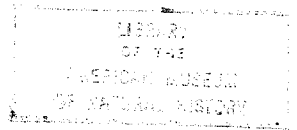


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The Earliest Iguanine Lizard (Reptilia: Squamata) and its Bearing on Iguanine Phylogeny

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ABSTRACT

A new Early Miocene iguanian lizard from New Mexico is described. This specimen is the oldest demonstrable member of the iguanine clade as determined by its possession of derived characters of Iguaninae as a whole and those of its two primary subclades. The phylogenetic relationships among iguanines are reevaluated with the inclusion of this and another recently described fossil

iguanine. The fossil taxa increase the amount of phylogenetic resolution, and a single most parsimonious tree is found. The new fossil appears to be the sister group of *Dipsosaurus* and the clade formed by both taxa is the sister group of the remaining iguanines. Monophyly of the new taxon is poorly supported.

INTRODUCTION

Iguaninae (de Queiroz, 1987) equivalent to Iguanidae of Frost and Etheridge (1989), is a monophyletic taxon of primarily herbivorous lizards (squamate reptiles) reaching moderate to large maximum body sizes (ca. 550 mm SVL). Iguanines are distributed in the New World from the southwestern United States throughout most of Central America and northern South America, the West Indies, and in the Old World on islands in

the Fiji and Tonga groups (Etheridge, 1982; de Queiroz, 1987; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989). Despite the large size and sometimes dense populations of certain extant iguanines, recent reviews of purported iguanine fossils (Estes, 1983; de Queiroz, 1987) reveal a sparse fossil record. Although several older fossils may represent remains of iguanines (Olson, 1937; Estes, 1963; Stevens, 1977), until now the oldest

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ones that can be assigned to this taxon unequivocally are Late Pliocene in age (de Queiroz, 1987; Norell, 1989). The discovery of an Early Miocene fossil iguanine, reported here, is therefore significant in that it extends the clade's temporal record and provides new information about character transformations and phylogenetic relationships at the base of the iguanine clade.

GEOLOGICAL OCCURRENCE

The specimen was collected in the Tesuque Formation, Skull Ridge Member, by J. C. Blick in 1940. It is part of the extensive Frick Collection, now housed in the American Museum of Natural History. The type locality lies in Santa Fe County, New Mexico (see Galusha and Blick, 1971, figs. 2, 9, and 17).

The Skull Ridge Member of the Tesuque Formation has produced a diverse early Barstovian mammalian fauna (Galusha and Blick, 1971; Tedford, 1981). Current estimates indicate that the Barstovian Land Mammal Age is between 11.6 and 16.5 million years. This places the Barstovian in the early middle Miocene era (Tedford et al., 1987).

The Tesuque beds have also produced a diverse but unstudied reptile fauna. Included in the assemblage are common late Tertiary North American lizard taxa (see Norell, 1989), including *Elgaria*-like gerrhonotines, *Eumeces*-like skinks, and *Ameiva/Cnemidophorus*-like teiids (Norell, 1989). In addition to these is a well-preserved cranium of small undescribed iguanian.

SYSTEMATIC PALEONTOLOGY

REPTILIA
SAURIA
LEPIDOSAURIA
SQUAMATA
IGUANIA
IGUANINAE

Armandisaurus explorator, new taxon

Figures 1 and 2

HOLOTYPE: AMNH-FAM 8799. (AMNH = American Museum of Natural History; FAM = Frick American Museum).

ETYMOLOGY: *Armand* (French), proper name, + *sauros* (Greek), lizard, and *explorator* (Latin), one who investigates, after our

friend and colleague, Jacques Armand Gauthier (the famous French explorer), in honor of his contributions to the study of reptile phylogeny and to express our thanks for bringing the specimen to our attention.

LOCALITY OF HOLOTYPE: White Operation Ridge, Santa Fe County, New Mexico, USA.

DATE COLLECTED: 1940, by J. C. Blick.

DIAGNOSIS: Although *Armandisaurus explorator* differs from all other iguanines, monophyly of this taxon is dubious. It possesses three characters that are interpretable as diagnostic apomorphies: a small but distinct ventral process of the squamosal, the absence of pterygoid teeth, and a reduced number of premaxillary teeth (fewer than 7); however, the synapomorphic status of these characters is ambiguous. The first may be a retained ancestral condition, and a distinct ventral process is also present in *Amblyrhynchus* and *Iguana*. The second character is variable in *Dipsosaurus* and pterygoid teeth are also absent in most *Conolophus*. The third character, number of premaxillary teeth, is based on population modes and thus must be scored tentatively in a single specimen; a reduced number of premaxillary teeth also occurs in *Sauromalus* and *Ctenosaura defensor*. *Armandisaurus* differs from *Dipsosaurus* and all other iguanines except *Brachylophus* in having a broad interpterygoid vacuity. It differs from *Brachylophus* and all other iguanines except *Dipsosaurus* in lacking a lateral process of the palatine posterior to the infraorbital foramen.

DESCRIPTION OF THE HOLOTYPE: Our purpose is not to describe the anatomy of the holotype exhaustively. Rather, we will concentrate on specific features of phylogenetic interest, which are relevant to determining the relationships of *A. explorator*. This discussion follows the terminology of iguanid cranial morphology provided by Oelrich (1956) and de Queiroz (1987).

The articulated cranium and mandibles are preserved in a lithic sandstone nodule. The skull and mandibles are well preserved, and all of the major cranial elements are present. Parts of seven cervical vertebrae are present posterior to the occiput. The ventral portion of the skull was not freed from the enclosing matrix because this would risk severely damaging the specimen. Rather than attempting to free the entire skull from the matrix, we

concentrated on preparing specific features of interest.

CRANIUM: The cranium is subtriangular in outline and relatively short (figs. 1, 2). Its domed profile more closely resembles that of most other iguanines than the dorsoventrally compressed skull of *Sauromalus*. The dorsal surface of the rostrum has been eroded and much of the palatal region cannot be exposed without damaging the specimen. The ventral surface of the premaxilla is not exposed. Anteriorly the premaxilla is broadly convex, rather than flat. A thin nasal process slopes backward; it cannot be determined whether this process was covered by the nasals as in *Amblyrhynchus* and *Conolophus* because of damage to the nasal bones. Six premaxillary teeth are present, which are trifold with small lateral cusps.

The nares are relatively small; that is, they are not enlarged as in some species of *Cyclura*. Most of both nasals are obliterated by weathering but impressions in the matrix indicate that they were relatively short. No frontonasal openings are apparent near the frontonasal suture; but their absence cannot be determined with certainty. The septomaxilla is hidden inside the unprepared nasal capsule.

Although the anterior portions of the prefrontals are absent, matrix impressions indicate that they did not border the nares as in some *Cyclura*. Inside the orbit, on the anterior orbital wall, the prefrontal is separated from the jugal by contact of the lacrimal and palatine posterior to the lacrimal foramen.

