

# AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY  
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024  
Number 3211, 25 pp., 6 figures, 1 table  
November 19, 1997

## Braincase and Phylogenetic Relationships of *Estesia mongoliensis* from the Late Cretaceous of the Gobi Desert and the Recognition of a New Clade of Lizards\*

MARK A. NORELL<sup>1</sup> AND GAO KEQIN<sup>2</sup>

### ABSTRACT

A description of a newly discovered partial skeleton of *Estesia mongoliensis* with a relatively well-preserved braincase is provided and allows a reassessment of the relationships of this taxon with other varanoids. Analysis of a data set of 89 characters across 19 ingroup taxa rejects the previously suggested *Estesia mongoliensis*–Varanidae sister-group relationship, revealing instead that *Estesia mongoliensis* is a member of a distinct clade of lizards including the extant *Heloderma* and its fossil relatives. This clade can be diagnosed by the following

unequivocal derived characters: (1) foramen ovale located anterior to spheno-occipital tubercle; (2) pterygoid lappet of quadrate present; and (3) vertebral neural spine narrow and tall. Several other characters diagnose sequential less inclusive groups and therefore also support an *Estesia mongoliensis*–*Heloderma* relationship. Recognition of the new clade necessitates revision of the definition and diagnosis of the Helodermatidae. The name Helodermatidae is restricted to the descendants of the last common ancestor of the extant taxa *Heloderma suspectum* and *Heloderma horridum*.

### INTRODUCTION

As one of the most significant discoveries of nondinosaurian and nonmammalian fossil

vertebrates from the Gobi Desert, *Estesia mongoliensis* is known from the Upper Cretaceous

\* This is publication no. 25 of the Mongolian Academy of Sciences—American Museum of Natural History joint paleontological project.

<sup>1</sup> Chairman and Associate Curator, Department of Vertebrate Paleontology, American Museum of Natural History.

<sup>2</sup> Frick Postdoctoral Fellow, Department of Vertebrate Paleontology, American Museum of Natural History.

Djadoktha and Barun Goyot formations and from an undetermined unit at Ukhaa Tolgod (Dashzeveg et al., 1995), Mongolia. Norell et al. (1992) provided a cladistic analysis of *Estesia mongoliensis* and other varanoid taxa based on the work of Pregill et al. (1986) consisting of 80 characters and five basic taxa. In that study, the most parsimonious tree placed *Estesia mongoliensis* as a sister-taxon to the Varanidae (sensu Pregill et al., 1986). However, the next most parsimonious tree placed *Estesia mongoliensis* as the sister-taxon of helodermatids. Furthermore, Norell et al.'s analysis was compromised by two factors. First, only 33 out of 80 characters in the data matrix could be scored on the type skull. To generate a more robust phylogenetic hypothesis, more complete specimens are necessary to reveal information on these missing data and more characters must be examined in closely related taxa. Secondly, Norell et al. (1992) included a nonmonophyletic Necrosauridae\* in their analysis. Although removal of this taxon had no effect on the preferred topology, inclusion of such a taxon may cause character ambiguities, especially when characters are variable among necrosaurids.

During the 1993 field-season of the Mongolian-American Museum Expeditions to the Gobi Desert, a partial skeleton and associated braincase of *Estesia mongoliensis* (MAE 14, IGM 3/15; see Figs. 1–3) was collected from the Khermeen Tsav locality, which is stratigraphically in the Upper Cretaceous Barun Goyot Formation (provisionally late Campanian in age; e.g., Fox, 1978; Lillgraven and McKenna, 1986, but see discussion in Norell et al., 1992: 3–5). Because the braincase of the holotype (IGM) M3/14 is crushed (see Norell et al., 1992), the newly discovered of the braincase provides information for revising the diagnosis and reassessing the phylogenetic relationships of this taxon within the Varanoidea.

An analysis of 89 characters across 19 in-group taxa produces results favoring an *Estesia mongoliensis*–helodermatid clade over the *Estesia mongoliensis*–Varanidae sister-group relationship previously suggested. Placement of *Estesia mongoliensis* as the sister group of helodermatids necessitates a change in definition of the Helodermatidae and reinterpretation of several characters that

were regarded as diagnostic for the group. Abbreviations are given in appendix 1.

## SYSTEMATIC PALEONTOLOGY

SQUAMATA OPPEL, 1811

SCINCOGEKKONOMORPHA SUKHANOV, 1961

ANGUIMORPHA FÜRBRINGER, 1900

VARANOIDEA CAMP, 1923

Unnamed taxon including all the descendants of the last common ancestor of *Heloderma* and *Estesia mongoliensis*.

*Estesia mongoliensis* Norell et al., 1992  
Figures 1–3

HOLOTYPE: (IGM) M3/14, a well-preserved skull with mandible.

TYPE LOCALITY AND HORIZON: Lizard Hill, Khulsan, Mongolia (43°29'19"N, 101°08'44"E); Upper Cretaceous Barun Goyot Formation.

REVISED DIAGNOSIS: For characters shared with closely related taxa see Phylogenetic Conclusions.

Distinguished from *Heloderma* and its fossil relatives in having the following autapomorphies: presence of a distinct single, median palatal trough formed by vomers; long median contact of vomers; presence of extensive convex surface medial to posterior ridge on posterior surface of quadrate; no distinct articular; foramen ovale located far anterior to spheno-occipital tubercle; spheno-occipital tubercle strongly elongate and posterolaterally oriented.

REFERRED SPECIMEN: No. IGM 3/15, partial skeleton with well-preserved braincase. IGM 3/15 is referred to *Estesia mongoliensis* on the basis of apomorphic characteristics shared with the type specimen. One of the most diagnostic areas of the skull of *Estesia mongoliensis* is the suspensorium. The quadrate is unique in both its size and in the possession of an "extensive convex surface medial to the posterior ridge on the posterior surface of the quadrate" (Norell et al., 1992: 5).

The articular fossa of the mandible is also unique in *Estesia mongoliensis*. As noted by Norell et al. (1992: 15):

In squamates generally the articular forms the articular fossa and is the bony ossification of the posterior end of Meckel's cartilage. In

*Estesia mongoliensis*, the articular is apparently not present. Because the element was found in articulation with the quadrate, it is reasonable to believe that this element is in fact lacking rather than an artifact of preservation.

The Khermeen Tsav specimen IGM 3/15 corroborates this view, as the quadrate is preserved in articulation with the ramus. Preparation of the articular fossa anterior to the quadrate reveals a deep cavity, identical to the type specimen. Both specimens now provide strong evidence that the articular was not present, or not ossified, in adults of *Estesia mongoliensis*. Absence of the articular and the morphology of the quadrate provide the basis for referral of IGM 3/15 to the taxon *Estesia mongoliensis*.

Locality and Horizon: Khermeen Tsav, Mongolia; Barun Goyot Formation (Late Cretaceous: late Campanian). Additional specimens have been collected from Bayn Dzak (Djadoktha Formation) and Ukhua Tolgod (undefined unit, see Dashzeveg et al., 1995).

## DESCRIPTION OF THE BRAINCASE

The newly discovered IGM 3/15 is the first specimen that shows braincase structures in *Estesia mongoliensis*. The specimen consists of the otico-occipital portion of the braincase; the cartilaginous anterior orbitotemporal part is not preserved. Although incomplete, the braincase shows little distortion, and foramina and sutures are easily recognizable.

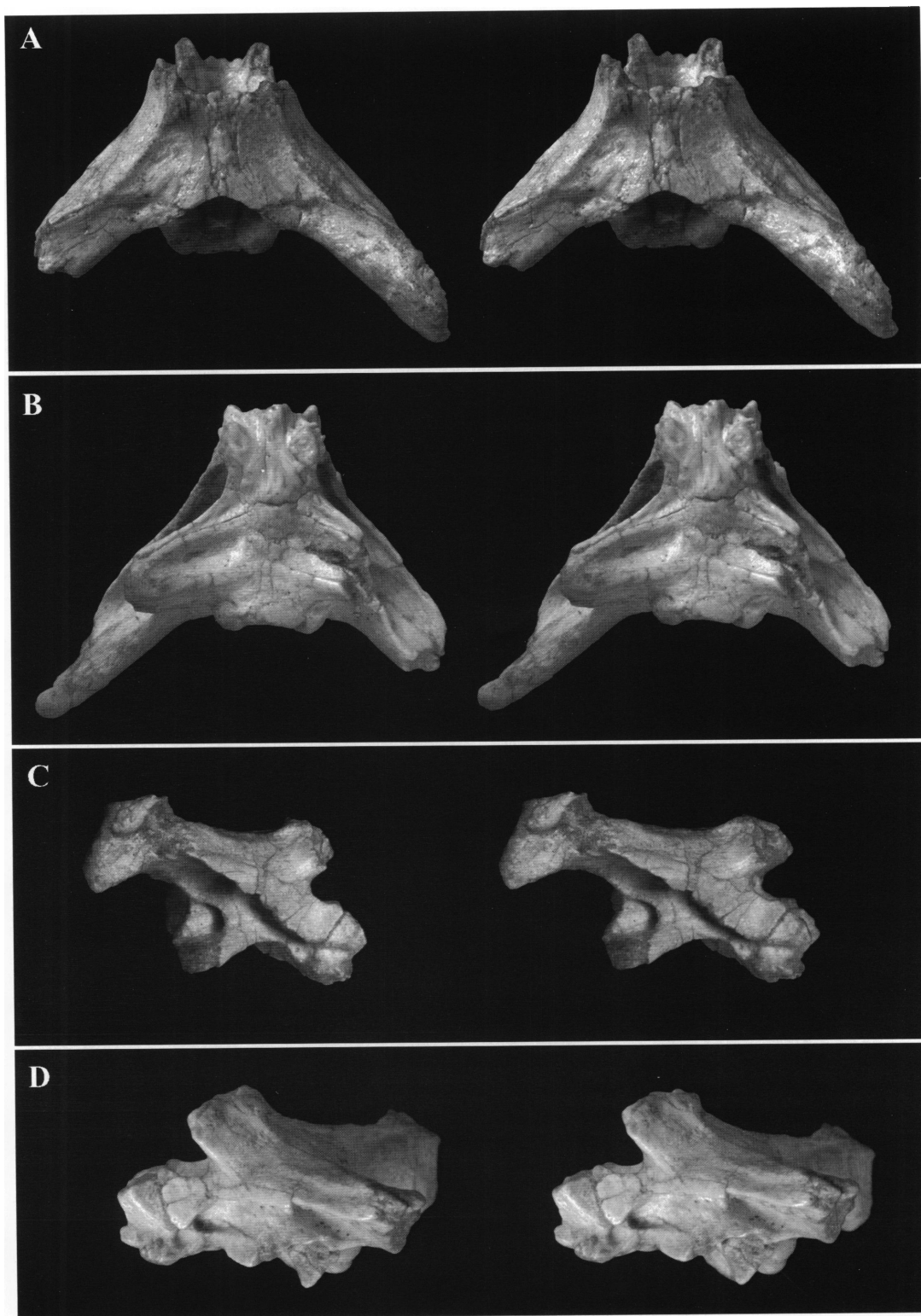
**Supraoccipital**—The supraoccipital is well exposed in dorsal view (fig. 1A) as the parietals are not preserved. The element is roughly trapezoidal and has a very small sagittal crest on its dorsal surface as in the type specimen. McDowell and Bogert (1954: 104) regarded the lack of a dorsal sagittal crest as a distinctive feature of anguimorphans, but Jollie (1960) noted that such a crest is present in *Varanus niloticus* (Varanidae) and *Ophisaurus attenuatus* (Anguidae); consequently, independent loss of this crest may have evolved in different clades within the Anguimorpha.

