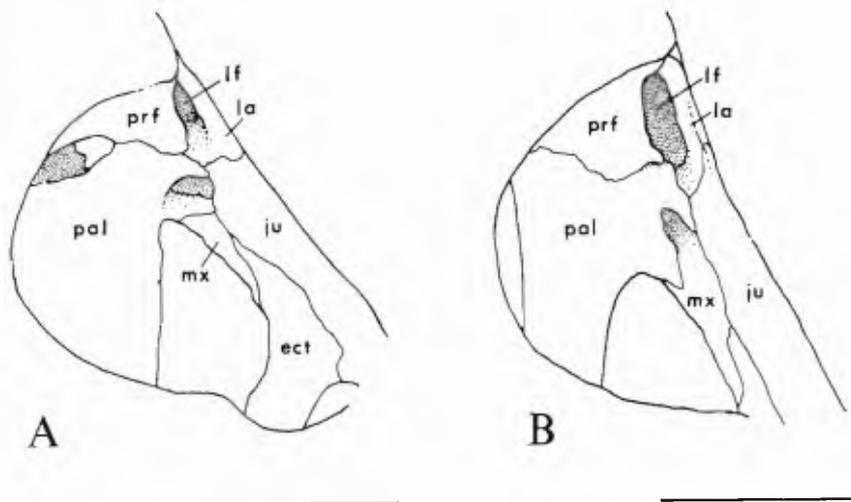
FIGURE 2. Posterodorsal views of the anterior orbital region of A, *Sauromalus australis* (KdQ 072) and B, *Enyalioides praestabilis* (USNM 22583) illustrating differences in the relative size of the lacrimal foramen (character 5). Abbreviations: ect = ectopterygoid; ju = jugal; lf = lacrimal foramen; mx = maxilla; pal = palatine; prf = prefrontal. Bar = 5 mm.

Presence of a lacrimal is the most common condition among non-iguanian squamates, but the lacrimal is absent in gekkonids, dibamids, snakes and several other squamate taxa (Estes et al., 1988). A discrete lacrimal is also absent in xantusiids, but here the bone appears to have fused to the prefrontal rather than to have disappeared. Although the lacrimal is absent in sphenodontidans, it is present in the rhynchocephalian *Gephyrosaurus* and in other more distantly related fossil lepidosauromorphs. This character distribution suggests that the presence of a lacrimal is primitive within iguanids, although the evidence is somewhat equivocal.

The lacrimal foramen pierces the anterior wall of the orbit between the lacrimal and the prefrontal, connecting the orbit with the nasal capsule. In most iguanids this foramen is relatively small, but in a few it is enlarged. Intermediates between the two extremes occur but are rare. The size of the lacrimal foramen may be related to the presence or size of the lacrimal bone because a large lacrimal foramen occurs only in those taxa in which the lacrimal bone is small or absent. The correlation is not perfect, however, for the lacrimal is present (although small) in taxa with the largest lacrimal foramina (e.g. *Enyalioides*), and *Phrynosoma* has a small lacrimal foramen even though it lacks a lacrimal bone. The lacrimal foramen in chamaeleontids and most agamids, except *Uromastyx* and *Leiolepis*, is very large.

Judging from the size of the lacrimal foramen in non-iguanian lepidosaurs, a large lacrimal foramen is derived within Iguanidae. The lacrimal foramen of nearly all other squamates is small, although that of some varanoids (in which the lacrimal bone is large and the lacrimal foramen is
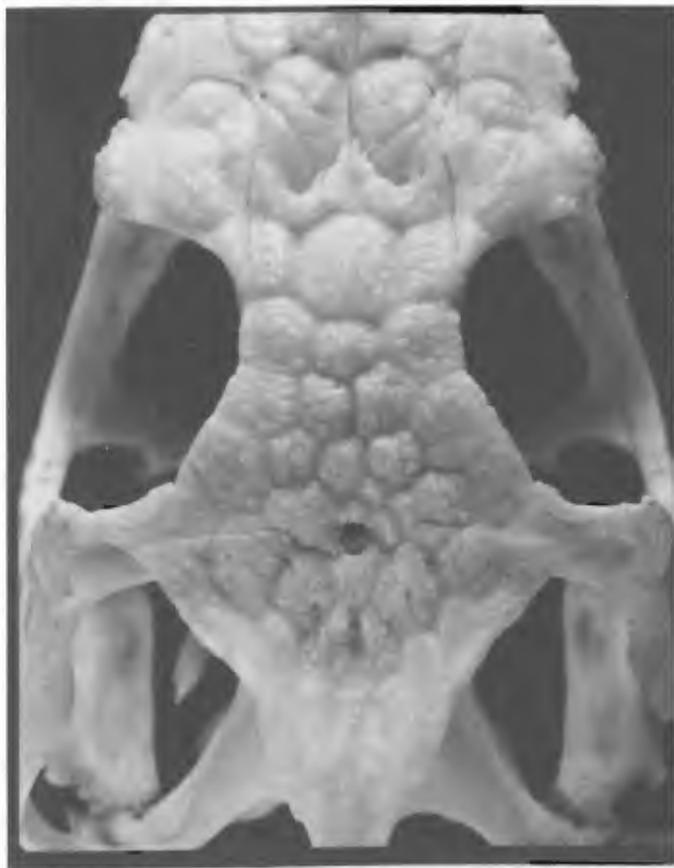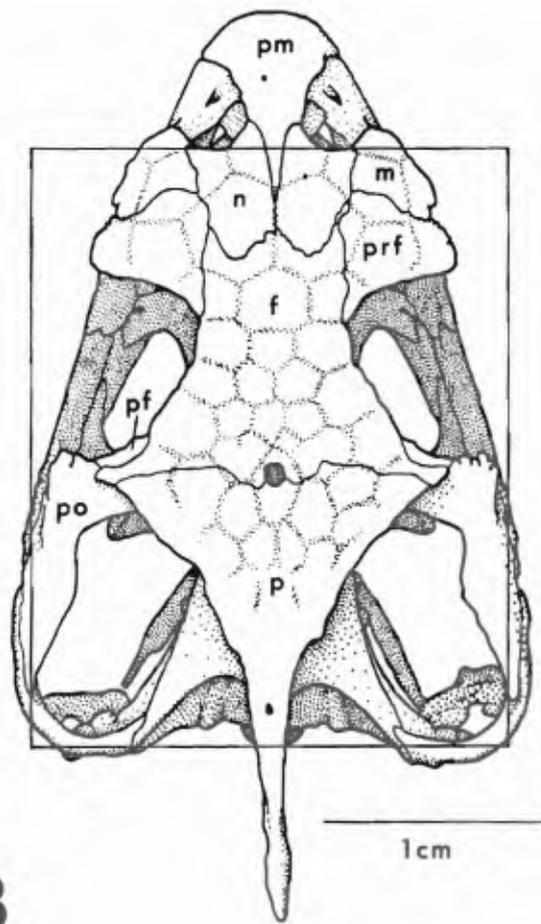
FIGURE 3. Dorsal views of the skull of *Laemanctus serratus* (AMNH 44982) illustrating rugosities that reflect the pattern of overlying epi-dermal scales on the surface of the dermal roof (character 7). The area represented in the photograph (A) is the area within the box in the line drawing (B). Abbreviations: f, frontal; m, maxilla; n, nasal; p, parietal; pf, postfrontal; pm, premaxilla; po, postorbital; prf, prefrontal.

double) approaches the large size seen in some iguanids. *Sphenodon* also has a small lacrimal foramen despite the fact that it has no lacrimal bone. Unfortunately, the anterior orbital wall of fossils is rarely figured so that data are currently unavailable for most extinct lepidosauromorphs.

Postfrontal (6). Like the lacrimal, the iguanid postfrontal is a small bone of the orbital margin whose presence varies within the group. Unlike iguanids, in which the postfrontal is usually present, agamids and chamaeleons both lack a postfrontal.

Judging from the condition in non-iguanian squamates and more distantly related lepidosauromorphs, the presence of a postfrontal is almost certainly primitive within iguanids, its absence derived. Among non-iguanian squamates, the postfrontal seems to be absent only in taxa possessing highly modified skulls: some snakes, some amphisbaenians, and *Dibamus* (but not *Anelytropsis* according to Greer, 1985). In a few other non-iguanian squamates no separate postfrontal is discernable; however, based on the morphology of the single bone in the postfrontal-postorbital region, these are probably cases in which the postfrontal has fused to the postorbital. The postfrontal is also present in all non squamate lepidosauromorphs in which the morphology of the postorbital region is known.

The absence of a discrete postfrontal can, theoretically, occur either through loss of the ossification center itself or through its fusion to a neighboring bone, namely the frontal or postorbital. Because these different processes have a similar result, i.e. the absence of a discrete postfrontal element, there is a potential problem of treating convergent characters as synapomorphies. Unfortunately, we lack developmental data that might be used to choose among these alternative processes of "loss." Furthermore, because of the small size of the postfrontal and its variable morphology in iguanids, it is difficult to choose among these alternatives without making assumptions about the appropriate taxa to choose for comparison (i.e., about phylogenetic relationships within the Iguanidae). Therefore, until more information becomes available, we will simply consider the absence of a discrete postfrontal to be a single derived character.

Surface of dermal roofing bones (7) (Fig. 3). In most iguanids the outer surface of the dermal roofing bones of the skull are smooth or nearly so, but in some taxa rugosities develop that reflect the pattern of the overlying epidermal scales. Ontogenetically these rugosities characteristically appear in juvenile animals on the dorsal surface of the frontal and parietal bones near the frontoparietal suture, thence spreading (in the most extreme cases) to include the entire frontal and parietal roof, the postfrontals, postorbitals, jugals, lacrimals, prefrontals, maxillae, nasals and premaxilla. Extreme hypertrophy of the fine, scroll-like rugae may obscure epidermal scale sutures in large individuals of some species. Similar rugosities are present in many chamaeleons and a few agamids, (e.g. *Gonocephalus*). The surface rugosities that appear on the skull in very large individuals of the teiids *Tupinambis* and *Ameiva* appear to be of the same type.

Although Camp's (1923:395-397) discussion of osteoderms in lizards concerns only their presence in non-iguanian lizards, in a footnote (p. 396) he stated that "Osteoderms are developed only over the skull in the Lacertidae, Xantusiidae, Xenosauridae, and in some Iguanidae." However, iguanians appear not to have the same type of dermal ossifications found among non-iguanian lizards. In the latter, intramembranous ossifications may appear within the dermis and later fuse or not with the underlying bones where the skin passes over the skull. Among iguanians we have found such ossifications only in very large *Amblyrhynchus cristatus*. In contrast, the dermal rugosities found in some iguanids, agamids, chamaeleons, and perhaps some large teiids appear to be formed in a different way, by elaboration from the cranial periosteum itself. The skull bones of *Sphenodon* and other lepidosauromorphs are nearly smooth.

Because the skull roofing bones are smooth in *Sphenodon*, and in most non-iguanian squamates they are either smooth or fused with true dermal ossifications, we consider smooth dermal skull bones to be primitive within Iguanidae, the presence of rugae that reflect the epidermal scale pattern derived.
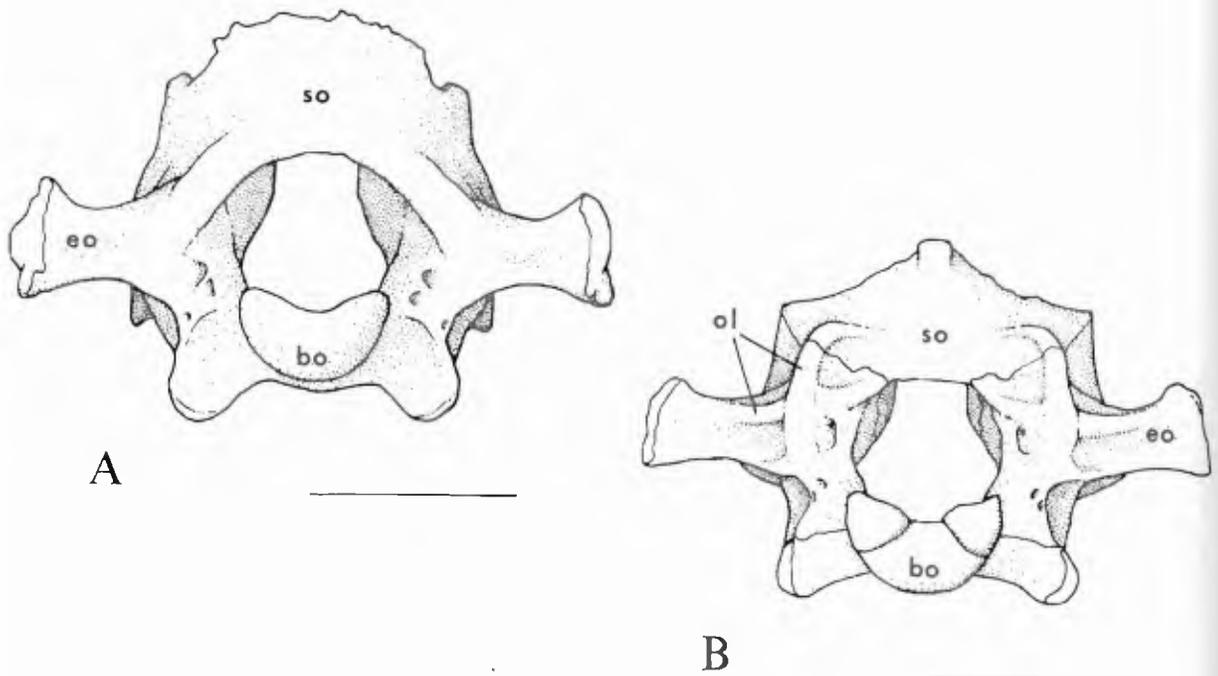
FIGURE 4.   Posterior views of iguanid braincases illustrating variation in the prominence of the superficial outlines of the osseous labyrinth (character 8).   A, *Brachylophus fasciatus* (AMNH 17701), in which outlines of the labyrinth are barely visible.   B, *Uranoscodon superciliosus* (KdQ 124), in which outlines of the osseous labyrinth are raised well above the rest of the surface of the braincase.   Abbreviations: bo = basioccipital; eo = fused exoccipital and opisthotic; ol = superficial outlines of osseous labyrinth; so = supraoccipital.   Bar = 5 mm.

Bony labyrinth (8) (Fig. 4).   The superficial outlines of the inner ear's osseous labyrinth are barely or not at all discernible on the top and sides of the braincase in most iguanids, but in some they are quite conspicuous, rising well above the outer surface of the braincase.   About the same range of variation is found in agamids, and in chamaeleons the labyrinth is moderately conspicuous.

Among non-iguanian squamates the osseous labyrinth outlines cannot be seen or are only vaguely apparent in all forms examined except in some xantusiids and gekkonids. In *Sphenodon* they cannot be seen at all.   Since a conspicuous bony labyrinth raised well above the braincase outer surface occurs only in some iguanids, agamids, xantusiids and gekkonids this condition is considered derived.

Supratemporal (9). The supratemporal of most iguanids lies on the anterolateral surface of the supratemporal process of the parietal. In contrast, the supratemporal of some *Oplurus* and *Enyalius* has roughly equal portions exposed on the anterolateral and the posteromedial surfaces of the parietal, and in iguanines it lies mostly on the posteromedial surface. Because the supratemporal of "primitive eosuchians" and *Paliguana* lay in a depression along the posteromedial surface of the parietal (Carroll, 1977), this condition might seem, upon cursory examination, to be primitive for iguanids. The supratemporal is absent in *Sphenodon* and most other sphenodontidans and is either

absent or not preserved in kuehneosaurs and *Gephyrosaurus* (Gauthier et al., 1988). Closer examination reveals the posteromedially located supratemporals of early lepidosauromorphs and some iguanids to be only superficially similar. In all non iguanian squamates (except mosasaurs) in which this region has not been greatly modified, the supratemporal is like that of most iguanids, lying along the anterolateral surface of the supratemporal process of the parietal. The posterior end of the bone lies deeper than it does in those of the early lepidosauromorphs mentioned above, including the sphenodontidan *Clevosaurus* (Robinson, 1973). Furthermore, the squamate supratemporal also wraps around the ventral edge of the supratemporal process of the parietal and wholly separates the squamosal from the paroccipital process while contacting the cephalic condyle of the quadrate (Robinson, 1967). Despite the posterior location of the supratemporal in iguanines (and mosasaurs - see Camp, 1942, figs. 1,9; Russell, 1967, figs. 12,17,20), and approached in some *Oplurus* and *Enyalius*, the posterior end of this bone wraps around the ventral edge of the supratemporal process of the parietal onto its lateral surface and wholly separates the squamosal from the paroccipital process while contacting the cephalic condyle of the quadrate, as in other squamates. Thus, the posterior location of the supratemporal described here for some iguanids is but one variant of a condition present in all squamates. Since the alternative condition, an anterolaterally located supratemporal, is found both in iguanids and in nearly all other squamates that have not obviously modified this region further, the posteromedially located supratemporal seems to be derived within Iguanidae.

Coronoid (10) (Fig. 5). Gauthier et al. (1988) argued that the squamate coronoid bone is derived relative to those of other lepidosauromorphs in that it alone generally forms the entire coronoid eminence (sometimes the dentary also contributes to the eminence). Primitively within the Lepidosauromorpha, the coronoid bone forms only the medial part of the eminence and the surangular forms its lateral portion. In addition to forming the entire coronoid eminence, the coronoid bone of many squamates extends laterally so that it sits atop the dentary and the surangular. In many iguanids this lateral extension is highly developed, forming a large, blade-like lateral process that extends well down the labial face of the mandible so that the coronoid straddles the rest of the lower jaw (Etheridge, 1966, fig. 2). In some iguanids the lateral process of the coronoid is much smaller and less blade-like, and in others it is lacking entirely. Living agamids and chamaeleontids lack a lateral process of the coronoid, but a large one is present in an extinct Cretaceous acrodont iguanian (Borsuk-Bialynicka and Moody, 1984).

Among non-iguanian squamates the presence of a large lateral process of the coronoid is by far the most common condition, although it is absent in some amphisbaenians, some snakes, and in *Dibamus* (Estes et al., 1988). The coronoid bone of all other lepidosauromorphs forms only the medial part of the coronoid eminence so that these taxa lack the lateral coronoid process. Thus, the evidence from outgroup taxa is equivocal concerning the primitive condition of the iguanid coronoid. We provisionally consider the absence of the coronoid lateral process to be primitive, primarily because this interpretation is more congruent with other characters within anoloid iguanids. For iguanids as a whole, this interpretation may well be incorrect (compare Estes et al., 1988).

Fusion of Meckel's groove (11) and *closure of Meckel's groove* (12) (Fig. 6). In iguanid lizards the dentary portion of Meckel's groove may be open, exposing Meckel's cartilage medially from the anterior end of the splenial to the mandibular symphysis, or closed but not fused for all or part of the distance from splenial to symphysis, or fused for all or part of the distance. Meckel's groove is open anterior to the splenial (or angular) throughout its length in agamids (Moody, 1980) and chamaeleons, in many autarchoglossans (e.g., teiids, lacertids, cordylids, scincids, anguids, xenosaurids, varanids, helodermatids), and in rhynchocephalians. In geckos it is closed and fused. The presence of a fully open Meckel's groove is considered primitive within Iguanidae, and probably also within squamates and lepidosaurs; various degrees of closure and fusion represent progressively derived states.
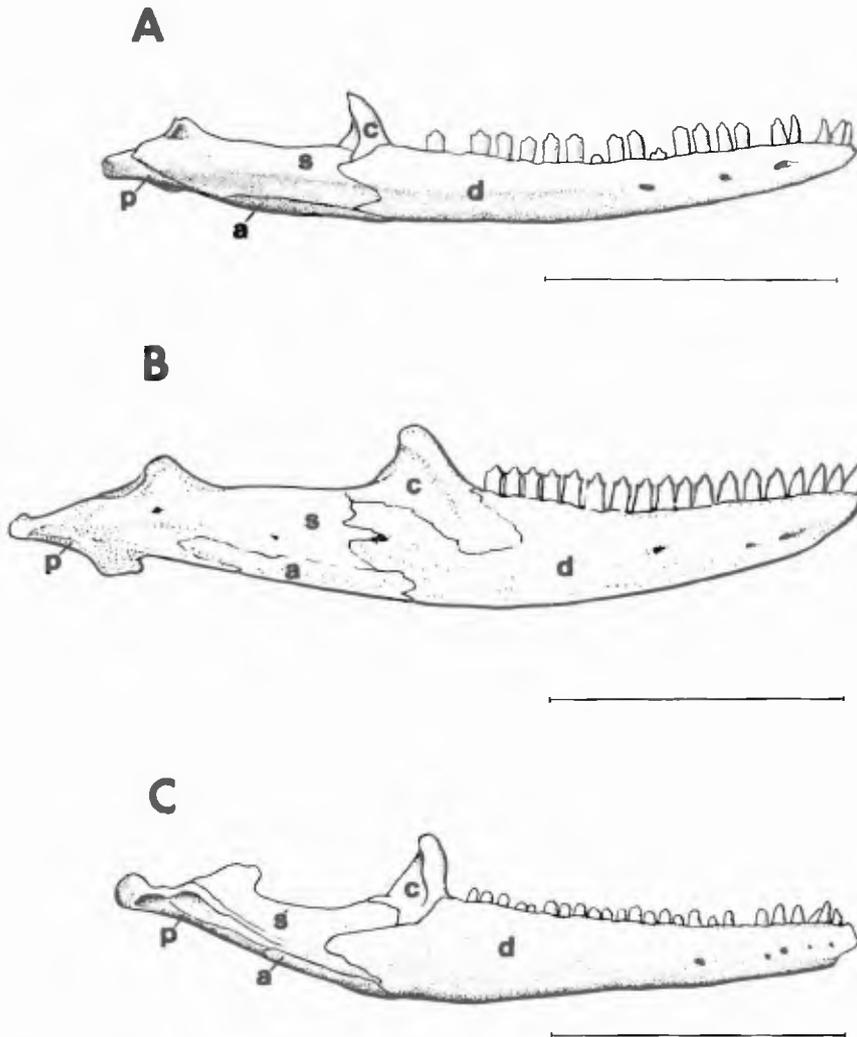
FIGURE 5.   Labial views of the right mandibles of iguanids illustrating variation in the coronoid labial process (character 10) and the posterior extent of dentary (character 16).   A, *Polychrus marmoratus* (RE 346) 10.0, 16.0.   B, *Hoplocercus spinosus* (RE 1263) 10.2, 16.1.   C, *Sceloporus magister* (RE 503) 10.0, 16.2. Abbreviations: d = dentary; c = coronoid; s = surangular; a = angular; p = prearticular. Bar = 5 mm.

Splenial presence (13) and *splenial size* (14) (Fig. 6). A splenial bone may be present or absent in iguanids. When present (in Recent forms) it may extend forward to a point about one-third of the way back from the mandibular symphysis along the dentary tooth row, and back to a point just posterior to the posterior medial process of the coronoid, or it may be variously reduced. In the Eocene iguanid *Parasauromalus* the splenial extends forward to the mandibular symphysis (Estes, 1983b). In Recent agamids the splenial may underlie 40 to 50 percent of the dentary tooth row at maximum size, or be variously reduced, absent, or fused (Moody, 1980), but in a Cretaceous acrodont iguanian the splenial reaches the mandibular symphysis (Borsuk-Bialynicka & Moody, 1984). A separate splenial is absent in chamaeleons (Moody and Rocek, 1980; pers. obs.). Among
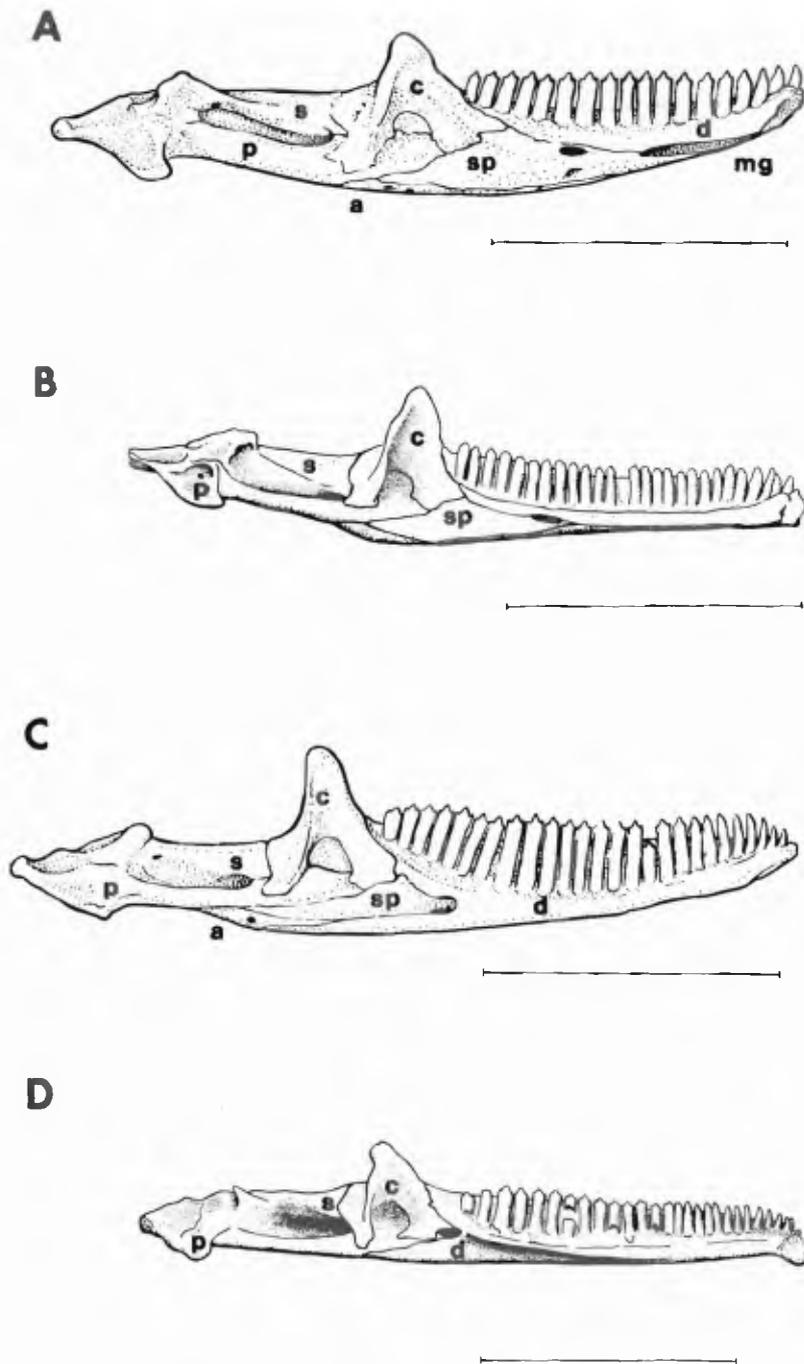
FIGURE 6. Lingual views of the left mandibles of iguanids illustrating variation in the fusion of Meckel's groove (character 11), closure of Meckel's groove (character 12), splenial presence (character 13), splenial size (character 14), and angular (character 15). A, *Hoplocercus spinosus* (RE 1263) 11.0, 12.0, 13.0, 14.0, 15.0. B, *Sceloporus magister* (RE 503) 11.0, 12.1, 13.0, 14.1, 15.0. C, *Leiocephalus melanochloris* (MCZ 5954) 11.1, 12.2, 13.0, 14.1, 15.0. D, *Anolis garmani* (SDSNH 63925) 11.1, 12.2, 13.1, 14.na, 15.4. Abbreviations: sp = splenial; mg = Meckel's groove; others as in Fig. 5. Bar = 5 mm.

autarchoglossans a large splenial underlying 50 to 100 percent of the dentary tooth row occurs in some forms of most families, e.g., lacertids, teiids, cordylids, xenosaurids, varanids, scincids and anguids. A splenial is absent in rhynchocephalians (Gauthier et al., 1988).

According to Romer (1956) the splenial takes part in the mandibular symphysis in various "primitive" reptiles, and thus it seems that the presence of a large splenial is primitive for iguanids and squamates, reduction or loss of the splenial derived.

Angular (15) (Fig. 6). In some iguanid lizards the angular bone is a large element composed of a plate-like portion on the lateral face of the mandible and a lanceolate process that extends ventromedially to terminate some distance anterior to the most posterior dentary tooth, suturing with the splenial on the medial face of the mandible. In other iguanids the anterior process is shorter or absent entirely, or the angular bone itself is lacking. A large angular is present in all agamids (Moody, 1980) and chamaeleons, in most scleroglossans and in rhynchocephalians. The presence of a large angular is considered primitive within Iguanidae and probably also within squamates and lepidosaurs, with transformations leading to reduction or loss of the element.