The fused frontals are narrow between the orbits and longer than wide. The parietal foramen lies mostly within the frontal with its posteriormost end contacting the frontoparietal suture. The lateral edge of the frontal forming the dorsal orbital border is smoothly curved. The cristae cranii form a continuous arc from the frontal onto the prefrontals. Small postfrontal bones lie at the posterodorsal angle of the orbits. A postfrontal "knob" is not apparent.

The postorbital contacts the parietal behind the postfrontal; it is excluded from the infratemporal fenestra by contact of the squamosal and the jugal. The parietal roof is short and trapezoidal and lacks a midsagittal crest posteriorly; these features change ontogenetically in iguanians, and the magnitude of

change is correlated with body size (de Queiroz, 1987). The supratemporal wraps ventrally around the posterior supratemporal process of the parietal, and as in all iguanines, a greater amount of the bone is exposed posteromedially than anterolaterally.

Much of the maxillae has been destroyed by weathering. They are tall, concomitant with the domed profile of the skull, and contain a row of supralabial foramina. The lateral surfaces of the maxillae are more or less flat, rather than convex, ventral to the supralabial foramina. Anteriorly, the premaxillary process of each maxilla is horizontal, rather than being curved dorsally as in *Ctenosaura*. The lacrimal is of moderate relative size, that is, not as small as in *Amblyrhynchus* and *Conolophus*.

The jugal forms the ventral margin of the orbit and contacts the squamosal posteriorly along the ventral margin of the temporal bar. The squamosal is long and thin with a distinct ventral process posteriorly; this process is proportionally smaller than those of *Iguana* and *Amblyrhynchus*.

As indicated above, much of the palate could not be freed of matrix without severely damaging the specimen. Nevertheless, several phylogenetically informative characters (de Queiroz, 1987) are visible. The infraorbital foramen is bordered dorsally by a lateral process of the palatine that contacts the jugal and ventrally by the maxilla (fig. 3); there is no lateral process of the palatine posterior to the foramen. The medial borders of the pterygoids are not strongly curved anterior to the basiptyergoid articulation, and the interptyergoid vacuity thus narrows gradually. The pterygoids also lack teeth, and they appear to separate the palatines and ectopterygoids from mutual contact near the posteromedial borders of the suborbital fenestrae.

Only the floor of the braincase has been exposed. The parabasisphenoid rostrum cannot be seen in its entirety, but appears to be relatively long, at least in comparison with that of *Amblyrhynchus*. The cristae ventrolaterales are constricted posterior to the basiptyergoid processes. Posterolateral processes of the parabasisphenoid are large, nearly reaching the sphenoccipital tubercles.

MANDIBLE: *Armandisaurus explorator* has seven pairs of mandibular bones, as do all other iguanines. The splenial is relatively short

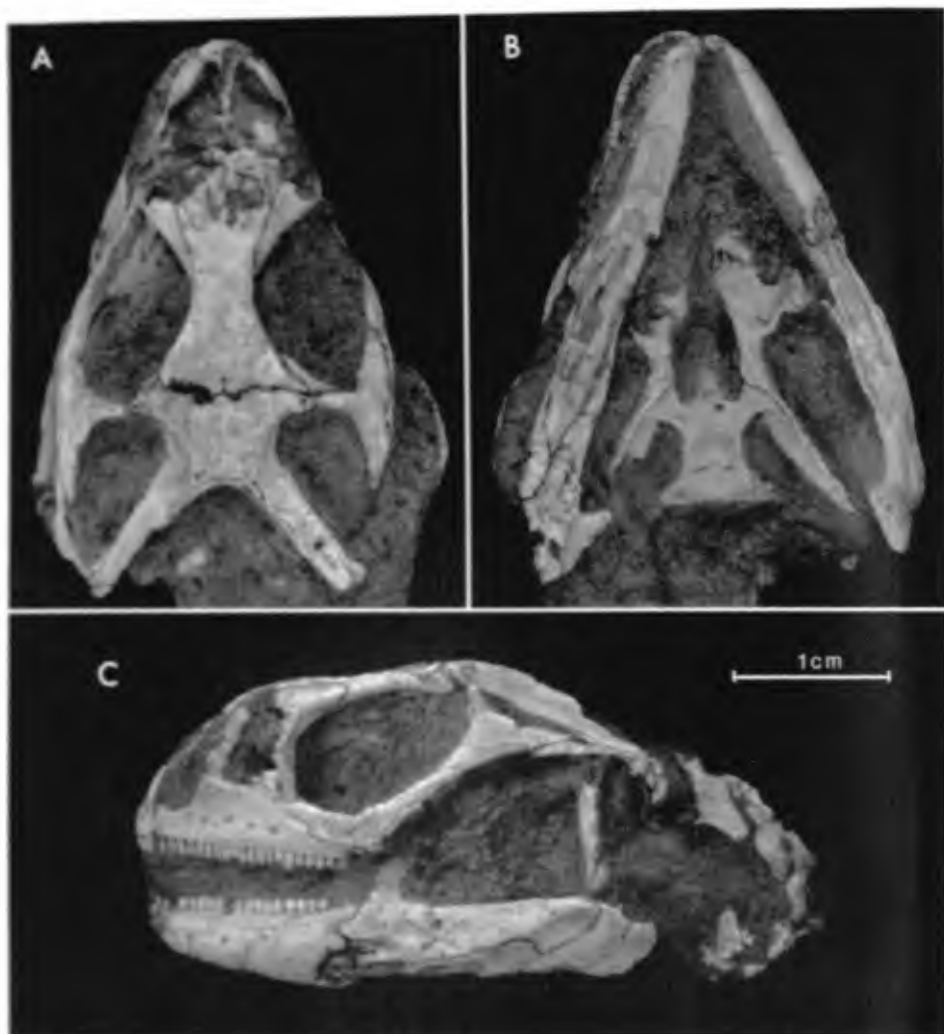


Fig. 1. The holotype specimen of *A. explorator*. (A) Dorsal view of cranium. (B) Ventral view of cranium. (C) Lateral view of cranium.

anteroposteriorly, and Meckel's groove is closed and fused. A row of mental foramina lie in a line approximately halfway between the dorsal and ventral borders of the dentary, a condition found in all other iguanines except *Amblyrhynchus* (de Queiroz, 1987). The dentary and the surangular lie at approximately the same level anterior and posterior to the coronoid eminence. Although visible only on the right side and incomplete ventrally, the splenial appears to be of about the same relative size as in other iguanines except

Sauromalus. The anterior inferior alveolar foramen lies at the anterior end of the splenial, on its suture with the dentary. The labial process of the coronoid is distinct but small, extending less than halfway down the lateral surface of the mandible. Posterolaterally the angular is broadly exposed and is wide posteriorly. The anterior extent of the surangular on the lateral surface of the mandible cannot be determined, nor can it be determined whether the surangular is exposed below the coronoid lingually. Posteriorly a large angular