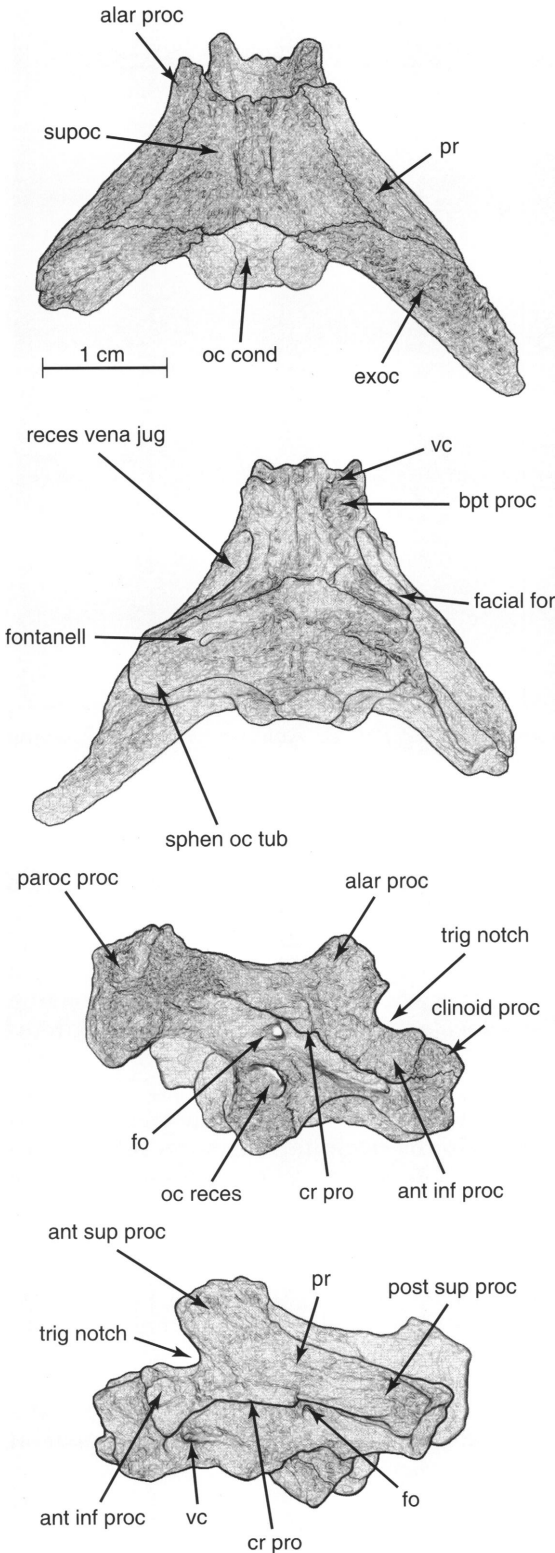
The supraoccipital in *Estesia mongoliensis* arises anterodorsally at a very low angle, giv-

ing the dorsal surface of the bone a very gentle slope. The processus ascendens (Oelrich, 1956; processus anterior tecti of various authors) is broken off, but the base on the left process indicates it was more dorsally than anteriorly directed. Laterally, the bone is sutured with the prootic and the suture runs along a crest extending from the base of the processus ascendens lateroposteriorly to the point near the dorsal tip of the paroccipital process. As commonly seen in other lizards, the posterior border of the supraoccipital is notched in dorsal view and forms most of the dorsal margin of the foramen magnum. The supraoccipital/exoccipital suture meets the supraoccipital/prootic suture at a Y-shaped joint on the dorsal surface of the skull at the base of the paroccipital process.

**Exoccipital**—As in most other lizards, the opisthotic fuses with the exoccipital to form a compound element, which (following terminology of Oelrich, 1956) we call the exoccipital. This element forms the lateral rim of the foramen magnum, part of the occipital condyle, part of the posterior rim of the occipital recess, and the entire paroccipital process, which lies lateral to the foramen magnum. Fusion of the two bones occurs during early stages of lizard ontogeny and it is debatable which is the primary element contributing to the formation of the compound bone (for example, see e.g., Jollie, 1960). However, a consensus exists that the exoccipital forms the lateral margin of the foramen magnum (de Beer, 1985) and at least the base of the paroccipital process. The paroccipital process of *Estesia mongoliensis* is proportionally longer than that in *Varanus* and is more posteriorly than laterally directed.

This compound element can clearly be delimited from its adjacent elements. In dorsal view, it makes sutural connection with the supraoccipital anteriorly and with the posterior superior process of the prootic laterally (fig. 1A). In posterolateral view, a ventrolaterally directed process involves the formation of the spheno-occipital tubercle and marks the posterior rim of the occipital recess (this rim is termed "crista tuberalis" in Oelrich, 1956). The anterolateral rim of the occipital recess is termed "crista interfrenetralis," which is notched anteriorly in lateral





view (fig. 1C). It is worth noting that there is a significant difference in ventral exposure of the exoccipital between *Varanus* and *Heloderma*. The exoccipital exposed in ventral view in *Varanus* is roughly fan-shaped and has an oblique suture medially with the basioccipital, while the same bone in *Heloderma* has little exposure in ventral view and the exoccipital/basioccipital suture is horizontal.

In posterior view, the exoccipital on each side contributes to slightly less than  $\frac{1}{3}$  of the occipital condyle (fig. 1F). Lateral to the foramen magnum is a slitlike aperture in which the vagus and hypoglossal foramina are separated by a bony septum. Differing from the confluent condition in the Varanidae (McDowell and Bogert, 1954; Pregill et al., 1986), in *Estesia mongoliensis* these two foramina are clearly separate inside and outside the braincase. Anterior to the interior openings for the vagus and hypoglossal nerves, a large foramen at the floor of the braincase is the perilymphatic foramen, which opens at the suture between the prootic and exoccipital.

**Prootic**—In lateral view, the prootic is tri-radiate, with a large posterior process (Oelrich, 1956; = paroccipital process of Jollie, 1960), a much shorter alar or anterior superior process, and an anterior inferior process (fig. 1C, D). This configuration differs from the condition in extant varanids, in which the prootic develops an extra posterior inferior process or crest. The anterior superior process is broken on both sides of the specimen, but the anterior inferior process is completely preserved. The latter process contributes little to the attachment of the pila antotica. The triradiate condition is widely distributed in basal iguanians (Oelrich, 1956; personal obs.) and most scleroglossans.

The trigeminal notch (= facial notch of Jollie, 1960) at the anterior margin of the prootic (between the superior and the in-

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Fig. 1. Braincase of *Estesia mongoliensis* (IGM 3/15). A, dorsal view showing Y-shaped suture between supraoccipital, paraoccipital, and prootic; B, ventral view; C, right lateral view; D, left lateral view. Abbreviations, see appendix 1.

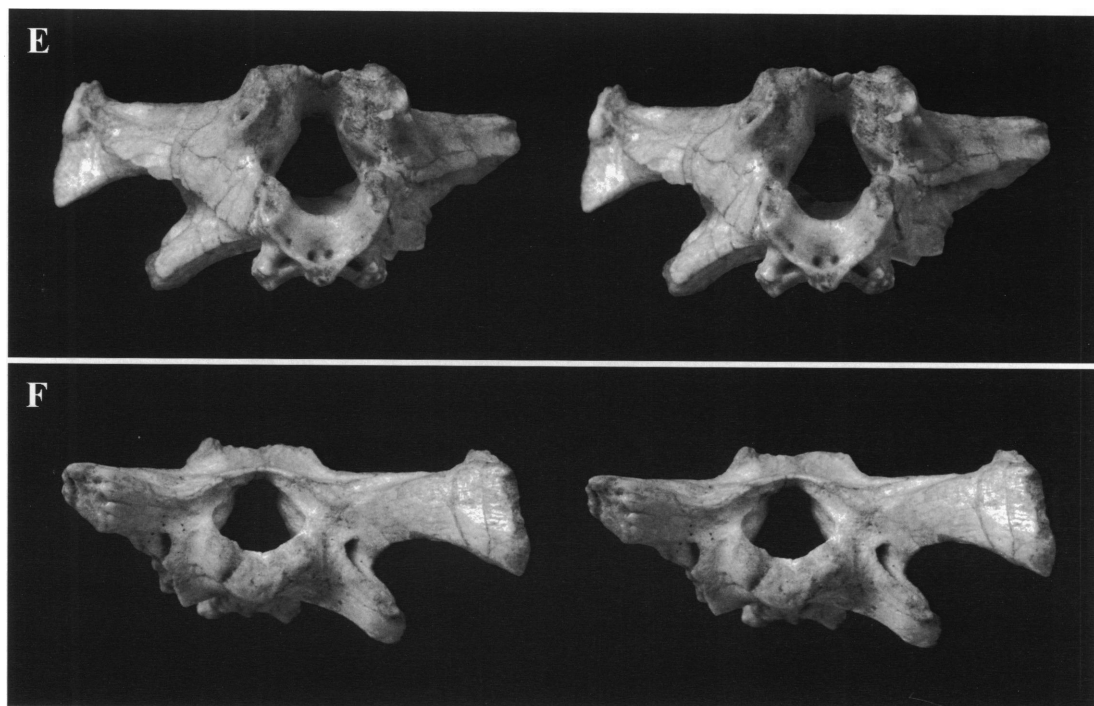
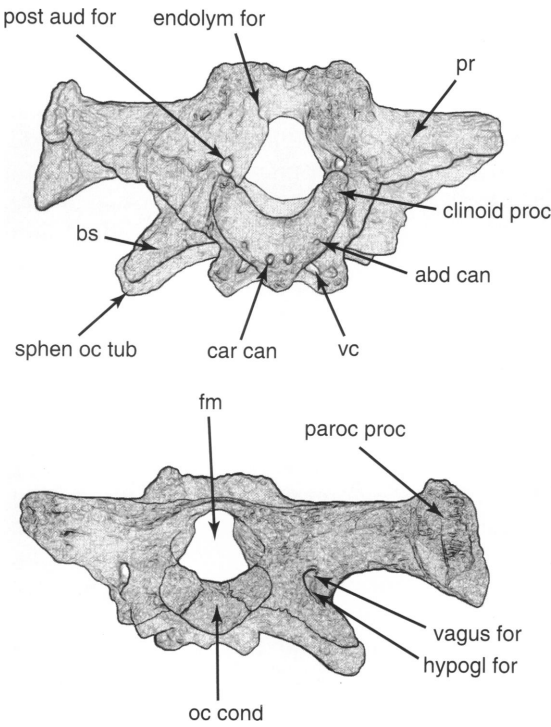