Posterior extent of dentary (16) (Fig. 5). In iguanids the posterior limit of the dentary on the labial face of the mandible may lie between a point below the superior apex of the coronoid and a point about 75 percent of the distance between the coronoid superior apex and the center of the articular fossa. In agamids and chamaeleons the dentary extends posteriorly well beyond the coronoid, occupying 30 percent or more of the distance between the coronoid superior apex and center of the articular fossa. Among scleroglossans the dentary fails to reach the level of the coronoid superior apex in teiids, lacertids, anguids, xenosaurids, helodermatids, and varanids. It reaches the coronoid apex or extends up to 30 percent beyond in scincids and cordylids, and in gekkonids and xantusiids it may extend up to 60 percent beyond the coronoid apex. In *Sphenodon* the dentary terminates below the articular fossa.

If our outgroup comparisons were to end here we might conclude that the elongate dentary of *Sphenodon*, agamids and chamaeleons and some scleroglossans is primitive for the lepidosaurs (*sensu* Gauthier et al., 1988); however, since the jaws of *Sphenodon* and the acrodont iguanians are conspicuously derived in other features we have included more distantly related lepidosauromorphs in our comparisons. The dentary fails to reach the level of the coronoid superior apex in *Youngina capensis*, *Paliguana whitei*, and *Icarosaurus siefkeri*, but in *Cteniogenys antiquus* it extends perhaps 30 percent of the distance to the articular fossa. Thus we hypothesize that a relatively short dentary, one that reaches or stops short of the coronoid superior apex is primitive in lepidosauromorphans and in iguanids, with longer dentaries representing progressively derived states.

Palatine teeth (17) and *pterygoid teeth* (18). When present, iguanid palatal teeth are confined to the palatines and pterygoids; vomerine teeth are never present. Palatine teeth are known in only nine genera of iguanids. In contrast, most iguanids possess pterygoid teeth, and when only one pair of palatal bones bears teeth, it is generally the pterygoids. Agamids and chamaeleontids lack both palatine and pterygoid teeth (Moody, 1980).

Although the presence of numerous teeth on the vomers, palatines and pterygoids appears to be primitive for lepidosaurs (Gauthier et al., 1988), the conclusion that the presence of palatine and pterygoid teeth is primitive for iguanids is less clear. Palatine teeth are absent in most non-iguanian squamates but are present in some anguids, *Heloderma*, *Lanthanotus*, and most snakes (Estes, et al., 1988). They are also present in rhynchocephalians and other early lepidosauromorphs (Gauthier et al., 1988). Unlike palatine teeth, pterygoid teeth are present in a wide variety of non-iguanian squamates; however, they are also commonly absent. Although *Sphenodon* and its closest relatives lack pterygoid teeth, Triassic sphenodontidans, *Gephyrosaurus* , and other early lepidosauromorphs have them (Gauthier et al., 1988). Thus, evidence provided by outgroups is equivocal concerning the primitive presence of iguanid palatine and pterygoid teeth. It is tempting
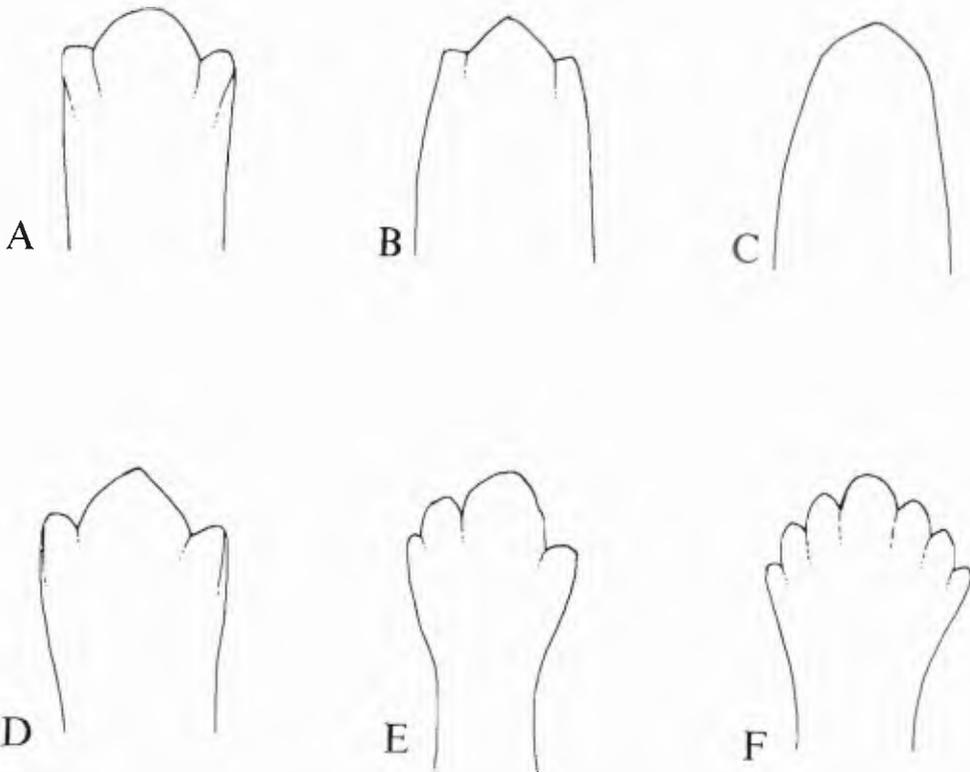
FIGURE 7. Lingual views of iguanid posterior dentary teeth illustrating variation in the morphology of the tooth crowns (character 19). A, *Morunasaurus annularis* (MCZ 146375) 19.0. B, *Cophosaurus texanus* (SDSNH 35251) 19.1b. C, *Phrynosoma coronatum* (MVZ 137780) 19.2b. D, *Basiliscus basiliscus* (KdQ 122) 19.1a. E, *Conolophus subcristatus* (MVZ 77314) 19.2a. F, *Sauromalus obesus* (MVZ 100404) 19.2a. The teeth illustrated are from the right tooth row, between one-half and three-quarters of the way back, and are not drawn to scale.

to invoke a "law" of evolutionary irreversibility and assume that the presence of palatal teeth is primitive for squamates and that such teeth have been lost convergently on numerous occasions rather than allow palatal teeth to be lost and regained, in which case the presence of palatal teeth could not be assumed to be primitive for iguanids. However, among living squamates, vomerine teeth are present only in *Ophisaurus apodus* (Rieppel, 1980) where they have almost certainly been regained. Furthermore, since the genetic and developmental bases for the formation of palatal teeth are unknown, it would be premature to assume that these structures cannot be regained during the course of evolution. Although the evidence is equivocal we follow the traditional interpretation that the absence of palatine and pterygoid teeth is derived within Iguanidae.

Crowns of posterior marginal teeth (19) (Fig. 7). Extremes in the morphology of iguanid marginal tooth crowns are highly divergent, ranging from blunt and peglike to lanceolate with serrated edges. A common tooth crown morphology in iguanids is tricuspid with a large apical cusp, smaller anterior and posterior cusps, and more or less parallel sides. Within single jaws the teeth may range from more or less homodont to markedly differentiated by region. Because maximum cuspation is generally reached near the posterior ends of the tooth rows, we have compared the teeth in this region. Unlike those of iguanids, the posterior marginal teeth of agamids and chamaeleons are not replaced (Edmund, 1969). For this reason, the crowns are often worn extensively, obscuring their original morphology. Nevertheless, a tricuspid crown similar to that of many
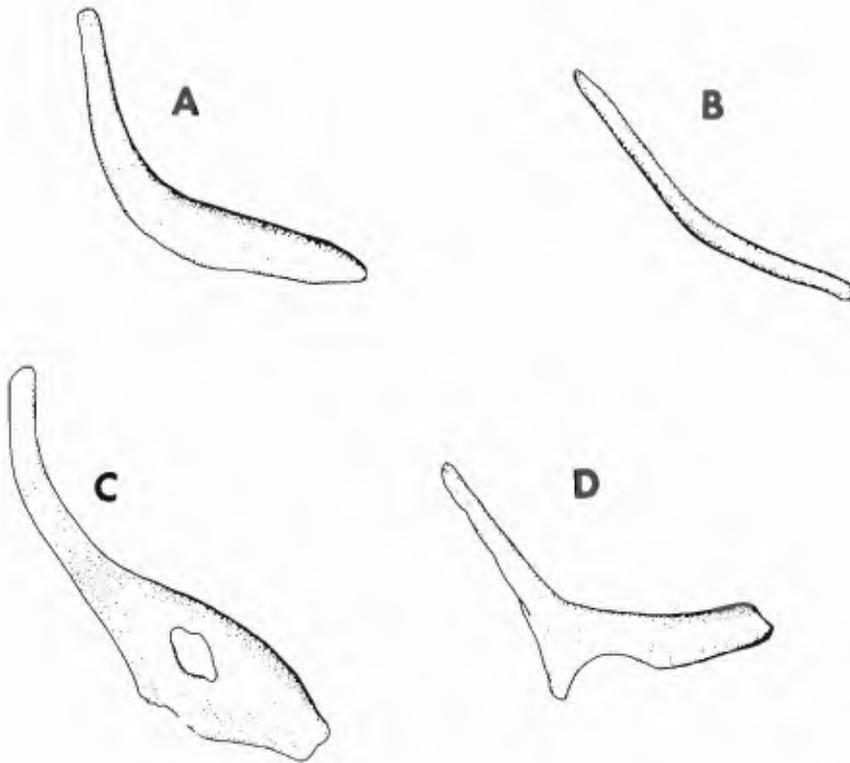
FIGURE 8.   Lateral view of the right clavicles of iguanids illustrating variation in clavicle shape (character 21), clavicular fenestration (character 22), and clavicle lateral margin (character 23). A, *Hoplocercus spinosus* (RE 1263) 21.0, 22.0, 23.0.   B, *Polychrus marmoratus* (RE 346) 21.1, 22.0, 23.0.   C, *Basiliscus plumifrons* (RE 427) 21.0, 22.1, 23.1b.   D, *Sceloporus magister* (RE 503) 21.0, 22.0, 23.1a.

iguanids can be seen in many agamids and most chamaeleons. The teeth of the agamid *Uromastyx* have a unique crown morphology (see Robinson, 1979), and those of many agamids lack cusps. In contrast to the teeth of those iguanids that lack cusps, the teeth of these agamids are strongly eliptical in cross section rather than being nearly circular.

The diversity of tooth crown morphologies seen in non-iguanian squamates is even greater than that seen in iguanians, making an unambiguous assessment of the primitive iguanid condition nearly impossible. The only tooth crown morphologies seen in iguanids that are also widespread in non-iguanian squamates are the tricuspid and the simple, peg-like crowns. In more distantly related lepidosauromorphs the teeth are generally simple and conical (Carroll, 1975; Colbert, 1970; Currie, 1980; Evans, 1980; Gow, 1975; Robinson, 1962), although an entirely different crown morphology is seen in certain sphenodontidans (Cocude-Michel, 1963; Gauthier et al., 1988; Robinson,1976).

Although the outgroup evidence for our position is ambiguous, we treat the tricuspid tooth crown as primitive within iguanids. We hypothesize two independent modifications of this primitive morphology, one involving reduction and eventual loss of the anterior and posterior cusps and a second involving broadening of the tooth crowns and an increase in cuspation.

Second ceratobranchials (20). The second ceratobranchials in iguanids vary in length from a pair of short, vestigial horns to elongate rods that extend back beyond the level of the clavicles to

underlie the interclavicle and sternum (Cope, 1900, pl.2). In most forms they do not exceed the first ceratobranchials in length and terminate far short of the pectoral girdle. The second ceratobranchials of agamids also vary considerably in length, the more elongate ones, as in iguanids, characteristically associated with an extensile gular fan (Moody, 1980). The second ceratobranchials are absent in chamaeleons. Second ceratobranchials are short or absent in scleroglossans and in *Sphenodon* they are short (Cope, 1892; Tanner & Avery, 1982). Therefore, second ceratobranchials that fail to reach the level of the clavicles are considered primitive within Iguanidae and squamates, longer elements derived.

Clavicle (21), *clavicular fenestra* (22) and *clavicle lateral margin* (23) (Fig. 8). The most common form of the clavicle in iguanid lizards is that of a simple, curved and somewhat flattened bar, widest in the middle or proximally, without a fenestra, and with the lateral margin forming a smooth curve. In a few iguanids the clavicle is expanded proximally and sometimes a fenestra penetrates the expanded part; in some the lateral margin forms an obtuse angle or bears a hook-like process near its middle, and in others the clavicle is a slender rod throughout its length. In most agamids the clavicle is a slender, rod-like element, but in several genera it is expanded proximally, usually with a fenestra (Moody, 1980). Postembryonic chamaeleons lack clavicles. A distinctively different clavicle shape is of common occurrence among non-iguanian squamates (e.g. teiids, xantusiids, lacertids, cordylids, scincids, gekkonids, anguids): the proximal part is expanded and flat, with a large, well defined fenestra, the distal part more slender, with a hook-like process projecting from its lateral margin. The posterior border of the fenestra may be interrupted to varying degrees, and the hook-like processes may be reduced or absent, the two modifications occurring independently of one another (Lécuru, 1968b; pers. obs.). In *Sphenodon* the clavicle is flattened, tapered at both ends, unfenestrate, with the lateral margin forming a smooth curve.

We consider a simple, curved, somewhat flat and unfenestrated clavicle with the lateral margin forming a smooth curve, present in *Sphenodon* and most iguanids, to be primitive within Iguania, the presence of a rod-like clavicle, a clavicular fenestra, and/or an angular lateral margin to be derived. A proximally expanded, fenestrate clavicle may be primitive within scleroglossan lizards.

Interclavicle (24). The iguanid interclavicle is a T- or arrow-shaped bone with paired lateral processes and a single median posterior process. Variation in the angle between the median and posterior processes and the proximity of the former to the clavicles have been used as systematic characters in other studies of iguanids (Etheridge, 1959); however, we have chosen to ignore this variation in the present analysis because the continuous nature of the variation makes it difficult to recognize discrete character states. The length and posterior extent of the posterior process of the interclavicle also varies within Iguanidae (Etheridge, 1964, figs. 4-5). In most iguanids the posterior process is long, extending posteriorly beyond an imaginary line passing through the lateral corners of the sternum, and often covers the sternal fontanelle ventrally. In contrast, the posterior process of the interclavicle of some iguanids is short, not extending as far posteriorly as the lateral corners of the sternum. Both long and short posterior processes of the interclavicle occur in agamids; chamaeleontids lack the interclavicle altogether.

Although variation in the posterior extent of the interclavicle in non-iguanian squamates is as great as that seen in iguanids (Lécuru, 1968b), the conditions seen in more distantly related taxa suggest that a long interclavicle is primitive for iguanids. In *Sphenodon* and certain well-preserved Jurassic Rhynchocephalia (Cocude-Michel, 1963) the interclavicle extends posteriorly beyond the lateral corners of the sternum, although not as far beyond this point as in many iguanids. The interclavicle of *Saurosternon* also extends far posteriorly (Carroll, 1977) as does that of the younginiform *Hovasaurus* (Currie, 1981). In most other fossil lepidosauromorphs the interclavicle is either fragmentary or completely unknown.

Scapular (25) and *posterior coracoid* (26) *fenestrae*. Along the anterior margin of the iguanid scapulocoracoid on each side of the pectoral girdle lie two, three, or four fenestrae, or emarginations if they are not bounded anteriorly by the cartilaginous epicoracoids (Savage, 1958, fig. 5). From dorsal to ventral these are (1) the scapular fenestra, which lies within the scapula, (2) the scapulocoracoid fenestra, which lies on the border between the scapula and the coracoid, (3) the anterior (primary) coracoid fenestra, which lies within the coracoid, and (4) the posterior (secondary) coracoid fenestra, which also lies within the coracoid but is located posterior and ventral to the anterior coracoid fenestra. The scapulocoracoid and anterior coracoid fenestrae are present in all iguanids, and nearly all squamates, but the presence of the scapular and posterior coracoid fenestrae is each variable. In agamids, the posterior coracoid fenestra is present and the scapular fenestra is absent (Moody, 1980). The presence of fenestrations in the scapulocoracoid of chamaeleontids is difficult to assess because the pectoral girdle in these lizards is highly modified. The anterior and posterior coracoid emarginations are absent, and the scapular and scapulocoracoid emarginations appear to be present (Lécuru, 1968a).

Lécuru (1968a) summarized the distributions of the various scapulocoracoid fenestrations in lizards. Outside of Iguania the scapular fenestra is present in gekkonids and is variably present in anguids, scincids and teiids. The posterior coracoid fenestra occurs in gymnophthalmids, teiids, and varanids, and is variably present in gekkonids and in *Lanthanotus* (Lécuru, 1968a; Rieppel, 1980). Because the absence of both scapular and posterior coracoid fenestrae is the prevalent condition in non-iguanian squamates and because lepidosauromorphs other than squamates lack all four scapulocoracoid fenestrations (Gauthier, et al., 1988), we consider the absence of both scapular and posterior coracoid fenestrae to be primitive within iguanids.

Sternal fontanelle (27). The cartilaginous sternum of most iguanids is penetrated by a single median fontanelle (Etheridge, 1964, figs. 4-5). Although the fontanelle is occasionally absent or reduced to a few tiny holes, it is most commonly present and is relatively small and narrow, only slightly wider than the posterior process of the interclavicle which frequently covers the fontanelle ventrally. In contrast, the sternal fontanelle of some iguanids is large, that is, it is much wider than the posterior process of the interclavicle and occupies a large area in the posterior part of the sternum. When a sternal fontanelle is present in agamids it is generally unlike that of other iguanians and most other squamates in that it is double. Chamaeleons lack a sternal fontanelle.

A single, large median sternal fontanelle is unknown in lepidosauromorphs other than iguanids and is therefore considered to be derived within Iguanidae. Most non-iguanian squamates lack the fontanelle altogether or when present it is generally small, as in most iguanids (Lécuru, 1968b). *Sphenodon* also lacks a sternal fontanelle as do the few other rhynchocephalians in which the sternum is preserved (Cocude-Michel, 1963). There is similarly no evidence of a fontanelle in the sterna of more distantly related lepidosauromorphs such as *Saurosternon* (Carroll, 1977) and the younginiform *Hovasaurus* (Currie, 1981) in which the sternal plates remain paired into postembryonic development.

Numerical transformations in serial homologues: cervical ribs (28), *sternal ribs* (29), *presacral vertebrae* (30) *and lumbar vertebrae* (31). Counting back from the atlas, the first vertebra with bony ribs attached to the sternum by cartilaginous inscriptional ribs is number 9 in iguanids, other lizards except chamaeleons, *Lanthanotus* and *Varanus*, and in *Sphenodon*. The vertebrae anterior to this are designated cervical vertebrae (Hoffstetter and Gasc, 1969), some of which bear bony ribs with short, distal cartilages that end free. In iguanids, the first vertebra to bear ribs is the third (= first postaxial), fourth or fifth. In agamids it is the fifth or sixth (Moody, 1980), and in chamaeleons the third or fourth, but in this family the number of cervical vertebrae is reduced to five. Among other squamates the most anterior rib pair is located on the axis in *Dibamus* and some snakes, on the third vertebra in some gekkonids, pygopodids, scincids, anguids and *Xenosaurus*,

and on the fourth or fifth in others; in *Sphenodon* it is located on the fourth (Hoffstetter and Gasc, 1969). Because *Sphenodon* and the great majority of squamates lack ribs on the axis it seems likely that they have reappeared in *Dibamus* and some snakes. However, no iguanids have axial ribs, and we consider a maximum number of six cervical rib pairs to be primitive, lower numbers progressively derived.

In iguanids, agamids and most scleroglossan lizards, but not in *Sphenodon*, there develops a ventral pair of parallel or diverging cartilaginous rods posterior to the sternum that characteristically form articulations with short extensions of the posterolateral corners of the sternal plate, and are joined by one or more pairs of cartilaginous inscriptional ribs. The ventral cartilages are usually continuous with the inscriptional ribs, not forming articulations, and may or may not continue beyond the most posterior rib connection (see figures in Lécuru, 1968a). Hoffstetter and Gasc (1969) use the term "mesosternum" for the ventral rods, and "xiphisternum" for the portion of the rod that projects beyond the last rib connection, stating that the xiphisternum is always paired. However, as shown by Etheridge (1962, 1964) the pattern of inscriptional rib attachments may vary greatly even within species, and includes various asymmetries in the posterior free projections. We prefer the term "xiphisternum" for the paired ventral rods because it refers to them unambiguously, independent of their inscriptional rib connections.

We have not used transformations in numbers of xiphisternal inscriptional rib attachments as systematic characters because individual variation is high in some taxa but apparently low in others, and we have insufficient data from large samples. Nevertheless, we feel justified in including in our analysis numerical changes in presacral vertebral number because their transformations are uncoupled from those of the sternal inscriptional ribs, although both are constrained to develop within myosepta. Rare individual variants from the modal number of presacral vertebrae retain the modal number of sternal, xiphisternal and, when present, post-xiphisternal inscriptional chevrons ("parasternum" of Hoffstetter and Gasc, 1969 and others). The reverse is also true: loss or gain of sternal, xiphisternal or inscriptional chevrons does not disturb the number of presacral vertebrae. Most iguanids have 24 presacral vertebrae (including atlas and axis), with a range of 21 to 26. Hoffstetter and Gasc (1969) tabulated presacral vertebral numbers for most lizard families. In agamids the usual number is 24 or 23 with a range of 20 to 25, and in chamaeleons the range is 16 to 23. Hoffstetter and Gasc (1969) consider 24 to be the "fundamental number", with an increase in "the rest of the Lacertillia" (i.e., scleroglossans): 26 is the modal number in scincomorphans and geckos, 29 in anguinomorphans, with much higher numbers in the serpentine scleroglossans. According to Romer (1956) "such eosuchians as have well preserved columns appear to have had a count of about 24 presacrals and in rhynchocephalians in general there are characteristically 23 to 25." We consider 24 to be the primitive number of presacrals in iguanids, and higher or lower numbers derived.

All of the post-sternal presacral vertebrae bear articulating ribs in most iguanids but one or more vertebrae immediately anterior to the sacrum may be ankylosed to their ribs or lack them. Ribs are present on all post-sternal presacrals in agamids, with one or two vertebrae immediately anterior to the sacrum bearing fused ribs in some species (Moody, 1980). Chamaeleons characteristically have one or more post-sternal presacrals with short, fused ribs. In *Sphenodon* and the autarchoglossan families Scincidae and Lacertidae, all post-sternal presacrals have articulating ribs but one or more ribs may be lacking or fused in other autarchoglossan families (Hoffstetter and Gasc, 1969). We consider the presence of articulating ribs on all post-sternal presacral vertebrae to be primitive within iguanids, fusion or loss of ribs derived.

Post-xiphisternal inscriptional rib pattern (32). This term refers to all of the elements of calcified cartilage imbedded within the myocommata of the flank and abdominal musculature, lateroventral to the distal extremities of the dorsal bony ribs and posterior to the cartilaginous inscrip-

tional ribs attached to the xiphisternum (mesosternum) or, in the absence of xiphisternal connections, to the sternum. These elements are thought to be posterior serial homologues of the inscriptional cartilages that extend down from the bony ribs and join the sternum or xiphisternum, or end free in the cervical musculature (Etheridge, 1965a). Although Etheridge (1965a) recognized four patterns of inscriptional rib connections in the Iguanidae, we recognize two stages of a single transformation series.

In most iguanids the post-xiphisternal ribs end free in the abdominal or flank musculature, and characteristically the anterior one to three pairs are long, curve forward to enter the rectus myocomata, but fail to meet medially. These are followed by progressively shorter elements that become reduced to mere tips of calcified cartilage at the extremities of the posterior bony ribs (Etheridge, 1965a, fig. 1A). There is significant variation in the lengths of the anterior segments; all may be very short, as in *Phrynosoma*, while in some *Ophryoessoides* and most iguanines there may be from one to four anterior pairs that meet, overlap, or join to form continuous chevrons (Etheridge, 1965a, fig. 1B).

The second pattern is like that found in chamaeleons. A series of midventrally continuous chevrons tied to the bony ribs is followed by one or more chevrons that do not extend up into the flank musculature and fail to join the dorsal bony rib of their corresponding segment (see Etheridge, 1965a, fig. 2A). Or, less frequently, there are no inscriptional ribs at all posterior to the attached chevrons. As a common individual variant of this pattern the chevrons may be followed by one or more paired or unilateral splint-like elements that contact neither one another at the ventral midline, nor their corresponding dorsal ribs. The post-xiphisternal inscriptional ribs of *Chalarodon* and *Oplurus* consist entirely of paired series of isolated, splint-like elements (Etheridge, 1965a, fig. 2B).

Like most iguanids, most other lizards appear to have free-ending post-xiphisternal cartilages. Moody's (1980:74, 77) statement that abdominal inscriptional ribs are absent in the Agamidae may refer to the absence of a chamaeleon-like pattern of continuous chevrons in that family. In agamids the post-xiphisternal inscriptional ribs are characteristically all very short, but the anterior ones may be noticeably longer (e.g., *Physignathus*), though apparently in no case do they penetrate the rectus musculature. In gekkonids this pattern occurs in all save *Uroplatus* (Camp, 1923; pers. obs.). In most geckos examined the post-xiphisternal inscriptional ribs are uniformly short, but the anterior ones are noticeably elongate in *Naultinus* and *Gekko*; only in *Uroplatus* are there midventrally continuous chevrons. Free-ending ribs are also present in all anguimorphans and most scincomorphan lizards and *Sphenodon*. Characteristically the cartilages are uniformly short, though in the teiid *Dracaena* the anterior ones are longer. The inscriptional cartilages of *Sphenodon*, not to be confused with their more superficial gastralia of dermal bone, are in two segments, a short proximal one and a flat, cruciform distal segment oriented anteromedially; the pairs of distal segments are widely separated medially (Hoffstetter and Gasc, 1969).

Midventrally continuous post-xiphisternal inscriptional chevrons occur in chamaeleons and some iguanids, *Uroplatus*, and some scincomorphans. In the latter they occur for the most part in serpentine forms such as some gymnophthalmids, dibamids, some scincids (Camp, 1923) and some cordylids (Berger-dell'Mour, 1984), where they often show patterns of oddly-shaped elements. As Camp (1923) pointed out, midventral inscriptional ribs are best developed in ascalabotans (i.e., Iguania + Gekkota) specialized for arboreal life, and in autarchoglossans specialized for limbless locomotion. Because midventrally separate, free-ending post-xiphisternal inscriptional ribs occur in almost all gekkonids, all anguimorphans, most scincomorphans, and *Sphenodon*, we consider this to be the primitive iguanid pattern. The chamaeleon-like pattern of midventrally continuous chevrons is considered derived within the Iguanidae, and the pattern of isolated pairs of splint-like ribs is considered derived from the chamaeleon-like pattern.

Caudal vertebra type (33) and *caudal autotomy* (34). Linear differentiation in the caudal verte-bral column with respect to the presence, number, shape, size and orientation of the transverse pro-cesses and their positional relationships to the planes of fracture in lizards have been described and illustrated by Etheridge (1967). Four types are recognized in the Iguanidae: the *Sceloporus*-type with a single pair of processes located anterior to the fracture plane on vertebrae throughout most of the column; the *Iguana*-type with two pairs of diverging processes with the fracture plane locat-ed in between, present on one or more of the anterior autotomic vertebrae; the Beta *Anolis*-type with a single pair of anterolaterally oriented, usually terminally bifurcate processes posterior to the plane of fracture throughout most of the column, and a fourth type lacking processes on the auto-tomic vertebrae. Two non-homolgous types are thought to be represented by the fourth; in some species the first autotomic vertebra is occasionally asymmetric, with a short process on one side located anterior to a partly developed fracture plane (the *Basiliscus*-type), and in others it is located posteriorly (the Alpha *Anolis*-type). Nonautotomic sequences with laterally oriented processes throughout most of the column are identified as the *Sceloporus*-type, those with anterolaterally oriented processes as Beta *Anolis*, and those with one or more vertebrae bearing two pairs of di-verging processes are identified as the *Iguana*-type, but in the absence of processes throughout most of the column nonautotomic caudal sequences cannot be identified as either the *Basiliscus*-type or Alpha *Anolis*-type.