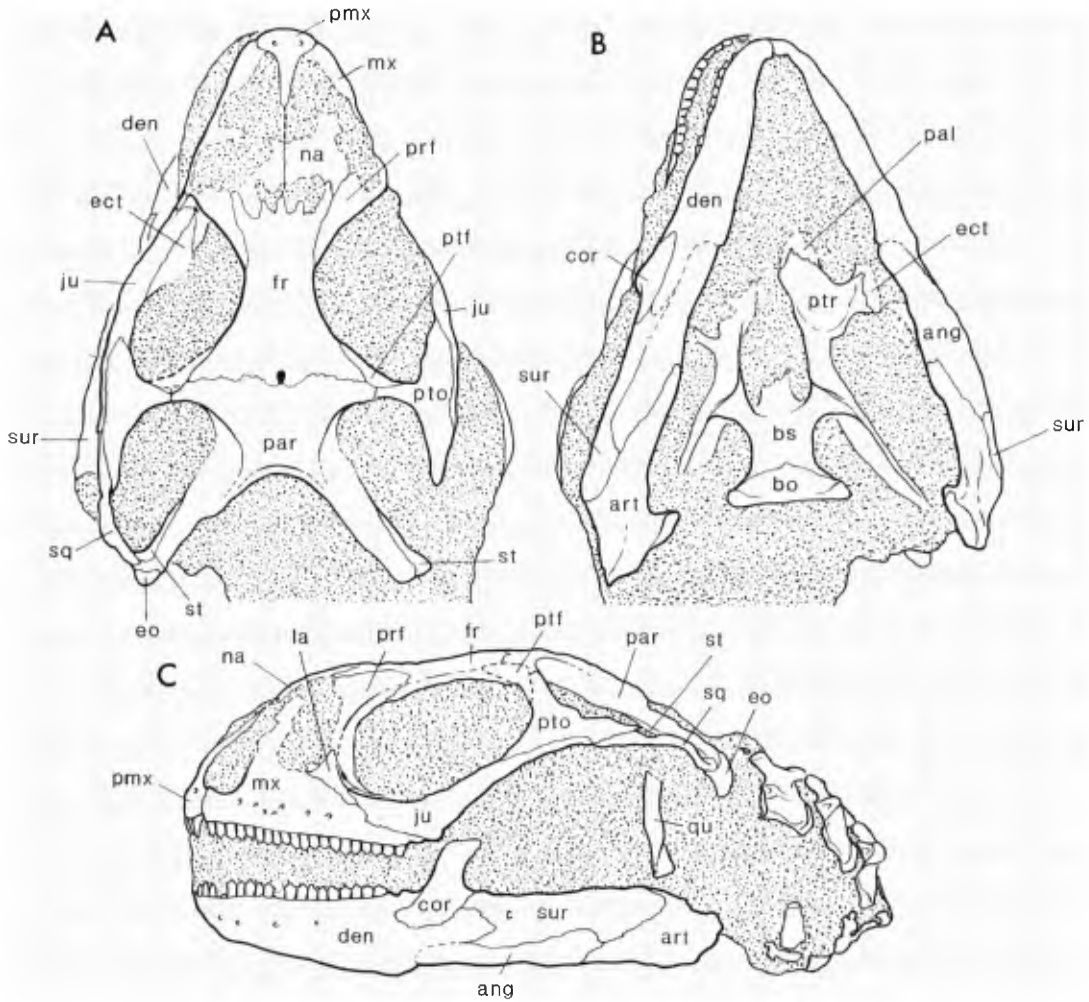


Fig. 2. Schematic representation of *A. explorator*. (A) Dorsal view of cranium. (B) Ventral view of cranium. (C) Lateral view of cranium.

Abbreviations: ang angular, art prearticular, bo basioccipital, bs basisphenoid, cor coronoid, den dentary, ect ectopterygoid, eo exoccipital, fr frontal, ju jugal, la lacrimal, mx maxilla, na nasal, pal palatine, par parietal, prf prefrontal, pmx premaxilla, ptr pterygoid, pto postorbital, qu quadrate, sur surangular, sq squamosal, st supratemporal.

process is present and the retroarticular process is triangular, as in most iguanines.

TEETH: The teeth are heterodont. The anterior teeth are weakly tricuspid and blunt. The posterior marginal teeth appear trifid with flaring tooth crowns (fig. 4), resembling the condition in some fossil *Dipsosaurus* species (see Norell, 1989: fig. 8). When small lateral cusps are present in other taxa, however, they are often visible only in lingual view. It

is not possible to rule out the presence of additional cusps, because the lingual surfaces of *Armandisaurus* are not visible.

VERTEBRAE: Parts of seven cervical vertebrae are exposed and resemble those of most iguanines in having relatively high neural spines. Like the vertebrae of *Dipsosaurus*, the zygosphenes are connected to the prezygapophyses by a continuous arc of bone (compare fig. 5 with de Queiroz, 1987: fig. 36). In

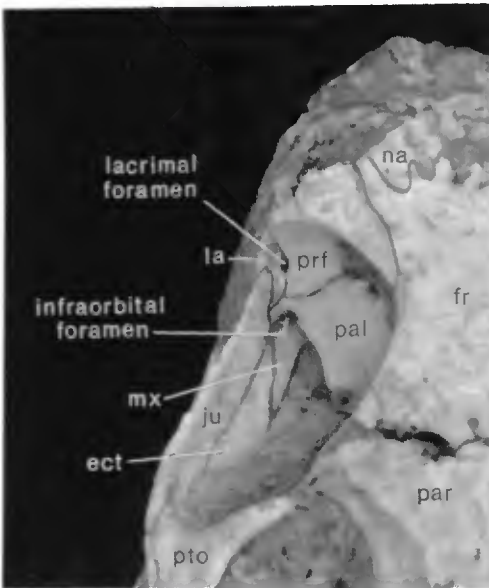


Fig. 3. Arrangement of bones surrounding the infraorbital foramen on the left anterior floor of the orbit in postero-oblique view. Compare with de Queiroz (1987: fig. 17). Abbreviations same as in fig. 2.

other iguanines, the prezygapophyses and the zygosphenes are separated by a deep notch (de Queiroz, 1987).

DISCUSSION

Referral of *Armandisaurus* to *Iguania* is based on its possession of all 6 of the 14 diagnostic apomorphies (Estes et al., 1988)

that can be scored in this fossil: fused frontals, frontals strongly constricted between orbits, broad frontal shelf underlying nasals, post-frontal reduced and confined to orbital margin, parietal foramen anteriorly displaced (at or anterior to the suture), fingerlike angular process of prearticular. Prefrontal bosses ("knobs"), another supposedly diagnostic apomorphy of *Iguania* (Estes et al., 1988), are not evident in *Armandisaurus*, but this is true of many iguanians, especially small ones.

Referral of *Armandisaurus* to Iguaninae is based on its possession of both (out of 5) diagnostic apomorphies (de Queiroz, 1987) that can be scored in this fossil: crowns of posterior marginal teeth laterally compressed and anteroposteriorly flared, supratemporal lies primarily on posteromedial surface of supratemporal process of parietal.

