Assembling the Squamate Tree of Life: Perspectives from the Phenotype and the Fossil Record

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ABSTRACT

We assembled a dataset of 192 carefully selected species—51 extinct and 141 extant—and 976 apomorphies distributed among 610 phenotypic characters to investigate the phylogeny of Squamata ("lizards," including snakes and amphisbaenians). These data enabled us to infer a tree much like those derived from previous morphological analyses, but with better support for some key clades. There are also several novel elements, some of which pose striking departures from traditional ideas about lizard evolution (e.g., that mosasaurs and polyglyphanodontians are on the scleroglossan stem, rather than parts of the crown, and related to varanoids and teiids, respectively). Long-bodied, limb-reduced, "snake-like" fossorial lizards—most notably dibamids, amphisbaenians and snakes—have been and continue to be the chief source of character conflict in squamate morphological phylogenetics. Carnivorous lizards (especially snakes, mosasaurs and varanoids) have proven a close second. Genetic data, presumably less burdened by the potential for adaptive convergence related to fossoriality, were expected to resolve these conflicts. Although recent gene phylogenies seem to do so, they also differ radically from any phylogeny based on the phenotype, especially for the most ancient crown squamate divergences that occured during the latter half of the Mesozoic. Our study relied on traditionally prepared specimens as well as high-resolution computed tomography scans that afforded unprecendented access to the cranial anatomy of Squamata. This, along with the inclusion of stem fossils, provided an unparalleled sample of the phenotype enabling us to more fully explore the extreme incongruences between molecular and morphological topologies for the squamate tree of life. Despite this extensive new database, we were unable to find morphological support for the major rearrangement of the deep divergences in Squamata proposed by recent molecular studies. Instead, our data strongly support the same fundamental topology suggested by most previous morphological studies—an Iguania–Scleroglossa basal split, a sister-group relationship between Gekkota and Autarchoglossa, and the divergence between Anguimorpha and Scincomorpha—and documents the extreme degree of morphological homoplasy required by those molecular topologies.

KEYWORDS

Rhynchocephalia, Squamata, Iguania, Polyglyphanodontia, Scleroglossa, Gekkota, Autarchoglossa, Scincomorpha, Anguimorpha, Mosasauria, Serpentes, phylogeny, morphology, fossils, biogeography, divergence times, homoplasy, evolution, taxon sampling, morphology vs. molecules.

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Introduction

With his "Essai d'une Classification Naturelle des Reptiles," Alexandre Brongniart (1800a, 1800b), a collaborator of Georges Cuvier, set the stage for all later discussions of "reptile" classification. Applying Cuvier's method of dichotomized classification (called *méthode naturelle* by Cuvier [1817:10]) to extant tetrapods (except birds and mammals), he recognized four "orders" later adopted by Duméril (1806) in his classic *Zoologie Analytique*: *Chéloniens*, *Sauriens*, *Ophidiens* and *Batraciens*. Because of an error in the dissection of the caecilian, "lizard" and snake hearts jointly undertaken by Cuvier, Brongniart, and F.M. Daudin, snakes were separated from "lizards," but the long-bodied, limbless caecilian amphibians were included within snakes (Daudin 1926; Rieppel 1987b).

The "order Squamata" was introduced by Oppel (1811:14) to encompass "Saurii" (with distinct limbs and nondilatable maxillary bones) and "Ophidii" (lacking external limbs and characterized by dilatable maxillary bones). Oppel's (1811:19) "Saurii" included the crocodilians (which will not be further commented on here). More important is his grouping of "lizards" and snakes within one order, which he based on the insight that hardly any single character unambiguously differentiates "lizards" from snakes. For *Ophisaurus* (considered an intermediate between snakes [*Ophi-*] and "lizards" [*-saurus*] by F.M. Daudin [*O. ventralis,* Daudin 1803:346]), and *Anguis fragilis* (both of which Duméril [1806] had grouped with other "lizards"), Oppel (1811:17) confessed difficulty in deciding whether these should be arranged "at the end of the lizard [series], or at the beginning of the snake [series]...nature herself seems not to have placed great weight on the character of [the presence or absence] of limbs." But whereas he continued to group *Ophisaurus* and *Anguis* with "lizards," he included the (mostly) limbless amphisbaenians with snakes (Oppel 1811:53), as Brongniart (1800a) had done before him. Oppel's early (1811) efforts in his "arrangement of reptiles" introduced themes that still resonate in contemporary discussions of squamate phylogeny, in particular the potential relationships of snakes to other limb-reduced and long-bodied taxa within Squamata.

Although the Cuvierian scheme of classification portrayed "affinities" in terms of a dichotomous hierarchy, the image of an underlying "series" of forms still dominated comparative biology well into the 19th century (Daudin 1926), as can be seen from Oppel's (1811) concerns about the continuity of the "lizard" with the snake "series." Louis Agassiz, in his famous *Essay on Classification* (1857), emphasized continuity of limb reduction in squamates, citing the graded series of intermediates between "lizards" and snakes as evidence for the completeness (plenitude) of the scheme of nature, which for him was ultimately rooted in Divine thought. Such views, of course, were famously opposed by Charles Darwin. Noting the presence of rudimentary hindlimbs in some basal snakes, Darwin was satisfied that "on my view of descent with modification, the origin of rudimentary organs is simple" (Darwin 1859:206). The gradual transition from limb-reduced "lizards" to snakes pointed to descent with modification. This pattern of thought was interrupted, though, by Cope (1869:253), who referred monitor-like, marine lizards from the Cretaceous to his Pythonomorpha based on the fact that mosasaurs have an intramandibular joint in the lower jaw, as well as a loose mandibular symphysis, as do some snakes such as pythons. Later, Cope (1872) used similarities of inferred jaw mechanics in support of the phylogenetic derivation of snakes from mosasaurs. Cope (1878, 1895a, 1895b, 1896) continued to defend his gradualistic scenario linking the feeding mechanics of mosasaurs with those of macrostomatan snakes like boas and pythons against criticisms such as those of Owen (1877, 1878) and Baur (1895, 1896).

The subsequent discovery of basal mosasaurs such as "aigialosaurs" and dolichosaurs—the latter approaching snakes more closely in general body proportions than the highly derived Mosasauridae, and exhibiting various stages of limb size reduction and body elongation (Kornhuber 1873, 1901; Gorjanovic-Kramberger 1901; Nopcsa 1903, 1908; Janensch 1906)—from early mid-Cretaceous marine sediments of southern Europe, seemed to lend further support to Cope's earlier theory of snake origins. With the discovery of *Pachyophis woodwardi* from the early Upper Cretaceous of Bosnia-Herzogevina, Nopcsa (1923) believed he had finally found the critical transitional species between basal mosasaurs and snakes, which in his view also necessarily implied a marine origin of snakes (Nopcsa 1925).

Meanwhile, Camp's (1923) monograph on the classification of lizards was an important milestone, the first modern attempt at a broad-scale analysis of squamate relationships (Underwood 1971). Much of the later work on lizard classification based on morphology can be seen as refining Camp's (1923) results. What Camp's (1923) monograph established for "lizard" classification, Underwood's (1967) seminal contribution provided for snake classification; it is the foundation for contemporary investigations of snake interrelationships. Camp's (1923) basic subdivision of squamates into Ascalabota (Iguania and Gekkota) and Autarchoglossa (Scincomorpha and Anguimorpha) provided an important basis for additional broad-scale investigations in search of monophyletic higher taxa, as did Underwood's (1967) classification of snakes into three "grades": Scolecophidia (blind snakes), Henophidia (pipe snakes, file snakes, boas and pythons), and Caenophidia (higher snakes). Camp's (1923:313) derivation of snakes "from anguimorphid, grass-living lizards" kept their origin close to the mosasaurs (which were associated in Camp's concept of Anguimorpha), yet derived them from terrestrial, rather than marine, ancestors.

With his comparative studies of the development of the eye in squamates, Walls (1940, 1942) cast new light on the question of the origin of snakes, an analysis that was most comprehensively dealt with in Bellairs and Underwood's (1951) review. According to Walls (1940, 1942), the development and anatomy of the eye in snakes are unique in numerous and important ways. The structure of the eye in snakes differs greatly from that of other squamates—indeed, from that of most other vertebrates. This led Walls to suggest that the snake eye may have redeveloped from a rudimentary (reduced) eye that would characterize a secretive, or burrowing, snake ancestor. The hypothesis of a burrowing ancestry for snakes was further supported by Bellairs and Underwood (1951), who pulled together an impressive body of data derived from various organ systems in support of that hypothesis. Their influential review was followed by another milestone in the history of squamate research, the monographic study of "anguinomorph 'lizards'" by McDowell and Bogert (1954). This monograph not only made important improvements to Camp's (1923) original lizard phylogeny with respect to the composition and interrelationships of Anguimorpha, but also proposed the earless "monitor" *Lanthanotus borneensis* as the extant quadrupedal "lizard" most closely related to snakes. Interpreted by McDowell and Bogert (1954:54) as a "living aigialosaurian," the particular habits of *Lanthanotus*, a secretive creature found on the banks of the Sarawak River in Borneo, would nicely bridge the gap between a terrestrial and secretive origin and a (semi-) aquatic origin of snakes.

Motivated by Walls' (1940, 1942) discoveries concerning the eye of squamates, Senn and Northcutt (1973) set out to investigate optic centers and related structures in the forebrain and mid-brain of squamates. Their findings supported Walls' (1940, 1942) conclusions in significant ways, adding that brain anatomy indicates relationships of snakes with scincomorph, limb-reduced and burrowing lizards such as the dibamids *Anelytropsis* and *Dibamus*, and the "feyliniid" skinks. In a later contribution, Northcutt (1978) expanded the survey of fore- and mid-brain organization in squamates within a phylogenetic context. He found dibamids to be most closely related to scincids, the two sharing a common root with snakes (amphisbaenians were not included in this study, but see also Rage 1982). Further support for a burrowing ancestry of snakes derived from studies of head miniaturization in squamates (Rieppel 1984a, 1984b).

Another important milestone in the understanding of squamate diversity was the publication by Estes (1983) of a compendium on terrestrial fossil "lizards" and amphisbaenians (nonmarine squamates exclusive of snakes). (The corresponding, yet far less voluminous, "snake volume" was compiled by Rage [1984].) The Estes (1983) volume contained no phylogenetic analysis, and is in part outdated by modern standards. Nevertheless, the book is still a classic reference, presenting rich material on the fossil record on all major groups of non-ophidian terrestrial lizards.

The first explicitly apomorphy-based cladistic analysis of squamate reptile interrelationships was that of Estes et al. (1988), which set the stage for all subsequent phylogenetic work on squamates. This analysis recovered the paraphyly of Camp's (1923)

Ascalabota, because Gekkota was recognized to be the sister group of Autarchoglossa (see also Gauthier 1982) and grouped in a clade named Scleroglossa. The study further clarified the composition of major squamate clades outside (i.e., Iguania) and within (i.e., Gekkota, Scincomorpha, Anguimorpha) Scleroglossa, but left some difficult-to-resolve squamate clades as "Scleroglossa incertae sedis," i.e., the "snake-like" amphisbaenians, dibamids and snakes. For dibamids, a scincoid relationship was considered possible (Rieppel 1984b), whereas amphisbaenians were considered of possible lacertoid relationships (Gauthier 1984; Schwenk 1988). Snakes were considered more likely to be anguimorph than scincomorph relatives (Estes et al. 1988:235).

The study of higher-level squamate relationships by Estes et al. (1988) was accompanied by two more landmark cladistic studies at around the same time: the study by Etheridge and de Queiroz (1988) published in the same "Camp Symposium" volume as the Estes et al. (1988) monograph, and the even more comprehensive analysis published the following year by Frost and Etheridge (1989) that laid the foundations of all subsequent investigations of iguanian phylogeny.

The hypothesis of a marine origin of snakes from mosasaurs was revitalized by the redescription of two specimens of *Pachyrhachis problematicus* (Caldwell and Lee 1997; Lee and Caldwell 1998), a fossil snake with fully differentiated, if very reduced, hindlimbs, from early Upper Cretaceous marine sediments of the Middle East (for the original description of the material see Haas 1979, 1980a, 1980b). As two additional species of mid-Cretaceous snakes with hindlimbs became known (Rage and Escuillié 2000; Tchernov et al. 2000), a debate developed as to whether these snakes were, indeed, transitional fossils linking snakes with mosasaurs (Carroll 1988) or whether they were derived taxa, i.e., macrostomatan snakes related to boas and pythons (the debate is summarized and referenced in Rieppel et al. 2003).

The first global analysis of squamate interrelationships that included mosasaurs as well as *Pachyrhachis problematicus* (Lee 1998) corroborated a mosasaur sister-group relationship to snakes, indicating that the signal that would link snakes with burrowing squamates such as dibamids or amphisbaenians was due to convergence. The data set assembled by Lee (1998) contained a noteworthy morphological signal in support of a relationship of snakes with fossorial squamates such as amphisbaenians and dibamids, a signal that was broken only by downweighting those characters thought to be correlated with the "burrowing ecomorph" (Lee 1998). Later, morphological analyses of the characters that supported a relationship of snakes with mosasaurs became the subject of criticism by Rieppel and Zaher (2000a) who, after revising relevant character codings, again recovered an amphisbaenian-dibamid-snake clade. Hallermann (1998) lent further support to dibamid—amphisbaenian relationships of snakes through his study of the nasal capsule and associated structures—anatomy that had not been included in previous analyses. The same signal continued to emerge from several unrelated cladistic analyses of squamate relationships that were not primarily concerned with snake origins (e.g., Evans and Barbadillo 1998; Kearney 2003a).

While the 1980s witnessed the first important applications of explicit phylogenetic methods to the (morphology-based) study of extant squamate phylogeny, our understanding of squamate evolution exploded in the 1990s because of the expeditions to the Upper Cretaceous of Mongolia that discovered the most remarkable and abundant quantity of fossil lizards ever found, representing nearly all major squamate clades (except for mosasaurians, snakes and amphisbaenians; Norell et al. 1992; Norell and Gao 1997; Gao and Norell 1998, 2000; Norell 2004; Conrad and Norell 2006, 2007, 2008; Norell et al. 2008; Conrad et al. 2010; Conrad et al. 2011). These paleontological discoveries have not had much influence on current discussions of squamate phylogeny (which tend to be largely molecular-based today), but have provided key insights into our understanding of ancestral states for the surviving diversity of Squamata. The significance of these discoveries encompasses an immense increase in our knowledge of taxonomic diversity, anatomical disparity, biogeography, and patterns of extinction and origination, as well as establishing minimum divergence times of many major squamate clades. These fossils have overturned key ideas about squamate character evolution; the "semilunate" postfrontal, for example, previously thought to be diagnostic of Scleroglossa

(Gauthier 1982; Estes et al. 1988), is still present in stem iguanids from the Gobi Desert if not in any crown iguanian today (Gao and Norell 2000). We have accordingly included several of these fossils in our analysis.

In 2004, multi-gene molecular studies of Squamata drastically altered all previous ideas about deeper squamate relationships (Townsend et al. 2004; Vidal and Hedges 2004). In these molecular studies, Iguania no longer represents a basal squamate clade, but is instead related to either Anguimorpha or Serpentes, or both, and nested well inside Squamata. Subsequent molecular work supported a non-monophyletic Scincomorpha indicated in the earlier studies, yet yielded variable placements of Iguania as sister to either Serpentes (Wiens et al. 2010, fig. 6), Anguimorpha (Vidal and Hedges 2005; Fry et al. 2006; Kumazawa 2007), Gekkota (Voronov et al. 2011), Anguimorpha plus Scincidae (Douglas et al. 2010), or Anguimorpha plus Serpentes (Wiens et al. 2010, fig. 5; Müller et al. 2011). Albert et al. (2009) obtained a tree in which Iguania is not monophyletic, with Acrodonta and Serpentes forming a clade that is sister to all other crown squamates, and with Iguanidae forming a clade with Scincomorpha. These molecular studies raise new questions and concerns about deeper squamate phylogeny and evolution during the Mesozoic Era.

Comparisons of morphological and molecular signals for squamate interrelationships are remarkably incongruent—perhaps more so than for any other vertebrate group. Whatever the outcome of a future combined analysis, the high degree of discordance between morphological and molecular data warrants scrutiny and discussion. Squamates may even provide a perfect case study for exploring the causes of such extreme data incongruence. As a result, we wished to re-examine phenotypic data in lizards to determine whether any characters could be discovered in support of the novel groupings found in recent molecular analyses. Our study (part of the "Deep Scaly" Assembling the Tree of Life project) was intended to investigate the early-diverging squamate clades and their relationships to one another. Issues of interest include the following: the placement of extinct mosasaurs and polyglyphanodontians; potential interrelationships among fossorial squamates, especially snakes, dibamids and amphisbaenians; potential interrelationships among carnivorous squamates, particularly snakes, varanoids and mosasaurians; the monophyly of Iguania, Scleroglossa and Autarchoglossa; the early phylogeny of snakes; and the placement of certain age-calibrating fossils.

Materials and Methods

Specimen Preparation

Most skull characters were scored using computed tomography (CT) scans, which vastly improved access to internal cranial anatomy relative to traditional methods. Specimens were scanned at the High-Resolution X-ray Computed Tomography Facility at The University of Texas at Austin using a FeinFocus microfocal X-ray source. However, the tiny *Anelytropsis papillosus* and *Liotyphlops albirostris* were scanned separately by W. Hagadorn at Amherst College using a Skyscan 1172 microfocus X-ray CT scanner. Scanning parameters were individually optimized and thus varied across specimens. The datasets were re-sliced and rendered in three dimensions using VGStudioMax® (Volume Graphics, Heidelberg, Germany). Reslice, rotation, and cutaway animations were generated and distributed in QuickTime® format. The CT data and more detailed scan parameters are available from author J.A. Maisano; all visualizations will be available at the Digital Morphology website (DigiMorph.Org. c2002–2012).

Postcranial osteological characters were scored primarily using cleared and double-stained specimens, prepared following the general methodology of Dingerkus and Uhler (1977) and Maisano (2008). Observations of both cranial and postcranial characters were supplemented by examining dry skeletal preparations, as well as fossils that could not be scanned, or scanned poorly, and had to be prepared by hand. Characters of the tongue were scored based on alcohol-preserved and fresh specimens. Characters relating to the use of the tongue during feeding, and for cleaning the eye, were scored by J.A. Gauthier from captive specimens. For this study 1,319 specimens were examined (Appendix 1).

Taxon Sampling

Phenotypic characters were ultimately meant to be integrated with gene sequences for the same exemplar species considered in this Assembling the Tree of Life project, so taxon sampling was constrained largely by tissue availability. We used an exemplar approach based on single species, fossil and Recent, though composites were scored in a few instances (e.g., "*Clidastes*"). We selected 192 exemplar species (141 extant and 51 extinct) for analysis (see Appendix 1). We used three species, two extinct and one extant, of Rhynchocephalia to represent the outgroup (see "The Outgroup" in Results and Discussion below). For extant species, we sampled large "adult" individuals, but had to rely on available specimens for extinct species. In both instances, we calibrated ontogenetic stage by braincase fusion, supplemented by fusions in the limb girdles and fusions between long bone secondary ossification centers and their respective diaphyses. This required that we ignore potentially informative ontogenetic information, except in rare instances.

Extant species of Squamata were selected from traditional categorical ranks: two species for each "family" and one for each "subfamily." Selection of species within those categorical ranks was informed by previous phylogenetic analyses, so that, within the bounds of tissue availability, we selected species for their ability to inform ancestral states in their respective "family" and "subfamily." Extinct species were selected under the same criteria, as well as on the basis of completeness and availability of material for study, and ultimately by whether or not they scanned well with CT imaging.

Exemplar selection by categorical rank led to some expected distortions, especially when it came to sampling fossorial squamates. Highly modified taxa, such as those constrained by head-first burrowing and life underground, tend to be accorded "higher" ranks because they look "so different" from other lizard "families" and "subfamilies," sometimes resulting in a disproportionate presence in our sample. The fossorial skink *Feylinia polylepis*, for example, is accorded either its own "subfamily" or "family" in traditional taxonomies because of its highly specialized "fossorial" ecomorphology (e.g., Gans 1975). It is nonetheless related to other, less modified, sub-Saharan African skinks (Whiting et al. 2003; Brandley et al. 2005), which we will refer to informally as "scelotines." Although ultimately squamate systematists want to know where *Feylinia polylepis* fits into the "lizard tree of life," this scelotine exemplar overly complicates our more modest goal of determining where Scincidae fits into the squamate tree. In that case, the more "snake-like" scelotine *Feylinia polylepis* (missing so much pertinent data owing to evolutionary transformation) proved far less useful than the much less modified—and accordingly informative—anatomy available in the more "lizard-like" scelotine *Amphiglossus splendidus*.

Character Sampling

Interrelationships among every species in our analysis are not the focus of this study and thus we did not include characters necessary to resolve relationships within many clades. Instead, we assembled all characters that had proven useful for basal squamate relationships published at the start of our project (finalized in January 2006), and added new characters that we discovered during the course of this study. We also tried to fill in anatomical gaps for species that previously were scored as "missing data," such as important fragmentary fossils and extant species too rare to permit "destructive" sampling. CT imaging gave us unparalleled access to squamate cranial anatomy, enabling us to pursue these questions to a degree heretofore impossible. We have only scratched the surface of the wealth of anatomical data available in these CT scans. Much more morphological study will certainly prove informative to future studies of squamate phylogeny.

Morphological investigation produced 610 characters composed of a total of 976 apomorphies. Most are osteological characters of the skull, a major source of squamate morphological characters in previous comprehensive studies (e.g., Estes et al. 1988; Lee 1998; Conrad 2008), but postcranial characters are also sampled, as well as a few soft-anatomical characters. Virtually all characters (more than 99%) are scored based on our own observations of specimens prepared specifically for this study. Literature observations were, however, used for some characters in some fossil taxa, particularly mosasaurians. We include a list of characters scored with images for each state (for qualitative characters), except for "absence" (Appendix 2).

Data Analysis

Most characters are described qualitatively and coded as binary or multi-state. Multi-state characters that involve continuous quantitative variation (e.g., relative bone length, number of teeth or vertebrae) are ordered from lowest to highest values, or vice versa. All other characters describing qualitative variation (e.g., presence or absence of fangs, frontals paired or fused) are unordered. Characters are coded so that they could be analyzed by both parsimony and Bayesian methods. Unfortunately, available versions of MrBayes (v. 3.0; Ronquist and Huelsenbeck 2003) did not allow step matrices or more than five ordered character states (more than five unordered states are, however, available in more recent versions). It was therefore not possible to use frequency coding for polymorphic characters or gap-weighting for quantitative characters (despite some advantages of these methods). A few multi-state morphological characters had to be recoded for the Bayesian analysis by lumping the full range of variation into just five bins (states).

The decision to bin quantitative characters sometimes obscured variation that we expected to be informative for our study based on previous analyses. All morphological analyses to date have, for example, found that an increase from 24 to 26 presacral vertebrae diagnoses a major squamate clade: Scleroglossa. However, when the full range of variation in vertebral number among our squamate exemplars (which ranges from fewer than 23 to more than 219) was divided into just five bins of about 40 vertebrae each, that effectively concealed this information. In a few instances, we accordingly divided certain characters, such as "presacral vertebral number," into several characters (e.g., characters 454 to 458), each with the five bins (states) permitted in MrBayes at the time. In other cases, such as variation in tooth number (characters 419 to 421), we parceled the observed variation equally among five bins. This was not an ideal choice either; in the dentary, for example, a tooth count somewhere between 18 to 28 teeth seems to be ancestral for lizards, but that variation is distributed between two bins in our analysis (apomorphies 421[2], 10 to 20 teeth, and 421[3], 21 to 35 teeth]. Ideally, future analyses of these data will implement software packages that provide a sufficient number of states to encompass the full range of variation, including species-level polymorphism.

Given our focus on early divergences among lizards, sample sizes within species were generally limited (*n*=1 for characters from CT scans, but greater for characters observable in all 1,319 specimens used in this study). When denser samples of species revealed polymorphism, we coded using the "polymorphic method" (reviewed in Wiens 1999), given that frequency methods would be difficult to implement in MrBayes and the "majority method" can only be applied arbitrarily to a frequency of 50%.

This dataset was assembled in MacClade v. 4.08 (Maddison and Maddison 2005). Parsimony analyses were conducted with PAUP* v. 4.0 Beta 10 (Swofford 2002) for Macintosh PPC, and the Bayesian analysis with MrBayes v. 3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). All analyses of the dataset were conducted on a Mac® Pro 3.1 with a 2.8GHz Quad-Core Intel Xeon processor and 32GB RAM, running Mac OS® X (v. 10.5.8). The matrix was first analyzed with a parsimony ratchet (Nixon 1999) command file built in PAUPRat (Sikes and Lewis 2001) in PAUP* v. 4.0 Beta 10 (Swofford 2002) with 20 independent runs of 200 iterations each (10 runs with 10% of the characters reweighted in each iteration, and 10 runs with 20% of the characters reweighted with each iteration). We used the set of trees from the parsimony ratchet as the starting point for a heuristic search with the three rhynchocephalians (*Sphenodon punctatus*, *Kallimodon pulchellus* and *Gephyrosaurus bridensis*) constrained as a monophyletic outgroup. The default settings in PAUP* v. 4.0 Beta 10 (Swofford 2002) were used, except for the following: pset collapse=minbrlen; opt=deltran; mstaxa=polymorph; hsearch enforce=yes; start=current; nreps=1. The bootstrap (BP) analysis was conducted with 1,000 iterations and a time limit of 3,600 seconds per iteration. The Bremer support (BS) index was determined in PAUP* v. 4.0 Beta 10 (Swofford 2002), with a command file built in TreeRot v. 3 (Sorenson and Franzosa 2007). Bootstrap values more than 70% (e.g., Hillis and Bull 1993, and caveats therein) and Bayesian posterior probabilities (PP) more than 90% are considered strongly supported. The Bayesian analysis used the default settings for 50 million generations and runs were checked for convergence with the "sump" command using a "burnin" value of 50%. We also consider clades strongly supported when they share phenotypic apomorphies that seem unique and unreversed on all reasonably supported trees stemming from this analysis. In the taxon deletion experiments, we used the set of most parsimonious trees from the initial parsimony analysis as the starting point for the heuristic search with the taxa of interest pruned from those trees.

We used the Wilcoxon sign-ranked test (Templeton 1983) to compare selected alternative hypothesized topologies (e.g., Iguania as sister to Anguimorpha [Wiens et al. 2010]). As a nonparametric test, the inferences of rejection are actually very conservative and will not reject all topologies that are significantly different. Conversely, any topologies that are significantly different are rejected with confidence.

Results and Discussion

The heuristic search found a total of 112 trees with a length of 5,430 steps (consistency index [CI] = 0.2066; homoplasy index [HI] = 0.8203; CI excluding uninformative characters = 0.2060; HI excluding uninformative characters = 0.7940; retention index [RI] = 0.7936; and rescaled consistency index [RCI] = 0.1640). See the strict consensus (Figure 1) and the Adams consensus of those trees derived from maximum parsimony analysis as implemented in PAUP* (Figure 2).

Note that only some synapomorphies—those identified as "unambiguous" in PAUP*—are discussed here. Even that list will often be reduced to just those synapomorphies that we anticipate will survive wider analyses. All clades inferred in this study are diagnosed in Appendix 4.

Below we focus solely on new insights into squamate evolution, for which we found reasonably good support (more than 70% BP, more than 90% PP), and contrast them with the results of the most recent comprehensive morphological analysis of squamate phylogeny (Conrad 2008; we refer the reader to that publication for a detailed history of the ideas on the subject). We will also consider alternative results emerging from a completely unordered maximum parsimony (Figure 3), as well as Bayesian analyses (Figure 4), of our dataset where appropriate, evaluate our findings in light of their sensitivity to taxon sampling (see "Taxonomic Inclusion/Exclusion Experiments" below), and compare our tree to those recently derived from gene sequence data (see "Morphology vs. Molecules" below).

The Outgroup

We used three species of Rhynchocephalia, two extinct and one extant, to represent "the outgroup" in our maximum parsimony and Bayesian analyses (when that option was available). Stretching aproximately 350 million years from the Recent down to near the Permian–Triassic boundary, then up again toward the late Jurassic when unambiguous crown lizards first appear, the vast timespan separating crown *Sphenodon punctatus* from crown Squamata constitutes the single longest branch among living amniotes. It should come as no surprise, then, that Rhynchocephalia was once a remarkably diverse and disparate group of diapsid reptiles that we are only just beginning to understand (e.g., Cocude-Michel 1963; Evans 1980, 1981; Rasmussen and Callison 1981; Fraser and Walkden 1984; Carroll 1985; Fraser 1986, 1988, 1989; Whiteside 1986; Sues et al. 1994; Wu 1994; Reynoso 2000; Apesteguía and Novas 2003; Simon and Kellner 2003). The clade dominates the fossil record of Lepidosauria during the Triassic and Jurassic, with the squamate branch becoming abundant, in a classic pattern evolutionary relay, only much later during the Cretaceous.

The entire clade is represented today by a single living species, *Sphenodon punctatus,* which persists only as small, bottle-necked populations on a few islands off the coast of New Zealand (Hay et al. 2010). We accordingly chose to estimate ancestral states for Rhynchocephalia by adding two extinct species in an effort to shorten that immense branch length: the Early Jurassic *Gephyrosaurus bridensis* and the Late Jurassic *Kallimodon pulchellus*. Ranging from 10 autapomorphies in our most basal rhynchocephalian, *G. bridensis*, to as many as 21 autapomorphies in Recent *S. punctatus,* none of these species affords a clear picture of an unmodified example of the root of the *Sphenodon* stem. We agree with Townsend et al. (2004) that caution should be exercised when relying entirely on data from living *Sphenodon punctatus* as the sole representative of this ancient (more than 220-million-year-old) clade. For the 610 characters used in this analysis, for example, *Sphenodon punctatus*

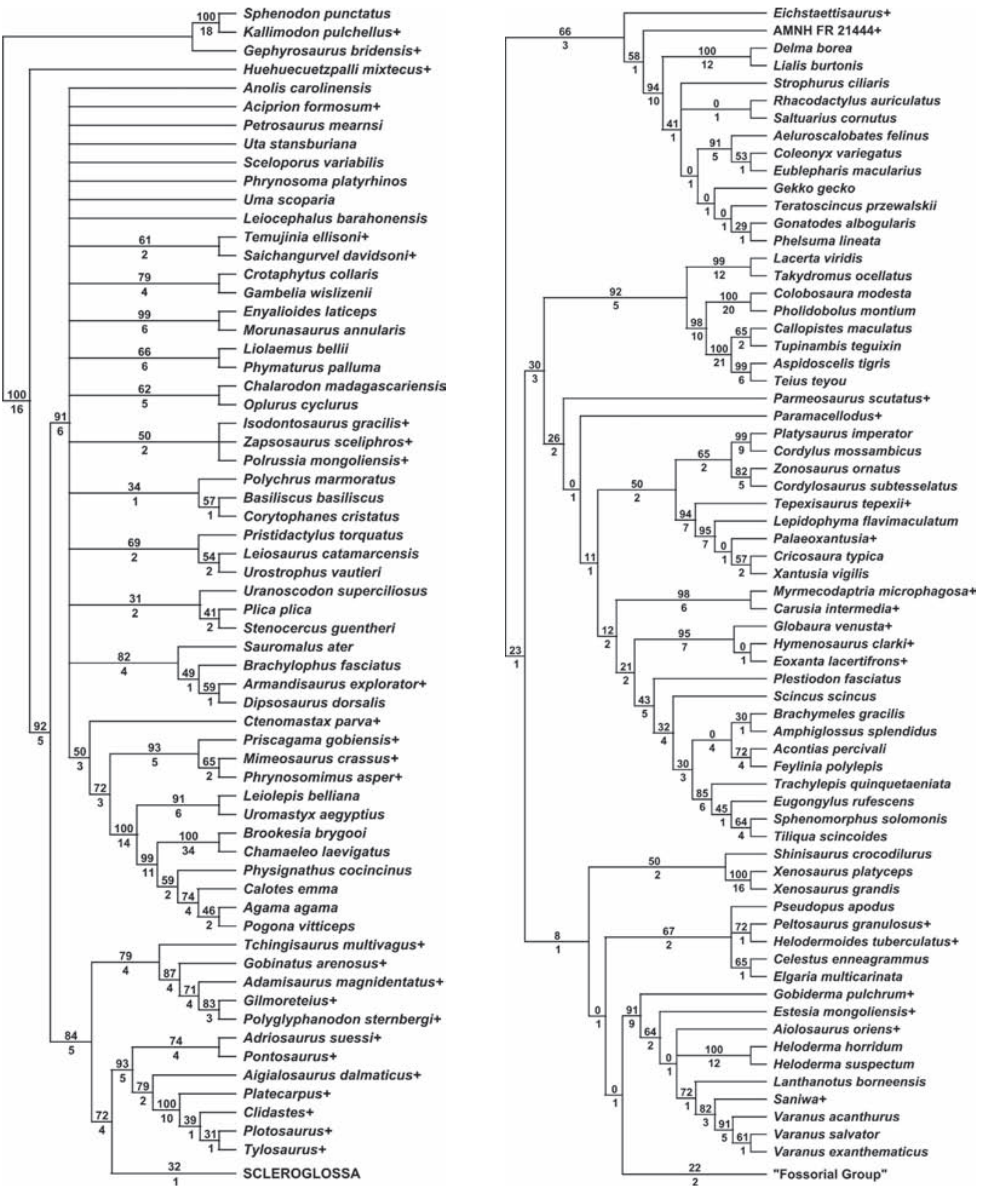

Figure 1. Maximum parsimony strict consensus tree for Squamata. Continued on next page.

displays from 37 to 55 autapomorphies relative to the ancestral lepidosaur.

We normally enforced monophyly of Rhynchocephalia and accordingly did not test that proposition in most analyses. Nevertheless, in a few analyses we simply rooted the resulting tree between ingroup and outgroup species. In that context, as in those based on wider analyses, we can identify 10 unambiguous synapomorphies, one of which (65[1]) is unique and unreversed on our tree (i.e., CI = 1.00), that arose along the deepest known branch on the stem of this clade (see Appendix 4). These include characters associated with a unique masticatory system, including a mobile snout tip and sawing bite, which began to evolve in rhynchocephalians early in the

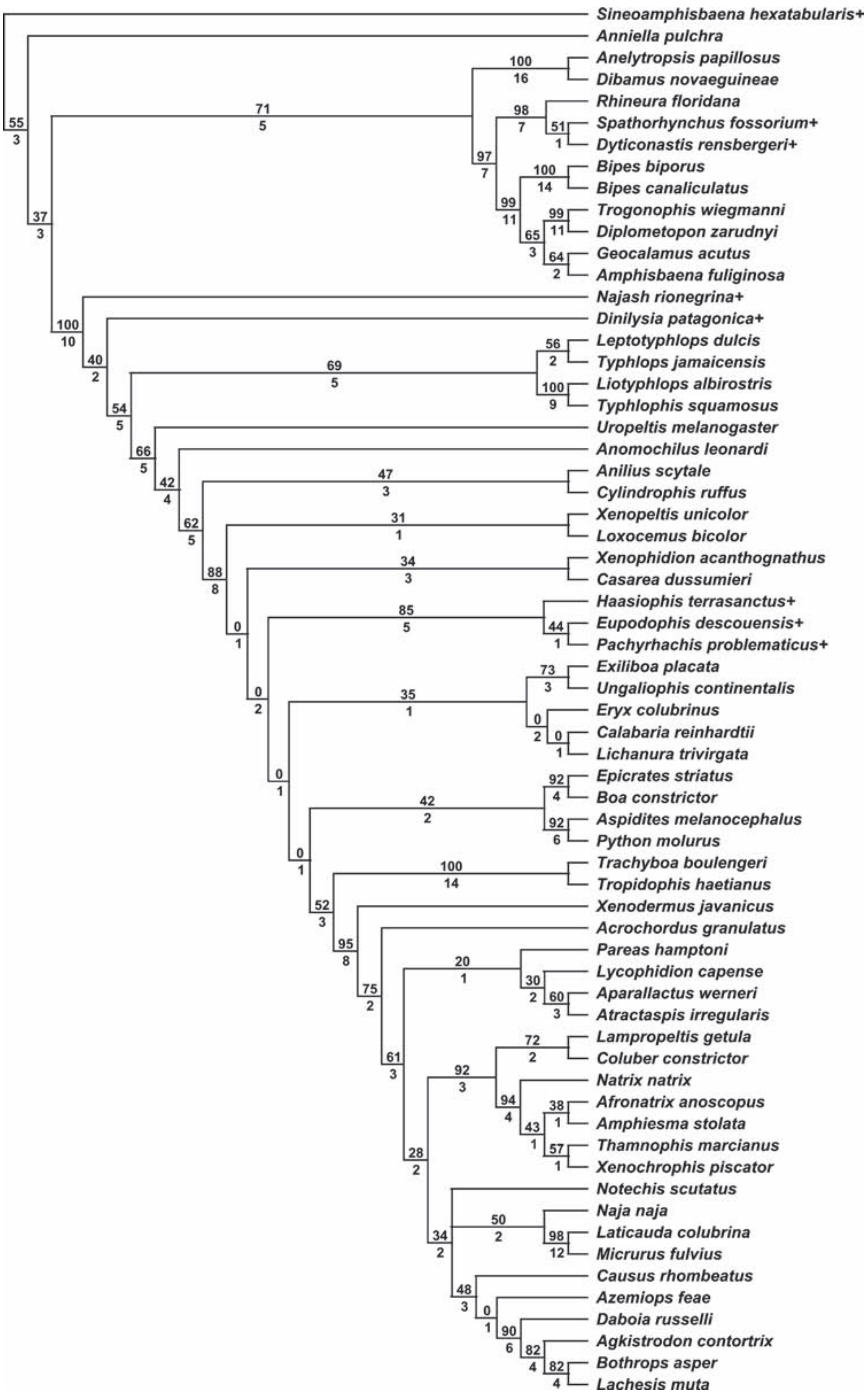

Figure 1 continued. Maximum parsimony strict consensus tree for Squamata.

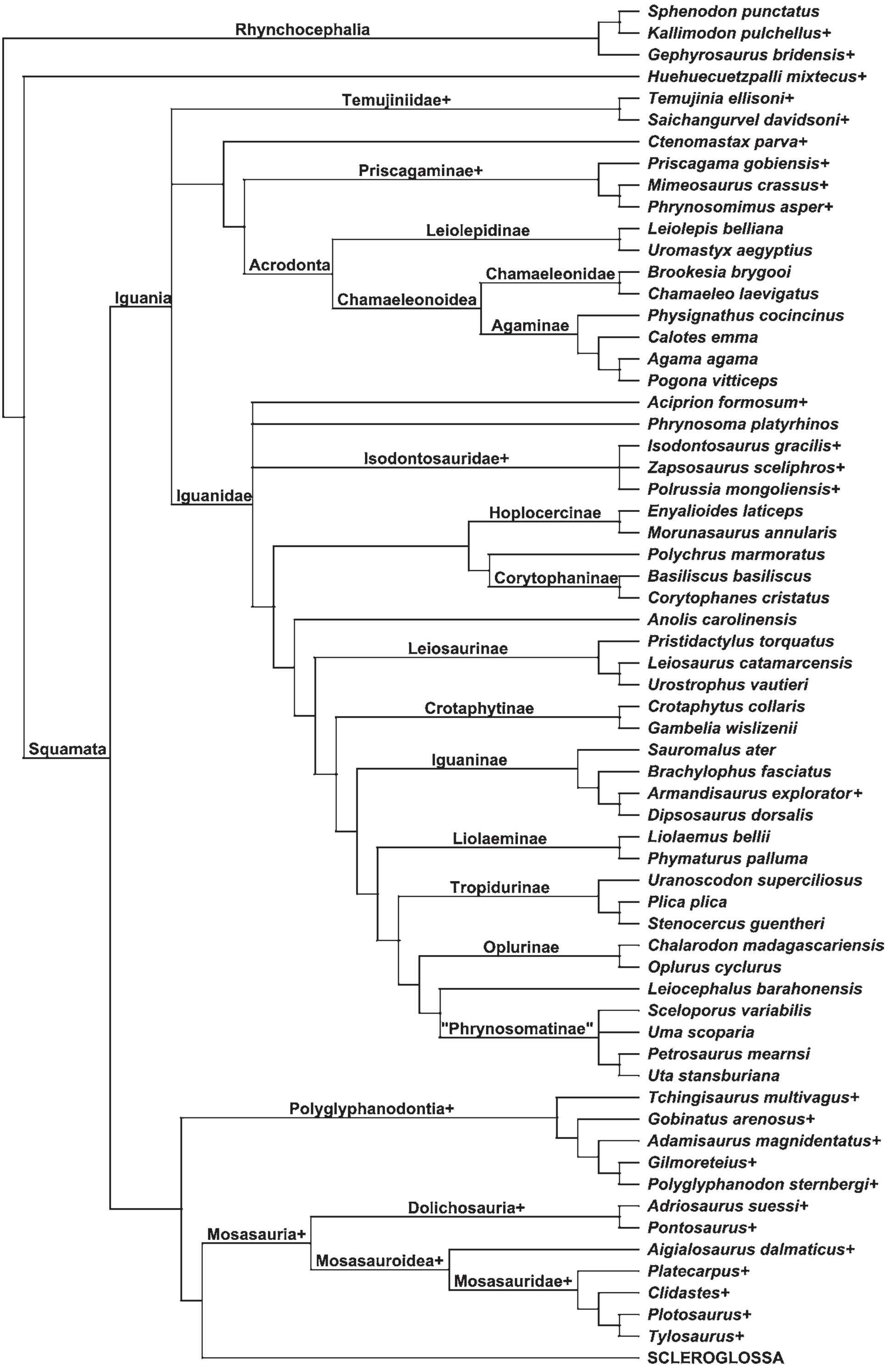

FIGURE 2. Maximum parsimony Adams consensus tree for Squamata. Continued on next page.

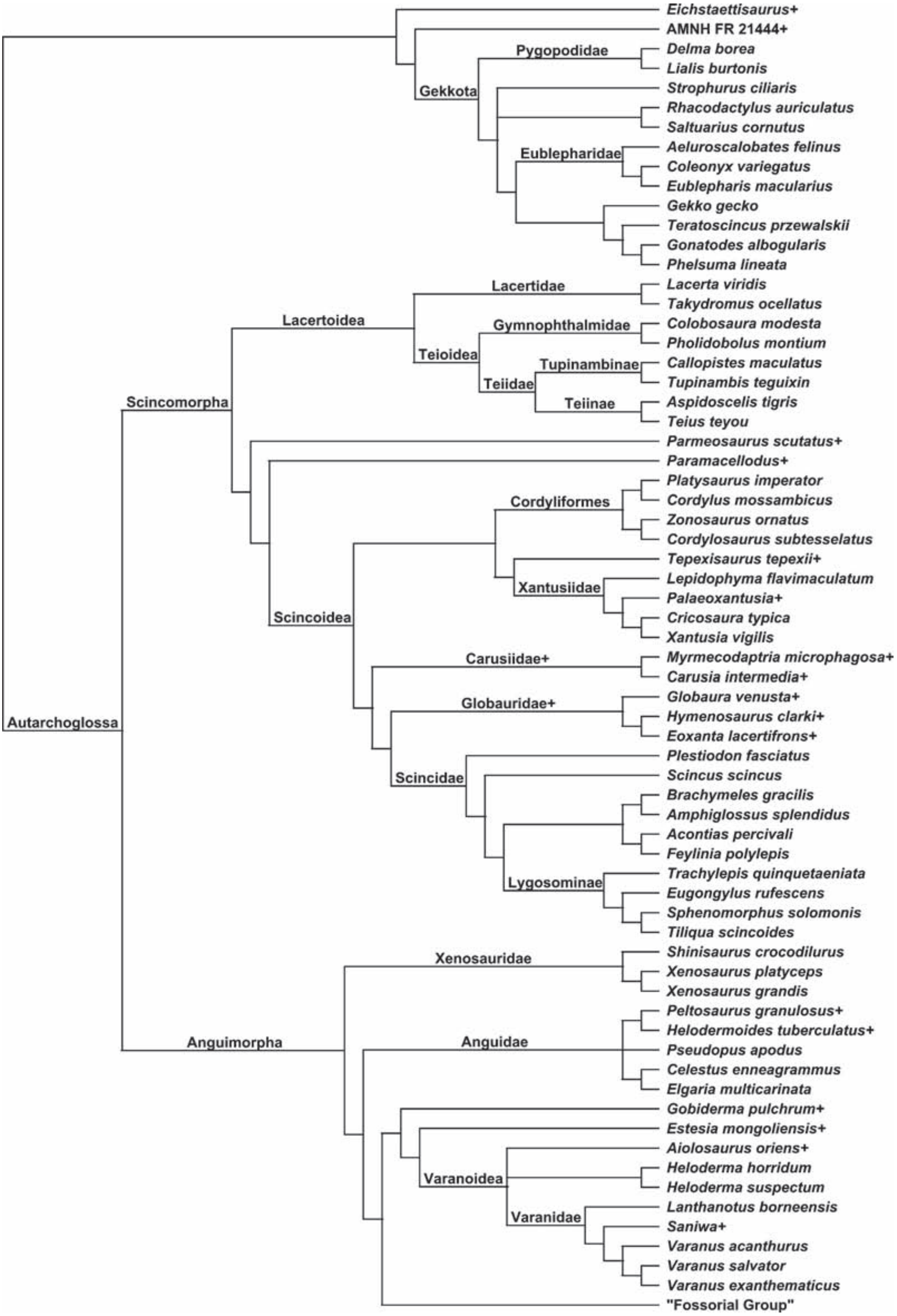

FIGURE 2 CONTINUED. Maximum parsimony Adams consensus tree for Squamata. Continued on next page.

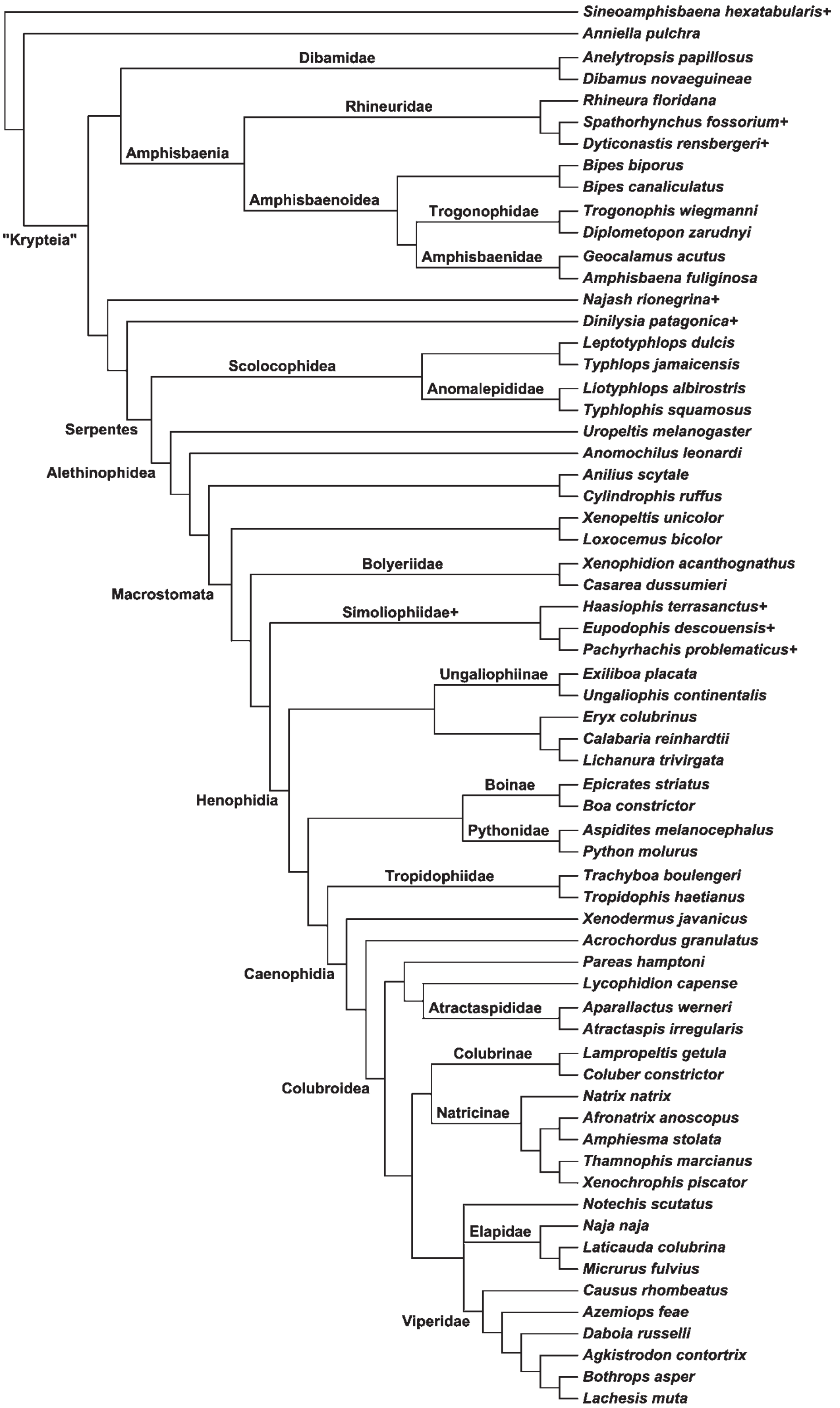

FIGURE 2 CONTINUED. Maximum parsimony Adams consensus tree for Squamata.

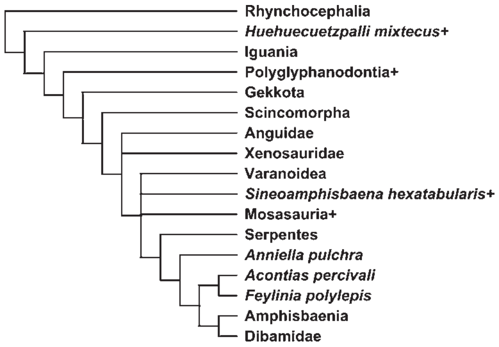

Figure 3. Maximum parsimony majority rule consensus tree from completely unordered analysis of Squamata.

Triassic. We recovered Sphenodontida within Rhynchocephalia, and with strong support (100% BP, 100% PP, 18 BS; 22 unambiguous synapomorphies, including a CI = 1.00 synapomorphy, 65[2]), indicating that Recent *Sphenodon punctatus* shared an ancestor with the Upper Jurassic *Kallimodon pulchellus* that was not also shared by the basalmost rhynchocephalian side branch represented by the Lower Jurassic species *Gephyrosaurus bridensis* (see Appendix 4).

STEM SQUAMATA

Given the antiquity of the squamate stem—which must extend deep into the Triassic—surprisingly few stem fossils can be referred with any confidence to that great branch of the lepidosaur tree. *Huehuecuetzpalli mixtecus*, from the Early Cretaceous of Mexico, seems to be one of these (Reynoso 1998). This species is reasonably well known by the standards of Mesozoic lizard paleontology, as it is represented by two fairly complete skeletons, with some patches of skin impressions, of juvenile and nearly adult individuals. *H. mixtecus* apparently represents an entirely extinct side branch off the squamate stem. All major living clades of lizards—Iguania, Gekkota, Scincomorpha and Anguimorpha—diverged by the Late Jurassic (Estes 1983; Conrad 2008). Albian-age *H. mixtecus* must therefore have been separated from the surviving branch of the lizard tree by anywhere from 25 to 50 million years. Unsurprisingly, it displays several distinctive autapomorphies (see Appendix 4).

Huehuecuetzpalli mixtecus is joined to the lizard crown by 20 unambiguous squamate synapomorphies (100% BP, 100% PP, 16 BS; see Appendix 4). Three of those are unique and unreversed on our tree: 177(1), 181(1) and 295(1). Among these diagnostic characters are many of those involved in the kinetic masticatory system unique to lizards. *H. mixtecus* is, however, also quite primitive in many ways; for example, skin impressions indicate that it retained a mid-dorsal row of spiny scales, a feature diagnostic of lepidosaurs that is retained today only among iguanian lizards and *Sphenodon punctatus* (scleroglossans generally lack the mid-dorsal scale row originally present in Reptilia; Gauthier, Kluge and Rowe 1988). The upper temporal arch of *H. mixtecus* displays a mixture of ancestral and derived traits; the postorbital, for example, still fits into a V-shaped recess on the lateral face of the squamosal as in diapsids ancestrally; in crown lizards, however, the postorbital lies largely dorsal to the squamosal at their articulation (Arnold 1998), with the postorbital terminating on the medial surface, rather than on the lateral face, of the squamosal. The temporal-arch ramus of the lizard squamosal differs further in being rod-like in section, rather than plate-like as in *H. mixtecus* and other diapsids. Its squamosal is nevertheless distinctly lizard-like in having a peg at its posterior tip, on which pivots the mobile (streptostylic) quadrate uniquely diagnostic of crown lizards (Robinson 1967).

CROWN SQUAMATA

Huehuecuetzpalli mixtecus shares a few apomorphies characteristic of (at least some) iguanians, such as fused hourglass-shaped frontal bones and a small subtriangular postfrontal bone confined to the orbital rim (Reynoso 1998). Nonetheless, it seems to lie well outside the lizard crown, because it lacks—so far as it is preserved—the 13 unambiguous synapomorphies that diagnose Squamata (8 CI = 1.00 synapomorphies; 92% BP, 100% PP, 5 BS). There are 59 morphological synapomorphies that distinguish crown Squamata from the last common ancestor of crown Lepidosauria in this analysis (see Appendix 4). Gauthier, Estes and de Queiroz (1988) proposed even more (74) and Estes et al. (1988) added an additional 10, bringing the total to 84 squamate synapomorphies several decades ago. The lower number found here reflects the absence of diagnostic soft anatomical characters not assayed in this analysis. In any case, this morphological "long branch" simultaneously

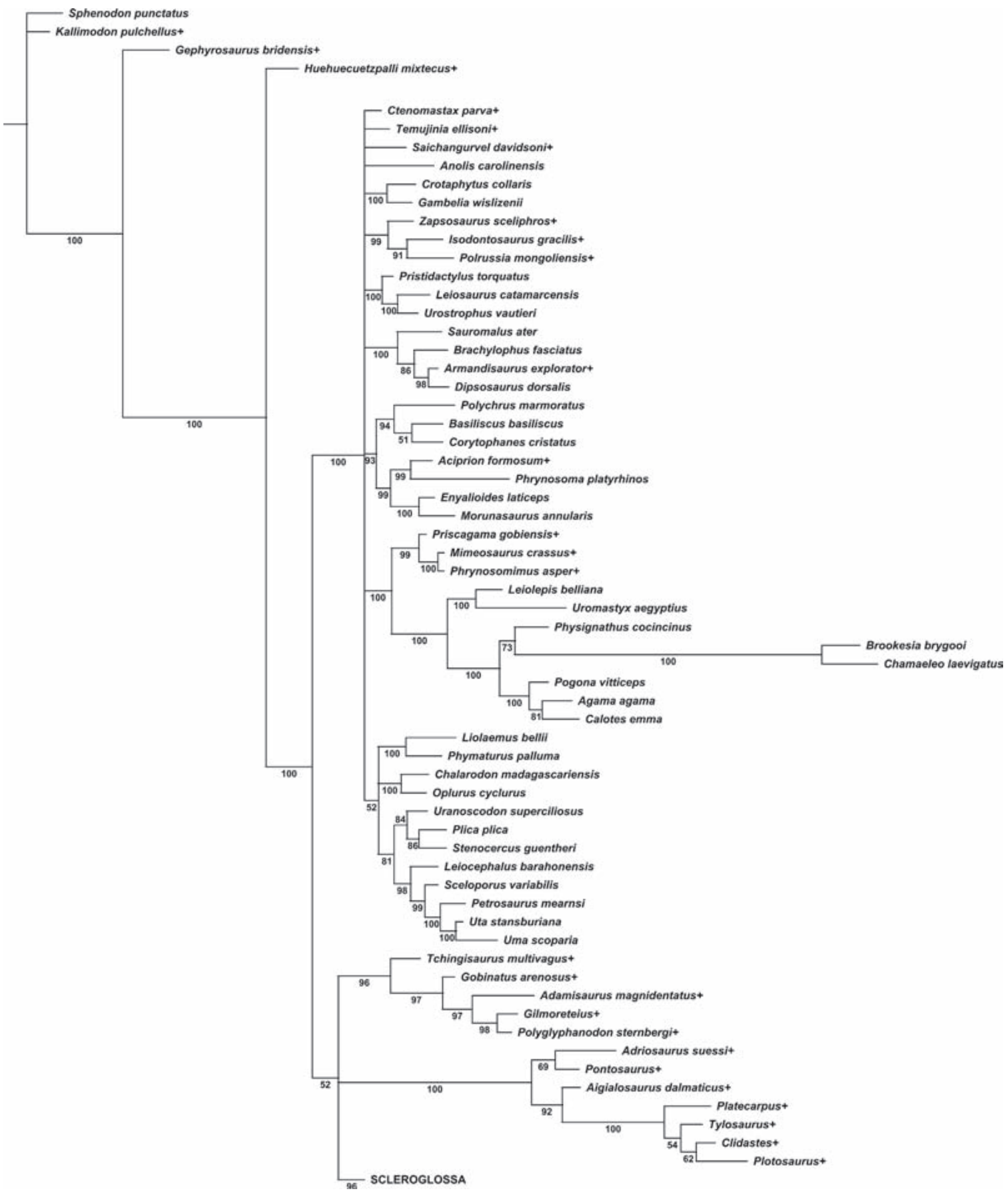

FIGURE 4. Bayesian tree for Squamata. Continued on next page.

underscores our confidence in squamate monophyly while highlighting just how little we know about their evolutionary origins.

CROWN IGUANIA

The earliest diversification of Iguania is poorly resolved in both maximum parsimony (see Figures 1, 2 and 3) and Bayesian (see Figure 4) analyses. As will be argued below, however, at least some of this is due to the excessive influence of two rogue species (*sensu* Nixon and Wheeler 1992). The following discussion of iguanian evolution will therefore be based largely on the Adams concensus tree (see Figure 2).

Smith (2009a) provided the most recent analysis of early divergences within Iguania based on the phenotype. We direct the reader to that publication for an overview of the history of ideas on this seemingly intractable problem in lizard systematics (see also Conrad and Norell 2007;

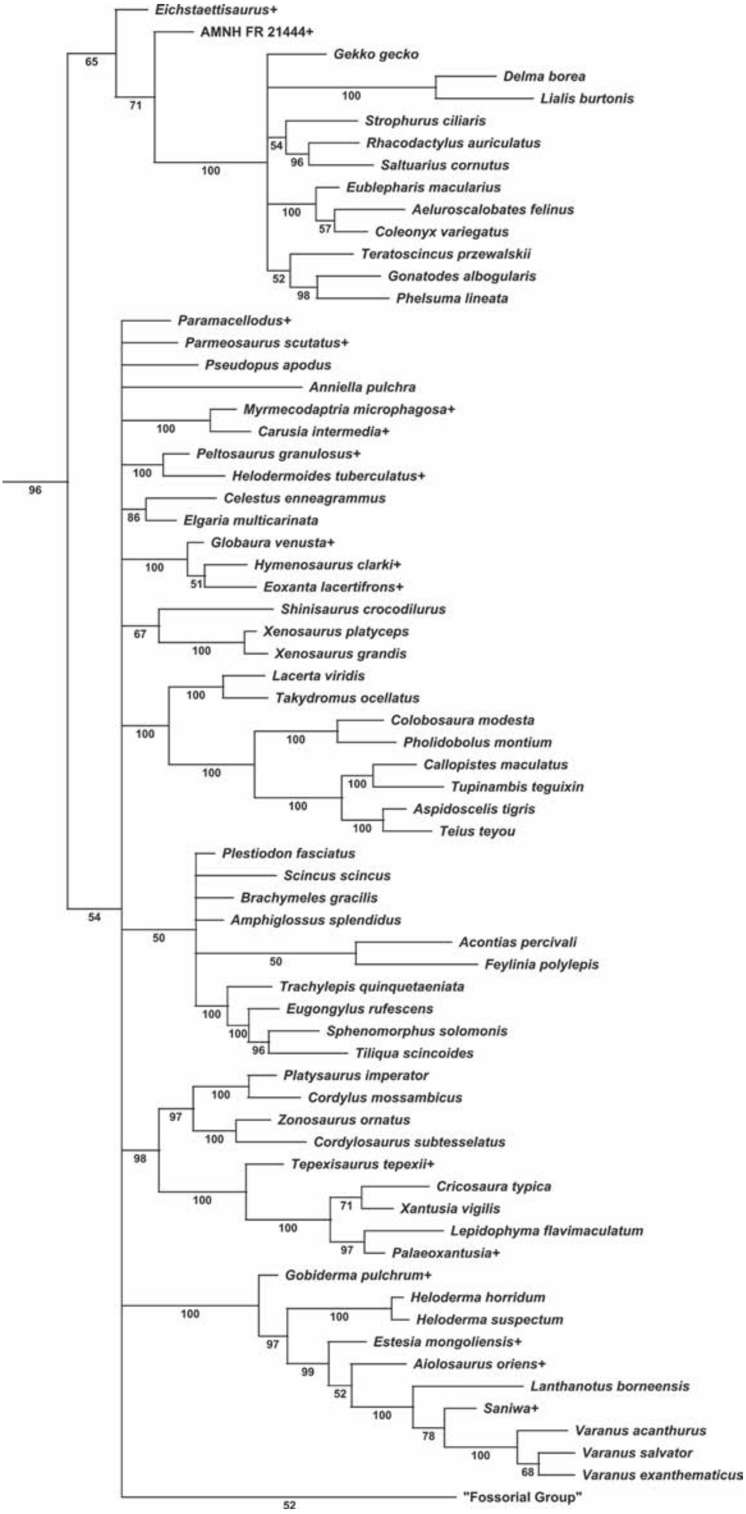

FIGURE 4 CONTINUED. Bayesian tree for Squamata. Continued on next page.

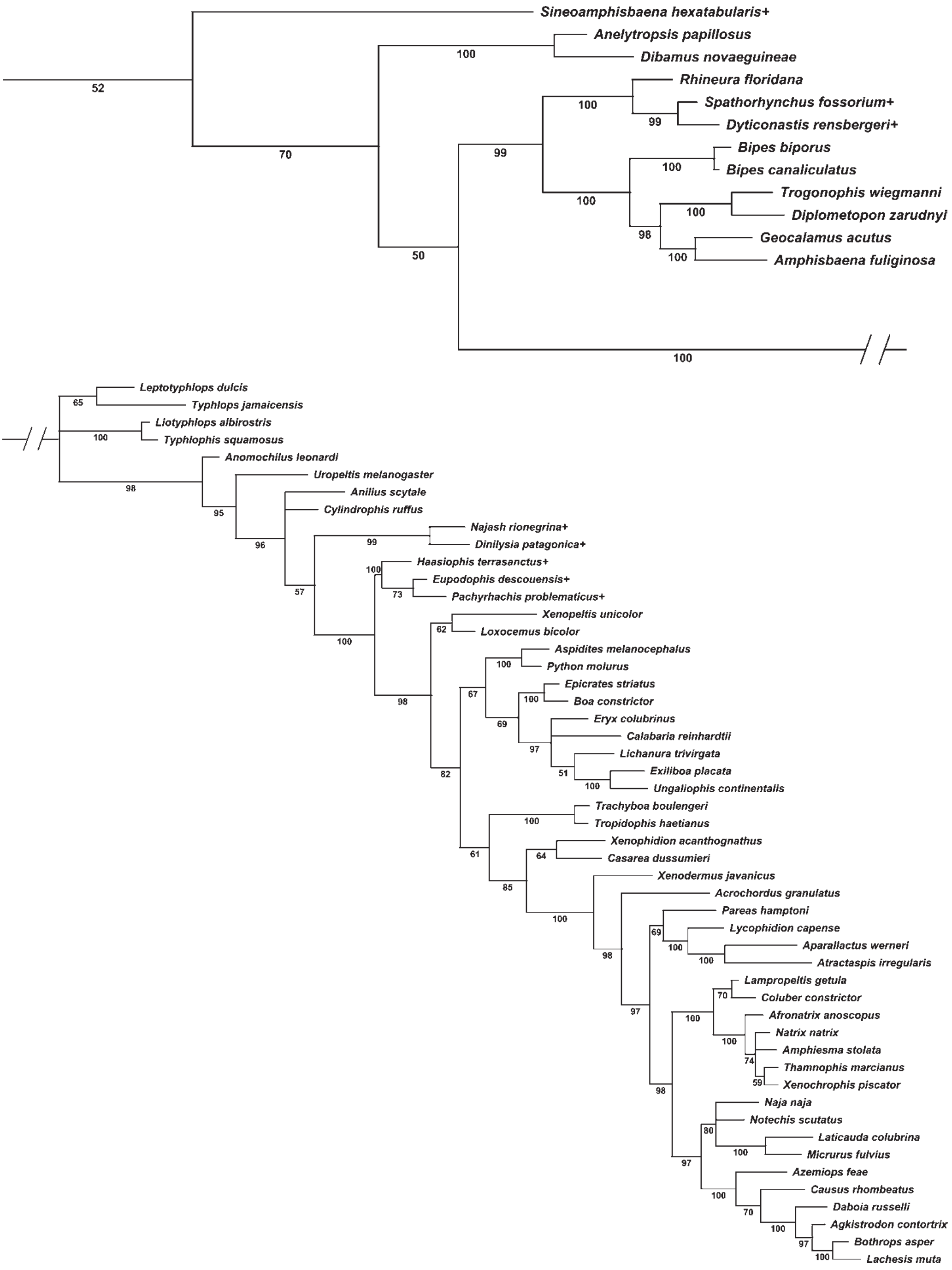

FIGURE 4 CONTINUED. Bayesian tree for Squamata.

Conrad 2008). Smith (2009a) scored 145 parsimony-informative characters for 33 species, including two extinct lizards from the Late Cretaceous, selected for their completeness and capacity to inform ancestral states in Iguania. We scored 46 species, including nine basal forms from the Late Cretaceous. Unfortunately, only 15 species are shared by both datasets, so they cannot be compared directly. Moreover, Smith's (2009a) characters were more disparate than ours, as he derived important data from the literature that were not considered in our analysis. Conrad (2008) looked at a denser sample of Cretaceous species, but many of his terminal taxa were composites, rendering his analysis even less comparable to ours. Nevertheless, these datasets were designed to address the same problem, namely, the Late Cretaceous to early Paleogene radiation of Iguania, a well-supported clade composed of subclades long recognized in morphological datasets, even as relationships among those subclades continue to defy our best efforts to resolve them (e.g., Etheridge 1960; Etheridge and de Queiroz 1988; Frost and Etheridge 1989; Schulte et al. 2003; Conrad and Norell 2007; Conrad 2008; Smith 2009a; see Figures 1 to 4).

Despite that uncertainty, we found 21 unambiguous synapomorphies supporting Iguania, in keeping with the results of all previous phylogenetic analyses (91% BP, 100% PP, 6 BS; see Appendix 4). One of these is a further modification to the lizard kinetic system that is uniquely iguanian: character 79(1), a kinetic joint between the postorbital-squamosal, as evidenced by a loose sutural gap between them that is wider than that between the postorbital and postfrontal, or between the postorbital and jugal (reversed inside acrodontans). Smith (2009a) proposed another synapomorphy for this clade: a coronoid anteromedial process that fits into a sulcus beneath the tooth-bearing border of the dentary below the posteriormost few teeth (and wraps around its ventral margin apically; see our character 388). As Smith (2009a) observed, this character may be of particular importance because, for the first time, it would enable us to justifiably refer isolated dentaries—among the most durable and thus common elements in the lizard fossil record—to an iguanian very near to or within the crown, thereby providing a key calibration point for squamate divergence-time estimation. Smith (2009a) proposed that this character evolved before the iguanian crown did, because he regarded *Saichangurvel davidsoni* as sister to the total-clade including crown Iguania (see also Gao and Norell 2000; Conrad and Norell 2007). In our analysis, however, *S. davidsoni* (and its relative *Temujinia ellisoni*) seems to be the basalmost divergence on the stem of Iguanidae rather than the stem of Iguania (see below). Although we differ in detail, we agree that these Cretaceous fossils are central to further understanding of iguanian phylogenetics, owing to their antiquity and overall plesiomorphic skeletal anatomy.

STEM ACRODONTA

Our conclusion that *Saichangurvel davidsoni* is on the iguanid stem (see below) rests partly on our interpretation of the Late Cretaceous *Ctenomastax parva* (Gao and Norell 2000) as a stem acrodontan (50% BP, 3 BS). *C. parva* shares several apomorphies with Priscagaminae and Acrodonta (see Appendix 4): 419(2) premaxillary tooth count reduced to 4 to 6; 417(1) anterior maxillary fangs that are conspicuously enlarged relative to adjacent teeth; and 436(1), V-shaped wear facets of maxillary teeth impressed on lateral face of dentary between dentary teeth. Gao and Norell (2000) remarked on the seemingly reduced rate of tooth replacement in *C. parva*, another feature commonly associated with “acrodonty” in lepidosaurs (e.g., Robinson 1976).

Although the teeth are technically “pleurodont” in implantation in stem acrodontans, the marginal dentition displays several characters seen only in Acrodonta among lizards. For example, in external view, most of the maxillary dentition is composed of short, subtriangular tooth crowns that diminish in size anteriorly and show little evidence of replacement. As in crown acrodontans (Robinson 1976), new tooth positions are evidently added at the back of the tooth row during ontogeny. That is to say, in *Ctenomastax parva,* as in living acrodontans, the smallest (and oldest) teeth lie anteriorly while the largest (and newest) teeth arise posteriorly as the lizard grows. There is, moreover, a marked transition between this larger dental module and a much smaller module at the front of the maxillary dentition that produces a more or less enlarged set of pleurodont “fangs”; e.g., see figure for character state 120(1). The caniniform teeth in this part of the maxilla may be apomorphic in their size, but they are decidedly plesiomorphic in their more normal columnar shape and more regular pattern of replacement. This suite of characters in the maxillary dentition is unique to Acrodonta (with subsequent loss of maxillary fangs in chameleons).

“Acrodont” dentitions—if one defines them narrowly as having “teeth that lie apically on the tooth-bearing bones" as does Cope (1900)—arose at least four different times on our tree (e.g., Sphenodontida, Acrodonta, Trogonophidae, Macrostomata). However, the stem of Acrodonta in the Late Cretaceous is clearly not "acrodont" in that sense. There are other ways that "acrodont" can be conceptualized; Luan et al. (2009), for example, defined it in terms of tooth–jaw fusion in the absence of attachment bone (which we track indirectly with character 430, "absence of tooth replacement," to which this feature is said to be related causally). Perhaps the term "acrodont" should be avoided until a consensus is reached on this point.

In any case, caution should be exercised when referring isolated tooth-bearing bones from deep in the Mesozoic to crown Acrodonta (and thus to the iguanian and squamate crowns) solely because they have "acrodont" teeth. A distinct caniniform region on the maxilla could be more definitive, especially as it arose along the acrodontan stem long before the fully developed dental anatomy characterizing the acrodontan crown. The earliest examples of maxillae with these features are currently known only from the Paleogene of Laurasia (Early Eocene of Europe [Delfino et al. 2008] and North America [Smith 2009b]). That being said, the presence of two successive sisters to crown Acrodonta in the Upper Cretaceous of Asia indicates an earlier history for its stem that is only beginning to come to light.

We agree with Smith (2009a) that Mongolian Cretaceous Priscagaminae (93% BP, 99% PP, 5 BS) *sensu* Borsuk-Bialynicka and Moody (1984), including *Phrynosomimus asper* (see also Conrad 2008), constitutes a clade that is sister to crown Acrodonta (see also Frost and Etheridge 1989). Priscagamines and acrodontans share six apomorphies (72% BP, 100% PP, 3 BS) that remain plesiomorphic in *Ctenomastax parva* (see Appendix 4).

CROWN ACRODONTA

The crown clade Acrodonta (Cope 1864) has always been well-supported in morphology (e.g., 100% BP, 100% PP, and 14 BS in the present analysis) and more recently in gene sequences (e.g., 100% BP and 100% PP in Okajima and Kumazawa 2010), as well as in analyses combining morphology and molecules (e.g., Schulte et al. 2003). We recognize 26 synapomorphies as diagnostic of crown acrodontans relative to Priscagaminae, with an additional nine separating their ancestor from that shared with *Ctenomastax parva*, and yet another 11 synapomorphies separating the currently known base of the acrodont stem from the last iguanian ancestor. Thus, crown Acrodonta can be diagnosed by 46 unambiguous synapomorphies, one of which—266(1)—is unique and unreversed on our tree, relative to the last ancestor it shared with crown Iguanidae (see Appendix 4). Diversification at the very base of the iguanian crown was apparently well under way before the Campanian in the Upper Cretaceous of Asia.

CROWN LEIOLEPIDINAE

Moody's (1980) proposal that *Leiolepis* and *Uromastyx* are remnants of one of the most ancient clades within Acrodonta finds additional support in our analysis from 14 unambiguous synapomorphies (91% BP, 100% PP, 6 BS), including: 82(2), postorbital jugal ramus reduced, not reaching ventral to level of quadrate head; 147(1), jugal laps over external suborbital margin of maxilla (CI = 1.00); 204(1), presence of septomaxilla lateral flange; 420(2), maxillary tooth count reduced to 7 to 15 teeth; 424(1), marginal teeth fused to each other; 439(1), basihyal ventral to braincase; 482(1), sternal fontanelle double; 484(1), xiphisternum lost; and 572(0), dermal skull bones smooth (see Appendix 4 for complete list).

Conrad (2008) relied on a composite *Uromastyx* and Smith (2009a) used only *Leiolepis belliana* as terminal taxa, so these datasets did not test Moody's (1980) hypothesis. Although typically placed near the base of the acrodontan tree in analyses of gene sequences, there is little consensus and generally poor support for alternative placements of *Uromastyx* and *Leiolepis*. For example, the maximum parsimony analysis of Schulte et al. (2003) placed *Uromastyx acanthinurus* with *Hydrosaurus* sp. as sister to all other Agaminae, whereas *Leiolepis guentherpetersi* + *Leiolepis belliana* were placed inside Agaminae. Their maximum likelihood analysis, on the other hand, placed these species, as well as the chameleons, inside Agaminae but not with one another as a monophyletic Leiolepidinae; those alternatives were, however, poorly supported. More recently, Okajima and Kumazawa (2010) analyzed complete mitochondrial genomes to argue that *Leiolepis guttata* was closer to Agaminae than was *Uromastyx benti*, albeit in only 58% of maximum likelihood bootstrap replicates. We tentatively accept leiolepidine monophyly, though basal acrodont divergences are not broadly supported across datasets, and require further scrutiny.

CROWN CHAMAELEONOIDEA (*TAXON NOVUM*)

Perhaps the most noteworthy result in our analysis of iguanian phylogenetics is the inferred sister relationship between Chamaeleonidae and Agaminae (100% BP, 100% PP, 11 BS) to the exclusion of Leiolepidinae (see Appendix 4). We propose "Chamaeleonoidea" (*taxon novum*) for this clade; it is supported by 16 unambiguous synapomorphies, three of which are unique and unreversed on our tree (marked by an asterisk), such as: 81(1)*, a postorbital—ectopterygoid contact; 78(3), a squamosal that lies in a trough beneath the postorbital; 139(1)*, an enlarged lacrimal foramen; 284(1)*, ectopterygoid posterior process extends past coronoid apex; 412(1), premaxillary teeth that are distinctly smaller than the maxillary teeth; 442(0), the loss of free epibranchials in the hyoid; and 489(1), a tall and narrow scapula. Schwenk and Bell (1988) also suggested that the ability to project the entire tongue, and not just the foretongue, out of the mouth during prey capture might be diagnostic not just of chameleons, but of all chamaeleonoid acrodontans.

Conrad (2008) did not recover this topology; indeed, his analysis yielded a novel arrangement in which Chamaeleonidae is nested well inside the clade we refer to as Agaminae. Smith's (2009a) maximum parsimony analysis agreed with our findings, but his Bayesian analysis did not (i.e., *Leiolepis belliana* [Leiolepidinae] joined the chameleon *Brookesia superciliaris* [Chamaeleonidae] as sister to Agaminae). With Bremer supports of "1" at best, and bootstrap values always less than 50%, neither Conrad (2008) nor Smith (2009a) provided a compelling case for early divergences within Acrodonta. Further testing of ideas about the character concepts involved, as well as their proposed distributions across acrodontans and outgroups, awaits integration of their morphological data with our own.

Molecular-based trees seem equally discordant and poorly supported, although Okajima and Kumazawa (2010) recently analyzed whole mitochondrial genomes from 12 disparate chameleon and nine nonchameleon acrodontan species and found strong support (100% BP, 100% PP) for the traditional acrodontan classification in which *Leiolepis guttata, Uromasyx benti* and Agaminae are united to the exclusion of Chamaeleonidae. Wiens et al. (2010) recovered the same topology in a Bayesian analysis of their molecular and combined datasets. But they also recovered the opposite topology—viz., our Chamaeleonoidea—in parsimony analyses of the same two datasets. Combining their genotypic with our phenotypic data may help to resolve this apparent conflict.

CROWN AGAMINAE

The diverse and widespread clade to which we restrict "Agaminae" emerged as one of Moody's (1980) key insights into acrodontan systematics. The clade has a unique (CI = 1.00) epiotic foramen in the braincase (our character 304[1]) that is present universally among agamids and found nowhere else among amniotes (Bell et al. 2009). We identified additional support for this clade, including three CI = 1.00 synapmorphies (marked by an asterisk): 107(1)*, a vertical lappet of the parietal that extends laterally to overlap the postorbital and form the anteromedial margin of the upper temporal fenestra; 154(2), a broad contact between the jugal and the squamosal; 344(1), a medial aperture of the recessus scala tympani that lies entirely within the opisthotic; 390(0), a coronoid restricted to the medial aspect of the mandible; and 407(1)*, retroarticular process slopes posterodorsally to the tip. Support indices for this clade are surprisingly weak, however, as it appears in only 59% of bootstrap replicates and with a Bremer support of 2 in our maximum parsimony analyses. It is not recovered in the Bayesian analysis (see Figure 4). This circumstance appears to reflect the highly modified anatomy of its sister clade, the Chamaeleonidae (i.e., see 73 autapomorphies in Appendix 4), which hinders placement of apomorphies relevant to the diagnosis of Agaminae.

As noted above, Conrad (2008) did not recover this clade, but his alternative topology was also poorly supported. Smith (2009a), on the other hand, recovered Agaminae with good support in both maximum parsimony (78% BP) and Bayesian analyses (92% PP). Analyses of mitochondrial sequence data seem equally problematic. Macey et al. (Macey, Schulte and Larson 2000; Macey, Schulte, Larson, Anajeva et al. 2000) found very modest support for Agaminae (61% BP), but that clade was not recovered by Schulte et al. (2003, albeit with a poorly supported alternative hypothesis). Nevertheless, Okajima and Kumazawa's (2010) analyses of entire mitochondrial genomes revealed strong support for Agaminae (100% BS, 100% PP), albeit with limited taxon sampling. Data from the nuclear genome may help adjudicate this point.

Within Agaminae, we found nine synapomorphies (74% BP, 100% PP, 4 BS; see Appendix 4) supporting a subclade containing the vast majority of Old World acrodontans (more than 400 species). That subclade does not include the apparently basal Australasian species represented here by *Physignathus cocincinus* (removing chameleons to counter the influence of uncertainty caused by evolutionary transformation increases support for *P. cocincinus* being basal to other agamines to 83% BP, as predicted by our tree; see Figures 1 to 4). This subclade is represented in our analysis by examplars from the major agamine radiations in Australia (*Pogona vitticeps*), in the tropics of eastern Asia (*Calotes emma*), and across more arid reaches of southern and western Asia and then into Africa (*Agama agama*). These three agamine radiations regularly emerge in analyses using mitochondrial gene sequences (e.g., Macey, Schulte and Larson 2000; Macey, Schulte, Larson, Anajeva et al. 2000; Schulte et al. 2003; Okajima and Kumazawa 2010), even though relations among the earlier-diverging crown acrodontans (such as *Physignathus*, chameleons and leiolepidines) remain more ambiguous.

We agree with Raxworthy et al. (2002) and Hugall and Lee (2004) that it is unlikely that the geographic distribution of any crown acrodontans reflects the breakup of Pangaea (Macey, Schulte, Larson, Anajeva et al. 2000). On the contrary, they appear Laurasian in origin because two acrodontan stem-clades were in Asia during the Upper Cretaceous, where the sister to all other crown acrodontans, the Leiolepidinae, still lives today (except for a few species of *Uromastyx* in North Africa).

STEM IGUANIDAE

TEMUJINIIDAE (*TAXON NOVUM*)

The spectacular skeleton of *Saichangurvel davidsoni* (Conrad and Norell 2007) and several fairly complete crania referred to *Temujinia ellisoni* (Gao and Norell 2000) seem to comprise a clade diagnosed by two synapomorphies (61% BP, 2 BS): 160(1), squamosal extends anterior to level of epipterygoid, and 165(1), squamosal ascending process absent. Both characters display a very modest degree of homoplasy within the squamate crown. Nevertheless, this pair of changes in squamosal form does not co-occur elsewhere in Squamata. With so few characters at play, the Bayesian analysis naturally left their relationships unresolved at the very base of Iguania. *S. davidsoni* and *T. ellisoni* are without doubt the most important paleobiological discoveries in iguanian evolution, rivaled only by *Huehuecuetzpalli mixtecus* for the potential to illuminate the very root of the squamate tree.

This clade, hereafter referred to as Temujiniidae (*taxon novum*), may lie on the iguanid stem, rather than the iguanian stem as generally thought (Conrad 2008; Smith 2009a). Given that these Cretaceous species are very primitive overall, and that they lie very near to the root of the iguanian crown in any case, the dearth of potential synapomorphies supporting one or the other hypothesis is perhaps to be expected. We found only two that might serve to support our hypothesis that Temujiniidae is related to crown Iguanidae: 372(1), the upper and especially lower borders of Meckelian canal at mid-dentary approach closely to restrict that canal in front of a reduced splenial, and 470(2), caudal autotomic septum posterior to caudal rib.

The second potential synapomorphy is problematic on two counts: first, acrodontans do not have fragile tails, so we must await the discovery of stem species still retaining this feature to justify conclusions about where a particular position for the fracture plane arose in the iguanian tree. Second, nearly every permutation of fracture-plane position exists among iguanians today, so our optimization requires a firm grasp of ingroup relationships that we do not yet possess.

Our argument for constriction of the Meckelian sulcus on the dentary just anterior to the splenial (and concomitantly "reduced anterior extent of the splenial") stands on firmer footing. The dentary of *Temujinia ellisoni* is distinctly more like that characteristic of Iguanidae in this respect, whereas the dentary in the stem acrodontans *Priscagama gobiensis,* and to a lesser extent *Ctenomastax parva,* still retain a relatively unconstricted Meckelian sulcus (and an accordingly longer overlying splenial bone). Even considering subsequent modification within crown iguanians during the past 65 million years, this particular morphology is otherwise present only in crown Iguanidae among iguanians. Weakly supported, that tree topology emerges only sporadically in our analyses (e.g., when the rogue species *Sineoamphisbaena hexatabularis* is removed; see below), so we tentatively accept that Temujiniidae is the deepest known divergence off the stem of crown Iguanidae.

It may be noteworthy that in a 50% majority-rule consensus tree resulting from a completely unordered analysis, Temujiniidae is sister to all Iguania, rather than being on the iguanid stem. The key to this problem may lie in the interpretation of the anatomy of the postorbital and postfrontal bones among transformed living clades (e.g., chameleons) and incomplete fossils (e.g., isodontosaurids). That Temujiniidae might be on the stem of Iguania (Smith 2009a), rather than on the stem of Iguanidae, strikes us as a reasonable alternative hypothesis while these questions remain open.

Isodontosauridae

Our analysis identified five unambiguous synapomorphies that seem to unite three poorly known species from the Late Cretaceous of Mongolia *Isodontosaurus gracilis*, *Polrussia monogoliensis* and *Zapsosaurus sceliphros* (see Appendix 4). This putative clade is poorly supported in maximum parsimony analyses (50% BP, 2 BS), but strongly supported in Bayesian (99% PP). Moreover, Conrad and Norell's (2007) study yielded very different results, with *I. gracilis* outside Iguania, and *P. mongoliensis* and *Z. sceliphros* at markedly different, if still peribasal, positions within Iguanidae. Nevertheless, we find several of the characters supporting Isodontosauridae compelling, including: 59(1), frontoparietal fontanelle remains open in the adult (the presence of a frontoparietal fontanelle late in skeletal ontogeny is an apomorphy present in all crown iguanians; Maisano 2001); 245(1), infraorbital canal entirely within palatine; 399(1), surangular adductor fossa deep and extending more than half way down (nearly to the angular bone) on the external face of the mandible; and 572(0), loss of rugosities on dermal skull bones. We accordingly use "Isodontosauridae" (Alifanov 1993) to designate this clade.

No clear stem iguanians are known even though 22 synapomorphies suggest a long branch. Although the two crown clades are typically New and Old World in distribution today, our analysis indicates that Iguania is Asian in origin. Crown Iguanidae does indeed seem to be exclusively New World (North American, originally). However, all successive sister clades—Isodontosauridae, Temujiniidae, and Pan-Acrodonta—are Asian (i.e., Mongolian), suggesting that stem iguanids invaded the New World from Asia after the end-Cretaceous mass extinction. The rapid subsequent radiation and spread across the New World of iguanids—reaching Brazil by the Late Paleocene (Estes and Price 1973)—could explain why relationships among the familiar iguanid subclades have been so difficult to unravel from the perspective of nearly 65 million years later.

CROWN IGUANIDAE (OR PLEURODONTA)

Missing data in stem fossils, as well as some character conflict exacerbated by poor resolution of iguanid ingroup relationships, render diagnosis of crown Iguanidae problematic (see Figures 1 to 4). Indeed, most of the 112 alternative trees for all Squamata stem from this basal polytomy. Although problems with character discordance are real enough, the more resolved Adams consensus (see Figure 2) suggests that two exemplar species from crown Iguanidae play outsized roles in this conundrum: the extinct species *Aciprion formosum* and the extant species *Phrynosoma platyrhinos*.

Both are missing a lot of data, but for very different reasons. The fossil could be especially helpful because it is so primitive and would therefore root deep in the tree, thereby affording a clearer picture of ancestral states at key points in iguanid phylogeny. Unfortunately, the best specimen for this species is a single, incomplete, and badly fractured skull (The Deep Scaly Project 2011).

Although the latter species is very well known, it contributes even more uncertainty to this analysis owing to its highly modified morphology (e.g., 51 autapomorphies for *Phrynosoma platyrhinos*; see branch length in Figure 4). Removing either rogue species moves Temujiniidae to the iguanid stem from the less resolved basal trichotomy in the Adams consensus.

At this point, we would only call attention to two internested nodes within Iguanidae that we will refer to as the "iguanine" node and the "spiny lizard" node. Although poorly supported statistically, they have interesting sets of shared apomorphies with relatively low levels of homoplasy (on any of the published iguanid trees). The "iguanine" node, which contains iguanines and hoplocercines, plus the spiny lizards, is supported by two striking synapomorphies: 80(1), a mobile joint between the postorbital and the skull roof, in which the postorbital barely underlaps the parietal at the frontoparietal suture, and 246(1), a palatine foramen that enters the palatine dorsally toward its anterior end to pass anteroventrolaterally into the infraorbital canal. The "spiny lizard" node, which includes oplurines, liolaemines, *Leiocephalus*, tropidurines and phrynosomatines, shares those two apomorphies, as well two additional unambiguous synapomorphies (albeit more variable in distribution): 258(2), pterygoids broadly separated at their palatal bases, but only moderately separated anteriorly; and 468(1), reduced zygosphene-zygantrum intervertebral articulations.

In a 50% majority rule consensus of a completely unordered analysis of our dataset, there is weak indication of two (or three) major groups within Iguanidae that are broadly consistent with those emerging from the more detailed study of Smith (2009a). One potential clade includes the corytophanines, polychrotines and leiosaurines. The other contains most of the living iguanids, including what may be three additional subclades: iguanines + hoplocercines; oplurines + liolaemines; and *Leiocephalus* + tropidurines + phrynosomatines.

The position of crotaphytines is more problematic in our view; this clade could be sister to all other crown iguanids, or root along the base of one of the deeper iguanid subclades outlined above, but particularly the "iguanine node."

Some problems in phylogenetics may be hard to resolve from the perspective of survivors in the present biota, especially if these species diverged rapidly and long ago; basal iguanid phylogeny may be one of these. Distinctive and long-recognized subclades in the New World (with long-distance dispersals from the Americas to Madagascar and Fiji) are unknown among well-studied lizard faunas in the Upper Cretaceous of the western interior of North America. But they differentiated rapidly and became abundant there during the Paleogene, with a few acrodontan and iguanid species dispersing across the North Atlantic at the Paleocene–Eocene Thermal Maximum (e.g., Conrad 2008; Smith 2009a, 2009b, 2011), apparently after stem iguanids dispersed to North America from Asia following the Cretaceous–Paleogene (K–Pg) mass extinction.

STEM SCLEROGLOSSA

We found mixed support values (84% BP, 52% PP, 5 BS) for the sister clade to Iguania. It is composed of one extant clade (Scleroglossa) plus two extinct clades (hereafter referred to as "Polyglyphanodontia" and "Mosasauria"; see below). Support for the known total group of Scleroglossa (Pan-Scleroglossa) is strong in the maximum parsimony analyses, but weak in the Bayesian analysis; nevertheless, one synapomorphy—437(1)—is unique and unreversed on our tree. Polyglyphanodontians and mosasaurians are two entirely extinct lizard clades that, to our surprise, appear as stem scleroglossans in this analysis, rather than as parts of the scleroglossan crown as widely thought. If correct, then (at least) half the basal cladistic diversity of the squamate crown extant in the Mesozoic—viz., Iguania, Polyglyphanodontia, Mosasauria and Scleroglossa—did not survive the K–Pg boundary. As we discuss below, however, relationships among the latter three clades, especially the position of mosasaurians, are not as clearcut. In our all-species maximum parsimony analysis, mosasaurs are closer to crown scleroglossans (72% BP, 4 BS) than are polyglyphanodontians, but crown Scleroglossa is poorly supported (32% BP, 1 BS). The opposite situation obtains in the Bayesian analysis, as stem Scleroglossa is only weakly supported, whereas support for crown Scleroglossa is strong (96% PP).

We identify nine unambiguous synapomorphies, one of which—38(1)—is unique and unreversed on our tree, that join these three clades to the exclusion of Iguania (see Appendix 4): 39(1), frontal subolfactory process depth 43% to 53% of distance from skull roof to palatine; 83(1), postorbital–jugal joint kinetic, with jugal reduced to no more than a tab-like dorsal tip that lies distal to the postorbital (CI = 1.00); 114(3), maxilla facial process enlarged (facial process more than 37% of maxilla length); 205(1), septomaxilla medial flange present; 250(2), choanal fossa extends about half way back on palatine; 305(1), alar process of prootic present; 455(2), at least 26 presacral vertebrae; 507(1), interclavicle anterior process present; and 555(1), tibia distal epiphysis notched for astragalo-calcaneum articulation.

Note that the ancestral iguanian is uniformly plesiomorphic for these features. As in diapsids generally, all iguanians in our analysis, including the Cretaceous fossils where known, retain state 0 for characters 83, 205, 305 and 555. One can, however, occasionally find examples of a particular scleroglossan trait arising independently among today's 1,025 living species of iguanians (as of 1 August 2011 [Uetz 1995–2011]). But these occurrences are rare, scattered and can in no case be regarded as ancestral for Iguania.

State 1 of character 39, for example, appears independently in the crotaphytine *Gambelia wislizenii* and the leiosaurine *Pristidactylus torquatus*, and in an even more derived state 3 in the liolaemine *Liolaemus belli*. State 3 of character 114 is also present in the iguanine *Brachylophus fasciatus* and the polychrotine *Anolis carolinensis*. A more derived state 3 of character 250 is present in the leiolepidine acrodontan *Uromastyx aegyptius* and in the polychrotine iguanid *Polychrus marmoratus*. State 2 of character 455 also appears independently in the polychrotine *Polychrus marmoratus*. Finally, state 1 of character 507 is present in crown acrodontans, and it appears independently in *Leiocephalus barahonensis* and in the tropidurine *Stenocercus guentheri*.

POLYGLYPHANODONTIA

Extinct Polyglyphanodontia (Alifanov 2000) in our analysis—possibly including *Sineoamphisbaena hexatabularis,* but certainly including *Tchingisaurus multivagus*, *Gobinatus arinosus*, *Adamisaurus magnidentatus*, *Gilmoreteius* (= *Macrocephalosaurus*) spp. and *Polyglyphanodon sternbergi*—is well supported (see eight unambiguous synapomorphies in Appendix 4; 79% BP, 96%PP, 4 BS). *P. sternbergi* from the Campanian of North America is nested well inside this fundamentally Asian clade of lizards. Unlike the case with iguanians, in which isolated scleroglossan apomorphies can appear sporadically, all our polyglyphanodontian exemplars share all of the classic scleroglossan features so far as they are preserved (see Appendix 4). These include: 305(1), a prootic alar process of the braincase; 455(2), the addition of at least two more vertebrae to the presacral column; and 555(1), the characteristic ridge-and-groove joint between the tibia and ankle (i.e., astragalus).

We find, however, that polyglyphanodontians also lack several other apomorphies associated with crown Scleroglossa (that are also present in mosasaurians; see below and Appendix 4). These include the following: 83(2), jugal tapers smoothly to apex and is joined loosely to the postorbital (forming a mobile joint unique and unreversed in scleroglossans); 285(2), ectopterygoid dorsal process absent; 360(2), pronounced subdental gutter; and 394(1), coronoid anterolateral dentary process present.

Perhaps most important, polyglyphanodontians still possess an ascending process on the squamosal, unlike the ancestral scleroglossan in which that process was lost (165[1]). This primitive feature is retained by all iguanians (except temujiniids), in the squamate stem species *Huehuecuetzpalli mixteca* and all Rhynchocephalia. In what seems to be an artifact of sampling, however, character 165 is equivocal on the shortest tree. That is because mosasaurians are sister to scleroglossans in our analysis, and they display both states. Dolichosaurs have scleroglossan state 1, the classic "hockey-stick" shaped squamosal of Robinson (1967), and so do some basal examples of their sister clade, the mosasauroids. Unfortunately, the basal species that was included, *Aigialosaurus dalmaticus*, cannot be scored for this character with any confidence. Instead, we relied on exemplars at hand, viz., highly modified latest Creteceous mosasauroids readily available in the Niobrara collections of Yale University's Peabody Museum of Natural History. That subclade is diagnosed in part by secondary re-evolution of an ascending process (McDowell and Bogert 1954; Russell 1967; Bell 1997).

Finally, polyglyphanodontians lack an additional 10 unambiguous synapomorphies of crown

Scleroglossa that also seem to be plesiomorphic in the mosasaurians we sampled (see Appendix 4 and "Scleroglossa" below).

Polyglyphanodontians lack at least 16 scleroglossan synapomorphies, leading us to infer that, far from being stem teiids (e.g., Estes 1983; Gauthier 1984; Conrad 2008), this group diverged from other lizards before the origin of crown Scleroglossa (see also "morphology tree" in Lee 2009). These conspicuously different placements for Polyglyphanodontia differ significantly when imposed on our strict consensus tree (Templeton's test p=0.0026). This placement in the squamate tree requires that polyglyphanodontians extend back into the Late Jurassic, when crown scleroglossans first appear in the fossil record (e.g., the stem gekkotan *Eichstaettisaurus*, the stem scincoid *Paramacellodus*, the stem anguimorph *Dorsetisaurus*, and the earliest mosasaurian *Proaigialosaurus*). So far, however, polyglyphanodontians are known only from the Upper Cretaceous (when terrestrial sediments become more common in North America), by which time lizards had replaced sphenodontidans as the most abundant lepidosaurs in terrestrial ecosystems.

According to their relative abundance in fossil faunas (e.g., Gao and Norell 2000), polyglyphanodontians are overwhelmingly the dominant clade of Late Cretaceous lizards on land in Asia. They appear much less abundant in penecontemporaneous sediments in North America (Nydam et al. 2010). But if one recognizes that highly modified tooth crowns mark only part of Polyglyphanodontia, it may be that several putative "teiid" species based on isolated tooth-bearing bones with simple tricuspid crowns and slightly swollen tooth shafts might actually represent less modified polyglyphanodontians (i.e., see "boreoteioids" of Nydam et al. 2007; Nydam and Voci 2007; Nydam et al. 2010).

MOSASAURIA

One of the most startling results of our analysis is a sister group relationship between Scleroglossa and Mosasauria (the latter including Dolichosauria and Mosasauroidea, a clade represented by *Aigialosaurus dalmaticus* + Mosasauridae in our study). They share six unambiguous synapomorphies with crown scleroglossans that are absent in polyglyphanodontians, including the following (see Appendix 4): 83(2), jugal tapers to apex, and loosely joined to postorbital (CI = 1.00); 285(2), ectopterygoid dorsal process absent; 360(2), pronounced subdental gutter; and 394(1), coronoid anterolateral dentary process extends anteriorly to overlap dentary past level of tooth row.

Caldwell (1999) also arrived at this conclusion early on in his extensive and ongoing studies of mosasaur phylogeny (see also Gauthier 1984), but later abandoned that idea in favor of a snake—mosasaur union inside varanoid anguimorphs (e.g., Lee and Caldwell 2000). The varanid—mosasaur connection is the more traditional view, as indicated by the fact that descriptions of mosasaur species have historically relied almost invariably on extant *Varanus* alone for comparisons, virtually ignoring the rest of living squamates (e.g., Williston 1917; McDowell and Bogert 1954; Russell 1967). The gross resemblance of the skulls of extant *Varanus* and extinct mosasaurians is admittedly striking at first glance.

Nevertheless, if mosasaurs and varanids are related as tradition dictates, then one might expect that, just like all other varanoids, mosasaurians should share apomorphies with other anguimorphs, other autarchoglossans, and other scleroglossans. That is to say, any given mosasaurian is expected to have not only those synapomorphies inherited from the ancestral mosasaurian, but also those inherited from the ancestral anguimorph, the ancestral autarchoglossan and the ancestral scleroglossan as well. This need not be the case in every instance, as evolutionary reversals can and do occur with some frequency, especially in diminutive or gigantic lizards whose patterns of growth might subject them to paedomorphosis. Indeed, specialized host-specific parasites may degenerate to the degree that they "lose" so much anatomy as to effectively erase their phylogenetic histories from their phenotypes.

This does not seem to be the case here, however, at least for the characters and species sampled in this analysis. Of the 30 unambiguous synapomorphies that arose along the branch leading from the ancestral scleroglossan to the ancestral anguimorph, for example, the mosasaurians we sampled have only three of them (10%). Extinct mosasaurians are highly modified marine lizards, so one might expect a fair bit of missing data owing to evolutionary overprinting beyond that due to incomplete preservation. And, indeed, mosasaurs cannot be scored for 17% (6 of 36) of our squamate "backbone" characters. Even if mosasaurs in fact had the apomorphic states for all those missing entries, it seems anomalous that no more than 25% of the total number of relevant characters would be consistent with a mosasaur–anguimorph grouping. Evolutionary reversals are common enough in lizard phylogeny and, indeed, *Varanus* has apparently reversed one scleroglossan synapomorphy (among 10). But *Varanus* also possesses 90% of the apomorphies diagnostic of crown Scleroglossa, while mosasaurians have none.

That being said, we think it especially revealing that mosasaurians have all seven of the unambiguous synapomorphies uniting extinct *Saniwa* with extant *Varanus* among the total-group varanoids in this analysis (see Appendix 4). In that respect, earlier workers would seem entirely justified in comparing mosasaurians only to crown *Varanus*, even though the former clade is entirely Mesozoic in age while the latter is confined to the Neogene. Stem varanoids extend back into the Upper Cretaceous, but the earliest mosasaurians are much older (Upper Jurassic). And although the earliest mosasaurians have, for example, the long snout and retracted nares that seem especially varanid-like, the most basal stem varanoids certainly do not (e.g., *Gobiderma pulchrum*). Thus, as the phylogenetic scope widens, so does the degree of anomaly (Templeton's test $p = 0.0192$ when Mosasauria is joined to Varanidae in our strict consensus tree). That is to say, mosasaurians have only 30% (3 of 10) of the unambiguous synapomorphies (for which they can be scored) that unite crown Varanidae (= *Lanthanotus*, *Saniwa* and *Varanus*). *Varanus*, in contrast, has every single one of them. Thus, *Varanus* displays just the sort of hierarchically internested distribution of synapomorphies that one expects of a descendant of a varanoid anguimorph autarchoglossan scleroglossan, but mosasaurians do not. That is why we find the apomorphies shared by mosasaurians and total-clade *Varanus* so revealing, as this decidedly nonhierarchical pattern is just what one might expect to see in cases of convergence, rather than homology.

We note finally that some morphological analyses recovered snakes nested inside dolichosaur mosasaurians (Caldwell 2000; Lee and Caldwell 2000; Palci and Caldwell 2010). Our dataset never supports such a placement, even when all other fossorial species aside from snakes are excluded from the analysis (for further discussion see "Taxonomic Inclusion/Exclusion Experiments" below). Moreover, when snakes are grafted to the *Adriosaurus suessi* branch among marine dolichosaur mosasaurians, that requires 40 additional steps on our tree. It thus seems unlikely that snakes are dolichosaurs. That does not, however, negate a possible sister group relationship between snakes and mosasaurians as a whole; they could still have shared a carnivorous ancestor that was fully terrestrial.

CROWN SCLEROGLOSSA

Iguania is unambiguously the sister to Scleroglossa in all our analyses, because they are united by a minimum of 25 and a maximum of 43 synapomorphies, five of which are unique and unreversed on our tree: 83(2), 437(1), 200(1), 600(1) and 604(1) (see Appendix 4). Every morphology-based phylogenetic analysis since Gauthier (1982) has arrived at the same conclusion—that lizards traditionally grouped as Gekkota and Autarchoglossa comprise a clade that is sister to Iguania within Squamata. This hypothesis represented a significant departure from the traditional classification of lizards.

For most of the 20th century, herpetological thinking was dominated by the concept of "Ascalabota," a group including only iguanians and gekkotans, and explicitly excluding any autarchoglossan lizards (including mosasaurians, snakes, dibamids and amphisbaenians; Camp 1923). Note that Camp's "skiogram" matched the topology found in later phylogenetic analyses of the lizard phenotype; however, it was Camp's classification, and not his "tree," that held sway in the field (e.g., McDowell and Bogert 1954; Underwood 1971). Questions about Camp's classification began to appear in the precladistic literature. These include Robinson's (1967) discovery of the "hockey-stick shaped" squamosal in gekkotans and autarchoglossans, and Sukhanov's (1976) finding of shoulder-musculature characters shared by gekkotans and scincomorphs that are not present in iguanians (anguimorphs were not included in his analysis, so monophyly of Autarchoglossa and its possible connection to "Scincogekkonomorpha" were not tested). An explicit hypothesis for a gekkotan–autarchoglossan sister relationship emerged with phylogenetic systematics. To recognize that shift in thinking, Estes et al. (1988) coined the taxon name "Scleroglossa" for a gekkotan-autarchoglossan crown clade with keratinized foretongues (Schwenk 1988).

Scleroglossa is distinguished from both mosasaurians and polyglyphanodontians by 10 unambiguous synapomorphies (see Appendix 4), among which are the following: 82(1), a shortened jugal process of the postorbital; 90(2), temporal muscles originating from the ventral surface of parietal table and supratemporal process; 128(1), orbitonasal fenestra margin vertical; 162(1), base of temporal ramus of squamosal lies against supratemporal process of parietal; 188(2), quadrate slopes anteroventrally; 200(1), dorsal expansion of septomaxilla (to house an enlarged vomeronasal organ; CI = 1.0); 241(2), palatine barely overlaps pterygoid laterally and pterygoid does not extend well anterior to the ectopterygoid–jugal–maxilla juncture (i.e., a kinetic pterygopalatine joint); 258(2), moderately broad separation between pterygoids; 272(1), crescentic curve to the ectopterygoid in dorsal view; and 502(1), strongly angulated clavicles.

We propose two additional synapomorphies for this clade: character 600(1), a flatter (and keratinized) tongue tip modified for vomeronasal olfaction, and 604(1), prey prehension no longer mediated entirely by a fleshy tongue, but instead relying mainly on jaws. Schwenk's (1988) classic (and perhaps correlated) characters in the gross anatomy and use of the tongue in feeding are unlikely to be preserved in extinct stem scleroglossans, and are accordingly regarded as "equivocal" by PAUP*. Nevertheless, the inability of these characters to resolve relationships of extinct polyglyphanodontians and mosasaurians to crown scleroglossans in no way reduces their utility for addressing the earliest divergence in the squamate crown. These two soft-tissue synapomorphies, as well as character 200(1), add unambiguous support for placing crown Iguania outside of a clade composed of crown Scleroglossa, as all three are unique and unreversed (CI = 1.00) on our tree.

The monophyly of Scleroglossa relative to Iguania emerging from studies of the phenotype stands in stark contrast to most recent molecular analyses that consistently place iguanians high up in the lizard tree next to anguimorphs and snakes. The evolutionary consequences of this alternative will be considered below (see "Molecules vs. Morphology").

Within Scleroglossa, we recover a primary split between the total clades encompassing crown Gekkota on the one hand and crown Autarchoglossa on the other (albeit with poor support for the latter clade; see below).

STEM GEKKOTA

The Late Jurassic *Eichstaettisaurus* (*E. schroederi* + *E. gouldi*) from Europe is the most basal stem gekkotan, followed by an unnamed stem gekkotan (AMNH FR 21444) from the Early Cretaceous of Mongolia. Long thought to be a stem gekkotan (Estes 1983), *Eichstaettisaurus* has been placed in a wider variety of positions in recent phylogenetic analyses, though most often near the scleroglossan root (e.g., Conrad 2008), consistent with its overall primitive form. Nevertheless, *Eichstaettisaurus* shares six unambiguous apomorphies with crown gekkotans in our analysis: 38(1), frontal subolfactory processes arch beneath the brain (but do not contact on midline); 88(0), parietals paired; 161(1), squamosal temporal ramus broadly contacts parietal supratemporal process; 419(4), 10 or more premaxillary teeth; 420(4), 31 or more maxillary teeth; and 470(2), caudal autotomic septum posterior to the caudal rib. *Eichstaettisaurus* also has another distinctive gekkotan feature—259(0), smooth skull bones—although that character is ambiguous on our tree. Statistical support is predictably modest (66% BP, 65% PP, 3 BS) given its antiquity, overall primitiveness and state of preservation. Nonetheless, we find the connection to Gekkota compelling given the unique collection of apomorphies visible in *Eichstaettisaurus. E. schroederi,* in particular, is strikingly like crown gekkotans in having relatively short metapodials compared to zeugopodia and digits in both forelimbs and hindlimbs. That morphology is common among arboreal lizards today (e.g., *Polychrus marmoratus*, *Chamaeleo calyptratus* and *Gekko gecko*).

The incomplete skull AMNH FR 21444 appears to be another stem gekkotan (58% BP, 71% PP, 1 BS) that is nearer to, but still outside of, the gekkotan crown (Conrad and Norell 2007). It shares with crown Gekkota two additional gekkotan apomorphies: 95(1), parietal postparietal projection present, and 158(1), jugal remnant depressed on supradental shelf of maxilla at level of ectopterygoid.

CROWN GEKKOTA

Support for the gekkotan crown is strong (94% BP, 100% PP, 10 BS) despite the missing data introduced by Mesozoic stem gekkotans. In his groundbreaking cladistic analysis of crown gekkotan phylogeny, Kluge (1987) recognized the same four "gekkonid subfamilies" he found in 1967. This time, however, he inferred an Australian clade comprised of "snake-like" Pygopodidae and "lizard-like" Diplodactylinae. We likewise recover Pygopodidae (100% BP, 100% PP, 12 BS), but as the sister taxon to all other crown gekkotans, rather than nested within them; the same result was obtained by Kluge (1967). We also recover a monophyletic Eublepharidae (91% BP, 100% PP, 5 BS), including *Aeluroscalabotes felinus*, in a peribasal position within crown Gekkota. The Bayesian analysis (see Figure 4) also supports two additional clades, one composed of *Gonatodes albogularis* and *Phelsuma lineata* (98% PP) and another including *Rhacodactylus auriculatus* and *Saltuarius cornutus* (96% PP), as in the maximum parsimony analyses (which is otherwise less resolved; see Figure 1). This doubtless reflects that our character sampling did not target gekkotan interrelationships, but rather the position of total-group gekkotans in the squamate tree.

The molecular analysis by Donnellan et al. (1999) also placed a monophyletic Pygopodidae as the sister taxon to all Australian geckos included in their analysis. However, a more broadly based analysis of gekkotan interrelationships using molecular data (Han et al. 2004) recovered a monophyletic pygopod clade nested within gekkotans, as the sister group of a clade that comprises the carphodactylines *Carphodactylus*, *Nephrurus* and *Phyllurus*.

CROWN AUTARCHOGLOSSA

Autarchoglossa *sensu* Estes et al. (1988) refers to a scleroglossan crown clade that includes traditional Scincomorpha and Anguimorpha, but excluding crown Gekkota. It is diagnosed by 12 unambiguous synapomorphies in our analysis (see Appendix 4). Conrad (2008) also recovered this clade on the basis of five unambiguous synapomorphies: (1) presence of dermal sculpturing on the frontal and parietal; (2) fused premaxillae; (3) angulated jugal; (4) posteroventral process on jugal; (5) articular-prearticular fused to the surangular. We sampled all but one of these characters (i.e., character 3). In our analysis, however, character 2—our 1(1)—is a squamate synapomorphy and character 5—our 401(1)—may be a scleroglossan synapomorphy. We confirm autarchoglossan synapomorphies 1 (Estes et al. 1988) and 4 (Smith 2006) in Conrad's (2008) list, corresponding to our characters 572(2) and 155(1), respectively. To those two, we add the following unambiguous synapomorphies: 117(1), a posterodorsally trending ridge on the medial side of the facial process of the maxilla that demarcates the anterior and dorsal limits of a shallow oval fossa (nasolacrimal fossa) bordered by the lacrimal and infraorbital canals posteriorly; 208(2), nervus ethmoidalis enclosed in anterior half of the septomaxillae; 217(1), vomer encapsulates the vomeronasal organ posteriorly and medially; 275(2), ectopterygoid with slot laterally that clasps the maxilla; and 607(1), rectus abdominis muscles insert into hinges between transverse ventral scale rows.

Despite the diversity of synapomorphies for this clade, Autarchoglossa is poorly supported statistically in our analysis (23% BP, 54% PP, 1 BS). The enigmatic *Sineoamphisbaena hexatabularis* (which we think might be a burrowing polyglyphanodontian) contributes disproportionately to uncertainty on this point, as do snake-like autarchoglossans generally, and branch-shortening stem fossils in particular. Indeed, removing fossorial lizrds from the analysis raises bootstrap support for Autarchoglossa to 67% BP, and removing stem fossils increases it to 80% BP (82% BP when both are excluded). Nevertheless, in our "all-species" Bayesian analysis basal autarchoglossan phylogeny is poorly unresolved (see Figure 4).

A series of evolutionary innovations including a relatively longer body, increased reliance on vomero-olfaction for sensory cues and attachment of the segmented abdominal muscles to the skin, apparently set the stage for the explosion of snake-like clades unique to Autarchoglossa within Amniota.

CROWN SCINCOMORPHA

A clade composed of lizard species here referred to as "Scincomorpha" (as defined by Estes et al. 1988) emerged from our analysis. Such a grouping, invariably including at least the limbed members of crown clades Scincidae, Cordylidae, Gerrhosauridae, Lacertidae, Gymnophthalmidae and Teiidae, has a venerable history in herpetology, both in traditional classifications (e.g., Gray 1845; Cope 1864, 1900; Camp 1923), and in explicitly phylogenetic taxonomies (e.g., Estes et al. 1988; Conrad 2008). As discussed below, Xantusiidae has posed a special challenge.

Despite the endurance of this hypothesis, and the 13 unambiguous synapomorphies we found for this clade (see Appendix 4), Scincomorpha is poorly supported in our analysis (30% BP, 3 BS). However, a closer look suggests that this is due largely to missing data in the fossorial forms and stem fossils. Thus, when fossorial species are omitted, bootstrap proportions rise to 74%. Bootstrap proportions naturally improve a bit more, to 77%, on removal of some necessarily branch-shortening stem scincoids (i.e., *Paramacellodus*, *Parmeosaurus*, *Carusia* and *Myrmecodaptria*).

Molecular datasets often strongly support scincomorph paraphyly, however, with lacertoids and then scincoids (always including fossorial *Acontias* and *Feylinia*) as successive sisters to a clade composed of anguimorphs + snakes + iguanians (Townsend et al. 2004; Vidal and Hedges 2005; Lee 2009; Wiens et al. 2010). Given the apparent strength of this alternative signal in molecular datasets, there is surprisingly little support for scincomorph paraphyly in the morphological datasets assembled to date.

With that noteworthy caveat, we otherwise obtain strong support for the primary division within Scincomorpha between the Lacertoidea and Scincoidea of Estes et al. (1988). Indeed, lacertoids and scincoids each show 100% bootstrap support, at least in analyses excluding fossorial forms and branch-shortening stem species. Even when such species are included, lacertoids retain good support (92% BP, 100% PP, 5 BS), but scincoids are very poorly supported (26% BP, 2 BS). This discrepancy likely reflects that, unlike the case with scincoids, there are no branch-shortening "intermediate" stem lacertoids in our analysis.

CROWN LACERTOIDEA

Lacertoidea is composed of Old World Lacertidae (99% BP, 100% PP, 12 BS) and New World Teioidea: 98% BP, 100% PP, 10 BS, and two CI = 1.00 characters, 314(1) and 441(1). Within teioids, Teiidae (100% BP, 100% PP, 21 BS, and one CI = 1.00 synapomorphy, 233[1]) is sister to Gymnophthalmidae (100% BP, 100% PP 20 BS, and one CI = 1.00 synapomorphy, 226[1]). These clades have been recognized universally in previous morphological studies (e.g., Presch 1974a, 1974b, 1983, 1988; Rieppel 1980a, 1980b; Estes et al. 1988; Gao and Fox 1991; Denton and O'Neill 1995; Lee 1998, 2000, 2005, 2009; Conrad 2008). Within Teiidae, the traditional subclades Teiinae (99% BP, 100% PP, 6 BS) and Tupinambinae (65% BP, 100% PP, 2 BS) are also recovered. All these lacertoid clades are uncontroversial (their diagnoses are detailed in Appendix 4).

STEM SCINCOIDEA

Late Cretaceous *Parmeosaurus scutatus* (a stem autarchoglossan in Conrad 2008) and Late Jurassic *Paramacellodus* (a stem anguimorph in Conrad 2008) are inferred to be the basalmost stem scincoids here. That inference is, however, very poorly supported in our analysis (26% BP, 2 BS), since these species, particularly *Paramacellodus*, are poorly known and deeply plesiomorphic in any case. Both species nevertheless display a distinctive scincoid synapomorphy: 367(1), a prominent process of the dentary overlapping the coronoid anterodorsolaterally. They also have the infaorbital canal in a more medial position, entirely enclosed in the palatine (245[1]), as in all scincoids except for some xantusiids. However, lacertids also have this character, although teioids (and amphisbaenians) are apparently plesiomorphic in this regard. The history of this trait within Scincomorpha (and Autarchoglossa) is thus unclear (an infraorbital canal confined to the palatine is also present in Anguimorpha and Serpentes, but not in Mosasauria; it also arose independently in Isodontosauridae within Iguania).

Osteoderms covering the body of *Parmeosaurus scutatus* obscure much of its anatomy; this species requires more careful study than given here. Specimens referred to as *Paramacellodus* (following Evans and Chure 1998) are unmistakably stem scincoids in our estimation, even if statistical support is poor. *Paramacellodus* shows only two unambiguous synapomorphies of crown scincoids (see Appendix 4): 95(1), postparietal projection near midline of parietal, and 149(0), jugal covered by maxilla and no longer exposed laterally below the orbit.

Interestingly, the type specimen of *Paramacellodus* (*P. oweni* Hoffstetter 1967) has rectangular body osteoderms similar to those of *Parmeosaurus scutatus*, especially in being larger dorsally but with smaller, and presumably "compound," osteoderms ventrally (i.e., ventral scales similar in size to the dorsal scales are invested by several smaller rectangular osteoderms lying side-by-side). Other "paramacellodids" apparently do not have any body osteoderms (Estes 1983; Richter 1994); we found none associated with either specimen here referred to *Paramacellodus*. According to Evans and Chure (1998), paramacellodids are united by a derived tooth form. However, presence or absence of body osteoderms could unite them with different clades within Scincoidea. More data are needed to resolve this apparent conflict regarding the monophyly of this putative clade of Late Jurassic and Early Cretaceous stem scincoids.

STEM XANTUSIIDAE

Total-group xantusiids (Pan-Xantusiidae) lie embedded among scincoids as sister to cordyliforms in our tree (50% BP, 98% PP, 2 BS), as in diverse molecular datasets (Vicario et al. 2003; Whiting et al. 2003; Townsend et al. 2004; Vidal and Hedges 2005; Raselimanana et al. 2009; Lee 2009). We agree with Conrad (2008) that xantusiids are scincomorphs as proposed by Estes et al. (1988). But unlike Estes et al. (1988), and most subsequent morphological analyses (e.g., Conrad 2008), xantusiids are here allied with scincoids rather than lacertoids (see also Evans and Barbadillo 1997, 1998; Evans and Chure 1998). Support for this placement is admittedly weak (11% BP, 1 BS), but that seems merely to reflect missing data in stem fossils, rather than conflict in the data.

CROWN XANTUSIIDAE

Xantusiid monophyly is supported universally in molecular datasets. Crown Xantusiidae is also strongly supported in our analysis of the phenotype (95% BP, 100% PP, 7 BS), as is the position of the Early Cretaceous fossil *Tepexisaurus tepexii* (Albian of Puebla, Mexico) along its stem (94% BP, 100% PP, 7 BS, and one CI = 1.00 synapomorphy, 282[1]). Conrad (2008) inferred that the Mexican *T. tepexii* was the earliest divergence along the autarchoglossan stem, but that hypothesis had little support (i.e., 1 BS). Nydam and Fitzpatrick (2009) recently made a compelling case for placing Contogeniidae, a newly recognized lizard clade ranging from early in the Upper Cretaceous (Cenomanian) to the Middle Paleocene (Tiffanian) of North America, on the xantusiid stem.

Within Xantusiidae, our data support the Cuban endemic *Cricosaura typica* as sister to North American *Xantusia vigilis*, contrary to molecular data (e.g., Vicario et al. 2003). Support for our hypothesis is weak, however (57% BP, 71% PP, 2 BS). An extinct species of *Palaeoxantusia* from the Late Eocene (Chadronian) White River Formation (all from "Al's Pocket," Loan Tree Gulch, Natrona County, Wyoming, USA; see Appendix 1) is sister to those two, again with weak support (1 BS), with extant *Lepidophyma flavimaculatum* sister to all other crown xantusiids.

The deeply nested position of *Cricosaura typica* seems to be an artifact of sampling, however, with relationships among the remaining three xantusiids constant throughout. Given only these four species, the two smallest, *Cricosaura typica* and *Xantusia vigilis*, tend to associate in morphological analyses (e.g., Conrad 2008) based mainly on shared size-related character states inferred to be paedomorphic in analyses with denser taxon sampling. Those apomorphies shared by the two larger (i.e., more normal-sized) xantusiid species, *Lepidophyma flavimaculatum* and *Palaeoxantusia* sp., are actually "xantusiine" synapomorphies that are absent in Cuban *C. typica*, the basal sister to extant xantusiids still dwelling on mainland North America where the crown clade originated (Hedges et al. 1991; Vicario et al. 2003; Gauthier et al. 2008). In that hypothesis, apomorphies shared by *Lepidophyma* and *Palaeoxantusia* sp. in our analysis (see Appendix 4) are actually xantusiine synapomorphies that fail to develop in the diminutive species of *Xantusia,* such as *X. vigilis*. Although absent in smaller, more derived species of *Xantusia*, those diagnostic xantusiine apomorphies are still present in the larger and more basal species of *Xantusia* not included in the present analysis (e.g., *X. riversiana* and *X. henshawi*; Gauthier et al. 2008). The "absence" of these characters in *C. typica* is plesiomorphy, but their "absence" inside *Xantusia* is apomorphy.

The definitive presence of a stem xantusiid in the Early Cretaceous of North America (in southern Mexico), and of its cordyliform sister clade in the Late Cretaceous of Africa (i.e., Madagascar; Krause et al. 2003), suggests that the clade stemming from their last common ancestor had already achieved its current (now widely disjunct) geographic distribution by the end of the Mesozoic Era.

CROWN CORDYLIFORMES

Setting aside for the moment the question of snake and polyglyphanodontian relationships, Conrad's (2008) trees also differ from ours in placing crown clade Cordyliformes as sister to Lacertoidea (which also includes Xantusiidae and Polyglyphanodontia, according to Conrad). Our analysis instead places cordyliforms within Scincoidea, as proposed by Estes et al. (1988), and as also inferred in molecular datasets (e.g., Vicario et al. 2003; Whiting et al. 2003; Vidal and Hedges 2005; Lee 2009; Wiens et al. 2010).

Since McDowell and Bogert (1954), the composition of the clade here referred to as Cordyliformes (*sensu* Lang 1991) has been uncontroversial (e.g., Estes et al. 1988; Harvey and Gutberlet 1995; Mouton and Van Wyck 1997; Frost et al. 2001; Odierna et al. 2002; Lamb et al. 2003; Vicario et al. 2003; Conrad 2008). Support for Cordyliformes in our analysis is thus surprisingly weak (65% BP, 97% PP, 2 BS; see Appendix 4), though this could reflect uncertainty stemming from missing data in extinct stem scincoids. Cordylidae, here represented by *Cordylus mossambicus* and *Platysaurus imperator*, is strongly supported in our analysis (99% BP, 100% PP, 9 BS), as is Gerrhosauridae, represented by *Cordylosaurus subtesselatus* and *Zonosaurus ornatus* (82% BP, 100% PP, 5 BS). The former gerrhosaur species is exceptionally small for a cordyliform, and has accordingly "lost" (in the sense of "fails to develop") some characteristic cordyliform apomorphies normally appearing later in ontogeny; it thereby reduces support values for Cordyliformes as a whole (e.g., 100% BP if deleted, but. 65% BP if included). As with the basal xantusiid *Cricosaura typica*, *Cordylosaurus subtesselatus* serves as another example of the perils of relying on a highly modified species, even if it is "basal" in a cladistic sense, in the effort to infer ancestral states.

STEM SCINCIDAE

CARUSIIDAE

A surprising result of our study is that two markedly modified species from the Late Cretaceous of Mongolia, *Myrmecodaptria microphagosa* (a stem autarchoglossan in Conrad 2008) and *Carusia intermedia* (a stem xenosaur anguimorph autarchoglossan in Conrad 2008), are strongly supported as a clade (98% BP, 100% PP, 6 BS). These two species display nine unambiguous synapomorphies, including the following (see Appendix 4): 6(1), premaxilla with multiple ethmoidal foramina (exiting through premaxillary body); 36(1), fused frontals; 42(1), frontal subolfactory processes delimit a deep, narrow canal for the olfactory tracts across most of orbits; 62(2), postfrontal fused to postorbital; 108(2) prominent parietal epipterygoid processes extend ventrally to level of prootic alar process; and 137(1), lacrimal absent. This particular combination of apomorphies is compelling, even if all of them appear elsewhere in Squamata. We accordingly refer both species to Carusiidae (Borsuk-Bialynicka 1987).

Perhaps more surprising, Carusiidae seems to lie along the stem of Scincidae in our all-species analysis, albeit with very weak support (12% BP, 2 BS). Regardless, note that they share five unambiguous synapomorphies that are distinctly scincid: 1(0), paired premaxillae; 67(1), postfrontal supratemporal shelf; 82(2), postorbital jugal ramus very reduced, not reaching ventrally to level of quadrate head; 160(1), squamosal extends anterior to level of epipterygoid; and 275(1), ectopterygoid abuts posteromedial corner of maxilla.

Carusiids also share one or another of these apomorphies with other lizard clades to which they have been allied previously. As Gao and Norell (1998) noted, for example, they share paired premaxillae with gekkotans and anteriorly lengthened squamosals and narrow, fused frontals with xenosaurs. They are inferred to be autarchoglossans on the Bayesian tree, but their relationships among basal autarchoglossans are otherwise unclear (see Figure 4).

GLOBAURIDAE

Another surprising result of our analysis is that two species in Conrad's (2008) "Bainguidae," *Eoxanta lacertifrons* and *Globaura venusta*, are here united with *Hymenosaurus clarki* in a well-supported clade (95% BP, 100% PP, 7 BS). (Note that although the four specimens referred to *Eoxanta lacertifrons* are here scored collectively, they derive from different localities and might include two species, or perhaps the same species sampled at two different times during its history; the holotype ZPAL MgR-III/37 and referred ZPAL MgR-III/38 are from Khermeen Tsav, while referred ZPAL MgR1/74 and ZPAL MgR-I/61 are from Khulsan [Borsuk-Bialynicka 1988]; the latter specimen in particular seems to have relatively broader bones that constitute the temporal arcade.) This clade, informally designated "Globauridae," is known only from the Late Cretaceous of Mongolia. It is supported by eight unequivocal synapomorphies, including the following (see Appendix 4): 29(1), nasal terminates posterior to end of maxillary tooth row or vomer tip; 56(2), frontoparietal suture interdigitation moderately developed; 124(1), maxilla posterior process confined to the anterior half of the orbit; and 379(1), anterior inferior alveolar foramen dorsal to posterodorsal to anterior mylohyoid foramen in the splenial.

Globauridae seems to be sister to crown Scincidae (Alifanov 2000), although support is very weak (21% BP, 2 BS) owing in part to missing data in carusiids. In spite of seemingly poor support, Globauridae is united with Scincidae by five unequivocal synapomorphies and could have as many as five additional synapomorphies supporting that hypothesis (see Appendix 4): 67(2), postfrontal supratemporal shelf extending posteriorly further than laterally across the upper temporal fenestra; 76(1), postorbital widens posteriorly to partly occlude upper temporal fenestra; 94(1), enlarged parietal nuchal fossa; 97(1), bifid parietal supraoccipital process; and 128(2), prefrontal orbitonasal margin slopes ventromedially in cross section.

CROWN SCINCIDAE

Monophyly of quadrupedal Scincidae has never seriously been in doubt—unlike the case with some limbless fossorial forms often allied to Scincidae—and has now been tested extensively with molecular sequence data (e.g., Whiting et al. 2003; Brandley et al. 2005). However, Scincidae (43% BP, 50% PP, 5 BS, but two CI = 1.00 synapomorphies, 581[1], 601[1]) has heretofore proven difficult to diagnose morphologically (e.g., Estes et al. 1988).

In addition to three correlated and potentially redundant characters related to the mosaic ("compound") nature of the metaplastic bones (osteoderms) investing their cycloid scales (575[2], 577[2], 578[2]; Estes et al. 1988), we identified an additional eight unambiguous synapomorphies for crown Scincidae, among which are the following (see Appendix 4): 18(2), anterior width of nasals less than nasofrontal joint width; 69(1), postorbital narrows anteriorly; 157(1), jugal medial ridge pronounced, with base of that ridge projecting laterally behind ectopterygoid in dorsal view; 161(1), squamosal temporal ramus broadly contacts parietal supratemporal process; 231(1), palatines in contact anteriorly; 249(2), intermediate duplicipalatinate palatine bones (*sensu* Rieppel et al. 2008); and 573(1), palpebral bone lies below supraorbital scales (and their osteoderms).

Although we included a total of 10 skinks in our analysis, we made little effort to resolve relationships within this clade. We focused instead on identifying where skinks belong among squamates. As a consequence, we found good support for only three scincid subclades, one of which is the long-recognized Lygosominae (85% BP, 100% PP, 6 BS; Greer 1970). Within the latter, we also found some support (64% BP, 96% PP, 4 BS) for a clade including *Sphenomorphus solomonis* (*Sphenomorphus* group) and *Tiliqua scincoides* (*Egernia* group). The third group includes the only fossorial scincids in this study, viz., the acontine *Acontias percivali* and the scelotine *Feylinia polylepis* (72% BP, 50% PP, 4 BS). Molecular datasets are, however, unanimous in regarding these two species as more distantly related within Scincidae (e.g., Whiting et al. 2003; Brandley et al. 2005); they apparently did not share a long-bodied and reduced-limbed fossorial ancestor, an ecomorphology that is the primary source of characters that seem to unite them in our study (see Appendix 4).

As expected, these two fossorial skinks proved to be pivotal tree-changing taxa in our analysis. Like other highly modified forms, they are primary sources of both missing data and character conflict—so much so that even minor changes in taxon and character sampling will remove them from Scincidae and place them in a group composed of other snake-like squamates, or draw other snake-like squamates (including snakes) into Scincidae (see "Taxonomic Inclusion/Exclusion Experiments" below).

Although we found good support for a sister-group relationship between *Acontias percivali* and *Feylinia polylepis,* the accuracy of that hypothesis is doubtful as they never root at the same points on the scincid tree when added individually (see "Snake-like Autarchoglossans" and "Taxonomic Inclusion/Exclusion Experiments" below). Indeed, when *Acontias percivali* is removed (along with other fossorial squamates), *Feylinia polylepis* groups with *Amphiglossus splendidus* in a sub-Saharan African clade of skinks that emerges in all molecular datasets (e.g., Whiting et al. 2003; Brandley et al. 2005).

Given these circumstances, we are surprised to recover a fully resolved tree for Scincidae, at least in the Adams consensus of the full dataset (see Figure 2). That tree is, however, very poorly supported; Scincidae, for example, emerges in only 38% of the bootstrap partitions. Nevertheless, a more focused analysis including only the traditional scincomorphs produces the same topology with much better support, indicating a promising avenue for future research. That is to say, using lacertoids as a monophyletic outgroup to scincoids reveals a clearer signal in our dataset that is not apparent in the all-species analysis. Support for Scincidae, for example, rises from 38% to 93% BP. Support also increases to 73% BP for a group including all skinks apart from *Plestiodon fasciatus*. And if uncertainty is reduced by removing fossorial forms (i.e., *Acontias* and *Feylinia*)—which is effectively what we accomplished by confining the analysis to scincomorphs alone in the first place—support rises to 70% BP for a sister-group relationship between *Scincus scincus* and the remaining skinks, consistent with a morphology-based hypothesis first proposed by Griffith et al. (2000; see also Giovannotti et al. 2009).

Finally, we find it particularly revealing that among the "six unambiguous synapomorphies" that Conrad (2008:104) used to diagnose his Scinciformes (traditional skinks plus most of the "fossorial autarchoglossans" of our analysis), three of those apomorphies are in fact plesiomorphic in basal snakes: 83(2), expansive nuchal fossa extends well onto parietal table; 181(1), dentary Meckel's canal partly closed; and 207(1), broad mandible retroarticular process. The other three are plesiomorphic in basal skinks, even if present in snakes: 192(0), coronoid process short and broad; 221(1), replacement teeth posterolingual in position; and 277(2), loss of humerus ectepicondylar groove and foramen ("?" in snakes). This indicates that it is specifically the apomorphies of fossorial skinks, rather than the apomorphies of skinks per se, that draw other snake-like fossorial lizards into Conrad's "Scincophidia."

CROWN ANGUIMORPHA

Anguimorpha *sensu* Estes et al. (1988) on our tree includes species traditionally referred to Xenosauridae, Anguidae and Varanoidea (see McDowell and Bogert 1954; Rieppel 1980a, 1980b; Gauthier 1982). But it also includes a novel collection of species, namely, all snake-like forms except for pygopod gekkotans, albeit with very little support (8% BP, 1 BS; see Figures 1–3). The inclusion of snakes in Anguimorpha is not unusual, because the roots of that idea run deep in herpetology (e.g., Camp 1923; McDowell and Bogert 1954; see also the review in Rieppel 1988). However, that Anguimorpha might also include the putative polyglyphanodontian *Sineoamphisbaena hexatabularis*, as well as Dibamidae and Amphisbaenia and, under certain species-sampling regimes, the skinks *Acontias percivali* and *Feylinia polylepis*, is novel indeed. This part of our tree will be discussed at length below. At this point, it is only necessary to emphasize that most of the uncertainty here stems from the "fossorial autarchoglossans" (see below) and to a lesser extent conflicting data on the position of *Shinisaurus crocodilurus* near the basal diversification of Anguimorpha. Missing data in the basalmost scincoids, *Parmeosaurus* and *Paramacellodus*, are also contributing to uncertainty in character optimizations at the root of Anguimorpha. The influence of these species will be discussed below (see "Fossorial Autarchoglossans" and "Taxonomic Inclusion/Exclusion Experiments"). Note that this rather more expansive composition for Anguimorpha is not supported by the Bayesian analysis (see Figure 4).

CROWN XENOSAURIDAE

We recover a monophyletic Xenosauridae (including *Shinisaurus crocodilurus*, albeit with weak support [50% BP, 67% PP, 2 BS]), as in most previous analyses, but *contra* Conrad (2008) and Conrad et al. (2010).

CROWN ANGUIDAE

With the conspicuous exception of *Anniella pulchra*, there is also reasonable support (67% BP, 2 BP; one CI = 1.00 synapomorphy, 576[1]) for monophyly of Anguidae in our study. There is good support for extinct Glyptosaurinae (i.e., *Peltosaurus granulosus* + *Helodermoides tuberculatus*; 70% BP, 100% PP, 1 BS) in agreement with Sullivan (1979) and more comprehensive recent studies (Conrad and Norell 2008; Conrad et al. 2010). We also found modest support (65% BP, 86% PP, 1 BS) for an anguid subclade composed of the exclusively New World Gerrhonotinae and Diploglossinae (Gauthier 1982).

Surprisingly, *Anniella pulchra,* a species traditionally allied to anguids, appears near the base of the other fossorial squamates leading to Serpentes, although support for that novel arrangement is poor in the maximum parsimony analysis (55% BP, 3 BS) and nonexistent in the Bayesian analysis. Relationships among basal clades of Anguidae remain unresolved in our view (e.g., Sullivan 1979, 1987; Gauthier 1982; Good 1987; Macey et al. 1999; Wiens and Slingluff 2001; Conrad 2008; Conrad and Norell 2008; Conrad et al. 2010; Wiens et al. 2010).

STEM VARANOIDEA

Our chief departure from current views based on morphology (Norell and Gao 1997; Conrad 2008; Conrad et al. 2010; Conrad et al. 2011) relates to the composition of "Monstersauria," a clade that encompasses crown *Heloderma* and its stem. The two Cretaceous Mongolian "monstersaur" species included in our analyses—*Gobiderma pulchrum* and *Estesia mongoliensis*—are not associated with the *Heloderma* stem in this study (*contra* Conrad et al. 2011). *G. pulchrum* is the first to diverge from the line leading to the varanoid crown in all analyses (see Figures 1–4); this species seems to be the best example of an early stem varanoid currently known. In the maximum parsimony tree, *G. pulchrum* is followed successively by another "monstersaur," *Estesia mongoliensis*, and then *Aiolosaurus oriens*, in more crownward positions (see Figures 1 and 2).

There is strong support for *Gobiderma pulchrum* as the basalmost stem varanoid in our analysis (91% BP, 100% PP, 9 BS). However, the stem position of *Estesia mongoliensis* relative to crown Varanoidea has less support (64% BP, 2 BP) in the maximum parsimony analysis. Support for that hypothesis naturally rises when *Ailosaurus oriens*, with all its missing data, is excluded from the analysis. In contrast, the Bayesian analysis strongly supports (99% PP) *E. mongoliensis* on the varanid stem inside crown Varanoidea (see Figure 4). In no case does *E. mongoliensis* join the *Heloderma* stem.

We cannot tell whether or not *Aiolosaurus oriens*—known only from a very incomplete skull—is part of the varanoid crown in either maximum parsimony (see Figure 2) or Bayesian (see Figure 4) analyses. Nevertheless, all evidence indicates that *Aiolosaurus* shared an ancestor with Varanoidea that was not shared by either *Estesia* or *Gobiderma*. Interestingly, in the 50% majority rule consensus of a completely unordered analysis of our dataset, *Aiolosaurus oriens* moves onto the varanid stem just inside Varanoidea, instead of being sister to the latter clade. Otherwise, the anguimorph part of our tree is unaffected by assumptions about character-state order.

The varanoid stem was already disparate, diverse, and abundant by the Upper Cretaceous (e.g., Borsuk-Bialynicka 1984; Pregill et al. 1986; Lee 1997a; Gao and Norell 2000; Conrad et al. 2010). If extinct *Cherminotus longifrons* is indeed on the stem of extant *Lanthanotus borneensis*, then the basalmost varanoid crown divergences, first between total-clade *Heloderma* and total-clade Varanidae and then between total-clade *Lanthanotus* and total-clade *Varanus*, would have taken place earlier than the K–Pg boundary. Because our study included only one exinct taxon (*Saniwa*) that is unquestionably part of the varanid crown, however, we can only confirm with any confidence that the *Lanthanotus*–

Varanus split must have taken place by the Early Eocene at the latest, well after the K–Pg boundary. Adding our characters to a dataset based on a denser sample of anguimorph species and characters (i.e., Conrad et al. 2010) could provide further insights on these and other problems in anguimorph phylogenetics. In any case, the varanoid stem apparently has deep roots in Asia.

CROWN VARANOIDEA

This clade stems from the last common ancestor of the extant species of *Heloderma*, *Lanthanotus* and *Varanus* in our analysis (72% BP, 97% PP, 1 BS). *Saniwa,* a composite here based on two species from the North American Eocene (the large species *Saniwa ensidens* [Rieppel and Grande 2007; Conrad et al. 2008] and a dwarf species represented by AMNH 8688 and AMNH 8691) lies on the *Varanus* stem (82% BP, 78% PP, 3 BS; and one CI = 1.00 synapomorphy, 140[2]). Although we consider only three species, our tree for *Varanus* (91% BP, 100% PP, 5 BS) matches that of the comprehensive analysis of the anguimorph phenotype by Conrad et al. (2010). Like Conrad et al. (2010), we recover a tree in which Australian *Varanus acanthurus* is sister to a weakly supported clade composed of tropical Asian *V. salvator* + African *V. exanthematicus* (61% BP, 68% PP, 1 BS). When molecular data are added to their dataset, however, the tropical Asian clade of *Varanus* is sister to a clade composed of the Australian and African clades (Conrad et al. 2010, fig. 26). That is an unusual geographic distribution in the biota of the Old World, however, as Australian and African taxa generally stem from adjacent Asia, in closer agreement with the phenotypic phylogeny for *Varanus* recovered here and in Conrad et al. (2010).

FOSSORIAL AUTARCHOGLOSSANS

As with all previous morphological analyses of squamates in the cladistic era (e.g., Estes et al. 1988; Evans and Barbadillo 1998; Hallermann 1998; Lee 1998; Rieppel and Zaher 2000a; Kearney 2003a; Conrad 2008), we found a group composed of most of the long-bodied, limb-reduced "snake-like" squamates (including Serpentes). In our analysis, this group lies deeply embedded in Anguimorpha, whereas Conrad (2008) recovered a similar group, but found it nested deep inside Scincomorpha (within Scincidae). Regardless of its placement, this putative clade of snake-like forms is very poorly supported (e.g., 22% BP, 2 BS in our maximum parsimony analysis). The traditional view acknowledges six strongly supported and long-recognized clades that are often associated with this "fossorial group": Serpentes; Amphisbaenia and Dibamidae; two independent lines of limbless skinks (*Feylinia polylepis* and *Acontias percivali*); a limbless anguid (*Anniella pulchra*); and the remarkably modified Cretaceous species *Sineoamphisbaena hexatabularis* (with several modifications to the skull, if not the postcranium, that seem associated with burrowing). In some manipulations of our dataset, we could also find another snake-like anguid, *Pseudopus apodus,* and even the snake-like pygopod gekkotans, occasionally joining this group (see "Taxonomic Inclusion/Exclusion Experiments" below).

The group composed of Serpentes, Amphisbaenia and Dibamidae—hereafter referred to as the "Krypteia" (the "hidden," owing to their generally secretive habits)—is often recovered, although its monophyly has been met with some skepticism regarding whether the apomorphic resemblances they share are due to phylogeny or to convergence related to a fossorial lifestyle (Lee 1998; Conrad 2008; but see Rieppel and Zaher 2000a). Our analysis may heighten that suspicion because *Anniella pulchra* and *Sineoamphisbaena hexatabularis* are also recovered as part of this group. As mentioned above, it takes very little change to our dataset to get *Feylinia polylepis* and *Acontias percivali* to join them as well (nine additional steps on the maximum parsimony tree if the fossorial group is simply grafted to *Acontias* following Conrad [2008]; Templeton's test p= 0.3475). Although one or more of those species may have been grouped together in previous morphological studies, none but snakes and *Anniella pulchra* have ever been placed in Anguimorpha as in our analysis.

Scleroglossans are exceptional for repeatedly producing ecomorphic "snakes." Nearly every major clade of Autarchoglossa, for example, includes one or more snake-like subclades (e.g., Wiens and Slingluff 2001; Brandley et al. 2008). In those cases in which clades include both "lizard-like" and "snake-like" forms, as among skinks and gekkotans, for example, it has often been easier to discern their relationships and to reveal that their shared snake-like habitus is due to convergence. Groups composed entirely of snake-like forms, such as the krypteians, are another matter. Many of these snake-like species are also small, especially the fossorial forms, and are accordingly often missing phylogenetically informative characters that normally appear later in lizard development. Moreover, their skulls are often streamlined, consolidated and reinforced to withstand the demands of using the head to enter the substrate (Rieppel 1984a), and their sensory systems, including their brains (e.g., Northcutt 1978), are accordingly modified to apprehend and process cues encountered in that medium (e.g., reduced eyes; elaborate vomero-olfactory systems; thick stapes suited to reception of sound waves traveling through dense soil rather than thin air).

The fossorial group includes a succession of taxa on our tree (see Figures 1 and 2), beginning with the first divergence, *Sineoamphisbaena hexatabularis*, followed by *Anniella pulchra*, and then a group composed of the "krypteians," which includes snakes (Serpentes) as sister to a group composed of Dibamidae (*Anelytropsis papillosus* and *Dibamus novaeguieae*) plus Amphisbaenia (see below). Among the snake-like lizards in our analysis, three distinctive fossorial clades—the crown clades of Amphisbaenia (97% BP, 99 % PP, 7 BS) and Dibamidae (100% BP, 100% PP, 16 BS), and (total-group) Serpentes (100% BP, 100% PP, 10 BS)—have often emerged as a clade in morphological analyses. Alternative hypotheses for "deeper" relationships among diverse clades of fossorial lizards have never enjoyed much support in anatomy. Our analysis proved no different; support values for most groupings identified here (including one encompassing *S. hexatabularis* plus most of the fossorial autarchoglossan lizards in our study) are uniformly low (10%–47% BP, 2–3 BS). Only one group (that including Dibamidae plus Amphisbaenia) rises above that to 71% BP (5 BS; but see below).

Interestingly, a version of Krypteia also emerged in the Bayesian analysis. As in the maximum parsimony analysis, *Sineoamphisbaenia hexatabularis* is the first to diverge, with similarly low support (52% PP). Amphisbaenians and Serpentes are sisters, with Dibamidae sister to both of them as in Conrad (2008), but with equally poor support (50% PP and 70% PP, respectively). Note also that "Krypteia" is very poorly supported (37% BP, 3 BS) in the maximum parsimony analysis, even though it has 13 unambiguous synapomorphies (see Appendix 4). That there are so many apomorphic resemblances shared by these three clades reveals why they have been so persistent in morphological phylogenies. Nevertheless, a closer look at these characters illustrates why support levels have never been particularly compelling to many squamate systematists.

Consider the following putatively unambiguous synapomorphies of Krypteia: 18(1), nasal width reduced anteriorly, subequal to nasofrontal joint width; 137(1), lacrimal loss; 142(1), jugal loss; 182(2), narrow overlap of pterygoid and quadrate; 188(4), quadrate slopes anteriorly more than 135%; 234(0), vomer attaches over entire face of palatine; 348(1), vagus foramen close to medial aperture of the recessus scalae tympani, with the hypoglossal foramina extending posterior to the vagus; 392(1), reduced splenial overlap of coronoid (below tooth row); 456(4) 89 or more presacral vertebrae; 463(1), cervical ribs start on vertebrae number 3; and 572(0), dermal skull bones smooth.

All three "core krypteian" clades are distinctive among squamates for being on conspicuously long branches in both morphological (see Appendix 4) and molecular datasets (e.g., Wiens et al. 2010). Moreover, all of these characters display considerable homoplasy across Squamata, regardless of favored topology. And perhaps most troubling, more than half—i.e., 7 of 13, or 54%: 18(1), 142(1), 182(2), 188(4), 234(0), 457(1) and 572(0)—of these putative synapomorphies must immediately reverse inside Krypteia in at least some basal taxa. If complete jugal loss is, for example, truly synapomorphic of Krypteia, then that bone must not only reappear in the earliest rhineurids (sister to the rest of the amphisbaenians), but it must once again form a fully differentiated postorbital bar from a condition in which that element was entirely absent. And then that fully developed jugal must once again undergo reduction from the Paleogene toward the Recent to the vestige left in *Rhineura floridana* today (Kearney et al. 2005). There is also the question of potential redundancy among some of these characters; nearly half of them (6 of 13, or 46%)

appear to reflect paedomorphosis—viz., miniaturization or fossoriality: 137(1), 142(1), 182(2), 348(1), 392(1) and 572(0)—and almost a quarter of them (3 of 13, or 23%) correlate with body elongation: 456(4), 457(1) and 463(3). (Total exceeds 100% as some characters; e.g., 142, can fall under more than one category, such as fossoriality and reversal.)

It is equally instructive to confine analysis to snake-like lizards only (see Conrad [2008] for another version of such an analysis). Topological relations among those species are nearly identical in "all-species" and "fossorial species only" trees (see Figures 1 and 5). The most conspicuous exception is that the fossorial skinks, *Feylinia polylepis* and *Acontias percivali,* form a clade that is sister to Dibamidae + Amphisbaenia. Support values improve dramatically in some instances; for example, bootstrap proportion rises from 47% to 100% for monophyly of fossorial autarchoglossans. This makes sense to us in that the former value depends on "snake-like" and "fossorial" characters alone, while the latter reflects addition of congruent sclergoglossan and autarchoglossan synapomorphies as well. There is thus a deeper signal in these data that still reflects the "all-species" tree: viz., that *Sineoamphisbaena hexatabularis* (a burrowing polyglyphanodontian) is sister to snake-like scleroglossans; that pygopods (snake-like gekkotans) are sister to snake-like autarchoglossans; and that Autarchoglossa is composed of two main branches, snake-like scincomorphs and snake-like anguimorphs. Scincomorphs in this instance are represented by fossorial scincids (*Feylinia* and *Acontias*), and perhaps dibamids and amphisbaenians, while anguimorphs are represented by anguids (*Pseudopus* and *Anniella*) and Serpentes. This problem will be further explored below in the section describing our taxonomic inclusion/exclusion experiments.

Molecular analyses strongly support the idea that the three "core krypteians" are a polyphyletic assemblage of different clades of unrelated fossorial squamates. Wiens et al. (2010), for example, placed amphisbaenians within lacertoids (although could not recover amphisbaenian monophyly), dibamids at the base of squamates, and snakes with anguimorphs (as well *Feylinia polylepis* and *Acontias percivalli* with scincids and *Anniella pulchra* with anguids).

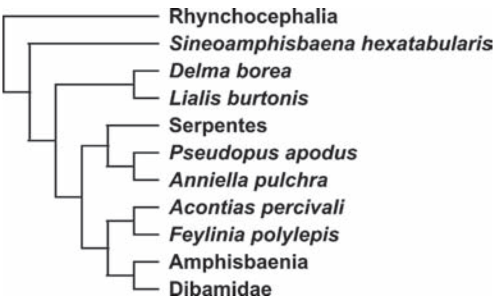

FIGURE 5. Maximum parsimony tree including only snake-like lizards.

