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Estesia mongoliensis, a New Fossil Varanoid from the Late Cretaceous Barun Goyot Formation of Mongolia¹

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ABSTRACT

A new lizard from the Late Cretaceous Barun Goyot Formation was collected during the 1990 joint Mongolian American paleontological expedition to the Gobi Desert, Mongolia. This lizard is referable to a clade containing the extant genera *Lanthanotus*, *Heloderma*, and *Varanus*, as well as several poorly known extinct taxa including *Cher-*

minotus and *Saniwa*. Although the phylogenetic relationships among these taxa are uncertain, preliminary analysis suggests that the new taxon is the sister group to *Lanthanotus* and *Varanus*. Further, it displays the unusual feature of longitudinal grooves on the teeth, identical to the grooves used for venom conduction in *Heloderma*.

INTRODUCTION

One of the great Mesozoic and Tertiary fossil-producing regions in the world is the Gobi Desert of Mongolia. Since their discovery by field parties of the American Museum in 1923, the Mesozoic beds from this region have produced spectacular skeletons of fossil vertebrates (see Andrews, 1932; Kielan-Ja-

worowska and Dovchin, 1968). Among these are Cretaceous mammals and exquisitely preserved dinosaurs. Often overlooked, remains of lizards are among the most numerous fossils encountered at some localities.

Mongolian lizard fossils have been described by Gilmore (1943) (from specimens

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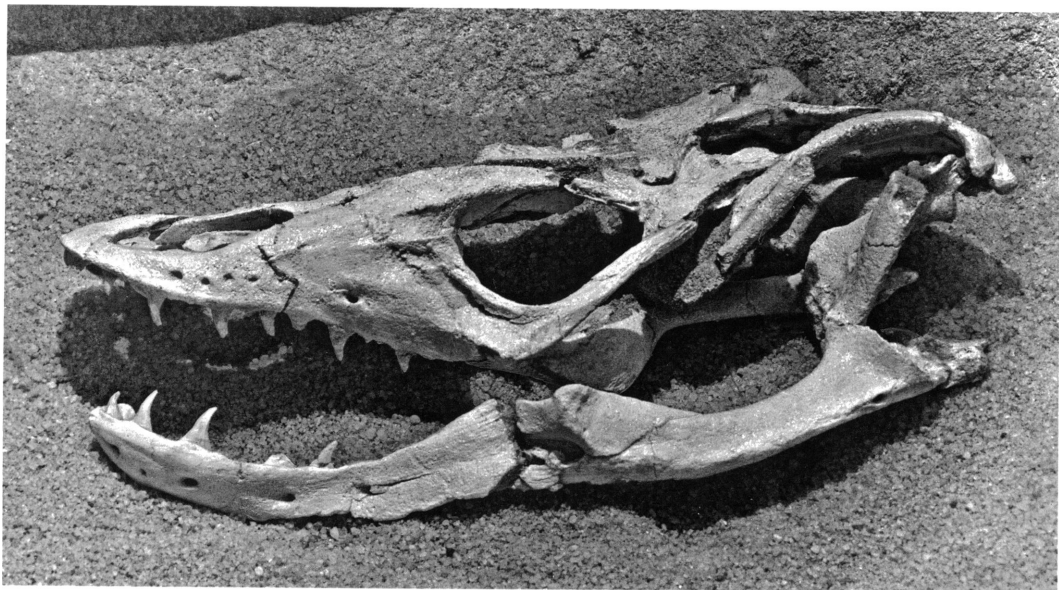


Fig. 1. The type skull of *Estesia mongoliensis*.

collected by the American Museum Central Asiatic expeditions) and Borsuk-Bialynicka (1984) and Sulimski (1972, 1975, 1978) (from specimens collected by the Polish-Mongolian expeditions). Here, we describe a new fossil lizard collected in June 1990, near Khulsan in the Barun Goyot Formation by a field party from the Mongolian Academy of Sciences and the American Museum of Natural History (fig. 1). This specimen, a nearly complete skull, displays features that may aid in deciphering the relationships among anguimorph lizards.

Such complete specimens of fossil lizards are generally rare. Where they exist, phylogenetic study is often hampered by a lack of detailed knowledge of extant taxa, making both determination of character polarity and the choice of appropriate outgroup taxa difficult. Among lizards phylogenetically affiliated with the taxon described herein (the Varanoidea), significant progress in resolving relationships has been accomplished (Rieppel, 1980; Gauthier, 1982; and Pregill et al., 1986). Nonetheless, much more work, including development of a phylogeny within the Varanidae, a detailed analysis of *Saniwa*, and a comprehensive review of "necrosaurids" is needed.

Our purpose is to provide a diagnosis and

comparative description of this new taxon and place it in a phylogenetic context. Comments regarding its explicit phylogenetic relationships are preliminary until a detailed reanalysis of the relationships among living and fossil anguimorphs is accomplished. In the following discussion, nomenclatural terminology follows Pregill et al. (1986), where the varanoids include descendants of the last common ancestor of *Heloderma*, *Lanthanotus*, and *Varanus*, and Varanidae is restricted to the descendants of the last common ancestor of *Lanthanotus* and *Varanus*. The morphological terminology follows Oelrich (1956) and Mertens (1942).

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History
RE	Collection of Richard Etheridge
MAN	Collection of Mark Norell
MAS	Mongolian Academy of Sciences

LOCALITY, GEOLOGIC SETTING, AND HISTORICAL BACKGROUND

In 1990, after an absence of nearly 60 years, the American Museum of Natural History resumed exploration in outer Mongolia

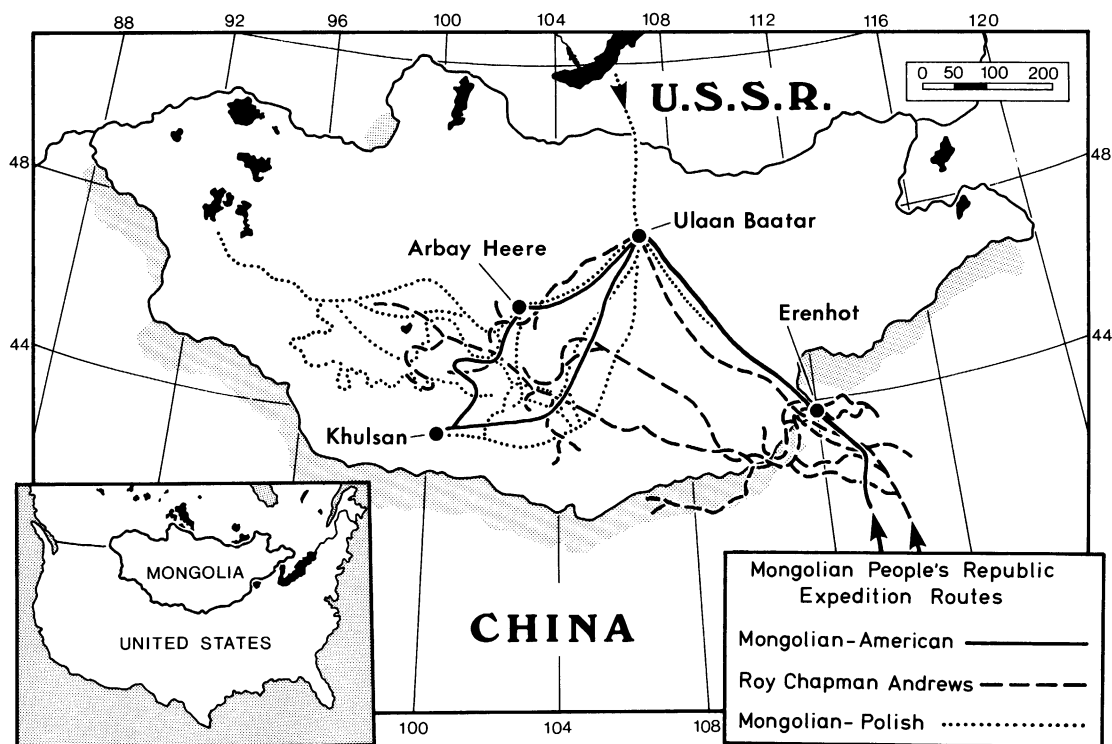


Fig. 2. Map of Mongolia, showing routes of American Museum Central Asiatic Expedition, the Polish-Mongolian Expedition, and the Mongolian-American Museum Expedition of 1990.

(Mongolian People's Republic until 1991; now simply Mongolia), in collaboration with the Mongolian Academy of Sciences. A reconnaissance of south-central Mongolia was undertaken in the early summer of 1990 (fig. 2). During this reconnaissance, the field party composed of Dr. Demberelyin Dashzeveg of the Mongolian Academy of Sciences, and Malcolm McKenna, Mark Norell, and Michael Novacek of the American Museum of Natural History visited the locality of Khulsan, explored in 1965 by the Polish-Mongolian Expeditions, although fossils were not found there until 1970 (fig. 3). The Khulsan locality yielded a well-preserved skull and mandibles and part of a front leg of a large varanoid lizard in addition to specimens of other lizards and dinosaurs. The varanoid specimen lay in a steep cliff face about 3 km downstream from the 1971 Polish-Mongolian Expedition's Khulsan camp (Gradzinski and Jerzykiewicz, 1972). Also recovered at this site were associations of dinosaur eggs, a skeleton of *Protoceratops*, the skull of a nearly

complete, but badly weathered ankylosaurid skeleton, and several skulls of small lizards.