Armandisaurus possesses several other derived characters of iguanines, but these characters are diagnostically ambiguous because they are not restricted to iguanines (Etheridge and de Queiroz, 1988). The dentary portion of Meckel's groove is closed and fused anterior to the splenial. The splenial does not extend anterior to the dentary tooth row midpoint. Palatine teeth are absent. Zygosphenzygantrum articulations are present. In addition, a labial process of the coronoid is present, but we interpret this character as plesiomorphic for *Iguania* (contra Etheridge and de Queiroz, 1988).

In order to explore the phylogenetic affinities of *A. explorator* within Iguaninae, we

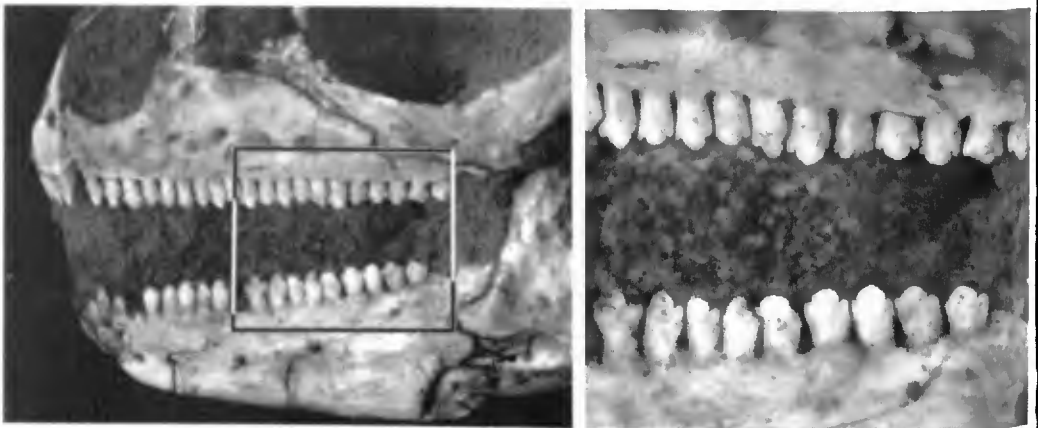


Fig. 4. Left cheek teeth of *A. explorator*. Enlarged area on right is 2× that on left.

modified de Queiroz's (1987) original data set for reanalysis (a discussion and summary of this new matrix are provided in the appendix). This data set was analyzed using PAUP version 3.0 for the Macintosh. The branch-and-bound option was used, guaranteeing that the most parsimonious tree would be found. The trees were rooted with a hypothetical ancestor constructed from the polarity decisions used by de Queiroz (1987) based on outgroup conditions in a series of unresolved outgroup taxa. This ancestor includes some characters that could not be polarized. Characters were treated as unordered, unless specified differently, and variation within basic taxa was treated as requiring additional state changes.

Two analyses were performed. One duplicated de Queiroz's original study (which was restricted to extant species) with negligible modifications to his data matrix (see appendix). The analysis of 90 characters (minimum of 102 character transformations) restricted to the extant taxa resulted in two trees with lengths of 158+ steps (fig. 6). The two trees differ only in the placement of *Dipsosaurus* and *Brachylophus* relative to the remaining iguanine taxa. These taxa swap places as the sister group to the remaining Iguaninae. These two trees are topologically identical to those recovered by de Queiroz (1987). A second analysis included the fossil taxa *A. explorator* and *Pumilia novaceki** [Norell, 1989; the asterisk (*) indicates that evidence for monophyly is lacking (Gauthier et al., 1988)]. Inclusion of the fossil taxa *Armandisaurus* and *P. novaceki** resulted in the recovery of a single tree of 161+ steps (fig. 7). This tree is identical, apart from the inclusion of the fossil taxa, to one of the two trees recovered in the analysis without fossils.

Enough characters are present on the type specimen of *A. explorator* to place it in a specific phylogenetic position within the iguanines. Within iguanines, *A. explorator* is the sister group to *Dipsosaurus* by virtue of two unambiguous character changes [an anteriorly located parietal foramen (character 13) and the absence of a lateral process of the palatine posterior to the infraorbital foramen (22)], and an additional eight ambiguous characters (9, 18, 28, 46, 47, 58, 79, 80), six of which could not be scored in *Armandi-*

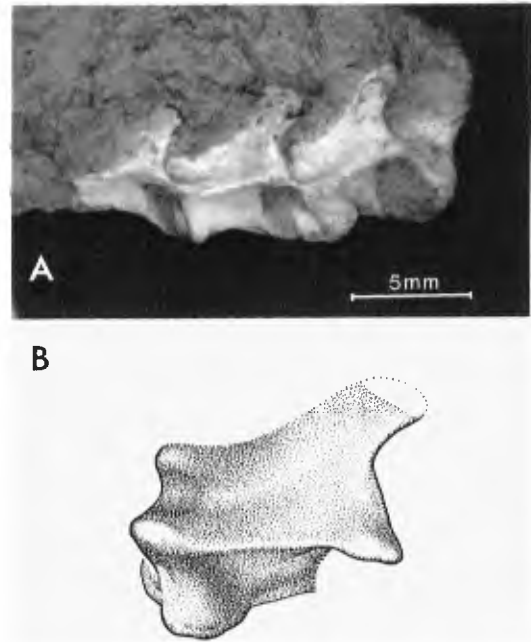


Fig. 5. Cervical vertebra of *A. explorator* showing the condition in which the prezygophyses and the zygosphenes are connected by a continuous arc of bone. Bottom is restored third cervical in lateral aspect.

saurus (9, 28, 46, 58, 79, 80). Character ambiguity results from the multiple equally parsimonious possible optimizations of homoplasious characters and missing data. The fossil *Pumilia novaceki** is placed as the sister group to *Iguana* on the basis of the synapomorphic presence of two unambiguous characters—an enlarged ventral process of the squamosal (18) and serrate marginal teeth (42)—as well as seven ambiguous characters (45, 57, 73, 77, 83, 84).

The incorporation of fossils into other analyses has demonstrated that fossil taxa sometimes can modify phylogenetic conclusions based exclusively on extant taxa (Gauthier et al., 1988; Doyle and Donoghue, 1987; Donoghue et al., 1989). Most of the studies demonstrating phylogenetic rearrangement with the addition of fossils have dealt with lineages that diverged much earlier than those in the present study.