CROWN AMPHISBAENIA

Amphisbaenia is strongly supported—97% BP, 99% PP, 7 BS, and four CI = 1.00 synapomorphies: 221(1), 264(1), 320(2), 414(2)—in our analysis, as might be expected. Amphisbaenians are exceptional among squamates for living in permanent burrow systems that they construct with their heads (Gans 1978). Monophyly is strongly supported even when all (snake-like) postcranial characters are deleted from the analysis. Indeed, the composition and many diagnostic characters for this unique "burrow-dwelling" clade of lizards have been discussed for more than a century (Gray 1825; Cope 1861; Gans 1978) and well-documented phylogenetically (e.g., Kearney 2003a). We list here diagnoses for Amphisbaenia, which included a long body and the absence of functional hindlimbs, and its major subclades—including extant *Rhineura floridana* plus two of its Paleogene stem species, as well as extant *Bipes*, Trogonophidae and Amphisbaenidae (see Appendix 4).

Relationships among the most ancient amphisbaenian clades are controversial. Our data afford a new perspective on the problem. Morphology initially seemed to indicate that *Bipes*, the only amphisbaenian with functional forelimbs, was sister to all other amphisbaenians in which no more than vestiges of the pectoral apparatus remain (Kearney 2003a). Later, either North American Rhineuridae (Kearney and Stuart 2004; Macey et al. 2004), or Old World Trogonophidae (Conrad 2008), both of which lack functional forelimbs, were considered basal. Our analysis of the phenotype agrees with all gene sequence data indicating that *Rhineura floridana* is the sole survivor of the North American ramus leading from earliest divergence within Amphisbaenia (e.g., Kearney and Stuart 2004; Macey et al. 2004; Townsend et al. 2004; Vidal and Hedges 2005; Hembree 2006; Vidal et al. 2008).

Surprisingly, amphisbaenian monopyhyly is never recovered in recent molecular analyses. Wiens et al. (2010), for example, analyzed 15,794 characters from 22 nuclear loci and still inferred that Lacertidae lies inside Amphisbaenia, and with strong support (98% BP, 100 PP). That is to say, all datasets recover an amphisbaenian subclade composed of *Bipes,* Trogonophidae and Amphisbaenidae (=Amphisbaenoidea; see below). But there is also a strong signal, so far emerging only in molecular datasets, that requires that a diverse clade composed of lizards with quintessentially "lizard-like" body plans, Lacertidae, is even more closely related to amphisbaenoids than is the unquestionably amphisbaenian *Rhineura floridana.*

Two fossil skulls from the Paleogene, *Spathorhynchus fossorium* (Berman 1973) and *Dyticonastis rensbergeri* (Berman 1976), are crown amphisbaenians allied to *Rhineura floridana* with strong support (98% BP, 100% PP, 7 BS). These two fossils form a clade on our shortest tree (see also Kearney 2003a); that grouping is poorly supported in the maximum parsimony analysis (51% BP, 1 BS), but strongly supported (99% PP) in the Bayesian analysis. Note that the few characters supporting their monophyly (such as the jugal forming a complete postorbital bar) may well be simple plesiomorphies that are only regarded as apomorphic reversals when amphisbaenians are embedded among krypteians (that otherwise lack any vestige of the jugal bone). Regardless, these fossils are proof of the great antiquity and once widespread occurrence of rhineurids across North America during much of the Cenozoic. They apparently failed to reach Europe during the faunal interchange of the Paleocene–Eocene Thermal Maximum, as only nonrhineurid amphisbaenians are reported in Europe and adjacent North Africa from the Late Paleocene onward (Augé 2005).

Amphisbaenoidea—a clade composed of *Bipes* (*B. biporus* and *B. canaliculatus*), Trogonophidae (*Trogonophis weigmanni* and *Diplometopon zarudnyi*) and Amphisbaenidae (*Geocalamus acutus* and *Amphisbaena fuliginosa*)—is strongly supported in our tree: 99% BP, 100% PP, 11 BS, and one CI = 1.00 synapomorphy, 127(1). That agrees with strongly supported molecular hypotheses noted above: North American *Bipes* is sister to Old World Trogonophidae + Amphisbaenidae. We also recover a clade—here termed "Afrobaenia" (*taxon novum*)—composed of Trogonophidae + Amphisbaenidae inferred by Kearney (2003a) from phenotypic data and also from genetic data (Kearney and Stuart 2004). Afrobaenians have good support in our all-species analyses (65% BP, 98% PP, 3 BS) and better support (76% BP) when the analysis is confined to the traditional lacertoid and amphisbaenian exemplars in our study (see below). According to Vidal et al. (2008), African Amphisbaenidae crossed the South Atlantic late in the Paleogene to invade South America. That amphisbaenid subclade is diverse and widespread in South America today, and it even successfully invaded and diversified in the West Indies later in the Neogene.

Extant *Rhineura floridana* has no functional limbs, although vestiges of the hindlimbs only remain internally (Kearney 2002). Amphisbaenian tree topology requires either that North American *R. floridana* lost its forelimbs independently of Old World amphisbaenians, or that functional forelimbs re-evolved in *Bipes*. If amphisbaenians are in fact related to dibamids and snakes, then a parsimony argument would dictate that forelimbs must have re-evolved in *Bipes*, regardless of amphisbaenian ingroup relationships. Even if amphisbaenians have no close connection to other fossorial autarchoglossans, as molecular (and some morphological) data indicate, we are still faced with the problem posed by the peculiarities of the forelimbs and girdles of *Bipes*. The morphology of the hand (e.g., with its distinctive 2-3-3-3-3 phalangeal formula consistent with repeated digit II identities) and shoulder girdle (e.g., unfenestrated scapulocoracoid) have led some to suggest forelimb reappearance (see discussion in Kley and Kearney 2007). Current evidence is inconclusive on this point. Articulated amphisbaenian fossils from the Paleogene could prove pivotal. Fossils of *Spathorhynchus fossorium*, an Eocene stem rhineurid, are sufficiently abundant to offer a real chance of finding an articulated or associated specimen and decisively test the alternative hypotheses of forelimb evolution in Amphisbaenia.

Multi-locus genetic analyses commonly place Lacertidae inside Amphisbaenia. But branch-length asymmetry is a conspicuous feature of basal lacertoid phylogeny in sequence data (e.g., Wiens et al. 2010). A recent study based on two nuclear loci (*rag-1* and *c-mos*), but also including morphology (albeit with some composite character codings) and a potentially intermediate fossil, favored a sister relationship between Lacertidae and Amphisbaenia (Müller et al. 2011). We focus narrowly on this problem by confining analysis to all the lacertoids in our study, adding amphisbaenians, and rooting the resulting tree on a clade composed of the basal Mesozoic scincoids, i.e., *Paramacellodus* and *Parmeosaurus scutatus*. A 10,000 pseudoreplicate bootstrap search yields a single most-parsimonious tree with good support overall (not shown, as it is the traditional scincomorph topology in Figure 1). One of the admittedly weaker groups inferred, a teioid + amphisbaenian clade at 65% BP, with Lacertidae as sister to both of them, fails to support lacertids as being either sister to or nested within amphisbaenians. We accordingly regard a teioid + amphisbaenian clade of Estes et al. (1988) as a viable alternative to the "lacertibaenian" hypothesis. Amphisbaenian relationships should prove an illuminating test case in which to explore potential causes for the strongly conflicting signals in genetic and phenotypic data (see further discussion below in "Taxonomic Inclusion/Exclusion Experiments").

STEM SERPENTES

We recover the Upper Cretaceous species *Najash rionegrina* and *Dinilysia patagonica* as successive stem species to crown Serpentes in the maximum parsimony analysis. Although the hypothesis that *Najash* and *Dinilysia* are related to snakes is strongly supported in our analysis (100% BP, 100% PP, 10 BS), support for a *Dinilysia* + Serpentes clade exclusive of *Najash* is weak, largely because of noncomplementary remains in these fossils. As expected given the intermediate morphology and the incomplete preservation of these two stem snakes, crown Serpentes exclusive of *Najash* and *Dinilysia* has only very modest statistical support (54% BP, 5 BS). We find that hypothesis compelling nonetheless, as crown Serpentes can be diagnosed by 11 unambiguous synapomorphies, at least two of which—53(1) and 310(1)—are unique and unreversed on our tree. Still, the Bayesian analysis infers *N. rionegrina* and *D. patagonica* as a strongly supported clade (99% PP) that is poorly supported (57% PP) as diverging from the macrostomatan stem inside alethinophidians (see Figure 4). None of this affects our confidence in the monophyly of crown snakes with respect to any other crown squamates, as they are united by at least seven unique and unreversed (CI = 1.00) characters in our tree.

CROWN SERPENTES

Because there has been some controversy regarding the phylogenetic position of *Najash rionegrina* and *Dinilysia patagonica* in the snake tree, we list some synapomorphies they lack that unambiguously place them outside of crown snakes (see Appendix 4 for a full list; CI = 1.00 synapomorphies are denoted by an asterisk): 40(1), frontal subolfactory process sutured to parasphenoid; 53(1)*, frontal with anteroposteriorly narrow, blunt prefrontal process off the lateral base of the subolfactory process extending into prefrontal socket; 101(1), parietal supratemporal process reduced, less than 25% of parietal width; 106(1), parietal supraorbital process present; 241(4), tongue-in-groove interlocking pterygopalatine joint; 275(0), ectopterygoid lies dorsally along supradental shelf of maxilla; 310(1)*, crista tuberalis and crista prootica combine to surround the stapedial footplate and the lateral aperture of recessus scalae tympani; 332(2), basipterygoid process (and synovial palatobasal articulation) absent; 390(1), coronoid does not extend onto lateral face of surangular; and 461(3), cervical intercentra absent (except on atlas-axis).

Within crown Serpentes, we recover a basal divergence between Scolecophidia (69% BP, 5 BS) and Alethinophidia (66% BP, 5 BS), a signal that was also recovered by previous morphology-based analyses (Rieppel 1988; Cundall et al. 1993; Caldwell and Lee 1997: Zaher 1998; Tchernov et al. 2000). The sister-group relationship between Scolecophidia and Alethinophidia was not recovered by Caldwell and Palci (2010), however, who instead found scolecophidians nested within macrostomatan snakes (and accordingly regarding them to be "regressed macrostomatans").

CROWN SCOLECOPHIDIA

Within Scolecophidia, the anomalepidids *Liotyphlops alba* and *Typhlophis squamosus* clearly form a clade: 100% BP, 100% PP, 9 BS, and two CI = 1.00 synapomorphies, 197(2) and 303(1). There is more modest support (56% BP, 65% PP, 2 BS) for a group composed of the leptotyphlopid *Leptotyphlops dulcis* and the typhlopid *Typhlops jamaicensis*. Three of those synapomorphies are, however, unique and unreversed on our tree: 236(1), 270(1) and 298(1). Vidal et al. (2010) found the same tree based on molecular data. This topology contrasts with the molecular signal reported by Vidal and Hedges (2002), where anomalepidids are the sister-taxon to typhlopids, with leptotyphlopids being the sister-taxon of those two. Vidal and Hedges' (2002) scolecophidian topology was found by Cundall et al. (1993), Scanlon and Lee (2000), and Lee and Scanlon (2002) on morphological grounds. Our Bayesian analysis places typhlopids + leptotyphlopids and anomalepidids at the very base of Serpentes, but cannot resolve their relationships further (see Figure 4).

CROWN ALETHINOPHIDIA

Relative to scolecophidians and, so far as they are preserved, the stem snakes *Dinilysia patagonica* and *Najash rionegrina*, alethinophidian snakes share 22 unambiguous synapomorphies, three of which are unique and unreversed on our tree (see Appendix 4; CI = 1.00 synapomorphies denoted by an asterisk): 12(1), long internasal process clasped between descending nasal laminae; 41(1), descending lamina off frontal subolfactory process (continuation of frontal enclosure of optic nerve) lies dorsolateral to parasphenoid; 45(1), medial frontal pillar separated from subolfactory process by gap (see notes in Appendix 2); 57(3), frontoparietal suture dorsal outline deeply bowed posteriorly into U or W; 106(2), parietal supraorbital process deeply clasping frontal orbital margin; 119(2)*, maxilla ligamentously attached to palatine by a prominent palatine process of maxilla and distinct maxillary process of palatine (with the former lying anterior to the latter); 206(1), septomaxilla median flange long, extends posteriorly to anteroposterior level of anterior margin of prefrontal; 207(1), septomaxilla posterior process on laterally ascending flange long, extends posteriorly deep to prefrontals; 208(1), nervus ethmoidalis medialis enclosed in septomaxilla anteriorly; 219(1), margin of vomer at opening of vomeronasal organ curled downward; 224(1)*, vomer septum (vertical lamina) height partly separating olfactory chambers; 242(1), palatine anterior "dentigerous" process present only as short extension of palatine anterior to maxillary process; 323(1)*, an "ophidiosphenoid" ossification present in braincase; 351(2), perilymphatic foramen faces laterally; 361(1), single mental foramen exits dentary (sometimes more); 387(0) coronoid eminence formed by surangular and coronoid bones; 389(1), coronoid bone small and strap-like; 392(2) anteromedial ventral margin of coronoid (at/behind end of tooth row) does not contact splenial; 393(0), coronoid posteromedial process absent; 397(1), single extenal surangular foramen; 400(1), surangular dorsal margin rises steeply anterodorsally to coronoid, with apex reaching above level of tooth crowns; and 429(1), replacement teeth erupt horizontally, and then rotate through ninety degrees about the base into their functional position.

"ANILIOIDEA"

Traditional "Anilioidea"—represented by *Uropeltis melanogaster, Cylindrophis ruffus* and *Anilius scytale* in our analysis—is widely held to comprise a basal clade of alethinophidian snakes (Scanlon and Lee 2000; Tchernov et al. 2000; Apesteguìa and Zaher 2006; Wilson et al. 2010). They are polyphyletic in our study, however, and paraphyletic according to Cundall et al. (1993), and in some analyses in Lee and Scanlon (2002). In agreement with most morphological analyses, we found that first *Anomochilus leonardi*, and then a clade composed of *C. ruffus* and *Anilius scytale* (47% BP, 3 BS), diverged from the line leading to the rest of Alethinophidia, albeit with poor support in each case. Surprisingly, in our maximum parsimony analysis, *C. ruffus* is the sister taxon to *Anilius scytale*, rather than *U. melanogaster* as in most other analyses. In our maximum parsimony study, *U. melanogaster*, and not *Anomochilus leonardi* (Cundall et al. 1993), is sister-taxon to all other alethinophidians. But that topology is reversed in our Bayesian analysis, in which *Anomochilius leonardi* is strongly supported (98% PP) as the deepest alethinophidian crown divergence (see Figure 4), consistent with Cundall et al. (1993).

All morphology-based analyses of snake interrelationships (except Caldwell and Palci

2010) have concluded that "anilioids" are located outside Macrostomata (a name here attached to the clade stemming from the last common ancestor of *Loxocemus bicolor*, *Xenopeltis unicolor* and *Coluber constrictor*). This contrasts with molecular studies that found *Anomochilus*, *Cylindrophis* and uropeltines variably nested within Macrostomata (Wilcox et al. 2002; Lawson et al. 2004; Vidal and David 2004; Gower et al. 2005; Wiens et al. 2008; but not Vidal and Hedges 2002).

CROWN MACROSTOMATA

Compared to "anilioids" and scolecophidians and, so far as they are preserved, *Diniliysia patagonica* and *Najash rionegrina*, 24 unambiguous synapomorphies diagnose Macrostomata, two of which are unique and unreversed on our tree (CI = 1.00 synapomorphies marked with an asterisk). Because the point has been so controversial, we list them here: 18(2), nasal anterior width less than frontal anterior width; 115(2), loss of maxilla facial process; 170(3), supratemporal lies dorsally on parietal (or braincase alone); 174(1), supratemporal tip extends freely posterior to oto-occipital; 185(2), quadrate 70-74% of braincase depth; 194(3), fenestra ovalis opens posterolaterally; 203(1), septomaxilla with long posterodorsally directed, blade-like process (medial flange) extending nearly to frontal; 208(0), nervus ethmoidalis medialis passes dorsal to septomaxilla; 210(1), cupola for vomeronasal organ closed medially (even if only narrowly); 224(2)*, vomer septum (vertical lamina) nearly completely separating olfactory chambers along with septomaxilla and nasal; 247(1), choanal process of palatine touches or abuts the vomer without articulation; 248(1), choanal process of palatine forms a short vertical or horizontal lamina; 256(2), palatine teeth enlarged, similar in size to marginal teeth; 260(1), pterygoid articulates with palatine in a tongue-in-groove joint; 265(1), quadrate ramus of pterygoid blade-like and with distinct longitudinal groove for insertion of the protractor pterygoidei muscle; 268(2), pterygoid teeth enlarged, similar in size to marginal teeth; 274(1)*, anterior end of ectopterygoid located dorsal to maxilla, invading the dorsal surface of the maxilla to a variable degree; 299(2), temporal muscles spread onto supraoccipital to form a Y-shaped crest; 300(2), supraoccipital nuchal crest spreads laterally onto oto-occipital; 324(2), dorsum sellae enclosed in a distinct fossa, a cup-like depression walled laterally and ventrally by the basisphenoid and anteriorly by the parasphenoid rostrum; 337(0), posterior opening of Vidian canal within the basisphenoid; 351(0), perilymphatic foramen faces ventrally; 387(2), coronoid eminence formed mainly by surangular; and 420(3), maxillary tooth count 16 to 27.

XENOPELTIS + *LOXOCEMUS*

In most morphology-based analyses, *Xenopeltis unicolor* and *Loxocemus bicolor* are successive sisters to other crown macrostomatans (Cundall et al. 1993; Tchernov et al. 2000; Wilson et al. 2010). In the present analysis, however, New World *Loxocemus* and Old World *Xenopeltis* form a clade (see also Scanlon and Lee 2000; Lee and Scanlon 2002), albeit with very poor support (31% BP, 62% PP, 1 BS). That they are closer to other extant macrostomatans than to "anilioids," scolecophidians and stem snakes seems secure (88% BP, 98% PP, 8 BS; see Appendix 4). But just where they fit among basal macrostomatans, and in particular relative to marine simoliophiids, is considerably less clear (see "Simoliophiidae" below). In sharp contrast, molecular studies have found *Xenopeltis* and *Loxocemus* variably nested within booid henophidians (Wilcox et al. 2002; Lawson et al. 2004; Vidal and David 2004; Vidal and Hedges 2004; Wiens et al. 2008).

CROWN BOLYERIIDAE

An important result of our study is the first discovery of morphological support for a unique phylogenetic relationship between the Southeast Asian *Xenophidion acanthognathus* and the two species of Bolyeriidae endemic to the Seychelles deep in the Indian Ocean. This result was suggested on molecular grounds by Lawson et al. (2004) and is supported in morphology by the development of a unique mobile joint between the anterior and posterior halves of a bipartite maxillary bone in *X. acanthognathus*, *Casarea dussumieri* and *Bolyeria multocarinata*. This character—125(1)—unequivocally supports (CI = 1.00) the sister-group relationship of *Xenophidion* with *Casarea* in our study. Six additional unambiguous, if considerably more homoplastic, characters also support this clade (see Appendix 4): 8(0), small ethmoidal foramen pierces body of premaxilla to palatal surface; 45(3), medial frontal pillar fused with subolfactory process; 343(1), ventral crest on basioccipital; 510(1), pubis absent; 516(1), ischium absent; and 520(1), ilium absent. One might reasonably question the independence of the last three apomorphies, since suppression of the cartilaginous pelvic girdle eliminates all three ossifications that normally appear within it later in ontogeny. We are inclined to accept the bolyeriid affinities of *X. acanthognathus* even though that hypothesis is poorly supported statistically (34% BP, 64% PP, 3 BS).

Our maximum parsimony tree (see Figures 1 and 2) has Bolyeriidae as sister to Henophidia, which is used here for a clade including traditional "booids" and Caenophidia, rather than to designate a "morphological grade" in snake evolution, as in Underwood (1967). That puts bolyeriids in a more basal position within Macrostomata than indicated by previous morphology-based analyses (Cundall et al. 1993; Scanlon and Lee 2000; Tchernov et al. 2000; Lee and Scanlon 2002; Apesteguìa and Zaher 2006; Wilson et al. 2010). However, our morphological data agree with molecular analyses (Vidal and Hedges 2002; Lawson et al. 2004; Gower et al. 2005; Wiens et al. 2008)—with the exception of Wilcox et al. (2002)—that tend to place bolyeriids more basally within Macrostomata.

Some bolyeriid apomorphies, such as loss of all vestiges of the pelvic limbs and girdles, are also shared with caenophidian snakes. Such characters may be noteworthy in that bolyeriids are often inferred to be nearer to caenophidians than are other basal macrostomatans (e.g., Wilson et al. 2010). Some pelvic elements and femora, at least, are widely distributed among basal macrostomatans, including the tropidophiids identified here as the sister to Caenophidia in our maximum parsimony analysis. If the maximum parsimony tree is correct, then bolyeriids lost the last remnants of their legs and pelvis independently of caenophidians. There is reason to doubt such a deep position (one that is distal to henophidians) for bolyeriids, however. A 50% majority rule consensus tree derived from a completely unordered maximum parsimony analysis of our dataset results in bolyeriids moving inside Henophidia closer to caenophidians than to booids (as sister to Tropidophiidae + Caenophidia). In the Bayesian analysis, moreover, bolyeriids are sister to Caenophidia (85% PP), with tropidophiids as sister to both of them (see Figure 4). Support is not particularly compelling in either case, raising new questions for future study.

SIMOLIOPHIIDAE

Represented in our analysis by *Eupodophis descouensis*, *Haasiophis terrasanctus*, and *Pachyrhachis problematicus*, we recover a clade of marine snakes, the Simoliophiidae (Rieppel and Head 2004), with hindlimbs like those of stem snakes. These species are especially noteworthy for having had more elements of the hindlimb (including toes) than any other crown snake. This clade is strongly supported in our analysis (85% BP, 100% PP, 5 BS), particularly impressive given the imperfect preservation of the few articulated fossils available. Simoliophiids have unmistakable anterior dorsal vertebrae with exceptionally long and posterodorsally tapering neural spines. That should help identify distarticulated simoliophiid remains from elsewhere in sediments deposited along the margins of the Tethys Sea during the Late Cretaceous.

As in some (Tchernov et al. 2000; Apesteguìa and Zaher 2006; Conrad 2008; Wilson et al. 2010), but not all (Caldwell and Lee 1997; Lee 2000, 2005; Scanlon and Lee 2000; Lee and Scanlon 2002), previous analyses, we find support in maximum parsimony analyses (60% BP, 4 BS) for simoliophiids being on the alethinophidian branch relative to scolecophidians, and thus crown snakes. That signal is much stronger in the Bayesian analysis (98% PP) and in the completely unordered maximum parsimony analysis (85% BP). We note that among the 22 unambiguous synapomorphies uniting Alethinophidia, Simoliophiidae has 62% of those preserved (8 of 13), including two of the CI = 1.00 synapomorphies. But simoliophiids are apparently plesiomorphic for 39% of the rest (5 of 13), and are missing data for nearly half of them (9 of 22). There is, moreover, additional strong support for simoliophiids being allied to macrostomatan snakes within alethinophidians (88% BP, 100 PP, 8 BS). As with the alethinophidian question, simoliophiids are missing significant data (9 of 24, or 38%). Nevertheless, simoliophiids have two-thirds of the preserved macrostomatan synapomorphies (10 of 15), but are plesiomorphic for one-third of them (5 of 15). Unlike the case with alethinophidian synapomorphies for which simoliophiids appear plesiomorphic, this need not be viewed as character discordance (i.e., if simoliophiids are sister to, rather than nested in, crown Macrostomata; see Figure 4).

All of our tree topologies for basal snakes also imply that the fully differentiated hindlimbs in simoliophiids pose a potential violation of Dollo's law (Coates and Ruta 2000). Like stem snakes, simoliophiids retain most osseous components, including ankle bones and toes, in their small legs. They are certainly snake-like in being nonfunctional as weight-bearing appendages, although they could still be used to synchronize copulation as in basal snakes today. In any case, simoliophiids are remarkable among crown snakes for having reasonably well-differentiated external appendages easily recognizable as hindlimbs. Rudiments of various hindlimb and girdle components are scattered widely among basal crown snakes; *Leptotyphlops dulcis*, for example, can have the full complement of pelvic elements, as well as a femur and a partly developed tibia and fibula (J.A. Maisano, pers. obs.; see also List 1966). Moreover, reduction and loss of various hindlimb and girdle elements must have taken place several times within snakes in any reasonably supported tree (e.g., see losses inside Scolecophidia [List 1966]). "Loss" in the sense of near suppression of external expression of the hindlimbs—leaving nothing more than a scaly spur capping the femur externally—occurs at least seven times on our maximum parsimony tree. However, if anilioids comprise a clade (e.g., Wilson et al. 2010), and if simoliophiids are sister to Macrostomata (see Figure 4), then there would still have been three such "losses" among crown snakes (in scolecophidians, in anilioids, and in macrostomatans), if in fact simoliophiids retained the ancestral snake's external hindlimbs, and did not re-evolve them.

Although our analysis firmly places simoliophiids in a clade with crown macrostomatans, it is less clear whether they are part of that crown clade. Because of some character conflict, but also because of uncertainty from nonpreservation and evolutionary transformation, the position of simoliophiids is unstable in our analyses; sometimes they are sister to crown Macrostomata, sometimes just inside that crown, and sometimes they are sister to Henophidia, as in our shortest maximum parsimony tree (see Figure 1). However, none of these alternatives has much support.

What is nonetheless clear is that, regardless of these uncertainties, snakes are terrestrial, and not marine, in origin. That is to say, the stem snakes *Najash rionegrina* and *Dinilysia patagonica* are found in terrestrial sediments, as are the oldest unambiguous (stem?) snake fossils (isolated vertebrae) from the Aptian–Albian of Europe (Cuny et al. 1990), the Cenomanian of Africa (Werner and Rage 1994) and the Albian–Cenomanian boundary of North America (Gardner and Cifelli 1999; Nydam 2002). All living Scolecophidia, *Anomochilus leonardi*, and "anilioids" are still found in terrestrial settings today. And all of these terrestrial snakes appear basal to one or more internested subclades of snakes that include marine Simoliophiidae.

CROWN HENOPHIDIA

This clade, which includes all crown macrostomatans except for *Xenopeltis* and *Loxocemus*, has poor statistical support in our maximum parsimony analysis. We nevertheless found four unambiguous synapomorphies for Henophidia: 33(1), nasal dorsal lamina in narrow contact with frontal; 184(1), quadrate stylohyal process on medial face of quadrate present as oval disc; 327(1), parasphenoid rostrum distinctly I-beam shaped, strongly compressed laterally, abruptly narrows at trabeculae; and 363(1), dentary single mental foramen displaced caudally.

CROWN BOOIDEA

Relationships at the base of Henophidia are fully resolved in our maximum parsimony tree (see Figure 1), but most details of that topology are poorly supported. The exceptions are the strongly supported Pythonidae (92% BP, 100% PP, 6 BS; see also Kluge 1993b), represented in this analysis by *Aspidites melanocephalus* and *Python molurus*, and Boinae (92% BP, 100% PP, 4 BS; see also Kluge 1991), represented here by *Boa constrictor* and *Epicrates striatus*. Support for relationships among traditional erycines (Kluge 1993a) is, however, uniformly poor, the signal weak and discordant. Nevertheless, one of the four unambiguous synapomorphies for Erycinae—473(1) a pterapophysis on the caudal vertebrae—is unique and unreversed on our tree (see Appendix 4).

We also recover good support (73% BP, 100% PP, 3 BS) for the sister group relationship of the North American dwarf boas *Ungaliophis continentalis* and *Exiliboa placata*. They are united by seven unambiguous synapomorphies: 2(0), premaxilla palatal shelf not bifid posteriorly; 12(3), nasal descending lamina abuts posteroventral base of premaxilla; 41(0), frontal subolfactory process descending lamina not in contact with parasphenoid rostrum; 84(2), postorbital contribution to posterior orbital margin reduced to 53% to 66%; 344(1), medial aperture of the recessus scala tympani entirely in opisthotic; 389(2), coronoid bone lost; and 416(0), maxillary tooth crown height constant throughout tooth row.

The dwarf boas (Ungaliophiinae) are sister to Erycinae in our maximum parsimony analysis (see Figure 1), although support for that hypothesis is very poor (21% BP, 1 BS). Surprisingly, erycines do not group with boines. Instead, the boines are poorly supported (42% BP, 2 BS) as the sister taxon of the pythons on our shortest tree (see also Wilson et al. 2010). However, the Bayesian analysis reveals a more traditional arrangement for Booidea (see Figure 4), in which Erycinae, including Ungaliophiinae, is strongly supported (97% PP) as sister to Boinae (69% PP), and those two primary clades of Boidae (67% PP) are, in turn, sister to Pythonidae. New World *Lichanura trivirgata* and Ungaliophiinae are grouped in the Bayesian tree, with Old World *Calabaria reinhardtii* and *Eryx colubrinus* diverging more basally.

CROWN TROPIDOPHIIDAE

We find strong support for Tropidophiidae (100% BP, 100% PP, 14 BS), represented in our analysis by *Trachyboa boulengeri* and *Tropidophis haetiana*. We also find much more modest support (52% BP, 3 BS) for North American tropidophiids being the sister group to crown Caenophidia. One of the nine unambiguous synapomorphies supporting that placement is, however, unique and unreversed on our tree; only tropidophiids and caenophidians have an ectopterygoid flange on the maxilla (character 121[1]; see Appendix 4).

A henophidian clade composed exclusively of Tropidophiidae and Caenophidia can be diagnosed as follows: 12(3), nasal descending lamina abuts posterodorsal base of premaxilla; 91(1), anterolateral corner of parietal temporal fossa terminates posteriorly, dorsal and ventral margins of temporal fossa converge behind frontal, so parietal table extends as flat surface toward orbital margin, and temporal muscles are confined laterally; 101(2), parietal supratemporal process absent; 121(1), maxilla suborbital process widens below articulation with ectopterygoid (CI = 1.00); 363(2), single mental foramen on dentary displaced further caudally; 389(2), loss of coronoid bone; 398(3), adductor fossa on mandible faces dorsolaterally, lateral wall below medial wall; 404(0), retroarticular process on mandible present; and 466(1), vertebral pedicles present through most of the vertebral column.

Despite unconvincing statistical support, we regard a possible tropidophiid + caenophidian clade as a reasonably well-supported hypothesis, at least with respect to most other basal henophidians. That being said, first bolyeriids and then tropidophiids are successive sisters to crown Caenophidia in our Bayesian analysis. Statistical support for that arrangment is not much better. Moreover, two of the apomorpies shared by Tropidophiidae + Caenophidia in the maximum parsimony analysis are also present in bolyeriids—91(1) and 404(0)—and another three are variably present in bolyeriids: 101(2), 389(2) and 466(1).

In either case, the traditional “dwarf boa” group composed of ungaliophiines and tropidophiids is clearly polyphyletic. Both clades are confined to tropical climes in North America and the West Indies today. That accordingly raises questions about the relationships of fossils from the Paleogene of the western interior of North America (e.g., Hecht 1959), as well as in Europe (e.g., Rage and Augé 2003), North Africa (e.g., Augé and Rage 2006), and even South America (Rage 1998), that have been assigned to the “dwarf boas” (i.e., Tropidophiidae). They could serve as key calibration points for divergence time estimates in snake phylogeny, such as the origin of Caenophidia. And they could add important new data to what could be termed the “Great North Atlantic Interchange” that occurred during the Paleocene–Eocene Thermal Maximum (e.g., Smith 2009a, 2009b). Their phylogenetic relationships should be carefully reconsidered.

A tropidophiid–caenophidian relationship was found in some earlier morphology-based analyses of snake interrelationships (Cundall et al. 1993; Tchernov et al. 2000; Apesteguía and

Zaher 2006; Wilson et al. 2010), whereas other morphological analyses found tropidophiids nested inside booids (Scanlon and Lee 2000; Lee and Scanlon 2002). In stark contrast to hypotheses derived from phenotypic data (but see Siegel et al. 2011), gene-sequence analyses have retrieved tropidophiids either as sister to *Anilius scytale* (Vidal and David 2004; Vidal and Hedges 2004; Wiens et al. 2008), as sister to all other alethinophidians (Gower et al. 2005), or as sister to all other alethinophidians except for *A. scytale* (Wilcox et al. 2002; Lawson et al. 2004). As might be expected, moving Tropidophiidae next to *A. scytale* on the strict consensus tree yields a significantly poorer explanation of our data (Templeton's test p<0.0001).

CROWN CAENOPHIDIA

Monophyly of crown Caenophidia is strongly supported in our analysis (95% BP, 100% PP, 8 BS; see Appendix 4). Within Caenophidia, *Xenodermus javanicus* is sister to a clade composed of *Acrochordus granulatus* + Colubroidea, and with good support (75% BP, 98% PP, 2 BS; see Appendix 4).

The position of *Acrochordus* as sister taxon of colubroids has been tested repeatedly by previous analyses of morphology (Cundall et al. 1993; Scanlon and Lee 2000; Tchernov et al. 2000; Lee and Scanlon 2002; Apesteguìa and Zaher 2006; Wilson et al. 2010) and molecules (Vidal and Hedges 2002; Wilcox et al. 2002; Lawson et al. 2004; Vidal and David 2004; Gower et al. 2005; Wiens et al. 2008; Sanders et al. 2010). When xenodermatids (*Stoliczkaia*: Vidal and David 2004; *Xenodermus*: Wiens et al. 2008) are included in the analysis, however, molecular data favor *Acrochordus* as sister to a clade composed of xenodermatids + colubroids, reversing relationships inferred from the phenotype in our analysis.

CROWN COLUBROIDEA

Support for crown Colubroidea within Caenophidia is only modest in our maximum parsimony analysis (61% BP, 3 BS), but strong in the Bayesian analysis (97% PP). Colubroids also have one among their 14 potential synapomorphies that is unique and unreversed on our tree (character 606[3], mineralized hemipenial spines; see Appendix 4). Unfortunately, although the hemipenial spines are definitely not mineralized in tropidophiids or in other basal snakes (with the possible exception of *Uropeltis melanogaster*), and they are heavily mineralized in colubroids, we have yet to determine which state applies to either Xenodermatidae or *Acrochordus*.

Our character and taxon sampling was not designed to resolve colubroid interrelationships, so we can only make some preliminary observations about this nearly uncharted realm in squamate systematics on the basis of morphology. Recent molecular analyses (e.g., Pyron et al. 2010) indicate that Viperidae and Elapidae are nested inside "Colubridae" because that taxon has traditionally been conceived as that collection of caenophidians that are neither vipers nor elapids. Support for colubrid paraphyly is modest in our maximum parsimony analyses (61% BP, 3 BS), but strong in our Bayesian analysis (98% PP).

We find a clearer signal for several other clades within Colubroidea. For instance, we have good support for a succession of Old World vipers diverging from the line leading to the New World branch of Crotalinae (82% BP, 97% PP, 4 BS for *Agkistrodon contortrix*, *Bothrops asper* and *Lachesis muta*). Their nearest relative among the Asian vipers in our analysis is *Daboia russelli*, and with strong support (90% BP, 100% PP, 6 BS).

We also recover a largely African clade of colubroid snakes, the Lamprophiidae (Kelly et al. 2009; Pyron et al. 2010). It includes the "boodontine" *Lycophidion capense* as well as disparate members of the southern African clade Atractaspididae (60% BP, 100% PP, 3 BS for *Atractaspis irregularis* and *Aparallactus werneri*). Statistical support for lamprophiid monophyly is mixed; it is very weak in maximum parsimony analyses (30% BP, 2 BS) but very strong in the Bayesian analysis (100% PP). A clade including these three African species is nevertheless supported by three unambiguous synapomorphies in our analyses, including a CI = 1.00 synapomorphy (character 224[3], vomer septum reduced so that only the ventral edge remains; 30% BP, 100% PP, 2 BS; see Appendix 4).

We get strong support (98% BP, 100% PP, 12 BS) for an elapid clade composed of the New World *Micrurus fulvius* and the Old World *Laticauda colubrina*, including one character that is unique and unreversed on our tree (CI = 1.00; character 224[4], vomer septum with V-shaped notch separating dorsal and ventral rami; see Appendix 4). Asian *Naja naja* and Australian

Notechis scutatus are apparently basal relative to that clade, but support is weak, so much so that we are unable to securely place the latter species in Elapidae in the strict consensus emerging from the maximum parsimony analysis. However, *Notechis scutatus* joins the other elapids in a basal polytomy with *Naja naja* in the Bayesian tree, though support is still comparatively weak (80% PP).

We infer strong support for a monophyletic, if narrowly circumscribed, Colubridae (92% BP, 100% PP, 3 BS). It includes the subclades Colubrinae (72% BP, 70% PP, 2 BS for *Coluber constrictor* and *Lampropeltis getula*) and Natricinae (94% BP, 100% PP, 4 BS, and one CI = 1.00 synapomorphy, 27[1] for *Natrix natrix*, *Afronatrix anoscopus*, *Amphiesma stolata*, *Thamnophis marcianus* and *Xenochrophis piscator*).

Although much uncertainty remains, our trees (see Figures 1–4) lend further credence to a proposed Asian origin for caenophidian snakes (Cadle 1987). To date, there is no convincing evidence that crown caenophidians, much less the colubroid crown, were extant during the Upper Cretaceous (*contra* Rage and Werner 1999; see Head et al. 2005). In the context of the maximum parsimony tree (see Figures 1 and 2), the age of Caenophidia currently relies on snake vertebrae from the Early Eocene of India (Rage et al. 2008) that can only be safely attributed to the "colubroid" total group (whether in or outside of crown Colubroidea cannot be determined; J.J. Head, pers. comm.). Nevertheless, colubroids did not secure the preeminence they enjoy today until much later in the Neogene (Holman 2000). Other carnivorous anguimorphs assumed those roles in the Paleogene, including large-bodied glyptosaurine anguids, stem species of both *Heloderma* and *Varanus,* and basal henophidian snakes related to living boines and erycines. These other anguimorph lines slowly gave way to colubroids as the primary squamate predators during the Eo-Oligocene transition. The primacy of Colubroidea was not realized fully until the Miocene, at least in North America (Holman 2000). The curious delay in that remarkable diversification, producing nearly 3,000 species alive today, has yet to be explained.

Completely Unordered Analysis

Some general comments on trees resulting from a "completely unordered" analysis are in order, primarily because a 50% majority rule consensus of 272,453 trees suggests a somewhat more traditional placement for mosasaurians. In this tree (see Figure 3), Mosasauria emerges from a polytomy inside Anguimorpha including the usual suspects, the total-groups Varanoidea and Serpentes, but also the putative fossorial polyglyphanodontian *Sineoamphisbaena hexatabularis*, and a snake-like clade composed of the fossorial anguid *Anniella pulchra*, the fossorial skinks *Feylinia polylepis* and *Acontias percivali*, and fossorial Dibamidae + Amphisbaenia.

Predictably, trees resulting from our "partly unordered" (see Figures 1, 2 and 4) and our "completely unordered" (see Figure 3) analyses differ in length (5,430 steps and 4,974 steps, respectively) as well as in degree of resolution (112 trees and 10,304 trees, respectively). In both analyses, characters that could be said to differ in kind (e.g., vertebrae amphicoelous or procoelous) are unordered. In the "completely unordered" analysis, however, those multi-state characters that could be said to differ by degree (e.g., 24 or 26 or 28 presacral vertebrae, and so on) are unordered as well.

We chose to order adjacent states in the latter class of characters according to insights derived from studying patterns of polymorphism in extant lizard populations (e.g., Gauthier et al. 2008). For example, although presacral vertebral counts could differ within species, the range of variation is invariably tightly constrained (i.e., individual *Dipsosaurus dorsalis* might have 24 or 25 presacral vertebrae, but they never have 240). Evolutionary change can only occur within the confines of the available polymorphism (which itself can evolve), thereby constraining the path of evolutionary change (Wagner and Stadler 2003). We therefore elected to order adjacent states in series, effectively treating a change from 24 to 26 presacrals as being less costly than a transition from 24 to 240 presacrals (in terms of amount of evolutionary change implied). Moreover, if a character actually evolves in an ordered series, preliminary modeling suggests that if treated as unordered, the chance of positively misleading results increases with the number of states (Merck 1999). Finally, failing to acknowledge that, for example, a lizard with 26 presacrals is more like one with 28 (or 240) than either is to a lizard with only 24 presacrals, seems to abrogate the very concept of synapomorphy.

Taxonomic Inclusion/Exclusion Experiments: The Effects of Sampling

If the goal is a complete phylogeny for Squamata, there can be no justification for ignoring any species, either fossil or Recent. Nevertheless, given that our analysis has already "removed" at least 97% of all living lizard species, and that our sample is unlikely ever to be complete so far as extinct species are concerned, we must justify our choice of exemplars and consider its phylogenetic consequences. Our primary goal in exemplar selection is to bracket ancestors of undisputed lizard clades. That effort proved fraught with difficulties, however, not the least of which is the distinct possibility that these exemplars might themselves be highly modified. Indeed, the older the divergence, the greater the chance that we may be faced with just this eventuality. For example, no living chameleon looks remotely like the ancestral acrodontan (see Figure 4). Nor does the skeleton of fossorial *Acontias percivali* look much like that of any quadrupedal skink (see Figure 4). Bearing that in mind, it may be instructive to explore the degree to which the topology of the present tree depends on the particular species included here.

We performed a series of inclusion/exclusion experiments in the manner of Gauthier et al. (1988b) to discover which branches of our tree are relatively insensitive to taxon sampling, and to identify those exemplars producing the most dramatic effects on tree topology. It is important to emphasize that while some species may prove unstable within fairly narrow limits (e.g., *Shinisaurus crocodilurus* moves from sister to *Xenosaurus* to the base of the varanoid stem under certain deletion regimes), the traditional composition of most squamate clades (such as Iguania, Acrodonta, Iguanidae, Polyglyphanodontia, Mosasauria, Gekkota, Xantusiidae, Amphisbaenia, Dibamidae, Cordyliformes, Teioidea, Varanoidea and Serpentes) is not affected by these manipulations. We therefore focus discussion on those taxa with the most marked influence on relationships among the early squamate divergences that are the primary subjects of our study.

The Importance of Fossils

We begin by deleting all Recent ingroup species to see whether data available in extinct species reveal the same topology as in our all-species analysis. In this "fossils only" analysis (Figure 6), we find 12 equally parsimonious trees whose strict consensus closely matches that derived from the "all-species" analysis (see Figure 1). That is to say, *Huehuecuetzpalli mixtecus* is still sister to crown Squamata, Iguania is sister to all other squamates, and extinct Polyglyphanodontia (except *Sineoamphisbaena hexatabularis*) is still outside of crown Scleroglossa. Likewise, Gekkota remains the sister to traditional autarchoglossans, and the latter is composed of traditional anguimorphs and scincomorphs. But there are some conspicuous differences: Serpentes joins Mosasauria outside of crown Scleroglossa, and *S. hexatabularis* joins Amphisbaenia as sister to xantusiids among scincoid scincomorphs. *S. hexatabularis* is a pivotal taxon here as in the "all-species" analysis, because removing it reproduces the "fossils-only" tree topology, except that amphisbaenians now join snakes as sister to mosasaurians (not shown).

We then removed all fossils from both the ingroup and outgroup to assess their influence on tree topology (Figure 7). The strict consensus of 296 trees still recovers the fundamental Iguania–Scleroglossa split, the sister-group relationship between Gekkota and Autarchoglossa, and the divergence between Anguimorpha and Scincomorpha. From the base of Anguimorpha, however, we retrieve a polytomy in which *Shinisaurus crocodilurus*, *Xenosaurus*, and Anguidae (aside from *Anniella*) diverge from crown Varanoidea + Krypteia. Within Krypteia, relationships among basal Serpentes are most dramatically affected by the absence of fossils—Scolecophidia is paraphyletic and basal macrostomatan and especially basal henophidian relationships are almost completely unresolved (not shown). The stem-snakes *Najash rionegrina* and *Dinilysia patagonica* apparently play central roles in resolving basal crown snake phylogeny.

Character combinations supplied by both fossil and Recent species are necessary to recover the better-resolved tree for Squamata emerging from the entire dataset.

The Mosasaur Problem

We are unable to recover the traditional topology of mosasaurs nesting in or near varanoid

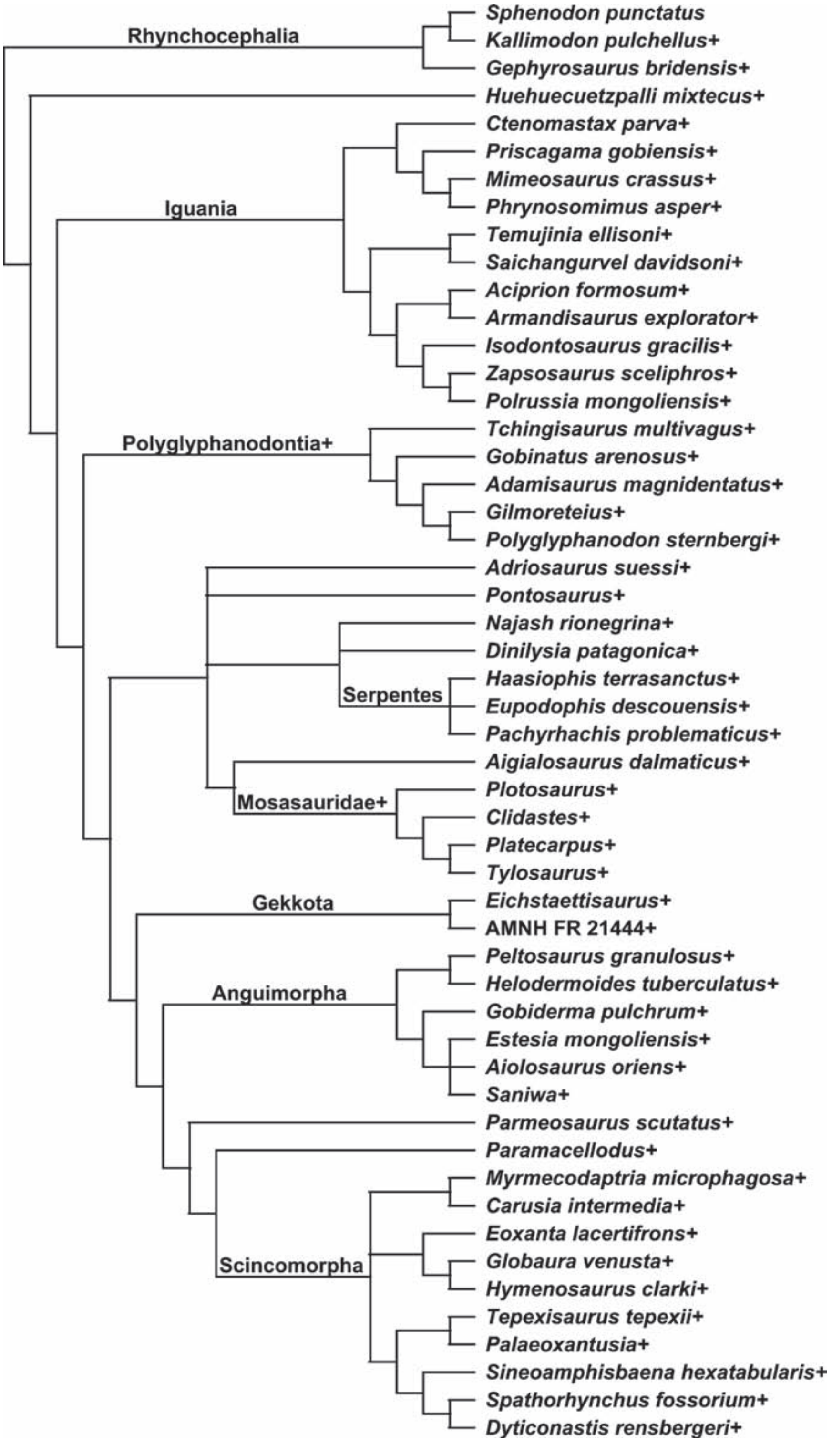

Figure 6. Maximum parsimony strict consensus tree including only ingroup fossils.

anguimorphs (e.g., Conrad et al. 2010) in most of our experiments. However, when we include snakes, but exclude other snake-like squamates (limb-reduced lizards with more than 50 presacral vertebrae), mosasaurians join snakes as sister to total-clade Varanoidea (Figure 8). Note that in no case did mosasaurians join crown Varanoidea, however, indicating that at least some of the apomorphies Mosasauria shares with Varanidae, and especially *Saniwa* + *Varanus*, must be convergent (see "Mosasauria" above).

The attraction of mosasaurians to snakes apparently underlies all of these topologies, however, as excluding snakes invariably leads mosasaurians to move outside crown Scleroglossa (Figure 9). Mosasaurians—at least those species in this analysis—apparently do not share enough apomorphies with any anguimorph subclade, including varanoids, to lead them to join Anguimorpha without the benefit of apomorphies shared specifically with snakes (which always group with anguimorphs when considered on their own; see below).

It may be revealing that the only way to obtain mosasaurians with total-group varanoids is to exclude all other anguimorphs (including total-group snakes) from this taxonomic subsample. In this experiment, however, that yields an unresolved trichotomy among the gekkotans, the scincomorphs and the mosasaurians + total-group varanoids at the base of Scleroglossa (not shown).

We tested traditional hypotheses for the placement of Mosasauria within Anguimorpha with the Wilcoxon sign-ranked test compared to our shortest tree (Templeton 1983). Mosasauria as sister to Varanidae can be rejected (p=0.0192). However, we cannot reject the idea that Mosasauria is either basal to the varanoid stem (p=0.0964), the snake stem (p=0.3365), or the stem of the entire "Fossorial Group" including snakes (p=0.7270). Nor can we reject the hypothesis that mosasaurians represent a basal divergence from the anguimorph stem (p=0.0550). These results indicate convergence for those apomorphies shared by mosasaurians, *Lanthanotus* and *Varanus* that are not also present in *Heloderma*. Nevertheless, that leaves open questions about alternative relations for mosasaurians nested inside Scleroglossa, particularly in or next to Anguimorpha, including a more or less distant connection to snakes.

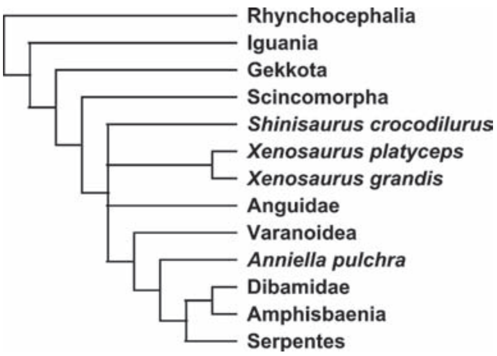

FIGURE 7. Maximum parsimony strict consensus tree including only extant species.

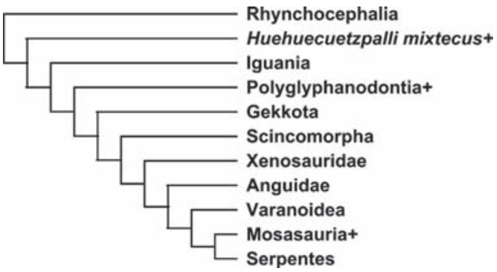

FIGURE 8. Maximum parsimony tree including Mosasauria and Serpentes, but excluding all other snake-like species.

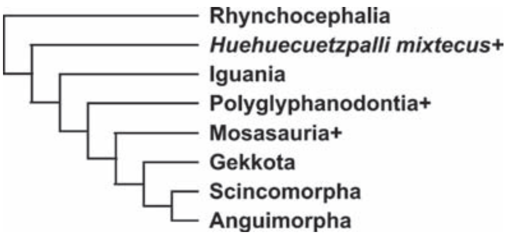

FIGURE 9. Maximum parsimony tree including Mosasauria, but excluding Serpentes and other snake-like species.

The striking apomorphies shared by carnivorous varanoids and mosasaurians likely explain why descriptions of species from the latter clade invariably involve comparisons with species of the former. But our inclusion/exclusion experiments and Templeton's tests highlight the dangers of confining comparisons of mosasaurians to crown varanids in general, and to *Varanus* in particular. Our tree might suffer from inadequate sampling, but that criticism applies equally to trees derived by excluding either all nonanguimorph squa-

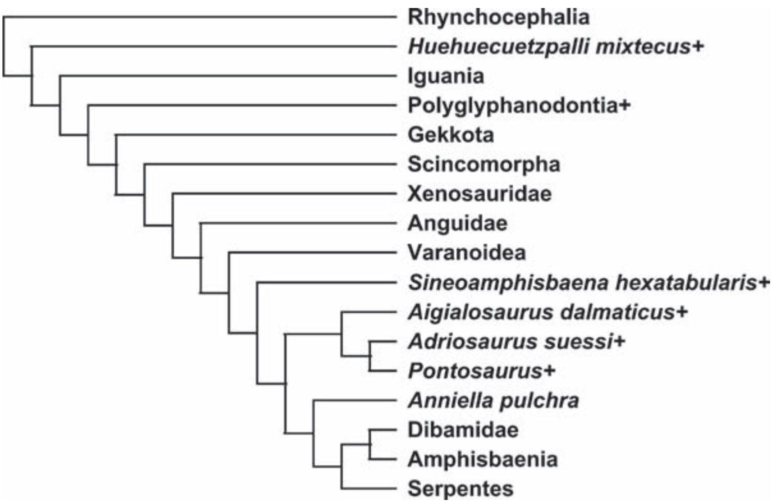

FIGURE 10. Maximum parsimony tree including basal Mosasauria (*Aigliosaurus dalmaticus* and the dolichosaurs *Pontosaurus* spp. and *Adriosaurus suessi*), but excluding derived Mosasauridae.

mates (e.g., Caldwell and Palci 2010), or all snakes (e.g., Conrad et al. 2010), from the analysis.

The phylogenetic implications of this subsampling routine are apparently unrelated to our sample of mosasaurians. That is to say, the trees described above—at least in the absence of snake-like squamates (and *Sineoamphisbaena hexatabularis*)—are the same whether or not one includes all mosasaurians in the analysis or just the most basal species (but see below). That does not, however, necessarily mean that the anomalous position of mosasaurians in the tree derived from our all-species analysis is unaffected by over-sampling of the latest, and most derived, mosasaurids (i.e., late Upper Cretaceous species of *Clidastes*, *Tylosaurus*, *Platycarpus* and *Plotosaurus*). We test this hypothesis by excluding them, thereby reducing Mosasauria to the least modified species in our analysis, namely, the most primitive mosasauroid, viz., Early Cretaceous *Aigialosaurus dalmaticus*, plus the dolichosaurs *Pontosaurus* (*P. kornhuberi* + *P. lesinensis sensu* Caldwell 2006) and *Adriosaurus suessi sensu* Lee (2000; see also Caldwell and Palci 2010).

In this series of experiments, we first delete the derived mosasaurids and, indeed, we recover the more basal mosasaurians near the root of the fossorial autarchoglossan group that is sister to total-group varanoids as in the all-species analysis (Figure 10). That relationship persists whether using only dolichosaurs or the basal mosasauroid *Aigialosaurus dalmaticus* as the sole mosasaurian exemplars (not shown). In contrast, confining the mosasaurian sample to derived mosasaurids has some remarkable consequences. First, Krypteia now emerges from inside Anguidae, predictably, with the snake-like and fossorial *Anniella pulchra* as its sister taxon and then the snake-like *Pseudopus apodus* as its first outgroup. Second, derived mosasaurids move outside of Scleroglossa as in the all-species analysis but, most surprising, with *Sineoamphisbaena hexatabularis* as their sister. Deleting *S. hexatabularis* yields the same result—krypteians emerge from inside Anguidae. But if both *Anniella pulchra* and *S. hexatabularis* are excluded, that results in an even more dramatic shift: although most other details of our all-species tree are conserved, krypteians switch from deeply nested within anguid anguimorphs to deeply nested among scincid scincomorphs (Figure 11) as inferred by Conrad (2008; thus, an "Anguiophidia" can replace "Scincophidia" depending on the fossorial species included). As discussed below, however, that result depends crucially on fossorial skinks. Without them, krypteians cannot root inside scincid scincomorphs as they do not otherwise share particular apomorphic resemblances with less modified basal skinks.

The Problem of Snake-like Squamates

As should be evident by now, fossorial squamates proved to be the chief source of character discor-

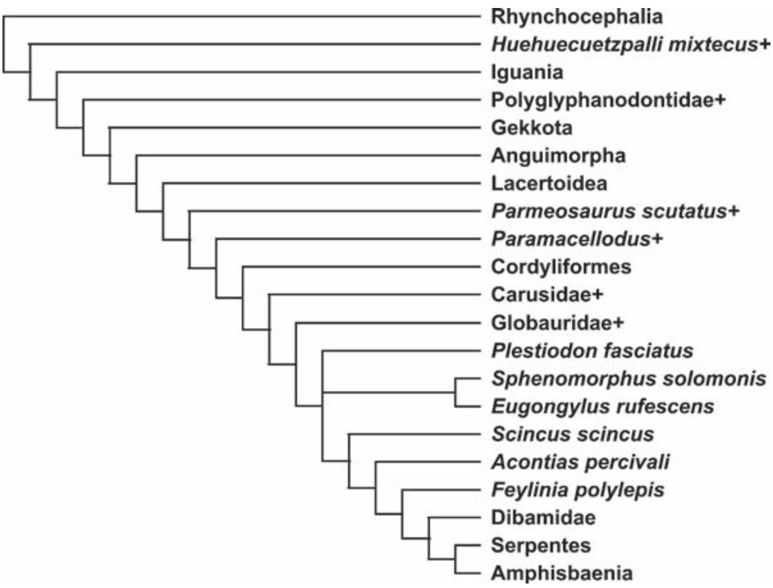

FIGURE 11. Maximum parsimony strict consensus tree excluding Mosasauria, *Anniella pulchra* and *Sineoamphisbaena hexatabularis*.

dance in all analyses. Thus, we excluded them entirely to examine their influence. Provided one overlooks the still-unresolved "iguanid problem," this experiment results in a single fully resolved tree for the rest of Squamata (Figure 12). Topological relations among species are identical to those in our all-species analysis, but this time with much stronger support for many clades (e.g., crown Scleroglossa increases from 32% to 76% BP and crown Autarchoglossa from 23% to 68%; support values rise even more, to 100% and 96% BP, respectively, when branch-shortening stem fossils are also removed).

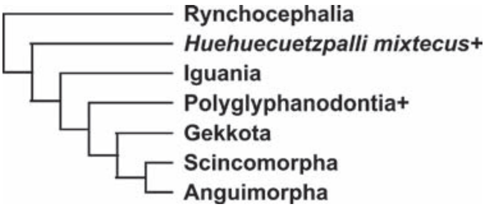

FIGURE 12. Maximum parsimony tree excluding all snake-like species.

This is essentially the same tree found by Estes et al. (1988) after they excluded snake-like squamates. Lee (1998) arrived at a similar conclusion for relationships among fossorial squamates by downweighting characters correlated with fossoriality. That these analyses might arrive at similar conclusions is perhaps unsurprising, because they are functionally the same (i.e., either removing "ecomorph taxa" or downweighting "ecomorph characters"). Nevertheless, analyses concluding that krypteians comprise a clade (e.g., Zaher and Rieppel 2000; Kearney 2003a; Conrad 2008) are burdened by no more appealing assumptions (e.g., that apomorphies independent of fossoriality, such as those in tongue anatomy, that disperse the snake-like clades elsewhere on the lizard tree, should be accorded no more weight than the potentially correlated "snake-like" apomorphies, such as body elongation and limb reduction, that group them).

If krypteians and other fossorial squamates are placed correctly on our tree, then that entails another consequence that we will now examine. If snakes, for example, are placed accurately on our tree, then we predict that when all other snake-like squamates are excluded, any given snake, or group of snakes, will still nest inside (or next to) Anguimorpha. That is to say, congruent synapomorphies should be distributed hierarchically across the lizard tree. And that is invariably the case (if mosasaurians are removed so as not to complicate the test). Indeed, snakes remain related

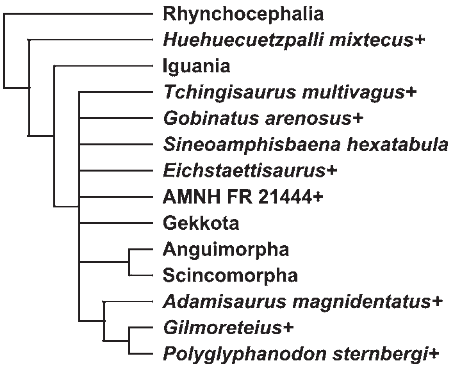

Figure 13. Maximum parsimony strict consensus tree including *Sineoamphisbaena hexatabularis* and excluding all snake-like lizards.

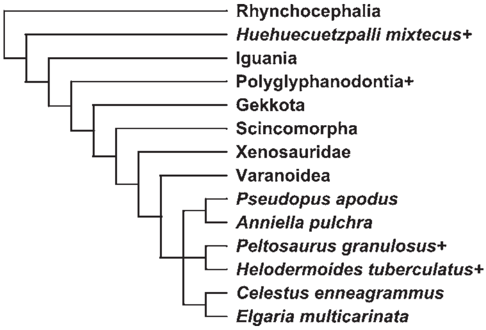

Figure 14. Maximum parsimony strict consensus tree including snake-like anguids *Pseudopus apodus* and *Anniella pulchra*, but excluding all other snake-like lizards.

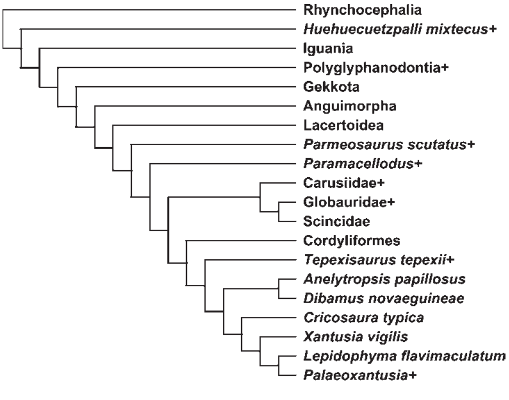

Figure 15. Maximum parsimony tree including snake-like Dibamidae (*Anelytropsis papillosus* and *Dibamus novaeguineae*), but excluding all other snake-like lizards.

to anguimorphs even when all varanoids are removed from the analysis (leaving only xenosaurids and anguids as exemplars of Anguimorpha). Snakes also nest inside anguimorphs when the analysis includes only anguids and snakes, or only xenosaurids and snakes. The anguimorph affinities of snakes thus seem robust not just because of the number of apomorphies they share, but also because snakes display the same hierarchically internested pattern among those synapomorphies expected of any anguimorph (unlike the case with mosasaurians).

When this same procedure is applied to the other fossorial lizards in our analysis, however, they are seldom related as our "all-species" tree would predict; viz., unlike snakes, most never group with other, especially nonvaranoid, anguimorphs. When all snake-like squamates (and mosasaurians) are removed from the analysis, and each well-supported fossorial clade is then added independently, *Sineoamphisbaena hexatabularis* groups with polyglyphanodontians (Figure 13; at least in the 50% majority rule consensus), *Anniella pulchra* and *Pseudopus apodus* group with anguids (Figure 14), *Feylinia polylepis* and *Acontias percivali* group with skinks (e.g., see Figure 1), and dibamids lie within scincoids on the xantusiid stem (Figure 15; the xantusiid line would thereby join the ranks of so many other autarchoglossan clades in having produced a fossorial ecomorph).

That most burrowing lizards that are supposed to be related fail to root at the same point on the tree when added individually is suggestive. It raises the possibility that given the excessive "attraction" supplied by numerous, and perhaps redundant, phenotypic characters that seem to unite all fossorial snake-like lizards, their shared snake-like habitus might perhaps be better explained by adaptive convergence rather than common ancestry. Similarly, if snakes are really related to skinks as part of Scincophidia (Conrad 2008), then why are there no characters supporting that position for snakes alone, without benefit of apomorphies seen only in the most fossorial species of skinks? And why should snakes almost invariably nest within anguimorphs (see Figures 1, 2 and 4), but fossorial *Feylinia polylepis* and *Acontias percivali* nest among scincid scincomorphs (see Figures 1, 2 and 4), if they are related to one another as predicted by the "Scincophidia" hypothesis (Conrad 2008)?

To answer these questions, we tested Scincophidia in a constrained analysis with Scincomorpha and Serpentes in a constrained polytomy, with all other fossorial taxa removed. If *Feylinia polylepis* and *Acontias percivali* do not matter as a link between skinks and snakes, then the test should retain the relationship between Serpentes and Scincidae. However, the result has Serpentes as sister to Scincomorpha, not embedded inside Scincidae, and the Templeton's test ($p=0.0453$) allows us to reject this topology compared to an unconstrained analysis with the fossorial taxa removed.

Amphisbaenians may prove an exception. Under the same exclusion regime outlined above, they remain sister to total clade Varanoidea within Anguimorpha, just like snakes do when included on their own. This seems to strengthen the case for the amphisbaenian branch being correctly placed in the lizard tree, unlike the situation with most other fossorial squamates. In striking contrast to snakes, however, amphisbaenians nest in Scincomorpha when we remove total-clade Varanoidea. Thus, micropredaceous amphisbaenians seem drawn particularly to macropredaceous Varanoidea rather than to anguimorphs generally, as snakes are. That, in turn, suggests that convergence in correlated characters—such as fewer, taller-crowned, sharply pointed, recurved and widely spaced "prehensile" teeth with interdental replacement—may underlie the amphisbaenian + total-clade varanoid association, rather than common-ancestry relationships.

This dissonance prompts the general, if not universal, suspicion among morphologists about the accuracy of the placement of fossorial lizards in their trees (e.g., Estes et al. 1988; Lee 1998; Kearney 2003a). Granted, such arguments might be raised against any grouping of fossorial squamates. But the case for monophyly seems more secure for those snake-like clades bolstered by unique character systems (e.g., the nasopharynx of Dibamidae, fore-and-aft rectilinear locomotion of Amphisbaenia, and the feeding apparatus of Serpentes) that strongly support monophyly even without benefit of characters related to their being "snake-like" in general appearance.

That is not the case for characters supporting Krypteia, however, where shared apomorphies relate almost exclusively to similar solutions to problems posed by the challenges of life underground. Even among those that might qualify as having little to do with fossoriality per se—for example, character 497(1), the position of the posterior opening of the Vidian canal on the braincase—dibamids and amphisbaenians may have the most derived state, 497(3), but the position of this opening is highly variable in snakes, with stem snakes showing both state 0 (*Diniliysia patagonica*) and state 1 (*Najash rionegrina*). Moreover, derived states for character 497 are not unique to krypteians among squamates; state 1 is, for example, also common among anguimorphs.

Snake-like clades nearly always group with one another regardless of the mix of species added. There seem to be two components to this signal; one relates to being snake-like in the sense of having a long body and reduced limbs, and the other reflects fossoriality as expressed in miniaturization and other modifications (such as dense skull bones and short tails) related to head-first burrowing (see Rieppel 1984a). Camp (1923) observed that there are two classes of "snake-like" lizards, long-tailed surface dwellers and short-tailed burrowers (see also Wiens and Slingluff 2001; Brandley et al. 2008). Thus, some snake-like but nonfossorial species, such as the long-tailed gekkotan *Lialis burtonis*, may not always group with committed burrowers in our analyses (although they will when all other gekkotans are excluded). Fossorial species will, however, frequently group together in analyses because both signals conspire to the same end.

In our analysis, for example, the fossorial anguid *Anniella pulchra* groups with the grass-swimming anguine *Pseudopus apodus* (when no other fossorial species are included). Indeed, apart from Gauthier (1982), morphological analyses have been unanimous in placing *Anniella pulchra* with the most fossorial anguine, *Anguis fragilis* (e.g., Conrad and Norell 2008; Conrad et al. 2010). Nevertheless, although fossorial *Anniella pulchra* always groups with anguids, it never joins grass-swimming anguines, much less fossorial *Anguis fragilis*, in analyses using allozymes (Good 1987) or gene sequences (e.g., Wiens and Slingluff 2001; Wiens et al. 2010; Conrad et al. 2010).

We believe that this series of experiments lays bare the central challenge in squamate phylogenetics based on morphology: Is homology expressed in the carnivorous adaptations that snakes share with mosasaurians, and with varanoids, or does homology reside in the fossorial adaptations that snakes share with other burrowing squamates, or neither? It is this conundrum that squamate systematists hoped to overcome by adding gene-sequence data to the mix of phenotypic character systems traditionally used to address this problem.

Molecules vs. Morphology

Depending on one's outlook, hopes for improved understanding of squamate phylogeny based on molecular data were somewhat justified: the distinctive core fossorial clades widely supported across morphological data sets—dibamids, amphisbaenians and snakes—never group together in molecular trees. However, not only was the morphological analogue of "long-branch attraction" seemingly overcome with the aid of gene sequence data, so were the very foundations of modern ideas about lizard evolution derived from the phenotype: instead of being sister to all other crown squamates, Iguania was placed high in the lizard tree next to anguimorphs and snakes (with strong support from several genes, including nuclear and mitochondrial; e.g., Townsend et al. 2004; Vidal and Hedges 2004, 2005; Lee 2009; Okajima and Kumazawa 2010; Wiens et al. 2010). This is a particularly interesting problem we now consider in more detail.

Beginning with the publications of Vidal and Hedges (2004, 2005), a radically different picture of squamate phylogeny based on DNA sequence data began to emerge. This initial result was corroborated and refined by Townsend et al. (2004) with much denser taxon sampling, and later still with a marked increase in the sample of species and nuclear loci investigated (Wiens et al. 2010). Our tree derived from phenotypic data and that inferred from the most comprehensive nuclear sequence dataset (Wiens et al. 2010) agree on the following clades: Iguania, including a sister-group relationship between chameleons and agamines, with leiolepidines as their sister, and a monophyletic Iguanidae; Gekkota, and its sister-group relationship with Autarchoglossa (except Iguania); Scincoidea, with a sister-group relationship of xantusiids and cordyliforms, and their sister relationship to Scincidae; Lacertoidea, and the sister-goup relationship of teioids and lacertids (even if the latter are part of Amphisbaenia); Anguimorpha (not including snakes); and Serpentes, as well as a monophyletic Alethinophidia and Colubroidea.

Nevertheless, the results of studies based on sequence data differ radically from all morphology-based phylogenetic analyses of squamates in fundamental ways. Lee (2009) was the first to address squamate phylogeny by concatenating morphological and molecular data, but discounted the apparent discordance between them owing to poor support in the mtDNA results. Wiens et al. (2010) also performed analyses combining Conrad's (2008) morphological dataset with their nuclear gene sequences to find strong support for the new molecular tree topology. In the case of Scleroglossa in particular, such conspicuous incongruence is not so easily dismissed (e.g., Templeton's test $p<0.0001$). Both signals—that the iguanian branch lies near the top of the lizard tree in all genetic datasets but at its base in all phenotypic datasets—are strongly supported, which is what makes them so interesting, if there can be only one Tree of Life.

The inference that Dibamidae might be sister to all other squamates is another conspicuous difference (e.g., Townsend et al. 2004; Wiens et al. 2010). Dibamids are so modified that we could believe almost anything about them based on the character systems that we investigated. Nevertheless, we find little anatomical support for such a basal placement among squamates in our dataset. For example, much has been made of an apparent plesiomorphy in the dibamid tongue (e.g., Vidal and Hedges 2005). Although it is true that dibamids lack the notched tongue-tip present in all other squamates (except chameleons), their tongues are otherwise entirely scincomorphan in being flattened, with ventrolateral plicae, and in being covered with keratinized scales bearing crenellated apical edges (at least in *Anelytropsis papillosus;* the tongue in *Dibamus novaeguineae* lacks discrete scales and is composed of simple keratinized ridges apparently formed by fusion among adjacent scales; Schwenk 1988). Indeed, there is a significant difference (Templeton's test $p=0.0135$) between our morphological and all molecular topologies when we place Dibamidae and Gekkota basal to other squamates as inferred in molecular analyses.

Heloderma poses another conspicuous difference, because there has never been any indication in morphological phylogenetics in nearly two centuries of intensive study that this clade is anything but a varanoid anguimorph (e.g., Wiegmann 1834; Conrad et al. 2010; see Figure 1). Wiens et al. (2010), however, inferred that *Heloderma* lies on an "anguioid" branch with *Xenosaurus grandis* plus Anguidae, and with strong support (100% BP, 100% PP). These alternatives are significantly different (Templeton's test $p<0.0007$). Wiens et al. (2010) also found the Chinese xenosaur *Shinisaurus crocodilurus* to be closer to Varanidae than is *Heloderma*. This requires convergence in all the classic varanoid synapomorphies, including a deeply bifid and highly protrusible foretongue, a characteristic snout with retracted nares, prehensile teeth with infolded bases (plicidentine), a distinctive intramandibular jaw joint, and a powerful tail absent caudal fracture planes (see extensive list in Conrad et al. 2010). There are, moreover, no data in morphology supporting *Heloderma* as sister to a group composed of *Xenosaurus* plus Anguidae. Although we found some support for a *S. crocodilurus* plus *Xenosaurus* clade (i.e., Xenosauridae), we also noted some contrary evidence in our dataset suggesting that the former species is sister to all varanoids, including *Heloderma* (see also Conrad 2008; Conrad et al. 2010).

Most surprising, molecular analyses uniformly infer a non-monophyletic Amphisbaenia, which would require convergent evolution in more than 50 unique morphological synapomorphies (Kearney 2003a). Wiens et al. (2010), for example, recovered *Lacerta viridis* inside Amphisbaenia, i.e., lacertids are the sister group of amphisbaenoids, with *Rhineura floridana* as sister to both of them, and with strong support (98% BP, 100% PP). Imposing this topology on our strict consensus tree indicates a significant difference (Templeton's test $p<0.0001$). That incongruity disappears, however, when their gene sequence data are combined with Conrad's (2008) phenotypic evidence that, like ours (see Figures 1–4), strongly supports monophyly of Amphisbaenia as the composition of that clade is traditionally understood (Rhineuridae + Amphisbaenoidea, but not Lacertidae; $p<0.0001$). The Bayesian analysis in Wiens et al. (2010) suggests that conspicuous branch-length asymmetry and attendant long-branch attraction may underlie this problem. Although we did not recover Amphisbaenia among lacertoids in our analysis, even when it was the only fossorial clade included, there are data, including the morphology of the tongue, indicating lacertoid, if not specifically lacertid (Müller et al. 2011), relations for this clade (see "Amphisbaenia" above and Estes et al. 1988).

There are also some conspicuous differences between molecular and morphological trees for snakes, particularly as regards the position of Tropidophiidae. We found reasonably good support for tropidophiids being sister to Caenophidia, and thus nested well inside Henophidia and Macrostomata (see Figures 1–4). But genetic data from mtDNA (e.g., Wilcox et al. 2002) and nuclear DNA sequences (e.g., Vidal and Hedges 2002; Wiens et al. 2008) consistently place tropidophiids deep in the snake tree among basal alethinophidians (e.g., 98% BP for an *Anilius scytale* + *Trophidophis melanurus* group in Vidal and Hedges 2002; more than 94% for *Anilius scytale* + *Tropidophis haetinaus* and *Trachyboa boulengeri* in Wiens et al. 2008). That topology differs significantly from ours (Templeton's test $p<0.0001$).

Even considering the cases listed above in which we have strongly supported alternative hypotheses, they pale by comparison to the fundamental disagreement about the positions of *Huehuecuetzpalli mixtecus* and Iguania in the lizard tree. We found strong support for the Early Cretaceous fossil species *H. mixtecus* as sister to crown Squamata, and for Iguania as sister to all other crown squamates (see Figures 1–4). In sharp contrast, however, Wiens et al. (2010; see also Lee 2009) found weak support (53% BP) that *H. mixtecus* was sister to Iguania, and reasonably good support (69% BP) that this group was sister to a clade composed of snakes (and mosasaurs) + anguimorphs.

If that hypothesized position for Iguania within Squamata is accurate, however, it requires from 51 to 69 evolutionary reversals in diverse character systems, that is to say, cases in which iguanians must re-evolve the unmodified ancestral lepidosaurian conditions still retained by Rhynchocephalia (and *H. mixtecus*). And if Iguania lies inside a clade composed of anguimorphs + snakes (e.g., Vidal and Hedges 2005), that requires from 55 to 77 reversals. Worse still, placing *H. mixtecus* on the iguanian stem (e.g., Wiens et al. 2010) on that tree requires from 88 to 147 morphological reversals. We searched exhaustively for phenotypic character evidence that might support the new molecular signal for these novel groups during the course of this study, but found not a single synapomorphy, ambiguous or otherwise, that could support gene trees in which either Iguania or *H. mixtecus* lies nested within either Autarchoglossa or Scleroglossa, much less that they shared an ancestor with any part of Anguimorpha.

Conclusions

There are roughly 9,000 species of Squamata alive today (Uetz 1995–2011). With the exception of Aves, no other living clade of diapsid reptiles is remotely near as diverse. Given that the squamate stem must extend deep into the Triassic, there are presumably a significant number of extinct species that could be added to the "total group" of Squamata (viz., Pan-Squamata). We studied only 192 of them, too often from a CT scan of a single adult specimen (although our complete sample consisted of 1,319 specimens; see Appendix 1). Nevertheless, those 192 species were selected carefully in an effort to bracket ancestral states for well-supported squamate clades identified in previous studies. This shortcoming in taxon sampling is offset somewhat by the diversity of character data that we assembled. We also significantly increased the number of phenotypic characters over that used in the most recent comprehensive study of the problem (i.e., 610 compared with 363 in Conrad 2008). And we illustrated all states (except "absence") for nearly every (qualitative) character, essentially typifying our character concepts by tying them to specific images instead of trying to describe them with words alone. We trust that this will facilitate addition of more species to the squamate dataset and eventually overcome the constraints of the present study.

Our tree (Figure 1) may offer the best argument for the adequacy of our sample of characters and taxa. Lizard systematists will be familiar with much of its topology. They might contest the position of a species here or there, especially of an incomplete fossil (e.g., *Sineoamphisbaena hexatabularis*), or of an extant species within larger clades whose interrelationships were not investigated fully (e.g., Iguanidae, Gekkota, Scincidae and Caenophidia). Or they might have good reason to question the placement of some major branches on that tree (e.g., Dibamidae, Amphisbaenia and Mosasauria). But its deeper divergences among less modified forms are nearly universal components in phylogenies based on the phenotype (see review in Conrad 2008). In our view these include the following: *Hueheucuetzpalli mixtecus* is a stem squamate; Iguania is sister to Scleroglossa; Polyglyphanodontia is on the scleroglossan stem; Gekkota is sister to Autarchoglossa; Scincomorpha is sister to Anguimorpha; and Serpentes is either close to or nested within Anguimorpha. Of course, the exact composition of these clades can be controversial, especially considering the plethora of taxonomies proposed for various groupings of snake-like squamates since Cuvier's time. Nevertheless, the major outlines of the squamate tree that diversified during the latter half of the Mesozoic remain intact despite these rogue elements (*sensu* Nixon and Wheeler 1992)—most notably Mosasauria, *Sineoamphisbaena hexatabularis* and several snake-like taxa—whose influence is confined largely to altering relationships among one another in an otherwise remarkably stable and well-supported tree (see Figure 12).

Some groups emerging from molecular phylogenies pose radically different hypotheses (e.g., the "Toxicofera" of Vidal and Hedges 2005). The markedly dissimilar positions of *Huehuecuetzpalli mixtecus*, Iguania, Dibamidae and Tropidophiidae, and the nonmonophyly of Amphisbaenia, Scincomorpha and Varanoidea present some of the most striking examples of discordance between genetic and phenotypic phylogenies anywhere in the vertebrate tree.

The relationship of Iguania according to gene-sequence data poses a particular challenge in evolutionary biology (see, for example, Schwenk and Wagner 2004). According to ideas about squamate evolution based on the phenotype, iguanians resemble amniotes generally in lacking a dense series of internested synapomorphies that arose along the branch leading toward the more chemosensory-oriented and longer-bodied anguimorphs (and snakes) from the more visually oriented and longer-limbed ancestral squamate (Gauthier et al. 2011). These include the following disparate set of apomorphies from across the phenotype, which are shared by scleroglossan squamates adapted to markedly different environments, including swimming in the ocean, gliding through the air or burrowing underground: lateral enclosure of the olfactory tracts of the forebrain by the frontals; a restricted orbitonasal fenestra; a septomaxilla that is expanded and convex where it overlies the enlarged vomeronasal organ, encapsulating that organ medially and posteriorly, overlapping the palatal shelf of the maxilla posterior to the margin of the palatal opening of the vomeronasal organ, and with a medial flange enclosing the ethmoidal nerve anterodorsally; a vomeronasal nerve that exits the vomeronasal organ via a canal on the dorsal surface of the vomer; a prominent choanal fold on the palatine; the ventral origin of the temporal muscles on the parietal table and its supratemporal process; a squamosal lacking an ascending process and with its main shaft lying against the parietal supratemporal process; the jugal broadly separated from the squamosal on the upper temporal bar; a kinetic jugal-postorbital joint; a postorbital bone with a shortened jugal ramus; a broad facial process of the maxilla; a crescentic ectopterygoid with a slot medially clasping the supradental shelf of the maxilla; a reduced pterygopalatine joint, with the former bone barely underlapping the latter laterally; a broad interpterygoid vacuity; a braincase with an alar process on the prootic and in which the posterior auditory foramen is enclosed entirely in the prootic; an axial skeleton in which there are at least two vertebrae that have been added to the presacral column, bringing the total to at least 26 vertebrae; a pectoral girdle with an anterior process on the interclavicle and a clavicle that is strongly angulated, curving anteriorly away from the scapulocoracoid; a notch on the distal epiphysis of the tibia received by a corresponding ridge on the astragalus; rectus abdominis muscles that insert into the hinges between the transverse ventral scale rows; loss of the mid-dorsal scale row; and a flattened and keratinized foretongue with a reduced role in prey prehension and an increased role in vomero-olfaction.

Thus, it is not a simple matter of iguanians re-evolving lingual prey prehension as some have suggested (e.g., Townsend et al. 2004). None of these synapomorphies can reasonably be inferred to have been present in either iguanians or rhynchocephalians ancestrally, nor are they present in any other diapsids (or turtles). According to molecular trees, however, they must all have reversed along the iguanian stem, even though they are not localized to any particular anatomical region, organ system or functional unit, nor do they stem from the same embryonic sources or appear at the same time during ontogeny. Moreover, most of them would not qualify as candidates for paedomorphosis, because they do not characterize early stages in squamate ontogeny. The list of reversals is of course even longer for *Huehuecuetzpalli mixtecus*, since this Early Cretaceous species lacks not only all of these scleroglossan and autarchoglossan novelties, but also all of the synapomorphies diagnosing crown Squamata (so far as they are preserved in this fossil species).

This case study leads to a fundamental question for systematists: Can it be the case that such a broad sample of the phenotype through time is so misleading as to be overturned so fundamentally by gene sequence data? If recently established squamate molecular trees are accurate, and if such unprecedented levels of homoplasy in disparate anatomical systems of organisms pursuing very different lifestyles is possible in morphological evolution, then systematists and others must reassess the utility of the phenotype for investigating fundamental questions in evolutionary history. Why, for example, would anyone expect that an apparently primitive stem fossil, such as *Huehuecuetzpalli mixtecus*, would be useful for calibrating divergence times, or for assessing past biogeographic distributions from the fossil record? These are seminal questions for reconstructing the Tree of Life. Simply adding these datasets together in a "combined analysis" hardly does justice to the depth of the quandary; such strongly supported incongruence begs for explanation in and of itself.

One might attribute this discordance to a misplaced root on the lizard molecular tree, given the roughly 350 million years separating living *Sphenodon punctatus* from the lizard crown. But that cannot be a complete explanation, because simply re-rooting that tree between *Hueheucuetzpalli mixtecus* and Squamata will not resolve all the discordance. It also seems unlikely that the problem reflects inadequate sampling of the species and genes available in the Recent biota, since the discordance only grows stronger with increasing samples of both. Nevertheless, branch-length asymmetries readily apparent in molecular datasets (e.g., Wiens et al. 2010; see Figure 4) raise the specter of long-branch attraction. Bayesian and maximum likelihood analyses may perform better than maximum parsimony in such circumstances (Felsenstein 2004), but that hardly renders them immune to this source of error.

Whatever the explanation might be, all indications are that the contrary signal appears genome-wide. Note that most species of the major reptilian clades (*Sphenodon punctatus*, Crocodylia and Testudines) tend to be much longer-lived than are most species of Squamata (Castenet 1994). Generation time, and its potential influence on rates of molecular evolution (Smith and Donoghue 2008), could play such a genome-wide role. And, indeed, there are indications in both mitochondrial (e.g., Jiang et al. 2007) and nuclear genes (e.g., Hugall et al. 2007) that lizards in general, and snakes and iguanians (especially acrodontans) in particular, display conspicuously high rates of molecular evolution compared to other reptiles (indeed, in what might be a consequence of their very small population sizes, snake rates exceed those of all other vertebrates according to Jiang et al. [2007]). There is also the possibility that rates of molecular evolution could be altered episodically by drastic changes in population size in survivors of mass extinctions (see Bromham 2009). The core "krypteian" clades whose phylogenetic relationships engender the most controversy seem to have survived the asteroid impact 65 million years ago, when fossorial habits and a low metabolism might have proved a distinct advantage. They now rank among the longest branches anywhere in the lizard tree in both the genotype (Wiens et al. 2010) and phenotype (see Figure 4).

It is not clear to us that simply conducting "combined analyses" of genetic and phenotypic characters adequately addresses these issues. The potential explanatory power in character congruence led us to combine evidence from disparate phenotypic systems. Wiens et al. (2010) also concatenated their multi-gene datasets and added them to Conrad's (2008) phenotypic dataset including fossil and Recent species. Given the staggering disparity in the number of characters in each case, however, that effectively amounts to simply imposing the molecular tree on the morphological dataset rather than a genuine search for consilience or for an explanation of significant congruence.

Moreover, on key points of contention described above, we anticipate that imposing the phenotypic tree on the genetic dataset will explain much more of these data than vice versa. Of course, an apomorphy can be optimized on any phylogeny by some criterion; in that sense, the anomalous position of Iguania on molecular trees can be said to "explain" the absence in Iguania of all those phenotypic novelties arising along the scleroglossan branch as "evolutionary reversals."

In our view, however, support for the position of any given taxon in a phylogeny is not just a matter of the total number of characters supporting any particular branch of the Tree of Life. We also expect that, far more often than not, those synapomorphies should appear hierarchically during phylogeny, arising in a series of ancestors and then passed along to all their descendants. That is simply not the case for iguanians in gene trees, however, because there seem to be no phenotypic synapomorphies indicating that they are either scleroglossans or autarchoglossans, as there are for the anguimorphs and snakes to which iguanians are allied in all gene trees.

Donoghue et al. (1989; and see Gauthier, Kluge and Rowe 1988) argued that such asymmetric patterns of homoplasy are just what one might expect for taxa that are misplaced on a phylogenetic tree. The inexplicable and highly asymmetric patterns of evolutionary reversal in the phenotype required by the placement of Iguania (and *Huehuecuetzpalli mixtecus*) in gene trees, with little or no supporting evidence in the phenotype—especially of the hierarchically internested kind that evolutionists expect—may prove to be just such a case.

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Appendix 1: Specimens Examined

Institutional abbreviations used:

AMNH	American Museum of Natural History, New York, NY, USA
BSPG	Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany
CAS	California Academy of Sciences, San Francisco, CA, USA
CM	Carnegie Museum of Natural History, Pittsburgh, PA, USA
DINO	Dinosaur National Monument, National Park Service, Dinosaur, CO, USA
FMNH	Field Museum of Natural History, Chicago, Illinois, USA
FRIM	Forest Research Institute Malaysia, Kepong, Malaysia
GM	Geiseltal Museum, Halle, Germany
IGM-MAS	Institute of Geology, Mongolian Academy of Sciences, Ulan Bator, Mongolia
IGM-UNAM	Instituto de Geología Universidad Nacional Autónoma de México, Mexico City, Mexico
KU	University of Kansas Natural History Museum, Lawrence, KS, USA
LACM	Los Angeles County Museum, Los Angeles, CA, USA
MACN	Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina

MAE	Mongolian Academy of Sciences–American Museum of Natural History Expeditions, field numbers
MUCP	Museo de Geologia y Paleontologia, Universidad Nacional del Comahue, Neuquen, Argentina
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley, CA, USA
ROM	Royal Ontario Museum, Toronto, Canada
TCWC	Texas Cooperative Wildlife Collection, Texas A&M University, College Station, TX, USA
TMM	Texas Memorial Museum, Austin, Texas, USA
TNHC	Texas Natural History Collection, University of Texas, Austin, Texas, USA
UCMP	University of California Museum of Paleontology, Berkeley, CA, USA
UF	University of Florida, Gainesville, FL, USA
UMMZ	University of Michigan Museum of Zoology, Ann Arbor, MI, USA
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
UTA	University of Texas at Arlington, Arlington, TX, USA
YPM	Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA: YPM HERR, Division of Vertebrate Zoology Herpetology Reptile Collection
ZPAL	Palaeobiological Institute, Polish Academy of Sciences, Warsaw, Poland

Outgroup
Rhynchocephalia
Gephyrosaurus bridensis: scored from Evans (1980, 1981)
Kallimodon pulchellus: BSPG 1887 VI 1, 1887 VI 2, 1908 I 76, 1922 I 15
Sphenodon punctatus: FMNH 11113, 22180, 197942, YPM HERR 009194, 010645–010647, 011419, 011420, 011431, 011432, 012896

Ingroup
Huehuecuetzpalli mixtecus: IGM-UNAM 7389, 4185A, B (scored from photographs by J.A. Gauthier)

Iguania
Stem acrodontans
Ctenomastax parva: IGM-MAS 3/61, 3/62

Priscagaminae
Priscagama gobiensis: IGM-MAS 3/77, 3/78, 3/80, MAE 98–154
Mimeosaurus crassus: IGM-MAS 3/74–3/76
Phrynosomimus asper: IGM-MAS 3/81, 3/83

Acrodonta
Leiolepidinae
Leiolepis belliana: FMNH 181071, 191791, USNM 205722, YPM HERR 010622, 012129
Uromastyx composite: *U. aegyptia*: FMNH 22214, 31031, 78661, YPM HERR 010522, 011104, 011161; *U. hardwickii:* FMNH 592, 42234, YPM HERR 011539

Agaminae
Agama agama: CAS 130806, 130808, FMNH 47531, 62382, 62403, YPM HERR 011094, 011453, 011641, 011642, 011875, 011876, 011952, 013255, 013338, 017847, 017936, 017937
Pogona vitticeps: FMNH 257083, ROM 22699, YPM HERR 009062, 010393, 011029, 011045, 011154, 011190, 011290, 012139, 013487–013489, 016629, 017075
Calotes emma: FMNH 180369, 185431, 196208, 252264
Physignathus cocincinus: FMNH 252297, 252300, 252303, YPM HERR 011193, 011218, 012089, 012230, 014378, 014495, 014499, 014954

Chamaeleonidae
Brookesia brygooi: FMNH 260015, 260017, UMMZ 210964
Chamaeleo composite: *C. calyptratus*: FMNH 66181, 66182, 66198, TNHC 62768, YPM HERR 010309, 011106, 011279; *C. laevigatus*: FMNH 47572; *C.* sp.: FMNH 22391

Stem iguanids
Temujiniidae
Temujinia ellisoni: IGM-MAS 3/63–3/66, 3/68–3/70
Saichangurvel davidsoni: IGM-MAS 585

Isodontosauridae
Zapsosaurus sceliphros: IGM-MAS 3/71
Polrussia mongoliensis: IGM-MAS 3/73
Isodontosaurus gracilis: IGM-MAS 3/84–3/87, 3/90–3/92, 3/94

Crown Iguanidae
Corytophaninae
Basiliscus vittatus: FMNH 165545, 165538, 165622, YPM HERR 011132, 010428, 011129, 010429, 010992, 010993, 011006, 012810
Corytophanes cristatus: FMNH 21794, 69226, 69227, 206165, 229589, 229601, YPM HERR 010443, 011095, 011183, 011184, 015184–015186

Crotaphytinae
Crotaphytus collaris: FMNH 8950, 22301, 22396, 48667, 117111, 117113, KU 188421, YPM HERR 010745, 011185, 011208, 011535, 012160, 014968, 014973, 014975, 015050
Gambelia wislizenii: CAS 89540, 200856, TMM M-9023, MVZ 173647, YPM HERR 010367, 011219, 012504, 014380, 017133, 017475, 017476, 017479, 017480, 017481, 017483, 017484, 017515–017517, 017545

Hoplocercinae
Enyalioides laticeps: FMNH 31354, KU 122103, 122108, 14793
Morunasaurus annularis: USNM 200739, 200752, 200767, 200770

Iguaninae
Armandisaurus explorator: AMNH 8800
Brachylophus fasciatus: FMNH 181270, UMMZ 181270, 181271
Dipsosaurus dorsalis: CAS 195765, 195772, FMNH 249784, YPM HERR 010988–010991, 011128, 011244, 012081, 012082, 012732, 012811, 013232, 013364–013367, 013527, 013814, 014376, 107614, 017776–017778, 017782–017786, 017858
Sauromalus ater: CAS 174700, TMM M-9022, FMNH 31015, TMM M8950, TNHC 18483, YPM HERR 010327, 011067, 011194, 011623–011625, 013407, 013786, 015372, 017083

Leiosaurinae
Leiosaurus catamarcensis: CM 65003
Pristidactylus torquatus: FMNH 134133, 202335, 206964, YPM HERR 011031
Urostrophus vautieri: FMNH 83576

Liolaeminae
Leiolaemus composite: *L. bellii*: MVZ 125659; *L. elongatus*: FMNH 6558, MVZ 246623
Phymaturus palluma: FMNH 209123, KU 161972, MVZ 247092

Oplurinae
Chalarodon madagascariensis: FMNH 72612, TMM M8509, YPM HERR 011951, 012866
Oplurus cyclurus: FMNH 72640, 75620, YPM HERR 011252, 012861

Phrynosomatinae
Petrosaurus mearnsi: FMNH 8431, 37720, 216151, LACM 127316, YPM HERR 011052, 011081, 012809, 016961, 017675, 017677, 017722
Phrynosoma platyrhinos: FMNH 1209, 31289, 37718, 216163, TNHC 18496, YPM HERR 010378, 010387, 011016, 011017, 011157, 011224, 011245, 011956, 011957, 013375–011377, 015367–016369, 017471, 017474
Sceloporus variabilis: CM 18383, FMNH 70941, 70946, 122866, KU 67295, YPM HERR 013181, 013182, 013203
Uma composite: *U. scoparia*: FMNH 1203, 218757, YPM HERR 010369, 010388, 011001, 011002, 013894, 015375, 016815; *U. notata:* YPM HERR 011536 (for caudal vertebrae fracture plane)
Uta stansburiana: FMNH 98465, 213914, USNM 239332, 239335, YPM HERR 010441, 010484, 010996, 011004, 011005, 011292–010294, 012146, 010147, 012165, 013893, 014974, 015363–015365, 015903, 016151, 016678, 016688, 016690, 017135, 017140, 017141, 017718, 017724–017727, 017730, 017985

Polychrotinae
Anolis carolinensis: FMNH 242279, 242297, 242298, YPM HERR 010713, 011068, 011325, 011382–011385, 011394–011399, 014925–014943, 016024
Polychrus marmoratus: FMNH 42501, 49845, 49848, YPM HERR 010620, 013340, 013556, 014659, 014950

Tropidurinae
Leiocephalus barahonensis: KU 147421, 242347, 242359, USNM 260564
Stenocercus guentheri: FMNH 27674, KU 147409, 147421
Plica plica: CAS 93243, FMNH 31355, 56019, KU 167449, YPM HERR 012859, 016071, 016072
Uranoscodon superciliosus: USNM 288891, 531654, YPM HERR 010489, 010491, 011872, 011873, 012871

Stem scleroglossans
Polyglyphanodontia
Adamisaurus magnidentatus: IGM-MAS 3/96, 3/100, 3/105, 3/113, 3/115–3/117
Gilmoreteius (=*Macrocephalosaurus*) (composite): scored from Sulimski, 1975: IGM-MAS 3/132, 3/134
Gobinatus arenosus: IGM-MAS 3/126
Polyglyphanodon sternbergi: scored from Gilmore, 1942, USNM 16585, YPM VP 003230
Sineoamphisbaena hexatabularis: scored from Wu et al., 1996, and Kearney, 2003
Tchingisaurus multivagus: IGM-MAS 3/129

Mosasauria
Adriosaurus (composite): scored from Caldwell, 2000, and Lee and Caldwell, 2000
Pontosaurus (composite): scored from Pierce and Caldwell, 2004, and Caldwell, 2006
Platecarpus (composite): scored from Williston, 1898, and Russell, 1967
Clidastes (composite): *Clidastes propython*: YPM VP 001319, and scored from Williston, 1898, and Russell, 1967
Tylosaurus (composite): scored from Williston, 1898, and Russell, 1967
Plotosaurus (composite): UCMP 32778 and scored from Camp, 1942, 1951, Lindgren et al., 2007, and Lindgren et al., 2008

Scleroglossa
Stem gekkotans
Eichstaettisaurus (composite): *Eichstaettisaurus schroederi*: BSPG 1937 I 1a,b; *E. gouldi*: scored from Evans et al., 2004
Unnamed stem gekkotan: AMNH FR 21444

Gekkota
Carphodactylidae
Saltuarius cornutus: FMNH 57498, 57500, 57501, 57503, UMMZ 127590

Diplodactylidae
Rhacodactylus auriculatus: CAS 205486, MCZ 18011, YPM HERR 017620, 017621, 013895, 017746
Strophurus ciliaris: FMNH 215488, LACM 56800, 56822, 56857, YPM HERR 010211

Eublepharidae
Aeluroscalabotes felinus: FMNH 146103, 146141, 146157, YPM HERR 011373, 016058–016060
Coleonyx variegatus: MVZ 197984, YPM HERR 9213, 14383, 010368, 010487, 010976–010987, 011069–011073, 011079, 011080, 011085, 011086, 011350, 011351, 013539, 013540, 014383, 016038, 016612, 017854, 017855
Eublepharus maculatus: CM 67524, 1310, FMNH 215851, TMM M8946, UMMZ 172893, 180452, YPM HERR 013253, 013259, 016479

Gekkonidae
Gekko gecko: FMNH 31008, 186818, 213417, 215535, 216546, YPM HERR 011138, 014687
Phelsuma lineata: FMNH 260100, 260104, 260107, UMMZ 127728, YPM HERR 018238
Teratoscincus composite: *T. przewalski*: CAS 17103, 167390, 167393, 167394; *T. scincus* (tongue): YPM HERR 013715

Pygopodidae
Delma borea: USNM 128679
Lialis composite: *L. burtonis*: FMNH 166958, USNM 213030, YPM HERR 000800 (tongue); *L. jicari* (tongue): YPM HERR 010270, 013916, 013917

Sphaerodactylidae
Gonatodes albogularis: FMNH 55929, MVZ 83380, USNM 338131

Autarchoglossa
Amphisbaenia
Amphisbaenidae
Amphisbaena fuliginosa: FMNH 22847, 40015, YPM HERR 016696

Bipedidae
Bipes biporus: CAS 126478, 142262, 151601, UMMZ 180437, 180440, YPM HERR 012844
Bipes canaliculatus: FMNH 105037, 105038, 105042, 134753

Stem rhineurids
Dyticonastis rensbergeri: UCMP 76881
Spathorhynchus fossorium: USNM 26317, CM 37242, 42233–42239

Rhineuridae
Rhineura floridana: FMNH 31774, 263913, KU 74136, UF 21110, 51811, 63388, 132744, 135623, YPM HERR 13690

Trogonophiidae
Diplometopon zarudnyi: FMNH 64429, 263882
Trogonophis wiegmanni: CAS 135944, 135954, FMNH 109462

Anguimorpha
Anguidae
Anniella pulchra: FMNH 42144, 130481, 139475, MVZ 33857
Celestus enneagrammus: FMNH 108860, 111101
Elgaria multicarinata: FMNH 23173, 23601, MVZ 140604, TMM M8974, M8975, YPM HERR 010799, 011025, 011026, 011036, 011456, 014550, 014098, 016777, 017008, 017176, 017345
Helodermoides tuberculatus: CM 1050, 51344, USNM 13861, 13869
Peltosaurus granulosus: AMNH FR 1710, 8138, 42913, FMNH 27072, USNM 13870, YPM VP 001060, 001061, 011393
Pseudopus apodus: FMNH 15680, 22088, 22359, 184449, 216745, YPM HERR 010621, 012870, 016248

Stem serpents
Dinilysia patagonica: MACN-RN 1013, 1014, MUCP v38 and scored from Caldwell and Albino, 2002
Najash rionegrina: scored from Apesteguía and Zaher, 2006

Serpentes
Scolecophidia
Leptotyphlopidae
Leptotyphlops dulcis: FMNH 40959, 41792, TNHC 60638, UMMZ 149633, YPM HERR 006172

Typhlopidae
Typhlops jamaicensis: KU 269915, 269916, USNM 12378

Anomalepididae
Liotyphlops albirostris: FMNH 216257
Typhlophis squamosus: USNM 289090

Alethinophidia
Anilius
Anilius scytale: KU 140152, USNM 204078, 204079, YPM HERR 010767

Anomochilus
Anomochilus leonardi: FRIM 0026

Cylindrophis
Cylindrophis ruffus: FMNH 60958, 252714, 259183, YPM HERR 013484, 013587

Uropeltinae
Uropeltis melanogaster: FMNH 167048–167051

Macrostomata
Bolyeriidae
Casarea dussumieri: UMMZ 190285
Xenophidion acanthognathus: FMNH 235170

Loxocemus
Loxocemus bicolor: FMNH 104800, LACM 150325, 150329, YPM HERR 013879, 013880

Simoliophiidae
Eupodophis descounensi: scored from Rage and Escuillié, 2000
Haasiophis terrasanctus: scored from Rieppel et al., 2003
Pachyophis woodwardi: YPM VP 058078

Pachyrhachis problematicus: scored from Polcyn et al., 2005

Xenopeltis
Xenopeltis unicolor: FMNH 131714, 148900, 233396, YPM HERR 011459, 013588

Henophidia
Boinae
Boa constrictor: FMNH 31182, UMMZ 184028, 184030, YPM HERR 011148–011150, 012323, 010579, 010580, 010584, 010865, 10866–010868, 011126, 011179, 011180, 011755, 011774, 014695
Epicrates striatus: UMMZ 182528, USNM 59918

Erycinae
Calabaria reinhardtii: FMNH 117833, YPM HERR 011098, 011178, 017935
Eryx colubrinus: FMNH 63117, YPM HERR 016057, 016615, 016603, 016996, 017174, 017270
Lichanura trivirgata: LACM 126004, YPM HERR 012869, 016171, 010876, 012869, 012892, 017076, 017837, 017918

Pythonidae
Aspidites melanocephalus: FMNH 97055
Python molurus: FMNH 8925, TNHC 62769, YPM HERR 010752, 010871, 011849, 010587, 010871, 011189, 011233, 012545, 012605, 014414, 017989

Tropidophiidae
Trachyboa boulengeri: FMNH 131266
Tropidophis haetianus: KU 69424, TNHC 64040, UF 99114, YPM HERR 013579, 013584–013586

Ungaliophiinae
Exiliboa placata: FMNH 207669
Ungaliophis continentalis: UTA 50569

Caeneophidia
Acrochordus
Acrochordus granulatus: FMNH 201350, 202059E, KU 040064, YPM HERR 010675, 012238, 012239, 012932

Atractaspididae
Aparallactus werneri: FMNH 250437, 250439, 250440, 250442
Atractaspis irregularis: FMNH 62204

Colubrinae
Coluber constrictor: FMNH 73944, 135284, YPM HERR 010596, 010597, 010684, 010820, 011099, 011100, 013381, 015908, 016019, 016605, 017925, 017962
Lampropeltis getula: FMNH 8500, 95184, 194430, YPM HERR 010326, 010717, 011359, 013026, 013573, 013574, 016689, 017145, 017468, 017469

Elapidae
Laticauda composite: *L. colubrina*: FMNH 13812, 13819, 202810; *L. laticauda*: YPM HERR 010590 (for vertebrae number)
Micrurus fulvius: FMNH 39479, 44928, 45812, YPM HERR 010685, 015911, 014096
Naja naja: FMNH 22468, 140060, YPM HERR 010677, 010776
Notechis scutatus: FMNH 11124, 11126, 215857, YPM HERR 013645

Lamprophiinae
Lycophidion capense: FMNH 58322, 78205, 78210

Natricinae
Afronatrix anoscopus: FMNH 179339, 179341
Amphiesma stolata: FMNH 109121, 120720, 120724, YPM HERR 010668, 011261, 015138
Natrix natrix: FMNH 30522, 30524, 30525
Thamnophis marcianus: FMNH 26260, 47069, 47071, YPM HERR 011529, 012141, 013942, 013943, 017834
Xenochrophis piscator: FMNH 120698, 120701, 179132, YPM HERR 011258, 011260, 011266

Pareatidae
Pareas composite: *P. hamptoni*: FMNH 105558, 128304; *P. margaritophorus*: YPM HERR 13498 (for vertebrae number)

Viperidae
Agkistrodon contortrix: FMNH 166644, YPM HERR 011527, 011541, 013252, 015910, 017983
Azemiops feae: FMNH 218627
Bothrops asper: FMNH 3480, 31162, YPM HERR 015031, 015032
Causus rhombeatus: FMNH 74241
Daboia russelli: FMNH 121447, 140146, 140147
Lachesis muta: FMNH 31178, YPM HERR 011656

Xenodermatidae
Xenodermus javanicus: FMNH 158613, 222889; YPM HERR 017634, 017642, 017643

Stem varanoids
Aiolosaurus oriens: IGM-MAS 3/171
Estesia mongoliensis: IGM-MAS 3/14, 3/15
Gobiderma pulchrum: IGM-MAS 3/55, 3/57, 3/59

Varanoidea
Heloderma
Heloderma horridum: FMNH 31366, TNHC 64380, UMMZ 182092, YPM HERR 010618, 016804, 016820
Heloderma suspectum: FMNH 22232, 213066, 229925, TNHC 62766, UMMZ 180473, YPM HERR 010718, 011201, 011357, 012895, 014352, 011490, 016816, 016819, 016829, 017178, 017982, 017984

Varanidae
Lanthanotus borneensis: FMNH 130981, 134711, 148589, YPM HERR 012673
Saniwa (composite): AMNH FR 8688, 8691, FMNH PR 2378
Varanus acanthurus: FMNH 97862, 218083, UTA 13015, YPM HERR 014951
V. exanthematicus: FMNH 47537, 58299, 229530, YPM HERR 010299, 010812, 011062, 011063, 011141, 011187, 011191, 013558, 013940, 014353

V. salvator: FMNH 22204, 31358, 35144, 152229, 223194, YPM HERR 010756, 010834, 011022, 011043, 011044, 011064, 011147, 011177, 011773, 013993

Xenosauridae
Shinisaurus crocodilurus: FMNH 215541, 234242, UF 68983, 71700, UMMZ 182160, YPM HERR 010846, 012816, 012817, 016844–016851, 017860, 017861
Xenosaurus grandis: FMNH 117105, 123702, 211832, 211833, YPM HERR 012818, 017680, 017859
X. platyceps: UF 60965, 60967, UTA 23594

Dibamidae
Anelytropsis papillosus: FMNH 100410, TCWC 45503
Dibamus novaeguineae: CAS 26937, 27069, 27070

Scincomorpha
Lacertoidea
Gymnophthalmidae
Colobosaura modesta: USNM 341978
Pholidobolus montium: FMNH 197865, KU 141610, 141612, UMMZ 189852, 193352

Lacertidae
Lacerta viridis: TMM M-9024, FMNH 66649, 66650, 66655, YPM HERR 005764, 011490, 012858
Takydromus sexlineatus (=T. ocellatus): FMNH 252372, 252376, 255513, TMM M8515, YPM HERR 011213, 013655, 013656, 016214, 016215, 017893, 017895, 017943

Teiidae
Aspidoscelis tigris: CAS 181811, FMNH 98502, 161622, USNM 248375, YPM HERR 001379, 011000, 011020, 011040, 011537, 012167, 012168, 013342, 013343, 013374, 014971, 015371, 016679, 016683, 016684, 016686, 016687, 017152, 017498–017509
Callopistes maculatus: FMNH 9975, 53726, 223688, TMM M8461, YPM HERR 012825, 013014, 016094
Teius teyou: FMNH 10407, 10412, 10873, MVZ 128176, YPM HERR 013708–013710, 013936–013939
Tupinambis teguixin: FMNH 22392, 22393, 22416, 31279, 213660, YPM HERR 010400, 010746, 011378, 012249, 012806, 012815

Stem scincoids
Paramacellodus (composite): DINO 14864, 15914
Parmeosaurus scutatus: IGM-MAS 3/138–3/140, 3/142, 3/143,

Scincoidea
Cordylidae
Cordylus mossambicus: YPM HERR 012670, 013408, 015387, 016154, 016155, 016221, 016258, 017006
Platysaurus imperator: YPM HERR 012507, 012534, 012669, 013493, 013813, 013818, 013819, 014885, 014886
Gerrhosauridae:
Zonosaurus ornatus: FMNH 259998, 260000, YPM HERR 016809, 012535, 012671, 017172, 017173
Cordylosaurus subtesselatus: FMNH 74082, YPM HERR 017098

Stem xantusiids
Tepexisaurus tepexi: IGM-UNAM 7466 (scored from photographs taken by J.G.)

Xantusiidae
Cricosaura typica: USNM 138495, 138498,
Lepidophyma flavimaculatum: FMNH 13002, 49271, LACM 128570, YPM HERR 012233, 012814, 013231, 013256, 013261, 014875, 014877, 015189, 016089, 016158, 016160–016161, 016165–016170, 016172–016195, 017079, 017092
Palaeoxantusia sp.: AMNH 42914, USNM 10600, 214717, 214719, 214721, 547842
Xantusia vigilis: KU 154141, LACM 123671, YPM HERR 9262, 9263, 010994, 010995, 013506, 013541, 013543, 016207, 016673, 016674, 017136, 017164, 017166–017169, 017810, 017814, 017816, 017817, 0171819, 017820, 017821, 017824–017826

Stem scincids
Carusiidae
Carusia intermedia: IGM-MAS 3/16–3/18, 3/20, 3/22–3/26, 3/28, 3/29
Myrmecodapatria microphagosa: IGM-MAS 3/95

Globauridae
Eoxanta lacertifrons: ZPAL MgR-I74, II37,III38, III61, 3/168
Hymenosaurus clarki: IGM-MAS 3/53
Globaura venusta: IGM-MAS 3/160, 3/164

Scincidae
Acontias percivali: CM 53646, 53651, YPM HERR 012687, 013918, 016251, 016521, 016792, 017082, 017085, 017095, 017096, 017926
Amphiglossus splendidus: FMNH 72804, 72807, 72808
Brachymeles gracilis: CAS 92856, 92860, FMNH 52642, 52648, UF 53604, 61595, YPM HERR 011981
Feylinia polylepis: FMNH 81939, 120967, 120967, 120968
Plestiodon fasciatus: CAS 71563, CM 67126, FMNH 118859, YPM HERR 001492, 012539, 012543, 012544, 012689, 016023, 017264, 017876
Scincus (composite): *Scincus scincus*: TMM M-9025, FMNH 72290, 216011, UF 83518, YPM HERR 011027, 011415, 011900, 012686; *S. mitranus*: YPM HERR 013565 (for cervical rib shape)

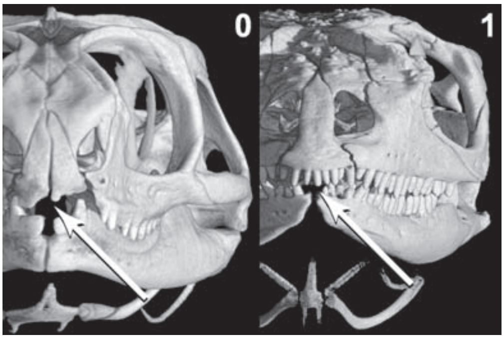
Lygosominae
Eugongylus rufescens: CAS 118116, 118753, FMNH 142306, YPM HERR 008966, 010639
Sphenomorphus solomonis: CAS 110090, 110097, 110102, YPM HERR 008962
Tiliqua scincoides: FMNH 22091, 22092, 57518, 97839, YPM HERR 012880, 010623, 013770, 017866–017868
Trachylepis quinquetaeniata: CAS 154616, YPM HERR 012688, 013562, 013892, 013909–013914, 013921–013926, 013931, 016256, 016257, 017931

Appendix 2

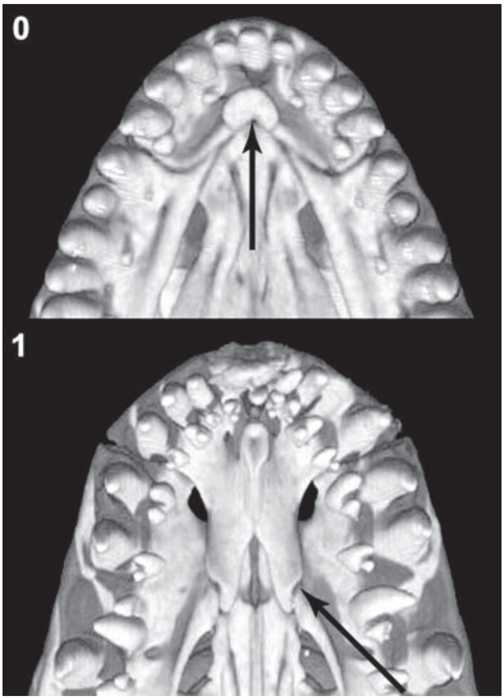
Characters Used in Analysis of Squamate Phylogeny

State "0" for binary qualitative characters generally corresponds to the presumed ancestral condition for Lepidosauria based on its presence among ingroup species as well as a succession of late Paleozoic and early Mesozoic outgroups (viz., Kuehneosauridae, *Paliguana whitei, Saurosternon bainii, Prolacerta broomi, Youngina capensis,* and *Claudiosaurus germaini*). Authorship for characters reflects the first explicit use of a character (or state) as a synapomorphy (or "shared derived character") in lepidosaur systematics. Many of them were first discovered and described by previous generations of squamate morphologists; we acknowledge that there is thus an argument to be made for awarding authorship of these "characters" in a purely descriptive sense. That said, several of these characters have been modified subsequent to their original publication as character concepts improved with deeper understanding of the anatomy, variation and distribution among lizard species.

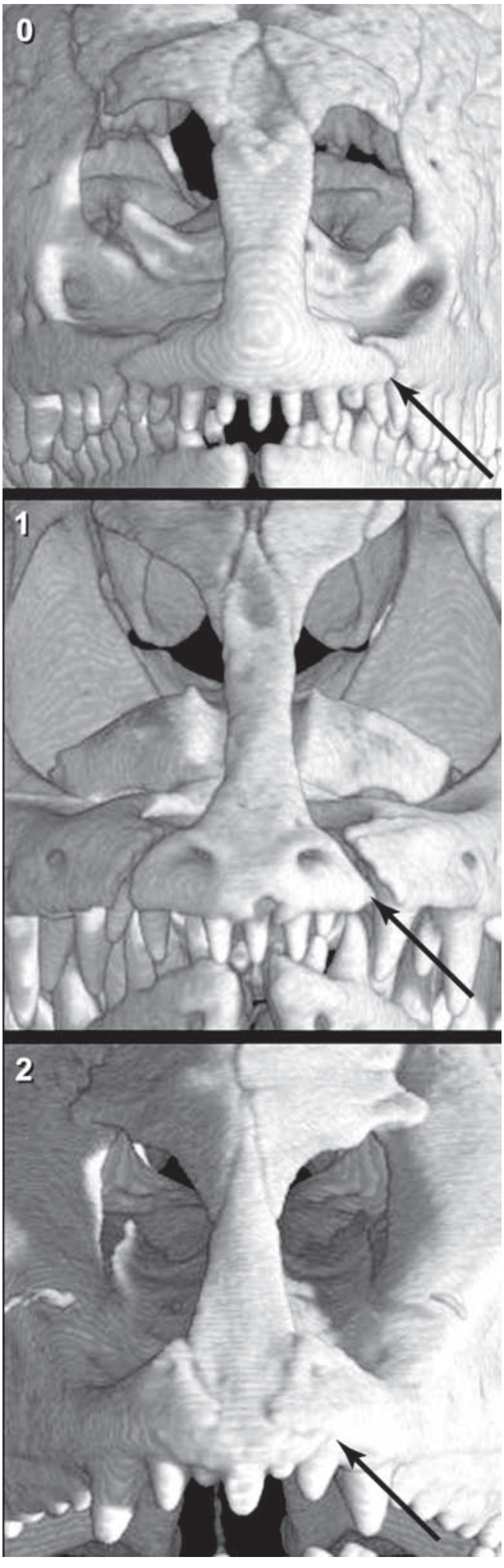
A superscript "N" (^{N}) denotes new characters (or states) discovered during the course of this study. Character states are unordered except as noted. Multistate characters tracking differences in degree or quantity are generally ordered arbitrarily from least to most, or vice versa, and are generally not illustrated. See Appendix 5 for sources for those few squamate characters and character states derived from the literature. Arrows in figures point to specific anatomical qualities; when state "0" denotes the "absence" of a feature it is generally not figured, so the number of states figured may not always match the number of states listed under each character description. States are generally assigned based on their presence in "adult" specimens as defined with respect to body size and skeletal fusions broadly associated with sexual maturation and skeletal maturity in squamates (Maisano 2002a, 2002b, 2002c). The character description is located directly below the figure to which it refers. Not all descriptions are illustrated. A few character states are not illustrated. Most illustrations are derived from three-dimensional reconstructions of the CT scans acquired for this study. These reconstructions, available at the University of Texas, Austin, Digital Morphology library website (DigiMorph.Org. c2002–2012), were produced by J.A. Maisano.



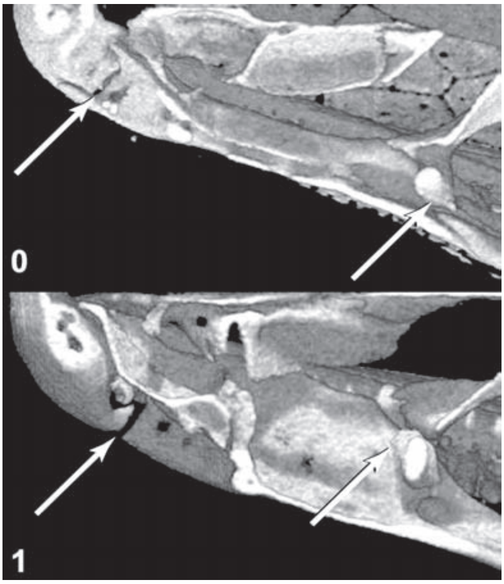
1. Premaxilla: (0) paired (*Sphenodon punctatus*, anterior view); (1) fused (*Urostrophus vautieri*, anterior view). Gauthier, Estes and de Queiroz (1988).



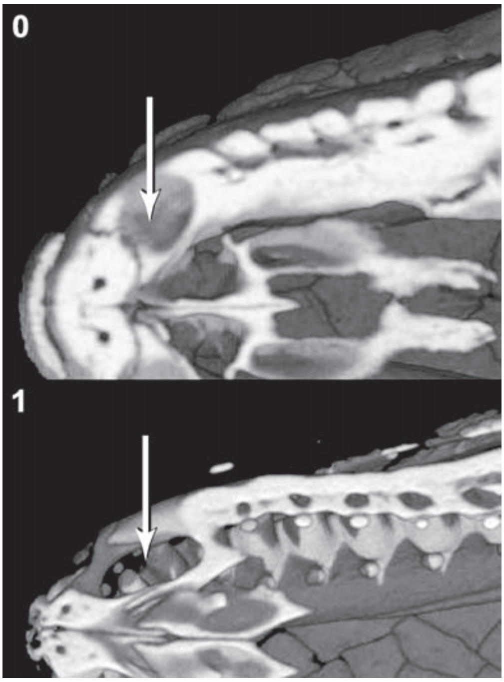
2. Premaxilla palatal shelf: (0) not bifid posteriorly (*Xenosaurus platyceps*, ventral close-up of anterior palate); (1) bifid posteriorly (*Varanus salvator*, ventral close-up of anterior palate). Rieppel (1980a).



3. Premaxilla maxillary process development: (0) normal size (*Lacerta viridis*, anterior close-up of snout); (1)^N reduced (*Varanus acanthurus*, anterior close-up of snout); (2) absent (*Calotes emma*, anterior close-up of snout). Moody (1980) (ordered).



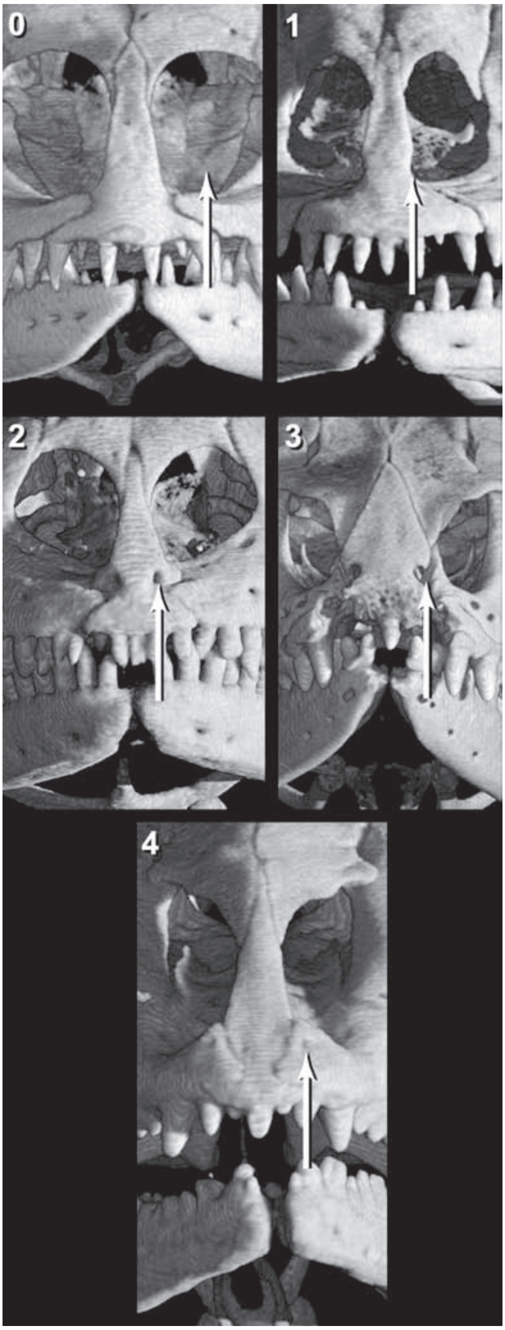
4. Premaxilla maxillary process length relative to level of palatine-maxilla suture^N: (0) premaxilla medial to level of palatine-maxilla suture (*Cordylosaurus subtesselatus*, dorsal close-up cutaway view of snout); (1) premaxilla extends lateral to level of palatine-maxilla suture (*Colobosaura modesta*, dorsal close-up cutaway view of snout).



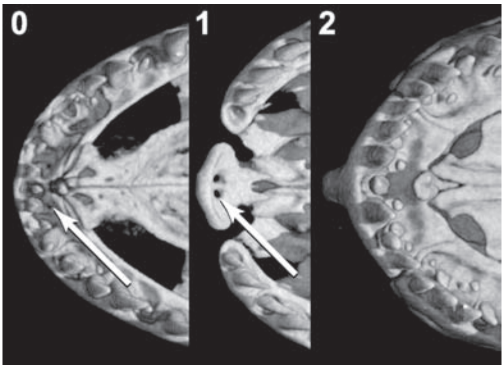
5. Premaxillary-maxillary fenestra: (0) absent (*Elgaria multicarinata*, dorsal close-up cutaway view of snout); (1) present

(*Pseudopus apodus*, dorsal close-up cutaway view of snout). Gauthier (1982).

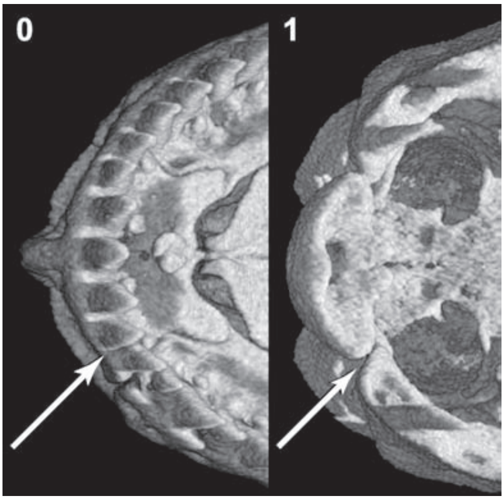
6. Premaxilla body anterior ethmoidal foramina number: (0) two; (1) four or more. Lee (1998).



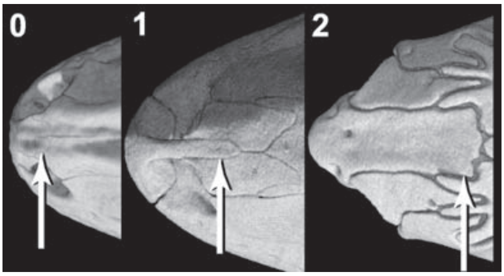
7. Premaxilla body anterior ethmoidal foramina exit via: (0) external naris (*Gambelia wislizenii*, anterior close-up of snout), (1) premaxilla notch (*Petrosaurus mearnsi*, anterior close-up of snout), Lee (2000); (2) premaxilla body (*Phymaturus palluma*, anterior close-up of snout), Hallermann (1998); (3)^{N} between premaxilla and maxilla (*Physignathus cocincinus*, anterior close-up of snout); (4)^{N} in maxilla (*Calotes emma*, anterior close-up of snout) (ordered).



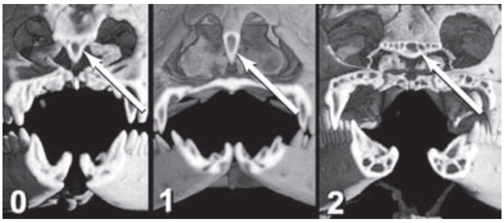
8. Premaxilla body ventral ethmoidal foramen^{N}: (0) small (*Gambelia wislizenii*, ventral close-up of anterior palate); (1) large (*Cylindrophis ruffus*, ventral close-up of anterior palate); (2) absent (*Anelytropsis papillosus*, ventral close-up of anterior palate).



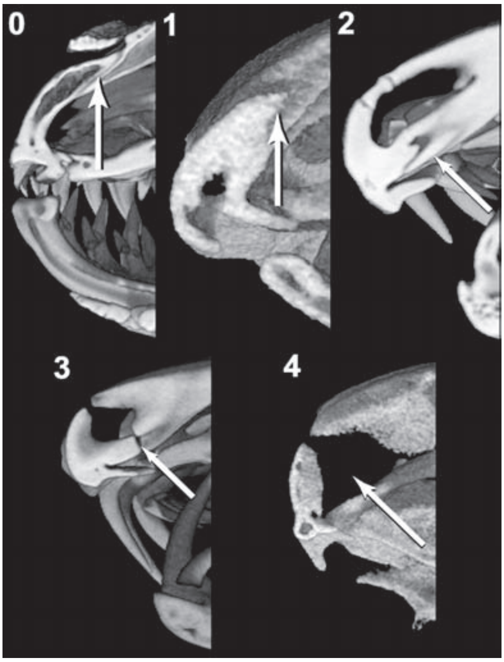
9. Premaxilla-maxilla suture: (0) firm (*Dibamus novaeguineae*, ventral close-up of anterior palate); (1) loose (*Anomochilus leonardi*, ventral close-up of anterior palate). Cundall (1995).



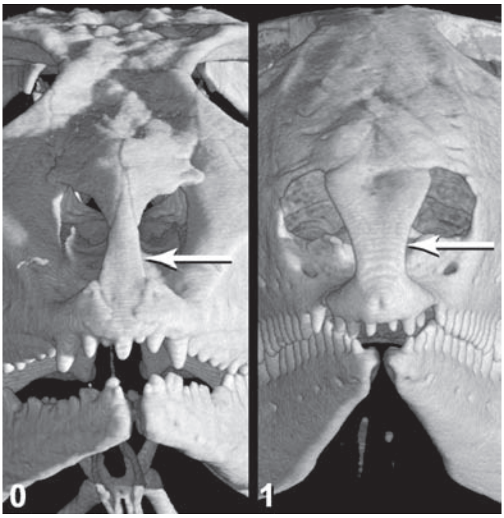
10. Premaxilla internasal process length: (0) less than half nasal length (*Rhacodactylus auriculatus*, dorsal close-up of snout); (1) more than half way to frontal between nasals (*Gonatodes albogularis*, dorsal close-up of snout); (2) nearly to, or articulates with, frontal (*Trogonophis weigmanni*, dorsal close-up of snout). Kearney (2003b) (ordered).



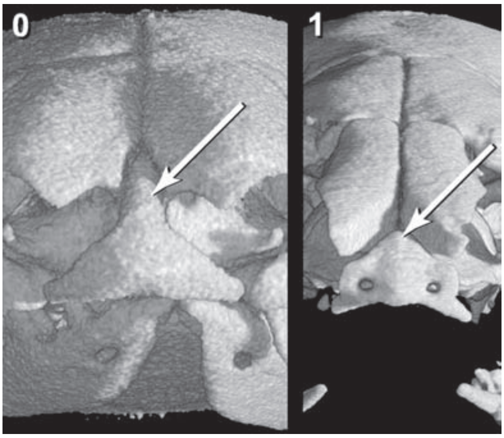
11. Premaxilla internasal process shape in cross-section[N]: (0) subtriangular (*Pristidactylus torquatus*, anterior close-up cutaway view of snout); (1) compressed (*Teratoscincus przewalskii*, anterior close-up cutaway view of snout); (2) depressed (*Polychrus marmoratus*, anterior close-up cutaway view of snout).



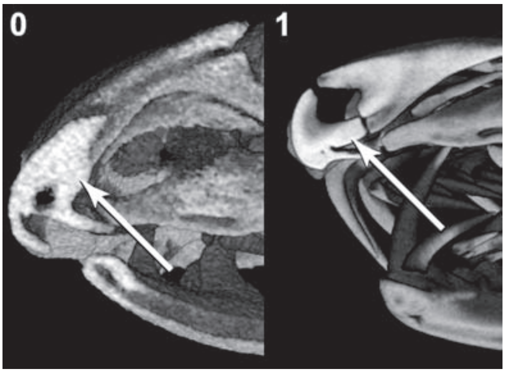
12. Premaxilla internasal process position relative to nasal descending lamina: (0) premaxilla internasal process lies at level of nasals on skull roof (*Heloderma horridum*, lateral close-up cutaway view of snout); (1) long internasal process clasped between descending nasal laminae (*Anomochilus leonardi*, lateral close-up cutaway view of snout); (2)[N] short overlap between premaxilla and nasal lamina (*Boa constrictor*, lateral close-up cutaway view of snout); (3)[N] lamina abuts posteroventral base of premaxilla (*Epicrates striatus*, lateral close-up cutaway view of snout); (4) loss of nasal descending lamina contact with premaxilla (*Pareas hamptoni*, lateral close-up cutaway view of snout). Cundall et al. (1993) (ordered).



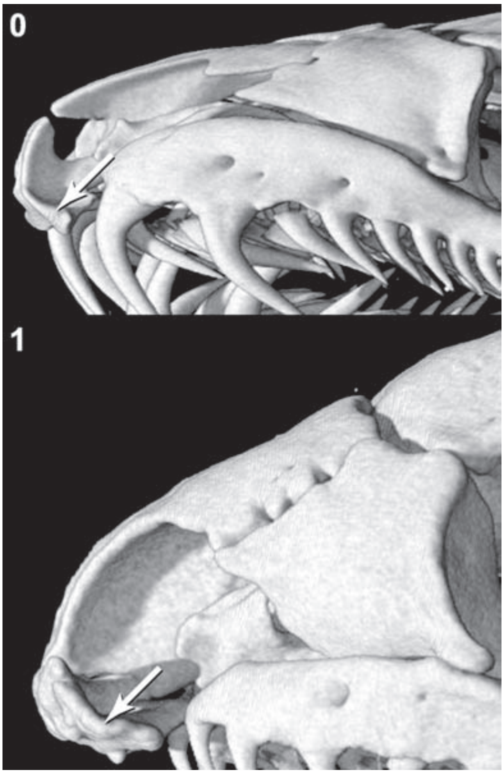
13. Premaxilla internasal process shape in anterior view[N]: (0) tapers apically or parallel-sided across nares (*Calotes emma*, anterior close-up of snout); (1) widens across nares (*Teius teyou*, anterior close-up of snout).



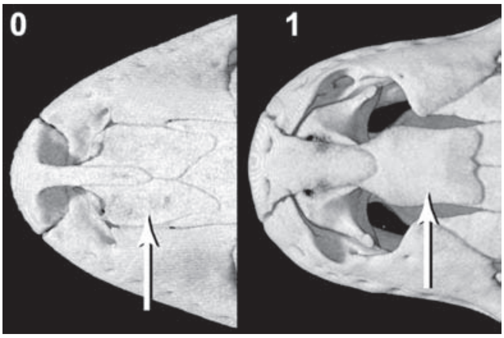
14. Premaxilla internasal process size^{N}: (0) well developed (*Anomochilus leonardi*, anterior close-up of snout); (1) very reduced/absent (*Atractaspis irregularis*, anterior close-up of snout).



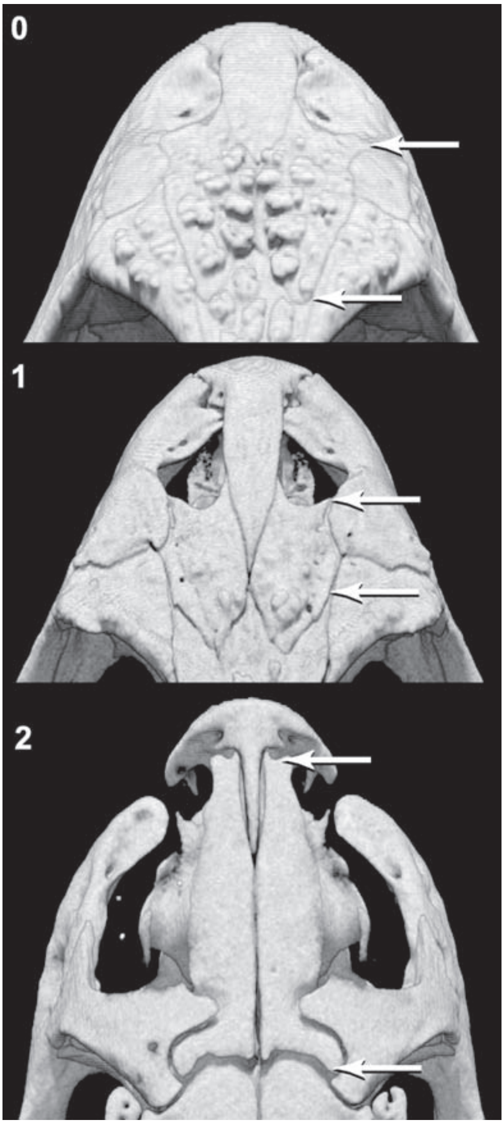
15. Premaxilla internasal process bifid in lateral view, with ancestral dorsal ramus joined by a deeper ventral ramus (premaxillary keel of Lee and Scanlon 2002) extending posteriorly off base of internasal process: (0) absent (*Anomochilus leonardi*, lateral close-up cutaway view of snout); (1) present (*Epicrates striatus*, lateral close-up cutaway view of snout). Cundall et al. (1993).



16. Premaxilla: (0) without conspicuous vertical margin on maxillary process (*Epicrates striatus*, lateral close-up of snout); (1) with conspicuous vertical margin on maxillary process (*Calabaria reinhardtii*, lateral close-up of snout). Kluge (1993a).

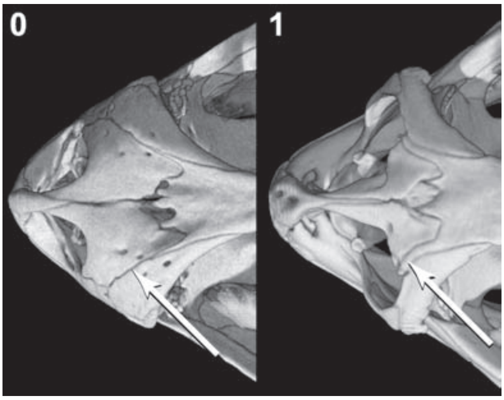


17. Nasals: (0) paired (*Gonatodes albogularis*, dorsal close-up of snout); (1) fused (*Lanthanotus borneensis*, dorsal close-up of snout). Pregill et al. (1986). Species in which the premaxilla internasal process contacts the frontal are scored (?), as nasals bisected by the premaxilla internasal process overprint both of the conditions described in the character and prevent the scoring of either condition.

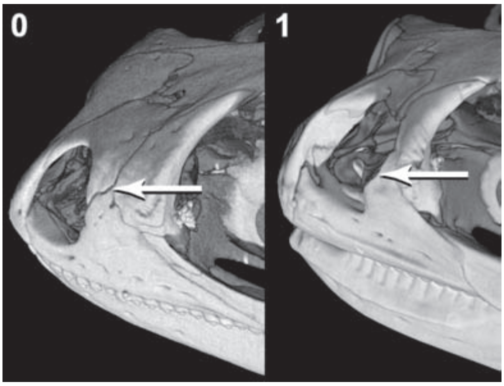


18. Nasals anterior width: (0) exceeds nasofrontal joint width (*Pristidactylus torquatus*, dorsal close-up of snout); (1) is subequal to nasofrontal joint width (*Urostrophus vautieri*, dorsal close-up of snout) Gauthier (1982); (2)^{N} less than anterior frontal width (*Loxocemus bicolor*, dorsal close-up of snout) (ordered).

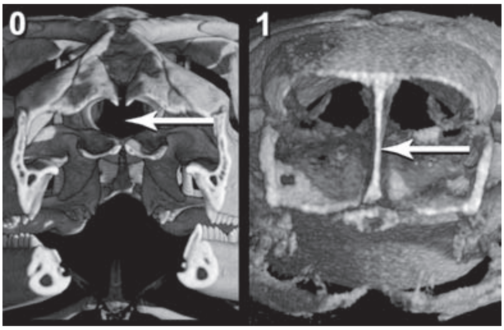
In snakes with kinetic nasofrontal joints, comparison is between the anterior width of the nasals vs. the anterior width of the frontals.



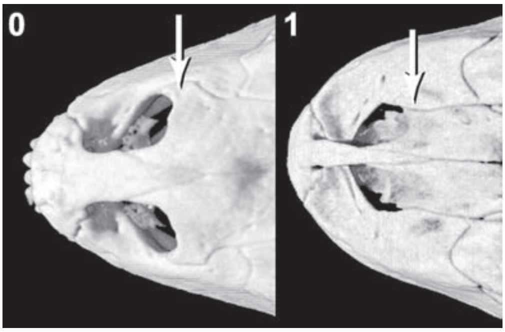
19. Nasal-prefrontal suture: (0) present (*Dipsosaurus dorsalis*, dorsal close-up of snout); (1) absent (*Uromastyx aegyptius*, dorsal close-up of snout). Estes et al. (1988).



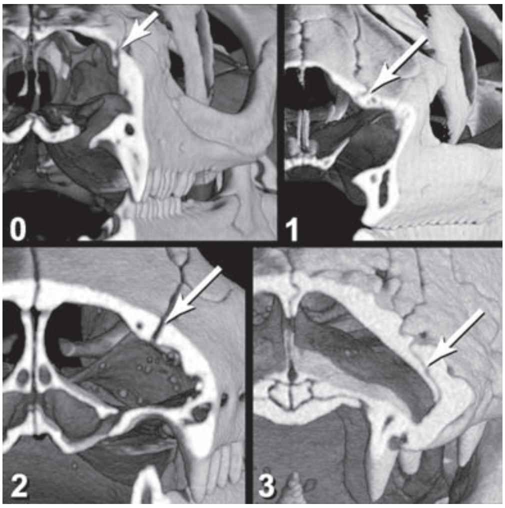
20. Nasal-maxilla suture: (0) present (*Dipsosaurus dorsalis*, oblique lateral close-up of snout); (1) absent (*Uromastyx aegyptius*, oblique lateral close-up of snout). Estes et al. (1988).



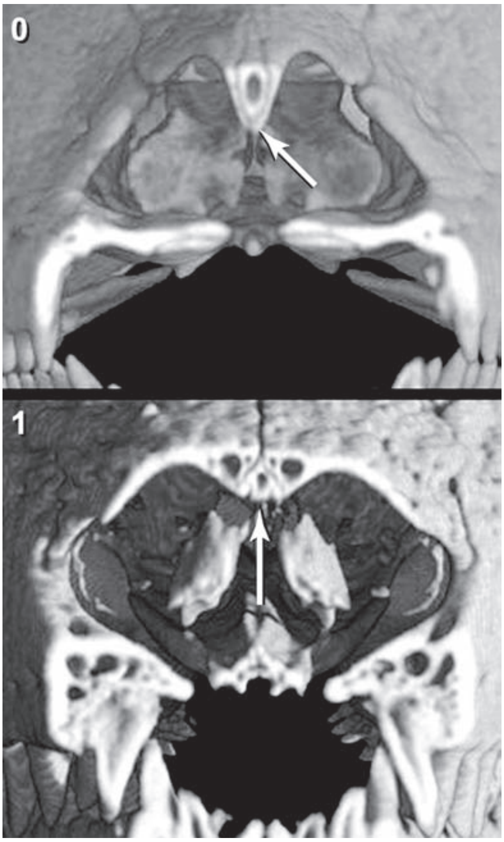
21. Nasal descending lamina^{N}: (0) absent (*Plica plica*, anterior close-up cutaway view of snout); (1) present, with descending lamina extending below level of nasal-maxilla suture (*Typhlophis squamosus*, anterior close-up cutaway view of snout).



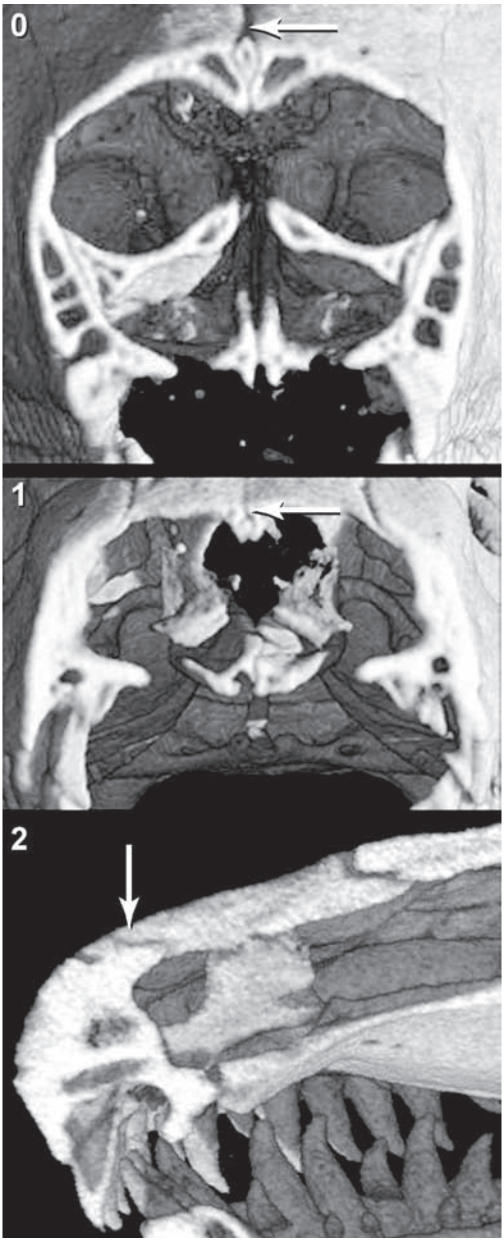
22. Nasal supranarial process in dorsal view^N: (0) well-developed (*Basiliscus basiliscus*, dorsal close-up of snout); (1) reduced/absent (*Petrosaurus mearnsi*, dorsal close-up of snout).



23. Nasal-maxilla suture in cross section anteriorly^N: (0) maxilla overlaps nasal at roof of nasal chamber (*Sauromalus ater*, anterior close-up cutaway view of snout); (1) nasal partly overlaps maxilla dorsally (*Agama agama*, anterior close-up cutaway view of snout); (2) nasal abuts maxilla (*Anelytropsis papillosus*, anterior close-up cutaway view of snout); (3) nasal underlaps maxilla to floor of narial chamber (*Rhineura floridana*, anterior close-up cutaway view of snout).

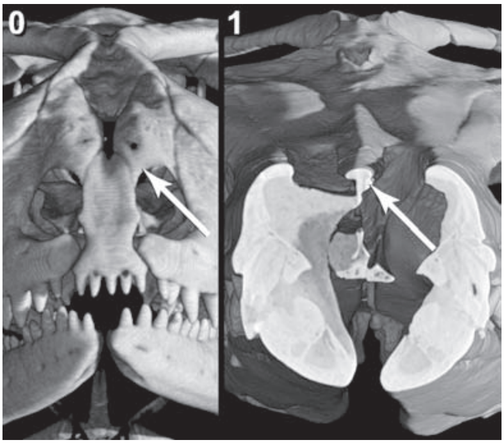


24. Nasals ventral contact beneath premaxillary internasal process^N: (0) broad contact below (*Teratoscincus przewalskii*, anterior close-up cutaway view of snout); (1) or not in contact except near apex (*Brachylophus fasciatus*, anterior close-up cutaway view of snout).

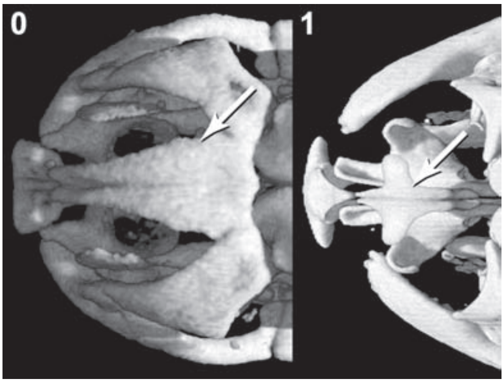


25. Nasals dorsal contact over premaxilla internasal process^N: (0) no contact (*Aspidoscelis tigris*, anterior close-up cutaway view of snout); (1) in contact over apex (*Phymaturus palluma*, anterior close-up cutaway view of snout); (2) broadly in contact (*Dibamus novaeguineae*, lateral close-up cutaway view of snout) (ordered).

Figures for states (1) and (2) appear similar as they differ only in degree, with overlap in the former confined to the apex of the internasal process only, and the later covering nearly the entire internasal process along its articulation with the nasal bones.

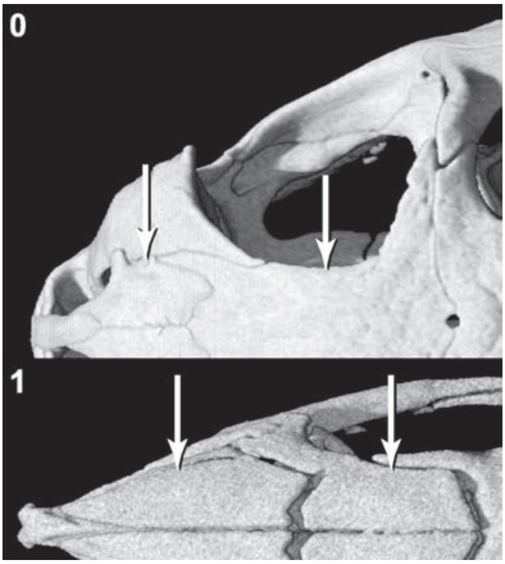


26. Nasals reduced to narrowly elliptic elements attached to either side of premaxilla internasal process: (0) absent (*Plica plica*, anterior close-up view of snout); (1) present (*Plotosaurus bennisoni*, anterior close-up cutaway view of snout). Bell (1997).

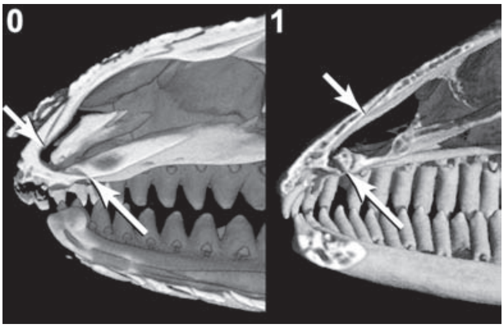


27. Nasal shape^N: (0) not small and cruciform (*Xenophidion acanthognathus*, dorsal close-up of snout); (1) small and cruciform (*Thamnophis marcianus*, dorsal close-up of snout).