Fig. 1 (continued). Braincase of *Estesia mongoliensis* (IGM 3/15). E, Anterior view; F, Occipital view. Abbreviations, see appendix 1.

ferior processes) shows no significant differences from that of other varanoids. The crista prootica, which forms the postero-ventral margin of the bone, is a thin and relatively straight crest that extends from the ventral border of the anterior inferior process to near the tip of the posterior superior process. Medial to the crista prootica is the well-developed "recessus venae jugularis" (of Oelrich, 1956; = vena capitis lateralis of Jollie, 1960), which constitutes a trough for the internal jugular vein and the openings of several cranial nerves (see Oelrich, 1956; Jollie, 1960). The prootic forms the arched roof and the lateral wall of the recessus vena jugularis.

Within the recessus vena jugularis lie several nerve openings. Anteriorly, close to the prootic/basisphenoid suture is the posterior opening of the vidian canal (carotid foramen of Jollie, 1960; entocarotid-vidian canal of McDowell and Bogert, 1954). The position of this opening varies taxonomically within the Varanoidea. In *Lanthanotus borneensis*, according to 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). In *Varanus* it penetrates the basisphenoid and is close to the base of the basiptyergoid process, whereas in *Heloderma* the opening is "located far back at the posterior extremity of the lateroventral surface of the sphenoid" (McDowell and Bogert, 1954: 40), i.e., at the prootic/basisphenoid suture and close to the occipital recess on the sphenoccipital tubercle. A single foramen for the facial nerve (VII) is located posterodorsal to the vidian canal and at the level of the trigeminal notch. Within the Varanoidea, *Heloderma* has a single facial foramen exposed in lateral view, but *Varanus* has double openings for the facial nerve (Jollie, 1960). Because of the development of a posterior inferior process of the prootic, the two foramina are not exposed in lateral view. Presence of double facial foramina is probably derived at the level of Varanidae, as the condition also occurs in *Lanthanotus borneensis* (Rieppel, 1980a).



Anteroventral to the facial foramen and anterodorsal to the posterior opening of the vidian canal is the carotid fossa, which is an elongate recess separated from the facial foramen by a clearly defined bony ridge. Such a carotid fossa occurs in basal anguimorphans (anguids), is strongly reduced in *Xenosaurus grandis*, *Shinisaurus crocodi-*

*lurus* (McDowell and Bogert, 1954), and *Heloderma*, but is absent in *Varanus* and *Lanthanotus borneensis* (McDowell and Bogert, 1954). Therefore, lack of a carotid fossa is diagnostic for the Varanidae. The third and posteriormost foramen in the recessus venae jugularis is the foramen ovale (fenestra vestibuli), the anterior border of which is formed by a ridge of the prootic descending from the arched roof of the recessus venae jugularis. The foramen ovale in *Estesia mongoliensis* is located far anterior to the tip of the sphenoccipital tubercle (fig. 1C), while in *Varanus* the foramen is slightly posterior to the tubercle. In iguanians, scincomorphans, and basal anguimorphans, the foramen ovale is at the same level with the tubercle. Therefore, we interpret the anterior location of the foramen in *Estesia mongoliensis* as a derived condition. As in most other lizards, the prootic marks the anterior and dorsal margin of the foramen ovale, whereas the posterior and ventral border is formed by the exoccipital.

The internal wall of the prootic is smooth and shows no indication of a supratrigeminal process. Such a process is best known in basal iguanians (for example, Oelrich, 1956), greatly reduced in some scincomorphans (for example, *Tupinambis teguixin*, AMNH-DHI 141941) but well developed in some scincids (for example, *Tiliqua nigrolutea* AMNH-DHI 99684), and virtually lost in anguimorphans (Jollie, 1960). Estes

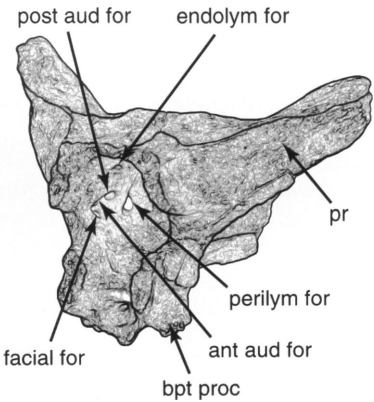


Fig. 2. Anteromedial view of the braincase of *Estesia mongoliensis* (IGM 3/15) showing acoustic recess of the prootic. Abbreviations, see appendix 1.



et al. (1988: 153) interpreted the presence of a supratrigeminal process as "an iguanian synapomorphy that has been lost in chamaeleontids and a few iguanids\* and agamids\*." However, presence of this process in other lizard families (Scincidae: *Eumeces* and *Mabuya*, see Rao and Ramaswami, 1952: fig. 16; Teiidae: *Tupinambis*, according to Jollie, 1960) may indicate that its presence is a synapomorphy of a more inclusive taxon—the Squamata.

Three foramina are clearly identifiable on the inner surface of the prootic (see fig. 1D, 2). These lie in a single shallow depression, which is termed the acoustic recess by Oelrich (1956). The posteriormost and the largest is the posterior auditory foramen for CN VIII. Anterior to this and close to the trigeminal notch are two smaller openings: the facial foramen and the anterior auditory foramen. Taxonomically significant variations in size and relative location of these foramina can be observed in extant varanoids: in *Heloderma* (e.g., MAN 9), the facial and the anterior auditory foramina are roughly equal in size and the posterior auditory foramen is slightly larger than the former two. The three foramina are closely located and all open in the same recess. In *Varanus* (e.g., AMNH-DVP-CA 2994 and AMNH-DHI 109498), on the other hand, the facial foramen is enlarged compared to the posterior auditory foramen. The latter foramen is located far back on the exoccipital side of the prootic/exoccipital suture and there is an additional fourth foramen closely associated with it.

Another foramen visible in anteromedial view is the endolymphatic foramen, which forms a passageway for the endolymphatic duct. In *Estesia mongoliensis* this foramen penetrates the inner surface of the supraoccipital as in other lizards.

**Basioccipital**—The basioccipital in *Estesia mongoliensis* has a unique configuration in comparison with other varanoids: It has an unusually strong spheno-occipital tubercle (basal tubera of Romer, 1956; tuberculum sphenooccipitale of Jollie, 1960) that is more posterolaterally than ventrally directed (fig. 1B). In extant varanoids (e.g., *Varanus* and *Heloderma*), this tubercle is greatly reduced, ventrally directed, and shifted anteriorly. The posterolateral direction of the tubercle in *Es-*

*tesia mongoliensis* implies a different orientation of the longus capitis muscles (Romer, 1956) in this Cretaceous lizard from that of other known fossil and extant varanoids. The ventral surface of the basioccipital in *Estesia mongoliensis* has a paired depression which is deep and laterally elongate. Such a depression is extremely shallow or simply absent in extant varanoids. On the floor of each depression, and close to the basisphenoid/basioccipital suture, is a tadpole-shaped small pit (broken on the left side of the specimen), which almost penetrates the floor of the occipital recess. This is probably the remnant of the basicranial fontanelle. According to Jollie (1960: 4), "the basioccipital is very thin in this region or just behind this suture because of the basicranial fenestra of the chondrocranium" and "a minute opening here can occur in many species as a variant."

Owing to the elongation of the spheno-occipital tubercle and the posterolateral process of the basisphenoid, the basioccipital has a long sutural contact with the basisphenoid, which is strongly arched anteriorly. This morphology is very similar to the so-called "obtusely angulate" (McDowell and Bogert, 1954: 21) suture in basal anguimorphans, but is different from the straight line suture in *Varanus* and *Lanthanotus borneensis*. The new specimen of *Estesia mongoliensis* shows no "X ossicle" (see Jollie, 1960 for discussion) posterolaterally between the basisphenoid and basioccipital; such a "X ossicle" is well developed in *Varanus* (e.g., *Varanus komodoensis*, AMNH-DHI 109498) but absent in *Heloderma*.

Dorsal to the spheno-occipital tubercle is a large occipital recess (of Oelrich, 1956; "recessus scalae tympani" of Siebenrock, 1894, and Romer, 1956; fenestra cochlearis of Jollie, 1960). As in extant varanoids (e.g., *Varanus* and *Heloderma*), the anterior border of the recess (crista interfenestralis, Sæve-Söderbergh, 1947) in *Estesia mongoliensis* is formed by the exoccipital. However, comparison of *Estesia mongoliensis* with extant varanoids shows significant differences in the shape and orientation of the recess. The recess is vertically elliptical in *Heloderma* and oblique in *Varanus*. In *Estesia mongoliensis*, the anterior border of the recess is strongly arched anteriorly, and the recess itself is es-



entially posteriorly oriented. Owing to the posterior elongation of the spheno-occipital tubercle, the posterior border of the recess (crista tuberalis of Säve-Söderbergh, 1945, 1947) is less well-defined and more dorsally located than in *Varanus* or *Heloderma*. Posteriorly, the basioccipital contributes a small portion to the occipital condyle (slightly more than  $\frac{1}{3}$ , differing from *Varanus* and *Heloderma*, in which over  $\frac{1}{2}$  of the condyle is composed of this element).

