THE POWER AND UTILITY OF MORPHOLOGICAL CHARACTERS IN SYSTEMATICS: A FULLY RESOLVED PHYLOGENY OF *XENOSAURUS* AND ITS FOSSIL RELATIVES (SQUAMATA: ANGUIMORPHA)

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ABSTRACT. *Xenosaurus* is an enigmatic clade of Mexican and Central American lizards distinguished by knob-like scalation and flattening of the head and body associated with living in cracks within cliff faces. The position of *Xenosaurus* within the larger clade Anguimorpha is difficult to determine owing to a combination of primitive features and a unique, highly modified anatomy that obscures useful characters. Evidently, the phylogenetic stem of *Xenosaurus* represents a long independent history of evolution. Fortunately, several fossil taxa exist that can elucidate this history. These taxa include the extinct *Exostinus lancensis* (Cretaceous), *Exostinus serratus* (Oligocene), and *Restes rugosus* (Paleocene), the latter two known from substantial, cranial material (Bhullar, 2007; 2010). Using osteological and alcohol-preserved specimens, fossils, and high-resolution x-ray CT scans thereof, I attempted to reconstruct the relationships of the three fossil taxa and the six extant species of *Xenosaurus* that are available in U.S. collections.

Despite the considerable phylogenetic importance of *Xenosaurus* and its stem, this is the first phylogenetic analysis of the group. An exhaustive search of the skeleton, including osteoderms embedded in the skin visualized using CT scanning, yielded 274 new characters, substantially more than have been used previously in gross anatomy–based analyses of such a restricted group of reptiles. The great number of characters is largely the result of the availability of disarticulated skeletal material, CT scans showing internal bone structure and bones embedded in the skin, and attention to subtle anatomical differences whose validity could be assessed in terms of intraspecies variation because of the availability of large sample sizes for certain taxa.

My results suggested that *R. rugosus* is sister to the other xenosaurs, resolving a polytomy with other Anguimorpha recovered by previous work. *Exostinus lancensis* is problematic in that it may represent several distinct taxa, but it was recovered as sister to *E. serratus + Xenosaurus*, making *Exostinus* paraphyletic. *Exostinus serratus* emerged as sister to *Xenosaurus*. *Xenosaurus* comprises a northern clade consisting of *Xenosaurus newmanorum* and *Xenosaurus platyceps*; the remaining taxa are united as a southern clade. Within the southern clade, *Xenosaurus agrenon* and *Xenosaurus rectocollaris* are sister to *Xenosaurus grandis* and *Xenosaurus rackhami*. North–south splits within Xenosauridae mirror those of several other lizard clades and may be the legacy of the equatorial contraction of early Tertiary tropical forests. The fully resolved nature of the phylogeny and the congruence of the extant portion with molecular results indicates the continued relevance and efficacy of morphological systematics when an exhaustive anatomical analysis is performed to search for new characters.

Key words: Xenosaurs, Xenosauridae, squamates, lizards, extinct, paleontology, Anguimorpha, systematics, *Shinisaurus*

INTRODUCTION

Phylogenetic analysis using gross morphological characters, while once the standard approach to systematics, has in the last two decades been complemented by the huge number of characters (albeit with a very limited number of character states) available from the morphology of nucleic acids, or "molecular" data. Ancient fossil taxa, of course, can generally be included in phylogenetic analyses only when morphological data are in play, but for extant organisms the huge number of individual characters available from DNA sequences compared with the characters available from gross morphology has led to suggestions that morphological analyses are woefully inaccurate and obsolete (Scotland et al., 2003).

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Indeed, early morphology-based analyses in particular often utilized only a few dozen characters—but still their resolving power could be considerable (Gauthier et al., 1988). However, far longer character lists and far better resolution can be achieved with the detailed consideration of the near-infinite aspects of organismal morphology at all scales. Here, I employ an exhaustive search for the characters most relevant to fossil taxa—those derived from skeletal anatomy—in an attempt to resolve the phylogeny of the enigmatic clade *Xenosaurus* and its fossil relatives.

Xenosaurus ("knob-scaled lizards") consists of unusual flat-bodied crevice-dwelling lizards distributed throughout Mexico and northern Central America. The relationships of the species within *Xenosaurus* and extinct taxa with affinities to the clade have not been treated in a published phylogenetic analysis. Two studies, by Gauthier (1982) and Conrad (2008; see also Conrad et al., 2011), presented hypotheses of relationships along the phylogenetic stem of *Xenosaurus*, although both dealt primarily with relationships within the larger clade Anguimorpha as a whole. In the first of these studies, Gauthier (1982) suggested that the Oligocene fossil taxon *Exostinus serratus* is sister to *Xenosaurus* to the exclusion of the Cretaceous *Exostinus lancensis* and the Paleocene *Restes rugosus* (*Exostinus rugosus* prior to reassignment in that work) but left the relationships of the latter two taxa unresolved. These taxa are described fully under Materials and Methods. A preferred hypothesis in which *R. rugosus* is sister to the remaining taxa and *E. lancensis* is sister to *E. serratus* was provided by Conrad (2008). Finally, an unpublished master's thesis (Canseco Márquez, 2005) included a hypothesis of relationships among the extant species of *Xenosaurus* based on squamation. That study included more species of *Xenosaurus* than were available to me, but for those which were included by Canseco Márquez (2005) and by me in this study, the phylogenetic hypotheses recovered for relationships within *Xenosaurus* is

identical. I did not include the characters from that study here in deference to the author of the work, who is preparing it for publication.

Hypotheses of the phylogeny of Anguimorpha as a whole were provided by McDowell and Bogert (1954) and Gauthier (1982). Those hypotheses were not explicitly tested by the authors, although Gauthier (1982) presented his hypothesis with an explicitly cladistic frame of reference. Anguimorpha was subjected to explicit phylogenetic analysis by several authors, some of whom used gross anatomical characters (Rieppel, 1980; Estes et al., 1988; Lee, 1998; Evans and Barbadillo, 1998; Gao and Norell, 1998; Conrad, 2005, 2008; Conrad et al., 2011) and others of whom used nucleic acid structure (Macey et al., 1999; Wiens and Slingluff, 2001; Townsend et al., 2004; Conrad et al., 2011).

In a cladistic framework, the phylogeny posited by McDowell and Bogert (1954) has an initial split between Varanoidea (here Platynota) and Diploglossa, the latter of which includes the remainder of Anguimorpha. The arrangement suggested that Varanoidea is split between *Heloderma* and *Lanthanotus borneensis* + *Varanus*, whereas Diploglossa is split between Diploglossinae and a trichotomy of Gerrhonotinae + Anguinae + Xenosauridae. Xenosauridae was used in the sense of *Shinisaurus crocodilurus* + *Xenosaurus*. A similar phylogeny was presented by Rieppel (1980), with Varanoidea sister to a clade whose first split is between Gerrhonotinae and all other taxa, with the latter then split into Xenosauridae and Diploglossinae + Anguinae. Xenosauridae was not nested within Anguidae in the topology presented by Gauthier (1982). Instead, he posited a trichotomy of Varanoidea, Xenosauridae, and Anguidae, the last consisting of Anguinae and Gerrhonotinae + Diploglossinae. The trichotomy was resolved by Estes et al. (1988) to Anguidae on one branch and Xenosauridae + Varanoidea on the other. The same topology was recovered by Lee (1998). According to Evans and Barbadillo (1998),

the initial split is between Xenosauridae and the remaining anguimorphs (in addition, Gekkota is nested within Anguimorpha, an unusual result that was not recovered in other studies). This topology, without the nested Gekkota, was also recovered by Gao and Norell (1998), as was the placement of the Mongolian taxon *Carusia intermedia* (Borsuk-Bialynicka, 1984) as the sister to Xenosauridae. Finally, a similar topology was recovered by Conrad (2005, 2008), save that *S. crocodilurus* and its extinct relative *Bahndwivici ammoskius* are sister to Varanoidea, leaving the initial split in Anguimorpha between *Xenosaurus* plus its allied extinct taxa and the remainder of Anguimorpha. *Carusia intermedia* emerged in the 2005 study as the sister taxon to Anguimorpha, and in the 2008 and 2011 studies as the sister to *Xenosaurus* and its extinct relatives. Within Anguidae, Anguinae and Diploglossinae are sister taxa to the exclusion of Gerrhonotinae.

Among the studies based on nucleic acid structure, the same data set was used by Macey et al. (1999) and Wiens and Slingluff (2001). Both groups recovered the same overall topology for Anguimorpha. The initial split according to those studies is a trichotomy among *Varanus*, *Heloderma*, and the remainder of Anguimorpha. The latter clade is split between *S. crocodilurus* and *Xenosaurus* + Anguidae. Within Anguidae, Anguinae and Gerrhonotinae are sister taxa to the exclusion of Diploglossinae. Several years after the publications of those focused studies on Anguimorpha, the first molecular structure–based phylogenies of all of Squamata appeared (Townsend et al., 2004; Vidal and Hedges, 2005). In general, most of the trees recovered in those analyses have the initial split in Anguimorpha between *S. crocodilurus* + Varanidae and Anguidae + *Heloderma* + *Xenosaurus* in some combination. An Anguidae + *Heloderma* clade appears more often than a *Heloderma* + *Xenosaurus* clade. The molecular structure–based phylogenies are thus broadly congruent with the newest gross anatomy–based phylogenies, save for the unprecedented nonmonophyly of Varanoidea, a clade supported by numerous gross anatomical apomorphies (summarized by Gao and Norell, 1998; Conrad, 2005, 2008; Conrad et al., 2011).

Regarding outgroups to Anguimorpha, the gross anatomy–based and molecular structure–based phylogenies differ strikingly. All of the gross anatomy–based phylogenies have Anguimorpha as part of a monophyletic Scleroglossa (*sensu* Estes et al., 1988), with Iguania sister to that large clade. The appropriate outgroups to Anguimorpha would thus be found within "Scincomorpha" (whose monophyly is not universally supported), at least a part of which is, in most gross anatomy–based phylogenies, more closely related to Anguimorpha than is Gekkota. The molecular structure–based phylogenies, on the other hand, generally recover Iguania as more closely allied to Anguimorpha than any "scincomorph" clade, sometimes with Serpentes intervening.

Given the potential importance of *Xenosaurus* and its extinct relatives to resolving the phylogeny of Anguimorpha and thereby of Squamata as a whole, this study is directed at resolving the problematic relationships within the highly autapomorphic crown clade and its stem. The extinct taxa are particularly important to my analyses because they can break up the phylogenetic "long branch" leading to *Xenosaurus* (Gauthier et al., 1988). Two other factors were important to the viability of the study. First, museum collections in the United States have sufficient skeletal and wet-preserved specimens of extant *Xenosaurus* to allow a reasonable sampling of taxa and some assessment of intraspecific variation. Furthermore, some of the skeletal specimens I used were disarticulated. Many of the characters identified here would have been impossible to see in articulated skeletons. Finally, high-resolution CT scanning technology allowed the digital disarticulation of fossils in matrix and the visualization of osteoderms within the skin of extant specimens.

MATERIALS AND METHODS

Ingroup

The focus of the present study is *Xenosaurus* and its extinct relatives, also referred to herein as "xenosaurs" (*Shinisaurus* and its extinct relatives are likewise called "shinisaurs"). The term Xenosauridae is used exclusively to refer to the "traditional" clade, including xenosaurs and shinisaurs as sister taxa, a topology only supported by one of the two analyses performed here. The characters included are limited in large part to those pertinent to relationships within the xenosaur ingroup. Most of the 274 characters I describe and score (Table 1) are new or newly defined; derivation from previous literature is noted in the character descriptions. The extinct taxa are particularly important in light of the highly derived nature of the crown clade; they provide the opportunity to break up "long branches" and resolve problematic clades (Rowe, 1986; Gauthier et al., 1988).

Xenosaurus. Twelve extant species of *Xenosaurus* were included in the unpublished external anatomy–based phylogenetic analysis by Canseco Márquez (2005); two of those are undescribed, and I was unable to obtain four—*Xenosaurus arboreus*, *Xenosaurus sanmartinensis*, *Xenosaurus phalaroanthereon*, and *Xenosaurus penai*—from U.S. collections. Most species of *Xenosaurus* were once classified as subspecies of *Xenosaurus grandis* Gray 1856. Summaries of the taxonomic history of the group were provided by King and Thompson (1968), Ballinger et al. (2000), and Canseco Márquez (2005). The taxa used in my study (see Table 1) are *Xenosaurus newmanorum* Taylor 1949 (Fig. 1), *Xenosaurus platyceps* King and Thompson 1968 (Fig. 2), *Xenosaurus rackhami* King and Thompson 1968 (as *Xenosaurus grandis rackhami*) (Fig. 3), *X. grandis* (Fig. 4), *Xenosaurus agrenon* King and Thompson 1968 (as *Xenosaurus grandis agrenon*), and *Xenosaurus rectocollaris* Smith and Iverson 1993 (Fig. 5). Alcoholic specimens were available for all taxa, and skeletal material was available for

all but *X. rectocollaris*. To supplement the skeletal material, I used high-resolution x-ray CT scans of the heads and bodies of all species save *X. agrenon*, for which the wet-preserved specimens were filled with metal shot that interfered with the scanning process. The scans were performed at the High-Resolution CT Scanning Facility at The University of Texas at Austin (UTCT) and allowed visualization of the articulated skeletons with the osteodermal armor in place.

Exostinus serratus. The included specimens, from the Oligocene of Colorado and Wyoming, were described by Bhullar (2008; 2010), as was the history of this taxon.

Exostinus lancensis. This is the most problematic taxon included in the study. It was described by Gilmore (1928) and Estes (1964) on the basis of fragmentary material from the Late Cretaceous of Wyoming and Montana. A summary of the history of the taxon until 1983 was provided by Estes (1983). Following that work, the only additional information on the anatomy of the taxon was provided by Gao and Fox (1996) on the basis of specimens from the western interior of Canada. Scoring here is based on those descriptions and on a number of undescribed specimens from the western United States in the collections of the American Museum of Natural History. For the purposes of this study, all of these disparate specimens are assumed to represent the same taxon. However, *E. lancensis* requires additional study. In particular, most of the American Museum specimens from the Lance Formation of Wyoming conform well to the descriptions of *E. lancensis* in the literature. However, frontals that are clearly associated with the characteristic parietals based on size, osteodermal sculpturing, and fit of the articular surfaces are large and unfused, whereas Gao and Fox (1996) described the anterior portion of a fused frontal that is nearly the same size. For the purposes of this study, frontal fusion is assumed to be ontogenetically variable in *E. lancensis*, but work on this taxon continues.

Restes rugosus. This taxon was described as *Exostinus rugosus* by Gilmore (1942) and further by Estes (1965). It was renamed *R. rugosus* by Gauthier (1982). It is known primarily from a single well-preserved but disarticulated specimen, YPM PU 14640 from the late Paleocene of Wyoming. Isolated frontals that Gauthier (1982) referred to the taxon were suggested to belong instead to a shinisaur or a platynotan by Smith (2006b). *Restes rugosus* was never fully described, nor has it been examined since the work of Gauthier (1982). The analysis here utilizes a low-resolution CT scan of the YPM PU 14640 block, which I found to contain a surprising amount of unexposed material. I had access to one additional specimen, an anterior section of a maxilla (UMMP 73565) from the Paleocene of Wyoming.

Outgroup

Anguimorpha. Because of the unresolved state of the larger clade Anguimorpha, it was necessary to use a variety of anguimorph taxa in the analysis. In general, the focus was upon extant taxa to minimize missing data, and because I was not attempting to resolve anguimorph relationships definitively. However, because *S. crocodilurus* was traditionally allied to *Xenosaurus* in Xenosauridae, the analysis includes two described fossil shinisaurs—*B. ammoskius* from the Eocene of Wyoming (Conrad, 2005, 2008) and *Merkurosaurus ornatus* from the Miocene of the Czech Republic (Klembara, 2008). These are the only included taxa that I scored entirely from the literature. I also included three anguids—the diploglossine *Celestus enneagrammus* (part of the clade sister to all other diploglossines; Macey et al., 1999), the anguine *Ophisaurus ventralis*, and the gerrhonotine *Elgaria multicarinata*. I excluded the problematic glyptosaurs (see Conrad, 2005, 2008) and *Anniella* (Wiens and Slingluff, 2001; Conrad, 2005, 2008). Within Varanidae, *L. borneensis* and the monitor lizard species *Varanus niloticus* and

Varanus exanthematicus were used (Fuller et al., 1998; Ast, 2001; Pianka and King, 2004). Helodermatidae is scored as a composite taxon. *Heloderma suspectum* suffices for scoring most characters of this clade. However, for two characters (96 and 97), the derived nature of *H. suspectum* affected the resolution of xenosaur phylogeny. The anterior (frontal and pre-orbital) skull roof osteoderms of extant *Heloderma* are highly domed, but those of *Primaderma nessovi* Nydam 2000, *Gobiderma pulchra* Borsuk-Bialynicka 1984, and *Eurheloderma gallicum*, primitive taxa on the stem of *Heloderma*, are flat and plate-like (Hoffstetter, 1957; Gao and Norell, 2000; Nydam, 2000). The domed state of the extant taxa rendered ambiguous the nature of the flattened skull roof osteoderms of *R. rugosus*, whereas scoring the primitive state for the helodermatid lineage results in a most parsimonious hypothesis that *R. rugosus* is primitive relative to *Xenosaurus* + *E. lancensis* and pulls it out of a trichotomy with those taxa. In these cases, as noted, scoring was performed as though the ancestral states for the entire helodermatid lineage were being considered. When greater access to the skeletal material of these stem taxa is possible, they should be broken out and scored separately.

Outside of Anguimorpha. One non-anguimorph was used as an outgroup. A possible choice according to Conrad (2005) would be *C. intermedia* (Gao and Norell, 1998, 2000). However, *C. intermedia* is not universally agreed to lie outside of Anguimorpha and still cannot be as thoroughly scored as an extant taxon. Because of the overwhelming molecular scale support for an Anguimorpha + Iguania clade, I chose the iguanian *Pristidactylus torquatus* as my additional outgroup. No previous gross anatomical phylogenetic analysis has used this topology.

Variation

The assessment of intraspecies variation, including but not limited to ontogenetic

TABLE 1. CHARACTER MATRIX FOR PHYLOGENETIC ANALYSIS OF *XENOSAURUS* AND ITS FOSSIL RELATIVE.

Xenosaurus spp.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
serratus	2	0	1	?	0	?	2	3	1	0	1	0	0	?	0	0	0	?	1	?	2	1	0	1	2	0	0	0	?	?	?
rugosus	2	?	?	?	?	?	?	?	1	?	1	?	?	?	?	?	?	?	1	?	2	?	?	1	2	?	?	?	?	?	?
lancensis	1	?	?	?	?	?	?	?	1	?	1	?	?	?	?	?	?	?	1	?	?	?	?	1	?	?	?	?	?	?	?
newmanorum	2	1	1	1	0	1	2	4	2	1	1	0	1	1	0	1	1	1	1	0	4	2	1	1	2	1	0	1	2	2	1
platyceps	2	1	1	1	0	1	2	4	2	1	2	0	1	1	1	1	1	1	1	1	4	2	1	1	2	0	1	0	2	2	1
agrenon	2	1	1	1	0	1	2	4	2	1	2	1	0	1	0	1	1	0	1	1	3	1	1	1	2	1	1	0	1	2	1
rectocollaris	2	1	1	1	0	1	2	4	2	1	2	1	0	1	0	1	1	0	1	1	3	1	1	1	2	1	1	0	1	2	1
rachhami	2	1	1	1	1	1	2	4	2	1	2	1	0	1	1	1	1	0	1	1	3	1	1	1	2	1	1	0	1	2	1
grandis	2	1	1	1	1	1	2	4	2	1	2	1	0	?	0	0	1	0	0	2	3	1	1	1	2	?	1	0	1	2	1
ornatus	0	0	1	?	0	1	0	?	0	1	2	?	0	?	0	0	1	?	0	2	2	1	1	1	0	0	0	0	2	2	?
ammoskius	0	0	?	?	0	?	0	0	0	0	0	?	0	0	0	?	1	0	0	2	2	0	0	0	2	0	1	?	2	2	0
crocodilurus	0	0	?	?	1	1	?	0	0	0	0	?	0	0	0	?	0	0	0	2	2	1	0	0	0	0	1	?	2	2	0
multicarinata	?	0	?	0	0	?	1	0	0	0	0	?	0	0	0	1	0	0	0	0	1	0	0	0	2	?	0	?	1	1	0
ventralis	?	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	0	0	0	1	0	0	0	1	2	0	0	?	2	0	0
enneagrammus	?	0	0	0	0	0	0	0	0	0	0	?	0	0	1	1	0	0	0	2	0	0	0	0	2	0	0	?	2	2	0
suspectum	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	0	0	0	1	4	0	0	1	2	0	0	?	2	1	0
borneensis	0	0	1	0	0	1	1	0	0	0	0	?	0	1	0	0	0	?	0	0	0	0	0	0	3	1	0	?	0	0	0
niloticus	0	0	0	0	0	1	1	0	0	0	0	?	0	1	0	0	0	?	0	0	1	0	0	0	2	0	0	?	1	0	0
exanthematicus	0	0	0	0	0	0	0	0	0	0	0	?	0	1	0	0	0	?	0	0	1	0	0	0	2	0	0	?	0	0	0
torquatus	?	0	0	1	0	0	0	0	0	0	0	?	0	1	0	0	0	?	0	1	2	0	0	0	0	0	1	0	2	1	0

Xenosaurus spp.	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62
serratus	?	?	?	?	?	?	?	?	?	?	?	2	1	0	1	?	0	0	1	1	1	1	1	2	4	0	0	1	2	3	4
rugosus	?	?	?	?	?	?	?	?	?	?	?	0	?	0	0	?	?	0	0	1	2	1	0	3	4	0	1	1	1	1	2
lancensis	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	0	0	1	2	?	0	?	?	0	?	?	?	?	3
newmanorum	1	1	1	1	1	1	0	1	0	1	1	3	1	0	1	1	0	1	0	1	2	1	0	2	5	1	1	0	0	1	4
platyceps	1	1	1	1	0	1	1	0	0	1	0	3	1	0	0	1	0	0	0	1	2	1	1	2	3	1	1	1	1	2	4
agrenon	1	1	1	1	0	2	1	1	1	0	0	1	1	0	2	1	0	0	0	1	2	1	1	2	1	1	1	1	0	1	4
rectocollaris	1	1	1	1	1	2	1	0	0	0	0	1	1	0	2	1	0	0	0	1	2	1	1	2	2	1	2	1	2	1	4
rachhami	1	1	1	1	1	2	1	0	0	0	0	1	1	0	1	1	0	0	0	1	2	1	1	2	4	0	1	1	1	1	4
grandis	1	1	1	1	1	2	1	0	0	0	0	1	1	1	1	0	0	1	0	1	2	1	1	1	3	3	1	1	1	1	4
ornatus	?	1	1	1	1	2	?	0	?	1	?	0	1	?	1	1	1	1	0	1	2	1	0	2	?	0	0	1	1	0	0
ammoskius	?	1	1	1	?	0	?	0	?	1	0	2	1	0	0	0	1	1	0	1	2	0	0	1	2	0	1	0	0	0	0
crocodilurus	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	1	0	0	0	0	2	0	0	2	2	0	0	0	0	0	0
multicarinata	1	0	0	0	0	0	0	0	0	0	0	2	1	1	0	1	1	1	0	1	2	0	0	2	4	0	0	0	0	0	1
ventralis	1	0	0	0	0	0	0	0	0	0	0	3	0	0	1	1	1	0	0	0	0	0	0	4	6	0	0	0	0	0	0
enneagrammus	1	0	0	0	0	0	0	0	0	0	0	3	0	0	0	1	0	1	0	0	0	0	0	3	2	0	0	0	0	0	0
suspectum	1	1	0	0	0	0	0	1	0	0	0	3	1	0	1	0	0	0	0	1	1	0	0	3	4	0	0	0	1	1	4
borneensis	1	0	0	0	0	0	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	5	6	0	0	0	1	1	0
niloticus	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	1	0	0	3	0	1	0	0	0	1	0
exanthematicus	0	0	0	0	?	0	?	0	0	0	0	0	1	1	0	0	?	0	0	0	0	0	0	2	0	0	0	0	0	0	0
torquatus	0	0	0	0	?	0	?	0	?	0	0	0	0	1	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	2	0

TABLE 1. CONTINUED.

Xenosaurus spp.	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93
serratus	0	5	0	1	1	2	2	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0
rugosus	1	7	0	1	1	1	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
lancensis	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0
newmanorum	0	B	1	1	1	3	1	0	0	1	1	1	2	2	0	1	1	0	0	?	0	1	1	1	2	2	0	0	1	0	1
platyceps	0	B	0	1	1	3	1	0	0	1	1	1	2	2	0	2	1	0	1	0	1	?	2	1	2	1	1	0	1	1	1
agrenon	0	9	0	1	1	0	1	0	0	1	0	1	1	0	1	2	0	0	0	0	1	0	1	1	2	1	0	0	1	1	1
rectocollaris	0	B	0	1	1	0	1	0	0	1	0	1	1	1	1	2	0	1	0	0	1	0	1	1	1	0	0	0	1	1	1
rackhami	0	9	1	1	1	0	1	0	0	1	0	2	1	1	1	2	0	1	1	1	?	0	1	1	4	4	0	1	1	1	1
grandis	0	9	1	1	1	0	0	1	0	1	0	2	1	1	1	2	0	0	1	1	?	0	1	1	1	1	0	1	1	1	1
ornatus	1	9	?	?	1	0	?	1	1	1	1	2	2	1	1	2	1	0	?	1	0	1	2	1	2	?	0	0	1	1	0
anmoskius	1	8	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	5	0	0	1	1	1
crocodilurus	1	5	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	?	0	0	0	0	0	2	5	0	0	1	1	?
multicarinata	0	A	1	0	0	0	1	0	0	0	0	2	0	2	1	0	0	0	?	0	1	0	1	0	2	5	0	0	0	0	?
ventralis	0	9	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	0	0	5	0	0	0	0	?
enneagrammus	0	6	0	0	0	0	0	0	0	0	0	1	0	2	2	2	0	0	0	0	0	0	0	0	2	5	1	0	0	?	?
suspectum	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	?	?
borneensis	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?
niloticus	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	1	1	0	0	?	?
exanthematicus	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	2	0	0	0	0	0	?	0
torquatus	0	9	0	0	1	1	0	0	0	0	1	0	0	0	0	0	?	?	?	0	0	0	0	0	0	5	0	0	1	1	1

	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124
serratus	2	0	1	3	2	1	1	1	0	0	0	1	1	1	2	?	?	?	?	1	1	?	?	?	?	?	?	?	?	0	2
rugosus	?	0	0	2	0	0	0	0	?	?	?	0	0	0	1	0	1	1	1	1	1	?	?	?	?	?	?	?	?	0	1
lancensis	?	0	1	3	0	0	1	0	?	?	?	1	0	0	0	?	3	0	0	1	1	1	3	0	0	0	?	?	?	0	?
newmanorum	2	1	1	3	1	1	1	0	0	0	1	1	0	0	1	2	2	3	0	1	1	0	0	1	0	0	0	1	1	0	2
platyceps	2	1	1	3	1	1	0	0	0	0	1	1	0	0	1	2	3	3	0	1	1	1	3	1	0	0	0	0	1	0	2
agrenon	2	0	1	3	1	0	0	0	0	0	1	1	0	0	1	2	2	2	0	1	0	1	3	0	0	0	0	1	0	0	2
rectocollaris	2	0	0	3	1	0	1	0	1	0	1	0	1	0	1	1	0	0	1	1	1	1	1	0	0	0	1	0	0	1	2
rackhami	2	0	0	3	1	1	0	1	1	1	1	1	1	0	1	1	2	1	1	1	1	2	2	0	0	0	0	1	0	0	2
grandis	2	0	1	3	1	1	0	0	1	1	1	1	1	0	1	1	2	1	1	1	0	1	1	0	0	0	0	1	0	0	2
ornatus	2	0	0	1	0	0	0	?	1	0	1	0	0	0	0	2	2	0	1	0	0	0	0	0	0	0	1	0	0	0	2
anmoskius	1	0	3	3	1	1	1	0	0	1	1	1	0	0	0	1	1	1	1	0	1	1	1	1	1	0	1	1	?	0	0
crocodilurus	0	0	0	1	1	0	0	?	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	?	0	1
multicarinata	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
ventralis	0	0	0	0	?	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
enneagrammus	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
suspectum	0	0	0	0	?	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
borneensis	0	0	0	0	?	0	1	1	1	1	1	1	1	0	1	1	2	1	0	1	1	0	0	0	0	1	1	0	?	0	0
niloticus	0	0	0	0	?	0	1	0	0	0	1	1	1	0	2	0	0	0	0	0	1	0	0	0	0	1	1	0	?	0	0
exanthematicus	0	?	1	3	?	?	0	1	0	0	1	1	1	0	2	0	0	0	?	0	0	0	0	0	0	1	1	0	?	0	0
torquatus	1	0	1	3	0	1	0	0	0	1	0	0	0	0	0	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0

TABLE 1. CONTINUED.

Xenosaurus spp.	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155
serratus	1	0	0	0	1	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
rugosus	0	0	0	1	1	1	1	2	0	?	?	?	?	?	0	0	0	0	0	1	1	?	?	?	?	?	?	?	?	?	?
lancensis	1	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	C	?	1	0	1	?	0	3	1
newmanorum	1	0	1	1	1	1	1	2	0	0	2	1	1	0	1	0	0	1	1	0	2	1	4	0	1	0	0	1	0	3	1
platyceps	1	0	1	1	1	1	1	2	0	0	0	1	1	0	1	0	1	1	0	0	2	1	3	2	2	0	1	0	0	2	1
agrenon	1	1	0	1	1	1	1	2	0	1	0	1	1	1	1	0	0	0	0	1	2	1	0	3	1	1	1	0	0	2	2
rectocollaris	1	1	0	1	1	1	0	2	0	1	0	1	1	1	1	1	0	0	0	1	2	1	0	3	1	1	1	0	0	1	2
rackhami	1	0	1	1	1	1	1	2	1	1	0	1	1	1	2	1	0	0	0	0	2	1	2	3	0	1	1	1	1	1	0
grandis	1	1	1	1	1	1	1	2	1	1	1	0	0	0	2	1	0	0	0	0	2	?	5	2	0	0	1	1	1	1	0
ornatus	?	?	1	?	?	?	0	2	1	1	1	0	0	0	2	2	1	1	1	0	2	1	5	4	0	0	1	1	1	1	0
ammoskius	?	?	0	0	0	0	0	1	1	0	2	1	1	1	2	0	0	0	0	0	0	0	6	4	0	0	2	0	0	0	2
crocodilurus	0	1	0	0	0	0	0	0	0	1	2	1	0	0	2	0	0	0	0	?	?	0	9	3	0	0	1	0	0	0	0
multicarinata	?	0	0	0	0	0	0	1	0	0	2	0	0	1	1	0	0	0	0	0	0	0	3	7	1	0	1	0	0	1	1
ventralis	?	0	0	0	1	0	0	1	0	0	2	0	0	0	0	0	0	0	0	1	0	0	7	7	1	0	0	0	0	1	1
enneagrammus	?	0	0	0	0	0	0	0	0	0	2	0	0	0	2	0	0	0	1	0	1	0	4	7	1	0	0	0	0	1	2
suspectum	1	1	0	1	1	0	0	0	0	0	2	0	0	1	2	0	0	0	0	0	0	0	3	4	1	0	0	0	0	2	0
borneensis	?	0	0	0	0	0	0	0	0	0	2	0	0	0	2	0	0	0	0	0	2	0	8	7	0	0	0	0	0	3	2
niloticus	?	0	0	0	0	0	0	0	1	1	2	0	1	1	0	0	0	0	0	0	0	0	4	5	0	0	1	0	0	1	1
exanthematicus	?	0	0	0	0	1	0	0	1	2	0	0	0	0	0	0	0	0	0	2	2	0	5	0	0	0	0	0	0	0	1
torquatus	?	0	0	0	1	0	0	1	0	0	2	0	0	0	?	0	0	0	0	0	0	0	1	5	0	0	1	1	0	3	2

	156	157	158	159	160	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185	186
serratus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1
rugosus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	1
lancensis	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1
newmanorum	0	1	1	1	1	1	1	1	1	1	0	2	1	3	0	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0	1
platyceps	0	1	1	0	0	1	1	1	1	0	2	2	1	3	0	0	1	2	0	1	1	0	1	0	0	1	2	1	0	0	1
agrenon	0	2	0	1	1	1	0	0	2	1	2	2	1	3	0	1	1	2	0	0	1	0	0	1	0	1	1	0	0	0	1
rectocollaris	0	2	0	1	1	1	0	0	2	0	2	2	1	3	0	0	1	2	0	0	0	1	1	1	1	1	2	1	0	0	1
rackhami	1	2	0	1	1	1	2	2	3	1	3	2	2	1	1	1	1	1	2	1	0	0	1	0	1	0	2	1	1	1	1
grandis	1	1	1	1	1	1	2	2	2	2	3	3	2	2	1	1	1	1	0	?	0	0	0	0	1	2	2	1	1	0	1
ornatus	0	1	?	1	1	1	2	2	2	0	3	3	2	2	0	1	1	1	0	0	?	0	?	0	1	2	2	0	0	0	1
ammoskius	0	?	0	1	0	0	1	2	0	0	1	1	1	3	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1
crocodilurus	0	0	1	0	0	0	1	1	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0
multicarinata	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	1	0	1	0	1	0	0	2	2	1	0	0	0
ventralis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	1	1	2	1	0	1	1
enneagrammus	1	1	0	0	0	0	0	0	2	0	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	2	1	0	1	1
suspectum	0	2	0	0	0	0	0	0	2	0	0	0	0	0	1	1	2	2	0	0	1	0	0	0	1	2	1	0	0	1	0
borneensis	1	0	0	0	1	0	1	2	3	1	0	0	0	1	1	1	2	2	0	0	1	0	0	0	1	0	1	0	0	1	1
niloticus	1	0	0	0	1	0	0	0	2	0	0	0	0	1	0	0	2	2	0	1	0	0	0	0	2	2	2	0	1	1	0
exanthematicus	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	2	1	0	0	0	0
torquatus	1	0	0	0	1	0	1	1	1	0	2	?	?	0	0	0	0	2	0	0	?	0	0	0	0	0	2	0	0	0	0

Tᴀʙʟᴇ 1. Cᴏɴᴛɪɴᴜᴇᴅ.

Xenosaurus spp.	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210	211	212	213	214	215	216	217
serratus	0	?	?	0	1	0	0	1	1	1	0	0	0	1	0	0	0	0	0	?	0	1	1	1	?	?	?	?	?	?	?
rugosus	0	?	?	1	0	0	1	0	1	1	0	0	0	0	?	0	0	1	1	0	0	0	0	1	1	1	1	1	1	0	?
lancensis	?	?	?	1	1	?	2	0	1	1	0	?	?	?	?	?	?	1	2	1	1	?	?	1	1	1	1	1	?	0	?
newmanorum	1	0	0	0	0	0	2	0	1	1	1	1	1	1	1	1	0	0	2	1	1	1	1	1	1	1	1	2	2	0	1
platyceps	1	0	0	0	0	0	3	0	0	0	0	0	0	1	1	1	0	1	2	0	1	1	1	1	1	1	1	2	2	0	1
agrenon	0	1	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	1	1	1	1	1	2	0	1	1
rectocollaris	0	0	0	0	1	0	2	0	0	0	0	1	0	0	0	0	0	0	2	0	0	1	1	1	2	1	1	2	2	1	0
rackhami	0	0	0	0	0	0	2	0	0	1	1	0	1	1	1	1	1	0	2	0	0	1	1	1	1	1	1	1	1	1	0
grandis	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	2	0	0	1	1	1	2	1	?	?	?	0	0
ornatus	0	?	?	0	0	?	1	0	2	0	0	1	1	1	1	0	0	1	2	0	0	1	0	0	2	1	0	0	0	0	2
ammoskius	?	?	?	0	?	0	1	0	2	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	3
crocodilurus	0	1	0	0	0	0	1	0	2	1	0	0	0	0	?	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	2
multicarinata	0	0	0	0	0	0	3	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3
ventralis	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	?	6
enneagrammus	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0
suspectum	0	1	1	0	0	0	0	0	2	0	0	1	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
borneensis	0	0	1	0	0	0	2	0	2	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	5
niloticus	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
exanthematicus	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1
torquatus	?	0	0	?	0	0	0	2	0	0	0	?	0	1	0	0	?	0	?	0	0	0	0	0	0	0	0	0	1	B	1

Xenosaurus spp.	218	219	220	221	222	223	224	225	226	227	228	229	230	231	232	233	234	235	236	237	238	239	240	241	242	243	244	245	246	247	248
serratus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
rugosus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?
lancensis	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	0	2	?	?	?	?	?	?	?	?	?	?	?	2	1	?
newmanorum	1	1	0	0	0	1	1	1	2	1	1	1	1	1	1	0	1	?	1	1	0	1	0	0	0	1	1	0	1	1	1
platyceps	1	1	0	2	1	0	1	0	2	1	1	1	1	1	0	0	0	?	0	0	1	0	0	0	1	0	0	0	1	1	?
agrenon	1	0	0	1	0	0	0	0	2	1	0	0	1	0	0	0	0	0	1	1	1	0	1	0	?	1	?	0	1	1	0
rectocollaris	1	0	0	1	1	0	0	0	2	1	1	1	1	1	0	0	0	?	0	1	0	0	0	0	0	0	0	0	1	1	2
rackhami	1	1	1	1	1	0	0	1	1	1	1	1	1	0	1	0	1	?	0	1	0	2	0	0	1	1	1	0	1	1	3
grandis	1	0	1	1	1	0	0	0	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1	1	1	1	0	1	1	3
ornatus	?	0	?	1	1	1	?	?	1	1	?	1	1	?	?	1	0	?	0	0	0	0	0	1	0	0	1	?	1	1	?
ammoskius	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	?	0	0	0	0	1	0	0	0	0	0	0	0	0
crocodilurus	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	?	0	0	0	0	1	0	0	0	1	0	3	3	3
multicarinata	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	3	1	3
ventralis	0	0	0	?	0	0	0	0	?	?	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	3
enneagrammus	1	1	0	1	1	0	1	2	2	2	1	1	1	1	1	1	1	?	1	1	0	2	0	0	1	1	0	1	1	1	2
suspectum	1	0	0	0	1	1	0	2	2	2	1	1	1	0	0	0	1	?	0	0	0	0	1	0	0	0	0	0	1	1	3
borneensis	0	0	0	2	1	0	0	2	2	2	0	0	1	1	1	1	0	?	0	0	1	0	1	0	0	1	1	1	0	0	3
niloticus	1	0	0	1	0	0	0	0	2	1	1	1	1	1	0	0	0	?	0	0	0	0	0	0	0	0	0	1	0	0	?
exanthematicus	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	1	1	?	0	1	1	0	0	0	0	0	0	0	1	0	?
torquatus	0	0	0	1	0	1	1	0	1	1	0	0	1	1	1	1	1	?	0	0	1	2	1	1	1	1	1	0	0	1	1

TABLE 1. CONTINUED.

Xenosaurus spp.	249	250	251	252	253	254	255	256	257	258	259	260	261	262	263	264	265	266	267	268	269	270	271	272	273	274
serratus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
rugosus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
lancensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
newmanorum	0	0	1	0	0	0	1	0	0	3	0	0	1	0	0	2	1	1	1	0	1	1	0	1	0	0
platyceps	0	0	1	0	0	1	1	1	0	4	0	1	1	1	1	2	?	2	0	1	0	1	0	1	0	0
agrenon	?	0	0	?	?	?	0	?	?	?	1	?	?	?	?	?	?	?	2	2	1	2	1	2	2	0
rectocollaris	3	1	0	1	1	0	0	1	1	2	1	?	?	?	?	4	2	1	2	2	1	2	0	2	0	0
rackhami	6	1	0	3	2	?	0	3	1	2	1	2	?	?	1	3	3	1	2	2	1	2	0	2	2	0
grandis	3	1	0	2	2	?	1	2	1	2	?	3	?	?	?	3	3	?	2	2	1	2	0	2	2	0
ornatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
ammoskius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
crocodilurus	2	1	0	0	2	0	0	2	0	1	1	2	?	?	1	1	2	0	2	1	1	2	0	2	1	0
multicarinata	4	0	0	0	0	0	0	0	0	3	1	0	?	?	?	?	?	1	0	0	0	0	0	2	0	−1
ventralis	3	0	0	0	0	1	0	0	0	3	1	0	?	?	?	?	?	?	0	0	0	0	0	0	0	−1
enneagrammus	3	0	0	0	0	0	1	0	0	3	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	−1
suspectum	5	0	1	4	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	−1
borneensis	6	0	0	4	?	?	?	1	?	2	?	?	0	?	0	1	0	?	?	?	1	3	0	0	0	−1
niloticus	?	?	?	4	?	?	?	?	?	?	?	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?
exanthematicus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	2	?	?	?	?	?	0
torquatus	?	?	?	?	?	?	4	4	?	0	3	3	?	?	?	4	3	?	2	2	0	0	0	0	0	0

variation, is an important but often overlooked aspect of character discovery for phylogenetic analysis (Barahona and Barbadillo, 1998; Wible, 2003; Bever, 2005, 2006, 2008). Large sample sizes representing a good sample of the populations of the species were not possible to obtain for all taxa here examined, but such samples were available for enough taxa to phylogenetically bracket several clades. Specifically, samples of 10 or more specimens, spanning most of postnatal ontogeny, were available for *V. exanthematicus*, *E. multicarinata*, *H. suspectum*, *X. platyceps*, and *X. grandis*. I also had a large sample of *X. rackhami* (see Supplementary Information), although very young individuals were lacking. When statements are made in the character descriptions regarding ontogenetic variation, they refer to the taxa listed above as being present as large samples or clades bracketed by them.

Observed variation is noted in the character descriptions. For most taxa scored, multiple specimens were available for examination (see specimen list in Supplementary Information). As might be expected, in general, sample sizes were low for the extinct taxa—one in the cases of *R. rugosus* (save for a small fragment of maxilla, UMMP 73565) and *B. ammoskius*. The weakest part of the extant ingroup in terms of variation assessment was the *X. agrenon* + *X. rectocollaris* clade. For each of these taxa, I had only a single skeletal specimen (but multiple wet specimens). However, I discovered multiple unique synapomorphies for the clade, and their position in my results is consistent, as mentioned above, with that recovered by other researchers using different sources of data from gross anatomy. In general, I was conservative in defining characters; most of the characters described in this work vary little within species for which multiple individuals were available. Any variation that was present is noted.

Another aspect of variation is the assessment of the relative ontogenetic age of the specimens examined, which affects the scoring of some characters. Within Squamata and more specifically Anguimorpha,
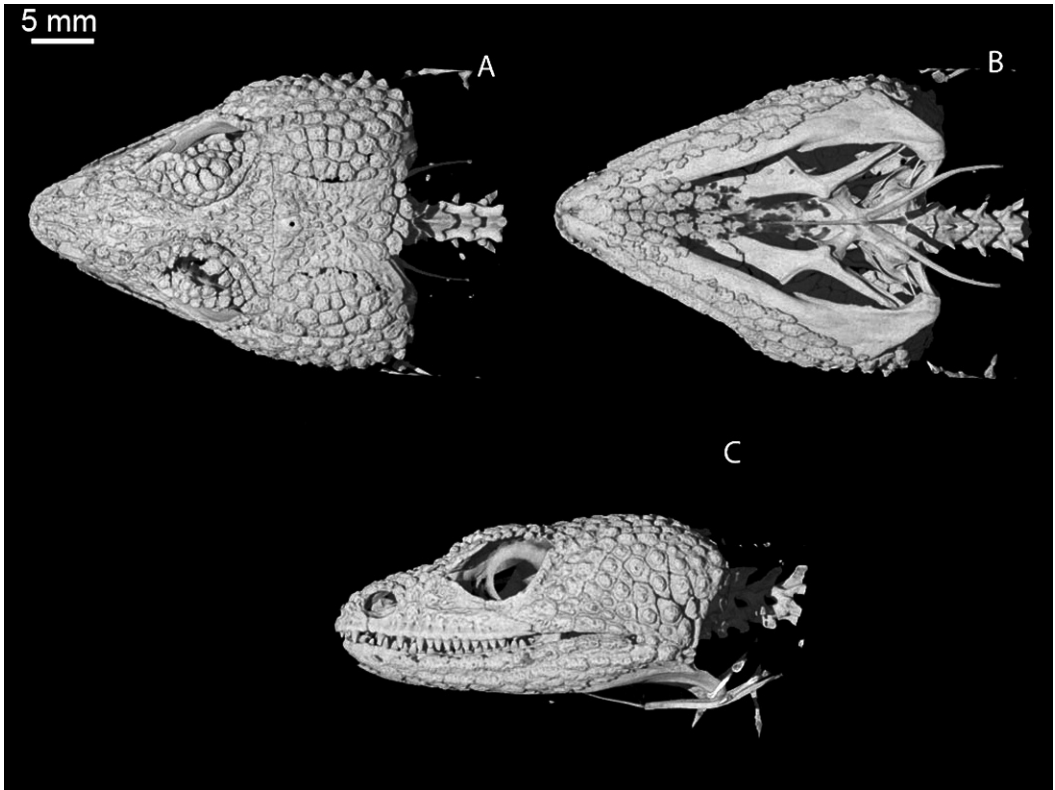
Figure 1.   Cranium of *Xenosaurus newmanorum*, CT scan of UMMZ 126056. A, Dorsal, anterior to the left. B, Ventral, anterior to the left. C, Left lateral, anterior to the left. Illustrates characters 114(1), 151(0), 184(0), 247(1), 248(1), 249(0), 251(0), 252(0), 255(1), 256(0), 257(0), 258(3), 259(0), 260(0), 261(1), 262(0), 263(0), 264(2).

several general ontogenetic trends can be bracketed as ancestral for the clade (Bever et al., 2005; Bhullar, 2006; Bhullar and Smith, 2008, for Anguimorpha). Ontogenetic age can thus be inferred for fossils and extant specimens without age data. *Merkurosaurus ornatus* specimens range from "subadults" with unfused frontals and proportionally shorter supratemporal processes of the parietal to large, mature adults with fused frontals, heavy osteodermal sculpturing, and long supratemporal processes (Klembara, 2008). The single known specimen of *B. ammoskius* appears to be a relatively mature adult based on the prominent osteodermal sculpturing on the skull roof and the proportionally great length of the supratemporal processes. The Yale *R.*

rugosus likewise has fully fused frontals and strong osteodermal sculpturing upon both the frontal and the maxillae, suggesting that it is a large, mature individual. Most specimens of *E. lancensis* have parietals that are heavily sculptured and rectangular in overall outline and are large compared with those of other xenosaurs, suggesting fairly advanced ontogenetic stages, but the frontals are unfused save in a few individuals, indicating immaturity (taking into account the cautionary notes regarding this taxon made earlier). Finally, the known specimens of *E. serratus* are approximately the same size as adults of other xenosaurs and bear heavy osteodermal sculpturing and generally "mature adult" proportions of the cranial elements.
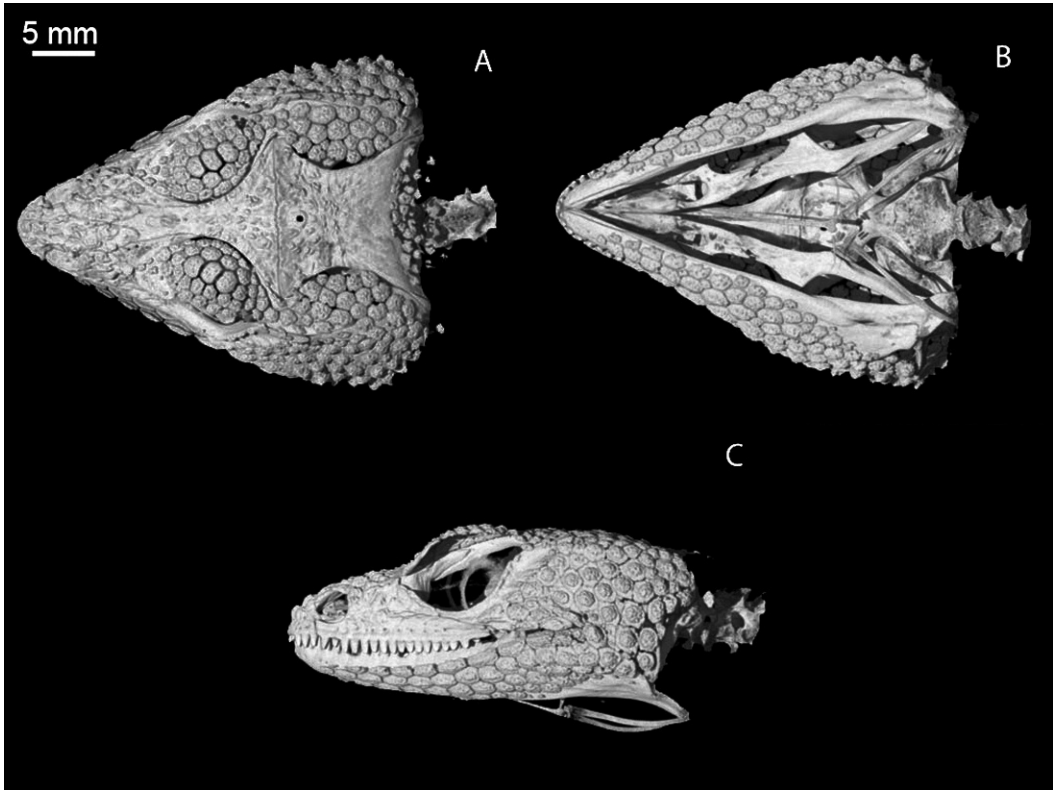
Figure 2.   Cranium of *Xenosaurus platyceps*, CT scan of UTA 23594, courtesy of Deep Scaly Project (2007; images from original data processing). A, Dorsal, anterior to the left. B, Ventral, anterior to the left. C, Left lateral, anterior to the left. Illustrates characters 26(1), 248(0), 250(0), 253(0), 254(1), 258(4), 260(1), 262(1), 263(1).

Analyses

Instead of a single preferred starting hypothesis, I use two, generating results referred to as Analysis 1 and Analysis 2 in the descriptions and discussions that follow. Starting conditions for Analysis 1 were inspired by phylogenies of Anguimorpha on the basis of nucleic acid structure, notably that of Townsend et al. (2004), which remains the most thorough and thoughtful analysis of these data. To generate Analysis 1, I used a constraint tree fixing extant taxa in the topology discussed previously for molecular studies (with an Anguidae + Helodermatidae clade instead of a Helodermatidae + *Xenosaurus* clade or a trichotomy) and leaving relationships among

xenosaurs, as well as among *Shinisaurus* and its extinct relatives, free to vary. To generate Analysis 2, I initially intended to constrain relationships based on a preferred gross anatomy–based phylogenetic hypothesis for Anguimorpha, but I found that my characters alone, with *P. torquatus* specified as the outgroup, generated a hypothesis identical to that of Conrad (2005, 2008), with one major difference: *Shinisaurus* and its extinct relatives are not sister to Varanoidea but are united with xenosaurs in the traditional Xenosauridae. This result obtained with overwhelming support even after the experimental addition of the characters uniting shinisaurs with varanoids in Conrad's analyses (2005, 2008; results not shown).
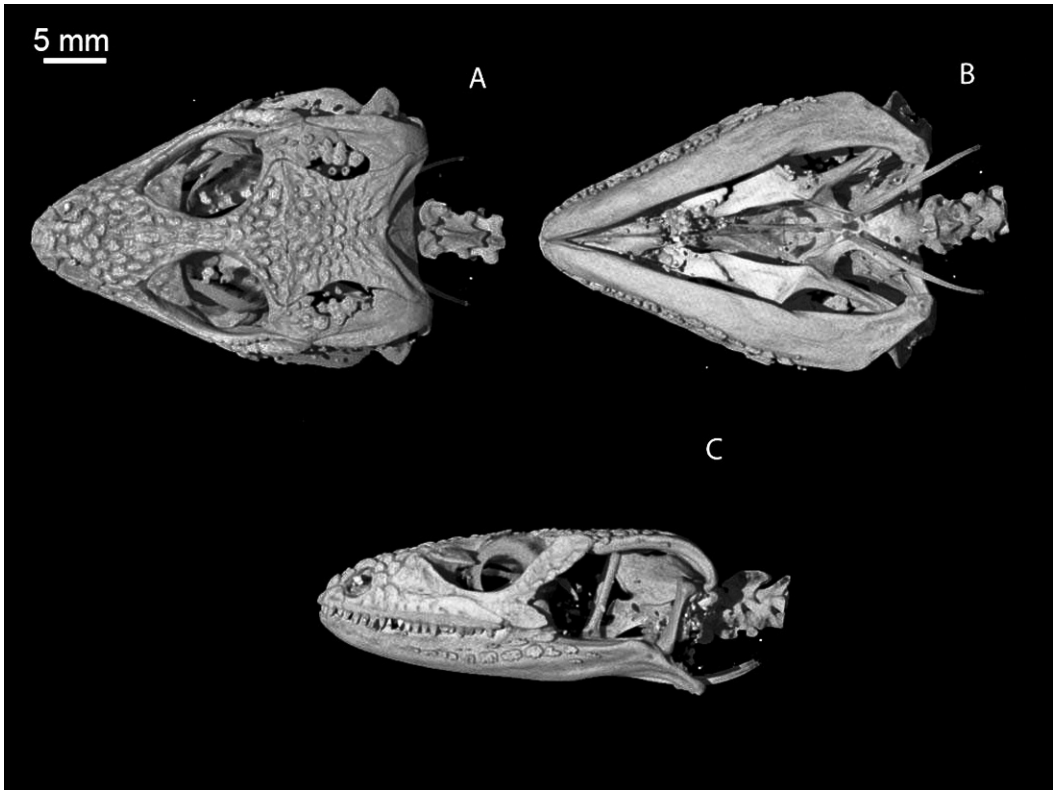
Figure 3.   Cranium of *Xenosaurus rackhami*, CT scan of UTEP 4555. A, Dorsal, anterior to the left. B, Ventral, anterior to the left. C, Left lateral, anterior to the left. Illustrates characters 28(0), 123(0), 133(1), 135(2), 249(6), 252(3), 256(3), 264(3).

Both analyses proceeded using the parsimony heuristic search option in PAUP* v. 4.0b10, with default options save that tree bisection and reconnection (TBR) branch swapping was enabled with 1,000 random addition sequences (Swofford, 2001). Bootstrap analyses were run with default settings save the parsimony settings noted above and the specification of 200 replicates. Each set of conditions yielded a single most parsimonious tree under all three character state optimization options, mercifully obviating calculations of consensus.

Ingroup relationships were identical in the results of Analysis 1 and Analysis 2. Because Analysis 2 was essentially unconstrained save for the specification of an uncontroversial outgroup, I was able to use a nonparametric Wilcoxon signed ranks test (Templeton test), automated through PAUP*, to assess whether the overall tree topologies (including the outgroups) were significantly different in terms of character support and evolution (Templeton, 1983; Larson, 1994).

