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New materials of *Estesia mongoliensis* (Squamata: Anguimorpha) and the evolution of venom grooves in lizards

HONG-YU YI^{1,2} AND MARK A. NORELL^{1,2}

ABSTRACT

New specimens of the fossil lizard *Estesia mongoliensis* are described from the Upper Cretaceous of Mongolia. Phylogenetic analysis of 86 anguimorph taxa coded with 435 morphological characters and four genes confirms the placement of *Estesia mongoliensis* in a monophyletic Monstersauria. Extant monstersaurs, the genus *Heloderma*, are the only extant lizards bearing venom-transmitting teeth with a deep venom groove in the rostral carina. Compared to the crown group, stem monstersaurs are morphologically more variable in venom-delivery apparatus. This study has found that *Estesia mongoliensis* has two shallow grooves in the rostral and caudal carinae of its dentary teeth, demonstrating a primary venom-delivery apparatus. A summary of venom-delivering tooth specialization in the Anguimorpha is provided, and related morphological characters are optimized on the strict consensus tree resulting from the combined morphological and molecular analysis of anguimorph phylogeny. The phylogeny supports a single origination of venom grooves in the Monstersauria, and indicates that grooved teeth are currently the only reliable venom-delivery apparatus to be recognized in fossil lizards.

KEY WORDS: *Estesia mongoliensis*, Monstersauria, venom groove, Anguimorpha

INTRODUCTION

Estesia mongoliensis is the oldest fossil squamate with dental grooves comparable to venom grooves in extant species. Squamate reptiles, commonly known as lizards, snakes, and amphis-

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baenians, are highly diverse in predation and defense strategies, including venom use in snakes and lizards. Venomous snakes use marginal teeth for venom delivery, from large, highly specialized hollow fangs in vipers and elapids, to regular-sized teeth with shallow venom grooves in rear-fanged snakes. In extant lizards, only members in the genus *Heloderma* have grooved marginal teeth used for venom delivery. Extant *Heloderma* is low in diversity and restricted in geographic distribution. *Heloderma suspectum* is endemic to southwestern United States and northern Sonora, Mexico, and *Heloderma horridum* is found in Mexico from southern Sonora into Guatemala (Uetz, 2012). In contrast, fossil monstersaurs (Norell and Gao, 1997), phylogenetically allied to *Heloderma*, are found in North America (Stevens, 1977; Pregill et al., 1986), Europe (Hoffstetter, 1957), and Asia (Norell et al., 1992; Norell and Gao, 1997; Conrad et al., 2011b).

The clade Monstersauria (sensu Conrad et al., 2011a) is a group of mostly large and carnivorous anguimorph lizards, including extant *Heloderma* and stem taxa (Norell and Gao, 1997). Monstersaurs differ from other anguimorph lizards in the possession of venom grooves in their marginal teeth and thick mound-shaped osteoderms fused to the skull. Venom grooves are specialized dental grooves that extend from the root of a tooth to its tip, and are used for venom delivery in extant *Heloderma*. Venom grooves in fossil monstersaurs are shallower than the extant condition, and demonstrate more morphological variations of the venom-delivery apparatus along its evolutionary path. The fossil record of monstersaurs in North America dates back to the Late Cretaceous. In the Cenozoic, fossil monstersaurs are commonly known from the Oligocene and Miocene. Fragmentary materials are known from Nevada (Brattstrom, 1954), the Pleistocene of southern California (Gensler, 2001), and the Mio-Pliocene of Tennessee (Mead et al., 2012). *Heloderma texana* is known from the Miocene of Texas (Stevens, 1977) and is represented by articulated skulls. The grooved marginal teeth and thickened osteoderms of *H. texana* closely resemble those in extant *Heloderma*. *Lowesaurus matthewi* is known from the Oligocene to the Miocene of Colorado and Nebraska (Gilmore, 1928; Yatkola, 1976; Pregill et al., 1986), represented by isolated skull elements and trunk vertebrae. In this study we also include an unnamed taxon from the Miocene of Florida (UF 206579; Bhullar and Smith, 2008) that has grooved teeth resembling those of extant *Heloderma*. Mesozoic records of monstersaurs in North America include *Palaeosaniwa canadensis* (Gilmore, 1928; Estes, 1983; Balsai, 2001), *Paraderma bogerti* (Estes, 1964), and *Primaderma nessovi* (Nydam, 2000). Conrad et al. (2011b) also included *Parasaniwa wyomingensis* (Gilmore, 1928; Estes, 1983) as a basal monstersaur. Among the four taxa, only *Paraderma* is suggested to bear dental “venom grooves” (Gao and Fox, 1996).

Eurheloderma gallicum is the only monstersaurian taxon known from Europe. Hoffstetter (1957) reported this taxon from the Late Eocene/Early Oligocene beds of France. It is known to have grooved marginal teeth, but detailed description of these grooves is lacking. In Asia, fossil monstersaurs have been discovered at several localities in the Upper Cretaceous of the Mongolian Gobi Desert (Gao and Norell, 2000). *Estesia mongoliensis* is the largest monstersaur (skull length of the holotype reaching 150 mm), represented by several skulls and postcranial materials (Norell et al., 1992; Norell and Gao, 1997). *Estesia mongoliensis* has grooved teeth but

no osteoderms on the skull. *Gobiderma pulchrum* (Borsuk-Bialynicka, 1984; Gao and Norell 2000; Conrad et al., 2011b), represented by articulated skulls and skeletons, has mound-shaped osteoderms that are fused to the skull, but lacks grooved teeth. *Gobiderma pulchrum* has been assigned to various anguimorph lineages by different authors (Borsuk-Bialynicka, 1984; Pregill et al., 1986), but the recent work (Conrad et al., 2011b), based on several new specimens, found strong support for this taxon as a basal monstersaur.

Estesia mongoliensis was first described by Norell et al. (1992) as the sister group to *Lanthanotus* and Varanidae (fig. 1), but Norell and Gao (1997) found it more closely related to *Heloderma*, with new braincase characters. The latter authors did note, however, that *Estesia mongoliensis* groups with Varanidae in a tree only two steps longer than the most parsimonious tree. Several subsequent studies generally found *Estesia mongoliensis* as a monstersaur (Conrad, 2008; Conrad et al., 2011a, 2011b; Nydam, 2000), although Yi and Norell (2010) reported that *Estesia mongoliensis* grouped with varanoids (but see discussions below). In this study, we report new materials of *Estesia mongoliensis*, including a three-dimensionally preserved skull. Aside from filling in gaps in morphological codings of *Estesia mongoliensis*, our goals include: (1) to evaluate the monstersaurian affinity of *Estesia mongoliensis*, and (2) to discuss evolution of dental characters relating to venom grooves in the Anguimorpha.

Specimens reported here were discovered from the Ukhha Tolgod locality in the Gobi Desert of Mongolia. In the Late Cretaceous, Ukhha Tolgod was a drainage basin populated by stable sandstones, ephemeral ponds, or small lakes. The fossil bearing beds are pale orange alluvial fans formed by water-induced collapse of eolian dunes (Dingus et al., 2008). Paleoclimatic analyses suggest an arid habitat (Montanari et al., in press), similar to that of extant *Heloderma suspectum* (the gila monster). Ukhha Tolgod has produced abundant fossil lizards (Gao and Norell, 2000) including members of Iguanomorpha, Gekkonomorpha, Scincomorpha, and Anguimorpha. This study provides the first detailed descriptions of *Estesia mongoliensis* from Ukhha Tolgod as previously described specimens were from Khulsan (Upper Cretaceous Barun Goyot Formation; Norell et al., 1992), Khermeen Tsav (Upper Cretaceous Barun Goyot Formation; Norell and Gao, 1997), and Bayn Dzak (Upper Cretaceous Djadokhta Formation; Norell and Gao, 1997) in the Gobi Desert of southern Mongolia.

INSTITUTIONAL ABBREVIATIONS: **IGM** or **M**, Mongolian Institute of Geology, Ulaan Baatar, Mongolia; **AMNH**, American Museum of Natural History, New York.

SYSTEMATIC PALEONTOLOGY
SQUAMATA OPPEL, 1811
ANGUIMORPHA FÜRBRINGER 1900
MONSTERSAURIA NORELL AND GAO, 1997
Estesia mongoliensis Norell et al., 1992

HOLOTYPE: IGM 3/14, a skull with mandible.

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

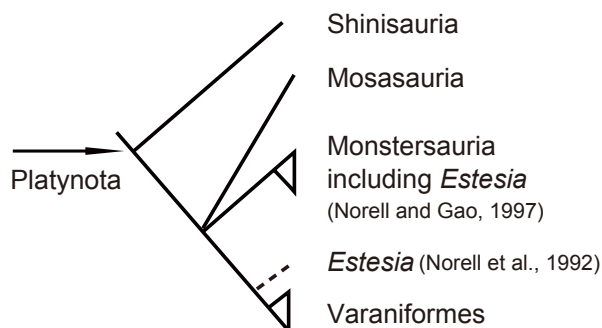


FIGURE 1. Two possible phylogenetic positions for *Estesia mongoliensis* suggested in previous studies. The cladogram of the Platynota follows Conrad (2008).

character no.]-[state no.): absence of dermal sculpture on the maxilla (8-0); absence of dermal sculpture on the prefrontal (9-0); apex of the nasal process of the maxilla positioned posterior to midpoint of the maxilla along the lateral margin (26-1); nasal process of the maxilla weakly inclined in lateral view, with the posterior border of the naris not distinct from the ventral border (27-1); presence of a posterolateral flange on the lacrimal in lateral view (40-1); large lacrimal foramen, being approximately two times the smallest diameter of the palatine foramen, or larger (42-1); absence of a posteroventral process in the jugal (46-1); dorsal margin of the supratemporal process of the parietal narrow and bladelike (79-0); sphenoid housing the posterior opening of the Vidian canal (143-0); retroarticular process of the articular posteriorly broad (204-1); vertebrae with a weak precondylar constriction (229-1); absence of a midline dorsal ridge or keel on the supraoccipital (393-0); presence of grooves extending from root to tip on marginal teeth on the rostral and caudal carinae (429-2); length of edentulous posterodorsal rim on the dentary being longer than one-third of its total length (431-1); presence of lateral processes at the base of nasal process of the premaxilla, with the processes contacting the maxilla (434-2).

DESCRIPTION

IGM 3/196 consists of a skull with associated mandibles, preserved in three dimensions (figs. 2, 4). IGM 3/760 preserves fragments of one front limb, nine vertebrae and dorsal ribs (fig. 8). No osteoderms are found associated with either of the specimens.

SKULL

The skull of IGM 3/196 is dorsoventrally flattened with little compression. The outline of the skull features an elongate round snout, and laterally expanded orbits, which is seen in all monstersaurs except *Gobiderma pulchrum*. The premaxilla, maxillae, jugals, and septomaxillae are preserved in articulation. Posterior to the frontal, the skull roof and entire braincase are

NEWLY REFERRED SPECIMENS:
IGM 3/196, a skull with mandible, preserved three-dimensionally; IGM 3/760, partial axial skeletons including dorsal vertebrae with articulating ribs and an incomplete left forelimb. Both specimens were collected from the Upper Cretaceous Djadokhta Formation at Ukhha Tolgod, Mongolia.

