PHYLOGENY AND SYSTEMATICS OF SQUAMATA (REPTILIA) BASED ON MORPHOLOGY
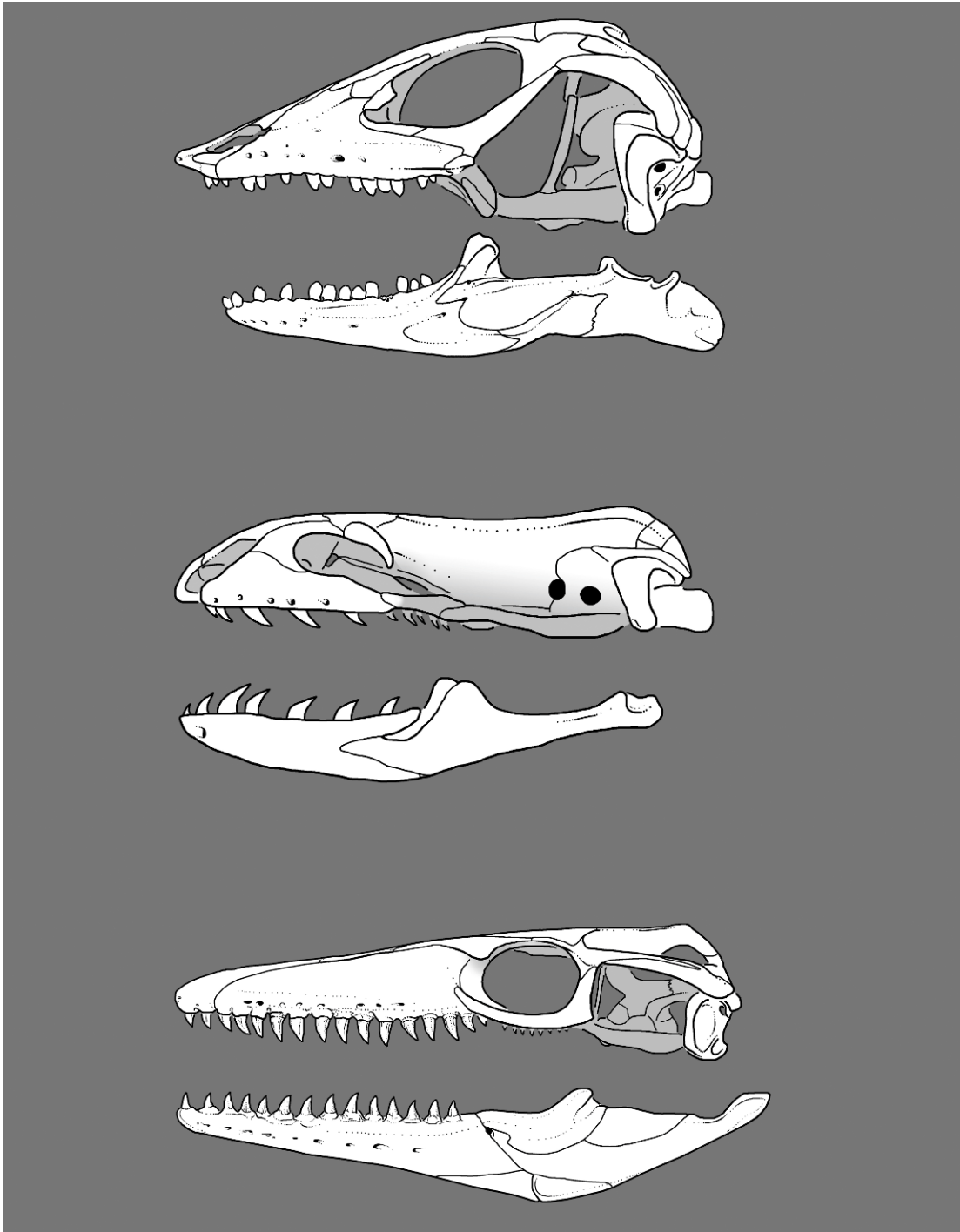
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Skulls of three squamates suggested as close to the origins of snakes: *Scincus scincus* (Scincomorpha) (top); *Cylindrophis ruffus* (Serpentes) (middle); *Mosasaurus hoffmanni* (Anguimorpha) (bottom).

CONTENTS

ABSTRACT

Squamata (amphisbaenians, "lizards", mosasaurs, and snakes) is an extremely diverse clade with a rich fossil record. There is little consensus about the interrelationships of the major squamate clades (i.e., Iguania, Gekkota, Scincomorpha, Anguimorpha, Amphisbaenia, and Serpentes), or even the membership of some of these clades. Morphology-based cladistic analyses typically agree only that the major dichotomy in extant squamates is between Iguania and all other taxa. The phylogenetic placement of Amphisbaenia and Serpentes is particularly problematic. Incomplete taxon sampling is likely a major contributing factor to the absence of a consensus about squamate interrelationships. This study examines squamate relationships using 222 ingroup taxa scored for 363 morphological characters. Analysis of these data recovered 2,213 equally short trees with a length of 3,273 steps and a retention index of 0.7164. The results confirm the monophyly of the clades Scleroglossa (extant squamates exclusive of Iguania), Gekkota, Scincomorpha, Lacertoidea, Scincoidea, Anguimorpha, Carusioidea, Platynota, and Varanoidea. Novel results include the identification of a clade containing Scincidae sensu lato, Dibamidae, Amphisbaenia, and Serpentes; identification of a Mesozoic clade containing *Bainguis*, *Eoxanta lacertifrons*, *Globaura venusta*, and *Myrmecodaptria*; and identification of *Dalinghosaurus* as a basal shinisaur. A new taxonomic scheme is outlined. The names Iguanomorpha, Scincogekkonomorpha, Evansauria, and Mosasauriformes are applied to the stem-based groups including Iguania, Scleroglossa, Autarchoglossa, and Mosasauria, respectively. The importance of strict rigidity within taxonomy is questioned; taxonomy is most useful as a tool for communication about organisms or groups of organisms.

INTRODUCTION

SUBJECT MATTER AND GOALS

Squamata (amphisbaenians, "lizards", mosasaurs, and snakes) represents a morphologically and ecologically diverse clade with a rich fossil record. The smallest known squamates are no more than 18 mm in snout-to-vent length (Hedges and Thomas, 2001) and the largest known fossil form probably exceeded 17 m in total length (Lingham-Soliar, 1995). Squamates are very speciose in extant faunas with approximately 8,000 species spreading to every country except Iceland (Bauer, 2003; Gans, 2003; Shine, 2003; Uetz, 2007). Moreover, the diversity of form throughout the last 160 million years of known squamate history rivals that of mammals. Different squamates have become adapted for fossoriality, terrestriality, arboreality, and for the near-shore, open-water, and reef marine environments (see Lingham-Soliar, 1992b, 1995, 1999b; Caldwell, 1996, 2000; Caldwell and Lee, 1997, 2004; Caldwell and Cooper, 1999; Lee et al., 1999b; Kley, 2000, 2001, 2006; Caldwell and Albino, 2001; Lee and Scanlon, 2002b; Voris and Murphy, 2002; Bauer, 2003; Gans, 2003; Kearney, 2003a; Shine, 2003; Alfaro et al., 2004; Kearney et al., 2005; Uetz, 2007). Such diversity in morphology, biogeography, and ecology paired with a relatively deep fossil record and numerous extant taxa makes Squamata an extremely attractive group for evolutionary studies. Unfortunately, there is currently no clear picture of squamate phylogenetic relationships. This problem is due, in part, to incomplete sampling of squamates in recent phylogenetic analyses. Incomplete morphological documentation of some problematic taxa is also a major problem. A few landmark works have looked at squamates in fantastic detail (e.g., Parker, 1878, 1879; Bellairs, 1949; Oelrich, 1956; Jollie, 1960) and recent application of high-resolution x-ray tomography has helped to demystify problematic taxa and otherwise hidden morphology (see the recent work on the braincase of *Shinisaurus crocodilurus* by Bever et al., 2005a and of the cranial anatomy of *Rhineura hatcheri* by Kearney et al., 2005, for example).

Many extant and fossil taxa are problematic for understanding squamate evolution because they are poorly known morphologically, because they possess no fossil record, and/or because they possess a combination of character states making their referral difficult. Dibamidae, a clade of bizarre fossorial squamates, is one example of such a taxon. That is, Dibamidae is a well-described extant clade whose affinities are in nearly constant flux.

This paper presents a phylogenetic analysis of the squamate groups and offers a new taxonomic scheme. Although future discoveries and incorporation of new evidence will offer variations in parts of the tree, the current study is based on the most extensive morphological data matrix currently available. Broad taxonomic sampling in this analysis is one way to analyze the phylogenetic positions of some particularly problematic taxa (e.g., necrosaurs, snakes, amphisbaenians); that is, to avoid constraining those problematic taxa within or outside of their historical placements.

Taxonomy is a tool for communication about groups of things (organisms, in this case). To this end, I find that taxonomy is most effective when names remain meaningful between phylogenetic hypotheses, even if there are some differences in group membership. Empirical studies always offer the possibility of changes (radical or trivial) in broader scale relationships, and a given taxonomic scheme remains useful only if it is flexible enough to accommodate these changes while maintaining continuity of meaning (see Rieppel, 2005, 2006). Utility is a worthy prize for which rigid structure may be sacrificed. This is especially true in something so subjective (and semantic) as taxonomy. Having said that, I do employ taxon name definitions below with the hope that they will be employed—so long as the terminology remains useful. Thus, the taxonomic scheme accompanying my squamate phylogenetic hypothesis is designed to be useful even in the face of some topological changes to the tree. It is constructed to be useful for neontologists (e.g., herpetologists) and paleontologists alike, and to remain relatively consistent with the current taxonomic usage of both those groups of scientists.

My three overarching aims for this study are:

1. Produce a morphological phylogenetic data matrix for the major squamate groups, more exclusive groups with problematic history, and numerous fossils of debated history.
2. Produce a phylogenetic hypothesis of squamate relationships based on this morphological data matrix.

3. Offer a revised taxonomy taking into consideration previous studies and problematic areas in the current topology, and stabilize existing names that lack clear or precise definitions.

HISTORICAL ANALYSES

History provides a useful frame on which to rest new ideas. Because Squamata is a conspicuous extant clade, it has been the focus of numerous phylogenetic studies and taxonomic treatments over the past 13 decades or so. Some of the more inclusive and influential ones are reviewed here.

PRECLADISTIC STUDIES: Wallace (1876a, 1876b) provides an early comprehensive view of "family"-level squamate systematics, identifying 27 lizard "families" (his Lacertilia) and 24 snake "families". Importantly, many of these groups are retained in modern systematic treatments, although often with some modifications of membership.

Squamate systematics were extensively analyzed by two papers appearing just at the turn of the last century (Cope, 1900; Fürbringer, 1900a), but the real landmark paper is that of Camp (1923). Using extant taxa and numerous fossil groups, Camp constructed a branching diagram (a "skiogram") (Camp, 1923: 333) that has been compared to a cladogram (Moody, 1985), identifying several groups that are still supported in modern analyses (fig. 1). That diagram illustrates iguanians branching off from the rest of squamates first, followed by a dichotomy between Gekkota and Autarchoglossa (containing Scincomorpha and Anguimorpha) (Camp, 1923). Romer (1956, 1966), Estes (1983), and Carroll (1988a, 1988b suggested three similar taxonomic schemes for squamates containing several "infraorders". Carroll's (1988a, 1988ba) incarnation of this scheme is seen in table 1. This system largely corresponds to that in the popular literature (e.g., Whitfield, 1982), and web resources such as the TIGR Reptile Database (Uetz, 2007) and Animal Diversity Web (Myers, 2001). Herpetologists usually employ similar schemes (see, for example, Behler and King, 1979, Kent and Miller, 1997, and Pough et al., 2005).

ESTES ET AL., 1988: Camp's (1923) systematic scheme as modified by later authors
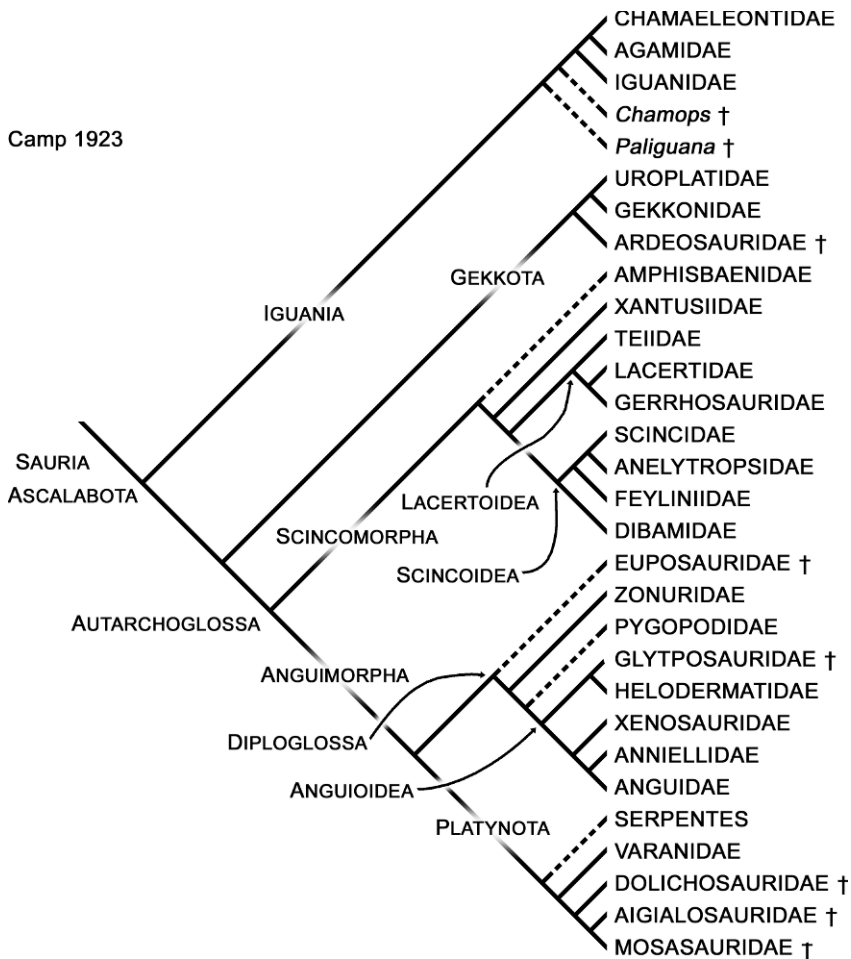
Fig. 1.   Camp's ''skiogram''; the evolutionary history of squamates as envisioned by Camp (1923), often heralded as the first approximation of a cladogram. Some higher level taxon names (e.g., Rhiptoglossa, Xantusioidea) have been omitted. Note that much of the taxonomy employed here is still used in modern phylogenetic taxonomy. Fossil taxa denoted by daggers (†).

(Romer, 1949, 1956; Carroll, 1988a, 1988ba) remained the mainstay of lizard interrelationships until the widespread use of cladistics over the last two decades. The new standard for squamate relationships is that of Estes et al. (1988). Like Camp (1923), this analysis identified Gekkota as the sister-taxon to the Autarchoglossa, with Iguania representing the most basal extant squamate lineage. The most often cited diagram from Estes et al. (1988: fig. 6) (fig. 2A) was not a consensus cladogram of relationships, but rather, as Estes et al. state, a preferred ''conservative'' hypothesis of interrelation-

ships (Estes et al., 1988:140). The Estes et al. (1988) data set actually supports a somewhat different phylogenetic topology in which an amphisbaenian-dibamid-snake clade is the sister group to Scleroglossa (fig. 2B).

Estes et al. (1988) did not use fossil taxa as part of the ingroup in their analysis. Despite this, Estes et al. (1988) remains an extremely important study used as the basis of recent morphology-based cladistic analyses, including this one.

Eight additional morphology-based analyses (Wu et al., 1996; Evans and Barbadillo, 1998, 1999; Lee, 1998; Caldwell, 1999a; Lee

TABLE 1
The Taxonomic Scheme of Carroll (1988a)

Superorder: Lepidosauria
  Order: Sphenodontida
  Order: Squamata
    Suborder: Lacertilia
      Infraorder: Eolacertilia
        Family: Paliguanidae
        Family: Kuehneosauridae
        Family: Fulengidae

Infraorder: Iguania
        Family: Euposauridae
        Family: Arretosauridae
        Family: Iguanidae
        Family: Agamidae
        Family: Chameleontidae

Infraorder: Nyctisauria (Gekkota)
        Family: Ardeosauridae
        Family: Bavarisauridae
        Family: Gekkonidae
        Family: Pygopodidae

Infraorder: Leptoglossa (Scincomorpha)
        Family: Paramacellodidae
        Family: Xantusiidae
        Family: Teiidae
        Family: Scincidae
        Family: Lacertidae
        Family: Cordylidae (incl. Gerrhosauridae, Zonuridae)
        Family: Dibamidae

Infraorder: Annulata
        Family: Olidogodontosauridae
        Family: Amphisbaenidae
        Family: Rhineuridae
        Family: Hyporhinidae
        Family: Bipedidae
        Family: Trogonophidae

Infraorder: Diploglossa (Anguimorpha)
        Family: Paravaranidae
        Family: Bainguidae
      Superfamily: Anguioidea
        Family: Anguidae
        Family: Anniellidae
        Family: Xenosauridae
        Family: Dorsetisauridae
      Superfamily: Varanoidea (Platynota)
        Family: Necrosauridae
        Family: Helodermatidae
        Family: Varanidae
        Family: Lanthanotidae
        Family: Aigialosauridae
        Family: Dolichosauridae
        Family: Mosasauridae

TABLE 1
(*Continued*)

Suborder: Serpentes
    Infraorder: Scolecophidia
        Family: Typhlopidae
        Family: Leptotyphlopidae

Infraorder: Henophidia
      Superfamily: Simoliopheoidea
        Family: Lapparentopheidae
        Family: Simoliopheidae
      Superfamily: Anilioidea
        Family: Aniliidae
        Family: Uropeltidae
      Superfamily: Booidea
        Family: Dinilysiidae
        Family: Xenopeltidae
        Family: Boidae
        Family: ?Palaeophidae
      Superfamily: Acrochordoidea
        Family: Acrochordidae
        Family: Nigeropheidae

Infraorder: Caenophidia
      Superfamily: Colubroidea
        Family: Anomalopheidae
        Family: Russellopheidae
        Family: Elapidae
        Family: Viperidae

and Caldwell, 2000; Evans et al., 2005; Evans and Wang, 2005) that have addressed a broad range of squamate taxa and included significant fossil data are reviewed here and used for comparisons below. All of these analyses have drawn from the character list presented in Estes et al. (1988). Lee (1998) and Lee and Caldwell (2000) are essentially one analysis with the latter study including a few additional fossil taxa. Evans and Barbadillo (1998, 1999) are literally the same analysis with similar findings, except that the Evans and Barbadillo (1999) analysis included the fossil taxon *Hoyalacerta sanzi*. Evans et al. (2005) and Evans and Wang (2005) updated this analysis with broader taxon sampling and recovered a different hypothesis. Finally, I will also review two recent molecular analyses (Townsend et al., 2004; Vidal and Hedges, 2005) that turn the morphological trees on their collective (figurative) heads.

Wu et al. (1996) citing problems with unscoreable characters (''missing data'' of
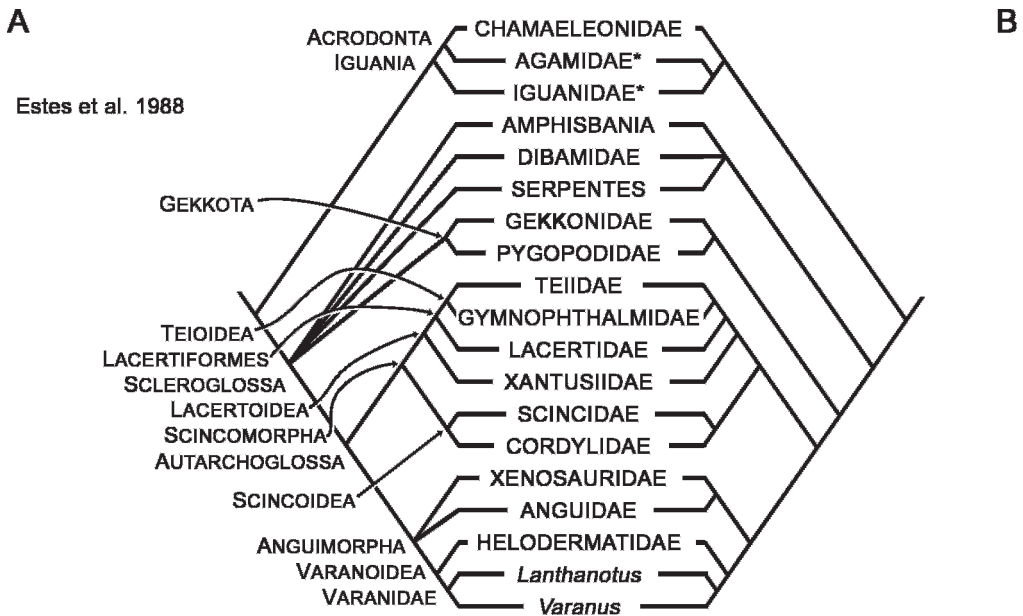
Fig. 2.   Hypotheses of squamate interrelationships, based on morphology, as presented by Estes et al. (1988) and separately derived from their data. The cladogram on the left represents the "conservative cladogram of squamate relationships" as reported by Estes et al. (1988: 140, fig. 6). The right side shows the relationships recovered when the Estes et al. (1988) data matrix is run in PAUP* (Swofford, 2001) using a heuristic search (parsimony) and TNT (Goloboff et al., 2003) using the traditional search.

their usage, see Kearney and Clark, 2003), modified the analysis of Estes et al. (1988) by excluding non-osteological characters, adding 22 new characters, and including the fossil taxa *Adamisaurus magnidentatus*, *Eoxanta lacertifrons*, *Globaura venusta*, Macrocephalosauridae (=Gilmoreteiidae; Langer, 1998), Polyglyphanodontidae, *Sineoamphisbaena hexatabularis*, and *Slavoia darevskii*. Their most inclusive analysis (for taxa and characters) yielded 28 shortest trees. They found *Sineoamphisbaena hexatabularis* to be the sister-group to their terminal group "other amphisbaenians" and suggested placement of the Xantusiidae with Scincoidea (sensu Estes et al., 1988) (fig. 3).

Evans and Barbadillo (1998) included the major groups used by Estes et al. (1988), but added the fossil taxa *Ardeosaurus* (unspecified species inclusion), *Bavarisaurus macrodactylus* (=*Homoesaurus macrodactylus* of Wagner, 1852), *Eichstaettisaurus schroederi*, *Meyasaurus diazromerali*, *Paramacellodus* (presumably including taxa from several localities, including those described in

Prothero and Estes, 1980; Broschinski and Sigogneau-Russell, 1996; Evans and Barbadillo, 1998; Evans and Chure, 1998a; Averianov and Skutchas, 1999), and *Scandensia ciervensis* to the analysis. Additionally, they not only included Rhynchocephalia, Kuehneosauridae, and a "paliguanid" (*Saurosternon*) as outgroups, but also the relatively recently described *Marmoretta* (these outgroups omitted from fig. 4). Characters from this analysis were taken from both Estes et al. (1988) and Gauthier et al. (1988a) with one novel character included, though many of the character states were reported as "parsimony uninformative" (Evans and Barbadillo, 1998). The analysis recovered six most parsimonious trees. A strict consensus leaves only the relative positions of *Eichstaettisaurus* and *Scandensia ciervensis* unresolved with respect to more nested squamates (fig. 4). The results showed that *Ardeosaurus*, *Bavarisaurus*, and *Eichstaettisaurus* constitute basal members of Squamata. Additionally, Evans and Barbadillo (1998) retrieved the novel position. A contemporary study (Lee,

Fig. 3. Hypothesis of squamate interrelationships, based on morphology, as presented by Wu et al. (1996). Fossil taxa denoted by daggers (†).

1998; see below) found dibamids and amphisbaenians to be close to Gekkota, and snakes as falling within Anguimorpha. A subsequent analysis (Evans and Barbadillo, 1999) included the taxon *Hoyalacerta sanzi* and resulted in three shortest trees. The variation between these trees occurred only between the relative placements of *Hoyalacerta sanzi* and *Eichstaettisaurus* with respect to each other, *Ardeosaurus*, and Iguania (fig. 5). The rest of the tree was consistent with the earlier study (Evans and Barbadillo, 1998).

Lee (1998) and Lee and Caldwell (2000) analyzed very similar data sets with the latter subdividing some of the taxa included in the former (Xenosauridae, Mosasauroidea, Gekkonidae, and Agamidae) and adding four additional fossil taxa (*Adriosaurus*, *Aphanizocnemus*, *Dolichosaurus longicollis*, and *Pa-*

chyophis woodwardi). Both character lists draw heavily from Estes et al. (1988), but with additions and modifications. Unlike Evans and Barbadillo (1998), these analyses include numerous limbless terminal taxa and aquatic fossil forms. The Lee (1998) analysis found two most parsimonious trees with the only unresolved node occurring between Scincidae, Cordyliformes (Cordylidae of his usage), and Anguimorpha (fig. 6). Lee and Caldwell (2000) produced 12 most parsimonious trees with the same polytomy as in Lee (1998), and another between Dolichosauridae, *Aphanizocnemus*, and a clade including *Adriosaurus* and snakes (fig. 7). Both analyses fail to retrieve a monophyletic Scincomorpha, place amphisbaenians, dibamids, and xantusiids near Gekkota, and hypothesize that snakes are derived from the mosasaurid-varanid clade.
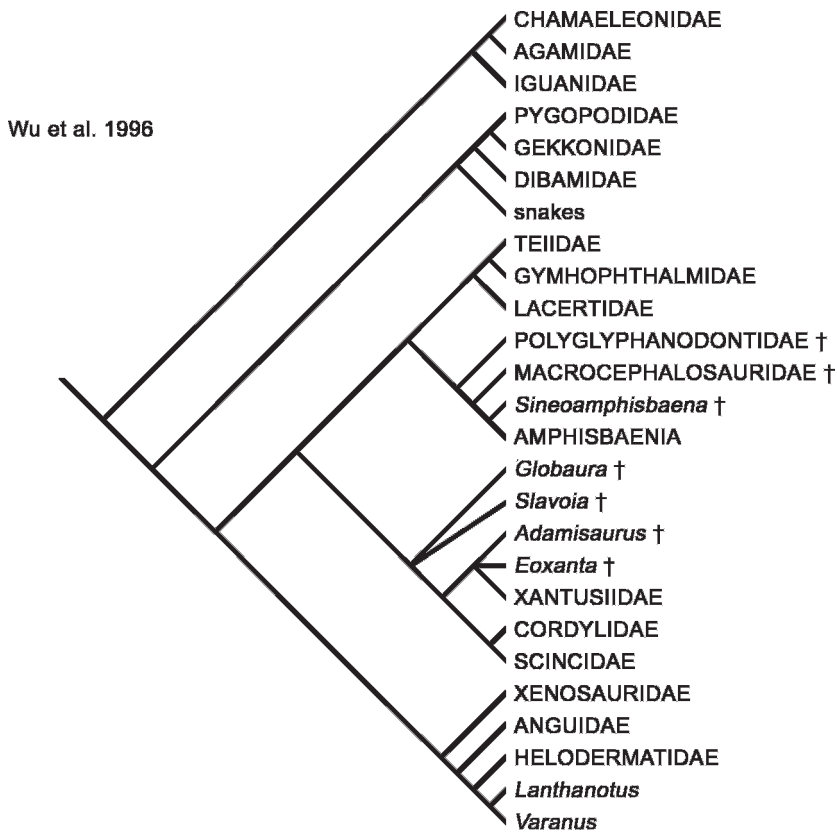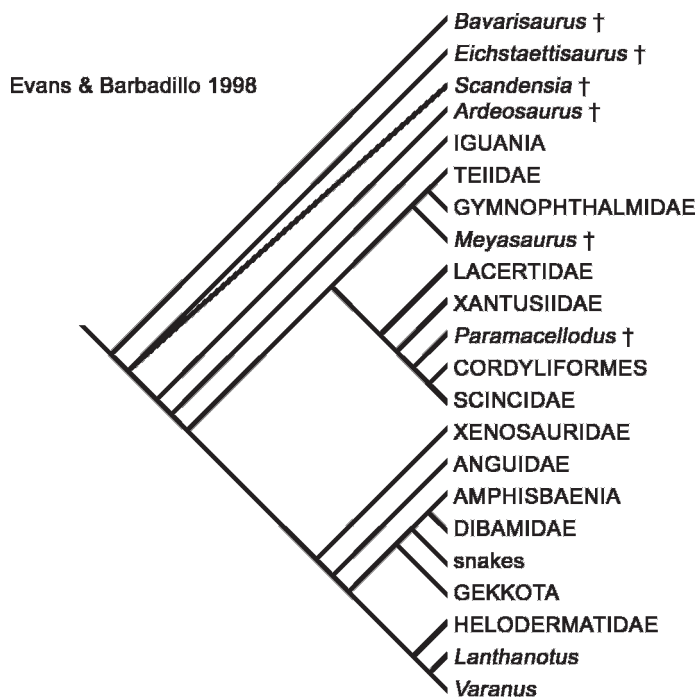
Fig. 4. Hypothesis of squamate interrelationships, based on morphology, as presented by Evans and Barbadillo (1998). Fossil taxa denoted by daggers (†).

Caldwell (1999a) analyzed a set of taxa similar to that of Estes et al. (1988), but added the fossil taxa *Coniasaurus*, *Dinilysia patagonica*, *Estesia*, and Mosasauroidea. Additionally, he divided Gekkonidae sensu Estes et al. (1988) into Eublepharinae and Gekkonoidea sensu Kluge (1987), and extant snakes into Scolecophidia and Alethinophidia to help analyze the position of *Dinilysia patagonica*. This analysis recovered 18 equally short trees whose strict consensus shows limited resolution (fig. 8). However, this analysis did offer support for some clades questioned by Lee (1998) and later by Lee and Caldwell (2000). Scincomorpha, Scincoidea, and Lacertoidea (all sensu Estes et al., 1988) were supported in the strict consensus. Additionally, this analysis supported a sister-taxon relationship between *Dinilysia patagonica* and alethinophidians, suggested the paraphyly of Xenosauridae (sensu Estes et al., 1988), and suggested that *Lanthanotus borneensis*, *Estesia*, and *Varanus* were successively more remote outgroups to *Heloderma*. The latter is significant because *Lanthanotus*

borneensis typically has been considered to be more closely related to *Varanus* than to *Heloderma*, and because *Estesia* was first considered a close relative of the *Varanus-Lanthanotus borneensis* clade (Norell et al., 1992) and then a monstersaur (Norell and Gao, 1997; Gao and Norell, 1998, 2000; Nydam, 2000).

Evans et al. (2005) have offered one of the most recent broad-scale analyses of squamate phylogeny. Similar in composition to the analyses of Evans and Barbadillo (1998, 1999), this analysis has added three taxa (*Yabeinosaurus tenuis*, *Parviraptor*, and *Aigialosaurus*) and some new characters. The resulting study is one of the most fossil-inclusive studies so far published and the phylogenetic hypothesis (fig. 9A) shows significant differences from the Evans and Barbadillo (1998, 1999) studies. Importantly, Gekkota is found to be a basal clade within Scleroglossa, the amphisbaenian-dibamid-snake clade is the sister-taxon to *Aigialosaurus* (and, presumably, other mosasauroids) within Anguimorpha (above the level of
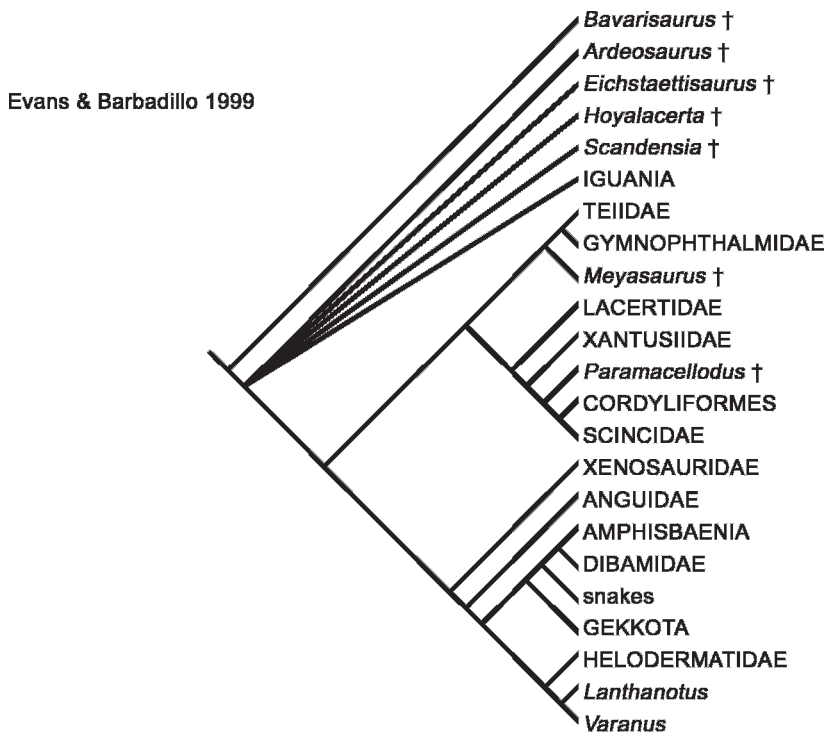
Fig. 5. Hypothesis of squamate interrelationships, based on morphology, as presented by Evans and Barbadillo (1999). Note that this is essentially the same tree as in Figure 4, but with the addition of *Hoyalacerta sanzi* and the collapse of several nodes at the base of squamates. Fossil taxa denoted by daggers (†).

Shinisaurus and *Xenosaurus*), and there is an extinct clade composed of *Eichstaettisaurus*, *Hoyalacerta sanzi*, *Parviraptor*, and *Scandensia ciervensis* at the base of Anguimorpha.

Evans and Wang (2005) offer another derivation from the Evans and Barbadillo (1998, 1999) matrices. This analysis includes the fossil taxa *Carusia intermedia*, Mosasauroidea, and *Dalinghosaurus longidigitus*, but not *Yabeinosaurus tenuis* nor *Scandensia ciervensis* (fig. 9B). Similar to Caldwell (1999a), this study finds mosasauroids to be basal to Scleroglossa. It also recovers a Carusioidea (sensu Gao and Norell, 1998) and suggests that *D. longidigitus* and a clade consisting of *Eichstaettisaurus*, *Hoyalacerta sanzi*, and *Parviraptor* are successively more remote outgroups to Carusioidea. A monophyletic Scincomorpha is the sister taxon to Gekkota in this analysis and is nested within Anguimorpha as the sister-group to a clade containing snakes, dibamids, amphisbaenians, and non-carusioid anguimorphs.

MOLECULAR ANALYSES: Townsend et al. (2004) and Vidal and Hedges (2005) have recently offered a higher-level analysis of extant squamate relationships based on molecular evidence (fig. 10). Both of these analyses find Gekkota and *Dibamus* to be basal radiations of squamates. Townsend et al. (2004) suggest that Gekkota is the basalmost lineage; Vidal and Hedges (2005) suggest that *Dibamus* (Dibamidae of their usage; because *Anelytropsis papillosus* was not included, *Dibamus* is a more accurate taxon indicator) is more basal. Both analyses suggest that cordylids, xantusiids, and scincids form a clade that was the next to diverge. Amphisbaenians are hypothesized to be nested within Lacertiformes (sensu Estes et al., 1988) as the sister-group to a clade composed of snakes, iguanians, and anguimorphs. Although there is some question about the exact placement of snakes, each study suggests that they are close to an Iguania-Anguimorpha clade.
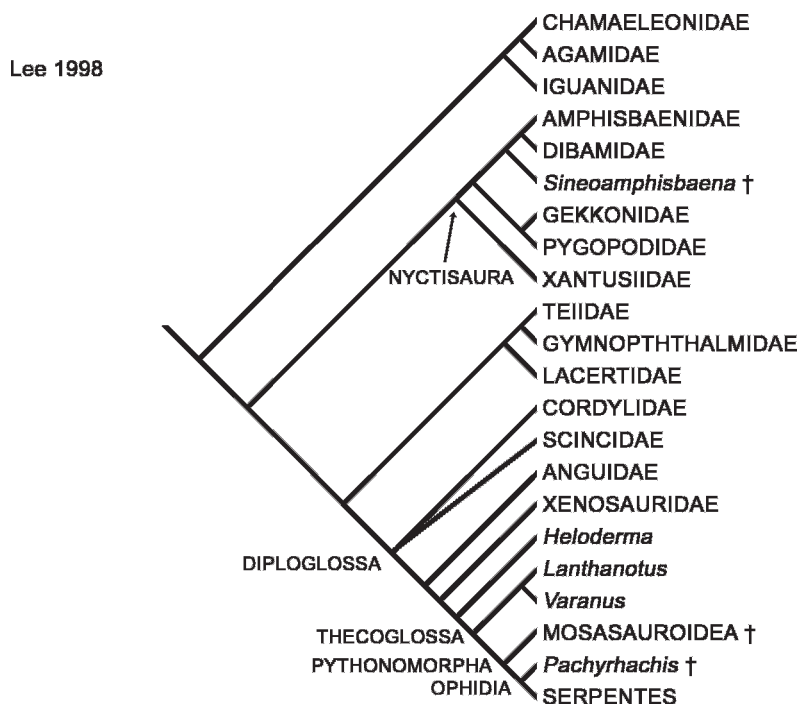
Fig. 6. Hypothesis of squamate interrelationships, based on morphology, as presented by Lee (1998) with some of the accompanying taxonomy, especially as it differs from that of Estes et al. (1988). Note that Serpentes exclusive of *Pachyrhachis problematicus* is constrained to be monophyletic. Fossil taxa denoted by daggers (†).

The basal position of gekkotans and dibamids in these analyses is intriguing in part because of parallels with some historical discussions of the plesiomorphic squamate form. Earlier, noncladistic, discussions of dibamid and gekkotan morphology often characterized them as a puzzling combination of plesiomorphic and apomorphic character states that might be close to the plesiomorphic squamate form (see Estes, 1983; Kluge, 1983, 1987; Rieppel, 1984b; Greer, 1985). This has been influenced, to some degree, by the late fusion (or absence of fusion) of some braincase elements in dibamids and the persistence of notochordal vertebrae in some gekkotans.

COMPARISONS: Although all of the described morphology-based analyses agree on points such as the monophyly of Gekkota, Varanoidea, and Scleroglossa, there remains virtually no consensus about higher-level relationships. Xantusiidae, Cordyliformes, Scincidae, Dibamidae, Amphisbaenia, Serpentes, Mosasauroidea, and Xenosauridae are extremely problematic. This, despite a common dependence on the Estes et al. (1988) character list. Differing taxonomic inclusions are likely a major contributing factor to the absence of consensus among these phylogenetic hypotheses. Taxonomic sampling in these studies is seemingly dependent upon the specific problem the authors are addressing, probably because no more inclusive data matrices of squamates (including fossils) exist. Wu et al. (1996) were interested in the cladistic position of *Sineoamphisbaena hexatabularis* as it relates to Amphisbaenia and the *Gilmoreteius*-type scincomorphs it resembles, so they included teiioid fossils. Evans and Barbadillo (1998, 1999) were examining basal squamates and taxa previously believed to be related with scincomorphs and/or "stem" Gekkota. Accordingly, they included "bavarisaurid" and "ardeosaurid" taxa and *Scandensia ciervensis*, *Hoyalacerta sanzi*, and *Paramacellodus*.
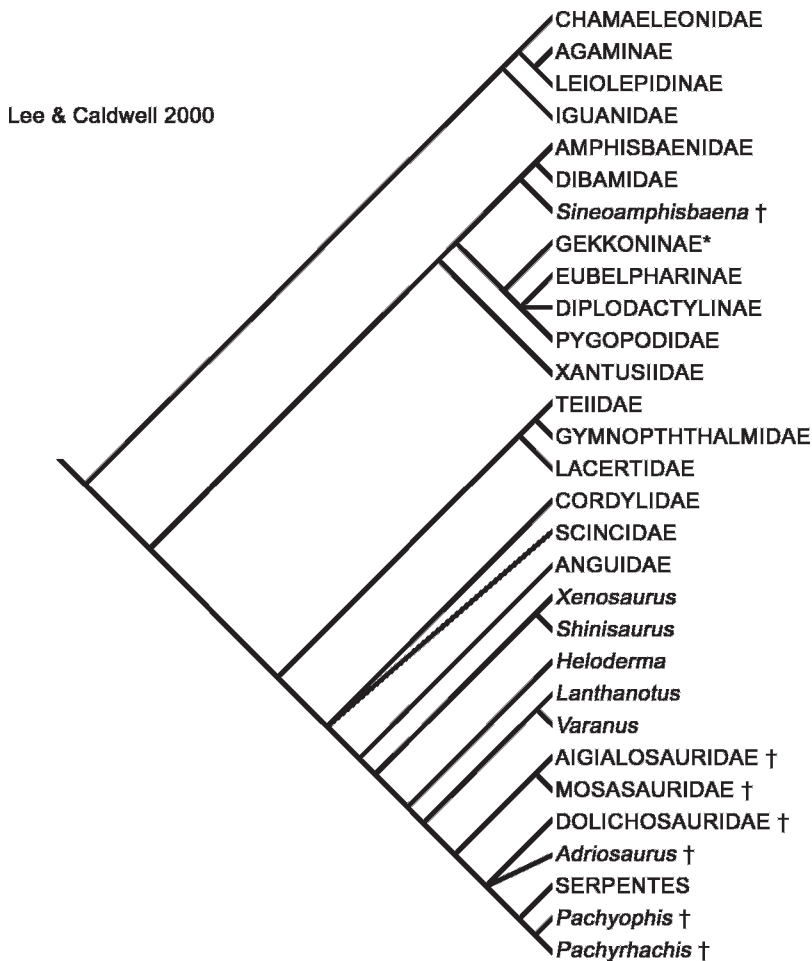
Fig. 7. Hypothesis of squamate interrelationships, based on morphology, as presented by Lee and Caldwell (2000). This analysis was similar to that of Lee (1998), but several fossil taxa were added near the base of Mosasauroidea, and Agamidae and Gekkota were further divided into their presumed constituent clades. Note that Serpentes exclusive of *Pachyrhachis problematicus* and *Pachyophis woodwardi* is constrained to be monophyletic. Fossil taxa denoted by daggers (†).

Lee (1998), Caldwell (1999a), and Lee and Caldwell (2000) were primarily concerned with the relative position of specific limbless taxa. Thus, Lee (1998) included Mosasauroidea, *Pachyrhachis problematicus*, and *Sineoamphisbaena hexatabularis*. Lee and Caldwell (2000) included these taxa and added *Adriosaurus*, *Aphanizocnemus*, and Dolichosauridae such that their analyses were sensitive to testing the position of those particular taxa within Anguimorpha. Caldwell (1999a) focused somewhat on snakes and mosasauroids, but helped to balance these taxonomic selections by including *Estesia*. Evans et al.

(2005) and Evans and Wang (2005) both included numerous fossil taxa, but were still closely examining the positions of specific taxa. Comparable analyses not observed in detail here include those also testing the specific placement of new fossil taxa (e.g. Nydam, 2000; Reynoso and Callison, 2000).

There is very little overlap of fossil taxa included in the analyses described above. *Sineoamphisbaena hexatabularis* was included in three analyses (Wu et al., 1996; Lee, 1998; Lee and Caldwell, 2000) and Mosasauroidea was included in three (Lee, 1998; Caldwell, 1999a; Lee and Caldwell, 2000), but no other

Caldwell 1999

CHAMAELEONIDAE
AGAMINAE
other iguanians
ALETHINOPHIDIA
Dinilysia †
SCOLECOPHIDIA
MOSASAUROIDEA †
Coniasaurus †
GEKKONOIDEA
EUBLEPHARINAE
DIBAMIDAE
AMPHISBAENIA
TEIIDAE
GYMNOPHTHALMIDAE
LACERTIDAE
XANTUSIIDAE
CORDYLIDAE
SCINCIDAE
ANGUIDAE
Shinisaurus
Xenosaurus
Varanus
Estesia †
Lanthanotus
Heloderma

Fig. 8. Hypothesis of squamate interrelationships, based on morphology, as presented by Caldwell (1999a). Fossil taxa denoted by daggers (†).

taxon appeared in more than two of these six studies. *Adamisaurus magnidentatus*, *Adriosaurus*, *Aphanizocnemus*, *Coniasaurus*, *Dinilysia patagonica*, Dolichosauridae, *Eoxanta lacertifrons*, *Estesia*, *Hoyalacerta sanzi*, *Paramacellodus*, *Parviraptor*, *Meyasaurus diazromerali*, *Scandensia ciervensis*, *Slavoia darevskii*, and *Yabeinosaurus* each appeared in only one analysis. Of course, the molecular studies included no fossil taxa at all; this is significant given the findings of Gauthier et al. (1988b) (see below). Different taxonomic sampling in these analyses is equivalent to asking different phylogenetic questions, so different answers (in the form of phylogenetic hypotheses) should be expected. The question then becomes: Are we asking the appropriate questions to find the information we desire? The answer is ''yes'' when the goal is to place specific fossil taxa within a subset of Squamata. However, to more fully test the relative positions of any group of taxa, more inclusive sampling is necessary.

BROADLY SAMPLING FOSSILS

Gauthier et al. (1988b) clearly demonstrate that fossils are important for inclusion in a phylogenetic analysis because they affect character polarities throughout the tree. They posit that intermediate forms offer new information regarding character state changes throughout a tree (Gauthier et al., 1988b). They further outline the difficulties with using only extant taxa as outgroups in an analysis; the possibility of polymorphism and the derived condition of many taxa (Gauthier et al., 1988b). Both pose problems, but the latter is especially important because it is easy to think of some extant animals as primitive, even though they are not. The duck-billed platypus (*Ornithorhynchus anatinus*) repre-

A

Evans et al. 2005

Bavarisaurus †
Ardeosaurus †
Yabeinosaurus †
IGUANIA
GEKKOTA
TEIIDAE
GYMNOPHTHALMIDAE
Meyasaurus †
LACERTIDAE
XANTUSIIDAE
Paramacellodus †
CORDYLIDAE
SCINCIDAE
Scandensia †
Eichstaettisaurus †
Parviraptor †
Hoyalacerta †
Xenosaurus
Shinisaurus
Dorsetisaurus †
ANGUIDAE
HELODERMATIDAE
Lanthanotus
Varanus
Aigialosaurus †
DIBAMIDAE
AMPHISBAENIA
SERPENTES

B

Evans & Wang, 2005

Bavarisaurus †
Ardeosaurus †
IGUANIA
MOSASAUROIDEA †
Shinisaurus
Xenosaurus
Carusia †
Dalinghosaurus †
Eichstaettisaurus †
Hoyalacerta †
Parviraptor †
SCINCOIDEA
PARAMACELLODIDAE †
LACERTOIDEA
GEKKOTA
AMPHISBAENIA
DIBAMIDAE
SERPENTES
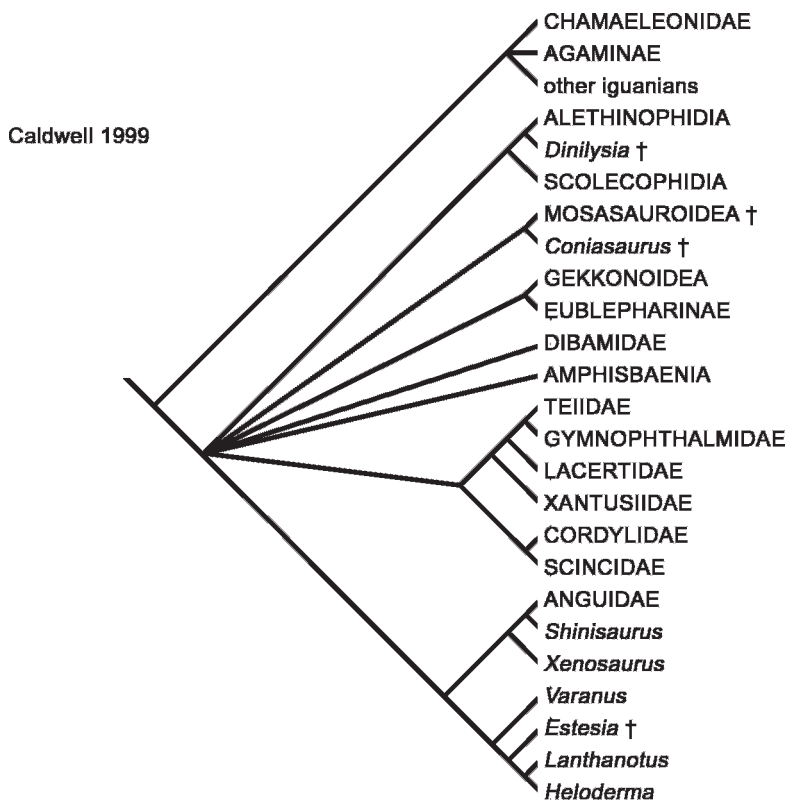*Dorsetisaurus* †
ANGUIDAE
HELODERMATIDAE
VARANIDAE

Fig. 9.   Hypothesis of squamate interrelationships, based on morphology, as presented by Evans et al. (2005). Fossil taxa denoted by daggers (†).

A

Townsend et al., 2004

GEKKOTA
Dibamus sp.
CORDYLIDAE
Xantusia vigilis
SCINCIDAE (s.l.)
AMPHISBAENIA
Eremias scripta
Cnemidophorus tigris
Leposoma parietale
SERPENTES
IGUANIA
Xenosaurus grandis
ANGUIDAE
Heloderma suspectum
Shinisaurus crocodilurus
VARANIDAE

B

Vidal & Hedges 2005

GEKKOTA

LACERTIBAENIA

BIFURCATA
UNIDENTATA

EPISQUAMATA   LATERATA

TOXICOFERA

Sphenodon punctatus
Dibamus
Gekko vittatus
Gehyra mutilata
Lialis
Cordylus
XANTUSIIDAE
Plestiodon
AMPHISBAENIA
LACERTIDAE
Gymnophthalmus underwoodi
TEIIDAE
Cylindrophis rufus
Liasis savuensis
IGUANINAE (s.s.)
Anolis sagrei
Leiocephalus barahonensis
Anniella pulchra
Heloderma suspectum
Varanus

Fig. 10. Hypotheses of squamate interrelationships, based on molecular data, as presented by **(A)** Townsend et al. (2004) and **(B)** Vidal and Hedges (2005). Note that the "leaf" taxa of each tree have been modified somewhat for this analysis from those presented in the original study. In **(A)**, some clades have been collapsed and the "leaves" are labeled as the most exclusive taxon name for which taxa are sampled (e.g., the clade containing gekkonids, pygopodids, and eublepharids are collapsed into a clade termed "Gekkota" here). The tree in **(B)** has been modified in a slightly different way. The "leaves" of the tree as presented in the original study (Vidal and Hedges, 2005) usually suggested a broader taxon than was represented by their data. Consequently, the appropriate taxon names are put on the tree for those taxa represented by the study (e.g., "Scincidae" is replaced here by *Plestiodon* sensu Smith, 2005).

sents an ancient and basal lineage of Mammalia. However, nobody actually considers the platypus "primitive"; this extremely derived mammal lacks teeth as an adult, possesses a bizarrely specialized snout and venomous spurs (Manger and Pettigrew, 1995; Attenborough, 2002; Dawkins, 2004) among other features that certainly were not present in truly primitive mammals (Desui, 1991; Luo et al., 2002; Rich et al., 2005).

Further analysis led Gauthier et al. (1988b) to suggest that some taxa were important and others unimportant for reconstructing character polarities within their data matrix. That is, inclusion of some taxa has more effect on tree topology than others and some taxa may be excluded with no extended effects. This seems to imply that only some fossil taxa need to be included in a given analysis, but that is not the intention of Gauthier et al. (1988b). Indeed, the point is that such analyses are context sensitive, meaning that different taxonomic samplings have the potential to produce different results. Additional data (as from fossils) can render the "unimportant" taxa "important." Gauthier et al. (1988b) show that their so-called "unimportant" taxa could only be identified *a posteri*, underscoring the necessity of increased taxon sampling.

That increasing taxon sampling is beneficial was recently challenged by an evolutionary model using DNA evidence (Rosenberg and Kumar, 2001). However, subsequent analyses reveal errors in the original interpretations of this model and provide further confirmation for the importance of broad taxonomic sampling (Pollock et al., 2002; Zwickl and Hillis, 2002).

Two major conclusions may be drawn from these studies:

1. Fossils are important for inclusion in phylogenetic analyses
2. As many taxa as possible should be included.

When viewed in conjunction, these first two conclusions support a third:

3. As many *fossil* taxa as possible should be included in any given phylogenetic analysis.

Even if fossil taxa include a large number of unknown or unscoreable character states, their inclusion may be useful. Incompletely known taxa with unexpected character state combinations are sometimes omitted from analyses because they may reduce resolution in a strict consensus (Nixon and Wheeler, 1992). However, this type of taxonomic deletion is problematic because taxa with few scoreable characters still offer important data for reconstructing character polarities (Kearney and Clark, 2003; Wiens, 2003), although incompletely known taxa whose character scoring completely overlap with another taxon in the matrix, may be safely removed from an analysis (Wilkinson, 1995; Kearney and Clark, 2003). Similarly, soft tissue (or molecular) characters remain important in analyses including large numbers of fossils if taxa and characters are well sampled overall (Kearney and Clark, 2003; Wiens, 2003).

Given the context-sensitive nature of phylogenetic analyses and that the cladistic positions of included taxa are somewhat interdependent, the published phylogenetic analyses of squamates described above have obvious conflicts with one another. Each of those studies includes only a few fossil taxa and the inclusion of many more would be expected to retrieve a different conceivably more accurate picture of the interrelationships (see Pollock et al., 2002; Zwickl and Hillis, 2002).

That being said, the current study does not examine all of the described fossil squamates that are diagnosable to species. Taxa of unquestioned affinity or that are nested members of well supported clades have been omitted in some cases, but may be included in future versions of this data matrix by myself or others.

MATERIALS AND METHODS

BREADTH OF THE ANALYSIS

This study was undertaken with the goal of analyzing the phylogenetic relationships and interrelationships of major squamate groups with more focus given to problematic groups. The historical analyses described above have helped shape this analysis. Iguanians are a problematic group whose ingroup relationships remain uncertain and without consen-
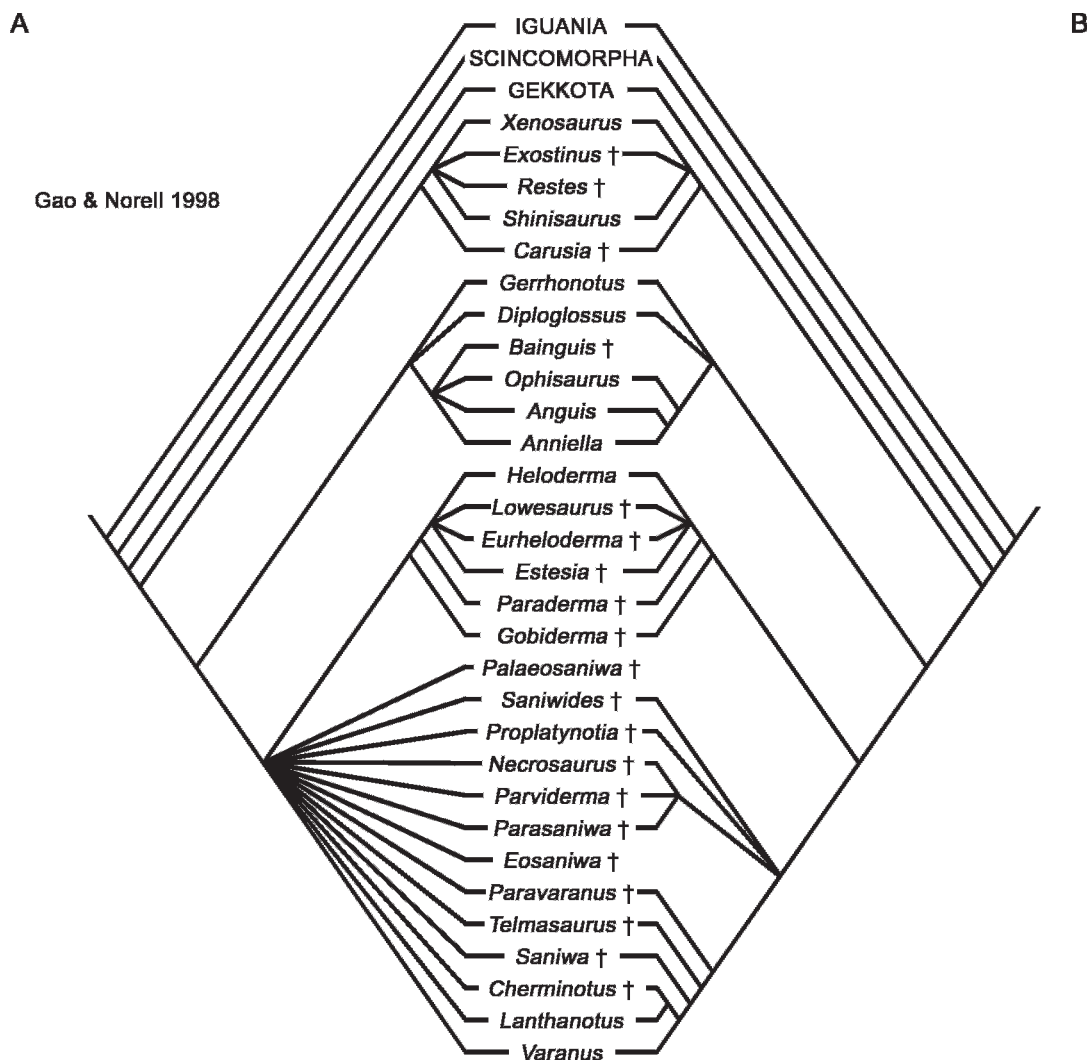
Fig. 11. Hypotheses of anguimorph interrelationships, based on morphology, as presented by Gao and Norell (1998). The cladogram on the left **(A)** is a more inclusive analysis; **(B)** is the analysis after the removal of *Bainguis parva*, *Eosaniwa koehni*, *Palaeosaniwa canadensis*, and *Restes rugosus*. Fossil taxa denoted by daggers (†).

sus (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989; Macey et al., 1997; Frost et al., 2001; Schulte et al., 2003; Conrad and Norell, 2007a). As described above, the structure (or monophyly) of various scleroglossan groups have not reached consensus. Snake origins are an important problem for understanding almost any area of squamate phylogeny. Indeed, even if a researcher were interested only in anguimorph phylogenetics, she or he would be forced to examine all of

Squamata based on the problem of snake origins in the context of recent phylogenetic analyses.