Inapplicable and unknown data were both scored as ? under the default settings in PAUP* v. 4.0b10. Failing to distinguish between the two can be problematic because character states from applicable taxa can "bleed" to inapplicable taxa during optimization, but the alternative strategy of "absence coding" is also problematic (Strong and Lipscomb, 1999). Specifically, in such a case, inapplicability can be optimized as a synapomorphy when multiple taxa are scored as inapplicable for a single character. In several cases within this
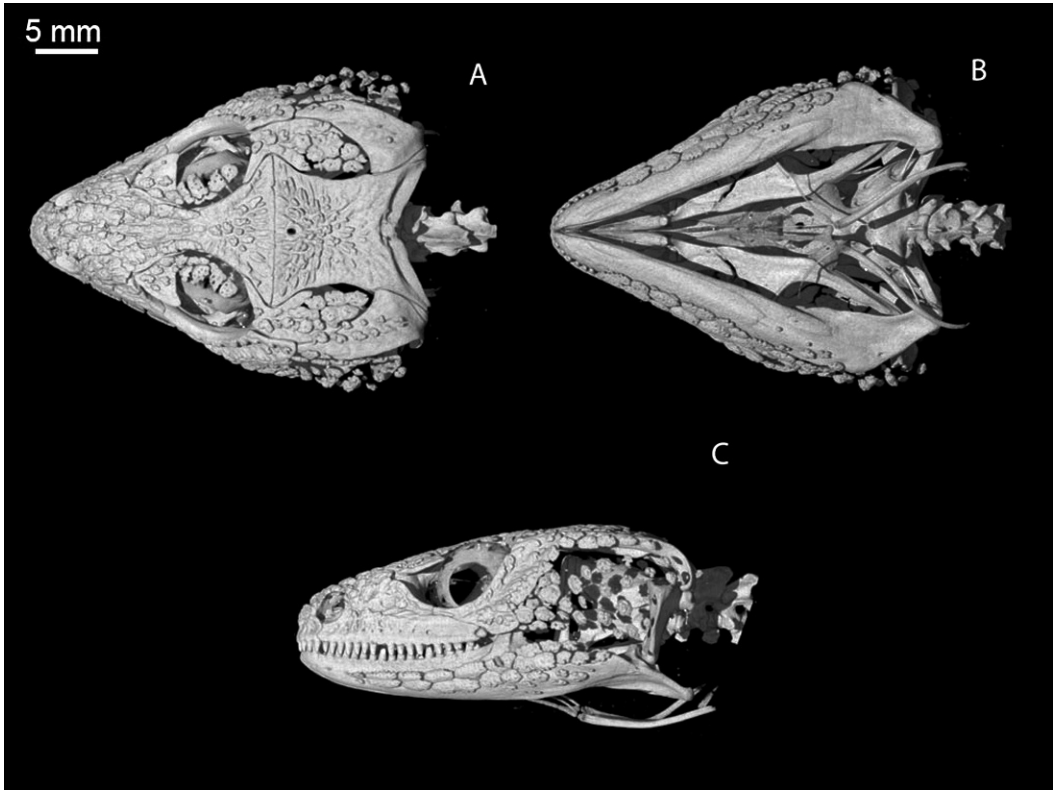
Figure 4.   Cranium of *Xenosaurus grandis*, CT scan of FMNH 123704, courtesy of Deep Scaly Project (2007; images from original data processing). A, Dorsal, anterior to the left. B, Ventral, anterior to the left. C, Left lateral, anterior to the left. Illustrates characters 135(1), 248(3), 250(1), 251(1), 252(2), 253(2), 256(2), 260(3).

analysis, this presence/absence scoring would be redundant with another character.

Multistate characters are discretizations of quantitative continua (counts or measurements) and were run as ordered, although the unordered setting was used to test the robusticity of the results. Mesquite v. 2.01 (Maddison and Maddison, 2008) was used to construct the character matrix and to trace character evolution. The process of discretizing continua necessarily leads to artificial bins, and the cutoffs for each character state are different to capture different levels of quantitative distinction among taxa. However, when more than two character states exist, the intervals are even. Even intervals prevent "cooking" of the data by selectively expanding some bins to encompass extra taxa. I first described most of the characters expressed as numerical values in less precise or more "qualitative" terms (all valid "qualitative" characters can be expressed in quantitative terms; see Wiens, 2001). The numerical values serve to give additional precision to these differences; essentially, after describing the differences in the states of a character in comparative or "qualitative" terms, I searched for a numerical expression of these differences. This process explains why the cutoffs for different values are not always "standard" intervals of 5 or 10, for instance (though, as noted, they are always regular intervals). The logical next step would be to attempt quantification of all characters and to score them using more advanced numer-
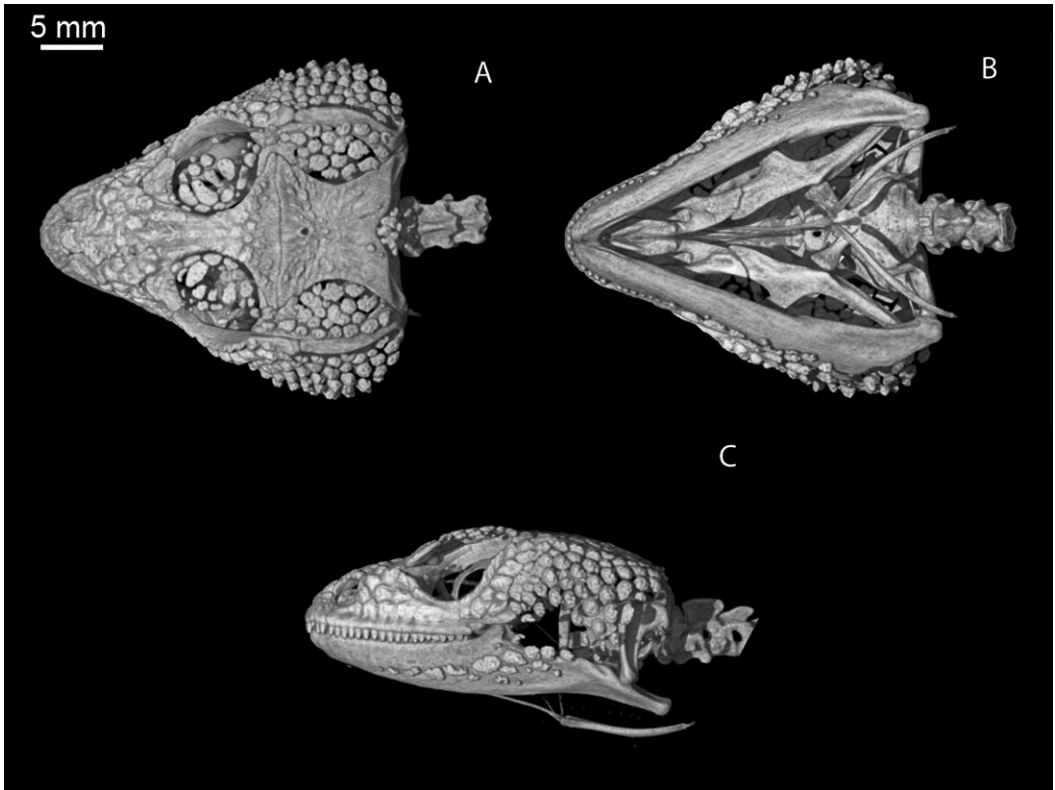
Figure 5. Cranium of *Xenosaurus rectocollaris*, CT scan of UF 51443. A, Dorsal, anterior to the left. B, Ventral, anterior to the left. C, Left lateral, anterior to the left. Illustrates characters 87(1), 123(1), 135(0), 165(2), 248(2), 249(3), 252(1), 253(1), 254(0), 255(0), 256(1), 257(1), 258(2), 259(1), 260(2), 264(4).

ical methods such as gap-weighting (Wiens, 2001). For the purposes of the present study, however, this analysis takes a middle ground.

Institutional Abbreviations

AMNH, American Museum of Natural History, New York; CAS, California Academy of Sciences, San Francisco; NAUQSP-JIM, Northern Arizona University Quaternary Sciences Program, Jim I. Mead collection (now housed at East Tennessee State University, Johnson City); FMNH, Field Museum of Natural History, Chicago; MCZ, Harvard Museum of Comparative Zoology, Cambridge; MVZ, Museum of Vertebrate Zoology, The University of California at Berkeley; TMM, Vertebrate Paleontology Laboratory, Texas Natural Science Center, The University of Texas at Austin; UF, Florida Museum of Natural History, Gainsville; TNHC, Texas Natural History Collections, The University of Texas at Austin; UMMZ, University of Michigan Museum of Zoology, Ann Arbor; USNM, National Museum of Natural History, Washington, DC; UTA, The University of Texas at Arlington Herpetological Collections, Arlington; UTEP, The University of Texas at El Paso Natural History Collections, El Paso; YPM, Yale Peabody Museum of Natural History, New Haven, Connecticut.

CHARACTER DESCRIPTIONS

Extended descriptions of characters and their distribution are contained in the electronic supplementary material. All char-

Figure 6.   Analysis 1 tree with bootstrap values greater than 50%.

acters refer to the condition in relatively large "adult" individuals, except where noted. Measurements are given to define some character states; most states, however, are illustrated, and the figures should be used as primary guides in scoring specimens. Intraspecific variation was accounted for by measurements of additional individuals and by simple visual comparison when possible. Where angles to a plane or an edge are given, the acute component is provided.

Comments on variation follow the character descriptions when variation that would affect scoring was evident. Given the low sample sizes of some of the taxa included in this study, the comments are certainly incomplete. An intensive study of variation in the characters used in this study is warranted but beyond the scope of the current work.

Description of the evolution of characters references both terminal taxa and clades that are supported by both resultant phylogenetic hypotheses (Figs. 6, 7), i.e., Anguimorpha, Anguidae, Varanidae, *S. crocodilurus* + *B. ammoskius* + *M. ornatus*, and all subclades within the clade *Xenosaurus* + *E. serratus*. *Varanus exanthematicus* + *Varanus niloticus* is referred to as *Varanus* where scorings do not differ in *Varanus salvator*, a taxon on the other branch from the basal split of *Varanus* (Fuller et al., 1998; Ast, 2001). *Bahndwivici ammoskius* was scored based on the description by Conrad (2006), and *M. ornatus* from that by Klembara (2008).

When character states are identified as synapomorphies of various clades, these statements are to be understood given the limitations of the taxon sampling for this study;

Figure 7.   Analysis 2 tree with bootstrap values greater than 50%.

thus, most stated synapomorphies of clades outside of *Xenosaurus* and its stem are likely to represent synapomorphies of more inclusive clades or may not be valid with the inclusion of the vast array of additional extant and extinct taxa within Anguimorpha (Conrad et al., 2011). Most characters are new; if a version of the character appeared in a previous analysis, the original analysis is cited parenthetically after the short description. The only characters that appeared in some form in previous analyses are 62, 91, 117, 124, 134, 145, 149, 189, 218, 224, 231, 246, and 272. Of those, only 91, 149, and 189 are essentially unmodified. The full taxon–character matrix is depicted in Table 1.

Dentition, General

1. Dentition: Tooth form (0) entirely unicuspid with pointed apices (Fig. 8A); (1) chisel-shaped (see Gao and Fox, 1996); (2) chisel-shaped, some bicuspidity (Fig. 8B).

Variation. Considerable ontogenetic variation occurs in tooth form. Bicuspidity develops during postnatal ontogeny in *Xenosaurus* and in Anguidae. However, whereas early (postnatal)-stage anguid teeth are nearly conical, in early-stage *Xenosaurus,* the chisel shape already obtains. The teeth of iguanians in general do not undergo a unicuspid-to-multicuspid transition during postnatal ontogeny, although the extremity of development of the cusps may increase with ontogenetic age. Moreover, in no observed taxon do the teeth progress during ontogeny from multicuspid to unicuspid. Thus, the fossils with bicuspid teeth *R. rugosus*
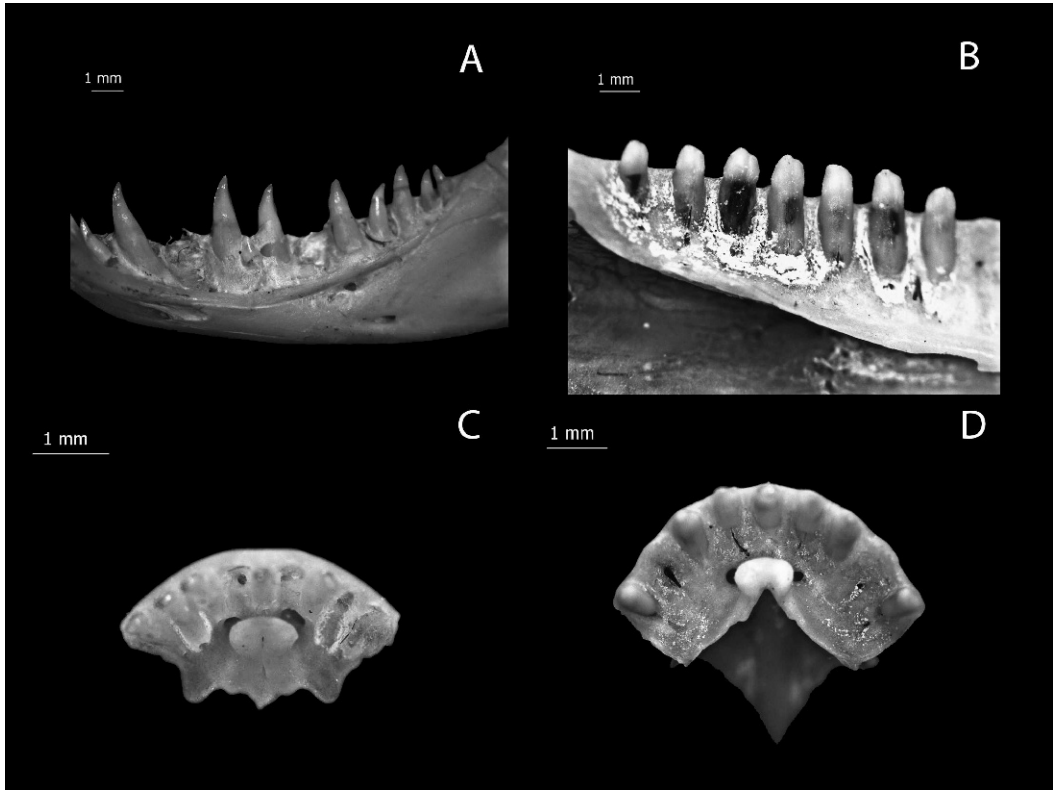
Figure 8.   A, Right dentary of *Shinisaurus crocodilurus* MVZ 204291, medial, anterior to the left. Illustrates character 1(0). B, Left dentary of *Xenosaurus newmanorum* uncatalogued NAUQSP-JIM specimen, medial, anterior to the right. Illustrates character 1(2). C, Premaxilla of *Elgaria multicarinata* TMM-M 8993, ventral, anterior to the top. Illustrates characters 2(0), 14(0). D, Premaxilla of *Xenosaurus newmanorum* uncatalogued NAUQSP-JIM specimen, ventral, anterior to the top. Illustrates characters 2(1), 14(1).

and *E. serratus* are scored as such and the inferred late ontogenetic stages of the fossil shinisaurs are beyond those at which the transition from unicuspid to multicuspid occurs in any observed extant specimen. Little variation occurs across broad ontogenetic stages in the general form of the teeth.

Evolution. Under both phylogenetic analyses, state (0), unicuspid teeth, is plesiomorphic within Anguimorpha as suggested by Gauthier (1982). Furthermore, under most hypotheses for the placement of Anguimorpha that have been suggested, having unicuspid teeth is a synapomorphy along the angui-

morph stem. If *C. intermedia* is on the anguimorph stem as suggested by Conrad (2005) and if the blunt, multicuspid state of the teeth of that taxon (Gao and Norell, 1998) is homologous to that of most other Scleroglossa, then this synapomorphy can be constrained to the internode between *C. intermedia* and Anguimorpha. However, various Mesozoic squamates with unicuspid teeth are placed by some phylogenetic analyses as a sister clade to all other Scleroglossa (Evans et al., 2005; but see Conrad, 2008), potentially complicating the optimization of unicuspidity. The chisel shape of the tooth crowns is a synapomorphy of

Xenosaurus and its fossil relatives. The presence of chisel-shaped teeth without bicuspidity in *E. lancensis* is either a primitive character of that taxon with bicuspidity a synapomorphy of *Xenosaurus* and an autapomorphy of *R. rugosus*, or the chisel-shaped state lacking bicuspidity is an autapomorphy of *E. lancensis* with the bicuspid chisel-shaped morphology as a synapomorphy of *Xenosaurus + Retes rugosus*.

Premaxilla

The premaxilla is unknown for *R. rugosus* and *E. lancensis*.

2. Premaxilla: Curvature of rostral arc in horizontal plane (0) relatively broad (Fig. 8C); (1) relatively acute (Fig. 8D).

    Variation. The premaxillae of most taxa become slightly less acute during ontogeny, but even early neonates of non-xenosaurs do not show the acute morphologies of adult *Xenosaurus*.

    Evolution. Acute curvature is a synapomorphy of *Xenosaurus* under both analyses.

3. Premaxilla: Height of dentigerous arc at suture of dermal surface to lateral (dermal) surface of maxilla: (0) dorsoventrally short, about one-fifth or less of mediolateral width between contralateral sutures (Fig. 9A); (1) tall, about one quarter or more of mediolateral width between contralateral sutures (Fig. 9B).

    Evolution. Under Analysis 1, two alternative hypotheses of character evolution each require three steps. In the first hypothesis of character evolution, the proportional tallness of the dentigerous arc is a synapomorphy of Anguimorpha. The shortness of the dentigerous arc is then a synapomorphy of Anguidae + Helodermatidae and of *Varanus*. In the second hypothesis of character evolution, relative tallness is independently a synapomorphy of *Xe-*

nosaurus + E. serratus, *S. crocodilurus + M. ornatus*, and *L. borneensis*. Under Analysis 2, relative tallness is a synapomorphy of Xenosauridae, independently of *L. borneensis*.

4. Premaxilla: Angle to the horizontal in transverse plane of lateral edges of rostral body connecting portion (0) low, 40° or lower (Fig. 9A); (1) high, greater than 40° (Fig. 9C).

    Evolution. Taking into account the relatively vertical condition in *P. torquatus* and the wide distribution of that condition in other non-anguimorph Squamata and sphenodontians (Evans, 1980; Fraser, 1982; Whiteside, 1986), a low angle to the horizontal of the lateral edges is a synapomorphy of Anguimorpha under both analyses. According to Analysis 1, a high angle to the horizontal within Aguimorpha is independently a synapomorphy of *E. serratus + Xenosaurus* and of *S. crocodilurus + M. ornatus*. According to Analysis 2, a high angle to the horizontal is a synapomorphy of Xenosauridae.

5. Premaxilla: Dorsolateral angle of dentigerous arc (0) formed by meeting of relatively straight edges, not produced into wedge (Fig. 9A); (1) produced into small wedge (Fig. 9B).

    Variation. The degree of development of the produced wedges varies within broad ontogenetic stages of *X. rackhami* and *X. grandis* but is always greater than that of the taxa scored as (0).

    Evolution. Under both analyses, production into wedges is a synapomorphy of *X. grandis + X. rackhami* and of *S. crocodilurus + M. ornatus*.

6. Premaxilla: Major premaxillary ethmoid canals (0) partially or completely bounded by connective tissue only, not fully surrounded by ossified premaxilla (Fig. 9D, left side); (1) bony, surrounded by ossified premaxilla (Fig. 9D, right side).
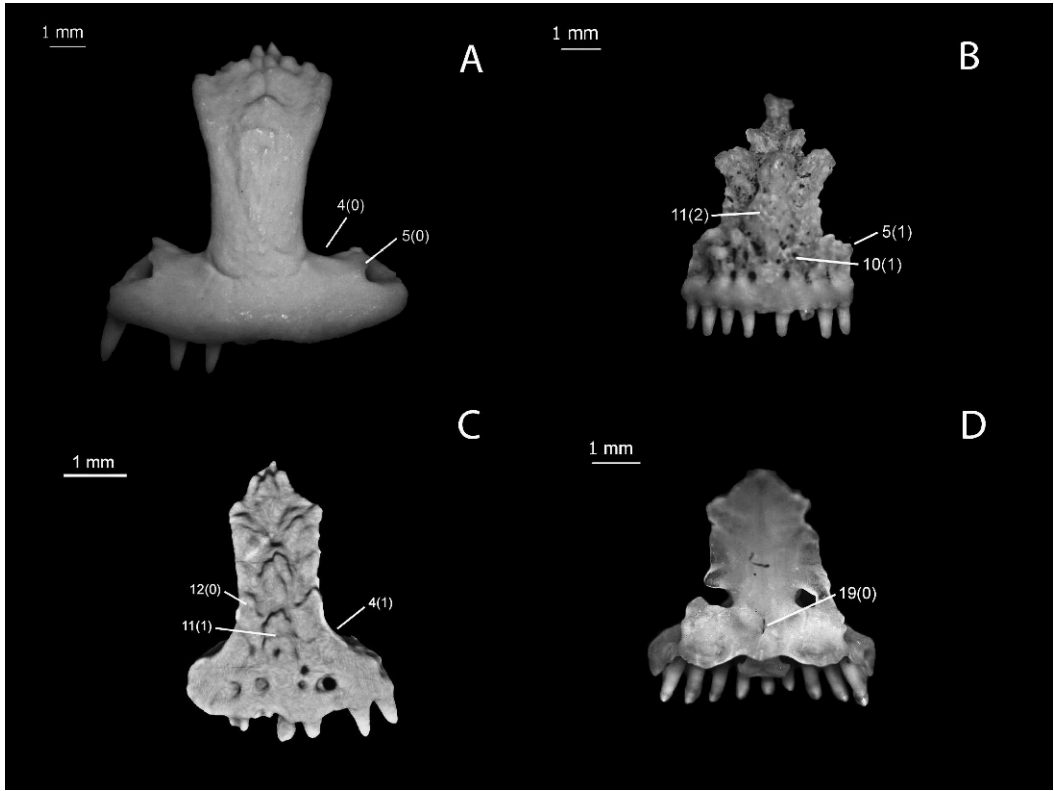
Figure 9.   A, Premaxilla of *Heloderma suspectum* TMM-M 9001, anterior. Illustrates characters 3(0), 4(0), 5(0), 7(0), 8(0), 9(0), 21(0). B, Premaxilla of *Xenosaurus grandis* NAUQSP-JIM 1460, anterior. Illustrates characters 3(1), 5(1), 7(2), 9(2), 10(1), 11(2), 12(1). C, Premaxilla of *Exostinus serratus*, CT scan of USNM v16565, anterior. Illustrates characters 4(1), 8(3), 9(1), 11(1), 12(0), 13(0). D, Premaxilla of *Elgaria multicarinata* TMM-M 8993, posterior. Illustrates characters 6(0), 6(1), 19(0).

Variation. The enclosure does not transform during postnatal ontogeny, but its does vary to some extent within taxa. Specifically, in one *S. crocodilurus* specimen examined, UF 71623, the enclosure is incomplete on one side. Enclosure is also present on one side in a single very large individual of *E. multicarinata*, TMM-M 8993 (Fig. 9D). In general, extremely large individuals, at least within anguimorphs, tend to develop extra flanges of bone that sometimes close previously open grooves for nerves and vasculature (personal observation).

Evolution. Under Analysis 1, enclosure of the medial ethmoidal canals is a synapomorphy of *Xenosaurus* + *E. serra-* *tus* and of *S. crocodilurus* + Varanidae. Under Analysis 2, enclosure is a synapomorphy of Xenosauridae and an autapomorphy of *L. borneensis*. The hypothesis that Varanidae and its stem ancestrally showed enclosure of the canals is complicated by the existence of taxa along the stems of the two varanoid lineages (and perhaps Varanoidea as a whole) from the Cretaceous of Mongolia and the early Paleogene of Europe, including *Estesia mongoliensis*, *Aiolosaurus oriens*, *G. pulchra*, and *Necrosaurus* sp., that do not appear to show the morphology (Estes, 1983; Borsuk-Bialynicka, 1984; Norell et al., 1992; Norell and Gao, 1997; Gao and Norell, 1998,
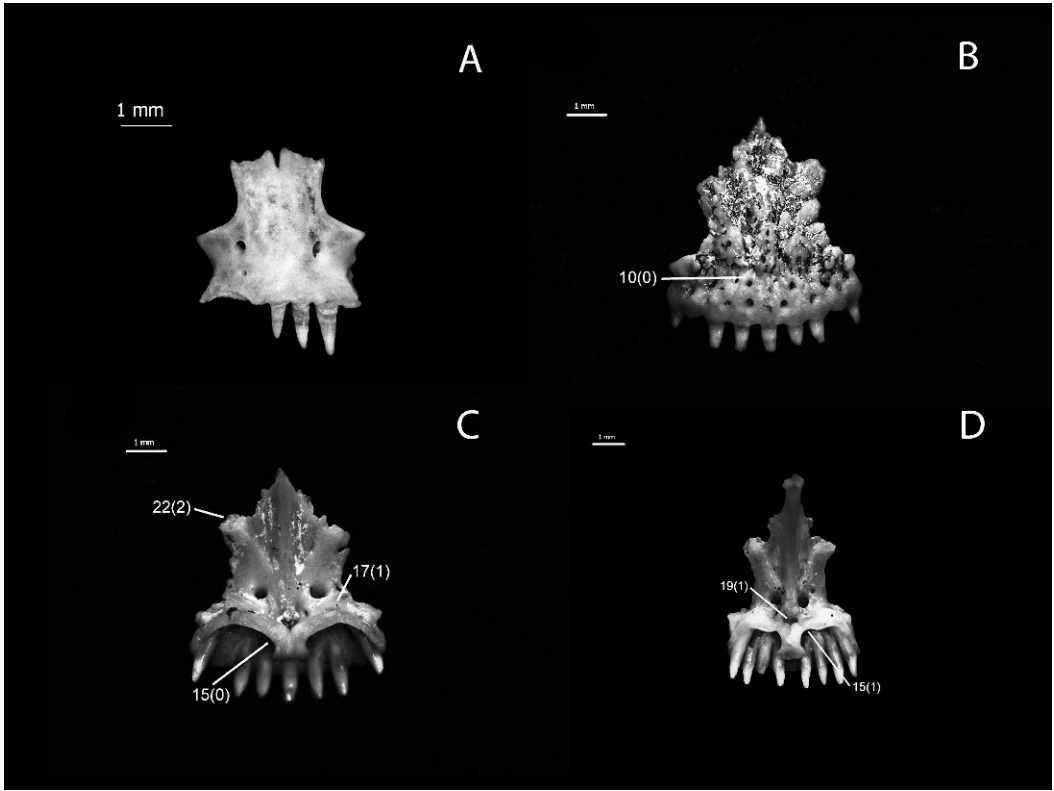
Figure 10.   A, Premaxilla of *Shinisaurus crocodilurus* UF 72805, anterior. Illustrates characters 7(1), 9(0), 11(0). B, Premaxilla of *Xenosaurus newmanorum* uncatalogued NAUQSP-JIM specimen, anterior. Illustrates characters 8(4), 10(0), 13(1). C, Premaxilla of *Xenosaurus newmanorum* uncatalogued NAUQSP-JIM specimen, posterior. Illustrates characters 15(0), 16(1), 17(1), 18(1), 22(2), 23(1). D, Premaxilla of *Xenosaurus grandis* NAUQSP-JIM 1460, posterior. Illustrates characters 15(1), 16(0), 18(0), 19(1).

2000). However, the issue is resolved if Varanoidea is not monophyletic, as in Analysis 1, and most or all of these taxa lie along the helodermatid stem, as was suggested for *E. mongoliensis* and *G. pulchra* (Norell and Gao, 1997; Gao and Norell, 1998; Conrad, 2004, 2005, 2008).

7. Premaxilla: Number of anterior foramina collinear with main row of maxillary labial foramina (0) none (Fig. 9A); (1) two (Fig. 10A); (2) more than two (Fig. 9B).

Variation. Other than the variation in the degree of enclosure noted for Character 6, the number of lower foramina does not vary in observed specimens of those taxa scored as possessing two (but see variation in upper foramina noted under Character 8). Slight variation occurs in the number of foramina within the species of *Xenosaurus*—from three to five, for example, in *X. rackhami*. No variation that would affect scoring was evident.

Evolution. Under both analyses, the possession of several lower anterior foramina is a synapomorphy of *E. serratus* + *X. grandis*. Under Analysis 1, the ancestral state for the entire group, for *Xenosaurus* + Anguidae, and for *S. crocodilurus* + Varanidae is ambiguous between no foramina and two foramina. The ancestral state for Anguidae + Helodermatidae is no foramina. Under

Analysis 2, a lack of foramina is ancestral for the entire group and for Anguimorpha and two foramina is a synapomorphy of Varanidae; the ancestral state for Xenosauridae is ambiguous between no foramina and two foramina.

8. Premaxilla: Number of anterior foramina dorsal to main row of maxillary labial foramina (0) none (Fig. 9A); (1) one; (2) two; (3) three (Fig. 9C); (4) four or more (Fig. 10B).

    Evolution. Under both analyses, the presence of one to three dorsal foramina is a synapomorphy of *E. serratus* + *Xenosaurus* and an increased number of such foramina is a further synapomorphy of *Xenosaurus*. Absence of foramina is an autapomorphy of *X. rectocollaris*.

9. Premaxilla: Anterior surface of premaxilla just dorsal to teeth (0) flush with remainder of anterior surface (Fig. 9A); (1) raised into supradental thickening (Fig. 9C); (2) supradental thickening pronounced (Fig. 9B).

    Variation. Little noticeable variation was evident, save that very young individuals of *Xenosaurus* have a slightly less pronounced thickening.

    Evolution. Under both analyses, the presence of the premaxillary supradental thickening is a synapomorphy of *Xenosaurus* + *E. serratus*. The presence of a more pronounced thickening is a synapomorphy of *Xenosaurus*.

10. Premaxilla: Surface ventral to rostral osteoderm (0) rugose (Fig. 10B); (1) bearing discrete fused osteoderms (Fig. 9B).

    Variation. Osteoderms fuse to the premaxilla during postnatal ontogeny, but are present in mid-sized and large specimens within the species that possess them.

    Evolution. Under both analyses, rugosity of the surface ventral to the rostral osteoderm is a possible synapomorphy of *E. serratus* + *Xenosaurus*; fusion of osteoderms in this region is a synapomorphy of the southern clade of *Xenosaurus*.

11. Premaxilla: Rostral osteoderm (0) absent (Fig. 10A); (1) oval and mediolaterally narrow (Fig. 9C); (2) rounded and mediolaterally wide (Fig. 9B).

    Variation. Other than the ontogenetic fusion of osteoderms to the premaxilla, I observed no intraspecific variation in this character.

    Evolution. Under both analyses, presence of a narrow rostral osteoderm is a synapomorphy of *E. serratus* + *Xenosaurus*. A rounded shape to the osteoderm is a synapomorphy of the southern clade of *Xenosaurus*.

12. Premaxilla: Distinct flanking osteoderms dorsolateral to rostral osteoderm (0) present (Fig. 9C); (1) absent (Fig. 9B).

    Evolution. Under both analyses, the presence of flanking osteoderms is a synapomorphy of *E. serratus* + *Xenosaurus*. Their absence is a synapomorphy of the southern clade of *Xenosaurus*.

13. Premaxilla: Rostral osteoderm and flanking osteoderms (when present) (0) smoothly domed or weakly keeled (Fig. 9C); (1) strongly keeled (Fig. 10B).

    Variation. The keel appears to form first during osteoderm development (unpublished observation), and as evidenced by juvenile *X. platyceps*, this character does not transform postnatally.

    Evolution. Under both analyses, a relatively smooth and rounded morphology is the primitive state for the rostral osteoderm, with strong keeling a synapomorphy of the northern clade of *Xenosaurus*.

14. Premaxilla: Medial edges of vomerine processes oriented in a horizontal plane

(0) more mediolaterally (Fig. 8C); (1) more anteroposteriorly (Fig. 8D).

Evolution. Under Analysis 1, mediolateral orientation is a synapomorphy of Anguidae and of *S. crocodilurus* (or a more inclusive shinisaur-related clade). Under Analysis 2, more ambiguity exists. With one possible hypothesis of character evolution, an anteroposterior orientation is ancestral, with a mediolateral orientation an autapomorphy of *S. crocodilurus*. A mediolateral orientation is then either a synapomorphy of Anguidae + Varanoidea with an anteroposterior orientation a synapomorphy of Varanidae, or a mediolateral orientation is a synapomorphy of Anguidae and an autapomorphy of Helodermatidae. The second hypothesis of character evolution is that a mediolateral orientation is ancestral. An anteroposterior orientation is thus an autapomorphy of *P. torquatus* and a synapomorphy of *E. serratus* + *Xenosaurus* on the one hand and Varanidae on the other.

15. Premaxilla: Medial edges of vomerine processes near midline convergence (0) straight, without dorsoventral bow (Fig. 10C); (1) with dorsoventral bow (Fig. 10D).

    Evolution. Under both analyses, the bowing or inflection is a synapomorphy of *X. rackhami* + *X. grandis*.

16. Premaxilla: Stalk of incisive process (0) relatively long, length similar to or greater than diameter (Fig. 10D); (1) relatively short, length shorter than diameter (Fig. 10C).

    Variation. Some variation does occur across ontogenetic stages within taxa; in particular, a few individuals of *X. rackhami* and *X. grandis* show shorter processes. However, the vast majority of specimens where adequate samples are available have incisive processes of approximately uniform relative length.

Evolution. Under both analyses, shortness of the stalk of the incisive process is a synapomorphy of the northern clade of *Xenosaurus* and an autapomorphy of *X. rectocollaris*. Under Analysis 1, shortness is a synapomorphy of Helodermatidae + Anguidae and an autapomorphy of *L. borneensis*. Under Analysis 2, shortness is a synapomorphy of Anguidae + Varanoidea. Within this clade, a longer morphology is a synapomorphy of *Varanus*.

17. Premaxilla: Accessory processes dorsal to vomerine processes (0) absent (Fig. 11A); (1) present (Fig. 10C).

    Evolution. Under both analyses, presence of the accessory dorsal processes is a synapomorphy of *Xenosaurus*.

18. Premaxilla: Accessory processes dorsal to vomerine processes (0) relatively short, nub-like (Fig. 10C); (1) relatively long and slender (Fig. 10D).

    Evolution. Under both analyses, relative length of the processes is a synapomorphy of the northern clade of *Xenosaurus*.

19. Premaxilla: Fossa for rostral process of nasal septum (0) relatively mediolaterally narrow (Fig. 9D); (1) relatively mediolaterally wide (Fig. 10D).

    Variation. Although the shape of the fossa varies somewhat among individuals, no variation so great as to affect the scoring of the character was evident.

    Evolution. Under both analyses, relatively great width of the fossa is a synapomorphy of *E. serratus* + *Xenosaurus*.

20. Premaxilla: Angle of rise of nasal process in sagittal plane (0) relatively low (Fig. 11B); (1) intermediate (Fig. 11C); (2) relatively great (Fig. 11D).

    Evolution. Under both analyses, a moderate angle is ancestral and a high angle is a synapomorphy of *S. crocodilurus* + *M. ornatus* and an autapomorphy of Helodermatidae. Also under both analyses, a low angle is a synapomorphy
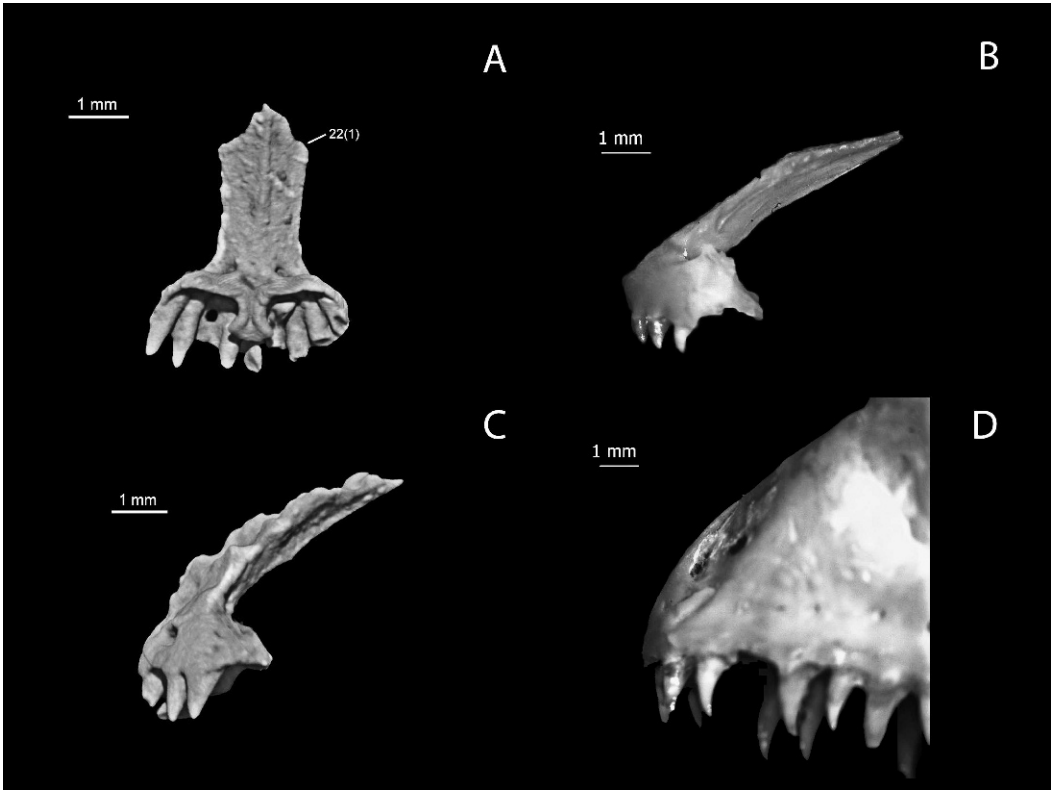
Figure 11.   A, Premaxilla of *Exostinus serratus*, CT scan of USNM v16565, posterior. Illustrates characters 17(0), 22(1), 23(0), 24(1). B, Premaxilla of *Elgaria multicarinata* TMM-M 8993, left lateral, anterior to the left. Illustrates character 20(0). C, Premaxilla of *Exostinus serratus*, CT scan of USNM v16565, left lateral, anterior to the left. Illustrates character 20(1). D, Rostrum of *Shinisaurus crocodilurus* MVZ 204291, left lateral, anterior to the left. Illustrates character 20(2).

of the northern clade of *Xenosaurus* and of *Varanus*. Under Analysis 1, a low angle is a synapomorphy of *E. multicarinata* + *O. ventralis*. Under Analysis 2, a low angle is either a synapomorphy of Anguidae with a moderate angle an autapomorphy of *C. enneagrammus* or an autapomorphy of *E. multicarinata* and of *O. ventralis*.

21. Premaxilla: Mediolateral width of nasal process at base (0) two to three tooth positions (Fig. 9A); (1) between four and five tooth positions (Fig. 12A); (2) five tooth positions (Fig. 11A); (3) between five and six tooth positions (Fig. 10D); (4) six or more tooth positions (Fig. 10C).

Variation. The values scored for this character are approximate; it can be difficult to determine precisely whether all or most of a tooth lies within the span of the nasal process. The character may need refining in the future. Nevertheless, at least comparatively, the scorings are sound.

Evolution. Under both analyses, a width of about five tooth positions is ancestral. This is largely a consequence of the state in *P. torquatus* and may seem unusual given the classical gross anatomy–based hypothesis of squamate phylogeny, in that many non-angui-morph scleroglossans have narrow nasal
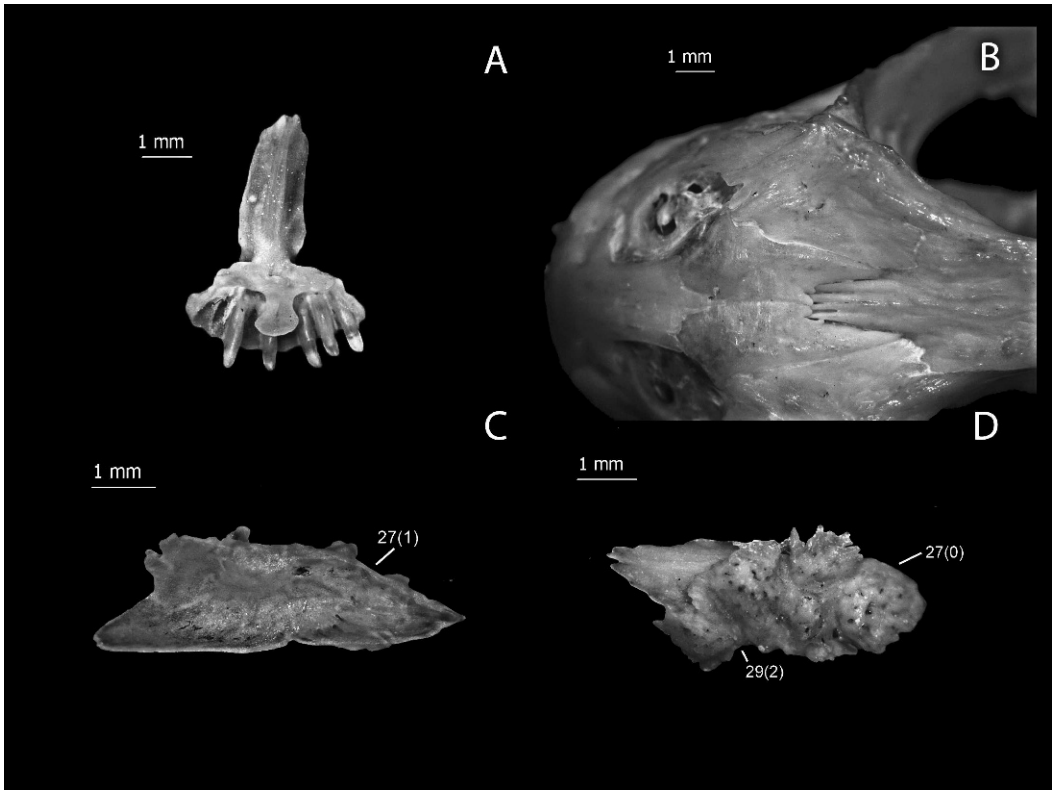
Figure 12.   A, Premaxilla of *Elgaria multicarinata* TMM-M 8958, posterior and slightly left lateral. Illustrates characters 21(1), 22(0), 24(0). B, Rostrum of *Shinisaurus crocodilurus* MVZ 204291, dorsal, anterior to the left. Illustrates characters 26(0), 67(0). C, Left nasal of *Xenosaurus grandis* NAUQSP-JIM 1460, ventral, anterior to the left. Illustrates character 27(0). D, Left nasal of *Xenosaurus platyceps* UF 45622, dorsal, anterior to the left. Illustrates characters 27(1), 28(1), 29(2).

processes. However, in support of the inference here presented, a relatively wide-based nasal process is shared by a host of primitive iguanians on the one hand (Polychrotinae, Corytophaninae, Hoplocercinae, *Leiolepis,* and *Uromastyx,* among others) and by *C. intermedia*, sometimes suggested to be the extinct sister taxon to Anguimorpha (Gao and Norell, 1998, 2000; Conrad, 2005, 2008). Under both analyses, a width of between five and six tooth positions is a synapomorphy of *Xenosaurus* and six or more is a synapomorphy of the northern clade of *Xenosaurus,* as well as an autapomorphy of *L. borneensis*. Under Analysis 1, a width of two to three tooth positions is a synapomorphy of Anguidae, and a width of between four and five tooth positions is an autapomorphy of *E. multicarinata*. A width of between four and five tooth positions is also a synapomorphy of *Varanus*, and a width of two to three an autapomorphy of *V. niloticus*. However, this result might be skewed by the unusual width of the snout of *V. exanthematicus*. Under Analysis 2, a width of between four and five tooth positions is a synapomorphy of Anguidae + Varanoidea; a width of two to three is a synapomorphy of *O. ventralis* + *C. enneagrammus* and an autapomorphy of both Helodermatidae and *V. niloticus*.

22. Premaxilla: Dorsolateral flare at contact with dermal surface of nasal (0) absent or minimal (Fig. 12A); (1) present with distinct dorsal wedge separated (Fig. 11A); (2) pronounced (Fig. 10C).

    Evolution. Under both analyses, a pronounced premaxillary flare is a synapomorphy of the northern clade of *Xenosaurus.* Under Analysis 1, the flaring morphology is a synapomorphy of *E. serratus* + *Xenosaurus.* Additionally, either the flare is a synapomorphy of *M. ornatus* + *S. crocodilurus* and no flare is an autapomorphy of *B. ammoskius,* or the flare is an autapomorphy of both *M. ornatus* and *S. crocodilurus.* Under Analysis 2, the flaring morphology is a synapomorphy of Xenosauridae, and the lack of a flare is an autapomorphy of *B. ammoskius.*

23. Premaxilla: Anterior portions of nasal facets (0) shallowly impressed (Fig. 11A); (1) deeply impressed (Fig. 10C).

    Evolution. Under both analyses, deep impression is a synapomorphy of *Xenosaurus* and an autapomorphy of *M. ornatus.*

24. Premaxilla: Keel between nasal facets (0) dorsoventrally extensive (Fig. 12A); (1) restricted to dorsal portion of nasal process (Fig. 11A).

    Evolution. Under Analysis 1, relatively great extent of the keel is unambiguously a synapomorphy of *E. multicarinata* + *O. ventralis.* At the initial split of the tree, the ancestral state is ambiguous. If the ancestral state is great extent, then restriction is either a synapomorphy of Anguimorpha with great extent an autapomorphy of Varanidae, or restriction is a synapomorphy of both Anguidae + *Xenosaurus* and *S. crocodilurus* + *M. ornatus.* If the ancestral state is restriction, then great extent is an autapomorphy of *P. torquatus* and a synapomorphy of Varanidae. Under Analysis 2, great extent is ancestral and restriction is a

synapomorphy of Xenosauridae and an autapomorphy of both *C. enneagrammus* and Helodermatidae.

25. Premaxilla: Tooth position count, average rounded to nearest integer, (0) 7; (1) 8; (2) 9; (3) more than nine.

    Variation. Premaxillary tooth position count does vary, and the character scored is the average value for the individuals examined. However, even in those taxa whose count did vary, the variants always possessed one fewer tooth position than the average (and modal) number. Furthermore, these nonmodal variants were rare.

    Evolution. Under both analyses, having more than nine tooth positions is an autapomorphy of *L. borneensis.* Under Analysis 1, the ancestral state is ambiguous. If it is eight or nine tooth positions, then having seven tooth positions is an autapomorphy of *P. torquatus,* and the other transformations are as described below for the case in which eight or nine is ancestral for Anguimorpha. If seven tooth positions is the ancestral state, an increased number is a synapomorphy either of Anguimorpha or of Anguidae + *Xenosaurus.* Two possibilities obtain if an increased number of either eight or nine is a synapomorphy of Anguimorpha. If eight, then having nine tooth positions is a synapomorphy of Anguidae + *Xenosaurus* and of Varanidae, and having seven tooth positions is a synapomorphy of *S. crocodilurus* + *M. ornatus.* If nine, then only the two-step transformation along the *Shinisaurus* stem need occur.

Nasal

The nasal is unknown for *E. lancensis,* *R. rugosus*, and *M. ornatus.*

26. Nasal: Contacts contralateral nasal at dermal surface (0) extensively, along at least a quarter of its medial margin (Fig. 12B); (1) barely or not at all (Fig. 2A).

Variation. In younger individuals of *V. exanthematicus*, the nasals are barely in contact, but in medium to large individuals, they show extensive contact. The nasals of *Varanus* in general are unusual in their morphology and their contacts, concomitantly with the retracted nares characteristic of the clade (McDowell and Bogert, 1954; Estes et al., 1988).

Evolution. Under both analyses, a small amount of contact is a synapomorphy of *Xenosaurus* and an autapomorphy of *V. niloticus*.

27. Nasal: Posterior tapered portion (in horizontal plane) (0) mediolaterally wider at base than long along long axis of nasal (Fig. 12C); (1) longer than wide (Fig. 12D).

Evolution. Under Analysis 1, the longer-than-wide morphology is ancestral, with wider-than-long a synapomorphy of *Xenosaurus* + Anguidae and, within that clade, longer-than-wide a synapomorphy of the southern clade of *Xenosaurus*. Under Analysis 2, the ancestral state for Anguimorpha is ambiguous. If the ancestral state is wider-than-long, then the longer-than-wide morphology is a synapomorphy of *B. ammoskius* + *S. crocodilurus* and the southern clade of *Xenosaurus*. If the ancestral state is longer-than-wide, then wider-than-long is a synapomorphy of Anguidae. Furthermore, wider-than-long is either a synapomorphy of *E. serratus* + *Xenosaurus* and longer-than-wide a synapomorphy of the southern clade of *Xenosaurus,* or wider-than-long is an autapormophy of *E. serratus* and a synapomorphy of the northern clade of *Xenosaurus*.

28. Nasal: Osteoderms of lateral row posterior to enlarged anterolateral osteoderm (0) comparable in size to or smaller than osteoderms of medial row (Fig. 3A); (1) larger and more prominent than osteoderms of medial row; anterolateral osteoderm especially large (Fig. 12D).

Evolution. Under both analyses, greater size and prominence of the lateral row is a synapomorphy of the northern clade of *Xenosaurus*.

29. Nasal: Anterior portion of lateral edge corresponding to underlying lateral bend of cartilaginous nasal capsule (0) with no change in angle or with deflection in horizontal plane away from the midline of a few degrees relative to the posterior portion of the lateral edge (Fig. 13A); (1) with slight deflection from posterior portion of about 10°; (2) with notable bend, deflecting from the posterior portion by about 40° (Fig. 12D).

Evolution. Under both analyses, ancestral character states are ambiguous between a change in angle of 10° and 40° across most of the tree. Under Analysis 1, the only unambiguous synapomorphy is the lack of a change in angle uniting *Varanus*. Under Analysis 2, the ambiguity along the stem of Varanoidea shifts to no change in angle/slight change in angle.

Septomaxilla

Unfortunately, the septomaxilla is unknown in all of the extinct taxa. In general, this element is neglected in studies of squamate osteology. It received the most attention in work dealing with the complex olfactory organs of lizards (Stebbins, 1948; Bellairs, 1949; Hallerman, 1994; Bernstein, 1999). A few characters are used in current phylogenetic works on Serpentes (Lee and Scanlon, 2002). In the course of this investigation, I was able to identify a number of informative characters in the septomaxilla. In part, this stems from the unusually complex septomaxilla of *Xenosaurus*, in and upon which several canals and ridges are formed that do not appear on the septomaxillae of most other squamates.

30. Septomaxilla: Posteromedial corner of cupular portion (0) with a long para-
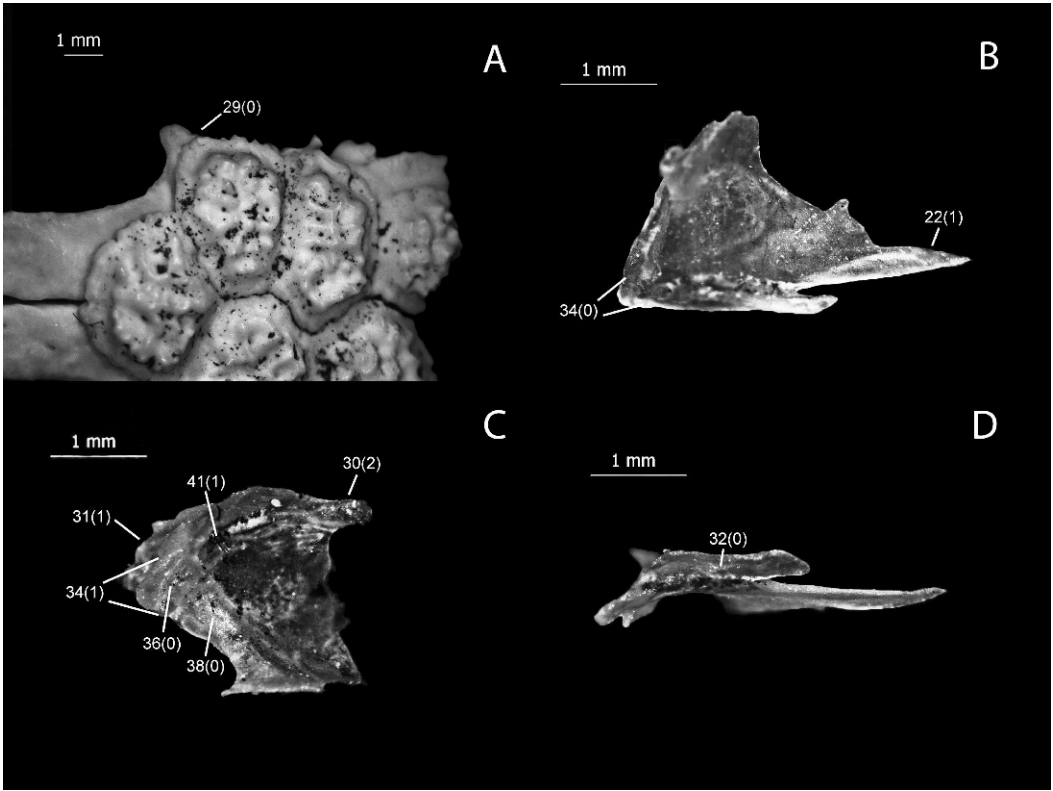
Figure 13.   A, Nasals of *Heloderma suspectum* TMM-M 9001, dorsal, anterior to the left. Illustrates character 29(0). B, Right septomaxilla of *Elgaria multicarinata* TMM-M 8958, dorsal, anterior to the left. Illustrates characters 30(0), 31(0), 34(0). C, Left septomaxilla of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, dorsal, anterior to the left. Illustrates characters 30(2), 31(1), 34(1), 36(0), 38(0), 41(1). D, Right septomaxilla of *Elgaria multicarinata* TMM-M 8958, medial, anterior to the left. Illustrates character 32(0).

septal process, several times as long as mediolaterally wide at base (Fig. 13B); (1) sending back moderate-length or short process, about twice as long as mediolaterally wide at base; (2) process absent or reduced to minor projection of corner, septomaxilla roughly an equilateral triangle in overall shape (Fig. 13C).

Variation. The process becomes longer during postnatal ontogeny, but its proportions are consistent with the scoring for most of ontogeny.

Evolution. Under both analyses, moderate length of the process is ancestral and absence is a synapomorphy of *Xenosaurus.* Under Analysis 1,

great length is a synapomorphy of Varanidae. Great length is also either a synapomorphy of Anguidae with moderate length an autapomorphy of *C. enneagrammus,* or great length is an autapomorphy of Helodermatidae and *O. ventralis + E. multicarinata.* Under Analysis 2, great length is a synapomorphy of Anguidae + Varanoidea, and moderate length is an autapomorphy of *C. enneagrammus.*

31. Septomaxilla: Deflection of bone away from rostral process of nasal septum to form distinct anteromedial surface (0) absent (Fig. 13B); (1) present (Fig. 13C).
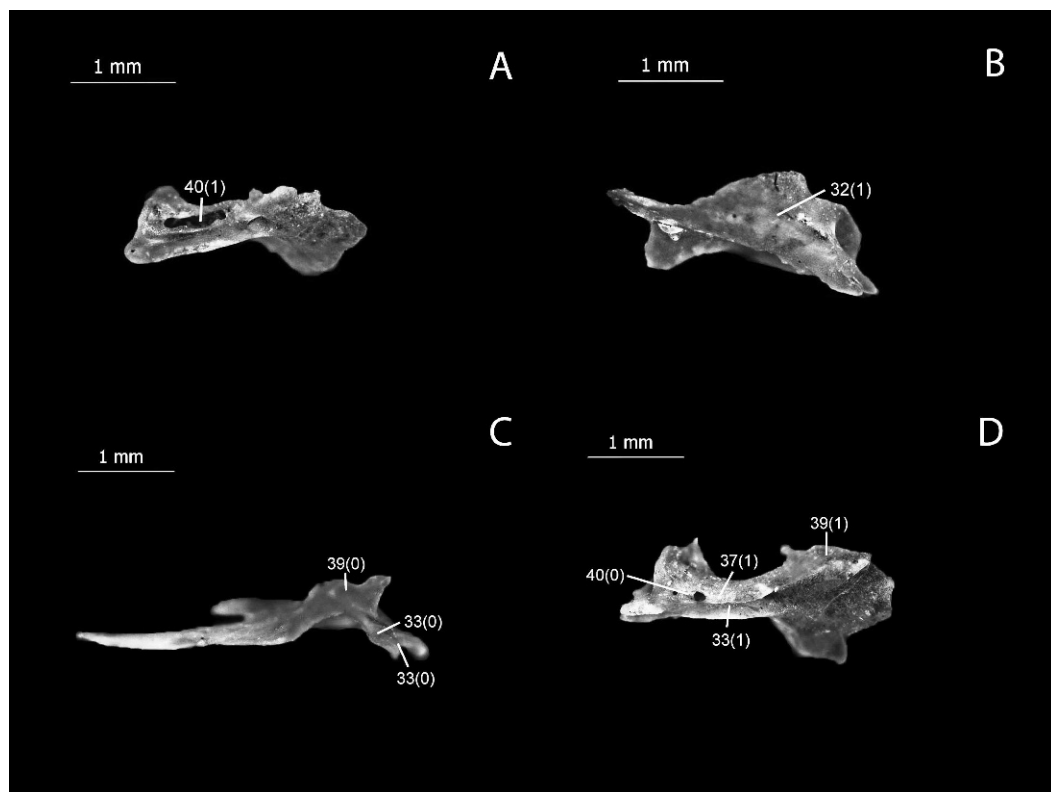
Figure 14. A, Left septomaxilla of *Xenosaurus rackhami* UTEP-OC "MALB" 388, lateral, anterior to the left. B, Left septomaxilla of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, medial, anterior to the right. Illustrates characters 32(1), 40(1). C, Right septomaxilla of *Elgaria multicarinata* TMM-M 8958, lateral, anterior to the right. Illustrates characters 33(0), 37(0), 39(0). D, Left septomaxilla of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, lateral, anterior to the left. Illustrates characters 33(1), 37(1), 39(1), 40(0).