Chamaeleons and agamids lack caudal fracture planes. Single processes throughout most of the column occur in chamaeleons and most agamids; in other agamids processes are limited to a short series present only at the anterior end of the column (Moody, 1980). Almost all gekkonids have autotomic caudal vertebrae with processes anterior to the fracture plane. Among autarchol-glossans the *Iguana*-type sequence occurs in most teiids, gymnophthalmids, lacertids and cordylids. Paired, converging processes are present in most anguids, and in most scincids the processes are split transversely by the fracture plane but do not converge or diverge. All varanoids lack fracture planes and have single processes throughout most of the column. In *Sphenodon* single, short pro-cesses are present with the fracture plane passing through the anterior base of the processes or im-mediately in front of them.

The *Sceloporus* pattern was considered by Etheridge (1967) to be primitive for squamates. We adopt this position here, although out-group comparisons provide no strong evidence for it. Among scleroglossans this pattern occurs with certainty only in gekkonids; it appears elsewhere in lacertids and xantusiids but is presumably derived through loss of the posterior pair of split pro-cesses in these families. Most autarchoglossans have split processes of one sort or another, the *Iguana*-type, converging types such as anguids, or split but unmodified processes as in most scin-cids. Etheridge's (1967) observation that the *Sceloporus*-type occurs in *Sphenodon* appears to be incorrect, or there may be more individual variation than we are aware of; in our two specimens the majority of the processes are posterior to the fracture planes. Hoffstetter and Gasc (1969) point out that autotomic caudal vertebrae in which the septum divides the transverse processes into two parts are known in the upper Jurassic genus *Paramacellodus* (Hoffstetter, 1967), and suggest that this condition may be primitive for lizards. We follow Etheridge (1967) in considering the *Iguana*-type and the *Basiliscus*-type independently derived from the *Sceloporus*-type. Because both types of caudal sequence found in *Anolis* are unique to that genus and share the condition of having the transverse processes, when present, posterior to the plane of fracture, and all forms have one or the other, we have combined the two as a single state, the *Anolis*-type, for this analysis.

Planes of fracture facilitate caudal autotomy in most iguanids and in most scleroglossans save varanoids, and in sphenodontids both Recent and extinct. We follow Etheridge (1967) and other authors in this volume in considering the presence of caudal autotomy to be primitive within le-pidosaurs, squamates, and iguanids.

Nuchal endolymphatic sacs (35). In most vertebrates the endolymphatic sacs are confined to the cranial vault and anterior vertebral canal, but in some iguanids, agamids, chamaeleons and gekkonids a derived condition exists in which paired outpocketings of the endolymphatic sacs protrude posteriorly into the anterior axial musculature of the neck. In iguanids these sacs extend back between the supraoccipital and parietal (Etheridge, 1959, fig. 6). In agamids they exit through a special foramen, the epiotic foramen, and only in *Cophotis ceylanica* do they reach the musculature of the neck (Moody, 1980). Small sacs exiting between the parietal and supraoccipital bones have recently been reported for several species of the chamaeleonid genus *Brookesia* but were not observed in *Chamaeleo* (Moody, 1983b). In gekkonids, nuchal endolymphatic sacs are present in the Gekkoninae and Sphaerodactylinae, absent in the Eublepharinae and Diplodactylinae, and when present may exit either through the vagus foramen or, as in iguanids, between the supraoccipitals and parietal (Kluge, 1967). Camp's (1923:114) observation that nuchal endolymphatic sacs are present in *Xantusia vigilis* has not been confirmed (Kluge, 1967; personal observation), and Savage (1963:5-7) did not mention them in his characterization of the Xantusiidae. It may be best to assume they are absent until demonstrated otherwise. We concur with Kluge (1967) that the different points of exit of the nuchal endolymphatic sacs in the Gekkonidae suggest their independent origins within that family, and that their origins in the Gekkonidae and Iguanidae are separate. We also conclude that the derivations of nuchal endolymphatic sacs in iguanids and agamids are independent because of their different exit locations from the cranial vault.

Scale surface microstructure: scale organs (36) and *subdigital scales* (37). Published data on the microstructure of the keratinized outer epidermal surface (Oberhaüchten) of scales are now available for many lizards and snakes, and *Sphenodon* (see Peterson, 1984, and references therein), and we have augmented them with unpublished SEM photographs and data on many others provided by Jane Peterson and Ernest Williams. We have personally examined with a light microscope, under oil emersion (970X), the dorsal body scales, scales from the loreolabial region and subdigital scales from representatives of all iguanid genera save *Phrynosaura*, 21 genera of agamids and 22 species of *Chamaeleo*. For this analysis we include characteristics of the surface microstructure of two special areas of the skin, the scale organs and subdigital scales.

Peterson (1984) recognized four patterns of scale surface microstructure based on differences in cell shape, the arrangement of cell boundaries, and micro-ornamentation of the cell surface: (1) a honeycomb pattern formed by elevated boundaries of polygonal, juxtaposed cells, (2) a spinulate pattern characterized by juxtaposed cell boundaries, and relatively flat cells covered with minute, densely packed spinules, (3) a lamellate pattern of cells elongated transverse to the proximo-distal axis of the scale, with overlapping borders and little or no surface ornamentation; the distal cell boundaries may be serrated (lamellate/dentate pattern), and 4) irregular, polygonal cells with juxtaposed cell boundaries, or a combination of lamellate or juxtaposed boundaries, with a light surface texture created by pits and grooves.

Two of these patterns have been found in the Iguanidae, a honeycomb pattern, by far the most common, and a spinulate pattern. Intermediate morphologies are known in a few species of *Sceloporus* and *Tropidurus*. Scale organs of iguanids with a honeycomb Oberhaüchten are bare, multicellular, and rather large, often 50 to 90 microns in diameters. Relatively few iguanids with a spinulate Oberhaüchten have these large, bare sense organs, and those that do (some *Sceloporus* and *Tropidurus*) have congeners with a honeycomb pattern on the general scale surface. In other iguanids with a spinulate pattern the sense organs are also spinulate and usually smaller in diameter, 15 to 40 microns, and the height of the spinules always higher, 5 to 15 microns, than the background spinulation. The scale organ spines may be distributed evenly or unevenly over the surface of the organ, or those in the center may be markedly longer, and in some twisted together to form a long, central filament. The latter type, with a long, twisted central filament, occurs only

in oplurines and anoles, and in the latter there is also a second type of scale organ, much larger, and covered entirely with uniformly low spinules.

Iguanids with a honeycomb Oberhaüchten exhibit this pattern on the subdigital scale surfaces also. Most iguanids with a spinulate pattern also have subdigital spinules or structures modified therefrom. The subdigital spinules may be essentially like those of the general body scale surface, or more elongate and differentiated into several morphological types (see Peterson and Williams, 1981, for terminology, illustrations and descriptions of different subdigital spinules). Spinulate iguanids with congeners that have a honeycomb pattern have honeycombed subdigitals. Maderson (1970), working with histological sections, stated that all iguanids examined except *Anolis, Chamaeleolis* and *Phenacosaurus* have a "lamellate Oberhaüchten which is seen in section as a series of teeth." He reported that in *Anisolepis grilli* and *Chamaelinorops wetmorei* (= *C. barbouri*) only the digital lamellar scales bear spinules, while the rest of the body shows a dentate Oberhaüchten. We do not know how the dentate condition described for histological sections might appear in surface view, but SEM photographs of both these species clearly show their overall scale surface to be spinulate, and both scale organ as well as subdigital spinules to be elongate. Maderson (1970) also reported the presence of short setae on the subdigital surface of *Polychrus acutirostris*, but Peterson (pers. comm.) failed to confirm their presence in SEM photographs.

All agamids examined have a honeycomb pattern that includes the scale organs and subdigital scales. *Lophocalotes ludekingi*, the only agamid with unkeeled subdigital scales, is typical of other members of the family (E. Williams, pers. comm., 1986). In some agamids the scale organs have a centrally located, multicellular spike up to 10 microns thick at the base. A spinulate pattern has been reported for the Chamaeleontidae (Schelich and Kästle, 1979), but a broader survey of the family by Ernest Williams found some species with a honeycomb pattern and others that are intermediate. Scale organs have not been found in all chamaeleons, but where present they are either bare or spinulate. The only SEM study of chamaeleon subdigital scales is that of Schelich and Kästle (1979), who found some modifications of the spinules in the only form examined. Our studies using the light microscope showed elongate subdigital spinules in all of chamaeleons examined, but we were unable to determine the presence or extent of their morphological differentiation.

Both the honeycomb and spinulate patterns have been found among non-iguanian squamates, but other patterns are far more common. A spinulate pattern occurs in all gekkotans, although in some gekkonids certain areas of the integument are bare, and in pygopods spinules are confined to the boundaries of the scales. Both gekkonids and pygopods have spinulate scale organs, with the central spinules twisted to form one or two filaments. Elongate and differentiated subdigital spines occur in gekkos, but their morphology is quite different from those found in iguanids. Among the remaining lizard families a honeycomb Oberhaüchten is known in the Varanidae (*Varanus*), Xenosauridae (*Xenosaurus, Shinisaurus*), Cordylidae (*Cordylus* but not *Gerrhosaurus*), and Scincidae (*Tropidophorus brookei*, dorsal surface only). A spinulate pattern has been found only in the teiid genus *Kentropyx* (Williams, unpubl.). Spinulate subdigital scales have been reported for the scincid genus *Prasinohoema*, but they do not appear to be homologous with the subdigital spinules of iguanids (Williams and Peterson, 1982). According to Peterson (1984) the Oberhaüchten of *Sphenodon* is comparable to the lamellate pattern found in many non-iguanian squamates.

In summary, a honeycomb pattern is widespread in iguanids, universal in agamids, present in some chamaeleons and a few non-iguanian lizards. A spinulate pattern occurs in some iguanids and chamaeleons, gekkotans, and a single teiid genus. Other surface morphologies predominate in the remaining lizard families and *Sphenodon*. Thus, outgroup comparisons provide no compelling evidence for considering either the honeycomb or spinulate pattern to be primitive for the Iguanidae. For the present we consider a honeycomb pattern with bare scale organs and subdigital scales

to be primitive within iguanids because this polarity assessment is more congruent with other characters. More elongate scale organ spinules and more elongate and differentiated subdigital spinules are considered to represent progressively more derived states.

Distal subdigital scales (38), *subdigital scale surface macrostructure* (39) and *subdigital pads* (40). On the subdigital surface of all iguanids and most other lizards the scales are arranged in a single row parallel to the digital axis. In the great majority of iguanids the subdigital scales are distinctly multicarinate; only within the anoloid group do some forms have smooth or faintly keeled subdigital scales. Multicarinate subdigital scales occur in all agamids save *Lophocalotes ludekini*, in which they are smooth. In chamaeleons the digits as well as the palmar and plantar surfaces are covered with transverse rows of small, convex scales.

The subdigital scales are essentially smooth in gekkonids, xantusiids, gymnophthalmids, anguids, xenosaurids, helodermatids and amphisbaenians. Varanids have transverse rows of smooth, convex scales encircled by granules. Subdigitals are smooth, or with a single keel in teiids, lacertids and scincids, and have one or several keels in cordylids. The subdigital scales of *Sphenodon* are smooth and irregular in size and arrangement.

The great majority of non-iguanian lizards appear to have a single row of subdigitals that are smooth or with a single keel; the distinctly multicarinate subdigitals of most iguanians are found in few. Thus, outgroup comparisons provide no compelling reason to think that either smooth or multicarinate subdigital scales are primitive for Iguania. However, since smooth subdigitals occur only within the anoloid group, and since multicarinate subdigitals occur in oplurines and morunasaurs, possible sister taxa of anoloids, and in *Polychrus*, the sister taxon of all other anoloids, a polarity of keeled to smooth is more congruent with other characters. Although we consider all multicarinate subdigitals to be homologous characters in the Iguanidae, the structural details are not the same in all forms that have them (Peterson, pers. com.). In our own analysis it is for those few taxa with multicarinate subdigitals structurally different from most other iguanids that reversal from smooth to multicarinate is required. More detailed studies of keel macrostructure may help to resolve the question of homologies. In some iguanids with smooth subdigitals, the scales are lamellar-like and form a distal, raised pad under phalanges 2 and 3 (Peterson, 1983, fig. 9). This condition is unique to the anole iguanids within squamates, and we here consider it derived from smooth.

In a few iguanids, the distal one to three scales of each digit are longitudinally divided by a distinct median groove, also unique among iguanians, and here considered derived from the usual undivided distal subdigitals in most iguanids and other lizards.

Femoral pores (41) and *preanal pores* (42). Macroscopic, holocrine follicular glands (femoral pores), present in both sexes and seasonally active in males, are present on the ventral surfaces of the thighs in 27 iguanid genera, and as a single row on the anterior margin of the vent (preanal pores) in 3 others. The remaining iguanids lack both. Femoral and/or preanal pores are also present in some agamids, gekkonids, teiids, gymnophthalmids, lacertids, cordylids, xantusiids, scincids and amphisbaenians (Camp, 1923; Maderson, 1970, Moody, 1980). Maderson (1970) recognized two histologically and developmentally distinct types of holocrine glands in lizards: generation glands, including escutcheon scales and beta glands, and follicular preanal organs, including femoral-inguinal pores and preanal (precloacal) pores. He believed that tubular preanal organs were probably derived from generation glands, and that in gekkonids they have probably been derived more than once. However, generation glands are known with certainty only in gekkonids and the iguanid species *Leiocephalus psammodromus*, although "specialized scales" thought probably to be generation glands were seen in other tropidurine iguanid genera (Alexander and Maderson, 1972). According to Moody (1980) the "callous glands" are uniquely derived in the Agamidae, and are structurally similar to generation glands. We agree with Kluge (1982) that because generation

glands are known only in gekkonids and iguanids, and since presumably homologous preanal organs (femoral and preanal pores) occur in iguanids, agamids, and many scleroglossan families, presence of the latter is a synapomorphy for squamates that is retained in ancestral iguanids; their absence is the result of loss.

Although both femoral and preanal pores in iguanids are follicular holocrine glands, seasonally active in males, we do not know if the preanal pores found in a few iguanid genera represent a displaced segment of the femoral-inguinal series, or have appeared de novo. However, our analysis would remain the same with either position, and we have simply considered that the absence of preanal pores is primitive, their presence derived.

Transverse gular fold (43). Many iguanids possess a transverse gular fold extending across the posterior gular region just anterior to the shoulders (Smith, 1946, fig. 45). In some iguanids there are two folds in the gular region (Darrel Frost, pers. comm.), the second lying just anterior to the one just described. We hereafter use the term gular fold to refer only to the more posterior fold. This fold is usually more distinct and often has enlarged scales along its edge and encloses reduced scales within the fold. Some iguanids lack the gular fold (Smith, 1946, fig. 44), and in others it is present laterally but absent medially.

The presence of a transverse gular fold is variable in non-iguanian squamates. It occurs in at least some agamids, cordylids (incomplete), gymnophthalmids, helodermatids, lacertids, teiids, varanids, xantusiids, and xenosaurids. *Sphenodon* also has a gular fold. Thus, data from the most pertinent outgroups suggest that the presence of a transverse gular fold is primitive for iguanids although the evidence is somewhat equivocal.

Middorsal scale row (44). In many iguanid lizards there is a row of scales aligned middorsally. The row may be continuous from the occiput to well out onto the tail, or interrupted, most commonly in the shoulder and hip region. Characteristically, middorsal scales are larger than those adjacent to them and may increase greatly in size ontogenetically, but in some adult iguanids (e.g., *Proctotretus*) the middorsal scales are scarcely different in size and form from adjacent scales.

A row of scales alligned middorsally is present in some agamids and in all chamaeleonids. Except for some snakes, non-iguanian squamates appear to lack a middorsal scale row, although it may have been present in mosasaurs (Williston, 1899). *Sphenodon* has a row of scales aligned middorsally but interrupted in the shoulder and hip region.

Not all middorsal scale row morphologies are alike. The neatly aligned row of enlarged, peaked or keeled middorsals of most iguanines, morunasaurs, basiliscines and most tropidurines is unlike that of *Polychrus peruvianus*, in which consecutive middorsal scales are separated by smaller paravertebrals that contact medially on the posterior back, of *Aperopristis*, which has a discontinuous row of tubercles posteriorly, or of some anoles, in which there is a double row of alternating enlarged scales. With uncertainty we include all middorsal scale rows as homologous characters, and although the primitive condition of this character is ambiguous, we tentatively consider the presence of a row of scales aligned middorsally to be primitive within Iguanidae.

Interparietal scale (45). An interparietal scale, i.e., a scale overlying the parietal foramen and possessing a central convexity, is present in most iguanids and agamids and in many scleroglossans and *Sphenodon*. In most iguanids it is small, not wider than the interorbital width, and not conspicuously larger than adjacent scales, but in some it is conspicuously larger than adjacent scales and wider than the interorbital width (Smith, 1946, fig. 47, 49). A small interparietal scale is present in those agamids that have one (Moody, 1980), and in chamaeleons it is absent. Among scleroglossans the interparietal scale, when present, is usually smaller than adjacent scales, and in *Sphenodon* it is also small. We conclude that a small interparietal scale is primitive in iguanids, its absence resulting from loss, or if very large, resulting from increased size.

Superciliary scales (46) and *subocular scales* (47). The scales of the dorsal and lateral surfaces

of the head in most iguanid lizards form a regionally differentiated and more-or-less symmetrical pattern such that specific groups may be recognized as loreals, loreolabials, superciliaries, suboculars, supraoculars, etc. In these, the superciliaries characteristically form a row of elongate and broadly overlapping scales, and the orbit is bordered below by a single subocular at least three times longer than high (Smith, 1946, fig. 36). Other iguanids exhibit various degrees of undifferentiated head scales, including shorter superciliaries with little or no overlap, and a row of subequal suboculars (Smith, 1946, fig. 37). No agamids have head scales as highly differentiated as those in most iguanids, although in many agamids the superciliaries are elongate and overlapping, and in *Leiolepis* there is an elongate subocular as well. The head scales of chamaeleons are relatively undifferentiated, and in none are there elongate, overlapping superciliaries or an elongate subocular.

The head scales of non-iguanian squamates vary greatly, from minutely and uniformly granular to large, symmetrical plates. But in those with highly differentiated head scales their patterns are not easily comparable to the common pattern of iguanids, and in none of them have we found elongate and overlapping superciliaries or an elongate subocular (Friederich, 1978). The head scales of *Sphenodon* are small, heterogenous and exhibit little regional differentiation.

Because relatively undifferentiated head scales occur in *Sphenodon* and some non-iguanian squamates, this pattern might be considered primitive within iguanids. However, the head scales of *Sphenodon*, chamaeleons, gekkonids and others that exhibit little or no differentiation are not strictly comparable, and it may be inappropriate to lump them all into the same character state. Differentiated head scales, including elongate superciliaries and an elongate subocular, are present in at least some members of all of the major iguanid generic groups that we recognize save the morunasaurs. The elongate, overlapping superciliaries of iguanids are very similar to those of agamids which have them, and the elongate subocular of iguanids is similar to that of *Leiolepis*. Thus, either head scale differentiation or dedifferentiation must have occurred multiple times within the Iguania. The functional significance and developmental basis of different head scale patterns are not known, but the independent acquisition of closely similar, highly organized patterns seems less likely than the independent loss of such a pattern. With some hesitation we take the position that elongate, overlapping superciliaries and an elongate subocular are primitive within Iguanidae, and that short, non-overlapping superciliaries and subequal suboculars are derived.

Ulnar nerve pathway (48) and *dorsal shank muscle innervation* (49). Jullien and Renous-Lécuru (1972) surveyed variation in the pathway of the ulnar nerve and the innervation of the dorsal muscles of the shank in lizards. Two alternative pathways of the ulnar nerve exist in this group (Jullien and Renous-Lécuru, 1972, fig. 1). In one, designated the lacertid type (L), the ulnar nerve separates from the n. flexor brachialis proximally in the limb and passes between the m. triceps and the m. coracobrachialis. The nerve then emerges superficially in the elbow region before plunging deep into the antebrachial muscles. The second ulnar nerve pathway is designated the varanid type (V). In this pattern the ulnar nerve separates from the n. flexor brachialis distally in the limb and thus passes with the main trunk of the n. flexor brachialis between the m. coracobrachialis and the m. biceps. Although ulnar nerve morphologies intermediate between these two types occur in certain lizards, they are apparently lacking in iguanians. Both types, L and V, occur in iguanids. Agamids have the lacertid pattern while chamaeleons have the varanid pattern.

The dorsal muscles of the shank in lizards also exhibit two primary patterns of innervation (Jullien and Renous-Lécuru, 1972, fig. 2; the two types of innervation appear to be incorrectly labeled in this figure). When present, the n. peroneus emerges from the thigh near the knee, between the insertions of the m. iliotibialis and m. iliofibularis. It passes superficial to the m. gastrocnemius, the m. peroneus longus, and the m. peroneus brevis before moving deep between the m. peroneus brevis and the m. extensor digitorum communis. The n. peroneus may be present or absent. In contrast, the deep n. interosseous, a prolongation of the sciatic trunk, is always present.

This nerve invariably supplies the ventral shank muscles, and sometimes it also emits a branch that passes dorsally between the tibia and fibula to innervate the dorsal muscles of the shank. The condition in which the n. peroneus alone innervates the dorsal shank muscles is designated type A. When the n. peroneus is absent and a branch of the n. interosseous innervates the dorsal shank muscles the condition is designated type B. Intermediates between these two patterns exist in iguanians; that is, sometimes both nerves supply the dorsal shank muscles. Because such intermediates are rare and because one or the other of the two nerves is the primary source of innervation in these intermediate cases, we recognize only two states for this character, A and B. Although both states occur in iguanids, agamids and chamaeleons possess only type B.

Non-iguanian squamates are not particularly informative concerning the primitive condition of this character in iguanids. For the forelimb as well as the hindlimb, both alternative conditions occur commonly in non-iguanian squamates. However, in all other tetrapods that have been examined (urodeles, anurans, mammals, turtles, crocodiles, and *Sphenodon*) only patterns L and A occur. Therefore, it appears that these are the primitive conditions within iguanids. Although Jullien and Renous-Lécuru (1972) surveyed most of the iguanid genera in their study of innervation patterns, they did not examine *Aperopristis, Aptycholaemus, Chamaelinorops, Sator, Gambelia, Tapinurus, Ophryoessoides,* and *Vilcunia.* We have dissected representatives of all of these genera.

Appendix 1 lists the 49 characters discussed above with their various states. The distribution of these character states among iguanid genera is given in Appendix 2 .

THE MAJOR GROUPS

Although minimum step methods yield highly resolved phylogenetic trees, or cladograms (see Results of Computer Analysis), the character basis for many of the supposed monophyletic groups resulting from minimum step analyses are based on characters that must later reverse one or more times within the group, or must arise independently one or more times in other groups, or both. Recognition of such groups is expected to be very sensitive to the addition or deletion of certain characters, or to reinterpretation of character polarities. The tenuous nature of such groups makes us hesitant to accept them as phylogenetic realities. Therefore, in order to highlight what we feel are the best supported phylogenetic relationships and at the same time indicate problems in need of further study, we leave certain relationships unresolved, even though they are "resolvable" by minimum step methods.

Given the inadequacies of our primary character list in resolving the relationships among the iguanid genera, we recognize eight major groups of these genera. The names employed for these eight groups and subsets of them above the level of our basic taxa are meant to be informal appellations and not formal taxonomic names. It is unfortunate that group names ending in "ines" came into informal usage in correspondence among those of us working with iguanid systematics, and later in print (for his apology see Etheridge, 1964). While the ability to diagnose these groups might suggest the usefulness of formal taxonomic names, and the lack of resolution of their interrelationships a reason for assigning them equal ranks, we prefer at this time to retain the traditional informal group names until other possible relationships among the major groups can be more fully explored. In any case, although we have had limited success in finding evidence for more inclusive monophyletic groups, that is, for establishing relationships among the major groups, we feel that the monophyletic status of the eight major groups is reasonably well supported.

Within each of the major groups there is generally a larger body of character data that bears on intergeneric relationships, but for which we have been unable to survey all or even most of the iguanid genera. For this reason, we have not included these characters in our primary character list, although we do provide a list of them along with references in each group discussion. The apo-

morphic states of these characters are usually unambiguous based on outgroup comparison with other major groups of iguanids, and, therefore, we have not presented detailed arguments for our polarity decisions as we did for the characters in our primary list. We have also omitted many other characters, mostly generic synapomorphies, from the primary character list. This was done even in cases in which the characters had been surveyed for most or all of the iguanid genera, in order to keep the character matrix at a manageable size. Of course, these generic synapomorphies provide evidence only for the monophyly of particular genera, not for relationships among them.

In the following discussions we provide a list of genera included within the eight major groups of iguanids, their number of species in parentheses, a brief description of their range, and a word or two about their habits. The term "arboreal" refers to life in vegetation above ground, but not necessarily in trees; "terrestrial" refers to living on the ground in a variety of habitats but not restricted to any one in particular; "saxicolous" and "arenicolous" refer to life restricted to rocky and sandy habitats, respectively. A brief discussion of each group follows in which we address some or all of the following: evidence for the monophyly of the group, the monophyletic status of the genera within the group, and relationships among the genera within the group.

The Anoloids (Fig. 9)

Polychrus (7) Nicaragua southward through South America to northwestern Perú west of the Andes and to the east to southern Bolivia, Paraguay, northern Argentina and southeastern Brazil. Arboreal.

Enyalius (6) Atlantic forests of eastern Brazil from Paraiba southward to Río Grande do Sul; one species disjunct in southwestern Amazonian Basin in Brazil. Arboreal.

Pristidactylus (8) Western-central Chile where arboreal in relict *Nothofagus* and *Araucaria* forest, and disjunct forms in western and central Argentina where terrestrial-saxicolous.

Diplolaemus (3?) Patagonian Argentina from Mendoza southward to southern Santa Cruz and adjacent eastern Chile. Terrestrial-saxicolous.

Leiosaurus (2) Western central Argentina from Catamarca southward to Río Negro. Terrestrial.

Aperopristis (1) Western central Argentina from Catamarca southward to La Pampa. Terrestrial.

Urostrophus (2) Disjunct in northern Argentina, eastern Bolivia and southeastern Brazil. Arboreal.

Anisolepis (2) Southeastern Brazil, Uruguay and northern central Argentina. Arboreal.

Aptycholaemus (1) Northern Argentina and eastern Paraguay. Arboreal.

Chamaeleolis (3+) Cuba and the Isla de Pinos. Arboreal.

Phenacosaurus (3) Northwestern South America at high altitudes. Arboreal.

Chamaelinorops (1) Southwestern Hispaniola. Arboreal.

Anolis (170+) Southeastern United States; throughout the West Indies; northeastern and northwestern México southward to Ecuador west of the Andes and to the east to Bolivia, northern Paraguay and southeastern Brazil, and various Pacific islands. Mostly arboreal, a few terrestrial, saxicolous, semi-aquatic.

The monophyly of anoloids (Node 1, Fig. 10) is indicated by their possession of endolymphatic sacs that extend back between the parietal and occipital bones into the neck musculature, a condition unique within the family and found elsewhere only in some chamaeleontids and some gekkonids, together with other derived characters shared with othergroups.