**Basisphenoid**—In keeping with the development of a large lateral process of the basioccipital, the basisphenoid (of Oelrich, 1956; parasphenoid or para-basisphenoid of others) has a slender and greatly elongate posterolateral process attached to the anterior surface of the basioccipital (fig. 1B). The basipterygoid process is broken on both sides but the base seems to indicate the process was probably short and anterolaterally oriented. Anterior to the base of the process is the anterior foramen of the vidian canal. In primitive anguimorphans and helodermatids, there is a well-developed lateral crest (crista trabecularis) dorsal to the foramen, which separates the canal from the sella turcica (or pituitary fossa), so that the foramen is ventral to the floor of the recess. Contrary to this condition, varanids have a derived condition in which the canal is anterolateral or medial to the crest. *Estesia mongoliensis* retains the primitive condition with a strong crest separating the canal from the sella turcica.

Deep in the sella turcica are two small foramina that occur side by side and penetrate the dorsum sellae: these are the anterior inferior carotid foramina (fig. 1E). They are very small, rounded, and close to one another, differing from the condition in extant *Heloderma* and *Varanus*, in which the foramina are enlarged and more laterally located, clearly branching from the vidian canal. No retractor crest is developed between the anterior inferior carotid foramina as seen in extant varanoids.

The parasphenoid process (rostrum or cultriform process of other authors) is largely missing, probably because of its slenderness and poor ossification. According to McDowell and Bogert (1954), extant *Heloderma* and *Lanthanotus borneensis* have an unossified parasphenoid process (formed by trabecular

cartilage), while the process in *Varanus* is a bony structure.

Dorsolateral to the deep sella turcica is the small but clearly defined clinoid process of the basisphenoid. As is typical of other lizards, it sutures with the anterior inferior process of the prootic posteriorly and has a facet for articulation with the cartilaginous pila antotica dorsally. The abducens canal opens on the medial surface of the clinoid process very close to the lateral crest of the sella turcica. In most lizards, including *Varanus*, the abducens canal opens deep inside the sella turcica, while in *Heloderma*, it opens directly on the crest.

### VERTEBRAL COLUMN

The vertebral column of *Estesia mongoliensis* was previously unknown, as the holotype has no postcranial skeleton preserved. The newly recovered IGM 3/15 includes 12 associated vertebrae (fig. 3), which provide information on the vertebral morphology of *Estesia mongoliensis*. Three articulated vertebrae are identifiable as the posteriormost cervical and the first two anterior dorsals. Identification of the cervical is based on the presence of a pit below the condyle for the unfused hypocentrum and the presence of a well-developed midventral ridge on the centrum; this identification is further supported by the presence of a well-developed neural crest anterior to the spine dorsally. Generally such a crest is shorter and more vertical in dorsal vertebrae than in cervicals. This cervical centrum shows no hypapophysis fused onto its ventral surface; instead, a small posteroventral "chip" indicates the intercentrum may contact the condyle. There is no indication of prominent basal peduncles, which is a derived condition for extant *Lanthanotus* and *Varanus* (Rieppel, 1980b) and at least fossil *Saniwa* (Gilmore, 1922). Neither the cervical nor the anterior dorsals show any tendency toward elongation, and in this aspect they differ from more derived varanids (Hoffstetter and Gasc, 1967, 1969).

Other associated and articulated vertebrae are the dorsals and the first sacral; the latter is broken but shows a robust sacral rib fused to the vertebra. The dorsal vertebrae are definitely the varanoid type: they have a well-

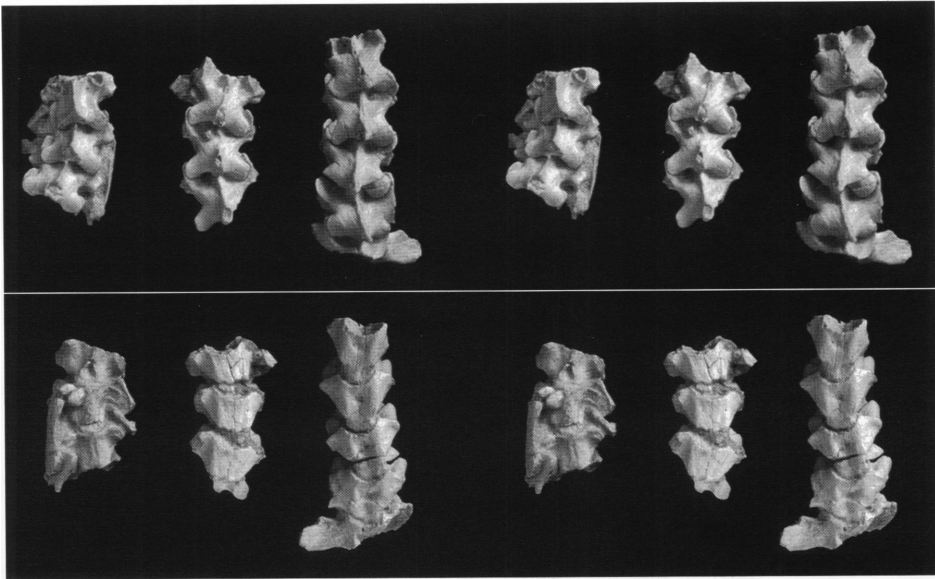


Fig. 3. Vertebral column of *Estesia mongoliensis* (IGM 3/15). **Top**, Dorsal view; **Bottom**, Ventral view.

defined condyle, which is flanged and constricted from the centrum body, and the articulation between the vertebrae is oblique (Estes, 1983; Estes et al., 1988). The diapophysis and parapophysis are fused, providing a tubercular attachment for a single-headed dorsal rib.

All neural spines are broken, but the preserved base clearly indicates that they are more rodlike than crown-shaped, and are probably tall and rise at an acute angle. Such a configuration resembles helodermatids but differs from varanids, in which the spine is crownlike or platelike. The ventral surface of the centrum shows variation along the length of the column. Cervical and anterior dorsal vertebrae have a midventral ridge, whereas those of the middle portion of the column have flattened ventral surfaces, and those close to the sacrals have a shallow depression in which two tiny openings can be observed.

#### PHYLOGENETIC RELATIONSHIPS

Phylogenetic relationships of *Estesia mongoliensis* with other varanoids were examined by constructing a matrix of 89 characters (table 1). Characters were derived from a variety of sources as discussed in appendix 3. Our approach differs from that of Norell

et al. (1992) and Pregill et al. (1986), in that instead of including a single set of character conditions for the Necrosauridae\*, we coded characters for a wide variety of "necrosaurid" and other relevant taxa (table 1).

All of the trees were rooted using Anguinae as an outgroup. Anguinae was used as the basal outgroup by both Pregill et al. (1986) and Norell et al. (1992). Because Xenosauridae has also been considered a close relative of the crown group (Estes et al., 1988), inclusion of it in a rooting scheme is important. However, because of a paucity of relevant xenosaur taxa available for this study, we do not consider it here; this outgroup scheme will be employed in another work (Gao and Norell in prep.), which will combine the data presented here with data for a number of xenosaur and putative xenosaur taxa.

Although fragmentary, a number of fossil taxa have variously been considered part of this crown group (table 1). Many of these have been allocated to the Necrosauridae\*, a nonmonophyletic grade group whose members have traditionally been considered primitive varanoids (Hoffstetter, 1962; Estes, 1983). Many of these taxa are exceedingly incomplete, resulting in much missing data

(see table 1). The addition of such fossils may have the positive effect of clarifying relationships (Gauthier et al., 1988). However, it may also produce extremely high numbers of equally parsimonious trees (Gauthier, 1986; Nixon and Wheeler, 1992; Novacek, 1992). Several approaches have been suggested for dealing with such data sets and a few of these were implemented here.

Our initial analysis concerned only *Estesia mongoliensis*, *Heloderma*, *Varanus*, and *Lanthanotus borneensis* under the search conditions listed in appendix 2. This analysis produced a single tree of 104 steps (fig. 4A). This tree supports an *Estesia mongoliensis*–*Heloderma* sister-taxon relationship, favoring the B-tree from a previous analysis (Norell et al., 1992).

This tree is separated from the next shortest trees by two steps. The tree in Figure 4B, of length 106, places *Estesia mongoliensis* as the sister-taxon of the Varanidae (*Varanus* and *Lanthanotus borneensis*), the position preferred by Norell et al. (1992). A tree three steps longer than the most parsimonious tree (fig. 4C, length = 107) positions *Estesia mongoliensis* as the sister taxon of the Varanoidea (Varanidae + Helodermatidae). The next cluster of longer trees have lengths greater than 114.

When the complete data set of all taxa and all characters was analyzed, 395 shortest trees (length = 131) were discovered. Strict consensus of these trees resulted in the poorly resolved consensus tree (fig. 5). However, a significant element of structure present in this tree is a clade composed of a four-taxon (*Eurheloderma gallicum*, *Lowesaurus matthewi*, *Heloderma*, and *Estesia mongoliensis*) polytomy, followed by *Paraderma bogerti* and *Gobiderma pulchrum*. We name this clade the Monstersauria (see below).

An obvious method to subvert the influence of taxa that have copious amounts of missing data and create large numbers of trees is simply to eliminate them from the analysis. Such elimination must proceed with caution, consider the example where inclusion of a fragmentary fossil taxon resulted in the discovery of fewer most parsimonious trees and a more resolved consensus solution (Norell and De Queiroz, 1991). In our analysis, one taxon, *Palaeosaniwa canadensis*,

had 79 missing entries (eight more than the next least-complete taxon, *Parasaniwa wyomingensis*). Consequently, we implemented the TAXEQ2 algorithm (Wilkinson 1995a, 1995b), which examines data sets for taxa whose character distributions render them phylogenetically equivocal in an analysis. This process found *Palaeosaniwa canadensis* to be equivalent to *Lanthanotus borneensis*, *Saniwa*, and *Varanus*. *Palaeosaniwa candidensis* can therefore be safely eliminated (according to Wilkinson), if these three index taxa are retained.

Elimination of *Palaeosaniwa canadensis* resulted in 25 trees of length 131 (CI = 0.679, RI = 0.714). The strict consensus of these trees (fig. 6) is somewhat more resolved than the uncultured analysis. It supports not only a monophyletic Monstersauria clade, but its sister clade composed of (Varanidae + *Saniwa* + *Telmasaurus grangeri*) + (*Proplatynotia longirostrata* + *Saniwides mongoliensis*). These two groups together form a major anguimorph clade, which is more or less equivalent to the Platynota of other authors. The relationships of several other taxa (e.g., *Necrosaurus*, *Parviderma*, *Parasaniwa*) remain unresolved.

