



A DIVERSE NEW ASSEMBLAGE OF LATE EOCENE SQUAMATES (REPTILIA) FROM THE CHADRON FORMATION OF NORTH DAKOTA, U.S.A.

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ABSTRACT

The current fossil record of squamates across the Eocene/Oligocene boundary in central North America is perplexing in that it shows a marked increase in species richness in response to climatic cooling and drying, which is contrary to both the European record and expectation. A diverse, new squamate assemblage from the late Eocene Chadron Formation of the Medicine Pole Hills, North Dakota, provides new insight into these changes. Nineteen squamate species are described, fourteen of which were previously unknown. The acrodontan, varanid, and diploglossine anguid are previously unreported holdovers from the early Eocene. The Medicine Pole Hills local fauna is one of the most species-rich squamate assemblages yet reported from the fossil record.

Late Eocene iguanids are remarkable for both their species-level and higher taxonomic diversity: among their numbers are a phrynosomatine (fence lizards and relatives), a polychrotine (anoles and relatives), and a crotaphytine (collared and leopard lizards). The polychrotine, interpreted as the earliest-known representative of the *Polychrus* lineage, indicates that at least one subgroup of Iguanidae shows a historical biogeographic pattern similar to that of North American scincomorph and anguimorph lizards. The increasing numerical dominance of iguanid species has been considered a hallmark of herpetofaunal modernization in central North America, but this measure appears inadequate in light of these data.

Including the new fauna, the record of central North American squamates, like the European record, shows a decrease in richness across the Eocene/Oligocene boundary. However, many uncorrected sampling biases remain that may distort our picture of the squamate response to Eocene/Oligocene climate change. Sampling-standardized studies are indicated.

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INTRODUCTION

The past decades have witnessed considerable multidisciplinary attention to climate change around the Eocene/Oligocene boundary and the causes and consequences of associated biotic change. This is partly due to a re-calibration of the North American terrestrial record (Prothero and Swisher 1992; Swisher and Prothero 1990), extensive study of deep-sea cores (e.g., Thomas 1992; Lear et al. 2000), and debate over bolide impacts (see discussion in Prothero 1994).

Wolfe (e.g., 1978, 1992) argued early on from paleobotanical data that climatic deterioration was not limited to the Eocene/Oligocene boundary interval: the middle/late Eocene boundary was also marked by a decrease in mean annual temperature (MAT) and an increase in mean annual range of temperature (MART) in many areas on the fringe of the North American continent. According to his studies, amelioration during the late Eocene was followed by another marked deterioration in the earliest Oligocene.

How apparent climatic change along the North American periphery was reflected in its interior is a matter of some contention. Hutchison (1982, 1992) could accept a moderate drop in MAT ($<5^{\circ}\text{C}$) as an explanation for the observed decrease in maximum carapace length in testudinid turtles; but he also argued that in the early Oligocene, mean winter temperature could not have been below 13°C , because the relatively large terrestrial turtles (>30 cm carapace length) known from that time could not burrow to escape lower temperatures. Similarly, Evanoff et al. (1992) concluded that there was a minor drop in MAT in the early Oligocene (from 16.5°C in the late Eocene) based on the terrestrial gastropod fauna near Douglas, Wyoming. Contrariwise, Wolfe (1992) found that, between the late Eocene and early Oligocene in Colorado, MAT decreased from ~ 12.5 to $\sim 4.5^{\circ}\text{C}$; the magnitude of this drop (8°C) is comparable to what he found in the Pacific Northwest and elsewhere in North America (Wolfe 1978). The late Chadronian Ruby flora of Montana had a great many conifers and indicates a MAT of $\sim 12^{\circ}\text{C}$ and a probable MART of $<16^{\circ}\text{C}$ (Wolfe 1992). These pre-deterioration values already exceed the limits suggested by Hutchison (1982) for the early Oligocene.

A change in mean annual precipitation (MAP) across the Eocene/Oligocene boundary seems less controversial. Studies of palaeosols (e.g., Retallack 1992; Sheldon and Retallack 2004) imply that MAP gradually dropped by $\sim 50\%$ between 36

and 27 Ma, by which time MAP values in Nebraska likened modern-day values.

The transformation of North American squamate assemblages during the Tertiary has not been investigated in detail (Hutchison 1992), but broad shifts in assemblage composition may relate to climate change. Gauthier (1982) noted a general replacement of Paleogene mesic-adapted lizards (especially anguimorphs) by Neogene xeric-adapted lizards (especially iguanids). Holman (2000) described an analogous shift from booid- to colubroid-dominated assemblages around the same time. Many of the common Paleogene squamate taxa moved south and are found today in the southeastern United States and Central America (Estes 1970; Savage 1960).

Despite increasing aridity and cooler temperatures, squamate diversity appears to increase across the Eocene/Oligocene boundary in central North America (10 to 17 species: Sullivan and Holman 1996)¹. A temperature decrease of only $\sim 5^{\circ}\text{C}$ is related to a moderate decrease in lizard species richness in modern North American deserts (Pianka 1967). The pattern seen in the North American fossil record, however, may be vitiated by differences in sampling, indicated by Lazarus taxa in the Chadronian (Sullivan and Holman 1996).

In this paper, I report on a new and very diverse fauna from the Chadronian of North Dakota, the Medicine Pole Hills local fauna (l.f.). Many new lizard morphotypes are identified, and three are formally named. Extensive comparisons are made with the disarticulated skeletons of extant taxa in order to estimate their phylogenetic position. I then evaluate the effects of this new fauna on our understanding of squamate species richness across the Eocene/Oligocene boundary.

GEOLOGIC SETTING AND PALEOENVIRONMENT

The White River Group of the Great Plains includes the Chadron and Brule Formations of late Eocene to Miocene age. It reaches its maximum thickness in northwestern Nebraska, decreases in thickness northward, and disappears in northern North Dakota (Larson and Evanoff 1998). Pioneer Trails Regional Museum (PTRM) (Bowman, North Dakota) locality V89002 is located in the Medicine

1. Actually, the increase is even greater than reported, for the helodermatid *Lowesaurus matthewi*, known from two Orellan specimens (Estes 1983; Pregill et al. 1986), was not included in Sullivan and Holman's (1996) tally.

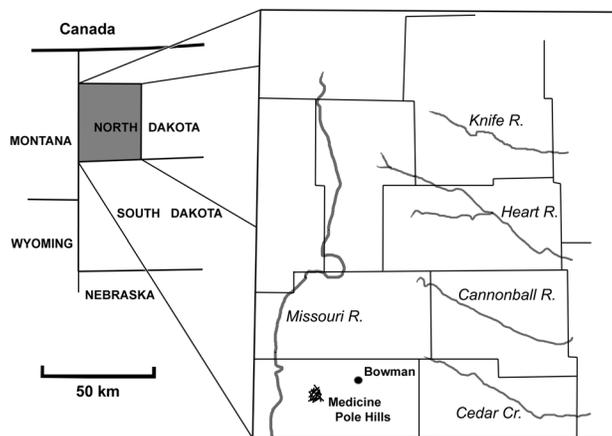


Figure 1. Geographic map of the northern plains states, showing the location of the Medicine Pole Hills in North Dakota (after Hoganson et al. 1998). New specimens described in this paper are deposited in the Pioneer Trails Regional Museum in Bowman, North Dakota.

Pole Hills of southwestern North Dakota (Figure 1; South Rhame quadrangle). The lower part (Chalky Buttes Member) of the Chadron Formation, remnant of a former sedimentary "blanket" (Trimble 1980), caps those hills in many places (Murphy et al. 1993; Pearson 1993), and V89002 is located on one of the hilltops. Fossils were first reported from the area some 80 years ago (Leonard 1922), and since 1989 the Pioneer Trails Regional Museum has conducted excavations at V89002.

The sediment is a brownish, poorly sorted, poorly consolidated, generally medium- to fine-grained sandstone (Pearson 1993). A 2.5 m local section (Figure 2) shows two trough cross-bedded units (units 2 and 6); unit 5 is composed of sediment indistinguishable from that of unit 2. Along the bedding planes are strewn gray mudballs, often comprising 15% of total rock volume. The troughs of units 2 and 6 have trends at high angle ($\sim 80^\circ$) to one another. Unit 3 is a fine-grained, parallel-bedded sandstone. Unit 4 displays planar cross-bedding.

Rapidly shifting channels that deposit planar and trough cross-bedded sandstone units (lithofacies Sp and St of Miall 1996) are characteristic of the distal reaches of some modern braided rivers (Einsele 1992), and I postulate that this section was deposited as part of a braidbelt environment. Parallel-bedded units, like unit 3, are also deposited in such environments during waning flood stages (Einsele 1992: 45). The mudballs probably derive from the underlying Paleocene strata (Kihm personal commun., 2004). Many fossils are quite

worn, presumably by stream abrasion. The similar color (creamy to tannish yellow) and preservation of nearly all specimens argue for a single provenance.

The Medicine Pole Hills l.f. is taphonomically similar in many ways to the Calf Creek l.f. of Saskatchewan (Holman 1972, 1976). The Cypress Hills Formation, which yields the Calf Creek l.f., is also interpreted as a braidbelt deposit (Leckie and Cheel 1989). As at V89002, the bone in the Cypress Hills Formation is set in a poorly sorted matrix that also contains mudballs torn from interfluvial (Leckie and Cheel, op. cit.), although I interpret the Medicine Pole Hills fossil horizons as fluvial in origin rather than as debris flows. All fossils were collected from units 1 and 2 by dry-screening quarried sediment; fossils of the Calf Creek l.f. were also collected by screening (Holman 1972). Neither deposit appears to exclude particular size classes, both preserving everything from large brontotheriids to small marsupials (Storer 1996; Kihm et al. 2001; Pearson, personal commun., 2001).

The Chadron Formation in the Medicine Pole Hills and the Cypress Hills Formation in the Calf Creek area are both Chadronian in age, although more carefully considered, they may differ by 1 m.y. or so. The leptomerycid artiodactyls present in the Medicine Pole Hills l.f., including a probable early form of *Leptomeryx yoderi*, suggest an early Chadronian age for these deposits (Heaton and Emry 1996; Hoganson et al. 1998). In contrast, the Calf Creek l.f. contains *L. speciosus* and *L. mam-*

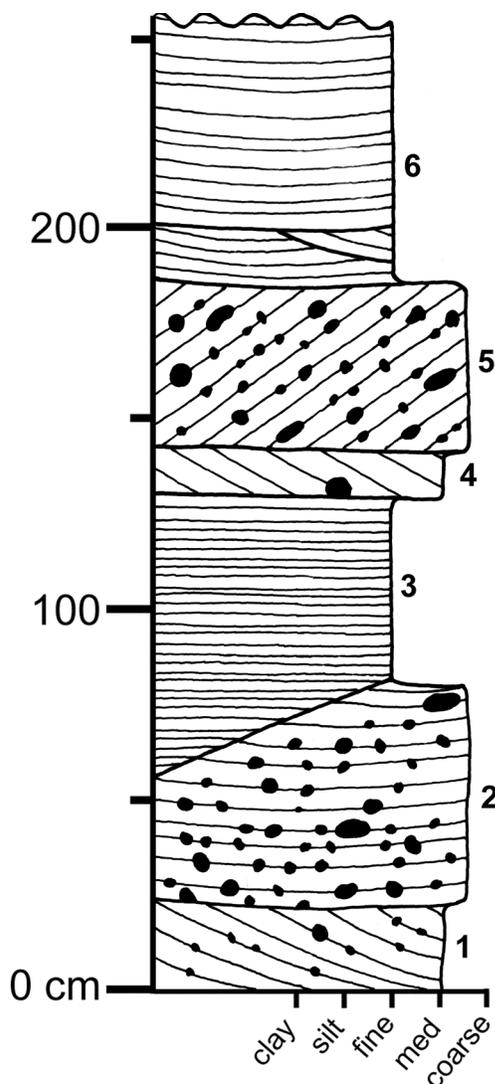


Figure 2. Stratigraphic section at PTRM locality V89002. Grain size (clay, silt, and fine, medium, and coarse sand) is indicated by width of the section. Fine intra-unit lines illustrate sedimentary structure (planar and trough cross-bedding and horizontal lamination). Numbers 1–6 on the right correspond to unit numbers used in text. The black marks in units 1, 2, 4, and 5 represent mudballs in their relative volumetric proportions.

mifer (Storer 1996), which are indicative of a medial Chadronian age (Emry et al. 1987).

INSTITUTIONAL ABBREVIATIONS

American Museum of Natural History (AMNH), Carnegie Museum of Natural History (CM), Florida Museum of Natural History (UF), Pioneer Trails Regional Museum (PTRM), Senckenberg-Museum, Frankfurt-am-Main (SMF), Saskatchewan Museum of Natural History (SMNH), University of California Museum of Pale-

ontology (UCMP), United States National Museum (USNM), Yale Peabody Museum – Princeton Collection (YPM-PU), Yale Peabody Museum – Vertebrate Paleontology (YPM-VP), Yale Peabody Museum – Vertebrate Zoology (YPM-VZ).

SYSTEMATIC PALEONTOLOGY

When fossils of poor quality are given formal taxonomic designations several difficulties may arise. The type material of the new taxon may be diagnostic when described even though in absolute terms it is not, leading to later abandonment of the name. Considered in this way, "diagnostic" is really a time-dependent descriptor that could be defined as "distinguishable from all known (Recent and fossil) forms whose relevant parts have been studied thus far." For example, the taxon *Lestophis anceps* Marsh (1885) was named on the basis of vertebrae from the Bridger basin of Wyoming, but later work has shown that these rhineurid vertebrae possess no unique features, rendering *L. anceps* a *nomen dubium* (Estes 1983). How diagnostic a particular specimen is depends on how many distinctive features it displays and can be expected to correlate with completeness.

More problems may arise when the description of a new taxon on the basis of undiagnostic material is later supplemented by information from much more complete specimens, which subsequently become closely associated with the name of the taxon. The discovery of a new taxon, from which the type material of the first cannot be distinguished, would thus render the first name invalid, but one hesitates to strike down the first name because most scientists in considering the taxon think not of the type but rather of the more complete and well-described specimens.

Many of the taxa described herein, especially on the basis of jaws, are currently diagnostic—that is, there are currently no other taxa whose morphology is known (by me) to match theirs. But given their incomplete nature and the incomplete study of the skeletal material of extant species, it seems likely that future workers could find other species that, were they fragmentary, would look identical to those from Medicine Pole Hills. When they cannot even reasonably be compared ("cf.") to an existing genus or species, I use an informal nomenclatural system. Each name designates the probable phylogenetic affinity and includes an abbreviation, appended with a number, for the locality name from which the specimens derive. For example, "Iguanid MPH-1" indicates that the

taxon is probably an iguanid and derives from the Medicine Pole Hills locality.

These appellations are viewed only as a temporary solution to the need for a name. The taxa described herein were almost certainly distinct species, regardless of whether they can be linked to species from another location (e.g., Smith 1994). The informal name refers only to material from the "type" (that is, original) locality, where distinctions in informal designation likely represent real biological divisions and, conversely, where similarity probably indicates common membership in a real biological set. This treatment thus differs from that of Hutchison (e.g., 1998), whose early Eocene turtle taxon Emydid P, for instance, is based on a much better geographic assessment and sample size.

In this section, I follow the metataxon convention of Gauthier et al. (1988) and Schulte et al. (2003), whereby an asterisk following a taxon name indicates that the monophyly of that taxon as presently constituted is open to reasonable dispute. Because the use of a rankless hierarchy in a faunal description is likely to confuse any reader not intimately familiar with the taxonomy of a group of organisms, the following rankless hierarchy is provided, with the lowest taxonomic level, species, in bold. If more than two taxa appear at the same level, this indicates that relationships among them are not resolved. The hierarchy is not repeated in the systematic treatment: only the lowest taxonomic level is given.

I have attempted to restrict taxon names to those that refer to clades. My use of these names is equivalent to that of Estes et al. (1988). For the purposes of the discussion, Amphisbaenia is viewed as nested within Scincomorpha, related to Lacertoidea (e.g., Camp 1923; Schwenk 1988; Townsend et al. 2004). With only two exceptions, taxon names refer to the crown clade; for Rhineuridae, I follow Kearney (2003), and for Helodermatidae, Pregill et al. (1986). Within Iguanidae, I follow the conventions recommended by Macey et al. (1997), Zug et al. (2001), and most recently Schulte et al. (2003). Polychrotinae* and Tropicodurinae* *sensu* these authors are considered metataxa, following Frost et al.'s (2001) and Schulte et al.'s (2003) analyses. Note in particular that I am using Iguanidae in the old sense for all living pleurodont iguanians, not in the sense of Frost and Etheridge (1989), who restricted that name to certain genera (Iguaninae *sensu* de Queiroz 1987). Despite the author's discontent in following the Linnaean system generally and the binomial in partic-

ular, and the attendant necessity to create "dummy" higher taxa—e.g., genera—for the reception of new species that cannot be accommodated in existing taxa, no official alternative yet exists; thus, with some reluctance, one new genus for a new species is proposed.

Squamata Oppel (1811)
 Iguania Cuvier (1817)
 Acrodonta Cope (1864)
*Tinosaurus** Marsh (1872)
***Tinosaurus* sp.**
 Iguanidae Oppel (1811)
 Polychrotinae* (Frost and Etheridge 1989)
Polychrus Merrem (1820)
Polychrus charisticus sp. nov.
Iguanid MPH-1
Iguanid MPH-2
 Phrynosomatinae (Frost and Etheridge 1989)
***Tuberculacerta pearsoni* gen. et sp. nov.**
cf. *Aciprion* sp.
Iguanid MPH-3
Iguanid MPH-4
Cypressaurus Holman (1972)
***Cypressaurus* sp.**
 Autarchoglossa Wagler (1830)
 Scincomorpha Camp (1923)
 Scincoidea Oppel (1811)
Scincoid MPH-1
 Xantusiidae Baird (1858)
Palaeoxantusia Hecht (1956)
"*Palaeoxantusia*" borealis
 Holman (1972)
 Amphisbaenia Gray (1844)
 Rhineuridae (Vanzolini 1951)
Spathorhynchus Berman (1973)
cf. *Spathorhynchus* sp.
Rhineura Cope (1861)
cf. *Rhineura* sp.
 Anguimorpha Fürbringer (1900)
Anguimorph MPH-1
 Anguidae Gray (1825)
 Diploglossinae Cope (1864)
Diploglossine MPH-1
 Glyptosaurinae (Marsh 1872)
Peltosaurus Cope (1872)
cf. *Peltosaurus* sp.
Helodermoides Douglass (1903)
***Helodermoides* sp.nov.?**
 ?Xenosauridae Cope (1866)

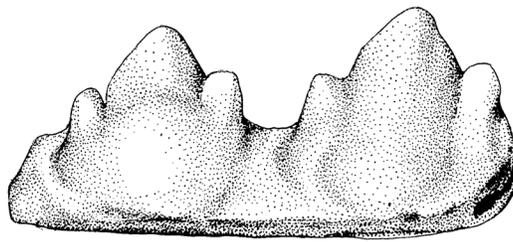


Figure 3. *Tinosaurus* sp., jaw fragment in lingual view (PTRM 2038). Scale bar equals 1 mm.

Xenosaurid MPH-1

Varanidae Gray (1827)

*Saniwa** Leidy (1870)

***Saniwa edura* sp. nov.**

Tinosaurus sp.

(Figure 3)

Referred specimens. PTRM 2038 (jaw fragment), Figure 3

Description. A thorough description of this specimen was provided by Pearson (1998), who wrote:

The referred specimen PTRM-2038 is a fragment of bone ... with two tricuspid, acrodont teeth. The anterior tooth measures 0.87 mm in width and the posterior tooth 1.06 mm, as measured at their widest point. The teeth are laterally compressed with three antero-posteriorly aligned cusps, the median being the tallest at 0.95 mm for the anterior and 1.12 mm for the posterior tooth. The teeth are separated with a spacing of 0.27 mm at the narrowest point and 0.35 mm at the level of the jaw parapet. The total space occupied by both teeth ... equals 2.07 mm. The anterior tooth extends 0.50 mm above the parapet of the jaw and the posterior tooth 0.64 mm. Both teeth exhibit sub-equal lateral cusps.... The bases of the teeth are broad and fused to the dorsal margin of the [jaw] at a slight angle. ... The presence of lateral cusps on both teeth indicates the specimen originated from the mid-

dle, or more posterior portion, of the [jaw]. (p. 37)

The specimen is illustrated in Figure 3.

