Supporting Information Corrected March 15, 2013

# ONLINE SUPPLEMENTARY MATERIAL 1

## Contents

# 1. Faunal List, Upper Maastrichtian of Western North America

Based on literature (1-6) and museum specimens (see SI 3 for complete references and specimen numbers) . Species in bold are either named or recognized here for the first time.

Table S1.

IGUANIA
- Iguanidae incertae sedis
  - ***Pariguana lancensis***

POLYGLYPHANODONTIA
- Polyglyphanodontia incertae sedis
  - ***Obamadon gracilis***

- Polyglyphanodontidae
  - *Polyglyphanodon sternbergi*

- Chamopsiidae
  - *Chamops segnis*
  - *Leptochamops denticulatus*
  - *Meniscognathus altmani*
  - *Haptosphenus placodon*
  - *Stypodontosaurus melletes*
  - ***Tripennaculus* n. sp.**
  - **Frenchman chamopsiid**
  - *Peneteius aquilonius*
  - ***Socognathus brachyodon***
  - **Laramie chamopsiid**

SCINCOMORPHA
- Scincomorpha incertae sedis
  - ***Lonchisaurus trichurus***

- Scincoidea incertae sedis
  - *Estescincosaurus cooki*

- Globauridae
  - *Contogenys sloani*

ANGUIMORPHA
- Xenosauridae

- *Exostinus lancensis*

Anguidae
- *Odaxosaurus piger*
- “*Gerrhonotus*” sp.

Platynota incertae sedis
- *Litakis gilmorei*
- *Colpodontosaurus cracens*
- *Palaeosaniwa* sp.
- *Paraderma bogerti*
- ***Cemeterius monstrosus***
- *Parasaniwa wyomingensis*

OPHIDIA

Coniophidae
- *Coniophis precedens*

Alethinophidia incertae sedis
- ***Cerberophis rex***
- **Lance Snake**

SQUAMATA INCERTAE SEDIS
- ***Lamiasaura ferox***
- **Sweetwater County lizard**

## 2. Stratigraphy

### A. Maastrichtian

The Cretaceous lizards included in this study come from the Hell Creek Formation of Montana, the Lance and Ferris formations of Wyoming, the Frenchman Formation of Saskatchewan, the Scollard Formation of Alberta, the Laramie Formation of Colorado, and the North Horn Formation of Utah. All formations are inferred to be late Maastrichtian in age and contain typical late Maastrichtian faunas (i.e., Lancian Land Vertebrate Age). Age constraint (Table S2) is based on several lines of evidence, including radiometric dating, magnetostratigraphy, palynostratigraphy, and vertebrate biostratigraphy, which is primarily based on mammalian faunas.

#### i. Frenchman Formation

The entire Frenchman Formation is constrained on the basis of magnetostratigraphy to the final reversed interval of the Cretaceous, C29r (7), which spans the final 300,000 years of the Cretaceous (8) and so the Frenchman lizards are no older than 300,000 years. It is unclear where the Gryde locality (which produced the Frenchman lizards discussed here) lies in section, but it lies 20 meters up the exposed outcrop, and the entire formation is a little more than 50 meters thick in this area (9). This suggests that the Gryde lizards date to significantly less than 300,000 years before the K-Pg boundary.

#### ii. Lance Formation

There are fewer constraints on the age of the Lance Formation in eastern Wyoming because no radiometric dates or magnetostratigraphic studies have been published. Here, the K-Pg claystone occurs just below the basal lignite in the Fort Union Formation, at the very top of the Lance Formation; it displays the signature features of the Chicxulub impact, including an iridium anomaly, a layer of spherules, shock-metamorphosed mineral grains, and the abrupt disappearance of many pollen species, followed by the appearance of a layer rich in fern spores (10). In this area, the Lance Formation is roughly 2,500 feet thick, and UCMP V5620 (Lull 2) lies 2,100 feet above the base of the Lance, and UCMP V5711 (Bushy Tailed Blowout) lies in the top half of the formation (11). Based on some assumptions that are admittedly simplistic, i.e. that the Lance was deposited at a constant rate over the final 1.3 Ma of the Cretaceous, as found for the Hell Creek Formation of North Dakota (8), this would indicate ages of ~200,000 and >650,000 years before the K-Pg boundary for UCMP V5620 and UCMP V5711, respectively. The occurrence of the marsupial *Glasbius* in both sites, a genus that appears between 900,000 and 600,000 years before the K-T boundary in Montana (12) also supports a latest Maastrichtian age, assuming that the introduction of *Glasbius* occured more or less simultaneously across the region. Palynostratigraphic studies of this area (13) also show that UCMP V5620 lies well above the first occurrence of pollen species that occur in the Latest Cretaceous in North Dakota. These are *Striatopollis tectatus* and *Liliacidites altmurus*. In the Hell Creek Formation, these species appears about 40 meters below the boundary (14), which would correspond 500,000 years before the K-Pg boundary (8). Again, assuming that they appeared simultaneously across the region, then this would support a latest Maastrichtian age for the lizards occurring in the Lull 2 locality.

The same assumptions regarding stratigraphy would suggest an age of ~200,000 years before the K-Pg boundary for the Black Butte assemblage in Sweetwater County, southern Wyoming (UW V-79032) which lies 33 meters below the K-T transition in a 233 meter section (15).

### iii. Hell Creek Formation

The Hell Creek of Garfield/McCone Counties in Montana spans the final 1.8 million years of the Cretaceous (12); unfortunately no published stratigraphic data are available for the localities that produced the lizards described here. No stratigraphic data are available for the lizards from Carter County and Dawson County, Montana, but similar ages are assumed here.

### iv. Scollard Formation

The Cretaceous portion of the Scollard can be constrained to the final 1.5 million years of the Cretaceous (16).

### v. Laramie Formation

The Laramie site UCM 77062 is the oldest site in this study, dating to 2.5 Ma before the K-T (17).

### vi. North Horn Formation.

The age of the Cretaceous exposures of the North Horn Formation in Utah remains uncertain, but on the basis of the mammal fauna it is assigned to the Late Maastrichtian (18).

### vii. Bighorn Basin Lance

The stratigraphy of the Bighorn Basin sites is not well-known but they contain characteristic 'Lancian' mammals (19) suggesting a Late Maastrichtian age; furthermore the occurrence of *Glasbius* in the Hewitt's Foresight locality (19) supports this assignment.

### viii. Ferris Formation

Finally, the age of the Cretaceous part of the Ferris Formation is not well-constrained, but on the basis of the fauna these assemblages are late Maastrichtian in age (20). The sole lizard reported from the Ferris, *Odaxosaurus*, occurs high in section but given that it crosses the K-Pg boundary, the precise age of this specimen is not an issue.

It should be kept in mind that the the point here is not to make definitive claims about the precise age of last occurrence for each taxon, but rather to emphasize that the fauna described here is as close as one can possibly come to providing a picture of what the squamate fauna looked like just before the K-T impact, within the inevitable constraints imposed by an imprecise understanding of the chronostratigraphy of these formations, and an extremely patchy fossil record. Given that a number of lizard genera appear to have stratigraphic ranges of 10 Ma or more (SI3), it is unlikely that a significant percentage of the species described here became extinct in the hundreds of thousands of years that separate these localities from the K-T boundary, and the various localities can also be assumed to represent, more or less, a picture of a single fauna rather than a succession of faunas.

### B. Paleocene

The ages of the Palaeocene localities are less of an issue: a survivor is a survivor regardless of whether it occurs a few tens of thousands of years after the K-T boundary, or millions of years later. Therefore, for the purposes of inferring survival and for rarefaction, the analysis of Paleocene species lumped together localities from the Puercan and Torrejonian land vertebrate ages, a period spanning some 4 million years (21), because relatively few Puercan localities are known. Inferences of Puercan and Torrejonian age have previously been made on the basis of the co-occurring mammals. Insofar as this lumping of assemblages might tend to bias the study, treating these various assemblages as a single fauna would inflate Paleocene diversity and make the fauna appear more diverse and less well-sampled than it really is. Given that this would bias the study against the conclusion we are investigating (i.e. a major drop in diversity from the Maastrichtian to Palaeocene) we argue that this assumption is conservative.

The Bug Creek fauna, however, is problematic in representing a mixed assemblage (22, 23) containing Palaeocene and reworked Maastrichtian species. For examining Paleaocene diversity, we assumed the Bug Creek lizard fossils were Palaeocene if they were (a) from species known to cross the K-Pg boundary based on undisputed Palaeocene fossils occurring elsewhere, or (b) they represented species entirely unknown from the Maastrichtian. Although it is conceivable that some of these specimens could be reworked from the Maastrichtian, in this case, it would only bias the data against the conclusions of this paper by inflating Paleocene diversity, and in this sense our assumptions are again conservative.

**Table S2.** Stratigraphically highest occurrences for species failing to cross the K-T boundary. Occurrence data: Estes (4); Gao and Fox (6), this study (SI3).

| Taxon | Occurrence | Date |
|---|---|---|
| *Chamops segnis* | Frenchman Fm., SK | ≥300,000 years before K-T |
| *Leptochamops denticulatus* | Frenchman Fm., SK | ≥300,000 years before K-T |
| *Meniscognathus altmani* | Frenchman Fm., SK | ≥300,000 years before K-T |
| *Haptosphenus placodon* | Frenchman Fm., SK | ≥300,000 years before K-T |
| *Tripennaculus* sp. | Frenchman Fm., SK | ≥300,000 years before K-T |
| Frenchman chamopsiid | Frenchman Fm., SK | ≥300,000 years before K-T |
| *Paraderma bogerti* | Frenchman Fm., SK | ≥300,000 years before K-T |
| *Parasaniwa wyomingensis* | Frenchman Fm., SK | ≥300,000 years before K-T |
| *Lamiasaura ferox* | Lance Formation, Sweetwater County, WY | ≥200,000 years before K-T (?) |
| Sweetwater Lizard | Lance Formation, Sweetwater County, WY | ≥200,000 years before K-T (?) |
| *Cemeterius monstrosus* | UCMP V5620, Lance Fm., WY | ≥250,000 years before K-T(?) |
| *Litakis gilmorei* | UCMP V5620, Lance Fm., WY | ≥250,000 years before K-T(?) |
| *Palaeosaniwa canadensis* | UCMP V5620, Lance Fm., WY | ≥250,000 years before K-T(?) |
| *Colpodontosaurus cracens* | UCMP V5620, Lance Fm., WY | ≥250,000 years before K-T(?) |
| *Estescincosaurus cooki* | UCMP V5620, Lance Fm., WY | ≥250,000 years before K-T(?) |
| Lance snake | UCMP V5711, Lance Fm., WY | ≥650,000 years before K-T(?) |
| *Lonchisaurus trichurus* | UCMP V5711, Lance Fm., WY | ≥650,000 years before K-T(?) |
| *Pariguana lancensis* | UCMP V5711, Lance Fm., WY | ≥650,000 years before K-T(?) |
| *Stypodontosaurus melletes* | Scollard Fm., AB | ≥1.5 Ma before K-T |
| *Cerberophis rex* | UCMP V80096, Hell Creek Fm., MT | ≥1.8 Ma before K-T |
| *Obamadon gracilis* | UCMP V74116, Hell Creek Fm., MT | ≥1.8 Ma before K-T |
| *Peneteius aquilonius* | UCMP V74116, Hell Creek Fm., MT | ≥1.8 Ma before K-T |
| Laramie chamopsiid | UCM 77062, Laramie Fm., CO | ~2.5 Ma before K-T |
| *Socognathus brachyodon* | Lance Formation, Park County, WY | Late Maastrichtian |
| *Polyglyphanodon sternbergi* | North Horn Formation, UT | Late Maastrichtian |

# 3. Species Descriptions

**Institutional abbreviations.** AMNH, American Museum of Natural History, New York, New York; UCM, University of Colorado Museum, Boulder, Colorado; UCMP, University of California Museum, Berkeley, California; USNM, Smithsonian Institution National Museum of Natural History, Washington, DC; YPM, Yale Peabody Museum, New Haven, Connecticut; YPM-PU, Yale Peabody Museum, Princeton University collection.

REPTILIA Laurenti, 1768

SQUAMATA Oppel, 1811

IGUANIA Cope 1864

IGUANIDAE Oppel 1811

*Pariguana* new genus

**Etymology.** The genus name is derived from Greek *para*, near, and the genus name *Iguana*.

**Diagnosis.** As for the type and only species.

**Type species.** *Pariguana lancensis*.

*Pariguana lancensis* new species

**Etymology.** The specific name refers to the Lance Formation.

**Diagnosis.** Small iguanid characterized by the following combination of characters: teeth tall, slender, with tapering crowns and weak accessory cusps; coronoid extends forward on lateral surface of jaw beneath last tooth, Meckelian groove constricted suddenly ahead of anterior inferior alveolar foramen.

**Holotype.** AMNH 22208, partial mandible.

**Locality and Horizon.** UCMP V5711, Bushy Tailed Blowout; upper Maastrichtian Lance Formation, Niobrara County, eastern Wyoming.

**Description.** The type and only known specimen consists of the posterior half of a dentary and the associated parts of the splenial, coronoid, and angular. The dentary is weakly bowed in lateral view and extends posteriorly well beyond the toothrow and below the coronoid. In medial view, the Meckelian groove is broad posteriorly, but exhibits a sharp taper just ahead of the anterior inferior alveolar foramen, where the splenial is pinched between the subdental ridge and the ventral margin of the dentary. This distinctive taper distinguishes *Pariguana* from the Paleocene iguanid *Swainiguanoides milleri* (24). The subdental ridge is also flat medially, in contrast to the more rounded subdental ridge of *Swainiguanoides*. The ventral margin of the dentary wraps beneath the splenial, an iguanian synapomorphy. The splenial has a large, elliptical anterior inferior alveolar foramen, and below and slightly behind it a smaller mylohyoid foramen. A long, slender sliver of the angular extends well forward between the splenial and angular. The coronoid extends beneath the subdental ridge medially, and on the lateral surface of the dentary there is a facet where the coronoid would extended onto the dorsolateral surface of the dentary. This anterolateral process of the dentary is a derived feature seen in a number of crown iguanids.

There are 13 tooth positions preserved, and the complete mandible would probably have had between 20 and 30 teeth. Implantation is pleurodont. Several teeth bear large resorption pits at their bases, and four teeth in the back of the jaw are short and implanted at odd angles, a pathology. Tooth crowns are tall and slender, with tapered tips. The tip is tricuspid, with a broad, blunt central cusp flanked by tiny mesial and distal cusps. Medially, the accessory cusps are separated from the central cusp by grooves. The teeth generally resemble those of *Swainiguanoides*, but differ in having a narrower crown.

**Discussion.** *Pariguana* can be referred to the Iguania on the basis of the constriction of the Meckelian groove by the ventral margin of the dentary. *Pariguana* exhibits two features that are found in crown Iguanidae but not among stem Iguanidae from the Cretaceous of Mongolia (e.g. *Temujinia*, *Zapsosaurus*): anterior extension of the coronoid beneath the toothrow on the lateral surface of the jaw, and posterior extension of the dentary beneath the coronoid process. On this basis, *Pariguana* appears to represent either the sister taxon of crown Iguanidae, or a member of the crown; in the present analysis Pariguana is the sister taxon to Hoplocercidae. Given the uncertainty over the relationships of crown iguanids, and the limited material available for Pariguana, this conclusion should be considered tentative. Although *Pariguana* closely resembles the Paleocene *Swainiguanoides milleri*, it differs in the strongly tapering shape of the Meckelian groove, the flat subdental ridge, and in having more strongly tapered tooth crowns.

The earliest and most primitive known iguanids and acrodonts are Asian, suggesting that the Iguania originated in Asia and later migrated into North America (25). Until now, the earliest known iguanids were Paleocene, which suggested that this migration occurred in the Palaeocene (25) the presence of *Pariguana* in the Maastrichtian of North America shows that this immigration event had occurred prior to the end of the Cretaceous. The end-Cretaceous mass extinction appears to have eliminated the Asian iguanids, but spared the North American lineage, leading to a North American radiation of iguanids in the Palaeogene.

Although Gao and Fox (6) identify several Cretaceous lizards as iguanids, these specimens do not exhibit any derived features that allow confident referral to either Iguania or Iguanidae. In particular, the Maastrichtian fossils they refer to Iguanidae can be referred to *Tripennaculus*, an unusual polyglyphanodontian with strongly tricuspid teeth (26); the others appear to represent polyglyphanodontians as well. Accordingly, *Pariguana* represents the earliest definitive evidence of Iguanidae in North America.

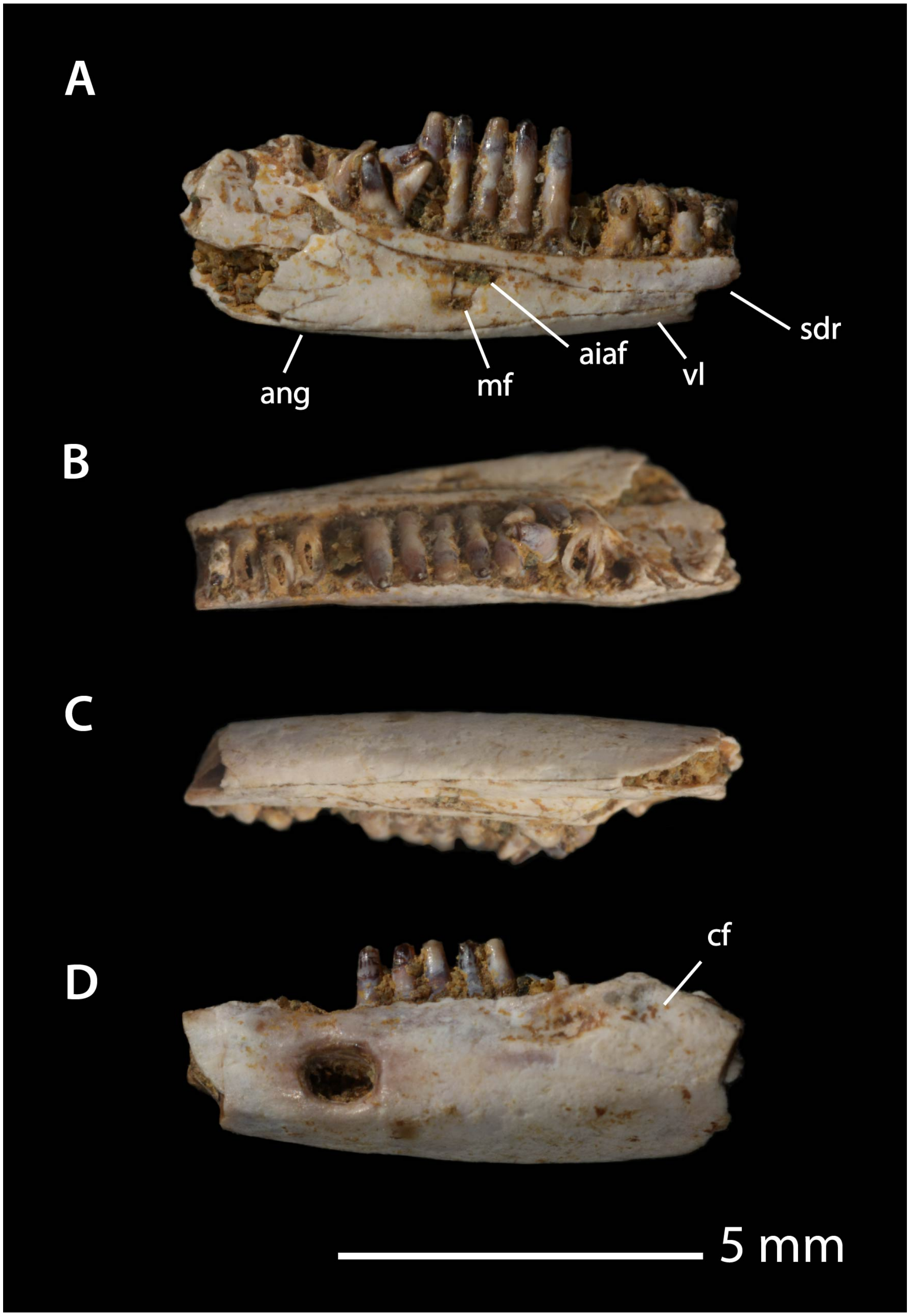


**Fig. S1.** *Pariguana lancensis* n. gen et sp., AMNH 22208 left dentary. In **A**, medial view; **B**, dorsal view; **C**, ventral view, **D**, lateral view. Abbreviations: aiaf, anterior inferior alveolar foramen; cf, coronoid facet; mf, mylohyoid foramen; sdr, subdental ridge; vl, ventral lip of dentary.

## POLYGLYPHANODONTIA Alifanov 2000

**Definition.** *Polyglyphanodon sternbergi* and all species closer to *Polyglyphanodon sternbergi* than to any extant species. This taxon includes Borioteiioidea as defined by Nydam et al. (27). However, Borioteiioidea is a node-based taxon, whereas Polygyphanodontia is a stem-based taxon, and would therefore include any species which were found to lie along the stem of Borioteiioidea.

## POLYGLYPHANODONTIA INCERTAE SEDIS

### *Obamadon* new genus

**Etymology.** The genus name refers to Barack Hussein Obama and *odon* (Greek) = tooth, in reference to the tall, straight teeth, and the manner in which Mr. Obama has acted as a role model of good oral hygiene for the world.

**Diagnosis.** As for the type and only species.

**Type species.** *Obamadon gracilis*.

### *Obamadon gracilis* new species

**Etymology.** From the Latin *gracilis*, slender.

**Diagnosis.** Small polyglyphanodontian characterized by the following combination of characters: dentary slender, symphysis weakly developed, tooth implantation subpleurodont, teeth lack basal expansion, tooth crowns with a tall central cusp separated from accessory cusps by deep lingual grooves.

**Holotype.** UCMP 128873, right dentary.

**Referred Material.** UW 44954, partial dentary.

**Locality and Horizon.** Holotype: UCMP V 74116, Baldy Butte; upper Maastrichtian Hell Creek Formation, Garfield County, Montana. Referred specimen: UW 81013, Hewitt's Foresight One, upper Maastrichtian Lance Formation, Bighorn Basin, Park County, Wyoming.

**Description.** The holotype consists of a partial dentary with five teeth, missing the posterior end. The dentary is relatively long and slender in lateral view when compared to the deep dentary seen in most polyglyphanodontians. The dorsal margin is straight in lateral view, in contrast it is curved in many other polyglyphanodontians (e.g. *Leptochamops denticulatus* and *Socognathus unicuspis*).

The dentary bears a large mental foramen at its tip, and at least seven smaller foramina on its lateral surface. The dentary symphysis is typical of polyglyphanodontians in being V-shaped, but the symphysis is small and weakly developed, a primitive feature. The symphysis is weakly angled relative to the jaw, such that the left and right dentaries would have diverged at an angle of approximately 60º.

The Meckelian canal is deep and broad except at the tip of the jaw, where it is constricted by the subdental ridge. The subdental ridge is narrow posteriorly, becomes deep as it approaches the fourth tooth position, and then tapers again towards the tip of the jaw. The subdental ridge projects dorsally to form a low, narrow subdental shelf. The ventral surface of the subdental ridge bears a distinctive slot-and-ridge articulation for the splenial, with a distinct slot on the subdental ridge to receive the dorsal margin of the splenial, and a low ridge medial to the slot that would have inserted into a V-shaped groove on top of the splenial. This configuration is a derived feature of polyglyphanodontians (e.g., *Chamops segnis*, *Socognathus brachyodon*).

There are five teeth preserved in the jaw with perhaps 15 or 16 tooth positions. The back of the dentary is missing, but the total tooth count was likely between 20 and 25. Teeth implant in a subpleurodont fashion, extending less than halfway down the medial surface of the mandible. In this respect, *Obamadon* is comparable to *Meniscognathus* and *Leptochamops*, but more primitive than advanced chamopsiids such as *Chamops* and *Socognathus*. Teeth are secured to the jaw with a strong basal deposition of cementum. In contrast to most other polyglyphanodontians, there are multiple open tooth positions, suggesting ongoing tooth replacement. This may represent a primitive feature of *Obamadon*, or it could be that the animal was still actively growing and had not yet received the adult set of teeth. No replacement pits are visible in any of the implanted teeth.