In the present case, the inclusion of fossils does not contradict the phylogeny based on extant taxa alone, but it does increase resolution. Only 32 percent of de Queiroz's char-

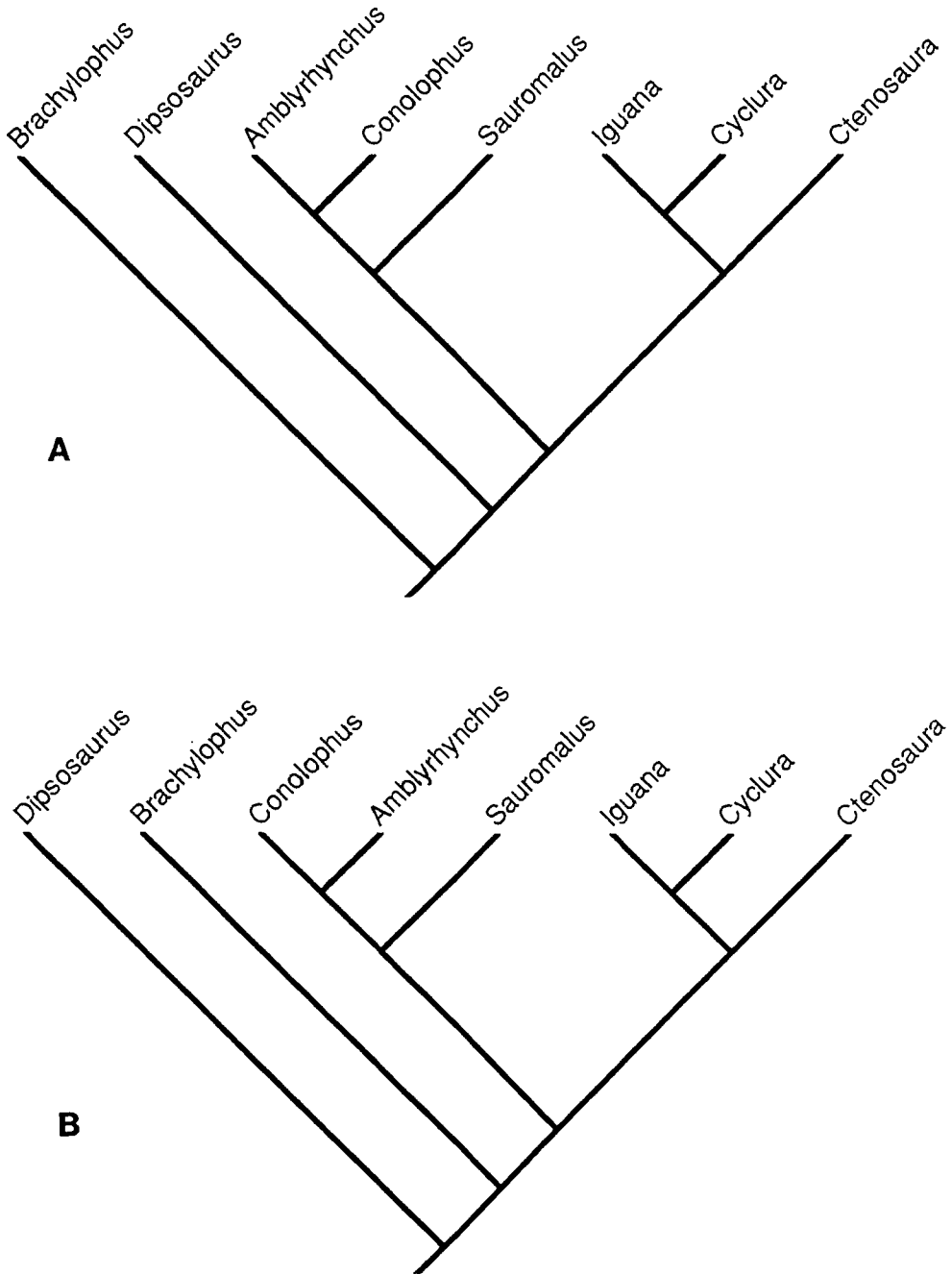


Fig. 6. Two minimum-length trees found during reanalysis of de Queiroz's (1987) data for extant iguanines. CI (excluding uninformative characters) = 0.543. The positions of *Sauromalus* and *Ctenosaura* are dubious (de Queiroz, 1987).

acters could be scored in *Armandisaurus* and 30 percent in *Pumilia novaceki**. These fossils clarify the relationships among *Brachylophus*, *Dipsosaurus*, and the remaining igua-

nines. *Armandisaurus*, not *P. novaceki**, is critical to resolving these relationships. If *Armandisaurus* is included but *P. novaceki** is not, the same topology is recovered as if both

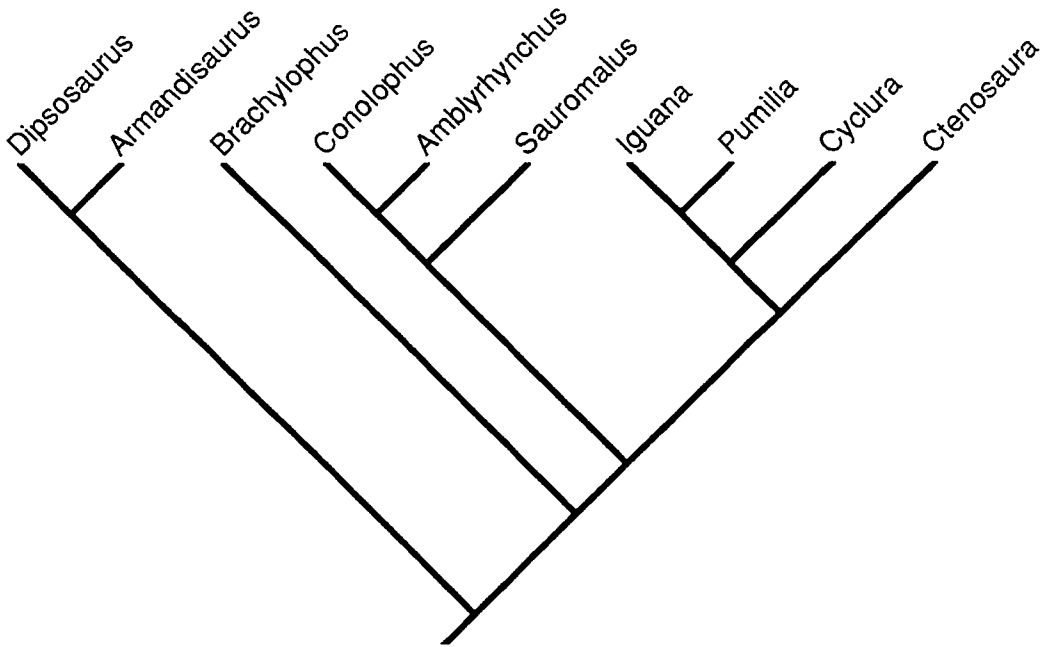


Fig. 7. Minimum-length tree found by analysis of extant and extinct iguanines. CI (excluding uninformative characters) = 0.527. The positions of *Sauromalus* and *Ctenosaura* are dubious as discussed by de Queiroz (1987).

fossil taxa were included. However, if *P. novaceki** is included without *Armandisaurus*, the relationships in question remain unresolved.