The specimen was collected in the Barun Goyot Formation (Gradzinski and Jerzykiewicz, 1972; Efremov, 1950, 1954, 1955). Exposures at the locality are orange pink to light brown, cross bedded and poorly indurated sands, with occasional small pebbles. These beds have been considered Late Cretaceous, middle Campanian in age, based on multituberculates (Kielan-Jaworowska, 1974). "Comparative studies of dinosaurs and mammals" (Gradzinski et al., 1977) suggest that the Barun Goyot Formation is younger than the Djadokhta Formation at the Flaming Cliffs locality (Berkey in Granger and Gregory, 1923). Lillegraven and McKenna (1986), however, argued that "the Djadokhta and Barun Goyot formations are approximately equivalent in age, respectively, to the older and younger parts of the North American Judithian." These authors stress that determination of absolute ages and faunal stages is tenuous. Correlation based on higher taxa

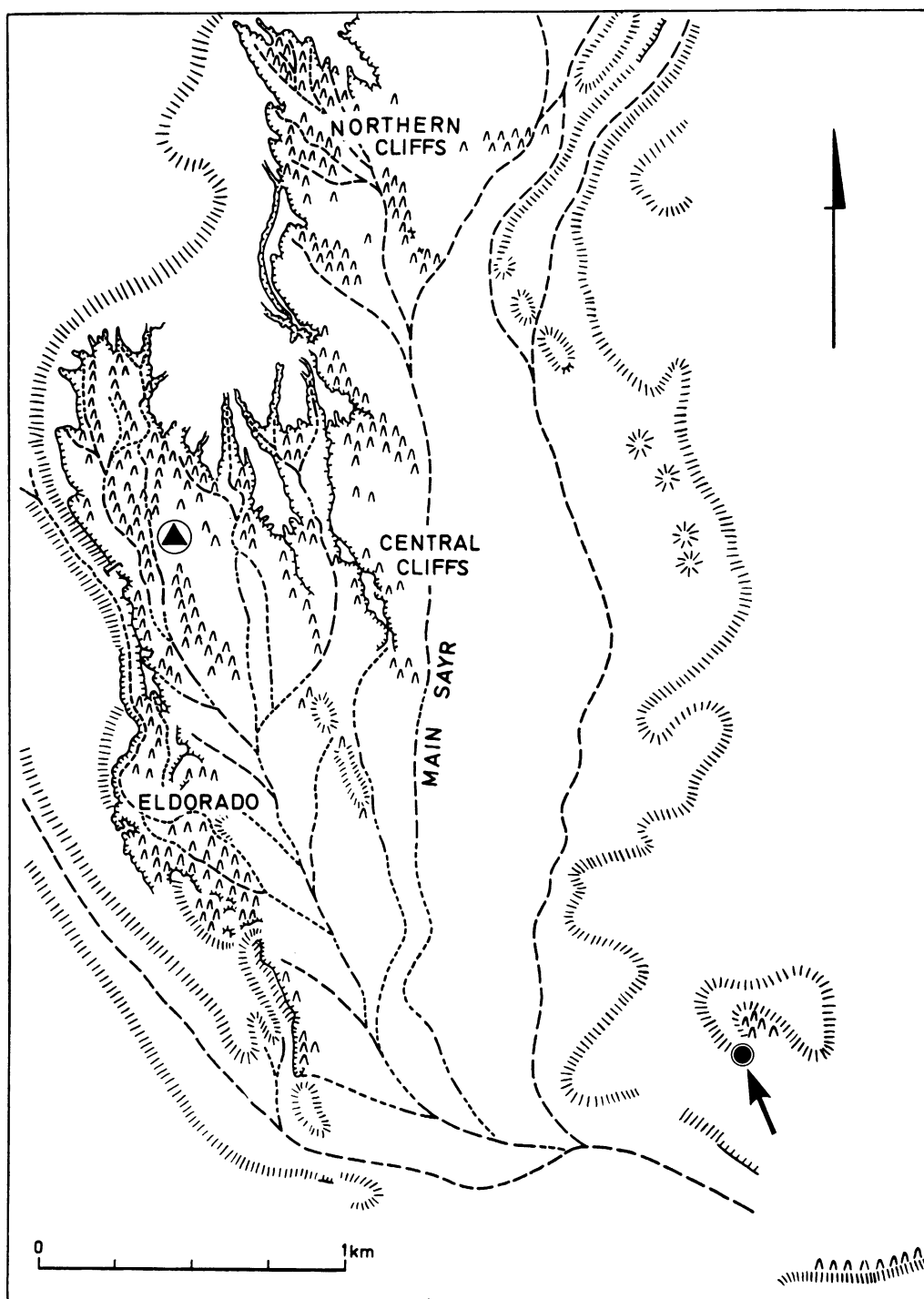


Fig. 3. Map of the general region of Khulsan showing the locality where the specimen was collected. Modified from Gradzinski and Jerzykiewicz (1972).

of dinosaurs and mammals is difficult, no radiometric or magnetostratigraphic evidence is available, and the beds do not intertongue with any known fossiliferous marine sediments (Lillegraven and McKenna, 1986).

SYSTEMATIC PALEONTOLOGY

REPTILIA

SAURIA

LEPIDOSAURIA

SCLEROGLOSSA

ANGUIMORPHA

VARANOIDEA

Estesia mongoliensis, new taxon⁴

Figures 4–7

HOLOTYPE: M 3/14; a skull and mandibles.

ETYMOLOGY: *Estes* (proper name), and *mongoliensis*, geographic location, after Richard Estes in honor of his timeless contributions to the study of fossil lizards.

LOCALITY OF HOLOTYPE: Lizard Hill, Khul-san, South Gobi Aimak, Mongolia. 43°29'19"N, 101°08'44"E (fig. 1). 4741' MSL.

DATE COLLECTED: June 1990, by M. C. McKenna, M. A. Norell, and M. J. Novacek (AMNH), and D. Dashzeveg (MAS).

DIAGNOSIS OF NEW TAXON: Referable to the Varanoidea on the basis of the following derived characters: nasal and maxillary bones with little or no contact, large subolfactory processes of the frontal, a lack of dental resorption pits, sharply pointed plicidentine teeth, a long vomer with narrow palatal shelves, and a short, wide palatine that contacts the ectopterygoid to exclude the maxilla

⁴ Following Queiroz and Gauthier (1990 and ms.) higher taxonomic categories are not recognized. Besides other difficulties discussed in these papers, recognition of taxonomic categories implies a sort of equivalence between categories of same rank. This extension includes the categories included in the Linnean binomial. The binomial *Estesia mongoliensis*, therefore, should not be considered a strict Linnean binomial composed of a species (*E. mongoliensis*) in the genus *Estesia*. Rather, *Estesia mongoliensis* is a two-part taxonomic name. If this is troublesome to some readers, the name *Estesia mongoliensis* can be considered equivalent to a Linnean binomial, however, the senior author makes no such claim.

from the border of the suborbital fenestra (Pregill et al., 1986). Can be differentiated from all other varanoids by the following combination of derived characters: venom grooves on the teeth, and a lack of cranial osteoderms. *Estesia mongoliensis* is unique among squamates in possessing an extensive convex surface medial to the posterior ridge on the posterior surface of the quadrate.

COMPARATIVE DESCRIPTION OF HOLOTYPE: The skull is a well-preserved cranium of an adult individual. There is no trace of free or fused osteoderms accompanying the specimen. The roof of the skull, especially the parietal and the frontals, may have been sculptured, or the crenulated surface may be an effect of weathering. The lateral surfaces of the maxillae and the dentaries are smooth as in *Varanus*.

The right side of the skull is badly weathered and only a few elements remain. The posterior region (i.e., braincase) is crushed; however, the left side of the skull and the left mandible are nearly complete. Lateral surfaces of the skull and dentaries are smooth, whereas the skull roof is covered with fine striations, somewhat like those found in large adult *Varanus*. The occipital region of *Estesia mongoliensis* is crushed and the fragmentary occipital condyle has been rotated into the braincase.

OPENINGS OF THE SKULL

Large, protracted nares are characteristic of *Estesia mongoliensis* and other varanoids. The nares reach posteriorly almost to the anterior margin of the orbits. Reminiscent of the Varanidae is the large circular orbit. The supratemporal fenestrae are small. On the palatal surface, the suborbital fenestra is short and elliptical. The exchoanal fenestra is long and thin, extending posteriorly to the back of the tooth row. The pyriform recess is narrow anteriorly and extends to the level of the fourth posterior maxillary tooth.