Remarks. *Tinosaurus** is a poorly diagnosed taxon erected for small- to medium-sized Paleogene squamates that evince acrodont tooth implantation and tricuspid posterior teeth (Estes 1983). It represents one or more incursions of acrodont iguanians into North America during a time of widespread faunal interchange (Gauthier 1982) that resulted from decreased latitudinal temperature gradients (Greenwood and Wing 1995). The type specimen (now at USNM) of the type species (*T. stenodon* Marsh 1872) is from the Bridgerian of North America. Barring multiple invasions by Acrodonta, the North American taxa may constitute an exclusively monophyletic group (though this cannot be demonstrated with apomorphies at present). The relations of these taxa to Asian and European species referred to *Tinosaurus** are also unclear, but the North American taxa would remain the name-bearers.

Pearson (1998) compared PTRM 2038 to *T. stenodon*. There is presently not enough material to justify specific assignment. This specimen is the latest known record of Acrodonta in the New World (Pearson 1998).¹

Polychrus charisticus sp. nov.

(Figure 4.1–5)

Holotype. PTRM 1841 (partial right maxilla), Figure 4.1–2

1. Though Hutchison (1992) carefully included the faunal list of Emry (1973), which had been neglected by other authors (Estes 1983; Sullivan and Holman 1996), he mistakenly stated (p. 456) that Emry listed "cf. *Tinosaurus*" from the Flagstaff Rim area of Wyoming; the taxon in question was actually cf. *Thinosauros*, considered synonymous with *Saniwa** (Estes 1983).

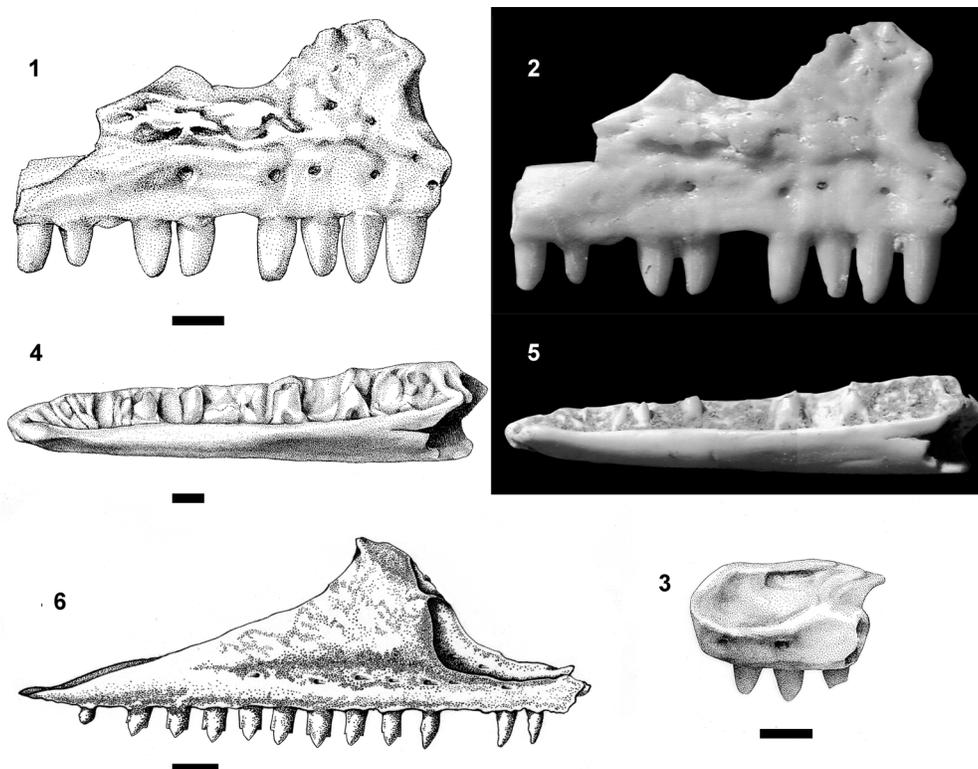


Figure 4. *Polychrus charisticus* sp. nov., (1) Illustration and (2) photograph of holotype, partial right maxilla in lateral view (PTRM 1841). (3) Paratype, premaxillary process of a right maxilla in dorsolateral view (PTRM 5373). Anterior to right. Note lip overhanging the lateral margin. (4) Illustration and (5) photograph of paratype, edentulous right dentary in medial view (PTRM 5351). The AIAF is represented by the notch at the posterior margin of the medial face of the dentary. The anterior-most one or two teeth are not discernible in this view. The specimen has subsequently been damaged. (6) Right maxilla of extant *Polychrus marmoratus* in lateral view (YPM R13556). Scale bars equal 1 mm.

Paratypes. PTRM 2637 (right dentary fragment); 1990 (partial right dentary); 2596 (left dentary fragment); 1418 (right dentary fragment); 2673 (right dentary fragment); 5351 (edentulous right dentary), Figure 4.4–5; 5400 (jaw fragment); 1997 (right maxilla fragment); 5372 (left maxilla fragment); 5373 (right maxilla fragment), Figure 4.3; 5374 (partial right maxilla)

Locality and horizon. PTRM V89002, Chalky Buttes Member, Chadron Formation (late Eocene), North Dakota, USA

Distribution. Thus far known only from type locality.

Diagnosis. A polychrotine iguanid with a dorsolaterally projecting lip of bone on lateral margin of premaxillary process of maxilla; dorsal surface of premaxillary process concave, bounded medially by crista transversalis; anterior inferior alveolar foramen of maxilla small; base of nasal process excavated anteriorly; anterior margin of nasal process vertical, overhangs premaxillary process; nasal process rugose, with small facet on anterior

margin for articulation with nasal; teeth conical, tapering, with striated crowns and squarish cross-section posteriorly; Meckelian groove closed and extensively fused anteriorly and posteriorly; and a weak, discontinuous sulcus dentalis along most of the tooth row that is bounded medially by a sharp lip of bone.

Differs from *Polychrus acutirostris*, *P. guttuosus* and *P. marmoratus* in having conical, unicuspid teeth and greater overlap of the premaxilla onto the dorsal surface of the premaxillary process of the maxilla. Also differs from *P. guttuosus* and *P. marmoratus* in having a rugose nasal process of the maxilla. Also differs from *P. acutirostris* in having a more vertical nasal process and a less extended premaxillary process of the maxilla.

Etymology. *charistikos*, Gr. "giving freely," in reference to the permission given by the landowner, Jeff Oakland, for excavation of the specimens.

Description of holotype. The teeth of the maxilla are moderately robust, high-crowned and, as far as they are preserved, unicuspid, tapering apically.

Weak labial and occasionally lingual striae are visible on the crowns despite heavy wear to the tips. The anterior teeth are slightly recurved, the more posterior teeth essentially straight (Figure 4.1–2). The palatal shelf is not wide. The palatine process is very weak, but there is a relatively large facet, developed on its dorsal surface and extending onto the main of the palatal shelf, that marks the articulation with the palatine. The superior alveolar foramen (SAF) is not well separated from the jugal groove, and it is set in a short gutter (see also below under *Cypressaurus* sp.). The nasal process, covered with irregular rugosities (interspersed with small foramina) above the labial foramina, has a nearly vertical anterior margin that even projects out over the premaxillary process (Figure 4.1). On the anterodorsal margin of the nasal process is a small but distinct facet that marks the articulation with the nasal. The maxillary anterior inferior alveolar foramen (AIAF) opens along this margin above the level of the premaxillary process.

Description of paratypes. Further information on the maxilla comes from PTRM 1841, 5373, and 5374. The crest for attachment of the vomer and the lamina transversalis anterior (Oelrich 1956)—here called the *crista transversalis*—is well developed, crossing the palatal shelf anteromedially, then extending nearly to the anterior end of the bone along its medial margin. The dorsal surface of the premaxillary process is concave, bounded by ridges medially and laterally (Figure 4.3). A second foramen—filled with sediment and continued by a small groove anteriorly—lies just lateral to the *crista transversalis*; it is probably for the subnarial artery (see Oelrich, 1956). A small lip of bone projects dorsolaterally to overhang part of the maxillary wall in all specimens. The premaxillary process is especially long, extending well beyond the anterior limit of the concavity on its dorsal surface (Figure 4.3). This anterior extension bears a facet dorsally for articulation with the premaxilla. Its anterior margin is somewhat concave in dorsal aspect. A ventral facet for articulation with the premaxilla is also present.

PTRM 5351 (Figure 4.4–5) is one of the largest dentaries. Though the bone itself is well preserved, only the bases of non-resorbed teeth remain; their crowns were likely broken during the screening process. Eighteen tooth spaces occupy 14.0 mm; the more anterior teeth are mesiodistally compressed (their bases are elliptical). The posterior teeth have broader bases and a squarish outline. There is a narrow, shallow, and discontinuous sub-

dental gutter (sulcus dentalis) bordered medially by a sharp lip of bone. The dentary does not grow much taller posteriorly, and the dental parapet is low. Posteriorly, the dentary is broken at the level of the AIAF. Only the anterior portion of this foramen is preserved, and it is slit-like and narrow; a small groove extends anteriorly from it. The foramen is located in the upper half of the medial face of the dentary. The Meckelian groove is closed and extensively fused anteriorly. The anterior-most end of the dentary curves only slightly medially, not strongly and abruptly. There are five irregularly spaced labial foramina, the last of which is positioned between the twelfth and thirteenth teeth (from symphysis). There are a few fine, irregularly oriented grooves on the external surface of the dentary, which are probably artifactual. There is also a shallow, longitudinal groove on the ventral surface of the dentary. The ventral border of the dentary is nearly flat. The anterior opening of the Meckelian canal is highly restricted.

Other referred specimens supplement the description above. Tooth crowns in PTRM 5200 (only slightly worn) taper considerably toward their tips, even as posteriorly as tooth 13 (the last tooth preserved in this specimen). There is no indication at this point of tricuspid crowns. PTRM 1990 has two reasonably well-preserved teeth, at positions four and five (from symphysis). Each has a faint mesial crest descending the tooth crown, disappearing above the dental parapet. The fifth tooth has fine, vertical striations about midway up the lingual side of the crown and coarser striae on the labial side; the tip of the crown, though slightly worn, bears no indication of accessory cusps.

Remarks. The extensive (>50%) closure and fusion of the Meckelian groove in *Polychrus charisticus* is a derived feature it shares with the polychrotine taxa *Anolis* and *Polychrus* as well as with many iguanines and tropidurines (Etheridge and de Queiroz 1988). The extent of anterior fusion of the groove is matched, among living taxa, only by *Anolis*, *Polychrus*, and some *Leiocephalus*. The dentary of *P. charisticus* also appears (dorsoventrally) short posteriorly, but as the end of the bone is not preserved, it is not known how much taller it would become; nor is a dentary tooth count obtainable. Dentary tooth counts vary from 21 to 26 teeth in living *Polychrus* I have seen (26 in *P. acutirostris*, 24 in *P. gutturosus*, 21 in *P. marmoratus*).

The maxilla of *Polychrus charisticus* is distinctive and furnishes a number of useful characters. Especially noteworthy is the evident overlapping of the

premaxilla onto the premaxillary process of the maxilla. In the few living iguanians where a dorsal overlap surface is evident on the premaxillary process—only *Polychrus* and the hoplocercine *Enyalioides oshaughnessyi* (where it is highly developed)—, the premaxilla has a posterolateral recess formed by the development above the primitive articulation surface of a flange that overlaps the maxilla. The premaxillary overlap was evidently more highly developed in *P. charisticus* than in *P. marmoratus* and *P. guttuosus*.

The moderately concave dorsal surface of the premaxillary process, and the dorsolaterally projecting lip of bone on its lateral margin, are seen in all examined *Polychrus* (see Appendix). A dorsal excavation is also found in many tropidurines (*Plica*, *Uracentron*, *Tropidurus*, *Microlophus*). In the latter taxa, however, the premaxillary process curves strongly medially toward its anterior end and lacks a dorsolaterally projecting ridge. A dorsal excavation is also seen in *Enyalioides oshaughnessyi* and many iguanines; but in iguanines the lateral crest bounding this dorsal excavation curves medially across the dorsal surface of the process. The excavation of the anterior base of the nasal process proceeds to such an extent in *Polychrus marmoratus* (Figure 4.6) and *P. guttuosus* (especially) that the lateral surface of the nasal process slightly overhangs the premaxillary process, as in *P. charisticus* (Figure 4.1). This was not observed in any other iguanian and is not well developed in *P. acutirostris*.

The superior alveolar foramen (SAF) is partially "roofed" in *Polychrus charisticus*, as in other disarticulated specimens of *Polychrus*, *Anolis*, many tropidurines (*Microlophus*, *Plica*, *Tropidurus*, *Uracentron*; less so in *Uranoscodon*), and phrynosomatines (see Appendix). In most other iguanians examined, including the agamid *Uromastix hardwickii* and *Leiocephalus*, there is a gutter developed on the dorsal surface of the palatal shelf of the maxilla that extends far anteriorly toward the anterior end of the nasal process, and the superior alveolar nerve penetrates the maxilla in several places along the floor and anterior end of this gutter (see, e.g., Figure 11.3). Limited out-group comparison and the restricted distribution of the covered or "roofed" condition of the SAF in Iguanidae suggest that the former condition is derived and could serve to unite *Anolis* and *Polychrus*. The state of the SAF is unknown in leiosaurs and para-anoles (*sensu* Etheridge and de Queiroz 1988).

The irregular, nearly pustulose rugosities on the lateral surface of the nasal process in *Polychrus charisticus* also occur in some *Anolis*, some *Polychrus* (e.g., *P. acutirostris*), some *Leiocephalus*, some *Phrynosoma*, and some *Laemanctus*. In most iguanians, however, rugosities, when present, are restricted to the frontal and perhaps parietal. Extensive development of rugosities is considered derived in Iguania (Etheridge and de Queiroz 1988), but their complicated distribution in certain taxa (*Anolis*, *Polychrus*) disallows, at present, the use of this feature as an apomorphy uniting them.

The nasal facet on the anterior margin of the nasal process, seen in *Polychrus charisticus*, is also found in other *Polychrus* (Figure 4.6), corytophanines, *Oplurus cuvieri*, and *Enyalioides oshaughnessyi*. The derived nature of the maxilla in *Anolis*—which shows, for instance, a strong, low-angle canthal crest and a sharply medially bent nasal process—makes it difficult to ascertain whether this feature is primitive for *Anolis*, *Polychrus*, and Corytophaninae but lost due to transformation in *Anolis*. Stem representatives of *Anolis* would help to clarify this problem. In other iguanids, the nasal generally does not leave a distinct facet on the anterior margin of the nasal process; if it leaves a mark at all, it is an arcuate depression on the anteromedial surface of the nasal process. Out-group comparison with Agamidae and *Sphenodon punctatus* suggests that the presence of an anterior facet is primitive. It appears to have been lost, then, in *Anolis*, *Pristidactylus torquatus* (unknown in other leiosaurs), *Chalarodon madagascariensis*, *Crotaphytinae*, *Phrynosomatinae*, and *Tropidurinae**.

Striations of the tooth crown are uncommon in Iguania, yet not as rare as commonly conceived. I have observed them labially and lingually in a number of *Anolis* (e.g., *A. biporcatus*, *A. extremus*, *A. garmani*), in all *Polychrus*, and in some *Crotaphytus*. They are also found in the early Eocene *Parasauromalus olseni* (see Gilmore 1928) and some *Sceloporus* (e.g., *S. cyanogenys*) and *Tropidurus* (e.g., *T. hispidus*). Distinct striations are interpreted as primitive for *Polychrus* and may independently have evolved in the other taxa listed above. The new species also likens *Polychrus* in the possession of a distinct if discontinuous sulcus dentalis that extends far posteriorly and whose medial border is a sharp lip of bone.

Several other features are primitive or of uncertain polarity and can do no more than exclude *Poly-*

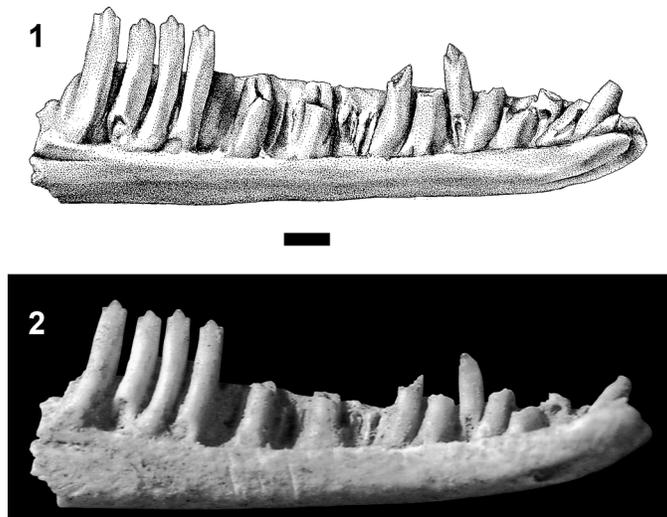


Figure 5. Iguanid MPH-1, (1) illustration and (2) photograph of left dentary in medial view (PTRM 1822). The notch or the posterior margin of the medial face of the dentary does not represent the AIAF. The first tooth is scarcely visible in this view. Scale bar equals 1 mm.

chrus charisticus from crown *Anolis*. For instance, the anterior margin of the nasal process of the maxilla is very steep in *P. charisticus*, as it is in many iguanids; but in *Anolis*, as well as some *Polychrus* (e.g., *P. acutirostris*, but not *P. marmoratus* or *P. guttuosus*), the margin rises more gradually posteriorly. As in *Anolis* and *Polychrus*, the crista transversalis is tall, a feature also seen in taxa like Phrynosomatinae.

In summary, *Polychrus charisticus* is united with *Anolis* and *Polychrus* by (1) extensive fusion of the Meckelian groove, both anteriorly and posteriorly, and (2) at least partial roofing of the SAF on the dorsal surface of the maxilla. *Polychrus charisticus* is united with living *Polychrus* by (1) extension of the premaxillary process of the maxilla, together with (2) dorsal overlap of the premaxillary process by the premaxilla, (3) slight overhang of the premaxillary process by the anterior margin of the nasal process, (4) the dorsolaterally projecting lip of bone on the lateral margin of the premaxillary process, and (5) lingual and labial tooth crown striations. The evident tuberculation of the dermal skull bones is not grossly inconsistent with this placement, as this feature appears in many taxa in both *Anolis* and *Polychrus* (though it cannot be concluded to be primitive for them). Known autapomorphies of *P. charisticus* are (1) the simplified tooth crowns, and (2) possibly the greater extent of overlap of the premaxillary process by the premaxilla. There are presently no features that would place the new species inside or outside crown *Polychrus*, and I have conservatively placed the

new species in that taxon. If further information were to show the new species to lie outside crown *Polychrus*, *charisticus* could be removed.

Oddly, *Polychrus* is a predominantly South American taxon. Only one of six species, *P. guttuosus*, is found north of the Isthmus of Panama (according to the EMBL Database; see Köhler 2000). The sister-taxon of *P. guttuosus*, according to Frost et al. (2001), is *P. femoralis*, known exclusively from South America (EMBL Database; Lehr 2002). This small clade, in turn, was found to be the sister-taxon to remaining species of *Polychrus*. *Polychrus guttuosus* may be a fairly recent immigrant to Central America. If *Polychrus charisticus* is correctly referred, the story becomes more complex. Regardless of whether Polychrotinae* is paraphyletic (Frost et al. 2001), it seems that some members of the group had a longer history in North America than previously thought. *P. charisticus* would provide a good candidate for the estimation of divergence times in Iguania using molecular methods, provided that the position of *Polychrus* in Iguanidae is secured.

Size alone would not contravene the referral of Vertebra Type 1 (see below) to this species.