Since McDowell and Bogert's (1954) landmark study, the conventional wisdom has been that snakes are derived anguimorphs. Importantly, the only broad cladistic analysis of terrestrial anguimorphs (including fossils) have not included mosasaurs or snakes (e.g., Gao and Norell, 1998; fig. 11) and those analyses including mosasaurs and snakes

include few, if any, terrestrial fossil forms (Lee, 1997, 1998, 2000; Caldwell, 1999a, 2000; Lee and Caldwell, 2000; Rieppel and Zaher, 2000a) (e.g., see figs. 6–8). Numerous recent papers provide data suggesting that snakes are derived varanoids (Forstner et al., 1995; Lee, 1997, 1998; Lee et al., 1999a; Caldwell, 2000; Lee, 2000; Lee and Caldwell, 2000; Lee and Scanlon, 2001; Scanlon and Lee, 2002; Caldwell and Dal Sasso, 2004), but others have re-examined the issue and found that the characters or character codings supporting this hypothesis are problematic (Zaher and Rieppel, 1999a, 1999b, 2002; Rieppel and Zaher, 2000a, 2000b, 2001; Rieppel et al., 2003). Caldwell (1999a) finds snakes and mosasauroids to fall outside of Anguimorpha (fig. 8), and some studies place snakes with Amphisbaenia, Dibamidae, and Gekkota within Anguimorpha (e.g., Evans and Barbadillo, 1998, Rieppel and Zaher, 2000a).

Suggestions that Gekkota or Gekkota and Scincomorpha are nested within Anguimorpha (Evans and Barbadillo, 1998, 1999) (figs. 4, 5) carry important implications and require broad sampling of anguimorphs. The possibility of geckos being derived anguimorphs (Evans and Barbadillo, 1998), or closely related to scincomorphs (Caldwell, 1999a), or forming the sister group to Autarchoglossa (Estes et al., 1988) is important for understanding anguimorph outgroups. Evans and Wang (2005) suggested not only that geckos were nested anguimorphs, but also that scincomorphs may be.

Given all of this, the current study samples most densely within Iguania and Anguimorpha. Snakes, a very diverse group representing over one-third of extant squamates, are not densely sampled, but snake monophyly is virtually unquestioned. McDowell and Bogert (1954) were the last to suggest non-monophyly of snakes, suggesting that some scolecophidians might be more closely related to anguid lizards than to other snakes (see below). The analysis presented below is sensitive to that possibility.

TAXON SAMPLING

Many taxa included in this analysis are coded at the species level, but some are scored at supraspecific levels, including relatively inclusive levels such as ''family'' or, less commonly, at groups more inclusive than previously outlined ''families''. Except in the cases of very small, morphologically homogenous clades, and coursely sampled morphologic character lists, at least some of the morphological diversity for a given group will not be coded when taxa are collapsed and coded supraspecifically. This type of coding requires assumptions regarding monophyly of the group and, usually, some of the phylogenetic relationships within the group. In the current analysis, I have focused on groups that are more problematic. For instance, macrostomatan snakes are universally identified as a monophyletic group. However, McDowell and Bogert (1954) suggested that scolecophidians were polyphyletic with Typhlopidae (including Anomalepidae given their usage) being nested within Anguidae (Anguinidae of their usage). Thus, in the current analysis, representatives of the three scolecophidian groups and ten other snake taxa are included and anguids are also sampled heavily. By contrast, most extant macrostomatans were included as a single terminal group here.

Published analyses have guided my selection of species exemplars for scoring supraspecific groups in this analysis. Given a clade with some resolution of basal taxa, collapsing the taxa into one unit is beneficial logistically because it reduces the total number of included taxa. Even so, future versions of this analysis will include more species-level codings, therefore relying less on the hypotheses of prior analyses. Below, explanations are offered both for taxon selection and character scoring. The explanations for taxon sampling specifically address those taxa that appear only as generic names.

THE OUTGROUP: Carroll (1988b) describes a ''Suborder'' Eolacertilia as the sister taxon to other squamates, but Eolacertilia has been rejected as paraphyletic or polyphyletic (Estes et al., 1988; Gauthier et al., 1988a). As described by Estes (1983), this ''Eolacertilia'' includes Paliguanidae, Kuehneosauridae, *Fulengia*, *Lacertulus*, and *Litakis*. Carroll (1988b) includes these taxa and *Colubrifer*.

I have omitted the so-called eolacertilians for various, case-specific reasons. Carroll

(1975, 1977, 1988a, 1988b) regards "paliguanids" as very important for understanding the origin and early evolution of lepidosaurs. Other authors have followed this opinion and have described new "paliguanids", including *Blomosaurus* (Tatarinov, 1978) and *Kudnu* (Bartholomai, 1979). Even so, "Paliguanidae" is widely regarded as a paraphyletic taxon and, unfortunately, the preservation of specimens constituting the known "paliguanid" genera (including *Paliguana*, *Palaeagama*, and *Saurosternon*) makes it impossible to characterize them except through plesiomorphy (Benton, 1985; Gauthier et al., 1988a; Rieppel, 1994). Thus, their position within Lepidosauromorpha is currently impossible to ascertain with any kind of precision. *Fulengia* is not a lepidosaur, but instead is a juvenile sauropodomorph dinosaur (Evans, 1989). *Litakis* is based only on a dentary fragment lacking both the surangular margin and the symphysial portion (Estes, 1964). Thus, although probably representing a taxon of interest, *Litakus* is far too fragmentary to be informative for this analysis. *Lacertulus* has not been convincingly shown to be a squamate or lepidosaur (Carroll and Thompson, 1982; Estes, 1983; Carroll, 1988a; Gauthier et al., 1988a). *Colubrifer* has been shown to be a procolophonian, probably *Owenetta* (Evans, 2001).

Kuehneosauridae is a monophyletic assemblage (Robinson, 1962, 1967) and usually considered to be close to squamate ancestry (Robinson, 1962, 1967; Gauthier et al., 1988a; Rieppel, 1994; Evans, 2003). However, recent analyses have brought even this relationship into question, suggesting kuehneosaurids are the outgroup to Sauria (the archosauromorph-lepidosauromorph clade) (Müller, 2003, 2004b). Thus, kuehneosaurids have been omitted from this analysis.

Rhynchocephalia is the immediate sistergroup to Squamata and is used as the outgroup in this analysis. *Sphenodon punctatus* and *S. guntheri* represent the only two living species of this ancient and historically diverse clade. Although *Sphenodon* differs from squamates in numerous aspects of its morphology that have been interpreted as plesiomorphic for Lepidosauria (Romer, 1966; Carroll, 1988b), comparisons with Triassic and Jurassic rhynchocephalians demonstrate that some of its supposedly plesiomorphic characteristics are actually derived (Evans, 1980, 1981; Fraser, 1982; Fraser and Walkden, 1984; Whiteside, 1986; Fraser, 1988; Carroll and Wild, 1994; Sues et al., 1994; Reynoso, 1996; Wilkinson and Benton, 1996; Evans and Sigogneau-Russell, 1997; Reynoso, 2000, 2003; Evans et al., 2001; Fraser, 2002). There is general agreement that *Gephyrosaurus*, *Diphydontosaurus*, *Planocephalosaurus*, and *Rebbanasaurus* are the most basal Rhynchocephalia (Sues et al., 1994; Reynoso, 1996; Wilkinson and Benton, 1996; Evans and Sigogneau-Russell, 1997; Reynoso, 2000; Evans et al., 2001). These taxa have been used to score the group wherever possible, with *Sphenodon* being used to supplement these codings.

Marmoretta is a recently described lepidosauromorph from the Middle Jurassic of Skye, Scotland (Evans, 1991; Waldman and Evans, 1994). It resembles kuehnoesuarids, but is somewhat less specialized based on the known remains (Evans, 1991; Waldman and Evans, 1994). However, given the uncertainty regarding the placement of kuehneosaurids, this taxon was not included as an outgroup. Rhynchocephalia stands as the sole outgroup for the phylogenetic analysis performed here, but character codings are given for *Marmoretta* and Kuehneosauridae (see appendix 2).

STEM SQUAMATES: Most known squamates fit within one of the seven major radiations (Iguania, Gekkota, Lacertoidea, Scincoidea, Anguimorpha, Amphisbaenia, and Serpentes), but some fossil taxa defy placement within any of these groups. Recent descriptive and phylogenetic work suggests that some fossil taxa fall outside of the crown-group represented by this framework. Among these are *Huehuecuetzpalli mixtecus* (Reynoso, 1998), *Hoyalacerta sanzi* (Evans and Barbadillo, 1999; Evans et al., 2004), *Scandensia ciervensis*, "bavarisaurids", and "ardeosaurids" (Evans and Barbadillo, 1998, 1999; however, see Conrad, 2004c; Conrad and Norell, 2006a, 2007b). Accordingly, these taxa have been included in this analysis with the latter two taxa being represented by most of their constituent taxa: *Ardeosaurus brevipes*, *Bavarisaurus macrodactylus*, *Eichstaettisaurus*, and *Yabeinosaurus tenuis* are

not closely related to Gekkota (Evans and Barbadillo, 1997, 1998, 1999; Evans et al., 2005; Conrad and Norell, 2006a) (see figs. 4, 5, 9), contra earlier some earlier taxonomic treatments (e.g., Kluge, 1967, 1983, Estes, 1983). These taxa are included individually in the current analysis. Published data were used for scoring *A. brevipes* (Hoffstetter, 1966; Mateer, 1982; Estes, 1983; Evans and Barbadillo, 1998), *B. macrodactylus* (Estes, 1983; Evans, 1994b; Evans and Barbadillo, 1998), and *Y. tenuis* (Endo and Shikama, 1942; Young, 1958; Evans et al., 2005). Note that much of the data for *Y. tenuis* comes from an excellent recent study by Evans et al. (2005). *Eichstaettisaurus* is scored as a single taxon based on published descriptions (Hoffstetter, 1966; Estes, 1983; Evans and Barbadillo, 1998; Evans et al., 2004) and photos kindly supplied by Sterling J. Nesbitt. The ''bavarisaurid'' *Palaeolacerta bavarica* is not included in the current analysis because it lacks complete, available, descriptions. *Tijubina pontei* is an incompletely known taxon that is apparently similar to *Huehuecuetzpalli mixtecus* (Bonfirm-Júnior and Marques, 1997; Bonfirm-Júnior and Avilla, 2002; Bonfirm-Júnior and Rocha-Barbosa, 2006). It may be included in future versions of this analysis, pending further studies.

IGUANIA: Monophyly of Iguania as defined by Estes et al. (1988) is universally accepted. However, the precise relationships of the iguanian clades remain problematic. Importantly, most analyses not treating Iguania as a single taxon assume a basal dichotomy of iguanians with an ''iguanid'' group forming the sister group to Acrodonta (agamas and chameleons) and usually break Iguania into the three taxa Iguanidae, Agamidae, and Chamaeleontidae (Estes et al., 1988; Wu et al., 1996; Lee, 1998, 2000; Caldwell, 1999a; Caprette et al., 2004). The former two taxa are usually highlighted with an asterisk (*) to indicate their possible paraphyly. Lee and Caldwell (2000) divided Agamidae into two taxa in an attempt to eliminate paraphyletic taxa, but (like many other analyses) coded all nonacrodont iguanians as single unit.

Current understanding of iguanian phylogeny is rudimentary at best. Only three morphological analyses have been performed with the hopes of sorting out the broad-scale
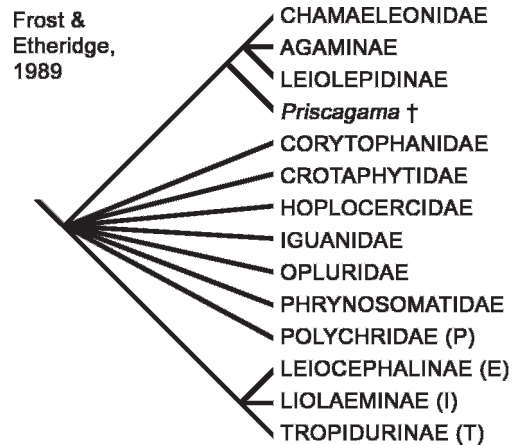
Fig. 12. Hypothesis of iguanian interrelationships, based on morphology, as presented by Frost and Etheridge (1989). As recently described by Schulte et al. (2003), iguanian relationships are a problematic area, seeming to defy any attempt to recover strong node supports. The letters in parentheses are implemented for easy comparison with Figure 11 (below). Fossil taxon denoted by a dagger (†).

iguanian interrelationships. The first of these (Etheridge and de Queiroz, 1988) excluded acrodontans. A superior study (from a taxonomic sampling perspective) considered 35 extant iguanians and one fossil (Frost and Etheridge, 1989). Although Frost and Etheridge (1989) did not fully resolve the interrelationships of the iguanian groups (fig. 12), the strict consensus of their trees did show support for a number of clades that are used in this analysis, including Corytophanidae, Phrynosomatidae, Crotaphytidae, Iguanidae (sensu stricto) and Tropidurinae (sensu stricto). A recent molecular study (Schulte et al., 2003) (fig. 13) provides independent support for many (but not all) of the groups identified by Frost and Etheridge (1989).

Despite the consensus that Acrodonta is monophyletic, questions remain regarding the relationships of Agaminae (sensu Frost and Etheridge, 1989: 32–33), *Leiolepis*, *Physignathus*, *Uromastyx*, and Chamaeleonidae (Frost and Etheridge, 1989; Macey et al., 1997, 2000; Honda et al., 2000). The monophyly of Chamaeleonidae, on the other hand, has never been questioned. Indeed, the clade seems to be universally viewed as a very
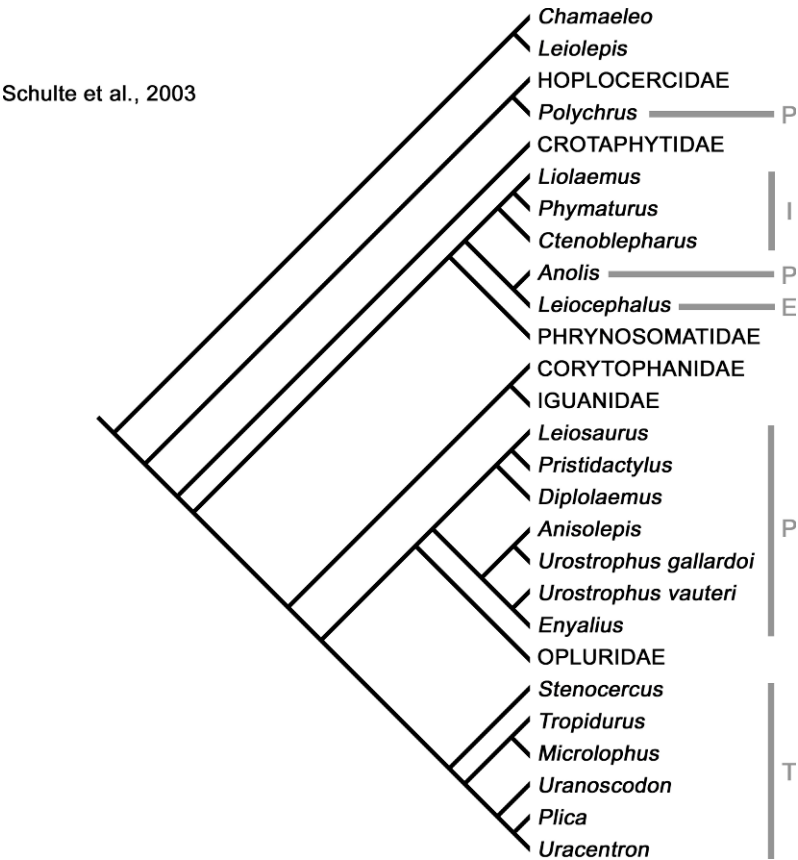
Fig. 13. Hypothesis of iguanian interrelationships, based on molecular data, as presented by Schulte et al. (2003). The gray letters correspond with those in Figure 10. They refer to clades recovered by Frost and Etheridge (1989): (E) Leiocephalinae; (I) Liolaeminae; (P) Polychrotidae, polyphyletic here; (T) Tropidurinae. Note that Tropiduridae sensu Frost and Etheridge (1989) included leiocephalines, liolaemines, and tropidurines, but these taxa do not form a clade in the Schulte et al. (2003) analysis.

distinctive radiation of peculiar squamates (Hillenius, 1978; Moody and Rocek, 1980; Rieppel, 1981b, 1987; Estes et al., 1988; Frost and Etheridge, 1989; Macey et al., 2000; Townsend and Larson, 2002; Bauer, 2003; Uetz, 2007). *Brookesia superciliaris* and *Rhampholeon spectrum* were used in this analysis because of their apparently basal position within Chamaeleonidae in morphological- and molecular-based studies (Rieppel, 1981b, 1987; Townsend and Larson, 2002). Three representative "agamids" were coded in this analysis: *Agama agama*, *Physignathus cocincinus*, and *Uromastyx* (coded based primarily on *U. aegyptius*).

Priscagamids are a group of Late Cretaceous iguanians showing similarities with extant agamas. Three priscagamines were included in the present analysis: *Priscagama gobiensis* (probably including *Chamaeleognathus iordanskyi* and *Cretagama Białynickae* of Alifanov, 1996, and maybe *Pleurodontagama aenigmatodes* of Borsuk-Białynicka, 1996 based on data in Gao and Norell, 2000); *Mimeosaurus crassus* (probably including *Gladidenagama semiplana*); and *Phrynosomimus asper*. Data used for coding the individual priscagamids comes from previous descriptive studies (Borsuk-Białynicka and Moody, 1984; Alifanov, 1989b, 1996; Borsuk-Białynicka, 1996; Gao and Norell, 2000) and observation of specimens (see appendix 1).

Tikiguania estesi, known only from a dentary, is highly important in that it may

be a Triassic iguanian (Datta and Ray, 2006), but is too incomplete to be coded meaningfully here. Its relationships must be tested by an analysis sampling basal rhynchocephalians and acrodontans more intensely.

Three representative hoplocercids were scored. These were *Enyalioides* (based on *E. palpebralis* and *E. laticeps*), *Hoplocercus spinosus*, and *Morunasaurus annularis*.

Camp (1923) considered *Euposaurus* to be a relative of anguimorphs (see fig. 1), Carroll (1988b) hypothesized that it was an iguanian, and Gauthier et al. (1988a: 97) suggested it to be a rhynchocephalian possibly close to "clevosaurs". Evans (1993) has shown that the three species of *Euposaurus* represent a non-diagnostic lepidosaur and two relatively derived rhynchocephalians.

GEKKOTA: Gekkota is similar to Iguania in that there is complete consensus regarding the monophyly of a clade including Pygopodinae, Diplodactylinae, Gekkoninae, and Eublepharinae, but gekkotan interrelationships remain problematic. Few fossil forms represent this group and previously attributed forms ("ardeosaurids" and "bavarisaurids") have been removed (Evans and Barbadillo, 1997, 1998), leaving the scoring of Gekkota to rest mainly upon extant forms. The extant taxa are scored based on a number of studies dating from the last 40 years (Kluge, 1967, 1969, 1974, 1983, 1987; Estes, 1983; Estes et al., 1988; Schwenk, 1988; Bauer, 1989; Rieppel, 1992; Hutchinson, 1997; Uetz, 2007) as well as upon preserved specimens. Three representative species are coded for Eublepharidae. These were chosen based on the phylogenetic hypotheses of morphology- (Grismer, 1988) and molecular-based studies (Ota et al., 1999). Included are two basal species (*Aeluroscalabotes felinus* and *Coleonyx mitratus*) and a more derived eublepharine (*Hemitheconyx caudicinctus*). The representative gekkonines were chosen similarly, based on the phylogenetic hypotheses presented by Kluge (1967, 1983, 1987) and Han et al. (2004).

Numerous fossil forms, besides those mentioned above, have been attributed to the Gekkota, but most are too incomplete for species level diagnosis. Noteworthy, though, are *Gobekko cretacicus*, *Hoburogekko suchanovi*, and *Pygopus hortulanus*. Of these three taxa, only *Gobekko cretacicus* is included in the current analysis, being represented by a relatively complete skull (Borsuk-Białynicka, 1990). *Hoburogekko* is represented by a partial skull and mandible showing enough features to demonstrate that it is a gekkotan (Alifanov, 1989a, 2000), but there are no characteristics that may diagnose it specifically or distinguish it from gekkonines, pygopods, or diplodactylines (Conrad and Norell, 2006a). *Pygopus hortulanus* is represented only by a dentary resembling (but distinct from) extant *Pygopus* species (Hutchinson, 1997). Although not included as a separate taxon in this analysis, this fossil offers important biostratigraphic information regarding the age of the pygopod lineage.

SCINCOMORPHA: Scincomorpha is a diverse and speciose assemblage of lizards that may or may not represent a monophyletic group exclusive of Gekkota and/or Anguimorpha. Recent studies testing scincomorph monophyly in the broader context of squamates have produced both support for (Estes et al., 1988; Presch, 1988; Wu et al., 1996; Evans and Barbadillo, 1998; Caldwell, 1999a; Vicario et al., 2003; Evans and Wang, 2005; Evans et al., 2005) (see figs. 2–5, 8, 9) and evidence against it (Lee, 1998, 2000; Lee and Caldwell, 2000; Townsend, 2002; Townsend et al., 2004; Vidal and Hedges, 2005) (see figs. 6, 7, 10). Most of these studies agree that Lacertidae, Gymnophthalmidae, and Teiidae form a clade (Lacertiformes of Estes et al., 1988). Presch (1988) places Lacertidae with Scincidae, Cordyliformes [as used by, for example, Lang, 1991; Mouton and Wyik van, 1997; Cooper and Steele, 1999; Odierna et al., 2002; Lamb et al., 2003; Cordylidae of Presch's (1988) usage and that of some other authors; Cordylidae and Gerrhosauridae], and Xantusiidae. Xantusiidae is particularly problematic and has been suggested as having affinities with the lacertiforms (Estes et al., 1988; Caldwell, 1999a) (figs. 2 and 8, respectively), with Cordyliformes and Scincidae (Presch, 1988; Evans and Barbadillo, 1998; Vicario et al., 2003; Townsend et al., 2004; Vidal and Hedges, 2005) (see figs. 4, 10), or with Gekkota (Lee, 1998, 2000; Lee and Caldwell, 2000) (figs. 6, 7). Scincidae and Cordyliformes are typically suggested as being closely related, but some analyses have

found no support for this clade, instead recovering a polytomy between these taxa and Anguimorpha (Lee, 1998, 2000; Lee and Caldwell, 2000).

Polyglyphanodontidae is a Cretaceous radiation of teiid-like lizards that has been suggested as forming a subfamily of Teiidae, possibly close to the Teiinae (Estes, 1983; Gao and Norell, 2000; though see Sulimski, 1975; Alifanov, 1993a). More recently, it has been shown that *Sineoamphisbaena hexatabularis*, previously identified as a basal amphisbaenian (Wu et al., 1996; Lee, 1998), probably represents a derived member of this radiation (Kearney, 2003a, 2003b).

Because of the disagreement about placement of polyglyphanodontines and *Sineoamphisbaena hexatabularis* with regard to Teiidae and other squamates (respectively), Teiidae is broken into Teiinae and Tupinambinae. These two taxa are well recognized as sister taxa and they have been scored based on numerous specimens (appendix 1) and literature (Estes, 1964, 1983; Estes et al., 1988; Uetz, 2007). *Adamisaurus magnidentatus*, *Gobinatus*, *Cherminsaurus*, *Gilmoreteius* (=*Macrocephalosaurus*), *Polyglyphanodon*, and *Sineoamphisbaena hexatabularis* are also included, as well as the possible teiid *Chamops* (Estes, 1964, 1983; Gao and Fox, 1996) are included here. *Bicuspidon numerosus* (Nydam and Cifelli, 2002) and *Peneteius aquilonius* (Nydam et al., 2000) are also probable teiioids known from remains of similar incompleteness as *Chamops*. These taxa may be included in future iterations of this matrix. *Chamops* is included here and *B. numerosus* and *P. aquilonius* are not, in part, because the latter taxa are unquestioned as polyglyphanodontines, whereas there is some question as to the placement of *Chamops* within squamates (summarized in Estes, 1983; Gao and Fox, 1996).

Gymnophthalmidae is retained as a separate taxon following most recent studies and scored based mainly on published accounts (Presch, 1976, 1983, 1988; Estes et al., 1988; Kizirian, 1996; Kizirian and McDiarmid, 1998; Kizirian and Cole, 1999; Montero et al., 2002; Bell et al., 2003). The morphology of this important and intriguing group is understudied and deserves more attention.

Lacertidae is included as a single taxon. Data for Lacertidae comes not only from observations of preserved specimens, but also from literature regarding extant forms (Estes, 1983; Estes et al., 1988; Borsuk-Białynicka et al., 1999; Müller, 2001; Barbadillo and Martínez-Solano, 2002) and regarding the fossils *Succinilacerta* (Borsuk-Białynicka et al., 1999) and *Dracaenosaurus croizeti* (Müller, 2004a).

Representatives from each of the three extant xantusiid genera (*Cricosaura*, *Lepidophyma*, and *Xantusia*) are included in this analysis. Coding is based in part from observation of specimens and also on the literature (Rieppel, 1984a; Peterson and Bezy, 1985; Estes et al., 1988; Maisano, 2003a, 2003b, 2003c, 2003d). *Palaeoxantusia* is included and scored with the assumption that all three named species (*P. fera*, *P. allisoni*, and *P. kyrentos*) represent an exclusive, monophyletic, clade (Hecht, 1956; Schatzinger, 1980; Estes, 1983).

Cordyliformes includes only a few extant taxa and very few fossil forms. This is only one of six taxa scored above the level of ''family'' in this analysis, this because of the relatively low diversity known for the clade and its universal acceptance as monophyletic (McDowell and Bogert, 1954; Romer, 1956; Presch, 1988; Lang, 1991; Mouton and Wyik van, 1997; Odierna et al., 2002; Maisano, 2003e; Uetz, 2007).

Scincidae represents one of the most speciose and morphologically diverse ''families'' of squamates, yet in most cladistic analyses they are coded as a single taxon. There remains some debate about the topology of scincid interrelationships, but several monophyletic groups may be recognized. Greer (1970) recognized the four ''subfamilies'' Feyliniinae, Acontinae, Scincinae, and Lygosominae, but suggested that his Scincinae might be paraphyletic. Rieppel (1981a, 1982,; 1984c) described the skull and jaw adductor musculature in Acontinae and Feyliniinae, concluding that the former were derived scincids, but that the latter represented the sister lineage to the Scincidae; the Feyliniidae. Based on similarities in brain morphology, Northcutt (1978) suggested a close relationship between dibamids, scincids, and snakes (fig. 14). Hallermann (1998) alone has used morphology to test the monophyly of a clade containing the main lineage of
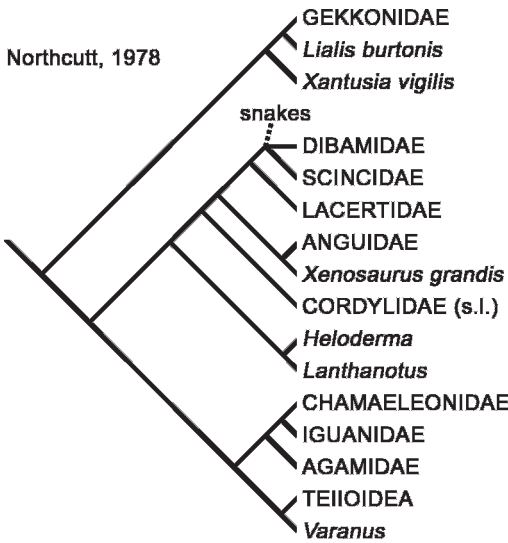
Fig. 14. Northcutt's (1978) vision of squamate interrelationships based on his studies of brain morphology.

skinks, acontines, and feyliniines, but was unable to resolve the interrelationships of these groups (fig. 15). Recent molecular work (Whiting et al., 2003) suggests that Acontinae

is the sister taxon to other scincids, with Feyliniinae forming a sister group to a clade including *Scelotes* and *Proscelotes* (fig. 16), genera regarded as scincines by Greer (1970). Although this paints a confusing picture of scincid interrelationships, in reality these three studies are complementary and seem to identify four major clades of "scincids," including a *Feylinia* clade, an *Acontias* clade, a *Scelotes-Proscelotes* clade, and a larger radiation including genera such as *Scincus*, *Eumeces*, *Lygosoma*, *Mabuya*, *Plestiodon*, and *Tiliqua*. These four clades are referred to here as Feyliniidae, Acontidae, Scelotidae, and Scincidae, respectively, and taxa were selected for scoring based on the topology presented in Greer (1970) and Whiting et al. (2003). These were scored based on observations of specimens (appendix 1) and published data (Greer, 1970; Haas, 1973; Rieppel, 1981a, 1982, 1984c).

In addition to these extant clades of scincomorphs, many additional fossil taxa have been referred to the group, but whose familial affinities are less clear than those described above. Many of the appropriately
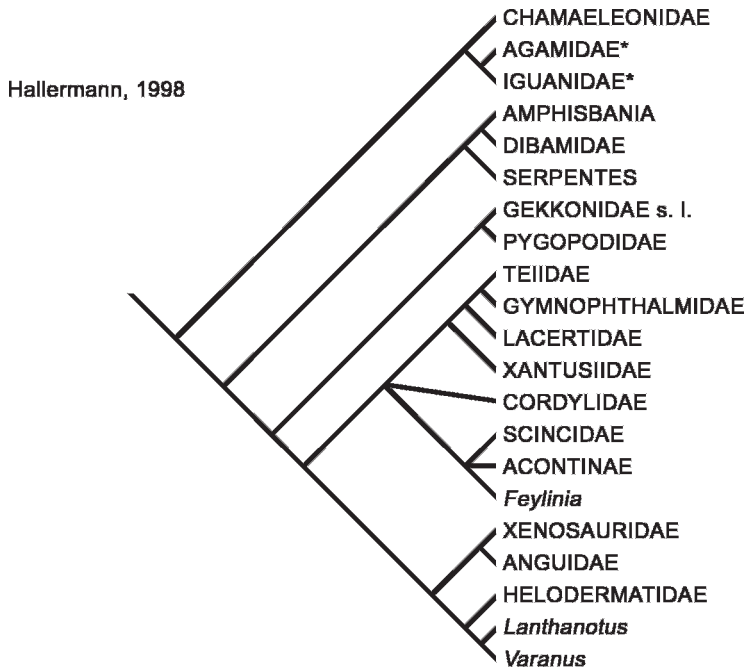
Fig. 15. Hypothesis of squamate interrelationships, based on morphology, as presented by Hallermann (1998).
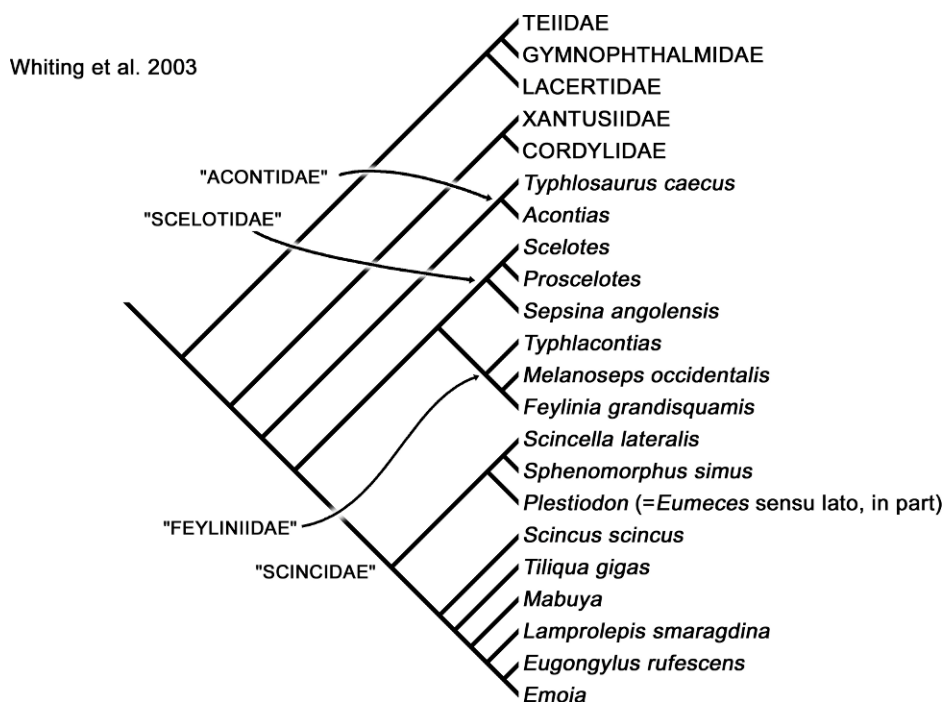
Fig. 16.   Hypothesis of scincomorph interrelationships, based on molecular data, as presented by Whiting et al. (2003). Suprageneric taxon names in quotation marks are the ''family'' names applied to the scincoid groups in the text of the current study. This tree was used to guide selection of exemplars for the identified ''family'' groups. Note that *Plestiodon* is used following Smith (2005).

complete representatives are included in this analysis to offer some additional context for the more clearly resolved fossils, to aid in reconstructing scincomorph nodes, and thus help determine if Scincomorpha is holophyletic. Included in this analysis are *Becklesius hoffstetteri*, *Eoxanta lacertifrons*, *Eolacerta robusta*, *Globaura venusta*, *Meyasaurus diazromerali*, *Paramacellodus oweni*, *Parmeosaurus scutatus*, *Pseudosaurillus* (*P. becklesi* and *P.* sp. of Estes, 1983), *Sakurasaurus shokawensis*, *Slavoia darevskii*, *Tchingisaurus multivagus*, and *Tepexisaurus tepexii*. Several of these taxa have been redescribed based on new material recovered from Cretaceous rocks in the Gobi desert over the last several years (Gao and Norell, 2000). Gao and Norell (2000) described several new scincomorph taxa from the Gobi, including *Hymenosaurus*, *Parmeosaurus scutatus*, and *Tchingisaurus multivagus*. *Eolacerta* was recently redescribed (Müller, 2001) and primary coding for this taxon is based on that excellent paper. Evans and Barbadillo

(1996) have shown that specimens referred to *Meyasaurus diazromerali* and *Ilerdaesaurus* represent a the single taxon (*Meyasaurus diazromerali*) included here. *Becklesius hoffstetteri* includes most of the material referred to *Macellodus brodiei* (Estes, 1983). Monophyly of *Pseudosaurillus* as described by Estes (1983) is ambiguous, and thus *P. becklesi* and *P.* sp. are included as separate taxa.

Numerous fossil scincomorphs are represented by partial mandibles or skull bits; these are omitted from the present analysis, but may be included in future versions of the data set. Notable examples of this include *Estescincosaurus* (=*Sauriscus*) (Sullivan and Lucas, 1996), *Peneteius*, *Leptochamops*, *Contogenys*, and *Palaeoscincosaurus*.

ANGUIMORPHA: Anguimorpha is represented by only about 181 extant species in the five clades *Xenosaurus*, *Shinisaurus*, Anguidae, *Heloderma*, and Varanidae. Even so, extant anguimorphs rival scincomorphs in morphological diversity. The genus *Varanus* alone rivals terrestrial mammals in its size

range (Pianka, 1995). The interrelationships and inclusion or exclusion of other taxa, both extant and fossil, are more contentious. Most studies suggest a monophyletic Varanoidea including *Heloderma*, *Lanthanotus borneensis*, and *Varanus* to the exclusion of Anguidae and *Xenosaurus* (e.g. Lee, 1998; fig. 6), but recent molecular studies call even this into question (Macey et al., 1999; Townsend, 2002; Townsend et al., 2004; Vidal and Hedges, 2005) (see fig. 10).

In addition to these extant anguimorph clades, two major fossil groups have been identified. These are the Mosasauroidea and the Necrosauridae (=Parasaniwidae of Estes, 1964). Besides these, a number of miscellaneous taxa that seem to defy placement in any previously defined group have been described.

Many recent phylogenetic analyses have coded Xenosauridae as a single taxon including *Shinisaurus* (Estes et al., 1988; Wu et al., 1996; Evans and Barbadillo, 1998; Lee, 1998, 2000). New data show this to be potentially misleading. It relies upon and incorporates erroneous morphological characterizations for *Shinisaurus*, *Xenosaurus*, or both (Conrad, 2004a, 2006a, 2006b). Consequently, *Shinisaurus* and *Xenosaurus* are here scored as separate taxa. *Xenosaurus* is scored from observations of both *X. platyceps* and *X. grandis* as well as from the literature (Barrows and Smith, 1947; McDowell and Bogert, 1954; King and Thompson, 1968; Rieppel, 1980a; Gao and Norell, 1998; Ramos et al., 2000; de Oca et al., 2001). Additionally, four fossil taxa have been referred to the Xenosauridae. *Restes rugosus* (Gauthier, 1982; =*Exostinus rugosus* of Gilmore, 1942a) is represented by most of the dermal bones of the skull roof and included here, coded from the literature (Estes, 1975, 1983; Gauthier, 1982). Gauthier (1982) questioned the monophyly of *Exostinus serratus* and *E. lancensis*. Both are included here, with codings for *E. serratus* based mainly on Gilmore (1928) and Estes (1964, 1983), and *E. lancensis* based on Gilmore (1928), Gauthier (1982), Estes (1964, 1976, 1983), and Gao and Fox (1996). A fossil genus based on incomplete dentaries from the Cretaceous, *Oxia*, has additionally been referred to Xenosauridae (Gao and Nessov, 1998), but this material is non-diagnostic and is omitted here.

Recent analyses suggest that *Carusia* (the senior synonym of *Shinisauroides* as shown by Gao and Norell, 1998), sometimes considered an unusual scincomorph (Borsuk-Białynicka, 1985; Alifanov, 2000), is actually an anguimorph close to Xenosauridae (Gao and Hou, 1996; Gao and Norell, 1998, 2000; but see Conrad, 2006b) (fig. 11). This taxon is included in the current analysis. The possible carusioid relative *Dalinghosaurus longidigitus* is included based on published data (Ji, 1998; Ji and Ji, 2004; Evans and Wang, 2005).

Shinisaurus crocodilurus is included and its osteology and external morphology is scored almost exclusively from observations of skeletonized and preserved specimens, supplemented by data from the excellent study of Bever et al. (2005a). Muscle characters and other morphological data are derived from the published literature (McDowell and Bogert, 1954; Haas, 1960; Rieppel, 1980a; Zhang, 1991; Zhao et al., 1999). The recently described *Bahndwivici ammoskius* is included based on direct observations summarized by Conrad (2006b).

Monophyly of Anguidae is unquestioned, but no cladistic analysis has ever tested the relationships and interrelationships of the entire anguid clade. Based on molecular data (Macey et al., 1999; Wiens and Slingluff, 2001) and overall similarity (Uetz, 2007), the extant genera may be divided into the Gerrhonotinae (*Abronia*, *Barisia*, *Coloptychon*, *Elgaria*, *Gerrhonotus*, and *Mesaspis*), the Diploglossinae (*Celestus*, *Diploglossus*, and *Ophiodes*), and the Anguinae (*Anguis*, *Ophisaurus*, and *Pseudopus*), with *Anniella* representing its own lineage or nested in one of the others. Indeed, Macey et al. (1999) and Wiens and Slingluff (2001) demonstrate paraphyly of *Ophisaurus* with respect to both *Pseudopus* and *Anguis*, and paraphyly of *Diploglossus* with respect to the other diploglossines (fig. 17). More broadly, a fossil radiation close to extant anguids, the glyptosaurs, is usually overlooked entirely. For example, Gao and Norell (1998) include representative members of the four major clades of extant Anguidae in their analysis, but did not address glyptosaurs.

A   **B**

Macey et al. 1999   Wiens & Slingluff 2001

Heloderma suspectum
Varanus griseus
Shinisaurus crocodilurus
Xenosaurus grandis
Anniella (2 sp.)
Celestus enneagrammus
Diploglossus bilobatus
Diploglossus pleei
Ophiodes striatus
Sauresia agasepsoides
Wetmorena haetiana
Barisia imbricata
Gerrhonotus liocephalus
Abronia oaxacae
Mesaspis moreleti
Elgaria (5 sp.)
Ophisaurus koellikeri
Anguis fragilis
Pseudopus apodus
Dopasia harti
Ophisaurus ventralis
"Ophisaurus" attenuatus

Fig. 17.   Hypotheses of anguid interrelationships, based on molecular data, as presented by **(A)** Macey et al. (1999) and **(B)** Wiens and Slingluff (2001).

Because of the poorly understood relationships of this clade as a whole, numerous taxa are included here. Included here are the extant taxa *Anguis fragilis*, *Anniella pulchra*, *Ophisaurus ventralis*, *O. attenuatus*, *Pseudopus apodus*, *Dopasia harti*, *Diploglossus millepunctatus*, *Celestus costatus*, *Ophiodes* sp., *Gerrhonotus liocephalus*, *Abronia deppii*, and *Barisia imbricata* from specimens (see appendix 1). Additional data was taken from the literature for *A. pulchra* (Coe and Kunkel, 1906; McDowell and Bogert, 1954; Bellairs, 1970; Rieppel, 1978, 1980b; Gao and Norell, 1998), and *A. fragilis* (Bellairs, 1970; Rieppel, 1980b; Iordansky, 1997; Gao and Norell, 1998). Published codings and descriptions were used for *G. multicarinata*, *Ab. mixteca*, *P. apodus*, *Di. lessonae*, and *Ophiodes striatus* (Meszoely, 1970; Rieppel, 1980a; Gao and Norell, 1998).

Taxonomy and scoring of fossil taxa comes from their associated reference literature and observation of specimens. Taxa included paired with the literature that was used to code or supplement their codings here are *Apodosauriscus minutus* (Gauthier, 1982), *Arpadosaurus gazinorum* (Meszoely, 1970), *Bainguis parvus* (Borsuk-Białynicka, 1984; Gao and Hou, 1996), *Glyptosaurus sylvestris* sensu Sullivan (1979, 1986, 1989) (Gilmore, 1928; Sullivan, 1979,1986, 1989; Estes, 1983), *Helodermoides tuberculatus* (Gilmore, 1928; Sullivan, 1979, 1986, 1989; Estes, 1983), *Melanosaurus maximus* (Estes, 1983), *Odaxosaurus* sensu Gauthier (1982) (Meszoely, 1970; Sullivan, 1979; Gauthier, 1982; Estes, 1983), *Ophisauriscus quadrupes* (Sullivan et al., 1999), *Paragerrhonotus ricardensis* (Estes, 1963, 1983), *Paraglyptosaurus princeps* (Sullivan, 1979), *Parophisaurus pawneensis* (Sullivan, 1987), *Peltosuarus granulosus* sensu Estes (1983) (Gilmore, 1928; Estes, 1964, 1983), *Proglyptosaurus huerfanensis* sensu Sullivan (1989) (Sullivan, 1979, 1989), *Proxestops jepseni* sensu Gauthier (1982) (Estes, 1964, 1983; Gauthier, 1982), and *Xestops*

vagans sensu Sullivan (1979) (Meszoely, 1970; Meszoely et al., 1978; Sullivan, 1979; Estes, 1983) (see appendix 1).

Noteworthy exclusions from this analysis include the gerrhonotine genera *Coloptychon* and *Mesaspis* among extant forms. *Placosaurus* and *Paraplacosauriops* were recently reviewed (Augé and Sullivan, 2006; Sullivan and Augé, 2006) and will be included in future versions of this analysis. *Eodiploglossus* (Gauthier, 1982) awaits redescription.

Heloderma includes the extant beaded lizard (*H. horridum*) and the Gila monster (*H. suspectum*). These species and the fossil *H. texana* are included in the present analysis as individual taxa in order to determine their positions relative to one another. Extant *Heloderma* are scored primarily based on observations of specimens (appendix 1). *Heloderma texana* was scored based on published descriptions (Estes, 1983; Pregill et al., 1986) and digital scans (Maisano, 2001a).

Although *Heloderma* is the sole extant genus of Helodermatidae, a number of fossil taxa have been associated with this clade. The following taxa are included based on observations of specimens and published data: *Estesia mongoliensis* (Norell et al., 1992; Norell and Gao, 1997; Gao and Norell, 1998, 2000; Nydam, 2000), *Eurheloderma gallicum* (Hoffstetter, 1957; Estes, 1983; Norell and Gao, 1997; Gao and Norell, 1998; Nydam, 2000), *Gobiderma pulchrum* (Borsuk-Białynicka, 1984; Gao and Norell, 1998, 2000), *Lowesaurus matthewi* (Gilmore, 1928; Estes, 1983; Pregill et al., 1986; Gao and Norell, 1998), *Paraderma bogerti* (Estes, 1964; Gao and Fox, 1996; Nydam, 2000), and *Primaderma nessovi* (Cifelli and Nydam, 1995; Nydam, 2000). Both extant species of *Heloderma* are included and are scored based on observations of specimens and also on published data (McDowell and Bogert, 1954; Bogert and Del Campo, 1956; Rieppel, 1980a; Pregill et al., 1986; Bernstein, 1999).

Varanidae includes at least 45 extant species (Pianka, 1995; Fuller et al., 1998; Ast, 2001) and possibly more than 60 (Uetz, 2007) in the two genera *Lanthanotus borneensis* and *Varanus*. Although the affinities of the monospecific *Lanthanotus borneensis* have been problmatic in the past (McDowell

and Bogert, 1954), a consensus opinion has arisen that it is the extant sister taxon to *Varanus* (Rieppel, 1980a; Pregill et al., 1986; Lee, 1997, 1998; Evans and Barbadillo, 1998; Gao and Norell, 1998; Lee and Caldwell, 2000; though see Caldwell, 1999a) (figs. 6–9, 11). *Lanthanotus borneensis* was scored based on observations of specimens and on published descriptions (McDowell and Bogert, 1954; Haas, 1973; Rieppel, 1980a, 1980b, 1983; Maisano, 2001b; Maisano et al., 2002).

Recently, molecular data have been employed to identify clades within *Varanus*, with some consistency of results (Fuller et al., 1998; Ast, 2001, 2002; Pepin, 2001). Ast (2002) is the most recent of these analyses and also the most species-inclusive. Multiple species of *Varanus* are included in the present analysis to help identify some of the broader relationships among *Varanus*, because of their relatively certain monophyly based on comparisons of various analyses, and to test their monophyly exclusive of similar taxa such as *Megalania prisca*, *Saniwa ensidens*, and *Saniwides mongoliensis*; something not previously tested. Species used for coding these taxa were selected based on the cladistic relationships suggested by molecular data (Ast, 2001, 2002; Pepin, 2001) and were scored based on observations of specimens and published data (Mertens, 1942a, 1942b, 1942c; Bellairs, 1949; McDowell and Bogert, 1954; Bellairs, 1970; Haas, 1973; Rieppel, 1980a; Jenkins and Goslow, 1983; Zaher and Rieppel, 1999a). In addition to these other taxa, one fossil species described as *Varanus rusingensis* (Clos, 1995) is included because it is the earliest known specimen that may be reliably referred to *Varanus*.

Numerous fossils have been referred to the Varanidae and many are included here. *Megalania prisca* is the largest-known terrestrial lizard and may belong within crown group *Varanus* (Hecht, 1975; Molnar, 1990, 2004; Lee, 1995). This taxon is incomplete, but the characters for which it may be coded show non-synonymous coding with other observed taxa.

Several species have been referred to *Saniwa*, but only the type species (*S. ensidens*) and a possible ''necrosaurid'' (below) are included here based on published descriptions (Gilmore, 1928; Estes, 1983; see also the

necrosaurid literature used below). Estes (1983) regarded *S. agilis* as a probable synonym of *S. ensidens*. The type specimens for *S. brooksi*, *S. crassa*, *S. grandis*, *S. orsmaelensis*, and *S. paucidens* are isolated vertebrae or a series of several vertebrae that are probably too incomplete for generic or specific diagnosis (Estes, 1983; Augé, 2005); these taxa are not included here. Vertebrae from the Eocene of Kirghizia have been referred to ?*Saniwa* sp. (Averianov and Danilov, 1997), but these lack varanid characteristics and are otherwise non-diagnostic. *Saniwa australis* is a nomen dubium (Báez and de Gasparini, 1977; Estes, 1983) and is not included.

A European fossil broadly resembling varanids has been described as *Saniwa feisti* (Stritzke, 1983). Although probably not representing a *Saniwa*, this taxon is relatively completely known (Stritzke, 1983; Keller and Schaal, 1992) and is included in the analysis.

Saniwides mongoliensis, *Telmasaurus grangeri*, and *Cherminotus longifrons*, all from the Gobi, show varanid affinities and are included here based observations of specimens and published descriptions (Gilmore, 1943; Estes, 1983; Borsuk-Białynicka, 1984; Gao and Norell, 2000). Gao and Norell (2000) have added two new Gobi lizards to the Varanidae. One of these, *Aiolosaurus*, is included in this analysis; the other was deemed too incompletely known by Gao and Norell (2000) to be named and is not included here.

Palaeosaniwa canadensis represents a problematic taxon identified variably as a varanid (Gilmore, 1928; Estes, 1964, 1983) or a helodermatid (Balsai, 2001). Regardless, it is included in this analysis based on the original descriptions (Gilmore, 1928; Estes, 1964, 1983) and on a recently described new specimen (Balsai, 2001).

Various fossils too incomplete to be included here have been referred to the Varanidae. Noteworthy is the Middle Miocene *Iberovaranus catalaunicus* (Hoffstetter, 1969; Estes, 1983).

Dolichosauridae is a group of Cretaceous lizards with reduced limbs and an overall morphology that looks to be intermediate between terrestrial varanids and the fully aquatic mosasaurs (Romer, 1966; Carroll, 1988b; Caldwell, 2000; Lee and Caldwell, 2000). Most of the taxa referred to as dolichosaurids have been recently redescribed and all are included here at the generic level or below. Included are *Adriosaurus suessi* (=*Acteosaurus crassicostatus*) (Lee and Caldwell, 2000; Caldwell and Lee, 2004), *Coniasaurus* (based on both *C. crassidens* and *C. gracilodens*) (Bell et al., 1982; Caldwell, 1999b; Caldwell and Cooper, 1999), *Dolichosaurus longicollis* (Caldwell, 2000), *Eidolosaurus trauthi* (Nopcsa, 1923a), and *Pontosaurus* (=*Hydrosaurus*) (Kornhuber, 1873; Dal Sasso and Pinna, 1997). Dal Sasso and Pinna (1997) described *Aphanizocnemus*, demonstrating some affinities with *Adriosaurus* and *Dolichosaurus longicollis* (Lee and Caldwell, 2000).

Aigialosauridae is usually considered a paraphyletic assemblage of basal mosasauroids forming successively more proximal outgroups to Mosasauridae (Bell, 1997; Lee, 1997; Caldwell, 1999a; Dutchak, 2005, 2006; Dutchak and Caldwell, 2006), but some analyses (Caldwell, 1996, 2000; Bardet et al., 2003) recover an aigialosaurid clade. Because of this ambiguity and to avoid misinterpretation of the basal character polarities for a single-taxon aigialosaur group, the aigialosaur species are included individually here. *Aigialosaurus dalmaticus* is the only species of *Aigialosaurus* included and it is scored from Carroll and DeBraga (1992). There is some question as to the generic and/or specific distinctiveness of *Opetiosaurus buchichi* from *A. dalmaticus* (Carroll and DeBraga, 1992; Caldwell, 1996, 2000), although recent work suggests more convincingly that they are distinct (Dutchak, 2005, 2006; Dutchak and Caldwell, 2006). Both are included based primarily on the descriptions of Carroll and DeBraga (1992), Dutchak (2005), and Dutchak and Caldwell (2006). *Carsosaurus marchesetti* seems to represent a taxon distinct from *Aigialosaurus* and *Opetiosaurus* and is here included based on recent descriptive works (Carroll and DeBraga, 1992; Caldwell, 1996, 2000). *Tethysaurus nopcsai* is a recently described lizard of a similar ''grade'' as aigialosaurids (Bardet et al., 2003) also included in the analysis.

Proaigialosaurus has been lost (Carroll and DeBraga, 1992) and is not included in the present analysis. The recently described
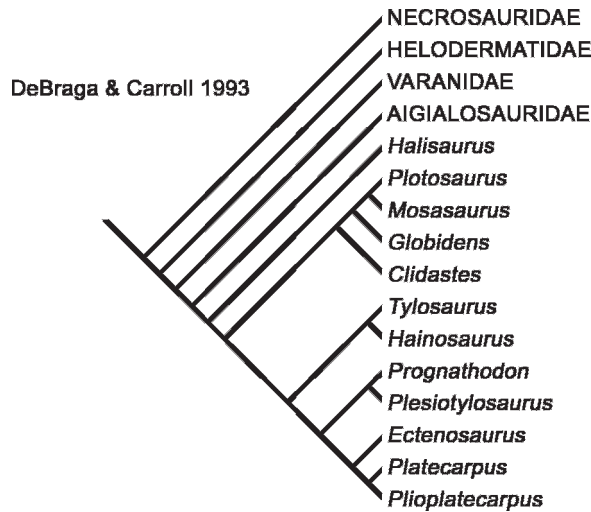
Fig. 18. Hypothesis of mosasaur interrelationships as presented by DeBraga and Carroll (1993). Note that Helodermatidae and Varanidae include extant taxa, but all other taxa are fossils.

Dallasaurus turneri (Bell and Polcyn, 2005) and *Russellosaurus coheni* (Polcyn and Bell, 2005) will be included in future analyses.

Mosasauridae is a Late Cretaceous radiation of large aquatic lizards. Existing phenetic groupings and cladistic systematic analyses (Russell, 1967; Carroll, 1988b; DeBraga and Carroll, 1993; Bell, 1997) have been limited in scope to mostly North American and European taxa and have had conflicting results (DeBraga and Carroll, 1993; Bell, 1997) (figs. 18, 19). Given this, scoring a single-taxon Mosasauridae would be difficult; so multiple mosasaurid taxa are scored for this analysis based on previous descriptive and phylogenetic studies. *Halisaurus arambourgi*, *H. platyspondylus* and *Eonatator sternbergii* (=*Halisaurus sternbergii*) are included as separate taxa based on recent descriptive works (Russell, 1967; DeBraga and Carroll, 1993; Holmes and Sues, 2000; Bardet and Suberbiola, 2001; Bardet et al., 2005). Debate continues over the distinctiveness of these taxa at both the generic and specific level (Caldwell, 1996; Lingham-Soliar, 1996; Bell, 1997; Holmes and Sues, 2000; Bardet and Suberbiola, 2001), but they are not identical in coding and so each is included.

Clidastes liodontus is included mainly on data from Russell (1967). Multiple species of *Clidastes* have been described (Russell, 1967; Bell, 1997) and may form a paraphyletic grade (Bell, 1997; Christiansen and Bonde, 2002). Only *C. liodontus* is used here based mainly on accessibility of descriptions and specimens.

Ectenosaurus clidastoides was initially considered a species of *Platecarpus*, but Russell (1967) identified it as representing an independent lineage. This species is included and scored based on photos of Sternberg Museum VP 40 generously provided by M. J. Everhart (personal commun.) and data in Russell (1967) and DeBraga and Carroll (1993).

Data for both species of *Globidens* (*G. alabamaensis* and *G. dakotensis*) were used to score the single-taxon *Globidens* (Gilmore, 1911; Russell, 1967, 1975; Bell, 1997; Lingham-Soliar, 1999a). *Carinodens* is not included because it is very incompletely known and strongly resembles *Globidens* in scoreable features (Lingham-Soliar, 1999a). *Carinodens* and other mosasaurids not included here may be included in future incarnations of this analysis.