REVISED DIAGNOSIS: A monstersaurian lizard differing from other members of the group in the following character states ([character

eroded away. The skull roofing bones have no fused osteoderms, but show shallow surface striations like those in the holotype (Norell et al., 1992). Most of the palatal bones are preserved, with only the posterior part of basisphenoid missing (fig. 3A).

PREMAXILLA: The premaxilla consists of a horizontal maxillary process and a nasal process rising about 30° from the level of the maxillary process. The maxillary process bears nine tooth positions as reported for the holotype (IGM 3/14, Norell et al., 1992). A premaxilla-maxilla aperture is not present. In ventral view, a short bipartite vomerine process is present in the middle of the maxillary process. The nasal process of the premaxilla is slender; posteriorly it tapers and inserts between the nasals. Two small projections are present at the base of the nasal process where it branches off from the maxillary process. The lateral projections abut the premaxilla-maxilla suture, forming two small openings (fig. 3B, dorsal view). The presence of the premaxilla projections is an autapomorphy for *Estesia mongoliensis*. *Heloderma* and *Gobiderma pulchrum* do not possess similar structures; the premaxilla is not preserved for *Heloderma texana*, *Lowesaurus matthewi*, and *Eurheloderma gallicum*. The function of these projections is unclear, but the size and position of the apertures formed by the projections is comparable to the ethmoidal foramina of extant *Heloderma*, *Lanthanotus borneensis*, *Varanus*, and *Shinisaurus crocodilurus*. In extant anguimorph lizards, similar lateral projections are known only in *Diploglossus* (Rieppel, 1980: fig. 18), but the projections are not as extensive as those in *Estesia mongoliensis*, and not in contact with the maxilla.

Major anguimorph clades demonstrate considerable variation in the contacts between the premaxilla and nasal. In the Monstersauria (and squamates in general), the premaxilla lies on the surface of the nasals with no additional ventral process extending beneath the nasals (fig. 4A, B, D, E). *Varanus*, however, demonstrates a derived condition where the premaxillary process of the nasal embraces the premaxilla along its lateral margins (fig. 4C). Correspondingly the nasal process of the premaxilla divides into dorsal and ventral branches to interlock with the nasal. This is also seen in some fossils allied to varanids (sensu Conrad et al., 2011a), e.g., *Aiolosaurus oriens* (Gao and Norell, 2000: fig. 34A). Mosasaurs show an additional hyper-derived condition where the nasals are greatly reduced or lost (Russell, 1967). IGM 3/196 shows that *Estesia mongoliensis* has a horizontal articulation surface between the premaxilla and nasal, resembling the condition in *Heloderma* and other monstersaurs.

NASAL: The nasals are paired, thin, and elongate, contacting the premaxilla anteriorly and the frontal posteriorly. Another apomorphy of *Estesia mongoliensis* shown in IGM 3/196 is that the nasals taper anteriorly and suture beneath the premaxilla. In other monstersaurs with nasals preserved (e.g., *Heloderma*, *Gobiderma pulchrum*), the anterior tips of left and right nasals remain separate and do not completely suture along the midline. Posteriorly, the nasals contact the frontals in a straight suture, although details of this suture are obscured by erosion.

MAXILLA: The maxilla forms most of the lateral margin of the rostrum. It is roughly triangular in lateral view, with a long and low premaxillary process and a relatively short posterior process ending abruptly anterior to the orbit (fig. 2). The premaxillary process is dorsoventrally flat. In dorsal view, the premaxillary process curves medially to give the snout a blunt shape. The medial curving begins at the level of the fourth posterior tooth position.



FIGURE 2. Lateral view of IGM 3/196. Scale bar = 10 mm.

The premaxillary process notches anteriorly, articulating with the premaxilla and the septomaxilla (fig. 3A, B). The posterior (nasal) process gradually rises from the premaxillary process. In lateral view, the margin of the bony naris is weakly inclined posteriorly. Most monstersaurs, e.g., *Heloderma* and *Eurheloderma gallicum*, have steeply inclined nasal processes. In comparison, varanid lizards have weakly inclined nasal processes developed in conjunction with a posterior retraction of the nares. “Retracted nares” is a common character used in anguimorph matrices (Estes et al., 1988; Norell et al., 2007; Conrad et al., 2011b). In general, true retraction is thought to only appear in varanids. Correlated features that develop with naris retraction include weakly inclined lateral naris margins, a fused nasal that tapers posteriorly, and anterior processes of the frontal contributing to the naris margins. Nares of extant *Heloderma* extend more posteriorly than the primitive anguimorph condition, but are generally treated as not retracted, due to the extensive connective tissues between the nasal and prefrontal (see discussion in Estes et al., 1988: char. 2). Discoveries of fossil monstersaurs have revealed variation in the extent of narial posterior elongation (Hoffstetter, 1957; Norell et al., 1992; Conrad et al., 2011b), and so there is a call for a more precise definition of “retracted nares.” In this study, “retracted nares” is used when the posterior margins of the nares not only invade the space between the nasal and maxilla, but also incorporate the anterior margins of the frontal. Note that “retraction” cannot be assumed only by the weak inclination of the nasal process of the maxilla. In this context, *Estesia mongoliensis* has a

varanidlike, low and posteriorly inclined, maxilla, but does not develop full naris retraction because the frontals do not contribute to the narial margin.

In ventral view, the maxilla contacts the premaxilla and vomer anteriorly. Posteriorly, it is excluded from the infraorbital fenestra by the palatine and ectopterygoid. Eleven tooth positions are observed on each maxilla.

SEPTOMAXILLA: The septomaxilla is subtriangular in dorsal view. It is concave medially with a low ridge, resembling the shape of the septomaxilla in other monstersaurs. In contrast, the septomaxilla of *Varanus* (fig. 4C) is convex in the middle. The septomaxilla of IGM 3/196 lies on top of the maxilla and vomer, and housed Jacobson's organ within it. Like in *Heloderma* and *Gobiderma pulchrum* (Conrad et al., 2011b), the low medial flange of the septomaxilla does not contact the premaxilla or nasal dorsally. Due to preservation, the septomaxilla is unknown in *Eurheloderma gallicum*, *Primaderma nessovi*, and *Paraderma bogerti*. The septomaxilla can be provisionally described in *Heloderma texana* (Pregill et al., 1986) with further preparation on reported materials; unfortunately, the only CT-scanned specimen (TMM 40635-230) seems to lack this element.

PREFRONTAL: The prefrontal has a dorsal process extending along the orbit anteroposteriorly, and a ventral process forming part of the anterior wall of the orbit. The dorsal processes on both sides are badly weathered. The ventral process of the prefrontal surrounds a single lacrimal foramen with the lacrimal and palatine. Like the holotype of *Estesia mongoliensis* (Norell et al., 1992: fig. 10A), the prefrontal, lacrimal, and jugal of IGM 3/196 meet at a single point on the ventral margin of lacrimal foramen. In anguimorph lizards, the plesiomorphic morphology lacks contact between the prefrontal and jugal. In derived monstersaurs (extant *Heloderma*), the jugal extensively contacts with the prefrontal (Norell et al., 1992; fig. 10C). *Estesia mongoliensis* demonstrates an intermediate morphology between the derived and primitive conditions.

LACRIMAL: The lacrimal is triangular in lateral view and forms the lateral margin of the orbit. IGM 3/196 has a single lacrimal foramen, surrounded by the lacrimal, prefrontal, and jugal. On the holotype of *Estesia mongoliensis*, the lacrimal foramen appears as a small slit due to lateral compression, but IGM 3/196 shows that the lacrimal foramen is clearly larger than the palatine foramen. The presence of a single posterior lacrimal foramen is plesiomorphic in the Anguimorpha and squamates in general (Estes, et al., 1988). In anguimorph lizards, only *Lanthanotus borneensis* and *Varanus* demonstrate a derived condition with double posterior lacrimal foramina. *Heloderma* and *Gobiderma pulchrum* (Conrad et al., 2011b) both have one posterior lacrimal foramen, and the same condition is found in *Estesia mongoliensis*.

JUGAL: The jugal is angular with a short suborbital process and a long tapering postorbital process. The suborbital process extends along the medial side of the maxilla, excluding the maxilla from the orbital rim. Dorsally, the postorbital process of the jugal is smooth and rodlike, and tapers towards the postorbitofrontal. No posterior process develops at the base of postorbital process. The postorbital process contacts the postorbitofrontal to form a complete orbital rim. In anguimorph lizards, a greatly reduced jugal (that does not contact the postorbitofrontal) is a synapomorphy of *Varanus*. A complete orbital rim is plesiomorphic

and shared by major anguimorph clades and possibly some fossils allied to varanids (e.g., *Saniwa ensidens*). The medial side of the jugal bears a distinct fossa for muscle attachment. This fossa exists in most anguimorphs, generally projecting medially. In *Estesia mongoliensis* and extant *Heloderma*, this distinct fossa faces posteriorly, largely due to the unique lateral expansion of the skull posterior to the rostrum. No dermal rugosities are preserved on the jugal.

VOMER: Both vomers, elongate and rodlike, are preserved in IGM 3/196. The vomer is more than twice the length of the palatine, in keeping with elongation of the snout. Vomer elongation is also present in *Heloderma*, *Varanus*, *Lanthanotus*, and allied fossil taxa including *Gobiderma* (the Deep Scaly Project, 2011a; digital morphology accessed through <http://www.digimorph.org>), *Ovoogurvel* (Norell et al., 2007), and *Paravaranus angustifrons* (Borsuk-Bialynicka, 1984: pl. 1). All mosasaurs have an elongate snout, but the proportion between vomer and palatine remains unclear for many species. In other anguimorph clades, the vomer is shorter than the palatine.

In IGM 3/196, the vomer contacts the premaxilla and maxilla at its anterior tip, but has no contact with the maxilla along its lateral edge. In *Varanus* the vomer contacts the maxilla anterolaterally to form a complete floor for the chamber enclosing Jacobson's organ (Rieppel et al., 2008). This is termed the neochoanate condition in Lakjer (1927). In *Heloderma* and *Lanthanotus borneensis* the vomer does not contact the lingual process of the maxilla, forming the incomplete neochoanate condition (Lakjer, 1927). The holotype of *Estesia mongoliensis* appears to show a "neochoanate condition" (Norell et al., 1992: fig. 4), but the less distorted skull of IGM 3/196 indicates that the contact in the holotype is due to lateral deformation of the skull and *Estesia mongoliensis* actually has an incomplete neochoanate condition.

On the ventral surface of the anterior tip of the vomer are two lacrimal grooves (sensu Oelrich, 1956) surrounding a lacrimal duct. In anguimorph lizards, the plesiomorphic morphology is that two anteroposterior ridges border the lacrimal groove (fig. 5C). In extant *Heloderma*, the ridges are reduced to small knobs, and the lacrimal groove is not prominent (fig. 5B). In fossil monstersaurs, *Estesia mongoliensis* and *Goboderma pulchrum* retained the plesiomorphic condition (fig. 5A). The vomers in other fossil members remain unknown.