The resolution of relationships at the base of the iguanine clade provided by inclusion of *Armandisaurus* results from the particular combination of characters in this fossil. In addition to sharing several derived characters with *Dipsosaurus*, *Armandisaurus* appears to retain the ancestral form of the interpterygoid vacuity, a condition retained also by *Brachylophus*. Before discovery of *Armandisaurus*, the derived condition of the interpterygoid vacuity shared by all iguanines except *Brachylophus* was interpretable as a synapomorphy of a group represented by all iguanines except *Brachylophus* (fig. 6A). An equally parsimonious hypothesis, however, had *Dipsosaurus* rather than *Brachylophus* as the sister group of all other iguanines (fig. 6B). Under this alternative hypothesis, the derived condition of the interpterygoid vacuity exhibits some form of homoplasy: either it arose independently in *Dipsosaurus* and in the common ancestor of *Amblyrhynchus* through *Ctenosaura* (Iguanini), or it arose once in the

common ancestor of all iguanines and reverted to the ancestral form in *Brachylophus*. Because *Armandisaurus* retains the ancestral condition of the interpterygoid vacuity and also appears to be the sister group of *Dipsosaurus*, the derived morphology of the interpterygoid vacuity in *Dipsosaurus* and Iguanini is most parsimoniously interpreted as homoplasy regardless of whether *Brachylophus* or *Dipsosaurus* is the sister group of other iguanines. Thus, in removing the derived condition of the interpterygoid vacuity as potential support for the hypothesis that *Brachylophus* is the sister group of other iguanines (fig. 6A), the evidence favors the alternative that *Dipsosaurus* (plus *Armandisaurus*) is the sister group of all other iguanines (fig. 7).

The formal naming of *Armandisaurus explorator* presents a common problem in the taxonomy of fossils. Although a newly discovered fossil may be distinct from all currently recognized taxa, evidence that it represents a separate monophyletic taxon may be weak. Naming a new superspecific taxon for such a fossil is similar to naming a meta taxon, a practice that has been discouraged

(Gauthier et al., 1988). Because higher (monophyletic) taxa cannot be ancestral, metasppecies are the only taxa to which new metataxonomic names should be applied—not to suggest that they are ancestors, but only to indicate that they are not demonstrably monophyletic and might not ever be (Donoghue, 1985; de Queiroz and Donoghue, 1988). Nonmonophyletic taxa and metataxa other than species should not be newly named. Nevertheless, we are constrained by current definitions of taxon names and binomial nomenclature. According to the current definition of the name "*Dipsosaurus*" as the clade stemming from the most recent common ancestor of the extant populations (de Queiroz, 1987), *A. explorator* is not part of *Dipsosaurus*. However, because the genus name is a part of the binomial, we must either (1) abandon binomial nomenclature, (2) redefine "*Dipsosaurus*," or (3) coin a new generic name for a species the monophyly of which is poorly supported. We have chosen the third option in order to preserve, at least for the present, binomial nomenclature and the phylogenetic meaning of "*Dipsosaurus*." We realize that referral of any new specimens to the taxon *Armandisaurus explorator* will be tenuous until its monophyly is better supported on the basis of derived characters.

CONCLUSIONS

Armandisaurus explorator, from the early middle Miocene of New Mexico, is the earliest fossil that is unambiguously referable to the Iguaninae. Not only does it possess all the diagnostic apomorphies of Iguaninae for which the condition is determinable, but it also possesses derived characters suggesting a sister-group relationship with *Dipsosaurus*. The particular combination of ancestral and derived characters possessed by *A. explorator* resolves relationships at the base of the iguanine clade that were unresolved based on information derived from extant taxa alone. Monophyly of *A. explorator* is poorly supported.

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- An intermediate state has been added to character 18 to describe the condition in *Armandisaurus*; this state is considered the ancestral condition. (2) His characters 22–24 have been combined into a single multistate character (our character 22). (3) His characters 34 and 35 have been combined into a single multistage character (our character 32). (4) His characters 52 and 53 have been combined into a single multistate character (our character 48). (5) His character 51 (our character 47) has been changed from 1 to 0, 1 for *Dipsosaurus* in light of study of additional specimens from Baja California, which usually have pterygoid teeth. Unless otherwise indicated, all characters were treated as unordered.

1. Ventral surface of premaxilla. 0) bears large posterolateral process; 1) posterolateral process absent.
2. Posteroventral crests of premaxilla 0) small, do not continue up the sides of the incisive process and are not pierced by foramina for maxillary arteries; 1) large, continue up sides of incisive process and are pierced or notched by foramina for maxillary arteries.
3. Anterior surface of rostral body of premaxilla. 0) broadly convex; 1) nearly flat.
4. Nasal process of premaxilla I. 0) slopes backwards; 1) nearly vertical.
5. Nasal process of the premaxilla II. 0) wholly or partly exposed dorsally between nasals; 1) covered dorsally between nasals.
6. Size of nasals and nasal capsule. 0) nasal capsule of moderate size, nasals relatively small; 1) nasal capsule enlarged, nasals relatively large.
7. Bones in anterior orbital region. 0) lacrimal contacts palatine behind lacrimal foramen; 1) prefrontal contacts jugal behind lacrimal foramen.
8. Frontal. 0) longer than wide, or length approximately equal to width; 1) wider than long.
9. Paired openings at or near frontonasal suture. 0) absent; 1) present.
10. Crista cranii on ventral surface of frontal. 0) extend in a smooth, continuous curve from frontal onto prefrontals; 1) frontal portions project anteriorly forming a step between frontal and prefrontal portions.
11. Paired cristae on ventral surface of frontal. 0) absent or weakly developed; 1) strongly developed, united as a single median crest anteriorly and together with the cristae cranii forming pockets in the anteroventral surface of the frontal.

APPENDIX

Characters used in phylogenetic analysis. Character numbers refer to the data matrix in table 1. These characters have been modified from de Queiroz (1987) as follows: (1)

TABLE 1
 Data Matrix for the Iguanine Lizards Including the Fossil Taxa *A. explorer* and *P. novaceki**
 (Numbered columns refer to characters in appendix)