Goronyosaurus nigeriensis is an overlooked taxon that has appeared in no previous analyses of squamate or mosasaur relationships. Originally described as *Mosasaurus nigeriensis* (Azzaroli et al., 1975), *Goronyosaurus* is currently a monospecific taxon whose anatomy was reviewed and clarified by Soliar (1988). This mosasaurid was coded
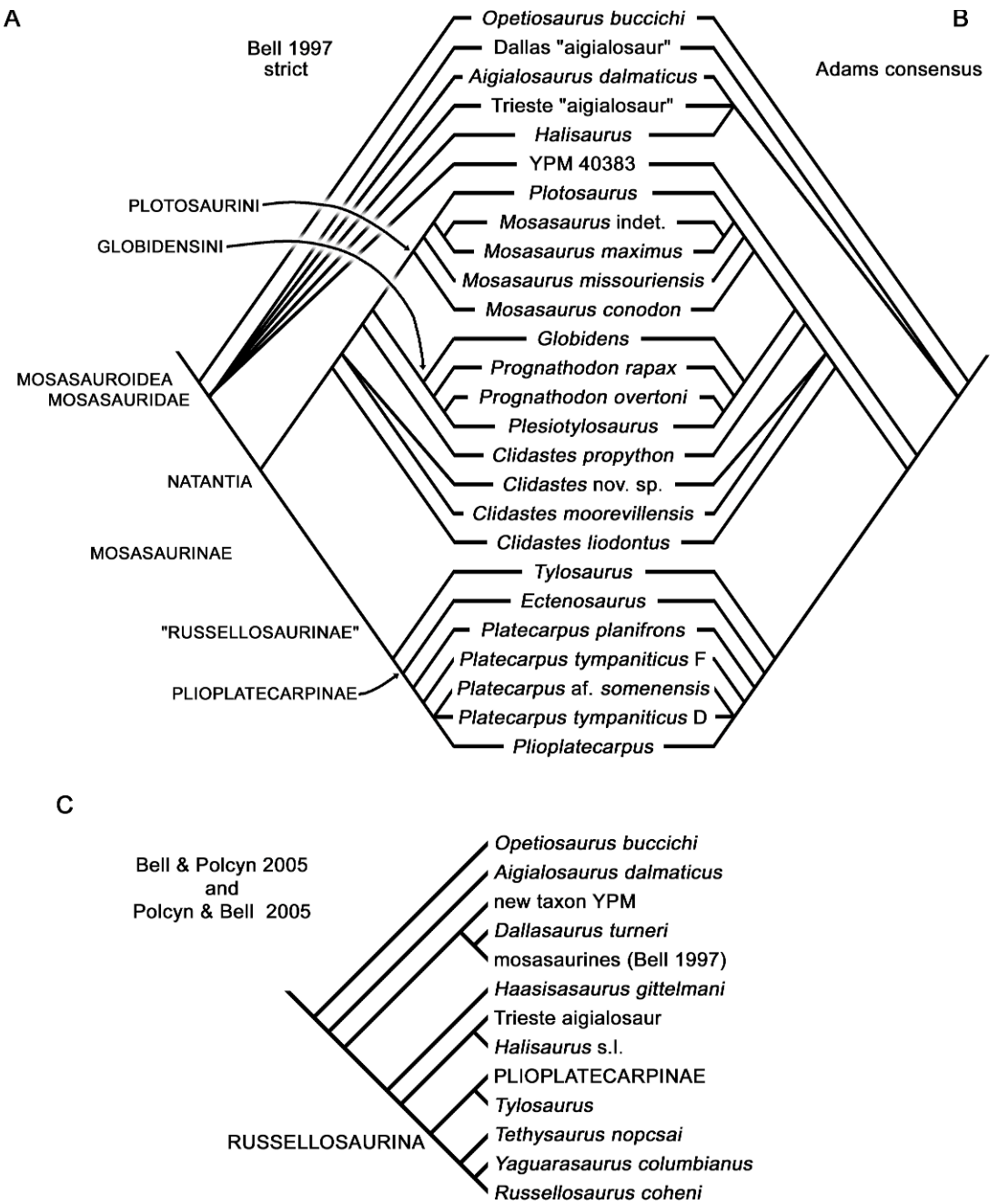
Fig. 19.   Hypothesis of mosasaur interrelationships as presented by **(A–B)** Bell (1997) and **(C)** Bell and Polcyn (2005) and Polcyn and Bell (2005). Note that the taxon labeled ''mosasaurines (Bell 1997)'' refers to *Clidastes*, Globidensini, and Plotosaurini from **(A)**. All displayed taxa are fossils.

based on descriptive works (Swinton, 1930; Azzaroli et al., 1975; Soliar, 1988; Lingham-Soliar, 1991, 1999b, 2002).

Hainosaurus is included here based on a recent redescription of *H. bernardi* from a nearly complete skeleton (Lingham-Soliar, 1992a) and on the account given by Russell (1967). *Hainosaurus gaudryi* (Lingham-Soliar, 1992a) and *H. pembinensis* (Nicholls, 1988; Lingham-Soliar, 1992a) may or may not be distinct from *H. bernardi*; only *H. bernardi* is included in this analysis.

Lakumasaurus antarcticus represents the only relatively complete squamate currently known from Antarctica. It has been briefly described as a basal tylosaurine and this description was used for coding character states in this analysis (Novas et al., 2002).

*Moanasaurus mangahouangae* is a mosasaurid from New Zealand that encompasses specimens previously attributed to *Mosasaurus flemingi* and *Rikisaurus tehoensis*. This taxon is scored based on published descriptions of these specimens (Wiffen, 1980, 1990).

Under its recent usage, the name *Mosasaurus* represents a speciose assemblage of mosasaurids probably not representing a monophyletic group to the exclusion of *Plotosaurus* (Bell, 1997; Christiansen and Bonde, 2002; Bell and Polcyn, 2005; Polcyn and Bell, 2005). Russell (1967) reviewed all of the then-described species of *Mosasaurus*. Based on this review, *M. conodon*, *M. ivoensis*, and *M. missouriensis* are relatively incompletely known taxa that are difficult to differentially diagnose. The position of these taxa must be further analyzed elsewhere. The two species of *Mosasaurus* included in this analysis, *M. hoffmanni* and *M. lemonnieri*, are based on reasonably complete specimens. *Mosasaurus maximus* has been convincingly shown to be synonymous with *M. hoffmanni* (Mulder, 1999) and so specimens and descriptions of both species are used for coding *M. hoffmanni* (Russell, 1967; Lingham-Soliar, 1995; Bell, 1997; Mulder, 1999). Lingham-Soliar (2000) rejects the synonymy of *M. lemonnieri* with *M. conodon* and his descriptive work is used for coding *M. lemonnieri* here.

Platecarpus is another relatively speciose group of mosasaurids probably not representing a holophyletic clade with respect to

other taxa. *Plioplatecarpus* has been demonstrated to fall within the *Platecarpus* radiation (Bell, 1997; Christiansen and Bonde, 2002; Bell and Polcyn, 2005; Polcyn and Bell, 2005). As described by Russell (1967), *Platecarpus tympaniticus* probably represents the senior subjective synonym for *P. ictericus* and *P. coryphaeus* (=*P. abruptus*) (but see Christiansen and Bonde, 2002). *Platecarpus planifrons* is not included in this analysis, pending full description of a new specimen. Here, *Platecarpus* has been scored based on *P. tympaniticus* and its subjective synonyms based on published data (Williston, 1910; Russell, 1967) and examination of specimens.

Plioplatecarpus is presumed to be a monophyletic radiation of mosasaurids, but is known from relatively few good specimens. Here, *Plioplatecarpus* was scored using data presented in previous descriptive and phylogenetic works of various specimens and species, especially *P. primaevus* sensu Holmes (1996) (Russell, 1967; Burnham, 1991; Lingham-Soliar, 1992b; Holmes, 1996; Bell, 1997; Christiansen and Bonde, 2002).

Plotosaurus (=*Kolposaurus* of Camp, 1942) is known from two species, *Plotosaurus bennisoni* and *P. tuckeri*, that may form a single species. Apparently, they are a monophyletic group scored here as a single taxon based on the original description (Camp, 1942).

Prognathodon is a speciose genus of large-bodied mosasaurids (Russell, 1967; Lingham-Soliar and Nolf, 1989; Bell, 1997; Christiansen and Bonde, 2002). The monophyly of this genus has been tested and corroborated (Christiansen and Bonde, 2002). Recent studies (Bell, 1997; Bell and Polcyn, 2005; Polcyn and Bell, 2005) have suggested that the poorly known *Plesiotylosaurus crassidens* (not included here) may belong within this radiation. Two representative species of *Prognathodon*, *P. overtoni* and *P. solvayi*, have been scored individually here based on previous phylogenetic codings and descriptions (Bell, 1997; Christiansen and Bonde, 2002) and published descriptions (Russell, 1967; Lingham-Soliar and Nolf, 1989).

Based on a recent analysis (Novas et al., 2002), *Tylosaurus proriger* and *T. nepaeolicus* may not represent a monophyletic assemblage with respect to *Hainosaurus*. Because of

this uncertainty, these two species must be treated separately. However, *T. nepaeolicus* is in need of redescription, so only *T. proriger* is included here and coded based on observations of specimens (appendix 1) and published literature (Osborn, 1899; Russell, 1967; Bell, 1997).

Various other mosasaurs have been described and named based on inferior remains and are omitted here. Notable among these are *Amphekepubis* and *Pluridens*. *Amphekepubis* is a pelvis with a few associated vertebrae that may or may not be diagnostic (Russell, 1967). *Pluridens* is represented by a single dentary from Niger that is probably diagnostic of a new taxon (Lingham-Soliar, 1998), but it is too incomplete for meaningful inclusion here.

Necrosauridae is generally acknowledged as a problematic group that may not represent a monophyletic assemblage (Pregill et al., 1986; Norell et al., 1992; Evans, 1994a; Lee, 1997; Gao and Norell, 1998; Conrad, 2005b). Although incompletely known, most ''necrosaurids'' preserve enough informative morphology for specific diagnosis and are included in this analysis. Included taxa have been scored primarily on published descriptions (but see appendix 1). Besides *Necrosaurus*, the taxa included here and their associated references are *Colpodontosaurus* (Estes, 1964, 1983), *Eosaniwa* (Estes, 1983; Gao and Norell, 1998; Rieppel et al., 2007), *Parasaniwa* (Gilmore, 1928; Estes, 1964, 1975, 1976; Gao and Fox, 1996; Gao and Norell, 1998), *Parviderma* (Borsuk-Białynicka, 1984; Gao and Norell, 1998), and *Proplatynotia* (Borsuk-Białynicka, 1984; Gao and Norell, 1998). *Necrosaurus* itself may or may not represent a monophyletic group. *Necrosaurus cayluxi*, *N. eucarinatus*, and *Saniwa feisti* (possibly a *Necrosaurus*, see above) have been coded as separate taxa based on published data (Hoffstetter, 1943; Haubold, 1977; Rage, 1978; Estes, 1983; Stritzke, 1983; Keller and Schaal, 1992; Augé, 2005).

Several taxa of a similar ''grade'' to necrosaurs have been described and are included here. *Paravaranus angustifrons* was suggested as having possible affinities with Mosasauroidea by Alifanov (2000); this was independently confirmed by a recent analysis (Rieppel et al. 2007). It is included here and was coded based on its original description (Borsuk-Białynicka, 1984). *Dorsetisaurus purbekensis* was coded based on Hoffstetter (1967a). *Parviraptor* is a problematic taxon of this ''grade,'' that may or may not represent a single taxon (Evans, 1994a). A possible anguimorph from Portugal, *Lisboasaurus estesi* (Seiffert, 1973) needs re-evaluation and redescription and is not included here.

DIBAMIDAE: Dibamidae exhibits low diversity, including only about 18 species in *Dibamus* and *Anelytropsis papillosus* (Das and Lim, 2005; Uetz, 2007). Dibamids are important for inclusion in this analysis because of their uncertain affinities. Importantly, no broad-scale cladistic analysis has addressed the monophyly of Dibamidae, despite some relatively plesiomorphic character states in *Anelytropsis papillosus* and their disparate ranges (Rieppel, 1984b; Greer, 1985; Uetz, 2007). Consequently, published descriptions were used to score *Dibamus novaeguineae* (Gasc and Renous, 1979; Rieppel, 1984b; Greer, 1985) and *Anelytropsis papillosus* (Greer, 1985) separately in this analysis. There are no known fossil dibamids.

AMPHISBAENIA: Amphisbaenia is a bizarre clade of mostly limbless squamates whose interrelationships have been recently re-analyzed very thoroughly (Kearney, 2001, 2003a; Kearney and Stuart, 2004). These analyses are the basis for dividing amphisbaenian diversity into the five taxonomic units (Rhineuroidea, Trogonophidae, Amphisbaenidae, *Bipes*, and *Blanus*) scored here. Also based on the topology of Kearney (2001, 2003a), taxa near the bases of these major lineages were used to score those lineages from the literature (Zangerl, 1944; Gans, 1960; Montero and Gans, 1999; Kearney, 2001, 2002, 2003a; Maisano, 2003f, 2003g, 2003h, 2003i; Kearney and Maisano, 2004) and from direct observations of specimens. Taxa excluded from consideration also follows that of Kearney (2003a). Future versions of this analysis will include multiple species from each of the major amphisbaenian lineages.

SERPENTES: Although the monophyly of snakes (=Ophidia sensu Caldwell and Lee, 1997) is unquestioned, the interrelationships

of the major snake taxa are not. Because Cretaceous limbed marine snakes may represent primitive snakes (Caldwell and Lee, 1997; Lee, 1997, 1998; Lee et al., 1999a, 1999b; Caldwell, 2000; Lee and Caldwell, 2000; Rage and Escuillé, 2000; Scanlon and Lee, 2000) or derived alethinophidians (Zaher and Rieppel, 1999b, 2002; Rieppel and Zaher, 2000a, 2000b, 2001; Tchernov et al., 2000; Rieppel et al., 2003), reliably reconstructing the ancestral states for snakes and scoring them as a single taxon is not a viable option if the idea is to test the phylogenetic placement of snakes within squamates. For the purposes of this study, snakes are broken up into 12 separate taxa: Anilioidea, *Dinilysia patagonica*, *Eupodophis descouensi*, *Haasiophis terrasanctus*, *Leptotyphlops goudottii*, *Liotyphlops albirostris*, ''other macrostomatans'', *Pachyophis woodwardi*, *Pachyrhachis problematicus*, *Typhlops lineolatus*, *Wonambi naracoortensis*, and *Xenopeltis unicolor*. All taxa based mainly upon extant species (Anilioidea, macrostomatans, and scolecophidians) were scored via a combination of observations of specimens (appendix 1) and published literature.

Three representative scolecophidians are included based on specimens and published data (Evans, 1955; List, 1966; Parker and Grandison, 1977; Scanlon and Lee, 2000; Tchernov et al., 2000; Kley, 2006). Anilioidea is of questionable monophyly, supported by recent analyses (Scanlon and Lee, 2000; Tchernov et al., 2000; Lee and Scanlon, 2002a) and is tentatively accepted here. Most of the coding for Anilioidea comes from published literature (Rieppel, 1977, 1979; Rieppel and Zaher, 2000a, 2002; Scanlon and Lee, 2000; Tchernov et al., 2000; Lee and Scanlon, 2002a). Tchernov et al. (2000) found *Pachyrhachis problematicus* and *Haasiophis terrasanctus* to be nested within Macrostomata. To make this analysis sensitive to that possibility, extant Macrostomata was broken into *Xenopeltis* [with supplementary codings from the literature (Scanlon and Lee, 2000; Tchernov et al., 2000; Lee and Scanlon, 2002a)] and a group informally termed ''other macrostomatans'' to receive all other extant taxa traditionally considered to be macrostomatans (see Rieppel and Zaher, 2000a; Scanlon and Lee, 2000; Tchernov et

al., 2000; Lee and Scanlon, 2002a; codings also based on data taken from these studies).

Fossil snakes were coded based on the following literature: *Dinilysia patagonica* (Estes et al., 1970; Rage, 1984; Caldwell and Albino, 2001, 2003), *Eupodophis descouensi* (Rage and Escuillé, 2000; Rieppel et al., 2003; Rieppel and Head, 2004), *Haasiophis terrasanctus* (Tchernov et al., 2000; Rieppel et al., 2003), *Pachyophis woodwardi* (Nopcsa, 1923a; Lee et al., 1999b; Caldwell and Albino, 2001; Rage and Escuillie, 2002; Rieppel et al., 2003; Rieppel and Head, 2004), *Pachyrhachis problematicus* (Zaher and Rieppel, 1999b, 2002; Lee and Caldwell, 2000; Rieppel and Zaher, 2000a; Caldwell and Albino, 2001; Polcyn et al., 2005a, 2005b), *Wonambi naracoortensis* (Scanlon and Lee, 2000; Rieppel et al., 2002).

DATA ANALYSIS

PRINCIPLE TREE SEARCHES: The data matrix used in this analysis is very large and a PAUP* (Swofford, 2001) analysis of the data set would take months. Goloboff et al. (2003) offer an alternative, a program called T.N.T. (tree analysis using new technology), which is very efficient at analyzing this type of data set (Hovenkamp, 2004). T.N.T. was used here with the specifications given below.

CONSENSUS TREES AND APOMORPHY LISTS: T.N.T. does not offer the option of reconstructing Adams consensus trees. The principle trees were exported from T.N.T. to PAUP* (Swofford, 2001) for reconstruction of Adams consensus trees and for the reconstruction of an apomorphy list.

VIEWING TREES: Principle trees were primarily viewed in TreeViewX, version 0.4 (Page, 2004). This program was used to quickly view the principle trees and to discover the alternative placements of some volatile taxa (e.g., basal varanoids; see below).

DEFORMATION COMPARISONS AND DECAY INDICES: Deformation comparisons (see below) were performed using the program Mesquite (Maddison and Maddison, 2006), a program which allows easy movement of branches within a tree with simultaneous reports of length change. Decay indices (Bremer support) were calculated using the

"Suboptimal Search" criteria in T.N.T. (Goloboff et al., 2003).

INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History; FMNH, Field Museum of Natural History; GM, Geiseltal Museum of the Martin-Luther-Universität in Halle/Saale (Germany); IGM, Institute of Geology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; REE, Richard E. Etheridge Collection; UF, University of Florida, Florida State Museum.

CHARACTER LIST FOR SQUAMATA

Below is a list of morphological characters used in this study. Each character and some of the character states are followed by an abbreviation identifying the publication from which the character or character state was taken. This reference does not always correspond with the original use of a particular character or character state, but rather the specific study used to derive the character as used in this study. The abbreviations are listed below with their corresponding study listed afterward. A dash (-) and a number representing the character number from the original study follow these abbreviations in most cases. Some characters come from studies that did not include character lists; a dash and number do not follow abbreviations associated with these characters. Abbreviations are present after all of the character descriptions, but some character states are followed by abbreviations indicating that these character states were not originally identified for that character or were not identified for that character in the cited study.

CITATION ABBREVIATIONS

AM, Abdala and Moro, 2003; B, Bell, 1997; B82, Branch, 1982; B86, Beuchat, 1986; BB, Borsuk-Białynicka, 1983; C99, Caldwell, 1999a; CDB, Carroll and DeBraga, 1992; CN, Conrad and Norell, 2006a; CRG, Conrad et al., 2007; C06, Conrad, 2006b; DBC, DeBraga and Carroll, 1993; E, Estes et al., 1988; E83, Estes, 1983; Eagam, characters

from Estes et al., 1988 that do not appear in the larger list of characters, but that are found only in the section describing Agamidae*; Eanguim, characters from Estes et al., 1988 that do not appear in the larger list of characters, but that are found only in the section describing Anguimorpha; EB98, Evans and Barbadillo, 1998; Echam, characters from Estes et al., 1988 that do not appear in the larger list of characters, but that are found only in the section describing Chamaeleonidae; EdQ88, Etheridge and de Queiroz, 1988; Egek, characters from Estes et al., 1988 that do not appear in the larger list of characters, but that are found only in the section describing gekkotans; FE, Frost and Etheridge, 1989; Ga82, Gauthier, 1982; Ga84, Gauthier, 1984; Ga88, Gauthier et al., 1988a; GN98, Gao and Norell, 1998; GN00, Gao and Norell, 2000; Gr85, Greer, 1985; Gr88, Grismer, 1988; H93, Harvey, 1993; Ke, Kearney, 2003a; Kl87, Kluge, 1987; L98, Lee, 1998; LC00, Lee and Caldwell, 2000; M70, Meszoely, 1970; MB54, McDowell and Bogert, 1954; McG, McGuire, 1996; NG, Norell and Gao, 1997; PGG86, Pregill et al., 1986; R80, Rieppel, 1980a; R84, Rieppel, 1984a; R80L, Rieppel, 1980b; Rs80, Rieppel, 1980c; RZ, Rieppel and Zaher, 2000a; S, Schwenk, 1988; TC00, Tchernov et al., 2000; Y76, Yatkola, 1976.

CHARACTER DESCRIPTIONS

1. Skull, percentage of total length made up by antorbital snout (DBC-2): (0) <30%; (1) >30%; (2) >45%; (3) >50%. The structure of this character allows that it be ordered. Logically, if a snout is 50% of the total skull length, then it is also more than 30% or 45%. The character states used for this character are somewhat arbitrarily delimited, but are descriptive. They largely follow the character states put forward in DeBraga and Carroll (1993).

2. Skull, rostrum anterior to the bony external nares (new/extensively modified): (0) short, absent; (1) four tooth positions long or more. This character refers to the amount of the premaxilla extending anterior to the anterior margin of the septomaxilla. Most lepidosaurs possess a small portion of premaxilla anterior to the septomaxilla, but certain forms [e.g., *Huehuecuetzpalli mixtecus* (fig. 20), *Varanus*] possess a more significant rostrum.
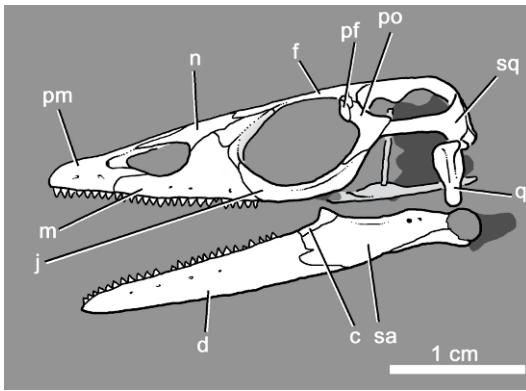
Fig. 20. Reconstruction of the skull of *Huehuecuetzpalli mixtecus mixtecus* in left lateral view, modified after Reynoso (1998). Missing portions are reconstructed as semi-opaque shadows.

3. Skull, muzzle shape (NG-33): (0) tapering; (1) blunt and rounded. This character describes the presence or absence of linear, subparallel, lateral surfaces of the snout in dorsal view. The absence of flat, subparallel surfaces is considered the derived state for this analysis.

4. Skull, supratemporal crest (Ga82-25): (0) absent; (1) present, forming a distinct angle between the dorsal and lateral faces of the skull (a postorbital canthal crest).

5. Skull, interorbital septum (Ke-27): (0) present; (1) absent. I treat this character exactly as in Kearney (2003a).

6. Nares, posterior elongation invading contact between prefrontal and nasals or such that they open extensively dorsally (E-2): (0) absent (fig. 21); (1) present (fig. 22B). This differs somewhat from the description given by Estes et al. (1988: character 2). They discuss only the condition of the posterior nareal border approaching the frontal. Theoretically, the frontal could approach the naris without the latter being greatly posteriorly expanded. As used here, this character also helps to identify the anterior elongation of the premaxillary process of the maxilla without overlapping with the character describing the anteroposterior placement of the nasal process of the maxilla. There are some difficulties in scoring the condition of the external naris in *Heloderma* (Pregill et al., 1986). Based on the work of Pregill et al. (1986) and similarities the nasal-prefrontal-maxillary morphology in *Estesia mongoliensis* (see Norell et al., 1992; fig. 4), each of these taxa has been scored with the plesiomorphic state.

Caldwell et al. (1995) describe apparent narial retraction as the result of snout elonga-

tion and/or topological changes in some skull roofing bones. The current character takes this into account in describing the reduction of contact between the nasals and prefrontals. Other characters described by Caldwell et al. (1995) are also accounted for in this character list (see characters relating to the nasals, prefrontals, and maxillae). Note, however, that Caldwell's (1995) characterization of the processes leading to apparent narial retraction in *Varanus* (in contrast to mosasauroids or other taxa with apparent narial retraction) includes morphological characteristics that are present in only some *Varanus*. For example, not all *Varanus* possess anteriorly elongate nasals (see figures in Mertens, 1942b).

7. Dermal sculpturing (E-129): (0) irregular (vermiculate); (1) pitted; (2) bumps/hornlets. Treatment of this character, again, differs somewhat from that of Estes et al. (1988). They coded for the presence or absence of vermiculate sculpturing, but here sculpturing is described with three character states and applies not only to the osteoderms, but also the dermal skull roofing bones. If there is no sculpturing whatever, then the taxon is scored "-" or "inapplicable" for this character because the three following characters (8–10) code for the presence or absence of sculpturing on various skull bones.

8. Dermal sculpturing, maxilla (CN-5): (0) absent; (1) present.

9. Dermal sculpturing, prefrontal (CN-6): (0) absent; (1) present.

10. Dermal sculpturing, parietal/frontal (E-129): (0) absent; (1) present on frontal and parietal.

11. Premaxilla, fusion into single element (LC00-1): (0) absent, paired premaxillae; (1) present. Estes et al. (1988) define this character based on ontogeny. Very little ontogenetic data are known for most fossil taxa, making this character virtually impossible to score for any taxa without fused premaxillae. Given a taxon with paired premaxillae, one might appeal to the immaturity of the specimen. I have chosen to leave out the ontogenetic component of the character description and implemented the following conventions for scoring it. When taxa appear, from other indicators, to represent adults, I have scored them for this character. When they appear to be somatically immature, but with fused premaxillae, I have scored them as possessing character state "1". When they appear immature and possess paired premaxillae, I have refrained from scoring them and thus leave the "?" in place. Thus, the only conditions under which fossil taxa are coded as "0" for this
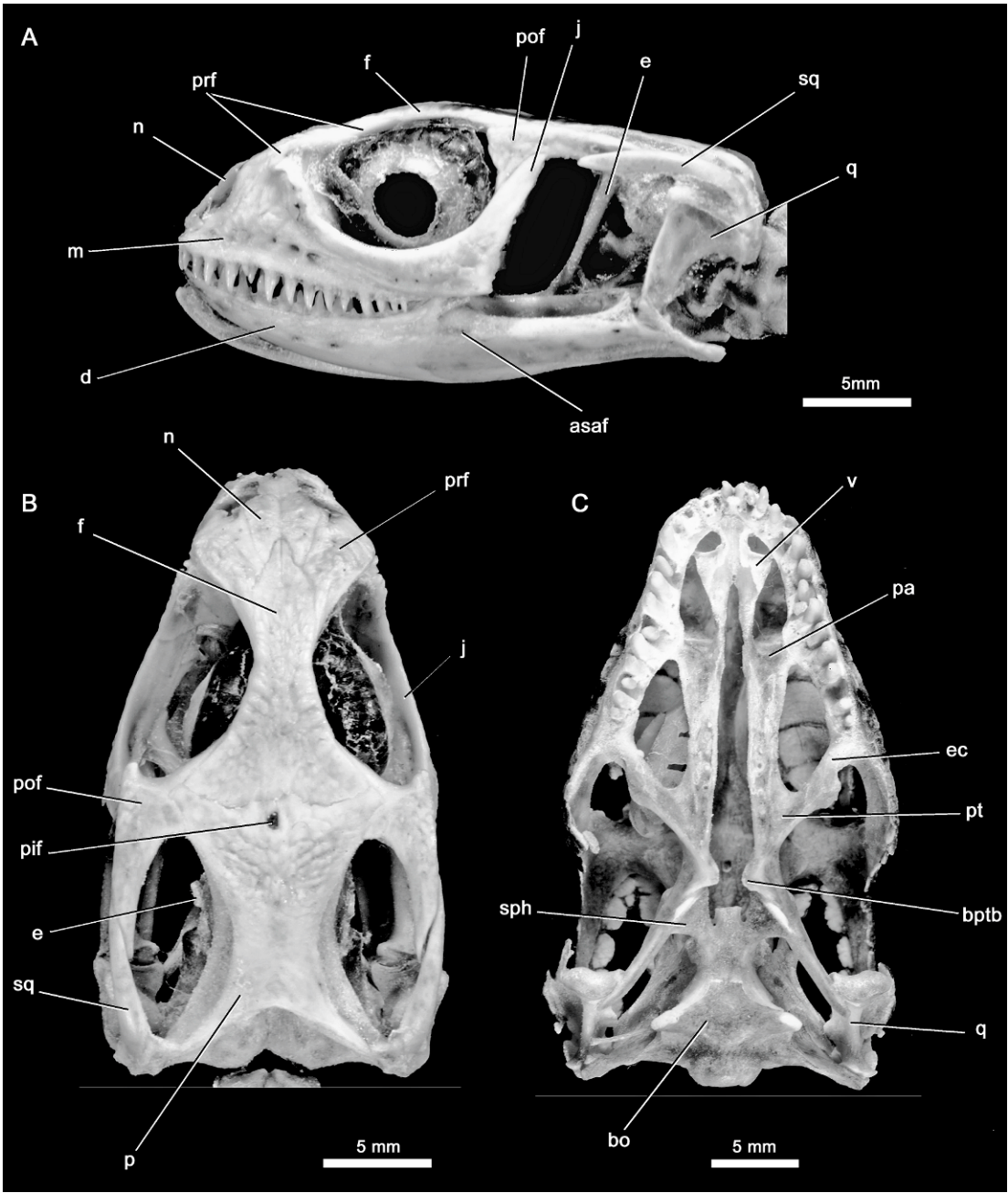
Fig. 21.   Skull of *Shinisaurus crocodilurus* in **(A)** right lateral (reversed to be left lateral) view, **(B)** dorsal view, and **(C)** ventral view. **(A)** and **(B)** UF 62316, and **(C)** UF 62497. Modified after Conrad (2004a).

character are when they appear to be adults and have paired premaxillae.

12. Premaxilla, mediolateral breadth of nasal process (B-4): (0) absent; (1) broad, widest plane; (2) narrow, narrowest plane; (3) narrow at its base, but spatulate posteriorly. This character is an attempt at quantifying the relative breadth of the nasal process of the
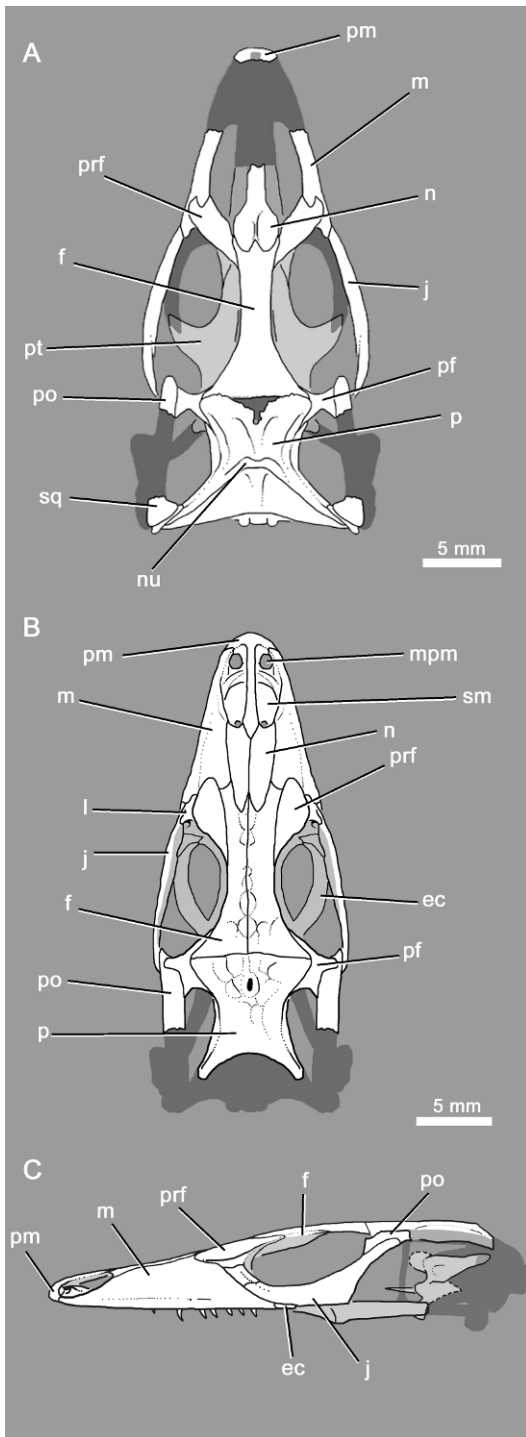
Fig. 22. Skulls of **(A)** *Paravaranus angustifrons* in dorsal view and *Proplatynotia longirostris* in **(B)** dorsal and **(C)** left lateral views. Modified after

premaxilla. Bell (1997) presented this character making comparisons between the internarial bar (=nasal process) of the premaxilla and the premaxillary rostrum of mosasauroids. Here, it is somewhat reformulated to be comparable to other groups of squamates.

13. Premaxilla, external contact with the frontal(s) (LC00-2): (0) absent, (1) present, (2) contact overlain by nasals. This character is modified from that of Lee and Caldwell (2000) in that the contact is specified, here, to be external. It retains the same distribution as in the previous study, but allows for the possibility of a contact with the frontal ventrally, invisible in dorsal view.

14. Premaxilla, incisive process (GN98-46): (0) single; (1) bilobed or bipartite; (2) absent.

15. Premaxilla, rostrum anterior to the premaxillary teeth (DBC-4): (0) absent (fig. 23A, D); (1) present, conical and short (extending for about 1 tooth position) (fig. 23B, E); (2) cylindrical and elongate (extending for about the length of two tooth positions) (fig. 23C, F). This character was modified by Bell (1997) who divided it into two characters, effectively ordering the three character states above. I do not use the latter approach. The rostrum anterior to the premaxillary teeth is not necessarily homologous in states (1) and (2).

16. Premaxilla, contact with maxilla (L98-3; RZ-3): (0) sutural; (1) nonsutural (fig. 24).

17. Premaxilla-maxilla aperture (M70): (0) absent; (1) present (fig. 22B). This structure, a hole between the premaxilla and maxilla, has been referred to by a variety of names, including premaxillary foramen (Meszoely, 1970). Gao and Norell (1998: 44–45) favor the term used here, which helps to avoid confusion with the premaxillary foramen of lizards lacking the hole between the premaxilla and maxilla.

18. Premaxilla, contact with the nasal (FE-1): (0) premaxilla(e) overlaps the nasal(s); (1) nasal(s) overlap the premaxilla(e); (2) premaxilla(e) does not reach the nasal(s).

19. Nasals, presence as discrete elements (DBC-12): (0) present; (1) absent. This is a modification of DeBraga and Carroll (1993: character 12), Bell (1997: character 8) and Lee and Caldwell (2000: character 21). Although there is some ambiguity left in the character by the current wording, it allows for either of the two possibilities (nasals fused to the premaxilla or nasals absent) to be scored. Because it is not

←

Borsuk-Białynicka (1984). Missing portions are reconstructed as semi-opaque shadows.
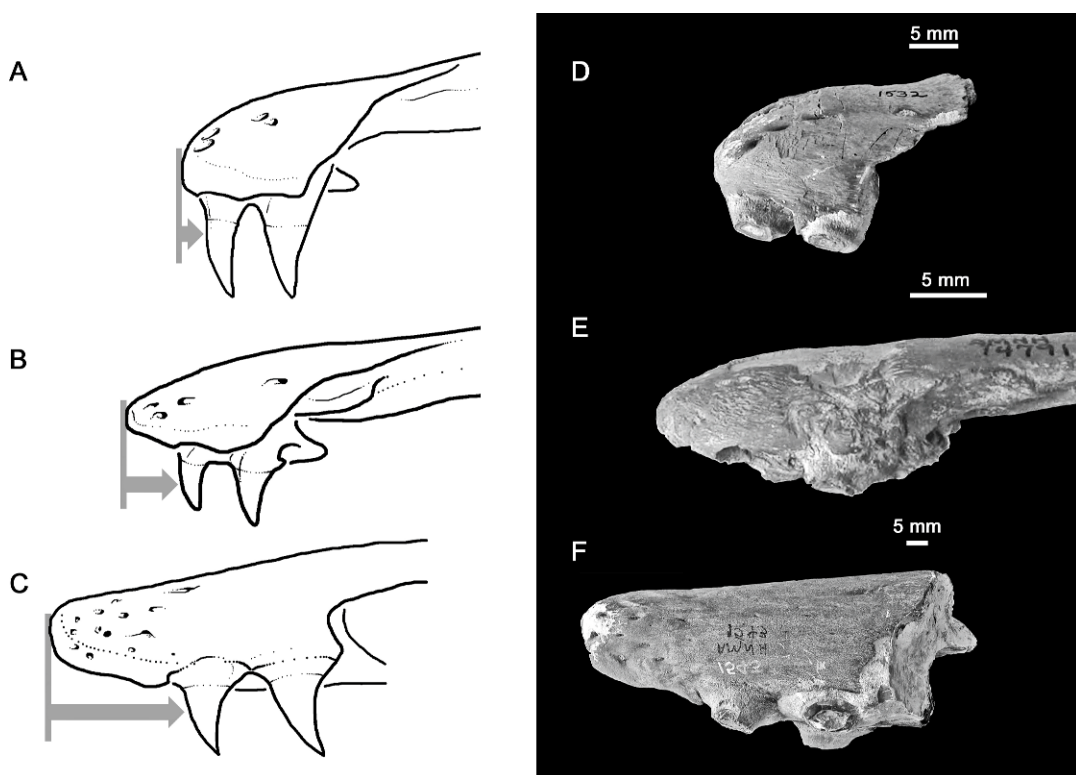
Fig. 23. Line drawings and photos of selected mosasaurid premaxillae in lateral view, showing the relative lengths of the rostrum (see character 15) as illustrated by the gray arrows. **(A)**, **(D)** *Platecarpus tympaniticus*, character state 15(0). **(B)**, **(E)** *Clidastes* sp., character state 15(1). **(C)**, **(F)** *Tylosaurus proriger*, character state 15(2). **(A–C)** redrawn after Russell (1967). Photos of **(D)** AMNH FR1532; **(E)** AMNH FR14791; and **(F)** AMNH FR3451 (reversal of right lateral view).

believed that these two possibilities co-exist as independent character states, but instead that either one or the other is the case for all taxa for which the nasals are indistinct (known only within mosasauroids), the correct identification of one or the other of these character states is not imperative.

20. Nasals (E-3): (0) paired (e.g., fig. 22B); (1) fused to one another (fig. 22A). Estes et al. (1988) define this character (like character 11) based on ontogeny. This character is treated in much the same manner as character 11 (above).

21. Nasals, internasal contact (GN98-2): (0) extensive; (1) less than one-half of their length.

22. Nasal, anterior border (Gr88-2): (0) concave, forming the posterior border of the external naris; (1) lacking anterolateral narial process. Some squamates possess an anterolateral prong of the nasal bone such that the nasal forms the entire posterior border of the external naris (state 0). Other taxa lack this process and

the posterior border of the external naris has contributions from the prefrontal, frontal, or maxilla (state 1).

23. Nasofrontal suture, articulated shape in dorsal view (C06-7): (0) M-shaped (nasals forming a posterior wedge); (1) frontal forms an anterior wedge (fig. 21B); (2) transverse (fig. 24B); (3) W-shaped (fig. 22A, B). Some authors discuss the presence of a nasal shelf of the frontal as a synapomorphy of iguanians (Estes et al., 1988). However, such a shelf is present in many squamates, including all of the observed taxa having states 1 and 3 in this analysis.

24. Nasofrontal fontanelle (new/extensively modified): (0) absent (e.g., figs. 21B, 24B), (1) present (fig. 25).

25. Maxilla, anteromedial process lying between vomers and premaxillae (Egek-12): (0) absent; (1) present. Estes et al. (1988) include this character in their diagnosis of
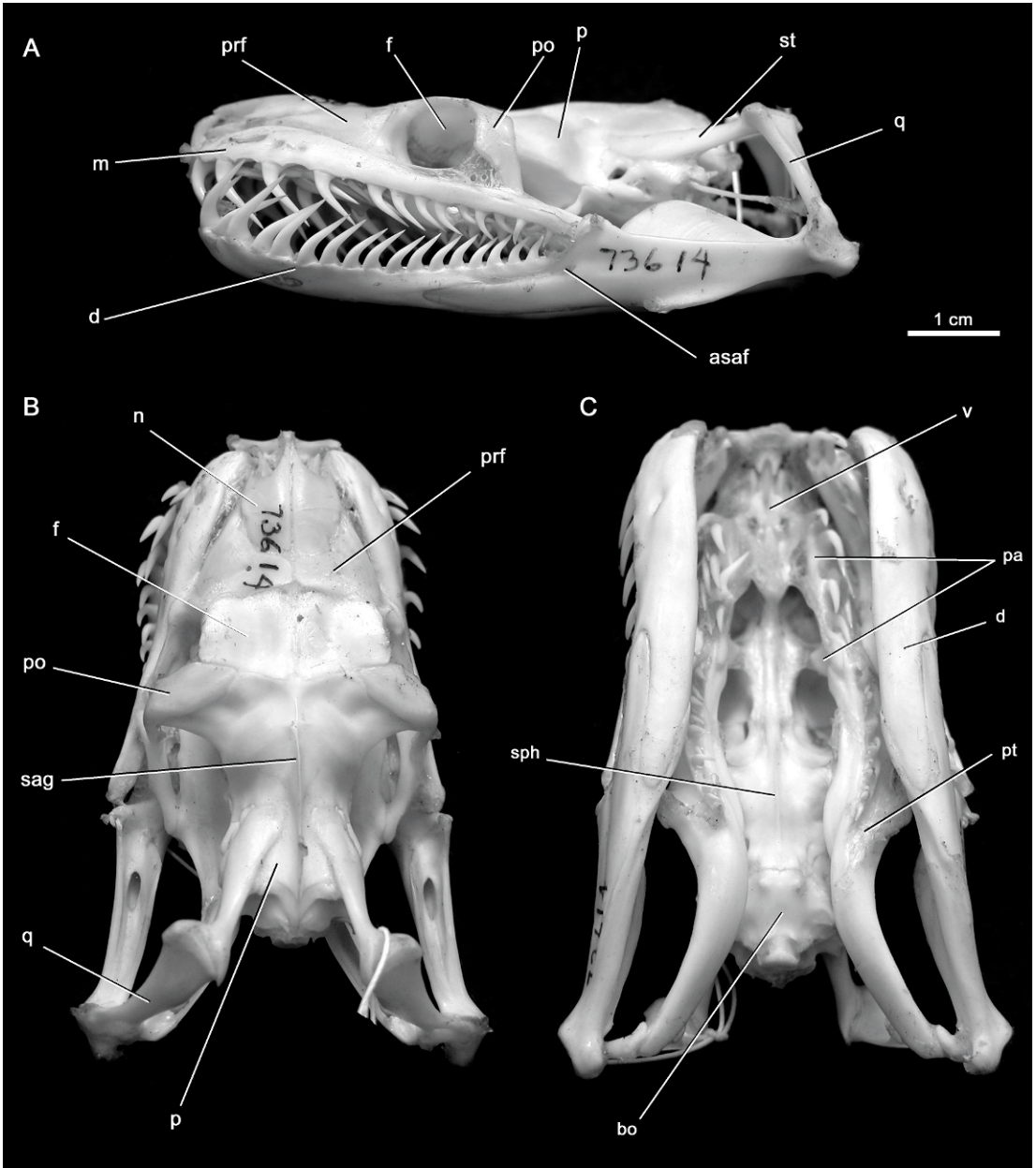
Fig. 24.   Skull and mandibles of *Boa constrictor* (AMNH R73614) in **(A)** left lateral view, **(B)** dorsal view, and **(C)** ventral view.

Gekkota, although it did not make it into their larger list of characters for their overall analysis.

26. Maxilla, strong medial processes posterior and posteroventral to the nasal process of the premaxilla (FE-2): (0) absent; (1) present. Al-though this character was not explicitly defined by Frost and Etheridge (1989), it seems a natural outgrowth of character 2 in their analysis.

27. Maxillae, contact at midline behind nasal process of premaxilla (FE-2): (0) absent; (1) present.

28. Maxilla, nasal process (RZ-5): (0) at or anterior to midpoint of maxilla (fig. 26A); (1) posterior to midpoint of maxilla (fig. 26B); (2) dorsal and ventral margins subparallel (TC00-29) (fig. 24A); (3) maxilla very short, presence or absence of a nasal process implicit. Rieppel and Zaher (2000a), believed this character to be the same as describing a presence or absence of a retracted naris. However, *Dinilysia patagonica* and anilioids possess a retracted external naris (see character 6), but not a posteriorly positioned maxillary nasal process. Conversely, *Hemitheconyx caudicinctus*, *Proplatynotia longirostrata*, *Estesia mongoliensis* (see description under character 6, above), and rhineurids possess a posterior nasal process, but not a retracted naris. Thus, this character varies independently from other characters in the analysis. State 2 was added based on descriptions in the supplementary data of Tchernov et al. (2000).

29. Maxilla, nasal process inclination (CN-17): (0) steeply inclined, posterior border of the naris distinct from ventral border (e.g., Figs. 26, 27); (1) weakly inclined, posterior border of the naris not distinct from the ventral border (no strong angle between the two faces) (figs. 28B, 29C, E). This character may, at first, seem to be correlated with a retracted naris, but this is not the case. A variety of taxa from each of the major squamate clades possess a strongly angled anterior margin of the nasal process in lateral view (e.g. *Leiolepis belliana*, *Pygopus lepidopus*, *Tupinambis nigropunctatus*, *Cordylus polyzonus*, and *Pseudopus apodus*). However, many taxa show much gentler slope to the anterior margin of the nasal process, including *Hemitheconyx caudicinctus*, *Xantusia henshawi*, and *Gobiderma pulchrum* without concomitant posterior placement of the maxillary nasal process.

30. Maxilla, overlap of prefrontal (new/extensively modified): (0) only anteriorly; does not include a supraorbital component (fig. 30A, C, D); (1) extensive, extends beyond the lacrimal and/or lacrimal foramen (fig. 30B). In a few taxa, the maxillary overlap of the prefrontal has increased such that the former overlaps the latter in a way that it partly encircles the orbit.

31. Maxilla, contact with vomer posterior to the fenestra vomeronasalis externa (E-42): (0) absent (paleochoanate condition); (1) present (neochoanate condition).

32. Maxilla, palatine flange (CN-19): (0) medial flaring absent (fig. 21C); (1) medially flared from the lateral border of the internal nares (fig. 29A); (2) present, expanded poster-
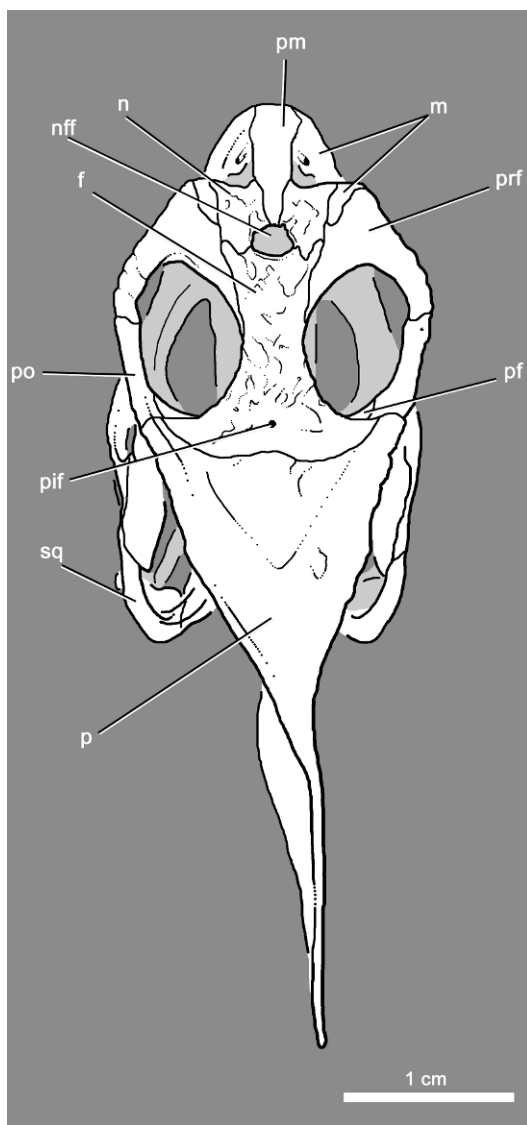
Fig. 25. Skull of *Corytophanes cristatus* (FMNH 22093) in dorsal view. Note the presence of a nasofrontal fontanelle (see character 23).

omedially beyond the posterolateral process of the maxilla (fig. 31C). This character addresses the palatal portion of the maxilla. Various squamates possess a medial, usually obtuse and pointed projection of the maxilla that contacts the palatine and carries the posterior part of the infraorbital canal (see Oelrich, 1956; Conrad, 2004a; Bever et al., 2005a, 2005b). Feyliniids and dibamids alone are known to have state 2 in which this palatal ramus of the maxilla extends posteriorly beyond the lateral maxillary exposure.
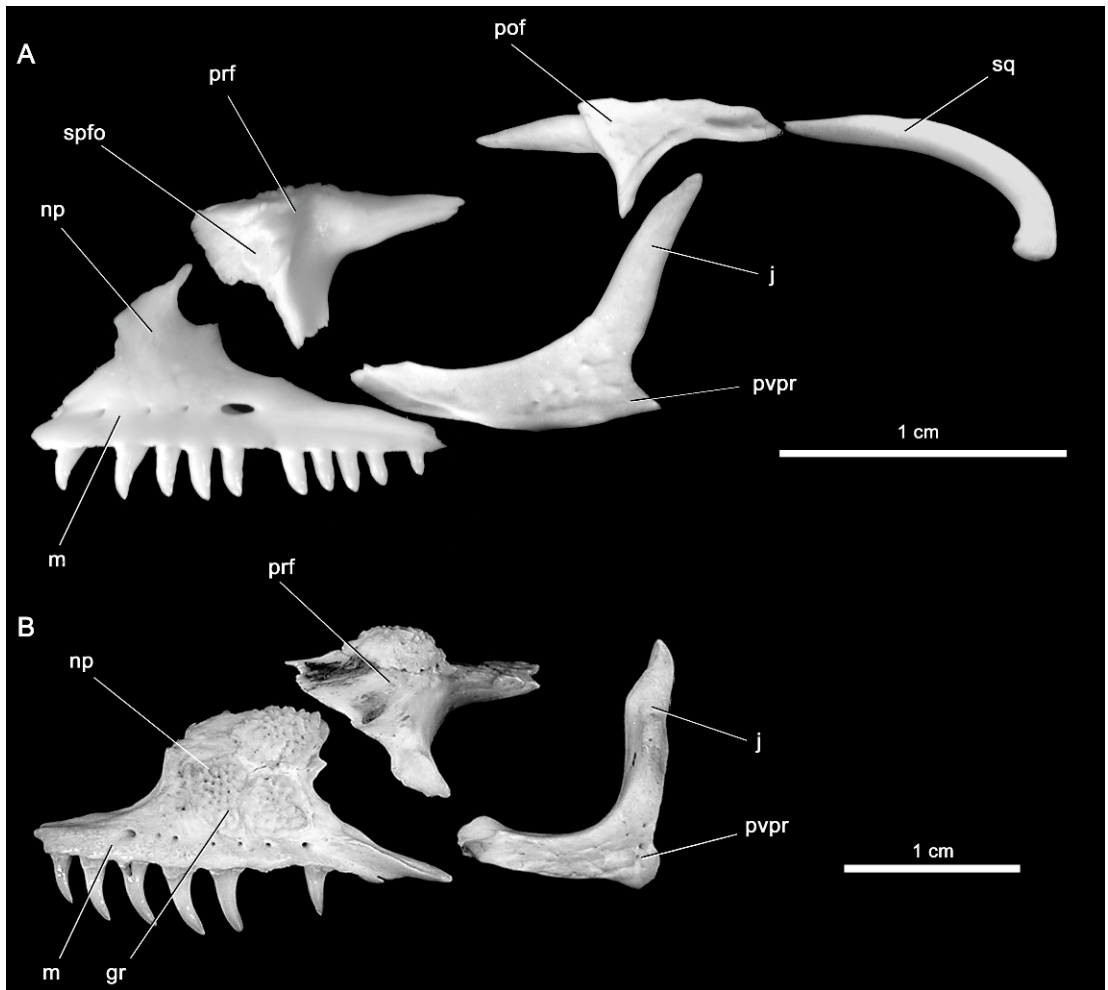
Fig. 26.   Some paired dermal skull bones of **(A)** *Shinisaurus crocodilurus* (UF 57112) and **(B)** *Heloderma suspectum* (AMNH R142627) in left lateral view for comparison. Note that *Heloderma* lacks a postorbital and has a very reduced squamosal that is not figured here.

33. Maxilla, posterior extent of tooth row (E-27): (0) beyond anterior one-fourth of the orbit (e.g., fig. 27); (1) terminates at anterior border of the orbit (fig. 31).

34. Prefrontal, dorsolateral tuberosity (Ga84): (0) absent; (1) present.

35. Prefrontal, supraorbital ridge (DBC-13): (0) absent; (1) present. The supraorbital ridge is a laterally projecting shelf on the dorsolateral margin of the prefrontal, extending antriorly from the orbit.

36. Prefrontal, pares frontales contact at midline (Gr88-011): (0) absent; (1) present.

37. Prefrontal, contact with postorbitofrontal (E-5): (0) absent; (1) present.

38. Prefrontal, blocks contact between maxilla and nasal (C06-10): (0) absent (e.g., fig. 29B); (1) present, extends anteriorly to reach the naris (fig. 21B); (2) present, contacts the premaxilla.

39. Prefrontal, contact with jugal (R80-24): (0) absent; (1) present.

40. Prefrontal, subpalpebral fossa (C06-11): (0) absent (fig. 26B); (1) present (fig. 26A).

41. Lacrimal (E-28): (0) present, large and extending for more than one-half the distance to the external naris; (1) present, discrete, and limited to orbital margin (fig. 30D); (2) present on orbital margin, but fused to the prefrontal (fig. 30A, C); (3) absent (figs. 24A, 30B); (4)
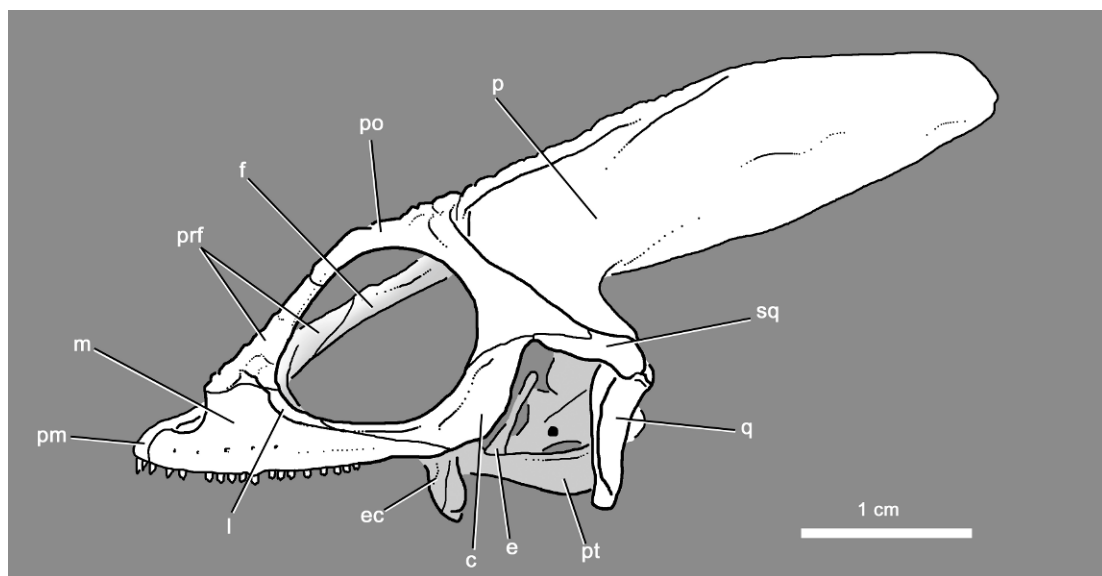
Fig. 27.   Skull of *Corytophanes cristatus* (FMNH 22093) in left lateral view.

present, but reduced to a nubbin that is supported by soft tissue and fails to contact the prefrontal. Within Rhynchocephalia, *Gephyrosaurus* possesses a distinct lacrimal (Evans, 1980) (fig. 32A), but most sphenodontidans including *Diphydontosaurus* (Whiteside, 1986), *Planocephalosaurus* (Fraser, 1982), *Paleopleurosaurus* (Carroll, 1985), and *Sphenodon*, possess a fused lacrimal-prefrontal. Character state (0) is included here based on previous ideas about the close relationship of Kuehneosauridae with squamates (see Romer, 1956, 1966; Robinson, 1967; Estes, 1983; Gauthier, 1984; Estes et al., 1988; Gauthier et al., 1988a). This relationship has been recently challenged (Müller, 2003, 2004b). The character state is retained for easy inclusion of kuehneosaurids or the "paliguanid" *Paliguana whitei** (see Carroll, 1975, 1977, 1988a; Gauthier, 1984) in later analyses. State 4 is difficult to assess in some cases. I have observed it only in *Hoplocercus spinosus* and in *Enyalioides* and it is clear that the very reduced lacrimal might easily be overlooked or lost because it was held in place almost exclusively by soft tissue. High-resolution x-ray tomography might serve as a tool to search for a vestigial/rudimentary lacrimal in various taxa apparently possessing state 3 of this character just as it has in the identification of the palpebral in *Lanthanotus borneensis* (Maisano, 2001b; Maisano et al., 2002) and the confirma-

tion of its absence in *Heloderma* (see Bonine, 2005).

42. Lacrimal, posterolateral flange (new/extensively modified): (0) absent; (1) present.

43. Lacrimal, foramen (RZ-10): (0) single; (1) double.

44. Lacrimal foramen, size (FE-6): (0) small; similar in size to palatine foramen; (1) large; distinctly larger than the palatine foramen.

45. Jugal (RZ-12): (0) present; (1) absent (figs. 30B, 31).

46. Jugal, anterior extension (LC00-18): (0) no further than if forming the anterior border of the orbit; (1) extends anteriorly beyond the margin of the orbit and not contiguous with the prefrontal and/or lacrimal suture.