PALATINE: Both palatines are preserved in IGM 3/196; they are wider than long with the vomerine branch shorter than the maxillary branch. The palatine is posteriorly located; the vomeropalatine suture extends to the level of the posteriormost tooth position in the maxilla. In *Heloderma* the vomeropalatine suture extends posterior to the last maxillary tooth. In *Varanus*, the vomerine process of the palatine generally extends more forward compared to that in *Estesia mongoliensis* and *Heloderma*. No obvious tooth patch is preserved on the palatine of IGM 3/196. One single tooth can be observed on the right palatine near its suture with the pterygoid, but it is unclear whether the palatine teeth form a single row, multiple rows, or a patch. The holotype of *Estesia mongoliensis* seems to bear a tooth patch on the palatine (Norell et al., 1992), but weathering of its ventral surface precludes conclusive descriptions of this character.

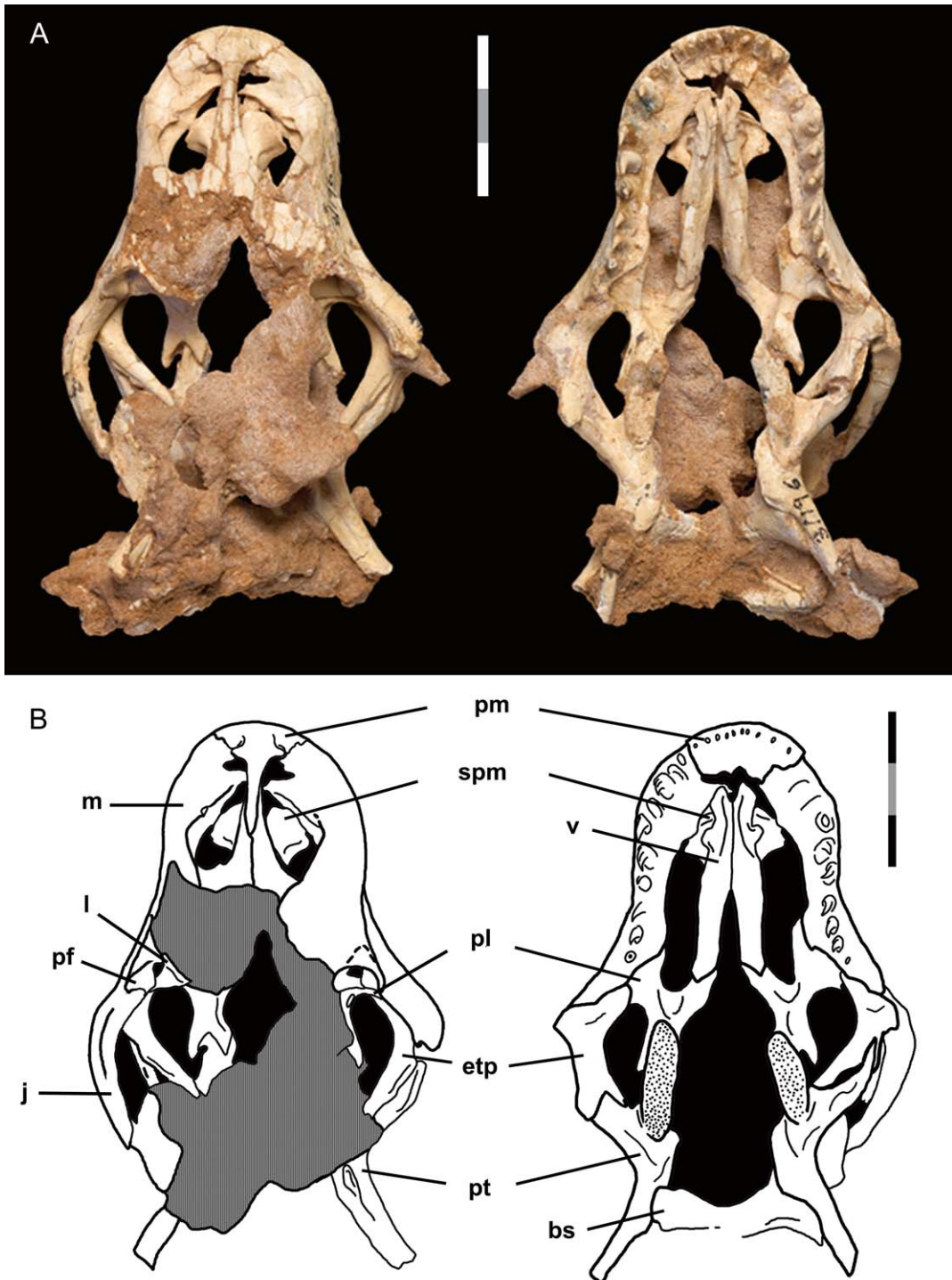


FIGURE 3. A. Skull of IGM 3/196 in dorsal and ventral view (scale bar = 10 mm). B. Line drawings of the skull of IGM 3/196 in dorsal and ventral view (scale bar = 10 mm). Abbreviations are listed in appendix 6.

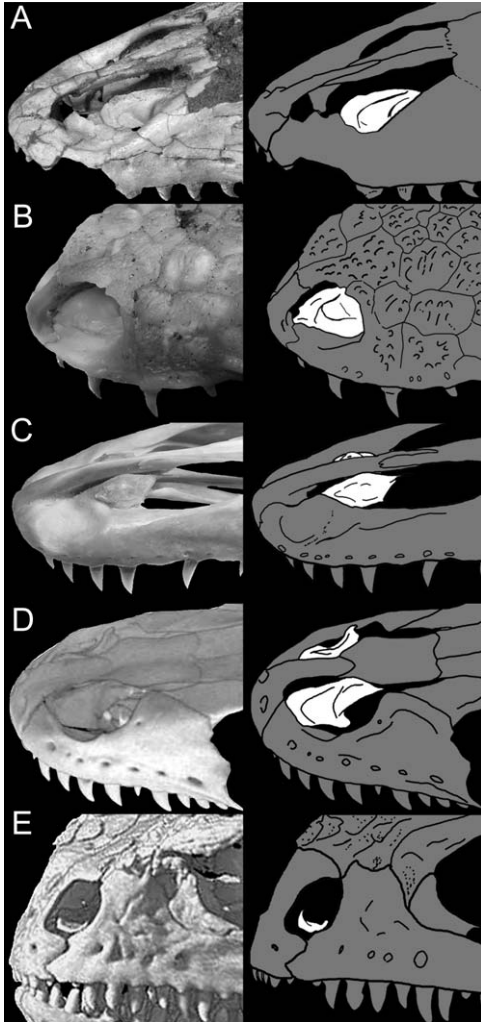


FIGURE 4. Comparisons of snout morphologies in the Anguimorpha, with the septomaxilla highlighted in white. **A.** *Estesia mongoliensis* (IGM 3/196); **B.** *Heloderma suspectum* (AMNH R-147173); **C.** *Varanus salvadorii* (AMNH R-59873); **D.** *Lanthanotus borneensis* (the Deep Scaly Project, 2011b); **E.** *Shinisaurus crocodilurus* (Bever et al., 2005). Not to scale.

goid, which is visible in lateral view (fig. 2). In dorsal view, the ectopterygoid fits into a distinct groove on the dorsal surface of the pterygoid that terminates anterior to the epipterygoid.

MANDIBLE

Both mandibular rami of IGM 3/196 are preserved. The left ramus is nearly complete, curving ventrally and medially. Articulating the left mandibular ramus to the skull shows that

PTERYGOID: Both pterygoids are preserved on IGM 3/196, although most of their posterior processes (quadrate processes) are weathered away. The pterygoid is triradiate, with the palatine and ectopterygoid processes projecting anteriorly and the quadrate process projecting posteriorly. The palatine process elevates to form a flat platform dorsal to its contact with the ectopterygoid process. This platform is covered by a patch of teeth, resembling the pterygoid tooth patch in *Gobiderma pulchrum*. The presence of palatal teeth is variable among individuals in *Heloderma suspectum*, but when present, the teeth are arranged in a single row. *Eurheloderma gallicum* possess a single row of teeth on the pterygoid (Hoffstetter, 1957). The pterygoids of other fossil monstersaurs remains unknown. The dorsal surface of the pterygoid has a distinct groove running along the ectopterygoid process to the terminus of the quadrate process, as seen in *Heloderma* and *Lanthanotus borneensis*, but this groove is absent in *Varanus*.

ECTOPTERYGOID: The ectopterygoid consists of a short anterior process and two posterior processes. The anterior process contacts the palatine medially, excluding the maxilla from participation in the margin of the suborbital fenestra. The contact between the ectopterygoid and palatine is less extensive in *Estesia mongoliensis* compared to *Heloderma*. The ectopterygoid diverges posteriorly into dorsal and ventral processes, embracing the anterolateral process of the pterygoid. The ventral branch is short and sutures with the pterygoid nearly vertically. The dorsal branch resembles that of *Heloderma* in that it extends about two thirds of the length of the ectopterygoid process of the ptery-

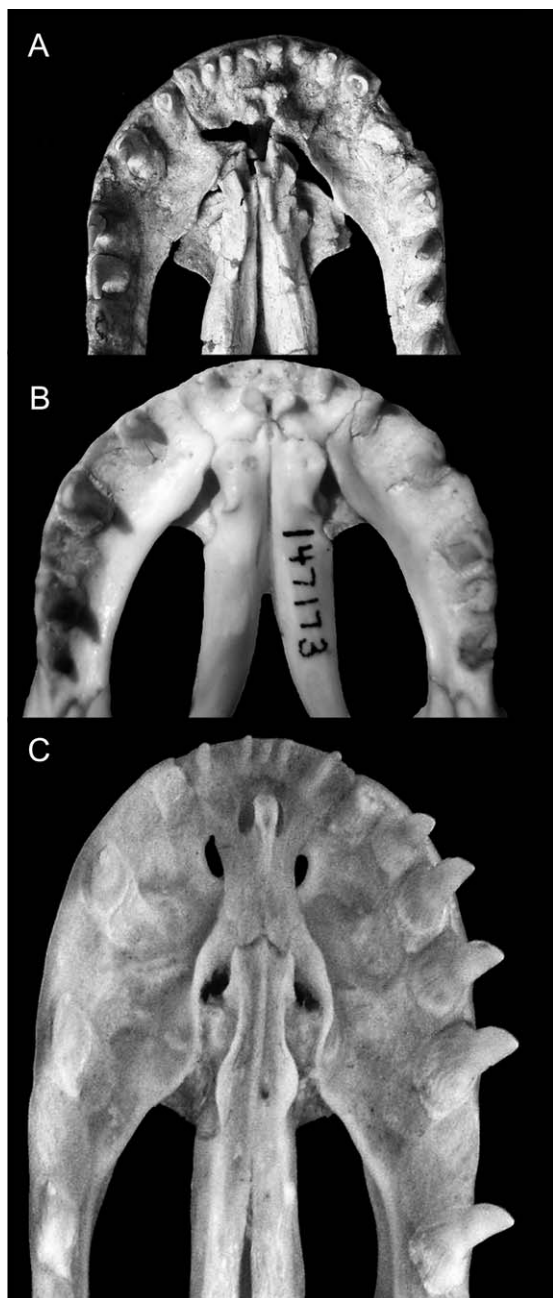


FIGURE 5. Comparisons of anterior palate of: (A) *Estesia mongoliensis* (IGM 3/196); (B) *Heloderma suspectum* (AMNH R-147173); and (C) *Varanus salvadorii* (AMNH R-59873). Not to scale.

mongoliensis shares with other monstersaurs the following characters: extensive height (measuring about half as long as the length) and a distinct medial inflection at the symphysis that

the dentary and coronoid have kept their original life position, whereas the postdentary elements have shifted anteriorly (fig. 6). The right dentary and coronoid are complete, but their medial surface is hidden by postdentary elements that shifted ventral to the dentary. Neither the splenial or angular is preserved on either side. The mandibular fossa of IGM 3/196 is deep and elongate in medial view. Extant *Heloderma* and *Varanus* have an elongate mandibular fossa; in *Lanthanotus borneensis*, the mandibular fossa is restricted and nearly covered by a ventral lappet of the surangular in the lingual surface.