Iguanid MPH-1 (Figure 5)

Referred specimens. PTRM 1822 (left dentary), Figure 5; 2605 (right dentary fragment); 2743 (edentulous left dentary); 5231 (partial right dentary); 5334 (left dentary fragment); 5352 (partial

right dentary); 5353 (right dentary fragment); 5354 (partial right dentary); 5724 (maxilla fragment)

Description. The most complete specimen, PTRM 1822, is also one of the larger dentaries. There are spaces for 20 teeth in the ~10.8 mm of tooth row; at least one more tooth appears to have been present behind the twentieth. The teeth are relatively tall, and both anterior and posterior teeth are mesial-distally compressed (Figure 5). The eighth tooth (from symphysis) has distinct mesial and distal "shoulders," separated from the central cusp by very weak, vertical grooves that anticipate more posterior tooth morphology. Posterior teeth have strong mesial and distal accessory cusps, both separated from the central cusp by grooves. The crowns are parallel-sided (i.e., not flared). There is a slight concavity on the lingual side of each tooth, matched by a slight convexity on the labial side; thus, the cutting edges are directed somewhat lingually. The bases of the posterior teeth are slightly bulbous or protrusive. There is a weak sulcus dentalis anteriorly, but no subdental shelf or gutter posteriorly. The Meckelian groove is closed and fused, though it is impossible to determine precisely how far posteriorly, because the dentary is broken. A narrow, longitudinal groove extends anteriorly from the break, just ventral to the tooth row; this groove penetrates entirely through the medial wall of the dentary and may be artifactual. The external surface of the dentary is quite smooth; it is perforated by eight irregularly spaced labial foramina, the posterior-most of which is located at the level of the boundary between teeth 18 and 19 (from symphysis). The dentary does not curve strongly medially at its anterior end (i.e., it is not "hooked"). The anterior opening of the Meckelian canal is elongate.

Other specimens provide more information. In PTRM 5231, approximately the same size as PTRM 1822, the fifth and sixth teeth (from symphysis) have distinct "shoulders" separated by grooves. (The crown of the fourth tooth is broken; the third is resorbed.) PTRM 5353 is the medial segment of a small dentary, with tooth crown morphology similar to that of PTRM 1822. Interestingly, the crowns of the teeth are nearly translucent; this peculiarity is matched by PTRM 5354, a small partial dentary. PTRM 5354 also confirms the presence of posterior labial foramina. PTRM 2743, a highly weathered, edentulous partial dentary, preserved no indication of a medial, longitudinal groove on the dentary.

Remarks. This species is considered an iguanid because it possesses distinctly tricuspid teeth (grooves separating accessory cusps from the central cusp are present both labially and lingually), which are mesiodistally compressed and show pleurodont implantation. A number of other squamates have been described as having "tricuspid" teeth, such as scincoids, but in most of these taxa labial grooves bounding accessory cusps are not developed (the xantusiid *Lepidophyma* is an exception). In other taxa with distinctly tricuspid teeth, such as some teiids, they are mesiodistally expanded and tend to show considerable basal cementum. Most acrodont iguanians also have distinctly tricuspid teeth, but they show acrodont tooth implantation and are mesiodistally expanded. These remarks apply to other iguanids described below.

Iguanid MPH-1 is easily distinguished from *Polychrus charisticus* by several features. The teeth of the former are weakly tricuspid anteriorly (essentially unicuspid), and are closely spaced distally (widely spaced); the dental parapet is relatively higher (lower); the labial foramina extend far posteriorly (not far posteriorly); and the anterior opening of the Meckelian canal is elongate (constricted). Fusion of the Meckelian groove is a derived character in Iguania (Etheridge and de Queiroz 1988). Because this state was achieved independently multiple times, it is by itself of little systematic utility; as noted above, extensive fusion of the Meckelian groove appears also in Iguaninae, *Anolis*, *Polychrus*, and many tropidurines. There are otherwise few derived characters in the jaw elements that would constrain the affiliation of Iguanid MPH-1.

Size cannot disbar the referral of Vertebra Type 1 (see below) to this taxon.

Iguanid MPH-2 (Figure 6)

Referred specimens. PTRM 2602 (right dentary), Figure 6

Description. The tooth row of this dentary is 15.0 mm long, and the depth of the dentary at the ultimate tooth is 4.6 mm. Twenty-three tooth positions, with one complete and one partial tooth in place, are preserved (Figure 6). The complete tooth is located in the latter half of the tooth row. It is relatively low-crowned. As preserved, the crown is relatively blunt, in part due to wear and to breakage of its mesial edge; there is no trace of a distal accessory cusp on the crown. Thus, cheek teeth in

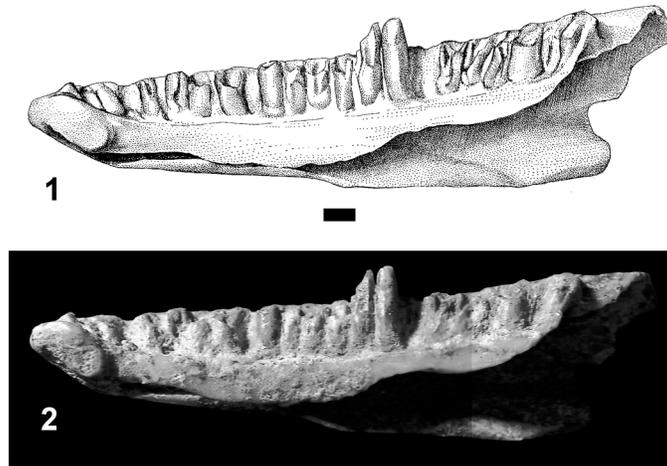


Figure 6. Iguanid MPH-2, (1) illustration and (2) photograph of right dentary in medial view (PTRM 2602). Note the coronoid notch that continues onto the labial surface of the dentary. The first tooth is not visible in this view. Scale bar equals 1 mm.

Iguanid MPH-2 were probably unicuspid or weakly tricuspid (this cannot be better constrained, due to the extent of wear). There is a narrow subdental shelf that spans much of the tooth row. The Meckelian groove is open, except for a space of ~2.5 mm in the anterior half of the dentary, where the dorsal and ventral flanges close on one another. A small groove (Figure 6) is present on the ventral surface of the dorsal flange at the level of the eighteenth tooth (from symphysis), marking the position of the AIAF, which would also then have been in contact with the splenial. The Meckelian groove is widely open posteriorly. The anterior end of the dentary is markedly inturned ("hooked").

Immediately posterior to the tooth row is a notch for the coronoid (Figure 6) which continues for a short distance onto the labial surface of the dentary. There was evidently no strong, anterior blade of the coronoid in this species, nor is there a large dorsal process of the dentary to brace the coronoid anteriorly. Several labial foramina penetrate the dentary's external surface; these tiny holes are irregularly spaced and extend >50% along the tooth row. The lateral surface of the dentary is otherwise smooth.

Remarks. The nearest relatives of Iguanid MPH-2 are obscure. Primitively, species of the phrynosomatine taxon *Phrynosoma* tend to have especially deep dentaries (Van Devender and Eshelman 1979), which may also apply to the *Phrynosoma* stem [e.g., *Paraphrynosoma greeni* (Holman 1987) from the early Oligocene of Colorado]. PTRM 2602 appears relatively deep, but the depth/length ratio

is actually much closer to iguanids generally and does not suggest a relationship to *Phrynosoma*.

The small, deep, labial coronoid notch is likewise not currently diagnostic. A strong labial coronoid blade on the dentary is typical in members of *Anolis* (pers. obs.), Iguaninae (pers. obs.), *Leiocephalus* (Etheridge 1966; Pregill 1992; pers. obs.), and hoplocercines (Estes et al. 1988, figure 16; pers. obs.); a weaker one is found in some phrynosomatines and tropidurines (pers. obs.), and a blade is generally absent in members of *Polychrus*, *Pristidacylus*, *Corytophaninae*, *Crotaphytinae*, and *Oplurinae* that I have examined.

Finally, partial closure without fusion of the Meckelian groove is a derived feature also appearing in several iguanid clades. It is evident in a number of crotaphytines, *Basiliscus*, phrynosomatines, and oplurines (Etheridge and de Queiroz 1988) and in some liolaemins (Etheridge, personal commun., 2002). While on biogeographic grounds it is unlikely that Iguanid MPH-2 is a tropidurine or oplurine, this apomorphy cannot itself diagnose the species described here. Better specimens are also desirable before the species is formally named.

Tuberculacerta gen. nov.

Type species. *Tuberculacerta pearsoni* sp. nov. (by monotypy)

Diagnosis. As for type and only known species.

Etymology. *tuberculum*, L., diminutive of *tuber*, L. "swelling, bulb," plus *lacerta*, L. "lizard," referring to the tuberculated snout of this squamate.

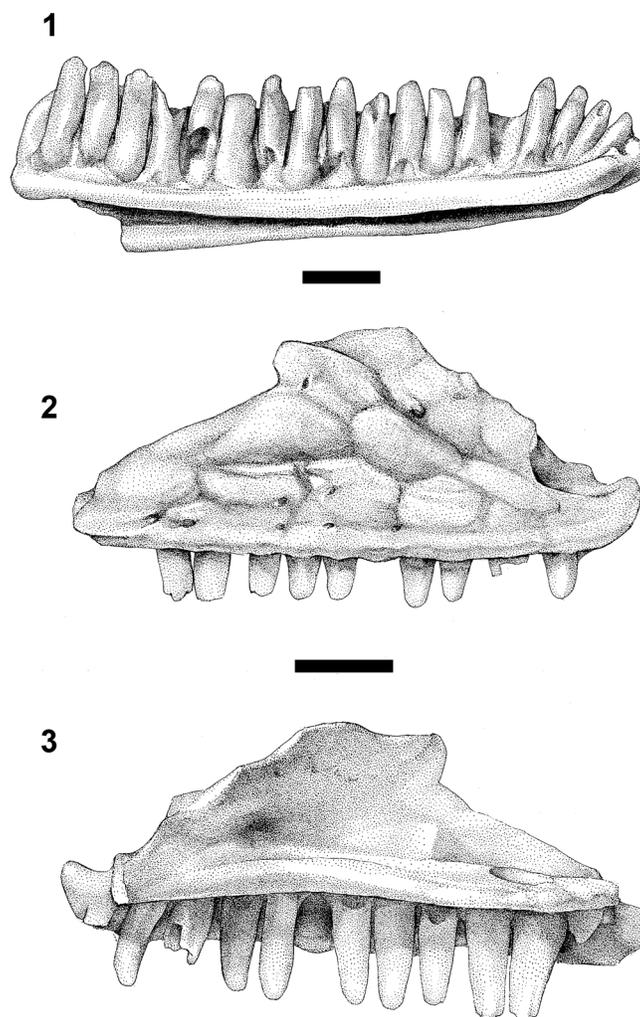


Figure 7. *Tuberculacerta pearsoni* gen. et sp. nov. (1) Holotype, left dentary in medial view (PTRM 5296). The IMS cannot be seen in this view because it is nearly perpendicular to the plane of the page. (2) Paratype, right maxilla in lateral view (PTRM 1429). (3) Same specimen in medial view. The broken palatine facet is located anterior and medial to the SAF. The SAF is not set in a "gutter." Scale bars equal 1 mm.

Tuberculacerta pearsoni sp. nov.
(Figure 7)

Holotype. PTRM 5296 (left dentary), Figure 7.1

Paratypes. PTRM 1432 (left dentary fragment); 5326 (right dentary); 5355 (left dentary); 1429 (right maxilla), Figure 7.2–7.3

Locality and horizon. PTRM V89002, Chalky Buttes Member, Chadron Formation (late Eocene), North Dakota, USA

Distribution. Known only from type locality

Diagnosis. A small iguanid with parallel-sided to weakly tapering, tricuspid posterior teeth; >19 dentary teeth in total; subhorizontal intramandibular septum that extends far posteriorly; Meckelian groove narrow but open, faces ventrally near sym-

physis; lateral surface of maxilla adorned with large tubercles; sharp bend in the nasal process of the maxilla (see below); dorsal surface of the premaxillary process of the maxilla excavated; crista transversalis strong.

Etymology. Named in honor of Dean A. Pearson (PTRM), whose diligent work and kind permission has made this study possible.

Description of holotype. PTRM 5296 is a relatively complete left dentary, missing only its posterior-most end. The preserved tooth row is 8.0 mm long and contains 19 tooth spaces, with all but the first and sixth teeth in place. The teeth are moderately high crowned (Figure 7.1). The crowns are generally worn, but a couple of the posterior teeth retain mesial and distal cusps in addition to the

main central cusp. The posterior crowns are parallel-sided to weakly tapering. Anteriorly there is a weak subdental shelf, but this shelf gradually disappears posteriorly. The Meckelian groove is entirely open; for most of its length it is directed ventromedially, but anteriorly it is directed ventrally. There is a prominent medial "hook" to the dentary at its anterior end. The intramandibular septum (IMS) extends far posteriorly and is present as far back as the dentary itself is preserved. The IMS is oriented nearly horizontally. Externally, there are six labial foramina, the last at the level of the fourteenth tooth.

Description of paratypes. PTRM 1432 and 5326 are smaller than PTRM 5296 and poorly preserved, but PTRM 5355, a still smaller specimen, provides more information on the pattern of tooth crown morphology in the dentary. The ninth and tenth teeth (from symphysis) are partially preserved, and weak grooves mesially and distally indicate that those teeth had at least weak "shoulders," if not distinct cusps. PTRM 5355 also has a somewhat better-developed subdental shelf posteriorly. All three of these specimens show a long, subhorizontal IMS, as seen in PTRM 5296.

PTRM 1429 is a well-preserved right maxilla (referred to the same taxon as the dentaries on the basis of size and tooth morphology). Twelve tooth positions and nine teeth are preserved (Figure 7.2–3). The teeth are unicuspid anteriorly, but the tenth and eleventh teeth are tricuspid, with parallel-sided to weakly tapering crowns; where precisely the transition occurs is difficult to estimate, because of wear on some more anterior teeth. The crowns are moderate in height. The nasal process is broad and shows a strong canthal crest (Figure 7.2); it is "bent," in other words, divided into an anterodorsally facing surface and a laterally facing one. Posteriorly, there is a facet on the medial surface of the nasal process for articulation with the prefrontal. Anteriorly, the nasal process is continuous with the well-developed crista transversalis. The nasal process shows large, well-developed dermal rugosities, which presumably indicate the margins of epidermal scales, down to just above the main row of labial foramina, of which there are six. The premaxillary process is broken medially at the level of the subnarial arterial foramen. The dorsal surface of the process is excavated. The AIAF lies just dorsal and medial to this pit, at the base of the nasal process. The palatine process, as preserved, is insignificant, but the sharp-bordered facet visible on its dorsal surface (Figure 7.3) and the tapering of the palatal shelf medial to this facet suggest that

it has been broken. Its original extent is unknown. The SAF is "roofed" (see above under *Polychrus characteristicus*) and opens posteriorly near the end of the nasal process (Figure 7.3). The posterior end of the maxilla is broken, but it retains part of the moderately deep groove for articulation with the jugal. This groove extends anteriorly to the level of the SAF.

Remarks. The elongate IMS of *Tuberculacerta pearsoni* is noteworthy. To evaluate this feature in iguanids, I measured two lengths in each of over 50 isolated dentaries, including representatives of all major clades except Liolaemini. The first length is that from the symphysis to the end of the IMS; the second, from the symphysis to the end of the tooth row. The ratio between these measurements was ≥ 0.69 in all phrynosomatines (usually >0.80) and >0.80 in *Anolis*, *Pristidactylus torquatus*, Oplurinae, and *Leiocephalus*. A ratio of <0.69 was found in all other clades, including *Polychrus*, Corytophaninae, Crotaphytinae, *Enyalioides oshaughnessyi*, Iguaninae, and Tropidurini (*Uracentron*, *Uranoscodon*, *Microlophus*, *Tropidurus*, *Plica*). In cases where two specimens of the same species were examined (*Phrynosoma asio*, *Gambelia wislizenii*), the ratio differed by no more than 7%. In the four agamids examined, the ratio was between 0.60 and 0.70. An extended IMS—defined here as one showing a ratio of greater than ~ 0.7 —is tentatively interpreted as independently synapomorphic of some part of Polychrotinae*, Oplurinae, *Leiocephalus*, and Phrynosomatinae, pending evaluation in Liolaemini. The posterior end of the most complete dentary in the sample, PTRM 5296, is not preserved; one can nevertheless say that the IMS extends to the level of the nineteenth dentary tooth, further than in all iguanids with a "short" IMS (ratio less than ~ 0.7).

In the maxilla of *Tuberculacerta pearsoni*, as in all phrynosomatines examined, the SAF is "roofed." As discussed above, this morphology appears to be synapomorphic of *Anolis* and *Polychrus*, of parts of Tropidurinae*, and of Phrynosomatinae.

The nasal process of the maxilla of *Tuberculacerta pearsoni* is distinctive in being strongly bent medially and continuous with the crista transversalis at its anterior base. A bend like this, which corresponds to a strong canthal crest, is well developed in all examined members of Phrynosomatinae with the exception of some *Phrynosoma* (*P. cornutum*, *P. platyrhinos*). As discussed below, the nasal process in these species of *Phrynosoma* departs strongly from the primitive condition. Among other

iguanians examined, a sharp bend is present in Tropicurini but is weak in *Leiocephalus* and oplurines; it is weak or absent in many *Polychrus* (*P. guttuosus*, *P. marmoratus*), Crotophytinae, Iguaninae, and *Enyalioides oshaughnessyi*. In the case where a sharp bend is absent, the nasal process of the maxilla is essentially a vertical flange that may curve slightly medially at its dorsal terminus. On the other hand, a sharp bend is present in *Anolis* (even better developed here) and in Corytophaninae; in *Anolis*, the anterodorsal surface of the nasal process is continuous with the crista transversalis, as in Phrynosomatinae, whereas in Corytophaninae the bend occurs high and in a nearly coronal plane, such that the (small) dorsally facing surface is not continuous with the crista. Outgroup comparison suggests that the presence of a sharp bend is derived in Iguanidae where it occurs. Thus, the distribution within Iguania of a sharp bend in the maxilla suggests that it is primitive for Phrynosomatinae (and also Tropicurini and *Anolis*) and has been transformed beyond recognition in some members of the eponymous clade *Phrynosoma*. Absence in *T. pearsoni* of a closed and fused Meckelian groove (primitive for Tropicurinae and Polychrotinae*) suggests in turn that it is related to Phrynosomatinae; this conclusion is consistent with the extended IMS and "roofed" SAF discussed above.

Rugosities on the nasal process of the maxilla, as seen in *Tuberculacerta pearsoni*, also occur in some species of *Phrynosoma*. Rugosities on the dermal bone in *Phrynosoma* generally extend far beyond the frontal, regardless of whether they reach the nasal process, which is highly reduced in many species. Among other iguanids examined, some members of Polychrotinae* and Crotophytinae have the best-developed dermal rugosities. Pregill (1992) has also discussed them in some species of *Leiocephalus* but determined them not to be primitive for that clade; Etheridge and de Queiroz (1988) and Lang (1989) furthermore noted them in *Lae-manctus serratus*. Extreme development of rugosities on the dermal skull bones may be a synapomorphy of *Phrynosoma* or part of its stem, and their presence in *T. pearsoni* might suggest that this species belongs on that stem.

This evidence tying *Tuberculacerta pearsoni* to the stem of *Phrynosoma* is tenuous. In any case, the new taxon lacks at least two synapomorphies of (crown) *Phrynosoma*, namely, a medially facing anterior extent of the Meckelian groove (Van Devender and Eshelman 1979) and a high dentary depth/length ratio. Many species of *Phrynosoma*

furthermore possess an open Meckelian groove (*P. modestum* is an exception), a characteristic that distinguishes them from other phrynosomatines. An open Meckelian groove is primitive for Iguania (Etheridge and de Queiroz 1988), but it is important to determine whether its occurrence in *Phrynosoma* is symplesiomorphic or secondary. If closure of the Meckelian groove was acquired twice in Phrynosomatinae—once in the *Uta-Urosaurus-Sceloporus* clade and once in "sand lizards" (*sensu* Frost and Etheridge 1989)—then an open Meckelian groove in *T. pearsoni* only excludes it from these clades; if closure is a synapomorphy of Phrynosomatinae and reversed in *Phrynosoma*, then the open Meckelian groove could unite *T. pearsoni* with *Phrynosoma*. The (uncertain) phylogenetic position of *Petrosaurus* is crucial to addressing this question.