47. Jugal, shape (GN98-13): (0) angulated (e.g., fig. 21B); (1) little angulation; curved (figs. 20, 29E); (2) reduced to a small splint barely extending beyond the posterior margin of the maxilla (fig. 29C).

48. Jugal, posteroventral process (GN98-14): (0) present (fig. 26); (1) absent (fig. 29E).

49. Jugal, postorbital branch (Ga82-27): (0) without anterior or posterior flanges (fig. 26); (1) dilated (fig. 27).

50. Jugal, postorbital process rugosities (GN98-17): (0) absent; (1) present.

51. Jugal, contact with the postorbitofrontal (E-32): (0) present; (1) absent.

52. Jugal, relationship to maxilla (C06-14): (0) mostly medially; (1) mostly dorsally; (2)
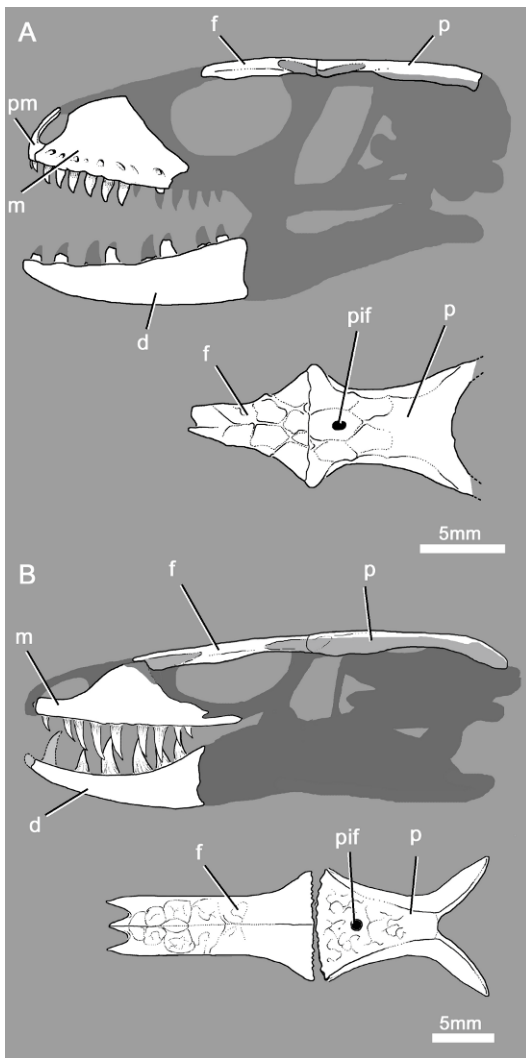
Fig. 28. Reconstructed skulls in left lateral view and frontals and parietals in dorsal view of two "necrosaurs". **(A)** *Parasaniwa wyomingensis*; and **(B)** "*Necrosaurus*" *eucarinatus*. Drawn after **(A)** Estes (1964), and **(B)** Kuhn (1940) and Estes (1983). Missing portions are reconstructed as semi-opaque shadows.

jugal reduced and lying mostly posterior to the maxilla. In some taxa, the posteroventral part of the maxilla laterally overlies the jugal (state 0). In others, the jugal lies mostly dorsal to the posteromedial part of the maxilla, the latter being mediolaterally broadened (state 1; fig. 26). The anterior (suborbital) ramus of the jugal is reduced in some taxa such that the bone

lies mostly posterior to the maxilla and has limited dorsal or medial overlap with it.

53. Jugal-squamosal contact (E-18): (0) absent (fig. 29E); (1) present (fig. 27). Rhynchocephalians are coded as apomorphic for this condition even though *Sphenodon* does not possess this contact. The relatively basal rhynchocephalians *Gephyrosaurus*, *Planocephalosaurus*, *Clevosaurus*, *Paleopleurosaurus*, and *Pleurosaurus* show state 1.

54. Quadratojugal (new/extensively modified): (0) present; (1) absent.

55. Frontals (E-6): (0) separate in adults (figs. 22B, 31B); (1) fused in adults (figs. 22A, 32B, 33, 34). Basal rhynchocephalians (*Gephyrosaurus*, *Diphydontosaurus*, *Planocephalosaurus*) possess fused frontals (Evans, 1980; Fraser, 1982; Whiteside, 1986) (fig. 32B). *Paleopleurosaurus* appears to be the most basal rhynchocephalian possessing paired frontals (Carroll and Wild, 1994) like those of *Sphenodon*.

56. Frontal, anterior constricted neck (DBC-19): (0) absent; (1) present.

57. Frontals, shape as a unit (CN-33): (0) anterior and posterior borders subequal in width (figs. 31B, 32B); (1) rhomboid (fig. 34); (2) concave lateral margins, minimum width less than three-fifths of the posterior border width (fig. 33); (3) tapering posteriorly. The condition "triangular" in *Lowesaurus matthewi* (Pregill et al., 1986) is questionable because of breakage; scored trapezoidal here. State 2 is not identical to the derived state of character 58. This character refers to the shape of the frontal unit as a whole; specifically comparing the anterior and posterior widths of the unit. *Shinisaurus crocodilurus* possesses concave lateral margins on the frontal (character 57, state 2), but because the frontal does not expand mediolaterally anterior to this lateral margin, it is also scored as state (0) for character 58. Other taxa share this combination of character states.

58. Frontals, constriction between orbits (E-7): (0) absent, interorbital margin linear; (1) present, anterior portion of the frontal is hourglass shaped.

59. Frontal, dorsal keel (B-12): (0) absent (fig. 29); (1) low, weakly developed (fig. 34); (2) tall, well developed.

60. Frontal, dorsoventral inflation (CRG-36): (0) absent; (1) present. Some taxa (e.g., *Anolis carolinensis*; see The Deep Scaly Project, 2006) possess dorsoventrally inflated frontals with large internal cavities. These cavities are entirely within the frontal and do not form canals between the frontals and other bones, nor do they house the olfactory tract.
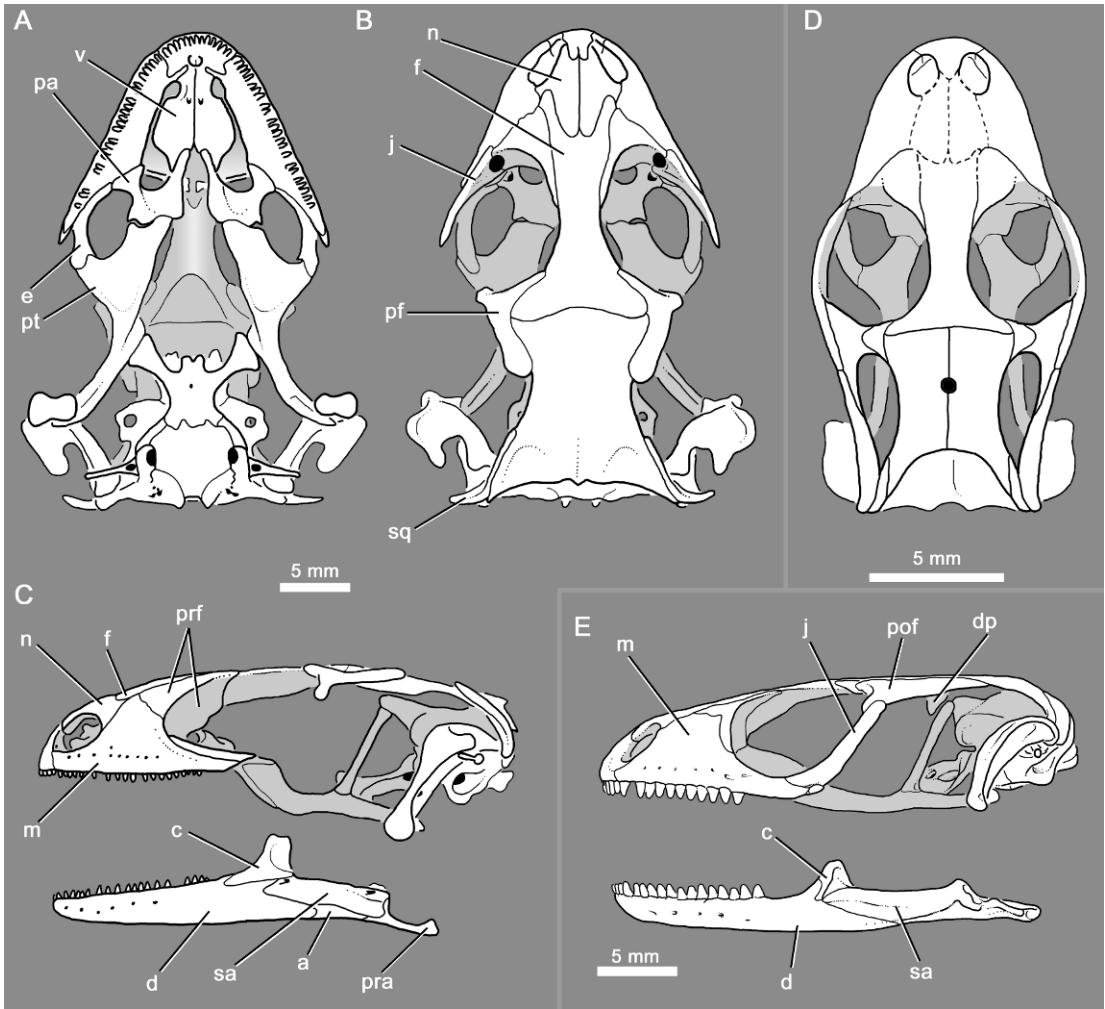
Fig. 29.   Skulls of a modern gecko and two taxa traditionally considered closely related to gekkotans. **(A–C)** Skull of *Hemitheconyx caudicinctus* in ventral, dorsal, and left lateral view (with lower jaw), respectively. **(D)** Skull of *Eichstaettisaurus schroederi* in dorsal view. **(E)** Skull and lower jaw of *Xantusia henshawi* in left lateral view. Note that the ectopterygoid is visible posterior to the maxilla and ventral to the jugal in **(E)**. **(A–C)** modified after Rieppel (1984a) and Maisano (2003j), **(D)** redrawn from Evans et al. (2000), Evans et al. (2004), and photos kindly supplied by Sterling Nesbitt, and **(E)** modified after Maisano (2003a).

61. Frontals, subolfactory processes (E-10): (0) ventral downgrowths; (1) partly surrounding the olfactory tracts; (2) contact the parasphenoid (RZ-54). State (1) describes the ventromedial growth of the subolfactory processes wherein they grow toward, and may approach, one another. State (2) addresses a condition wherein the frontal partly underlies the olfactory tract, but the processes contact part of the braincase (the parasphenoid portion of the sphenoid). Taxa with state (2) cannot be scored for character 62 (below) and are coded as (-) for that character.

62. Frontals, subolfactory processes contact at midline (E-10): (0) absent; (1) present (fig. 29A).

63. Frontal, medial pillar separating the olfactory tracts (Rs80): (0) absent, (1) present.
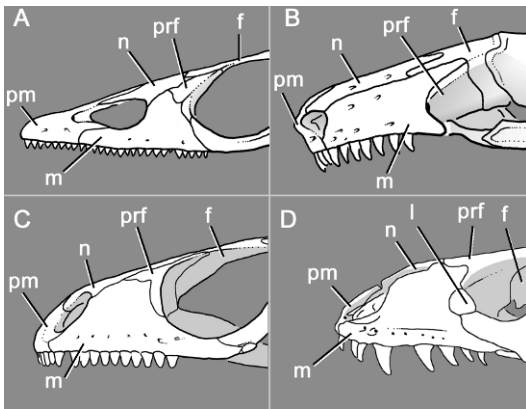
Fig. 30. Snouts of selected squamates in left lateral view to show relative snout lengths and details of the arrangements of snout bones. **(A)** *Huehuecuetzpalli mixtecus mixtecus*, **(B)** *Dibamus novaeguinea*, **(C)** *Xantusia henshawi*, and **(D)** *Heloderma suspectum*. Not to scale but drawn to the same approximate depth. Redrawn or modified from **(A)** Reynoso (1998), **(B)** Rieppel (1984b), **(C)** Maisano (2003a), and **(D)** Rieppel (1980a).

64. Frontals, contact between the medial pillar and lateral subolfactory flanges (Rs80): (0) absent, (1) present.

65. Frontals, contact the maxilla anteriorly (E-4): (0) absent (figs. 21B, 24B); (1) present (figs. 22B, 29B, 31B).

66. Frontals, participation in the orbitonasal foramen (C99-7): (0) absent, prefrontals with large contributions; (1) present, prefrontals largely blocked from the orbitonasal fenestra. Note that character state (1) is not redundant with the presence of a frontal-palatine contact (see below). State (1) suggests the presence of strong descending processes of the frontals along the medial surfaces of the prefrontals that may or may not co-occur with the frontal-palatine contact.

67. Frontal, contact with palatines (Ga82-82): (0) absent; (1) present.

68. Frontal, invaded by external nares (B-5): (0) absent; (1) present. This is a further transformation of character 6.

69. Frontals, parietal tabs (C99-9): (0) absent; (1) present (fig. 33); (2) present, elaborated into dorsomedial extensions on top of the parietals (fig. 34).

70. Frontoparietal suture, dorsal view (EB98-131): (0) U-shaped, anteriorly arched; (1) transverse; (2) W-shaped; (3) U-shaped, posteriorly arched. Most other rhynchocephalians possess a U- or even W-shaped frontoparietal suture.
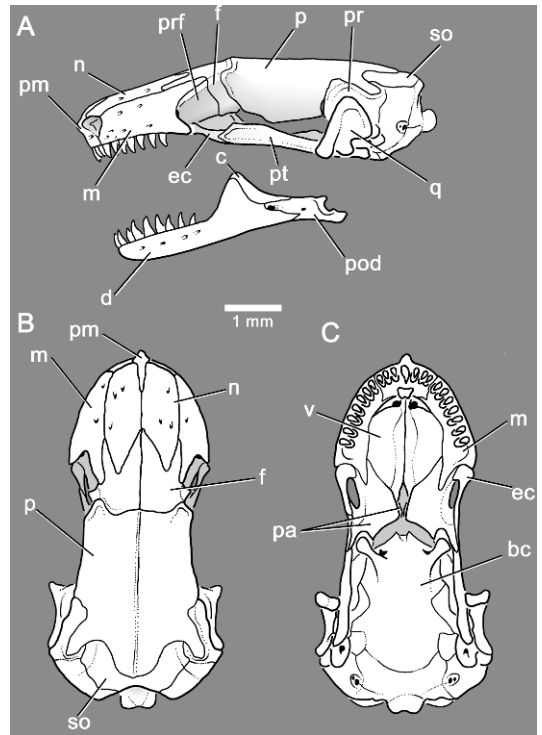
Fig. 31. The skull of *Dibamus novaeguineae* in **(A)** left lateral view (with mandible), **(B)** dorsal view, and **(C)** ventral view. Modified primarily after Rieppel (1984b) with consideration of data from Greer (1985).

71. Frontoparietal fontanelle (new/extensively modified): (0) absent; (1) present.

72. Parietal, lateral flange at the frontoparietal suture (new/extensively modified): (0) gently curved, laterally tapering; (1) with broad, squared, lateral tabs such that the postfrontal margin of the frontal is parallel with the postfrontal margin of the parietal.

73. Parietals (E-21): (0) paired (fig. 29D); (1) fused (fig. 29B). Rhynchocephalians appear to have fused parietals primitively. This is the case for *Gephyrosaurus* (Evans, 1980) (fig. 32B), *Planocephalosaurus* (Fraser, 1982), and *Paleopleurosaurus* (Carroll and Wild, 1994). *Diphydontosaurus* has been reported to possess fused parietals (Whiteside, 1986), although the same author illustrated a midline suture. Regardless, rhynchocephalians are scored with state (1).

74. Parietal, frontal tabs (C99-17): (0) absent; (1) present within the contact and visible dorsally; (2) present on the ventral surface.

75. Parietal, median adductor crest expressed as a keel (FE-10): (0) absent; flat
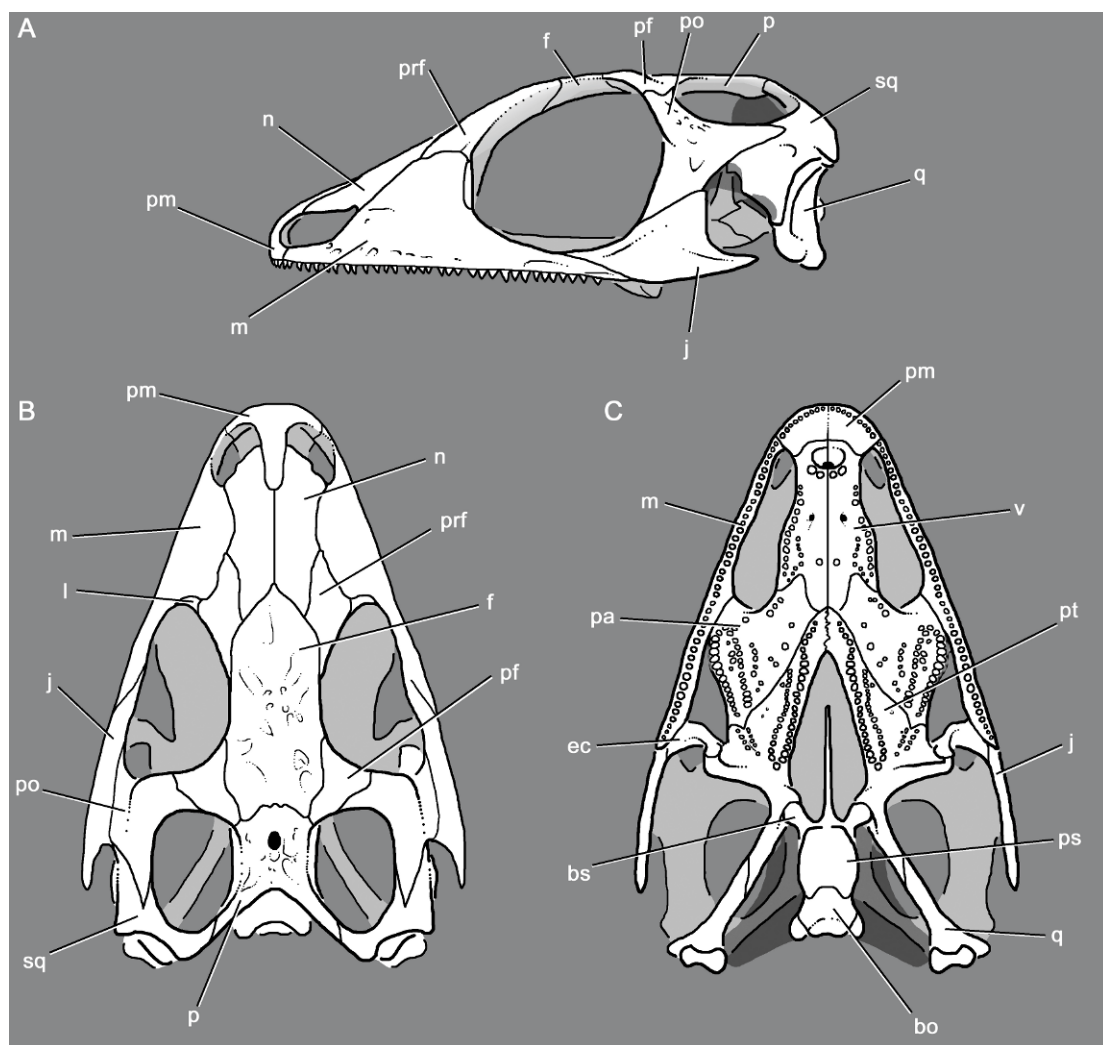
Fig. 32. Skull of a basal rhynchocephalian, *Gephyrosaurus bridensis*, in **(A)** left lateral, **(B)** dorsal, and **(C)** ventral views. All redrawn and modified after Evans (1980). Palate modified after the individual elements drawn in Evans (1980), not the composite reconstruction. Missing portions are reconstructed as semi-opaque shadows.

parietal table extends to the posterior margin; (1) present. Taxa in which the jaw adductors originate from the ventral surface of the parietals cannot be scored for this character because of redundancy with character 86 (see below). Note that this median crest is not homologous with the sagittal crest seen in some taxa wherein the jaw adductors do not contribute to the crest.

76. Parietal, decensus parietalis (E-23): (0) weakly developed/absent (fig. 29C); (1) present as anteroposteriorly elongate crest (fig. 33); (2) present, anteroposteriorly narrow ventral projection (figs. 29E, 35, 36A).

77. Parietal, pineal foramen (E-26): (0) within parietal; (1) within frontal; (2) at frontoparietal suture; (3) absent.

78. Parietal fossa, posterior margin (CN-46): (0) open, crests extend posterolaterally; (1) closed, crests meet at midline; (2) absent. The parietal fossa is a dorsal concavity on the ventral surface of the parietal occurring poste-
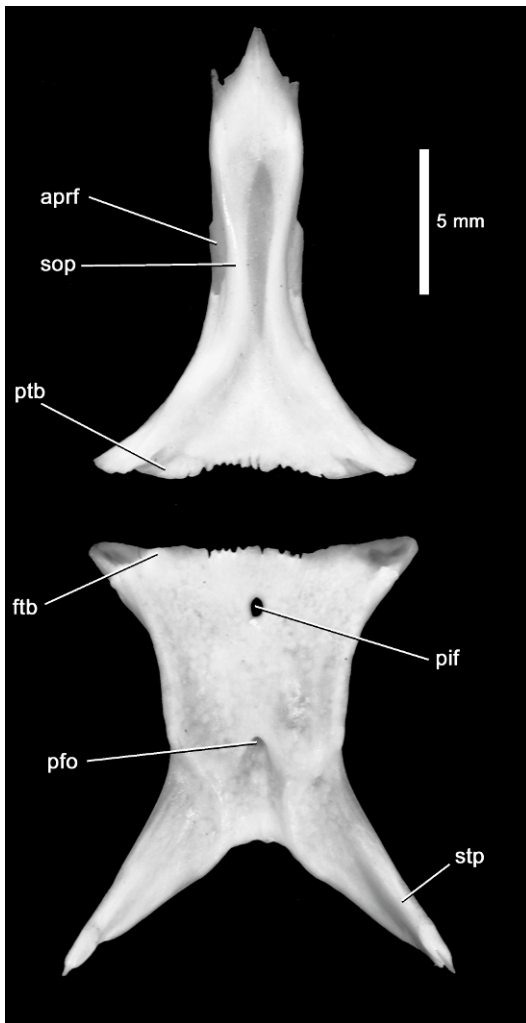
Fig. 33. Ventral views of the frontal (top) and parietal (bottom) of *Shinisaurus crocodilurus* (UF 57112).

Fig. 34. Dorsal view of part of an articulated skull of *Mosasaurus hoffmanni* (drawn after Lingham-Soliar, 1995).

rior to the pineal foramen (when the latter is present) and is flanked by the cristae postfovealis. In some taxa (e.g., *Xenosaurus*, *Glyptosaurus*) these crests extend posteromedially to and contact one another at midline posterior to the parietal fossa.

79. Parietal, posterior flange (not associated with a sagittal, jaw adductor, crest) (CN-47): (0) absent; (1) present.

80. Parietal, supratemporal processes length from the level of the parietal notch compared to the parietal anterior to that point (Ga82-30): (0) greater than one-half (fig. 28B); (1) less than one-half (fig. 29B); (2) absent (fig. 24).

81. Parietal, dorsal margin of the supratemporal process (GN98-33): (0) narrow and bladelike; (1) broad and flat.

82. Parietal, transverse posterior margin between the supratemporal processes (CN-50): (0) present (fig. 36B); (1) absent (fig. 33).

83. Parietal, nuchal fossa (GN00): (0) absent (fig. 22B); (1) present, visible in dorsal view (fig. 22A); (2) present and extending substantially onto the skull table (fig. 36B).

84. Parietal, contact with supratemporal arch (C99-15): (0) only at the anterior and posterior extremes (figs. 21B, 32B); (1) increased contact anteriorly and posteriorly (fig. 36B).

85. Parietal, contact with the supraoccipital (TC00-37): (0) no bony contact (contact only via the processus ascendens tecti synotici) (fig. 36B); (1) bony contact present and extensive; the supraoccipital becomes incorporated into the skull roof (figs. 24B, 31).

86. Parietal, origin of the jaw adductor musculature (E-54): (0) dorsally (figs. 21, 22, 24); (1) ventrally (fig. 34B, D, 36B).

87. Supratemporal (Egek-10): (0) present (figs. 21B, 24B, 36); (1) absent (figs. 29B, 31).

88. Supratemporal, length relative to depth (extensively modified after Ga82-86; CN-55): (0) less than 2.5 times as long as deep; (1) more than 3 times as long as deep. The arbitrary
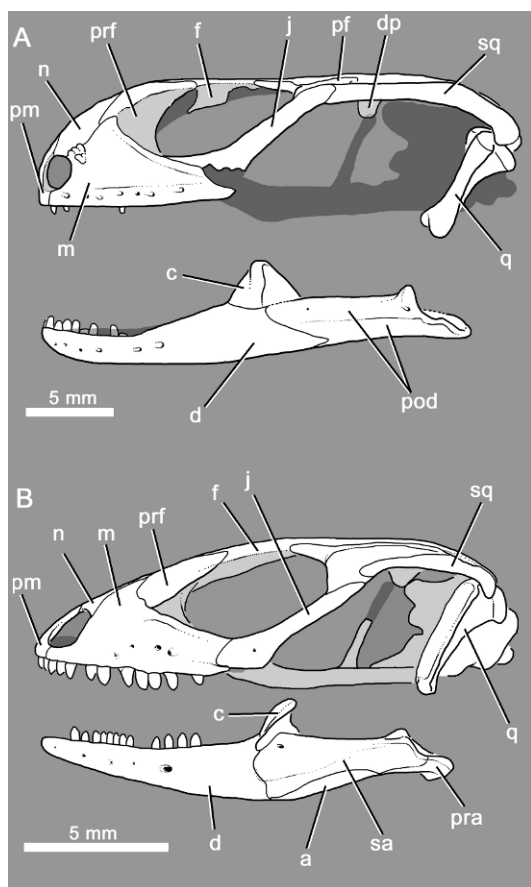
Fig. 35. Left lateral views of the skulls of **(A)** *Myrmecodaptria microphagosa*; and **(B)** *Globaura venusta*. Modified after **(A)** Gao and Norell (2000) and **(B)** Borsuk-Białynicka (1988).

numbers implemented here are used as an alternative to the even more arbitrary descriptions sometimes used, including "elongate" and "short".

89. Postfrontal/postorbital, forking of medial surface (RZ-25): (0) absent; (1) present.

90. Postorbital/postfrontal tubercle (McG-7): (0) absent (figs. 25, 29D); (1) present. In some taxa, an anterodorsal tuberosity is present near the postorbital-postfrontal contact at the posterolateral margin of the orbit. This tubercle marks a point of strong connection between the integument and skull bones during dissection.

91. Postfrontal (E-12): (0) present; (1) absent.

92. Postfrontal shape (new/extensively modified): (0) anteroposteriorly elongate (fig. 29B); (1) irregularly shaped, not elongate in medio-

lateral or anteroposterior planes (fig. 25); (2) mediolaterally developed bar bordering the orbit and supratemporal fenestra (fig. 22A). Note that state (1) appears primarily in iguanians and has not yet been observed in taxa lacking a postorbital.

93. Postfrontal, contact with the parietal (E-15): (0) absent; (1) present; (2) present for more than one-half the parietal table length. This ordered character addresses the presence or absence of a postfrontal-parietal contact and amount of contact between these bones.

94. Postorbitofrontal, fusion (E-14): (0) absent; postorbital and postfrontal exist as distinct elements (figs. 22, 25); (1) present (figs. 21B, 34).

95. Postorbital (may be fused with the postfrontal) (E-16): (0) present (figs. 21, 35B); (1) absent (figs. 35A, 36).

96. Postorbital, posterior extent (E83): (0) less than one-half the length of the supratemporal fenestra; (1) more than one-half the length of the supratemporal fenestra; (2) more than ¾ the length of the supratemporal fenestra; (3) contacts the supratemporal, partly or completely blocking the squamosal from contacting the supratemporal fenestra.

97. Postorbital, contribution to the postorbital bar (E-17): (0) one-half or more; (1) less than one-half.

98. Squamosal (RZ-40): (0) present; (1) absent.

99. Squamosal, contact with postorbitofrontal (or postorbital or postfrontal)—completion of the supratemporal arch (RZ-38): (0) present (e.g., fig. 29D); (1) absent (fig. 29B, C).

100. Squamosal, dorsal process (C99-25): (0) present; (1) absent.

101. Palpebral bone (E-36): (0) absent; (1) present, a single ossification articulating with or located near the prefrontal.

102. Septomaxilla (Echam-12): (0) present; (1) absent.

103. Septomaxilla, medial flange (RZ-87): (0) short/absent; (1) long.

104. Septomaxilla, contact with the osseous nasal cavity roof (FE-54): (0) absent; (1) present.

105. Palate, orientation of the ectopterygoid (CN-68): (0) mostly mediolaterally; (1) oriented anterolaterally (at more than 30 degrees from perpendicular to sagittal for the skull). Future work should address the utility of this character and the way it is scored in taxa for which the maxillary tooth row terminates anterior to the orbit (e.g., *Varanus*).

106. Vomers, fusion: (0) absent (fig. 37B); (1) present, intervomerine suture lost (fig. 37A).
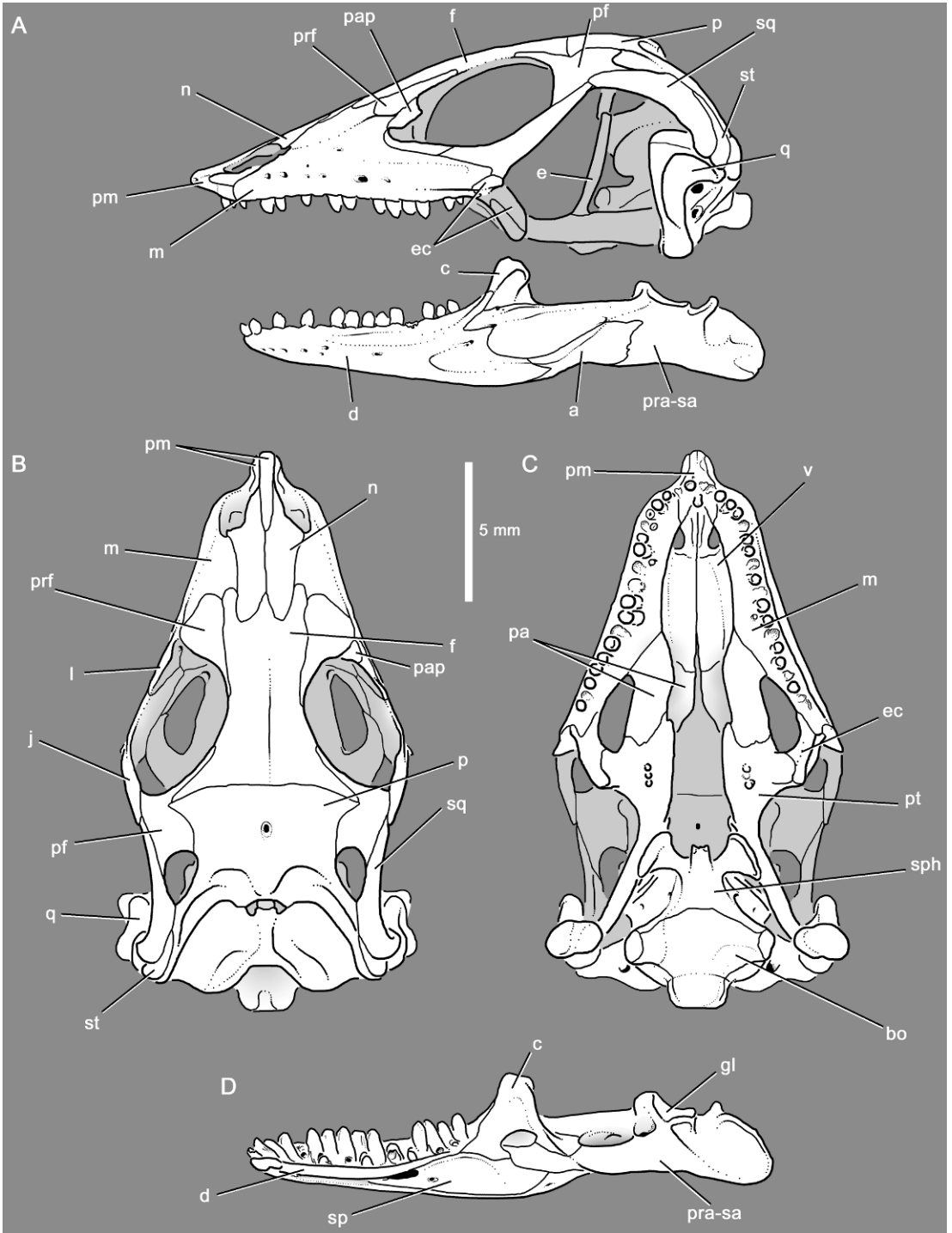
Fig. 36. Skull of *Scincus scincus* (AMNH R2245) in **(A)** left lateral view (with mandible), **(B)** dorsal view, **(C)** ventral view, and **(D)** mandible in medial view. Note the presence of a partly developed secondary palate [character state 114(1)].
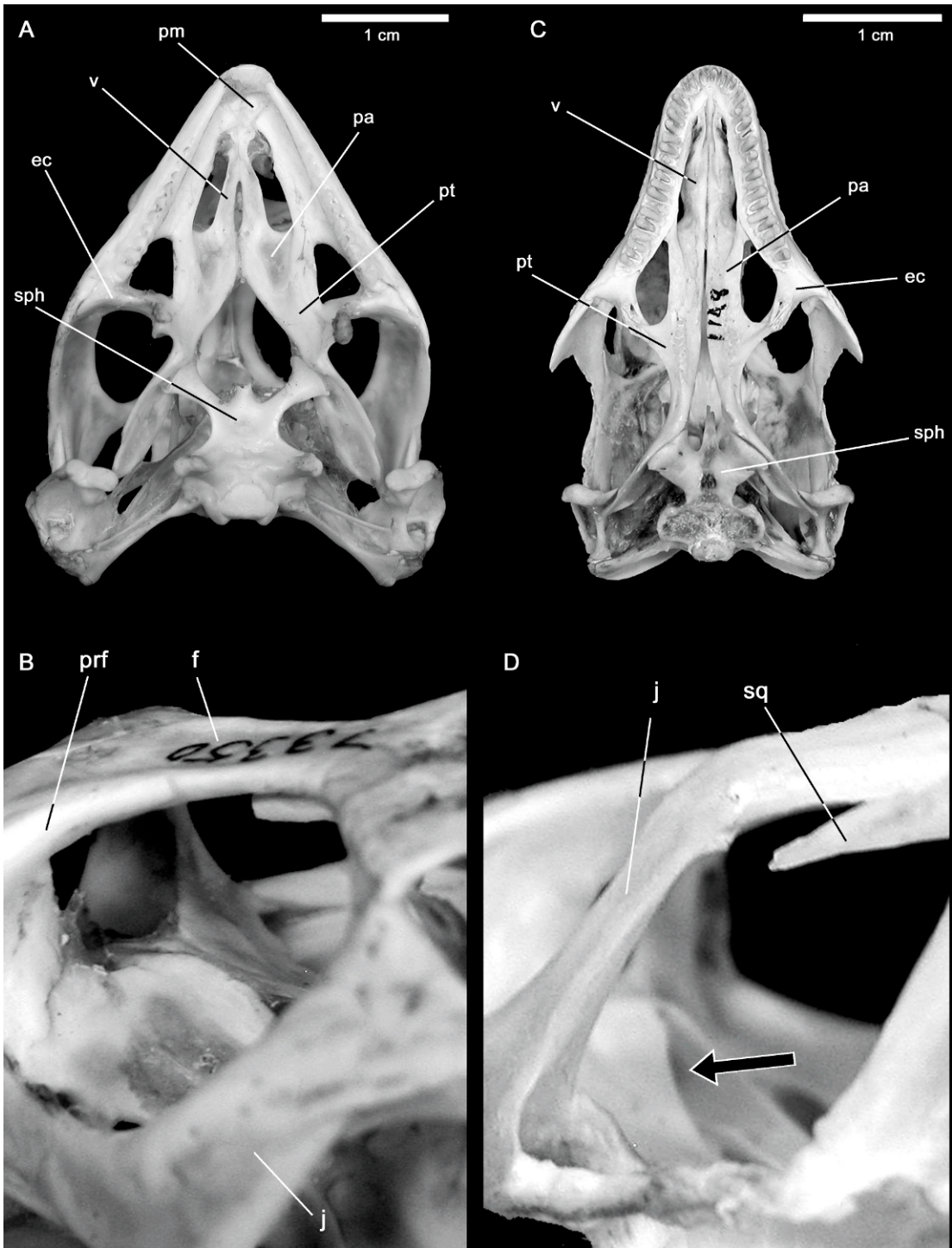
Fig. 37.   **(A)** Skull of *Uromastyx* sp. (AMNH R73350) in ventral view; note the fusion of the vomers and broad interpertygoid vacuity [character states 106(1) and 123(0), respectively]. **(B)** Posterolateral view through the right orbit of *Uromastyx* sp. (AMNH 73350) showing the midline contact of the palatal bones

107. Vomer, shape (RZ-93): (0) platelike (broad, flat); (1) rodlike (narrow and sub-cylindrical).

108. Vomer, articulation with the palatine (R84): (0) relatively broad (subequal in breadth to the contact with the maxilla) (figs. 32C, 37C); (1) relatively narrow (about one-half the breadth of the contact with the maxilla) and movable (e.g., fig. 29A); (2) absent (TR-47) (fig. 24C).

109. Vomerine teeth (Ga88-22): (0) present; (1) absent.

110. Palatines, medial expansion anteriorly (Ga82-84): (0) absent; (1) present. As used here, this character is meant to describe the ante-romedially oriented margin of the palatine in some taxa. This results in an anterior constriction (or even closure) of the pyriform recess in some taxa. Estes et al. (1988) used a similarly worded character (E-43) to describe a secondary palate. The secondary palate is treated separately in the present analysis (see character 114 below).

111. Palatine, length (GN98-51): (0) longer than wide; (1) subequal in length and width; (2) deeper than long.

112. Palatine, length relative to the vomer (L98-98): (0) subequal; (1) only two-thirds the length. Character state (1) has been modified from Lee (1998).

113. Palatines, choanal groove (RZ-101): (0) very short/absent; (1) distinct, elongate.

114. Palatine, secondary palate formed around choanal groove (E-43): (0) absent (fig. 21C); (1) present, ventromedial fold partly hides the choanal groove (fig. 36C); (2) present, ventromedial processes hide most or all of the dorsomedial processes (fig. 31C). The character states here have been modified to help identify the degree of the secondary palate formation. Of course, the cutoff points for the individual character states are somewhat arbitrary, but they are descriptive.

115. Palatine, teeth (E-82): (0) present, patches; (1) absent; (2) present, single line. Although some authors may treat this as two characters or as an ordered character to help emphasize the difference between the presence and absence of teeth, it is not clear that it is a larger evolutionary change to go from patches of teeth to teeth being absent than from patches of teeth to a single line. Consequently, this character is treated as unordered, as is character 118 addressing pterygoid teeth. Lepidosaurs apparently possess patches of palatine teeth plesiomorphically (Evans, 1980; Estes, 1983; Whiteside, 1986; Estes et al., 1988; Fraser, 1988; Gauthier et al., 1988a; Wilkinson and Benton, 1996). Note that studies by Mahler and Kearney (2006a, 2006b) found evidence for non-independence of palatal teeth on different palatal bones. However, this character (115) and character 118 do not co-vary in every circumstance, so they are treated separately.

116. Pterygoid, contact with jugal (GN98-54): (0) absent; (1) present.

117. Pterygoid, ventromedial process (GN98-32): (0) absent; (1) present.

118. Pterygoid, teeth (E-83): (0) arranged in multiple rows or patches (fig. 36C); (1) in a single line; (2) absent (fig. 21C).

119. Pterygoid, contact with vomer: (0) present (fig. 32C); (1) absent (fig. 29A).

120. Pyriform recess, midline contact of vomers (C06-22): (0) present, invaded by pyriform recess (fig. 21C); (1) present, contact for their length (figs. 24C, 34C); (2) present, contact anteriorly and posteriorly) (fig. 37A); (3) absent. This and the following two characters are used to define the forward extent of the pyriform recess.

121. Pyriform recess, midline contact of palatines (CN-81): (0) absent; (1) present.

122. Pyriform recess, midline contact of pterygoids (new/extensively modified): (0) absent; (1) present. Scoring of *Saniwa ensidens* is based on Gilmore's (1928: 61) discussion of skull distortion and his plate 4.

123. Pyriform recess, broadest point compared to the distance from basicranial joint to quadrate (CN-82): (0) greater than one-half; (1) less than one-half.

124. Ectopterygoid, contact with the palatine anterior to the suborbital fenestra (E-45): (0) absent (fig. 38C); (1) present (fig. 38A); (2) present, contact broader than suborbital fenestra (fig. 38B); (3) present, closes suborbital fenestra (Ke-99). This character is modified to accommodate the special morphology of diba-mids and some skinks or skink-like taxa.

←

and the absence of a secondary palate [character state 114(0)]. **(C)** Skull of *Lacerta viridis* (AMNH R1148) in ventral view. Note the absence of a distinct palatine flange of the maxilla and narrow pyriform recess [character states 32(0) and 123(1), respectively]. **(D)** Posterolateral view through lateral temporal vacuity of *Tiliqua nigrolutea* (AMNH R99684) with the presence of a secondary palate indicated by an arrow [character state 114(2)]. Note that **(B)** and **(D)** are not to scale.

125. Ectopterygoid, contact with the palatine posterior to the suborbital fenestra (new/extensively modified): (0) absent; (1) present (fig. 31C).

126. Ectopterygoid, lateral exposure posterior to the maxilla (MB54): (0) absent (e.g., fig. 29C); (1) present (e.g., figs. 29E, 36A).

127. Braincase, ventral sagittal ridge or crest on the sphenoid and basioccipital (TC00-77): (0) absent; (1) present.

128. Braincase, spheno-occipital epiphyses (NG-27): (0) absent; (1) present. Kearney (2003a: 32) gives a summary of the treatment of these elements in the literature. This character should be further examined (perhaps in a developmental framework) to determine its exact utility.

129. Braincase, fenestra ovalus location (NG-25): (0) above/slightly posterior to the spheno-occipital tubercle; (1) anterior to the spheno-occipital tubercle.

130. Braincase, azygous orbitosphenoid (Ke-105): (0) absent; (1) present. Originally, state (1) of this character was considered an amphisbaenian synapomorphy (Kearney, 2001, 2003a). However, new morphological studies suggest a narrower distribution for it (Kearney et al., 2005).

131. Braincase, ossified part of the occipital condyle (Egek-9): (0) single unit made of basioccipital and otooccipitals; ovoid or subovoid (e.g., figs. 36, 39); (1) bipartite, constructed primarily by otooccipitals with little contribution from the basioccipital (fig. 29A); (2) formed only by the basioccipital (GN00). Although Kluge (1987) takes issue with this character, the phenotypes for states (0) and (1) are readily observed in exemplars of skeletonized and CT-scanned squamate samples (see Maisano, 2003k; Kley, 2004; and Conrad and Norell, 2006a).

132. Braincase, anterior extension of crista prootica (E-52): (0) terminates on or just ventral to the inferior process; (1) extends onto the basipterygoid process; (2) crista prootica absent. This character is treated as unordered because there is no clear nested set of primary homologies inherent to the character and because it is possible to hypothesize a direct transformation from state (0) to state (2).

133. Braincase closure (Ke-29): (0) open (e.g., fig. 36); (1) parietal downgrowths and anterior extensions of prootics (fig. 40); (2) parietal downgrowths (figs. 24A, 31A).

134. Epipterygoid (E-47): (0) present; (1) absent.

135. Supraoccipital, processus ascendens tecti synotici (Egek-11): (0) present; (1) absent.

136. Prootic, supratrigeminal process (E-50): (0) absent or faint ridge; (1) distinct, anterior process visible in lateral view; (2) extensive, with a downgrowth that closes the trigeminal foramen.

137. Prootic, crista alaris (Ke-79): (0) absent; (1) present, short (dorsoventral depth greater than anteroposterior length); (2) present, elongate (dorsoventral depth less than anteroposterior length).

138. Prootic, crista prootica (RZ-66): (0) well-developed; laterally and ventrally projecting parts; (1) reduced; extending mostly laterally; (2) absent.

139. Prootic, perforation of the crista prootica (CN-91): (0) absent; (1) present. Although this character state had been illustrated previously (e.g., Rieppel, 1984a; Grismer, 1988), it was not used in a phylogenetic analysis until very recently (Conrad and Norell, 2006a). This perforation carries a branch of the trigeminal nerve.

140. Prootic, entocarotid fossa (GN98-30): (0) present as distinct a fossa within the recessus vena jugularis; (1) reduced/absent. As defined here, this refers to a depression on the lateral surface of the braincase posterior to the Vidian canal as opposed to the carotid fossa (below), which is located on the anterior surface of the sphenoid.

141. Prootic, external facial foramen (NG-20): (0) single; (1) double (presence of an external facialis canal). Conrad (2004a) and Bever et al. (2005a) term this character differently for some taxa, including *Shinisaurus crocodilurus*. Bever et al. (2005a) point out that the double external opening of the facial foramen in some specimens of *Shinisaurus* and some *Varanus exanthematicus* is the result of the fusion between a ventral flange of the crista prootica with a lateral extension of the prootic; the medial opening of the facial foramen is single. Thus, they argue that there is not a true bifurcation of the facial foramen, but rather that a superficial canal is formed near the external surface of the braincase (Bever et al., 2005a: 15–16). Certainly, the account of the morphology offered by Bever et al. (2005a) is accurate and I accept this interpretation of the morphology. Regardless of whether this morphology is termed a ''double facialis foramen'' (Rieppel and Zaher, 2000b: 504), a bifurcated facial foramen (Conrad, 2004a), or a facialis canal (Bever et al., 2005a), this character is coded here based on the apparent phenotype of the external opening of the facial foramen.

142. Sphenoid, carotid fossa (NG-22): (0) present; (1) absent. Because the basisphenoid
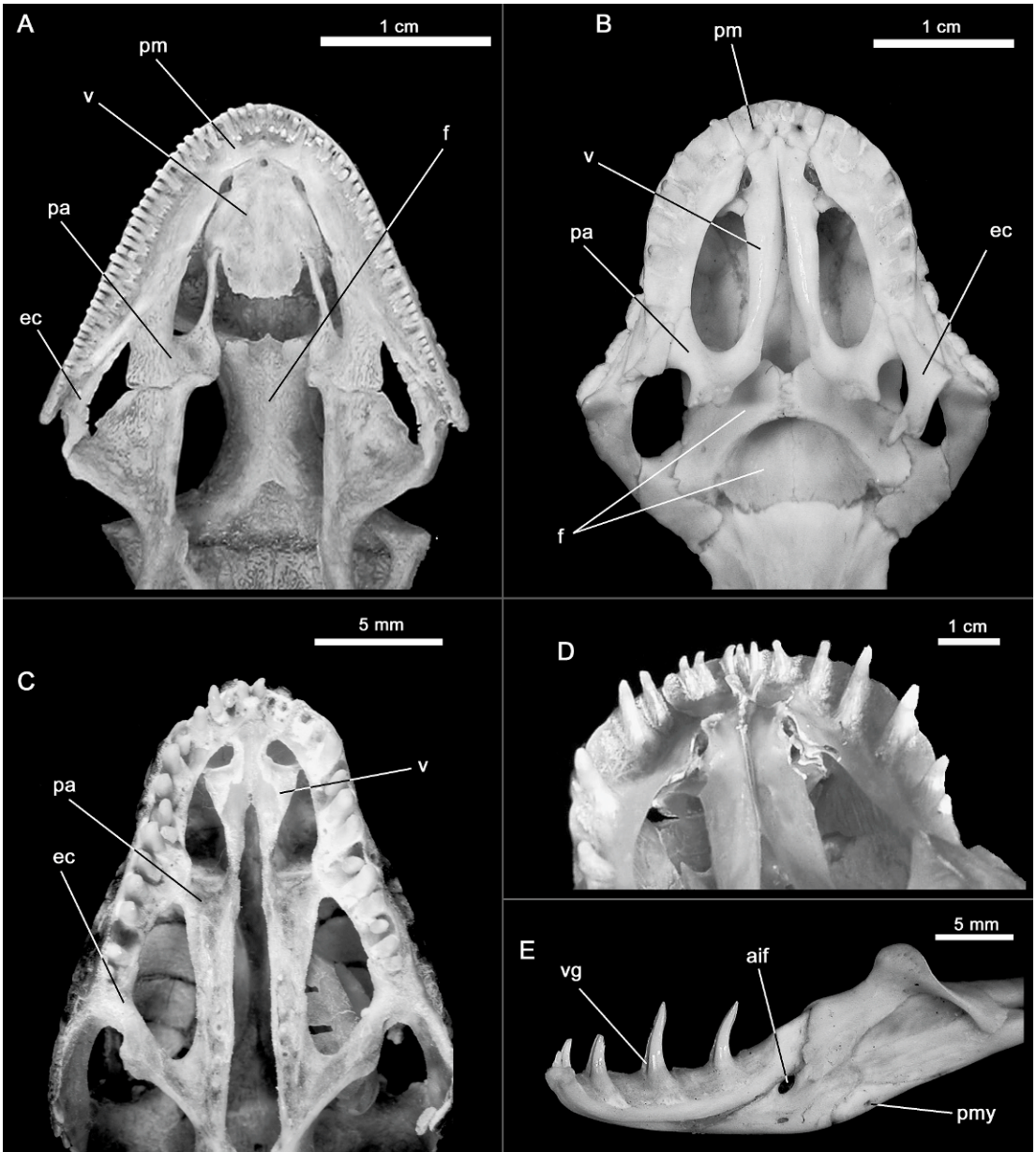
Fig. 38.   Ventral view of the anterior part of the skull in **(A)** *Gekko gecko* (AMNH R141109), **(B)** *Heloderma suspectum* (AMNH R74778), and **(C)** *Shinisaurus crocodilurus* (UF 62497). **(D)** Posteroventral of the skull of *Heloderma horridum* (FMNH 98468) highlighting the pronounced increase in tooth length between the premaxilla and maxilla. **(E)** Medial view of the right mandible of *Heloderma suspectum* (AMNH R74778).

and parasphenoid usually fuse in squamates, that compound structure is here referred to as the sphenoid, following some recent studies (Bever et al., 2005a; Conrad and Norell, 2006a).

143. Sphenoid, posterolateral ventral flanges laterally overlying basioccipital (**BB**): (0) absent (fig. 31C); (1) present (fig. 36C); (2) fusion of basioccipital to the sphenoid. Many squamates
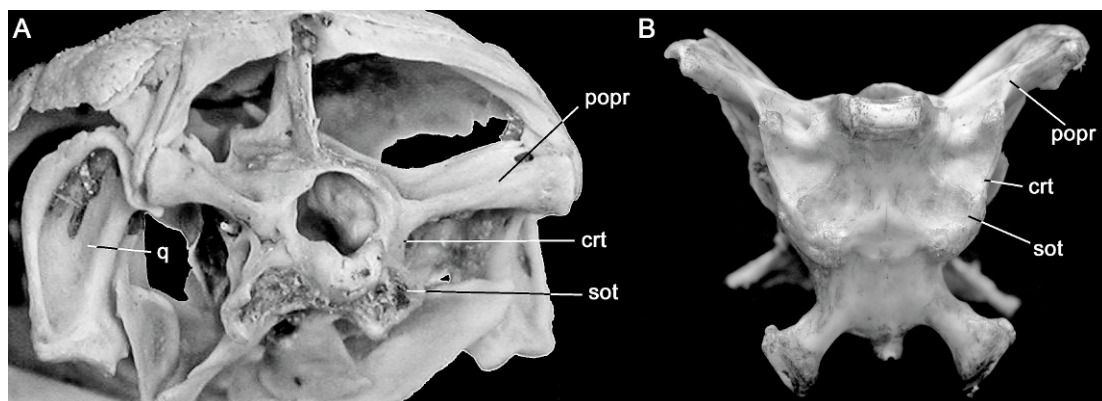
Fig. 39. The braincases in two autarchoglossans. **(A)** Posterolateral view of the posterior part of the skull in *Lacerta viridis* (AMNH R1148) in left posterolateral view. **(B)** Posteroventral view of the braincase in *Varanus* sp. (AMNH, uncatalogued specimen). Note the absence of an enlarged crista tuberalis in **(A)** [character state 149(0)] and its presence in **(B)** [character state 149(1)].

show a condition in which tapering processes of the sphenoid extends posterolaterally along the ventral surface of the braincase and ventrally overlies the basioccipital. These processes of the sphenoid often extend onto the spheno-occipital tubercles. The presence or absence of these processes cannot be determined in taxa wherein the sphenoid and basioccipital fuse. This character possesses no clear set of nested homologies and is left unordered.

144. Sphenoid, enclosure of the lateral head vein (E-52): (0) absent/incomplete; (1) present. Here, character 52 (E-52) of Estes et al. (1988) is broken up into two characters. This character (the current study's character 144) addresses only the actual encircling of the lateral head vein by the sphenoid as discussed by Conrad and Norell (2006a).

145. Sphenoid, anterior opening of Vidian canal (NG-18): (0) ventral to dorsum sella; (1) in the floor of the braincase, dorsal to the dorsum sella. The derived state (1) has been described and illustrated by Rieppel (1978).

146. Sphenoid, relationship with the posterior opening of the Vidian canal (E-53): (0) houses it; (1) shares it with the prootic; (2) posterior opening of the Vidian canal occurs within the prootic; (3) sphenoid and parietal share the posterior opening of the Vidian canal.

147. Parasphenoid, teeth (GA88-31): (0) present; (1) absent. This character is informative only as characterizing lepidosaurs; that is, with the inclusion of kuehneosaurids (see appendix 1)

148. Basipterygoid processes, length (RZ-74): (0) long, extending beyond main body of

the sphenoid; (1) short, expressed as short nubbins that are more than 2 times as wide as long and not extending anterior to the main body of the sphenoid; (2) absent.

149. Basioccipital, crista tuberalis development (RZ-79): (0) medially concave (fig. 39A); (1) medially flat, inclusion in the paroccipital process more lateral than on the spheno-occipital tubercle (fig. 39B). This character describes the ''webbing'' of bone that extends between the ventrolateral margins of the braincase posteriorly and the paroccipital processes of the otooccipital. In some cases, this bony lamina may be extensive such that its lateral margin is more or less linear and extends diagonally from the basioccipital to the paroccipital processes.
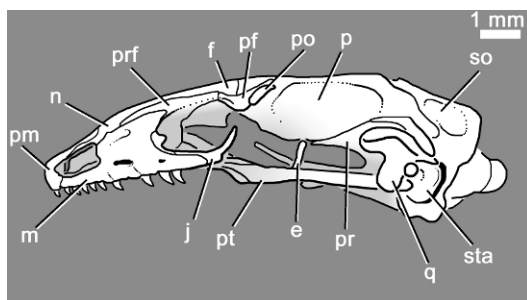
Fig. 40. Skull of *Anguis fragilis* in left lateral view. Compare the closure of the braincase with that of *Dibamus novaeguineae* (fig. 31), which lacks the anterior projections of the prootics. Modified after Rieppel (1980a).

150. Basioccipital, spheno-occipital tubercle (NG-23): (0) short and ventrally directed; (1) elongate and posterolaterally directed.

151. Basioccipital, location of the spheno-occipital tubercle (RZ-76): (0) posteriorly, crista tuberalis nearly vertical; (1) anteriorly, crista tuberalis posterodorsally inclined.

152. Basioccipital, canal or groove for basalar artery (DBC-34): (0) absent; (1) present.

153. Otooccipital, hypoglossal foramen (L98-69): (0) separated from vagus foramen; (1) both the hypoglossal and vagus nerves passing through internally subdivided canal or completely confluent. Lee (1997, 1998) and Rieppel and Zaher (2000a) left a small chance of confusion about the scoring of this character in their version of state (1) for this character. Lee described it as the condition wherein the hypoglossal foramen is ''very close to or confluent with [the] jugular foramen on [the] external surface of the braincase,'' (Lee, 1998: 392). ''Very close'' is open to interpretation. The presence or absence of confluence may even be problematic in the case of this character because the hypoglossal and vagus nerves often share a canal that is further subdivided for these nerves. Thus, the wording of state (1) as presented here.

154. Otooccipital, closure of the occipital recess (RZ-70): (0) open; (1) closed. Rieppel and Zaher (2000a; 2000b) offer discussions of this feature and related surrounding structures (e.g., the crista circumfenestralis of snakes), clarifying problematic areas of primary homology through detailed anatomical descriptions.

155. Otooccipital, ventral view of the occipital recess (CN-98): (0) hidden by spheno-occipital tubercle in ventral view; (1) visible in ventral view. This character is designed to further describe the relative development and orientation of the spheno-occipital tubercle.

156. Stapes, internal (quadrate) process lost (E-141): (0) present; (1) absent.

157. Stapes, shape of shaft (TC00-60): (0) straight; (1) angulated.

158. Extracolumella, anterior elongation (Ke-82): (0) absent; (1) present.

159. Quadrate, suspension (RZ-49): (0) monimostylic (fig. 32A); (1) streptostylic and supported by the squamosal, supratemporal, and paroccipital process of the otooccipital (e.g., fig. 36A); (2) suspended mainly from supratemporal (figs. 24, 40); (3) suspended mainly from otooccipital (fig. 31); (4) suspended mainly from squamosal. This character was discussed at some length by Rieppel and Zaher (2000a) who further listed historical references regarding this morphological area in various squamates.