CRANIAL BONES

The premaxilla is composed of a dentigerous maxillary process, a nasal arch, and a vomerine process. Anteriorly the premaxilla is thin dorsoventrally. In fact, it is so thin that there is no flat anteriorly directed surface

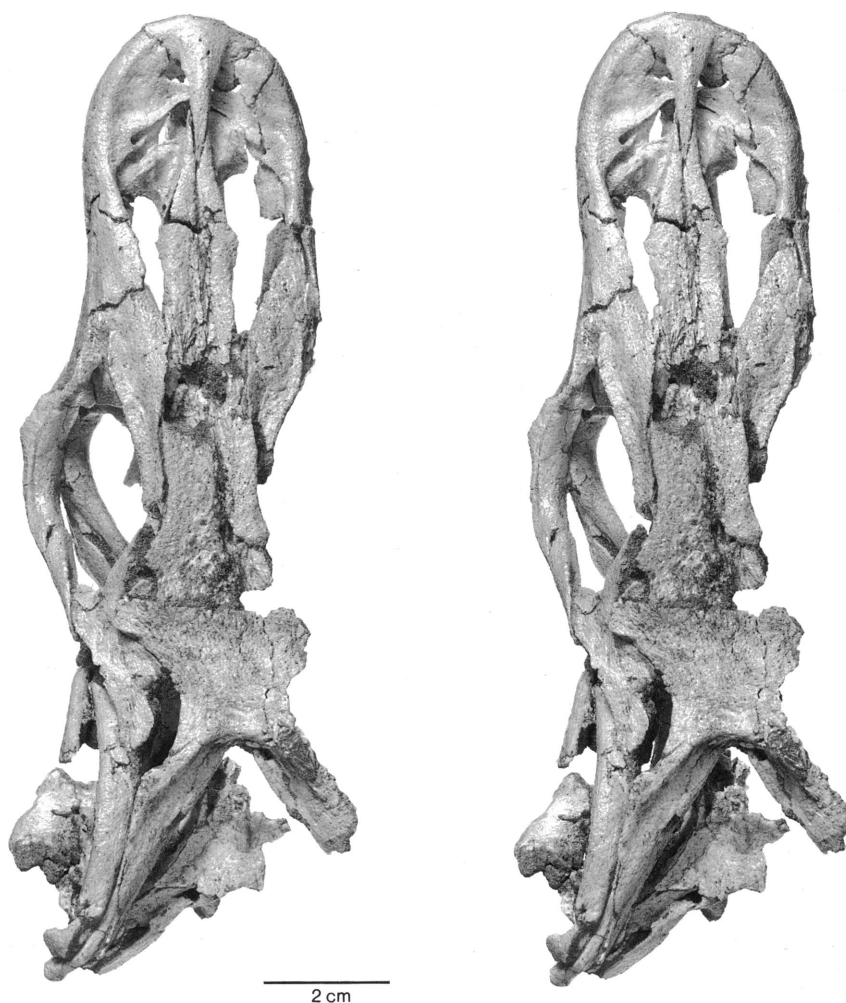


Fig. 4. Dorsal view of *Estesia mongoliensis*. For abbreviations see Appendix 1.

dorsal to the tooth row and ventral to the floor of the narial chamber. The premaxilla is not pierced anteriorly by medial ethmoidal foramina, a condition also seen in *Heloderma* and some *Varanus* (e.g., *Varanus gouldi*). The nasal process is long and tapers posteriorly, contacting the nasal arch between the paired nasal elements. The nasal process is triangular in cross section, with ventrally directed apex. Whether the nasal arch of the premaxilla contacts the frontal beneath the nasals cannot be determined. Posterolateral to the base of the nasal process lie small foramina for the medial ethmoidal nerves and the sub-

narial branches of the maxillary arteries (Oelrich, 1956).

Ventrally, the vomerine process is short, as in *Heloderma* and *Lanthanotus*; thus the premaxilla is wider than long. A reflected winglike incisive process lies along the midline posteroventrally. As in *Lanthanotus*, *Heloderma*, and some *Varanus*, the premaxillary-maxillary aperture (between the maxilla and the premaxilla) and the premaxillary foramen (lateral to the incisive process) are absent. Both of these are found in *Varanus* (fig. 8B). The dentigerous process bears positions for nine teeth.

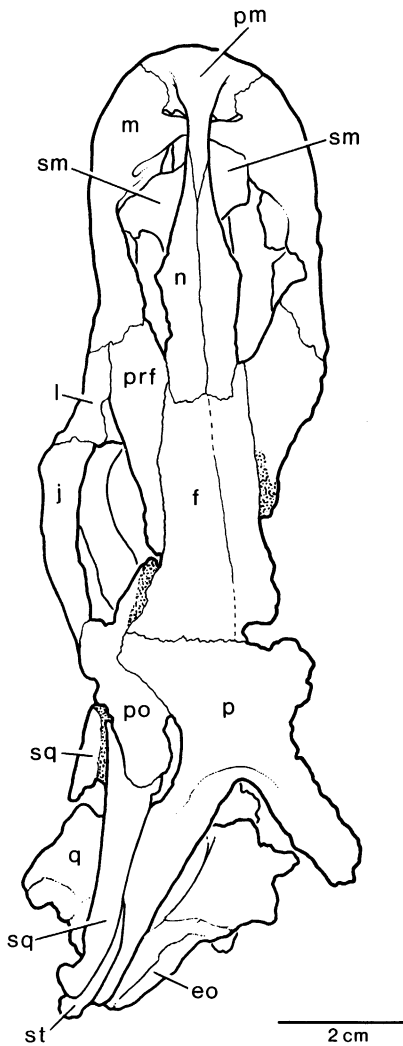


Fig. 4-(Continued).

The nasal is long and thin, contacting the frontal posteriorly and the nasal process of the premaxilla anteriorly. The nasal process of the premaxilla enters an anterior notch between the nasal bones; the nasal forms the posteromedial border of the nares. Posteriorly, lateral to the midline on the internarial bar, the nasal thins and overhangs the narial chamber. The nasals are not fused into a single element along the midline as in *Varanus* and adult *Lanthanotus*. Posteriorly the nasals are divided by an anterior process of the frontal. The frontonasal suture is posterolaterally transverse. This suture ends at the posterior

angle of the naris. Therefore, a nasal-maxillary contact, if present, was not extensive and lay at the posterior angle of the naris. In *Heloderma* this condition is sometimes variable on opposite sides of the same specimen.

The septomaxilla of *Estesia mongoliensis*, as in *Varanus*, is elaborate. The bone lies on top of the vomers and contacts the septomaxillary branch of the maxilla anteriorly. Dorsally the septomaxilla contacts the premaxillary branch of the nasal on the internarial bar. The dorsal surface of the septomaxilla is elaborated with a series of crests, the largest of which is a median ridge that lies on the medial edge of the bone. A prominent boss lies anteriorly, dorsal to a ventral concavity. Along the median edge, a canal runs along the long axis of the bone.

The prefrontal is very large. Dorsally it may form the posterior angle of the naris, excluding the maxilla from contact with the nasal. Above the orbit the prefrontal forms the anterior two-thirds of the orbital border, contacting the postorbital-postfrontal compound bone above the orbit as in *Heloderma* and *Lanthanotus*. The dorsal surface is somewhat concave laterally, forming a supraciliary ridge that runs anteriorly onto the rostrum. The anterior wall of the orbit is formed by the palatine process of the prefrontal. The palatine process also forms the anterior part of the subolfactory process (fig. 9). Ventrally the prefrontal contacts the palatine. The orbitonasal fenestra was apparently very small.

Palpebrals are not preserved on the holotype of *Estesia mongoliensis*. In *Varanus* the palpebral lies in a large prefrontal fossa between the lacrimal and the prefrontal on the anterodorsal orbital rim. The presence of a similar fossa in *Estesia mongoliensis* suggests that large palpebral bones may have been present.

The frontal is paired and parallel-sided, with a posterolateral postorbital process. Laterally the frontal is excluded from the supra-orbital rim by contact of the prefrontal and the postorbital. The anterior articulation of the frontal with the nasal is not preserved. Ventrally, a large subolfactory process is present; however, unlike in varanids and helodermatids, the processes fail to meet either anteriorly or posteriorly to form an osseous subolfactory canal. Instead the subolfactory



Fig. 5. Palatal view of *Estesia mongoliensis*. For abbreviations see Appendix 1.

processes are intermediate between the more primitive anguid condition of subolfactory processes that do not approach each other, and the derived condition seen in the Varanoidea (fig. 9).

In *Estesia*, as in other varanoids, the postorbital and postfrontal form a single bone. This compound bone has four rami: an anterior supraorbital ramus that contacts the prefrontal above the orbit, a lateral postorbital ramus that meets the jugal to form a postorbital bar, a supratemporal ramus that, with the squamosal, forms the supratemporal arcade, and a short parietal ramus that lies

on the lateral surface of the parietal. The postorbital ramus is short and tapers laterally. It contacts the anterior surface of the jugal's postorbital process. The supraorbital ramus is very broad and extends above the orbit to contact the prefrontal. Posteriorly, the supratemporal and parietal rami form a wide, gently laterally concave dorsal surface before they separate. The supratemporal ramus is wide and longer than the parietal ramus, extending about one-third the length of the supratemporal fenestra. Posteromedially the supratemporal ramus is very thin and overhangs the supratemporal fenestra. The lateral

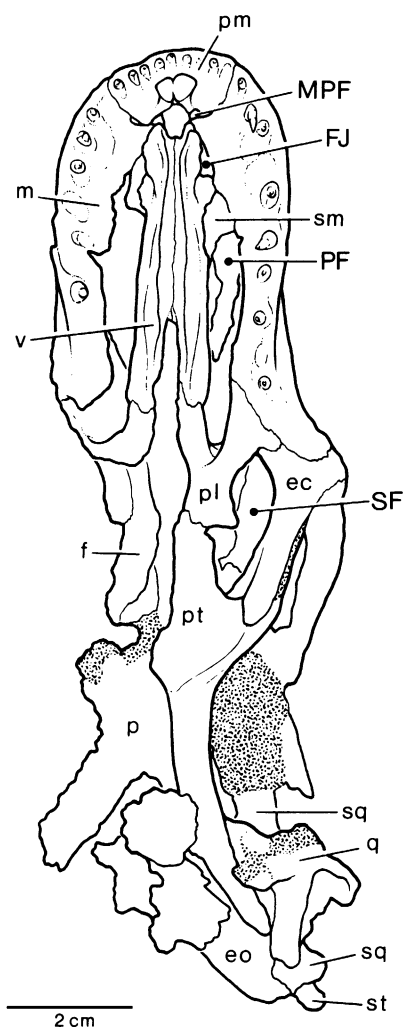


Fig. 5—(Continued).

surface of the supratemporal ramus is contacted by the squamosal. How much of the lateral surface of the postorbital contacted the squamosal cannot be determined because of poor preservation. The parietal ramus abuts the anterolateral margin of the parietal and forms the anterior angle of the supratemporal fenestra.