A maxilla of *Tuberculacerta pearsoni* preserving the palatine process is desirable. If it is a phrynosomatine, as the evidence above suggests, it should have a strong and triangular palatine process. In most phrynosomatines (excepting *Petrosaurus mearnsi* and some *Sceloporus* like *S. clarkii* and *S. serrifer*) the palatine process is moderate to large in size and triangular. This morphology also obtains in oplurines, crotophytines, and many tropicurines (although in *Leiocephalus* and *Uranoscodon* the process tends to be blunt), but contrasts with the morphology in Polychrotinae*, Corytophaninae, Crotophytinae, Iguaninae, and *Enyalioides oshaughnessyi*, where the process is blunt, rounded, and poorly developed. One can conclude, minimally, that a strong, triangular palatine process is primitive for Phrynosomatinae.

In summary, *Tuberculacerta pearsoni* possesses a larger suite of characters uniting it with Phrynosomatinae than with any other taxon, including (1) an elongate IMS, (2) a sharp bend in the nasal process of the maxilla, creating an anterodorsally facing surface that is continuous with the crista transversalis, and (3) a "roofed" SAF. Within Phrynosomatinae, *T. pearsoni* is tenuously united with *Phrynosoma* by the well-developed rugosities of the facial bones. The open Meckelian groove does not contravene this placement.

Tuberculacerta pearsoni has at least one autapomorphy that distinguishes it from all extant phrynosomatines examined, namely, the dorsal excavation of the premaxillary process of the maxilla. A slight depression is evident in the premaxillary process of *Cophosaurus texana* and *Urosaurus graciosus*, but it is not as well devel-

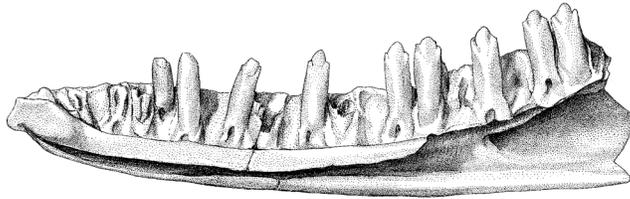


Figure 8. cf. *Aciprion* sp., right dentary in medial view (PTRM 5198). The first tooth position is not discernible in this view. Scale bar equals 1 mm.

oped as in *T. pearsoni*; in most phrynosomatines examined, the premaxillary process is flat and may or may not slope slightly ventrolaterally.

Thus far, the earliest record of Phrynosomatinae seems to be the early Oligocene *Paraphrynosoma greeni* (Holman 1987), which was also suggested to lie on the stem of *Phrynosoma*.

cf. *Aciprion* sp.
(Figure 8)

Referred specimens. PTRM 5198 (right dentary), Figure 8; 2054 (left dentary fragment); 2594 (partial left dentary); 5202 (partial right dentary); 2095 (left maxilla fragment); 5356 (right maxilla fragment); 5401 (left maxilla fragment); ?5396 (left maxilla fragment)

Description. PTRM 5198 is a right dentary missing only its posterior-most end (Figure 8). It preserves 23 tooth spaces (with nine teeth); the length of the tooth row as preserved is 10.9 mm. The teeth are moderate in height. There are well-developed mesial and distal accessory cusps on the crowns of the posterior teeth, but the crowns are not flared. These cusps are much weaker on the more anterior teeth but nevertheless visible on tooth nine. The posterior crowns do not abut one another. The posterior-most tooth is somewhat shorter than the anterior-most, reflecting a decrease in tooth size toward the back of the tooth row. Five middle teeth occupy a length of 5.4 mm. Anteriorly, a moderately developed subdental gutter is present, which is reduced, but still present, posteriorly. The IMS extends to under the twentieth tooth space (9.2 mm along the tooth row). The Meckelian groove is open along the entire dentary; however, it narrows considerably in the middle. The anterior end of the dentary turns abruptly medially (it is "hooked"). On the external surface, there is a linear indentation, running longitudinally just below the parapet of the jaw. There are five labial foramina, the last located at the level of the fourteenth tooth space. The

remaining specimens provide little more information on dentary morphology, although it is worth noting that PTRM 2594, nearly the same size as PTRM 5198, lacks an external, longitudinal indentation.

The maxilla of cf. *Aciprion* sp. is not represented by equally well-preserved material. (Maxillae were referred to the same taxon as the dentaries on the basis of size and tooth morphology.) PTRM 2095 has essentially the same tooth morphology as the dentaries described above. It is a middle fragment of maxilla; it is quite worn and does not preserve the nasal process. The roof of bone covering the posterior course of the superior alveolar foramen is broken, giving the foramen the superficial appearance of being set in a "gutter"; it was not. PTRM 5356 is a slightly more posterior fragment that preserves the anterior part of the jugal groove, which is only moderately deep.

Remarks. Cf. *Aciprion* sp. compares closely in many details with the equi-sized *Aciprion formosum* from the early Oligocene of Colorado (YPM 4663, YPM-PU 10015). Cf. *Aciprion* sp. had >23 teeth in the dentary, versus 25 in YPM-PU 10015. Tooth morphology, especially the position and nature of the transition from unicuspid to tricuspid crowns, and tooth spacing are similar in the two taxa. The only significant dental difference between the two appears to be tooth crown height, which is lower in cf. *Aciprion* sp. The two taxa additionally share a similar symphyseal structure. *A. formosum* does differ from cf. *Aciprion* sp. in that it has only a weak subdental shelf; additionally, in *A. formosum* the Meckelian groove is closed (but not fused) for several millimeters in the anterior half of the dentary, while in cf. *Aciprion* sp., the groove merely narrows.

As in *Aciprion formosum* (see Estes 1983), there are few features of cf. *Aciprion* sp. that permit ready phylogenetic placement. The apparently high IMS/tooth row length ratio (~0.8?) is sugges-

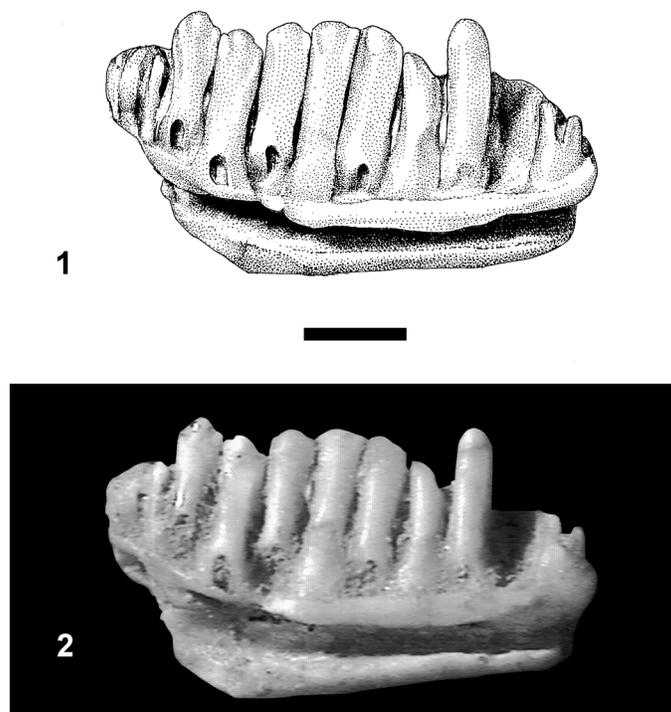


Figure 9. Iguanid MPH-3, (1) illustration and (2) photograph of partial left dentary in medial view (PTRM 5357). Crowns of teeth, like the bone itself, are heavily worn but clearly abut on one another. Scale bar equals 1 mm.

tive of affinities with Phrynosomatinae/Oplurinae/Tropidurini or with *Anolis* (see above under *Tuberculacerta pearsoni*).

Iguanid MPH-3 (Figure 9)

Referred specimens. PTRM 5357 (partial left dentary), Figure 9; 5178 (partial left dentary); 5267 (left dentary fragment)

Description. PTRM 5357 is the posterior segment of a left dentary (Figure 9). It is generally well worn, with bone edges and tooth crowns rounded. Ten tooth positions and seven teeth are preserved. The teeth are moderately high-crowned. The anterior-most tooth was either unicuspid or weakly tricuspid. The teeth become more strongly tricuspid posteriorly; the crowns begin to flare and actually contact one another to form a continuous cutting surface. Due to the incomplete preservation, it is unclear where along the dentary the transition in tooth crown morphology occurs. Five middle teeth occupy 4.6 mm. There is a very weak subdental shelf anteriorly. The Meckelian groove is open throughout the preserved length of dentary. PTRM 5178 and 5267 provide no further details.

Remarks. Iguanid MPH-3 is very similar to cf. *Aciprion* sp. By comparison with the latter, how-

ever, Iguanid MPH-3 is distinguished by having more closely spaced teeth and slightly flared tooth crowns that, in the posterior part of the jaw, contact one another. The IMS appears to be posteriorly extensive in this taxon, but better-preserved and more complete specimens must be found before any systematic determination can be made.

Iguanid MPH-4 (Figure 10)

Referred specimen. PTRM 2041 (partial left dentary), Figure 10

Description. PTRM 2041, the middle segment of a left dentary, is heavily worn. Fourteen tooth positions and nine teeth are preserved. The teeth are worn to rounded stumps, so no distinct morphology is apparent (Figure 10); they are, however, not closely spaced. There is the slightest of subdental gutters along most of the length of the tooth row. The Meckelian groove gently closes anteriorly. The IMS extends posteriorly to under the tenth preserved tooth.

Remarks. Iguanid MPH-4 is poorly preserved, and little can be said about the characteristics of this morphotype. As the tooth crowns are worn away, tricuspid teeth cannot be used to refer it to Iguanidae; instead, complete closure (without

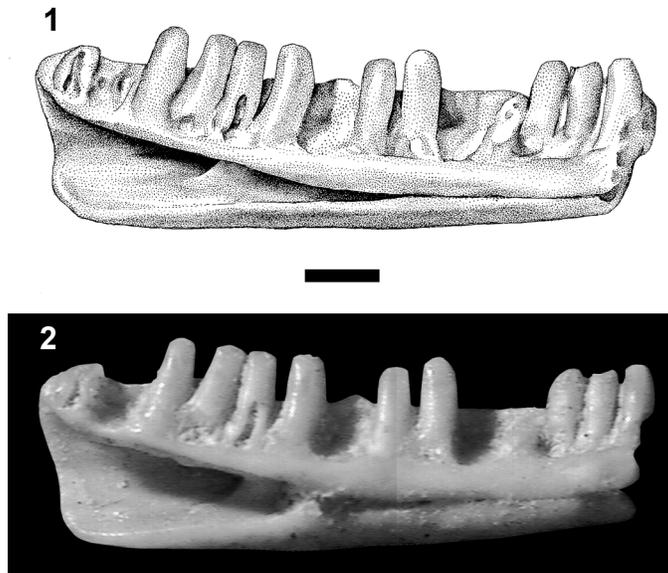


Figure 10. Iguanid MPH-4, (1) illustration and (2) photograph of partial left dentary in medial view (PTRM 2041). Teeth and bone are heavily worn. Scale bar equals 1 mm.

fusion) of the Meckelian groove must be used (I am unaware of any non-iguanid that shows this feature). It is distinguished from most other taxa described here by gentle closure, without fusion, of the Meckelian groove and from *Cypressaurus* sp. (see below) by the more robust teeth.

Cypressaurus sp.
(Figure 11)

Referred specimens. PTRM 2623 (partial left maxilla), Figure 11; 5321 (dentary fragment)

Description. PTRM 2623 is the medial portion of a left maxilla. The four complete teeth are high-crowned, with ~50% of their height projecting above the parapet of the jaw. The tooth crowns are slightly worn, but they are distinctly tricuspid. The crowns taper slightly toward their apices (Figure 11.1–2). The palatine process of the maxillary shelf is weak. There is a small groove along the dorsal surface of its anterior margin that represents the articulation with the palatine. The SAF is set in a gutter (Figure 11.3; see also discussion under *Polychrus charisticus* and *Tuberculacerta pearsoni*). The jugal groove is quite deep; it extends anteriorly to the posterior end of the gutter but is separated from it by a small ridge. The external surface of the nasal process is smooth and has four labial foramina as preserved.

The dentary fragment has three teeth with the same general tooth form as PTRM 2623; the crowns are somewhat worn. The ventral portion of the dentary is not preserved.

Remarks. The monotypic *Cypressaurus hypsodontus* Holman (1972) was described on the basis of two partial dentaries from the medial Chadronian of Saskatchewan. PTRM 2623 is referred to *Cypressaurus* on the basis of its high tooth crowns, a derived feature. In *C. hypsodontus*, the central cusp of each tooth appears higher than in PTRM 2623, but this difference could be the result of wear. Also in *C. hypsodontus*, the tooth crowns do not appear to taper toward the apex (see Holman 1972, figure 2), unlike in PTRM 2623. More and better specimens are desirable to clarify whether these differences indicate the presence of two different taxa.

Scincoid MPH-1
(Figure 12)

Referred specimens. PTRM 5359 (partial right dentary), Figure 12; 5358 (right dentary fragment)

Description. Both specimens are small. PTRM 5359 is a partial right dentary with 13 full tooth positions and five relatively complete teeth (Figure 12). The IMS extends posteriorly to under the fifth tooth from the rear. A facet for the splenial, on the underside of the subdental shelf, extends to under the eighth tooth from the rear. There is a weak subdental shelf, but no sulcus dentalis. Two labial foramina are present, the posterior-most under the seventh tooth from the rear.

Tooth replacement is intradental ("iguanid" type of McDowell and Bogert 1954). The teeth, as preserved, are relatively blunt (especially in PTRM

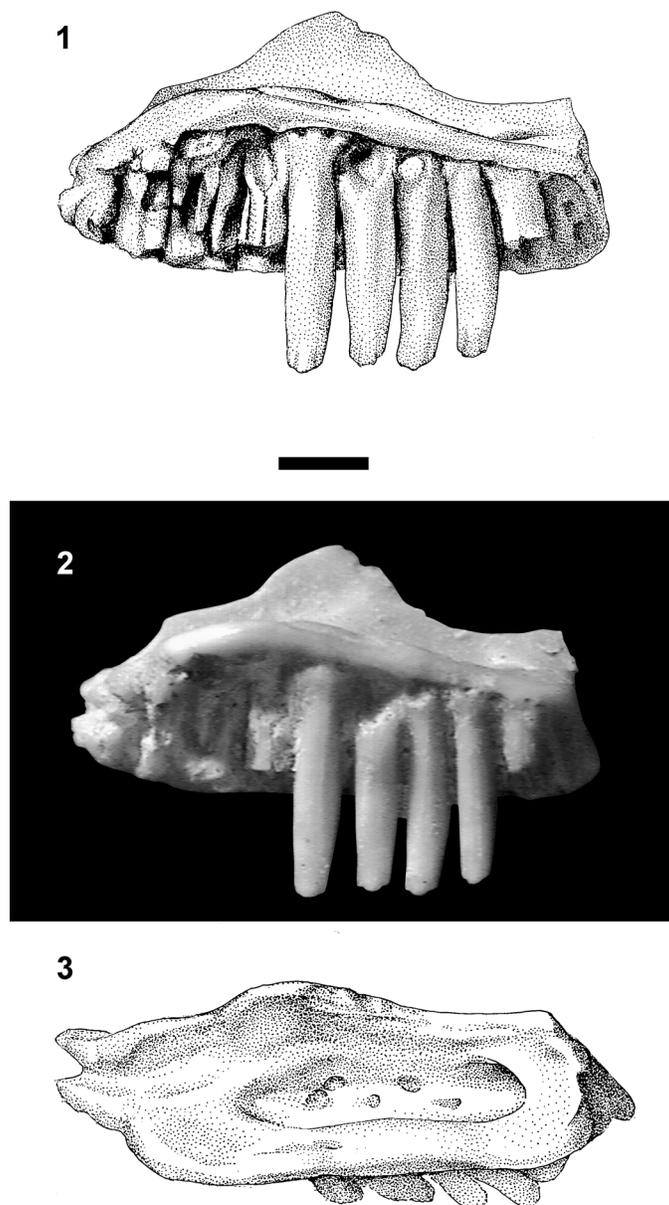


Figure 11. *Cypressaurus* sp., (1) illustration and (2) photograph of partial left maxilla in medial view (PTRM 2623). Teeth taper slightly toward their tips. (3) Same specimen in dorsomedial view. The jugal groove is deep, and the superior alveolar foramen is set in a "gutter." Scale bar equals 1 mm.

5358, which is worn) and low-crowned. Many teeth are especially broad at the base, tapering toward their crowns. The crowns themselves show a moderate central cusp bordered by strong mesial and weaker distal crests that curve labially around the main cusp, forming "shoulders." The lingual, but not labial, surfaces of the crowns are striated.

Remarks. Scinoid MPH-1 is distinguished from heretofore described Paleogene scinoid lizards by the tapering of the teeth toward their apices, and

the absence of a sulcus dentalis. The primary reason for allying it with Scincoidea is general tooth form, which, as described, consists of a main central cusp, striated lingually and bordered by "shoulders" (not distinct accessory cusps). Clearly, better specimens are desirable.

"Palaeoxantusia" borealis Holman (1972)
(Figure 13)

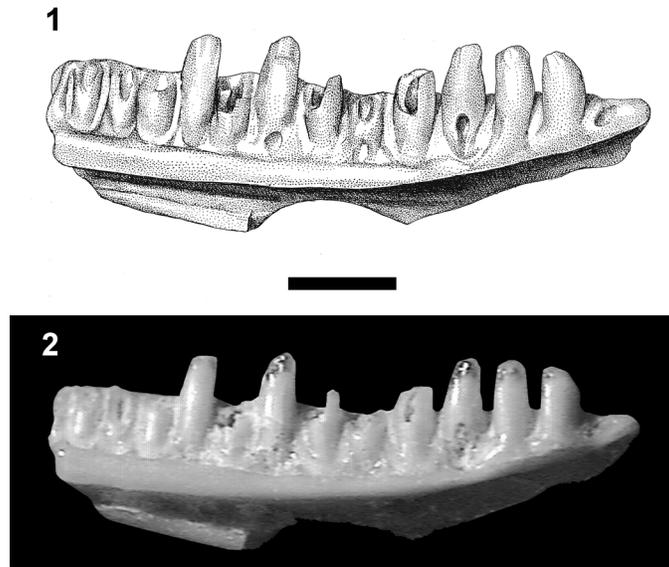


Figure 12. Scincoid MPH-1, (1) illustration and (2) photograph of partial right dentary in medial view (PTRM 5359). Scale bar equals 1 mm.

Referred specimens. PTRM 2720 (partial left dentary), Figure 13.1; 5360 (edentulous left dentary); 5361 (partial right dentary), Figure 13.2; 2074 (medial portion of right maxilla); 5284 (left dentary fragment); 5288 (partial right dentary); 2074 (right

maxilla fragment); 2713 (partial right maxilla); 5298 (right maxilla fragment); 5387 (right dentary fragment)

Amended diagnosis. As in Holman (1972), except that the AIAF is located at or behind the ultimate

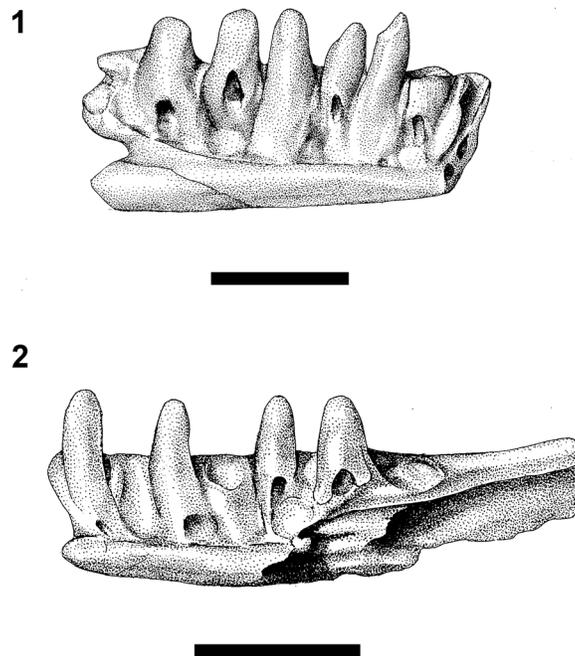


Figure 13. "*Palaeoxantusia*" *borealis*, (1) partial left dentary in medial view (PTRM 2720). No indication of a splenial is preserved in this specimen. The thin line extending anteriorly from the AIAF is a fracture. (2) Partial right dentary in medial view (PTRM 5361). Scale bars equal 1 mm.

dentary tooth in most members (see below) and tooth crowns are striated lingually.