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Amblyrhynchus</i>	1	0	1	1	1	1	1	1	0	0	0	1	0
<i>Brachylophus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Conolophus</i>	0	1	0	0	1	0	1	0	0	1	0	0	0
<i>Ctenosaura</i>	0	0	0	0	0	0	0,1	0	0	0,1	0	0	0,1
<i>Cyclura</i>	0	0	0	0	0	0	0,1	0,1	0	0	0	0	0,1
<i>Dipsosaurus</i>	0	0	0	0	0	0	0	0	1	0	0	0	2
<i>Iguana</i>	0	0	0	0	0	0	0	0,1	0	0	0	0	0
<i>Sauromalus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Armandisaurus</i>	?	?	0	0	?	0	0	0	?	0	?	0	1
<i>Pumilia</i>	?	?	0	0	0	0	?	0	0	?	?	0	2
<i>Ancestor</i>	0	0	0	0	0	0	0	0	0	?	?	0	0
Taxon	14	15	16	17	18	19	20	21	22	23	24	25	26
<i>Amblyrhynchus</i>	0	1	0	2	0	0	1	1	2,3	1	0	1	0
<i>Brachylophus</i>	0	0	0	0	2	0	0	0	3	0	0	0	0
<i>Conolophus</i>	1	0	0	1	2	0	0	1	2	1	1	0	0
<i>Ctenosaura</i>	0	0	1	0	2	0	0	0	2,3	1	0	0	0
<i>Cyclura</i>	0	0	0	0	2	1	0	0	2	1	0	0	1,2
<i>Dipsosaurus</i>	0	0	0	0	2	0	0	0	1	1	0	0	0
<i>Iguana</i>	0	0	0	0	0	1	0	0	2	1	0	0	2
<i>Sauromalus</i>	0	0	0	0	2	0	0	0	0,2,3	1	0	0	0
<i>Armandisaurus</i>	0	0	0	0	1	0	?	?	1	0	0	0	0
<i>Pumilia</i>	0	0	0	0	0	1	0	?	?	1	?	?	2
<i>Ancestor</i>	0	0	0	0	1	0	0	0	0	0	0	0	0
Taxon	27	28	29	30	31	32	33	34	35	36	37	38	39
<i>Amblyrhynchus</i>	0	0	1	1	0	2	1	1	0	0	1	1	0
<i>Brachylophus</i>	0	0	0	0	0	1	1	0	0	0	0	0	0
<i>Conolophus</i>	0	0	0	0	0	0	2	1	0	0	1	0	0
<i>Ctenosaura</i>	1	0	0	0	0	0	0	0	0	0,1	0	0	0
<i>Cyclura</i>	0	0	0	0	0	0	0	0	0	1	0,1	0	0
<i>Dipsosaurus</i>	0	1	0	0	0	0	0	0	0	0	0	0	1
<i>Iguana</i>	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Sauromalus</i>	0	0	0	0	1	0	0	1	1	0	0	0	0
<i>Armandisaurus</i>	0	?	?	0	0	0	0	0	?	?	?	0	0
<i>Pumilia</i>	0	?	?	0	?	0	0	0	0	?	?	0	0
<i>Ancestor</i>	0	0	0	0	0	0	0	0	0	1	?	0	?

TABLE 1—(Continued)

Taxon	79	80	81	82	83	84	85	86	87	88	89	90
<i>Amblyrhynchus</i>	0	1	0	1	0	0	0	0	0	1	0	0
<i>Brachylophus</i>	1	0	0	0	1	0	0	0	0	0	0	0
<i>Conolophus</i>	1	0	0	0	0	0	0	0	0	0	0	0
<i>Ctenosaura</i>	1	2	0	0	0,1	0	0	0	0,1	0	1	0
<i>Cyclura</i>	1	0	0	0	0	0	0	0	1	0	0,1	0
<i>Dipsosaurus</i>	2	2	0	0	0	0	0	0	0	0	0	0
<i>Iguana</i>	1	0	0	0	1	1	0	0	0	0	0	0
<i>Sauromalus</i>	0	0	1	0	0	0	1	1	0	0	0	1
<i>Armadisaurus</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pumilia</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ancesor</i>	?	?	0	0	?	0	?	0	0	0	?	?

12. Dorsal border of the orbits. 0) more or less smoothly curved; 1) wedge shaped.
13. Position of parietal foramen. 0) on the frontoparietal suture; 1) variable; 2) within the frontal bone. (ordered).
14. Supratemporals. 0) extend anteriorly more than halfway across the posterior temporal fossae; 1) extend anteriorly no more than halfway across the posterior temporal fossae.
15. Maxilla I. 0) relatively flat or concave laterally; 1) flares outward ventral to the row of supralabial foramina.
16. Maxilla II. 0) premaxillary process of maxilla lies roughly in the same plane as the remainder of the maxilla; 1) premaxillary process of maxilla curves dorsally.
17. Lacrimal. 0) large; 1) intermediate; 2) small. (ordered).
18. Ventral process of the squamosal. 0) large; 1) intermediate; 2) small or absent. (ordered).
19. Squamosal. 0) separated from or barely contacting dorsal end of tympanic crest of quadrate; 1) abuts against dorsal end of tympanic crest of quadrate.
20. Septomaxilla. 0) flat or with a weak ridge on anterolateral surface; 1) with a pronounced longitudinal crest.
21. Anterodorsal surface of the palatines. 0) with a low medial ridge; 1) with a high medial crest.
22. Infraorbital foramen. 0) between palatine and maxilla with a process of the palatine projecting laterally or posterolaterally behind the foramen; 1) between palatine and maxilla without such a process; 2) between palatine and jugal; 3) entirely within palatine. (ordered 1-0-2-3).
23. Pterygoids. 0) medial borders relatively straight anterior to the pterygoid notch, interpterygoid vacuity narrows gradually; 1) medial borders curve sharply toward the midline anterior to the pterygoid notch, interpterygoid vacuity narrows abruptly.
24. Ectopterygoids. 0) fail to contact palatines near posteromedial corners of suborbital fenestrae; 1) usually contact palatines near posteromedial corners of suborbital fenestrae.
25. Parasphenoid rostrum. 0) long; 1) short.
26. Cristae ventrolateralis of parabasisphenoid. 0) strongly constricted behind basiptyergoid process; 1) intermediate; 2) widely separated.
27. Posterolateral process of parabasisphenoid. 0) present and large; 1) small or absent.
28. Laterally directed points on cristae interfenestralis. 0) absent; 1) present.
29. Stapes. 0) thin; 1) thick.
30. Relative heights of dorsal borders of dentary and surangular on either side of coronoid eminence. 0) approximately equal; 1) dorsal bor-