DENTARY: The dentary bulges outward laterally. In dorsal view, the symphyseal facet for the opposing mandibular ramus is nearly vertical to the long axis of the rest of the dentary. The medial inflection of the dentary begins at the second tooth position anteriorly. Medially, Meckel's groove is open at least in the anterior half of the dentary, according to the position of the articulation facet for the surangular below the last dentary tooth. The opening of the intramandibular septum lies posterior to the last dentary tooth below the descending subdental shelf, or suprameckelian lip (Bhullar and Smith, 2008). The posterior margin of the intramandibular septum of the dentary is U-shaped and smooth, without the eminence reported in some Miocene helodermatids (Bhullar and Smith, 2008). Both dentaries bear eight tooth positions. The mandibular teeth are loosely arranged and modified pleurodont with basally infolded plicidentine. In lateral view, six alveolar foramina pierce the lateral wall of the dentary, with the last foramen lying posterior to the level of the last tooth. The dentary of *Estesia*

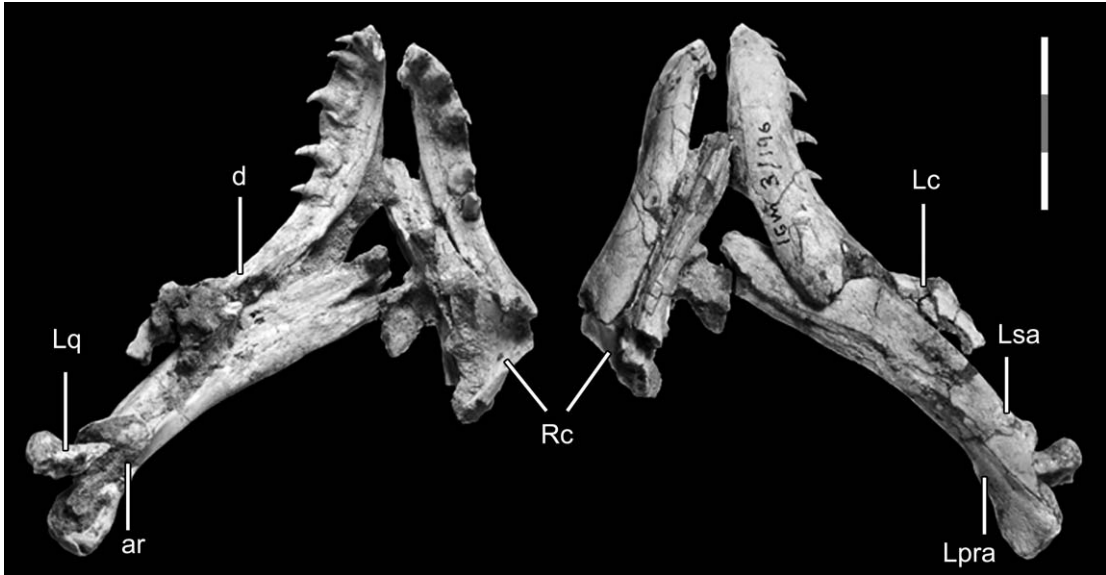


FIGURE 6. The mandible of IGM 3/196 in dorsal and ventral views. Scale bar = 10 mm; abbreviations are listed in appendix 6.

gives the snout a round outline (not distinct in *Gobiderma pulchrum*). Compared to other monstersaurs, *Estesia mongoliensis* is unique in having a long edentulous posterior rim in the dentary. The tooth row occupies only about two thirds the length of the dentary (figs. 2, 7), which is much shorter than that in *Heloderma* and *Gobiderma pulchrum* (see IGM 3/55).

CORONOID: The coronoid is fragmentary on the left side; the right coronoid is obscured by other overlying bones. The labial branch of the coronoid is short, overlapping the dorsal part of the dentary-surangular suture. The lingual process is long, as shown in the right coronoid. The angular process of the coronoid is not well preserved on either side, but shows a general shape similar to that of the holotype (Norell et al., 1992).

SURANGULAR: The surangular is exposed on the left mandibular ramus, although it shifted anteriorly postmortem. Consequently, presence of an anterior surangular foramen cannot be confirmed. A posterior surangular foramen is located near the surangular-prearticular suture. In lingual view, the surangular forms most of the dorsal margin of the mandibular fossa, whereas the angular forms the ventral margin.

PREARTICULAR: The prearticular extends from the posterior margin of the dentary to the posterior end of the mandible. In ventral view, a prominent triangular medial process of the prearticular coextends with the glenoid process of the mandible, as seen in *Heloderma*, *Lanthanotus borneensis*, and *Varanus*. The retroarticular process is equal in both length and width, and is much shorter than in extant *Heloderma*. Piercing the medial surface of the retroarticular process is a foramen that transmits the chondra tympani nerve in some extant lizards (Oelrich, 1956).

ARTICULAR: The articular is well ossified, forming the anterior wall of the glenoid fossa. Its exposed surface is rough, suggesting the attachment of cartilage in life. The purported loss

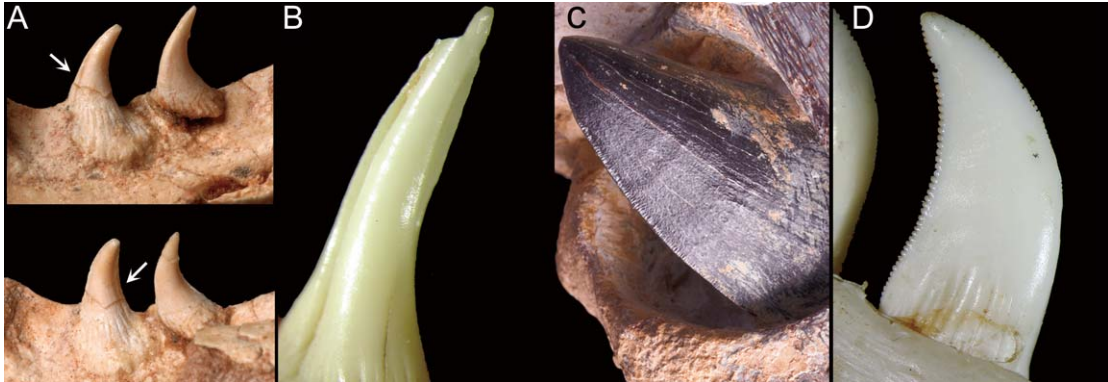


FIGURE 7. Tooth specializations (grooves and serrations) in the Anguimorpha. **A.** *Estesia mongoliensis* (IGM 3/196), with arrows pointing to tooth grooves and flanges on the anterior and posterior carinae of a dentary tooth. **B.** Dentary tooth of *Heloderma suspectum* (AMNH R-71082). **C.** Dentary tooth of *Tylosaurus proriger* (AMNH FR 1543). **D.** Dentary tooth of *Varanus komodoensis* (AMNH R-37909). Not to scale.

of the articular in *Estesia mongoliensis* reported in previous studies (Norell et al., 1992; Norell and Gao, 1997) is probably due to incomplete ossification or preservation.

DENTITION

Similar to *Heloderma*, *Estesia mongoliensis* has larger teeth lying in the middle of the tooth row. The premaxillary teeth are distinctly smaller than the maxillary teeth. All teeth are recurved. They are neither as elongate nor as cylindrical as those of extant *Heloderma*. IGM 3/196 reveals a new character shared by *Estesia mongoliensis* and extant *Heloderma*: distinct flanges (“trenchant margins delimited from main tooth shaft,” as mentioned in Pregill et al., 1986) on the rostral and caudal carinae of the dentary teeth, forming sharp cutting edges (fig. 7B). Such flanges are not known in other anguimorphs. When describing tooth morphology in this study, “rostral” refers to the direction toward the mandibular symphysis, whereas “caudal” (“distal” in Bhullar and Smith, 2008) refers to the direction toward the retroarticular process in the mandible. Extant *Heloderma* lizards bear the most extensive flanges that are expanded at the tooth tip. These flanges are not the same structures as the venom grooves. Although venom grooves in *Heloderma* develop associated with the flanges, the flanges can also be observed in taxa that do not bear venom grooves (*Primaderma nessovi*; Nydam, 2000). *Estesia mongoliensis* bears flanges and grooves in the marginal teeth, and these structures are most prominent in large teeth. IGM 3/196 has several teeth that clearly show flanges that delimit the main tooth shaft and extend from the tooth root to the tip (fig. 7A). Tooth flanges in *Estesia mongoliensis* are not as wide as those in extant *Heloderma*, indicating the primitive condition of this structure. Similar flanges are also observed in *Palaeosaniwa canadensis* (Pregill et al., 1986; Balsai, 2001) and UF 206579 (Bhullar and Smith, 2008). The presence of tooth flanges in other monstersaurs remains uncertain, although they are probably not present in *Gobiderma pulchrum*. Stevens (1977) reported venom grooves of *Heloderma texana*, but it is impossible to tell whether a flange develops

with the groove because the reported teeth were broken and no crowns are preserved. In Hoffstetter's (1957) description of teeth in *Eurheloderma gallicum*, a flange develops on the rostral carinae, but the caudal flange is not mentioned.

Compared to the tooth flanges, venom grooves are better documented in the Monstersauria, and have been summarized in various studies (Pregill et al., 1996; Nydam, 2000). IGM 3/196 provides new information of the venom grooves of *Estesia mongoliensis*. On large dentary teeth of IGM 3/196, grooves extending from the tooth root to the tip can be observed on both the rostral and caudal carinae (fig. 7A), with the caudal one much deeper than the rostral. In extant *Heloderma*, however, the deep venom groove is present only on the rostral carina. The caudal groove is sometimes observed (especially in *Heloderma horridum*), but the caudal groove is always shallower than the rostral when present. All other monstersaurs with venom grooves have deep root-to-tip tooth grooves in the rostral carina. These taxa include *Lowsaurus matthewi* (Gilmore, 1928; Pregill et al., 1986), *Eurheloderma gallicum* (Hoffstetter, 1957), *Heloderma texana* (Stevens, 1977), *Paraderma bogerti* (Gao and Fox, 1996) and the unnamed specimen UF 206579 (Bhullar and Smith, 2008).