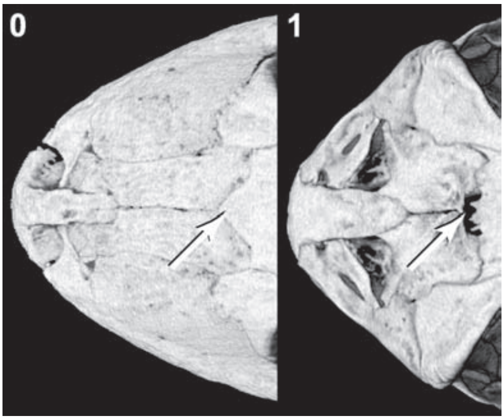
In those few mosasaurians in which nasals are known, they may be reduced in size but are not cruciform in shape, and are accordingly scored as state (0).



28. Nasal length relative to frontal length^{N}: (0) nasals shorter than frontals (*Agama agama*, dorsal close-up of anterior skull); (1) nasals longer than frontals (*Uropeltis melanogaster*, dorsal close-up of anterior skull).

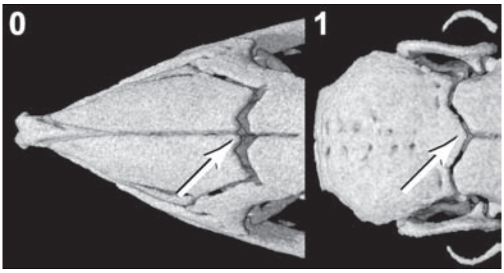


29. Nasal anterior extent toward premaxilla^{N}: (0) nasal extends anterior to maxillary tooth row or vomer (*Pseudopus apodus*, lateral close-up cutaway view of snout); (1) nasal terminates posterior to end of maxillary tooth row or vomer tip (*Polychrus marmoratus*, lateral close-up cutaway view of snout).

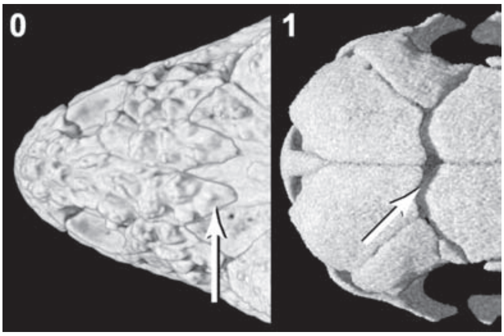


30. Nasofrontal fontanelle: (0) absent, frontal and nasal firmly sutured (*Strophurus ciliaris*, dorsal close-up of snout); (1) present, poorly ossified suture between nasal and frontal on midline (*Uranoscodon superciliosus*, dorsal close-up of snout). Moody (1980).

This character, like virtually all others in this analysis, is scored in adult individuals. A “fontanelle” of sorts in this position may be present in incompletely ossified juveniles.

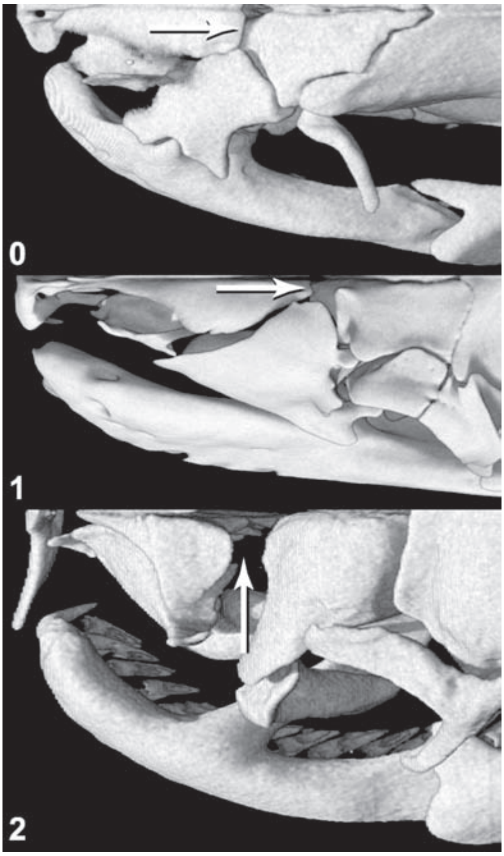


31. Nasofrontal suture shape^{N}: (0) without V-shaped nasal process into frontal midline (*Uropeltis melanogaster*, dorsal close-up of snout); (1) with prominent V-shaped nasal process into frontal midline (*Liotyphlops albirostris*, dorsal close-up of snout).

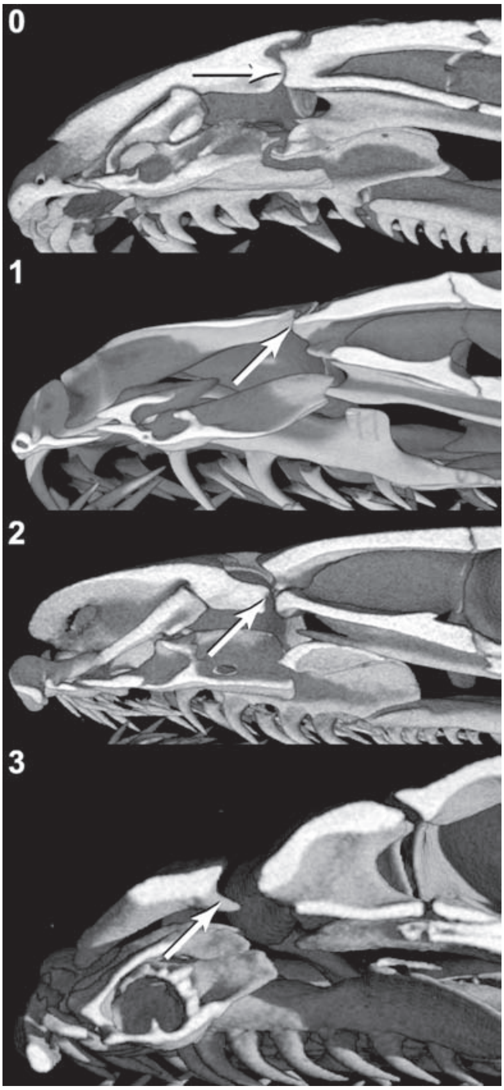


32. Nasal-frontal articulation dorsally^{N}: (0) nasals suture in two V-shaped recesses of anterodorsal end of frontal

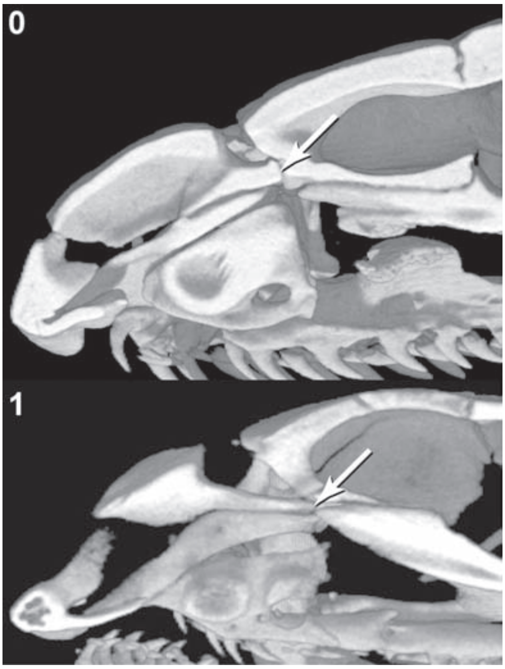
(*Xenosaurus platyceps*, dorsal close-up of snout); (1) nasals overlap only onto narrow horizontal shelf dorsally on frontals (*Anomochilus leonardi*, dorsal close-up of snout).



33. Nasal dorsal lamina: (0) in broad contact with dorsal frontal lamina (*Cylindrophis ruffus*, dorsal close-up view of anterior skull); (1) in narrow (medial, point-) contact with frontal (*Python molurus*, dorsal close-up view of anterior skull); (2) not in contact with frontal (*Acrochordus granulatus*, dorsal close-up view of anterior skull). Rieppel (2007) (ordered).

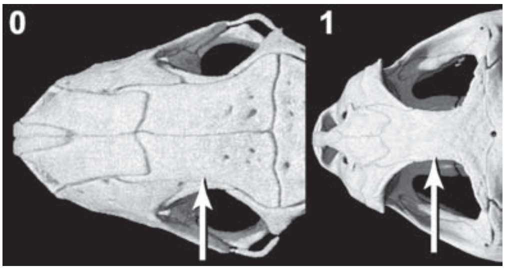


34. Nasal medial (vertical) flange: (0) in extensive dorsoventral contact with medial frontal flange (*Anilius scytale*, lateral close-up cutaway view of anterior skull); (1) in dorsal contact only (*Python molurus*, lateral close-up cutaway view of anterior skull); (2) in ventral contact only (*Tropidophis haetianus*, lateral close-up cutaway view of anterior skull); (3) not in contact with frontal (*Acrochordus granulatus*, lateral close-up cutaway view of anterior skull). Rieppel (2007).

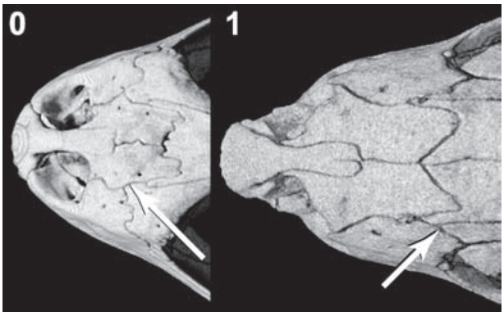


35. Nasal medial (vertical) flange, ventral contact with frontal: (0) abutting (*Lampropeltis getula*, lateral close-up cutaway view of anterior skull); (1) reduced to point contact (*Causus rhombeatus*, lateral close-up cutaway view of anterior skull). Rieppel (2007).

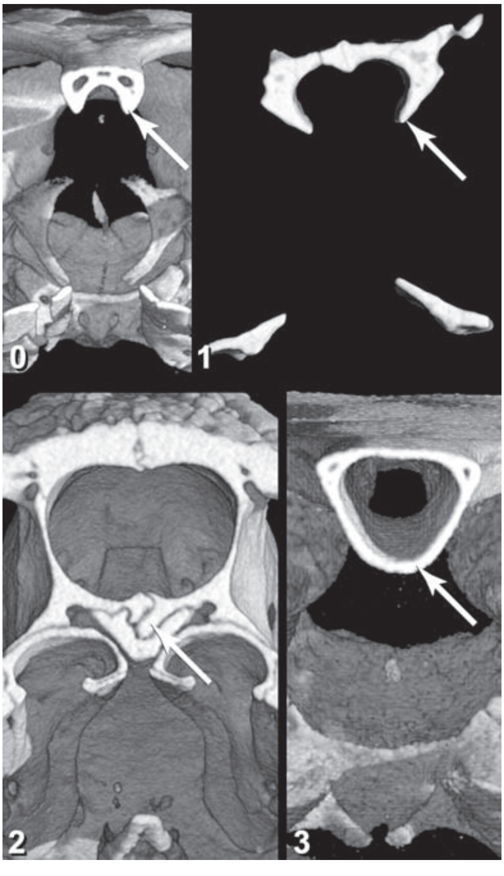
Character 34(2) correlates with 35(1) in that the "point contact" is always "ventral". However, because "ventral contact" 34(2) can be either "abutting" 35(0) or a "point contact" 35(1), they are treated separately.



36. Frontals: (0) paired (*Acontias percivali*, dorsal close-up of anterior skull); (1) fused (*Agama agama*, dorsal close-up of anterior skull). Estes et al. (1988).



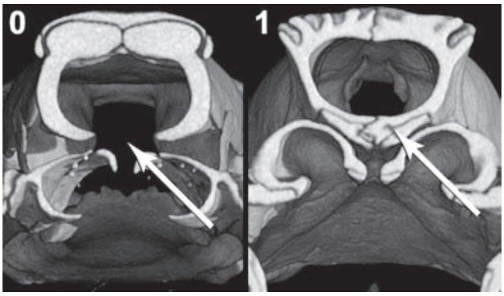
37. Frontal-maxilla suture: (0) frontal separated from maxilla by nasal-prefrontal contact (*Stenocercus guentheri*, dorsal close-up of snout); (1) frontal contacts maxilla, separating nasal from prefrontal (*Anniella pulchra*, dorsal close-up of snout). Gauthier (1982).



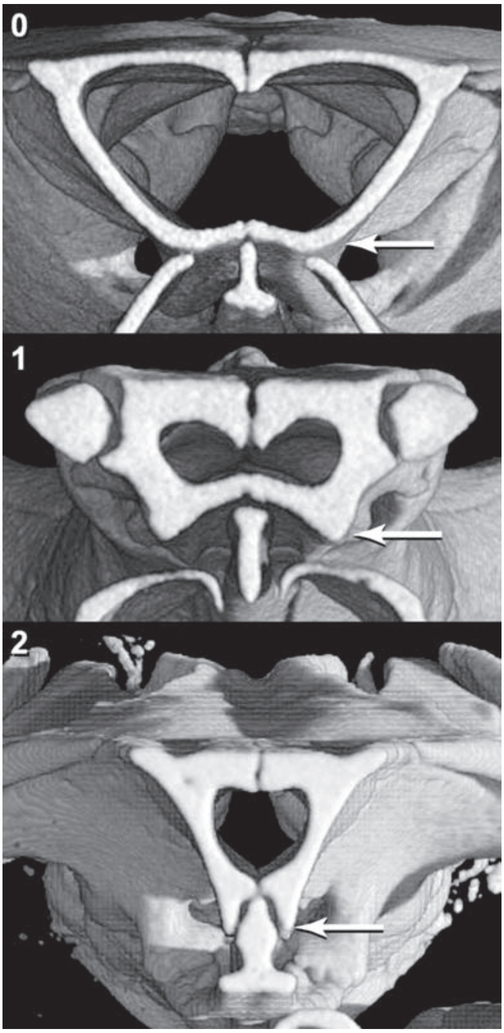
38. Frontal subolfactory processes: (0) absent (*Liolaemus bellii*, anterior close-up cutaway view of frontals); (1) arch beneath brain but do not contact (*Saniwa* sp., anterior close-up cutaway view of frontals); (2) arch beneath brain to articulate on ventral midline (*Rhineura floridana*, anterior close-up cutaway view of frontals); (3) arch beneath brain and fuse on ventral midline (*Coleonyx variegatus*, anterior close-up cutaway view of frontals). Pregill et al. (1986) (ordered).

39. Frontal subolfactory process depth: (0)^{N} 25–35%; (1)^{N} 42–53%; (2)^{N} 58–68%; (3)^{N} 75–85%; (4)^{N} more than 89%. Gauthier (1982) (ordered).

To track the ventral depth of the frontal subolfactory process, we measured CT cross-sections from the maximum ventral limit of the subolfactory process to the dorsal surface of the palatine, then divided that by the distance from the dorsal surface of the frontal (sans any overlying osteoderms) to the dorsal surface of the palatine, and subtracted that value from 100.

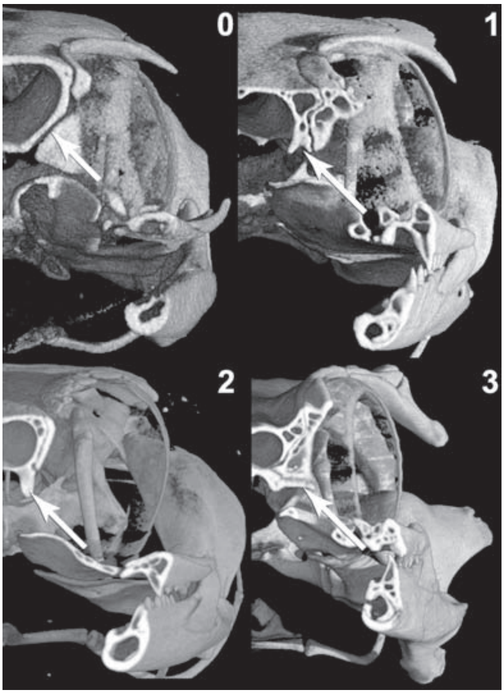


40. Frontal subolfactory process-parasphenoid suture: (0) absent (*Anelytropsis papillosus*, anterior close-up cutaway view of snout); (1) present (*Amphisbaena fuliginosa*, anterior close-up cutaway view of snout). Lee (1998).

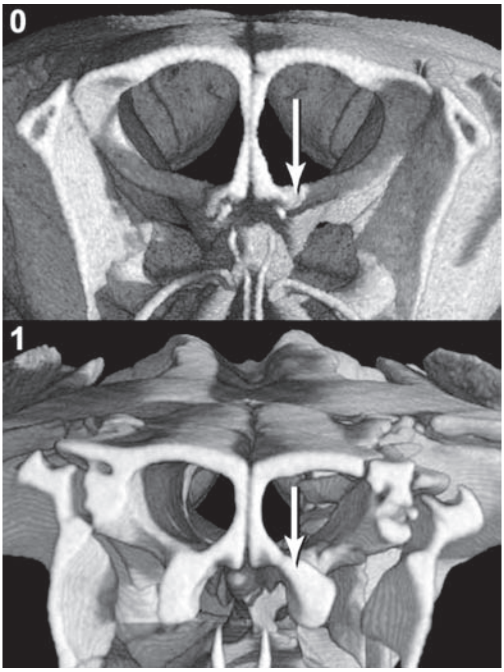


41. Frontal subolfactory process descending lamina-parasphenoid rostrum relationship^{N}: (0) absent (*Casarea dussumieri*, anterior close-up cutaway view of frontals); (1) descending lamina off frontal subolfactory process (continuation of frontal enclosure of optic nerve) lies dorsolateral to parasphenoid (*Anilius scytale*, anterior close-up cutaway view of frontals); (2) descending lamina off frontal subolfactory process tightly clasps parasphenoid dorsolaterally (*Thamnophis marcianus*, anterior close-up cutaway view of frontals) (ordered).

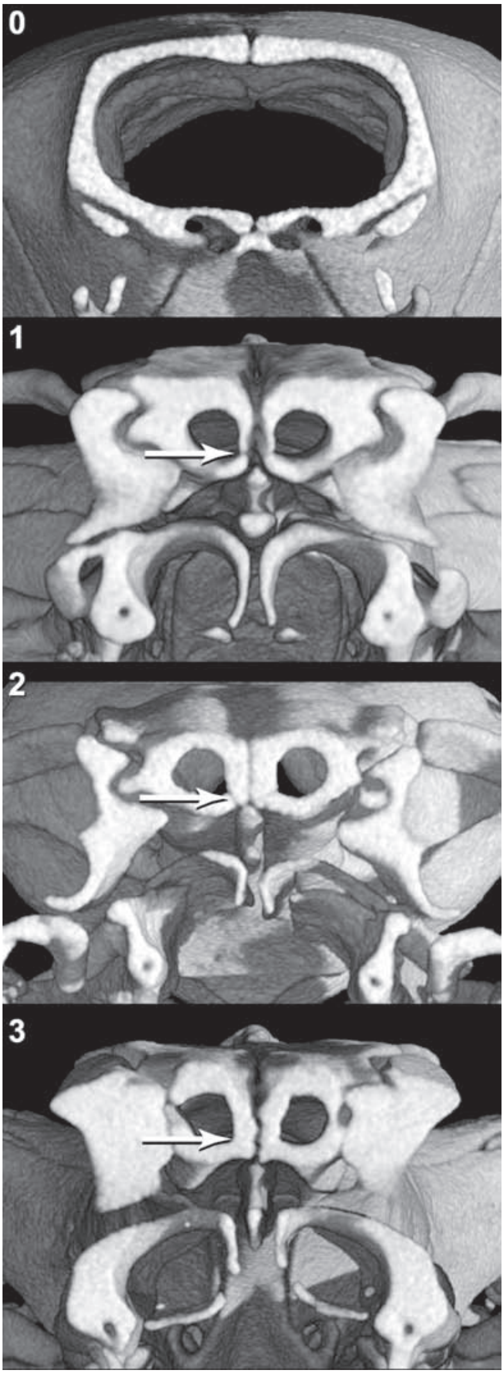
42. Frontal subolfactory processes delimit deep narrow canal across most of orbit^{N}: (0) absent (*Crotaphytus collaris*, anterior close-up cutaway view of skull); (1) present (*Carusia intermedia*, anterior close-up cutaway view of skull).



43. Frontal subolfactory process prefrontal lamina^{N}: (0) absent (*Delma borea*, anterior close-up cutaway view of skull); (1) knob-like process at anteromedial rim of subolfactory process with prefrontal facet (*Phelsuma lineata*, anterior close-up cutaway view of skull); (2) conspicuous descending lamina off subolfactory process articulating just behind prefrontal (*Teratoscincus przewalskii*, anterior close-up cutaway view of skull); (3) produced into shelf supporting prefrontal ventrally (*Rhacodactylus auriculatus*, anterior close-up cutaway view of skull) (ordered).

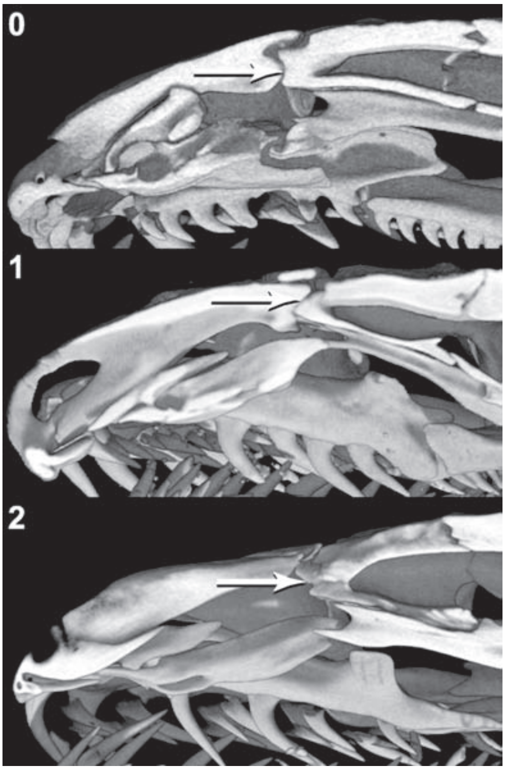


44. Frontal subolfactory process: (0) straight (*Pareas hamptoni*, anterior close-up cutaway view of frontals); (1) forms thickened anterolaterally projecting flange (*Natrix natrix*, anterior close-up cutaway view of frontals). Rieppel (2007).

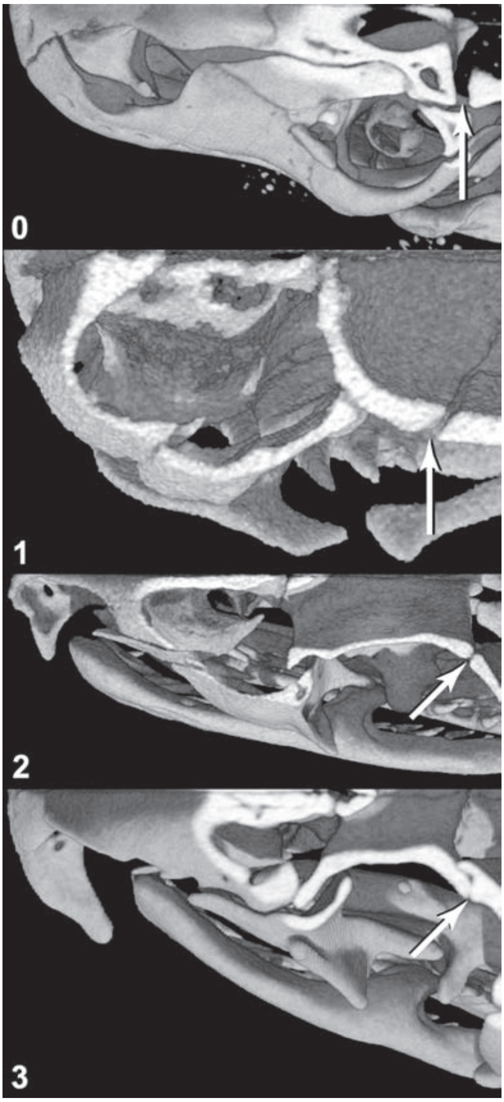


45. Frontal medial pillar: (0) absent (*Typhlops jamaicensis*, anterior close-up cutaway view of frontals); (1) separated anteriorly from subolfactory process by gap (*Cylindrophis ruffus*, anterior close-up cutaway view of frontals); (2) sutured to subolfactory process (*Trachyboa boulengeri*, anterior close-up cutaway view of frontals); (3) fused with subolfactory process (*Anilius scytale*, anterior close-up cutaway view of frontals). Rieppel (2007) (ordered).

States (1) and (2) in character 45 may be difficult to distinguish (R. Nydam, pers. comm.), or are simply scored incorrectly (J. Head, pers. comm.), in some basal alethinophidians.



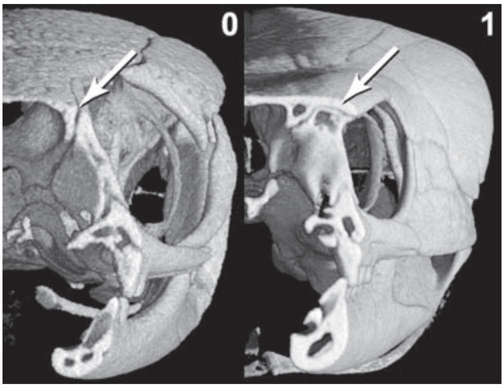
46. Frontal medial flange separating olfactory tracts: (0) vertically positioned (*Anilius scytale*, lateral close-up cutaway view of anterior skull); (1) slants forward (anterior margin of subolfactory process in front of anterior margin of frontal dorsal lamina) (*Boa constrictor*, lateral close-up cutaway view of anterior skull); (2) slants backwards (anterior margin of subolfactory process behind anterior margin of frontal dorsal lamina) (*Python molurus*, lateral close-up cutaway view of anterior skull). Rieppel (2007).



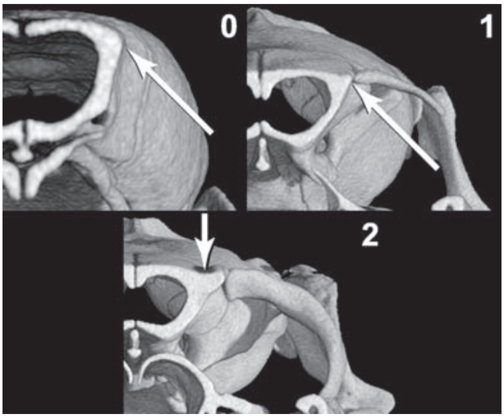
47. Frontal descending process-parietal contact, in horizontal section[N]: (0) no contact (*Lanthanotus borneensis*, dorsal close-up cutaway view of anterior skull); (1) parietal overlaps frontal laterally (*Anomochilus leonardi*, dorsal close-up cutaway view of anterior skull); (2) frontal descending process abuts parietal (*Lichanura trivirgata*, dorsal close-up cutaway view of anterior skull); (3) frontal descending process overlaps parietal laterally, at least in part (*Eryx colubrinus*, dorsal close-up cutaway view of anterior skull).

48. Frontal interorbital width/frontoparietal suture width I: (0)[N] 14-19%; (1)[N] 20-22%; (2)[N] 24-26%; (3)[N] 28-34%; (4)[N] 36-40%. Estes et al. (1988) (ordered) Scores for charcters 48 and 49 determined with straight line measurements at the narrowest part of the frontal between the orbits, and between the lateral contact between the forntal and parietal, even if the suture is not straight.

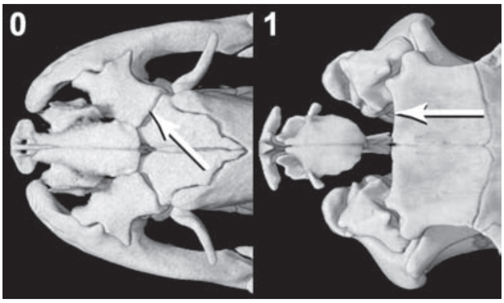
49. Frontal interorbital width/frontoparietal suture width II: (0)^N less than 44%; (1)^N 44-47%; (2)^N 50-53%; (3)^N 55-58%; (4)^N 60-63%. Estes et al. (1988) (ordered).



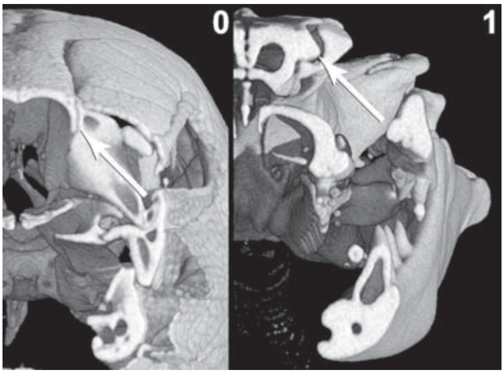
50. Frontal broadly overlaps prefrontal dosally: (0) absent (*Cricosaura typica*, anterior close-up cutaway view of skull); (1) present (*Lepidophyma flavimaculatum*, anterior close-up cutaway view of skull). Crother et al. (1986).



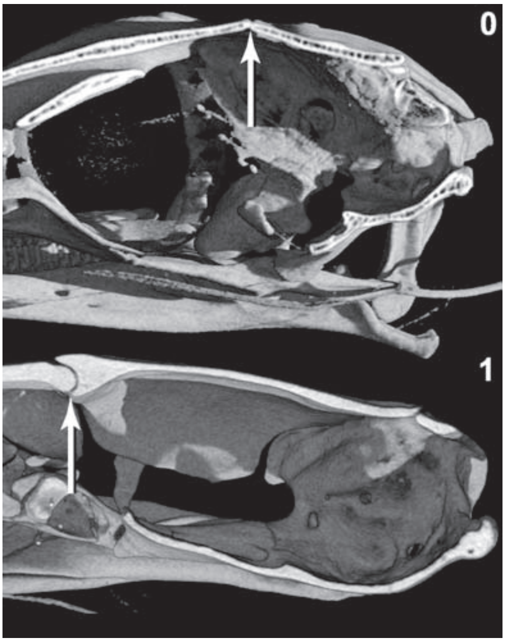
51. Frontal supraorbital shelf: (0) absent (*Leptotyphlops dulcis*, anterior close-up cutaway view of skull); (1)^N present (*Exiliboa placata*, anterior close-up cutaway view of skull); (2)^N present and demarcated medially by narrow shallow longitudinal furrow often bearing line of foramina on the dorsal surface of the frontal (*Tropidophis haetianus*, anterior close-up cutaway view of skull). Smith (2009a) (ordered).



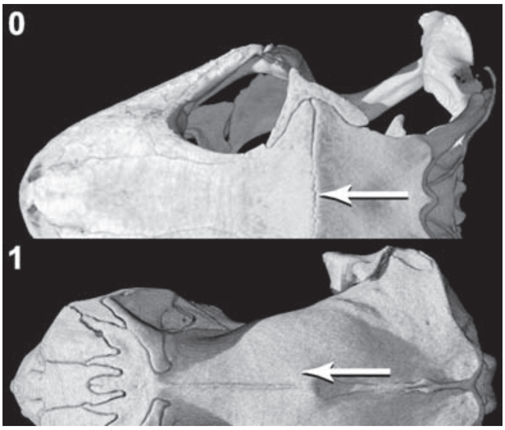
52. Frontal anterior margin shape^N: (0) mainly trends anteromedially (*Cylindrophis ruffus*, dorsal close-up of snout); (1) broadly transverse (*Bothrops asper*, dorsal close-up of snout).



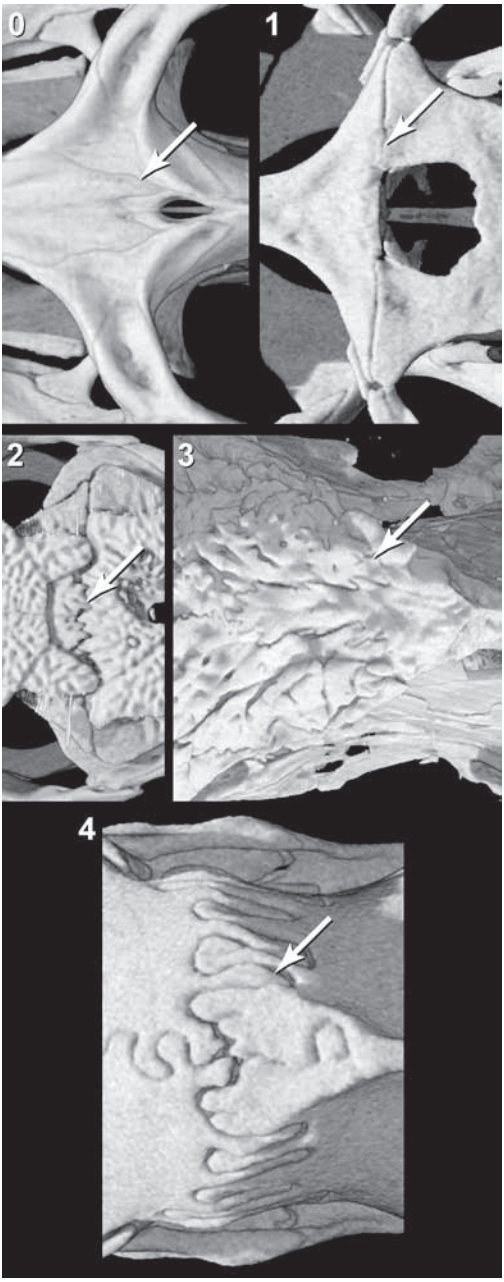
53. Frontal anteroposteriorly narrow, blunt prefrontal process off lateral base of subolfactory process extends into prefrontal socket^N: (0) absent (*Scincus scincus*, anterior close-up cutaway view of skull); (1) present (*Anilius scytale*, anterior close-up cutaway view of skull).



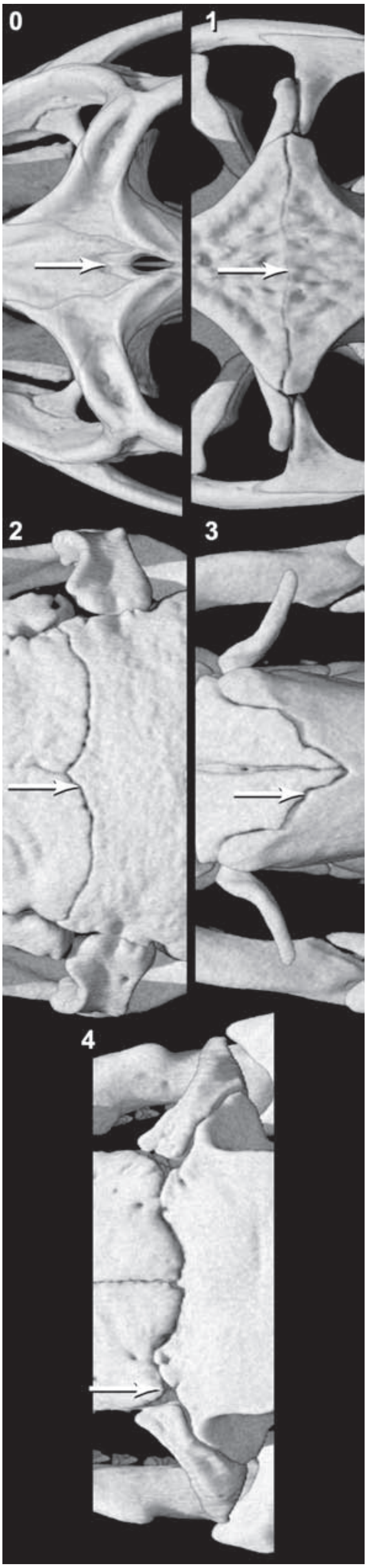
54. Frontal posterior margin convex and parietal anterior margin concave, in mid-sagittal section^{N}: (0) absent (*Aeluroscalabotes felinus*, lateral close-up cutaway view of posterior skull); (1) present (*Anelytropsis papillosus*, lateral close-up cutaway view of posterior skull).



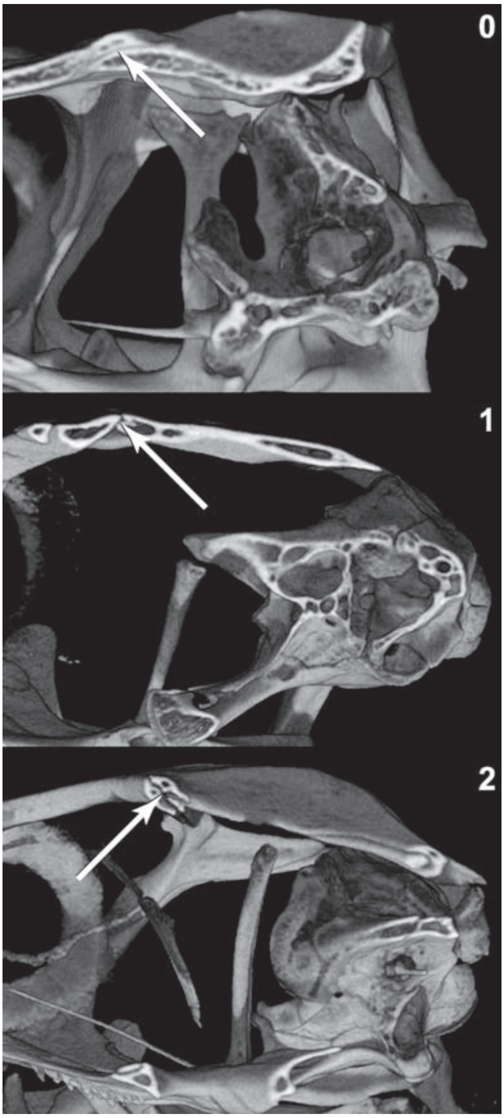
55. Frontoparietal suture: (0) separate (*Strophurus ciliaris*, dorsal view of skull); (1) fused (*Bipes canaliculatus*, dorsal view of skull). Kearney (2003b).



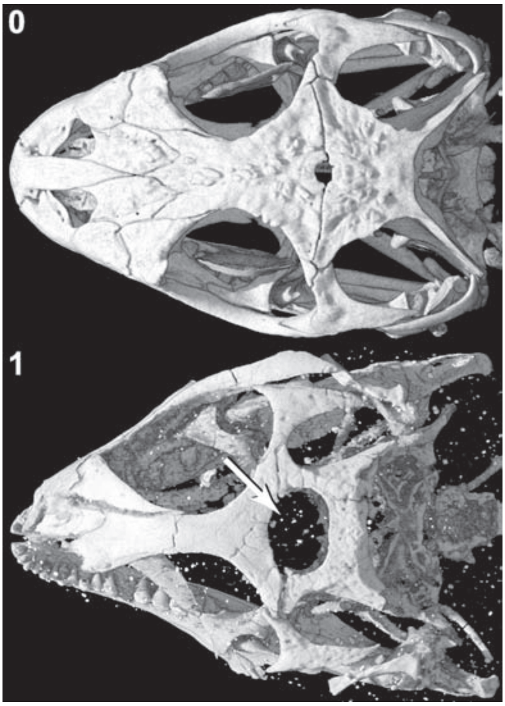
56. Frontoparietal suture interdigitation: (0) frontal overlaps parietal dorsally (*Sphenodon punctatus*, dorsal close-up of frontoparietal suture); (1) lightly interdigitate or simple abutment (*Petrosaurus mearnsi*, dorsal close-up of frontoparietal suture); (2)^{N}moderate interdigitation (*Pseudopus apodus*, dorsal close-up of frontoparietal suture); (3)^{N} strong interdigitation (*Spathorhynchus fossorium*, dorsal close-up of frontoparietal suture); (4) deeply interdigitate (*Geocalamus acutus*, dorsal close-up of frontoparietal suture [Kearney 2003b]). Estes et al. (1988).



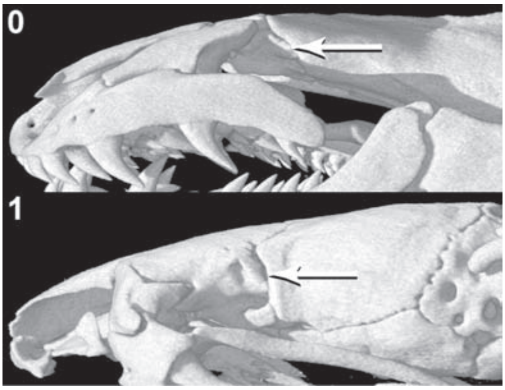
57. Frontoparietal suture dorsal outline: (0) bowed anteriorly/inverted U (*Sphenodon punctatus*, dorsal close-up of frontoparietal suture); (1) roughly transverse (*Morunasaurus annularis*, dorsal close-up of frontoparietal suture); (2) shallow U or W bowed posteriorly (*Calabaria reinhardtii*, dorsal close-up of frontoparietal suture); (3) deeply bowed posteriorly U or W (*Cylindrophis ruffus*, dorsal close-up of frontoparietal suture); (4)^{N} frontal postero-dorsolateral corner protrudes posterolaterally (*Lampropeltis getula*, dorsal close-up of frontoparietal suture). Gauthier, Estes and de Queiroz (1988).



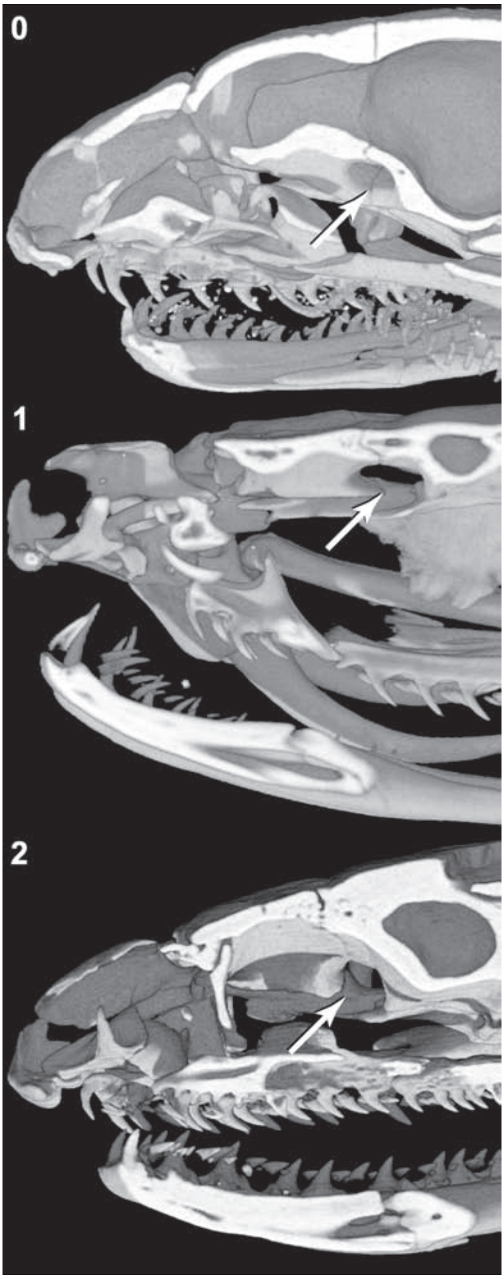
58. Frontal parietal lateral overlap^{N}: (0) frontal deeply overlaps parietal (*Sphenodon punctatus*, lateral close-up cutaway view of frontoparietal suture); (1) frontal barely overlaps parietal laterally (*Eublepharis macularius*, lateral close-up cutaway view of frontoparietal suture); (2) frontal underlaps parietal laterally (*Gambelia wislizenii*, lateral close-up cutaway view of frontoparietal suture).



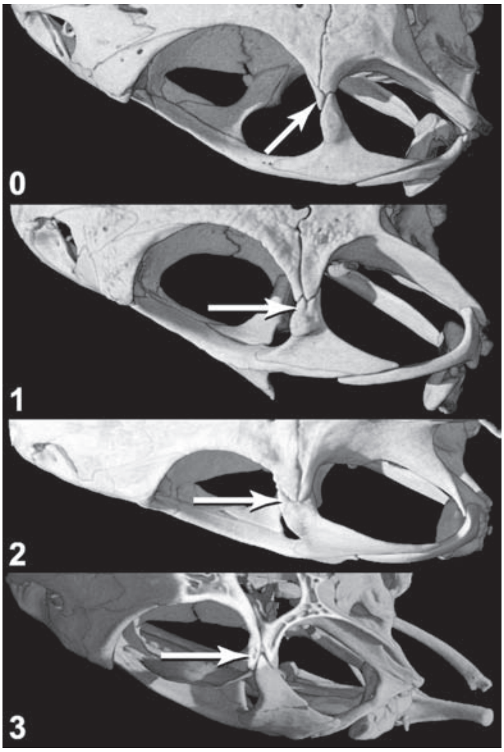
59. Frontoparietal fontanelle in adult^{N}: (0) absent (*Urostrophus vautieri*, dorsal view of skull); (1) present (*Isodontosaurus gracilis*, dorsal view of skull).



60. Frontoparietal suture expression in medial wall of orbit: (0) strongly inclined anteriorly (*Anilius scytale*, lateral close-up of anterior skull); (1) vertical or slightly inclined anteriorly (*Atractaspis irregularis*, lateral close-up of anterior skull). Kluge (1983b).



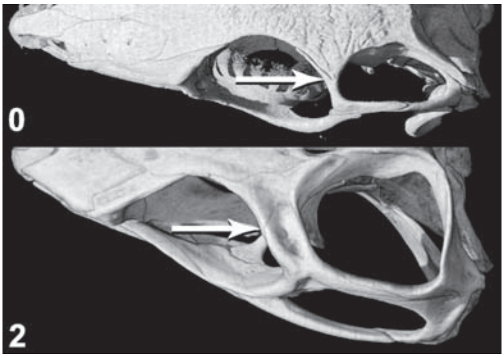
61. Frontal suboptic shelves-parietal contact^{N}: (0) parasagittal shelves (suboptic shelves) pass from posterior base of frontal subolfactory processes on either side of the dorsal edge of the parasphenoid to near contact, or overlap, parietal medially below optic foramen (*Calabaria reinhardtii*, lateral close-up cutaway view of anterior skull); (1) frontal suboptic processes widely separated from parietal on either side of the midline at the ventral junction of frontal, parietal and parasphenoid (*Bothrops asper*, lateral close-up cutaway view of anterior skull); (2) suboptic shelves absent (*Lampropeltis getula*, lateral close-up cutaway view of anterior skull).



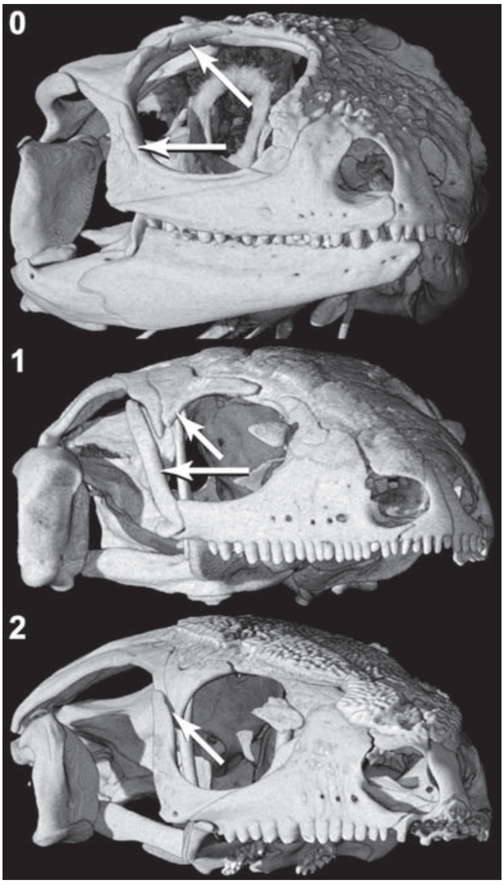
62. Postfrontal: (0) present (*Dipsosaurus dorsalis*, dorsal view of skull); (1) absent (*Crotaphytus collaris*, dorsal view of skull); (2) fused to postorbital (*Basiliscus basiliscus*, dorsal view of skull); (3)^N fused to frontal (*Agama agama*, dorsal view of skull). Estes et al. (1988).

63. Postfrontal shape: (0) triradiate (notched distally or not), with subequal frontal and parietal processes wrapping around frontoparietal suture (*Colobosaura modesta*, oblique dorsal close-up view of anterior skull); (1)^N parietal process much shorter than frontal process (*Temujinia ellisoni*, oblique dorsal close-up view of anterior skull); (2) parietal process absent, postfrontal subtriangular (*Urostrophus vautieri*, oblique dorsal close-up view of anterior skull). Estes et al. (1988) (ordered).

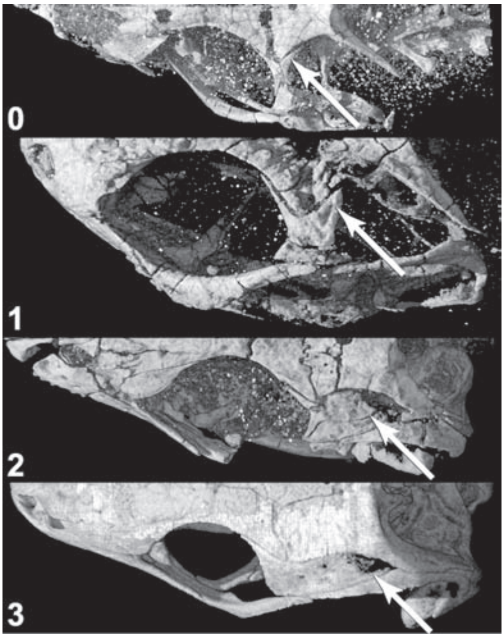
64. Postfrontal distal shape^{N}: (0) tapering to point (passing anterior to postorbital) (*Colobosaura modesta*, oblique dorsal close-up view of anterior skull); (1) bifid (clasps postorbital) (*Temujinia ellisoni*, oblique dorsal close-up view of anterior skull).



65. Postfrontal relative to parietal table^{N}: (0) ventrolateral (*Aspidoscelis tigris*, dorsal view of skull); (1) dorsal overlap present (*Gephyrosaurus* in Evans 1980, fig. 12A); (2) dorsal overlap extensive (*Sphenodon punctatus*, dorsal view of skull) (ordered).

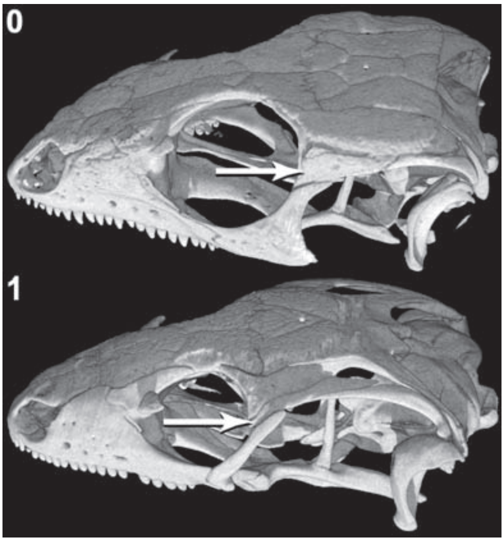


66. Postfrontal-jugal articulation^{N}: (0) widely separated (*Leiosaurus catamarcensis*, anterior oblique view of skull); (1) nearly in contact, but still separated (*Sphenomorphus solomonis*, anterior oblique view of skull); (2) in contact (*Pseudopus apodus*, anterior oblique view of skull) (ordered).

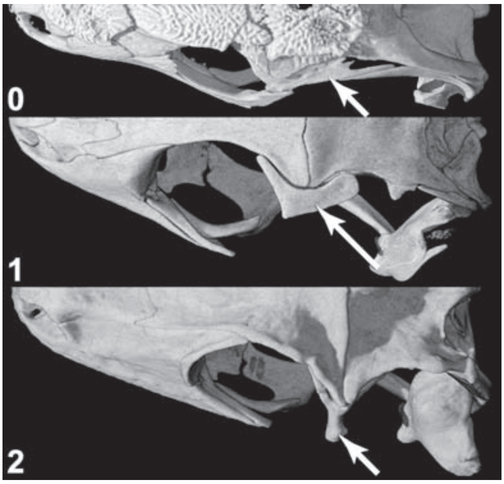


67. Postfrontal supratemporal shelf: (0) absent (*Tchingisaurus multivagus*, dorsal view of skull); (1)$^{\text{N}}$ present as thin shelf extending over anterodorsal corner of supratemporal fenestra (*Carusia intermedia*, dorsal view of skull); (2)$^{\text{N}}$ extending posteriorly further than laterally across upper temporal fenestra (*Globaura venusta*, dorsal view of skull); (3) to (nearly) occlude upper temporal fenestra (*Plestiodon fasciatus*, dorsal view of skull). Estes et al. (1988) (ordered).

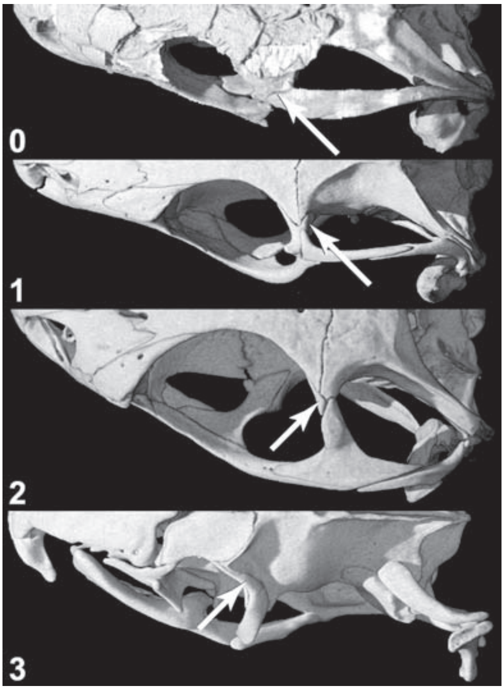
68. Postorbital: (0) present; (1) lost. Estes et al. (1988).



69. Postorbital shape$^{\text{N}}$: (0) widens anteriorly (*Lacerta viridis*, oblique lateral view of skull); (1) narrows anteriorly (*Sphenomorphus solomonis*, oblique lateral view of skull). Snakes lack a squamosal process, but the postorbital has a conspicuous ventral reach behind the orbit, and they are accordingly regarded as having a "wide" postorbital anteriorly.

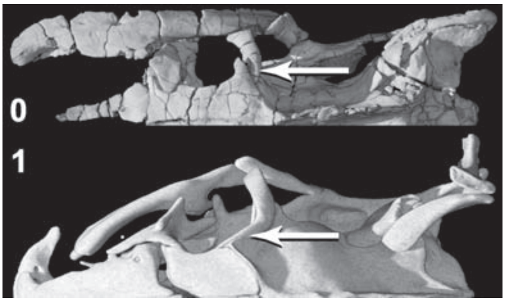


70. Postfrontal broad and flat$^{\text{N}}$: (0) not (*Pseudopus apodus*, dorsal view of skull); (1) often very broad, always anteroposteriorly extensive and flat, with postorbital process reduced to nub (*Eublepharis macularius*, dorsal view of skull); (2) with a shaft that is club-shaped distally (*Rhacodactylus auriculatus*, dorsal view of skull) (ordered).

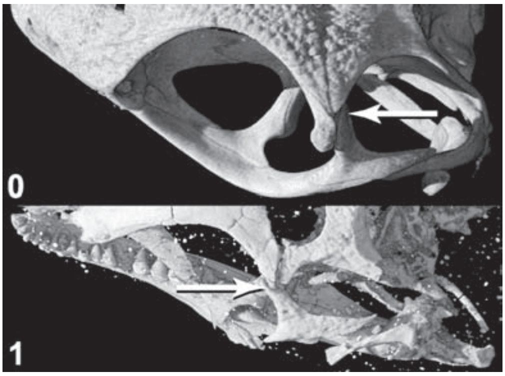


71. Postorbital-parietal contact: (0) postorbital entirely distal, separated by postfrontal from parietal (*Elgaria multicarinata*, dorsal view of skull); (1) postorbital with discrete process extending toward parietal behind postfrontal

(*Callopistes maculatus*, dorsal view of skull); (2) postorbital contacts parietal ventrolaterally at frontoparietal suture (*Dipsosaurus dorsalis*, dorsal view of skull); (3)^N or postorbital dorsolaterally behind frontoparietal suture (*Eryx colubrinus*, dorsal view of skull). Smith (2009a, 2009b).

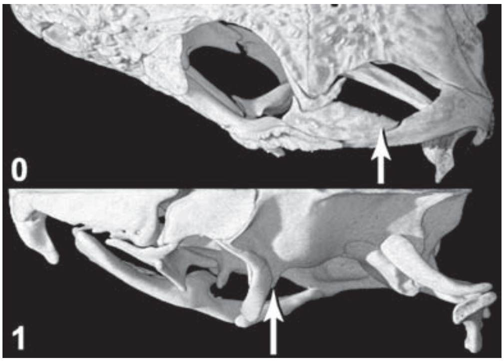


72. Postorbital shape at skull roof contact^N: (0) postorbital abuts parietal dorsolaterally at narrow contact (*Dinilysia patagonica*, dorsal view of skull); (1) with a long anterodorsally curving head (that often extends past level of frontoparietal suture midline) (*Eryx colubrinus*, dorsal view of skull).

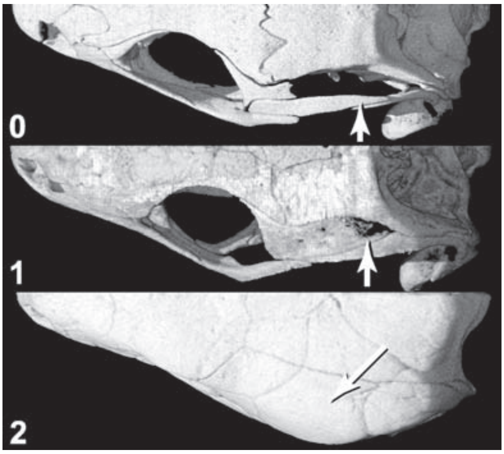


73. Postorbital with small compressed tab at apex passing across frontoparietal suture^N: (0) absent (*Enyalioides laticeps*, dorsal view of skull); (1) present (*Isodontosaurus gracilis*, dorsal view of skull).

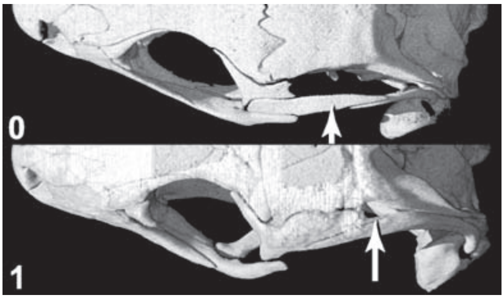
74. Postorbital, dorsomedial head: (0) undivided (*Cylindrophis ruffus*, oblique lateral close-up of anterior skull); (1) divided into two heads (*Trachyboa boulengeri*, lateral close-up of anterior skull). Kluge (1993b).



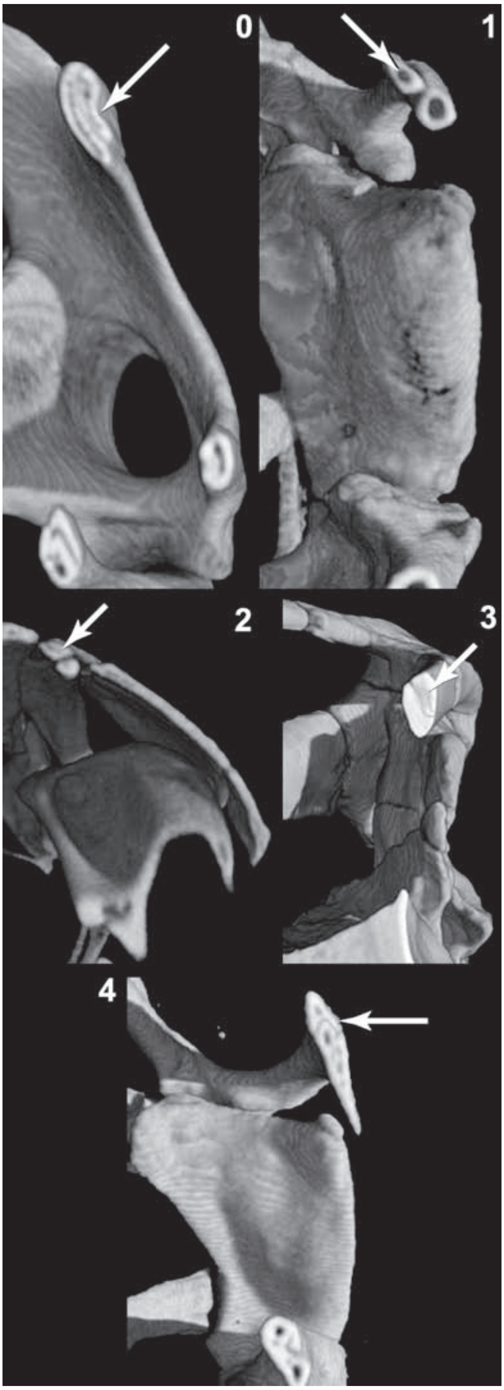
75. Postorbital squamosal process: (0) present (*Xenosaurus platyceps*, dorsal close-up of skull); (1) absent (*Eryx colubrinus*, dorsal close-up of skull). Estes et al. (1988).



76. Postorbital restricts upper temporal fenestra (UTF): (0) absent, postorbital tapers to tip (*Pholidobolus montium*, dorsal view of skull); (1)^N partly occludes UTF, as postorbital expands medially posteriorly (*Plestiodon fasciatus*, dorsal view of skull); (2) enlarged postorbital completely occludes UTF (*Lepidophyma flavimaculatum*, dorsal view of skull). Estes et al. (1988).

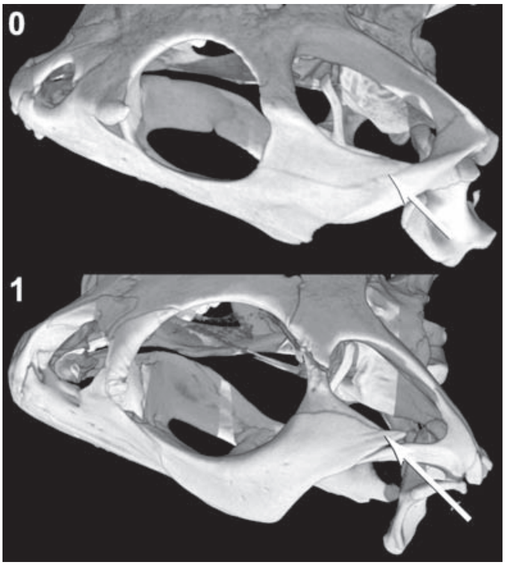


77. Postorbital (nearly) excludes squamosal from upper temporal fenestra: (0) absent (*Pholidobolus montium*, dorsal view of skull); (1) present (*Eugongylus rufescens*, dorsal view of skull). Wu et al. (1996).



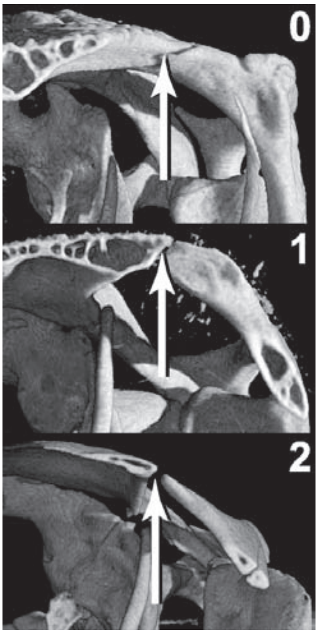
78. Postorbital overlaps squamosal: (0) laterally into V-shaped recess in squamosal (*Sphenodon punctatus*, anterior close-up cutaway view of skull); (1) dorsomedially as slender tapering rod attached superficially (*Chalarodon madagascariensis*, anterior close-up cutaway view of skull); (2)^N dorsally (*Platysaurus imperator*, anterior close-up cutaway view of skull); (3)^N postorbital in long V-shaped trough dorsally and then rotating dorsolaterally posteriorly (*Plotosaurus*

bennisoni, anterior close-up cutaway view of skull); (4)N squamosal lies in trough beneath postorbital (*Calotes emma*, anterior close-up cutaway view of skull). Arnold (1998).

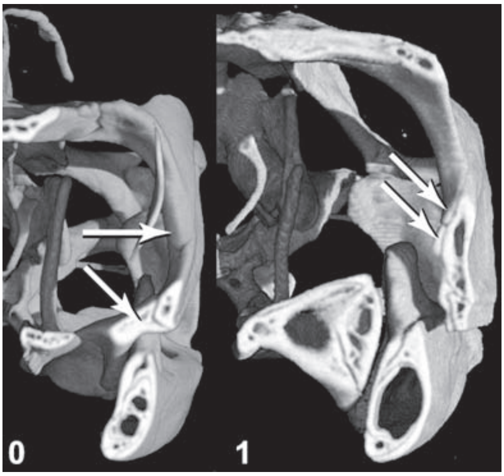


79. Postorbital-squamosal suture: (0) firm, suture no wider than those among surrounding elements (*Pogona vitticeps*, oblique dorsal view of skull); (1) loose, sutural gap wider than that between postorbital and postfrontal, or postorbital and jugal (*Uromastyx aegyptius*, oblique dorsal view of skull). Arnold (1998).

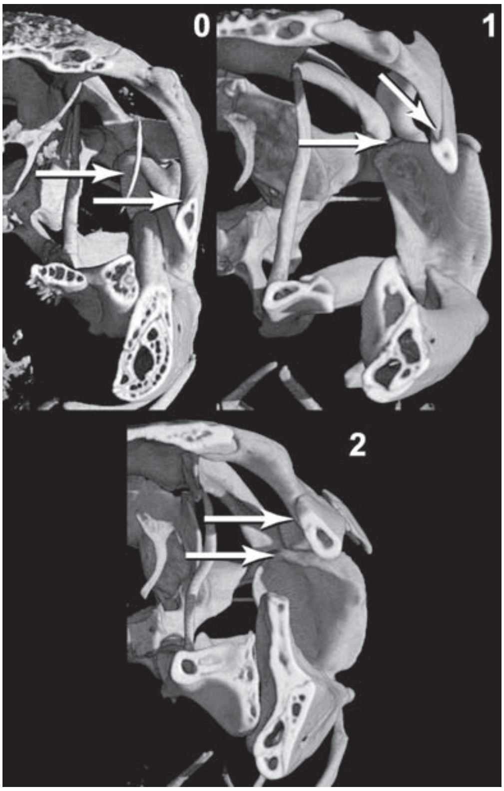
These bones are held together by considerable connective tissue in iguanians generally. In dried skeletal preparations, that tissue shrinks, drawing the two bones together. Nick Arnold found this kinetic joint by manipulating spirit-preserved specimens, but no one studying dried skulls appears to have noticed it. Our discovery of this apomorphy, quite independently of Arnold's insight, was an unforeseen benefit of CT-scanning wet specimens.



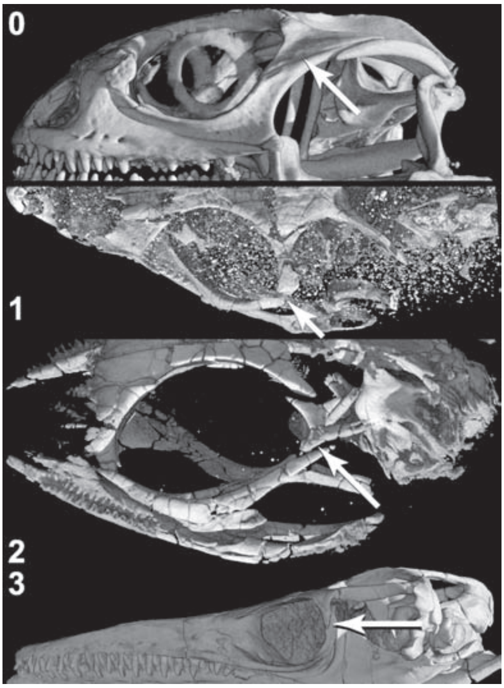
80. Postorbital firmly sutured to skull roofing bones (postfrontal or parietal): (0) present (*Polychrus marmoratus*, anterior close-up cutaway view of skull); (1) postorbital barely underlaps parietal at frontoparietal suture (equals mobile joint of Arnold 1998) (*Enyalioides laticeps*, anterior close-up cutaway view of skull); (2)N postorbital tapers to blunt tip separated from parietal (*Liolaemus belliii*, anterior close-up cutaway view of skull). (Smith 2009a, 2009b) (ordered).



81. Postorbital-ectopterygoid contact: (0) absent (*Basiliscus basiliscus*, anterior close-up cutaway view of skull); (1) present (*Calotes emma*, anterior close-up cutaway view of skull). Moody (1980).

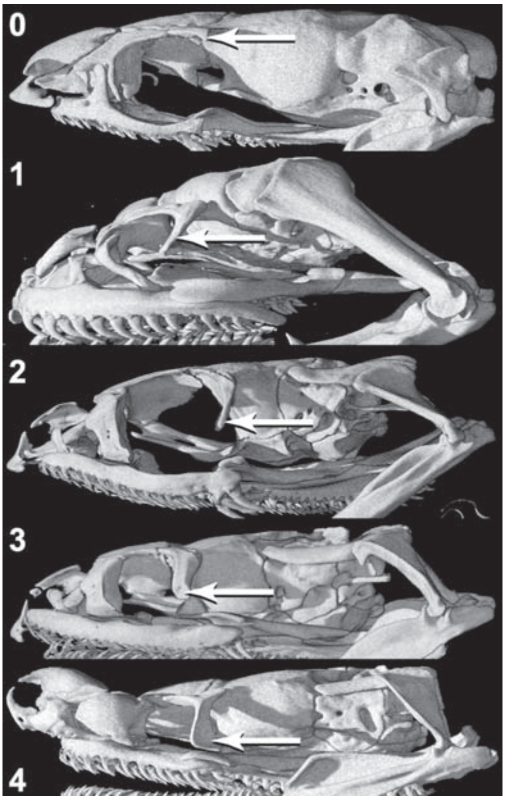


82. Postorbital jugal ramus: (0) extends ventral to quadrate head (*Brachylophus fasciatus*, anterior close-up cutaway view of skull); (1)^N level with quadrate head (*Morunasaurus annularis*, anterior close-up cutaway view of skull); (2) or above quadrate head (*Leiolepis belliana*, anterior close-up cutaway view of skull). Estes et al. (1988) (ordered).



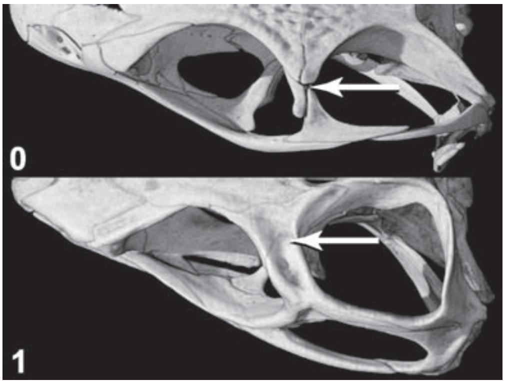
83. Postorbital-jugal suture^N: (0) long, firm, immobile, tonque-in-groove suture, with jugal largely ventrolateral to postorbital (*Crotaphytus collaris*, lateral view of skull); (1) short abutting suture, with jugal reduced to tab-like dorsal tip that lies distal to postorbital (*Tchingisaurus multivagus*, dorsal view of skull); (2) jugal tapers smoothly to apex, which is loosely joined to lateral face of postorbital via connective tissue (AMNH 21444, oblique dorsal view of skull); (3) postorbital with process extending lateral to tapering apex of jugal (*Plotosaurus bennisoni*, lateral view of skull) (ordered).

As with character 79, this kinetic joint between postorbital and jugal is readily visible in CT scans of wet scleroglossans. It went unnoticed by those studying dried skeletons because the elastic connective tissue from which it forms shrinks during preparation, drawing the two bones into close contact.

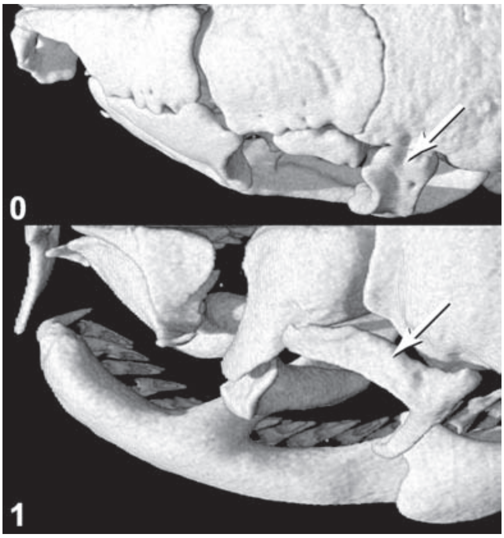


84. Postorbital contribution to posterior orbital margin: (0)^{N} less than 39% (*Aparallactus werneri*, lateral view of skull); (1)^{N} 39-52% (*Acrochordus granulatus*, lateral view of skull); (2)^{N} 53-66% (*Amphiesma stolata*, lateral view of skull); (3)^{N} 67-80% (*Afronatrix anoscopus*, lateral view of skull); (4) more than 80% (*Xenodermus javanicus*, lateral view of skull). Lee and Caldwell (1998) (ordered).

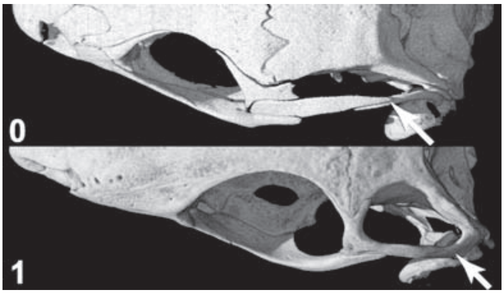
Postorbital length was measured along the midshaft of the element from the apex of its contact with the skull roof to its ventral tip. The length of the posterior orbital margin was measured from the same point dorsally to the dorsal edge of the maxilla ventrally.



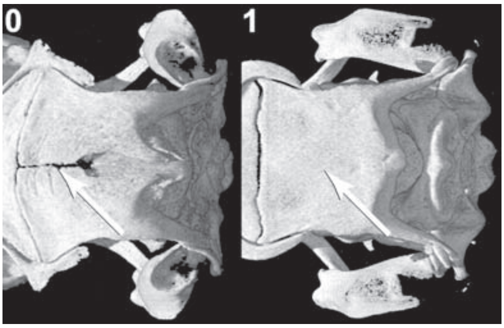
85. Postorbital spreads onto dorsal surface of postfrontal^{N}: (0) absent (*Morunasaurus annularis*, dorsal view of skull); (1) present (*Sphenodon punctatus*, dorsal view of skull).



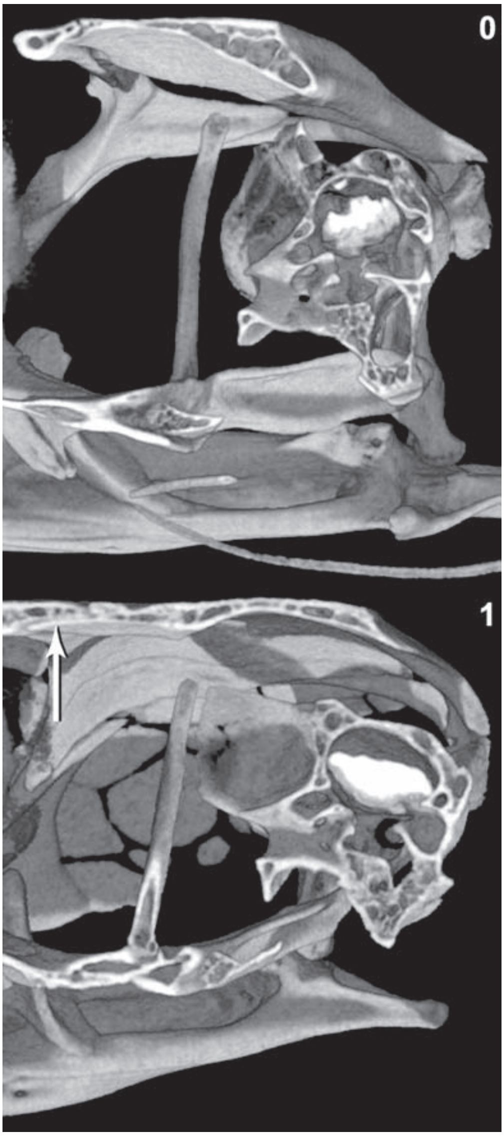
86. Postorbital dorsal part, above lateral wing of parietal: (0) uniformly narrow (*Calabaria reinhardtii*, dorsal close-up of anterior skull); (1) broadened (*Acrochordus granulatus*, dorsal close-up of anterior skull). Kluge (1993a).



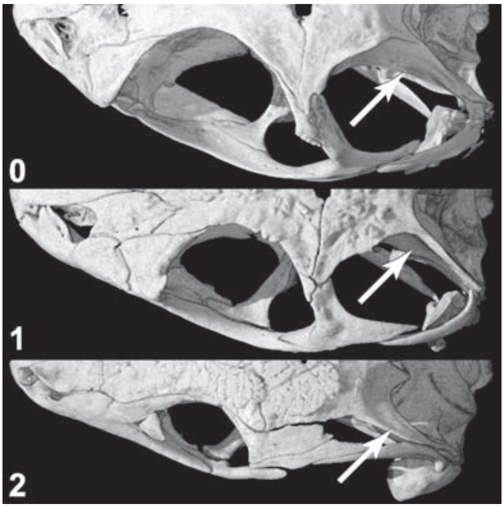
87. Postorbital extent posteriorly^{N}: (0) to end of parietal table or less (*Pholidobolus montium*, dorsal view of skull); (1) posterior to parietal table (*Teius teyou*, dorsal view of skull).



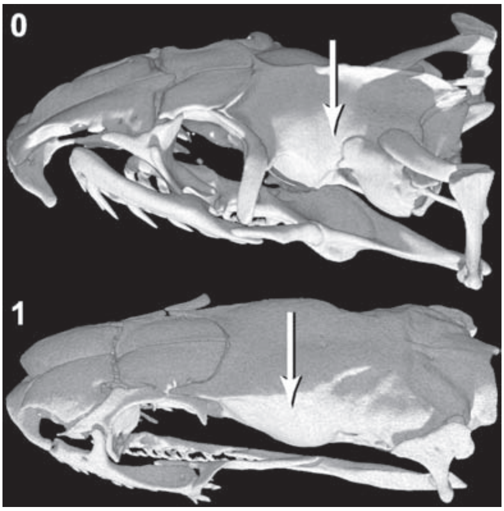
88. Parietal fusion: (0) paired (*Strophurus ciliaris*, dorsal close-up view of posterior skull); (1) fused (*Coleonyx variegatus*, dorsal close-up view of posterior skull). Gauthier, Estes and de Queiroz (1988).



89. Parietal ventral lappet: (0) poorly developed or absent (*Gambelia wislizenii*, lateral close-up cutaway view of posterior skull); (1) prominent V-shaped, flat process (*Lacerta viridis*, lateral close-up cutaway view of posterior skull). Estes et al. (1988).

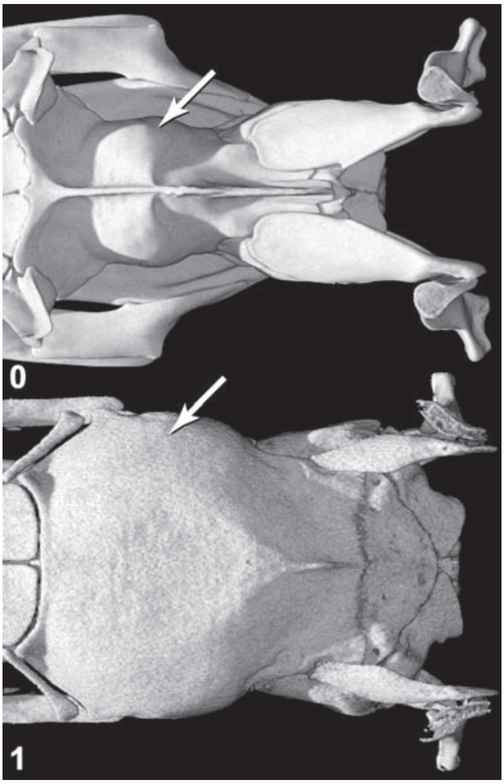


90. Parietal temporal muscles originate: (0) dorsally on parietal table and supratemporal process of parietal (*Uranoscodon superciliosus*, dorsal view of skull); (1)^{N} ventrally on parietal table and dorsally on supratemporal process (*Urostrophus vautieri*, dorsal view of skull); (2) ventrally on parietal table and supratemporal process (*Sphenomorphus solomonis*, dorsal view of skull). Gauthier (1982) (ordered).

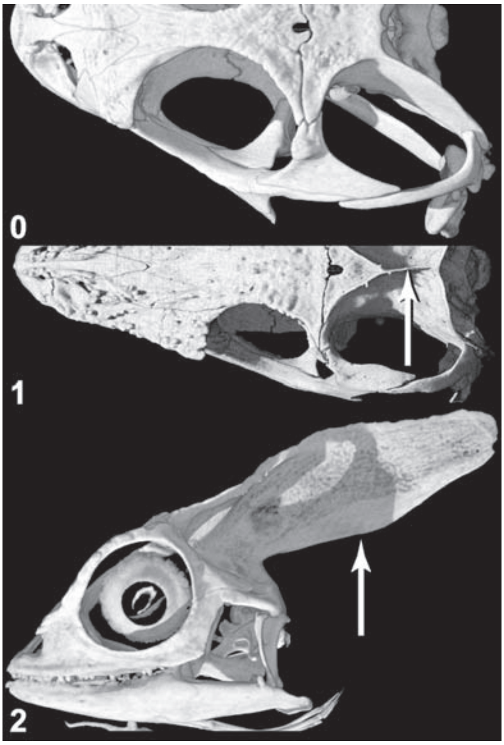


91. Parietal temporal fossa shape^{N}: (0) temporal muscles originate dorsally across entire parietal table all the way to frontal anteriorly (at least laterally) (*Eryx colubrinus*, oblique lateral view of skull); (1) anterolateral corner of temporal fossa terminates posteriorly, dorsal and ventral margins of temporal fossa converge behind frontal, so parietal table extends as flat surface toward orbital margin, and temporal muscles are confined laterally (*Aparallactus werneri*, oblique lateral view of skull).

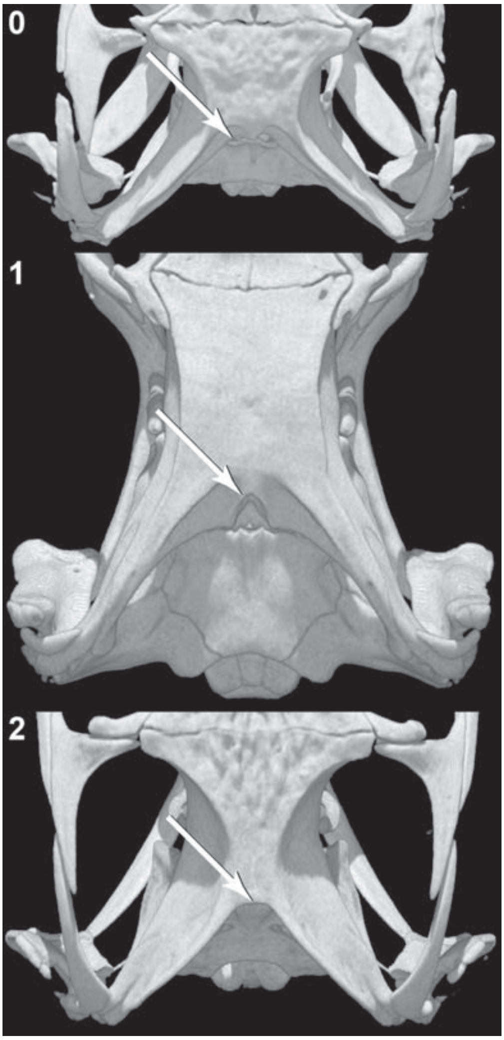
This character tracks an apomorphy arising inside Serpentes, and is accordingly considered "not applicable" (?) in other lizards. The apomorphic condition from which it arises in stem snakes—in which the jaw muscles converge on the midline to form a sagittal crest over most of their origin on the parietal table—is tracked by character 93(1).



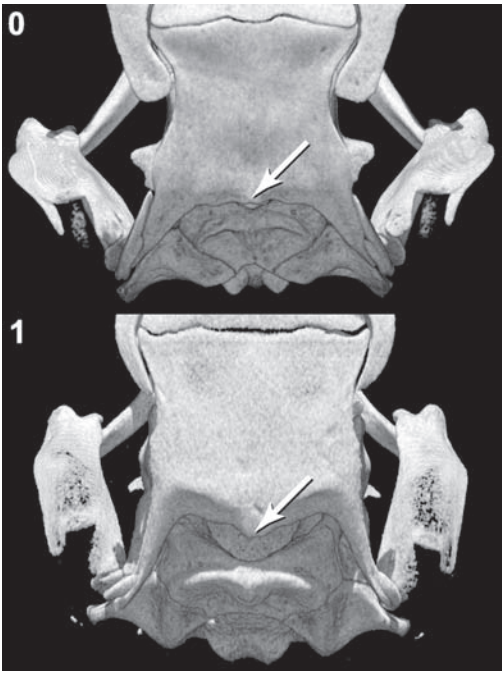
92. Parietal, middle third: (0) narrow in dorsal view (*Python molurus*, dorsal close-up of posterior skull); (1) wide in dorsal view (*Lichanura trivirgata*, dorsal close-up of posterior skull). Kluge (1993a).



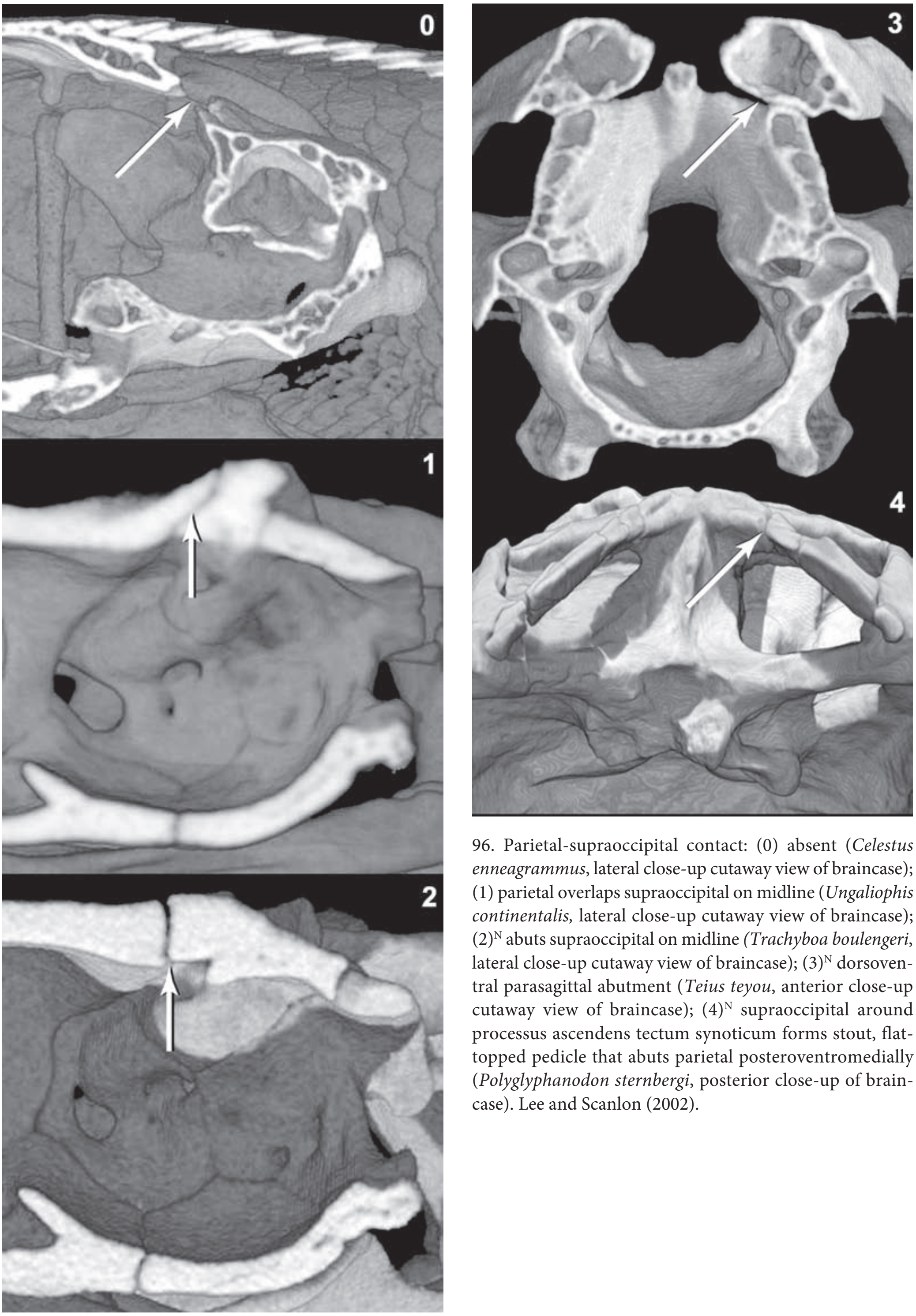
93. Parietal sagittal crest: (0) absent (*Crotaphytus collaris*, dorsal view of skull); (1) present (*Anolis carolinensis*, dorsal view of skull); (2) projecting dorsally (*Corytophanes cristatus*, lateral view of skull). Etheridge and de Queiroz (1988) (ordered).



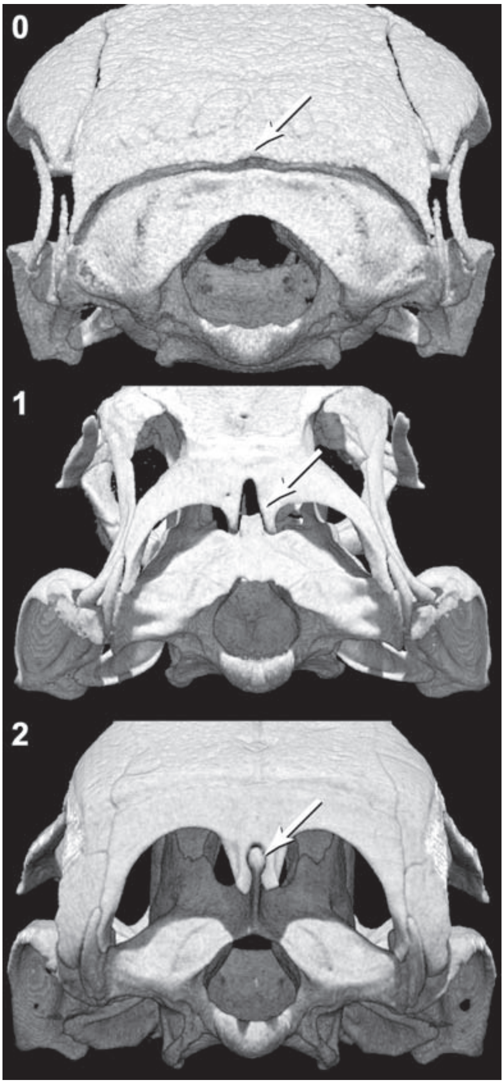
94. Parietal nuchal fossa width^{N}: (0) narrow (*Sauromalus ater*, dorsal close-up view of parietal); (1) wide (*Lanthanotus borneensis*, dorsal close-up view of parietal); (2) overgrown by parietal (nearly) to midline (*Morunasaurus annularis*, dorsal close-up view of parietal).



95. Parietal postparietal projection near midline (bifid distally or not; see character 97)^{N}: (0) absent (*Eublepharis macularius*, dorsal close-up of parietal); (1) present (*Coleonyx variegatus*, dorsal close-up of parietal).

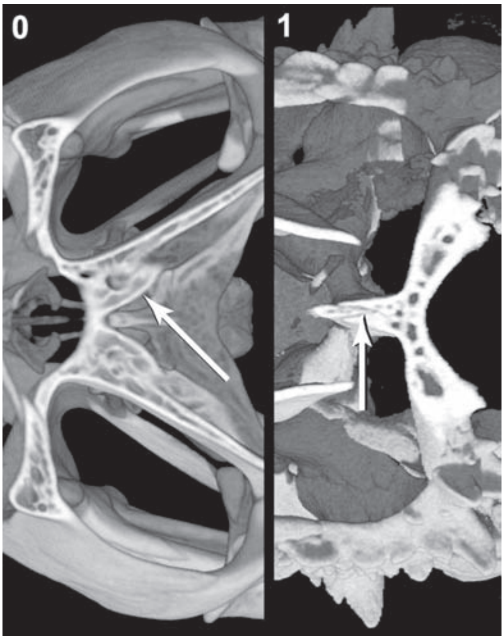


96. Parietal-supraoccipital contact: (0) absent (*Celestus enneagrammus*, lateral close-up cutaway view of braincase); (1) parietal overlaps supraoccipital on midline (*Ungaliophis continentalis,* lateral close-up cutaway view of braincase); (2)^{N} abuts supraoccipital on midline *(Trachyboa boulengeri*, lateral close-up cutaway view of braincase); (3)^{N} dorsoventral parasagittal abutment (*Teius teyou*, anterior close-up cutaway view of braincase); (4)^{N} supraoccipital around processus ascendens tectum synoticum forms stout, flat-topped pedicle that abuts parietal posteroventromedially (*Polyglyphanodon sternbergi*, posterior close-up of braincase). Lee and Scanlon (2002).

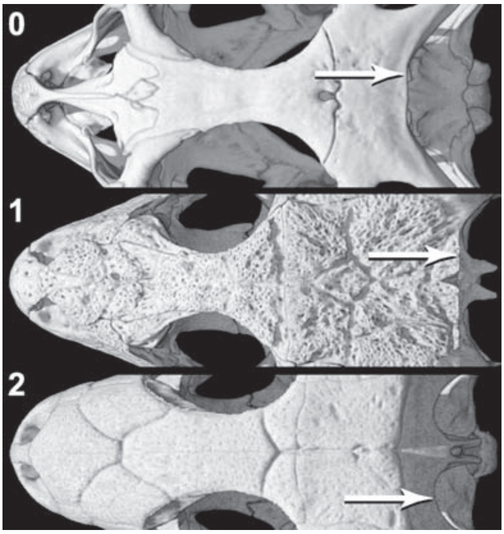


97. Parietal bifid supraoccipital process: (0) absent (*Cricosaura typica*, oblique posterior view of braincase); (1)^{N} present (*Amphiglossus splendidus*, oblique posterior view of braincase); (2) clasping supraoccipital crest (*Zonosaurus ornatus*, oblique posterior view of braincase). Lang (1991) (ordered).

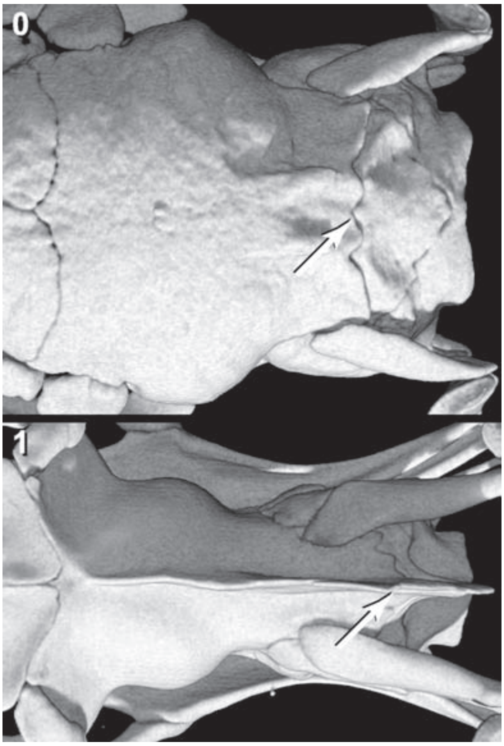
The parietal supraoccipital process may clasp the processus ascendens of the tectum synoticum in some scincoids (e.g., *Amphiglossus*). But that is not the same as the supraocciptial crest to which it attaches in others. *Zonosaurus*, for example, has both structures on its supraoccipital, and the bifid process clasps only the latter. Nevertheless, these states were ordered to capture the fact that the crest arises immediately behind, and indeed may be continous with, the ascending process, and the same "bifid process" of the parietal clasps the supraoccipital on the anterodorsal midline in either case.



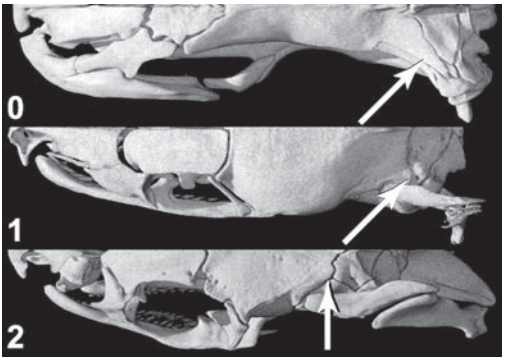
98. Parietal descending lamina articulates with supraoccipital ascending lamina^{N}: (0) absent, parietal descending lamina is anterior to supraoccipital ascending lamina (*Pogona vitticeps*, dorsal close-up cutaway view of braincase); (1) present, parietal descending lamina is posterior to the supraoccipital ascending lamina (*Brookesia brygooi*, dorsal close-up cutaway view of braincase).



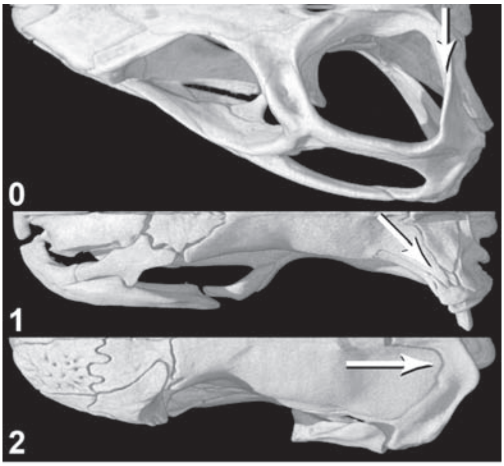
99. Parietal extent over braincase in dorsal view: (0) does not cover occiput (*Uromastyx aegyptius*, dorsal close-up view of skull); (1) covers nearly all of occiput (*Cordylus mossambicus*, dorsal close-up of skull); (2) with emarginate lateral fossae (*Zonosaurus ornatus*, dorsal close-up of skull), Lang (1991). Estes et al. (1988) (ordered).



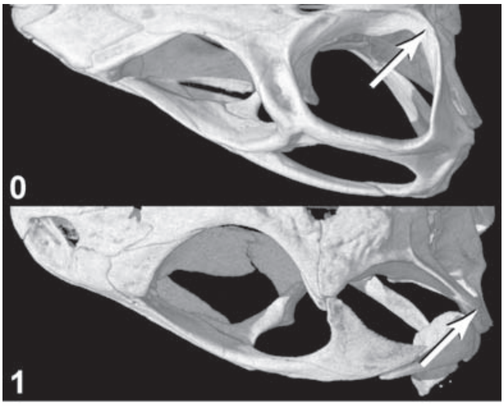
100. Parietal posterior margin, in dorsal view: (0) does not form an elongate, slender and pointed posterior process (*Calabaria reinhardtii*, dorsal close-up of posterior skull); (1) does form an elongate, slender and pointed posterior process (*Epicrates striatus*, dorsal close-up of posterior skull). Kluge (1993a).



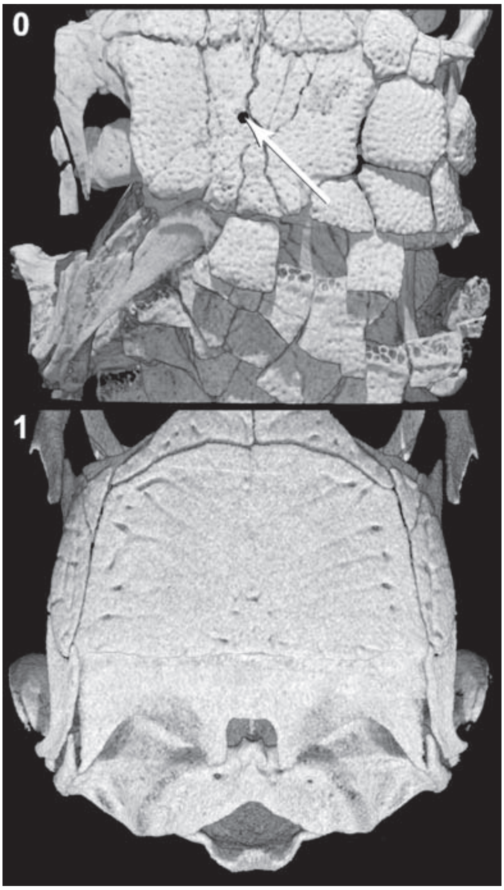
101. Parietal supratemporal process length: (0) well-developed (*Anilius scytale*, dorsal view of skull); (1) reduced, less than 25% of parietal width (*Lichanurus trivirgata*, dorsal view of skull); (2) absent (*Amphiesma stolata*, dorsal view of skull), Tchernov et al. (2000). Estes et al. (1988) (ordered).



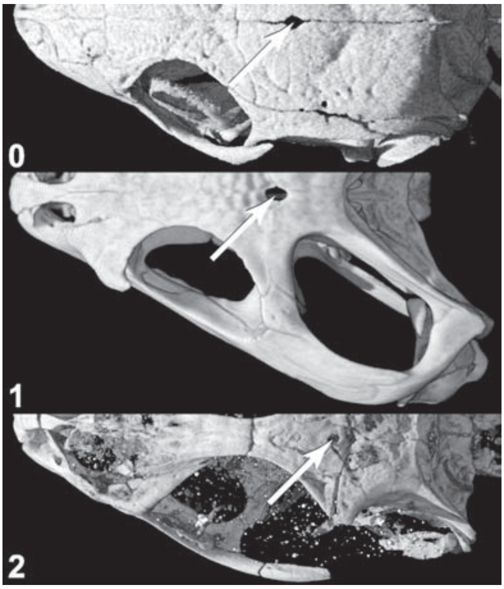
102. Parietal supratemporal process orientation^{N}: (0) directed laterally (*Sphenodon punctatus*, dorsal view of skull); (1) directed posterolaterally (*Anilius scytale*, dorsal view of skull); (2) directed posteriorly (*Amphisbaena fuliginosa*, dorsal view of skull) (ordered).



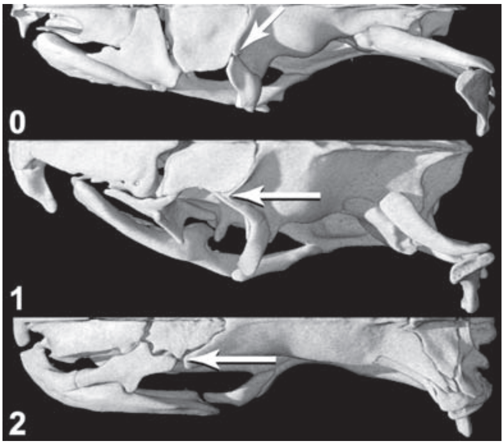
103. Parietal contribution to back of the upper temporal fenestra^{N}: (0) short supratemporal process, parietal only forms about half of the upper temporal fenestra posterior arch, with supratemporal forming distal half (*Sphenodon punctatus*, dorsal view of skull); (1) long parietal supratemporal process extends distally to near the quadrate head (*Sceloporus variabilis*, dorsal view of skull).



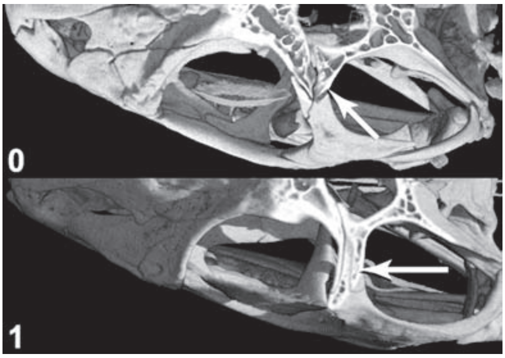
104. Parietal foramen: (0) present (*Peltosaurus granulosus*, AMNH 8138, dorsal close-up of parietal); (1) absent (*Cordylosaurus subtesselatus*, dorsal close-up of parietal). Estes et al. (1988).



105. Parietal foramen position: (0) in parietal (*Xantusia vigilis*, dorsal view of skull); (1) at frontoparietal suture (*Pogona vitticeps*, dorsal view of skull); (2) in frontal (*Armandisaurus* sp., dorsal view of skull). Estes et al. (1988) (ordered).



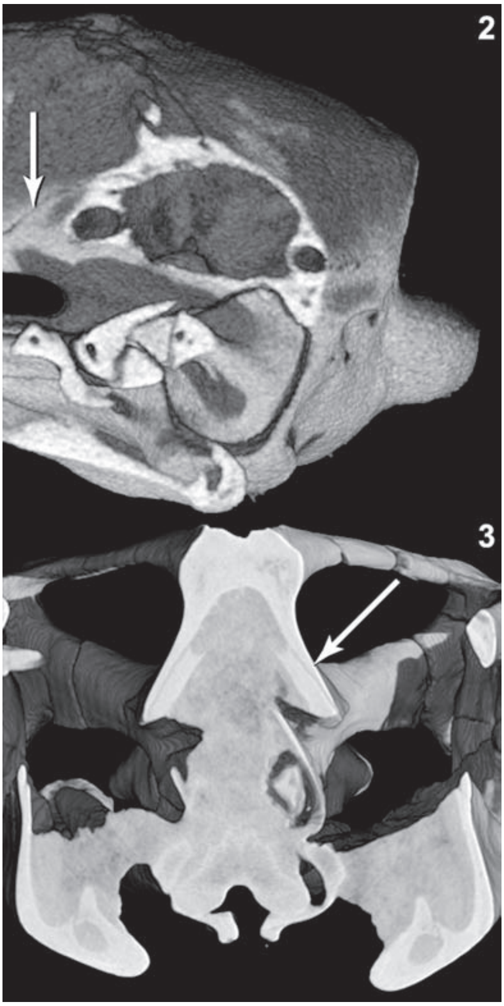
106. Parietal supraorbital process: (0) absent (*Epicrates striatus*, dorsal view of skull); (1) present (*Eryx colubrinus*, dorsal view of skull); (2) deeply clasping frontal orbital margin (*Anilius scytale*, dorsal view of skull). Tchernov et al. (2000) (ordered).



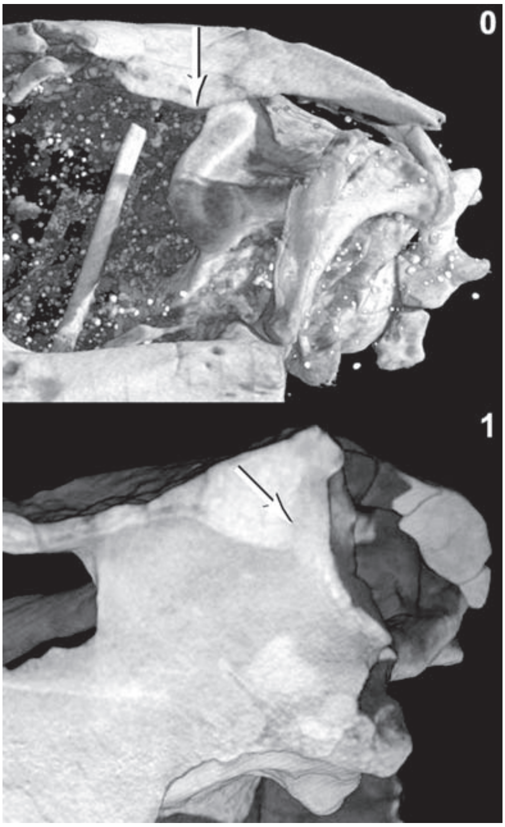
107. Parietal postorbital process^{N}: (0) absent; parietal barely, if at all, laps behind postorbital apex in horizontal section (*Urostrophus vautieri*, dorsal cutaway view of skull); (1) parietal vertically oriented lappet extends laterally to overlap postorbital to form anteromedial margin of upper temporal fenestra (*Calotes emma*, dorsal cutaway view of skull).

108. Parietal epipterygoid process: (0) absent (*Oplurus cyclurus*, lateral close-up cutaway view of posterior skull);

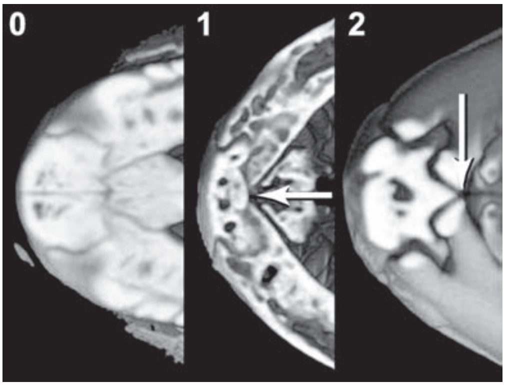
(1)^{N} distinct process (*Zonosaurus ornatus*, lateral close-up cutaway view of posterior skull); (2) reaches alar process of prootic (*Eugongylus rufuscens*, lateral close-up cutaway view of posterior skull). Estes et al. (1988) (ordered).



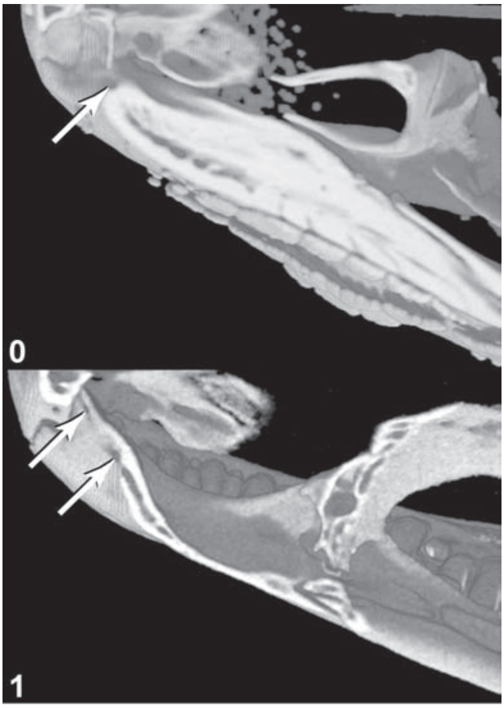
109. Parietal-prootic contact: (0) absent (*Shinisaurus crocodilurus*, lateral close-up cutaway view of braincase); (1)^{N} contact at apex of alar process (*Tupinambis teguixin*, lateral close-up cutaway view of braincase); (2) extensive conformable contact, with parietal overlapping prootic laterally throughout length (*Anniella pulchra*, lateral close-up cutaway view of braincase); (3)^{N} discrete ventral process of parietal overlaps prootic alar process laterally (*Plotosaurus bennisoni*, anterior close-up cutaway view of braincase). Lee (1998).



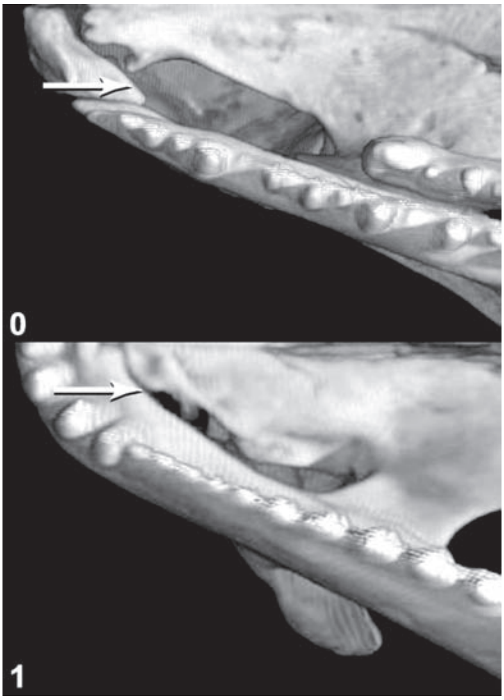
110. Parietal ventral triangular downgrowths of temporal muscle origin overlap prootic laterally, with latter abutting former medially, just anterior to supraoccipital^{N}: (0) absent (*Armandisaurus explorator*, lateral close-up view of braincase); (1) present (*Polyglyphanodon sternbergi*, lateral close-up cutaway view of braincase).



111. Maxilla (post-) premaxillary process contact: (0) not in contact (*Tiliqua scincoides*, dorsal close-up cutaway view of snout); (1) in contact, or nearly so, but always excluding premaxilla from vomer dorsally (*Uranoscodon superciliosus*, dorsal close-up cutaway view of snout); (2)^{N} in contact and vertically expanded (*Uromastyx aegyptius*, dorsal close-up cutaway view of snout). Estes et al. (1988).



112. Maxilla premaxillary process dorsal surface grooved (often enclosed) for passage of a deeper and more internally placed ramus of the subnarial artery: (0) absent (*Gekko gecko*, dorsal close-up cutaway view of snout); (1) present (*Urostrophus vautieri*, dorsal close-up cutaway view of snout). Smith (2009a, 2009b).

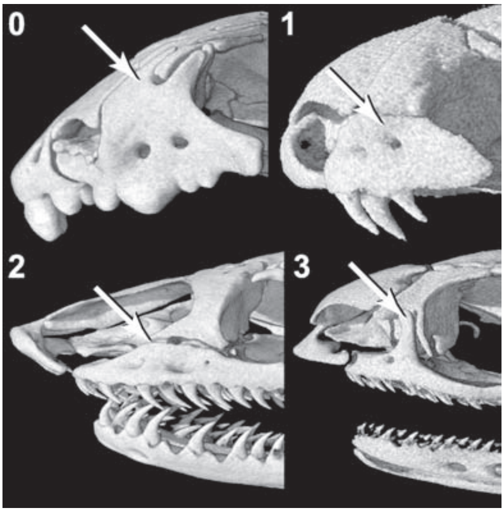


113. Maxilla and vomer: (0) do not meet at anterior margin of fenestra exochoanalis (*Sphenodon punctatus*, ventral

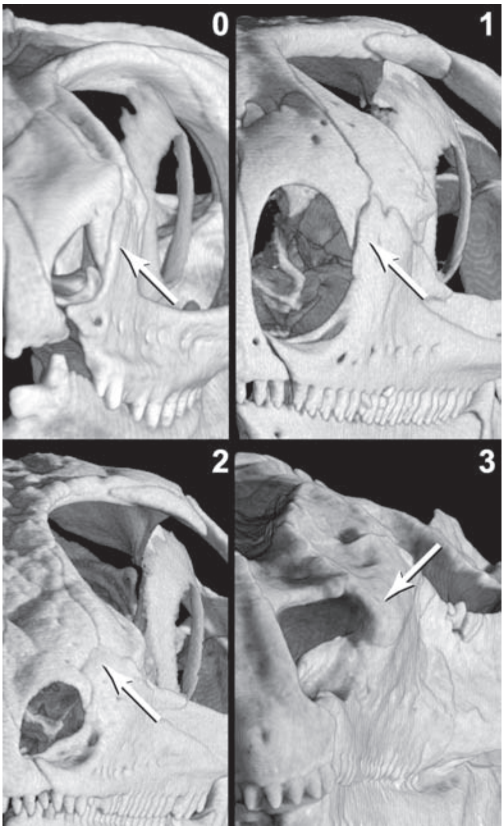
close-up of snout); (1) meet at anterior margin of fenestra exochoanalis (*Pogona vitticeps*, ventral close-up of snout). Rieppel et al. (2008).

114. Maxilla facial process length/maxilla length: (0)^N 10-15%; (1)^N 16-23%; (2)^N 25-36%; (3) 38-55%; (4)^N more than 56%. Gauthier (1982) (ordered).

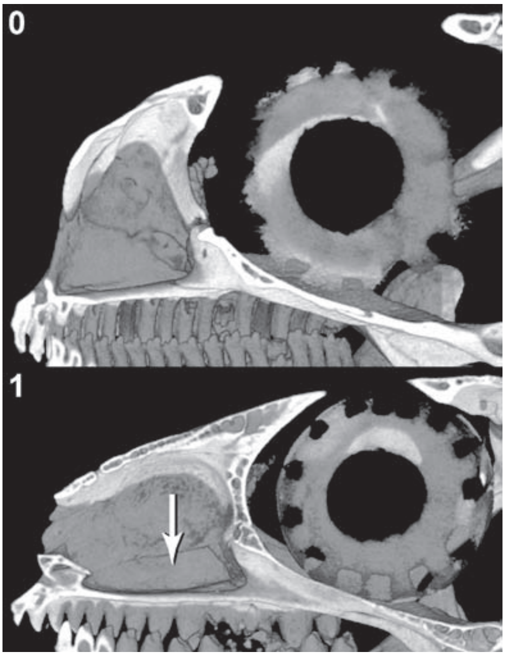
Maxilla length measured just above base of tooth row from premaxillary articulation to posterior terminus of the element. Maxilla facial process length measured from mid-height of narial margin to edge of jugal articulation.



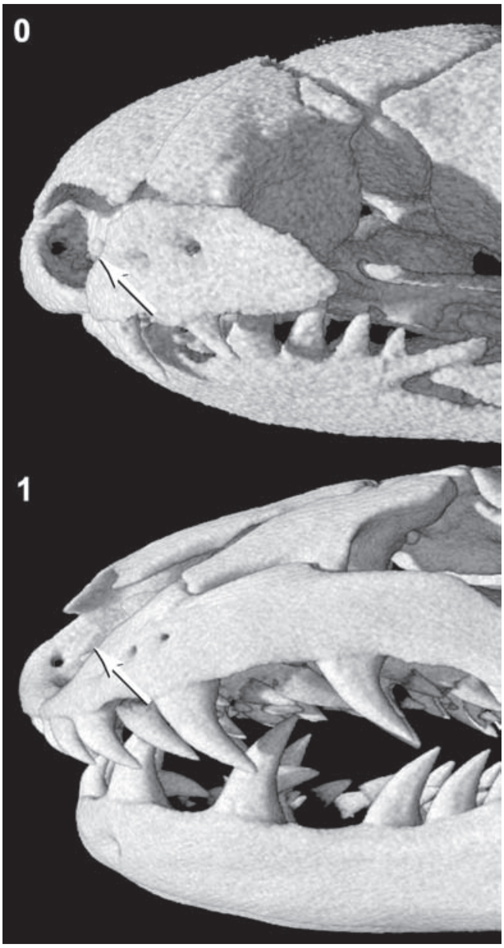
115. Maxilla facial process height: (0) tall, to skull roof (*Trogonophis weigmanni*, lateral close-up of snout); (1)^N reduced (*Anomochilus leonardi*, lateral close-up of snout); (2) absent (*Loxocemus bicolor*, lateral close-up of snout); (3)^N columnar process received in longitudinal concavity on anterior face of prefrontal (*Aparallactus werneri*, lateral close-up of snout). Tchernov (2002) (ordered).



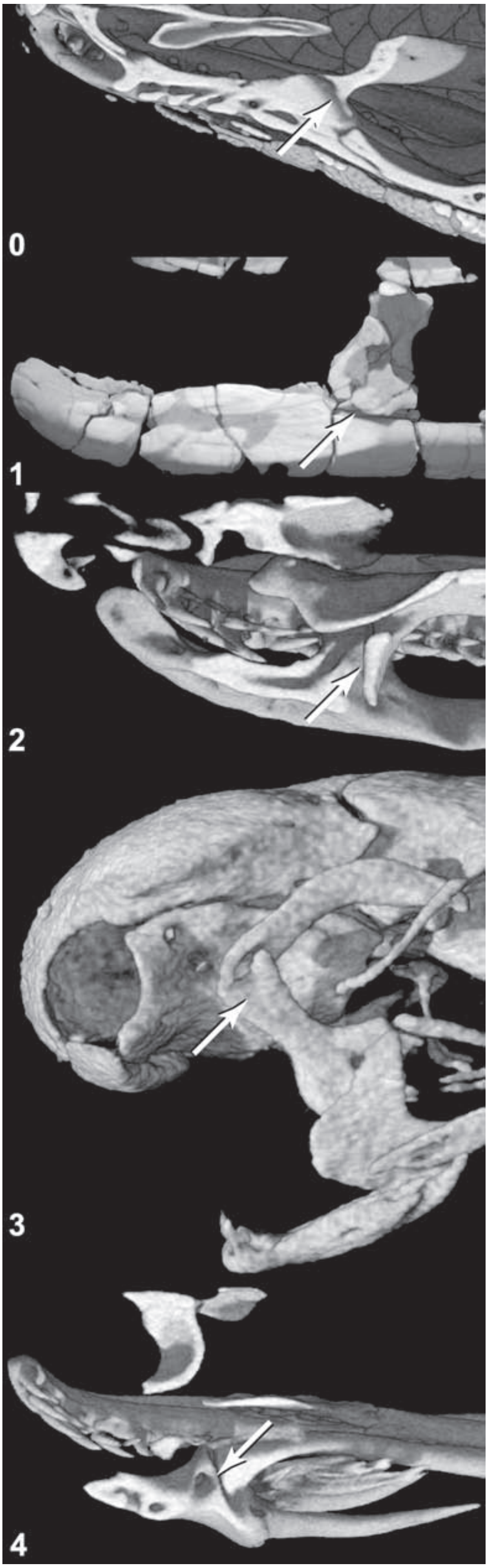
116. Maxilla facial process apical surface faces: (0) laterally (*Sphenodon punctatus*, anterior close-up of snout); (1) dorsolaterally (*Dipsosaurus dorsalis*, anterior close-up of snout); (2)^N anterodorsally (*Leiocephalus barahonensis*, anterior close-up of snout); (3)^N large, triangular, dorsally directed surface sharply set off from nearly vertical external surface of facial process (*Polyglyphanodon sternbergi*, anterior close-up of snout). Smith (2009a).



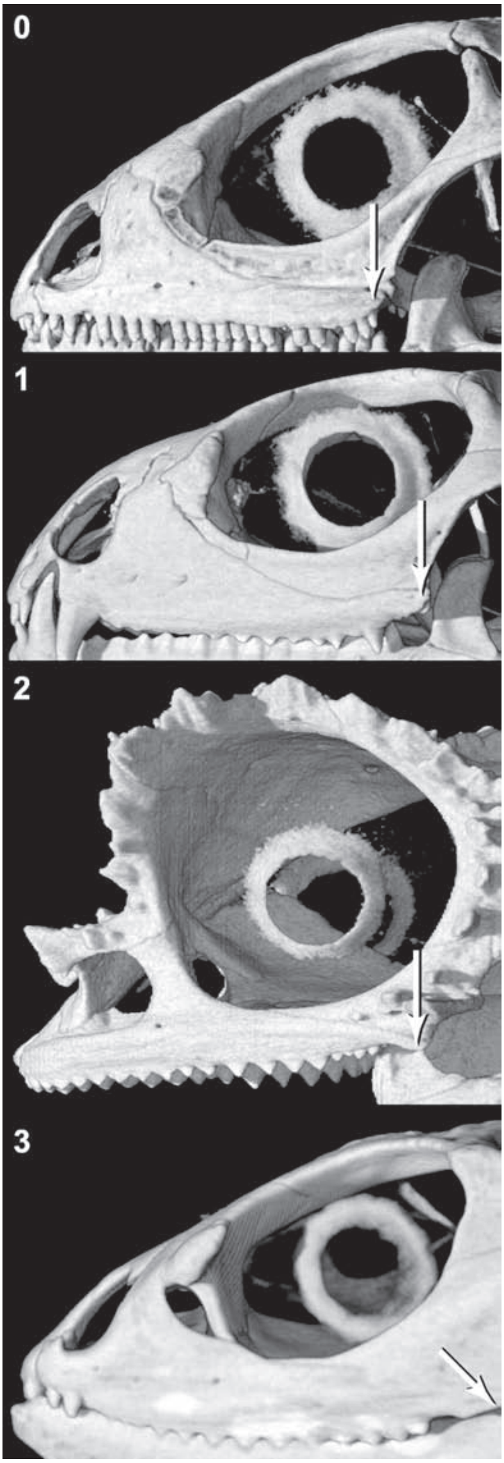
117. Maxilla facial process medial face with a posterodorsally trending ridge demarcating the anterior limits of a shallow, oval fossa—the naso-lacrimal fossa—bordered by the lacrimal and infraorbital canals posteriorly: (0) absent (*Dipsosaurus dorsalis*, lateral close-up cutaway view of anterior skull); (1) present (*Teius teyou, lateral* close-up cutaway view of anterior skull). Gauthier (1982).



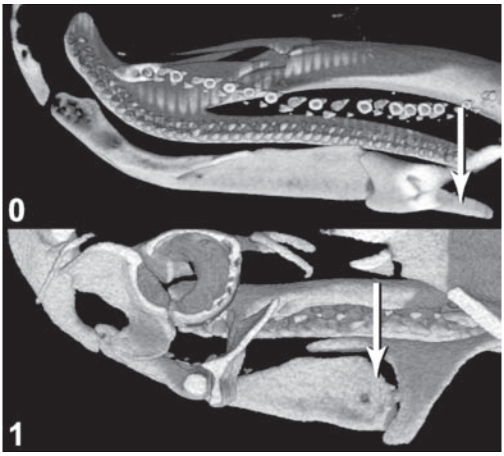
118. Maxilla narial margin rises at: (0) high angle (*Anomochilus leonardi*, lateral close-up of snout); (1) low angle (*Anilius scytale*, lateral close-up of snout). Pregill et al. (1986).



119. Maxilla firmly sutured to palatine: (0) present (*Pseudopus apodus*, dorsal close-up cutaway view of snout); (1)^N prominent palatine process of maxilla (*Dinilysia patagonica*, dorsal close-up cutaway view of snout [mirrored]); (2) loosely ligamentous connection via projecting palatine process of maxilla and distinct maxillary process of palatine, with the former lying anterior to the latter (*Loxocemus bicolor*, dorsal close-up cutaway view of snout); (3)^N maxilla free of palatine, suspended from prefrontal (*Liotyphlops albirostris*, lateral close-up of snout); (4) maxilla rotates to erect fang (*Azemiops feae*, dorsal close-up cutaway view of snout), Kardong (1994). Cundall et al. (1993).



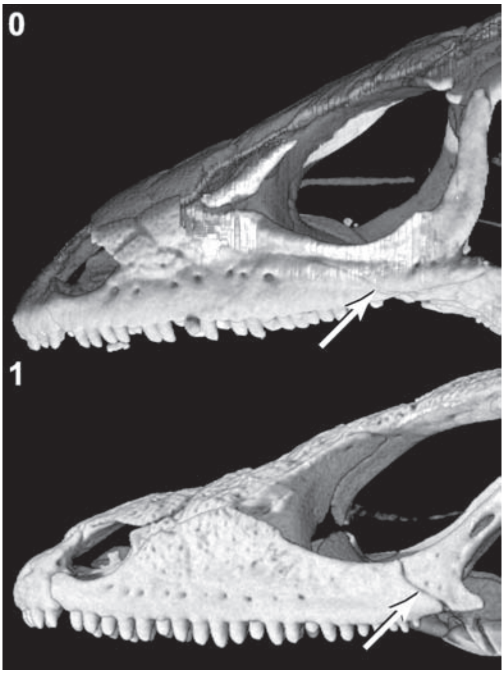
120. Maxilla suborbital ramus extends posteriorly: (0) to roughly midorbit (or anterior) (*Chalarodon madagascariensis*, lateral close-up of anterior skull); (1)^{N} to posterior quarter of orbit (*Leiolepis belliana*, lateral close-up of anterior skull); (2)^{N} to posterior edge of orbit (*Brookesia brygooi*, lateral close-up of anterior skull); (3) posterior to orbit (or frontoparietal suture) (*Pogona vitticeps*, lateral close-up of anterior skull). Lee and Scanlon (2002) (ordered).



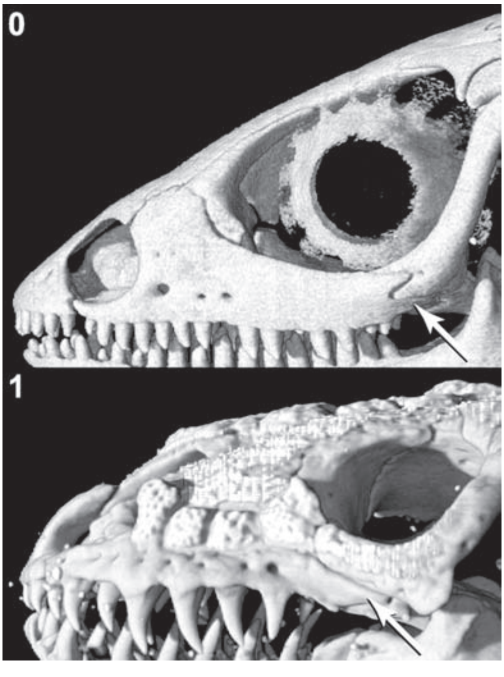
121. Maxilla suborbital process width ventral to ectopterygoid: (0) tapers posteriorly (*Xenopeltis unicolor*, dorsal close-up cutaway view of snout); (1) widens below articulation (i.e., ectopterygoid flange) (*Aparallactus werneri*, dorsal close-up cutaway view of snout). Kluge (1991).

122. Jugal depth below orbit^{N}: (0) jugal suborbital ramus not much deeper dorsoventrally below mid-orbit than postorbital ramus is wide anteroposteriorly (*Heloderma suspectum*, lateral view of skull); (1) jugal very deep below orbit (*Polyglyphanodon sternbergi*, lateral view of skull).

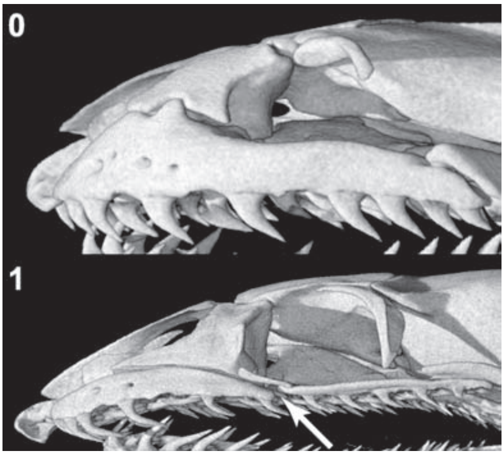
Polyglyphanodontians have a robustly constructed m. pterygoideus insertion reflected in an extensive ectopterygoid-pterygoid overlap deep to the maxilla and jugal. The robust construction of the jugal and maxilla lateral to this insertion—reflected particularly in the depth of the jugal suborbital ramus—may represent a correlated response to what must have been a massive jaw adductor.



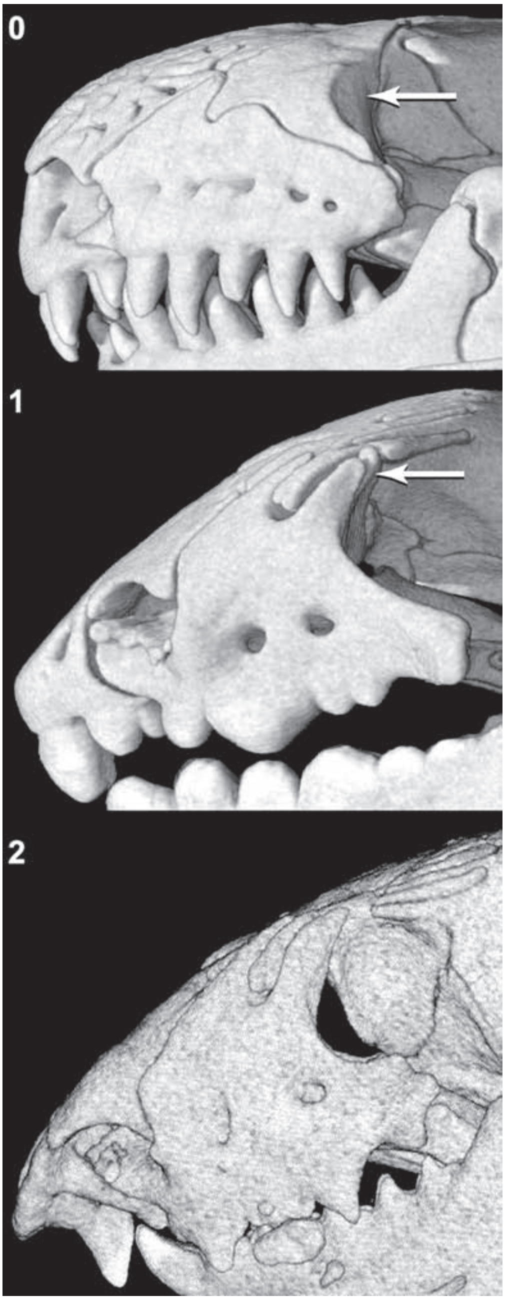
123. Maxilla suborbital process tip shape at jugal articulation^{N}: (0) suborbital margin slopes smoothly to tip (*Elgaria multicarinata*, lateral close-up of snout); (1) with distinct step or V-shaped notch distally at jugal articulation (*Cordylus mossambicus*, lateral close-up of snout).



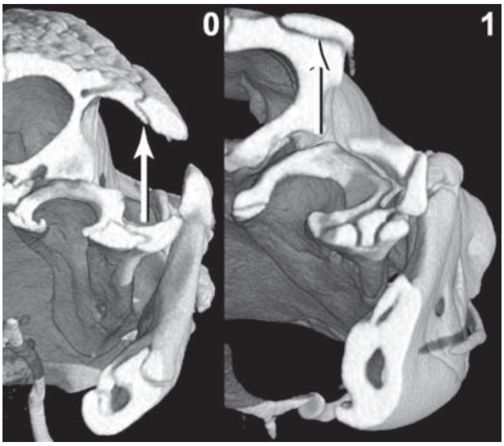
124. Maxilla posterior process shortens: (0) to midorbit or longer (*Pholidobolus montium*, lateral close-up of snout); (1) to anterior half of oribit (*Heloderma suspectum*, lateral close-up of snout).



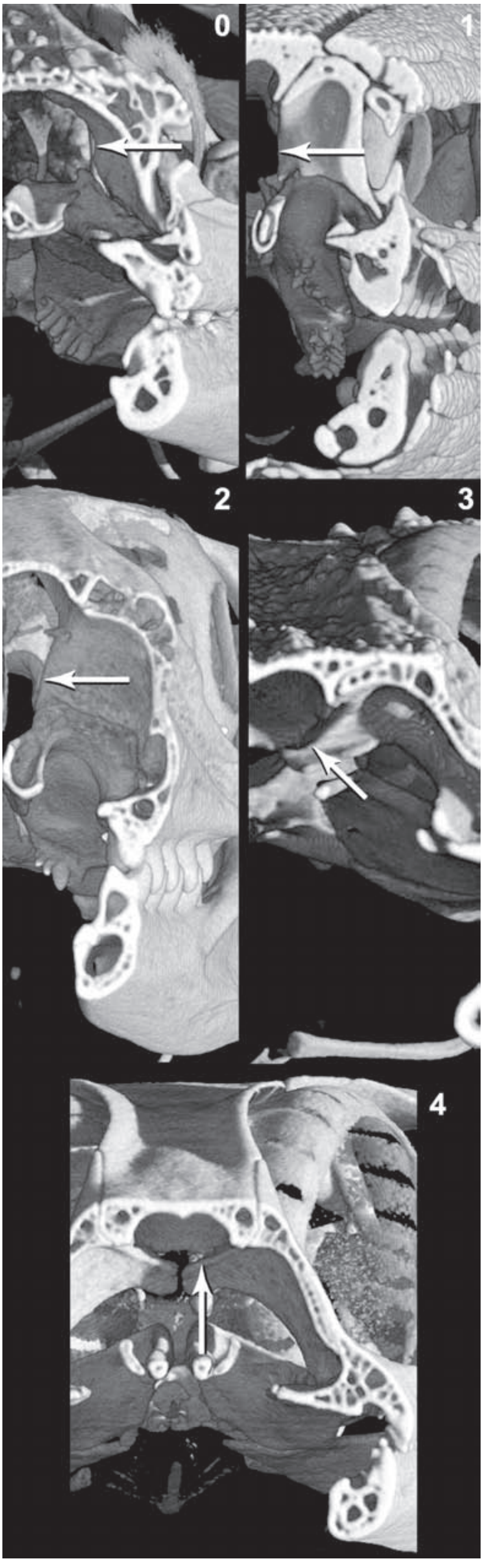
125. Maxilla, intramaxillary joint: (0) absent (*Cylindrophis ruffus*, lateral close-up of snout); (1) present (*Casarea dussumieri*, lateral close-up of snout). Cundall and Irish (1989).



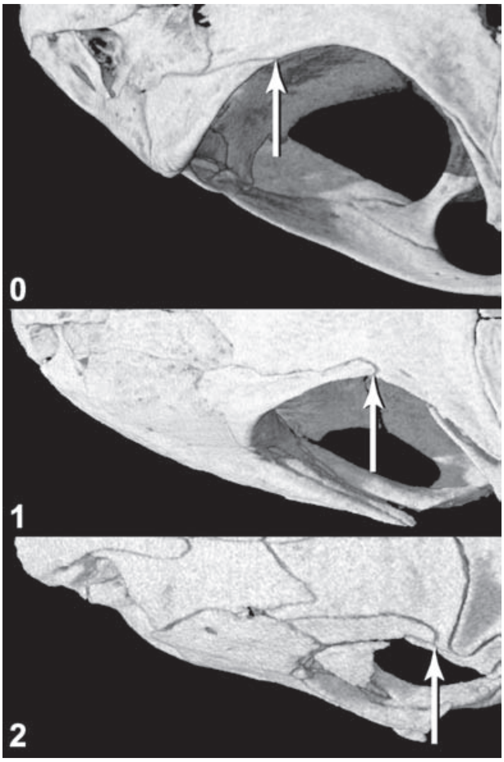
126. Prefrontal: (0) present (*Amphisbaena fuliginosa*, lateral close-up of snout); (1)^{N} reduced (*Trogonophis weigmanni*, lateral close-up of snout); (2) absent (*Diplometopon zarudnyi*, lateral close-up of snout). Kearney (2003a) (ordered).



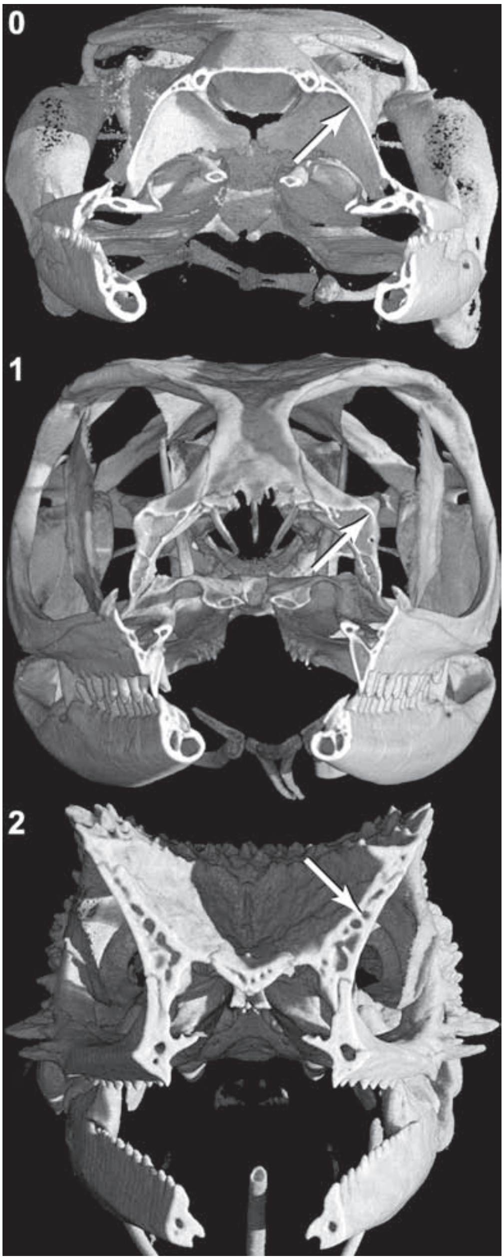
127. Prefrontal broadly overlaps frontal posterodorsally^{N}: (0) absent (*Rhineura floridana*, anterior close-up cutaway view of snout); (1) present (*Amphisbaena fuliginosa*, anterior close-up cutaway view of snout).



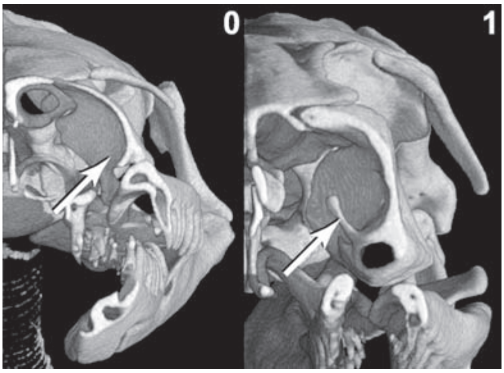
128. Prefrontal orbitonasal margin^{N}: (0) slopes ventrolaterally (*Leiosaurus catamarcensis*, anterior close-up cutaway view of snout); (1) vertical (*Pseudopus apodus*, anterior close-up cutaway view of snout); (2) slopes ventromedially (*Teius teyou*, anterior close-up cutaway view of snout); (3) extends beneath subolfactory processes (*Saltuarius cornutus*, anterior close-up cutaway view of snout); (4) extends to near contact with its opposite on midline (*Aeluroscalabotes felinus*, anterior close-up cutaway view of snout) (ordered).



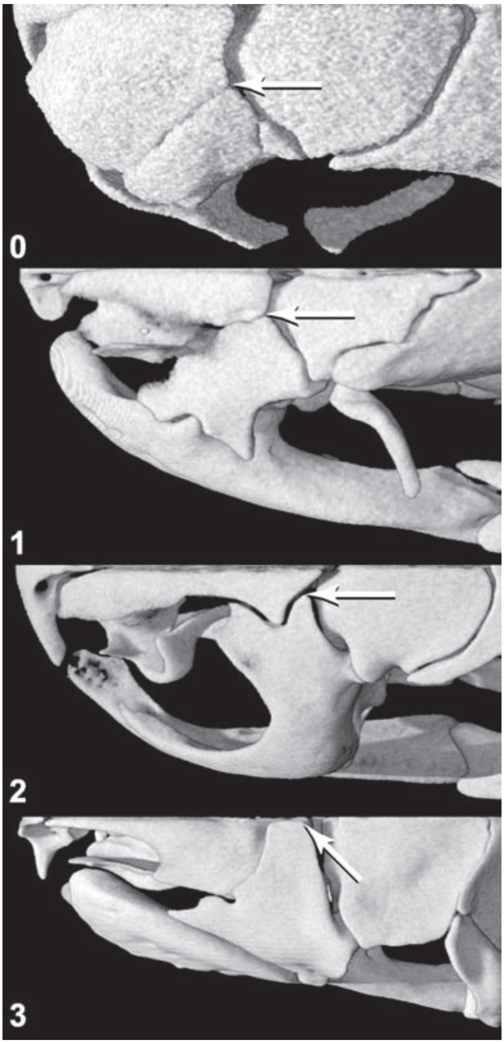
129. Prefrontal posterior extent along orbital margin: (0) terminates in anterior half of orbit (*Uranoscodon superciliosus*, dorsal close-up of orbit); (1)^{N} extends to midorbit (*Strophurus ciliaris*, dorsal close-up of orbit); (2) extends posterior to midorbit (*Anniella pulchra*, dorsal close-up of orbit), Lee et al. (2009). Estes et al. (1988) (ordered).



130. Prefrontal boss: (0) absent (*Coleonyx variegatus*, anterior cutaway view of skull); (1) present (*Uranoscodon superciliosus*, anterior cutaway view of skull); (2)^N in projecting canthal crest (*Brookesia brygooi*, anterior cutaway view of skull). Gauthier (1984) (ordered).

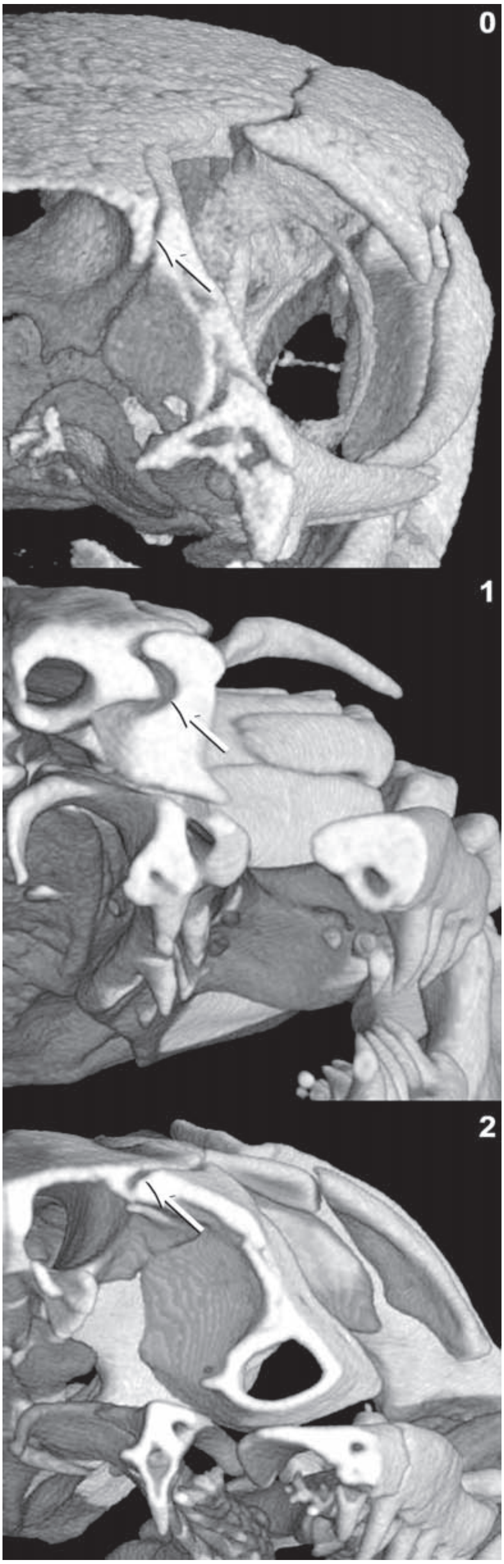


131. Prefrontal nasolacrimal cornu^N: (0) absent (*Exiliboa placata*, anterior close-up cutaway view of snout); (1) present (*Amphiesma stolata*, anterior close-up cutaway view of snout).



132. Prefrontal medial extent across anterior margin of frontal: (0) prefrontal extends 50% or less across frontal

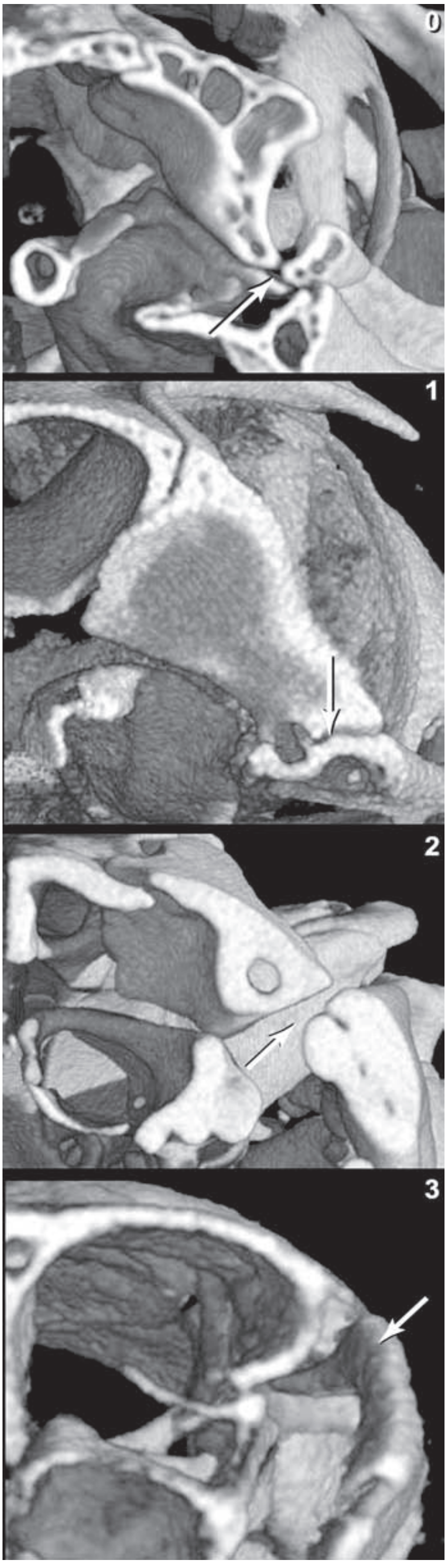
anterior width (*Anomochilus leonardi*, dorsal close-up of anterior skull); (1)^N extends 50% to 65% across frontal anterior width (*Cylindrophis ruffus*, dorsal close-up of anterior skull); (2)^N extends 65% to 75% across frontal anterior width (*Xenopeltis unicolor*, dorsal close-up of anterior skull); (3) extends 85% or more across frontal to approach midline (*Epicrates striatus*, dorsal close-up of anterior skull). Cundall et al. (1993) (ordered).