160. Quadrate, pterygoid lappet (E-37): (0) present; (1) absent.

161. Stapes, position of stapedial artery (E-145): (0) anteriorly; (1) pierces stapes; (2) posteriorly. This character is scored based primarily on data in Estes et al. (1988). The perforate stapes in Kuehneosauridae (Evans, 1980; Gauthier et al., 1988a) indicates character state 1 for that taxon.

162. Quadrate, tympanic crest (RZ-51): (0) greater than or equal to the length of the posterior crest of the quadrate; (1) shorter than posterior crest of the quadrate at the dorsal head; (2) tympanic crest absent. The wording of this character as presented here is meant to reduce ambiguity. Essentially, the quadrate crest is broad/extensive (0), reduced (1), or absent (2).

163. Quadrate, suprastapedial process (DBC-39): (0) absent (e.g., figs. 36, 40); (1) present (fig. 41).

164. Quadrate, infrastapedial arch (DBC-41, 43): (0) absent (e.g., figs. 36, 40); (1) present (fig. 41); (2) present, contacts the suprastapedial process.

165. Extracolumellar tissue, calcification (LC00-65): (0) absent; (1) present. Coding of this character is somewhat tentative, although it appears that no extant squamates possess a calcified portion of the extracolumellar tissue and only *Aigialosaurus dalmaticus* and *Platecarpus tympaniticus* have been reported as possessing such among fossil taxa.

166. Mandible; fusion of articular, prearticular, and surangular (RZ-129): (0) absent (e.g., fig. 35); (1) present (articular-prearticular-surangular as a single unit) (fig. 36A, D). Although it may be at least partly related to ontogeny, this character is retained and it was scored as follows: If adults and/or late juveniles (staged based on other morphological indicators) lack fusion of the articular, prearticular, and surangular as observed and/or reported in the literature, they are coded with state (0); state (1) is coded for any taxon showing fusion of these elements. *Gephyrosaurus* (Evans, 1980) shows the unfused condition, but *Diphydontosaurus* (Whiteside, 1982) and other basal sphenodontidans possess the derived condition.

167. Mandible, symphysis (RZ-110): (0) present; (1) absent (fig. 24C). In extant squamates, the absence of a bony symphysis between the dentaries is accompanied by an elastic, soft-tissue connection between them.

168. Mandible, adductor fossa orientation (RZ-137): (0) medial margin low and rounded; (1) distinct vertical flange.

169. Mandible, adductor fossa expansion (E-81): (0) absent; (1) present.

170. Mandible, intramandibular septum (L98-116): (0) absent; (1) present. This character is modified from the form in Lee (1998) and Rieppel and Zaher (2000a), each of which described the posterior extent of the intramandibular septum.

171. Mandible, intramandibular septum ventral margin (M70): (0) absent; (1) posteroventral margin sutured; (2) posteroventral margin free. *Lowesaurus matthewi* is scored based on the description and figures in Yatkola (1976).

172. Mandible, anterior surangular foramen (CN-109): (0) present; (1) absent.

173. Mandible, external border of the anterior surangular foramen (CN-110): (0) formed only by the surangular; (1) margin with coronoid contribution; (2) with dentary contribution; (3) with coronoid and dentary contribution; (4) anterior surangular foramen absent. Because there is no clear set of nested homology statements for this character, it is treated as unordered.

174. Mandible, groove associated with anterior surangular foramen (CN-111): (0) absent; (1) present.

175. Mandible, posterior mylohyoid foramen (CN-112): (0) present; (1) absent.

176. Mandible, position of posterior mylohyoid foramen (FE-24): (0) anterior to the coronoid apex (fig. 38D); (1) posterior to the coronoid apex.

177. Mandible, glenoid (DBC-54): (0) formed at least primarily by articular; (1) formed equally by articular and surangular. This character cannot be scored for taxa in which the articular-prearticular and surangular are fused.

178. Dentary, shape of long axis (DBC-67): (0) ventrally convex (e.g., fig. 21A); (1) straight (e.g., fig. 36A).

179. Dentary, anteroventral surface (Ga82-59): (0) narrow, depth greater than width; (1) broader than tall with splenial and Meckel's canal slightly visible laterally.

180. Dentary, posterior extent (EB98-213): (0) to the level of the posterior margin of the coronoid process (eminence) (e.g., fig. 36A); (1) extends to or beyond the midpoint of mandible between the coronoid eminence and the articular condyle (fig. 31A).

181. Dentary, Meckel's canal (E-55): (0) open; (1) partly closed; (2) closed and fused.

182. Dentary, subdental shelf (E-58-59): (0) present; (1) absent; (2) present, enlarged (E-58). The subdental shelf is a lingual extension of the dentary originating from the area on which the dentary teeth attach. Estes et al. (1988) note that the subdental shelf is present in *Gephyrosaurus*, but suggest that other rhynchocephalians lack it. However, descriptions and figures in Whiteside (1986) suggest that a shelf is also present in *Diphydontosaurus*.

183. Dentary, contribution to the anterior inferior alveolar foramen (E1964): (0) dentary does not contribute; (1) dentary contributes to dorsal border; (2) dentary forms anterior and dorsal border; (3) discrete foramen absent. *Eurheloderma gallicum* is scored from figure 3B in Hoffstetter (1957).

184. Dentary, posterodorsal coronoid process(es) (RZ-113): (0) large and extensively overlying the coronoid eminence of the coronoid (fig. 31A); (1) small (not approaching the dorsal terminus of the coronoid eminence nor significantly overlapping it) (fig. 36A); (2) absent (fig. 35A).

185. Dentary, angular and surangular processes (E-63): (0) absent (fig. 29E); (1) present and distinct (fig. 29C). This is modified from Estes et al. (1988) in which a third character state (notches present, reduced) was included. Here this has been treated strictly as a binary character. A wavy suture is coded as (0); only the presence of distinct notches is considered to represent state (1). The structure of the intramandibular hinge and anterior end of the surangular in mosasauroids and their closest relatives makes this character inapplicable to that group (see character 191). The compound bone in snakes tapers anteriorly and helps to complete the hinge mechanism laterally.

186. Dentary, angular process compared to surangular process (Ga82-41): (0) angular and surangular processes terminate at about the same posterior level; (1) angular process terminates more anteriorly; (2) angular process extends more posteriorly (figs. 29C, 36A).

187. Dentary, principle support (RZ-119): (0) coronoid, surangular, and prearticular; (1) prearticular; (2) surangular.

188. Splenial (Ke-124): (0) present, discrete; (1) absent; (2) present, fused to the postdentary bones (Gr85).

189. Splenial, extent of anteromedial walling of Meckel's canal (E-67): (0) extends for more than two-thirds of the dentary; (1) extends for less than one-half of the dentary.

190. Splenial, posterior extent (E-66): (0) extends posterior to the apex of the coronoid (fig. 36D); (1) terminates at, or anterior to, the coronoid apex (fig. 38E).

191. Splenial, overlap with postdentary bones (RZ-121): (0) overlap, no hinge with angular (fig. 36D); (1) abutting, splenial re-
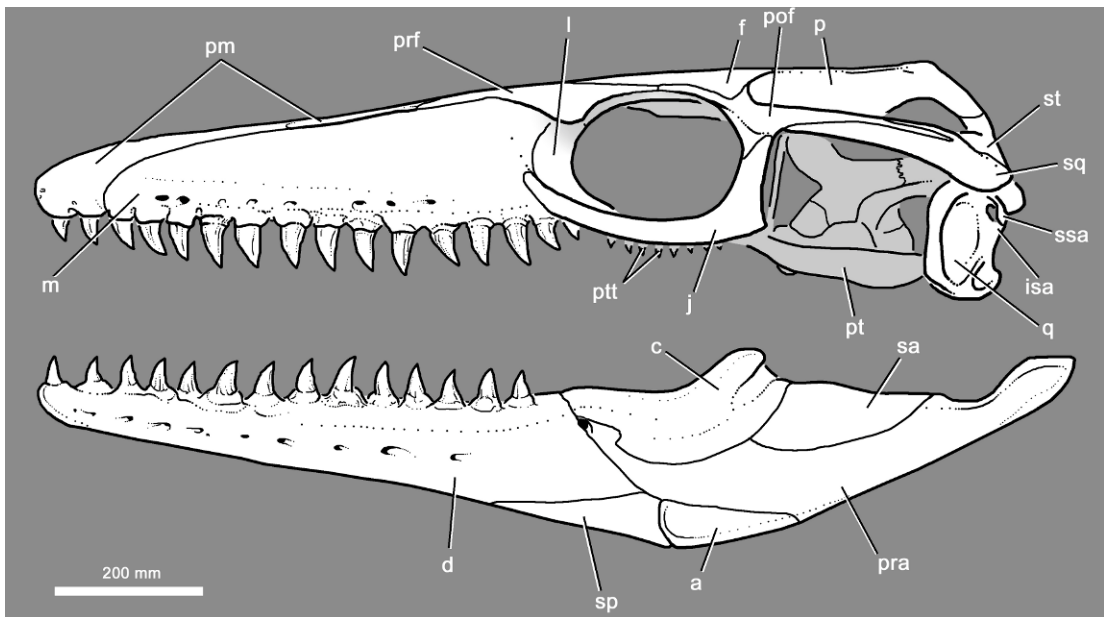
Fig. 41. Skull of *Mosasaurus hoffmanni*, the largest known squamate, in left lateral view. Modified after Lingham-Soliar (1995).

ceives angular (figs. 41, 42A); (2) abutting, angular receives splenial (fig. 42B). This character follows the descriptions given in Rieppel and Zaher (2000a) and is unordered. Thus, no assumption is made about whether or not the condition seen in snakes (state 2) is derived from the plesiomorphic condition or from the mosasaur-style intramandibular hinge (state 1). Although Rieppel and Zaher (2000a) score Scolecophidia as plesiomorphic for this character, data in List (1966) and Kley (2004) suggest state 2 for at least some members of this taxon.

192. Coronoid, height of coronoid at process relative to the length of the mandible (CN-125): (0) short, broad; (1) tall, narrow. This is an imperfect attempt to quantify the character states "coronoid process tall" and "coronoid process short". Every attempt has been made, though, for internal consistency within the present analysis.

193. Coronoid, posterior extent of the labial flange (CN-126): (0) absent (fig. 31A); (1) extends mostly labially (fig. 29C, E), does not overlap the posterior margin of the coronoid process in lateral view; (2) extends beyond the posterior margin of the coronoid process in lateral view

194. Coronoid, anterior end (E-70): (0) clasps the dentary; (1) butts against dentary.

195. Coronoid, ventral margin (RZ-128): (0) flat or concave; (1) dorsally convex.

196. Coronoid, long and low anterior process (E-69): (0) absent (e.g., fig. 35); (1) present (figs. 20, 41).

197. Coronoid, medially exposed contact with the anterior inferior alveolar foramen (new): (0) absent (fig. 36D); (1) present (fig. 38E). In some taxa, the anterior ramus of the coronoid is exposed anteriorly between the splenial and the dentary to the level of the anterior inferior alveolar foramen and contributes to its margin.

198. Coronoid, posterior overlap by surangular (E-71): (0) absent (figs. 29C, 30); (1) present (figs. 20, 29E, 35, 36).

199. Surangular, anterodorsal buttress of coronoid (DBC-57): (0) absent (e.g., fig. 36A); (1) present (fig. 41).

200. Surangular, anterior border when disarticulated (E-61): (0) tapering; (1) expanded anterodorsally with vertical anterior margin.

201. Surangular, anterior extension into mental canal (Ga82-75): (0) absent; (1) present.

202. Angular (RZ-132): (0) present; (1) absent.

203. Prearticular crest (E-73): (0) absent; (1) present.

204. Prearticular crest with imbedded angular process (E-73): (0) absent; (1) present.

205. Articular, orientation of the retroarticular process along its long axis (E-75): (0) posteriorly directed; (1) medially deflected.

206. Articular, medial offset of retroarticular process with lateral notch (E-77): (0) absent; (1) present.

207. Articular, retroarticular process with posterior broadening (E-78): (0) absent; (1) present.

208. Articular, presence of a deep fossa on the dorsal or dorsomedial surface of the retroarticular process (the retroarticular process pit) (E-74): (0) present; (1) absent.

209. Articular, tubercle on the medial margin of the retroarticular process (E-76; GN00): (0) absent; (1) present as a tubercle; (2) present, elaborated into a fingerlike process.

210. Articular, torsion of the retroarticular process (GN98-70): (0) absent; (1) present; (2) present and strongly twisted.

211. Dentition, spacing (C06-33): (0) closely spaced (fig. 26A); (1) widely separated; spaces between tooth bases greater than one-half the width of a tooth shaft (figs. 22C, 26B); (2) tightly packed (ctenodont) (figs. 20, 29A, C, 38A).

212. Dentition, form of middle and posterior marginal teeth (Ga82-34): (0) straight, pointed; (1) triangular; (2) trenchant, curved; (3) incipient cusps on posterior teeth; (4) teeth with multiple crowns; (5) globidont; (6) squared dorsal margin. Premaxillary teeth and anterior maxillary and dentary teeth tend to be the most variable in their form, whereas more posterior marginal teeth are usually more uniform with one another (although often different from the more anterior teeth).

213. Dentition, waist on marginal teeth (new/extensively modified): (0) absent (e.g., fig. 38E); (1) present (e.g., fig. 43).

214. Dentition, marginal tooth implantation (RZ-146): (0) labially pleurodont (e.g., fig. 37C); (1) acrodont (fig. 37A); (2) modified pleurodont; (3) enclosed by expanded interdental ridge; (4) subacrodont. The terminology used in this character and its scoring are based on several recent studies and may be slightly different from traditional usage (Zaher and Rieppel, 1999a; Rieppel and Zaher, 2000a).

Borsuk-Białynicka (1996) described a condition of tooth permanency in some squamates that is, apparently, related to acrodonty and posterior extension of the dentary as exemplified by *Pleurodontagama aenigmatodes* (possibly a young *Priscagama gobiensis* as discussed by Gao and Norell, 2000) (Borsuk-Białynicka, 1996). Posterior extent of the dentary and presence of acrodont dentition do not invariably co-vary, so both of these characters are included in the current analysis.

215. Dentition, caniniform teeth (Eagam-1): (0) absent; (1) present.

216. Dentition, anterior marginal teeth (DBC-53): (0) generally perpendicular to the long axis of the jaw; (1) procumbent.

217. Dentition, expanded bases on marginal teeth (RZ-149): (0) absent; (1) present, main shafts of teeth somewhat separated.

218. Dentition, plicidentine (E-86): (0) absent; (1) present. *Proplatynotia* and *Paravaranus* coded as per Gao and Norell (1998). Note that there is some question about the homology of basally ridged teeth in some taxa and the relationship of this to true plicidentine (Kearney and Rieppel, 2006). Presence of plicidentine can only be assessed in the context of a broken/sectioned tooth clearly showing the presence or absence of dentine folds or, in some cases, in high-resolution x-ray computed tomography scans (Kearney and Rieppel, 2006).

219. Dentition, crown striations (M70): (0) absent; (1) present. Striations are present most commonly in anguids, but are also present in the pleurodont teeth of *Diphydontosaurus* (Whiteside, 1986) and many mosasaurs (e.g., *Mosasaurus hoffmanni*; fig. 41). Because of possible asymmetric wear on teeth, crown striations are coded as a single character in the present analysis.

220. Dentition, venom groove (PGG86-30): (0) absent (fig. 36D); (1) present (fig. 38E). Nydam (2000) carefully reviews the morphology of the various relevant taxa for this character and the codings given in this analysis are based mainly on that study.

221. Dentition, replacement (E-85): (0) develop lingually, large resorption pit; (1) posterolingually, resorption pit; (2) posterolingually, no resorption pit.

222. Dentition, enlarged median premaxillary tooth more than half again the diameter of the other premaxillary teeth (Ke-114): (0) absent; (1) present. Kearney (2001, 2003a, 2003b) takes issue with the previous coding of this character, her discussions are used as a basis for the codings in the present analysis.

223. Dentition, premaxillary teeth compared to maxillary teeth (RZ-156): (0) similar (e.g., fig. 38A); (1) markedly smaller (e.g., fig. 38B–D); (2) absent. Note that snakes sometimes lack premaxillary teeth (state 2).

224. Dentition, maxillary teeth (new): (0) present; (1) absent.

225. Dentition, dentary teeth (new): (0) present; (1) absent. Coding of the presence or absence of maxillary and dentary teeth is not redundant with other dental characters. Taxa lacking maxillary and dentary teeth are coded
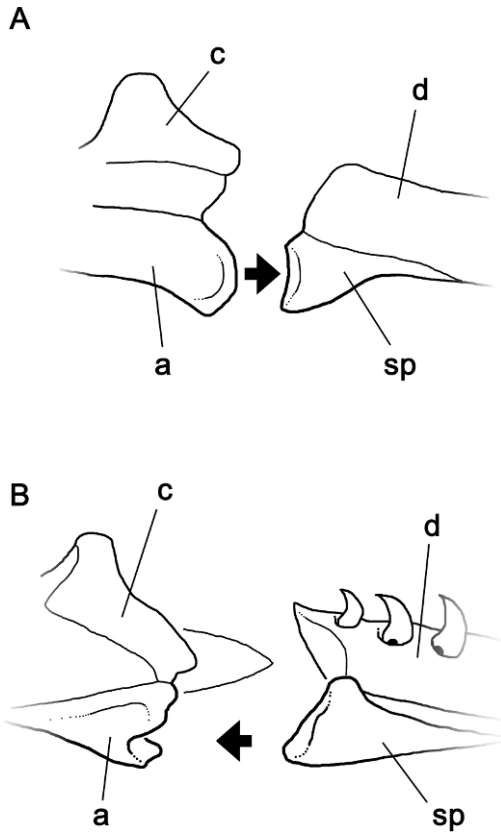
Fig. 42. Diagrammatic illustration of the construction of the intramandibular joint in mosasaurs and snakes. **(A)** The mosasaur condition in which the splenial receives a projection of the angular. **(B)** The snake condition in which the angular receives a projection of the splenial. Modified after Rieppel and Zaher (2000a: figs. 7, 8).

as "-" or "unknown due to change" in this analysis for characters associated specifically with maxillary or dentary teeth. No taxon included in this study lacks both maxillary and dentary teeth.

226. Dentition, chisel shaped posterior teeth (M70): (0) absent; (1) present.

227. Hyoid, second ceratobranchial (E-91): (0) present; (1) absent.

228. Hyoid, second epibranchials (E-90): (0) present; (1) absent.

229. Epihyal, shape (Egek-20): (0) small, triangular; (1) large, winglike.

230. Notochord, in adults (Kl87-2): (0) persistent; (1) obliterated.

231. Vertebrae, centrum morphology (Kl87-1): (0) amphiplatyan; (1) amphicoelous; (2) procoelous. Examination of published descrip-

tions and specimen observations confirm that a persistent notochord is not always concomitant with amphicoelous vertebrae (see, for example, Evans, 1994a).

232. Vertebrae, neural spines (GN98-78; Ke03-134): (0) short and broad; (1) tall and narrow; (2) absent. State (2) is used for those taxa in which there is no projection above the level of the neural canal roof.

233. Vertebrae, precondylar constriction (E-94): (0) absent; (1) present, weakly constricted; (2) strongly constricted to less than 80% of the maximum condylar diameter.

234. Vertebrae, obliqueness of condyles (E-92): (0) absent/weak, posterior apex of condyle visible; (1) moderate, articulating condylar surface slightly visible in ventral view; (2) strong, articulating surface not visible in ventral view.

235. Vertebrae, zygosphenes-zygantra (RZ-169): (0) absent; (1) present, zygosphene articular surface faces dorsolaterally (fig. 44A); (2) present, zygosphene articular surfaces face ventrolaterally (fig. 44B). Rieppel and Zaher (2000a) pointed out the difference in structure between some taxa possessing these accessory articulations. There is no reason to assume primary homology between the two types of accessory articulation described here. Thus, there is no clear nested set of homologies and this character is considered unordered. Retaining this character as unordered further allows assessment of whether the presence/absence of zygosphenes-zygantra is a viable character; that is, whether or not one morphology of zygosphenes evolved from the other.

236. Vertebrae, presacral number (E-105, 106): (0) 25 or fewer; (1) 26; (2) 27 or more. More work is needed to help identify the informative character states for this character. Although the character is informative as used here and similarly used in recent publications (Evans and Barbadillo, 1998; Gao and Norell, 1998; Lee, 1998; Lee and Caldwell, 2000), its conception is imperfect.

237. Presacral vertebrae, notching of synapophyses: (0) absent; (1) present.

238. Presacral vertebrae, length of transverse processes: (0) short, subequal or shorter than centrum; (1) more than the length of the centrum. This character is informative only with the inclusion of *Marmoretta* and Kuehneosauridae (see appendix 1).

239. Atlas, dorsal margin (CN-158): (0) horizontal; (1) posteroventrally inclined. This character is used to describe the dorsal margin of the atlas neural spine when in articulation and with the skull held horizontally.
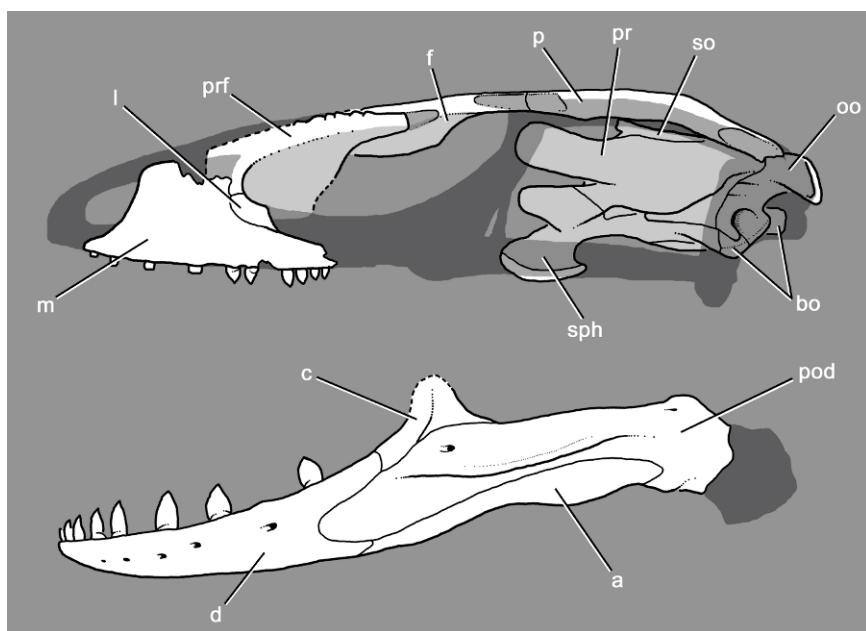
Fig. 43. The skull of *Dorsetisaurus purbeckensis* as reconstructed based on the individual elements illustrated and described in Hoffstetter (1967a). Note that the dentary teeth are much larger than the corresponding maxillary teeth. Reconstructed portions are shown as semi-opaque shadows.

240. Atlas, lateral process (CN-159): (0) well defined with some posterior overlap of the axis; (1) small, a "hill-like" projection; (2) absent.

241. Cervical vertebrae, length relative to the dorsal vertebrae (L97-103): (0) cervical vertebrae subequal to or shorter than the dorsal vertebrae; (1) more elongate than the dorsal vertebrae.

242. Cervical vertebrae (E-107, 108): (0) 8; (1) 7 or fewer; (2) 9; (3) 10 or more.

243. Cervical, intercentra (E-97): (0) intervertebral; (1) sutured to the posterior part of the preceding centrum; (2) fused to posterior part of preceding centrum; (3) fused to the succeeding centrum (CN-161); (4) absent.

244. Cervicals, hypapophyseal keel (EB98-149): (0) absent; (1) present.

245. Dorsal vertebrae, pachyostosis (LC00-196): (0) absent; (1) present.

246. Dorsal vertebrae, intercentra (EB98-86): (0) present; (1) absent.

247. Sacral vertebrae, functional (DBC-72): (0) present; (1) absent. "Functional" sacral vertebrae are defined here as those whose sacral ribs contact the ilium, anchoring the pelvis to the vertebral column.

248. Cloacal vertebrae, lymphapophyses (LC00-209): (0) absent; (1) present.

249. Caudal vertebrae, dorsoventral height (including the neural spines and chevrons) (CDB—mosasauroid character 9): (0) unexpanded; (1) expanded, creating a sculling organ (depth of proximal and mid caudal vertebrae, including chevrons, greater than 3 times length of centrum).

250. Caudal vertebrae, zygapophyses and transverse processes (CDB5): (0) well developed, zygapophyses extending more one-fourth the length of centrum; (1) reduced, creating greater flexibility of the trunk and tail. This character complex describes the flexibility of the tail. Greater flexibility is typically associated with the further development of the tail as a sculling organ (see character 249).

251. Caudal vertebrae, transverse processes (E-100-102): (0) single (fig. 45A, B, D); (1) double, diverging (fig. 45C); (2) double converging; (3) absent.

252. Caudal vertebrae, autotomy planes (E-103): (0) present on (or between) the transverse process(es) (fig. 45A, C); (1) present posterior to the transverse process(es) (fig. 45B); (2) absent; (3) present anterior to transverse processes

(fig. 45D). Species and even specimens are sometimes polymorphic for this character.

253. Caudal vertebrae, pedestals for chevrons (RZ-183): (0) bulges; (1) well-developed, expressed as relatively deep and discrete pedestals.

254. Chevrons, position (RZ-185): (0) at the posteroventral margin of the centrum; (1) anterior to the posteroventral margin of the centrum; (2) fused to vertebrae (GN98-83).

255. Ribs, anteroventral pseudotuberculum (LC00-207): (0) absent; (1) present.

256. Ribs, posterodorsal pseudotuberculum (LC00-208): (0) absent; (1) present.

257. Ribs, expansion and flattening of the anterior presacral ribs (CN-166): (0) absent; (1) present.

258. Ribs, postxiphisternal inscriptional ribs (FE-40): (0) contacting the dorsal ribs, not contacting at midline; (1) contacting dorsal ribs, one or more pairs confluent at midline; (2) free dorsally, confluent ventrally. Some taxa scored for this character based on Torres-Carvajal (2004).

259. Postcloacal bones (E-125): (0) absent; (1) present.

260. Clavicles, shape (RZ-196): (0) rodlike; (1) expanded proximally with notch or fenestra; (2) absent.

261. Clavicle, angulation (E-116): (0) straight, without angulation; (1) strongly curved/angled.

262. Coracoid, anterior (primary) coracoid emargination (E-112): (0) absent; (1) present.

263. Coracoid, posterior (secondary) emargination (E-113): (0) absent; (1) present.

264. Epicoracoid cartilage, contact with suprascapula (E-114): (0) present; (1) absent.

265. Scapula, size relative to the coracoid (DBC-95): (0) scapula subequal to, or larger than the corocaoid; (1) scapula smaller than the coracoid; (2) scapula and coracoid absent.

266. Scapula, secondary scapular fenestra formed by a scapular epicoracoid bar (E-111): (0) absent; (1) present.

267. Sternum, rib attachments (E-109): (0) five; (1) four; (2) three; (3) two or fewer. Taxa lacking sterna cannot be scored for this character.

268. Interclavicle (E-118): (0) present; (1) absent.

269. Interclavicle, anterior process (E-120): (0) absent; (1) present, single; (2) present, double.

270. Interclavicle, lateral arms (E-119): (0) present; (1) absent.

271. Sternum (Ke-146): (0) present, articulates with pectoral girdle; (1) present, reduced and does not articulate with the pectoral girdle; (2) absent.

272. Sternum, proximity to the lateral arms of the interclavicle (FE-33): (0) separated by more than one-third the posterior process of the interclavicle; (1) separated by one-third or less the length of the posterior process. *Xenosaurus* is coded as polymorphic; an illustration in Renous-Lécuru (1968) indicates derived condition for *X. grandis*, but *X. platyceps* has the plesiomorphic state.

273. Sternum, fontanelle (E-121): (0) absent; (1) present. Some taxa were coded based on Renous-Lécuru (1968).

274. Xiphisternum, branching (this character is derived from figures and descriptions in Renous-Lécuru, 1968; Estes et al., 1988; and Etheridge and de Queiroz, 1988; CN-179): (0) more than one branching; (1) one branching; (2) unbranched.

275. Humerus, shape (DBC-104): (0) elongate, sub-cylindrical, and twisted such that distal ends at right angles to one another; (1) flattened; hourglass-shaped; (2) flattened—with square, ends expanded but equal; (3) flattened; rhomboid, distal end more expanded; (4) humerus absent.

276. Humerus, deltopectoral crest (DBC-107): (0) single continuous projection; (1) separate, but joined by a lamina; (2) separate, not joined by a lamina. Ordered by DeBraga and Carroll (1993), but not ordered here.

277. Ectepicondylar foramen (EB98-103): (0) foramen (fig. 46A); (1) groove; (2) absent altogether (fig. 46B).

278. Forelimb, zeugopodium (CN-181): (0) present; (1) absent.

279. Radius, preaxial ridge (DBC-113): (0) absent; (1) thin, rounded, lamina extending for more than one-half the anterior margin; (2) present, rounded and extending for less than one-half the anterior edge; (3) present, greatly expanded with an anteroproximal apex.

280. Ulna, articulation with intermedium (DBC-111): (0) absent, intermedium does not contact the ulna; (1) present, no facet; (2) present, with a distinct intermedium facet on the ulna.

281. Carpus, intermedium (Egek-24): (0) present; (1) absent.

282. Manus, first metacarpal (DBC-116): (0) similar in robustness to other metacarpals; (1) robust, more than 1.5 times wide as the other metacarpals.

283. Manus, orientation of the fifth digit relative to the others (DBC-119): (0) fifth digit not greatly divergent; (1) at greater than 70 degrees from fourth digit.

A

B
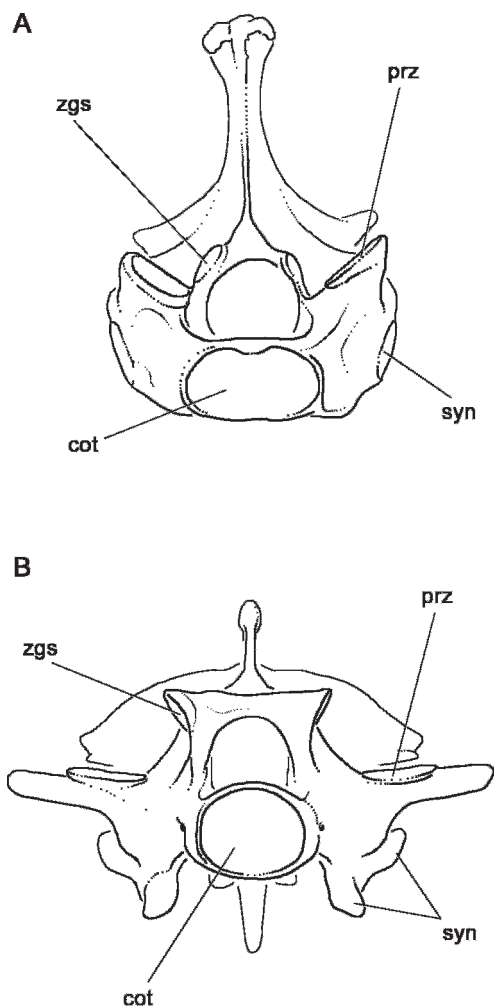
Fig. 44.   Anterior view of two vertebrae bearing zygosphenes. **(A)** *Necrosaurus cayluxi* possesses dorsolaterally oriented zygosphenes [character state 235(1)]. **(B)** *Natrix natrix* possesses ventrolaterally oriented zygosphenes [character state 235(2)]. Modified after **(A)** Rage (1978) and **(B)** Parker and Grandison (1977).

284. Pelvis (RZ-207): (0) fused into a single ossification such that the sutre lines have become indistinct; (1) strongly sutured, but with distinct suture lines visible; (2) nonsutural contacts. Many taxa have fused the pelvis so tightly that sutures are not visible in the acetabulum or on the medial surface of the pelvis (state 0). Many others have sutures visible (state 1). Other taxa, especially those adapted to aquatic lifestyle and/or limb-reduced taxa, have lost sutural contacts altogether (2). In the latter,

the bones of the pelvis may contact one another, but are not sutured.

285. Pubis, relative length of the symphysial portion compared to the tubercular portion (E-124): (0) shorter than; (1) subequal to, slightly longer than; (2) more than one-half again as long.

286. Pubis, distal shape (DBC-125): (0) expanded and fanlike; (1) slender. This character is problematic because the derived state as described by DeBraga and Carroll (1993) seems to be plesiomorphic. This character is included here with some reservations, but is coded consistently within the analysis. Taxa that lack an ossified pubis are not coded, even if a cartilaginous element is present.

287. Ilium, anterior process (RZ-208): (0) present; (1) absent.

288. Femur, distal condyles (DBC-132): (0) separate and distinct such that the distal part of the femur is a single convex entity; (1) confluent.

289. Femur, shape (DBC-130): (0) cylindrical with moderately expanded proximal and distal ends; (1) flattened, breadth of distal end more than one-quarter the bone's length; (2) femur absent.

290. Pes (CN-186): (0) present with digits and/or metatarsals (fig. 47A); (1) absent (fig. 47B); (2) tarsal element(s) only. Gasc and Renou (1979) illustrate a single distal element in *Dibamus*.

291. Pes, relative positions of the medial and lateral plantar tubercles on metatarsal V (R80L; C06-44): (0) even with one another or overlapping levels; (1) lateral tubercle distally placed; (2) lateral tubercle distally placed, approaching condyle; (3) greatly shortened metatarsal V precludes identification. Rieppel (1980b) originally identified the distal placement of the lateral plantar tubercle in the varanid *Lanthanotus borneensis*. Later, the same character state was observed in shinisaurids (Conrad, 2005a, 2006a, 2006b). This character has now been scored across squamates and the derived states have been observed in various taxa.

292. Astragalus and calcaneum, fusion (L98-215): (0) separate; (1) fused; (2) absence of a bony calcaneum. Lee and Caldwell (2000) scored *Aphanizocnemus* as possessing a separate astragalus and calcaneum, but this is ambiguous based on the description by Dal Sasso and Pinna (1997). Many aquatic taxa apparently lack a calcaneum (Russell, 1967; Bell, 1997; however see Caldwell, 1996). However, because ossification of various distal appendicular elements is reduced in these forms, it seems possible
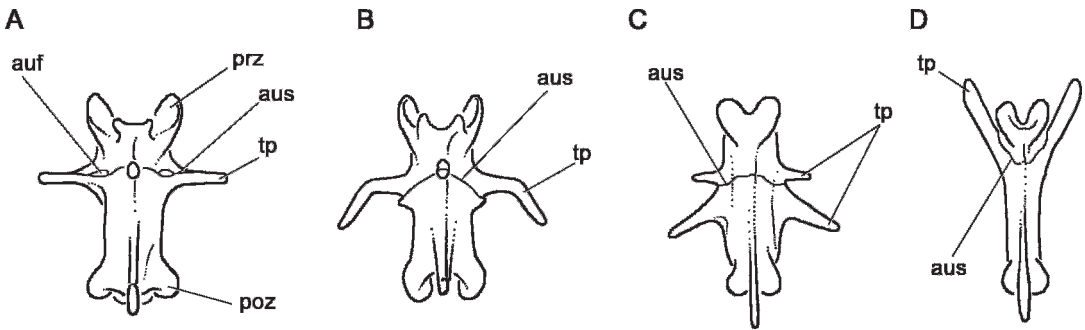
Fig. 45. Dorsal view of the various caudal vertebrae possessing autotomy planes. **(A)** *Shinisaurus crocodilurus* (UF 57712) possesses character states 251(0) and 252(0); **(B)** *Gekko* sp. possesses character states 251(0) and 252(1); **(C)** *Dipsosaurus dorsalis* possesses character states 251(1) and 252(0); and **(D)** *Anolis sagrei* possesses character states 251(0) and 252(3). The vertebra in **(A)** is modified from Conrad (2006a), **B–D** are redrawn from Estes et al. (1988). Not to scale.

that a cartilaginous calcaneum might have originally been present.

293. Egg teeth (KL87-15): (0) single; (1) double; (2) absent.

294. Femoral/precloacal pores (E-144): (0) absent; (1) present.

295. Integument, gular fold with distinctive midventral squamation (FE-47): (0) absent (figs. 48, 49B); (1) present (fig. 50).

296. Integument, annular rings (dermal/epidermal) in the body squamation (Ke-3): (0) absent; (1) present.

297. Integument, scale organ ornamentation (FE-52; H93): (0) absent; (1) spinules; (2) spikes. Original character from Frost and Etheridge (1989); character state ''spikes'' added from Harvey (1993).

298. Squamation, cephalic scales (E-147; M70): (0) absent; (1) small and irregularly shaped (figs. 48, 49); (2) enlarged plates (fig. 51). The character state (0) absent does not occur in any taxon used here, although some gekkotans possess only lightly keratinized dermal tubercles that do not follow the traditional definition of a scale. This character is considered unordered.

299. Squamation, contact between frontal and parietal scale (M70): (0) absent; (1) present. Meszoely et al. (1978) report that the plesiomorphic condition occurs in *Peltosaurus*. Lacertids are coded here with consideration of data from *Succinilacerta succinea*, an Eocene lacertid preserved in Baltic amber (Borsuk-Białynicka et al., 1999).

300. Squamation, middorsal scale row (E-146): (0) differing from surrounding scales, elongate with apices (fig. 50); (1) similar to surrounding scales (figs. 48, 49, 51, 52).

301. Squamation, cycloid scales (E-148): (0) absent; (1) present.

302. Squamation, cephalic scale fusion (Ke-5): (0) absent; (1) present. This character addresses the presence or absence of expansive head shields that incorporate (and obscure the boundaries of) individual head scales such as labials or superciliaries (or others).

303. Squamation, imbrication (M70): (0) absent (fig. 49); (1) present (fig. 51).

304. Squamation, lateral fold in body (MB54): (0) absent; (1) present.

305. Squamation, dorsal body osteoderms (E-127): (0) absent (figs. 48, 50); (1) present (figs. 49, 51, 52).

306. Squamation, dorsal compound osteoderms (E83): (0) absent; (1) present. Taxa lacking dorsal body osteoderms cannot be scored for this character.

307. Squamation, ventral body osteoderms (E-126): (0) absent; (1) present.

308. Squamation, ventral compound osteoderms (E83): (0) absent; (1) present. Taxa lacking ventral body osteoderms cannot be scored for this character.

309. Osteoderms, grooves separating osteoderms on maxilla (Y76-5): (0) absent (fig. 26A); (1) present (fig. 26B).

310. Squamation, osteoderm thickening (C06-48): (0) absent, osteoderms thin plates or noncalcified (fig. 51); (1) present, irregularly shaped (fig. 22B); (2) present, polygonal mounds (fig. 52); (3) absent, osteoderms wormlike (vermiform). State 3 has been carefully described in the literature (Smith, 1935; McDowell and Bogert, 1954; Auffenberg, 1981; Erickson et al., 2003). Fig. 49 has photos of monitor lizards that would, presumably, possess

vermiform osteoderms, but their presence is not obvious from external view (unlike the large thickened osteoderms in taxa such as *Heloderma*; fig. 52)

311. Squamation, bony tubercles (new/extensively modified): (0) absent; (1) present as individual bony tubercles; (2) large osteoderms covered with individual bony tubercles. Tubercular osteoscutes and bony tubercles have been variably described for numerous taxa and are present in xenosaurids (state 1) and glyptosaurs (state 2), for example.

312. Squamation, keeled osteoderms on body (C06-47): (0) absent; (1) present.

313. Eyeball (Ke-10): (0) complete and exposed; (1) reduced, covered by a head scale; (2) reduced, not externally visible. Although most of the fossil taxa included in this analysis probably possessed state (0), it is impossible to be sure for all except some of those preserved in amber. To minimize assumptions about fossil taxa, this character has been left as "?"s for nonamber specimens.

314. Eye, movable eyelid (Ke-11): (0) present; (1) absent, eyelids fused into a spectacle or brill.

315. Eye, scleral ossicles (Ke-12): (0) present; (1) absent. The number, orientation, morphology, and interrelationships of squamate scleral ossicles have not been included in this matrix as yet. Future iterations of this analysis will address those morphological features, but they require further consideration.

316. Glossus, filamentous tongue papillae (S-6, 7, 8, 9): (0) absent; (1) peglike; (2) individual papillae dorsally asymmetrical, forming points.

317. Glossus, division of the foretongue (E-137): (0) absent; (1) notched more than 10% of length; (2) notched more than 20%; (3) notched more than 40%; (4) notched more than 50% of length. The character states delimited here are slightly modified from Estes et al. (1988). The states for this character both here and in Estes et al. (1988) are arbitrary in their delimitation.

318. Glossus, foretongue retracts within hindtongue at zone of invagination (E-136): (0) absent; (1) present. Many of the tongue characters listed here (including this one) are taken from or modified after both Estes et al (1988) and Schwenk (1988).

319. Glossus, cross-section of tongue (E-138): (0) rounded and glandular; (1) flattened foretongue; (2) keratinized and mushroom shaped foretongue cross-section.

320. Gland of Gabe (GN98-102): (0) absent; (1) present.

321. Ear, external ear opening (auricular depression or canal) (Ke-13): (0) present; (1)
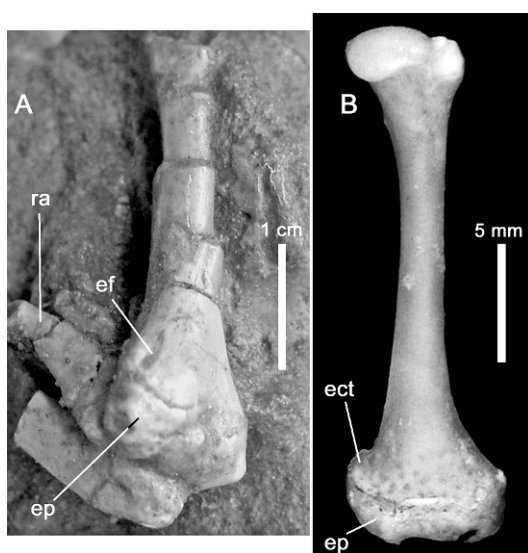
Fig. 46. Left humeri of **(A)** *Telmasaurus grangeri* (AMNH FR6643) in anterodorsal view; and **(B)** *Lacerta viridis* (AMNH R1148) in dorsal view. Note the absence of a ectepicondylar foramen and groove [character state 277(2)] in **(B)**.

absent. For a further discussion of this character, see Greer (2002).

322. Inner ear, thickening of the neural limbus of cochlear duct (Eanguim-14): (0) absent; (1) present. This character is scored based on data presented in Miller (1966), Wever, (1978), and Estes et al. (1988).

323. Inner ear, ciliary restraint for hair cells (E-140): (0) tectorial, lacking sallet systems; (1) tectorial and sallet; (2) more than one-half hair cells inertial.

324. Seromucus glands in inferior labial glands (Eanguim-16): (0) absent; (1) present.

325. Endolymphatic sacs, extension into the nuchal musculature (Kl67-C; EdQ88-35): (0) absent; (1) present, the endolymphatic sacs exit through an aperture between the supraoccipital and parietal; (2) present, the endolymphatic sacs exit through the epiotic foramen; (3) present, the endolymphatic sacs exit through the vagus foramen.

326. Hemipenis, symmetry (B82): (0) present; (1) absent.

327. Hemipenis, sulcus (B82): (0) simple; (1) divided.

328. Hemipenis, dorsal asulcal ornamentation (B82): (0) absence; (1) simple flounces; (2) bifurcated flounces.

329. Hemipenis, m. retractor lateralis posterior substantial situation within hemipeneal sheath (FE-63): (0) absent; (1) present.
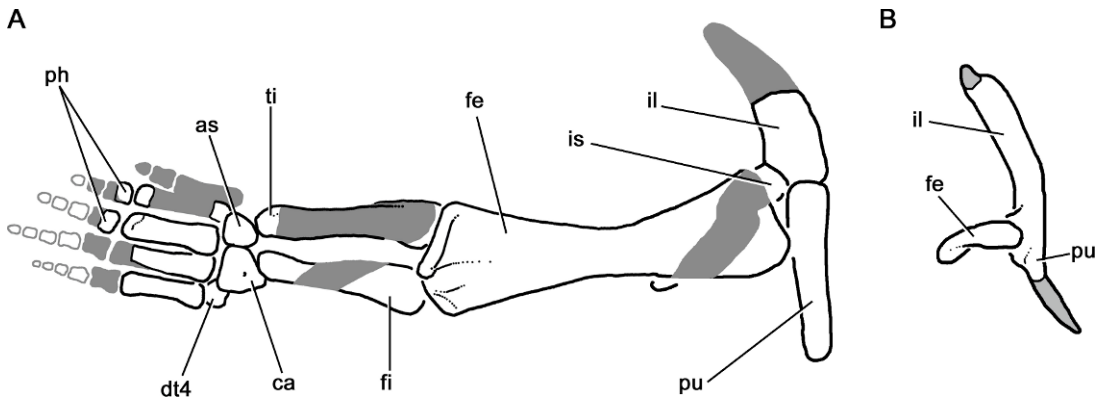
Fig. 47.   Hind limbs **(A)** *Haasiophis terrasanctus* and **(B)** *Blanus cinereus*. The hind limb of *Haasiophis terrasanctus*, a snake is well developed with tarsals, metatarsals, and phalanges [character state 290(0)]. The hind limb of *Blanus* is composed only of a femur without distal elements such as a pes [an exemplar of character state 290(1)]. Note that the dark gray represents unknown or heavily reconstructed portions and the light gray (in **B**) represents cartilaginous elements. The gray outlines represent portions that are hypothesized to have originally been present, but for which there is not direct evidence. Modified after **(A)** Tchernov et al. (2000) and Rieppel et al. (2003), and **(B)** Kearney (2002).

330. Hemipenis, horns (B82): (0) absent; (1) present, simple; (2) present, multicusped.

331. Hemibacula (GN98-99): (0) absent; (1) present.

332. Neurology, ulnar nerve position (J72; E-142): (0) "lacertid" style; (1) "varanid" style.

333. Neurology, dorsal leg muscles (J72; E-143): (0) peroneal nerve present; (1) peroneal nerve absent, interosseus innervation.

334. M. anterior mandibulae externus (MAME) profundus origin (GN98-93): (0) supratemporal and parietal; (1) supratemporal only. Data used here were derived from various sources in the literature for different squamate groups (Haas, 1960, 1973; Rieppel, 1980a, 1980d, 1980e, 1981a, 1981b, 1982, 1984a; Estes et al., 1988; Gao and Norell, 1998; Abdala and Moro, 2003).

335. Meatal closure muscle (Kl87-12): (0) absent; (1) present, L-shaped; (2) present, O-shaped.

336. M. extracolumellaris (E-135): (0) absent; (1) present.

337. Myology, anterior extension of m. adductor mandibulae posterior (E-131): (0) no further than the posterior margin of Meckel's canal; (1) anterior to the posterior one-fourth of the dentary.

338. Myology, m. pseudotemporalis superficialis origin (E-132): (0) lateral and anterior margins of the supratemporal fossa; (1) also along the medial margin of the temporal fenestra.

339. M. levator pterygoidii, insertion (GN98-96): (0) extends posteriorly beyond the columellar fossa; (1) restricted anterior to the columellar fossa.

340. M. pseudotemporalis profundus, anterior head (E-133): (0) absent; (1) present, not expanded; (2) present, expanded.

341. M. pseudotemporalis superficialis, origin (E-132): (0) limited to the anterior one-half of the supratemporal fenestra; (1) extends far posteriorly, onto the posterior one-third of the supratemporal fenestra.

342. Bodenaponeurosis, base contact with mandibular fossa (GN98-98): (0) present; (1) absent, attached only to the caudomesial edge of the coronoid Coding from Gao and Norell, 1998 after Lakjer (1926), Haas (1973), and Rieppel (1980a).

343. M. constrictor colli coverage of first ceratobranchials (GN98-92): (0) absent; (1) present.

344. M. genioglossus lateralis, morphology (GN98-95): (0) not separate bundles, not inserting on the hyobranchials; (1) separate bundles, some inserting on the hyobranchials.

345. M. rectus abdominis lateralis (E-134): (0) absent; (1) present.

346. M. episterno-cleido-mastoideus insertion (GN98-91): (0) mainly on the paroccipital process; (1) extensively on parietal.

347. Urinary bladder (B86): (0) present, complete; (1) present, vestigial; (2) absent. Coded largely after data summarized by Beuchat (1986).

348. M. levator anguli oris (AM03-3): (0) present; (1) absent.

Fig. 48.   *Uromastyx dispar maliensis* (= *Uromastyx maliensis* of the usage of Joger and Lambert, 1996). **(A)** Broad view of the body except the tail tip. **(B)** Detail of the head. Note the character states 198(1) (compare with fig. 51) and 300(1) (compare with fig. 50), among others visible in this figure. Specimen housed at Dickerson Park Zoo in Springfield, Missouri. Photo by R. M. Shearman.

349. M. levator anguli oris, aponeurosis (AM03-10): (0) present; (1) absent.

350. Adductor mandibulae externus, tendinous system (AM03-12): (0) absent; (1) present.

351. M. adductor mandibulae posterior (AM03-32): (0) present; (1) absent.

352. M. pseudotemporalis superficialis (AM03-36): (0) present; (1) absent.

353. M. protractor pterygoidei (AM03-51): (0) present; (1) absent.

354. M. retractor pterygoidei (AM03-53): (0) present; (1) absent.

355. M. intermandibularis anterior superficialis (AM03-54): (0) absent; (1) present.

356. M. intermandibularis anterior profundus aponeurosis (AM03-55): (0) absent; (1) present.

357. M. depressor mandibulae profundus (AM03-65): (0) present; (1) absent.

358. M. mandibulohyoideus II (AM03-76): (0) absent; (1) present.

359. M. mandibulohyoideus III (AM03-81): (0) absent; (1) present.

360. M. branchiohyoideus aponeurosis (AM03-83): (0) absent; (1) present.

361. M. ceratohyoideus (AM03-84): (0) absent; (1) present.

362. Muscle "X" (AM03-86): (0) absent; (1) present.

363. M. sternohyoideus (AM03-92): (0) absent; (1) present.

364. Biogeography: (0) global; (1) Madagascar; (2) South America; (3) North America/Central America; (4) Europe/western Asia; (5) sub-Saharan Africa; (6) northern Africa/Arabia; (7) India; (8) East Asia; (9) Australia.

THE CHARACTERS OF ESTES ET AL. (1988)

Many of the characters used in this analysis are directly or indirectly derived from the character list provided by Estes et al. (1988). Estes et al. (1988) used 148 morphological characters in their analysis, 139 of which are covered by the characters used in this analysis. Each of the nine excluded characters will be discussed here.

ESTES ET AL. (1988) CHARACTER 40: "Median contact of septomaxillae: (0) separated by a gap filled by the cartilaginous internarial septum; (1) septomaxillae meet or nearly meet on midline in a raised crest"
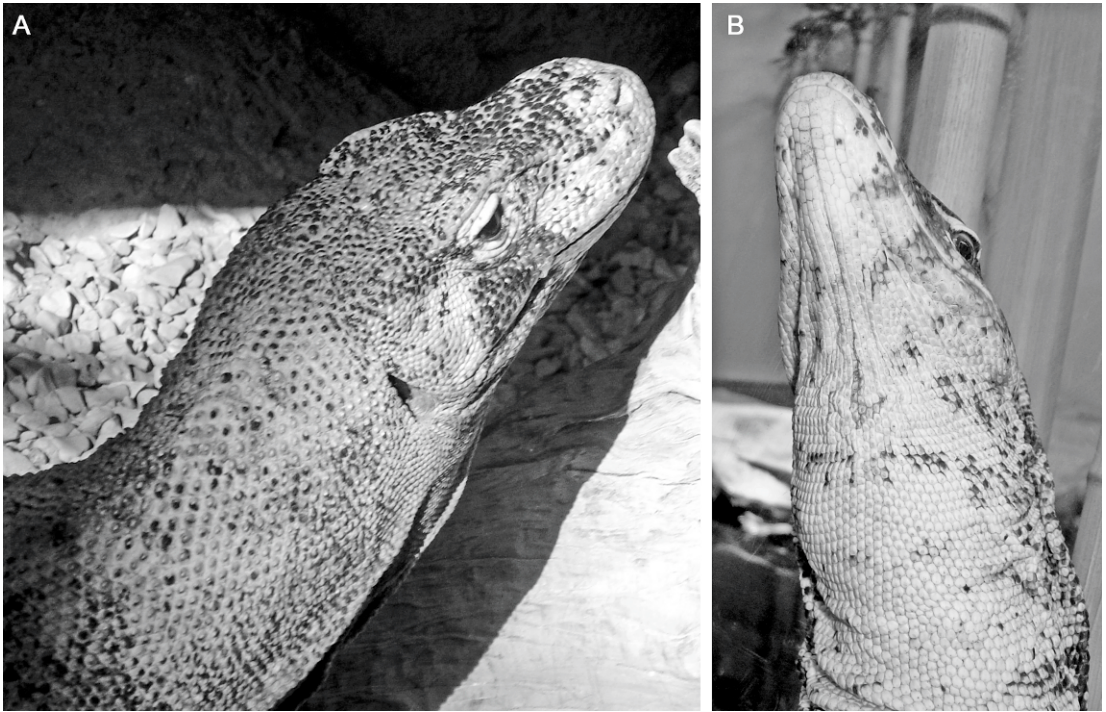
Fig. 49. The head of two species of *Varanus*. **(A)** Dorsolateral view of the head and neck in *Varanus komodoensis* exhibiting character states 3(1), 298(1), 300(1), and 310(3). **(B)** Ventrolateral view of the head of *Varanus salvator* exhibiting character states 3(0) and 295(0) (compare with fig. 50). Specimens housed at **(A)** the Audubon Zoo in New Orleans, Louisiana, and **(B)** photographed at AMNH, part of the collection from Clyde Peeling's Reptiland in Allenwood Pennsylvania. Photos by R. M. Shearman.

(Estes et al., 1988: 129). The character states included in this description are vague and, as pointed out by Rieppel and Zaher (2000a), an internarial septum always separates the septomaxillae.

ESTES ET AL. (1988) CHARACTER 51: "Opisthotic-exoccipital fusion: (0) bones remain separate or fuse to exoccipitals relatively late in postembryonic ontogeny; (1) fuse to exoccipital in embryo or in early postembryonic ontogeny, or the two bones develop from a single ossification center" (Estes et al., 1988: 130). This character was omitted because of the extremely limited data available to determine character states. Additionally, the derived state apparently refers to two non-homologous conditions.

ESTES ET AL. (1988) CHARACTER 57: "Meckel's canal exposure ventrally: (0) opens medially for entire length; (1) opens ventrally anterior to anterior inferior fora-

men" (Estes et al., 1988: 130). Scoring of this character is difficult and may be variable within a specimen. Moreover, the ventral surface of the mandible is dependent upon the orientation of the naturally articulated mandible, something not always immediately apparent.

ESTES ET AL. (1988) CHARACTER 62: "Medial view of prearticular with dentary and splenial removed: (0) prearticular extends nearly to anterior end of surangular, well anterior to coronoid bone; (1) reduced not extending well anterior to the coronoid bone" (Estes et al., 1988:131). The character states of this character are dependent upon the anterior extensions of the coronoid and the surangular, each of which being the subject of other independently varying characters.

ESTES ET AL. (1988) CHARACTER 88–89: "Scleral ossicle number I: (0) more than 14 ossicles; (1) 14 ossicles or fewer […] Scleral
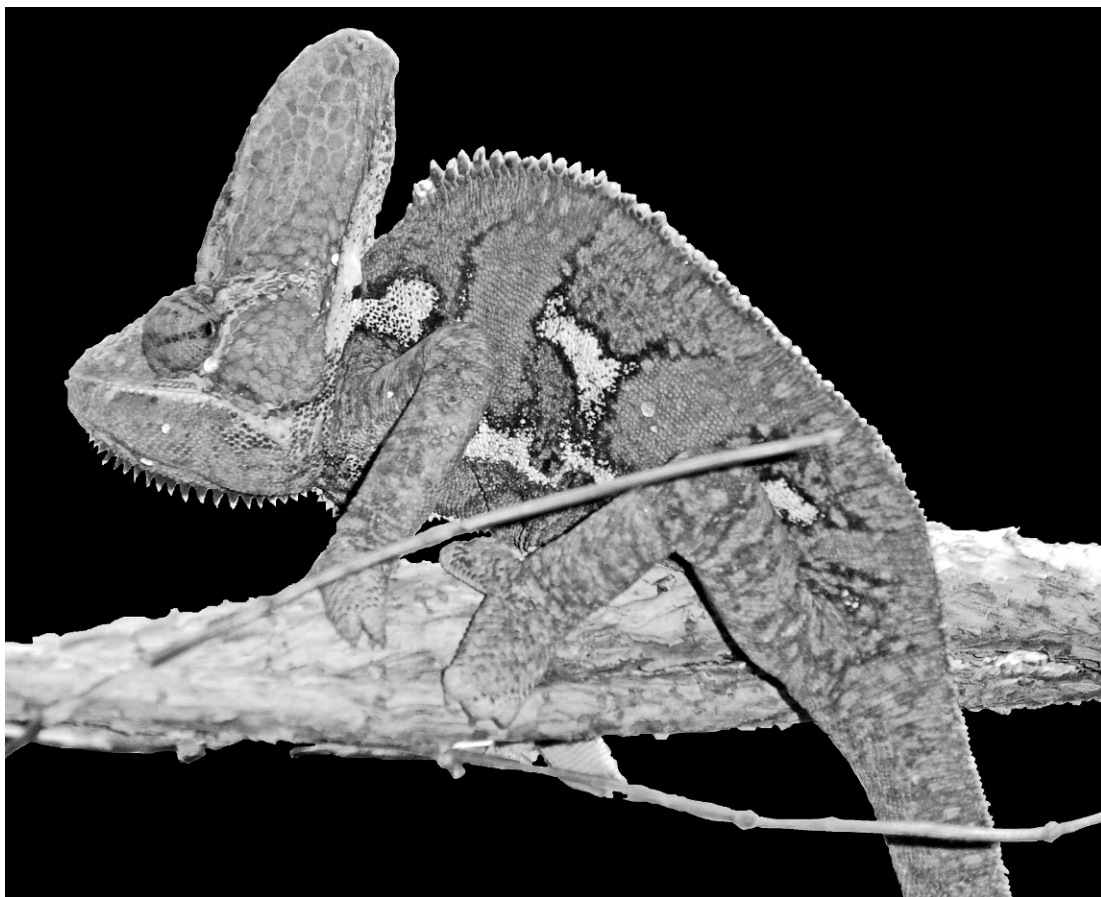
Fig. 50.   *Chamaeleo calyptratus*, exhibiting character state 295(0), 298(1), and 300(0). Specimen photographed at AMNH, part of the collection from Clyde Peeling's Reptiland in Allenwood Pennsylvania. Photo by R. M. Shearman.

ossicle number II: (0) 14 ossicles ore more; (1) fewer than 14 ossicles'' (Estes et al., 1988: 132). These two characters possess overlapping character states. Inclusion of this character could be accomplished in the future with further subdivision of the number of scleral ossicles.