Evolution. Under both analyses, the presence of the anteromedial surface is a synapomorphy of *Xenosaurus*.

32. Septomaxilla: Medial ethmoidal nerves and vasculature (0) running in connective tissue near surface of septomaxilla, not enclosed by bone (Fig. 13D); (1) enclosed by septomaxilla (Fig. 3.32B).

Evolution. Under Analysis 1, enclosure is a synapomorphy of *Xenosaurus* + Anguidae and an autapomorphy of *L. borneensis*. Under Analysis 2, enclosure may be ancestral, in which case lack of enclosure is an autapomorphy of *P. torquatus* and *S. crocodilurus*. If enclosure is not ancestral, it is a synapomorphy of Anguimorpha or a synapomorphy of *Xenosaurus* and of Anguidae + Varanoidea. Under any of these hypotheses of character evolution, lack of enclosure is a synapomorphy of *Varanus*.

33. Septomaxilla: Lateral ethmoidal nerves and vasculature (0) running in connective tissue near surface of septomaxilla, not enclosed by bone (Fig. 14C); (1) enclosed by septomaxilla (Fig. 14D).

Evolution. Under Analysis 1, lateral enclosure is either a synapomorphy of Anguidae + *Xenosaurus*, with lack of
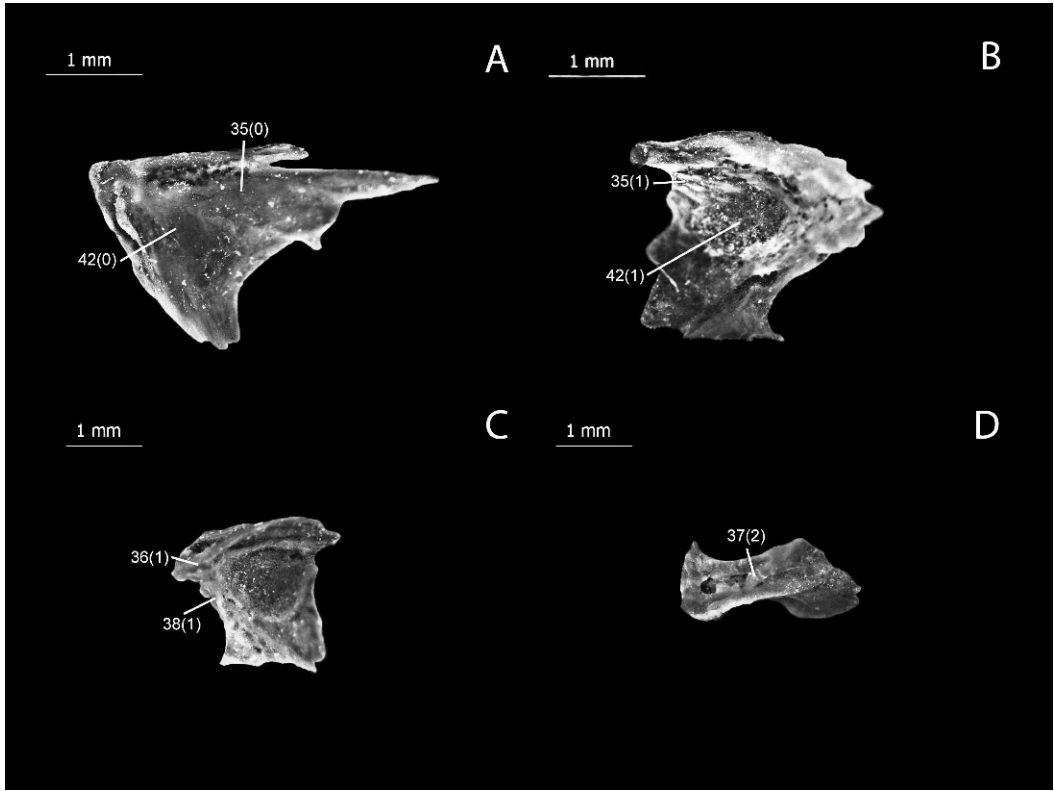
Figure 15.   A, Right septomaxilla of *Elgaria multicarinata* TMM-M 8958, ventral, anterior to the left. Illustrates characters 35(0), 42(0). B, Right septomaxilla of *Elgaria multicarinata* TMM-M 8958, lateral, anterior to the right. Illustrates characters 35(1), 42(1). C, Left septomaxilla of *Xenosaurus grandis* NAUQSP-JIM 1460, dorsal, anterior to the left. Illustrates characters 36(1), 38(1), 41(0). D, Left septomaxilla of *Xenosaurus grandis* NAUQSP-JIM 1460, lateral, anterior to the left. Illustrates character 37(0).

enclosure a synapomorphy of Anguidae, or lateral enclosure is a synapomorphy of *Xenosaurus* and an autapomorphy of Helodermatidae. Under Analysis 2, only the latter hypothesis of character evolution is most parsimonious.

34. Septomaxilla: Dorsal ridges following anterolateral and anteromedial edges (0) absent or low (Fig. 13B); (1) high and sharp (Fig. 13C).

    Evolution. Under both analyses, a high, sharp morphology is a synapomorphy of *Xenosaurus*.

35. Septomaxilla: Ventral surface posterior to vomeronasal cupula (0) smooth (Fig. 15A); (1) impressed into longitudinal grooves by vomeronasal nerve (Fig. 15B).

    Variation. The sulci become more deeply incised during ontogeny but are present in even the youngest individuals examined.

    Evolution. Under both analyses, the presence of vomeronasal nerve impressions is a synapomorphy of *Xenosaurus*.

36. Septomaxilla: Anteroposterior length of flattened dorsal region near anterior apex, in front of capsular depression. Measured as proportion of total anteroposterior length of septomaxilla from

anterior apex back along anteroposterior axis: (0) 0.35 or greater (Fig. 13C); (1) less than 0.35 (Fig. 15C).

Variation. The lamina of bone posterior to the cupular region of the septomaxilla lengthens slightly during ontogeny, so the ratios above should be taken to apply to fairly mature individuals.

Evolution. Because no other squamate possesses the flattened region, the ancestral state within *Xenosaurus* is ambiguous.

37. Septomaxilla: Ratio of dorsoventral height of anterolateral face at shortest level to anteroposterior length of face (0) less than 0.10 (Fig. 14C); (1) 0.10 to 0.50 (Fig. 14D); (2) greater than 0.50 (Fig. 15D).

    Evolution. A dorsoventrally short anterolateral face with a height-to-length ratio of less than 0.10 is ancestral under both analyses. Also under both analyses, a ratio of 0.10 to 0.50 is a synapomorphy of *Xenosaurus* and a ratio greater than 0.50 is a synapomorphy of the southern clade of *Xenosaurus*.

38. Septomaxilla: Anterolateral dorsal ridge continuing from lateral wing (0) broad and rounded (Fig. 13C); (1) narrow and sharp (Fig. 15C).

    Evolution. The ancestral state within *Xenosaurus* is ambiguous.

39. Septomaxilla: Ratio of anteroposterior length of lateral wing to anteroposterior length of septomaxilla along anteroposterior axis from level of anterior apex to level of back of lateral wing (0) greater than 0.55 (Fig. 14C); (1) 0.55 or less (Fig. 14D).

    Evolution. Under both analyses, a ratio of 0.55 or less is a synapomorphy of the northern clade of *Xenosaurus* and an autapomorphy of Helodermatidae.

40. Septomaxilla: Anterolateral ethmoid canal (0) open only at round terminal foramina (Fig. 14D); (1) open along much of anterolateral face as long fissure (Fig. 14A).

    Evolution. Under both analyses, closure is the primitive state and the existence of the fissure is a synapomorphy of the southern clade of *Xenosaurus*.

41. Septomaxilla: Canal paralleling and running lateral to the medial edge of the septomaxilla or to the anteromedial dorsal ridge (when visible) (0) absent (Fig. 15C); (1) present (Fig. 13C).

    Evolution. Under both analyses, presence of the canal is a synapomorphy of the northern clade of *Xenosaurus*.

42. Septomaxilla: Ratio of mediolateral width of vomeronasal cupula at its widest level to width of septomaxilla at that level (0) 0.45 or greater (Fig. 15A); (1) less than 0.45 (Fig. 15B).

    Evolution. Under both analyses, a ratio of less than 0.45 is a synapomorphy of the northern clade of *Xenosaurus*.

Maxilla

The maxilla is only partially preserved in *E. lancensis* and *M. ornatus*.

43. Maxilla: Medial premaxillary process, portion projecting beyond dental gutter, (0) anteroposteriorly very short, about twice as tall at posterior end as long (Fig. 16A); (1) short, about as tall as long; (2) intermediate length, about two-thirds as tall as long (Fig. 16B); (3) long, about half as tall as long (Fig. 16C).

    Variation. The medial premaxillary process becomes slightly dorsoventrally taller during ontogeny, but despite this, no variation that would affect scoring was evident.

    Evolution. Under both analyses, a very short process is ancestral for the
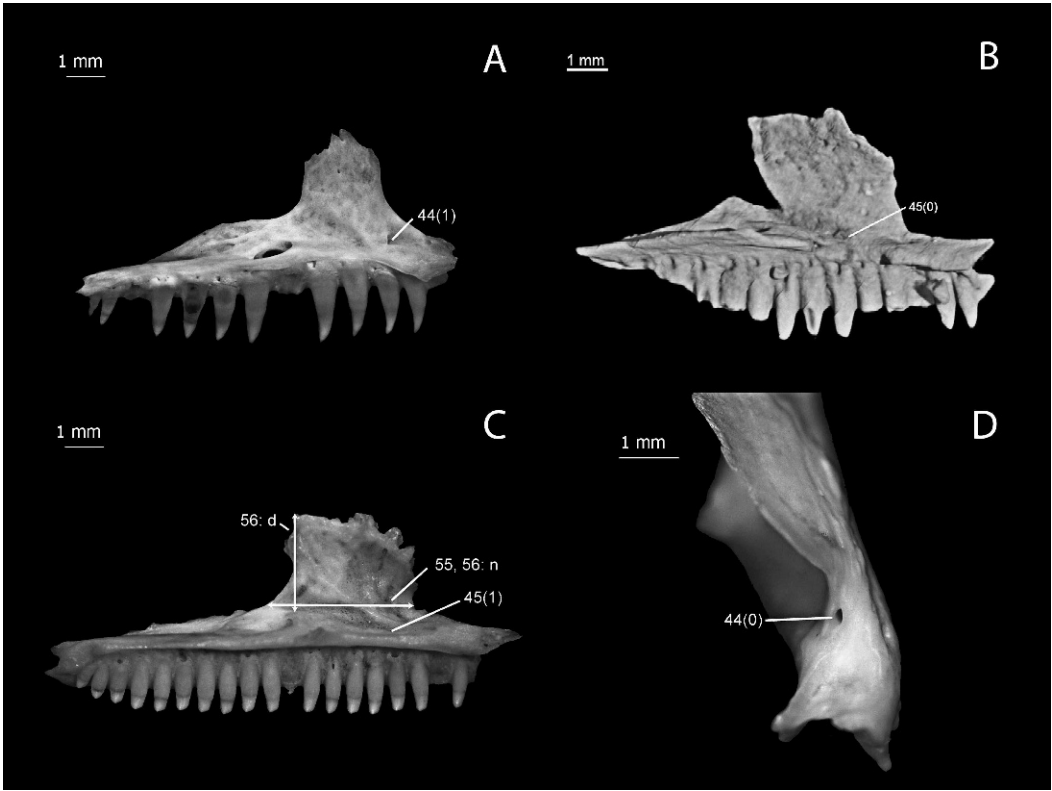
Figure 16.   A, Left maxilla of *Shinisaurus crocodilurus* UF 72805, medial, anterior to the right. Illustrates characters 43(0), 44(1), 46(2), 63(1). B, Left maxilla of *Exostinus serratus*, CT scan of USNM v16565, medial, anterior to the right. Illustrates characters 43(2), 45(0), 46(1), 60(1), 63(0). C, Left maxilla of *Xenosaurus platyceps* UF 45622, medial, anterior to the right. Illustrates characters 43(3), 45(1), 55 (n for numerator, d for denominator), 56 (n for numerator, d for denominator), 60(0). D, Left maxilla of *Elgaria multicarinata* TMM-M 8958, anterior. Illustrates character 44(0).

entire group and for Anguimorpha and a long process is a synapomorphy of the northern clade of *Xenosaurus*. The ancestral states for *Xenosaurus* + *E. serratus* and *Xenosaurus* are ambiguous between short and intermediate. Under Analysis 1, the ancestral state for Anguidae + Xenosauridae is ambiguous among very short, short, and intermediate, as is that for *Xenosaurus* + *R. rugosus*. The long morphology is a synapomorphy of Anguidae + Helodermatidae, and intermediate length is an autapomorphy of *E. multicarinata*. Under Analysis 2, the ancestral states for Anguidae + Varanoidea and Varanoidea are ambiguous among very short, short, and intermediate lengths. The long morphology is a synapomorphy of *O. ventralis* + *C. enneagrammus* and an autapomorphy of . Along the other branch of Anguimorpha, the ancestral state for Xenosauridae and for *Xenosaurus* + *R. rugosus* is the very short morphology.

44. Maxilla: Major anterior foramen for contents of infraorbital canal (ethmoidal nerve and accompanying structures) (0) exiting onto lamina intercristalis, lateral to crista transversalis (Fig. 16D); (1) exiting posteromedial to crista transversalis (Fig. 16A).

Evolution. Under both analyses, the ancestral state of the character is ambiguous. However, the medial foramen is not widespread outside of Anguimorpha, and I tentatively suggest that the ancestral state is for the exit to be in the upper region of the lamina intercristalis. Under Analysis 1, a medial exit is then a synapomorphy of Anguimorpha and a lateral exit is a synapomorphy of Anguidae. Under Analysis 2, the ancestral state for Anguimorpha is ambiguous.

45. Maxilla: Anterior end of lacrimal recess (0) relatively posterior, greater than one quarter of the way to the posterior end of the facial process (Fig. 16B); (1) relatively anterior, one quarter of the way back or less (Fig. 16C).

    Evolution. Under both analyses, the relatively anterior morphology is ancestral for the total group and the relatively posterior morphology is ancestral for *Xenosaurus + R. rugosus*, with the relatively anterior morphology a synapomorphy of *Xenosaurus*. Under Analysis 1, the ancestral state for Anguidae + *Xenosaurus* and for the clades within Anguidae is ambiguous. Under Analysis 2, the relatively posterior morphology is a synapomorphy of *O. ventralis + C. enneagrammus*.

46. Maxilla: Anterior portion of dorsal margin of lacrimal recess—posterodorsal rise in plane of facial process (0) shallow, 30° or less (Fig. 17A); (1) moderate, between 30° and 35° (Fig. 16B); (2) steep, 35° and greater (Fig. 16A).

    Evolution. Under both analyses, a shallow angle of 30° or less is ancestral. In the absence of data for *B. ammoskius*, a steep angle of 35° or greater is an autapomorphy of *S. crocodilurus*. An angle between 30° and 35° is a synapomorphy of *Xenosaurus*, and an angle of 35° or greater is a synapomorphy of *X. agrenon + X. rectocollaris*.

47. Maxilla: Articular facet posterior to facial process (0) mediolaterally narrow, hardly differentiated from sharp dorsal edge of maxilla (Fig. 17B); (1) mediolaterally wide, with a distinct dorsally facing table (Fig. 17C).

    Evolution. Under Analysis 1, the wide morphology is a synapomorphy of *E. serratus + Xenosaurus* and of *S. crocodilurus + B. ammoskius*. Under Analysis 2, the ancestral state for Xenosauridae is ambiguous.

48. Maxilla: Mediolaterally expanded facet posterior to facial process: (0) for lacrimal; (1) for jugal.

    Evolution. Because of widespread missing data, the ancestral state for the character is ambiguous at all levels.

49. Maxilla: Width of palatal shelf at widest level (measured in horizontal plane perpendicular to axis of toothrow) (0) less than one-fifth length of maxillary toothrow (Fig. 17D); (1) one-fifth length of maxillary toothrow or greater (Fig. 18A).

    Evolution. Under both analyses, a wide palatal shelf is an autapomorphy of *E. serratus*.

50. Maxilla: Posterior end of tooth row (0) relatively straight, collinear with more anterior portion (Fig. 17D); (1) medially deflected (Fig. 18A).

    Evolution. Under both analyses, medial deflection is an autapomorphy of *E. serratus*.

51. Maxilla: Infraorbital canal (0) round for entire length, confined to medial, steep portion of palatal shelf (see *E. multicarinata*, The Deep Scaly Project [2007], coronal slices 35–124); (1) mediolaterally expanded and oval for portion of length, extending above flattened, horizontal lateral portion of palatal shelf (Fig. 18B).

    Evolution. Under both analyses, an expanded canal is a synapomorphy of
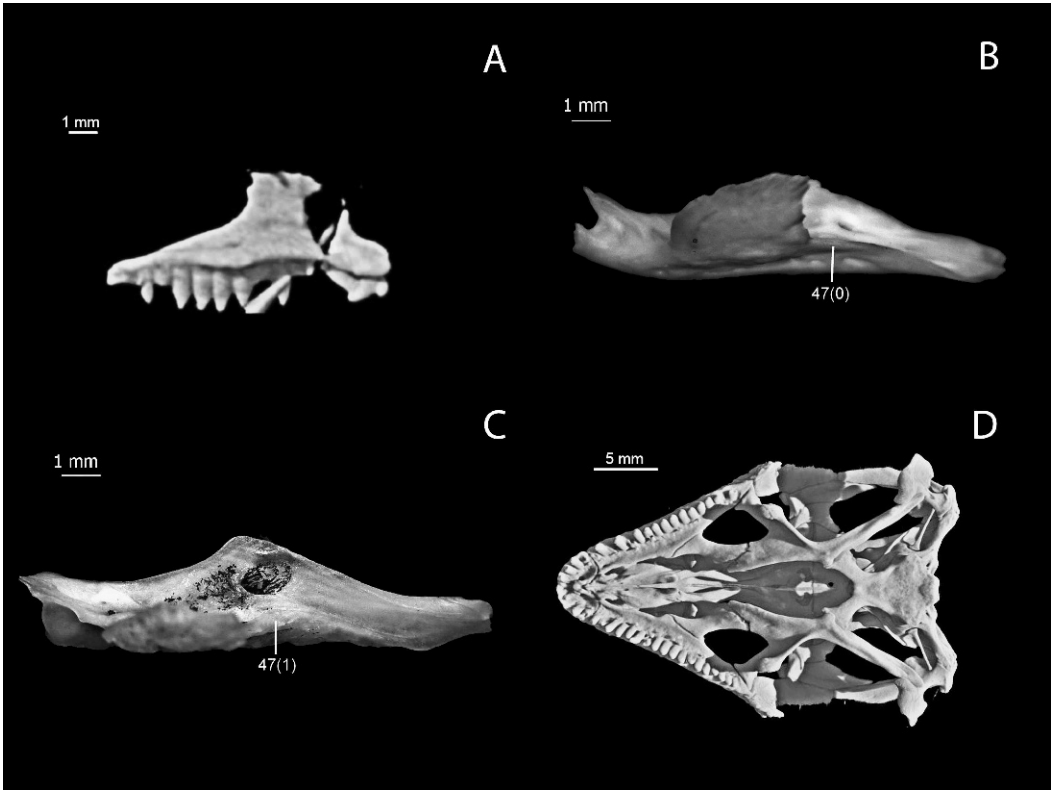
Figure 17.   A, Left maxilla of *Restes rugosus*, CT scan of YPM PU 14640, medial, anterior to the right. Illustrates character 46(0). B, Left maxilla of *Elgaria multicarinata* TMM-M 8958, dorsal, anterior to the left. Illustrates character 47(0). C, Left maxilla of *Xenosaurus grandis* NAUQSP-JIM 1460, dorsal, anterior to the left. Illustrates character 47(1). D, Skull of *Xenosaurus newmanorum*, CT scan of UMMZ 126056, ventral, anterior to the left. Illustrates characters 49(0), 50(0), 93(1).

Xenosaurus + R. rugosus and of *Varanus*, and an autapomorphy of *C. enneagrammus*.

52. Maxilla: Supradental thickening (0) absent (Fig. 18C); (1) weak, low ridge above teeth (Fig. 18D); (2) strong, rounded ridge above teeth, differentiated dorsally by groove (Fig. 19A).

    Variation. The ridge becomes stronger with increasing age.

    Evolution. Under both analyses, weak development is an autapomorphy of *E. serratus*. Under Analysis 1, the ancestral state for the entire group is ambiguous between absence of the thickening and the weakly developed morphology, as are the ancestral states for Anguimorpha and Anguidae + Helodermatidae. Strong development is a synapomorphy of *Xenosaurus + R. rugosus* and of *S. crocodilurus + M. ornatus*. Under Analysis 2, absence is the ancestral state for the entire group and for Anguimorpha and Anguidae + Varanoidea. Within Varanoidea, weak development is an autapomorphy of Helodermatidae. Strong development is a synapomorphy of Xenosauridae.

53. Maxilla: Major labial foramina: (0) posteriormost one or more foramina abruptly larger than others (Fig. 19B); (1) nearly the same size, with only a subtle and gradual trend of posterior enlargement (Fig. 19A).
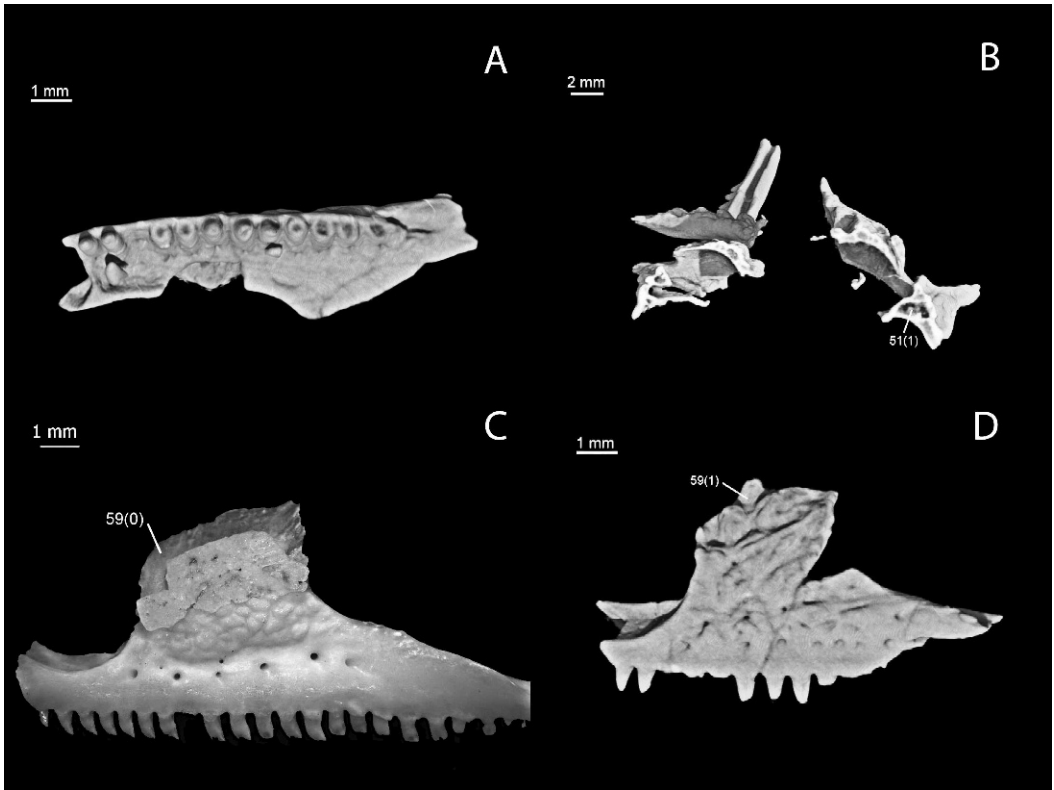
Figure 18.   A, Left maxilla of *Exostinus serratus*, CT scan of USNM v16565, ventral, anterior to the left. Illustrates characters 49(1), 50(1). B, Cutaway near posterior end of infraorbital canal of rostrum of *Exostinus serratus*, CT scan of USNM v16565, anterior. Illustrates character 51(1). C, Left maxilla of *Elgaria multicarinata* TMM-M 8993, lateral, anterior to the left. Illustrates characters 52(0), 54(0), 59(0), 61(0), 62(1). D, Left maxilla of *Exostinus serratus*, CT scan of USNM v16565 lateral, anterior to the left. Illustrates characters 52(1), 54(1), 57(0), 58(0), 59(1), 61(3), 62(4).

Evolution. Under both analyses, rough equivalence in size along the entire row is a synapomorphy of *Xenosaurus + R. rugosus*.

54. Maxilla: Foramina (0) concentrated in single row of labial foramina (Fig. 18C); (1) present in two rows—ventral labial foramina and dorsal row upon lower portion of facial process (Fig. 18D).

Evolution. Under both analyses, the ancestral state for *Xenosaurus + E. serratus* and for the southern clade of *Xenosaurus* is ambiguous, such that presence of the dorsal row could either be an autapomorphy of *E. serratus* and a synapomorphy of the southern clade of *Xenosaurus* or a synapomorphy of *Xenosaurus + E. serratus*, with lack of a dorsal row a synapomorphy of the northern clade of *Xenosaurus*.

55. Maxilla: Ratio of length of facial process along base (at dorsoventral level of inflection toward horizontal between rami of lacrimal) to total length of maxilla from anterior edge of facial process at that dorsoventral level to posterior end of maxilla (Fig. 16C) (0) 0.20 to less than 0.30; (1) 0.30 to less than 0.40; (2) 0.40 to less than 0.50; (3) 0.50 to less than 0.60; (4) 0.60 to less than 0.70; (5) 0.70 to less than 0.80.

Variation. As the orbit becomes proportionally smaller during growth,
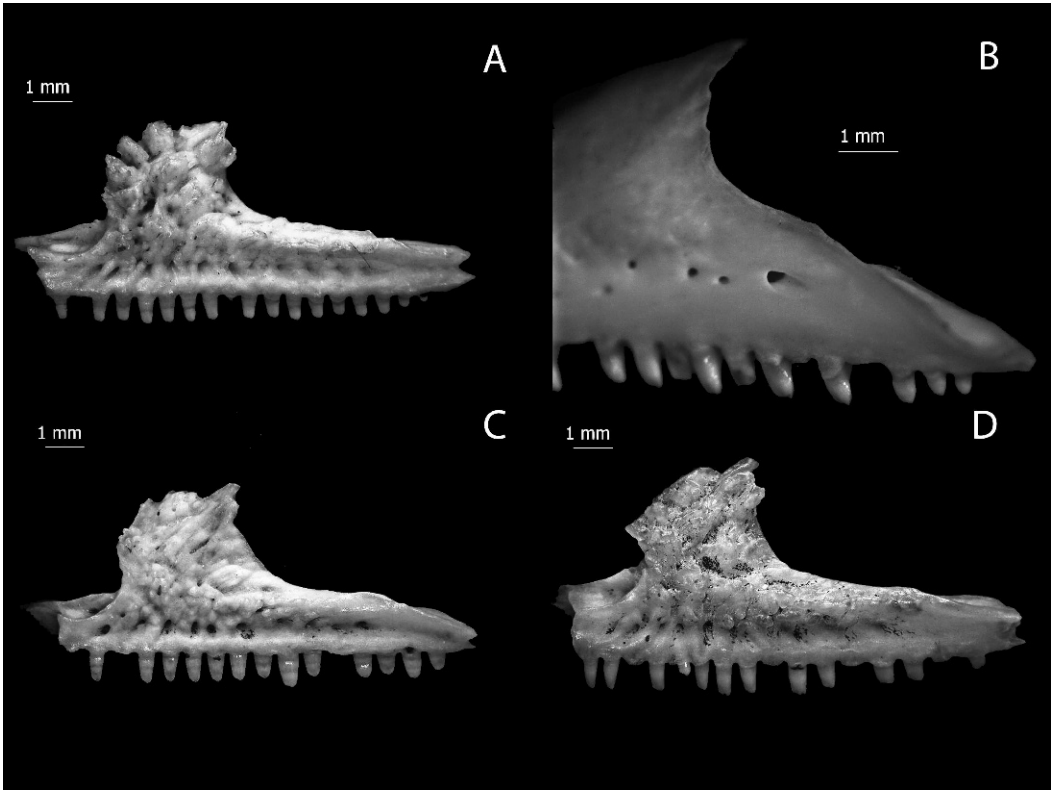
Figure 19.   A, Left maxilla of *Xenosaurus platyceps* UF 45622, lateral, anterior to the left. Illustrates characters 52(2), 53(1), 57(1), 61(2). B, Left maxilla of *Elgaria multicarinata* TMM-M 8958, lateral, anterior to the left. Illustrates character 53(0). C, Left maxilla of *Xenosaurus rackhami* UTEP-OC "MALB" 388, lateral, anterior to the left. Illustrates character 58(2). D, Left maxilla of *Xenosaurus grandis* NAUQSP-JIM 1460, lateral, anterior to the left. Illustrates character 58(3).

the posterior suborbital portion of the maxilla shortens relative to the remainder of the bone. However, this transformation occurs largely during early ontogenetic stages, and I scored this character on relatively large individuals.

Evolution. Under both analyses, state 1 is autapomorphic for *X. agrenon*, *X. grandis*, and *B. ammoskius*, state 4 is autapomorphic for *O. ventralis*, and state 5 is autapomorphic for *L. borneensis*. Under Analysis 1, the ancestral state for the entire group is ambiguous among state 0, state 1, state 2, and state 3. The ancestral state for Anguimorpha is ambiguous between state 2 and state 3, as is that for *S. crocodilurus* + Varanidae, Varanidae, *Varanus*, *Xenosaurus*

+ Anguidae, and *Xenosaurus* + *R. rugosus*. The ancestral state for *S. crocodilurus* + *B. ammoskius* is state 2, as is that for *E. serratus* + *Xenosaurus* and all nodes therein. Finally, the ancestral state for Anguidae is state 3, making state 2 an autapomorphy of *E. multicarinata*. Under Analysis 2, the ancestral state for the entire group is ambiguous among state 0, state 1, and state 2. The ancestral state for Xenosauridae and all nodes therein is state 2, and state 3 is autapomorphic for *R. rugosus*. The ancestral state for Anguidae + Varanoidea and for Anguidae is ambiguous between state 2 and state 3. The ancestral state for *O. ventralis* + *C. enneagrammus* is state 3, as is that for

Varanoidea, making state 2 autapomorphic for *V. exanthematicus*.

56. Maxilla: Ratio of length of facial process along base (at dorsoventral level of posterior inflection toward horizontal) to greatest height posterior to nasal facet (Fig. 16C) (0) 0.50 to less than 0.75; (1) 0.75 to less than 1.00; (2) 1.00 to less than 1.25; (3) 1.25 to less than 1.50; (4) 1.50 to less than 1.75; (5) 1.75 to less than 2.00; (6) 2.00 to less than 2.25.

Evolution. Under both analyses, state 0 is a synapomorphy of *Varanus* and state 6 is an autapomorphy of *L. borneensis* and of *O. ventralis*. State 2 is an autapomorphy of *C. enneagrammus* and a synapomorphy of *S. crocodilurus* + *B. ammoskius*. Furthermore, the ancestral state for *Xenosaurus* is ambiguous between state 3 and state 4. Within *Xenosaurus*, state 5 is autapomorphic for *X. newmanorum,* and state 2 is synapomorphic for *X. agrenon* + *X. rectocollaris*, with state 1 an autapomorphy of *X. agrenon*. Under Analysis 1, the ancestral state for the entire group is ambiguous among state 1, state 2, and state 3. The ancestral state for Anguimorpha is state 2. State 4 is a synapomorphy of *Xenosaurus* + Anguidae. Under Analysis 2, the ancestral state for the entire group is ambiguous among state 0, state 1, state 2, state 3, and state 4. The ancestral states for Anguimorpha and Xenosauridae are ambiguous among the last three of those states. That for Anguidae + Varanoidea is state 4. The ancestral state for *Xenosaurus* + *R. rugosus* is ambiguous between state 3 and state 4.

57. Maxilla: Narial margin of facial process (0) dorsoventrally tall, horizontal portion about as extensive as or less extensive than vertical portion (Fig. 18D); (1) dorsoventrally short, horizontal margin more extensive than vertical portion (Fig. 19A).

Evolution. Under both analyses, a proportionally short vertical margin is a synapomorphy of *Xenosaurus*. Under Analysis 1, a short vertical margin is a synapomorphy of Varanidae and an autapomorphy of Helodermatidae. Under Analysis 2, a short vertical margin is a synapomorphy of Varanoidea.

58. Maxilla: Vertical portion of narial margin of facial process (0) failing to tilt anterodorsally beyond the vertical by more than a few degrees (Fig. 18D); (1) tilting slightly beyond the vertical to form a dorsal overhang of the naris by the facial process with a slight anterior eminence (Fig. 19A); (2) tilting beyond the vertical to form a dorsal overhang with a pronounced but rounded anterior eminence (Fig. 19C); (3) tilting beyond the vertical to form a marked dorsal overhang with a pronounced and sharply pointed anterior eminence (Fig. 19D).

Variation. Smaller individuals of *X. rackhami* do not show as much anterior projection of the overhang as large adults, which were scored.

Evolution. Under both analyses, a slight overhang is a synapomorphy of *Xenosaurus*, a moderately pronounced overhang is a synapomorphy of *X. rackhami* + *X. grandis*, and a very pronounced overhang is an autapomorphy of *X. grandis*.

59. Maxilla: Posterior portion of nasal facet upon facial process (0) curving smoothly in transverse plane, following general curvature of facial process (Fig. 18C); (1) distinctly folded toward the vertical relative to remainder of facial process, forming an upturned posterior tab of the nasal facet (Fig. 18D).

Evolution. Under Analysis 1, the upturned tab is a synapomorphy of *Xenosaurus* + *R. rugosus* and of *S. crocodilurus* + *B. ammoskius*. Under Analysis 2, the upturned tab is a synapomorphy of Xenosauridae.

60. Maxilla: Highest point of facial process: (0) prominent, posterior corner between
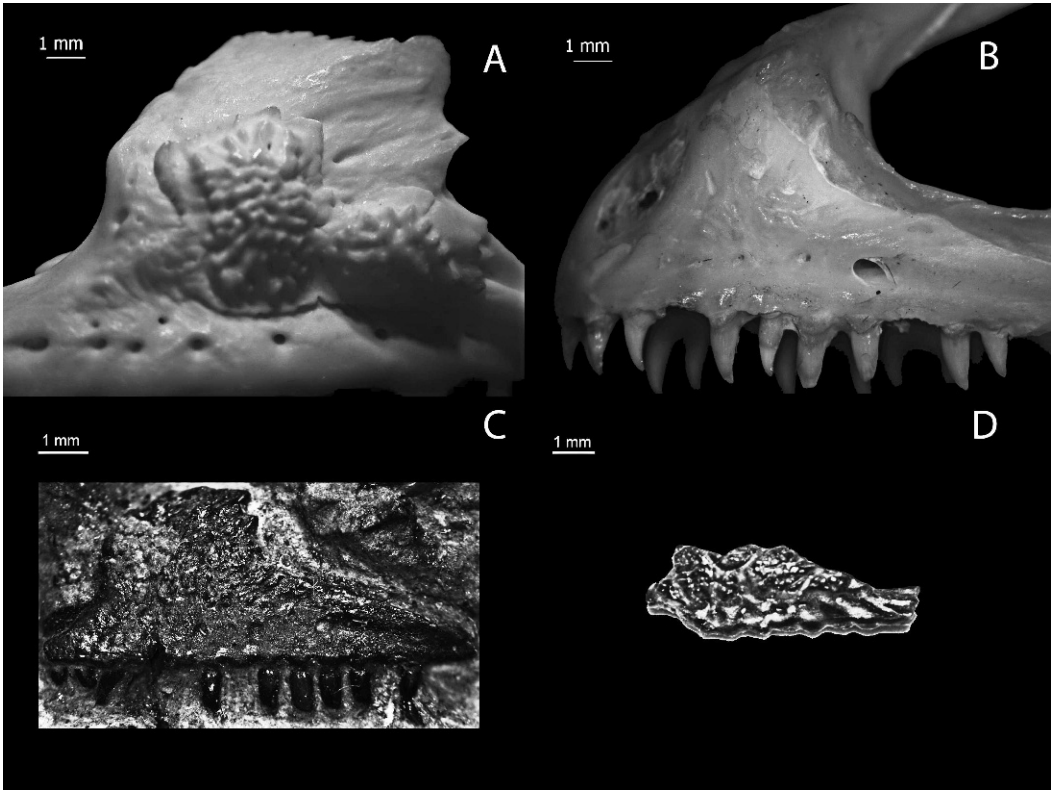
Figure 20.   A, Left maxilla of *Heloderma suspectum* TMM-M 9001, lateral, anterior to the left. Illustrates character 61(1). B, Left maxilla of *Shinisaurus crocodilurus* MVZ 204291, lateral, anterior to the left. Illustrates characters 62(0), 118(1). C, Left maxilla of *Restes rugosus* YPM PU 14640, lateral, anterior to the left. Illustrates character 62(2). D, Fragmentary left maxilla of *Exostinus lancensis* AMNH 8498, lateral, anterior to the left. Illustrates character 62(3).

prefrontal facet and orbital (posterior) edge (Fig. 16C); (1) dorsal edge of facial process nearly horizontal (Fig. 17A); (2) upturned tab of nasal facet (Fig. 16B).

Evolution. Under both analyses, the ancestral state for the entire group is for the highest point to be the corner between the prefrontal facet and orbital edge. The ancestral state for *Xenosaurus* + *R. rugosus* is a horizontal dorsal edge of the facial process, with the upturned tab of the nasal facet the highest point autapomorphically in *E. serratus* and *X. rectocollaris.* The corner between the prefrontal facet and orbital edge the highest point synapomorphically in the northern clade of *Xenosaurus.* Under

Analysis 1, the ancestral state for Anguidae + *Xenosaurus* is ambiguous between the prefrontal facet/orbital edge corner and a horizontal dorsal edge, as is the ancestral state for Anguidae + Helodermatidae. A horizontal dorsal edge is an autapomorphy of *L. borneensis.* Under Analysis 2, a horizontal dorsal edge is a synapomorphy of *Xenosaurus* + *R. rugosus,* and the ancestral state for Varanoidea is ambiguous between the prefrontal facet/orbital edge corner and a horizontal dorsal edge.

61. Maxilla: Canthal crest (0) absent (Fig. 18C); (1) minimally developed: abrupt medial fold of facial process, but no projecting ridge (Fig. 20A); (2)

projecting as a low ridge (Fig. 19A); (3) projecting as an extensive, strong ridge (Fig. 18D).

Variation. The crest, when present, becomes somewhat stronger with age, and the scoring here represents the condition in relatively large individuals.

Evolution. Under both analyses, the ancestral state for the entire group is ambiguous between slight and moderate development of the crest. The ancestral state for Anguimorpha is moderate development. Also under both analyses, lack of a crest is a synapomorphy of Anguidae, a moderately developed crest is an autapomorphy of *X. platyceps*, and an extensive crest is an autapomorphy of *E. serratus*. Under Analysis 1, the ancestral state for *S. crocodilurus* + Varanidae is ambiguous between lack of a crest and slight development. Under Analysis 2, lack of a crest is a synapomorphy of *S. crocodilurus* + *M. ornatus* and of *Varanus*.

62. Maxilla: Osteoderms upon facial process (0) absent (Fig. 20B); (1) present as nearly continuous sculptured plate or a small number of rectangular plates (Fig. 18C); (2) present as sculptured plate with sculpture concentrated into low mounds (Fig. 20C); (3) present as several low, polygonal (generally more edges than rectangles) tesserae (Fig. 20D); (4) present as pronounced mounds (Fig. 18D). This character was described and scored as "rugosity absent or present" by Conrad (2005, 2008).

Variation. Fusion of osteoderms to dermal elements proceeds during postnatal ontogeny, and mound-shaped osteoderms develop from flat lattices of bone (personal observation). Thus, relatively large individuals were scored.

Evolution. Under both analyses, the ancestral state for the entire group and for Anguimorpha is no osteodermal fusion. The ancestral state for *Xenosaurus* + *R. rugosus* is a sculptured plate concentrated into scattered low mounds. The low, polygonal, tesselated morphology is a synapomorphy of *E. lancensis* + *Xenosaurus*, and the pronounced mound-shaped morphology is a synapomorphy of *E. serratus* + *Xenosaurus* and an autapomorphy of Helodermatidae. The latter result is consistent with the presence of low, polygonal tesserae instead of pronounced mounds in primitive helodermatids (Hoffstetter, 1957). Under Analysis 1, the ancestral state for Anguidae + *Xenosaurus* is ambiguous among all four states. The ancestral state for Anguidae is ambiguous between state 0 and state 1. Under Analysis 2, the ancestral state for Xenosauridae is the absence of fused osteoderms; presence of a few large sculptured plates is an autapomorphy of *E. multicarinata*. Note, however, that the apparently primitive (Conrad, 2005, 2008) glyptosaurid anguids generally have large sculptured plate-like osteoderms fused to the facial process (Meszoely, 1970; personal observation).

63. Maxilla: Tooth height (0) short, less than half of tooth extending beyond margin of bone (Fig. 16B); (1) tall, half or more of tooth extending beyond margin of bone (Fig. 16A).

Evolution. Under both analyses, the ancestral state is ambiguous at all nodes whose branches have mixed states. However, this is largely a result of incomplete taxon sampling, as few non-anguimorph squamates have tall teeth.

64. Maxilla: Tooth count (average, rounded to nearest integer) (0) 7; (1) 8; (2) 9; (3) 10; (4) 11; (5) 12; (6) 13; (7) 14; (8) 15; (9) 16; (A) 17; (B) 18.

Variation. As noted, average values were scored. Ontogenetic increase in tooth number was previously documented for some squamates (Edmund, 1969; Ananjeva et al., 2003), but it was not in abundant evidence for the taxa I examined.
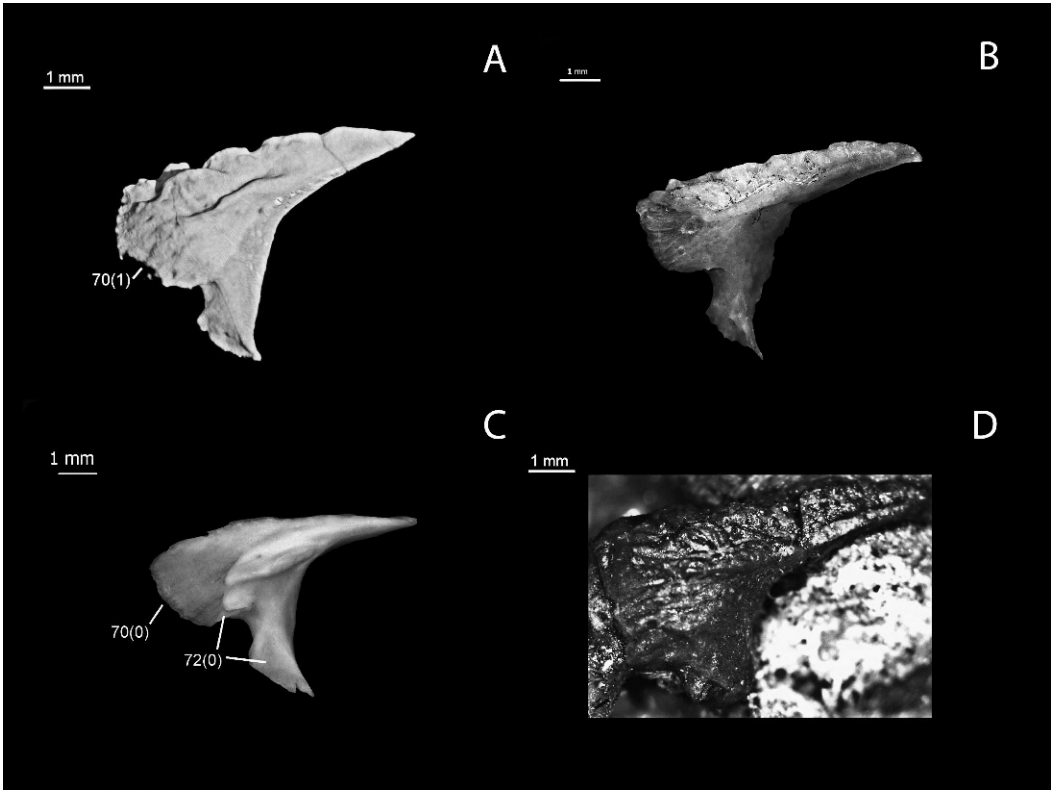
Figure 21.   A, Left prefrontal of *Exostinus serratus*, CT scan of USNM v16565 lateral, anterior to the left. Illustrates characters 65(0), 68(2), 69(2), 70(1), 71(1). B, Left prefrontal of *Xenosaurus grandis* NAUQSP-JIM 1460, lateral, anterior to the left. Illustrates characters 65(1), 68(0). C, Left prefrontal of *Elgaria multicarinata* TMM-M 8958, lateral, anterior to the left. Illustrates characters 66(0), 69(0), 70(0), 71(0), 72(0). D, Left prefrontal of *Restes rugosus* YPM PU 14640, lateral, anterior to the left. Illustrates characters 66(1), 69(1).

Evolution. Under both analyses, a count of seven is an autapomorphy of Helodermatidae, nine is an autapomorphy of *V. exanthematicus*, 12 is an autapomorphy of *E. serratus* and *S. crocodilurus*, and 17 is an autapomorphy of *E. multicarinata*. Additionally, a count of 16 is a synapomorphy of *Xenosaurus* and a count of 18 is a synapomorphy of the northern clade of *Xenosaurus*, as well as an autapomorphy of *X. rectocollaris*. Under Analysis 1, the ancestral state for the entire group is ambiguous from 13 to 16, and that for Anguimorpha is ambiguous between 13 and 14. The ancestral state for *S. crocodilurus* + Varanidae is ambiguous from 12 to 14, and a count of 15 is an autapomorphy of *B. ammoskius*. A count of 11 is a synapomorphy of Varanidae. Along the other major anguimorph lineage, a count of 16 is a synapomorphy of *E. multicarinata* + *O. ventralis*. Under Analysis 2, the primitive state for the entire group is ambiguous from 14 to 16. A count of 11 is a synapomorphy of Varanoidea.

Prefrontal

The prefrontal is unknown for *E. lancensis* and *M. ornatus*.

65. Prefrontal: Frontal process (0) relatively short and broad-based at divergence from main body of prefrontal, about twice as long along long axis as wide at base perpendicular to long axis (Fig. 21A); (1) relatively long and nar-
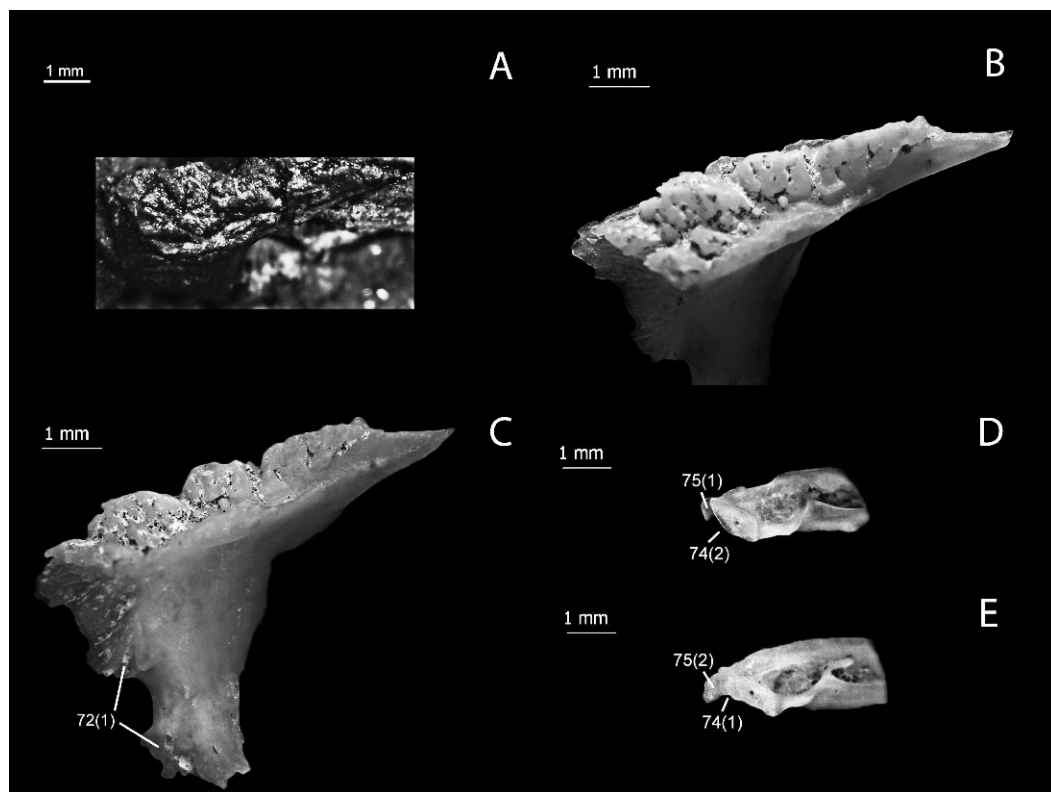
Figure 22.   A, Left prefrontal of *Restes rugosus* YPM PU 14640, dorsal, anterior to the left. Illustrates characters 67(1), 68(1). B, Left prefrontal of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, dorsolateral, anterior to the left. Illustrates character 68(3). C, Left prefrontal of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, lateral, anterior to the left. Illustrates character 72(1). D, Left vomer of *Xenosaurus grandis* NAUQSP-JIM 1460, dorsolateral, anterior to the left. E, Left vomer of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, same view. D and E illustrate characters 73(0), 73(1), 74(1), 74(2), 75(1), 76(2).

row-based, about two-and-a-half times as long as wide (Fig. 21B).

Variation. The frontal process becomes relatively shorter and more stout with age, and this character was scored on relatively large individuals. Large adults were available for all taxa scored as having long frontal processes.

Evolution. Under both analyses, a long frontal process is an autapomorphy of *O. ventralis* and of *X. newmanorum* and a synapomorphy of *X. grandis + X. rackhami*.

66. Prefrontal: Row of osteoderms along lateral edge of dermal surface (0) absent (Fig. 21C); (1) present (Fig. 21D).

Variation. Osteoderms fuse to the prefrontal postnatally.

Evolution. Under Analysis 1, presence of a lateral row of osteoderms is a synapomorphy of *S. crocodilurus + B. ammoskius* and of *Xenosaurus + R. rugosus*. Under Analysis 2, presence of the lateral row is a synapomorphy of Xenosauridae.

67. Prefrontal: Distinct osteodermal pattern of two small osteoderms adjacent to nasal facet and longer, lateral row of four with anteriormost laterally displaced, (0) absent (Fig. 12B); (1) present (Fig. 22A).

Variation. Osteoderms fuse to the prefrontal postnatally.

Evolution. Under both analyses, the "two and four" pattern is a synapomorphy of *Xenosaurus + R. rugosus*.

68. Prefrontal: Osteoderms (0) low, barely domed, with flat appearance (Fig. 21B); (1) moderately pronounced, with some doming (Fig. 22A); (2) pronounced with domes and low keels (Fig. 21A); (3) pronounced with high domes and sharp keels (Fig. 22B).

    Variation. Osteoderms become more domed during postnatal ontogeny, but as mentioned in the description for character 13, the keel forms early.

    Evolution. Under both analyses, the moderately pronounced morphology is ancestral. The low, barely domed morphology is a synapomorphy of *S. crocodilurus + B. ammoskius*. The ancestral states for *Xenosaurus + E. serratus* and for *Xenosaurus* are ambiguous between the moderately pronounced morphology and the domed and moderately keeled morphology. The low morphology is a synapomorphy of the southern clade of *Xenosaurus* and the highly domed and highly keeled morphology a synapomorphy of the northern clade.

69. Prefrontal: Canthal crest (0) absent (Fig. 21C); (1) present as distinct ridge (Fig. 21D); (2) present as sharp, pronounced ridge (Fig. 21A).

    Evolution. Under both analyses, a sharp, pronounced morphology is an autapomorphy of *E. serratus*. Under Analysis 1, a distinct crest is a synapomorphy of *S. crocodilurus + B. ammoskius* and of *Xenosaurus + R. rugosus*. Under Analysis 2, it is a synapomorphy of Xenosauridae.

70. Prefrontal: Emargination or straight edge in maxillary flange (0) dorsoventrally extensive, representing over half of entire edge length of flange (Fig. 21C); (1) dorsoventrally restricted, less than half of entire edge length (Fig. 21A).

Variation. The maxillary flange is extremely thin early in postnatal ontogeny, and in young individuals, it may be damaged or only partially ossified. This character is best scored on relatively large individuals.

Evolution. Under both analyses, the restricted morphology is an autapomorphy of *E. serratus* and of Helodermatidae.

71. Prefrontal: Lacrimal foramen (0) relatively unconstricted, margins remain divergent (Fig. 21C); (1) relatively constricted, margins become nearly parallel (Fig. 21A).

    Evolution. Under both analyses, the parallel morphology is an autapomorphy of *E. serratus*.

72. Prefrontal: Lacrimal facets (0) relatively smooth (Fig. 21C); (1) adorned with complex ridges and bumps (Fig. 22C).

    Variation. When the complex adorned morphology is present, it tends to be more pronounced in older individuals.

    Evolution. Under both analyses, the adorned morphology is a synapomorphy of *Xenosaurus + R. rugosus*.

Vomer

The vomer is unknown in *E. serratus*, *E. lancensis*, *R. rugosus*, and *M. ornatus*. It is not visible in the single known specimen of *B. ammoskius* (Conrad, 2006).

73. Vomer: Anterior facet for medial premaxillary process of maxilla (0) less than three times as long along its long axis as tall perpendicular to long axis (Fig. 22D); (1) three or more times as long as tall (Fig. 22E).

    Evolution. Under both analyses, the elongated morphology is a synapomorphy of the northern clade of *Xenosaurus*.

