Taxonomic Revision of *Carusia* (Reptilia: Squamata) from the Late Cretaceous of the Gobi Desert and Phylogenetic Relationships of Anguimorphan Lizards

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ABSTRACT

New specimens of lizards collected by the Mongolian Academy of Sciences–American Museum of Natural History Expeditions from the Gobi Desert include a large sample of superbly preserved cranial material of *Carusia intermedia*. Study of these specimens resolves problematic aspects of the cranial morphology and phylogenetic relationships of this poorly known lizard taxon. Analyses of 105 morphological characters across 30 selected ingroup and three outgroup taxa yield a phylogeny. This result refutes a previously suggested ?Scincomorphan relationship of *Carusia*, instead supporting placement of this taxon in the Anguimorpha. A new lizard clade including the basal *Carusia* and the crown group Xenosauridae is recognized. This clade occupies the basalmost position within the Anguimorpha. Recognition of this taxon as a basal anguimorphan resolves the Xenosauridae/Anguidae/Varanoidea polytomy. Relationships of platynotan taxa known from the Gobi Desert are also discussed and problems with these taxa are addressed.

INTRODUCTION

Among the Late Cretaceous lizards known from the Gobi Desert, *Carusia intermedia* (Borsuk-Bialynicka, 1985) is a phylogenetically important but problematic taxon. Previous work on the phylogenetic relationships of this taxon was hampered by uncertainty concerning the cranial morphology of *Carusia*. Borsuk-Bialynicka (1985) originally

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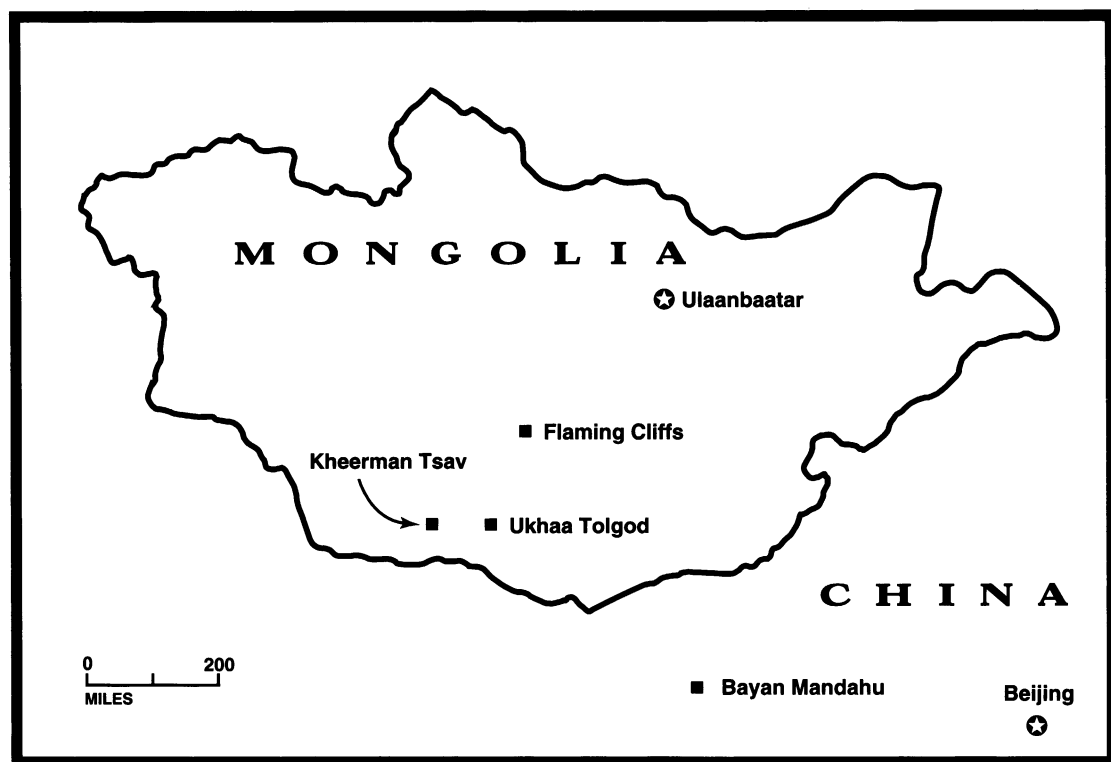
Fig. 1. Map of the Gobi Desert showing fossil localities where specimens of *Carusia intermedia* were collected.

classified *Carusia* (= *Carolina*) in its own family (Carusiidae), and referred it to the ?Scincomorpha, although she indicated that it also shares several characters with extant xenosaurids. Later, the same author (Borsuk-Bialynicka, 1991a: 9) considered the Carusiidae as "either a sister-group of the Xenosauridae or an autarchoglossan taxon convergent to this family," and consequently, placed *Carusia* in "Carusiidae (?Xenosauridae)" in a faunal list (Borsuk-Bialynicka, 1991b). More recently, Alifanov (1993) listed *Carusia* [sic] under Xenosauridae but gave no explanation. None of these authors have provided evidence (i.e., characters) to justify their classifications.

Recent discoveries of a large number of well-preserved specimens of *Carusia* from Ukhaa Tolgod (Dashzeveg et al., 1995) and other localities (fig. 1) in the Gobi Desert are important, as these specimens add new data clarifying the cranial morphology and relationships of this taxon. This paper de-

scribes these specimens and provides an assessment of the phylogenetic relationships of this taxon based on analyses of 105 morphological characters across 30 selected ingroup taxa and three outgroups. The results of our analyses refute a previously suggested hypothesis of a possible scincomorphan relationship of *Carusia*, and instead support inclusion of the taxon in the Anguimorpha. Within the Anguimorpha, *Carusia* is placed as the basal taxon to a newly recognized clade (Carusioidea). Furthermore, the Carusioidea is the sister taxon to the crown group Xenosauridae. Because many of the Gobi lizards apparently represent basal taxa of various anguimorphan clades (for example, *Estesia mongoliensis*—see Norell et al., 1992; Norell and Gao, 1997), including them in the analyses yields important results providing insight into the taxonomic and phylogenetic framework of the Anguimorpha, as discussed in the later sections in this paper.

Institutional and other abbreviations used in the paper are as follows: AMNH, American Museum of Natural History, New York; MAE, specimens collected for the Mongolian Academy of Sciences–American Museum of Natural History Paleontological Expeditions to be cataloged into IGM collections; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland; IGM, Institute of Geology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia.

SYSTEMATIC PALEONTOLOGY

SQUAMATA OPPEL, 1811

SCINCOGEKKONOMORPHA SUKHANOV, 1961

ANGUIMORPHA FÜRBRINGER, 1900

CARUSIOIDEA, NEW TAXON

DEFINITION: The last common ancestor of *Carusia*, Xenosauridae, and all of its descendants.

DIAGNOSIS: The new taxon Carusioidea can be diagnosed by the following derived characters: frontals fused; lateral border of frontals constricted between orbits; presence of jugal-squamosal contact below supratemporal arch; presence of cranial osteoderms with vermiculate rugosities; postorbital branch of jugal sculptured; anterior tapering of surangular strongly reduced; and surangular extends anteriorly slightly beyond coronoid eminence.

Many of these characters were included in the diagnosis of Xenosauridae (e.g., Estes, 1983; Estes et al., 1988), but recognition of *Carusia* as a basal taxon outside the crown group Xenosauridae in this paper necessitates the revision of the diagnosis of the crown clade (see discussion on results of phylogenetic analyses).

CARUSIIDAE BORSUK-BIALYNICKA, 1987

Carolinidae Borsuk-Bialynicka, 1985: 153.

Carusia Borsuk-Bialynicka, 1987, nom. subst. [pro. *Carolina* Borsuk-Bialynicka, 1985 (non Thomson, 1880)]

TYPE SPECIES: *Carolina intermedia* Borsuk-Bialynicka, 1985.

RANGE: Upper Cretaceous Djadochta, Barun Goyot formations, and Ukhaa Tolgod (unidentified geological unit), Gobi Desert.

DIAGNOSIS: As for the type and only known species (see below).

REMARKS: Borsuk-Bialynicka (1985) named *Carolina*, but later (1987) suggested substituting *Carusia* for *Carolina*, which is preoccupied. Another name associated with *Carusia* is *Shinisauroides* Borsuk-Bialynicka, 1985. Because the latter name is based on specimens that show no autapomorphies and only minor variations from the former taxon, Gao and Hou (1996) suggested synonymizing *Shinisauroides* with *Carusia*. Our new collections mainly from Ukhaa Tolgod, like those from Bayan Mandahu in China, provide further evidence in favor of synonymizing *Shinisauroides* with *Carusia*.

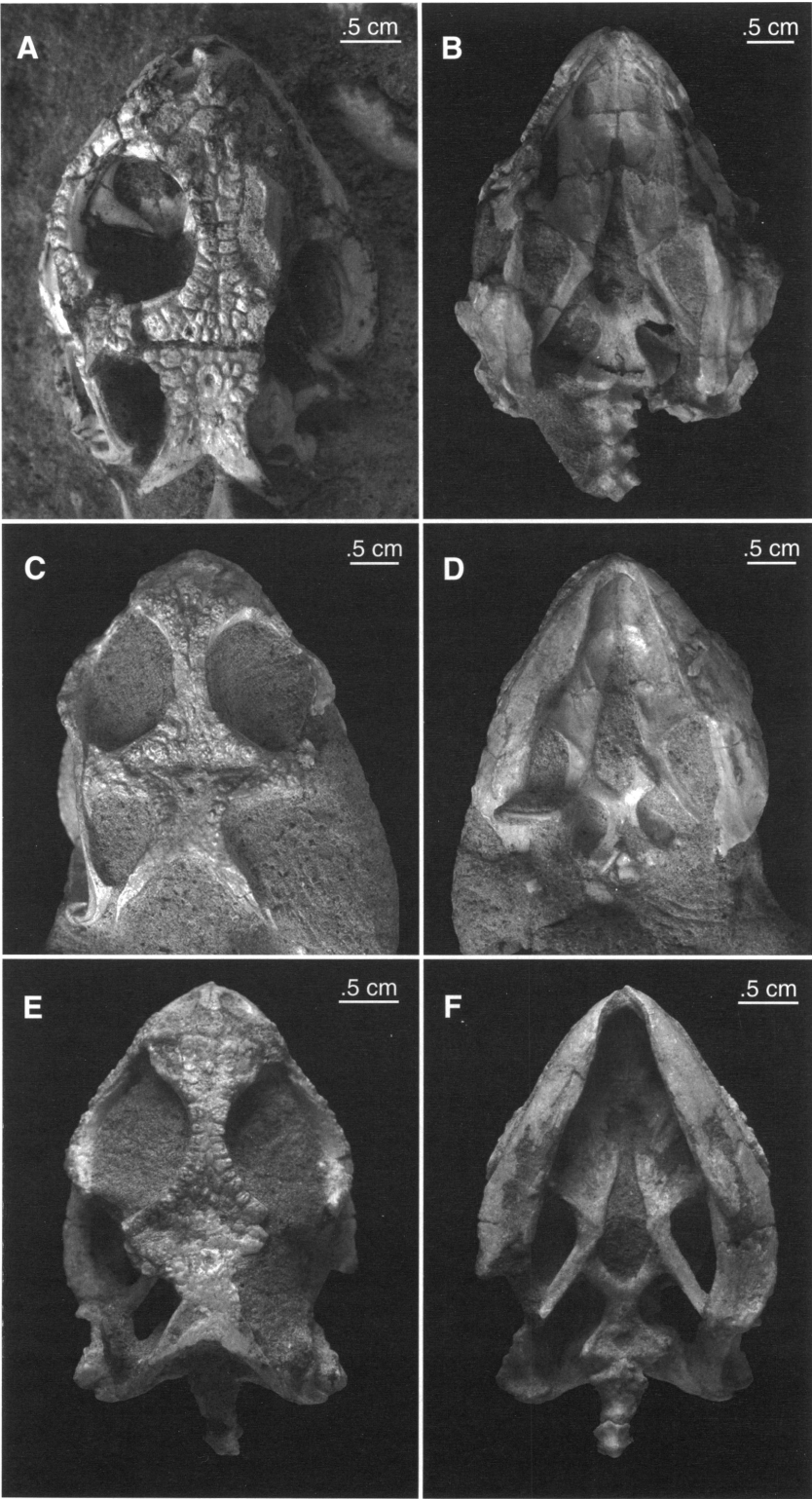### *Carusia intermedia* Borsuk-Bialynicka, 1985
Figure 2–6

HOLOTYPE: ZPAL MgR-III/34, incomplete skull with mandibles.

TYPE LOCALITY AND HORIZON: Khermeen Tsav, Gobi Desert, Mongolia; Upper Cretaceous Barun Goyot Formation (late Campanian). See comments concerning the age of these faunas in Norell et al. (1992).

KNOWN DISTRIBUTION: Upper Cretaceous Djadochta, Barun Goyot formations, and Ukhaa Tolgod (unidentified geological unit), Gobi Desert.

DIAGNOSIS: Sharing with extant xenosaurids the following derived characters: strong interorbital constriction of fused frontals; jugal-squamosal contact; dermal vermiculate rugosities on skull roof elements; postorbital branch of jugal ornamented.

Distinguished from all other closely related taxa including *Xenosaurus* and *Shinisaurus* by the following autapomorphies: lacrimal absent, with anteroventral process of jugal contacting prefrontal; maxilla contributes to formation of ventral border of orbit; caudoventral process of jugal ventrally directed; fenestra exochoanalis distinctively short and elliptic; presence of midline contact of palatines anteriorly; palatine rectangular and strongly widened, suppressing suborbital fenestra into narrow and elongate opening; presence of vertical crest anteriorly on quad-

rate; condyle-fossa articulation for both squamosal and supratemporal with cephalic condyle of quadrate; descending process of parietal subrectangular, elongated, and laterally compressed; epipterygoid slanted strongly posterodorsally; marginal process of supraoccipital prominent and well-ossified; presence of strong adductor crest dorsolaterally on surangular; marginal teeth extremely fine, numerous, and having comblike arrangement; strong posterior extension of neural spone of axis over entire third cervical.

REFERRED SPECIMENS: Nearly complete skulls with mandibles—MAE 95-5, 95-52, 94-38, 40/93-90, 94-26, 96-9, 96-122, 96-191; incomplete skulls with mandibles— MAE 35/93-167, 115/93-93, 241/93-130, 104/93-158, 33/93-167, 470/93-134, 92/93-104, 231/93-99, 414/93-111, 311/93-127, 36/93-129, 314/93-127, 37/93-129, 94-27, 94-49-1, 94-101, 95-72, 96-17, 96-40, 96-50, 96-52, 96-65, 96-109, 96-196; incomplete mandibles—MAE 94-49-2, 95-51, 61/93-130 (total: 35, all from Ukhaa Tolgod and adjacent localities). In addition, two incomplete skulls with mandibles (MAE 67 and 71) represent the only specimens of *Carusia* from the classic Flaming Cliffs (Bayn Dzak) locality.

NEW SPECIMENS FROM UKHAA TOLGOD

Borsuk-Bialynicka (1985) provided the original description of *Carusia intermedia*, on the basis of the type and then only known specimen collected from Khermeen Tsav by the Polish-Mongolian Palaeontological expeditions. Because of the incompleteness of these specimens, and ambiguities between the description and the specimens themselves, a number of cranial characters of *Carusia* require further elaboration. It is clear that these ambiguities have substantially obscured the phylogenetic relationships of this poorly known but phylogenetically important lizard taxon. New specimens described here are significant, not only because of the large

sample from different localities, but also because the exceptional quality of preservation reveals new information relevant to the morphology and relationships of this taxon.

Among the skulls from the Ukhaa Tolgod locality, six (MAE 95-5, 95-52, 40/93-90, 94-38, 241/93-130, 96-191) are the best preserved in terms of overall completeness; another (MAE 115/93-93) shows the best-preserved palatal region and braincase (figs. 2, 3). It is mainly on these specimens that the following description is based.

DERMAL ROOF ELEMENTS

Most of the dermal roofing elements are heavily covered with an incrustation of small and vermiculate osteoderms, as in extant xenosaurids. This somewhat complicates the description of sutural boundaries among skull elements. Nevertheless, the extent of the collection allows removal of some of the osteoderms on some specimens to confirm these relationships.

Premaxilla—One of the uncertainties about the skull morphology of *Carusia* is the nature of its premaxillae: Borsuk-Bialynicka (1985: 154, 161) described the premaxillae as paired in *Carusia* but "fused in midline with increasing age" in *Shinisauroides* (junior synonym of *Carusia*, see above). This raises the question about the ontogenetic fusion of this element, as the two names mentioned above are treated as the same taxon in this paper. Our new specimens from Ukhaa Tolgod, like those from Bayan Mandahu (Gao and Hou, 1996), include both small (MAE 36/93-129, 241/93-130, 37/93-129) and large skulls (MAE 115/93-93, 94-38, 33/93-167, 35/93-158, 104/93-158) that clearly show a paired condition of the premaxillae. Several other small and large skulls (MAE 95-5, 95-52, 35/93-167, 231/93-99, 414/93-111) with eroded surfaces look as if the premaxillae were "fused." Yet in palatal view these specimens show a paired condition. Therefore, we conclude that the "fused"

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Fig. 2. Skull of *Carusia intermedia*: MAE 95-5, dorsal view (**A**); MAE 115/93-93, ventral view (**B**); MAE 95-52, dorsal (**C**) and ventral (**D**) views; MAE 94-38, dorsal (**E**) and ventral (**F**) views.
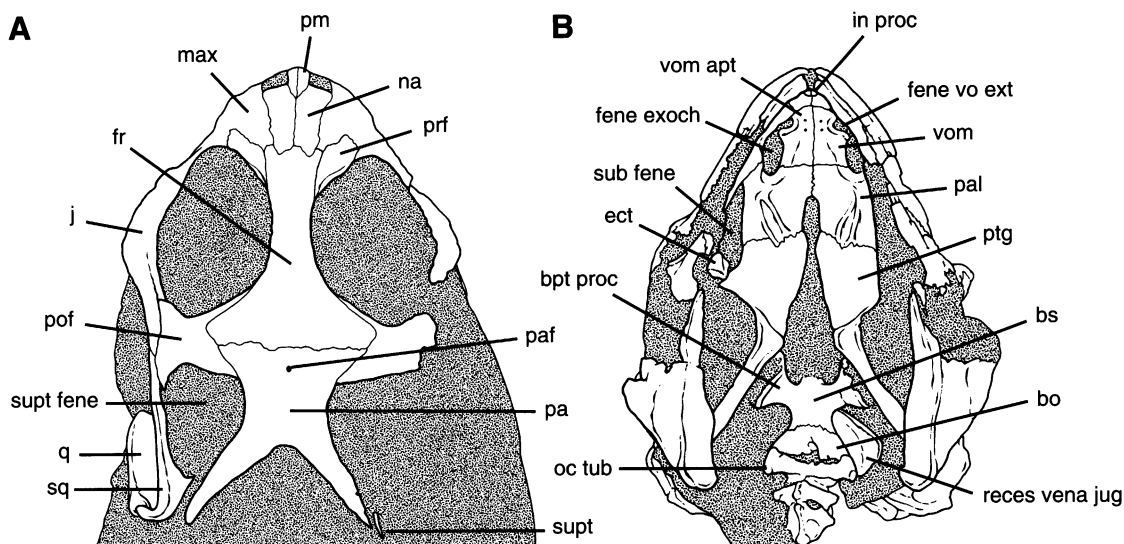
Fig. 3. Skull of *Carusia intermedia*: dorsal view (**A**), based on MAE 95-52; ventral view (**B**), based on MAE 115/93-93.

Abbreviations used in this and the following figures: **alar proc,** alar process of prootic; **bo,** basioccipital; **bpt proc,** basipterygoid process; **bs,** basisphenoid; **des pa,** descensus parietalis; **ect,** ectopterygoid; **ept,** epipterygoid; **fene exoch,** fenestra exochoanalis; **fene vo ext,** fenestra vomeronasalis externa; **fo,** foramen ovale; **fr,** frontal; **hyp for,** hypoglossal foramen; **in proc,** incisive process; **inf proc,** inferior process of prootic; **j,** jugal; **marg proc,** marginal process of supraoccipital; **max,** maxilla; **na,** nasal; **oc tub,** spheno-occipital tubercle; **pa,** parietal; **paf,** parietal foramen; **pal,** palatine; **paroc proc,** paroccipital process; **pm,** premaxilla; **pof,** postorbitofrontal; **prf,** prefrontal; **proc ascd,** processus ascendens; **ptg,** pterygoid; **q,** quadrate; **reces vena jug,** recessus vena jugularis; **semi can,** semicircular canal; **sq,** squamosal; **sub fene,** suborbital fenestra; **supt,** supratemporal; **supt fene,** supratemporal fenestra; **vom,** vomer; **vom apt,** vomerine aperture.

condition described by Borsuk-Bialynicka is the result of weathering.

The premaxillae are fused in all iguanians and some scincogekkonomorphs, but are paired in some gekkonids (Kluge, 1967), extinct ardeosaurids, and bavarisaurids (Estes, 1983; Mateer, 1982; Evans, 1994), some scincids (Greer, 1970), and in the primitive anguimorphan *Carusia* (this paper). Estes et al. (1988) inferred the ontogenetic fusion of the premaxillae as a squamate synapomorphy and the paired condition in some gekkonids and scincids as character reversals. We accept this interpretation.

In *Carusia*, the dorsal process of the premaxilla is well developed, and is nearly vertical owing to the high profile of the snout. Dorsally, the process wedges slightly into the midline suture between the nasals. Five or six premaxillary teeth are present. In keeping with the paired condition of the premaxillae, the incisive process is bipartite in palatal

view (best shown on MAE 115/93-93, 95-52, 414/93-111). A premaxillary foramen (within the premaxilla) is absent, but a small fossa is developed laterally at the base of the incisive process. A premaxillary–maxillary aperture (at the suture between the two elements) is also absent as in extant xenosaurids.

Nasal—Like most anguimorphans (except for the extant varanids), the nasals are paired in *Carusia*. The two bones are only slightly divided anteriorly by the dorsal processes of the premaxillae, and posteriorly by an anteromedial process of the frontal (e.g., MAE 95-52, 93-93, 93-167). The sutural contact is much longer than half the length of the nasals, and in this respect differs from extant xenosaurids. In *Xenosaurus* and *Shinisaurus*, the nasals are deeply separated anteriorly by the dorsal process of the premaxilla and posteriorly by an anteromedial process of the frontal (McDowell and Bogert, 1954); there-

fore, the midline contact of the nasals is significantly shorter than half the length of the nasal bone. The nasal in *Carusia* contacts the dorsal process of the maxilla laterally, but is separated from the prefrontal by a slender anterolateral process of the frontal (best shown in MAE 231/93-99, 115/93-93, 95-52, and 96-50). The loss of a nasal-prefrontal contact has been recognized as a scincomorphan synapomorphy (Estes et al., 1988), but independent occurrences of this character are known in several anguimorphans (e.g., *Diploglossus*, *Proplatynotia*, and *Saniwides*) other than *Carusia*.

Frontal—The frontals are fused in *Carusia*, and are strongly constricted between the orbits. Laterally, the frontal contributes to a small portion of the dorsal rim of the orbit, since it has extensive sutural contact with the prefrontal anteriorly and with the fused postorbitofrontal posteriorly. The frontal has a well-developed subolfactory process. Borsuk-Bialynicka (1985: 154) described this structure: "extending medioventrally the subolfactory processes of the frontals fuse in the midline . . . . they extend down to the palatines anteriorly." This description contradicts her figure (Borsuk-Bialynicka, 1985: fig. 2) in which the subolfactory processes are close to the ventral midline but not in contact nor fused.

Our examination of the new specimens (e.g., MAE 314/93-127, 241/93-130, 94-38, 95-5) concurs with Borsuk-Bialynicka's illustration in that the subolfactory processes are not fused. The processes are ventromedially close to the midline but remain clearly separated by a narrow space, and the anterior extension of the process does not contact the palatine bone (best shown on MAE 314/93-127). Some anguimorphans (e.g., *Heloderma*, *Varanus*; see Estes et al., 1988 for analysis) show ventral contact and fusion of the subolfactory processes, yet others (see Norell et al., 1992: fig. 9) display a condition more similar to that in *Carusia*. Anteroventrally, a slender descending process of the frontal extends downward and attaches to the medial margin of the prefrontal, restricting the contribution of the prefrontal to the orbitonasal fenestra.

Lateral to the frontal and posterior to the prefrontal, two specimens (MAE 40/93-90 and 95-5) preserve well-ossified palpebral bones. Presence of palpebrals on other specimens is indicated by a distinct notch at the anterodorsal corner of the orbit.

Prefrontal—The prefrontal in *Carusia* has a relatively short but strong frontal process extending to a point slightly anterior to the midlevel of the dorsal rim of the orbit. Anteroventrally, this element forms the entire anterior wall of the orbit and extends downward to contact the widened palatine. The anteromedial margin of this bone does not form the lateral border of the orbitonasal fenestra, but is sutured to a descending process of the frontal. In dorsal view, the prefrontal contacts the maxilla and the frontal, but has no contact with the nasal (see above). As in *Xenosaurus*, the prefrontal is dorsally exposed posterior to the nasal process of the maxilla. This condition is sharply different from *Shinisaurus*, in which the prefrontal has a strong anterior extension entering the narial opening (see McDowell and Bogert, 1954).