133. Prefrontal-frontal suture in cross-section^N: (0) prefrontal arcs gently about anterolateral frontal margin along

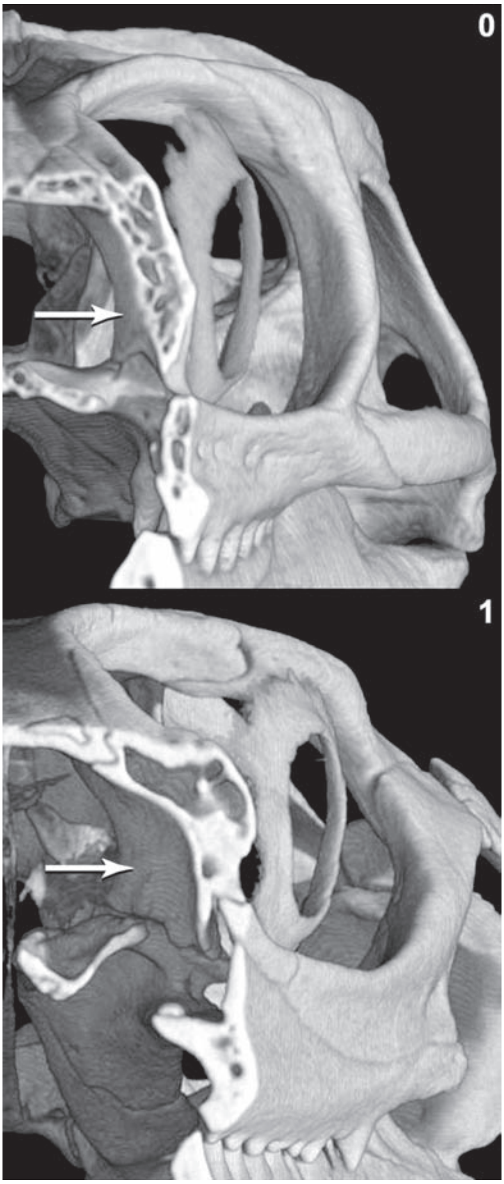
entire anteroposterior length (*Cricosaura typica*, anterior close-up cutaway view of snout); (1) prefrontal strongly bifid, clasps frontal posteriorly then spreads dorsally and reduced ventrally anteriorly (*Cylindrophis ruffus*, anterior close-up cutaway view of snout); (2) frontal clasps prefrontal in V-shaped notch (*Xenocrophis piscator*, anterior close-up cutaway view of snout) (ordered).

134. Prefrontal length relative to height$^{\mathrm{N}}$: (0) long anteroposteriorly (*Lichanura trivirgata*, lateral close-up of anterior skull); (1) short anteroposteriorly (*Micrurus fulvius*, lateral close-up of anterior skull).

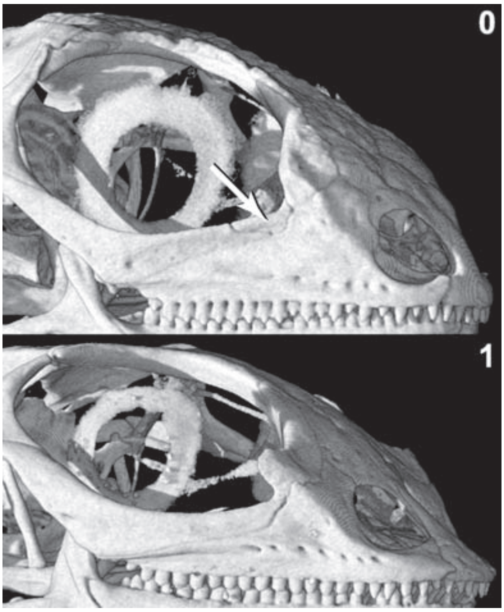


135. Prefrontal-maxilla articulation: (0) prefrontal posteroventromedial corner narrowly (or not at all) in contact with

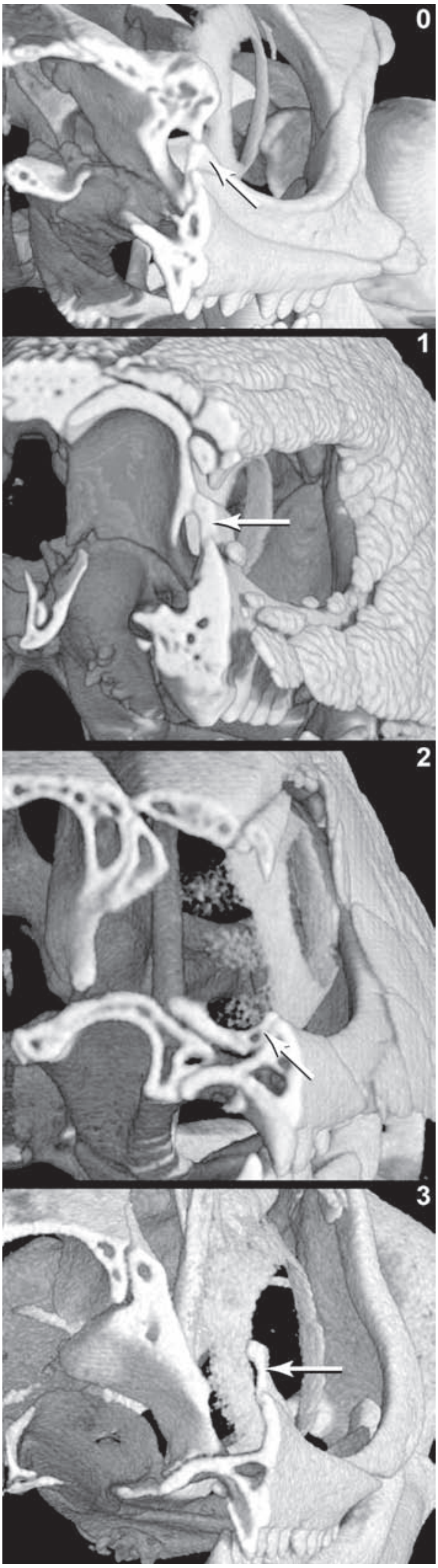
maxilla lateral to palatine (*Oplurus cyclurus*, anterior close-up cutaway view of snout); (1)^N prefrontal broadly contacts maxilla supradental shelf lateral to palatine (*Delma borea*, anterior close-up cutaway view of snout); (2) prefrontal has mobile contact with maxilla (*Anilius scytale*, anterior close-up cutaway view of snout); (3)^N rod-like prefrontal arched dorsally, bifid at each end, with mobile joints at maxilla and frontal (prefrontal functionally part of upper jaw) (*Liotyphlops albirostris*, anterior close-up cutaway view of snout). Tchernov et al. (2000).



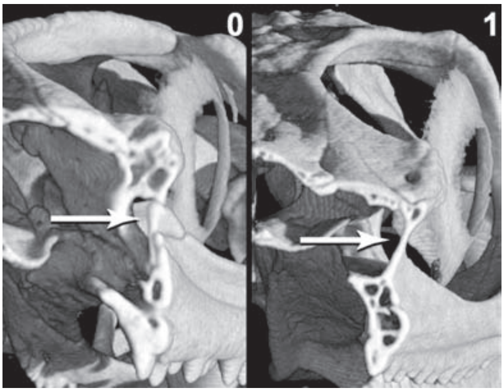
136. Prefrontal arcs about orbitonasal fenestra, with posteroventromedial corner curving inwards toward palatine in cross-section^N: (0) absent (*Sphenodon punctatus*, anterior close-up cutaway view of snout); (1) present (*Leiolepis belliana*, anterior close-up cutaway view of snout).



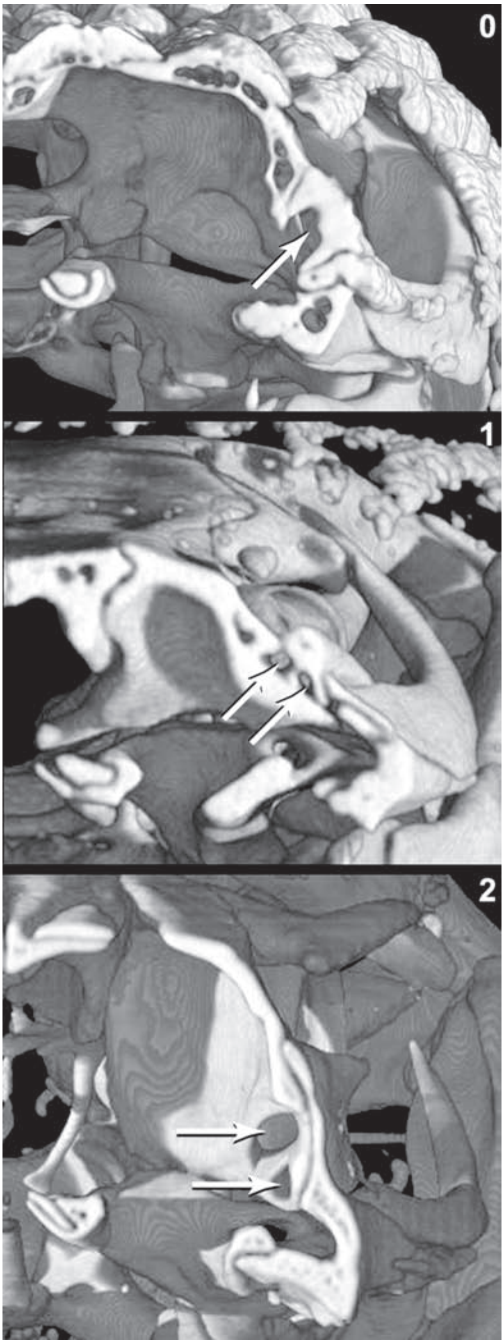
137. Lacrimal: (0) present (*Leiocephalus baharonensis*, oblique lateral close-up of snout); (1) absent (*Uma scoparia*, oblique lateral close-up of snout). Estes et al. (1988).



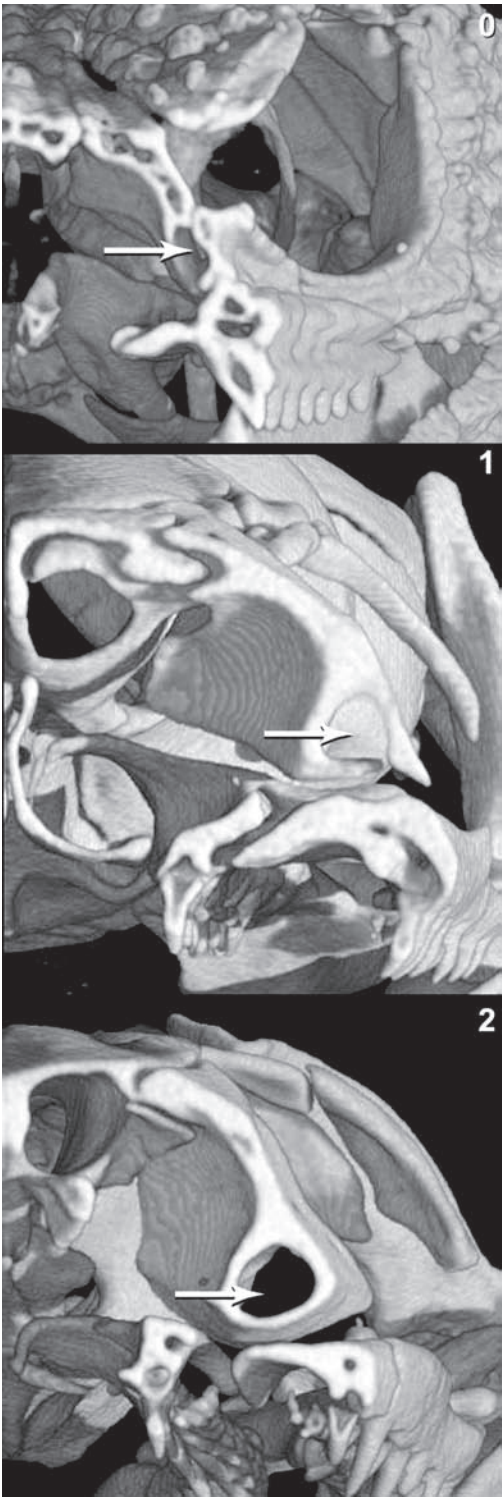
138. Lacrimal position relative to lacrimal duct^{N}: (0) lacrimal with broad exposure laterally, reaching from lateral floor of lacrimal duct up the medial face of the maxilla to contact a lateral process of the prefrontal that roofs the lacrimal duct in cross section (*Crotaphytus collaris*, anterior close-up cutaway view of snout); (1) lacrimal arches over the lacrimal duct to replace the prefrontal dorsally, broadly floors the lacrimal duct with a medial process posteriorly passing up the lateral face of the prefrontal (*Pseudopus apodus*, anterior close-up cutaway view of snout); (2) lacrimal reduced to floor of lacrimal duct and lingual surface of maxilla, and barely, if at all, exposed laterally (*Zonosaurus ornatus*, anterior close-up cutaway view of snout); (3) lacrimal bone reduced ventrally, confined mainly to dorsolateral corner of lacrimal duct (*Colobosaura modesta*, anterior close-up cutaway view of snout). The complexity of lacrimal morphology is difficult to illustrate from any single view. We recommend perusal of animations available on the University of Texas, Austin, Digital Morphology library website (DigiMorph.Org. c2002–2012).



139. Lacrimal foramen size: (0) small (*Dipsosaurus dorsalis*, anterior close-up cutaway view of snout); (1) large (*Calotes emma*, anterior close-up cutaway view of snout). Moody (1980).



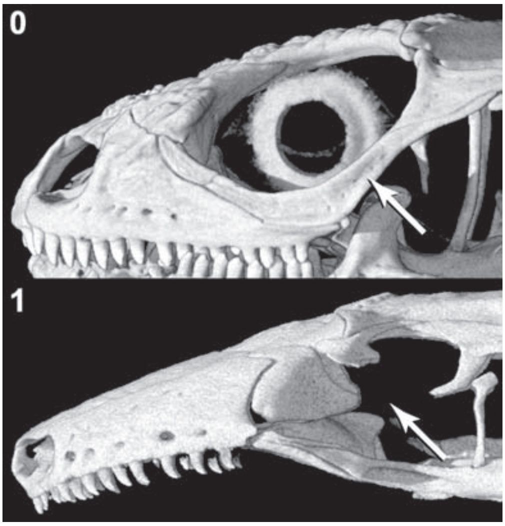
140. Lacrimal foramen number: (0) one (*Heloderma horridum*, anterior close-up cutaway view of snout); (1) divided on orbital surface (*Lanthanotus borneensis*, anterior close-up cutaway view of snout); (2) divided through to olfactory surface (*Varanus salvator*, anterior close-up cutaway view of snout). Pregill et al. (1986) (ordered).



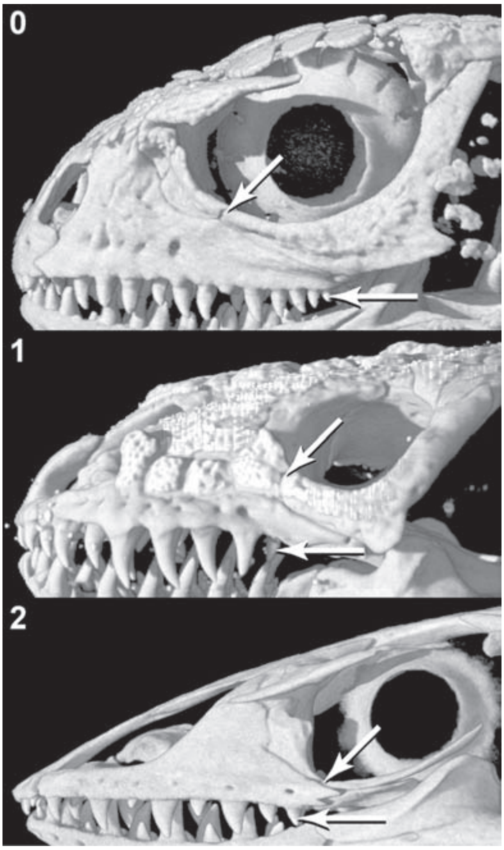
141. Lacrimal duct position: (0) between prefrontal and lacrimal (*Xenosaurus platyceps*, anterior close-up cutaway view of snout); (1)^{N} enclosed in prefrontal, except ventrally (*Loxocemus bicolor*, anterior close-up cutaway view of

snout); (2) enclosed entirely in prefrontal (*Xenochrophis piscator*, anterior close-up cutaway view of snout). Lee (1998) (ordered).

Varanidae is scored (0) for the larger lacrimal duct only.

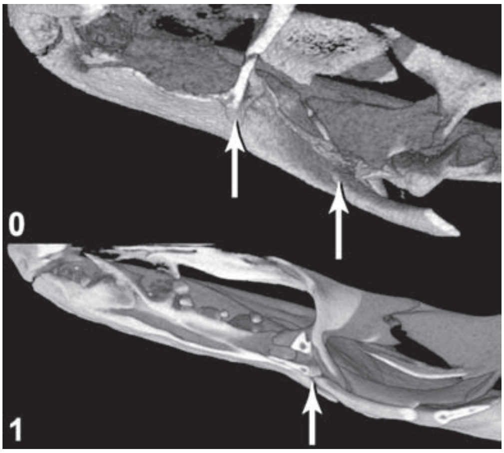


142. Jugal: (0) present (*Oplurus cyclurus*, lateral close-up of anterior skull); (1) absent (*Feylinia polylepis*, lateral close-up of anterior skull). Estes et al. (1988).



143. Jugal extent anteriorly with respect to tooth row^{N}: (0) jugal broadly overlaps level of posterior maxillary tooth row (*Shinisaurus crocodilurus*, lateral close-up of anterior skull); (1) jugal overlaps the most posterior maxillary tooth (*Heloderma suspectum*, lateral close-up of anterior skull); (2) jugal just reaches base of, or stops short of, the most posterior maxillary tooth (*Varanus acanthurus*, lateral close-up of anterior skull) (ordered).

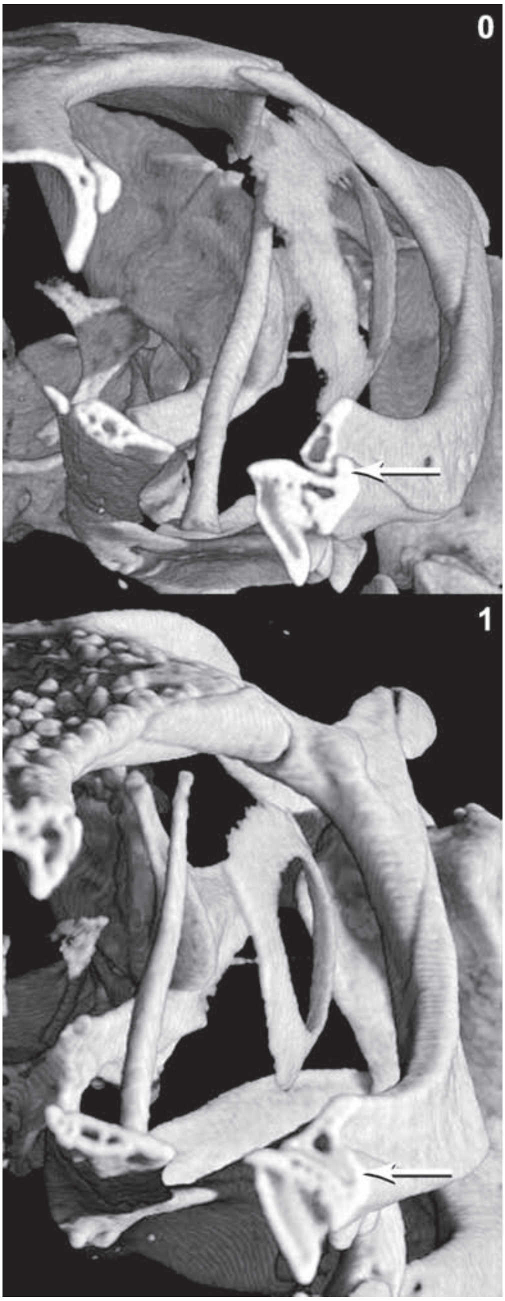
R. Nydam (pers. comm.) pointed out to us that although the jugal terminates well behind the last tooth in *Varanus* and *Saniwa*, it just overlaps the last tooth base in *Lanthanotus;* we altered the description of that state accordingly. We also rechecked our varanoid CT scans, and confirmed that the jugal overlaps the entire tooth in *Heloderma suspectum*. In *H. horridum*, however, the jugal stops short of the last maxillary tooth, and should have been scored as state (2) rather than (1). There is some uncertainty on that point, however, as *H. horridum* has fewer maxillary teeth than any other helodermatid (Pregill et al. 1986), so it might be difficult to distinguish “reduction of the anterior extent of the jugal” from “reduction of the posterior extent of the maxillary tooth row” in that species. Also, *Aiolosaurus* was scored as state (1) even though it lacks a jugal, because the juncture between the palatine and maxilla is nicely preserved, as is the fossa for the attachment of the last maxillary tooth. Given the situation in *Lanthanotus*, however, future iterations of this dataset will change the score for *Aiolosaurus* to (?).



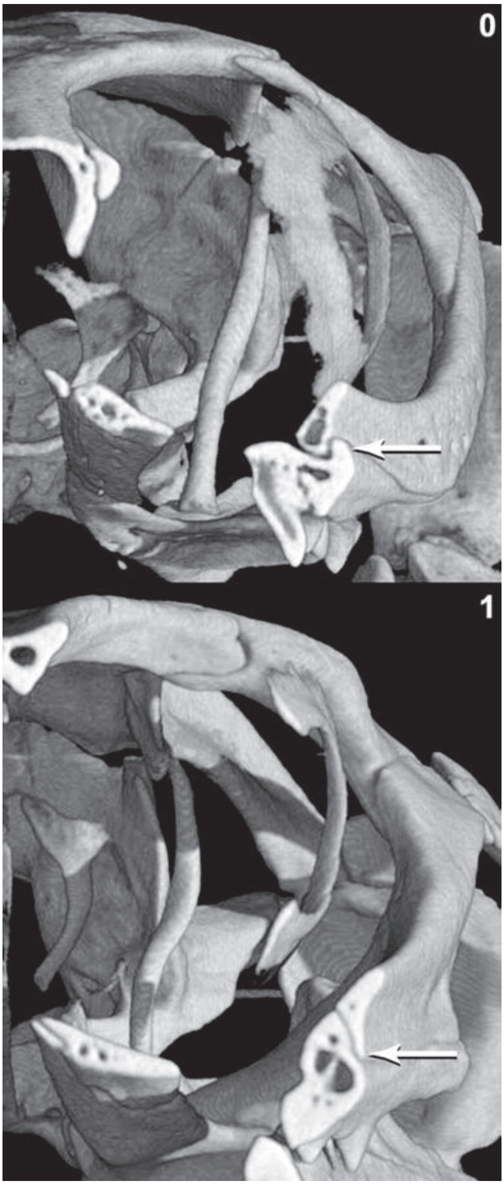
144. Jugal anterior extent^N: (0) broadly separated from prefrontal (*Cricosaura typica*, dorsal close-up cutaway view of anterior skull); (1) reaches level of prefrontal (*Varanus acanthurus*, dorsal close-up cutaway view of anterior skull).

145. Jugal-lacrimal overlap^N: (0) jugal lateral to lacrimal (*Basiliscus basiliscus*, anterior close-up cutaway view of orbit); (1) jugal medial to lacrimal (*Aspidoscelis tigris*, ante-

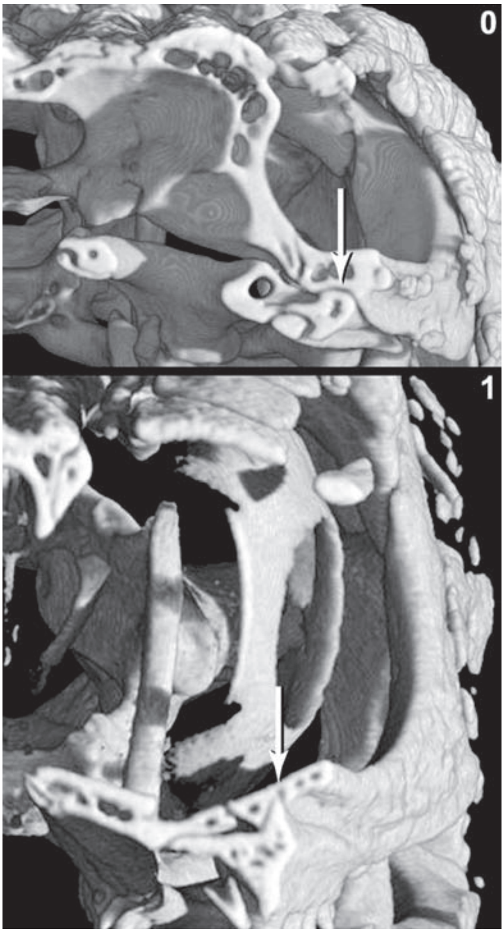
rior close-up cutaway view of orbit); (2) jugal ventral to lacrimal (*Zonosaurus ornatus*, anterior close-up cutaway view of orbit).



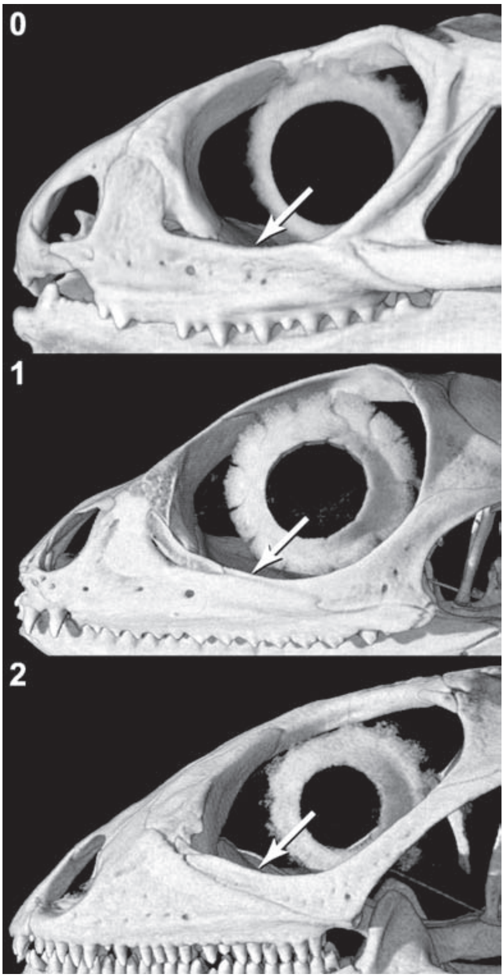
146. Jugal articulation with maxilla in cross-section^{N}: (0) rounded ventral margin of jugal and shallow and more rounded contour of the maxilla supradental shelf (*Liolaemus bellii*, anterior close-up cutaway view of snout); (1) acute ventral margin of jugal lies in narrow longitudinal groove on dorsal surface of maxillary supradental shelf (*Pristidactylus torquatus*, anterior close-up cutaway view of snout).



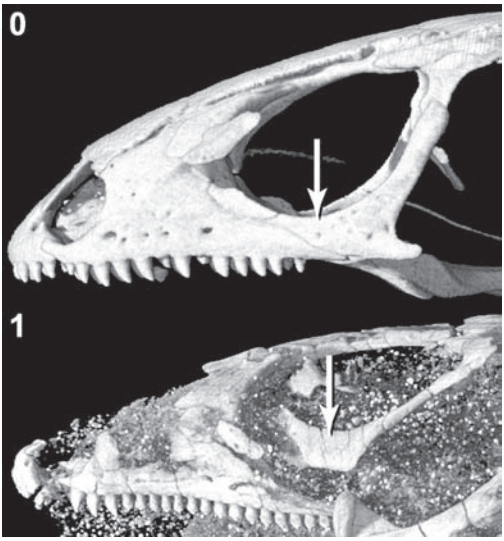
147. Jugal lateral extent over maxilla in cross-section^{N}: (0) maxilla suborbital border wraps dorsally around jugal external margin (*Liolaemus bellii*, anterior close-up cutaway view of snout); (1) jugal laps over external suborbital margin (*Leiolepis belliana*, anterior close-up cutaway view of snout).



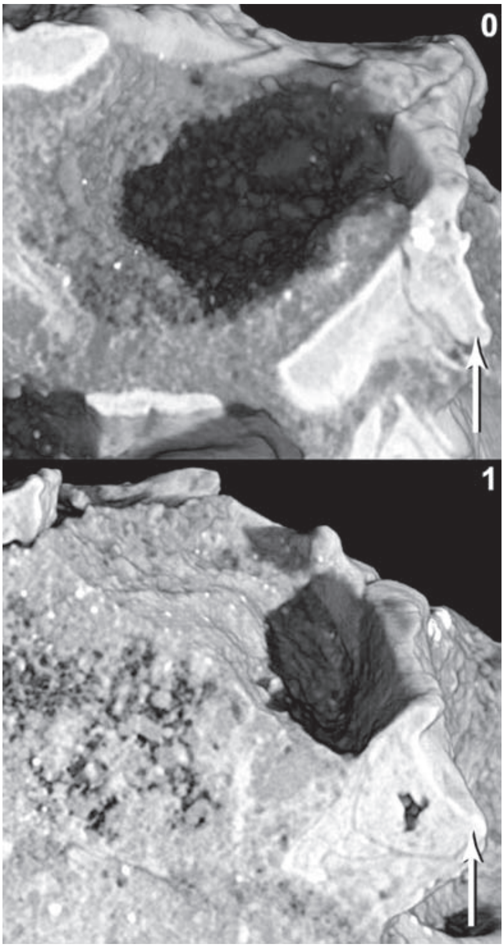
148. Jugal with inverted V-shaped notch clasping suborbital edge of maxilla^N: (0) absent (*Heloderma horridum*, anterior close-up cutaway view of orbit); (1) present (*Shinisaurus crocodilurus*, anterior close-up cutaway view of orbit).



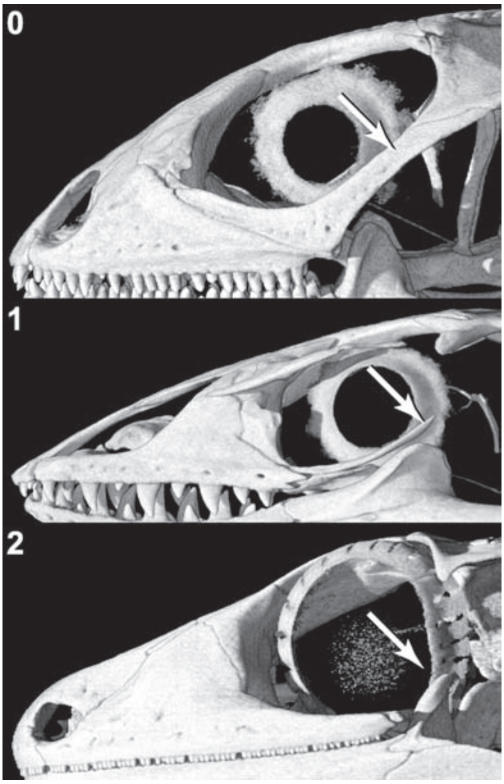
149. Jugal lateral exposure below orbit: (0) absent (*Sphenodon punctatus*, lateral close-up of anterior skull); (1)^N partly exposed above orbital margin of maxilla (*Physignathus cocincinus*, lateral close-up of anterior skull); (2) entirely exposed above orbital margin of maxilla (*Sceloporus variabilis*, lateral close-up of anterior skull). Estes et al. (1988) (ordered).



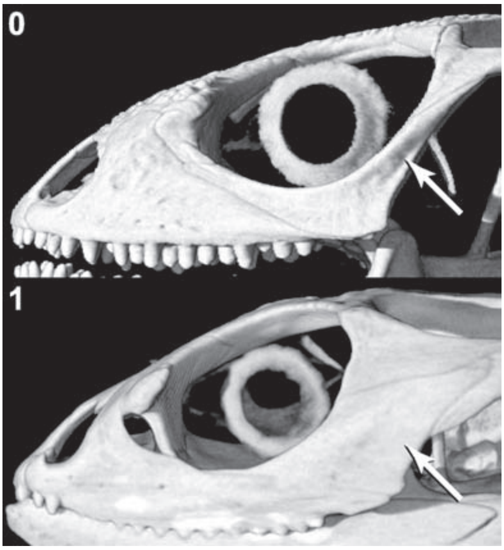
150. Jugal suborbital ramus^{N}: (0) shallow (*Celestus enneagrammus*, lateral close-up of anterior skull); (1) deep (*Tchingisaurus multivagus*, lateral close-up of anterior skull).



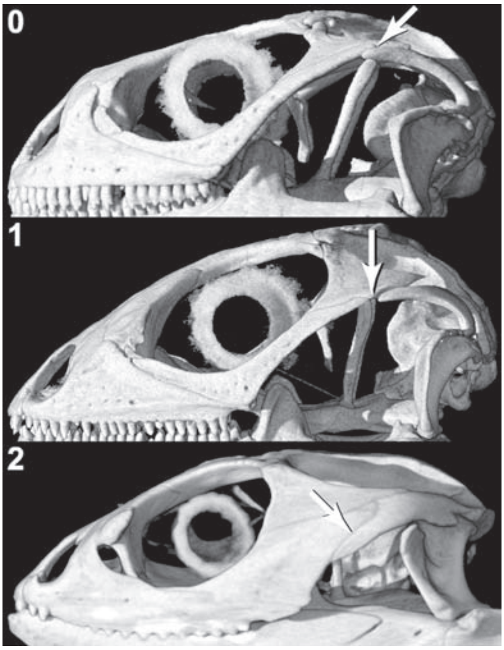
151. Jugal suborbital boss: (0) absent (*Priscagama gobiensis*, anterior close-up cutaway view of orbit); (1) present (*Mimeosaurus crassus*, anterior close-up cutaway view of orbit). Borsuk-Białynicka and Moody (1984).



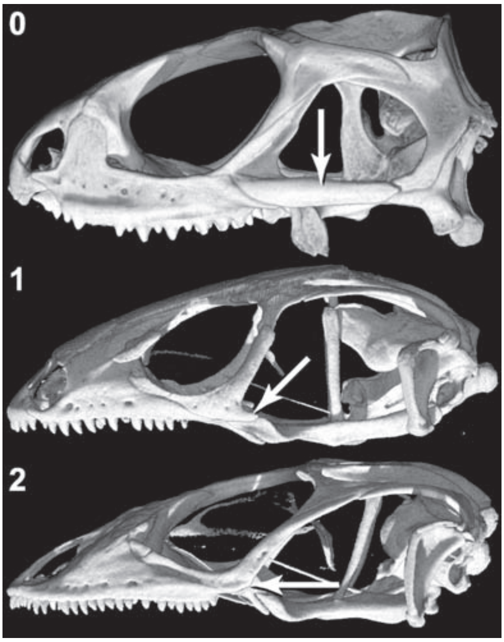
152. Jugal postorbital ramus development: (0) complete bony postorbital bar (*Sceloporus variabilis*, lateral close-up of anterior skull); (1) incomplete bony postorbital bar (*Varanus acanthurus*, lateral close-up of anterior skull); (2) bony postorbital bar absent (*Aeluroscalabotes felinus*, lateral close-up of anterior skull). Estes et al. (1988) (ordered).



153. Jugal postorbital ramus shape in lateral outline: (0) narrow (*Pristidactylus torquatus*, lateral close-up of anterior skull); (1) wide (*Pogona vitticeps*, lateral close-up of anterior skull). Gauthier (1982).

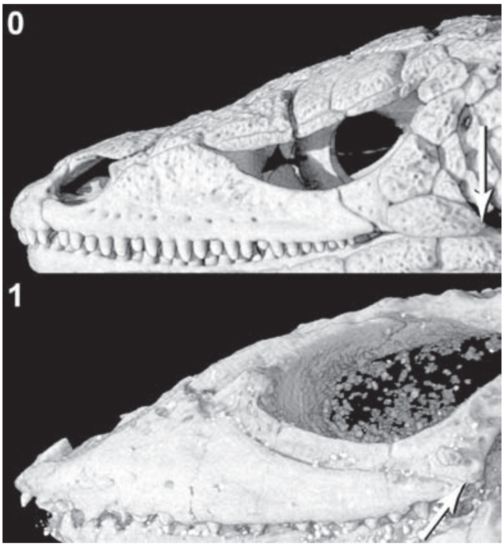


154. Jugal contacts squamosal: (0) present (*Phymaturus palluma*, lateral view of skull); (1) absent (*Sceloporus variabilis*, lateral view of skull), Gauthier (1982); (2)^{N} broad contact (*Pogona vitticeps*, lateral view of skull).

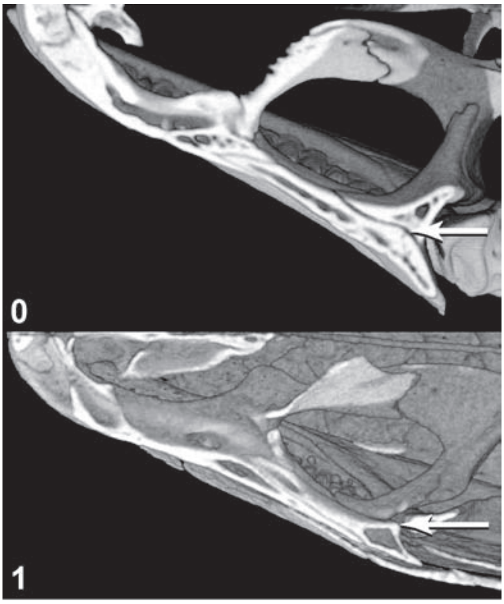


155. Jugal posterior process: (0) complete lower temporal bar (*Sphenodon punctatus*, lateral view of skull); (1) reduced to a discrete bony posterior process (*Celestus enneagram-*

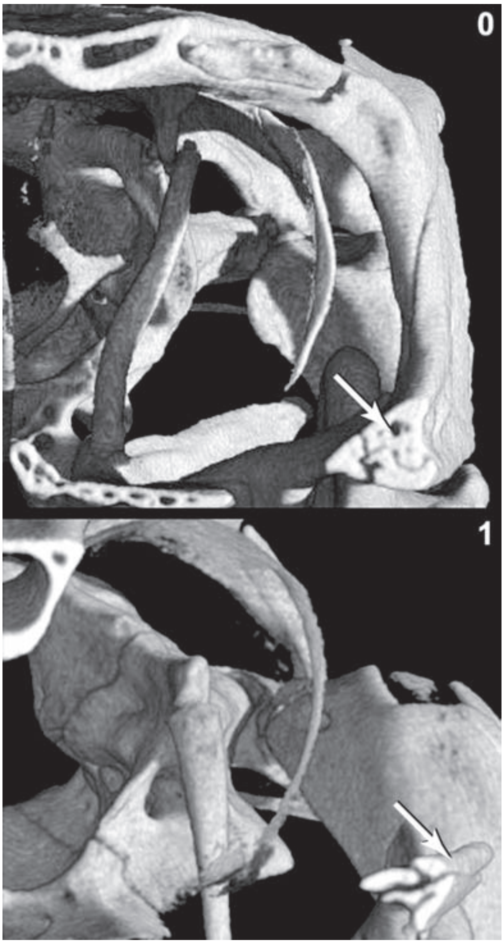
mus, lateral view of skull), Gauthier, Estes and de Queiroz (1988); (2) absent (*Petrosaurus mearnsi*, lateral view of skull). Benton (1984) (ordered).



156. Jugal posterior process orientation^N: (0) more posterior in orientation (*Cordylus mossambicus*, lateral close-up of anterior skull); (1) more ventral in orientation (*Priscagama gobiensis*, lateral close-up of anterior skull).

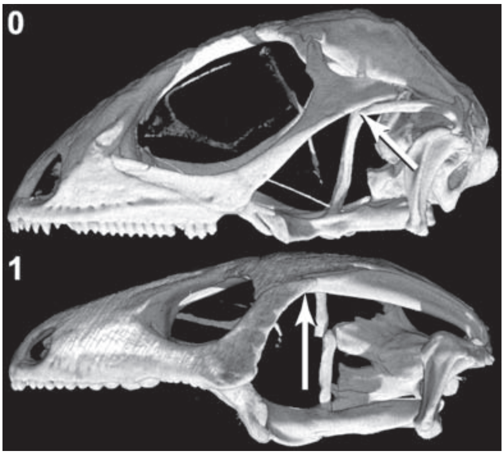


157. Jugal medial ridge^N: (0) medial ridge weak, jugal lateral to ectopterygoid at base in dorsal view (*Crotaphytus collaris*, dorsal close-up cutaway view of anterior skull); (1) medial ridge pronounced, base of medial ridge projects behind ectopterygoid base in dorsal view (*Plestiodon fasciatus*, dorsal close-up cutaway view of anterior skull).

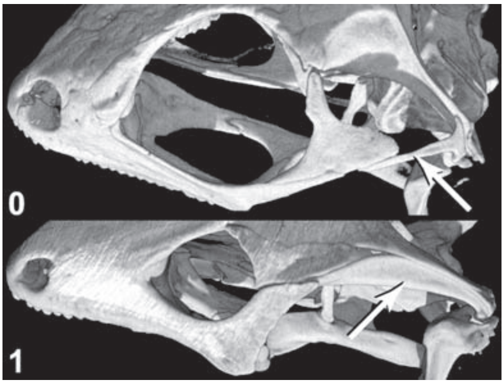


158. Jugal cross-section at level of ectopterygoid^N: (0) subtriangular (*Anolis carolinensis*, anterior close-up cutaway view of orbit); (1) depressed (*Eublepharis macularius*, anterior close-up cutaway view of orbit).

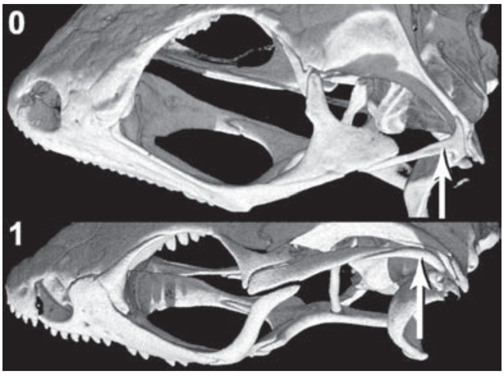
159. Squamosal: present (0), absent (1). Estes et al. (1988).



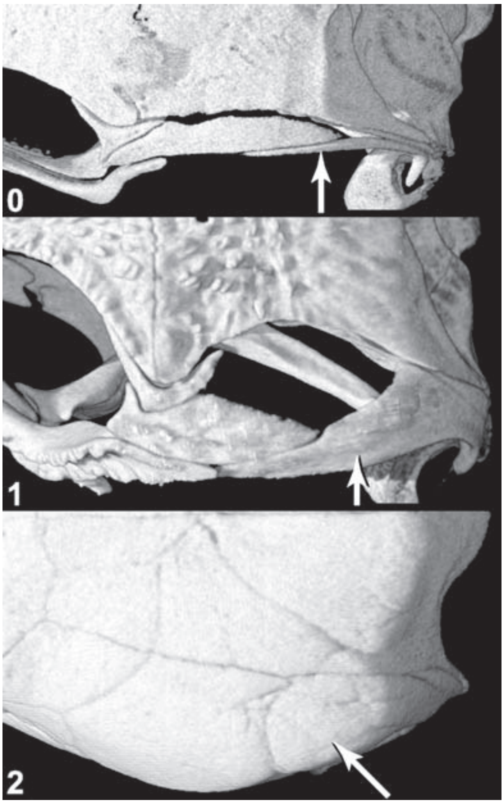
160. Squamosal length relative to epipterygoid position^N: (0) squamosal does not extend anterior to level of epipterygoid (*Leiocephalus barahonensis*, lateral view of skull); (1) squamosal extends anterior to level of epipterygoid (*Tiliqua scincoides*, lateral view of skull).



161. Squamosal temporal ramus-parietal contact^N: (0) temporal ramus diverges from parietal supratemporal process (*Leiocephalus barahonensis*, oblique dorsal view of skull); (1) temporal ramus broadly contacts parietal supratemporal process (*Tiliqua scincoides*, oblique dorsal view of skull).



162. Squamosal base of temporal ramus^N: (0) diverges from parietal (*Leiocephalus barahonensis*, oblique dorsal view of skull); (1) base lies against parietal (*Pholidobolus montium*, oblique dorsal view of skull).

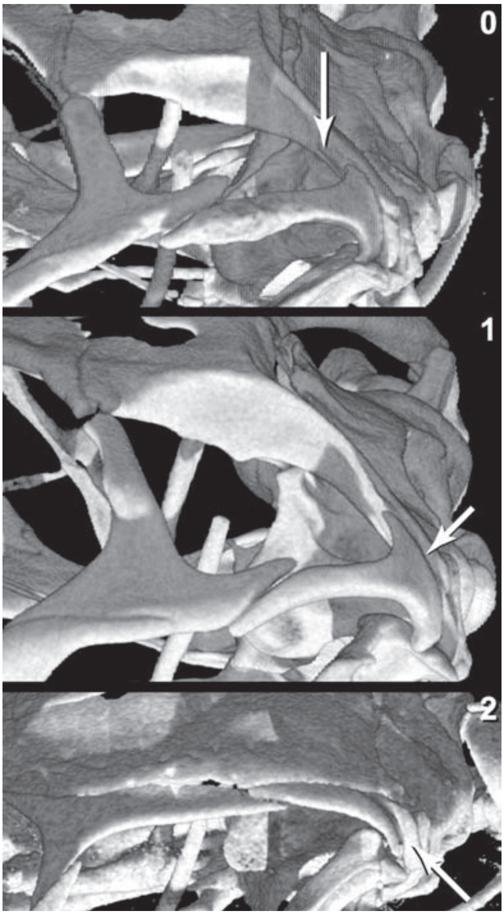


163. Squamosal temporal ramus width^N: (0) slender (*Colobosaura modesta*, dorsal close-up of posterior skull); (1) widens posteriorly (*Xenosaurus platyceps*, dorsal close-up of posterior skull); (2) widens anteriorly with medial shelf along parietal that roofs posterior end of upper temporal fenestra (*Lepidophyma flavimaculatum*, dorsal close-up of posterior skull).

164. Squamosal temporal ramus shape^{N}: (0) compressed (*Colobosaura modesta*, anterior close-up cutaway view of temporal region); (1) depressed (*Xantusia vigilis*, anterior close-up cutaway view of temporal region).

165. Squamosal ascending process: (0) present (*Leiocephalus barahonensis*, oblique dorsal close-up of temporal region); (1) absent (*Tiliqua scincoides*, oblique dorsal close-up of temporal region). Gauthier (1982).

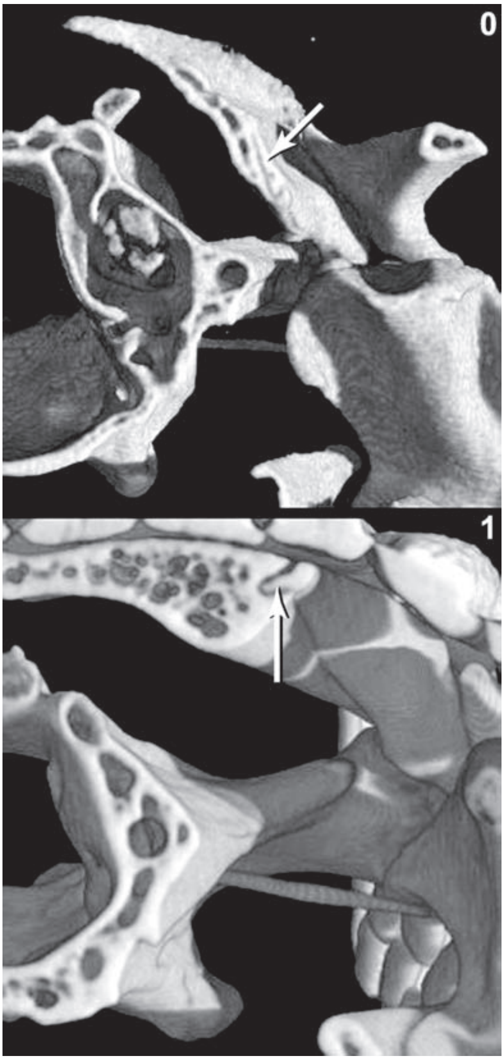
166. Supratemporal: (0) present; (1) absent. Estes et al. (1988).



167. Supratemporal shortens^N: (0) supratemporal longer than squamosal-parietal contact (*Uta stansburiana*, oblique dorsal view of temporal region); (1) supratemporal shorter than squamosal-parietal contact (*Uma scoparia*, oblique dorsal view of temporal region); (2) supratemporal very small (*Xantusia vigilis*, oblique dorsal view of temporal region) (ordered).

168. Supratemporal lengthens: (0) posterior to level of parietal notch (*Uta stansburiana*, oblique lateral view of temporal region); (1) near to level of parietal notch (*Leiocephalus barahonensis*, oblique lateral view of temporal region); (2) anterior to level of parietal notch (*Rhacodactylus*

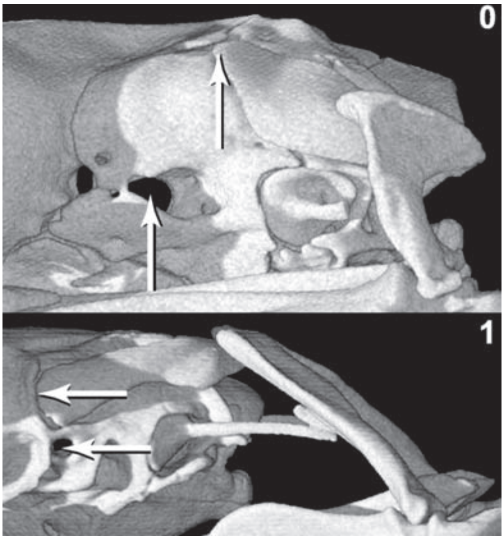
auriculatus, oblique lateral view of temporal region). Pregill et al. (1986) (ordered).



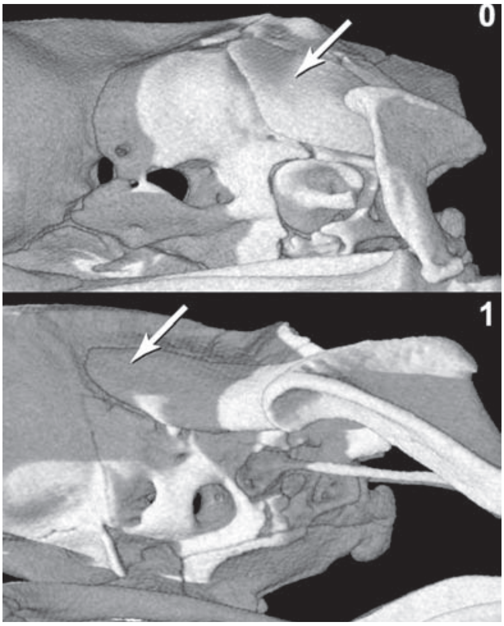
169. Supratemporal anterior suture with parietal shape: (0) supratemporal lies flat against supratemporal process of parietal (*Anolis carolinensis*, anterior close-up cutaway view of temporal region); (1) inserts in slot in supratemporal process of parietal (*Heloderma horridum*, anterior close-up cutaway view of temporal region). Frost and Etheridge (1989).

170. Supratemporal position on parietal: (0) partly ventral (*Tupinambis teguixin*, anterior close-up cutaway view of

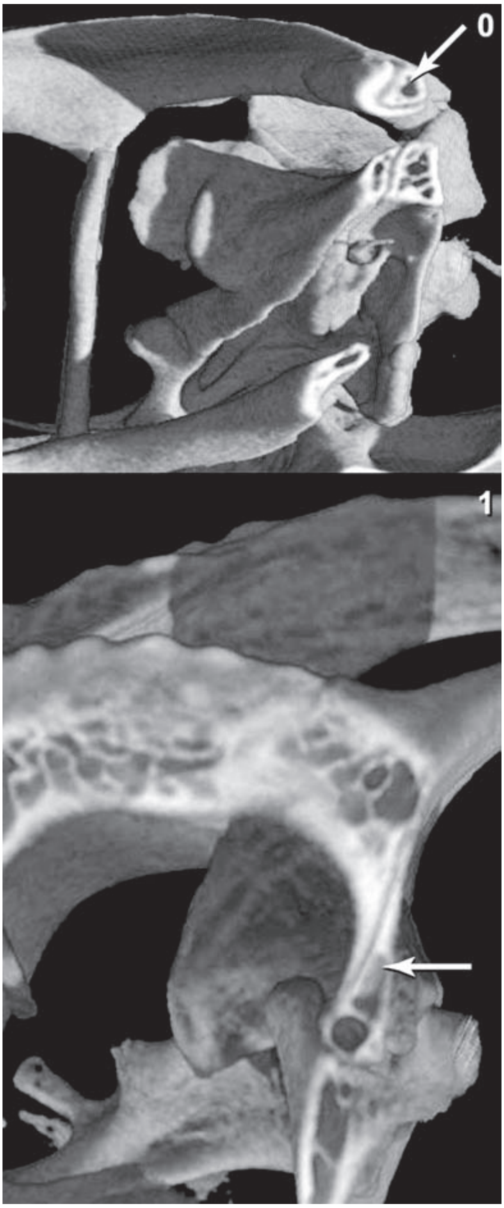
temporal region); (1) ^{N} partly ventrolateral (*Lacerta viridis*, anterior close-up cutaway view of temporal region); (2) all lateral (*Cordylosaurus subtesselatus*, anterior close-up cutaway view of temporal region), Etheridge and de Queiroz (1988); (3) ^{N} dorsolateral (on either parietal or braincase alone) (*Loxocemus bicolor*, anterior close-up cutaway of temporal region). de Queiroz (1987).



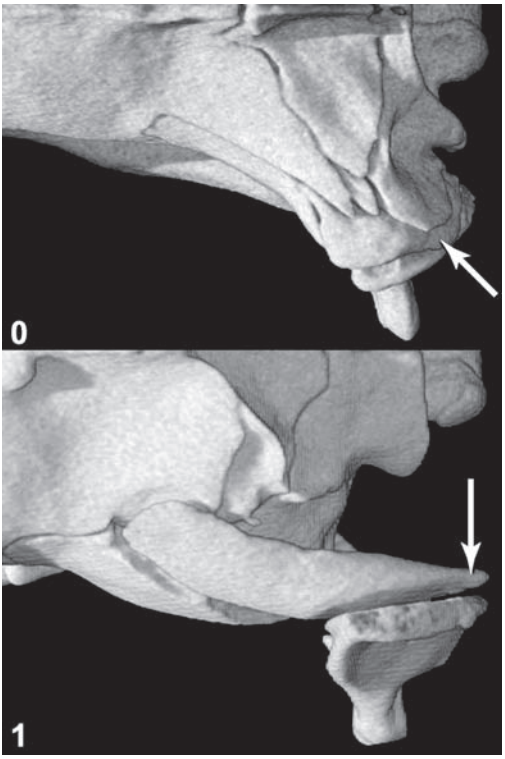
171. Supratemporal anterior terminus: (0) posterior to level of trigeminal nerve exit (*Casarea dussumieri*, lateral close-up of temporal region); (1) anterior to level of trigeminal nerve exit (*Agkistrodon contortrix*, lateral close-up of temporal region). Tchernov et al. (2000).



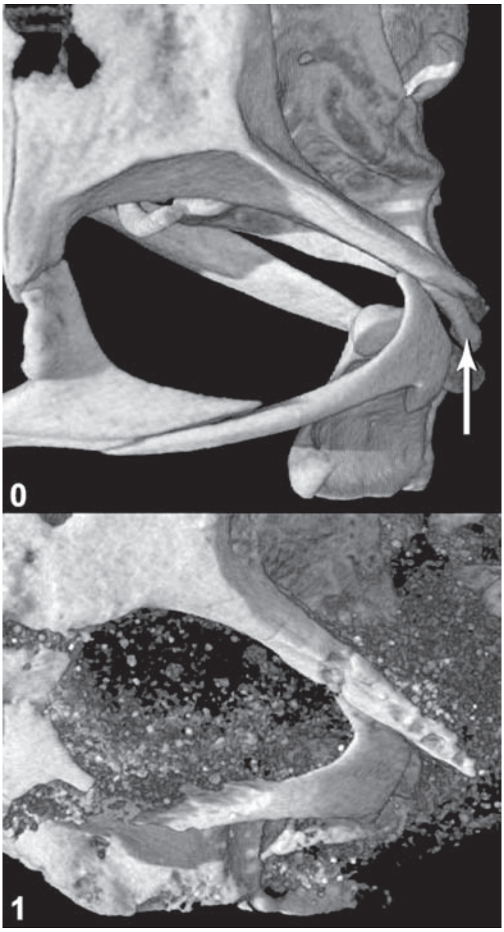
172. Supratemporal anterior extent in snakes without supratemporal process of parietal^{N}: (0) supratemporal does not extend anterior of posterior border of parietal table (*Casarea dussumieri*, lateral close-up of temporal region); (1) supratemporal extends anterior of posterior border of parietal table (*Coluber constrictor*, lateral close-up of temporal region). Not scored in snakes where supratemporal is absent.



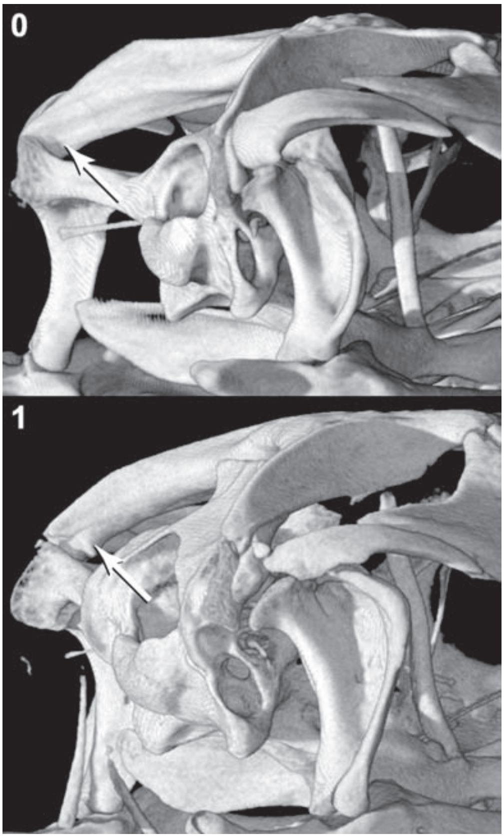
173. Supratemporal orientation: (0) anterior to quadrate head (*Callopistes maculatus*, lateral close-up cutaway view of temporal region); (1) dorsal to quadrate head (*Chamaeleo laevigatus*, lateral close-up cutaway view of temporal region). Rieppel (1987a).



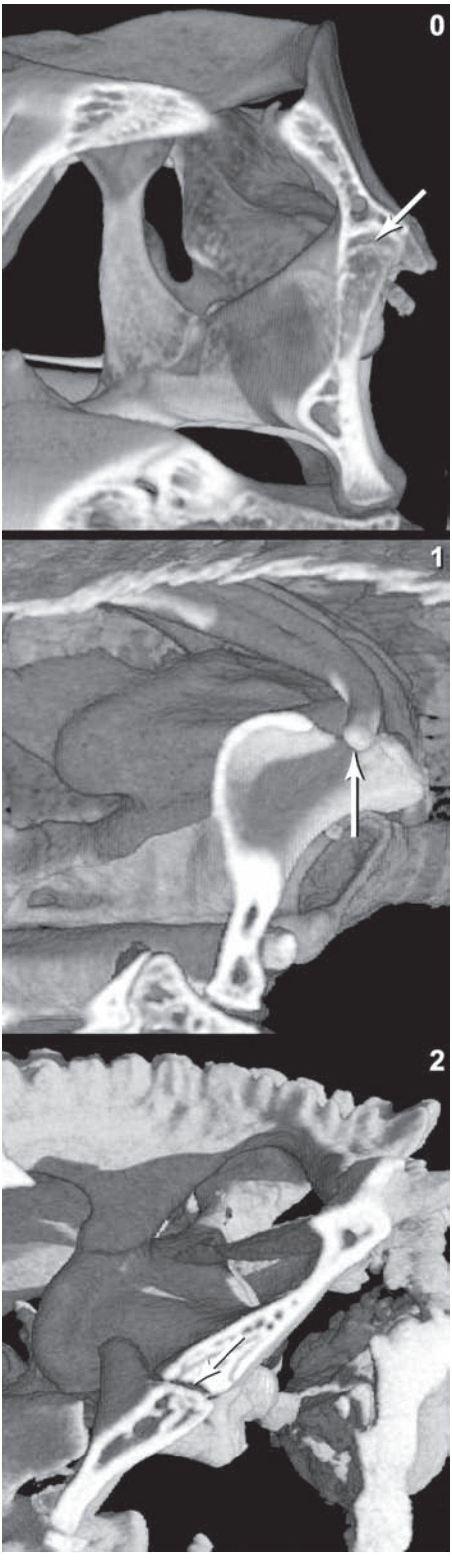
174. Supratemporal free posteriorly: (0) supratemporal ends near attachment to braincase (*Anilius scytale*, dorsal close-up of temporal region); (1) extends freely posterior to oto-occipital (*Loxocemus bicolor*, dorsal close-up of temporal region). Kluge (1991).



175. Supratemporal hidden in dorsal view^{N}: (0) supratemporal at least partly exposed dorsally on lateral side of parietal supratemporal process (*Gambelia wislizenii*, dorsal close-up of temporal region); (1) slender and hidden completely from view by parietal-squamosal contact dorsally (*Adamisaurus magnidentatus*, dorsal close-up of temporal region).

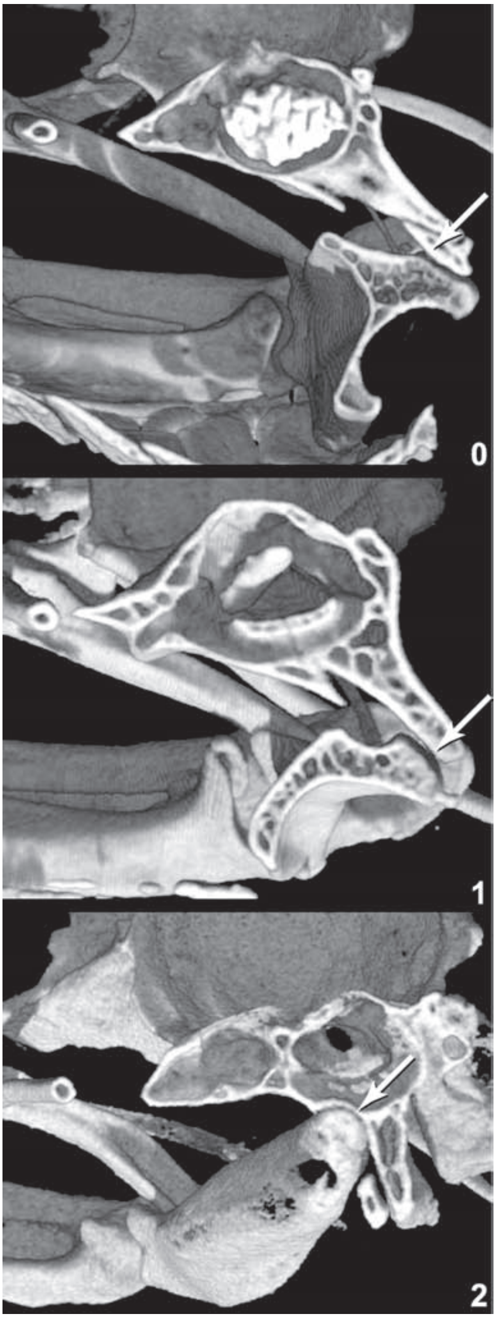


176. Supratemporal posterior exposure on parietal supratemporal process: (0) narrow or absent (*Plica plica*, oblique lateral view of temporal region); (1) present broadly (*Dipsosaurus dorsalis*, oblique lateral view of temporal region). Etheridge and de Queiroz (1988).

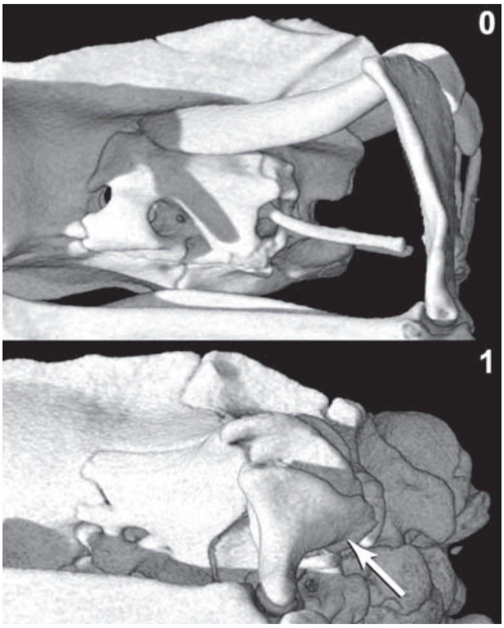


177. Quadrate head attachment: (0)^{N} tapering peg-like head loosely attached in socket formed largely by squamosal (*Sphenodon punctatus*, lateral close-up cutaway view of

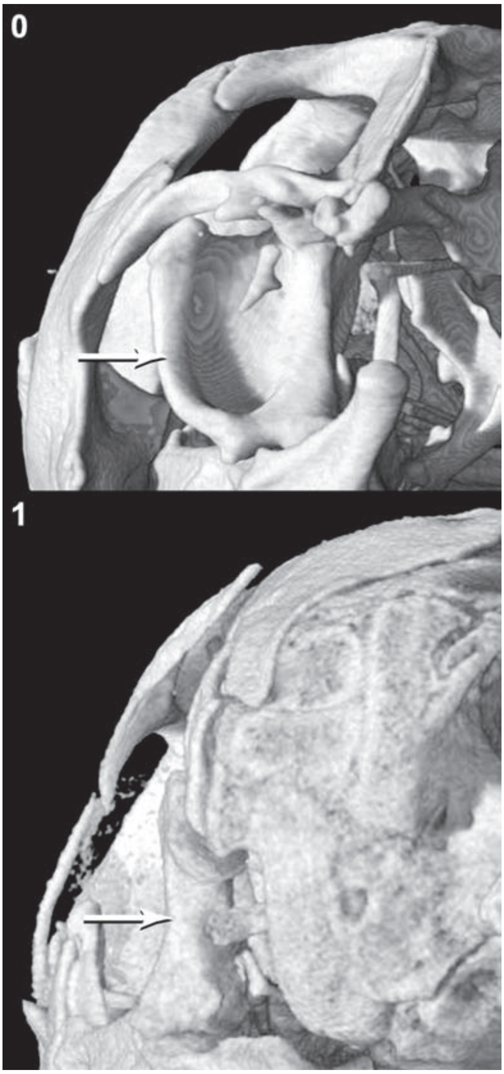
temporal region); (1) quadrate head pivots on slender tapering tip of squamosal (*Amphiglossus splendidus*, lateral close-up cutaway view of temporal region) (Gauthier 1984); (2)^{N} bluntly abuts supratemporal and squamosal (*Brookesia brygooi*, lateral close-up cutaway view of temporal region). *Sphenodon* retains the ancestral ball and socket suspensorium of Diapsida. In contrast, the quadrate head remains unmodified and firmly attached to the skull in captorhinids and turtles.



178. Quadrate head suspension: (0) supratemporal and squamosal separate quadrate head from braincase (except narrowly beneath tip of supratemporal) (*Cordylus mossambicus*, dorsal close-up cutaway view of temporal region); (1)^{N} quadrate head abuts braincase ventral to supratemporal (*Shinisaurus crocodilurus*, dorsal close-up cutaway view of temporal region); (2) quadrate head broadly contacts braincase anteriorly (*Gonatodes albogularis*, dorsal close-up cutaway view of temporal region).

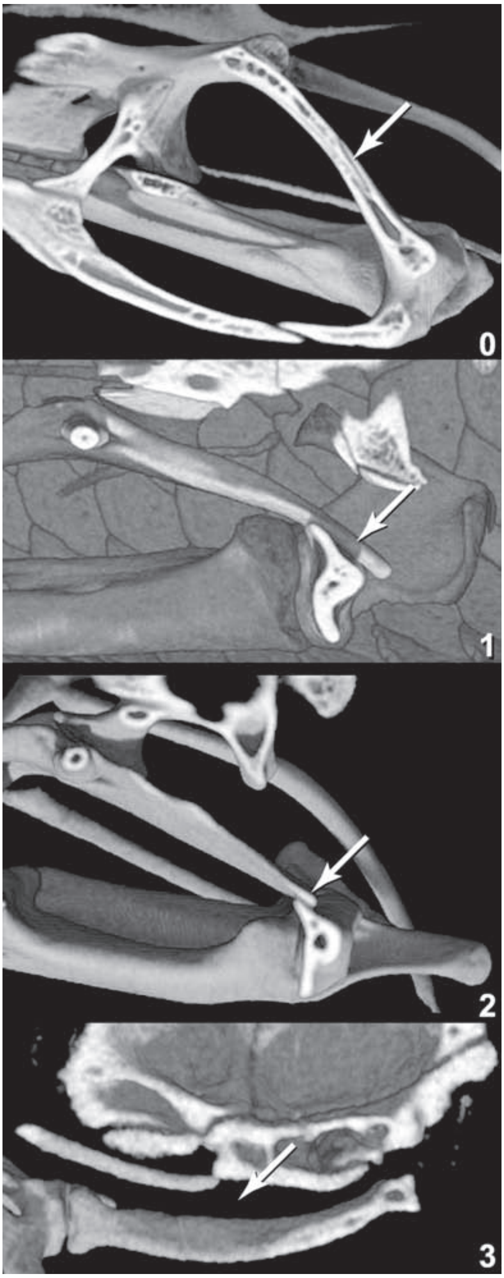


179. Quadrate suprastapedial process: (0) absent (*Anilius scytale*, lateral close-up of braincase); (1) present (*Epicrates striatus*, lateral close-up of braincase). Lee (1998).

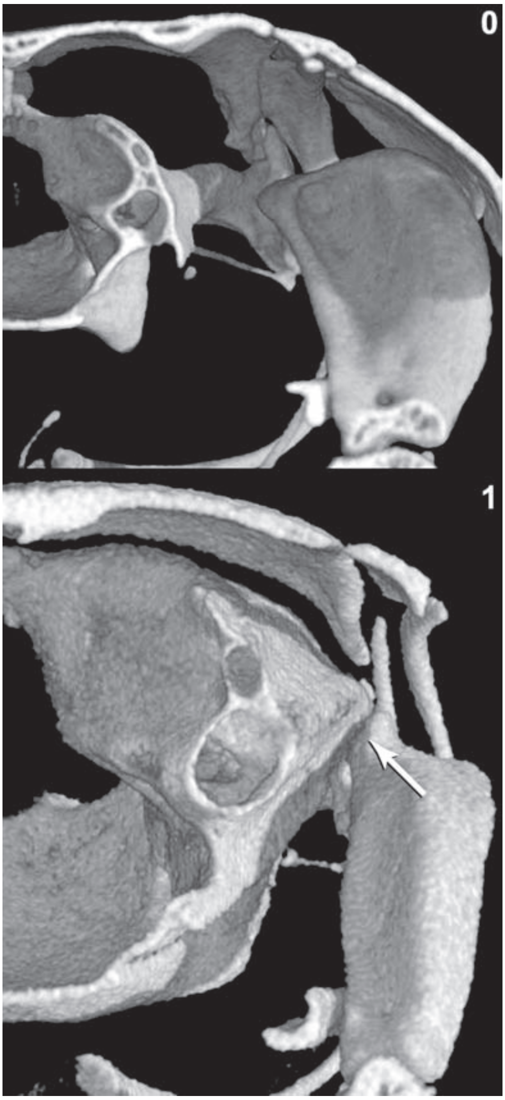


180. Quadrate lateral conch: (0) present (*Agama agama*, oblique posterior close-up of temporal region); (1) absent (*Acontias percivali*, oblique posterior close-up of temporal region). Benton (1984).

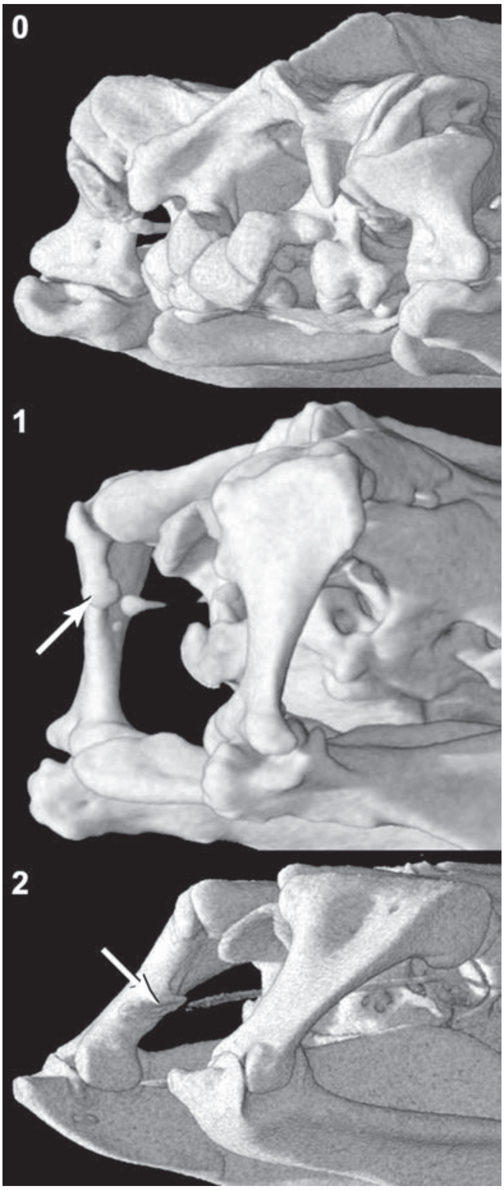
181. Quadratojugal: (0) present; (1) absent. Benton (1984).



182. Quadrate-pterygoid overlap^{N}: (0) extensive (*Sphenodon punctatus*, dorsal close-up cutaway view of temporal region); (1) short overlap or small lappet (*Pseudopus apodus*, dorsal close-up cutaway view of temporal region), Gauthier (1984); (2) very narrow overlap or lappet absent (*Basiliscus basiliscus*, dorsal close-up cutaway view of temporal region), Benton (1984); (3)^{N} no overlap, ligamentous connection only (*Leptotyphlops dulcis*, dorsal close-up cutaway view of temporal region) (ordered).

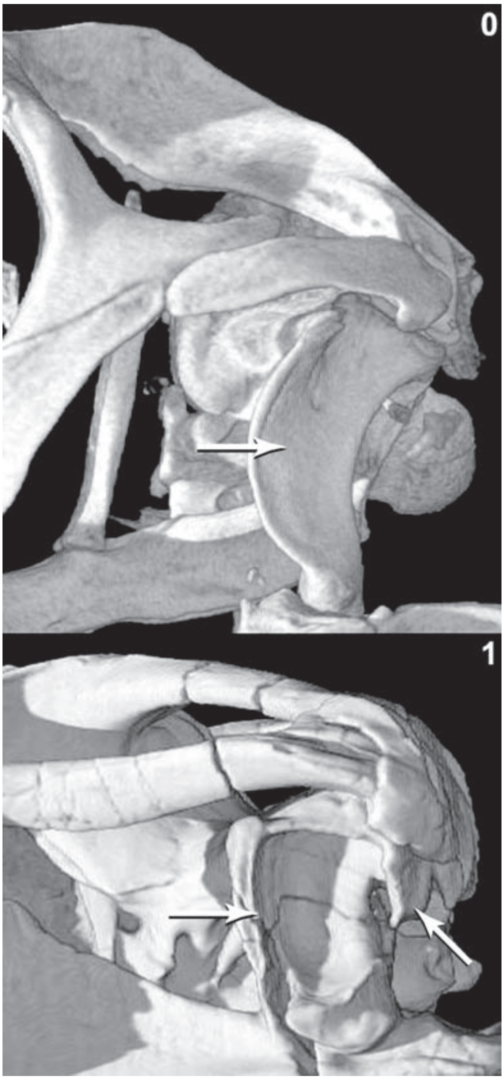


183. Quadrate accessory process arising off anteromedial edge near quadrate head abuts braincase in region of horizontal semicircular canal: (0) absent (*Platysaurus imperator*, anterior close-up cutaway view of temporal region); (1) present (*Cricosaura typica*, anterior close-up cutaway view of temporal region).



184. Quadrate stylohyal process on medial face of quadrate: (0) absent (*Anilius scytale*, oblique posterior close-up of temporal region); (1) present as oval disc (*Ungaliophis continentalis*, oblique posterior close-up of temporal region); (2)^{N} present as narrow cylindrical ridge (*Lycophidion capense*, oblique posterior close-up of temporal region). Rieppel (1980b) (ordered).

185. Quadrate height to braincase depth ratio (braincase depth measured from near the quadrate head)^{N}: (0) less than 50%; (1) 50–59%; (2) 60–69%; (3) 70–79%; (4) more than 79%. (ordered).



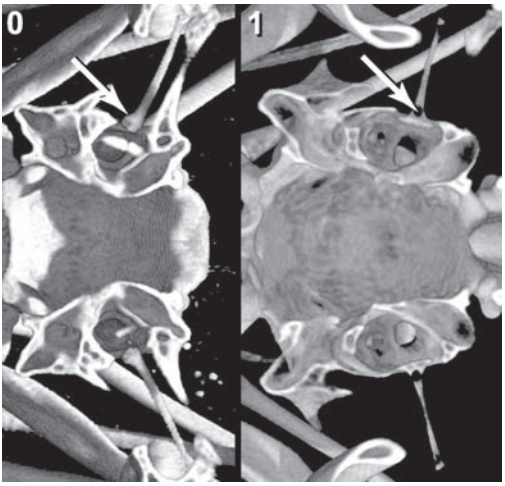
186. Quadrate "pythonomorph": (0) bowed more or less, but not in both lateral and posterior views (*Uranoscodon superciliosus*, lateral close-up of temporal region); (1) massive, and strongly bowed anteriorly in lateral view and laterally in posterior view, throughout length, and with prominent ventrally-directed suprastapedial process forming cavum tympani (*Plotosaurus bennisoni*, lateral close-up of temporal region). DeBraga and Carroll (1993).

187. Quadrate foramen size^{N}: (0) large (*Sphenodon punctatus*, anterior close-up cutaway view of temporal region); (1)

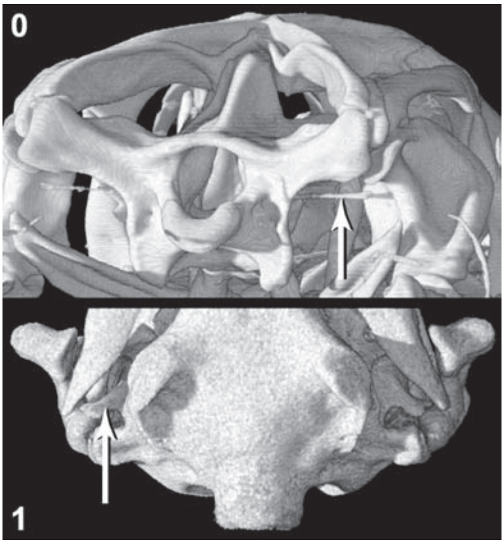
small (*Delma borea*, anterior close-up cutaway view of temporal region); (2) tiny (*Leiolepis belliana*, anterior close-up cutaway view of temporal region) (ordered).

188. Quadrate slopes anteroventrally (more than 90° equals anterior slope from quadrate head)$^{\mathrm{N}}$: (0) vertical to posterior slope; (1) 94–107°; (2) 108–121°; (3) 122–135°; (4) more than or equal to 136° (ordered).

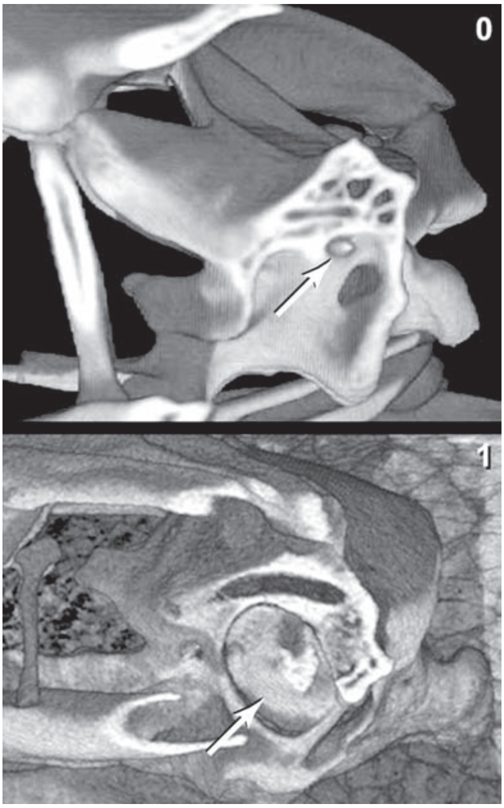
189. Quadrate slopes posteroventrally (less than 90° equals posterior slope from quadrate head): (0) vertical to anterior slope (87–93°); (1)$^{\mathrm{N}}$ 86–68°; (2)$^{\mathrm{N}}$ 67–49°; (3)$^{\mathrm{N}}$ 48–31°; (4)$^{\mathrm{N}}$ less than 30°. Kluge (1993) (ordered).



190. Stapes: (0)$^{\mathrm{N}}$ imperforate (*Enyalioides laticeps*, dorsal close-up cutaway view of braincase); (1)$^{\mathrm{N}}$ perforate (*Teratoscincus przewalskii*, dorsal close-up cutaway view of braincase). Gauthier, Estes and de Queiroz (1988).

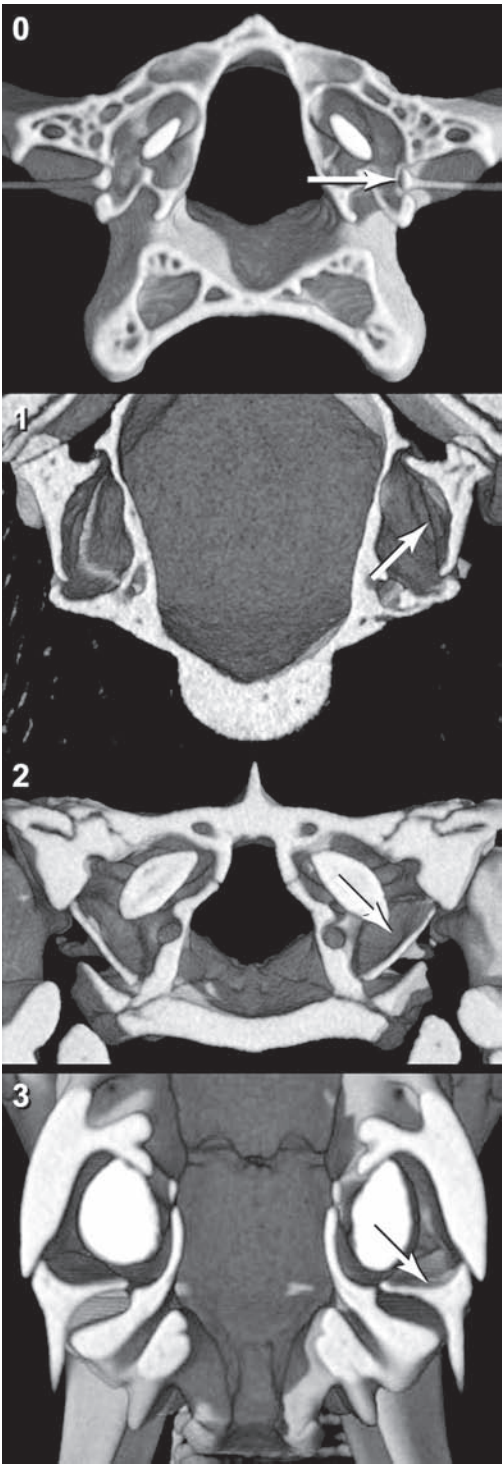


191. Stapedial shaft: (0) long and slender (*Tupinambis teguixin*, oblique posterior close-up of braincase); (1) short and thick (*Feylinia polylepis*, ventral close-up of braincase). Lee (1998).



192. Stapedial footplate: (0) small (*Tupinambis teguixin*, lateral close-up cutaway view of braincase); (1) large (*Feylinia polylepis*, lateral close-up cutaway view of braincase). Lee (1998).

193. Stapedial footplate: (0) does not fill fenestra ovalis (*Leiolepis belliana*, anterior close-up cutaway view of braincase); (1) fills fenestra ovalis (*Anniella pulchra*, lateral close-up cutaway view of braincase). Lee (1998).

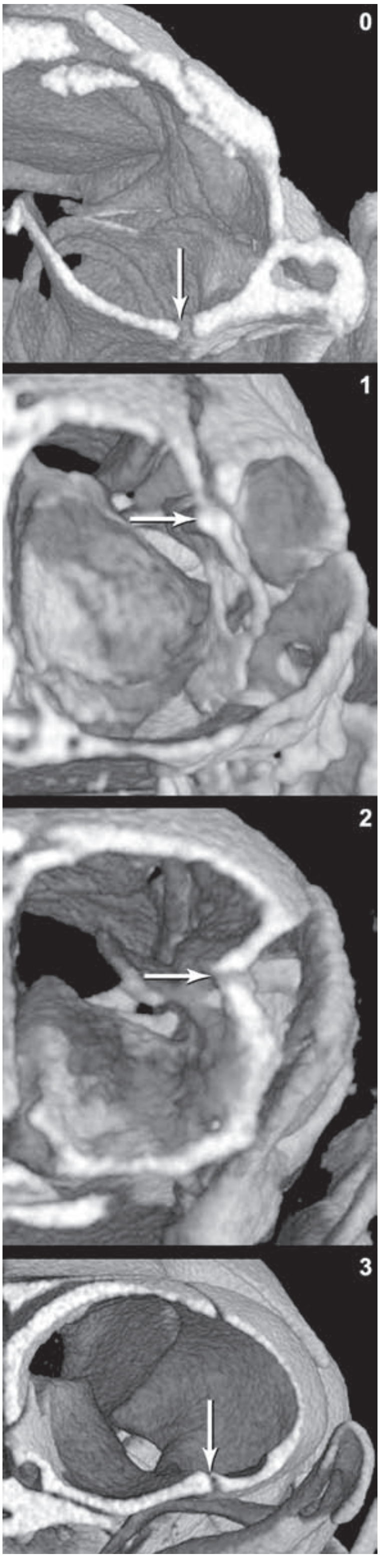


194. Fenestra ovalis orientation: (0) opens directly laterally (*Leiolepis belliana*, anterior close-up cutaway view of braincase); (1) opens anterolaterally^{N} (*Anniella pulchra*, dorsal close-up cutaway view of braincase); (2) opens ventrolaterally (*Anilius scytale*, anterior close-up cutaway view of

braincase); (3) opens posterolaterally^N (*Python molurus*, dorsal close-up cutaway view of braincase). Gauthier, Estes and de Queiroz (1988).

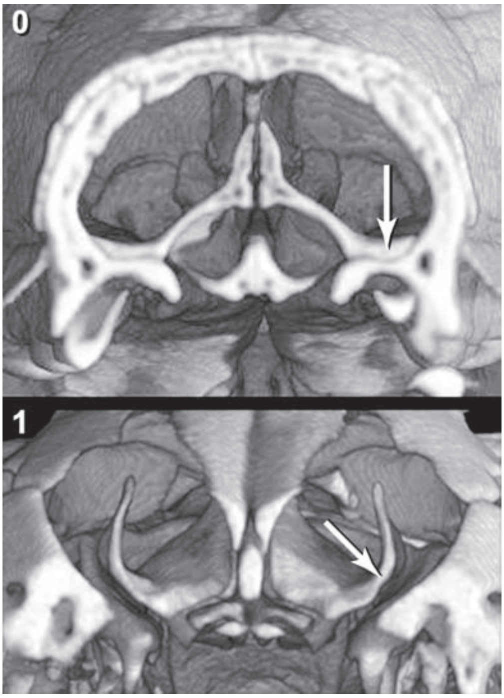
195. Extracolumella: (0) present; (1) absent. Rieppel (1980a).

196. Septomaxilla: (0) present; (1) absent. Estes et al. (1988).

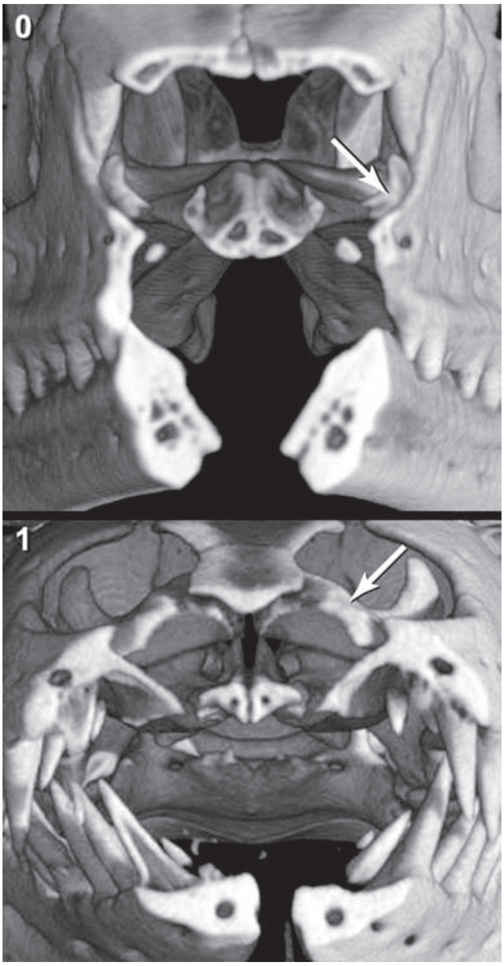


197. Septomaxilla dorsolateral contacts^N: (0) no contacts (*Dibamus novaeguineae*, anterior close-up cutaway view of

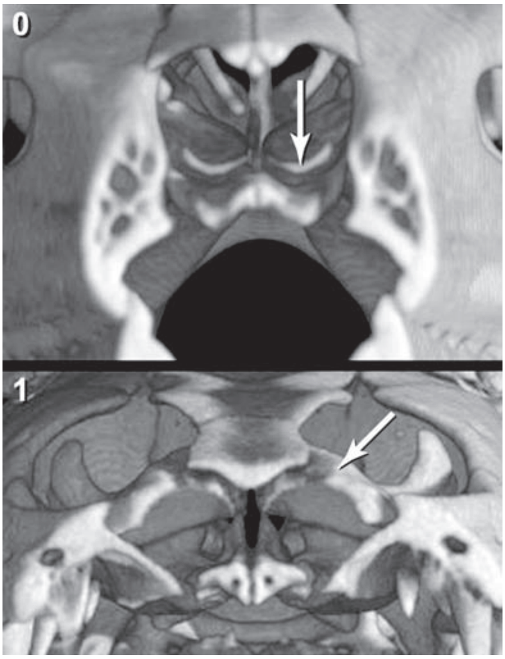
snout); (1) abuts laterally with prefrontal and nasal (*Leptotyphlops dulcis*, anterior close-up cutaway view of snout); (2) abuts laterally with nasal only (*Liotyphlops albirostris*, anterior close-up cutaway view of snout); (3) abuts laterally with prefrontal only (*Typhlops jamaicensis*, anterior close-up cutaway view of snout).



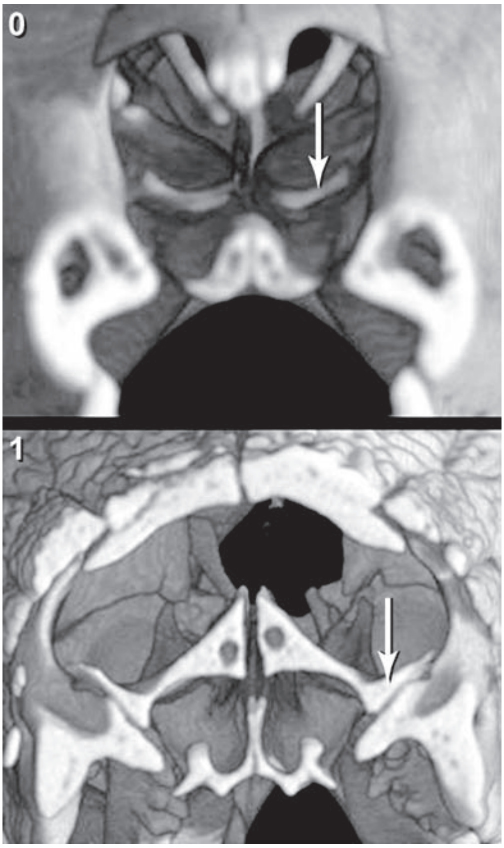
198. Anterior end of septomaxilla: (0) meets maxilla in immovable joint (*Tiliqua scincoides*, anterior close-up cutaway view of snout); (1) mobile, septomaxilla not contacting maxilla (*Cylindrophis ruffus*, anterior close-up cutaway view of snout). Lee (1998).



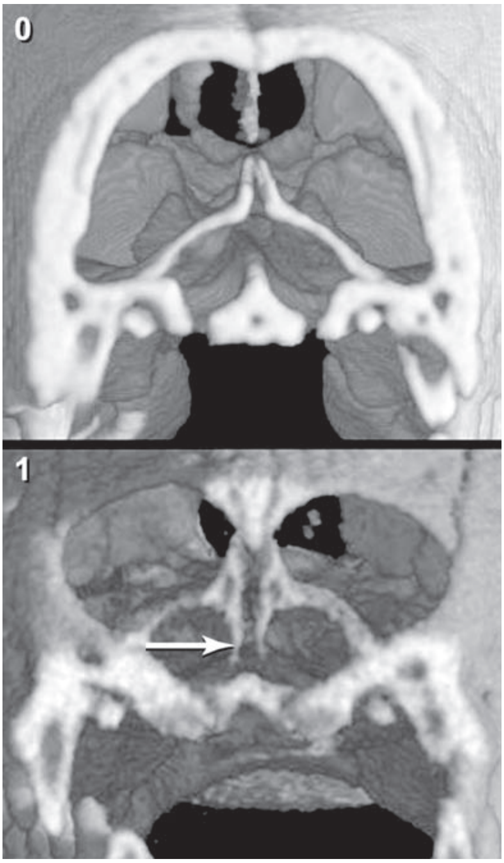
199. Septomaxilla position relative to vomeronasal organ: (0) occupies a lateral position, not contributing to nasal cavity or to roofing of vomeronasal organ (*Sphenodon punctatus*, anterior close-up cutaway view of snout); (1) occupies a more medial position, contributing to nasal cavity and roofing vomeronasal organ (*Lanthanotus borneensis*, anterior close-up cutaway view of snout). Gauthier, Estes and de Queiroz (1988).



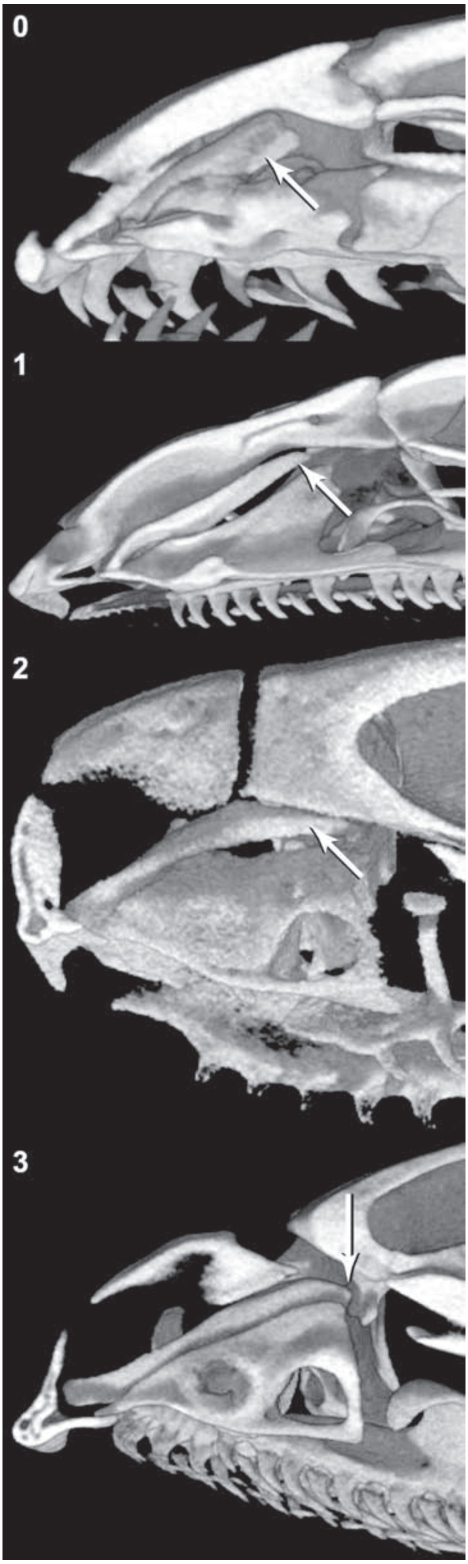
200. Septomaxilla, dorsal expansion: (0) flat or weakly convex, vomeronasal organ small (*Pogona vitticeps*, anterior close-up cutaway view of snout); (1) expanded and convex, reflecting large size of vomeronasal organ (*Lanthanotus borneensis*, anterior close-up cutaway view of snout). Gauthier, Estes and de Queiroz (1988).



201. Septomaxilla: (0) does not contact the dorsal surface of the palatal shelf of the maxilla (*Pogona vitticeps*, anterior close-up cutaway view of snout); (1) contacts the dorsal surface of the palatal shelf of the maxilla (*Pseudopus apodus*, anterior close-up cutaway view of snout). Lee (1998).

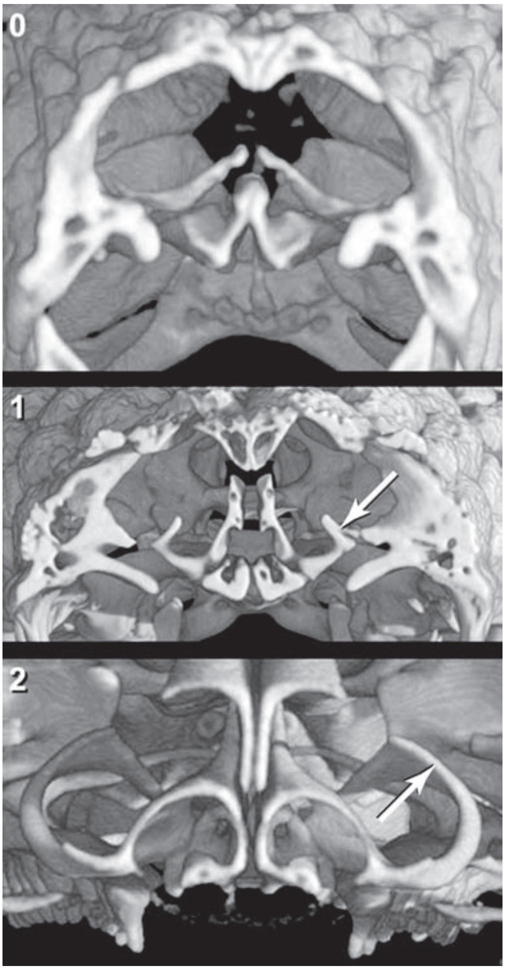


202. Septomaxilla divides vomeronasal organ^{N}: (0) absent (*Lepidophyma flavimaculatum*, anterior close-up cutaway view of snout); (1) present (*Xantusia vigilis*, anterior close-up cutaway view of snout).

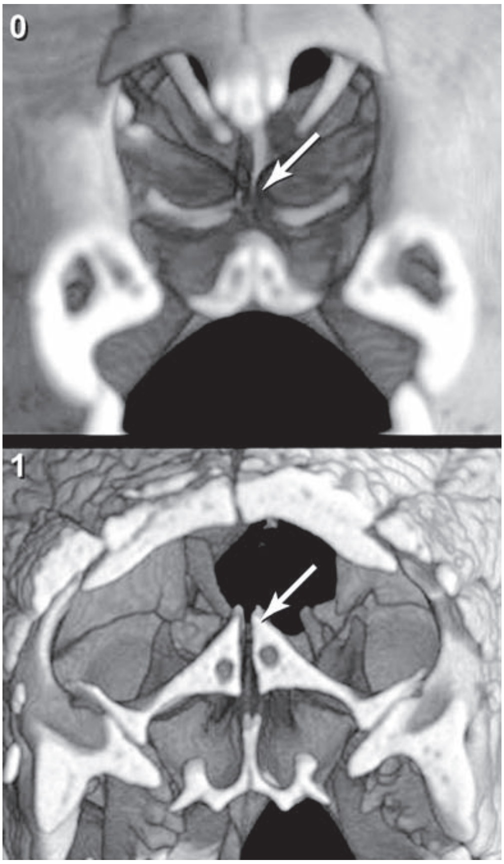


203. Septomaxilla medial flange produced into a long, posterodorsally directed, blade-like process: (0) absent

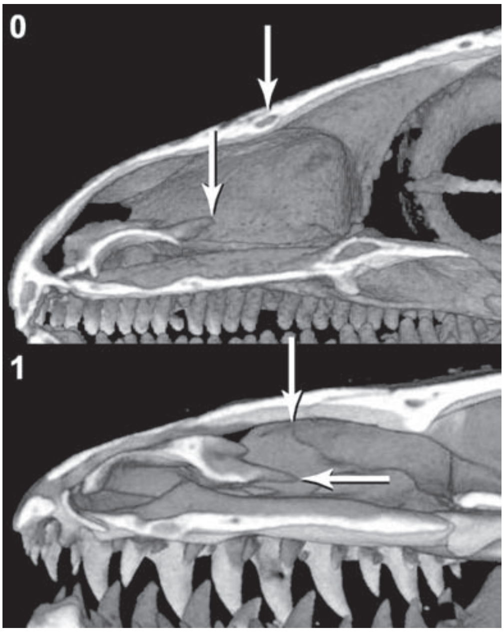
(*Cylindrophis ruffus*, lateral close-up cutaway view of snout); (1)^{N} present, but nasal intercedes between septomaxilla and frontal (*Xenopeltis unicolor*, lateral close-up cutaway view of snout); (2) extends to frontal beneath nasal (*Pareas hamptoni*, lateral close-up cutaway view of snout), Tchernov et al. (2000); (3)^{N} develops an expanded faceted articulation with the frontal (*Amphiesma stolata*, lateral close-up cutaway view of snout). Caldwell (1999) (ordered).



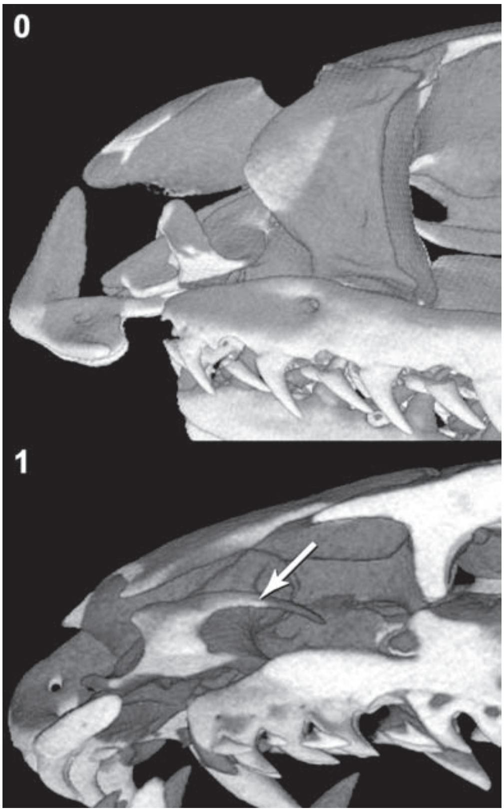
204. Septomaxilla lateral flange: (0) absent (*Xenosaurus platyceps*, anterior close-up cutaway view of snout); (1)^{N} present (*Heloderma horridum*, anterior close-up cutaway view of snout); (2)^{N} reaches well above roof of vomeronasal organ (*Xenopeltis unicolor*, anterior close-up cutaway view of snout). Lee (1997a) (ordered).



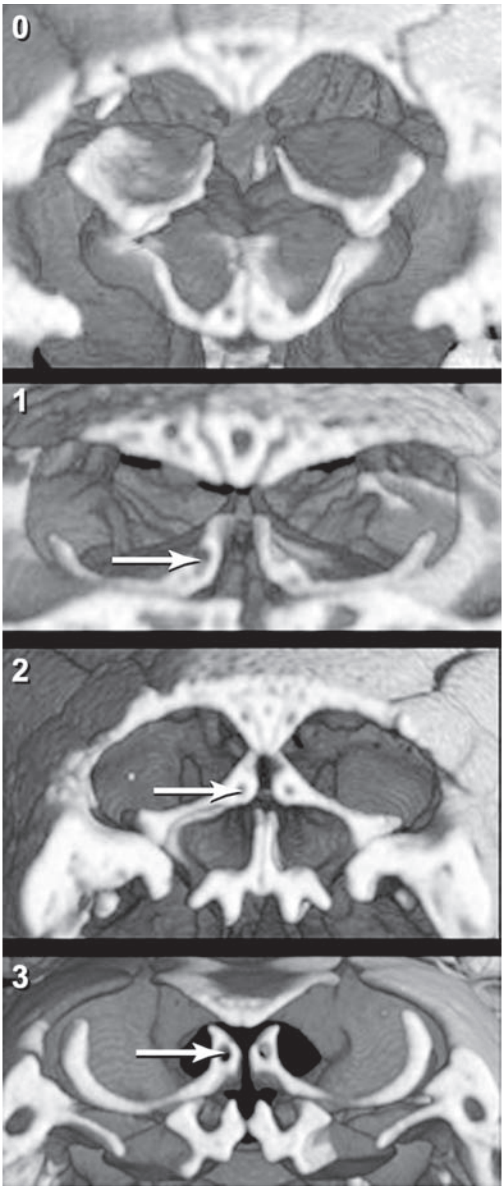
205. Septomaxilla medial flange: (0) absent (*Pogona vitticeps*, anterior close-up cutaway view of snout); (1) present (*Pseudopus apodus*, anterior close-up cutaway view of snout). Estes et al. (1988).



206. Septomaxilla, posterior extent of medial flange: (0) short, not reaching level of prefrontal (*Plestiodon fasciatus*, lateral close-up cutaway view of snout); (1) long, extends posteriorly to anteroposterior level of anterior margin of prefrontal (*Lanthanotus borneensis*, lateral close-up cutaway view of snout). Lee (1998). Short in scolecophidians, but medial to prefrontal: coded (0).

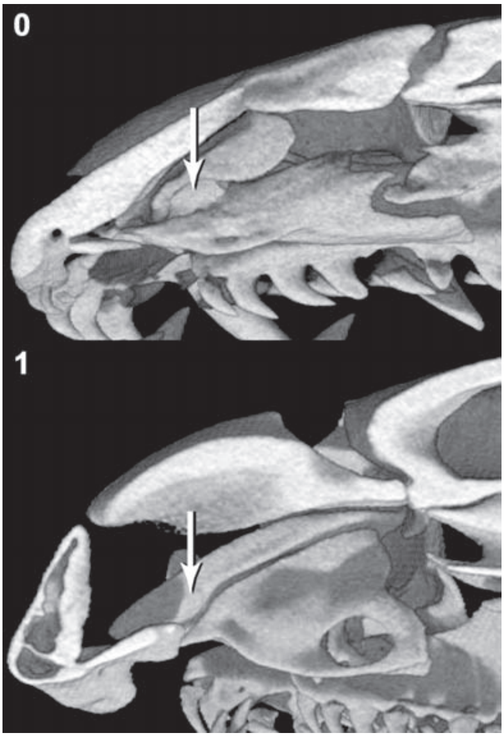


207. Septomaxilla posterior process on laterally ascending flange: (0) short or absent (*Coluber constrictor*, lateral close-up cutaway view of snout); (1) long, extends posteriorly deep to prefrontals (*Anilius scytale*, lateral close-up cutaway view of snout). Caldwell (1999).

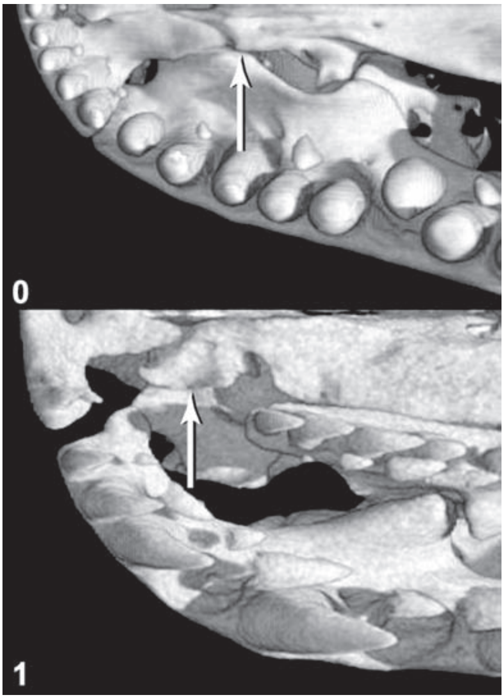


208. Nervus ethmoidalis medialis^{N}: (0) above septomaxilla (*Stenocercus guentheri*, anterior close-up cutaway view of snout); (1) enclosed in septomaxilla anteriorly (*Cordylus mossambicus*, anterior close-up cutaway view of snout); (2) in anterior half of septomaxilla (*Elgaria multicarinata*, anterior close-up cutaway view of snout); (3) enclosed posteriorly in septomaxilla (*Lanthanotus borneensis*, anterior close-up cutaway view of snout) (ordered).

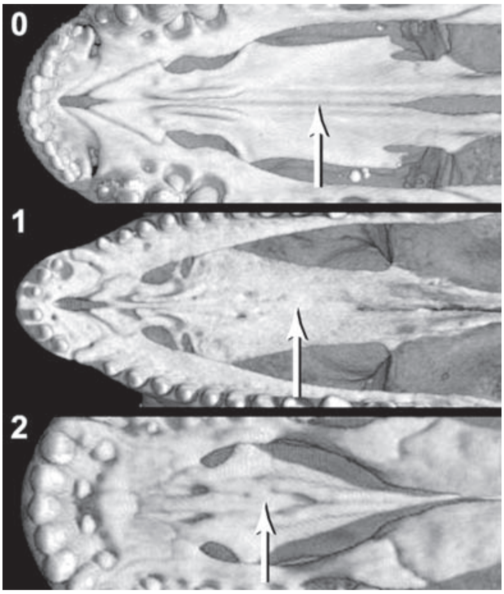
209. Vomeronasal organ, concha: (0) simple diverticulum of nasal capsule; (1) completely separated from nasal capsule, with fungiform body. Gauthier, Estes and de Queiroz (1988).



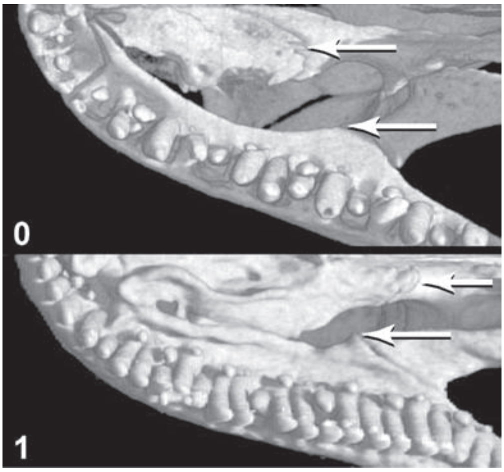
210. Vomeronasal organ, cupola: (0) fenestrated medially, even if only narrowly (*Anilius scytale*, lateral close-up cutaway view of snout); (1) closed medially (*Coluber constrictor*, lateral close-up cutaway view of snout). Cundall et al. (1993).



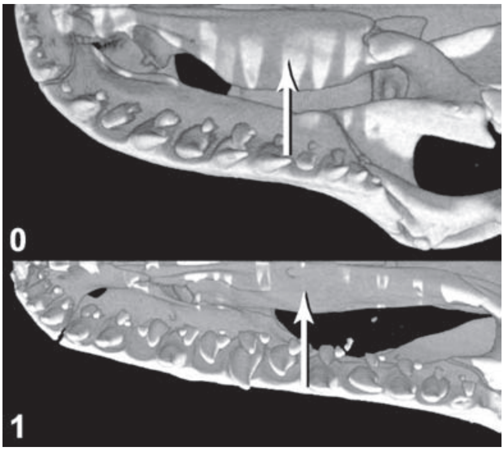
211. Vomeronasal organ and mushroom body: (0) not fully enclosed by septomaxilla and vomer (*Varanus exanthematicus*, ventral close-up of palate); (1) fully enclosed by septomaxilla and vomer only (*Anilius scytale*, ventral close-up of palate). Estes et al. (1988).



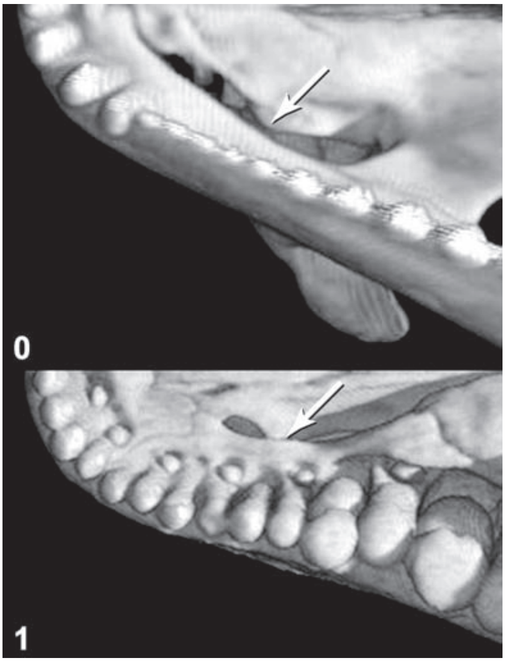
212. Vomer fusion: (0) absent (*Tupinambis teguixin*, ventral close-up of palate); (1) partial (*Teius teyou*, ventral close-up of palate); (2) fully fused (*Tiliqua scincoides*, ventral close-up of palate). Estes et al. (1988).



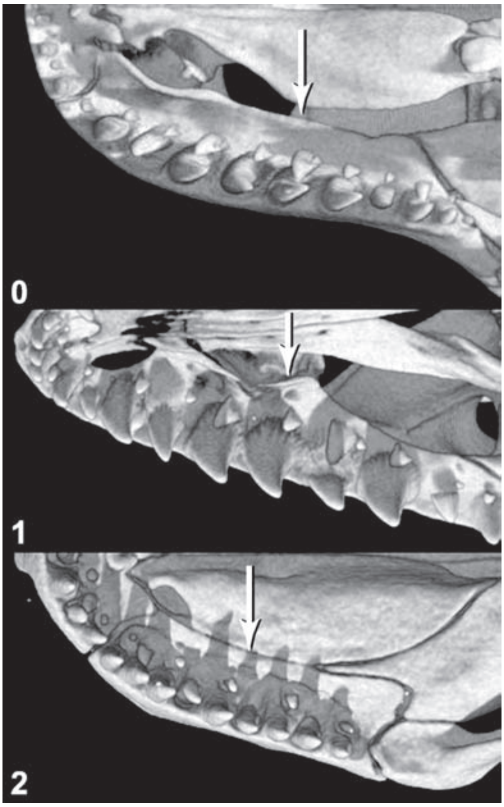
213. Vomer size: (0) vomer extends backwards no further than anteriormost contact of palatine with maxilla (*Liolaemus bellii*, ventral close-up of palate); (1) vomer extends backwards beyond anteriormost contact of palatine with maxilla (*Elgaria multicarinata*, ventral close-up of palate). Estes et al. (1988).



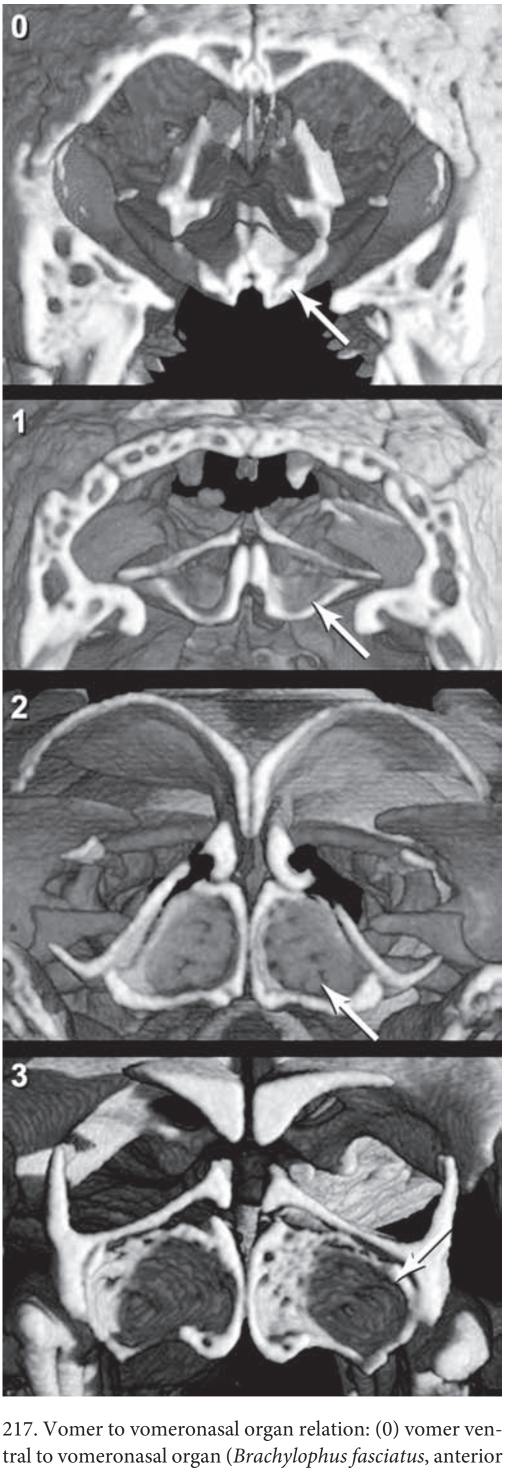
214. Vomer: (0) main portion plate-like (*Lanthanotus borneensis*, ventral close-up of palate); (1) main portion rod-like (*Varanus salvator*, ventral close-up of palate). Lee (1998).



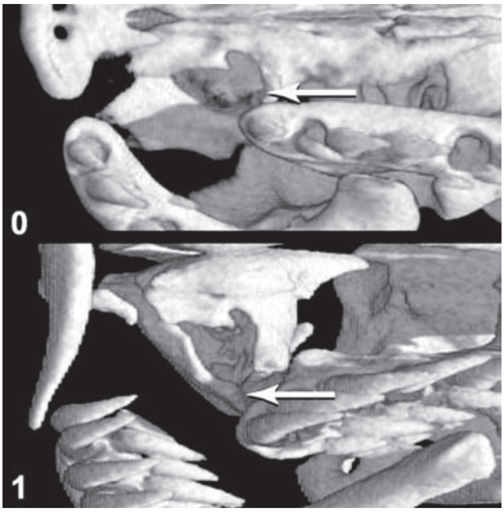
215. Vomer overlaps (dorsally) the palatal shelf of the maxilla behind posterior margin of opening of vomeronasal organ: (0) absent (*Pogona vitticeps*, ventral close-up of snout); (1) present (*Tiliqua scincoides*, ventral close-up of snout). Gauthier, Estes and de Queiroz (1988).



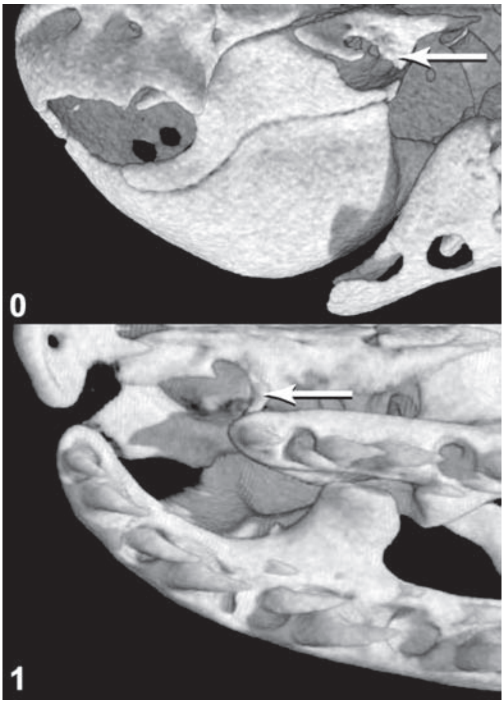
216. Vomer: (0) does not establish any sutural contact with the palatal shelf of the maxilla behind the incisura Jacobsoni (*Lanthanotus borneensis*, ventral close-up of palate); (1) establishes narrow contact with the palatal shelf of the maxilla behind the incisura Jacobsoni (*Varanus acanthurus*, oblique ventral close-up of palate); (2) establishes broad contact with the palatal shelf of the maxilla along the entire length of the lateral margin of vomer (*Anelytropsis papillosus*, oblique ventral close-up of palate). Rieppel et al. (2008) (ordered).



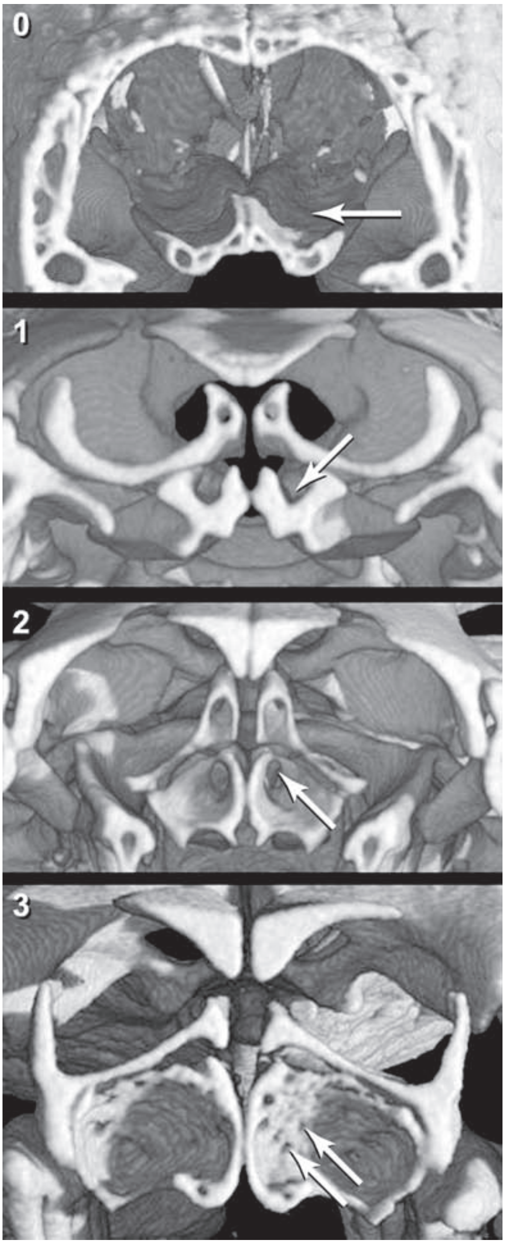
217. Vomer to vomeronasal organ relation: (0) vomer ventral to vomeronasal organ (*Brachylophus fasciatus*, anterior close-up cutaway view of snout); (1) encapsulates vomeronasal organ posteriorly and medially (*Cordylus mossambicus*, anterior close-up cutaway view of snout); (2) with margins enclosing posterior wall sloping ventrolaterally (*Xenodermus javanicus*, anterior close-up cutaway view of snout); (3) further expanded laterally to completely encapsulate vomeronasal organ posteriorly (*Acrochordus granulatus*, anterior close-up cutaway view of snout). Rieppel et al. (2008) (ordered).



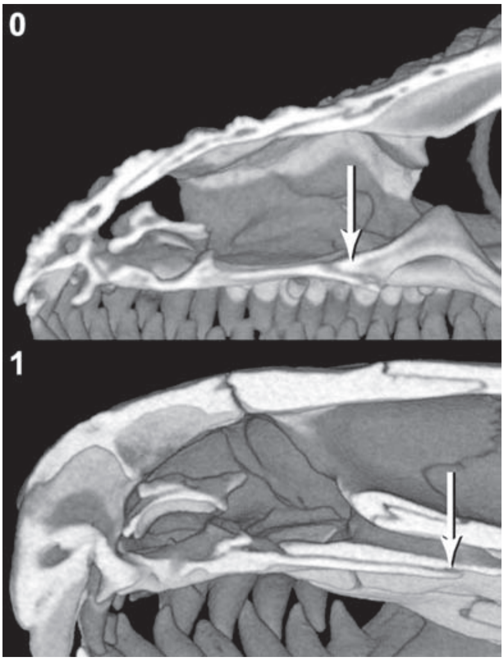
218. Vomer meets septomaxilla: (0) at posterior margin of opening of vomeronasal organ (*Cylindrophis ruffus*, ventral close-up of palate); (1) at lateral margin of opening of vomeronasal organ (*Acrochordus granulatus*, ventral close-up of palate). Tchernov et al. (2000).



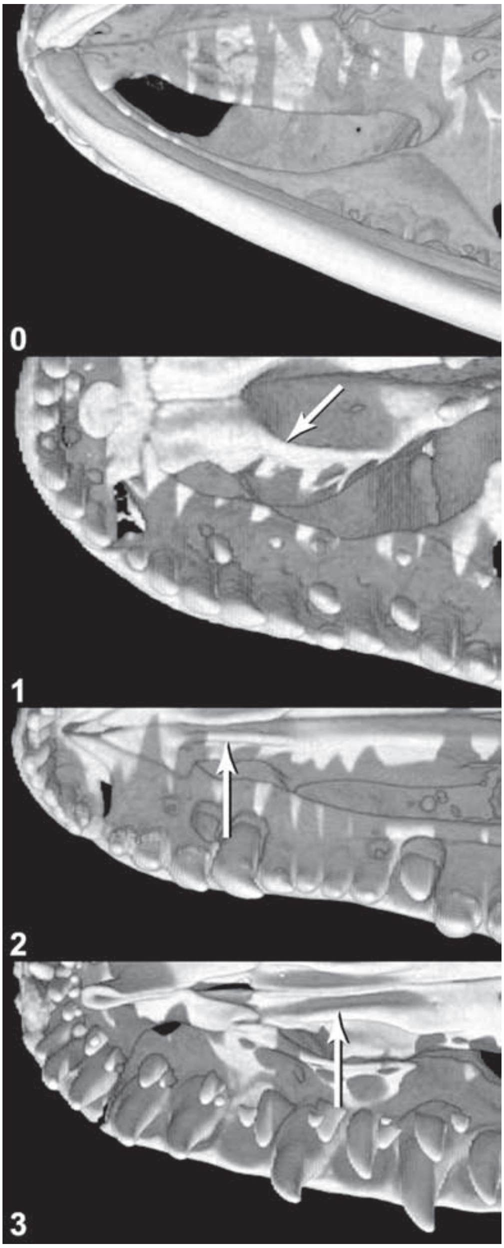
219. Margin of vomer at opening of vomeronasal organ^{N}: (0) flat (*Typhlops jamaicensis*, ventral close-up of palate); (1) curled downwards (*Cylindrophis ruffus*, ventral close-up of palate).



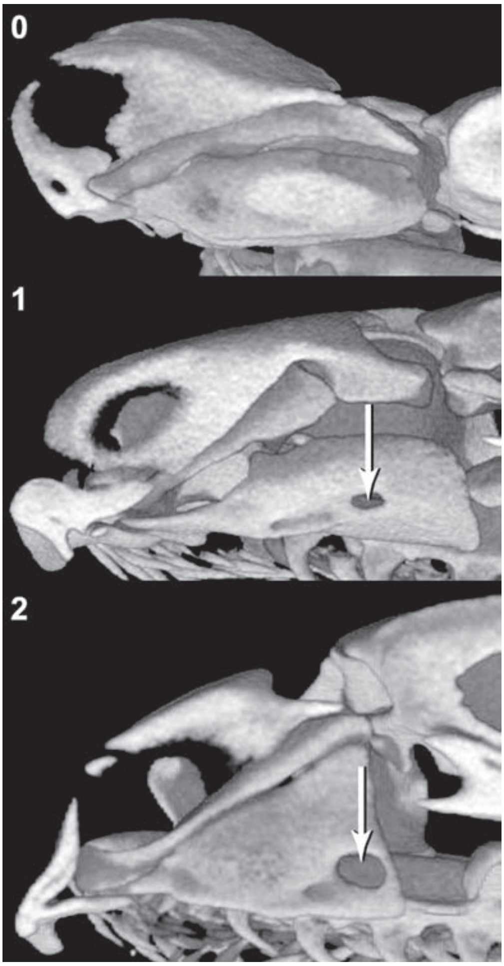
220. Vomeronasal nerve exit: (0) dorsal to vomer (*Brachylophus fasciatus*, anterior close-up cutaway view of snout); (1) via canals dorsally on vomer (*Lanthanotus borneensis*, anterior close-up cutaway view of snout); (2) via foramen at back end of vomer (*Cylindrophis ruffus*, anterior close-up cutaway view of snout); (3) via sieve-like arrangement of foramina through back end of vomer (*Acrochordus granulatus*, anterior close-up cutaway view of snout). Rieppel et al. (2008) (ordered).



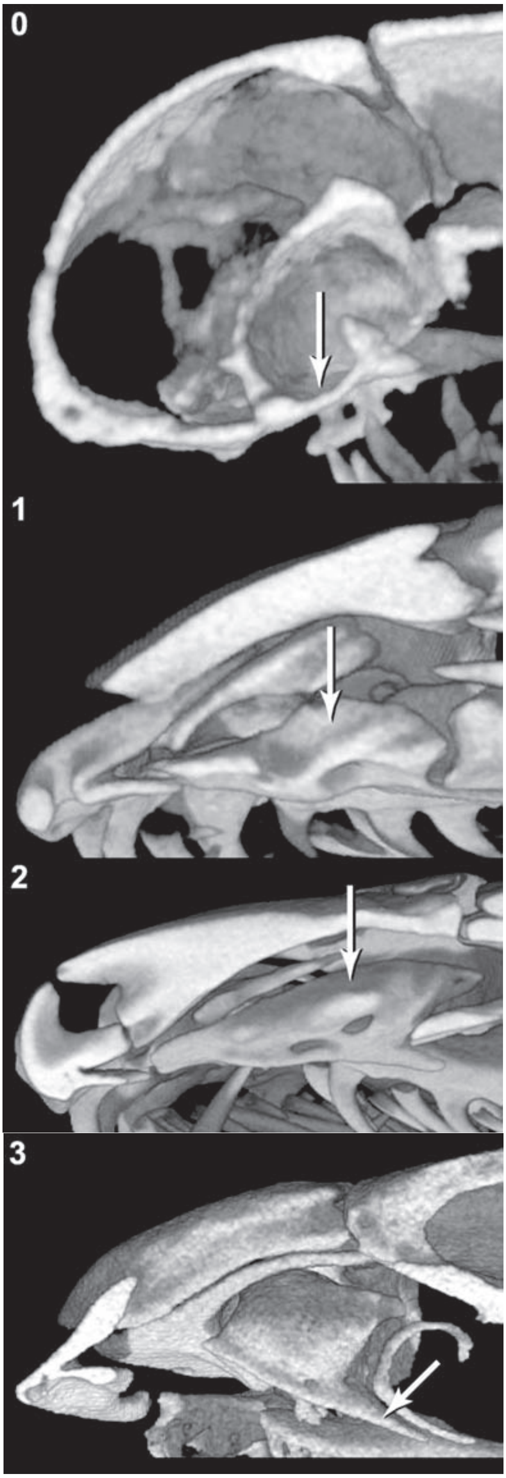
221. Vomer degree underlap of palatine: (0) just at tips (*Xenosaurus platyceps*, lateral close-up cutaway view of snout); (1) extending posteriorly to level of maxilla-ectopterygoid first contact (*Amphisbaena fuliginosa*, lateral close-up cutaway view of snout). Kearney (2003a).

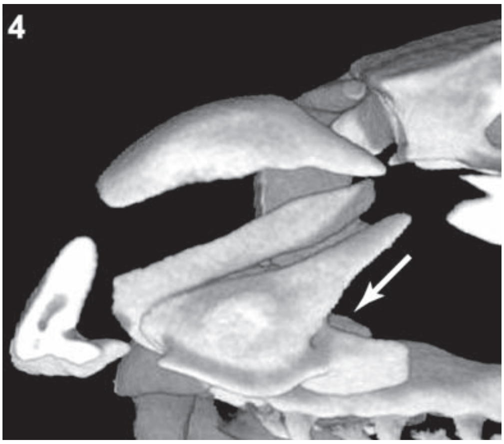


222. Vomer ventral longitudinal ridges^{N}: (0) absent (*Gambelia wislizenii*, ventral close-up of palate); (1) long and converge toward midline, well-developed below vomeronasal nerve exit from septomaxilla (*Celestus enneagrammus*, ventral close-up of palate); (2) short parasagittal ridges anteriorly on vomer at level of vomeronasal duct opening (*Tupinambis teguixin*, ventral close-up of palate); (3) discrete parasagittal canals anteriorly on vomer delimited by lateral and median ridges (*Varanus salvator*, ventral close-up of palate).

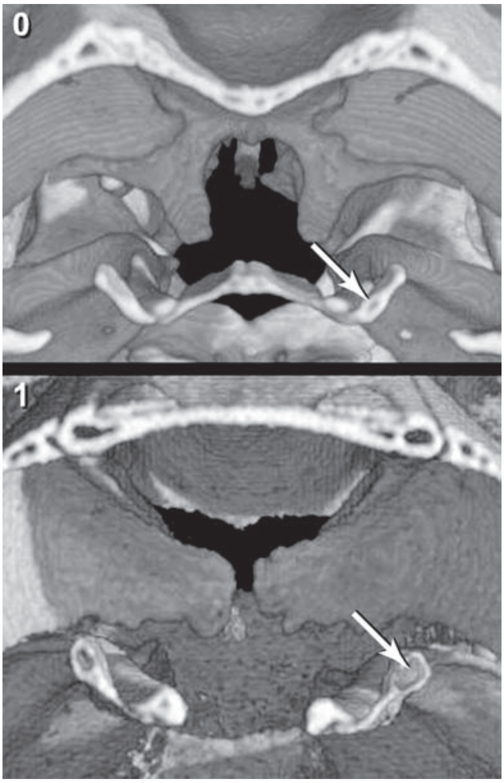


223. Vomer septum transversely fenestrate^{N}: (0) absent (*Xenodermus javanicus*, lateral close-up cutaway view of snout); (1) present (*Tropidophis haetianus*, lateral close-up cutaway view of snout); (2) at posteroventral corner of vomer septum (*Afronatrix anoscopus*, lateral close-up cutaway view of snout) (ordered).



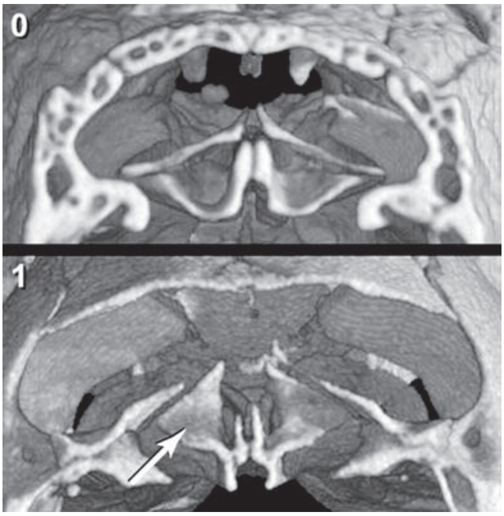


224. Vomer septum (vertical lamina) height^{N}: (0) low, not forming septum (*Leptotyphlops dulcis*, lateral close-up cutaway view of snout); (1) partly separating olfactory chambers (*Cylindrophis ruffus*, lateral close-up cutaway view of snout); (2) nearly completely separating olfactory chambers along with septomaxilla and nasal (*Epicrates striatus*, lateral close-up cutaway view of snout); (3) only ventral edge of septum remains (*Aparallactus werneri*, lateral close-up cutaway view of snout); (4) V-shaped notch separates dorsal and ventral rami of vomer septum (*Laticauda colubrina*, lateral close-up cutaway view of snout).

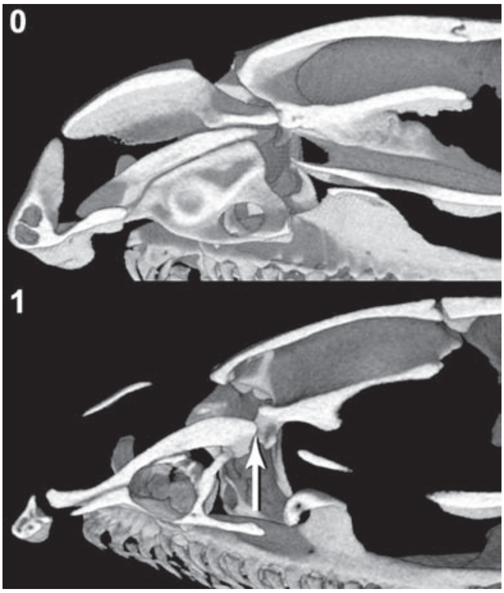


225. Vomer, posterodorsal margin forms expanded hollow flange^{N}: (0) absent (*Rhacodactylus auriculatus*, anterior

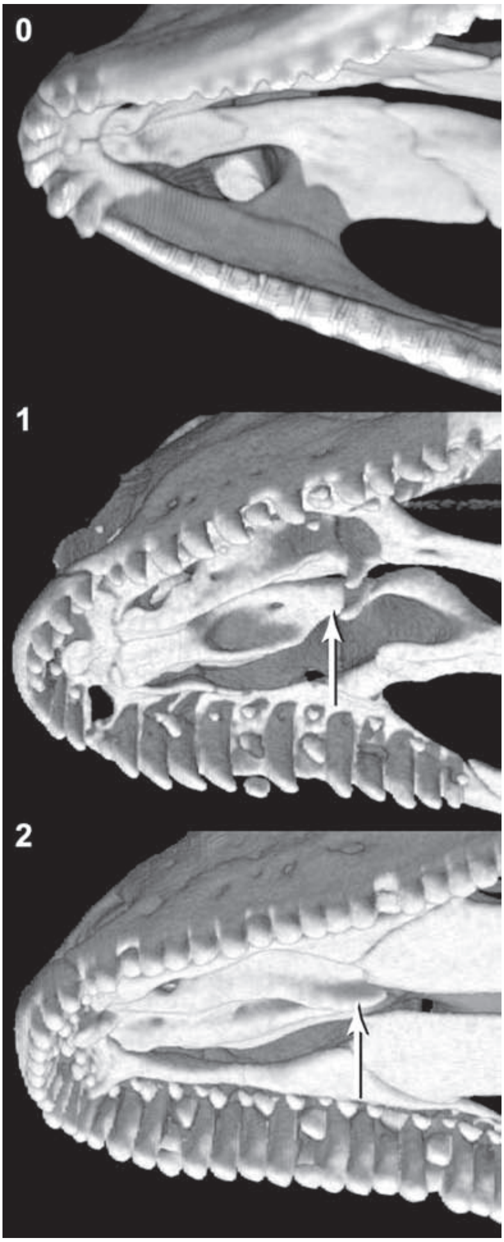
close-up cutaway view of snout); (1) present (*Coleonyx variegatus*, anterior close-up cutaway view of snout).



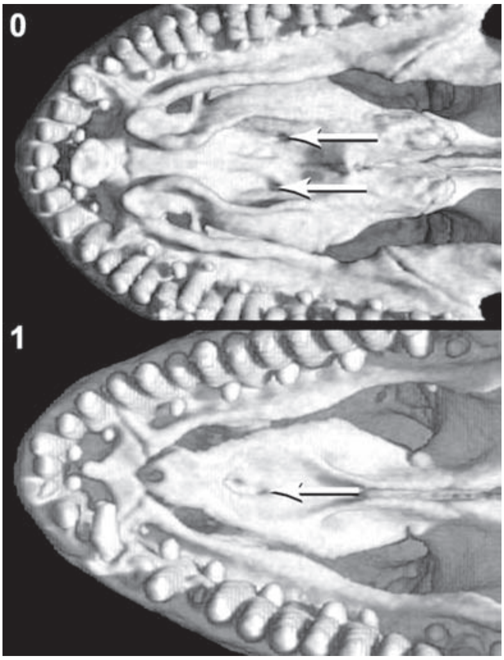
226. Vomer, transverse flange rises vertically to meet septomaxilla and encloses vomeronasal organ posteriorly: (0) absent (*Cordylus mossambicus*, anterior close-up cutaway view of snout); (1) present (*Colobosaura modesta*, anterior close-up cutaway view of snout).



227. Vomer contact with subolfactory process of frontal: (0) absent (*Coluber constrictor*, lateral close-up cutaway view of snout); (1) present (*Amphiesma stolata*, lateral close-up cutaway view of snout). Rieppel (2007).

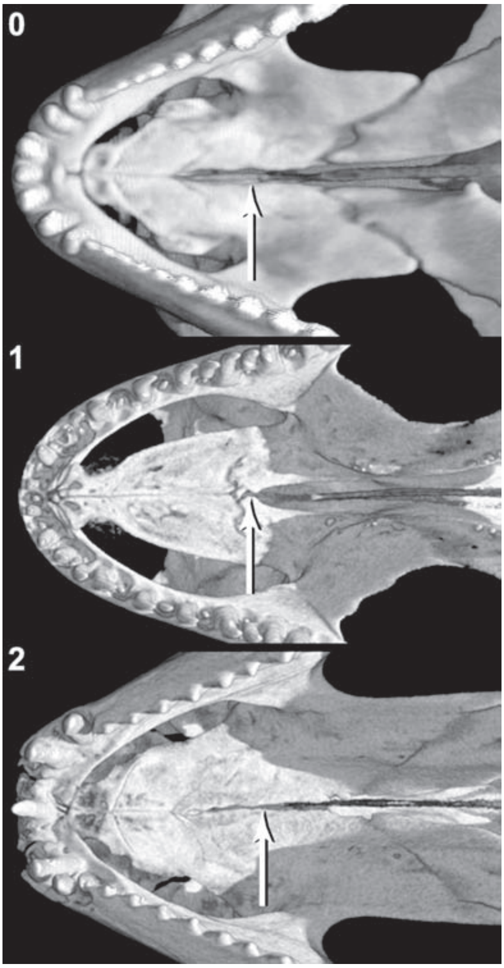


228. Vomer, descending tubercle (or ridge) at vomero-palatine junction^{N}: (0) absent (*Pogona vitticeps*, oblique ventral view of palate); (1) tubercle present (*Celestus enneagrammus*, oblique ventral view of palate); (2) ridge/tubercle present on vomer and/or adjacent palatine (*Eugongylus rufescens*, oblique ventral view of palate).

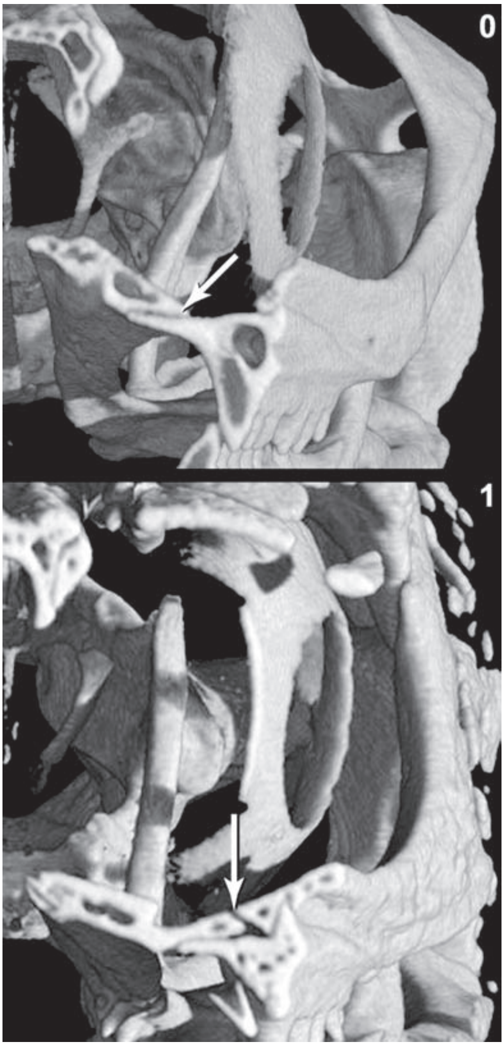


229. Vomer, foramina on palatal surface near midline^{N}: (0) paired (*Elgaria multicarinata*, ventral close-up of palate); (1) single (*Lepidophyma flavimaculatum*, ventral close-up of palate).

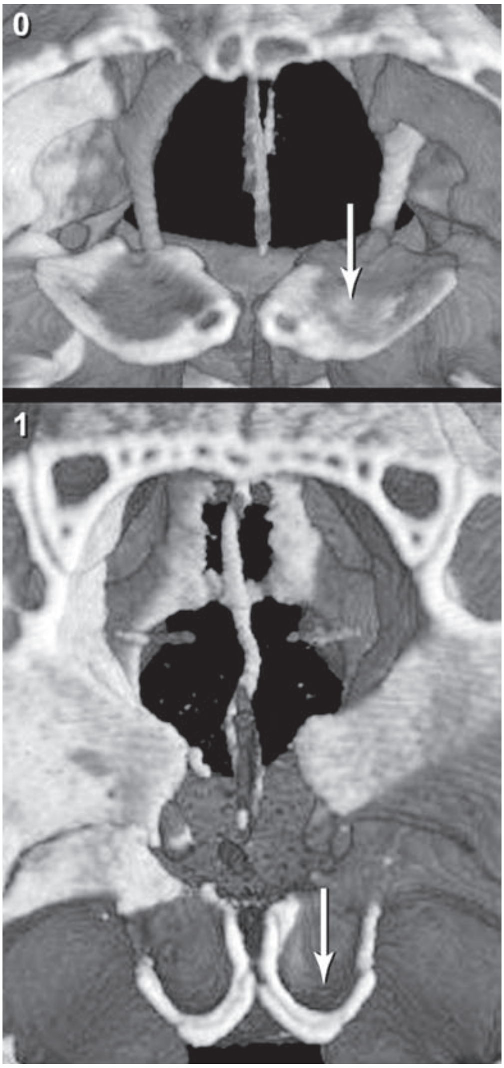
230. Vomer, teeth: (0) present; (1) absent. Gauthier, Estes and de Queiroz (1988).



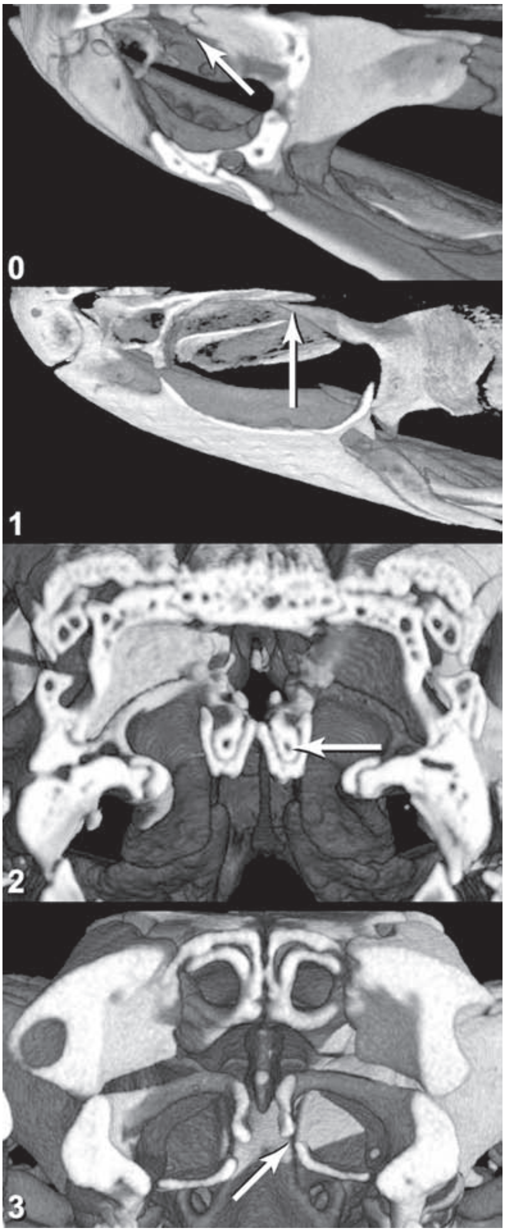
231. Palatines: (0) separated (*Pogona vitticeps*, ventral close-up of palate); (1) anterior contact only (*Gambelia wislizenii*, ventral close-up of palate); (2) contact extends to midpoint, or beyond (*Physignathus cocincinus*, ventral close-up of palate). Lee (1998) (ordered).