The parietal is hourglass shaped, with an extensive parietal table. Anteriorly it contacts the frontals. A pineal foramen is absent, although a pineal fossa is present posteriorly just anterior to the angle of the supratemporal processes, more or less in the same position as it is in *Telmasaurus grangeri* (see Estes,

1983) and *Heloderma*. Laterally, the parietal is concave; the temporal musculature attached to a concave surface on the lateral side of the bone. Posteriorly, a long supratemporal process forms the posterior border of the supratemporal fenestra. Near its posterior end the supraorbital process is hook shaped and lies in a groove in the supratemporal. The posterior end of the supraorbital process forms a small knob.

The supratemporal of *Estesia* lies on the lateral surface of the supratemporal process of the parietal. The supratemporal is almost as broad as the supratemporal process of the parietal and extends anteriorly almost to the margin of the posterior part of the parietal table. The supratemporal is not visible in dorsal view; it fails to reach the dorsal margin of the parietal and the supratemporal process of the parietal is ventrally oriented where the supratemporal overlaps it. Posteriorly the supratemporal underlies the ventral surface of the parietal's supratemporal process and is also exposed slightly on the supraoccipital process' medial surface. Here, the supratemporal is wedged between the parietal and the paroccipital process of the exoccipital. Laterally, the supratemporal is wedged between the squamosal and the posterior part of the parietal's supratemporal process. Ventrally the supratemporal isolates the supraorbital process of the parietal from the quadrate's cephalic condyle.

In lateral view the maxilla of *Estesia* is triangular. The bone forms most of the floor of the olfactory chamber and borders the anterolateral and lateral margins of the naris. The narial margins are rounded and smooth. Anteriorly the maxilla contacts the premaxilla and is dorsoventrally thin. The anterior floor of the narial chamber is flat. Just posterior to the premaxillary narial arch, in the narial chamber, a medial process of the maxilla forms the posterior wall of the maxillo-premaxillary aperture. Posteriorly this process is elevated and contacts the septo-maxilla. This elevated area continues laterally as a small ridge posterior to which arises a single anterior inferior alveolar foramen. The nasal process emanates from the bone posteriorly. It contacts the prefrontal, the lacrimal, and the jugal in a dorsoventral diagonal suture. A row of large mental foramina

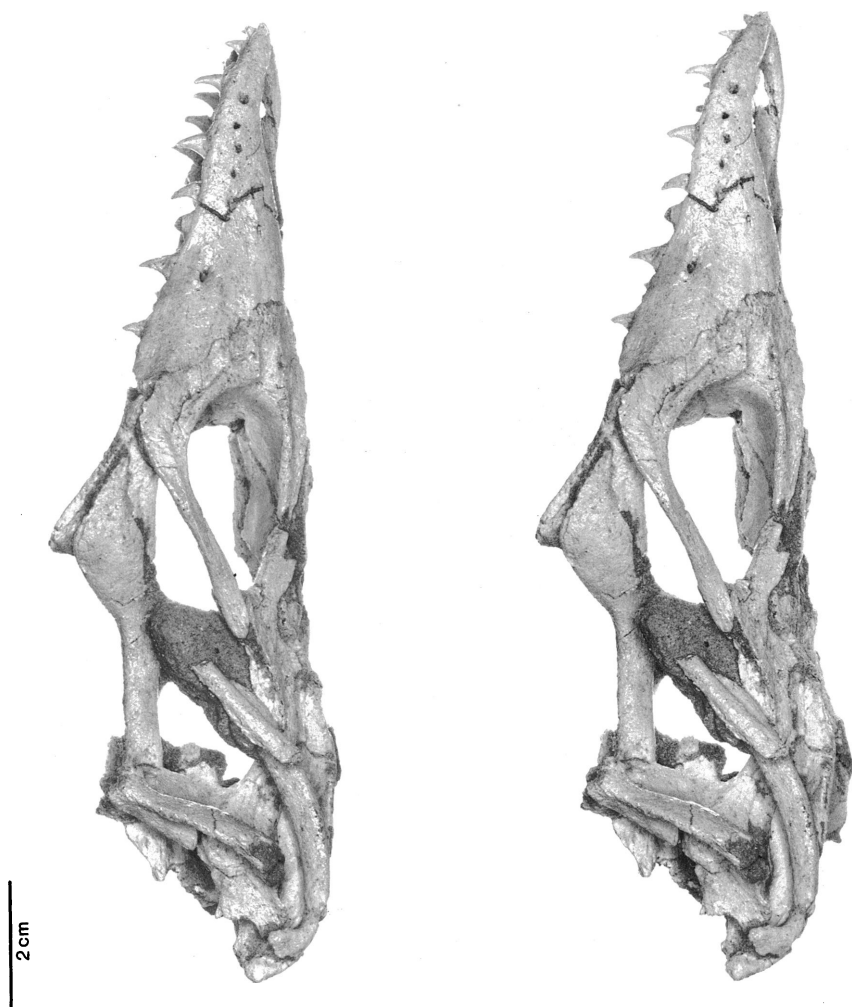


Fig. 6. Left lateral view of *Estesia mongoliensis*. For abbreviations see Appendix 1.

lie dorsal to the tooth row and posteriorly the maxilla overhangs the tooth row. On the palatal surface the maxilla contacts the premaxilla and vomer anteriorly and the ectopterygoid and palatine posteriorly, and forms the lateral margin of the long and thin extrachoanal fenestra. Lateral to the tooth row the maxilla forms a wide palatal shelf that tapers posteriorly. Anteriorly, just posterior to the premaxillary contact, the maxilla and the vomer border the incisive foramen. Eleven tooth positions were present on the maxilla.

The lacrimals are trapezoidal and contact the prefrontal dorsally and medially, the

maxilla anterolaterally, and the jugal ventrally. The posterior margin of the lacrimal forms the anterior rim and wall of the orbit and bears a pronounced posterior spine as in living *Varanus*. In *Varanus*, *Lanthanotus*, and *Saniwa* the lacrimal is perforated by a pair of posterior lacrimal foramina (Gabe and St. Girons, 1976). In *Varanus* the larger dorsal foramen lies on the margin of the lacrimal and the prefrontal, whereas the ventral foramen, usually smaller, is completely enclosed by the bone. In *Lanthanotus* the foramina are equal in size and lie entirely within the lacrimal (contra Rieppel, 1980). *Estesia*

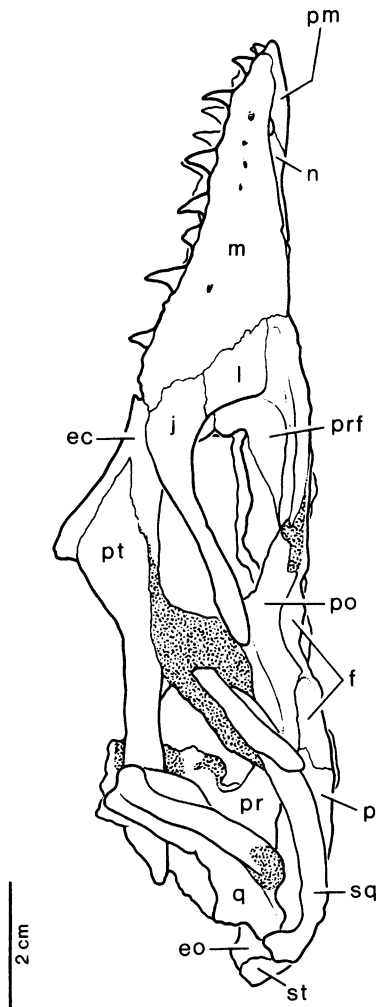


Fig. 6-(Continued).

mongoliensis displays the primitive condition of a lacrimal that is perforated along the suture with the prefrontal by a single slitlike lacrimal foramen (fig. 10).

The jugal forms the entire ventral and posterior orbital border. In lateral view it is dorsoventrally concave, wide anteriorly, and tapered posteriorly. This lateral concavity forms an everted rim on the anteroventral orbital border. Inside the orbit, the jugal is broad and contacts the ectopterygoid medially. On its ventral surface is a large fossa, also present in *Heloderma*. Posterodorsally the jugal thins and contacts the postorbital-postfrontal to form a complete postorbital bar as in *Lan-*

thanotus and *Heloderma*. The jugal apparently did not form any of the supratemporal arcade, yet on the lateral surface of the postorbital it may have contacted the postorbital process of the squamosal.

The squamosal of *Estesia* is a thick, heavy bone that, as in *Varanidae*, forms most of the supratemporal arcade. Anteriorly it contacts the lateral surface of the postorbital-postfrontal in a groove along that bone's lateral edge. Posteriorly the bone is much heavier than in *Varanus*, although it is similarly hooked and contacts the dorsal surface of the quadrate.

The quadrate of *Estesia* is very large. Neither the articular nor cephalic condyles are preserved. A large outer conch (absent in *Varanus*) forms the tympanic crest. The anterior surface of the quadrate is extensive; wider ventrally than dorsally. A median longitudinal (dorsoventral) depression and a lateral reflected edge form an undulating surface. The posterior crests divide the posterior surface medially. Lateral to the posterior crest lies a large concave depression that tapers ventrally to the articular condyle. Medial to the posterior crest, the posterior surface of the quadrate forms an extensive convex surface.

The vomer is long and thin and articulates with the palatine at the level of the last maxillary tooth. The vomers are medially confluent for about half of their length; they lack the lateral processes of *Lanthanotus*. As in *Varanus*, small crests are present posteriorly on the ventral surface; however, the vomers are keeled for their entire length, lacking the ventral surface found in other varanoids. Where the vomers meet anteriorly a deep fossa is present. On the anterior wall of this fossa lies a pair of vomerine foramina. Anteriorly the vomer meets the incisive process of the premaxilla. A small vomeronasal foramen is present between the vomer and the maxilla, lateral to which lie the lacrimal crests that are similar to those found in *Varanus*. Laterally the vomer forms the medial border of the exocoanal foramen. The dorsal surface of the vomer is hidden inside the cranium.