## PHYLOGENETIC CONCLUSIONS

The focus of this paper was a reevaluation of the phylogenetic position of *Estesia mongoliensis*. In the process we discovered that this taxon was not the sister taxon to the Varanidae as presented by Norell et al. (1992), but rather was a member of a distinct clade of lizards that includes the extant *Heloderma* and its fossil relatives. This identical clade was found in our analyses by using both a complete and a revised data set. Within this well-supported new clade, *Gobiderma pulchrum* is the sister taxon to the remaining members of the clade, followed by *Paraderma bogerti*.

We name this clade the Monstersauria (monster in reference to the Gila monster *Heloderma suspectum*). The new clade, supported by numerous characters, is defined as all of the descendants of the last common ancestor of *Gobiderma pulchrum* and *Heloderma suspectum*. This clade can be diagnosed by the derived characters as discussed

TABLE 1—Data Matrix

	0	10	20	30
Anguillidae	0	0	0	0
Santia	1	0	1	0
Necrosaurus	?	0	1	1
Paravaranus	?	0	?	?
Proplatynotia	0	0	?	0
Paroiderma	?	0	?	?
Gobiderma	0	0	?	?
Santoides	0	0	?	1
Paraderma	?	?	?	?
Parasantia	?	?	?	?
Eosantia	?	?	?	?
Cherninotus	0	1	?	?
Eurheloderma	?	?	?	?
Loavesaurus	?	?	?	?
Heloderma	0	1	?	?
Palaeosantia	?	?	?	?
Telmisaurus	1	1	?	?
Varanus	1	1	?	?
Lanthanotus	0	1	?	?
Estesia	0	1	?	?

	40	50	60
Anguillidae	0	0	0
Santia	1	1	1
Necrosaurus	?	?	?
Paravaranus	?	?	?
Proplatynotia	?	?	?
Paroiderma	?	?	?
Gobiderma	0	1	?
Santoides	1	1	?
Paraderma	?	?	?
Parasantia	?	?	?
Eosantia	?	?	?
Cherninotus	1	1	?
Eurheloderma	?	?	?
Loavesaurus	?	?	?
Heloderma	?	?	?
Palaeosantia	?	?	?
Telmisaurus	1	1	?
Varanus	1	1	?
Lanthanotus	1	1	?
Estesia	0	1	?

	70	80
Anguillidae	0	0
Santia	0	0
Necrosaurus	0	0
Paravaranus	0	0
Proplatynotia	?	?
Paroiderma	?	?
Gobiderma	?	?
Sentoides	?	?
Paraderma	?	?
Parasantia	?	?
Eosantia	?	?
Cherninotus	?	?
Eurheloderma	?	?
Loxosaurus	?	?
Heloderma	?	?
Palaeosantia	?	?
Telmasaurus	?	?
Varanus	?	?
Lanthanotus	?	?
Estesia	?	?

below, determined from the strict parsimony analysis of the complete data set including all taxa and characters.

COMMENTS ON GOBIDERMATIDAE  
LEE, 1997

Another important difference between the two taxa concerns their frontals. *Parviderma*

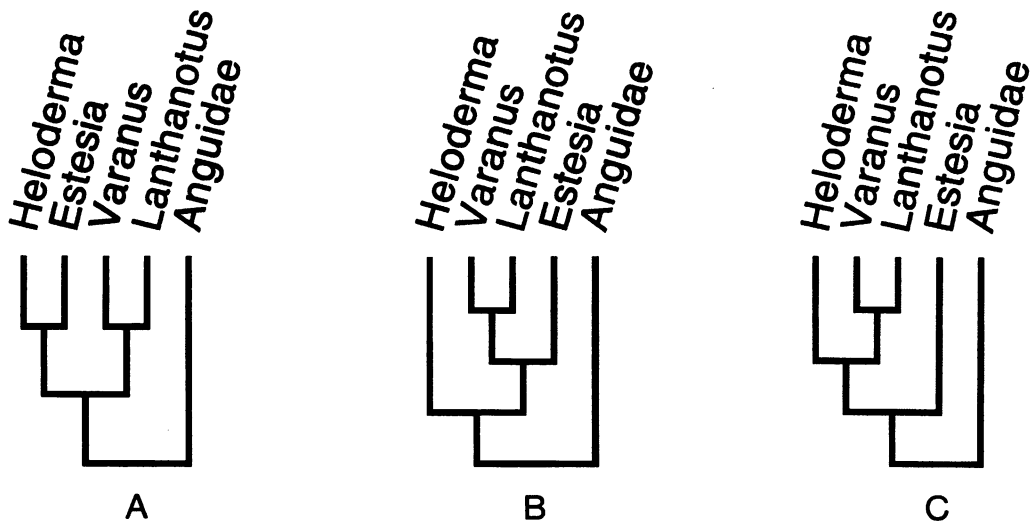


Fig. 4. Phylogenetic relationships of *Estesia mongoliensis* and other varanoids: A, Phylogenetic hypothesis (length 104) showing *Estesia mongoliensis*—*Heloderma* sister-taxon relationship; B, Slightly less parsimonious hypothesis (length 106) placing *Estesia mongoliensis* as the sister taxon to the Varanidae as preferred by Norell et al., 1992; C, Tree of length 107 placing *Estesia mongoliensis* as the sister taxon to the Varanoidea (Varanidae + Helodermatidae).

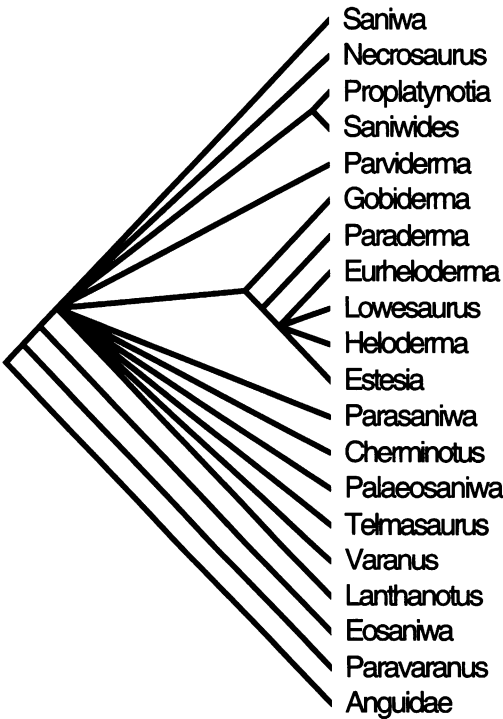


Fig. 5. Strict consensus of 395 shortest trees (131 steps) using the entire data set in table 1.

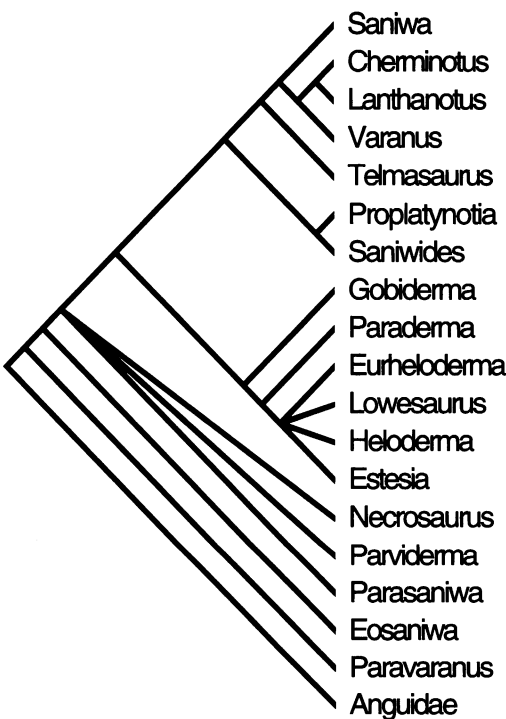


Fig. 6. Strict consensus of 25 trees (131 steps) with *Palaeosaniwa canadensis* eliminated.

*inexactum* has fused frontals, while all well-preserved specimens of *Gobiderma pulchrum* clearly show a paired condition as in other monstrosaurians. One referred fragment (MgR-I/54) is said to have fused frontals, but the suture in dorsal view may have been obscured as a matter of preservation. The specimen is only shown in dorsal view, but a ventral view may well show a paired condition. A similar case is known for *Telmasaurus grangeri*, in which one of the specimens (MgR-I/65) is described as having fused frontals (Borsuk-Bialynicka 1984) but in ventral view the specimen clearly shows a paired condition (GK personal obs.). We know of no convincing evidence that indicates any specimen of *Gobiderma pulchrum* has fused frontals.

Lee (1997: 60) claimed that "the two taxa share a distinct (autapomorphic) pattern of tubercular osteoderms concentrated in a circular zone centred around the frontoparietal suture." Lee's assertion is not supported; the skull roof elements of *Gobiderma pulchrum* have extensive subconical osteoderms with pitted surfaces, sharply different from the sculpture in *Parviderma inexactum*, which Borsuk-Bialynicka (1984: 38) described as "arranged in small-plate pattern" and "is quite similar to that present on the frontals of young *Gerrhonotus*." These important differences in patterns of osteodermal sculpture between the two taxa are best figured in Borsuk-Bialynicka (1984: fig. 27H, I).

As discussed above, we found no support for grouping *Gobiderma pulchrum* with *Parviderma inexactum*, and the Gobidermatidae as Lee (1997) proposed is in fact an artificial taxon.

#### CHARACTERS DIAGNOSTIC OF THE MONSTROSAURIA

These characters are unique to this clade of lizards within the study group. All of these characters displayed a CI of 1 and could be scored on *Gobiderma pulchrum* and other monstrosaur taxa.

Character 25. Foramen ovale located above or slightly posterior to the sphenoccipital tubercle (0), or anterior to the tubercle (1).

A foramen ovale anterior to the sphenoccipital tubercle occurs in *Gobiderma pulchrum*, *Heloderma*, and *Estesia mongoliensis*. Although scored as unknown for *Paraderma bogerti*, *Eurheloderma gallicum*, and *Lowesaurus matthewi*, our analyses show that this character is best interpreted as a monstrosaurian synapomorphy.

Character 32. Pterygoid lappet of quadrate absent (0), or present (1).