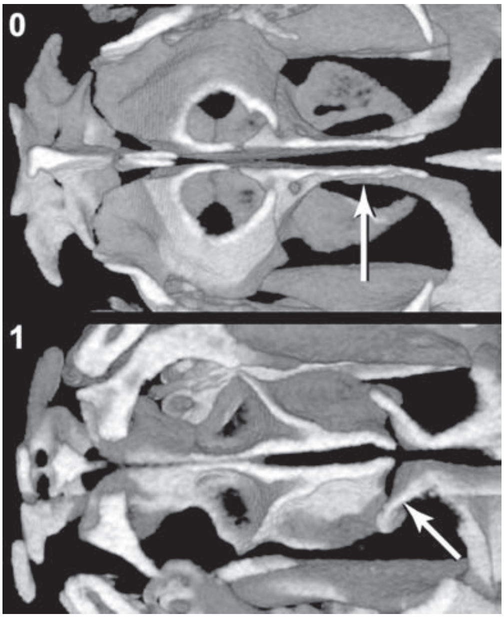
232. Palatine relative to maxilla-lacrimal-jugal articulation^{N}: (0) palatine sits medial to lacrimal and/or jugal and maxilla in cross section (*Leiocephalus barahonensis*, anterior close-up cutaway view of orbit); (1) palatine inserts between lacrimal and/or jugal and maxilla in cross section (*Shinisaurus crocodilurus*, anterior close-up cutaway view of orbit).



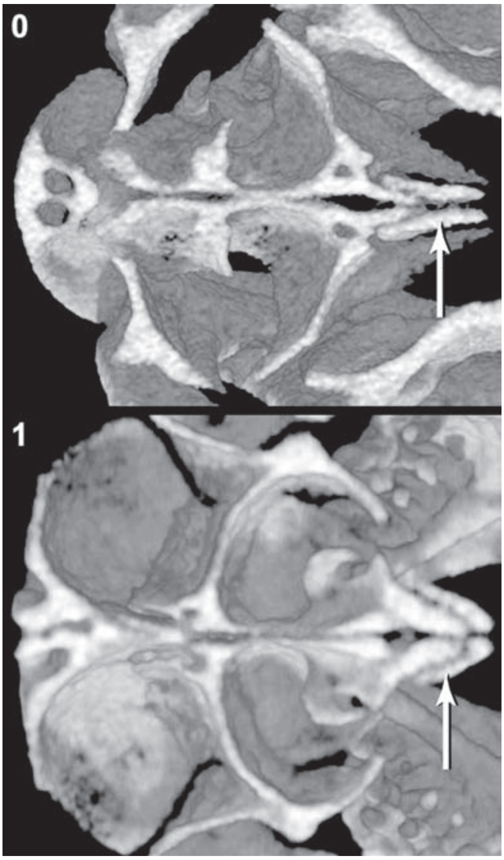
233. Palatine dorsal canal^{N}: (0) shallow longitudinal sulcus (*Leiocephalus barahonensis*, anterior close-up cutaway view of snout); (1) upturned lateral and medial edges of palatine demarcate deep, narrow canal ending in enclosed fossa (*Aspidoscelis tigris*, anterior close-up cutaway view of snout).



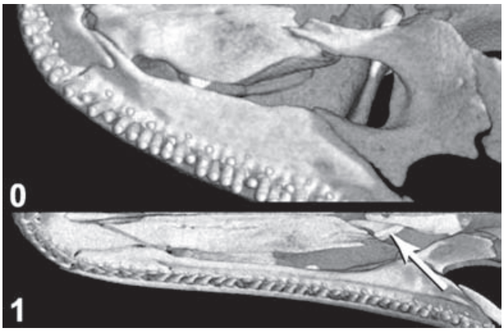
234. Palatine, vomerine process dorsally on vomer: (0) vomer attaches over entire face of vomerine process of palatine (*Crotaphytus collaris*, dorsal close-up cutaway view of snout); (1) narrow slender tip of palatine loosely attached to vomer (*Coleonyx variegatus*, dorsal close-up cutaway view of snout) Rieppel et al. (2008); (2)^{N} long slender palatine process clasped in groove on dorsal surface of vomer (*Elgaria multicarinata*, anterior close-up cutaway view of snout); (3) ventral edge of vomerine process of palatine attached ligamentously between bifid palatine process of vomer (*Anilius scytale*, anterior close-up cutaway view of snout), Cundall et al. (1993).



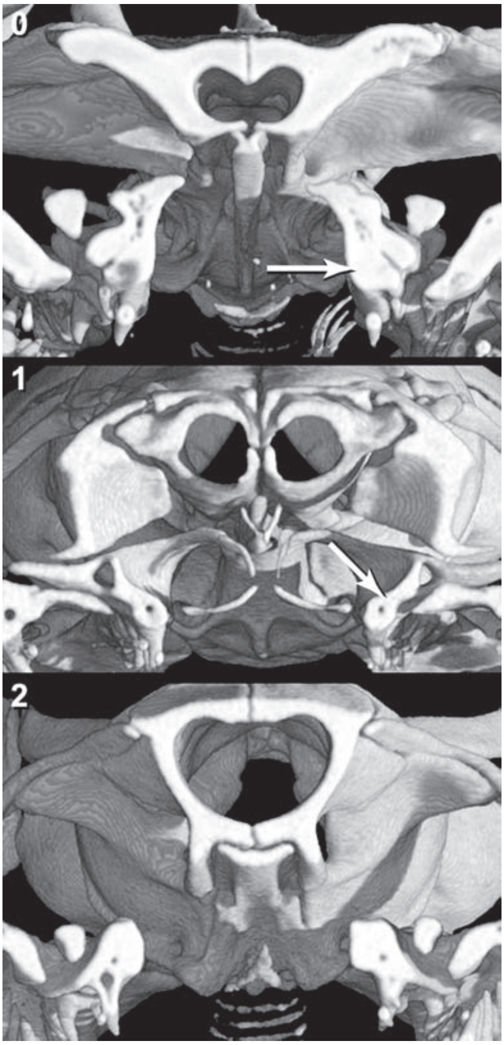
235. Palatine, vomerine process buttresses vomer^{N}: (0) palatine vomerine process tapers anteromedially (*Exiliboa placata*, dorsal close-up cutaway view of snout); (1) splays laterally at tips to buttress vomer posteriorly (*Trachyboa boulengeri*, dorsal close-up cutaway view of snout).



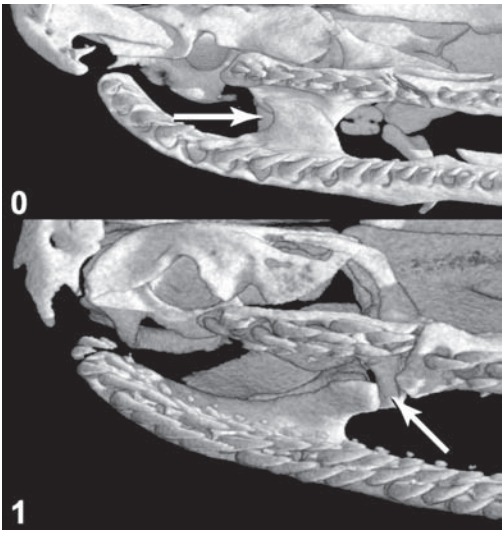
236. Palatine, vomerine process passes vomer^{N}: (0) medial to vomer tines (*Anomochilus leonardi*, dorsal close-up cutaway view of snout); (1) lateral to vomer tines (posteromedial process of vomer) (*Leptotyphlops dulcis*, dorsal close-up cutaway view of snout).



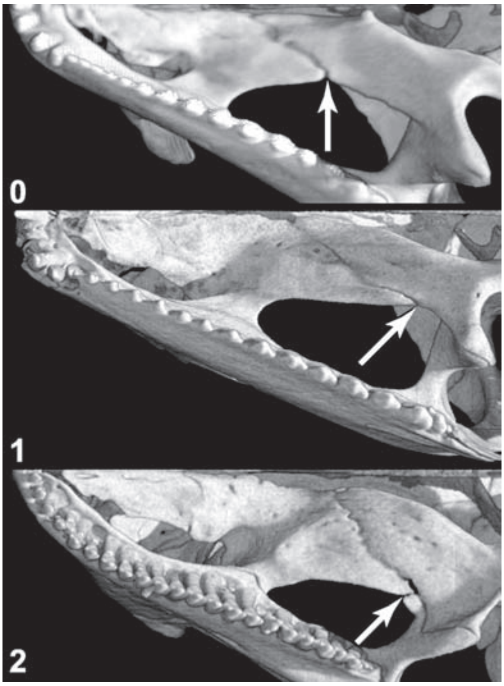
237. Ventral projections from anterior end of palatine, near palatine-vomer suture^{N}: (0) absent (*Eublepharis macularius*, ventral close-up view of palate); (1) present (*Lialis burtonis*, ventral close-up view of palate).



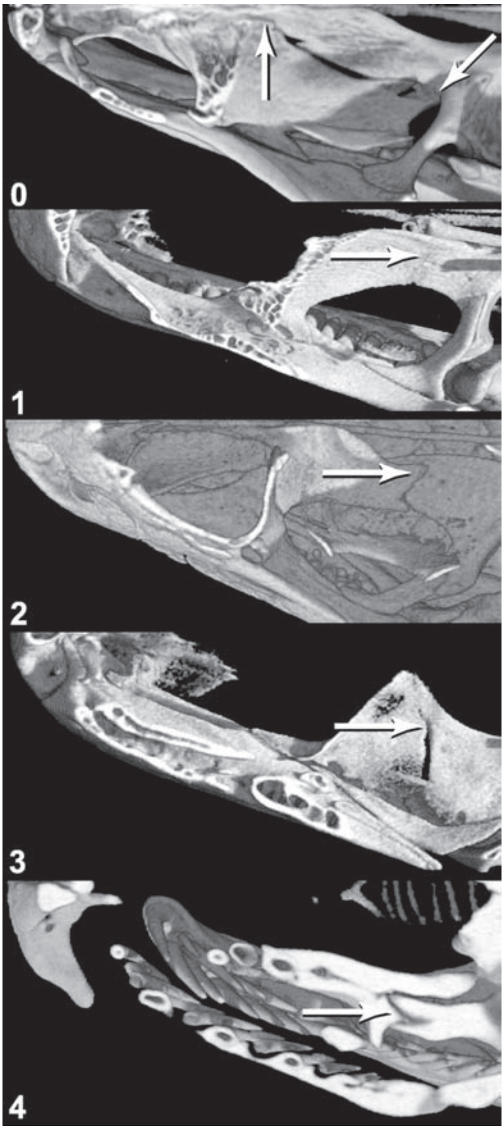
238. Ventromedial extension from maxillary process of palatine (choanal processes of palatine): (0) present but not descending ventromedially (*Boa constrictor*, anterior close-up cutaway view of snout); (1) present and descending ventromedially to reach in between (or close to) posterior tips of vomers (*Loxocemus bicolor*, anterior close-up cutaway view of snout); (2) absent (*Eryx colubrinus*, anterior close-up cutaway view of snout). Cundall et al. (1993) (ordered).



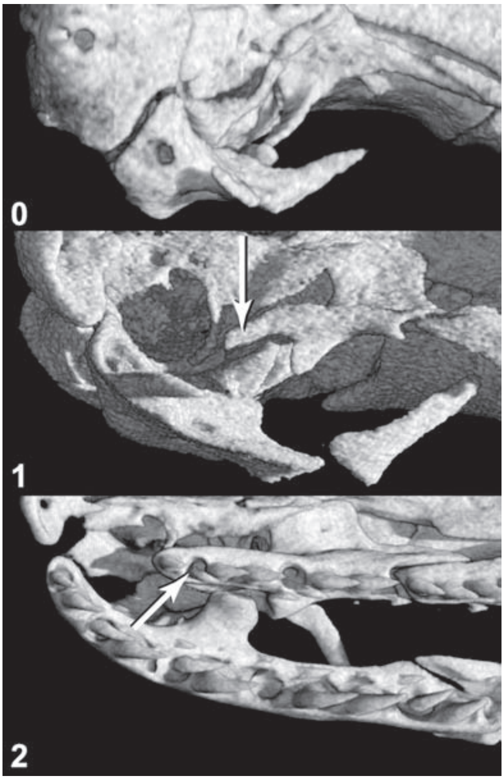
239. Maxillary process of palatine: (0) is situated anterior to the posterior end of palatine (*Loxocemus bicolor*, ventral close-up of palate); (1) is situated at the posterior end of the palatine (*Exiliboa placata*, ventral close-up of palate). Tchernov et al. (2000).



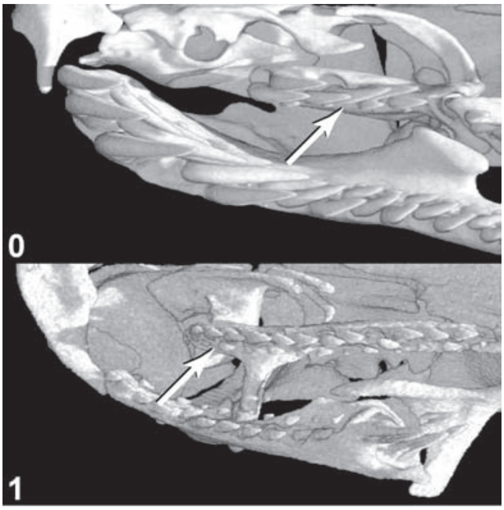
240. Palatine contribution to suborbital fenestra^{N}: (0) reduced posteromedially, and pterygoid broadly exposed in suborbital fenestra (*Pogona vitticeps*, ventral close-up of palate); (1) palatine extends posteriorly along lateral edge of pterygoid so that pterygoid narrowly enters suborbital fenestra (*Physignathus concincinus*, ventral close-up of palate); (2) palatine fully excludes pterygoid from border of suborbital fenestra (*Dipsosaurus dorsalis*, ventral close-up of palate).



241. Palatine-pterygoid overlap: (0) palatine overlaps pterygoid at tip and ectopterygoid near base, otherwise lateral in position (*Sphenodon punctatus*, dorsal close-up cutaway view of snout); (1)^{N} palatine overlaps pterygoid dorsally from lateral to near medial margin of pterygoid, with loose abutment laterally (*Polychrus marmoratus*, dorsal close-up cutaway view of snout); (2)^{N} palatine barely overlaps pterygoid laterally and pterygoid does not extend well anterior to ectopterygoid-jugal-maxilla juncture (*Plestiodon fasciatus*, dorsal close-up cutaway view of snout); (3)^{N} palatine barely overlaps pterygoid, joint nearly transverse (*Phelsuma lineata*, dorsal close-up cutaway view of snout); (4) complex pattern of clasping projections (*Eryx colubrinus*, dorsal close-up cutaway view of snout). Cundall et al. (1993).

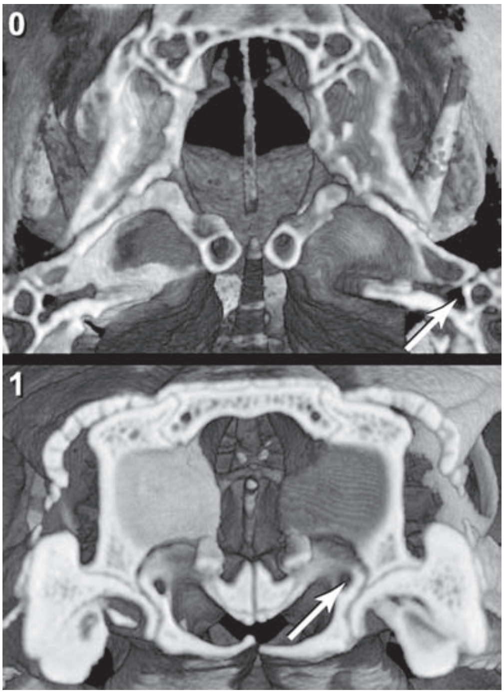


242. Palatine anterior "dentigerous" process: (0) absent (*Leptotyphlops dulcis*, ventral close-up of palate); (1) present only as short extension of palatine anterior to maxillary process (*Anomochilus leonardi*, ventral close-up of palate), Lee and Scanlon (2002); (2) present (with teeth) (*Cylindrophis ruffus*, ventral close-up of palate). Cundall et al. (1993) (ordered).

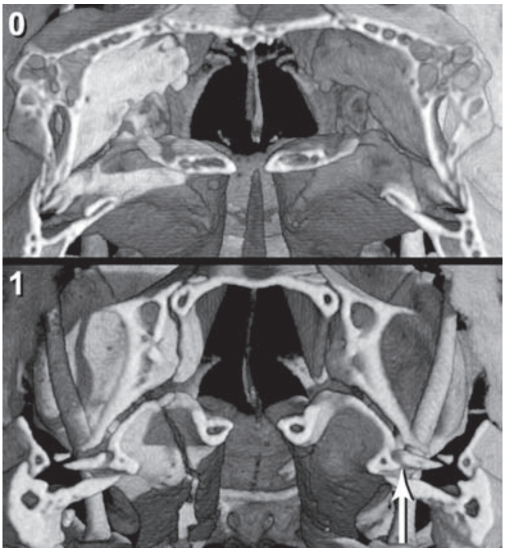


243. Palatine dentigerous process reduction^{N}: (0) long, bearing six or more teeth (*Epicrates striatus*, ventral close-up view of palate); (1) short, bearing five or fewer teeth. (*Aparallactus werneri*, ventral close-up view of palate).

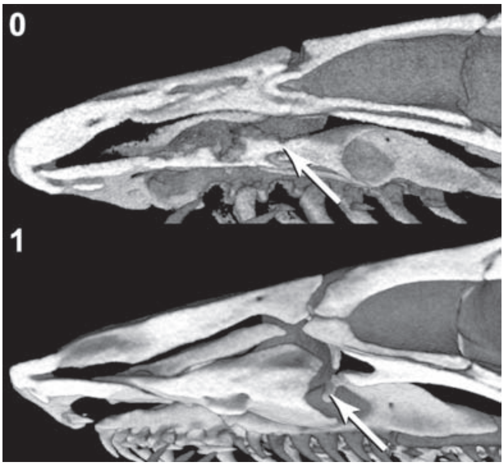
244. Infraorbital canal divides anteriorly in palatine^{N}: (0) single foramen anteriorly (*Elgaria multicarinata*, anterior close-up cutaway view of snout); (1) double anteriorly, with medial palatine ramus small and lateral large (*Cordylus mossambicus*, anterior close-up cutaway view of snout).



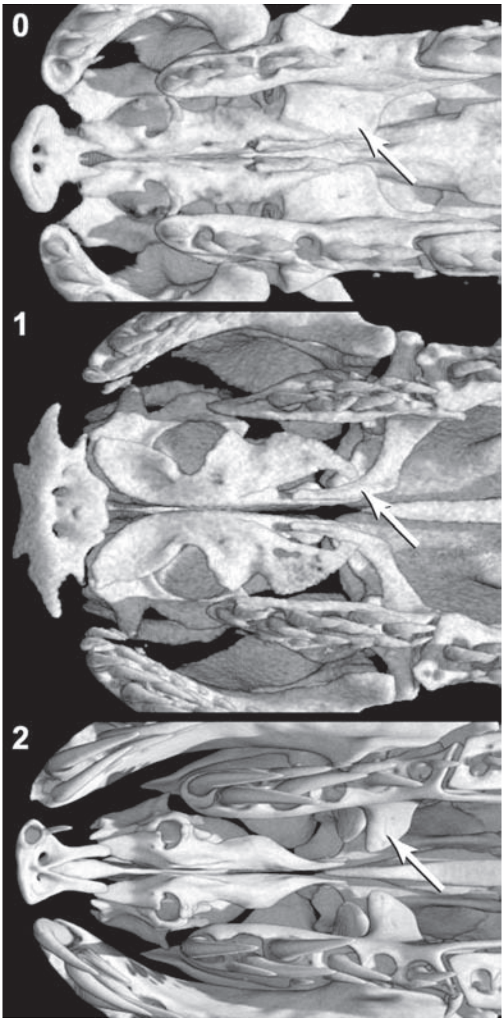
245. Infraorbital canal position: (0) lateral, between palatine and dorsal surface of supradental shelf of maxilla (*Chalarodon madagascariensis*, anterior close-up cutaway view of snout); (1) medial, entirely in palatine (*Tiliqua scincoides*, anterior close-up cutaway view of snout). de Queiroz (1987).



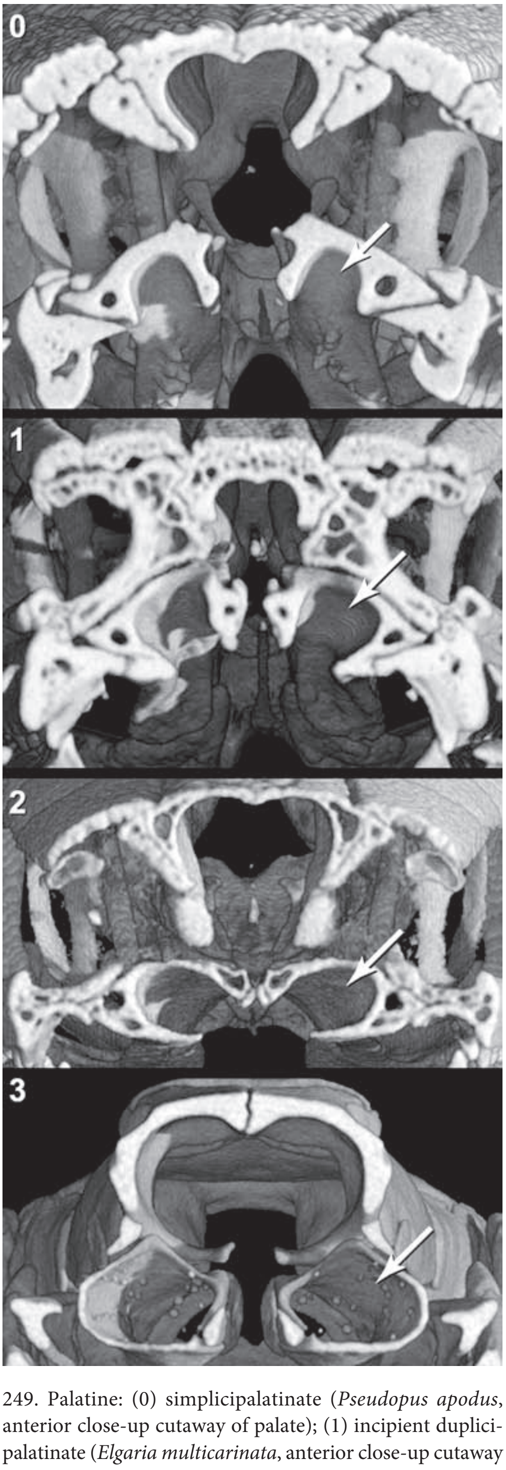
246. Palatine foramen^{N}: (0) absent (*Gambelia wislizenii*, anterior close-up cutaway view of snout); (1) present, enters palatine dorsally toward its anterior end to pass anteroventrolaterally into the infraorbital canal (*Liolaemus bellii*, anterior close-up cutaway view of snout).



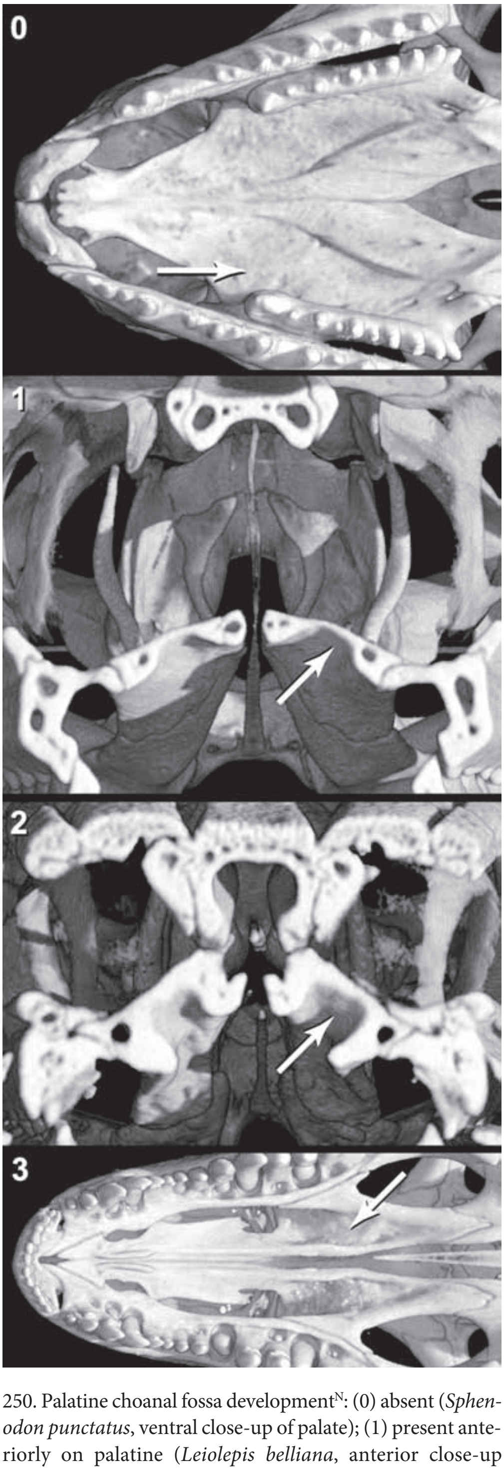
247. Palatine, choanal process: (0) curves medially and meets the vomer in a well-defined articular facet (*Uropeltis melanogaster*, lateral close-up cutaway view of snout); (1) touches or abuts the vomer without articulation, or remains separated from vomer (*Loxocemus bicolor*, lateral close-up cutaway view of snout). Tchernov et al. (2000).



248. Palatine, choanal process: (0) forms an extensive concave surface dorsal to the ductus nasopharyngeus (*Cylindrophis ruffus*, ventral close-up of palate); (0) narrows to form a curved finger-like process (*Exiliboa placata*, ventral close-up of palate); (2) forms a short vertical or horizontal lamina that does not reach the vomer (*Python molurus*, ventral close-up of palate). Tchernov et al. (2000) (ordered).

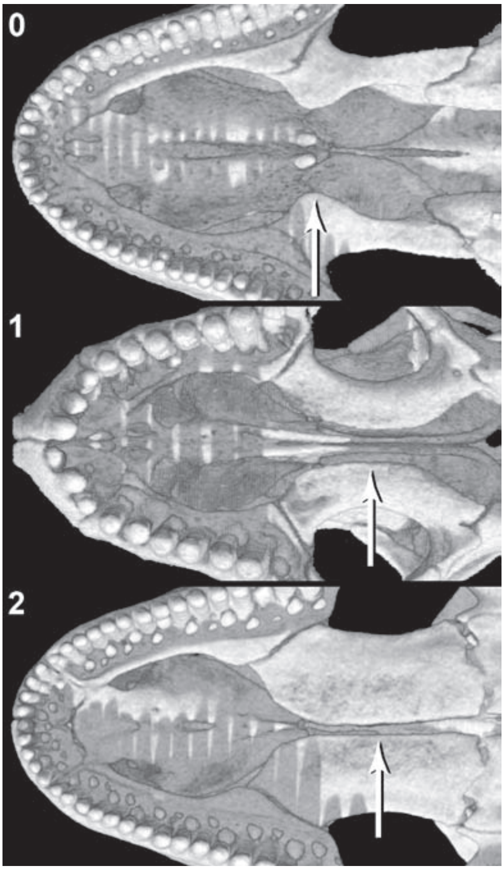


249. Palatine: (0) simplicipalatinate (*Pseudopus apodus*, anterior close-up cutaway of palate); (1) incipient duplicipalatinate (*Elgaria multicarinata*, anterior close-up cutaway of palate); (2) intermediate (*Plestiodon fasciatus*, anterior close-up cutaway of palate); (3) fully duplicipalatinate (*Anelytropsis papillosus*, anterior close-up cutaway of palate). Rieppel et al. (2008).



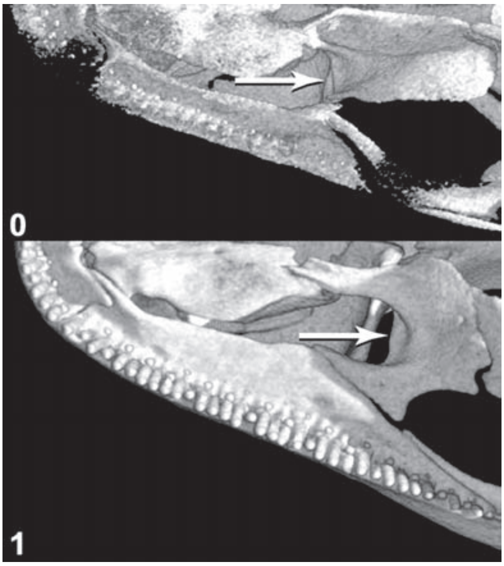
250. Palatine choanal fossa development^{N}: (0) absent (*Sphenodon punctatus*, ventral close-up of palate); (1) present anteriorly on palatine (*Leiolepis belliana*, anterior close-up cutaway view of snout); (2) extending about half way back on palatine (*Elgaria multicarinata*, anterior close-up cutaway view of snout); (3) fully developed to end of element (*Tupinambis teguixin*, ventral close-up of palate) (ordered).

Snakes that can be scored are given a 3 as they have a well-developed choanal fossa, although modification of the palatine precludes application of the state as defined in most snakes.

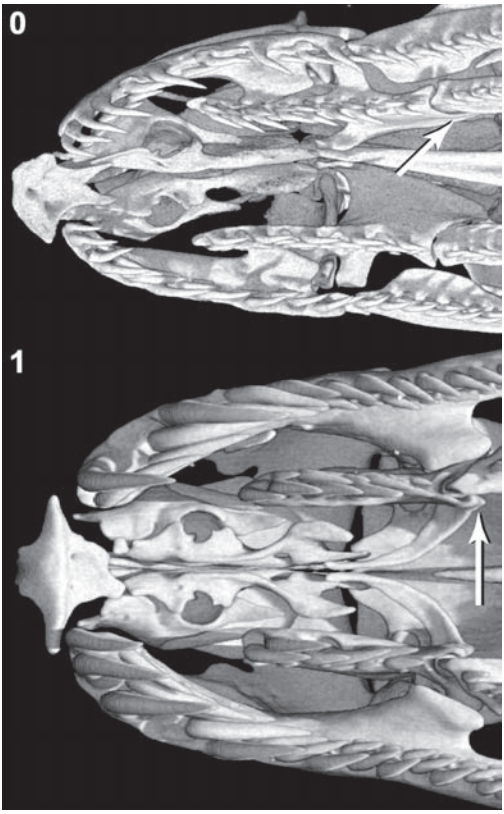


251. Palatine, subchoanal process medial edge shape in ventral view^N: (0) present only on anterior one-third of palatine (*Plestiodon fasciatus*, ventral close-up view of palate); (1) roughly arcuate (*Acontias percivali*, ventral close-up view of palate); (2) roughly parasagittal (*Sphenomorphus solomonis*, ventral close-up view of palate) (ordered).

This character assesses the anteroposterior extent of character 249, which describes how closely the palatine subchoanal processes approach on the midline.



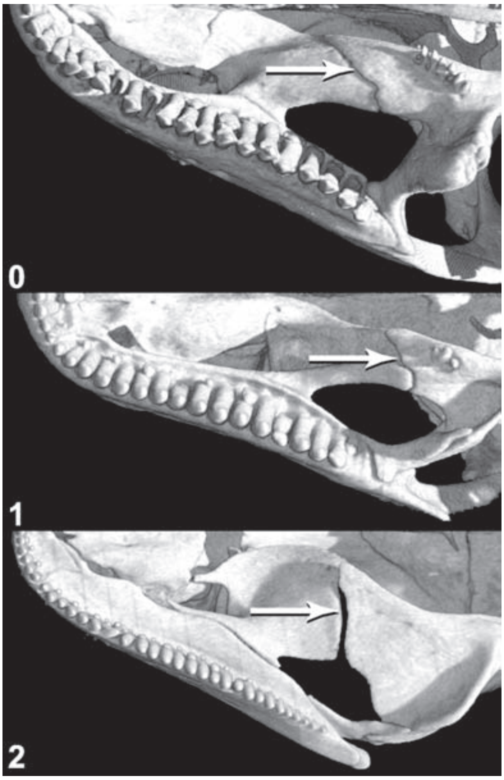
252. Palatine, posterior emargination of anterodorsal margin of choanal fossa^N: (0) anterior to anteroposterior midpoint of palatine-maxilla suture (*Delma borea*, ventral close-up of palate); (1) extends posterior to anteroposterior midpoint of palatine-maxilla suture (*Eublepharis macularius*, ventral close-up of palate).



253. Posteromedial process of palatine: (0) long, overlaps at least two pterygoid teeth (*Casarea dussumieri*, ventral close-

up of palate); (1) short, overlaps no more than one pterygoid tooth (*Epicrates striatus*, ventral close-up of palate). Kluge (1993a).

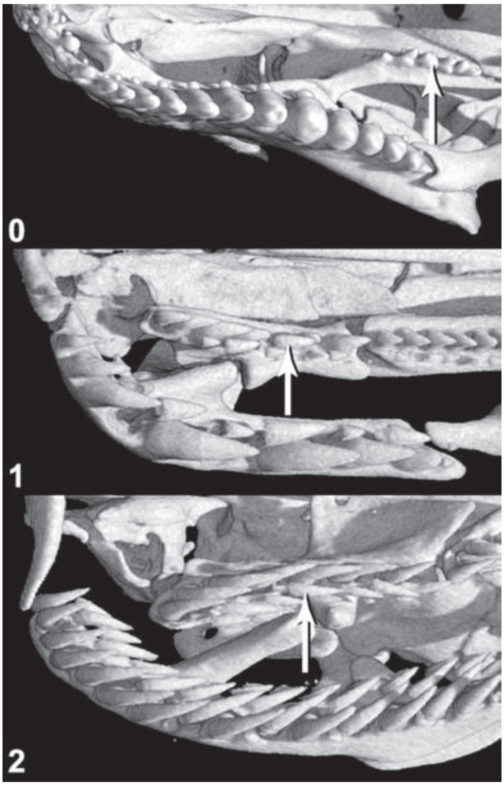
Uropeltis melanogaster, Calabaria reinhardtii and *Anomochilus leonardi* have no pterygoid teeth, but still have a long overlap and are accordingly scored 0.



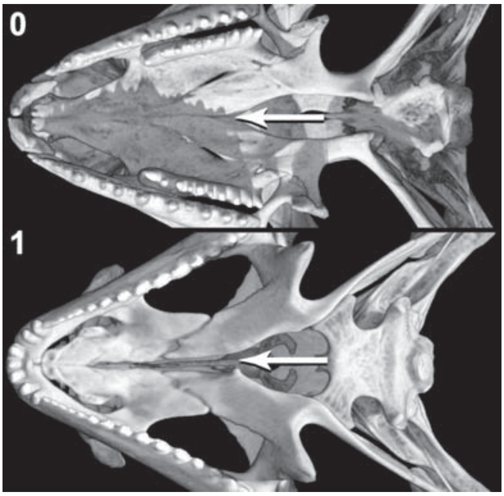
254. Palatine, shape of posterolateral margin at pterygoid suture^N: (0) unmodified (*Brachylophus fasciatus*, ventral close-up of palate); (1) palatine with discrete surface set off from choanal fold, extending along lateral margin from maxillary to pterygoid sutures (*Zonosaurus ornatus*, ventral close-up of palate); (2) transversely broad palatine at pterygo-palatine suture strongly restricts suborbital fenestra (*Teratoscincus przewalskii*, ventral close-up of palate).

This character tracks two separate transformations and is in any case coded incorrectly. State 1 is scored as present in all scincomorphs, but applies only to cordyliforms and scincids. State 2 arises inside gekkotans. These errors will have to be corrected in ensuing versions of this matrix.

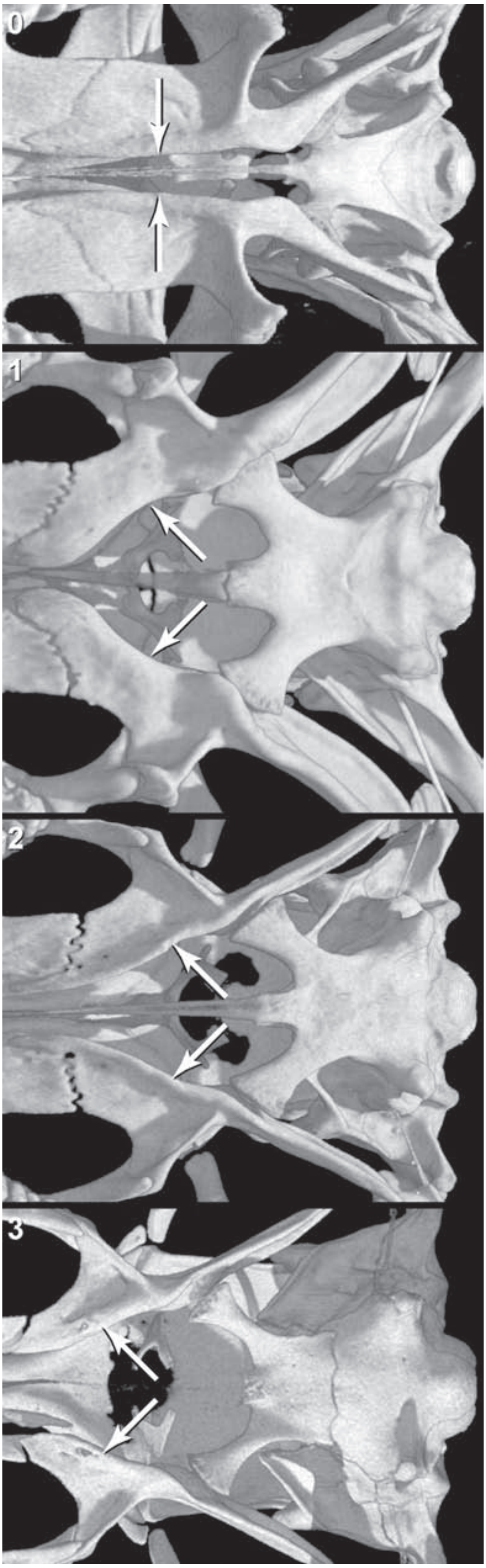
255. Palatine teeth: (0) present; (1) absent. Gauthier (1982).



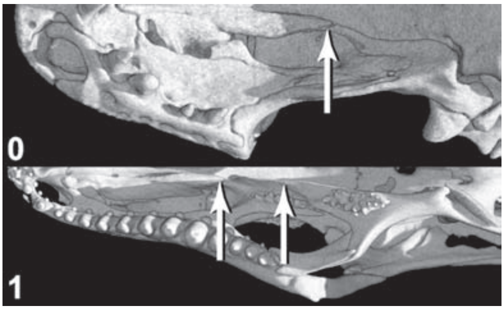
256. Palatine teeth size: (0) small conical denticles (*Pseudopus apodus*, ventral close-up of palate); (1) enlarged, but smaller than marginal teeth^N (*Anilius scytale*, ventral close-up of palate); (2) highly enlarged, similar in size to marginal teeth^N (*Acrochordus granulatus*, ventral close-up of palate). Lee (1998) (ordered).



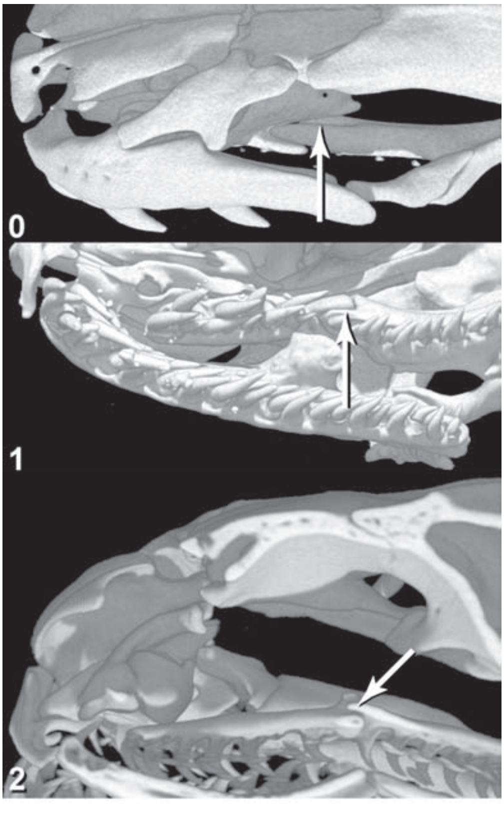
257. Pterygoids: (0) contacting each other (*Sphenodon punctatus*, ventral view of palate); (1) palatal rami fully separated (*Pogona vitticeps*, ventral view of palate). Estes et al. (1988).



258. Pterygoid separation on midline: (0)^{N} pterygoids narrowly separated for most of their length (*Calotes emma*, ventral veiw of palate); (1)^{N} broad at base, narrow anteriorly (*Sauromalus ater*, ventral view of palate); (2)^{N} broad at base, but not as narrowly separated anteriorly (*Uma scoparia*, ventral view of palate); (3)^{N} broad throughout length (*Liolaemus bellii*, ventral view of palate). Estes et al. (1988) (ordered).

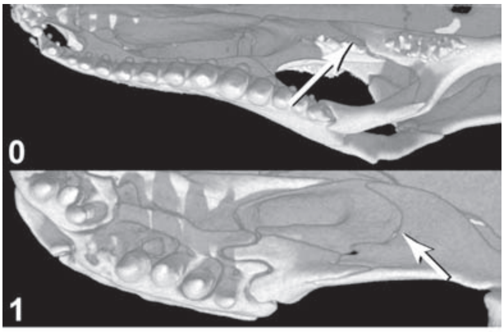


259. Pterygoid, palatine ramus: (0) contacts vomer (*Rhineura floridana*, ventral close-up of palate); (1) does not contact vomer (*Pseudopus apodus*, ventral close-up of palate). Gauthier, Estes and de Queiroz (1988).



260. Pterygoid-palatine joint; length of complex pattern of projections in snakes: (0) long (*Anilius scytale*, oblique dorsal close-up view of anterior skull); (1) medium (*Boa*

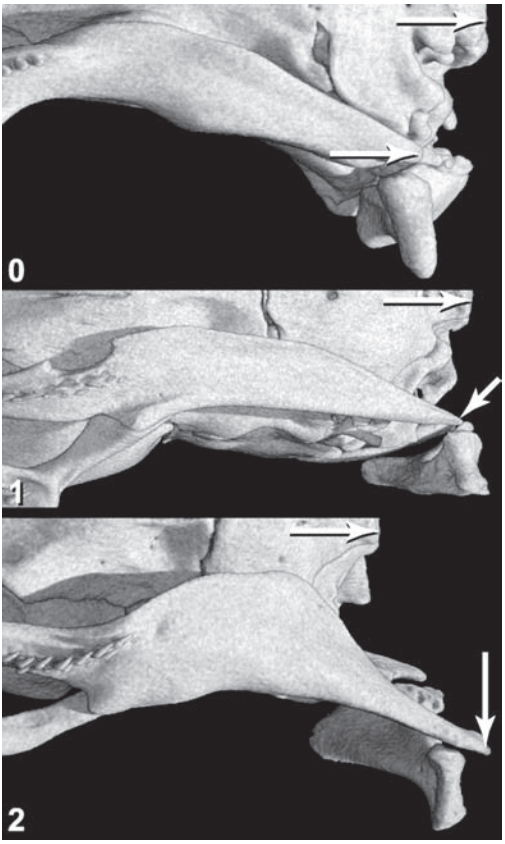
constrictor, ventral close-up view of anterior skull); (2) short (*Notechis scutatus*, lateral close-up cutaway view of anterior skull). Rieppel et al. (2002) (ordered).



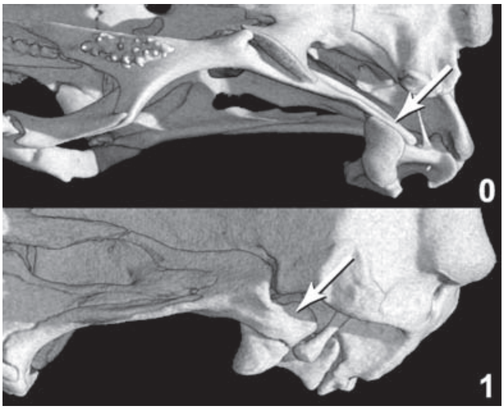
261. Pterygoid, palatine ramus clasps pterygoid ramus of palatine: (0) absent (*Pseudopus apodus*, ventral close-up of palate); (1) present (*Amphisbaena fuliginosa*, ventral close-up of palate). Wu et al. (1996).

This character corresponds to the lateral process of the palatine ramus of the pterygoid (absent or present). The palatine ramus of the pterygoid in *Feylinia polylepis* does not actually clasp the pterygoid ramus of the palatine, but the extensive lateral contact of the pterygoid with the palatine is here regarded to be state 1.

262. Pterygoid transverse process and ectopterygoid (pterygoideus muscle insertion) nearly as deep as mandible (at least 80% mandible depth), and ectopterygoid transversely broad, covering most of transverse process of pterygoid in anterior view$^{\mathrm{N}}$: (0) absent (*Gobinatus arenosus*, anterior close-up cutaway view of skull); (1) present (*Adamisaurus magnidentatus*, anterior close-up cutaway view of skull).



263. Pterygoid posterior extent$^{\mathrm{N}}$: (0) pterygoid does not reach level of occipital condyle (*Anilius scytale*, ventral close-up of posterior skull); (1) pterygoid reaches level of occipital condyle (*Casarea dussumieri*, ventral close-up of posterior skull); (2) pterygoid reaches well posterior to level of occipital condyle (*Tropidophis haetianus*, ventral close-up of posterior skull) (ordered).

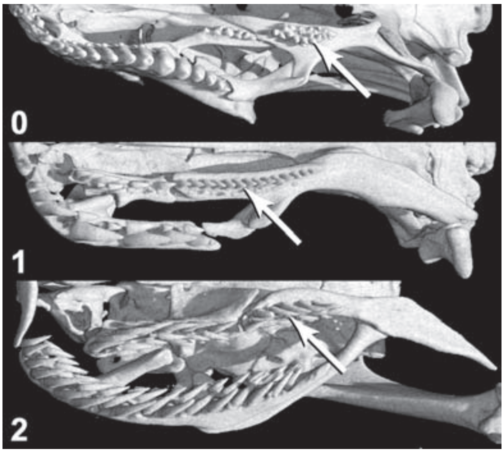


264. Pterygoid, quadrate ramus short and small, tightly wrapping around posteromedial (ventromedial if quadrate horizontally oriented) surface of quadrate: (0) absent (*Pseudopus apodus*, ventral close-up of posterior skull); (1) present (*Rhineura floridana*, ventral close-up of posterior skull). Wu et al. (1996).

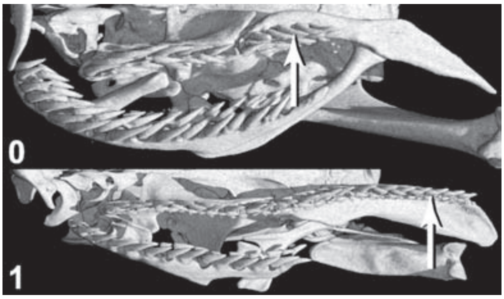
265. Pterygoid, quadrate ramus: (0) robust, rounded or triangular in cross-section, but without groove (*Cylindrophis ruffus*, ventral close-up of posterior skull); (1) blade-like and with distinct longitudinal groove for the insertion of the protractor pterygoidei muscle (*Coluber consrictor*, ventral close-up of posterior skull). Tchernov et al. (2000).

266. Pterygoid, ventral flange ("wing-shaped extension") of quadrate ramus ^{N}: (0) absent (*Sceloporus variabilis*, lateral view of skull); (1) present (*Chamaeleo laevigatus*, lateral view of skull).

267. Pterygoid teeth: (0) present; (1) absent. Pregill et al. (1986).

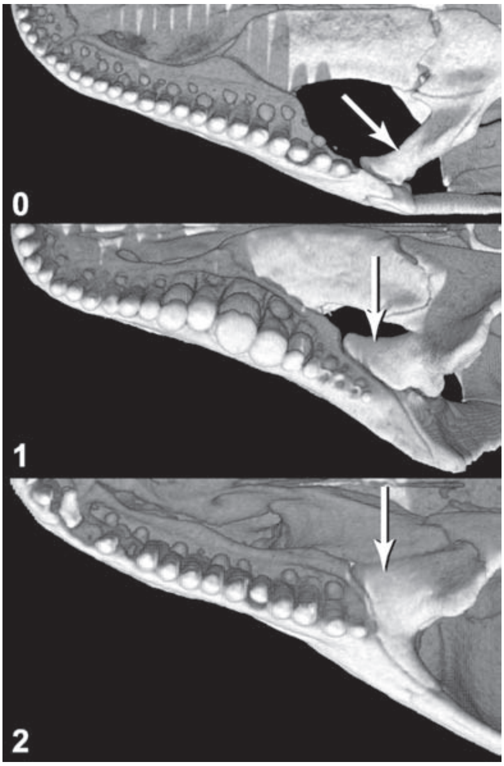


268. Pterygoid teeth: (0) small conical denticles (*Pseudopus apodus*, ventral view of skull); (1) enlarged, but smaller than marginal teeth^N (*Anilius scytale*, ventral view of skull); (2) highly enlarged, similar in size to marginal teeth^N (*Acrochordus granulatus*, ventral view of skull). Lee (1998) (ordered).

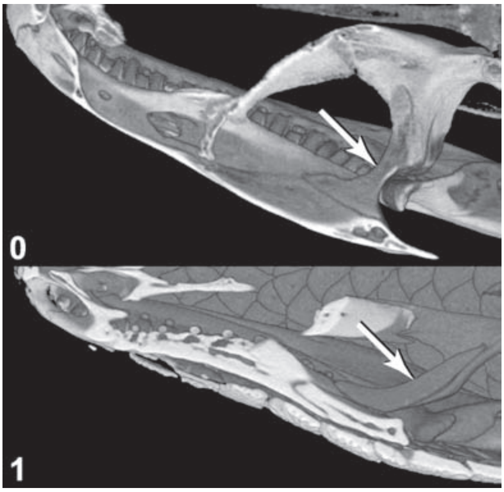


269. Pterygoid teeth: (0) restricted to palatal ramus of pterygoid (*Acrochordus granulatus*, ventral view of skull); (1) extend posteriorly onto quadrate ramus of pterygoid (*Coluber constrictor*, ventral view of skull). Mahler and Kearney (2006).

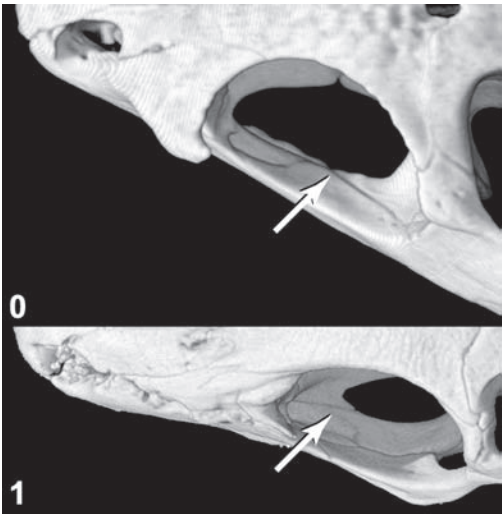
270. Ectopterygoid^N: (0) present; (1) absent.



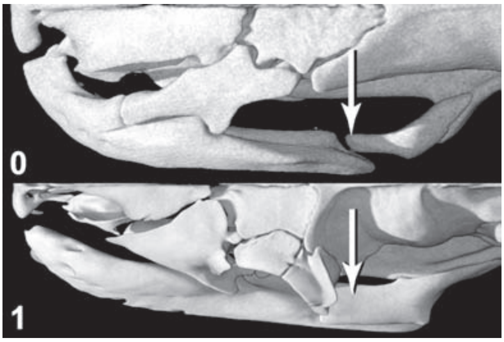
271. Ectopterygoid size and restriction of suborbital fenestra: (0) ectopterygoid relatively slender, fenestra widely open (*Sphenomorphus solomonis*, ventral close-up of palate); (1) ectopterygoid enlarged medially, restricting suborbital fenestra (*Tiliqua scincoides*, ventral close-up of palate); (2) ectopterygoid highly enlarged medially, closing suborbital fenestra (*Lepidophyma flavimaculatum*, ventral close-up of palate). Estes et al. (1988) (ordered).



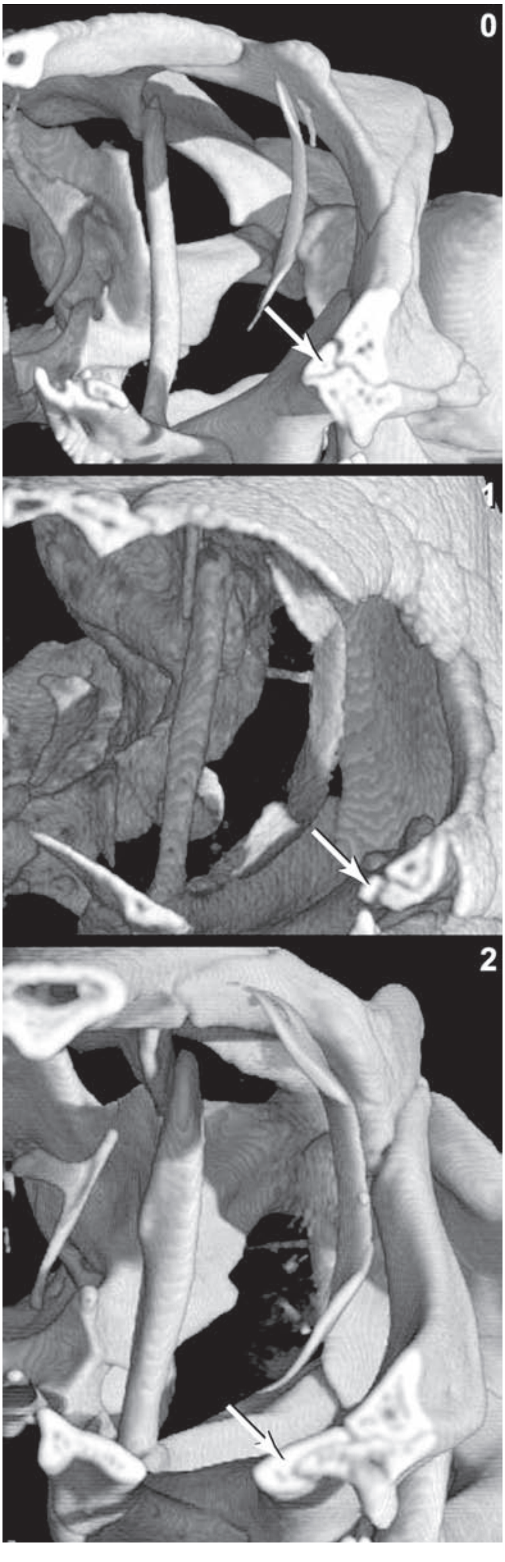
272. Ectopterygoid angulation in dorsal view: (0) nearly orthogonal (*Uranoscodon superciliosus*, dorsal close-up cutaway view of snout); (1) obtuse angle (including crescentic curve) (*Pseudopus apodus*, dorsal close-up cutaway view of snout). Smith (2009b).

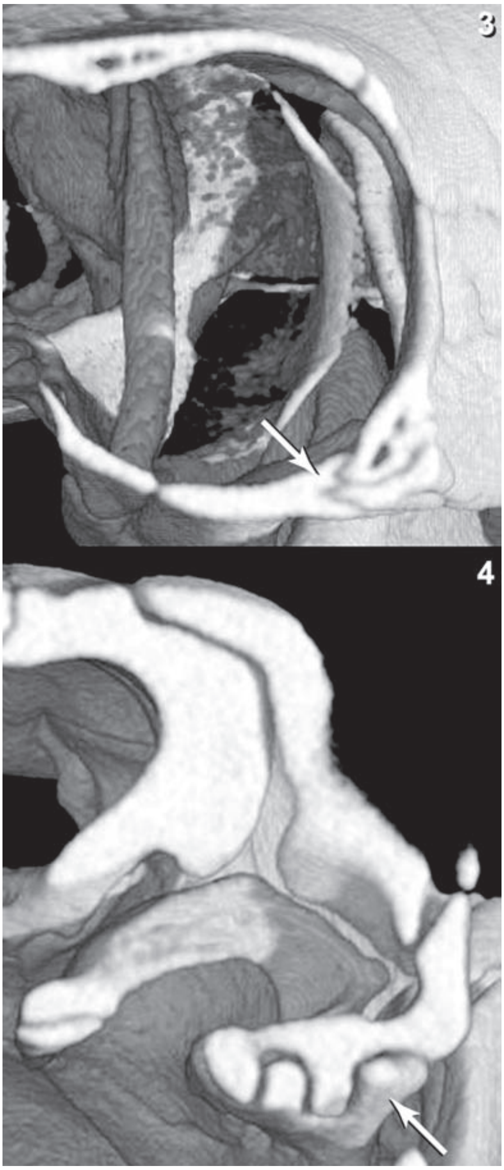


273. Ectopterygoid anterior length: (0) well separated from palatine above maxilla (*Pogona vitticeps*, dorsal close-up of anterior skull); (1) near to or in contact with palatine (*Tupinambis teguixin*, dorsal close-up of anterior skull). Estes et al. (1988).



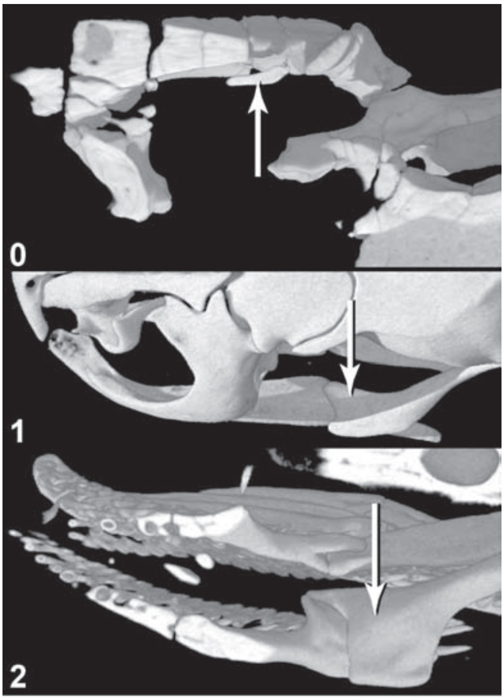
274. Anterior end of ectopterygoid: (0) restricted to posteromedial edge of maxilla (*Anilius scytale*, dorsal close-up of anterior skull); (1) located dorsal to maxilla, invading the dorsal surface of the maxilla to variable degrees (*Python molurus*, dorsal close-up of anterior skull). Tchernov et al. (2000).



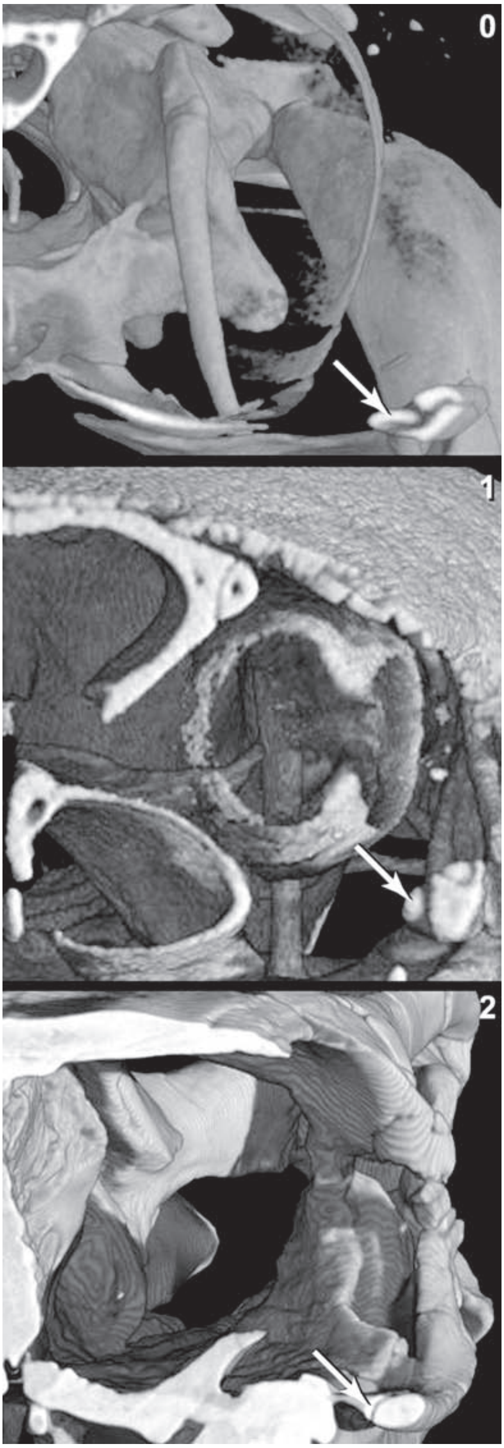


275. Ectopterygoid-maxilla suture: (0) ectopterygoid lies dorsally along supradental shelf of maxilla (*Crotaphytus collaris*, anterior close-up cutaway view of orbit); (1)^N ectopterygoid abuts posteromedial corner of maxilla (*Plestiodon fasciatus*, anterior close-up cutaway view of orbit); (2) ectopterygoid with slot laterally clasping maxilla (*Tupinambis teguixin*, anterior close-up cutaway view of orbit); (3)^N ectopterygoid overlapping maxilla more ventrally than dorsally (*Lepidophyma flavimaculatum*, anterior close-up cutaway view of orbit); (4)^N interdigitating suture, with maxilla at least partly overlapping ectopterygoid dorsally (*Amphisbaena fuliginosa*, anterior close-up cutaway view of orbit). Smith (2009b).

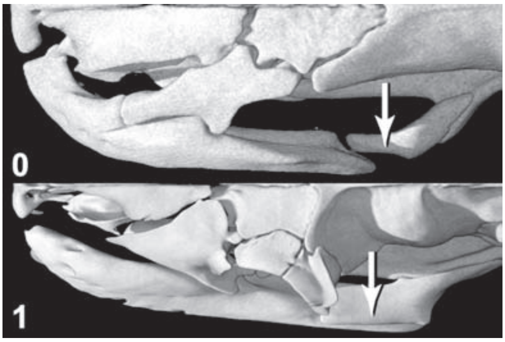
276. Ectopterygoid maxillary process shape in dorsal view$^{\mathrm{N}}$: (0) tapers or parallel-sided (*Anilius scytale*, dorsal close-up cutaway view of snout); (1) widens anteriorly (*Trachyboa boulengeri*, dorsal close-up cutaway view of snout); (2) to more than three times wider anteriorly relative to ectopterygoid shaft (*Lycophidion capense*, dorsal close-up cutaway view of snout) (ordered).



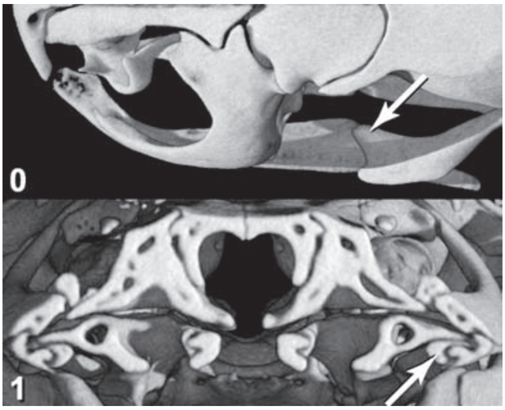
277. Ectopterygoid maxillary process anterior notch$^{\mathrm{N}}$: (0) tapers forward of maxilla contact (*Dinilysia patagonica*, dorsal dorsal close-up cutaway view of snout); (1) notched anteriorly (*Xenopeltis unicolor*, dorsal close-up cutaway view of anterior skull); (2) with large, rectangular, lateral ramus produced directly laterally (*Xenocrophis piscator*, dorsal close-up cutaway view of anterior skull) (ordered).



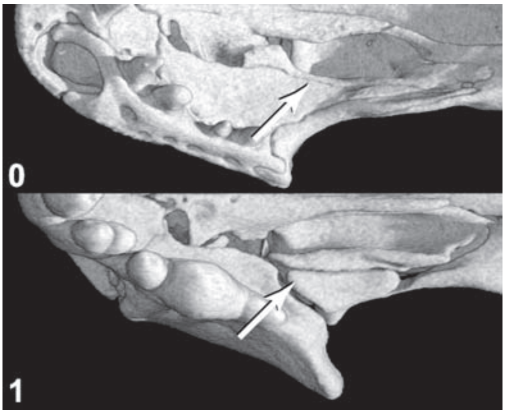
278. Ectopterygoid-maxilla posterior process suture$^{\mathrm{N}}$: (0) ectopterygoid medial and mainly dorsal to maxilla (*Teratoscincus przewalskii*, anterior close-up cutaway view of orbit); (1) ectopterygoid abuts maxilla on posteromedial edge only (*Brachymeles gracilis*, anterior close-up cutaway view of orbit); (2) ectopterygoid contacts jugal only (*Plotosaurus bennisoni*, anterior close-up cutaway view of orbit) (note that state 1 in this series is redundant with 275[1]).



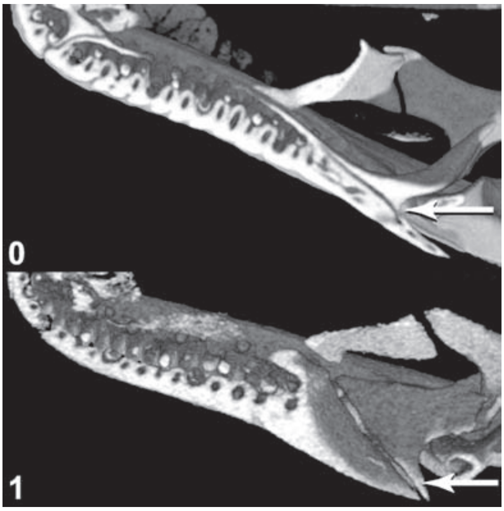
279. Lateral edge of maxillary ramus of ectopterygoid: (0) slopes medially (*Anilius scytale*, dorsal close-up of anterior skull); (1) straight (*Python molurus*, dorsal close-up of anterior skull). Tchernov et al. (2000).



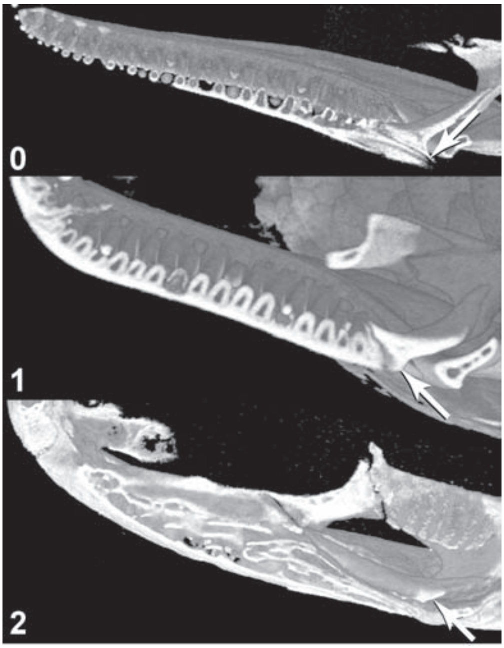
280. Ectopterygoid, prefrontal and palatine relations^N: (0) ectopterygoid does not underlap palatine posteriorly below prefrontal (*Xenopeltis unicolor*, dorsal close-up of anterior skull); (1) ectopterygoid underlaps palatine below prefrontal (*Lanthanotus borneensis*, anterior close-up cutaway view of snout).



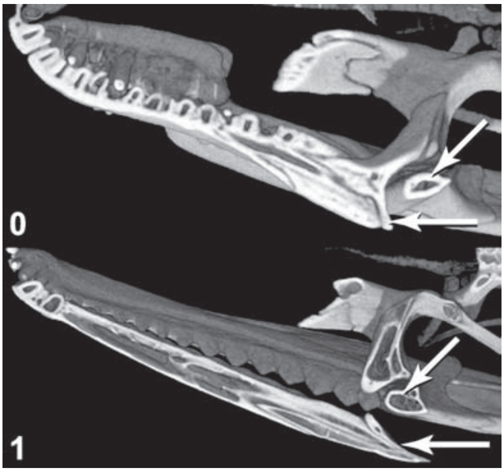
281. Ectopterygoid-palatine ventral articulation^N: (0) palatine-maxilla contact excludes ectopterygoid (*Rhineura floridana*, ventral close-up of palate); (1) ectopterygoid anterior process largely separates palatine from maxilla posteriorly (*Trogonophis weigmanni*, ventral close-up of palate).



282. Ectopterygoid hooked posterior process flat and exposed dorsally, ventrally and laterally^N: (0) absent (*Platysaurus imperator*, dorsal close-up cutaway view of anterior skull); (1) present (*Cricosaura typica*, dorsal close-up cutaway view of anterior skull).



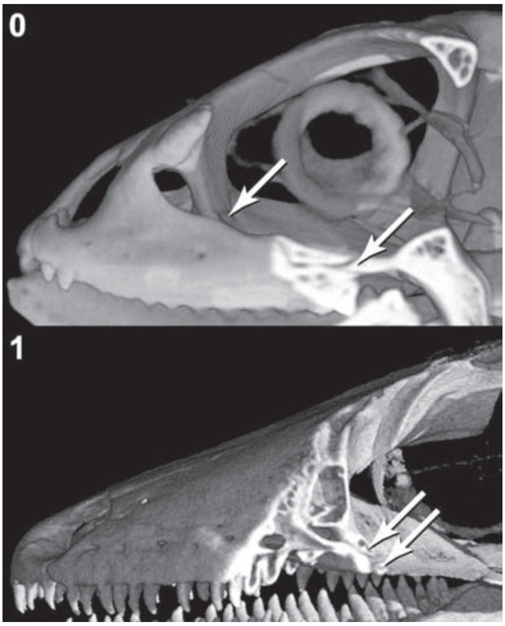
283. Ectopterygoid posterior process: (0) prominent (*Takydromus ocellatus*, dorsal close-up cutaway view of snout); (1)^N small lateral knob (*Zonosaurus ornatus*, dorsal close-up cutaway view of snout); (2) absent (*Strophurus ciliaris*, dorsal close-up cutaway view of snout) (ordered). Smith (2009b).



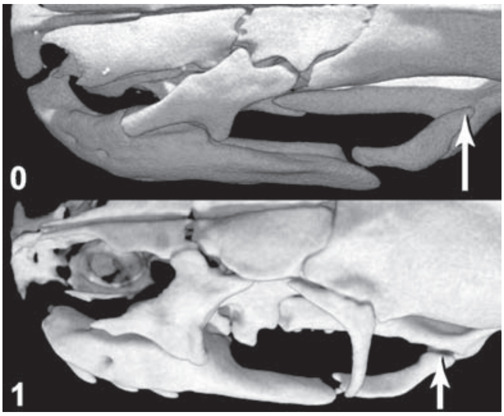
284. Ectopterygoid posterior process lengthens^{N}: (0) does not extend past coronoid apex (*Oplurus cyclurus*, dorsal close-up cutaway view of anterior skull); (1) extends past coronoid apex (*Physignathus cocincinus*, dorsal close-up cutaway view of anterior skull).

285. Ectopterygoid dorsal process height^{N}: (0) tall (*Pogona vitticeps*, anterior close-up cutaway view of orbit); (1) short

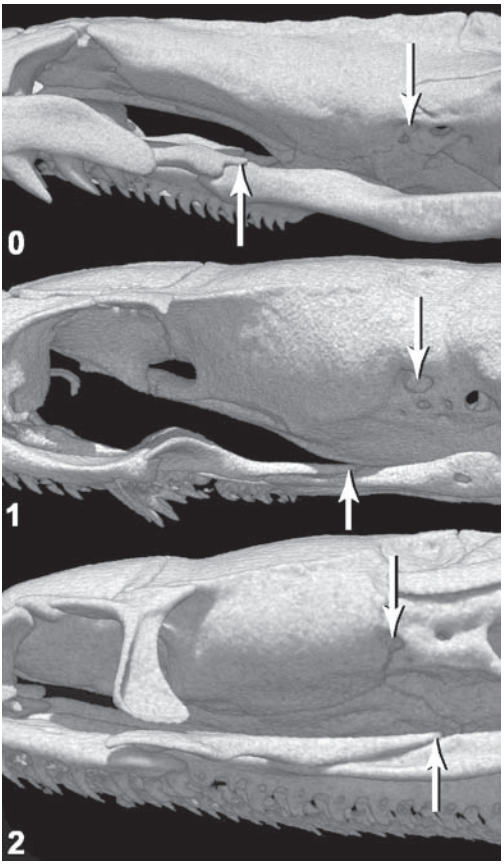
(*Basiliscus basiliscus*, anterior close-up cutaway view of orbit); (2) absent (not extending up medial face of jugal) (*Elgaria multicarinata*, anterior close-up cutaway view of orbit) (ordered).



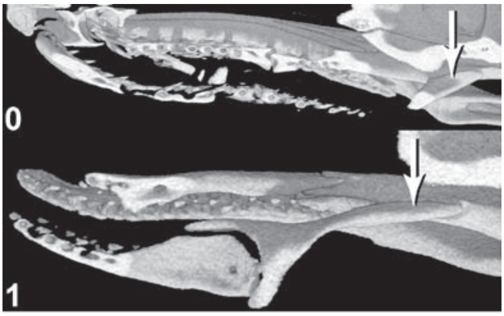
286. Ectopterygoid^{N}: (0) does not contact prefrontal (*Pogona vitticeps*, lateral close-up cutaway view of anterior skull); (1) contacts prefrontal at base of orbit (*Phelsuma lineata*, lateral close-up cutaway view of anterior skull).



287. Ectopterygoid-pterygoid contact: (0) predominantly dorsal (*Anilius scytale*, dorsal close-up of anterior skull); (1) predominantly lateral (*Ungaliophus continentalis*, dorsal close-up of anterior skull). Tchernov et al. (2000).

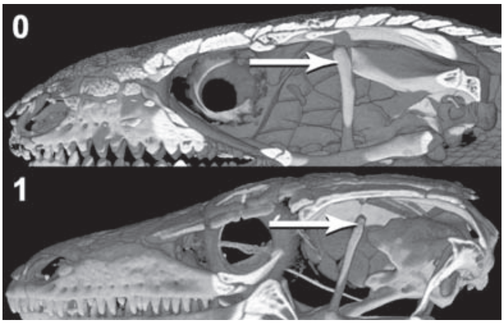


288. Ectopterygoid pterygoid process length^{N}: (0) short (*Anilius scytale*, lateral close-up of skull); (1) longer, but still anterior to trigeminal foramen (*Aparallactus werneri*, lateral close-up of skull); (2) longest, extending posterior to trigeminal foramen (*Xenodermus javanicus*, lateral close-up of skull) (ordered).



289. Ectopterygoid overlap of pterygoid^{N}: (0) short (*Uropeltis melanogaster*, dorsal close-up cutaway view of skull); (1) long (*Xenopeltis unicolor*, dorsal close-up cutaway view of skull).

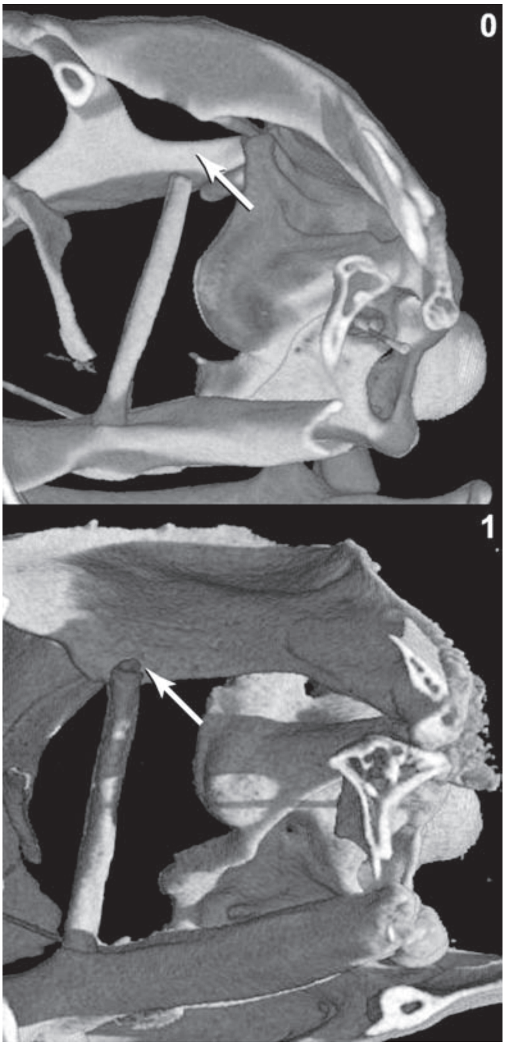
290. Epipterygoid: (0) present; (1) absent. Estes et al. (1988).



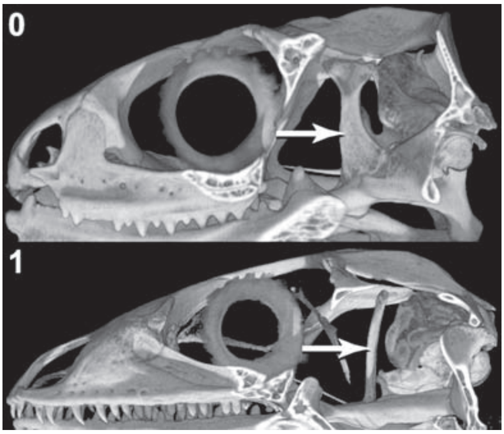
291. Epipterygoid, in resting position^{N}: (0) located lateral to prootic (even if only narrowly so) (*Pseudopus apodus*, lateral cutaway view of skull); (1) located entirely anterior to prootic (*Platysaurus imperator*, lateral cutaway view of skull).

292. Epipterygoid relative to alar process of prootic^{N}: (0) epipterygoid anterolateral to prootic alar process (*Gonatodes albogularis*, lateral close-up cutaway view of braincase); (1) epipterygoid abuts anteroventral tip of alar process (*Teratoscincus przewalskii*, lateral close-up cutaway view of braincase).

293. Epipterygoid shortens^{N}: (0) long (reaches nearly to level of top of braincase, or above quadrate head, or more than half distance between pterygoid and parietal table) (*Petrosaurus mearnsi*, lateral close-up cutaway view of braincase); (1) short (reaches only to level of quadrate head, barely to semicircular canal, or half or less of distance between pterygoid and parietal table) (*Phrynosoma platyrhinos*, lateral close-up cutaway view of braincase).

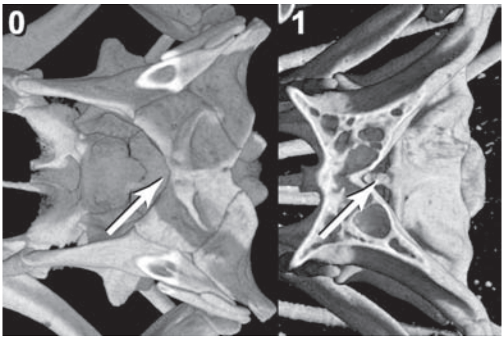


294. Epipterygoid-parietal contact^N: (0) absent (*Uma scoparia*, lateral close-up cutaway view of braincase); (1) overlaps parietal temporal muscle origin (*Anolis carolinensis*, lateral close-up cutaway view of braincase).

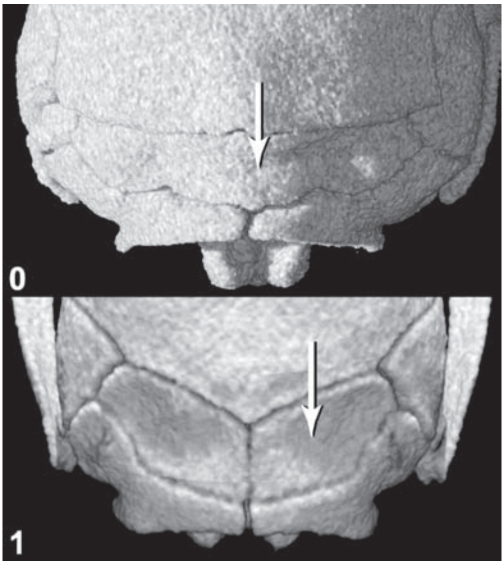


295. Epiptergyoid: (0) expanded dorsoventrally and ventrally (*Sphenodon punctatus*, lateral cutaway view of skull); (1) columelliform (*Pogona vitticeps*, lateral cutaway view of skull). Estes et al. (1988).

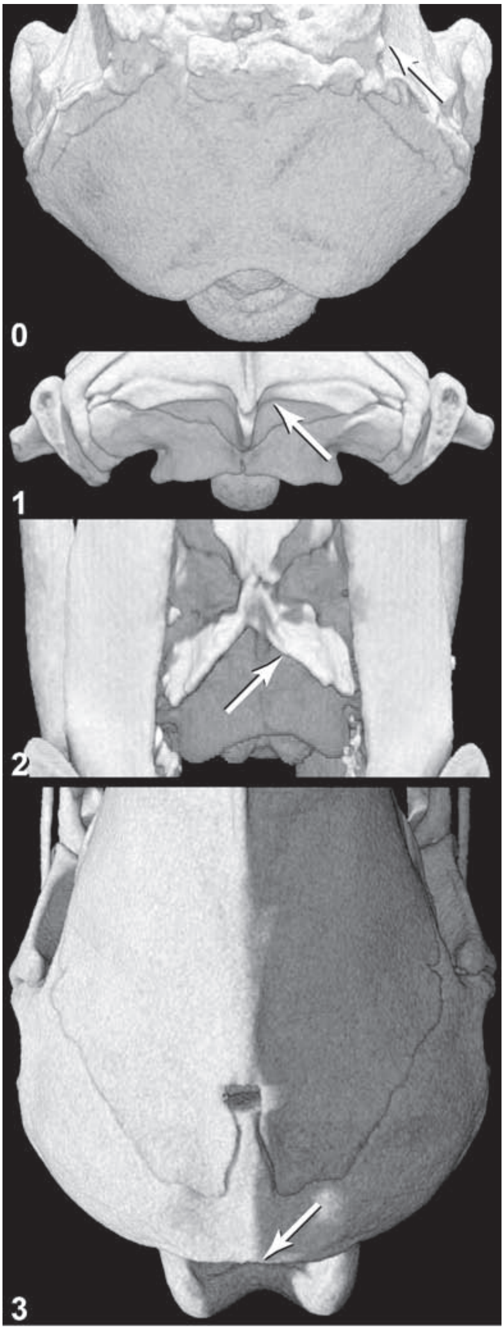
296. Braincase fusion: (0) unfused in adult; (1)^N opisthotic and prootic fused in adult; (2) complete braincase fusion in adult. Gauthier (1984).



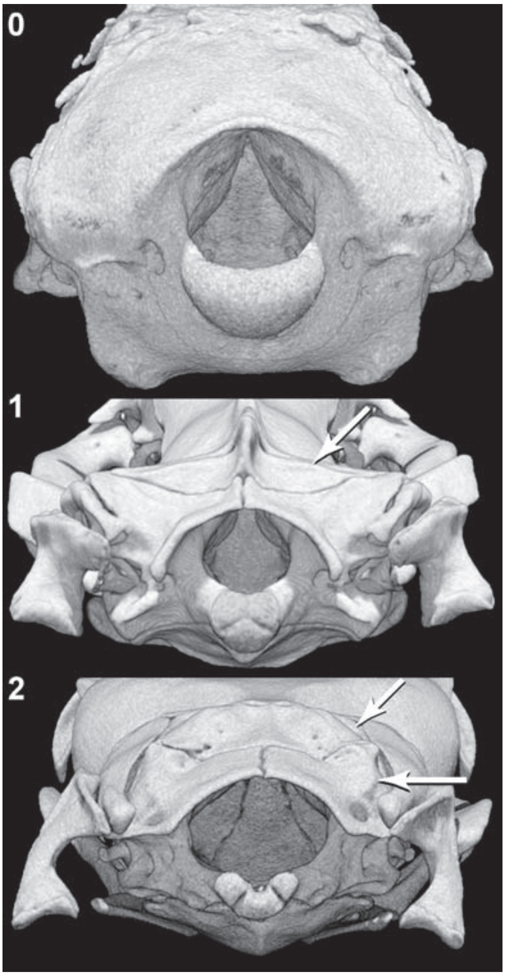
297. Processus ascendens of synotic tectum: (0) absent (*Eublepharis macularius*, dorsal close-up cutaway view of braincase); (1) present (*Enyalioides laticeps*, dorsal close-up cutaway view of braincase). Estes et al. (1988).



298. Supraoccipital: (0) single (*Anomochilus leonardi*, dorsal view of posterior skull); (1) double (*Leptotyphlops dulcis*, dorsal view of posterior skull). Estes et al. (1988).

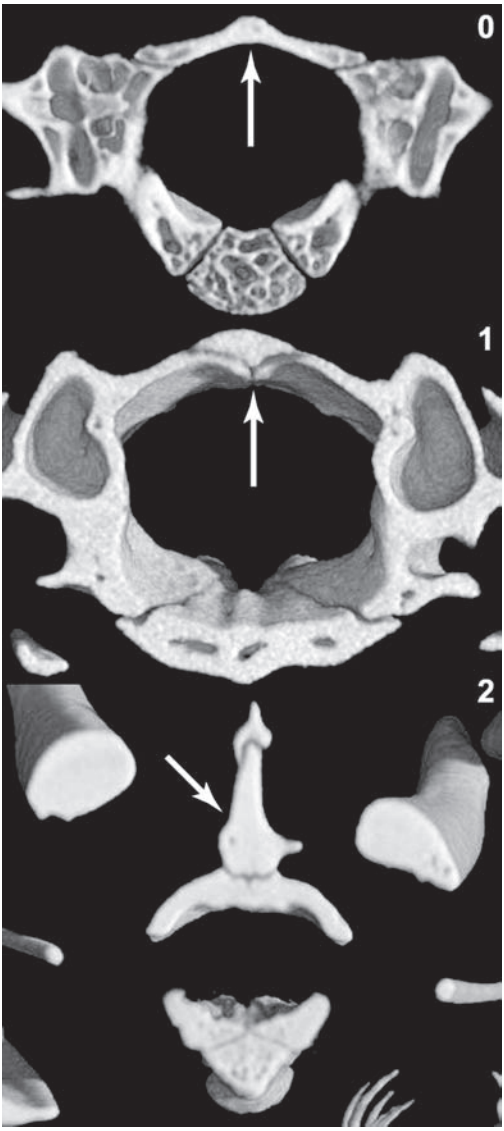


299. Supraoccipital origin of temporal muscles^{N}: (0) restricted to parietal (*Anniella pulchra*, dorsal close-up of posterior skull); (1) spread onto supraoccipital contacting nuchal crest in roughly T-shaped outline (*Cylindrophis ruffus*, dorsal close-up of posterior skull); (2) spread onto supraoccipital to form Y-shaped crest (*Thamnophis marcianus*, dorsal close-up of posterior skull); (3) temporal muscles spread onto braincase dorsally, but sagittal and nuchal crests join to form roughly anchor-shaped outline (*Geocalamus acutus*, dorsal close-up of posterior skull).

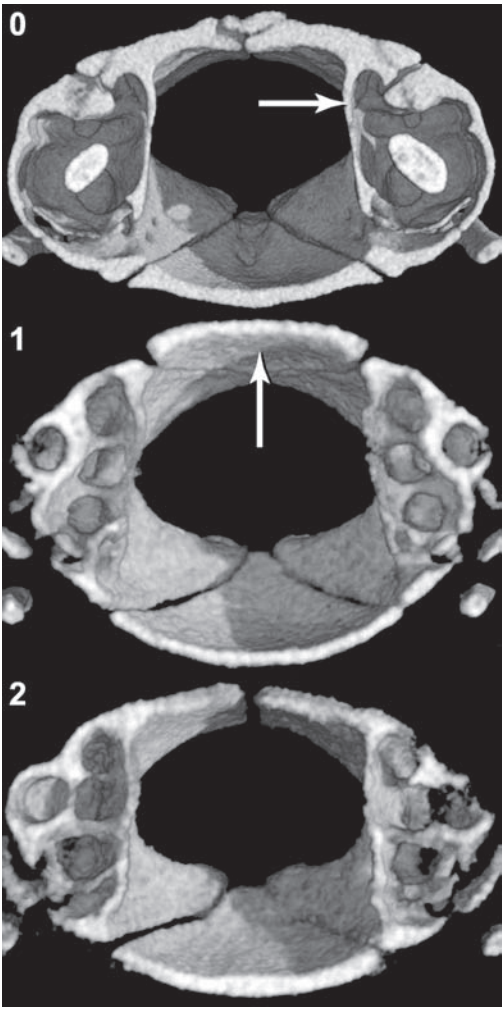


300. Supraoccipital nuchal crest lateral extent^{N}: (0) absent (*Anniella pulchra*, oblique posterior view of skull); (1) present on supraoccipital (*Cylindrophis ruffus*, oblique posterior view of skull); (2) present on supraoccipital and otoccipital (*Casarea dussumieri*, oblique posterior view of skull) (ordered).

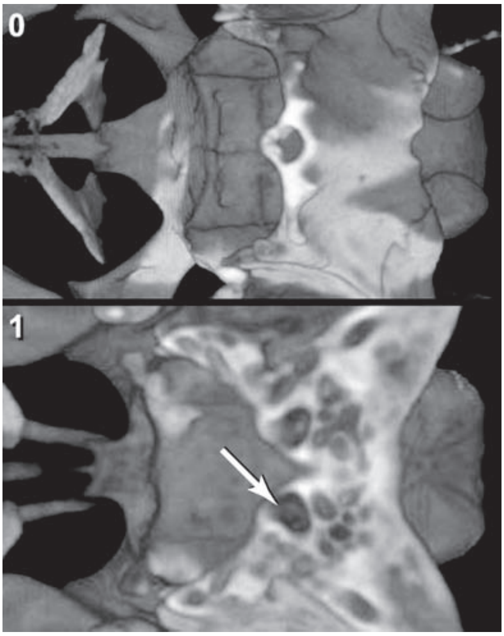
301. Supraoccipital crest: (0) absent (*Lanthanotus borneensis*, lateral close-up cutaway view of posterior skull); (1) present (*Lepidophyma flavimaculatum*, lateral close-up cutaway view of posterior skull), Estes et al. (1988); (2) meets ventral parietal (*Chamaeleo laevigatus*, lateral close-up cutaway view of posterior skull). Rieppel (1981) (ordered).



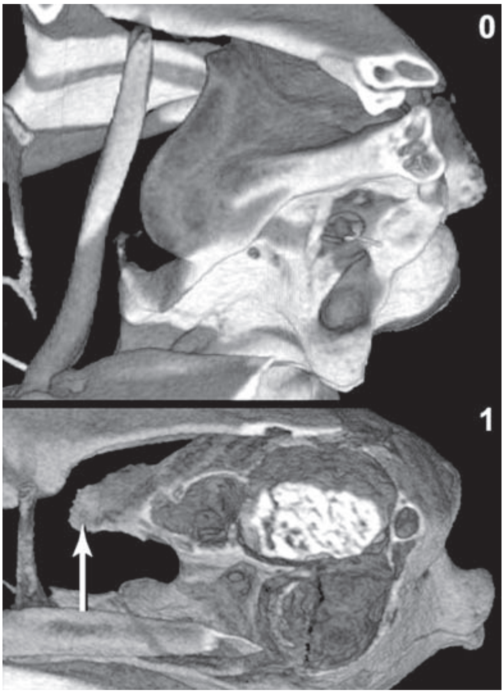
302. Supraoccipital relative to oto-occipital on midline: (0) overlaps oto-occipital laterally (*Physignathus cocincinus*, anterior close-up cutaway view of braincase; (1) laps over oto-occipital on midline as part of sagittal crest (*Casarea dussumieri*, anterior close-up cutaway view of braincase) Lee and Scanlon (2002); (2) that is, in turn, capped by the parietal, so that all three bones are visible in cross section (*Boa constrictor*, anterior close-up cutaway view of braincase). Kluge (1991) (ordered).



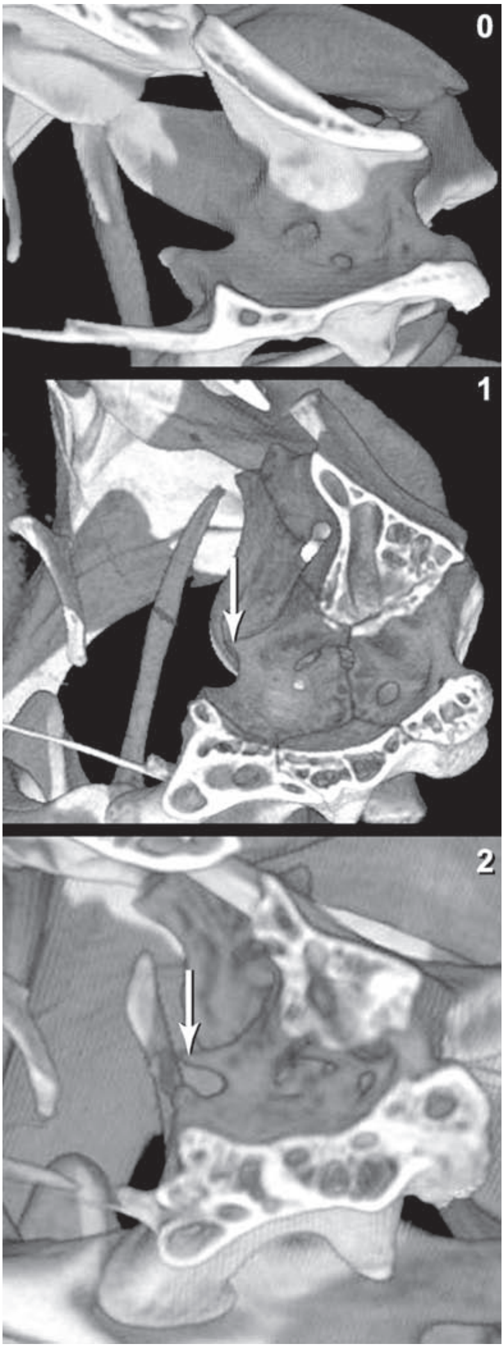
303. Supraoccipital contribution to internal sidewall of neurocranium^{N}: (0) participates in sidewall (*Typhlops jamaicensis*, anterior cutaway view of braincase); (1) absent, only dorsal plate remains (*Liotyphlops albirostris*, anterior cutaway view of braincase); (2) dorsal plate absent (*Typhlophis squamosus*, anterior cutaway view of braincase) (ordered).



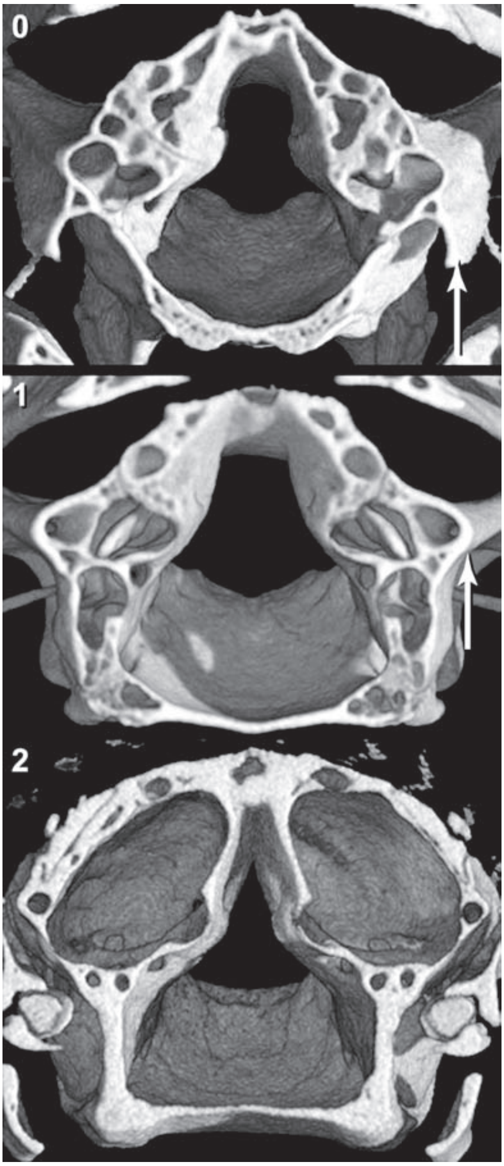
304. Epiotic foramen: (0) absent (*Uromastyx aegyptius*, dorsal close-up cutaway view of braincase); (1) present (*Pogona vitticeps*, dorsal close-up cutaway view of braincase). Moody (1980).



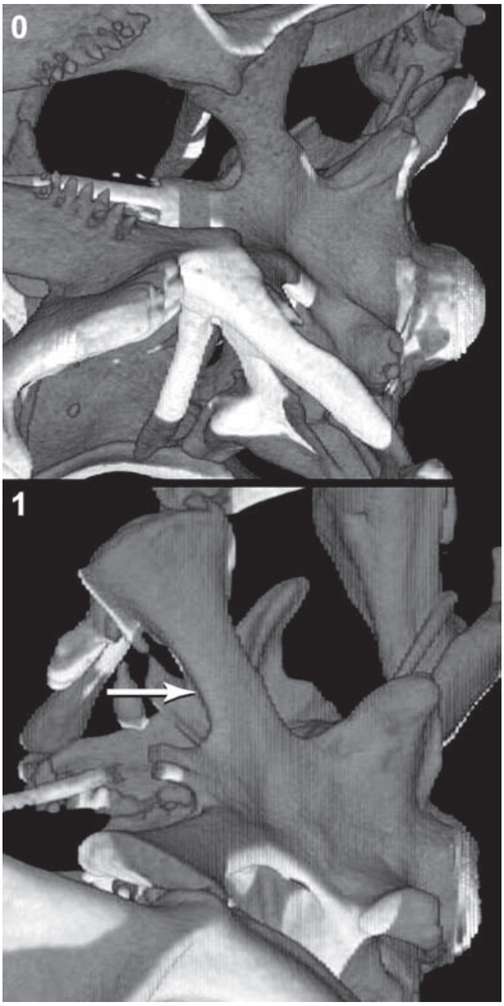
305. Prootic, alar process: (0) small or absent (*Dipsosaurus dorsalis*, lateral close-up cutaway view of braincase); (1) prominent (*Acontias percivali*, lateral close-up cutaway view of braincase). Gauthier (1982).



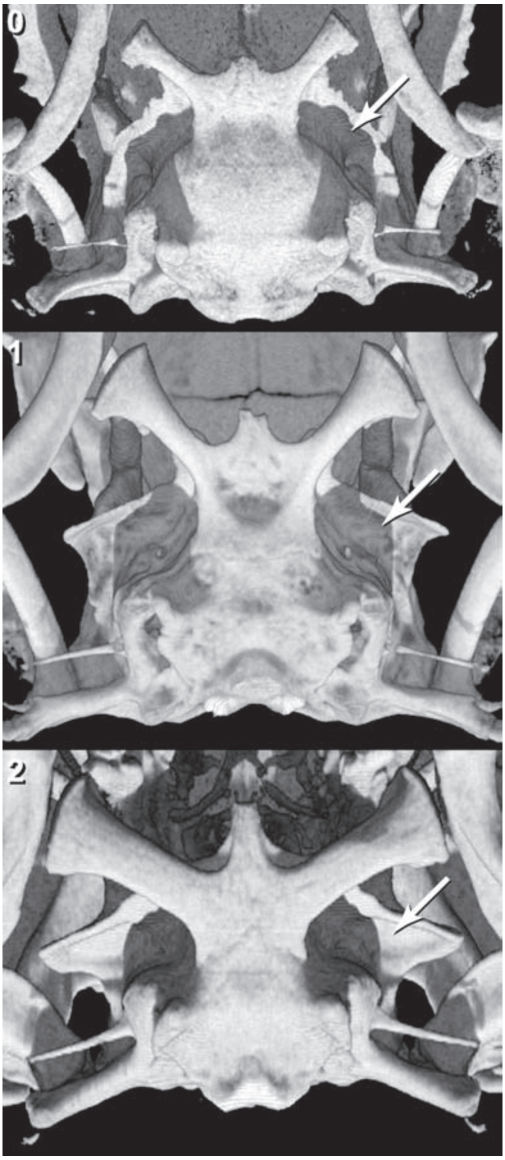
306. Prootic, supratrigeminal process: (0) absent (*Tupinambis teguixin*, lateral close-up cutaway view of braincase); (1) weakly developed, not projecting beyond cupola anterior (*Physignathus cocincinus*, lateral close-up cutaway view of braincase), Moody (1980); (2) present as a finger-like projection above trigeminal notch, projecting beyond cupola anterior (*Pogona vitticeps*, lateral close-up cutaway view of braincase). Estes et al. (1988) (ordered).



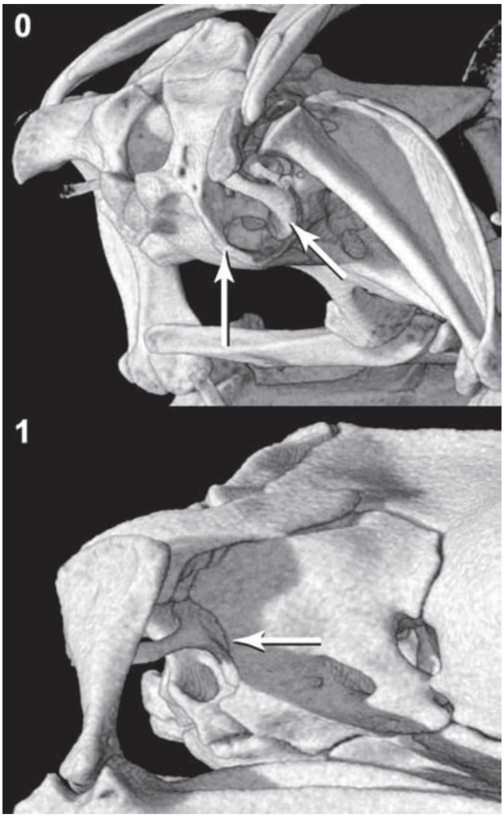
307. Crista prootica (ridge on lateral surface of the prootic, overhanging facial foramen): (0) well-developed lateral flange (*Callopistes maculatus*, anterior close-up cutaway view of braincase); (1) reduced to weak ridge (*Varanus acanthurus*, anterior close-up cutaway view of braincase); (2) absent (*Anniella pulchra*, anterior close-up cutaway view of braincase). Presch (1988). This character should be (ordered), but was not so designated in the dataset.



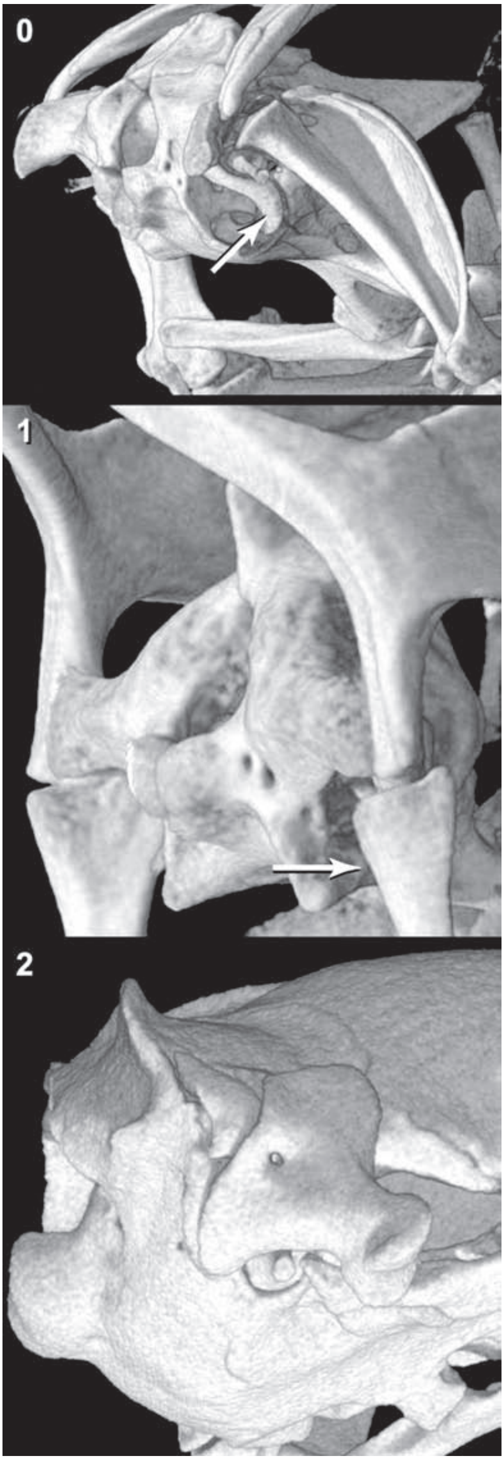
308. Crista prootica: (0) does not extend onto basipterygoid process (*Brachylophus fasciatus*, oblique ventral close-up of braincase); (1) extends onto basipterygoid process forming open or closed bony canal (*Gekko gecko*, ventral close-up of braincase). Estes et al. (1988).



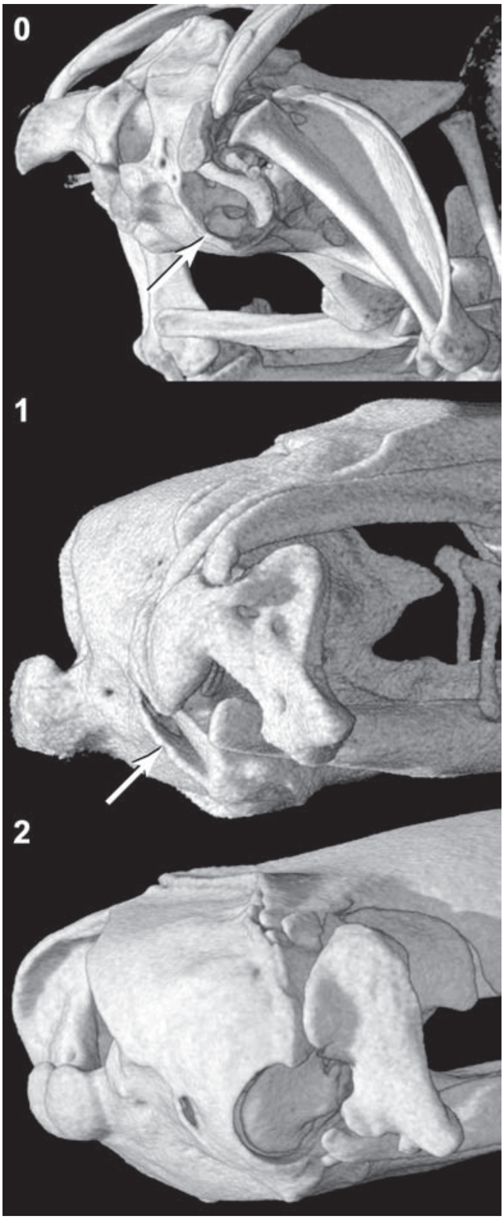
309. Crista prootica aliform in outline in ventral view (extended butterfly shape): (0) absent (*Phelsuma lineata*, ventral view of braincase); (1) present (*Teratoscincus przewalskii*, ventral view of braincase); (2)$^{\mathrm{N}}$ prominent, extending further laterally (*Saltuarius cornutus*, ventral view of braincase). Estes et al. (1988) (ordered).



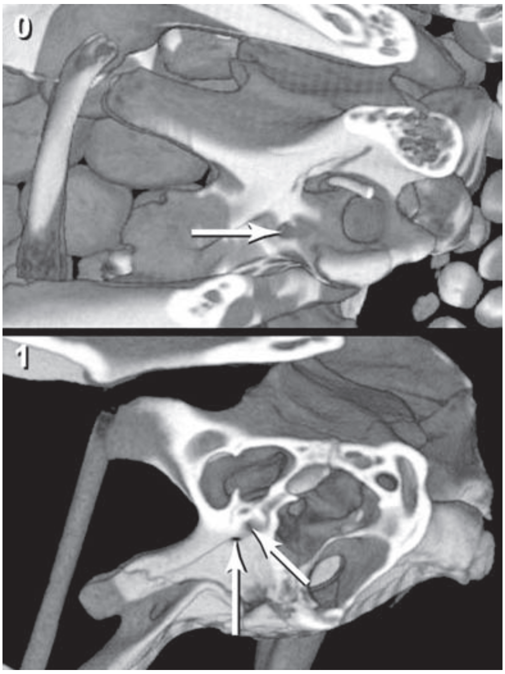
310. Crista tuberalis and crista prootica: (0) separate (*Eublepharis macularius*, oblique lateral close-up of braincase); (1) combined to surround stapedial footplate and lateral aperture of recessus scalae tympani (*Exiliboa placata*, lateral close-up of braincase). Estes et al. (1988).



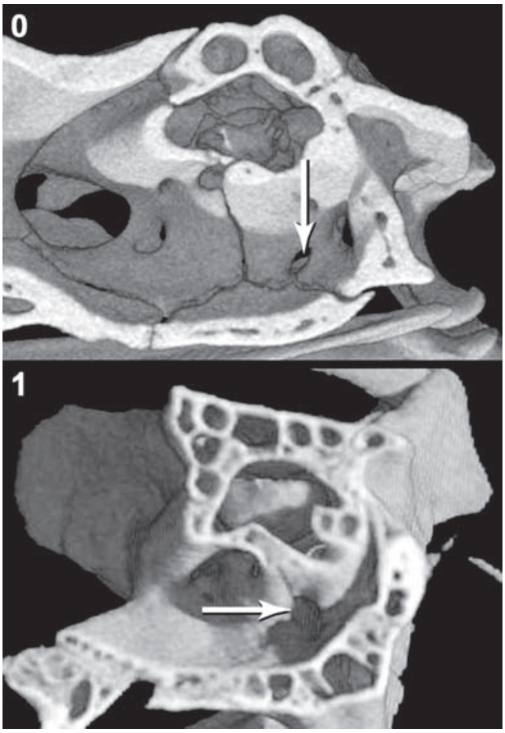
311. Crista interfenestralis: (0) prominent (*Eublepharis macularius*, oblique lateral close-up of braincase); (1) reduced (*Chamaeleo laevigatus*, oblique lateral close-up of braincase) Rieppel (1981); (2) absent^{N} (*Bipes biporus*, oblique lateral close-up of braincase). Rieppel (1984a) (ordered).



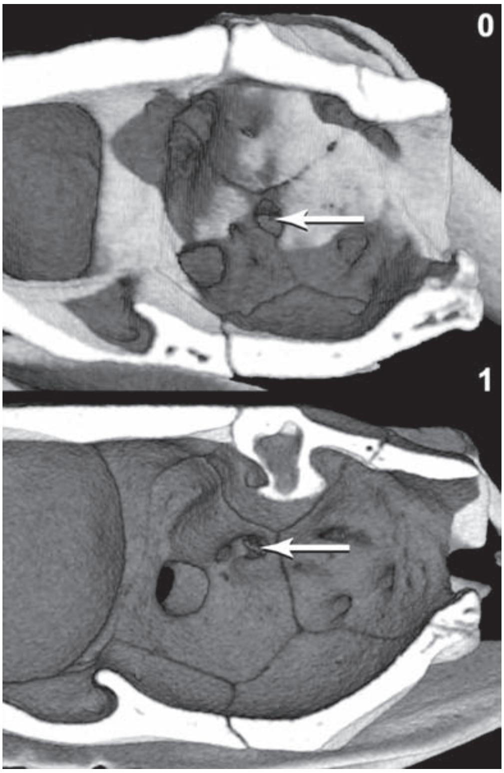
312. Crista tuberalis: (0) prominent (*Eublepharis macularius*, oblique lateral close-up of braincase); (1) reduced (*Feylinia polylepis*, oblique lateral close-up of braincase); (2) absent (*Anelytropsis papillosus*, oblique lateral close-up of braincase). Rieppel (1984a) (ordered).



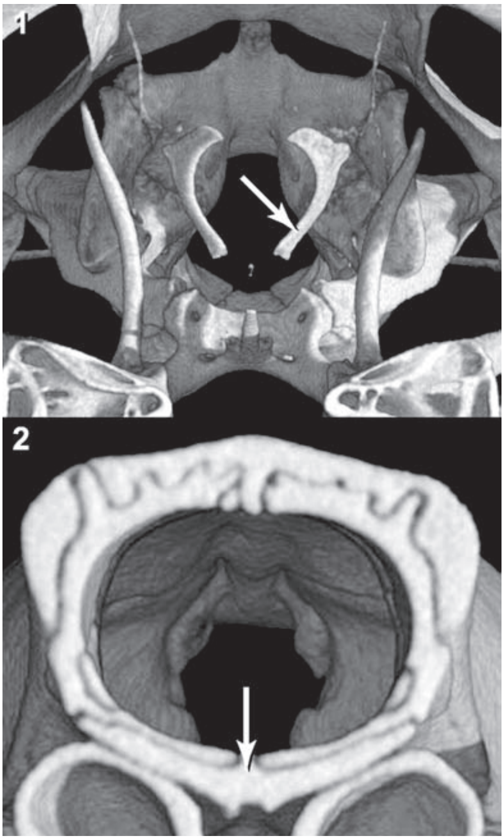
313. Facial foramen (lateral exit on prootic for the facial or VII cranial nerve): (0) single (*Heloderma horridum*, lateral close-up cutaway view of braincase); (1) double (*Varanus acanthurus*, lateral close-up cutaway view of braincase). Lee (1998).



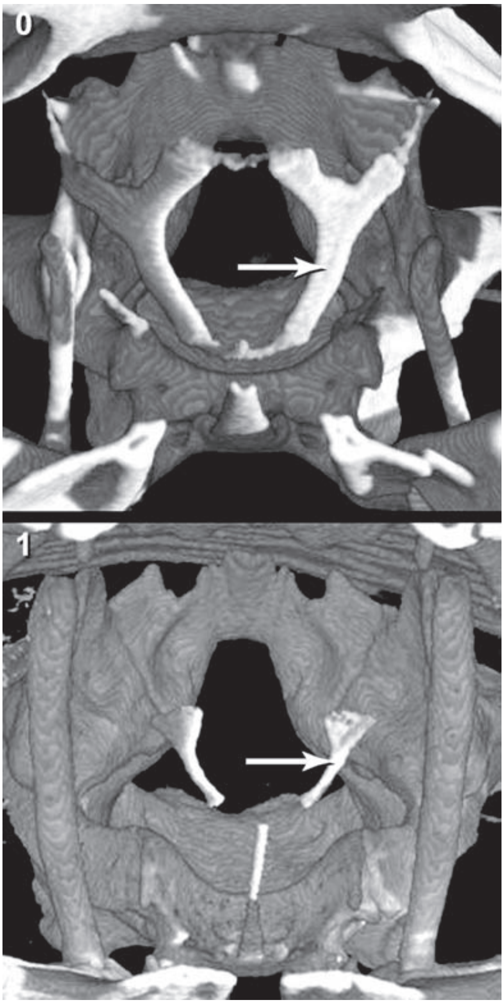
314. Prootic participates in medial aperture of the recessus scala tympani (MARST): (0) absent (*Casarea dussumieri*, lateral close-up cutaway view of braincase); (1) prootic forms part of MARST (*Callopistes maculatus*, lateral close-up cutaway view of braincase). Gauthier and Bell (unpubl. data).



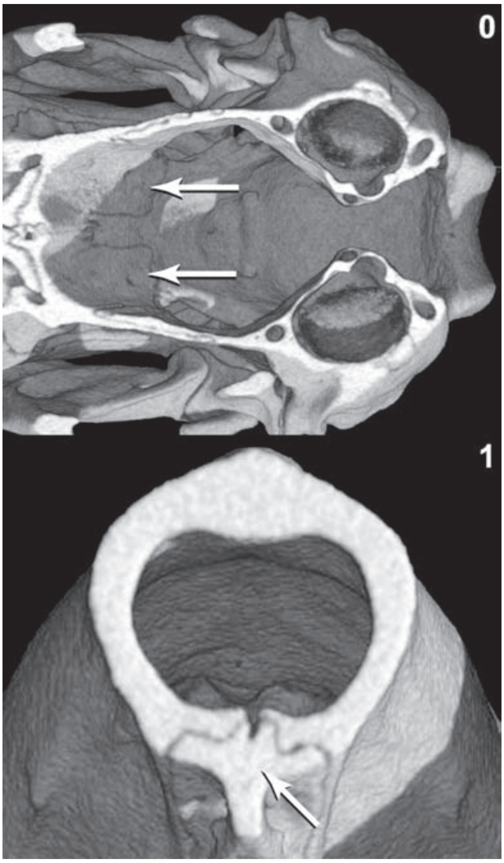
315. Posterior auditory foramen^{N}: (0) bordered by opisthotic (=oto-occipital) posteromedially (*Acrochordus granulatus*, lateral close-up cutaway view of braincase); (1) enclosed entirely in prootic (*Azemiops feae*, lateral close-up cutaway view of braincase).



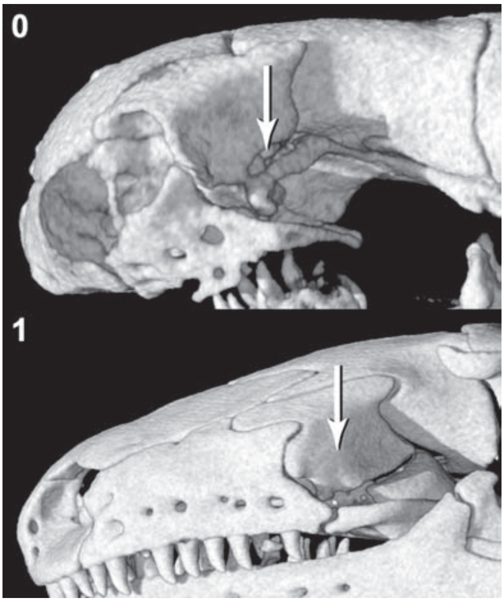
316. Orbitosphenoid, calcified/ossified: (0) absent; (1) present (*Physignathus cocincinus*, anterior close-up cutaway view of braincase); (2) expanded to floor the braincase (*Amphisbaena fuliginosa*, anterior close-up cutaway view of braincase). Wu et al. (1996) (ordered).



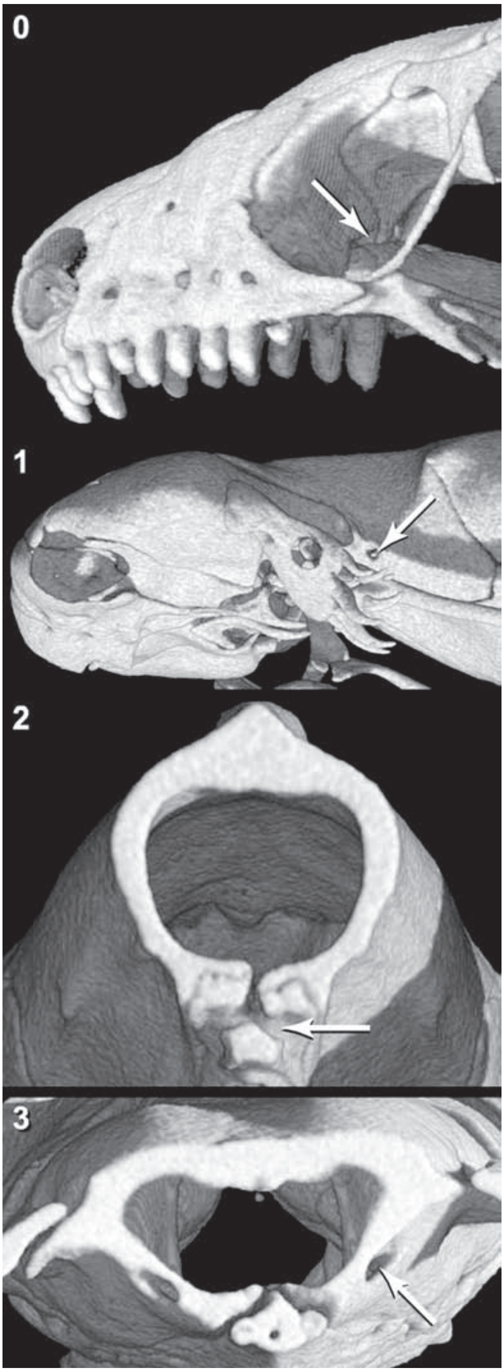
317. Orbitosphenoid^{N}: (0) well developed (*Agama agama*, anterior close-up cutaway view of braincase); (1) reduced (*Celestus enneagrammus*, anterior close-up cutaway view of braincase).



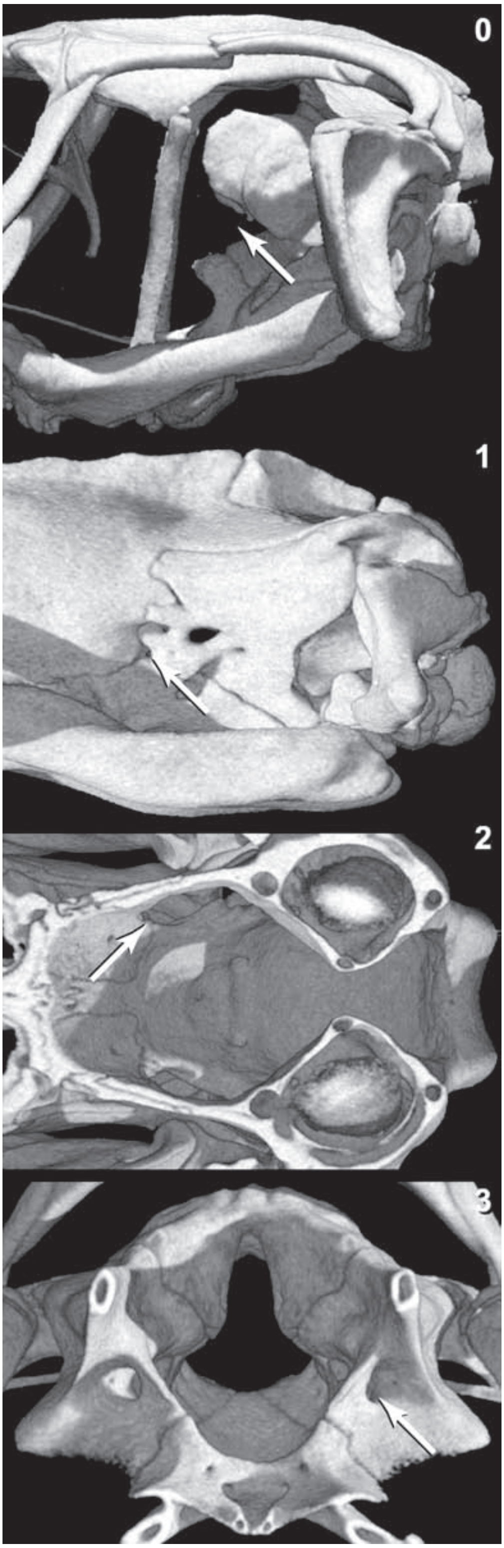
318. Orbitosphenoid^{N}: (0) paired (*Rhineura floridana*, dorsal close-up cutaway view of braincase); (1) single (fused ventrally) (*Trogonophis weigmanni*, anterior close-up cutaway view of braincase).



319. Optic foramen: (0) present (*Leptotyphlops dulcis*, lateral close-up of anterior skull); (1) absent (*Anelytropsis papillosus*, lateral close-up of anterior skull). Rieppel (1984b).

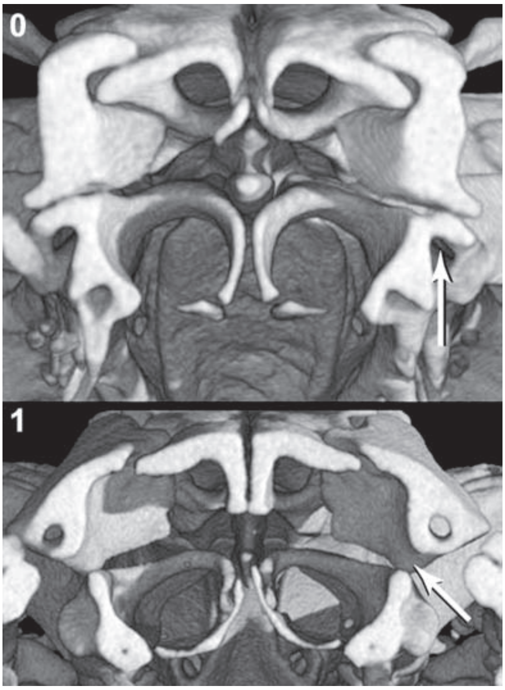


320. Optic foramen: (0) not fully enclosed by bone (*Acontias percivali*, lateral close-up of anterior skull); (1) enclosed partly or entirely by frontals (*Typhlops jamaicensis*, oblique lateral close-up of anterior skull); (2) entirely within orbitosphenoid (*Trogonophis weigmanni*, anterior cutaway close-up view of orbit); (3) entirely within parietal (*Acrochordus granulatus*, anterior cutaway close-up view of orbit). Wu et al. (1996).

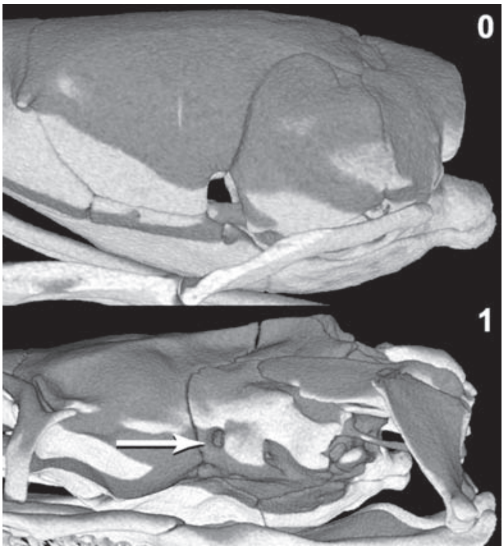


321. Trigeminal foramen or foramina: (0) anterior margin not enclosed in bone (*Callopistes maculatus*, lateral close-up of braincase); (1) anterior margin enclosed by descend-

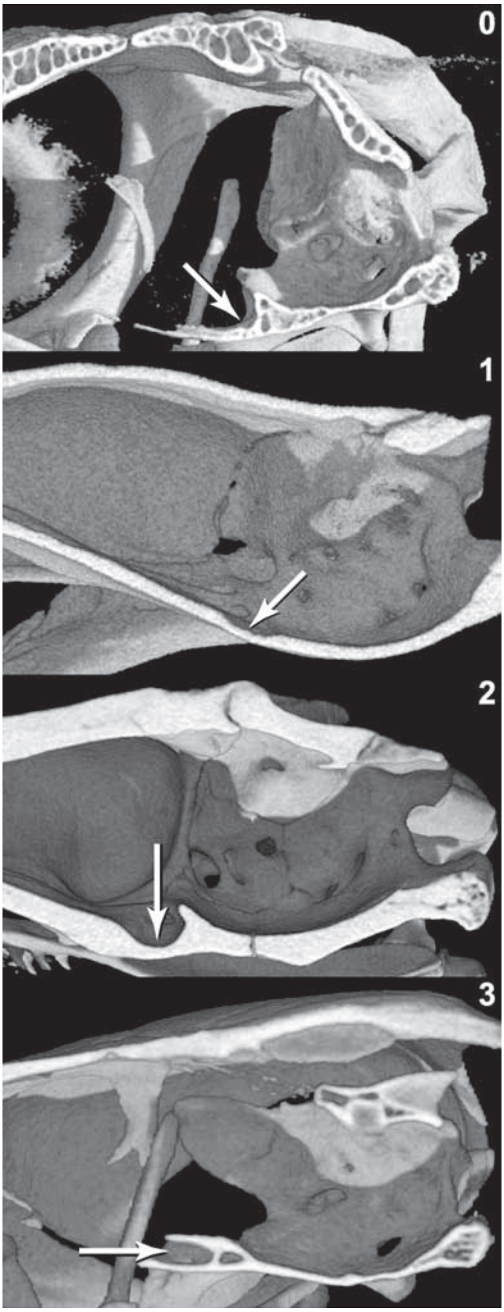
ing flange of parietal (*Anilius scytale*, lateral close-up of braincase); (2) anterior margin enclosed by orbitosphenoid (*Rhineura floridana*, dorsal close-up cutaway of braincase); (3) enclosed by prootic (*Eublepharis macularius*, anterior close-up cutaway of braincase). Wu et al. (1996).



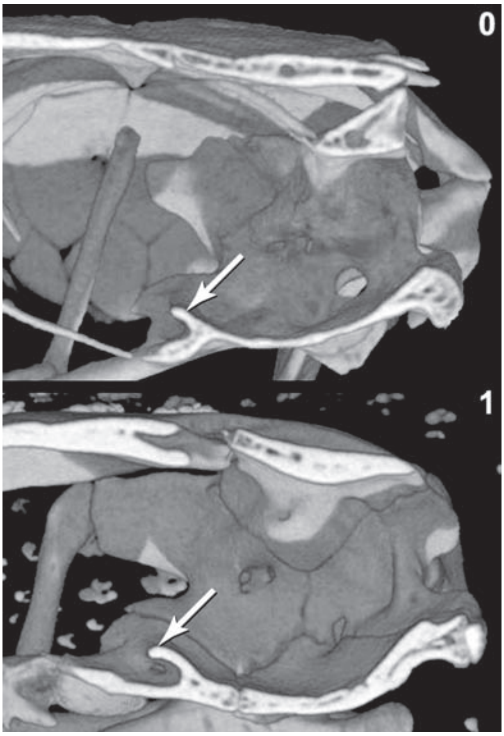
322. Trigeminal nerve maxillary branch: (0) pierces the lateral (maxillary) process of the palatine (*Cylindrophis ruffus*, anterior close-up cutaway view of snout); (1) passes dorsally between the palatine and the prefrontal (*Anilius scytale*, anterior close-up cutaway view of snout). Tchernov et al. (2000).



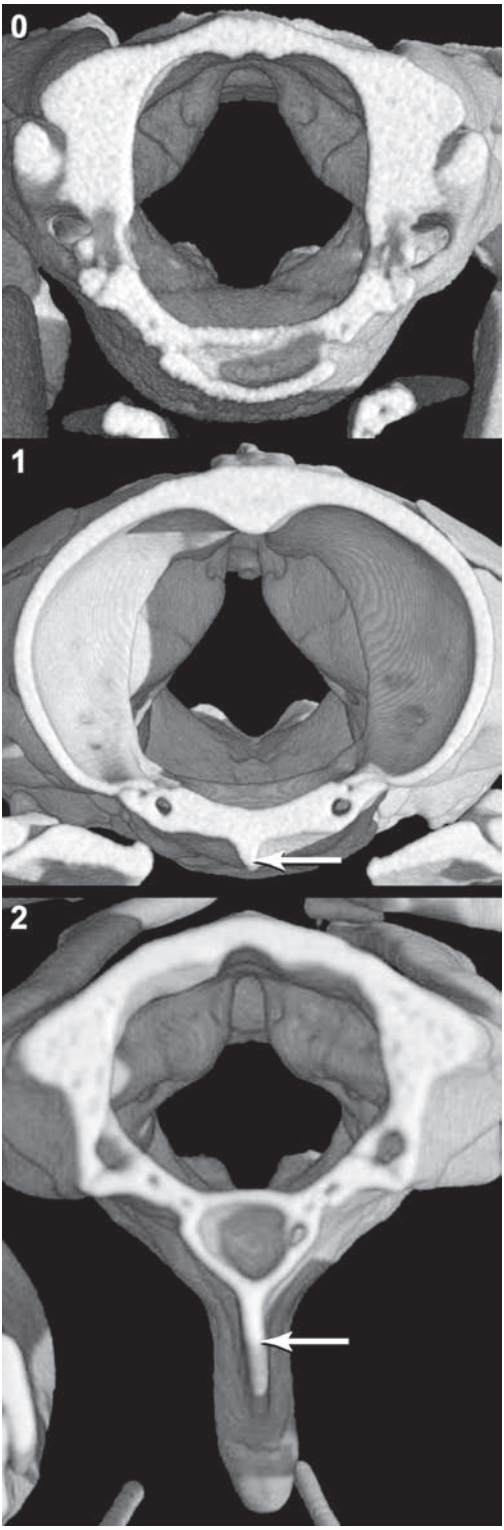
323. Ophidiosphenoid (equals "laterosphenoid" or "pleurosphenoid"): (0) absent (*Typhlops jamaicensis*, lateral close-up of braincase); (1) present (*Tropidophis haetianus*, lateral close-up of braincase). Rieppel (1976).



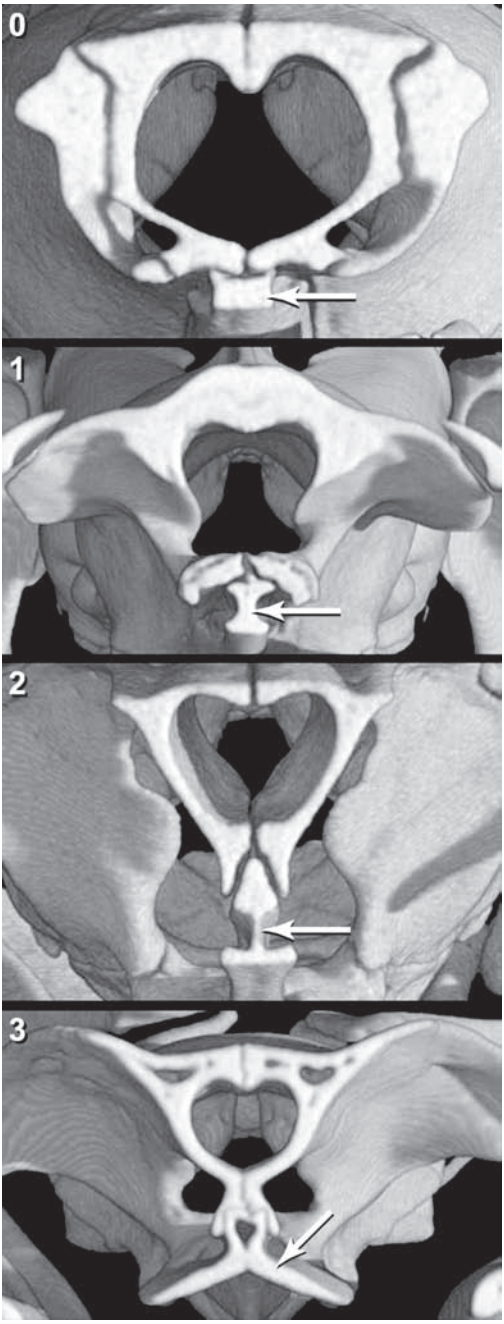
324. Dorsum sellae shape in longitudinal cross-section: (0) crista sellaris forms posterior wall, usually low and vertically disposed with more or less anterior slope (*Polychrus marmoratus*, lateral close-up cutaway view of braincase); (1) dorsum sellae poorly differentiated with, at most, shallow fossa with low crista sellaris (*Uropeltis melanogaster*, lateral close-up cutaway view of braincase); (2) enclosed in distinct fossa, a cup-like depression walled laterally and ventrally by the basisphenoid and anteriorly by the parasphenoid rostrum^N (*Loxocemus bicolor*, lateral close-up cutaway view of braincase); (3) completely enclosed tube-like dorsum sellae (*Lepidophyma flavimaculatum*, lateral close-up cutaway view of braincase), C.J. Bell (pers. comm.). Rieppel (1979a).



325. Dorsum sella fossa roofed posteriorly by crista sellaris (not scored in species with reduced/absent crista sellaris)^N: (0) fossa only modestly roofed by crista sellaris (*Platysaurus imperator*, lateral close-up cutaway view of braincase); (1) roofing more extensive over deep fossa (*Lanthanotus borneensis*, lateral close-up cutaway view of braincase).

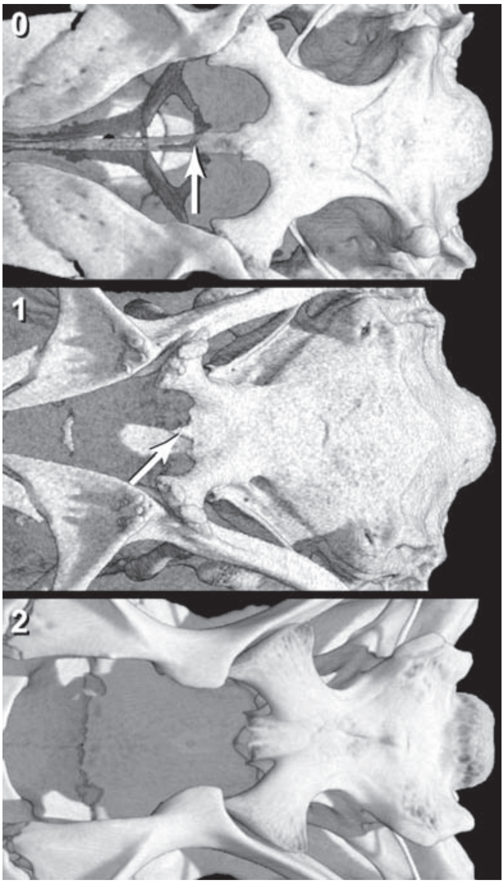


326. Parabasisphenoidal keel: (0) absent (*Lycophidion capense*, anterior close-up cutaway view of braincase); (1) present below dorsum sellae (*Loxocemus bicolor*, anterior close-up cutaway view of braincase); (2)^{N} deep keel (*Daboia russelli*, anterior close-up cutaway view of braincase). Kluge (1991) (ordered).

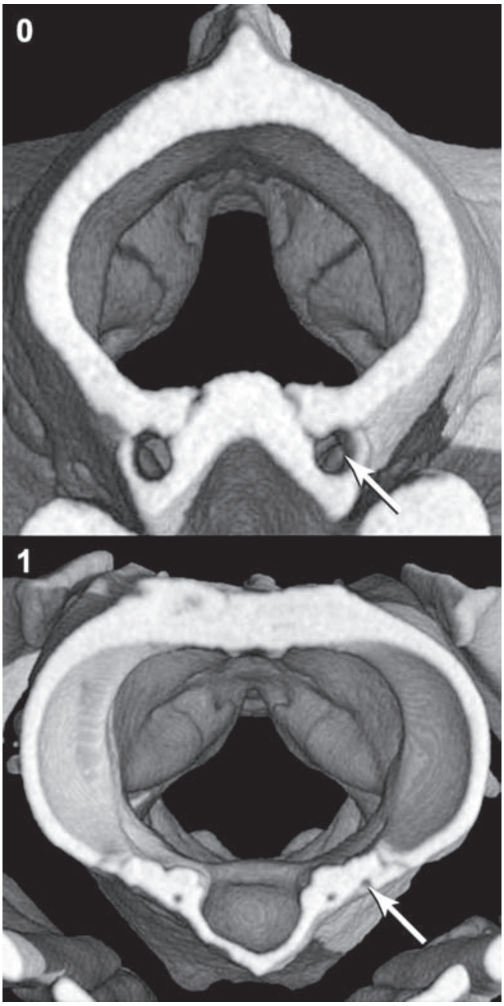


327. Parasphenoid rostrum in cross-section below posterior frontal articulation: (0) somewhat subrectangular (*Loxocemus bicolor*, anterior close-up cutaway view of midskull); (1)^{N} distinctly I-beam shaped, strongly compressed laterally, abruptly narrows at trabeculae (*Python molurus*, anterior close-up cutaway view of midskull); (2)^{N} with an arrowhead-shaped apex in cross-section (*Amphiesma

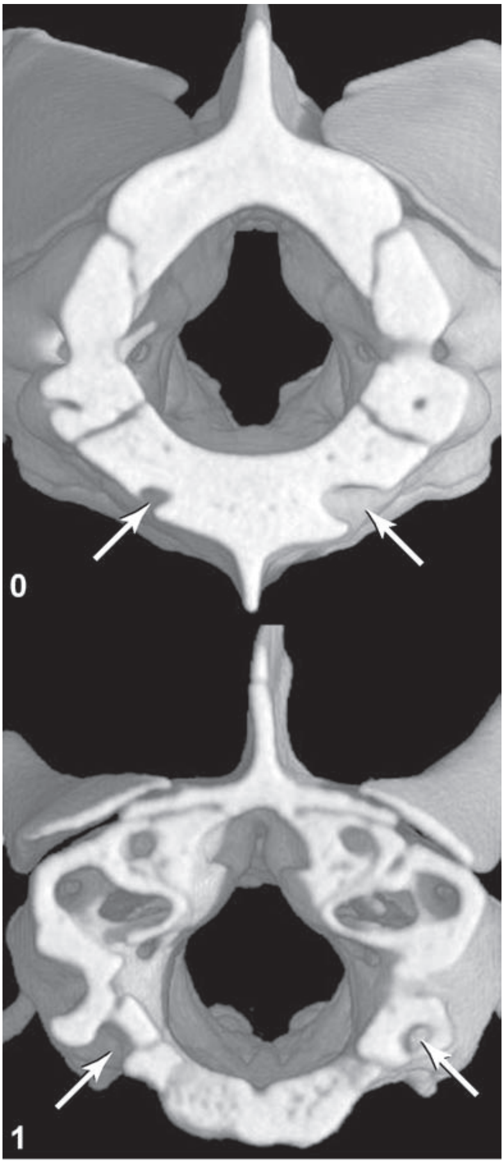
stolata, anterior close-up cutaway view of midskull); (3)^N with prominent ventrolaterally directed alae (*Daboia russelli*, anterior close-up cutaway view of midskull). Tchernov et al. (2000).



328. Cultriform process^N: (0) long (*Dipsosaurus dorsalis*, ventral close-up of posterior skull); (1) short (*Colobosaura modesta*, ventral close-up of posterior skull); (2) absent (*Heloderma horridum*, ventral close-up of posterior skull) (ordered).



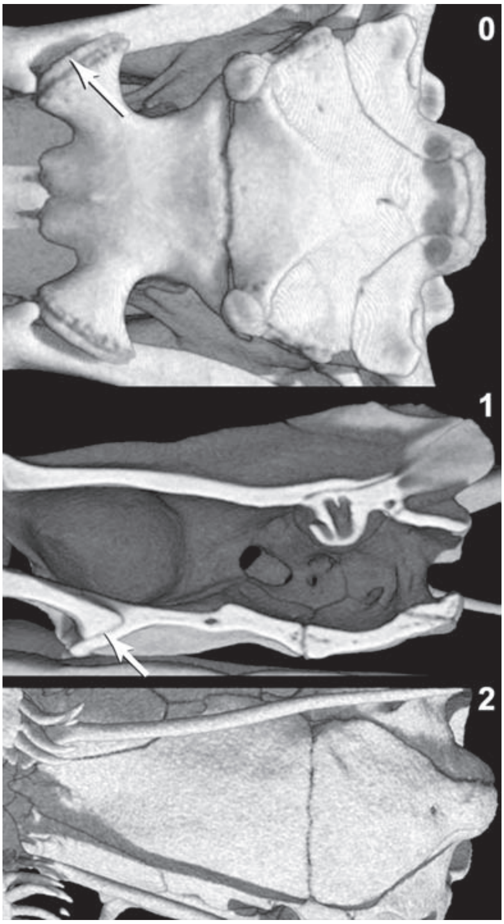
329. Vidian canal rostral opening^N: (0) roofed by parietal (*Anilius scytale*, anterior close-up cutaway view of braincase); (1) exits via parasphenoid rostrum only (*Xenocrophis piscator*, anterior close-up cutaway view of braincase).



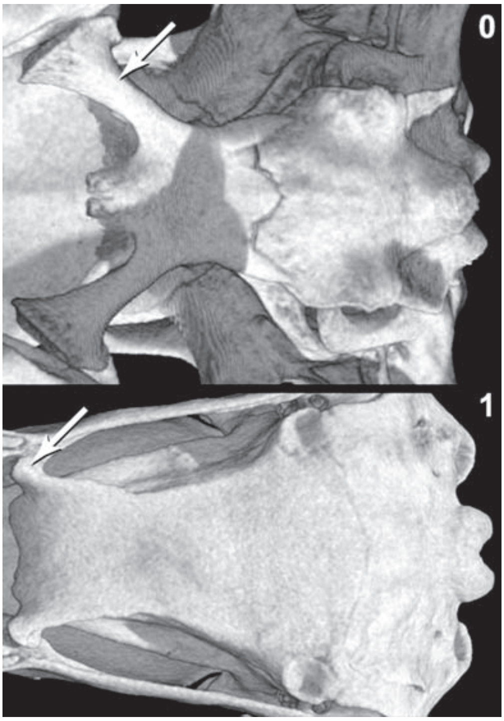
330. Vidian canal opening on right side: (0) is not larger than that of left Vidian canal (*Python molurus*, anterior close-up cutaway view of braincase); (1) is larger than that of the left Vidian canal (*Epicrates striatus*, anterior close-up cutaway view of braincase). Kluge (1993a).

Scored as per Kluge (1993a).

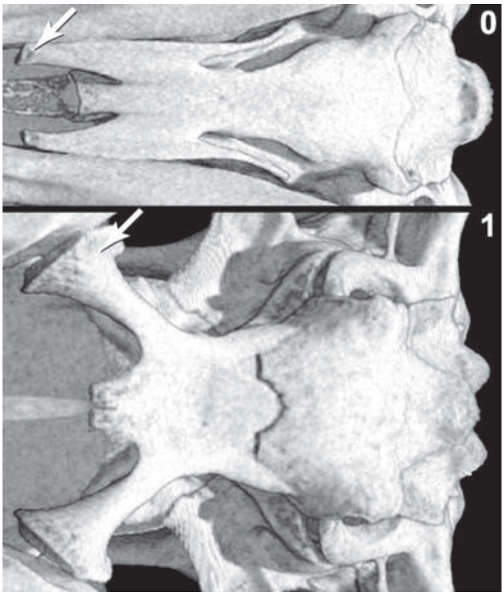
331. Trabeculae cranii: (0) tropibasic; (1) platybasic. Rieppel (1984a).



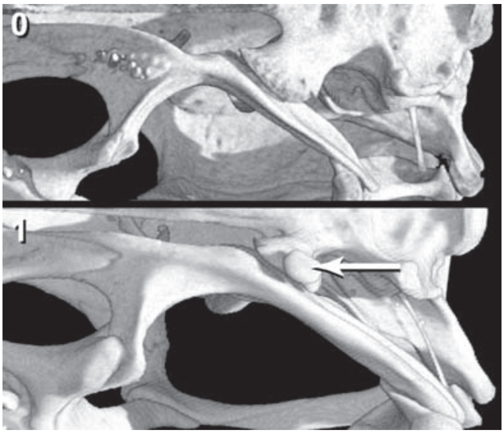
332. Basipterygoid process (and synovial palatobasal articulation): (0) present, formed by ossified basitrabecular process (*Lanthanotus borneensis*, ventral close-up of braincase); (1) present, formed by outgrowth from parabasisphenoid (no basitrabecular process known; synovial palatobasal articulation absent) (*Epicrates striatus*, lateral close-up cutaway view of braincase); (2) basipterygoid process absent (*Typhlops jamaicensis*, ventral close-up of braincase). Rieppel (1980b).



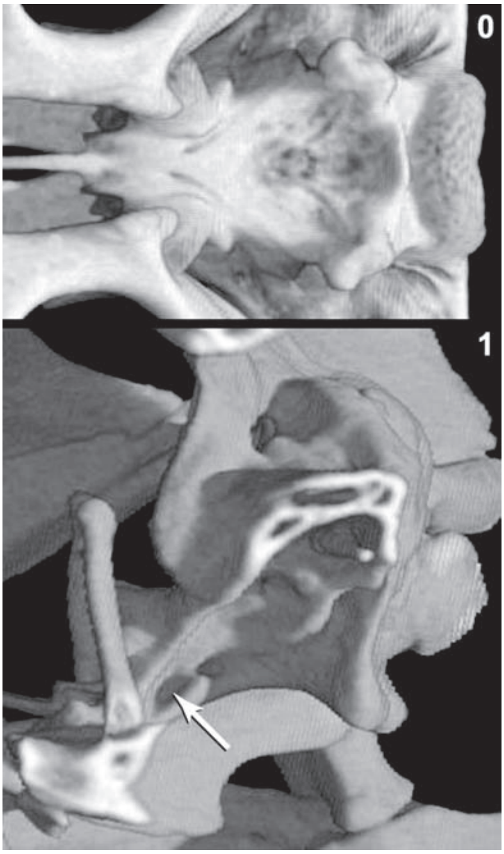
333. Basipterygoid process: (0) long, i.e., projecting far beyond the body of the basisphenoid (*Eublepharis macularius*, ventral close-up of braincase); (1) short, i.e., not projecting very far beyond the body of the basisphenoid (*Anelytropsis papillosus*, ventral close-up of braincase). Lee (1998).