Lacrimal and Lacrimal Foramen—Another uncertain point concerns the presence or absence of the lacrimal; presence of this element in the holotype is uncertain (Borsuk-Bialynicka, 1985). New specimens (e.g., MAE 36/93-129, 241/93-130, 314/93-127) show that the lacrimal is absent in correlation with a strong anterior extension of the jugal. The absence of a lacrimal in several lizard groups can either be explained as fusion with the prefrontal or simple loss (see Jollie, 1960; Estes et al., 1988 for discussion). Several small individuals (e.g., MAE 36/93-129, 96-50) show the same condition as that present in large individuals, indicating that fusion or loss of this element in *Carusia* is not related to ontogeny. Estes et al. (1988: 149) cited Presch (1980) for the lacrimal-prefrontal fusion in some gymnophthalmids and Romer (1956) for fusion in amphisbaenians, and pointed out that the elements are separate in all nonsquamate lepidosauromorphs. Accordingly, the loss or fusion of the lacrimal in *Carusia* is another independently acquired character. Because all extant xenosaurids (*Xenosaurus* and *Shinisaurus*) have a well-developed lacrimal as a separate element (McDowell and Bogert, 1954; Rieppel, 1980a), the absence of the lacrimal in *Carusia* is autapomorphic.

Associated with the problem of presence or absence of the lacrimal is the number and relative location of lacrimal foramina. Examination of the new specimens including the four best-preserved skulls mentioned above, indicates that a single lacrimal foramen is located between the prefrontal and maxilla. Below the lacrimal foramen is the opening for the infraorbital canal. Within Squamata, double lacrimal foramina occur only in *Varanus*, *Lanthanotus* (Rieppel, 1980a; Estes et al., 1988; Norell et al., 1992), and closely related fossil taxa (*Saniwa* and possibly *Telmasaurus*; see character analysis below).

Maxilla—As in extant xenosaurids, the maxilla in *Carusia* has a high nasal process. A large part of the maxilla is covered with osteoderms. The maxilla is vertical with the exception of the nasal process which bends dorsomedially to contact the nasal and prefrontal. The nasal process is primitively located above the anterior part of the maxillary tooth row, as in extant xenosaurids (see Rieppel, 1980a: figs. 20, 21; personal obs. of specimens of *Xenosaurus grandis*: AMNH 98122, 103212). The premaxillary process of this element extends anteriorly, overlapping the lateral process of the premaxilla. This pattern of maxilla-premaxilla articulation is probably primitive, since it is present in many scincomorphans (e.g., Scincidae, Cordylidae, and Lacertidae). In extant xenosaurids, the premaxillary process of the maxilla may have a nearly vertical suture with the premaxilla (*Xenosaurus*) as in many anguimorphans, or it extends ventral to the premaxilla (*Shinisaurus*, McDowell and Bogert, 1954: fig 4; Rieppel, 1980a: fig. 20).

The posterior process of the maxilla covers most of the anteroventral process of the jugal laterally, and forms a large part of the ventral border of the orbit. In this aspect, *Carusia* is different from extant xenosaurids, in which the ventral border of the orbit is formed by jugal and lacrimal. The lateral surface of the maxilla is smooth ventrally, but its dorsal part, slightly above the lateral foramina, is covered by osteodermal sculpture.

Jugal—In *Carusia*, the anteroventral process of the jugal extends along the medial side of the maxilla. This condition differs from that seen in extant xenosaurids by the absence of a widened postorbital bar and by the orientation of the posteroventral process. In *Carusia* it is directed ventrally, instead of posteriorly. Borsuk-Bialynicka (1985: 156) stated: "the jugal contributes the posterior one third to the suborbital margin and is medioventral to this margin in the anterior part of the orbit." Undistorted specimens (e.g., MAE 241/93-130, 94-38, 115/93-93, 95-52) show that the anteroventral process is deep, but barely exposed dorsally in lateral view. Because the lacrimal is absent, the process is strongly elongate, extending anteriorly along the inner side of the posterior process of the maxilla. The anterior end of the process contacts the prefrontal above the opening for the infraorbital canal or below the lacrimal foramen. In sharp contrast to extant xenosaurids and many other lizards, both the anteroventral process of the jugal and the posteroventral process of the maxilla are involved in the formation of the entire lateroventral border of the orbit in *Carusia*. The postorbital branch of the jugal is more robust than the anteroventral process in terms of thickness, and, like other skull roof elements, it is laterally sculptured. The dorsal extremity of the jugal twists to horizontal and contacts the squamosal beneath the supratemporal arch (best shown on MAE 95-5, 95-52, 96-191). The jugal bears a strong caudoventral process, but it is neither triangular nor posteriorly directed, in contrast to the condition seen in extant *Xenosaurus* and *Shinisaurus* (see Rieppel, 1980a).

In comparison with other groups of lizards, the jugal in *Carusia* retains a primitive morphology, i.e., it is strongly angulated (see McDowell and Bogert, 1954) in keeping with the presence of a strong posteroventral process. The angulation is lost in those gekkotans that have a remnant jugal and in several scincomorphan groups (see Estes et al., 1988); strongly reduced in some anguids and entirely lost in others; and lost in all varanoids with the exception of *Heloderma*.

Postorbital and Postfrontal—The postorbital and postfrontal are not preserved on the holotype of *Carusia intermedia* (Borsuk-Bialynicka, 1985). Six specimens in the new collection (MAE 40/93-90, 104-93/158, 241/93-130, 95-5, 95-52, 96-191) show that the two elements are fused as in extant xeno-

saurids and many other anguimorphans. The fusion of the postorbital with postfrontal occurs independently in at least six groups of lizards (see Estes et al., 1988 for comments). In *Carusia*, the fused elements are forked dorsally and clasp the frontoparietal suture. Laterally, the fused elements contact the postorbital branch of the jugal, and contact the anterior process of the squamosal to form a well-developed supratemporal arch (best shown on MAE 95-5, 95-52); however, the posterior process is so short that most of the arch is formed by the long anterior process of the squamosal. The short posterior process of the postorbitofrontal is similar to the condition seen in *Xenosaurus* (differing only in a narrower width), but different from *Shinisaurus*, which has an elongate process forming a large part of the supratemporal bar.

Parietal—The parietal is nearly complete on seven specimens (MAE 94-38, 33/93-167, 40/93-90, 95-5, 95-52, 96-122, and 96-191), and partially preserved on several others. The parietal table is slightly constricted at its middle portion as in *Shinisaurus*, but differs sharply from the latter in having no parietal flange (see below). Anteriorly, the parietal of *Carusia* forms a transverse frontoparietal suture as in extant xenosaurids. A small parietal foramen is located just posterior to that suture. Posteriorly, a strong supratemporal process is of about the same length as the parietal table. This condition differs from that in *Xenosaurus* and *Shinisaurus* where the process is half, or less, the length of the parietal table. Most of the specimens show elongation of the parietal table as in *Shinisaurus*, but variation (a shorter parietal table) is present in some specimens (e.g., MAE 95-52, 96-191). This variation is not size related, because both conditions occur in large individuals and may be caused by some other factor (i.e., sexual dimorphism).

Borsuk-Bialynicka (1985: 154, fig. 5) ambiguously described and figured *Carusia* as having a "huge triangular" or "finger-like" descensus parietalis, which is the same structure as the "cranial wall laminae" of Jollie (1960) or the "parietal downgrowths" of Estes et al. (1988). Preparation of several new specimens (MAE 33/93-167, 92/93-104, 104/93-158, 115/93-93, 241/93-130, 94-38, 95-5, 96-52, 96-122) confirms the presence of the

robust ventral process of the parietal, but it is neither "huge triangular" nor "fingerlike"; instead, it can be more appropriately described as subrectangular and laterally compressed, about one-third to one-half of the length of the epipterygoid (see fig. 4B). Such a configuration of the descensus parietalis differs significantly not only from the ventral or lateral flange in many anguimorphan groups (e.g., in anguids, xenosaurids, *Heloderma*, and *Varanus*), but also from the pointed and fingerlike condition in many scincomorphans, and is diagnostic of *Carusia intermedia*. Presence of prominent downgrowths of the parietal has been interpreted as a scincomorphan synapomorphy (Estes et al., 1988), but congruence with other characters in our analyses indicates that it is independently derived in *Carusia intermedia* (see analysis results below). A similar but much shorter structure is seen in a highly specialized Solomon Islands skink *Corucia zabrata* (AMNH 140797), but this occurrence is apparently independent from that in *Carusia intermedia*.

Squamosal—The squamosal is not preserved on the holotype and other specimens included in the original description of *Carusia*; therefore, the morphology of this element was previously unknown. Among the new specimens, a complete squamosal is preserved on the left side of MAE 95-5, 95-52, and 96-191; on the right side of MAE 33/93-167, and partially preserved on several others (e.g., MAE 35/93-167, 94-38). These specimens show that the squamosal in *Carusia* is much more slender than in *Shinisaurus*, and is distinctly different from the strongly widened condition in *Xenosaurus*. It retains a primitive anguimorphan morphology, as in *Shinisaurus*, in which the squamosal is separated from the parietal by the splintlike supratemporal; this condition is different from that in *Xenosaurus*, in which a strong dorsal process of the squamosal contacts the parietal (McDowell and Bogert, 1954). Extending anteriorly to contact the fused postorbitofrontal as well as the posterodorsal process of the jugal, the strongly elongate anterior process forms most of the supratemporal arch, while the extremely short posterior process of the postorbitofrontal contributes only slightly to the supratemporal arch. A strong downward

bending of the posterior process makes it more cane-handle than hockey-stick shaped in lateral view, as in extant xenosaurids. The dorsal process of the squamosal in *Carusia* is small, and its appearance is intermediate between that in *Xenosaurus* where it is strong and hooked, and in *Shinisaurus* where it is nearly lost (see McDowell and Bogert, 1954; Rieppel, 1980a).

A significant difference in the morphology of the squamosal in *Carusia* and in extant xenosaurids is its lack of a well-defined canthal crest. Presence of such a crest has been recognized as a xenosaurid synapomorphy (McDowell and Bogert, 1954; Gauthier, 1982; Estes et al., 1988). In *Carusia*, a very poorly defined crest is seen on two specimens (MAE 95-5, 33/93-167), but it is hardly recognizable on several others (e.g., MAE 95-52, 96-191); therefore, we conclude that this taxon lacks a well-defined canthal crest. This is one of the characters that indicates a basal position of *Carusia* within the clade leading to modern xenosaurids.

Supratemporal—The supratemporal was previously unknown for *Carusia* (Borsuk-Bialynicka, 1985), but is well-preserved on several specimens in the new collection (e.g., MAE 115/93-93, 40/93-90, 94-38, 95-52, 96-191, 96-196). A large part of this splint of bone is wedged between the squamosal and the supratemporal process of the parietal, with its anterior extension terminating at about midlength of the supratemporal process of the parietal. Wedged between the paroccipital process and the squamosal, the posterior part of this bone slightly thickens, and distally terminates as a small condyle that fits in a small pit on the quadrate.

Several authors (Barrows and Smith, 1947; McDowell and Bogert, 1954) have described a small, peculiar ossicle (or ossified intercalary; see Jollie, 1960), lying between the supratemporal and the paroccipital process on top of the quadrate, in extant *Xenosaurus* and *Shinisaurus*. This ossicle is absent in *Carusia* (e.g., MAE 115/93-93, 94-38, and 40/93-90); however, the posterior thickening of the supratemporal may indicate a fusion of the ossicle with the latter element as in some *Xenosaurus* (e.g., AMNH 103212).

Quadrate—As shown on several speci-

mens (e.g., MAE 95-5, 115/93-93, 94-38, 95-52), the quadrate is relatively straight as in extant xenosaurids and some other lizard groups (see Jollie, 1960), lacking a strong concave conch on its posterior margin. However, the dorsal end of the quadrate has a cephalic condyle, which is not as massive as in xenosaurids. Dorsally on the condyle are two pits, each having a foramen inside (clearly shown on 95-5, see fig. 2A). The laterally located, larger pit, accepts the condyle of the squamosal, and the medially located smaller one is for the joint with the condyle of the supratemporal. Such paired foramina are probably unique for *Carusia*, as a single foramen is known for some iguanians, teiids, scincids, amphisbaenians (see Jollie, 1960), and helodermatids (personal obs.). In extant xenosaurids, the cephalic condyle has a smooth surface without pits (personal obs. of AMNH 98122: *Xenosaurus grandis*; *Shinisaurus crocodilurus*, S. E. Evans, personal commun. 1997).

Anteriorly, the quadrate has a prominent vertical crest (see e.g., fig. 2A), extending from the dorsal end to the ventral condyle. This crest divides the anterior surface of the lateral conch into two parts, with the medial half about twice to three times the width of the lateral half. Presence of this vertical crest is probably another unique feature of the quadrate in *Carusia*, pending an investigation of the condition in *Shinisaurus*. Examination of two specimens (AMNH 98122, 103212) shows that such a crest is absent in *Xenosaurus*. Functionally, such a crest may provide a strong attachment area (origin) for the quadrate aponeurosis and/or the 3a portion of the MAME profundus. Extant xenosaurids lack this crest, as these muscles originate dorsally on the anterior edge of the cephalic condyle (see Rieppel, 1980a). Lateral to this crest in *Carusia* is the tympanic crest, which is thin and straight (rather than arched) in both lateral and posterior views. Dorsally, the crest ends with a small tubercle and is connected to the horizontal lateral border of the cephalic condyle. In *Xenosaurus*, the dorsal part of the tympanic crest is thick and ends with a strong tubercle that is separated from the cephalic condyle by a notch (e.g., AMNH 103212; see also Rieppel, 1980a: fig. 21). Near the ventral condyle, the tympanic

crest turns medially toward the ventral condyle and has a small notch. This notch is for the attachment of the lateral collateral ligament (Oelrich, 1956). Roughly at the same level and on the anterior surface is a small, rounded quadrate foramen for the anastomotic branch of the anterior tympanic vein and the posterior condylar artery (Oelrich, 1956). Within Xenosauridae, this foramen is present in *Shinisaurus* (S. E. Evans, personal commun. 1997), but is absent in *Xenosaurus* (AMNH 98122, 103212). The only known absent condition in other squamates is in Late Cretaceous *Sineoamphisbaena hexatabularis* (see Wu et al., 1996).

Posteromedial to the tympanic crest is a well-developed fossa that is commonly seen in many other lizards. The posterior crest is much more developed than the anterior crest and is relatively straight, differing from the strongly arched condition of extant xenosaurids. This crest separates the fossa of the lateral conch from the medial crest, which serves as the origin of the adductor posterior muscle (Oelrich, 1956). The medial crest of the quadrate is also straight and has a flat posterior surface rather than a fossa; therefore, no inner conch is developed. In this respect *Carusia* differs from extant xenosaurids. Development of an inner and an outer conch of the quadrate is a unique character of extant xenosaurids (McDowell and Bogert, 1954: 27).

Ventrally, the distal condyle is slightly saddle-shaped with a lateral epicondyle. In posterior view, ventral to the end of the posterior crest, is a small triangular depression for the posterior flaplike buttress of the articular fossa in the lower jaw. Posteriorly above the level of pterygoquadrate joint is the posterior opening for the quadrate foramen, which is close to the edge of the medial crest.

Palpebral—As indicated earlier, a fully ossified palpebral bone is preserved on two specimens (MAE 95-5, 40/93-90). On MAE 95-5, the palpebral is preserved on the right orbit, but it apparently has been displaced as it seems to be the left side element. Only the ventral surface is exposed, and it is smooth and slightly concave. Anteriorly the bone is slightly thickened, and has an articular surface, which matches the distinct notch dorsal to the prefrontal at the anterior corner of the orbit. The bone is more or less rectangular, but has a very prominent posterolateral process. As the prefrontal has a strong frontal process covering a large part of the anteromedial rim of the orbit, the palpebral probably has little or no articulation with the frontal. A palpebral bone is developed in anguimorphans (except *Heloderma* and *Lanthanotus*), and is also known in scincoid and lacertid scincomorphans (see Estes et al., 1988: character 36).

PALATAL ELEMENTS

Vomer—The vomers are wide and paired (e.g., MAE 94-38, 241/93-130, 115/93-93, 95-52), with a clear midline suture. Independent fusion of the vomers occurs in some iguanians, gekkotans, some scincomorphans, and some anguimorphans excluding xenosaurids (for citations and discussion, see Jollie, 1960; Estes et al., 1988; Norell et al., 1992). In *Carusia*, the vomer anteriorly contacts the premaxilla by a slightly arched suture and anterolaterally contacts the anteromedial process of the maxilla. Posteriorly, the vomer is delimited from the palatine by a transverse suture. The ventral surface of the vomer is flat, except for its posterolateral part, which is curved dorsally for the internal narial opening. No vomerine teeth are present in any of the specimens, but each of the paired vomers is perforated by two small vomerine apertures (best shown in MAE 115/93-93, 95-52), through which passed small veins from the posterior part of the Jacobson's organ (Bahl, 1937). Extant xenosaurids have two apertures (Barrows and Smith, 1947; Rieppel, 1980a: figs. 20, 21), one on each side, as in most anguimorphans; therefore, the double aperture condition in *Carusia* is probably autapomorphic for this taxon.

In comparison with other anguimorphs, the vomer of *Carusia* is primitively short, extending posteriorly no more than one-third the length of the maxillary tooth row. Xenosaurids (and anguids as well) have vomers that extend posteriorly to the midlevel of the tooth row, whereas varanoids have a strong elongation of the vomer as well as the internal narial opening (fenestra exochoanalis). In varanoids both structures reach the posterior end of the tooth row (see Rieppel, 1980a;

Estes et al., 1988). In *Carusia*, the internal naris is distinctively short and elliptical. Such a configuration of the fenestra is unique at least among anguimorphans and probably among lizards as well. The internal naris is anteriorly connected with the opening of the Jacobson's organ (fenestra vomeronasalis externa), as no vomer-maxilla contact separates the two structures (figs. 2B, 3B).

Palatine—The palatine is very wide, and it laterally suppresses the suborbital fenestra (contra Borsuk-Bialynicka, 1985: fig. 2B). Anteriorly, it has a horizontal suture with the vomer and anterolaterally an oblique suture with the palatal process of the maxilla. The paired palatines have a short midline contact behind the vomer-palatine suture anteriorly (see fig. 2B, 3B), but are separated by the pyriform recess (or interpterygoid vacuity) posteriorly. Laterally, this element forms most of the medial border of the suborbital fenestra, which has little contribution from the pterygoid. Posteriorly, the palatine-pterygoid suture (unclear on the holotype, see Borsuk-Bialynicka, 1985: fig. 2) is shown on several of the new specimens (e.g., MAE 241/93-130, 94-38, 115/93-93, 95-52). This suture is transverse in dorsal view, but forms an irregular wavy line in palatal view, with a short anteromedial process of the pterygoid overlapping the palatine. The palatine is toothless, although some specimens show slanting ridges on their ventral surfaces (e.g., 115/93-93, 94-38).

Pterygoid—Anteriorly, the pterygoid is strongly widened and fan-shaped, lacking a sharp bifurcation of the palatal process from the lateral process. On the lateral edge of the anterior expansion of the pterygoid, the weakly developed pterygoid flange is a thin and low crest, which laterally joins the slightly thickened ectopterygoid. Pterygoid teeth are present, but strongly reduced. They are recognizable as a remnant row near the border of the pyriform recess (e.g., MAE 115/93-93, 241/93-130, 95-52). *Shinisaurus* has a single row of pterygoid teeth (see McDowell and Bogert, 1954: fig. 4), but *Xenosaurus* lacks them.

As in many other anguimorphans, the quadrate process in *Carusia* is slender and abruptly turns laterally at the base of the anterior fan-shaped expansion. Medially the process is concave, with a groove allowing the basipterygoid process to slide backward to some degree. The mesopterygoid fossa is considered primitive, since its anteroventral border lacks a prominent projection. In xenosaurids, helodermatids, varanids, and most anguids, such a projection is well developed (see Rieppel, 1980a) to enhance the basipterygoid process/pterygoid joint.

Ectopterygoid—The ectopterygoid is a small bone. It has a slender anterior process extending along the ventromedial border of the jugal. This process forms part of the lateral border of the suborbital fenestra but does not contact the palatine anteriorly; thus, the maxilla narrowly enters the lateral margin of the fenestra (the maxilla contributes to at least half the length of the fenestra in extant xenosaurids). A posteromedial process forms the posterior border of the fenestra. A ventral process articulates with the pterygoid and contributes to a small part of the pterygoid flange. The ectopterygoid has a small lateral projection against the medial surface of the jugal, but is not exposed laterally at the ventral edge of the skull (see figs. 2B, 3B).

Barrows and Smith (1947: 240) stated that the ectopterygoid in *Xenosaurus* "extends as a knob to the exterior between the jugal and the maxilla at the ventral extremity of this suture." McDowell and Bogert (1954: 26) listed "entrance of the ectopterygoid into the lateral border of the skull beneath the jugal" as one of the 17 "most impressive" resemblances between *Shinisaurus* and *Xenosaurus*. Phylogenetic analyses (Rieppel, 1980a; Estes et al., 1988) have shown that the lateral exposure of the distal head of the ectopterygoid is a xenosaurid synapomorphy. Since the lateral exposure of the ectopterygoid does not occur in basal *Carusia* as described above, this character apparently evolved within the carusioid clade; however, because it cannot be assessed in other fossil taxa (*Exostinus*, *Restes*), the exact level of inclusiveness for this character within the carusioid clade cannot be determined in this study.

Epipterygoid—An epipterygoid is well preserved on several specimens (e.g., MAE 241/93-130, 104/93-158, 115/93-93, 94-38; see fig. 4B). In *Carusia*, this element is obliquely positioned, which differs from the nearly vertical position in *Shinisaurus* and

Xenosaurus (see McDowell and Bogert, 1954: fig. 4; Rieppel, 1980a: fig. 21). In keeping with the oblique position, the dorsal end of the epipterygoid attaches to the lateral surface of the alar process of the prootic, rather than to the anterior border as in *Xenosaurus*. Without distortion, MAE 115/93-93 (on both sides) shows that the epipterygoid has no contact with the more anteromedially located downgrowths of the parietal. This condition is also shown on several other well-preserved specimens (e.g., MAE 94-38, 96-122, 96-196), with the exception of MAE 241/93-130, in which the dorsal end of the epipterygoid has been slightly dislocated, facilitating contact with the parietal process. As in extant xenosaurids and many other lizards, the epipterygoid has a ventral "foot" which fits into a small pit (fossa columella) at the base of the quadrate process of the pterygoid.
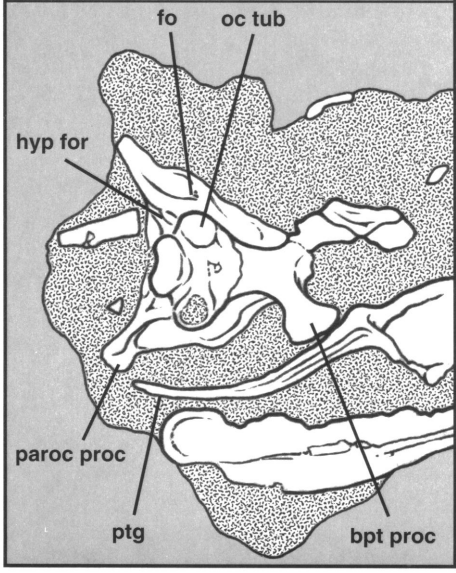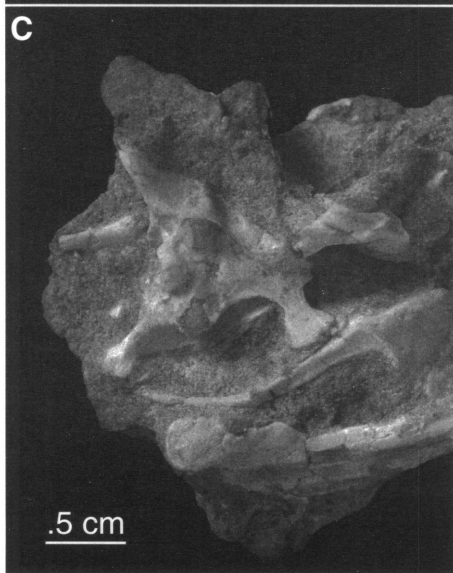
BRAINCASE

The braincase is preserved on several specimens (e.g., MAE 94-38, 115/93-93, 40/93-90, 95-5, 95-52, 33/93-167, and 96-122). As in many other lizards, the supraoccipital is roughly a hexagonal element in dorsal view, roofing the posterior part of the braincase and forming the dorsal margin of the foramen magnum. Anterodorsally, the supraoccipital bears a prominent bony processus ascendens (= processus anterior tecti of Jollie, 1960), with a short supraoccipital crest on its dorsal surface. The posterior semicircular canals are clearly recognizable on both sides of specimens such as MAE 115/93-93 (fig. 4A). The supraoccipital of *Carusia* differs from that of *Xenosaurus* and *Shinisaurus* in having a prominent and well-ossified marginal process anterolateral to the processus ascendens. Such a marginal process is poorly defined in *Ctenosaura pectinata* (Oelrich, 1956: fig. 7), calcified in large iguanians (see Jollie, 1960), and ossified but small in some scincids (e.g., AMNH 37830: *Mabuya agilis*; AMNH 99684: *Tiliqua nigrolutea*) and anguids (see Rieppel, 1980a: figs. 16–18). The ossification and elongation of this process in *Carusia* are probably derived conditions for this taxon among scincogekkonomorphs.