AXIAL SKELETON

VERTEBRAE: IGM 3/760 (fig. 8) preserves 10 dorsal vertebrae associated with ribs, and a fragmentary right forelimb. Although *Estesia mongoliensis* lacks diagnostic characters in the postcrania, the most obvious feature is the large size of the skeleton. IGM 3/760 is referred to *Estesia mongoliensis* for its large size and constricted articular condyles of the vertebrae resembling other reported postcrania of this species (Norell and Gao, 1997). The centra of the dorsal vertebrae are constricted posteriorly, and bear distinct articular condyles. The articulation surfaces between the vertebrae are oblique, so in lateral view the condyle of the proceeding vertebra lies below the articulation surface of the more posterior element. The parapophysis and hypopophysis are fused for articulation with single headed ribs. All neural arches are broken; however, the preserved bases indicate that the neural arches are narrow dorsally. Ribs are single headed, and slightly curved back.

FORELIMB: IGM 3/760 provides information on limb elements of *Estesia mongoliensis* for the first time. The manus of the right forelimb is preserved with the vertebral column. The carpals and metacarpals are well ossified, and are not particularly reduced or elongate in proportion to the body trunk, indicating that *Estesia mongoliensis* had limbs at least as powerful as extant monstersaurs or varanids. The suture between the carpals also indicates this individual is an adult, as these elements fuse at somatic maturity. The exact count of wrist elements cannot be determined due to preservation. Four carpals are preserved; they are the medial centrale and distal carpals 2–4 based on shape comparison to extant anguimorph lizards.

PHYLOGENETIC ANALYSIS

Estesia mongoliensis is analyzed in a matrix of the Anguimorpha. Morphological phylogenies have consistently assigned *Estesia mongoliensis* and the Monstersauria to the monophy-

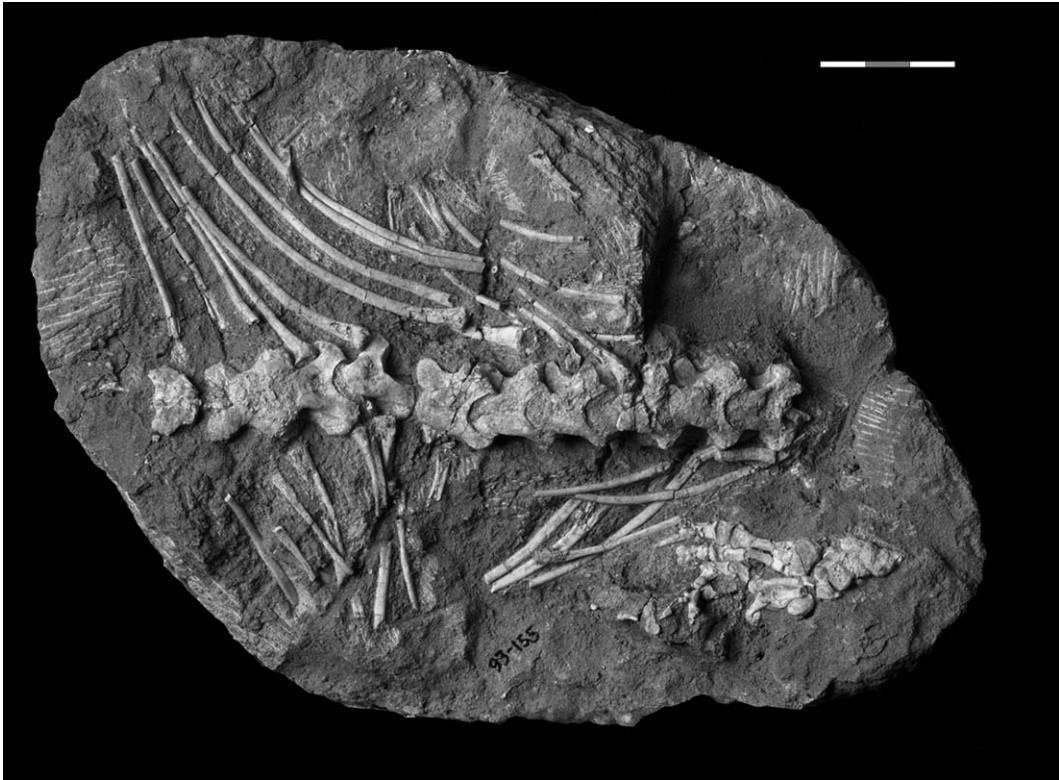


FIGURE 8. Postcrania of *Estesia mongoliensis* (IGM 3/760). Scale bar = 10 mm.

letic Platynota (sensu Conrad et al., 2011a). The clade Platynota includes extant *Shinisaurus crocodilurus*, *Heloderma*, *Varanus*, and their fossil relatives (Pregill et al., 1986; Conrad, 2008; Conrad et al., 2011a). Molecular phylogenies (Wiens et al., 2010), however, have failed to find a monophyletic Platynota. The most recent combined analysis (morphological and molecular) phylogeny (Conrad et al., 2011b) also found the Monstersauria as the sister group to Anguinae and Carusoidea, instead of as a member of Platynota. We analyze *Estesia mongoliensis* in a matrix of extant and fossil anguimorphs, coded with morphological and molecular data. To explore its possible phylogenetic positions, we broadly sampled major clades of the Anguimorpha.

The data matrix includes 86 taxa coded with 435 morphological characters and four genes (two nuclear and two mitochondrial genes). Five outgroups were used: *Sphenodon punctatus*, *Gephyrosaurus bridensis*, *Eolacerta robusta*, *Aspidoscelis tigris*, and *Xantusia vigilis*. The 81 ingroup taxa consist of 11 extant and 35 fossil species, covering every major anguimorph lineage (“Family” or “Subfamily” level). Snakes have not been included in this analysis, as their phylogenetic position remains contentious. In recent squamate phylogenies, morphological studies have shown mixed results on the position of snakes. Conrad (2008) found snakes outside the Anguimorpha, but Gauthier et al. (2012) found them nested within the Anguimorpha with other limbless taxa. Recent total-evidence studies on squamates (Wiens et al., 2010) and

anguimorph lizards (Conrad et al., 2011a), incorporating molecular data, both found snakes outside the Anguimorpha.

All taxa are coded to species level except *Paraglyptosaurus*, *Mosasaurus*, *Clidastes*, *Tylosaurus*, and the unnamed UF 206579 of Bhullar and Smith (2008). For lineages that are diverse, and whose monophyly is well supported (e.g., *Varanus*), we take sample species representative of their major geographic regions.

Most of the morphological characters (417 of 435) are derived from Conrad et al. (2011a), describing morphological variation in the Squamata; 10 additional characters are chosen from Gao and Norell (1998) and Bhullar and Smith (2008), describing variation in the Anguimorpha; eight new characters are added based on direct observations in this study. All morphological characters are treated as unordered. Molecular sequences of extant taxa are obtained from GenBank (Benson et al., 2011). The four genes included are RAG1 (partial coding sequence, ~2800 bp), BDNF (partial coding sequence, ~670 bp), ND1 (the complete coding sequence, ~968 bp) and ND2 (the complete coding sequence, ~1037 bp). We chose both nuclear and mitochondrial genes that can be coded with the most taxa sampled in this study. Sequence alignment was completed in MUSCLE (Robert, 2004) using the default values for transition, transversion, and gap opening.

Descriptions and codings of the new morphological characters are provided in appendix 1. For a complete list of character descriptions and codings of all morphological data, an executable NEXUS file can be downloaded from the TreeBASE (Morel, 1996) record of this study (appendix 2: URL to TreeBASE record). The TreeBASE record also includes aligned molecular sequences for download. Specimens of extant species used for morphological coding are listed in appendix 3. GenBank accession numbers are provided in appendix 4.

The combined morphology and molecular matrix is analyzed in POY 4.1.2 (Varón et al., 2010), with molecular sequences read as prealigned. Morphology-only analysis is completed in TNT (Willi Hennig Society edition, Goloboff et al., 2008), using new technology search (20 cycles each of ratchet, drift, and tree fuse). The search was set to find the shortest trees 500 times.

RESULTS: The combined analysis yielded 90 topologically unique most parsimonious trees (MPTs) of 9479 steps. The strict consensus tree (fig. 9) was imported into PAUP v. 4.0b10 (Swofford, 2001) for reconstructing apomorphies at each node. The strict consensus tree recognizes monophyletic clades of Monstersauria, Anguinae, Carusioidea, Shinisauria, Mosasauria, and Varanidae. Note that some clades (e.g., Shinisauria) are collapsed in figure 9 to simplify the display of the tree, but they all represent several species in the original matrix. The polytomy at the base of the Anguimorpha rendered the relationship between the Monstersauria and Anguinae unresolved. *Estesia mongoliensis* is recognized as a basal monstersaur.

The morphology-only analysis returned 4160 MPTs of 1429 steps. The resulting strict consensus tree (fig. 10) also supports *Estesia mongoliensis* as a basal member of a monophyletic Monstersauria, and recognizes monophyletic Mosasauria, *Varanus*, Lanthanotinae, Shinisauria, and Anguinae. However, a monophyletic Platynta, exclusive of the Anguinae in the Angui-