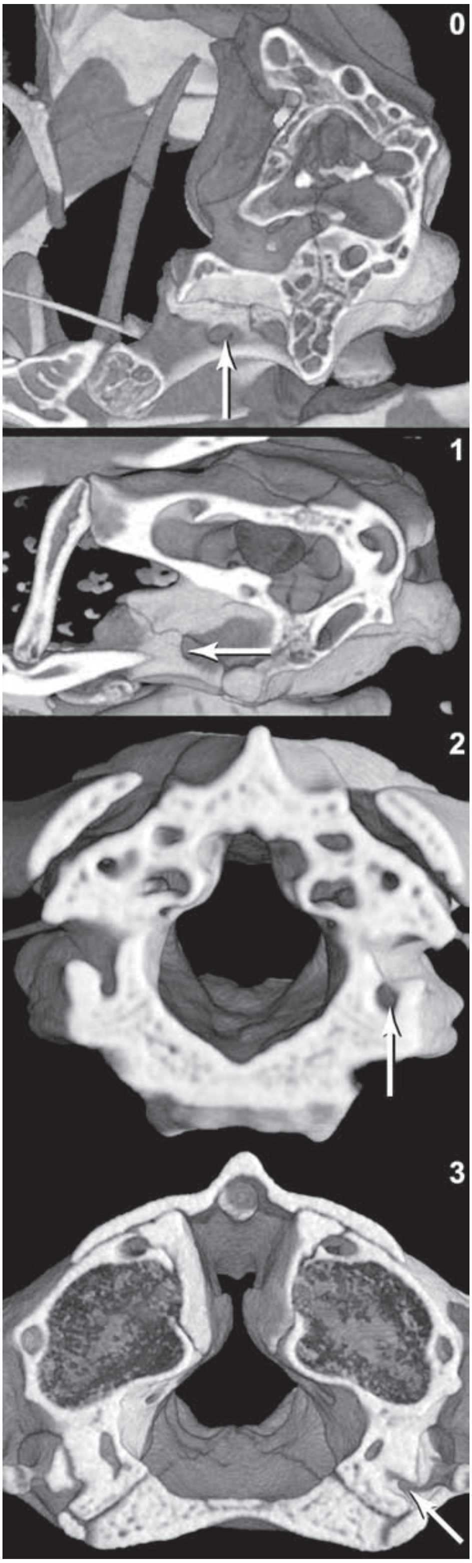
334. Basipterygoid process: (0) not expanded at distal end (*Lialis burtonis*, ventral close-up of braincase); (1) distal end expanded (*Eublepharis macularius*, ventral close-up of braincase). Lee (1998).



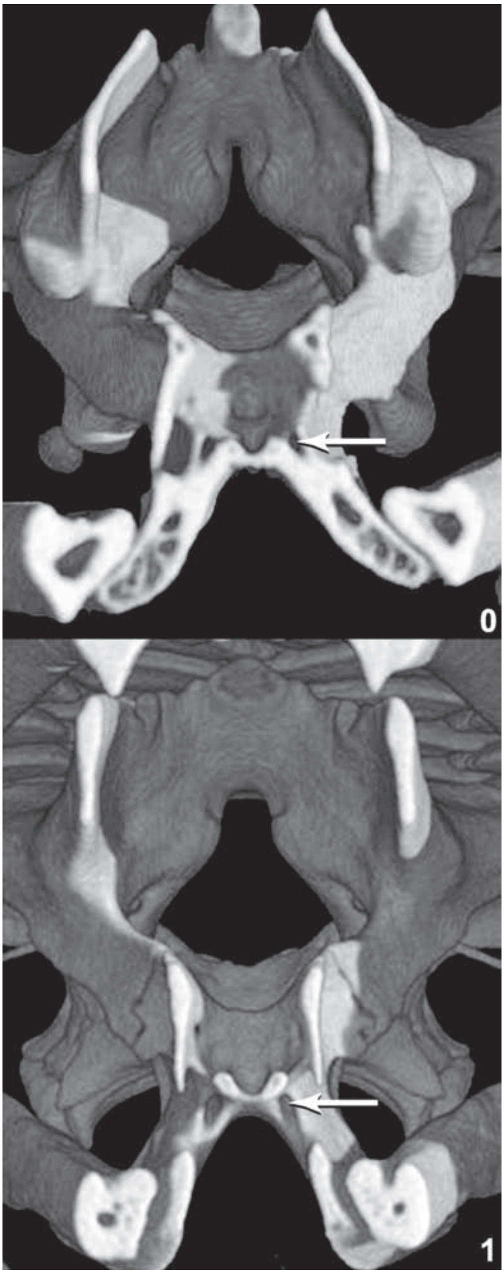
335. Sesamoid bone at basipterygoid-pterygoid articulation$^{\mathrm{N}}$: (0) absent (*Lacerta viridis*, ventral close-up of braincase); (1) present (*Tupinambis teguixin*, ventral close-up of braincase).



336. Vidian canal formed by the basisphenoid enclosing the internal carotid artery, and the base of the palatine artery, as they pass over the basipterygoid process: (0) absent (*Sphenodon punctatus*, ventral close-up of braincase); (1) present (*Agama agama*, lateral close-up cutaway view of braincase). Estes et al. (1988).

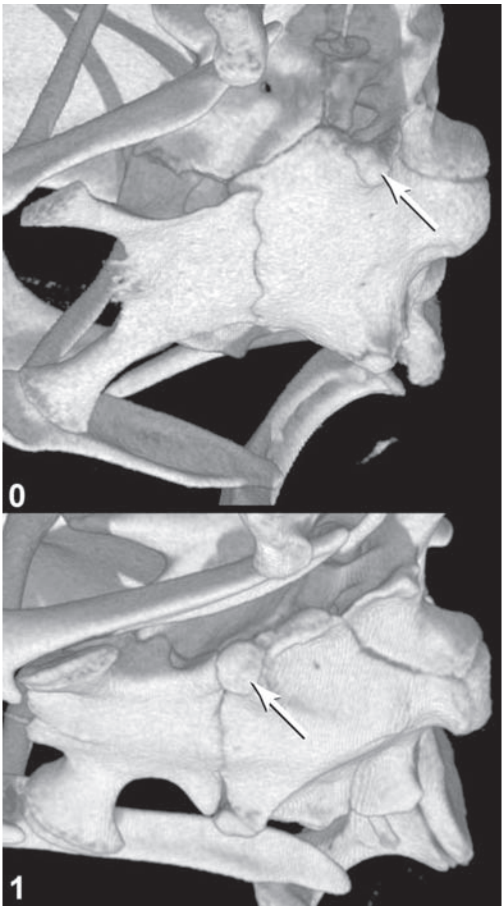


337. Vidian canal caudal opening: (0) within basisphenoid (*Physignathus cocincinus*, lateral close-up cutaway view of braincase); (1) anterior margin at basisphenoid-prootic suture (*Lanthanotus borneensis*, lateral close-up cutaway view of braincase; (2) entirely within prootic (*Notechis scutatus*, anterior close-up cutaway view of braincase); (3) the dibamid-amphisbaenian condition (*Trogonophis weigmanni*, anterior close-up cutaway view of braincase). *Anniella pulchra* coded (0) *fide* Toerien (1950). Estes et al. (1988) (ordered).

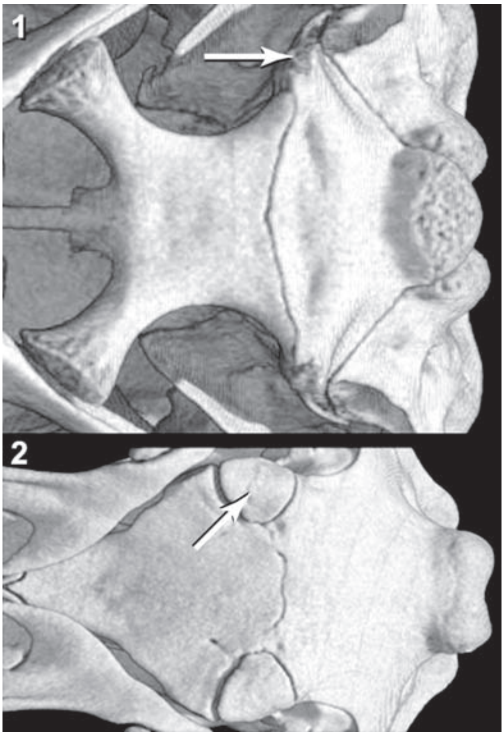


338. Carotid artery exits rostral end of Vidian canal: (0) at same level (or slightly above) as the remnant of the embryonic neurocranial trabeculae (*Elgaria multicarinata*, ante-

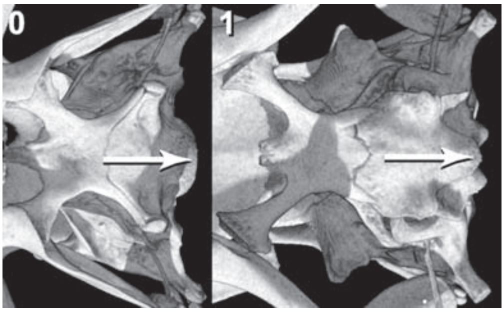
rior close-up cutaway view of braincase); (1) below the level of the remnant of the embryonic neurocranial trabeculae (*Pseudopus apodus*, anterior close-up cutaway view of braincase). Conrad and Norell (2008).



339. Basal tubera position^N^: (0) posterolateral, with apex on lateral edge of basioccipital just behind base of prootic-opisthotic suture (*Liolaemus bellii*, oblique ventral close-up of braincase); (1) anteromedial, with apex at lateral juncture of sphenoid and basioccipital, anterior and medial to prootic-opisthotic suture (*Lanthanotus borneensis*, oblique ventral close-up of braincase).

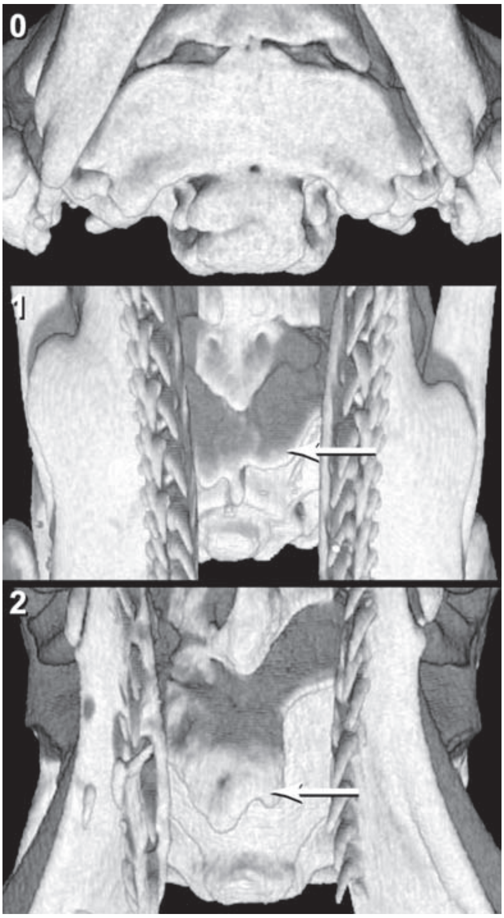


340. Apophyseal ossification (Element "X") caps basal tubera^{N}: (0) absent; (1) present (*Physignathus cocincinus*, ventral close-up of braincase); (2) huge (*Amphisbaena fuliginosa*, ventral close-up of braincase) (ordered).

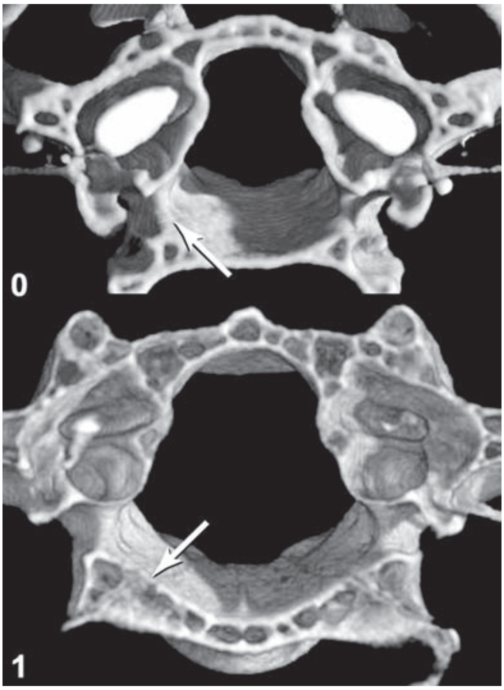


341. Occipital condyle: (0) posterior surface of condyle straight in ventral view (*Gambelia wislizenii*, ventral close-up of braincase); (1) posterior surface of condyle concave in ventral view (*Eublepharis macularius*, ventral close-up of braincase). Lee (1998).

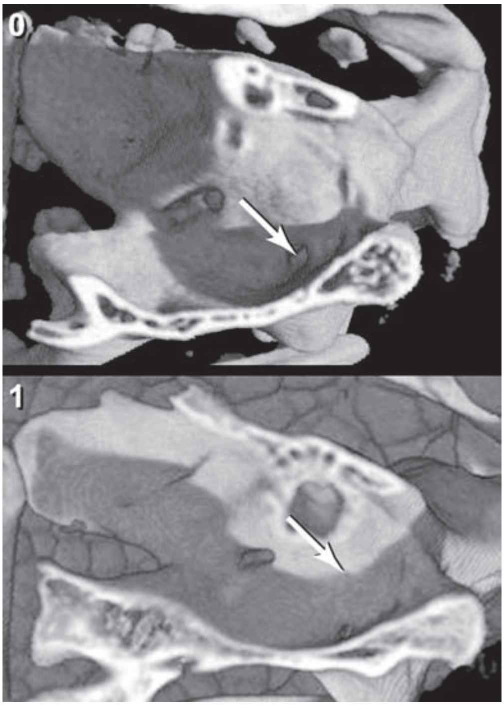
342. Basioccipital: (0) contributes to ventral border of foramen magnum (*Eublepharis macularius*, anterior close-up cutaway view of occipital condyle); (1) excluded from ventral border of foramen magnum by contact of exoccipitals (*Cylindrophis ruffus*, anterior close-up cutaway view of occipital condyle). Rieppel (1979c).



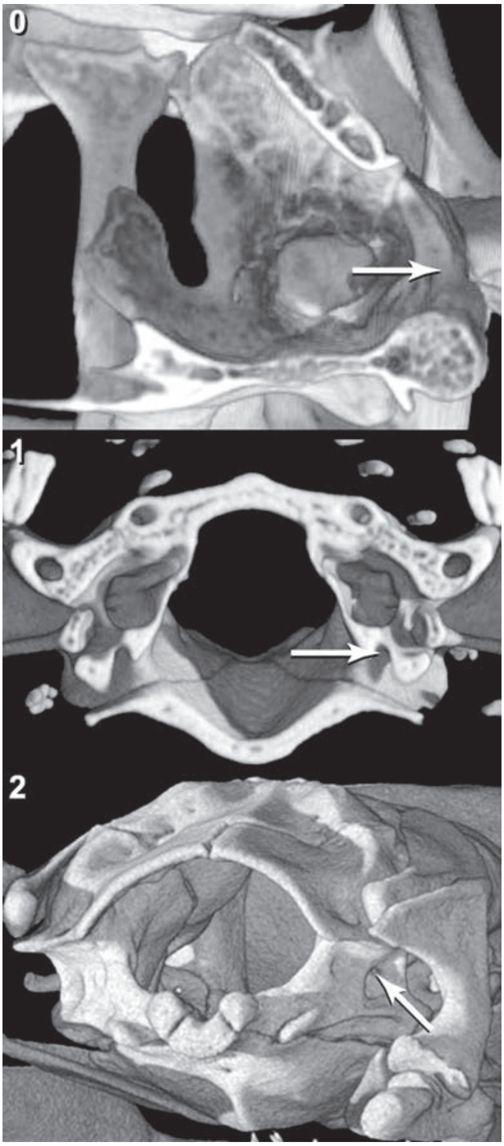
343. Basioccipital ventral keel: (0) absent (*Anilius scytale*, ventral close-up of braincase); (1) crest (*Thamnophis marcianus*, ventral close-up of braincase); (2)^{N} keel (*Agkistrodon contortrix*, ventral close-up of braincase). Kluge (1991) (ordered).



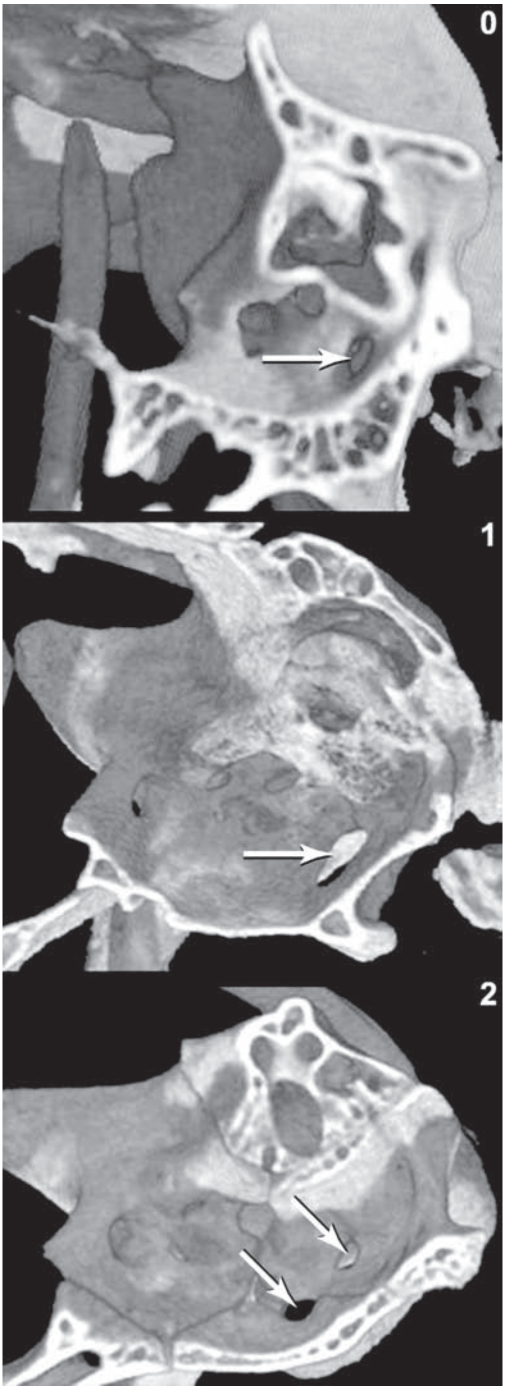
344. Medial aperture of the recessus scala tympani (MARST): (0) between basioccipital and opisthotic (*Pristidactylus torquatus*, anterior close-up cutaway view of braincase); (1) entirely in opisthotic (*Uranoscodon superciliosus*, anterior close-up cutaway view of braincase). Gauthier and Bell (in prep.).



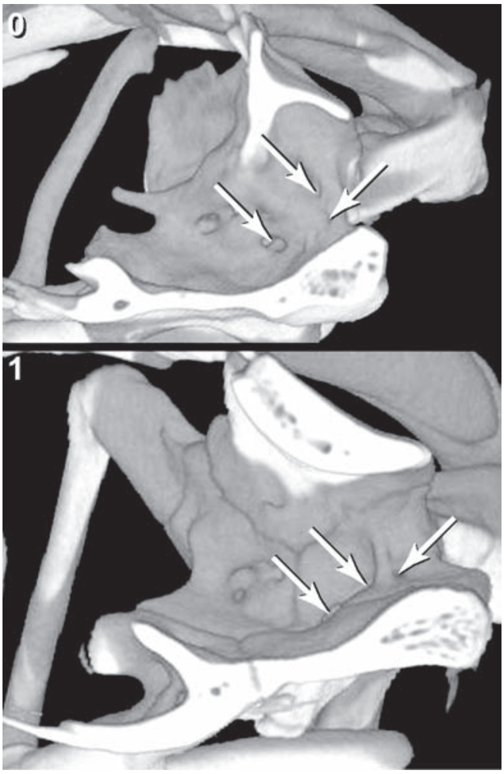
345. Cranial nerve IX exits braincase via: (0) MARST internally and lateral aperture of recessus scala tympani (LARST) externally (*Xenosaurus grandis*, lateral close-up cutaway view of braincase); (1) exits dorsal to MARST then out LARST (*Tiliqua scincoides*, lateral close-up cutaway view of braincase). Gauthier and Bell (in prep.).



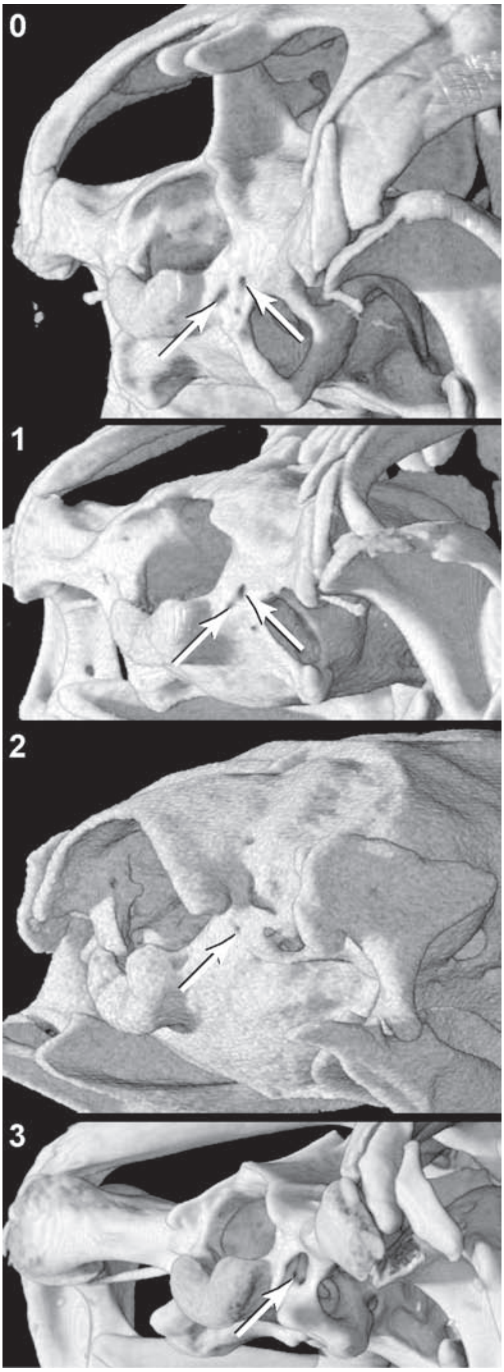
346. Cranial nerve IX exits braincase via: (0) foramen magnum (*Sphenodon punctatus*, lateral close-up cutaway view of braincase); (1) laterally via LARST (*Lanthanotus borneensis*, anterior close-up cutaway view of braincase); (2) posteriorly via vagus (=jugular) foramen (*Casarea dussumieri*, oblique posterior view of braincase). Rieppel (1985) (ordered).



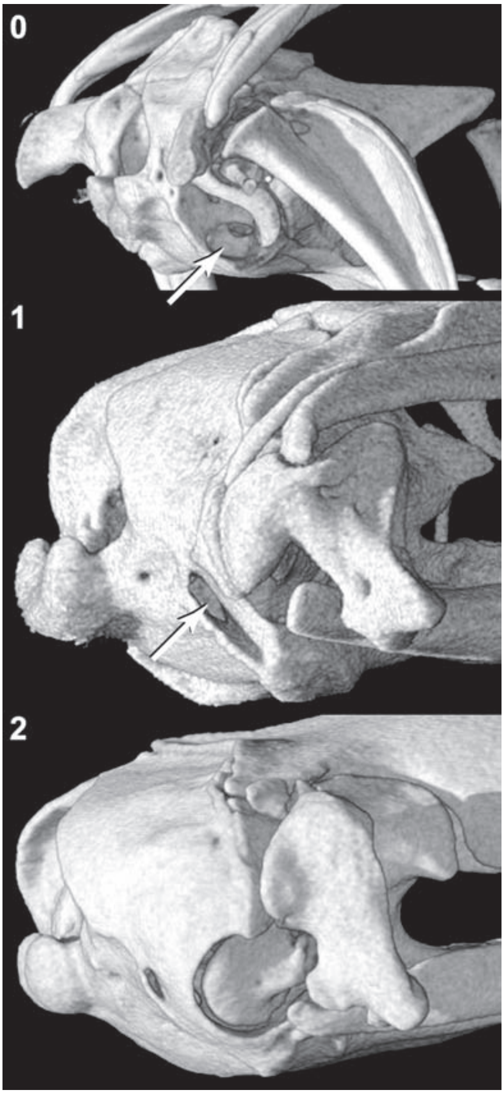
347. Medial aperture of the recessus scalae tympani (MARST) subdivided, IX cranial nerve exits posteriorly: (0) absent (*Brachylophus fasciatus*, lateral close-up cutaway view of braincase); (1) large oval MARST undivided, with IX cranial nerve exiting at posterodorsal end (*Gonatodes albogularis*, lateral close-up cutaway view of braincase); (2) MARST divided into anterior and posterior openings by bony process, with IX cranial nerve exiting via posterodorsal foramen (*Eublepharus macularius*, lateral close-up cutaway view of braincase). Gauthier and Bell (in prep.) (ordered).



348. Vagus foramen (="jugular foramen" in other amniotes) far from MARST^{N}: (0) with hypoglossal foramina lying below and between them medially (*Sauromalus ater*, lateral close-up cutaway view of braincase); (1) vagus foramen closer to MARST, with hypoglossal foramina extending posterior to vagus (*Varanus exanthematicus*, lateral close-up cutaway view of braincase).

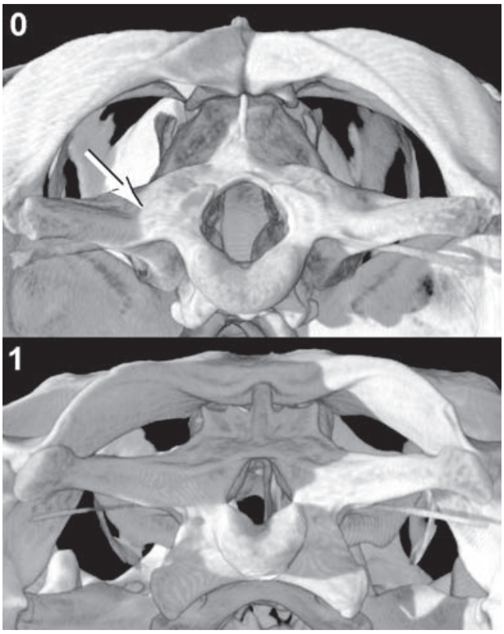


349. Hypoglossal (XII) foramina exit(s) relative to vagus (X–XI) foramen on external surface of braincase: (0) hypoglossal foramina separated from vagus (=jugular) foramen (*Zonosaurus ornatus*, oblique posterior close-up of braincase) (Conrad 2008); (1)^{N} at least one hypoglossal foramen emerges from the same fossa as the vagus foramen (*Amphiglossus splendidus*, oblique posterior close-up of braincase); (2)^{N} only one hypoglossal foramen still exits separately from the vagus foramen fossa (*Aparallactus werneri*, oblique posterior close-up of braincase); (3) all three hypoglossals emerge from the same fossa as the vagus foramen (*Heloderma horridum*, oblique posterior close-up of braincase). Lee (1997a) (ordered).



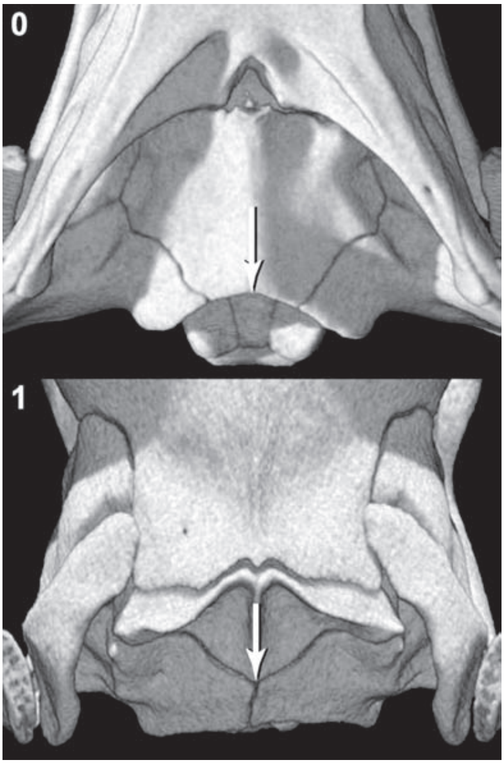
350. LARST (lateral aperture of recessus scalae tympani): (0) open (*Eublepharis macularius*, oblique lateral close-up of braincase); (1) small (*Feylinia polylepis*, oblique lateral close-up of braincase), Rieppel (1981); (2) closed (*Anelytropsis papillosus*, oblique lateral close-up of braincase). Rieppel (1984b) (ordered).

351. Perilymphatic foramen faces: (0) ventrally (*Eublepharis macularius*, anterior close-up cutaway view of braincase); (1) medially (*Typhlops jamaicensis*, anterior close-up cutaway view of braincase); (2) laterally (*Anilius scytale*, lateral close-up cutaway view of braincase); (3) posteriorly (*Trogonophis weigmanni*, anterior close-up cutaway view of braincase). Rieppel (1979a).

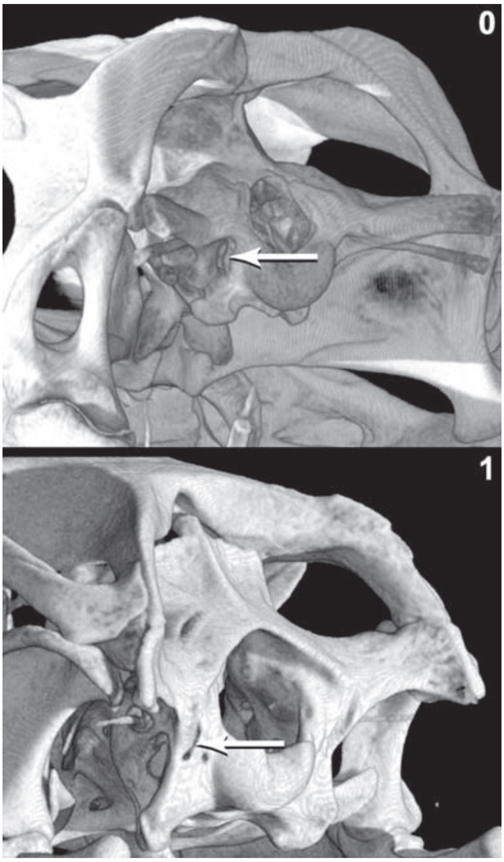


352. Opisthotic-exoccipital fusion to form oto-occipital: (0) incompletely fused or separate in adult (*Sphenodon punctatus*, posterior close-up view skull); (1) completely fused early in post-hatching ontogeny (*Pogona vitticeps*, posterior close-up view skull). Estes et al. (1988).

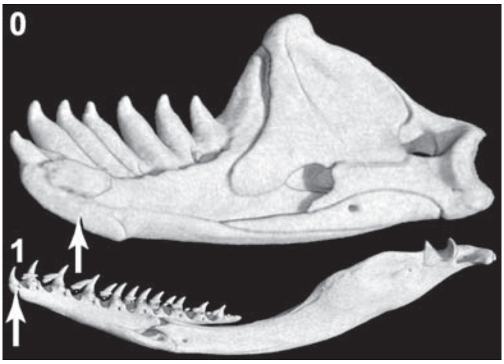
In extant amniotes generally, dense lamellar bone covers the occipital condyle late in ontogeny, so that one cannot distinguish among the three bones—the exoccipitals dorsolaterally and the basioccipital midventrally—involved in forming the occipital condyle. This event enables determination of (near) adult size in fossil amniotes.



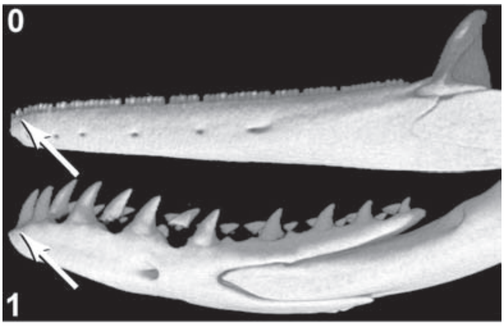
353. Oto-occipitals (exoccipital part) contact above foramen magnum to exclude supraoccipital: (0) absent (*Lanthanotus borneensis*, dorsal close-up of posterior skull); (1) present (*Exiliboa placata*, dorsal close-up of posterior skull). Estes et al. (1988).



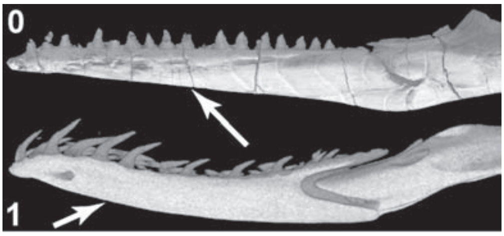
354. Metotic fissure: (0) open (*Sphenodon punctatus*, oblique posterior close-up of braincase); (1) subdivided by contact of basal plate and otic capsule (*Teius teyou*, oblique posterior close-up of braincase). Gauthier, Estes and de Queiroz (1988).



355. Mandibular symphysis: (0) anterior tips of dentary with distinct flat symphyseal area (*Amphisbaena fuliginosa*, medial view of mandible); (1) anterior tips of dentary smoothly rounded and without distinct symphyseal area (*Coluber constrictor*, medial view of mandible). Lee (1998).

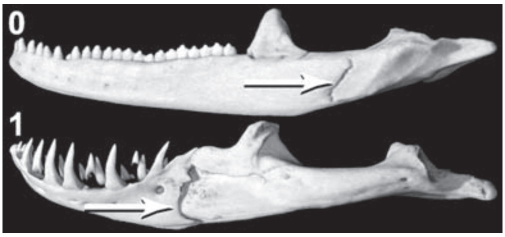


356. Dentary anterodorsal edge of dental parapet at tip^N: (0) straight (*Aeluroscalabotes felinus*, lateral close-up of anterior mandible); (1) tipped down (and medially) (*Lampropeltis getula*, lateral close-up of anterior mandible).

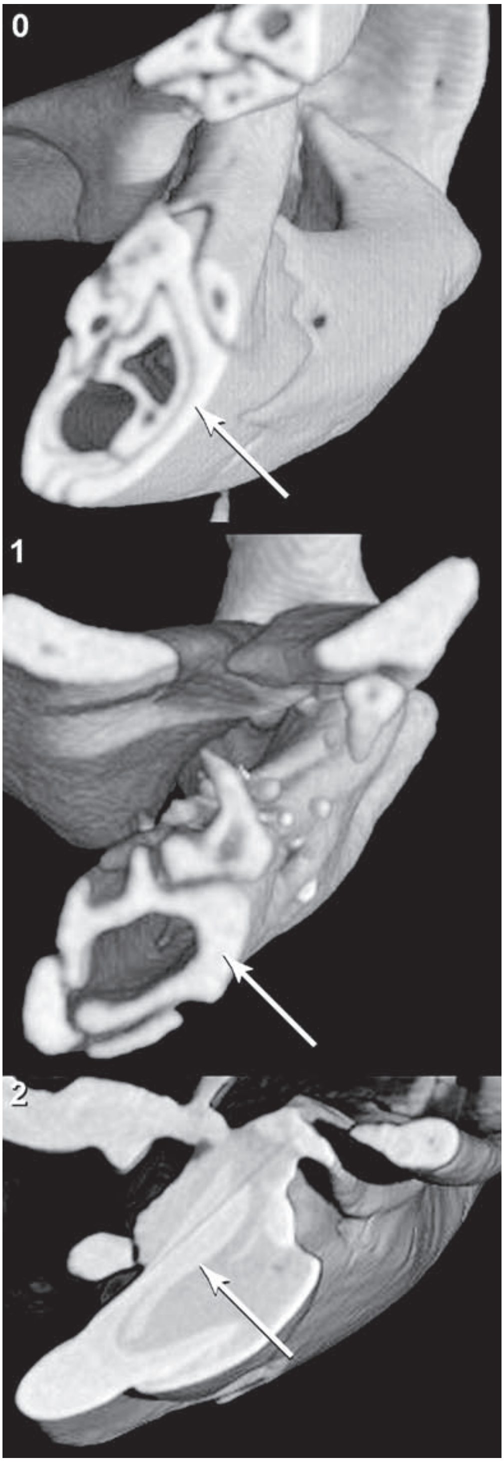


357. Dentary bowed ventrally along long axis: (0) straight to slightly bowed (*Plotosaurus bennisoni*, lateral close-up of anterior mandible); (1) distinctly bowed ventrally *Caserea dussumieri*, lateral close-up of anterior mandible). Conrad (2008).

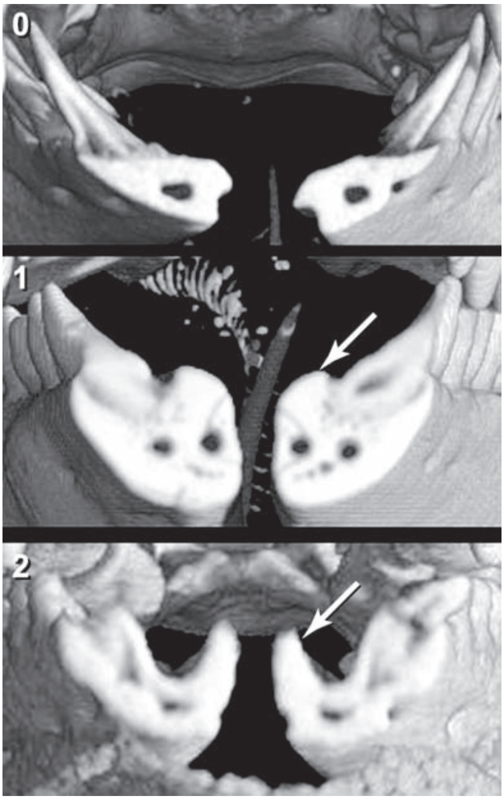
The degree of ventral bowing is nearly continuous and can even be more difficult to parse in cases where dentary shape is markedly transformed (e.g., some scolecophidians). It is most obvious in those cases where both dorsal and ventral margins are bowed ventrally (e.g., *Caserea dussumieri*), though they do not always coincide. Scored as 1 in those snakes with the dentary tipped down (and medially) at its terminus, so long as dental parapet remains bowed ventrally near the middle of the element. Scored as 0 in those snakes in which the dentary may be bowed ventrally but has a nearly horizontal dental parapet dorsally.



358. Dentary overlaps postdentary bones laterally: (0) extensive (*Plica plica*, lateral view of mandible); (1) reduced (*Heloderma horridum*, lateral view of mandible). Gauthier (1982).



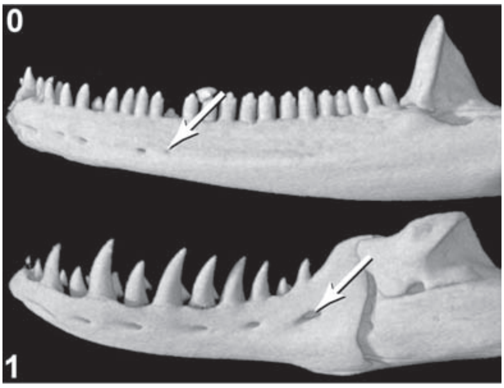
359. Dentary suspended from: (0) overlapping parts of coronoid, surangular, prearticular, splenial and angular (*Morunasaurus annularis*, anterior close-up cutaway view of mandible); (1) surangular (*Calabaria reinhardtii*, anterior close-up cutaway view of mandible); (2) prearticular (*Plotosaurus bennisoni*, anterior close-up cutaway view of mandible). Gauthier (1982).



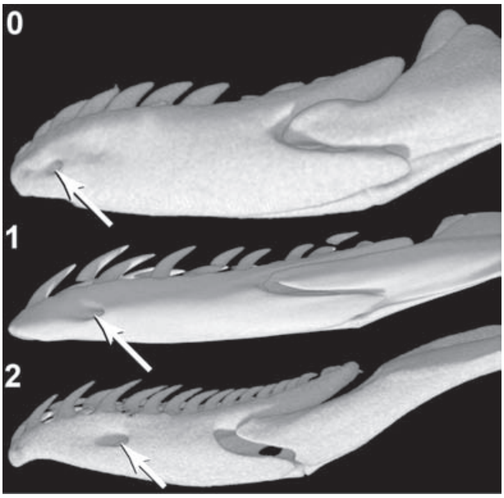
360. Dentary subdental shelf/gutter development in anterior part of dentary: (0) subdental shelf absent (*Lanthanotus borneensis*, anterior close-up cutaway view of dentary); (1) weakly developed subdental shelf (*Tupinambis teguixin*, anterior close-up cutaway view of dentary); (2) pronounced subdental gutter (*Amphiglossus splendidus*, anterior close-up cutaway view of dentary). Estes et al. (1988) (ordered).

R. Nydam (pers. comm.) argues that *Tupinambis* and *Amphiglossus* differ only in the amount of dental tissue filling their subdental gutters, which are otherwise equally well developed.

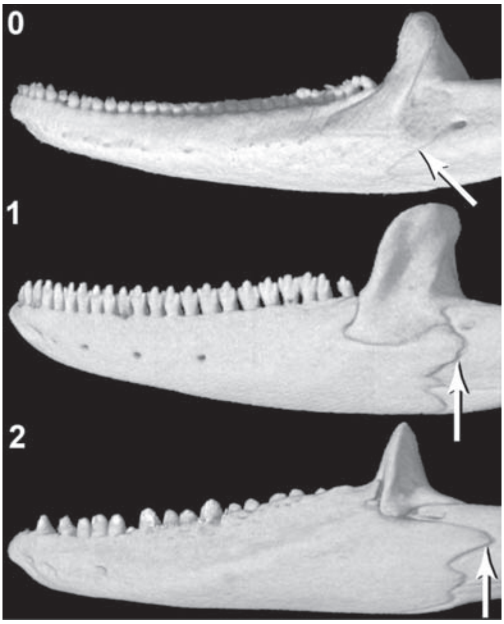
361. Dentary, number of mental foramina on lateral surface: (0) none^{N}; (1) one; (2) two^{N}; (3) three^{N}; (4) four or more. Lee (1998) (ordered).



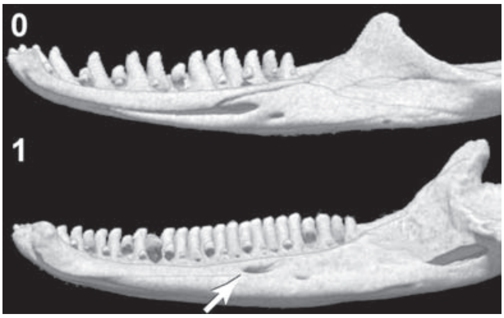
362. Dentary, size of posteriormost mental foramen^{N}: (0) same size as others (*Uranoscodon superciliosus*, lateral close-up of anterior mandible); (1) enlarged relative to others (*Lanthanotus borneensis*, lateral close-up of anterior mandible).



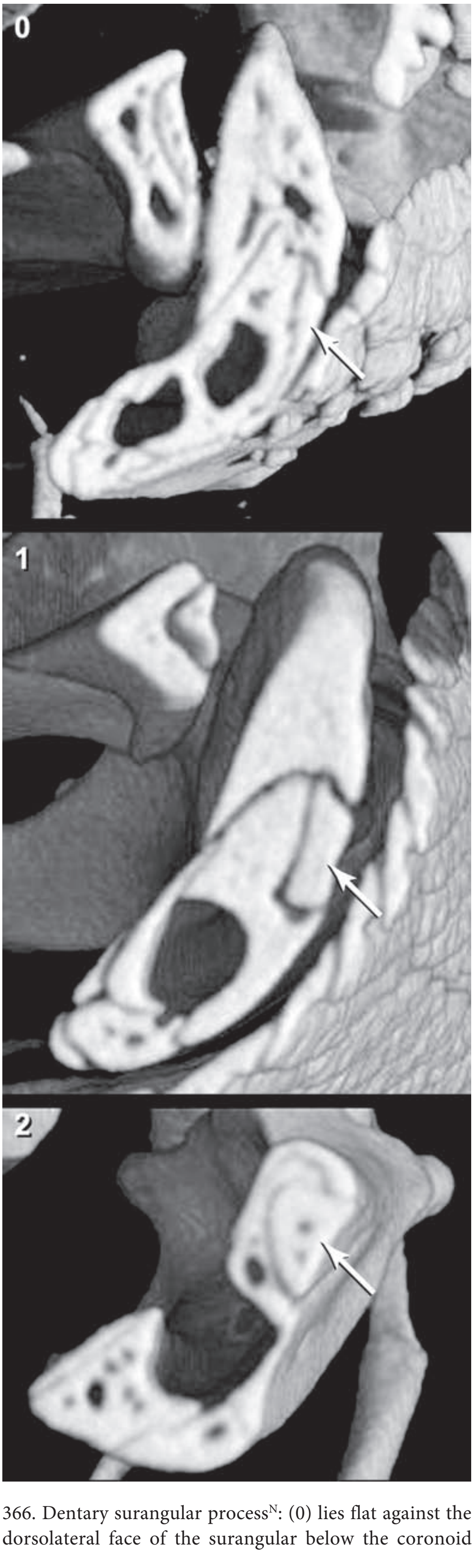
363. Dentary mental foramen position^{N}: (0) near tip of dentary (*Cylindrophis ruffus*, oblique lateral close-up of anterior mandible); (1) displaced caudally (*Python molurus*, oblique lateral close-up of anterior mandible); (2) displaced further caudally (*Tropidophis haetianus*, lateral view of mandible).



364. Dentary coronoid process posterior termination^{N}: (0) below (or anterior) to level of coronoid apex (*Enyalioides laticeps*, lateral close-up of anterior mandible); (1) just behind level of coronoid apex (*Dipsosaurus dorsalis*, lateral view of mandible); (2) well posterior to level of coronoid apex (*Leiosaurus catamarcensis,* lateral close-up of anterior mandible).

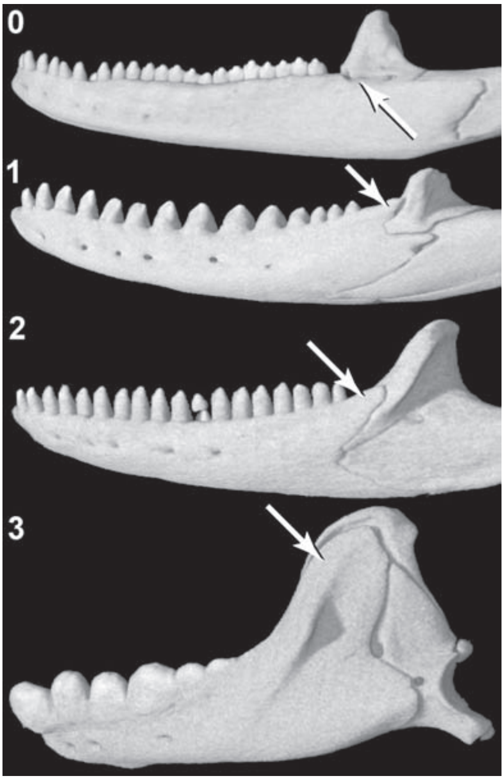


365. Dentary subdental shelf hooks around anterior rim of the anterior inferior alveolar foramen: (0) absent (*Celestus enneagrammus*, medial close-up of anterior mandible); (1) present (*Elgaria multicarinata*, medial close-up of anterior mandible). Gauthier (1982).



366. Dentary surangular process^{N}: (0) lies flat against the dorsolateral face of the surangular below the coronoid

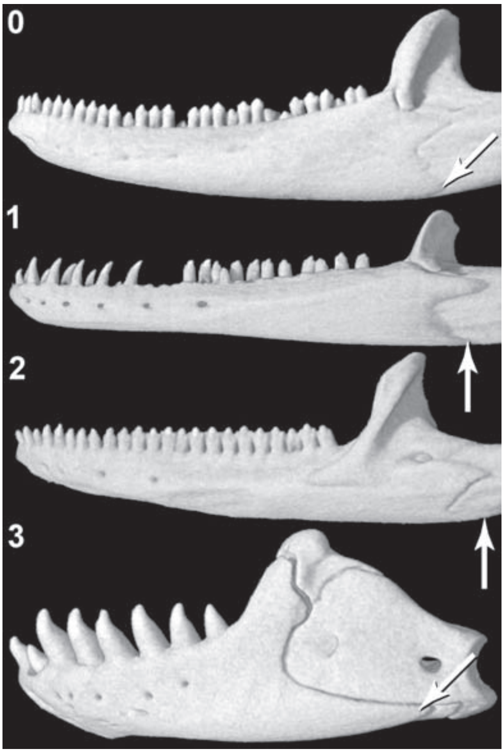
(*Xenosaurus grandis*, anterior close-up cutaway view of mandible); (1) set in a posterodorsally trending groove, open dorsally, that supports it from below on the dorsolateral face of the surangular below the coronoid (*Pseudopus apodus*, anterior close-up cutaway view of mandible); (2) set in deep V-shaped, laterally-facing recess on dorsolateral face of surangular behind coronoid (*Leiolepis belliana*, anterior close-up cutaway view of mandible).



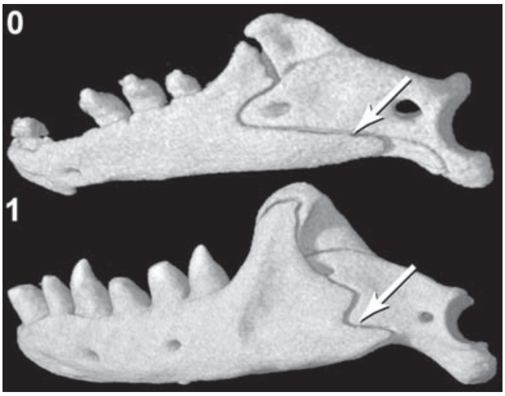
367. Dentary coronoid process posterodorsal extension: (0) absent or with only small dorsal extension (*Plica plica*, lateral close-up of anterior mandible); (1) large, but extending between lateral and medial processes of coronoid (*Pseudopus apodus,* lateral close-up of anterior mandible; (2) large, but extending dorsally to overlap most of anterolateral surface of coronoid (*Zonosaurus ornatus*, lateral close-up of anterior mandible); (3) extremely well developed, covering almost entire lateral surface of coronoid (*Trogonophis weigmanni*, lateral view of mandible). Estes et al. (1988) (ordered).

368. Dentary angular process reduced; (0) angular process extends to or past coronoid apex^{N} (*Lacerta viridis*, lateral view of mandible); (1) anterior to coronoid apex (*Anniella pulchra*, lateral view of mandible); (2) anterior to level of coronoid bone (*Pseudopus apodus*, lateral view of mandible). Gauthier (1982) (ordered).

Regarded as indeterminable in species with an intramandibular joint, which is scored elsewhere.

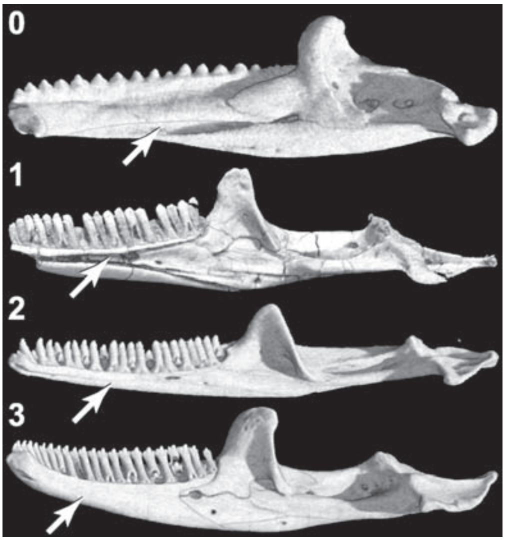


369. Dentary posterior termination on latral face of mandible: (0) below (or anterior to) level of coronoid apex (*Basiliscus basiliscus*, lateral close-up of anterior mandible); (1) just posterior to coronoid apex (*Gambelia wislizenii*, lateral close-up of anterior mandible); (2) well posterior to level of coronoid apex (*Leiocephalus barahonensis*, lateral close-up of anterior mandible); (3) nearly to posterior surangular foramen (*Amphisbaena fuliginosa*, lateral view of mandible (ordered). Etheridge and de Queiroz (1988).

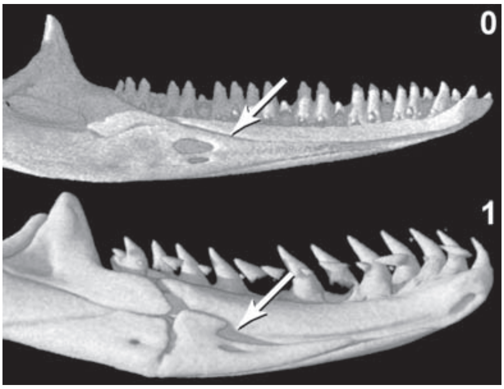


370. Dentary angular process prominently bifid$^{\mathrm{N}}$: (0) absent (*Geocalamus acutus*, lateral view of mandible); (1) present (*Bipes canaliculatus*, lateral view of mandible).

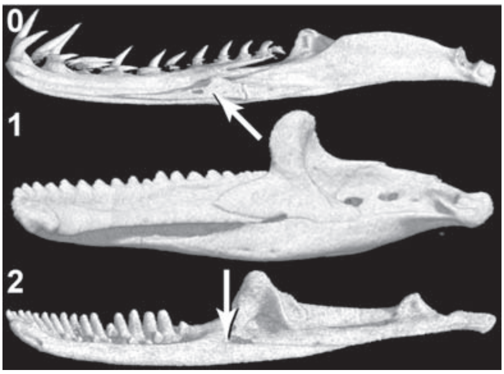
371. Meckel's canal: (0) opens medially for most of length (*Callopistes maculatus*, medial view of mandible); (1) opens ventrally anterior to anterior inferior alveolar foramen (*Anniella pulchra*, ventral view of mandible). Gauthier (1982).



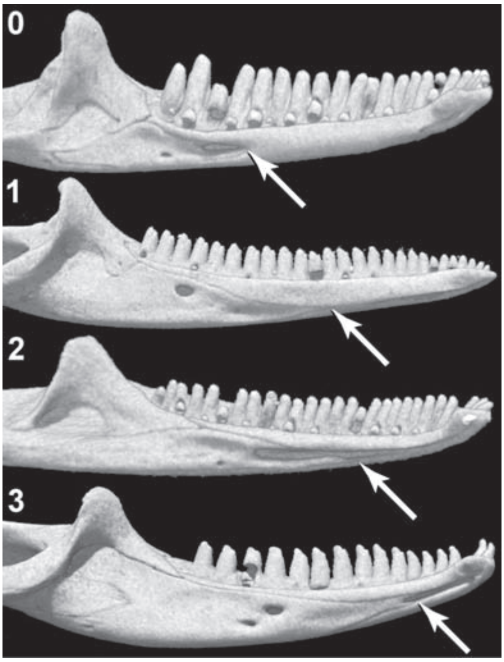
372. Dentary restricts Meckel's canal: (0) does not restrict or enclose Meckelian canal (*Brookesia brygooi*, medial view of mandible); (1)$^{\mathrm{N}}$ lower dentary border of Meckel's canal folds up to approach closely upper border to restrict canal (*Temujinia ellisoni*, medial view of mandible); (2) upper and lower borders form sutural contact anterior to splenial (*Uta stansburiana*, medial view of mandible); (3) Meckel's canal closed and fused anterior to splenial (*Dipsosaurus dorsalis*, medial view of mandible). Etheridge and de Queiroz (1988) (ordered).



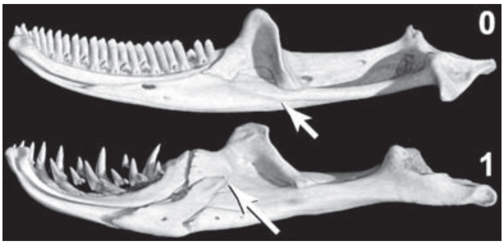
373. Splenial attachment to dentary above Meckel's canal: (0) close throughout length (*Colobosaura modesta*, medial close-up of anterior mandible); (1) loose, with dorsal dentary suture confined to posterodorsal corner of splenial (*Cylindrophis ruffus*, medial close-up of anterior mandible). Pregill et al. (1986).



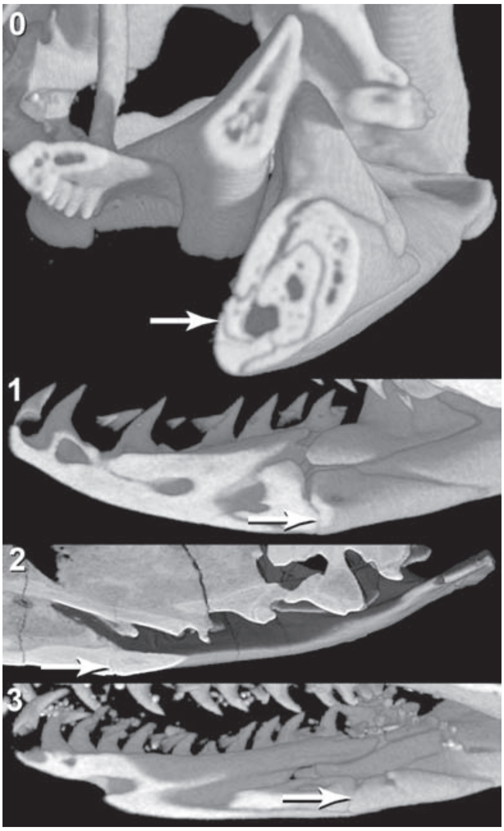
374. Splenial: (0) present (*Lichanura trivirgata*, medial view of mandible); (1) absent (*Brookesia brygooi*, medial view of mandible); (2)$^{\mathrm{N}}$ fused to dentary (*Cricosaura typica*, medial view of mandible). Gauthier, Estes and de Queiroz (1988).



375. Splenial anterior extent: $(0)^{N}$ around one-third (or less) length relative to dentary tooth row (*Sphenomorphus solomonis*, medial close-up of anterior mandible); (1) about one-half (*Aspidoscelis tigris*, medial close-up of anterior mandible); $(2)^{N}$ about two-thirds (*Plestiodonh fasciatus*, medial close-up of anterior mandible); $(3)^{N}$ three-fourths (or more) (*Callopistes macularius*, medial close-up of anterior mandible). Estes et al. (1988) (ordered).

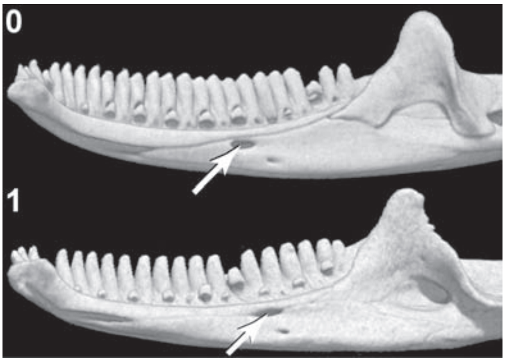


376. Splenial posterior extent: (0) extends posteriorly to or beyond apex of coronoid (*Morunasaurus annularis*, medial view of mandible); (1) does not extend posteriorly to apex of coronoid (*Heloderma horridum*, medial view of mandible). Pregill et al. (1986).

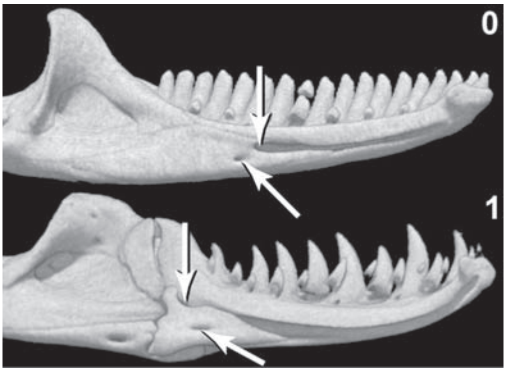


377. Splenial-angular articulation: (0) splenial overlaps angular (*Crotaphytus collaris*, anterior close-up cutaway view of skull); (1) with ball on splenial (below level of posterior mylohyoid foramen) fitting into socket on angular (*Cylindrophis ruffus*, anterior close-up cutaway medial view of mandible); (2) with ball on angular fitting into socket on splenial (*Plotosaurus bennisoni*, medial close-up cutaway view of right mandible); (3) flat, abutting joint (*Calabaria reinhardtii*, medial view of right mandible).

The posteroventral end of the splenial abuts a ventromedially positioned notch in the angular in *Lanthanotus borneensis*, comparable to none of the joints described here, longstanding opinion to the contrary (e.g., McDowell and Bogert 1954). The joint visible in an intact *L. borneensis* mandible is superficial only. The angular otherwise overlaps the splenial internally, as in lizards generally.



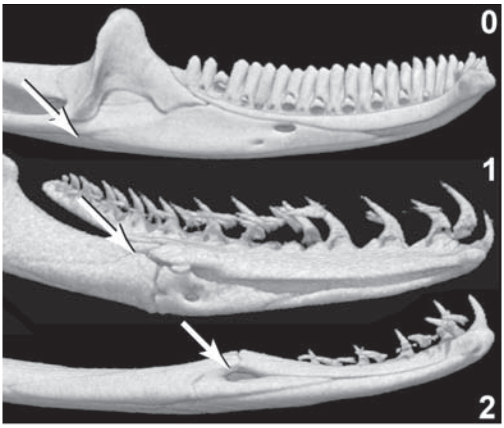
378. Splenial anterior inferior alveolar foramen (aiaf) position relative to dentary^N: (0) enclosed entirely in splenial (*Morunasaurus annularis*, medial close-up of anterior mandible); (1) between splenial and dentary (*Xenosaurus grandis*, medial close-up of anterior mandible). Scored as "missing" in those species in which the dorsal margin of the splenial, or the entire element, is reduced anterior to the aiaf. Some species, particularly stem acrodontans, but also *Shinisaurus crocodilurus*, have the aiaf in a high position, between the dentary and splenial, as in state 1, but still have the aiaf narrowly enclosed in the splenial as in state 0.



379. Splenial anterior inferior alveolar foramen position relative to anterior mylohyoid foramen^N: (0) anterodorsal (*Zonosaurus ornatus*, medial close-up of anterior mandible); (1) dorsal to posterodorsal (*Lanthanotus borneensis*, medial close-up of anterior mandible).

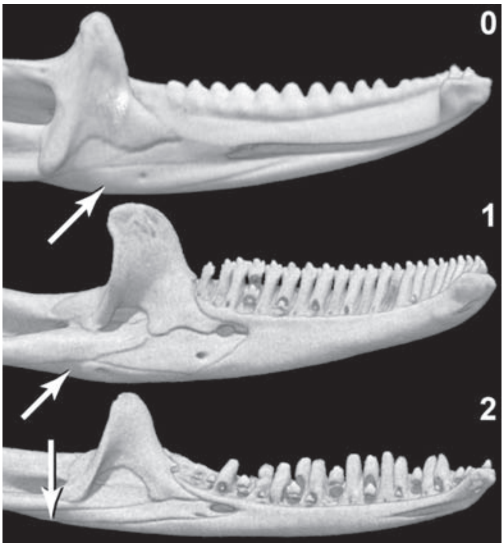
380. Angular: (0) present; (1) absent. Estes et al. (1988).

381. Angular posterior extent: (0) reaches mandibular condyle (*Geocalamus acutus*, medial view of mandible); (1) does not reach mandibular condyle (*Heloderma horridum*, medial view of mandible). Gauthier, Estes and de Queiroz (1988).

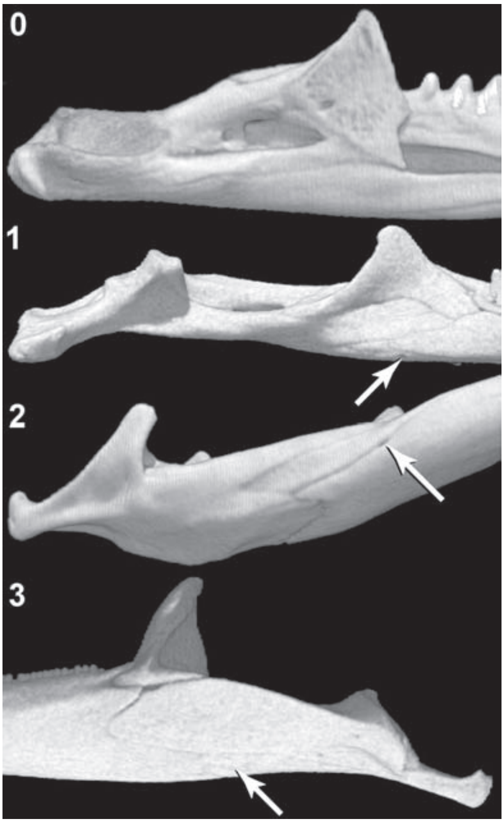


382. Angular taller anteriorly, closely approaching coronoid (or, if coronoid absent, tooth-bearing margin of dentary above Meckelian canal)^N: (0) absent, angular broadly separated from coronoid (*Morunasaurus annularis*, medial close-up of anterior mandible); (1) present (*Trachyboa boulengeri*, medial close-up of anterior mandible); (2) with finger-like process over-arching Meckel's canal (*Agkistrodon contortrix,* medial close-up of anterior mandible).

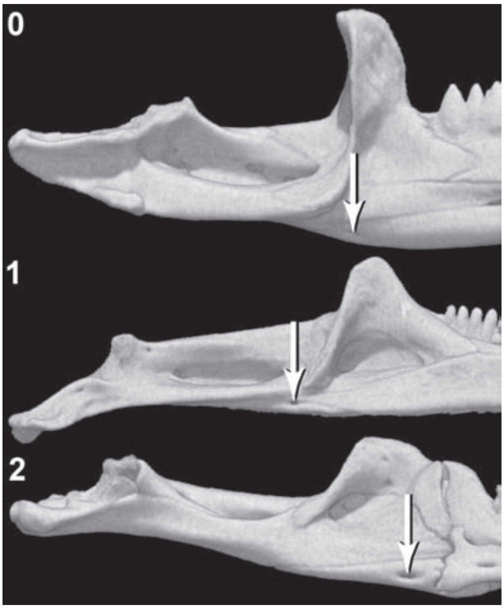
Gephyrosaurus scored based on *Diphyodontosaurus*. Scored as state 2 in those snakes conserving the same splenioangular shape, including a finger-like process of the angular, even when both elements are reduced in size and thereby separated from the tooth-bearing border of the dentary.



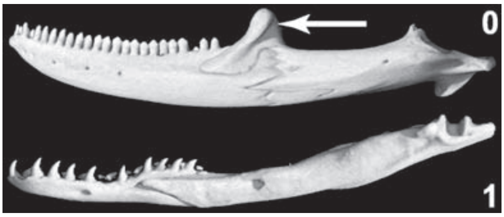
383. Angular medial exposure (relative degree of medial exposure scored with the teeth pointing straight up): (0) broad (*Pogona vitticeps*, medial close-up of anterior mandible); (1)$^{\mathrm{N}}$ reduced (*Dipsosaurus dorsalis*, medial close-up of anterior mandible); (2) narrow (*Liolaemus bellii*, medial close-up of anterior mandible). Lee (1998).



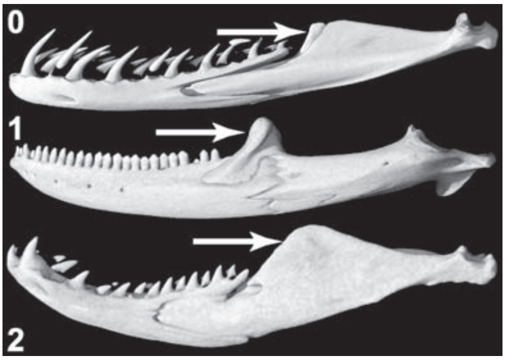
384. Posterior mylohyoid foramen position$^{\mathrm{N}}$: (0) absent: (*Sphenodon punctatus*, medial close-up of posterior mandible); (1) medial (*Celestus enneagrammus*, medial close-up of posterior mandible; (2) ventral (*Plica plica*, ventral close-up of posterior mandible); (3) lateral (*Aeluroscalabotes felinus*, lateral close-up of posterior mandible).



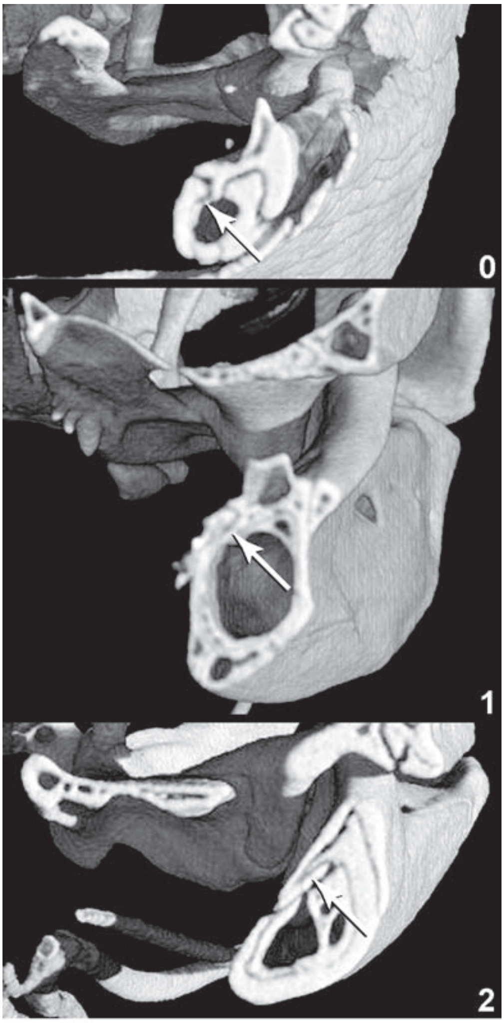
385. Posterior mylohyoid foramen position relative to coronoid apex: (0) below *(Leiolepis belliana*, medial close-up of posterior mandible); (1) posterior (*Cordylus mossambicus*, medial close-up of posterior mandible); (2) anterior (*Lanthanotus borneensis*, medial close-up of posterior mandible). Frost and Etheridge (1989).



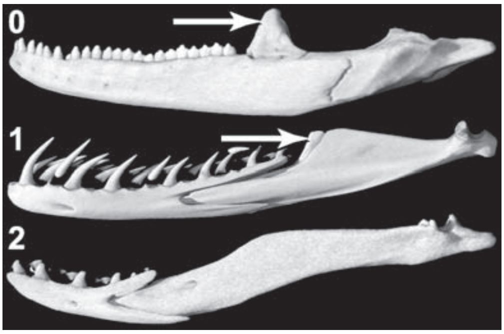
386. Coronoid eminence: (0) present (*Morunasaurus annularis*, lateral view of mandible); (1) absent (*Naja naja*, lateral close-up of posterior mandible). Gauthier, Estes and de Queiroz (1988).



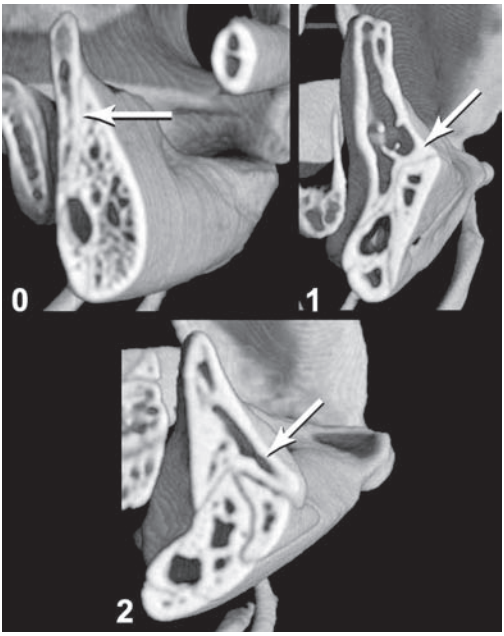
387. Coronoid eminence composition: (0) formed by both surangular and coronoid (*Python molurus*, lateral view of mandible); (1) formed exclusively by coronoid (*Morunasaurus annularis*, lateral view of mandible); (2) formed exclusively by surangular^{N} (*Ungaliophis continentalis*, lateral view of mandible). Gauthier, Estes and de Queiroz (1988).



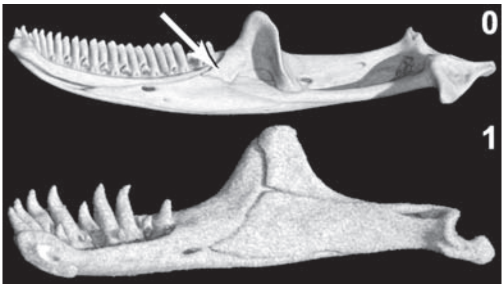
388. Coronoid anteromedial process fits into sulcus beneath tooth-bearing border of dentary (at or behind end of tooth row): (0) absent (*Celestus enneagrammus*, anterior close-up cutaway view of mandible); (1)^{N} present (*Teius teyou*, anterior close-up cutaway view of mandible); (2) and wraps around ventral margin of dentary tooth-bearing border at apex posteriorly (*Anolis carolinensis*, anterior close-up cutaway view of mandible). Smith (2009a) (ordered).



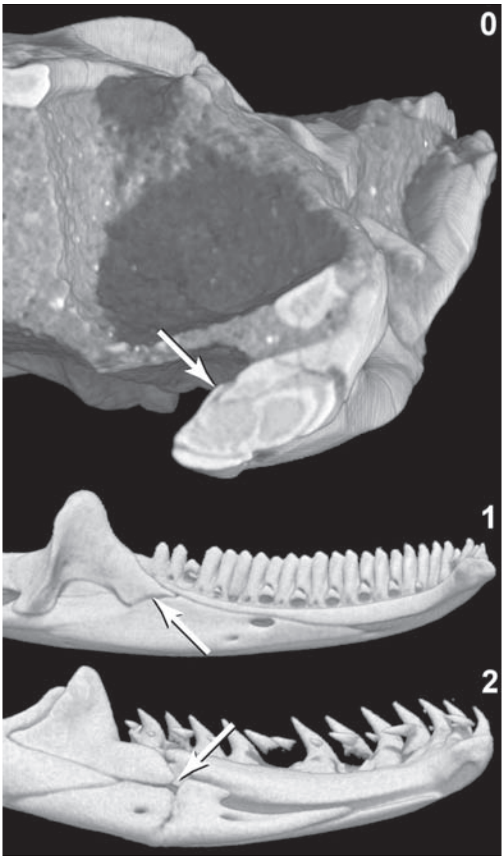
389. Coronoid bone^{N}: (0) present, well developed (*Plica plica*, lateral view of mandible); (1) present, small and strap-like (*Python molurus*, lateral view of mandible); (2) absent (*Micrurus fulvius*, lateral view of mandible) (ordered).



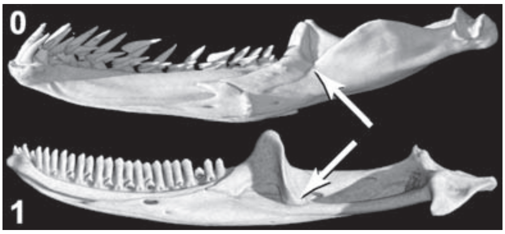
390. Coronoid-surangular articulation: (0) coronoid restricted to medial aspect of mandible (*Sphenodon punctatus*, anterior close-up cutaway view of mandible); (1)^{N} coronoid extends onto dorsal surface of surangular (*Leiolepis belliana*, anterior close-up cutaway view of mandible); (2) coronoid arches over dorsal margin of mandible to reach lateral face of surangular (*Crotaphytus collaris*, anterior close-up cutaway view of mandible). Estes et al. (1988) (ordered).



391. Coronoid, anteromedial process: (0) present (*Morunasaurus annularis*, medial view of mandible); (1) absent (*Dibamus novaeguineae*, medial view of mandible). Lee (1998).



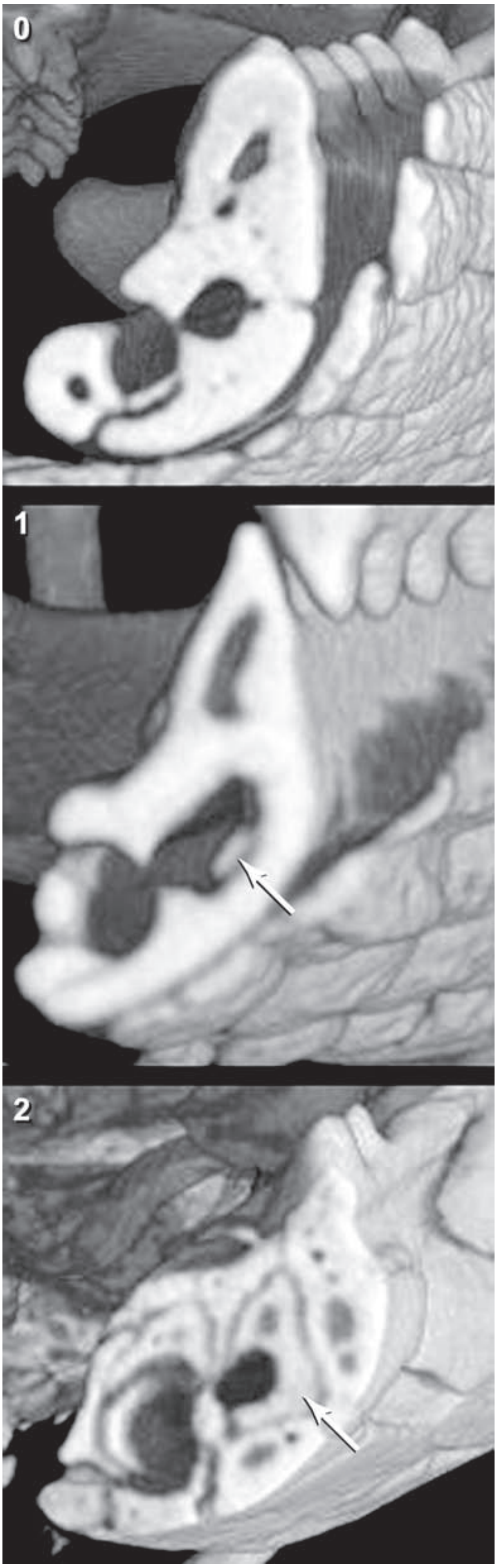
392. Coronoid, anteromedial ventral margin (at/behind end of tooth row): (0)^{N} overlapped by splenial (*Temujinia ellisoni*, anterior close-up cutaway view of mandible); (1)^{N} abuts splenial (*Morunasaurus annularis*, medial close-up of anterior mandible); (2) does not contact splenial (*Cylindrophis ruffus*, medial close-up of anterior mandible). Lee (1998) (ordered).



393. Coronoid, posteromedial process: (0) absent (*Boa constrictor*, medial view of mandible); (1) present (*Morunasaurus annularis*, medial view of mandible). Lee (1998).

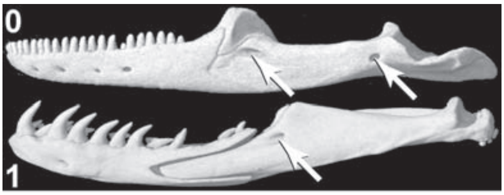
394. Coronoid, anterolateral dentary process^{N}: (0) absent (*Stenocercus guentheri*, lateral view of mandible); (1) present (*Morunasaurus annularis*, lateral view of mandible); (2) overlaps dentary past level of tooth row (*Anolis carolinensis*, lateral view of mandible). (ordered).

395. Coronoid, shape of anterolateral dentary process^{N}: (0) extends anteroventrally and smoothly tapers into dentary (*Morunasaurus annularis*, lateral view of mandible); (1) extends anteriorly, with dorsal and ventral margins more parallel sided, terminating in a blunt edge anteriorly (*Heloderma horridum*, lateral view of mandible).



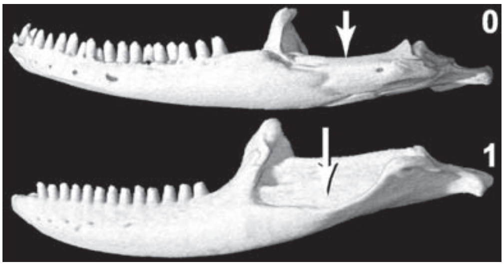
396. Surangular inserts into dentary lateral to the intramandibular septum, entering the intramandibular canal

(which houses the alveolar branch of the inferior alveolar nerve, according to Oelrich 1956): (0) absent (*Pseudopus apodus*, anterior close-up cutaway view of mandible); (1)^N present slightly (*Xenosaurus platyceps*, anterior close-up cutaway view of mandible); (2) present deeply (*Peltosaurus granulosus*, anterior close-up cutaway view of mandible). Gauthier (1982) (ordered).

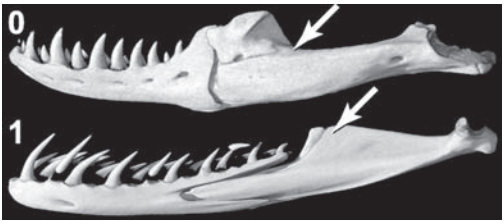


397. Surangular, external foramina^N: (0) two foramina, anterior and posterior (*Brachymeles gracilis*, lateral view of mandible); (1) single foramen (anterior surangular foramen) (*Aspidites melanocephalus*, lateral view of mandible).

398. Adductor fossa: (0) faces dorsomedially, medial wall below lateral wall (*Plica plica*, anterior close-up cutaway view of mandible); (1) faces dorsally, medial/lateral walls same height (*Naja naja*, anterior close-up cutaway view of mandible); (2) no distinct medial wall^N (*Amphisbaena fuliginosa*, anterior close-up cutaway view of mandible); (3)^N faces dorsolaterally, lateral wall below medial wall (*Pareas hamptoni*, anterior close-up cutaway view of mandible). Lee (1998).

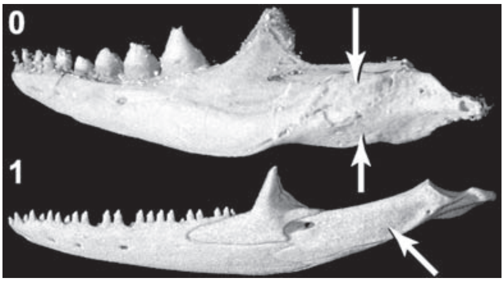


399. Surangular adductor fossa on external face of mandible: (0) shallow and extends ventrally no more than halfway down (*Urostrophus vautieri*, lateral view of mandible); (1) deep and extends ventrally more than half way down (nearly to angular bone) (*Lepidophyma flavimaculatum*, lateral view of mandible). Gauthier (1984).

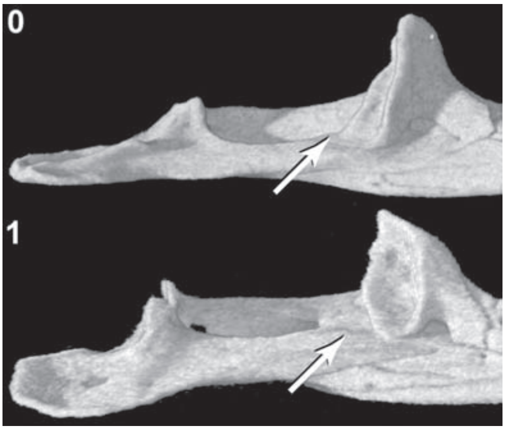


400. Surangular dorsal margin^N: (0) nearly horizontal, rising somewhat toward the coronoid, anterodorsal edge set below level of tooth crowns (*Lanthanotus borneensis*, lateral view of mandible); (1) rises steeply anterodorsally to coronoid, with apex reaching above level of tooth crowns (*Amphisbaena fuliginosa*, lateral view of mandible).

The character is not scored in species lacking a coronoid eminence to avoid redundancy.

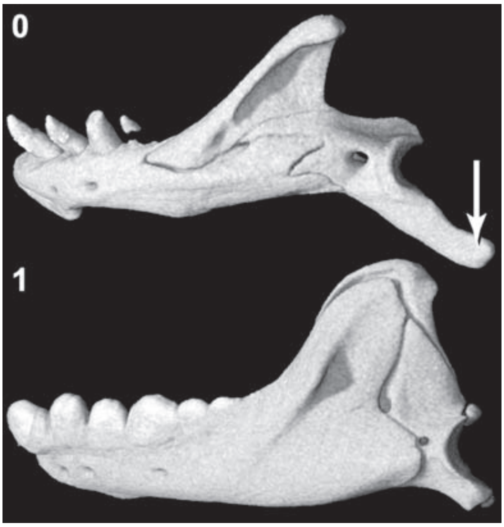


401. Prearticular and surangular fused in adult^N: (0) separate (*Adamisaurus magnidentatus*, lateral view of mandible); (1) fused (*Colobosaura modesta*, lateral view of mandible).



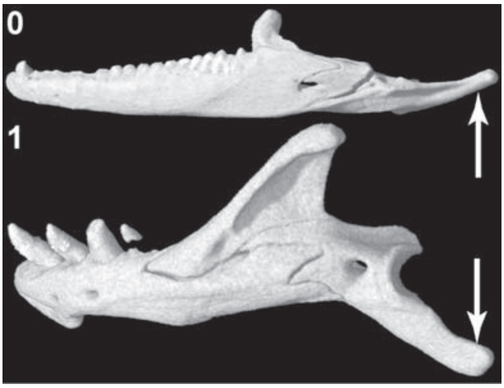
402. Prearticular broadly contacts surangular behind posteromedial process of coronoid, restricting mandibular adductor fossa anteriorly^{N}. (0) absent (*Sphenomorphus solomonis,* medial close-up of posterior mandible; (1) present (*Acontias percivali*, medial close-up of posterior mandible). Although *Feylinia polylepis* has an exceptionally long coronoid posteromedial process, the prearticular and surangular are broadly in contact, resulting in the posterior placement of the adductor fossa. It is accordingly scored as state 1.

403. Prearticular crest: (0) absent (*Takydromus ocellatus*, dorsal close-up of posterior mandible); (1) present (*Lepidophyma flavimaculatum*, dorsal close-up of posterior mandible). Estes et al. (1988).



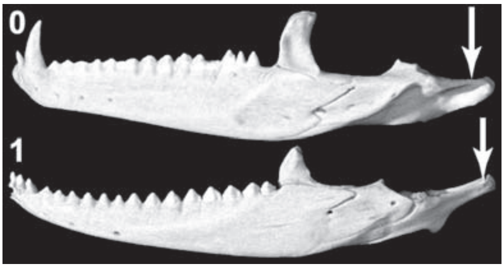
404. Retroarticular process: (0) present (*Rhineura floridana*, lateral view of mandible); (1) very short or absent (*Trogonophis weigmanni,*, lateral view of mandible). Gauthier, Estes and de Queiroz (1988).

405. Retroarticular process orientation (scored with teeth pointing straight up): (0) not inflected medially (*Aeluroscalabotes felinus*, dorsal view of mandible); (1) inflected medially (*Cordylus mossambicus*, dorsal view of mandible). Estes et al. (1988).



406. Retroarticular process orientation in lateral (or posterior) view: (0) extends straight posteriorly (*Agama agama*,

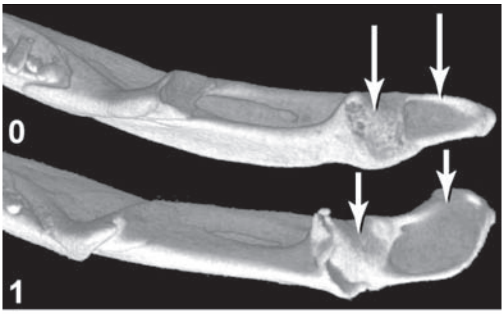
lateral view of mandible); (1) inflected ventrally (*Rhineura floridana*, lateral view of mandible). Gauthier (1982).



407. Retroarticular process dorsal surface ^{N}: (0) horizontal (*Leiolepis belliana*, lateral view of mandible); (1) inclined posterodorsally (*Physignathus cocincinus*, lateral view of mandible).

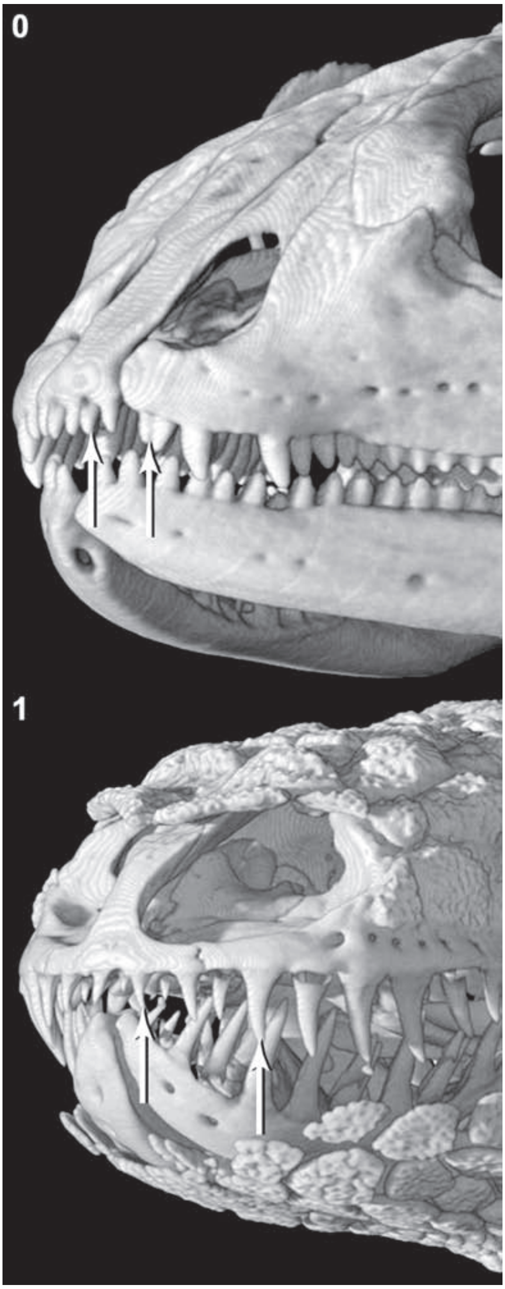
408. Retroarticular process emarginate distally: (0) absent (*Brachymeles gracilis*, dorsal view of mandible); (1) present (*Hymenosaurus clarki*, dorsal view of mandible). Gao and Norell (2000).

409. Retroarticular process, lateral notch forming waist proximally: (0) absent (*Uranoscodon superciliosus*, dorsal view of mandible); (1) present (*Gekko gecko*, dorsal view of mandible). Estes et al. (1988).

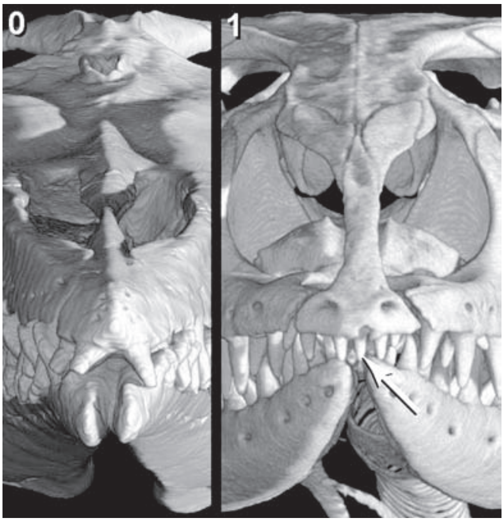


410. Retroarticular process breadth (greatest width) relative to mandibular condyle (glenoid): (0) narrower (*Lacerta viridis*, dorsal close-up of posterior mandible); (1) wider (*Amphiglossus splendidus*, dorsal close-up of posterior mandible). Estes et al. (1988).

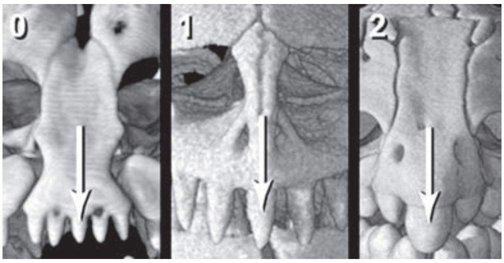
411. Prearticular, pterygoideus process (=angular process of Oelrich 1956) (i.e., part of retroarticular process): (0) absent (*Takydromus ocellatus*, dorsal view of mandible); (1) present (*Liolaemus bellii,* dorsal view of mandible). Estes et al. (1988).



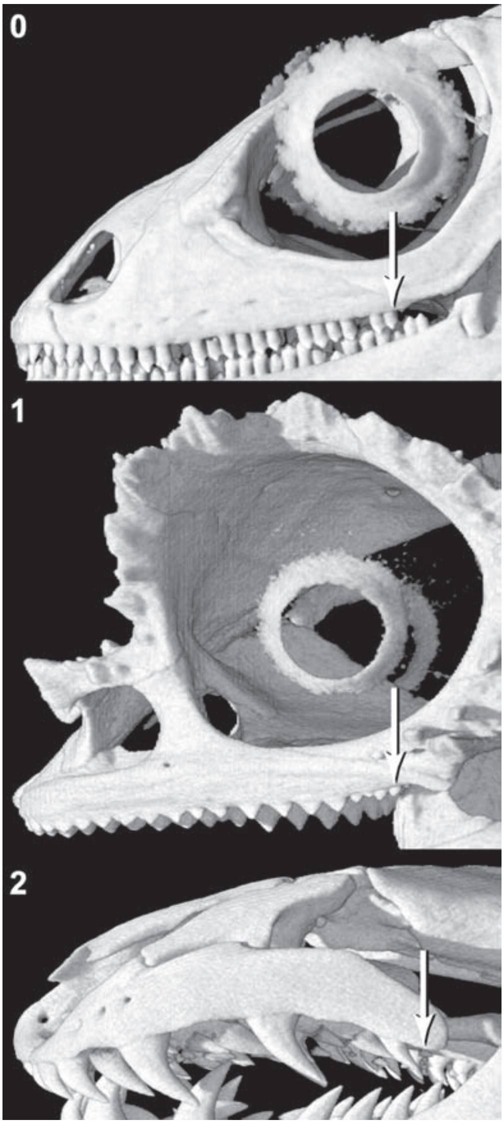
412. Premaxillary teeth (apart from median tooth): (0) similar size or larger than anterior maxillary teeth (*Plica plica*, oblique anterior close-up of snout); (1) distinctly smaller than anterior maxillary teeth (*Heloderma horridum*, oblique anterior close-up of snout). Pregill et al. (1986).



413. Median premaxillary tooth: (0) absent (*Plotosaurus bennisoni*, anterior close-up of snout); (1) present (*Varanus acanthurus*, anterior close-up of snout). Lee (1998).

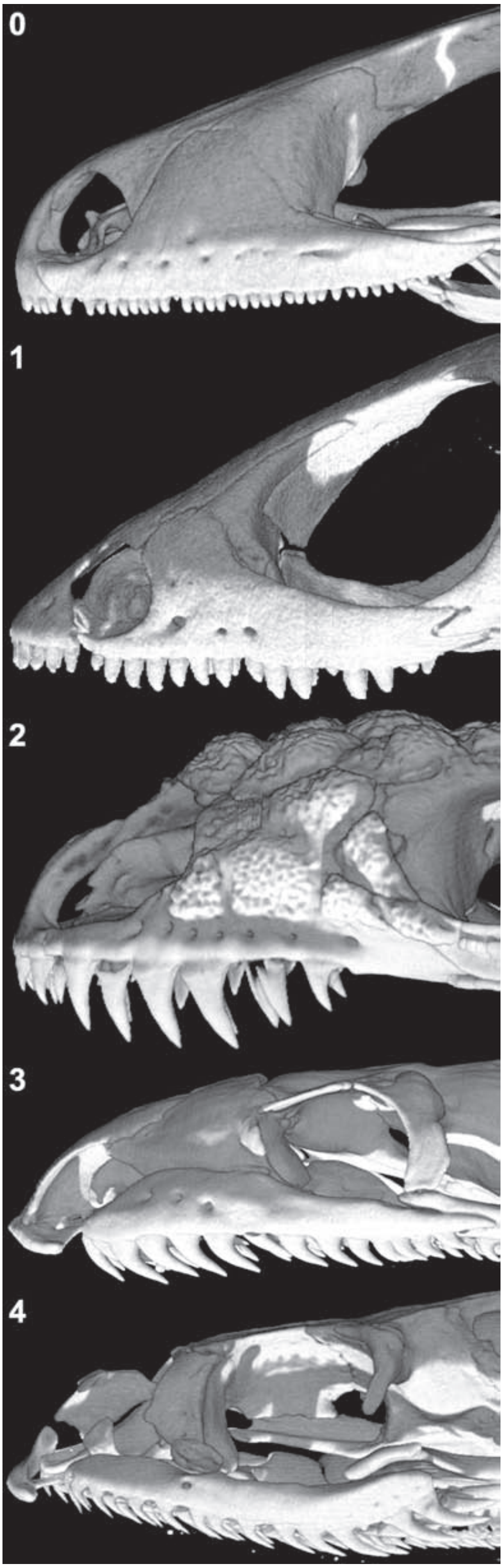


414. Enlarged median tooth on fused premaxilla: (0) median tooth same size as other premaxillary teeth (*Plica plica*, anterior close-up of snout); (1) slightly enlarged median premaxillary tooth (*Dibamus novaeguineae*, anterior close-up of snout); (2) greatly enlarged median premaxillary tooth (*Amphisbaena fuliginosa*, anterior close-up of snout). Lee (1998) (ordered).



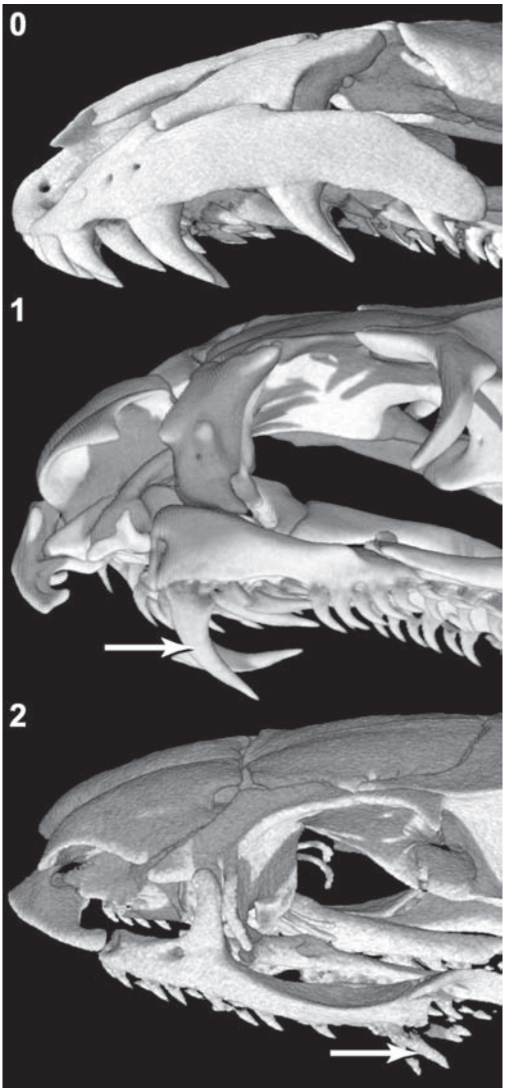
415. Maxillary tooth row extent posteriorly^{N}: (0) to roughly midorbit (or anterior) (*Basiliscus basiliscus*, lateral close-up of anterior skull); (1) to posterior third of orbit (*Brookesia brygooi*, lateral close-up of anterior skull); (2) posterior to orbit (*Anilius scytale*, lateral close-up of anterior skull) (ordered).

The posterior limit of the tooth row is partly correlated with the posterior extension of the maxilla (character 120), as without a maxilla, there can be no teeth. Nevertheless, the posterior limit of the tooth row can terminate well before the posterior limit of the maxilla (character 124), so the characters are scored separately (see also character 418 below).



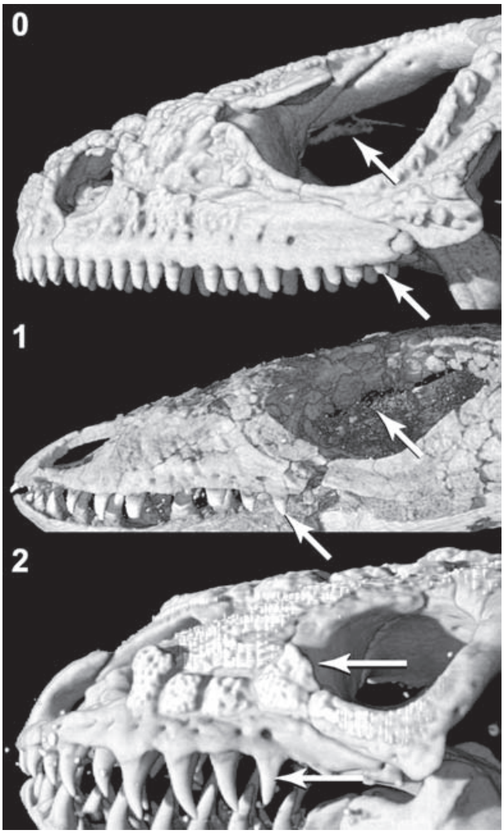
416. Maxillary tooth crown height^{N}: (0) constant throughout tooth row (*Eublepharis macularius*, lateral close-up of

anterior skull); (1) length varies, resulting in sinuous occlusal surface (*Pholidobolus montium*, lateral close-up of anterior skull); (2) length varies, resulting in convex occlusal surface (*Heloderma horridum*, lateral close-up of anterior skull); (3) length decreases posteriorly (*Aspidites melanocephalus*, lateral close-up of snout); (4) length increases posteriorly (*Thamnophis marcianus*, lateral close-up of anterior skull).



417. Maxilla, enlarged teeth ("fangs") (relative to adjacent teeth)^{N}: (0) absent (*Anilius scytale*, lateral close-up of anterior skull); (1) present on anterior maxilla (*Notechis scutatus*, lateral close-up of anterior skull); (2) present on posterior maxilla (*Aparallactus werneri*, lateral close-up of anterior skull).

Fangs of uncertain position on the maxilla—i.e., whether they are "front" or "rear" fangs—are scored as indeterminable. Unlike elapids, viperids have only fangs, and no other teeth, on the maxilla, so it cannot be determined whether or not those fangs are in the front or rear of the tooth row. *Lycophidion capense*, in which the single fang is neither at the anterior nor posterior end of the maxilla but in the middle of the tooth row, is also scored as indeterminable for this character.



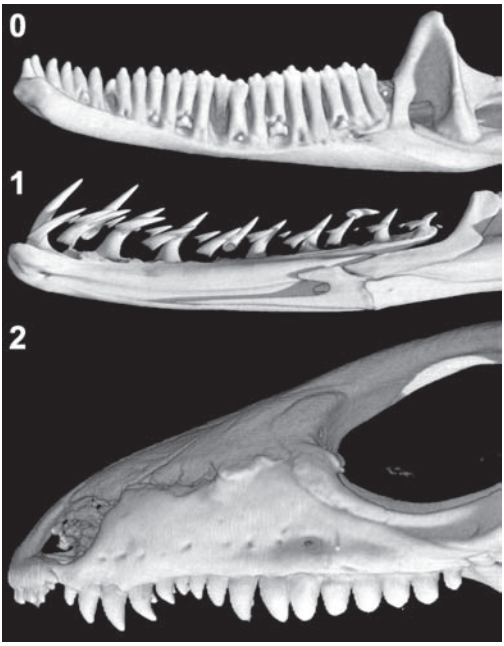
418. Maxilla tooth row length: (0) to or behind midorbit (*Xenosaurus grandis*, lateral close-up of anterior skull); (1)^{N} anterior to midorbit (*Gobiderma pulchrum*, lateral close-up of anterior skull); (2) anterior to orbit (*Heloderma suspectum*, lateral close-up of anterior skull). Pregill et al. (1986) (ordered).

Unlike character 415, which tracks a lengthening tooth tow, this character traces a shortening tooth row. Both start from a condition in which the tooth row extends roughly to the level of middle of the orbit.

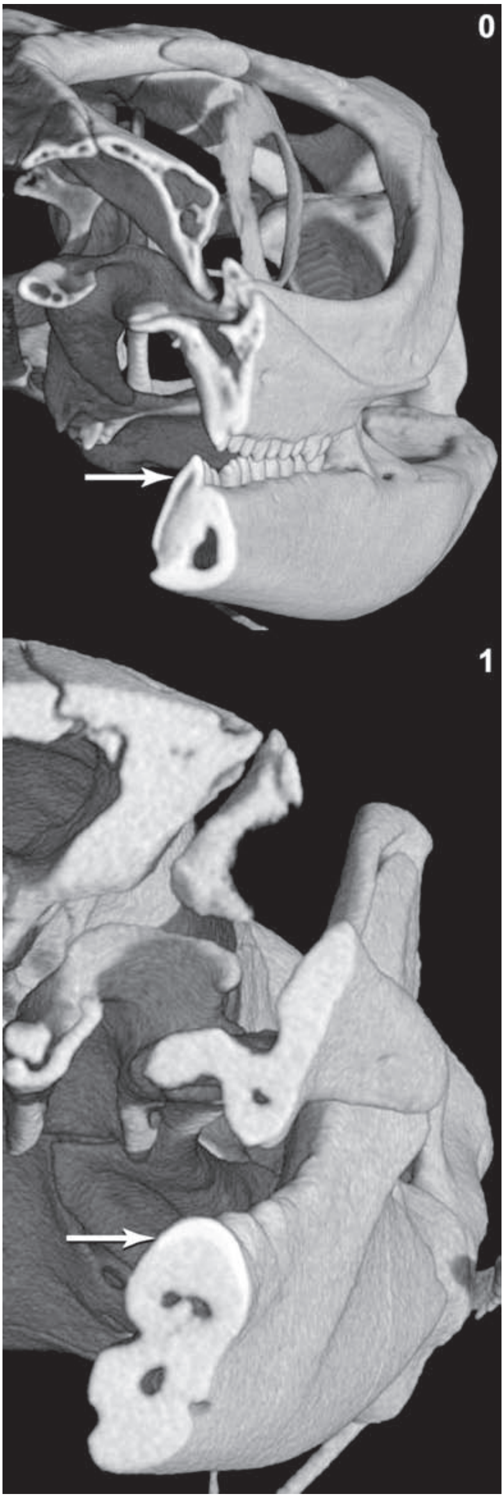
419. Premaxillary tooth count: (0)^{N} none; (1)^{N} one to three; (2)^{N} four to six; (3)^{N} seven to nine; (4)^{N} 10 or more. de Queiroz (1987) (ordered).

420. Maxillary tooth count: (0) 0, Conrad (2008); (1)^{N} 2–5; (2)^{N} 7–15; (3)^{N} 16–27; (4)^{N} 31 or more. Lee (1998) (ordered).

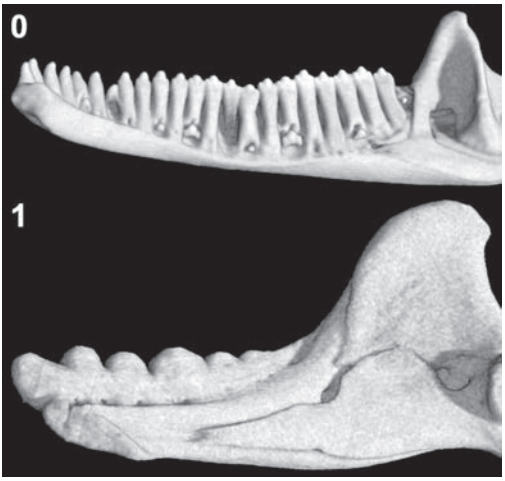
421. Dentary tooth count: (0) 0, Conrad (2008); (1)^{N} 4–9; (2)^{N} 10–20; (3)^{N} 21–35; (4)^{N} 36 or more. Lee (1998) (ordered).



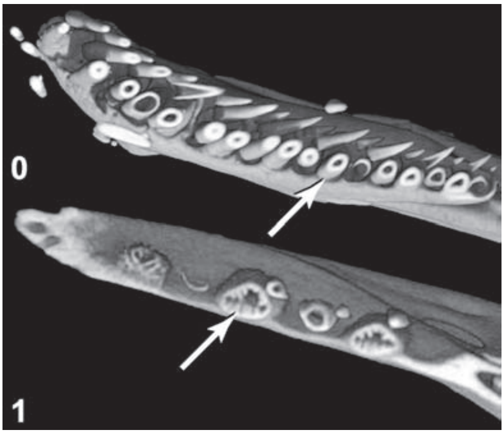
422. Marginal teeth^N: (0) all vertical (*Plica plica*, medial close-up of anterior mandible); (1) all recurved (*Python molurus*, medial close-up of anterior mandible); (2) anterior teeth recurved and posterior teeth vertical (*Tupinambis teguixin*, lateral close-up of snout).



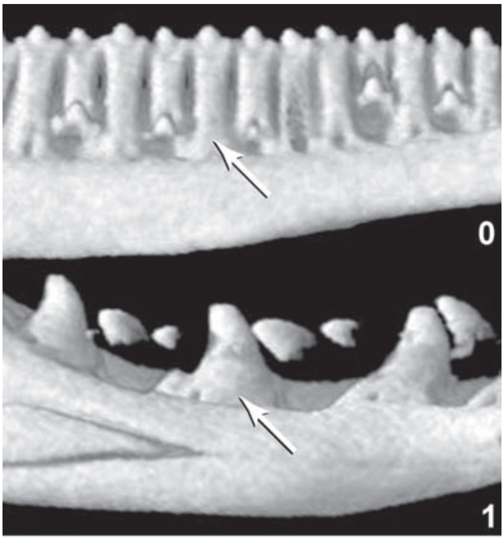
423. Position of marginal teeth relative to tooth-bearing element: (0) on medial side of tooth-bearing element (*Plica plica*, anterior close-up cutaway view of snout); (1) near/on apical margin of tooth-bearing element (*Trogonophis weigmanni*, anterior close-up cutaway view of snout). Estes et al. (1988).



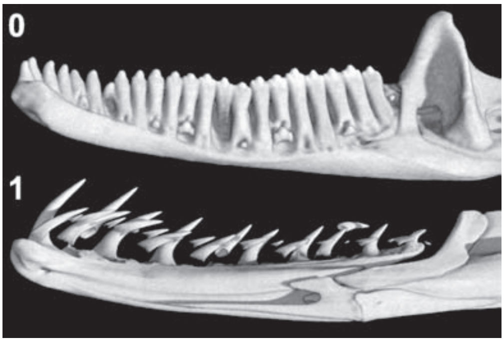
424. Fusion of marginal teeth^N: (0) unfused to each other (*Plica plica*, medial close-up of anterior mandible); (1) fused to each other (*Trogonophis weigmanni,* medial close-up of anterior mandible).



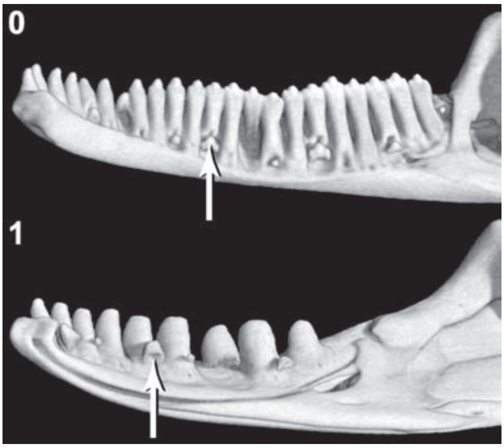
425. Bases of marginal teeth: (0) smooth, dentine and enamel not infolded (*Boa constrictor*, dorsal close-up cutaway view of anterior mandible); (1) dentine and enamel infolded into pulp cavity (“plicidentine’), resulting in longitudinal grooves externally at base of teeth (*Varanus acanthurus*, dorsal close-up cutaway view of anterior mandible). Pregill et al. (1986).



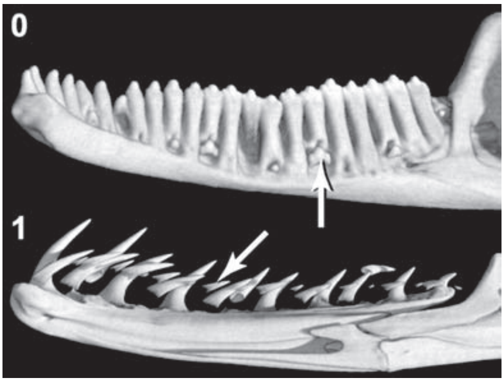
426. Bases of marginal teeth expanded: (0) absent (*Leiocephalus barahonensis*, medial close-up view of anterior mandible); (1) present (*Micrurus fulvius*, medial close-up view of anterior mandible). Conrad (2008).



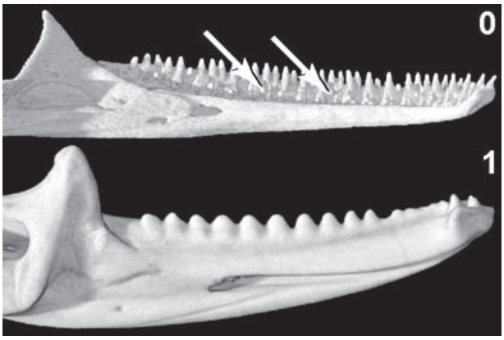
427. Marginal tooth spacing: (0) crowns closely spaced (*Plica plica*, medial close-up of anterior mandible); (1) crowns separated by large gaps (*Python molurus*, medial close-up of anterior mandible). Lee (1998).



428. Position of replacement teeth: (0) lingual (*Plica plica*, medial close-up of anterior mandible); (1) posterolingual (*Varanus exanthematicus*, medial close-up of anterior mandible). Pregill et al. (1986).

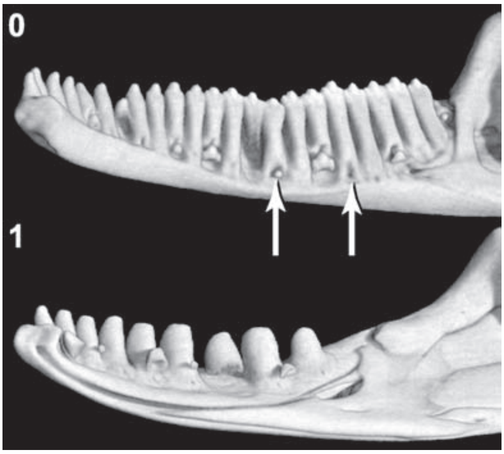


429. Orientation of replacement teeth: (0) erupt upright, growing straight upwards into functional position (*Plica plica*, medial close-up of anterior mandible); (1) erupt horizontally, and then rotate through 90° about the base into functional position (*Python molurus*, medial close-up of anterior mandible). Lee (1997b).

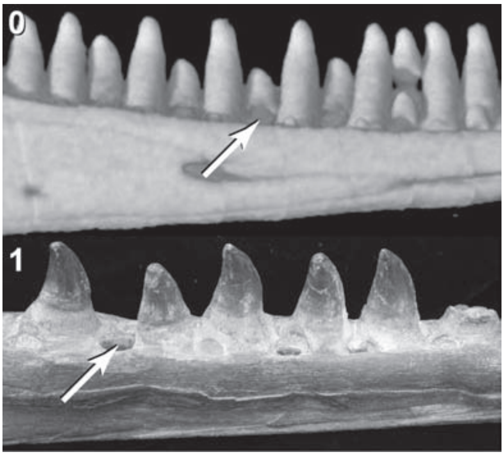


430. Tooth replacement^{N}: (0) present (*Coleonyx variegatus*, medial close-up of anterior mandible); (1) absent (*Pogona vitticeps*, medial close-up of anterior mandible).

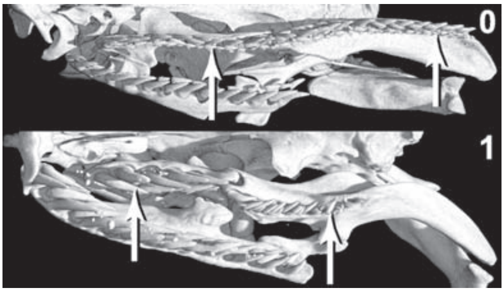
R. Nydam (pers. comm.) noted that *Polyglyphanodon*, here scored as ? because of the poor quality of our CT-scanned specimen, is well known to lack tooth replacement.



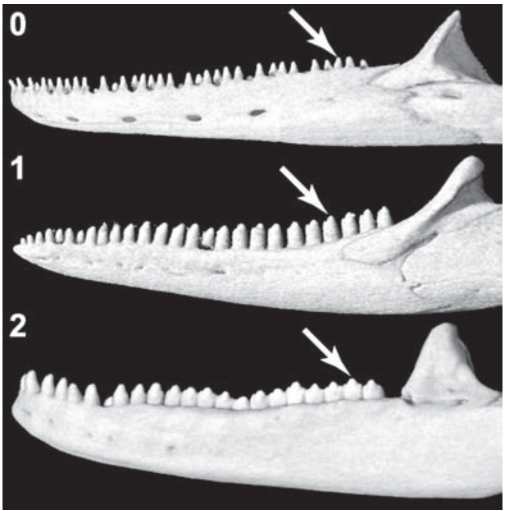
431. Resorption pits: (0) present (*Plica plica*, medial close-up of anterior mandible); (1) absent (*Varanus exanthematicus*, medial close-up of anterior mandible). Pregill et al. (1986).



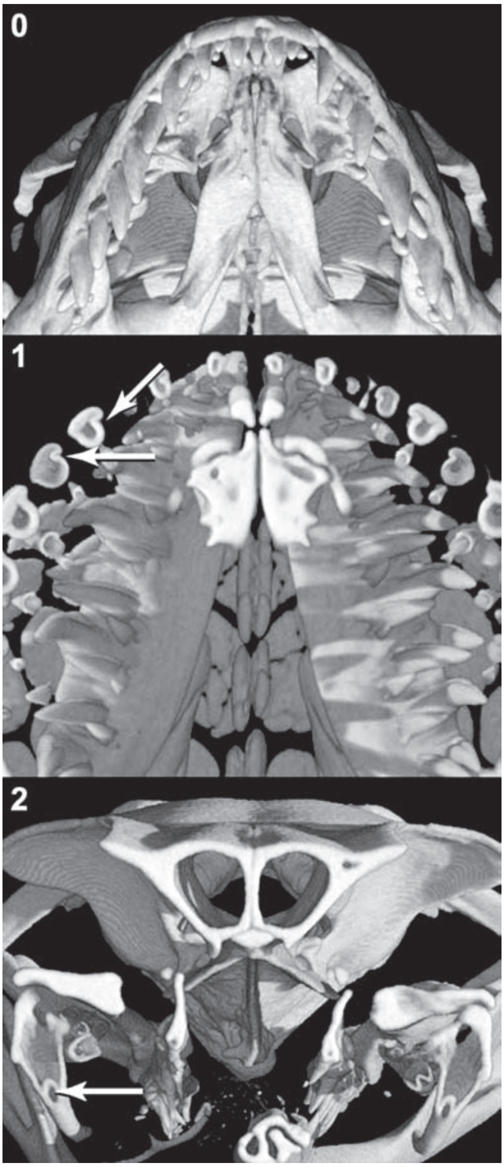
432. Development of resorption pits: (0) at base of teeth (*Platysaurus imperator*, medial close-up of mandible); (1) on bony tooth pedicel (*Clidastes propython*, medial close-up of mandible). Rieppel and Zaher (2000a).



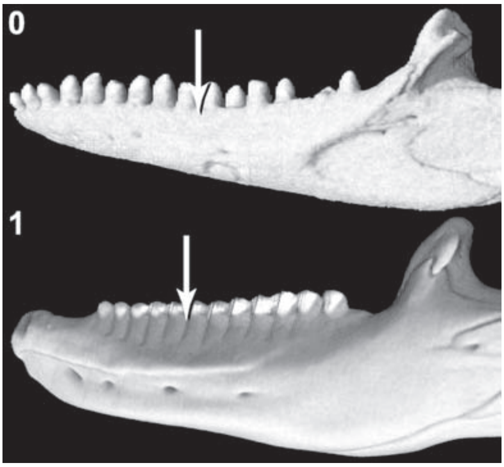
433. Palatal teeth: (0) constant in size across palatal tooth row (*Coluber constrictor*, ventral view of skull); (1) decrease in size posteriorly (*Boa constrictor*, ventral view of skull). Mahler and Kearney (2006).



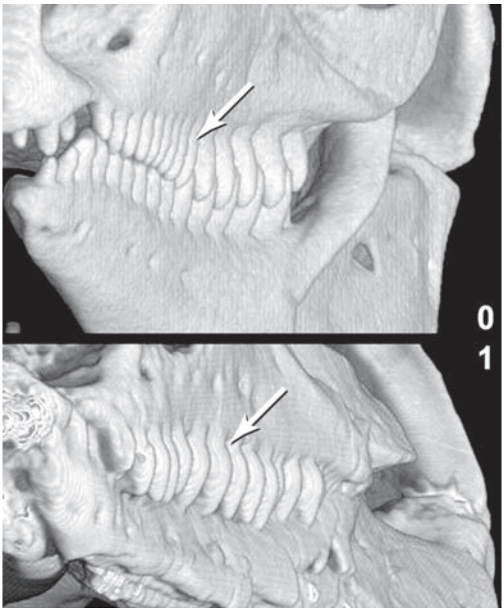
434. Cusps on posterior teeth^{N}: (0) unicuspid (*Coleonyx variegatus*, lateral close-up of anterior mandible); (1) bicuspid (*Aspidoscelis tigris*, lateral close-up of anterior mandible); (2) tricuspid (*Plica plica*, lateral close-up of anterior mandible).



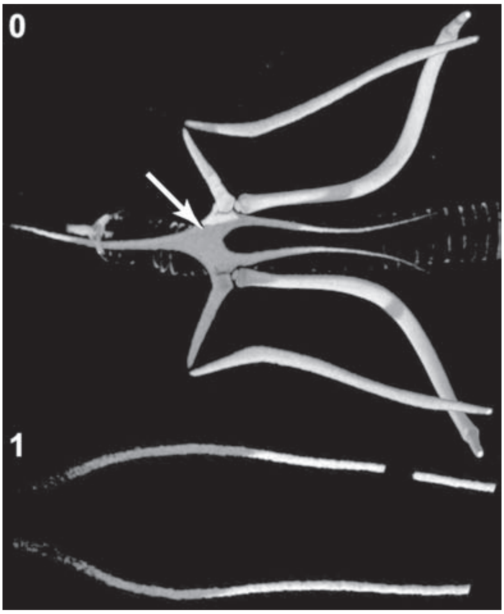
435. Venom groove on anteromedial surface of teeth^{N}: (0) absent (*Varanus acanthurus*, ventral close-up of snout); (1) present, unenclosed (*Heloderma horridum*, dorsal close-up cutaway view of snout); (2) present, enclosed tube (*Agkistrodon contortrix*, anterior close-up cutaway view of snout) (ordered).



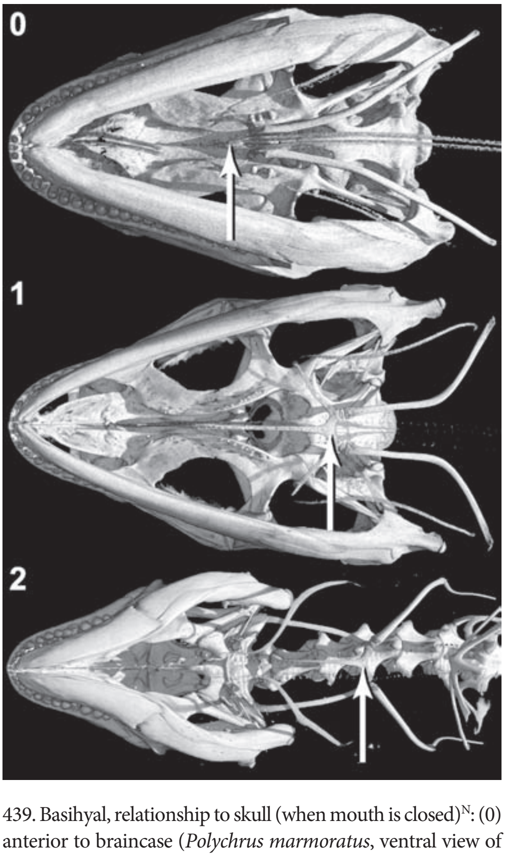
436. V-shaped wear facets of maxillary teeth incised on lateral face of dentary between dentary teeth: (0) absent (*Scincus scincus*, lateral close-up of anterior mandible); (1) present (*Uromastyx aegyptius*, lateral close-up of anterior mandible). Evans et al. (2002).



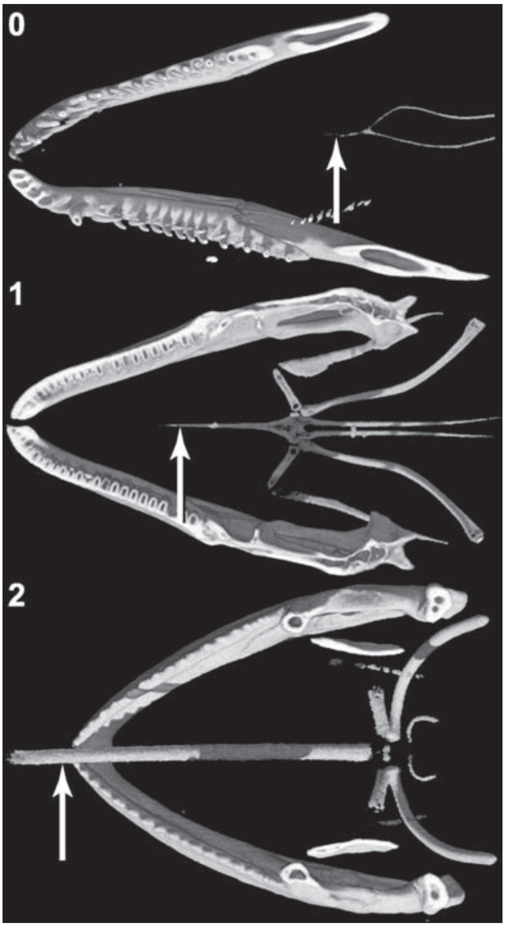
437. Teeth swollen, set off from tooth shafts above jaw parapet^{N}: (0) absent (*Teius teyou*, anterior close-up view of snout); (1) present (*Gobinatus arenosus*, anterior close-up view of snout).



438. Basihyal^{N}: (0) present (*Sauromalus ater*, dorsal view of hyoid apparatus); (1) absent (*Azemiops feae*, dorsal view of hyoid apparatus).

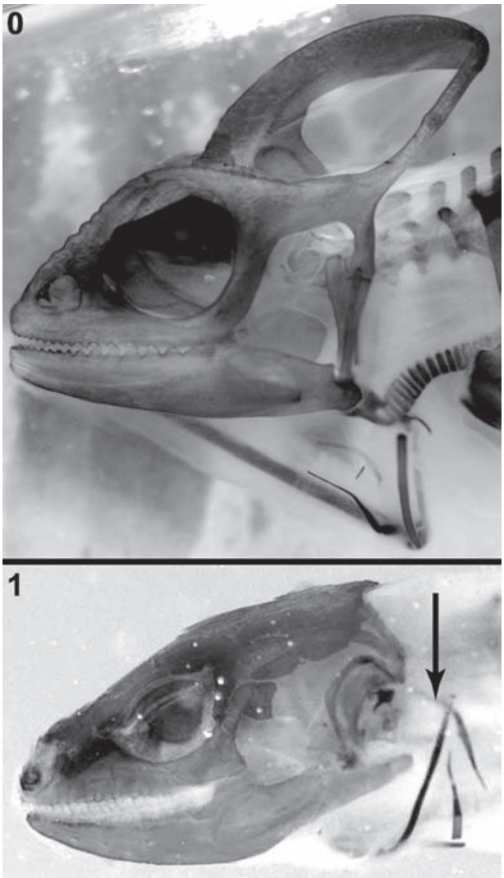


439. Basihyal, relationship to skull (when mouth is closed)^{N}: (0) anterior to braincase (*Polychrus marmoratus*, ventral view of hyoid apparatus); (1) ventral to braincase (*Gambelia wislizenii*, ventral view of hyoid apparatus); (2) posterior to braincase (*Varanus exanthematicus*, ventral view of hyoid apparatus).

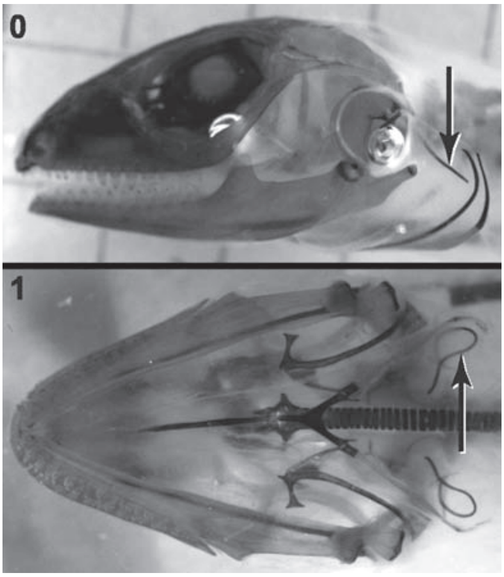


440. Hyoid, lingual process length^{N}: (0) short (*Lamprophis fuliginosus*, dorsal view of hyoid apparatus); (1) medium (*Leiocephalus barahonensis*, dorsal view of hyoid apparatus); (2) long (*Brookesia brygooi*, dorsal view of hyoid apparatus) (ordered).

441. Hyoid, distal part of lingual process: (0) not detached (*Gambelia wislizenii*, dorsal view of hyoid apparatus); (1) detached (*Tupinambis teguixin*, dorsal view of hyoid apparatus). Schwenk (1988).

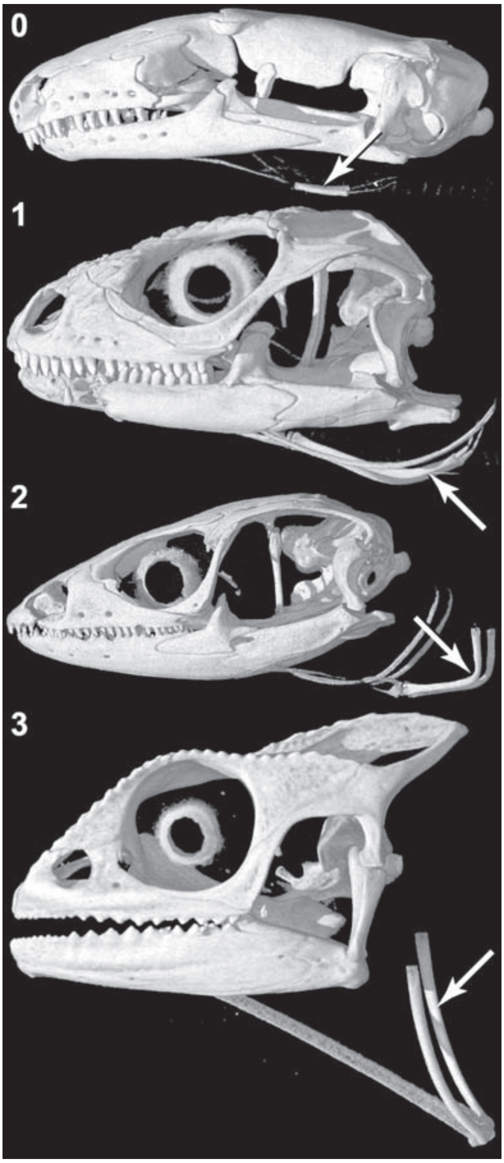


442. Free epibranchials (=second epibranchial): (0) absent (*Chamaeleo calyptratus*, lateral view of head); (1) present (*Lacerta viridis*, lateral view of head). Gauthier, Estes and de Queiroz (1988).

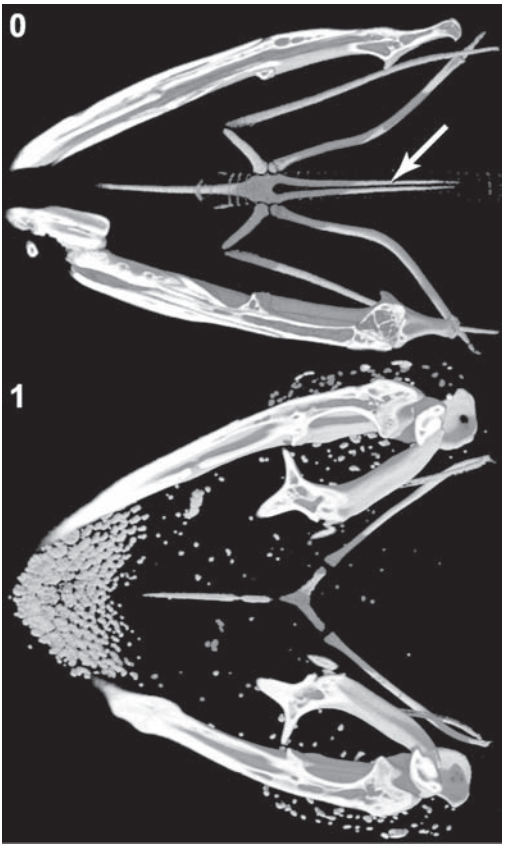


443. Free epibranchial^{N}: (0) simple (short or sigmoidal) (*Teius teyou*, lateral view of skull); (1) complex (has hooks or processes, and/or doubles back on itself) (*Phelsuma lineata*, ventral view of skull).

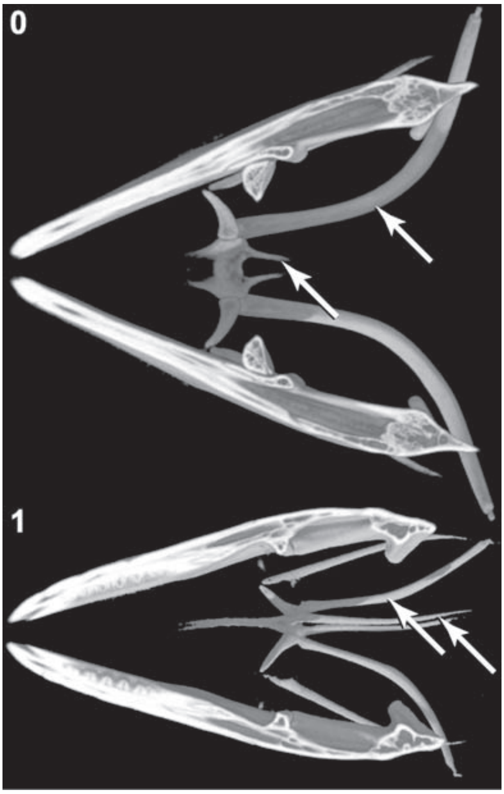
444. First epibranchial^{N}: (0) shorter than first ceratobranchial (*Leiolepis belliana*, lateral view of skull); (1) longer than or nearly equal to first ceratobranchial (*Varanus exanthematicus*, lateral view of skull).



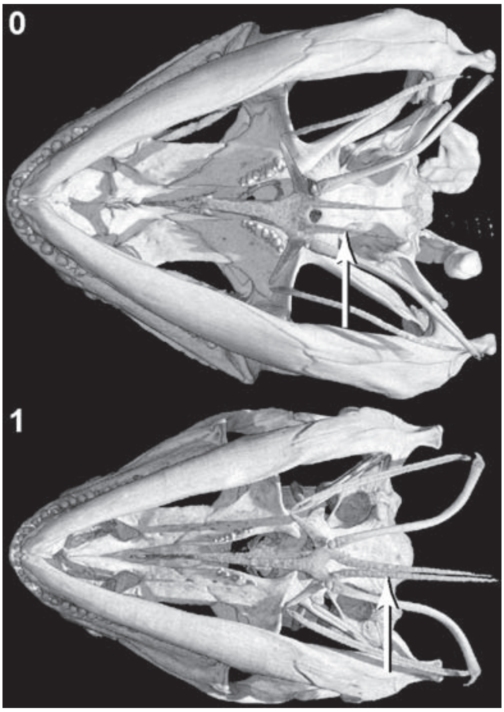
445. First ceratobranchial (in lateral view)^{N}: (0) no dorsolateral angulation (*Anelytropsis papillosus*, lateral view of skull); (1) weak dorsolateral angulation (has a distinct bend) (*Oplurus cyclurus*, lateral view of skull); (2) strong dorsolateral angulation (90° or more) (*Colobosaura modesta*, lateral view of skull); (3) entire element straight or oriented vertically (*Chamaeleo laevigatus*, lateral view of skull).



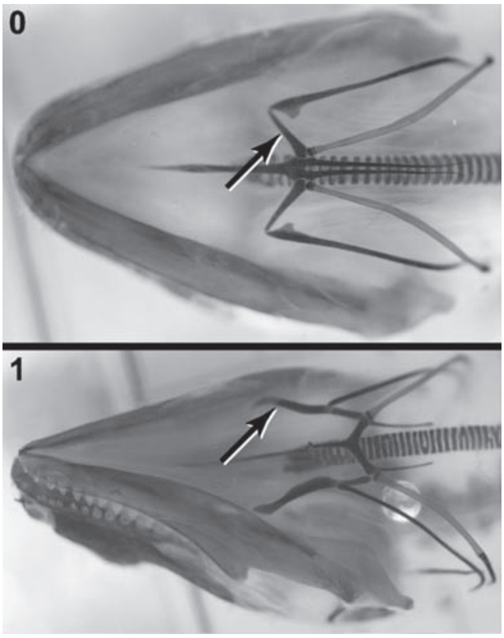
446. Second ceratobranchials: (0) present (*Oplurus cyclurus*, dorsal view of hyoid apparatus); (1) absent (*Gekko gecko*, dorsal view of hyoid apparatus). Estes et al. (1988).



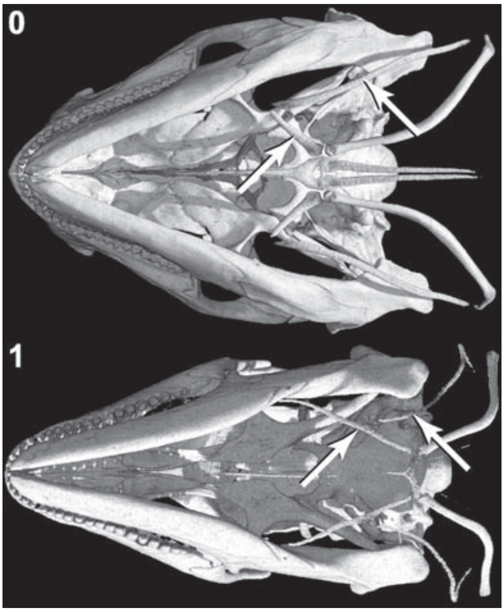
447. Second ceratobranchial: (0) shorter than first ceratobranchial (*Pogona vitticeps*, dorsal view of hyoid apparatus), Lang (1989); (1) nearly equal to or longer than first ceratobranchial (*Basiliscus basiliscus*, dorsal view of hyoid apparatus). Etheridge and de Queiroz (1988).



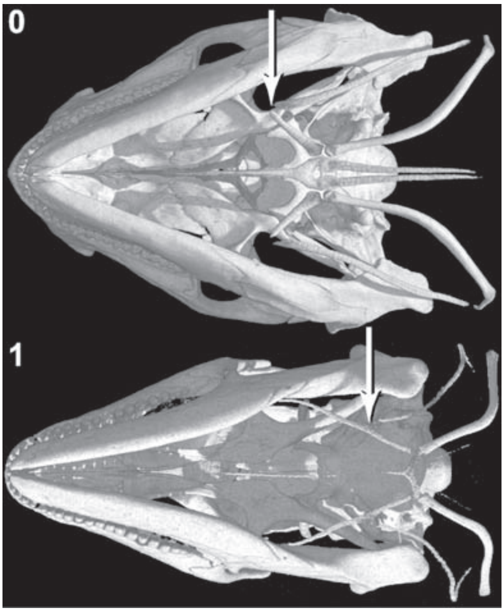
448. Second ceratobranchial apposed on midline: (0) absent (*Leiosaurus catamarcensis*, ventral view of hyoid apparatus); (1) present (*Chalarodon madagascariensis*, ventral view of hyoid apparatus). McGuire (1996).



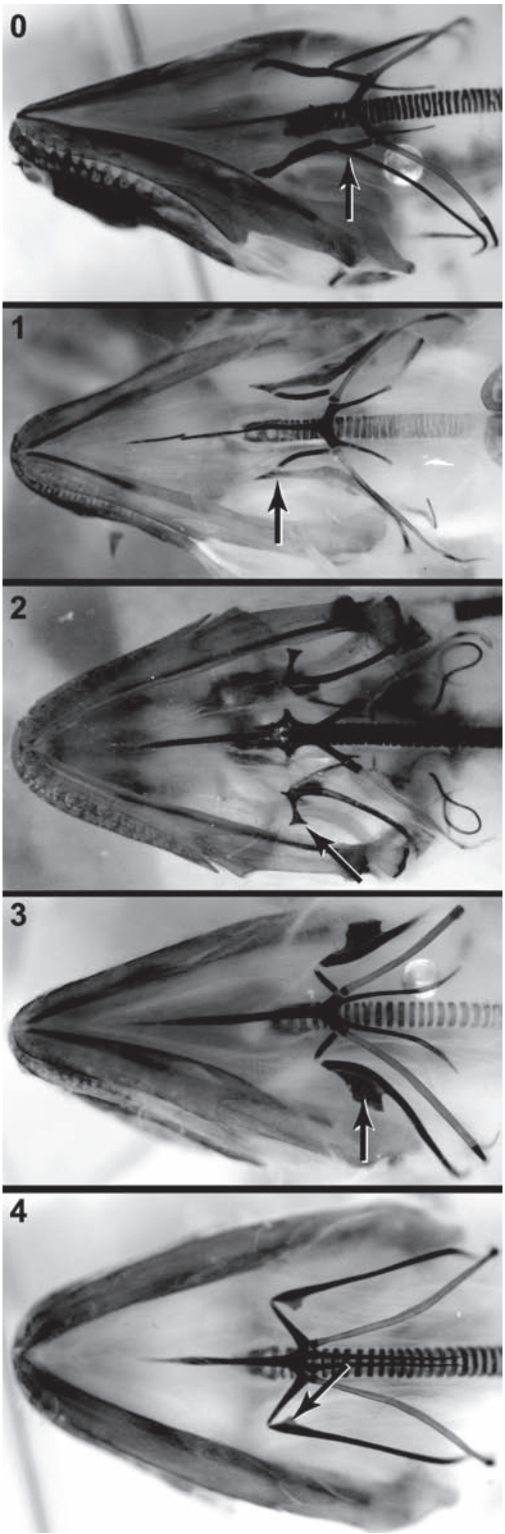
449. Large, wing-like hyoid cornu: $(0)^N$ absent (*Pristidactylus torquatus*, ventral view of hyoid apparatus); $(1)^N$ present (*Teius teyou*, ventral view of hyoid apparatus). Kluge (1987).



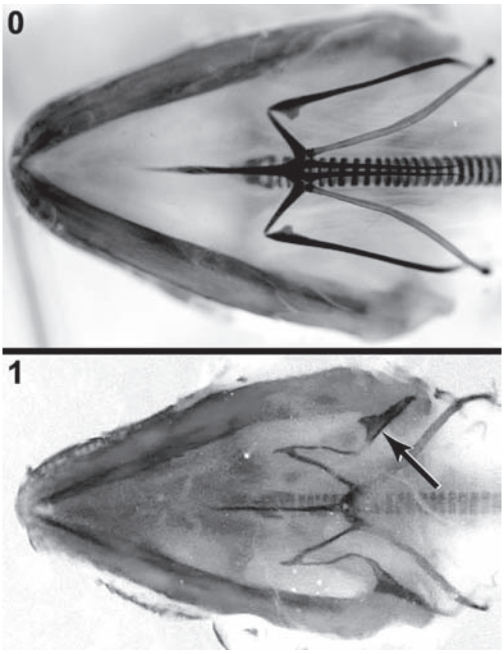
450. Hyoid cornu: $(0)^N$ less than the length of the epihyal (*Dipsosaurus dorsalis*, ventral view of hyoid apparatus); $(1)^N$ greater than or equal to the length of the epihyal (*Pholidobolus montium*, ventral view of hyoid apparatus). Presch (1988).



451. Epihyal^N: (0) meets hyoid cornu at (or near) its distal end (*Dipsosaurus dorsalis*, ventral view of hyoid apparatus); (1) meets hyoid cornu along its body (*Pholidobolus montium*, ventral view of hyoid apparatus).



452. Epihyal^{N}: (0) expansion or elaboration at proximal end absent (*Teius teyou*, ventral view of hyoid apparatus); (1) simple expansion at proximal end present (*Plestiodon fasciatus*, ventral view of hyoid apparatus); (2) hook-like elaboration at proximal end present (*Phelsuma lineata*, ventral view of hyoid apparatus); (3) lateral flange at proximal end present (*Lacerta viridis*, ventral view of hyoid apparatus); (4) medial flange at proximal end present (*Pristidactylus torquatus*, ventral view of hyoid apparatus).



453. Lateral flange at midpoint of epihyal^{N}: (0) absent (*Pristidactylus torquatus*, ventral view of hyoid apparatus); (1) present (*Elgaria multicarinata*, ventral view of hyoid apparatus).

454. Presacral vertebrae number reduction: (0) 24 or more presacrals; (1) 23 presacrals, Etheridge and de Queiroz (1988); (2) fewer than 23 presacrals. Estes et al. (1988) (ordered).

455. Presacral vertebrae number increase I: (0) 24 or fewer; (1) 25; (2) 26; (3)^{N} 27; (4)^{N} 28 or more. Estes et al. (1988) (ordered).

For characters 455–458, in the absence of a sacral attachment, the last trunk vertebra in here considered to be the first bearing a distally bifid rib.

456. Presacral vertebrae number increase II: (0) 32 presacrals or fewer; (1) 33–39; (2) 50–55; (3) 61–84; (4)^{N} 89 or more. Lee and Scanlon (2002) (ordered).

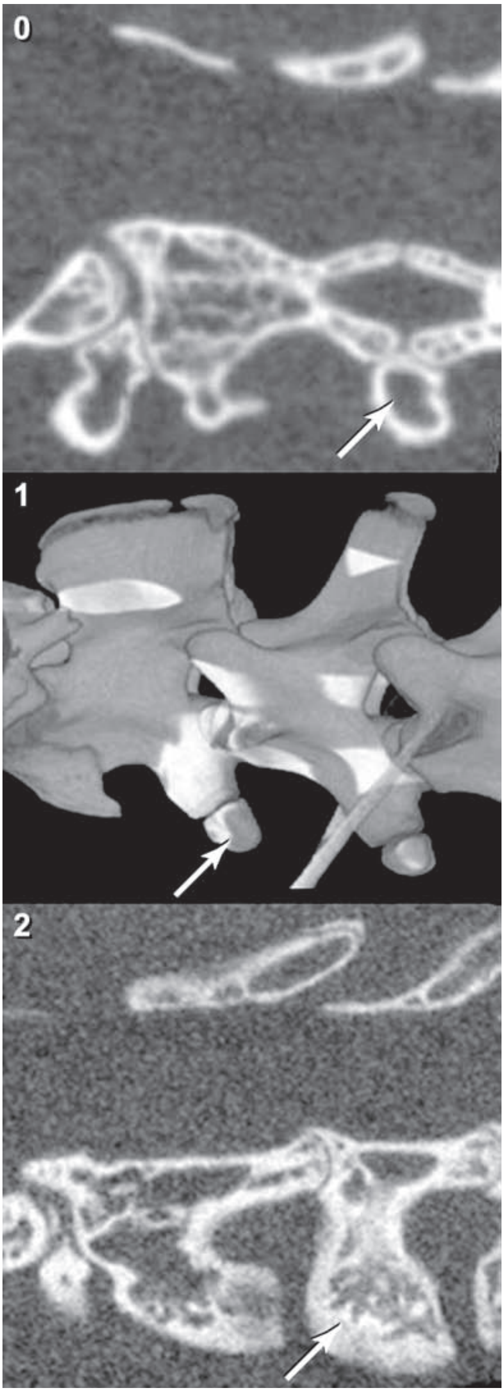
457. Presacral vertebrae number increase III: (0) less than 104; (1)^{N} 118–132 (2)^{N} 144–156; (3)^{N} 168–180; (4)^{N} 184 or more. Lee and Scanlon (2002) (ordered).