The tooth crowns themselves are columnar. In contrast to chamopsiids, the bases of the crowns are only slightly wider than the tips. In this respect, the teeth resemble those of *Tripennaculus eatoni* (26). Teeth are strongly tricuspid. There is a tall, conical central cusp, which is very slightly recurved; it is separated from small, low mesial and distal cusps by deep grooves on the lingual surface of the tooth. Here again, the teeth closely resembles *Tripennaculus*. However, *Tripennaculus* is distinguished by taller mesial and distal cusps, which bear ridges that extend down the inside of the tooth as distinct blades. *Tripennaculus* is also distinguished by closely packed, posteriorly curved tooth crowns.

**Discussion.** *Obamadon* is identified as a polyglyphanodontian on the basis of the V-shaped dentary symphysis, interlocking slot-and-ridge articulation for the splenial, and subpleurodont tooth implantation. Although this specimen has previously been referred to *Leptochamops* (28) it is clearly more primitive than *Leptochamops* and other taxa referred to the Chamopsiidae in the weak development of the dentary symphysis and the lack of barrel-shaped tooth crowns. The current analysis places *Obamadon* near the base of the Polyglyphanodontia, although it is possible that it represents a basal chamopsiid. The well-developed tricuspid teeth, grooves on the teeth, and lack of barrel-shaped tooth crowns all suggest affinities with *Tripennaculus*, although the short, straight teeth and small accessory cusps preclude referral to that genus.

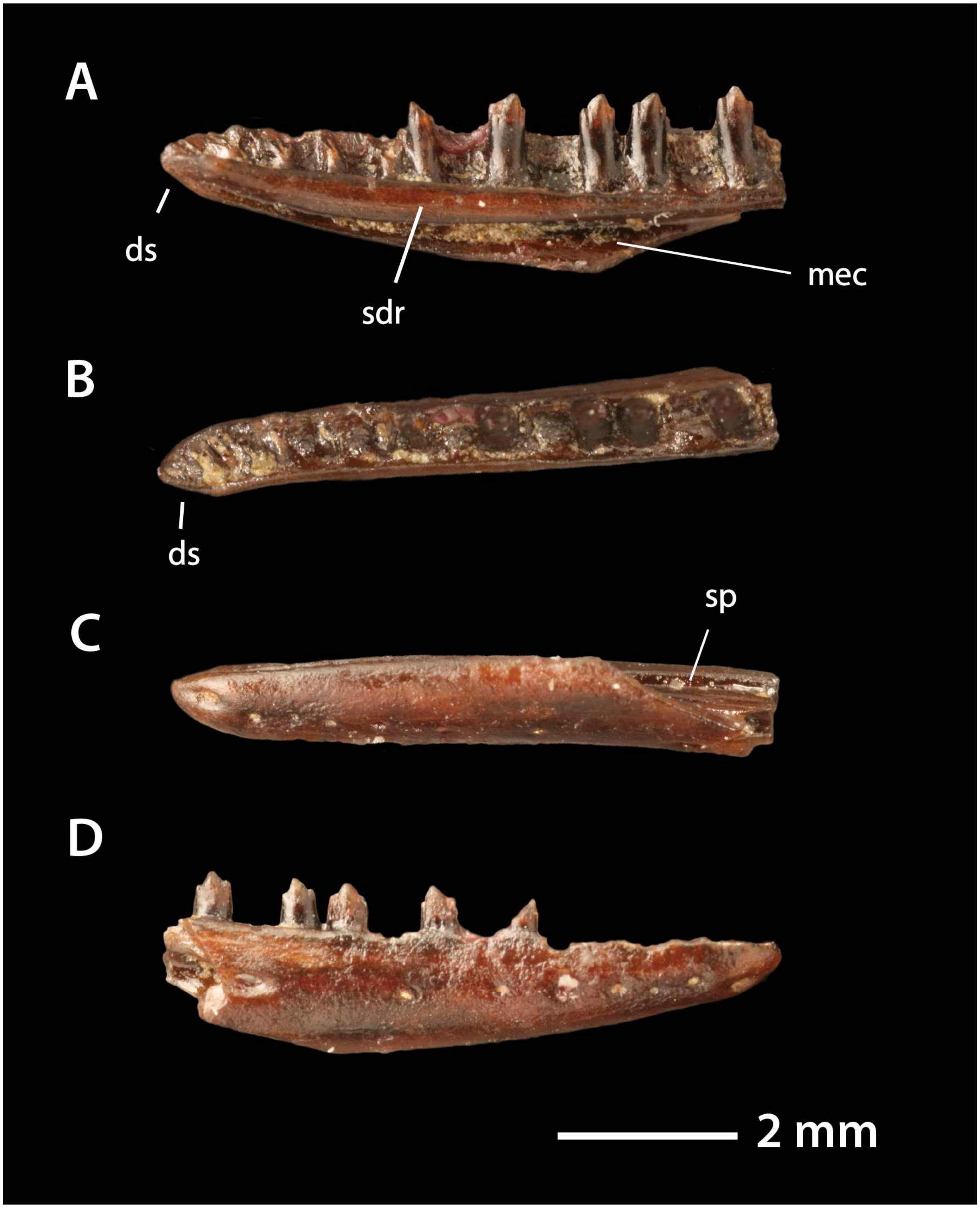


**Fig. S2.** *Obamadon gracilis* n. gen et sp. (Polyglyphanodontia) left dentary. In **A**, medial view; **B**, dorsal view; **C**, ventral view, **D**, lateral view. Abbreviations: ds, dentary symphysis; mec, Meckelian fossa; sdr, subdental ridge; sp, splenial contact.

## CHAMOPSIIDAE Denton and O'Neill 1995

**Definition.** *Chamops segnis* and all species closer to *Chamops segnis* than to *Polyglyphanodon sternbergi*.

Denton and O'Neill (29) defined Chamopsiinae as the node-based taxon containing *Chamops segnis*, *Prototeius stageri*, *Leptochamops denticulatus*, and *Meniscognathus altmani*, but the published phylogenetic analysis only included *Prototeius* and *Chamops*. Nydam et al. (30) later raised the Chamopsiinae to family rank. They also questioned whether *Prototeius* is closely related to *Chamops*, and so the monophyly of the Chamopsiinae as originally defined remains an open question. Nydam et al.'s redefinition of Chamopsiinae includes a list of species, but not a formal definition. The current study did find that the North American taxa form a clade, but the affinities of *Prototeius* are beyond the scope of this analysis, and given that its relationships remain unclear, a new stem-based definition for the name is proposed here that largely conforms to the original intent of Denton and O'Neill while remaining robust against changes in tree topology.

## *Socognathus* Gao and Fox 1996

**Revised Diagnosis.** Polyglyphanodontian characterized by the following combination of characters: long, straight dentary that is dorsoventrally shallow and labiolingually expanded, massive dentary symphysis, short, robust crowns with reduced mesial and distal cusps.

**Type species.** *Socognathus unicuspis* Gao and Fox 1996

## *Socognathus brachyodon* new species

**Etymology.** Greek *brachy*, short, and *odon*, tooth.

**Diagnosis.** *Socognathus* with posterior teeth having strongly swollen, weakly tricuspid crowns.

**Holotype.** YPM PU 16724, dentary (Fig. S2)

**Referred Specimens**. YPM-PU 21375, dentary.

**Locality and Horizon.** Polecat Bench, Sec. 31, T57N, R98W; Late Maastrichtian Lance Formation, Bighorn Basin, Park County, Wyoming.

**Description.** The holotype of *Socognathus brachyodon* (YPM-PU 16724) consists of a virtually complete dentary with all teeth preserved (Fig. S1). The dentary is relatively large, being 21 mm in length. As with *Socognathus unicuspis* (6), the jaw is relatively long, straight and shallow in lateral view; the dentary's depth at midpoint is about 20% of its length. *S. brachyodon* also resembles *S. unicuspis* in having a robust mandible; the lateral surface of the dentary is strongly convex and projects laterally well beyond the toothrow. Half a dozen small mental foramina are present on the lateral surface of the mandible.

Medially, the symphysis is well-developed. It is V-shaped with facets extending above and below the Meckelian canal, a derived feature of polyglyphanodontians. The ventral facet is enlarged, a derived feature shared with *Socognathus unicuspis* (6) and, to a lesser degree, *Chamops segnis* (4). The symphysis is angled relative to the long axis of the dentary, such that the two halves of the mandible would have diverged at approximately a 90º angle. The skull of *Socognathus* therefore would have been relatively short and broad. In ventral view, the dentary is strongly curved inward near the symphysis, but posteriorly the jaw is bowed inwards, as is typical of polyglyphanodontians.

The Meckelian canal is typical of polyglyphanodontians in being broadly open along the length of the jaw to accommodate a large splenial. The intramandibular septum terminates near the midpoint of the jaw, as in *Chamops*, and is concealed by the subdental ridge in medial view. The subdental ridge is typical of polyglyphanodontians. It is developed as a flat plate with a sharp dorsal edge that projects upwards to form a subdental shelf medial to the teeth. In medial view it is shallow posteriorly and becomes deeper anteriorly, where it projects ventrally to constrict the Meckelian canal at the tip of the jaw.

On the ventral surface of the subdental ridge there is a complex system of slots and ridges. A long slot between the subdental ridge and the intramandibular septum would have received the splenial. Medial to this slot there is a long ridge, which would have inserted into a corresponding slot atop the splenial. A similar arrangement is seen in other polyglyphanodontians, including *Chamops*, *Leptochamops*, *Tchingisaurus*, and as described above, *Obamadon*.

The dentary contains 19 teeth. As in other polyglyphanodontians, teeth implant high on the dentary, with the tooth bases extending about a third of the way down the medial surface of the dentary. In this feature, *S. brachyodon* is intermediate between the condition in primitive polygyphanodontians such as *Leptochamops* and *Meniscognathus*, where the teeth extend slightly less than halfway down the dentary (subpleurodont) and the more derived *Chamops* and *Haptosphenus*, in which the teeth lie along the dorsal margin of the jaw (subacrodont). In contrast to the typical squamate condition, in which multiple tooth positions are empty and replacement foramina are present, all tooth positions are occupied by a tooth, and replacement foramina are absent. This indicates that tooth replacement is greatly reduced or absent in adults, a derived character shared with most other polyglyphanodontians.

Tooth crowns are small and slender anteriorly, then become taller and more robust near the middle of the jaw, developing the typical ‘barrel-shaped’ crowns seen in other Chamopsiidae; they then become shorter again at the back of the jaw. The swelling of the crowns is more well-developed than in *Socognathus unicuspis*, in which the crowns are more columnar. Anterior teeth are unicuspid, with a central cusp and weak mesial and distal ridges. Posterior teeth have accessory cusps. The accessory cusps are more well-developed than in *Socognathus unicuspis*, but are reduced compared to polyglyphanodontians such as *Chamops*, *Haptosphenus*, and *Leptochamops*. Reduced accessory cusps appears to be a derived feature, and is shared with *Stypodontosaurus* and the Frenchman chamopsiid, suggesting that these animals may form a clade.

**Systematics.** *Socognathus brachyodon* shares numerous features with Polyglyphanodontia, including development of the dentary symphysis dorsal and ventral to the Meckelian canal, a subdental slot and ridge for the splenial, and subpleurodont implantation. The subacrodont tooth implantation and swollen tooth crowns indicate chamopsiid affinities. The robust symphysis suggests that *Socognathus* is most closely related to derived Chamopsiidae including *Chamops* and *Haptosphenus*, while the reduced accessory cusps suggests affinities with *Stypodontosaurus* and the Frenchman chamopsiid.

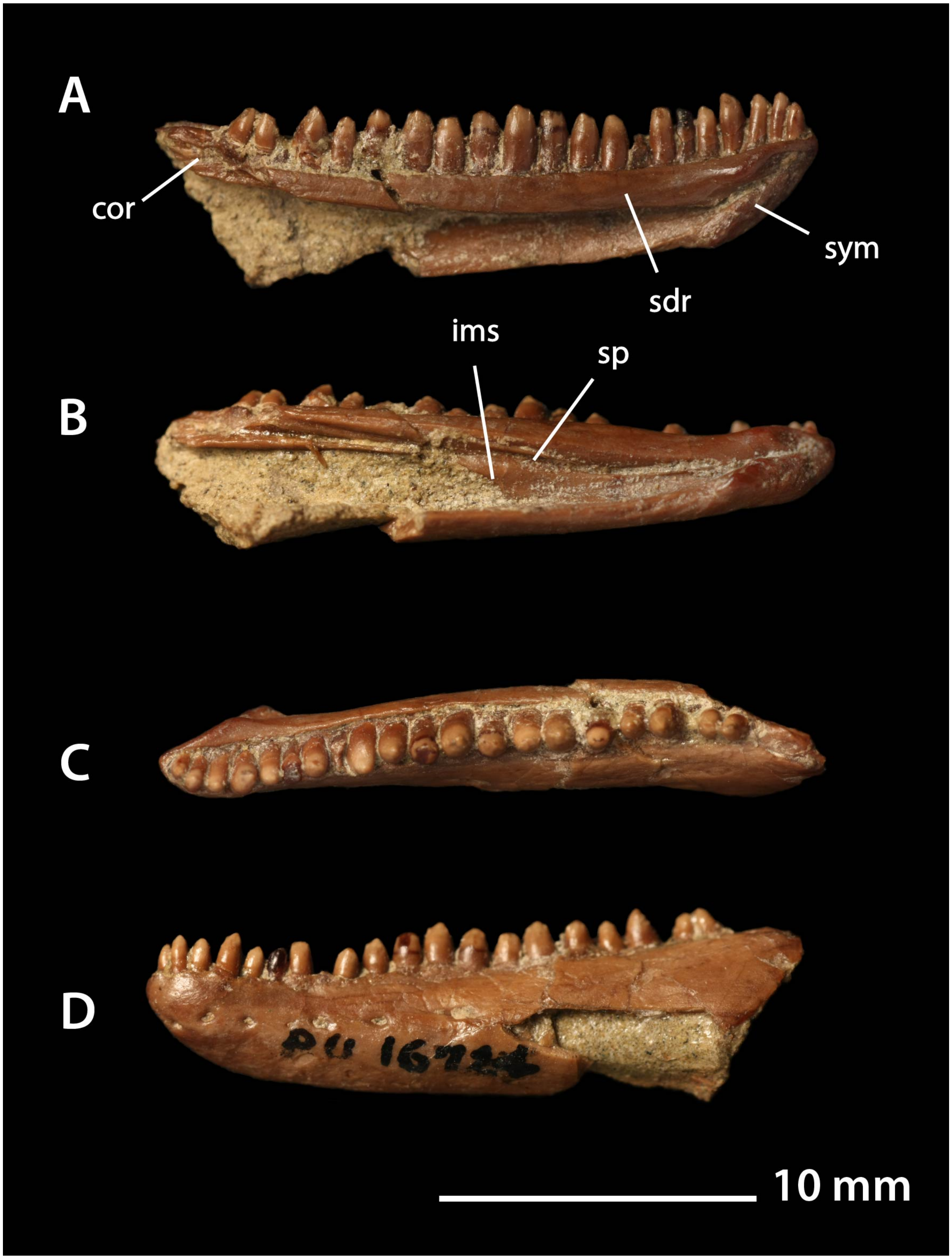


**Fig. S3.** *Socognathus brachyodon* n. sp, YPM-PU 16724 left dentary. **A**, medial view; **B**, ventromedial view; **C**, dorsal view, **D**, lateral view. Abbreviations: cor, coronoid facet; ims, intramandibular septum; sdr, subdental ridge; sym, dentary symphysis.

## Laramie Chamopsiid

**Material.** UCM 42164, dentary.

**Horizon and Locality.** UCM 77062, upper Maastrichtian Laramie Formation, Weld County, Colorado.

**Diagnosis.** Chamopsiid with slender teeth in the anterior half of the jaw, and greatly enlarged teeth in the posterior half of the jaw; dentary tapers strongly anteriorly and dentaries weakly divergent in dorsal view.

**Description.** This species is known from a single, poorly preserved jaw (Fig. S4). The jaw appears to have been relatively long and slender, and the symphyseal region is strongly tapered in lateral view. The symphysis has the typical V-shaped configuration of polyglyphanodontians, however while the dorsal facet is robust, the ventral facet is more weakly developed, as in *Leptochamops*. The symphysis is weakly angled with respect to the dentary, such that the two dentaries would have diverged at an angle of roughly 45º. As in other chamopsiids, the subdental ridge is shallow posteriorly and deep anteriorly where it constricts the Meckelian canal. The subdental ridge supports a prominent subdental shelf.

There are 17 preserved teeth but the total number was probably 20 or more. Teeth are implanted in a strongly subacrodont fashion, similar to the condition in *Chamops*. All tooth positions are occupied and no teeth exhibit resorption pits, indicating cessation of replacement, as in other Chamopsiidae. Teeth are short and moderately robust anteriorly; towards the back of the jaw the teeth become broad and massive, and are 2-3 times the diameter of the anterior teeth. The crowns are heavily worn postmortem such that the enamel is missing, but the anterior teeth appear to have been unicuspid, and posterior teeth are strongly tricuspid.

**Discussion.** The Colorado chamopsiid can be assigned to Polyglyphanodontia on the basis of the V-shaped dentary symphysis and to Chamopsiidae on the basis of the subacrodont tooth implantation. Despite the poor preservation, the extreme disparity in size between anterior and posterior teeth makes this specimen unlike any of the other known chamopsiids; neither does the shape of the dentary match that of any of the other species. This specimen therefore appears to represent a distinct species, but better material is needed to characterize this taxon.

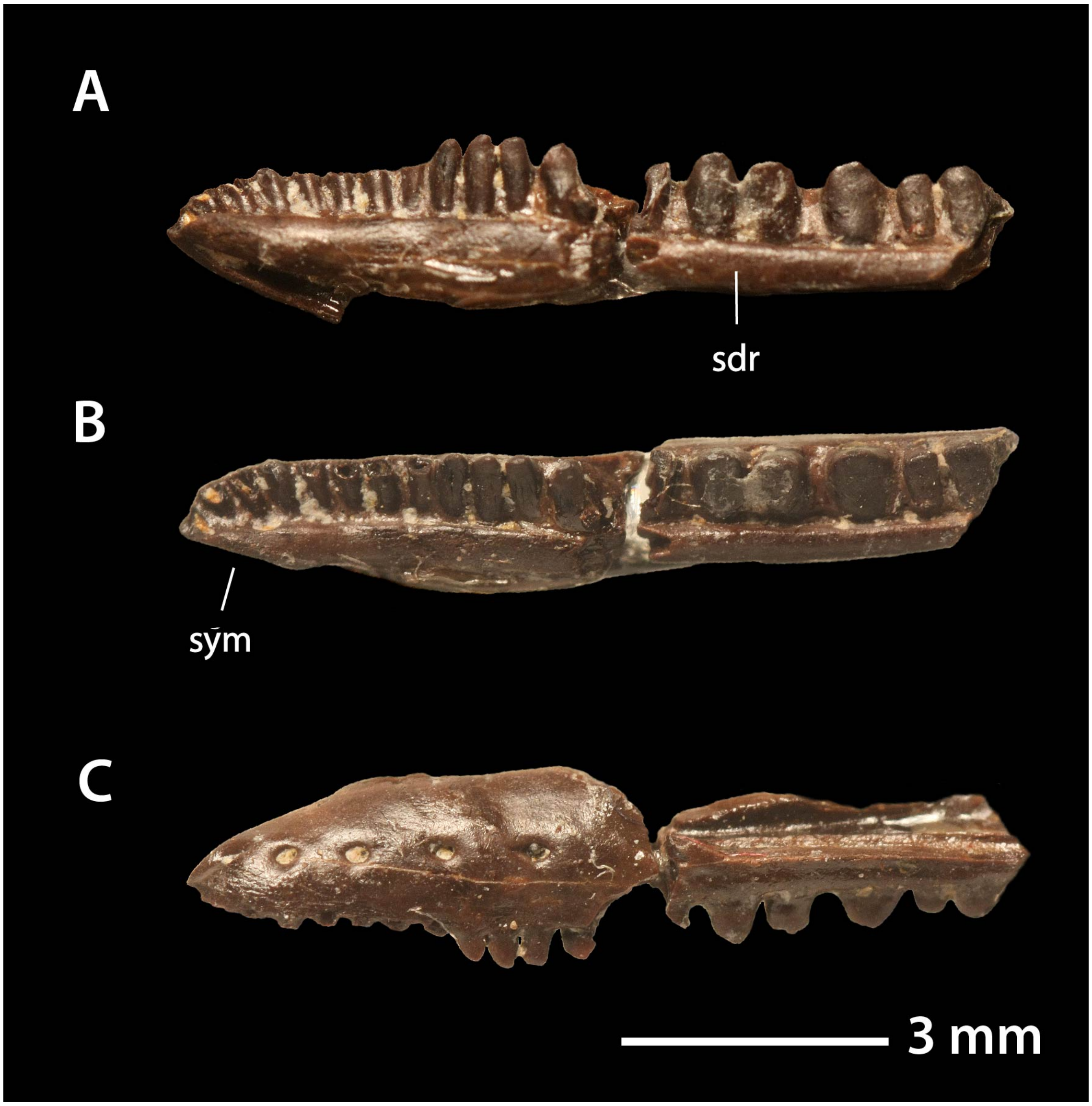


**Fig. S4.** Colorado chamopsiid UCM 42164, right dentary. **A**, medial view; **B**, dorsal view; **C**, lateral view. Abbreviations: sdr, subdental ridge; sym, dentary symphysis.

### *Tripennaculus* Nydam and Voci 2007

**Revised diagnosis.** Small polyglyphanodontian with strongly tricuspid tooth crowns bearing tall mesial and distal cusps separated from central cusp by grooves; teeth slender and closely packed (26), accessory cusps with lingual ridges developed as strong blades, mesial cusp larger than distal cusp, basal expansion of crowns absent.

### *Tripennaculus* new species

**Other identifications.**"Iguanidae new genus and species B" Gao and Fox 1996; "Family incertae sedis, new genus and species B" Gao and Fox 1996

**Diagnosis.** *Tripennaculus* differing from *Tripennaculus eatoni* Nydam and Voci 2007 in having relatively taller central cusps, mesial and distal cusps shorter, tip of tooth lacking the strong mesiodistal expansion seen in *T. eatoni*.

**Referred Material.** SMNH P1927.916, SMNH P1927.980, SMNH P 1927.998, SMNH P1927.885, posterior dentaries; SMNH P1927.886, SMNH P2004.90, anterior dentaries.

**Locality and Horizon.** Gryde Locality; Late Maastrichtian Frenchman Formation, Saskatchewan.

**Comments.** Four specimens (SMNH P1927.916, SMNH P1927.980, SMNH P 1927.998, and SMNH P1927.885) were described as "Iguanidae new genus and species B" by Gao and Fox (6) on the basis of the tricuspid teeth and the morphology of the subdental ridge. However, tricuspid teeth also occur in polyglyphanodontians, and the apparent reduction of tooth replacement in the specimens implies polyglyphanodontian affinities. Furthermore, the teeth closely resemble the polyglyphanodontian *Tripennaculus* (26) in exhibiting the following combination of features: teeth tall, closely packed and lacking basal swelling of the crown, tall mesial and distal cusps bearing bladelike ridges lingually, accessory cusps separated from main cusp by deep grooves, mesial cusps enlarged relative to distal cusps (6). The specimens are also comparable in size (tooth crowns ~ 1mm in height). Accordingly, we refer these dentaries to *Tripennaculus*. The teeth of the Frenchman species are slightly taller and the central cusp is more well-developed than in *T. eatoni*, suggesting that they represent a distinct species. Nydam (pers. comm., 2012) suggests that this species is distinct from and unrelated to *Tripennaculus*. We are of the opinion that the numerous shared features suggest that the two form a clade to the exclusion of other polyglyphanodonts. Given the differences in tooth morphology a new genus may be warranted. However, we have not examined the original material personally and are therefore hesitant to name either a new genus or a new species.