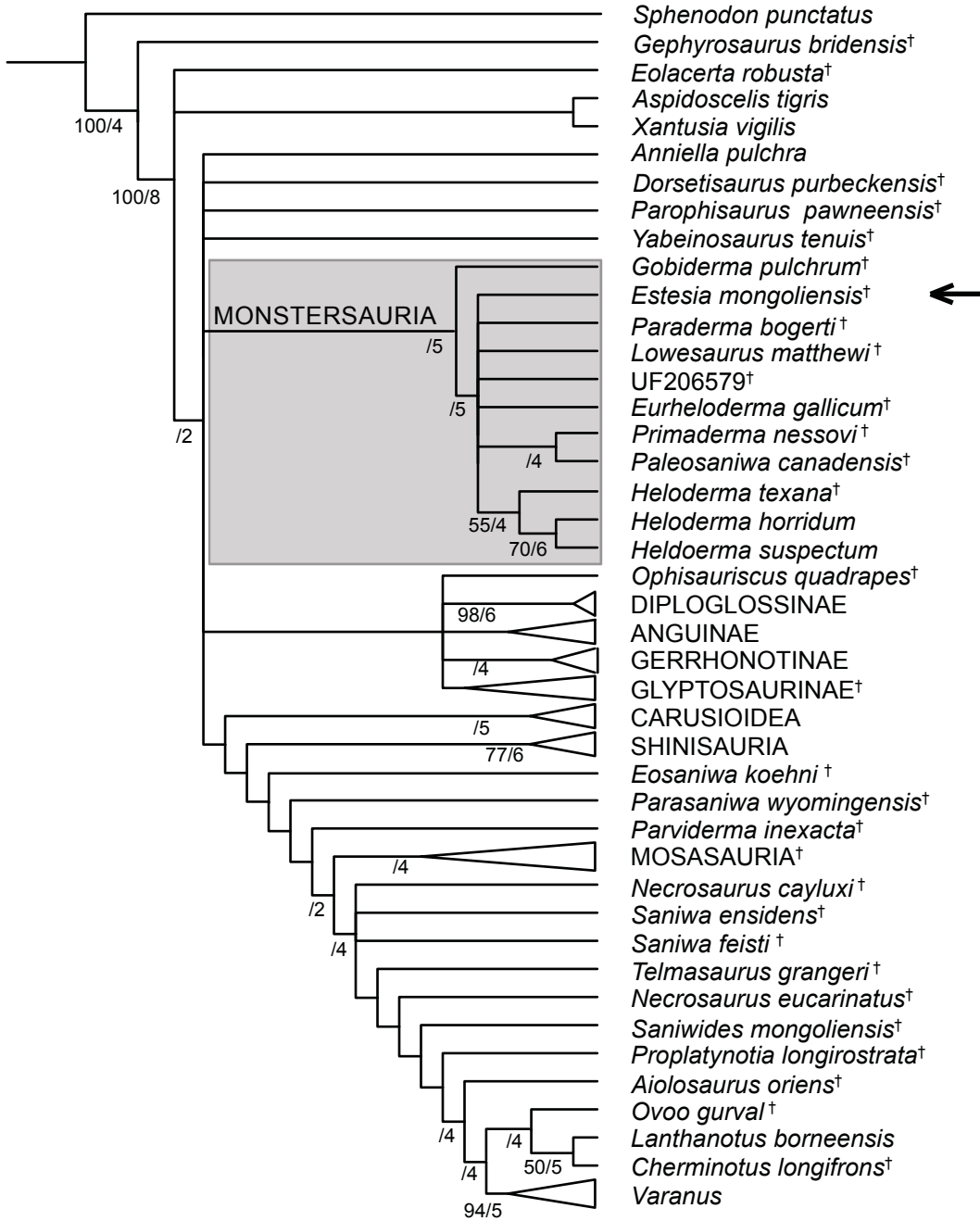


FIGURE 9. The strict consensus tree of the combined analysis of morphological and molecular data. Support values are labeled beneath branches. The number written before the slash is bootstrap value; the number written after the slash is Bremer support. Only bootstrap values above 50% are listed, so some branches show only Bremer support values.

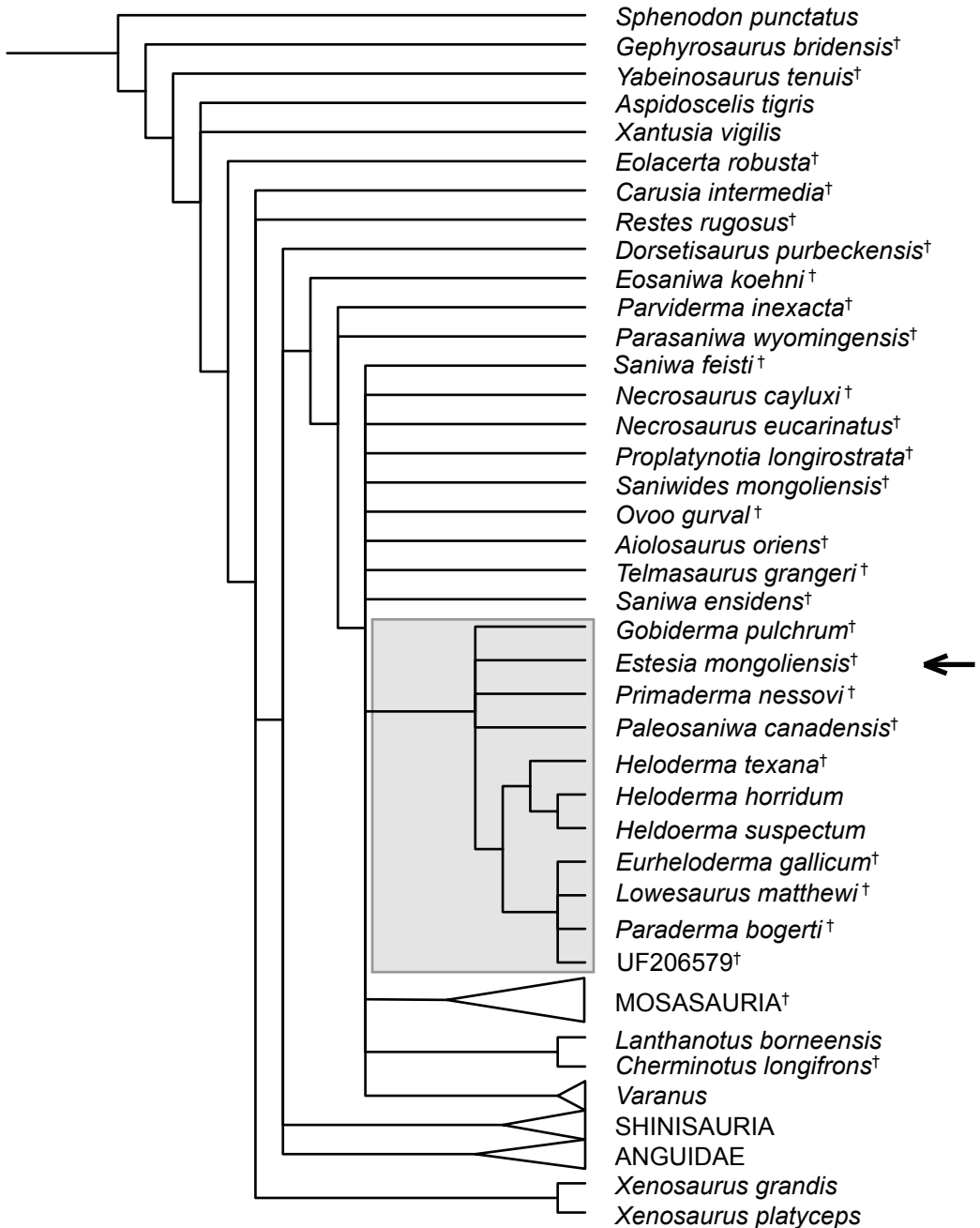


FIGURE 10. The strict consensus tree of the morphology-only analysis. The clade in grey shade is the Monstersauria.

morpha, is not recovered. The Monstersauria, Mosasauria, and varanids form a monophyletic clade that does not include the Shinisauria.

DISCUSSION

ESTESIA MONGOLIENSIS AS A BASAL MONSTERSAUR

As mentioned before, previous studies report varying phylogenetic positions for *Estesia mongoliensis* (Norell et al., 1992; Norell and Gao, 1997; Conrad et al., 2011a; Yi and Norell, 2010), but these studies differ in taxon and character sampling. In a preliminary analysis (Yi and Norell, 2010), we suggested that *Estesia mongoliensis* is the most basal member of the Varaniformes (sensu Conrad, 2008), but our subsequent work shows that this was probably due to inadequate taxon sampling. In comparison to the matrix used in Yi and Norell (2010), the current matrix is updated in several aspects: first, we expanded our taxon sampling to genus level in the Anguimorpha, including broad sampling in the Mosasauria. Although *Estesia mongoliensis* never grouped with mosasaurs, adding mosasaurs in the matrix changed the character optimization of *Varanus*-like characters (e.g., the fusion of nasals). In the updated data matrix, *Estesia mongoliensis* “shifted back” to the Monstersauria, possibly due to the extra steps of reversals required if *Estesia mongoliensis* remained within the Varaniformes.

In addition to expanded taxon sampling, we added eight new morphological characters based on the observations in this study; we also updated the characters codings for *Gobiderma pulchrum* based on the recent work by Conrad et al. (2011b). *Gobiderma pulchrum* has been assigned to different positions in the anguimorph phylogeny by different authors. When first reported by Borsuk-Bialynicka (1984), *Gobiderma pulchrum* was considered as a “necrosaurian grade” anguimorph lizard, convergent with Helodermatidae. Pregill et al. (1986) argued that it should be more closely related to *Xenosaurus*. Conrad et al. (2011b) provided detailed descriptions on the morphology of *Gobiderma pulchrum* based on new specimens, supporting the monstersaurian affinity of this taxon. Updating character codings for *Gobiderma pulchrum* not only augmented information for this particular taxon, but also changed optimizations of “*Heloderma*-like” characters in the anguimorph tree. Finally, the current data matrix included molecular characters to further explore the possible phylogenetic positions for *Estesia mongoliensis* within a total evidence framework.

The morphology-only and combined analysis supported *Estesia mongoliensis* as a basal monstersaur. The strict consensus tree of the combined analysis recovered 34 unambiguous morphological synapomorphies for the Monstersauria (appendix 5).

INGROUP RELATIONSHIPS OF THE MONSTERSAURIA

The strict consensus trees of the morphology-only (fig. 10) and combined analysis (fig. 9) both support *Heloderma texana* as the sister group to the two extant *Heloderma* species. The morphological tree further recovers a monophyletic group consisting of *Eurheloderma gallicum*, *Lowesaurus matthewi*, *Paraderma bogerti*, and UF 206579. The ingroup relation-

ships of the Monstersauria, shown in both strict consensus trees, suggest a complex biogeographic history of the group. First, in the Late Cretaceous, the two Asian species (*Gobiderma pulchrum* and *Estesia mongoliensis*) do not form a monophyletic clade; neither do the three North American species (*Primaderma nessovi*, *Paraderma bogerti*, and *Palaeosaniwa canadensis*). Second, among the Cenozoic North American taxa, only *Heloderma texana* is closely related to the extant species; the other two taxa (*Lowesaurus matthewi* and UF 206579) are probably more closely related to the European taxon *Eurheloderma gallicum* and the Late Cretaceous North American taxon *Paraderma bogerti*, according to the morphology-only analysis. Inferring from the morphological consensus tree, extant monstersaurs are most closely related to North America fossil taxa, and the European taxon *Eurheloderma gallicum* likely dispersed from North America. Tracing back the evolutionary history to the Mesozoic, the geographic region for the origin of the Monstersauria remains unclear due to the uncertainty in the phylogenetic relationships between basal taxa. However, monstersaurs clearly had a cosmopolitan distribution across Laurasia in the Cretaceous. The available fossil record shows that Asian monstersaurs became extinct after the Cretaceous, and the current phylogeny indicates no dispersal event out of Asia.

CHARACTER EVOLUTION OF VENOM-RELATED TOOTH SPECIALIZATIONS IN THE ANGUIMORPHA

Lizards are traditionally considered as nonvenomous except for extant *Heloderma*. Discoveries of fossil monstersaurs reveal that the origin of the lizard venom system possibly dates back to the Cretaceous (Norell et al., 1992; Norell and Gao, 1997; Balsai, 2001). Recent biochemical studies (Fry et al., 2006, 2012) show intriguing results that *Varanus* and some iguanids share several toxin proteins with snakes. This suggests that the evolution of a venom system in lizards has a longer and more complex evolution history than previously considered, and fossils are essential for illustrating this history. Since venom glands and toxin proteins are rarely preserved in fossils, morphological characters of venom delivery (tooth characters), when used with caution, are a reliable source of data for inferring whether a fossil was venomous. We suggest the incorporation of phylogenetic information when inferring venom use in fossils. A morphological character can be used as an indicator for venom use in fossils when all the following criteria are met: (1) the fossil and extant species are included in a monophyletic group; (2) the venom-related character is a synapomorphy of the monophyletic group including the fossil and extant taxa; (3) in the monophyletic group, the venom-related morphology is associated with venom use in all extant taxa that are venomous.