Description. None of the Medicine Pole Hills specimens approaches the quality of the holotype spleniodentary of "*Palaeoxantusia borealis*" (SMNH 1435). The most complete specimen, PTRM 5360, is edentulous and broken just posterior to the ultimate tooth and lacks a splenial; it displays many features seen in the other specimens from the Medicine Pole Hills l.f. It is relatively small, with a tooth-row length of 4.0 mm; the height of the dentary at the ultimate tooth is 1.1 mm. A sulcus dentalis is well developed. Twelve tooth positions are present. The AIAF is situated just behind the ultimate tooth (more clearly seen in PTRM 2720: Figure 13.1). There are five labial foramina. PTRM 5361 shows the long, horizontal posterior extension of the dentary beyond the tooth row (Figure 13.2).

The teeth of most specimens are rather worn; they are blunt and unicuspid and do not preserve details of crown morphology. The teeth of a couple of specimens retain traces of the weak "shoulders" that lie mesial and distal to the central cusp. The ultimate maxillary tooth of PTRM 5298 and 5387 present clear examples of weak striations near the base of the crown.

Remarks. This Medicine Pole Hills xantusiid compares well to "*Palaeoxantusia borealis*", and it is referred to that taxon. The specimens described here are smaller than those from the Calf Creek l.f. (Medicine Pole Hills: mean dentary depth at ultimate tooth ~1.1 mm, $n = 4$; Calf Creek: mean depth ~1.3 mm, $n = 6$). However, there is much overlap at the lower end of the Calf Creek size range, and a 20% difference in linear dimensions would translate into an approximately 75% difference in volume (and hence, mass), which accounts for the overall slender appearance of the Medicine Pole Hills specimens. It is possible that, if the specimens are correctly referred, "*P.*" *borealis* exhibits an inverse correlation of size (mass) to latitude—and, hence, temperature—conforming to Bergmann's rule (Bergmann 1847), which is disputed in squamates (e.g., Angilletta et al. 2004). Alternatively, none of the specimens in the sample may be fully grown. Only one of the largest specimens from Calf Creek (depth ~1.5 mm) evinces complete fusion of the splenial to the dentary and can be interpreted as more-or-less fully adult. Unfortunately, none of the specimens preserves the splenial at all (this fact may indicate that the splenial

was not yet fused, i.e., that all the specimens are from juveniles).

Fossil xantusiid species are typically based on the dentary or spleniodentary, and there are precious few features in this bone upon which phylogenetic hypotheses can be based (Vicario et al. 2003). Thus, it is important to point out a feature not yet described that may provide some constraint on the relationships of fossil xantusiids. In the earliest-known of these, "*Palaeoxantusia fera*", from the middle Paleocene of Wyoming (Estes 1976; Sullivan 1982), the AIAF is located under the ultimate or penultimate dentary tooth in all specimens for which this character is clearly scorable ($n = 4$ and 9, respectively). The same holds true for the large Bridgerian form "*P. fera*" (YPM-PU 17506, $n = 3$) and the Bridgerian type of *P. fera* (AMNH 3815; Hecht 1956). The only specimen that appears to violate this generalization is AMNH 3821, from the same locality as the type of *P. fera*; it appears, then, that middle Eocene "*Palaeoxantusia*" exhibits some polymorphism. "*Palaeoxantusia kyrentos*" and "*P.*" *allisoni* from the Uintan of California also display an anterior foramen (see Schatzinger 1980, text-figures 1,4). Among extant xantusiids, the anterior position of the AIAF is seen in *Lepidophyma flavimaculatum* (pers. obs.); some *Xantusia riversiana* (three of eight) also approach the condition. In all "*Palaeoxantusia borealis*" from both the Medicine Pole Hills (Figure 13.1) and Calf Creek, in contrast, the AIAF is located just behind the ultimate dentary tooth. This posterior position—it may be defined as the case in which the foramen is entirely located behind the midline of the ultimate tooth—is also seen in the living basal (Hedges and Bezy 1993; Vicario et al. 2003) member *Cricosaura typica* (see Savage 1963, figure 8), *Xantusia downsi* (see Norell 1989, figure 14), and *X. vigilis*, *X. arizonae*, *X. henshawi*, and a significant proportion of *X. riversiana* (pers. obs.). Given Vicario et al.'s (2003) recent phylogeny of Xantusiidae, it seems possible that the posterior position is primitive for *Xantusia* and partially reversed in *X. riversiana*. The only other small xantusiid, *Cricosaura typica*, must independently have acquired this feature, implying that it might simply be related to absolute size. On the other hand, the posterior position in one paratype of *P. fera* and many *X. riversiana* indicates that this need not be the case. Size correlation also suggests that an anterior shifting of the foramen ought to be visible during development.

Estes (1983: 125) concluded that "*Palaeoxantusia borealis*" was inadequately diagnosed and might be

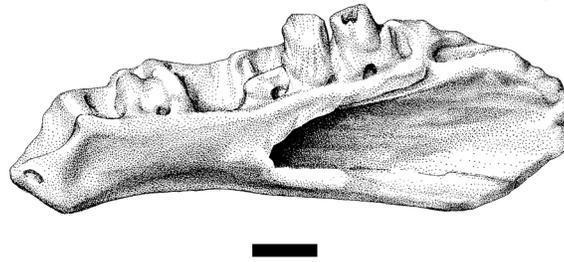


Figure 14. Cf. *Spathorhynchus* sp., right dentary in medial view (PTRM 1793). The bone is heavily worn, and no details of tooth morphology are preserved. Scale bar equals 1 mm.

synonymous with *P. fera*. The validity of "*P. borealis*" is confirmed, and its diagnosis is amended above.

cf. *Spathorhynchus* sp.
(Figure 14)

Referred specimens. PTRM 1793 (right dentary), Figure 14; 1825, 5364–5370, 5638, 5639, 5662, 5667, 5671, 5672, 5691 (trunk vertebrae)

Description. The worn dentary is relatively large, the tooth row measuring 6.2 mm in length. There are eight tooth positions, but only the sixth and seventh teeth are even partially preserved (Figure 14). They are subpleurodont and slightly separated from the interior edge of the dentary by a weak subdental shelf. Their bases are inflated and confluent, rather square in coronal section. The first and fourth tooth bases are the largest. The splenial notch extends to the boundary between the fourth and fifth teeth. The interior of the dentary has a small ridge that extends ventrally from the top of the Meckelian canal; an intramandibular septum is therefore not well developed posteriorly. The Meckelian groove is closed and fused. There is a small, medially facing notch, just posterior to the last tooth, which is confluent with the well-defined coronoid fossa on the labial surface of the bone, thus excluding the possibility of a long labial process of the dentary. The coronoid fossa actually comprises two conjoined fossae, the boundary between which is marked by a faint ridge. The medial, shallower one is confluent with the aforementioned notch posterior to the last tooth; the lateral, deeper one extends anteriorly to the level of the boundary between the sixth and seventh teeth. The coronoid fossa as a whole is triangular in shape, with the apex pointed forward. Two, widely spaced labial foramina are present, one each below the second and fifth teeth. The mandibular symphysis is weak.

The best-preserved vertebra (PTRM 5364) is large, measuring 7.5 mm in length (along neural arch) and somewhat wider anteriorly than posteriorly (10.2 mm at prezygapophyses vs. 9.1 mm at postzygapophyses). The prezygapophyses are oriented in a nearly coronal plane. A midline keel runs along the entirety of the neural arch; the keel ends in a projection (partially broken) from the posterior end of the arch. The posterior end is flared and markedly taller than the anterior end. On the dorsal surface of the posterior half of the neural arch run linear ridges (or "flutings": Gans 1978) which diverge posteriorly from the midline. The ridges match corresponding structures on the ventral surface of the arch (a convexity above matches a concavity below), and thus, viewed from behind, the edge of the arch appears crinkled. (This ventral mirroring of flutings is present in many, but not all, vertebrae referred to cf. *Rhineura* sp.) The centrum is depressed. The condyle has a constricted neck. There is no hypapophyseal ridge; only the right subcentral arterial foramen is present, and it is located close to the synapophysis, well away from the midline. The synapophyses are hemispherical. The vertebrae (including PTRM 5364) typically have a small indentation just above the synapophysis on their lateral side. Most referred vertebrae are only two-thirds the size of PTRM 5364.

Remarks. The low tooth count and subpleurodont tooth implantation are sufficient to refer this species to *Amphisbaenia*. Unfortunately, the polarity of many character state changes seen within *Amphisbaenia* is equivocal because of uncertain in-group and out-group relationships (Estes et al. 1988; Kearney 2003); this complicates discussion of relationships. The determination of whether many features are primitive or derived in *Rhineuridae* depends crucially on the position that that taxon occupies. Despite these phylogenetic difficulties, a plethora of rhineurid *amphisbaenians* has been

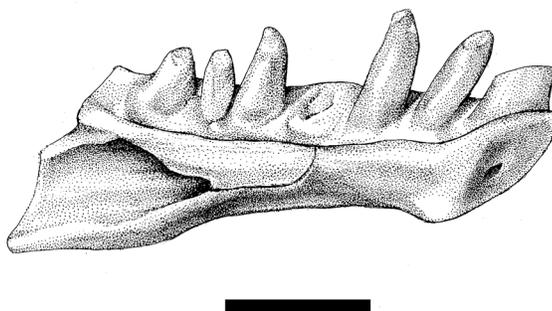


Figure 15. Cf. *Rhineura* sp., left dentary in medial view (PTRM 5248). The thin line extending anteriorly from the AIAF is a fracture. Scale bar equals 1 mm.

named from the late Eocene through Oligocene of North America, generally based on more-or-less complete skulls. PTRM 1793 shares with many of these fossil rhineurids—including the middle Eocene *Spathorhynchus fossorium* Berman (1973), early Oligocene *Rhineura hatcheri* (Kearney et al. 2005), Miocene *Rhineura sepultura* Holman (1979), and extant *R. floridana* (Cope 1892, figure 5; pers. obs.)—enlargement of the first and fourth dentary teeth. In "Rhineuridae sp. indet." from the late Paleocene of Wyoming (Estes 1975), only the fourth tooth appears to be enlarged (pers. obs.). *Hyporhina tertia* has enlarged first and fourth "maxillary teeth" (Berman 1972: 8); whether this applies to the dentary is unclear. The first and fourth dentary teeth appear to be enlarged in *Jepsibaena minor* (YPM-PU 13460; pers. obs.). It is probable that specified tooth enlargement is diagnostic of a clade including part of the stem of *R. floridana*, though precisely how much of the stem is at this point difficult to assess. The late Paleocene "Rhineuridae sp. indet." is the earliest taxon to display apomorphy one (fourth tooth enlarged); apomorphy two (first tooth enlarged) is first known in the early Eocene *J. minor*. Kearney (2003) concluded that all these North American forms were more closely related to *R. floridana* than to any other living amphisbaenian.

Cf. *Spathorhynchus* sp. can be excluded from described species of *Rhineura* by the primitive retention of eight dentary teeth. *Spathorhynchus fossorium* and the late Eocene *S. natronicus* also retain the presumably primitive state of eight dentary teeth (Berman 1973, 1977) and are both relatively large, with tooth row lengths somewhat less than 10 mm. Thus, of described coeval rhineurids, PTRM 1793 compares best to *Spathorhynchus*

natronicus; due to poor preservation, however, I refer the specimens to cf. *Spathorhynchus* sp.

The largest vertebra, PTRM 5364, is considerably larger than one would expect in relying on the dentary alone. This fact suggests that the animal represented by PTRM 1793 was not yet fully grown. Cf. *Spathorhynchus* sp. may be the same as the large rhineurid taxon described as *Lestophis* sp. nr. *L. anceps* by Holman (1972) based on vertebrae. [Estes (1983), with good cause, declared *Lestophis* a *nomen dubium*.] Berman (1972) stated that ridges are present on the neural arches of vertebrae in rhineurids, to which list Estes (1976) added *Amphisbaena* (in *A. alba*, this is particularly true of the more anterior vertebrae). Kearney (2003) recently found dorsal ridges to be present also in *Aulura*, *Dalophia*, *Leposternon*, and *Monopeltis*, which she regarded as basal in Rhineuroidea. Flutings are not always reflected on the underside of the neural arch, but this is conceivably related to size.

Interestingly, amphisbaenian vertebrae—from both cf. *Spathorhynchus* sp. and cf. *Rhineura* sp. (see below)—appear to be unusually abundant in the Medicine Pole Hills l.f. Iguanids, though they are much more diverse and numerically abundant (based on jaw elements), are represented by (relatively) far fewer vertebrae. The same might be true of the amphisbaenians in the Calf Creek l.f., which are represented by 58 and 43 vertebrae (small and large, respectively; Holman 1972). Even considering that a given amphisbaenian typically has more than three times as many vertebrae as a non-fossorial squamate (<30 precloacal vertebrae in non-fossorial taxa versus often >100 in amphisbaenians; Hoffstetter and Gasc 1969), the difference appears anomalous.

cf. *Rhineura* sp.
(Figure 15)

Referred specimens. PTRM 5248 (left dentary), Figure 15; 5322 (right dentary fragment); 5725 (left dentary); 1422, 1434, 1438, 1443–1445, 1553, 1796, 1812, 1813, 1828, 1831, 1851, 2023, 2042, 2067, 5171, 5180, 5216, 5235, 5238, 5348 (12 specimens), 5362, 5363, 5384–5386, 5668, 5673, 5674, 5686–5688 (trunk vertebrae)

Description. The most complete specimen, PTRM 5248, has a tooth row length of 3.0 mm. There are seven tooth positions (Figure 15), although the fourth tooth is missing. Of these seven, the first and fourth are enlarged relative to the others. The teeth are subpleurodont and conical, tapering uniformly toward their crowns; these crowns, preserved only on the third and fifth teeth, are slightly recurved. There is a narrow, shallow sulcus dentalis. The symphysis is relatively large, expanded relative to the part just distal to it and has a small posteroventral projection. The Meckelian groove is closed and fused, and the splenial notch extends anteriorly to the level of the boundary between the fifth and sixth teeth. A fossa for the labial coronoid blade extends anteriorly to the level of the seventh (last) tooth.

PTRM 5322 is approximately the same size as PTRM 5248, though it is broken (just?) in front of the anterior margin of the splenial notch and preserves only the first through fifth teeth. The first and fourth teeth are enlarged. The symphysis is relatively large, and it has a posteroventral projection as in PTRM 5248.

The vertebrae of cf. *Rhineura* sp. are quite abundant and typical of rhineurid vertebrae. Vertebral flutings (see above under cf. *Spathorhynchus* sp.) are present but are only rarely reflected on the underside of the neural arch (e.g., in PTRM 5171), and then only weakly. The subcentral arterial foramina are typically located along the anterior third to fourth of the centrum. As in cf. *Spathorhynchus* sp., there is typically an indentation dorsal to the synapophysis on the lateral side of the vertebrae.

Remarks. The referral of these specimens to cf. *Rhineura* sp. is based on small size, tooth count, and age. The reduction to seven dentary teeth is a derived feature within Rhineuridae (see above). Cf. *Rhineura* sp. is therefore closer to *Rhineura* than are various Paleogene forms like *Jepsibaena minor* (8 dentary teeth) and *Spathorhynchus* spp. (8). No known North American Eocene rhineurid has seven dentary teeth, but Gilmore (1928)

describes early Oligocene *Rhineura hatcheri* (CM 423A and B) as having seven. *Hyporhina antiqua* (YPM-PU 11390) also has seven dentary teeth, but that species lacks the expanded symphysis seen in *J. minor* and cf. *Spathorhynchus* sp. (pers. obs.) The enlargement of the first and fourth teeth places cf. *Rhineura* sp. firmly on the rhineurid line, and its possession of only seven dentary teeth indicates that it is derived relative to *Spathorhynchus*.

Sullivan and Holman (1996) synonymized many early Oligocene rhineurid taxa, arguing that the characters used to distinguish fossil amphisbaenians, including tooth count, may be related solely to ontogenetic stage and therefore "taxonomically insignificant" (p. 362). This point is well taken, for it is widely recognized, for instance, that tooth count increases with absolute size during development in many squamates. (I am not aware of any such study specifically on amphisbaenians.) Estes (1983) was correct in stating that taxonomic and systematic revision of Paleogene amphisbaenians is needed.

Nevertheless, the dismissal of tooth count data in rhineurid systematics seems not yet to be warranted. Granted, extant *Rhineura floridana* has only six dentary teeth, and it is also smaller than many of its presumed early Paleogene relatives, which have eight dentary teeth. But *Rhineura floridana*'s small size is itself an evolutionary change. Its small size and low tooth count may be informative for both alpha taxonomy and systematics, even if the two characters are developmentally correlated and might be considered a single character complex. In other words, ontogenetic correlation is by itself an insufficient basis for discarding character information in the referral of fossil forms. Additionally, in the particular case of Rhineuridae, absolute size is clearly a poor predictor of tooth count: the large Eocene *Spathorhynchus* as well as small *Jepsibaena minor* have eight dentary teeth, whereas the large Miocene *Macrorhineura* and small extant *Rhineura floridana* have but six.

Cf. *Rhineura* sp. might be the same as the small rhineurid species noted by Holman (1972) in the Calf Creek l.f., which was represented only by vertebrae.

Anguimorph MPH-1
(Figure 16)

Referred specimens. PTRM 5375 (partial left dentary), Figure 16; PTRM 1824 (partial right dentary); PTRM 5376 (anterior left dentary fragment)

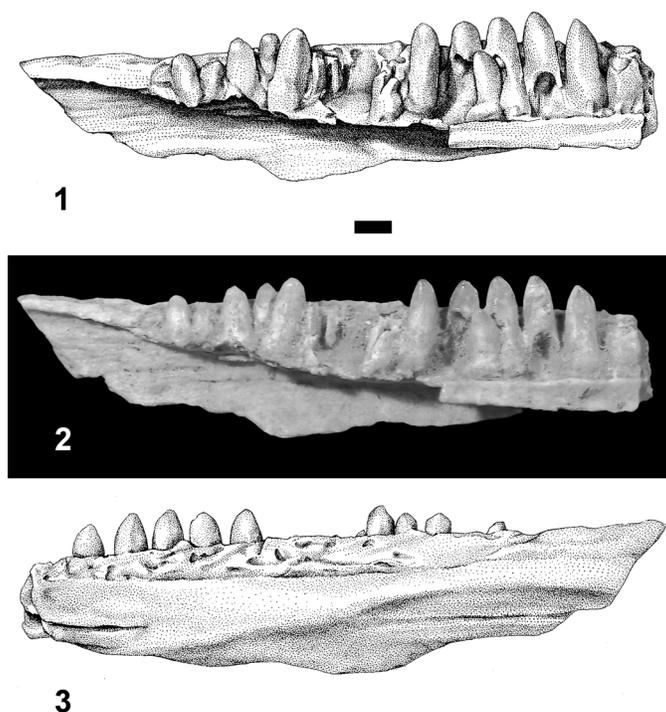


Figure 16. Anguimorph MPH-1, (1) illustration and (2) photograph of partial left dentary in medial view (PTRM 5375). The crowns of the teeth are striated lingually. (3) Same specimen in lateral view. Note the planation of the ventrolateral wall of the dentary. Scale bar equals 1 mm.