74. Vomer: Anterior facet for medial premaxillary process of maxilla (0) abruptly diverging ascending portion of ventral edge absent (Fig. 23A); (1) abruptly
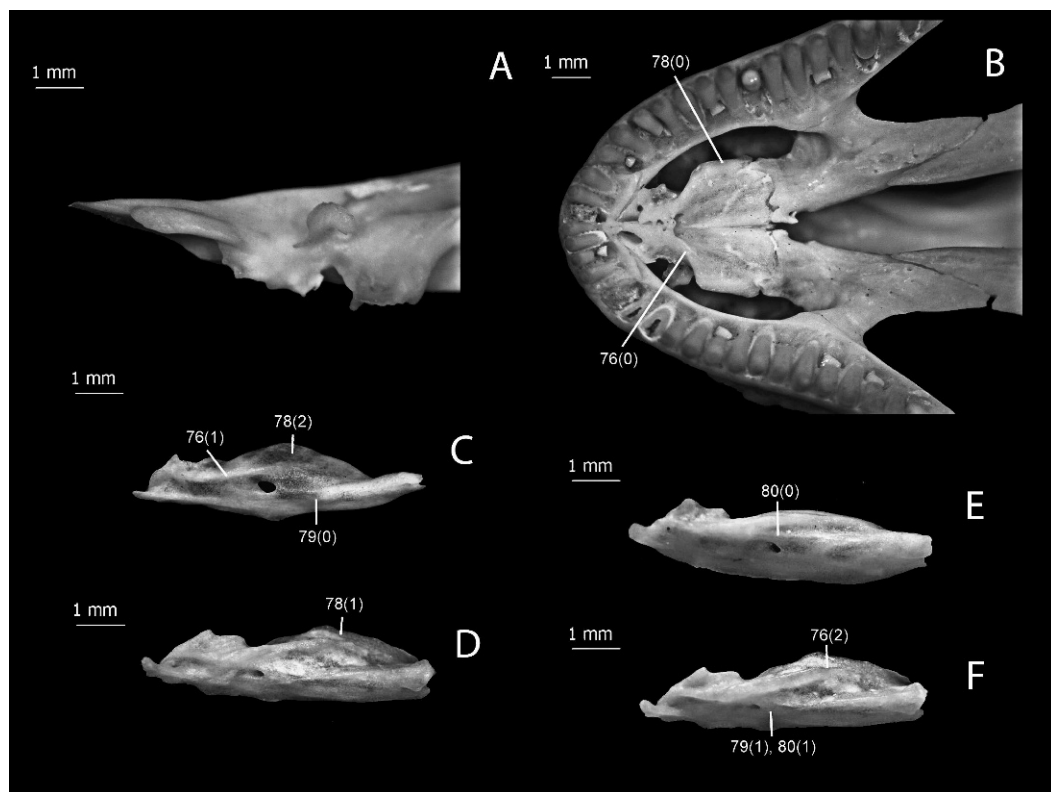
Figure 23.   A, Left vomer of *Varanus exanthematicus* TMM-M 8956, dorsolateral, anterior to the left. Illustrates characters 74(0), 75(0). B, Rostrum of *Pristidactylus torquatus* CAS 85234, ventral, anterior to the left. Illustrates characters 76(0), 78(0), 87(0). C, Left vomer of *Xenosaurus rackhami* UTEP-OC "MALB" 388, ventromedial, anterior to the left. D, Left vomer of *Xenosaurus platyceps* UF 45622, same view. C and D illustrate characters 76(1), 77(0), 78(1), 78(2), 79(0), 81(0), 81(1), 82(0), 82(1), 83(0), 83(1). E, Left vomer of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, same view. F, Left vomer of *Xenosaurus platyceps* UF 45622, same view. E and F illustrate characters 76(2), 79(1), 80(0), 80(1).

diverging ascending portion of ventral edge relatively short, beginning over halfway to medial limit of facet (Fig. 22E); (2) ascending portion relatively long, beginning less than halfway to medial limit of facet (Fig. 22D).

Evolution. Under both analyses, the ancestral states for the entire group and for Anguimorpha are ambiguous between absence and the short morphology. The ancestral state for the southern clade of *Xenosaurus* is ambiguous between the short and long morphologies, and the long morphology is an autapomorphy of *E. multicarinata*. Under Analysis 1, the ancestral state for *S. crocodilurus* +

Varanidae is ambiguous between absence and the short morphology. The ancestral state for Varanidae is absence. Along the other major branch of Anguimorpha, the ancestral state for *Xenosaurus* + Anguidae is ambiguous between absence and the short morphology, but the short morphology is the ancestral state for *Xenosaurus* and for Anguidae.

75. Vomer: Anterior process from anteromedial corner (0) absent (Fig. 23A); (1) present, short—about as long along long axis as wide perpendicular to it (Fig. 22D); (2) present, long—longer along long axis than wide perpendicular to long axis (Fig. 22E).

Evolution. Under both analyses, presence of a short process is a synapomorphy of *Xenosaurus,* and a long process is a synapomorphy of the northern clade of *Xenosaurus.*

76. Vomer: Lateral parasagittal crest on ventral surface (0) short, extends about a third of the way to the back of the vomer (Fig. 23B); (1) intermediate length, extends about half of the way to the back of the vomer (Fig. 23C); (2) long, extends about two-thirds of the way to the back of the vomer (Fig. 23F).

     Evolution. Under both analyses, the ancestral state for the entire group is ambiguous between short and intermediate length. The ancestral state for *Xenosaurus* is the intermediate morphology, with the short morphology an autapomorphy of *X. agrenon* and the long morphology a synapomorphy of the northern clade. Under Analysis 1, the ancestral state for Anguimorpha is ambiguous between short and intermediate length. The ancestral state for *Xenosaurus* + Anguidae is intermediate length, that for Anguidae is ambiguous between intermediate length and the long morphology, and that for Varanidae is the short morphology. Under Analysis 2, intermediate length is ancestral for Anguimorpha. The long morphology is a synapomorphy of *O. ventralis* + *C. enneagrammus,* and the short morphology is a synapomorphy of Varanidae.

77. Vomer: Lateral parasagittal crest (0) extends largely dorsoventrally (Fig. 23C); (1) folds medially as a tall flange, underhanging much of the vomer (Fig. 24A).

     Evolution. Under both analyses, the medial folding is an autapomorphy of *X. agrenon.*

78. Vomer: Mediolateral width of lateral flange bordered medially by lateral parasagittal crest at widest anteroposterior level (0) narrow, less than half that of remainder of vomer (Fig. 23B); (1) intermediate, one half of that of remainder of vomer to just under equal to that of remainder of vomer (Fig. 23D); (2) wide, equal to or wider than that of remainder of vomer (Fig. 23C).

     Evolution. Under both analyses, the narrow morphology is ancestral for the entire group and for Anguimorpha. The intermediate morphology is ancestral for *Xenosaurus* and the wide morphology is a synapomorphy of the southern clade of *Xenosaurus.* Under Analysis 1, the ancestral state for *Xenosaurus* + Anguidae is ambiguous between narrow and intermediate, and the ancestral state for Anguidae is ambiguous between intermediate and wide. Under Analysis 2, the ancestral state for Anguidae + Varanoidea and for Xenosauridae is narrow, making the intermediate morphology a synapomorphy of Anguidae and the wide a synapomorphy of *O. ventralis* + *C. enneagrammus.*

79. Vomer: Medial parasagittal crest (0) ends posterior to vomerine foramen (Fig. 23C); (1) ends at level of, or anterior to, vomerine foramen (Fig. 23F).

     Evolution. Under both analyses, termination at or anterior to the vomerine foramen is a synapomorphy of the northern clade of *Xenosaurus.*

80. Vomer: Medial parasagittal crest extending to or past level of vomerine foramen (0) passes lateral to foramen (Fig. 23E); (1) passes medial to foramen (Fig. 23F).

     Evolution. Given the restricted distribution of the character states, it is impossible to infer the ancestral state of this character.

81. Vomer: Vomerine foramen (0) small, mediolateral width less than one-eighth mediolateral width of vomer at same level (Fig. 23D); (1) large, mediolateral width one-eighth mediolateral width of vomer at same level or greater (Fig. 23C).
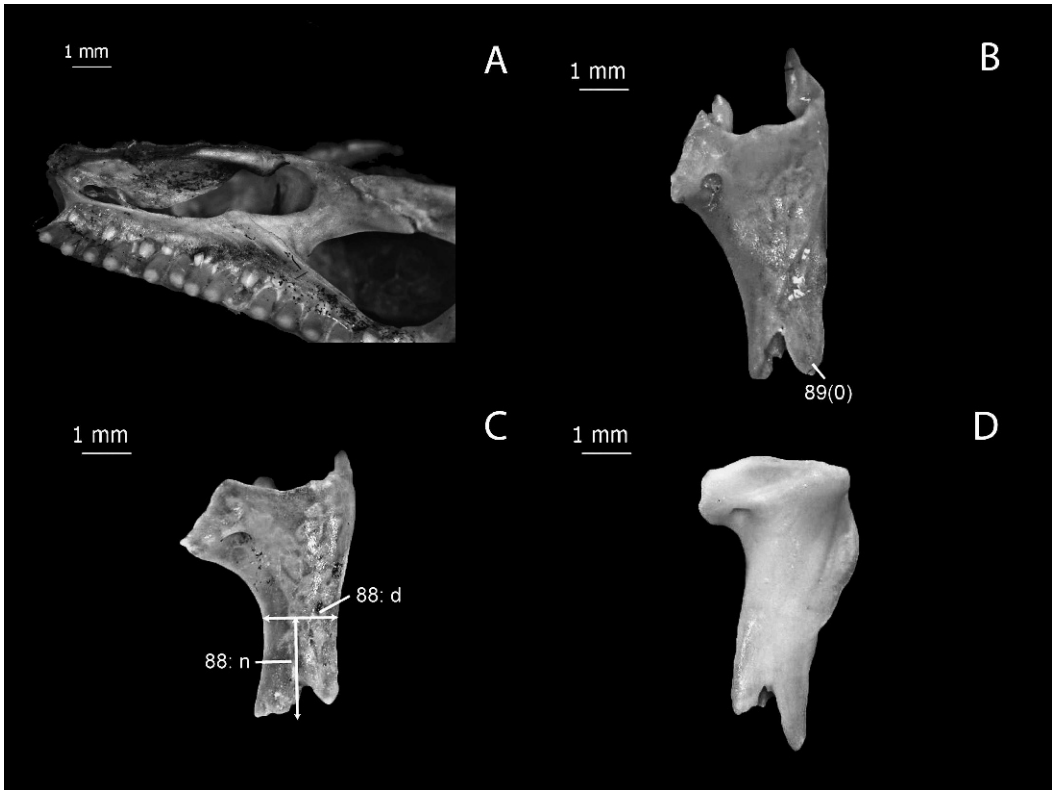
Figure 24.   A, Rostrum of *Xenosaurus agrenon* UTACV r45008, ventral, anterior to the left. Illustrates character 77(1). B, Left palatine of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, dorsal, anterior to the top. C, Left palatine of *Xenosaurus grandis* NAUQSP-JIM 1460, same view. D, Left palatine of *Elgaria multicarinata* TMM-M 8958, same view. B through D illustrate characters 84(0), 84(1), 85(0), 85(1), 85(2), 86(0), 86(1), 88 (n for numerator, d for denominator), 89(0).

Evolution. Under both analyses, a large foramen is an autapomorphy of *X. rackhami*.

82. Vomer: Posterior end of palatine process (0) nearly straight in horizontal plane (Fig. 23D); (1) bowed laterally (Fig. 23C).

Evolution. Under both analyses, lateral bowing is a synapomorphy of *X. grandis* + *X. rackhami*.

83. Vomer: Palatine process, width measured by ratio of mediolateral width to widest mediolateral width of vomer, (0) mediolaterally wide, ratio 0.44 or greater (Fig. 23D); (1) mediolaterally narrow, ratio less than 0.44 (Fig. 23C).

Evolution. Under both analyses, the ancestral state for the entire group is the wide morphology, as is that for Anguimorpha. The ancestral state for the southern clade of *Xenosaurus* is ambiguous, with the narrow morphology either a synapomorphy of the entire clade and the wide morphology an autapomorphy of *X. rectocollaris* or the narrow morphology an autapomorphy of *X. agrenon* and a synapomorphy of *X. grandis* + *X. rackhami*. Under Analysis 1, the narrow morphology is an autapomorphy of *S. crocodilurus*. Under Analysis 2, the ancestral state for Xenosauridae is ambiguous.

Palatine

The palatine is unknown in *E. serratus*, *E. lancensis*, *R. rugosus*, and *M. ornatus*. It is

not visible in the single known specimen of *B. ammoskius* (Conrad, 2006).

84. Palatine: Choanal margin (0) straight or convex anteriorly in horizontal plane (Fig. 24D); (1) concave anteriorly in horizontal plane (Fig. 24C).

    Evolution. Under both analyses, anterior concavity is a synapomorphy of the northern clade of *Xenosaurus* and an autapomorphy of *X. grandis*. Under Analysis 1, anterior concavity is an autapomorphy of Helodermatidae and of *L. borneensis*. Under Analysis 2, the ancestral states for Varanoidea and Varanidae are ambiguous, with anterior concavity either a synapomorphy of Varanoidea and convexity or linearity a synapomorphy of *Varanus* or anterior concavity an autapomorphy of Helodermatidae and *L. borneensis*.

85. Palatine: Eminence in choanal margin (0) absent (Fig. 24D); (1) small and located medial to the mediolateral midpoint of the margin (Fig. 24C); (2) large, broadly curved, and located around the mediolateral midpoint of the margin (Fig. 24B).

    Evolution. Under both analyses, absence of the eminence is ancestral for the entire group and the small, medial morphology is a synapomorphy of *Xenosaurus*. The large, broad morphology is a synapomorphy of the northern clade of *Xenosaurus*.

86. Palatine: Maxillary process (0) about as anteroposteriorly long as mediolaterally wide (Fig. 24D); (1) distinctly anteroposteriorly longer than mediolaterally wide (Fig. 24C).

    Evolution. Under both analyses, the longer-than-wide morphology is a synapomorphy of *Xenosaurus*.

87. Palatine: Pterygoid process ventral surface (0) bearing teeth (Fig. 23B); (1) bearing midline ridge or groove (Fig. 5B); (2) smooth (Fig. 25A). Presence or absence of palatine teeth was character 82 of Estes et al. (1988).

    Variation. I did not have ontogenetic series for taxa that possess palatine teeth, but the palatal teeth upon the pterygoid of *E. multicarinata* increase in number during postnatal ontogeny.

    Evolution. Under both analyses, the ancestral state for the entire group is ambiguous among the three states, but the ancestral state for Anguimorpha is absence of teeth and ridges. The presence of ridges in *X. rectocollaris*, and of teeth in *O. ventralis* and *L. borneensis*, is autapomorphic for each of these taxa.

88. Palatine: Pterygoid process, ratio of length along long axis beginning at posterior end of base of vomerine process to width perpendicular to long axis at constriction behind base of vomerine process (Fig. 24C) (0) 1.1 or less; (1) greater than 1.1 to 1.2; (2) greater than 1.2 to 1.3; (3) greater than 1.3 to 1.4; (4) greater than 1.4 to 1.5; (5) greater than 1.5.

    Variation. The pterygoid process in some but not all taxa becomes relatively wider with age, and all scorings were performed on relatively large individuals.

    Evolution. Under both analyses, the ancestral state for *Xenosaurus* is ambiguous between state 1 and state 2. State 0 is a synapomorphy of *X. agrenon* + *X. rectocollaris*, and state 4 is an autapomorphy of *X. rackhami*. Under Analysis 1, the ancestral state for the entire group is ambiguous among all states, as is that for Anguimorpha and *Xenosaurus* + Anguidae, as well as *Shinisaurus* + Varanidae. State 0 is a synapomorphy of Varanidae and an autapomorphy of Helodermatidae. Under Analysis 2, state 5 is ancestral for the entire group, Anguidae + Varanoidea, and Xenosauridae. State 0 is a synapomorphy of Varanoidea.
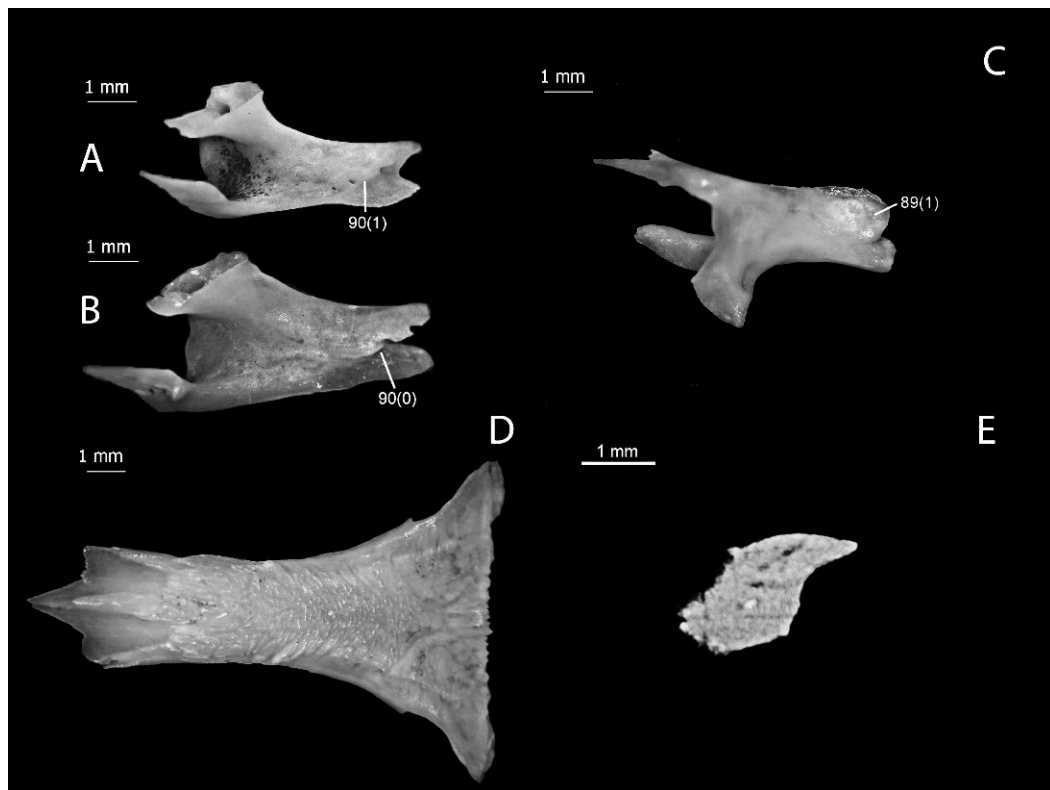
Figure 25.   A, Left palatine of *Xenosaurus rackhami* UTEP-OC "MALB" 388, ventral, anterior to the left. B, Left palatine of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, same view as A. A and B illustrate characters 87(2), 90(0), 90(1). C, Left palatine of *Xenosaurus platyceps* UF 45622, dorsal, anterior to the left. Illustrates character 89(1). D, Frontal of *Elgaria multicarinata* TMM-M 8958, dorsal, anterior to the left. Illustrates characters 91(0), 94(0), 97(0), 104(1), 108(0). E, Anterior tip of frontal of *Exostinus serratus*, CT scan of USNM v16565, ventral, anterior to the left. Illustrates character 93(0).

89. Palatine: Dorsomedial tongue for ptery-goid articulation (0) anteroposteriorly longer than mediolaterally wide at base (Fig. 24B); (1) mediolaterally wider at base than long (Fig. 25C).

Evolution. Under both analyses, the wider-than-long morphology is anautapomorphy of *X. platyceps*. Under Analysis 1, the wider-than-long morphology is a synapomorphy of Varanidae and an autapomorphy of Helodermatidae. Under Analysis 2, it is a synapomorphy of Varanoidea.

90. Palatine: Anterior to mediolateral divergence of dorsomedial and ventrolateral tongues for pterygoid articulation, medial edge of dorsoventrally diverging ventrolateral tongue (0) raised into sharp, underhanging ridge (Fig. 25B); (1) raised into low ridge with little if any underhang (Fig. 25A).

Evolution. Under both analyses, the low, rounded morphology is a synapomorphy of the southern clade of *Xeno-saurus*.

Frontal

91. Frontal: Frontals (0) remain unfused throughout ontogeny (Estes et al., 1988, Fig. 13B); (1) fuse at some point during ontogeny (Fig. 25D).

Variation. Frontal fusion occurs during ontogeny; in the taxa (specified in Materials and Methods) for which very

young postnatal specimens were available, a seam and sometimes a split at the anterior end still remained.

Evolution. Under both analyses, the fused morphology is ancestral for the entire group. Under Analysis 1, pairing is a synapomorphy of Varanidae and of Anguidae + Helodermatidae, with the fused morphology an autapomorphy of *E. multicarinata.* Under Analysis 2, the ancestral state for Anguidae + Varanoidea is ambiguous; either the paired morphology is a synapomorphy of that clade, and fused morphology is an autapomorphy of *E. multicarinata,* or the paired morphology is a synapomorphy of *O. ventralis* + *C. enneagrammus* and of Varanoidea.

92. Frontal: Frontals in taxa where fusion occurs (0) remain separate for some period of time postnatally; (1) fuse prenatally.

    Variation. This character depends upon the recognition of ontogenetic variation. It is possible that unrecognized individual variation occurs regarding when and whether fusion occurs, in particular among the extinct taxa.

    Evolution. Under both analyses, the ancestral state for the entire group is prenatal fusion. Postnatal fusion is an autapomorphy of *E. lancensis* and of *M. ornatus.*

93. Frontal: In taxa with fused frontals, frontals fuse and raised seam at line of fusion vanishes (0) only at most advanced ontogenetic stages (Fig. 25E); (1) by attainment of approximately two-thirds of ''adult'' size of frontals (Fig. 17D).

    Variation. As noted, this character is scored based on the nature of inferred ontogenetic variation.

    Evolution. Under both analyses, the ancestral state for the entire group and for Anguimorpha is early disappearance of the seam. Under Analysis 1,

the ancestral state for *E. lancensis* + *Xenosaurus* and for *E. serratus* + *Xenosaurus* is ambiguous, and late disappearance is an autapomorphy of *M. ornatus.* Under Analysis 2, the ancestral state for Xenosauridae is ambiguous.

94. Frontal: Constriction (0) weak, ratio of widest mediolateral width of frontal table anterior to level of greatest constriction to width at greatest constriction less than 1.15 (Fig. 25D); (1) moderate, ratio 1.15 to 1.7; (2) strong, ratio greater than 1.7 (Fig. 26A).

    Variation. In many taxa, including *S. crocodilurus,* the frontals in younger individuals are considerably more constricted than in older individuals, concomitant with the relatively larger size of the eyes. Individuals scored here were relatively large adults.

    Evolution. Under both analyses, the ancestral state for the entire group and for Anguimorpha is moderate constriction, and weak constriction is an autapomorphy of *S. crocodilurus.* Under Analysis 1, weak constriction is a synapomorphy of Varanidae and of Anguidae + Helodermatidae, and strong constriction is a synapomorphy of *E. serratus* + *Xenosaurus* and an autapomorphy of *M. ornatus.* Under Analysis 2, weak constriction is a synapomorphy of Anguidae + Varanoidea, and the ancestral state for Xenosauridae is ambiguous between weak and strong constriction.

95. Frontal: Osteoderms (0) lacking keels or with weak keels (Fig. 26A); (1) strongly keeled, at least in part (Fig. 26B).

    Variation. Osteoderms fuse to the frontal postnatally in most taxa, but the keel may be the first part of each osteoderm to form.

    Evolution. Under both analyses, the keeled morphology is a synapomorphy of the northern clade of *Xenosaurus.*

96. Frontal: Orbital rows of osteoderms along lateral edges (0) flat and rectan-
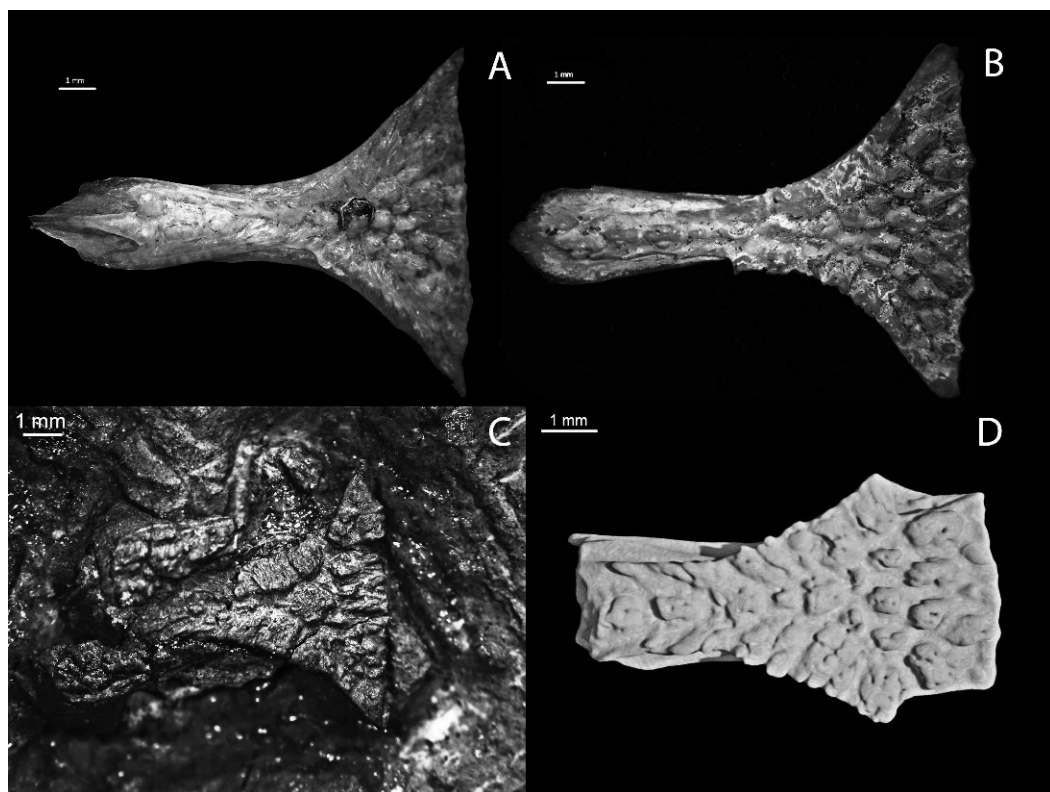
Figure 26.   A, Frontal of *Xenosaurus grandis* NAUQSP-JIM 1460, dorsal, anterior to the left. Illustrates characters 94(2), 95(0), 102(1), 103(1). B, Frontal of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, dorsal, anterior to the left. Illustrates characters 95(1), 96(1), 97(3), 98(1), 99(1), 100(0), 102(0), 103(0), 108(1). C, Frontal of *Restes rugosus* YPM PU 14640, dorsal, anterior to the left. Illustrates characters 96(0), 97(2), 98(0), 99(0). D, Frontal of *Exostinus serratus*, CT scan of AMNH 1608, dorsal, anterior to the left. Illustrates characters 98(2), 100(1), 108(2).

gular (Fig. 26C); (1) small and domed (Fig. 26B).

Variation. Osteoderms fuse to the frontal postnatally in most taxa.

Evolution. Under both analyses, the ancestral state for the entire group is ambiguous and the ancestral state for Anguimorpha is flat and rectangular. The domed morphology is a synapomorphy of *E. lancensis + Xenosaurus,* and the flat, rectangular morphology is an autapomorphy of *X. rectocollaris.*

97. Frontal: Osteoderms in center of expanded posterior portion of frontal (0) all flat and plate-like (Fig. 25D); (1) some flat and plate-like, others broad and domed (Klembara, 2008); (2) some flat and plate-like, others small and domed (Fig. 26C); (3) all small and domed (Fig. 26B).

Variation. Osteoderms become fused to the frontal and become more domed during ontogeny.

Evolution. Under both analyses, the ancestral state for the entire group is ambiguous among all three states, and that for Anguimorpha is ambiguous between state 1 and state 2. State 2 is ancestral for *R. rugosus + Xenosaurus*, and state 3 is a synapomorphy of *E. lancensis + Xenosaurus* and an autapomorphy of *B. ammoskius.* Under Analysis 1, the ancestral states for *S. crocodilurus* + Varanidae and for *Xenosaurus* + Anguidae are ambiguous like Anguimorpha. State 0 is

ancestral for Anguidae + the helodermatid lineage. Under Analysis 2, the ancestral state for Xenosauridae is ambiguous like Anguimorpha, and the ancestral state for Anguidae + Varanoidea is state 0.

98. Frontal: Region of strong development of orbital rows of osteoderms along lateral edges (0) restricted, extending anteriorly only up to greatest constriction of frontal table or ending posterior to it (Fig. 26C); (1) intermediate, extending anteriorly past greatest constriction of frontal table and for less than a third of the length of the prefrontal facet (Fig. 26B); (2) extensive, extending anteriorly past greatest constriction of frontal table and for about a third of the length of the prefrontal facet (Fig. 26D).

   Variation. Osteoderms fuse to the frontal during postnatal ontogeny.

   Evolution. Under both analyses, the ancestral state for the entire group is a restricted extent. The intermediate morphology is a synapomorphy of *S. crocodilurus* + *B. ammoskius* and of *E. serratus* + *Xenosaurus*, and the extensive morphology is an autapomorphy of *E. serratus*.

99. Frontal: Transverse rows of osteoderms in posterior expanded portion (0) two to three (Fig. 26C); (1) four or more (Fig. 26B).

   Evolution. Under both analyses, the ancestral state for the entire group is ambiguous, and four or more rows is a synapomorphy of *E. serratus* + *Xenosaurus*.

100. Frontal: Posteriormost transverse row of osteoderms in posterior expanded portion (0) similar in prominence to more anterior rows (Fig. 26B); (1) less prominent than more anterior rows (Fig. 26D).

   Variation. No variation affecting scoring was evident, save, most likely, the ontogenetic variation already noted in osteoderm characters.

   Evolution. Under both analyses, the reduced prominence of the posteriormost row is either a synapomorphy of *E. lancensis* + *Xenosaurus*, with similar prominence a synapomorphy of *Xenosaurus*, or it is an autapomorphy of *E. lancensis* and of *E. serratus*.

101. Frontal: Distance from posterior end of prefrontal facet to posterior end of frontal (0) relatively great, 2.25 or more times length of posterior sharply tapering portion of prefrontal facet (Fig. 27A); (1) relatively small, fewer than 2.25 times length of posterior portion of facet (Fig. 27B).

   Evolution. Under both analyses, a relatively small distance is an autapomorphy of *E. serratus*. Under Analysis 1, that character state is also an autapomorphy of Helodermatidae and a synapomorphy of Varanidae. Under Analysis 2, it is a synapomorphy of Varanoidea.

102. Frontal: Anterior mediolaterally tapered tip of frontal (0) mediolaterally wider at base than anteroposteriorly long (Fig. 26B); (1) longer than wide (Fig. 26A).

   Evolution. Under both analyses, longer than wide is a synapomorphy of the southern clade of *Xenosaurus*.

103. Frontal: Internasal spine (0) closely approaching anterior tip of frontal (Fig. 26B); (1) halting posterior to anterior tip with frontal extending beyond it for half or more of the length of the spine, forming an extensive anterior lamina (Fig. 26A).

   Evolution. Under both analyses, a posterior termination of the spine is a synapomorphy of *X. rackhami* + *X. grandis*.

104. Frontal: Posteriorly, medial and lateral edges of nasal facets converge (0) at a relatively wide angle of 70° or greater (Fig. 27C); (1) at a relatively narrow angle of less than 70° (Fig. 25D).
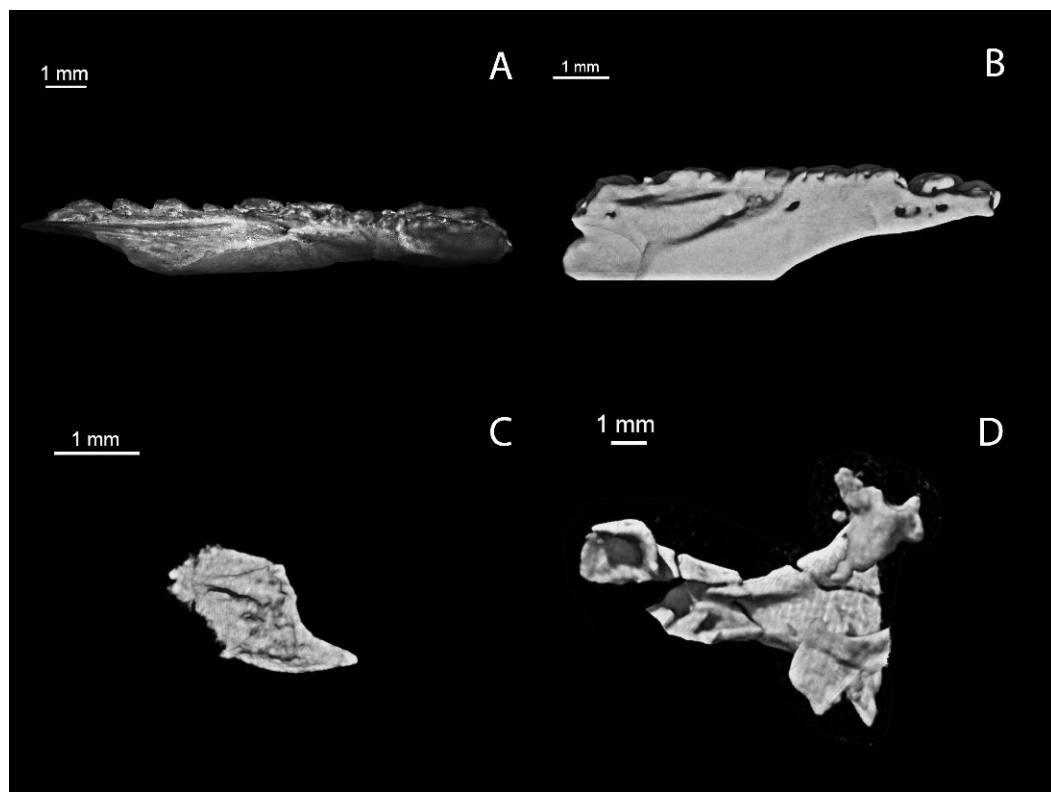
Figure 27. A, Frontal of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, left lateral, anterior to the left. Illustrates characters 101(0), 106(0), 107(0). B, Frontal of *Exostinus serratus*, CT scan of AMNH 1608, left lateral, anterior to the left. Illustrates characters 101(1), 106(1), 107(1). C, Anterior tip of frontal of *Exostinus serratus*, CT scan of USNM v16565, dorsal, anterior to the left. Illustrates character 104(0). D, Frontal of *Restes rugosus*, CT scan of YPM PU 14640, ventral, anterior to the left. Illustrates character 105(0).

Evolution. Under Analysis 1, the ancestral states for all clades with mixed character distribution are ambiguous. Under Analysis 2, the ancestral state for the entire group is a relatively narrow angle, as is that for Anguimorpha. The ancestral state for Xenosauridae is ambiguous. On the other branch of Anguimorpha, the ancestral state for Anguidae + Varanoidea is a relatively narrow angle, with the wider morphology a synapomorphy of *C. enneagrammus + O. ventralis* and an autapomorphy of *Lanthonotus borneensis*.

105. Frontal: Ventral edges of cristae cranii, at closest approach in a horizontal plane, separated by (0) greater than one-third of the mediolateral width of the frontal at that anteroposterior level (Fig. 27D); (1) one-third or less of the mediolateral width of the frontal (Fig. 28A).

Evolution. Under both analyses, wide separation is the primitive state for the entire group and for Anguimorpha. Under Analysis 1, close approach is a synapomorphy of *S. crocodilurus + *Varanidae and of *E. lancensis + Xenosaurus*. Under Analysis 2, close approach is a synapomorphy of Varanidae, and the ancestral state for Xenosauridae is ambiguous.

106. Frontal: Cristae cranii deepen anterior to expanded portion of frontal to (0)
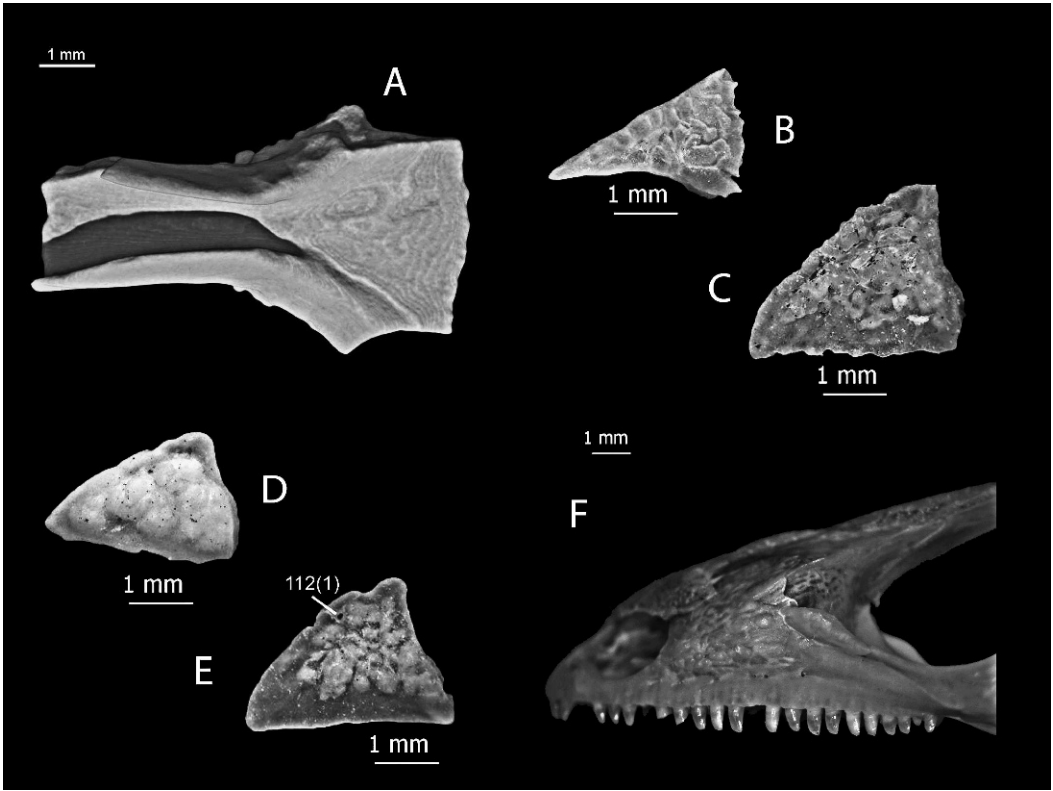
Figure 28.   A, Frontal of *Exostinus serratus*, CT scan of AMNH 1608, ventral, anterior to the left. Illustrates character 105(1). Left palpebrals, dorsal, anterior to the top: B, *Elgaria multicarinata* TMM-M 8958; C, *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen; D, *Xenosaurus agrenon* UTACV r45008; E, *Xenosaurus grandis* NAUQSP-JIM 1460. B through D illustrate characters 109(0), 109(1), 110(0), 110(1), 111(0), 111(1), 112(0), 112(1), 113(0), 113(1). F, Rostrum of *Elgaria multicarinata* CAS 85234, left lateral, anterior to the left. Illustrates character 114(0).

less than twice their dorsoventral height along the expanded portion (Fig. 27A); (1) equal to or greater than twice their dorsoventral height along the expanded portion (Fig. 27B).

Evolution. Under both analyses, shallow cristae cranii are ancestral for the entire group and for Anguimorpha, and the deep morphology is an autapomorphy of *E. lancensis*. Under Analysis 1, the deep morphology is a synapomorphy of Varanidae and of Anguidae + Helodermatidae. Under Analysis 2, the deep morphology is a synapomorphy of Anguidae + Varanoidea.

107. Frontal: Angle of posterior descent of cristae cranii just behind horizontal portion of ventral edges (0) less than 40° (Fig. 27A); (1) 40° or greater (Fig. 27B).

Evolution. Under both analyses, a steep slope is an autapomorphy of *E. serratus*. Under Analysis 1, a steep slope is a synapomorphy of Varanidae and an autapomorphy of Helodermatidae. Under Analysis 2, it is a synapomorphy of Varanoidea.

108. Frontal: Cristae cranii project laterally beyond dermal table of frontal (0) not at all (Fig. 25D); (1) only in region of greatest constriction (Fig. 26A); (2) extensively beginning in region of greatest constriction and extending nearly to anterior tip of frontal (Fig. 26D).

Evolution. Under both analyses, no projection is the ancestral state for the entire group and for Anguimorpha. Moderate projection is a synapomorphy of *E. serratus* + *Xenosaurus*, and extensive projection is an autapomorphy of *E. serratus* and a synapomorphy of *Varanus*. Under Analysis 1, moderate projection is a synapomorphy of Varanidae and an autapomorphy of Helodermatidae. Under Analysis 2, moderate projection is a synapomorphy of Varanoidea.

Palpebral

The palpebral is unknown for *M. ornatus*, *B. ammoskius*, *E. lancensis,* and *E. serratus*. It is absent in *P. torquatus* and Helodermatidae and is so reduced in *L. borneensis* that its morphology in relation to the characters described here is unscorable (Maisano et al., 2002).

109. Palpebral: Overall shape: (0) mediolaterally elongate triangle with lateral constriction caused by step in posterior margin (Fig. 28B); (1) mediolaterally shorter triangle without lateral constriction caused by step in posterior margin (Fig. 28C).

    Evolution. Under both analyses, the mediolaterally elongate morphology is a synapomorphy of Anguimorpha, and the more equilateral morphology is a synapomorphy of *R. rugosus* + *Xenosaurus* and an autapomorphy of *O. ventralis.*

110. Palpebral: Posterior edge (0) with relatively straight or smoothly curving margin (Fig. 28E); (1) with wavy margin (Fig. 28D); (2) with ragged margin (Fig. 28C).

    Evolution. Under both analyses, the wavy morphology is an autapomorphy of *X. agrenon,* and the ragged morphology is a synapomorphy of the northern clade of *Xenosaurus.*

111. Palpebral: Fused osteoderms (0) absent (Fig. 28B); (1) present as slight dorsal rugosities (Fig. 28E); (2) present across most of dorsal surface; less coverage upon anterior two-thirds and along anterior edge (Fig. 28D); (3) strong across dorsal surface, including anterior portion, with distinct, tall row along anterior edge (Fig. 28C).

    Variation. Osteodermal fusion to dermal elements, including the palpebral, occurs postnatally, although relatively small specimens of *X. platyceps* already show some dorsal rugosity.

    Evolution. Under both analyses, a slight dorsal rugosity is a synapomorphy of *R. rugosus* + *Xenosaurus*, a moderately strong covering of osteoderms is a synapomorphy of *Xenosaurus*, and a strong covering is a synapomorphy of the northern clade of *Xenosaurus.*

112. Palpebral: Foramen near anterior edge, just lateral to mediolateral level of apex of slight concavity in posterior margin (0) absent (Fig. 28C); (1) present (Fig. 28E).

    Evolution. Under both analyses, presence of the foramen is a synapomorphy of *X. rackhami* + *X. grandis.*

113. Palpebral: Strong s-curve to medial edge in horizontal plane, with anterior emargination and posterior bulge accompanied by dorsoventral deepening (0) absent (Fig. 28B); (1) present (Fig. 28D).

    Variation. In some large adult *E. multicarinata*, the medial edge of the palpebral displays a slight s-curve, but not to the extent of the taxa scored as (1).

    Evolution. Under both analyses, the ancestral state for the entire group is ambiguous, as is that for Anguimorpha. Under Analysis 1, the ancestral state for *R. rugosus* + *Xenosaurus* is presence of the s-curve, with all mixed nodes ambiguous. Under Analysis 2, the ancestral state for Xenosauridae is presence of an s-curve, and that for Anguidae + Varanoidea is absence.

Lacrimal

The lacrimal is unknown for all of the extinct taxa save *B. ammoskius*, but some of
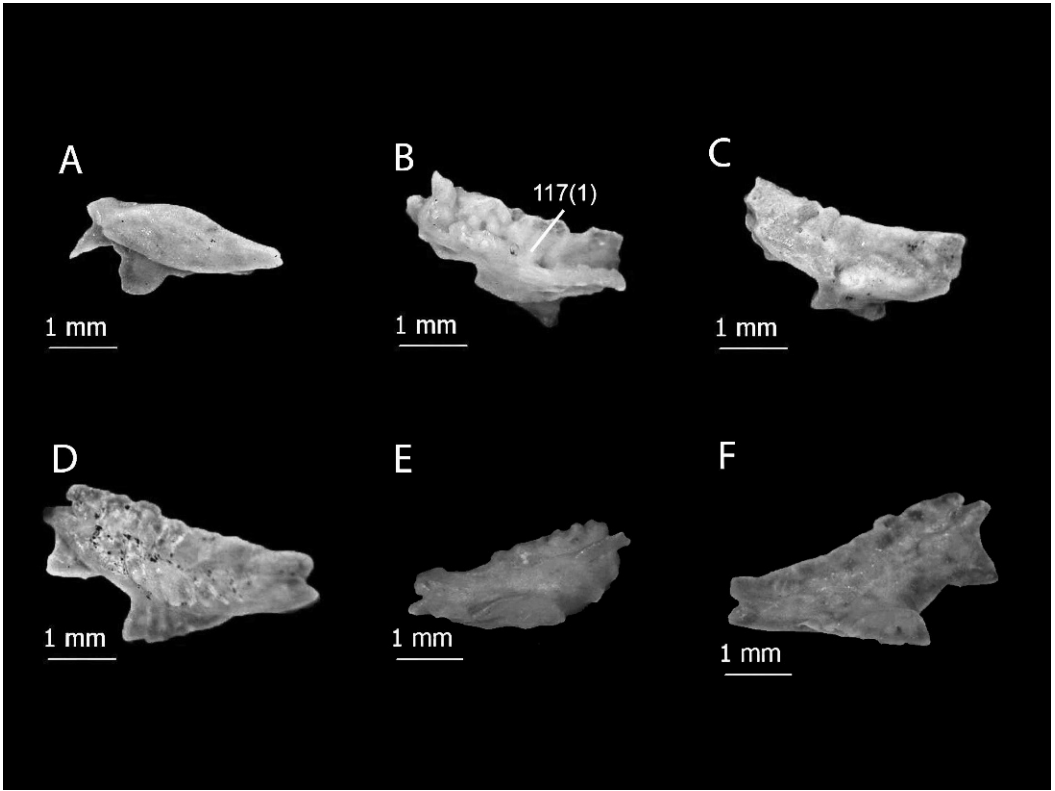
Figure 29.   Left lacrimals, lateral, anterior to the left: A, *Elgaria multicarinata* TMM-M 8958; B, *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen; C, *Xenosaurus agrenon* UTACV r45008; D, *Xenosaurus grandis* NAUQSP-JIM 1460. A through D illustrate characters 115(0), 115(1), 116(0), 116(1), 116(2), 116(3), 117(0), 117(1), 120(0), 120(1), 121(0), 121(1), 122(0), 122(1). Left lacrimals, medial, anterior to the right: E, *Xenosaurus platyceps* UF 45622; F, *Xenosaurus grandis* NAQSP-JIM 1460; E and F illustrate characters 119(0), 119(1), 122(0), 122(1).

its basic dimensions can be inferred from the morphology of the maxilla and prefrontal. This is the method by which character 114 is scored for all taxa.

114. Lacrimal: Size relative to maxilla (0) small, around one-quarter length of maxilla or smaller (Fig. 28F); (1) large, around one-third length of maxilla (Fig. 1C).

   Evolution. Under both analyses, a relatively large lacrimal is a synapomorphy of *R. rugosus* + *Xenosaurus*.

115. Lacrimal: Angle between antorbital and suborbital rami measured along lower margin (0) high, greater than 135° (Fig. 29A); (1) low, less than 135° (Fig. 29C).

   Evolution. Under both analyses, an angle of less than 135° is a synapomorphy of *X. rackhami* + *X. grandis*.

116. Lacrimal: Fused osteoderms (0) absent (Fig. 29A); (1) present as slight rugosities (Fig. 29C); (2) present as low mounds (Fig. 29B); (3) present as tall mounds, some of which bear keels (Fig. 29D).

   Variation. Osteoderms become fused to dermal elements postnatally.

   Evolution. Under both analyses, the presence of fused osteoderms as slight rugosities is a synapomorphy of *Xenosaurus*, low mounds is an autapomorphy of *X. grandis*, and tall, sometimes keeled

mounds is a synapomorphy of the northern clade of *Xenosaurus*.

117. Lacrimal: Subpalpebral fossa (0) absent (Fig. 29A); (1) present (Fig. 29B).

Evolution. Under Analysis 1, the fossa is a synapomorphy of *Xenosaurus* and of *S. crocodilurus* + *B. ammoskius*. Under Analysis 2, it is a synapomorphy of Xenosauridae.

118. Lacrimal: Subpalpebral fossa (0) contained entirely in lacrimal (Fig. 1C); (1) extending onto adjacent elements (Fig. 20B).

Evolution. Under both analyses, most nodes optimize ambiguously. The ancestral state for the southern clade of *Xenosaurus* is containment within the lacrimal.

119. Lacrimal: Lacrimal foramen (0) large, expanse at greatest extent is half or more of length of antorbital ramus of lacrimal (Fig. 29F); (1) small, less than half as extensive as antorbital ramus (Fig. 29E).

Evolution. Under both analyses, the small, constricted morphology is an autapomorphy of *X. platyceps*.

120. Lacrimal: Dorsal and ventral prefrontal processes (0) project as prominent wedges beyond main body of lacrimal in sagittal plane (Fig. 29A); (1) barely project if at all beyond body of lacrimal in sagittal plane (Fig. 29B).

Evolution. Under both analyses, lack of projection or minor projection is ancestral for the entire group, and projection is an autapomorphy of *X. newmanorum*, *E. multicarinata*, and *X. grandis*. Under Analysis 1, projection is an autapomorphy of Helodermatidae and a synapomorphy of Varanidae. Under Analysis 2, it is a synapomorphy of Varanoidea.

121. Lacrimal: Lacrimal canal (0) deeply incised into medial surface of lacrimal, with strong overhanging and/or underhanging ridges, the latter formed by flange of ventral prefrontal process (Fig. 29A); (1) shallowly incised, with marginal ridges only in anteriormost portion (Fig. 29B).

Evolution. Under both analyses, the ancestral state for the entire group is ambiguous. Under Analysis 1, shallow incision is ancestral for Anguimorpha, and deep incision is a synapomorphy of Anguidae. Under Analysis 2, the ancestral state for Anguimorpha is ambiguous, as are those for Anguidae + Varanoidea and Varanoidea.

122. Lacrimal: Posteriorly, ventral prefrontal process (0) diminishes mediolaterally (Fig. 29D); (1) expands mediolaterally (Fig. 29B).

Evolution. Under both analyses, mediolateral expansion along a posterior cline is a synapomorphy of the northern clade of *Xenosaurus*.

Jugal

The jugal is unknown for *M. ornatus*.

123. Jugal: Postorbital ramus (0) long axis relatively straight (Fig. 3C); (1) long axis broadly curved in sagittal plane (Fig. 5C).

Evolution. Under both analyses, sagittal curvature is an autapomorphy of *X. rectocollaris*.

124. Jugal: Fused osteoderms or osteodermal sculpturing (0) absent (Fig. 30A); (1) present on ventral two-thirds of postorbital ramus (Fig. 30B); (2) present on all of postorbital ramus (Fig. 30C). This character was scored as presence or absence of sculpturing by Estes et al. (1988).

Variation. Osteoderms fuse to the jugal during early postnatal ontogeny.

Evolution. Under both analyses, the ancestral state for the entire group and for Anguimorpha is a lack of sculpturing or fused osteoderms and that for *R. rugosus* + *Xenosaurus* is partial cover-
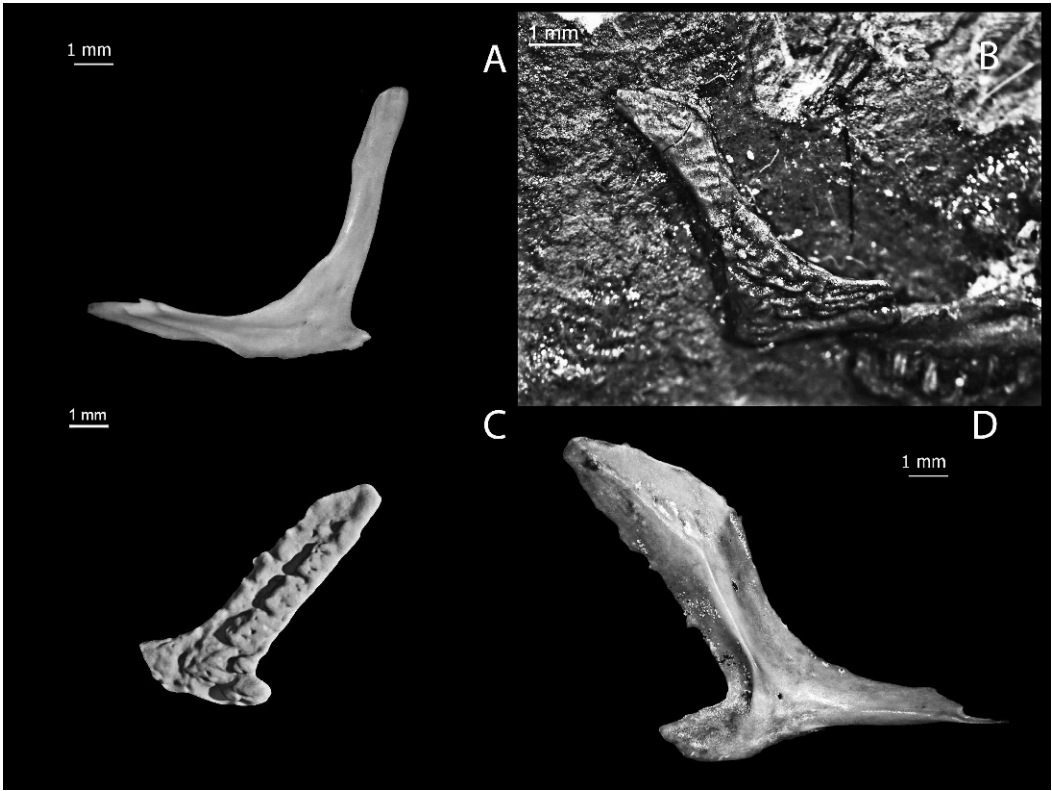
Figure 30.   A, Left jugal of *Elgaria multicarinata* TMM-M 8958, lateral, anterior to the left. Illustrates character 124(0). B, Right jugal of *Restes rugosus* YPM PU 14640, lateral, anterior to the right. Illustrates characters 124(1), 125(0), 132(2), 133(0). C, Left jugal of *Exostinus serratus*, CT scan of AMNH 1608, lateral, anterior to the left. Illustrates characters 124(2), 125(1), 132(1). D, Left jugal of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, medial, anterior to the right. Illustrates characters 126(0), 128(1).

age. Having osteoderms upon the entire dermal surface is a synapomorphy of *E. serratus* + *Xenosaurus*. Under Analysis 1, partial coverage is an autapomorphy of *S. crocodilurus*. The ancestral state for *Xenosaurus* + Anguidae and for Anguidae + Helodermatidae is ambiguous between absence and partial coverage. Under Analysis 2, partial coverage is an autapomorphy of Helodermatidae; the ancestral state for Xenosauridae and for *S. crocodilurus* + *M. ornatus* is ambiguous between absence and partial coverage.

125. Jugal: Fused osteoderms (0) relatively unconsolidated, vermiculate plate with a few mounds (Fig. 30B); (1) mostly

consolidated into discrete osteoderms (Fig. 30C).

Variation. Osteoderms fuse to the jugal during early postnatal development.

Evolution. Under both analyses, all mixed internal nodes are ambiguous regarding ancestral states.