Lateral to the braincase floor, a recessus

vena jugularis (of Oelrich, 1956; vena capitis lateralis of Jollie, 1960) is well developed. The lateral wall (crista prootica) of this troughlike recess is broken in several specimens, but is well preserved on several others (e.g., MAE 115/93-93, 96-122). The well-preserved specimens show that the recess is relatively wide and deep in comparison with the greatly reduced groove in *Xenosaurus*. Anterior to the prootic bulge (otic capsule), the trough turns medially and ends as a fossa above the base of the basipterygoid processes of the basisphenoid (entocarotid fossa of McDowell and Bogert, 1954). Such a fossa is well developed in most lizards but is nearly or entirely lost in extant xenosaurids, helodermatids, varanids (McDowell and Bogert, 1954), and some anguids (e.g., *Anniella*). Two foramina open into the recessus vena jugularis: one is the posterior foramen of the vidian canal, which opens on the medial wall of the recess and at the basisphenoid-prootic suture anteriorly within the recess. The same foramen in *Xenosaurus* (AMNH 98122, 103212) and *Shinisaurus* (Rieppel, 1980a: fig. 20) opens roughly at the same position as in *Carusia*. Another foramen, the facial foramen, is more posterolaterally located, and opens on the roof of the recess (best shown on MAE 115/93-93, 96-122) within a fossa anterolateral to the otic capsule. In *Xenosaurus*, this foramen opens at a similar position in relation to the bulge of the otic capsule, but it opens in a shallow groove because the fossa is absent.

In lateral view and dorsal to the recessus vena jugularis, the anterior inferior process, trigeminal notch, and the alar process of the prootic are clearly identifiable (contra Borsuk-Bialynicka, 1985). These structures are best shown on MAE 115/93-93 (fig. 4B) without distortion, while other specimens often have the anterior part of the prootic missing as a matter of preservation. The alar process is close to (or nearly in contact with) the ventral process of the parietal. Posterior to the alar process, the anterior and the external semicircular canals end at the anterior ampullar recess, which is slightly posterodorsal to the trigeminal notch. This location of the anterior ampullar recess is similar to the condition in *Shinisaurus* (see Rieppel, 1980a: fig. 20), but in a significantly lower position
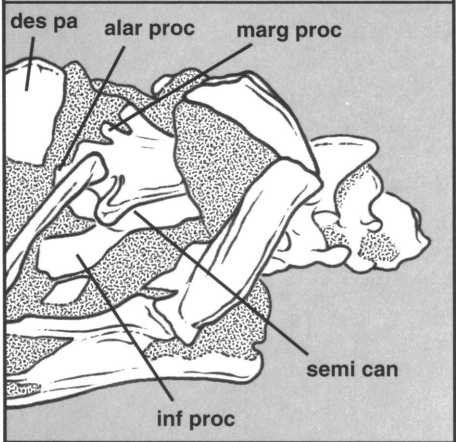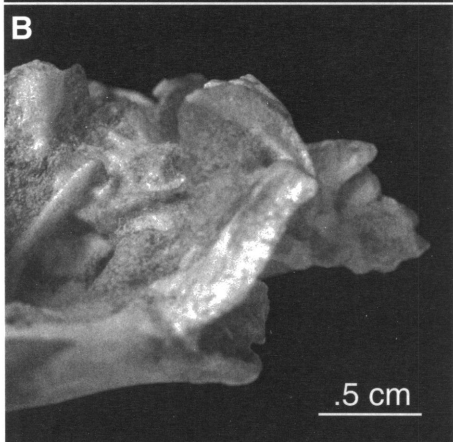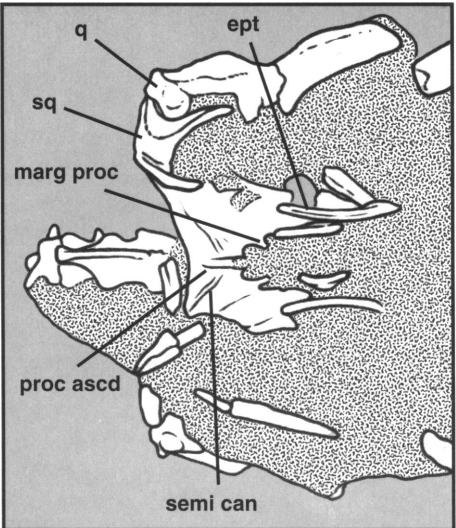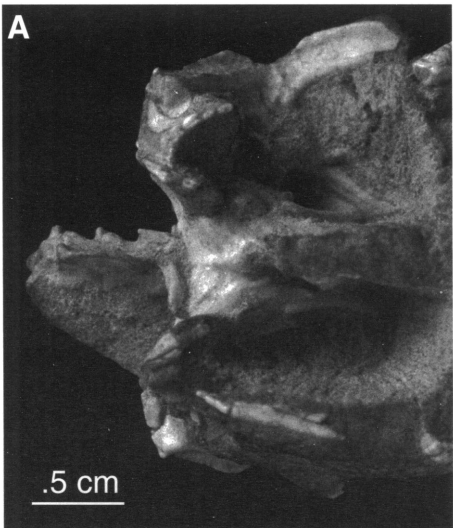
than in *Xenosaurus*, in which the recess is clearly dorsal to the trigeminal notch.

In ventral view, the basioccipital and basisphenoid contribute about equally to the formation of the braincase floor (figs. 3B, 4C). The two elements are separated by an angulate and laterally diagonal suture as in extant xenosaurids (see Rieppel, 1980a: figs. 20, 21) and many other lizard groups. Anteriorly, the basipterygoid processes diverge from the base of the basisphenoid forming a Y-shaped bifurcation. Between the basipterygoid processes, only the base of the parasphenoid process is ossified (e.g., MAE 115/93-93) and slightly bent dorsally. Posteriorly, a basicranial fontanelle or foramen (best shown on MAE 94-38, 40/93-90) is a round opening between the spheno-occipital tubercles (see also Borsuk-Bialynicka, 1985). Such a foramen is present in extant *Shinisaurus* (McDowell and Bogert, 1954; Rieppel, 1980a: fig. 20), but is absent in *Xenosaurus*. The spheno-occipital tubercles are much stronger than those in *Xenosaurus*, and have no distinct epiphysis as in the latter taxon. The so-called "distinct epiphysis" mentioned in Borsuk-Bialynicka (1985: 158) is not present on any of the new specimens for this study. The occipital recess (recessus scalae tympani of Siebenrock, 1894; Romer, 1956) is on the posterolateral aspect of the spheno-occipital tubercle, and is ventromedial to the foramen ovale. The recess opens posterolaterally, and is two to three times the size of the foramen ovale (in *Xenosaurus* the recess is only slightly larger than the foramen ovale). Several specimens (e.g., MAE 94-38, 95-5, 115/93-93) show the footplate of the stapes in the foramen ovale, and one of them (MAE 115/93-93) even has part of the stapes bridging the gap between quadrate and the prootic.

In occipital view, the exoccipital is fused with the opisthotic. This compound element contributes to the lateral border of the foramen magnum and the lateral part of the occipital condyle; however, a suture with the basioccipital is undetectable as the result of fusion (e.g., MAE 115/93-93, 96-122; see Jollie, 1960, for discussion). Laterally, most of the exoccipital contributes to the paroccipital process, which is posterolaterally directed and relatively short. Medioventrally at the base of the process is the fissurelike vagus or jugular foramen (X, XI). The hypoglossal foramen (XII), much smaller and rounded, is more ventrally located and opens at the dorsal border of the occipital recess (best shown on MAE 96-122). In *Xenosaurus* (e.g., *Xenosaurus grandis* AMNH 98122, 103212) the number of openings for the hypoglossal (XII) nerve varies from two to three (see also Barrows and Smith, 1947). A variable number of hypoglossal nerve foramina is also known for other lizards (see e.g., Jollie, 1960).

CRANIAL OSTEODERMS

Like extant xenosaurids, *Carusia* has well-developed osteodermal incrustation covering the major skull roofing elements. The osteoderms are most prominent around the orbit, but do not cover the ventral part of the maxilla where the alveolar foramina are located. Structurally, the osteoderms are subdivided into small units and are ornamented with vermiculate sculpture, as in extant xenosaurids. Minor variation in terms of thickness of the osteoderms can be observed among specimens. Generally, relatively robust skulls are more heavily ornamented than lightly built ones. In addition, extent and thickness of the osteodermal ornamentation are related to ontogenetic development. For instance, a juvenile specimen (MAE 96-50) has only weakly developed osteoderms, while large individuals (adults) have significantly heavier ornamentation.

LOWER JAW

On the holotype, sutures of the dentary-postdentary elements of *Carusia intermedia* are difficult to delimit (see Borsuk-Bialynicka, 1985), and some important structures (such as the mandibular foramen) were in-

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Fig. 4.   Braincase of *Carusia intermedia*: dorsal (**A**), lateral (**B**), and ventral (**C**) views. A and B from MAE 115/93-93, and C from MAE 96-122.

correctly reconstructed. The new collections provide a much better preserved and larger sample of specimens, which allows accurate delimitation of the mandibular elements and reveals phylogenetically important mandibular characters.

The largest element of the lower jaw, the dentary, laterally forms slightly over one-half of the anterior part of the mandible. The lateral surface of the dentary is smooth, and carries a row of irregularly arranged mental foramina. Posterodorsally, the dentary has a small coronoid process (dental lappet of Borsuk-Bialynicka, 1985), which slightly overlaps the anterior surface of the coronoid (MAE 115/93-93, 92/93-104, 94-38, 104/93-158, 95-51, 95-52, 95-72), as in *Shinisaurus* and *Xenosaurus* (see Rieppel, 1980a: figs. 20, 21). It must be emphasized that this is not the same condition as in scincomorphans (contra Borsuk-Bialynicka, 1985), in which the coronoid process of the dentary overlaps the lateral process of the coronoid laterally. The coronoid of *Carusia* lacks a well-defined lateral process, and the posteroventral process of the dentary does not extend posterior to the level of the apex of the coronoid process (fig. 5A).

Medially, the subdental shelf is relatively robust, but it lacks a dorsal ridge and the sulcus dentalis is lost (e.g., MAE 94-49-2). As in extant xenosaurids, the Meckelian canal is covered by a well-developed splenial, but anteriorly is open ventrally. The anterior inferior alveolar foramen is elongate, and located slightly anterior to the midpoint of the dentary tooth row. Although close to the splenial-dentary suture, this foramen penetrates the splenial—a primitive feature, as in most scincomorphans. In extant anguids and xenosaurids this foramen opens at the suture between the dentary and splenial. A much smaller and rounded anterior mylohyoid foramen is posteroventral to and close to the anterior inferior alveolar foramen (MAE 94-49-2, 233/93-99; see fig. 5B). Below the anterior third of the dentary tooth row, the anterior end of the splenial is notched (contra Borsuk-Bialynicka, 1985: fig. 3) with the dorsal spikelike process slightly longer than the ventral one (MAE 94-38). The posterior extension of the splenial terminates anterior to the posteromedial process of the coronoid,
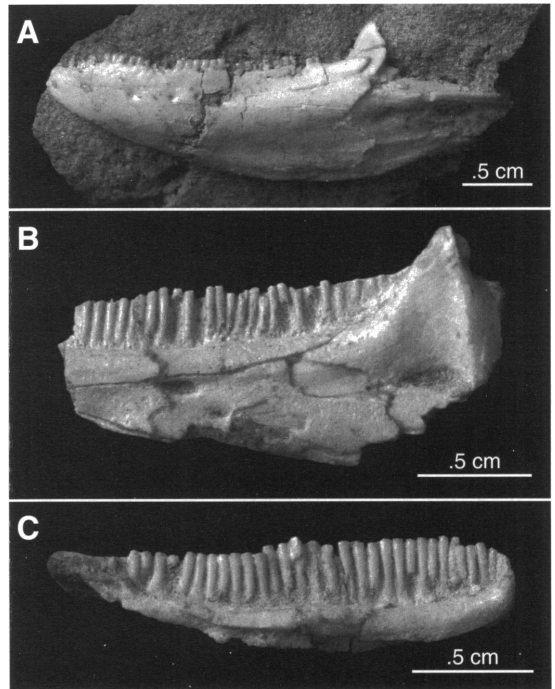
Fig. 5. Lower jaw of *Carusia intermedia*: MAE 95-51, lateral view of left mandible (**A**); MAE 94/49-2, incomplete right mandible, medial view (**B**) showing anterior inferior alveolar foramen and anterior mylohyoid foramen; MAE 61/93-130, medial view (**C**) showing unworn tooth crowns.

but slightly posterior to the dorsal eminence of the coronoid. In anguimorphans, this morphology of the splenial is seen in anguids and xenosaurids, but not in helodermatids and varanids in which the splenial terminates anterior to the dorsal process of the coronoid. The coronoid in *Carusia* has a robust anteromedial process, the anterior end of which extends below the subdental shelf and is medially overlapped by the dorsal part of the splenial (fig. 5B).

Some fragmentary specimens (e.g., MAE 94-101), where the Meckelian canal is exposed, show that a small but clearly defined intramandibular septum is vertically directed and is roughly at the midlevel of the tooth row. Presence of such a septum is an anguimorphan synapomorphy (e.g., Estes et al., 1988). Another systematically significant character of the lower jaw is the articulation of the dentary with postdentary elements

(Gauthier, 1982; Estes et al., 1988). The dentary-postdentary articulation, in lateral view, is best shown on two specimens (MAE 95-51, 95-72), which reveal that the articulation in *Carusia* is essentially of anguimorphan style: presence of a dorsal (coronoid) and a ventral (surangular) notch on the posterior margin of the dentary (Estes et al., 1988). However, the notches (especially the coronoid notch) in *Carusia* are small and are not as well developed as in other anguimorphans.

The postdentary part of the mandible is preserved in several specimens (e.g., MAE 94-38, 95-5, 95-52, 104/93-158, 96-50, 96-122). These specimens show that the postdentary part of the jaw is strongly constricted at its ventral border, and is strongly twisted ventromedially, so that the posteriormost part is nearly horizontal. Anterodorsally at the surangular-coronoid suture is the anterior surangular foramen exposed in lateral view (e.g., MAE 95-5, 94/49-1). Anterodorsal to this foramen is the very small dorsal process of the coronoid bone, which is anteriorly covered by a small coronoid process of the dentary. In lateral view, the coronoid sits in a small coronoid notch of the dentary. Posterior to the coronoid, the surangular has a strong lateral crest (adductor crest of Borsuk-Bialynicka, 1985), extending from a point lateral to the anterior surangular foramen to slightly anterior to the craniomandibular joint (see figs. 2A, 5A). Presence of such a strong crest is a unique character for *Carusia intermedia* as Borsuk-Bialynicka (1985) has recognized. Functionally, such a crest provides strong insertion for a powerful adductor muscle to move a very heavily built lower jaw.

As Borsuk-Bialynicka (1985) correctly described for the holotype, many adult specimens have the surangular fused with the articular-prearticular; the line of fusion is clearly marked with a ridge (e.g., MAE 115/93-93). However, the fusion is obviously an ontogenetic feature, since a juvenile specimen (MAE 96-50) has a clear suture separating the two elements. The posterior surangular foramen is located slightly anterolateral to the craniomandibular joint, again exposed in lateral view. The angular is slightly smaller than the surangular, and is sutured to the latter even in adults (e.g., MAE 95-51, 95-52, 95-72, 94-38). It has a pointed anteroventral process, which ventrally intervenes between the dentary and splenial, and extends to a level slightly anterior to the posterior end of the tooth row. A large part of the angular is a thin tongue attached on the ventrolateral surface of the surangular, and posteriorly it ends at a point slightly anteroventral to the posterior surangular foramen.

Posterior to the quadratomandibular joint, a retroarticular process (best shown on MAE 115/93-93) is short and relatively wide, but clearly different from the widened condition in anguids. In shape, the process is more similar to that in *Shinisaurus* (Rieppel, 1980a: fig. 20) than in *Xenosaurus*, in which the process is much more slender and elongate. *Carusia* differs from extant xenosaurids that have a medially deflected (see Rieppel, 1980a: figs. 20, 21) retroarticular process; in *Carusia* it is essentially posteriorly directed (see e.g., figs. 2B, 3B). The dorsal surface of the retroarticular process is concave, and has a small foramen (foramen chorda tympani) behind the small buttress (flap) that reinforces the craniomandibular articulation (see above).

The mandibular fossa is reduced to a narrow slit (contra Borsuk-Bialynicka, 1985; see later discussion) as in extant xenosaurids (e.g., *Xenosaurus*, AMNH 98122), and the mandibular fossa is oriented more dorsally than medially (see fig. 2A).

MARGINAL TEETH

The marginal teeth of *Carusia intermedia* were poorly known, because the holotype has damaged crowns (see Borsuk-Bialynicka, 1985). Fortunately, a large number of new specimens show that one of the distinct characters for this lizard taxon is the presence of numerous marginal teeth with a comblike arrangement. The maxillary teeth are best preserved on MAE 96-164, and dentary teeth with unworn crowns are preserved on several specimens (e.g., MAE 95-51, 94-49-2, 96-40, 61/93-130). These specimens show that the crowns are not simply conical as previously illustrated (Borsuk-Bialynicka, 1985: fig. 3), but are more or less chisel-shaped with a small and low central cusp and a lateral crest on each side of the cusp (figs. 5C, 6). The crown surfaces are smooth, without
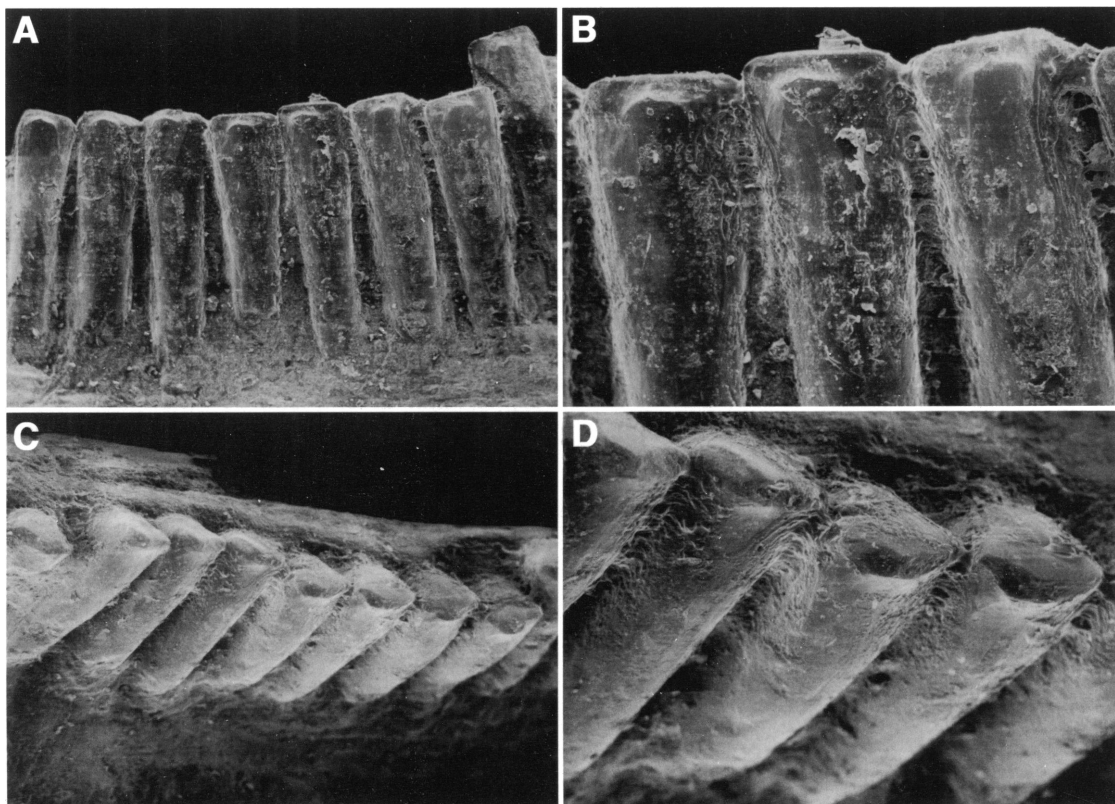
Fig. 6.   SEM photographs showing crown pattern of dentary teeth in *Carusia intermedia* (MAE 61/ 93-130): **(A)** lingual view of posterior dentary teeth, ×23; **(B)** higher magnification of three posterior teeth, lingual view, ×54; **(C)** occlusal view of posterior dentary teeth, ×23; **(D)** high magnification of four posterior teeth, ×50.

lingual or labial striations. The tooth shaft is anteroposteriorly compressed, but lacks the strong shoulder seen in some fossil anguids (e.g., *Odaxosaurus*, see Estes, 1964). In medial view, these teeth are highly pleurodont with over two-thirds of the tooth height attached to the lateral parapet of the jaw. In terms of tooth count, the maxillary tooth row comprises at least 32 teeth (e.g., MAE 104/ 93-158, 115/93, 94-38), whereas the dentary has about 37 (e.g., MAE 115/93-93).

As seen in many other anguimorphans, each tooth has a small basal foramen (alveolar foramen). Replacement teeth are developed interdentally at the base of the functional teeth, rather than within replacement pits; therefore, no evidence indicates a direct or "iguanid" pattern of replacement in *Carusia* (contra Borsuk-Bialynicka, 1985). This replacement pattern is similar to that seen in extant *Xenosaurus* (e.g., AMNH 103212), except that the interdental position of the replacement teeth is more pronounced than in the latter taxon. Nonetheless, like many other primitive anguimorphans (see Rieppel, 1978), it falls in the category of the so-called intermediate condition (Edmund, 1960).

CERVICAL VERTEBRAE

Cervical vertebrae including the atlas-axis complex are preserved in at least two prepared specimens (MAE 115/93-93, 94-38). The atlas consists of the first intercentrum sutured to the two half neural arches. This vertebra forms a ring that articulates directly with the occipital condyle. The posterior zygapophysis of the atlas is a spikelike structure

in lateral view, but medially has a horizontal articular surface for the anterior zygapophysis of the axis. The atlas has a relatively strong transverse process, which is a similar size to that of the axis. Such a process is well developed in comparison to those in other anguimorphans (see Rieppel, 1980a). The neural arch lacks a prominent anterior process and a posterior lappet, and in these aspects the atlas of *Carusia* differs from that of *Xenosaurus* (see e.g., Rieppel, 1980a).

The axis has a crown, with a posterior extension over nearly the entire third cervical. Such a strong posterior extension of the crown is unique for *Carusia*, and sharply different from all other anguimorphans in which the extension terminates at the same level, or slightly dorsal to, the posterior condyle of the axis (see Rieppel, 1980a: figs. 26, 27). The odontoid process is fused with the axis, resembling other primitive anguimorphans but differing from the varanoid condition (see Rieppel, 1980a). The second intercentrum is incompletely preserved on MAE 115/93-93, but is likely to be fused to the centrum of the atlas and is now broken along that plane. The third intercentrum is not preserved, but is probably free from the centrum, since an articular surface is identifiable on MAE 115/93-93. The axis is short, and has a transverse process that is about the same length as that of the atlas.

PHYLOGENETIC ANALYSES AND RESULTS

One of the goals of this study is to resolve the phylogenetic relationships of the anguimorphan lizard taxa (including *Carusia*) from the Gobi Desert. Besides *Carusia*, nine other anguimorphan taxa from the Gobi are included in our analyses, among which *Estesia* is the only taxon whose relationship has been resolved (Norell and Gao, 1997). Among others, two (*Paravaranus* and *Bainguis*) were previously classified as "preanguimorphan grade," three (*Proplatynotia, Parviderma,* and *Gobiderma*) as "necrosaurian grade," and three others (*Cherminotus, Telmasaurus,* and *Saniwides*) as "modern platynotan grade" (see Borsuk-Bialynicka, 1984).

To resolve these phylogenetic relation-

ships, a matrix containing 105 characters across 33 taxa (including 30 ingroup and three outgroup taxa) was constructed (see table 1). The characters were polarized using the Scincomorpha, Gekkota, and Iguania as successive outgroups, based on the phylogenetic framework presented by Estes et al. (1988). We used PAUP version 3.1.1 (Swofford, 1993) to analyze the data set; tracing character evolution was facilitated by using MacClade version 3.03 (Maddison and Maddison, 1992). To analyze such a large data set, we used the PAUP Heuristic search option under several different search strategies.