Description. The most complete specimen of this taxon is PTRM 5375. It is large, the tooth row being 13.7 mm long as preserved. A weak, narrow sulcus dentalis (Figure 16.1–2) is present at the anterior end of the bone. Fourteen or fifteen tooth positions are preserved. The teeth are pleurodont and low-crowned, less than one-third of their height projecting above the parapet of the jaw. The tooth crowns are striated lingually, and small mesial and distolabial crests descend the crowns (the mesial crest is much stronger), creating a V-shaped cutting edge. Except for the most posterior teeth, the crowns are discolored and somewhat transparent. They are bluntly pointed (in part due to wear), slightly recurved, weakly labiolingually compressed, and a little concave lingually near the juncture between crown and shaft. The teeth become progressively smaller and more blunt posteriorly and lose the crown-shaft concavity. The excavated base of the third preserved tooth with the incoming replacement tooth not directly below it indicates an interdental mode of replacement. The Meckelian groove is open. Though much of the shelf that supports the teeth has been broken posteriorly, a thin

upper remnant of the IMS is evident; its original extent is unknown.

Externally, labial foramina are not readily identifiable in PTRM 5375, but a groove runs along much of the length of the dentary in the expected position of these foramina (Figure 16.3). The posterior, ventrolateral surface of the dentary is flattened, or planated; the plane of flattening is parallel to the longitudinal axis and oblique to a sagittal plane. Articulation surfaces with the postdentary bones are not apparent.

The two other specimens are far less complete, but both of them confirm the tooth morphology of this taxon. Additionally, PTRM 1824 displays the planated, external dentary surface and labial groove in the position of the labial foramina. There appear to be a couple of foramina present along the groove; whatever their number, they are small. Its two remaining teeth also exhibit discoloration of the crowns. PTRM 5376 exhibits a weak anterior sulcus dentalis but does not preserve the portion of the dentary that is planated in the other two specimens. No discoloration of the tooth crowns is evident in this specimen.

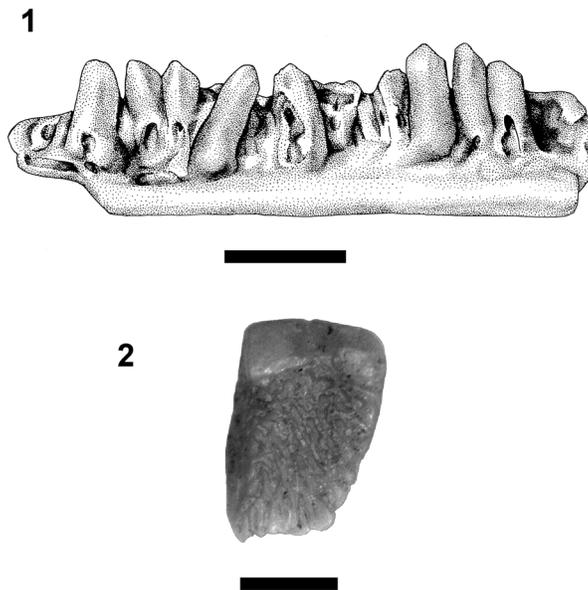


Figure 17. Diploglossine MPH-1, (1) Left dentary fragment in medial view (PTRM 1807). (2) Osteoderm in external view (PTRM 5377). Scale bars equal 1 mm.

Remarks. The interdental mode of tooth replacement unites this new species with Anguimorpha (cf. Estes et al. 1988). Its tooth morphology is unique, but the V-shaped cutting edge is found in Anguinae and some anterior teeth in *Xenosaurus* (Gauthier, 1982; pers. obs.). In possessing lingually striated tooth crowns it also likens anguids, *Xenosaurus*, and many *Varanus* (pers. obs.). Many other features, such as osteodermal characteristics and the state of the IMS posteriorly, cannot yet be evaluated. Oddly, nearly all anguimorphs possess at least a moderate subdental shelf along most of the dentary. That this shelf is essentially lacking in Anguimorph MPH-1 would seem to be autapomorphic.

Relationships among anguimorphs generally and anguid subclades in particular are not well resolved (e.g., Camp 1923; Rieppel 1980; Gauthier 1982; Macey et al. 1999; Wiens and Slingluff 2001; Townsend et al. 2004), which also limits our understanding of character evolution within the group. Preserved features in Anguimorph MPH-1 appear only to disbar it from membership in particular anguid subclades: from Diploglossinae and Gerhonotinae, by its lack of bicuspid teeth; from Glyptosaurinae by its tooth morphology; and from *Anniella*, by its higher tooth count and tooth morphology. In all these respects, Anguimorph MPH-1 is primitive relative to known representatives of

these groups. Although its tooth form and lack of a significant subdental shelf render Anguimorph MPH-1 distinctive, better specimens are required before a formal new name can be applied.

Diploglossine MPH-1
(Figure 17)

Referred specimens. PTRM 1807 (left dentary fragment), Figure 17.1; 1823 (jaw fragment); 5378 (osteoderm), Figure 17.2

Description. PTRM 1823 is a fragment of either a right dentary or a left maxilla. The bit of bone to which the two preserved teeth are attached is worn. The crown of the first tooth is also worn, but the second does not project as high—it is probably an incompletely emplaced replacement tooth—and appears largely undamaged. This second (posterior) tooth bears a distinct mesial crest, offset from the rest of the tooth crown by a shallow groove. The main tooth cusp is distally displaced and slightly labiolingually compressed. The lingual surface of the crown is smooth, but near the base of the crown, on its mesial side, there are coarse striations; the striae do not extend onto the lingual side, possibly a result of wear. The bases of both teeth are missing, so it is difficult to estimate crown height.

There are 13 tooth positions, with eight teeth, preserved in PTRM 1807, a left dentary fragment (Fig-

ure 17.1). The teeth are considerably smaller than in PTRM 1823. They are of moderate height, and the lingual surfaces of the crowns are apparently unstriated. All but the anterior-most teeth have strong mesial crests; on posterior teeth these crests are so expanded that the crowns are mesiodistally longer than the shafts. A few teeth appear fully implanted, their labial margins flush with the parapet of the jaw; lingual to these teeth is a moderate subdental shelf. Many of the preserved teeth are incompletely emplaced replacement teeth and have bulbous, rounded bases that are not strongly fused to the dentary; they also sit away from the parapet of the jaw over the subdental shelf. The relative position of replacement teeth is difficult to determine posteriorly, where the tooth pattern is distorted. The anterior-most tooth, however, is excavated distolingually, indicating an interdental (anguimorph) pattern of tooth replacement.

The osteoderm, PTRM 5378 (Figure 17.2), is rectangular and unkeeled, ~2.2 mm in length. Its sculpturing consists of variably linked, apically flattened tesseræ that are separated by grooves; where they merge, they create a vermiculate sculpture. The anterodorsal edge of the gliding surface was oblique to the anterior margin, but there is no indication of a posterior projection of the gliding surface. This surface is approximately one-fourth the length of the whole osteoderm.

Remarks. The jaw fragments constitute the primary evidence for the presence of a diploglossine in this assemblage. Strong development of the mesial tooth crests, often with the development of a secondary cusp, diagnoses Diploglossinae and possibly Gerrhonotinae (within Anguidae) as well as *Xenosaurus* and its stem (Gauthier 1982); only diploglossine anguids have apomorphically shorter, stocky teeth, often with expanded crowns that are mesiodistally longer than their shafts. An undamaged osteoderm with a posterior projection of the gliding surface would be desirable to buttress this conclusion (cf. Hoffstetter 1962; Gauthier 1982). The sculpturing of the osteoderm, however, is similar to that of the (stem) diploglossine *Eodiploglossus borealis* Gauthier (1982) from the early Eocene of Wyoming; and in living diploglossines and *E. borealis*, not all the osteoderms have a posterior projection. There is presently little that would permit a more specific determination of the taxon, nor is it known whether it lies on the stem of Diploglossinae or in the crown. It represents the latest-known occurrence of the diploglossine lineage in central North America.

cf. *Peltosaurus* sp.

Referred specimens. PTRM 2606 (partial left dentary); PTRM 2617 (partial right maxilla); 5272 (jaw fragment); 5381 (right maxilla); 5685 (right frontal fragment)

Description. PTRM 2606 is the anterior two-thirds of a left dentary. Fourteen tooth positions and two teeth (numbers 4 and 10, from symphysis) are preserved. Both teeth, like the dentary itself, are streamworn, and details of crown morphology are lacking. The apex of tooth 10, however, is somewhat labiolingually compressed. The crowns are moderate in height, projecting less than 50% above the parapet of the jaw. There is a moderately developed subdental shelf, without attendant sulcus dentalis; this shelf is largely broken anteriorly. The Meckelian groove is ventrally located on the anterior portion of the dentary. There are six, irregularly spaced labial foramina on the external surface. There is also a small indentation at the posterolateral margin of the preserved portion, but the generally streamworn character of the specimen suggests that this feature may represent a rounded fracture rather than the anterior edge of an articular surface or fossa.

PTRM 5381 is a small, nearly complete but somewhat worn right maxilla. The premaxillary process is broken near the base of the nasal process. Eleven tooth positions and seven complete or partial teeth are preserved. The teeth are widely spaced, but it is impossible to estimate crown height. Both the crowns and the shafts are somewhat recurved. The crowns are unicuspid, blunt, and without labial or lingual striations, which may or may not be due to abrasion. They decrease in height posteriorly such that the posterior-most teeth are exceedingly small. The dorsal surface of the maxilla is divided into anterior and posterior segments by an oblique ridge on the interior surface of the nasal process and dorsal surface of the main body of the maxilla. The SAF is located at the level of the posterior edge of the nasal process. The foramen is set in a short groove and is covered anteriorly by the dorsal roof of the maxilla. The palatine process is only weakly developed and is located at about the same level as the superior alveolar foramen; on its dorsal surface is a shallow facet for articulation with the palatine. Laterally, there are four labial foramina and several other foramina, irregularly spaced, on the slightly irregular surface of the nasal process. There are no osteoderms fused to the surface of the nasal process, probably a result of the small size of the indi-

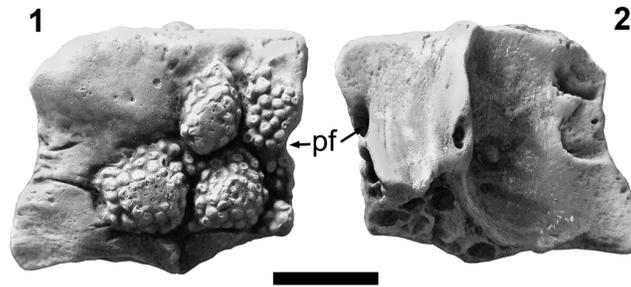


Figure 18. *Helodermoides* sp. nov.?, Partial left parietal in dorsal (1) and ventral (2) views (PTRM 1825). **pf**, parietal foramen. Scale bar equals 5 mm.

vidual. Another poorly preserved maxilla (PTRM 2617) appears to have weak striations on the lingual surface of one anterior tooth.

The frontal fragment (PTRM 5685) is heavily worn, but it certifies the existence of a non-glyptosaurine glyptosaurine in the Medicine Pole Hills l.f. A thin strip along the orbital margin is devoid of the tuberculated osteodermal crust that otherwise covers the bone. A small foramen pierces the lateral margin of the orbit.

Remarks. These specimens are compared to *Peltosaurus* on the basis of glyptosaurine tooth form, size, and geologic age. PTRM 2606 shares with specimens of *Peltosaurus granulatus* robust teeth, similar tooth spacing, and similar size, but more complete teeth, as on the maxilla, seem rather more recurved than in *P. granulatus*. The lack of striations on most teeth may be attributable to stream abrasion, a phenomenon that may also account for the lack of striations on *Peltosaurus* sp. from the Cypress Hills Formation of Saskatchewan (see Lambe 1908; cf. Estes 1983). *Peltosaurus* is rare in late Eocene sediments, though one would expect a "melanosaurin" glyptosaurine to be present somewhere on stratigraphic grounds.

Helodermoides sp. nov.?
(Figure 18)

Referred specimens. PTRM 1825 (left parietal fragment): Figure 18; 5647, 5709 (cephalic osteoderms)

Description. PTRM 1825 is a left, anterior fragment of parietal. Its edges and surfaces are in places smoothed by abrasion, including the tops of the osteoderms (Figure 18.1). There are four relatively complete, tall, bulbous, tuberculated osteoderms coössified with the dorsal surface. The osteoderms are vaguely polygonal, with subrounded corners, and separated from one another by deep grooves. They are undercut in places, and some isolated tubercles occur in the grooves. Sev-

eral osteoderms are missing from the anterolateral part of the bone. The left edge of the parietal foramen (Figure 18.1–2, **pf**) is visible, perforating the first, large, median osteoderm. In medial view, the parietal fragment has a hemispherical cavity, about 2.5 mm in diameter, that excavates both osteoderm and underlying bone. It opens dorsally through the osteoderm and ventrally through a short canal into the cranial cavity. On the ventral surface of the parietal, the anterior ridges (Figure 18.2) are well developed. The distance between the median plane and the anterior ridge is less than that between the anterior ridge and the lateral edge of the parietal (i.e., the triangular inter-ridge area is small). There are two notches, rounded at their medial apices, on the anterolateral part of the ventral surface; they are confluent with the anterolateral edge of the bone and constitute articulation facets for the postfrontal and possibly also the postorbital.

PTRM 5647 and 5709, hexagonal cephalic osteoderms, are also referred to this taxon.

Remarks. The more-or-less hexagonal osteoderms of PTRM 1825 are sufficient to refer it to Glyptosaurini. As Sullivan (1979) noted, tall, bulbous osteoderms, among other features, serve to distinguish the presently monotypic *Helodermoides tuberculatus* from other glyptosaurins. Sullivan also argued (op. cit.) that *H. tuberculatus* is diagnosed by "closure of the supratemporal fenestra," a phenomenon that in Glyptosaurini deserves further investigation. The primitive condition is illustrated by *Paraglyptosaurus princeps* ("*Glyptosaurus hillsi*": Gilmore 1928, figure 63; and "*G. rugosus*": Meszoely 1970, figure 16B; see Sullivan 1979 for nomenclature), in which the postfrontal articulation on the parietal is a single notch restricted to the latter bone's anterior-most end. Sullivan (1979, figure 10h) figures complete closure of the supratemporal fenestra in one specimen of *Helodermoides* (USNM 214736). The condition in PTRM 1825 is

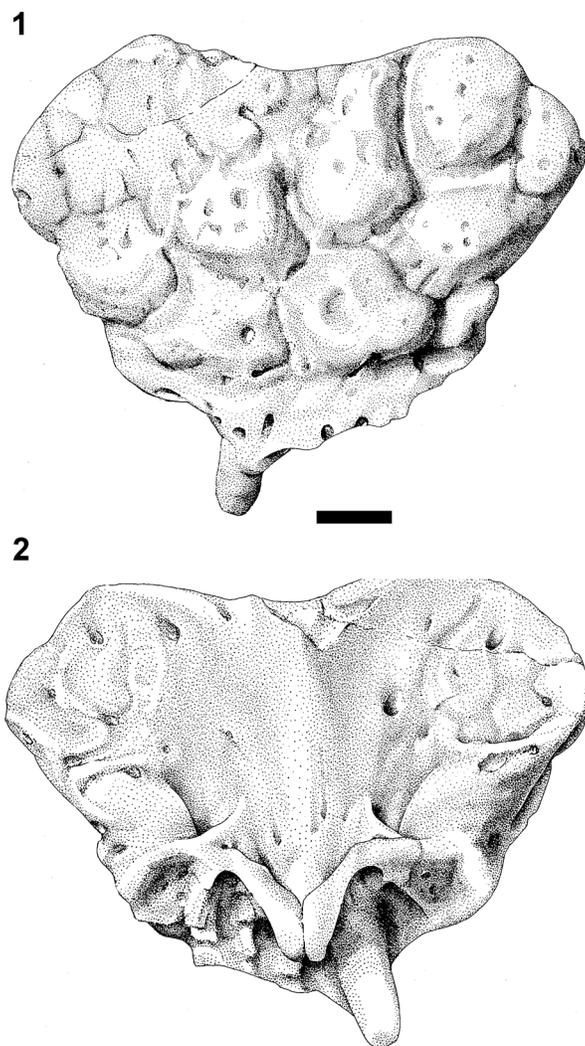


Figure 19. Xenosaurid MPH-1, Premaxilla in dorsal (1) and ventral (2) views (PTRM 1986). Scale bar equals 1 mm.

intermediate, for although the two notches on the ventral surface suggest some closure, the bone thins out laterally, and there are no other obvious articulation surfaces. Sullivan is surely correct that extensive closure of the supratemporal fenestra by increased articulation of the temporal bones is a derived feature in Anguillidae. The seemingly significant difference in supratemporal closure between specimens (PTRM 1825 and AMNH 8706 vs. USNM 214736) suggests specific difference. However, because the type specimen of *H. tuberculatus* (CM 707) consists only of frontals, a determination of which form is new is not yet possible. *Helodermoides* is a previously known and in

this sense unproblematic taxon from the Chadronian.

Xenosaurid MPH-1
(Figure 19)

Referred specimens. PTRM 1986 (premaxilla), Figure 19; 5371 (dermal skull bone fragment)

Description. PTRM 1986 is a slightly worn but relatively complete premaxilla. The dorsal surface is covered by coössified osteoderms, worn on their outer surfaces (Figure 19.1). The osteoderms are broad and rounded and separated by narrow valleys. They tend to be flatter toward the midline and more conical laterally and do not extend to the extreme lateral margins of the bone. Tiny pocks

and perhaps foramina pierce them. The anteroventral margin of the bone, below the fused osteoderms, is perforated by several small foramina. The posterolateral borders of the premaxilla appear unbroken. The dorsal nasal process is broken near its tip. On the ventral margin, there are spaces for seven teeth, including one midline tooth (Figure 19.2). Only one tooth, the first, right, paired tooth, is preserved, and it is short, the crown worn and blunt. The incisive process is narrow and bilobed, unfused even basally, where the right and left portions are strongly apposed; it lies immediately behind the median tooth alveolus. The ventral premaxillary foramina are located lateral to the incisive process and posterior to the first pair of premaxillary tooth alveoli. The posterior premaxillary foramina are larger than the ventral ones, with which they connect internally (Bahl 1937). Broad dorsal wings extend from the midline to the lateral edge of the bone, covering the typical location of the external nares. The wings are thinner between the thick midline and the thick lateral margins. Small grooves present on both sides of the ventral surface mark articulations with the premaxillary processes of the maxillae.

PTRM 5371 is a thin, rectangular fragment of a skull bone, 5.5×2.5 mm. It is referred to the same taxon as the premaxilla on the basis of size and similar osteoderms. All of the osteoderms are flatter than on the premaxilla, however: none is bulbous. One long edge is unbroken and is grooved for an articulation along the whole of its preserved length. In internal (ventral?) aspect, this same edge is distinguished by a moderately high ridge. Its appearance suggests that the element may bound the supratemporal fenestra (a parietal fragment, or postfrontal), which might have been partially closed.

Remarks. These specimens are referred to an undetermined xenosaurid with some hesitation. In possessing multiple anterior foramina the premaxilla likens *Xenosaurus* but differs from most other anguimorphs. But unlike *Xenosaurus platyceps* and *X. grandis*, which have nine premaxillary teeth (like most anguimorphs), Xenosaurid MPH-1 has but seven. Uncertain phylogenetic relationships within Anguimorpha, however, and the presence of only seven premaxillary teeth in *Shinisaurus crocodilurus*, render it uncertain whether nine teeth in *Xenosaurus* is primitive or derived. Gilmore (1941) reported only eight in *Exostinus serratus*.

An alternative hypothesis is that this species is a helodermatid, which would be consistent with the

more bulbous character of the osteoderms on the premaxilla. The absence of the "coralline" sculpturing characteristic of *Heloderma* might then be interpreted as artifactual (i.e., it has been removed by abrasion). The premaxilla is too small (especially considering the fusion of the osteoderms) to be attributed to *Helodermoides* and moreover lacks any indication of tubercles. There is presently no evidence that would tie the specimens to any other species in the fauna.

Regardless of its affinities, the broad posterolateral wings of the premaxilla of Xenosaurid MPH-1 are unlike anything known in squamates. The external nares must have been displaced a considerable distance posteriorly as a result of their presence; furthermore, the maxilla necessarily articulates on the ventral surface of the premaxilla rather than the dorsal surface, as in most lizards.

Saniwa edura sp. nov.