Polychrus retains femoral pores, a primitive honeycomb Oberhaüchten, and a short dentary, but otherwise has a large number of derived states, including the third and fourth toes of equal
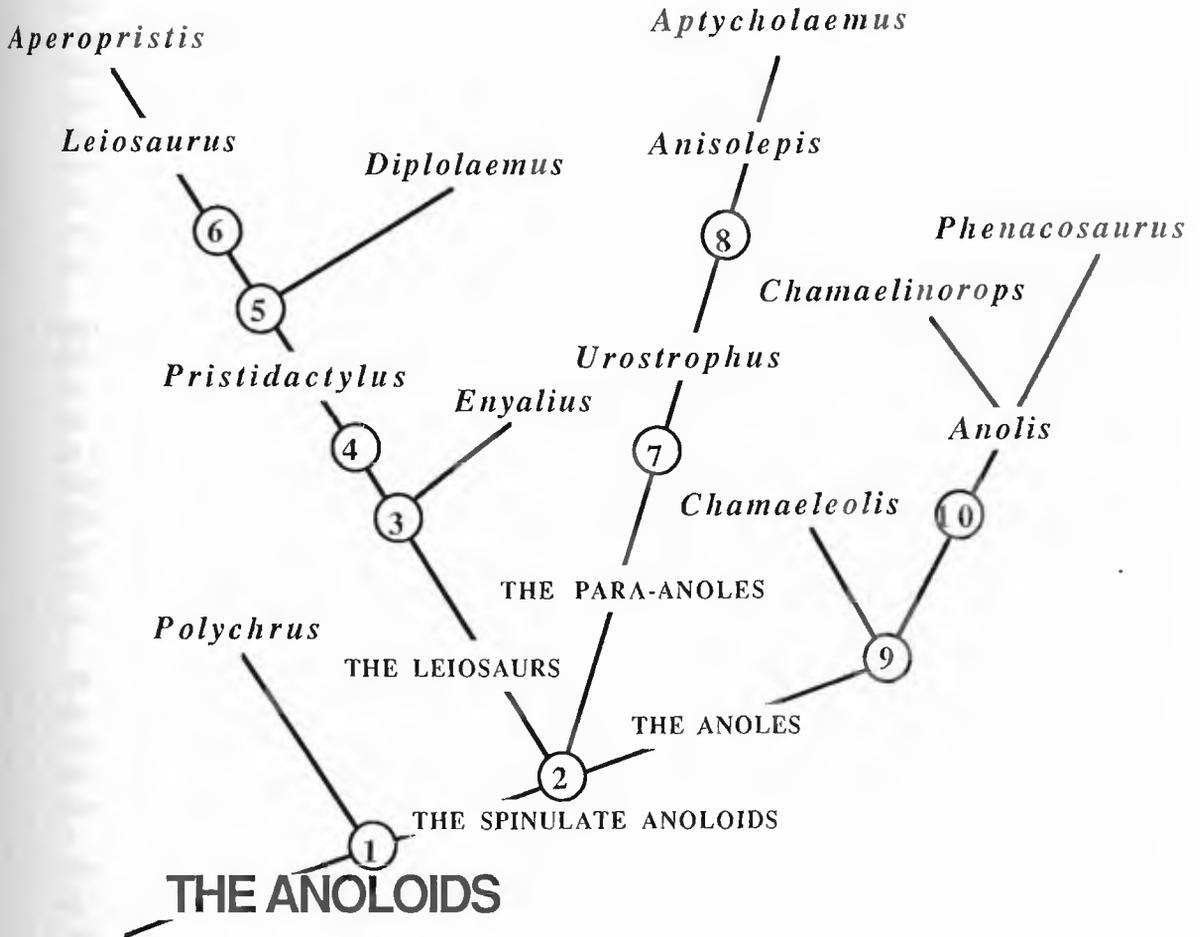
FIGURE 9. Relationships of the anoloid iguanid lizards.

length, unique within the family. Gorman et al. (1969) found a karyotype consisting almost entirely of acrocentric chromosomes, also possibly unique within Iguanidae, in the three species examined. *Polychrus* is considered the sister taxon of the remaining anoloids.

The remaining anoloids (Node 2) all lack femoral pores, have a longer dentary, and exhibit derived conditions of the Oberhaüchten. The Oberhaüchten cells of the general body surface have flat margins and are covered with short spinules, and the spinules of the scale organs and subdigital surfaces are variously elongate and differentiated.

The genera *Enyalius*, *Pristidactylus*, *Diplolaemus*, *Leiosaurus*, and *Aperopristis* appear to form a clade (Node 3) specified by divided distal subdigital scales, unique among iguanids, and several other derived states shared with other groups. We refer to them informally as the "leiosaurs." *Enyalius* is unique within anoloids in having conical throat scales, and the remaining genera (Node 4) all possess transversely expanded, lamellar-like supradigital scales (Fig. 11), also unique within

anoloids. *Aperopristis* is unique in having an undifferentiated rostral, *Diplolaemus* has lost pala-
tine and pterygoid teeth, and *Pristidactylus* is characterized by the presence of enlarged and pectinate
proximal subdigital scales, absent in other anoloids. A more comprehensive analysis of leiosaur
relationships has been conducted by Etheridge (1984), using additional characters, with *Enyalius* as
the outgroup and each of the species of *Pristidactylus*, *Leiosaurus* and *Aperopristis* as terminal
taxa. The three Chilean species of *Pristidactylus*, *P. alvaroi*, *P. valeriae*, and *P. torquatus* were
seen as diverging early. East of the Andes *P. casuhatiensis*, *P. achalensis*, *P. scapulatus*, and
P.fasciatus appear progressively more closely related to the clade formed by *Diplolaemus*, *Leio-
saurus* and *Aperopristis* (Node 5). *Leiosaurus catamarcensis* and *Aperopristis paronae* are sister
taxa that form the sister clade (Node 6) of *Leiosaurus belli*. The species of *Diplolaemus* share a
number of synapomorphies. According to this interpretation *Pristidactylus* and *Leiosaurus* are par-
aphyletic.

Of the remaining anoloids, *Chamaeleolis*, *Phenacosaurus*, *Anolis* and *Chamaelinorops*, known
as the "anoles" (Node 9), are strongly linked by a large number of derived characteristics, including
the unique expanded subdigital lamellae and pad, and greatly elongate second ceratobranchials that
support an extensile gular fan. *Urostrophus*, *Anisolepis* and *Aptycholaemus* are weakly linked
(Node 7) by the loss of both the middorsal scale row and caudal autotomy, possibly also by the
presence of a prehensile tail. We tentatively recognize them as a monophyletic group, the "para-
anoles." The para-anoles share with anoles a reduction in the number of sternal ribs, more exten-
sive fusion of Meckel's groove, and taller, more highly differentiated subdigital spines. They share
with the leiosaurs the presence of a small secondary coracoid fenestra and an angular anterior mar-
gin of the clavicle. For the present we cannot resolve the relationships of anoles, para-anoles and
leiosaurs.

Within the para-anoles no synapomorphy specifies *Urostrophus*, and that genus may be para-
phyletic. *Anisolepis* and *Aptycholaemus* (Node 8) both have tapered marginal tooth crowns and
have lost the posterolateral processes of the basisphenoid, and also differ markedly from *Urostro-
phus* in having strongly keeled ventral scales and a much longer tail. No derived state specifies
Anisolepis, thus the relationships of *Anisolepis undulatus*, *A. grilli*, and *Aptycholaemus
longicauda* remain unresolved.

Within the anoles *Chamaeleolis* is unique in its retention of a small angular bone and palatine
teeth, but its monophyly is indicated by highly modified marginal teeth, a peculiar casque-like pa-
rietal bone, and loss of caudal autotomy. *Anolis* may be paraphyletic with respect to *Chamaelin-
orops* and *Phenacosaurus* (Node 10).

The Morunasaurs (Fig. 10)

Enyalioides (7) Panamá, western Columbia and Ecuador, and the upper Amazon Basin of Co-
lombia, Ecuador and Perú. Terrestrial and arboreal.

Morunasaurus (2) Panamá, western Colombia and Ecuador. Terrestrial.

Hoplocercus (1) Southeastern Brazil. Terrestrial.

The morunasaurs (Node 1, Fig. 12) are persistantly primitive in some regards, especially in
the mandible, and were figured in a basal position in Etheridge's "Old Tree" (Fig. 1). However,
they share with anoloids and oplurines the chamaeleon-like pattern of post-xiphisternal inscription-
al ribs, and monophyly of morunasaurs is indicated by their greatly enlarged nasal scale (Etheridge,
1969, fig. 11B), unique within the family. Based upon our original data set, relationships within
morunasaurs remained obscure, so we attempted a more comprehensive analysis using additional
characters and the ten morunasaur species as terminal taxa. If we consider as derived within moru-
nasaurs: dorsolateral crests of enlarged scales, heterogenous scalation, a shorter, more spiny tail, a
compressed tail or a depressed tail, and the iliac blade more elongate and anterior iliac process re-

· *Hoplocercus*

Morunasaurus

②

Enyalioides

①
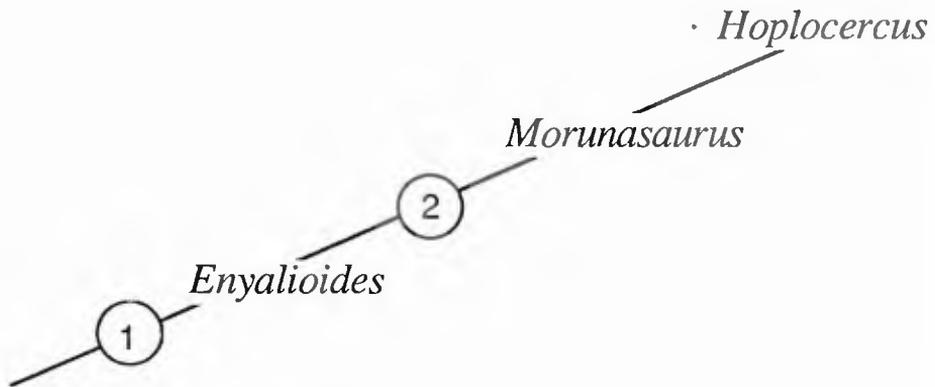
THE MORUNASAURS

FIGURE 10. Relationships of the morunasaur iguanid lizards.

duced (in addition to the original data set), then the species of morunasaurs appear to form a graded series. *Enyalioides laticeps* is the sister taxon of the remaining morunasaurs with *E. praestabilis*, *E. oshaughnessyi*, *E. microlepis* and *E. cofanorum*, *E. palpebralis*, *E. heterolepis*, *Morunasaurus annularis* and *M. groi*, progressively more closely related to *Hoplocercus spinosus*.

Chalarodon   *Oplurus*

①
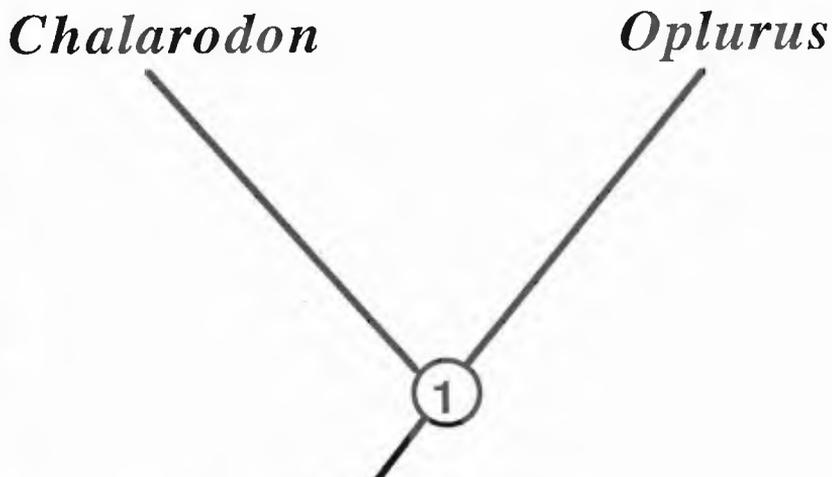
THE OPLURINES

FIGURE 11. Relationships of the oplurine iguanid lizards.

According to this analysis, in addition to a large nasal scale, a large lacrimal foramen and posterior marginal tooth crowns that are flared and deeply cusped, often with a fourth secondary cusp, are synapomorphies of the morunasaur group. However, in *M. groi* the teeth have reverted to straight sided crowns with moderate secondary cusps, the primitive state, and in *H. spinosus* the tooth crowns have become tapered with small secondary cusps, and the lacrimal foramen is somewhat reduced. Transformations that originate within *Enyalioides* and are continued or exaggerated in *Morunasaurus* and *Hoplocercus* are the development of heterogenous dorsal scalation and a shorter, spinier tail. A compressed tail, characteristic of all *Enyalioides* except *E. laticeps*, reverts to rounded in *M. groi* and becomes depressed in *H. spinosus*, and the dorsolateral crests, also present in all *Enyalioides* save *laticeps*, are lost (or obscured) in *H. spinosus*. The anterior iliac spine becomes elongate in *M. annularis*, *M. groi* and *H. spinosus* (Node 2), the middorsal scale row is lost in *M. groi* and *H. spinosus*, and in *H. spinosus* caudal autotomy has been lost. Thus *Enyalioides* and *Morunasaurus* are both paraphyletic according to this analysis.

The Oplurines (Fig. 11)

Oplurus (6) Arid and semiarid southwestern Madagascar and Grand Comore Island. Terrestrial, saxicolous, arboreal.

Chalarodon (1) Arid and semiarid western and southwestern Madagascar. Terrestrial.

Monophyly of the Malagasy iguanids (Node 1, Fig. 13) is indicated by the reduction of their chamaeleon-like post-xiphisternal inscriptional ribs to a series of paired splints, and a change in the ulnar nerve pathway to lie deep to the limb muscle, both unique within the family. *Oplurus* is specified by a single derived state, the loss of a middorsal scale row, and *Chalarodon* by reduction of the sternal ribs to three pair and acquisition of a moderately distinct bony labyrinth. However, *Chalarodon* shares a number of derived states with at least some of the species of *Oplurus*. If the middorsal scale row of *Chalarodon* were to be considered a secondary acquisition there would be no basis for the recognition of this genus apart from *Oplurus*, i.e., *Oplurus* would be paraphyletic.

The Tropidurines (Fig. 12)

Phymaturus (4) Disjunct in the high cordilleras and precordilleras of central Chile and adjacent western Argentina, and on various volcanic tablelands in Patagonian Argentina. Saxicolous.

Vilcunia (2) Disjunct, high cordilleras of Santa Cruz Province, southern Argentina. Terrestrial and saxicolous.

Liolaemus (90+) High cordilleras of southern Perú and Bolivia, southward in the mountains and lowlands to the coast in Chile and Argentina to northern Tierra del Fuego, and eastward through Paraguay, Uruguay and southeastern Brazil. Terrestrial, saxicolous, arenicolous, and arboreal.

Ctenoblepharis (1) Coastal central Perú. Arenicolous.

Leiocephalus (22) Cuba and the Isla de Pinos, the Bahama Islands, and Hispaniola; late Pleistocene of Jamaica, Puerto Rico and most of the Leeward Islands, and Miocene of Florida. Terrestrial and saxicolous.

Stenocercus (31) Middle and lower Andean slopes from Colombia southward to northern Argentina. Terrestrial and saxicolous.

Ophryoessoides (6+) Middle and lower Atlantic Andean slopes from Colombia southward to Bolivia and the western Amazonian Basin. Terrestrial and arboreal.

Proctotretus (3) Disjunct in northern central Argentina and northeastern Argentina through Uruguay to southeastern Brazil. Terrestrial.

Uranoscodon (1) Northeastern South America in the Guianas and Amazonian Basin. Arboreal.
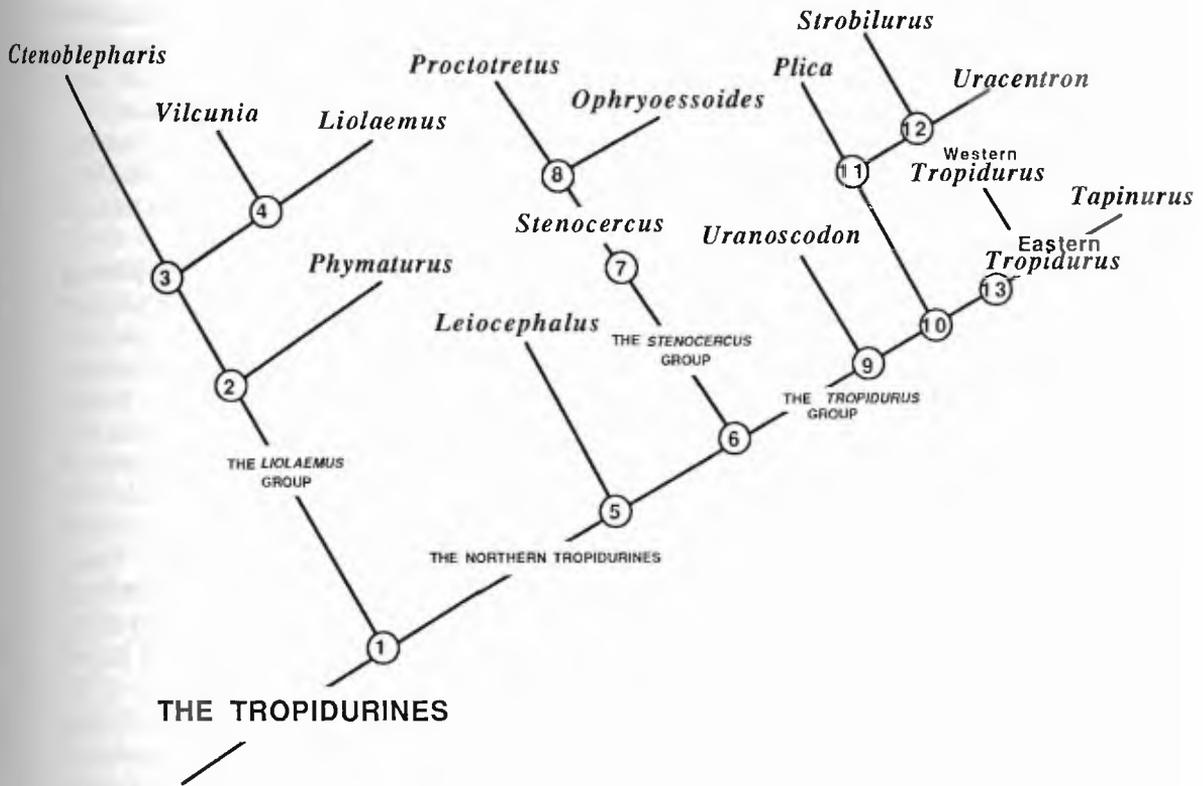
FIGURE 12. Relationships of the tropidurine iguanid lizards.

Tropidurus (26+) Most of South America east of the Andes (except the upper Amazon Basin) southward to northern Argentina, Uruguay and southeastern Brazil; west of the Andes from Ecuador southward to northern Chile and the Galápagos Archipelago. Terrestrial, saxicolous, arenicolous, and arboreal.

Tapinurus (2) Eastern central Brazil. Saxicolous.

Plica (2) South America in the Guianas and Amazon Basin. Arboreal.

Strobilurus (1) Eastern central Brazil. Arboreal.

Uracentron (2) South America in the Guianas and Amazon Basin. Arboreal.

The tropidurines (Node 1, Fig. 14) cannot be specified by any single, derived character state, but monophyly of the group is supported by a unique combination of derived characters, including the acquisition of a large sternal fontanelle and the loss of femoral pores. The initial branching within the tropidurines forms two clades, the primarily austral *Liolaemus* group (Node 2) and the remaining tropidurines, here referred to as the Northern Tropidurines (Node 5).

For purposes of our analysis we have recognized the following genera within the *Liolaemus* group: *Phymaturus*, *Liolaemus*, *Vilcunia* and *Ctenoblepharis*. We follow Laurent (1982) in the synonomy of *Pelusaurus* with *Liolaemus*, and also his (Laurent, 1984) restriction of *Ctenoblepharis* to *C. adspersus*. Laurent (1984) also revived *Phrynosaura*, proposed the genus *Ceiolaemus* and revived *Ortholaemus* as a subgenus of *Liolaemus*. Our sample includes representatives of *Ceiolaemus* and both subgenera of *Liolaemus*, but no representatives of *Phrynosaura*. We are unable to distinguish *Ceiolaemus* from *Liolaemus* with the characters used in this analysis and have therefore included the former within the latter.

Members of the *Liolaemus* group share a number of derived characters including the presence of preanal pores, unique within the family, and a coronoid labial blade (the latter may be primitive; see discussion of this character). Preanal pores occur in all save *Vilcunia* and *Liolaemus lineomaculatus*. Because *Vilcunia* and *L. lineomaculatus* share derived characteristics with *Ctenoblepharis* and *Liolaemus* and none with *Phymaturus* that are not characteristic of the entire group, preanal pores are here considered to have been lost in *Vilcunia* and *L. lineomaculatus*, a conclusion also reached by Laurent (1984). *Phymaturus* is a genus of herbivorous lizards with tricuspid premaxillary teeth and deeply cusped marginal teeth (often with a fourth cusp). Tricuspid premaxillary teeth have been used to distinguish *Phymaturus* from *Liolaemus* (Boulenger, 1885a); however, some species of the latter have been found by us to possess a dentition like that of *Phymaturus*. Monophyly of *Phymaturus* is indicated by their short interclavicle median process and fragmented subocular and superciliary scales. The remaining members of the *Liolaemus* group (Node 3) have a shorter splenial, have lost their gular fold, and acquired overlap of the premaxillary nasal process by the nasal bones.

Ctenoblepharis differs from *Liolaemus* and *Vilcunia* in having acquired a proximally expanded and sometimes perforate clavicle, and a number of other derived features, but retains a large angular; the latter two genera (Node 4) have a reduced angular and have acquired a posterior coracoid fenestra. *Vilcunia* appears to be closely allied to *Liolaemus*, retaining a shorter dentary but having acquired a peculiar serrate form of dorsal body scales (Cei and Scolaro, 1982). The large and widespread genus *Liolaemus* differs from *Vilcunia* only in having a longer dentary and lacking serrate body scales.

The Northern Tropidurines (Node 5) share the acquisition of a scapular fenestra. In addition all save the extinct *Leiocephalus apertosulcus* (Etheridge, 1965b) and *L. anonymus* (Pregill, 1984) have Meckel's groove closed and fused; in *Phymaturus*, *Ctenoblepharis* and most *Liolaemus* it is unfused. Three monophyletic groups are recognized: *Leiocephalus*, the *Stenocercus* group and the *Tropidurus* group.

Monophyly of *Leiocephalus* is indicated by its V-shaped adult parietal roof, unique within the tropidurine group, but its relationships with other tropidurines is not entirely resolved. It shares the presence of a labial coronoid blade (possibly primitive) with the *Liolaemus* group, and the premaxillary-nasal overlap, loss of a gular fold and a shorter splenial with the *Ctenoblepharis* + *Vilcunia* + *Liolaemus* clade. However, the retention of a middorsal scale row and the absence of preanal pores indicate that the derived states *Leiocephalus* shares with *Liolaemus* et al. may be convergent. With the remaining tropidurines *Leiocephalus* shares a scapular fenestra and shorter splenial. On this basis, but with little confidence, we link *Leiocephalus* with the remaining tropidurines to form the Northern Tropidurines, sister taxon to the *Liolaemus* group.

Linkage of the *Stenocercus* and *Tropidurus* groups (Node 6) is weakly specified by the acquisition of a posterior coracoid fenestra, a state that also occurs in *Liolaemus* and *Vilcunia*. The *Stenocercus* group (Node 7), including *Stenocercus*, *Ophryoessoides* and *Proctotretus*, is weakly specified by the presence of a longer dentary. *Proctotretus* and *Ophryoessoides* share an angular lateral

margin of the clavicle and loss of the transverse gular fold; however, both states are found in some species of *Stenocercus*, and no single character or combination of characters will specify this genus. Thus, *Stenocercus* may be paraphyletic.

For our analysis of the *Tropidurus* group (Node 8) we have used the following terminal taxa: *Uranoscodon*, *Plica*, *Uracentron*, *Strobilurus*, *Tapinurus*, the species of *Tropidurus* west of the Andes (Western *Tropidurus*) and the species of *Tropidurus* east of the Andes (Eastern *Tropidurus*). All members of the clade possess a greatly enlarged interparietal scale, found elsewhere in the family only in sceloporines. *Uranoscodon* is considered to be the sister taxon of the remaining members of the group, having retained a relatively primitive mandible, but specified by its fragmented suboculars and superciliaries and reduced sternal fontanelle. Two additional subgroups remain (Node 9), collectively differing from *Uranoscodon* by reduction in the angular bone and further elongation of the dentary. *Plica*, *Strobilurus* and *Uracentron* (Node 10) are considered to form a monophyletic group based on their expanded tooth crowns, still smaller angular, and moderately enlarged lacrimal foramen. *Plica* is specified by a shorter interclavicle and fragmented suboculars, its sister taxon, *Uracentron* and *Strobilurus* (Node 11), by their shorter, spiny tail and shorter splenial. *Strobilurus* has lost the angular bone, while in *Uracentron* the tail has become shorter still and nonautotomic, its middorsal scale row and parietal foramen lost.

Monophyly of the widespread *Tropidurus* + *Tapinurus* assemblage (Node 12), is indicated by the absence of a complete transverse gular fold. The Western *Tropidurus* species (west of the Andes in Ecuador, Perú, northern Chile and the Galápagos Archipelago) are the only representatives of the *Tropidurus* group west of the Andes, and differ from other tropidurines in consistently having a clavicular fenestra. However, we point out that although a clavicular fenestra is used here to specify Western *Tropidurus*, one is variably present in *Uranoscodon*, *Plica* and *Uracentron*; it is absent in our single skeleton of *Strobilurus*. In *Uranoscodon* it is absent only in some adults. Thus, the presence of a clavicular fenestra may be primitive within the *Tropidurus* group, being lost in Eastern *Tropidurus* and *Tapinurus*, and variably lost in others. *Tapinurus* exhibits a large number of derived characters but many occur as well in some Eastern *Tropidurus*. Since no combination of derived characters will specify the Eastern *Tropidurus*, whether *Tapinurus* is included or not, this group, and *Tropidurus* as a whole may be paraphyletic.

The Iguanines (Fig. 13)

Amblyrhynchus (1) Rocky coasts of islands in the Galápagos Archipelago, Ecuador. Terrestrial, saxicolous, semiaquatic.

Brachylophus (2) Islands in the Fiji and Tonga groups in the southwestern Pacific Ocean. Arboreal.

Conolophus (2) Islands in the Galápagos Archipelago, Ecuador. Terrestrial.

Ctenosaura (4) Coasts of México from Sonora and southern Baja California on the West and Tamaulipas on the East south through most of Central America to Panamá as well as various offshore islands. Terrestrial, arboreal.

Cyclura (8) Various islands in the Greater Antilles and the Bahamas as well as Anegada Island. Terrestrial.

Dipsosaurus (1) Deserts of the southwestern United States in southeastern California, southern Nevada, southwestern Utah, and western Arizona, southward into México to northwestern Sinaloa and the southern tip of Baja California, as well as various islands in the Gulf of California. Terrestrial.

Enyaliosaurus (5) Disjunct in western and southern México and northern Central America. Terrestrial, arboreal.

Iguana (2) Low elevations from Sinaloa and Veracruz, México southward through Central
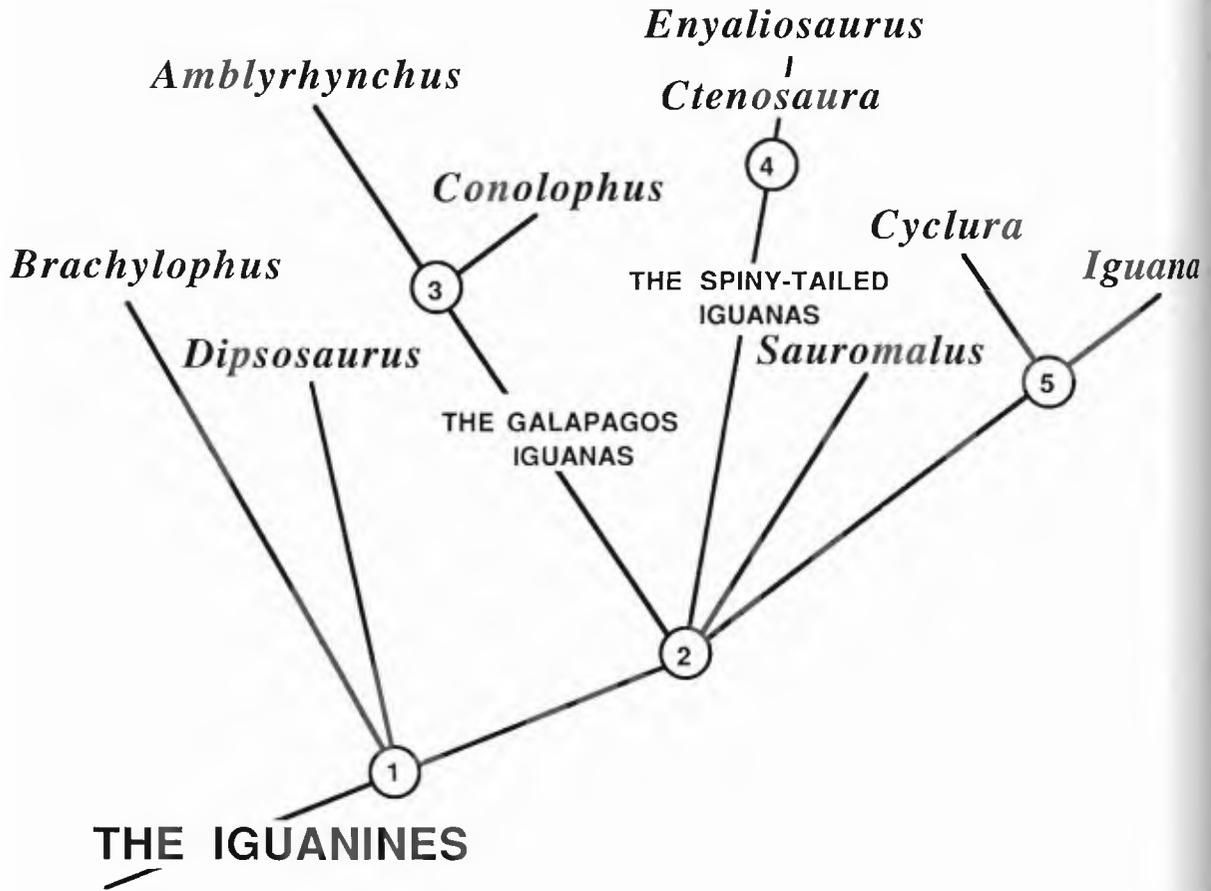
FIGURE 13. Relationships of the iguanine iguanid lizards.