458. Presacral vertebrae number increase IV: (0) less than 193; (1)^{N} 197–209; (2)^{N} more than 219. Lee and Scanlon (2002) (ordered).

459. Cervical vertebra number reduction: (0) six or more; (1)^{N} five; (2)^{N} four; (3)^{N} three; (4)^{N} two. Estes et al. (1988) (ordered).

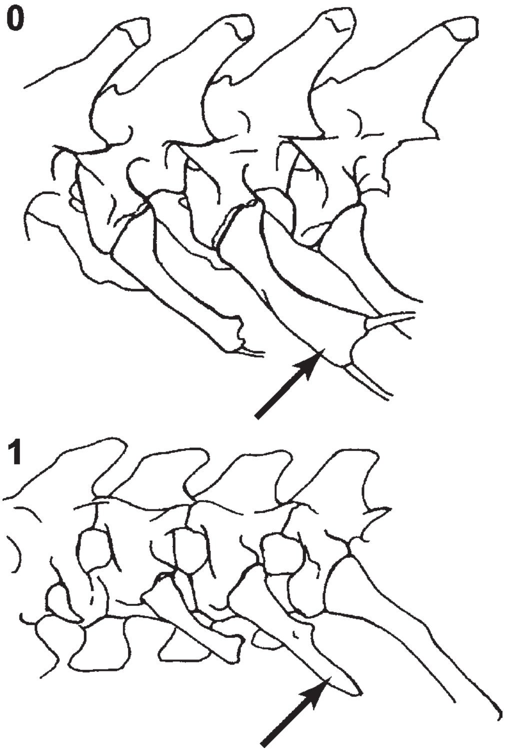
For characters 459–460, "cervical" refers to those anterior vertebrae retaining a primitive rib morphology (short and broad, with pointed cartilaginous apices); the two following ribs between the shoulders that are distinctly longer, narrower, and have blunt, unfinished bony apices, are here considered post-cervical. That yields a primitive count of six for lizards and other amniotes, rather than the usual count of eight based on the first vertebrae whose cartilaginous ventral rib segment contacts the cartilaginous sternum (see character 477).

460. Cervical vertebrae number increase: (0) six or fewer; (1)^{N} seven; (2)^{N} eight or more. Pregill et al. (1986) (ordered).



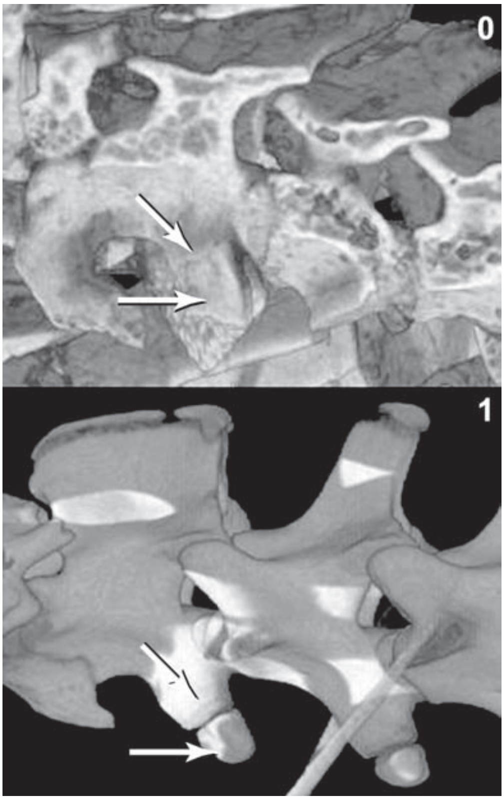
461. Cervical intercentrum position: (0) intercentral (*Teratoscincus przewalskii,* sagittal slice through cervical vertebrae); (1) posterior end of preceding centrum (*Varanus exanthematicus*, lateral view of cervical vertebrae); (2) anterior end of following centrum (*Colobosaura modesta*, sagittal slice through cervical vertebrae); (3)^{N} absent. Estes et al. (1988).

Based on late embryos of *Bothrops asper* (UMMZ 175987) and *Lichanura trivirgata* (YPM HERR 012892), crown snakes are regarded as having lost all trunk intercentra except in the atlas-axis complex; only pedicels, downgrowths of the pleurocentra, remain. The cartilaginous pedicles in these species are continuous with the pleurocentra, while intercentra are separate condensations sutured to the pleurocentra. Moreover, ossification spreads distally from the body of the pleurocentra into the pedicles, rather than arising from a separate center of ossification as in intercentra.

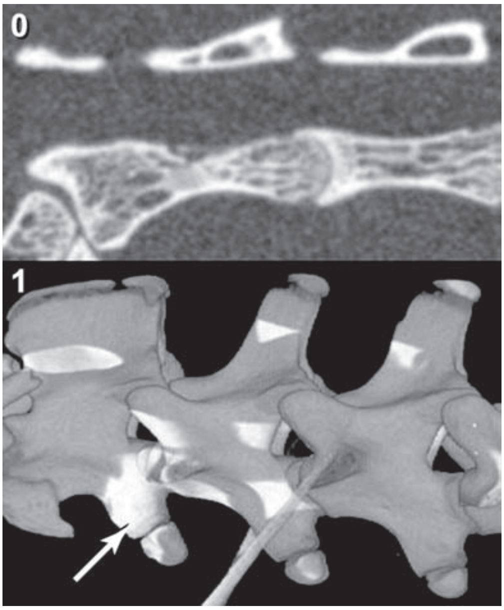


462. Cervical rib ossified portion shape^{N}: (0) widens distally, at least in last cervical (*Scincus mitratus*, lateral view of cervical vertebrae); (1) tapers distally (*Crotaphytus collaris*, lateral view of cervical vertebrae).

463. Cervical ribs start on vertebra number: (0) two; (1) three; (2) four; (3) five; (4) six. Estes et al. (1988) (ordered).



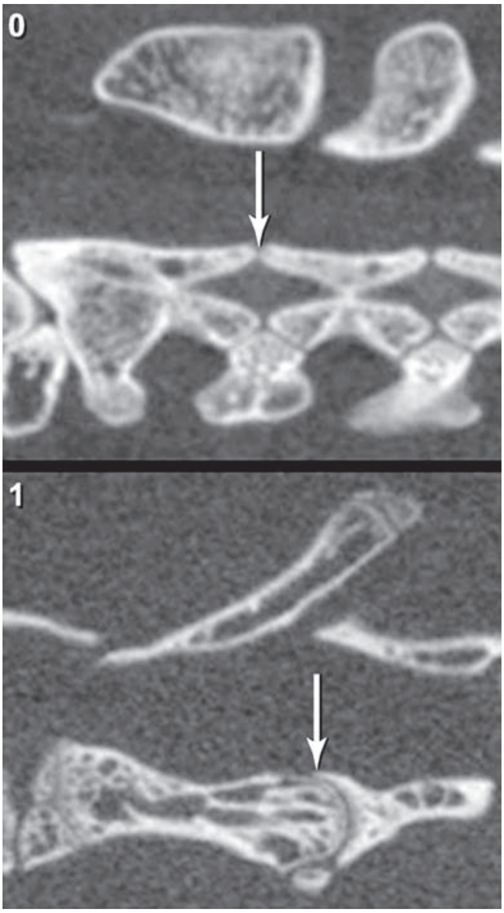
464. Cervical intercentrum length relative to pedicle length^{N}: (0) intercentrum longer than pedicle (*Peltosaurus granulosus*, lateral cutaway view of cervical vertebrae); (1) intercentrum shorter than pedicle (*Varanus exanthematicus*, lateral view of cervical vertebrae).



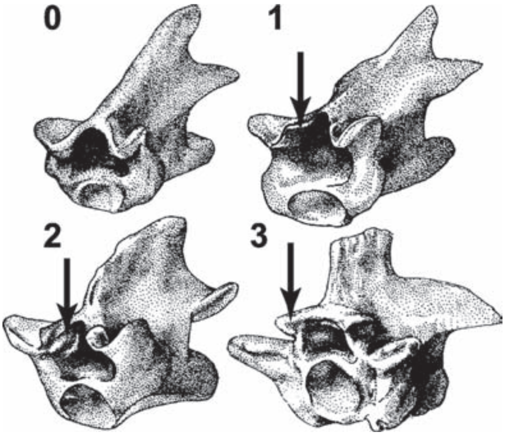
465. Cervical pedicle (outgrowth of pleurocentrum to which intercentrum may attach): (0) absent (*Agama agama*, sagit-

tal slice through cervical vertebrae); (1) projecting ventrally with discrete fore and aft margins (*Varanus exanthematicus*, lateral view of cervical vertebrae). Pregill et al. (1986).

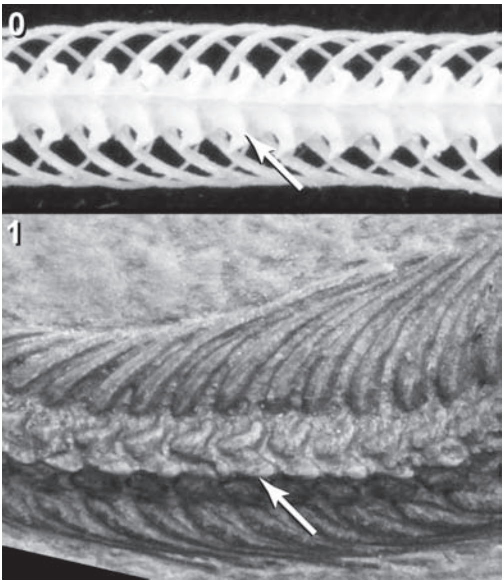
466. Vertebral pedicle ("hypapophysis") posterior extent^{N}: (0) in anterior half of vertebral column; (1) throughout vertebral column.



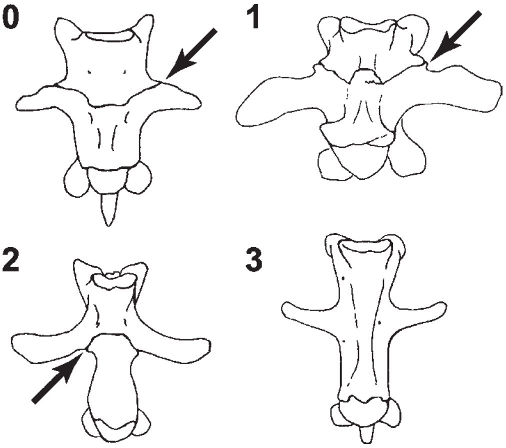
467. Vertebral centrum articulation: (0) amphicoelous (and notochordal) (*Gecko gekko*, sagittal slice through cervical vertebrae); (1) procoelous (*Gambelia wislizenii*, sagittal slice through cervical vertebrae). Gauthier, Estes and de Queiroz (1988).



468. Zygosphene-zygantrum accessory intervertebral articulations: (0) absent (*Brachymeles gracilis*, oblique anterior view of vertebra); (1) dorsolaterally directed facet continuous with prezygapophyseal articulation located just up edge of neural arch (*Trachylepis quinquetaeniata*, oblique anterior view of vertebra), Gauthier, Estes and de Queiroz (1988); (2)^{N} tall, laterally directed facet continuous with prezygapophyseal articulation and extending as high as top as neural canal (*Gambelia wislizenii*, oblique anterior view of vertebra); (3)^{N} separate facet set on distinct pedicle and facing ventrolaterally (*Tropidophis haetianus*, oblique anterior view of vertebra), de Queiroz (1987). Estes et al. (1988) (ordered).

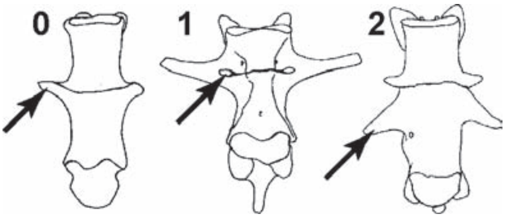


469. Vertebrae (and ribs), mid-dorsals are pachyostotic: (0) absent (*Pareas margaritophorus*, dorsal view of trunk vertebrae); (1) present (*Pachyophis woodwardi*, dorsal view of trunk vertebrae). Rieppel and Head (2004).

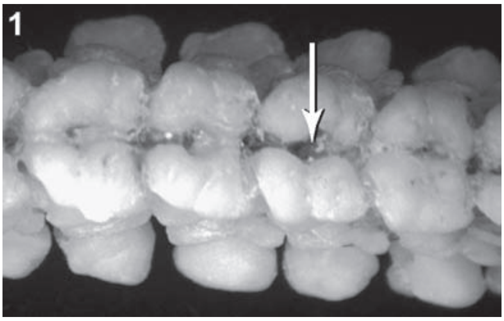


470. Caudal autotomic septum position relative to caudal rib: (0) within caudal rib (*Trachylepis quinquetaeniata*, ventral view of caudal vertebra); (1) anterior to caudal rib (*Zonosaurus ornatus*, ventral view of caudal vertebra); (2) posterior to caudal rib (*Uma notata*, ventral view of caudal vertebra); (3) absent (*Polychrus marmoratus*, ventral view of caudal vertebra). Estes et al. (1988).

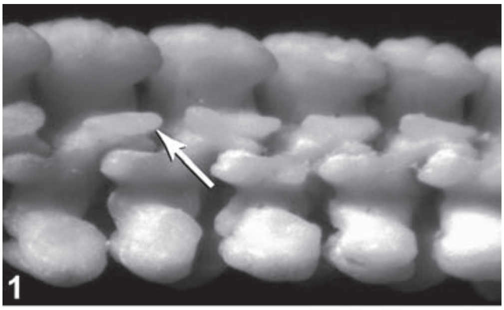
Fracture plane position could be regarded as a continuous variable. Exemplars chosen to typify states 0 and 1 indicate the arbitrary distinction used here, i.e., is any part of the rib traversed by the autotomic septum?.



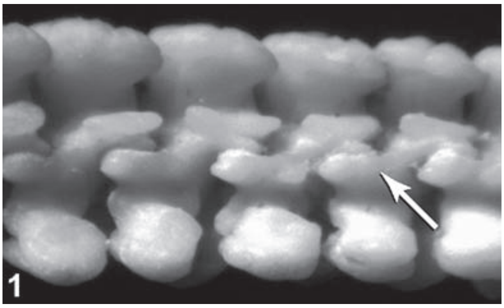
471. Caudal rib (transverse process) shape: (0) single rib without basal foramen (*Scincus scincus*, ventral view of caudal vertebra); (1)^{N} foramen passing through base of rib (*Shinisaurus crocodilurus*, ventral view of caudal vertebra); (2) divergent bifid ribs on some caudals (*Sauromalus ater*, ventral view of caudal vertebra). Estes et al. (1988).



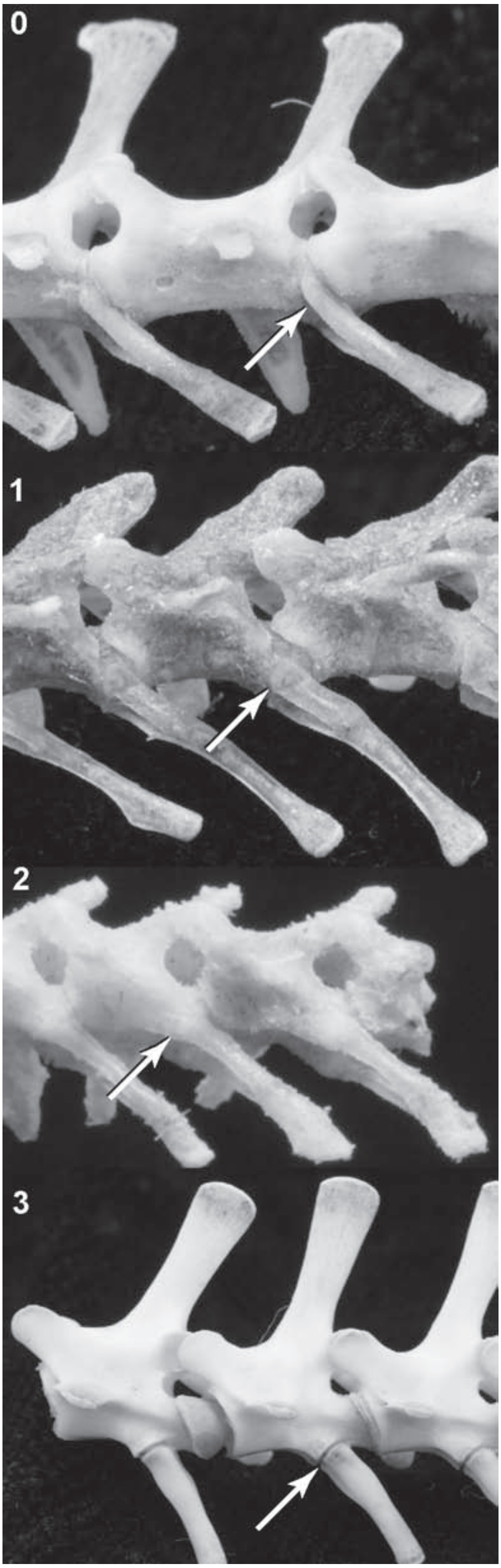
472. Posterior caudal vertebrae, groove on dorsal surface of neural spines: (0) absent; (1) present (*Lichanura trivirgata*, dorsal view of posterior caudal vertebrae). Kluge (1993a).



473. Caudal vertebrae, pterapophysis: (0) absent; (1) present (*Lichanura trivirgata*, lateral view of posterior caudal vertebrae). Kluge (1993a).



474. Caudal vertebrae, distal tip of anterior zygapophyses: (0) undifferentiated; (1) elaborated into a horizontal blade. (*Lichanura trivirgata*, lateral view of posterior caudal vertebrae). Kluge (1991).

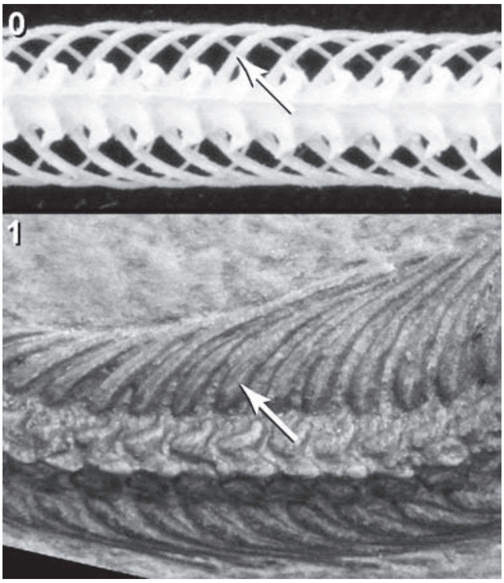


475. Caudal haemal arch (intercentrum) position: (0) intercentral, pedicles feeble/absent (*Physignathus cocincinus*, left lateral view of caudal vertebrae); (1)^{N} contacting mainly condyle but also distinct pedicles beneath preceding centrum (*Zonosaurus ornatus,* left lateral view of caudal vertebrae); (2)^{N} mainly contacting pedicles on preceding centrum but still bordering condyle (*Brachymeles gracilis*, left lateral view of caudal vertebrae); (3) well forward of condyle on preceding centrum (*Varanus exanthematicus*, left lateral view of caudal vertebrae). Pregill et al. (1986) (ordered).

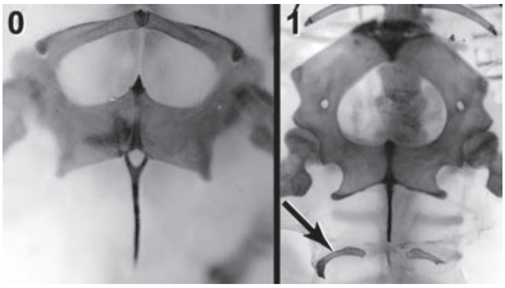
We suspect that crown snakes, with the possible exception of *Eupodophis* (Rieppel and Head 2004), lack haemal arches (intercentra) for reasons noted above (see character 460). The paired structures in snakes, that may bend inward to contact on the midline in males (Keiser 1970) and thus appear to be haemal arches, are instead regarded to be pedicles, viz., outgrowths of the vertebral pleurocentrum. In either case, they are set beneath preceding centra and accordingly scored as state 2 in snakes.

476. Caudal haemal arch pedicle length: (0) short; (1) long. Pregill et al. (1986).

477. Vertebra whose rib first attaches to sternum: (0) seventh (or more anteriorly); (1) eighth; (2) ninth. Estes et al. (1988) (ordered).

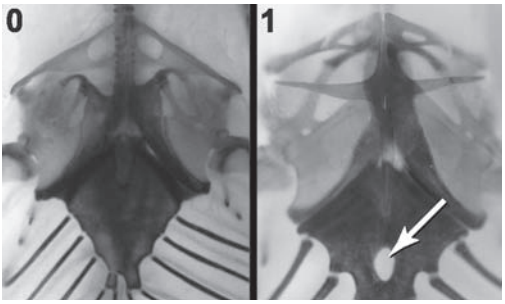


478. Trunk ribs pachyostotic: (0) slender, cancellous ribs (*Pareas margaritophorus*, dorsal view of trunk); (1) thick, dense ribs (*Pachyophis woodwardi*, dorsal view of trunk). Caldwell (1999).

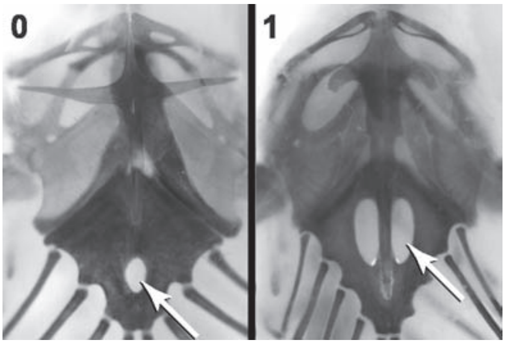


479. Postcloacal bones: (0) absent (*Pristidactylus torquatus*, ventral view of pelvic girdle); (1) present (*Saltuarius cornutus*, ventral view of pelvic girdle). Estes et al. (1988).

480. Sternum: (0) present; (1) absent. Lee (1998).

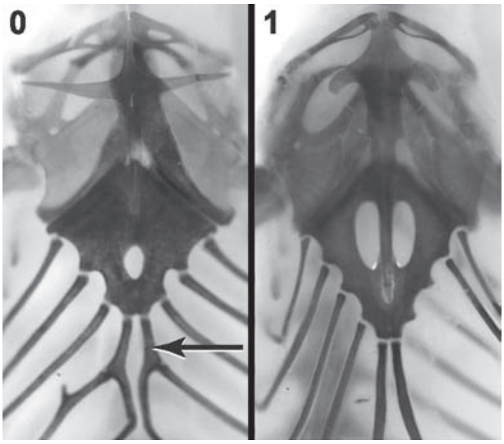


481. Sternal fontanelle: (0) absent (*Phelsuma lineata*, ventral view of sternum); (1) present (*Lacerta viridis*, ventral view of sternum). Estes et al. (1988).

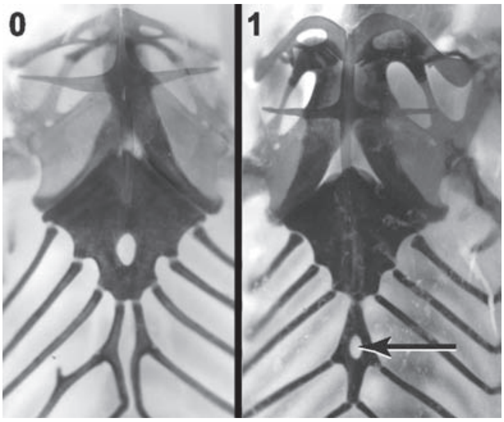


482. Sternal fontanelle number: (0) single (*Lacerta viridis*, ventral view of sternum); (1) double (*Leiolepis belliana*, ventral view of sternum). Moody (1980).

483. Number of rib attachment points to sternum (including attachment of xiphisternum): (0)^{N} five; (1)^{N} four; (2)^{N} three; (3)^{N} two or fewer. Gauthier, Estes and de Queiroz (1988) (ordered).



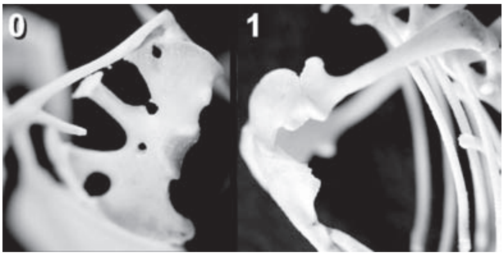
484. Xiphisternum: (0)^{N} present (*Lacerta viridis*, ventral view of sternum); (1) absent (*Leiolepis belliana*, ventral view of sternum). Gauthier, Estes and de Queiroz (1988).



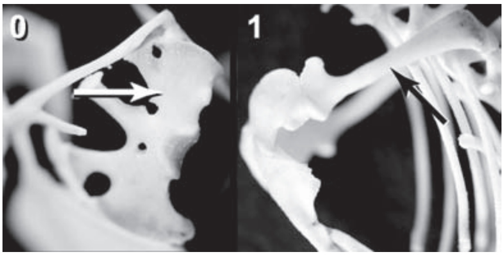
485. Xiphisternal fontanelle^{N}: (0) absent (*Lacerta viridis*, ventral view of sternum); (1) present (*Amphiglossus splendidus*, ventral view of sternum).

486. Number of xiphisternal rib attachment points^{N}: (0) none; (1) one; (2) two; (3) three; (4) four. (ordered).

487. Number of postxiphisternal (or poststernal) inscriptional ribs united along the ventral midline to form continuous chevron shaped structures: (0) 0; (1)^{N} 1–4; (2)^{N} 5–11; (3)^{N} 12–30; (4)^{N} more than 31. Estes et al. (1988) (ordered).

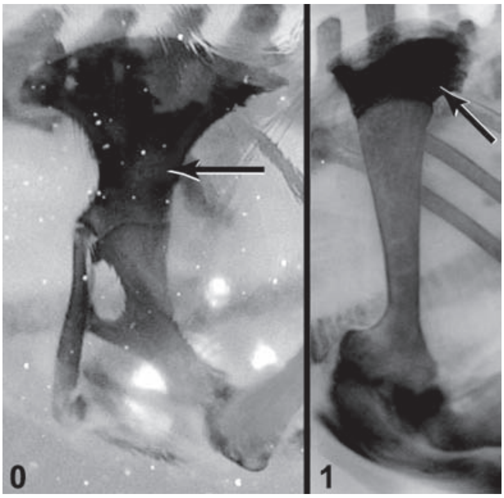


488. Scapulocoracoid: (0) large (*Sauromalus ater*, ventrolateral view of scapulocoracoid); (1)^N reduced (*Chamaeleo* sp., ventrolateral view of scapulocoracoid); (2) absent. Lee (1998) (ordered).

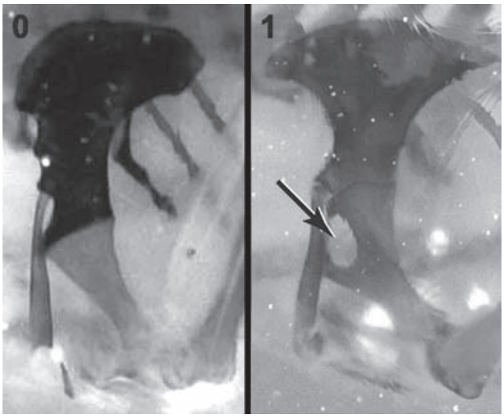


489. Scapula: (0) short and wide (*Sauromalus ater*, ventrolateral view of scapulocoracoid); (1) elongate and thin (*Chamaeleo* sp., ventrolateral view of scapulocoracoid). Grismer (1988).

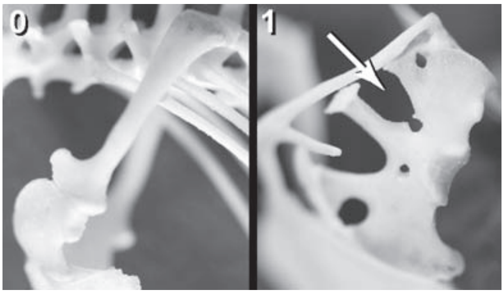
490. Suprascapular cartilage^N: (0) present; (1) absent.



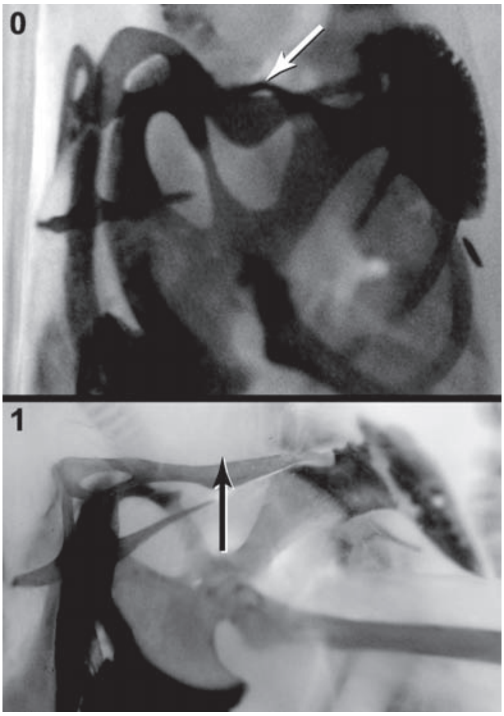
491. Suprascapula: (0) large (approximately equal to length of scapula) (*Uranoscodon superciliosus*, lateral view of scapula); (1) small (*Chamaeleo calyptratus*, lateral view of scapula). Estes et al. (1988).



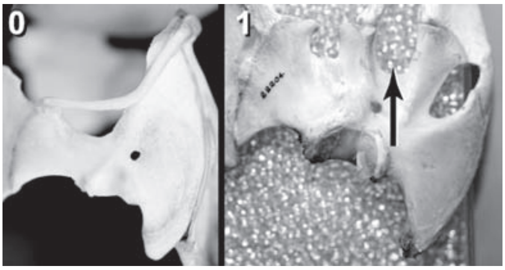
492. Scapula, emargination on anterodorsal edge (scapular fenestra): (0) absent (*Lacerta viridis*, lateral view of scapula); (1) present (*Uranoscodon superciliosus*, lateral view of scapula). Estes et al. (1988).



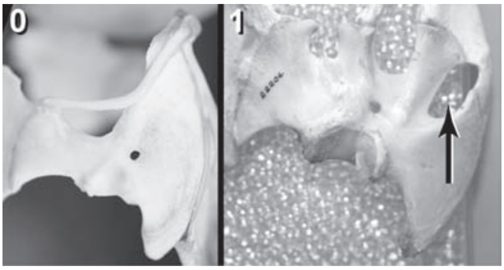
493. Scapulocoracoid emargination: (0) absent, (*Sphenodon punctatus*, vental view of pectoral girdle); (1) present, (*Cordylus mossambicus*, ventrolateral view of pectoral girdle). Gauthier, Estes and de Queiroz (1988).



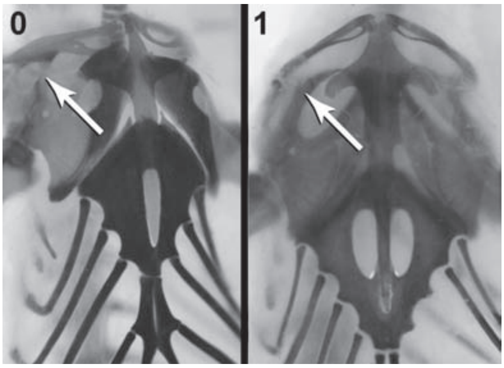
494. Scapulocoracoid emargination$^{\mathrm{N}}$: (0) closed by cartilage (*Amphiglossus splendidus*, ventrolateral view of scapulocoracoid); (1) open (*Lacerta viridis*, ventrolateral view of scapulocoracoid); (2) closed by scapula and coracoid.



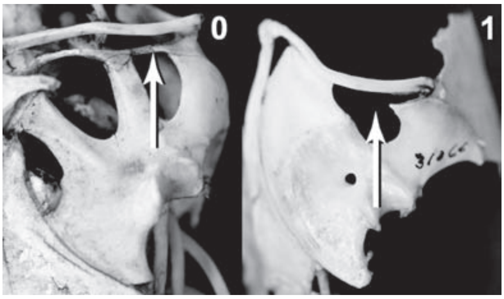
495. Coracoid, anterior (primary) emargination (fenestra): (0) absent (*Heloderma suspectum*, ventrolateral view of scapulocoracoid); (1) present (*Varanus salvator*, ventrolateral view of scapulocoracoid). Pregill et al. (1986).



496. Coracoid, posterior (secondary) emargination (fenestra): (0) absent (*Heloderma suspectum*, ventrolateral view of scapulocoracoid); (1) present (*Varanus salvator*, ventrolateral view of scapulocoracoid). Pregill et al. (1986).

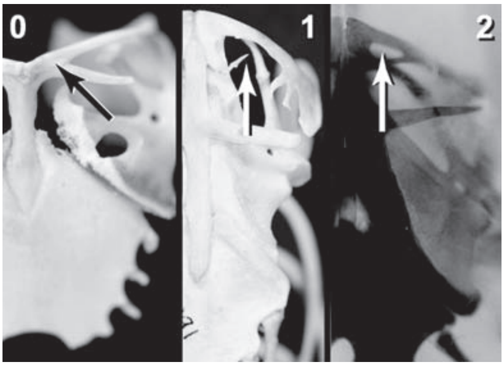


497. Coracoid size$^{\mathrm{N}}$: (0) enlarged, extending anteriorly to level of clavicles (*Teius teyou*, ventral view of pectoral girdle); (1) not enlarged, not extending anteriorly to level of clavicles (*Leiolepis belliana*, ventral view of pectoral girdle).



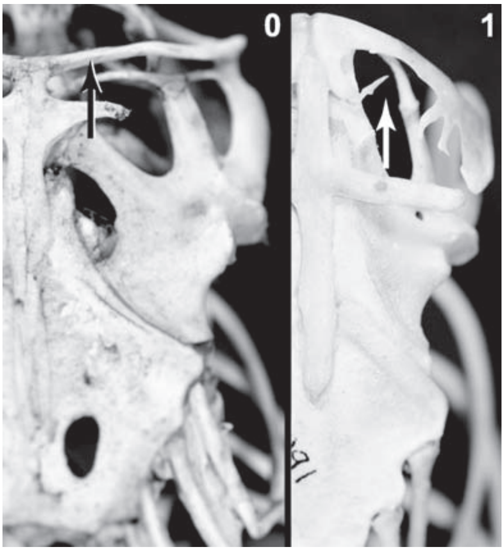
498. Epicoracoid cartilage extent: (0) contacts mesoscapula and suprascapula (*Uromastyx aegyptius*, ventrolateral view of scapulocoracoid); (1) does not contact mesoscapula and suprascapula (*Heloderma horridum*, ventrolateral view of scapulocoracoid). Pregill et al. (1986).

499. Clavicle: (0) present; (1) absent. Estes et al. (1988).

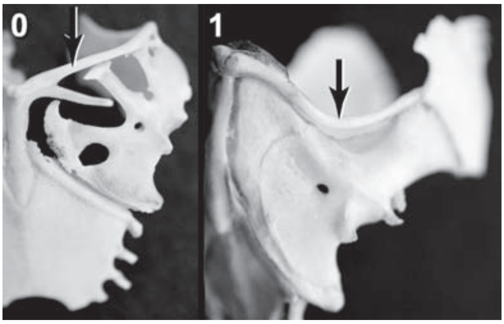


500. Clavicle: (0) no notch or fenestration present (*Sauromalus ater*, ventral close-up of pectoral girdle); (1)$^{\mathrm{N}}$ notch present (*Tiliqua scincoides*, ventral close-up of pectoral girdle); (2) fenestration present (*Lacerta viridis*, ventral

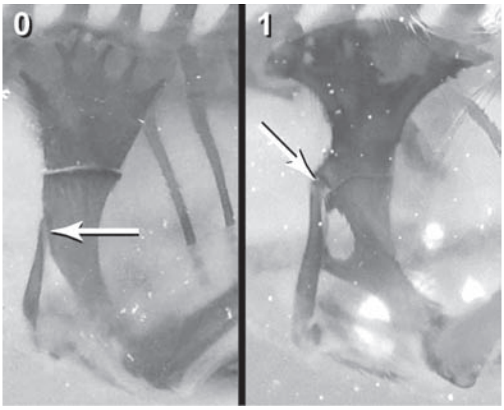
close-up of pectoral girdle). Etheridge and de Queiroz (1988).



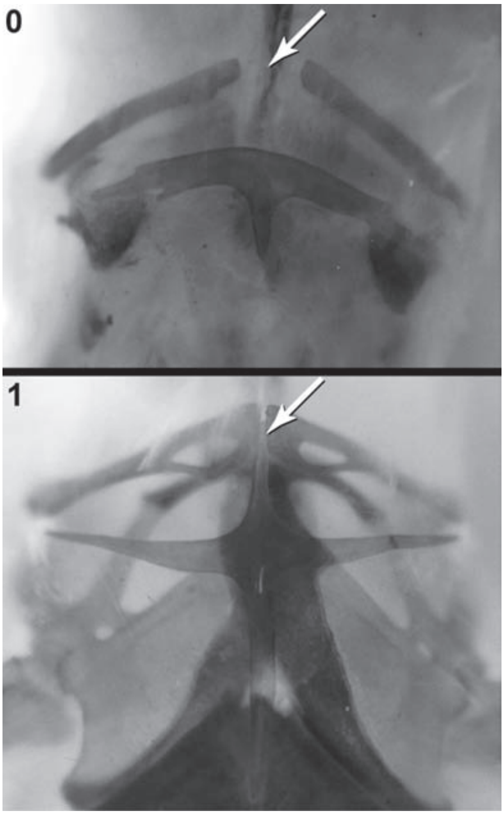
501. Clavicle: (0) rod-like (*Uromastyx aegyptius*, ventral close-up of pectoral girdle); (1) greatly expanded proximally (*Tiliqua scincoides*, ventral close-up of pectoral girdle). Gauthier (1982).



502. Clavicular angulation: (0)^{N} simple curved rod, following contour of scapulocoracoid (*Sauromalus ater*, ventrolateral view of scapulocoracoid); (1) strongly angulated, curving anteriorly away from scapulocoracoid (*Heloderma suspectum*, ventrolateral view of scapulocoracoid). Estes et al. (1988).

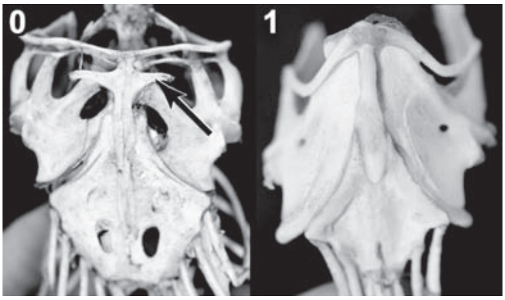


503. Distal clavicle articulation: (0) with scapula (*Physignathus cocincinus,* lateral view of scapula); (1) with suprascapula (*Uranoscodon superciliosus*, lateral view of scapula; (2)^{N} no distal articulation. Gauthier, Estes and de Queiroz (1988).

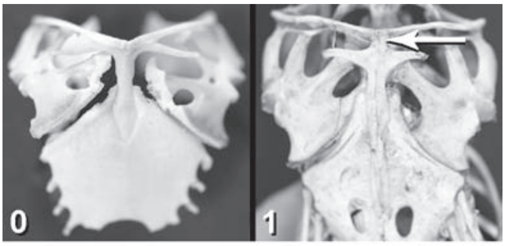


504. Clavicles, medial contact^{N}: (0) clavicles do not meet on midline (*Psuedopus apodus*, ventral view of pectoral girdle); (1) clavicles meet on midline (*Lacerta viridis*, ventral view of pectoral girdle).

505. Interclavicle: (0) present; (1) absent. Estes et al. (1988).

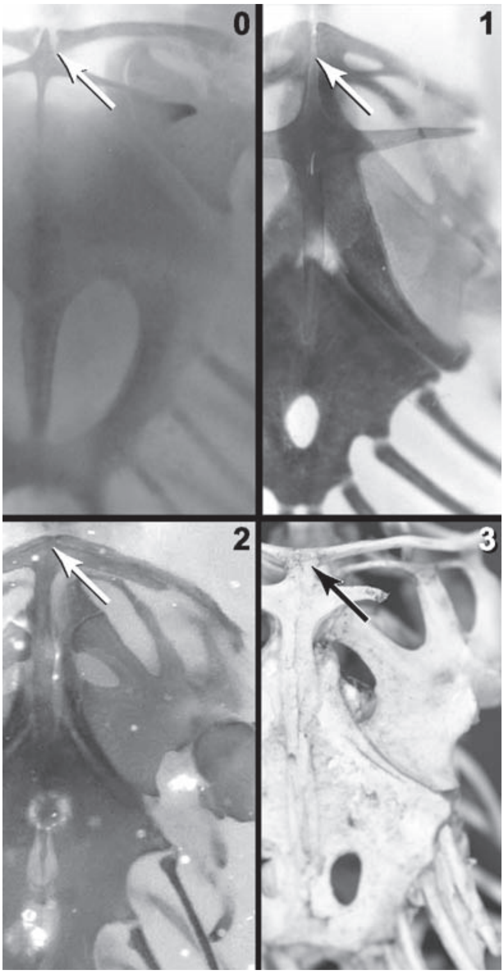


506. Interclavicle lateral process: (0) present (*Uromastyx aegyptius*, ventral view of pectoral girdle); (1) absent (*Heloderma suspectum*, ventral view of pectoral girdle). Estes et al. (1988).



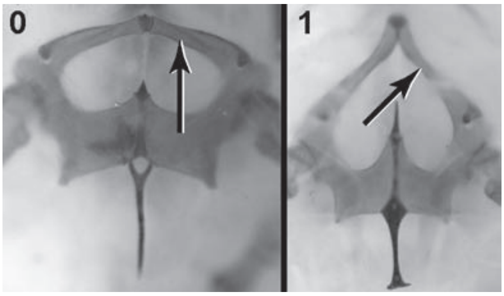
507. Interclavicle anterior process (extending beyond lateral process): (0)^{N} absent (*Sauromalus ater*, ventral view of pectoral girdle); (1)^{N} present (*Uromastyx aegyptius*, ventral view of pectoral girdle). Gauthier (1982).

508. Interclavicle anterior process, length (as ratio of interclavicle length): (0)^{N} 0.01-0.20; (1) more than 0.20. Gauthier (1982).

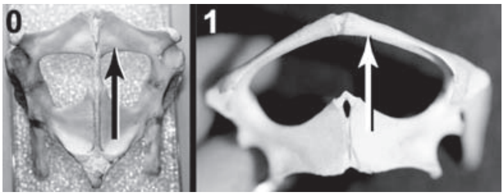


509. interclavicle, anterior end^{N}: (0) ventral to clavicles (*Agama agama*, ventral close-up of pectoral girdle); (1) dorsal to clavicles (*Lacerta viridis*, ventral close-up of pectoral girdle); (2) abuts clavicles (*Uranoscodon superciliosus*, ventral close-up of pectoral girdle); (3) lies posterior to clavicles (*Pseudopus apodus*, ventral close-up of pectoral girdle).

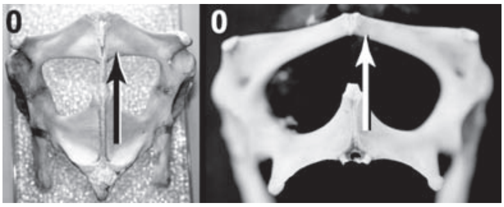
510. Pubis: (0)^{N} present; (1)^{N} absent. Lee (1998).



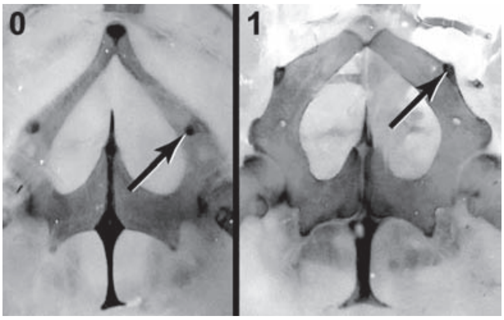
511. Pubis, symphyseal process orientation in ventral view: (0)^{N} medially directed (*Pristidactylus torquatus*, ventral view of pelvic girdle); (1)^{N} anteromedially directed (*Lacerta viridis*, ventral view of pelvic girdle). Estes et al. (1988).



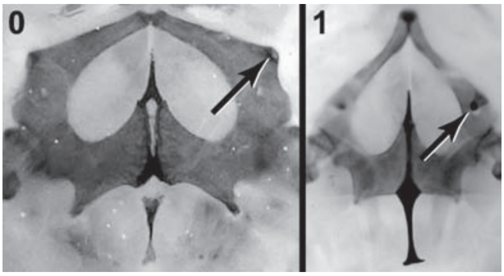
512. Pubis, symphyseal process: (0)^{N} thick (*Varanus salvator*, ventral view of pelvic girdle); (1)^{N} thin (*Tiliqua scincoides*, ventral view of pelvic girdle). Estes et al. (1988).



513. Pubis, symphyseal process: (0) expanded distally (*Varanus salvator*, ventral view of pelvic girdle); (1) tapered, not expanded distally) (*Sauromalus ater*, ventral view of pelvic girdle). DeBraga and Carroll (1993).

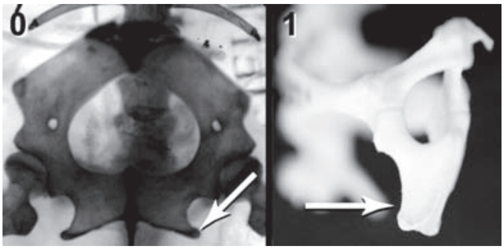


514. Pectineal (pubic) tubercle: (0)^{N} closer to acetabulum than to symphysis (*Lacerta viridis*, ventral view of pelvic girdle); (1)^{N} closer to symphysis than to acetabulum (or equal distance) (*Uranoscodon superciliosus*, ventral view of pelvic girdle). Estes et al. (1988).

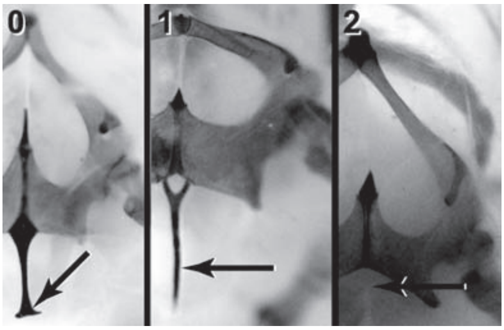


515. Pubis, tubercle orientation in ventral view^{N}: (0) anteriorly directed (*Morunasaurus annularis*, ventral view of pelvic girdle); (1) ventrally directed (*Lacerta viridis*, ventral view of pelvic girdle).

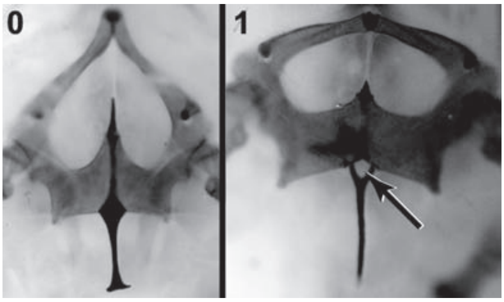
516. Ischium: (0)^{N} present; (1)^{N} absent. Lee (1998).



517. Ischial tubercle: (0)^{N} present (*Saltuarius cornutus*, ventral view of pelvic girdle); (1)^{N} absent, or continuous with hypoischial cartilage (*Chamaeleo* sp., ventrolateral view of pelvic girdle). Estes et al. (1988).

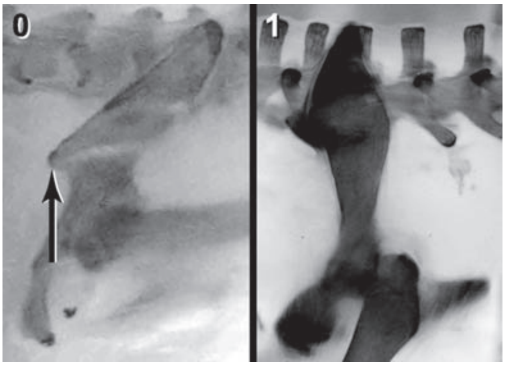


518. Hypoischium: (0) well developed (expanded at distal end) (*Lacerta viridis*, ventral view of pelvic girdle); (1) vestigial (no expansion at distal end) (*Pristidactylus torquatus*, ventral view of pelvic girdle); (2) absent (*Plestiodon fasciatus*, ventral view of pelvic girdle). Lee (2000) (ordered).

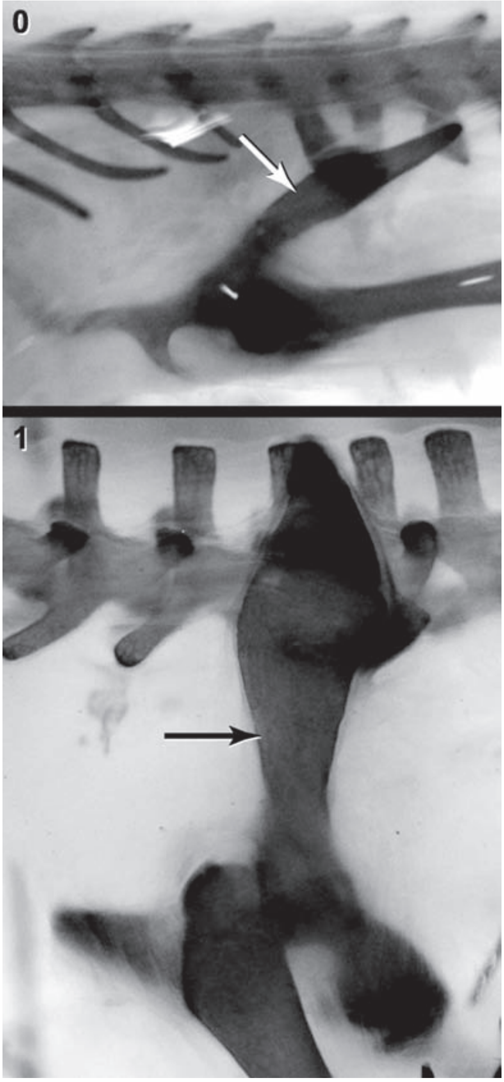


519. Hypoischial foramen^{N}: (0) absent (*Lacerta viridis*, ventral view of pelvic girdle); (1) present (*Pristidactylus torquatus*, ventral view of pelvic girdle).

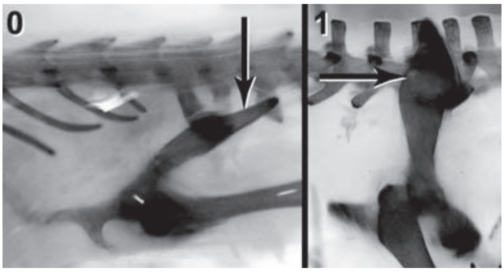
520. Ilium: (0)^{N} present; (1)^{N} absent. Lee (1998).



521. Ilium, tubercle: (0) present (*Crotaphytus collaris*, lateral view of pelvic girdle); (1) absent (*Chamaeleo calyptratus*, lateral view of pelvic girdle). Lee (1998).

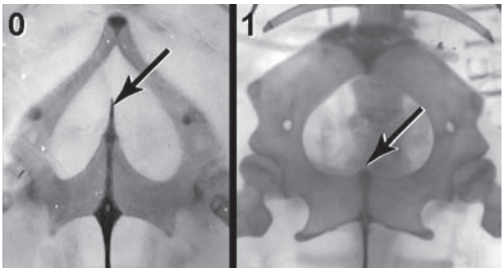


522. Ilium, blade orientation: (0) slopes posterodorsally (*Amphiglossus splendidus*, lateral view of pelvic girdle); (1)$^{\mathrm{N}}$ oriented vertically (*Chamaeleo calyptratus*, lateral view of pelvic girdle); (2)$^{\mathrm{N}}$ oriented anteriorly (Russell 1967, fig. 56). Bell (1997).

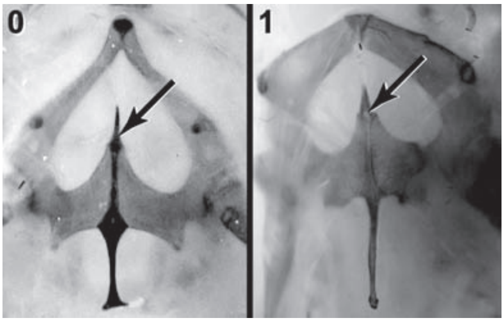


523. Ilium, dorsal ends blades: (0)$^{\mathrm{N}}$ not compressed laterally, and do not expand or converge dorsomedially (*Amphiglossus splendidus*, lateral view of pelvic girdle); (1)$^{\mathrm{N}}$ compressed laterally, suprailiac cartilages expanded into triangular plates that converge dorsomedially (*Chamaeleo calyptratus*, lateral view of pelvic girdle). Estes et al. (1988).

524. Pelvic elements (ilium, ischium, pubis): (0) in close sutural contact throughout postnatal ontogeny and co-ossified into a single pelvic bone late in postnatal ontogeny; (1) distinct elements weakly united in non-sutural contacts (Lee 1998). Gauthier, Estes and de Queiroz (1988).



525. Hyperischium$^{\mathrm{N}}$: (0) present (*Lacerta viridis*, ventral view of pelvic girdle); (1) absent (*Saltuarius cornutus*, ventral view of pelvic girdle).



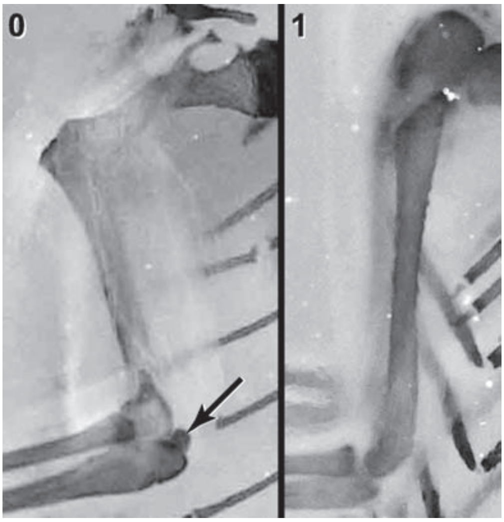
526. Hyperischial foramen$^{\mathrm{N}}$: (0) absent (*Lacerta viridis*, ventral view of pelvic girdle); (1) present (*Polychrus marmoratus*, ventral view of pelvic girdle).

527. Epiphyses on long bones: (0) present; (1) absent. Gauthier, Estes and de Queiroz (1988).

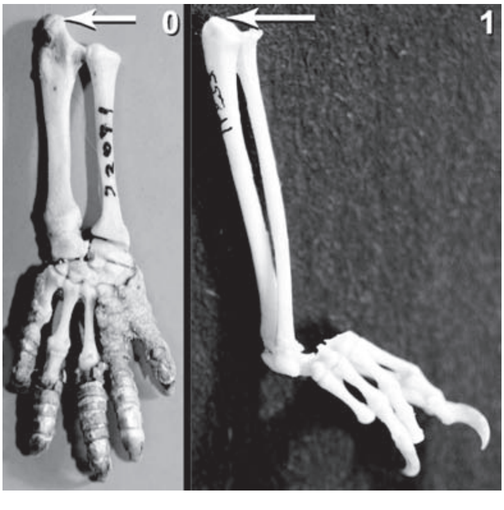
528. Proximal forelimb long bones (humerus, radius and ulna): (0)^N present; (1)^N absent. Lee (1998).

529. Ratio of radius/ulna to humerus^N: (0) 0.50–0.61; (1) 0.62–0.97; (2) 0.98–1.10. (ordered).

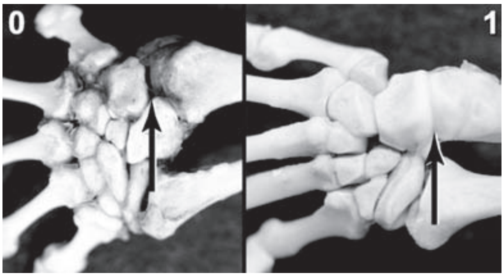
530. Ectepicondylar foramen: (0) present; (1) absent. Estes et al. (1988).



531. Ulnar patella^N: (0) present (*Oplurus cyclurus*, lateral view of upper forelimb); (1) absent (*Chamaeleo calyptratus*, lateral view of upper forelimb).

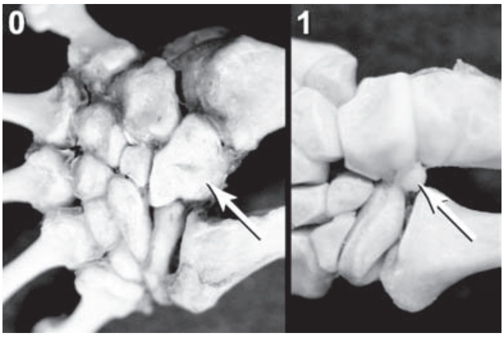


532. Ulna, olecranon process on proximal epiphysis: (0)^N prominent (*Tiliqua scincoides*, dorsal view of lower forelimb); (1) short or absent (*Chamaeleo* sp., lateral view of lower forelimb). Gauthier, Estes and de Queiroz (1988).

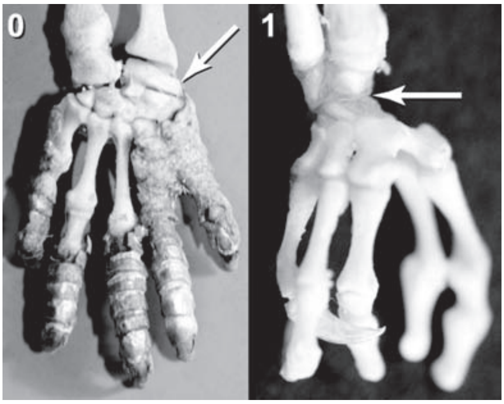


533. Unla, enlarged distal epiphysis that is nearly hemispherical in profile and fits into a concomitantly enlarged depression on the ulnare: (0) absent (*Sphenodon punctatus*, dorsal view of carpus); (1) present (*Tupinambis teguixin*, dorsal view of carpus). Gauthier, Estes and de Queiroz (1988).

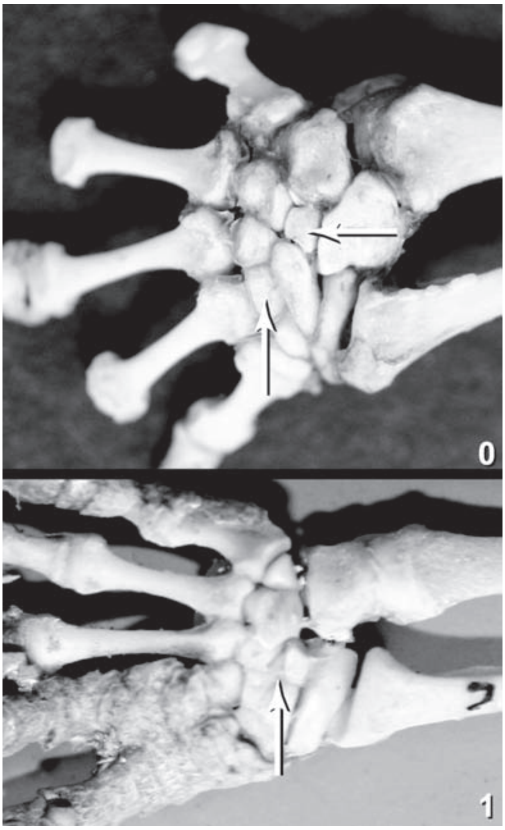
534. Radius, styloid process: (0) absent; (1) present on posterolateral surface of distal epiphysis. Gauthier, Estes and de Queiroz (1988).



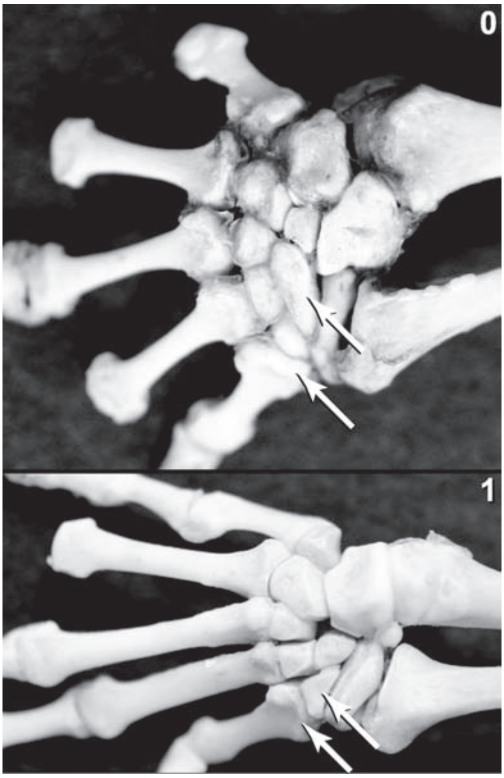
535. Carpal intermedium: (0) large (*Sphenodon punctatus*, dorsal view of carpus); (1)^N small (*Tupinambis teguixin*, dorsal view of carpus); (2)^N absent. Gauthier, Estes and de Queiroz (1988) (ordered).



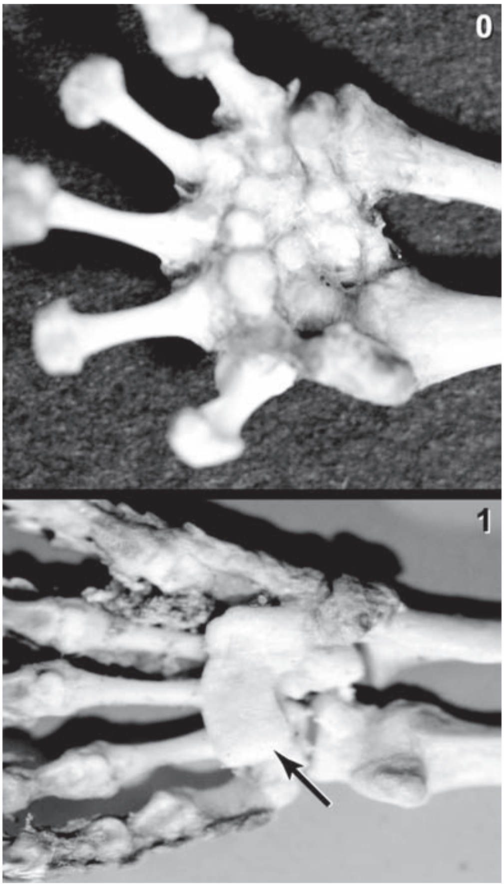
536. Ball and socket intercarpal joint formed by large central carpal or lateral centrale (ball) and radiale, ulnare and pisiform (socket): (0) absent (*Tiliqua scincoides*, dorsal view of manus); (1) present (*Chamaeleo* sp., dorsal view of manus). Estes et al. (1988).



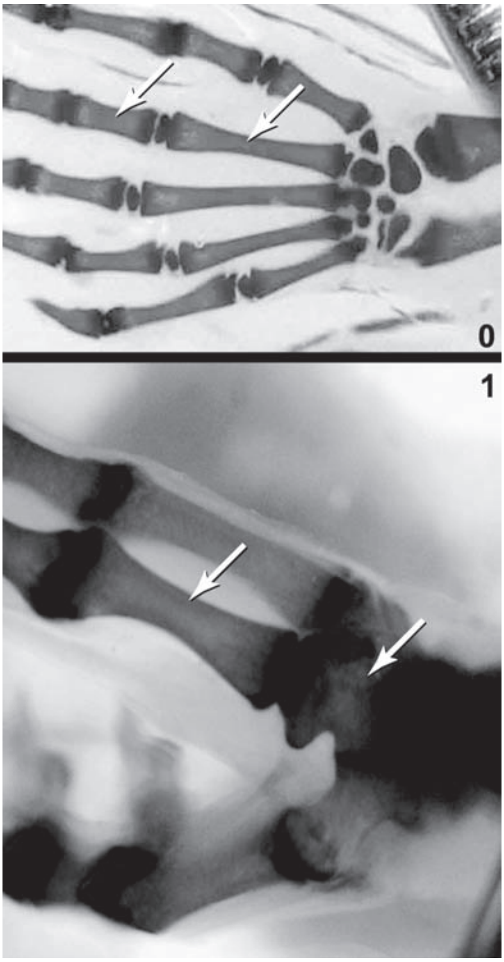
537. Lateral centrale in hand: (0) separated from second distal carpal (*Sphenodon punctatus*, dorsal view of carpus); (1) contacting second distal carpal (*Tiliqua scincoides*, dorsal view of carpus). Gauthier, Estes and de Queiroz (1988).



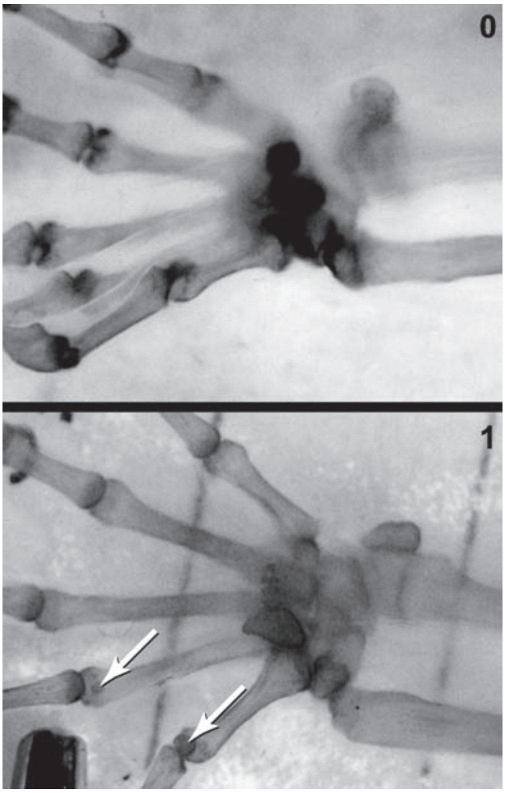
538. Proximal end of first metacarpal: (0) separated from medial centrale (*Sphenodon punctatus*, dorsal view of carpus); (1) contacting medial centrale (*Tupinambis teguixin*, dorsal view of carpus). Gauthier, Estes and de Queiroz (1988).



539. Palmar sesamoid^{N}: (0) absent (*Sphenodon punctatus*, ventral view of carpus); (1) present (*Tiliqua scincoides*, ventral view of carpus).



540. Metacarpals II–IV: (0) longer than proximal phalanges (*Physignathus cocincinus*, dorsal view of manus); (1) shorter than proximal phalanges (*Chamaeleo calyptratus*, dorsal view of manus). Estes et al. (1988).

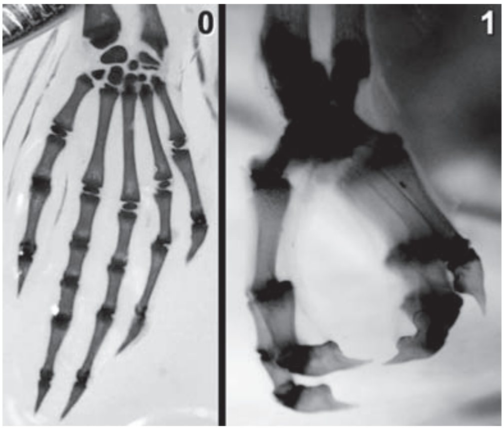


541. Metacarpals, sesamoids ventral to distal heads$^{\mathrm{N}}$: (0) absent (*Lacerta viridis*, ventral view of manus); (1) present (*Xenosaurus grandis*, ventral view of manus).

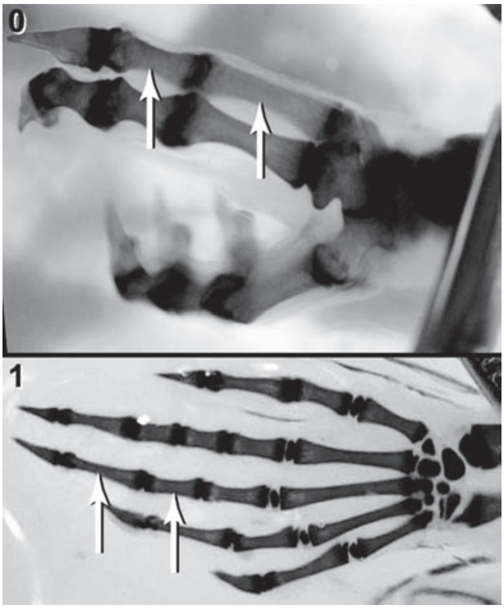
542. Phalangeal count, reduction in manus digits II–IV$^{\mathrm{N}}$: (0) three, four, five; (1) reduced to three in digits III and IV; (2) reduced to four in digit IV; (3) reduced to three in digit III and four in digit IV.

543. Phalangeal count, digit V of manus$^{\mathrm{N}}$: (0) three; (1) two; (2) four.

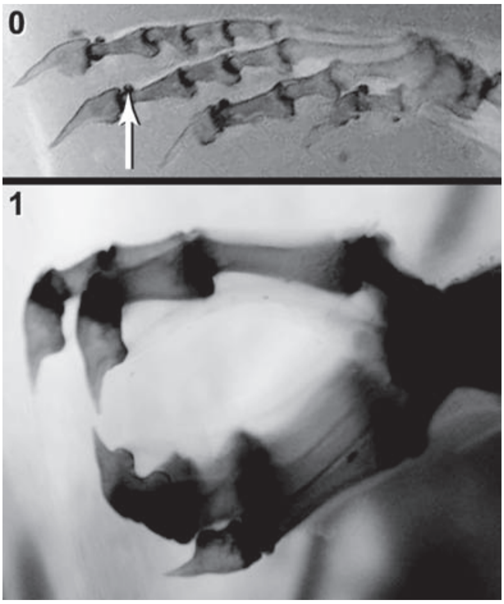
544. Hyperphalangy in manus: (0) absent; (1)$^{\mathrm{N}}$ present in more than one digit; (2)$^{\mathrm{N}}$ present only in digit 1; (3)$^{\mathrm{N}}$ present only in digit 5. Bell (1997).



545. Opposing digits in manus: (0) digits nonopposing (*Physignathus cocincinus*, dorsal view of manus); (1) digits 1, 2 and 3 opposing digits 4 and 5 (*Chamaeleo calyptratus*, dorsal view of manus). Estes et al. (1988).

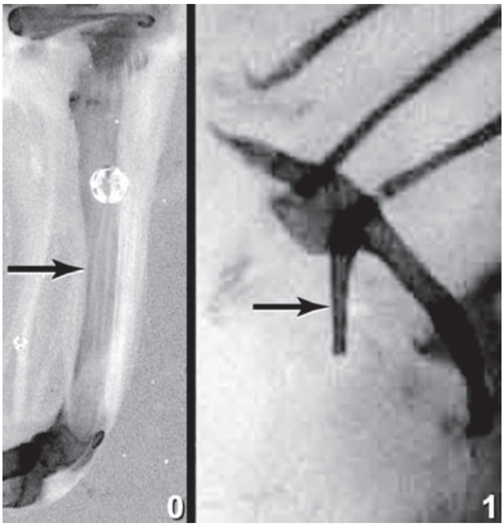


546. Penultimate phalanges in hand$^{\mathrm{N}}$: (0) shorter than or equal to antepenultimate (*Chamaeleo calyptratus*, dorsal view of manus); (1) longer than antepenultimate (*Physignathus cocincinus*, dorsal view of manus).

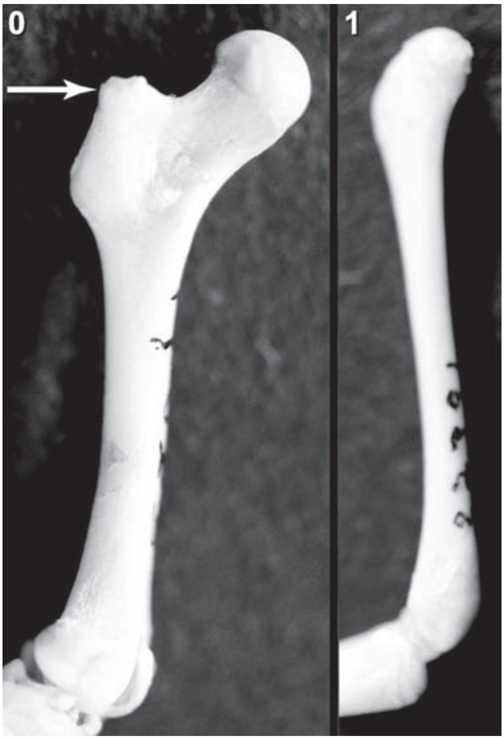


547. Sesamoids dorsal to distal heads of penultimate phalanges (manus)^N: (0) present (*Crotaphytus collaris*, lateral view of manus); (1) absent (*Chamaeleo calyptratus*, dorsal view of manus).

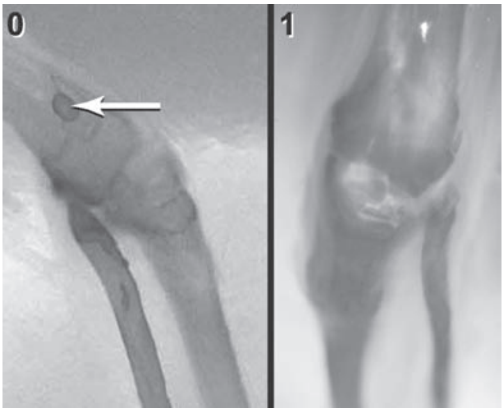
548. Femur: (0)^N present; (1)^N absent. Lee (1998).



549. Femur: (0) curved in dorsoventral plane (*Crotaphytus collaris*, postaxial view of femur); (1) not curved in dorsoventral plane (*Lialis burtonis*, ventral view of femur). Lee (1998).

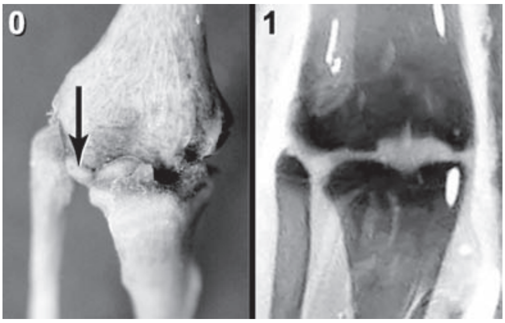


550. Femur, internal trochanter: (0) well developed as a prominent, distinct head (*Tiliqua scincoides*, preaxial view of femur); (1) poorly developed or absent (*Chamaeleo* sp., preaxial view of femur). Estes et al. (1988).

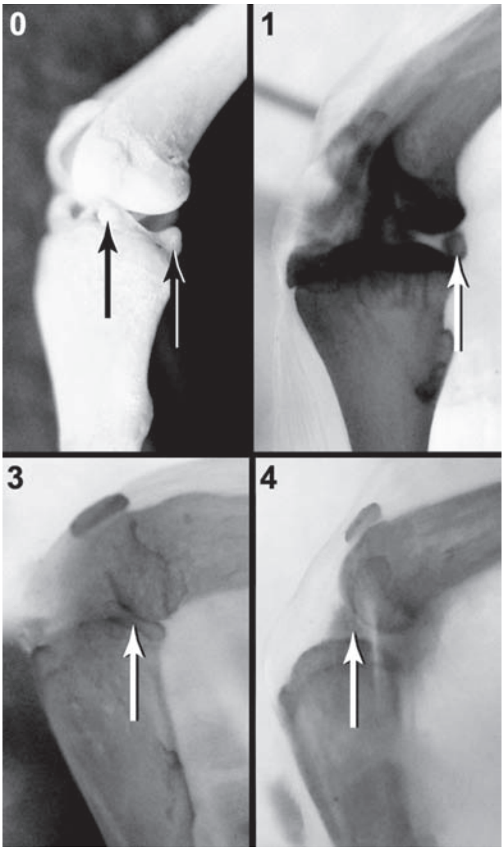


551. Tibial patella^N: (0) present (*Crotaphytus collaris*, superior view of knee); (1) absent (*Agama agama*, superior view of knee).

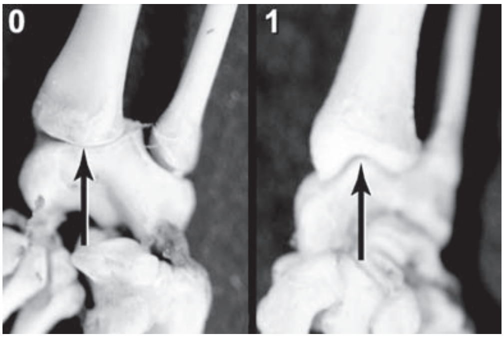
552. Tibial lunula^N: (0) present (*Heloderma suspectum*, superior view of knee); (1) absent.



553. Fibular lunula^N: (0) present (*Heloderma suspectum*, superior view of knee); (1) absent (*Uranoscodon superciliosus*, superior view of knee).

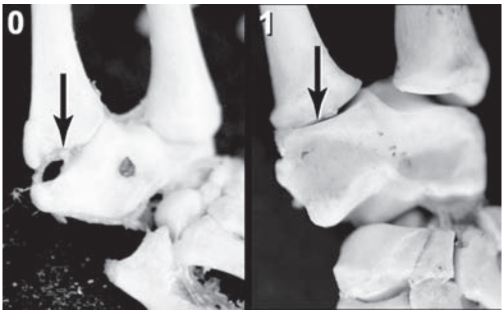


554. Dorsal and ventral tibiofemoral lunulae^N: (0) both present and separate (*Tiliqua scincoides*, preaxial view of knee); (1) ventral present, dorsal absent (*Teius teyou*, preaxial view of knee); (2) both absent; (3) both present and fused (*Xenosaurus grandis*, preaxial view of knee); (4) dorsal present, ventral absent (*Oplurus cyclurus*, preaxial view of knee).

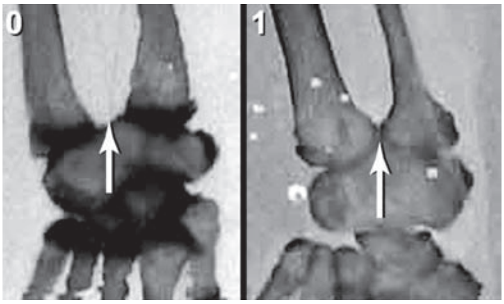


555. Tibia, notching of distal epiphysis: (0) notch not present, epiphysis gently convex for astragalocalcaneal articulation (*Sauromalus ater*, superior view of tarsus); (1) distinct notch present, fitting onto a ridge on the astragalocalcaneum (*Tiliqua scincoides*, superior view of tarsus). Estes et al. (1988).

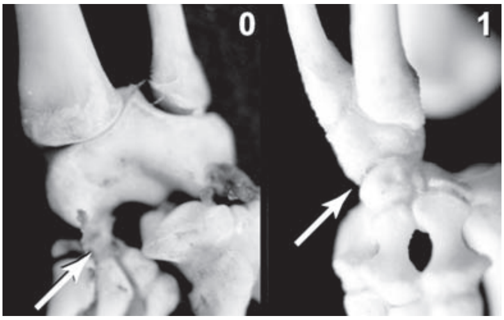
Reynoso (1998) scored the derived state as present in the stem lizard *Huehuecuetzpalli mixtecus*. We made two separate week-long trips to the Instituto de Geología Universidad Nacional Autónoma de México to study these specimens, and close examinations of the color and texture of this putative "notch" led us to conclude that it was formed by calcite precipitation—which surrounds several areas on these specimens, including the feet—and not in the bone. The putative scleroglossan "notch" is, moreover, present in only one of the four *H. mixtecus* tibiae, while the other three are unambiguously "flat" as in iguanians, as Reynoso (1998) acknowledged. When the notch is feebly developed, it can be difficult to discern in the supra-axial view most often exposed in *H. mixtecus* tibiae; with a 'notch' this prominent, however, it would be no less visible subaxially.



556. Fibulo-astragalar joint: (0) occupies less than half of distal end of fibula (*Sphenodon punctatus*, superior view of tarsus); (1) involves most of distal end of fibula (*Tupinambis teguixin*, superior view of tarsus). Gauthier, Estes and de Queiroz (1988).



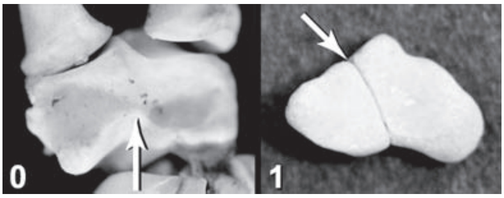
557. Tibia and fibula^{N}: (0) remain widely separated at distal ends (*Elgaria multicarinata*, superior view of tarsus); (1) very close or in contact at distal ends (*Oplurus cyclurus*, superior view of tarsus).



558. Ball and socket intertarsal joint formed by distal tarsal 4 (ball) and astragalocalcaneum (socket): (0) absent (*Sauromalus ater*, superior view of tarsus); (1) present (*Chamaeleo sp.*, superior view of tarsus). Estes et al. (1988).

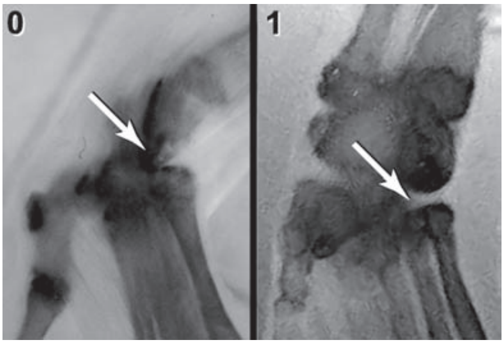
559. Third distal tarsal^{N}: (0) present; (1) absent.

560. Second distal tarsal: (0) present; (1) absent. Gauthier, Estes and de Queiroz (1988).

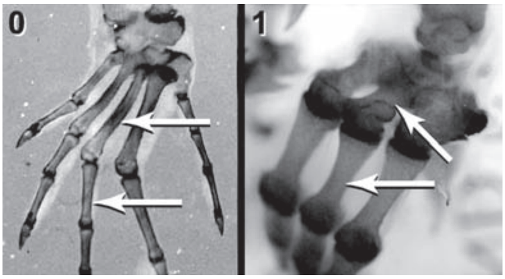


561. Astragalus and calcaneum: (0) fused with no suture visible in adult (*Tupinambis teguixin*, supraxial view of astragalocalcaneum) Gauthier, Estes and de Queiroz (1988) (1) co-ossified with suture visible (*Sphenodon punctatus*, superior view of astragalocalcaneum); (2) separated. Lee (1998).

We note that it may be that those squamates with state 1 represent subterminal ontogenetic stages (in which the suture is still visible), and that the proximal tarsal would fuse indistinguishably as in other full-grown lepidosaurs. Proximal tarsals are reported in only one simoliophiid (*Pachyrhachis problematicus*); without separate means of assessing ontogenetic stage of this extinct snake, the state in this species is ambiguous in our view. Mosasaurians pose the same challenge. However, many specimens have yet to show the expected fusion, suggesting that failure to fuse, or even to ossify completely as in *Tylosaurus* (Russell 1967)—i.e., paedomorphosis—may indeed characterize this clade.

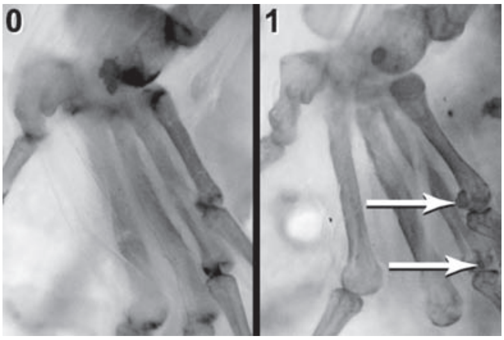


562. Sesamoid between metatarsal I and astragalocalcaneum (ventrally)^{N}: (0) present (*Agama agama*, postaxial view of tarsus); (1) absent (*Crotaphytus collaris*, postaxial view of tarsus).



563. Metatarsals II–IV: (0) longer than proximal phalanges (*Lacerta viridis*, dorsal view of pes); (1) shorter than proximal phalanges (*Chamaeleo calyptratus*, dorsal view of pes). Estes et al. (1988).

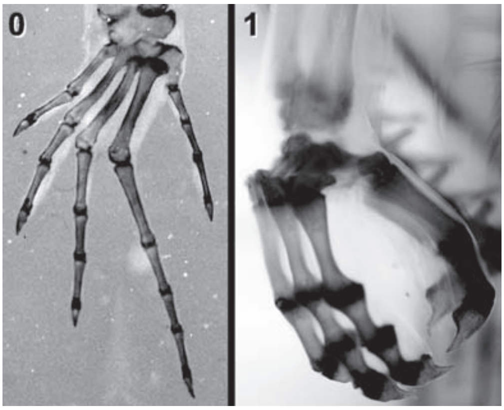
564. Metatarsal V: (0) hooked (*Tupinambis teguixin*, dorsal view of tarsus); (1) broad proximally, but not hooked. Gauthier, Estes and de Queiroz (1988). *Haasiophis terrasanctus* is the only snake in which this feature might be preserved. It is scored as state (1) following Rieppel et al. (2003). However, there are only four metatarsals preserved in that specimen, so we cannot be sure that the fifth was actually present. Moreover, although we also scored *Clidastes* as lacking a hooked fifth metatarsal, and left the other mosasaurians unscored, it is hooked in all mosasaurians in which this element is preserved according to Russell (1967). We will alter the dataset accordingly in future studies.



565. Metatarsals, sesamoids ventral to distal heads^{N}: (0) absent (*Lacerta viridis*, ventral view of pes); (1) present (*Xenosaurus grandis*, ventral view of pes).

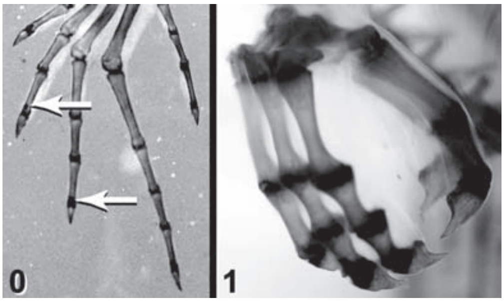
566. Phalangeal counts, reduction in pes^{N}: (0) two, three, four, five, four; (1) reduced to three phalanges in digits III, IV and V; (2) reduced to four phalanges in digit IV and three phalanges in digit V; (3) reduced to two phalanges in digit V; (4) reduced to three phalanges in digit V.

567. Hyperphalangy in digits of pes: (0) absent; (1)^{N} present in more than one digit; (2)^{N} present only in digit V. Bell (1997).

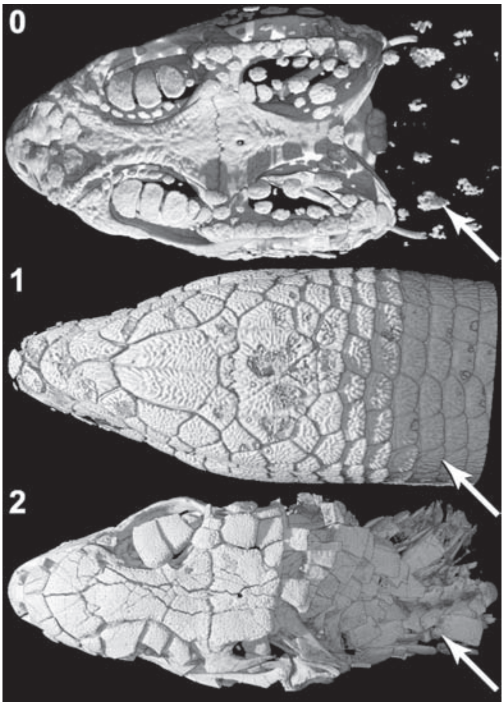


568. Opposing digits in pes: (0) digits non-opposing (*Lacerta viridis*, dorsal view of pes); (1) digits 1 and 2 opposing digits 3, 4 and 5 (*Chamaeleo calyptratus*, dorsal view of pes). Estes et al. (1988).

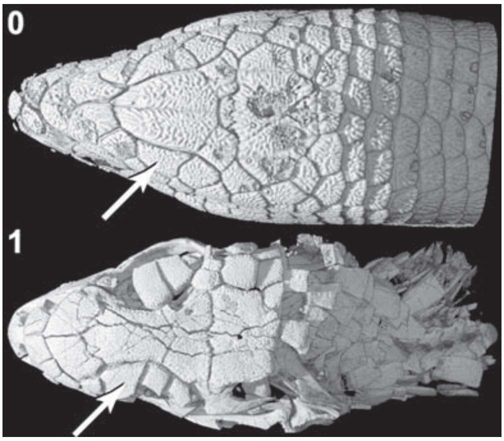
Both K. Smith (pers. comm.) and R. Nydam (pers. comm.) questioned the wisdom of scoring a “zygodactyl” manus and pes separately. We concur, and will alter future datasets accordingly.



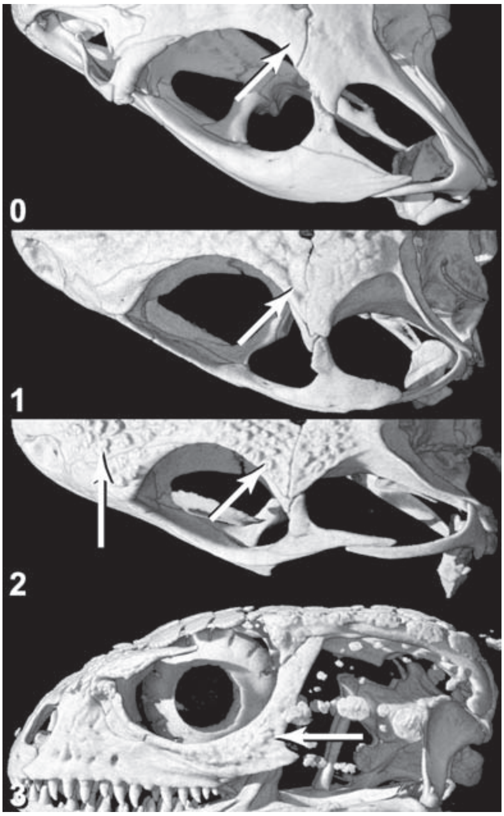
569. Sesamoids dorsal to distal heads of penultimate phalanges^{N}: (0) present (*Lacerta viridis*, dorsal view of pes); (1) absent (*Chamaeleo calyptratus*, dorsal view of pes).



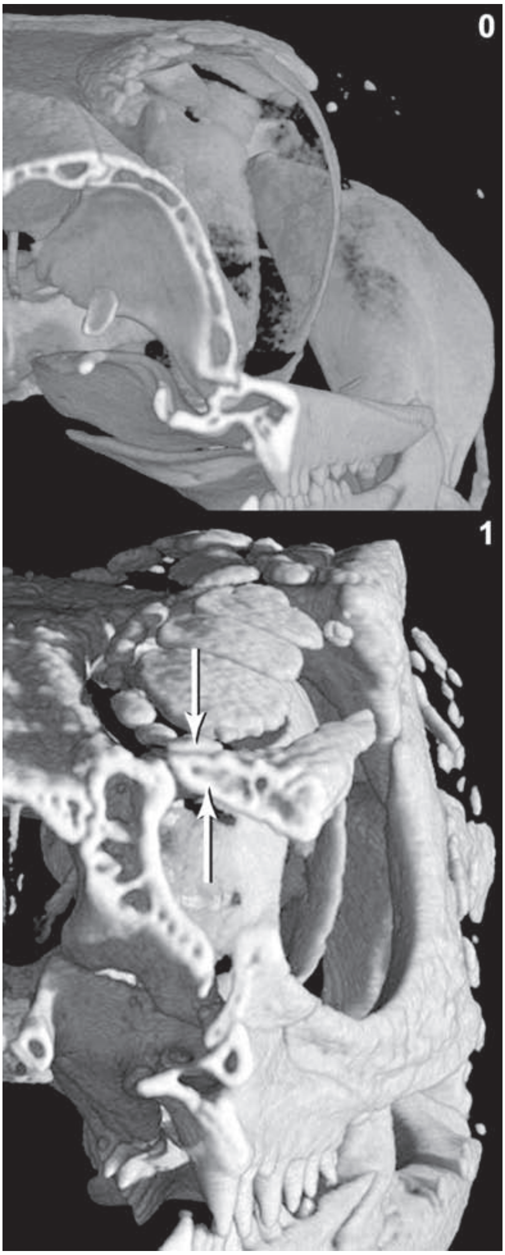
570. Osteoderms on body (and/or tail): (0) not imbricate (*Shinisaurus crocodilurus*, dorsal view of head and neck); (1) imbricate, with gliding surface anteriorly (*Pseudopus apodus*, dorsal view of head and neck); (2) imbricate anteroposteriorly (with gliding surface), but interdigitate laterally (*Peltosaurus granulosus*, dorsal view of head and neck). Gauthier (1982) (ordered).



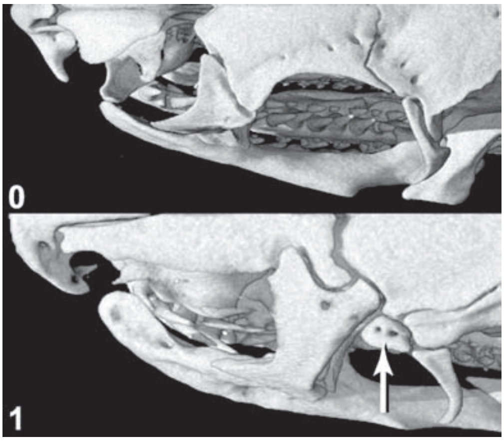
571. Osteoderm ornamentation: (0) vermiculate or smooth (*Pseudopus apodus*, dorsal view of head and neck); (1) tuberculate (*Peltosaurus granulosus*, dorsal view of head and neck). Gauthier (1982).



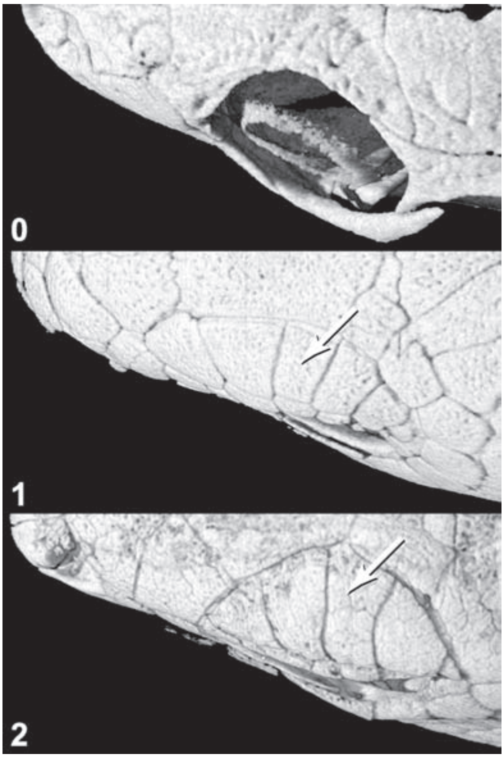
572. Dermal skull bone ornamentation: (0) smooth (*Uromastyx aegyptius*, dorsal view of skull); (1) lightly rugose about frontoparietal suture (*Leiocephalus barahonensis*, dorsal view of skull); (2) present over dorsum (*Pristidactylus torquatus*, dorsal view of skull); (3)^{N} present on jugal postorbital bar (*Shinisaurus crocodilurus*, lateral view of skull). Estes et al. (1988) (ordered).



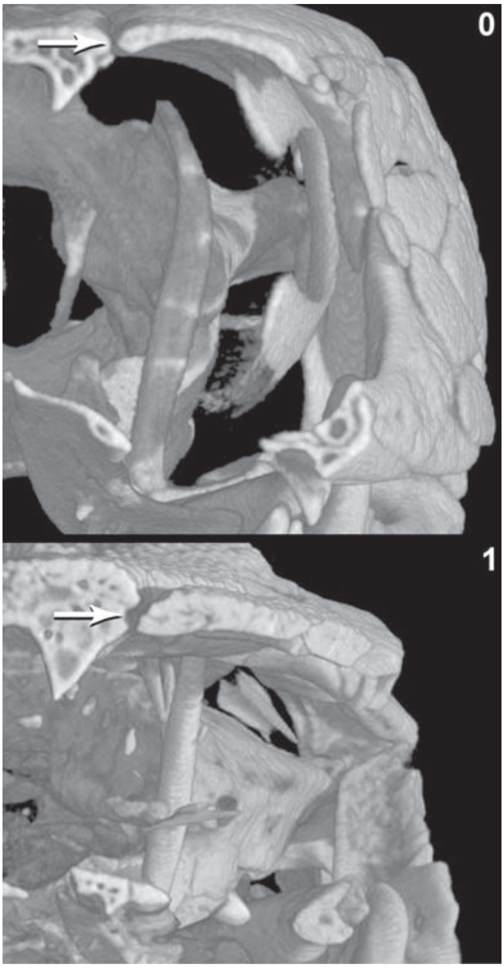
573. Palpebral osteoderm below supraorbital scales (and their osteoderms): (0) absent (*Teratoscincus przewalskii*, anterior close-up cutaway view of orbit); (1) present (*Shinisaurus crocodilurus*, anterior close-up cutaway view of orbit). Pregill et al. (1986).



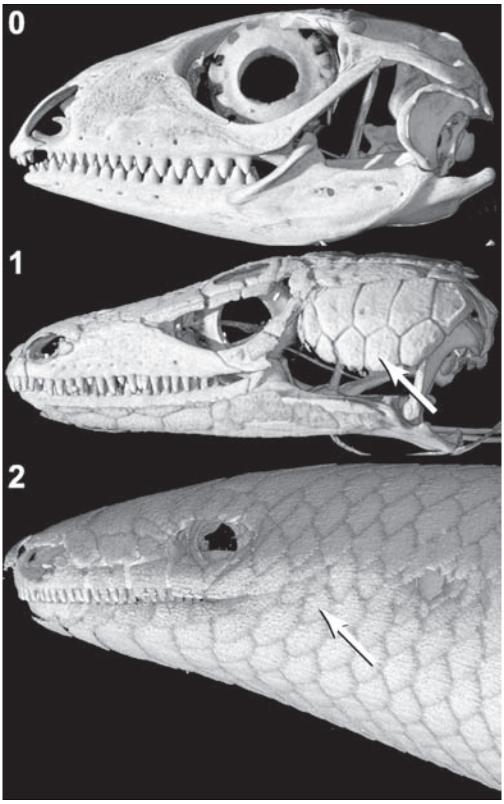
574. Supracilliary osteoderm (pierced vertically by foramina)^{N}: (0) absent (*Coluber constrictor*, dorsal close-up of anterior skull); (1) present (*Loxocemus bicolor*, dorsal close-up of anterior skull).



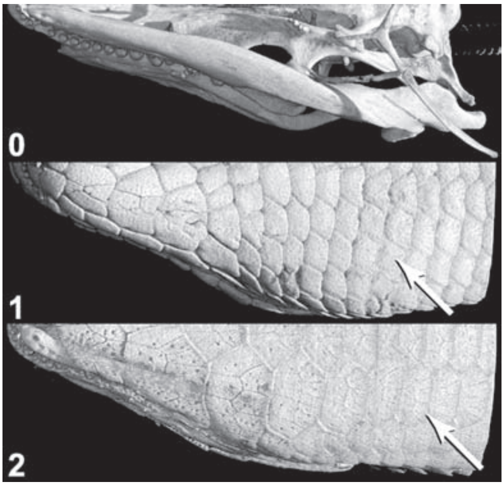
575. Osteoderms inside supraorbital scales: (0) absent (*Xantusia vigilis*, dorsal close-up of anterior skull); (1) single (*Celestus enneagrammus*, dorsal close-up of anterior skull); (2) compound (*Trachylepis quinquetaeniata*, dorsal close-up of anterior skull). Estes et al. (1988).



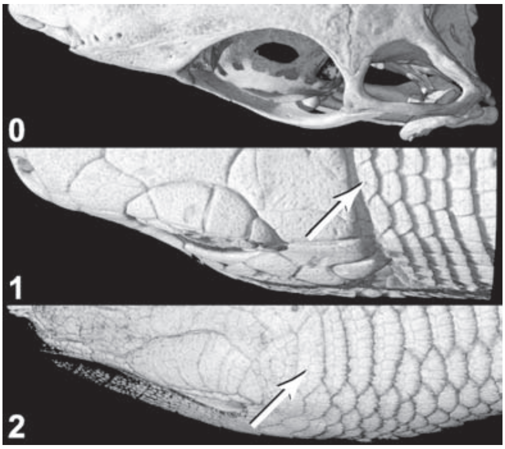
576. Supraorbital osteoderms insert into sulcus along frontal supraorbital margin: (0) absent (*Lacerta viridis*, anterior close-up cutaway view of orbit); (1) present (*Peltosaurus granulosus*, anterior close-up cutaway view of orbit).



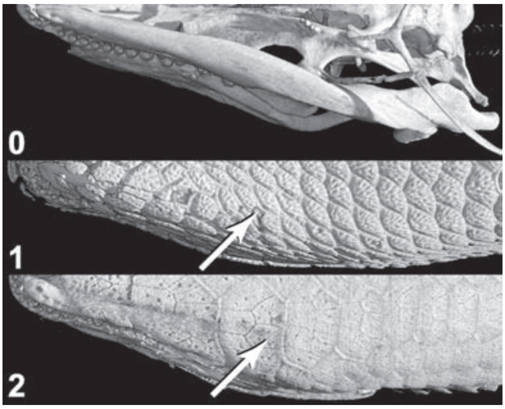
577. Osteoderms in cheek scales: (0) absent (*Teius teyou*, lateral view of skull); (1) single (*Platysaurus imperator,* lateral view of skull); (2) compound (*Brachymeles gracilis*, lateral view of skull). Estes et al. (1988).



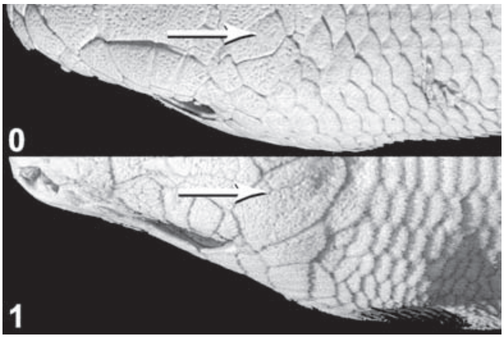
578. Osteoderms in gular scales^{N}: (0) absent (*Teius teyou*, ventral view of skull); (1) single (*Elgaria multicarinata*, ventral view of skull); (2) compound (*Cordylosaurus subtesselatus*, ventral view of skull).



579. Osteoderms in dorsal scales: (0) absent (*Teius teyou*, dorsal view of skull); (1) single (*Zonosaurus ornatus*, dorsal view of skull); (2) compound (*Scincus scincus*, dorsal view of skull). Gauthier (1982).

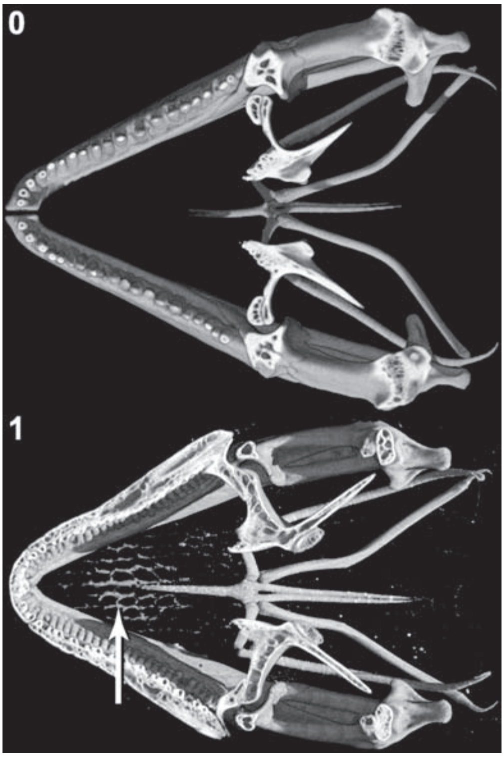


580. Osteoderms in ventral scales: (0) absent (*Teius teyou*, ventral view of skull); (1) single (*Pseudopus apodus*, ventral view of skull); (2) compound (*Cordylosaurus subtesselatus*, ventral view of skull). Gauthier (1982).



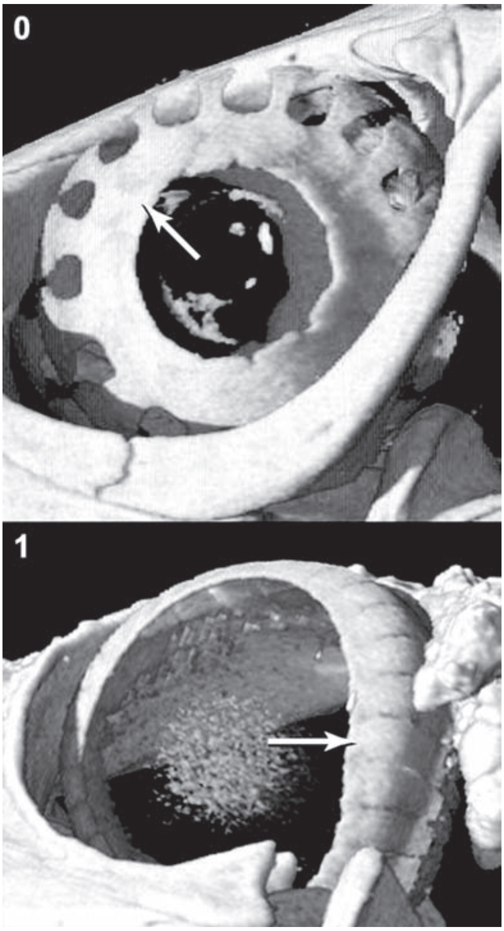
581. Osteoderms in skull roof scales: (0) single (*Celestus enneagrammus*, dorsal view of skull); (1) compound (*Amphiglossus splendidus*, dorsal view of skull). Gauthier (1982).

582. Osteoderms invest imbricate caudal scales^{N}: (0) absent; (1) present.

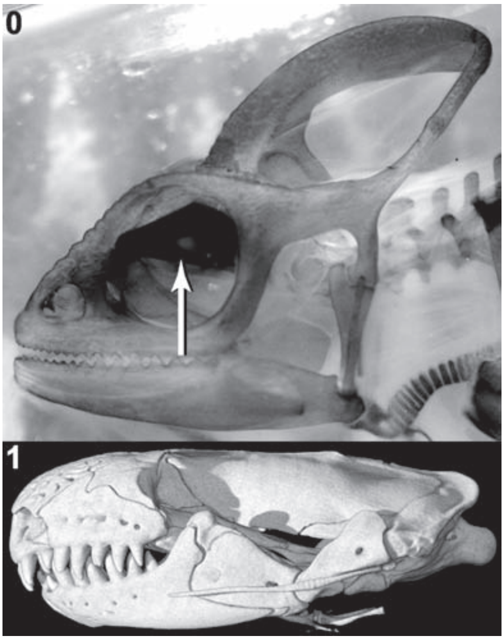


583. Mineralized cranial scales hinges^{N}: (0) absent (*Crotaphytus collaris*, dorsal cutaway view of skull); (1) present (*Enyalioides laticeps*, dorsal cutaway view of skull).

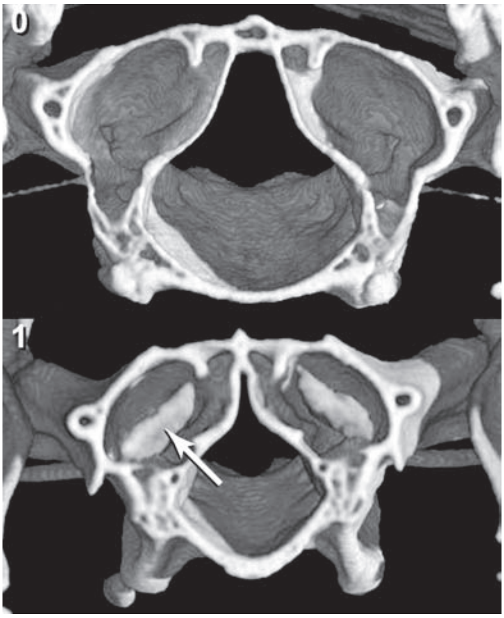
584. Scleral ossicle count: (0)^{N} 16 or more; (1)^{N} 14–15; (2)^{N} 12–13; (3)^{N} 11 or fewer. Pregill et al. (1986) (ordered).



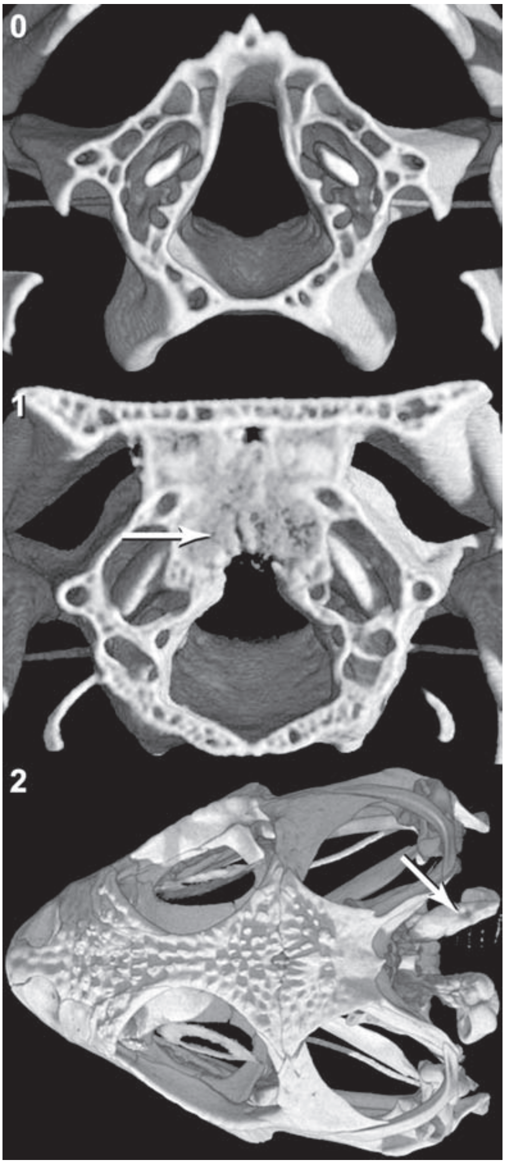
585. Scleral ossicles: (0) complex and irregular in shape (*Callopistes maculatus*, lateral close-up of scleral ring); (1) square or rectangular in shape (*Saltuarius cornutus*, lateral close-up of scleral ring). Lee (1998).



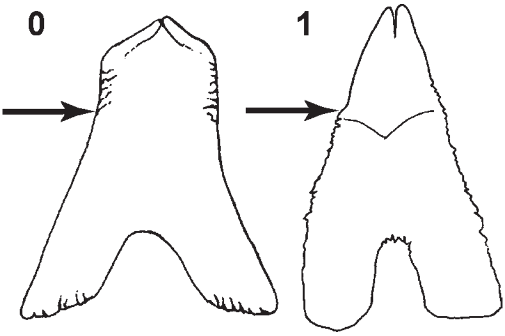
586. Interorbital septum: (0) present (*Chamaeleo calyptratus*, lateral view of skull); (1) absent (*Amphisbaena fuliginosa*, lateral view of skull). Hallermann (1998).



587. Statolithic masses^{N}: (0) absent (*Celestus enneagrammus*, anterior close-up cutaway view of braincase); (1) present (*Elgaria multicarinata*, anterior close-up cutaway view of braincase).

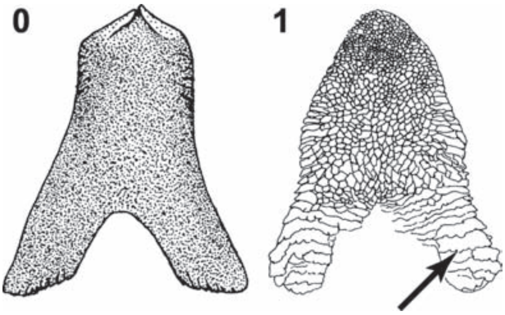


588. Calcified endolymph: (0) absent (*Leiolepis belliana*, anterior close-up cutaway view of braincase) Moody (1980); (1) present, but confined to occiput (*Aeluroscalabotes felinus*, anterior close-up cutaway view of braincase) Hallerman (1994); (2) present, extends posteriorly into neck (*Leiosaurus catamarcensis*, dorsal view of skull). Estes et al. (1988) (ordered).

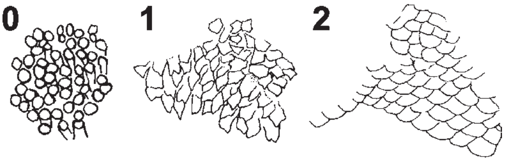


589. Foretongue retracts into hind tongue: (0) absent (*Dipsosaurus dorsalis*, dorsal view of tongue); (1) present (*Elgaria multicarinata*, dorsal view of tongue); (2) tongue can be retracted entirely into buccal cavity below larynx. Schwenk (1988) (ordered).

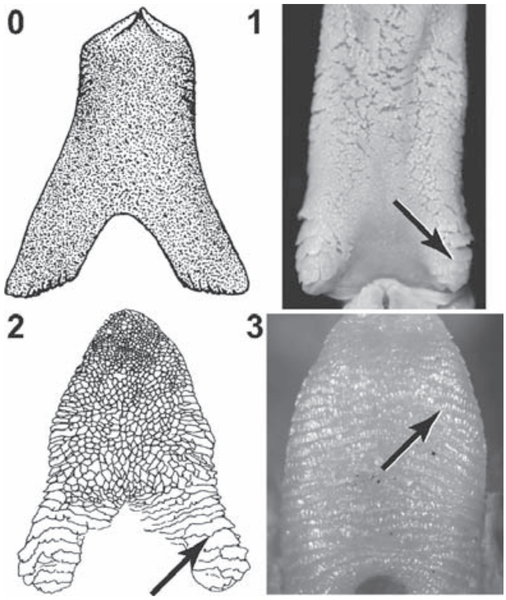
590. Tongue tip notching, as percentage of tongue length: (0) no notch; (1)^N less than 10%; (2)^N 10–20%; (3)^N 20–40%; (4)^N more than 45%. Schwenk (1988) (ordered).



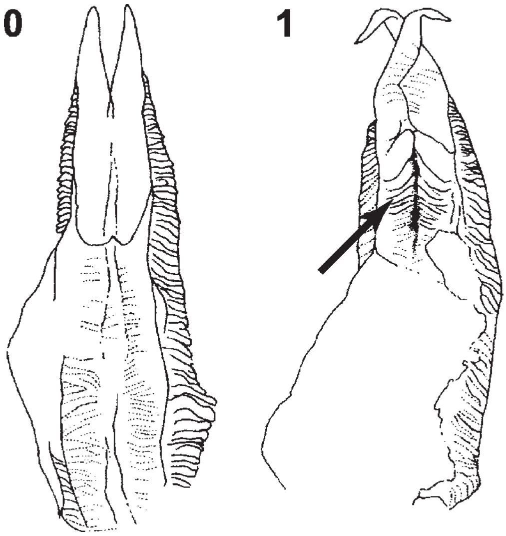
591. Tongue papilla crenellated: (0) continuous smooth distal edges of papilla (*Dipsosaurus dorsalis*, dorsal view of tongue); (1) crenellated distal edge (*Cordylus mossambicus*, dorsal view of tongue). Schwenk (1988).



592. Tongue papilla shape: (0) long, filamentous, and densely packed papilla (*Dipsosaurus dorsalis*, close-up of papilla); (1) shorter, larger, somewhat compressed and tipped caudally (scale-like papilla) (*Cordylus mossambicus*, close-up of papilla); (2) deeply imbricate flat scales (*Amphisbaena fuliginosa*, close-up of papilla). Schwenk (1988) (ordered).

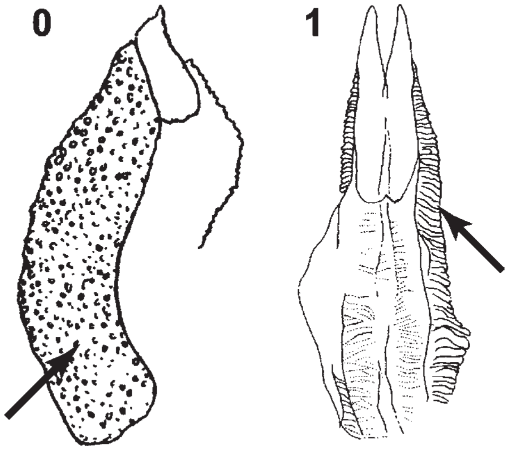


593. Hindtongue epithelium: (0) discrete papilla (filamentous or scale-like) (*Dipsosaurus dorsalis*, dorsal view of tongue); (1)^{N} transverse plicae confined to lateral margins of posterior lobes (*Lialis burtonis*, dorsal view of hindtongue); (2) transverse plicae extend across hindtongue (*Cordylus mossambicus*, dorsal view of tongue); (3) and into the anterior half of the tongue (*Anelytropsis papillosus*, dorsal view of tongue). Schwenk (1988) (ordered).

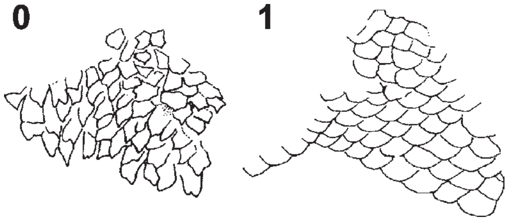


594. Infralingual folds: (0) absent (*Lacerta viridis*, dorsal view of tongue); (1) present (*Callopistes maculatus*, dorsal view of tongue). Harris (1985).

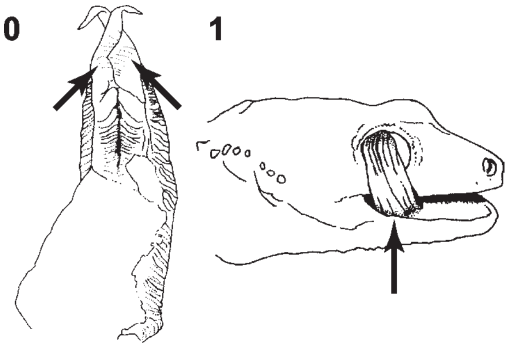
There are many tiny "folds" along each of the hypoglossal muscles in *Rhacodactylus*, *Lialis* and *Eublepharis*.



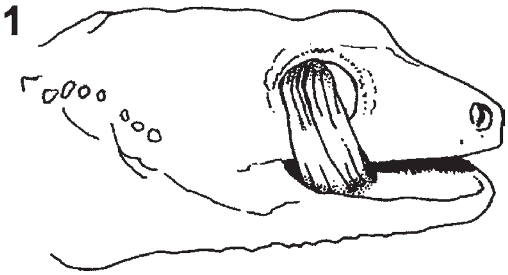
595. Papilla on ventrolateral margins of entire tongue^{N}: (0) papillose (*Dipsosaurus dorsalis*, lateral view of tongue); (1) plicate (transverse scale rows) (*Lacerta viridis*, dorsal view of tongue). Plicae passing around dorsolateral margins of posterior lobes formed from broad and/or fused papillae in gekkotans; those running along the entire ventrolateral margins of tongue are composed of fused scale-like papillae in scincomorphs (Schwenk 1988).



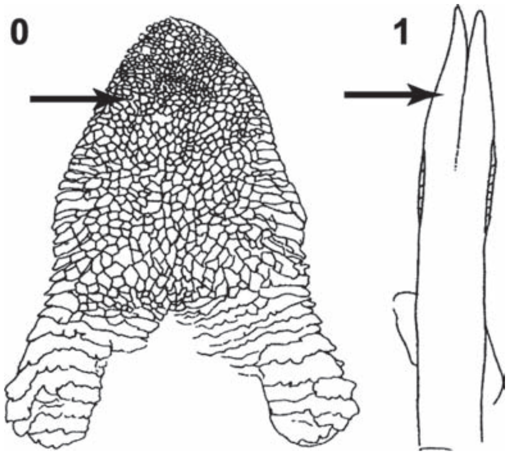
596. Tongue papilla arrangement: (0) not in oblique rows (*Cordylus mossambicus*, close-up of papilla); (1) arranged in regular oblique rows (*Amphisbaena fuliginosa*, close-up of papilla). Schwenk (1988).



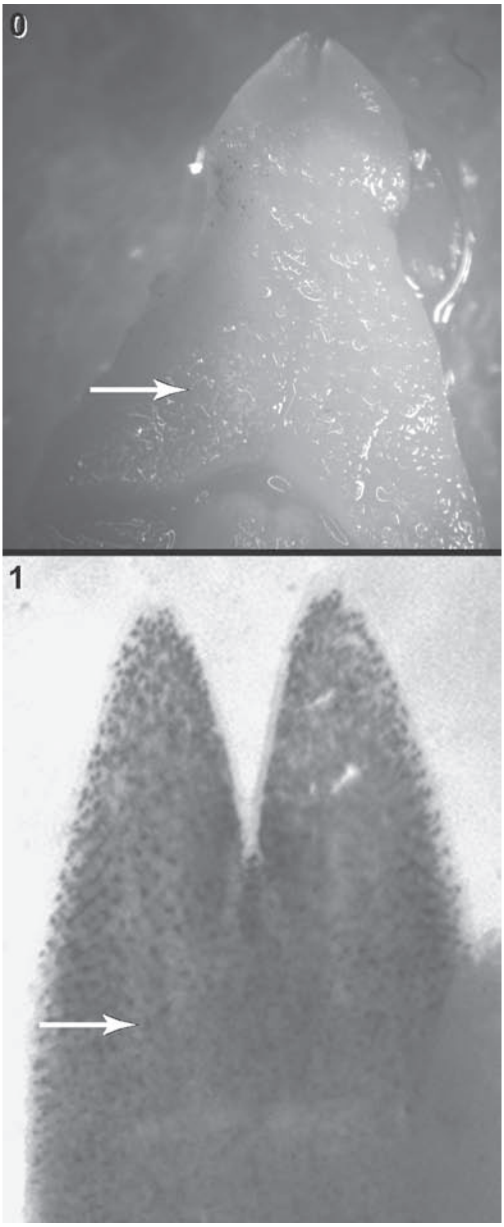
597. Hypoglossal muscle: (0) paired and smooth ventrally (*Callopistes macularius*, dorsal view of tongue); (1)^{N} multiple, and with fine transverse grooves beneath each muscle bundle (*Gekko gecko*, ventral view of tongue). Schwenk (1988).



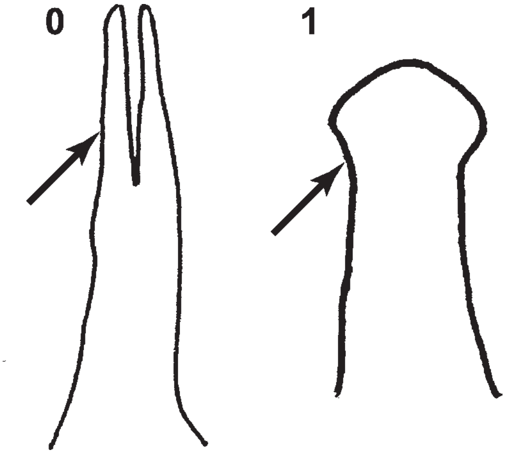
598. Facial tongue wiping (tongue acts as an accessory eyelid): (0) absent; (1) present (*Gekko gecko*). Greer (1985b) All scores are pers. obs. J.A. Gauthier.



599. Foretongue surface: (0) papillose (*Cordylus mossambicus*, dorsal view of tongue); (1) smooth (*Leptotyphlops dulcis*, dorsal view of tongue). Schwenk (1988).

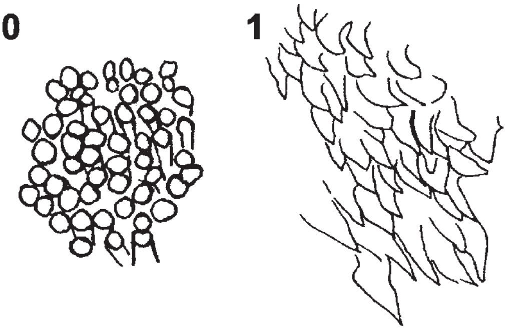


600. Foretongue filamentous epithelium anterior extent: (0) extends to tongue tip as long filaments (*Dipsosaurus doralis*, dorsal view of tongue); (1) those overlying chemosensory part of tongue are depressed to varying degree (*Lialis jicari*, dorsal view of tongue). Schwenk (1988).



601. Arrowhead tongue tip: (0) tongue lateral margins continuous at tip (*Tupinambis teguixin*, dorsal view of tongue); (1) notched just behind tip (*Tiliqua scincoides*, dorsal view of tongue). Schwenk (1988).

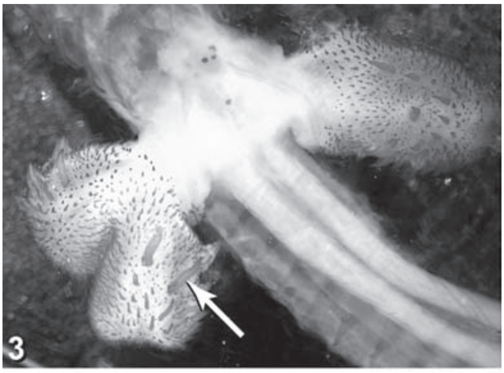
602. Tongue width across posterior notch/maximum tongue length: (0)^{N} 50–60%; (1)^{N} 40–44%; (2)^{N} 30–35%; (3)^{N} 22–25%; (4)^{N} less than 12%. Schwenk (1988) (ordered).



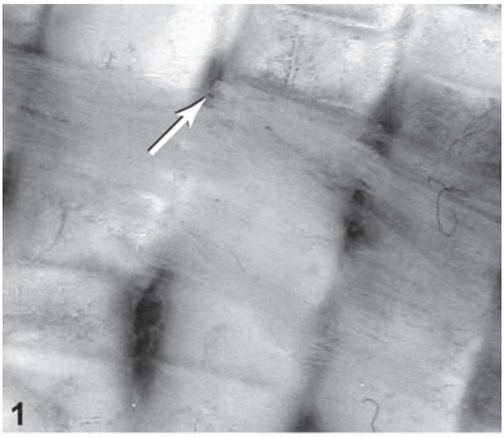
603. Hind tongue papilla: (0) not sharply pointed (*Dipsosaurus dorsalis*, close-up of papilla); (1) sharply pointed (*Elgaria multicarinata*, close-up of papilla). Schwenk (1988).

604. Prey prehension: (0) crickets (or larger animals) taken primarily with tongue; (1) primarily with jaws. Schwenk (1988) All scores are pers. obs. J.A. Gauthier.

605. Amniote penis: (0) absent; (1) hemipenis present. Gauthier, Estes and de Queiroz (1988). See character 606(3).



606. Hemipenis mineralizations^{N}: (0) absent; (1) comb-like; (2) sleeve-like; (3) spine-like (*Causus rhombeatus*, cleared and alizarin-stained hemipenis).



607. Rectus abdominis muscles: (0) not attached to belly skin; (1) attached to hinges between ventral transverse scale rows (*Callopistes maculatus*, close-up internal view of belly skin showing insertions of fragments of m. rectus abdominis). Bhullar (2009).

608. Ulnar nerve pathway: (0) superficial to limb muscles; (1) deep to limb muscles. Jullien and Renous-Lécuru (1972) See Appendix 5.

609. Dorsal shank muscle innervation: (0) peroneal nerve; (1) interosseous nerve. Jullien and Renous-Lécuru (1972) See Appendix 5.

610. Ovipary vs. ovovivipary/vivipary: (0) ovipary; (1) ovovivipary to vivipary. See Appendix 5.

Appendix 3:
Taxon and Character Matrix
Used in Analysis of Squamate Phylogeny

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#NEXUS
BEGIN DATA;
        DIMENSIONS NTAX=192 NCHAR=610;
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?00??????? ?????????? ??0??00??? ????0????? 00??3?00?? ?????????? ??1???????
??0??????? 1????????? ??00000??0 00???????? ?????????? ?????????? ??????1???
?????????? ?????????? ?????????? ????00???? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?3000?0000 ?????????? ?????????? ??????????

Leiolepis_belliana 1020003000 00000?0000 0011100010 000??10000 000?0?0300
000001120? ?32000000? 2?0?000110 020???0100 ??0000000? 0110100000 2012020001
0000000?01 0000010000 0000001120 0002200000 0000000000 0?00001010 1100102000
0000000010 00010??01? 0100000??0 00?0000001 00000?0??0 10?0000001 ?0?01?111?
0000?11??0 000?2000?0 ?00000?0?0 1001121000 0000010000 0000100?0 0?0000?0??
0001010000 0?00010100 0101000001 40?2020010 0000000??0 1001001001 0110?00010
1000000000 100?101022 3011000??1 ???2010011 0100100110 0000000000 003?0?1003
0???0?1000 1101??0000 0010101002 00110010{13}0 0{01}11000{01}10 0000000010
0011201110 0000010000 0010011001 010000000? ?0000?0000 ?002001001 0000000000
0?00100010

Uromastyx_aegyptius 102000{23}002 00?00?0011 0??1100010 000??1?000 000?0?0400
000001120? ?1????00? 2?0?000?10 020???0100 ??0200000? 0110100000 20120?0000
0010000?01 0000011?00 0001?01010 0010200000 0000000000 0?00001010 1200?02200

0000000010 00010??01? 0010000??0 00?0000001 01000?0??2 10?0000003 ?0?01?111?
0000?11??0 000?2000?0 ?00010?0?0 0000121000 0000010000 0000010??0 0?0000?0??
0001010001 0001010110 0101000000 40?2021010 0000000??0 1001201001 0110?00000
?000000000 000?00?012 2011000??1 ???0010011 0100100000 0000000000 003?0?1003
0???0?1000 11010?0000 0010111000 0011001000 0110000{01}00 0000{01}10010
0011201110 0000010000 0012011001 {01}10000000? ?0000?0000 ?0020010?? ??????????
????100??0

Brookesia_brygooi 10200??200 ?0000?1001 0??1100000 000??10000 000?0?0??1
000002300? ??????000? ??0?000400 100????100 ??0200011? 00?0100?0? 2010000002
0000000?22 03?1011?10 0000?00010 001120000? 0000000??? 0?10?02001 1310002400
00?2?1???? ?????????? ?10000???? 00?00?0001 10000?0??1 10?0000001 ?0?01?111?
000??11??0 000?0000?0 ?001?0?0?1 ????20000 20000010?0 1100?100?0 0?0000?2??
0001010100 0?00010101 0101000000 30?2020010 00?1??0??0 ?011201001 0?10?00000
1001?????? 110?100013 2010000??1 ???2010022 00?031??01 1002000010 002?0?1003
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Chamaeleo_laevigatus 102000320? ?0000?0001 0??1100010 000??10000 000?0?0??1
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0000000?22 00?1011?10 0000?10020 000020000? 0000000??? 0?10?02001 1310?0?100
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000??11??0 000?0000?0 ?00100?0?1 ?????2?000 2000010000 100??110?0 0?0000?2??
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0?????0000 0?300{34}2110 100?00111? ????1????0 00010012?0 11101?0021 111121??01
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Physignathus_cocincinus 1020003200 00000?0000 0?11100000 000??10000 000?0?0300
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0000000?01 0000010010 0000000010 0002100000 0000000000 0?00001010 1200002000
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Agama_agama 1020004200 ?0000?0100 0?11100010 000??10000 000?0?0300 000001120?
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0000010010 0000?00010 0012100000 0000000000 0?00001010 1200102010 0000000010
00000??01? 0000000??0 00?0000001 00000?0??0 10?0010001 ?0?01?111? 0000?11??0
000?0000?0 ?00100?0?0 101?121000 0001010000 0000010??0 0?0000?0?? 0001010000
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1?0?101003 2010000??1 ???0010001 00?0001100 0001000000 103?0?1003 0???0?1000
1110020010 1011100100 0000001000 0010000110 0000000010 0011201110 0000010000
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Calotes_emma 1020004200 00000?0100 0?11100010 000??10000 000?0?0300 000001120?
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000?0000?0 ?00100?0?0 101?121000 0001020000 0000010070 0?0000?0?? 0001010101
0001010100 0101000001 40?2020010 0000000??0 1001201000 0110?00010 1000001000
1110101013 2010000??1 ???0010001 00?0101100 0001000000 103?0?1003 0?????1000
1120030010 1011101100 00010010{12}0 0011000010 0000000010 0011201110 0000010000
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Pogona_vitticeps 1020004200 00000?0000 0?11100010 000??10000 000?0?0300
000001120? ?32000000? 2?0?000400 100???0100 ??0000000? 0110101000 2011020003
0000000?01 0000011?10 0000?00010 0012200000 0000000000 0?00001010 1200102010
0000000010 00000??01? 0000000??0 00?0000001 00000?0??0 10?0010001 ?0?01?111?
0000?11??0 000?0000?0 ?00100?0?0 0010121000 0001020000 000001?0?0 0?0000?0??
0001010000 0001010100 0101000001 40?2020010 0000000??0 1001201000 0110?00010
0000001000 1110101013 2010000??1 ???001000? 00?0100000 00?0100000 103?0?1003
0???0?1000 1100?200?0 0011101100 0000001010 0?101000?0 0000??0010 0011201110
0000010000 0??0011001 000000000? ?1000?0000 ?002001001 0000000000 000010???0

Temujinia_ellisoni ????????0? 0????????? ???????0?? ?00??1?000 000?0?0100
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???0?????? ?????????? 0????????? ?????????? ?0???????0 ?0?0000001 ?0?01?1?1?
?000?01??0 000?0000?0 ?000?0?0?0 ?00????000 100???0000 00??????0? 0?0000????
?00101?00? 0?00??0?00 0?01??0001 ???0000000 0100200100 1001001102 0010?00000
?000000000 1???0000?3 2000000000 00?2000??? ?????????? ?????????? 0???0?12??
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?1?00?0000 ?????????? ?????????? ??????????

Saichangurvel_davidsoni ?0000???00 00000?0000 000??0001? 00???10000 0??????200
0???011??? ?011000000 0?0?00?1?0 ??0?0?01?0 ??000?000? 0110100000 11?102?000
0000000?01 ?00?0?0000 000100??20 00002?0001 000010000? 0?00001??0 1??0??????
?????????? ?????????? ?????????? ?????????? ?????????? 1???0????? ??????????
?0???????0 ?00?0000?0 ?????????0 ??00?2?000 00???????? ?????????? ??????????
?????????? ?????????? ???????00? ??????0??? ??00?0???0 ?0???01?0? 0?1????0?0
?000??0?0? ?01000003? ?000000??? ???20????? ????1????? ???0000000 ?01???1102
0??????0?? ???????010 ??1?11??0? ??1??????0 111??0???0 0000??0010 00???0??10
??0?01?00? 0????110?? ??00???0?? ?1000?0?00 ?0???????? ?????????? ??????????

Isodontosaurus_gracilis 10000???00 ??000?0000 000??00010 000??10000 000?0?0200
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0000000011 0000?00000 0001000020 00022?000? 00??01???? ??????1?10 120??0????
?????????? ?0???????? 0????????? ?????????? ?0???????0 ????1???0? ????1?1???
?0?0?01??0 000?0000?0 ?000?0?0?0 ?00?12??00 00?????000 00???????? 0?0000????
?0010??00? ??0??????0 ??01000001 40?0020000 0100200000 1001201102 0010?00010
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?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?0000?0000 ?????????? ?????????? ??????????

Zapsosaurus_sceliphros ?????????? ??????0??? ?????0?0?? ?00??1?000 000???0100
000001121? ?1????000? 2?0?000??0 000????1?0 ??010?000? 0110100?0 ????02??00
0?00000?01 ?000??00?? ?0???????0 ?00?????0? ??00?00?00 0?00001?10 ??0??0????
?????????? ?????????? 0????????? 0????????? ?????????? ?????????? ??????1???
?0?0??1??0 000?0000?0 ?00010?0?0 ??0?1???00 00?????00 ?????????? 0?000?????
?001???00? 0?00??0??? ??0?000??0 40?0000?00 ?3001?0??? ?001001?02 ??1??0?010

0000000000 1?????00?? 30000000?0 00?2000??? ?????????? ?????????? 0???0?1???
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?0??0?0000 ?????????? ?????????? ??????????

Polrussia_mongoliensis ?????????? ?????????? ???????0?? ?0???10000 000???0000
0000011?1? ?1?????00? ??1?0001?? ?00???01?0 ??020?000? 0110100?0 ????02??00
0000000?01 ?000???0?? ?001?00020 00002?000? 000000???? ??????1?10 ??0??0????
?????????? ?????????? 0????????? ?????????? ?????????0 ?0??1???0? ????101???
?000?000?0 000?0000?0 ?????0?0?0 ??0?12??00 0???????00 ?????????? ??0???????
?0010????? ??0??????? ????00001 ???0000?01 03000000?0 1002001?02 0?10??0010
?000?10000 1???0000?2 2000000000 0000000??? ?????????? ?????????? 0???0?1???
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
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Basiliscus_basiliscus 1000002000 00000?0000 0001000010 000??10000 000?0?0300
000001120? ?2??0?000? 2?0?000110 000???0100 ??22?0000? 0110200000 1112020000
0000000001 0000000000 0001010020 00002?0000 0000000?00 0?00001010 120000?000
0000000010 00000??01? 0000000??0 00?0000001 10000?0??0 10?0000001 ?0?01?101?
0000?00000 000?0000?0 000010?0?0 1000121000 0000020000 0000?100?0 0?0000?0??
0001010000 0001010000 0101000001 40?0?00000 030010?000 1001001200 0010?00000
0000000000 1010000033 3000000000 0002000001 0??0100100 0000000000 012?0?130?
0?????1000 10{01}0030100 1011101102 1011000?10 0010000110 00000{01}0010
?0112011?0 0000010000 ?0?0011001 {01}?0000000? ?1000?0000 ?0010010?? ???????0??
????10?010

Corytophanes_cristatus 1000002000 20000?0000 000??00011 000??10000 000?0?0200
000001120? ?2??0?000? 2?0?000110 000???0100 ??22?0000? 0010200000 1?12020000
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000?000010 00000??01? 0?00000??0 00?0000001 10000?0??0 10?0000001 ?0?01?121?
0000?01??0 000?0000?0 00001??0?0 001?121000 0000011000 0000?100?0 0?0000????
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0011201110 0000010000 1010011001 000000000? ?2000?0000 ?001001001 000000?00?
0?0010?010

Polychrus_marmoratus 100001200? 20000?0000 000?000011 000??10000 000?0?0?10
000001120? ?2??0?000? 2?0?000110 000???0100 ??0200000? 0111?00000 1012020000
0000000001 0000000200 0001000120 00012?0000 0000000000 0?00001010 1200102100
0000000010 000?0???1? 0000000??0 00?0000001 00000?0??0 10?0000003 ?0?01?121?
0000?00000 000?0000?0 ?00010?0?0 101?121000 0000110?0 0000100?0 0?0000?0??
0001010000 0000010000 01010000?1 40?0000000 ?300000100 1012001202 0010?00000
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0???101000 10200320{01}0 0010101000 000{01}000?00 00100011{01}0 0000010010
0011201110 0000010000 0010011001 010000000? ?2000?0000 ?001001101 000??0?00?
0?00100010

Anolis_carolinensis 10000?0002 00000?01?0 0001000010 000??11000 000?0?0?10
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0000000001 0000000000 0001010120 0000100000 0000000200 0?00001010 1200002000
0000000010 00010??01? 0000000??0 00?0000001 00000?0??0 10?0000001 ?0?21?101?
0000?01?00 000?0000?0 000010?0?0 1001121000 0000010000 0000?100?0 0?0000?0??

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0???101000 {01}?{12}00{23}1010 0011101100 001000{01}?{02}0 0010000010 0000000010
0011201110 0000010000 0010011001 000000000? ?2000?0000 ?001001101 0000000000
000010?010

Leiosaurus_catamarcensis 1000002002 00000?0100 0001000010 000??10000 000?0?0300
000001120? ?020000000 2?0?000110 000?0?0101 ??0000000? 0110100000 1111020000
0000000001 0000000000 0001010020 0000200000 0000000100 0?00001010 1200002100
0000000010 00000??01? 0000000??0 00?0000001 20000?0??0 10?0000001 ?0?01?111?
0000?00100 000?0000?0 ?00010?0?0 0000121000 0000010000 0000?100?0 0?0000?0??
0001010001 1001010000 0101000001 30?2000010 0300000100 1001001202 0010?00000
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0?????1000 ?????????? ????1???0? ?0??00???0 0??0?0???0 ??00??00?? ??11?011?0
????0??0?? ????01?001 ??00???0?? ?2000?0000 ?00?0?12?? ?????????? ????10?01?

Pristidactylus_torquatus 10000?0002 00000?0000 0001000010 000??10010 000?0?0300
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0000000001 0000000000 0001010020 0001200000 0000000100 0?00001010 120010?200
0000000010 00000??01? 0000000??0 00?0000001 10000?0??0 10?0000001 ?0?01?111?
0000?00000 000?0000?0 ?00010?0?0 1000121000 0000010000 0000?100?0 0?0000????
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0011201110 0000010000 0010011001 010000000? ?2000?0000 ?001001201 000000?00?
0?00100010

Urostrophus_vautieri 10000?0002 00000?0100 0001000010 000??10000 000?0?0400
000001120? ?020000000 2?0?000110 000?0?0101 ??0000000? 0110100000 1112020000
0000000001 0000000000 0001010020 0001200000 0000000200 0?00001010 1200102200
0000000010 00000??01? 0000000??0 00?0000001 10000?0??0 10?0000001 ?0?01?111?
0000?00000 000?0000?0 ?00010?0?0 1000121000 0000010000 00000110?0 0?0000?2??
0001010001 1000010000 0101000001 40?2000010 0300000000 1001101202 0010?00000
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0?????1000 ?????????? ????1???0? ?0??00???0 0??0?0???0 ??0???00?? ??11?011?0
????0??0?? ????01?001 ??00???0?? ?2000?0000 ?00?0?12?? ?????????? ????10?010

Aciprion_formosum 10000???00 00?00?0000 000??0001? 000??10000 000???0300
000001120? ?1????000? 2?0?0001?1 000???0100 ??020?000? 0110100?0 11?1020000
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?000??0??0 000?0000?0 ?00010?0?? ?????2??00 00????0000 00???????? 0?0000????
?00????00? 000???0??0 ??01?00001 ???1000100 02001?0000 1001201202 ?010?00000
0000000000 1???0000?3 ?000000000 00?2000??? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?1000?00?? ?????????? ?????????? ??????????

Crotaphytus_collaris 10000?0000 0000000000 0101100010 000??10000 000?0?0000
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0000000001 0000000000 0001010020 0000200000 0000000010 0?00001010 1200102100
0000000010 00000??01? 0000000??0 00?0000001 10000?0??0 10?0000001 ?0?01?111?
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0001010000 0000010000 0101000001 40?10?0110 0200100110 1001001202 0110?00000
0000000000 100?000023 2200000?00 0002000001 0100100100 0400000000 012?0?1303
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Gambelia_wislizenii 10000?0000 00000?0000 0101000010 000??10010 000?0?0000
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0?????1000 1000020000 0111110102 1011000?20 0010000110 0000000010 0011201110
0000010000 0010011001 010000000? ?0000?0000 ?001001001 0000000000 000010?010

Enyalioides_laticeps 1000002000 20100?0000 0001000011 000??10000 000?0?0200
000001120? ?020000000 2?0?000111 000?0?0100 ??0200000? 0110100000 1111010000
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0?????1000 1000021000 0011100100 0011000?20 0010000010 0000000010 0011201110
0000010000 0000011001 {01}10000000? ?200101100 00110010?? ?????????? ????10?010

Morunasaurus_annularis 100000200? 20000?00?0 0101000011 000??11000 000?0?0200
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0000?00000 001?0000?0 000010?0?0 1001121000 0000011000 0000?100?0 0?0000?0??
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0?????1000 1000020000 0111111100 0011000?10 0110000000 {01}000010010 0011201110
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Brachylophus_fasciatus 1000000000 00000?0000 0001100010 000??10000 000?0?0?10
000001120? ?020000000 2?0?000111 000?0?0100 ??0200000? 0110100000 1113010000
0000000?01 0000010000 0001200020 0000200000 0000000000 0?00011010 1200102000
0000000010 00000??01? 0000000??0 00?0000001 11000?0??0 10?0010001 ?0?01?111?
0000?00100 000?0000?0 ?00010?0?0 1000121000 0000010000 0000?100?0 0?0000?0??
000101000{01} 0?0{01}010000 0101000001 40?1000000 0300000100 1001001102
0012000010 1000000000 100?000023 2000000000 0002000001 0100101100 0400000000
013?0?1303 2?????1000 1000021000 011{01}101{01}00 0011000?20 0010000000
0000000010 0011201110 0000010000 ???011001 1?0000000? ?2000?0000 ?0010010??
?????????? ????10?000

Armandisaurus_explorator ?000001000 00000?0000 0001?00010 ?00??10000 000?0?0200
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???0?00?10 0?000??0?? ?000000??0 00??00?001 0?000?0??0 10?0010001 ?0?01?111?
00?0?01??0 000?0000?0 ?00010?0?0 10001??000 00000?0000 0000?????0 0?00?0????
?001?1000? 0000??0??0 0?01000001 40?1000000 0300001?0 ?001001102 0012000000

?0???????? ?01?000033 ?000000000 00?2000??? ?????????? ?????????? ??????1?0?
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?1000?00?? ?????????? ?????????? ??????????