(Figure 20)

Holotype. PTRM 5379 (partial left dentary), Figure 20.1

Paratype. PTRM 5380 (partial parietal), Figure 20.2–3

Locality and horizon. PTRM V89002, Chalky Buttes Member, Chadron Formation (late Eocene), North Dakota, USA

Distribution. Thus far only known from type locality.

Etymology. L. *eduro*, meaning "to last, endure, persist," in reference to its status as the last known varanid in North America

Diagnosis. A varanid lizard with teeth that are laterally compressed somewhat obliquely to the jaw axis and have strongly recurved tooth crowns, ventromedially expanded tooth bases, and coarse if discontinuously expressed infoldings along the tooth base labially and lingually; dentary with a wide subdental shelf posteriorly; frontoparietal suture weakly anteriorly convex; and dorsal surface of parietal highly rugose.

Description of holotype. PTRM 5379 is the medial portion of a large left dentary, preserving six tooth positions with three partial to near-complete teeth (Figure 20.1). The bases of the teeth are expanded posteromedially. They show coarse but discontinuously expressed infoldings; they are visible externally at the very base and then further up the shaft, but are subdued in between. Each tooth has one small, basal nutrient foramen, located distal to the anteroposterior mid-point of the tooth.

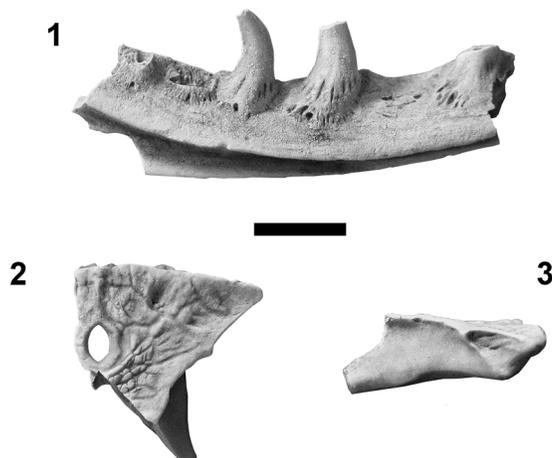


Figure 20. *Saniwa edura* sp. nov., (1) Holotype, partial left dentary in medial view (PTRM 5379). Partial right parietal in dorsal (2) and lateral (3) views (PTRM 5380). Scale bar equals 5 mm.

The crowns lack serrations and are strongly recurved and labiolingually compressed, giving rise to mesial and distal carinae. The best-preserved tooth is the fourth, which shows a peculiar crown morphology. In the upper crown of this tooth, the plane of compression is not quite parallel to the dentary; rather, the anterior edge is rotated labially $\sim 20^\circ$. A rigorous tooth count is unobtainable owing to incomplete preservation; by comparison with *Varanus*, the decreasing size of the posterior-most tooth bases and the rise of the subdental shelf indicate that the last preserved tooth is close to or at the end of the tooth row, and the narrowing of the Meckelian groove anteriorly suggests that probably 5–7 more teeth were present there. Tooth count may not have differed much from extant *Varanus*. Posteriorly, the subdental shelf is wide, about equal to the width of the tooth bases there. The Meckelian groove is in a ventral position anteriorly, and there is no indication how far anteriorly the splenial extended. The IMS extends posteriorly to the end of the preserved part of the dentary. The posterior, dorsolateral surface is strongly beveled, presumably just anterior to where the coronoid fit. Several labial foramina are present, the posterior-most being the largest.

Description of paratype. PTRM 5380 is the well-preserved, right side of a large, azygous parietal, referred to the same species on the basis of size and varanid morphology. The anterior margin of the bone—the frontoparietal suture—is weakly convex. Its dorsal surface is distinctly rugose, perhaps reflecting a strong attachment of epidermal

scales (Figure 20.2). On the anterior portion of the bone, rugosities are bounded by widely spaced grooves, perhaps indicating the presence of relatively large scales. Posterolateral to the parietal foramen, tuberculae are smaller and more clearly developed (Figure 20.2) but probably smaller than individual epidermal scales. The parietal foramen is surrounded by a raised ridge nearly hexagonal in shape. The foramen was probably covered by a single, hexagonal interparietal scale and is relatively large (1.9×1.1 mm). A weak, longitudinal ridge extends anteriorly from the ridge surrounding the foramen to the frontoparietal suture (where it may have continued onto the frontal). Posteriorly, the jaw adductor musculature originates in the supratemporal fossa, whereas anteriorly the parietal table overhangs the fossa. On the anterolateral surface of the bone is a triangular notch for the attachment of the postfrontal (Figure 20.3); its limit is marked by a bump in the margin of the parietal table in dorsal view (Figure 20.2). Along the edge of ventral crista runs a small groove.

Remarks. *Saniwa edura* was probably close in size to, or slightly larger than, *Saniwa ensidens* Leidy (1870), the most well-known North American fossil varanid. The dentary of *S. edura* is slightly larger than that of the type specimen of *S. ensidens*: Gilmore (1928) notes that in the holotype of *S. ensidens*, three dentary teeth take up a total of 11.0 mm, whereas in PTRM 5379, three middle dentary teeth take up ~ 12 mm. There are at least three partial parietals of *Saniwa** known [YPM 1074 (illustrated in Gilmore 1928, plate 9, figure

11), YPM 1059 (mentioned by Gilmore), and YPM 613], which Estes (1983) suggested were referable to *S. ensidens*. PTRM 5380 is smaller than them and clearly belonged to an animal smaller than the one that produced the dentary.

The dentary of *Saniwa edura* is similar to that of *S. ensidens* in having a wide subdental shelf posteriorly. In contrast, in living *Varanus* (except *V. komodoensis*) the shelf is much narrower toward the posterior end of the dentary. The parietal of *Saniwa edura* distinguishes it from *Saniwa ensidens*. In YPM 1074 and 613, the lateral edges of the parietal table are sharp and upturned (Gilmore 1928), whereas in PTRM 5380 they are flat. This feature is virtually unknown in extant *Varanus* (it was only observed in *V. niloticus* and large *V. exanthematicus*, which have blunt, upturned edges). Additionally, the parietal table is rugose in *S. edura*, whereas it is smooth in *S. ensidens* and most *Varanus* (less well-developed rugosities of similar form are seen in *V. prasinus*). Comparison of tooth morphology is difficult owing to incomplete preservation of the type material of *S. ensidens* (Caldwell 2003).

Some aspects of the anatomy of *Saniwa edura* are rendered uncertain due to its poor preservation. For example, some modern species (e.g., *Varanus melinus*) and *Palaeosaniwa canadensis* have serrations on the mesial and distal tooth carinae; it is possible that such were present on PTRM 5379 but have been lost to stream abrasion. Similarly, many living *Varanus* show distinct lingual striations on the tooth crown; these were not observed in the holotype of *S. edura*. Several other features are primitive. For instance, the narrow grooves, extending anteriorly along ventrolateral edges of the parietal, were found in all varanoids examined and in extant taxa appear to correspond to the taeniae marginales of the synotic tectum. Likewise, the dorsal origin of the adductor musculature is shared with *Lanthanotus* and *Varanus* (Estes et al. 1988) together with fossil "necrosaurids" (Estes 1983).

Several medium-sized varanid species have been described from the middle Eocene, all now assigned to *Saniwa** (see Gilmore 1928). The new species is also assigned to that taxon on the basis of overall similarity. Although *Saniwa** presently has no known synapomorphies (Estes 1983), neither can it be shown to be paraphyletic. Assignment of *edura* to *Saniwa** is a conservative solution: should new evidence later show *Saniwa** to be paraphyletic, *edura* can always be removed.

These specimens constitute the latest certain record of Varanidae in North America (cf. Estes 1983; Sullivan and Holman 1996). Brattstrom (1955) and Schatzinger (1975) have described *Saniwa brooksi* from the Uintan of California on the basis of vertebrae and a jaw fragment. Emry (1973) reported *Saniwa* sp. and ?*Thinosaurus* (= *Saniwa*) sp. from the White River Formation (Chadronian) of Wyoming but did not describe or cite specimens.

ADDITIONAL MATERIAL

A great many "lizard" vertebrae are known from V89002. One morphotype deserves special attention. Its description separate from the taxa described above is not intended to imply that it represents a different taxon, only that their attribution to a particular taxon is not yet fully warranted.

Vertebra Type 1 (Figure 21)

Referred specimens. PTRM 1829, 2073, 5629, 5633, 5657 (posterior presacral vertebra, Figure 21), 5663

Description. PTRM 5657 is a well-preserved posterior presacral vertebra. The neural arch surrounds a large, rounded neural canal. The neural crest is low anteriorly but rises posteriorly into a moderately developed, posteriorly inclined spine (Figure 21.1, 3). The anterior border of the neural arch is strongly concave. Posteriorly, the neural spine is mirrored on the underside of the neural arch by a small ridge that does not extend into the neural canal. Accessory articulations (zygosphenes and zygantra) are well developed. The zygosphenes are oriented ventrolaterally, at an angle of ~40° to the prezygapophyses. The zygosphenes are continuous with the prezygapophyses; that is, there is no notch separating zygosphenes from prezygapophysis (Figure 21.3). The articular surfaces of the pre- and postzygapophyses are rounded (Figure 21.1–2). There is a pair of tiny foramina below the prezygapophyses on the anteromedial edge of the neural arch.

On the ventral surface are well-developed, bilateral subcentral impressions, giving rise to a mid-sagittal ridge (Figure 21.2). The ridge is not rounded but rather squared off in cross-section, and a narrow, shallow, longitudinal groove runs along its length. In other words, the ridge appears weakly paired (Figure 21.2). No subcentral foramina are present. Ridges of bone run posterovertrally from the small, rounded synapophyses

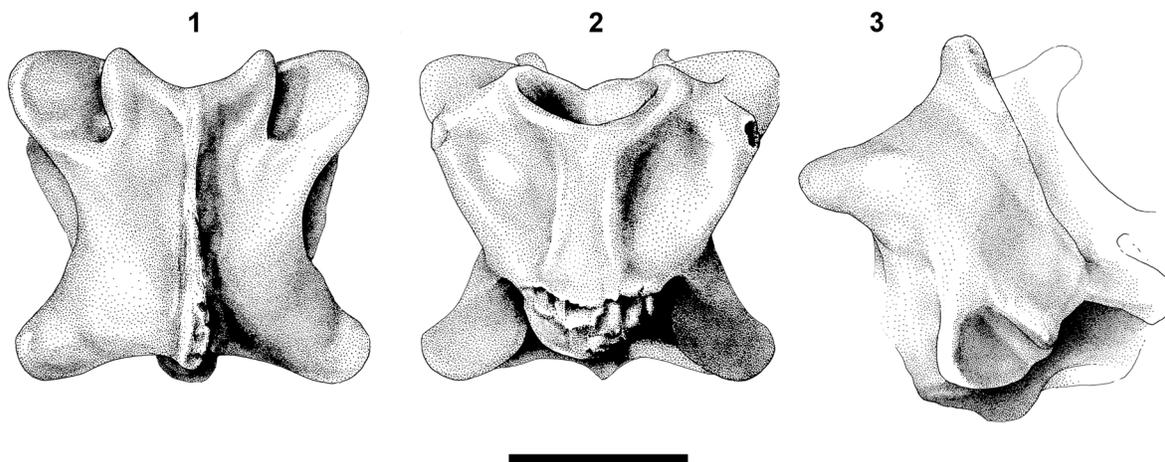


Figure 21. Vertebra Type 1, Posterior presacral vertebra in (1) dorsal, (2) ventral and (3) anterodorsolateral views (PTRM 5657). Scale bar equals 3 mm.

toward the condyle, bounding the subcentral impressions laterally. The centrum is moderately depressed. Half of the specimens referred here have a paired ventral ridge (PTRM 5629, 5657, 5663).

Remarks. It is tempting to try to refer these lizard vertebrae to a species described above (since they were surely produced by one of them). The largest iguanids in the locality are *Polychrus charisticus*, Iguanids MPH-1 and -2, and cf. *Aciprion* sp. *P. charisticus*, Iguanid MPH-1, and cf. *Aciprion* sp., represented by 12, 9, and 8 specimens (respectively), are also the most abundant iguanids in the locality, rendering them good candidates for referral. (Certain other lizard taxa in the fauna are also large enough to have produced the vertebrae—even too large—but the clades to which these species generally lack accessory articulations and/or subcentral impressions. For a discussion of vertebrae in Squamata, see Hoffstetter and Gasc 1969). For the moment, I decline (semi-)formally to associate the vertebrae.

The most notable feature of Vertebra Type 1 is the development of zygosphene–zygantral accessory articulations. Zygosphenes and zygantra have evolved several times within Squamata, most notably in Iguania, Teiidae, and Serpentes (Hoffstetter and Gasc 1969; Estes et al. 1988). Within Iguanidae, they appear in all iguanines, some "*Enyalioides*," crotaphytines, and corytophanines (de Queiroz 1987) as well as some members of Tropidurinae* (e.g., *Uranoscodon superciliosus*) and Polychrotinae* (e.g., *Anolis equestris*, *Poly-*

chrus). In lacking complete separation of zygosphene from prezygapophysis, Vertebra Type 1 has a condition intermediate between having no accessory articulations and having advanced ones (see de Queiroz 1987, figure 36), as in the extant iguanine *Dipsosaurus dorsalis*.

The squaring and pairing of the mid-sagittal ventral ridge is more restricted in distribution. I have observed it in some corytophanines, crotaphytines, some *Sauromalus obesus*, and *Dipsosaurus dorsalis*, especially on the more posterior presacral vertebrae; it appears to be absent in the large iguanines (including juveniles). The significance of this feature is uncertain.

DISCUSSION

Referral of Fragmentary Specimens

The difficulty in systematizing many of the taxa described above reflects not only the fragmentary nature of the specimens but also the fact that published anatomical data on isolated bones of squamates is meager. Fossil iguanids are known from a few good Tertiary specimens (e.g., *Parasauromalus olseni*, *Aciprion formosum*), and morphological cladistic analyses of Iguania have focused on gross skeletal characteristics of extant species. Thus, there are no characters in the maxilla *per se* that have been argued to diagnose iguanid clades. I have attempted to redress the problem by comparison with disarticulated Recent and fossil specimens. Much work, however, remains to be accomplished.

Known Richness in Squamate Assemblages

The fossil record has yielded squamate assemblages of greatly differing species richness, in part because sample sizes differ. In the Medicine Pole Hills l.f., 17 lizard and 2 amphisbaenian species have been described. Additionally, four snake taxa have been identified on the basis of numerous vertebrae. Thus, when all squamate taxa are included—that is, when squamates are not split into paraphyletic, partially ecomorphic groups like "Lacertilia"—the Medicine Pole Hills l.f. has about 23 species and is one of the most diverse fossil squamate assemblages heretofore described. The second most diverse assemblage is the Ukhaa Tolgod assemblage from the Late Cretaceous of Mongolia, from which 21 taxa have been described. Notably, the Ukhaa Tolgod assemblage completely lacks snakes (Gao and Norell 2000).

Squamate Species Richness across the Eocene/Oligocene Boundary

Sampling and richness. Particularly relevant to this inquiry is the fact that there are no microvertebrate quarries from which squamate assemblages have been described in the lower Oligocene. The one well-studied quarry from the upper Eocene, which produced the Calf Creek l.f. (Holman 1972), was not very diverse. This fact has two effects on the study of richness. First, it greatly increases the number of known specimens for a few late Eocene taxa without greatly increasing the total number of species. Second, it might lead one to conclude that the late Eocene is in fact better studied than the early Oligocene, because microvertebrate quarries often produce much higher diversities of small taxa than surface collections (e.g., Silcox and Rose 2001). However, this conclusion is not necessarily warranted. Calf Creek is the most northerly locality of those compiled by Sullivan and Holman (1996). Negative latitudinal gradients in species richness are a pervasive feature of nearly all higher taxa in the modern world (e.g., Pianka 1966; Rosenzweig 1995), including reptiles (Kiestler 1971; Pianka 1977), and they have also been described from the fossil record (e.g., Crane and Lidgard 1989). One can reasonably assume that squamate richness was likewise deployed in the late Eocene and therefore conclude that the Calf Creek l.f. should be the least rich of all sampled faunas. In other words, it may contribute relatively little to total richness while superficially bettering sampling by inflating the number of specimens.

Sampling statistics for the late Eocene and early Oligocene clarify these points. Counting skull

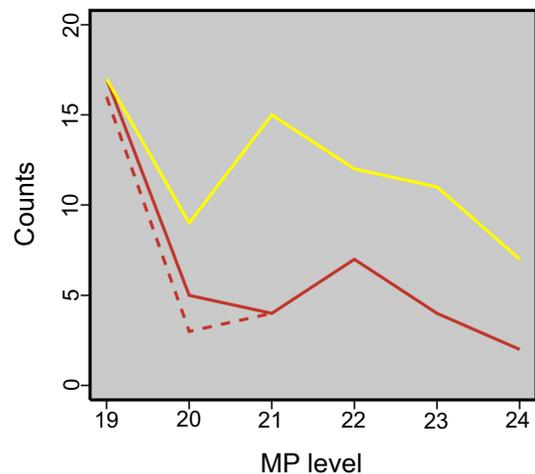


Figure 22. Sampling and the European record of squamate diversity. The *Grande Coupure* and Eocene/Oligocene boundary are basically the boundary between standard levels MP 20 and MP 21 (MP = *Mammifères Paléogène*). Solid yellow line is number of localities; solid (dashed) red line is maximum (minimum) number of taxa per level. The number of fossiliferous localities for each level was compiled from Schmidt-Kittler (1987). Data on squamate diversity come from Rage and Augé (1993); "maximum" number of taxa includes questionable occurrences excluded from the "minimum," following these authors.

elements alone, there are 109 published squamate specimens from the Chadronian and 93 from the Orellan (compiled from Estes 1983; Holman 1972; Sullivan and Holman 1996). In terms of specimen counts, the Chadronian appears to be better sampled. However, when large specimens—especially glyptosaurine anguils—are removed from the samples (they are much easier to pick up in surface collecting), then sampling counts decline to 66 specimens from the Chadronian and 78 from the Orellan. Even so, frequency distributions of the number of specimens per species (glyptosaurines removed) show that in the Chadronian, two (25%) of the species are represented by ≥ 10 specimens, both of them from the Calf Creek l.f. In the Orellan, two (only 11%) of the species are represented by ≥ 10 specimens.

The situation appears to be quite different in Europe, where the major terrestrial faunal break is known as the *Grande Coupure* (Stehlin 1909). Rage (1984; 1986) and Rage and Augé (1993) have argued that squamate richness in Europe plummets across the Eocene/Oligocene boundary. Richness drops from 16–17 taxa in level MP19 (see Schmidt-Kittler 1987), to 3–5 in MP20 and 4 in MP21 (Figure 22) (Rage and Augé 1993). (These

estimates do not include boid taxa A–M that Rage included in his 1984 tabulation and would increase the magnitude of the change.) One way to examine sampling issues is by comparing the number of well-correlated localities at each level to species richness. There are 17 such localities for MP19, 9 for MP20, and 15 for MP21 (Figure 22; compiled from Schmidt-Kittler 1987). It is not necessarily the case that all of these localities have produced described squamate fossils, but the numbers do suggest a decrease in sampling from MP19 to MP20, which may account for the drop in richness at that time. However, richness remains low in MP21 despite many more localities for that level. A drop in richness near the Eocene/Oligocene boundary in Europe is probably robust to increased sampling.

North American Record of Species Richness Revisited. With these new data, the current central North American record of squamates is at least qualitatively consonant with the European record and is furthermore consistent with expectation. There are now 25 known Chadronian squamates in comparison with 18 in the Orellan (Table 1). Of the Chadronian taxa, 11 were previously described, and 14 are new. Other Lazarus taxa remain unaccounted for (Table 1). Snake vertebrae from the Medicine Pole Hills l.f. have not yet been described, which will further increase known squamate richness in the Chadronian. However, sampling in the Chadronian is now also better than in the Orellan, so it is difficult to know whether these differences are real.