The same locality has also produced two anterior dentary fragments (SMNH P1927.886, SMNH P2004.90) identified by Gao and Fox as "Family incertae sedis, new genus and species B". These are here referred to *Tripennaculus* n. sp. on the basis of co-occurrence, small size, and the distinctive tall, closely packed, curved crowns. Although these specimens lack strongly tricuspid crowns, this feature varies along the jaw in polyglyphanodontians; accessory cusps tend to be well-developed posteriorly and weakly developed or absent anteriorly. Accordingly these elements probably represent the anterior part of the dentary of *Tripennaculus*, but complete jaws are necessary to test this referral.

## Frenchman Chamopsiid

**Other identifications.** “Family incertae sedis, new genus and species A” Gao and Fox 1996

**Material.** SMNH P1927.880, dentary.

**Locality and Horizon.** Gryde Locality; Late Maastrichtian Frenchman Formation, Saskatchewan.

**Comments.** Gao and Fox (6) described a partial dentary as “Family incertae sedis, new genus and species B”. The dentary appears to have the characteristic polyglyphanodontian symphysis, and exhibits the subacrodont implantation characteristic of derived Chamopsiidae. Gao and Fox (6) suggested that this specimen might be related to Paramacellodidae or Cordylidae, but phylogenetic analysis supports its placement in Chamopsiidae. Accessory cusps are reduced, as in *Socognathus* and *Stypodontosaurus*. The distinctive teeth- in which mesial and distal ridges wrap around a blunt central cusp- closely resemble those of *Stypodontosaurus*, suggesting a relationship between the two, but the teeth are much taller, supporting Gao and Fox’s identification of this jaw as a distinct species.

### SCLEROGLOSSA Estes, Gauthier and de Queiroz 1988

### AUTARCHOGLOSSA Wagler 1830

### ANGUIMORPHA Fürbringer 1900

### PLATYNOTA Baur 1890

### *Cemeterius* new genus

**Etymology.** Latin *cemeterium*, in reference to the type locality of Graveyard Coulee.

**Diagnosis.** As for the type and only species.

**Type species.** *Cemeterius monstrosus*.

### *Cemeterius monstrosus* new species

**Etymology.** Latin *monstrosus*, monstrous.

**Diagnosis.** Large stem varanoid characterized by a deep, massively constructed jaw, teeth short, unserrated, robust, and labiolingually expanded.

**Holotype.** USNM 25870, partial right dentary bearing two teeth (Fig. S5).

**Referred specimens.** AMNH 2366, anterior end of maxilla; YPM 1063, partial parietals; UCMP 49954, isolated tooth.

**Locality and Horizon.** The type is from Graveyard Coulee; upper Maastrichtian Hell Creek Formation, Dawson County, Montana; AMNH 2366 also comes from the Hell Creek of Dawson County. YPM 1063 is from the upper Maastrichtian Lance Formation, Niobrara County, Wyoming. UCMP 49954 is from UCMP V 5620, Lull 2, upper Maastrichtian Lance Formation, Niobrara County, Wyoming.

**Description.** The type consists of a dentary missing the anterior and posterior ends (Fig. S5). The dentary is shorter (estimated length ~ 50 mm) than that of *Palaeosaniwa* (UCMP 130716) (estimated length ~64 mm) but it is far more robustly constructed. The ventral margin is strongly curved, indicating a bowed mandible, and the jaw tapers anteriorly, indicating a very short, deep mandible; this condition is approached in *Paraderma* and *Labrodioctes* (6) but it is taken to a greater extreme in *Cemeterius*. Two small mental foramina are preserved. Medially there is a deep, robust subdental ridge; as in *Paraderma* and *Labrodioctes*; the subdental ridge is shallow and thin in *Palaeosaniwa*. Ventrally the subdental ridge bears a ridge for the splenial. The ridge terminates anteriorly between the two preserved teeth, indicating that the splenial was short; posteriorly the splenial contact tapers out where the anterior inferior alveolar foramen would have passed between the splenial and dentary.

The Meckelian fossa is deep and broad posteriorly, in contrast with the narrower fossa in *Paraderma*. The Meckelian fossa is also broad in *Labrodioctes* (6), but not to the same extreme as seen here. The intramandibular septum appears to have been located near the back of the jaw, as in other anguimorphs (31). The medial surface of the septum bears a prominent ridge. Posteriorly, the ventral edge of the Meckelian groove is bounded by a distinct facet running along the ventromedial edge of the dentary, which would have contacted the ventral edge of the splenial. A similar facet may be present in *Labrodioctes* (6). Anteriorly the Meckelian fossa tapers to a narrow groove that wraps onto the ventral surface of the dentary, as in other anguimorphs.

One tooth and part of a second are preserved, alternating with spaces for two more. Comparisons with other stem varanoids suggest the presence of three more teeth posteriorly and three or four anteriorly, for a tooth count of 10-11, comparable to *Paraderma* and *Labrodioctes*. Teeth implant in a pleurodont fashion in a broad dental gutter, as in other anguimorphs (32). Tooth bases are heavily infolded, as in Varanoidea and stem varanoids, including *Parasaniwa*, *Paraderma*, and *Palaeosaniwa*. Each tooth preserves a basal foramen but replacement pits are not visible. In contrast to the labiolingually compressed teeth of other stem varanoids, the tooth is robust and labiolingually expanded to give the tooth a U-shaped section. The tooth crown is short, massive, and hooked posteriorly, closely resembling the teeth of *Labriodioctes* (6). As in *Palaeosaniwa* and other stem varanoids, anterior and posterior carinae extend the full length of the crown, but the tooth lacks the bladelike cross section and microserrations found in stem varanoids such as *Palaeosaniwa* (4, 6), *Primaderma* (33), and *Parasaniwa* (UCMP 47744). Heavy apical wear is found in both the type and the referred tooth. Tooth wear is uncommon in carnivorous lizards, but frequently occurs in crocodylians and tyrannosaurids (NRL, pers obs.) and suggests an unusual feeding mode in *Cemeterius*.

A fragment of the maxilla (AMNH 2366) can be referred to *Cemeterius* on the basis of its size, robust construction, and the presence of the distinctive labiolingually expanded tooth bases. The premaxillary process is short and the facial process is highly rugose, as in *Paraderma* and *Parasaniwa*; these features are acquired independently in *Heloderma*.

Parts of the parietals (YPM 1063) are also preserved (2). They are too large to belong to either *Paraderma* or *Parasaniwa*, and their massive construction precludes referral to *Palaeosaniwa*, allowing referral to *Cemeterius*. The parietal dorsal surface bears a series of large osteoderms that are sculptured with pits and ridges; there is a large parietal foramen. The anterior surface of the parietal reveals a strongly interdigitating contact with the frontal. Well developed attachments for the supratemporal muscles are present dorsolaterally, similar to the condition in Parasaniwa (4); in parietals referred to *Paraderma* the supratemporal muscles attach ventrally (6).

**Discussion.** *Cemeterius* can be referred to Anguimorpha on the basis of the ventral position of the Meckelian groove anteriorly. Reduction of the subdental shelf allows referral to the Anguidae + Varanoidea clade. Infolded tooth bases, absence of replacement pits, a bowed dentary, and well-developed carinae all indicate platynotan

affinities. Phylogenetic analysis supports placement of *Cemeterius* with *Parasaniwa*, *Palaeosaniwa*, and *Paraderma* along the stem of Varanoidea. Among basal platynotans, *Cemeterius* is most similar to the Campanian *Labrodioctes* but differs in having a much shorter, more robust mandible and shorter teeth. The possibility exists that *Cemeterius* is descended from *Labriodioctes*, as the Campanian *Labrodioctes* is plesiomorphic relative to the Maastrichtian *Cemeterius*.

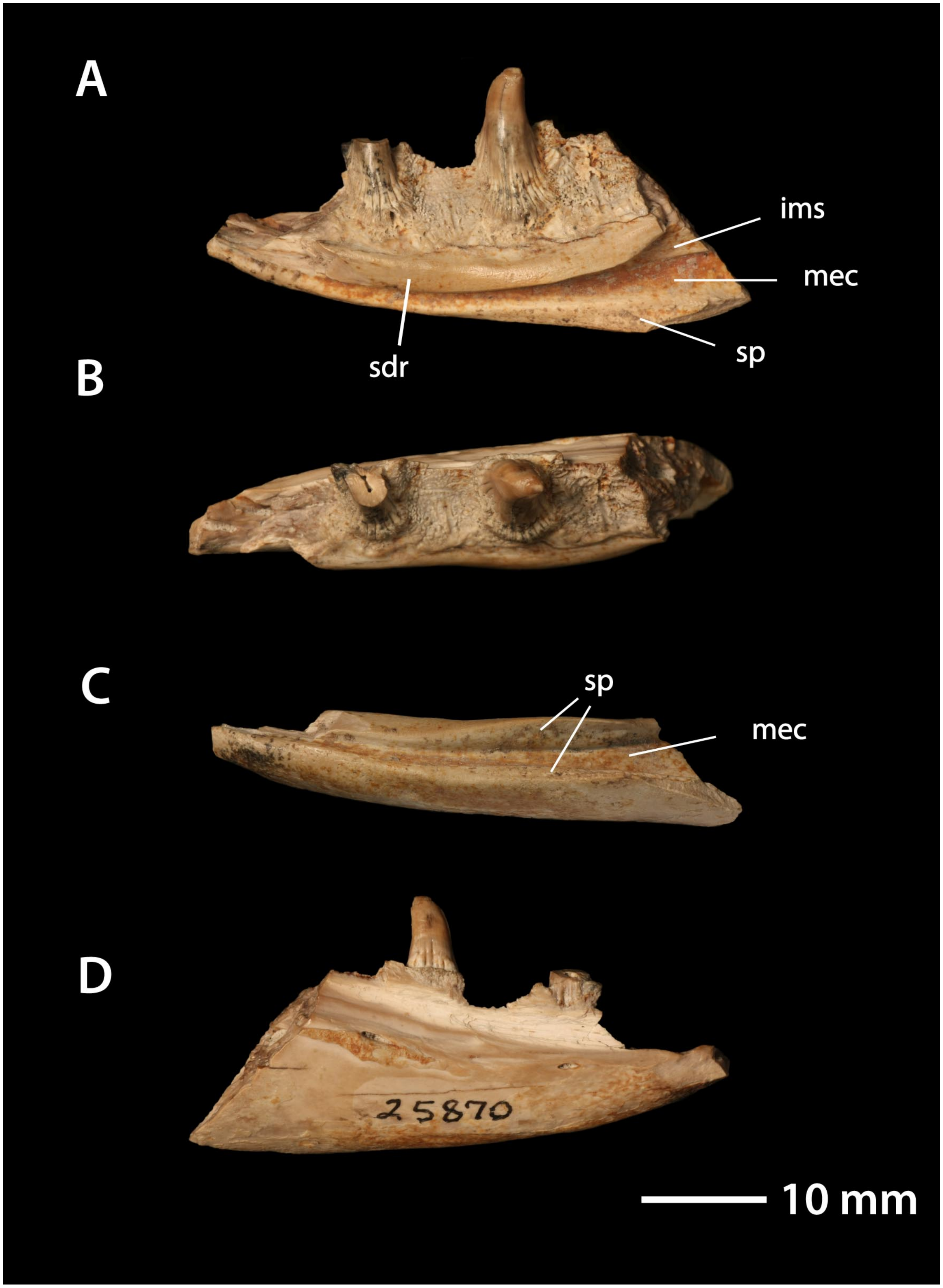


**Fig. S5.** *Cemeterius monstrosus* n. gen. et sp. USNM 25870, right dentary. **A**, medial view; **B**, dorsal view; **C**, ventral view, **D**, lateral view. Abbreviations: ims, intramandibular septum; mec, Meckelian fossa, sdr, subdental ridge; sp, splenial contact.

SERPENTES Linnaeus, 1758

ALETHINOPHIDA Nopsca 1923

*Cerberophis* new genus

**Etymology.** Cerberus, a snake-tailed guardian of the underworld in Greek mythology, and Greek *ophis*, snake.

**Diagnosis.** As for species.

**Type species.** *Cerberophis rex*

*Cerberophis rex* new species

**Etymology.** Greek *rex*, king.

**Diagnosis.** Medium-sized (~ 2 m long) alethinophidian characterized by trunk vertebrae with a broad, flat ventral surface, hypertrophied synapophyses, large, massive prezygapophyses bearing rudimentary prezygapophyseal processes and anterior ridges; neural arch bearing prominent dorsolateral ridges and a moderately tall neural spine.

**Holotype.** UCMP 130696, trunk vertebra.

**Locality and Horizon.** UCMP V80096, Scrap Hill; upper Maastrichtian Hell Creek Formation, Garfield County, Montana.

**Description**. The holotype vertebra measures 9 mm in length from the cotyle to the condyle, and would have measured 16 mm across the prezygapophyses, making *Cerberophis* comparable in size to a large *Boa constrictor*. In terms of proportions, the vertebrae are very short, low, and broad, much like those of the basal alethinophidian *Dinilysia patagonica* (34).

The centrum is typical of snakes in having a deep, cup-shaped anterior cotyle and a prominent, ball-shaped posterior condyle. The condyle is slightly wider than tall and faces posteriorly rather than posterodorsally, as is typical of snakes. The condyle is separated from the centrum by a groove; this groove is characteristic of Madtsoiidae and crown Alethinophidia (34).The ventral surface of the centrum is unusual in being extremely broad and almost perfectly flat except for a sharp, bladelike haemal keel that extends from the cotyle to the condyle. This bladelike keel indicates that the vertebra comes from the anterior part of the trunk vertebrae, behind the series of elongate hypapophyses found in the anteriormost trunk. As a result, the length and mass estimates (which are based on the maximum diameter of the trunk vertebrae) almost certainly underestimate the size of *Cerberophis*. To either side of the haemal keel are a pair of small subcentral foramina, a typical snake feature. On the ventrolateral aspect of the centrum are the subcentral ridges; these extend forward from the condyle and then turn strongly laterally to connect to the synapophyses. The right synapophysis is damaged and the left is pathological, but the synapophyses appear to have been massively constructed. What is left of the right synapophysis indicates that the synapophysis is divided into a knob-like dorsal facet and a planar ventral facet, as is typical of snakes. Paracotylar fossae, on the anterior surface of the synapophyses, are rudimentary.

The zygapophyses are the most unusual and distinctive feature of this snake. The prezygapophyseal articular facet is rhomboidal in shape and unusually large and broad, being roughly 5 mm wide proximodistally and 3.5 mm wide anteroposteriorly. Articular facets lie about 30° above the horizontal plane. Just below the articular facet is a rudimentary prezygapophyseal process. Below and anterior to this process, a ridge extends mediolaterally across the front of the prezygapophysis; this ridge appears to be an autapomorphy of *Cerberophis*.

The zygosphene-zygantrum joint is well-developed. The zygosphene is moderately robust, unlike like the massive, wedge-shaped structures seen in Madtsoiidae and Boidae, and bears relatively small articular facets, which lie at approximately 45° from the vertical. Inside the zygantrum are a small pair of foramina; it is unclear whether parazygantral foramina are present due to breakage of the neural arch.

The neural arch is relatively low and broad. It defines a triangular neural canal with ventrolateral canals, a snake feature. The neural spine is low and bladelike anteriorly but broken posteriorly; it may have been relatively tall, although not to the degree seen in boids and madtsoiids. The neural spine appears to have become wider and more robust posteriorly, suggesting a low neural spine that was subtriangular in dorsal view, similar to that of *Dinilysia*. On either side of the neural spine there are a pair of prominent dorsolateral ridges, a feature shared with the stem snake *Najash*, the basal alethinophidian *Dinilysia*, and Madtsoiidae.

**Discussion**. The distinct separation between the condyle and centrum suggests that *Cerberophis rex* represents an alethinophidian more derived than *Dinilysia*. Dorsolateral ridges, a feature shared with *Najash*, *Dinilysia*, and Madtsoiidae, suggest a basal position within Alethinophidia, as found by Longrich et al. (35).

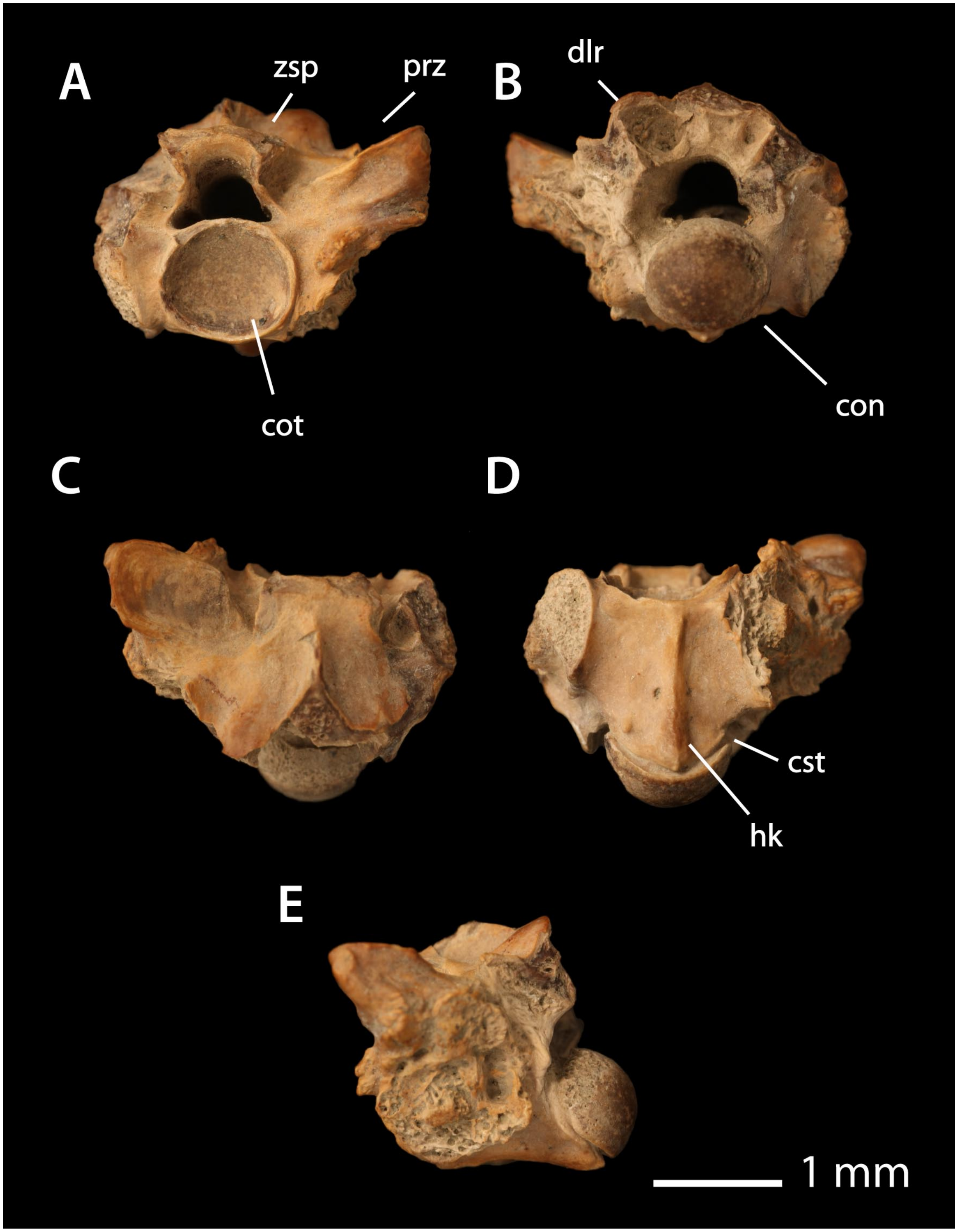


**Fig. S6.** *Cerberophis rex*, n. gen. et sp. UCMP 130696, anterior trunk vertebra. In **A**, anterior view; **B**, posterior view; **C**, dorsal view; **D**, ventral view; **E** left lateral view. Abbreviations: con, condyle; cot, cotyle; cst, constriction; dlr, dorsolateral ridge; hk, haemal keel; zsp, zygosphene.

## Lance Snake

**Material.** AMNH 28457, vertebra.

**Locality and Horizon.** UCMP V-5711, Bushy Tailed Blowout, upper Maastrichtian Lance Formation, Niobrara County, Wyoming.

**Diagnosis.** Small alethinophidian with a rudimentary neural spine and a moderately elongate, subtriangular centrum, weakly developed paracotylar fossae.

**Description.** The Lance Snake is represented by a single trunk vertebra, AMNH 28457. The condyle is typical of snakes in being taller than wide, strongly ball-shaped, and oriented posteriorly. It is strongly separated from the centrum by a distinct groove running between the centrum and the condyle, a derived feature shared with Madtsoiidae and crown Alethinophidia, but absent from basal snakes such as *Coniophis* (35) and Scolecophidia. The condyle is also much larger than the condyle of the stem snake *Coniophis*. The cotyle is a distinct cup, as is typical of snakes.

The ventral surface of the centrum bears a narrow keel. Such a keel is typically seen in snakes in the anterior part of the trunk vertebrae, just behind those vertebrae bearing elongate hypapophyses, indicating that the vertebra comes from this region. The keel is flanked by a pair of small subcentral foramina. The overall shape of the centrum is relatively elongate, and expanded anteriorly to give it a roughly triangular shape. In contrast, the centrum is more subrectangular in *Coniophis*. Synapophyses are characteristic of snakes in being double-headed, with a prominent, ball-shaped dorsal facet and a planar ventral facet, whereas those of *Coniophis* are simple and undivided (35). The ventral facet of the synapophysis is placed close to the cotyle and projects distinctly ventrally, to the level of the ventral margin of the cotyle, as is typical of Alethinophidia. The anterior surfaces of the synapophyses bear shallow paracotylar fossae (whereas those of *Coniophis* are prominent) but paracotylar foramina are absent. The neural canal has a distinctly triangular shape, another snake feature. The zygapophyses and posterior margin of the neural arch are broken away, but a well-developed zygosphene is present, indicating that the Lance snake had the characteristic zygosphene-zygantrum joint found in all snakes. The neural spine is extremely reduced, without even a trace of the neural spine on the anterior half of the neural arch.

**Dicussion.** The Lance Snake is distinguished from *Coniophis* by the large, double-headed synapophyses and the large, well-differentiated posterior condyle. The distinct separation of the condyle and centrum is an alethinophidian feature. Recent work on Late Maastrichtian snakes (35) places the Lance Snake in Alethinophidia.