126. Jugal: Ridge between orbital and adductor surfaces (0) at or posterior to midline of postorbital ramus of jugal (perpendicular to its long axis), orbital surface relatively sagittally oriented (Fig. 30D); (1) anterior to midline, orbital surface relatively transversely oriented (Fig. 31A).

Figure 31. A, Left jugal of *Xenosaurus agrenon* UTACV r45008, medial, anterior to the right. Illustrates characters 126(1), 127(0). B, Left jugal of *Xenosaurus platyceps* UF 45622, medial, anterior to the right. Illustrates characters 127(1), 130(1), 131(1). C, Left jugal of *Exostinus serratus*, CT scan of AMNH 1608, medial, anterior to the right. Illustrates characters 126(0), 128(0), 129(1), 131(0). D, Left jugal of *Shinisaurus crocodilurus* UF 72805, medial, anterior to the right. Illustrates characters 129(0), 130(0).

Evolution. Under both analyses, the ancestral state for the entire group is a location at or posterior to the midline. The ancestral states for the southern clade of *Xenosaurus* and for *S. crocodilurus* + *M. ornatus* are ambiguous and a location anterior to the midline is an autapomorphy of Helodermatidae.

127. Jugal: Base of postorbital ramus (0) less extensive perpendicular to its long axis than base of suborbital ramus or approximately as extensive (Fig. 31A); (1) more extensive than base of suborbital ramus (Fig. 31B).

Evolution. Under both analyses, the more extensive morphology is an autapomorphy of *X. platyceps* and of *X. grandis*.

128. Jugal: Adductor surface (0) expands ventrally (Fig. 31C); (1) diminishes ventrally, resulting in a longer quadratojugal process (Fig. 30D).

Evolution. Under both analyses, ventral diminishment is a synapomorphy of *Xenosaurus*.

129. Jugal: Foramen piercing table at junction of maxillary, orbital, and adductor surfaces (0) absent (Fig. 31D); (1) present (Fig. 31C).

Evolution. Under both analyses, the ancestral states for the entire group and for Anguimorpha are absence of the foramen. Under Analysis 1, the ancestral state for *S. crocodilurus* + Varanidae is

absence of the foramen; that for Anguidae + *Xenosaurus* is ambiguous, as is that for Helodermatidae + Anguidae and all nodes therein. Under Analysis 2, presence of the foramen is a synapomorphy of *E. serratus* + *Xenosaurus* and of *C. enneagrammus* + *O. ventralis*.

130. Jugal: Foramen piercing adductor surface just posterior to table at junction of maxillary, orbital, and adductor surfaces (0) absent (Fig. 31D); (1) present (Fig. 31B).

    Evolution. Under both analyses, the ancestral states for the entire group and for Anguimorpha are ambiguous. Under Analysis 1, the ancestral state for *S. crocodilurus* + Varanidae and for Anguidae + Helodermatidae is absence of the foramen. Under Analysis 2, the ancestral state for Anguidae + Varanoidea is absence, and that for Xenosauridae is ambiguous.

131. Jugal: Anterior expansion at meeting of anterior and dorsal edges of postorbital ramus (0) absent (Fig. 31C); (1) present (Fig. 31B).

    Evolution. Under both analyses, the ancestral states for *R. rugosus* + *Xenosaurus* and *E. lancensis* + *Xenosaurus* were ambiguous. The ancestral state for *Xenosaurus* is expansion. Lack of expansion is an autapomorphy of *X. rectocollaris*.

132. Jugal: Tip of postorbital ramus (0) without strong change in sagittal angle at level of postorbital facet (Estes et al., 1988, Fig. 13B); (1) moderately projected posteriorly at beginning of level of postorbital facet by less than 20° to long axis of majority of postorbital ramus (Fig. 30C); (2) strongly projected posteriorly beginning at level of postorbital facet by 20° or more to long axis of majority of postorbital ramus (Fig. 30B).

    Evolution. Under both analyses, the ancestral state for the entire group and

for Anguimorpha is moderate posterior projection, as is that for shinisaurs. The ancestral state for Varanidae is lack of projection, and that for *R. rugosus* + *Xenosaurus* is ambiguous between moderate and strong projection. Under Analysis 1, the ancestral state for *S. crocodilurus* + Varanidae is moderate projection, as is that for *Xenosaurus* + Anguidae. The ancestral state for Anguidae + Helodermatidae and for Anguidae is ambiguous between no and moderate projection. Under Analysis 2, the ancestral state for Anguimorpha, Anguidae + Varanoidea, and Xenosauridae is moderate projection. A lack of projection is an autapomorphy of *C. enneagrammus* and a synapomorphy of Varanoidea.

133. Jugal: Posterior edge of postorbital ramus (0) straight or smoothly curved (Fig. 30B); (1) abruptly angled toward the vertical at level of postorbital facet (Fig. 3C).

    Evolution. Under both analyses, abrupt vertical angulation is a synapomorphy of *X. rackhami* + *X. grandis*.

Postorbital/Postfrontal

The postorbital and postfrontal are unknown in *M. ornatus*, *E. serratus*, and *E. lancensis*. The postorbital is unknown in *B. ammoskius*. Only the postfrontal ossifies in Helodermatidae and *L. borneensis*.

134. Postorbital/Postfrontal: Postorbital and postfrontal (0) remain separate well after hatching/birth or throughout ontogeny (Fig. 32A); (1) fuse in late prenatal or early postnatal ontogeny (Fig. 32B) (see character 14 of Estes et al., 1988).

    Variation. As noted, this character involves the assessment of the ontogenetic stage of a specimen. Justifications for age assessments of the fossils were given in Materials and Methods.

    Evolution. Under both analyses, the ancestral state for the entire group
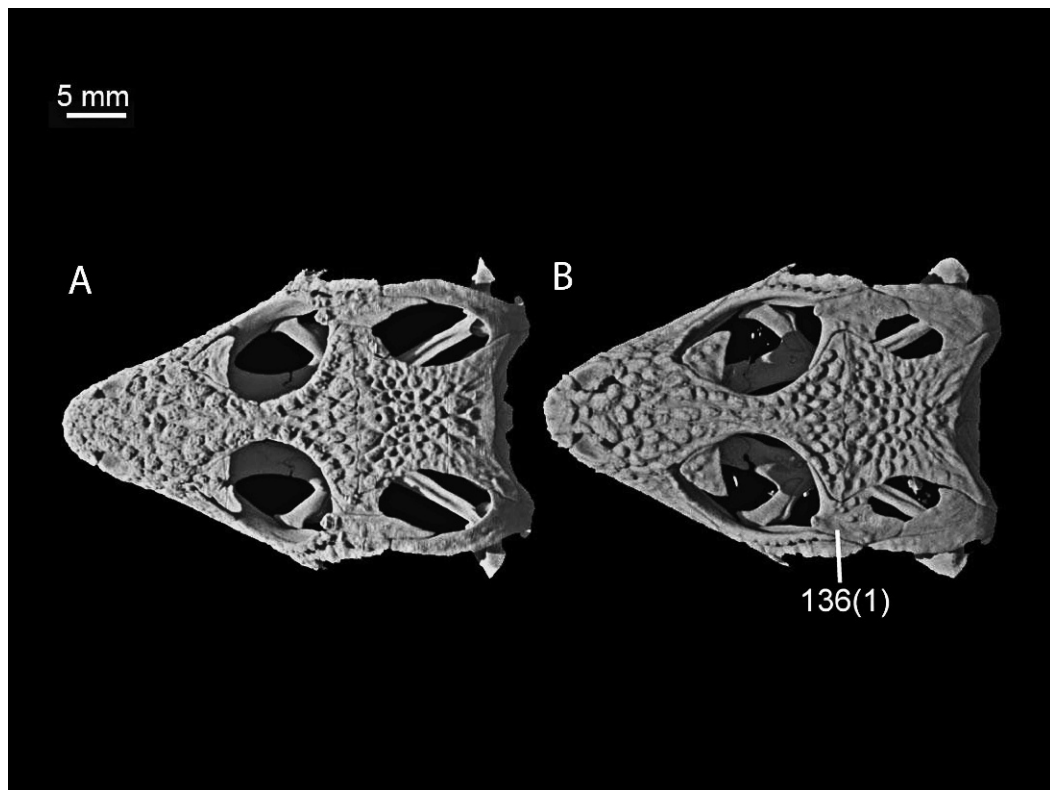
Figure 32.   Skulls, dorsal, anterior to the left: A, *Xenosaurus newmanorum*, CT scan of UMMZ 126056; B, *Xenosaurus rackhami*, CT scan of UTEP 4555. A and B illustrate characters 134(0), 134(1), 136(1), 138(0), 139(1), 139(2), 140(0), 140(1), 141(0), 141(1), 142(1), 165(1), 165(3), 166(0), 166(1).

and for Anguimorpha is lack of fusion, and early fusion is a synapomorphy of the southern clade of *Xenosaurus*. Under Analysis 1, the ancestral state for *S. crocodilurus* + Varanoidea is ambiguous. Under Analysis 2, early fusion is a synapomorphy of *Varanus* and an autapomorphy of *S. crocodilurus*.

135. Postorbital/Postfrontal: Angle of post-frontal "clasp" of frontoparietal suture (taken between long axes of anterior and posterior processes of postfrontal) (0) less than 80° (Fig. 5A); (1) 80° to 85° inclusive (Fig. 4A); (2) greater than 85° (Fig. 3A).

Evolution. Under both analyses, state 2 is ancestral for the entire group. The ancestral state for *Xenosaurus* is ambiguous between state 2 and state 1.

State 0 is a synapomorphy of *X. agrenon* + *X. rectocollaris* and an autapomorphy of *X. platyceps*.

136. Postorbital/Postfrontal: Dorsal ridge adjacent to lateral edge of postorbital (0) absent (Fig. 33A); (1) present (Fig. 32B).

Evolution. Under both analyses, absence of a ridge is the ancestral state for the entire group and for Anguimorpha. Under Analysis 1, presence of a ridge is a synapomorphy of *Xenosaurus* and an autapomorphy of *S. crocodilurus*. Under Analysis 2, the ancestral state for Xenosauridae is ambiguous.

137. Postorbital/Postfrontal: Postorbital (0) relatively flat, lying largely in horizontal plane (Fig. 33A); (1) bearing deep
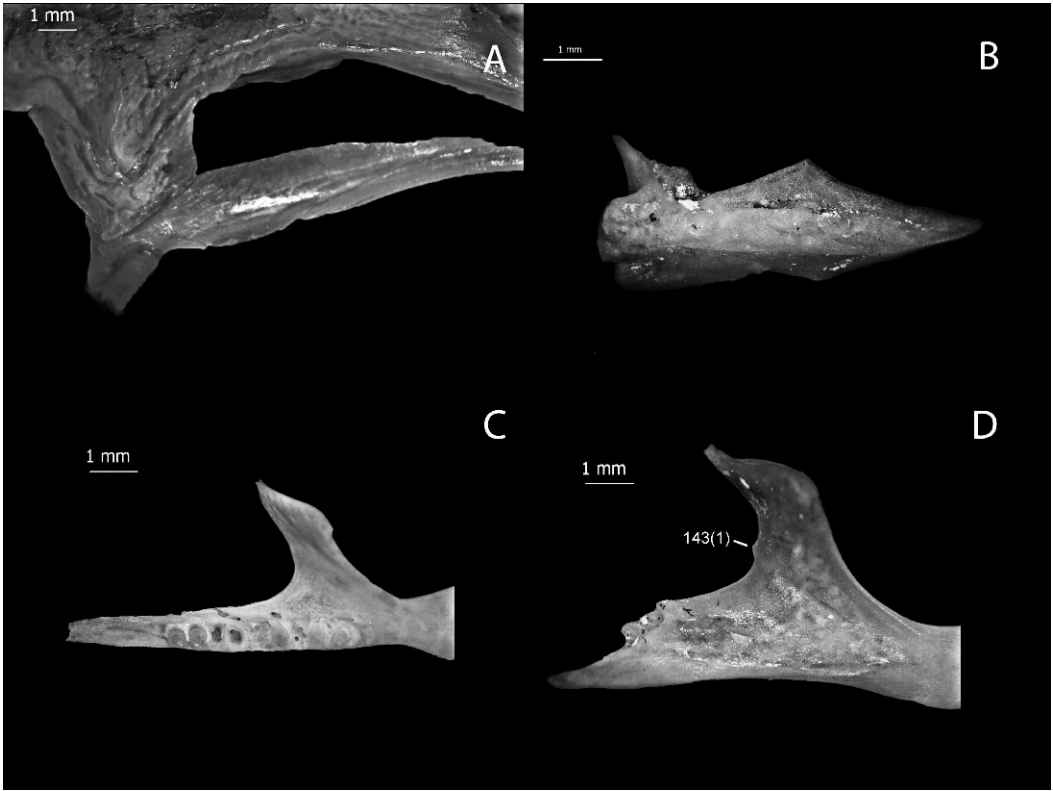
Figure 33.   A, Temporal region of *Elgaria multicarinata* CAS 85234, dorsolateral, anterior to the left. Illustrates characters 136(0), 137(0), 139(0), 142(0). B, Left postorbital of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, dorsolateral, anterior to the left. Illustrates character 137(1). C, Left pterygoid of *Shinisaurus crocodilurus* UF 72805, ventral, anterior to the left. Illustrates characters 143(0), 145(0). D, Left pterygoid of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, ventral, anterior to the left. Illustrates characters 143(1), 145(2).

flange descending from lateral edge, creating a surface in the sagittal plane, perpendicular to the main body of the bone (Fig. 33B).

Evolution. Under both analyses, the flat morphology is ancestral for the entire group and for Anguimorpha. Under Analysis 1, presence of a flange is a synapomorphy of *Xenosaurus* and an autapomorphy of *S. crocodilurus*. Under Analysis 2, the ancestral state for Xenosauridae is ambiguous.

138. Postorbital/Postfrontal: Tip of postorbital process of postfrontal (0) pointed, formed by meeting of smoothly curving medial and lateral edges (Fig. 32A); (1) squared-off because of posterior

inflection of medial edge in horizontal plane (Fig. 32B).

Evolution. Under both analyses, the ancestral state for the entire group and for Anguimorpha is pointed, and the squared-off morphology is a synapomorphy of the southern clade of *Xenosaurus* and an autapomorphy of *S. crocodilurus*. Under Analysis 1, the squared-off morphology is a synapomorphy of *Varanus* and an autapomorphy of Helodermatidae. Under Analysis 2, the ancestral state for Varanoidea is ambiguous.

139. Postorbital/Postfrontal: Narrowness of postorbital measured by ratio of anteroposterior length to mediolateral width

just posterior to divergence of posterior process of postfrontal (0) 4.0 or greater (Fig. 33A); (1) between 2.5 and 4.0 (Fig. 32A); (2) 2.5 or less (Fig. 32B).

Evolution. Under both analyses, the ancestral state of the entire group and of Anguimorpha is the narrow morphology, and the wide morphology is a synapomorphy of *X. rackhami* + *X. grandis*. Under Analysis 1, intermediate width is a synapomorphy of *Xenosaurus* and an autapomorphy of *S. crocodilurus*. Under Analysis 2, the ancestral state for Xenosauridae is ambiguous between the narrow and intermediate morphologies.

140. Postorbital/Postfrontal: Posterior end of squamosal process of postorbital (0) pointed (Fig. 32A); (1) rounded (Fig. 32B).

Evolution. Under both analyses, the rounded morphology is an autapomorphy of *X. rackhami*.

141. Postorbital/Postfrontal: Posterior end of squamosal process of postorbital (0) gently curved medially in horizontal plane or not curved medially (Fig. 32A); (1) strongly curved medially in horizontal plane, resulting in sharp change in angle of medial edge (Fig. 32B).

Evolution. Under both analyses, strong curvature is a synapomorphy of *X. rackhami* + *X. grandis*.

142. Postorbital/Postfrontal: Lateral edge of postorbital (0) straight or nearly straight in horizontal plane (Fig. 33A); (1) broadly curved in horizontal plane (Fig. 32B).

Evolution. Under both analyses, the ancestral state for *Xenosaurus* is ambiguous.

Pterygoid

The pterygoid is unknown in *E. lancensis* and *E. serratus* and is not substantially visible in *B. ammoskius*.

143. Pterygoid: Margin of pterygoid bordering infraorbital fenestra (0) smoothly curved (Fig. 33C); (1) bearing small eminence just medial of posterior apex (Fig. 33D).

Evolution. Under both analyses, presence of an eminence is a synapomorphy of the northern clade of *Xenosaurus* and an autapomorphy of Helodermatidae.

144. Pterygoid: Medial and lateral edges of vomerine process posterior to oblique anterior edge (0) weakly divergent (by 20° or less) in horizontal plane (Fig. 34A); (1) strongly divergent (by greater than 20°) in horizontal plane (Fig. 34B).

Evolution. Under both analyses, strong divergence is an autapomorphy of *R. rugosus* and of *C. enneagrammus*.

145. Pterygoid: Bears (0) large row or patch of teeth (Fig. 33C); (1) one or two small teeth, sometimes bilaterally asymmetrical (Fig. 34B); (2) no teeth (Fig. 33D). Presence or absence of pterygoid teeth was character 83 of Estes et al. (1988).

Variation. Pterygoid teeth often increase in number with age (personal observation), and observations on this character were made using relatively large individuals. Additionally, when teeth are highly reduced, their presence can vary from side to side in an individual or from individual to individual in a species (e.g., *C. enneagrammus*).

Evolution. Under both analyses, reduction of pterygoid dentition is a synapomorphy of *Xenosaurus* + *R. rugosus* and an autapomorphy of *C. enneagrammus*. Absence of pterygoid dentition is a synapomorphy of *Xenosaurus* and of *Varanus*.

Ectopterygoid

The ectopterygoid is unknown for all extinct taxa in the study (not sufficiently exposed in *B. ammoskius*).
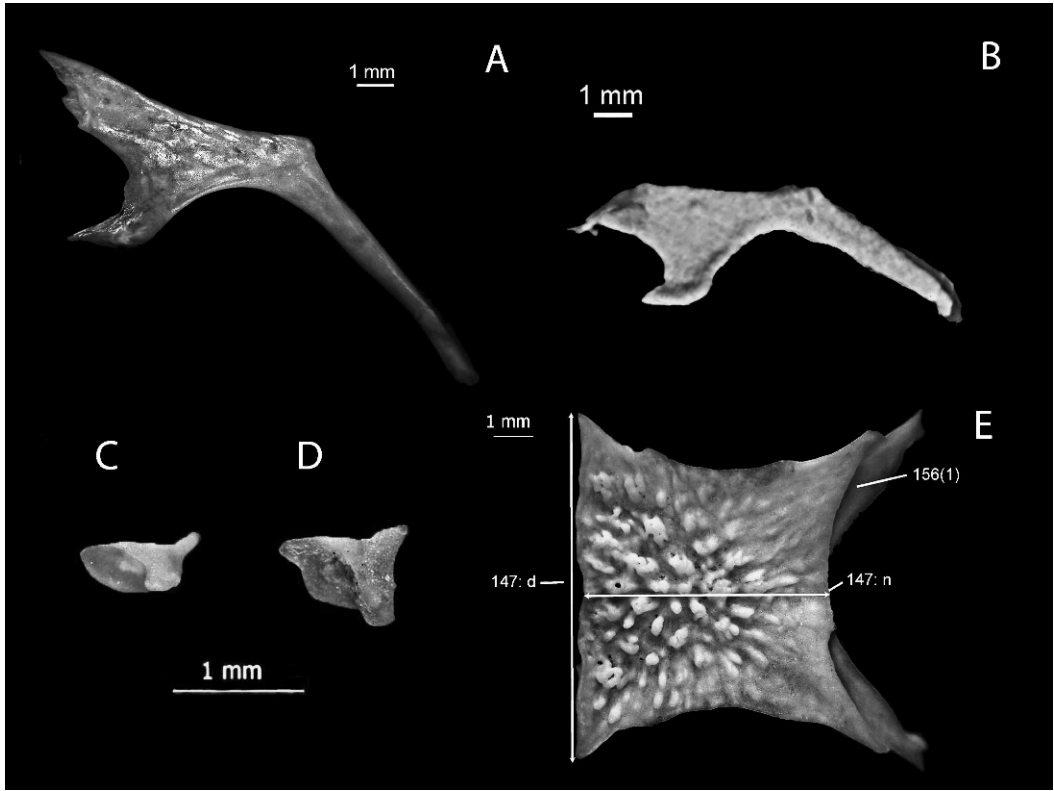
Figure 34.   Right pterygoids, ventral, anterior to the left: A, *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen. Illustrates character 144(0). B, *Restes rugosus*, CT scan of YPM PU 14640. Illustrates characters 144(1), 145(1). Left ectopterygoids, maxillary articulation surfaces, anterior to the left: C, *Elgaria multicarinata* TMM-M 8958; D, *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen. C and D illustrate characters 146(0), 146(1). E, Parietal of *Xenosaurus rackhami* UTEP-OC "MALB" 388, dorsal, anterior to the left. Illustrates characters 147 (n for numerator, d for denominator), 150(0), 151(1), 153(1), 154(1), 156(1).

146. Ectopterygoid: Prominent descending projection of maxillary process (0) absent (Fig. 34C); (1) present (Fig. 34D).

Evolution. Under both analyses, presence of a descending projection is a synapomorphy of *Xenosaurus*.

Parietal

The parietal is unknown in *R. rugosus* and *E. serratus*.

147. Parietal: Ratio of anteroposterior length along midline (to apex of meeting of supratemporal processes) to mediolateral width at frontoparietal suture (Fig. 34E) (0) less than 0.70; (1) 0.70 to less than 0.75; (2) 0.75 to less than 0.80; (3) 0.80 to less than 0.85; (4) 0.85 to less than 0.90; (5) 0.90 to less than 0.95; (6) 0.95 to less than 1.00; (7) 1.00 to less than 1.05; (8) 1.05 to less than 1.10; (9) 1.10 to less than 1.15; (A) 1.15 to less than 1.20; (B) 1.20 to less than 1.25; (C) 1.25 or greater.

Variation. The length-to-width ratio of the parietal body increases with growth, especially in the earlier parts of ontogeny (personal observation). Thus, care must be taken to use relatively large adult individuals in scoring this character.

Evolution. Under both analyses, the ancestral state for the entire group is ambiguous among state 1, state 2, state

3, and state 4. The ancestral state for Anguimorpha is ambiguous between state 3 and state 4. Additionally, the ancestral state for *S. crocodilurus + M. ornatus* is state 5. State 6 is a synapomorphy of *S. crocodilurus + B. ammoskius*, and state 9 is an autapomorphy of *S. crocodilurus*. The ancestral state for Anguidae is ambiguous between state 3 and state 4. State 7 is an autapomorphy of *O. ventralis*. State C is an autapomorphy of *E. lancensis.* The ancestral state for *Xenosaurus* is ambiguous between state 3 and state 4. A reduced ratio is a synapomorphy of the southern clade of *Xenosaurus*, whose ancestral state is ambiguous between state 1 and state 2. State 0 is a synapomorphy of *X. agrenon + X. rectocollaris*. State 8 is an autapomorphy of *L. borneensis,* and state 0 is an autapomorphy of *V. exanthematicus*. Under Analysis 1, the ancestral state for *S. crocodilurus +* Varanidae is ambiguous between state 4 and state 5, and that for *Varanus* is state 4. The ancestral state for *Xenosaurus +* Anguidae and for Anguidae + Helodermatidae is ambiguous between state 3 and state 4. Under Analysis 2, the ancestral state for Anguidae + Varanoidea is ambiguous between state 3 and state 4, as is that for Varanoidea and all nodes therein. The ancestral state for Xenosauridae is ambiguous among state 3, state 4, and state 5, as is that for *Xenosaurus + E. lancensis*.

148. Parietal: Ratio of anteroposterior length of supratemporal processes beginning at apex of their meeting to mediolateral width at widest separation of processes (Fig. 35A) (0) less than 0.20; (1) 0.20 to less than 0.25; (2) 0.25 to less than 0.30; (3) 0.30 to less than 0.35; (4) 0.35 to less than 0.40; (5) 0.40 to less than 0.45; (6) 0.45 to less than 0.50; (7) 0.50 or greater.

Variation. The posterior portion of the parietal becomes relatively more elongate with growth, especially in early ontogeny (personal observation), so it is important to score this character on relatively large adults.

Evolution. Under both analyses, the ancestral state for Varanidae is state 5, and state 7 is an autapomorphy of *L. borneensis*. State 7 is a synapomorphy of Anguidae. The ancestral state for *S. crocodilurus + M. ornatus* is state 4, and state 3 is an autapomorphy of *S. crocodilurus*. Finally, the ancestral state for *Xenosaurus* is ambiguous between state 2 and state 3. The ancestral state for the northern clade of *Xenosaurus* is state 2, and state 0 is an autapomorphy of *X. newmanorum*. In the southern clade, state 1 is an autapomorphy of *X. grandis*. Under Analysis 1, the ancestral state for the entire group, Anguimorpha, *S. crocodilurus +* Varanidae, and *Xenosaurus +* Anguidae is ambiguous between state 4 and state 5. Under Analysis 2, the ancestral state for the entire group, Anguimorpha, Anguidae + Varanoidea, and Varanoidea is state 5. State 4 is an autapomorphy of Helodermatidae. On the other branch of Anguimorpha, state 4 is a synapomorphy of Xenosauridae.

149. Parietal: Attachment areas for adductor musculature (0) dorsolateral or lateral, without extensive overhanging flange; (1) ventral, roofed over by flange of parietal table (Fig. 35B) (see character 54 of Estes et al., 1988).

Variation. Although the overhanging flange in those taxa with ventral origin often becomes relatively more extensive with age, I did not observe intraspecies variation that would alter the scoring of the character.

Evolution. Under both analyses, the ancestral state for *Xenosaurus + E. lancensis* is ventral origin. Under Analysis 1, the ancestral state for the entire group and for Anguimorpha is dorsal origin, and ventral origin is a synapomorphy of *Xenosaurus +* Anguidae.
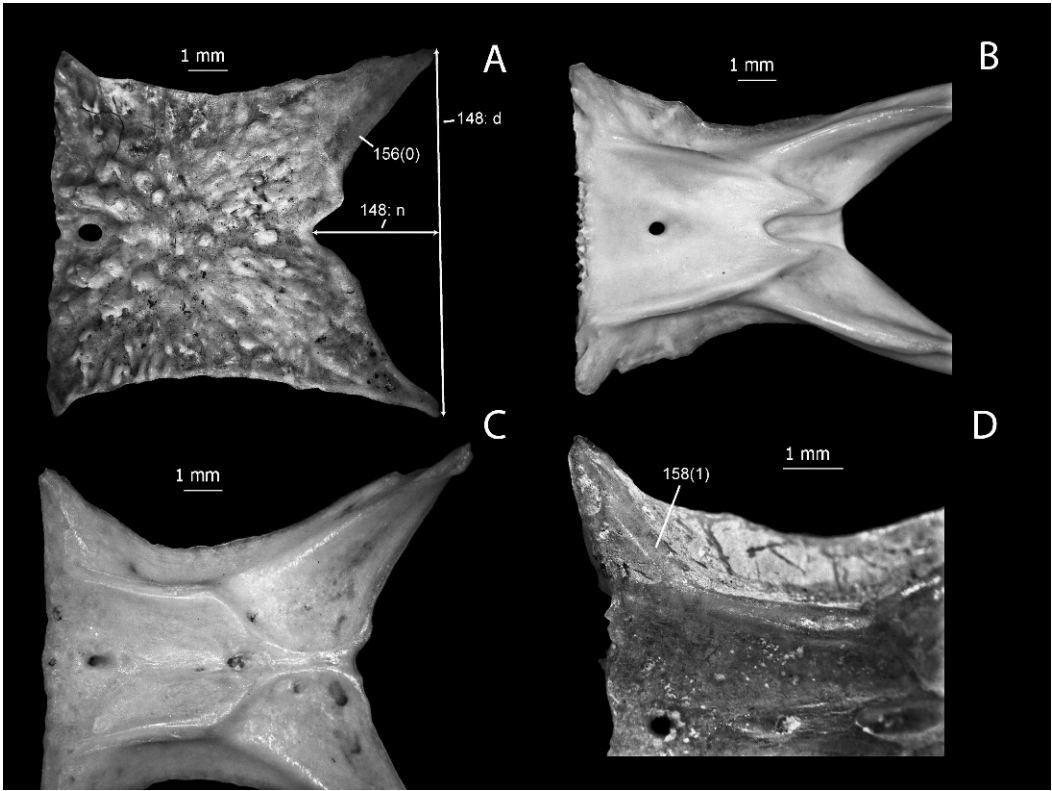
Figure 35.   A, Parietal of *Xenosaurus agrenon* UTACV r45008, dorsal, anterior to the left. Illustrates characters 148 (n for numerator, d for denominator), 150(1), 152(1), 153(0), 155(2), 156(0). B, Parietal of *Elgaria multicarinata* TMM-M 8958, ventral, anterior to the left. Illustrates characters 149(1), 152(0), 155(0), 157(0). C, Parietal of *Xenosaurus platyceps* UF 45622, ventral, anterior to the left. Illustrates characters 154(2), 155(1), 157(1). D, Parietal of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, ventral, anterior to the left. Illustrates characters 154(3), 158(1).

Note that this is dependent upon the use of an iguanian as the immediate anguimorph outgroup. Most scleroglossans show ventral origin (Estes et al., 1988). Under Analysis 2, the ancestral state for all mixed nodes is ambiguous.

150. Parietal: Lateral edges forming margins of supratemporal fenestrae (0) strongly curved in a horizontal plane (Fig. 34E); (1) weakly curved, especially anterior to apex of temporal emargination (Fig. 35A).

Variation. In the taxa showing lateral or dorsolateral origin of the adductor musculature (character 149-0), the degree of emargination increases with age as the braincase becomes relatively smaller and the adductor chamber relatively larger.

Evolution. Under both analyses, relatively weak curvature is an autapomorphy of *X. agrenon*.

151. Parietal: Number of osteoderms on each side lateral to midline osteoderm just posterior to parietal foramen (0) three (Fig. 1A); (1) two (Fig. 34E); (2) one (Conrad, 2006, fig. 2A).

Evolution. Under both analyses, the ancestral state for the entire group is ambiguous between three osteoderms and two osteoderms. The ancestral

state for shinisaurs is two osteoderms and one osteoderm is an autapomorphy of *M. ornatus*.

152. Parietal: Parietal foramen (0) set far back from frontoparietal suture, considerably posterior to anterolateral extensions of parietal bearing postfrontal facets (Fig. 35B); (1) set close to frontoparietal suture, at anteroposterior level of anterolateral extensions bearing postfrontal facets (Fig. 35A).

Variation. State 0 reportedly occurs in some *S. crocodilurus* (J. L. Conrad, personal communication), although not in the specimens examined.

Evolution. Under both analyses, the ancestral state for the entire group and for Anguimorpha is ambiguous. Under Analysis 1, the ancestral state for *Xenosaurus* + Anguidae and for Helodermatidae + Anguidae is ambiguous. The ancestral state for *E. multicarinata* + *O. ventralis* is relatively posterior placement. Under Analysis 2, the ancestral state for *S. crocodilurus* + Varanoidea is the relatively posterior placement, with placement close to the frontoparietal suture an autapomorphy of *S. crocodilurus*. The ancestral state for Anguidae + Helodermatidae is ambiguous. Under Analysis 2, the ancestral state for Anguidae + Varanoidea is relatively posterior placement.

153. Parietal: Parietal foramen (0) relatively large (Fig. 35A); (1) small, barely larger than tiny nutrient foramina (Fig. 34E).

Evolution. Under both analyses, the small morphology is an autapomorphy of *X. rackhami*.

154. Parietal: Anterior edge in horizontal plane (0) convex (Conrad, 2006, fig. 2A); (1) relatively straight (Fig. 34E); (2) slightly concave (Fig. 35C); (3) strongly concave (Fig. 35D).

Evolution. Under both analyses, the ancestral state for the entire group is ambiguous among straight, slightly

concave, and strongly concave. The ancestral state for shinisaurs is relatively straight and a convex morphology is an autapomorphy of *B. ammoskius*. The ancestral state for Anguidae and xenosaurs is also straight, with convex an autapomorphy of *E. lancensis*, slightly concave a synapomorphy of the northern clade of *Xenosaurus*, and strongly concave an autapomorphy of *X. newmanorum*. Strongly concave is an autapomorphy of *L. borneensis*. Under Analysis 1, the relatively straight morphology is ancestral for Anguimorpha, and slightly concave is an autapomorphy of Helodermatidae. Under Analysis 2, the ancestral state for Anguimorpha is ambiguous between relatively straight and slightly concave.

155. Parietal: Notch in posterior edge of parietal at meeting of medial edges of supratemporal processes (0) absent (Fig. 35B); (1) weak, more than four times as mediolaterally wide as anteroposteriorly long (Fig. 35C); (2) strong, four times or less as mediolaterally wide as anteroposteriorly long (Fig. 35A).

Evolution. Under both analyses, the ancestral state for the entire group and for Anguimorpha is ambiguous between weakly notched and strongly notched, as are the ancestral states for Varanidae and Anguidae. The absence of a notch is a synapomorphy of shinisaurs and an autapomorphy of *E. multicarinata*, Helodermatidae, and *V. exanthematicus*. The ancestral state for *E. lancensis* + *Xenosaurus* is weakly notched. The strongly notched morphology is a synapomorphy of *X. agrenon* + *X. rectocollaris,* and absence of a notch is a synapomorphy of *X. rackhami* + *X. grandis*. Under Analysis 1, the ancestral state for shinisaurs + Varanidae is ambiguous between weakly and strongly notched, as is that for *Xenosaurus* + Anguidae. Under Analysis 2, the ancestral state for Xenosauridae is weakly notched.
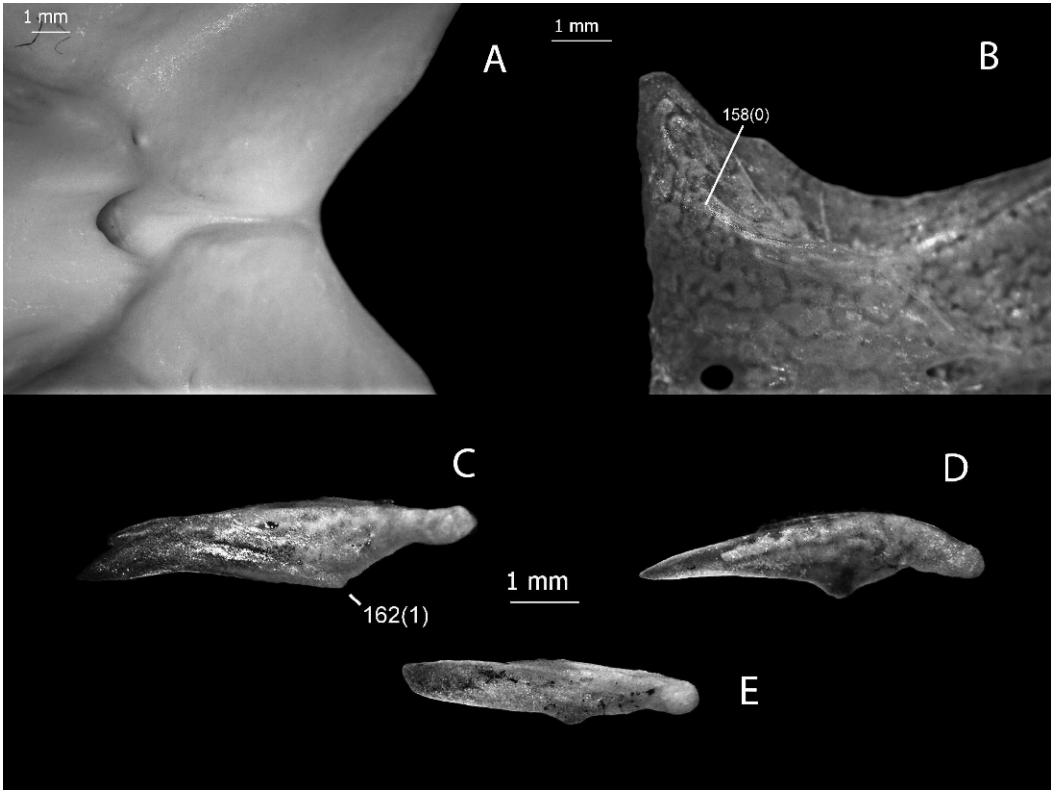
Figure 36.   Parietals, ventral, anterior to the left: A, *Heloderma suspectum* TMM-M 9001. Illustrates character 157(2). B, *Xen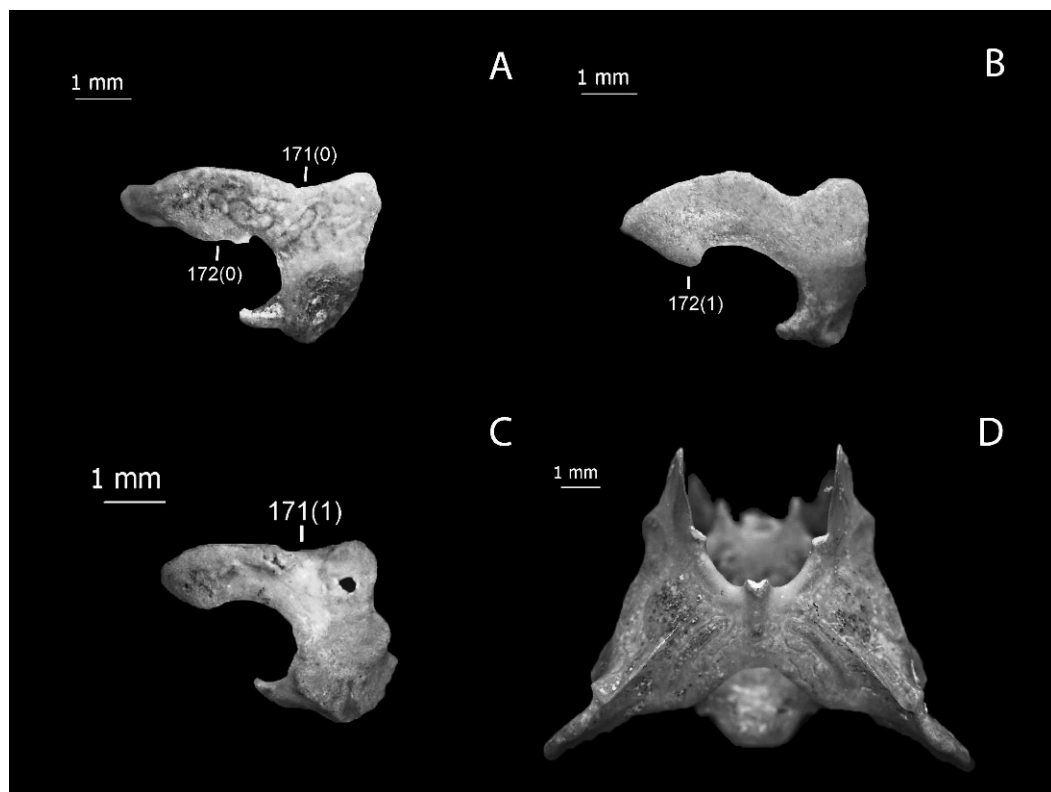osaurus grandis* NAUQSP-JIM 1460. Illustrates character 158(0). Left supratemporals, lateral, anterior to the left: C, *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen; D, *Xenosaurus grandis* NAUQSP-JIM 1460. E, *Xenosaurus agrenon* UTACV r45008. C through E illustrate characters 159(0), 159(1), 160(0), 160(1), 161(1), 162(1), 163(0), 163(1), 163(2).

156. Parietal: Dorsal fossae for m. articulo-parietalis attachment (0) shallow, only slightly stepped down from parietal table (Fig. 35A); (1) deep, divided from parietal table by sharp ridge along at least part of fossa (Fig. 34E).

   Variation. The relative depth of the fossae increases somewhat with age, most prominently in the early stages of postnatal ontogeny.

   Evolution. Under both analyses, the ancestral condition for the entire group is ambiguous, and the deep morphology is a synapomorphy of *X. rackhami + X. grandis* and an autapomorphy of *C. enneagrammus*. Under Analysis 1, the ancestral state for Anguimorpha is ambiguous, and the ancestral state for

Xenosaurus + Anguidae is the shallow morphology. Under Analysis 2, the ancestral state for Anguimorpha is the shallow morphology, and the deep morphology is a synapomorphy of Varanidae.

157. Parietal: Ventral excavations on supratemporal processes for transversospinalis group muscles (0) widely separated by sulcus processi ascendentis (Fig. 35B); (1) moderately separated; bridged by flange of parietal extending posteriorly past sulcus processi ascendentis but do not approach each other closely, leaving between them a broad triangular wedge of cerebral table (Fig. 35C); (2) approach each other closely, leaving between them only a thin ridge of cerebral table (Fig. 36A).

Evolution. Under both analyses, widely separated is the ancestral state for the entire group and for Anguimorpha. The ancestral state for *E. lancensis* + *Xenosaurus* is moderately separated, and that for the southern clade of *Xenosaurus* is ambiguous between moderately separated and closely approaching. Closely approaching is an autapomorphy of Helodermatidae. Under Analysis 1, the ancestral state for *Xenosaurus* + Anguidae is ambiguous between closely approaching and moderately separated. Under Analysis 2, the ancestral state for Xenosauridae is widely separated, and moderately separated is a synapomorphy of *Xenosaurus* + *E. lancensis*.

158. Parietal: Ventral ridges contacting taeniae marginales (0) also bound adductor attachment surface medially for entire length (Fig. 35D); (1) diverge just posterior to level of prefrontal facet from ridge delineating medial margin of adductor attachment surface (Fig. 36B).

Evolution. Under both analyses, divergence is a synapomorphy of the northern clade of *Xenosaurus*.

Supratemporal

The supratemporal is unknown for all extinct taxa save *B. ammoskius*, in which a negligible amount of its morphology is visible.

159. Supratemporal: Anterior edge (0) dorsoventrally short, less than half greatest height of supratemporal (Fig. 36D); (1) dorsoventrally tall, more than half greatest dorsoventral height of supratemporal (Fig. 36C).

Evolution. Under both analyses, the ancestral state for the entire group and for Anguimorpha is the short morphology. Under Analysis 1, the ancestral state for *Xenosaurus* is ambiguous, and the tall morphology is an autapomorphy of *S. crocodilurus*. Under Analysis 2, the tall morphology is a synapomorphy of Xenosauridae and the short mor-

phology is a synapomorphy of *X. rackhami* + *X. grandis*.

160. Supratemporal: Foramen piercing lateral surface near ridge dividing squamosal facet and adductor attachment surface about two-thirds of the way to posterior end of supratemporal (0) present (Fig. 36E); (1) absent (Fig. 36D).

Evolution. Under both analyses, the ancestral state for the entire group is ambiguous, and absence of the foramen is a synapomorphy of *X. rackhami* + *X. grandis*. Under Analysis 1, the ancestral state for Anguimorpha is ambiguous, and the ancestral state for *Xenosaurus* + Anguidae is presence of the foramen. Under Analysis 2, the ancestral state for Anguimorpha is presence of the foramen, and absence is a synapomorphy of Varanidae and of *X. rackhami* + *X. grandis*.

161. Supratemporal: Foramen piercing lateral surface (0) above (Fig. 37A); (1) below ridge dividing squamosal facet and adductor attachment surface (Fig. 36E).

Evolution. Under both analyses, a ventral position is a synapomorphy of *Xenosaurus*.

162. Supratemporal: Ventral flange wrapping under supratemporal process of parietal (0) smoothly curved along ventromedial edge (Fig. 37A); (1) produced into wedge (Fig. 36C).

Evolution. Under both analyses, the ancestral state for the entire group and Anguimorpha is smoothly curved. Under Analysis 1, production into a wedge is an autapomorphy of *S. crocodilurus* and a synapomorphy of *Xenosaurus*. Under Analysis 2, production into a wedge is a synapomorphy of Xenosauridae.

163. Supratemporal: Wedge-shaped ventral flange wrapping under supratemporal process of parietal (0) small and nublike (Fig. 36E); (1) squat, obtuse wedge
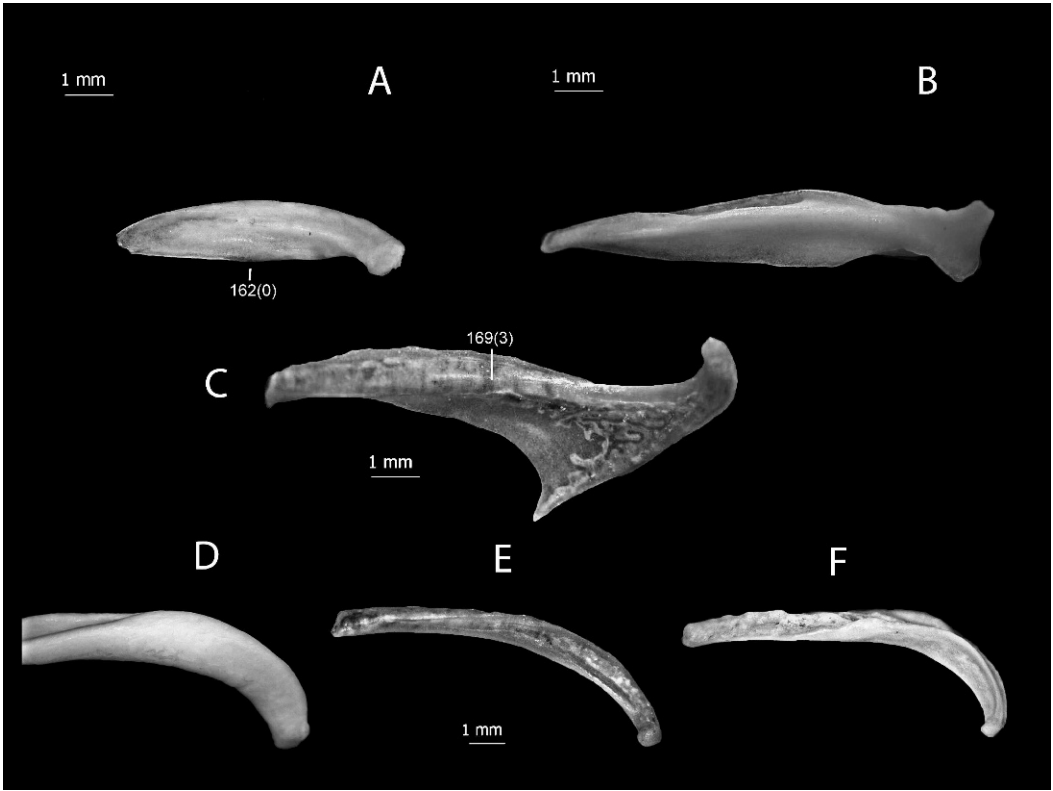
Figure 37.   A, Left supratemporal of *Elgaria multicarinata* TMM-M 8958, lateral, anterior to the left. Illustrates characters 161(0), 162(0). Left squamosals, ventral, anterior to the left: B, *Elgaria multicarinata* TMM-M 8958. Illustrates character 164(0). C, *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen. Illustrates characters 164(1), 167, 169(3). Left squamosals, lateral, anterior to the left: D, TMM-M 8956. Illustrates characters 165(0), 168(0), 169(0). E, *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen; F, *Xenosaurus grandis* NAUQSP-JIM 1460. E illustrates 168(1) and F illustrates 168(2).

(Fig. 36C); (2) sharp, more acute wedge (Fig. 36D).

Evolution. Under both analyses, the ancestral state is squat and obtuse. The small, nub-like morphology is a synapomorphy of *X. agrenon* + *X. rectocollaris,* and the sharp, acute morphology is a synapomorphy of *X. rackhami* + *X. grandis.*

Squamosal

The squamosal is unknown for all of the extinct taxa.

164. Squamosal: Posterior portion (0) unexpanded mediolaterally (Fig. 37B); (1) mediolaterally expanded (Fig. 37C). The presence or absence of a canthal crest in the temporal region was mentioned as a possible synapomorphy of Xenosauridae by Estes et al. (1988).

Evolution. Under both analyses, expansion is the ancestral state for the entire group and for Anguimorpha. Under Analysis 1, narrowness is a synapomorphy of Varanidae and of Anguidae + Helodermatidae. Under Analysis 2, narrowness is a synapomorphy of Anguidae + Varanoidea.

165. Squamosal: Dorsal ridge adjacent to lateral edge (0) absent (Fig. 37D); (1) relatively low (Fig. 32A); (2) intermediate height (Fig. 5A); (3) pronounced (Fig. 32B).

Evolution. Under both analyses, presence of a low ridge is a synapomorphy of *Xenosaurus*, presence of a ridge of intermediate height is a synapomorphy of the southern clade of *Xenosaurus*, and presence of a sharp ridge is an autapomorphy of *X. rackhami.*

166. Squamosal: Dorsal ridge adjacent to lateral edge (0) most prominent posteriorly (Fig. 32A); (1) most prominent anteriorly (Fig. 32B).

Evolution. Under both analyses, anterior prominence is an autapomorphy of *X. agrenon* and of *X. rackhami.*

167. Squamosal: Width, assessed by ratio of mediolateral width at anteroposterior level of closure of supratemporal fenestra to anteroposterior length of squamosal (Fig. 37C) (0) 0.15 or less; (1) 0.15 to 0.30; (2) 0.30 to 0.40; (3) 0.40 or above.

Evolution. Under both analyses, the ancestral state for the entire group and for Anguimorpha is ambiguous between state 1 and state 2. The ancestral state for *Xenosaurus* is state 2, and state 3 is a synapomorphy of *X. rackhami + X. grandis.* Under Analysis 1, the ancestral state for *Shinisaurus* + Varanidae is state 1, and state 0 is a synapomorphy of Varanidae. Under Analysis 2, state 0 is a synapomorphy of Anguidae + Varanoidea.

168. Squamosal: Suspensorial end curvature in a sagittal plane (0) without abrupt terminal hook (Fig. 37D); (1) terminal hook present and reaches the vertical or only slightly beyond the vertical (Fig. 37E); (2) terminal hook progresses well beyond the vertical, folding under the remainder of the squamosal and extending anteriorly for a short distance (Fig. 37F).

Evolution. Under both analyses, curvature of the hook to near the vertical is a synapomorphy of *Xenosaurus,* and curvature well beyond the vertical is a synapomorphy of *X. rackhami + X. grandis.*

169. Squamosal: Ventral ridge dividing attachment surface for m. anguli oris 1a and m. adductor mandibularis externus superficialis 1b from that for m. adductor mandibularis externus medialis and m. adductor mandibularis externus profundus (0) absent (Fig. 37D); (1) uniformly weak (Fig. 38A); (2) sharp only in posterior portion of squamosal (Fig. 38B); (3) sharp and well-defined for most of length of squamosal (Fig. 37C).

Evolution. Under both analyses, absence of a ridge is ancestral for the entire group and for Anguimorpha. A sharp ridge is an autapomorphy of *E. multicarinata,* and a ridge of mixed prominence is ancestral for *X. rackhami + X. grandis,* whereas a weak ridge is an autapomorphy of *X. rackhami.* Under Analysis 1, a sharp ridge is an autapomorphy of *S. crocodilurus.* The ancestral state for *Xenosaurus* is ambiguous between a ridge of mixed prominence and a sharp ridge, as is that for the southern clade of *Xenosaurus.* Under Analysis 2, a sharp ridge is a synapomorphy of Xenosauridae, and a ridge of mixed prominence is a synapomorphy of *X. rackhami + X. grandis.*

Quadrate

The quadrate is unknown in the fossil xenosaurs and in *M. ornatus.*

170. Quadrate: Two-thirds or more of the way down its dorsoventral height, lateral edge of tympanic crest (0) abruptly angles medially in plane of the crest, possibly associated with attachment of lateral collateral ligament and other connective tissue (Fig. 38C); (1) curves smoothly without abrupt medial angulation (Fig. 38E).

Evolution. Under both analyses, lack of a medial deflection is a synapomorphy of Varanidae and of *X. agrenon + X.*
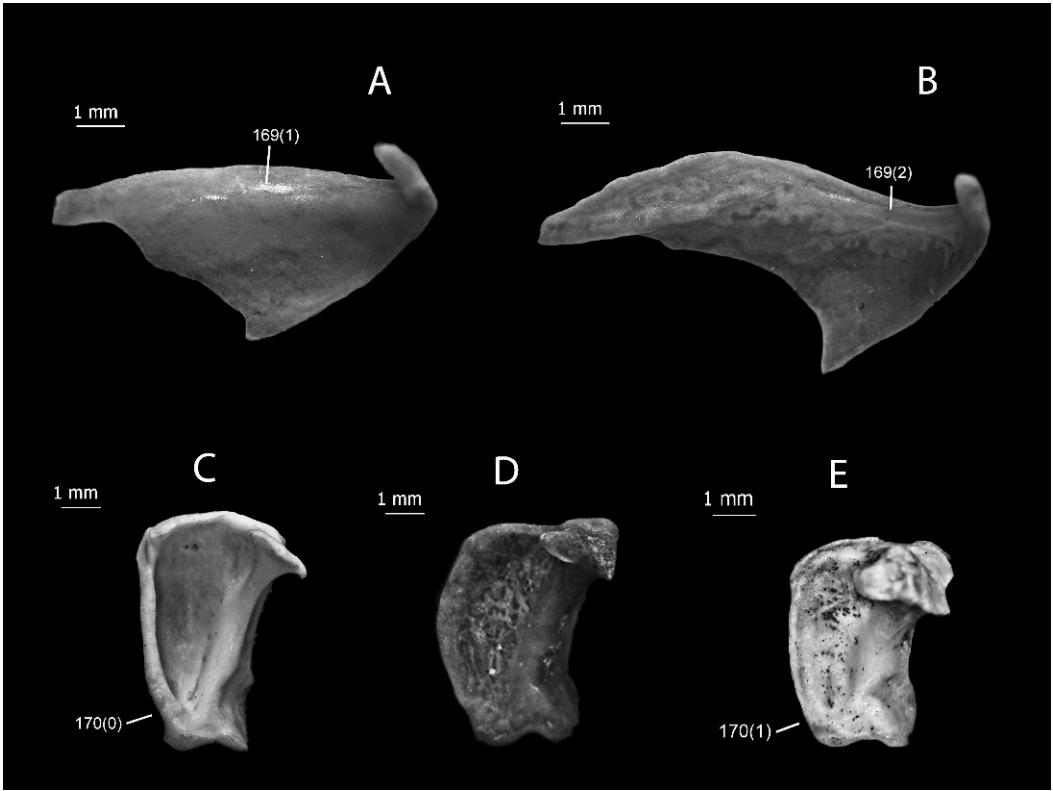
Figure 38.   Left squamosals, ventral, anterior to the left: A, *Xenosaurus rackhami* UTEP-OC "MALB" 388. Illustrates character 169(1). B, *Xenosaurus grandis* NAUQSP-JIM 1460. Illustrates character 169(2). Left quadrates, posterior: C, *Elgaria multicarinata* TMM-M 8958; D, *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen. C and D illustrate characters 170(0), 173(0), 173(1). E, *Xenosaurus agrenon* UTACV r45008. Illustrates character 170(1).

rectocollaris. Under Analysis 1, the ancestral state for Anguidae is ambiguous. Under Analysis 2, lack of a deflection is a synapomorphy of *C. enneagrammus + O. ventralis*.

171. Quadrate: Anteromedial emargination of dorsal surface of cephalic condyle (0) relatively deep, enclosing angle of 35° or more (Fig. 39A); (1) relatively shallow, enclosing angle of less than 35° (Fig. 39C).

    Evolution. Under both analyses, the shallow morphology is a synapomorphy of *X. agrenon + X. rectocollaris*.

172. Quadrate: Posterior eminence from lateralmost portion of dorsal surface of cephalic condyle (0) small, rounded bump (Fig. 39A); (1) pronounced wedge (Fig. 39B).

    Evolution. Under both analyses, the ancestral state for the entire group is ambiguous; that for Anguimorpha is the small, bump-like morphology; and the wedge morphology is a synapomorphy of *X. rackhami + X. grandis*.