America and South America to southern Brazil and Paraguay; in the Caribbean northward through the Lesser Antilles to the Virgin Islands. Arboreal.

Sauromalus (6) Deserts of the southwestern United States in southern California, Utah, and Nevada and western and central Arizona southward in México into western Sonora and eastern Baja California to its southern end, as well as various islands in the Gulf of California. Terrestrial, saxicolous.

The wide and disjunct geographical distribution of iguanines (Node 1, Fig. 15) might lead one to doubt the monophyly of this group. Nevertheless, iguanine monophyly is supported by numerous shared, derived characters. At least three hypothesized iguanine synapomorphies seem to be related to the herbivorous diets of these lizards: large body size, flared and often polycuspate marginal teeth, and transverse folds or valves in the colon. In addition, iguanine monophyly is supported by two characters not obviously related to herbivory: two pairs of parallel or diverging transverse processes on some of the caudal vertebrae and a posteriorly located supratemporal bone.

Relationships within the iguanine group are presented in greater detail elsewhere (de Queiroz, 1987). For this reason, we include only some of the relevant data in this report.

Eight of the nine commonly recognized iguanine genera can be diagnosed with derived characters, and thus each of these eight genera appears to be monophyletic. In *Dipsosaurus*, the parietal foramen has moved into the frontal bone, and the outlines of the osseous labyrinth have become moderately distinct. *Brachylophus* has lost caudal autotomy septa, a derived character shared with the Galápagos iguanas and *Iguana delicatissima*, and has acquired elongated inscriptional cartilages on the second and third postxiphisternal ribs. Both *Brachylophus* and *Dipsosaurus* lack a posterior coracoid fenestra, indicating that they are outside of the clade formed by the remaining iguanine genera. The elongate, strongly overlapping superciliary scales of *Dipsosaurus* suggest that this taxon diverged earlier than *Brachylophus* from the rest of the iguanines, but it is not clear that elongated superciliaries are primitive within iguanines. For this reason, we leave the relationships among *Brachylophus*, *Dipsosaurus*, and the remaining iguanines unresolved.

The remaining iguanines (Node 2) share a posterior coracoid fenestra, although the fenestra is occasionally reduced or even absent in *Amblyrhynchus* and *Sauromalus*. Within this latter group, the Galápagos iguanas, *Amblyrhynchus* and *Conolophus* (Node 3), have often been considered closely related. This relationship is supported by several derived characters including coverage of the premaxillary spine between the nasal bones, the absence of caudal autotomy septa, and cuspate premaxillary teeth. Monophyly of *Amblyrhynchus* is attested to by numerous derived characters including the presence of separable skull osteoderms in large specimens, apparently unique within iguanids. *Conolophus* is less highly modified morphologically than *Amblyrhynchus* but also has its own derived characters. These include contact of ectopterygoid and palatine at the posteromedial corner of the suborbital fossa and the reduction or loss of pterygoid teeth.

Iguana and *Cyclura* share a derived morphology of the basisphenoid, and highly cuspate marginal teeth, suggesting that they are sister taxa (Node 5). Monophyly of *Iguana* is supported by the presence of a gular crest, while that of *Cyclura* is suggested by the peculiar toe combs, a condition approached but not attained by some other iguanines. Members of this genus also share an increase in the number of premaxillary teeth.

The spiny-tailed iguanas (Node 4) share reduced posterior processes of the basisphenoid, indicating that they share a unique common ancestry. Nevertheless, the recognition of two separate genera of spiny-tailed iguanas is problematic. Although the monophyly of *Enyaliosaurus* can be supported by derived characters, recognition of *Enyaliosaurus* as separate from *Ctenosaura* would leave the latter without derived characters except for those characteristic of both taxa. Based on the characters used in this study one might argue that the parietal roof of *Ctenosaura* is derived relative to that of *Enyaliosaurus*. However, since adult *Conolophus*, *Cyclura*, and *Iguana* also have Y-shaped parietal roofs, it is likely that this character is a synapomorphy of a more inclusive group and that *Enyaliosaurus* has acquired triangular or trapezoidal roofs secondarily. Given the Y-shaped parietal roofs in two of the three taxa most likely to be the sister group of the spiny-tailed iguanas, the derived small size of *Enyaliosaurus*, and the apparent correlation of parietal roof shape with body size, we consider *Enyaliosaurus* to be a subgroup of *Ctenosaura* rather than its sister group.

Monophyly of *Sauromalus* is supported by numerous derived characters including a short posterior process of the interclavicle, loss of the middorsal scale row, and reduction in the number of premaxillary teeth. The relationships among *Sauromalus*, the Galápagos iguanas, the spiny-tailed iguanas, and *Iguana* plus *Cyclura* are uncertain. This is attributable to the lack of a congruent pattern of the distributions of derived characters within this group (Node 2). For example, *Sauromalus*, *Iguana*, and *Cyclura* share highly cuspate posterior marginal teeth, but a derived parietal roof is shared by *Iguana*, *Cyclura*, *Conolophus*, and *Ctenosaura*. For this reason, we leave the relationships at this level (Node 2) unresolved.
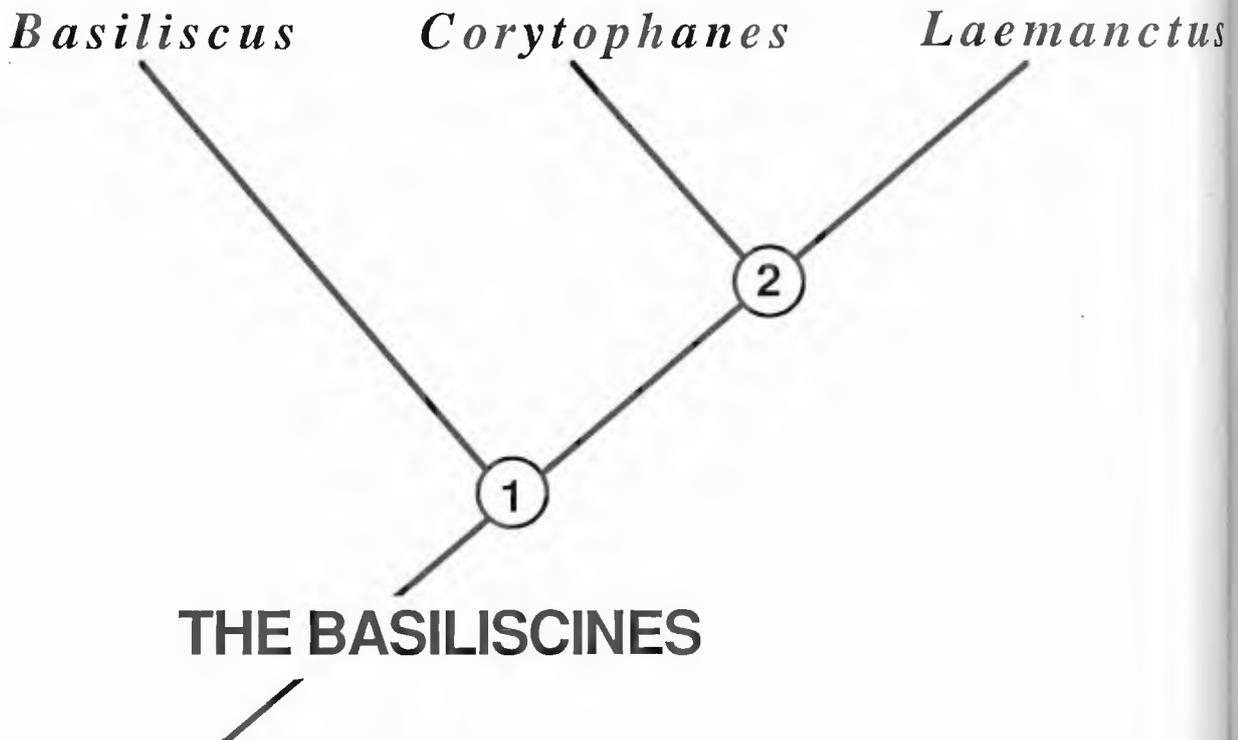
FIGURE 14.   Relationships of the basiliscine iguanid lizards.

The Basiliscines (Fig. 14)

Basiliscus (4) Along the coasts of southern México from Jalisco and southern Tamaulipas to the Isthmus of Tehuántepec, then southward throughout Central America to northwestern South America. Arboreal, semiaquatic.

Corytophanes (3) Central Veracruz and San Lúis Potosi, México, southward through Central America to northwestern Colombia. Arboreal.

Laemanctus (2) Atlantic lowlands from Tamaulipas, México, to northwestern Honduras. Arboreal.

Basiliscines (Node 1, Fig. 16) are basically arboreal, Central American iguanids whose collective monophyly is indicated by one feature that is both unique and derived within the family, the posteriorly extended skull crest formed by the parietal bone. Basiliscines also share a unique combination of other derived characters, including the presence of medially expanded and often fenestrate clavicles and the absence of femoral pores, each of which is shared with some other non-basiliscine iguanids.

The three basiliscine genera are very distinct, and the monophyly of each is supported by diagnostic derived characters. *Basiliscus* has expanded crowns on their posterior marginal teeth and free flaps of skin on the margins of the pedal digits (Maturana, 1968). The latter structures presumably aid these animals in their famous runs across the surface of water (Laerm, 1973). *Laemanctus* has extensive development of scale impressions on the dermal skull roof (Fig. 3) and reduction in the

Crotaphytus   *Gambelia*
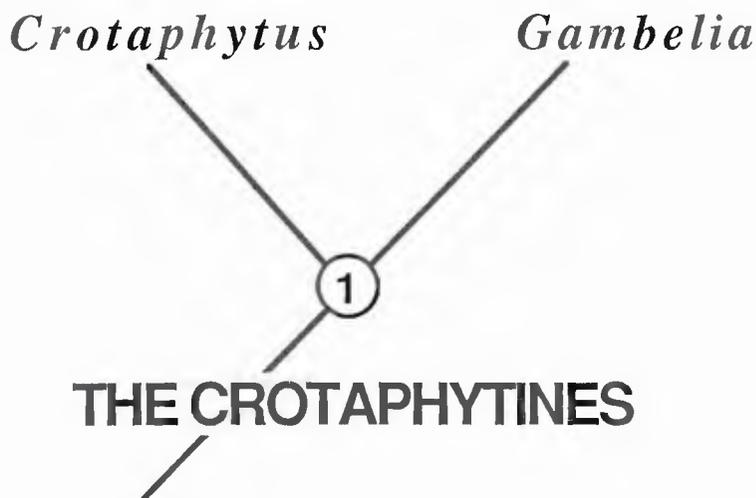
THE CROTAPHYTINES

FIGURE 15. Relationships of the crotaphytine iguanid lizards.

number of keels on the subdigital scales. *Corytophanes* is highly modified from the ancestral basi-liscine condition, especially in its cranial morphology, although it also exhibits postcranial modi-fications. Some of the obvious synapomorphies of *Corytophanes* are the reduction of the preorbi-tal portion of the skull, the development of orbital processes on the prefrontal and postorbital bones, closure of the posttemporal fossae, and elongation of the scapulae resulting in a shift in the dorsal articulations of the clavicles from the suprascapular cartilages to the scapulae.

Our analysis suggests that *Corytophanes* and *Laemanctus* shared a more recent common ances-tor with one another than either did with *Basiliscus*. These relationships are supported by numer-ous derived characters shared by *Corytophanes* and *Laemanctus* including loss of autotomy septa in the caudal vertebrae, reduction of the angular process of the mandible, acquisition of a sharp canthal ridge, and reduction or loss of the septomaxillary bones. In addition, the bones of the dermal roof in both of these taxa have more extensive development of rugosities reflecting the pattern of the overlying epidermal scales, but these rugosities develop during postembryonic ontogeny and can-not always be seen in small specimens. Although many characters support a sister group relation-ship between *Corytophanes* and *Laemanctus*, this hypothesis of relationships is incongruent with at least some other characters. Specifically, it requires either that the postfrontal bones and ribs on the third cervical vertebrae have been lost convergently in *Basiliscus* and *Corytophanes* or that the derived condition was present in the ancestral basiliscine and has reversed in *Laemanctus*.

One noteworthy feature about character distributions within basiliscines is the frequent occur-rence of characters that are fixed in certain taxa but polymorphic in others. For example, the den-tary portion of Meckel's groove is invariably closed and fused in postembryonic *Corytophanes*, but this condition also occurs in some *Basiliscus* and *Laemanctus*. Other such characters include cervi-cal ribs, splenial size and the position of the parietal foramen. Although sampling error involving characters that are actually variable in all of the taxa cannot be ruled out as the explanation for this phenomenon, it is possible that the novel features in question first arose as polymorphisms and later became fixed in certain clades.

Subsequent to the completion of this study in 1982, a more detailed phylogenetic analysis of basiliscines has been completed by Mathias Lang at San Diego State University. According to Lang (in litt.) "the modified character data set greatly supports the *Corytophanes* + *Laemanctus* clade with *Basiliscus* being the sister taxon."

The Crotaphytines (Fig. 15)

Crotaphytus (4) Western and central North America. Terrestrial.

Gambelia (2) Western North America. Terrestrial.

Crotaphytines (Node 1, Fig. 17) are western and central North American lizards with basically terrestrial habits. They retain two primitive features seen in few other iguanids, the presence of palatine teeth and ribs on the third cervical vertebra. Although none of the derived characters that are characteristic of crotaphytines is unique within Iguanidae, they share the unique combination of the lack of postfrontal bones and a middorsal scale row and the presence of posterior coracoid fenestrae and female gravid coloration. In any case, the unity of the crotaphytine group is not controversial. In fact, the most persistent taxonomic controversy concerning crotaphytines is whether *Gambelia* should be recognized as a separate genus or should be synonymized with *Crotaphytus*.

Both *Crotaphytus* and *Gambelia* possess derived characters supporting their separate monophyletic status. *Crotaphytus* has lost autotomy septa in its caudal vertebrae and possesses short posterolateral processes of the basisphenoid; *Gambelia* has ventromedially expanded and fenestrate clavicles. If this evidence as well as that supporting the monophyly of the crotaphytines as a whole is accepted, then the question of whether *Gambelia* deserves separate generic status rests solely on a subjective judgment about the amount of difference that calls for generic distinction. We recognize two genera simply because they are easily distinguished osteologically.

The Sceloporines (Fig. 16)

Callisaurus (1) Arid regions of Baja California, the northwestern mainland of México, and the southwestern United States. Terrestrial.

Cophosaurus (1) Arid and semiarid regions of the southwestern United States and northern central México. Terrestrial.

Holbrookia (3) Arid and semiarid regions of the central and southwestern United States and northern México. Terrestrial.

Petrosaurus (2) Baja California, México and southern California in the United States. Saxicolous.

Phrynosoma (13) Extreme southern Canada, the western and central United States, most of México, including Baja California, south to western Guatemala. Terrestrial.

Sator (2) Cerralvo, Santa Cruz, and San Diego Islands in the Gulf of California. Terrestrial.

Sceloporus (64) North and Central America from Pacific to Atlantic coasts and from the northern United States to eastern Panamá. Terrestrial, arboreal, saxicolous.

Uma (4) Deserts of southeastern California and southwestern Arizona in the United States; México in northeastern Baja California and northwestern Sonora as well as southeastern Coahuila and southeastern Chihuahua and adjacent Coahuila. Arenicolous.

Urosaurus (9) From southwestern Wyoming southward through much of the southwestern United States and northern México to the tip of Baja California and along the west coast of mainland México to the Isthmus of Tehuantepec as well as the Tres Marias Islands and the Revillagigedo Archipelago. Arboreal, saxicolous.

Uta (6) From southern Washington southward through the southwestern United States to the Cape region of Baja California, some islands in the Gulf of California, and the northwestern and northcentral mainland of México. Terrestrial.

Sceloporines (Fig. 18) are basically inhabitants of arid and semiarid regions in western and central North America. Because of their accessibility to North American herpetologists, scelopo-
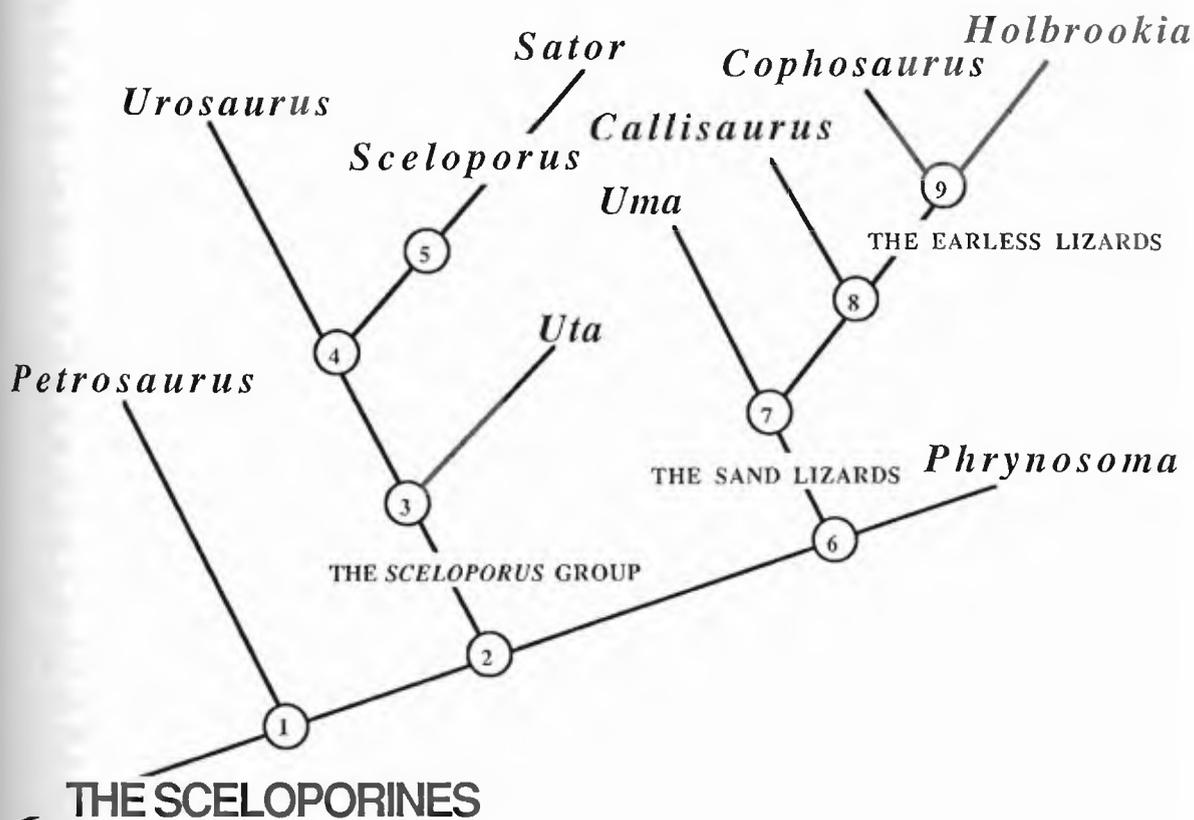
FIGURE 16. Relationships of the sceloporine iguanid lizards.

rines are among the most thoroughly studied of the major groups of iguanids. Although sceloporines as a group (Node 1) possess no known unique, derived feature or features, the unique combination of an enlarged sternal fontanelle, the absence of a middorsal scale row, reduction in the number of presacral vertebrae, and other derived characters, as well as the geographical unity of the group, indicate that the sceloporines are monophyletic.

Except for *Sceloporus*, all of the sceloporine genera have derived characters supporting their monophyly, and most of the intergeneric relationships within this group can be resolved on the basis of the distribution of derived characters among sceloporine genera. Monophyly of *Petrosaurus* is supported by the short neural spines of the presacral vertebrae. This taxon is thought to be the sister group of all other sceloporines because its members retain a fourth pair of sternal ribs and a relatively small sternal fontanelle, the absence of a nasal valve, and "shimmy" burial behavior.

The sister group of *Petrosaurus* (Node 2) consists of two large primary clades. Members of

the *Sceloporus* group (Node 3) share derived clavicular hooks and keeled, imbricate dorsal body scales. Our data suggest an alternative to previously published hypotheses about relationships within this group. *Sceloporus* supposedly differs from *Uta*, *Urosaurus*, and *Sator* in its lack of a transverse gular fold (Smith, 1946), presumably a derived character, yet both Mittleman (1942) and Smith (1946) considered each of these other three genera to have originated within *Sceloporus*. For *Sator* this problem is obviated since its members lack a true gular fold (Darrel Frost, pers. comm.). Even if this fold is "possible," as stated in the original generic diagnosis given by Dickerson (1919:468), it is less evident than in some *Sceloporus* (e.g., *S. couchi*). Although the (presumably primitive) presence of a fold anterior to the true gular fold is supposed to be another feature separating *Sator* from *Sceloporus* (Dickerson, 1919), it is present in some *Sceloporus* (e.g., *S. merriami*), albeit less well developed than in *Sator*. In addition, certain biochemical data have been interpreted as indicating that some *Sceloporus* are more closely related to *Sator* than either are to other *Sceloporus* (Wyles and Gorman, 1978). Thus, if *Sator* is considered to be distinct from *Sceloporus* rather than a subset of it, *Sceloporus* lacks diagnostic derived characters and may even be paraphyletic. On the other hand, if *Sator* is considered a subgroup of *Sceloporus*, then the two taxa form a monophyletic group (Node 5) diagnosed by the loss of the gular fold. Both *Uta* and *Urosaurus* retain gular folds, indicating that they are not derived from within *Sceloporus-Sator*. The interosseous innervation of the dorsal shank muscles, the enlarged dorsal scales, and the belly patches of the males in *Sceloporus-Sator* and *Urosaurus* suggest a sister group relationship between these groups (Node 4).

Phrynosoma and the sand lizards (Node 6) share the loss or reduction of various skeletal elements, both cranial and postcranial, as well as modifications in the trunk musculature presumably associated with burrowing habits (Blackburn, pers. comm.). The monophyly of *Phrynosoma* is highly corroborated. In addition to the characters that have emerged from our analysis, an extensive list of synapomorphies for this taxon can readily be compiled from the work of Presch (1969), on skeletal morphology, and Blackburn (pers. comm.), on head and trunk musculature.

The sand lizards (Node 7) share numerous derived characters, many of which are presumably related to the enhancement of burrowing in loose sand. These include the scoop-shaped head, keeled and oblique labial scales, and the countersunk lower jaw. Monophyly of *Uma* is supported by the dedifferentiation of the head scales and the acquisition of digital fringe scales, although the latter also occur in some populations of *Callisaurus* (Schmidt, 1922). Monophyly of *Callisaurus* is supported by its very long limbs. *Callisaurus* and the earless lizards (Node 8) share reduced secondary cusps on the posterior marginal teeth and modifications in the columellar apparatus of the middle ear, derived characters not present in *Uma*.

A close relationship between the earless lizards, *Cophosaurus* and *Holbrookia*, (Node 9), has been highly controversial. However, those available data that lend themselves to phylogenetic analysis are congruent (de Queiroz, 1981), and it appears that much of the controversy has resulted from the inappropriate use of retained primitive characters and overall similarity as evidence for a sister group relationship between *Callisaurus* and *Cophosaurus*. These two genera share no derived characters that are not also found in *Holbrookia*, whereas monophyly of the earless lizards is supported by the earless condition itself as well as other modifications of the ear region and the head and trunk musculature. Compared with *Holbrookia*, *Cophosaurus* retains a relatively primitive ear morphology, but its monophyly is supported by the posterior placement of the lateral black bar.

RELATIONSHIPS OF THE MAJOR GROUPS

Although considerably more data and more refined methods of analysis have become available during the past 20 years, our picture of the relationships among the iguanid genera has changed little. The same major generic groupings recognized by Etheridge on the Old Tree are still with

us, and for the most part their relationships with one another remain uncertain. Minimum step methods resolve the relationships among the groups, but the character basis for this resolution is weak. Although we prefer to leave many of the relationships among the major groups of iguanids unresolved, we comment on some previous hypotheses about relationships among genera that fall into more than one of our major groups as well as offer some new hypotheses about intergroup relationships.

Several hypotheses about relationships among iguanid genera belonging to more than one of our major groups have been offered previously. Both Mittleman (1942) and Smith (1946) offered phylogenies for the genera of iguanids occurring in North America. It is difficult to evaluate many aspects of these phylogenies, since iguanids not found in North America were omitted. Nevertheless, certain propositions can be evaluated in light of our data.

Common to the Mittleman (1942) and Smith (1946) phylogenies are the notions that sceloporines plus crotaphytines are derived from within iguanines and that crotaphytines are derived from within sceloporines near *Petrosaurus* (contrast Savage, 1958; Etheridge, 1964). The authors of these hypotheses provided no evidence linking *Sauromalus, Dipsosaurus*, or *Ctenosaura*, the iguanines supposedly closest to sceloporines and crotaphytines, with these latter groups. Furthermore, the presence of caudal vertebrae with two pairs of transverse processes and of colic folds or valves, derived characters unique to iguanines within Iguanidae, are evidence against the notion that any other iguanids have their origins within iguanines (i.e., that iguanines are paraphyletic). Numerous other characters in which iguanines are derived relative to sceloporines specifically contradict the specific hypothesis of a sceloporine origin from within iguanines.

The hypothesis of a sceloporine ancestry for crotaphytines is similarly untenable on the basis of the numerous characters, such as reduction in the number of presacral vertebrae, enlarged sternal fontanelle, the sink trap nasal apparatus, and the modified karyotype, in which sceloporines are derived relative to crotaphytines. The supposed relationship between crotaphytines and *Petrosaurus* seems to be based only on Mittleman's (1942:112) unspecified declaration that they are "almost identical on superficial examination". Except for the short neural spines, we have been unable to identify characters in which *Petrosaurus* is derived relative to the ancestral sceloporine. In contrast, members of *Sceloporus* group, the sand lizards, and the horned lizards have all undergone extensive modification since this common ancestor. The purported similarity between *Petrosaurus* and crotaphytines may represent the retention of features that existed in the common ancestor of both crotaphytines and sceloporines.

Avery and Tanner (1971) seem to have suggested that iguanines are derived from within oplurines. Although their discussion is ambiguous, their diagram of phylogenetic relationships (Avery and Tanner, 1971, fig. 37) shows iguanines branching off from the line leading to *Oplurus* after it had diverged from *Chalarodon*. Our data contradict not only an hypothesis of iguanine origins from within oplurines but also one of a close relationship between these two groups. As a group, oplurines possess numerous characters that are derived relative to iguanines (and vice versa) including at least two characters, postxiphisternal inscriptional ribs consisting entirely of floating splint-like elements and the deep path of the ulnar nerve, that are derived relative to all other iguanids. In addition, tabulation of the numbers of derived characters shared by *all* pairs of the eight major groups of iguanids (Appendix 3) reveals that iguanines share only one derived character with oplurines, which is fewer than or equal to the number that iguanines share with any of the other major groups. The converse is also true: oplurines share fewer derived characters with iguanines than with any other major group. Furthermore, the one derived character shared by iguanines and oplurines, loss of ribs from the third cervical vertebra, is also shared with morunasaurs, basiliscines, and sceloporines, as well as with many anoloids, crotaphytines, and tropidurines. There is little reason to hypothesize an oplurine ancestry for iguanines.

Etheridge (1964) proposed a sister group relationship between sceloporines and tropidurines and between this group and crotaphytines. These relationships contrast with those proposed on the Old Tree, in which sceloporines and crotaphytines were considered to form a monophyletic group with tropidurines as its sister group. Of all the major groups of iguanids, sceloporines share more derived characters with tropidurines than does any other major group of iguanids, and if the presence of a coronoid lateral blade is considered primitive within iguanids, then tropidurines along with basiliscines and iguanines also share the most derived characters with sceloporines (Appendix 3). However, only one of these derived characters, the enlarged sternal fontanelle, is shared only by sceloporines and tropidurines among the major groups of iguanids.