The first run used the complete data set with all the taxa and characters included. This analysis terminated at the MAXTREES limit (32,700). Strict consensus of the 32,700 equally short trees (TL = 256, CI = 0.543, RI = 0.794) shows that two major clades among our ingroup taxa are supported (fig. 7A): the most basal anguimorphan clade (Carusioidea), and its sister group (an unnamed new clade) consisting of the Anguidae and Platynota. Grouped in the Anguidae are not only the four selected taxa (*Gerrhonotus, Diploglossus, Ophisaurus,* and *Anguis*) normally classified in the family, but also *Bainguis* from the Gobi and *Anniella* (see discussion below). Within the Platynota, the Monstersauria is the only well-supported clade, as suggested by our previous analyses (Norell and Gao, 1997), while 13 other fossil and extant taxa are unresolved.

An obvious cause of this polytomy is that some of the fossil taxa have large amounts of missing data (see table 1). Inclusion of such taxa in a phylogenetic analysis often produces extremely high numbers of equally parsimonious trees (Gauthier, 1986; Nixon and Wheeler, 1992; Novacek, 1992). To generate hypotheses with better resolution and to test the influence of missing data on our result, we ran several analyses with successive deduction of taxa.

Among the fossil taxa included in our analysis, *Palaeosaniwa* is the most problematic. It is a poorly represented taxon based on very fragmentary material (Gilmore, 1928; Estes, 1983; Gao and Fox, 1996), and contains about 90% missing entries in our data set. With *Palaeosaniwa* deleted, the number of equally short trees was reduced to

TABLE 1

Taxon–Character Data Matrix (see appendix 1 for character description)

	1									10										20										30					35
Scincomorph	0/1	0	1	0	1	0/1	0	0	0	0	0	0/1	0	0	0	0	0	0	0/1	0	0	0	1	0	0/1	0	0/1	0	0	0	0/1	0	0	0	0
Iguania	0/1	0	0	1	0	1	0	0	0	0	1	1	1	1	0	9	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0/1	0	0/1	0
Gekkota	0	0/1	0/1	1	1	0/1	1	1	0	1	1	1	2	1	9	1	0	0	0	9	3	1	3	1	1	0	0	1	0	0	0	0	0	0	0
Carusia	0	1	1	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	1	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0
Exostinus	?	?	?	1	1	1	?	?	0	0	0	1	?	?	1	?	1	0	1	0	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?
Restes	?	?	?	0	1	0	?	?	0	?	0	0	?	?	1	?	1	0	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Necrosaurus	?	0	0	1	1	0	?	?	0	0	2	1	1	1	1	0	0	0	1	0	?	0	?	0	0	0	0	0	0	1	1	1	1	1	1
Paravaranus	?	2	2	1	2	1	1	1	0	0	2	2	2	?	0	?	?	0	1	0	?	?	?	?	0	1	1	1	?	1	1	1	1	1	?
Bainguis	?	?	?	1	0	1	1	1	1	0	0	2	2	?	?	1	?	0	?	1	?	?	?	?	0	0	0	1	?	1	?	?	?	?	1
Proplatynotia	0	1	1	0	2	0	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	?	0	0	0	0	0	0	0	0	0	0	0	0	1
Parviderma	?	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	?	0	0	0	0	0	1	1	0	0	1	?	?	?	?
Gobiderma	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	1	0	1	0	0
Saniwides	0	1	1	2	0	1	1	2	0	0	0	2	1	2	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1
Paraderma	?	?	?	1	?	?	?	?	0	?	1	?	?	?	?	?	?	?	?	?	?	0	?	?	?	1	?	?	?	?	?	?	?	?	?
Parasaniwa	?	?	?	1	1	0	?	?	0	?	0	1	?	?	0	?	?	?	?	?	?	0	?	?	?	0	?	?	?	?	?	?	?	?	?
Eosaniwa	?	?	?	1	?	?	?	?	0	?	0	0	?	?	?	?	?	?	?	?	?	0	?	?	?	0	?	?	?	?	?	?	?	?	?
Cherminotus	0	2	2	0	1	1	2	1	0	0	3	2	2	2	1	0	1	0	0	?	9	0	3	1	1	0	0	0	1	2	0	1	0	1	1
Eurheloderma	?	?	?	1	?	?	?	?	0	?	2	1	?	?	?	?	1	0	?	?	?	1	?	0	1	1	0	1	0	?	1	?	?	?	?
Lowesaurus	?	?	?	2	1	0	2	2	1	0	2	1	1	1	0	0	0	0	1	0	?	0	?	0	0	0	0	0	1	?	1	1	0	1	0
Heloderma	0	0	0	2	2	1	1	1	0	1	3	1	0	1	1	1	1	0	1	0	9	1	3	0	1	0	0	0	1	?	0	1	0	1	0
Saniwa	1	2	2	0	0	1	3	3	2	0	0	2	0	1	1	0	0	0	0	0	0	1	0	1	1	1	0	0	2	?	0	1	0	1	1
Telmasaurus	?	?	?	2	1	0	3	3	2	0	0	2	0	0	1	0	0	0	0/1	0	0	1	0	0	0	0	0	1	2	?	1	1	1	1	1
Varanus	1	2	2	0	0	1	3	3	2	1	1	2	1	1	1	1	1	0	1	1	9	1	3	1	0	0	1	1	2	1	1	1	1	1	1
Lanthanotus	0	2	2	2	1	0	3	2	2	0	0	2	0	1	0	1	0	0	1	0	1	0	1	0	0	0	1	1	2	0	1	1	1	1	0
Estesia	0	2	2	0	1	0	3	2	1	0	1	2	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	1	0	1	0
Xenosaurus	0	1	0	1	0	1	1	1	0	0	0	1	0	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0
Shinisaurus	0	1	0	1	1	1	1	1	1	1	1	0	0	2	1	1	1	1	1	0	1	0	0	0	0	0	1	0	0	1	0	1	0	1	1
Gerrhonotus	0	0/1	0/1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0/1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Diploglossus	1	0/1	1	1	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0/1	0/1	0	1	0	0	0	0	1	0	0	0	0	0	0	0
Ophisaurus	1	0	0	0	0	0	0	0	0	0	0	2	0	0	1	1	1	0	0	1	0	0	2	0	1	0	0	0	0	1	0	1	0	0	1
Anguis	1	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0/1	0	2	0/1	1	0	2	2	1	0	0	1	0	1	0	1	0	1	1	1
Anniella	0	0	0	1	1	1	0	0	1	0	1	1	1	1	1	0	1	1	0	1	9	1	3	1	0	0	0	0	2	2	0	1	0	1	1

TABLE 1—(Continued)

Taxon	40										50										60										70
Scincomorph	0/1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Iguania	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Gekkota	0	0/1	0	0	0	0	0	0	0	0	0	0/1	0	0	0	0	0/1	1	1	1	0	0/1	0	1	0	1	0	0	0	1	0
Carusia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0/1	0	1	0	0	0	0	1	0	1	0	0	0	1	0	0
Exostinus	?	?	?	?	0	0	0	0	0	0	0	0	0	1	1	0	?	?	1	?	1	1	1	1	1	?	0	1	1	1	?
Restes	?	?	?	?	0	0	?	0	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?
Necrosaurus	?	0	?	1	0	1	1	1	?	1	0	?	?	?	?	?	?	?	1	?	1	?	2	1	1	?	?	?	?	?	?
Paravaranus	?	0	?	?	0	1	1	0	0/1	0	0	?	?	?	?	?	?	?	1	?	1	?	1	1	1	?	?	?	?	0	?
Bainguis	?	?	?	?	0	1	1	?	?	2	2	?	?	?	?	?	?	?	1	?	1	?	2	1	1	1	?	?	?	?	?
Proplatynotia	?	0	1	?	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	2	0	1	1	1	0	1	1	0
Parviderma	?	0	?	1	1	1	1	1	?	1	1	?	?	1	?	?	?	1	1	1	1	1	2	1	1	1	1	?	0	1	?
Gobiderma	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1
Saniwides	0	0	0	1	1	1	1	1	0	0	0	1	0	0	0	0	1	1	1	1	1	1	2	0	1	0	0	0	1	1	0
Paraderma	?	1	1	1	1	1	1	1	?	?	?	?	?	1	?	?	?	1	1	1	1	1	2	0	1	1	?	?	1	1	?
Parasaniwa	?	?	?	?	1	1	1	?	?	1	1	?	?	1	?	?	?	1	1	?	1	1	2	0	1	1	?	?	1	1	?
Eosaniwa	?	0	?	?	?	0	0	0	?	1	1	0	0	0	1	1	?	1	0	?	1	1	2	0	1	?	?	?	1	0	0
Cherminotus	0	1	?	?	1	1	1	2	2	2	1	?	?	1	?	?	?	1	2	1	1	1	2	0	1	1	1	1	1	1	1
Eurheloderma	?	1	?	?	1	1	1	2	2	2	1	?	?	1	?	?	?	1	2	?	1	1	2	1	1	1	1	?	0	1	1
Lowesaurus	?	1	?	1	1	1	1	2	2	1	1	?	?	0	?	?	?	1	2	1	1	1	2	0	1	1	1	1	1	1	0
Heloderma	1	1	0	1	1	1	1	2	2	2	2	0/1	1	1	0	1	2	1	2	1	1	1	2	1	1	1	1	1	1	1	0
Saniwa	0	?	1	1	1	1	1	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	2	0	1	0	0	0	1	1	0
Telmasaurus	0	?	1	?	1	1	1	?	?	?	?	?	?	0	?	?	?	1	2	?	1	1	2	0	1	1	?	?	1	1	?
Varanus	0	0	1	1	1	2	1	2	1	2	2	1	1	0	1	1	2	2	2	2	1	1	2	0	1	1	1	1	1	1	0
Lanthanotus	0	1	1	1	1	2	1	2	1	2	2	1	0/1	1	0	1	2	2	2	2	1	1	2	0	1	1	1	1	1	1	1
Estesia	1	1	0	1	1	2	1	2	1	2	1	0	?	1	1	?	?	?	1	?	2	1	2	1	1	?	?	?	?	?	?
Xenosaurus	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1
Shinisaurus	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
Gerrhonotus	0	0	0	1	0	1	1	0	0	1	1	0/1	0	0	0	1	1	1	0	1	0	1	1	1	1	0	1	0	1	1	1
Diploglossus	0	0	0	1	0	0/1	1	0/1	0	1	1	0	1	0	0	1	1	0	1	0	0	0	1	1	0	0	0	0	1	1	1
Ophisaurus	0	0	0	1	0	1	1	0	0	1	0/1	1	0	1	0	1	1	2	0	0	0	0	2	0	1	1	0	1	1	1	1
Anguis	0	0	0	1	0	2	2	2	0/1	2	1	0/1	1	1	1	0	1	1	2	2	2	2	1	1	0	0	0	1	1	1	1
Anniella	0	0	1	0	0	0	0	2	2	2	0	1	1	1	1	0	1	1	2	1	2	2	1	1	0	1	0	1	1	1	1

TABLE 1—(Continued)

	80										90										100					105
Scincomorph	0	0/1	0/1	0/1	0	0	0	0	0	0	0/1	0	0/1	0	0	0/1	?	0	0	0	0	1	0	0	0	0
Iguania	0	0	0	0	0	0	0	0/1	0/1	0	0	0	0	0	0/1	0	0	0	0	0	0/1	0	0	0	0/1	0
Gekkota	1	0	0	0	0	0	0	0	0/1	0/1	1	0	0	0	0	0/1	?	0	0	0	0	0/1	?	?	0	0
Carusia	0	2	1	0	0	0	?	0	0/1	1	1	0	?	0/1	0	?	0/1	0	0	0	?	?	?	?	?	?
Exostinus	?	2	1	1	0	0	?	?	?	1	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?
Restes	?	2	1	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Necrosaurus	?	1	0	1	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Paravaranus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bainguis	1	0	1	1	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	2	?	?	?	?	?
Proplatynotia	?	0	1	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Parviderma	?	1	1	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Gobiderma	1	2	2	1	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Saniwides	1	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Paraderma	?	2	2	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Parasaniwa	?	2	2	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eosaniwa	1	?	?	?	?	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cherminotus	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eurheloderma	?	2	2	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lowesaurus	?	2	2	1	1	0	1	1	1	9	0	1	?	1	1	1	1	2	1	2	2	0	1	1	1	0
Heloderma	1	2	0	1	0	1	0	0	9	1	0	1	1	0	0/1	0	0	1	0	0	0/1	1	1	1	1	0
Saniwa	1	?	?	0	1	1	1	0	1	1	0	?	?	?	1	?	?	?	?	?	2	1	?	?	?	?
Telmasaurus	?	?	1	1	0	1	1	1	1	1	1	?	1	1	1	1	1	2	1	2	2	1	1	1	1	1
Varanus	1	2	1	0	0	1	1	1	0/1	1	2	0	1	1	1	0/1	1	1	1	2	2	1	1	1	1	1
Lanthanotus	1	2	0	0	1	1	1	?	1	1	2	0	1	1	1	0	0	1	1	2	2	?	1	1	1	1
Estesia	?	?	?	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Xenosaurus	1	2	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	1
Shiniscaurus	1	2	1	1	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	0	0	1
Gerrhonotus	1	1	0	0	2	0	0	2	0	0	1	0	0	1	0	1	1	1	1	1	1	1	0	0	1	0
Diploglossus	1	0	1	0	2	0	0	2	0	0	1	1	0	1	0	1	1	1	0	1	1	2	1	0	1	1
Ophisaurus	1	0	1	0	2	0	0	2	0	0/2	1	0	0	0	0	0	0	1	1	1	1	2	0	0	1	1
Anguis	1	0	1	0	2	0	0	2	9	2	2	1	1	0	0	1	0	1	1	1	1	3	0	0	?	1
Anniella	1	0	0	1	0	0	0	2	9	2	2	1	9	0	0	0	0	0	0	1	1	0	?	0	0	1

32,171 (TL = 256, CI = 0.543, RI = 0.794). The strict consensus tree of these shows much better resolution among platynotan taxa than our first analysis, and once again supports the monophyly of Carusioidea, Anguidae (with *Bainguis* and *Anniella*), and Platynota. Within Platynota, a significant topological change is the grouping of five taxa (the Varanoidea, see discussion below) as a sister group to *Paravaranus*. Varanoidea (equivalent to the Varanidae of previous authors, e.g., Estes, 1983) includes *Cherminotus* and *Lanthanotus* as sister groups followed by *Varanus*, *Saniwa*, and *Telmasaurus* (fig. 7B). Six fossil taxa (*Necrosaurus*, *Proplatynotia*, *Parviderma*, *Saniwides*, *Parasaniwa*, and *Eosaniwa*) form an unresolved position at the base of Platynota.

For our third run, we further revised the data set by eliminating three more taxa (*Restes*, *Bainguis*, and *Eosaniwa*) each of which contains 80–84% missing entries in the data matrix. This analysis discovered 180 equally short trees (TL = 253, CI = 0.549, RI = 0.791). The strict consensus of the 180 equally parsimonious trees shows no significant topological change except that *Necrosaurus–Parviderma–Parasaniwa* are grouped as monophyletic (compare fig. 7B with 7C). This grouping is weakly supported by two character states: frontals are fused (6-1), and lateral borders of frontals are constricted between orbits (7-1). This grouping is the direct result of eliminating *Eosaniwa* from the analysis. Elimination of *Restes* has no significant effect on topology of the carusioid clade, but removal of *Bainguis* resolved an *Anniella–Anguis* clade within the Anguidae and *Ophisaurus* is placed as the sister taxon to this group (see fig. 7C).

In our fourth analysis, we deleted five more taxa (*Exostinus*, *Parasaniwa*, *Paraderma*, *Eurheloderma*, and *Lowesaurus*) so that our data set contained no taxa with more than 70% missing data. Four equally parsimonious trees were found. The removal of the five taxa that have already grouped with their related clades has no significant effect, and the strict consensus of the four equally short trees (TL = 250, CI = 0.548, RI = 0.773) displays a simplified pattern of the cladogram resulting from our third run: the Carusioidea remain as the most basal angui-

morphan clade, in which *Carusia* is shown as the sister group of a *Xenosaurus–Shinisaurus* clade (Xenosauridae). Within the Monstersauria, *Gobiderma* remains in the most basal position, but *Estesia* is placed as the sister group of *Heloderma* as a result of the removal of three taxa in this clade (*Paraderma*, *Eurheloderma*, and *Lowesaurus*). Other taxa have the same positions as in our third analysis (figs. 7C, 7D).

As discussed above, the following groupings of our ingroup taxa are stable throughout our analyses: (1) Carusioidea are placed as the most basal anguimorphan clade; (2) Anguidae are placed as the sister group of the Platynota, and the two groups together form a major anguimorphan clade as the sister taxon of Carusioidea; (3) Monstersauria is well supported as monophyletic, enhancing the results from our previous study; and (4) Varanoidea is monophyletic in all trees in which the highly problematic taxon *Palaeosaniwa* is deleted. The evidence supporting these groupings is presented below in a discussion of each of these clades.

Those taxa with large amounts of missing data may or may not have significant impact on the entire parsimonious framework of our analyses, depending on the type of characters scored for these taxa. For example, *Palaeosaniwa* contains about 90% missing data in our data set, and inclusion of this taxon in our analyses causes not only an extremely high number of most parsimonious trees (that a computer with memory of 40 MB RAM and one GB Hard-Drive cannot handle), but also poor resolution of the relationships of the platynotan taxa involved. On the other hand, *Bainguis*, containing the second highest number of unknown entries (about 85%) in our data set, can be grouped with other anguinines within the Anguidae. The real difference is that the 15% known characters scored for *Bainguis* contain several pivotal ones that support its grouping with other anguids. Therefore, it is not only the amount of, but also the type of, missing data that may have crucial effect on the phylogenetic results (Gauthier et al., 1988). Evidently, removal of those taxa (with large amounts of missing data) that are already grouped with their related taxa does simplify the topology of that particular clade, but has no significant

A

Iguania
Scincomorpha
Gekkota
Shinisaurus
Exostinus
Restes
Xenosaurus
Carusia
Anguis
Anniella
Bainguis
Ophisaurus
Diploglossus
Gerrhonotus
Palaeosaniwa
Eosaniwa
Parasaniwa
Saniwides
Telmasaurus
Saniwa
Varanus
Cherminotus
Lanthanotus
Heloderma
Lowesaurus
Eurheloderma
Estesia
Paraderma
Gobiderma
Necrosaurus
Parviderma
Paravaranus
Proplatynotia

B

Iguania
Scincomorpha
Gekkota
Shinisaurus
Exostinus
Restes
Xenosaurus
Carusia
Anguis
Anniella
Bainguis
Ophisaurus
Diploglossus
Gerrhonotus
Eosaniwa
Parasaniwa
Saniwides
Heloderma
Lowesaurus
Eurheloderma
Estesia
Paraderma
Gobiderma
Necrosaurus
Parviderma
Proplatynotia
Paravaranus
Cherminotus
Lanthanotus
Varanus
Saniwa
Telmasaurus

C

Iguania
Scincomorpha
Gekkota
Shinisaurus
Exostinus
Xenosaurus
Carusia
Anniella
Anguis
Ophisaurus
Diploglossus
Gerrhonotus
Heloderma
Lowesaurus
Eurheloderma
Estesia
Paraderma
Gobiderma
Saniwides
Proplatynotia
Necrosaurus
Parviderma
Parasaniwa
Paravaranus
Cherminotus
Lanthanotus
Varanus
Saniwa
Telmasaurus

D

Iguania
Scincomorpha
Gekkota
Shinisaurus
Xenosaurus
Carusia
Anniella
Anguis
Ophisaurus
Diploglossus
Gerrhonotus
Heloderma
Estesia
Gobiderma
Saniwides
Proplatynotia
Necrosaurus
Parviderma
Paravaranus
Cherminotus
Lanthanotus
Varanus
Saniwa
Telmasaurus

impact on the entire parsimonious framework. This pattern is shown in several major clades in our phylogenetic results: *Restes* and *Exostinus* in Carusioidea, *Bainguis* in Anguidae, *Paraderma* and *Eurheloderma* in Monstersauria.

PHYLOGENETIC RELATIONSHIPS OF *CARUSIA*

EVIDENCE SUPPORTING INCLUSION OF *CARUSIA* IN THE ANGUIMORPHA

The original assignment of *Carusia* to the "?Scincomorpha" was based on several supposedly shared derived characters with the scincomorphans (Borsuk-Bialynicka, 1985: 169). To clarify the phylogenetic status of *Carusia*, we list and address each of these problematic characters:

1. Overlap of dentary on the lateral surface of coronoid (Borsuk-Bialynicka 1985: character 5):

Borsuk-Bialynicka (1985) cited Estes et al. and used this character to support a possible scincomorphan relationship of *Carusia*. To discuss this problem, two different characters in Estes et al. (1988: characters 60, 71) must be clearly distinguished: one (character 60) is described as "dorsal extension of coronoid process of dentary" and the other (character 71) as "dentary overlap of coronoid lateral process." Estes et al. (1988) interpreted the lateral coronoid process of the dentary extending onto anterolateral surface of coronoid (the first character) as a scincoid synapomorphy with independent acquisition in other groups including xenosaurids; and they interpreted the lateral process of the coronoid overlapped anteriorly by the dentary (the second character) as a scincomorphan synapomorphy, with convergence in several other groups including some anguids. Because a lateral process of the coronoid is not developed (or poorly defined) in *Carusia*, character 71 is irrelevant to this taxon. Moreover, the optimization of this character as a scincomorphan synapomorphy is equivocal, as Estes et al. (1988: 159) pointed out "it is equally simple, however, to interpret it as separate synapomorphies of xantusiids and scincoids, with reversal in some scincids." The character pertinent to *Carusia* is character 60, in which the derived state also occurs in some anguids (*Ophisaurus apodus*) and xenosaurids (Estes et al., 1988).

Our observations of several well-preserved specimens (e.g., MAE 104/93-158, 94-38, 95-51) indicate that the condition in *Carusia* is similar to that in extant xenosaurids, and our analyses found no evidence to support homology of the *Carusia* condition with the condition in scincomorphans. Instead, a large number of other characters strongly support an anguimorphan relationship of this taxon (see discussion below).

2. Widely open mandibular fossa (Borsuk-Bialynicka 1985: character 6):

According to Estes et al. (1988: 160) "an inflated, widely open fossa is a synapomorphy of the Lacertiformes, with independent occurrence within scincids." It is not a scincomorphan synapomorphy. More importantly, the actual fossa in *Carusia* is narrow and shallow without a crest connecting it with the posteroventral process of the coronoid. Examination of well-preserved specimens (e.g., MAE 95-5, 95-52) clearly shows the mandibular fossa in *Carusia* is, similar to the condition in *Xenosaurus*, narrow and shallow. In some smaller specimens (e.g., MAE 94-38) the fossa is slightly wider than in adults, but it is clearly different from the inflated condition in lacertiformes. It also lacks a sharp ventral border. Therefore, this character provides no support of a scincomorphan relationship of *Carusia*.

←

Fig. 7. Phylogenetic relationships of *Carusia* within the Anguimorpha based on analysis of 105 characters (see table 1 and appendix 1 for data). (A) Strict consensus of 32,700 shortest trees from the complete data set, TL = 256, CI = 0.543, RI = 0.794; (B) strict consensus of 32,171 trees with elimination of *Palaeosaniwa*, TL = 256, CI = 0.543, RI = 0.794; (C) strict consensus of 180 trees with further elimination of *Restes*, *Bainguis*, and *Eosaniwa*; TL = 253, CI = 0.549, RI = 0.791; (D) strict consensus of four trees with elimination of the above-mentioned and five other taxa (*Exostinus*, *Parasaniwa*, *Paraderma*, *Eurheloderma*, and *Lowesaurus*), TL = 252, CI = 0.552, RI = 0.778.

3. Paired premaxillae:

Borsuk-Bialynicka listed this as a shared derived character with the Scincomorpha (Borsuk-Bialynicka, 1985: 169, 171; fig. 8B) and interpreted it as "most probably a result of character reversal." However, the paired condition is not a scincomorphan synapomorphy and cannot be used to support a scincomorphan relationship of *Carusia* (see Estes et al., 1988 for evaluation). Given the fact that a fused condition occurs in iguanians (basal squamates), and a paired condition occurs in sphenodontids (the closest sister group of Squamata), the paired condition in some scincogekkonomorphs (some skinks, gekkonids) and the fused condition in others is not unambiguous within the squamate groups. Optimization of this character at the scincogekkonomorph level remains equivocal, and the evolution of this character within the Squamata merits further investigation.

4. Parietal downgrowths:

Borsuk-Bialynicka (1985: fig. 5) ambiguously described and figured *Carusia* as having a "huge triangular descensus parietalis" in the text, but "fingerlike descensus parietalis" in the diagnosis. The structure in question is what Estes et al. (1988) called "parietal downgrowths" and what Jollie (1960) called the "cranial wall laminae" or "descending process." Camp (1923: 393) noted that these processes are slender and long in skinks. Estes et al. (1988: 207) listed "pointed ventral downgrowths of the parietal extend to (or just medial to) the epipterygoids" as a scincomorphan synapomorphy, but also admitted the ambiguity of this interpretation as they stated that "this character could be interpreted in several ways" (Estes et al., 1988: 147).