Two tooth characters have been used to indicate venom use in anguimorph lizards: deep root-to-tip venom grooves and serrations on the tooth carina. In the Anguimorpha, venom grooves are present only in monstersaurs and are connected with the specialized venom gland in extant species. Serrated teeth have recently been suggested as an aid for venom delivery in *Varanus komodoensis*, and are used as a morphological evidence for venom use in the fossil *Varanus priscus*, the largest known terrestrial lizard (Fry et al., 2012). However, the distribution

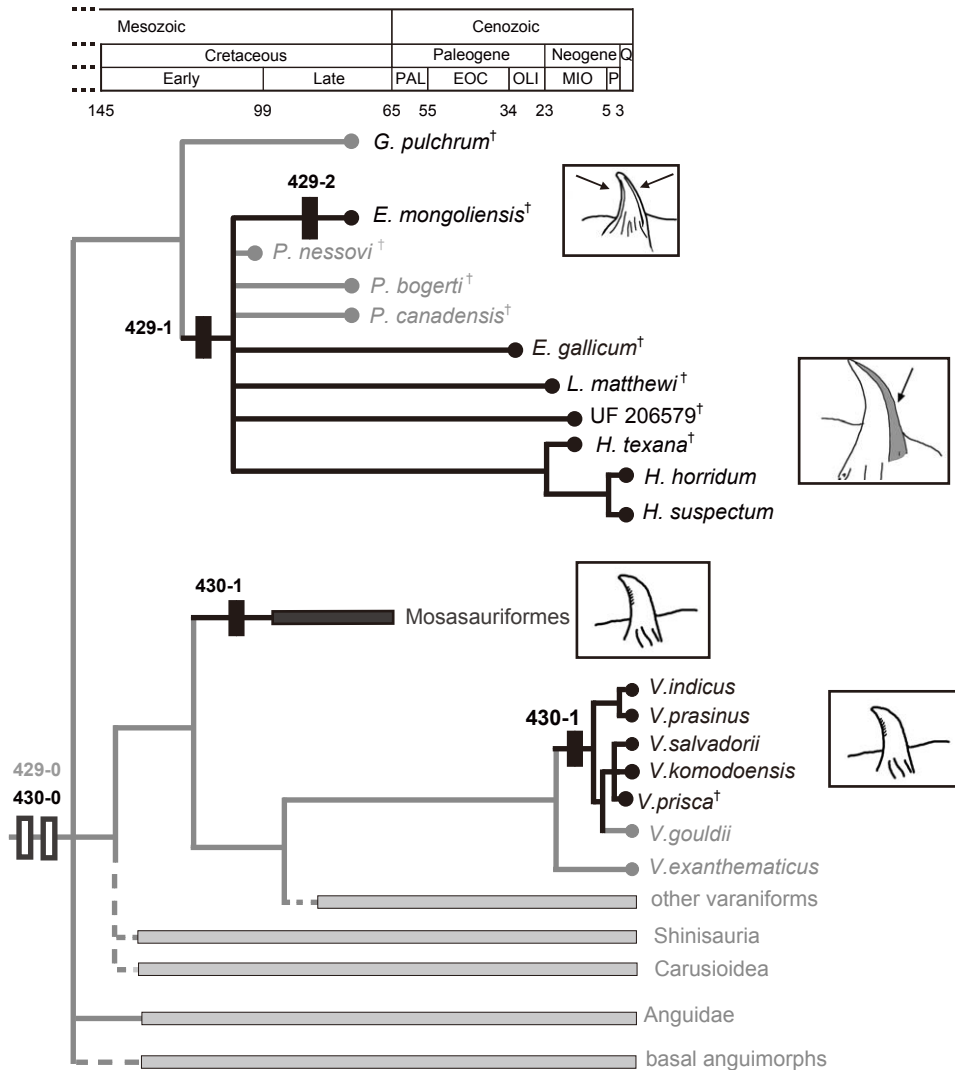


FIGURE 11. Character evolution of tooth specializations in the Anguimorpha. The labels on the branches indicate the origination of derived states as optimized on the tree (ACCTRAN optimization). Clades in black are those with specializations (derived states) on the marginal teeth. Clades in gray are those that show the plesiomorphic state of the corresponding characters: Character 429 – root-to-tip grooves in marginal teeth: (0) absent; (1) present, at anterior carina; (2) present, at anterior and posterior carinae. Character 430 – serrations on marginal teeth: (0) absent; (1) present.

of tooth serrations in the Anguimorpha is yet to be fully sampled. We included the above two characters in our analyses of anguimorph phylogeny (fig. 11). Optimization of the two characters on the strict consensus tree of the combined analysis shows that base-to-tip groove originated once in the Monstersauria, whereas tooth serrations originated twice, independently in *Varanus* and the Mosasauria.

In the anguimorph phylogeny (fig. 11), the Monstersauria is monophyletic and *Estesia mongoliensis* falls within a clade including *Heloderma*. Root-to-tip tooth grooves are clearly used for venom delivery in extant *Heloderma*. As a result, we propose that *Estesia mongoliensis* has a venom system comparable to extant taxa.

Presence of serrated teeth in *Varanus* is a weakly supported indication for venom use in fossil taxa. Fry et al. (2006) suggested the Komodo dragon (*Varanus komodoensis*) is venomous, with oral glands secreting “venom proteins” that are also found in some snakes. A following paper by Fry et al. (2009) tied the shearing effect of tooth serrations (fig. 7D) to venom distribution during predation in *Varanus komodoensis*, and further suggested the Pleistocene fossil *Varanus priscus* (with serrated teeth) was venomous. It is noteworthy, however, although *Varanus priscus* and *Varanus komodoensis* both fall within a *Varanus* subclade in our anguimorph phylogeny (fig. 11), not every extant species of this clade bears serrated teeth. *Varanus gouldii* is a medium-sized carnivorous lizard lacking serrated teeth, as does *Varanus exanthematicus*. The genus *Varanus* has more than 80 extant species, only four of which are documented to have protein-secreting oral glands (“venom glands” of Fry et al., 2012). Whether protein-secreting oral glands are present in the *Varanus* species without serrated teeth is yet to be studied. In addition, the anguimorph phylogeny (fig. 11) shows that serrated teeth originated twice in the Anguimorpha, once in *Varanus* and once in the Mosasauria (fig. 7C). The Mosasauria is an extinct anguimorph lineage with no other morphological indication for venom use. Finally, serrated teeth are widely distributed in non-venomous reptiles, especially among large predators (crocodylians and dinosaurs), casting doubt on the direct relationship between serrated teeth and venom use. In summary, the information on the distribution of serrated tooth and protein-secreting oral glands in the Squamata is currently so patchy that using serrated teeth to indicate venom use in squamates remains tentative at best.

CONCLUSION

The current phylogeny supports the Monstersauria as a monophyletic anguimorph clade, including *Estesia mongoliensis* as a basal member. Presence of tooth flanges developed with venom grooves is recognized as a new monstersaurian synapomorphy in this study. *Estesia mongoliensis* has venom grooves comparable to extant *Heloderma*, but has the deeper root-to-tip groove in the caudal tooth carina, revealing morphological variations of lizard venom-delivery apparatus that are not recorded in extant species. Tracing venom use in fossils can be tough because venom glands hardly fossilize, so tooth characters need to be used with caution. According to morphological and phylogenetic comparisons in anguimorph lizards, more information is needed before considering serrated tooth edge as an indication for venom use in fossil lizards, as it remains unclear for the distribution of this character in fossil and extant clades. On the other hand, a root-to-tip tooth groove is a reliable indication for venom use, as it is phylogenetically conservative with a single origination in the Anguimorpha, and is clearly related to venom delivery in extant species.

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APPENDIX 1

DESCRIPTIONS AND CODINGS OF NEW CHARACTERS

NEW CHARACTERS DEVELOPED IN THIS STUDY: Character 428 to 435 of the morphological matrix are newly developed and coded with direct observations. The characters are listed below with codings for each taxon. Descriptions and codings of all morphological and molecular characters are contained in a NEXUS file provided in appendix 2.

428. Dentition, root-to-tip flanges on anterior and posterior carinae of marginal teeth: (0) absent; (1) present.
429. Dentition, root-to-tip grooves in marginal teeth: (0) absent; (1) present, on anterior carina; (2) present, on anterior and posterior carinae.
430. Dentition: serrated edges on marginal teeth: (0) absent; (1) present.
431. Dentary: length of edentulous posterodorsal rim: (0) short, less than one third the total length of dentary; (1) long, more than one third of the total length of dentary.
432. Premaxilla, mediolateral width of nasal process: (0) broad, height smaller than width, tapering posteriorly; (1) broad, height smaller than width, with posterior tip expanding and forming a fanlike shape; (2) narrow, height larger than width (rodlike).
433. Premaxilla, articulation surface with the nasal: (0) mainly horizontal; (1) mainly vertical, nasals embrace premaxilla in lateral view; (2) nasals lost or greatly reduced.
434. Lateral process of premaxilla at the base of its nasal process: (0) absent; (1) present; (2) extensive, contacting the maxilla.
435. Vomer: medial canals near the anterior tip: (0) absent; (1) present.

<i>Sphenodon punctatus</i>	?0000000
<i>Gephyrosaurus bridensis</i>	?000??0?
<i>Estesia mongoliensis</i>	12010021
<i>Gobiderma pulchrum</i>	?0000?0?
<i>Heloderma suspectum</i>	11000000
<i>Heloderma horridum</i>	11000000
<i>Heloderma texana</i>	?10??0??
<i>Eurheloderma gallicum</i>	?1??????
<i>Lowesaurus matthewi</i>	?1??????
<i>Paraderma bogerti</i>	????????
<i>Primaderma nessovi</i>	101?????
<i>Parviderma inexacta</i>	?0?0????
<i>Palaeosaniwa canadensis</i>	101?????
<i>Parasaniwa wyomingensis</i>	?0??0???