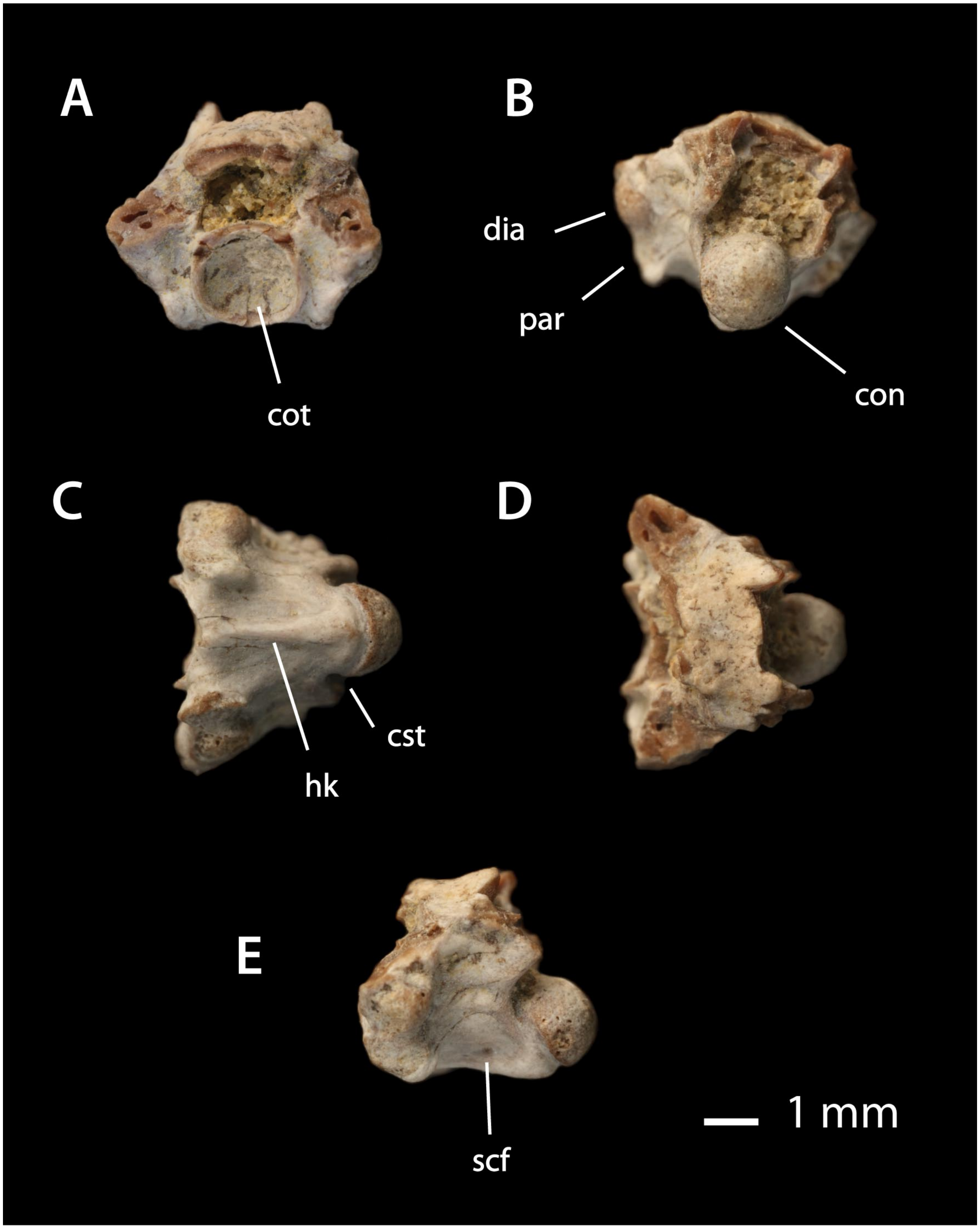


**Fig. S7.** Lance Snake, AMNH 28457, anterior trunk vertebra. In **A**, anterior view; **B**, posterior view; **C**, ventral view; **D**, dorsal view; **E** lateral view. Abbreviations: con, condyle; cot, cotyle; cst, constriction; dia, diapophysis; hk, haemal keel; par, parapophysis, scf, subcentral foramen.

## SCINCOMORPHA Camp 1923

## SCINCOMORPHA INCERTAE SEDIS

### *Lonchisaurus* new genus

**Etymology.** The genus name is derived from the Greek *Lonchus*, 'spear', in reference to the Lance Formation that produced the holotype, and *saurus*, lizard.

**Diagnosis.** As for species.

**Type species.** *Lonchisaurus trichurus*.

### *Lonchisaurus trichurus* new species

**Etymology.** The species name is derived from the Greek *trichos*, hairy and *uros*, tail, in reference to the Bushy Tailed Blowout locality (UCMP V-5711).

**Diagnosis.** Lizard characterized by the following combination of characters: dentary long, low, and weakly bowed in lateral view; tooth crowns robust and weakly recurved, with weakly pointed crowns; tooth bases wider labially than lingually, tooth replacement reduced, lateral overlap of dentary by coronoid.

**Holotype.** AMNH 15446, left dentary.

**Locality and Horizon.** UCMP V-5711, Bushy Tailed Blowout, Niobrara County, Wyoming; upper Maastrichtian Lance Formation.

**Description.** The dentary is relatively long and low. In lateral view, the dorsal margin of the jaw is nearly straight while the lower margin is curved, and the dentary tapers strongly anteriorly. Six small mental foramina are present externally. Along the posterodorsal margin of the jaw, there is a narrow facet where the coronoid would have lapped onto the lateral surface of the jaw, extending lateral to the the final two tooth positions. Medially, a well-developed dentary symphysis is present dorsal to the Meckelian canal but not ventrally, as is typical of squamates. The symphysis is angled such that the dentaries would have diverged at an angle of roughly 60º.

The Meckelian canal is deep and expanded in the back of the jaw but strongly constricted in the anterior half of the dentary. The subdental ridge is extremely slender posteriorly and gradually becomes deeper towards the tip of the mandible. It defines a well-developed subdental shelf medial to the teeth. The ventral surface of the subdental ridge bears a very broad surface which presumably articulated with the splenial. A similar broad articulation between the dentary and the splenial occurs in *Paramacellodus*.

There are 20 closely packed tooth positions, with teeth implanting in a pleurodont fashion. Teeth are relatively short, rising only a third of their height of above the dental parapet. Teeth are similar in length from the middle to the back of the jaw, but become more robust posteriorly. Tooth shafts are columnar, and very weakly curved posteriorly, such that tips angle backwards in lateral view. Crowns bear blunt points. A number of teeth are broken and their cross sections are visible in dorsal view. The teeth have relatively thick walls and the bases are labiolingually expanded. The tooth bases have a distinctive cross-section, being slightly wider labially than lingually, giving them a slight subtriangular or teardrop shape.

**Discussion.** The present analysis places *Lonchisaurus* near the base of Scincomorpha, but beyond this its affinities are unclear.

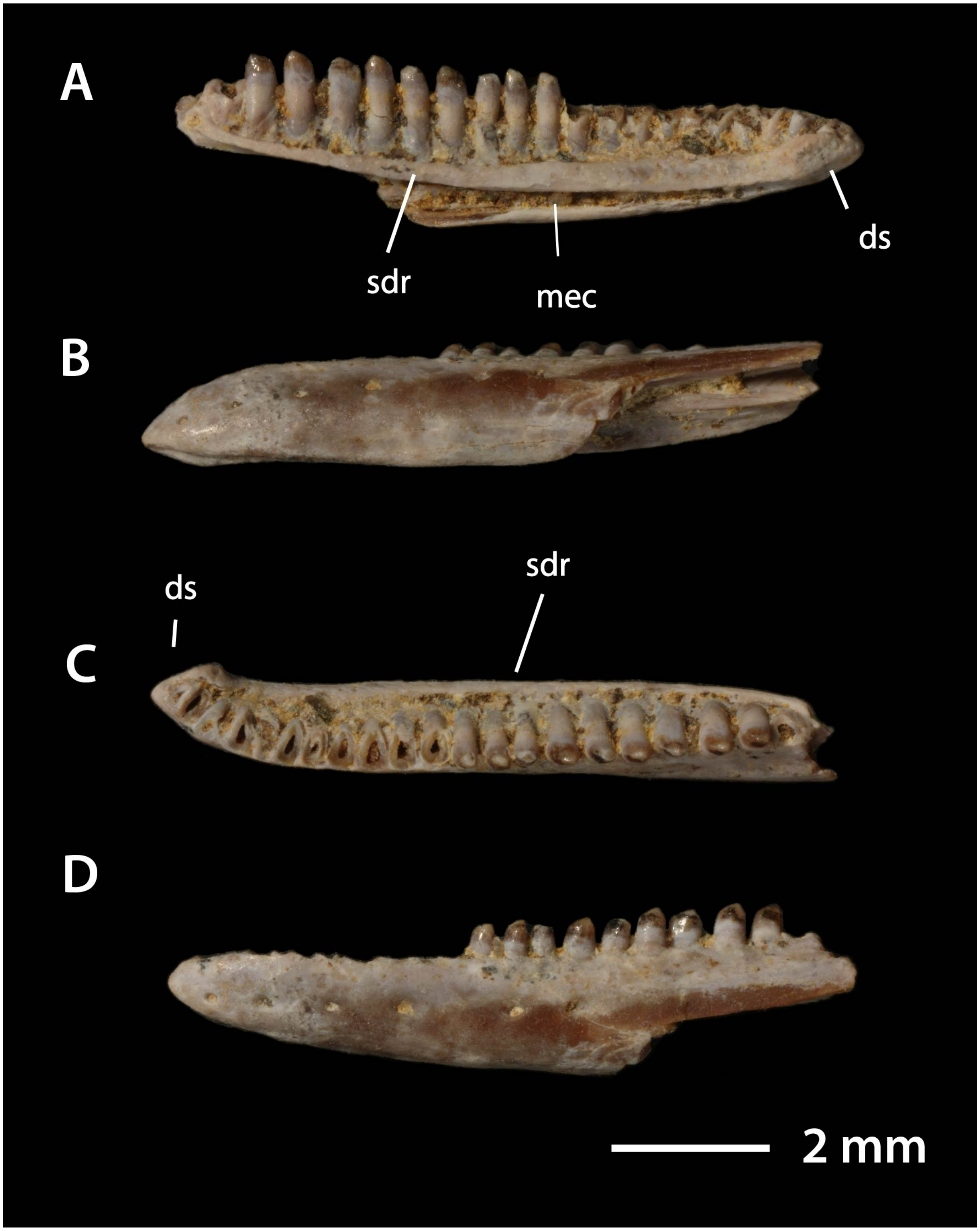


**Fig. S8.** *Lonchisaurus trichurus* gen. et sp. nov. AMNH 15446, dentary. In **A**, medial view; **B**, ventral view; **C**, dorsal view; **D**, lateral view. Abbreviations: ds, dentary symphysis; mec, Meckelian canal; sdr, subdental ridge.

## SQUAMATA INCERTAE SEDIS

### *Lamiasaura* new genus

**Etymology.** *Lamia*, a fierce demon from Greek mythology, in reference to the wicked appearance of the teeth, and Greek *saurus*, lizard.

**Diagnosis.** As for species.

**Type species.** *Lamiasaura ferox*.

### *Lamiasaura ferox* new species

**Etymology.** Greek *ferox*, fierce.

**Holotype.** UW 25116A

**Locality and Horizon.** UW V-79032; upper Maastrichtian Lance Formation, Sweetwater County, Wyoming.

**Diagnosis.** Dentary straight and strongly tapered in lateral view; teeth widely spaced, with weakly recurved crowns, crowns with a distinct bottleneck constriction between the base and apex; low mesial and distal cusps, and distinct ridges on the lingual surface.

**Description.** The dentary is relatively gracile in its construction, and tapers strongly in lateral view. The anterior and posterior ends of the dentary are missing, but the jaw appears to have been relatively long and slender. The Meckelian canal is deep. Dorsally it is bounded by a thin subdental ridge. Ten tooth positions are present in the preserved jaw fragment; implantation is pleurodont. One tooth position is unoccupied, three teeth have large replacement pits. Replacement pits are located lingually.

Teeth have robust, columnar bases, but taper slightly above the dental parapet before becoming columnar again, giving them a shape similar to a rifle cartridge or a wine bottle. Although tooth base is distinctly broader than the tip of the crown, the condition in *Lamiasaura* differs from that of the Chamopsiidae, in which it is the base of the crown that is inflated, rather than the tip that is tapered. The apex of the tooth bears a weakly pointed central cusp, with mesial and distal carinae extending about a quarter of the way down the crown. The lingual surface of the crown bears a few striations, but the teeth are smooth externally.

**Discussion.** The affinities of *Lamiasaura* remain unclear. The pointed, widely-spaced crowns are similar to those of Platynota and the ridged crowns are anguid-like, but the medial position of the Meckelian groove and the lingual position of the replacement teeth argue against anguimorph affinities. The current analysis unites *Lamiasaura* with Iguania on the basis of a single character, the short splenial. *Lamiasaura* may represent a distinct, extinct lineage of lizard; however more complete material is needed.

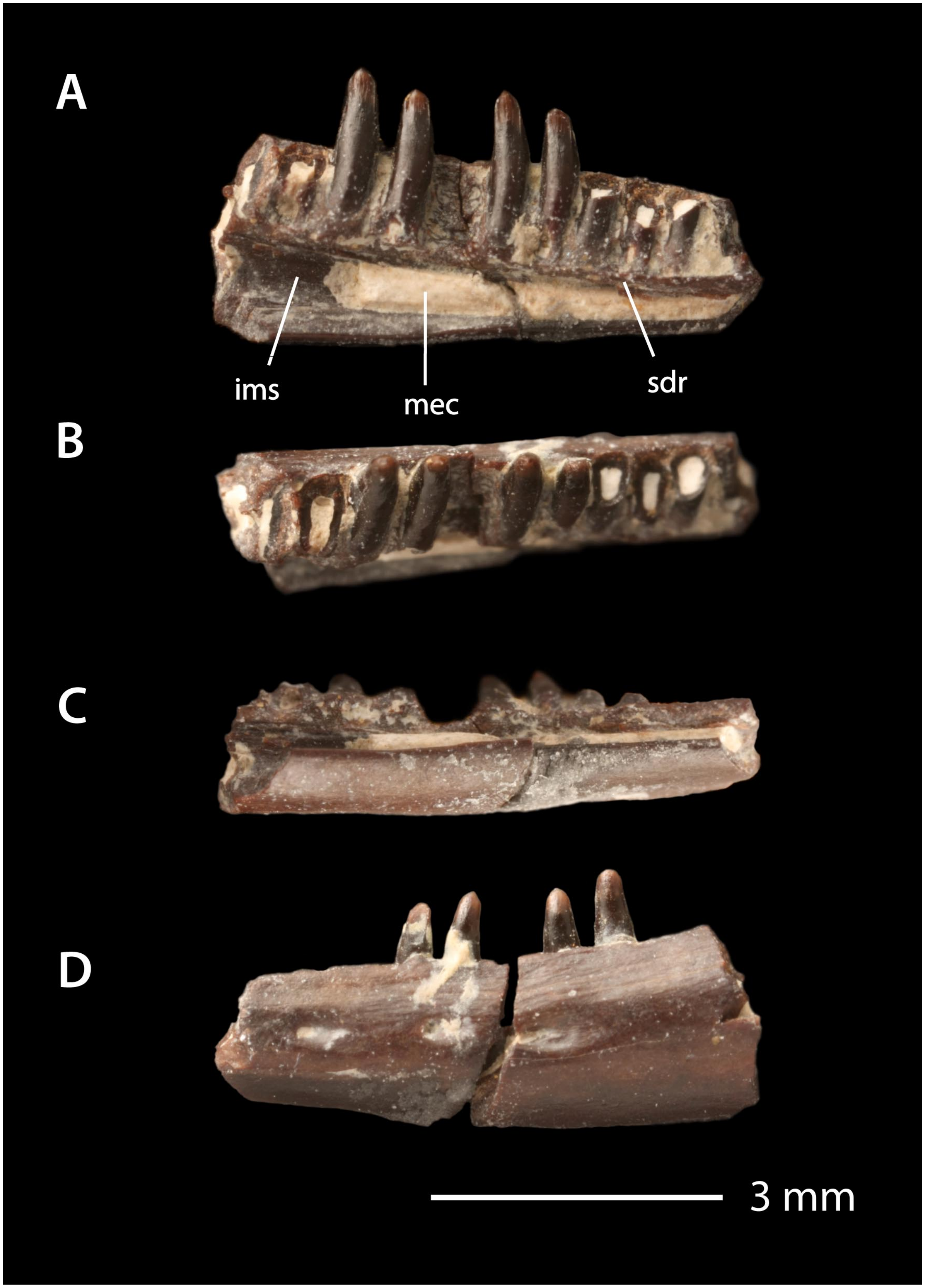


**Fig. S9.** *Lamiasaura ferox*, UW 25116A, left dentary. **A**, medial view; **B**, dorsal view; **C**, ventral view; **D**, lateral view. Abbreviations: ims, intramandibular septum; mec, Meckelian canal, sdr, subdental ridge.

## Sweetwater County Lizard

**Material.** UW 25116B, left dentary.

**Locality and Horizon.** UW V-79032; upper Maastrichtian Lance Formation, Sweetwater County, Wyoming.

**Diagnosis.** Lizard characterized by the following combination of characters: relatively long, slender dentary, mental foramina large and numerous, subdental ridge strongly rounded, shallow posteriorly and deep anteriorly, pleurodont implantation, anterior teeth small and strongly procumbent.

**Description.** The only known specimen of this species an edentulous dentary missing its posterior end. The dentary is long and low in lateral view, tapering strongly towards the tip. The dental parapet is relatively straight in lateral view, while the ventral margin is gently curved. The external surface of the jaw is strongly rounded. There are eight mental foramina, which are large and born in deep depressions. Medially, there is a small symphysis. The Meckelian canal is broad posteriorly, but becomes a narrow slot anteriorly, indicating a short splenial. The subdental ridge is very slender posteriorly, becomes deeper anteriorly, and then tapers rapidly as it approaches the symphysis. The medial surface of the subdental ridge forms a broad, strongly rounded lip, similar to that of many scincomorphs. The ventral surface of the subdental shelf bears a broad ventral surface to contact the splenial, again resembling some scincomorphs. Teeth are implanted in a pleurodont fashion. Sixteen tooth positions are present but there were probably between 20-25 in total. There are multiple open tooth positions, and several teeth bear large, subcircular replacement pits.

**Discussion.** UW 25116B cannot be referred to any previously described species, but the poor preservation of the specimen makes it inadequate to serve as a type of a new species. Phylogenetic analysis was unable to determine the affinities of this lizard. *Aocnodromeus corrugatus* from the late Campanian of Alberta (6) resembles the Sweetwater Lizard in the overall shape of the mandible, although it lacks either the enlarged mental foramina or the broad, rounded subdental ridge seen in UW 25116B. The prominent subdental shelf and broad contact for the splenial suggest that UW 25116B might represent a scincomorph.

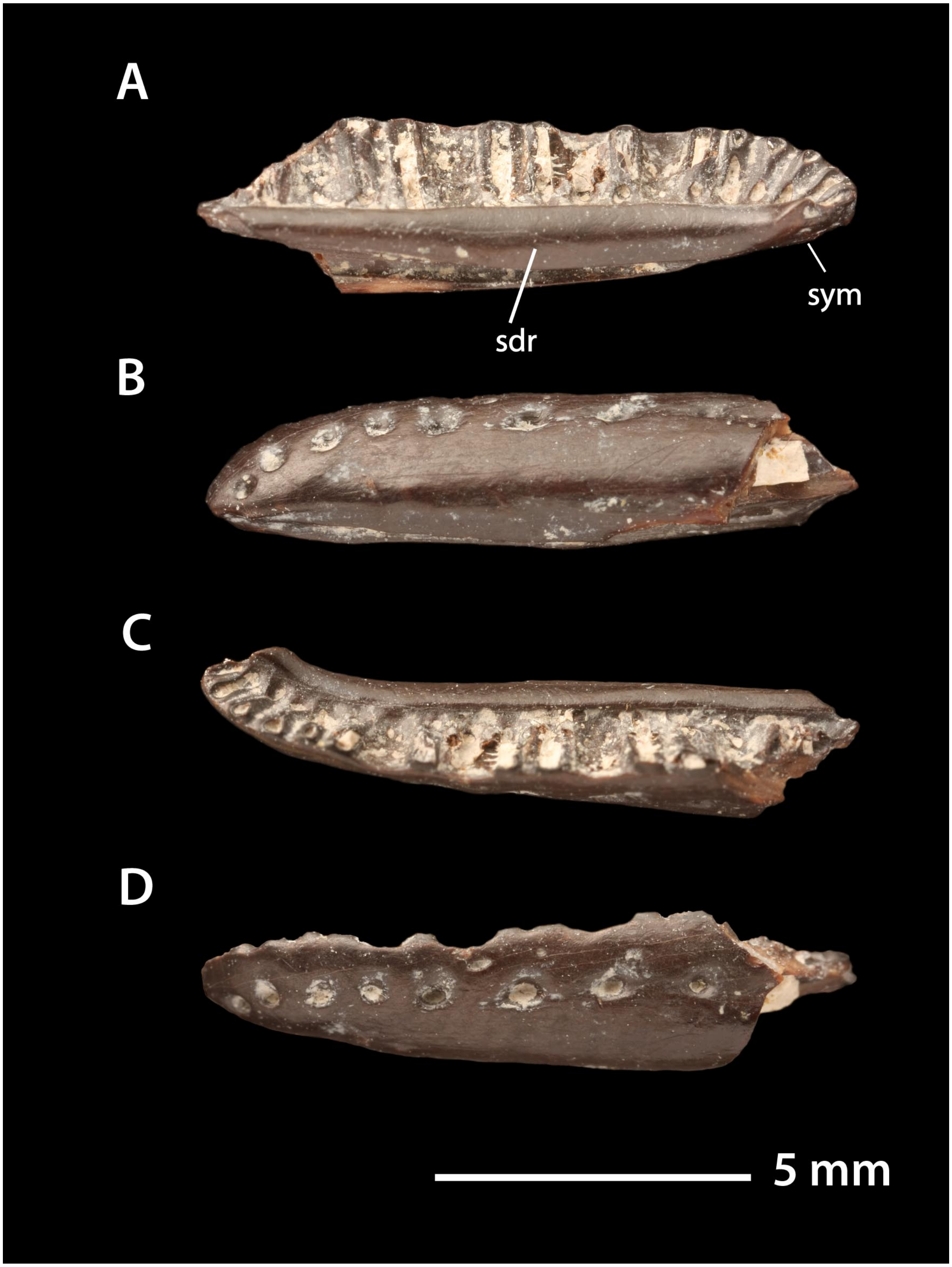


**Fig. S10.** Sweetwater County Lizard, UW 25116, left dentary. In **A**, medial view; **B**, ventromedial view; **C**, dorsal view, **D**, lateral view. Abbreviations: sdr, subdental ridge; sym, dentary symphysis.

## 4. Phylogenetic Analysis

### a. Revisions to Gauthier et al. (2012) matrix

89. Parietal ventral lappet: *Tchingisaurus multivagus* 0->1, *Gobinatus arenosus* 0->?, *Polyglyphanodon sternbergi* 0->?

89. unordered => ordered

93. *Anniella pulchra* 1->0

117. *Dinilysia patagonica* ?=>0

360. subdental shelf: *Shinisaurus crocodilurus*, 2->1, *Xenosaurus grandis*, 2->1, *Xenosaurus platyceps*, 2->1

372. *Zapsosaurus sceliphros*: 3->2

388. Subdental slot for coronoid: *Shinisaurus crocodilurus* 1->0, *Xenosaurus grandis* 1->0, *Xenosaurus platyceps* 1->0, *Peltosaurus granulosus* 1->0, *Helodermoides tuberculatus* 1->0.