Functionally, such a downgrowth of the parietal probably serves as the point of origin of the temporal muscle, and occurs in all lizards that have a ventral origin of the muscle (contra Estes et al., 1988). For example, the downgrowths in *Heloderma* are present in the form of low crests, while those in teiids, scincids, and xantusiids are present as prominent processes. In *Carusia*, the downgrowths are more prominent than in *Xenosaurus*, and are different from those in *Shinisaurus*, which are lateral flanges. As de-

scribed above, the ventral process of the parietal in *Carusia* is robust but not "huge triangular" or "fingerlike." It is subrectangular, laterally compressed, and ventrally free from both the epipterygoid and the alar process of the prootic (best shown on MAE 115/93-93). The shape and robustness of this process are unique for *Carusia* within Anguimorpha, and a similar condition in *Corucia zebrata* (Scincidae) is apparently convergent.

5. Other relevant characters:

Other characters that Borsuk-Bialynicka (1985) treated as "important differences" include: Lack of alar process of the prootic, large vomer-palatine contact, and retention of a subdental shelf. We offer the following comments on these characters:

1) Presence of an alar process of the prootic occurs in all non-iguanian lizards (Gauthier, 1982; Estes, 1983; Borsuk-Bialynicka, 1983; Estes et al., 1988), and development of an elongated and anterodorsally orientated alar process is a synapomorphy of the Scleroglossa (Estes et al., 1988) with no reversals known (Borsuk-Bialynicka, 1984). If this interpretation is accepted, the supposed lack of an alar process in *Carusia* (if true) offers no phylogenetic information for relationships, but a secondary loss would be an autapomorphy solely for this particular taxon. Moreover, a specimen with a well-preserved braincase (MAE 115/93-93) clearly shows that *Carusia* does indeed have a well-defined alar process, while other specimens show that the absence of such a process is an artifact of preservation.

2) Extensive vomer-palatine contact is a direct result of lateral expansion of the palatal elements, which is autapomorphic for *Carusia* and hence offers no information for recognition of the relationships of this taxon.

3) Retention of a reduced subdental shelf occurs in all extant xenosaurids (see McDowell and Bogert, 1954: fig. 4; Rieppel, 1980a: figs. 20, 21) and their fossil relatives (see e.g., Gauthier, 1982; Gao and Fox, 1996), and is a plesiomorphic character state within the Anguimorpha. More importantly, the reduced subdental shelf in *Carusia* lacks a dorsal ridge that normally borders a deep sulcus dentalis in most scincomorphans; this feature, together with the great reduction of

the sulcus dentalis, differs from the scincomorphan condition in which both the ridge and sulcus dentalis are well developed in most cases.

From the above discussion, we found no convincing evidence for inclusion of *Carusia* in the Scincomorpha. On the other hand, we noticed the following character states strongly indicate an anguimorphan relationship of *Carusia*:

- incisive process of premaxilla bipartite (46-1; reversal in *Anniella*);
- presence of both coronoid and surangular notch (56-1);
- surangular extends anteriorly beyond coronoid eminence (58-1-2);
- presence of intramandibular septum within Meckelian canal (62-1);
- Meckelian canal opens ventrally anterior to anterior inferior alveolar foramen (66-1);
- strong reduction of mandibular fossa (67-1);
- cephalic osteoderms present (72-1-2);
- ossified palpebrals present (74-1; reversals in *Heloderma* and *Lanthanotus*, respectively. Although scored as unknown for some fossil taxa, our analyses indicate that the derived state is unequivocally diagnostic of the Anguimorpha).

Several other anguimorphan synapomorphies (see Estes et al., 1988) cannot be scored for *Carusia*. These include: number of presacral vertebrae more than 26 (80-1); body osteoderms present dorsally (90-1); m. geniomyoideus present (94-1); foretongue cleft for 10–20% of length (100-1). In addition to the characters listed above, the anguimorphan relationship of *Carusia* is further supported by a suite of derived characters that it shares with extant xenosaurids (see below).

PHYLOGENETIC POSITION OF *CARUSIA* WITHIN
ANGUIMORPHA

Within the Anguimorpha, the following derived character states diagnose a clade including *Carusia* and xenosaurids (Carusioidea): frontals fused into a single element (6-1; unequivocal, but independently acquired

in several other anguimorph subgroups); lateral border of frontals strongly constricted between orbits (7-1; unequivocal, the derived condition is known for all carusioid taxa); presence of jugal-squamosal contact on supratemporal arch (12-1; missing data in *Exostinus* and *Restes* have no effect on interpretation of the derived state as diagnostic of the carusioid clade); postorbital branch of jugal sculptured (17-1; unequivocal, the derived state occurs in all taxa in the carusioid clade); postorbital/postfrontal fusion present (20-1; although coded as unknown for *Exostinus* and *Restes*, the derived state is unequivocally diagnostic of the carusioid clade); surangular weakly tapered anteriorly in lateral view (57-1; unequivocal, derived condition is known for all carusioid taxa but *Restes*); cephalic osteoderms fragmented and thickened as subconical mounds (72-2; unequivocal, but convergent in Monstersauria); and dermal rugosities with vermiculate sculpture (73-1; unequivocal, the derived state is scored for all taxa in the carusioid clade). Most of these characters are listed in Estes et al. (1988) as xenosaurid synapomorphies (but see discussion elsewhere).

In this study, the monophyly of the Xenosauridae (*Xenosaurus* and *Shinisaurus*, possibly plus *Exostinus* and *Restes*) is supported by another set of derived character states (see below). Lack of these characters places *Carusia* outside this crown clade, and the results of our analyses indicate a basal position of *Carusia* within a more inclusive clade (see fig. 7A–D). In this case, the name Xenosauridae can be associated unambiguously with the crown clade using a node-based definition (see de Queiroz and Gauthier, 1992). As *Carusia* is evidently not part of the crown clade, we exclude it from the Xenosauridae. This placement requires emendation of the diagnosis of the Xenosauridae (see below) and naming the more inclusive taxon, which includes the most recent common ancestor of *Carusia* and Xenosauridae, and all its descendants. We name this more inclusive clade Carusioidea from the existing name Carusiidae (Borsuk-Bialynicka, 1987). The new taxon Carusioidea is diagnosed by a suit of derived characters including several that were previously

included in the diagnosis of Xenosauridae (see diagnosis of Carusioidea above). Within the new clade, *Carusia* is distinguished from its closely related fossil taxa as well as extant xenosaurids by an array of autapomorphies. These include: lost lacrimal; strongly widened palatal elements; presence of midline contact of the palatines anteriorly; strongly suppressed suborbital fenestra; vertical crest on anterior surface of quadrate, etc. (see diagnosis).

The results of this study support an alternative hypothesis that Borsuk-Bialynicka (1991a) suggested, but refute the original assessment of *Carusia* to ?Scincomorpha. The basal position of *Carusia* in the Carusioidea indicates that it represents a primitive taxon of this depauperate anguimorphan clade.

DEFINITION AND DIAGNOSIS OF XENOSAURIDAE

DEFINITION: Xenosauridae Cope, 1886, can be defined as the most recent common ancestor of *Xenosaurus* and *Shinisaurus* and all its descendants. Results of our analyses show that two fossil taxa (*Exostinus* and *Restes*) are members of the crown clade, and hence, these are included in the Xenosauridae as previously suggested (e.g., Gauthier, 1982; Estes, 1983). As *Carusia* is clearly outside the crown group, we exclude it from the Xenosauridae (for discussion of phylogenetic definition of taxa, see de Queiroz and Gauthier, 1992; Bryant, 1996).

DIAGNOSIS: The Xenosauridae as defined above can be unambiguously diagnosed by the following derived character state: postorbital branch of jugal strongly widened (16-1; the derived state is scored for all the fossil and extant xenosaurid taxa included in our analyses).

The following characters are also interpreted as diagnostic for the clade, but are uncertain because of missing data in fossil taxa *Exostinus* and *Restes*: paired nasals with limited midline contact ½ or less length of the element (2-1); ectopterygoid exposed laterally on ventral edge of skull wall (18-1); presence of canthal crest on temporal arch (21-1); entocarotid fossa in recessus vena jugularis strongly reduced (30-1); distinct medial projection anteroventral to mesopterygoid fossa present to enhance basipterygoid process/pterygoid articulation (32-1); anterior extension of supratemporal reaches level of apex of parietal notch (34-1); and second epibranchial absent (105-1; missing data in *Exostinus*, *Restes*, and *Carusia* as well). Depending on the actual condition in *Exostinus* and *Restes*, these character states could either be diagnostic for the Xenosauridae as defined above or for the subgroups of the four taxa.

Several other characters previously included in the diagnosis of the Xenosauridae are now recognized as diagnostic of the more inclusive clade Carusioidea (see above).

REMARKS: The Xenosauridae include only four extant species in two genera that are widely separated in geographic distribution and have very different lifestyles (Gauthier, 1982). The Asian *Shinisaurus* is represented by a single species (*Shinisaurus crocodilurus*) in southern China, and is nocturnal and semiaquatic; it lives near mountain streams in forested areas, largely feeding on small fish, frogs, and tadpoles (Fan, 1931; Zhang and Tang, 1985; Zhao and Adler, 1993). North American *Xenosaurus* includes three species that are confined to eastern Mexico. These live in mountainous regions, and are insectivorous and nocturnal (see King and Thompson, 1968; Mattison, 1989). The two genera were previously referred to separate families (Xenosauridae Cope, 1886, and Shinisauridae Ahl, 1929), but later were grouped in the same family by McDowell and Bogert (1954). The family Xenosauridae of McDowell and Bogert, however, is polyphyletic because it included *Necrosaurus* (Necrosauridae*) and *Melanosaurus* (Anguidae). Hu et al. (1984) compared 26 characters in *Shinisaurus* and *Xenosaurus*, and argued for placing *Shinisaurus* in its own family. In a recent cladistic analysis of squamate phylogeny, Estes et al. (1988) listed 12 synapomorphies (but see diagnosis above) shared by *Xenosaurus* and *Shinisaurus*. Currently the monophyly of the Xenosauridae, consisting of these two taxa, is widely accepted. This study corroborates Gauthier (1982) and Estes (1983) in showing that two fossil taxa (*Exostinus* and *Res-*

tes) are also members of this group, as they share at least one unambiguous synapomorphy with the extant taxa of the clade, and several other character states listed above may well support this grouping.

Estes et al. (1988) cited Costelli and Hecht (1971) concerning a xenosaurid synapomorphy: carotid fossa reduced; however, no such character is ever mentioned in the original paper, which is about postcranial osteology of *Shinisaurus*. In fact, McDowell and Bogert (1954: 22) stated that an "entocarotid-fossa" is reduced in *Xenosaurus* and nearly absent in *Shinisaurus*. As a basal carusioid, *Carusia* retained the primitive condition with a well-defined entocarotid fossa within the recessus vena jugularis. This character along with several others cannot be scored for *Exostinus* and *Restes*, although our analyses showed these are members of the Xenosauridae. Estes et al. (1988) also listed another character (cervical intercentra fused to posterior part of preceding centrum) as a xenosaurid synapomorphy, but ambiguously suggested it to be an anguimorphan synapomorphy in their character analysis. The ambiguity of this character cannot be clarified at present, although it has been suggested as an anguioid synapomorphy (Rieppel, 1980a).

FOSSIL RECORD OF THE CARUSIOIDEA

Carusioidea have a poor fossil record in comparison with other anguimorphan groups (Anguidae and Platynota), in terms of temporal and spatial continuity. Nonetheless, the scattered fossil records provide important paleontological data for tracing the evolutionary history of this small and poorly understood lizard group.

NORTH AMERICA: North American fossil xenosaurids were reviewed by Gauthier (1982) and recent discoveries from western Canada extended the North American record of the group from Maastrichtian to early Campanian (Gao and Fox, 1996).

Two fossil taxa (*Exostinus* and *Restes*) are known from specimens collected from Late Cretaceous and Early Tertiary deposits in North America. The first discovery of fossil xenosaurids was documented by Cope (1873), who named *Exostinus serratus*

based on specimens from the middle Oligocene White River Formation, Logan County, Colorado. The genus *Exostinus* also includes species based on specimens from Late Cretaceous beds: *Exostinus lancensis* Gilmore, 1928, from the Lancian or late Maastrichtian horizon mainly in Wyoming, Montana (see Estes, 1983: 131), and Alberta (Gao and Fox, 1996). The oldest North American xenosaurid record is of Aquilan or early Campanian age, from the Milk River Formation in southern Alberta. Jaw fragments and isolated skull elements, such as the jugal or frontal, show characteristic ornamentation of vermiculate dermal rugosities. However, these specimens offer little information about their lower-level relationships with other xenosaurid taxa, and are identified as "gen. et sp. undet."

A second genus, *Restes* Gauthier, 1982, is known from the upper Paleocene–lower Eocene horizons in Wyoming. The type species (*Exostinus rugosus* Gilmore, 1942) was based on a fragmentary right maxilla with five teeth from the Polecat Bench Formation, and was originally placed in the family Iguanidae. Estes (1963, 1975) relocated *Exostinus rugosus* to the Xenosauridae, and Gauthier (1982) erected a new genus for this particular taxon.

Estes (1964, 1975, 1983) and Gauthier (1982) presented convincing evidence indicating close relationships among the North American fossil xenosaurids *Exostinus* (Late Cretaceous) and *Restes* (late Paleocene–early Eocene) with extant *Xenosaurus*. Gauthier (1982: 10) stated that "the living species of the family diverged prior to the end of the Cretaceous." Our study indicates that *Carusia* and another fossil taxon (*Oxia*, see discussion below) are the known Cretaceous relatives of the Xenosauridae.

CENTRAL ASIA: In the Gobi Desert, *Carusia* is known from both the Djadochta and Barun Goyot formations, and from the Ukhaa Tolgod locality (unidentified geological unit), which may range from middle to late Campanian in age, and are roughly correlated to the Judithian and part of the Edmontonian beds, respectively, in the Western Interior of North America (e.g., Fox, 1978; Lillegraven and McKenna, 1986; but see also Norell et al., 1992). Now *Carusia*

is known from more than 40 skulls with mandibles (Borsuk-Bialynicka, 1985; Gao and Hou, 1996; this paper), and a study of the exceptionally well-preserved skulls in this paper provides strong evidence to place *Carusia* as the basal taxon of the carusioid clade.

Nessov (1985) named *Oxia karakalpakensis* and tentatively referred it to "Lacertilia incertae sedis," based on several disarticulated dentaries from the Kyzylkum Desert, Uzbekistan. This problematic taxon is possibly related to the Xenosauridae (Nessov and Gao, 1993), but lack of knowledge of its skull elements seems to weaken a definite referral of it to any familial group (Gao and Nessov, 1998). The type Khodzhakul locality is stratigraphically in the lower part of the Khodzhakul Formation, which has been determined as late Albian in age (Nessov, 1988; Nessov et al., 1994). Therefore, *Oxia* may represent the geologically oldest known member of the carusioid clade. However, because the status of this taxon is uncertain at this stage, we excluded it from our analyses.

PHYLOGENETIC RELATIONSHIPS AND DIAGNOSES OF THE MAJOR ANGUIMORPHAN CLADES

The Anguimorpha are a relatively small group of lizards with slightly over 100 extant species (Mattison, 1989), but the group has received considerable attention because of its comparably rich fossil record and its potential relationships with snakes (see Estes et al., 1988). Previous studies have shown that the monophyly of the Anguimorpha is well supported by a large number of osteological and soft anatomical characters (see Estes et al., 1988; Rieppel, 1988 for list of characters and discussion), but the interrelationships among its subgroups (Anguidae, Xenosauridae, and Varanoidea) are still controversial (Estes et al., 1988).

The Anguimorpha were traditionally subdivided into the Diploglossa and Platynota (Camp, 1923). After a series of revisions, the monophyly of the Platynota (Varanoidea of various authors, but see below) including the Helodermatidae and Varanidae, was well corroborated. It is problematic whether

snakes are part of the Platynota; if so, the contents of the Platynota need be amended to include this taxon. The two major anguimorphan groups were revised by McDowell and Bogert (1954). Unfortunately, their "major specializations" of the Diploglossa contained only plesiomorphic characters at the anguimorphan level (see McDowell and Bogert, 1954; fig. 43).

ANGUIOIDEA AND THE ANGUIDAE/XENOSAURIDAE/VARANOIDEA POLYTOMY

Camp (1923) included in his Anguioidea five familial groups (Xenosauridae, Anguidae, Anniellidae, Glyptosauridae, and Helodermatidae). McDowell and Bogert (1954) classified three groups (Anguidae, Anniellidae, and Xenosauridae) in their Anguioidea or Diploglossa. However, Gauthier (1982) found no shared derived character states that delimit the Anguioidea, and more recent analysis by Estes et al. (1988) resulted in an Anguidae/Xenosauridae/Varanoidea polytomy (see also Rieppel, 1988).

In this study, the recognition of the Carusioidea (including the crown clade Xenosauridae) as the basal anguimorphan clade, and the resolution of the Xenosauridae/Anguidae/Varanoidea trichotomy represents major progress in our understanding of anguimorphan phylogeny. Among the 105 characters used in our phylogenetic analyses, Carusioidea may share with Anguidae a single derived character state: cervical intercentrum fused to posterior part of preceding centrum (77-2). Yet this is problematic because this character is coded as uncertain for *Carusia*, *Exostinus*, and *Restes*, making its position within the Carusioidea dependent on the optimization of a missing value. Three other characters shared by these two clades are primitive at the anguimorphan level: presence of both a coronoid and a surangular notch (56-1); m. geniomyoideus present but completely superficial to m. genioglossus medialis (94-1); and foretongue cleft for 10–20% of length (100-1). Our analyses found no evidence supporting the grouping of Carusioidea with Platynota.

In contrast, Anguidae share with Platynota at least five derived character states that are absent in Carusioidea. These derived

character states diagnose an unnamed an-guimorphan clade, which includes the tra-ditionally defined Anguidae and Platynota:

- premaxillary teeth abruptly smaller than maxillary teeth (39-1, unequivo-cal);
- vomer/maxillary contact behind aper-ture of Jacobson's organ forming neo-choanate palate (48-1, unequivocal with reversal in *Heloderma*);
- surangular extending anteriorly well beyond coronoid eminence (58-2, un-equivocal);
- subdental shelf strongly reduced as a slope of tooth-bearing border (64-2, unequivocal);
- rib attached on sternum no more than three pairs (88-1, equivocal, further transformed in Varanidae).

All the above character states, except for the last one, are unambiguously diagnostic of the unnamed anguimorphan clade, which includes all but the carusioid subclades. In the case of the last character state (88-1), ambiguity is created by missing data in fos-sil taxa. This character is scored for all ex-tant anguids (nonapplicable for *Anniella*), helodermatids, and varanids, but is un-known for all the fossil taxa in the unnamed new clade. Therefore, it could be a syna-pomorphy of the new clade (with further modification in the Varanidae) or indepen-dently diagnostic for the Anguidae and Hel-odermatidae, depending on the actual con-dition of the fossil taxa.

RELATIONSHIPS OF *ANNIELLA* AND THE STATUS OF ANNIELLIDAE

The highly specialized *Anniella* was first described by Gray (1852) as a member of the Scincidae; however, because of the ex-tensive modification of its skull morphology in association with its burrowing habits, the taxonomic position of this interesting lizard has been in constant debate ever since. Cope (1864) first established the Anniellidae and placed it with the Anelytropsidae and Acon-tiidae, but later (Cope, 1892, 1900) grouped the family with the Amphisbaenidae. Bou-lenger (1884) recognized its close relation-ships with the Anguidae, and this view was

supported by various authors (Baur, 1894; Coe and Kunkel, 1906; Camp, 1923; To-erien, 1950; McDowell and Bogert, 1954; Gauthier, 1982; Estes, 1983; Good, 1987) with slightly different interpretations of its relationships within the group. Baur (1894) considered the closest relative of *Anniella* to be *Anguis*, but Camp (1923) pointed out, based on throat musculature, the close sim-ilarity of *Anniella* with *Gerrhonotus*. In their major revision of anguimorphan clas-sification, McDowell and Bogert (1954) fur-ther supported the *Anniella—Anguis* rela-tionship and regarded the former derived from the latter: "However, the retention of several primitive features in the anatomy of the skull (and of the head musculature) fa-vour the hypothesis of a common ancestry of *Anniella* and *Anguis* rather than the de-scent of *Anniella* from *Anguis*" (Rieppel, 1980a: 62). A more recent analysis of mo-lecular data (Good, 1987) indicates that *An-niella* is outside the anguid clade.

Although the close relationship of *An-niella* with anguids is supported by most au-thors, Malan (1946) questioned it, based on differences in nasal anatomy, while Bellairs (1949) supported Cope (1864) and argued that the genus comes much closer to the bur-rowing skinks than to *Anguis* or *Ophisau-rus*. An *Anniella*—Acontinae (burrowing skinks) relationship is supported by karyo-typic similarities of the two groups (Bezy and Wright, 1971), but allozyme analysis supports grouping *Anniella* with anguids (Good, 1987). In terms of ranking, some au-thors treated the small group of lizards as a separate family (e.g., McDowell and Bogert, 1954; Rieppel, 1980a), while others treated it as a subfamily within the Anguidae (e.g., Gauthier, 1982; Estes, 1983).

Results of our analyses support the inclu-sion of *Anniella* in the Anguidae on the ba-sis of the following unequivocal synapo-morphies of the Anguidae:

- ventral border of the subdental shelf notched, forming anterior and dorsal rim of the anterior inferior alveolar fo-ramen (65-1; Estes, 1964; the unnotched condition in *Diploglossus* is interpreted as reversal);
- retroarticular process of the mandible

widened posteriorly (69-1; Estes et al., 1988; convergent in Gekkota);

- retroarticular process of the mandible twisted (70-1; McDowell and Bogert, 1954);
- caudal chevrons fused to centrum (83-2; unique; Hoffstetter and Gasc, 1969);
- strong elongation of symphysial process of pubis present (89-1; Estes et al., 1988; character 124; convergent in scincomorphs);
- presence of both dorsal and ventral body osteoderms (90-2; Gauthier, 1982; all the included taxa of anguids are scored as (2) with no convergence known for other anguimorphans).

Most of the above characters, with the exception of the last, cannot be scored for the fossil taxon *Bainguis*, but our analyses show that these are unequivocal synapomorphies at the anguid level. In addition, the derived condition of another character (cervical intercentrum fused to posterior part of preceding centrum, 77-2; Hoffstetter and Gasc, 1969) is known for all anguid taxa but *Bainguis*; however, missing data in *Carusia* make it indecisive as an anguid synapomorphy. It cannot be ascertained whether this is a shared derived feature of the Anguidae and Carusioidea or independently diagnostic for the Anguidae and Xenosauridae.

Within the Anguidae, *Anniella* can be further grouped with the Anguinae based on the following derived character states:

- jugal strongly reduced with little or no angulation (13-1; McDowell and Bogert, 1954; unequivocal with convergence in gekkotans and advanced platynotans);
- posteroventral process of jugal nearly lost (14-1; McDowell and Bogert, 1954; unequivocal with convergence in gekkotans, *Estesia*, and advanced platynotans);
- postorbital excluded from entering orbit (19-1; Rieppel, 1980a; equivocal as both primitive and derived conditions occurred in *Diploglossus*; the derived state can be interpreted as an anguinine synapomorphy convergent in some *Diploglossus* species, or diagnostic for a

more inclusive clade with reversal in the latter species);

- presence of distinct medial projection anteroventral to mesopterygoid fossa to enhance basipterygoid/pterygoid articulation (32-1; Rieppel, 1980a; unequivocal, although scored as unknown for *Bainguis*; convergent in Xenosauridae and Platynota);
- tympanic crest of quadrate reduced (35-1; McDowell and Bogert, 1954; unequivocal with convergence in advanced platynotans);
- anterolateral process of pterygoid extended to contact jugal (54-1; unequivocal with missing data in *Bainguis*; convergent in Monstersauria).
- interclavicle vestigial or entirely lost in adults (86-2; McDowell and Bogert, 1954; unknown for *Bainguis* and uncertain in *Ophisaurus*).

In addition, several other character states are also diagnostic of the Anguinae: supratemporal fenestra strongly reduced and nearly closed (25-2), recessus vena jugularis strongly reduced (30-1), and anterior head of m. pseudotemporalis profundus present and expanded (97-2). But further modification of all these character states occurs in *Anniella*.

Within the Anguinae, grouping of *Anniella* with *Anguis* (with exclusion of *Bainguis*) is supported by two characters (see below), and an alternative placement of *Anniella* as the sister group of the Anguinae makes the tree five steps longer. *Anniella* shares with *Anguis* the following two derived character states:

- maxillary tooth number nine or less (44-2, equivocal because of the unknown condition in *Bainguis*; it could be diagnostic for a more inclusive clade including the latter fossil taxon);
- anterior extension of splenial retracted posterior to midpoint of tooth row (59-1; unambiguously diagnostic of the clade, convergent in gekkotans and platynotans with reversal in *Paravaranus*).