The palatines are longer than wide as in other varanoids. The palatine is "Y"-shaped with anterior vomerine and maxillary processes and a posterior pterygoid process. Dor-

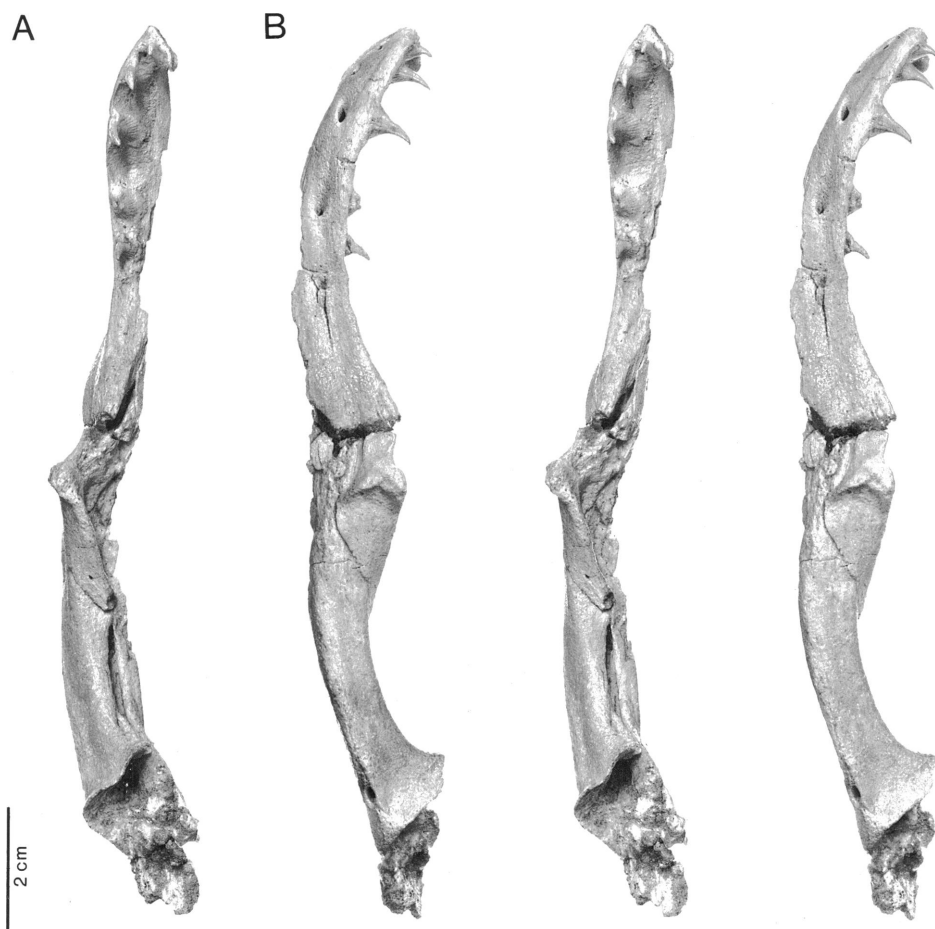


Fig. 7. Dorsal and labial view of *Estesia mongoliensis*. For abbreviations see Appendix 1.

sally the ascending prefrontal process contacts the prefrontal, and the lacrimal and jugal dorsolaterally. The maxillary process extends anteriorly to the level of the second tooth, unlike in *Heloderma* where the entire tooth row lies anterior to the palatine. As in *Heloderma* and in juvenile *Varanus* and *Lanthanotus*, the vomerine process is shorter than the maxillary process. Between the maxillary and vomerine process a small ventral fossa is formed by a shelf of bone overhanging the crux, ventral to contact with the lacrimal. The dorsal surface forms the anteroventral floor of the orbit. Anteriorly, immediately ventral to contact with the lacrimal on the anteroventral wall of the orbit, the pterygoid

is perforated by a conspicuous infraorbital foramen.

The pterygoid is "Y"-shaped with large transverse and palatine processes anteriorly, and a long thin quadrate process posteriorly. The ectopterygoid process is ventrally concave, with an elevated lateral margin forming a ridge similar to the condition in *Heloderma*. Dorsally the pterygoid overlies the ectopterygoid, as in *Heloderma*, but not as in *Varanus* where the pterygoid lies in a notch of the ectopterygoid anteriorly. The ectopterygoid process fails to reach the ectopterygoid-jugal contact, as it does in *Heloderma*. The transverse process extends further anteriorly than the ectopterygoid process. A large, rugose,

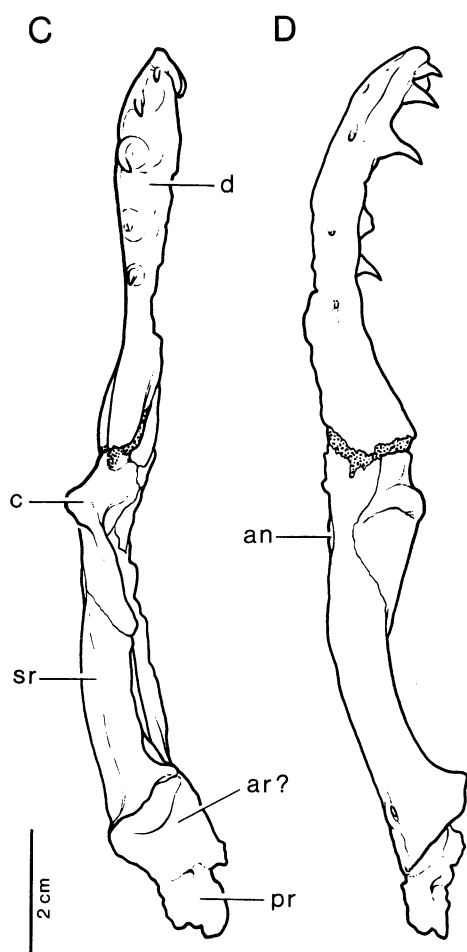


Fig. 7-(Continued).

elevated platform is prominent ventrally. There is no evidence that pterygoid teeth were present in life. The quadrate process is long, thin, and tapers posteriorly. It is ventrally oriented and its medial surface is dorsoventrally concave. The dorsal surface of the pterygoid is not visible except anteriorly as a convex floor of the orbit.

The ectopterygoid is robust, as in *Heloderma*, with anterior maxillary and palatine processes. The palatine process abuts the palatine, excluding the maxilla from participation in the suborbital fenestra. However, unlike *Heloderma*, the anterior palatine process does not extend anteriorly between the maxilla and the palatine. Anterolaterally, a large maxillary process is present. Posteriorly the ectop-

terygoid forks into a short, heavy, ventral pterygoid process and a long, thin, dorsal process. The ectopterygoid process of the pterygoid articulates into this fork and a large palatine process covers most of its surface.

The bones of the braincase are very fragmented and most are not preserved. Those present are featureless because of crushing and distortion. Nevertheless, fragments of the basioccipital, the exoccipital, and the opisthotic are preserved in a jumbled mass inside of the braincase area.

MANDIBLE

The better preserved left mandible is fragmentary ventrolingually. The retroarticular process is fragmented posteriorly. The right dentary is only preserved anteriorly.

The mandible is long, thin, and smooth (fig. 7). The entire lower jaw is curved, especially far anteriorly and just anterior to the articular fossa. Both ventral surfaces are severely weathered. The lateral surface of the dentary is smooth and contains a row of four large mental foramina. Lateral to the tooth row, a thin lamina of bone forms a shallow dental parapet. Posterior to the tooth row, the dentary is robust, dorsoventrally concave, and long relative to that of other varanoids, being three-fourths as long as the tooth-bearing segment of the dentary. A small coronoid process fills a groove on the anterior margin of the coronoid. This process is developed to the same degree as in *Varanus* but not so large as in *Heloderma*. The loose connection between the dentary and the posterior elements and the groove on the anterior coronoid margin suggests that kinesis along this margin was possible.