- der of dentary well above that of surangular.
31. Splenial. 0) large; 1) small.
 32. Anterior inferior alveolar foramen. 0) between splenial and dentary, the coronoid may or may not contribute to its posterior margin; 1) entirely within the dentary in some specimens (others state 0); 2) between splenial and coronoid. (ordered 1→0→2).
 33. Labial process of the coronoid. 0) small; 1) intermediate; 2) large.
 34. Angular I. 0) extends far up the labial surface of the mandible and is largely visible in lateral view; 2) does not extend far up the labial surface of the mandible and is barely visible in lateral view.
 35. Angular II. 0) wide posteriorly; 1) narrow posteriorly.
 36. Surangular. 0) exposed laterally only about as far forward as the apex of the coronoid or the anterior slope of this bone and never anterior to the to the last dentary tooth; 1) exposed laterally well anterior to the apex of the coronoid and often anterior to the last dentary tooth.
 37. Lingual exposure of the surangular between ventral processes of coronoid. 0) a dome-shaped portion exposed; 1) largely or completely covered by prearticular.
 38. Angular process of prearticular. 0) increases substantially in relative size during postembryonic ontogeny, becoming a prominent structure in adults; 1) increases only slightly in relative size during postembryonic ontogeny, remaining relatively small even in adults.
 39. Retroarticular process. 0) tympanic and medial crests converge posteriorly to give the process a triangular outline in both juveniles and adults; 1) tympanic and medial crests converge posteriorly in juveniles, but the posterior ends separate during ontogeny so that the process assumes a quadrangular outline in adults.
 40. Number of premaxillary teeth. 0) fewer than seven; 1) seven; 2) more than seven. (ordered).
 41. Crowns of premaxillary teeth. 0) lateral cusps small or absent; 1) lateral cusps large.
 42. Crowns of posterior marginal teeth. 0) tricuspid; 1) four cusped; 2) polycusped (5 to 10 cusps); 3) serrate. (ordered).
 43. Crowns of tricuspid posterior marginal teeth II. 0) individual lateral cusps much smaller than apical cusp; 1) individual lateral cusps relatively large, subequal to apical cusp in size.
 44. Pterygoid teeth I. 0) entire row lies along the ventromedial edge of the pterygoid adjacent to the interpterygoid vacuity. 1) posterior portion of row displaced laterally.
 45. Pterygoid teeth II. 0) entire row single throughout ontogeny; 1) posterior portion of row doubles ontogenetically; 2) entire row doubles ontogenetically.
 46. Pterygoid teeth III. 0) anterior portion of tooth patch present; 1) absent (posterior end of suborbital fenestra used as a reference point).
 47. Pterygoid teeth IV. 0) usually present; 1) usually absent.
 48. Hyoid I. 0) second ceratobranchials short, often less than two-thirds the length of the first ceratobranchials; 1) intermediate, from two-thirds the length of the first ceratobranchials to slightly longer than the first ceratobranchials; 2) long, much longer than the first ceratobranchials. (ordered).
 49. Hyoid II. 0) second ceratobranchials in medial contact with one another for most or all of their lengths; 1) separated from one another medially for most or all of their lengths.
 50. Neural spines of presacral vertebrae. 0) tall, making up more than 50% of the total vertebral height. 1) short making up less than 50% of the total vertebral height.
 51. Zygosphenes. 0) connected to prezygapophyses by a continuous arc of bone; 1) separated from zygapophyses by a deep notch.
 52. Sacrum I. 0) posterolateral process of second pleuropophyses (usually) present; 1) (usually) absent.
 53. Sacrum II. 0) foramina in the ventral surface of the second pleuropophyses (usually) present; 1) (usually) absent.
 54. Number of caudal vertebrae. 0) more than 40; 1) fewer than 40.
 55. Autotomy septa in caudal vertebrae. 0) present; 1) absent.
 56. Beginning of the autotomic series of caudal vertebrae or beginning of the series of caudal vertebrae with two pairs of transverse processes. 0) at or before the 10th caudal vertebrae; 1) at or behind the 10th caudal vertebrae.
 57. Thin, midsagittal processes on the dorsal surface of the caudal centra anterior to the neural spines. 0) relatively large and present well beyond the anterior third of the caudal sequence; 1) relatively small and confined to the anterior fifth of the caudal sequence.
 58. Postxiphisternal inscriptional ribs. 0) do not form continuous chevrons; 1) variably form continuous chevrons; 2) invariably form continuous chevrons. (ordered).
 59. Suprascapulae. 0) situated primarily in a vertical plane and forming a continuous arc with the scapulocoracoids; 1) situated primarily in a horizontal plane and forming an angle with the scapulocoracoids.

60. Scapular fenestrae. 0) large, invariably present; 1) small or absent.
61. Posterior coracoid fenestrae. 0) usually absent; 1) usually present.
62. Clavicles. 0) wide, with a prominent lateral shelf; 1) narrow, the lateral shelf small or absent.
63. Posterior process of the interclavicle. 0) extends posteriorly beyond the lateral corners of the sternum; 1) does not extend beyond the lateral corners of the sternum.
64. Lateral process of the interclavicle. 0) usually forming angles of less than 75° with the posterior process and giving the interclavicle the shape of an arrow; 1) forming an angle of between 75 and 90° with the posterior process and giving the interclavicle the shape of a T.
65. Sternal fontanelle. 0) present and of moderate size; 1) small or absent.
66. Sternum-xiphisternum. 0) sternum diamond shaped (quadrilateral), the xiphisterna in close proximity; 1) intermediate; 2) sternum pentagonal, the xiphisterna widely separated. (ordered).
67. Pelvic girdle. 0) long and narrow; 1) short and broad.
68. Anterior iliac process. 0) large; 1) small.
69. Osteoderms. 0) absent; 1) present.
70. Heart. 0) does not extend posterior to the transverse axillary plane; 1) extends posterior to the transverse axillary plane.
71. Subclavian arteries (de Queiroz, 1987). 0) covered ventrally by the posterior end of the *M. rectus capitis anterior*; 1) not covered by the *M. rectus capitis anterior*.
72. Dorsal aorta. 0) right and left systemic arches unite to form the dorsal aorta above the heart; 1) origin of dorsal aorta posterior to the heart.
73. Coeliac artery. 0) arises from the dorsal aorta anterior to and separate from the two mesenteric arteries; 1) arises posterior to the mesenterics between the mesenterics or continuous with one or the other of the mesenterics.
74. Colic wall. 0) forms one or more transverse valves; 1) forms numerous irregular transverse folds.
75. Colic valves. 0) all valves semilunar; 1) one or more circular valves (semilunar valves may be present or absent).
76. Rostral scale. 0) median and azygous; 1) subdivided by a median suture.
77. Scutellation of snout region. 0) consists of many small scales subequal in size to those of superorbital and temporal regions; 1) consists of relatively few large scales.
78. Dorsal head scales. 0) flat or slightly convex; 1) pointed and conical.
79. Superciliary scales (Etheridge and de Queiroz, 1988). 0) Quadrangular and nonoverlapping; 1) intermediate; 2) elongate and strongly overlapping. (ordered).
80. Subocular scales (Etheridge and de Queiroz, 1988). 0) all subequal in size; 1) one or two suboculars moderately elongate; 2) one subocular very long, the rest shorter. (ordered).
81. Anterior auricular scales. 0) all relatively small or one row slightly enlarged; 1) one row of scales anterior to the tympanum pointed and greatly enlarged, extending posteriorly over tympanum.
82. Gular fold. 0) conspicuous; 1) weakly developed.
83. Dewlap. 0) small or absent; 1) present and large.
84. Gular crest. 0) absent; 1) present.
85. Middorsal scale row. 0) present; 1) absent.
86. Pedal subdigital scales I. 0) anterior keels larger than posterior ones, scales asymmetrical; 1) anterior and posterior keels approximately equal in size, scales roughly symmetrical with respect to the long axis of the toe.
87. Pedal subdigital scales II. 0) individual scales entirely separate; 1) scales with greatly enlarged anterior keels fused anteriorly at bases.
88. Toes. 0) unwebbed; 1) partially webbed.
89. Caudal squamation. 0) caudal scales in adjacent verticils approximately equal in size, smooth or keeled but not spinous; 1) tail bears whorls of enlarged, strongly spinous scales.
90. Cross-sectional body shape. 0) laterally compressed or cylindrical; 1) strongly depressed.

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