McDowell and Bogert (1954: 124; fig. 41) described the two taxa as similar in hav-

ing a long and broad cultriform process extending well forward to the level of the posterior border of the suborbital fenestrae, but figured *Anguis* as having a short process. McDowell and Bogert (1954) also noted that the skull structure of *Anniella* shows some convergence toward platynotans. Among the six characters that they mentioned, four are derived: marginal tooth row entirely antorbital (43-2), recurved and fanglike teeth (not included in our data set), midline contact of the descending processes of the frontals below the olfactory tracts (see description of character 9), ectopterygoid contacting palatine to exclude maxilla from suborbital fenestra (55-1). We add four other characters to their list: vomer strongly elongated reaching level of posterior end of tooth row (47-1), posterior extension of choana approaches or reaches posterior end of maxillary tooth row (49-2), increased number of cervical vertebrae (76-1-2; Bell et al., 1995), and mesosternum absent (87-1). McDowell and Bogert (1954) also mentioned two other characters that *Anniella* convergently shared with platynotans: retention of traces of sutures between major postdentary elements and presence of a bony palpebral. The former character is clearly plesiomorphic and individually (or ontogenetically) variable in *Anniella* (see Jollie, 1960), and the latter is an anguimorphan synapomorphy (Estes et al., 1988) and thus also primitive at the anguid level.

Our analysis concurs with that of McDowell and Bogert (1954) and found no evidence to support grouping *Anniella* with Platynota. On the other hand, *Anniella* retained a large number of primitive character states in comparison with platynotans. The most conspicuous among these are: lack of plicidentine infolding on the tooth bases (40-0); surangular in lateral view tapered anteriorly in keeping with lack of intramandibular hinge (57-0); anterior process of coronoid is not elongate, nor extensively dorsally exposed (63-0); and retention of autotomic septum in caudal vertebrae (81-0).

Nonetheless, our results show relatively strong support for placement of *Anniella* in the Anguidae; a weakly supported *Anguis*— *Anniella* sister group relationship needs further investigation (especially in relation to *Bainguis*, see below). Our analyses, which are based on morphological data, differ from molecular analyses (e.g., Bezy and Wright, 1971; Good, 1987) in terms of the relationships of *Anniella* with other anguids.

RELATIONSHIPS OF *BAINGUIS*

One of the problematic taxa in our analysis is *Bainguis*, in which about 85% of the characters used in this analysis cannot be scored. This poorly understood taxon was first classified in the Banguidae, which was included in the "preanguimorphan grade" (Borsuk-Bialynicka, 1984), but later regarded as "an anguid relative" (Borsuk-Bialynicka, 1991a: 9). Our analysis of the complete data set supports the latter interpretation. *Bainguis* shares with all other anguids one unequivocal character state: body osteoderms present both dorsally and ventrally (90-2); several other recognized anguid synapomorphies (e.g., 69-1, 70-1, 77-2, 83-2, 89-1) could not be scored for *Bainguis* because of missing data. Nonetheless, an anguid relationship of this problematic taxon is probably the best interpretation based on the available evidence. In addition, our analyses revealed further evidence in resolving the relationships of *Bainguis* within the Anguidae. It can be grouped with *Anniella* in the Anguinae on the basis of the following unequivocal character states: jugal strongly reduced without angulation (13-1); posteroventral process of jugal nearly or entirely lost (14-1); postorbital excluded from entering the orbit (19-1, see discussion above); and tympanic crest of quadrate strongly reduced (35-1). Within the Anguinae, *Bainguis* shares with *Anniella* a single character state: origin of temporal musculature on dorsolateral aspect of parietal table (26-0). Although coded as (0), our analyses shows that the condition in these two anguimorphan taxa must be interpreted as apomorphic reversal.

DEFINITION AND DIAGNOSIS OF PLATYNOTA

DEFINITION: The term Platynota used here refers to a clade that includes the most recent common ancestor of Monstersauria and Varanidae, and all its descendants.

Camp's (1923) Platynota contains Vara-

noidea and Mosasauroidea. McDowell and Bogert (1954) used the term Platynota as an alternate name of Varanoidea, and a similar usage is seen in other major publications (e.g., Rieppel, 1980a, 1988; Estes, 1983; Borsuk-Bialynicka, 1984). Lee (1997: 78) provided a stem-based definition of the Platynota: "*Heloderma, Lanthanotus* and *Varanus*, and all taxa more closely related to these forms than to other anguimorphs."

DIAGNOSIS: The Platynota as defined above are diagnosed by an array of derived character states: presence of distinct medial projection anteroventral to mesopterygoid fossa to enhance basipterygoid process/pterygoid articulation (32-1; Rieppel, 1980a; convergent in the Xenosauridae and Anguinae); presence of plicidentine infolding at marginal tooth bases (40-1; McDowell and Bogert, 1954; unequivocal, scored for all taxa included except *Eosaniwa, Proplatynotia, Paravaranus*); marginal teeth widely spaced with expanded tooth bases (41-1; McDowell and Bogert, 1954; unequivocal, scored for all taxa but uncertain in *Eosaniwa*); replacement teeth developed posteriorly without presence of resorption pits (42-1; unequivocal as above); maxillary tooth row entirely antorbital or slightly suborbital with no more than three tooth positions (43-1-2; unequivocal, with reversal in *Eosaniwa*; further transformation in advanced monstersaurians and varanids); maxillary teeth number 10–13 (44-1; unequivocal, reversal in *Eosaniwa* and further modified in *Heloderma* and *Cherminotus* independently); vomer strongly elongated approaching level of posterior end of tooth row (47-1; unequivocal, although several fossil taxa coded as unknown); palatal shelf of vomer narrow (50-1; unequivocal, in spite of missing data in several fossil taxa; reversal in *Lanthanotus*); palatine equally wide as long as (51-1; missing data in nine ingroup taxa have no effect on interpretation of this state as unambiguously diagnostic of the Platynota); ectopterygoid in palatal view contacting palatine and excluding maxilla from entering suborbital fenestra (55-1; equivocal because of missing data in *Parviderma* and *Parasaniwa*; depending on the actual condition in these, the derived state could be a platynotan synapomorphy or independently

diagnostic for Monstersauria and a clade including Varanoidea and its closely related forms); development of intramandibular hinge (56-2; unequivocal, missing data in seven taxa have no effect on interpretation of the derived state as unambiguously diagnostic of the clade); surangular blunt anteriorly in lateral view (57-1; unequivocal, with reversal in *Eosaniwa*); anterior extension of splenial retracted to or posterior to midpoint of tooth row (59-1; unequivocal, with convergence in the Gekkota and within the Anguinae, reversal in *Paravaranus*); posterior extension of splenial terminates anterior to or below coronoid eminence (60-1; unequivocal, no reversal in both outgroup and ingroup taxa); splenial-dentary suture loose, with much connective tissue between the two bones (61-1; unequivocal as the above character); anterior process of coronoid elongated and extensively exposed dorsally (63-1; unequivocal, convergent in Gekkota); extensive medial exposure of angular bone (68-1; although up to ten taxa contain missing data, known distribution of the derived state in other nine taxa indicates it is unambiguously diagnostic of the Platynota); lacrimal duct double (75-1; the derived state can only be scored for extant *Heloderma, Varanus,* and *Lanthanotus,* but it is best interpreted as a platynotan synapomorphy on congruence with other characters); cervical intercentrum sutures to posterior part of preceding centrum (77-1; equivocal, as only five out of 19 included taxa can be scored for this character); autotomy on caudal vertebrae absent (81-1; besides the three extant taxa, *Saniwa* is the only fossil taxon that can be determined to have the derived condition. Missing data in a large number of fossil taxa make its status as a platynotan synapomorphy uncertain).

The following characters cannot be scored in any of the fossil taxa, but have been interpreted as diagnostic of the Platynota based on their distribution in three extant taxa of the group (*Heloderma, Varanus, Lanthanotus;* see Rieppel, 1980a; Estes et al., 1988): epicoracoid fails to contact suprascapula and mesoscapula (84-1); mesosternum absent (87-1); m. episterno-cleidomastoideus has extensive insertion on parietal (91-1); origin of 3b-layer of MAME

profundus from supratemporal only (93-1); m. geniomyoideus present and invades deep to m. genioglossus medialis (94-2; ambiguity of this character state is created by *Lanthanotus*, which shows a primitive condition as in extant xenosaurids and anguids); m. genioglossus lateralis subdivided into separate bundles and insert into hyobranchials (95-1); foretongue deeply cleft from 20% up to 50% of length (100-2); carotid duct absent (101-1); gland of Gabe present (102-1); cochlear duct robust and broad, limbus elongate and heavy (103-1); ulnar nerve deep in forearm (104-1).

MONSTERSAURIA—A WELL-SUPPORTED PLATYNOTAN CLADE

The taxonomic and phylogenetic treatments of this important platynotan clade have been covered in our previous paper (see Norell and Gao, 1997), in which the Monstersauria is defined as "all of the descendants of the last common ancestor of *Gobiderma pulchrum* and *Heloderma suspectum*." In this study, analyses of a more extensive data set using a different outgroup scheme reinforce conclusions from our previous study, showing that Monstersauria is a well-supported platynotan clade. Adding new evidence supporting the monophyly of Monstersauria, the diagnosis of this important clade can be revised as follows:

Anterior extension of supratemporal reaches level of apex of parietal notch (34-1); this character state cannot be interpreted as unequivocal: Monstersauria shares this character state with Varanidae, but nine nonmonstersaurian taxa were coded as unknown because of missing data. Depending on the actual condition of these taxa, the derived condition in Monstersauria and Varanidae may be independently acquired, or may be diagnostic for Platynota with reversal in *Telmasaurus*.

Pterygoid lappet of quadrate present (36-1, unequivocal); the pterygoid lappet is present in *Gobiderma, Heloderma*, and *Estesia*. Although coded as unknown for *Paraderma, Eurheloderma*, and *Lowesaurus*, our analyses show that the derived state unambiguously diagnoses the monstersaurian clade.

Anterolateral process of pterygoid extended dorsally on ectopterygoid to contact jugal (54-1, unequivocal); this character state has the same distribution as character 36, but independent acquisition occurs in some anguids.

Cephalic osteoderms fragmented and thickened as subconical mounds (72-2, unequivocal); the character state is scored for all monstersaurian taxa except for *Estesia*, and the same character state occurs in all carusioid taxa. Our analyses indicate that it is separately diagnostic for both clades.

Dermal rugosities present with conspicuously pitted surfaces (73-2, equivocal); within the monstersaurian clade, this character state has the same distribution as character 72. The same character state also occurs in some advanced platynotans. McDowell and Bogert (1954) recognized this feature as characteristic for Varanoidea based on its presence in *Heloderma, Varanus*, and *Lanthanotus*; however, our analyses indicate it is possibly diagnostic for Monstersauria with independent acquisition in *Parasaniwa* and Varanidae, or it is diagnostic for the more inclusive Platynota with reversals in *Necrosaurus, Parviderma*, and *Proplatynotia*.

Neural spines narrow and tall (78-1, unequivocal); in *Heloderma* and closely related *Eurheloderma*, the neural spines are narrow and tall (Pregill et al., 1986). The same morphology is known for *Estesia, Paraderma*, and *Gobiderma* (Norell and Gao, 1997; Gao and Fox, 1996); therefore, it is unambiguously diagnostic for the monstersaurian clade.

Foramen ovale located anterior to the spheno-occipital tubercle (see Norell and Gao, 1997). This character state is known in *Gobiderma, Estesia*, and *Heloderma*; and it is diagnostic for the Monstersauria.

With elimination of *Palaeosaniwa* and *Eosaniwa*, our analyses indicate that Monstersauria may well be the most basal platynotan clade. This clade retains platynotan synapomorphies but lacks several derived character states that may diagnose an unnamed new clade, which includes our Varanoidea and several closely related fossil taxa (see below).

AN UNNAMED NEW PLATYNOTAN CLADE

The unnamed new taxon, consisting of the Varanoidea and several closely related taxa, represents a derived platynotan clade and forms the sister group of Monstersauria (see fig. 7B–D). The following character states can be scored for most but not all the fossil taxa included in the group, and are potentially diagnostic of the clade:

- jugal strongly reduced without angulation (13-1; equivocal because of missing data in *Necrosaurus*, *Parviderma*, and *Parasaniwa*; it could be diagnostic for a less inclusive clade excluding the abovementioned three taxa);
- posteroventral process of jugal lost (14-1; equivocal as character 13 with the same ingroup distribution);
- supratemporal process of parietal in dorsal view narrow with sharp crest (33-1; this is one of the unequivocal character states that diagnose the unnamed clade, as missing data in several fossil taxa apparently have no effect on this interpretation);
- tympanic crest of quadrate reduced (35-1; equivocal with a similar distribution as characters 13 and 14);
- peduncles on cervical and caudal vertebrae present (82-1; unequivocal on the basis of its distribution among the five taxa that can be scored);
- caudal chevrons suture to centrum (83-1; unequivocal as character 82).

The following character states, mostly soft anatomy, can only be scored for the extant taxa (*Varanus* and *Lanthanotus*); therefore, whether they are strictly diagnostic of the Varanidae or of a more inclusive clade cannot be ascertained:

- ribs attached on sternum two pairs or fewer (88-2);
- m. constrictor colli extensively cover first ceratobranchials (92-1);
- insertion of m. levator pterygoidii restricted anteriorly (96-1);
- anterior head of m. pseudotemporalis profundus present and expanded (97-2);
- hemibacula present (99-1).

Within this unnamed platynotan clade, positions of those taxa included in our Varanoidea and their sister group *Paravaranus* are very stable throughout our analyses; those taxa with unstable positions within this clade are discussed below.

PROBLEMATIC TAXA WITHIN THE PLATYNOTAN CLADE

Within the unnamed platynotan clade, several fossil taxa are problematic with poorly resolved relationships. Three taxa (*Palaeosaniwa*, *Parasaniwa*, and *Eosaniwa*), from the Upper Cretaceous of North America and Tertiary of Europe, are known from very fragmentary material and each contains a large amount of missing data. *Palaeosaniwa* is classified in the Varanidae, on the basis of a precondylar constriction in the vertebrae (Gilmore, 1928; Estes, 1983), and recent discoveries of referred jaw material support this placement (Gao and Fox, 1996). *Parasaniwa* and *Eosaniwa* have been classified in the possibly paraphyletic Necrosauridae* (Gilmore, 1928; Estes, 1964, 1983; Gao and Fox, 1996).

Three other taxa (*Proplatynotia*, *Parviderma*, and *Saniwides*) from the Upper Cretaceous of the Gobi Desert, and one (*Necrosaurus*) from the Tertiary of Europe are also problematic. These are apparently members of the sister clade of the Monstersauria (see fig. 7B–D); however, the definite relationships within that clade as well as with other closely related taxa are not well resolved. Although our analyses revealed possible grouping of *Parviderma* with *Necrosaurus* and *Parasaniwa*, the robustness of this hypothesis needs to be tested. As for *Proplatynotia* and *Saniwides*, our analyses failed to reveal evidence for their possible grouping with other related taxa. Resolving the relationships of these important but problematic taxa largely depends on discovery of new and better preserved fossil specimens.

The phylogenetic framework we constructed for platynotan taxa differs substantially from that presented in Lee (1997), in terms of the position of several important taxa. The conflicting results are partially a consequence of our different coding of character states. For instance, nasal process of

the maxilla in *Telmasaurus* is coded (0) in Lee (1997: character 8), but we treated it as missing data as no fossil specimen known has this part preserved. The same process in *Proplatynotia* and *Saniwides* shows a very similar condition (located at the posterior part of the maxilla), but Lee coded the two taxa differently (0 for the former and 1 for the latter). *Saniwa* is coded (1) based on Gilmore's (1928) restoration, but a better preserved specimen at hand (AMNH-DVP 8688) clearly shows (0) condition. *Estesia* is clearly illustrated and described as "the nasal process emanates from the bone posteriorly," but is scored (0) in Lee (1997). We offer the following comments on these taxa with different interpretations:

PROPLATYNOTIA: We found no evidence for placing *Proplatynotia* as the most basal platynotan clade (see Lee, 1997: fig. 15). Lee's unnamed clade A includes "all platynotans except *Proplatynota* [sic]", and is diagnosed by two character states: (1) palatine short, half as long as vomer; (2) subdental shelf absent. The first character state is indecisive in *Proplatynotia*, because on both sides the posterior end of the vomer is incomplete. Considering the broken tip of the vomer, the palatine may well be half the length of the vomer. The second character is coded incorrectly for *Proplatynotia*. The subdental shelf in *Proplatynotia*, as in other platynotans (and also anguids), is strongly reduced to a slope without a dorsal ridge. This condition of the strongly reduced subdental shelf is termed "the tooth-bearing border" in Estes (1964) and Borsuk-Bialynicka (1984: 34), but "subdental shelf absent" in Estes et al. (1988).

Our study revealed that *Proplatynotia* acquired several derived character states that are absent in Monstersauria: nasal process of maxilla located at posterior part of maxilla (5-2), jugal strongly reduced without angulation (13-1), and posteroventral process of jugal nearly or entirely lost (14-1). These character states, in congruence with others, strongly indicate a more derived position of *Proplatynotia* than the Monstersauria. Results of our analyses show that *Proplatynotia* together with *Saniwides* rooted at the node of an unnamed platynotan clade (see fig. 7C, D).

PARAVARANUS: In Lee's (1997) cladogram, this taxon is placed as the most basal clade of his Clade A and outside his Varanoidea; however, this placement gains no support from the available data on this taxon. Here we list Lee's nine diagnostic features of his Varanoidea and place our comments in brackets following each character description:

(1) Posterior end of maxilla does not reach middle of orbit. [Lee (1997: character 9); the actual condition in *Paravaranus* is uncertain, as Borsuk-Bialynicka (1984: 16) described: "the posterior limit of the maxilla and its sutures with neighboring bones cannot be established with any certainty because of its state of preservation." Coding as (0) in Lee's data matrix is inappropriate, even if Borsuk-Bialynicka's (1984: pl. 1, fig. 1c) reconstruction is followed.]

(2) Supratemporal large. [Lee (1997: character 26); not preserved on real specimen and undescribed in Borsuk-Bialynicka (1984), but coded as (0) in Lee's matrix probably based on restoration of the skull (Borsuk-Bialynicka, 1984: fig. 2).]

(3) Maxilla enters suborbital foramen. [This primitive character state is obviously misplaced here, as the derived condition is the maxilla excluded from the foramen. Borsuk-Bialynicka (1984: 18) clearly described the condition in *Paravaranus*: "the exact extension of ectopterygoid cannot be established due to damage," while Lee (1997: character 66) coded (0) for this taxon.]

(4) Surangular, when disarticulated, with flat anterior end. [Lee (1997: character 82): missing data in *Paravaranus*.]

(5) Marginal teeth with carinae. [Lee (1997: character 87); the teeth in *Paravaranus* are too poorly preserved to be scored for this character.]

(6) Plicidentine present. [See item above.]

(7) Fewer than 13 maxillary teeth. [Lee (1997: character 92); Borsuk-Bialynicka (1984: 19) stated: "neither in the maxilla nor in the dentary can the number of teeth be established." We treated this character as missing data for the taxon, while Lee coded (0) for it.]

(8) Pelvic elements separate, not co-ossified into single innominate bone. [Lee

(1997: character 130): missing data in *Paravaranus*.]

(9) Thirteen or fewer scleral ossicles. [Lee (1997: character 142): missing data in *Paravaranus*.]

None of these characters interpreted as varanoid features can be positively scored for *Paravaranus* as primitive states; and hence, no evidence supports Lee's exclusion of this taxon from his Varanoidea. Contrary to Lee's cladogram, the results of our analyses support grouping *Paravaranus* with our Varanoidea as sister groups. In all our analyses except for the first run (incorporating all taxa and all characters), this grouping is supported by the following unequivocal character states: nasals fused (2-2); nasal and prefrontal bones separated by gap (3-2); nasal and maxillary bones separated by gap (4-1); and in keeping with the last two characters, prefrontal enters the external narial opening as a consequence of strong retraction of nares (10-2).

PARVIDERMA: Lee (1997) grouped *Parviderma* with *Gobiderma* in the Gobidermatidae. As we have pointed out in our previous paper (Norell and Gao, 1997), this is an artificial taxon. Contrary to Lee (1997: 60) who asserted that there are "no major differences between them except for a size difference," *Parviderma* clearly displays several cranial features distinctly different from those in *Gobiderma* and other monstersaurian taxa, for example, temporal muscles originate dorsolaterally rather than ventrally on the parietal table; frontals fused rather than paired (see comments in Norell and Gao, 1997). This study indicates that *Parviderma* is grouped with *Necrosaurus* and *Parasaniwa*, and the three together form a monophyletic clade. This grouping is weakly supported by two character states: the frontals are fused (6-1), and the lateral borders of the frontals are constricted between the orbits (7-1).

SANIWIDES: Borsuk-Bialynicka (1984) named *Saniwides mongoliensis* and referred it to the Varanidae. The most characteristic feature of this species is the enlargement of the prefrontal, but this diagnostic feature is not included in the diagnosis. In terms of dentition, this species is described as having 16 maxillary teeth (Borsuk-Bialynicka,

1984: 55), but this is apparently overestimated. Both a photograph of the holotype and a partially restored drawing of the skull (Borsuk-Bialynicka, 1984: fig. 14) show that the maxillary tooth row has no more than 13 positions.

Based on the available data on this taxon, our analyses failed to find evidence supporting its referral to either Varanidae or Varanoidea; instead, we place it (together with *Proplatynotia*) at the base of an unnamed clade, which is the sister group of the Monstersauria. *Saniwides* shares several character states with varanoids: nasal process of the maxilla located at the posterior part of the bone (5-2), and strongly reduced tympanic crest of the quadrate (35-1); but our analyses indicate that these are diagnostic of a more inclusive clade including varanoids and their relatives. On the other hand, *Saniwides* retains several primitive character states that place it outside the varanoid clade: prefrontal not entering external narial opening (10-0), posterior lacrimal foramen single rather than double (38-0), and very weak basal infolding of the teeth (see Borsuk-Bialynicka, 1984).

VARANOIDEA—A DERIVED PLATYNOTAN CLADE

DEFINITION: The most recent common ancestor of *Telmasaurus* and Varanidae, and all its descendants. Adopting a crown-group definition, our usage of Varanoidea as defined above differs from the usage of other authors (e.g., McDowell and Bogert, 1954; Rieppel, 1980a; Estes, 1983; Estes et al., 1988), who in most cases used Varanoidea as alternative name for Platynota (see also Lee, 1997).

DIAGNOSIS: The Varanoidea as defined above can be diagnosed by the following derived character states: subolfactory processes of frontals closely approach or contact posteromedially (9-3; scored for all the ingroup taxa and are unambiguously diagnostic of the clade); entocarotid fossa within recessus vena jugularis essentially lost (30-2; unequivocal, scored for all the ingroup taxa except *Saniwa*); posterior lacrimal foramen double (38-1; unequivocal, although coded as unknown for *Cherminotus*); pre-

condylar constriction of vertebrae present (79-1; equivocal as the derived condition is also scored for the problematic taxon *Palaeosaniwa*; see discussion below).

DISCUSSION: Throughout our analyses, a very stable platynotan clade besides Monstersauria is Varanoidea, which is represented by five taxa. This clade was not recognized in our first analysis, which included all the taxa in the data set. The monophyly of this well-supported clade was apparently disguised by the problematic taxon *Palaeosaniwa*, which contains about 90% missing data in our matrix. Among the 10% characters scored for *Palaeosaniwa*, presence of precondylar constriction of vertebrae (79-1) may be considered informative; however, the unknown condition in most of the Gobi platynotan taxa evidently obscured the phylogenetic value of this character.

As shown in all the strict consensus trees (fig. 7B–D) except the tree resulting from our first analysis, our Varanoidea includes *Cherminotus* and *Lanthanotus* as sister groups followed by *Varanus*, *Saniwa*, and *Telmasaurus*. The latter two taxa were previously classified in the Varanidae by various authors (see Gilmore, 1828, 1943; Estes, 1983; Borsuk-Bialynicka, 1984; Gao and Fox, 1996), but are excluded from this group as they are not members of the crown-group Varanidae. Outside the varanoid clade is its sister taxon *Paravaranus*. This sister-group relationship is supported by four character states: nasal bones fused (2-2); nasal and prefrontal bones separated by gap (3-2); nasal and maxillary bones separated by gap (4-1); and prefrontal enters external narial opening owing to strong narial retraction (10-2). However, because all these character states are more or less related to narial retraction and all cannot be ascertained for *Telmasaurus* or *Palaeosaniwa*, the robustness of this sister-group hypothesis merits further investigation. Six other fossil taxa (*Necrosaurus*, *Proplatynotia*, *Parviderma*, *Saniwides*, *Parasaniwa*, and *Eosaniwa*) are apparently more remotely related to Varanoidea than *Paravaranus* within the Platynota.