Only a small fragment of the left splenial is preserved and no features of interest are apparent. The coronoid is a large element situated dorsal to the surangular. Anterior to the low coronoid eminence lies a short dentary process. Labially the dentary process is not extensive dorsoventrally; however, on the lingual surface the dentary process is extensive and platelike with a tongue that underlies the splenial. Lingually just ventral to the coronoid eminence is a large excavated area. Posteriorly this area is bordered dorsally by the extensive surangular process of the cor-

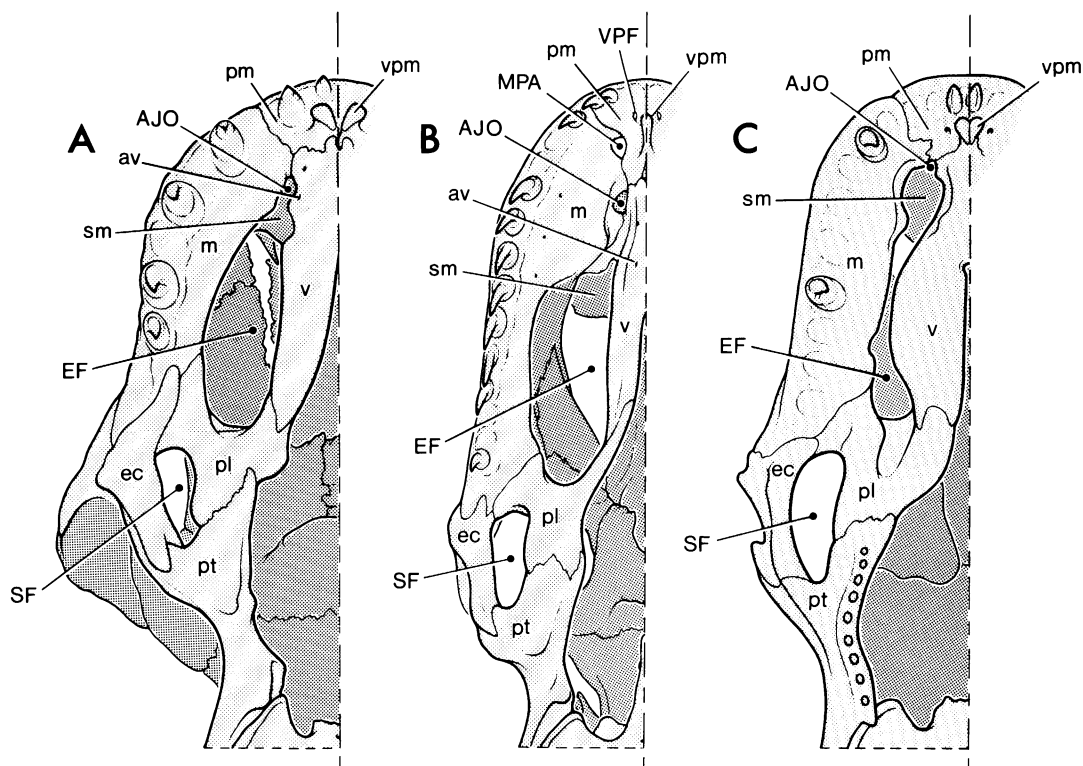


Fig. 8. Palatal views of (A) *Heloderma suspectum* (MAN 9), (B) *Varanus komodoensis* (AMNH 37912), and (C) *Lanthanotus borneensis* (RE 1445).

onoid. Laterally, a vertical ridge runs ventrally from the coronoid eminence, posterior to which lies the triangular lateral exposure of the surangular process.

The angular is extremely fragmented, represented only by splinters of bone. The surangular forms most of the lateral and posteroventral surface of the mandible posterior to the coronoid. The surangular is large and curved, and the posterior part of the mandible is arch shaped. A large posterior surangular foramen pierces the surangular anterolateral to the articular fossa and emerges medially in the mandibular fossa. An anterior surangular foramen is not present.

The prearticular is exposed on the lingual surface of the mandible; in lingual aspect it forms much of the posteroventral surface of the mandible. It is robust dorsally and forms the lateral medial border of the mandibular fossa. Posteriorly it forms the flat and thin (although crushed) retroarticular process.

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 mandible 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.

TEETH

The teeth of *Estesia mongoliensis* are typical of varanoids in being plicidentine, and recurved with sharp points (Pregill et al., 1986). The tooth bases are expanded and tooth replacement occurs from the back; consequently resorption pits are not present. The ventromedial surface of each tooth is perforated by a small nutrient foramen. As in *Heloderma*, the premaxillary teeth (of which there are nine) are markedly smaller than the

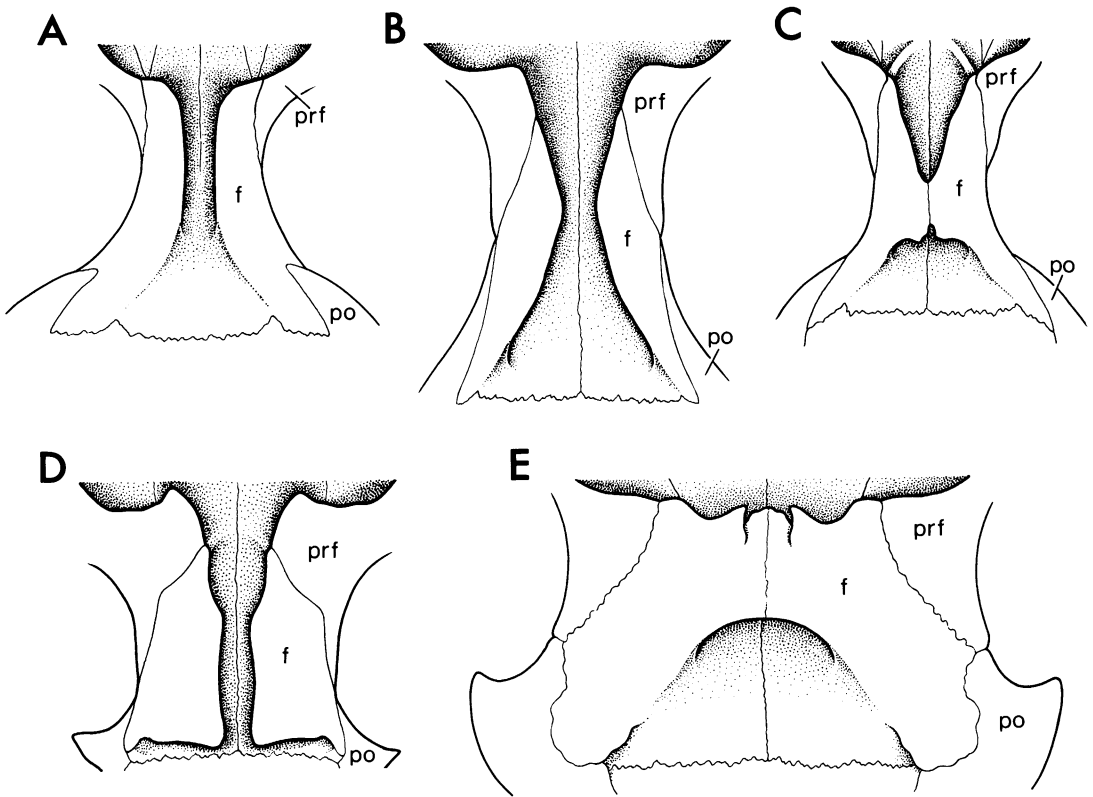


Fig. 9. The subolfactory processes of (A) *Elgaria multicarinatus* (MAN 7), (B) *Estesia mongoliensis*, (C) *Varanus salvator* (MAN 48), (D) *Lanthanotus borneensis* (RE 1445), and (E) *Heloderma suspectum* (MAN 9).

cheek teeth. The maxillary and dentary teeth are widely spaced. There are positions for nine maxillary teeth. The left dentary contains five tooth positions; the right dentary is incomplete but has four teeth. As in *Heloderma*, the largest teeth in the dentary tooth row occur in the middle of the tooth row (positions 3 and 4), giving the tooth row an arched aspect [compare fig. 8 in Pregill et al. (1986) with fig. 11 here].

The most interesting feature of the teeth is the presence of deep longitudinal grooves that run the entire length of each tooth on both the anterior and posterior tooth surfaces (fig. 11). These grooves are also present in extant *Heloderma* and its close helodermatid relatives. For instance, in *Paraderma bogerti* "an incipient groove is present on the antero-medial margin near the base" of the best preserved tooth (Pregill et al., 1986). In extant *Heloderma* these grooves are functionally re-

lated to the transmission of venom with the saliva. Pregill et al. (1986) were cautious in suggesting that this groove was used as a venom-conducting structure in taxa closely related to *Heloderma*, because, obviously, this cannot be observed in fossil taxa. However, the correlation is impressive and it is possible that *Estesia mongoliensis* shared with *Heloderma* the ability to conduct salivary venom through its grooved teeth.

DISCUSSION

Estesia mongoliensis displays a suite of primitive and derived characters that invite comparison with other anguimorphs. Yet it is difficult to evaluate these similarities in a phylogenetic context until a detailed analysis of additional taxa is completed. These taxa include the purported varanines from the Cretaceous of Mongolia *Telmasaurus gran-*

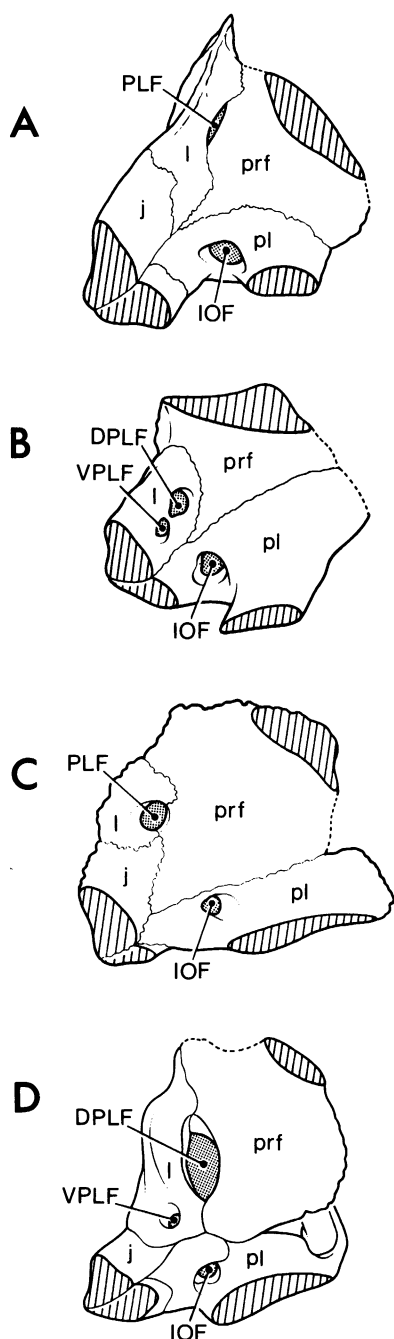


Fig. 10. The anterior orbital wall in (A) *Estesia mongoliensis*, (B) *Lanthanotus borneensis* (RE 1445), (C) *Heloderma suspectum* (MAN 9), and (D) *Varanus komodoensis* (AMNH 37912). The posterior lacrimal foramen is primitively single in *Estesia mongoliensis* and *Heloderma suspectum*. The derived paired condition is seen in *Varanus* and *Lanthanotus borneensis*.

geri and *Saniwides mongoliensis*, the Cretaceous Mongolian putative lanthanotine *Chermonotus longifrons*, the "necrosaurids" *Gobiderma pulchrum*, *Proplatynota longirostrata*, and *Parviderma*, and the poorly studied North American taxon *Saniwa*. The marine "platynotan" lizards (e.g., mosasaurs and aigialosaurs) also need be considered. Nevertheless, an initial approximation of the phylogenetic position of *Estesia mongoliensis* can be attempted.