If the presence of a coronoid labial process is considered primitive, then the greatest number of derived characters found in all crotaphytines is shared with sceloporines, as well as with anoloids, oplurines, basiliscines, and morunasaurs (Appendix 3). However, only one of these, the absence of a middorsal scale row, is shared by all sceloporines and crotaphytines but does not characterize any of the other major groups as a whole. Crotaphytines share only one derived character with tropidurines as a whole, an elongated dentary. This character is also found in many other iguanids including all oplurines, morunasaurs and sceloporines. Thus, if the enlarged sternal fontanelle is considered a synapomorphy of sceloporines and tropidurines, then there is little reason to consider crotaphytines to be closely related to this group. Likewise, if the absence of a middorsal scale row is considered a synapomorphy of crotaphytines and sceloporines, then there is little reason to consider tropidurines to be closely related to this group. Acceptance of the monophyly of a group composed of crotaphytines, sceloporines and tropidurines requires that one or the other or both of these characters exhibit homoplasy at the level of the relationships among these three groups.

Based on variation within our basic taxa (iguanid genera), size of the sternal fontanelle is a less plastic character than presence or absence of a middorsal scale row. On the other hand, assuming a Gondwanan origin for iguanids (Estes, 1983a), the North American distribution of sceloporines and crotaphytines is additional evidence for a close relationship between these groups. Perhaps this issue will be resolved upon determination of the level at which the derived characters that are shared by more than just these three groups exist as synapomorphies. At present we offer no such resolution.

Etheridge (Old Tree, 1964) also proposed a close relationship between iguanines and basiliscines. For the characters considered here and considering the presence of the lateral coronoid blade to be primitive, iguanines share the greatest number of their derived characters with basiliscines, morunasaurs, and sceloporines (Appendix 3). Basiliscines share the largest number of their derived characters with morunasaurs. Iguanines, oplurines, and sceloporines share one less derived character with basiliscines than do morunasaurs (Appendix 3). In light of these ambiguities and the fact that many of the the derived characters involved are shared by more than just two of the major groups, it would be premature to consider a close relationship between basiliscines and iguanines anything more than a hypothesis in need of further testing.

One new hypothesis that has emerged from this study is the possibility of a close relationship among morunasaurs, oplurines and anoloids. Morunasaurs share with anoloids and oplurines the chamaeleon-like pattern of post-xiphisternal inscriptional ribs and an interosseus dorsal leg innervation. But the relationships within this larger group (for which we have no name) are not clear. Morunasaurs share with anoloids rugose dermal roofing bones, and on this basis morunasaurs and anoloids together may be considered the sister taxon of oplurines. However, oplurines share with all anoloids save *Polychrus* an Oberhaüchten with flat cell margins and a spinulate surface, and the loss of femoral pores, whereas *Polychrus* retains the primitive honeycomb Oberhaüchten and femoral pores found in morunasaurs. *Polychrus* is linked with other anoloids primarily on the basis of their nuchal endolymphatic sacs, absent in both morunasaurs and oplurines. If we postulate that

oplurines lack nuchal endolymphatics as a result of loss, then oplurines may be nested within the anoloids. Thus, if morunasaurs, anoloids and oplurines indeed form a monophyletic group, then their relationships within this group remain unresolved.

Although chameleon-like post-xiphisternal inscriptional ribs are found within the Iguanidae only in morunasaurs, oplurines and anoloids, an interosseus dorsal leg innervation occurs as well in basiliscines, crotaphytines, and some members of the tropidurines and sceloporines. If all of our generic groupings are in fact monophyletic, then the derived condition of the nerve must have evolved several times within the family, as it clearly has in other lizard families (Renous, 1978). For this reason we do not consider that the interosseus nerve in basiliscines, crotaphytines and the morunasaur-anoloid-oplurine clade provides strong support for a more inclusive monophyletic group.

COMPUTER ANALYSIS OF THE PRIMARY CHARACTER LIST

The shortest tree that we could find for our list of 49 characters is presented in Fig. 17. This tree was found by using the Wagner.S program in the PHYSYS package, and required 368 character transformations (steps), which is 283 more than the minimum of 85. The consistency index was 23.098 and the F-ratio 104.307. The apomorphies that arise at each stem and terminal taxon are given in Appendix I. For reasons discussed in the Methods section we do not accept this minimum step tree as our preferred phylogenetic hypothesis, nor do we feel obligated to comment on it in detail. We present it for the sake of completeness and invite comparison with our phylogenetic conclusions.

SUMMARY AND CONCLUSIONS

Because this is the first attempt to bring together the diverse data that bear on the phylogenetic relationships among all genera of iguanid lizards, the task is far from complete. Nevertheless, we have offered some explicit hypotheses about intergeneric relationships as well as character data relevant to these hypotheses. According to our analysis, every iguanid species can be placed in one of eight "major generic groups," each of which appears to be monophyletic but which neither includes nor is included within any of the others (Fig. 18). Although derived characters support the monophyly of many iguanid genera, many other genera lack diagnostic synapomorphies, and there is evidence that some of these are actually paraphyletic. Iguanidae itself currently lacks diagnostic synapomorphies, and it too may be paraphyletic. For this reason, the study of relationships within iguanids bears on higher systematic issues within Squamata, specifically, the relationships among all iguanians. We hope that our study not only answers some questions about relationships within Iguanidae but also provides a framework and data for biogeographical analysis, identifies systematic problems in need of further study, and reveals characters that bear both on these issues and on ones that transcend the boundaries of Iguanidae.

ACKNOWLEDGEMENTS

FIGURE 17. Wagner Tree of Iguanidae based on data matrix in Table 2.

Amblyrhynchus
Conolophus
59
Iguana
Cyclura
60
Ctenosaura
62
Enyaliosaurus
Dipsosaurus
64
Sauromalus
66
Brachylophus
69
Uranoscodon
71
Polychrus
68
Corythophanes
65
Laemanctus
63
Basiliscus
61
Plica
72
Uracentron
70
Strobilurus
67
Eastern Tropidurus
73
Western Tropidurus
76
Leiocephalus
77
Vilcunia
75
Liolaemus
74
Proctotretus
78
Ophryoessoides
79
Stenocercus
80
Tapinurus
81
Sceloporus
82
Sator
84
Urosaurus
86
Uta
90
94

FIGURE 18. The New Tree, illustrating the relationships of iguanid lizard genera based on the present study.

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APPENDIX 1. Iguanid Characters and Character States.

The following is a list of 49 characters and their states used in our initial phylogenetic analysis. We recognize these characters because it is convenient to do so, for each one does not necessarily represent a phylogenetically significant unit, i.e. a single transformation series. We hypothesize that the 49 characters actually represent 58 transformation series, and we indicate these transformation series to the right of each of the 49 characters. In order to set up a data matrix for Wagner analysis on a computer each transformation series was treated as a single character. Thus, some of our original characters had to be broken up into more than one character each. Transformation series involving more than one derived state were further broken up under additive binary coding. We give the codings used in the computer analysis to the right of each state for those characters that were recoded to make all entries binary. The number 9 stands for not applicable (e.g., position of parietal foramen when absent).

1. Premaxilla-nasal relationship. 0 -> 1
    0. Premaxillary spine exposed dorsally between nasal bones.
    1. Premaxillary spine mostly or completely overlapped by nasal bones.
2. Position of parietal foramen. 0 -> 1a; 0 -> 1b; 0 or 1a or 1b -> 1c
    0. At the frontoparietal suture. (000)
    1a. Entirely within the frontal. (100)
    1b. Entirely within the parietal. (010)
    1c. Absent (001)
3. Adult parietal roof shape. 0 -> 1 -> 2 -> 3
    0. Trapezoidal, lateral borders widely separated posteriorly. (000)
    1. Triangular, the lateral borders forming a V. (100)
    2. Y-shaped, with a median crest. (110)
    3. Y-shaped, the median crest forming a posteriorly projecting vertical blade. (111)
4. Lacrimal bone. 0 -> 1
    0. Present.
    1. Absent.
5. Lacrimal foramen. 0 -> 1 -> 2
    0. Small. (00)
    1. Intermediate. (10)
    2. Large. (11)
6. Postfrontal bone.   0 -> 1
    0. Present
    1. Absent.
7. Surface of dermal roofing bones. 0 -> 1 -> 2
    0. Smooth. (00)
    1. Frontal (at least posteriorly) and parietal roof with distinct surface rugosities that reflect the pattern of epidermal scales. (10)
    2. Rugosities extending onto other dermal skull bones in addition to frontal and parietal. (11)
8. Osseous labyrinth.   0-> 1 -> 2
    0. Superficial outlines of osseous labyrinth obscure, not raised well above surface of occipital bones. (00)
    1. Intermediate. (10)
    2. Superficial outlines of osseous labyrinth very distinct, raised well above surface of occipital bones. (11)
9. Supratemporal position.   0 -> 1 -> 2
    0. Supratemporal bone mostly overlaps lateral surface of supratemporal process of parietal. (00)

      1.   Intermediate. (10)

      2.   Supratemporal bone mostly overlaps medial surface of supratemporal process of parietal. (11)

10. Coronoid lateral process.   0 -> 1 -> 2

      0.   Coronoid bone without a process overlapping the posterolateral surface of the dentary. (00)

      1.   Coronoid bone with a small, irregular process overlapping the posterolateral surface of the dentary. (10)

      2.   A large, blade-like process of the coronoid bone descends over posterolateral surface of the dentary. (11)

11. Fusion of Meckel's groove.   0 -> 1

      0.   Meckel's groove open, or closed but not fused (a suture remaining) between anterior end of splenial and mandibular symphysis.

      1.   Meckel's groove fused anterior to the splenial, all the way to the symphysis or not.

12. Closure of Meckel's groove.   0 -> 1 -> 2

      0.   Meckel's groove open between anterior end of splenial and mandibular symphysis. (00)

      1.   Meckel's groove closed but not fused anterior to splenial for half or less the distance between the splenial and mandibular symphysis. (10)

      2.   Meckel's groove closed for more than half the distance between the splenial and mandibular symphysis. (11)

13. Splenial presence.   0 -> 1

      0.   Present.

      1.   Absent.

14. Splenial size.   0 -> 1 -> 2

      0.   Splenial extends forward at least to midpoint of dentary tooth row. (00)

      1.   Splenial extends forward to a point between dentary tooth row midpoint and most posterior dentary tooth. (10)

      2.   Anterior extremity of splenial not extending as far forward as most posterior dentary tooth. (11)

15. Angular.   0 -> 1 -> 2 -> 3 -> 4

      0.   Anterior process of angular long, its suture with the splenial usually on the medial face of the mandible. (0000)

      1.   Anterior process of intermediate length, its suture with the splenial usually on the ventral face of the mandible. (1000)

      2.   Anterior process short or nearly absent; its suture with the splenial usually on the lateral face of the mandible. (1100)

      3.   Anterior process of angular absent; posterior process greatly reduced. (1110)

      4.   Angular absent. (1111)

16. Posterior extent of dentary.   0 -> 1 -> 2

      0.   Dentary not extending beyond a point below the superior apex of the coronoid. (00)

      1.   Dentary extends beyond superior apex of coronoid but not beyond a point 30 percent of the distance between coronoid apex and center of articular fossa. (10)

      1.   Dentary extends beyond a point 30 percent of distance from coronoid apex to center of articular fossa. (11)

17. Palatine teeth.   0 -> 1

      0.   Present.

      1.   Absent.

18. Pterygoid teeth.   0 -> 1

      0.   Present.

      1.   Absent.

19. Crowns of posterior marginal teeth.   0 -> 1a -> 2a; 0 -> 1b -> 2b

      0.   Tricuspid, with more or less parallel sides. (0000)

    1a. Tricuspid, with distinctly expanded crowns.   (1000)

    2a. Crowns distinctly expanded, with four or more cusps. (1100)

    1b. Tricuspid, with distinctly tapered crowns and very small secondary cusps. (0010)

    2b. Cusps lacking. (0011)

20. Second ceratobranchials. 0 -> 1
- 0. Short, not extending beyond clavicles, or if longer not associated with an extensile gular fan.
- 1. Long, extending beyond clavicles, almost always associated with an extensile gular fan.

21. Clavicle. 0 -> 1
- 0. Flat, with a wide lateral flange.
- 1. Slender, lateral flange greatly reduced or absent.

22. Clavicular fenestra. 0 -> 1
- 0. Absent.
- 1. Present.

23. Clavicular lateral margin. 0 -> 1a; 0 -> 1b
- 0. Lateral margin of clavicle irregular, or forming a smooth curve. (00)
- 1a. Lateral margin of clavicle distinctly angular, with an acute projection at the apex of the angle. (10)
- 1b. Lateral margin of clavicle expanded ventromedially. (01)

24. Interclavicle posterior median process. 0 -> 1
- 0. Extending posteriorly beyond posterolateral corners of sternum.
- 1. Not extending beyond lateral corners of sternum.

25. Scapular fenestra. 0 -> 1
- 0. Absent.
- 1. Present.

26. Posterior coracoid fenestra. 0 -> 1
- 0. Absent.
- 1. Present.

27. Sternal fontanelle. 0 -> 1 -> 2
- 0. Absent or small, nor much wider than the interclavicle posterior median blade width. (00)
- 1. Intermediate. (10)
- 2. Large, much wider than interclavicle posterior median blade width. (11)

28. Cervical ribs. 0 -> 1 -> 2
- 0. First pair on vertebra number 3. (00)
- 1. First pair on vertebra number 4. (10)
- 2. First pair on vertebra number 5. (11)

29. Number of sternal rib pairs. 0 -> 1 -> 2
- 0. Four.   (00)
- 1. Three. (10)
- 2. Two.   (11)

30. Total number of presacral vertebrae. 0 -> 1a -> 2a; 0 -> 1b
- 0. Twenty-four. (000)
- 1a. Twenty-three. (100)
- 2a. Twenty-two or fewer. (110)
- 1b. Twenty-five or more. (001)

31. Lumbar vertebrae. 0 -> 1a; 0 -> 1b
- 0. All with free articulating ribs. (00)
- 1a. One or more with ribs absent. (10)
- 1b. One or more with ribs fused. (01)

32. Post-xiphisternal inscriptional rib pattern.   0 -> 1 -> 2
    0. *Sceloporus* pattern. (00)
    1. *Chamaeleon* pattern. (10)
    2. *Oplurus* pattern. (11)
33. Caudal vertebral types.   0 -> 1a; 0 -> 1b; 0 -> 1c
    0. *Sceloporus* type. (000)
    1a. *Iguana* type. (100)
    1b. *Basiliscus* type. (010)
    1c. *Anolis* type. (001)
34. Caudal autotomy.   0 -> 1
    0. Present.
    1. Absent.
35. Nuchal endolymphatic sacs.   0 -> 1
    0. Absent.
    1. Present.
36. Scale organs.   0 -> 1 -> 2 -> 3
    0. Smooth or with spinules less than 1 micron tall. (000)
    1. Spinulate, with short spines less than 3 microns tall. (100)
    2. Spinulate, with spikes about 5 microns tall. (110)
    3. Spinulate, with a single, long twisted filament. (111)
37. Subdigital scale sufrace microstructure.   0 -> 1 -> 2 -> 3
    0. Honeycombed, smooth, or with spinules not more than 1 micron tall. (000)
    1. Spinulate, with spines at least 2 micron tall; taller spikes and prongs present or not. (100)
    2. Spinulate, with differentiated seta-prongs. (110)
    3. Spinulate, with differentiated setae. (111)
38. Distal subdigital scales.   0 -> 1
    0. Distal two or three subdigital scales without a median groove.
    1. Distal two or three subdigital scales with a median groove.
39. Subdigital scale surface macrostructure.   0 -> 1
    0. Distinctly carinate.
    1. Smooth or faintly carinate.
40. Subdigital pads.   0 -> 1
    0. No distal pad raised under phalanges 2 and 3.
    1. A distal pad raised under phalanges 2 and 3.
41. Femoral pores.   0 -> 1
    0. Present.
    1. Absent.
42. Preanal pores.   0 -> 1
    0. Absent.
    1. Present.
43. Transverse gular fold.   0 -> 1 -> 2
    0. Present, strong and continuous. (00)
    1. Weak, faint medially. (10)
    2. Absent. (11)
44. Midorsal scale row.   0 -> 1 -> 2
    0. Present, continuous. (00)
    1. Present but discontinuous. (10)
    2. Absent. (11)
45. Interparietal scale.   0 -> 1; 0 -> 1b
    0. Small, not wider than interorbital width. (00)
    1a. Large, wider than interorbital width. (10)
    1b. Absent. (01)

46. Superciliary scales. 0 -> 1 -> 2
    0.   Elongate and strongly overlapping (00)
    1.   Intermediate. (10)
    2.   Quadrangular, nonoverlapping. (11)
47. Subocular scales. 0 -> 1 -> 2
    0.   One subocular elongate, at least three times longer than high. (00)
    1.   One or two elongate, between two and three times longer than high. (10)
    2.   All suboculars more or less subequal in size. (11)
48. Ulnar nerve pathway. 0 -> 1
    0.   Superficial to limb muscle ("L").
    1.   Deep to limb muscle ("V").
49. Dorsal shank muscle innervation. 0 -> 1
    0.   From peroneal nerve ("A").
    1.   From interosseous nerve ("B").

APPENDIX 2. Iguanid Character States - Data Matrix for the character states scored for forty-nine characters representing fifty-eight transformation series.   Genera are listed in the order in which they were entered into the PHYSYS program. The number of each character and the number(s) of each state or states listed below the characters correspond to the numbered characters and states described in Appendix 1; na = not applicable. Intrageneric variation is indicated by a listing of two or more states for one character. Only the most primitive state found in each genus was used in the Wagner analysis. Character states were scores separately for *Tropidurus* species east and west of the Andes.

Taxon	Number															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Enyalioides	0	0	0	0	2	0	1	0	0	2	0	0	0	0	0	1
Morunasaurus	0	0,1c	0	0,1	2	0	1	0	0	2	0	0	0	0	0	1
Hoplocercus	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	1
Oplurus	0	0	0	0	0	0,1	0,1	0	0,1	0	0,1	0,1,2	0	0,1	0,1	1,2
Chalarodon	0	0	0	0	0	1	0	1	1	0	1	2	0	1	1	2
Polychrus	0	0,1c	0	0,1	0	1	2	2	0	0	1	2	0	1	0	0,1
Enyalius	0	0	0	0	0	0	2	2	0,1	0	1	2	0	1	0	2
Leiosaurus	0	0	0	0	0	1	2	2	0	0	1	2	0	1	0	2
Aperopristis	0	0	0	0	0	0	2	2	0	0	1	2	0	1	0	2
Diplolaemus	0	0	0	0	0	0	1	2	0	0	1	2	0	1	0	2
Pristidactylus	0	0	0	0	0	0	2	1,2	0	0	1	2	0	1	0	2
Urostrophus	0	0	0	0	0	0	2	2	0	0	1	2	0	1	0	2
Anisolepis	0	0	0	0	0	0	2	2	0	0	1	2	0	1	0	2
Aptycholaemus	0	0	0	0	0	0	2	2	0	0	1	2	0	1	0	2
Chamaeleolis	0	0	3	0	0	0	2	2	0	2	1	2	0	2	3	2
Phenacosaurus	0	0	0	0	0	0	2	2	0	2	1	2	0	2	4	2
Chamaelinorops	0	0	0	0	0	1	1	2	0	2	1	2	1	na	4	2
Anolis	0	0,1b	0,1,2	0	0	0,1	0,1,2	2	0	2	1	2	0,1	2,na	4	1,2

Taxon	Number															
	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Enyalioides	1	0	2a	0	0	0	0,1b	0	0,1	0	0	1	0	0	0	1
Morunasaurus	1	0	1a,2a	0	0	0	0	0	0,1	0,1	0	1	0	0	0	1
Hoplocercus	1	0	1b	0	0	0	0	0	0	0	0	1	0	0	0	1
Oplurus	0,1	0	0,1a	0	0,1	0	0,1	0	0,1	0	0	2	0	0	0	2
Chalarodon	1	0	0	0	1	0	0	0	1	0	0	1	1	0	0	2
Polychrus	1	0,1	0	0,1	1	0	0	0	0,1	0	0	2	2	1b	1b	1
Enyalius	0,1	0	0,1b	0	0	0	1a	0	0	1	0	0,1	0	0	1a	1
Leiosaurus	0,1	0	1b	0	0	0	1a	0	0	1	0	0,1	0	0	0	1
Aperopristis	1	0	1b	0	0	0	1a	0	0	1	0	0,1	0	0	0	1
Diplolaemus	1	1	1b	0	0	0	1a	0	0	1	0	1	0	0	0	1
Pristidactylus	0,1	0	0,1a,b	0	0	0	1a	0	0	1	0	0,1	0	0	0,1a,1b	1
Urostrophus	0,1	0	0	0	0	0	1a	0	0	1	0	1	1	0	0,1a	1
Anisolepis	0,1	0	1b	0	0	0	1a	0	0	1	0	1	1	0	0,1a	1
Aptycholaemus	1	0	1b	0	0	0	1a	0	0	1	0	1	1	0	0	1
Chamaeleolis	0	0	2b	1	1	0	0	1	0	0	0	2	1	0	0	1
Phenacosaurus	1	2	0	1	1	0	0	0	0	0	0	2	2	2a	1a	1
Chamaelinorops	1	1	0	1	0	0	1a	0	0	0	0	2	1	0	1a	1
Anolis	1	0,1	0	1	0,1	0	0,1a	0	0	0	0	2	1	0,1a	1a	1

Taxon	Number																
	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
Enyalioides	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	1
Morunasaurus	0	0	0	0	0	0	0	0	0	0	0	0,2	1b	2	2	0	1
Hoplocercus	0	1	0	0	0	0	0	0	0	0	0	2	0	2	2	0	1
Oplurus	0	0	0	3	2	0	0	0	1	0	0	2	0	0	0	1	1
Chalarodon	0	0	0	3	2	0	0	0	1	0	0	0	0	0	0	1	1
Polychrus	1b	1	1	0	0	0	0	0	0	0	2	0,2	0,1b	2	1	0	1
Enyalius	1b	0,1	1	1	1	1	0,1	0	1	0	0	0,1	0	1	0,1,2	0	1
Leiosaurus	0	1	1	1	1	1	0,1	0	1	0	0	2	0	2	2	0	1
Aperopristis	0	1	1	1	1	1	0	0	1	0	0	0	0	2	2	0	1
Diplolaemus	0	0	1	1	1	1	1	0	1	0	0	2	0	1	0,1,2	0	1
Pristidactylus	0	0	1	1	1	1	0,1	0	1	0	0	1,2	0	1	0,1,2	0	1
Urostrophus	0	1	1	2	2	0	1	0	1	0	0	2	0	1	0,1	0	1
Anisolepis	0	1	1	2	2	0	1	0	1	0	0	2	0	1	0	0	1
Aptycholaemus	0	1	1	2	2	0	1	0	1	0	2	2	0	1	0	0	1
Chamaeleolis	1c?	1	1	3	3	0	1	1	1	0	2	2	0	1	2	0	1
Phenacosaurus	1c?	1	1	3	3	0	1	1	1	0	2	0	0	2	2	0	1
Chamaelinorops	1c	1	1	3	3	0	1	1	1	0	2	2	0	1	2	0	1
Anolis	1c	0,1	1	3	3	0	1	1	1	0	2	0,1,2	0	0,1	2	0	1

Taxon	Number															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Amblyrhynchus	1	0	1	0	0	0	0	0	2	2	1	2	0	1	0	0
Conolophus	1	0	2	0	0	0	0	0	2	2	1	2	0	1	0	0,1
Brachylophus	0	0	0,1	0	0	0	0	0	2	2	1	2	0	1	0	1
Iguana	0	0	2	0	0	0	0	0	2	2	1	2	0	1	0	1
Cyclura	0	0	2	0	0	0	0	0	2	2	1	2	0	1	0	0
Ctenosaura	0	0	2	0	0	0	0	0	2	2	1	2	0	1	0	0,1
Enyaliosaurus	0	0	0,1	0	0	0	0,2	0	2	2	1	2	0	1	0	0,1
Sauromalus	0	0,1a	0	0	0	0	0	0	2	2	1	2	0	1	0	0,1
Dipsosaurus	0	1a	0	0	0	0	0	1	2	2	1	2	0	1	0	1
Basiliscus	0	1a	3	0	0	1	0	1	0	1	0,1	1,2	0	0	0	0,1
Laemanctus	0	0,1a	3	0	0	0	2	2	0	1	0,1	1,2	0	0,1	0	1
Corytophanes	0	1a	3	0	0	1	1	2	0	1	1	2	0	1	0	1
Petrosaurus	0	0	0	0	0	0	0	0	0	1	0	1,2	0	1	0	1
Sceloporus	0	0	0	0	0	0	0	0	0	1	0	1,2	0	1	0	2
Sator	0	0	0	0	0	0	0	0,1	0	1	0	2	0	1	0	1,2
Uta	0	0	0	0	0	0	0	1	0	1	0	2	0	1	0	1,2
Urosaurus	0	0	0	0	0	0	0	1	0	1	0,1	2	0	1	0	1,2
Callisaurus	0	0	0	1	1	1	0	1	0	1	0	2	0	1	0	2
Holbrookia	0	0	0	1	1	1	0	1	0	1	0	2	0	1	0	2
Cophosauru	0	0	1	1	1	1	0	1	0	1	0	2	0	1	0	1
Uma	0	0	0	1	1	1	0	1	0	1	0	2	0	1	0	1
Phrynosoma	0,1	0	0	1	0	1	2	0	0	1	0	0,1,2	0,1	1	0-4	1,2

Taxon	Number															
	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Amblyrhynchus	1	0	1a	0	0	0	0,1a	1	1	1	0	2	0	0	0	0
Conolophus	1	0,1	2a	0	0	0,1	0	0,1	1	1	0	2	0	0	0	0
Brachylophus	1	0	1a,2a	0	0	0	0	0	1	0	0	2	0	0	0	0
Iguana	1	0	2a	0	0	0	0	0	1	1	0	2	0	0	0	0
Cyclura	1	0	2a	0	0	0	0	0	1	1	0	2	0	0	0	0
Ctenosaura	1	0	2a	0	0	0	0	0	1	1	0	2	0	0	0	0
Enyaliosaurus	1	0	2a	0	0	0	0	0	1	1	0	2	0	0,1b	0	0
Sauromalus	1	0	2a	0	1	0	0	1	1	1	0	2	0	0	0	0
Dipsosaurus	1	0,1	2a	0	0	0	0	0	1	0	0	2	0	0	0	0
Basiliscus	1	0	1a	0	0	1	1b	0	0	0	2	0	0	0	0	0
Laemanctus	1	0	0	0	0	1	1b	0	0	0	0	1,2	0,1	0	1a	0
Corytophanes	1	0	0	0	0	1	1b	0	0	0	0	1,2	0,1	0,1a,2a	0,1a	0
Petrosaurus	1	1	0	0	1	0	0	0	0	0	1	1	0	1a	0	0
Sceloporus	1	1	0,1b,2b	0	1	0	1a	0	0,1	0	2	1	1	1a	0	0
Sator	1	1	0	0	1	0	1a	0	0	0	2	1	1	1a	0	0
Uta	1	1	0	0	1	0	1a	0	0	0	2	1	1	1a	0	0
Urosaurus	1	1	1b	0	1	0	1a	0	0	0	2	1	1	1a	0	0
Callisaurus	1	1	1b	0	1	0	0	1	1	0	2	2	1	1a	0	0
Holbrookia	1	1	1b	0	1	0	0	1	1	0	2	2	1	1a	0	0
Cophosaurus	1	1	1b	0	1	0	0	1	1	0	2	2	1	1a	0	0
Uma	1	1	0.	0	1	0	0	1	1	0	2	2	1	1a	0	0
Phrynosoma	1	1	1b,2b	0	1	0	0	1	0	0	2	1,2	1,2	0,1a	0,1b	0