CONCLUSIONS

Newly collected Late Cretaceous fossil lizards from Ukhaa Tolgod and other local-

ities in the Gobi Desert include some 35 specimens that are referred to *Carusia intermedia*. These well-preserved skulls with mandibles provide the core material for clarification of the taxonomic and phylogenetic uncertainties of this important but poorly understood taxon. Our study of *Carusia* and cladistic analyses of 105 characters across 33 selected taxa yielded important results concerning the relationships of the anguimorphan lizard taxa from the Gobi, and substantially changes the phylogenetic framework of the major anguimorphan clades. The conclusions of this study can be summarized as follows:

(1) Study of new specimens of *Carusia* revealed pivotal characters that refute the previously suggested ?Scincomorpha relationship, but strongly indicate an anguimorphan relationship of this taxon. Within the Anguimorpha, *Carusia* is placed as the basal taxon of a newly recognized clade, Carusioidea, and the sister group of Xenosauridae.

(2) Recognition of Carusioidea as the most basal anguimorphan clade and hence resolving the Xenosauridae/Anguidae/Varanoidea polytomy represents major progress in understanding the relationships of the major anguimorphan clades.

(3) The problematic Gobi taxon *Bainguis* and extant *Anniella* are grouped with anguinines in the Anguidae, and the latter group is recognized as the sister taxon of Platynota.

(4) Analyses of more extensive data sets using different outgroup schemes reinforce conclusions from our previous study, and furnish stronger support for monstersaurian monophyly.

(5) Within the Platynota, *Paravaranus* is recognized as the sister taxon of the redefined Varanoidea, in which the resolved relationships of our selected taxa are: [(*Cherminotus* + *Lanthanotus*) + *Varanus* + *Saniwa* + *Telmasaurus*].

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REFERENCES

Alifanov, V. R.
  1993. Some peculiarities [sic] of the Cretaceous and Palaeogene lizard faunas of the Mongolian People's Republic. Kaupia 3: 9–13.

Bahl, K. N.
  1937. Skull of *Varanus monitor* (Linn.). Rec. Indian Mus. 34: 133–174.

Barrows, S., and H. M. Smith
  1947. The skeleton of the lizard *Xenosaurus grandis* Gray. Univ. Kansas Sci. Bull. 31: 227–281.

Baur, G.
  1894. The relationship of the lacertilian genus *Anniella*, Gray. Proc. U.S. Natl. Mus. 17: 345–351.

Bell, C. J., J. I. Mead, and L. P. Fay
  1995. Neogene history of *Anniella* Gray, 1852 (Squamata, Anniellidae) with comments on postcranial osteology. Copeia 1995(3): 719–726.

Bellairs, A. d'A.
  1949. Observations on the cranial anatomy of *Anniella*, and a comparison with that of other burrowing lizards. Proc. Zool. Soc. London 119: 887–904.

Bezy, R. L., and J. W. Wright
  1971. Karyotypic variation and relationships of the California legless lizard *Anniella pulchra* Gray (Reptilia: Anniellidae). Herpetol. Rev. 3: 71–72.

Bezy, R. L., G. C. Gorman, Y. J. Kim, and J. W. Wright
  1977. Chromosomal and genetic divergence in the fossorial lizards of the family Anniellidae. Syst. Zool. 26: 57–71.

Borsuk-Bialynicka, M.
  1983. The early phylogeny of Anguimorpha as implicated by craniological data. Acta Paleontol. Pol. 28: 31–42.
  1984. Anguimorphans and related lizards from the Late Cretaceous of the Gobi Desert. Palaeontol. Pol. 46: 5–105.
  1985. Carolinidae, a new family of xenosaurid-like lizards from the Upper Cretaceous of Mongolia. Acta Palaeontol. Pol. 30: 151–176.
  1987. *Carusia*, a new name for the Later Cretaceous lizard *Carolina* Borsuk-Bialynicka, 1985. Ibid. 32: 153.
  1991a. Questions and controversies about saurian phylogeny, Mongolian perspective. Univ. Oslo Contrib. Paleontol. Mus. 364: 9–10.
  1991b. Cretaceous lizard occurrences in Mongolia. Cretaceous Res. (1991)12: 607–608.

Boulenger, G. A.
  1884. Synopsis of the families of the existing Lacertilia. Ann. Mag. Nat. Hist. (5)14: 117–122.

Bryant, H. N.
  1996. Explicitness, stability, and universality in the phylogenetic definition and usage of taxon names: a case study of the phylogenetic taxonomy of the Carnivora (Mammalia). Syst. Biol. 45: 174–189.

Camp, C.
  1923. Classification of the lizards. Bull. Am. Mus. Nat. Hist. 48: 289–481.

Card, W., and A. G. Kluge
  1995. Hemipeneal skeleton and varanid lizard systematics. J. Herpetology 29: 275–280.

Coe, W. R., and B. W. Kunkel
  1906. Studies on the California limbless liz-
          ard, *Anniella*. Trans. Connecticut Acad.
          Arts Sci. 12: 349–403.
Cope, E. D.
  1864. On the characters of the higher groups
          of Reptilia, Squamata and especially of
          the Diploglossa. Proc. Acad. Nat. Sci.
          Philadelphia 1864: 224–231.
  1873. Synopsis of new vertebrata from the
          Tertiary of Colorado, obtained during
          the summer of 1873. Washington, D.C.:
          US Govt. Printing Office.
  1892. The osteology of the Lacertilia. Proc.
          Am. Philos. Soc. 30: 185–222.
  1900. The crocodilians, lizards and snakes of
          North America. Annu. Rep. U.S. Natl.
          Mus. 1898: 151–1294.
Costelli, J. Jr., and M. K. Hecht
  1971. The postcranial osteology of the lizard
          Shinisaurus: the appendicular skeleton.
          Herpetology 27: 87–98.
Dashzeveg, D., M. J. Novacek, M. A. Norell, J.
          M. Clark, L. M. Chiappe, A. Davidson,
          M. C. McKenna, L. Dingus, C. Swish-
          er, and P. Altangerel
  1995. Extraordinary preservation in a new
          vertebrate assemblage from the Late
          Cretaceous of Mongolia. Nature 374:
          446–449.
de Queiroz, K., and J. Gauthier
  1992. Phylogenetic taxonomy. Annu. Rev.
          Ecol. Syst. 23: 449–480.
Edmund, A. G.
  1960. Tooth replacement phenomena in the
          lower vertebrates. R. Ontario Mus. Life
          Sci. Contrib. 52: 1–190.
  1969. Dentition. *In* C. Gans, A. Bellairs and
          T. Parsons (eds.), Biology of the Rep-
          tilia 1 (Morph. A): 117–200. New
          York: Academic Press.
Eldredge, N.
  1984. Simpson's inverse: Bradytely and the
          phenomenon of living fossils. *In* N.
          Eldredge and S. M. Stanley (eds.), Liv-
          ing fossils: 272–277. Berlin: Springer-
          Verlag.
Estes, R.
  1963. A new gerrhonotine lizard from the
          Pliocene of California. Copeia 1963:
          676–680.
  1964. Fossil vertebrates from the Late Creta-
          ceous Lance Formation, eastern Wyo-
          ming. Univ. California Publ. Geol. Sci.
          49: 1–180.
  1975. Lower vertebrates from the Fort Union
          Formation, late Paleocene, Big Horn

          Basin, Wyoming. Herpetology 31:
          365–385.
  1983. Sauria Terrestria, Amphisbaenia.
          Handb. Pälaoherpetologie, Pt. 10A: 249
          pp. Stuttgart: Gustav Fischer.
Estes, R., K. de Queiroz, and J. Gauthier
  1988. Phylogenetic relationships within Squa-
          mata. *In* R. Estes and G. Pregill (eds.),
          Phylogenetic relationships of the lizard
          families: 119–282. Stanford: Stanford
          Univ. Press.
Evans, S. E.
  1994. A new anguimorph lizard from the Ju-
          rassic and Lower Cretaceous of En-
          gland. Palaeontol. 37: 33–49.
Fan, T. H.
  1931. Preliminary report on the reptiles from
          Yaoshan, Kwangsi, China. Sun Yat-sen
          Univ. Dept. Biol. Bull. 11: 1–154.
Fox, R. C.
  1978. Upper Cretaceous terrestrial vertebrate
          stratigraphy of the Gobi Desert (Mon-
          golian People's Republic) and western
          North America. *In* C. R. Stelck and B.
          D. E. Chatterton (eds.), Western and
          Arctic Canadian biostratigraphy: 577–
          594. The Geol. Assoc. Canada Spec.
          Pap. 18.
Gabe, M., and H. Saint Girons
  1976. Contribution a la morphologie compa-
          rée des fosses nasales et de leurs an-
          nexes chez les lépidosauriens. Mem.
          Mus. Nat. Hist. Nat. (Zool.) 98: 1–87.
Gans, C.
  1978. The characteristics and affinities of the
          Amphisbaenia. Trans. Zool. Soc. Lon-
          don 34: 347–416.
Gao, K., and R. C. Fox
  1996. Taxonomy and evolution of Late Cre-
          taceous lizards from western Canada.
          Bull. Carnegie Mus. Nat. Hist. 33: 1–
          107.
Gao, K., and L. Hou
  1996. Systematics and taxonomic diversity of
          squamates from the Upper Cretaceous
          Djadochta Formation, Bayan Mandahu,
          Gobi Desert, People's Republic of Chi-
          na. Can. J. Earth Sci. 33: 578–598.
Gao, K., and L. A. Nessov
  1998. Early Cretaceous squamates from the
          Kyzylkum Desert, Uzbekistan. Neues
          Jahrb. Geol. Paleontol. 207: 1–21.
Gauthier, J.
  1982. Fossil xenosaurid and anguid lizards
          from the early Eocene Wasatch For-
          mation, southeast Wyoming, and a re-
          view of the Anguioidea. Univ. Wyo-
          ming Contrib. Geol. 21: 7–54.

1986. Saurischian monophyly and the origin of birds. California Acad. Sci. Mem. 8: 1–55.

Gauthier, J., A. G. Kluge, and T. Rowe
1988. Amniote phylogeny and the importance of fossils. Cladistics 4: 105–209.

Gilmore, C. W.
1928. Fossil lizards of North America. Natl. Acad. Sci. Mem. 22: 1–201.
1942. Paleocene faunas of the Polecat Bench Formation, Park County, Wyoming, Pt. II. lizards. Proc. Am. Philos. Soc. 85: 159–167.
1943. Fossil lizards of Mongolia. Bull. Am. Mus. Nat. Hist. 81: 361–384.

Good, D. A.
1987. An allozyme analysis of anguid subfamilial relationships (Lacertilia: Anguidae). Copeia 1987: 696–701.

Gray, J. E.
1852. Descriptions of several new genera of reptiles, principally from the collection of H.M.S. Herald. Annu. Mag. Nat. Hist. 10: 440.

Greer, A.
1970. A subfamilial classification of scincid lizards. Bull. Mus. Comp. Zool. 139: 151–184.

Grismer, L. L.
1988. Phylogeny, taxonomy, classification, and biogeography of eublepharid geckos. In R. Estes and G. Pregill (eds.), Phylogenetic relationships of the lizard families: 369–469. Stanford: Stanford Univ. Press.

Haas, G.
1973. Muscles of the jaws and associated structures in the Rhynchocephalia and Squamata. In C. Gans (ed.), Biology of the Reptilia, Vol. 4: morphology D (T. S. Parsons, ed.): 285–490. New York: Academic Press.

Hecht, M. K., and J. Costelli, Jr.
1969. The postcranial osteology of the lizard Shinisaurus 1. the vertebral column. Am. Mus. Novitates 2378: 21 pp.

Hecht, M. K., and R. Hoffstetter
1962. Note préliminaire sur les amphibien et les sqamates du Landenien spérieur et du Tongrien de Belgique. Bull. Inst. Royal Sci. Nat. Belgique 38: 1–30.

Hoffstetter, R.
1957. Un saurien hélodermatidé (Eurheloderma gallicum nov. gen. et sp.) dans la faune fossile des Phosphorites du Quercy. Bull. Soc. Géol. France 7: 775–786.

Hoffstetter, R., and J-P. Gasc
1969. Vertebrae and ribs of modern reptiles. In C. Gans, A. d'A. Bellairs, and T. Parsons (eds.), Biology of the Reptilia, Vol. 1: morphology A: 201–310. New York: Academic Press.

Hu, Q.
1980. The anatomy of the nervous system of Shinisaurus crocodilurus Ahl (Reptilia: Sauria). Acta Herpetol. Sin. 4(2): 1–11.

Hu, Q., Y. Jiang, and E. Zhao
1984. A study of taxonomic position of Shinisaurus crocodilurus. Acta Herpetol. Sin. 3: 1–7.

Jollie, M.
1960. The head skeleton of the lizard. Acta Zool. 41: 1–64.

King, W., and F. G. Thompson
1968. A review of the American lizards of the genus Xenosaurus Peters. Florida State Mus. Bull. 2: 93–103.

Kluge, A.
1967. Higher taxonomic categories of gekkonid lizards and their evolution. Univ. Michigan Misc. Publ. Zool. 147: 1–221.

Lakjer, T.
1926. Studien über die trigeminus-versorgte kaumuskulatur der Sauropsiden. Copenhagen: C. A. Rietzel.

Lécuru, S.
1968a. Remarques sur le scapulo-coracoide des lacertiliens. Ann. Sci. Nat. (Zool.) 10: 475–510.
1968b. Étude des variations morphologiques du sternum, des clavicules et de l'interclavicule des lacertiliens. Ann. Sci. Nat. (Zool.) 10: 511–544.

Lee, M. S. Y.
1997. The phylogeny of varanoid lizards and the affinities of snakes. Philos. Trans. R. Soc. London B 352: 53–91.

Lillegraven, J. A., and M. C. McKenna
1986. Fossil mammals from the "Mesaverde" Formation (Late Cretaceous, Judithian) of the Big Horn and Wind River basins, with definitions of the Late Cretaceous Land Mammal "Ages." Am. Mus. Novitates 2840: 68 pp.

Maddison, W. P., and D. R. Maddison
1992. MacClade: analysis of phylogeny and character evolution. version 3.03. Sunderland, MA: Sinauer Associates.

Malan, M. E.
1946. Contributions to the comparative anatomy of the nasal capsule and the organ of Jacobson of the Lacertilia. Ann. Univ. Stellenbosch (A)24(4): 69–137.

Mateer, N. J.
    1982.   Osteology of the Jurassic lizard *Ardeosaurus brevipes* (Meyer). Palaeontology 25: 461–469.
Mattison, C.
    1989.   Lizards of the world. New York: Facts on File.
McDowell, S. B.
    1972.   The evolution of the tongue of snakes, and its bearing on snake origins. *In* T. Dobzhansky, M. Hecht and W. Steere (eds.), Evolutionary biology 6: 191–272.
McDowell, S. B., and C. M. Bogert
    1954.   The systematic position of *Lanthanotus* and the affinities of anguinomorphan lizards. Bull. Am. Mus. Nat. Hist. 105: 1–141.
Meszoely, C.
    1970.   North American fossil anguid lizards. Bull. Mus. Comp. Zool. 139: 87–149.
Nessov, L. A.
    1985.   Rare bony fishes, terrestrial lizards and mammals from the lagoonal zone of the Littoral lowlands of the Cretaceous of the Kyzylkum. Ann. All-Union Paleontol. Soc. (Leningrad) 28: 199–219.
    1988.   Late Mesozoic amphibians and lizards of Soviet Middle Asia. Acta Zool. Cracov. 31: 475–486.
Nessov, L. A., and K. Gao
    1993.   Cretaceous lizards from the Kyzylkum Desert, Uzbekistan. J. Vertebr. Paleontol. 13(3): 51A.
Nessov, L. A., D. Sigogneau-Russull, and D. E. Russell
    1994.   A survey of Cretaceous tribosphenic mammals from Middle Asia (Uzbekistan, Kazakhstan and Tajikistan), of their geological setting, age and faunal environment. Palaeovertebrata 23: 51–92.
Nixon, K. C., and Q. D. Wheeler
    1992.   Extinction and the origin of species. *In* M. J. Novacek and Q. D. Wheeler (eds.), Extinction and phylogeny: 119–143. New York: Columbia Univ. Press.
Norell, M. A., and K. Gao
    1997.   Braincase and phylogenetic relationships of *Estesia mongoliensis* from the Upper Cretaceous, Gobi Desert and the recognition of a new clade of lizards. Am. Mus. Novitates 3211: 25 pp.
Norell, M. A., M. C. McKenna, and M. J. Novacek
    1992.   *Estesia mongoliensis*, a new fossil varanoid from the Late Cretaceous Barun Goyot Formation of Mongolia. Am. Mus. Novitates 3045: 24 pp.
Novacek, M. J.
    1992.   Fossils as critical data for phylogeny. *In* M. J. Novacek and Q. D. Wheeler (eds.), Extinction and phylogeny: 46–88. New York: Columbia Univ. Press.
Oelrich, T. M.
    1956.   The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). Univ. Michigan Mus. Zool. Misc. Publ. 94: 1–122.
Pregill, G., J. Gauthier, and H. Greene
    1986.   The evolution of helodermatid squamates, with description of a new taxon and an overview of Varanoidea. Trans. San Diego Soc. Nat. Hist. 21: 167–202.
Presch, W.
    1980.   Evolutionary history of the South American microteiid lizards (Teiidae: Gymnophthalminae). Copeia 1980(1): 36–56.
    1988.   Phylogenetic relationships of the "Scincomorpha." *In* R. Estes and G. Pregill (eds.), Phylogenetic relationships of the lizard families: 471–492. Stanford: Stanford Univ. Press.
Rieppel, O.
    1978.   Tooth replacement in anguimorph lizards. Zoomorphologie 91: 77–90.
    1980a. The phylogeny of anguimorphan lizards. Denkschr. Schweiz. Naturforsch. Ges. 94: 1–86.
    1980b. The postcranial skeleton of *Lanthanotus borneensis* (Reptilia, Lacertilia). Amphibia-Reptilia 1: 95–112.
    1980c. The trigeminal jaw adductor musculature of *Tupinambis*, with comments on the phylogenetic relationships of the Teiidae (Reptilia, Lacertilia). Zool. J. Linn. Soc. 69: 1–29.
    1981.   The skull and the jaw adductor musculature in some burrowing scincomorph lizards of the genera *Acontias*, *Typhlosaurus* and *Feylinia*. J. Zool. London 195: 493–528.
    1983.   A comparison of the skull of *Lanthanotus borneensis* (Reptilia: Varanoidea) with the skull of primitive snakes. Z. Zool. Syst. Evolutionsforsch. 21: 142–153.
    1984.   The cranial morphology of the fossorial lizard genus *Dibamus* with a consideration of its phylogenetic relationships. J. Zool. London 204: 289–327.
    1988.   The classification of the Squamata. *In* M. J. Benton (ed.), The phylogeny and classification of the tetrapods, vol. 1: Amphibians, reptiles, birds: 261–293.

Syst. Assoc. Spec. Vol. 35A. Oxford: Clarendon Press.

Robinson, P. L.
1967. The evolution of the Lacertilia. Colloq. Int. CNRS 163: 395–407.

Romer, A.
1956. Osteology of the reptiles. Chicago: Univ. Chicago Press, 772 pp.

Siebenrock, F.
1894. Das Skelet der *Lacerta simonyi* Steind und der Lacertidenfamilie überhaupt. Sitzungsber. Math.-Nat. Kl. Acad. Wiss. Wien 103: 205–292.

Simpson, G. G.
1944. Tempo and Mode in Evolution. New York: Columbia Univ. Press.

Swofford, D. L.
1993. PAUP: phylogenetic analysis using parsimony, version 3.1.1. Washington D.C.: Smithsonian Inst.

Toerien, M. J.
1950. The cranial morphology of the Californian lizard—*Anniella pulchra* Gray. S. Afr. J. Sci. 46: 321–342.

Underwood, G.
1957. *Lanthanotus* and the anguinomorphan lizards: a critical review. Copeia 1957 (1): 20–30.

Wu, X-C., D. B. Brinkman, and A. P. Russell
1996. *Sineoamphisbaena hexatabularis*, an amphisbaenian (Diapsida: Squamata) from the Upper Cretaceous redbeds at Bayan Mandahu (Inner Mongolia, People's Republic of China), and comments on the phylogenetic relationships of the Amphisbaenia. Can. J. Earth Sci. 33: 541–577.

Yatkola, D. A.
1976. Fossil *Heloderma* (Reptilia, Helodermatidae). Occas. Pap. Mus. Nat. Hist. Univ. Kansas 51: 1–14.

Zhang, Y., and Z. Tang
1985. Biology of *Shinisaurus crocodilurus*. Acta Herpetol. Sin. 1985(4): 331–340.

Zhao, Er-mi, and K. Adler
1993. Herpetology of China. Soc. Study Amphib. Reptiles (in co-operation with the Chin. Soc. Study Amphib. Reptiles) Contrib. Herpetol. 10: 1–522.

APPENDIX 1

Characters used in the phylogenetic analysis in this paper (modified from Pregill et al., 1986; Norell and Gao, 1997; other sources of characters as cited below). Codings of characters for taxa included are explained as follows:

Anguidae: based on published data as cited below and our personal observation of AMNH-DVP collections;

Necrosaurus: based on published data summarized in Estes (1983);

Estesia mongoliensis: based on type (M 3/14) and IGM 3/15;

Saniwa: based on description and illustrations in Gilmore (1928), and our examination of AMNH-DVP 8688 and 8691 from the Oligocene of Bates Hole, Wyoming;

Eosaniwa: based on published data summarized in Estes (1983);

Palaeosaniwa canadensis: based on specimens in UALVP and RTMP collections (described in Gao and Fox, 1996);

Paraderma bogerti: based on the type and referred specimens described in Estes (1964), Gao and Fox (1996);

Eurheloderma gallicum: based on description and figures in Hoffstetter (1957) and Estes (1983);

Lowesaurus matthewi: based on description and figures in Yatkola (1976) and Pregill et al. (1986);

Heloderma: based on MAN 9 and AMNH-DVP 40 (both skull with postcranial skeleton);

Varanus: based on AMNH 109498 (*Varanus komodoensis*), AMNH-DVP 2994 (*Varanus salvator*) and AMNH-DVP 1201 (*Varanus niloticus*);

Lanthanotus borneensis: based on RE 1445 and published data in McDowell and Bogert (1954), Rieppel (1980a, 1980b, 1983);

Gobiderma pulchrum: based on MAE 95-29, 93-248, 96-163, and published data in Borsuk-Bialynicka (1984);

Bainguis parvus: based on the holotype described by Borsuk-Bialynicka (1984).

Codings of characters for other taxa from the Gobi (*Paravaranus angustifrons, Proplatynotia longirostrata, Parviderma inexacta, Saniwides mongoliensis, Telmasaurus grangeri,* and *Cherminotus longifrons*) are based on the published data in Borsuk-Bialynicka (1984); when illustrations contradicted descriptions, we made interpretations on the basis of description, photoplates, and specimen photographs at hand.

Codings of muscle characters are based on Camp (1923), Lakjer (1926), Oelrich (1956), Haas (1973), Rieppel (1980a, 1980c, 1984), and Pregill et al. (1986).

Cranial characters

1. Premaxillary-maxillary aperture absent (0), or present (1). [We use the term *aperture* to mean the structure that opens at

the premaxillary-maxillary suture rather than within the premaxilla. In lizards such as *Varanus* both the aperture and premaxillary foramen are present on the palate.]

2. Nasal bones paired and have extensive suture contact along midline (0), or paired with limited contact ½ or less length of the element (1), or fused (2). [McDowell and Bogert (1954: 26) noted for xenosaurids "nasals deeply separated posteriorly by a median anterior process of the frontal. In no other diploglossans is the separation of the nasals by the frontal so well developed." Our analysis indicates that state (1) is a xenosaurid synapomorphy, but we also noticed its independent occurrences in some anguids (see McDowell and Bogert, 1954; Rieppel, 1980a).]

3. Nasal and prefrontal bones in broad contact (0), or separated by contact of frontal with maxilla (1), or separated by gap (2). [Coding of this and character 11 below for *Gerrhonotus* based on Meszoely (1970), Rieppel (1980a), and Good (1987).]

4. Nasal and maxillary bones in broad contact (0), or entirely or largely separated by gap (1), or separated by prefrontal (2).

5. Nasal process of maxilla located at the anterior (0), or middle (1), or posterior part of maxilla (2).

6. Frontals are paired in adult stage (0), or fused (1). [This is one of the several most problematic characters in study of squamate phylogeny; see Estes et al. (1988) for discussion. Although for *Telmasaurus* the frontals are described as "firmly fused" (Borsuk-Bialynicka, 1984: 56), ventral view of the specimen MgR-I/65 clearly shows a midline suture (GK personal obs.); therefore, we coded (0) for this taxon.]

7. Lateral border of frontals more or less parallel-sided (0), or constricted between orbits and hourglass-shaped (1), or trapezoidal (2).

8. Subolfactory processes of frontals poorly defined (0), or well developed as lateral wall of olfactory tract (1). [McDowell and Bogert (1954) recognized the derived condition as a characteristic feature of anguimorphans.]