The analyses of the Varanoidea by Pregill et al. (1986) considered 80 characters. These characters include skeletal features, characters of the soft anatomy, and behavior. Results of their analysis indicate that *Lanthanotus* is the sister group to a monophyletic Varaninae. These taxa compose the Varanidae, whose sister group is the Helodermatidae, represented by the fossil taxa *Paraderma*, *Lowesaurus*, and *Eurheloderma* and the extant taxon *Heloderma*. This phylogeny is similar to the one proposed by McDowell and Bogert (1954) and Rieppel (1980) for this subset of anguimorph taxa.

The characters of Pregill et al. (1986) were scored for the holotype of *Estesia mongoliensis*. These characters are listed in appendix 1 and a matrix showing their distribution within the group is provided in table 1. Again, because our analysis is considered preliminary, no modifications to the codings or character descriptions of Pregill et al. (1986) were included in this paper. Characters were analyzed using David Swofford's PAUP 3.0L for the Macintosh. The exhaustive search option indicated that all possible trees were examined. Characters were polarized using the polarities of Pregill et al. (1986). These polarities were enforced by using the ancestor function (all zero) to root the tree. Until a detailed analysis of additional taxa can be completed Pregill et al.'s (1986) diagnoses for clades within the Varanoidea and classification are not modified.

The analysis yielded a unique tree of 71 steps. This tree (fig. 12A) indicated the basic topology of Pregill et al. (1986), Rieppel (1980), and McDowell and Bogert (1954) in advocating a sister-group relationship between *Lanthanotus* and *Varanus* (the Varanidae), with helodermatids as their sister group (the Varanoidea). *Estesia mongoliensis* is the

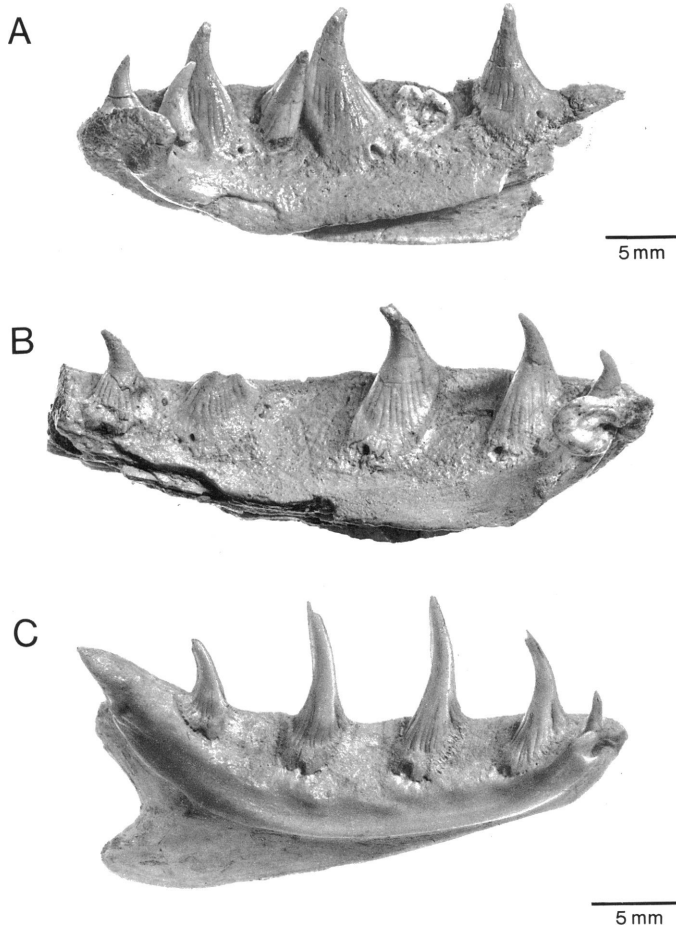


Fig. 11. The mandibular teeth of (A, B) *Estesia mongoliensis* and (C) *Heloderma suspectum* (MAN 9). Notice the enlarged medial teeth and the well-developed grooves. Possibly these grooves functioned as a poison delivery system.

sister group of the Varanidae. Four derived characters (characters 4, 5, 18, and 48) that could be scored in *Estesia mongoliensis* support this grouping. All of these characters are optimization independent. That is, the same characters support this node no matter what optimization criterion is implemented. These characters include the derived conditions of nasal and maxillary bones that fail to contact, a nasal process of the maxilla that rises from the posterior aspect of the maxillary, a narrow supratemporal process of the parietal, and no osteoderms fused to the skull.

The next closest tree has a length of 74 steps

(fig. 12B), 3 steps longer than the shortest tree and a retention index of 0.653. This tree indicates a sister-group relationship between helodermatids and *Estesia mongoliensis*. Two characters (numbers 30 and 14) that can be scored for *Estesia mongoliensis* unambiguously support the *Estesia* + helodermatid grouping. These characters are the insertion of the temporal musculature on the ventral surface of the parietal and presence of well-defined "venom" grooves on the teeth. Such grooves are widespread among helodermatids and lizards of necrosaurian grade. They are most developed in extant *Heloderma*;

TABLE 1
Data Matrix for Basic Taxonomic
Characters in Appendix 2

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Necrosauridae*	0	0	0	0	0, 1	0	0	0	0	0	0	0	0	1	0	?	?	0	?	?
<i>Heloderma</i>	0	0	1	0	0	1	1	1	0	1	1	1	1	0	0	0	0	0	1	0
<i>Lanthanotus</i>	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
Varanidae	1	1	1	1	1	0	1	0	1	0	0	0	0	1	1	1	1	1	1	1
<i>Estesia</i>	0	0	1	1	1	0	1	0	0	1	1	0	0	0	?	?	?	1	1	0

TABLE 1—(Continued)

Taxon	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Necrosauridae*	0	?	1	0, 1	1	0, 1	0, 1	0	0	0	1	1	0	0	0	0, 1	?	0	?	0
<i>Heloderma</i>	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	0	1	0
<i>Lanthanotus</i>	1	1	1	1	1	1	1	1	0	0	1	0	1	0	0	1	1	1	1	1
Varanidae	0	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1
<i>Estesia</i>	1	0	1	1	1	1	1	1	0	1	1	1	1	?	?	1	?	?	?	?

TABLE 1-(Continued)

[illegible]

TABLE 1-(Continued)

Taxon	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Necrosauridae*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Heloderma	0	1	0	0	1	0	0, 1	?	?	?	?	?	?	?	?	?	?	?	?	?
Lanthanotus	1	1	1	0	0	1	1	1	0	1	1	0	1	1	1	1	0	1	1	1
Varanidae	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1
Estesia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

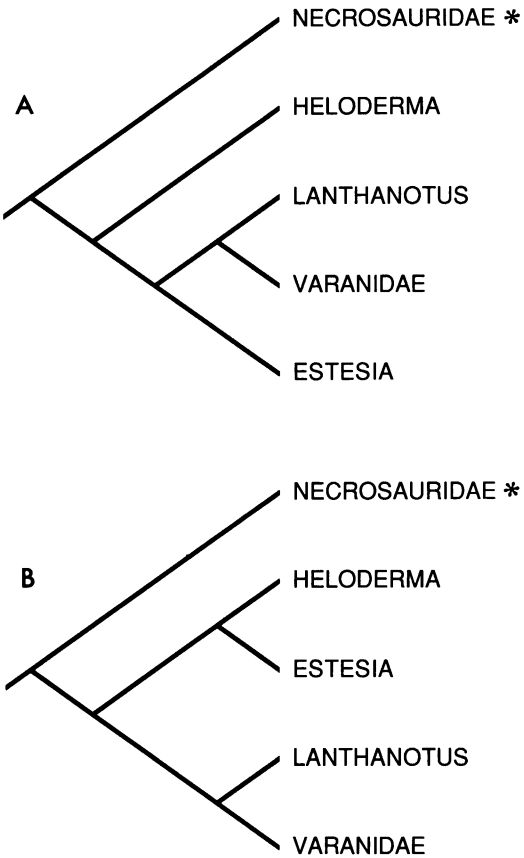


Fig. 12. (A) Minimum length tree for the data presented in table 1, (B) next shortest tree for the data presented in table 1.

however, they are also well developed in fossil relatives. The presence of venom grooves in *Estesia mongoliensis* is curious and, if the phylogeny in figure 12A is corroborated, one possible optimization of this character is that “venom grooves” are primitive for the Varanoidea.