<i>Aspidoscelis tigris</i>	?0000001
<i>Xantusia vigilis</i>	?0002?0?
<i>Eolacerta robusta</i>	?000??0?
<i>Yabeinosaurus tenuis</i>	?00?0?0?
<i>Carusia intermedia</i>	?0000000
<i>Xenosaurus grandis</i>	?0000001
<i>Xenosaurus platyceps</i>	?0??????
<i>Restes rugosus</i>	?0??????
<i>Bahndwivici ammoskius</i>	?0?0000?
<i>Shinisaurus crocodilurus</i>	?0001001
<i>Merkurosaurus omatus</i>	?000000?
<i>Dalinghosaurus longidigitus</i>	?0000000
<i>Saniwa feisti</i>	????0???
<i>Necrosaurus cayluxi</i>	?0??????
<i>Necrosaurus eucarinatus</i>	?0??????
<i>Proplatynotia longirostrata</i>	?0?0000?
<i>Paravaranus angustifrons</i>	?0??????
<i>Saniwides mongoliensis</i>	?0?02???
<i>Cherminotus longifrons</i>	?0?0200?
<i>Lanthanotus borneensis</i>	?0?00000
<i>Ovoo gurvel</i>	?00??000
<i>Aiolosaurus oriens</i>	?0?02?0?
<i>Telmasaurus grangeri</i>	?00?????
<i>Abronia deppii</i>	????????
<i>Abronia oaxacae</i>	?00000?1
<i>Anguis fragilis</i>	?000??0{01}
<i>Anniella pulchra</i>	??00100?
<i>Apodosauriscus minimus</i>	???0????
<i>Barisia imbricata</i>	?0000?01
<i>Celestus costatus</i>	?000??0?
<i>Diploglossus millepunctatus</i>	?0001011
<i>Dopasia harti</i>	?0001000
<i>Elgaria coerulea</i>	????????
<i>Elgaria multicarinata</i>	?0000001
<i>Gerrhonotus liocephalus</i>	?0000?01
<i>Ophisaurus attenuatus</i>	?0??????
<i>Ophisaurus ventralis</i>	?0001?0?
<i>Paragerrhonotus ricardensis</i>	?00?000?
<i>Parophisaurus pawneensis</i>	?000??0?
<i>Proglyptosaurus huerfanensis</i>	?00?0?01
<i>Ophisauriscus quadrupes</i>	????????

<i>Pseudopus apodus</i>	?000001
<i>Arpadosaurus gazinorum</i>	?0?????
<i>Glyptosaurus sylvestris</i>	?0?0????
<i>Helodermoides tuberculatus</i>	?0?0??0?
<i>Melanosaurus maximus</i>	?0?0??0?
<i>Odaxosaurus piger</i>	?00?????
<i>Paraglyptosaurus</i>	?001????
<i>Paraplacosauriops quercy</i>	?00?????
<i>Peltosaurus granulatus</i>	?000??0?
<i>Proxestops jepseni</i>	?00?????
<i>Xestops vagans</i>	?000????
<i>Dorsetisaurus purbeckensis</i>	?0??????
<i>Eosaniwa koehni</i>	?0?0????
<i>Dolichosaurus longicollis</i>	????????
<i>Adriosaurus suessi</i>	?0??????
<i>Aigialosaurus dalmaticus</i>	????????
<i>Tethysaurus nopcsai</i>	?0?02?0?
<i>Russellosaurus coheni</i>	?0??????
<i>Halisaurus arambougi</i>	?0?002??
<i>Mosasaurus</i>	?0{01}0220?
<i>Clidastes</i>	?0{01}022??
<i>Tylosaurus</i>	?01022??
<i>Saniwa ensidens</i>	????0???
<i>Varanus exanthematicus</i>	?0002?01
<i>Varanus gouldii</i>	?0002101
<i>Varanus indicus</i>	?0100001
<i>Varanus komodoensis</i>	?0102101
<i>Varanus prasinus</i>	??100101
<i>Varanus prisca</i>	?01?????
<i>Varanus salvadorii</i>	?0102101
UF 206579	?100????

APPENDIX 2

DATA MATRICES USED IN THIS STUDY

DATA MATRIX FOR THE COMBINED ANALYSIS: This nexus file includes 86 taxa coded to 435 morphological characters and four genes. The entire NEXUS file has been uploaded to TreeBASE (www.treebase.org); the TreeBASE datasets of this study are available online (<http://purl.org/phylo/treebase/phyloids/study/TB2:S12642>). The submitted version in TreeBASE includes codings for all morphological and molecular characters. Descriptions of all morphological characters are also included. Readers can view and download the whole matrix, morphological-only matrix, or molecular-only matrix from TreeBASE. The two strict consensus trees of this study are also included in the TreeBASE record as separate tree files.

ABBREVIATIONS USED IN CHARACTER DESCRIPTIONS: CMAN, the character is from Conrad et al. (2011a); GN, the character is from Gao and Norell (1998); BS, the character is from Bhullar and Smith (2008).

APPENDIX 3

SPECIMENS OF EXTANT SPECIES USED FOR CODING MORPHOLOGY

The following specimens are collections of American Museum of Natural History, New York, with specimen numbers that take the format AMNH R-0000. The institutional part of the following specimen numbers is omitted. *Abronia oaxacae* (R-93208); *Anguis fragilis* (R-154688); *Anniella pulchra* (R-1141112); *Barisia imbricata* (R-590); *Celestus costatus* (R-72358); *Diploglossus millepunctatus* (R-63557); *Gerrhonotus liocephalus* (R-106732); *Heloderma suspectum* (R-147173, R-71082); *Heloderma horridum* (R-154742); *Lanthanotus borneensis* (R-113983); *Ophisaurus ventralis* (R-57871); *Pseudopus apodus* (R-57958); *Shinisaurus crocodilurus* (R-44928); *Varanus exanthematicus* (R-140804); *Varanus gouldii* (R-82819); *Varanus indicus* (R-88066, R-142623); *Varanus komodoensis* (R-37909); *Varanus prasinus* (R-104683); *Varanus salvadorii* (R-59873); *Xenosaurus grandis* (R-19380).

APPENDIX 4

GENBANK ACCESSION NUMBERS USED IN THIS STUDY

RAG-1 (partial CDs, ~2800 bps): *Sphenodon punctatus* (AY662576); *Heloderma suspectum* (AY662606); *Aspidoscelis tigris* (AY662620); *Xantusia vigilis* (AY662642); *Xenosaurus grandis* (AY662607); *Shinisaurus crocodilurus* (AY662610); *Lanthanotus borneensis* (AY662609); *Anniella pulchra* (AY662605); *Ophisaurus attenuatus* (AY662602).

BDNF (partial CDs, ~670 bps): *Sphenodon punctatus* (GU457846); *Heloderma suspectum* (GU457856); *Heloderma horridum* (GU457855); *Aspidoscelis tigris* (EU402619); *Xantusia vigilis* (EU402620); *Shinisaurus crocodilurus* (GU457857); *Lanthanotus borneensis* (GU457859); *Anni-*

ella pulchra (GU457852); *Elgaria multicarinata* (GU457854); *Pseudopus apodus* (GU457851); *Varanus exanthematicus* (GU457861).

ND1 (complete CDs, ~968 bps): *Sphenodon punctatus* (NC_004815); *Heloderma suspectum* (AF407540); *Heloderma horridum* (AF407539); *Aspidoscelis tigris* (HM160771); *Xantusia vigilis* (HM160864); *Lanthanotus borneensis* (AF407541); *Anguis fragilis* (AF407536); *Anniella pulchra* (AF407537); *Ophisaurus attenuatus* (EU747729); *Varanus exanthematicus* (AF407496); *Varanus gouldii* (AF407502); *Varanus indicus* (AF407505); *Varanus komodoensis* (AF407510); *Varanus prasinus* (AF407519).

ND2 (complete CDs, ~1037 bps): *Sphenodon punctatus* (AY662533); *Heloderma suspectum* (AF407540); *Heloderma horridum* (AF407539); *Aspidoscelis tigris* (CTU71332); *Xantusia vigilis* (EU130271); *Xenosaurus grandis* (XGU71333); *Shinisaurus crocodilurus* (AF085604); *Lanthanotus borneensis* (AY662537); *Abronia oaxacae* (AF085615); *Anguis fragilis* (AF085622); *Anniella pulchra* (AF085606); *Barisia imbricata* (AF085613); *Elgaria multicarinata* (AF085620); *Gerrhonotus liocephalus* (AF085614); *Ophisaurus attenuatus* (AF085625); *Ophisaurus ventralis* (AF085626); *Pseudopus apodus* (AF085623); *Varanus exanthematicus* (AF407496); *Varanus gouldii* (AF407502); *Varanus indicus* (AF407505); *Varanus komodoensis* (AF407510); *Varanus prasinus* (AF407519).

APPENDIX 5

SYNAPOMORPHIES OF THE MONSTERSAURIA

According to the strict consensus tree of the combined analysis, the following 34 character states unambiguously support the monophyly of the Monstersauria ([character no.]-[state no.]):

The part of rostrum anterior to the septomaxilla is four tooth positions long or more (2-1); pitted dermal sculpturing (7-1); maxillae has strong medial processes behind the nasal process of the premaxilla, and separation of the two medial processes are subequal to the breadth of the nasal process of the premaxilla (24-1); posterior extent of maxillary tooth row terminates at anterior border of orbit (31-1); jugal runs mostly dorsally to maxilla (50-1); dorsal margin of the supratemporal process of the parietal is broad and flat (79-1); vomer is rodlike in shape (105-1); length of palatine equals as width (108-1); length of palatine is about two thirds the length of vomer (109-1); ectopterygoid is exposed behind maxilla in lateral view (123-1); fenestra ovalis locates anterior to the spheno-occipital tubercle in the braincase (126-1); the long axis of dentary is ventrally convex (175-0); subdental shelf of the dentary is absent (179-1); dentary contributes to dorsal border of the anterior inferior alveolar foramen (180-1); dentary has a small posterodorsal coronoid process(es) (181-2); the subcoronoid and surangular processes of the dentary are absent (182-0); splenial, anteromedial walling of Meckel's canal extends for less than one half of the dentary (186-0); posterior extent of the splenial terminates at or anterior to the coronoid apex (187-1); height of coronoid process is short and broad relative to the length of the mandible (189-0); anterior end of the coronoid butts against the dentary (191-1); coronoid has a long and low anterior process (193-1); anterior border of surangular, when disarticulated, expands anterodorsally with vertical anterior margin (197-1); marginal teeth are

widely separated with spaces between tooth bases greater than one half the width of a tooth shaft (208-1); marginal teeth are trenchant and curved (209-2); posterior marginal tooth implantation is modified pleurodont (211-2); marginal teeth have expanded bases with main tooth shafts somewhat separated (214-1); plicidentine is present in marginal teeth (215-1); replacement teeth develop posterolingually to the functional teeth with no resorption pit (217-2); length of the symphyseal portion of the pubis is subequal to or slightly longer than the tubercular portion (281-1); osteoderms are thickened as polygonal mounds (306-2); zygomatic arch alignment is bowed laterally (369-1); a fossa is present on the narial floor of the maxilla anterior to the level of the septomaxilla (378-1); surangular extends well beyond the coronoid eminence anteriorly (420-2); maxillary tooth number is between 10 and 13 (422-1).

APPENDIX 6

ANATOMICAL ABBREVIATIONS USED IN FIGURES

ar	articular
bs	basisphenoid
d	dentary
etp	ectopterygoid
j	jugal
l	lacrimal
Lc	left coronoid
Lpra	left prearticular
Lq	left quadrate
Lsa	left surangular
m	maxilla
pl	palatine
pf	prefrontal
pm	premaxilla
pt	pterygoid
Rc	right coronoid
spm	septomaxilla
v	vomer

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