173. Quadrate: Depression for tympanic cavity (0) strong, deeply concave posteriorly in horizontal plane (Fig. 38C); (1) weak, weakly concave posteriorly in horizontal plane (Fig. 38D).

    Variation. The depression for the tympanic cavity deepens with age, but relative differences can still be observed in early postnatal individuals.

Figure 39.   Left quadrates, dorsal, anterior to the top: A, *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen; B, *Xenosaurus grandis* NAUQSP-JIM 1460. A and B illustrate characters 171(0), 172(0), 172(1). C, *Xenosaurus agrenon* UTACV r45008. Illustrates character 171(1). D, Braincase of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, dorsal, anterior to the top. Illustrates characters 174, 181(0).

Evolution. Under both analyses, the shallow morphology is a synapomorphy of *Xenosaurus* and of Varanidae.

Braincase

The braincase is unknown for all extinct taxa save *B. ammoskius*, in which it is largely obscured.

174. Braincase: Ratio of greatest mediolateral width to anteroposterior length from posterior end of paroccipital process anteriorly to level of anterior end of alar process (Fig. 39C) (0) 1.20 or less; (1) between 1.20 and 1.50; (2) 1.50 or greater.

Variation. The proportions of the braincase vary significantly during ontogeny (Barahona and Barbadillo, 1998; Bever et al., 2005). In particular, the paroccipital processes become relatively longer with the relative expansion of the adductor chamber relative to the brain, and the alar processes of the prootic lengthen. This character must be evaluated on relatively large, adult individuals with fused braincases.

Evolution. Under both analyses, a ratio of 1.20 or less is an autapomorphy of *X. newmanorum*. Under Analysis 1, the ancestral state for the entire group and for Anguimorpha is 1.50 or greater. A ratio of 1.20 to 1.50 is an autapomorphy of *S. crocodilurus*, a synapomorphy of Anguidae, and a synapomorphy of *X. rackhami* + *X. grandis*. A ratio of 1.20 or
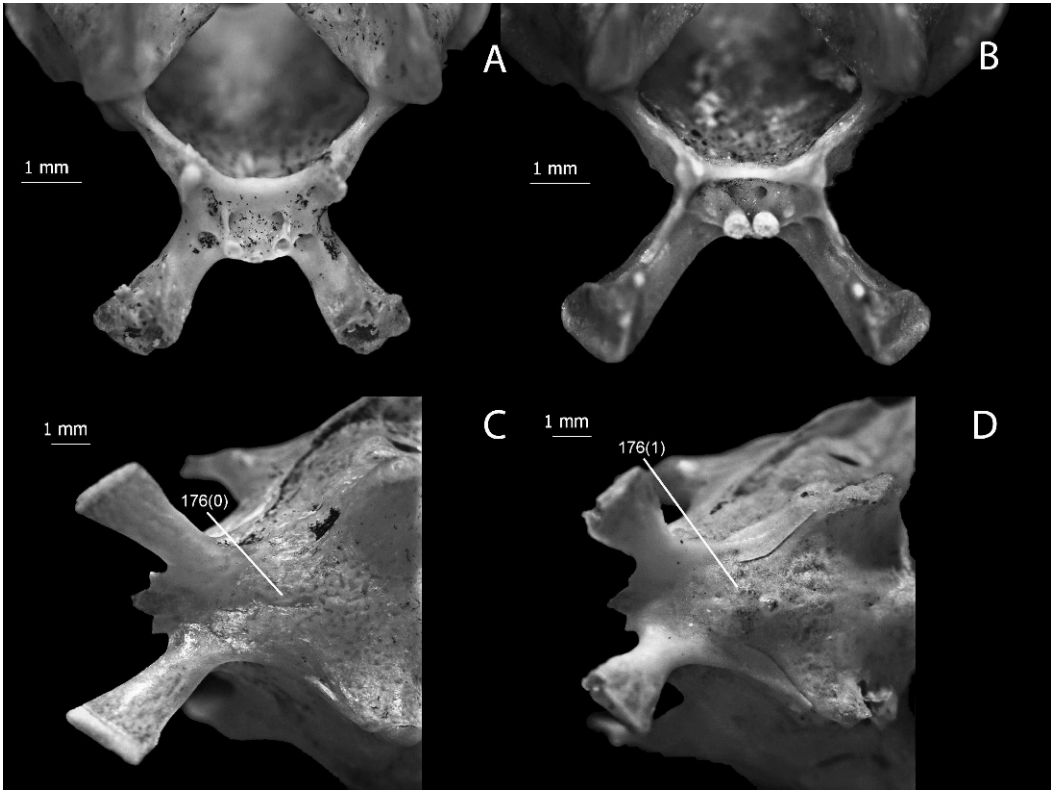
Figure 40.   A, Braincase of *Xenosaurus agrenon* UTACV r45008, anterior. Illustrates character 175(0). B, Braincase of *Xenosaurus platyceps* UF 45622, anterior. Illustrates character 175(1). C, Braincase of *Xenosaurus grandis* NAUQSP-JIM 1460, ventral, anterior to the left. Illustrates character 176(0). D, Braincase of *Xenosaurus agrenon* UTACV r45008, ventral, anterior to the left. Illustrates character 176(1).

less is a synapomorphy of *E. multi-carinata* + *O. ventralis*. Under Analysis 2, the ancestral state for the entire group and Anguimorpha is ambiguous between 1.20 to 1.50 and 1.50 or greater. The ancestral state for Anguidae is ambiguous between 1.20 or less and 1.20 to 1.50.

175. Braincase: Carotid fossa and retractor pits (0) shallow, barely excavated (Fig. 40A); (1) deeply excavated (Fig. 40B).

Variation. The carotid fossa and retractor pits deepen somewhat with age, and only relatively large adults were scored.

Evolution. Under both analyses, the shallow morphology is the ancestral state for the entire group and for Anguimorpha and the ancestral state for *Xenosaurus* is ambiguous. Under Analysis 1, the ancestral state for *Xenosaurus* + Anguidae and all mixed nodes therein is ambiguous. Under Analysis 2, the ancestral state for Xenosauridae and for Anguidae + Varanoidea is the shallow morphology. The deep morphology is an autapomorphy of *O. ventralis* and of Helodermatidae.

176. Braincase: Domed portion of ventral surface spanning sphenoid/basioccipital suture (0) divided into bilateral swellings with median groove (Fig. 40C); (1) projected into a single swelling without midline groove, bearing small tubercle slightly posterior to apex of dome in basioccipital region (Fig. 40D).

Figure 41. A, Braincase of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, left lateral, anterior to the left. Illustrates character 170(0). B, Braincase of *Xenosaurus rackhami* UTEP-OC "MALB" 388, left lateral, anterior to the left. Illustrates character 177(1). C, Braincase of *Xenosaurus grandis* NAUQSP-JIM 1460, left ventrolateral, anterior to the left. Illustrates character 178(0). D, Braincase of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, left ventrolateral, anterior to the left. Illustrates character 178(1).

Evolution. Under both analyses, the undivided morphology is an autapomorphy of *C. enneagrammus* and a synapomorphy of *X. agrenon* + *X. rectocollaris*. Under Analysis 1, the ancestral state for the entire group and for Anguimorpha is ambiguous. The ancestral state for *Xenosaurus* + Anguidae is the divided morphology. Under Analysis 2, the ancestral state for the entire group, Anguimorpha, Xenosauridae, and Anguidae + Varanoidea is the divided morphology.

177. Braincase: Sphenooccipital tubercles (0) rounded and blunt (Fig. 41A); (1) acutely pointed (Fig. 41B).

Variation. The sphenooccipital tubercles become more prominent with age, and their terminal shape forms in the later stages of postnatal ontogeny; this character should be scored on relatively large adults with fused braincases.

Evolution. Under both analyses, the pointed morphology is an autapomorphy of *O. ventralis* and of *X. rackhami*.

178. Braincase: Recessus vena jugularis (0) ends anteriorly behind anterior tip of alar process of sphenoid (Fig. 41C); (1) extends along entirety of lateral surface of alar process (Fig. 41D).

Variation. The recessus vena jugularis and the alar process of the sphenoid
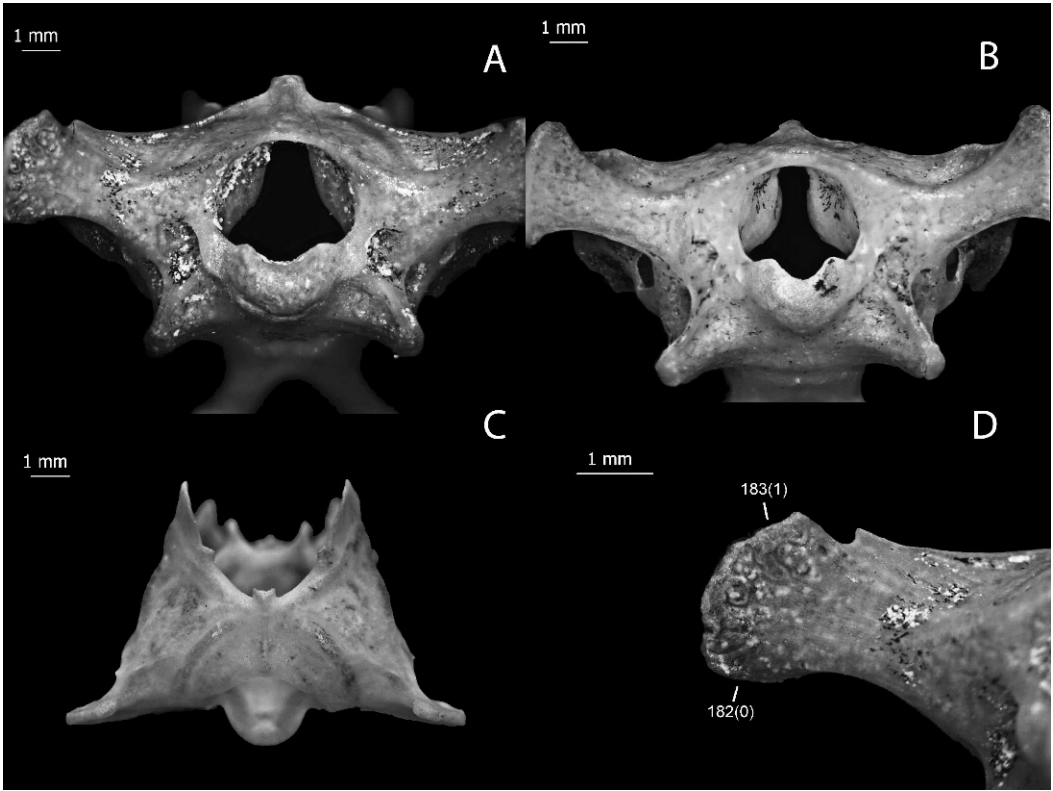
Figure 42.   A, Braincase of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, posterior. Illustrates characters 179(0), 180(0). B, Braincase of *Xenosaurus grandis* NAUQSP-JIM 1460, posterior. Illustrates characters 179(1), 180(1). C, Braincase of *Xenosaurus rackhami* UTEP-OC "MALB" 388, dorsal, anterior to the top. Illustrates character 181(1). D, Braincase of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, posterior. Illustrates characters 182(0), 183(1).

both develop largely after hatching. This character should be scored on relatively large adults.

Evolution. Under Analysis 1, extension to the anterior end of the alar process is an autapomorphy of *S. crocodilurus* and a synapomorphy of the northern clade of *Xenosaurus*. Under Analysis 2, the ancestral state for Xenosauridae is ambiguous and the ancestral state for the southern clade of *Xenosaurus* is ending posterior to the tip of the alar process.

179. Braincase: Constriction of odontoid recess (notochordal groove) in dorsal margin of occipital condyle, measured by angle through highest points of notch and deepest point (0) greater

than 120° (Fig. 42A); (1) 120° or less (Fig. 42B).

Variation. The recess becomes somewhat more constricted with age and should be scored on relatively large adults.

Evolution. Under both analyses, an angle of 120° or less is an autapomorphy of *O. ventralis* and a synapomorphy of *X. rackhami* + *X. grandis*.

180. Braincase: Cava capsulares within braincase (0) leave relatively wide space between them—mediolateral separation at closest approach greater than one-quarter mediolateral width of foramen magnum at that dorsoventral level (Fig. 42A); (1) approach closely—mediolateral separation at closest ap-
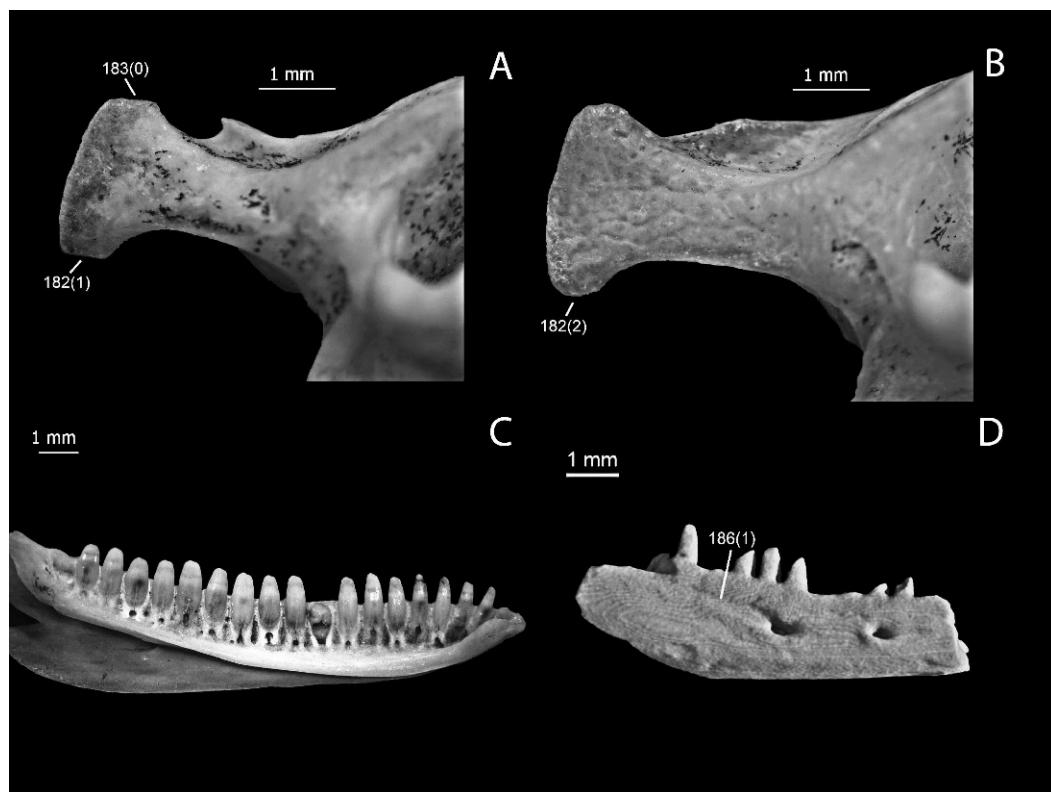
Figure 43.   A, Braincase of *Xenosaurus agrenon* UTACV r45008, posterior. Illustrates characters 182(1), 183(0). B, Braincase of *Xenosaurus grandis* NAUQSP-JIM 1460, posterior. Illustrates character 182(2). C, Left dentary of *Xenosaurus rackhami* UTEP-OC "MALB" 388, medial, anterior to the right. Illustrates characters 185(0), 197(1). D, Right dentary of *Exostinus serratus*, CT scan of AMNH 1608, lateral, anterior to the right. Illustrates characters 185(1), 186(1), 195(1), 196(1).

proach one-quarter or less mediolateral width of foramen magnum at that dorsoventral level (Fig. 42B).

Variation. The approach of the cava capsulares increases somewhat with age and should be scored in relatively large adults.

Evolution. Under both analyses, close approach is an autapomorphy of *O. ventralis* and of *X. grandis.*

181. Braincase: Paroccipital processes (0) distinctly posterolaterally directed (Fig. 39D); (1) only slightly posterolaterally directed, nearly oriented mediolaterally (Fig. 42C).

Variation. The posterior direction of the paroccipital processes tends to

increase with age and should be scored in relatively large adults.

Evolution. Under Analysis 1, the ancestral state for the entire group and Anguimorpha, as well as all internal mixed nodes, is ambiguous. Under Analysis 2, the ancestral state for the entire group and for Anguimorpha is lateral extension. Posterolateral extension is a synapomorphy of *C. ennea-grammus + O. ventralis* and an autapomorphy of *L. borneensis.* The ancestral state for Xenosauridae is ambiguous.

182. Braincase: Expanded tips of paroccipital processes—ventral projections (0) absent (Fig. 42D); (1) present, squared off or blunt (Fig. 43A); (2) present, long and pointed (Fig. 43B).

Variation. The projections become more prominent during early postnatal ontogeny and should be scored in relatively large adults.

Evolution. Under both analyses, absence of projections is an autapomorphy of *S. crocodilurus* and of *X. newmanorum.* Under Analysis 1, the ancestral state for the entire group and for Anguimorpha is ambiguous between squared off and long and pointed, as is that for *S. crocodilurus* + Varanidae, *Xenosaurus* + Anguidae, and *Xenosaurus.* Under Analysis 2, the ancestral state for the entire group and for Anguimorpha is long and pointed. Blunt or squared-off is an autapomorphy of Helodermatidae and a synapomorphy of Xenosauridae. Within Xenosauridae, the long and pointed state is a synapomorphy of *X. rackhami* + *X. grandis.*

183. Braincase: Expanded tips of paroccipital processes—dorsal projections (0) present as blunt or squared off tab (Fig. 43A); (1) low, barely divergent (Fig. 42D).

Variation. Dorsal projections tend to become more prominent during postnatal ontogeny and should be scored in relatively large adults.

Evolution. Under Analysis 1, the ancestral state for the entire group and all mixed nodes therein is ambiguous. Under Analysis 2, the ancestral state for the entire group and for Anguimorpha is presence of relatively extensive projections. The low and rounded morphology is a synapomorphy of Varanoidea and the northern clade of *Xenosaurus* and an autapomorphy of *C. enneagrammus.*

Dentary

184. Dentary: Anterior tip of dentary (0) relatively pointed in sagittal plane (Fig. 1A); (1) blunt, truncated, with steeply rising "chin" (genioglossus attachment area).

Evolution. Under both analyses, the ancestral state for the entire group and for Anguimorpha is the relatively pointed morphology. The ancestral state for *E. lancensis* + *Xenosaurus* is ambiguous, and the ancestral state for *Xenosaurus* is pointed.

185. Dentary: Posterior, rising section of dorsal edge of dentary extends for (0) more than six tooth positions (Fig. 43C); (1) six or fewer tooth positions (Fig. 43D).

Evolution. Under Analysis 1, the ancestral state for the entire group is ambiguous, and the ancestral state for Anguimorpha is six or fewer tooth positions. More than six tooth positions is a synapomorphy of *O. ventralis* + *E. multicarinata* and an autapomorphy of *M. ornatus.* The ancestral state for *Xenosaurus* + *E. lancensis* is ambiguous, as is that of *Xenosaurus* + *E. serratus.* Under Analysis 2, the ancestral state for the entire group and for Anguimorpha is more than six tooth positions. Six or fewer tooth positions is a synapomorphy of Varanoidea and *S. crocodilurus* + *B. ammoskius* and an autapomorphy of *C. enneagrammus*, *R. rugosus*, and *E. serratus.*

186. Dentary: Groove anterior to coronoid facet on lateral surface of dentary (0) shallow and short, not approaching posteriormost mental foramen (Fig. 44A); (1) deep and long, approaching or running to posteriormost mental foramen (Fig. 43D).

Evolution. Under both analyses, the ancestral state for the entire group and for Anguimorpha is the shallow, short morphology. Under Analysis 1, the deep, long morphology is a synapomorphy of *Xenosaurus* + *R. rugosus* and an autapomorphy of *S. crocodilurus.* Under Analysis 2, the deep, long morphology is a synapomorphy of Xenosauridae.
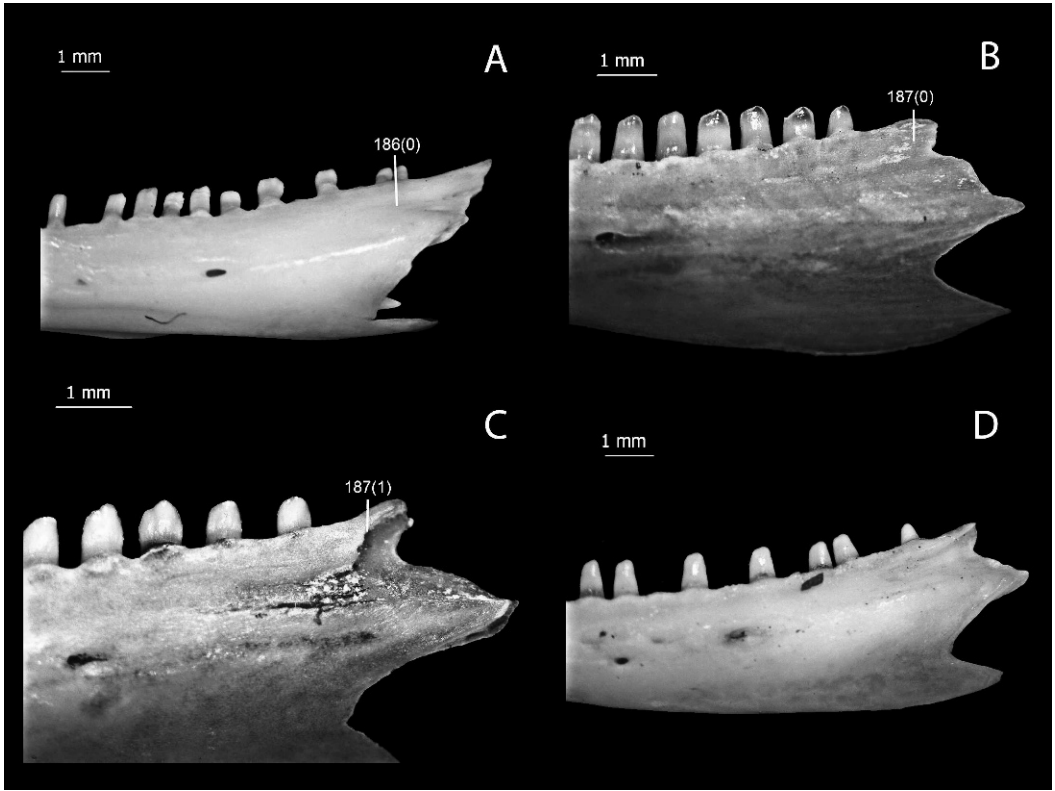
Figure 44.   A, Left dentary of *Elgaria multicarinata* TMM-M 8958, lateral, anterior to the left. Illustrates characters 186(0), 188(0). B, Left dentary of *Xenosaurus grandis* NAUQSP-JIM 1460, lateral, anterior to the left. Illustrates characters 187(0), 190(0). C, Left dentary of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, lateral, anterior to the left. Illustrates character 187(1). D, Left dentary of *Xenosaurus agrenon* UTACV r45008, lateral, anterior to the left. Illustrates characters 188(1), 189(1), 190(1).

187. Dentary: Lateral coronoid facet (0) shallowly impressed, surrounded dorsally and anteriorly by low ridge (Fig. 44B); (1) deeply impressed, surrounded by sharp ridge (Fig. 44C).

Evolution. Under both analyses, deep impression with a sharp ridge is a synapomorphy of the northern clade of *Xenosaurus* and an autapomorphy of *C. enneagrammus*.

188. Dentary: Coronoid process (0) extending posteriorly beyond surangular process (Fig. 44A); (1) ending anterior to tip of surangular process (Fig. 44D).

Evolution. Under both analyses, the ancestral state for the entire group is ambiguous, and that for Anguimorpha is extension beyond the surangular process. Ending anterior to the surangular process is a synapomorphy of *X. agrenon* + *X. rectocollaris* and an autapomorphy of *S. crocodilurus* and of Helodermatidae.

189. Dentary: Surangular notch between surangular and angular process (0) absent (Estes et al., 1988, fig. 11B); (1) present (Fig. 44D). Presence or absence of a surangular notch was character 63 of Estes et al. (1988).

Evolution. Under both analyses, the ancestral state of the entire group is ambiguous.

190. Dentary: Tip of angular process (0) pointed (Fig. 44B); (1) blunt and slightly bifurcated (Fig. 44D).
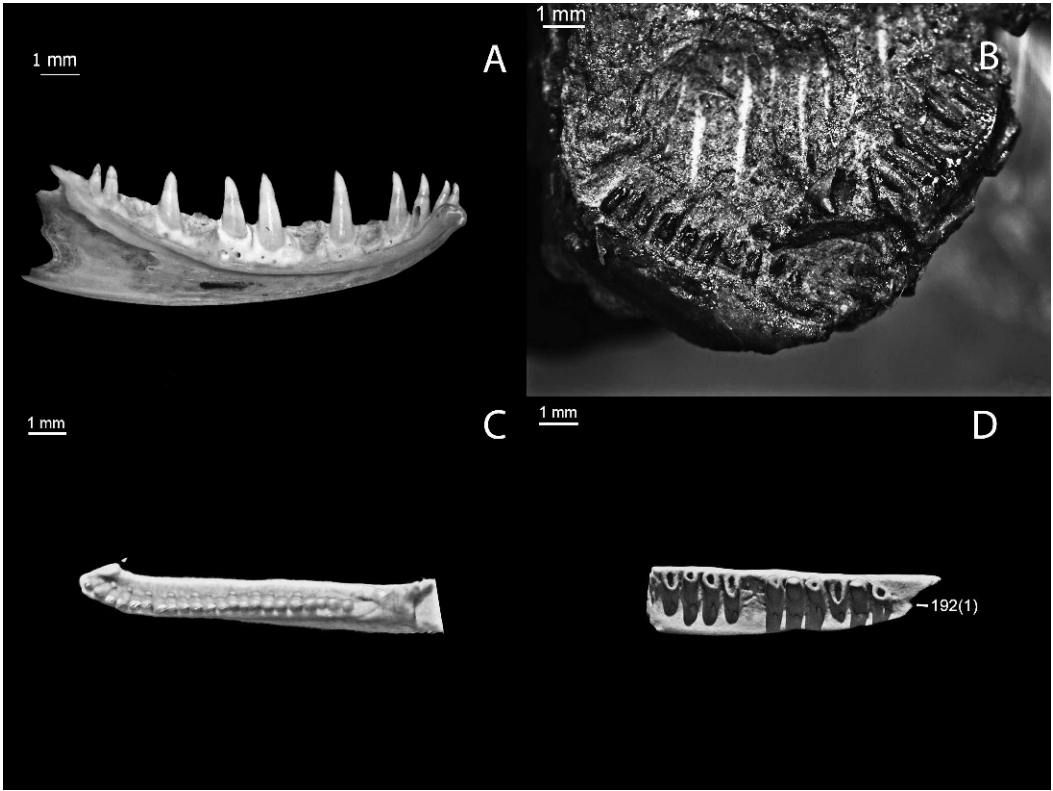
Figure 45.   A, Left dentary of *Shinisaurus crocodilurus* UF 72805, medial, anterior to the right. Illustrates characters 191(0), 193, 195(2). B, Left and right dentaries of *Restes rugosus* YPM PU 14640, lateral and medial, respectively, anterior to the left. Illustrates character 191(1). C, Left dentary of *Xenosaurus rectocollaris*, CT scan of UF 51443, dorsal, anterior to the left. Illustrates characters 192(0), 194(0). D, Right dentary of *Exostinus serratus*, CT scan of AMNH 1608, dorsal, anterior to the left. Illustrates characters 192(1), 194(1).

Evolution. Under both analyses, a blunt, slightly bifurcated angular process is a synapomorphy of *X. agrenon + X. rectocollaris*.

191. Dentary: Suprameckelian lip (0) becomes dorsoventrally taller anteriorly, but Meckel's groove remains fairly widely open (Fig. 45A); (1) becomes dorsoventrally tall anteriorly, restricting Meckel's groove to thin slit (Fig. 45B).

Evolution. Under both analyses, the ancestral state for *Xenosaurus + R. rugosus* and *Xenosaurus + E. lancensis* was ambiguous.

192. Dentary: Wedge-shaped process extending posteriorly from suprameckelian lip near posterior end of dental gutter (0) absent (Fig. 45C); (1) present (Fig. 45D).

Evolution. Under both analyses, the presence of a wedge-shaped process is an autapomorphy of *E. serratus*.

193. Dentary: Apex of posterior u-shaped emargination in intramandibular septum (Fig. 45A) at level of (0) third or fewer tooth position from back of dentary; (1) fourth tooth position from back; (2) fifth tooth position from back; (3) sixth or more tooth position from back.

Evolution. Under both analyses, the ancestral state for *Xenosaurus + R. rugosus* is at the level of the fourth tooth position from the back, and the

state for *Xenosaurus* + *E. lancensis* and *Xenosaurus* + *E. serratus* is ambiguous between the fourth and fifth tooth position from the back. The ancestral state for *Xenosaurus* is the fifth tooth position from the back. A position at the level of the fourth tooth position from the back is an autapomorphy of *X. grandis,* and one at the level of the sixth from the back is an autapomorphy of *X. newmanorum.* Finally, a position at the level of the sixth from the back is an autapomorphy of *E. multicarinata*. Under Analysis 1, the ancestral state for the entire group, for Anguimorpha, *S. crocodilurus* + Varanidae, *Xenosaurus* + Anguidae, and Anguidae + Helodermatidae, is the third or fewer tooth position from the back. A position at the level of the fourth tooth position from the back is a synapomorphy of *Xenosaurus* + *R. rugosus*, of *E. multicarinata* + *O. ventralis* and of *S. crocodilurus* + *M. ornatus*. Under Analysis 2, the ancestral state for the entire group and for Anguimorpha is ambiguous between the third and fourth tooth positions from the back. That for Xenosauridae is the fourth tooth position from the back, and that for Varanoidea is the third from the back.

194. Dentary: Posterior end of tooth row in horizontal plane (0) relatively straight or with slight medial inflection (Fig. 45C); (1) with marked medial inflection (Fig. 45D).

Evolution. Under both analyses, medial inflection is an autapomorphy of *E. serratus*.

195. Dentary: Tooth height (0) short, with one-third or less of most teeth extending above dorsal margin of dentary (Fig. 45A); (1) intermediate height, between one-third and half of most teeth extending above dorsal margin of dentary (Fig. 46A); (2) tall, with half or more of most teeth extending above dorsal margin of dentary (Fig. 46B).

Evolution. Under both analyses, the ancestral state for the entire group is ambiguous between tall and intermediate height, and the ancestral state for Anguimorpha is intermediate height. The ancestral state for *Xenosaurus* + *R. rugosus* is intermediate height, and the short morphology is a synapomorphy of *Xenosaurus*. Under Analysis 1, the ancestral state for *Xenosaurus* + Anguidae is intermediate height. The tall morphology is a synapomorphy of *S. crocodilurus* + Varanidae and an autapomorphy of Helodermatidae. Under Analysis 2, the ancestral state for Anguidae + Varanoidea and for Xenosauridae is intermediate height. The tall morphology is a synapomorphy of shinisaurs and of Varanoidea.

196. Dentary: Tooth height (0) declines drastically posteriorly, with two or three teeth anterior to most posterior tooth about half to two-thirds the height of tallest dentary teeth (Fig. 46A); (1) declines less, with teeth just anterior to most posterior tooth nearly the same height as tallest dentary teeth (Fig. 43D).

Evolution. Under both analyses, a precipitous decline is the ancestral state for the entire group and for Anguimorpha. Lack of a decline is ancestral for *Xenosaurus* + *R. rugosus* and for shinisaurs. A precipitous decline is a synapomorphy of *Xenosaurus*. Under Analysis 1, lack of a decline is a synapomorphy of *Xenosaurus* + *R. rugosus* and of shinisaurs. Under Analysis 2, lack of a decline is a synapomorphy of Xenosauridae.

197. Dentary: Shafts of teeth (0) do not change drastically in diameter posteriorly, save at anterior tip in premaxillary–maxillary occlusal transition (Fig. 46A); (1) increase markedly in diameter posteriorly (Fig. 43C).

Variation. The differentiation of shaft widths becomes more pronounced with age.

Evolution. Under both analyses, a marked posterior increase in diameter
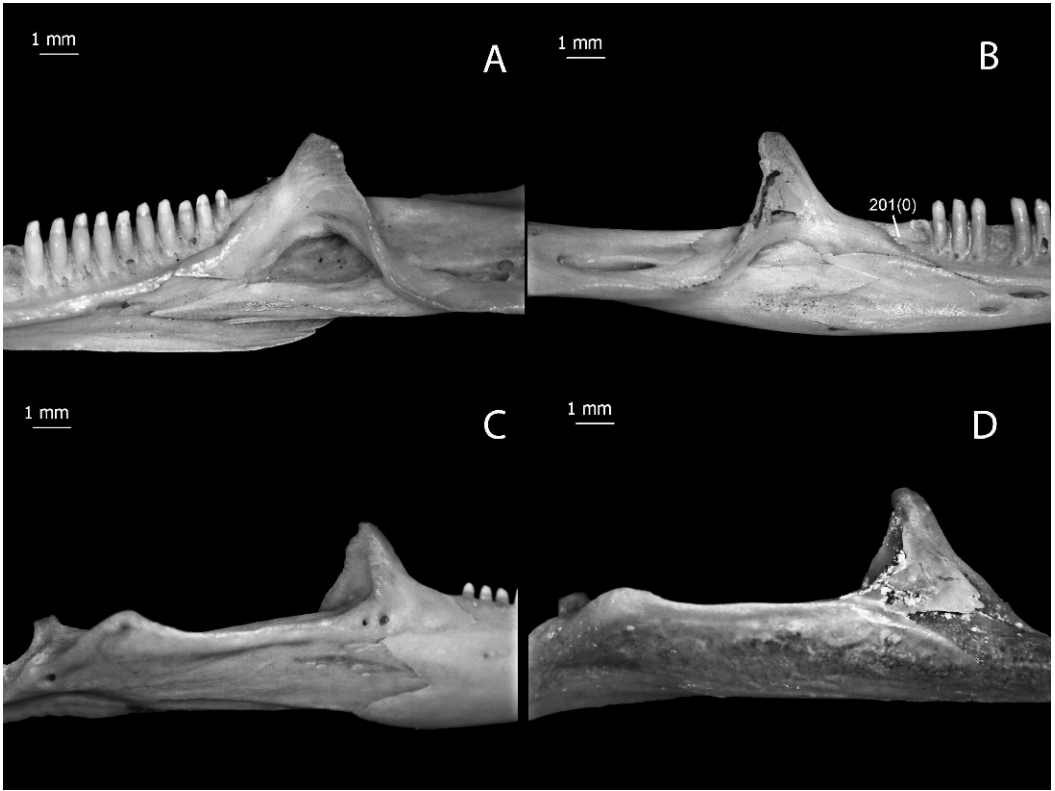
Figure 46.   A, Right mandible of *Xenosaurus platyceps* UF 45622, medial, anterior to the left. Illustrates characters 195(0), 196(0), 197(0), 200(1), 201(1), 202(1), 203(0), 204(0). B, Left mandible of *Elgaria multicarinata* CAS 54241, medial, anterior to the right. Illustrates characters 195(1), 200(0), 201(0). C, Right mandible of *Xenosaurus platyceps* UF 45622, lateral, anterior to the right. Illustrates characters 198(0), 199(1), 205(2), 206(1), 208(1). D, Right mandible of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, lateral, anterior to the right. Illustrates characters 198(1), 206(0), 207(1).

is a synapomorphy of *X. rackhami + X. grandis*.

Coronoid

The coronoid is unknown for *E. lancensis* and *M. ornatus*.

198. Coronoid: Anterolateral process (0) anteroposteriorly longer than dorsoventrally tall at base (Fig. 46C); (1) taller than long (Fig. 46D).

Evolution. Under both analyses, taller than long is an autapomorphy of *X. newmanorum*, of *X. agrenon*, and of *X. grandis*.

199. Coronoid: Posterolateral process: (0) ventral margin directed posterodorsally, resulting in taper for entire length

(Fig. 47A); (1) ventral margin directed straight posteriorly for most of length, resulting in a dorsoventrally extensive process (Fig. 46C).

Evolution. Under both analyses, a straight ventral margin and tall posterolateral process is a synapomorphy of *Xenosaurus*.

200. Coronoid: Posteromedial process (0) trending posteroventrally without strong bend toward the vertical (Fig. 46B); (1) becoming nearly vertical at tip, resulting in highly bowed appearance of coronoid arch (Fig. 47B).

Evolution. Under Analysis 1, the ancestral state for the entire group and
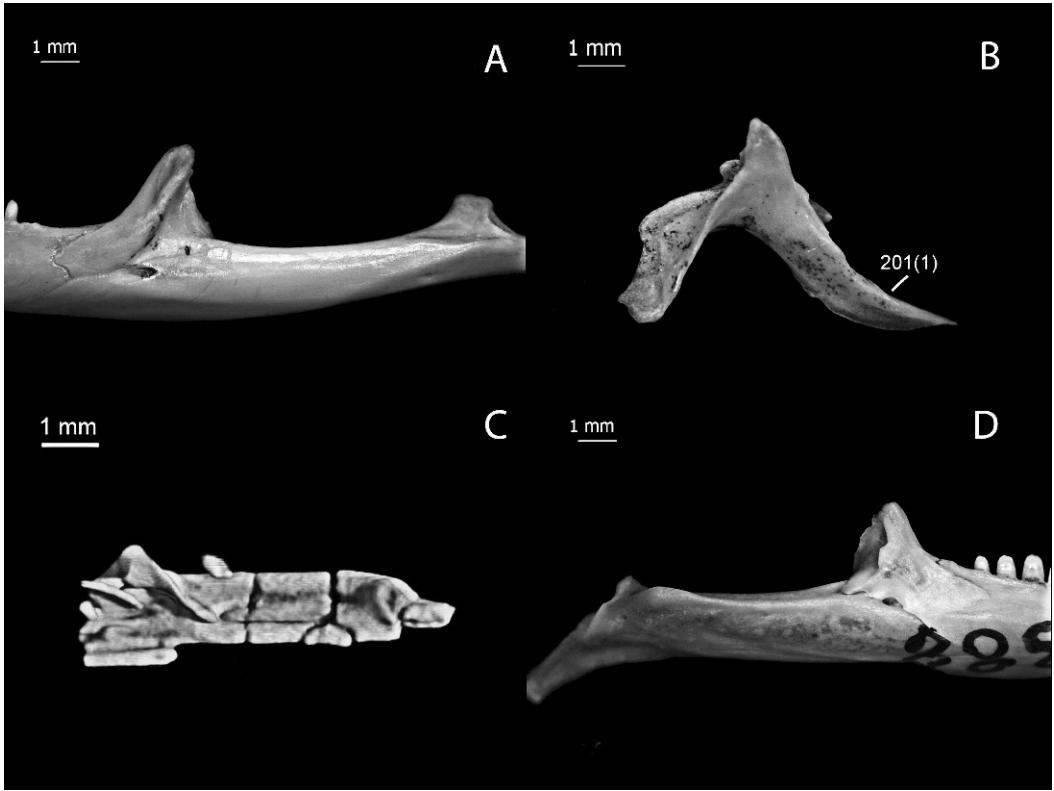
Figure 47.   A, Left mandible of *Elgaria multicarinata* CAS 54241, dorsolateral, anterior to the left. Illustrates characters 199(0), 205(0), 207(0), 208(0). B, Left coronoid of *Xenosaurus agrenon* UTACV r45008, medial, anterior to the right. Illustrates characters 200(1), 201(1), 202(0), 203(1). C, Right mandible of *Restes rugosus*, CT scan of YPM PU 14640, medial, anterior to the left. Illustrates character 204(1). D, Right mandible of *Xenosaurus rackhami* UTEP-OC "MALB" 388, lateral, anterior to the right. Illustrates character 205(1).

for Anguimorpha is ambiguous. The ancestral state for Anguidae + Helodermatidae is the relatively straight morphology. Under Analysis 2, the ancestral state for the entire group and for Anguimorpha is the bowed morphology. The straight morphology is a synapomorphy of Anguidae + Varanoidea and an autapomorphy of *R. rugosus*.

201. Coronoid: Anteromedial process (0) with abrupt constriction of dorsal and ventral margins about a third of the way toward anterior tip followed by continued taper (Fig. 46B); (1) gradually tapering without abrupt constriction or with slight step in dorsal, but not ventral, margin (Fig. 47B).

Evolution. Under both analyses, a gradual taper is a synapomorphy of *Xenosaurus* and of *Varanus*.

202. Coronoid: Anteromedial process (0) more than twice as long along long axis as tall perpendicular to long axis at widest level (Fig. 47B); (1) twice as long as tall or less, with thickened process restricting exposed portion anteriorly (Fig. 46A).

Evolution. Under both analyses, twice as long as tall or shorter is a synapomorphy of the northern clade of *Xenosaurus*. Under Analysis 1, twice as long as tall or shorter is a synapomorphy of *Varanus* and an autapomorphy of Helodermatidae. Under Analysis 2,

twice as long as tall or shorter is a synapomorphy of Varanoidea.

203. Coronoid: Medially facing flange extending posteriorly from posteromedial process for attachment of bodenaponeurosis; ratio of greatest width perpendicular to long axis to length along long axis (0) 0.25 or less (Fig. 46A); (1) greater than 0.25 (Fig. 47B).

Evolution. Under both analyses, an extensive flange is a synapomorphy of *X. agrenon + X. rectocollaris.*

204. Coronoid: Posterior end of posteromedial process (0) extends for short distance along prearticular (ventromedial) rim of adductor fossa (Fig. 46A); (1) ends anterior to adductor fossa (Fig. 47C).

Evolution. Under both analyses, termination anterior to the adductor fossa is a synapomorphy of the southern clade of *Xenosaurus* and an autapomorphy of *R. rugosus.*

205. Coronoid: Anterior surangular foramen (0) not overlapped by coronoid (Fig. 47A); (1) partially overlapped by coronoid, forming emargination in ventral margin of bone (Fig. 47D); (2) fully overlapped by coronoid, piercing through the bone (Fig. 46C).

Evolution. Under both analyses, partial overlap is an autapomorphy of *L. borneensis.* Complete overlap is a synapomorphy of *Xenosaurus,* and partial overlap is an autapomorphy of *X. rackhami.*

206. Coronoid: Anterior surangular foramen in coronoid (0) single (Fig. 46D); (1) double (Fig. 46C).

Evolution. Under both analyses, the paired morphology is an autapomorphy of *X. platyceps.*

Surangular/Prearticular/Articular

The surangular/prearticular/articular complex is unknown in *E. lancensis* and *M. ornatus.*

207. Surangular/prearticular/articular: Strong dorsal crest on surangular lateral to m. adductor externus medialis attachment table (0) absent (Fig. 47A); (1) present (Fig. 46D).

Variation. The crest becomes more prominent with age, and only relatively large adults should be scored.

Evolution. Under both analyses, presence of a crest is a synapomorphy of *Xenosaurus* and an autapomorphy of Helodermatidae.

208. Surangular/prearticular/articular: Posterior surangular foramen (0) anterior to articular (Fig. 47A); (1) at anteroposterior level of anterior edge of articular (Fig. 46C).

Evolution. Under both analyses, a position at the anterior edge of the articular is a synapomorphy of *Xenosaurus.*

209. Surangular/prearticular/articular: Fossa ventral to arc of medial coronoid facet (subcoronoid fossa) (0) shallow, only slightly impressed (Fig. 48A); (1) deep, forming a strongly impressed bowl-shaped cavity (Fig. 48B).

Evolution. Under both analyses, a deep subcoronoid fossa is a synapomorphy of *Xenosaurus + E. serratus.*

210. Surangular/prearticular/articular: Subcoronoid fossa (0) with no medial overhang at posterior end or only slight ridge developed there (Fig. 48A); (1) posteriorly continuing into bone as a blind pocket, sometimes pierced by a foramen, such that a portion of the medial wall of the surangular bearing the facet for the posteromedial process of the coronoid overhangs it (Fig. 48B).

Evolution. Under both analyses, lack of overhang is the ancestral state for the entire group and for Anguimorpha, and presence of an overhang is the ancestral state for *Xenosaurus + R. rugosus.* Under Analysis 1, the ancestral state for *Xenosaurus* + Anguidae and for Anguidae + Helodermatidae is ambiguous, and over-
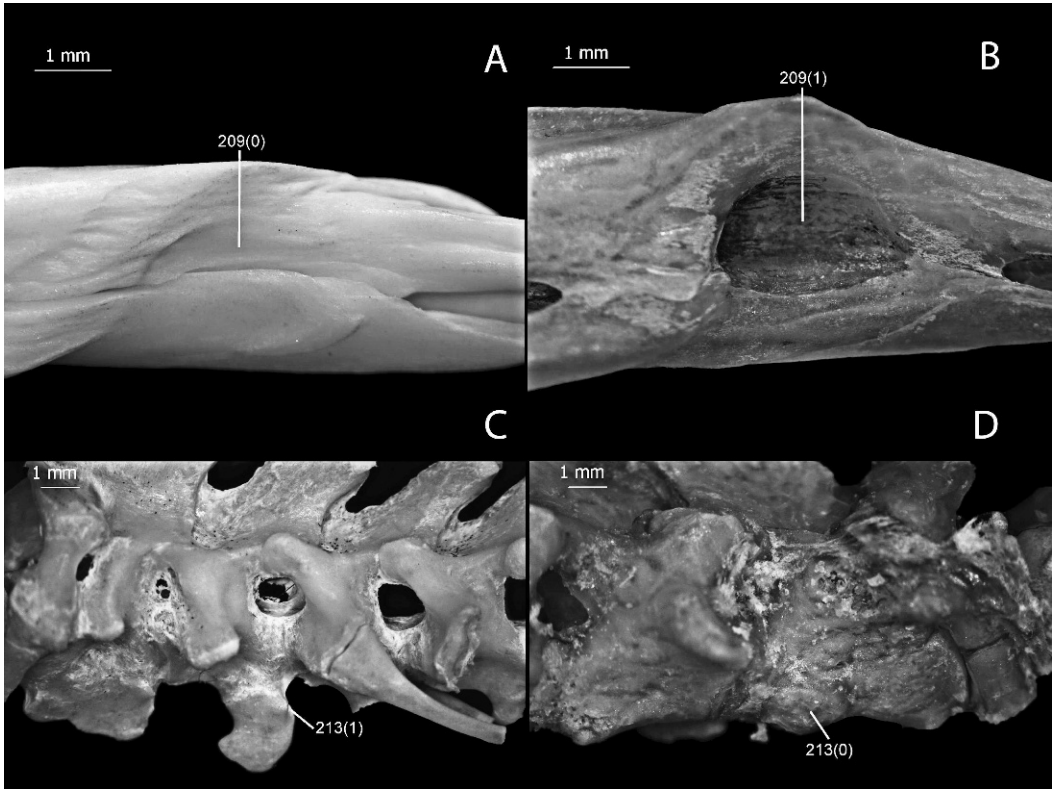
Figure 48.   A, Left postdentary elements of *Elgaria multicarinata* TMM-M 8958, medial, anterior to the right. Illustrates characters 209(0), 210(0). B, Left postdentary elements of *Xenosaurus grandis* NAUQSP-JIM 1460, medial, anterior to the right. Illustrates characters 209(1), 210(1). C, Cervical vertebrae of *Shinisaurus crocodilurus* MVZ 204291, left lateral, anterior to the left. Illustrates characters 212(0), 213(1). D, Cervical vertebrae of *Heloderma suspectum* CAS 513, right ventrolateral, anterior to the right. Illustrates characters 212(1), 213(0).

hang is an autapomorphy of *L. borneensis.* Under Analysis 2, overhang is a synapomorphy of *Xenosaurus + R. rugosus,* and the ancestral state for Varanoidea and Varanidae is ambiguous.

211. Surangular/prearticular/articular: Subcoronoid fossa (0) without foramina; (1) pierced by one or more small foramina; (2) pierced by one large posterior foramen serving as exit for canal from adductor fossa.

Evolution. Under both analyses, the ancestral state for the entire group is ambiguous, and that for Anguimorpha is one or more small foramina. A single large posterior foramen is a synapomorphy of *Xenosaurus.*

Cervical Skeleton

Most or all of the cervical skeleton is lacking in all fossils save *B. ammoskius.*

212. Cervical skeleton: Intercentra three and four (0) dorsoventrally taller than anteroposteriorly long (Fig. 48C); (1) anteroposteriorly longer than dorsoventrally tall (Fig. 48D).

Evolution. Under both analyses, the ancestral state for the entire group and for Anguimorpha is taller than long. Under Analysis 1, the ancestral state for *Xenosaurus* + Anguidae and for Anguidae + Helodermatidae is ambiguous. Under Analysis 2, longer than tall is a synapomorphy of
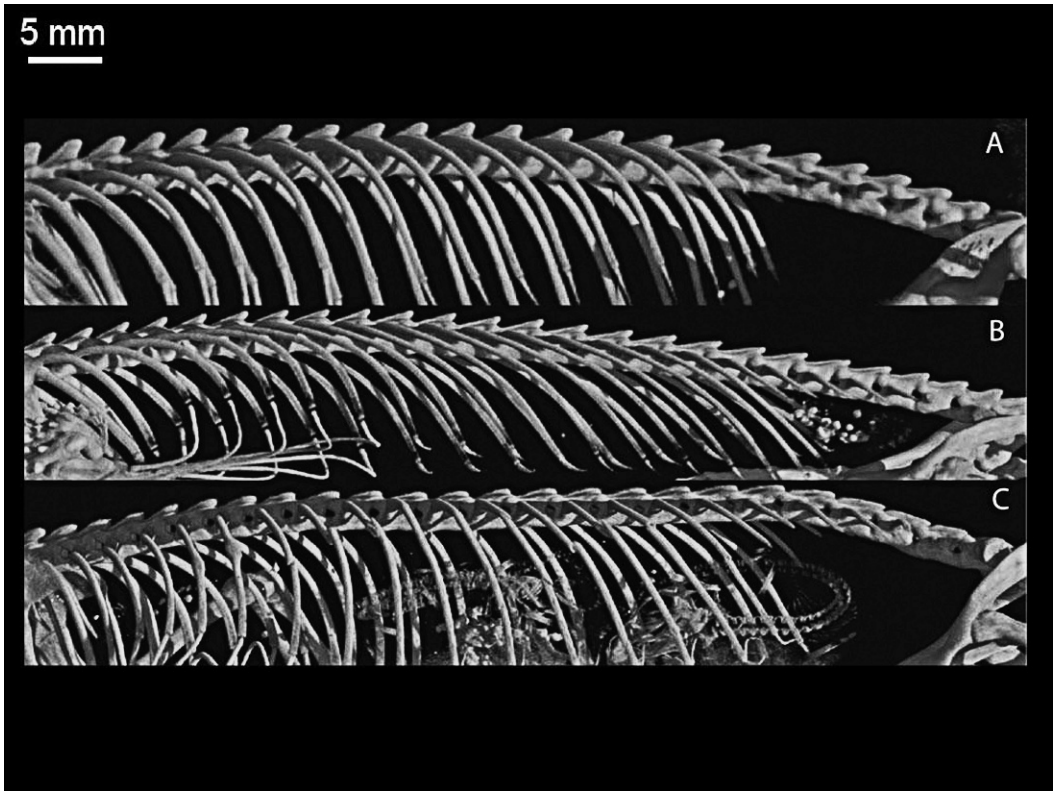
Figure 49.   Trunk skeletons, left lateral, anterior to the left: A, *Xenosaurus newmanorum*, CT scan of UMMZ 126057; B, *Xenosaurus platyceps*, CT scan of UF 25005; C, *Xenosaurus rectocollaris*, CT scan of UF 51443. A illustrates 214(1), 215(1), and 216(0). B illustrates 214(2), 215(2), and 216(0). C illustrates 214(2), 215(0), and 216(1).

Xenosaurus and an autapomorphy of Helodermatidae.

213. Cervical skeleton: Intercentra three and four (0) lateral surfaces gently contoured (Fig. 48D); (1) lateral surfaces bearing small transverse processes (Fig. 48C) (see Estes, 1983).

Evolution. Under both analyses, absence of transverse processes is the ancestral state for the entire group and for Anguimorpha. Under Analysis 1, presence of transverse processes is a synapomorphy of *Xenosaurus* and an autapomorphy of *S. crocodilurus*. Under Analysis 2, longer presence of transverse processes is a synapomorphy of Xenosauridae.

Trunk Skeleton

The trunk skeleton is unknown for all fossil taxa save *B. ammoskius* and *R. rugosus*. In the latter, only a few disarticulated vertebrae are preserved.

214. Trunk skeleton: Thoracic vertebral column, neural spines (0) tall, anterior edges sloping at about $45°$ to centrum; (1) spines in posterior third of thoracic column bearing long ribs low, anterior edges sloping at well under $45°$ (Fig. 49A); (2) all thoracic neural spines low, sloping at under $45°$ (Fig. 49B).

Variation. Neural spines heighten with age, especially during early postnatal ontogeny. This character should be scored on relatively large adults.

Evolution. Under both analyses, the low morphology in the posterior portion of the dorsal column is a synapomorphy of *Xenosaurus* + *R. rugosus*. The uniformly low morphology in the thoracic dorsal column is an autapomorphy of *X. platyceps* and of *X. rectocollaris*.

215. Trunk skeleton: Neural spines, posterodorsal projection formed by anteroventral slope of posterior edges (0) absent on most vertebrae, posterior edges of neural spines vertical or sloping posteroventrally (Fig. 49C); (1) well-developed, tip of neural spine blunt or rectangular (Fig. 49A); (2) well-developed, tip of neural spine produced into narrow finger-like process (Fig. 49B).

   Variation. Neural spines grow substantially during early postnatal ontogeny and so this character should not be scored on individuals less than about half of adult size.

   Evolution. Under both analyses, the ancestral state for the entire group and for Anguimorpha is the well-developed, blunt morphology. Absence is an autapomorphy of *X. rectocollaris,* and long, narrow production is an autapomorphy of *X. platyceps*.

216. Trunk skeleton: Lumbar neural spines (0) posteriorly sloped, anterior and posterior edges sloped with an anteroventral/posterodorsal orientation (Fig. 49A); (1) low, flat rectangles with weak, if any, slope (Fig. 49C).

   Evolution. Under both analyses, the low, rectangular morphology is a synapomorphy of *X. agrenon* + *X. rectocollaris*.

Caudal Skeleton

The caudal skeleton is unknown for all fossils save *B. ammoskius*.

217. Caudal skeleton: Caudal vertebral count (average, rounded to nearest integer) (0)

35 to 39; (1) 40 to 44; (2) 45 to 49; (3) 50 to 54; (4) 55 to 59; (5) 60 to 64; (6) 65 to 69; (7) 70 to 74; (8) 75 to 79; (9) 80 to 84; (A) 85 to 89; (B) 90 to 94.

   Variation. As noted, the values scored above are averages. A small amount of variation in caudal vertebral counts occurs. Furthermore, intact tails are present in a small fraction of specimens from modern skeletal collections and a smaller fraction still of fossils.

   Evolution. Under both analyses, the ancestral state for *Xenosaurus* is 40 to 44 and that for the southern clade of *Xenosaurus* is ambiguous between 35 to 39 and 40 to 44. A count of 60 to 64 is a synapomorphy of Varanidae, and a count of 90 to 94 a synapomorphy of *Varanus* or an autapomorphy of *V. exanthematicus*. A count of 65 to 69 is an autapomorphy of *O. ventralis*, and 35 to 39 is an autapomorphy of Helodermatidae. Under Analysis 1, the ancestral state for the entire group and for Anguimorpha is ambiguous between 40 to 44 and 45 to 49, as is that for *Xenosaurus* + Anguidae and Anguidae + Helodermatidae. A count of 50 to 54 is a synapomorphy of *E. multicarinata* + *O. ventralis*. The ancestral state for *S. crocodilurus* + Varanidae is 45 to 49. Under Analysis 2, the ancestral state for the entire group and for Anguidae is ambiguous between 45 to 49 and 50 to 54, as is that for Anguidae + Varanoidea and for Varanoidea. The ancestral state for Anguidae is 50 to 54. The ancestral state for Xenosauridae is 45 to 49, and 40 to 44 is a synapomorphy of *Xenosaurus*.