Taxon	Number																
	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
Amblyrhynchus	1a	1	0	0	0	0	0	0	0	0	1	0	0	2	1	0	0
Conolophus	1a	1	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0
Brachylophus	1a	1	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0
Iguana	1a	0,1	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0
Cyclura	·1a	0	0	0	0	0	0	0	0	0	0	0,1	0	1	2	0	0
Ctenosaura	1a	0	0	0	0	0	0	0	0	0	0	0,1	0	1	0	0	0
Enyaliosaurus	1a	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Sauromalus	1a	0	0	0	0	0	0	0	0	0	0	2	0	2	2	0	0
Dipsosaurus	1a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Basiliscus	1b	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	1
Laemanctus	1b	1	0	0	0	0	0	0	1	0	0,1,2	0,2	0	1	2	0	1
Corytophanes	1b	1	0	0	0	0	0	0	1	0	0	0	0	2	2	0	1
Petrosaurus	0	0	0	0	0	0	0	0	0	0	0	2	1a	0	0	0	0
Sceloporus	0	0	0	0	0	0	0	0	0	0	1,2	2	1a	0	0	0	1
Sator	0	0	0	0	0	0	0	0	0	0	2	2	1a	0	0	0	1
Uta	0	0	0	0	0	0	0	0	0	0	0	2	1a	0	0	0	0
Urosaurus	0	0	0	0	0	0	0	0	·0	0	0	2	1a	0	0	0	1
Callisaurus	0	0	0	0	0	0	0	0	0	0	0	2	1a	0	0	0	0
Holbrookia	0	0	0	0	0	0	0	0	0	0	0	2	1a	0	0	0	0
Cophosaurus	0	0	0	0	0	0	0	0	0	0	0	2	1a	0	0	0	0
Uma	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Phrynosoma	0	1	0	0	0	0	0	0	0	0	0	2	0	1	2	0	0

Taxon	Number															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Crotaphytus	0	0	0	0	0	1	0	1	0	1	0	0,1	0	0	0	1
Gambelia	0	0	0	0	0	1	0	1	0	1	0	2	0	0,1	0	1
Tropidurus (E)	0	0	0	0	0	0	0	0	0	0	1	2	0	1,2	1,4	2
Tropidurus (W)	0	0	0	0	0	0	0	0	0	0	1	2	0	1	1,2	2
Tapinurus	0	0	0	0	0	0	0	0	0	0	1	2	0	2	3	2
Uranoscodon	0	0	0	0	1	0	0	2	0	0	1	2	0	1	0	1
Plica	0	0	0	0	1	0	0	0	0	0	1	2	0	1	3,4	2
Uracentron	0	1c	0	0	1	0	0	0	0	0	1	2	0	2	2	2
Strobilurus	0	0	0	0	1	0	0	0	0	0	1	2	0	2	4	2
Ophryoessoides	0	0,1c	0	0	0	0	0,1	2	0	0	1	2	0	1	0	2
Stenocercus	0	0,1c	0	0	0	0	0,1	0,1	0	0	1	2	0	1	0,1,2	2
Proctotretus	0	0	0	0	0	0	0	0	0	0	1	2	0	1	0	2
Liolaemus	1	0	0	0	0	0	0,1	0	0	2	0,1	1,2	0	1	2,3,4	2
Vilcunia	1	0	0	0	0	0	0	0	0	2	1	1	0	1	2	1
Ctenoblepharis	1	0	0	0	1	0	0	1	0	2	0	1	0	1	0	1
Phymaturus	0	0	0	0	0	0,1	0	0	0	2	0,1	1	0	0	1	1
Leiocephalus	1	0,1a	1	0	0	0	0,1	0	0	2	1*	2*	0	1	1	2

* State 0 in some extinct species

Taxon	Number															
	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Crotaphytus	0	0	0	0	0	0	0	0,1	1	1	0	0,1	0	0	0	0
Gambelia	0	0	0	0	0	1	1b	0	1	1	0	1	0	0	0	0
Tropidurus (E)	1	0	0	0	0,1	0	0	0,1	0,1	0,1	2	1	0,1	0	0	0
Tropidurus (W)	1	0	0	0	0,1	1	0	0,1	1	1	2	1	1	0	0	0
Tapinurus	1	1	0	0	1	0	0	0	0	1	2	1	1	0	0	0
Uranoscodon	1	0,1	0	0	0	0,1	0	0	1	1	1	1	0,1	0	0	0
Plica	1	0,1	1a	0	0	0,1	0	1	1	1	2	1	0,1	0	0	0
Uracentron	1	1	1a	0	0	0,1	0	0	1	1	2	1	1	0	0	0
Strobilurus	1	1	1a	0	0	0	0	0	1	1	2	1	0,1	0	0	0
Ophryoessoides	1	0,1	0	0	0	0	1a	0	0,1	1	2	1	1	0	0	0
Stenocercus	1	0	0	0	0	0	0,1a	0	0,1	1	2	1	1	0	0	0
Proctotretus	1	0	0	0	0	0	1a	0	1	1	2	1	1	1a	0	0
Liolaemus	1	0,1	0,1a	0,10	0,1a	0	0	0	1	2	0,1	0,1	0,1a,1b	0	0	2a,1b
Vilcunia	1	1	0	0	0	0	1a	0	0	1	2	1	0	0	0	0
Ctenoblepharis	1	0	1b	0	0	0,1	1b	0	0	0	2	1	1	1a	0	0
Phymaturus	1	0	2a	0	0	0	1a	1	0	0	2	0,1	0	0	0	0
Leiocephalus	1	0,1	1a	0	0	0	0,1a	0	1	0	2	1	1	0	0	0

Taxon	Number															
	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
Crotaphytus	0	1	0	0	0	0	0	0	0	0	0	2	0	1	1,2	0	1
Gambelia	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	1
Tropidurus (E)	0	0	0	0	0	0	0	0	1	0	2	0,1,2	1a	0	0	0	0
Tropidurus (W)	0	0	0	0	0	0	0	0	1	0	2	0,1	1a	0	0	0	0
Tapinurus	0	0	0	0	0	0	0	0	1	0	2	2	1a	0	0	0	0
Uranoscodon	0	0	0	0	0	0	0	0	1	0	0	0	1a	1	2	0	1
Plica	0	0	0	0	0	0	0	0	1	0	0	0	1a	0	2	0	0
Uracentron	0	1	0	0	0	0	0	0	1	0	0	2	1a	0	0	0	0
Strobilurus	0	0	0	0	0	0	0	0	1	0	0	0	1a	0	0	0	0
Ophryoessoides	0	0,1	0	0	0	0	0	0	1	0	2	0	0,1b	0	0	0	0
Stenocercus	0	0	0	0	0	0	0	0	1	0	0,1,2	0,1	0,1b	0	0	0	0
Proctotretus	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0
Liolaemus	0	0	0	0	0	0	0	0	1	0,1	2	2	0	0	0	0	1
Vilcunia	0	0	0	0	0	0	0	0	1	0	2	2	0	0	0	0	1
Ctenoblepharis	0	0	0	0	0	0	1	0	1	1	2	2	0	1	2	0	1
Phymaturus	0	0	0	0	0	0	0	0	1	1	0	2	0	1	1,2	0	1
Leiocephalus	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0

APPENDIX 3

Pairwise comparisons of the number of derived characters shared by the major groups of i̧ nids. The comparisons involve only those derived characters that we consider to have been pre in the most recent common ancestor of all extant members of each major group (Appendix 4). two sets of comparisons differ in that the presence of a coronoid lateral blade is cosidered derived in the comparisons above the diagonal while it is considered primitive in comparisons below the diagonal. The first four letters of each major group name are used as abbreviations.

	Anol	Moru	Oplu	Trop	Igua	Basi	Crot	Scel
Anol	–	4	2	1	3	3	3	2
Moru	4	–	4	2	5	6	4	4
Oplu	2	4	–	2	1	3	2	2
Trop	1	2	2	–	2	3	1	4
Igua	3	4	1	2	–	5	2	5
Basi	3	5	4	3	4	–	3	4
Crot	3	3	3	1	1	3	–	3
Scel	2	3	3	4	4	4	3	–

APPENDIX 4

Listed below are the derived characteristics of each of the major suprageneric groups of iguanids, followed by lists of synapomorphies that characterize less inclusive monophyletic groups, and a list of those characters that vary within genera. Because relationships among the major suprageneric groups are unresolved, we include all of the derived states that characterize each of them, although some of these may be synapomorphies for monophyletic groups that are more inclusive than the groups under which they are listed. Numbered characters correspond to those used in our inclusive analysis; characters used only with restricted groups are indicated by an asterisk (*), followed by appropriate reference. Numbers that precede suprageneric taxa refer to the numbered nodes in the figures. Derived states that are unique within Iguanidae are indicated by a "U".

THE ANOLOIDS (Fig. 9)

Node 1. The Anoloids
07 Adult ·skull roofing bones acquire well-developed rugosities that reflect the pattern of overlying epidermal scales.
08 Osseous labyrinth becomes distinct externally.
11 Meckel's groove fuses.
12 Meckel's groove closes for more than half the distance between the mandibular symphysis and splenial.
14 Splenial fails to reach midpoint of dentary tooth row.
32 Post-xiphisternal inscriptional ribs become chamaeleon-like.
35 Nuchal endolymphatic sacs acquired. (U)
46 Superciliary sutures become less oblique.
49 Interosseous nerve innervates dorsal shank.

Polychrus
06 Postfrontal bone lost.
17 Palatine teeth lost.
21 Clavicle becomes slender.
28 Ribs lost from 3rd and 4th cervical vertebrae.
29 Sternal ribs reduced to 2.

30 Presacral vertebrae increase to 25-28.
31 Ribs fuse to lumbar vertebrae.
33 Transverse processes lost from all but anterior few caudal vertebrae.
34 Caudal autotomy septa lost.
43 Transverse gular fold lost.
47 Subocular becomes fragmented.
 * Unique karyotype consisting primarily of acrocentric chromosomes acquired (Gorman et al., 1969). (U)
 * Fourth toe reduced, equals third in length (Cope, 1900; pers. obs.). (U)
In some:
02 Parietal foramen lost.
04 Lacrimal bone lost.
16 Dentary elongates beyond superior apex of coronoid but less than 30 percent of the distance between the coronoid apex and center of articular fossa.
18 Pterygoid teeth lost.
20 Second ceratobranchials elongate.
26 Posterior coracoid fenestra acquired.
44 Middorsal scale row lost.
45 Interparietal scale lost.

Node 2. The Spinulate Anoloids
16 Dentary elongates, beyond 30 percent of distance between coronoid apex and center of articula- fossa.
36 Oberhäuchten becomes spinulate with flat cell boundaries; scale organ spinules taller than those of general scale surface.
37 Subdigital spinules elongate, at least 2 microns long.
39 Subdigital keels lost.
41 Femoral pores lost.

Node 3. The Leiosaurs
23 Lateral margin of clavicle becomes angular and hooked; possible synapomorphy with para- anoles.
26 A very small posterior coracoid fenestra acquired; possible synapomorpy with para-anoles.
38 Distal two or three subdigital scales acquire a longitudinal groove. (U)

Enyalius
 * Throat scales conical (pers. obs.). (U)
In some:
09 Supratemporal bone more or less equally overlaps medial and lateral surfaces of supratemporal process of parietal.
17 Palatine teeth lost.
19 Secondary cusps of marginal teeth reduced.
28 Ribs lost from 3rd cervical vertebra.
31 Lumbar ribs lost.
34 Caudal autotomy septa lost.
39 Subdigital scales become multicarinate; distal grooves obscured.
44 Middorsal scale row becomes interrupted; distal grooves obscured.
47 Subocular scale becomes fragmented.

Node 4. *Pristidactylus + Leiosaurus + Diplolaemus + Aperopristis*
 * Supradigital scales become transversly expanded, lamellar-like (pers. obs.). (U)
 * Proximal subdigital scales of toes 1-3 become enlarged and pectinate (pers. obs.).

Pristidactylus
In some:
08 Osseous labyrinth partly obscured.
17 Palatine teeth lost.
19 Posterior marginal tooth crowns become flared and deeply cusped.
19 Posterior marginal tooth crowns become blunt with minute cusps.
28 Ribs lost from 3rd cervical.
31 Ribs fused to lumbar vertebrae.
31 Ribs lost from lumbar vertebrae.
39 Subdigital scales become multicarinate.
44 Middorsal scale row becomes inconspicuous and interrupted in few, lost in most.
47 Subocular scale becomes fragmented.

Node 5. *Diplolaemus + Leiosaurus + Aperopristis*
19 Posterior marginal teeth become robust, with reduced secondary cusps.
34 Caudal autotomy septa partly fuse.
44 Middorsal scale row lost.
 * Proximal subdigital scales of toes remain swollen but no longer pectinate (pers. obs.).
 * Sexual dichromatism lost (pers. obs.).

Diplolaemus
07 Dermal roofing bone rugosities reduced.
17 Palatine teeth lost.
18 Pterygoid teeth lost.
28 Ribs lost from 3rd cervical vertebra.
In some:
47 Subocular scale becomes fragmented.

Node 6. *Leiosaurus + Aperopristis*
34 Caudal autotomy septa lost.
47 Subocular fragmented.
 * Dorsal body acquires distinctive fleur-de-lys pattern. (pers. obs.). (U)

Leiosaurus
In one (*L. catamarcensis*):
39 Subdigital scales become multicarinate.
 * Rostral scale undifferentiates (pers. obs.).

Aperopristis
39 Subdigital scales become multicarinate.
44 Middorsal row of enlarged tubercles acquired.
 * Rostral and mental scales undifferentiate, dorsal scales become markedly heterogeneous (pers. obs.).

Node 7. The Para-anoles
23 Lateral margin of clavicle becomes angular and hooked; possible synapomorphy with the leiosaurs.
26 A very small secondary coracoid fenestra acquired; possible synapomorphy with the leiosaurs.
29 Sternal ribs reduced to 3; possible synapomorphy with the anoles.
34 Caudal autotomy lost.
36 Scale organ spines at least 5 microns high; possible synapomorphy with the anoles.
37 Subdigital spinules differentiate, with seta-prongs; possible synapomorphy with the anoles.

44 Middorsal scale row lost.
* Sexual dichromatism lost (pers. obs.).

Urostrophus
No synapomorphies.

Node 8. *Anisolepis + Aptycholaemus*
36 Posterior marginal teeth slender, with tapered crowns and reduced secondary cusps.
* Posterolateral processes of basisphenoid lost (pers. obs.).
* A ventrolateral row of enlarged scales acquired (pers. obs.).
* Ventral body scales with sharp keels in parallel rows (pers. obs.)

Anisolepis
No synapomorphies.

Aptycholaemus
43 Transverse gular fold lost.
* External ear greatly reduced (Boulenger, 1891).
* Tail over three times head-body length (Boulenger, 1891).

Node 9. The Anoles
10 Coronoid labial blade acquired.
14 Splenial further reduced, not extending as far forward as posterior dentary tooth.
15 Angular reduced to tiny bone splint.
20 Greatly elongate second ceratobranchials associated with an extensile gular fan acquired.
21 Clavicles become slender.
28 Ribs lost from third and fourth cervical vertebrae.
29 Sternal ribs reduced to three; posible synapomorphy with para-anoles.
31 Ribs lost from lumbar vertebrae.
33 Anolis type caudal vertebrae acquired. (U)
36 Scale organs with a central filament of twisted spines; possible synapomorphy with oplurines.
37 Subdigital scales acquire differentiated setae; possible synapomorphy with para-anoles. (U?)
40 A distal pad raised under phalanges 2 and 3. (U)
43 Transverse gular fold lost.
47 Subocular scale fragments.

Chamaeleolis
03 Adult parietal roof forms a flat, projecting shelf. (U)
19 Adult posterior marginal teeth loose cusps.
24 Interclavicle median process becomes shorter.
34 Caudal autotomy lost.

Node 10. *Anolis + Phenacosaurus + Chamaelinorops*
15 Angular lost.
17 Palatine teeth lost.

Anolis
In some:
02 Parietal foramen moves into parietal.
03 Adult parietal roof becomes V-shaped or Y-shaped.
06 Postfrontal lost.
07 Dermal skull roof rugosities reduced or lost.

13 Splenial lost.
16 Dentary elongates to a point beyond 30 percent of the distance between coronoid superior apex and center of articular fossa.
18 Pterygoid teeth lost.
21 Clavicle reverts to flat.
23 Lateral margin of clavicle becomes angular.
30 Presacral vertebrae reduced to 23, 22 or 21.
34 Caudal autotomy lost.
39 Subdigital scales become multicarinate.
44 Middorsal scale row lost.

Phenacosaurus
18 Pterygoid teeth lost.
29 Sternal ribs reduced to two pairs.
30 Presacral vertebrae reduced to 22.
34 Caudal autotomy lost.
 * Tail becomes prehensile (Dunn, 1944).

Chamaelinorops
06 Postfrontal lost.
07 Dermal skull roof rugosities reduced.
13 Splenial lost.
18 Pterygoid teeth lost.
21 Clavicle reverts to flat.
23 Clavicle acquires an angular margin.
34 Caudal autotomy lost.
37 Subdigital spine and seta structure modified? (Peterson, 1983).
44 Middorsal scale row lost.
 * Zygapophyseal plates greatly expanded (Forsgaard, 1983). (U)

THE MORUNASAURS (Fig. 10)
Node 1. The Morunasaurs.
05 Lacrimal foramen enlarges.
07 Skull roofing bones become moderately rugose.
10 Coronoid labial blade acquired.
16 Dentary elongates.
17 Palatine teeth lost.
19 Teeth become expanded and multicusped.
28 Ribs lost from 3rd cervical vertebra.
32 Chamaeleon-like postxiphisternal inscriptional ribs acquired.
46 Superciliaries become subequal with vertical sutures.
47 Subocular scale fragments.
49 Dorsal shank nerve becomes interosseous.
 * Nasal scale greatly enlarged (Etheridge, 1969). (U)
 * Zygosphenes and zygantra acquired (pers. obs.).

Enyalioides
In some:
23 Lateral margin of clavicle becomes angular.
25 Scapular fenestra acquired.
 * Dorsolateral crest of enlarged scales acquired (Boulenger, 1885).
 * Dorsal body scalation becomes heterogenous (Boulenger, 1885).

* Tail becomes shorter, with well developed spines (Boulenger, 1885).
* Tail becomes compressed (Boulenger, 1885).

Node 2. *Morunasaurus + Hoplocercus*
  * Anterior iliac process reduced and iliac blade elongates (pers. obs.).
  * Dorsolateral crest of enlarged scales acquired (Boulenger, 1885).
  * Dorsal body scalation becomes heterogenous (Boulenger, 1885).
  * Tail becomes shorter, with well developed spines (Boulenger, 1885).

Morunasaurus

In some:
02 Parietal foramen lost.
04 Lacrimal bone lost.
19 Tooth crowns revert to straight sides, 4th cusp lost.
25 Scapular fenestra acquired.
26 Posterior coracoid fenestra acquired.
44 Middorsal scale row lost.
45 Interparietal scale lost.

Hoplocercus
05 Lacrimal foramen secondarily reduced.
07 Skull roof rugosities secondarily reduced.
19 Tooth crowns become tapered with small secondary cusps.
34 Caudal autotomy lost.
44 Middorsal scale row lost.
 * Anterior vidian canal opens on ventral basisphenoid (pers. obs.).
 * Dorsolateral crests lost (pers. obs.).
 * Tail becomes depressed, with very stout pines (Boulenger, 1885).
 * Tail reduced to one half head-body length, covered with stout spines (pers. obs.).

THE OPLURINES (Fig. 11)
Node 1. The Oplurines.
16 Dentary elongates.
28 Ribs lost from 3rd cervical vertebra.
32 Chamaeleon-like postxiphisternal inscriptional ribs reduced to paired splints. (U)
36 Oberhaüchten becomes spinulate, scale organ spines twist together to form central filament.
37 Subdigitals spinules become elongate and differentiated.
41 Femoral pores lost.
48 Ulnar nerve becomes deep to limb muscle. (U)
49 Dorsal shank nerve becomes interosseous.

Oplurus
44 Middorsal scale row lost.
In some:
06 Postfrontal lost.
07 Skull roof acquires moderate rugosities.
09 Supratemporal shifts to partly overlap lateral surface of supratemporal process of parietal.
11 Meckel's groove fuses.
12 Meckel's groove fuses more than half the distance between splenial and mandibular symphysis.
14 Splenial reduced.
15 Angular reduced.
16 Dentary becomes still longer.
17 Palatine teeth lost.
19 Tooth crowns expand.

21 Clavicle becomes slender.
23 Lateral margin of clavicle becomes angular.
25 Scapular fenestra acquired.

Chalarodon
06 Postfrontal lost.
08 Bony labyrinth becomes moderately distinct.
09 Supratemporal shifts to partly overlap lateral surface of supratemporal process of parietal.
11 Meckel's groove fuses.
12 Meckel's groove fuses for more than half the distance between mandibular symphysis and splenial.
14 Splenial shortens, fails to reach midpoint of dentary tooth row.
15 Anterior process of angular reduced.
16 Dentary becomes longer still.
17 Palatine teeth lost.
21 Clavicle becomes slender.
25 Scapular fenestra acquired.
28 Ribs lost from 4th cervicle vertebra.
29 Sternal ribs reduced to 3 pairs.

THE TROPIDURINES (Fig. 12)

Node 1. The Tropidurines.
12 Meckel's groove closes for half or less the distance between splenial and mandibular symphysis.
16 Dentary elongates.
17 Palatine teeth lost.
27 A large sternal fontanelle acquired.
41 Femoral pores lost.

Node 2. *Phymaturus + Ctenoblepharis + Liolaemus + Vilcunia*
10 Coronoid labial blade acquired.
23 Clavicle lateral margin becomes angular and projecting.
42 Preanal pores acquired. (U)
44 Middorsal scale row lost.
49 Dorsal shank nerve becomes interosseus.

Phymaturus
15 Anterior process of angular reduced.
19 Tooth crowns expand and become multicusped; premaxillary teeth become tricuspid.
24 Interclavicle median process shortens.
30 Presacral vertebrae increase to 25 or more.
46 Superciliary sutures become less oblique.
47 Subocular partly fragments.
In some:
06 Postfrontal lost.
11 Meckel's groove fuses.
28 Ribs lost from 3rd cervical vertebra.
47 Subocular becomes more fragmented.

Node 3. *Ctenoblepharis + Liolaemus + Vilcunia*
01 Nasal process of premaxilla overlapped by nasal bones.
14 Splenial reduced.
43 Transverse gular fold lost.

Ctenoblepharis
05   Lacrimal foramen moderately enlarges.
08   Bony labyrinth becomes moderately distinct.
19   Marginal tooth crowns become tapered with small secondary cusps.
23   Clavicle proximally expanded.
29   Sternal ribs reduced to 3.
30   Presacral vertebrae reduced to 23.
39   Subdigital scales become smooth.
46   Superciliaries become shorter with less oblique sutures.
47   Subocular fragments.
In some:
22   Clavicular fenestra acquired.

Node 4. *Vilcunia + Liolaemus*
15   Angular reduced.
26   Posterior coracoid fenestra acquired.

Vilcunia
11   Meckel's groove fused.
18   Pterygoid teeth lost.
28   Ribs lost from 3rd cervical vertebra.
30   Presacral vertebrae increase to 25.
42   Preanal pores lost.
 *   Posterior margin of dorsal scales with nibs (Cei and Scolaro, 1982). (U)

Liolaemus
16   Dentary further elongates.
In some:
07   Skull roof acquires moderate rugosities.
11   Meckel's groove fuses.
12   Meckel's groove fuses for more than half the distance between mandibular symphysis and splenial.
15   Angular further reduced or lost.
18   Pterygoid teeth lost.
19   Teeth expand and develop large cusps, some multicusped; premaxillary teeth tricusped.
19   Tooth crowns become tapered with small secondary cusps.
21   Clavicle becomes slender.
23   Lateral margin of clavicle reverts to a smooth curve.
28   Ribs lost from 3rd cervical vertebra.
29   Sternal ribs reduced to 3.
30   Presacral vertebrae increase to 25 or more.
42   Preanal pores lost.

Node 5. The Northern Tropidurines.
11   Meckel's groove closes and fuses for more than half the distance between mandibular symphysis and splenial. The extinct species *Leiocephalus apertosulcus* Etheridge (1965b) and *L. anonymus* Pregill (1984) are exceptions.
14   Splenial reduced.
25   Scapular fenestra acquired.
28   Ribs lost from 3rd cervical vertebra.
29   Sternal ribs reduced to 3.

Leiocephalus
01   Posterior process of premaxilla overlapped by nasal bones.
03   Adult parietal roof becomes V-shaped.
10   Coronoid labial blade acquired.
15   Anterior process of angular reduced.
16   Dentary becomes longer.
19   Tooth crowns expand, secondary cusps enlarge.
43   Transverse gular fold lost.
  *   Long free xiphisternal rods curve forward to underly xiphisternal ribs (Etheridge, 1966).
  *   First caudal fracture plane occurs at fourth or fifth caudal vertebra rather than seventh or eighth.
     (G. Pregill, pers. comm.).
In some:
02   Parietal foramen moves into frontal.
07   Skull roof becomes moderately rugose.
18   Pterygoid teeth lost.
23   Lateral margin of clavicle becomes angular.

Node 6. Unnamed.
26   Posterior coracoid fenestra acquired.

Node 7. *Proctotretus + Stenocercus + Ophryoessoides*
16   Dentary elongates.

Stenocercus
In some:
02   Parietal foramen lost.
07   Skull roof develops moderate rugosities.
08   Bony labyrinth becomes moderately distinct.
15   Angular reduced.
23   Lateral margin of clavicle becomes angular.
25   Scapular fenestra secondarily lost.
43   Transverse gular fold lost.
44   Middorsal scale row interrupted.
45   Interparietal scale lost.

Node 8. *Proctotretus + Ophryoessoides*
23   Lateral margin of clavicle becomes angular.
43   Transverse gular fold lost.

Proctotretus
30   Presacral vertebrae reduced to 23.

Ophryoessoides
08   Bony labyrinth becomes distinct.
In some:
02   Parietal foramen lost.
07   Skull roof becomes moderately rugose.
18   Pterygoid teeth lost.
25   Scapular fenestra secondarily lost.
34   Caudal autotomy lost.
45   Interparietal scale lost.

Node 9. The *Tropidurus* Group.
45 Interparietal scale greatly enlarges.

Uranoscodon
05 Lacrimal foramen moderately enlarges.
08 Osseous labyrinth becomes distinct.
27 Sternal fontanelle somewhat reduced.
46 Superciliary sutures become less oblique, superciliary crest strongly projecting, the last supercil-
    iary conspicuously enlarged.
47 Subocular fragments.
49 Dorsal shank nerve becomes interosseous.
In some:
18 Pterygoid teeth lost.
22 Clavicular fenestra acquired.
29 Sternal ribs revert to 4.

Node 10. Unnamed.
15 Angular reduced.
16 Dentary elongates.

Node 11. *Plica + Uracentron + Strobilurus.*
15 Angular further reduced.
16 Dentary further elongates.
19 Tooth crowns expand, secondary cusps enlarge.

Plica
24 Interclavicle median blade shortens.
47 Subocular fragments.
In some:
15 Angular lost.
18 Pterygoid teeth lost.
22 Clavicular fenestra acquired.
29 Sternal ribs revert to 4.

Node 12. *Strobilurus + Uracentron*
18 Pterygoid teeth lost.
23 Clavicle lateral margin becomes angular.
 * Proximal caudal scales become stout spines (Etheridge, 1968).

Strobilurus
15 Angular lost.
In some:
29 Sternal ribs revert to 4.

Uracentron
02 Parietal foramen lost.
15 Angular reduced or lost.
34 Caudal autotomy lost.
44 Middorsal scale row lost.
 * Tail becomes shorter than head-body length, covered with stout spines (Etheridge, 1968).
In some:
22 Clavicular fenestra acquired.

Node 13. *Tropidurus + Tapinurus*
43   Transverse gular fold lost.

Eastern *Tropidurus*
In some:
14   Splenial lost.
15   Angular further reduced or lost.
21   Clavicle becomes slender.
24   Interclavicle becomes shorter.
25   Scapular fenestra secondarily lost.
26   Posterior coracoid fenestra secondarily lost.
29   Sternal ribs revert to 4.
44   Middorsal scale row interrupted or lost.
  *   Scapula shortens, becomes inflected (pers. obs.).

Western *Tropidurus*
22   Clavicular fenestra acquired
In some:
15   Angular further reduced.
21   Clavicle becomes slender.
24   Interclavicle becomes shorter.
44   Middorsal scale row becomes interrupted.

Tapinurus
14   Splenial lost.
15   Angular further reduced.
18   Pterygoid teeth lost.
21   Clavicle becomes slender.
25   Scapular fenestra secondarily lost.
44   Middorsal scale row lost.
  *   Scapula shortens, becomes inflected (pers. obs.).
  *   Long, free xiphisternal rods curve forward to underly the xiphisternal ribs (Etheridge, 1966).