Dipsosaurus_dorsalis 100000{12}000 10000?0000 0001100010 000??10000 000?0?0200
000001120? ?020000000 2?0?000111 000?0?0100 ??0000000? 0110200000 1112010000
0000000?01 0000010000 0001000020 0000200000 0000000000 0?00011010 1200202100
0000000010 00000??01? 0000000??0 00?0000001 11000?0??2 10?0010001 ?0?01?111?
0000?01??0 001?0000?0 000010?0?0 1000121000 0000010000 0000010?0 0?0000?0??
0001010001 0000010000 0101000001 40?1000000 ?300000100 1011101102 0012000000
?000000000 100?000023 3000000000 00?2000001 0100101100 0000000000 013?0?1300
2???101000 1000020000 0111100100 0011000?20 0011000000 0000010010 0011201110
0000010000 0012011001 010000000? ?1000?0000 ?001001001 0000000000 000010?000

Sauromalus_ater 100000{12}000 00000?0000 0001000010 000??10000 000?0?0300
000001120? ?020000000 2?0?000111 010?0?0100 ??0000000? 0110100000 1012010000
0000000001 0000000000 0001000020 00002?0000 0000000000 0?00011010 120010?100
0000000010 00000??01? 0000000??0 00?0000001 01000?0??0 10?0010001 ?0?01?111?
0000?01??0 000?0000?0 ?00010?0?0 1000121000 0000020000 0000010?0 0?0000?0??
0001010000 1001010000 0101000001 30?0000000 0300000110 1001201102 0112000010
?000000000 100?000023 3000000000 00?2000001 0100100000 0100000000 013?0?1300
2???101000 0?00020000 0{01}10110000 0011000?20 0010000{01}10 0000000010
0011201110 0000010000 000?011001 0?0000000? ?2000?0000 ?001001001 000000?000
0?0010?000

Liolaemus_bellii 10000?0000 00000?0000 0001100010 000??10030 000?0?0100
000001121? ?020000000 2?0?000112 000?0?0100 ??0000000? 0110100000 0112020000
0000000101 0000000000 0001000020 00012?0000 0000000110 0?00001010 1200?02200
0000000010 00000??01? 0000000??0 00?0000001 10000?0??0 10?0010001 ?0?11?131?
0000?00000 000?0000?0 ?00010?0?0 1000120000 0000010000 0000010?0 0?0000?2??
0001010001 0000010000 0101000001 30?2001010 0300000100 1021101202 0012000000
?000000000 100?000023 2000000000 00?2000001 0100100000 0400000000 012?0?1102
0?????1000 10{01}0020000 0011111100 001100{01}0{12}0 0110000100 0000000010
0011201110 1000010000 0010011001 0000{01}0000? ?0000?0000 ?001001001 000??0??00
0?0?100011

Phymaturus_palluma 1000002000 00000?0000 0001100010 000??10000 000?0?0100
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0000000001 0000000000 0001000020 00002?0000 0000000101 0?00001010 1200102100
0000000010 00000??01? 0000000??0 00?0000001 10000?0??0 10?0010001 ?0?01?131?
0000?00000 000?0000?0 ?00010?0?0 1000121000 0000001000 0000?100?0 0?0000?0??
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0000000000 1010000013 3000000000 00?2000001 0100100000 0{014}00000000 002?0?1102
0?????1000 1000020000 001110{01}100 0010000?20 0{01}10000010 000000001{01}
0011201110 0000010000 0011011001 010000000? ?1000?0000 ?001001001 000??0??00
0?0?10?011

Chalarodon_madagascariensis 1000001000 00000?0000 0001000010 100??10000
000?0?0200 000001121? ?1?????00? 2?0?000112 000???0100 ??0000000? 0110100000
0112020000 0000000001 0000000000 0001000020 0000200000 0000000000 0?00001010
1200002000 0000000010 00000??01? 0000000??0 00?0000001 10000?0??0 10?0010001
?0?01?111? 0000?00000 000?0000?0 ?00010?0?0 1000121000 0000010000 0000010?0

0?0000?0?? 0001010001 0001010?00 0101000001 40?2000010 0300000000 1011101202
0110?00000 ?000000000 1010000033 3000000000 00?2000001 00?0101100 0000000000
012?0?1102 0?????1000 0?10040000 0111100100 0011000?20 0010000100 0000000010
0011201110 0000010000 001?011001 000000000? ?1000?0000 ?001001001 000000?00?
0?00100110

Oplurus_cyclurus 10000?0000 00000?0000 0001000010 100??10000 000?0?0400
000001120? ?1?????00? 2?0?000112 000???0100 ??0000000? 0110100000 0112020000
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0000000010 00000??01? 0000000??0 00?0000001 10000?0??0 10?0010001 ?0?00?111?
0000?00000 000?0000?0 ?00010?0?0 1000121000 0000010000 0000010?0 0?0000?0??
0001010001 0001010000 0101000001 40?2000?10 0100100000 1012001202 0110?00000
?000000000 1010000023 2000000000 00?2000001 0100100100 0400000000 012?0?1102
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000000?00? 0?0010?110

Petrosaurus_mearnsi 1000001000 00000?0100 0101000011 000??10000 000?0?0000
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0000000010 00000??01? 0000000??0 00?0000001 00000?0??0 10?0010001 ?0?01?121?
0000?01??0 000?0000?0 ?00010?0?0 1000121000 0000011000 0000010?0 0?0000?0??
0001010000 0000010010 01010000?1 40?2000010 0300000100 1012101202 0010?00000
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0000010000 0010011001 000000000? ?1000?0000 ?001001001 0000000000 0?00100000

Uta_stansburiana 10000?0000 00000?0000 0001000011 000??10000 000?0?0000
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0000000001 0000000000 0001000020 00012?0000 0000000001 0?00001010 1200202200
0000000010 00000??01? 0000000??0 00?0000001 00000?0??0 10?0010001 ?0?01?121?
0000?01??0 000?0000?0 000010?0?0 1000121000 0000011000 0000?100?0 0?0000?0??
0001010000 0000010000 01010000?1 40?1000010 0200000100 1012101202 0010?00000
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0???101000 1010020000 0011101100 0011000?00 0010000010 0000000010 0011201110
0000010000 0010011001 000000000? ?0000?0000 ?001001001 0000000000 0?0010?000

Sceloporus_variabilis 10000?0000 00000?0000 0001000011 000??10000 000?0?0100
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0000000001 0000000000 0001000020 0001200000 0000000001 0?00001010 1200102200
0000000010 00000??01? 0000000??0 00?0000001 10000?0??0 10?0010001 ?0?01?131?
0000?01??0 000?0000?0 000010?0?0 1000121000 0000010000 0000?100?0 0?0000?0??
0001010000 0?00010000 01010000?1 40?2000010 0200000100 1012101202 0010?00000
1000000000 1010000033 3000000000 00?2000001 0100100100 0401000000 012?0?1102
0????1000 1010030000 011{01}101{01}00 0011000?00 0010000010 0000000010
0011201110 {01}000010000 0010011001 0000{01}0000? ?1000?0000 ?0010010??
?????????? ????12??00

Phrynosoma_platyrhinos 1000001000 00000?0000 0??1100011 000??10000 000?0?0100
000001120? ?1?????00? 2?0?000111 000???0100 ??02?0?01? 0010100000 11110?0000
0001000001 0000001?00 0000?00020 00122?0000 00??001001 0?00001010 1200002400
000000?010 ????????1? 000000???? 00?00?0001 00000?0??0 10?0010001 ?0?21?121?

0000?01??0 000?0000?0 000010?0?0 001?120000 0000010000 0000010?0 0?0000?0??
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0???10?000 1020020000 0010100000 0011000?{02}0 0010000000 0000000010 0011201110
0210010000 0010011001 000004000? ?2000?0000 ?002001001 0000000000 0?00100000

Uma_scoparia 100000{12}000 00000?0000 0001100011 000??10000 000?0?0000 000001121?
?1?????00? 2?0?000112 000???0100 ??0000000? 0110100000 1112020000 0000000001
0000001?00 0001?00120 0001200000 0000001001 0?00001010 1200102100 0000000010
00000??01? 0000000??0 00?0000001 00000?0??0 10?0010001 ?0?01?121? 0000?01??0
000?0000?0 000010?0?0 1000121000 0000010000 0000010?0 0?0000?0?? 0001010000
0?01010000 01010000?1 40?1000010 0300000100 1001101202 0211000000 0000000000
100?000023 3000000000 00?2000001 0100101100 0401000000 002?0?1102 0???101000
1010020000 0111101100 0011000?00 0010000010 0000000010 0011201110 0000000000
0012011001 000000000? ?0000?0000 ?002001001 0000000000 0?0010?000

Leiocephalus_barahonensis 10000?0000 00000?0000 0001200010 000??10010 000?0?0200
000001120? ?020000000 2?0?000111 000?0?0100 ??0000000? 0110100000 1112020000
0000000001 0000000000 0001000020 0001200000 0000000100 0?00001010 1200102100
0000000010 00000??01? 0000000??0 00?0000001 10000?0??0 10?0010001 ?0?11?121?
0000?01??0 000?0000?0 ?00010?0?0 1001121000 0000010000 0000?100?0 0?0000?0??
0001010000 0?01010000 01010000?1 40?2000020 ?300000100 1012101202 0112000000
1000000000 1010000033 3000000000 00?2000001 0100101100 0400000000 012?0?1102
0???101000 1010030000 011110{01}100 0011001000 0010{01}00010 0000010010
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0?0010?000

Plica_plica 1010001000 20?00?0000 000?000011 000??10000 000?0?0300 000001120?
?020000000 2?0?000111 000?0?0100 ??0000000? 0110100000 1112020000 0000000001
0000000000 0001000020 00002?0000 0000000100 0?00001010 120010?100 0000000010
00000??01? 0000000??0 00?0000001 11000?0??0 10?0000001 ?0?11?121? 0000?00000
000?0000?0 000010?0?0 1000121000 0000010000 0000?100?0 0?0000?0?? 0001010000
0?01010000 01010000?1 40?2000020 ?3?00?0101 10?2101002 0110?00000 0000000000
1010000023 3000000000 00?2000001 0100101100 0100000000 002?0?1?02 0?????1000
1000020000 011{01}111{01}00 0011000?20 0000000010 0000000010 0011201110
0000010000 101{01}011001 010000000? ?1000?0000 ?001001001 000???00? 0?00100000

Stenocercus_guentheri 1000001000 00000?0100 0001000010 000??10000 000?0?0300
000001120? ?020000000 2?0?000111 000?0?0100 ??0000000? 0110100000 1012020000
0000000001 0000000000 0001000020 0001200000 0000000101 0?00001010 1200002100
0000000010 00000??01? 0000000??0 00?0000001 10000?0??0 10?0000001 ?0?11?101?
0000?00000 000?0000?0 ?00010?0?0 1000121000 0000010000 0000010?0 0?0000?0??
0001010000 0?01010000 01010000?1 40?20?0020 0300000100 1012101102 0110?00000
?000000000 100?000023 2000000000 00?2000001 0100100100 0400000000 002?0?1102
0?????1000 10100200{01}0 011111{01}100 0011001010 0010000010 0000000010
0011201110 000010000 001{02}011001 000000000? ?1000?0000 ?0010010?? ?????????
????10???0

Uranoscodon_superciliosus 10000?0000 00000?0000 0001000011 000??10000 000?0?0300
000001120? ?020000000 2?0?000111 000?0?0100 ??0000000? 0110100000 1112020000
0000000001 0000000000 0000000020 00002?0000 0000000001 0?00001010 1200102100
0000000010 00000??01? 0000000??0 00?0000001 10000?0??0 10?0000001 ?0?01?121?

0000?00000 000?0000?0 000010?0?0 1000121000 0000010000 00000100?0 0?0000?2??
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0?????1000 1010020000 0111111100 0011000?20 0010000000 0000000010 0011201110
0000010000 0010011001 010000000? ?0000?0000 ?001001001 000??0?00? 0?0010?010

Tchingisaurus_multivagus 10000?0?0? 0??00????? ???????0?0 0?0??0?010 000?0?0?10
0000021?0? ?001000000 0?0?00???0 0?1?0??1?0 ??000?000? 0110000?0 10?30?0000
0000000000 00000?0000 0001?00021 000?20100? ??0000???0 ??00001?10 1200?0????
?????????? ?????????? ?0?0?????? 00?000???0 ?0???????? ?0??1?00?? ????????1?
??00?0?00? ?????????0 ???????0?0 ??0?????00 00??1???0? ?????????? 0?0???????
?00??1???? ??0??????? ??????0001 ???0000000 0000300010 1002001102 0010?00000
0000000000 0010000033 ?000000??? ??02001??? ?????????? ?????????? 001?0?1???
?????????? ?????????? ????????0? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?2??0?000? ?????????? ?????????? ??????????

Gobinatus_arenosus 10000?0?00 00100?00?0 0??1?0000? 000??010?0 000?0?0?20
000002110? ?001000000 0?0?0001?0 0?1?0?1100 ??0104000? 0110000?0 20?303?000
0100000?00 00000?0000 0001100001 00002?100? 0000001000 0?00101?10 1200?0????
??????0??? ?000???0?? ??????0??0 00?000???? ?0???????? 10?00?00?2 ?0?0??1???
?000?000?0 ?01?0000?0 0000???0?0 ????1??000 0?????0000 00???????? 0?0000????
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0010000000 0???0001?2 3000000??? ???2001??? ?????????? ????????00 001?0?1???
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?1000?0000 ?????????? ?????????? ??????????

Adamisaurus_magnidentatus 10100???00 ?0100?00?0 000?000000 000??01040 000?0?0?10
0000021?0? ?001000000 1?0?000100 001?1?11?1 ??00004000? 0110000000 2013010001
0100000000 0000000000 0001100001 000?101000 00000010?? 0?00101?10 1?00?0????
???0?00010 ?0001??0?? ?0?0??0??0 00?000?0?1 00?00?0??0 10?0000002 ?0?01?000?
0100?01??0 101??000?0 10000??0?0 000012?000 00??1?0000 00???????? 0?0000????
?0010?000? 0?0???0??0 ??01?01000 40?00?0?20 00002000?0 1001001?02 0?10??0010
0010000?00 000?040122 1000000000 00?0001??? ?????????? ?????????? ????0?1???
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?0000?0000 ?????????? ?????????? ??????????

Gilmoreteius 10?00????0 ??00??0000 ?0???00000 ??0??000?0 000?0?0?30 0?00021?0?
?001000000 0?0?000100 001?0?11?0 ??0004000? 0110000001 ?01303?000 0100000000
?0?0000000 ?0011???01 0000101000 000001???? ??????1?10 1100?0???? ?????0?010
?000?????? ?0100????? 00?????001 0??00?0??1 10??00000? ????1?000? ?100?01??0
101???00?0 100?0??0?0 ?00?12?000 00??????00 ?0???????? 0?0??0?0?? ?0010???0?
0?0???0??0 ??01?0000? 40?0000?0? 0000?100?0 1?0??01?0? 0?10???0?0 ?010000?00
00??000133 3000000000 00?2001??? ?????????? ???0200000 ?01?0??2?? ???????0?0
???????0?? ????100?02 10?1001100 111??00??0 0000??00?? ?????0???0 ?00000?000
????110001 0?00?000?? ?1000?0000 ?0???????? ?????????? ??????????

Polyglyphanodon_sternbergi 1000001000 00000?00?0 0001000000 000??01040 000?0?0?20
000002110? ?001000000 0?0?000100 001?0?1101 ??00004000? 0110000001 2013030000
0100000000 0000000000 0001100001 000010100? 000001???? ??????1?10 1?00?0????
?????00010 10001??0?? ?010??0??0 00?000?001 20?00?0??1 10?000000? ????1?001?
0100?01??0 101??000?0 10000??0?0 ??0??2?000 00??????00 ?0???????? ??0000????
?001????0? 0?0???0??0 ?101000000 40?0000?00 00003100?0 1001001?0? 0?1??0?01?

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0010000?00 000?000133 30?0000??? ???2001??? ?????????? ???0200000 001?0?1200
0??????0?? ???????0?0 ?01?100?02 00??0010?0 ?????00??0 0000???01? 00?1?0??10
?00000?000 0??????0?? 1?00?000?? ?1000?0000 ?0???????? ?????????? ??????????

Sineoamphisbaena_hexatabularis 10000????0 ???0??0000 ????000000 ??0??001??
?????????? ????011?0? ?00??0000? ??0?011?00 ????0?10?2 ??01140?0? 1011?00???
?0??0??000 010000??1? ?0?0??0??? ?00?????01 000010??0? 0????1???? ????????01
1????0???? 11???????? ?????????? ???0?????? 0????????1 0???0????2 ?0??????1?
?0?01?13?? 1?0??01??0 2????000?? 100????0?? ???????000 00????2??? 220???????
?????0???? ??1001??01 100?????32 ?101?0000? ??????0??? 00???????? ?????0??0?
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?????????? ?????????? ?????????? ?????????? ?2000?0000 ?????????? ??????????
??????????

Adriosaurus_suessi 1?100???1? ?????????? ?????????? ??0??0???? ????0???10
0?0?0?1??? ????0?00?? 0?0?00???0 ???????1?0 ??0?0?000? ?1??000??? ????0??1??
????000?00 ?0???????? ?0???????? ????????0? ??0??????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
?????????0 ?????????? ?????????0 ??0?1??000 00???????? ?????????? ??????????
?????????? ?????????? ??0??????? ???0?????? ?????????? ?????????? ??????????
?????????? ?????????? ?1????1??0 ?????????? ?????????? ???0410003 ?11????3?3
0??????1?? ???????10? ?0??101?1? ????1????0 ?????0???0 ?000??001? ?????0???0
????0??011 ??????00?? ??0??300?? ?0??0?0?00 ?????????? ?????????? ??????????

Pontosaurus 10100?0?11 10000?0?11 ????0000?0 0????10??? ?0?????400 000001110?
?2??0?0000 0?0?0001?0 ??2???0100 ??0000000? 0110000??? 0???2??1?0 0000000?00
?0?0?????? ?001??0?20 00012??00? 000010000? 0?00001?10 1????1???? ??????0???
?????????? ?????????? ????0????? ?????????? ?????????? ?????????? ???0?0????
0????????? ???????0?0 ??0?10?000 0????????? ?????????? ?????????? ??????????
?????????? ??0??0???? ????000?0? 00?0112??0 10?1201?0? 0?111?0000 ??00000001
0?0?????2? ?100?01??? ???0??0??? ?????????? ???0410002 211?1??3?3 0???20?1?0
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?????00001 2?0???00?? ?0000?0?00 ?0???????? ?????????? ??????????

Aigialosaurus_dalmaticus ?????????? ????????11 ?????????0 ?????1???? ???????400
000?0?110? ?2??0?00?? 0?0?0001?0 ??3???01?0 ??020?0??? 0110000??? ????01?1?0
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?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????0 ?????????? ?????????? ?????????? ??????????
?????????? ??0??????? ??????01?2 ???0????00 ??00?????? ?10???1?0? ?????????0
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0???20?1?? ?????????? ?????????? ?????????0 ?????????0 10?0??002? ?????0???0
??0000?0?? ??????00?? ??0????0?? ?0000?0?00 ?0???????? ?????????? ??????????

Clidastes 1110012?02 1?000???11 ?????1???0 ?????100?0 000???0?11 10000??10?
?2??0?00?? 0?0?000300 003???1100 ??0202000? 011000003? 0???01?100 0001000020
0000??0000 0001000020 0001??0?0? 0000000000 0?00001010 1200?1???? ???0??????
?????????? ?????????? ?????????? ?????????0 1???0???0? ????1?10?? 00?0?001?0
?00????2?0 0???2??0?0 ?00??0?000 000?100000 10001????? 0?0000?0?? ?010?1000?
00010?0131 ?101?001?2 ???0000?00 0000?12??0 1101??10?2 02?11?0?01 ??00??????
000?000222 2100001110 01?0000??? ?????????? ???0410000 21001013?3 0??????0??
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???????10? ?01?????1? ????0????0 ?0?0?00??0 1201??101? 1???00???0 ???100?011
??????00?? ??01??10?? ?0000?0000 ?0?0?????? ?????????? ??????????

Platecarpus 1110012?02 1?000???11 ?????????0 ?????100?0 000???0??1 100?0??10?
?2??0?000? 0?0?001300 003???1100 ??1202000? 011000003? 0???01?100 0001000020
0000??000? 0001000020 00012?0?00 0000000000 0?00001010 1200?12??? 0??0??????
?????????? ?????????? 0??0?????1 ??0??????0 10??00000? ????1??0?? ?0????01?0
?00??002?0 00002??0?0 ?00?10?000 000?101000 10101????0 0?0000???? ?00??11001
00010?0131 0101000122 41?00?0?0? 0000?120?0 ?101201012 02011?1?00 ?000????0?
000?000222 3010001?00 0110000??? ?????????? ???0400000 21001013?3 0???20?1??
????????0? ??1?101?1? ????1????? ?????????0 12?1??101? ????00???? ????0??011
??????00?? 2?0???10?? ?0100?0000 ?0?31????? ?????????? ??????????

Plotosaurus 1?10012?02 10000???11 0????100?0 ?????100?0 000???0?01 10000??10?
?2??0?00?? 0?0?000300 003???11?0 ??0202000? 011000003? 00??010100 0001000?20
0000000000 000100?020 00012?010? 0000000000 0?0000?010 1200?1?00? ?????00010
?000???1?? ?0010?0??0 00?00000?? 10000????0 10?0000002 ?0?01?10?? 001??001?0
?11??0?2?0 00202??0?0 ??1?10?000 000???0000 ?0???????? 0?0000?0?? ?010?1000?
000?????3? ??01010122 41?0000?00 0000112000 1101201012 010110?001 ?000100001
000?000223 2210001100 0110000??? ?????????? ???0420000 21?01010?3 0?????????
?????????? ????????00 00??0????? ?????????0 12?1??101? ????00???1 ???100????
?????????? ??????1??? ?0000?0000 ?0???????? ?????????? ??????????

Tylosaurus 1110012?02 1?000???11 ?????1???0 ?????100?0 000???0?01 100?0??10?
?2??0?00?? 0?0?001300 003???1100 ??0202000? 011000003? 0???01?100 0001000?20
0000??000? ?011?00020 00012?0?0? 0000000000 0?00001010 1200?1???? ??????????
??00?????? ??????0??? ?????????? ?????????0 1???0???0? ????1?10?? 00?0?00100
?00??002?0 0???2??0?0 ?00??0?000 000??????? ??00?????? ?????0???? ??????????
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000?000222 2100001?00 0110000??? ?????????? ???0400000 21001010?3 0???30?0?0
???????100 101?001?1? ?????????0 ?????0???0 1201??101? 1???00???0 ???100?011
??????00?? 2?00??10?? ?0?00?0000 ?0?11????? ?????????? ??????????

Eichstaettisaurus 0?0?0?0?00 ?000??0100 0?0??000?0 000??001?0 0?0?0??100
00??01?10? ?00?000000 0?0?0001?0 0?2?0?00?2 ??0?0?000? 0110000??? 0??301?0?0
0000000?00 ?0????00?? 0001000?20 00002?000? 1100100100 0?00001??0 12?0?0????
?????????? ?????????? ?????????? ?????????? ?????????? 2????0???? ???0???3??
?0?0?0???0 ?10?0?00?0 ???02??000 ?00?1??000 00???????? ?????????? ??????????
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??00????0? 000?000044 ?0000?0??0 ???0?00??? ?????????? ???0400000 002?0??102
0??????0?? ???????00? ????????0? ?1???????0 00???0???0 0000??001? ?0??10???0
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AMNH_FR_21444 ?????????? ????????0? ???????0?0 000??00130 ?00?0?0300 000001010?
?00?000000 0?0?00???0 012???0002 ??0?1?000? 01100000?0 ?1??0???00 0000000200
?00?1???00 0001?00020 ?00?2??1?? ?????000?? 0????0???? ?????????? ???0??????
?????????? ??00?????? ???????0?? 00??????00 ???000?002 ?0?01?131? 00?0?01??0
010?0000?0 ?010200??0 ??0????000 0?0?100110 0????????0 3?000??2?? ?0010100??
??0???1??0 ??01?????? ????00???? 00002??000 10010?1?02 0?1????0?0 ??00??????
0???0??0?? ??00?00??? ?????????? ?????????? ?????????? ?????????? ??????????
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Delma_borea 1000001001 00100?0000 0120000000 000??10330 00000?0?20 000101410?
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00001?1?00 1010?00010 ?2????011? ?????1??00 ??00???210 1200401300 0000000011
00011??01? 0000000??1 00?0000001 00010?1??0 30?0000002 ?0?01?121? 0000?01??0
011??000?0 ??2?21?0?0 0001120000 0000101000 010??0???0 0?0000?0?? 0000010000
0?0?012000 0101000?2 30?2000020 030000?001 ???0?01002 0011000000 1000000000
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Lialis_burtonis 10010?0001 00000?02?0 0110000?0 000??11330 00100?0??0 0001011?0?
?0000?01?0 ?????????? ???????102 ??0210000? 01?1?00000 0014010000 0000000320
00001?1?00 11???????? ??????0?1? ?????1??00 ??00???210 1200401100 0000000011
00011??01? 0000000??1 00?0000001 0?010?1??0 30?0000012 00?01?121? 0000?01??0
010?3000?0 ??2?20?0?0 0000120000 0000101000 000?00???0 0?0110?0?? 0000010000
0?0?012000 01010100?2 40?2000020 030000?001 ???0?01002 0011000010 1000000000
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0?31??0110 000?00?100 01111????0 ?????0?2?0 1001??01?? ?????????? ???????011
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Strophurus_ciliaris 10000?0000 00000?0000 ?000000010 000??10330 00300?0300
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0000?01??0 011?2000?0 ??2?21?0?0 0100120000 0000100110 000??0???0 3?0000?2??
0001010000 100?012000 0101000?2 40?0000010 ?30010?001 1??3101002 0012000000
1000000000 0010000044 4000000000 00??00?001 0110100000 0200200000 ?02???0102
0????1000 0?10020010 0011100102 101101??10 0111000000 10001?0010 0011201110
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Rhacodactylus_auriculatus 10000?0000 00100?01?0 0100000000 000??11320 00300?0?11
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0010000011 00010??01? 0000000??0 00?0000001 00010?0??0 30?0000002 ?1?01?131?
0000?01??0 011?1000?0 ??2?21?0?0 0100120000 0000100120 000?00???0 3?0000?2??
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Saltuarius_cornutus 0000002000 20100?0000 0110000000 000??10330 00300?0301
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0010000011 00010??01? 0000100??0 00?0000001 00010?0??0 30?0000002 ?1?01?131?
0000?01??0 0?1?000??0 ??2?20?0?0 0100120000 0000100120 000??0???0 3?0000?2??
0001010000 1?0?012000 0101000?2 40?0000010 ?30000?0?1 1??0?01002 0012000000
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0????10{01}0 0?20{01}30000 0010110002 101101??10 0010000100 10001?0010 0011201100
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Aeluroscalobates_felinus 1000002000 00100?00?0 0000000000 000??11310 00100?0300
000001110? ?0000?01?1 ??0??????? ???????102 ??0000000? 0111?00000 0013010100

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Coleonyx_variegatus  10000?0000  00100000?0  0000000010  000??11310  00000?0300
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0000000011 00011??11? 0010000??0 00?0100001 00010?0??0 30?0000002 ?1?01?131?
0000?01??0 010?0000?0 ??2?20?0?0 0100120000 0000100110 000000???0 0?0000?2??
0001010000 1000012000 0101000??2 40?0000010 ?30000??01 1??3101002 0011000000
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0???0?1010 0?10020010 0012101002 1011001110 0010100 2?0 10001?0010 0011201100
1000010000  0000111001  000010000?  ?0000?0000  ?000?01001  0010001101  0001100??0

Eublepharis_macularius 10000?0000 00100?00?0 0010000000 000??11310 00000?0300
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0000000400 00001?0200 1001000010 ?2????0100 1100102002 0?00001210 1200402301
0000000011 00011??11? 0010000??0 00?0100001 00010?0??0 30?0000002 ?1?01?131?
0000?01??0 010?0000?0 ??2?20?0?0 0100120000 0000100110 000000???0 3?0000?2??
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0001100000

Teratoscincus_przewalskii 10000?0000 10000?0100 0100000000 000??00310 00200?0300
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0000?01??0 010?0000?0 ??2?20?0?0 0100120000 0000100110 000??0???0 3?0000?2??
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Gonatodes_albogularis  10000?0001  10000?01?0  0100000000  000??11320  00200?0400
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Phelsuma_lineata   10000?0000   00000?12?0   0120000000   000??11320   00100?0?10
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Gekko_gecko 10000?0000 00100?02?0 0100000000 000??11310 00200?0300 000001110?
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Lacerta_viridis 10000?0000 00100?02?0 0111000000 000??01040 000?0?0?10 000002100?
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Takydromus_ocellatus 1000001000 00000?02?0 0121000000 000??01010 000?0?0?10
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1230110001 0201101000

Colobosaura_modesta 1001101001 20100?00?0 0121000010 000??11020 000?0?0?20
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Pholidobolus_montium 1001101001 20100?01?0 0120000000 000??11330 00000?0300
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Callopistes_maculatus 10000?0000 00000?0000 0101000010 000??10000 000?0?0300
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Tupinambis_teguixin 10000?0000 00000001?0 0111000010 000??11000 000?0?0300
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0201101110

Aspidoscelis_tigris 10000?0000 00100?0100 0100000010 000??10000 000?0?0300
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Paramacellodus 100?002000 00000?01?0 01?00000?? 000??0?010 000?0?0??0 0000000???
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Parmeosaurus_scutatus 1000001?00 00000?0??0 0??0000000 000??01010 000?0?0?30
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0000?000?0 ?10?2000?0 00102??0?0 ?00?12?000 00????00?0 00???????? 0?0000????
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Tepexisaurus_tepexii 10000???0? ?????????? ?????????? ???????0?0 ?0????0?4?
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Cricosaura_typica 10000?0002 00000??200 012??00010 000??11330 00000?0?30
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Lepidophyma_flavimaculatum 10000?0000 00000?0200 0101200000 000??01040 000?0?0??1
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1011{12}01110 1000010000 0000110001 000010000? ?000??0000 ?001001001 1220110101
0?01101001

*Palaeoxantusia_*sp. 10000?0?00 10000?01?0 0???00000 000??01030 000?0?0?30
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?000?01??0 111?3000?0 01002??0?0 ??0?12?000 100????100 ?????????? 0?0000????
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1010??0??0 0010000232 2000000000 00?2000??? ?????????? ???020??00 002?0?1?0?
???????0?? ???????0?? ?????????? ?????????0 ?????0???0 1??0?????? ??????????
?????????? ?????????? ?????????? ?3000?0000 ?0???????? ?????????? ??????????

Xantusia_vigilis 10000?0200 1000000100 0121100000 000??01030 000?0?0?20
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0000?01??0 111?3000?0 010020?0?0 1000121000 1000101100 000010???0 0?0100?2??
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Platysaurus_imperator 1000012200 00000?01?0 0100000000 000??01030 000?0?0300
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0000000011 100110?11? 0010101??1 00?0000001 00000?0??0 30?1100003 ?0?11?131?
0000?01??0 011?2000?0 001020?0?0 1000121000 1000100000 000?1110?0 0?0000?0??
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0010000100 0000000200 0000?00000 0001101000 1120102002 0?00001010 1200202200
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Zonosaurus_ornatus 1000001000 00100?0100 0120000000 000??00030 000?0?0?30
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000?0?0400 000001010? ?00000000? ??0?021100 012?0?0102 ??0110202? 1111000?0
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1200?02300 0000000011 100010?21? 0010101??1 00?0000001 00000?0??0 20?0100003
?1?11?131? 0000?00000 011?2000?0 ??2?21?0?0 1000121000 1000100000 000?1110?0
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0110200?0 1000000001 000?000133 3000000000 00?0000012 0??011?000 01?0400000
?02?0?1?00 2?????10?0 ???????0?? ????1???0? ?????0???0 ?????0???0 ??00??00??
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000?101??0

Myrmecodaptria_microphagosa 0000012?00 00000?0??0 0?00?0000? ??0??11010 010?0?0300
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001000?100 0?00??1??? ?001?00000 0000200?01 010010010? 0?00001?10 ??0??0????
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0000?01??0 ?10?1000?0 001?2??0?0 ?????2??00 00???????? ?????????? ??0000????
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1000000000 0???0000?? ?000?0???? ???00?0??? ?????????? ?????????? ??????????
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Carusia_intermedia 0000012?00 00000?01?0 0000000000 000??11010 010?0?0100
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0010000100 0000001?00 0001?00000 0000100001 01001????? ??????1?10 1?0??0????
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?000?0???0 ?10??000?0 00102??0?0 ?0??12?000 00???????0 ?????????? 0?0000????
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1010???0?0 00??000043 3?00000?0? ????000??? ?????????? ?????????? 0???0?1???
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
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Globaura_venusta 0000002000 00000?01?0 0120000010 000??11010 000?0?0300
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0011000200 000000???? 0001?00000 0000110001 0100102002 0?00001010 1200?0????
?????????? ?????????? ?0?0?????1 00?000?2?1 00000????0 20?01000?3 ?0?11?131?
0000?00000 010?1000?0 001020?0?0 ?00??2?000 00????0000 ?????????? 0?0000????
?00101?00? ??0???0??0 ??01??0002 ?0?00?1000 0000200010 100?001?02 0?10000010
1000000101 000?000123 ?000000000 0002000??? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
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Hymenosaurus_clarki ?????????? ?????????? ?????????0 ??0??0?0?0 00??0?0?4?
0?000???0? ?0000120?0 0?0??????0 ??2????1?2 ??011?100? 01100000?0 ?0?301?000
00110???10 ?00??????? ?001?00000 000?11000? 010010???? ????001010 1200?0????
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ????10?3??
?000?000?0 010??000?0 00102??0?0 100?1??000 ???????000 ?1???????? 0?000?????
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1000000101 0???0001?? 2000?0???? ???2000??? ?????????? ?????????? ??????????
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Eoxanta_lacertifrons 0?000?0?00 00000?01?0 0121000010 000??01110 000?0?0?2?
000002110? ?000012000 0?0?01?1?0 0?2?0?0102 ??0000000? 0110000?00 0013011000
0011000200 0000000200 0001200000 0000110001 010?1???0? ??00??1??0 ?200002???
???0?00011 ?0001??2?? 00?0??1??1 00?000?20? ?0000?0??1 20?0100013 00?11?131?
?000?01??0 011?1000?0 00102??0?0 ??0?12?000 000???0000 ??00?????? 0?000?????
?00101000? 1000110?00 ?101?00002 40?0001000 0000100010 100110?102 0010?00010
?000???0?1 000?000122 2000000000 00?2000??? ?????????? ?????????? 00????1???
???????0?? ???????0?? ?????????? ?????????? ?????????? ?????????? ??????????
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Plestiodon_fasciatus 00000?0000 00000002?0 0120000000 000??01020 000?0?0?20
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0010000200 0000000200 0001200000 0001101001 1100102002 0?00001110 1200?02300
0000000011 100010?21? 0010101??1 00?0000201 10000?0??0 20?0100023 00?11?131?
0000?00000 010?1001?0 ?01020?0?0 0000121000 0000100100 0000?110?0 0?0000????
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0???201000 1?10021000 0011101102 1111001110 11001002?0 10001?0010 0011101110
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*Scincus_* ?02000{12}000 ?0000?02?0 0101000000 000??01020 000?0?0400 000001110?
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100010?21? 0010101??1 00?0000001 10000?0??2 20?0100023 00?01?131? 0000?00000
010?1001?0 ?01020?0?0 0000121000 0000100000 0000111?0 0?0000?1?? 0001010001
0000110000 01010100?2 40?0001010 0000100?00 1001101100 0010?00010 1000000001
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Brachymeles_gracilis 00000?0000 00000?02?0 0120000000 000??01030 000?0?0??0
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Acontias_percivali 0001001000 00000?01?0 0100000000 000??01230 000?0?0??1
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1102000011 100011?21? 0010111??? 00?0000201 20000?0??2 20?0100023 10??1?131?
0000?01??0 011?1001?0 ??2?21?0?0 1001121000 0000102??0 120010?0?0 0?01?0?2??
0011010??0 1000110?01 01010000?2 40?0001020 0300000?00 1001101000 0010?00010
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Amphiglossus_splendidus 0000001000 00000?02?0 0120000000 000??01030 000?0?0400
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0000?01??0 010?1001?0 ??2?20?0?0 0000121000 0000100000 0000111?0 0?0000?0??
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0300010000 0000110001 0100000001 0210202222 11010010?? ?????????? ???100???

Feylinia_polylepis 1000001000 00000?12?0 0100000100 000??01020 000?0?0??0
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?0?1000320 0000001?00 01???????? ????????01 ?100102002 0?00001111 1200102300
1112000011 100010?21? 0110111??1 00?0000201 2?000?0??? 20?0100033 10??1?131?
1000?01??0 111??1???0 ????20?0?0 1010121000 0000101000 110??0???0 0?01?0?1??
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1??????001 ??????31?1 ?0??00??00 00201????1 ?????1???0 100????1?? ??????????
???????1?? ?????????? ?????????1 0100202222 110??110?? ?????????? ????10????

Trachylepis_quinquetaeniata 00000?0000 00000?02?0 0100000000 000??11010 000?0?0300
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0000?01??0 010?1001?0 ???220?0?0 1000121000 0000100000 0000110?0 0?0000?0??
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1100000001 000?000033 3000000000 00?0000011 0110100000 0300200000 102?0?1100
0???201000 0?10120000 0111100102 1111001110 1100100?0 1000000010 ?011201110
?000010000 0001110001 1100?00001 0200202222 1101001001 1200100001 10011?0??0

Sphenomorphus_solomonis 00000?0000 00000?01?0 0120000000 000??11110 000?0?0?30
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0000?01??0 010?1001?0 ???220?0?0 0000121000 0000100000 000??110?0 0?0000????
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1200010000 0001110001 0 100100001 0210202222 1101001001 1210100?01 110?100???

Eugongylus_rufescens 10000?0000 00000?02?0 0120000000 000??11010 000?0?0400
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0001010000 0?01110010 01010000?2 40?0001020 0300000?00 1001101102 0010?00010
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0011{12}01110 1000010000 0000110001 0100100001 0210202222 1101001001 1200100?01
110?100??0

Tiliqua_scincoides 00010?0000 00000?00?0 0120000000 000??11010 000?0?0400
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1000?01??0 110?1001?0 ??2020?0?0 0000121000 0000100000 0000?110?0 0?0000?1??
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0?????1000 0?10121000 011110010{12} 11110011{12}0 11{01}01002?0 10000?0010
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100110?001

Shinisaurus_crocodilurus 1000002000 00000?0001 0??1100000 000??10010 010?0?0300
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Xenosaurus_platyceps 1000012002 20000??000 0101000000 000??10020 010?0?0100
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0000000100 0000000100 0001200020 0010101001 0011000?00 0?00001110 1100202200
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0011101001

Pseudopus_apodus 10001?0000 0000000000 0110000000 000??00010 000?0?0?40
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1???2??000 0?31??0100 001000?000 0010000?3? ?????????0 100{01}???1?? ??????????
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Peltosaurus_granulosus 1000002000 20000?01?0 0100000000 000??10040 000?0?0?10
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00?0?00011 ?00010?2?? 0010100??1 01?000?001 01020?0??0 20?0100002 ?0?000131?
0000?00000 010?2000?0 001020?0?0 100112?000 000?100000 00001????? 0?0000?2??
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Helodermoides_tuberculatus 1000??2?00 00100?0000 0101000000 000??00040 000?0?0?40
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1000110?1 0???0000?3 ?000000??0 00?0000??? ?????????? ?????????? ??????1???
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Anniella_pulchra  1000001000  00?00000?0  0000000100  000??01240  00000?0??0
000001120? ?0000??0?0 0?0?1????? ???2?0??100 ??1?02000? 0111?0??2? 0013011000
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0000?01??0 011?22?0?1 1??020?0?1 1???121000 00001020?? 1200?0???0 0?01?0?1??
0010010?00 0?01010021 1101000100 30?0111100 1000000100 1012001002 0011000000
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1???2??001 ??????0{12}?? ????????1? ????1????1 ?????1???0 1001???1?? ??????????
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Celestus_enneagrammus  1000101100  20100000?0  0100000000  000??01040  000?0?0?20
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0000000100 0000000100 0001200020 0001100001 1100101001 0?00001110 1100102300
0000000011 100010?21? 0010101??1 01?0000101 00020?0??0 20?0100012 00?01?111?
0000?00000 010?2000?0 001020?0?0 0000121000 0000100000 0000110?0 0?0000?0??
0001011001 0?00010000 0101000001 40?0011200 1000300100 1021001002 0011020000
1000110001 0010000032 2000000100 00?1000011 010011??00 0110410000 202???1001
0???2?1000 1110020000 011{01}100100 0111001110 1110100000 1000000010 1011{01}01110
0200010000 0000110001 {01}100020001 0210111111 0101000012 ???????0?? ????100??1

Elgaria_multicarinata  1000001000  00000?0000  0100000000  000??10040  000?0?0?10
000002120? ?000020000 0?0?000100 012?0?0102 ??0100000? 0110000000 0013011000
0000000300 0000000100 0001200020 0001100001 1100100001 0?00001110 1100102300
0000000011 100010?21? 0010101??1 01?0000101 10020?0??0 20?0100012 00?01?111?
0000?00000 010?2000?0 001020?0?0 0000121000 0000100000 0000110?0 0?0000?0??
0001011001 0?00010000 01010000?1 40?0110200 1000300100 1021201002 0011020010
1000110001 001?000033 3000000000 00?1000011 010011??00 0010400000 00200?1000
1???201000 0?10020000 0011100100 0111001110 1110100010 0000000010 1011101110
0000010000 0000110001 0100000001 0210111111 0101001012 0000000001 0011101000

Gobiderma_pulchrum  1000001?00  0000??0000  01?0000010  000??00120  000?0?0400
000002120? ?000010000 0?0?0001?0 0?2?0?0102 ??000?001? 0110000?0 0013011000
0001000110 0000000100 0001200?20 00012?0001 0100101200 0?00001?10 1100?0????
?????00011 1001???2?? 00?1??1??1 0??000???? 01020????0 ?0?0100002 ?0?000131?
?000?000?0 011?2000?0 00102??0?0 ??0?12??00 00?????000 00???????? 0?001?????
?00101?00? 1?0???0??0 ??01001100 40?0000?00 1010110?10 10??201002 00111?0000
0000000000 0110000132 2100111??0 1?00000??? ?????????? ?????????? ????0?1?0?
???????0?? ???????0?? ?????????? ?????????? ?????????? 1??0?????? ??????????
?????????? ?????????? ?????????? ?2001?111? 0?0??????? ?????????? ??????????

Estesia_mongoliensis  1000001000  00000?0201  01?1?0001?  ??0??00120  000?0?0400
0??002120? ?2??0?000? 0?0?00?1?0 0?2???0102 ??010?000? 0111?000?0 001301?100
0001000120 ?000??0100 0001??0?21 00012??001 0100101000 0?00001?10 110??0????
???0?0001? ?????????? ?01101???? 01????00?1 0???0????0 20??100002 ?0?0001?1?
0000?00000 011?2000?1 0010???0?? ???????000 000?1000?0 10001????? 0?0010????
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?00??1000? 0000010?30 ?101001100 40?0000?0? 10?0?????0 1???????02 0?111?0000
??00?????? 0110020232 2100111?0 1000000??? ?????????? ?????????? ?0????100?
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?1??0?00?? ?????????? ?????????? ??????????

Aiolosaurus_oriens  110?101000  00000?02?1  01?1000?1?  000???????  ??0?0????0
?????????? ?000010000 0???0001?0 0?????0??? ?????????? ??1???0??? 00??011100
0001000??0 0??0000100 001??00??0 ?0?1????0? 0100101?00 ??00001100 11?0?0????
?????0??11 ?0???0?2?? ?0?1??1??1 ???0?0???? ?1???????? ?0??10???? ??????????
?????????0 ??1?2??0?? ?????????0 ??0?1????? ?????????? ?????????? ??????????
?????????? ?????????? ????001100 40?0000?00 10100?0?10 1011201012 0011110000
0000000000 0110020222 2100111??0 10?0000??? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????

Heloderma_horridum  1000000000  0010000201  01?0000000  000??00240  00000?0??0
000002110? ?0000101?? ?????????? ???????102 ??0000000? 0111?00000 001?011000
0001000120 0000000100 0011200020 0001210000 ?1??100210 0?00001110 1100102200
0000000011 100110021? 0011001??1 01?0000001 01020?0??1 30?0100003 ?1?01?131?
0000?01??0 011?2000?1 101020?0?0 1001121000 0000101000 0000?110?0 0?0010?2??
0001011001 0?00010030 0101001100 41?0000?00 1010110?10 1001201002 0011100000
0000000000 0100020232 1100111000 1??0100011 010011??00 0000410001 212?1?1003
0???201000 0?11??0100 001?001100 011001??20 0010000000 0000000010 ?1110011?0
?000010000 000?110001 0?00?00000 ?200101110 0001001013 0001000001 0011101010

Heloderma_suspectum  10000?0000  00100?0201  01?0000000  000??00240  00000?0??0
000002110? ?0000101?? ?????????? ???????102 ??0000000? 0111?00000 001?011000
0001000120 0000000100 0011200020 0001110000 ????100210 0?00001110 1100?02300
0000000011 100110021? 0011001??1 01?0000001 01020?0??1 30?0100003 ?1?01?131?
0000?01??0 011?2000?1 101020?0?0 1001121000 0000101000 000010???0 0?0010?2??
0001011001 0?00010030 0101001100 41?0000?00 1010110?10 1001201002 0011100000
?000000000 0100020232 1100111?00 1??0100011 01{01}011??00 0000410001 212?0?1003
0???201000 0?11??0100 0011001100 011001??20 00000000{01}0 00000?0010 ?011101110
0000010000  000?110001  1?00000000  ?200101110  0002001013  000?000001 0011101010

Lanthanotus_borneensis 1100002000 00000?1111 01?1000010 000??00130 000?0?0??0
000001120? ?0000101?0 ?????????? ???????100 ??0103000? 0111?00000 001?011100
00?1000310 0000000101 0021200121 00012?0000 ?100100000 0?00001110 1100202200
0000000011 100211031? 0010001??1 01?0000001 010?0?0??0 20?0100003 ?1?001131?
0000?00100 011?2000?1 101020?0?0 0001121000 00001010?0 001010???0 0?0011?2??
0001011011 0000010130 0101001100 41?0000?00 1010010?10 1011201002 0111100000
?000000000 011?020222 2100111100 1?00000011 010011??01 0010410001 2031101003
0???312000 0?21??0000 0011101100 0110001?10 0000000010 1000000010 ?011201110
0200000000  ?00?110001  1100020000  ?010101110  0003?01014  0?0??00?1?  0111101100

Saniwa  1100101000  00000?1111  01??000?10  000??00120  0?0?0?0400  0000021?0?
?20001000? 0?0?0001?0 0?????01?0 ??0?0?000? 0110000?0 0013010100 00010???10
0000000101 0021200120 000?2??001 01?010?00? ??00001?10 ??0??0???? ?????00011
1?0110?0?? 0001011??1 01?000?001 01020?0??0 ?0?0100001 ?1?000131? 0000?000?0
?11??000?1 ?0102????0 ?00?121000 0?????1??0 ?????????? 0?0??0???? ?00????0??
0?0???0?30 ?101?011?0 41?0000?00 1010110?10 ?011201?02 0?11???000 000???????
0110000133 2100111??0 1??00000?? ????1????? ???0400001 202?101?03 0???312000
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0??00?0000  00????1?0?  ?????????0  ?????0???0  0000??0010  10?12011?0  ?000010000
????11?001  1?00?0000?  01100?0000  ?0????????  ??????????  ?????????

Varanus_salvator   1100101001   1000001211   01?1100010   000??0?220   00000?0?10
000002120?  ?2??0?00??  0?0?000100  ?2????0100  ??0200000?  0110000000  001?011100
0001000110  0000000102  0021200020  010?2?0001  0100100000  0?00001110  1100302200
0000000011  100010?01?  0011011??1  03?0000001  01020?0??0  20?0100001  ?1?01?131?
0000?01??0  011?2000?1  101020?0?0  0000121000  0000100000  00100110?0  0?0010?0??
0001011011  0000010130  0101001100  41?0000?00  1010110?10  1011201002  0011100000
?000000000  0110020232  2100111100  1??0000021  00?111??11  0410400002  2141101003
0???312000  0?21??0000  0010111100  00?0000?20  0001001100  0000000010  ?011201110
?000010000  ?00?110001  0?00?00000  ?110101111  0001?00024  ???????01?   04?110???0

Varanus_acanthurus   1110002002   10000??211   01?1000010   000??0?220   00000?0300
000001120?  ?2??0?00??  0?0?000100  ?2????0100  ??0000000?  0110000000  001?011100
0001000100  0000000102  0021000020  010?2?0001  0100100100  0?00001110  1100402200
0000000011  100010?31?  0011011??1  03?0000001  01020?0??0  20?0100001  ?1?01?131?
0000?01??0  011?2000?1  101020?0?0  0000121000  00001010?0  00100110?0  0?0011?0??
0001011011  0000010130  0101001100  41?0000?00  1010110?10  1011201002  0011100000
?000000000  011?020222  2100111100  1??0000021  00?101??11  0410400002  2031101003
0???312000  0?21??0000  0011111100  0100000?20  0010001100  0000000010  1011201110
0000010000  0000110001  010000000?  ?0100?0000  ?001001024  ???????01?   04?110???0

Varanus_exanthematicus  1100002001  100000?211  01?1100010  000??0?220  00000?0400
000002120?  ?20?0?00??  0?0?000100  ?2????0101  ??0000000?  0110000000  001?010100
0001000100  0000000102  0021200120  010?2?0001  0100100000  0?00001110  1100202200
0000000011  100110?01?  0011011??1  03?0000001  01020?0??0  20?0100001  ?1?01?131?
0000?01??0  011?2000?1  101020?0?0  0000121000  0000100000  00101110?0  0?0010?0??
0001010011  0000010130  0101001100  41?0000?00  1010210010  1011201002  0011100000
?000000000  0110000232  2000110100  1??0000021  00?111??11  0?00400002  2141101003
0???312000  0?20010000  0010111100  0100000?20  0001001100  0000000010  ?011201110
?000010000  ?00?110001  1100?4000?  ?1100?0100  ?001001024  ??????001?  04?1101100

Anelytropsis_papillosus  1000001200  10000002?0  0121000100  000??01040  000?0?0??0
0001011?0?  ?0000?01?0  ??????????  ???????100  ??0?10000?  11?1?0002?  0014011000
?001000100  00000?1?00  01????????  ??????????  ??????????  ????????11  1200202301
1112000011  100010?21?  0010121??1  00?0000001  0?0?0?0??2  ?0?0000033  ?0??1?111?
1000?01??0  111??2???0  0?2?20?0?0  1011120000  00000?2???  220??0??1?  0?01?0?2??
0010013??1  100?110122  ?0010100?2  40?0?01020  ?3?1?????1  ???2101?0{02}  1?10?00010
1000000000  0011000121  2100001100  00?0000000  ???001??0?  ???0441020  210???1?01
0??????00?  ??????????  ????????1?  ????1?????  ??????????  ???????1??  ??????11??
????0?????  ??????????  ??????????  ?0000?0000  ?00???1000  123011??01  000?10????

Dibamus_novaeguineae  1000002200  10100002?0  0121200100  000??01040  000?0?1??0
0001011?0?  ?1?????1??  ??????????  ???????100  ??0?11000?  11?1?1?02?  0014011000
?001000000  00000?1?00  01????????  ????????1?  ??????????  ????????11  1200202401
1112000011  100010?21?  0010122??2  00?0000001  0?0?0?0??2  ?0?0000033  20??1?111?
1000?01??0  111??2???0  0?2?21?0?1  ?????20000  00000?2???  2200?0??1?  0?01?0?2??
0010013??1  1?01110122  ?0010000?2  40?0?01020  ?3?1?????1  ???2101?02  1?10?00010
1100000000  0011000132  1100001100  00?0000011  00?101????  ???0441020  210???1?01
0??????000  0?31??41?0  100?00??1?  ????1????0  ?????01??0  1000??01??  ??????????
???????010  1112011?11  0?????????  ?0000?0000  ?00??01000  023??10?01  000?100??0
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Spathorhynchus_fossorium 1100002002 00000??0?0 0030000000 000??01241 00000????0
000003??0? ?000010170 ?????????? ???????1?0 ??1?00000? 0111?0??2? 001401??00
?0?1000220 0000??1?00 ?011?00020 00012?101? 1????0000? 0???00?111 1200?02400
11?2?00011 100010?2?? 0010101??1 10?0000001 00000?0??? 20?0000013 00??1?100?
1001?01??0 2?1?22???0 001020?0?1 ?????2??30 00??102??? 22??12?002 2?0100?0??
?2???13?02 100????132 3101000002 30?1000011 0300000000 1001001102 0112010010
1000010001 0112000212 1000001100 00?0000??? ?????????? ????????30 ?11???100?
???????0?? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?2000?0000 ?????1???? ?????????? ??????????

Dyticonastis_rensbergeri 1100012?01 00000?00?0 0030100000 000??01241 00000????0
000003??0? ?000010170 ?????????? ???????1?0 ??1?00000? 0111?0??2? 001401?000
?0?1000220 0000?0??00 0011?00020 00012?101? 1?0??0??0? 0???00?1?? ??????????
???2?00011 100010?2?? 0010111??1 10?0000001 00000?0??? 20?0000013 00??1?100?
10?1?01??0 2?1?22???0 001020?0?1 ??????0030 000?102??? 2200?2?002 2?0100?1??
?010013??2 1001??0?32 3101000002 30?1000021 0300000010 1011101102 0112010000
100001000? 0112000212 1000001?00 00?0000??? ?????????? ?????????? ??????1???
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?2000?0?00 0????1???? ?????????? ??????????

Rhineura_floridana 1100012000 ?0000?00?0 003?100000 000??01241 00000????0
000003??0? ?1?????1?? ?????????? ???????1?0 ??1?00001? 01?1?0??2? 001401??00
?0?1000220 0000??1?00 0021?0002? 01??20101? 11???0000? 0?000??111 1200002400
1112000011 100011?01? 0010101??1 10?0000001 00000?0??2 20?0000013 00??1?110?
1001?01??0 211?22???0 001021?0?1 ?????21030 0000102??? 210012?002 2?01?0?0??
0010013?02 1?01010132 31010000?0 30?0?00011 03??0???1? ???1001102 01110?0010
1000010000 0?12000211 1000001?00 00?0000011 00?011???? ???0441030 ?11???1002
0???20?001 ??????02?? ?????????1? ????1????? ?????????0 100????1?? ??????????
???????1?? ?????????? ?????????? ?2000?0000 ?00??11004 1200110?01 000?101??0

Bipes_biporus 1001002002 000000?1?0 0001000?00 000??11341 00000????0 00001???0?
?1?????1?? ?????????? ???????1?0 ??1?00001? 12?1?0??2? 001301?000 ?000001220
0000??1?00 01???????? ????????1? 0????0000? 0?000??111 1200002400 1112000011
100010?21? 0110011??1 1??0000001 0?000?0??2 20?0000013 00??1?121? 1001?01??0
211?41???0 1?2??20?0?1 ?????21031 0000102??? 210??2?102 2?01?0?1?? 0010013??2
1?0?010132 3101010??2 30?0?01011 00?1?????1 ??01001001 0?10?20011 1000000000
0012000131 1000000100 00?0000011 00?0100011 1000441030 ?12???1002 0???3??000
1030000110 000?001100 00201????1 ????012?0 1001??0001 0000201110 0102001011
?????????? ?????????? ?0000?0000 ?00??10004 1200?10001 0?01101?0

Bipes_canaliculatus 1001002002 00000??1?0 0001000?00 000??11341 00000????0
00001???0? ?1?????1?? ?????????? ???????1?0 ??1?00001? 12?1?0??2? 001301?000
?000001220 0000??1?00 01???????? ????????1? 0????0000? 0?000??111 1200002400
1112000011 100010?21? 0110011??1 10?0000001 0?000?0??2 20?0000013 0???1?121?
1001?01??0 211?41???0 1?2??20?0?1 ?????21031 0000102??? 210??2?102 2?01?0?1??
0010013??2 1?0?010132 3101010??2 30?0?01011 00?1?????1 ??01001001 0?10?20011
1000000000 0012000131 1000000100 00?0000011 00?0100011 1000440030 ?12???1002
0?????000 0?30000110 000?001100 00101????1 ????012?0 1001??0001 0000201110
0112001011 ?????????? ?????????? ?0000?0000 ?00??110?? ?????????? ???10???0

Trogonophis_wiegmanni 1101002002 00000??1?0 0001000000 000??01241 00000?????
000004??0? ?1?????1?? ?????????? ???????1?0 ??1?00000? 02?1?0??2? 001401?000

?00001?2?0 0000??1?00 01???????? ????????1? 0????02??? 0???0??111 1200202400
1112000011 100010?11? 0010011??1 10?0000001 1?000?0??2 20?0000013 ?0??1?111?
1001?01??0 211??001?0 1?2?20?0?1 ????120030 0000102??? 210012?102 2?01?0?0??
0010013?02 1{01}01010132 31010100?0 30?0?02030 00011????1 ?????00001 1100??0?11
10?1?????? 0012000121 1011000??1 ???0000011 00?0101011 ?0004300?0 ?12???1?03
0??????001 ??????02?? ????????1? ????1????1 ?????1???0 100????1?? ??????????
???????1?? ?????????? ?????????? ?0000?0000 ?00??11004 ???????0?? ???1101??1

Diplometopon_zarudnyi 1101002002 00000??1?0 0001000000 000??01241 00?00?????
00?004??0? ?1?????1?? ?????????? ???????1?0 ??1?00000? 12?1?0??2? 001401?000
?00002???? ??????1?00 ?1???????? ????????1? ?????1???? ????????11 1200002400
1112000011 100010?21? 0010111??0 10?0000001 1?000?0??2 20?0000013 ?0??1?111?
1001?01??0 211??001?? 1?2?20?0?1 ?????21031 0000102??? 2100?2?102 2?01?0?0??
0010013?02 1?01010132 31010000?0 30?0?02030 00011????1 ???1000001 1200??02?1
1??1?????? 0012000111 1011000??1 ??02010011 00?010101? ???0440030 ?11???1003
0??????000 0?31??01?0 100?????1? ????1????1 ?????1???0 100????1?? ??????????
???????1?? ?????????? ?????????? ?0000?0000 ?00??110?? ?????????? ????10???0

Geocalamus_acutus 1100002002 00?00??1?0 10?1000000 000??01241 00000?????
000004??0? ?1?????1?? ?????????? ???????1?0 ??1?00000? 02?1?0??2? 0014?0?000
?00001???0 000???1?00 01???????? ????????1? ?????1???? ????????01 1200002400
1112000011 100010?21? 0010011??1 12?00000?1 0?020?0??2 20?0000013 ?0??1?131?
1001?01??0 211?41???0 1?2?20?0?1 ?????21030 0000102??? 210??2?102 2?01?0?1??
02???13?02 1?0?010132 31010000?2 20?0?01030 00?1?????0 0000?00001 0?10?20211
10?1?????? 0012000111 10000?1100 00?0000010 00?0000011 100??????0 ??????1?0?
0??????001 ??????0101 ?00?00??1? ????1????? ?????????0 100????1?? ??????????
???????1?? ?????????? ?????????? ?0000?0000 ?00??110?? ?????????? ????10???0

Amphisbaena_fuliginosa 1000002001 00000?0100 1001100100 000??00241 00000????0
000004??0? ?1?????1?? ?????????? ???????1?0 ??1?00000? 02?1?0??2? 001401?000
?001001120 0000??1?00 01??00???? ????????1? ?????1???? ????????01 1200?02400
1112000011 100011?21? 0010111??1 12?0000001 00000?0??2 20?0000013 ?0??1?111?
1001?01??0 211?42???0 1?2?20?0?1 ?????20030 0000102??? 210??2?102 2?01?0?1??
02???13?02 1?0?010132 31010100?2 40?0?01030 00?1?????0 0001000101 0?10?202?1
10?1?????? 0012000221 1000000100 00?0000011 0??01000?? ??0?4200?0 ?12???100?
0???3??00? ?????????? ????????1? ????1????? ?????????? ???????1?? ??????????
?????????? ?????????? ?????????? ??000?0000 ?00??10004 1200110?01 000???1??0

Najash_rionegrina ?????????? ?????????? ?????????? ?????????? ?0????????
????0????? ?????????? ?????????? ???????1?0 001?010000 0111????20 ??????????
?????????? ?????????? ?????????? ????????1? ?????0?200 000?00???1 1300?0????
?112?????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
??0??????? ?????????? ?????????? ?????0?011 000??????0 1?0??0???? 1?0??000??
?1???11??0 ??0??????1 ?10101???? 200??????? 00?0?????? ?????????? ??????????
?????????? ?????????? 2?10?????? ?????????? ?????????? ?????????? ????101303
0???20?0?1 ?????????? ????????1? ????1????0 ?11??01??0 1001???1?? ??????????
???????010 ?????????? ?????????? ?0??????00 ?????????? ?????????? ??????????

Dinilysia_patagonica ????????10 ??????0201 1????001?0 ?10??00120 000???1??0
1100022?00 0000??0000 300010???0 0??40??100 001?010000 0111?00?2? 00?11??113
0000000200 0010201?00 11???????? ????????1? ?????00200 0?00?0?111 1300?0??0?
1112?0??1? ?????????? ?01??????? ???????0?1 0???0?0?00 20?01000?3 ?0?0011?10

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00000?0100 ?100200000 ?0101?1001 ?????0?011 010??????0 1?00?0??01 1?01000000
?1???10?00 0000??0?21 0111???110 2??0000?00 0010?13?10 1101202?02 0?10??00?0
1001?????? 0???2?00?2 ?110011??? ??0000???? ?????????? ???0?????? 2??01?130?
????20?0?? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?0?00?0000 ?????????? ?????????? ??????????

Leptotyphlops_dulcis 100001211? ?010011101 1????00100 1?0??00241 000?0?2??0
0?10012?01 01?????1?? ?????????? ???????100 000???0?00 2??1?1??2? 000?1??012
000000?200 0010201?00 ?1???????? ????????1? ?????1???? ????????01 130040?400
1012101?11 00?2100210 1000002002 01?0?00001 0?0001010? ?0?0100103 ?0??1?1310
0?000?1??1 ?????????? ?????????1 ?????00100 01000????1 ???010??01 1?01?00000
12???11??0 1001?2012? 01111??110 1??0??0?00 0010?13??0 1101201001 ?210??0?00
1000000000 0??????000 11000011?0 1??00?0021 00??01???? ???0444040 311?101303
0000???001 ??????02?? ????????1? ????1????0 ?1???01??0 1001??01?? ??????????
???????011 ?????????? ?????????? ?0000?0000 ?00??11024 ???0??001? 04?1101??0

Typhlops_jamaicensis 1000?011?? ?010010101 1????00000 0?0??00241 000?0?2??1
00?0012?0? 01?????1?? ?????????? ???????100 000???0?00 11?1?1??2? 0?0?????1?
????00?200 00?02?1??0 ?1???????? ????????1? ?????1???? ????????11 1300402400
1112103111 00?2100110 100?002002 ?1?0?0??0? 0????101?? 4????0110? ????1?1310
??000?1??1 ?????????0 ?????????1 ?????00100 0?000????1 ???010??01 1?01?00100
12???11??0 000102013? 11111??110 40?0??1?00 02?1??0??0 1000?01001 0110??0000
1100000000 0?????0?01 0100001100 1??00?0020 ?0??01???? ???04441?0 311?101303
0000???001 ??????02?? ????????1? ????1????1 ?????0???1 ???????1?? ??????????
???????1?? ?????????? ?????????? ?0000?0000 ?00??110?? ?????????? ????1?1??0

Liotyphlops_albirostris 100??121?? ?0?10011?1 1????00100 1?0??00241 000?0?2??0
1?10012?01 01?????00? ????10???? 0??4???100 000????000 2??1?1??2? 0?0?1???3?
?0??00??20 ????3?1??? ?1???????? ????????1? ?????1???? ????????11 130000?40?
1012102111 0002101310 100?002002 ?1?0?00?01 0?0???01?? ?0???0110? ????1?131?
?0000?1??0 010?021000 ??2?20?011 ?????10010 ?1100????1 ???0?0??01 1?01?001??
12????1??0 0001??012? 01111??110 2??0??0?00 00?1?????0 1????01000 0110??0?00
1000000000 0?????0?01 1100001100 0??00?0??? ?????????? ???0444130 311?101303
0000???0?? ??????0??? ?????????? ?????????0 ?????1???0 ???????1?? ??????????
???????1?? ?????????? ?????????? ?0000?0000 ?00??100?? ?????????? ??????????

Typhlophis_squamosus 100???21?? ?0?10011?1 1????00100 1?0??00241 000?0?2??0
1?10012?01 01?????00? ????10???? 0??4???100 000???0?00 2??1?0??2? 0?0?1???3?
?0??00??20 ????3?1??? ?1???????? ????????1? ?????1???? ????????11 130000?40?
1012102111 0002100310 100?002002 ???0?00??1 0?0???01?? ?0???0110? ????1?131?
?0000?1??0 010?021000 ??2?20?011 ?????10??? 0?200????1 ???0?0??01 1?01?001??
12????0??0 0001??012? 01111??110 2??0??0?00 00?1?????0 1????01000 0110??0?00
1000000000 0?????0?01 1100001100 0??00?0??? ?????????? ???0444130 311??01?0?
?000???0?? ??????0??? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?0000?0000 ?00??100?? ?????????? ??????????

Anomochilus_leonardi 11000?0110 1100000101 11?1000100 0100000231 1000121??0
1010013?00 01?????1?? ?????????? ???????100 000?010000 11?1?2??2? 000?1??020
000100?200 0010201?00 11???????? ????????1? ?????1???? ??0?????11 130000220?
1112100011 0002111110 1010002112 0101?00001 0?00000100 41?0100003 ?00?1?1310
00000?1??0 01??000000 ??2?20?0?1 ?????00011 01000????1 1?0000??01 1111?00100
12???11??0 1000020121 2111111110 1?000?0?00 0010?13??0 1101200010 ?200?21001
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1?00000000 0???020001 1100011?0 0??0000??? ?????????? ???0????30 311???1?0?
0000???0?? ??????0??? ?????????? ?????????0 ?????0???0 1??????1?? ??????????
???????1?? ?????????? ?????????? ?0000?0000 ?00??110?? ?????????? ?????????0

Anilius_scytale 1100??0110 1100000101 11?1000100 0100000231 1000301??0 1010023?00
01?????1?? ?????????? ???????100 001?010000 01?1?2???2? 000?1??123 000000?200
0010201?00 21???????? ????????1? ????00000 0?0000?111 1300002100 1112100111
0002111310 101?002002 0101?00001 0?03000100 4200100003 ?00?011310 00000?0100
0100100?10 ??2?200001 ????00011 01000????1 1?0010??01 1111?11000 12???11?00
1000020121 2111101110 1?00?02?10 00?1?????1 ?1?0?00010 0?00?21101 1?01??????
010?220022 2100011110 1?1000001? ?0??01???? ???0444230 311?101303 0000???001
??????02?? ????????1? ????1????? ?????0???0 1??????1?? ?????????? ???????0??
?????????? ?????????? ?0000?0000 ?00??11024 ????????1? 0???101??1

Cylindrophis_ruffus 1100??0110 1100000101 1???00100 0100000231 1000121??0
10100?3?00 01?????00? 31?010???? 0??1?0?100 001??10000 01?1?20?2? 000?1??123
000000??00 0110201?00 11???????? ????????1? ????00201 0?0000??11 1300002010
1?12100111 0002111310 1010002012 0101?00?01 0?03000100 4200100003 ?00?011310
00000?0100 0100011010 ??2?200001 ????00011 01000????1 1?0000??01 1011010?00
12???11?00 0110020121 2111101110 1?000?1?00 0010?11?10 1101200000 0200?21101
1?01?????? 0???220002 2100011110 1?000001?? ?0??01???? ???0444030 311?101303
0000???001 ??????02?? ????????1? ????1????0 ?1???0???0 100????1?? ??????????
???????0?? ?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 04?110???1

Uropeltis_melanogaster 1000001100 1100000101 11?1100100 0100000231 1000122??0
1010013?00 01?????1?? ?????????? ???????100 001??20000 2??1?2???2? 00??1??023
000000??00 0011201?00 11???????? ????????1? ?????1???? ????????11 1300002400
1112100011 0002111010 1000?02112 0001?000?1 0?0??00100 ?1?0100033 000?1?1310
00000?1??0 0100100000 ??2?200001 ?????2001? 0?000????1 1?0??0??01 1011?00000
12???12??0 ??0?020121 2111111110 1?000?1?00 0010?11??0 1101200010 0200?01001
1?01?????? 0???100002 1110011110 1??00001?? ?0??01???? ???04430?0 311?101303
0000???001 ??????02?? ????????1? ????1????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?0000?0000 ?00??110?? ?????????? ????1?????

Xenopeltis_unicolor 1100??0110 1100000201 1????0010? 0?1000?231 0000221??0
1010013?00 01?????10? ?????????? ???????100 001?010000 11?1?2???2? 000?2????3
000000??00 ?2102?1?00 11???????? ????????1? ????00203 0?010???11 1301202000
1113100111 0012111011 101?002012 0?02?00?01 0?030?0100 420010110? ??0?021311
00001?0200 0101011010 ??2?201111 ????00022 01000????1 1?0010??01 1012110000
12???10?00 0000020121 011110?110 1?0???0??0 0010??0??0 1000?1??2? ?????2110?
1?0000?000 000?200?44 4110010110 1?1000001? ?0??01???? ???0444030 311?101303
00002??001 ??????02?? ????????1? ????1????1 ?????1???1 ???????1?? ??????????
???????1?? ?????????? ?????????? ?0000?0000 ?00??11024 ???0??001? 04?110???0

Loxocemus_bicolor 1100??0110 1100000201 1????0010? 010000?231 1000211??0
1010013?00 01?????00? 31?110???? 0??3?1?100 001??20000 11?1?20?2? 000?2????23
000000??00 00102?1?00 11???????? ????????1? ????00203 0?010???11 1301402000
1113100111 0012111011 1010002012 0?02?00?01 0?030?0100 420010110? ?00?021311
00001?0200 0101011010 ??2?200211 ????00022 01000????1 1?0010??01 1012110000
11???10?00 1010020121 0111111110 1?000?0?00 0010?11??0 1101?02010 0200?21101
1?00000000 010?220013 2110011110 1?100001?? ?0??01???? ???04442?0 311?101303

000021?001 ??????02?? ????????1? ????1????0 ?1???0???0 1??????1?? ??????????
???????0?? ?????????? ?????????? ?0010?0000 ?00??11024 ???????01? 04?110???0

Xenophidion_acanthognathus 1100??001? 1100000201 1????0010? 0101?0?2?1 1000321??0
?010012?00 01?????1?? ?????????? ???????100 ?01??20000 2??1?1??2? 000?2???23
000010??00 00102?1?00 11???????? ????????1? ?????00203 01010???01 13002020?0
0113100111 001211121? 100?002012 0?02?00?01 0?03000100 420010110? ??0?021311
00101?0200 0101011010 ??2?200001 ?????00022 01000????1 1?0000??01 101100?000
12???11?00 ?0110?0121 0111111110 1?0?0?0??0 0010?11?10 1100?02?2? ?????2100?
1?0000?000 0???230003 2110011110 1?1000001? 00??01???? ???0443030 311?101303
0000???001 ??????02?? ????????1? ????1????1 ?????1???1 ???????1?? ??????????
???????1?? ?????????? ?????????? ?0000?0000 ?00??110?? ?????????? ??????????

Casarea_dussumieri 1100??0010 1100000201 1????0010? 0?2200?231 0000311??0
1010012?01 01?????00? 31?010???? 0??4?0?100 101??10000 11?1?10?2? 000?2???23
000010??00 00102?1?00 11???????? ????????1? ?????00103 00010???01 1300202010
1113100111 0022111011 101?002012 0?02?00?01 0?0???0000 420010110? ?00?011311
00101?0200 0101011010 ??2?200101 ?????00022 01000????1 1?0000??01 1012010000
12???10?00 0010020121 0111111110 1?000?0?00 0010?11?10 1101?1?010 ?100?21101
1?00000000 0???230003 2110011110 1?10000??? ?0??01???? ?????????0 ?????11???
?000????01 ??????02?? ????????1? ????1????1 ?????1???1 ???????1?? ??????????
???????1?? ?????????? ?????????? ?0000?0000 ??0??110?? ?????????? ?????????0

Haasiophis_terrasanctus ???00???10 ?????00211 1????001?0 010??00??1 ??????????
????022?0? ?1????000? 3?0010???0 ?????0?1?0 001?0?0000 0111?00??? 0???11?123
00?00???00 ?0?0??1?00 11???????? ????????1? ?????0020? 0?0000??01 1300?0????
???????1?? ?????????? ?????????? 0????????1 0???????1? ?20??????? ????021311
?0100?0200 ?101???010 0?2?201??1 ?????0?011 000??????? ?????0???? ??1??100??
?1???1???0 ??0??????? ??0?1?111? 1?0??00??? 0010?1??00 1?0??0101? 0100??1???
1?01?????? 0?0?2?00?3 31100111?? 1?100?0??? ?????????? ???04420?? ?13?1???13
0???21?101 ??????0??? ????????1? ????1????0 ?11??01??0 1001???1?? ??????????
???????011 ??????1011 ??01???0?? ?0000?0000 ?0???????? ?????????? ??????????

Eupodophis_descouensis 11200???10 ??00?0???? 1????????? ?????0???? ?0??1?????
????0????? ???????000 ?10010???0 ???4?1???? ?0???????? ??????0??? 0???1?????
0??0000??? ???02????? ?1???????? ????????1? ?????00??? ??0100???1 130??0????
?????0?1?? ?????????? 10?????00? 0????????? 0???0???1? 420???11?? ??????1?1?
???00?0??? ???1?1??0? ?????0???? ?????0???? ?????????? ?????0???? ??1??10???
?????1???? 1????????? ????1????? ?????????? ???0?????? ?????????? ??????????
1????????? 0?????0003 ?1?0?11??? ???00?0??? ?????????? ???04420?? 313?101313
???????001 ??????0??? ????????1? ????1????? ?????0???0 1001???1?? ??????????
???????011 ??????1??? ?????????? ????0?0000 00???????? ?????????? ??????????

Pachyrhachis_problematicus 1??00???1? ????????11 ?????????? ??0??00??? ??????????
????0?2?0? ?1????000? 310010???0 0??4?1?1?0 001???0000 0111?00??? 0???11?1?3
00?00???20 ?0?02?1?00 11???????? ????????1? ?????0020? 1?0100???1 130?40?00?
0????????? ?????????? ?????????? ?????????? 0???????1? ?20??????? ??????131?
?0200????0 ?10101?000 0?2?20???1 ?????0?0?? 0?0??????? ?????0???? ??????????
?????1???? ??0??????? ????11?11? 20??????0? 00?0?????? 1?0???1??2 ???????1??
1??1?????? 0??????0?2 2???01???? ???0??0??? ?????????? ?????????? 313?1?1?1?
???????101 ??????0??? ????????1? ????1????0 ?11??01??0 1001???1?? ??????????
???????011 ??????101? 1????????? ?0000?0000 ?????????? ?????????? ??????????

Exiliboa_placata 1000?0111? 1300100101 1????0010? 0?11?0?221 0000302??0
1010012?01 01?????00? 31?010???? 0??1?0?100 011??10000 11?1?1??2? 000?2???23
000000??00 00102?1?00 11???????? ????????1? ?????00203 0?010???01 1301202010
0113100111 0012111010 100?002012 0?02?00?01 0?03000110 420010110? ??1?021311
00101?0200 0101001010 ??2?200001 ?????00022 01000????1 1?0000??01 1112111000
12???10?00 0001020121 0111111110 1?2?0?0??0 0010?11?10 1101?02?2? ?????21101
1?01?????? 0???200003 3110011110 1?10000{01}?? 00??01???? ???0?????? 311???1???
0000???001 ??????02?? ????????1? ????1????? ?????????? ???????1?? ??????????
???????0?? ?????????? ?????????? ?0000?0000 ?00??110?? ?????????? ????1????1

Ungaliophis_continentalis 1000??011? 1300100201 1????0010? 0101?0?231 0000321??0
1010012?01 01?????00? 31?010???? 0??2?0?100 001??10000 11?1?10?2? 000?2???21
000000??00 01102?1?00 11???????? ????????1? ?????00203 0?010???01 1301402010
0113100111 0012101010 100?002012 0?02?00??1 0?03000110 420010110? ??0?021311
00101?0200 0101?01010 ??2?201001 ?????00022 01000????1 1?0010??01 1112111000
12???11?00 00010?0121 0111111110 1?1?0?0??0 0010??1??0 1100?02?2? ?????21101
1?01?????? 0???200002 2110011110 1?10000??? ?0??01???? ???0?????? 311???1???
0000???001 ??????02?? ????????1? ????1????0 ?????0???0 ???????1?? ??????????
???????0?? ?????????? ?????????? ?0000?0000 ?00??110?? ?????????? ????1????1

Eryx_colubrinus 1100??01?? 12?1?00201 1????0010? 0?1000?231 1000303??0 1?10012?01
01?????00? 31?010???? 0??4?0?100 001??10001 11?1?10?2? 000?2???23 000000??00
0??02?1?00 11???????? ????????1? ?????00203 0?010???01 1301402010 0113100111
0012110010 100?002012 ??02?00?01 0?030?0210 420??????? ??0?021311 00201?0200
0101000000 ??2?201001 ?????000?2 02000????1 1?0000??01 1112011001 11???10?00
0000020121 0111101110 1?100?0?00 0010?11?10 1101?00010 0100?21101 1?01??????
0???230002 2110011110 1?100001?? ?0??01???? ???0444030 311?101303 011121?001
??????02?? ????????1? ????1????0 ?1???0???0 ???????1?? ?????????? ???????0??
?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 04?11?1??1

Calabaria_reinhardtii 1100?0211? ?201?10201 1????0010? 010000?231 1000302??0
1010012?00 01?????00? 3??010???? 0??4?0?100 ?10??10000 11?1?00?2? 000?2???23
000000??00 00102?1?00 11???????? ????????1? ?????00203 0?010???01 1301102000
0113100111 0002111010 100?002012 ??02?00?01 0?03000110 41?010110? ??0?1?1311
00101?1??0 0101000000 ??2?201001 ?????00022 01000????1 1?0010??01 1112111001
11???10?00 1010020121 0111111110 1?100?0?00 0010?13?10 1101200010 0200?01101
1?01?????? 0???230003 2110011110 1??00001?? ?0??01???? ???04442?0 311?101303
001020?001 ??????02?? ????????1? ????1????0 ?1???0???0 ???????1?? ??????????
???????0?? ?????????? ?????????? ?0010?0000 ?00??11024 ???????01? 04?11?1??0

Lichanura_trivirgata 1100??011? ?200110201 1????0010? 0?2200?231 1000322??0
1010012?01 01?????00? 31?010???? 0??1?0?100 011??10000 11?1?10?2? 000?2???23
000000??00 00102?1?00 11???????? ????????1? ?????00203 0?010???01 1301302000
0113100111 0012110010 100?002012 ??02?00?01 0?03000110 421??0110? ??0?021311
00101?0200 0101000000 ??2?200001 ?????0002? 00000????1 1?0000??01 1112111000
12???10?00 0000020121 0101101110 1?1?0?0??0 0010?11?10 1101?00?2? ?????11101
1?01?????? 0???230003 2110011110 1?100001?? ?0??01???? ???0444230 311?101303
011121?001 ??????02?? ????????1? ????1????0 ?1???0???0 ???????1?? ??????????
???????0?? ?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 04?1101??1

Epicrates_striatus 1100??001? 1300100201 1????0010? 0?2200?221 1000212??0
1010012?00 01?????00? 31?010???? 0??3?1?100 001??10001 11?1?00?2? 000?2???23

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000000??00 03102?1?00 11???????? ????????1? ????00203 0?010???01 1301402010
0113100111 0012111011 100?002012 0?12?00?01 0?03000110 421010110? ??1?021311
00201?0200 0101011010 ??2?201001 ?????000?2 02000????1 1?0010??01 1112011001
11???10?00 1010020121 0111111110 1?100?0?00 0010?11?10 1101200010 0100?21101
1?01?????? 0???230003 2110011110 1?100001?? ?0??01???? ???04442?0 311?101303
000021?001 ??????02?? ????????1? ????1????0 ?1???0???0 ?0?0???1?? ??????????
???????011 ?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 0??110???1

Boa_constrictor   1100??001?   1200100201   1???00100   0?22000?1   1000213??0
1010012?00 01?????00? 31?010???? 0??4?1?100 001??10001 11?1?00?2? 000?2????23
000000??00 03102?1?00 11???????? ????????1? ????00203 0?010???01 130?202030
0113100111 0012111011 100?002012 ??02?00?01 0?0???0010 4210101 2?? ??1?021311
00201?0200 0101011010 ??2?201001 ?????000?2 02000????1 1?0010??01 1112011001
11???10?00 0110020121 0111110110 1?100?0?00 0010?11?10 1101200010 0100?21101
1?01?????? 0???230003 2110011110 1?100001?? ?0??01???? ???04442?0 311?101303
000021?001 ??????02?? ????????1? ????1????0 ?1???0???0 ???????1?? ??????????
???????0?? ?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 04?11?1??1

Aspidites_melanocephalus 1100??011? 1100000201 1????0010? 0111?0?231 1000221??0
1010012?00 01?????00? 31?110???? 0??4?1?100 001??20000 11?1?00?2? 000?2????23
000000??00 03102?1?00 21???????? ????????1? ????00203 1?010???01 1301402020
0113100111 0012111011 100?002012 0?02?00?01 0?0???0010 420010120? ??0?021311
00201?0200 0101011010 ??2?200211 ?????000?2 02000????1 1?0010??01 3012001010
11???11?00 10?0020121 0111111110 1?100?0?00 0010?11??0 1100?00010 0100?21101
1?01?????? 0???230002 2110011110 1?100001?? ?0??01???? ???04442?0 311?101303
0000???001 ??????02?? ????????1? ????1????0 ?????0???0 ???????1?? ??????????
???????0?? ?????????? ?????????? ?0010?0000 ?00??11024 ???????01? 04?11????0

Python_molurus   1100??011?   1100000201   1????0010?   0111?0?221   1000221??0
2010012?00 01?????00? 31?110???? 0??4?1?100 001??20001 11?1?0???2? 000?2????23
000000??00 03102?1?00 21???????? ????????1? ????00203 0?010???01 1301402010
0113100111 0012111010 101?002012 0?02?00?01 0?0???0010 420010120? ??0?021311
00201?0200 0101011010 ??2?201211 ?????000?2 02000????1 1?0010??01 3012011010
11???10?00 0010020121 0111111110 1?100?0?00 0010?11??0 1101?00010 0100?21101
1?01?????? 0???230013 2110011110 1?100001?? ?0??01???? ???04442?0 311?101303
000021?001 ??????02?? ????????1? ????1????0 ?1???0???0 ???????1?? ??????????
???????0?? ?????????? ?????????? ?0010?0000 ?00??11024 ???????01? 04?11????0

Trachyboa_boulengeri  1100??011?  1300100201  1????0010?  0?2200?231  000022??0
2010012?00 01?????00? 31?110???? 0??4?1?100 111??20000 2??1?0???2? 000?2????21
100000??00 00102?1?00 11???????? ????????1? ????00203 00010???01 1301402020
0113100111 0012111310 100?002002 0?12?00?01 0?031?0110 420010100? ??0?021311
00201?0200 0101011000 ??2?200201 ?????00022 01000????1 1?0000??01 3012111000
12???11?00 0011020121 0111111110 1?2?0?0??0 0010?11?10 1100?02??2? ?????2130?
1?00000000 0???130002 3110011110 1?10000??? ?0??01???? ???0441030 311?111303
0000???001 ??????02?? ????????1? ????1????0 ?????0???0 ???????1?? ??????????
???????0?? ?????????? ?????????? ?0000?0000 ?00??110?? ?????????? ????10???1

Tropidophis_haetianus 1100??011? 1300100201 1????0010? 0?2200?231 000022??0
2010011?00 01?????00? 31?110???? 0??4?1?100 111??20000 2??1?0???2? 000?2????21
100000??00 00102?1?00 11???????? ????????1? ????00103 00010???01 1301402020
0113100111 0012111310 100?002002 0?12?00?01 0?031?0110 420010100? ??0?021311
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00201?0200  0101011000  ???2200101  ?????00022  01000????1  1?0000??01  3012111000
12???11?00  0010020121  0111111110  1?2?0?0??0  0010?11?10  1101?02?2?  ?????2130?
1?000000?0  0???130003  3110011110  1?10000{01}??  ?0??01????  ???04441?0  311?111303
000021?001  ??????02??  ????????1?  ????1????0  ?1???0???0  ???????1??  ??????????
???????0??  ??????????  ??????????  ?0000?0000  ?00??11024  ???????01?  04?1101??1

Xenodermus_javanicus  1110??011?  ?300100111  1????0010?  0?23?0?2?1  1000301??0
1010012?01  01?????00?  31?110????  0??4?1?100  101??20000  2??1?00?2?  000?2???23
100000??00  10102?1?00  21????????  ????????1?  ?????00203  11010???01  1301402020
0113100111  0022111011  101?002113  0?02?0{01}?01  0?0???0010  42001?????  ??0?021312
00201?0210  0101021010  ???2201211  ?????00022  01000????1  1?0000??01  1011000?0
12???10??0  1011020121  0111111110  1?2?0?0??0  0010?1??10  1101?1??2?  ?????11301
1?00000000  0???200003  3110011110  1?00000010  00??01????  ???0443030  312?111303
000021?001  ??????02??  ????????1?  ????1????1  ?????1???1  ???????1??  ??????????
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Acrochordus_granulatus  1000??021?  ???1?00211  1????000??  ??23?0?2?1  1000322??0
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100000??00  0??12?1?00  21????????  ????????1?  ?????00203  11010???01  130?402030
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00201?0200  0101021000  ???2200201  ?????00022  01000????1  1?0?00??03  3112100000
12???10??0  000??20?21  1111110110  1?1?0?0??0  0010?11?10  1100?1??2?  ?????2130?
1?01??????  0???230003  2110011110  1?1000001?  ?0??01????  ???0444000  314?111303
000021?001  ??????02??  ????????1?  ????1????1  ?????1???1  ???????1??  ??????????
???????1??  ??????????  ??????????  ?0000?0000  ?00??11024  ???????01?  04?11?1??1

Pareas_hamptoni    1100??001?    ?400000111    1????0000?    0?13?0?231    1000302??0
1010011?01  21?????00?  31?010????  0??2?0?100  100??20000  2??1?00?2?  0?0?2????1
100000??20  10112?1?00  21????????  ????????1?  ?????00103  0?000???01  1302402030
0113100111  0022110011  101?003113  0?22?00?01  0?0???0000  ?2101?110?  ??0?021312
00201?0200  0101021010  ???2201211  ?????00022  01000????1  1?0000??01  1012100000
12???10??0  0011020121  0111111110  202?0?0??0  0010?1??10  120??1??2?  ?????2130?
1?00000000  0???1??002  2110011110  1?10000{01}??  ?0??01????  ???0444040  311?101303
0000???001  ??????02??  ????????1?  ????1????1  ?????1???1  ???????1??  ??????????
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Lycophidion_capense  1100??001?  ?400000111  1????0000?  0?23?0?231  1000301??0
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00201?0200  0101021000  ???2200111  ?????00022  01000????1  1?0010??01  1012100000
12???10??0  0011020121  0111111110  1?0?0?0??0  0310?1???0  ?20??1??2?  ?????2130?
1?00000000  0???230003  3110011110  1?0000001?  ?0??01????  ???04441?0  311?1?1303
0000???001  ??????02??  ????????1?  ????1????1  ?????1???1  ???????1??  ??????????
???????1??  ??????????  ??????????  ?0000?0000  ?00??11024  ???????01?  0????????0

Aparallactus_werneri  10000?0010  ??00000101  1????0000?  0?0000?221  1000301??0
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100000??00  10112?1?00  21????????  ????????1?  ?????02003  ??0?0???01  130?102100
1113100111  0022110011  101?003113  0??3?00?01  0?03000100  42001?11??  ??0?021312
00001?0200  0101021000  ???2200111  ?????20022  01000????1  1?0??0??01  ?011?00010
12???11?00  001?020121  0111110110  1?2?0?0??0  0210?13?10  1201?1??2?  ?????2130?
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1?00000000 0???242002 3110011110 1?10100020 00??01???? ???04420?0 311?101303
0000???001 ??????02?? ????????1? ????1????1 ?????1???1 ???????1?? ??????????
???????1?? ?????????? ?????????? ?0000?0000 ?00??11024 ????????1? 0???13???0

Atractaspis_irregularis 110??02010 ??01000111 1????0000? 0?0000?231 1000321??0
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1?01?????? 0??????001 0???01?110 ????200??? ?0??01???? ???0444230 311?1?1303
0000???001 ??????02?? ????????1? ????1????1 ?????1???1 ???????1?? ??????????
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Causus_rhombeatus 110???001? 1400000211 1????0000? 0?2210?2?1 2001223??0
2010011?01 21?????00? 31?010???? 0??4?0?100 100??10000 2??1?0??2? 0?0?????4?
????00??00 00212?1?00 21???????? ????????1? ?????00203 10010???01 1302402040
0113100111 0022110311 10??003113 ??12?00??1 0?0???02?0 4?0??????? ??1?021311
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12???10??0 0011020121 0111111110 0???0?0??0 0210?????0 1200?1??2? ??????130?
1?00100000 0???????01 3110011110 1?0020001? 00??01???? ???0442030 311?111303
0000???001 ??????02?? ????????1? ????1????1 ?????1???1 ???????1?? ??????????
???????1?? ?????????? ?????????? ?0000?0000 ?00??11024 ????????1? 0???13???0

Azemiops_feae 110??0101? 1400100211 1????0000? 0?1200?231 1000322??0 1010012?01
01?????00? 31?110???? 0??4?1?100 100??20000 2??1?00?2? 0?0?????4? ????00??10
10212?1?00 21???????? ????????1? ?????00203 10010???01 1302402020 0113100111
0022110011 10??003113 0?12?00?01 0?030?01?0 421??0110? ??1?021311 00201?0200
011?021000 ??2?200211 ?????00022 01000????1 1?0010??01 (13)?12100000 12???10??0
0011020121 0111101110 1?2?0?0??0 0010??1?10 1200?1??2? ?????2130? 1?00100000
0???????01 2110011110 1?10200010 00??01???? ???04430?0 311?111303 0000???001
??????02?? ????????1? ????1????1 ?????1???1 ???????1?? ?????????? ???????1??
?????????? ?????????? ?0000?0000 ?00??110?? ?????????? ????1????0

Daboia_russelli 110??0101? 1400100211 1????0000? 0?23?0?2?1 2000323??0
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0113100111 0022110011 10??003113 ??22?00??1 0?0???02?0 4?1??????? ??1?021311
00201?0200 011?021000 ??2?200211 ?????00022 01000????1 1?0010??01 1?12123000
12???10??0 1021020121 0111110110 1???0?0??0 0210??1??0 1200?1??2? ?????2130?
1?00100000 0???????01 2110011110 1?002001?? 00??01???? ???0443030 311?111303
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Agkistrodon_contortrix 100??0101? 1400100211 1????0000? 0?2210?2?1 10003?3??0
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00201?0200 011?021000 ??2?200111 ?????00022 01000????1 1?0010??01 1?12123000
12???10?00 0021020121 0111110110 1?2?0?0??0 0310??1??0 1200?1??2? ?????2130?
1?00100000 0???????01 2110011110 1?0020001? 00??01???? ???0442030 312?111303
000021?001 ??????02?? ????????1? ????1????1 ?????1???1 ???????1?? ??????????
???????1?? ?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 04?11????1

Bothrops_asper 110??0101? 1400100211 1????0000? 0?2210?2?1 0000302??0
2110011?00 11?????00? 31?010???? 0??0?0?100 100??10000 2??1?00?2? 0?0?????4?
????00??00 10?12?1?00 21???????? ????????1? ?????00203 10010???01 130240?040
0113100111 0022110011 10??003113 ??12?00?01 0?0???00?0 421???12?? ??1?021311
00201?0200 011?021000 ??2?200211 ?????00022 01000????1 1?0010??01 1?12123000
12???10??0 0021020121 0111100110 1???0?0??0 0310?????0 1200?1??2? ?????2130?
1?00100000 0???????01 2110011110 1?00200 1?? 00??01???? ???04441?0 312?111303
000021?001 ??????02?? ????????1? ????1????1 ?????1???1 ???????1?? ??????????
???????1?? ?????????? ?????????? ?0000?0000 ?00??10024 ????????1? 0???1????1

Lachesis_muta 110???001? 1400000211 1????0000? 0?23?0?2?1 0000302??0 2110011?01
11?????00? 31?010???? 0??0?0?100 100??10000 2??1?0??2? 0?0?????4? ????00??00
00?12?1?00 21???????? ????????1? ?????00203 10010???01 1302402030 0113100111
0022110011 10??003113 ??12?00??1 0?0???00?0 421???12?? ??1?021311 00201?0200
011?021000 ??2?200211 ?????00022 01000????1 1?0010??01 1?12123000 12???10??0
0021020121 0111100110 1???0?0??0 0010?????0 1200?1??2? ?????2130? 1?00100000
0???????01 2110011110 1?00200020 00??01???? ???0444230 312?111303 000021?001
??????02?? ????????1? ????1????1 ?????1???1 ???????1?? ?????????? ???????1??
?????????? ?????????? ?0000?0000 ?00??11024 ????????1? 0???1????0

Naja_naja 1000??001? 1300100211 1????0010? 0?2200?221 2001323??0 1010012?01
21?????00? 31?010???? 0??3?0?100 100??10000 2??1?00?2? 000?2????2? 100?00??00
12212?1?00 21???????? ????????1? ?????00203 10010???01 1302402030 0113100111
0022110011 100?003113 0?12?00??1 0?030?0000 ?20010120? ??1?021312 00201?0200
0101011?00 ??2?200211 ?????00022 01000????1 1?0000??01 1012100000 12???12?00
0011020121 0111111110 1?2?0?0??0 0310?11??0 1201?1??2? ?????2110? 1?00000000
0?????1?01 2110011110 1?00200{01}?? 00??01???? ???04441?0 312?111303 000021?001
??????02?? ????????1? ????1????1 ?????1???1 ???????1?? ?????????? ???????1??
?????????? ?????????? ?0000?0000 ?00??10024 ???????01? 04?113???0

Notechis_scutatus 110???001? 1400000211 1????0000? 0?2200?221 1001323??0
1010012?01 21?????00? 31?010???? 0??2?0?100 101??10000 2??1?00?2? 000?2?????
10??00??00 10212?1?00 21???????? ????????1? ?????00203 10010???01 1302402030
0113100111 0022110011 101?003113 ??12?00?01 0?0???02?0 420010???? ??1?021312
00201?0200 0101011?10 ??2?200211 ?????00022 01000????1 1?0000??01 1?12100000
12???12?00 1011020121 0111111110 1?2?0?0??0 0310?11??0 1200?1??2? ?????2110?
1?00000?00 0?????1?02 3110011110 1?002001?? 00??01???? ???04430?0 311?111303
000021?001 ??????02?? ????????1? ????1????1 ?????1???1 ???????1?? ??????????
???????1?? ?????????? ?????????? ?0000?0000 ?00??11024 ????????1? 0????????1

Laticauda_colubrina 1100??001? ?400000211 1????0000? 0?23?0?2?1 1000301??0
1110012?00 21?????00? 31?010???? 0??3?1?100 001??10000 2??1?10?2? 000?2????2?
10??00??00 03212?1?00 21???????? ????????1? ?????00203 10010???01 1300402020
0???100111 0020110011 101?003113 ???4?00??1 0?0???0200 42001????? ??1?021312
00201?0200 0101?00?00 ??2?201211 ?????000?2 01000????1 1?0000??01 1011000000
12???10?00 1011020121 0111110110 1?1?0?0??0 0310?13??0 1200?1??2? ?????0110?
1?00000000 0?????1?01 2110011110 1?10200010 00??01???? ???0444230 312?111303
0000???001 ??????02?? ????????1? ????1????1 ?????1???1 ???????1?? ??????????
???????1?? ?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 04?113???0

Micrurus_fulvius 1101??001? 1400000211 1????0000? 0?2200?221 1000321??0
1010013?00 21?????1?? ?????????? ???????100 001??10000 2??1?2???2? 000?2????2?

10??00??00 13112?1?00 21???????? ????????1? ????00203 10010???01 1301402020
0113100111 0022110011 101?003113 0??4?00?01 0?030?0000 ?20010110? ??1?021312
00201?0200 0101010?00 ??2?200111 ????00022 01000????1 1?0000??01 3111000010
12???10?00 1011020121 0111101110 1?2?0?0??0 0310?11?10 1200?1??2? ?????2110?
1?00000000 0???????01 2110011110 1?10200?0 00??01???? ???0444230 312?111303
0000???001 ??????02?? ????????1? ????1????1 ?????1???1 ???????1?? ??????????
???????1?? ?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 0??11????0

Natrix_natrix 1100??001? ?400000211 1????0100? 0?23?0?221 2001323??0 2010022?01
21?????00? 31?010???? 0??2?0?100 101??20000 2??1?00?2? 000?2???23 100000??00
10212?1?00 21???????? ????????1? ????00203 11010???01 1302402040 0113100111
0032110011 101?003113 0?22?00??1 0?0???0100 420010110? ??0?021312 00201?0210
0101022010 ??2?201211 ????00022 01000????1 1?0000??01 3012112010 12???10?00
0011020121 0111111110 1?2?0?0??0 0310?11?10 120??1??2? ?????2130? 1?00000000
0???242003 3110011110 1?000000?? ?0??01???? ???0443030 312?111303 0000???001
??????02?? ????????1? ????1????1 ?????1???1 ???????1?? ?????????? ???????1??
?????????? ?????????? ?0000?0000 ?00??10024 ????????1? 0???13???0

Afronatrix_anoscopus 1100??001? ?400000211 1????0100? 0?23?0?221 1001322??0
2010012?01 21?????00? 31?010???? 0??3?0?100 101??20000 2??1?00?2? 000?2???23
100000??00 10212?1?00 21???????? ????????1? ????00203 11010???01 1302402030
0113100111 0032110011 10??003113 0?22?01?01 0?0???0100 42001011?? ??0?021312
00201?0210 0101022010 ??2?200211 ????00022 01000????1 1?0000??01 3012112010
12???10?00 0011020121 0111110110 1?2?0?0??0 0310?1??10 1201?1??2? ?????2130?
1?00000000 0???242003 3110011110 1?00001?? ?0??01???? ???04420?0 311?1?1303
0000???001 ??????02?? ????????1? ????1????1 ?????1???1 ???????1?? ??????????
???????1?? ?????????? ?????????? ?0000?0000 ?00??110?? ????????? ????1????0

Amphiesma_stolata 1100?0101? ?400000211 1????0100? 0?23?0?221 2001323??0
2010012?0? 21?????00? 31?010???? 0??2?0?100 100??20000 2??1?00?2? 000?2???23
100000??00 10212?1?00 21???????? ????????1? ????00203 10010???01 1301402O?0
0113100111 0032110011 101?003113 0?22?01?01 0?0???0100 420010110? ??0?021312
00201?0210 0101022010 ??2?201211 ????00022 01000????1 1?0010??01 3012112010
12???10?00 0011020121 0111111110 1?2?0?0??0 0310?1??10 1201?1??2? ?????2130?
1?00000000 0???242003 3110011110 1?001001?? ?0??01???? ???0442030 312?111303
000021?001 ??????02?? ????????1? ????1????1 ?????1???1 ???????1?? ??????????
???????1?? ?????????? ?????????? ?0000?0000 ?00??110?? ????????? ???113???0

Thamnophis_marcianus 1100??001? ?400000211 1????0100? 0?23?0?221 2001323??0
2010012?00 21?????00? 31?010???? 0??2?0?100 101??20000 2??1?00?2? 000?2???23
100000??00 10212?1?00 21???????? ????????1? ????00203 11010???01 1301402040
0113100111 0032110011 101?003113 ??22?00??1 0?0???0100 42001?110? ??0?021312
00201?0210 0101022010 ??2?201211 ????00022 01000????1 1?0000??01 3012112010
12???11?00 1011020121 0111111110 1?2?0?0??0 0310?1??10 1201?1??2? ?????2130?
1?00000000 0???242003 3110011110 1?00001?? 00??01???? ???0442030 312?111303
000021?001 ??????02?? ????????1? ????1????1 ?????1???1 ???????1?? ??????????
???????1?? ?????????? ?????????? ?0000?0000 ?00??11024 ??????01? 04?113???1

Xenochrophis_piscator 1100??001? ?400000211 1????0100? 0?23?0?221 2001323??0
2010012?01 21?????00? 31?010???? 0??0?0?100 101??20000 2??1??0?2? 000?2???23
100000??00 10212?1?00 21???????? ????????1? ????00203 11010???01 1302402030
0113100111 0032110011 100?003113 ??22?00?01 0?0???0100 420010110? ??0?021312

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00201?0210 0101022010 ??2?201211 ????00022 01000????1 1?0000??01 3012112010
12???11?00 1011020121 0111111110 1?2?0?0??0 0310?11??0 1201?1???? ?????2130?
1?00000000 0???242003 3110011110 1?100001?? 00??01???? ???0442030 312?111303
000021?001 ??????02?? ????????1? ????1????1 ?????1???1 ???????1?? ??????????
???????1?? ?????????? ?????????? ?0000?0000 ?00??110?? ?????????? ????13???0

Lampropeltis_getula  1100??001?  1400000211  1????0000?  0?2200?221  2001323??0
2010014?01 21?????00? 31?010???? 0??3?0?100 101??20000 2??1?00?2? 000?2????23
100000??00 10212?1?00 21???????? ????????1? ????00203 11010???01 1302402?0
0113100111 0032110011 101?003113 ??22?00??1 0?0???0100 420010110? ??0?021312
00201?0210 0101021010 ??2?200211 ????00022 01000????1 1?0010??01 3012110010
1{12}???10?00 0011020121 0111111110 1?2?0?0??0 0310?1??10 120??1???? ?????2130?
1?00000000 0???240002 2110011110 1?100001?? 00??01???? ???04442?0 312?101303
000021?001 ??????02?? ????????1? ????1????1 ?????1???1 ???????1?? ??????????
???????1?? ?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 04?11????0

Coluber_constrictor  1100??001?  ?400000211  1????0000?  0?2200?221  2001323??0
2010024?01 21?????00? 31?010???? 0??3?0?100 101??20000 2??1?00?2? 000?2????23
100000??00 11212?1?00 21???????? ????????1? ????00203 11010???01 1302402030
0113100111 0032110011 101?003113 ??22?00?01 0?0???0000 420010100? ??0?021312
00201?0210 0101021010 ??2?200211 ????00022 01000????1 1?0010??01 3012100010
12???10?00 0011020131 0111111110 1?2?0?0??0 0310?1??10 1201?1???? ?????2130?
1?00000000 0???240002 2110011110 1?10000020 00??01???? ???0443?0 312?101303
000021?001 ??????02?? ????????1? ????1????1 ?????1???1 ???????1?? ??????????
???????1?? ?????????? ?????????? ?0000?0000 ?00??11024 ???????01? 04?113???0
;
END;
BEGIN ASSUMPTIONS;
         OPTIONS DEFTYPE = unord PolyTcount = MINSTEPS;
         TYPESET * UNTITLED = unord: 1-2 4-6 8-9 11 13-17 19-24 26-32 34-37 40 42
44 46-47 50 52-55 57 59-62 64 68-69 71-79 81 85-89 91-92 94-96 98 100 103-104 107
109-110 112-113 115-119 121-125 127 131 134-139 142 144-148 150-151 153-154 156-
166 169-177 179-181 183 186 190-202 205-207 209-215 218-219 221-222 224-230 232-
237 239-241 243-247 249 252-255 257 259 261-262 264-267 269-270 272-275 278-282
284 286-287 289-299 304-305 307-308 310 313-315 317-325 327 329-336 338-339 341-
342 344-345 348 351-359 362-363 365-367 370-371 373-374 376-381 383-387 391 393
395 397-413 416-417 422-434 436-439 441-453 461-462 464-467 469-474 476 478-482
484-485 489-517 519-528 530-534 536-569 571 573-583 585-587 591-592 594-601 603-
610, ord: 3 7 10 12 18 25 33 38-39 41 43 45 48-49 51 56 58 63 65-67 70 80 82-84
90 93 97 99 101-102 105-106 108 111 114 120 126 128-130 132-133 140-141 143 149
152 155 167-168 178 182 184-185 187-189 203-204 208 216-217 220 223 231 238 242
248 250-251 256 258 260 263 268 271 276-277 283 285 288 300-303 306 309 311-312
316 326 328 337 340 343 346-347 349-350 360-361 364 368-369 372 375 382 388-390
392 394 396 414-415 418-421 435 440 454-460 463 468 475 477 483 486-488 518 529
535 570 572 584 588-590 593 602;
END;
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Appendix 4: Squamate Clade Diagnoses

Synapomorphies for clades inferred in the PAUP* maximum parsimony analysis based on DELTRANS optimizations on the strict consensus tree (see Figure 1) are listed below. "Unambiguous" optimizations are in **bold** face, whereas "ambiguous" optimizations, resulting either from missing data (e.g., soft characters) or uncertainty about modes of character evolution (e.g., the prevalence of convergence vs. reversal in evolution), are listed in regular font. Characters that are unique and unreversed on this tree are denoted with an asterisk (*). Diagnoses for Rhynchocephalia, Sphenodontida, *Huehuecuetzpalli* + Squamata, and Squamata are optimized by hand using an outgroup succession composed of Kuehneosauridae, *Paliguana whitei, Saurosternon bainii, Prolacerta broomi, Youngina capensis* and *Claudiosaurus germaini*. In our experience, phylogenetic inference software packages using unrooted networks seldom produce reliable optimizations for basalmost nodes. They perform better when a hypothetical ancestor, or multiple outgroups plus apomorphies resolving their phylogenetic relationships—well beyond the scope of this analysis—are added.

Rhynchocephalia: **9(1), 29(1), 65(1)*, 120(1), 166(1), 256(1), 415(1), 364(1), 369(2), 374(1).**

Sphenodontida: **36(0), 65(2)*, 85(1), 88(0), 93(1), 102(0), 116(0), 155(0), 230(1),** 240(1), **254(2), 256(2),** 267(1), **354(2), 400(1), 404(1), 419(2), 420(2), 421(2), 423(1), 430(1), 463(1), 521(1), 572(0).**

***Huehuecuetzpalli mixtecus* + Squamata**: **57(1), 144(1), 149(2), 155(2), 177(1)*, 179(1), 181(1)*, 182(2), 295(1)*, 297(1), 381(1), 387(1), 390(2), 393(1), 493(1), 495(1), 513(1), 546(1), 556(1), 557(1).**

Squamata: **1(1), 56(1), 58(1), 78(1), 103(1)*,** 113(1), 114(2), 187(2), 199(1)*, 209(1)*, 240(1), 250(1), 255(1), 257(1), 259(1), 296(2), 336(1)*, 346(1)*, 352(1), 354(1)*, 384(1), 388(1), 413(1), **467(1), 475(1),** 503(1), 504(1), **533(1), 534(1),** 535(1), 537(1)*, 538(1)*, **546(1), 557(1), 560(1)*, 561(0),** 584(1), 590(1), 605(1)*.

Iguania: 24(1), 29(1), **58(2)**, 63(2), 71(2), **79(1), 80(1), 105(1),** 111(1), **112(1), 116(2), 130(1),** 188(1), **246(1), 258(2),** 267(1), 285(1), **291(1), 306(1),** 316(1), **372(2),** 378(1), **388(2), 411(1),** 413(1), 434(2), **448(1), 452(4), 462(1),** 463(2), **470(2), 481(1),** 494(1), 497(1), **509(2),** 519(1), 533(1), **535(2),** 553(1), 557(1).

***Ctenomastax parva* + Priscagaminae + Acrodonta: 62(2), 80(0), 188(0), 246(0), 372(0), 378(0), 413(0), 417(1), 419(2), 421(2), 436(1).**

Priscagaminae + Acrodonta: 3(1), 25(1), 48(2), 112(0), **120(1), 136(1), 285(0),** 388(1), **415(1).**

Priscagaminae: 146(1), 156(1), 369(0), **375(3), 572(3).**

***Mimeosaurus crassus* + *Phrynosomimus asper*: 151(1)*.**

Acrodonta: 3(2), 7(3), 23(1), 48(3), **62(3), 111(2),** 258(1), **266(1)*,** 348(1), **364(2), 366(2), 388(0), 390(1), 392(1), 401(1), 423(1), 430(1),** 452(0), 462(0), 468(0), 470(3), 475(0), 507(1), 509(1), 562(1), 584(2), 609(1).

Leiolepidinae: 82(2), 147(1)*, 204(1), 275(2), 420(2), 424(1), 439(1), 463(3), 482(1), **483(0), 484(1), 494(0), 498(0), 572(0).**

Chamaeleonoidea: 8(2), 78(4), 79(0), 81(1)*, 114(1), 120(2), 139(1)*, 144(0), **185(0),** 231(1), **284(1)*,** 385(2), **412(1),** 419(1), **442(0), 489(1), 551(1).**

Chamaeleonidae: 20(1), 50(1), 56(2), 57(3), 94(2), **98(1)*, 99(1), 114(0), 116(0), 129(2), 130(2), 134(1),** 137(1), **173(1)*, 177(2)*, 179(0), 180(1), 182(3), 183(1), 188(1), 194(2), 196(1)*, 212(1),** 240(1), **290(1), 301(2), 311(1), 328(2), 338(1), 350(1), 360(0), 361(3), 374(1), 383(1), 404(1), 417(0), 439(2),** 440(2), **445(3), 446(1), 454(2), 459(1), 477(0)*, 481(0), 483(2), 487(2), 488(1),** 491(1), **493(0), 495(0), 499(1), 505(1), 513(0), 514(1), 517(1), 518(2), 521(1), 522(1)*, 523(1)*, 530(1), 531(1), 532(1), 536(1)*, 539(0), 540(1), 545(1)*, 546(0), 547(1), 549(1), 558(1)*, 563(1)*, 568(1)*, 569(1).**

Agaminae: 107(1)*, 154(2), 304(1)*, 344(1), 390(0), 407(1)*, **413(1),** 447(1), 463(1), 503(0).

Calotes emma* + *Agama agama* + *Pogona vitticeps: **7(4), 120(3), 153(1), 246(1), 293(1), 434(0), 461(1),** 482(1), **562(0)**.

Agama agama* + *Pogona vitticeps: 149(1), **185(1), 189(1), 231(0), 401(0), 504(0).**

Temujiniidae: 63(1), 64(1), 71(0), 80(0), 160(1), 165(1).

Isodontosauridae: 59(1), 62(1), 80(0), 245(1), 364(0), 369(0), 378(0), 399(1), 420(2), 572(0).

***Polychrus marmoratus* + Corytophaninae: 7(2), 62(2), 80(0), 94(2), 246(0), 364(0), 369(0),** 372(3), **442(0), 452(0), 468(3), 470(3), 486(3),** 609(1).

Corytophaninae: 48(2), **93(2),** 105(2), **146(1), 188(0),** 231(1), **344(1), 375(1), 378(0), 390(1), 500(2), 501(1).**

Leiosaurinae: 10(2), 48(3), 80(0), 146(1), 168(1), 231(1), **246(0), 258(1), 267(0), 364(2),** 372(3), **421(2), 468(2), 572(2), 588(2),** 609(1).

***Leiosaurus catamarcensis* + *Urostrophus vautieri*: 18(1), 90(1), 340(1), 341(1), 448(0).**

Crotaphytinae: 22(1), 48(0), 62(1), 80(0), 146(1), 169(1), 231(1), **246(0), 258(1), 267(0), 375(1), 392(1),**

422(2), 468(2), 483(0), 492(1), 496(1), 497(0), 562(1), 609(1).

Hoplocercinae: **7(2), 11(2), 30(1),** 48(2), **94(2), 114(1), 116(1), 178(1), 188(2), 254(1), 258(3), 267(0), 294(1), 344(1), 364(0), 369(0), 372(1), 375(1), 378(0), 394(2), 447(1), 452(0), 468(2), 483(0), 553(0), 572(2), 583(1)*,** 609(1).

Iguaninae: 48(2), **116(1), 176(1)*, 232(1), 258(1), 369(0),** 372(3), **388(1), 394(2), 413(0), 419(2), 463(3), 468(3), 470(0), 471(2), 483(0).**

Brachylophus fasciatus* + *Dipsosaurus dorsalis* + *Armandisaurus explorator: **25(1), 136(1), 447(1),** 492(1), **519(0).**

Dipsosaurus dorsalis* + *Armandisaurus explorator*: *7(1), 105(2).

Liolaeminae: 25(1), 59(1), 80(2), 168(1), 231(1), **258(3), 267(0), 367(1), 383(2), 394(2), 419(2), 448(0),** 609(1), **610(1).**

Oplurinae: 31(1), 48(2), **62(1), 80(2), 111(0), 185(0), 188(0),** 231(1), **258(1), 267(0), 340(1), 344(1), 364(2), 378(0), 383(1), 392(1), 492(1), 519(0), 608(1),** 609(1).

Tropidurinae: **48(3),** 231(1), **246(0), 267(0), 344(1), 364(2),** 372(3), **383(1), 384(2), 385(1), 392(1), 419(2), 462(0), 492(1), 496(1).**

Plica plica* + *Stenocercus guentheri: 7(1), **168(1), 254(1), 369(2), 388(1).**

Polyglyphanodontia + Mosasauria + Scleroglossa: 36(0), **49(1), 56(2), 64(1),** 111(1), **150(1), 157(1), 375(3), 379(1),** 388(1), 434(2), **437(1)*.**

Polyglyphanodontia: 24(1), 37(1), 87(1), 96(4), **111(2), 122(1),** 145(1), **149(0),** 167(1), **175(1),** 273(1), **399(1), 403(1), 418(1).**

Adamisaurus magnidentatus* + *Gilmoreteius* + *Polyglyphanondon sternbergi: 39(4), **155(1), 257(0), 262(1)*,** 267(1), 271(1), **281(1), 360(0).**

Gilmoreteius* + *Polyglyphanodon sternbergi: 49(2), **110(1),** 116(3), **166(1),** 213(1), **240(1), 376(1),** 468(2), 500(2), 546(0).

Mosasauria + Scleroglossa: 48(3), **83(2)*, 285(2), 360(2), 394(1), 455(4), 521(1).**

Mosasauria: 3(1), 10(1), 11(1), 19(1), 20(1), 48(4), 62(2), 118(1), 154(1), **186(1)*, 296(0), 376(1), 377(2), 385(2), 395(1), 410(1), 419(2), 422(2), 427(1), 461(2), 462(1), 465(1), 468(3),** 470(3), **475(2), 478(1), 488(1),** 497(1), **549(1), 550(1), 561(2),** 572(0).

Dolichosauridae: 9(1), 456(1), 460(2).

Mosasauroidea: 83(3)*, 94(2), 358(1), **382(1),** 418(1), **546(0)**.

Mosasauridae: 2(1), 6(1), 7(2), 10(2), **50(1), 51(1), 78(3), 87(1),** 96(2), 109(3), **124(1), 129(2),** 268(1), 278(2), 311(1), 315(1), 344(1), 348(1), 349(3), 350(1), 359(2), 362(1), 392(2), 393(0), **418(2),** 420(2), 432(1)*, 433(1), **463(0),** 499(1), **522(2), 524(1), 527(1)*,** 567(1)*, 585(1).

Clidastes* + *Plotosaurus* + *Tylosaurus: 26(1)*, **333(1),** 334(0), **421(2),** 428(1), **478(0),** 531(1), 544(1).

Plotosaurus* + *Tylosaurus: 468(0).

Scleroglossa: 22(1), 36(1), **82(1), 90(2), 128(1), 162(1),** 165(1), **188(2), 200(1)*, 241(2), 258(2), 272(1),** 283(1), 375(2), 401(1), 439(1), 463(2), **502(1),** 508(1), 509(1), 533(1), 535(1), 600(1)*, 604(1)*.

***Eichstaettisaurus* + AMNH FR 21444 + Gekkota**: **38(1), 88(0), 161(1),** 258(3), **419(4), 420(4), 470(2),** 572(0).

AMNH FR 21444 + Gekkota: 39(3), **95(1),** 128(2), 135(1), **158(1),** 267(1), 347(1).

Gekkota: 36(1), 38(3), 68(1), 104(1), 128(3), 137(1), **141(1), 152(2),** 159(1), 178(2), 185(4), 204(1), 234(1), 241(3), **283(2),** 297(0), **347(2),** 369(1), **372(3), 375(1), 380(1),** 421(4), 518(1), 585(1), 588(1), 593(1), 597(1)*, 598(1).

Pygopodidae: **10(1), 54(1), 94(2), 129(2), 166(1), 187(1),** 220(1), **237(1)*, 258(2), 307(1), 334(0), 364(2), 369(2),** 375(0), 384(0), **422(1), 427(1),** 479(1), **505(1)**.

***Strophurus ciliaris* + *Rhacodactylus auriculatus* + *Saltuarius cornutus* + Eublepharidae + Gekkonidae: 43(2),** 70(1), 273(1), **292(1),** 308(1), 309(1), 328(2), **341(1),** 384(3), 385(1), 413(1), **443(1), 452(2), 455(2), 467(0),** 475(0), **500(2), 501(1), 502(0),** 525(1), 535(2), 584(0).

***Rhacodactylus auriculatus* + *Saltuarius cornutus*:** 13(1), 43(3), **50(1), 70(2),** 111(1), **114(1), 168(2), 188(3), 193(1),** 205(0), 252(1), **309(2),** 321(3), **409(1),** 539(0).

Eublepharidae + Gekkonidae: **37(1), 39(1), 88(1), 208(1), 213(1), 225(1)**, 252(1), 375(0), 539(0).

Eublepharidae: 13(1), **22(0), 43(1), 128(4),** 149(1), **159(0), 167(2), 170(2), 190(1), 450(1), 467(1),** 489(1), **515(1).**

Eubelpharus macularius* + *Coleonyx variegatus: **43(0), 137(0),** 138(2), **188(3), 273(0), 418(1),** 479(1), **557(1), 588(0).**

Gekkonidae: 18(1), 185(3), 254(2), 409(1), 439(0), 514(1), **584(1).**

Teratoscincus przewalskii* + *Gonatodes albogularis* + *Phelsuma lineatus: **144(0),** 149(1), **188(3),** 321(3), **420(3), 421(3).**

***Gonatodes albogularis* + *Phelsuma lineatus*:** **39(2), 190(1), 213(0), 249(1),** 286(1), **292(0), 309(0), 418(1).**

Autarchoglossa: **7(1), 117(1), 145(2),** 154(1), **155(1),** 201(1), **208(2), 215(1), 217(1),** 220(1), **245(1), 275(2),** 315(1), 316(1), 317(1), 413(1), **562(1), 572(2), 607(1).**

Scincomorpha: **18(1), 23(2), 37(1),** 213(1), **250(3), 254(1), 455(2), 500(2), 501(1), 511(1),** 512(1), **515(1), 591(1), 592(2),** 593(1), **595(1).**

Lacertoidea: **66(1), 89(1), 144(0), 145(1),** 157(1), 182(1), **222(2),** 291(1), 388(1), **394(2),** 434(1), **475(0), 481(1), 590(3),** 596(1), **602(2).**

Lacertidae: **18(2),** 24(1), **49(1),** 58(0), **67(3), 77(1), 82(0), 104(1), 123(1), 170(1), 206(1), 283(0),** 369(1), 379(1), 383(1), **452(3),** 494(1), 521(0), 573(1), **575(1), 577(1),** 593(2).

Teioidea: **36(1), 104(1), 128(3),** 178(1), **208(0), 231(1), 245(0),** 258(1), **314(1)*,** 383(2), 399(1), **403(1), 441(1)*, 449(1), 450(1), 451(1), 468(3), 471(2), 496(1), 530(1), 531(1), 590(4), 594(1), 608(1), 609(1).**

Gymnophthalmidae: **4(1), 5(1), 10(1), 11(2),** 13(1), 39(2), **56(0),** 58(0), **69(1), 94(1), 108(2), 135(1), 138(3), 149(1), 168(1),** 188(1), **226(1)*, 249(1), 338(1), 364(1),** 369(1), **384(3),** 385(1), 419(4), **445(2), 461(1),** 593(2), **606(1).Teiidae: 7(0), 23(0),** 29(1), **39(0), 56(2), 78(2), 90(0), 155(2), 233(1)*, 258(0), 261(1),** 268(1), **273(1), 281(1), 294(1), 317(0),** 335(1), **360(1), 412(1), 462(1), 508(0), 512(0), 514(1),** 521(0), **554(1), 593(0).**

Teiinae: 13(1), 37(0), **96(3),** 109(1), 114(4), **130(1), 162(0), 165(0),** 271(1), 368(1), 379(1), 502(0), **511(0), 591(0), 595(0), 602(3).**

Tupinambinae: 24(1), 87(1), **93(1), 94(2),** 188(1), **193(1), 344(1),** 375(3), 383(1), **416(1), 455(1),** 498(0), **535(2).**

***Parmeosaurus scutatus* + *Paramacellodus* + Scincoidea:** **367(1),** 385(1), **394(0),** 399(1), 570(1), **582(1).**

***Paramacellodus* + Scincoidea:** **95(1), 149(0).**

Scincoidea: **108(1), 123(1),** 138(2), 170(2), 258(3), 345(1), **369(1),** 494(1), 518(1).

Xantusiidae + Cordyliformes: **39(3), 76(2), 99(1), 101(1), 144(0), 161(1),** 167(2), 188(3), **273(1), 301(1), 396(1),** 593(2), 596(1).

***Tepexisaurus tepexii* + Xantusiidae:** **49(3), 62(2),** 267(1), **282(1)*, 283(0), 308(1), 372(2), 375(0), 385(0), 403(1),** 434(2), **531(1), 582(0).**

Xantusiidae: 7(0), 24(1), 25(1), 88(0), 104(1), 108(2), 135(1), 137(1), 141(1), 164(1), **183(1),** 212(2), 213(0), 220(0), 231(1), **240(2),** 245(0), 271(1), **275(3),** 307(1), 328(2), **369(2), 372(3), 374(2), 376(1), 380(1), 392(1), 420(2), 421(2),** 443(1), 447(1), 452(3), 468(0), 508(0), 518(2), 598(1).

***Palaeoxantusia* + *Cricosaura typica* + *Xantusia vigilis*:** **143(2), 244(1), 341(1), 418(1).**

***Cricosaura typica* + *Xantusia vigilis*:** **95(0), 123(0), 155(2),** 185(2), **240(1),** 291(1), 316(0), **324(1), 334(0), 385(1), 403(0), 434(0),** 513(0).

Cordyliformes: **77(1), 97(2), 114(4), 157(1),** 163(2), 383(1), 410(1), **575(1), 578(2).**

Cordylidae: **6(1), 7(2), 78(2), 82(2),** 185(2), **204(1), 208(1), 241(3), 244(1),** 267(1), **369(2), 399(0), 405(1), 406(1),** 470(1), **483(0), 500(0), 501(0),** 508(1), 577(1), **592(1).**

Gerrhosauridae: 37(0), **94(1), 99(2), 325(1), 394(1), 455(4), 573(1),** 577(2), **580(2).**

Carusiidae + Globauridae + Scincidae: **1(0), 67(1), 82(2), 160(1), 275(1).**

Carusiidae: **6(1), 7(2), 23(0), 36(1), 42(1), 62(2), 95(0),** 108(2), **137(1),** 154(0), **399(0).**

Globauridae + Scincidae: 66(1), **67(2), 76(1), 94(1), 97(1), 128(2),** 167(2), 228(2), 388(1), 410(1).

Globauridae: **29(1), 56(2), 108(0), 124(1),** 154(0), 156(1), 369(0), **379(1),** 413(0), 418(1), 419(2), 434(2).

***Hymenosaurus clarki* + *Eoxanta lacertifrons*:** **49(2),** 341(1), 375(1), 421(2).

Scincidae: **18(2), 39(2), 69(1),** 108(2), **157(1), 161(1),** 178(1), **231(1),** 249(2), **278(1),** 452(1), 475(2), 487(1), **513(0),** 518(2), 541(1), **573(1), 575(2), 577(2), 578(2),** 579(2), 580(2), 581(1)*, 601(1)*, 607(0).

***Scincus scincus* + *Brachymeles gracilis* + *Amphiglossus splendidus* + *Acontias percivali* + *Feylinia polylepis* + Lygosominae:** 48(4), **129(1), 240(2),** 375(1), 413(0), **455(3), 461(1), 485(1), 535(2), 593(0).**

***Brachymeles gracilis* + *Amphiglossus splendidus* + *Acontias percivali* + *Feylinia polylepis* + Lygosominae:** **128(3), 144(0), 251(1), 267(1), 283(2).**

***Brachymeles gracilis* + *Amphiglossus splendidus* + *Acontias percivali* + *Feylinia polylepis*:** **90(1), 129(2),** 369(2), 402(1), 418(1), 455(4), **468(0).**

***Brachymeles gracilis* + *Amphiglossus splendidus*:** 39(3), 114(4), **240(2), 384(2), 413(1),** 497(1), 541(0).

***Acontias percivali* + *Feylinia polylepis*:** 23(0), **180(1), 191(1), 192(1), 194(2), 216(1), 231(2), 273(1), 291(1), 311(1), 312(1), 316(0), 324(1),** 328(1), **350(1), 388(0),**

419(2), 420(2), 421(2), 445(0), 446(1), 456(3), 462(1), 463(1), 480(1), 488(1), **505(1), 528(1), 548(1), 572(1), 573(0).**

Lygosominae: 7(0), 36(1), 39(1), 62(2), 67(3), **77(1), 212(2), 249(3), 251(2), 349(1), 372(3), 452(3).**

***Eugongylus rufescens* + *Sphenomorphus solomonis* + *Tiliqua scincoides*:** 185(2), **258(2),** 369(2), **375(0), 461(2), 513(1),** 565(1).

***Sphenomorphus solomonis* + *Tiliqua scincoides*: 18(1), 114(4), 129(2), 231(2), 341(1),** 349(2), **413(1),** 492(1), **542(2).**

Anguimorpha (includes Fossorial forms: *Sineoamphisbaena hexatabularis* + *Anniella pulchra* + Krypteia): 56(2), 58(2), 138(1), 178(1), 182(1), **222(1), 232(1), 234(2), 340(1), 446(1), 461(2), 475(2), 575(1), 577(1),** 579(1), **589(1),** 590(2), **603(1).**

Xenosauridae: 7(2), 24(1), **36(1), 42(1), 101(1), 153(1),** 157(1), **375(3),** 388(1), **498(0), 508(0), 572(3),** 573(1), **610(1).**

***Xenosaurus*: 6(1), 10(2), 11(2),** 39(2), **48(2), 76(10, 82(2), 99(1), 154(0),** 160(1), **162(0), 163(1), 164(1), 165(0), 185(2), 228(1),** 258(3), **267(1),** 371(1), **378(1), 379(1),** 383(1), **385(1), 396(1), 406(1), 439(0),** 470(3).

Anguidae + Varanoidea + Fossorial forms: 39(2), **66(1),** 160(1), 213(1), **360(1),** 428(1), **456(1), 468(0).**

Anguidae: 49(1), 66(2), 77(2), 94(2), **161(1), 170(1), 188(3),** 337(1), **366(1),** 371(1), **378(1), 405(1), 406(1), 410(1), 453(1),** 570(1), 573(1), **576(1)*,** 578(1), **580(1), 582(1).**

Glyptosaurinae: 7(2), 39(4), **62(2), 108(1), 154(0),** 255(0), 338(1), **388(1),** 396(2), **570(2), 571(1).**

Gerrhonotinae + Diploglossinae: 39(4), **228(1), 232(0), 249(1), 258(1),** 368(2), **375(3), 383(2),** 396(2), **434(1),** 511(1), 512(1), 515(1), 531(1).

Pan-Varanoidea + Fossorial forms: 38(1), 129(1), 273(1), 294(1), 328(1), **349(2), 360(0), 375(1), 418(1), 361(3), 375(3), 401(0),** 410(1), 434(2), 573(1), **575(2), 577(2), 578(2),** 579(1).

***Gobiderma pulchrum* + *Estesia mongoliensis* + *Aiolosaurus oriens* + Varanoidea: 29(1),** 48(4), **124(1),** 155(2), **204(1), 214(1),** 255(0), 258(3), **325(1), 357(1),** 358(1), 371(1), **373(1), 376(1),** 379(1), **385(2), 395(1), 401(0),** 412(1), 422(1), **425(1), 426(1),** 427(1), **431(1).**

***Estesia mongoliensis* + *Aiolosaurus oriens* + Varanoidea: 18(2), 20(1),** 24(1), 104(1), **118(1),** 215(0), **280(1),** 349(3), **416(2), 418(2).**

***Aiolosaurus oriens* + Varanoidea: 143(1), 252(1), 281(1), 307(1),** 337(1), 460(1), 470(3), 494(1), 497(1), 590(3).

***Heloderma*: 7(0), 13(1), 24(0), 29(0), 38(2), 39(4), 58(1), 68(1), 118(0),** 129(2), 156(1), 160(0), **168(2), 169(1), 240(1), 241(3),** 250(3), **255(1), 267(1),** 291(1), 328(2), 362(1), 413(0), **421(1), 435(1), 462(1), 488(1), 495(0), 506(1),** 509(2), 521(0), 578(0), **609(1).**

Varanidae: 2(1), **17(1), 19(1), 90(0), 140(1)*, 143(2), 185(2), 313(1), 339(1)*, 348(1),** 362(1), 383(1), 450(1), **453(1),** 464(1)*, 465(1), **475(3), 476(1), 477(2)*,** 483(2), 535(2), 572(1), **573(1), 590(4), 599(1), 602(1), 608(1).**

***Saniwa* + *Varanus*: 10(1), 11(1), 38(2),** 82(1), **140(2)*, 152(1), 222(3), 255(1), 267(1),** 294(0), 328(0), 439(2), 442(0), 444(1), 449(1), 452(4), **460(2),** 463(3), 496(1), 503(0), 507(0), 509(2), 517(1), 518(1), 589(2), 602(4).

***Varanus salvator* + *Varanus exanthematicus*: 25(1),** 208(2), **307(0), 462(1), 463(4), 494(0),** 513(0), **514(1),** 578(1).

Fossorial forms (*Sineoamphisbaena hexatabularis* + *Anniella pulchra* + Krypteia): 56(1), 104(1), **180(1), 191(1), 192(1), 267(1), 307(2), 311(1), 312(2), 333(1), 334(0), 350(1), 575(0), 577(0).**

***Anniella pulchra* + Krypteia: 28(1),** 39(3), **75(1), 90(0), 93(1),** 109(2), **159(1),** 193(1), 250(3), 290(1), 291(1), 316(0), 324(10, 361(3), **419(2),** 421(1), 422(1), 427(1), 442(0), 445(0), 456(3), 459(3), 462(1), 480(1), **488(1),** 499(1), **505(1),** 524(1), **528(1),** 586(1).

Krypteia: 18(1), 24(1), **137(1), 142(1), 182(2), 188(4),** 194(2), **234(0),** 337(1), **348(1),** 379(1), **392(1), 394(0), 456(4), 457(1), 463(2),** 517(1), 549(1), 557(1), 559(1), **572(0),** 579(0).

Amphisbaenia + Dibamidae: 37(1), 39(4), 68(1), **114(4), 222(0), 240(2), 245(0), 258(1), 261(1), 271(1),** 276(1), **311(2), 337(3), 341(1),** 344(1), **350(2), 360(2), 369(1), 399(1),** 414(1)*, 483(3), 493(0), 495(0), **589(0),** 592(2), 595(1), 596(1), 603(0).

Amphisbaenia: 7(2), **22(0), 28(0),** 38(2), **40(1), 56(3),** 128(2), **129(2),** 185(0), **221(1)*,** 232(0), 249(1), **264(1)*, 271(2), 299(3), 316(2),** 320(2)*, **321(2), 340(2), 349(3),** 351(3), **396(1), 414(2)*, 422(0), 445(1),** 470(2), 590(4), 591(1).

Rhineuridae: 2(1), **18(0), 23(3),** 124(1), **142(0),** 143(1), 155(2), 157(1), **161(1), 259(0),** 276(2), 370(1), 372(3), 375(0), **388(1), 394(1), 406(1), 418(2),** 419(1), **572(2).**

***Spathorhynchus fossorium* + *Dyticonastis rensbergeri*: 10(2),** 328(1), **332(2), 379(0),** 410(1).

***Bipes*:** 4(1), **36(1), 38(3), 55(1)*, 99(1), 101(1), 114(3), 212(1),** 215(0), **258(2), 300(1),** 356(1), **370(1),** 380(1), **419(3), 480(0), 484(0),** 486(0), **489(1),** 497(1), **499(1),** 502(0), 518(2), **528(0),** 529(0), 530(1), 533(0), 534(0), 535(2), 542(1), 544(2), 546(0), 547(1), 550(1).

Amphisbaenoidea: **10(2),** 62(1), **102(2), 127(1)*,** 216(1), **275(4), 281(1),** 283(2), 312(1), **318(1),** 367(1), 374(1), **390(1), 396(2), 400(1),** 420(1), **427(0), 446(0),** 449(1), 450(1), 451(1), **463(2), 475(3),** 510(1).

Afrobaenia: 56(4), **369(3), 387(0), 398(2), 404(1),** 457(0), 548(1).

Trogonophidae: 2(1), 4(1), 126(1), **231(2), 276(0),** 278(1), **328(0), 360(0), 367(2),** 380(1), **391(1), 393(0), 423(1), 424(1), 430(1), 447(1),** 470(3), 516(1).

Amphisbaenidae: 21(1), 166(1), **179(0), 222(2), 332(2),** 381(0).

Dibamidae: 8(2), 11(1), **18(2), 23(2), 38(0), 54(1), 93(0), 95(1), 101(1),** 124(1), 129(0), **185(2), 190(1), 216(2),** 249(3), 276(2), 283(2), 297(0), 305(0), **319(1)*, 328(2), 345(1), 352(0), 361(4),** 367(1), **369(2),** 372(3), 374(1), 380(1), **384(2), 385(1), 391(1), 459(2), 463(0),** 470(1), **590(0), 593(3).**

***Najash rionegrina* + *Dinilysia patagonica* + Serpentes: 96(1), 168(2), 182(3), 296(0), 299(1), 300(1), 321(1), 328(0), 332(1),** 340(0), 356(1), **361(2),** 465(1), **468(3),** 470(3), 512(1).

***Dinilysia patagonica* + Serpentes:** 9(1), 20(1), 21(1), 32(1)*, 51(1), 57(2), 71(3), 84(3), 115(1), 119(1), 120(2), 128(2), 129(0), 133(1), 135(2), 141(1), 256(1), 268(1), 273(0), **302(1),** 320(1)*, **353(1),** 358(1), 359(1), 373(1), 376(1), 382(1), 385(2), 415(1), 418(0).

Serpentes: 8(1), 38(2), **40(1),** 47(2), **53(1)*,** 62(1), **101(1), 106(1),** 113(0), **166(1),** 195(1), 201(0), 204(2), 211(1), 215(0), 217(2), 220(2), **241(4),** 258(3), **275(0),** 283(2), 297(0), 305(0), **310(1)*,** 331(1)*, **332(2),** 346(2)*, 355(1)*, 390(1), 419(2), 457(3), **461(3),** 488(2), 550(1), 589(2), 590(4), 599(1), 602(4).

Scolecophidia: 39(4), **60(1), 93(0), 198(1),** 213(0), **248(1), 300(0),** 344(1), **420(1),** 457(4).

Leptotyphlophidae + Typhlopidae: 13(1), **16(1), 51(0),** 68(1), **185(4),** 236(1)*, **270(1)*, 298(1)*, 299(0),** 431(1), 439(2).

Anomalepididae: 7(2), **14(1),** 17(1), 31(1), 84(4), 101(2), **119(3), 129(2), 135(3),** 185(0), 192(0), 197(2)*, 208(3), 247(1), 276(2), 277(1), 289(1), **296(1), 303(1)*,** 328(1), 374(1), 390(0), 458(1), 587(0).

Alethinophidia: 11(1), **12(1), 41(1), 45(1), 57(3), 106(2), 119(2),** 185(0), **206(1), 207(1), 208(1), 219(1), 224(1)*, 242(1), 323(1)*, 351(2),** 357(1), **361(1),** 371(1), **387(0), 389(1),** 390(0), **392(2), 393(0), 397(1), 400(1),** 426(1), **429(1).**

***Anomochilus leonardi* + Cylindrophiidae + Macrostomata: 2(1), 7(0),** 47(1), **188(2), 396(2), 416(2).**

Cylindrophiidae + Macrostomata: 72(1)*, 120(3), **166(0), 188(1), 198(1), 234(3), 242(2), 255(0), 267(0), 279(1), 326(1), 398(1),** 413(0), **415(2), 421(2),** 431(1).

Cylindrophiidae: 101(0), 118(1), **208(3), 356(0), 404(1),** 457(4), **610(1).**

Macrostomata: 18(2), 45(2), **115(2), 170(3), 174(1), 185(2),** 188(0), **194(3), 203(1), 208(0), 210(1), 224(2)*, 247(1), 248(1), 256(2), 260(1), 265(1), 268(2), 274(1)*,** 276(1), 277(1), **299(2), 300(2), 324(2), 337(0), 351(0), 387(2), 420(3),** 423(1), 433(1), 476(1).

***Xenopeltis unicolor* + *Loxocemus bicolor*: 184(1),** 288(1), **289(1),** 325(1), **419(1),** 457(4).

Bolyeriidae + Simoliophiidae + Henophidia: 57(2), 84(4), **106(1), 179(0), 263(1),** 315(0), 392(1), **416(3).**

Bolyeriidae: 8(0), 45(3), 125(1)*, 343(1), 510(1), 516(1), 520(1), 548(1).

Simoliophiidae + Henophidia: 185(4), 191(0), **239(1), 287(1), 404(1).**

Simoliophiidae: 10(1), 101(0), 106(0), **115(1),** 118(1), **265(0), 387(1), 457(2), 463(3), 469(1).**

***Eupodophis descouensi* + *Pachyrhachis problematicus*: 86(1), 279(0).**

Henophidia: 12(2), 15(1), **33(1),** 47(2), **184(1),** 189(1), 213(0), **327(1), 363(1),** 457(4).

Ungaliophiinae + Erycinae: 45(3), 60(1), 210(0), 276(0), 322(1), 610(1).

Ungaliophiinae: 2(0), 12(3), 34(1), **41(0), 84(2),** 325(1), **344(1), 389(2), 416(0).**

Erycinae: 277(0), 279(0), 387(0), 438(1), **473(1).**

***Calabaria reinhardtii* + *Lichanura trivirgata*: 16(1), 92(1), 185(3), 189(0),** 325(1), **396(2), 458(2).**

Booidea + Tropidophiidae + Caenophidia: 34(2), **86(1),** 106(0), **263(2), 343(1).**

Booidea: 132(3), 302(2), 315(1), 332(1), **387(0),** 438(1), **458(2).**

Boidae: 8(0), 33(2), **46(1), 100(1), 243(1), 253(1), 322(1), 330(1),** 610(1).

Pythonidae: 12(1), 15(0), 34(1), **47(1),** 74(1), 96(2), **141(2),** 238(0), 248(2), 288(2), **289(1), 321(3), 329(1), 574(1).**

Tropidophiidae + Caenophidia: 12(3), 33(2), 74(1), **91(1),** 96(2), **101(2), 121(1)*,** 189(2), 288(1), **363(2), 389(2), 398(3), 404(0), 466(1).**

Tropidophiidae: 41(0), 51(2), 92(1), 120(1), 208(3), 210(0), 219(0), 223(1), 235(1)*, 248(0), **279(0),** 287(0), **321(3),** 325(1), **337(1), 415(1),** 421(3), 610(1).

Caenophidia: 19(1), 34(3), **45(3), 60(1), 141(2), 171(1), 203(2), 218(1), 220(3),** 238(0), **260(2), 276(2),** 288(2), **326(0), 327(0),** 344(1), **386(1),** 440(0), **510(1), 516(1), 520(1), 548(1).**

Acrochordus granulatus + Colubroidea: 28(0), 84(3), 134(1), 189(3), 207(0), 217(3), 239(0), 287(0), 325(1).

Colubroidea: 8(0), 12(4), 15(0), **61(2), 74(0), 86(0),** 131(1), 184(2), 213(1), **223(1),** 289(1), **382(2), 420(2),** 606(3)*.

Pareas hamptoni + _Lycophidion capense_ + Atractaspididae: 18(1), 46(0), 84(2), **466(0).**

Lycophidion capense + Atractaspididae: 47(1), 106(1), 115(3), 224(3)*, 279(0), 315(1), 372(2).

Atractaspididae: 33(0), 34(0), 93(0), 168(1), **191(1), 238(1), 337(1), 435(1).**

Viperidae + Elapidae + Colubridae: 39(2), 44(1), 47(3), 133(2), 238(1), 372(3), 457(3).

Viperidae + Elapidae + _Notechis scutatus_: 34(2), 96(1), 253(1), 384(0), 417(1), 433(0), **435(2).**

Viperidae: 93(0), **119(4), 260(1), 273(1), 372(2), 404(1),** 420(1).

Azemiops feae + _Daboia russelli_ + Crotalinae: 7(1), 15(1), 44(1), 243(1), 279(0), 315(1).

Daboia russelli + Crotalinae: 51(2), **52(1),** 57(1), 61(1), 84(2), **326(2),** 327(3), **343(2), 357(0), 610(1).**

Crotalinae: 35(1), **84(2), 238(0),** 248(2), **463(2).**

Bothrops asper + _Lachesis muta_: 41(0), 46(2), **47(2), 356(0), 457(4), 458(1).**

Naja naja + _Micrurus fulvius_ + _Laticauda colubrina_: 132(2), 276(1), **279(0),** 398(1), 420(1), **457(4), 458(1),** 463(2).

Micrurus fulvius + _Laticauda colubrina_: 44(0), 47(1), 60(0), 91(0), 106(1), 132(3), 184(1), 189(2), 224(4)*, 277(0), 324(1), 325(0), 341(1), 433(1), 458(2).

Colubridae: 41(2), 51(2), 172(1), **203(3),** 223(1), **269(1), 321(3), 329(1),** 416(4), 463(2).

Natricinae: 27(1)*, 84(2), **277(2), 287(1),** 326(1), **327(2), 417(2), 420(3),** 421(3), 433(0).

Afronatrix anoscopus + _Amphiesma stolata_ + _Thamnophis marcianus_ + _Xenocrophis piscator_: 438(1), 457(2).

Afronatrix anoscopus + _Amphiesma stolata_: 227(1)*.

Thamnophis marcianus + _Xenocrophis piscator_: 337(1), 341(1).

Colubrinae: 34(2), **57(4), 315(1), 466(0).**

Appendix 5:
Sources for State Assignments for Characters from the Literature

Characters 608 and 609

Jullien and Renous-Lécuru (1972): *Sphenodon punctatus, Physignathus cocincinus, Brachylophus fasciatus, Chalarodon madagascariensis, Crotaphytus collaris, Dipsosaurus dorsalis, Enyalioides laticeps, Morunasaurus annularis, Phymaturus palluma, Plica plica, Polychrus marmoratus, Sauromalus ater, Uma scoparia, Uranoscodon superciliosus, Urostrophus vautieri, Leiolepis belliana, Gecko gekko, Gonatodes albogularis, Eublepharis macularius, Lepidophyma flavimaculatum, Xantusia vigilis, Scincus scincus, Tiliqua scincoides, Lacerta viridis, Takydromus ocellatus, Callopistes maculatus, Pholidobolus montium, Teius teyou, Tupinambis teguixin, Elgaria multicarinata, Xenosaurus grandis, Heloderma horridum, Heloderma suspectum, Varanus exanthematicus, Lanthanotus borneensis.*

Etheridge and de Queiroz (1988): *Basiliscus, Corytophanes cristatus, Gambelia wislizenii, Morunasaurus annularis, Brachylophus fasciatus, Leiosaurus, Pristidactylus torquatus, Liolaemus, Oplurus cyclurus, Petrosaurus mearnsi, Phrynosoma platyrhinos, Uta stansburiana, Anolis carolinensis, Leiocephalus.*

Estes et al. (1988): *Bipes biporus.*

Character 610

Sphenodon punctatus (Packard et al. 1988); *Agama agama* (Daniel 1960); *Calotes emma* (Manthey and Schuster 1996); *Physignathus cocincinus* (Blake 1982); *Pogona vitticeps* (Johnson 2006); *Brookesia brygooi* (Nečas and Schmidt 2004); *Chamaeleo laevigatus* (Spawls et al. 2002); *Basiliscus basiliscus* (Rogner 1997); *Corytophanes cristatus* (Ream 1965); *Crotaphytus collaris* (Stebbins 2003); *Gambelia wislizenii* (Stebbins 2003); *Enyalioides laticeps* (Duellman 1978); *Brachylophus fasciatus* (Stacy et al. 2008); *Dipsosaurus dorsalis* (Muth 1980); *Sauromalus ater* (Stebbins 2003); *Leiolepis belliana* (Rogner 1997); *Uromastyx aegyptius* (Wilms 2005); *Pristidactylus torquatus* (Fitch 1970); *Urostrophus vautieri* (Rand 1982); *Liolaemus bellii* (Naya et al. 2008); *Phymaturus palluma* (Rogner 1997); *Chalarodon madagascariensis* (Blanc 1971); *Oplurus cyclurus* (Glaw and Vences 1994); *Petrosaurus mearnsi* (Stebbins 2003); *Phrynosoma platyrhinos* (Stebbins 2003); *Sceloporus variabilis* (Benabib 1994); *Uma* *scoparia* (Stebbins 2003); *Uta stansburiana* (Stebbins 2003); *Anolis carolinensis* (Hamlett 1952); *Polychrus marmoratus* (Rand 1982); *Leiocephalus barahonensis* (Schwartz and Henderson 1991); *Plica plica* (Vitt 1991); *Stenocercus guentheri* (Torres-Carvajal 2007); *Uranoscodon superciliosus* (Howland et al. 1990); *Ophisaurus apodus* (Rogner 1997); *Anniella pulchra* (Stebbins 2003); *Celestus enneagrammus* (Greene et al. 2006); *Elgaria multicarinata* (Stebbins 2003); *Cordylus mossambicus* (Branch 1998); *Platysaurus imperator* (Gray-Lovich 2005); *Dibamus novaeguineae* (Greer 1985a); *Aeluroscalabotes felinus* (Inger and Greenberg 1966); *Coleonyx variegatus* (Stebbins 2003); *Eublepharis macularius* (Rogner 1997); *Diplodactylus ciliaris* (Rogner 1997); *Saltuarius (Phyllurus) cornutus* (Rogner 1997); *Rhacodactylus auriculatus* (Rogner 1997); *Teratoscincus przewalskii* (Semenov and Borkin 1992); *Gekko gecko* (Rogner 1997); *Phelsuma lineata* (Glaw and Vences 1994); *Gonatodes albogularis* (Rogner 1997); *Cordylosaurus subtesselatus* (Branch 1998); *Zonosaurus ornatus* (Rogner 1997); *Pholidobolus montium* (Montanucci 1973); *Heloderma horridum* (Pianka et al. 2004); *Heloderma suspectum* (Stebbins 2003); *Lacerta viridis* (Arnold and Ovenden 2002); *Takydromus ocellatus* (Rogner 1997); *Delma borea* (Greer 1989); *Lialis burtonis* (Greer 1989); *Acontias percivali* (Branch 1998); *Eugongylus rufescens* (Greer 1989); *Plestiodon (Eumeces) fasciatus* (Tinkle et al. 1970); *Trachylepis (Mabuya) quinquetaeniata* (Branch 1998); *Scincus scincus* (Schleich et al. 1996); *Tiliqua scincoides* (Longley 1939); *Shinisaurus crocodilurus* (Kudryavtsev and Vassilyev 1998); *Aspidoscelis tigris* (Stebbins 2003); *Teius teyou* (Cruz et al. 1999); *Tupinambis teguixin* (Rogner 1997); *Lanthanotus borneensis* (Pianka et al. 2004); *Varanus acanthurus* (Pianka et al. 2004); *Varanus exanthematicus* (Spawls et al. 2002); *Varanus salvator* (Pianka et al. 2004); *Cricosaura typica* (Fong et al. 1999); *Lepidophyma flavimaculatum* (Savage 2002); *Xantusia vigilis* (Stebbins 2003); *Xenosaurus grandis* (Smith et al. 2000); *Xenosaurus platyceps* (Ballinger et al. 2000); *Amphisbaena fuliginosa* (Andrade et al. 2006); *Geocalamus acutus* (Spawls et al. 2002); *Bipes biporus* (Andrade et al. 2006); *Bipes canaliculatus* (Andrade et al. 2006); *Rhineura floridana* (Andrade et al. 2006); *Diplometopon zarudnyi* (Radaini 2007); *Trogonophis wiegmanni* (Andrade et al. 2006); *Acrochordus granulatus* (Voris and Glodek 1980); *Anilius scytale* (Cisneros-Heredia 2005); *Anomochilus leonardi* (Greene 1997); *Aparallactus werneri* (Alexander and Marais 2007); *Atractaspis irregularis* (Spawls et al. 2002); *Casarea dussumieri* (Bloxam and Tonge, 1986); *Boa constrictor* (O'Shea 2007); *Calabaria reinhardtii* (O'Shea 2007); *Epicrates striatus* (O'Shea 2007); *Eryx colubrinus* (Spawls et al. 2002); *Lichanura trivirgata* (Stebbins 2003); *Afronatrix anoscopus* (Luiselli and Akani 2002); *Amphiesma stolata* (Fitch 1970); *Coluber constrictor* (Stebbins 2003); *Lampropeltis getulus* (Stebbins 2003); *Lycophidion capense* (Branch 1998); *Natrix natrix* (Isaac 2003); *Pareas hamptoni* (J.C. Murphy and H.K. Voris, pers. comm., 2009); *Thamnophis marcianus* (Stebbins 2003*);* *Xenochrophis piscator* (Ji et al. 2001); *Xenodermus javanicus* (Smith 1943); *Cylindrophis ruffus* (Mehrtens 1987); *Laticauda colubrina* (Shetty and Shine 2002); *Micrurus fulvius* (Campbell 1973); *Naja naja* (Mehrtens 1987); *Notechis scutatus* (Mehrtens 1987); *Leptotyphlops dulcis* (Stebbins 2003); *Loxocemus bicolor* (Savage 2002); *Aspidites melanocephalus* (O'Shea 2007); *Python molurus* (O'Shea 2007); *Trachyboa boulengeri* (Lehmann 1970); *Tropidophis haetiana* (O'Shea 2007); *Exiliboa placata* (O'Shea 2007); *Ungaliophis continentalis* (O'Shea 2007); *Typhlops jamaicensis* (Schwartz and Henderson 1991); *Uropeltis melanogaster* (J.C. Murphy and H.K. Voris, pers. comm., 2009); *Agkistrodon contortrix* (Mehrtens 1987); *Azemiops feae* (Mehrtens 1987); *Bothrops asper* (Savage 2002); *Causus rhombeatus* (Branch 1998); *Daboia russelli* (Mehrtens 1987); *Lachesis muta* (Savage 2002); *Xenopeltis unicolor* (Mehrtens 1987).