218. Caudal skeleton: Caudal autotomy planes (0) present (Fig. 50A); (1) absent (Fig. 164). (See character 103 of Estes et al., 1988).

   Variation. Autotomy planes are formed in most taxa by the time of hatching.
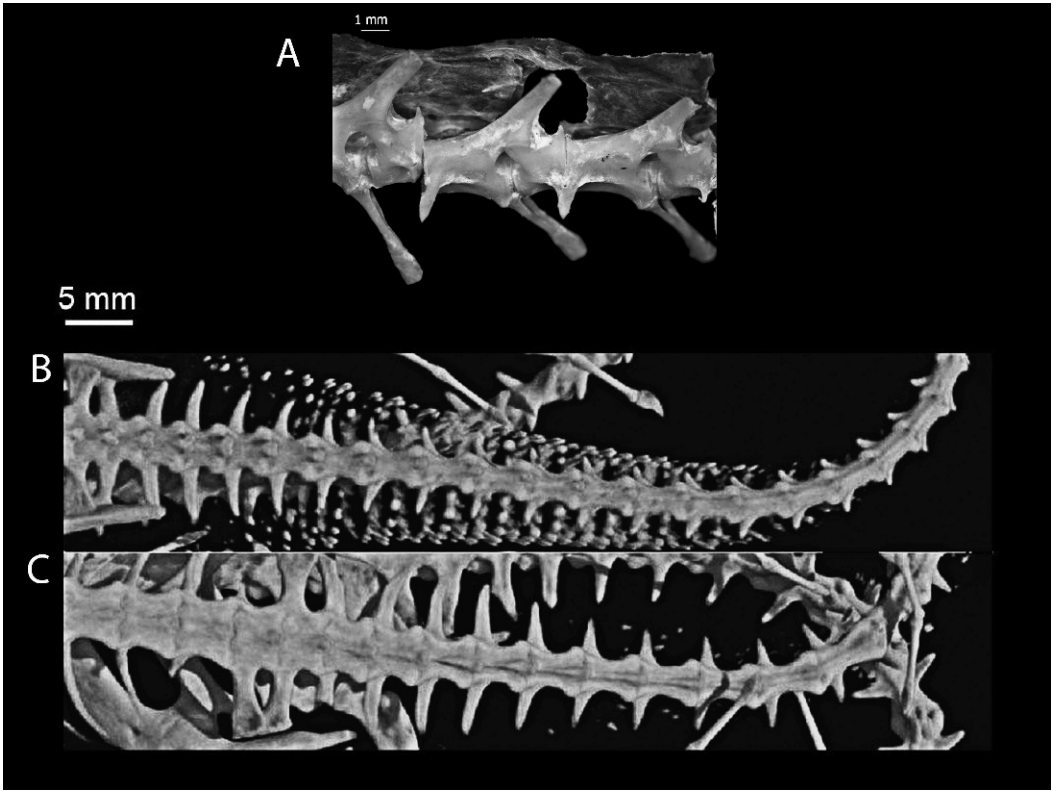
Figure 50.   A, Caudal vertebrae of *Shinisaurus crocodilurus* MVZ 204291, left lateral, anterior to the left. Illustrates character 218(0). Caudal vertebrae, dorsal, anterior to the left: B, *Xenosaurus newmanorum*, CT scan of UMMZ 126057; C, *Xenosaurus platyceps*, CT scan of UF 25005. B and C illustrate characters 218(1), 268(0), 268(1).

Evolution. Under Analysis 1, the ancestral state for the entire group and for Anguimorpha is ambiguous. Under Analysis 2, the ancestral state for the entire group and for Anguimorpha is presence of autotomy planes, and their absence is a synapomorphy of *Xenosaurus* and of Varanoidea.

Pectoral Girdle

The pectoral girdle is unknown for all extinct taxa save *B. ammoskius*.

219. Pectoral girdle: Scapulocoracoid emargination: (0) dorsal and ventral margins strongly diverging for most of length (Fig. 51A); (1) dorsal and ventral margins weakly diverging or nearly parallel for most of length (Fig. 51B).

Evolution. Under both analyses, weak or no divergence is a synapomorphy of the northern clade of *Xenosaurus* and of *Varanus*, as well as an autapomorphy of *C. enneagrammus*.

220. Pectoral girdle: Scapulocoracoid emargination; ratio of greatest height perpendicular to long axis to length along long axis (0) 0.70 or greater (Fig. 51C); (1) less than 0.70 (Fig. 51D).

Evolution. Under both analyses, the ancestral state for Anguidae is ambiguous, and a ratio of less than 0.70 is a synapomorphy of the northern clade of *Xenosaurus*.
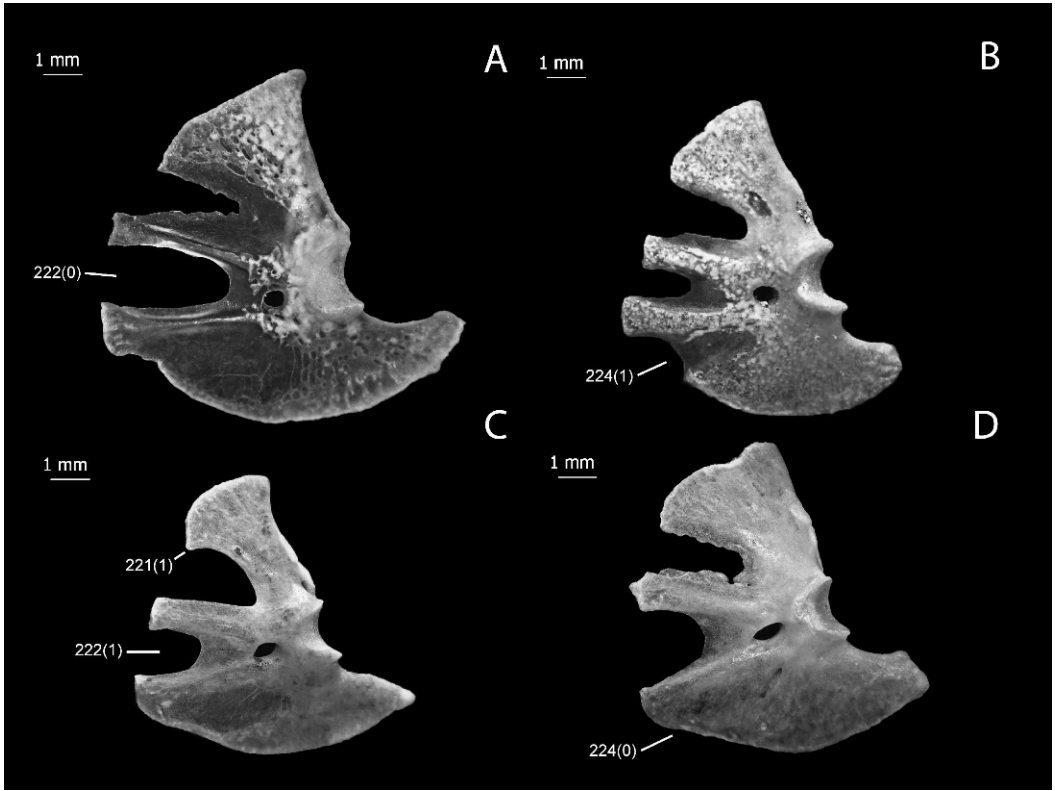
Figure 51. A, Left scapulocoracoid of *Elgaria multicarinata* TMM-M 8993, lateral, anterior to the left. Illustrates characters 219(0), 222(0), 223. B, Left scapulocoracoid of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, lateral, anterior to the left. Illustrates characters 219(1), 221(0), 224(1). C, Left scapulocoracoid of *Xenosaurus rackhami* UTEP-OC "MALB" 388, lateral, anterior to the left. Illustrates characters 220(0), 221(1), 222(1), 225(0). D, Left scapulocoracoid of *Xenosaurus platyceps* UF 45622, lateral, anterior to the left. Illustrates characters 220(1), 224(0), 225(1).

221. Pectoral girdle: Sharp hook-like overhang of scapulocoracoid emargination by scapula (0) absent (Fig. 51B); (1) present (Fig. 51C).

Evolution. Under both analyses, presence of an overhang is a synapomorphy of *X. rackhami + X. grandis.*

222. Pectoral girdle: Length of anterior coracoid emargination along long axis from apex of emargination to anterior end of dorsal margin (0) equal to or greater than length of remainder of scapulocoracoid along line of axis continued posteriorly from apex (Fig. 51A); (1) less than length of remainder of scapulocoracoid (Fig. 51C).

Evolution. Under Analysis 1, the ancestral state for the entire group and for Anguimorpha is ambiguous, as is that for all mixed internal nodes. Under Analysis 2, the ancestral state for the entire group and Anguimorpha is as long or longer than the remainder of the scapulocoracoid. Shorter than the remainder is a synapomorphy of *Xenosaurus* and of Varanoidea.

223. Pectoral girdle: Anterior coracoid emargination; ratio of greatest height perpendicular to long axis to length along long axis (Fig. 51B) (0) 0.50 or less; (1) between 0.50 and 0.85; (2) 0.85 or greater.

Evolution. Under both analyses, the ancestral state for the entire group and for Anguimorpha is between 0.50 and 0.85. The state 0.50 or less is an autapomorphy of *X. newmanorum,* whereas 0.85 or greater is an autapomorphy of *X. platyceps* and of *L. borneensis*. Under Analysis 1, the ancestral state for Anguidae + Helodermatidae and for Anguidae is ambiguous between 0.50 or less and between 0.50 and 0.85. The state 0.50 or less is a synapomorphy of *Varanus*. Under Analysis 2, the ancestral state for Anguidae + Varanoidea is ambiguous between states 0.50 or less and between 0.50 and 0.85.

224. Pectoral girdle: Posterior coracoid emargination (0) absent, ventral margin of coracoid curves smoothly (Fig. 51D); (1) present at least as abrupt anterior change in angle of ventral margin of coracoid toward the horizontal and straightening of curve (Fig. 51B) (see character 112 of Estes et al., 1988).

Evolution. Under both analyses, the ancestral state for the entire group is ambiguous, and that for Anguimorpha is absence of the emargination. Presence of the emargination is an autapomorphy of *X. newmanorum*, of *C. enneagrammus*, and of *L. borneensis*.

225. Pectoral girdle: Posterior end of coracoid (0) terminating in a point (Fig. 51C); (1) squared-off or blunt, attenuate (Fig. 51D).

Evolution. Under both analyses, the squared-off or blunt morphology is a synapomorphy of the northern clade of *Xenosaurus*.

226. Pectoral girdle: Clavicle, flattened tip of sternal ramus (0) in plane parallel or oblique to that of flattened portion of scapular ramus; (1) in plane nearly perpendicular to that of flattened portion of scapular ramus.

Evolution. Under both analyses, the nearly perpendicular morphology is a synapomorphy of the northern clade of *Xenosaurus*.

227. Pectoral girdle: Clavicle, corner between rami (0) projected into long, narrow process (Fig. 52A); (1) produced into distinct, moderately long eminence (Fig. 52B); (2) produced only slightly into small thickening or bump (Fig. 52C).

Evolution. Under both analyses, the ancestral state for the entire group and for Anguimorpha is ambiguous between production into a moderately long eminence and slight production. The long morphology is an autapomorphy of *S. crocodilurus* and of *E. multicarinata*. Under Analysis 1, the ancestral state for *S. crocodilurus* + Varanidae is ambiguous in the same way as Anguimorpha. The ancestral state for *Xenosaurus* + Anguidae is slight production, and moderate production is a synapomorphy of *X. rackhami* + *X. grandis*.

228. Pectoral girdle: Interclavicle, lateral processes (0) without proximal change in angle (Fig. 52A); (1) extending perpendicular to longitudinal body of interclavicle for short proximal stretch before abruptly angling backward (Fig. 52B).

Evolution. Under both analyses, the morphology involving a proximal transverse stretch and a posterior inflection is a synapomorphy of *Xenosaurus*.

229. Pectoral girdle: Interclavicle, angle of distal portion of lateral process to longitudinal body (0) 65° or less (Fig. 52B); (1) greater than 65° (Fig. 52C).

Evolution. Under both analyses, an angle greater than 65° is a synapomorphy of the northern clade of *Xenosaurus* and an autapomorphy of *X. rectocollaris* and of *L. borneensis*.

230. Pectoral girdle: Interclavicle, ratio of length of lateral process to length of posterior process (including section
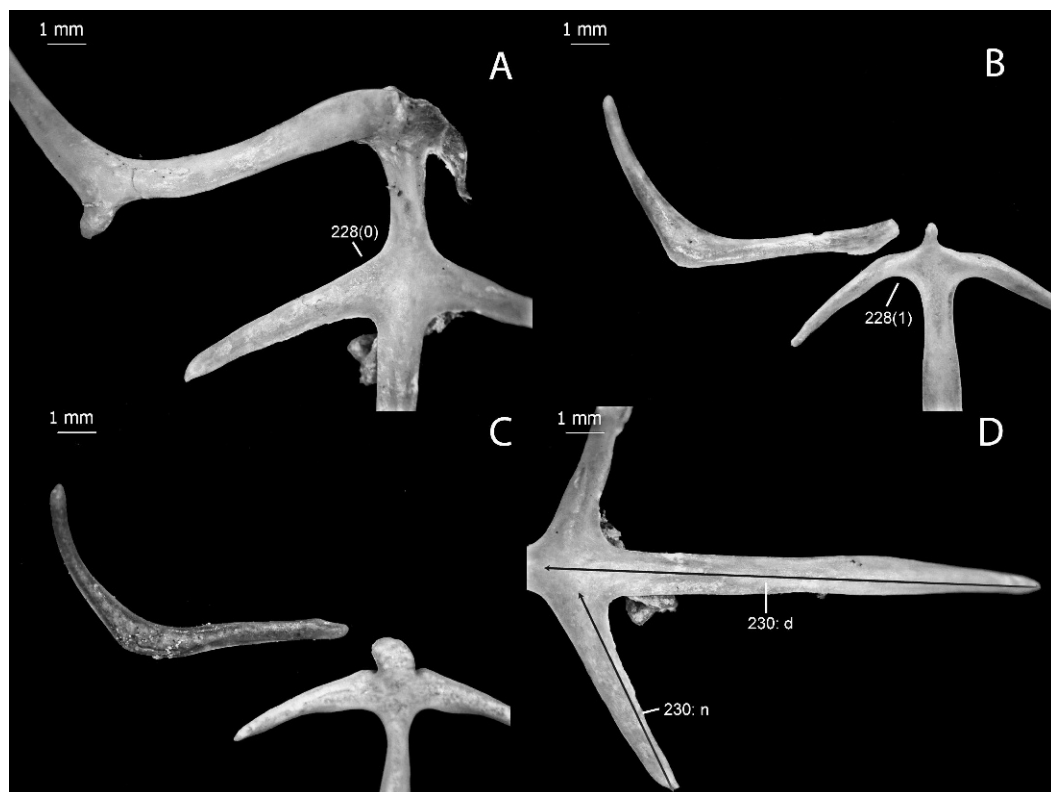
Figure 52.   A, Interclavicle and right clavicle of *Shinisaurus crocodilurus* MVZ 204291, ventral, anterior to the top. Illustrates characters 227(0), 228(0), 231(0). B, Interclavicle and right clavicle of *Xenosaurus rackhami* UTEP-OC "MALB" 388, ventral, anterior to the top. Illustrates characters 227(1), 229(0), 228(1). C, Interclavicle and right clavicle of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, ventral, anterior to the top. Illustrates characters 227(2), 229(1), 231(1). D, Interclavicle of *Shinisaurus crocodilurus* MVZ 204291, ventral, anterior to the left. Illustrates character 230 (n for numerator, d for denominator).

between lateral processes) (Fig. 52D) (0) 0.55 or greater; (1) less than 0.55.

Evolution. Under both analyses, the ancestral state for the entire group and for Anguimorpha is less than 0.55, and 0.55 or greater is an autapomorphy of *S. crocodilurus.* Under Analysis 1, the ancestral state for Anguidae + Helodermatidae and for Anguidae is ambiguous. Under Analysis 2, a ratio of 0.55 or greater is an autapomorphy of *E. multicarinata* and of Helodermatidae.

231. Pectoral girdle: Interclavicle, anterior process (0) prominent, several times as long as wide (Fig. 52A); (1) present as small eminence or absent (Fig. 52C)

(see character 120 of Estes et al., 1988).

Evolution. Under both analyses, the ancestral state for the entire group and for Anguimorpha is small size or absence. Prominence is a synapomorphy of Anguidae and an autapomorphy of *S. crocodilurus.*

Forelimb

The forelimb is unknown for all fossils but *B. ammoskius.*

232. Forelimb: Ulna, ratio of width perpendicular to long axis at narrowest part of shaft to length along long axis (0) 0.07 or less (Fig. 53A); (1) greater than 0.07 (Fig. 53B).

Figure 53.   Left ulnae, anterior, distal to the left: A, *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen; B, *Xenosaurus platyceps* UF 45622. A and B illustrate characters 232(0), 232(1). Right ilia, lateral, anterior to the right: C, *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen. Illustrates character 233(0). D, *Shinisaurus crocodilurus* MVZ 204291. Illustrates character 233(1).

Evolution. Under both analyses, relative width with a ratio greater than 0.07 is an autapomorphy of *X. platyceps*.

Pelvic Girdle

The pelvic girdle is unknown for *E. serratus*, *E. lancensis*, and *M. ornatus*. Only the ilium is preserved in *R. rugosus*; the taxon cannot be scored for the other elements. *Ophisaurus ventralis* has a vestigial pelvic girdle and could not be scored for these characters.

233. Pelvic girdle: Narrowing at tip of ilium (0) primarily resulting from change in angle in ventral margin of ilium (Fig. 53C); (1) primarily resulting from change in angle in dorsal margin (Fig. 53D).

Evolution. Under both analyses, tapering resulting from a dorsal change in angle is a synapomorphy of *S. crocodilurus* + *B. ammoskius*.

234. Pelvic girdle: Thyroid fenestra, ratio in plane of fenestra of longest antero-posterior length parallel to symphysis to widest mediolateral width perpendicular to symphysis (Fig. 54A) (0) less than 0.95; (1) from 0.95 to less than 1.20; (2) 1.20 or greater.

Evolution. Under both analyses, the ancestral state for the entire group and for Anguimorpha is between 0.95 and 1.20. A ratio of less than 0.95 is an
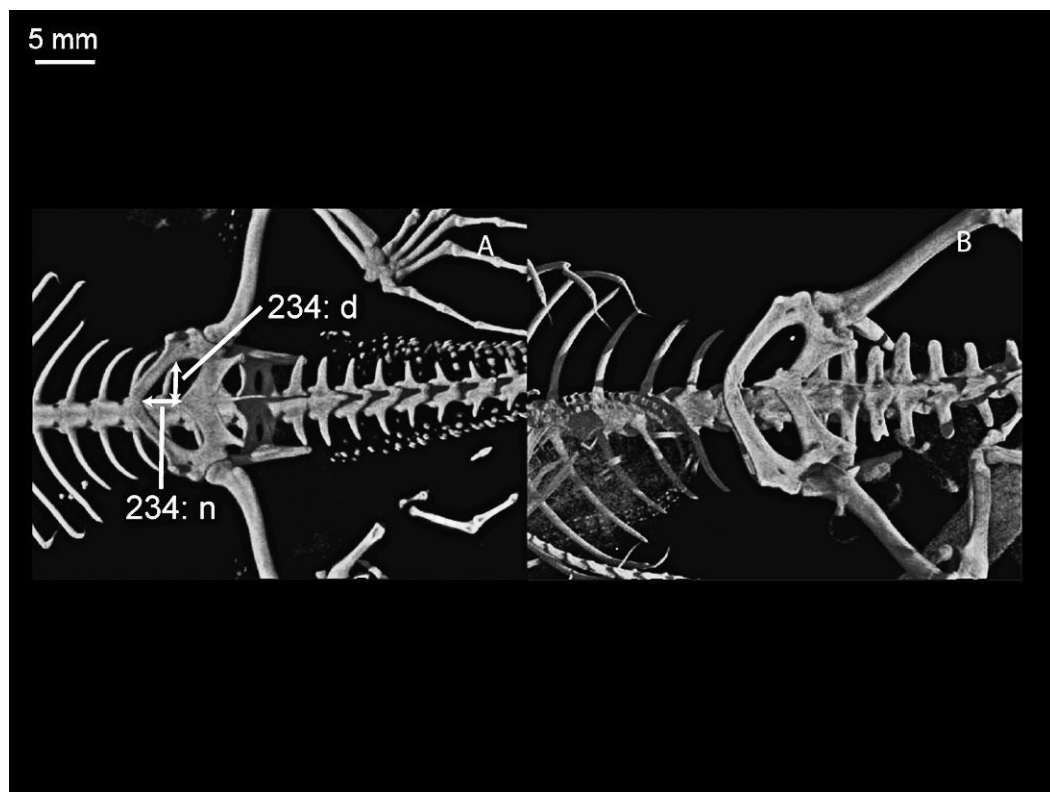
Figure 54.   Pelvic girdles and posterior axial skeletons, ventral, anterior to the left: A, *Xenosaurus newmanorum*, CT scan of UMMZ 126057; B, *Xenosaurus rectocollaris*, CT scan of UF 51443. A illustrates 234 (n for numerator, d for denominator), 235(1), 236(0), and 267(1). B illustrates 235(0), 236(1), and 267(2).

autapomorphy of *X. newmanorum*, of *X. rectocollaris*, and of *C. enneagrammus*. A ratio of 1.20 or greater is an autapomorphy of *X. platyceps*.

235. Pelvic girdle: Pubis, ratio of width perpendicular to long axis just medial to pectineal tubercle to length along long axis from tubercle to symphysis (0) greater than 0.38 (Fig. 54B); (1) 0.38 or less (Fig. 54A).

Evolution. Under both analyses, a ratio of 0.38 or less is an autapomorphy of *X. newmanorum* and of *C. enneagrammus*.

236. Pelvic girdle: Ischium (0) flat, broadly plate-like with constriction near mediolateral midpoint (Fig. 54A); (1) narrow, tapering medially with constriction

absent or weakly present far medially (Fig. 54B).

Evolution. Under both analyses, the narrow, tapering, unconstricted morphology is an autapomorphy of *X. rectocollaris*.

Hind Limb

The hind limb is unknown for all extinct taxa save *B. ammoskius*.

237. Hind limb: Femur, femoral neck in plane of knee flexion (0) wider perpendicular to long axis than long (Fig. 55A); (1) longer along long axis than wide (Fig. 55B).

Evolution. Under both analyses, longer-than-wide is an autapomorphy of *X. platyceps*.
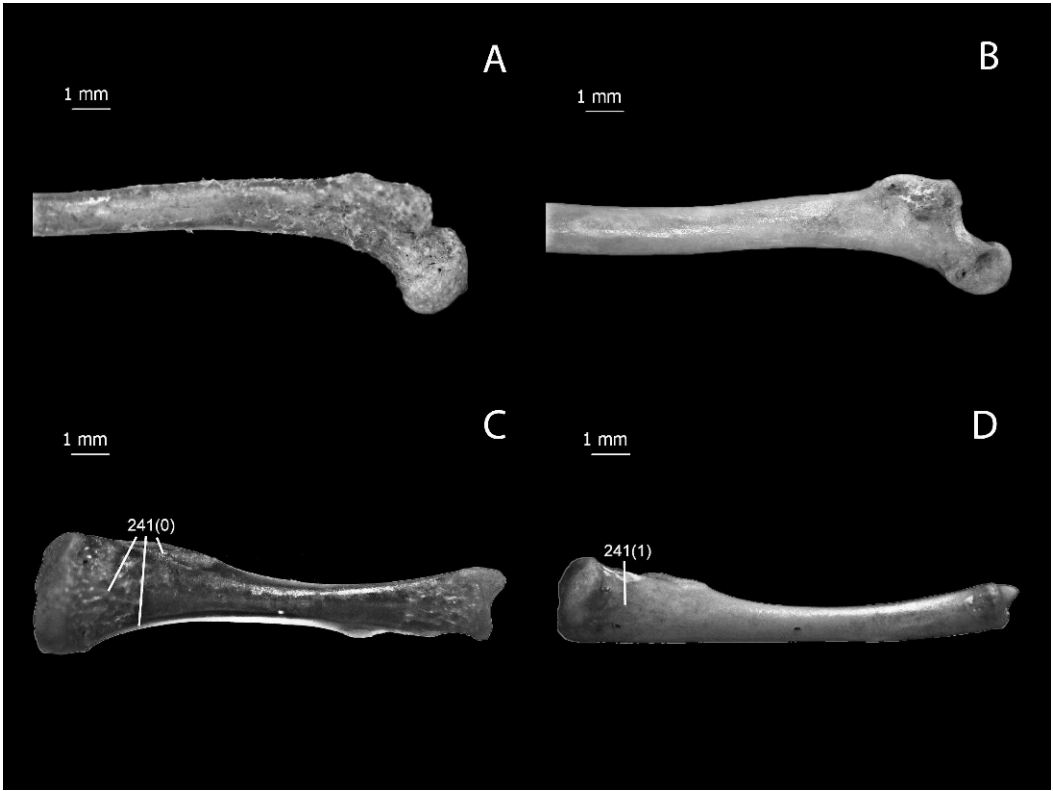
Figure 55.   Left femora, anterior, distal to the left: A, *Xenosaurus grandis* NAUQSP-JIM 1460; B, *Xenosaurus platyceps* UF 45622. A and B illustrate characters 237(0), 237(1). Left tibiae, flexor view, distal to the right: C, *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen; D, *Elgaria multicarinata* TMM-M 8958. C and D illustrate characters 238(0), 238(1), 239(0), 239(1), 240(0), 241(0), 241(1).

238. Hind limb: Tibia, width measured by ratio of anteroposterior length across extensor surface at proximal end, just distal to epiphysis, to proximodistal length (0) wide, 0.25 or greater (Fig. 55C); (1) narrow, less than 0.25 (Fig. 55D).

Evolution. Under both analyses, the ancestral state for the entire group and for Anguimorpha is ambiguous. Under Analysis 1, the ancestral state for *S. crocodilurus* + Varanidae and for Anguidae + Helodermatidae is 0.25 or greater. The ancestral state for *Xenosaurus* + Anguidae is ambiguous. Under Analysis 2, the ancestral state for Anguidae + Varanoidea is 0.25 or greater and that for Xenosauridae is ambiguous.

239. Hind limb: Tibia, anterior crest margin (0) straight or slightly convex (Fig. 55C); (1) concave in plane of crest (Fig. 55D).

Evolution. Under both analyses, the concave morphology is a synapomorphy of the northern clade of *Xenosaurus* and an autapomorphy of *X. agrenon*.

240. Hind limb: Tibia, anterior crest occupies (0) about one-quarter of shaft of tibia (Fig. 55C); (1) about one-fifth of shaft of tibia; (2) minimal portion of shaft, crest reduced to small distal eminence (Fig. 56A).

Evolution. Under both analyses, the ancestral state for the entire group is ambiguous among all three states. That
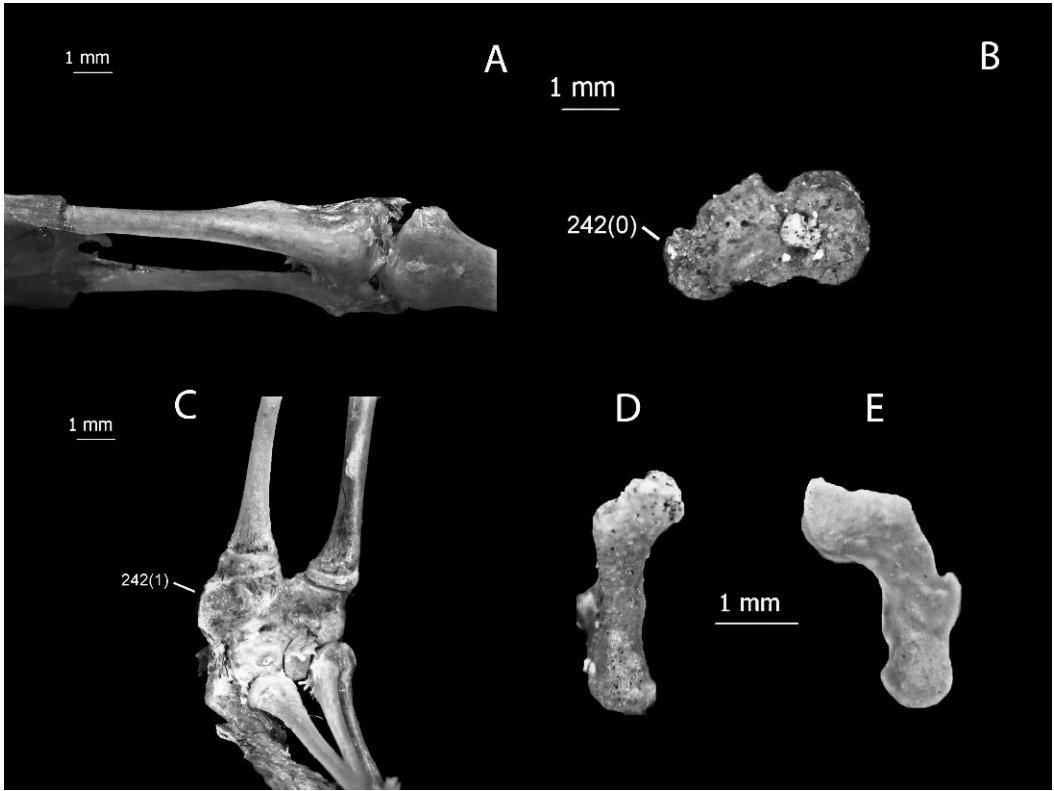
Figure 56.   A, Right lower hind limb of *Xenosaurus rackhami* MCZ 54317, flexor view, distal to the left. Illustrates character 240(2). B, Left astragalocalcaneum of *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen, flexor view, distal toward the bottom. Illustrates character 242(0). C, Left astragalocalcaneum of *Xenosaurus grandis* MVZ 128947, flexor view, distal toward the bottom. Illustrates character 242(1). Fifth metatarsals, extensor view, distal toward the bottom: D, left, *Xenosaurus newmanorum* NAUQSP-JIM uncatalogued specimen; E, right, *Elgaria multicarinata* TMM-M 8958.

for Anguimorpha is occupation of one-quarter of the shaft. Occupation of one-fifth of the shaft is an autapomorphy of *X. platyceps* and of *B. ammoskius*. Occupation of a minimal portion of the shaft as a small nub or eminence is an autapomorphy of *X. rackhami*.

241. Hind limb: Tibia, proximal sulci on flexor surface for attachment of m. semimembranosus and m. tibialis posterior among other muscles (0) forming distinct, shallow grooves (Fig. 55C); (1) barely incised, represented only by a flattening of tibial surface (Fig. 55D).

   Evolution. Under both analyses, the simple, flattened morphology is ancestral for the entire group and for Anguimorpha. Under Analysis 1, deep incision is a synapomorphy of *Varanus* or Varanidae and of Anguidae. Under Analysis 2, the ancestral state for Anguidae + Varanoidea is ambiguous.

242. Hind limb: Calcaneum, length of calcaneal heel measured by ratio of anteroposterior length to proximodistal width (0) long, 0.50 or greater (Fig. 56B); (1) short, less than 0.50 (Fig. 56C).

   Evolution. Under both analyses, the ancestral state for the entire group is ambiguous, and that for Anguimorpha is the long morphology. The short

morphology is a synapomorphy of the southern clade of *Xenosaurus* and an autapomorphy of *L. borneensis*.

243. Hind limb: Fifth metatarsal, flexo-extensor bending such that metatarsal is concave in the extensor direction (0) strongly arched, in part because of heavy development of expanded proximal end (Fig. 56E); (1) weak, creating a gentle, nearly horizontal arc (Fig. 56D).

    Evolution. Under both analyses, a weak flexo-extensor arch is a synapomorphy of *Xenosaurus*.

244. Hind limb: Fifth metatarsal, anteroposterior expansion of head measured by ratio of anteroposterior length at longest proximodistal level to proximodistal length of metatarsal (0) relatively great, 0.65 or greater (Fig. 56E); (1) relatively slight, less than 0.65 (Fig. 56D).

    Evolution. Under both analyses, the ancestral state for the entire group and for Anguimorpha is slight expansion. Under Analysis 1, relative expansion is a synapomorphy of Anguidae + Helodermatidae and of *Varanus*. Under Analysis 2, it is a synapomorphy of Anguidae + Varanoidea, and slight expansion is an autapomorphy of *L. borneensis* within that clade.

245. Hind limb: Fifth metatarsal, lateral plantar tubercle (0) nearly perpendicular to medial plantar tubercle in plane perpendicular to long axis of metatarsal; (1) at an acute angle to medial plantar tubercle.

    Evolution. Under both analyses, an acute angle is a synapomorphy of the southern clade of *Xenosaurus* and of Varanidae.

Osteoderms, General

These notes apply to all osteoderm character categories. Osteoderms could only be visualized on species of *Xenosaurus,* save *X. agrenon*, *S. crocodilurus*, *L. borneensis* from published x-rays (McDowell and Bogert,

1954) and CT scans (Maisano et al., 2002), Anguidae, and Helodermatidae, as well as the postcranium of *B. ammoskius*. When the southern clade of *Xenosaurus* is mentioned as having a character state in the osteoderm section, it should be understood that the state for *X. agrenon* is inferred. *Varanus* has osteoderms (McDowell and Bogert, 1954), but they are too small to visualize reliably with CT scanning, and alternative preparations were unavailable. Osteoderms are unknown for the remaining fossil anguimorphs, save some isolated osteoderms associated with *M. ornatus* (Klembara, 2008). *Pristidactylus torquatus* does not have significant free osteoderms as an adult; the condition in juveniles is unknown.

Regarding osteodermal variation, it is obvious that osteoderm patterns vary slightly with scalation patterns. Additionally, osteoderms develop postnatally for the most part; thus, it is important to score osteoderm characters on relatively large adult individuals.

246. Osteoderms: Domed osteoderms (0) absent; (1) largely circular; (2) some circular, but largely oval or obovate (see Conrad, 2005, 2008).

    Evolution. Under both analyses, the ancestral state for *Xenosaurus* + *R. rugosus* is domed and circular. Domed and circular plus oval is an autapomorphy of *E. lancensis*. Under Analysis 1, the ancestral state for the entire group and for Anguimorpha is domed and circular. Lack of domed osteoderms is a synapomorphy of *S. crocodilurus* + Varanidae and of Anguidae. Under Analysis 2, the ancestral state for the entire group and for Anguimorpha is ambiguous between absent and largely circular.

Cranial Osteoderms

247. Cranial osteoderms: Fused cranial osteoderms (0) absent; (1) present (Fig. 1A).

    Evolution. Under both analyses, absence of fused cranial osteoderms is a synapomorphy of Varanidae.

248. Cranial osteoderms: Supraorbital osteoderm longitudinal rows (0) five (Fig. 2A); (1) four (Fig. 1A); (2) three (Fig. 5A); (3) two (Fig. 4A).

Evolution. Under both analyses, two rows is ancestral for Anguimorpha. Three rows is an autapomorphy of *C. enneagrammus*. The ancestral state for *Xenosaurus* is ambiguous between three and two rows. Four rows is a synapomorphy of the northern clade of *Xenosaurus,* and five rows is an autapomorphy of *X. platyceps*.

249. Cranial osteoderms: Full supraorbital osteoderms in longitudinal row bearing largest osteoderms (0) eight (Fig. 1A); (1) seven; (2) six; (3) five (Fig. 5A); (4) four; (5) three; (6) two (Fig. 3A).

Evolution. Under both analyses, a count of eight is a synapomorphy of the northern clade of *Xenosaurus*. Two is an autapomorphy of *X. rackhami* and of *L. borneensis*. Four is an autapomorphy of *E. multicarinata,* and three is an autapomorphy of Helodermatidae. Six is an autapomorphy of *S. crocodilurus*. Under Analysis 1, the ancestral state for Anguimorpha is five, as is that for *S. crocodilurus* + Varanidae, *Xenosaurus* + Anguidae, and Anguidae + Helodermatidae. Under Analysis 2, the ancestral state for Anguimorpha is ambiguous among six, five, and four. The ancestral state for Xenosauridae is ambiguous between six and five. The ancestral state for Anguidae + Varanoidea is ambiguous between five and four, as is that for Anguidae. Three is a synapomorphy of Varanoidea

250. Cranial osteoderms: Supraorbital osteoderms in longitudinal row bearing largest osteoderms—largest osteoderms (0) less than twice as extensive along long axis as perpendicular to long axis (Fig. 2A); (1) twice as extensive or more along long axis as perpendicular to long axis (Fig. 4A).

Evolution. Under Analysis 1, the ancestral state for the entire group and for Anguimorpha is less than twice as long as wide. Twice as long as wide or more is a synapomorphy of the southern clade of *Xenosaurus* and an autapomorphy of *S. crocodilurus*. Under Analysis 2, the ancestral state for the entire group and for Anguimorpha is ambiguous. The ancestral state for Anguidae + Varanoidea is less than twice as long as wide.

251. Cranial osteoderms: Dorsal temporal osteoderms, peripheral rims (0) present (Fig. 1A); (1) absent (Fig. 4A).

Evolution. Under both analyses, presence of rims is a synapomorphy of the northern clade of *Xenosaurus* and an autapomorphy of Helodermatidae.

252. Cranial osteoderms: Dorsal temporal osteoderms (0) overlie entirety of dorsal temporal fenestra and dorsal surfaces of upper temporal arch bones (Fig. 1A); (1) overlie entirety of dorsal temporal fenestra and partially overlie dorsal surfaces of upper arch bones, but posterodorsal tip of jugal, lateral edge of postorbitofrontal, and anterolateral portion of squamosal lateral to mediolateral level of external edge of postorbitofrontal are exposed (Fig. 5A); (2) overlie dorsal temporal fenestra but leave exposed elements described in state 1 plus postfrontal portion of postorbitofrontal and most of squamosal (Fig. 4A); (3) only few and isolated, overlying dorsal temporal fenestra and posterior, median portion of postorbitofrontal (Fig. 3A); (4) absent.

Evolution. Under both analyses, the ancestral state for the entire group is ambiguous among all four states. The ancestral state for Anguimorpha is 0. State 4 is a synapomorphy of *Varanus*, state 1 is a synapomorphy of the southern clade of *Xenosaurus,* and state 2 is a synapomorphy of *X. rackhami* + *X. grandis*.

253. Cranial osteoderms: Transverse rows of osteoderms behind posterior edge of

parietal (0) spanning most of width of parietal (Fig. 2A); (1) restricted to mediolateral area spanned by notch at meeting of supratemporal processes (Fig. 5A); (2) absent (Fig. 4A).

Evolution. Under both analyses, absence is a synapomorphy of *X. rackhami* + *X. grandis*. Under Analysis 1, a span of most of the width of the parietal is ancestral for Anguimorpha, and a restricted span is a synapomorphy of the southern clade of *Xenosaurus*. Absence is an autapomorphy of *S. crocodilurus*. Under Analysis 2, the ancestral state for Anguimorpha and for Xenosauridae is ambiguous between a wide and a restricted span. The ancestral state for Anguidae + Varanoidea is a wide span.

254. Cranial osteoderms: Number of transverse rows of osteoderms behind posterior edge of parietal (0) two (Fig. 5A); (1) three (Fig. 2A).

Evolution. Under both analyses, three rows is an autapomorphy of *X. platyceps*. Under Analysis 1, three rows is an autapomorphy of Helodermatidae and of *L. borneensis*. Under Analysis 2, three rows is a synapomorphy of Varanoidea.

255. Cranial osteoderms: Lateral temporal osteoderms, peripheral rims (0) absent (Fig. 5C); (1) present (Fig. 1C).

Evolution. Under both analyses, the presence of rims is a synapomorphy of *Xenosaurus*. It is also an autapomorphy of *X. grandis* and of Helodermatidae.

256. Cranial osteoderms: Lateral temporal osteoderms, spacing—(0) closely packed (Fig. 1C); (1) separated by small gaps (Fig. 5C); (2) separated by gaps of one scale or more (Fig. 4C); (3) present only as small slivers of ossification (Fig. 3C); (4) absent.

Evolution. Under both analyses, the ancestral state for the entire group is ambiguous among the last four states. That for Anguimorpha is ambiguous

between separation by small and large gaps. Presence as only small slivers of ossification is autapomorphic for *X. rackhami*. Under Analysis 1, the ancestral state for *S. crocodilurus* + Varanidae is ambiguous between separation by small and large gaps. The ancestral state for *Xenosaurus* + Anguidae is ambiguous between close packing and separation by small gaps. Close packing is the ancestral state for Anguidae + Helodermatidae. Separation by small gaps is ancestral for the southern clade of *Xenosaurus*, and separation by large gaps is a synapomorphy of *X. rackhami* + *X. grandis*. Under Analysis 2, the ancestral state for Anguidae + Varanoidea is ambiguous between closely packed and separated by small gaps.

257. Cranial osteoderms: Lateral temporal osteoderms, coverage of quadratojugal region posterior to quadratojugal process of jugal (0) present (Fig. 1C); (1) absent (Fig. 5C).

Evolution. Under both analyses, noncoverage of the quadratojugal region is a synapomorphy of the southern clade of *Xenosaurus*.

258. Cranial osteoderms: Mandibular osteoderms (0) absent; (1) most of dentary exposed; only portions of postdentary bones extensively covered; (2) covering part of lateral face of mandible, including dentary and postdentary bones, but leaving large areas of dentary and postdentary bones exposed (Fig. 5B, C); (3) covering most of lateral face of mandible save for retroarticular process and pterygoideus insertion on surangular, present in three major longitudinal rows (Figs. 1B, C); (4) as with state 3 but with four major longitudinal rows (Figs. 2B, C).

Evolution. Under both analyses, the ancestral state for Anguimorpha is ambiguous between state 1 and state 2. The ancestral state for *Xenosaurus* is 2, and state 3 is a synapomorphy of

the northern clade of *Xenosaurus*, with state 4 an autapomorphy of *X. platyceps*. State 3 is also a synapomorphy of Anguidae. The ancestral state of most other nodes under both analyses is ambiguous between state 1 and state 2.

259. Cranial osteoderms: Mandibular osteoderms (0) with strong, sharp keels (Fig. 1B, C); (1) unkeeled or subtly keeled (Fig. 5B, C).

   Evolution. Under both analyses, strong keeling of the mandibular osteoderms is a synapomorphy of the northern clade of *Xenosaurus*.

260. Cranial osteoderms: Intermandibular osteoderms (0) present, well-developed (Fig. 1B); (1) present as multiple small ossifications (Fig. 2B); (2) present as one or two small ossifications (Fig. 5B); (3) absent (Fig. 4B).

   Evolution. Under both analyses, the well-developed morphology is an autapomorphy of *X. newmanorum,* and absence is a synapomorphy of *X. rackhami + X. grandis*. Under Analysis 1, the ancestral state for the entire group is ambiguous among multiple small ossifications, one or two small ossifications, and absence, and that for Anguimorpha is ambiguous between multiple and one or two small ossifications. The well-developed morphology is a synapomorphy of Anguidae + Helodermatidae and an autapomorphy of *L. borneensis*. Under Analysis 2, the ancestral state for the entire group is ambiguous between one or two small ossifications and absence. That for Anguimorpha is one or two small ossifications. The well-developed morphology is a synapomorphy of Anguidae + Varanoidea, and presence as multiple small ossifications is a synapomorphy of the northern clade of *Xenosaurus*.

261. Cranial osteoderms: Intermandibular osteoderms, well-developed portion (0) in posterior half of mandible; (1) in anterior half of mandible (Fig. 1A).

   Evolution. Under Analysis 1, posterior development is ancestral, and development in the anterior half of the mandible is a synapomorphy of the northern clade of *Xenosaurus* or of all xenosaurs. Under Analysis 2, the ancestral state is ambiguous across most of the tree, but the ancestral state of Varanoidea is posterior development.

262. Cranial osteoderms: Intermandibular osteoderms, lateral rows (0) present along entirety of tooth-bearing region of dentaries (Fig. 1B); (1) present only along anterior portion (Fig. 2B).

   Evolution. The ancestral state of the character is entirely ambiguous.

263. Cranial osteoderms: Intermandibular osteoderms (0) spanning mandibular rami for large portion of anteroposterior extent (Fig. 1B); (1) developed only laterally for most of extent (Fig. 2B).

   Evolution. Under both analyses, the ancestral state for Anguimorpha is ambiguous. Under Analysis 1, most internal nodes are ambiguous, save that the ancestral state for Anguidae + Helodermatidae is extensive development. Under Analysis 2, the ancestral state for Anguidae + Varanoidea is extensive development, and that for Xenosauridae is lateral development, making the extensive development in *X. newmanorum* an autapomorphy of that taxon.

Cervical Osteoderms

264. Cervical osteoderms: Cervical osteoderms (0) present dorsally in each scale (The Deep Scaly Project, 2007); (1) present dorsally in regularly spaced pattern, but not in each scale; (2) present dorsally as small ossifications concentrated anteriorly with occasional larger osteoderms interspersed (Fig. 1A); (3) present dorsally as small
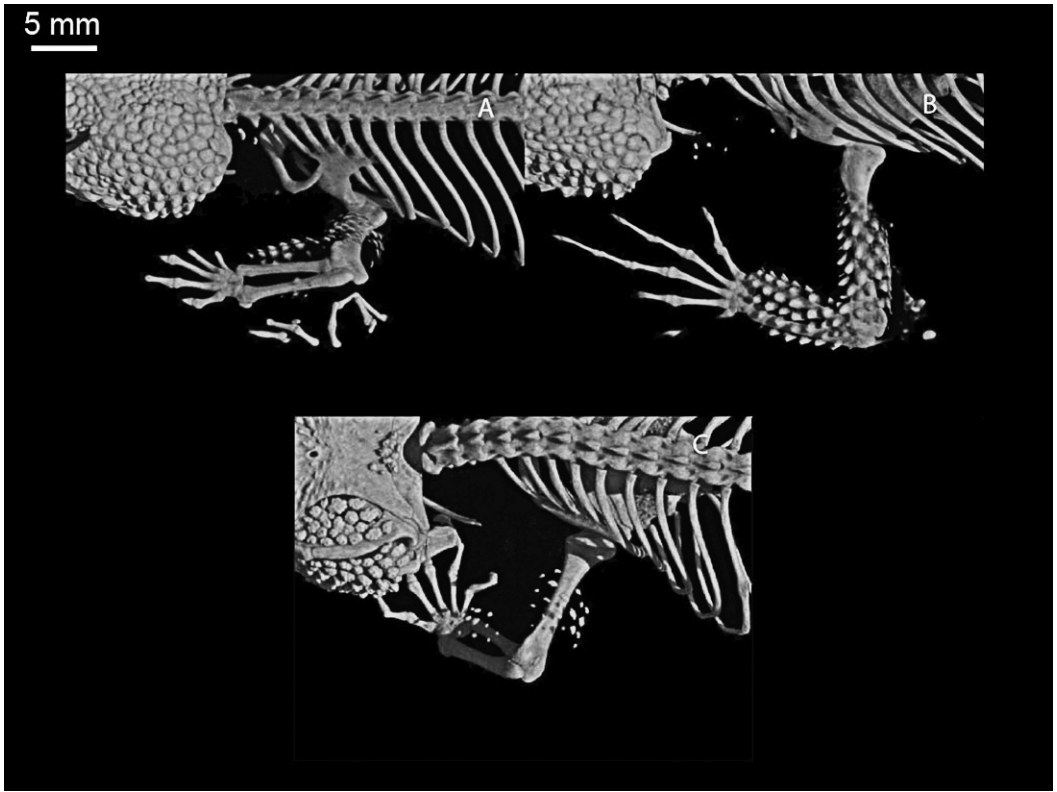
Figure 57.   Left pectoral limbs, extensor view, anterior to the left: A, *Xenosaurus newmanorum*, CT scan of UMMZ 126057; B, *Xenosaurus platyceps*, CT scan of UF 25005; C, *Xenosaurus rectocollaris*, CT scan of UF 51443. A illustrates 265(1) and 266(1). B illustrates 265(0) and 266(1). C illustrates 265(0) and 266(2).

ossifications (Fig. 3A); (4) absent (Fig. 5A).

Evolution. Under both analyses, the ancestral state for the entire group is ambiguous among the last four states, and that for Anguimorpha is ambiguous between 1 and 2. The ancestral state for *Xenosaurus* is 2, and state 3 is a synapomorphy of the southern clade of *Xenosaurus*. State 4 is an autapomorphy of *X. rectocollaris*. Under Analysis 1, the ancestral state for *S. crocodilurus* + Varanidae is 2, and that for Anguidae + Helodermatidae is 0. Under Analysis 2, the ancestral state for Anguidae + Varanoidea is ambiguous between 0 and 1, and that for Xenosauridae is ambiguous between 1 and 2.

Pectoral Osteoderms

265. Pectoral osteoderms: Osteoderms on pectoral limb (0) present on most of extensor surfaces of stylopod and zeugopod and more lightly distributed on flexor surface (Fig. 57B); (1) present on central two-thirds or more of extensor surfaces, but only marginally on flexor surfaces (Fig. 57A); (2) present only as narrow central band (about central one-third) of extensor surfaces, save for a few scattered ossifications over elbow (Fig. 57C); (3) absent.

Evolution. Under both analyses, the ancestral state for the northern clade of *Xenosaurus* is 1, and state 0 is an autapomorphy of *X. platyceps*. The ancestral state for the southern clade

of *Xenosaurus* is 2, and state 3 is a synapomorphy of *X. rackhami* + *X. grandis*. Under Analysis 1, the ancestral state for the entire group is ambiguous among 1, 2, and 3. That for Anguimorpha is ambiguous between 1 and 2. The ancestral state for Anguidae + Helodermatidae is 0. Under Analysis 2, the ancestral state for the entire group is ambiguous between 2 and 3, and that for Anguimorpha is 2. State 0 is a synapomorphy of Anguidae + Varanoidea, and state 1 is a synapomorphy of the northern clade of *Xenosaurus*.

266. Pectoral osteoderms: Osteoderms on pectoral limb (0) present as small nubs of ossification; (1) present as large rounded ossifications (Fig. 57A); (2) present as large rounded ossifications and in places as cone-shaped spicules (Fig. 57B).

    Evolution. Under both analyses, the ancestral state for the entire group is presence as large rounded ossifications. Presence as small nubs of ossification is an autapomorphy of *S. crocodilurus*, and presence as large rounded ossifications plus cone-shaped ossifications is an autapomorphy of *X. platyceps*.

Pelvic Osteoderms

267. Pelvic osteoderms: Osteoderms on pelvic limb (0) present on extensor surface of stylopod and scattered on flexor surface (McDowell and Bogert, 1954, plate 4); (1) present only on extensor surface of stylopod (Fig. 54A); (2) absent.

    Evolution. Under both analyses, the ancestral state for the northern clade of *Xenosaurus* is extensor presence only, and presence on the extensor and flexor surfaces is an autapomorphy of *X. platyceps*. Under Analysis 1, the ancestral state for the entire group and for Anguimorpha is ambiguous between presence on the extensor surface and absence. Presence on the flexor

and extensor surfaces is a synapomorphy of Anguidae + Helodermatidae and an autapomorphy of *L. borneensis*. Under Analysis 2, the ancestral state for the entire group and for Anguimorpha is absence, and presence on the extensor and flexor surfaces is a synapomorphy of Anguidae + Varanoidea. Presence on the extensor surface is a synapomorphy of the northern clade of *Xenosaurus*.

Caudal Osteoderms

268. Caudal osteoderms: Caudal osteoderms (0) in complete or nearly complete rings around anterior portion of tail and scattered over more posterior portion (Fig. 50B); (1) scattered in anterior portion of tail, sparse in more posterior portion (Fig. 50C); (2) absent.

    Evolution. Under both analyses, the ancestral state for the entire group is ambiguous between scattered and absent. That for Anguimorpha is scattered, as is that for *Xenosaurus*. Absence of cadual osteoderms is a synapomorphy of the southern clade of *Xenosaurus*, and complete rings thereof is an autapomorphy of *X. newmanorum*. Under Analysis 1, complete rings is a synapomorphy of Anguidae + Helodermatidae and an autapomorphy of *L. borneensis*. Under Analysis 2, complete rings is a synapomorphy of Anguidae + Varanoidea.

Scalation

Scalation is not informatively preserved on any of the extinct taxa.

269. Scalation: Canthus temporalis (0) scales no larger or more prominent than lateral and dorsal temporal scales, or barely so (Fig. 58A); (1) scales markedly larger and more prominent, canthus well-developed (Fig. 58B).

    Evolution. Under both analyses, the ancestral state for the entire group and for Anguimorpha is a lack of
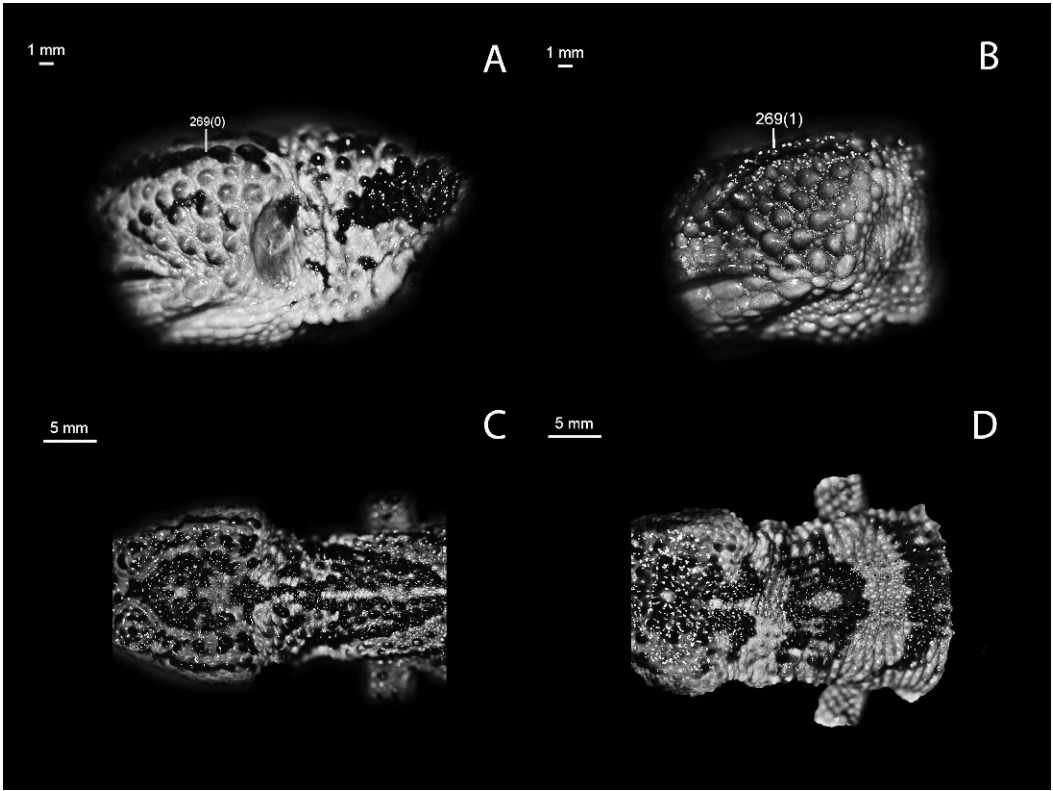
Figure 58.   Temporal and tympanic regions, left lateral, anterior to the left: A, *Xenosaurus newmanorum* UF 25006. Illustrates characters 269(0), 270(1). B, *Xenosaurus rackhami* UTEP 4555. Illustrates characters 269(1), 270(2). Necks, dorsal, anterior to the left: C, *Xenosaurus newmanorum* UF 25006. Illustrates character 271(0). D, *Xenosaurus rectocollaris* UF 51443. Illustrates character 271(1).

prominence. Under Analysis 1, the ancestral state for *S. crocodilurus* + Varanidae is ambiguous, and prominence of the canthus is a synapomorphy of the southern clade of *Xenosaurus*. Under Analysis 2, the ancestral state for Xenosauridae is ambiguous, and prominence is an autapomorphy of *L. borneensis*.