ESTES ET AL. (1988) CHARACTER 117: ''Dorsal articulation of clavicle: (0) articulates with scapula; (1) articulates with suprascapula'' (Estes et al., 1988: 133). Scoring this character relies heavily on the use of skeletonized specimens. Such specimens are usually desiccated, meaning that the clavicles may be pulled out of position through the shrinkage of soft tissue, introducing the

potential for erroneous observations of character states.

ESTES ET AL. (1988) CHARACTER 123: ''Notching of distal tibial epiphyses: (0) gently convex for astragalocalcaneal articulation; (1) tibial epiphysis more or less distinctly notched, fitting onto a ridge on the astragalocalcaneum'' (Estes et al., 1988: 133). The character states described for this character are vague and allow for much interpretation. However, a modified version of this character may be implemented in future analyses.

ESTES ET AL. (1988) CHARACTER 130: ''Epiphysis fusion: (0) fuse to diaphyses at same time or after fusion of braincase elements; (1) fuse to diaphyses prior to fusion

Fig. 51. *Tiliqua rugosa asper* (sensu Shea 1988; =*Trachydosaurus rugosus*). **(A)** Broad view of the body. **(B)** Detail of the head. Note the presence of character states 298(2), 305(1), 306(1), 307(1), 308(1), and 314(0). Specimen housed at the San Diego Zoo in Balboa Park, California. Photo by R. M. Shearman.

of braincase elements'' (Estes et al., 1988: 133). As with character 51 in Estes et al. (1988) (above), there are little data available to aid in meaningfully and accurately scoring this character and so it is omitted.

ANALYZING THE DATA

The morphological data set includes 363 morphological characters scored in 222 ingroup taxa (appendix 2) with the outgroup Rhynchocephalia. Seventeen characters were identified as parsimony uninformative. Multistate characters were treated as ordered only if they formed a clear set of nested homology statements (characters 1, 32, 59, 83, 93, 96, 111, 114, 124, 136, 137, 162, 164, 181, 280, 285, 313, 317, 323, and 330 were considered ordered in this analysis). The taxon-character matrix was analyzed via a new technology search using the ratchet option in the computer program T.N.T. (Goloboff et al., 2003) with the option set to find the shortest tree 1,000 times. The resulting trees were saved to RAM and two additional ratchet runs, each of 1,000 iterations were performed on these trees. The resulting 2,213 trees were used for the strict consensus cladogram (figs. 53, 54). The principle trees from the T.N.T. analysis were exported to the computer program PAUP* (Swofford, 2001) and Adams consensus trees were computed. Adams trees and strict consensus trees are reported here (figs. 55, 56) because they identify the groupings consistent within all trees. Because the current analysis does not include an exhaustive search, no majority rule trees are reported. Synapomorphies for each node in the Adams consensus tree were identified by PAUP* (Swofford, 2001) and unambiguous synapomorphies are reported below.

Fig. 52. *Heloderma suspectum* (*H. s. cinctum* sensu Bogert and Del Campo, 1956); anterior part of the body in dorsolateral view highlighting character states 298(1), 300(1), 305(1), 306(0), and 310(2). Specimen photographed at AMNH, part of the collection from Clyde Peeling's Reptiland in Allenwood Pennsylvania. Photo by R. M. Shearman.

Each of the 2,213 most parsimonious recovered trees from the T.N.T. (Goloboff et al., 2003) analysis have a length of 3,273 steps, a consistency index (excluding uninformative characters) of 0.1499 and a retention index of 0.7164 as reported by PAUP* (Swofford, 2001). Note that consistency index (CI) is inversely correlated with the number of included taxa in a given analysis (Klassen et al., 1991:446).

PHYLOGENY AND TAXONOMY

The revised phylogeny and taxonomy of Squamata presented here is intended to improve the current state of systematic understanding. Taxon name definitions used here are intended to follow the most common usage and allow for easy incorporation of new discoveries while also allowing for revision of phylogenetic hypotheses. This approach is in

contrast to the approach taken by Lee (1998) who suggests that the definitions of taxon names should be specific to each phylogenetic hypothesis (see the Introduction, above).

Importantly, the name Squamata itself is not defined here. Squamates are constrained to be monophyletic by outgroup and ingroup choice and so no diagnosis may be offered. Estes et al. (1988) defined the taxon as a crown group, but common usage of the name incorporates all non-rhynchocephalian members of the crown-node Lepidosauria. That is, my perception is that lepidosaurs are regarded as always being either rhynchocephalians or squamates, regardless of whether they fall within the squamate crown. The taxa included under Squamata would remain the same in the current analysis no matter if a node-based or stem-based definition were used.

Iguanomorpha Sukhanov, 1961
(figs. 54A, 55A, 56A)

DEFINITION: All taxa sharing a more recent common ancestor with *Iguana iguana* than with *Gekko gecko*, *Scincus scincus*, or *Varanus varius*.

DIAGNOSIS: Iguanomorphs are united by two unambiguous synapomorphies in the current analysis, 230(1) notochordal canal obliterated by centrum ossification, and 231(2) procoelous vertebrae.

COMMENTS: Sukhanov (1961), following earlier authors, described a basal dichotomy between iguana-like lizards and all other squamates. He referred to all iguana-like squamates as Iguanomorpha, a name that works well as a stem-defined group to include the crown iguanians and their fossil relatives. *Hoyalacerta sanzi* falls on the iguanomorph stem in this analysis, rather than in a position basal to other squamates as previously suggested (Reynoso, 1998; Evans and Barbadillo, 1999). Thus, it gives insight into character polarization at the base of the Iguanomorpha and is important for determining interrelationships within Iguania.

Iguania Cuvier, 1817
(figs. 54A, 55A, 56A)

DEFINITION: The most recent ancestor of extant taxa more closely related to *Iguana*

iguana than to *Gekko gecko* or *Varanus varius* and all descendants of that ancestor.

DIAGNOSIS: Iguania, as defined here, may be diagnosed by 11(1) premaxilla fusion (unpaired premaxilla), 34(1) presence of a prefrontal tuberosity, 117(1) ventromedial processes of the pterygoids, 244(1) hypapophyseal keels present on the cervical vertebrae, and 252(1) caudal autotomy planes present posterior to the transverse processes.

COMMENTS: Estes et al. (1988) defined Iguania as a node-based name describing "[t]he last common ancestor of Iguanidae*, Agamidae* and Chamaeleontidae and all of its descendants," with the caveat that Iguanidae and Agamidae might represent paraphyletic taxa. Even so, their definition was apparently intended to include all extant taxa closer to *Iguana* than to geckos, skinks, etc. The revised definition does that more precisely and does not rely upon metataxa.

Iguania exclusive of Phrynosomatidae
(figs. 55A, 56A)

DIAGNOSIS: The clade containing crown iguanians exclusive of phrynosomatids is diagnosed by 26(1) strong medial processes of the maxillae behind the nasal process of the premaxilla, 29(1) weakly inclined anterior margin of the maxillary nasal process, 83(1) presence of a nuchal fossa on the parietal table, 104(1) presence of a contact between the septomaxilla and the osseous roof of the nasal capsule, 181(2) closed and fused Meckel's canal, 261(1) angulated clavicle, and 263(1) a posterior coracoid emargination.

COMMENTS: The current analysis suggests that the basal dichotomy in Iguania is between Phrynosomatidae and other iguanians, the latter including acrodontans. Other recent analyses have suggested a basal dichotomy between Chamaeleontiformes (see below) and Pleurodonta (sensu Conrad et al., 2007; Conrad and Norell, 2007a; and see preliminary data in Conrad, 2005a) (=Iguanidae sensu lato). The different results appear to be caused, at least in part, by the inclusion of *Isodontosaurus* (also present in Conrad and Norell, 2007a) and by the inclusion of additional non-osteological character states (see below).

Opluridae + Tropidurinae +
Liolaemus + Leiocephalus
(figs. 55A, 56A)

DIAGNOSIS: This clade is supported by six unambiguous synapomorphies in the current analysis. These are presence of 9(1) dermal sculpturing on the prefrontal, 29(0) steeply inclined anterior margin of the maxillary nasal process, 121(1) midline contact of the palatines, 143(1) posterolateral sphenoid flanges ventrolaterally overlying the basioccipital, 180(1) elongate lateral portion of the dentary extending along the mandible to a point at least half way between the coronoid eminence and the mandibular glenoid, 185(0) dentary without a notch distinguishing coronoid and surangular processes, and 190(0) splenial extending far anteriorly.

COMMENTS: The current analysis does not recover unambiguous support for a monophyletic Tropiduridae sensu Frost and Etheridge (1989). Recent phylogenetic analyses have suggested the polyphyly of tropidurids and polychrotids (Frost et al., 2001; Schulte et al., 2003). However, two recent morphological analyses suggest tropidurid monophyly (Conrad et al., 2007; Conrad and Norell, 2007a). The first run of the current analysis also supports tropidurid monophyly, but the additional 1000 ratchet replicates lost support for this clade in each, the strict and the Adams consensuses. The presence of a clade containing all tropidurids sensu lato and oplurids is consistent with some networks recovered Frost and Etheridge (1989).

Opluridae Moody, 1983
(figs. 55A, 56A)

DIAGNOSIS: Oplurids (here represented by two specimens of *Oplurus quadrumcinctus*, *O. cyclurus*, and *Chalarodon madagascariensis*) are united in this analysis by five unambiguous character states. These are 47(0) presence of an angulated jugal, 60(1) a dorsoventrally inflated frontal, 263(0) absence of a posterior coracoid emargination, 332(1) ''varanid'' style ulnar nerve position, and 333(1) absence of a peroneal nerve.

COMMENTS: I refrain from defining Opluridae here, but it should be used to include *Oplurus madagascariensis* minimally in the future. The diagnosis above describes the taxa included in this analysis. A recent phylogenetic analysis (Conrad et al., 2007) suggest that *Oplurus* is the sister taxon to tropidurids (sensu Frost and Etheridge, 1989) and that *Chalarodon* is the sister-taxon to a clade containing the fossil taxa *Igua* and *Polrussia*. Titus and Frost (1996) recovered oplurid monophyly as does the current study, but this problem warrants further investigation.

Crotaphytidae + Iguanidae + Polychrotiformes
+ Hoplocercidae + Chamaeleontiformes
(figs. 55A, 56A)

DIAGNOSIS: This clade may be diagnosed by three unambiguous synapomorphies. These are 9(1) dermal sculpturing on the prefrontal, 29(0) steeply inclined anterior margin of the maxillary nasal process, and 90(1) presence of a postorbital tuberosity.

Chamaeleontiformes + Hoplocercidae
+ Polychrotiformes
(figs. 55A, 56A)

DIAGNOSIS: This clade is supported by five unambiguous synapomorphies: 21(1) nasals that are in contact for less than half their length in dorsal view, 52(0) jugal lying mostly medial (rather than dorsal) to the maxilla, 104(0) no contact between the septomaxilla and the osseous nasal cavity roof, 123(1) pyriform recess narrow (see the character description above), and 263(0) absence of a posterior coracoid emargination.

Polychrotiformes comb. nov.
(figs. 54A, 55A, 56A)

DEFINITION: All taxa sharing a more recent common ancestor with *Polychrus marmoratus* than with *Iguana iguana*, *Phrynosoma orbiculare*, or *Chamaeleo chamaeleon*.

DIAGNOSIS: The clade formed by Polychrotidae and Corytophanidae is joined by 47(0) presence of an angulated jugal, 174(1) presence of a groove extending anterior to the anterior surangular foramen, 260(1) clavicles proximally expanded and with a notch or fenestra, and 273(0) absence of a sternal fontanelle.
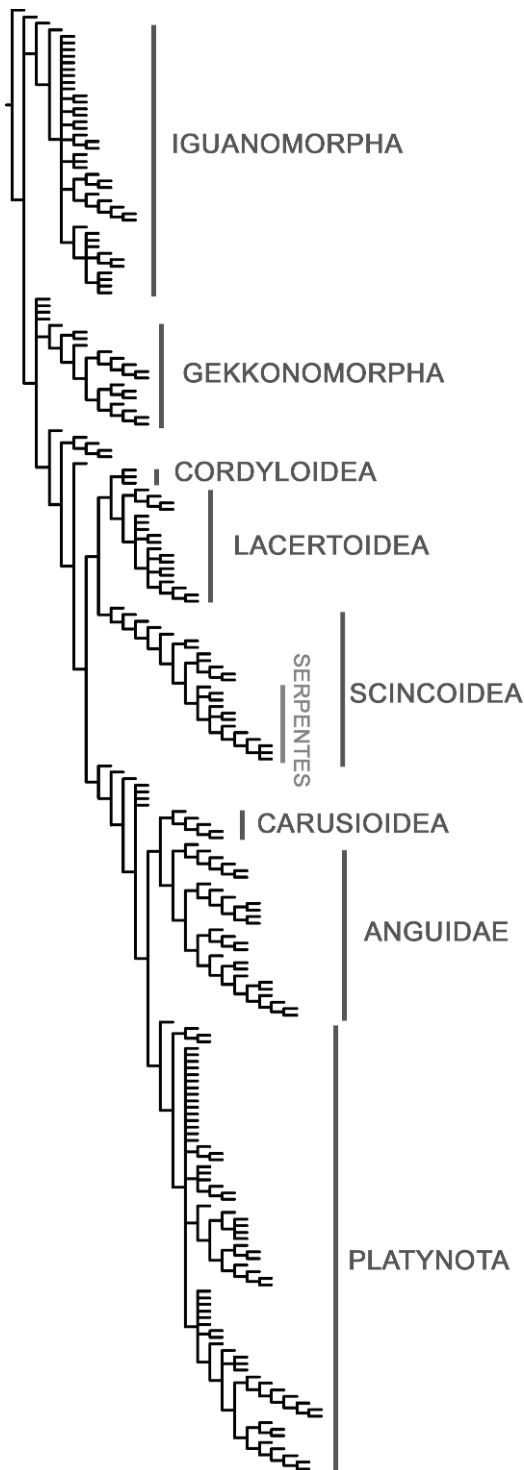
Fig. 53. Hypothesis of squamate interrelationships based on the current study. This figure shows

COMMENTS: Polychrotiformes as defined here includes a monophyletic Polychrotidae (sensu Frost and Etheridge, 1989 and Conrad et al., 2007; = "anoloids" of Etheridge and de Queiroz, 1988) and the Corytophanidae (= "basiliscines" of Etheridge and de Queiroz, 1988). Frost et al. (2001) previously alluded to a close relationship between polychrotids and corytophanids. Macey et al. (1997) and Frost et al. (2001) suggested the paraphyly of polychrotids with respect to corytophanids, but the taxonomic sampling of these studies was extremely limited, raising questions about the "reclassification" of iguanians proposed therein.

Note that the possible corytophanid *Geiseltaliellus* is currently being redescribed and that this taxon may be important for more completely understanding the plesiomorphic morphology of corytophanids (Smith, 2004).

Polychrotidae (Fitzinger, 1843)
(figs. 54A, 55A, 56A)

DIAGNOSIS: Seven unambiguous synapomorphies support polychrotid monophyly in this analysis. These are: 26(0) absence of strong medial processes of the maxilla posterior to the premaxillary nasal process, 252(3) caudal autotomy planes located anterior to the transverse processes (fig. 45D), 258(1) one or more pair(s) of postxiphisternal inscriptional ribs confluent at midline, 274(0) multiple xiphisternal branchings, 316(1) presence of peglike filamentous tongue papillae, 325(1) endolymphatic sacs extending into the nuchal musculature via the space between the supraoccipital and parietal, and 327(1) divided hemipeneal sulcus.

COMMENTS: Recent molecular studies have suggested the non-monophyly/non-ho-

←

entire tree at once; portions of the tree are shown individually in Figures 54 and 55. Note the presence of a clade containing cordyloids, lacertoids, and scincoids, to the exclusion of all other squamates. Serpentes (snakes) are shown here within Scincoidea (see also figs. 54C, 55C, and 56C). This figure also illustrates that anguimorphs are sampled most heavily within this analysis.

A

Brookesia
Rhampholeon
Physignathus
Agama
Uromastyx
Phrynosomimus †
Priscagama †
Mimeosaurus †
Isodontosaurus †
Enyalioides
Hoplocercus
Morunasaurus
Anolis vermiculatus
A. occultus
A. heterodermus
amber anole †
FMNH PR2379 †
ANISOLEPINAE
LEIOSAURINAE
Polychrus guttosus
P. marmoratus
P. femoralis
CORYTOPHANIDAE
IGUANIDAE
CROTAPHYTIDAE
IGM 3/858 †
Ctenomastax †
Temujinia †
Zapsosaurus †
Anchaurosaurus †
Oplurus AMNH R71452
Oplurus cyclurus
Oplurus AMNH R47944
Chalarodon
TROPIDURINAE
Stenocercus
Liolaemus
Leiocephalus
Igua †
Polrussia †
PHRYNOSOMATIDAE
Hoyalacerta †
Huehuecuetzpalli †

SCINCOGEKKONOMORPHA

IGUANOMORPHA
GEKKONOMORPHA
LACERTOIDEA
CORDYLOIDEA
SCINCOIDEA
CARUSIOIDEA
ANGUIDAE
SHINISAURIA
MONSTERSAURIA
VARANIFORMES
MOSASAURIA

Fig. 54.   Continued.

lophyly of Polychrotidae (Frost et al., 2001; Schulte et al., 2003), but morphological data continue to show support for polychrotid monophyly (Frost and Etheridge, 1989; Schulte et al., 2003; Conrad, 2005a; Conrad and Norell, 2007a; Conrad et al., 2007). These issues are discussed more fully by Schulte et al. (2003) and Conrad et al. (2007). Despite the presence of numerous unambiguous morphological synapomorphies supporting this clade here, I follow the relatively prudent approach exemplified by Schulte et al. (2003) and refrain from defining Polychrotidae. The name is used here in the same

←

C

Gilmoreteius †
Darchansaurus †
Sineoamphisbaena †
Polyglyphanodon †
Erdenetesaurus †
Cherminsaurus †
Gobinatus †
Tchingisaurus †
Adamisaurus †
TEIINAE
TUPINAMBINAE
GYMNOPHTHALMIDAE
Chamops †
LACERTIDAE
Palaeoxantusia †
Lepidophyma
Cricosaura
Xantusia
CORDYLIFORMES
Sakurasaurus †
Ornatocephalus †
Slavoia †
SCINCIDAE
SCELOTIDAE
FEYLINIIDAE
ACONTIDAE
Dibamus
Anelytropsis
TROGONOPHIDAE
RHINEURIDAE
AMPHISBAENIDAE
Blanus
Bipes
Leptotyphlops
Liotyphlops
Typhlops
Dinilysia †
Pachyophis †
Wonambi †
ANILIOIDEA
Xenopeltis
other macrostomatans
Eupodophis †
Haasiophis †
Pachyrhachis †

ANGUIMORPHA

IGUANOMORPHA
GEKKONOMORPHA
LACERTOIDEA
CORDYLOIDEA
SCINCOIDEA
CARUSIOIDEA
ANGUIDAE
SHINISAURIA
MONSTERSAURIA
VARANIFORMES
MOSASAURIA

Fig. 54. Continued.

Fig. 54. Continued.

E

Fig. 54.   Continued.

F

Dolichosaurus †
Aphanizocnemus †
Coniasaurus †
Adriosaurus †
Pontosaurus †
Opetiosaurus †
Aigialosaurus †
Carsosaurus †
Eidolosaurus †
Tethysaurus †
Eonatator sternbergi †
Halisaurus platyspondylus †
Halisaurus arambourgi †
Plotosaurus †
Goronyosaurus †
"Mosasaurus" lemonnieri †
Globidens †
Mosasaurus hoffmanni †
Rikisaurus †
Clidastes †
Lakumasaurus †
Hainosaurus †
Tylosaurus †
Platecarpus †
Plioplatecarpus †
Ectenosaurus †
Prognathodon solvayi †
P. overtoni †

IGUANOMORPHA
GEKKONOMORPHA
LACERTOIDEA
CORDYLOIDEA
SCINCOIDEA
CARUSIOIDEA
ANGUIDAE
SHINISAURIA
MONSTERSAURIA
VARANIFORMES
MOSASAURIA

Fig. 54.   Continued.

sense as Conrad et al. (2007); all descendants of the last common ancestor of the poly-chrotids identified by Frost and Etheridge (1989).

Hoplocercidae Frost and Etheridge, 1989
(figs. 54A, 55A, 56A)

DIAGNOSIS: The current analysis recovers five unambiguous synapomorphies for this clade. These are 44(1) enlarged lacrimal foramen (see character description above), 60(1) a dorsoventrally inflated frontal, 190(0) splenial extending anteriorly for more than two-thirds the dentary tooth row, 258(1) one or more pair(s) of postxiphisternal inscriptional ribs confluent at midline, and 285(2)

symphysial portion of the pubis more than half again as long as the tubercular portion.

COMMENTS: This analysis includes *Morunasaurus annularis*, *Hoplocercus spinosus*, and a composite *Enyalioides* scored from *E. palpebralis* and *E. laticeps*. A recent study by Wiens and Etheridge (2003) with extensive sampling of hoplocercid taxa suggests the monophyly of *Enyalioides*. Even so, future versions of this analysis will eliminate the composite coding of *Enyalioides* and likely include more species of *Morunasaurus*. Importantly, the Adams consensus (figs. 55, 56) supports the topology of Wiens and Etheridge based on their analysis using mixed scaling of meristic characters (Wiens and Etheridge, 2003: fig. 4).

A

a -- Iguanomorpha
b -- Iguania
c -- Polychrotiformes
d -- Chamaeleontiformes
e -- Acrodonta
f -- Priscagamidae

Brookesia
Rhampholeon
Physignathus
Agama
Uromastyx
Phrynosomimus †
Priscagama †
Mimeosaurus †
Isodontosaurus †
Enyalioides
Hoplocercus
Morunasaurus
Anolis vermiculatus
A. occultus
A. heterodermus
amber anole †
FMNH PR2379 †
ANISOLEPINAE
LEIOSAURINAE
Polychrus guttosus
P. marmoratus
P. femoralis
CORYTOPHANIDAE
IGUANIDAE
CROTAPHYTIDAE
IGM 3/858 †
Ctenomastax †
Temujinia †
Zapsosaurus †
Anchaurosaurus †
Oplurus AMNH R71452
Oplurus cyclurus
Oplurus AMNH R47944
Chalarodon
TROPIDURINAE
Stenocercus
Liolaemus
Leiocephalus
Igua †
Polrussia †
PHRYNOSOMATIDAE
Hoyalacerta †
Huehuecuetzpalli †

SCINCOGEKKONOMORPHA

IGUANOMORPHA
GEKKONOMORPHA
LACERTOIDEA
CORDYLOIDEA
SCINCOIDEA
CARUSIOIDEA
ANGUIDAE
SHINISAURIA
MONSTERSAURIA
VARANIFORMES
MOSASAURIA

Fig. 55. **(A–F)** Hypothesis of squamate interrelationships based on the current study; the Adams consensus with accompanying taxonomic scheme. Following (Brochu, 1999), parentheses indicate stem-based clade names, dots indicate node-based names.
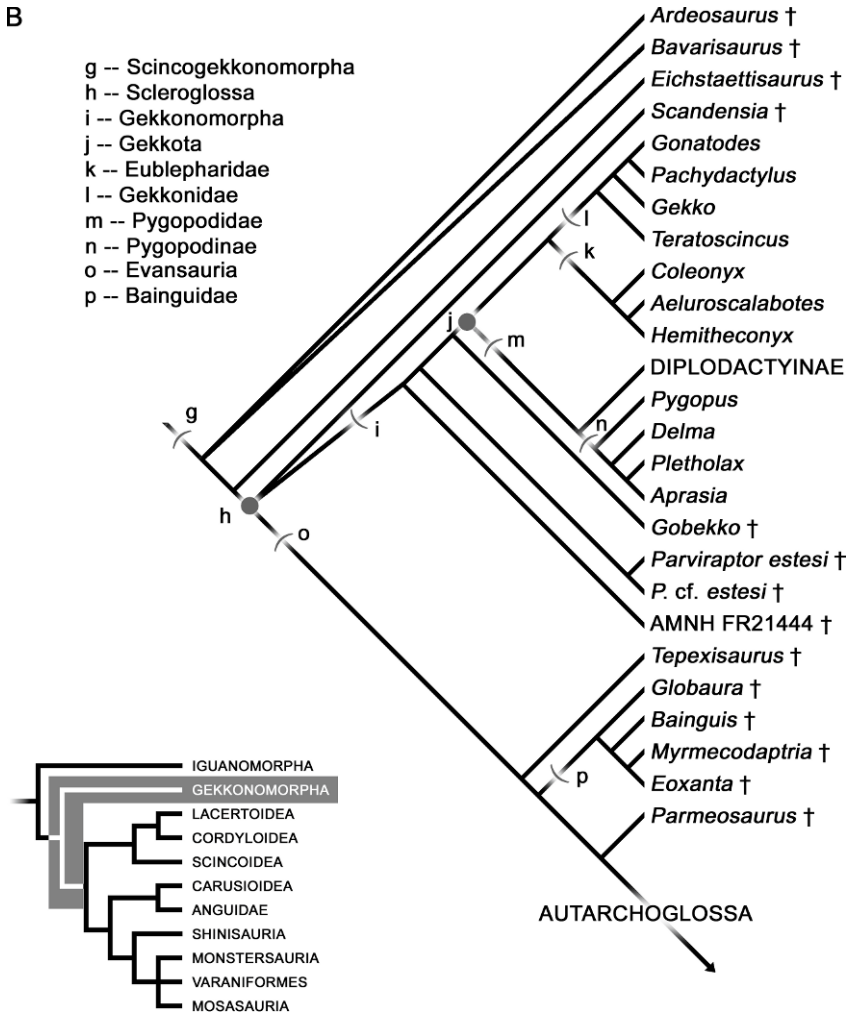
Fig. 55. Continued.

Given the absence of a fossil record for this clade and the somewhat limited sampling for it, I refrain from attaching a definition to this taxon name. The term ''Hoplocercidae'' is usually used to refer to all species within *Enyalioides*, *Hoplocercus*, and *Morunasaurus*; it is used here in that context.

Chamaeleontiformes comb. nov.
(figs. 54A, 55A, 56A)

DEFINITION: All taxa sharing a more recent common ancestor with *Chamaeleo*

chamaeleon than with *Hoplocercus spinosus*, *Polychrus marmoratus*, or *Iguana iguana*.

DIAGNOSIS: This stem-based taxon diagnosed by the following unambiguous synapomorphies: 27(1) absence of midline contact of the maxillae behind the premaxillary nasal process, 90(0) absence of a postorbital tuberosity, 117(0) absence of ventromedial processes (basipterygoid buttresses) on the pterygoid, 118(2) absence of pterygoid teeth, and 189(0) a shortened splenial (see character description above).

COMMENTS: Chamaeleontiformes, as defined here, is essentially equivalent to Cha-
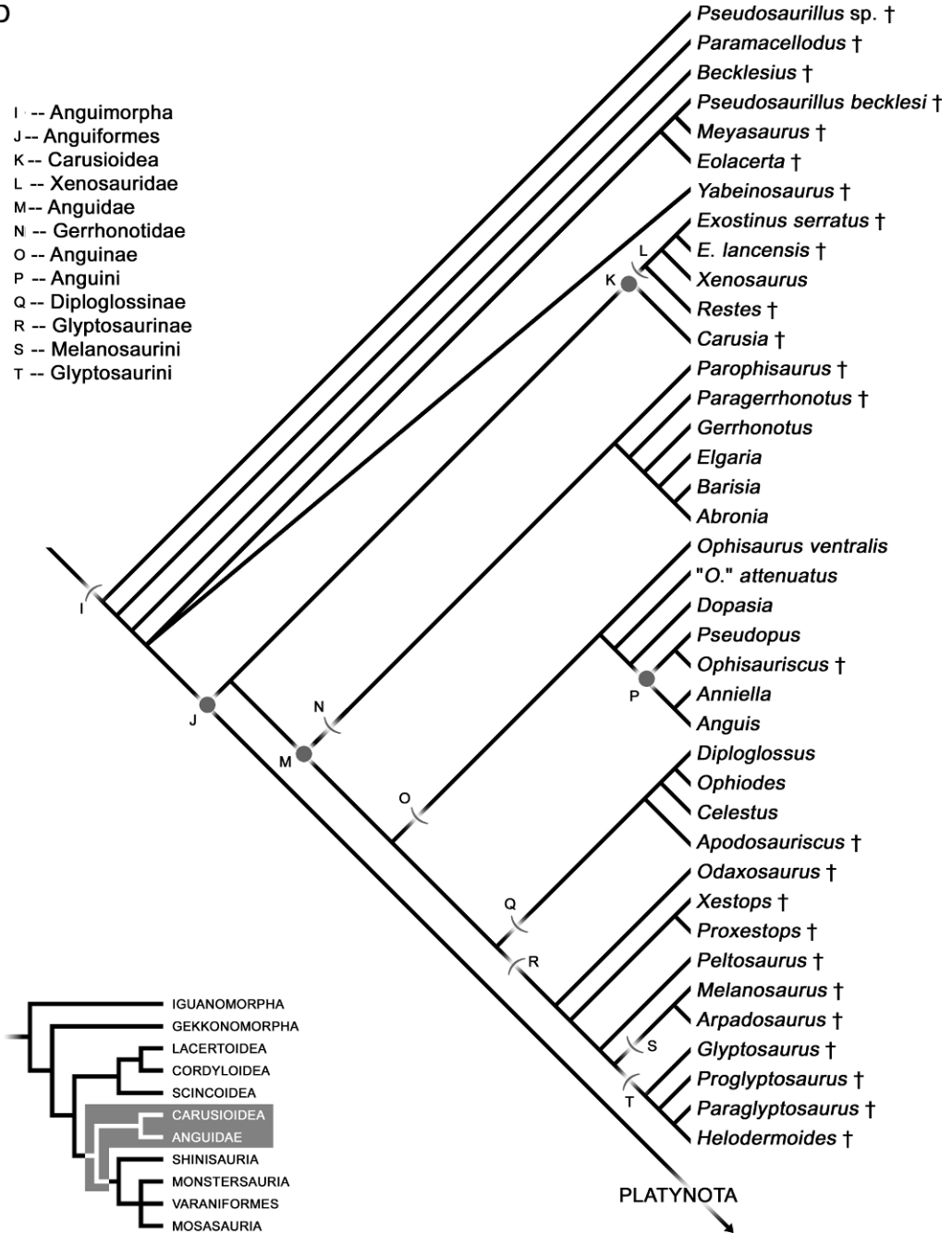
Fig. 55.   Continued.

Fig. 55. Continued.

maeleonidae as described by Frost and Etheridge (1989). Frost and Etheridge considered their Chamaeleonidae to be "equivalent to Acrodonta of Estes et al. (1988)" (Frost and Etheridge, 1989: 32), but explicitly included the *Priscagama gobiensis* and Priscagaminae as *incertae sedis*. Estes et al. (1988) defined Acrodonta as a crown group and in both Frost and Etheridge (1989) and, in the current analysis (figs. 16A, 17A, 18A), the

E

U -- Platynota
V -- Shinisauria
W-- Shinisauridae
X -- Varanoidea
Y -- Monstersauria
Z -- Helodermatidae
A -- Helodermatinae
B -- *Heloderma*
C -- Goannasauria
D -- Varaniformes
E -- Varanidae
F -- Lanthanotinae
G -- Varaninae
H -- *Varanus*
I -- Mosasauriformes

Dorsetisaurus †
Shinisaurus
Bahndwivici †
Dalinghosaurus †
Parasaniwa †
Parviderma †
Colpodontosaurus †
Heloderma suspectum
H. horridum
H. texana †
Lowesaurus †
Eurheloderma †
Estesia †
Paraderma †
Primaderma †
Gobiderma †
Palaeosaniwa †
"*Necrosaurus*" *eucarinatus* †
"*Saniwa*" *feisti* †
Necrosaurus cayluxi †
Proplatynotia †
Saniwides †
Telmasaurus †
Cherminotus †
Aiolosaurus †
Lanthanotus
Saniwa ensidens †
niloticus
exanthematicus
rusingensis †
olivaceus
griseus
prasinus
tristis
eremius
varius
komodoensis
salvadorii
prisca (="*Megalania*") †
Eosaniwa †
Paravaranus †

MOSASAURIA

IGUANOMORPHA
GEKKONOMORPHA
LACERTOIDEA
CORDYLOIDEA
SCINCOIDEA
CARUSIOIDEA
ANGUIDAE
SHINISAURIA
MONSTERSAURIA
VARANIFORMES
MOSASAURIA

Fig. 55.   Continued.

F

J -- Mosasauria
K -- Dolichosauridae
L -- Mosasauroidea
M -- Mosasauridae
N -- Halisaurinae
O -- Natantia
P -- Mosasaurinae
Q -- Plotosaurini
R -- Russellosaurina
S -- Tylosaurinae
T -- Plioplatecarpinae

Dolichosaurus †
Aphanizocnemus †
Coniasaurus †
Adriosaurus †
Pontosaurus †
Opetiosaurus †
Aigialosaurus †
Carsosaurus †
Eidolosaurus †
Tethysaurus †
Eonatator sternbergii †
Halisaurus platyspondylus †
Halisaurus arambourgi †
Plotosaurus †
Goronyosaurus †
"Mosasaurus" lemonnieri †
Globidens †
Mosasaurus hoffmanni †
Rikisaurus †
Clidastes †
Lakumasaurus †
Hainosaurus †
Tylosaurus †
Platecarpus †
Plioplatecarpus †
Ectenosaurus †
Prognathodon solvayi †
P. overtoni †

IGUANOMORPHA
GEKKONOMORPHA
LACERTOIDEA
CORDYLOIDEA
SCINCOIDEA
CARUSIOIDEA
ANGUIDAE
SHINISAURIA
MONSTERSAURIA
VARANIFORMES
MOSASAURIA

Fig. 55. Continued.

Priscagama gobiensis-like taxa fall outside the radiation of acrodonts. Thus, Chamaeleontiformes is used to name the clade Frost and Etheridge (1989) recognized as Chamaeleonidae.

Isodontosaurus gracilis is a chamaeleontiform according to the current analysis. *Isodontosaurus* bears an unusual combination apomorphic features making it somewhat problematic for phylogenetic placement (Gao and Norell, 2000) and also make it a reasonable intermediate between "iguanids*" and higher chamaeleontiforms. A more complete morphological treatment may add further evidence to support this phylogenetic hypothesis.

A recent analysis by Conrad and Norell (2007a) identifies a dichotomy between chamaeleontiforms and pleurodontans. In that analysis *Isodontosaurus gracilis* is found to be a basal iguanomorph. Further investigation may help to sort out the differences between this analysis and that one.

Although *Chamaeleo chamaeleon* is used in the definition of this taxon, it does not appear in the phylogenetic analysis. However, the monophyly chamaeleonids has never been questioned, and Chamaeleonidae is consistently cited as an unmistakable natural group (see the section on taxon sampling above; also see Hillenius, 1978; Moody and Rocek, 1980; Rieppel, 1981b, 1987; Estes et al., 1988; Frost and Etheridge, 1989; Macey et al., 2000).

All of the chamaeleontiforms currently included in the analysis are from Africa,
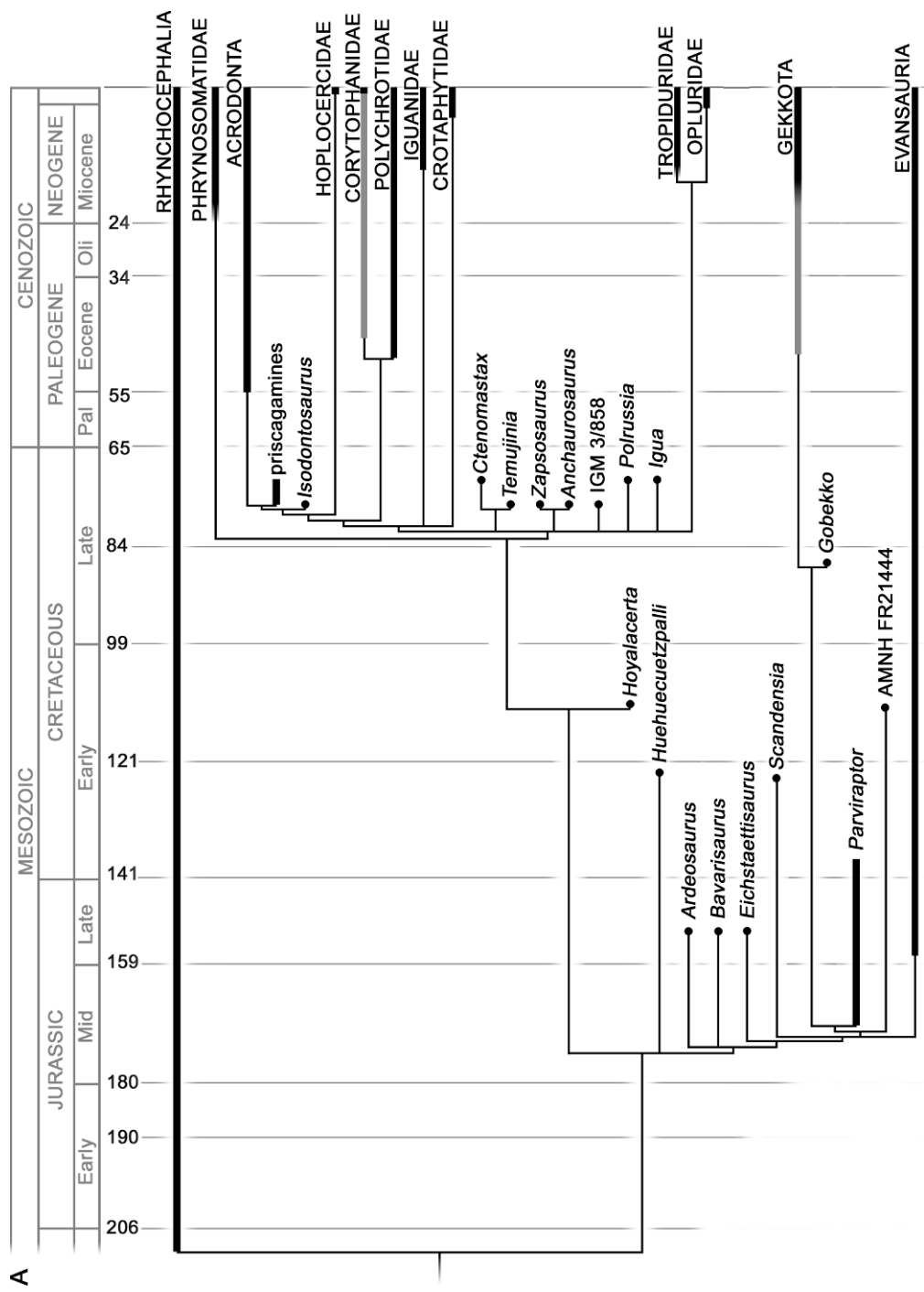
Fig. 56. (A–E) Temporally calibrated hypothesis of squamate interrelationships based on the Adams consensus with some taxa collapsed in the interest of space. Temporal ranges are approximate.
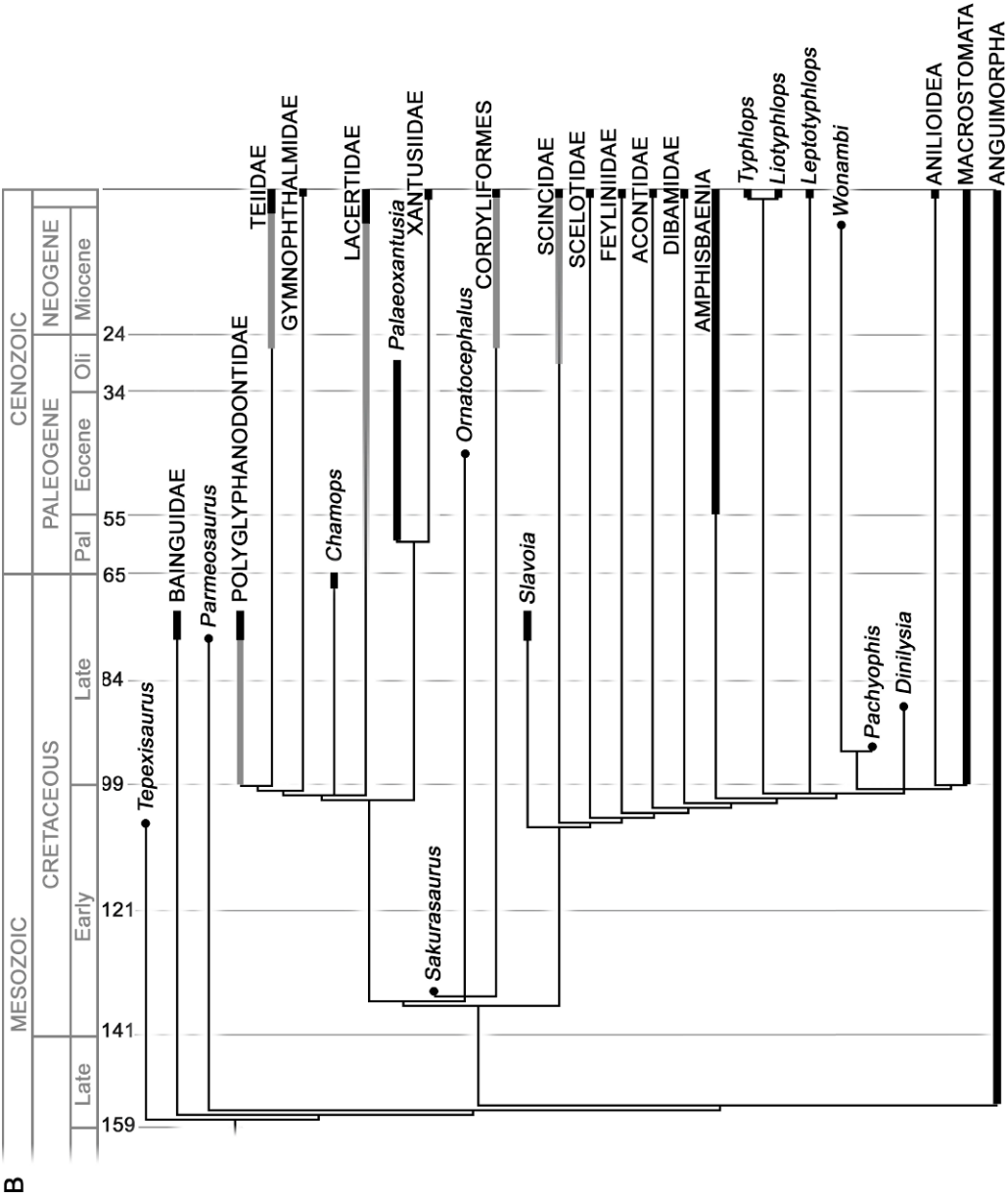
Fig. 56. Continued.
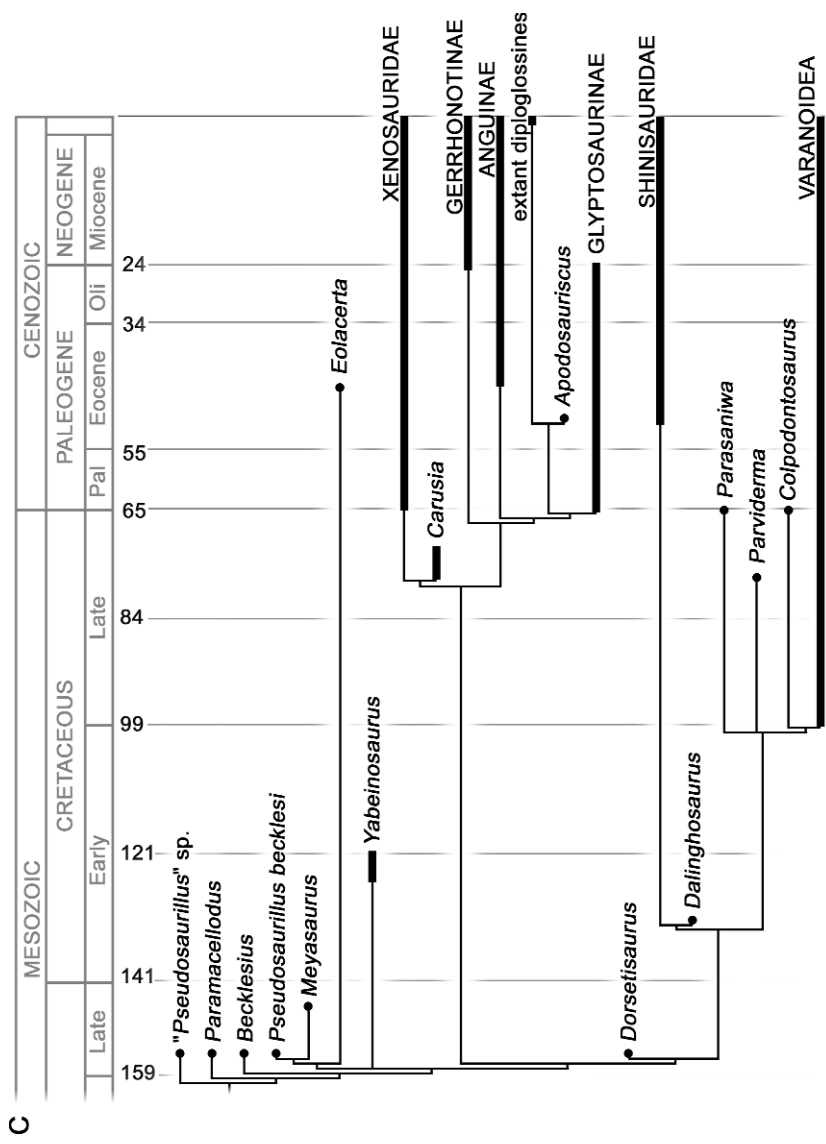
Fig. 56. Continued.
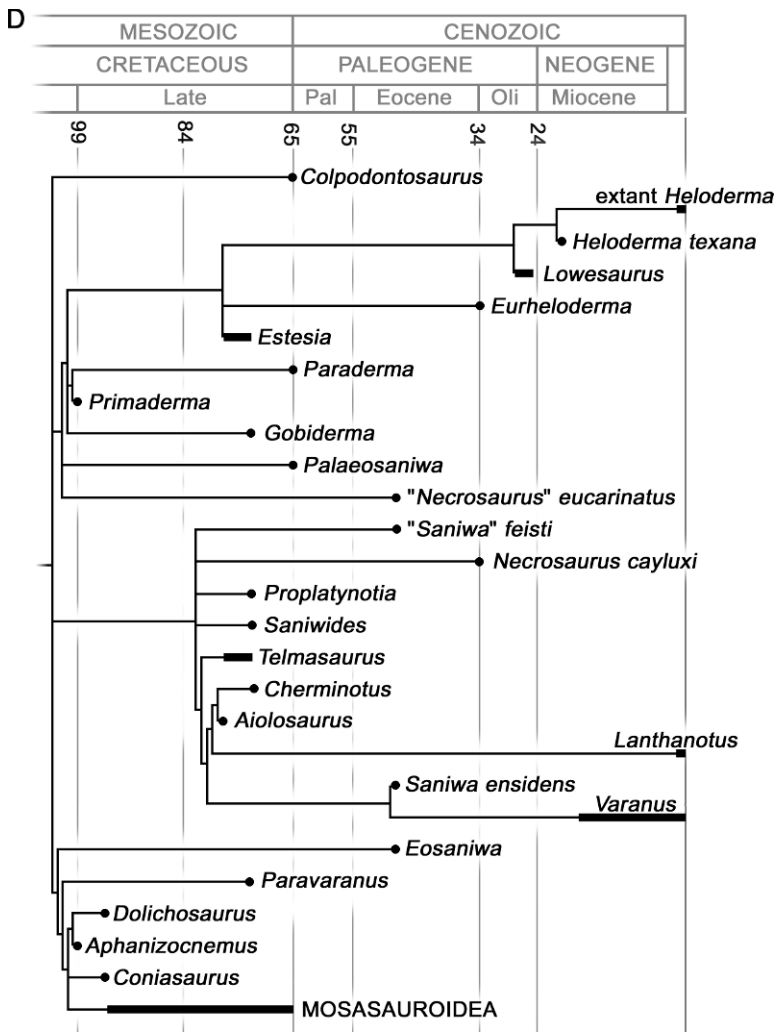
Fig. 56. Continued.

Asia, Australia, or Europe. The fossil priscagamids and the potential chamaeleontiform *Arretosaurus ornatus* (see below) are from Mongolia. *Tinosaurus* and *Pseudotinosaurus* were not included in the present analysis, but show some chamaeleontiform and/or acrodontan characteristics, including acrodont dentition with heterodonty (Marsh, 1872; Estes, 1983; Rage, 1987; Alifanov, 1993b; Augé and Smith, 1997; Li and Xue, 2002; Augé, 2003). The various species of *Tinosaurus* and *Pseudotinosaurus* are all poorly known; they are represented by fragmentary maxillae and dentaries that may or may not

be diagnostic at the generic or specific levels and probably do not form monophyletic groups. Even so, *Tinosaurus stenodon* (Marsh, 1872) is significant in that it probably represents the only known American chamaeleontiform.

Priscagamidae + Acrodonta
(figs. 54A, 55A, 56A)

DIAGNOSIS: An unnamed clade composed of chamaeleontiforms exclusive of *Isodontosaurus* is united by three unambiguous synapomorphies. These are 91(1) absence of a postfrontal, 214(1) presence of acrodont

dentition, and 215(1) presence of caniniform teeth.

Priscagamidae Borsuk-Białynicka and Moody, 1984
(figs. 54A, 55A, 56A)

DEFINITION: All taxa sharing a more recent common ancestor with *Priscagama gobiensis* than with *Agama agama*.

DIAGNOSIS: *Phrynosomimus asper*, *Mimeosaurus crassus*, and *Priscagama gobiensis* are united in this analysis to the exclusion of all other chamaeleontiforms based on three unambiguous synapomorphies: 8(1) presence of dermal sculpturing on the maxilla, 50(1) dermal rugosities on the postorbital process of the jugal, and 97(1) postorbital extending ventrally for less than one-half the orbital margin.

COMMENTS: Preliminary analyses (Conrad, 2005a) suggests that *Arretosaurus ornatus* shows some affinities with priscagamids. Inclusion of that taxon in a comprehensive analysis requires a re-visitation of its morphology.

Priscagama gobiensis + *Mimeosaurus crassus*
(figs. 54A, 55A, 56A)

DIAGNOSIS: *Priscagama gobiensis* and *Mimeosaurus crassus* share two unambiguous synapomorphies to the exclusion of *Phrynosomimus*. These are 29(1) weakly inclined anterior margin of the maxillary nasal process and 117(1) ventromedial processes of the pterygoids.

COMMENTS: Estes et al. (1988) identified three potential character states uniting Agamidae *sensu lato*. Of these, only the presence or absence of caniniform anterior maxillary and dentary teeth may be scored for priscagamids and only *Mimeosaurus crassus* shows the apomorphic state. Although this may indicate a relationship between *Mimeosaurus crassus* and agamids, the current analysis suggests priscagamid affinities.

Acrodonta Estes et al., 1988
(figs. 54A, 55A, 56A)

DEFINITION: This taxon is defined here as all descendants of the last common ancestor of all extant taxa more closely related to *Agama agama* and *Chamaeleo chamaeleon* than to *Gekko gecko*, *Varanus varius*, *Hoplocercus spinosus*, *Corytophanes cristatus*, *Polychrus marmoratus*, or *Iguana iguana*. This is in keeping with the definition originally proposed by Estes et al. (1988), who defined Acrodonta as all a node attached to their metataxon Agamidae* and the clade Chamaeleonidae.

DIAGNOSIS: The acrodontans included in this analysis are united by five unambiguous synapomorphies. These are 14(2) a bilobed premaxillary incisive process, 182(1) absence of a dentary shelf, 188(1) absence of a splenial, 261(0) straight (non-angulated) clavicle, and 272(1) a sternum that extends anteriorly, approaching the lateral arms of the interclavicle.

COMMENTS: Acrodonta here is scored from only a few species (two chamaeleonids and three "agamids"). Future versions of this data matrix will sample more broadly from within acrodontans and analyze the apparent paraphyly of the "agamids" recovered here.

Scincogekkonomorpha Sukhanov, 1961
(figs. 54B, 55B, 56A)

DEFINITION: All taxa sharing a more recent common ancestor with *Gekko gecko* and *Scincus scincus* than with *Iguana iguana*.

DIAGNOSIS: Scincogekkonomorphs are united by the 41(3) absence of the lacrimal (with notable reversals), 86(1) ventral origin of the jaw adductor musculature on the parietal, 92(0) an anteroposteriorly elongate postfrontal component of the postorbitofrontal, 100(1) absence of a dorsal process on the squamosal, and 101(1) presence of a palpebral.

COMMENTS: Scincogekkonomorpha is the sister taxon to Iguanomorpha in Sukhanov's (1961) taxonomic scheme. Scincogekkonomorpha has been used in some recent studies as a clade similar to or equivalent with Scleroglossa (Russell, 1988; Gao and Norell, 1998, 2000; Reynoso and Callison, 2000). Although Scleroglossa has been considered the sister taxon to iguana-like lizards, Estes et al. (1988) defined Scleroglossa as node-based taxon, anchoring it to extant taxa. Scincogekkonomorpha, as im-

plemented here, includes scleroglossans and their extinct sister-taxa. Use of this name is especially appropriate given the current topology of relationships (figs. 54–56), showing that the stem of this clade is mostly made up of taxa previously considered stem-geckos (e.g. *Bavarisaurus macrodactylus* and *Eichstaettisaurus schroederi*) or variably considered scincomorphs or geckos (*Ardeosaurus brevipes*) (see below).

Eichstaettisaurus schroederi + *Scandensia ciervensis* + Scleroglossa
(figs. 55B, 56A)

DIAGNOSIS: This clade (Scincogekkonomorpha exclusive of *Ardeosaurus* and *Bavarisaurus*) is diagnosed by 61(1) subolfactory processes of the frontal(s) partly surrounding the olfactory tract, 88(0) plesiomorphically possessing an anteroposteriorly short supratemporal, 97(1) postorbital extending ventrally for less than one-half the orbital margin, 260(1) clavicles proximally expanded and with a notch or fenestra, and 261(1) an angulated clavicle.

COMMENTS: *Ardeosaurus*, *Bavarisaurus*, and *Eichstaettisaurus* (fig. 29D) all have been considered basal members of the gecko-lineage (see Hoffstetter, 1964, 1967b, Kluge, 1967, 1983, 1987, Estes, 1983). Recent analyses have suggested that these taxa have nothing to do with gekkotans, but instead form a paraphyletic assemblage near the base of Squamata and/or Iguania (Evans and Barbadillo, 1997, 1998, 1999, Evans and Chure, 1998b, Evans et al., 2005), or that they are close to scleroglossans (Conrad, 2004c; Conrad and Norell, 2006a). Evans and Wang (2005) re-analyzed the data matrices of Evans and Chure (1998b) and Evans and Barbadillo (1997, 1998, 1999) after adding some taxa. They recovered the basal positions for *Bavarisaurus* and *Ardeosaurus*, but found *Eichstaettisaurus* to be a carusioid anguimorph (Evans and Wang, 2005). The current analysis includes all of the taxa used in the most recent of these studies (Evans and Wang, 2005; Evans et al., 2005), but supports a phylogenetic hypothesis more similar to that of Evans et al. (2005) and Conrad and Norell (2006a) who suggest that *Eichstaettisaurus* is a basal scincogekkonomorph.

Scleroglossa Estes et al., 1988
(figs. 54B, 55B, 56A)

DEFINITION: Estes et al. (1988) defined Scleroglossa as a node-based taxon including Gekkota and Autarchoglossa. I modify this definition here as follows: All descendants of the last common ancestor of *Gekko gecko*, *Scincus scincus*, and *Anguis fragilis*.

DIAGNOSIS: The unnamed, unresolved clade containing *Scandensia ciervensis*, Gekkonomorpha (sensu Conrad and Norell, 2006a), and Evansauria (see below) is diagnosed by 65(1) frontals with an anterior maxillary contact and 269(1) presence of a single anterior process of the interclavicle.