A pterygoid lappet of the quadrate is developed in *Gobiderma pulchrum*, *Heloderma* and *Estesia mongoliensis*. The same structure is coded as unknown for *Paraderma bogerti*, *Eurheloderma gallicum*, and *Lowesaurus matthewi*, but our analyses show that this is a monstrosaurian synapomorphy.

Character 61. Vertebral centra long and neural spines broad (0), or centra short and neural spines narrow and tall (1).

In *Heloderma* the trunk vertebrae are short in comparison with those of varanids, and the neural spines are narrow and tall (Pregill et al., 1986). The same morphology is also known for *Eurheloderma gallicum*, *Estesia mongoliensis*, *Paraderma bogerti*, and *Gobiderma pulchrum*. Our analyses indicate that this character is diagnostic of the monstrosaurian clade.

#### PROVISIONALLY DIAGNOSTIC CHARACTERS OF THE MONSTROSAURIA

These characters may be diagnostic of the Monstrosauria. However, because they either have a patchy distribution among taxa (a CI less than 1) or are missing in some ingroup taxa, their precise level of generality cannot be determined.

Character 14. Temporal musculature inserts centrally (0), or dorsally on parietal table (1).

Reversal to the primitive condition where the temporal musculature inserts ventrally on the parietal table is a synapomorphy of the Monstrosauria if it is separated from the basal varanoid node by one branch. All varanoids except for monstrosaurians display the derived condition. Consequently, reversal to the primitive condition may be synapomorphic for monstrosaurians depending on the topolog-



ical relationship of this clade to other varanoid taxa.

Character 23. Spheno-occipital tubercle short and ventrally directed (0), or elongate and posterolaterally directed (1).

The derived state of this character is present in *Estesia mongoliensis* and in *Gobiderma pulchrum*. *Heloderma* shows the outgroup condition and the condition cannot be assessed in the remaining Monstersauria. In other varanoid taxa, the condition is either missing or displays the outgroup condition. Therefore, an elongate posteriorly directed spheno-occipital tubercle is a synapomorphy of the Monstersauria and the condition is reversed in *Heloderma*, or in a clade composed of *Heloderma* and other closely related taxa if future fossil discoveries indicate the presence of the (0) state in them.

Character 40. Maxillary teeth number more than 13 (0), or 13 or less (1).

All the monstersaurian taxa are scored (1). The derived condition also occurs in varanids and some of the related fossil taxa. Our analyses indicate it could be independent synapomorphies for Monstersauria and a clade composed of varanids and some of their closely related fossil taxa, or it could be the synapomorphy for a more inclusive clade (Varanoidea) with reversal in the *Proplatynotia longironstrata*–*Saniwides mongoliensis* clade.

#### DIAGNOSTIC CHARACTERS OF UNNAMED CLADE MONSTERSAURIA EXCLUSIVE OF *GOBIDERMA* *PULCHRUM*

Within the Monstersauria, *Gobiderma pulchrum* is the sister taxon to an unnamed clade. This clade can be diagnosed by the unique occurrence of one character.

Character 33. Muzzle tapered, narrowing anteriorly (0), or blunt and rounded (1).

A blunt and rounded muzzle occurs in all Monstersauria except for the basal taxon *Gobiderma pulchrum*, which has a tapered muzzle. Occurrence of the same rostral configuration in the varanids *Cherminotus longifrons* and *Lanthanotus borneensis* is convergent.

#### PROVISIONALLY DIAGNOSTIC CHARACTERS OF UNNAMED CLADE MONSTERSAURIA EXCLUSIVE OF *GOBIDERMA PULCHRUM*

Character 42. Venom groove on marginal teeth absent (0), or present (1).

This is an important character but cannot be assessed in *Gobiderma pulchrum* at present. Depending on the actual condition in *Gobiderma pulchrum*, this character could be diagnostic of a less inclusive clade within the Monstersauria (exclusive of *Gobiderma pulchrum*), or an important feature supporting the monophyly of the new clade Monstersauria. Venom grooves are not found outside the Monstersauria.

#### CHARACTERS DIAGNOSING THE CROWN-GROUP MONSTERSAURIA

The crown group within the Monstersauria can be diagnosed by the unequivocal shared presence of one character. This clade is equivalent to the Helodermatidae of Estes et al. (1988); however, because we adopt the crown group concept of De Queiroz and Gauthier (1992), the name Helodermatidae is restricted to the descendants of the last common ancestor of the extant taxa *Heloderma suspectum* and *Heloderma horridum*.

Character 12. Parietal foramen present (0), or absent (1).

A parietal foramen is absent in *Eurheloderma gallicum*, *Lowesaurus matthewi*, *Heloderma*, and *Estesia mongoliensis* (absence of the foramen in *Lanthanotus borneensis* is considered convergent), but basal taxa of the monstersaurian clade (*Gobiderma pulchrum* and *Paraderma bogerti*) retain a primitive condition in having a parietal foramen.

#### PROVISIONALLY DIAGNOSTIC CHARACTERS OF THE CROWN- GROUP MONSTERSAURIA

Character 3. Nasal and prefrontal bones in broad contact (0), or with little or no contact (1).

The derived state occurs in *Heloderma* and *Estesia mongoliensis*, but it cannot be scored for other members of the the crown clade and

*Paraderma bogerti*, as well. The basal monstersaurian *Gobiderma pulchrum* shows primitive condition. Consequently, this character may diagnose the crown group in Monstersauria or a more inclusive clade, depending on the actual condition in *Paraderma bogerti*. Because the derived state occurs in Varanidae and their related fossil taxa, it may diagnose Varanoidea with reversal in *Gobiderma pulchrum*.

Character 4. Nasal and maxillary bones in broad contact (0), or with little or no contact (1).

Within Monstersauria, the derived condition of this character has the same distribution as character 3. Depending on the condition in other monstersaurians in which the character cannot be scored, the state (1) may diagnose the crown group or the crown group plus *Paraderma bogerti*. Outside the monstersaurian clade, the derived condition is convergently present in *Paravaranus*, Varanidae, and their fossil relative *Saniwa*.

Character 10. Prefrontal does not (0), or does (1) closely approach or contact postfrontal above orbit.

The derived condition of this character is present in *Estesia mongoliensis*, *Heloderma*, and *Lowesaurus matthewi*. The primitive condition is present in *Gobiderma pulchrum*, and in other monstersaurians it cannot be scored. Consequently the condition of the prefrontal contacting the postfrontal above the orbit may diagnose the crown clade in the Monstersauria that does not include *Paraderma bogerti* and *Gobiderma pulchrum*. The derived condition is also present in *Cherminotus longifrons*, *Lanthanotus borneensis*, and *Telmasaurus grangeri*.

#### DIAGNOSTIC CHARACTER OF *ESTESIA MONGOLIENSIS*

The following character from the data set used for the phylogenetic analysis is diagnostic for *Estesia mongoliensis*. Autapomorphies not included in the analysis are listed under Systematic Paleontology.

Character 5. Nasal process of maxilla rises from the middle (0), or posterior aspect of maxillary (1).

A problematic character is the retraction of the bony external narial opening in *Estesia mongoliensis* (correlated with posterior position of the nasal process of maxillary). Such a retraction has been recognized as a varanid synapomorphy (Pregill et al., 1986). However, close examination of the character among the taxa involved shows that the retraction in *Estesia mongoliensis* can be distinguished from the similar condition in *Varanus* and *Lanthanotus borneensis*; in the latter, the frontal enters into the margin of the narial opening, whereas in *Estesia mongoliensis* it does not. This difference, enhanced by the fusion of the nasals in *Varanus* and *Lanthanotus borneensis*, casts doubt on the possible homolog of the character in question between *Estesia mongoliensis* and the Varanidae. Nevertheless, we retain the coding of Norell et al., 1992 where they considered *Estesia mongoliensis* to have the same condition as Varanidae. Alteration of this coding scheme has no effect on resultant topologies.

#### PROVISIONALLY DIAGNOSTIC CHARACTERS OF *ESTESIA* *MONGOLIENSIS*

Character 24. Occipital recess elliptic, vertical, or oblique (0), or posteriorly elongated without clearly defined posterior border (1).

Modification of the occipital recess is a feature unique to *Estesia mongoliensis*. However it is missing in all other fossil monstersaurians.

Character 28. Basioccipital contributes slightly over  $\frac{1}{3}$  of the formation of occipital condyle (0), or over  $\frac{1}{2}$  of condyle (1).

The derived state in this character occurs in most of the taxa scored in this analysis where it can be observed. The reversed condition is found in *Lanthanotus borneensis* and in *Estesia mongoliensis*. Other than *Heloderma*, only *Paraderma bogerti* can be scored for this feature among monstersaurians. Both of these taxa display the derived condition. Reversal to the primitive condition may be diagnostic of either *Estesia mongoliensis*, or of *Estesia mongoliensis* and other crown-group Monstersauria.

Character 29. Supratemporal process of

parietal broad in dorsal aspect (0), or narrow (1).

The primitive condition is present in *Heloderma*, *Eurheloderma gallicum*, and *Gobiderma pulchrum*. It is missing in other Monstersauria. The derived condition in *Estesia mongoliensis* may be diagnostic for this taxon or for it and other members of crown-group Monstersauria where the character is missing.

#### DIAGNOSTIC CHARACTER OF THE HELODERMATIDAE

Character 41. Maxillary teeth greater than nine (0), or nine or fewer (1).

Reduction of maxillary tooth number to less than nine is characteristic of helodermatids. The derived condition also convergently occurs in *Cherminotus longifrons*, in which the maxillary tooth number is as low as eight.

#### PROVISIONALLY DIAGNOSTIC CHARACTERS OF THE HELODERMATIDAE

Character 13. Upper temporal arch present (0), or lost (1).

The derived condition is also found in *Lanthanotus borneensis* and *Cherminotus longifrons*. The primitive condition is found in *Estesia mongoliensis* and *Gobiderma pulchrum*; it is missing in other monstersaurs. Therefore it is provisionally diagnostic of the Helodermatidae until better specimens of *Lowesaurus matthewi* and *Eurheloderma gallicum* are collected.

Character 22. Carotid fossa present (0), or absent (1).

Among monstersaurs the derived state of the carotid fossa is uniquely present in helodermatids, although it is missing in *Eurheloderma gallicum* and *Lowesaurus matthewi*. Outside the Monstersauria the derived state is present in varanids and their fossil relative *Telmasaurus grangeri*. Like character 13, it is provisionally diagnostic of the Helodermatidae until more complete specimens of *Lowesaurus matthewi* and *Eurheloderma gallicum* are collected.