The apparent central North American drop in richness (~30%) is not as dramatic as that seen in Europe (>50%; Rage and Augé 1993). Climatic conditions across the Eocene/Oligocene boundary have not been as well studied in Europe, at least in part because of the discontinuous nature of the fossil record there. Collinson (1992) noted a generally large decrease in the richness of tropical and subtropical plant species and a sudden increase in the proportion of temperate palynomorphs at the Grande Coupure in the Paris Basin. These floral changes probably reflect cooling, but it is unclear how cooling in Europe compares with that in continental North America. Grimes et al. (2005) and Mosbrugger et al. (2005) recently demonstrated that MAT decreased by a few degrees celcius from the late Eocene to early Oligocene, primarily as a result of increased MART. Other factors besides temperature are doubtlessly involved in producing different results, such as the relatively large number of Asian immigrants in the earliest Oligocene of

Europe (Rage and Augé 1993) and the geography of late Eocene Europe.

Poor sampling in North America remains a great impediment to our understanding (see also Estes 1970; Hutchison 1992; Tihen 1964). There is little locality or stratigraphic information for older collections, screenwashing has been sporadic at best, and samples are generally geographically disjunct (geography, independently of time, can now influence the pattern). In this situation techniques like rarefaction that merely address the number of specimens rather than the pattern of their occurrence in space are inapplicable. Thus, an understanding of the response of squamate richness to Eocene/Oligocene climate change will require sampling-standardized collections from stratigraphically controlled localities in geographically restricted areas.

Composition of Late Eocene Squamate Assemblages. The Medicine Pole Hills l.f. is over three times as diverse as the Calf Creek l.f. It is possible that the difference partially reflects the age difference (~1 m.y.) between the localities. However, the difference in local richness is not as great as it appears. Rarefaction is a statistical technique that normalizes richness for sample size (e.g., Hurlbert 1971; Heck et al. 1975). It is appropriate here because we are comparing individual localities, and the results are directly interpretable because the deposits are roughly isotaphonomic. The two amphibaenian taxa from the Calf Creek l.f. are only known from (a disproportionate number of) vertebrae and constitute outliers in the specimen frequency distribution. Because differing specimen separate rarefaction curves were calculated and were derived for cranial elements alone and for all specimens using the program Analytic Rarefaction 1.3 (Holland 2001) (Figure 23). If the specimen sample size from the Medicine Pole Hills l.f. was the same as that from Calf Creek, the richness of the former would be reduced to 10.1 ± 2.8 species, for cranial specimens, versus 18.6 species when all specimens are considered; only three species are known from cranial remains at Calf Creek. The cranial comparison, because it does not rely on a frequency distribution with extreme outliers, is probably the more meaningful of the two analyses. Rarefaction reduces the apparent difference in species richness for cranial remains alone—16 species (19–3)—by more than half, to 7.1 species (10.1–3). The results are still consistent with a latitudinal gradient in local species richness.

Depending on the specific status of the taxa present, the Calf Creek and Medicine Pole Hills

Table 1. List of squamate taxa currently known from Chadronian and Orellan strata in North America (compiled from Estes 1983; Sullivan and Holman 1996; this study). An asterisk indicates that the taxon is known exclusively from the Medicine Pole Hills l.f.; a dagger indicates an uncertain record. Listing of taxa in the same row is not meant to imply direct descent, only that they cannot be excluded from the same lineage. Species-level taxon names are given where available; in cases where specimens from the Medicine Pole Hills l.f. cannot adequately be diagnosed to species level, but also cannot be excluded from a species already known from the Chadronian, only the previously known species is listed, with the conservative assumption that the specimen(s) in question do represent that species.

Chadronian	Orellan
<i>Tinosaurus</i> sp.*	
<i>Polychrus charisticus</i> sp. nov.*	
Iguanid MPH-1*	
Iguanid MPH-2*	
<i>Tuberculacerta pearsoni</i> gen. et sp. nov.*	<i>Paraphrynosoma greeni</i>
cf. <i>Aciprion</i> sp.*	<i>Aciprion formosum</i>
Iguanid MPH-3*	
Iguanid MPH-4*	
<i>Cypressaurus hypsodontus</i>	
" <i>Crotaphytus</i> " <i>oligocoenicus</i>	
Scincoid MPH-1*	Scincid, new taxon
" <i>Palaeoxantusia</i> " <i>borealis</i>	
cf. <i>Rhineura</i> sp.	<i>Rhineura hatcheri</i>
<i>Spathorhynchus natronicus</i>	
<i>Hyporhina tertia</i>	<i>Hyporhina antiqua</i>
	<i>Exostinus serratus</i>
Anguimorph MPH-1*	<i>Parophisaurus pawneensis</i>
Diploglossine MPH-1*	
cf. <i>Peltosaurus</i> sp.	<i>Peltosaurus granulatus</i>
<i>Helodermoides</i> sp. nov.?*	<i>Helodermoides</i> sp.
<i>Helodermoides tuberculatus</i>	
Xenosaurid MPH-1*	
	<i>Lowesaurus matthewi</i>
<i>Saniwa edura</i> sp. nov.*	
	<i>Coprophis dakotaensis</i>
<i>Boavus</i> sp.	<i>Boavus</i> cf. <i>occidentalis</i>
<i>Calamagras weigeli</i>	<i>Calamagras angulatus</i>
	<i>Calamagras murivorus</i>
	<i>Helagras orellanensis</i>
<i>Ogmophis compactus</i>	<i>Ogmophis compactus</i> †
	<i>Geringophis vetus</i>
	<i>Texasophis galbreathi</i>

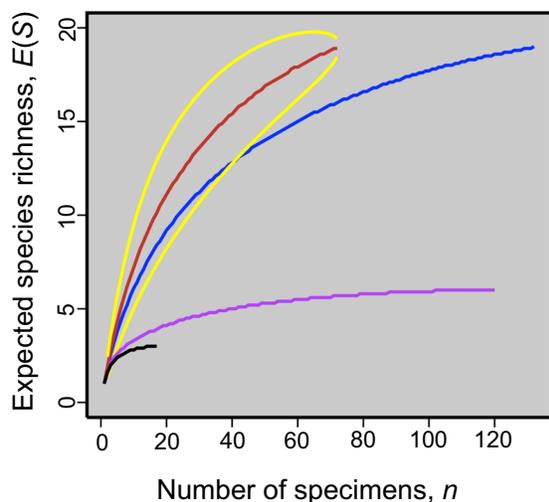


Figure 23. Rarefaction curves for the Calf Creek (C.C.) and Medicine Pole Hills (M.P.H.) local faunas. The blue line is for all specimens at M.P.H.; the red, for M.P.H. cranial elements only (see text), with associated the 95% confidence intervals in yellow. The purple line is for all elements at C.C.; the black, for C.C. cranial elements at only. Data from the Calf Creek l.f. derive from Holman (1972); data from the Medicine Pole Hills l.f. are from this study.

local faunas have up to five taxa in common, viz., a small and a large rhineurid, *Peltosaurus*, "*Palaeoxantusia*" *borealis*, and *Cypressaurus*. Calf Creek is conspicuous in lacking a xenosaurid, an acrodontan, a varanid, and a scincoid. (The latter four are represented by few specimens in the Medicine Pole Hills l.f., so their absence at Calf Creek is not altogether surprising.) Additionally, the largest anguid (*Helodermoides*) is seemingly absent in the Calf Creek l.f. Gilmore (1928: 120) noted the presence of "*Glyptosaurus* sp." in the "Cypress Hills"; Holman (1976) also listed this taxon without providing information on new specimens. Since the Cypress Hills Formation spans both the Duchesnean and Chadronian land-mammal "ages," and Gilmore provided no locality data for the specimen (a single cephalic osteoderm), the definitive presence of "*Glyptosaurus*" or *Helodermoides* cannot be supported with present data. Finally, the Calf Creek l.f. lacks the great diversity of iguanids seen in North Dakota.

The Medicine Pole Hills squamate assemblage is in some respects intermediate between early Eocene and Miocene faunas. There are two holdovers of early Eocene immigrants, the presumed relatives of the varanid *Saniwa* and the acrodontan *Tinosaurus*. These taxa are thought to have entered North America during the wet, warm

climate of the early Eocene (Estes 1983); they evidently persisted until near the end of the Eocene. Additionally, there are a number of more ancient North American lineages that remain, including a xantusiid and (probably) a xenosaurid. The former apparently disappears in central North America by the beginning of the Oligocene. Despite some similarities to early Eocene squamate assemblages, the Medicine Pole Hills l.f. is remarkable in its diversity of iguanids, in this respect more like the Miocene (Tihen 1964). Over 40% of the lizards are iguanids, as compared with an estimated 20% in the early Eocene Wasatch Formation of Wyoming (Gauthier 1982).

The transformation of central North American squamate assemblages over time has been described as showing a growing prominence of xeric-adapted lizards (especially iguanids). Tihen (1964) argued that modernization began in the late Oligocene and was centered in the early Miocene (Arikareean). Regardless of the poverty of sampling in the medial and late Oligocene, the data presented here superficially contradict Tihen's thesis in the high proportion of iguanids present in the Medicine Pole Hills l.f., but only if we assume that by modernization is meant "phrynosomatization." In other words, there is contradiction only if we are wed to the idea that late Eocene iguanids are of the type now inhabiting the western interior (i.e., phrynosomatine and crotaphytine). Of those taxa that can possibly be related to extant clades, one is a phrynosomatine (this study) and one a crotaphytine (Holman 1972; Estes 1983; McGuire 1996), but one is a polychrotine. Thus, at least one iguanid clade may show the same pattern as many scincormorph and anguimorph lizards, in which Eocene taxa retreated or became restricted to the south to become members of the modern Sierra-Madreal and Austroriparian herpetofaunas. An increased proportion of iguanids does not by itself imply that the Medicine Pole Hills squamate fauna is any meaningful sense "modern." That Iguanidae may show such a historical biogeographical pattern should not be surprising in view of the great variability in autecology within the clade.

CONCLUSIONS

A full understanding of change in squamate assemblage composition during the Tertiary is frustrated by sampling problems. It is very difficult even to assess the biases that currently affect the squamate record, much less to correct for them. Nevertheless, the squamates of the Medicine Pole Hills l.f. provide a great deal of new information on the

character of late Eocene assemblages. Fourteen previously unreported species are identified in this Chadronian fauna, including an acrodont iguanian, seven iguanids, a scincoid, a new anguimorph, a ?xenosaurid, a varanid, a diploglossine, and *Helodermoides*; another five are likely already known from that time (see Table 1). Of particular interest are the relatives of early Eocene immigrants from the Old World (*Tinosaurus*, *Saniwa**), a phrynosomatine (fence lizards and relatives), a polychrotine (anoles and relatives), and the last record of the stem-clade of Diploglossinae (galiwasps) in central North America. Three of the new species are named formally. The polychrotine, apparently a member of the *Polychrus* stem-clade, indicates that the transformation of squamate assemblages was not simply a gradual increase in the richness of iguanid taxa that are currently present in central North America (Phrynosomatinae, Crotaphytinae). Rather, some iguanids, like their counterparts in other parts of the squamate tree, may have had long histories in the area. This conclusion is completely consistent with the explicit recognition that Iguanidae has a great deal of intraclade variability in autecological preference. The fossil record now suggests that squamates in central North America, like those in Europe, suffered a drop in richness in response to Eocene/Oligocene climatic deterioration, but because of remaining sampling problems this observation must be treated with some circumspection. Sampling-standardized studies on new and existing collections are indicated.

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APPENDIX

Modern osteological specimens studied and referred to in this study are as follows.

Iguania

Iguanidae:

Corytophaninae: *Basiliscus basiliscus* (UF 99625, 99655), *B. galeritus* (UF 61491), *B. plumifrons* (UF 71704, 71725), *B. vittatus* (UF 44905, 61307, 140835), *Corytophanes cristatus* (UF 57011, 69072), *C. hernandesii* (UF 72492), *Laemanctus longipes* (UF 43115, 62082, 62561)

Crotaphytinae: *Crotaphytus baileyi* (YPM R11535), *C. collaris* (UF 11483, 11696, 100012, YPM R11208), *Gambelia wislizenii* (UF 51166, 54056, 56412, YPM R10367)

Hoplocercinae: *Enyalioides oshaughnessyi* (SMF 67590)

Iguaninae: *Amblyrhynchus cristatus* (UF 54782), *Brachylophus fasciatus* (UF 37578), *Conolophus subcristatus* (UF 11583), *Ctenosaura clarki* (UF 61948), *C. hemilopha* (UF 11477), *C. oedirhina* (UF 28530), *C. pectinata* (UF 62493), *C. similis* (UF 61966, 67982), *Cyclura cornuta* (UF 99656), *C. ricordi* (UF 86782), *Dipsosaurus dorsalis* (UF 55334, YPM R12811), *Sauromalus hispidus* (UF 38333), *S. obesus* (YPM R11623–11625), *S. varius* (UF 62313)

Oplurinae: *Chalarodon madagascariensis* (YPM R11951), *Oplurus cuvieri* (SMF 79191)

Phrynosomatinae: *Callisaurus draconoides* (UF 43122, 45140, YPM R11037), *Cophosaurus texana* (YPM R11523), *Holbrookia maculata* (UF 43839, 45139, YPM R11521), *Petrosaurus mearnsi* (YPM R12809), *Phrynosoma asio* (UF 60909, 62087), *P. cornutum* (UF 99225, YPM R11528), *P. modestum* (UF 55355, 56328, 60917), *P. platyrhinos* (YPM R11017), *Sceloporus clarkii* (UF 54914), *S. cyanogenys* (UF 35011), *S. formosus* (UF 62083), *S. grammicus* (UF 60671), *S. jarrovii* (UF 69154), *S. megalepidurus* (UF 99542), *S. poinsettii* (UF 50264), *S. serrifer* (UF 54560), *Uma notata* (YPM R11536), *Urosaurus graciosus* (YPM R11077), *Uta stansburiana* (YPM R12146)

Polycrotinae*: *Anolis acutus* (UF 62414), *A. armouri* (UF 99503–99504), *A. biporcatus* (UF 52563, YPM R12131), *A. brevirostris* (UF 99349, 99616), *A. capito* (UF 60346), *A. carolinensis* (UF 11132-1, 99671, 99750), *A. chlo-*

rocyanus (UF 42494, 99949), *A. coelestinus* (UF 99430–99431), *A. conspersus* (UF 63863), *A. cristatellus* (UF 99457, YPM R12048), *A. cybotes* (UF 99513, 99927), *A. distichus* (UF 99525, 99621), *A. equestris* (YPM R11195), *A. extremus* (UF 15017, 15019), *A. garmani* (UF 42404, 48915), *A. grahami* (UF 48997, 99166), *A. marmoratus* (UF 11712), *A. maynardi* (UF 21738, 63862), *A. lemuringus* (UF 99315), *A. lineatopus* (UF 11708-3, 48996), *A. lividus* (UF 11489, 48327), *A. olssoni* (UF 99681), *A. opalinus* (UF 48917–48918), *A. ortonii* (UF 68183, 68185), *A. pulchellus* (UF 99345), *A. richardii* (UF 144517), *A. ricordi* (UF 64820, 99672), *A. sagrei* (UF 99521, 99995), *A. scriptus* (UF 99541, 99565), *A. smaragdinus* (UF 99357, 99381), *A. wattsi* (UF 11488, 24019), *A. whitemani* (UF 99686), *Polychrus acutirostris* (SMF 24870), *P. gutturosus* (UF 49377), *P. marmoratus* (YPM R13556), *Pristidactylus torquatus* (YPM R11031)

Tropidurinae*: *Leiocephalus inaguae* (UF 99112, 99247), *L. lunatus* (UF 66071), *L. melanochlorus* (UF 60649, 71618), *L. personatus* (UF 99341, 99478), *L. punctatus* (YPM R11291), *L. schreibersii* (YPM R12128), *Microlophus occipitalis* (UF 99683), *Plica plica* (55718, 63244), *Plica umbra* (43638), *Tropidurus hispidus* (UF 61630, 69147), *T. torquatus* (UF 99338), *Uracentron azureum* (UF 66078, 68302), *Uranoscodon superciliosus* (YPM R10489, 11872).

Agamidae:

Leiolepidinae: *Leiolepis belliana* (YPM R10622, 12129), *Uromastix acanthinurus* (YPM R13525), *U. geeri* (YPM R13701), *U. hardwickii* (YPM R11539), *U. maliensis* (YPM R13524)

Agaminae: *Acanthosaura cracigera* (YPM R12142), *Agama agama* (YPM R11094), *A. atricollis* (YPM R13561), *Calotes versicolor* (YPM R12114), *Hypsilurus auritus* (YPM R12124), *Japalura splendida* (YPM R12100), *Lophognathus temporalis* (YPM R13891), *Physignathus cocincinus* (YPM R11218, 14495), *Xenagama taylori* (YPM R11327)

Chamaeleonidae: *Bradypodion fisheri* (YPM R13266), *Chamaeleo chamaeleon* (YPM

R10536), *C. oustaletii* (YPM R11214), *C. senegalensis* (YPM R12116), *Rhampholeon breviceaudata* (YPM R13594, 13815)

Gekkota:

Gekkonidae: *Eublepharis macularius* (YPM R11248), *Hemidactylus fasciatus* (YPM R10436), *Paroedura masobe* (YPM R11402), *Tarentola mauritanica* (YPM R11829)

Scincomorpha:

Scincidae: *Egernia cunninghami* (UF 64825), *Eumeces obsoletus* (UF 62556), *E. skiltonianus* (YPM R12151), *E. taeneolatus* (UF 61467), *Mabuya dissimilis* (UF 67813), *M. maculilabris* (UF 55342), *Scincus mitranus* (YPM R13500, 13565), *Tiliqua gigas* (UF 76243)

Cordylidae: *Cordylus cataphractus* (UF 68997), *C. giganteus* (YPM R12820), *C. warreni* (UF 57845), *Gerrhosaurus major* (YPM R13888)

Lacertidae: *Podarcis sicula* (YPM R13553, 13555, 13570)

Teiidae: *Callopiastes maculata* (YPM R12825), *Cnemidophorus tigris* (YPM R11020, 13374), *Dicrodon guttulatum* (UF 48447), *Kentropyx borckianus* (UF 99285)

Gymnophthalmidae: *Neusticurus bicarinatus* (UF 54554)

Anguimorpha

Anguinae:

Anguinae: *Anguis fragilis* (YPM R11030, 13572), *Ophisaurus attenuatus* (UF 57121), *O. compressus* (UF 68916, YPM R13504), *O. pseudo-*

pus (YPM R12870), *O. ventralis* (UF 52539, YPM R10638)

Anniellinae: *Anniella pulchra* (UF 51810)

Diploglossinae: *Celestus carraui* (UF 83555), *C. costatus* (UF 55485, 99990), *C. crusulus* (UF 21743), *C. curtissi* (UF 99395), *C. warreni* (UF 99396)

Gerrhonotinae: *Abronia aurita* (YPM R11222), *A. smithi* (YPM R11646), *Elgaria coerulea* (UF 61574), *E. multicaudata* (YPM R14098), *Gerrhonotus liocephalus* (YPM R11299), *Mesaspis gadovii* (UF 62782), *M. moreletii* (UF 541214, YPM R13661)

Xenosauridae: *Shinisaurus crocodilurus* (UF 68983, 71700, YPM R12817), *Xenosaurus grandis* (YPM R12818), *X. platyceps* (UF 60965)

Varanidae: *Lanthanotus borneensis* (YPM R12673), *Varanus albigularis* (YPM R13717, 13981), *V. beccari* (YPM R13267), *V. bengalensis* (YPM R11028, 11089), *V. doriensis* (YPM R13989), *V. dumerilii* (YPM R11203), *V. exanthematicus* (YPM R10812), *V. griseus* (YPM R10370), *V. indicus* (YPM R10381), *V. jobiensis* (YPM R11074), *V. melinus* (YPM R11202), *V. mertensi* (YPM R11658), *V. niloticus* (YPM R10775), *V. prasinus* (YPM R10328), *V. panoptes* (YPM R10394), *V. rudi-collis* (YPM R12235), *V. salvator* (YPM R10131, 11064), *V. storri* (YPM R11042), *V. tristis* (YPM R11175)

Helodermatidae: *Heloderma horridum* (YPM R10618), *H. suspectum* (UF 52565, YPM R11201, 14352)