413. Median premaxillary tooth: *Polyglyphanodon sternbergi* 0->1, *Adamisaurus magnidentatus* 0->1

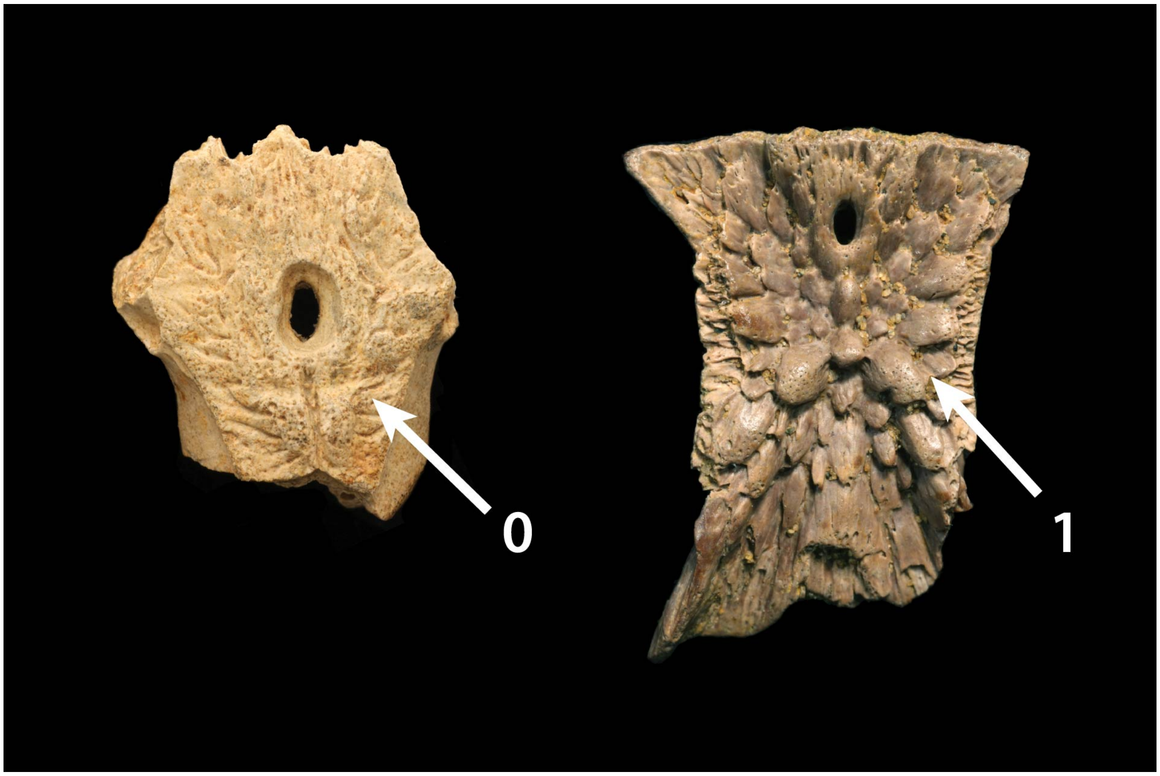
421. Dentary tooth count: *Peltosaurus granulosus* 3->2

434. Multicuspid teeth: *Cordylosaurus subtesselatus* 0->1

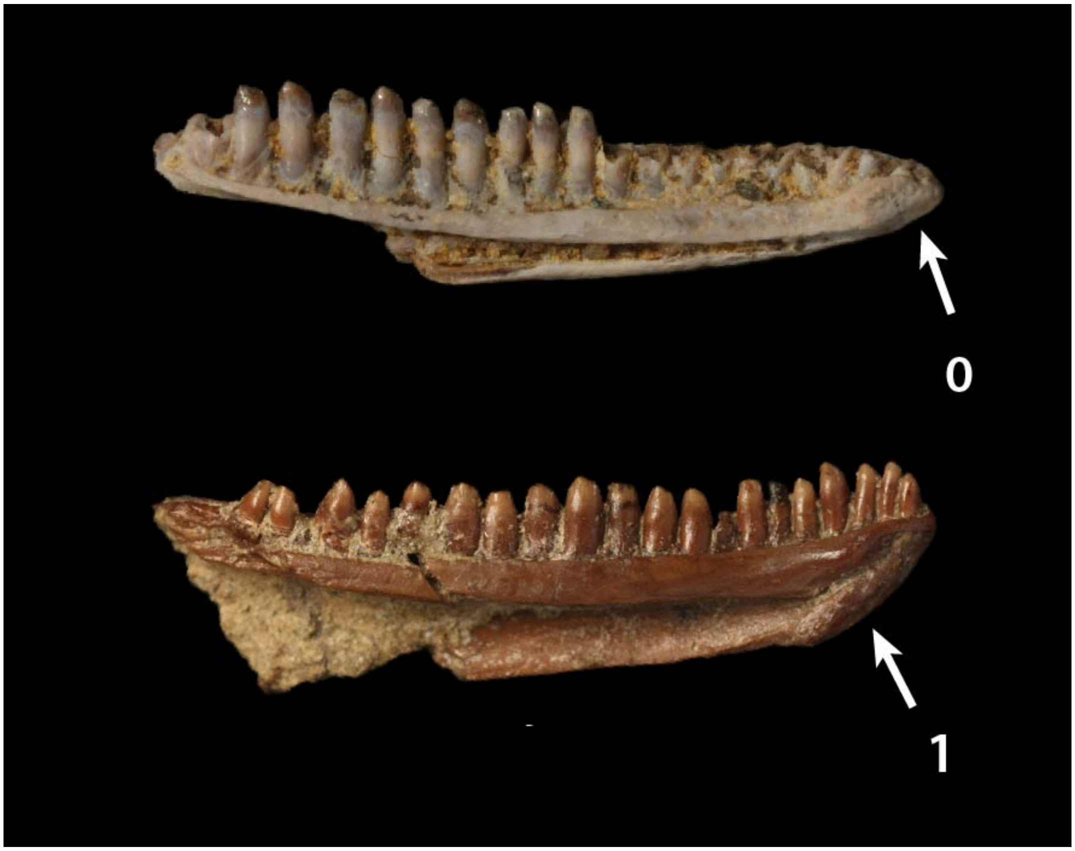
468. Zygosphene-zygantrum joint: *Gobiderma pulchra* ?->1

572. Dermal skull bone ornamentation: *Aiolosaurus oriens* ? => 0/1; *Gobiderma pulchrum* 2=>3.

## b. New Characters



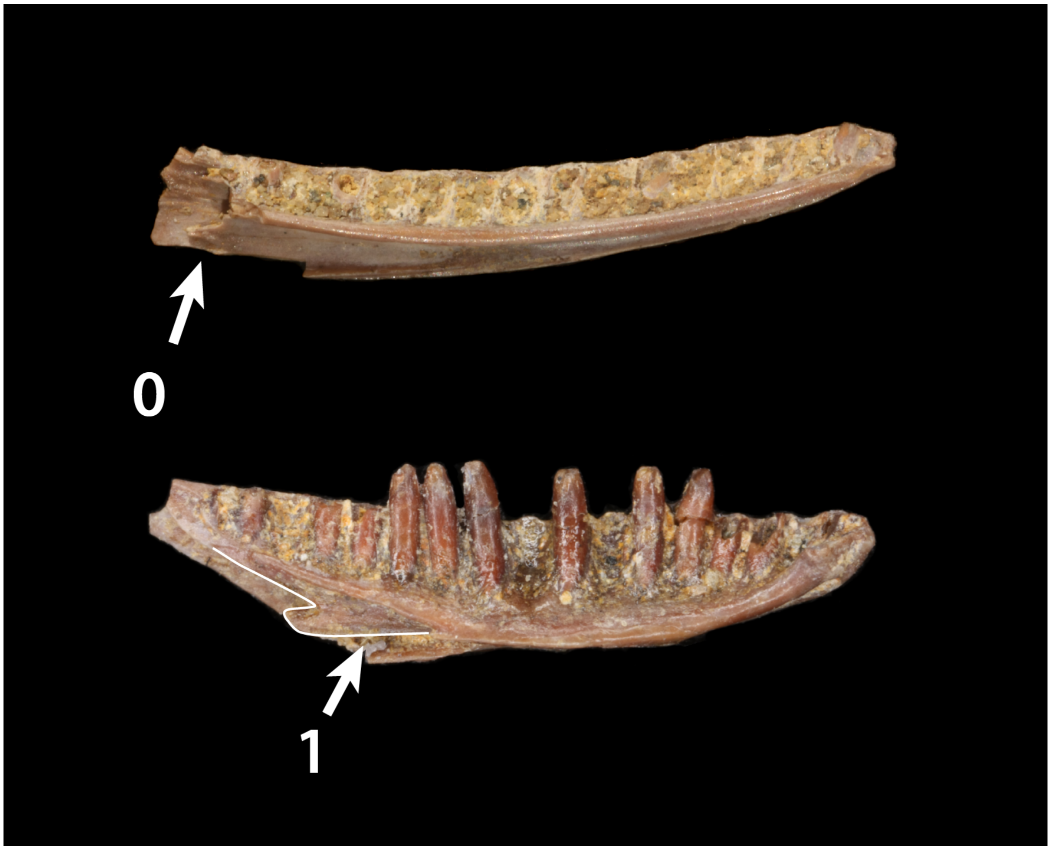
**611.** Frontoparietal sculpture: smooth or with low osteoderms/sculpturing (0) (shown in *Cemeterius monstrosus*), or with massive, prominently projecting osteoderms (1) (shown in *Exostinus lancensis*). This character refers to the development of the osteoderms on the dorsal surface of the skull as distinct, dorsally projecting tuberosities in *Exostinus* and *Xenosaurus*; a similar condition is seen in a number of other lizards (e.g. *Helodermoides*, *Heloderma*). Modified from Conrad (36).



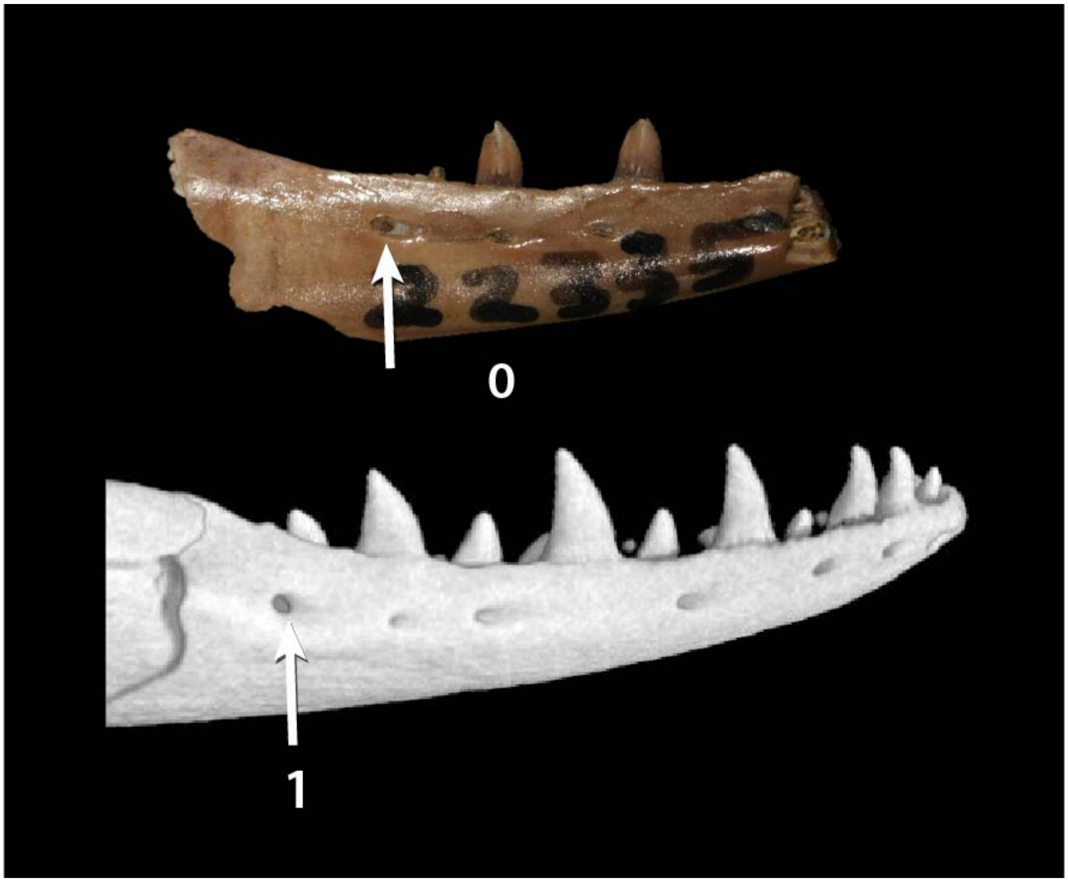
**612.** Dentary symphysis: dentary symphysis primarily developed dorsal to Meckel's groove (0) (shown in *Lonchisaurus trichurus*) or dentary symphysis V-shaped in medial view, with extensive accessory articular surface developed ventral to the Meckelian groove, and tip of dentaries contacting ventrally (shown in *Socognathus brachyodon*) (30). Polyglyphanodontians are characterized by a modified symphyseal morphology, where the symphysis extends dorsal and ventral to the Meckelian groove. A number of other lizards have convergently evolved this morphology, including Mosasauridae, Amphisbaenia, Dibamidae, and some Scincidae.

**613.** Dentary: subdental shelf abuts dorsal margin of splenial, or contact weakly developed (0) (shown in *Cemeterius monstrosus*) or subdental shelf with a slot for the dorsal margin of the splenial (1) (shown in *Socognathus brachyodon).* Polyglyphanodontians are characterized by a long slot below the subdental shelf that receives the dorsal margin of the splenial.

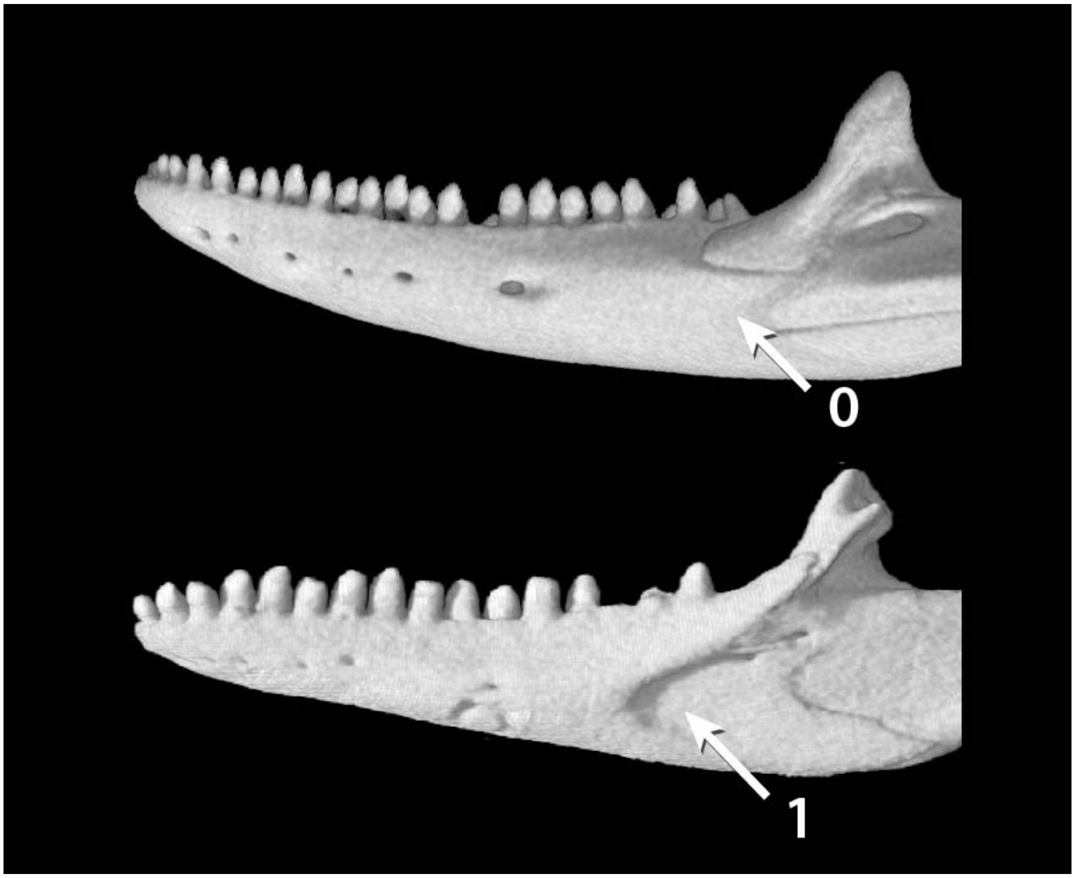
**614.** Intramandibular septum, caudal process: absent (0) (shown in *Socognathus brachyodon*), caudal process on posteroventral margin of intramandibular septum (1) (shown in *Colpodontosaurus cracens*). A process is present on the caudoventral margin of the intramandibular septum in *Shinisaurus*, Anguidae, and basal platynotans such as *Parasaniwa*.



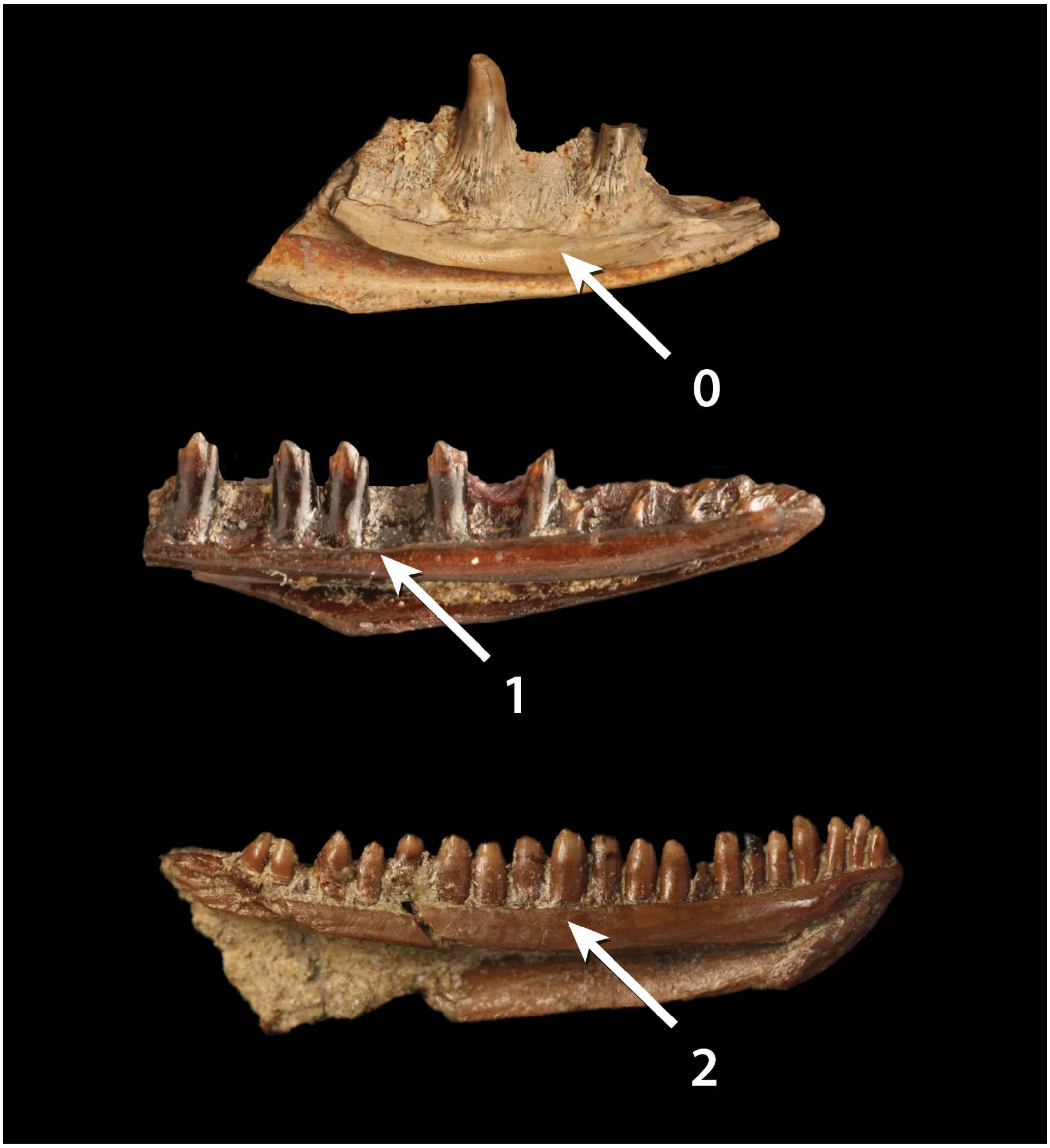
**615.** Intramandibular septum, attached ventrally (0) (shown in *Colpodontosaurus cracens*) or with extensive free ventral margin of intramandibular septum (2) (shown in “*Gerrhonotus*” sp.). (4). Anguids are characterized by a free ventral margin of the intramandibular septum.



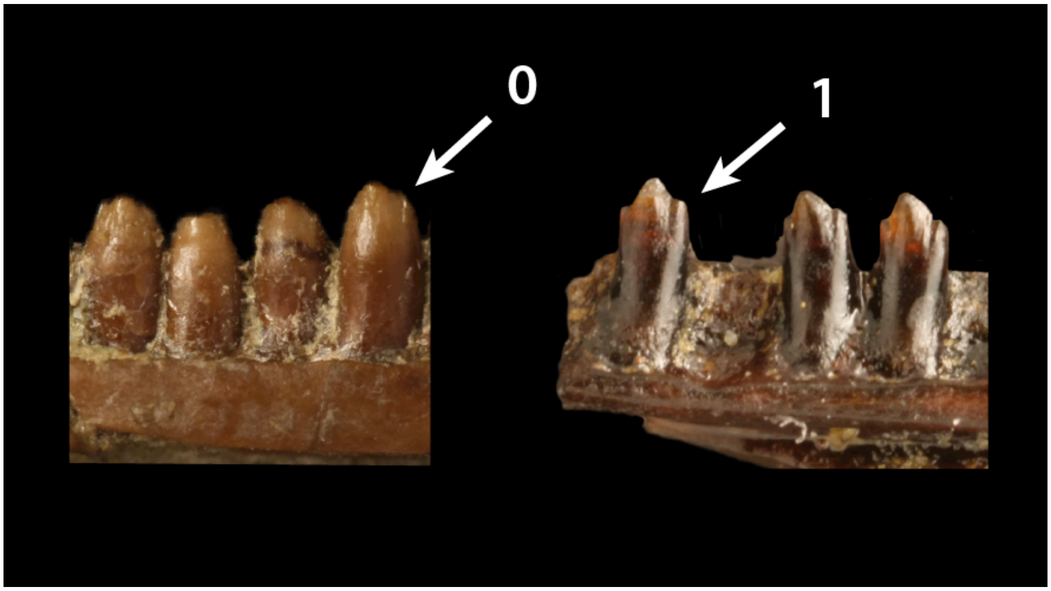
**616.** Dentary, mental foramina extend to back of mandibular toothrow absent (0) (shown in *Parasaniwa wyomingensis*) or present (1) (shown in *Varanus acanthurus*). In *Heloderma* and Varanidae, the last mental foramen is positioned at the back of the jaw; in contrast the mental foramen is more anteriorly located in Cretaceous stem Varanoidea. For taxa in which there is a complete toothrow, the derived condition is coded as present when the last mental foramen is present below the last tooth; for taxa in which the toothrow is shortened, the reference point is the back of the dentary.



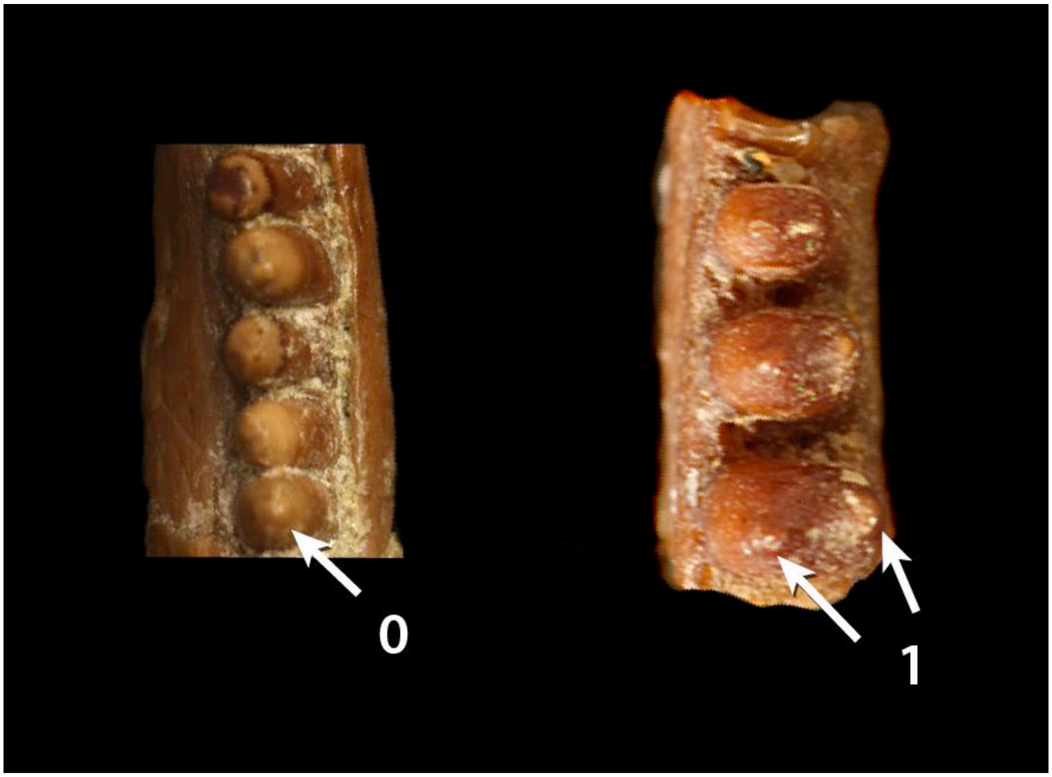
**617.** Dentary, adductor fossa on posterolateral surface of dentary: absent (0) (*Lacerta viridis*) or present (1) (*Scincus scincus*).