A difficulty with the minimum length tree is that Necrosauridae*, considered a basic taxon by Pregill et al. (1986), is not demonstrably monophyletic (Estes, 1983; Estes et al., 1988). The asterisk following Necrosauridae* is an indication that there is no evidence for or against monophyly, viz., a metataxon of Donoghue (1985) and Gauthier et al. (1988a). If necrosaurs are paraphyletic relative to other varanoids, local character polarities within higher varanoids will be mod-



Fig. 13. A reconstruction of *Estesia mongoliensis* preying on a nest of *Protoceratops*.

ified. For example, in the minimum length tree described above (fig. 12A), a synapomorphy uniting *Estesia mongoliensis* with Varanidae is the lack of osteoderms fused to the skull. Both conditions occur in the Necrosauridae*; however, if Necrosauridae* is paraphyletic, character polarity at this level may be modified and osteoderms present in helodermatids may be deemed apomorphic—thus invalidating the Varanidae + *Es-*

tesia mongoliensis synapomorphy of osteoderm loss. Until a hypothesis of monophyly for Necrosauridae* can be demonstrated or this grouping is abandoned due to paraphyly, an interim solution to this difficulty is to prune Necrosauridae* from the analysis. The resultant minimum length tree (exclusive of Necrosauridae*) is 17 steps shorter (length 54) than that in figure 12A and has a retention index of 0.677. Eliminating Necrosauridae*

from the analysis has no effect on tree topology or on the character evidence for an *Estesia mongoliensis* + Varanidae clade.

CONCLUSIONS

The presence of an additional varanoid in the Cretaceous of Mongolia is yet another indicator of the extensive Mesozoic radiation of this group in northern Asia. Such high varanoid diversity in a single region is unparalleled today. Extant varanoids are active, highly visual, carnivorous lizards that often prey on small or juvenile animals and often raid the nests of birds (Pregill et al., 1986). In the immediate vicinity of the type locality of *Estesia mongoliensis*, several aggregations (nests?) of small to medium sized dinosaurs were found. *Estesia mongoliensis*, like its modern relatives, probably also preyed on similar organisms; it is interesting that other Cretaceous varanoids (i.e., *Saniwa*) from the Judith River, Montana, have also been found in the direct proximity of dinosaur nests.

Although the environmental reconstruction in figure 13 is tantalizing, the discovery of *Estesia mongoliensis* is probably more important because it will aid in deciphering relationships among higher anguimorph lizards. By adding a new, excellently preserved taxon with unique character combinations near the base of the varanid-helodermatid radiation, the phylogenetic position of fragmentary, derived, and enigmatic taxa may be resolved (Gauthier et al., 1988b).

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APPENDIX 1

Anatomical Abbreviations Used in Figures

AJO	aperture for Jacobson's organ
av	vomerine aperture
DPLF	dorsal posterior lacrimal foramen
ec	ectopterygoid
EF	exochoanal fenestra
eo	exoccipital
f	frontal
IOF	interorbital foramen
j	jugal
l	lacrimal
m	maxilla
MPA	maxillo-premaxillary aperture
n	nasal
p	parietal
pl	palatine
PLF	posterior lacrimal foramen

APPENDIX 1—(Continued)

pm	premaxilla
po	postorbital + postfrontal
pr	prootic
prf	prefrontal
pt	pterygoid
q	quadrate
SF	suborbital fenestra
sm	septomaxilla
st	supratemporal
sq	squamosal
v	vomer
VPLF	ventral posterior lacrimal foramen
vpm	ventral process of maxilla

APPENDIX 2

**Character Summary of the Varanoidea, Scored on
Estesia mongoliensis in Table 1. From Pregill et
al., 1986**

Skull characters

1. Nasal bones paired (0), or fused (1).
 2. Nasal and prefrontal bones in broad contact (0), or with little or no contact (1).
 3. Nasal and maxillary bones in broad contact (0), or with little or no contact (1).
 4. Nasals and maxillary bones in narrow contact (0), or not in contact (1).
 5. Nasal process of maxilla rises from the middle (0), or posterior (1) aspect of maxillary.
 6. Frontal more or less parallel-sided (0), or trapezoidal (1).
 7. Subolfactory processes of frontals short, not in contact ventromedially (0), or well developed and closely opposed or contacting ventromedially (1).
 8. Subolfactory processes of frontals do not descend to contact each other anteromedially (0), or do so (1).
 9. Subolfactory processes of frontal do not descend to approach or contact each other posteromedially (0), or do so (1).
 10. Prefrontal does not (0), or does closely approach or contact postfrontal above orbit (1).
 11. Parietal foramen present (0), or absent (1).
 12. Postorbital present (0), or absent (1).
 13. Squamosal large, extending to postorbital (0), or small and reduced (1).
 14. Temporal musculature inserts ventrally (0), or dorsally (1) on parietal table.
 15. Supraoccipital not in broad contact with parietal (0), or with broad contact (1).
 16. Hypoglossal foramen not enlarged (0), or enlarged (confluent with vagal foramen) (1).
 17. Carotid duct present (0), or absent (1).
 18. Supratemporal process of parietal broad in dorsal aspect (0), or narrow (1).
 19. Supratemporal bone does not reach level of apex of parietal notch (0), or does (1).
-

APPENDIX 2—(Continued)

20. Quadrate with large outer conch (0), or conch reduced (1).
21. Muzzle tapered, narrowing anteriorly (0), or blunt and rounded (1).
22. Posterior lacrimal foramen single (0), or double (1).
23. Premaxillary teeth large (0), or abruptly smaller than maxillary teeth (1).
24. Plicidentine teeth absent (0), or present (1).
25. Teeth bluntly pointed (0), or sharply pointed, trenchant, recurved, and widely spaced (1).
26. Successional replacement teeth in resorption pits (0), or replacement teeth develop posteriorly, no resorption pits present (1).
27. Maxillary tooth row extends posteriad of orbit (0), or is entirely antorbital (1).
28. Maxillary teeth number 13 or more (0), or less than 13 (1).
29. Maxillary teeth greater than 9 (0), or less than/equal 9 (1).
30. Venom groove absent (0), or present (1).
31. Vomer short (0), or nearly twice the length of palatine (1).
32. Palatal shelves of vomer wide (0), or narrow (1).
33. Palatine longer than wide (0), or equally wide as long (1).
34. Palatine teeth present (0), or absent (1).
35. Pterygoid teeth present (0), or absent (1).
36. Ectopterygoid does not contact palatine anteriorly (0), or does to exclude maxilla from suborbital fenestra (1).
37. Dentary and surangular overlap considerably (0), or very little (1).
38. Coronoid and surangular processes of dentary well developed (0), or processes reduced (1).
39. Surangular tapered anteriorly (0), or blunt and expanded anterodorsally (1).
40. Surangular extends well beyond coronoid eminence (0), or does not (1).
41. Intramandibular septum (IMS) without posteroventral notch (0), or notched (1).
42. Splenial extends posterior of coronoid eminence (0), or does not (1).
43. Splenial-dentary suture firm (0), or loose, with much connective tissue between the two bones (1).
44. Splenial does not move with dentary (0), or does (1).
45. Coronoid without long anterolateral and anteromedial processes (0), or processes present (1).
46. Head scales large and plate-like (0), or partly or completely fragmented (1).
47. Osteoderms thin, plate-like (0), or rounded and thick (1).
48. Osteoderms fused to skull (0), or not (1).

Axial characters

49. Number of cervical vertebrae eight (0), or nine (1).
 50. Vertebral centra long and neural spines broad (0), or centra short and neural spines narrow and tall (1).
 51. Number of presacral vertebrae fewer than 30 (0), or more (1).
-

APPENDIX 2—(Continued)

52. Caudal vertebrae autotomic (0), or not (1).
53. Peduncles on cervical and caudal vertebrae short (0), or long (1).
54. Caudal chevrons and cervical hypapophyses (= intercentra) contact centrum condyle (0), or on centrum only (1).

Appendicular characters

55. Epicoracoid contacts suprascapula and mesoscapula (0), or not (1).
56. Anterior coracoid emargination present (0), or absent (1).
57. Posterior coracoid emargination absent (0), or present (1).
58. Clavicle loop-shaped medially (0), or gracile and not expanded (1).
59. Interclavicle with long anterior process (0), or process short or absent (1).
60. Mesosternum present (0), or absent (1).
61. Rib attachments on sternum more than three pairs (0), or three or fewer pairs (1).

Myological characters

62. M. episterno-cleido-mastoideus does not reach parietal (0), or has extensive insertion on parietal (1).
63. M. constrictor colli does not cover 1st ceratobranchials (0), or does (1).
64. Origin of MAME profundus from supratemporal and parietal (0), or supratemporal only (1).
65. Insertion of M. geniomyoideus is completely superficial to M. genioglossus medialis (0), or insertion

APPENDIX 2—(Continued)

- is at least partly deep to M. genioglossus medialis (1).
66. M. genioglossus lateralis single (0), or subdivided into separate bundles (1).
67. Insertion of M. levator pterygoidii extends posteriorly beyond columellar fossa of pterygoid (0), or does not (1).
68. Anterior head of M. pseudotemporalis profundus not enlarged (0), or enlarged (1).
69. Bodenaponeurosis with broad base (0), or narrow base attached only to caudomesial edge of coronoid (1).

Other characters

70. Hemipenis without paired horns as extensions of main retractor muscles (0), or with them (1).
71. Foretongue not deeply cleft (0), or deeply cleft (not less than 20% of length) (1).
72. Foretongue cleft for 20% of length or less (0), or not less than 40% of length (1).
73. Gland of Gabe absent (0), or present (1).
74. Calyciform duodenal cells simple (0), or sero-mucous type (1).
75. Cochlear duct not robust (0), or robust and broad, limbus elongate and heavy (1).
76. Ulnar nerve superficial (0), or deep (1) in forearm.
77. Second epibranchial present (0), or absent (1).
78. Ossified palpebrals present (0), or absent (1).
79. Scleral ossicles 14 (0), or fewer (1).
80. Lacrimal duct single (0), or double (1).

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