9. Subolfactory processes of frontals do not contact each other ventrally (0), extensive contact along midline (1), closely approach or contact anteromedially (2), or closely approach or contact posteromedi-

ally (3). [As large numbers of new specimens clearly show that the processes in *Carusia* are separate and do not contact along midline (contra Borsuk-Bialynicka, 1985: fused), we scored (0) for this taxon.]

10. Prefrontal not entering external narial opening (0), entering the opening owing to strong anterior extension of prefrontal (1), or entering opening owing to strong retraction of nares (2). [*Necrosaurus* is coded (0) because both the nasal and prefrontal contact the maxilla in this taxon (see Estes, 1983).]

11. Prefrontal does not (0), or does contact postfrontal above orbit (1). [The frontals of *Lowesaurus matthewi* has a prefrontal incision slightly separated from the postfrontal incision (Pregill et al., 1986). However, we do not consider this as positive evidence for a no-contact condition, because the incisions in *Estesia mongoliensis* are slightly separated but the two bones are in contact (see Norell et al., 1992). Coding of *Ophisaurus* based on McDowell and Bogert (1954).]

12. Jugal/squamosal contact on supratemporal arch absent (0), or present (1). [Optimization of this character is ambiguous; see Estes et al. (1988: character 18) for discussion.]

13. Jugal well developed and angulated (0), strongly reduced with little or no angulation (1). [See McDowell and Bogert, 1954 for description.]

14. Posteroventral process of jugal well developed (0), nearly or entirely lost (1). [Coding of *Gobiderma pulchrum* based on MAE 96-163.]

15. Postorbital arch complete (0), or broken (1). [See Rieppel (1980a: character 26). Conflicting data presented in Borsuk-Bialynicka (1984: 63, fig. 17) make the coding of this character for *Cherminotus* indecisive (See also character 20 below).]

16. Dilation of postorbital branch of jugal absent (0), or present (1). [Compared to the condition in extant *Shinisaurus* and *Xenosaurus* and their fossil relatives (*Exostinus* and *Restes*), the postorbital branch of the jugal in *Carusia* has no significant dilation; hence, we scored (0) for this taxon.]

17. Dermal ornamentation of postorbital branch of jugal absent (0), or present (1).

18. Ectopterygoid laterally concealed by maxilla and jugal (0), or exposed on ventral edge of skull (1). [See Rieppel

(1980a: character 49). Barrows and Smith (1947) initially identified this character in *Xenosaurus grandis*. McDowell and Bogert (1954) recognized this character as a xenosaurid feature, and noted its convergent occurrences in *Lanthanotus* and *Varanus*.]

19. Both postfrontal and postorbital (0), or only postfrontal enter the orbit (1). [See Rieppel (1980a: character 21). Based on data presented in Borsuk-Bialynicka (1984: 63), the character state in *Cherminotus* cannot be ascertained; thus, we treated it as missing data (see also character 16 above).]

20. Postorbital/postfrontal fusion absent (0), or present (1). [Fusion of the two elements independently occurs in several groups of lizards (see Estes et al., 1988, for character analysis). Our observations of two new specimens (MAE 220/93-248, 96-163) confirm that the two elements are separate in *Gobiderma pulchrum*. Several other taxa known from the Gobi (*Parviderma, Cherminotus,* and *Paravaranus*) cannot be scored for this character because of poor preservation of the specimen or conflicting data presented in the original publication (see Borsuk-Bialynicka, 1984). Fusion also occurs within *Anguis* and *Diploglossus* (Rieppel, 1980a). Coding of *Anniella* based on McDowell and Bogert (1954) and Rieppel (1980a), and *Necrosaurus* on Hecht and Hoffstetter (1962).]

21. Canthal crest on temporal arch absent (0), or present (1). [See McDowell and Bogert, 1954; Estes et al., 1988. Compared to extant xenosaurids, such a crest in *Carusia* is poorly defined on some (e.g., MAE 95-5, 33/93-167) but is hardly recognizable on several others (e.g., MAE 95-52, 96-191); thus, we scored (0) for this taxon.]

22. Parietal foramen present (0), or absent (1). [Coding of *Xenosaurus* is based on AMNH 98122 and 103212 (both *Xenosaurus grandis*). Conflicting data on this character for *Anguis* and *Anniella* reflect variable conditions in these taxa (see Camp; 1923: 394; Toerien, 1950; McDowell and Bogert, 1954: fig. 41; and Rieppel, 1980a).]

23. Descensus parietalis presents as a lateral flange of the parietal table (0), as ventral crest beneath the table (1), or as strongly elongated ventral process extending to or just medial to the epipterygoid (2). [See

text; see also Estes et al., 1988: character 23.]

24. Supratemporal arch present (0), or absent (1).

25. Supratemporal fenestra wide open (0), narrowed and elongated (1), strongly reduced and nearly closed (2), or entirely lost (3).

26. Origin of temporal musculature on dorsolateral aspect (0), or on ventral aspect of parietal table (1). [see Estes et al. (1988: character 54) for discussion.]

27. Hypoglossal foramen not enlarged (0), or enlarged and confluent with vagal foramen (1).

28. Posterior opening of vidian canal located at prootic/basisphenoid suture (0), or penetrates basisphenoid only (1). [See Estes et al. (1988: character 53). *Saniwa* is scored on the basis of AMNH 8691. Coding of *Lanthanotus* is based on McDowell and Bogert (1954: 41): "the entrance to the carotid-Vidian canal is in the anterior portion of the sphenoid" (contra Estes et al. (1988): at suture).]

29. Facial foramen in recessus vena jugularis single (0), or double (1). [A double foramen condition is known for *Varanus* and some *Ophisaurus* (Jollie, 1960), *Lanthonotus* (Rieppel, 1980a: character 59), and *Saniwa* (personal obs. of AMNH 8691). Rieppel (1980a) also added *Xenosaurus* and *Heloderma suspectum*. However, two specimens of *Heloderma suspectum* (MAN 9 and AMNH-DVP 40) show a single foramen; for the two specimens of *Xenosaurus grandis* (AMNH 98122, 103212) examined, the first shows a small bony bridge outside the main opening on the left side only, while the latter shows a single foramen on each side; therefore, we coded (0) for these taxa.]

30. Entocarotid fossa within recessus vena jugularis well developed (0), strongly reduced (1), or essentially lost (2). [Most lizards have a well-developed recessus vena jugularis, in which a distinct fossa occurs anteriorly at the entrance of the vidian canal. McDowell and Bogert (1954) identified this structure as the entocarotid fossa.]

31. Basioccipital/basisphenoid suture obtusely angulate and laterally diagonal (0), or roughly a straight line suture in keeping with anterior shifting of spheno-occipital tubercle (1). [See McDowell and Bogert (1954); see also Borsuk-Bialynicka (1984) for different optimization of this

character. Although *Heloderma* is coded (0) based on Rieppel (1980a: fig. 23), fusion of the two elements may occur in some individuals (e.g., MAN 9, AMNH-DVP 40).]

32. Distinct medial projection anteroventral to mesopterygoid fossa absent (0), or present to enhance basipterygoid process/pterygoid articulation (1). [Modified from Rieppel (1980a: character 53).]

33. Supratemporal process of parietal in dorsal aspect flat (0), or narrow with sharp crest (1). [Optimization of this character is equivocal, as many basal iguanians have narrow supratemporal process with sharp dorsal crest.]

34. Anterior extension of supratemporal does not (0), or does reach level of apex of parietal notch (1). [Optimization of this character is equivocal, because of widespread absence of a supratemporal in rhynchocephalians (see Estes et al., 1988, for citations) and variable conditions within basal iguanians. Although absent in most gekkotans, presence of a small supratemporal in most eublepharids (see Grismer, 1988) leads to our coding of (0) for this outgroup.]

35. Tympanic crest of quadrate large (0), or crest strongly reduced (1).

36. Pterygoid lappet of quadrate absent (0), or present (1). [Coding of *Gobiderma pulchrum* based on MAE 96-163.]

37. Muzzle tapered, narrowing anteriorly (0), or blunt and rounded (1).

38. Posterior lacrimal foramen single (0), or double (1). [Coding of *Gobiderma pulchrum* based on MAE 95-29, 93-248. *Cherminotus* is described as having "probably only one slit-like lacrimal foramen." Because of the uncertainty, the character cannot be confidently scored for this taxon and is treated as missing data.]

39. Premaxillary teeth large (0), or abruptly smaller than maxillary teeth (1). [Coding of *Gobiderma pulchrum* based on MAE 96-163.]

40. Plicidentine infolding of teeth absent (0), or present (1). [Although described as having no basal fluting (Borsuk-Bialynicka, 1984), the actual condition in *Paravaranus* cannot be ascertained because of poor preservation; and the anterior lower dentition in *Proplatynotia* seems to show very shallow infolding (GK, personal obs.). Because of the uncertainty, we treat the character as missing data in these taxa.]

41. Marginal teeth are not (0), or are widely spaced with expanded tooth bases (1). [Modified from Pregill et al. (1986: character 25).]

42. Replacement teeth developed entirely or partially in resorption pits (0), or developed posteriorly without presence of resorption pits (1). [State (0) corresponds to the so-called iguanid and intermediate methods, and state (1) is equivalent to the so-called varanid method of Edmund (1960). Because considerable overlapping of the iguanid and intermediate methods has been known within various groups of lizards (see Rieppel, 1978), we have chosen to combine the two replacement patterns in this analysis.]

43. Maxillary tooth row extends extensively suborbital (0), or slight suborbital with no more than three tooth positions (1), or entirely antorbital (2). [Coding of *Anniella* based on McDowell and Bogert's (1954: 122) description: "In *Anniella* the maxillary dentition does not extend posterior to the level of the lacrimal foramen" (contra McDowell and Bogert, 1954: fig. 42C; Rieppel, 1980a: fig. 22).]

44. Maxillary teeth number more than 13 (0), 10–13 (1), or nine or less (2). [State (1) is inferred for *Palaeosaniwa* from the lower dentition (see Estes, 1983; Gao and Fox, 1996), which normally has slightly higher number of teeth than the upper. *Shinisaurus* has 14 maxillary teeth (McDowell and Bogert, 1954). Coding of *Anguis* and *Anniella* is based on Edmund (1969) and Bell et al. (1995). *Proplatynotia* and *Saniwides* have no more than 13 maxillary teeth (contra Borsuk-Bialynicka, 1984).]

45. Venom groove on marginal teeth absent (0), or present (1). [This character remains undetermined for *Gobiderma pulchrum* in this study, awaiting preparation of a well-preserved specimen (MAE 96-163) for future revision.]

46. Incisive process of premaxilla as a single spine (0), or bipartite (1). [Coding of *Xenosaurus* based on Rieppel (1980a: character 5); but see also Barrows and Smith (1947: 230) who described the incisive process in *Xenosaurus* as "blunt, knobbed, sometimes bilobed."]

47. Vomer short of slightly elongated (0), or strongly elongated to nearly twice the length of palatine, reaching level of posterior end of tooth row (1).

48. Aperture of Jacobson's organ confluent

with internal narial opening (0), or separated from the narial opening by vomer-maxillary contact (1). [Modified from Rieppel (1980a: character 42). State (0) corresponds to the so-called palaeochoanate, and state (1) to neochoanate palate. See Rieppel (1983) and Estes et al. (1988: character 42) for discussion on *Lanthanotus*. Coding of *Xenosaurus* based on AMNH 98122 and 103212 (contra Rieppel, 1980a), and *Saniwa* on AMNH-DVP 8688.]

49. Posterior extension of choana ends far anterior (0), or ends close to or at posterior end of maxillary tooth row (1). [Modified from Rieppel (1980a: character 44).]

50. Palatal shelves of vomer wide (0), or narrow (1).

51. Palatine longer than wide (0), or equally wide as long (1).

52. Palatine teeth present (0), or absent (1). [*Lanthanotus* is coded as polymorphic, although some specimen may show toothless condition. For conflicting data see McDowell and Bogert (1954), Jollie (1960), and Rieppel (1980a).]

53. Pterygoid teeth present (0), or absent (1). [Small pterygoid teeth are developed in most anguids, *Shinisaurus*, and *Lanthanotus*; are rudimentary in some *Heloderma*, and are lost in *Xenosaurus*, *Varanus*, and some anguids. In *Carusia*, several specimens show remnant pterygoid teeth (see text). Independent loss of the pterygoid teeth apparently occurs many times in several squamate lineages (see Estes et al., 1988 for evaluation).]

54. Anterolateral process of pterygoid short and fits into a notch of ectopterygoid (0), or extended dorsally on ectopterygoid to contact jugal (1). [From McDowell and Bogert, 1954.]

55. Ectopterygoid in palatal view does not contact palatine anteriorly (0), or does, excluding maxilla from suborbital fenestra (1). [Coding of *Necrosaurus* based on Hecht and Hoffstetter (1962). According to Rieppel (1980a) and Hu et al. (1984), an ectopterygoid-palatine contact occurs in *Shinisaurus* dorsally (not ventrally) on the supradental shelf (but see also McDowell and Bogert, 1954: palatine and ectopterygoid rather widely separated). Nonetheless, the contact in *Shinisaurus* does not prevent the maxilla from entering the suborbital fenestra; thus, we coded (0) for this taxon. Coding of *Saniwa*

based on description in Gilmore (1928: 62, contra his pl. 3).]

56. Posterolateral end of dentary having no notch or one notch only (0), or presence of both a coronoid and a surangular notch (1), or notches strongly reduced or lost owing to development of intermandibular hinge (2). [Coding of *Eosaniwa* as is difficult, and we treated it as missing data. Judging from a restored left mandible (see Estes 1983: fig. 43A), it is likely derived from a double notch condition.]

57. Surangular in lateral view strongly tapered anteriorly (0), weakly tapered (1), or blunt in keeping with development of intermandibular hinge (2).

58. Surangular does not extend anteriorly beyond (0), or slightly beyond (1), or well beyond coronoid eminence (2).

59. Anterior extension of splenial far beyond midpoint of tooth row (0), retracted to or posterior to midpoint of tooth row (1). [Loss of splenial occurs within Iguania, Gekkota, and some scincomorphans; we coded the plesiomorphic state for these outgroup clades.]

60. Posterior extension of splenial beyond coronoid eminence (0), or terminates anterior to or below the eminence (1).

61. Splenial-dentary suture firm (0), or loose, with much connective tissue between the two bones (1).

62. Intramandibular septum within Meckelian canal absent (0), or present as oblique or vertical septum (1). [See Estes et al. (1988: character 56) for discussion. Coding of *Lowesaurus matthewi* based on description in Yatkola (1976).]

63. Anterior process of coronoid is not (0), or is elongate and extensively exposed dorsally (1). [State (1) of this character is a platynotan synapomorphy.]

64. Subdental shelf normally developed (0), or lost in keeping with fusion of dentary tube (1), or strongly reduced as a slope (2). [State (2) is equivalent to subdental shelf lost of Estes (1964), and subdental shelf absent of Estes et al. (1988).]

65. Ventral border of subdental shelf does not (0), or does notch to form dorsal and anterior border of anterior inferior aveolar foramen (1). [See Estes (1964, 1983) and Estes et al. (1988). *Xenosaurus* has the ventral edge of the shelf grooved, forming the dorsal but not much of the anterior border of the foramen.]

66. Meckelian canal open medially for entire length (0), or open ventrally anterior to

anterior inferior alveolar foramen (1), or completely closed as a dentary tube (2). [Because the known relationships clearly indicate that the closed conditions in some iguanids and some scincomorphans are independently derived within their clades, we scored (0) for Iguania and Scincomorpha.]

67. Strong reduction of mandibular fossa absent (0), or present (1). [A mandibular fossa or foramen is normally developed in most lizards, but strongly inflated in the Lacertiformes and some scincids (Estes et al., 1988). A strongly reduced fossa occurs in anguids, xenosaurids, and platynotans; therefore, state (1) is a putative synapomorphy of the Anguimorpha.]

68. Medial exposure of angular bone small (0), or extensive (1). [See Rieppel, 1980a: character 64.]

69. Retroarticular process not widened (0), or widened (1). [see Estes et al. (1988: character 78).]

70. Retroarticular process not (0), or strongly twisted (1). [See McDowell and Bogert (1954) and Rieppel (1980a: character 70).]

71. Retroarticular process posteriorly directed (0), or deflected medially (1). [Medial inflection of the retroarticular process occurs in gekkotans, scincoids, anguids, and varanoids (see Estes et al., 1988: character 75). However, our observation of specimens of *Xenosaurus* (AMNH 98122, 103212) and published figures of *Shinisaurus* (McDowell and Bogert, 1954: fig. 4; Rieppel, 1980a: fig. 20) led to our conclusion that the process is medially deflected in extant xenosaurids.]

72. Cephalic osteoderms absent (0), present as thin and platelike tesserae (1), or fragmented and thickened as subconical mounds (2). [Coding of *Anniella* based on Bellairs (1949), McDowell and Bogert (1954).]

73. Dermal rugosities absent (0), present with vermiculate sculpture (1), or present with conspicuously pitted surfaces (2). [McDowell and Bogert (1954) noted state (2) as "platynotan type of osteodermal sculpture."]

74. Ossified palpebrals absent (0), or present (1). [For character optimization see Estes et al. (1988: character 36). Known specimens of both *Gobiderma pulchrum* and *Estesia mongoliensis* have no palpebral bone preserved, although a notch may indicate presence of the element in these

taxa. Coding of *Saniwa* based on AMNH-DVP 8688, and *Necrosaurus* on Hecht and Hoffstetter (1962).]

75. Lacrimal duct single (0), or double (1). [*Saniwa* has double lacrimal foramina as in extant varanids (Gilmore, 1928; personal obs. of AMNH-DVP 8688). A single canal but double duct condition is known in *Heloderma* (Gabe and Saint Girons, 1976).]

Axial characters

76. Number of cervical vertebrae eight or less (0), nine (1), ten or more (2). [Having nine cervical vertebrae is a unique character state shared by *Varanus* and *Lanthanotus* (see Hoffstetter and Gasc, 1969; Rieppel, 1980b; Estes et al., 1988, for discussion). Highly specialized *Anniella* has 10–12 cervicals (see Bell et al., 1995).]

77. Cervical intercentrum intervertebral or fixed under anterior part of following centrum (0), sutured to posterior part of preceding centrum (1), or fused to posterior part of preceding centrum (2). [Although Estes et al. (1988: character 97) noted ontogenetic variable conditions in varanoids, we coded this character based on data presented in Hoffstetter and Gasc (1969), and Rieppel (1980a).]

78. Neural spines low and broad (0), or narrow and tall (1). [Coding of *Gobiderma pulchrum* based on MAE 96-163 and 254/92-33.]

79. Precondylar constriction of vertebrae absent (0), or present (1). [See Estes et al. (1988: character 94).]

80. Number of presacral vertebrae fewer than 26 (0), or 26 or more (1). [Analysis of extant groups indicates that number of presacral vertebrae exceeding 26 is a synapomorphy of Anguimorpha with reversals in *Shinisaurus* (Estes et al., 1988), which has 23 presacrals (Hecht and Costelli, 1969). Although Gilmore (1928) assumed *Saniwa* had the same number of presacrals as *Varanus*, we treated it as missing data because only 21 are preserved and the actual condition cannot be ascertained. Within the Anguimorpha, further modification of this character independently occurs in several taxa: in *Lanthanotus* and *Heloderma* the number of presacrals exceeds 30 (Rieppel, 1980b; Pregill et al., 1986), and *Anniella* has a range of 66–78 (Bell et al., 1995).]

81. Autotomy on caudal vertebrae present (0), or absent (1). [Autotomy is absent in

agamids, chamaeleontids, and some iguanids (Hoffstetter and Gasc, 1969); present in pygopodids and most gekkonids. Since autotomy normally starts from fifth caudal and no fracture is shown on an articulated second through 13th caudal series in *Saniwa ensidens* and isolated first caudal in *Saniwa grandis* (see Gilmore, 1928), we scored (1) for *Saniwa*. Autotomy is present in *Ophisaurus harti* and *O. ventralis*, but lost in *O. apodus*; we scored the primitive state for the genus.]

82. Peduncles on cervical and caudal vertebrae absent (0), or present (1).

83. Caudal chevrons contact centrum condyle (0), suture to centrum only (1), or fuse to centrum (2). [Coding of *Lanthanotus borneensis* based on Rieppel (1980b); but see conflicting data on this and several other taxa in Barrows and Smith (1947), Hoffstetter and Gasc (1969), and Hecht and Costelli (1969).]

Appendicular characters

84. Epicoracoid contacts suprascapula and mesoscapula (0), or not (1). [For discussion of this and the following pectoral girdle characters, see Camp (1923), Lécuru (1968a, 1968b), Hoffstetter and Gasc (1969), and Estes et al. (1988).]

85. Posterior coracoid emargination absent (0), or present (1). [Coding of *Carusia* based on MAE 95-52.]

86. Interclavicle T-shaped or anchor-shaped without anterior process (0), or cruciform with prominent anterior process (1), vestigious or entirely lost in adults (2). [Among outgroups, although some agamids have cruciform interclavicle most non-acrodontan iguanians show primitive state (0); the interclavicle is cruciform in most gekkonids, but it is lost in pygopodids. Among the ingroup taxa, we are unable to code the character for *Lanthanotus* because of conflicting data in the literature: McDowell and Bogert (1954: 24): "*Lanthanotus* lacks the transverse processes of the interclavicle"; Rieppel (1980b: 102, fig. 5): "modification of the primitive T-shaped interclavicle by developing a broad anterior crossbar"; Lécuru (1968b): "Une ancre dont l'extrémité est largement entaillée." Coding of *Carusia* is based on MAE 40/93-90. The nonapplicable condition in *Heloderma* (without lateral processes) is coded as (9). Coding of *Anguis* and *Anniella* is based on Camp (1923), and McDowell and Bogert (1954).]

87. Mesosternum present (0), or absent (1).

88. Rib attachments on sternum more than three pairs (0), or three pairs (1), or two or fewer pairs (2). [The primitive state of this character occurs in both *Shinisaurus* (Costelli and Hecht, 1971) and *Xenosaurus* (Barrows and Smith, 1947; Camp, 1923; contra Lécuru, 1968b: fig. 17). *Varanus* has two pairs of sternal ribs and a third pair attaching to the tip of the sternum, considered mesosternum; therefore, we scored (2) for this taxon.]

89. Strong elongation of symphysial process of pubis absent (0), or present (1). [Coding of anguids from Estes et al. (1988: character 124).]

90. Body osteoderms absent (0), present dorsally (1), or present both dorsally and ventrally (2). [See Estes et al., 1988: character 126 and 127.]

Soft anatomic characters

91. M. episterno-cleido-mastoideus inserts mainly on paroccipital process (0), or has extensive insertion on parietal (1).

92. M. constrictor colli does not (0), or does extensively cover first ceratobranchials (1).

93. Origin of 3b-layer of MAME profundus from supratemporal and parietal (0), or supratemporal only (1).

94. M. geniomyoideus absent (0), present but completely superficial to m. genioglossus medialis (1), or insertion at least partly invades deep to m. genioglossus medialis (2). [See Camp, 1923; McDowell, 1972; Haas, 1973; Rieppel, 1980a.]

95. M. genioglossus lateralis single bundle and not inserted into hyobranchial skeleton (0), or subdivided into separate bundles and inserted into hyobranchials (1). [According to Rieppel (1980a: 35), *Heloderma* has a distinct head of lateralis inserting into the head of the ceratohyal, so we changed Pregill et al.'s (1986) coding for this taxon.]

96. Insertion of m. levator pterygoidii extends posteriorly beyond columellar fossa of pterygoid (0), or restricted anteriorly (1).

97. Anterior head of m. pseudotemporalis profundus absent (0), or present but not expanded (1), present and expanded (2), or lost by fusion (3). [See Rieppel (1980a), Estes et al. (1988: character 133).]

98. Bodenaponeurosis with broad base extending onto lateral edge of mandibular fossa (0), or narrow base attached only to

caudomesial edge of coronoid (1). [Coding of *Varanus* based on Lakjer (1926), Haas (1973), and Rieppel (1980a).]

99. Hemibacula (mineralized horns of hemipenis) absent (0), or present (1). [See Card and Kluge (1995) for most recent review of this character.]

100. Foretongue not notched or cleft for less than 10% of length (0), cleft for 10–20% of length (1), or deeply cleft from 20% up to over 50% of length (2). [See Estes et al., 1988: character 137.]

101. Carotid duct present (0), or absent (1). [Ductus caroticus is absent in *Varanus* and *Heloderma* (Underwood, 1957), as well as in *Lanthanotus* (McDowell, 1972: 262). Presch (1988) cited Gans (1978) and coded (0) for Lanthanotidae.]

102. Gland of Gabe absent (0), or present (1).

103. Cochlear duct not robust (0), or robust and broad, limbus elongate and heavy (1).

104. Ulnar nerve superficial (0), or deep in forearm (1). [The state (0) is called the "lacertid type" and (1) the "varanid type"; see Estes et al. (1988) for explanation. Coding of *Shinisaurus* based on Hu (1980).]

105. Second epibranchial present (0), or absent (1). [See Camp, 1923.]