COMMENTS: The diagnosis of this clade is certainly influenced by the lack of resolution between its constituent groups and the relatively limited morphological understanding of *Scandensia ciervensis* (Evans and Barbadillo, 1998).

Gekkonomorpha Fürbringer, 1900b
(figs. 54B, 55B, 56A)

DEFINITION: Following Conrad and Norell (2006a), Gekkonomorpha is defined as all taxa sharing a more recent common ancestor with *Gekko gecko* than *Iguana iguana*, *Lacerta viridis*, *Scincus scincus*, *Anguis fragilis*, or *Varanus varius*.

DIAGNOSIS: Gekkonomorphs plesiomorphically share the following unambiguous synapomorphies: 79(1) posteromedial parietal flange, 131(1) occipital condyle bipartite and constructed primarily by the exoccipital portions of the otooccipitals, 136(2) presence of a distinct supratrigeminal process that anteriorly closes the trigeminal foramen, 144(1) sphenoid enclosing the lateral head vein, 151(1) anterior location for the sphenooccipital tubercle, and 207(1) retroarticular process that is posteriorly expanded (broadened).

COMMENTS: Cope (1900) and Fürbringer (1900a) used Nyctisaura to receive Gekkoninae and Eublepharinae. Lee (1998) recently redefined Nyctisaura such that it applies to a clade containing Xantusiidae and Gekkota to the exclusion of Rhynchocephalia, Iguanidae, Agamidae, *Leiolepis*, *Uromastyx*, Chamaeleonidae, Lacertidae, Teiidae, Gym-

nophthalmidae, Cordylidae, Scincidae, Anguidae, Xenosauridae, *Heloderma*, *Lanthanotus borneensis*, and *Varanus*. If not for this latter definition, Nyctisaura might be invoked for the clade referred to here as Gekkonomorpha. Gekkonomorpha is a name that is sometimes used informally to refer to extant geckos (Withers et al., 2000; Seligmann, 2002; Werner et al., 2002, 2004, 2005; Persaud et al., 2003; Gehr and Werner, 2005) and has been used more formally as well (Fürbringer, 1900b; Conrad and Norell, 2006a). Thus, this name is available and useful as a name for the stem-based group including geckos and their fossil relatives.

Parviraptor + *Gobekko cretacicus* + Gekkota
(figs. 54B, 55B, 56A)

DIAGNOSIS: The current analysis suggests that a clade formed by *Parviraptor*, *Gobekko cretacicus*, and Gekkota may be diagnosed by a single unambiguous synapomorphy: 108(1) vomer-palatine contact very narrow mediolaterally.

COMMENTS: The placement of *Parviraptor* (including *P. estesi* and *P.* cf. *estesi* of Evans, 1994a) within Gekkonomorpha is somewhat unexpected. *Parviraptor* was originally considered to be an anguimorph with platynotan affinities (Evans, 1994a; Evans and Wang, 2005). Recent studies have suggested that this is, instead, a basal scincogekkonomorph (Evans et al., 2005) or a basal member of the autarchoglossan lineage (Conrad and Norell, 2006a). Discovery of more complete remains of this intriguing animal would be a windfall for squamate anatomy and systematics.

Parviraptor Evans, 1994a
(figs. 54B, 55B, 56A)

DIAGNOSIS: *Parviraptor estesi* and *P.* cf. *estesi* are joined in this analysis by two unambiguous synapomorphies. These are 83(2) presence of an expansive nuchal fossa that extends well onto the parietal table and 214(2) "modified pleurodont" dentition (sensu Zaher and Rieppel, 1999a).

COMMENTS: I refrain from defining the clade *Parviraptor* as constituted here, preferring to leave that to the original describer of the specimens included in it. *Parviraptor*

estesi and *P.* cf. *estesi*, as described by Evans (1994a), are each represented by incomplete remains that may be diagnosed from one another and probably separated by several million years (Evans, 1994a). However, the present analysis supports Evans' (1994a) suggestion that these two taxa form a clade.

Gobekko cretacicus + Gekkota
(figs. 54B, 55B, 56A)

DIAGNOSIS: Gekkota and *Gobekko cretacicus* are united by 77(3) absence of a pineal foramen, 159(3) quadrate suspended mostly from the opisthotic, and 181(2) closed and fused Meckel's canal.

COMMENTS: The phylogenetic placement of *Gobekko cretacicus* has been cladistically analyzed only for the first time recently. A preliminary analysis of its relationships suggested the placement of this taxon as the sister-group to Gekkota (Conrad, 2005a), a view supported here. However, another recent study has suggested that *Gobekko cretacicus* falls within the gekkotan crown group (Conrad and Norell, 2006a), with the implication that crown-group gekkotans have been distinct since the Cretaceous. *Gobekko cretacicus* is known from an incomplete skull. A new study of the specimen and/or the discovery of more complete remains might help to more confidently place this animal in the context of gekkonomorph evolution.

Gekkota Cuvier, 1817
(figs. 54B, 55B, 56A)

DEFINITION: The most recent ancestor of extant taxa more closely related to *Gekko gecko* than to *Xantusia vigilis*, *Scincus scincus*, or *Varanus varius* and all descendants of that ancestor.

DIAGNOSIS: The present analysis yields two unambiguous synapomorphies for Gekkota, including 55(1) fused frontals and 80(1) short parietal supratemporal processes (see character description above).

COMMENTS: Estes et al. (1988) defined Gekkota as all descendants of the common ancestor of Gekkonidae and Pygopodidae. However, they considered Gekkonidae to include all limbed gekkotans. The revised definition used here maintains the apparent

intention of Estes et al. (1988) to include all extant geckos and pygopods, but does not make the same assumption about the primary gekkotan dichotomy.

Bauer et al. (2005) recently described an Eocene gecko preserved in Baltic Amber that represents the earliest known member of the crown gekkotan radiation. However, this taxon, *Yantarogekko balticus*, is not included in the current analysis because the current morphological data set is not sensitive enough to discriminate between *Y. balticus* and other gekkonids based on external morphology. Even so, the presence of *Y. balticus* is acknowledged in fig. 56A.

Gekkonidae + Eublepharidae
(figs. 54B, 55B)

DIAGNOSIS: Gekkonids and eublepharids are joined in this analysis by only two unambiguous synapomorphies. These are 73(1) fused parietals and 284(0) pelvic elements co-ossified (sutures lost).

COMMENTS: Numerous hypotheses for the interrelationships of the gekkotan clades have been put forward. Traditionally, a dichotomy has been described between limbed and limbless gekkotans (Kluge, 1967, 1983; Estes et al., 1988; Wu et al., 1996; Lee, 1998). However, Kluge (1987) suggested that the basal gekkotan dichotomy lay between eublepharids and all other gekkotans, with diplodactylines being the sister group to pygopodines. The latter hypothesis has been supported by one recent morphological study of gekkonomorph relationships (Conrad and Norell, 2006a). However, a recent molecular analysis (Han et al., 2004) with extensive taxonomic sampling offers some support for a new hypothesis in which eublepharids and gekkonids form the sister-clade to a Pygopodidae sensu Kluge (1987; see below). A recent analysis of diplodactylines raises questions about the monophyly of that group as it has been traditionally conceived (Donnellan et al., 1999). Importantly, the present phylogenetic analysis offers the same topological hypothesis for extant "families" as Han et al. (2004). Future versions of this data matrix will include more extensive sampling of gekkonids.

Gekkonidae Gray, 1825
(figs. 54B, 55B)

DEFINITION: All taxa sharing a more recent common ancestor with *Gekko gecko* than with *Pygopus lepidopus* or *Eublepharis hardwickii*.

DIAGNOSIS: The current analysis reveals six unambiguous synapomorphies for a clade minimally containing *Teratoscincus microlepis*, *Gekko gecko*, *Gonatodes albogularis*, and *Pachydactylus bibronii*. These are 26(1) the presence of strong medial processes of the maxillae posterior to the nasal process of the premaxilla, 104(1) presence of a contact between the septomaxilla and the osseous roof of the nasal capsule, 106(1) fused vomers, 113(0) absence of a distinct choanal groove on the palatine, 242(1) presence of seven or fewer cervical vertebrae, and 325(3) endolymphatic sacs extending into the nuchal musculature through the vagus foramen.

COMMENTS: Note that Gekkonoidea as used by Kluge (1987) and defined by Conrad and Norell (2006a) is taxonomically equivalent to Gekkonidae as defined here and with the present phylogenetic hypothesis. However, as discussed earlier, this result is acceptable to keep the meaning of the name consistent.

Conrad and Norell (2006a) suggested that *Teratoscincus* was closely related to pygopodids, but cautioned that a more inclusive analysis might reveal a different hypothesis. Indeed, the current analysis places *Teratoscincus microlepis* in a more traditional position as a member of the Gekkonidae. However, I will echo the cautionary statement of Conrad and Norell (2006a) in warning that the current sampling of gekkonids is relatively sparse and that more complete sampling is in order for future versions of this analysis. With that in mind, I will not further discuss gekkonid interrelationships here.

Eublepharidae Boulenger, 1883
(figs. 54B, 55B)

DEFINITION: All taxa sharing a more recent common ancestor with *Eublepharis hardwickii* than with *Gekko gecko* or *Pygopus lepidopus*.

DIAGNOSIS: The eublepharid taxa included in this analysis are joined by four unambiguous synapomorphies. These are 32(1) presence of a palatine flange of the maxilla, 36(1) pares frontales contact at midline, 74(2) frontal tabs of the parietal extending anteriorly onto the ventral surface of the frontal, and 211(2) teeth closely packed together (ctenodont).

COMMENTS: *Eublepharis hardwickii*, the type species for the type genus of Eublepharidae, is used in the definition of this group, even though *Eublepharis* does not appear in the present analysis. Morphological (Grismer, 1988) and molecular (Ota et al., 1999; Han et al., 2004) studies recover the monophyly of a clade including *Eublepharis*, *Aeluroscalabotes felinus*, *Coleonyx mitratus*, and *Hemitheconyx caudicinctus*. Thus, *E. hardwickii* is presumed to be a member of the clade represented by *A. felinus*, *C. mitratus*, and *H. caudicinctus* in the present analysis. This relationship will be further analyzed elsewhere.

Pygopodidae Gray, 1845
(figs. 54B, 55B)

DEFINITION: The most recent ancestor of extant taxa more closely related to *Pygopus lepidopodus* than to *Gekko gecko* or *Eublepharis hardwickii* and all descendants of that ancestor.

DIAGNOSIS: This analysis recovers six unambiguous synapomorphies for Pygopodidae, including 14(2) bilobed premaxillary incisive process, 22(1) absence of anterolateral processes on the nasals, 39(0) absence of a prefrontal-jugal contact, 114(1) presence of ventromedial fold on the palatine partly hiding the choanal groove in ventral view (rudimentary secondary palate), 185(0) dentary without a notch distinguishing coronoid and surangular processes, and 234(1) moderately oblique vertebral condyles and cotyles (see character description above).

COMMENTS: The current definition is a slight modification of that proposed by Kluge (1987) such that the anchor taxa are more specific. This is a more taxonomically inclusive definition than that of Estes et al. (1988) and includes diplodactyline geckos.

Pygopodinae Gray, 1845
(figs. 54B, 55B)

DEFINITION: All taxa sharing a more recent common ancestor with *Pygopus lepidopodus* than with *Carphodactylus laevis* or *Diplodactylus vittatus*.

DIAGNOSIS: In the present analysis, pygopodines are diagnosed by the following unambiguous synapomorphies: 21(1) nasals that are in contact for less than half their length in dorsal view, 33(1) a maxillary tooth row terminating at the level of the anterior border of the orbit, 57(0) anterior and posterior borders of the frontal of subequal width, 136(0) absence of a supratrigeminal process on the prootic, 143(2) fusion of the sphenoid and basioccipital, 151(0) posterior positioning of the spheno-occipital tubercle, 180(1) elongate lateral portion of the dentary extending along the mandible to a point at least half way between the coronoid eminence and the mandibular glenoid, 207(0) no posterior broadening of the retroarticular process, 230(1) notochordal canal obliterated by centrum ossification, 303(1) deeply imbricating scales, and 340(1) presence of an unexpanded head of the M. pseudotemporalis profundus.

Evansauria tax. nov.
(figs. 54B, 55B, 56B)

DEFINITION: All taxa sharing a more recent common ancestor with *Lacerta viridis* and *Varanus varius* than with *Gekko gecko* or *Iguana iguana*.

ETYMOLOGY: Named in honor of Susan E. Evans and her extensive work on the evolutionary history and systematics of lepidosaurs.

DIAGNOSIS: This taxon is diagnosed by 76(2) presence of an anteroposteriorly narrow decensus parietalis, 146(1) posterior opening of the Vidian canal located on the sphenoid-prootic suture, 185(0) dentary without a notch distinguishing coronoid and surangular processes, 209(1) presence of a tubercle on the medial margin of the retroarticular process, 230(1) notochordal canal obliterated by centrum ossification, 234(1) moderately oblique vertebral condyles and cotyles (see character description above), and

257(0) no expansion of the anterior presacral ribs.

COMMENTS: This taxon has been unidentified until now, mostly because most of the basal members of the clade have not previously appeared in cladistic analyses together. Importantly, each of the non-autarchoglossan evansaurs included here have been allocated to the clades Gekkota (*Myrmecodaptria microphagosa*), Lacertoidea (*Eoxanta lacertifrons lacertifrons*, *Globaura venusta*), Scincoidea (*Parmeosaurus scutatus multivagus*, *Tepexisaurus tepexii*), or Anguidae (*Bainguis parvus*) (see Borsuk-Białynicka, 1988; Gao and Hou, 1996; Gao and Norell, 1998, 2000; Reynoso and Callison, 2000).

Conrad and Norell (2006a) suggested that *Myrmecodaptria microphagosa* is a basal member of the autarchoglossan lineage; a hypothesis supported here, but in a slightly different phylogenetic context. Wu et al. (1996) suggested that *Globaura venusta* and *Eoxanta lacertifrons lacertifrons* are basal scincoids (contra Borsuk-Białynicka, 1988).

Bainguidae Borsuk-Białynicka, 1984
(figs. 54B, 55B, 56B)

DEFINITION: All taxa sharing a more recent common ancestor with *Bainguis parvus* than with *Lacerta viridis*, *Scincus scincus*, or *Varanus varius*.

DIAGNOSIS: Bainguids, as defined here, are united by five unambiguous synapomorphies, including 53(1) presence of a jugal-squamosal contact, 96(2) postorbital extending posteriorly for more than 3/4 the length of the supratemporal fenestra, 121(1) midline contact of the palatines, 193(1) coronoid labial flange present, but not greatly developed posteriorly, and 203(1) presence of a prearticular crest.

COMMENTS: Bainguidae was originally erected as a monospecific "family" described as possessing both scincomorph and anguimorph affinities, but conservatively placed as a member of a "preanguimorphan grade" (Borsuk-Białynicka, 1984). Later, *Bainguis parvus* was shown to have affinities with Anguidae (Borsuk-Białynicka, 1991; Gao and Hou, 1996; Gao and Norell, 1998) and Bainguidae was synonymized with Anguidae

(Alifanov, 2000). Gao and Norell (1998) alone have cladistically analyzed the position of *Bainguis parvus*. They provided evidence of anguine affinities for *Bainguis*, but cautioned that this poorly known taxon could not be scored for many of the anguid characters (Gao and Norell, 1998).

The current analysis is the first to include *Bainguis parvus* in a cladistic analysis with non-anguimorph fossils such as *Myrmecodaptria* and *Eoxanta lacertifrons*. Thus, this is the first analysis in which Bainguidae, as it is currently used, had the potential to be discovered. Given the relative completeness of our knowledge of *B. parvus*, prudence is exercised in the current definition of Bainguidae.

Note that the phylogenetic position of Bainguidae within Autarchoglossa is not strongly supported. A secondary analysis of only osteological characters (see below) suggested that bainguids are lacertoids. Further analysis of the position of Bainguidae is appropriate given this result and the convergences between this clade and the plesiomorphic condition for Scincomorpha and some of its constituent clades.

Bainguis parvus + *Eoxanta lacertifrons* +
Myrmecodaptria
(figs. 54B, 55B)

DIAGNOSIS: Bainguids exclusive of *Globaura venusta* are united by 143(1) the presence of posterolateral sphenoid flanges ventrolaterally overlying the basioccipital and 178(0) a dentary that is ventrally convex along its long axis.

Eoxanta lacertifrons + *Myrmecodaptria*
(figs. 54B, 55B)

DIAGNOSIS: This unnamed clade is united to the exclusion of other bainguids within Bainguidae by 209(0) the absence of a tubercle on the medial surface of the retroarticular process.

Parmeosaurus scutatus + Autarchoglossa
(figs. 54B, 55B, 56B)

DIAGNOSIS: *Parmeosaurus scutatus* and autarchoglossans share two unambiguous synapomorphies: 108(1) vomer-palatine con-

tact very narrow mediolaterally and 143(2) fusion of the sphenoid and basioccipital.

Autarchoglossa Wagler, 1830
(figs. 54C, 55C, 56B)

DEFINITION: *Lacerta viridis*, *Scincus scincus*, *Anguis fragilis*, and all descendants of their last common ancestor.

DIAGNOSIS: The current analysis recovers five unambiguous autarchoglossan synapomorphies: 10(1) presence of dermal sculpturing on the frontal and parietal, 11(1) premaxilla fused (unpaired), 47(0) presence of an angulated jugal, 48(0) presence of a posteroventral process on the jugal, and 166(1) articular-prearticular fused to the surangular.

COMMENTS: Estes et al. (1988) defined this clade phylogenetically following the general traditional usage of the name (e.g., Wagler, 1830; Camp, 1923); that definition is only made more precise here by implementing more specific anchor taxa.

Scincomorpha Camp, 1923
(figs. 54C, 55C, 56B)

DEFINITION: All taxa sharing a more recent common ancestor with *Scincus scincus* than with *Gekko gecko*, *Anguis fragilis*, or *Varanus varius*.

DIAGNOSIS: This clade is diagnosed by 114(1) presence of ventromedial fold on the palatine partly hiding the choanal groove in ventral view (rudimentary secondary palate), 285(2) symphysial portion of the pubis more than half again as long as the tubercular portion, 306(1) presence of compound osteoderms dorsally 308(1) and ventrally, 319(2) keratinized tongue with mushroom-shaped foretongue in cross section, 323(2) inner ear with more than one-half of the hair cells inert, 327(1) divided hemipeneal sulcus, and 360(0) absence of an aponeurosis for the M. branchiohyoideus.

COMMENTS: Although Estes et al. defined Scincomorpha as "[t]he last common ancestor of Scincidae, Cordylidae, Xantusiidae, Lacertidae, Teiidae, and Gymnophthalmidae, and all of its descendants" (Estes et al., 1988: 207), the definition is expanded here to include stem taxa. Such is more similar to the original usage of Camp (1923) who hypoth-

esized that Amphisbaenia is the sister taxon to scincomorphs sensu Estes et al. (1988), but included them in his Scincomorpha (see fig. 1). Scincomorpha is the sister group of Anguimorpha within the node-based Autarchoglossa. The name Leptoglossa (Cope, 1900) is available for the crown group scincomorph node, is suited for that purpose in identifying a soft-tissue characteristic, and has been implied as such in the past (Romer, 1956; Hu et al., 1984; Carroll, 1988b). Although the constituent taxa of that clade is the same as Scincomorpha in the present study's topology and Leptoglossa is not used or defined here, it is suggested for potential future use at that node.

Estes et al. (1988) considered Scincomorpha to be a dichotomy between Scincoidea and Lacertoidea, but scincomorph monophyly has been challenged more recently (Lee, 1998, 2000, 2005a, 2005b; Lee and Caldwell, 2000; Townsend et al., 2004; Vidal and Hedges, 2005). Lee (1998) and Lee and Caldwell (2000) suggested that scincomorphs are paraphyletic with respect to both a gekkotan-amphisbaenian-dibamid clade and to anguimorphs, representing three or four different lineages (Xantusiidae with "Annulata", Lacertiformes, Scincidae, and Cordylidae) (figs. 6, 7), although Lee (2005a) later found morphological support for a Scincidae-Cordyliformes clade. Molecular studies (Townsend et al., 2004; Vidal and Hedges, 2004, 2005) (fig. 10) and combined morphological-molecular analyses (Lee, 2005a, b) also suggest the non-monophyly of Scincomorpha. Importantly, Xantusiidae has been placed near Gekkota (Lee, 1998, 2000, 2005a, b; Lee and Caldwell, 2000) (figs. 6, 7), with Lacertiformes (Estes et al., 1988; Caldwell, 1999a) (figs. 2, 8), or associated with Scincidae and/or Cordyliformes (Wu et al., 1996; Evans and Barbadillo, 1997, 1998; Townsend, 2002; Vicario et al., 2003; Townsend et al., 2004; Vidal and Hedges, 2004, 2005) (figs. 3, 4, 10).

The taxonomy laid out for scincomorphs here is sensitive to the varying hypotheses of scincomorph interrelationships. The basic dichotomy recovered in this analysis is between a clade containing *Slavoia darevskii* and Scincidae sensu lato and a clade containing Cordyliformes, Xantusiidae, Lacerti-

formes, and several fossil relatives of these taxa. I apply names to three major stem-based clades below: Scincoidea, Cordyloidea, and Lacertoidea. Cordyloidea may become a subjective junior synonym of Scincoidea if the two are shown to form a clade exclusive of lacertoids, but Cordyloidea will never fall within Lacertoidea (see the definitions of these taxa below). This would more-or-less follow the usage of Estes et al. (1988). Xantusiids may move around the tree without disrupting the general meaning of any of the scincomorph group names, or of Gekko-nomorpha (see above). Although I have some confidence in clades described herein, I do not delude myself by thinking that alternative phylogenetic hypotheses are impossible or that they will not be proposed. The taxonomic framework offered here will allow continued communication about the groups to which they refer even in different phylogenetic contexts.

Lacertoidea + Cordyloidea
(figs. 54C, 55C, 56B)

DIAGNOSIS: Lacertoids and cordyloids are united in this analysis by 32(0) absence of a maxillary palatine flange, 80(1) short parietal supratemporal processes (see character description above), 96(2) postorbital extending posteriorly for more than 3/4 the length of the supratemporal fenestra, 251(1) double, divergent caudal transverse processes, 269(0) absence of an anterior process of the interclavicle, and 294(1) presence of large pores on the scales anterior to the cloaca and/or on the thigh.

COMMENTS: Estes et al. (1988) suggested a close relationship between scincids sensu lato and Cordyliformes (=Cordylidae of their usage and sensu lato) and found Xantusiidae to be more closely related to Lacertiformes. Recent molecular work has also suggested a close relationship between cordyliforms and scincids sensu lato, but further suggests that xantusiids are the sister-taxon to cordyliforms (Vicario et al., 2003; Townsend et al., 2004; Vidal and Hedges, 2005).

The current result of a lacertoid-cordyloid clade is somewhat unexpected. This may partly explain the molecular similarities between cordyliforms and xantusiids. Inclu-sion of fossil cordyloids and xantusiids also help to reveal this relationship by modifying character polarities and contributing to reconstruction of hypothetical ancestors. However, because of the consistent lack of consensus regarding the relationshiops of cordyloids, xantusiids, and lacertiforms to one another and to other squamate groups, it would not be surprising if further investigations with additional character data provided an hypothesis different from this one. With this in mind, no name is applied to this grouping of lacertoids and cordyloids.

Cordyloidea Fitzinger, 1826
(figs. 54C, 55C, 56B)

DEFINITION: All taxa sharing a more recent common ancestor with *Cordylus cordylus* than *Lacerta viridis* or *Anguis fragilis*.

DIAGNOSIS: Cordyloids share three unambiguous synapomorphies: 8(1) presence of dermal sculpturing on the maxilla, 166(0) absence of fusion between the articular-prearticular and the surangular, and 219(1) striated tooth crowns.

COMMENTS: Cordylidae sensu lato is now typically split into two ''families'' (Cordylidae sensu stricto and Gerrhosauridae), collectively referred to as Cordyliformes (Lang, 1991; Harvey and Gutberlet, 1995; Mouton and Wyik van, 1997; Cooper and Steele, 1999; Odierna et al., 2002; Lamb et al., 2003). The monophyly of a cordylid-gerrhosaurid clade exclusive of other extant taxa is unquestioned, rendering the usage of Cordyliformes or Cordylidae sensu lato somewhat semantic. Regardless, I use Cordyliformes here for the crown group, following recent usage, and employ Fitzinger's (1826) term Cordyloidea for the stem-based taxon including cordyliforms and their proximal fossil outgroups.

The current analysis is unable to resolve the relationships between cordyliforms, *Ornatocephalus metzleri*, and *Sakurasaurus shokawensis*. An analysis by Weber (2004) placed *O. metzleri* in an unresolved trichotomy with cordyliforms and scincids, with paramacello-dids as the outgroup. The current analysis does not recover a monophyletic scincoid clade as conceptualized by Weber (2004), but

does support the relationship between *O. metzleri* and cordyliforms. Evans and Manabe (1999) were prudent in their placement of *S. shokawensis*, suggesting only that it belonged within Scincomorpha; a hypothesis consistent with the current topology. The possibility that one or both of these fossil taxa belong within Cordyliformes will be analyzed elsewhere.

Lacertoidea Camp, 1923
(figs. 54C, 55C, 56B)

DEFINITION: All taxa sharing a more recent common ancestor with *Lacerta viridis* than with *Scincus scincus*, *Cordylus cordylus* (=*Zonurus cordylus*), or *Anguis fragilis*.

DIAGNOSIS: Lacertoids are diagnosed by 77(3) absence of a pineal foramen (with notable apparent reversals), 110(0) absence of anteromedial ''step'' to the palatine, 203(1) presence of a prearticular crest, 205(0) retroarticular process lacking medial deflection, 209(0) absence of a tubercle on the medial surface of the retroarticular process, 210(0) retroarticular process without torsion, 212(4) teeth with divided crowns/cusps, 303(0) body scales not deeply imbricating, 305(0) dorsal body osteoderms absent, 307(0) ventral body osteoderms absent, 337(0) M. adductor mandibulae posterior extending only to the posterior margin of Meckel's canal, and 341(1) origin of the M. pseudotemporalis superficialis extending onto the posterior one-third of the margin of the supratemporal fenestra.

COMMENTS: Estes et al. (1988) gave this taxon name a node-based definition including Xantusiidae and lacertiform taxa. Although the current topology would work with that definition and maintain the integrity of the taxon name as intended by Estes et al. (1988), Xantusiidae remains a problematic clade with a limited fossil record (Hecht, 1956; Estes, 1983). The relationships of xantusiids have been questioned and recent studies have suggested that their affinities lie with gekkotans, amphisbaenians, and dibamids (Lee, 1998, 2000, 2005a, 2005b; Lee and Caldwell, 2000) or with scincoids (Wu et al., 1996; Evans and Barbadillo, 1997, 1998; Vicario et al., 2003; Vidal and Hedges,

2004, 2005). If the former hypothesis is correct, then Lacertoidea sensu Estes et al. (1988) would become synonymous with Scleroglossa; if the latter is correct, then it would become synonymous with Scincomorpha sensu Estes et al. (1988). Even though the current topology supports the placement of Xantusiidae with many unambiguous synapomorphies, I find it prudent to modify the definition of Lacertoidea to allow for differing topologies with minimal disruption of taxonomy (see Scincomorpha above).

Xantusiidae Baird, 1859
(figs. 54C, 55C, 56B)

DEFINITION: *Xantusia vigilis*, *Cricosaura typica*, *Lepidophyma flavimaculatum*, *Palaeoxantusia kyrentos*, and all descendants of their last common ancestor.

DIAGNOSIS: Xantusiids, as defined here, are united by 89(0) contact between supratemporal arch bones and frontal and parietal unforked, 93(2) postfrontal contacting the parietal for more than one-half the length of the parietal table, 94(1) fused postorbitofrontal, 114(0) no development of the secondary palate, 126(1) ectopterygoid exposed on the lateral skull surface posterior to the maxilla, 180(1) elongate lateral portion of the dentary extending along the mandible to a point at least half way between the coronoid eminence and the mandibular glenoid, 181(2) closed and fused Meckel's canal, and 189(1) splenial not extending anterior to the midpoint of the dentary tooth row.

Xantusia + Cricosaura + Lepidophyma
(figs. 54C, 55C)

DIAGNOSIS: The extant xantusiids included in this analysis are united by seven unambiguous synapomorphies. These are 41(2) fusion of the lacrimal and prefrontal, 47(1) jugal curved (rather than angulated), 88(1) an elongate supratemporal, 97(0) postorbital with a robust descending process contributing at least one-half the posterior orbital border, 132(1) crista prootica extending anteriorly onto the basipterygoid process, 183(1) dentary forming the dorsal border of the anterior inferior alveolar foramen, and 202(1) absence of an angular.

Xantusia + *Cricosaura*
(figs. 54C, 55C)

DIAGNOSIS: According to the current analysis, *Xantusia* and *Cricosaura* share one unambiguous synapomorphy uniting them to the exclusion of *Lepidophyma*: 48(1) posteroventral process of jugal absent.

COMMENTS: Morphological data have previously suggested a sister taxon relationship between *Cricosaura* and *Lepidophyma*. Molecular data suggest a sister-group relationship between *Xantusia* and *Lepidophyma* (Hedges et al., 1991; Hedges and Bezy, 1993; Vicario et al., 2003). Recovery of a novel phylogenetic topology here may be related to the broader sampling of outgroup taxa compared to previous analyses. Even so, the composite coding of *Xantusia* in this matrix will be eliminated in future versions of this analysis to further analyze the current phylogenetic hypothesis.

Lacertiformes Estes et al., 1988
(figs. 54C, 55C, 56B)

DEFINITION: *Lacerta viridis*, *Teius teyou*, and all descendants of their last common ancestor.

DIAGNOSIS: Lacertiforms are united by 52(0) jugal lying mostly dorsal (rather than medial) to the maxilla, 160(0) presence of a pterygoid lappet on the quadrate, 169(1) expanded adductor fossa, 184(2) absence of a posterodorsal coronoid process on the dentary, 198(0) absence of a posterior overlap of the coronoid by the dentary, 287(0) presence of an anterior iliac process, 317(3) foretongue notched for more than 40 percent of its length, and 323(1) ciliary restraint system for the inner ear composed of tectorial and sallet systems.

COMMENTS: The definition applied to this taxon name follows that of Estes et al. (1988), but substitutes more specific anchor taxa. Although most recent phylogenetic analyses recover a clade containing Lacertidae and Teiioidea to the exclusion of other extant taxa, at least two do not (Evans and Barbadillo, 1998, 1999). Both of these studies suggest that lacertids are more closely related to a clade containing xantusiids, *Paramacellodus*, scincoids, and cordylids than to

teiioids. In this case, Lacertiformes includes scincoids and cordyloids and possibly would be considered a synonym of Leptoglossa (see Scincomorpha above).

Note that *Chamops segnis* is problematic. Observation of the principle trees saved from the analysis reveals that *C. segnis* may be the immediate outgroup of Lacertiformes, the sister-taxon to Lacertidae, a basal teiioid, the sister-taxon to Gymnophthalmidae, a basal macroteiid, the sister-taxon to Polyglyphanodontidae, or the sister-taxon to Teiidae. *Chamops segnis* may only be scored for characters 52 and 287 among those contributing to the lacertiform diagnosis and shares the lacertiform condition in both. A more complete understanding of this taxon may help to resolve this issue. *Prototeius stageri* is currently known from various skull bits associated based on size and proximity (Denton and O'Neill, 1995). Further study or more complete (articulated) remains are necessary to demonstrate that the known specimens belong to a single species.

Teiioidea Estes et al., 1988
(figs. 54C, 55C, 56B)

DEFINITION: All taxa sharing a more recent common ancestor with *Teius teyou* than with *Lacerta viridis*.

DIAGNOSIS: Teiioids are diagnosed by 80(0) elongate supratemporal processes (see character description above), 84(0) no increased contact between the supratemporal arches and the parietal, 121(1) midline contact of the palatines, 204(1) prearticular crest with imbedded angular crest, 263(1) a posterior coracoid emargination, 277(2) absence of an ectepicondylar groove and foramen, 317(4) foretongue notched for more than 50 percent of its length, 333(1) peroneal nerve absent, and 347(2) absence of the urinary bladder.

COMMENTS: Estes et al. (1988) defined this clade as a crown, node-based taxon anchored to teiids and gymnophthalmids. That definition is equivalent to Boulenger's (1885–1887) conception of Teiidae. Upon considering fossil taxa and implementing cladistic methodology, Presch (1983) questioned the holophyly of Teiidae sensu Boulenger and raised Gymnophthalminae to "family" rank, a

convention followed by many subsequent studies (e.g., Estes, 1983; Estes et al., 1988; Presch, 1988; Schwenk, 1988; Kizirian, 1996; Evans and Barbadillo, 1998; Kizirian and McDiarmid, 1998; Lee, 1998; Kizirian and Cole, 1999; Reynoso and Callison, 2000; Montero et al., 2002; Bell et al., 2003). The definition of Teiioidea is slightly expanded here to include fossil stem taxa that may be more closely related to teiids and gymnophthalmids than to lacertids.

Macroteiida tax. nov.
(figs. 55C, 56B)

DEFINITION: *Teius teyou*, *Polyglyphanodon sternbergii*, and all descendants of their last common ancestor.

ETYMOLOGY: *Macro*, (Latin) large; "-teiida" referring to the Teiidae, the extant radiation of macroteiids. Referring to "macroteiids", the common name given to extant, non-gymnophthalmid, teiioids (e.g., Presch, 1974, 1976, 1983, 1988; Vitt, 1982; Estes, 1983; Krause, 1985; Estes et al., 1988; Schwenk, 1988; White, 1990).

DIAGNOSIS: Macroteiids form a clade diagnosed by 66(0) prefrontals with large contributions to the orbitonasal fenestra, 92(2) postfrontal developed as a mediolaterally elongate bar forming the anterior margin of the supratemporal fenestra, 114(0) no development of the secondary palate, 124(1) ectopterygoid contacting the palatine in the suborbital fenestra, 166(0) absence of fusion between the articular-prearticular and the surangular, and 269(1) presence of a single anterior process of the interclavicle.

COMMENTS: The informal term "macroteiid" is formalized here as Macroteiida to encompass not only crown group teiids, but to include all of the known larger-bodied teiioids (fig. 55).

Teiidae Gray, 1827
(figs. 54C, 55C, 56B)

DEFINITION: *Teius teyou*, *Tupinambis teguixin*, and all descendants of their last common ancestor.

DIAGNOSIS: Teiidae share five unambiguous synapomorphies to the exclusion of polyglyphanodontids: 8(1) presence of der-

mal sculpturing on the maxilla, 100(0) presence of a dorsal process on the squamosal, 240(0) well-developed atlantal lateral processes, 243(3) cervical intercentra fused to the succeeding vertebrae, and 285(1) symphysial and tubercular portions of the pubis of subequal length.

COMMENTS: Estes et al. defined Teiidae as "the last common ancestor of the Teiinae and Tupinambinae … and all organisms sharing a more recent common ancestor with these taxa than with any other extant organisms" (Estes et al., 1988: 215). Polyglyphanodontids would be considered teiids under that definition. Indeed, polyglyphanodontids have been considered part of the Teiidae in the past (Estes, 1983; Presch, 1983; Gao and Norell, 2000; Nydam and Cifelli, 2005). However, *Polyglyphanodon*-like teiioids have also often been considered to constitute up to four separate "families" from teiids; Adamisauridae, Gilmoreteiidae (=Macrocephalosauridae; Langer, 1998), Mongolochamopidae (see Alifanov, 2000), and Polyglyphanodontidae (see Gilmore, 1942b; Sulimski, 1972, 1975, 1978; Alifanov, 1993a, 2000; Langer, 1998). Because of this precedent and because polyglyphanodontids sensu lato (see usage below) do not fall within the crown group Teiidae, I use the above definition for Teiidae.

Polyglyphanodontidae Gilmore, 1942b
(figs. 54C, 55C, 56B)

DEFINITION: *Adamisaurus magnidentatus*, *Gilmoreteius ferrugenous*, *Gobinatus arenosus*, *Polyglyphanodon sternbergii*, and all descendants of their last common ancestor.

DIAGNOSIS: Polyglyphanodontids are diagnosed by 9(0) absence of dermal sculpturing on the prefrontal, 77(0) pineal foramen lying within the parietal, 119(0) presence of a pterygoid-vomer contact, 122(1) pterygoids contact at midline, 213(1) marginal teeth waisted, 261(0) straight (non-angulate) clavicle, and 266(1) secondary scapular fenestra present.

COMMENTS: Estes (1983) and Presch (1983) considered the taxa contained here in Polyglyphanodontidae to be a subclade of Teiidae (see comments above for Teiidae). New data regarding the dentition of *Polyglyphanodon sternbergii* from an excellent study by Nydam

and Cifelli (2005) will be incorporated into future versions of this analysis.

Gobinatus arenosus + Tchingisaurus multivagus
(figs. 54C, 55C)

DIAGNOSIS: *Gobinatus arenosus* and *Tchingisaurus multivagus* form a clade exclusive of other polyglyphanodontids based on the presence of three unambiguous synapomorphies: 83(1) presence of a nuchal fossa on the parietal, 100(0) presence of a dorsal process on the squamosal, and 182(0) presence of a subdental shelf.

COMMENTS: The principle trees recovered in this analysis revealed two competing hypotheses for the placement of this clade; as the sister group to *Adamisaurus magnidentatus magnidentatus*, or as the sister taxon to a clade containing *Erdenetesaurus robinsonae* and *Cherminsaurus kozlowskii*. A forthcoming revision of the morphology of *Adamisaurus magnidentatus* may help resolve these interrelationships.

Polyglyphanodontinae Gilmore, 1942b
(figs. 54C, 55C)

DEFINITION: All taxa sharing a more recent common ancestor with *Polyglyphanodon sternbergii* than with *Adamisaurus magnidentatus* or *Teius teyou*.

DIAGNOSIS: The current analysis reveals five unambiguous synapomorphies uniting polyglyphanodontines as defined here. These are 39(1) presence of a jugal-prefrontal contact, 47(1) jugal curved (rather than angulated), 58(0) linear interorbital margins of the frontal, 96(1) postorbital extends posteriorly for more than one-half the length of the supratemporal fenestra, and 208(1) absence of a retroarticular process pit.

COMMENTS: Among the taxa included in this analysis, the strict consensus tree presented here (fig. 54C) supports only the inclusion of *Polyglyphanodon sternbergii*, *Gilmoreteius chulsanensis*, *Sineoamphisbaena hexatabularis*, and *Darchansaurus estesi* within Polyglyphanodontinae as described here. The Adams Rule tree (fig. 55C) shows that all of principle trees are consistent with the inclusion of *Erdenetesaurus robinsonae* and *Cherminsaurus kozlowskii*. However, the in-

clusion of *Gobinatus arenosus* and *Tchingisaurus multivagus* clade can be neither confirmed nor denied by the current data. *Gobinatus arenosus* possesses only two of the synapomorphies for Polyglyphanodontinae listed in the diagnosis above (prefrontal-jugal contact and curved jugal); *T. multivagus* shares none of them.

Erdenetesaurus + Cherminsaurus
(figs. 54C, 55C)

DIAGNOSIS: *Erdenetesaurus robinsonae* and *Cherminsaurus kozlowskii* share two unambiguous synapomorphies according to this analysis: 166(1) articular-prearticular fused to the surangular and 185(1) presence of distinct subcoronoid and surangular processes of the dentary.

COMMENTS: As described and diagnosed by Sulimski (1975), *E. robinsonae* and *C. kozlowskii* are very similar. By the same token, cranial osteology may be very conserved in otherwise morphologically different species among extant squamates (e.g., closely related species of *Anolis*, *Tiliqua*, and *Varanus*).

Polyglyphanodon + Sineoamphisbaena hexatabularis + Darchansaurus + Gilmoreteius
(figs. 54C, 55C)

DIAGNOSIS: This unnamed clade is united by 9(1) dermal sculpturing on the prefrontal, 26(0) absence of strong medial processes of the maxilla posterior to the premaxillary nasal process, and 57(0) anterior and posterior borders of the frontal of subequal width.

Sineoamphisbaena hexatabularis + Darchansaurus + Gilmoreteius
(figs. 54C, 55C)

DIAGNOSIS: The unnamed clade containing *Sineoamphisbaena hexatabularis*, *Darchansaurus*, and *Gilmoreteius chulsanensis* are united in this analysis by two unambiguous synapomorphies: 131(1) occipital condyle bipartite and constructed primarily by the exoccipital portions of the otooccipitals and 213(0) unwaisted marginal teeth.

Darchansaurus + Gilmoreteius
(figs. 54C, 55C)

DIAGNOSIS: This unnamed clade is united by 96(3) a postorbital that extends posteriorly to contact the supratemporal and 215(1) the presence of caniniform teeth.

Scincoidea Oppel, 1811
(figs. 54C, 55C, 56B)

DEFINITION: All taxa sharing a more recent common ancestor with *Scincus scincus* than with *Lacerta viridis* or *Anguis fragilis*.

DIAGNOSIS: This stem-based taxon is diagnosed by 14(2) bilobed premaxillary incisive process, 31(1) neochoanate condition, 83(1) presence of a nuchal fossa on the parietal, 96(0) postorbital extends posteriorly for less than one-half the length of the supratemporal fenestra, 114(2) ventromedial palatal folds of the palatine hiding most or all of the dorsomedial processes of the palatine, 121(1) midline contact of the palatines, and 195(0) straight ventral margin of the coronoid in medial view.

COMMENTS: Estes et al. (1988) assigned the name Scincoidea as a node using Cordylidae and Scincidae as anchor taxa. However, differing phylogenetic hypotheses have yielded a variety of placements for Cordyliformes, Xantusiidae, and Paramacellodidae (see above) (figs. 1–10). Moreover, given the present topology (figs. 53–56) and the Estes et al. (1988) definition, Scincoidea would include Lacertoidea. Implementation of the Estes et al. (1988) definition would require Scincoidea to become synonymous with Scincomorpha given the current analysis, or possibly with Lee's (1998) Diploglossa given some other recent analyses (Lee, 1998, 2000; Lee and Caldwell, 2000). The current definition ensures the presence of a Scincoidea including skinks and all their closest relatives.

Scinciformes comb. nov.
(figs. 54C, 55C)

DEFINITION: *Scincus scincus*, *Scelotes bipes*, *Acontias meleagris*, *Feylinia currori*, and all descendants of their last common ancestor.

DIAGNOSIS: Scinciformes, as defined here and in the context of the current topology, are united by six unambiguous synapomorphies. These are 83(2) presence of an expansive nuchal fossa that extends well onto the parietal table, 181(1) Meckel's canal partly closed, but unfused, 192(0) coronoid process short and broad, 207(1) retroarticular process that is posteriorly expanded (broadened), 221(1) replacement teeth occur posterolingually with a small resorption pit, and 277(2) absence of an ectepicondylar groove and foramen.

COMMENTS: Scinciformes, as defined here, includes all the taxa usually considered Scincidae, plus Dibamidae, Amphisbaenia, and Serpentes (figs. 53–56). Scincidae sensu lato, the Scincidae of most recent authors (Estes et al., 1988; Wu et al., 1996; Evans and Barbadillo, 1998; Lee, 1998, 2000; Caldwell, 1999a, 2000; Lee and Caldwell, 2000; Reynoso and Callison, 2000), is paraphyletic in the current topology with respect to the Dibamidae, Amphisbaenia, and Serpentes. Rather than simply including dibamids, amphisbaenians, and snakes within Scincidae to maintain the ''subfamilies'' Feyliniinae, Acontinae, and Scelotinae, the traditional ''subfamilies'' are treated as ''families'' of scinciforms in the current taxonomic scheme.

The recovery of a clade containing skinks, dibamids, amphisbaenians, and snakes is not totally surprising. Morphologists have noted, for decades, the similarities between various limbless and limb-reduced skinks and all, or subsets, of these groups (Camp, 1923; Senn and Northcutt, 1973; Northcutt, 1978; Rieppel, 1980d, 1981a, 1984b; Greer, 1985) (see figs. 1, 14). Hallermann (1998) offered the first study to analyze the monophyly of scincids sensu lato (fig. 15). However, this is the first morphological analysis to include the appropriate taxonomic sampling (including both extant and fossil groups) to analyze this possible relationship. Even so, further analysis is necessary, especially in light of recent molecular studies suggesting a possible relationship between Serpentes and Iguania and between Amphisbaenia and Lacertidae (Harris et al., 2001; Townsend et al., 2004; Vidal and Hedges, 2004, 2005).

The current phylogenetic hypothesis suggests that the individual clades of scinciforms (including the clades usually considered to constitute Scincidae sensu lato) must have

been distinct by the end of the Early Cretaceous (fig. 56B). This hypothesized antiquity is somewhat surprising based on the nature of the fossil record of scincids, scelotids, feyliniids, acontids, and dibamids. However, recent molecular and molecular/biogeographic studies suggest that some nested scincid (sensu stricto) lineages may have been distinct by the beginning of the Oligocene (Hickson et al., 2000). Also, the morphology of the Cretaceous *Contogenys* is consistent with extant scincids.

Scelotidae + Scincophidia
(figs. 54C, 55C, 56B)

DIAGNOSIS: Scinciforms exclusive of Scincidae (in the current sense) are united by 10(0) absence of dermal sculpturing from the frontal and parietal, 26(0) absence of strong medial processes of the maxilla posterior to the premaxillary nasal process, 52(1) jugal lying mostly medial (rather than dorsal) to the maxilla, 69(0) absence of parietal tabs on the frontal, 74(0) absence of frontal tabs on the parietal, 175(1) absence of a clear posterior mylohyoid fenestra, 267(3) two or fewer sternal ribs, and 302(1) fusion of cephalic scales.

Scincophidia tax. nov.
(figs. 54C, 55C, 56B)

DEFINITION: *Feylinia currori*, *Acontias meleagris*, *Dibamus novaeguineae*, and all descendants of their last common ancestor.

ETYMOLOGY: *Skinkos* (Greek; a kind of lizard), in reference *Scincus* and to the larger, including clade (Scincoidea); *fidi* (Greek; ''snake'') in reference to the name (Ophidia) sometimes used for snakes, as a suffix for snake group names (e.g., Scolecophidia), or as a descriptor in naming snakelike taxa (e.g., *Ophisaurus*, *Ophiodes*). The name refers to the body form of these squamates, elongate and often limbless.

DIAGNOSIS: This clade is diagnosed by 28(1) midpoint/apex of the maxillary nasal process posterior to the midpoint of the maxilla, 57(0) anterior and posterior borders of the frontal of subequal width, 81(1) broad, flat dorsal margins to the supratemporal processes of the parietal, 95(1) absence of the postorbital, 117(1) ventromedial processes of

the pterygoids, 181(2) closed and fused Meckel's canal, 261(0) straight (nonangulate) clavicle, and 268(1) absence of the interclavicle.

COMMENTS: A possible relationship between scincomorphs and dibamids has been recognized for more than a century (Cope, 1900; Fürbringer, 1900a; Camp, 1923; Rieppel, 1984b), but recent cladistic studies (Wu et al., 1996; Evans and Barbadillo, 1998; Lee, 1998, 2000; Caldwell, 1999a; Lee and Caldwell, 2000) have suggested that dibamids probably belong to the gekkonomorph lineage (figs. 3, 4, 6–8). Importantly, the older studies considered independent groups of Scincidae sensu lato, but the more recent studies (those which suggest dibamids are related to gekkotans) have treated Scincidae sensu lato as a single taxon. Acontidae, Amphisbaenia, Dibamidae, Feyliniidae, and Serpentes form a clade under the current phylogenetic hypothesis and are included here in the Scincophidia (figs. 57, 58). However, only acontids, feyliniids, and dibamids are used as anchor taxa because their relationship has been the longest recognized and because of the relatively volatile nature of amphisbaenians and snakes in phylogenetic analyses. If dibamids should be shown to be gekkonomorphs, then Scincophidia becomes a junior subjective synonym for Scleroglossa. In this way, the taxon name may be effectively eliminated in the event of the gekkonomorph-dibamids hypothesis is shown to be a strong one.

Acontidae + Dibamidae +
Amphisbaenia + Serpentes
(figs. 54C, 55C, 56B)

DIAGNOSIS: These taxa form a clade within scincophidians based on 67(1) presence of a frontal-palatine contact, 83(0) absence of a parietal nuchal fossa (interpreted here as a reversal), 86(0) dorsal origin of the jaw adductor musculature on the parietal, 153(1) hypoglossal and vagus foramina confluent or subdivided within a single canal, 162(1) short tympanic crest on the quadrate, 184(0) presence of a large, posterodorsal, coronoid process of the dentary, 192(1) presence of a tall, narrow, coronoid process, 198(0) absence of a posterior overlap of the coronoid by the dentary, 209(0) absence of a tubercle on the medial surface of the retro-

articular process, and 321(1) absence of an external ear.

Dibamidae + Amphisbaenia + Serpentes
(figs. 54C, 55C, 56B)

DIAGNOSIS: This mostly limbless clade of scincophidians is diagnosed by 5(1) presence of an interorbital septum, 41(3) absence of the lacrimal, 98(1) absence of a squamosal, 101(0) absence of a palpebral, 132(2) absence of a crista prootica, 133(2) braincase closure primarily through downgrowth of the parietals, 137(0) absence of the crista alaris prootica, 140(1) entocarotid fossa indistinct/absent, 145(1) anterior opening of the Vidian canal opens dorsally on the dorsum sella, 151(1) anterior location for the spheno-occipital tubercle, 155(1) occipital recess visible in ventral view (not hidden by spheno-occipital tubercles), 159(3) quadrate suspended mostly from the opisthotic, 162(2) absence of a tympanic crest, 232(2) absence of distinct neural spines, 256(1) presence of a posterodorsal pseudotuberculum on the ribs, 305(0) dorsal body osteoderms absent, 307(0) ventral body osteoderms absent, 313(1) eyeball reduced and covered externally by a head scale, and 319(1) a flattened foretongue (see character description above, Estes et al., 1988, and Schwenk, 1988).

Dibamidae Boulenger, 1884
(figs. 54C, 55C, 56B)

DEFINITION: *Anelytropsis papillosus*, *Dibamus novaeguineae*, and all descendants of their last common ancestor.

DIAGNOSIS: *Dibamus* and *Anelytropsis papillosus* form a clade diagnosed by 12(2) mediolateral breadth of the premaxillary nasal process less than the dorsoventral depth, 32(2) palatine flange expanded posteromedially beyond the posterolateral process of the maxilla, 33(1) maxillary tooth row terminates at the level of the anterior border of the orbit, 146(2) prootic alone houses the external posterior opening of the Vidian canal, 188(2) splenial present, but fused to the postdentary bones, and 234(0) absence of oblique vertebral condyles.

COMMENTS: Only one of about 20 named species of *Dibamus* (Uetz, 2007) was included

in this analysis (*D. novaeguineae*). More species, possibly one including more plesiomorphic features (e.g., *D. bourreti*; see Iordansky, 1985), will be included in the future. However, available material and descriptions suggests that *Anelytropsis papillosus* retains more plesiomorphic features than any observed *Dibamus*.

Amphisbaenia + Serpentes
(figs. 54C, 55C, 56B)

DIAGNOSIS: Amphisbaenians and snakes are hypothesized to form a clade exclusive of other squamates in this analysis; a clade diagnosed by 28(0) midpoint/apex of maxillary nasal process at or anterior to the midpoint of the maxilla, 79(0) absence of a midline parietal flange, 110(0) absence of medial "step" to the palatine, 114(0) no development of the secondary palate, 117(0) absence of ventromedial processes (basipterygoid buttresses) on the pterygoid, 131(1) occipital condyle bipartite and constructed primarily by the exoccipital portions of the otooccipitals, 134(1) absence of an epipterygoid, 182(1) absence of a dentary shelf, 254(2) chevrons fused to the vertebrae, 284(2) pelvic bones with nonsutural contacts, 289(2) absence of a femur (note that this is reversed both within Amphisbaenia and Serpentes), and 317(4) foretongue divided for more than 50 percent of its length.

COMMENTS: The sister-group relationship between amphisbaenians and snakes was recently recovered by Evans and Wang (2005), a result duplicated here. Other recent studies have suggested that amphisbaenians and dibamids form the sister-taxon to snakes (Evans and Barbadillo, 1997, 1998, 1999; Evans et al., 2005). This hypothesis is consistent with the terrestrial origin of snakes, a hypothesis further supported by the recent discovery of *Najash rionegrina* (Apesteguía and Zaher, 2006); a taxon that will be included in future versions of this analysis.

Amphisbaenia Gray, 1844
(figs. 54C, 55C, 56B)

DIAGNOSIS: The current analysis recovers the following unambiguous synapomorphies

for Amphisbaenia: 32(0) absence of a maxillary palatine flange, 37(1) prefrontal-postfrontal/postorbitofrontal contact present, 67(0) frontal not contacting the palatines, 74(1) frontal tabs of the parietal present dorsally, 108(0) broad vomer-palatine contact, 123(1) pyriform recess narrow (see the character description above), 124(3) ectopterygoid-palatine contact closes the suborbital fenestra, 128(1) spheno-occipital epiphyses present, 158(1) streptostylic quadrate suspension, 222(1) presence of an enlarged medial premaxillary tooth, 296(1) presence of annular rings along the length of the body, 301(0) presence of cycloid scales, and 303(0) body scales not deeply imbricated.

COMMENTS: Estes et al. (1988) defined Amphisbaenia as a node. This would mean that fossil taxa related to amphisbaenians, but falling outside of the crown-group, would not be considered part of Amphisbaenia. The matter is largely semantic, but neither this analysis, nor that of Estes et al. (1988) include taxonomic sampling complete enough to warrant a definition of the name Amphisbaenia. Kearney (2003a) performed the most complete recent analyses, by far, of amphisbaenians, but did not formally define Amphisbaenia. I refrain from attaching a definition to the name.

Amphisbaenidae + *Bipes* + *Blanus* (figs. 54C, 55C)

DIAGNOSIS: The current analysis recovers two unambiguous synapomorphies joining amphisbaenids, *Bipes biporus*, and the genus *Blanus*. These are 91(1) absence of a postfrontal and 252(0) caudal autotomy planes present on the transverse processes.

Bipes + *Blanus* (figs. 54C, 55C)

DIAGNOSIS: This unnamed clade is diagnosed, in this analysis, by 119(0) presence of a pterygoid-vomer contact, 158(0) absence of an anteriorly elongate extracolumella, 260(0) rodlike clavicles, 265(1) scapula shorter than the coracoid, and 289(0) cylindrical femur with moderately expanded proximal and distal ends.

Serpentes Linnaeus, 1766 (figs. 54C, 55C, 56B)

DEFINITION: *Typhlops lineolatus ater*, *Anomalepis mexicanus*, *Vipera aspis*, *Python molurus*, and all descendants of their last common ancestor.

DIAGNOSIS: This clade is diagnosed by 16(1) nonsutural contacts between the premaxilla and maxilla, 29(1) weakly inclined anterior margin of the maxillary nasal process, 31(0) paleochoanate condition, 61(3) subolfactory processes of the frontal contact the parasphenoid, 65(0) frontal fails to contact the maxilla, 91(1) absence of a postfrontal, 135(1) absence of a processus ascendens tecti synotici, 150(2) elongate, posterolaterally directed, spheno-occipital tubercles, 167(1) absence of a mandibular symphysis, 180(0) dentary extends posteriorly no further than the coronoid process, 181(0) Meckel's canal open, 184(2) absence of a posterodorsal coronoid process on the dentary, 187(2) dentary primarily supported by the surangular, 190(1) posterior terminus of the splenial at or anterior to the coronoid apex, 191(2) presence of an intramandibular joint in which the angular receives the splenial, 194(1) anterior end of coronoid abutting the dentary (rather than overlapping it), 210(0) retroarticular process without torsion, 214(2) "modified pleurodont" dental attachment (sensu Zaher and Rieppel, 1999a), and 235(2) presence of zygosphenes which face ventrolaterally (fig. 44B).

COMMENTS: The definition of Serpentes as a node containing extant snakes here is in keeping with those of previous such definitions and applications of the group name (Rage, 1984; Estes et al., 1988; Lee, 1997, 1998, 2000, 2001; Lee and Caldwell, 2000; Caldwell, 1999a; Apestiguía and Zaher, 2006). Under this definition, Ophidia might be invoked as a stem-based name to include taxa that would be identified as snakes, but which fall outside of the crown group (e.g., *Najash rionegrina*; Apestiguía and Zaher, 2006).