270. Scalation: Tympanum (0) unscaled; (1) covered with thin scales, becoming thinner toward middle of tympanum (Fig. 58A); (2) covered with thick scales but still differentiated from surrounding skin (Fig. 58B); (3) covered with thick scales and undifferentiated from surrounding skin (McDowell and Bogert, 1954, plate 1).

Variation. In *S. crocodilurus*, small juveniles have a tympanum that appears naked to the eye (Sprackland, 1993; Mägdefrau, 1997; Bever et al., 2005). It is possible that a thin layer of scales covers it, as in juvenile *X. grandis*. Relatively large adults should be scored for this character.

Evolution. Under both analyses, the nondifferentiated covering of thick scales in *L. borneensis* is an autapomorphy of that taxon. Under Analysis 1, the ancestral state for the entire group and for Anguimorpha is ambiguous between unscaled and covered with thin scales. A thick scaly covering is an autapomorphy of *S. crocodilurus*. The ancestral state for Anguidae + Helo-

dermatidae is unscaled, and the ancestral state for *Xenosaurus* is thinly scaled, with thickly scaled but differentiated a synapomorphy of the southern clade of *Xenosaurus*. Under Analysis 2, the ancestral state for the entire group and for Anguimorpha is unscaled, and increased scalation is a synapomorphy of Xenosauridae, whose ancestral state is ambiguous between lightly scaled and heavily scaled but differentiated.

271. Scalation: Skin around neck (0) conforms relatively tightly to underlying muscular structure (Fig. 58C); (1) puffs out considerably, such that neck appears wide and little differentiated from back of head (Fig. 58D).

    Evolution. Under both analyses, the loose collar-like morphology is an autapomorphy of *X. rectocollaris*.

272. Scalation: Lateral fold (0) absent; (1) present, relatively weakly developed, discontinuous; (2) present, well-developed, continuous along body. (Scored as lateral fold absent or present in Estes et al., 1988).

    Evolution. Under both analyses, lack of a fold is the ancestral state for the entire group and for Anguimorpha. Presence of a weak fold is a synapomorphy of *Xenosaurus*, and a strong fold is a synapomorphy of the southern clade of *Xenosaurus*. Under Analysis 1, a well-developed fold is a synapomorphy of *E. multicarinata + O. ventralis*. Under Analysis 2, the ancestral state for Anguidae is ambiguous among absent, weakly developed, and strongly developed.

273. Scalation: Dark markings on venter (0) absent; (1) present peripherally; (2) present across most of venter.

    Evolution. Under both analyses, lack of markings is the ancestral state for the entire group and for Anguimorpha. Under Analysis 1, peripheral markings

are an autapomorphy of *S. crocodilurus* and the ancestral state for the southern clade of *Xenosaurus* is ambiguous among absence, peripheral presence, and extensive presence, as is the state for *X. agrenon + X. rectocollaris*.

274. Scalation: Epidermal ridge microstructure (0) polygonal; (1) not arranged in regular polygons.

    Evolution. This character was scored from the work of Harvey (1991, 1993). Under both analyses, the ancestral state for the entire group and for Anguimorpha is polygonal microstructure. Under Analysis 1, a lack of polygonal arrangement is a synapomorphy of Anguidae + Helodermatidae. Under Analysis 2, the ancestral state for Anguidae + Varanoidea is ambiguous.

RESULTS

Ingroup Topology and Effects of Ordering

Analysis 1 and Analysis 2 yielded the same fully resolved topology for *Xenosaurus* and its extinct relatives (Figs. 6, 7). In the single recovered topology, *R. rugosus* is sister to all other xenosaurs, and *E. lancensis* is sister to *E. serratus + Xenosaurus*. Within *Xenosaurus*, the northern clade of *X. newmanorum + X. platyceps* is sister to the southern clade, which is divided into two additional clades: *X. agrenon + X. rectocollaris* and *X. rackhami + X. grandis*. Bootstrap values greater than 50% are given at the internal nodes. For both trees, all internal nodes for the ingroup had bootstrap values greater than 50%.

Analysis 1 yielded a single most parsimonious tree with a length of 924 steps (Fig. 6). Of the 274 characters used in the analysis, 253 were parsimony-informative and 21 were parsimony-uninformative. The tree consistency index was 0.4708 (0.3147 rescaled and 0.4573 excluding uninformative characters), the homoplasy index was 0.5292 (0.5427 excluding uninformative characters), and the retention index was

0.6685. The parametric bootstrap test resulted in values of greater than 50% for all ingroup nodes and for the nodes within the shinisaur clade. The other nodes were constrained.

Analysis 2 yielded a single most parsimonious tree with a length of 875 steps (Fig. 7). Of the 274 characters used in the analysis, 253 were parsimony-informative and 21 were parsimony-uninformative. The tree consistency index was 0.4971 (0.3488 rescaled and 0.4836 excluding uninformative characters), the homoplasy index was 0.5029 (0.5164 excluding uninformative characters), and the retention index was 0.7017. The parametric bootstrap test resulted in values of greater than 50% for all ingroup nodes, for Xenosauridae, for Anguidae + Varanoidea, and for Varanoidea and all nodes therein.

A comparison of the Analysis 1 and Analysis 2 trees using a Templeton test with the Analysis 2 tree as the best or unconstrained instance (see Materials and Methods) demonstrated that the toplogies were significantly different ($P < 0.0001$, Wilcoxon signed-rank statistic 556.0, $N = 70$, $Z = -4.3500$). As expected, the tree length of the unconstrained tree (Analysis 2) was less than that of the constrained tree (Analysis 1), and the consistency and retention indices were higher in the unconstrained tree, which also had a lower homoplasy index. The number of parsimony-informative and parsimony-uninformative characters was consistent between the two analyses, despite the differing outgroup topologies. Finally, in both analyses, bootstrap values for the ingroup nodes were all greater than 50%, with the lowest support (the only values less than 80%) being for the *Xenosaurus + E. serratus* node and the *Xenosaurus + E. lancensis* node. The internode bounded by these nodes was the only branch to collapse when characters were run unordered, as described below. Ingroup topologies were identical between the two trees.

When the matrix was run with all characters unordered, the internode be-tween *E. serratus + Xenosaurus* and *E. lancensis + Xenosaurus* collapsed. This somewhat unexpected result emphasizes that the position of *R. rugosus* as sister to all other xenosaurs here included is fairly robust, and that *E. lancensis* is known from specimens representing a relative paucity of phylogenetic information. At a glance, the loss of resolution of *E. serratus + Xenosaurus* seems absurd; *E. serratus* is nearly identical to *Xenosaurus* in several unique features. Notable among these is the highly domed form of the maxillary osteoderms, as opposed to the primitively flat osteoderms of *E. lancensis*. That distinction is represented in the scorings of character 62, a multistate character representing a morphocline from a flat plate-like morphology to a broken-up domed morphology. The nature of the problem lies in the status of *E. lancensis* as a "transitional form," uniquely displaying a broken-up but undomed morphology. In an unordered scheme, the transitional nature of this morphology is not recognized, and it instead becomes simply an autapomorphy. Indeed, a simplification of the character scoring to two states (not domed and *Xenosaurus*-like, or domed and *Xenosaurus*-like) results in a majority-rule consensus identical to the ingroup tree produced by the ordered data. Two other multistate characters, 46 (the steepness of the slanted dorsal margin of the lacrimal recess) and 108 (the lateral projection of the cristae cranii), likewise have states that are unambiguous synapomorphies of *E. serratus + Xenosaurus,* whereas *E. lancensis* has an intermediate state.

Outgroup Topology

The alliance of *S. crocodilurus* and the fossil *B. ammoskius* was established by Conrad (2005, 2006) and Conrad et al. (2011). My study also agrees with Conrad et al. (2011) in placing *M. ornatus* Klembara 2008 as sister to a *Shinisaurus + Bahndwivici* clade in a phylogenetic analysis. All other relationships were set using a constraint tree to generate Analysis 1 (see

Materials and Methods). However, Analysis 2 was generated by specifying only *P. torquatus* as an outgroup for the analysis and therefore generated a hypothesis of anguimorph relationships (Fig. 7). Under Analysis 2, the initial split of Anguimorpha is between the traditional Xenosauridae, including the *Xenosaurus* clade and the shinisaurs, and an Anguidae + Varanoidea clade. Anguidae consists of an Anguinae + Diploglossinae clade to the exclusion of Gerrhonotinae, and Varanoidea has its traditional topology of Helodermatidae + Varanidae, with Varanidae consisting of *L. borneensis* and *Varanus*.

Character States Supporting Clades and Terminal Taxa

Following are lists of character states supporting the focal clades in this study (synapomorphies) and terminal taxa (autapomorphies) under each hypothesis. Starred states (*) are unambiguous. Clade numbering is arbitrary, but clades common to both hypotheses (clades 1 to 22) have the same number under both listings. Character states unique to one hypothesis are denoted with a capital "U" (not marked as such when state being transitioned from is different), and states that differ between analyses in ambiguity are denoted with a lowercase "u."

When dealing with scores of ?, accelerated transformation (ACCTRAN) optimization is assumed. My character descriptions are worded with neither accelerated transition nor delayed transformation (DELTRAN) optimization in mind, and they are thus more complete guides to character distribution than the following lists. One exception obtains in the case of the character descriptions and in the lists below—when data are truly missing, instead of a character being inapplicable to the taxon (see Strong and Lipscomb, 1999), I use a DELTRAN-type assumption, placing ambiguous synapomorphies at more exclusive nodes instead of assuming early transformation. Those transformations are listed in brackets following the other transformations optimized at the

nodes in question. Specifically, those nodes are all of those for which one branch is completely extinct and therefore represented by incomplete fossils: *Xenosaurus + R. rugosus*, *Xenosaurus + E. lancensis*, *Xenosaurus + E. serratus*, *S. crocodilurus + M. ornatus*, and *S. crocodilurus + B. ammoskius*. Additionally, I use the same approach for the osteodermal characters of *X. agrenon* at the *X. agrenon + X. rectocollaris* node because data were unavailable regarding the osteoderms of *X. agrenon*.

Analysis 1

1. *Xenosaurus + Restes rugosus*: 1 0-2*; 51 0-1*; 52 1-2 U*; 53 0-1*; 59 0-1 U*; 64 6-7 U; 66 0-1 U*; 67 0-1*; 69 0-1 U*; 72 0-1*; 97 1-2; 109 0-1*; 111 0-1*; 113 0-1 U; 114 0-1*; 131 0-1; 132 1-2; 145 0-1*; 184 0-1; 186 0-1 U*; 191 0-1; 193 0-1 U*; 196 0-1 U*; 214 0-1*;

2. *Restes rugosus*: 43 2-0 U; 125 1-0 U; 144 0-1*; 204 0-1*

3. *Xenosaurus + Exostinus lancensis*: 62 2-3*; 93 1-0; 96 0-1*; 97 2-3*; 100 0-1; 105 0-1 U; 185 1-0 U; 193 1-2 [152 0-1];

4. *Exostinus lancensis*: 1 2-1; 92 1-0*; 147 4-C*; 154 1-0*; 246 1-2*

5. *Xenosaurus + Exostinus serratus*: 46 0-1*; 54 0-1; 62 3-4*; 93 1-0; 98 0-1*; 99 0-1*; 108 0-1*; 191 1-0 [7 1-2; 8 0-3; 9 0-1; 11 0-1; 19 0-1; 22 0-1 U; 47 0-1 U; 55 3-2 U; 63 1-0; 130 0-1; 68 1-2; 94 1-2 U; 111 1-2; 124 1-2; 200 0-1 U; 209 0-1]

6. *Exostinus serratus*: 49 0-1*; 50 0-1*; 52 2-1*; 60 1-2*; 61 1-3*; 64 7-5*; 69 1-2*; 70 0-1*; 71 0-1*; 98 1-2*; 101 0-1*; 106 0-1*; 107 0-1*; 108 1-2*; 131 1-0; 132 2-1; 185 0-1 U; 192 0-1*; 193 2-0; 194 0-1*

7. *Xenosaurus*: 2 0-1*; 8 3-4*; 9 1-2*; 10 0-1; 17 0-1*; 21 2-3*; 23 0-1*; 26 0-1*; 45 0-1*; 56 4-3; 57 0-1*; 58 0-1*; 64 7-9*; 93 0-1*; 100 1-0; 104 0-1; 128 0-1*; 184 1-0; 195 1-0*; 196 1-0*; 201 0-1* [30 1-2; 31 0-1; 34 0-1; 35 0-1; 37 0-1; 75 0-1; 85 0-1; 86 0-1; 116 0-1; 117 0-1 U; 135 2-1; 136 0-1; 137 0-1 U; 139 0-1 U; 142 0-1; 145 1-2; 146 0-1; 147 4-3; 148 4-2;

159 0-1 U; 161 0-1; 162 0-1 U; 165 0-1; 167 1-2; 168 0-1; 169 0-3 U; 173 0-1; 199 0-1; 205 0-2; 207 0-1; 208 0-1; 211 1-2; 213 0-1 U; 228 0-1; 238 0-1; 243 0-1; 248 3-2; 260 0-1 U; 261 0-1 U; 263 0-1 U; 264 1-2; 265 0-1 U; 268 0-1 U; 272 0-1]

8. Northern clade of *Xenosaurus*: 13 0-1*; 16 0-1*; 18 0-1; 20 1-0*; 21 3-4*; 22 1-2*; 28 0-1*; 29 1-2; 39 0-1*; 41 0-1*; 42 0-1*; 43 2-3*; 54 1-0; 60 1-0*; 64 9-B*; 68 2-3*; 73 0-1*; 75 1-2*; 76 1-2*; 79 0-1*; 84 0-1*; 85 1-2*; 95 0-1*; 110 0-2*; 111 2-3*; 116 1-3*; 122 0-1*; 143 0-1*; 154 1-2*; 158 0-1*; 178 0-1 U*; 187 0-1*; 202 0-1*; 219 0-1*; 220 0-1*; 225 0-1*; 226 0-1*; 229 0-1*; 239 0-1*; 248 2-1*; 249 3-0*; 251 0-1*; 255 0-1*; 258 2-3*; 259 1-0*; 267 2-1*

9. *Xenosaurus newmanorum*: 56 3-5*; 65 0-1*; 88 1-2; 135 1-2; 147 3-4; 148 2-0*; 154 2-3*; 174 2-0*; 181 1-0; 182 1-0*; 198 0-1*; 223 1-0*; 224 0-1*; 234 1-0*; 235 0-1*; 237 0-1*; 260 1-0*; 263 1-0 u; 268 1-0 u

10. *Xenosaurus platyceps*: 61 1-2*; 80 0-1; 89 0-1*; 118 0-1; 119 0-1*; 120 0-1*; 127 0-1*; 135 1-0*; 193 2-3*; 206 0-1*; 214 1-2*; 215 1-2*; 223 1-2*; 232 0-1*; 234 1-2*; 240 0-1*; 248 1-0*; 254 0-1*; 258 3-4*; 262 0-1; 265 1-0 u; 266 1-2*; 267 1-0*

11. Southern clade of *Xenosaurus*: 11 1-2*; 12 0-1*; 27 0-1 u*; 36 0-1; 37 1-2*; 38 0-1; 40 0-1*; 43 2-1; 68 2-0*; 74 1-2; 78 1-2*; 83 0-1 U; 90 0-1*; 102 0-1*; 126 0-1; 134 0-1*; 138 0-1*; 147 3-1*; 151 0-1; 157 1-2; 165 1-2*; 183 1-0 U; 204 0-1*; 217 1-0; 242 0-1*; 245 0-1*; 250 0-1 U*; 252 0-1*; 253 0-1 U*; 256 0-1 U*; 257 0-1*; 260 1-2 U*; 264 2-3*; 265 1-2 U*; 268 1-2*; 269 0-1 U*; 270 1-2 U*; 272 1-2*; 273 0-2

12. *Xenosaurus agrenon + Xenosaurus rectocollaris*: 46 1-2*; 56 3-2*; 88 1-0*; 135 1-0*; 142 1-0; 147 1-0*; 155 1-2*; 163 1-0*; 170 0-1*; 171 0-1*; 175 1-0; 176 0-1*; 188 0-1*; 190 0-1*; 203 0-1*; 216 0-1*;

13. *Xenosaurus agrenon*: 55 2-1*; 56 2-1*; 74 2-1; 76 1-0*; 77 0-1*; 110 0-1*; 148 2-3; 150 0-1*; 166 0-1*; 181 1-0; 198 0-1*; 217 0-1; 239 0-1*

14. *Xenosaurus rectocollaris*: 8 4-0*; 16 0-1*; 60 1-2*; 64 9-B*; 83 1-0; 87 2-1*; 96 1-0*; 123 0-1*; 131 1-0*; 148 2-1*; 214 1-2*; 215 1-0*; 229 0-1*; 234 1-0*; 236 0-1*; 271 0-1*; 273 2-0 [264 3-4]

15. *Xenosaurus grandis + Xenosaurus rackhami*: 5 0-1*; 15 0-1*; 58 1-2*; 65 0-1*; 82 0-1*; 103 0-1*; 112 0-1*; 115 0-1*; 133 0-1*; 139 1-2*; 141 0-1*; 151 1-2*; 155 1-0*; 156 0-1*; 159 1-0 u; 160 0-1*; 163 1-2*; 167 2-3*; 168 1-2*; 169 3-2 u; 172 0-1*; 174 2-1 U*; 179 0-1*; 182 1-2 u; 197 0-1*; 221 0-1*; 227 2-1 u*; 248 2-3; 252 1-2*; 253 1-2*; 256 1-2*; 260 2-3*; 265 2-3*

16. *Xenosaurus rackhami*: 56 3-4; 81 0-1*; 88 1-4*; 126 1-0; 135 1-2; 140 0-1*; 148 2-3; 153 0-1*; 165 2-3*; 166 0-1*; 169 2-1*; 177 0-1*; 205 2-1*; 240 0-2*; 249 3-6*; 252 2-3*; 256 2-3*

17. *Xenosaurus grandis*: 55 2-1*; 58 2-3*; 84 0-1*; 116 1-2*; 120 0-1*; 127 0-1*; 147 1-2; 157 2-1; 180 0-1*; 181 1-0; 193 2-1*; 198 0-1*; 255 0-1*

18. *Shinisaurus crocodilurus + Merkurosaurus ornatus*: 20 1-2*; 22 0-1 U; 25 2-0; 52 1-2 U*; 155 1-0*; 193 0-1 U*; 196 0-1 U*

19. *Shinisaurus crocodilurus + Bahndwivici ammoskius*: 47 0-1 U*; 98 0-1*; 147 5-6* [29 1-2; 55 3-2 U; 59 0-1 U; 66 0-1 U; 69 0-1 U; 117 0-1 U; 200 0-1 U; 218 1-0 U; 233 0-1]

20. *Merkurosaurus ornatus*: 7 1-0; 23 0-1*; 92 1-0*; 94 1-2 U*; 185 1-0 U*

21. *Bahndwivici ammoskius*: 22 1-0 U; 55 2-1*; 64 5-8* U; 97 1-3*; 134 1-0 U; 151 2-3*; 154 1-0*; 240 0-1*

22. *Shinisaurus crocodilurus*: 5 0-1*; 94 1-0*; 124 0-1 U*; 138 0-1*; 147 6-9*; 148 4-3*; 152 0-1 u* [14 1-0 U; 46 0-2; 83 0-1 U; 88 1-5 U; 93 0-1; 113 0-1 U; 126 0-1; 136 0-1 U; 137 0-1 U; 139 0-1 U; 159 0-1 U; 169 0-3 U; 174 2-1 U; 178 0-1 U; 182 1-0; 183 1-0 U; 186 0-1 U; 188 0-1; 213 0-1 U; 222 1-0 U; 227 2-0; 230 1-0;

231 1-0; 249 3-2 U; 250 0-1 U; 253 0-2; 256 1-2; 258 2-1; 260 0-2 U; 263 0-1 U; 265 0-2 U; 266 1-0; 268 0-1 U; 273 0-1 U]

23. *Xenosaurus* + Anguidae: 27 1-0*; 32 0-1*; 33 0-1; 43 0-2; 45 1-0; 56 2-4*; 60 0-1; 62 0-2; 78 0-1; 124 0-1; 125 0-1; 129 0-1; 149 0-1*; 157 0-1; 175 0-1; 210 0-1; 212 0-1

Analysis 2

1. *Xenosaurus* + *Restes rugosus*: 1 0-2*; 45 1-0 U*; 51 0-1*; 53 0-1*; 60 0-1 U*; 62 0-2 U*; 67 0-1*; 72 0-1*; 97 1-2; 109 0-1*; 111 0-1*; 114 0-1*; 131 0-1; 132 1-2; 145 0-1*; 191 0-1; 210 0-1 U*; 214 0-1*

2. *Restes rugosus*: 55 2-3 U*; 105 1-0 U; 136 1-0 U; 137 1-0 U; 139 1-0 U; 144 0-1*; 185 0-1 U*; 200 1-0 U*; 204 0-1*

3. *Xenosaurus* + *Exostinus lancensis*: 62 2-3*; 93 1-0; 96 0-1*; 97 2-3*; 100 0-1; 111 1-2; 125 0-1 U; 193 1-2 [152 0-1; 157 0-1 U; 184 0-1]

4. *Exostinus lancensis*: 1 2-1; 92 1-0*; 147 5-C*; 154 1-0*; 246 1-2*

5. *Xenosaurus* + *Exostinus serratus*: 46 0-1*; 54 0-1; 62 3-4*; 93 1-0; 98 0-1*; 99 0-1*; 108 0-1*; 191 1-0 [7 1-2; 8 0-3; 9 0-1; 11 0-1; 14 0-1 U; 19 0-1; 43 0-2 U; 63 1-0; 68 1-2; 124 1-2; 129 0-1 U; 130 0-1; 209 0-1]

6. *Exostinus serratus*: 49 0-1*; 50 0-1*; 52 2-1*; 60 1-2*; 61 1-3*; 64 7-5*; 69 1-2*; 70 0-1*; 71 0-1*; 98 1-2*; 101 0-1*; 106 0-1*; 107 0-1*; 108 1-2*; 131 1-0; 132 2-1; 185 0-1 u*; 192 0-1*; 193 2-0*; 194 0-1*

7. *Xenosaurus*: 2 0-1*; 8 3-4*; 9 1-2*; 10 0-1; 17 0-1*; 21 2-3*; 23 0-1*; 26 0-1*; 45 0-1*; 56 4-3; 57 0-1*; 58 0-1*; 64 7-9*; 93 0-1*; 100 1-0; 104 0-1; 128 0-1*; 184 1-0; 195 1-0*; 196 1-0*; 201 0-1* [30 1-2; 31 0-1; 33 0-1 U; 34 0-1; 35 0-1; 37 0-1; 75 0-1; 78 0-1 U; 85 0-1; 86 0-1; 88 5-1 U; 116 0-1; 135 2-1; 142 0-1; 145 1-2; 146 0-1; 147 5-3; 148 4-2; 161 0-1; 165 0-1; 167 1-2; 168 0-1; 173 0-1; 175 0-1 U; 199 0-1; 205 0-2; 207 0-1; 208 0-1; 211 1-2; 212 0-1 U; 217 2-1 U; 218 0-1 U; 222 0-1 U; 228 0-1; 238 0-1; 243 0-1; 248 3-2; 264 1-2; 272 0-1]

8. Northern clade of *Xenosaurus*: 13 0-1*; 16 0-1*; 18 0-1; 20 1-0*; 21 3-4*; 22 1-2*; 28 0-1*; 29 1-2; 39 0-1*; 41 0-1*; 42 0-1*; 43 2-3*; 54 1-0; 60 1-0*; 64 9-B*; 68 2-3*; 73 0-1*; 75 1-2*; 76 1-2*; 79 0-1*; 83 1-0 U; 84 0-1*; 85 1-2*; 95 0-1*; 110 0-2*; 111 2-3*; 116 1-3*; 122 0-1*; 143 0-1*; 154 1-2*; 158 0-1*; 183 0-1 U*; 187 0-1*; 202 0-1*; 219 0-1*; 220 0-1*; 225 0-1*; 226 0-1*; 229 0-1*; 239 0-1*; 248 2-1*; 249 2-0*; 250 1-0 U; 251 0-1*; 253 1-0 U; 255 0-1*; 256 1-0 U; 258 2-3*; 259 1-0*; 260 2-1 U; 265 2-1 U; 267 2-1*; 269 1-0 U; 270 2-1 U; 273 1-0 U

9. *Xenosaurus newmanorum*: 56 3-5*; 65 0-1*; 88 1-2; 135 1-2; 147 3-4; 148 2-0*; 154 2-3*; 174 1-0*; 181 1-0; 182 1-0*; 198 0-1*; 223 1-0*; 224 0-1*; 234 1-0*; 235 0-1*; 237 0-1*; 260 1-0*; 263 1-0 u*; 268 1-0 u*

10. *Xenosaurus platyceps*: 61 1-2*; 80 0-1; 89 0-1*; 118 0-1; 119 0-1*; 120 0-1*; 127 0-1*; 135 1-0*; 174 1-2 U; 193 2-3*; 206 0-1*; 214 1-2*; 215 1-2*; 223 1-2*; 232 0-1*; 234 1-2*; 240 0-1*; 248 1-0*; 254 0-1*; 258 3-4*; 262 0-1; 265 1-0 u*; 266 1-2*; 267 1-0*

11. Southern clade of *Xenosaurus*: 11 1-2*; 12 0-1*; 27 0-1 u; 36 0-1; 37 1-2*; 38 0-1; 40 0-1*; 43 2-1; 68 2-0*; 74 1-2; 78 1-2*; 90 0-1*; 102 0-1*; 126 0-1; 134 0-1*; 138 0-1*; 147 3-1*; 151 0-1; 157 1-2; 165 1-2*; 178 1-0 U; 204 0-1*; 217 1-0; 242 0-1*; 245 0-1*; 249 2-3 U; 252 0-1*; 257 0-1*; 264 2-3*; 268 1-2*; 272 1-2*; 273 1-2

12. *Xenosaurus agrenon* + *Xenosaurus rectocollaris*: 46 1-2*; 56 3-2*; 88 1-0*; 135 1-0*; 142 1-0; 147 1-0*; 155 1-2*; 163 1-0*; 170 0-1*; 171 0-1*; 174 1-2 U; 175 1-0; 176 0-1*; 188 0-1*; 190 0-1*; 203 0-1*; 216 0-1*

13. *Xenosaurus agrenon*: 55 2-1*; 56 2-1*; 74 2-1; 76 1-0*; 77 0-1*; 110 0-1*; 148 2-3; 150 0-1*; 166 0-1*; 181 1-0; 198 0-1*; 217 0-1; 239 0-1*

14. *Xenosaurus rectocollaris*: 2-0*; 16 0-1*; 60 1-2*; 64 9-B*; 83 1-0; 87 2-1*; 96 1-0*; 123 0-1*; 131 1-0*; 148 2-1*; 214

1-2*; 215 1-0*; 229 0-1*; 234 1-0*; 236 0-1*; 271 0-1*; 273 2-0 [264 3-4]

15. *Xenosaurus grandis + Xenosaurus rackhami*: 5 0-1*; 15 0-1*; 58 1-2*; 65 0-1*; 82 0-1*; 103 0-1*; 112 0-1*; 115 0-1*; 133 0-1*; 139 1-2*; 141 0-1*; 151 1-2*; 155 1-0*; 156 0-1*; 159 1-0 u*; 160 0-1*; 163 1-2*; 167 2-3*; 168 1-2*; 169 3-2 u*; 172 0-1*; 179 0-1*; 182 1-2 u*; 197 0-1*; 221 0-1*; 227 2-1 u; 248 2-3; 252 1-2*; 253 1-2*; 256 1-2*; 260 2-3*; 265 2-3*

16. *Xenosaurus rackhami*: 56 3-4; 81 0-1*; 88 1-4*; 126 1-0; 135 1-2; 140 0-1*; 148 2-3; 153 0-1*; 165 2-3*; 166 0-1*; 169 2-1*; 177 0-1*; 205 2-1*; 240 0-2*; 249 3-6*; 252 2-3*; 256 2-3*

17. *Xenosaurus grandis*: 55 2-1*; 58 2-3*; 84 0-1*; 116 1-2*; 120 0-1*; 127 0-1*; 147 1-2; 157 2-1; 180 0-1*; 181 1-0; 193 2-1*; 198 0-1*; 255 0-1*

18. *Shinisaurus crocodilurus + Merkurosaurus ornatus*: 20 1-2*; 25 2-0; 61 1-0 U*; 149 1-0 U; 151 0-2 U; 155 1-0*; 195 1-2*

19. *Shinisaurus crocodilurus + Bahndwivici ammoskius*: 94 2-1 U; 98 0-1*; 147 5-6*; 185 0-1 U*; [27 0-1 U; 29 1-2; 48 0-1 U; 56 4-2 U; 68 1-0 U; 118 0-1 U; 126 0-1; 233 0-1]

20. *Merkurosaurus ornatus*: 7 1-0; 23 0-1*; 47 1-0 U; 92 1-0*

21. *Bahndwivici ammoskius*: 22 1-0 U*; 55 2-1*; 64 5-8 U; 97 1-3*; 124 1-0 U; 151 2-3*; 154 1-0*; 240 0-1*

22. *Shinisaurus crocodilurus*: 5 0-1*; 64 7-5 U*; 94 1-0*; 134 0-1 U*; 138 0-1*; 147 6-9*; 148 4-3*; 152 0-1 U [32 1-0 U; 46 0-2; 93 0-1; 182 1-0; 188 0-1; 227 2-0; 230 1-0; 231 1-0; 253 1-2; 256 1-2; 258 2-1; 266 1-0]

23. Xenosauridae: 3 0-1*; 6 0-1*; 7 0-1; 22 0-1*; 24 0-1*; 47 0-1; 52 0-2*; 59 0-1*; 66 0-1*; 69 0-1*; 83 0-1; 93 1-0; 94 1-2; 104 1-0; 105 0-1; 113 0-1; 117 0-1*; 124 0-1; 136 0-1; 137 0-1; 139 0-1; 147 4-5; 148 5-4*; 159 0-1*; 162 0-1*; 169 0-3*; 178 0-1; 181 0-1; 182 2-1*; 186 0-1*; 196 0-1*; 213 0-1*; 250 0-1; 253 0-1; 256 0-1; 260 0-2; 261 0-1; 263 0-1; 265 0-2; 268 0-1; 269 0-1; 270 0-2*; 273 0-1

DISCUSSION

Relation to Previous Studies and Taxonomic Issues Raised

Under both starting hypotheses, xenosaurs formed a clade within Anguimorpha when allowed to vary across the entire tree, supporting the monophyly of the ingroup of six extant species of *Xenosaurus* and three extinct taxa relative to the other included taxa. The relationship of the extinct taxa to *Xenosaurus* is thus consistent with historical descriptions of the fossils suggesting xenosaur affinities. Of the two prior studies presenting explicitly phylogenetic hypotheses of relationships among extinct and extant xenosaurs, the position of *R. rugosus* outside of a clade including *Xenosaurus* and *E. serratus* is consistent with those of both Gauthier (1982) and Conrad (2005, 2008). *Restes rugosus* as sister to all other xenosaurs is specifically consistent with Conrad (2005, 2008). However, *E. serratus* as the immediate sister to *Xenosaurus* was suggested by Gauthier (1982) but not Conrad (2005, 2008), who recovered a monophyletic *Exostinus*. Note that the relationships of xenosaurs were a primary focus of Gauthier's but not Conrad's work (J. Conrad, 2008; personal communication).

A single recent study suggests an alliance of the Mongolian Cretaceous taxon *C. intermedia* with xenosaurs (Conrad, 2008). A full analysis using the characters identified in the present work will have to proceed after examination of fossil material, and in particular CT scans, of *C. intermedia*. More recent work has indicated that *C. intermedia* might not be an anguimorph (J. A. Gauthier, personal communication); thus, a broader spread of scleroglossan characters and taxa than used in this study might be required to establish its phylogenetic position.

As predicted by previous studies (Gauthier, 1982; Estes, 1983; Conrad, 2008), I recovered *Exostinus* as a paraphyletic group consisting of two successive sister taxa to *Xenosaurus*. Notwithstanding concerns about the assignment of specimens to *E.*

lancensis, that taxon would then require a new genus name, and *Exostinus* would become monotypic, including only *E. serratus*. I propose to resurrect the name *Harpagosaurus*, applied by Gilmore (1928) to a maxilla now referred to *E. lancensis* (Estes, 1964, 1983). A more formal definition will require further study of known material of *E. lancensis*, which may represent several taxa (Gao and Fox, 1996).

As already discussed, the recovery of a monophyletic Xenosauridae in generating Analysis 2 is consistent with most morphological phylogenetic hypotheses, but not with studies based on molecular structure or with hypotheses proposed by Conrad (2005, 2008). Aside from this result, the close relationship of *B. ammoskius* to *S. crocodilurus* was again confirmed (Conrad, 2006). Moreover, *M. ornatus*, *B. ammoskius* + *Shinisaurus* as recovered by Conrad et al. (2011). That result provides support for the shinisaur affinities of the taxon (Klembara, 2008).

Temporal Implications

Exostinus serratus, sister to *Xenosaurus*, is nearly identical to the crown clade in most aspects of its known anatomy. Many of the character states appearing in the crown clade had thus arisen by the age of the Orellan sediments from which *E. serratus* was collected (Swisher and Prothero, 1990). Thus far, no extinct taxa that fall within the crown clade *Xenosaurus* have been identified. This "genus" may be very ancient indeed, like some anguid "genera" (Estes, 1983; personal observation). *Exostinus lancensis*, from the Late Cretaceous, is the oldest extinct taxon on the stem of *Xenosaurus* according to this study. The known fossil record of Anguidae and Helodermatidae, the putative sister groups to the xenosaur lineage in Analysis 1, are consistent with a Mesozoic split. *Odaxosaurus piger* is a primitive glyptosaur from the Cretaceous (Meszoely, 1970; Gauthier, 1982; Estes, 1983), and the primitive helodermatids *G. pulchra* and *P. nessovi*

are from the Upper Cretaceous of Mongolia and the Albian-Cenomanian of Utah, respectively. (If *P. nessovi* is indeed a helodermatid, its presence in the Early Cretaceous would suggest significant ghost lineages for xenosaurs and anguids.) The fossil record of shinisaurs extends back to the late Paleocene/early Eocene (Smith, 2006b), leaving a longer ghost lineage for the shinisaur branch of the Xenosauridae in Analysis 2. However, a number of North American Cretaceous "platynotan" taxa known from fragmentary remains have yet to be fully examined in a phylogenetic context, and among these might be found part of the missing shinisaur lineage (Estes, 1983; K. T. Smith, personal communication; personal observation).

Some notable stratigraphic incongruities are present in the phylogenetic hypotheses recovered here. The Paleocene *R. rugosus* is sister to all remaining xenosaurs, including the Cretaceous *E. lancensis*. The *R. rugosus* lineage has yet to be recovered from the Mesozoic. However, *R. rugosus* itself appears to be exceedingly rare in Paleogene faunas (Smith, 2006b; K. T. Smith, personal communication), and this may apply to its predecessors, as well. The second incongruity is the closer relationship of *B. ammoskius* from the North American Eocene to the extant Asian *S. crocodilurus* than *Merkurosaurus ornatus* from the European Miocene (Conrad, 2006; Klembara, 2008). This might suggest an early Paleogene transatlantic dispersal of the *Merkurosaurus* lineage, much like that which has been suggested to have resulted in the appearance of the primitive helodermatid *E. gallicum* in the Eocene of France (Hoffstetter, 1957) and the iguanian *Geiseltaliellus* in the Eocene of Germany (K. T. Smith, personal communication). One would then expect to find the *Merkurosaurus* lineage in earlier European deposits and in Early Paleogene or Mesozoic North American deposits. The former has not yet been reported, but the latter expectation may be fulfilled by the host of shinisaur-related taxa being identified from screenwashed early

Eocene and late Paleocene North American microfaunas (Smith, 2006b). Alternatively, in the case of both shinisaurs and helodermatids, the North American and European representatives could have been derived from an unknown Asian stock. Primitive helodermatids were present in present-day Mongolia during the Late Cretaceous (Gao and Norell, 2000).

Finally, taxa farther down the stem of *Xenosaurus* than *R. rugosus* are notably lacking. As noted already, relatively primitive helodermatids and shinisaurs have been found, but another frustrating absence exists along the stem of Anguidae. The highly derived glyptosaurs are the only putative stem anguids known, and even that placement is not strongly supported, for they already possess most of the derived features of anguids (Conrad, 2005, 2008; Conrad et al., 2011; J. A. Gauthier, personal communication).

Biogeography of Xenosaurs

There is a striking difference in latitude between the locations of collections of the stem xenosaurs in this study, all of which were found in Colorado, Wyoming, and farther north still, and the present distribution of *Xenosaurus* in central and southern Mexico. That pattern obtains for other squamate taxa, as well—notably diploglossine anguids (Gauthier, 1982; Smith, 2006b; personal observation) and polychrotine iguanians (Smith, 2006a, 2006b). The apparent contraction of the ranges of parts of clades has been convincingly attributed to the contraction of megathermal climate zones during the global cooling following the Paleocene/Eocene thermal maximum by Smith (2006b).

Xenosaurus are, with few exceptions, crevice-dwelling lizards and are distributed along the great north–south-extending mountain ranges of Mexico. The initial split within *Xenosaurus* is a division between a northern clade, consisting of *X. newmanorum* and *X. platyceps* in the Sierra Madre Oriental, and a southern clade, consisting of the remaining taxa (King and Thompson,

1968; Canseco Márquez, 2005), of which the *X. agrenon* + *X. rectocollaris* clade is more to the west and the *X. grandis* + *X. rackhami* clade is more to the east, extending into Central America. *Xenosaurus rackhami* has a particularly wide distribution, and I observed more intraspecies variation in that species of *Xenosaurus* than in the others for which I had sample sizes larger than one or two. Further details of the biogeography of *Xenosaurus* were provided by Canseco Márquez (2005).

Comments on Ingroup Clades

Xenosauridae. Analysis 2, the unconstrained analysis, strongly recovered a monophyletic Xenosauridae in the classical sense, as also suggested, but not cladistically tested, by Smith (2006b). Many of the characters supporting the clade were not used by Conrad (2005, 2008). Two characters, the subpalpebral fossa and the mediolaterally expanded facet on the maxilla, are present in association with slightly different elements in the two taxa, but this does not invalidate their potential homology according to the tree. Several other characters, including the upfolded tab of the facial process of the maxilla, are unique within Squamata. Part of the difficulty of resolving the degree of relatedness between xenosaurs and shinisaurs is the poor fossil record along the stem of Anguimorpha. It is quite possible that the character states that seem so peculiar to the classical Xenosauridae are in fact ancestral for Anguimorpha as a whole.

Xenosaurus + *Restes rugosus*. The most inclusive clade of the xenosaur lineage already has the characteristic dentition of the group. Among the bones surrounding the nasal capsule, the maxilla shows a combination of plesiomorphic and derived features, notably a primitively platey, continuous osteodermal covering. The palpebral and prefrontal already display typical xenosaur morphologies. Likewise, the frontal and jugal bear several synapomorphies with the other xenosaurs, but they are

primitive in various respects, as well. What is preserved of the palate is intermediate between *Xenosaurus* and the remainder of Anguimorpha, in particular the persistence of remnants of the pterygoid dentition. *Restes rugosus* is the only fossil xenosaur to preserve any of the palate. The primitively long, narrow postorbital suggests that the supratemporal arch was not expanded and heavily ornamented as in *Xenosaurus*. It is thus likely that the general flattening of the head and possibly the body evident in the crown clade was not as developed in the ancestor of this more inclusive clade.

Differences in synapomorphies supporting the clade between Analysis 1 and Analysis 2 have largely to do with the issue of xenosaurid monophyly. In Analysis 1, several features shared by xenosaurs and shinisaurs optimize as convergent and are added to the apomorphy list for *Xenosaurus* + *R. rugosus*.

Restes rugosus. *Restes rugosus* displays a host of plesiomorphic characters for xenosaurs, exhibiting few obvious autapomorphies in its known anatomy. The most obvious of its autapomorphies is the unusually large angle of divergence of the medial and lateral edges of the palatine process of the pterygoid. It is unclear whether that morphology indicates a similarly peculiar morphology for the remainder of the palate, which is not preserved. In *Xenosaurus*, despite the widening of the head, the palatine process of the pterygoid is not particularly expanded.

Xenosaurus + Exostinus lancensis. *Exostinus lancensis* is not a well-known taxon, and this clade is supported largely by the more broken-up osteoderms on the maxilla and the *Xenosaurus*-like domed osteoderms of the frontal. The frontal is still unconstricted interorbitally compared with *E. serratus* and *Xenosaurus*, but the cristae cranii approach each other more closely than in *R. rugosus*. *Exostinus lancensis* is the only fossil xenosaur, unfortunately, to preserve the parietal. The supratemporal processes are broken and so could not be

scored, but they appear to have been short as in *Xenosaurus*.

Exostinus lancensis. This is a difficult taxon for reasons already stated, relating to incompleteness and difficulty in the assignment of specimens. Its recovered position closer to the crown clade than *R. rugosus* requires a reversal in tooth form from slightly bicuspid to unicuspid. However, despite the assertion of the most recent description that all teeth in *E. lancensis* are unicuspid (Gao and Fox, 1996), some AMNH specimens I examined for this study show an apical, longitudinal groove like that which extends basally from the division between the smaller mesial and the larger distal cusps in those xenosaurs that have a bicuspid morphology (e.g., AMNH 15366). The apices of the teeth of all of these specimens are damaged. Furthermore, although the skull roof osteoderms of *E. lancensis* are domed like those of *E. serratus* and *Xenosaurus*, their form is unusual. They are oval or obovate and on the parietal show a concentric distribution unique to *E. lancensis*.

Xenosaurus + Exostinus serratus. These two taxa are nearly identical in many aspects of their osteology, although only the rostral portions of the skull are known for *E. serratus*, and these incompletely. The osteoderms in general are of the characteristic *Xenosaurus* form and distribution. The dentition also has the form seen in primitive parts of the crown clade. However, the nares are primitively large and elongate; concomitantly, the nasal process of the premaxilla, although expanded, is not so expanded as in *Xenosaurus*, and the slope of the narial margin of the maxilla is gentler and longer. Unfortunately, premaxillae are unknown from other fossil xenosaurs.

Exostinus serratus. This is essentially a short-faced xenosaur, its rostrum autapomorphically short, reflected in features such its reduced tooth count. Additionally, the unusually wide palatal shelf of the maxilla suggests a particularly wide skull with the maxillae diverging from each other at a high angle. The lack of a posterior expansion of

the jugal is another strange autapomorphy. The various unique features of this taxon raise the question of whether xenosaurs were relatively diversified earlier than the crown radiation. In turn, it is unclear where less autapomorphic lineages more similar to the crown might be found.

Xenosaurus. *Xenosaurus*, in part because constituents are extant and thus much more completely known, is supported by a large number of synapomorphies. Notable are the mediolateral expansions of the nasal process of the premaxilla and the squamosal and the relative mediolateral widening of the parietal. Several bones, such as the septomaxilla and coronoid, are expanded and enclose more nerves and vasculature than the primitive state. The body is flattened and the neural spines relatively low; various other axial and appendicular synapomorphies also exist, such that the postcranium of *Xenosaurus* is fairly distinct among anguimorphs.

Northern clade of Xenosaurus. The northern clade of *Xenosaurus*, widely separated geographically from the remaining species, retains a number of ancestral characters that the southern clade has lost, notably the proportions of the skull roof bones. However, the taxa within the northern clade are united by a consistent suite of synapomorphies—more than the southern taxa. Among these synapomorphies are several features of the anterior maxilla and premaxilla. Furthermore, the heavy osteodermal armor of the northern clade optimizes as primitive if the heavily armored helodermatids and anguids are the immediate sister taxon to xenosaurs. However, it optimizes as derived or ambiguous if the more lightly armored shinisaurs are used.

Xenosaurus newmanorum. This is a large-bodied species (King and Thompson, 1968). Other than its large size, it is in general the less autapomorphic of the two examined species from the northern clade. It has a particularly tall head for *Xenosaurus*, possibly a primitive feature (Herrel et al., 2001). As the less autapomorphic part of the northern clade, which itself retains a number of ancestral characters, *X. newmanorum*

might be a better taxon to include in phylogenetic analyses than the commonly used *X. grandis* and *X. platyceps* (e.g., Conrad, 2008, who noted the shortcomings of scoring a composite "*Xenosaurus*" from *X. grandis* and *X. platyceps*—although these two taxa do bracket the clade).

Xenosaurus platyceps. This is the flattest species of *Xenosaurus*, in head and body. Several autapomorphies of the maxilla and skull roof relate to the particularly flat, wide head of the taxon, and unusual morphologies of the axial and appendicular skeletons might also relate to this marked dorsoventral compression.

Southern clade of Xenosaurus. The southern clade of *Xenosaurus* is united by a large number of synapomorphies, most of them relatively subtle, such as the proportions of osteodermal sculpturing and proportions of articular parts of the dermal cranial roof and sidewall. The ranges of some of the taxa within are considerably greater than those of the species within the northern clade (i.e., *X. rackhami*; King and Thompson, 1968), and the individual species as a whole are more morphologically divergent than the relatively similar *X. newmanorum* and *X. platyceps*.

Xenosaurus agrenon + Xenosaurus rectocollaris. This clade, consisting of two little-known taxa for which I had but one specimen each, is supported by the fewest synapomorphies of the clades within *Xenosaurus*. Nevertheless, some of these synapomorphies (e.g., the unusual notch in the posterior region of the parietal, the morphology of the central region of the basisphenoid, and the bizarre flattened neural spines of the lumbar region) are striking and unique, and the clade appears robust. In general, this clade shares several ancestral character states with the northern clade that are no longer present in the well-supported *X. rackhami* + *X. grandis* clade. In contrast to the meager osteodermal armor of the latter clade, the *X. agrenon* + *X. rectocollaris* clade shares relatively heavy armor with the northern clade.

Xenosaurus agrenon. This species is particularly little known, appearing exter-

nally very similar to *X. grandis*, but internally sharing a number of synapomorphies with *X. rectocollaris*. A distinct form of the supratemporal arch is one of the few autapomorphies distinguishing it from its common ancestor with that taxon.

Xenosaurus rectocollaris. This is the most unusual of the species of *Xenosaurus* at first glance. Its head is particularly short and stout, although the shortening appears to involve the postorbital dermal bones of the adductor/otic region, instead of the bones surrounding the nasal capsule as in *E. serratus*. Externally, the taxon is distinguished by a bold dark-on-light color pattern different from the light-on-dark patterns of the other species of *Xenosaurus*, and it bears a strange cuff of puffy tissue around its neck. It would be interesting to investigate possible ecological correlations of the singular anatomy of this animal.

Xenosaurus rackhami + Xenosaurus grandis. These two species share a number of synapomorphies, most strikingly a dramatic reduction of cranial osteoderms (postcranial osteoderms are absent). Certain other features distinct to *Xenosaurus*, such as the anteroposterior expansion of the tip of the jugal and the mediolateral expansion of the supratemporal arch, are at their most extreme in these two taxa, which are also perhaps the best represented in U.S. museum collections.

Xenosaurus rackhami. This species is slender of head and body compared with other *Xenosaurus*, and some individuals have particularly flat heads. In *X. rackhami*, the reduction of osteoderms is the extreme among examined *Xenosaurus*, and several peculiar autapomorphies of the skull roof and supratemporal bar, as well as the dentition, also obtain.

Xenosaurus grandis. This is a relatively unusual species of *Xenosaurus*, stout and robust where its sister taxon is slim and slight. The reduction of osteoderms is less extreme in *X. grandis*, and some of the autapomorphies of the taxon relate to its generally stout form. *Xenosaurus grandis* is the most common species of *Xenosaurus* in

U.S. collections, and the most heavily figured and described (notably by Barrows and Smith, 1947). It is generally used as the exemplar for *Xenosaurus*, and sometimes for the classical Xenosauridae as a whole (Wever, 1978; Estes et al., 1988). Considering the large number of apomorphies between *X. grandis* and the *Xenosaurus* ancestor, it is not the ideal choice. Only one recent study (Conrad, 2008; extended in Conrad et al., 2011) included a prudent combination of *X. grandis* and *X. platyceps*, bracketing *Xenosaurus*.

Morphological Characters in Phylogenetic Analysis and Specific Issues of Character Evolution

My analysis includes an unusual number of characters for such a restricted group of lizards (compared with, e.g., Rieppel and Zaher [2002] for uropeltid snakes, a group of similar size and high specialization). The surfeit of characters owes in part to my discovery of a number of informative features in previously unappreciated elements, such as the septomaxilla and the palpebral—these discoveries in turn owing to the availability of disarticulated skeletal material. Characters such as small foramina in these diminutive bones were remarkably invariant within taxa, and the fact that this seems counterintuitive suggests that a large number of characters dealing with subtle differences in anatomy are arbitrarily neglected in gross anatomical phylogenetics. Further work, in particular, on subtle features of disarticulated bones, could be immensely profitable in increasing the number of gross-scale characters to achieve greater parity with the size of molecular-scale datasets (Chippindale and Wiens, 1994). Already, work on subtle and tiny foramina dotting the dermatocranial elements of certain mammals has shown that the clustering of these foramina are consistent within taxa and appear to be phylogenetically informative (Wible, 2003; Kearney et al., 2005).

In addition to hypotheses of relationships, phylogenetic analyses provide a thorough

catalogue of anatomical changes in the structures utilized, whether at the gross, histological, or molecular scale—they are in some ways "shorthand" descriptions of anatomy. Several characters or character systems here examined stand out as potentially fruitful for additional study. The enclosure of the ethmoid nerves within the premaxilla (character 6) is unusual within Squamata. It is interesting that xenosaurs show both this character and very heavy osteodermal sculpturing—as do very old individuals of *E. multicarinata*. The appearance of xenosaur-like features in very late stage *E. multicarinata* might suggest a heterochronic relationship, wherein some characters of xenosaurs are peramorphic with respect to those of anguids and perhaps other anguimorphs.

The increased number of foramina in the premaxilla (characters 7 and 8) and maxilla (characters 53 and 54) in xenosaurs might suggest an increased acuity of integumentary sensation, perhaps related to the decreased utility of sight in the dark environments frequented at least by individuals of *Xenosaurus*. Increased numbers of foramina on the face have been suggested to imply great tactile acuity in amphisbaenians, as well (Kearney et al., 2005). The increased diameter of the infraorbital canal within xenosaurs (character 51) indicates an increase in the size of the contained neurovascular bundle, which includes the V_2 division of the trigeminal nerve. An enlarged canal for V_3 is associated with the enormously elaborated sensory capabilities of the platypus snout (Rowe et al., 2008).

The various septomaxillary characters identified herein are remarkably phylogenetically useful and consistent with regard to variation, considering the general neglect of this skeletal element in the non-snake squamate literature. Clearly the septomaxilla is complex and evolutionarily labile, and I predict that it will prove a rich source of characters for other clades, as well. The morphology in *Xenosaurus*, with its fully enclosed medial and lateral canals, is especially remarkable, and one wonders at the possible soft tissue and sensory correlates. The complete enclosure of the lateral canal in *Xenosaurus* and *Heloderma* recalls the sister taxon relationship between those taxa suggested by some analyses in molecular-scale studies (Townsend et al., 2004).

Several transformations in the temporal region, notably the lateral and ventral expansion of the postorbital and squamosal and the anteroposterior expansion of the jugal, occur along the stem of *Xenosaurus*. Seemingly accompanying these changes are the strong surangular crest and the subcoronoid fossa. Possibly these features are variously related to the enormously elaborated adductor musculature of *Xenosaurus* (Haas, 1960). If they are so related, they may together represent a complex of characters that are not fully independent from each other.

Finally, *Xenosaurus* shows a lack of depression in the posterior end of the quadrate for the tympanic cavity (character 173). Varanidae also display this character, but the quadrates of those taxa are heavily modified. Possibly the lack of depression is related to a reduction of the tympanic cavity also associated with the scaling over (and thus apparent functional impedance) of the tympanum (character 270). However, the depression remains in *Shinisaurus*, whose tympanum is also scaled over in adulthood.

Character nonindependence is a recurring problem in phylogenetic analysis (Martins and Garland, 1991; Schaffer et al., 1991; Huelsenbeck and Nielsen, 1999; McCracken et al., 1999). Given the level of integration among the parts of a multicellular (or unicellular) organism, it is unlikely that characters can ever be fully independent. Nevertheless, studies such as mine could profit from careful analysis of character correlation, taking into account ontogeny and the soft tissue relations of bones. The character list I provided is arranged by sensory capsule, for example, because most dermatocranial elements are involved in sheathing one of the three capsular regions (with the otic region being more complicated because of the additional

presence of the adductor chamber). Significant changes in the basic structure of one of the sensory capsules surely would produce complementary changes in multiple sheathing bones. Considering the ingroup of this study, a few other potential sources of nonindependence arise. The head of *Xenosaurus* is unusually wide, and this general change may be related to the mediolateral expansion of several dermatocranial elements and even the capture of previously external vascular and nervous structures by the septomaxilla. In *E. serratus*, the shortness and width of the snout could be related to several autapomorphies of the taxon. Osteodermal development obviously shows general trends, with most regions of osteoderms reduced, for example, in *X. grandis* + *X. rackhami*. However, these trends are not always uniform, preventing the scoring of a single combined character for the various potentially related transformations. For instance, cranial osteoderms are best developed in *X. newmanorum* and *X. platyceps*, especially in the former. Limb osteoderms, however, are more prominent and numerous in *X. platyceps*, whereas caudal osteoderms are more developed in *X. newmanorum*. Thus, neither taxon can been scored overall as having the most "highly developed" osteoderms, even if cranial and postcranial categories are established.

Finally, an initial foray into studies of the intraspecies variation of characters is made herein, although the attempt is basically limited to an effort to justify character selection and scoring. A great deal of additional work needs to be done on intraspecies variation in all vertebrates, for this variation is the raw material of evolution (Darwin, 1859; Bever, 2006 and references therein). In particular, compared with the attempts made here, further studies must incorporate larger sample sizes, greater ontogenetic spreads, and careful control of localities/populations and the temporal aspect of collection. *Xenosaurus* provides an interesting case study for population studies because pop-

ulations of the species are spatially restricted, often occupying a single rock cliff (Ballinger et al., 2000). That spatial restriction may account for the relatively large number of species of *Xenosaurus*, and it is not clear whether significant gene flow occurs among isolated populations (Lemos-Espinal et al., 2004). On a larger scale, aspects of variation can provide additional characters for phylogenetic analysis. In short, morphological characters for phylogenetic analysis are by no means exhausted, even in the most heavily studied clades. A push for careful, thorough anatomical analysis of as much of the body as possible, ranging from the microscopic scale to aspects of variation and behavior, will yield a vast number of additional characters. The limited exercise provided by this work demonstrates that even a thorough, bone-by-bone analysis of the skeleton alone can yield hundreds of novel characters and produce a fully resolved phylogeny with high support values. In this case, congruence with DNA-based analyses allows further confidence in the results, but considering the number of the characters and the high support for the morphological tree, incongruence would necessitate careful reconsideration not only of the morphological but also of the molecular data and analyses.

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