THE IGUANINES (Fig. 13)
Node 1. The Iguanines.
09   Supratemporal moves to the posterior surface of the supratemporal process of the parietal.
10   Coronoid develops a large lateral blade.
11   Borders of Meckel's groove fuse anterior to the splenial.
12   Meckel's groove becomes closed for more than half the distance between the splenial and the mandibular symphysis.
14   Splenial reduced, does not extend anteriorly beyond the dentary tooth row midpoint.
17   Palatine teeth lost.
19   Crowns of posterior marginal teeth expand and acquire one or more secondary cusps.
25   Scapular fenestra acquired.
28   Ribs lost from third and fourth cervical vertebrae.
33   Iguana-type caudal vertebrae acquired (U).
  *   Vertebrae acquire zygosphene-zygantrum articulations (Etheridge, 1964).
  *   Colon acquires transverse valves or folds (Iverson, 1980) (U).

Dipsosaurus
02   Parietal foramen moves into the frontal bone.

08 Outlines of osseous labyrinth become moderately distinct.
16 Dentary elongates.
In some:
18 Pterygoid teeth lost.

Brachylophus
16 Dentary elongates.
34 Caudal autotomy septa lost.
46 Length and overlap of superciliary scales reduced; possible synapomorphy with all other igua-
     nines except *Dipsosaurus*.
47 Subocular scale fragments.
 * Second and third postxiphisternal inscriptional ribs elongate (pers. obs.)
In some:
03 Adult parietal roof becomes triangular.
19 Crowns of posterior marginal teeth secondarily lose fourth cusps.

Node 2. Unnamed.
26 Posterior coracoid fenestra acquired.
46 Length and overlap of superciliary scales reduced; possible synapomorphy with *Brachylophus*.

Sauromalus
21 Clavicles become slender.
24 Posterior median process of interclavicle shortens.
44 Middorsal scale row lost.
46 Length and overlap of superciliary scales further reduced.
47 Subocular scale fragments; possible synapomorphy with Galápagos iguanas, *Iguana* and *Cyclura*.
 * Number of premaxillary teeth reduced to fewer than 7 (de Queiroz, 1987).
 * Teeth acquire numerous secondary cusps (de Queiroz, 1987); possible synapomorphy with *Iguana*
     and *Cyclura*.
 * Rostral scale becomes undifferentiated (Smith, 1946).
 * Body becomes strongly depressed (Boulenger, 1885a).
In some:
16 Dentary elongates.

Node 3. The Galápagos Iguanas
01 Premaxillary spine becomes overlapped between nasal bones.
03 Adult parietal roof becomes triangular; possible synapomorphy with *Iguana, Cyclura* and *Cteno-
     saura*.
34 Caudal autotomy septa lost.
47 Subocular scale fragments; possible synapomorphy with *Iguana, Cyclura* and *Sauromalus*.
 * Premaxillary teeth become tricuspid (de Queiroz, 1987).

Amblyrhynchus
19 Crowns of posterior marginal teeth secondarily lose fourth cusps; secondary cusps enlarge (de
     Queiroz, 1985).
24 Posterior median process of interclavicle shortens.
43 Transverse gular fold becomes weak.
46 Length and overlap of superciliary scales further reduced.
 * Separable skull osteoderms acquired in large individuals (de Queiroz, 1987).
 * Partial webbing acquired between digits (Boulenger, 1885a).
In some:
23 Lateral margins of clavicles become distinctly angular.

Conolophus
03   Adult parietal roof becomes Y-shaped; possible synapomorphy of a more inclusive group.
47   Subocular scale fragments further; possible synapomorphy of a more inclusive group.
 *   Ectopterygoid acquires contact with the palatine on the posteromedial surface of the suborbital fossa (de Queiroz, 1987).
In some:
16   Dentary elongates.
18   Pterygoid teeth lost.
22   Clavicular fenestrae acquired.
24   Posterior median process of interclavicle shortens.

Node 4. The Spiny-tailed Iguanas
03   Adult parietal roof becomes Y-shaped: possible synapomorphy of a more inclusive group.
 *   Posterolateral processes of the basisphenoid shortened (de Queiroz, 1987).
 *   Tail acquires whorls of spinous scales (Bailey, 1928).
In some:
16   Dentary elongates.
44   Middorsal scale row becomes discontinuous.

Ctenosaura
     No synapomorphies.

Enyaliosaurus
03   Adult parietal roof becomes triangular secondarily.
 *   Enlarged, spinous scales on anterodorsal surface of leg acquired (Bailey, 1928; Smith and Taylor, 1950).
In some:
03   Adult parietal roof reverts to trapezoidal.
07   Dermal skull roof acquires rugosities that reflect epidermal scale pattern.
30   Number of presacral vertebrae increases to 25.

Node 5. Unnamed.
03   Adult parietal roof becomes Y-shaped: possible synapomorphy of a more inclusive group.
47   Subocular scale fragments: possible synapomorphy of a more inclusive group.
 *   Teeth become highly cuspate (de Queiroz, 1987): possible synapomorphy with *Sauromalus*.
 *   Basisphenoid widens (Boulenger, 1890).

Cyclura
 *   Toes acquire comb scales (Barbour and Noble, 1916).
 *   Number of premaxillary teeth increases to more than 7 (de Queiroz, 1987).
In some:
44   Middorsal scale row becomes discontinuous.
 *   Tail acquires whorls of spinous scales (Barbour and Noble, 1916).

Iguana
16   Dentary elongates.
 *   Basisphenoid widens further (Boulenger, 1890).
 *   Gular crest acquired (de Queiroz, 1987).
In *I. delicatissima*:
34   Caudal autotomy septa lost.

THE BASILISCINES (Fig. 14)

02 Parietal foramen moves into the frontal bone.
03 Parietal roof becomes Y-shaped with the median crest forming a posteriorly projecting vertical blade (U).
08 Outlines of osseous labyrinth become moderately distinct.
10 Small lateral process of coronoid acquired.
12 Meckel's groove closes for at least half the distance between the anterior end of the splenial and the mandibular symphysis.
17 Palatine teeth lost.
22 Clavicular fenestrae acquired.
23 Lateral margins of clavicles become expanded ventromedially.
28 Ribs lost from third cervical vertebra, variably from fourth (polymorphism).
33 Transverse processes lost from autotomic caudal vertebrae.
41 Femoral pores lost.
47 Subocular scale fragments.
49 Muscles of dorsal shank acquire interosseous innervation.
 * Postorbital expands dorsomedially over the dorsolateral portion of the supratemporal fossa (pers. obs.).
 * Vertebrae acquire zygosphene-zygantrum articulations (Etheridge, 1964).

Basiliscus

06 Postfrontal bone lost.
19 Crowns of posterior marginal teeth expand.
28 Ribs lost from fourth cervical vertebra.
 * Midsagittal parietal crest of males extends dorsally above the plane formed by the edges of the parietal table (pers. obs.).
 * Articular surfaces of caudal zygapophyses form acute angles (pers. obs.). *
    Pedal digits acquire free dermal margins (Cope, 1900).

In some:

11 Borders of Meckel's groove fuse anterior to the splenial.
12 Meckel's groove closes for more than half the distance between the anterior end of the splenial and the mandibular symphysis.
16 Dentary elongates.
 * Males acquire dorsal crests supported by elongated neural spines on the body and tail (Maturana, 1962).

Node 2. *Corythophanes + Laemanctus*

07 Dermal roofing bones acquire rugosities that reflect the pattern of the overlying epidermal scales.
08 Outlines of osseous labyrinth become distinct.
16 Dentary elongates.
31 Ribs of last presacral vertebra reduced or lost.
34 Caudal autotomy septa lost.
46 Length and overlap of superciliary scales reduced.
 * Septomaxilla reduced (pers. obs.).
 * Sharp canthal ridge acquired (pers. obs.).
 * Parietal roof acquires a lateral shelf over the supratemporal fenestra for attachment of jaw adductor muscles (pers. obs.).
 * Jugal becomes expanded posteroventrally (pers. obs.).
 * Angular process of mandible reduced in size (pers. obs.).
 * Haemal arches expanded and compressed ventrally (pers. obs.).

Corytophanes
06   Postfrontal bone lost.
11   Borders of Meckel's groove fuse anterior to the splenial.
12   Meckel's groove closes for more than half the distance between the anterior end of the splenial and the mandibular symphysis.
14   Splenial reduced, does not extend anteriorly beyond the dentary tooth row midpoint.
46   Length and overlap of superciliary scales reduced so that they are quadrangular and nonoverlapping.
 *   Preorbital portion of skull reduced (pers. obs.).
 *   Septomaxillae further reduced, possibly absent (pers. obs.).
 *   Roof of nasal capsule between the posteromedial portions of the nasals and the anteromedial portion of the frontal remains uncovered by bone (pers. observ.).
 *   Prefrontal and postorbital bones acquire orbital processes that underlie the superciliary ridge (pers. obs.).
 *   Lateral shelves of parietal table extending over the supratemporal fenestrae become enlarged (pers. obs.).
 *   Postemporal fenestrae become closed (pers. obs.).
 *   Scapular blade lengthens so that the dorsal end of the clavicle articulates with the scapula rather than the suprascapular cartilage (pers. obs.).
In some:
28   Ribs lost from fourth cervical vertebra.
29   Sternal rib pairs reduced to three
30   Number of presacral vertebrae reduced to 23 or 22.
31   Ribs lost from last presacral vertebra.

Laemanctus
07   Dermal rugosities reflecting the overlying epidermal scales extend over the premaxilla, maxillae, nasals, prefrontals, postorbitals, and jugals.
31   Ribs lost from last presacral vertebra.
 *   Base of premaxillary spine becomes expanded so that the premaxilla is triangular rather than anchor-shaped in dorsal view (pers. observ.).
 *   Number of keels on subdigital scales reduced to one (Boulenger, 1885a).
In some:
02   Parietal foramen returns to the frontoparietal suture secondarily.
11   Borders of Meckel's groove fuse anterior to the splenial.
12   Meckel's groove closes for more than half the distance between the anterior end of the splenial and the mandibular symphysis.
14   Splenial reduced, does not extend anteriorly beyond the dentary tooth row midpoint.
28   Ribs lost from fourth cervical vertebra.
43   Transverse gular fold reduced or lost.
44   Middorsal scale row becomes interrupted or lost.

THE CROTAPHYTINES (Fig. 15)
Node 1. The Crotaphytines
06   Postfrontal bone lost.
08   Outlines of osseous labyrinth become moderately distinct.
10   Coronoid acquires a small lateral process.
16   Dentary elongates.
25   Scapular fenestra acquired.
26   Posterior coracoid fenestra acquired.
44   Middorsal scale row lost.

46 Length and overlap of superciliary scales reduced.
48 Muscles of dorsal shank acquire interosseous innervation.
 * Anterior marginal teeth become sharply pointed and recurved (pers. obs.).
 * Females acquire gravid coloration (Medica et al., 1973).

Crotaphytus
34 Caudal autotomic septa lost.
47 Subocular scale fragments.
 * Posterolateral processes of basisphenoid shorten (pers. obs.).
 * Sternal attachment points of xiphisternal rods displaced laterally (pers. obs.).
In some:
12 Meckel's groove becomes closed for less than half the distance between the anterior end of the splenial and the mandibular symphysis.
24 Posterior median process of the interclavicle reduced.
28 Ribs lost from the third cervical vertebra.
47 Subocular scale fragments further.

Gambelia
12 Meckel's groove becomes closed for more than half the distance between the anterior end of the splenial and the mandibular symphysis.
22 Clavicular fenestrae acquired.
23 Lateral margins of clavicles become expanded ventromedially.
24 Ribs lost from third cervical vertebra.
 * Posteromedial ventral process of coronoid becomes oriented posteroventrally rather than ventrally (M. Norell, pers. comm., 1982).
In some:
14 Splenial reduced, does not extend anteriorly beyond the dentary tooth row midpoint.

THE SCELOPORINES (Fig. 16)
Node 1. The Sceloporines
10 Small coronoid lateral process acquired.
12 Meckel's groove becomes closed anterior to the splenial for at least half the distance between the splenial and the mandibular symphysis.
14 Splenial reduced, does not extend anteriorly beyond the dentary tooth row midpoint.
16 Dentary elongates.
17 Palatine teeth lost.
18 Pterygoid teeth lost.
21 Clavicles become slender.
27 Sternal fontanelle becomes enlarged.
28 Ribs lost from third cervical vertebra.
30 Number of presacral vertebrae reduced to 23.
44 Middorsal scale row lost.
45 Interparietal scale enlarged.
 * Sink trap nasal apparatus acquired; nasal concha lost (Stebbins, 1948; Savage, 1958).
 * Scleral ossicle number 8 reduced in size (de Queiroz, 1982).
 * Loss of one pair of microchromosomes from the diploid karyotype (Gorman, 1973; Pauli et al., 1976).

Petrosaurus
 * Neural spines shorten (Etheridge, 1964).
In some:
12 Meckel's groove becomes closed for more than half the distance between the anterior end of the splenial and the mandibular symphysis.

Node 2. Unnamed
12 Meckel's groove becomes closed for more than half the distance between the splenial and the mandibular symphysis.
27 Sternal fontanelle further enlarged, becomes much wider than interclavicle median blade.
29 Sternal ribs reduced to three pairs.
  * Nasal valve acquired (Stebbins, 1948; Pauli et al., 1976).
  * "Shimmy" burial behavior acquired (Hall, 1973; Pauli et al., 1976).

Node 3. The *Sceloporus* Group
23 Lateral margins of clavicles acquire acute projections at the apices of their angles.
  * Body scales become keeled and imbricate (Mittleman, 1942).
  * Dorsal shank muscles acquire some interosseous innervation (Jullien and Renous-Lécuru, 1972).

Uta
08 Outlines of osseous labyrinth become moderately distinct.
  * Blue or black axillary spot acquired (Mittleman, 1942).
In some:
16 Dentary lengthens further.

Node 4. *Sceloporus* + *Sator* + *Urosaurus*
49 Dorsal shank muscles become entirely innervated by the interosseous nerve.
  * Dorsal scales become enlarged relative to laterals (Larsen and Tanner, 1975).
  * Males acquire distinct pink or blue lateral belly patches (Mittleman, 1942).

Urosaurus
08 Outlines of osseous labyrinth become moderately distinct.
19 Secondary cusps of posterior marginal teeth reduced.
In some:
16 Dentary lengthens further.

Node 5. *Sceloporus* + *Sator*
43 Transverse gular fold becomes interrupted medially.
16 Dentary lengthens further.

Sceloporus
In some:
19 Secondary cusps of posterior marginal teeth reduced or lost.
25 Scapular fenestrae acquired.
43 Transverse gular fold lost entirely.
  * Lateral body scales enlarge (Smith, 1946; Larsen and Tanner, 1975).

Sator
43 Transverse gular fold lost entirely.
In some:
08 Outlines of osseous labyrinth become moderately distinct.
16 Dentary becomes secondarily reduced.

Node 6. Unnamed (Sand Lizards + *Phrynosoma*)
04 Lacrimal bone lost.
06 Postfrontal bone lost.
24 Posterior median process of interclavicle shortens.

* Anterolateral processes of frontals covered laterally by nasals (Etheridge, 1964; Presch, 1969).
* Scleral ossicle number 6 reduced or lost (de Queiroz, 1982).
* M. adductor mandibulae externus medius extends anteriorly more than half the length of supra-temporal fossa (Costelli, 1973).
* Cranial fibers of the m. transversus insert along the xiphisternal rod and rib rather than in a sheet of fascia that attaches to the inner surfaces of the inscriptional ribs (D. Blackburn, pers. comm.).
* Half or more of the fibers of the m. costocoracoideus insert on the sternum rather than the ster-noscapular ligament (D. Blackburn, pers. comm.).
* M. obliquus internus inserts directly on the lateral portions of the sternal inscriptional ribs or directly on the bony ribs dorsal to their curvatures rather than by tendons on the sternum and the medial portions of the sternal inscriptional ribs (D. Blackburn, pers. comm.).
* M. omosternohyoideus pars superficialis differentiates (D. Blackburn, pers. comm.)
* Anterior fibers of m. retractor lateralis anterior of hemipenes reflected outwards or posteriorly before insertion (Arnold, 1984).
* Row of enlarged chinshields that increase in size posteriorly acquired (R. Montanucci, pers. comm.).

Phrynosoma
07 Dermal roofing bones acquire rugosities that reflect the pattern of the overlying epidermal scales.
19 Secondary cusps of posterior marginal teeth become reduced.
34 Caudal autotomy septa lost.
45 Interparietal scale secondarily reduced; other head scales secondarily dedifferentiate.
46 Length and overlap of superciliary scales reduced.
47 Subocular scale fragments into several of more-or-less equal size.
* Skull becomes much shorter and broader associated with shortening and widening of the premax-illary nasal process and increase in its slope, formation of an angle between anterior and poste-rior processes of nasals, widening of postorbital portion of frontal, widening of postorbitals, widening and thickening of parietal, shortening and deepening of jugals, enlargement of squa-mosals which project laterally over quadrates, vomers become triangular, shortening and broa-dening of palatines and pterygoids, expansion of ectopterygoids, quadrates become more hori-zontally oriented, reduction or loss of epipterygoids, reduction of suborbital and supratemporal fossae, shortening and broadening of braincase with straightening of basisphenoid-basioccipital suture, dorsoventral flattening of first ceratobranchials, reduction in length of second cerato-branchials (Presch, 1969).
* Frontal and prefrontals acquire enlarged processes that underlie superciliary ridges (Reeve, 1952; Etheridge, 1964; Presch, 1969; R. Montanucci, pers. comm.).
* Horns or tuberosities acquired on parietal, squamosals, and sometimes other skull elements (Reeve, 1952; Etheridge, 1964; Presch, 1969; R. Montanucci, pers. comm.).
* Retroarticular processes become vertically flattened or are lost (Etheridge, 1964; Presch, 1969).
* Body becomes wide and depressed associated with shorteneing and broadening of presacral verte-brae and sternum, elongation of thoracic ribs, transverse orientation of pubes, shortening of ilia which also become stouter (Etheridge, 1964; Presch, 1969).
* Second pair of sacral diapophyses become more slender (Presch, 1964).
* Tail becomes shorter associated with reduction in number of cuadal vertebrae to less than 25 (Etheridge, 1964; Presch, 1969; R. Montanucci, pers. comm.).
* Sternal fontanelle enlarged to extend anteriorly past widest part of sternum (Reeve, 1952; Ethe-ridge, 1964; Presch, 1969; R. Montanucci, pers. comm.).
* Posterior median process of interclavicle further shortened or lost (Etheridge, 1964; Presch, 1969, R. Montanucci, pers. comm.).
* Xiphisternal rib connections reduced to one or none (Etheridge, 1964; Presch, 1969).

* Suprascapulae reduced in width dorsally, rectangular rather than fan-shaped (Presch, 1969).
* Phalanges lots from digits 4 and 5 of manus (phalangeal formula 2,3,4,4,2) and digit 5 of pes (2,3,4,5,3) (pers. obs.).
* Superficial fascia at posterodorsal corner of infratemporal fossa reduced (Costelli, 1973).
* M. pseudotemporalis reduced in size (Costelli, 1973).
* M. obliquus externus arises directly from ribs rather than via intercostalis tendons (D. Blackburn, pers. comm.).
* M. obliguus externus pars profundus I and pars profundus II lost (D. Blackburn, pers. comm.).
* M. intercostales interni entirely absent between bony portions of ribs (D. Blackburn, pers. comm.).
* Most fibers of m. costocoracoideus insert directly on sternum rather than on sternoscapular ligament (D. Blackburn, pers. comm.).
* M. obliquus internus inserts on bony portions of ribs rather than on inscriptional cartilages (D. Blackburn, pers. comm.).
* M. constrictor colli becomes narrow but robust (D. Blackburn, pers. comm.).
* Extensive development of m. branchiohyoideus (D. Blackburn, pers. comm.).
* M. sternohyoideus pars superficialis becomes separate from m. omohyoideus throughout its length (D. Blackburn, pers. comm.).
* Dorsal scales become heterogeneous, with enlarged spinous scales interspersed with smaller scales (Reeve, 1952; R. Montanucci, pers. comm.).
* Dorsal scales on body and tail not arranged as distinct transverse rows.

In some:
01 Premaxillary spine becomes covered between nasal bones.
12 Meckel's groove opens secondarily.
13 Splenial bone lost.
14 Splenial bone becomes further reduced.
15 Angular bone undergoes various stages of reduction culminating in its loss.
16 Dentary lengthens further.
19 Secondary cusps of posterior marginal teeth lost.
28 Ribs lost from fourth cervical vertebra.
29 Sternal ribs reduced to two pairs.
30 Number of presacral vertebrae secondarily increased to 24.
31 Ribs become fused to posterior presacral vertebrae.

Node 7. The Sand Lizards
05 Lacrimal foramen enlarges.
08 Outlines of osseous labyrinth become moderately distinct.
25 Scapular fenestrae acquired.
28 Ribs lost from fourth cervical vertebra.
  * Dorsal head scales become somewhat dedifferentiated (pers. obs.).
  * Labial scales become elongate, keeled, obliquely oriented, and overlap one another (Smith, 1946; Axtell, 1958).
  * Black spots or bars acquired on the sides of the body and the ventral surface of the tail (Smith, 1946; Axtell, 1958; Clarke, 1965).
  * Lower jaw becomes countersunk (Smith, 1946).
  * Median, triangular postmental scale acquired (Smith, 1946).
  * Head becomes scoop-shaped (Smith, 1946).

Uma
45 Interparietal scale secondarily reduced; head sc   idarily further dedifferentiated.
  * Fringe scales acquired on digit margins (Cope, 1866).

Node 8. Unnamed (*Callisaurus* + The Earless Lizards)

19 Secondary cusps of the posterior marginal teeth become reduced.
 * Stapes becomes thicker and abuts against the posterior edge of the quadrate (Earle, 1961, 1962).
 * Females acquire gravid coloration (Clarke, 1965).

Callisaurus
16 Dentary lengthens further.
 * Limbs become very long (Pianka and Parker, 1972; pers. obs.).
In some:
 * Fringe scales acquired on the digit margins (Cope, 1896; Schmidt, 1922; Schmidt and Bogert, 1947).

Node 9. The Earless Lizards
 * External tympanic membrane becomes covered by scales (Earle, 1961, 1962).
 * Stapes become yet thicker (pers. observ.).
 * M. intermandibularis rostralis pars superficialis secondarily fails to differentiate (Camp, 1923; Blackburn, unpubl.).
 * M. constrictor colli reduced in width and thickness (Blackburn, unpubl.).

Cophosaurus
 * Lateral bars become more posteriorly placed (Clarke, 1965).

Holbrookia
16 Dentary lengthens further.
 * Fenestra rotunda of middle ear reduced (pers. obs.).
 * Anterior fibers of m. depressor mandibulae insert on the quadrate rather than the dorsal surface of the neck (Earle, 1961, 1962).
 * Body size reduced.
In some:
 * Tail spots secondarily lost (Clarke, 1965).

APPENDIX 5

Listed below are the apomorphies that arise at each node and terminal taxon in the computer generated tree given in Fig. 17.

STEM NO.	CHARACTERS
112	16.1, 28.1, 44.1, 44.2, 49.1
111	10.1, 46.1, 47.1
110	32.1, 36.1, 36.2, 36.3, 37.1, 37.2, 41.1
109	17.1
108	6.1, 8.1, 25.1, 26.1
107	8.1, 11.1, 12.1, 12.2, 14.1, 16.2, 17.1, 29.1
106	12.1, 14.1, 27.1, 27.2, 29.1
105	5.1, 10.2, 32.1, 46.2, 47.2
104	8.2, 35.1, 39.1
103	18.1, 21.1, 49.0
102	10.2, 41.1, 42.1
101	5.2, 7.1, 19.1a, 44.0, 44.0
100	7.1, 19.1b, 23.1a, 26.1, 36.2, 46.1
99	10.1, 10.2, 14.2, 15.1, 15.2, 15.3, 15.4, 20.1, 28.2, 31.1a, 40.1, 43.1, 43.2
98	30.1a, 45.1a, 46.0, 47.0
97	29.0, 36.1, 37.1, 38.1

96	7.2, 34.1
95	7.1, 34.1, 46.1, 47.1, 47.2
94	8.1, 12.2
93	7.2, 28.0, 39.0
92	17.0
91	7.2, 21.1, 37.3
90	23.1a
89	4.1, 5.1, 6.1, 24.1, 25.1, 28.2
88	34.1, 46.2, 47.1, 47.2
87	17.0, 19.0, 44.1
86	49.1
85	19.1b
84	8.0, 43.1
83	16.2
82	16.2
81	10.0, 11.1, 26.1, 30.0, 41.1, 49.0
80	18.0, 21.0, 44.0, 44.1, 45.0
79	43.2
78	25.1
77	15.1, 23.0
76	45.1a
75	1.1, 10.1, 10.2
74	29.0
73	12.1, 15.2, 25.0, 29.0, 44.1, 44.2, 49.1
72	43.0, 43.1
71	15.0, 16.1, 27.1, 46.1, 47.1, 47.2
70	5.1, 15.2, 15.3, 19.1a
69	9.1, 9.2, 10.1, 10.2, 19.1a, 27.0, 28.2, 33.1a, 41.0, 45.0
68	8.1, 8.2, 49.1
67	18.1
66	16.0, 19.2a
65	6.1, 7.1, 25.0, 26.0, 27.0, 33.1b, 34.1, 45.0
64	47.0, 47.1
63	3.1, 3.2, 3.3, 10.1, 22.1, 23.1b
62	3.1, 3.2
61	11.0, 12.1, 14.0
60	47.1, 47.2
59	1.1, 34.1

TERMINAL TAXA	CHARACTERS
Phrynosoma	4.1, 6.1, 7.1, 7.2, 12.0, 19.1b, 24.1, 34.1, 47.2
Uma	45.0
Urosaurus	19.1b
Sator	43.2
Sceloporus	12.1
Petrosaurus	27.1, 29.0
Dipsosaurus	2.1a, 8.1, 16.1, 26.0, 46.0
Sauromalus	21.1, 24.1, 44.1, 44.2, 46.2
Enyaliosaurus	44.1
Iguana	16.1

Brachylophus	26.0, 34.1
Amblyrhynchus	3.1, 19.1a, 24.1, 43.1, 46.2, 47.1
Corytophanes	2.1a, 46.2
Laemanctus	6.0, 7.2, 31.1a
Basiliscus	2.1a, 7.0, 8.1, 16.0, 19.1a, 28.2, 34.0, 46.0
Gambelia	12.1, 12.2, 22.1, 23.1b, 47.0
Crotaphytus	28.0, 34.1
Tapinurus	14.2, 15.1, 15.2, 15.3, 23.0, 43.2
Eastern *Tropidurus*	25.0, 26.0
Western *Tropidurus*	22.1
Uracentron	2.1c, 29.1, 34.1, 44.1, 44.2
Strobilurus	15.4
Plica	24.1, 47.1, 47.2
Uranoscodon	5.1
Leiocephalus	3.1, 19.1a, 26.0
Ophryoessoides	8.1, 8.2
Stenocercus	23.0, 43.0
Proctotretus	30.1a
Vilcunia	16.1, 18.1, 23.1a, 30.1b
Liolaemus	11.0, 28.0
Ctenoblepharis	1.1, 5.1, 8.1, 19.1b, 23.1b, 30.1a, 39.1, 43.1, 43.2, 47.2
Phymaturus	14.0, 15.1, 19.1a, 19.2a, 23.1a, 24.1, 28.0, 29.0, 30.1b
Chalarodon	6.1, 9.1, 15.1, 21.1, 25.1, 32.2, 44.0, 44.1, 48.1
Oplurus	28.2, 32.2, 48.1
Hoplocercus	19.1b, 34.1
Morunasaurus	45.1b
Enyaliodes	19.2a
Anolis	16.1, 33.1c, 37.3, 44.0, 44.1
Chamaelinorops	6.1, 13.1, 18.1, 23.1a
Phenacosaurus	18.1, 29.2, 30.1a, 30.2a, 44.0, 44.1, 46.2
Chamaeleolis	3.1, 3.2, 3.3, 15.3, 17.0, 19.1b, 19.2b, 24.1
Aptycholaemus	43.1, 43.2
Urostrophus	19.0
Aperopristis	44.0, 44.1
Leiosaurus	17.0
Diplolaemus	18.1
Pristidactylus	8.1
Enyalius	31.1a, 33.1b, 44.0
Polychrus	7.2, 16.0, 21.1, 28.2, 29.1, 29.2, 30.1b, 31.1b, 32.1, 35.1, 41.0, 43.1, 43.2, 46.2, 47.1