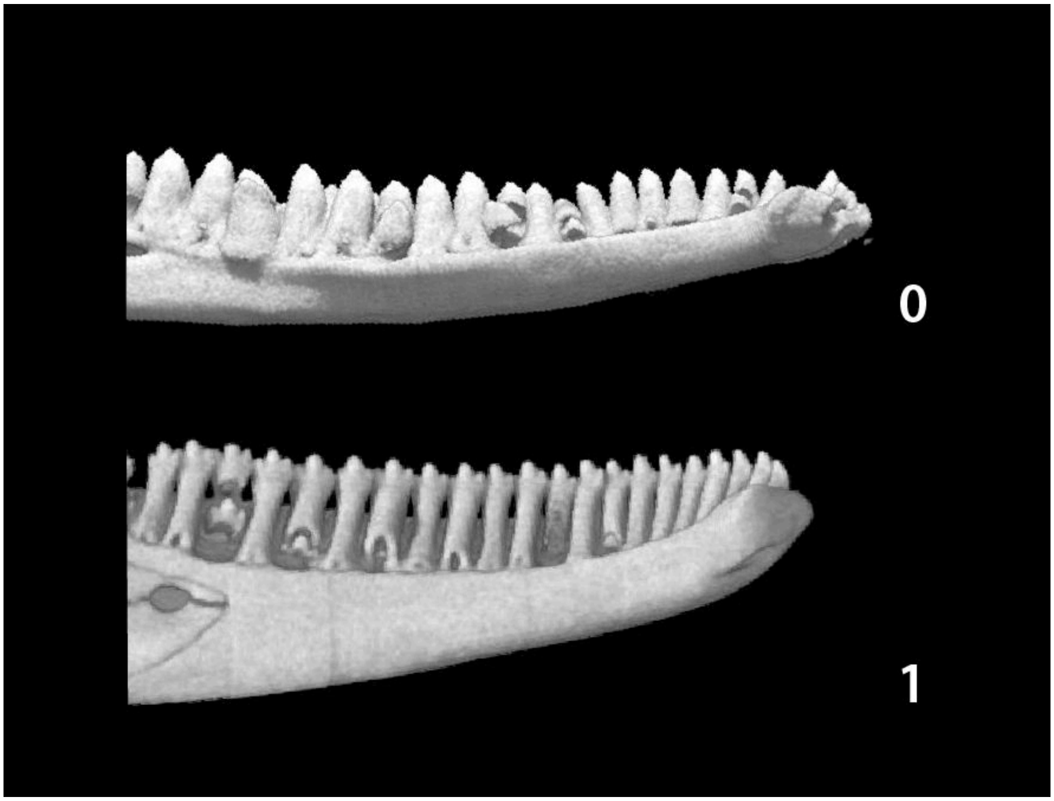
**618.** Dentary, tooth implantation: pleurodont (0), with teeth on medial surface of jaw, and tooth bases and subdental ridge extending at least 50% of the distance down the medial surface of the jaw (shown in *Cemeterius monstrosus*) or subpleurodont (1), with teeth subapically positioned, extending less than 50% down the medial surface of the jaw as measured at the middle of the toothrow (shown in *Obamadon gracilis*), or subacrodont/acrodont (2), with teeth extending 33% or less down the medial surface of the jaw (2) (shown in *Socognathus brachyodon*). Polyglyphanodontians are characterized by teeth that are positioned subapically (e.g, *Obamadon*, *Leptochamops*) to apically, as in *Polglyphanodon* and derived chamopsiids (e.g., *Socognathus*, *Chamops*). (ORDERED)



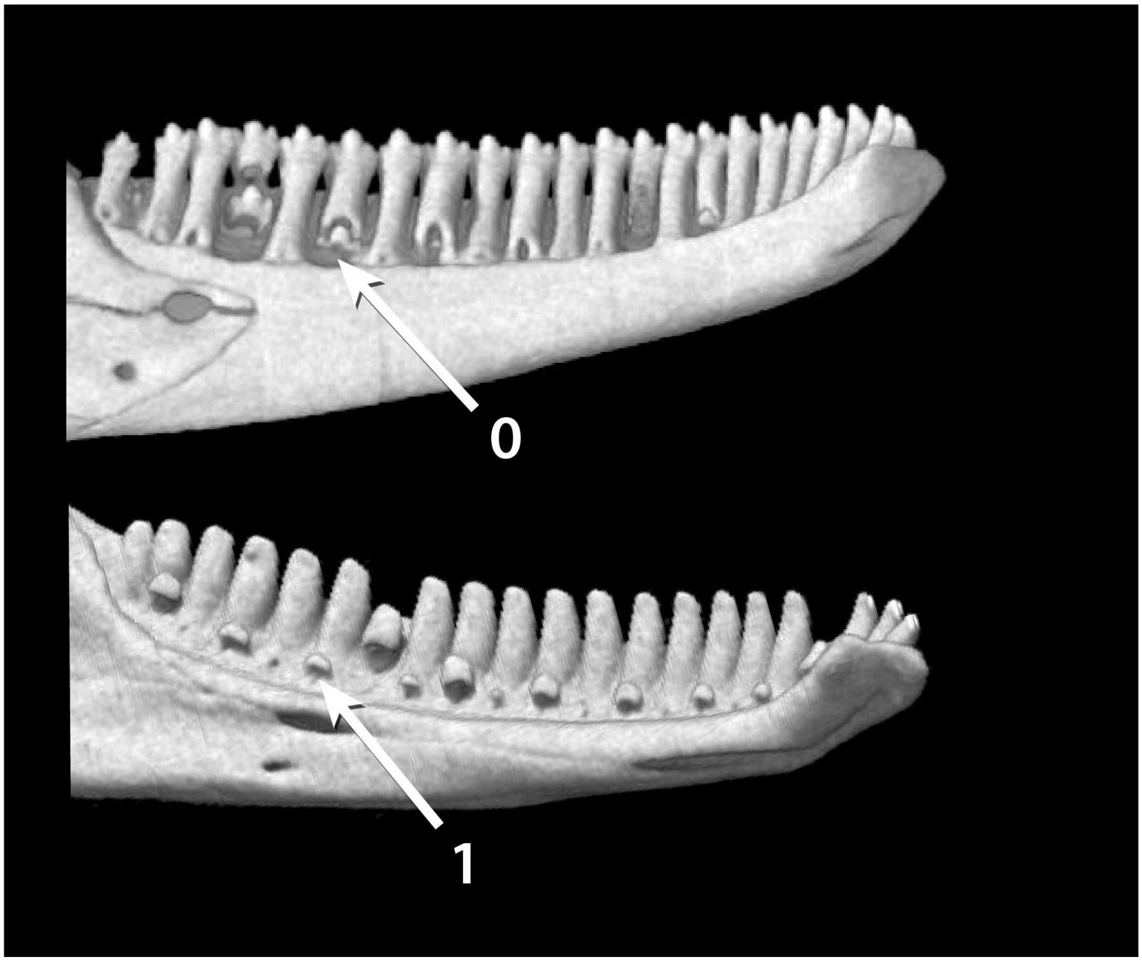
**619.** Teeth, crowns: unicuspid or with poorly differentiated accessory cusps (0) (shown in *Socognathus brachyodon*) or with distinct accessory cusps (1) (shown in *Obamadon gracilis*), Etheridge and de Queiroz 1988 (37). Primitively in lizards, the tooth has an apical cusp and low, bladelike mesial and distal cusps, whereas in a number of lizards, notably among many iguanas, polyglyphanodontians, and teioids, the accessory cusps are enlarged and distinctly separated from the main cusp by a conspicuous notch. Both states are coded as multicuspid by Gauthier et al. (2012: character 434). Character 622 is added here to differentiate between the two states. Primitively, polyglyphanodontians have state (1), but reduced accessory cusps appear to diagnose a subclade of Chamopsiidae (*Socognathus*, *Stypodontosaurus*, the Frenchman chamopsiid) and also occur in various Polyglyphanodontidae (e.g, *Polyglyphanodon*).



**620.** Teeth, crowns: accessory cusp developed lingual to tooth apex absent (0) (shown in *Socognathus brachyodon*) or present (1) (shown in *Peneteius aquilonius*) (27). In some lizards, the teeth have an accessory cusp developed medial to the apex of the tooth, which may be either separate from the main cusp (*Peneteius aquilonius*) or joined to it by a transverse blade (*Polyglyphanodon sternbergi*). *Teius teyou* has a similar morphology and is coded as having this condition, although here it appears to develop by medial rotation of the anterior accessory cusp lingually along with transverse expansion of the cutting surface of the tooth. By contrast, *Peneteius* and *Polyglyphanodon* retain accessory cusps in the standard mesial and distal position, which indicates that here the medial cusp is a novel structure.



**621.** Teeth, spatulate crowns absent (0) or present (1), Etheridge and de Queiroz, 1988 (37). Teeth with slender bases and labiolingually flattened, mesiodistally expanded crowns appear independently in a number of different lizards, notably among stem iguanids (*Isodontosaurus*), crown iguanids (e.g., *Dipsosaurus*) and Polyglyphanodontia (e.g., *Macrocephalosaurus chulsanensis*).



**625.** Replacement teeth: replacement teeth develop in association with replacement pits (0) or replacement teeth develop prior to onset of tooth replacement pit development, and outside of a replacement pit (1). Primitively in squamates, replacement teeth develop inside a replacement pit. In *Xenosaurus*, *Shinisaurus crocodilurus*, Anguidae, Varanoidea, and Serpentes, replacement teeth either develop prior to the development of an associated replacement pit, or replacement pits are absent.

### c. Materials Studied

Wherever possible, codings for Maastrichtian species were based on high-resolution digital photographs of the original material, typically shot at high magnification (1x-5x macro) and in multiple views. In a number of cases, however, codings are supplemented with, or based on material figured in, the literature, primarily Estes (4, 5, 38); and Gao and Fox (6). A full list of specimens and references used for coding is provided below.

Attribution of dissociated skeletal material follows Estes (39) and Gao and Fox (6); see also the supplementary information in Longrich et al. (35) for a detailed discussion of the rationale employed in referring dissociated material to a single species.

For all other species, the reader is referred to the material and methods section of Gauthier et al. (25).

***Pariguana lancensis***

Specimens: AMNH 22208, partial mandible

***Obamadon gracilis***

Specimens: UCMP 128873

***Tripennaculus* sp.**

Publications: Gao and Fox (6); "Iguanidae new genus and species (B)": p. 15, Figs 5G-J

***Leptochamops denticulatus***

Specimens: AMNH 22232, AMNH 22242, AMNH 22252, AMNH 22262, UCMP 46064, UCMP 46101, UCMP 47825, UCMP 49964, UCMP 49830, USNM 10749, dentaries; AMNH 25228, maxilla.

***Peneteius aquilonius***

Specimens: UCMP 124744
Publications: Estes (5), Nydam et al. (40)

**Frenchman polyglyphanodont**

Publications: Gao and Fox (6); "Family incertae sedis, new genus and species (B)": Fig. 25 D.

**Laramie polyglyphanodont**

Specimens: UCM 38828, dentary

***Meniscognathus altmani***

Specimens: AMNH 22106, maxilla; AMNH 25300, UCMP 46610, UCMP 49826, dentaries.

***Stypodontosaurus melletes***

Publications: Gao and Fox (6)

***Socognathus brachyodon***

Specimens: YPM-PU 16724, dentary; YPM-PU 21375, dentary.

***Haptosphenus placodon***

Specimens: AMNH 22222, anterior mandible; AMNH 129129, dentary.

***Chamops segnis***

Specimens: UCMP 49888, premaxillae; AMNH 26600, UCMP 49811, UCMP 49094, UCMP 46033, maxillae; UCMP 57418, frontals; AMNH 22005, UCMP 57147, parietals; UCMP 37146, quadrate; AMNH 22054, AMNH 15340, AMNH 22050, UCMP 46146, UCMP 49871, UCMP 49881, UCMP 46039, UCMP 49880, UCMP 71722, dentaries; UCMP 57149, vertebra; UCMP 57145, ilium.

***Lonchisaurus trichurus***

Specimens: AMNH 15446, dentary

***Lamiasaura ferox***

Specimens: UW 25116A, dentary

**Sweetwater Lizard**

Specimens: UW 25116B, dentary

***Estescincosaurus cooki***

Specimens: UCMP 46088, maxilla; UCMP 49994, dentary.

***Contogenys sloani***

Publications: Estes (38), Nydam and Fitzpatrick (41)

***Exostinus lancensis***

Specimens: AMNH 29777, AMNH 27056, UCMP 130731, frontals; UCMP 56093, parietals, AMNH 26686, UCMP 49848, UCMP 47829, dentaries.
Publications: Gao and Fox (6)

***Odaxosaurus piger***

Specimens: AMNH 22111, maxilla; AMNH 27072, parietals; AMNH 22055, UCMP 47756, dentaries.
Publications: Estes (4), Gao and Fox (6)

**“*Gerrhonotus*” sp.**

Specimens: AMNH 15441, maxilla; UCMP 49932, dentary
Publications: Estes (4)

***Litakis gilmorei***

Specimens*:* AMNH 22381, AMNH 15485, AMNH 15397, UCMP 47815, dentaries; UCMP 49798, maxilla.
Publications: Estes (4)

***Colpodontosaurus cracens***
Specimens: AMNH 15396, AMNH 15387, dentaries
Publications: Estes (4), Gao and Fox (6)

***Parasaniwa wyomingensis***
Specimens: AMNH 22164, UCMP 49799, YPM 3923, maxillae; UCMP 119286, frontals; AMNH 22012, AMNH 15555, parietals; AMNH 22362, AMNH 22335, AMNH 22698, AMNH 26655, UCM 43265, USNM 10797, USNM 10798, dentaries; AMNH 22801, vertebra.
Publications: Estes (4), Gao and Fox (6)

***Palaeosaniwa* sp.**
Specimens: UCMP 84144, dentary; UCMP 49955, UCMP 49958, teeth; UCMP 130717, dorsal vertebra.
Publications: Estes (1964), Balsai (42)

***Paraderma bogerti***
Specimens: AMNH 49940, maxilla; AMNH 49955, dentary; AMNH 26895, vertebra.
Publications: Estes (4), Gao and Fox (6)

***Cemeterius monstrosus***
Specimens: AMNH 2366, maxilla; YPM 1063, parietals; USNM 25870, dentary.

***Coniophis precedens***
Specimens: see Longrich et al. (35) for specimen list.

## d. Methods

Phylogenetic analysis of fossil lizards and *Coniophis* was conducted using a modified version of a recent, comprehensive phylogenetic analysis of squamata(25). To the existing matrix, we added 27 Maastrichtian lizards plus the snake *Coniophis*, and 12 additional characters, for a total of 219 species and 622 characters.

Phylogenetic analysis was conducted using PAUP 4.0 b10 (43)**.** The large number of taxa made a branch-and-bound search impractical; instead the analysis used the Parsimony Ratchet (44) implemented with the program PRAP2 (45). The analysis used 10 runs of the ratchet, set to 200 replicates per run with 25% character reweighting to generate a series of shortest trees. Then these trees were used as a starting point for a heuristic search with TBR to generate a total of 100,000 most parsimonious trees, from which the consensus was estimated. In addition to the strict consensus, the Adams consensus is presented, because several taxa (*Lonchisaurus*, the Sweetwater lizard, and *Phrynosoma*) act as wildcard taxa, causing resolution to break down in the strict consensus even though the trees are strongly in agreement about the placement of other species.

It proved impractical to examine the affinities of *Cerberophis* and the Lance Snake using the Gauthier et al. matrix (25). These snakes are known entirely on the basis of vertebrae whereas the matrix used here focuses largely on cranial morphology, and includes no vertebral characters that are specific to snakes among squamates. Instead, placement of these species follows Longrich et al. (35).

## e. Results

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Tree length = 5441
Consistency index (CI) = 0.1814
Homoplasy index (HI) = 0.8186
CI excluding uninformative characters = 0.1808
HI excluding uninformative characters = 0.8192
Retention index (RI) = 0.7927
Rescaled consistency index (RC) = 0.1438

Strict consensus of 100000 trees:

                                                         /---- Gephyrosaurus br
/--------------------------------------------------------+ /-- Sphenodon puncta
|                                                        \-+-- Kallimodon pulch
| /----------------------------------------------------------- Huehuecuetzpalli
| |                                         /----------------- Isodontosaurus g
| |                                         +----------------- Zapsosaurus scel
| |                                         +----------------- Polrussia mongol
| |                                         +----------------- Anolis carolinen
| |                                         +----------------- Aciprion formosu
| |                                         +----------------- Petrosaurus mear
| |                                         +----------------- Uta stansburiana
| |                                         +----------------- Sceloporus varia
| |                                         +----------------- Phrynosoma platy
| |                                         +----------------- Uma scoparia
| |                                         +----------------- Leiocephalus bar
| |                                         +----------------- Lamiasaura ferox
| |                                         |              /-- Temujinia elliso
| |                                         +--------------+-- Saichangurvel da
| |                                         |              /-- Crotaphytus coll
| |                                         +--------------+-- Gambelia wislize
| |                                         |              /-- Liolaemus bellii
| |                                         +--------------+-- Phymaturus pallu
| |                                         |              /-- Chalarodon madag
| |                                         +--------------+-- Oplurus cyclurus
| | /---------------------------------------+            /---- Polychrus marmor
| | |                                       +------------+ /-- Basiliscus basil
\-+ |                                       |            \-+-- Corytophanes cri
  | |                                       |            /---- Pristidactylus t
  | |                                       +------------+ /-- Leiosaurus catam
  | |                                       |            \-+-- Urostrophus vaut
  | |                                       |            /---- Pariguana lancen
  | |                                       +------------+ /-- Enyalioides lati
  | |                                       |            \-+-- Morunasaurus ann
  | |                                       |            /---- Uranoscodon supe
  | |                                       +------------+ /-- Plica plica
  | |                                       |            \-+-- Stenocercus guen
  | |                                       |          /------ Sauromalus ater
  | |                                       +----------+ /---- Brachylophus fas
  | |                                       |          \-+ /-- Armandisaurus ex
  | |                                       |            \-+-- Dipsosaurus dors
  | |                                       | /--------------- Ctenomastax parv
  | |                                       | |          /---- Priscagama gobie
  | |                                       | | /--------+ /-- Mimeosaurus cras
  | |                                       \-+ |        \-+-- Phrynosomimus as
  | |                                         | |          /-- Leiolepis bellia
  | |                                         \-+ /--------+-- Uromastyx aegypt
  | |                                           | |        /-- Brookesia brygoo
  | |                                           \-+  /-----+-- Chamaeleo laevig
  | |                                             \--+ /------ Physignathus coc
  \-+                                                \-+ /---- Calotes emma
    |                                                  \-+ /-- Agama agama
    |                                                    \-+-- Pogona vitticeps
    |                                             /----------- Obamadon gracili
    |                                             +----------- Leptochamops den
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|                                             +----------- Tripennaculus sp
|                                             |  /-------- Tchingisaurus mu
|                                             +--+ /------ Gobinatus arenos
|                                             |  \-+ /---- Adamisaurus magn
| /-------------------------------------------+    \-+ /-- Macrocephalosaur
| |                                           |      \-+-- POLYglyphanodon
| |                                           |      /---- Peneteius aquilo
| |                                           |      +---- Laramie polyglyp
| |                                           |      +---- Meniscognathus a
| |                                           \------+ /-- Haptosphenus pla
| |                                                  +-+-- Chamops segnis
| |                                                  | /-- Frenchman polygl
| |                                                  \-+-- Stypodontosaurus
| |                                                    \-- Socognathus brac
| |                                                    /-- Adriosaurus sues
| |                                           /--------+-- Pontosaurus
| | /-----------------------------------------+  /-------- Aigialosaurus da
| | |                                         \--+ /------ Platecarpus
| | |                                            \-+ /---- Clidastes
\-+ |                                              \-+ /-- Plotosaurus
  | |                                                \-+-- Tylosaurus
  | |  /-------------------------------------------------- Eichstaettisauru
  | |  +-------------------------------------------------- AMNH FR 21444
  | |  +-------------------------------------------------- Lacerta viridis
  | |  +-------------------------------------------------- Takydromus ocell
  | |  +-------------------------------------------------- Colobosaura mode
  | |  +-------------------------------------------------- Pholidobolus mon
  | |  +-------------------------------------------------- Paramacellodus
  | |  +-------------------------------------------------- Parmeosaurus scu
  | |  +-------------------------------------------------- Platysaurus impe
  | |  +-------------------------------------------------- Cordylus mossamb
  | |  +-------------------------------------------------- Zonosaurus ornat
  | |  +-------------------------------------------------- Cordylosaurus su
  | |  +-------------------------------------------------- Myrmecodaptria m
  \-+  +-------------------------------------------------- Carusia intermed
    |  +-------------------------------------------------- Globaura venusta
    |  +-------------------------------------------------- Hymenosaurus cla
    |  +-------------------------------------------------- Eoxanta lacertif
    |  +-------------------------------------------------- Plestiodon (Eume
    |  +-------------------------------------------------- Scincus scincus
    |  +-------------------------------------------------- Brachymeles grac
    |  +-------------------------------------------------- Amphiglossus spl
    |  +-------------------------------------------------- Estescincosaurus
    |  +-------------------------------------------------- Contogenys sloan
    |  +-------------------------------------------------- Lonchisaurus tri
    |  +-------------------------------------------------- Sweetwater Lizar
    |  |                                               /-- Acontias perciva
    |  +-----------------------------------------------+-- Feylinia polylep
    |  |                                               /-- Callopistes macu
    |  |                                             /-+-- Tupinambis tegui
    |  +---------------------------------------------+ /-- Aspidoscelis tig
    \--+                                             \-+-- Teius teyou
       |                                           /------ Trachylepis (Mab
       +-------------------------------------------+ /---- Eugongylus rufes
       |                                           \-+ /-- Sphenomorphus so
       |                                             \-+-- Tiliqua scincoid
       |                                           /------ Tepexisaurus tep
       |                                           | /---- Lepidophyma flav
       +-------------------------------------------+ +---- Palaeoxantusia "
       |                                           \-+ /-- Cricosaura typic
       |                                             \-+-- Xantusia vigilis
       |                                               /-- Delma borea
       |                                         /-----+-- Lialis burtonis
       |                                         | /------ Strophurus  cili
       |                                         | +------ Rhacodactylus au
       +-----------------------------------------+ +------ Saltuarius (Phyl
       |                                         | +------ Teratoscincus pr
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|                                         \-+------ Gekko gecko
|                                           |   /-- Gonatodes albogu
|                                           +---+-- Phelsuma lineata
|                                           | /---- Aeluroscalobates
|                                           \-+ /-- Coleonyx variega
|                                             \-+-- Eublepharis macu
|                                             /---- Exostinus lancen
| /-------------------------------------------+ /-- Xenosaurus platy
| |                                           \-+-- Xenosaurus grand
| |                                       /-------- Pseudopus (Ophis
| |                                       |   /---- Odaxosaurus pige
| | /-------------------------------------+ /-+ /-- Peltosaurus gran
| | |                                     | | \-+-- Helodermoides tu
\-+ |                                     \-+ /---- "Gerrhonotus" sp
  | |                                       \-+ /-- Celestus enneagr
  | |                                         \-+-- Elgaria multicar
  | | /-------------------------------------------- Shinisaurus croc
  | | +-------------------------------------------- Litakis gilmorei
  | | +-------------------------------------------- Colpodontosaurus
  \-+ |                        /------------------- Cemeterius monst
    | |                        | /----------------- Gobiderma pulchr
    | +------------------------+ +----------------- Palaeosaniwa sp.
    | |                        | +----------------- Paraderma bogert
    | |                        \-+----------------- Parasaniwa wyomi
    | |                          | /--------------- Estesia mongolie
    | |                          | | /------------- Aiolosaurus orie
    | |                          \-+ |          /-- Heloderma horrid
    \-+                            \-+ /--------+-- Heloderma suspec
      |                              \-+  /-------- Lanthanotus born
      |                                \--+ /------ Saniwa
      |                                   \-+ /---- Varanus acanthur
      |                                     \-+ /-- Varanus salvator
      |                                       \-+-- Varanus exanthem
      | /------------------------------------------ Sineoamphisbaena
      | | /---------------------------------------- Anniella pulchra
      | | |                                     /-- Anelytropsis pap
      | | |                            /--------+-- Dibamus novaegui
      \-+ |                            |      /---- Rhineura florida
        | |                            |  /---+ /-- Spathorhynchus f
        | | /--------------------------+  |   \-+-- Dyticonastis ren
        | | |                          |  |     /-- Bipes biporus
        \-+ |                          \--+ /---+-- Bipes canalicula
          | |                             | |   /-- Trogonophis wieg
          | |                             \-+ /-+-- Diplometopon zar
          | |                               \-+ /-- Geocalamus acutu
          | |                                 \-+-- Amphisbaena fuli
          | | /------------------------------------ Najash rionegrin
          \-+ +------------------------------------ Dinilysia patago
            | +------------------------------------ Anomochilus leon
            | +------------------------------------ Uropeltis melano
            | +------------------------------------ Coniophis praece
            | |                                 /-- Anilius scytale
            | +---------------------------------+-- Cylindrophis ruf
            | |                                 /-- Leptotyphlops du
            \-+                               /-+-- Typhlops jamaice
              +-------------------------------+ /-- Liotyphlops albi
              |                               \-+-- Typhlophis squam
              |                                 /-- Xenopeltis unico
              | /-------------------------------+-- Loxocemus bicolo
              | |                               /-- Xenophidion acan
              | | /-----------------------------+-- Casarea dussumie
              \-+ |                           /---- Haasiophis terra
                | |  /------------------------+ /-- Eupodophis desco
                \-+  |                        \-+-- Pachyrhachis pro
                  |  |                          /-- Exiliboa placata
                  |  |                      /---+-- Ungaliophis cont
                  \--+ /--------------------+ /---- Eryx colubrinus
```