Character 23. Spheno-occipital tubercle

small and ventrally directed (0), or elongate and posterolaterally directed (1).

The derived condition may be diagnostic for the Monstersauria—it is present in *Estesia mongoliensis* and *Gobiderma pulchrum* uniquely among varanoid taxa. However, copious missing data (in *Eurheloderma gallicum*, *Lowesaurus matthewi*, and *Paraderma bogerti*) somewhat confuses this issue. Nevertheless, if an elongate and posterolaterally directed spheno-occipital tubercle is primitive for the Monstersauria, reversal of this feature in helodermatids (or helodermatids and/or *Eurheloderma gallicum* and *Lowesaurus matthewi*) is a diagnostic character at this level.

Character 52. Splenial extends anteriorly to or beyond midpoint of tooth row (0), or posterior to midpoint (1).

Among monstersaurs this character can only be assayed in *Gobiderma pulchrum* (which shows the primitive condition) and in *Heloderma*, which shows the derived condition. The derived condition is also found in varanids. It is missing in most fossil taxa; therefore, depending on the nature of the missing data and topological constraints, this feature may be diagnostic of a more or less inclusive clade.

Character 62. Number of presacral vertebrae fewer than 30 (0), or more (1).

The derived state of this character occurs in *Heloderma* and in *Lanthanotus borneensis*, but is not present in *Saniwa* and *Varanus*. This feature is extremely problematic because it cannot be assessed in any fossil monstersaurs and it is known only in one other fossil varanoid (*Saniwa*). The use of this feature as a diagnostic character is therefore dependent on the phylogenetic placement of *Saniwa* as the sister taxon to the Varanidae until this character can be assessed in additional fossil taxa. Furthermore, the level at which it is diagnostic within monstersaurs is unclear until more ingroup fossils can be assayed.

Character 75. Insertion of *M. geniomyoideus* is completely superficial to *M. genioglossus medialis* (0), or at least partly deep to *M. genioglossus medialis* (1).

Derived states of this character are found in both *Heloderma* and *Varanus*. Obviously, it cannot be scored in any fossil taxon.

It can either be considered synapomorphic of both *Heloderma* and *Varanus* or as a character diagnosing the more inclusive clade Varanoidea. Both alternatives are supported in fundamental cladograms of equal length.

Character 79. Bodenaponeurosis with broad base (0), or narrow base attached only to caudomesial edge of coronoid (1).

This character has the same distribution and occurrence of missing data as Character 75.

Character 87. Ossified palpebrals present (0), or absent (1).

The derived condition is found in *Heloderma* and in *Lanthanotus borneensis*; the primitive condition is seen in *Varanus* and *Saniwa*. Because it is unknown in all fossil taxa but *Saniwa*, this character may be derived in a more general clade and lost in *Varanus* and *Saniwa*, or may be diagnostic of *Lanthanotus borneensis* and *Heloderma* individually.

Character 88. Scleral ossicles 14 (0), or fewer (1).

Reduced scleral ossicles have the same distribution as Character 87—the absence of ossified palpebrals.

#### CHARACTERS SUPPORTING A POSSIBLE GROUPING WITHIN HELODERMATIDS, THE CROWN GROUP

Other characters. Some other characters also seem to support a *Lowesaurus matthewi* + Helodermatidae clade. However, because they are unknown in *Eurheloderma gallicum*, this is somewhat conjectural.

Character 6. Frontal more or less parallel-sided (0), or trapezoidal (1). The derived condition of this feature occurs in helodermatids and *Lowesaurus matthewi*. The primitive condition occurs in all other varanoids where this character can be scored except for *Lanthanotus borneensis*. This feature is unknown in *Eurheloderma gallicum*.

Character 8. Subolfactory processes of frontals do not approach or contact each other anteromedially (0), or do so (1).

This character was figured by Norell et al. (1992) and has the same distribution as Character 6 above, except that the primitive con-

dition is also present in *Lanthanotus borneensis*.

#### CONCLUSIONS

*Estesia mongoliensis* is shown to be a member of a newly recognized and well-supported clade of lizards, the Monstersauria. This group is defined as the descendants of the last common ancestor of *Gobiderma pulchrum* and *Heloderma suspectum*, and is diagnosed by a set of derived characters. The new taxon Monstersauria contains the extant Helodermatidae, which comprise two species restricted to western North America as well as several fossil taxa. The extensive geographic (North America, Europe, and Asia) as well as temporal (Late Cretaceous to Recent) occurrence of these taxa indicates that this clade has a rich and diverse history.

#### ACKNOWLEDGMENTS

This paper is based on significant field discoveries from the Gobi Desert found by members of the Mongolian Academy of Science–American Museum of Natural History joint expeditions of the 1990s. We thank all those involved. We thank Marilyn Fox for preparation of specimens and Mick Ellison for preparation of photographs and drawings. We also thank John Wible and Guillermo Rougier for helpful discussion on terminology and evolution of cranial structures. This research was supported by the Frick Laboratory Endowment, the Department of Vertebrate Paleontology, American Museum of Natural History, NSF DEB 9300770, the IREX Foundation for International Research, the National Geographic Foundation, the Philip McKenna Foundation and Richard, Lynette and Byron Jaffe. Gao's work was supported by a Frick Research Fellowship of the American Museum of Natural History. Jim Clark (who also found the braincase), Darell Frost, Maureen Kearney, and Hans-Dieter Sues are thanked for their careful reviews of the manuscript.

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## APPENDIX 1

### Abbreviations

#### Anatomical:

Terminology follows Oelrich (1956) unless (otherwise) explicitly defined in the text. Abbreviations used in figures are explained as follows: **abd. can.** abducens canal; **alar proc.** alar process of prootic; **ant. aud. for.** anterior auditory foramen; **ant. inf. proc.** anterior inferior process of prootic; **ant. sup. proc.** anterior superior process of prootic; **bpt. proc.** basipterygoid process; **bo** basioccipital; **bs** basisphenoid; **car. can.** carotid canal; **clinoid proc.** clinoid process of basisphenoid; **cr. pro.** crista prootica; **endolym. for.** endolymatic foramen; **exoc.** exoccipital; **fm** foramen magnum; **fo**, fenestra ovalis; **hypogl. for.** hypoglossal foramen; **oc. cond.** occipital condyle; **oc. reces.** occipital recess; **perilym. for.** perilymphatic foramen; **pr.** prootic; **paroc. proc.** paroccipital process; **supoc** supraoccipital; **proc. as-**

**cend.** precessus ascendens; **post. aud. for.** posterior auditory foramen; **post. inf. proc.** posterior inferior process of prootic; **post. sup. proc.** posterior superior process of prootic; **reces. vena jug.** recessus vena jugularis; **sphen. oc. tub.** sphenoccipital tubercle; **supoc.** supraoccipital; **trig. notch** trigeminal notch of prootic; **vagus for.** vagus foramen; **vc** vidian canal.

#### *Institutional:*

AMNH-DVP	American Museum of Natural History, Department of Vertebrate Paleontology
AMNH-DVP-CA	American Museum of Natural History, Department of Vertebrate Paleontology comparative anatomy collection
AMNH-DHI	American Museum of Natural History, Department of Herpetology and Ichthyology
IGM	Institute of Geology, Mongolian Academy of Sciences, Ulan Bataar, Mongolia
MAE	Specimens from the Mongolian Academy of Sciences American Museum of Natural History Expeditions to be cataloged into the Institute of Geology, Mongolia collection
MAN	Personal collection of Mark A. Norell. Now transferred to the Department of Herpetology, American Museum of Natural History
PSS	Collection of the Polish Academy of Sciences, Paleontological Institute, Warsaw
RE	Personal collection of Richard Etheridge

## APPENDIX 2

### Phylogenetic Search Conditions

All of our trees were run using PAUP (Swoford, 1993) version 3.1, on a MacIntosh Power PC 8100 with 40 megabytes of RAM. As discussed in the text, trees were rooted using an outgroup (Anguidae), and the ingroup was constrained to be monophyletic. Trees were run using branch-and-bound search procedures except in the case of the analysis shown in figure 4, which was calculated using exact procedures.

## APPENDIX 3

### Characters Used in the Phylogenetic Analysis (modified from Pregill et al., 1986)

Numbers in parentheses indicate original characters enumerated in Pregill et al. (1986). Modifications of the original data set include elimination of two characters (40–41) owing to lack of phylogenetic value, and combination of several others (e.g., 3–4, 12–13, and 71–72) owing to character overlapping. Other modified and new characters added to the original data set are denoted with an asterisk. Codings of characters for taxa included are explained as follows:

*Anguidae*: based on published data in Rieppel (1980a) and Estes et al. (1988).

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

*Estesia mongoliensis*: based on type (M 3/14) and newly recovered 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 koehni*: 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 skulls 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).

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

Codings of 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 figure illustrations contradict descriptions, we made interpretations on the basis of description and photographs.



## Skull characters

**\*1.** Premaxillary foramen absent (0), or present (1). [From Rieppel (1980a: character 3). The opening misidentified as a premaxillary foramen in *Proplatynotis longirostrata* is in fact a premaxillary-maxillary aperture, as it opens at the premaxillary-maxillary suture, not within the premaxilla. Derived condition occurs within anguids, but we coded the plesiomorphic state for the taxon.]

**2** (1). Nasal bones paired (0), or fused (1). [Paired condition of the nasals in *Necrosaurus* is indicated by the double notched anterior border of the frontals (see Estes, 1983: fig. 43B).]

**3** (2). Nasal and prefrontal bones in broad contact (0), or with little or no contact (1).

**\*4** (3–4). Nasal and maxillary bones in broad contact (0), or with little or no contact (1).

**5** (5). Nasal process of maxilla rises from the middle (0), or posterior aspect of maxillary (1).

**6** (6). Frontal more or less parallel-sided (0), or trapezoidal (1).

**7** (7). Subolfactory processes of frontals short, not in contact ventromedially (0), or well developed and closely opposed or contacting ventromedially (1). [Coding of *Gobiderma pulchrum* based on MAE 95-29, 93-248.]

**8** (8). Subolfactory processes of frontals do not approach or contact each other anteromedially (0), or do so (1).

**9** (9). Subolfactory processes of frontals do not approach or contact each other posteromedially (0), or do so (1).

**10** (10). Prefrontal does not (0), or does closely approach or contact postfrontal above orbit (1).

**\*11.** Postorbital/postfrontal fusion absent (0), or present (1). [From Rieppel (1980a: character 20). Fusion of the two elements independently occurs in several groups of lizards (see Estes et al., 1988 for character analysis). Fusion also occurs within anguids (Rieppel, 1980a).]