```
                                | |                    \-+ /-- Calabaria reinha
                                | |                      \-+-- Lichanura trivir
                                | |                        /-- Epicrates striat
                                \-+                      /-+-- Boa constrictor
                                  | /--------------------+ /-- Aspidites melano
                                  | |                    \-+-- Python molurus
                                  | |                      /-- Trachyboa boulen
                                  \-+ /--------------------+-- Tropidophis haet
                                    | | /--------------------- Xenodermus javan
                                    \-+ | /------------------- Acrochordus gran
                                      \-+ | /----------------- Pareas hamptoni
                                        | | |            /---- Lycophidion cape
                                        \-+ +------------+ /-- Aparallactus wer
                                          | |            \-+-- Atractaspis irre
                                          | |            /---- Lampropeltis get
                                          \-+            +---- Coluber constric
                                            | /----------+ /-- Natrix natrix
                                            | |          | +-- Afronatrix anosc
                                            | |          \-+-- Amphiesma stolat
                                            | |            +-- Thamnophis marci
                                            \-+            \-- Xenochrophis pis
                                              | /------------- Notechis scutatu
                                              | |        /---- Naja naja
                                              | +--------+ /-- Laticauda colubr
                                              \-+        \-+-- Micrurus fulvius
                                                | /----------- Causus rhombeatu
                                                \-+  /-------- Azemiops feae
                                                  \--+ /------ Daboia russelli
                                                     \-+ /---- Agkistrodon cont
                                                       \-+ /-- Bothrops asper
                                                         \-+-- Lachesis muta

Adams consensus of 100000 trees:

                                                          /--- Gephyrosaurus br
/---------------------------------------------------------+/-- Sphenodon puncta
|                                                         \+-- Kallimodon pulch
| /----------------------------------------------------------- Huehuecuetzpalli
| |                                  /------------------------ Lamiasaura ferox
| |                                  |           /------------ Ctenomastax parv
| |                                  |           |        /--- Priscagama gobie
| |                                  |           | /------+/-- Mimeosaurus cras
| |                                  +-----------+ |      \+-- Phrynosomimus as
| |                                  |           | |       /-- Leiolepis bellia
| |                                  |           \-+ /-----+-- Uromastyx aegypt
| |                                  |             | |     /-- Brookesia brygoo
| |                                  |             \-+/----+-- Chamaeleo laevig
| |                                  |               \+ /----- Physignathus coc
| |/---------------------------------+                \-+ /--- Calotes emma
| ||                                 |                  \-+/-- Agama agama
| ||                                 |                    \+-- Pogona vitticeps
| ||                                 |                     /-- Temujinia elliso
| ||                                 | /-------------------+-- Saichangurvel da
| ||                                 | |                   /-- Isodontosaurus g
| ||                                 | +-------------------+-- Zapsosaurus scel
| ||                                 | | /-------------------- Polrussia mongol
| ||                                 | | +-------------------- Phrynosoma platy
\-+|                                 \-+ |              /----- Aciprion formosu
  ||                                   | |              | /--- Polychrus marmor
  ||                                   | |              +-+/-- Basiliscus basil
  ||                                   | +--------------+ \+-- Corytophanes cri
  ||                                   \-+              | /--- Pariguana lancen
  ||                                     |              \-+/-- Enyalioides lati
  ||                                     |                \+-- Morunasaurus ann
  ||                                     |/------------------- Anolis carolinen
  ||                                     ||               /--- Pristidactylus t
  ||                                     || /-------------+/-- Leiosaurus catam
```