**12** (11). Parietal foramen present (0), or absent (1).

**\*13** (12–13). Upper temporal arch present (0), or lost (1). [We have combined characters 12 and 13 of Pregill et al. (1986), because they overlap each other.]

**14** (14). Temporal musculature inserts ventrally (0), or dorsally on parietal table (1).

**15** (15). Supraoccipital not in broad contact with parietal (0), or with broad contact (1).

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

**17** (17). Carotid duct present (0), or absent (1). [Ductus caroticus is absent in *Varanus* and *Heloderma* (Underwood, 1957), as well as in *Lanthanotus borneensis* (McDowell, 1972: 262).]

**\*18.** Anterior opening of vidian canal ventral to sella turcica (0), or dorsal on the floor or within the sella turcica (1). [The anterior opening of the vidian canal in *Lanthanotus borneensis* is at a similar point as in *Heloderma* (see McDowell and Bogert, 1954: 41).]

**\*19.** Posterior opening of vidian canal located at prootic/basisphenoid suture (0), or penetrates basisphenoid only and close to the base of basiptyergoid process (1). [Modified from Estes et al. (1988: character 53); see discussion in text.]

**\*20.** Single facial foramen in recessus vena jugularis (0), or double (1). [Jollie (1960: 11) noted that most lizards have one facial foramen but *Varanus* and *Ophisaurus* have independently achieved a double foramina condition. Coding of *Lanthanotus borneensis* based on Rieppel (1980a).]

**\*21.** Prootic triradiate with straight crista prootica (0), or having a posterior inferior process (1).

**\*22.** Carotid fossa present (0), or absent (1). [From McDowell and Bogert (1954).]

**\*23.** Spheno-occipital tubercle short and ventrally directed (0), or elongate and posterolaterally directed (1).

**\*24.** Occipital recess elliptic, vertical, or oblique (0), or posteriorly elongated without clearly defined posterior border (1).

**\*25.** Foramen ovale located above or slightly posterior to the spheno-occipital tubercle (0), or anterior to the tubercle (1).

**\*26.** Basioccipital/basisphenoid suture obtusely angulate and laterally diagonal (0), or roughly a straight line suture (1). [See McDowell and Bogert (1954), and Borsuk-Bialynicka (1984) for detailed discussion of this character.]

**\*27.** "X ossicle" between basioccipital/basisphenoid/prootic absent (0), or present as a distinct element (1).

**\*28.** Basioccipital contributes slightly over  $\frac{1}{2}$  of the formation of occipital condyle (0), or over  $\frac{1}{2}$  of condyle (1).

**29** (18). Supratemporal process of parietal broad in dorsal aspect (0), or narrow (1).

**30** (19). Supratemporal bone does not reach level of apex of parietal notch (0), or does (1). [Coding of *Telmasaurus* according to Borsuk-Bialynicka (1984: fig. 16).]

**31** (20). Quadrate with large outer conch (0), or conch reduced (1).

**\*32.** Pterygoid lappet of quadrate absent (0), or present (1). [Coding of *Gobiderma pulchrum* based on MAE 96-163.]

**33** (21). Muzzle tapered, narrowing anteriorly (0), or blunt and rounded (1).

**34** (22). Posterior lacrimal foramen single (0), or double (1). [Borsuk-Bialynicka (1984: 43) not-

ed possible presence of a second lacrimal foramen in *Gobiderma pulchrum*. Our new specimens show a second small, blind pocket on right side only in MAE 95-29 but not in MAE 93-248 at all; therefore, we scored (0) for this taxon. Coding of *Cherminotus longifrons* is based on Borsuk-Bialynicka (1984: 64): "Probably only one slit-like lacrimal foramen is situated on the prefrontolacrimal suture."]

**35** (23). Premaxillary teeth large (0), or abruptly smaller than maxillary teeth (1).

**36** (24). Plicidentine teeth absent (0), or present (1).

**\*37** (25). Teeth slender and sharply pointed (0), or trenchant, with expanded base and widely spaced (1). [Modified from Pregill et al. (1986).]

**38** (26). Successional replacement teeth developed in association with resorption pits (0), or replacement teeth develop posteriorly, no resorption pits present (1). [Sixteen taxa were coded with (1), as lack of resorption pits indicates a varanid pattern of tooth replacement of these taxa. Because of poor known tooth morphology in *Eosaniwa koehni*, *Cherminotus longifrons*, and *Telmasaurus matthewi*, we coded (?) for these taxa.]

**39** (27). Maxillary tooth row extends extensively below orbit (0), or is antorbital or slightly below orbit with no more than three positions (1).

**\*40** (28). Maxillary teeth number more than 13 (0), or 13 or less (1). [Coding of *Palaeosaniwa* is inferred from the lower dentition (see Gao and Fox, 1996).]

**\*41** (29). Maxillary teeth greater than nine (0), or less than/equal nine (1).

**\*42** (30). Venom groove on marginal teeth absent (0), or present (1).

**43** (31). Vomer short (0), or nearly twice the length of palatine (1).

**44** (32). Palatal shelves of vomer wide (0), or narrow (1).

**45** (33). Palatine longer than wide (0), or equally wide as long (1).

**46** (34). Palatine teeth present (0), or absent (1).

**47** (35). Pterygoid teeth present (0), or absent (1).

**48** (36). Ectopterygoid does not contact palatine anteriorly (0), or does to exclude maxilla from suborbital fenestra (1).

**49** (37). Dentary and surangular overlap considerably (0), or very little (1).

**50** (38). Coronoid and surangular processes of dentary well developed (0), or processes reduced (1). [The coronoid and surangular processes in *Heloderma* are reduced in keeping with development of an intramandibular hinge.]

**51** (39). Surangular tapered anteriorly (0), or blunt and expanded anterodorsally (1).

**\*52**. Splenial extends anteriorly to or beyond midpoint of tooth row (0), or retracts posterior to midpoint (1).

**53** (42). Splenial extends posterior of coronoid eminence (0), or does not (1).

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

**55** (44). Splenial does not move with dentary (0), or does (1).

**56** (45). Coronoid without long anterolateral and anteromedial processes (0), or processes present (1).

**57** (46). Head scales large and platelike (0), or partly or completely fragmented (1).

**\*58** (47). Cephalic osteoderms thin, platelike (0), or thickened and fragmented as small elements (1).

**59** (48). Osteoderms fused to skull (0), or not (1). [To determine presence or absence of fused or unfused cranial osteoderms in *Estesia mongoliensis*, we reexamined the holotype skull and noticed a small scarlike structure at the base of the right supratemporal process. This "scar" can be counted as evidence of cranial osteoderms in *Estesia mongoliensis*, but it is indecisive as to whether the osteoderms were platelike or small elements divided by grooves as in extant *Heloderma*; nonetheless, the poor preservation of cranial osteoderms in the holotype skull provides no decisive evidence for understanding the pattern and fusion of the osteoderms to the skull.]

#### Axial characters

**\*60** (49). Number of cervical vertebrae eight or less (0), or nine (1). [See Estes et al. (1988: 171) for discussion.]

**61** (50). Vertebral centra long and neural spines broad (0), or centra short and neural spines narrow and tall (1).

**62** (51). Number of presacral vertebrae fewer than 30 (0), or more (1).

**63** (52). Caudal vertebrae autotomic (0), or not (1).

**64** (53). Peduncles on cervical and caudal vertebrae short (0), or long (1).

**65** (54). Caudal chevrons and cervical hypapophyses (= intercentra) contact centrum condyle (0), or on centrum only (1).

#### Appendicular characters

**66** (55). Epicoracoid contacts suprascapula and mesoscapula (0), or not (1).

**67** (57). Posterior coracoid emargination absent (0), or present (1). [Coding of *Lanthanotus borneensis* based on Rieppel (1980b).]

**68** (58). Clavicle loop-shaped medially (0), or gracile and not expanded (1).

**69** (59). Interclavicle with long anterior process (0), or process short or absent (1).

**70** (60). Mesosternum present (0), or absent (1).

**71** (61). Rib attachments on sternum more than three pairs (0), or three or fewer pairs (1).

### Myological characters

**\*72** (62). *M. episterno-cleido-mastoideus* inserts mainly on paroccipital process (0), or has extensive insertion on parietal (1).

**73** (63). *M. constrictor colli* does not cover first ceratobranchials (0), or does (1).

**\*74** (64). Origin of 3b-layer of *MAME profundus* from supratemporal and parietal (0), or supratemporal only (1). [Pregill et al. (1986) coded (0) for *Heloderma*, *Lanthanotus borneensis* and *Varanus*; we modified the description for more explicit explanation of the character and changed the codings of above-mentioned taxa based on Riepel's (1980a) work.]

**75** (65). Insertion of *M. geniomyoideus* is completely superficial to *M. genioglossus medialis* (0), or insertion is at least partly deep to *M. genioglossus medialis* (1).

**76** (66). *M. genioglossus lateralis* single (0), or subdivided into separate bundles (1).

**77** (67). Insertion of *M. levator pterygoidii* extends posteriorly beyond columellar fossa of pterygoid (0), or does not (1).

**78** (68). Anterior head of *M. pseudotemporalis profundus* not enlarged (0), or enlarged (1).

**79** (69). Bodenaponeurosis with broad base (0), or narrow base attached only to caudomesial edge of coronoid (1).

### Other characters

**80** (70). Hemipenis without paired horns as extensions of main retractor muscles (0), or with them (1). [See Card and Kluge (1995) for most recent review of this character.]

**\*81** (71–72). Foretongue cleft for 10–20% of length (0), or deeply cleft from 20% up to over 50% of length (1).

**82** (73). Gland of Gabe absent (0), or present (1).

**83** (74). Calyciform duodenal cells simple (0), or sero-mucous type (1).

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

**85** (76). Ulnar nerve superficial (0), or deep in forearm (1).

**86** (77). Second epibranchial present (0), or absent (1).

**87** (78). Ossified palpebrals present (0), or absent (1). [Coding of *Saniwa* based on AMNH-DVP 8688.]

**88** (79). Scleral ossicles 14 (0), or fewer (1).

**89** (80). Lacrimal duct single (0), or double (1). [*Saniwa* has double lacrimal foramina, but a single internal canal (Gilmore, 1928; personal observ. of AMNH-DVP 8688 (but see also Estes et al., 1988).]





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