```
||                                     \+ |             \+-- Urostrophus vaut
||                                      | |              /-- Crotaphytus coll
||                                      \-+ /------------+-- Gambelia wislize
||                                        | |         /----- Sauromalus ater
||                                        | |/--------+ /--- Brachylophus fas
||                                        \-+|        \-+/-- Armandisaurus ex
||                                          ||          \+-- Dipsosaurus dors
||                                          \+           /-- Liolaemus bellii
||                                           | /---------+-- Phymaturus pallu
\+                                           | |        /--- Uranoscodon supe
 |                                           \-+ /------+/-- Plica plica
 |                                             | |      \+-- Stenocercus guen
 |                                             \-+       /-- Chalarodon madag
 |                                               | /-----+-- Oplurus cyclurus
 |                                               \-+/------- Leiocephalus bar
 |                                                 \+ /----- Sceloporus varia
 |                                                  \-+ /--- Petrosaurus mear
 |                                                    \-+/-- Uta stansburiana
 |                                                      \+-- Uma scoparia
 |                                                 /-------- Obamadon gracili
 |                                                 +-------- Tripennaculus sp
 |                                                 |/------- Tchingisaurus mu
 |                                                 ++ /----- Gobinatus arenos
 |                                                 |\-+ /--- Adamisaurus magn
 | /-----------------------------------------------+  \-+/-- Macrocephalosaur
 | |                                               |    \+-- POLYglyphanodon
 | |                                               |/------- Leptochamops den
 | |                                               || /----- Peneteius aquilo
 | |                                               \+ +----- Laramie polyglyp
 | |                                                | +----- Meniscognathus a
 | |                                                \-+  /-- Haptosphenus pla
 | |                                                  | /+-- Chamops segnis
 | |                                                  \-+/-- Frenchman polygl
 | |                                                    \+-- Stypodontosaurus
 | |                                                     \-- Socognathus brac
 | |                                                     /-- Adriosaurus sues
 | |                                               /-----+-- Pontosaurus
 \-+ /---------------------------------------------+/------- Aigialosaurus da
   | |                                             \+ /----- Platecarpus
   | |                                              \-+ /--- Clidastes
   | |                                                \-+/-- Plotosaurus
   | |                                                  \+-- Tylosaurus
   | |/----------------------------------------------------- Sweetwater Lizar
   | ||                                            /-------- Eichstaettisauru
   | ||                                            +-------- AMNH FR 21444
   | ||                                            |     /-- Delma borea
   | |+--------------------------------------------+/----+-- Lialis burtonis
   | ||                                            || /----- Strophurus  cili
   | ||                                            || |  /-- Rhacodactylus au
   | ||                                            \+ +--+-- Saltuarius (Phyl
   \-+|                                             | | /--- Aeluroscalobates
     ||                                             \-+-+/-- Coleonyx variega
     ||                                               | \+-- Eublepharis macu
     ||                                               | /--- Teratoscincus pr
     ||                                               | +--- Gekko gecko
     ||                                               \-+/-- Gonatodes albogu
     ||                                                 \+-- Phelsuma lineata
     ||                                /-------------------- Lonchisaurus tri
     ||                                |                 /-- Lacerta viridis
     ||                                |            /----+-- Takydromus ocell
     ||                                |            |    /-- Colobosaura mode
     ||                                +------------+ /--+-- Pholidobolus mon
     \+                                |            | |  /-- Callopistes macu
      |                                |            \-+ /+-- Tupinambis tegui
      | /------------------------------+              \-+/-- Aspidoscelis tig
      | |                              |                \+-- Teius teyou
      | |                              |/------------------- Parmeosaurus scu
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| |                              |+------------------- Estescincosaurus
| |                              || /----------------- Paramacellodus
| |                              || |              /-- Platysaurus impe
| |                              \+ |             /+-- Cordylus mossamb
| |                               | |         /---+/-- Zonosaurus ornat
| |                               | |         |   \+-- Cordylosaurus su
| |                               \-+ /-------+ /----- Tepexisaurus tep
| |                                 | |       | | /--- Lepidophyma flav
| |                                 | |       \-+ +--- Palaeoxantusia "
| |                                 | |         \-+/-- Cricosaura typic
| |                                 | |           \+-- Xantusia vigilis
| |                                 \-+            /-- Myrmecodaptria m
| |                                   |/-----------+-- Carusia intermed
| |                                   ||        /----- Globaura venusta
| |                                   || /------+ /--- Hymenosaurus cla
\-+                                   \+ |      \-+/-- Eoxanta lacertif
  |                                    | |        \+-- Contogenys sloan
  |                                    \-+ /---------- Plestiodon (Eume
  |                                      | | /-------- Scincus scincus
  |                                      \-+ |     /-- Brachymeles grac
  |                                        | |    /+-- Amphiglossus spl
  |                                        \-+/---+/-- Acontias perciva
  |                                          ||   \+-- Feylinia polylep
  |                                          \+ /----- Trachylepis (Mab
  |                                           \-+ /--- Eugongylus rufes
  |                                             \-+/-- Sphenomorphus so
  |                                               \+-- Tiliqua scincoid
  |                                               /--- Exostinus lancen
  | /---------------------------------------------+/-- Xenosaurus platy
  | |                                             \+-- Xenosaurus grand
  | |                                         /------- Pseudopus (Ophis
  | |                                         |   /--- Odaxosaurus pige
  | | /---------------------------------------+ /-+/-- Peltosaurus gran
  \-+ |                                       | | \+-- Helodermoides tu
    | |                                       \-+ /--- "Gerrhonotus" sp
    | |                                         \-+/-- Celestus enneagr
    | |                                           \+-- Elgaria multicar
    | |/---------------------------------------------- Shinisaurus croc
    \-++---------------------------------------------- Litakis gilmorei
      |+---------------------------------------------- Colpodontosaurus
      ||                          /------------------- Cemeterius monst
      ||                          | /----------------- Palaeosaniwa sp.
      || /------------------------+ +----------------- Parasaniwa wyomi
      || |                        \-+ /--------------- Paraderma bogert
      \+ |                          | |/-------------- Gobiderma pulchr
       | |                          \-+| /------------ Estesia mongolie
       | |                            \+ | /---------- Aiolosaurus orie
       | |                             \-+ |       /-- Heloderma horrid
       | |                               \-+ /-----+-- Heloderma suspec
       | |                                 \-+/------- Lanthanotus born
       \-+                                   \+ /----- Saniwa
         |                                    \-+ /--- Varanus acanthur
         |                                      \-+/-- Varanus salvator
         |                                        \+-- Varanus exanthem
         | /------------------------------------------ Sineoamphisbaena
         | |/----------------------------------------- Anniella pulchra
         | ||                                      /-- Anelytropsis pap
         \-+|                                /-----+-- Dibamus novaegui
           ||                                |    /--- Rhineura florida
           ||                                |/---+/-- Spathorhynchus f
           \+ /------------------------------+|   \+-- Dyticonastis ren
            | |                              ||    /-- Bipes biporus
            | |                              \+ /--+-- Bipes canalicula
            | |                               | |  /-- Trogonophis wieg
            | |                               \-+ /+-- Diplometopon zar
            \-+                                 \-+/-- Geocalamus acutu
              |                                   \+-- Amphisbaena fuli
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| /------------------------------------- Najash rionegrin
| +------------------------------------- Coniophis praece
| |/------------------------------------ Dinilysia patago
\-+|                                 /-- Leptotyphlops du
  ||                                /+-- Typhlops jamaice
  \+ /------------------------------+/-- Liotyphlops albi
   | |                              \+-- Typhlophis squam
   \-+ /-------------------------------- Uropeltis melano
     | |/------------------------------- Anomochilus leon
     \-+|                            /-- Anilius scytale
       || /--------------------------+-- Cylindrophis ruf
       \+ |                          /-- Xenopeltis unico
        | | /------------------------+-- Loxocemus bicolo
        \-+ |                        /-- Xenophidion acan
          | | /----------------------+-- Casarea dussumie
          \-+ |                     /--- Haasiophis terra
            | |/--------------------+/-- Eupodophis desco
            \-+|                    \+-- Pachyrhachis pro
              ||                     /-- Exiliboa placata
              ||                  /--+-- Ungaliophis cont
              \+ /----------------+ /--- Eryx colubrinus
               | |                \-+/-- Calabaria reinha
               | |                  \+-- Lichanura trivir
               | |                   /-- Epicrates striat
               \-+                  /+-- Boa constrictor
                 | /----------------+/-- Aspidites melano
                 | |                \+-- Python molurus
                 | |                 /-- Trachyboa boulen
                 \-+/----------------+-- Tropidophis haet
                   || /----------------- Xenodermus javan
                   \+ | /--------------- Acrochordus gran
                    \-+ |/-------------- Pareas hamptoni
                      | ||          /--- Lycophidion cape
                      \-++----------+/-- Aparallactus wer
                        ||          \+-- Atractaspis irre
                        ||        /----- Lampropeltis get
                        \+        +----- Coluber constric
                         | /------+ /--- Natrix natrix
                         | |      | +--- Afronatrix anosc
                         | |      \-+/-- Amphiesma stolat
                         | |        \+-- Thamnophis marci
                         \-+         \-- Xenochrophis pis
                           | /---------- Notechis scutatu
                           | |      /--- Naja naja
                           | +------+/-- Laticauda colubr
                           \-+      \+-- Micrurus fulvius
                             | /-------- Causus rhombeatu
                             \-+/------- Azemiops feae
                               \+ /----- Daboia russelli
                                \-+ /--- Agkistrodon cont
                                  \-+/-- Bothrops asper
                                    \+-- Lachesis muta
```

## f. Discussion

### i. Placement of fossil forms.

The late Maastrichtian lizards are known on the basis of very limited material, primarily jaws, although in some cases other skull bones are also known, including maxillae, parietals, and frontals. Despite this, most species can be assigned to a major clade and often to more exclusive subclades; for instance, *Odaxosaurus piger* can be assigned to Anguimorpha, Anguidae, and Glyptosaurinae. The ability to place a species in a phylogeny therefore depends more upon a reliable phylogeny and the presence of informative synapomorphies than on the completeness of the material, and given that many of the characters that diagnose major clades relate to the jaws and teeth, the jaw remains can be highly informative. However, while it is often possible to assign fragmentary fossils to subclades, relationships within these subclades are sometimes difficult to resolve. It is this lack of resolution at the species level- particularly within the highly diverse Polyglyphanodontia- that is primarily responsible for the very large number of most-parsimonious trees found here.

Many of the relationships found here are in close agreement with previous systematic work, but there are also significant differences. Species previously assigned to Teiidae (4-6) are here found to be more closely related to *Polyglyphanodon*, as found by several recent studies (27, 30). However, the present analysis follows Gauthier et al. (25) in placing the Polyglyphanodontia not only away from Teiidae but outside of Scleroglossa entirely. *Tripennaculus* n. sp., previously referred to the Iguanidae (6), is also found to represent a polyglyphanodontian, as were several other lizards described by Gao and Fox (6).

The present analysis confirms Estes' supposition that *Estescincosaurus cooki* is related to the scincomorphs (4), and also places *Contogenys sloani* with scincoids as proposed by Estes (38). However, the present analysis was unable to confirm placement of *Contogenys* along the stem of Xantusiidae as previously suggested (41) and instead places it among the Globauridae, a group of stem scincoids.

Our results also corroborate the hypothesis that *Exostinus* represents an early member of the xenosaur lineage (4, 36, 46). The proposed anguimorph affinities of *Litakis gilmorei* (4) were also supported, as was the assignment of *Colpodontosaurus* to a basal position in Platynota (4, 36).

The analysis also corroborates the platynotan affinities of *Parasaniwa wyomingensis* (2) and in particular the hypothesis that *Parasaniwa* represents a stem varanoid (36). *Palaeosaniwa* is also referred to the Platynota (2, 4, 36, 42) but no derived characters were found to support referral to the Varanidae (4). Neither were any characters identified supporting referral to "Monstersauria" (36, 42, 47). Conrad (36) has argued that *Palaeosaniwa* shares a derived form of tooth implantation with *Heloderma* in which the tooth base extends past the lateral margin of the tooth-bearing element. However, this feature is clearly evident in some specimens of *Parasaniwa* (e.g., UCMP 49799) and *Varanus* (e.g., *Varanus panoptes* YPM 10394) and seems simply to be a result of the expansion of the tooth base in Platynota, which is taken to a greater or lesser degree in various species. *Paraderma* has also been referred to the Monstersauria (4, 36, 47) but again no characters were found to support this assignment; the extensive dermal armor shared by these forms and Helodermatidae may instead represent an anguimorph plesiomorphy.

Finally, *Coniophis precedens* is placed outside Serpentes as a basal member of the Ophidia, consistent with the findings of Longrich et al. (34). In the present analysis *Coniophis* is recovered as sister to *Najash rionegrina* rather than basal to *Najash*, although it should be noted that the present analysis was not primarily aimed at resolving the relationships of basal snakes (as was the goal with the Longrich et al. matrix).

A few species resist classification, however. Notably, *Lamiasaura ferox* and the Sweetwater Lizard could not be assigned to any major clade. In the case of the Sweetwater Lizard, the fossil may simply be too fragmentary. In the case of *Lamiasaura*, however, it may be that this unusual lizard simply does not belong to any major living group.

### ii. Relationships between major clades.

Another issue concerns the interrelationships of the the major clades. In particular, the placement of highly modified forms, such as the limbless lizards (Ophidia, Amphisbaenia, Dibamidae, Anniellidae) and the mosasaurs is complicated by morphological convergence (25), both in terms of specialization of the feeding apparatus for consuming relatively large prey, the evolution of a long body with reduced limbs, and in the case of the burrowing forms, specialization of the ears and the evolution of a highly reinforced braincase. The analysis consistently recovers a limbless clade (Serpentes, Amphisbaenia, Dibamidae, plus Anniellidae) but molecular data strongly suggests that the group is polyphyletic (48, 49) and many morphological characters are also at odds with this hypothesis (snakes, e.g., resemble varanoids but not amphisbaenians in lacking tooth replacement pits). The position of this 'clade' is also highly unstable, and earlier versions of this matrix have placed the limbless forms either next to Anguimorpha, inside Anguimorpha (the position found here) or inside Scincidae. The position of mosasaurs is also highly unstable, with Mosasauria variously being recovered outside Scleroglossa (as in Gauthier et al., 2012) or alongside the limbless forms (i.e. "Pythonomorpha"). Resolving these conflicts is beyond the scope of the present analysis, however it is important to note that the position of the fossils is robust to these tree changes, i.e. the fossils are consistently placed in the same major clades regardless of the order of branching between these clades.

A combined molecular-morphological analysis (49) could be effective in dealing with morphological convergence and help break up the limbless forms, but may introduce other artifacts, e.g., molecular data strongly supports placement of Helodermatidae with Anguidae (48) a topology strongly rejected by morphology (25). Molecules have also been unable to resolve the placement of snakes within squamata (48, 49) and strongly conflict with morphology on the interrelationships of the major clades (Iguania, Gekkota, Scincoidea, Lacertoidea, Anguimorpha, Serpentes) (25). The fact that both molecules and morphology recover the same major clades but arrive at fundamentally different hypotheses about their interrelationships is both puzzling and troubling. In particular, the inability to place snakes using either morphology or molecules strongly hints that a common problem is facing both data sets. It may be that a deep, ancient radiation- in which many branching events occur in a short window of time, producing lineages that persist for many tens of millions of years- is inherently vulnerable to long-branch attraction, either when dealing with morphology or molecules.

## 5. Resampling

To examine the effects of sampling on diversity, we conducted rarefaction analyses using occurrence data (SI Appendix 2) for late Maastrichtian and early Paleocene assemblages. Rarefaction was conducted using classic rarefaction, resampling fossil occurrence data, and sample-based rarefaction (50).

Classic rarefaction was conducted using the software program PAST (51); classic rarefaction suggests that the difference in diversity is not a function of number of occurrences. Instead, this analysis indicates that the Paleocene is undersampled relative to the Maastrichtian, because the Paleocene curve levels out with more specimens, while the Maastrichtian curve is still increasing. This suggests that rarity of fossils in the Paleocene (fewer fossils per locality, and therefore fewer species per locality) cannot explain the loss of diversity.

Sample-based rarefaction was conducted using the software program EstimateS (52). EstimateS conducts rarefaction of samples using analytical formulas (rather than resampling) to compute a species-accumulation (Mao-Tao) curve as a function of number of species versus number of localities. This analysis suggests that sampling (in terms of number of localities) does not explain the difference in diversity between the Maastrichtian and Paleocene; indeed, the Maastrichtian appears to be undersampled relative to the Paleocene (Fig. 3) so improved sampling in terms of more localities is predicted to increase the difference in species richness between the Maastrichtian and Paleocene assemblages.

## 6. Morphometric Analysis

Teeth chosen for morphometric analysis were the largest preserved teeth from the posterior half of the dentary tooth row of a representative specimen of the species. Where no well-preserved dentary teeth were available (e.g., *Coniophis*) maxillary teeth were used instead.

Landmarks (Fig. S11), were placed on photographs of teeth in lingual view at the apex of the tooth (landmark/LM 6) and the deepest point of the base (LM 2), the edges of the basal region (LM 3 and 4), and on the accessory cusps and troughs if present (LM 4, 5, 7, 8). For unicuspid teeth, all cusp landmarks (4-8) were placed at the apex of the single cusp of the tooth. If troughs were not present, landmarks were placed at the midpoints of the flat 'shoulder' regions. Landmarks were digitized with TPSDig (53) and a principle components analysis (PCA) was performed with TPSRelW (54) and MorphoJ (55). The first principle component axis explained 49.64% of the total variation in the sample. The second principle component axis explained 24.62% of the total variation in the sample. The remaining axes explained less than 15% of the total variation each.

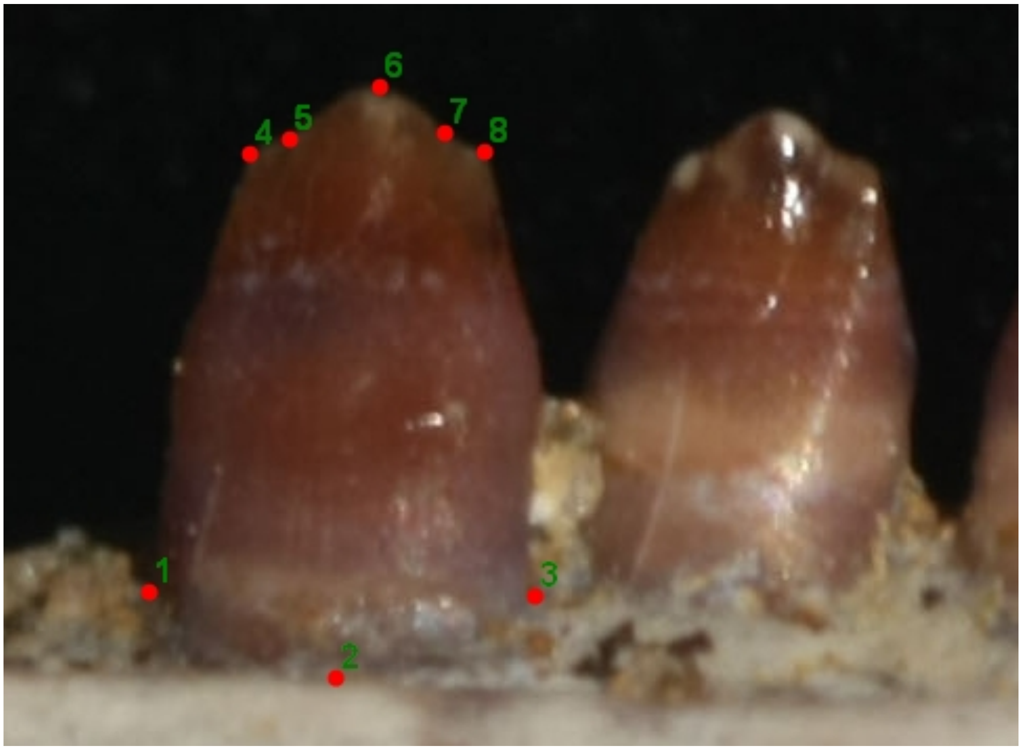

**Fig. S11.** Landmarks used for morphometric analysis of lizard tooth shape.

Metrics of disparity were calculated using scores for the first 5 principal coordinates (Table S3), which explain over 95% of the variation. Four metrics were calculated: sum and product of the ranges, and sum and product of the variances (56).

All four disparity metrics show a decrease across the K-Pg boundary (Table S3). In terms of tooth morphology, K-Pg survivors exhibit lower disparity in terms of sum of ranges, product of ranges, sum of variances, and product of variances (Fig. S12). All four metrics then increase with the addition of species that occur only in the Paleocene (here interpreted as opportunistic colonists that invaded the region following the extinction). Product of ranges is a metric of morphospace volume, therefore it can be concluded that morphospace occupation shows a decline between the Cretaceous and early Paleocene.

**Table S3.** Sum of ranges, product of ranges, sum of variances, and product of variances for species occurring in the Cretaceous, Cretaceous-Paleocene boundary crossers, and boundary-crossers plus Paleocene immigrants.

|  | Sum of Ranges | Product of Ranges | Sum of Variances | Product of Variances |
|---|---|---|---|---|
| K | 1.413 | 0.000982395 | 0.03194348 | 1.01E-12 |
| K-P | 0.702 | 4.31E-05 | 0.0163577 | 1.62E-13 |
| K-P + P | 0.989 | 0.000250231 | 0.02222938 | 2.57E-13 |

An F-test of variance found a difference in variance along PC1 between the Cretaceous fauna, K-Pg boundary crossers, and the survivor-immigrant fauna occuring in the basal Paleocene but the difference falls just short of significance ($p = .055$). Other PC axes showed no significant difference in variance. An MPMANOVA finds no difference in the means of the Cretaceous fauna, survivors, and Paleocene survivor-immigrant fauna, i.e., the overall position of forms in morphospace did not shift across the boundary.

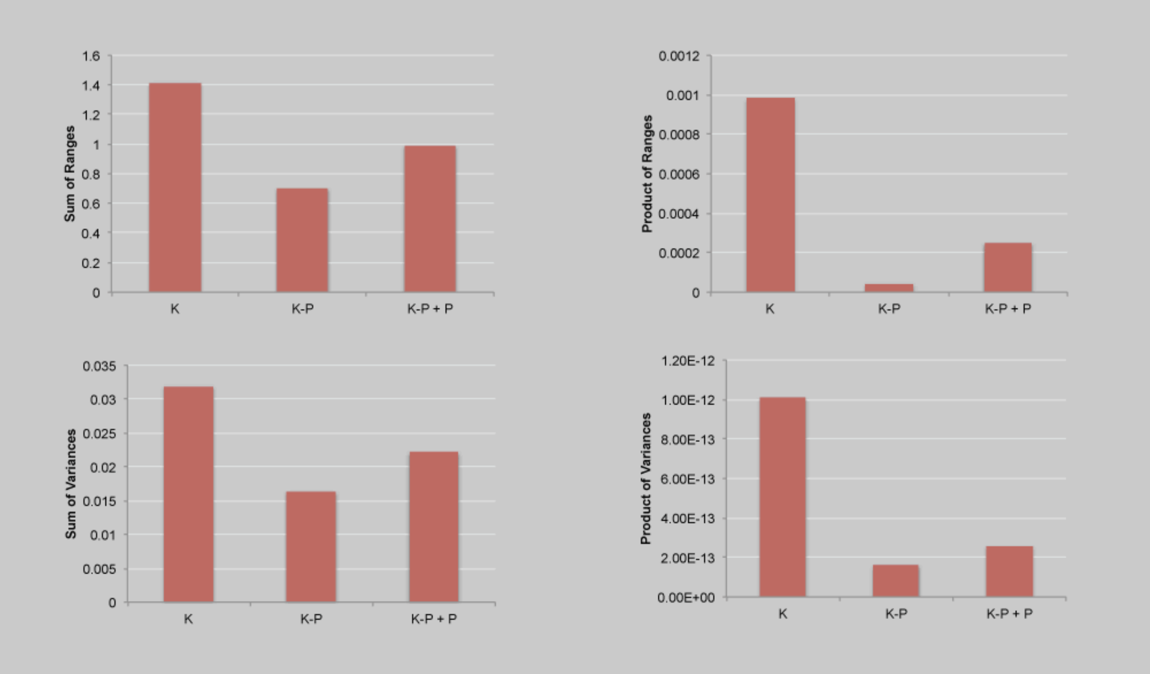

**Fig. S12.** Disparity metrics (sum of ranges, product of ranges, sum of variances, product of variances) for lizards occurring in the Maastrichtian (K), Maastrichtian-Paleocene boundary crossers (K-Pg), and boundary-crossers plus immigrant species found exclusively in the Paleocene (K-Pg + P).

To determine whether the decline in disparity is greater than would be expected for a randomly selected sample of survivors, we resampled the Maastrichtian data. Using the statistical software package R, we sampled 5 species, without replacement, from the Maastrichtian assemblage. For these 5 species, sum and product of ranges were computed, as well as sum and product of variances. This procedure was repeated 1000 times and then 95% confidence intervals were estimated.

Disparity metrics for the 5 boundary crossers are slightly smaller than predicted by random resampling, but the difference is not statistically significant, as the sum and product of ranges and the sum and product of variances all lie well within the 95% confidence interval estimated by resampling 5 species:

**Table S4.** Observed and predicted disparity for 5 species.

| | K-Pg, Actual | Resampled | 95% lower | 95% upper |
|---|---|---|---|---|
| Sum of Ranges | 0.700672423 | 0.809556 | 0.531975 | 1.115 |
| Product of Ranges | 4.26819E-05 | 6.13E-05 | 4.51E-06 | 2.31E-04 |
| Sum of Variances | 0.016313723 | 0.03249904 | 0.0127495 | 0.06929868 |
| Product of Variances | 1.58873E-13 | 1.11E-12 | 2.58E-15 | 7.74E-12 |

Similarly, resampling 15 species from the Maastrichtian morphospace shows that the sum and product of ranges and the sum and product of variances for the total Paleocene fauna (K-Pg boundary crossers plus species known only from the Paleocene) are not significantly smaller than expected for a fauna of this diversity:

**Table S5.** Observed and predicted disparity for 15 species.

| | K-Pg+Pg | Resampled | 95% lower | 95% upper |
|---|---|---|---|---|
| Sum of Ranges | 0.990275597 | 1.189427 | 0.966975 | 1.393 |
| Product of Ranges | 0.000251646 | 0.000448035 | 0.000156253 | 0.000896911 |
| Sum of Variances | 0.022264785 | 0.03181173 | 0.02164322 | 0.04154329 |
| Product of Variances | 2.58531E-13 | 1.01E-12 | 1.31E-13 | 3.12E-12 |

From the resampling analysis, it is clear that the difference in disparity is not significantly different from the disparity expected for a random sample. It might be tempting to view the reduction in morphospace occupation as the action of selection- with the extinction preferentially removing particular tooth morphotypes (e.g. ziphodont, brachyodont, and multicuspid teeth) presumably as a result of selection against particular ecological niches. However, the loss of morphospace volume can be explained entirely in terms of species extinction that is random- or at least, random with respect to tooth form.

The loss of disparity in tooth form can therefore be explained by the small sample of Paleocene species, but it does not follow that because this pattern is driven by sample size, it is a sampling artifact. The small sample of species, rather, reflects the fact that species richness is actually low in the Paleocene (Fig. 3, Fig. S11).

**Table S6.** Scores for first five principle coordinates for species studied.

| | | Range | ID | PC1 | PC2 | PC3 | PC4 | PC5 |
|---|---|---|---|---|---|---|---|---|
| AMNH 23222 | Haptosphenus | K | 1 | -0.195026366 | 0.010483201 | -0.032242697 | -0.004523803 | 0.011453454 |
| UCMP 49871 | Chamops | K | 2 | -0.121606919 | -0.04038776 | -0.051597332 | 0.023410464 | 0.038828615 |
| UCM 42164 | Laramie Poly | K | 3 | -0.136611494 | -0.05276157 | -0.093339448 | 0.007449891 | 0.04006077 |
| SMNH P1927.880 | Frenchman Poly | K | 6 | 0.016426866 | -0.076393481 | 0.007307202 | -0.078774598 | 0.004596469 |
| UCMP 128873 | Obamadon | K | 7 | -0.157917638 | 0.048816352 | 0.10247818 | 0.025022009 | -0.00369409 |
| AMNH 22208 | Pariguana | K | 8 | 0.080967304 | -0.113035903 | 0.009382069 | 0.025865341 | -0.009319269 |
| USNM 16514 | Leptochamops | K | 9 | -0.060633746 | -0.036146377 | 0.024734046 | 0.018727442 | 0.003889301 |
| UCMP 47815 | Litakis | K | 10 | 0.107927555 | -0.052352074 | -0.079729202 | 0.010898886 | -0.040748879 |
| UCMP 46610 | Meniscognathus | K | 11 | -0.143881532 | -0.060533113 | -0.009726981 | 0.037076348 | 0.015133632 |
| AMNH 15446 | Lonchisaurus | K | 12 | 0.010160234 | -0.035577666 | 0.015894903 | -0.081645419 | 0.016030464 |
| UALVP 29845 | Paraderma | K | 15 | 0.111604229 | 0.063293191 | -0.006295868 | 0.020470722 | -0.024826532 |
| UCMP 47744 | Parasaniwa | K | 16 | 0.103624467 | 0.155560534 | 0.057954104 | 0.025720732 | -0.044857372 |
| UCMP 124744 | Peneteius | K | 17 | -0.430724745 | 0.05478113 | -0.002487594 | 0.031278024 | -0.014670002 |
| OMNH 61334 | Polyglyphanodon | K | 18 | -0.092908453 | 0.154802516 | 0.090878954 | -0.170062743 | 0.006716576 |
| UCMP 49994 | Sauriscus | K | 19 | 0.02245623 | -0.028640194 | 0.075432409 | 0.036229143 | -0.007292206 |
| SMNH P1927.916 | Tripennaculus | K | 20 | -0.07910751 | -0.020138257 | 0.040772111 | 0.04153659 | -0.008158863 |
| YPM 16724 | Socognathus | K | 21 | -0.129846361 | -0.069939982 | -0.041000089 | 0.014366493 | 0.010539658 |
| UALVP 29844 | Stypodontosaurus | K | 22 | -0.193348075 | 0.096343031 | 0.058749818 | 0.012883449 | -0.029202653 |
| UCMP 49955 | Palaeosaniwa | K | 23 | 0.144913384 | 0.11143206 | 0.065173596 | 0.034960015 | 0.032518259 |
| USNM 25870 | Cemeterius | K | 24 | 0.075325862 | 0.133429485 | -0.039970269 | 0.001040236 | -0.027282072 |
| AMNH 22102 | Colpodontosaurus | K | 26 | 0.113954904 | -0.009920624 | -0.108161536 | 0.008757657 | 0.077392766 |
| UW 25116 | Lamiasaura | K | 37 | 0.023328561 | -0.066277056 | 0.050048824 | 0.046575165 | -0.015807232 |
| UW45055 | Contogenys | KP | 36 | 0.100278468 | -0.086885549 | 0.026785293 | -0.032152679 | -0.021247222 |
| UCMP 49932 | Gerrhonotus | KP | 0 | 0.117214197 | -0.0624476 | 0.015069906 | -0.007086744 | -0.001973489 |
| UCMP 53935 | Coniophis | KP | 4 | 0.139675173 | 0.122651833 | 0.053986761 | 0.052484741 | 0.09106432 |
| AMNH 26686 | Exostinus | KP | 5 | 0.021481751 | -0.029187493 | 0.047141863 | -0.085614432 | 0.043989792 |
| UCMP 47756 | Odaxosaurus | KP | 13 | 0.050066127 | -0.011714492 | 0.091946631 | 0.017738429 | -0.011692244 |
| MCZ 3681 | C. sloani | KP | 28 | 0.072511531 | -0.109118341 | -0.010077939 | -0.033816269 | -0.019520764 |
| YPM-PU 14243 | Provaranosaurus | P | 14 | 0.145375651 | 0.10015338 | 0.078128539 | 0.047466162 | 0.023782921 |
| AMNH 30799 | Chthonophis | P | 25 | 0.042873414 | 0.153064738 | -0.079955196 | -0.017769408 | -0.058980859 |
| YPM-PU 17035 | C. ekalakensis | P | 27 | 0.01237803 | -0.099482734 | -0.018043127 | 0.007399433 | -0.022154769 |
| YPM-PU 16777 | Oligodontosaurus | P | 29 | 0.019496349 | 0.148090284 | -0.141935217 | -0.018320713 | -0.014552927 |
| AMNH 12094 | Machaerosaurus | P | 30 | 0.119167283 | -0.044639817 | -0.059091166 | 0.012463994 | -0.037079255 |
| YPM-PU 19647 | Palaeoxantusia | P | 31 | 0.035006196 | -0.080324739 | 0.019582887 | 0.014415068 | -0.019342009 |
| UCM 35064 | Palaeoscincosaurus | P | 32 | -0.035000934 | -0.100271535 | -0.004385137 | -0.001589431 | -0.005241981 |
| UNM NP-596 | Plesiorhineura | P | 33 | 0.014684282 | 0.161473379 | -0.139945202 | -0.001491895 | 0.017864875 |
| AMNH 24339 | Proxestops | P | 34 | 0.003676228 | -0.101799323 | -0.004435501 | 0.003060556 | 0.003883499 |
| AMNH 12082 | Swainiguanoidea | P | 35 | 0.072039498 | -0.126399433 | -0.009028595 | -0.044448856 | -1.01E-04 |

## 7. Phylogenetic Independent Contrasts

Phylogenetic independent contrasts  (PIC) analyses were conducted using the PDTREE application included in the PDAP module of Mesquite 2.75 (57). A strict consensus tree for Maastrichtian species (Fig. S13) was used, with all branch lengths set to 1.

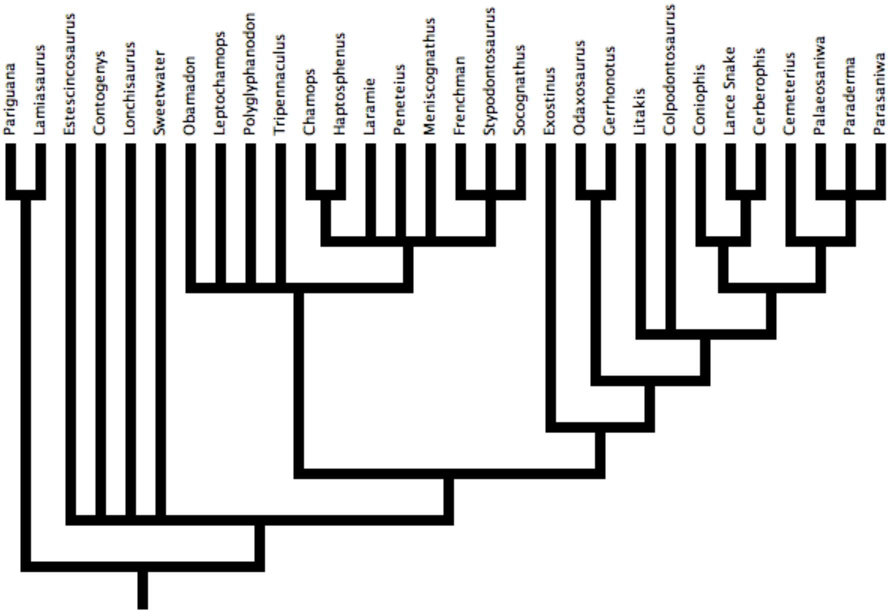

**Fig. S13.** Strict consensus used for PIC analyses.

When contrasts for tooth diameter (n=27) are regressed against contrasts for survivorship (Fig. S14), survivorship is found to be negatively correlated with tooth diameter (Pearson-Product-Moment Correlation Coefficient = -.1746) but the correlation is not significant (two-tailed p value = .3741).

Regressing contrasts for geographic range (n=29) on contrasts for survivorship (Fig. S14)  showed a positive relationship between range and survivorship (Pearson-Product-Moment Correlation Coefficient = .1062) but the correlation is not significant (two-tailed p value = .5762).

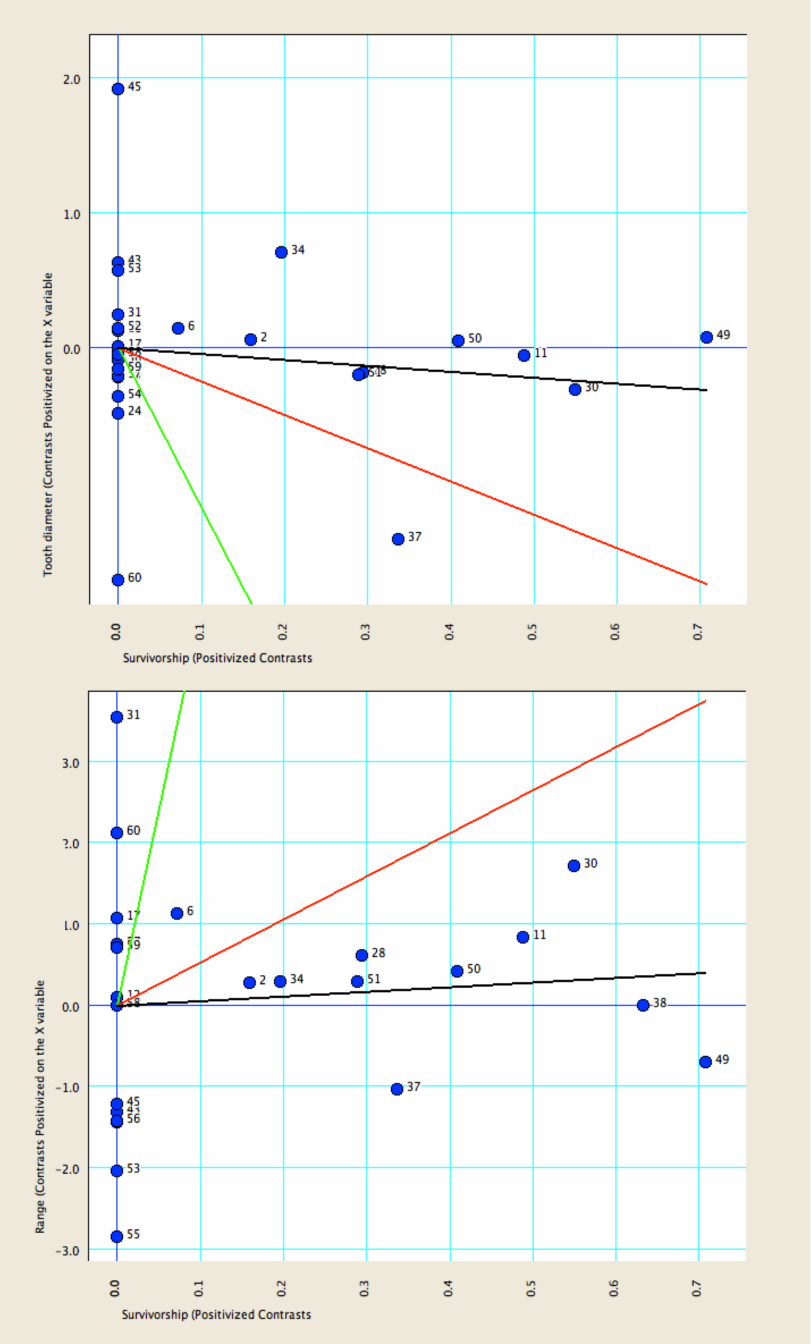

**Fig. S14.** Phylogenetic independent contrasts analyses. Top: contrasts for tooth diameter versus contrasts for survivorship. Bottom: contrasts for for geographic range versus contrasts for survivorship. Regression lines: ordinary least squares (58), major axis (green) and reduced major axis (red).

**Table S7.** Data for phylogenetic Independent Contrasts.

```
#NEXUS

BEGIN TAXA;
        TITLE Taxa;
        DIMENSIONS NTAX=30;
        TAXLABELS
                Pariguana Lamiasaura Estescincosaurus Contogenys Lonchisaurus Sweetwater
Polyglyphanodon Obamadon Leptochamops Tripennaculus Peneteius Laramie Meniscognathus
Haptosphenus Chamops Frenchman Stypodontosaurus Socognathus Exostinus Odaxosaurus
Gerrhonotus Litakis Colpodontosaurus Coniophis Lance_Snake Cerberophis Cemeterius
Palaeosaniwa Paraderma Parasaniwa
        ;
END;
BEGIN CHARACTERS;
        TITLE  Character_Matrix;
        DIMENSIONS  NCHAR=3;
        FORMAT DATATYPE = CONTINUOUS GAP = - MISSING = ?;
CHARSTATELABELS
                1 Survivorship,
                2 Range,
                3 Tooth_diameter ;
        MATRIX
        Pariguana         0.0 1.0 0.356
        Lamiasaura        0.0 1.0 0.421
        Estescincosaurus   0.0 2.0 0.373
        Contogenys        1.0 1.0 0.483
        Lonchisaurus      0.0 1.0 0.364
        Sweetwater        0.0 1.0 0.636
        Polyglyphanodon    0.0 1.0 1.267
        Obamadon          0.0 2.0 0.463
        Leptochamops      0.0 5.0 0.666
        Tripennaculus     0.0 1.0 0.384
        Peneteius         0.0 1.0 0.729
        Laramie           0.0 1.0 0.704
        Meniscognathus    0.0 3.0 0.558
        Haptosphenus      0.0 4.0 0.955
        Chamops           0.0 7.0 1.134
        Frenchman         0.0 1.0 0.553
        Stypodontosaurus   0.0 1.0 0.481
        Socognathus       0.0 1.0 1.11
        Exostinus         1.0 4.0 0.502
        Odaxosaurus       1.0 7.0 0.703
        Gerrhonotus       1.0 2.0 0.36
        Litakis           0.0 1.0 0.942
        Colpodontosaurus   0.0 2.0 0.722
        Coniophis         1.0 1.0 0.42
        Lance_Snake       0.0 1.0 ?
        Cerberophis       0.0 1.0 ?
        Cemeterius        0.0 2.0 3.507
        Palaeosaniwa      0.0 2.0 4.542
        Paraderma         0.0 5.0 2.119
        Parasaniwa        0.0 5.0 0.983
;
```

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