Liotyphlops albirostris + *Typhlops lineolatus* (figs. 54C, 55C, 56B)

DIAGNOSIS: *Liotyphlops albirostris* and *Typhlops lineolatus* (representatives of Anomalepidae and Typhlopidae, respectively, in
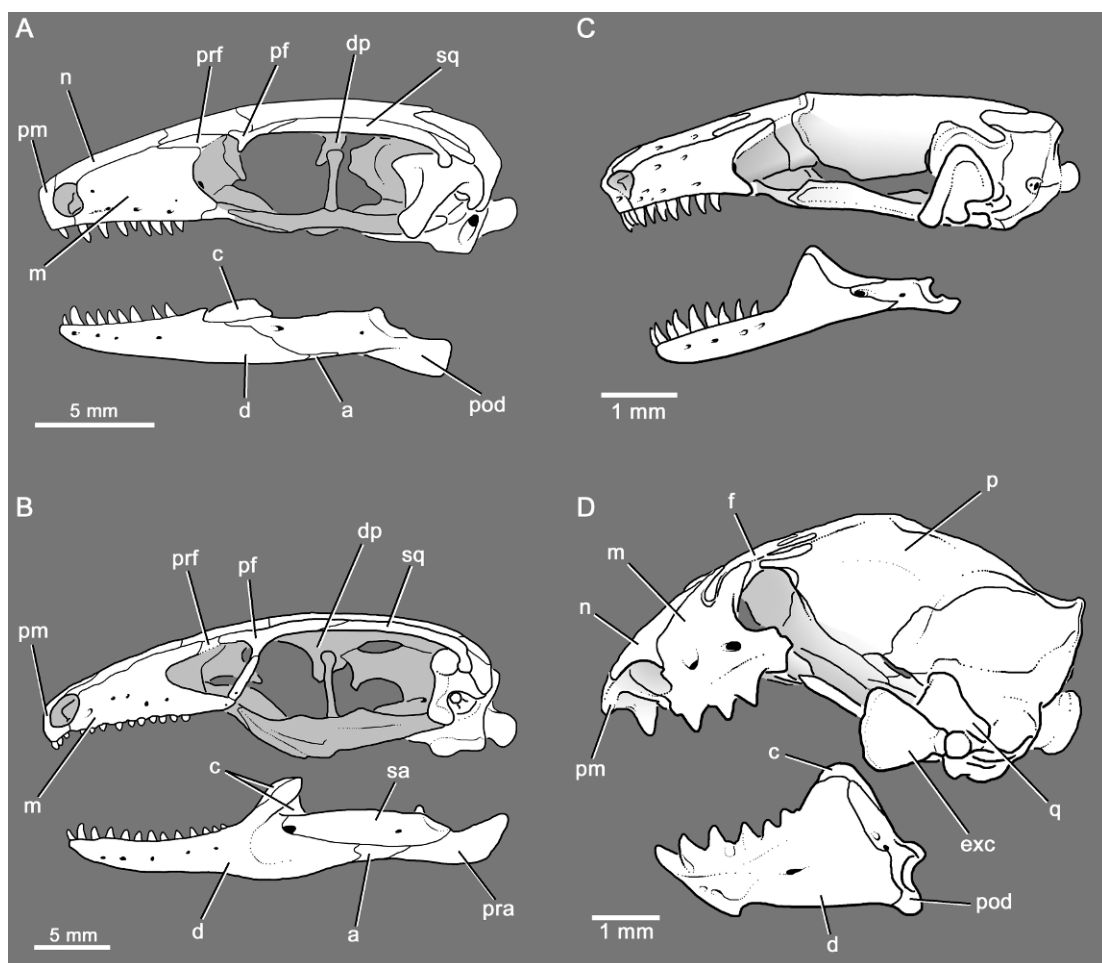
Fig. 57. The skulls of some representative, nonsnake scincophidians in left lateral view. **(A)** *Feylinia elegans*, **(B)** *Acontias plumbeus*, **(C)** *Dibamus novaeguineae*, and **(D)** *Diplometopon zarudnyi*. Note the progressive development of the descending processes of the frontals, descending processes of the parietals, and coronoid process of the dentary. Modified after **(A–B)** Rieppel, 1981a, **(C)** Rieppel (1984b) and Greer (1985), and **(D)** Maisano et al. (2005; 2006).

this analysis) are joined by three unambiguous synapomorphies. These are 28(3) extremely foreshortened maxilla, 111(2) palatine deeper than long, and 112(1) vomer much longer than the palatine.

COMMENTS: The current analysis finds support for Scolecophidia in a majority of the principle trees, but it is not supported in the strict nor the Adams consensus (figs. 54 and 55, respectively). In this analysis, *Leptotyphlops goudottii*, the only other putative scolecophidian included in this analysis, is

recovered as the sister-taxon to a clade composed of *Liotyphlops albirostris* and *Typhlops lineolatus*, as the sister taxon to all other snakes, or as the sister taxon to a clade containing Alethinophidia, *Dinilysia patagonica*, *Pachyophis woodwardi*, and *Wonambi naracoortensis*. Future analyses (with more inclusive taxon and character sampling) will more completely address this issue.

Note that McDowell and Bogert (1954) challenged the idea that typhlopids and anomalepids are snakes and suggested that
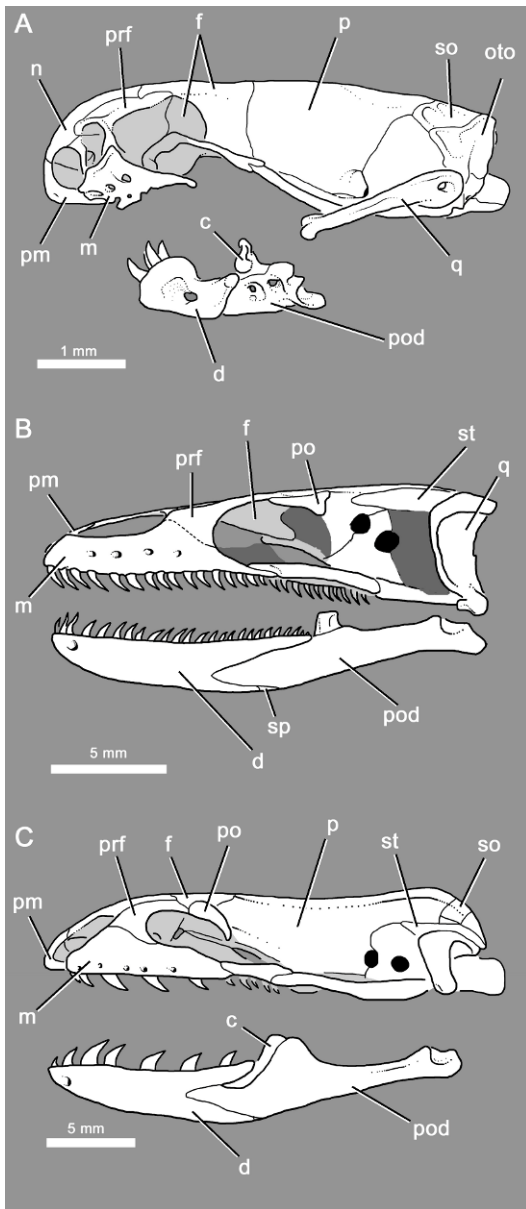
Fig. 58.   The skulls of three snakes that have, at some point, been considered close to the ancestral morphology for Serpentes. **(A)** *Leptotyphlops goudottii dulcis*, **(B)** *Haasiophis terrasanctus*, and **(C)** *Cylindrophis ruffus*. *Leptotyphlyops dulcis* is an extant burrowing form with greatly reduced eyes, *H. terrasanctus* is an aquatic Cretaceous fossil snake with legs, and *C. ruffus* is an extant burrower that is less specialized for fossoriality than *L. dulcis*. Modified after **(A)** Kley (2004; 2006), **(B)** Tchernov et al. (2000) and Rieppel et al. (2003), and **(C)** Rieppel (1983).

they are anguids. This hypothesis was never widely accepted and no subsequent study has recovered non-holophyly of snakes. Snake holophyly is analyzed and supported by this analysis.

Oculatophidia tax. nov.
(figs. 54C, 55C, 56B)

DEFINITION: All taxa sharing a more recent common ancestor with *Coluber constrictor* and *Anilius scytale* than with *Leptotyphlops goudottii bilineatus*, *Anomalepis mexicanus*, or *Typhlops lineolatus jaimacensis*.

ETYMOLOGY: *Oculatus* (Latin; ''having eyes'' or ''conspicuous''); *fidi* (Greek; ''snake'') in reference to the name (Ophidia) sometimes used for snakes and as a suffix for snake group names. The name used here is in reference to the basal dichotomy between blindsnakes (scolecophidians) and all other snakes (the group here named; nonblind snakes), and in reference to the more conspicuous nature of these snakes (as compared to blindsnakes) today and in the fossil record.

DIAGNOSIS: This clade is diagnosed by 6(1) posteriorly elongated nares, 74(1) frontal tabs of the parietal present dorsally, 87(0) presence of a supratemporal, 115(2) palatine teeth arranged in a single line, 118(1) pterygoid teeth arranged in a single line, 124(0) absence of a contact between the ectopterygoid and palatine anterior to the suborbital fenestra, 131(0) occipital condyle a single unit made of the otooccipitals and basioccipital, 159(2) quadrate suspended mainly from the supratemporal, 163(1) presence of a quadrate suprastapedial process, 168(1) adductor fossa with a distinct vertical flange, 192(0) coronoid process short and broad, 214(3) tooth bases enclosed by an expanded interdental ridge, and 232(0) presence of short and broad neural spines.

COMMENTS: The interrelationships between *Dinilysia patagonica*, Alethinophidia, and a clade containing *Pachyophis woodwardi* and *Wonambi naracoortensis* are unresolved in this analysis. Principle trees variably suggest that *Dinilysia patagonica* is the basal most member of this clade or that it is the

sister-taxon to the *Pachyophis woodwardi–Wonambi naracoortensis* clade. Future inclusion of more putative "madtsoiids" and *Najash* may help to more completely resolve these relationships.

Pachyophis woodwardi + *Wonambi naracoortensis*
(figs. 54C, 55C, 56B)

DIAGNOSIS: *Pachyophis woodwardi* and *Wonambi naracoortensis* share one unambiguous synapomorphy: 186(1) angular process of dentary terminates anterior to the level of the coronoid process.

COMMENTS: The relationship between *Pachyophis woodwardi* and *Wonambi naracoortensis* is only weakly supported, probably relating to the relative completeness of both taxa and the small amount of known morphological overlap. This possible relationship requires further study.

Alethinophidia Nopcsa, 1923b
(figs. 54C, 55C, 56B)

DEFINITION: The most recent ancestor of extant taxa more closely related to *Coluber constrictor* and *Anilius scytale* than to *Leptotyphlops goudottii bilineatus*, *Anomalepis mexicanus*, or *Typhlops lineolatus jaimacensis*.

DIAGNOSIS: Alethinophidians are diagnosed in this study by 110(1) palatines with medial expansion anteriorly, 126(0) absence of ectopterygoid exposure on the lateral surface of the skull behind the maxilla, and 143(1) posterolateral sphenoid flanges ventrolaterally overlying the basioccipital.

COMMENTS: Rage (1984) described a basal dichotomy in Serpentes between Scolecophidia and Alethinophidia, an approach to modern snakes informally applied by various authors (see Lee, 2001; Scanlon and Lee, 2002; Kelly et al., 2003). However, *Dinilysia patagonica* has been excluded from Alethinophidia whenever it is mentioned explicitly (e.g., Caldwell, 1999a; Rieppel et al., 2002, 2003; Apesteguía and Zaher, 2006). The current definition of Alethinophidia reflects the latter usage in which Alethinophidia is a node-based name including extant non-scolecophidian snakes.

Macrostomata Müller, 1831
(figs. 54C, 55C, 56B)

DEFINITION: All taxa sharing a more recent common ancestor with *Coluber constrictor* than with *Anilius scytale*, *Cylindrophis ruffus*, or *Uropeltis ceylanicus*.

DIAGNOSIS: The six unambiguous macrostomatan synapomorphies recovered in this analysis are 1(1) snout makes up greater than 30 percent of the total skull length, 28(2) dorsal and ventral margins of the maxilla subparallel, 64(1) presence of a contact between the medial frontal pillar and the lateral subolfactory flanges, 107(1) a rod-shaped vomer, 137(1) presence of a short crista prootica, and 178(0) dentary ventrally convex along its long axis.

COMMENTS: The definition of Macrostomata offered here is in line with the common usage of the name. Macrostomata is typically regarded as including all non-anilioid alethinophidians. Anilioid monophyly is not analyzed here, thus the type species from each of the three anilioid clades (*Anilius*, *Cylindrophis*, and Uropeltidae) are used in the definition. Anilioid monophyly will be further analyzed elsewhere.

Pachyrhachidae + "neo-Macrostomata"
(figs. 54C, 55C)

DIAGNOSIS: Pachyrhachids and more derived macrostomatans form a clade diagnosed by 108(2) absence of an articulation between the vomer and palatine, 127(1) presence of a ventral sagittal ridge on the sphenoid and basioccipital, and 163(0) absence of a suprastapedial process (interpreted as a reversal here).

Pachyrhachidae comb. nov.
(figs. 54C, 55C)
(*Pachyrhachis problematicus* from Haas, 1979)

DEFINITION: All taxa sharing a more recent common ancestor with *Pachyrhachis problematicus* than with *Coluber constrictor*.

DIAGNOSIS: *Pachyrhachis problematicus*, *Haasiophis terrasanctus*, and *Eupodophis descouensi* form a clade exclusive of other macrostomatans, diagnosed by 95(0) pres-

ence of a postorbital, 192(1) presence of a tall, narrow, coronoid process, and 290(0) presence of a pes with metatarsals and digits (see fig. 47).

Anguimorpha Fürbringer, 1900a
(figs. 54C, 55C, 56B)

DEFINITION: All taxa sharing a more recent common ancestor with *Anguis fragilis* and *Varanus varius* than with *Scincus scincus*, *Cordylus cordylus*, or *Iguana iguana*.

DIAGNOSIS: Anguimorphs are diagnosed by two unambiguous synapomorphies; 8(1) presence of dermal sculpturing on the maxilla and 209(0) absence of a tubercle on the medial surface of the retroarticular process.

COMMENTS: Estes et al. (1988) defined Anguimorpha as a crown-node, but the taxon is typically used to receive all nonscincomorph autarchoglossans and it is so defined here. Importantly, no previous analysis has addressed noncrown anguimorph relatives. Many of the basal most members of this clade were originally described as scincomorphs (e.g., ''*Pseudosaurillus*'' sp., *Paramacellodus oweni*, *Becklesius hoffstetteri*, *Pseudosaurillus becklesi*, *Meyasaurus diazromerali*, and *Eolacerta robusta*) or gekkotans (*Yabeinosaurus tenuis*) (see Endo and Shikama, 1942; Hoffstetter, 1967a; Prothero and Estes, 1980; Estes, 1983; Borsuk-Białynicka, 1985; Broschinski and Sigogneau-Russell, 1996; Evans and Barbadillo, 1998; Evans and Chure, 1998a; Averianov and Skutchas, 1999; Reynoso and Callison, 2000; Müller, 2001). The incomplete nature of taxa such as '''*Pseudosaurillus*' sp.'' (sensu Estes, 1983), *Paramacellodus oweni*, and *Becklesius hoffstetteri*, is probably to blame for the relative paucity of unambiguous anguimorph synapomorphies.

Anguimorpha exclusive of ''*Pseudosaurillus*'' sp.
(figs. 54D, 55D, 56C)

DIAGNOSIS: The clade containing all anguimorphs except ''*Pseudosaurillus*'' sp. may be diagnosed by 182(0) presence of a subdental shelf.

Anguimorpha exclusive of ''*Pseudosaurillus*'' sp. and *Paramacellodus oweni*

DIAGNOSIS: This clade is supported by only one unambiguous synapomorphy: 166(0) absence of fusion between the articular-prearticular and the surangular.

Eolacerta robusta + *Meyasaurus diazromerali* + *Pseudosaurillus beckelsi* + *Yabeinosaurus tenuis* + Anguiformes
(figs. 54D, 55D, 56C)

DIAGNOSIS: The clade formed by this unresolved trichotomy is here diagnosed by three unambiguous synapomorphies, including 26(0) absence of strong medial processes of the maxilla posterior to the premaxillary nasal process, 176(0) posterior mylohyoid foramen located anterior to the coronoid apex, and 185(1) presence of distinct subcoronoid and surangular processes of the dentary.

Eolacerta robusta + *Meyasaurus diazromerali* + *Pseudosaurillus beckelsi*
(figs. 55D, 56C)

DIAGNOSIS: This unnamed clade is diagnosed, in this analysis, by 21(1) nasals that are in contact for less than half their length in dorsal view and 203(1) presence of a prearticular crest.

Meyasaurus diazromerali + *Pseudosaurillus becklesi*
(figs. 55D, 56C)

DIAGNOSIS: These taxa share 182(2) presence of an enlarged subdental shelf and 277(2) absence of an ectepicondylar groove and foramen.

Yabeinosaurus tenuis + Anguiformes
(figs. 55D, 56C)

DIAGNOSIS: *Yabeinosaurus tenuis* and anguiforms form a clade exclusive of all other squamates diagnosed by 26(0) absence of strong medial processes of the maxilla posterior to the premaxillary nasal process, 176(1) position of the posterior mylohyoid foramen posterior to the coronoid apex, and 185(1) presence of distinct subcoronoid and surangular processes of the dentary.

COMMENTS: Evans et al. (2005) recently redescribed *Y. tenuis* and inserted it into some recent phylogenetic data matrices. They found *Y. tenuis* to be a basal scleroglossan or as the immediate outgroup to crown-squamates (Evans et al., 2005). The current analysis produces a markedly different result, suggesting that *Y. tenuis* is a basal anguimorph, close to the crown group.

Anguiformes Conrad, 2006b
(figs. 54D, 55D, 56C)

DEFINITION: *Anguis fragilis*, *Varanus varius*, and all descendants of their last common ancestor.

DIAGNOSIS: This analysis recovers five unambiguous synapomorphies for anguiforms. These are 74(0) absence of frontal tabs on the parietal, 76(1) presence of an anteroposteriorly elongate decensus parietalis, 198(0) absence of a posterior overlap of the coronoid by the dentary, 221(1) replacement teeth occur posterolingually with a small resorption pit, and 260(0) clavicles lacking proximal expansion; thus, rod-like.

COMMENTS: The phylogenetic topology presented in this analysis differs from that of Conrad (2006b) in the placement of *Carusia* and Xenosauridae. The earlier analysis found *Carusia* and Xenosauridae to be successively more proximal outgroups to a clade containing anguids, shinisaurids, and varanoids (Conrad, 2006b), but the present study recovers a monophyletic Carusioidea (sensu Gao and Norell, 1998, 2000; see below) as the sister-taxon to a clade containing modern anguids (figs. 54D, 55D). Regardless, the name Anguiformes is retained and maintains its meaning as a clade containing anguids and varanoids (among others) to the exclusion of more basal anguimorphs (e.g., *Yabeinosaurus*).

Note that Diploglossa might have been an alternative name for this clade or even for the clade described above as Anguimorpha if not for re-definition of that name (Lee, 1998). That definition, "The least inclusive clade containing [Cordylidae, Scincidae, Anguidae, Xenosauridae, Helodermatidae, *Lanthanotus borneensis*, and *Varanus*] to the exclusion of [Rhynchocephalia, Iguanidae, Agaminae, *Leiolepis*, *Uromastyx*, Chamaeleonidae, Xan-

tusiidae, Eublepharinae, Diplodactylinae, Gekkoninae, Pygopodidae, Lacertidae, Teiidae, and Gymnophthalmidae]" (Lee, 1998: 436) describes a paraphyletic group in this phylogenetic hypothesis. If that group name is made monophyletic by amending the definition to fewer excluded taxa, then the name becomes a synonym for Autarchoglossa. However, traditional usage of Diploglossa (see, for example Romer, 1956; Estes, 1983; Estes and Pregill, 1988; Uetz, 2007) does not intend the inclusion of scincomorphs such as Cordyliformes or Scincidae.

Carusioidea + Anguidae
(figs. 54D, 55D, 56C)

DIAGNOSIS: The current phylogenetic hypothesis suggests a sister-group relationship between carusioids and anguids based on 69(0) absence of parietal tabs on the frontal, 285(2) symphysial portion of the pubis more than half again as long as the tubercular portion, and 351(1) absence of the M. adductor mandibulae.

COMMENTS: Caldwell (1999a) recently recovered support for a monophyletic clade including xenosaurids and anguids in a clade roughly corresponding with the traditional usage of Anguioidea (McDowell and Bogert, 1954; Romer, 1956; Carroll, 1988b; Uetz, 2007). Importantly, analysis of a preliminary version of this data set did not recover a carusioid-anguid clade (Conrad, 2005a), nor did other recent osteological studies (Wu et al., 1996; Evans and Barbadillo, 1997, 1998; Gao and Norell, 1998; Lee, 1998, 2000, 2005a; Evans and Barbadillo, 1999; Conrad, 2004b, 2006b; Evans and Wang, 2005; Evans et al., 2005;). Importantly, Townsend (2002) offered preliminary results of an analysis based on molecular data supporting a similar hypothesis, published in full by Townsend et al. (2004). Although these analyses find *Heloderma* as the sister-taxon to Anguidae, a hypothesis not supported by the present morphological data set, they did consistently recover a clade containing *Xenosaurus* and Anguidae to the exclusion of *Shinisaurus* and Varanidae in their maximum-likelihood trees.

The greater taxonomic and character sampling of the present study as compared to previous morphological analyses suggests

greater credibility of the current phylogenetic hypothesis. This is bolstered by a general similarity between the phylogenetic topology supported by molecular data. Even so, the monophyly of the carusioid-anguid taxon and of Varanoidea should be further analyzed.

Carusioidea Gao and Norell, 1998
(figs. 54D, 55D, 56C)

DEFINITION: *Carusia intermedia*, *Xenosaurus grandis*, and all descendants of their last common ancestor.

DIAGNOSIS: *Carusia intermedia* and xenosaurids share the following unambiguous synapomorphies: 50(1) dermal rugosities on the postorbital process of the jugal, 53(1) presence of a jugal-squamosal contact, 55(1) fused frontals, 61(0) subolfactory processes present as simple ventral downgrowths, 94(1) fused postorbitofrontal, 96(0) postorbital extends posteriorly for less than one-half the length of the supratemporal fenestra, 100(0) presence of a dorsal process on the squamosal, 115(1) absence of palatine teeth, 166(1) articular-prearticular fused to the surangular, and 193(2) presence of a well-developed coronoid labial flange that extends posterior to the main body of the coronoid process in lateral view.

COMMENTS: Gao and Norell (1998) defined Carusioidea as a node anchored to *Carusia intermedia* and their Xenosauridae, the latter including *Shinisaurus crocodilurus* according to their analysis. Here, the definition is modified such that it is anchored to the type species of the Xenosauridae and *Carusia*.

The carusioid clade has remained largely untested since Gao and Norell (1998) proposed it. Conrad (2006b) found no support for the clade. The current analysis incorporates much broader taxonomic and character sampling, though, and recovers a monophyletic Carusioidea, albeit without the inclusion of *Shinisaurus crocodilurus*.

Xenosauridae Cope, 1886
(figs. 54D, 55D, 56C)

DEFINITION: All taxa sharing a more recent common ancestor with *Xenosaurus grandis* than with *Anguis fragilis*, *Carusia intermedia*, or *Varanus varius*.

DIAGNOSIS: Xenosaurids share two unambiguous synapomorphies: 126(1) ectopterygoid exposed on the lateral skull surface posterior to the maxilla and 212(3) presence of "shoulders" or incipient cusps on the posterior marginal teeth.

COMMENTS: Common usage and phylogenetic definitions of Xenosauridae have been anchored to *Xenosaurus* and *Shinisaurus* (McDowell and Bogert, 1954; Gauthier, 1982; Estes, 1983; Estes et al., 1988; Presch, 1988; Wu et al., 1996; Lee, 1998; Lee and Caldwell, 2000). However, *Shinisaurus* shows morphological affinities with platynotans (see below) and no special affinity for xenosaurids (Conrad, 2004a, 2004b, 2005a, 2006a, 2006b) (figs. 54–56). Recent molecular work supports a similar hypothesis, suggesting that *Shinisaurus* is related to varanids (Townsend et al., 2004) (fig. 10A).

Restes rugosus is usually considered to have affinities with *Xenosaurus* and was initially considered a species of *Exostinus* (Gilmore, 1942a; Estes, 1965, 1975). Although Conrad (2006b) was unable to resolve the placement of *R. rugosus*, perhaps due to the incompleteness of that and other taxa, the current analysis supports the hypothesis that it is a xenosaurid.

The current definition of Xenosauridae takes into account the problematic relationships of both *Shinisaurus* and *Restes*. Although the data analyzed here strongly suggest that *Shinisaurus* is not a member of the xenosaurid radiation, the current definition of Xenosauridae would allow inclusion of *Shinisaurus* should the topology of, for example, Lee and Caldwell (2000) (fig. 7) prove accurate.

Note that *Xenosaurus* is included here as a composite taxon based on observations of *X. grandis* and *X. platyceps*. Future versions of this data matrix may include codings for some individual *Xenosaurus* species.

Exostinus Cope, 1873
(figs. 54D, 55D)

DEFINITION: *Exostinus serratus*, *E. lancensis*, and all descendants of their last common ancestor.

DIAGNOSIS: The two included species of *Exostinus* are united by 310(1) presence of thickened, irregularly shaped, osteoderms.

COMMENTS: *Exostinus serratus* and *E. lancensis* are nearly identical in the 42 characters for which they may both be scored. *Exostinus lancensis* possesses more well-developed subolfactory processes than *E. serratus*, but this is the only observed coding difference between the two for this analysis. Given the incomplete nature of the remains for both species, however, more difference might appear with the discovery of more complete remains for one or both species. Indeed, a preliminary review of available material suggests that *Exostinus* may be a paraphyletic assemblage of three or more taxa (Bhullar, 2007).

Anguidae Gray, 1825
(figs. 54D, 55D, 56C)

DEFINITION: *Anguis fragilis*, *Gerrhonotus liocephalus*, *Diploglossus fasciatus*, and all descendants of their last common ancestor.

DIAGNOSIS: Anguids form a clade diagnosed by 9(0) absence of dermal sculpturing on the prefrontal, 10(0) absence of dermal sculpturing from the frontal and parietal, 31(1) neochoanate condition, 58(0) linear interorbital margins of the frontal, 67(1) presence of a frontal-palatine contact, 171(2) free posteroventral margin of the intramandibular septum, 183(2) dentary contributing to dorsal and anterior margin of the anterior inferior alveolar foramen, 207(1) retroarticular process that is posteriorly expanded (broadened), 210(2) strongly twisted retroarticular process, 254(2) chevrons fused to the vertebrae, and 304(1) presence of a lateral body fold.

COMMENTS: The definition of Anguidae used here follows that of Estes et al. (1988), but uses more specific anchor taxa. Note that if glyptosaurines are found to be outside of crown-anguids, then they must be considered distinct from Anguidae following this definition. However, the current analysis supports the general hypothesis of Gauthier (1982) that glyptosaurines are nested within extant anguids (figs. 54–56).

Gerrhonotinae McDowell and Bogert, 1954
(figs. 54D, 55D, 56C)

DEFINITION: All taxa sharing a more recent common ancestor with *Gerrhonotus liocephalus* than with *Anguis fragilis*, *Anniella pulchra*, or *Diploglossus fasciatus*.

DIAGNOSIS: The current analysis recovers five unambiguous gerrhonotine synapomorphies based on the included taxa, these are 88(1) supratemporal elongate, 173(1) coronoid contribution to the external border of the anterior surangular foramen, 186(1) angular process of dentary terminates anterior to the level of the coronoid process, 251(2) double, converging, caudal transverse processes, and 312(1) presence of keeled body osteoderms.

COMMENTS: The position of *Parophisaurus pawneensis* (=?*Xestops pawneensis* Gilmore, 1928; =*Pancelosaurus pawneensis* Meszoely, 1970; =*Odaxosaurus pawneensis* Meszoely et al., 1978) as a basal gerrhonotine in this analysis is unexpected. Sullivan (1987) regarded *P. pawneensis* as a proximal outgroup to the North American anguine *Ophisaurus*, but did not offer a cladistic analysis. Sullivan (1987) further cautioned, however, that *P. pawneensis* is a difficult taxon to interpret because it is relatively plesiomorphic in much of its known morphology. A preliminary phylogenetic study of squamates suggested that *P. pawneensis* is the sister-taxon to a clade containing Anguinae and Diploglossinae (Conrad, 2005a). Comparisons of *Parophisaurus pawneensis* (AMNH FR8711) with extant taxa reveal that *Parophisaurus pawneensis* more closely resembles *Ophisaurus ventralis* than *Gerrhonotus liocephalus* in muzzle shape, dermal sculpturing, possessing extensive internasal contact, and in the relative contribution of the dentary to the anterior inferior alveolar foramen margin, but this parsimony analysis interprets those similarities as plesiomorphies or convergence.

Gerrhonotines are interpreted by this analysis to be the basalmost lineage of Anguidae. Although *P. pawneensis* is from the Middle Oligocene, the gerrhonotine lineage must have been distinct by the Late Cretaceous.

Paragerrhonotus ricardensis + Extant Gerrhonotines
(figs. 54D, 55D)

DIAGNOSIS: This clade is supported by 7(1) presence of pitted dermal sculpturing, 21(1) nasals that are in contact for less than half their length in dorsal view, 55(1) fused frontals, and 183(1) dentary forming the dorsal border of the anterior inferior alveolar foramen.

Extant Gerrhonotine radiation
(figs. 54D, 55D)

DIAGNOSIS: The extant gerrhonotines used in this analysis are considered to form a clade exclusive of *Paragerrhonotus ricardensis* based on the presence of three unambiguous synapomorphies. These are 61(0) subolfactory processes present as simple ventral downgrowths, 219(1) striated tooth crowns, and 226(1) chisel shaped posterior teeth.

COMMENTS: The present analysis does not sample densely enough to meaningfully analyze the interrelationships of extant gerrhonotines. Therefore, this clade is not named and the further relationships of the gerrhonotines are not reported here.

Anguinae + Diploglossinae + Glyptosaurinae
(figs. 54D, 55D, 56C)

DIAGNOSIS: This unnamed clade is diagnosed by 8(0) absence of dermal sculpturing on the maxilla and 120(0) vomer contact posteriorly invaded by the pyriform recess.

Anguinae Gray, 1825
(figs. 54D, 55D, 56C)

DEFINITION: All taxa sharing a more recent common ancestor with *Anguis fragilis* than with *Diploglossus fasciatus*, *Gerrhonotus liocephalus*, or *Glyptosaurus sylvestris*.

DIAGNOSIS: Anguines are diagnosed by 74(1) frontal tabs of the parietal present dorsally, 84(1) increased contact between the parietal and supratemporal arch, resulting in reduction of the supratemporal fenestra, 117(1) presence of ventromedial processes of the pterygoids, 140(1) entocarotid fossa indistinct/absent, 233(1) presence of precon-

dylar constriction, 275(4) absence of a humerus, and 290(1) pes absent.

COMMENTS: Sullivan (1987) suggested that anguines were non-monophyletic, but with respect to which groups, he gave no indication. Indeed, Sullivan (1987: fig. 9) produced a phylogenetic diagram showing a monophyletic Anguinae (fig. 59). Ironically, the current topology (fig. 54–56) suggests that Sullivan's (1987) Anguinae is polyphyletic because *Parophisaurus*, nested taxa within Anguinae according to Sullivan, is a basal gerrhonotine according to the current analysis.

Anguinae exclusive of *Ophisaurus ventralis*
(figs. 54D, 55D)

DIAGNOSIS: Anguines exclusive of *Ophisaurus ventralis* form a clade diagnosed by 162(1) short tympanic crest on the quadrate, 183(1) dentary forming the dorsal border of the anterior inferior alveolar foramen, 239(0) horizontal dorsal margin of the atlas in lateral view, 264(1) absence of a contact between the epicoracoid and suprascapula, 265(1) scapula shorter than the coracoid, and 284(2) pelvic bones with nonsutural contacts.

Anguinae exclusive of *Ophisaurus ventralis* and ''*O.*'' *attenuatus*
(figs. 54D, 55D)

DIAGNOSIS: This unnamed clade is diagnosed by 126(1) ectopterygoid exposed on the lateral skull surface posterior to the maxilla, 186(1) angular process of dentary terminates anterior to the level of the coronoid process, and 251(2) double, converging, caudal transverse processes.

Anguini Augé, 2005
(figs. 54D, 55D)

DEFINITION: *Anguis fragilis*, *Pseudopus apodus*, and all descendants of their last common ancestor.

DIAGNOSIS: This clade is diagnosed by 47(1) jugal curved (rather than angulated), 67(0) frontal not contacting the palatines, 240(1) lateral processes of the atlas reduced, and 269(0) absence of an anterior process of the interclavicle.

COMMENTS: Anguins include *Anniella* and *Pseudopus apodus*; one of the more often sampled and illustrated species of ''*Ophi-*

saurus''. *Anniella* is sometimes separated into its own "family" Anniellidae (for a history of the phylogenetic and taxonomic placements of *Anniella*, see Gao and Norell, 1998). Importantly, the current analysis does not find a close relationship between *Anniella* and *Apodosauriscus minutus*, in contrast to the findings of Gauthier (1982). However, additional, undescribed, remains of *Apodosauriscus* (mentioned in Gauthier, 1982) will add critical data to the analysis and may bolster Gauthier's (1982) hypothesis upon their description. Even so, the current phylogenetic hypothesis reflects available data, suggesting that *Anniella* is an anguin close to *Anguis*.

Pseudopus apodus + Ophisauriscus quadrupes
(figs. 54D, 55D)

DIAGNOSIS: This unnamed clade is supported by 61(0) subolfactory processes present as simple ventral downgrowths, and 312(1) presence of keeled body osteoderms.

COMMENTS: Sullivan et al. (1999) recently redescribed *Ophisauriscus quadrupes* and offered important new details of its morphology from x-rays. These data help identify the presence of a limbed anguid (*Ophisauriscus*) nested within Anguini.

Anguis fragilis + Anniella pulchra
(figs. 54D, 55D)

DIAGNOSIS: This unnamed clade is supported by 14(0) single-lobed incisive process, 23(1) frontal forms a single anterior wedge, 39(0) absence of a prefrontal-jugal contact, 82(0) presence of a transverse posterior margin of the parietal between the supratemporal processes, 88(1) elongate supratemporal, 115(1) absence of palatine teeth, 175(1) absence of a clear posterior mylohyoid foramen, 183(2) dentary contributing to dorsal and anterior margin of the anterior inferior alveolar foramen, 189(1) splenial not extending anterior to the midpoint of the dentary tooth row, 211(1) marginal teeth widely separated, 233(0) absence of precondylar constriction in the vertebrae, and 304(0) absence of a lateral fold in the body squamation.

COMMENTS: As described by Gao and Norell (1998), the placement of *Anniella* (*A. pulchra* included here) has been problematic. However, the present analysis duplicates the

findings of Gao and Norell (1998) adding support for the hypothesis that *Anguis* and *Anniella* are sister taxa.

Diploglossinae + Glyptosaurinae
(figs. 54D, 55D, 56C)

DIAGNOSIS: The unnamed clade including diploglossines and glyptosaurines is diagnosed in this analysis by 166(1) articular-prearticular fused to the surangular, 201(1) angular extends anteriorly into the mental canal, and 254(1) anterior positioning of the chevrons.

Diploglossinae Cope, 1864
(figs. 54D, 55D, 56C)

DEFINITION: All taxa sharing a more recent common ancestor with *Diploglossus fasciatus* than with *Anguis fragilis*, *Glyptosaurus sylvestris*, or *Gerrhonotus liocephalus*.

DIAGNOSIS: The current analysis recovers two unambiguous synapomorphies for Diploglossinae as defined here: 178(0) dentary ventrally convex along its long axis and 186(1) angular process of dentary terminates anterior to the level of the coronoid process.

COMMENTS: The current analysis suggests a sister-group relationship between extant diploglossines and *Apodosauriscus minutus*, the latter having been originally described as close to *Anniella*. The current phylogenetic hypothesis should be further analyzed. Importantly, Wiens and Slingluff (2001) recovered a sister-taxon relationship between *Anniella* and diploglossines and Gauthier (1982) suggested that *Anniella* and *Apodosauriscus* are each other's closest known relatives.

Celestus costatus + Diploglossus millepunctatus + Ophiodes sp.
(figs. 54D, 55D)

DIAGNOSIS: The extant diploglossines included in this analysis form a clade diagnosed by 7(1) presence of pitted dermal sculpturing, 57(0) anterior and posterior borders of the frontal of subequal width, 61(0) subolfactory processes present as simple ventral downgrowths, 183(0) dentary does not contribute to the anterior inferior alveolar foramen margin, and 301(1) presence of cycloid scales.
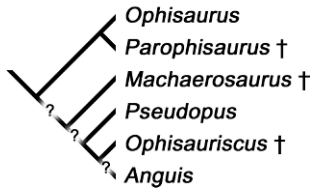
Fig. 59. Relationships of the anguine anguids according to Sullivan (1987). Fossil taxa denoted by daggers (†).

COMMENTS: The current analysis does not sample densely enough from diploglossines for further discussion of their relationships.

Glyptosaurinae Marsh, 1872
(figs. 54D, 55D, 56C)

DEFINITION: All taxa sharing a more recent common ancestor with *Glyptosaurus sylvestris* than with *Anguis fragilis*, *Diploglossus millepunctatus*, or *Gerrhonotus liocephalus*.

DIAGNOSIS: Glyptosaurinae is diagnosed by 10(1) presence of dermal sculpturing on the frontal and parietal, 82(0) presence of a transverse posterior margin of the parietal between the supratemporal processes, and 212(6) squared dorsal tooth margins.

COMMENTS: Gauthier (1982) and Conrad (2006b) provided the only prior cladistic analyses of glyptosaurine relationships with other anguid groups, but both of those analyses used composite codings for said groups. Based on preliminary phylogenetic analyses (including those reported in Conrad, 2004b, 2005a), *Peltosaurus granulosus* and Glyptosaurinae were treated separately and as individual taxa. However, the current analysis reveals that *P. granulosus* is nested within Glyptosarinae, as suggested by earlier studies (e.g., Gilmore, 1928; Meszoely, 1970; Meszoely et al., 1978; Sullivan, 1979, 1986; Estes, 1983).

Glyptosaurines exclusive of
Odaxosaurus piger
(figs. 54D, 55D)

DIAGNOSIS: Glyptosaurines exclusive *Odaxosaurus piger* form a clade diagnosed by 7(1) presence of pitted dermal sculpturing, 8(1) presence of dermal sculpturing on the maxilla, 171(1) sutured posteroventral margin of the intramandibular septum, 311(2) large osteoderms covered with bony tuber-

cles, and 312(1) presence of keeled body osteoderms.

COMMENTS: Glyptosaurines are often subdivided into a two "tribes"; the plesiomorphic Melanosaurini and the apomorphic Glyptosaurini (Meszoely, 1970; Meszoely et al., 1978; Sullivan, 1979, 1986; Augé and Sullivan, 2006; Sullivan and Augé, 2006). Melanosaurins sensu Sullivan (1979) were initially considered to form a monophyletic group. More recently, melanosaurins sensu lato have been suggested as a paraphyletic assemblage (Estes, 1983; Sullivan, 1986; Augé and Sullivan, 2006; Sullivan and Augé, 2006), a view supported by the current analysis (figs. 54D, 55D).

Proxestops jepseni + *Xestops vagans*
(figs. 54D, 55D)

DIAGNOSIS: This unnamed clade is supported by one unambiguous synapomorphy: 173(2) dentary contributing to the margin of the anterior surangular foramen.

COMMENTS: Neither of these species is well preserved. Gauthier (1982) suggested that *Proxestops jepseni* represents a good potential structural intermediate between the Cretaceous anguid *Odaxosaurus piger* and the Eocene *Xestops vagans*, a view supported by Estes (1983). The present analysis offers a phylogenetic hypothesis consistent with that scenario. Note that this analysis recovers autapomorphies for *X. vagans*, but none for *P. jepseni*. Although the fragmentary nature of known *P. jepseni* material is probably at least partly responsible for this result, it supports Gauthier's (1982) hypothesis.

Peltosaurus granulosus +
Melanosaurini + Glyptosaurini
(figs. 54D, 55D)

DIAGNOSIS: This unnamed clade is united by 55(1) fused frontals, 84(1) increased contact between the parietal and supratemporal arch, resulting in reduction of the supratemporal fenestra, and 170(0) absence of a distinct intramandibular septum.

Melanosaurini + Glyptosaurini
(figs. 54D, 55D)

DIAGNOSIS: Melanosaurins and glyptosaurins form a clade to the exclusion of

Peltosaurus granulosus diagnosed by 57(1) frontals rhomboid in dorsal view and 78(1) parietal fossa closed posteriorly.

Melanosaurini Sullivan, 1979
(figs. 54D, 55D)

DEFINITION: All taxa sharing a more recent common ancestor with *Melanosaurus maximus* than with *Glyptosaurus sylvestris*.

DIAGNOSIS: *Melanosaurus maximus* and *Arpadosaurus gazinorum* are united in this analysis based on one unambiguous synapomorphy: 88(1) supratemporal 3 times as long as deep.

COMMENTS: Estes (1983) suggested that any re-evaluation of the interrelationships of *A. gazinorum* and *M. maximus* must consider the possibility of the synonymy of the two. Indeed, the present analysis finds no diagnostic characters to separate these two taxa. However, the absence of autapomorphies for these taxa may be related to the incompleteness of *A. gazinorum* remains. If they are considered conspecific specimens, then Melanosaurini is taxonomically synonymous with *Melanosaurus maximus* in the present topology. However, the current definition of Melanosaurini allows for the addition of taxa if future discoveries produce new taxa more closely related to *M. maximus* than to *Glyptosaurus sylvestris*. The current definition also maintains the perceived spirit of usage set forth in Sullivan (1979).

Glyptosaurini Sullivan, 1979
(figs. 54D, 55D)

DEFINITION: All taxa sharing a more recent common ancestor with *Glyptosaurus sylvestris* than with *Melanosaurus maximus*.

DIAGNOSIS: This clade is diagnosed by 50(1) dermal rugosities on the postorbital process of the jugal, 80(1) short parietal supratemporal processes (see character description above), 298(1) small and irregularly shaped cephalic scales and 310(2) osteoderms thickened and expressed as polygonal mounds.

Glyptosaurins exclusive of *Glyptosaurus sylvestris*
(figs. 54D, 55D)

DIAGNOSIS: This unnamed clade is diagnosed by 47(1) jugal curved (rather than

angulated) and 48(1) posteroventral process of jugal absent.

Helodermoides tuberculatus + *Paraglyptosaurus princeps*
(figs. 54D, 55D)

DIAGNOSIS: *Helodermoides tuberculatus* and *Paraglyptosaurus princeps* form a clade diagnosed by the unambiguous synapomorphies 84(0) no increased contact between the supratemporal arches and the parietal and 226(0) posterior marginal teeth not chisel-shaped (reversal of an anguid synapomorphy).

Platynota Duméril and Bibron, 1839
(figs. 54E, 55E, 56C)

DEFINITION: All taxa sharing a more recent common ancestor with *Varanus varius* and *Heloderma horridum* than with *Anguis fragilis* or *Xenosaurus grandis*.

DIAGNOSIS: In the context of the current topology, this clade is diagnosed by 32(0) absence of a maxillary palatine flange, 86(0) dorsal origin of the jaw adductor musculature on the parietal, 178(0) dentary ventrally convex along its long axis, and 190(1) posterior terminus of the splenial at or anterior to the coronoid apex.

COMMENTS: Platynota has been considered by some to be an equivalent for Varanoidea (McDowell and Bogert, 1954; Romer, 1956; Estes, 1983; Carroll, 1988b). However, this term has also been used to refer to a more inclusive group than Varanoidea (Rieppel, 1980a; Pregill et al., 1986; Lee, 1997; Bernstein, 1999; Conrad, 2004a, 2006a, 2006b) as defined here. Gao and Norell (1998, 2000) defined this taxon as a node anchored to Monstersauria and Varanidae, synonymous with the traditional definition of Varanoidea. Gao and Norell (1998, 2000), in turn, applied the taxon name Varanoidea to a node anchored by *Telmasaurus grangeri* and Varanidae of their definition.

Molecular data offer phylogenetic hypotheses in which *Xenosaurus grandis* and anguids are closely related to *Heloderma suspectum*, and *Shinisaurus* is closely related to varanids (Townsend et al., 2004; Vidal and Hedges, 2004). The study of Vidal and Hedges (2005)

possessed weaker taxonomic sampling and did not analyze the phylogenetic position of *Shinisaurus* or *Xenosaurus*, but did support a sister-group relationship between *Heloderma suspectum* and *Anniella pulchra*. Given such topologies, Platynota and Varanoidea (below) are invalidated given their traditional understandings and their definitions here.

Platynota exclusive *Dorsetisaurus pubeckensis* (figs. 54E, 55E, 56C)

DIAGNOSIS: Platynotans exclusive of *Dorsetisaurus purbekensis* form a clade diagnosed by 55(1) fused frontals, 88(1) elongate supratemporal, 182(1) absence of a dentary shelf, 212(2) trenchant marginal teeth, and 217(1) presence of expanded bases on the marginal teeth.

Shinisauria comb. nov. (figs. 54E, 55E, 56C)

DEFINITION: All taxa sharing a more recent common ancestor with *Shinisaurus crocodilurus* than with *Anguis fragilis*, *Heloderma suspectum*, and *Varanus varius*.

DIAGNOSIS: Shinisaurids and *Dalinghosaurus longidigitus* form a clade diagnosed by 3(1) presence of a blunt muzzle, 23(1) frontal forms a single anterior wedge, 34(1) presence of a prefrontal tuberosity, 38(1) anterior flange of the prefrontal extending anteriorly to the margin of the external naris, 50(1) dermal rugosities on the postorbital process of the jugal, 61(0) subolfactory processes present as simple ventral downgrowths, 138(1) reduced crista prootica without a lateral descending portion, and 307(0) ventral body osteoderms absent.

COMMENTS: Evans and Wang presented analyses suggesting that *D. longidigitus* is the sister taxon to carusioids, the sister-taxon to *Eichstaettisaurus* in a clade that is the outgroup to carusioids, or that *D. longidigitus* is a basal scleroglossan (Evans and Wang, 2005: figs. 10, 12b, and 11b, respectively). The phylogenetic data matrices upon which these analyses were based (those presented in Gao and Norell, 1998; Lee, 1998; and a combination of Evans and Barbadillo, 1997, 1998, 1999; Evans and Chure, 1998b respectively) incorporated incomplete data from early descriptions of *Shinisaurus crocodilurus*

specimens as discussed by Conrad (2003, 2004a, 2006a, 2006b). Incorporation of corrected morphological data for *S. crocodilurus* as well as the addition of *Bahndwivici ammoskius* (Conrad, 2006b) are partly responsible for the novel hypothesis presented here (figs. 54E, 55E, 56D).

Shinisauridae Ahl, 1930 (figs. 54E, 55E, 56C)

DEFINITION: *Shinisaurus crocodilurus*, *Bahndwivici ammoskius*, and all descendants of their last common ancestor.

DIAGNOSIS: Shinisaurids are diagnosed by 58(0) linear interorbital margins of the frontal and 205(0) retroarticular process lacking medial deflection (a reversal).

COMMENTS: *Shinisaurus* has traditionally been considered a member of Xenosauridae (see above). Fan (1931) initially proposed the family Shinisauridae for *Shinisaurus crocodilurus* alone, but this group was demoted to subfamily by McDowell and Bogert (1954), a convention followed by many subsequent authors (Rieppel, 1980a; Gauthier, 1982; though see Hu et al., 1984). Given the extremely long missing history of the shinisaurid lineage and its potential to receive morphologically divergent taxa, the name Shinisauridae is applied here at the node containing *S. crocodilurus* and *Bahndwivici ammoskius* following Conrad (2006b).

Parasaniwa wyomingensis + *Parviderma inexacta* + Varanoidea (figs. 54E, 55E, 56C)

DIAGNOSIS: Platynotans exclusive of shinisaurs are diagnosed by 69(0) absence of parietal tabs on the frontal, 184(2) absence of a posterodorsal coronoid process on the dentary, 185(0) dentary without a notch distinguishing coronoid and surangular processes, 192(0) coronoid process short and broad, 194(1) anterior end of coronoid abutting the dentary (rather than overlapping it), 200(1) anterodorsally expanded surangular (vertical anterior margin), and 218(1) presence of plicidentine (as evidenced by internal view of teeth).

COMMENTS: Although the Adams consensus for this analysis shows an unresolved

trichotomy between *Parasaniwa wyomingen-sis*, *Parviderma inexacta*, and Varanoidea (fig. 55E), the volatile nature of some of the more incompletely known taxa that optimize in that tree as basal monstersaurs, mosasauriforms, or varaniforms, cause the strict consensus tree to show much less resolution (fig. 54E). The lack of resolution in the strict consensus tree derives mainly from the topological volatility of *Colpodontosaurus cracens*, *Eosaniwa koehni*, *Necrosaurus cayluxi*, "*Necrosaurus*" *eucarinatus*, *Palaeosaniwa canadensis*, *Paravaranus angustifrons*, *Parviderma inexacta*, and "*Saniwa*" *feisti*. All of these taxa, except *N. cayluxi*, *P. canadensis*, and "*S.*" *feisti* variably are recovered as basal platynotans (outside of Varanoidea), as basal goannasaurs and mosasauriforms (see below), or as basal mosasauriforms. *Palaeosaniwa canadensis* and *P. inexacta* are recovered in some trees as a clade near the base of Goannasauria (see below). "*Necrosaurus*" *eucarinatus* is the basalmost monstersaur in some trees. *Proplatynotia longirostrata* is variably an outgroup to varaniforms or a basal goannasaur. "*Saniwa*" *feisti* and *N. cayluxi* are always contiguous on the tree, either as a clade or as a paraphyletic group. They may be a proximal outgroup(s) to goannasaurs, basal varaniforms, or basal varanines.

The Adams consensus tree shows that all of the taxa discussed above are always members of Platynota above the level of shinisaurs. All of the shortest recovered trees are consistent with the possibility that *P. canadensis* and "*N.*" *eucarinatus* are monstersaurs, that "*S.*" *feisti*, *N. cayluxi*, *P. longirostrata*, and *Saniwides mongoliensis* are goannasaurs, and that *E. koehni* and *P. angustifrons* are mosasauriforms; this is, therefore, reflected in the Adams consensus tree (figs. 55E, 56E).

Varanoidea Camp, 1923
(figs. 54E, 55E, 56D)

DEFINITION: *Heloderma horridum*, *Lanthanotus borneensis*, *Varanus varius*, and all descendants of their last common ancestor.

DIAGNOSIS: Crown group platynotans form a clade (figs. 53E, 54E, 55E, 56E) diagnosed by 26(1) strong medial processes of the maxillae behind the nasal process of the premaxilla, 29(1) weakly inclined anterior margin of the maxillary nasal process, 55(0) paired (unfused) frontals, 111(1) palatine subequal in length and width, and 189(1) splenial not extending anterior to the midpoint of the dentary tooth row.

COMMENTS: The current definition of Varanoidea follows that of Estes et al. (1988), Norell et al. (1992), Lee (1997, 1998), Norell and Gao (1997), and Bernstein (1999), but uses the more specific anchor taxa as in Conrad (2006b). Gao and Norell (1998, 2000) used this taxon name in a more restricted sense, but theirs was not the common usage. See further comments at Platynota regarding usage of this definition.

Monstersauria Norell and Gao, 1997
(figs. 54E, 55E, 56D)

DEFINITION: All taxa sharing a more recent common ancestor with *Heloderma horridum* than with *Varanus varius*.

DIAGNOSIS: As defined in this analysis with the taxa included in Adams rule tree, this stem-based clade is diagnosed by 214(2) "modified pleurodont" dentition (sensu Zaher and Rieppel, 1999a) and 232(1) tall, narrow vertebral neural spines.

COMMENTS: Gao and Norell (1998) defined Monstersauria as a node-based taxon anchored to *Gobiderma pulchrum* and *Heloderma suspectum*. They re-iterated this definition later (Gao and Norell, 2000), but described their intention to include in this group "…Helodermatidae and its closely related fossil taxa…" (Gao and Norell, 2000: 92–93). Thus, their definition was used to encompass all of the then-recognized fossil relatives of *Heloderma*. Although the principle trees recovered in this analysis always recover monsteraurian status for *Gobiderma pulchrum*, *Paraderma bogerti*, and *Primaderma nessovi*, the principle trees support various positions for these taxa. Some trees support the hypothesis that *G. pulchrum* shares a more recent common ancestor with *Heloderma* than *Paraderma bogerti* or *Primaderma nessovi*, which, under the node-based definition, would place them outside of Monstersauria. The current definition is

intended to maintain and stabilize the originally intended use of the name Monstersauria.

Gobiderma pulchrum + *Paraderma bogerti* + *Primaderma nessovi* + Helodermatidae (figs. 55E, 56D)

DIAGNOSIS: This clade is diagnosed by 32(1) presence of a palatine flange of the maxilla, 160(0) presence of a pterygoid lappet on the quadrate, and 171(2) free posteroventral margin of the intramandibular septum.

Paraderma bogerti + *Primaderma nessovi* (figs. 55E, 56D)

DIAGNOSIS: These taxa are united in the current analyses by 309(1) presence of grooves separating the osteoderms on the maxilla.

COMMENTS: Monophyly of *Paraderma bogerti* and *Primaderma nessovi* to the exclusion of all other squamates is not recovered in all of the principle trees in this analysis (see comments above and below), but the close relationship of these two taxa is recovered by the Adams consensus. Note, though, that the only unambiguous synapomorphy for this clade is homoplastic in that it also forms part of the diagnosis for the clade of helodermatids including *Lowesaurus matthewi* and *Heloderma* (below).

Helodermatidae Gray, 1837 (figs. 54E, 55E, 56D)

DEFINITION: *Heloderma horridum*, *Lowesaurus matthewi*, *Eurheloderma gallicum*, and all descendants of their last common ancestor.

DIAGNOSIS: The node here referred to as Helodermatidae is diagnosed by seven unambiguous synapomorphies in the current analysis. These are 37(1) prefrontal-postfrontal/postorbitofrontal contact present, 57(1) frontals rhomboid in dorsal view, 77(3) absence of a pineal foramen, 115(1) absence of palatine teeth, 118(2) absence of pterygoid teeth (reversed in some *Heloderma suspectum*), 182(1) absence of a dentary shelf (fig. 38E), and 220(1) presence of a distinct venom groove in the dentary teeth (fig. 38E).

COMMENTS: Helodermatidae as defined here generally follows common usage (McDowell and Bogert, 1954; Bogert and Del Campo, 1956; Yatkola, 1976; Estes, 1983; Norell et al., 1992; Gao and Fox, 1996) and is similar to the usage of Pregill et al. (1986) who first applied this term to a node on a cladogram. This differs from the usage of some subsequent authors who prefer a crown based application of Helodermatidae (Norell and Gao, 1997; Gao and Norell, 1998, 2000).

Estes (1983) tentatively included *Paraderma bogerti* in his treatment of Helodermatidae, citing plesiomorphic characteristics and the then-forthcoming study by Pregill et al. (1986). Estes (1983) further cautioned that a parietal he had referred to *P. bogerti* (Estes, 1964) might be that of *Palaeosaniwa canadensis*. However, the parietal of *P. canadensis* is inconsistent with that morphology and the parietal is here tentatively considered to belong to *P. bogerti*. Pregill et al. (1986) included *Heloderma*, *Lowesaurus* (=*Heloderma*) *matthewi*, *Eurheloderma gallicum*, and *Paraderma bogerti* in their Helodermatidae. The latter usage is consistent with that of Estes et al., who defined it as a stem including "*Heloderma*, and all organisms sharing a more recent common ancestor with this taxon than with any other extant organisms," (Estes et al., 1988: 228). Given the phylogenetic topology presented here (figs. 54E, 55E) and a crown-based definition for Helodermatidae, helodermatids would be a subclade of *Heloderma*. Consequently, maintaining Helodermatidae in a traditional sense is advocated here.

The current application of Helodermatidae to the node specified above is beneficial given that all of the anchor taxa for the name were originally described as helodermatids (as opposed to "necrosaurids"/"parasaniwids"; e.g., *Paraderma bogerti* and *Gobiderma pulchrum*) and are retained as a monophyletic group in all of the principle trees recovered by this study (see also Augé, 2003). *Estesia mongoliensis* is variable in its placement in the current analysis. Different principle trees place it as the sister-taxon to *L. matthewi*, *E. gallicum*, the *L. matthewi* + *Heloderma* clade, or as the sister-taxon to Helodermatidae as defined here. This phylo-

genetic hypothesis owes, in part, to the relative quality of known *E. gallicum* and *L. matthewi*. Thus, *E. mongoliensis* may or may not be a helodermatid as the name is defined here, but it is certainly a monstersaur.

Lowesaurus matthewi + *Heloderma*
(figs. 55E, 56D)

DIAGNOSIS: This unnamed clade is diagnosed by 62(1) midline contact of the frontal subolfactory processes and 309(1) presence of grooves separating the osteoderms on the maxilla.

COMMENTS: *Lowesaurus matthewi* was initially described as *Heloderma matthewi* (Gilmore, 1928) and was, for many years, an unquestioned *Heloderma* species (Bogert and Del Campo, 1956; Pianka, 1967; Yatkola, 1976; Estes, 1983). However, Pregill et al. (1986) showed that they could recover no support for a sister-group relationship between the *matthewi* species and extant *Heloderma* exclusive of *Eurheloderma gallicum*, and erected a new genus for the Oligocene species.

Heloderma Wiegmann, 1829
(figs. 54E, 55E, 56D)

DEFINITION: *Heloderma suspectum* (fig. 52), *H. horridum*, *H. texana*, and all descendants of their last common ancestor.

DIAGNOSIS: Two unambiguous synapomorphies diagnose *Heloderma* as defined here. These are 57(0) anterior and posterior borders of the frontal of subequal width and 124(2) presence of a broad ectopterygoid-palatine contact anterior to the suborbital fenestra.

Heloderma horridum + *H. suspectum*
(figs. 54E, 55E, 56D)

DIAGNOSIS: Extant members of *Heloderma* form a clade to the exclusion of *Heloderma texana*. This clade is diagnosed by 32(0) absence of a maxillary palatine flange.

Goannasauria tax. nov.
(figs. 55E, 56D)

DEFINITION: All taxa sharing a more recent common ancestor with *Varanus varius* than with *Heloderma suspectum*.

ETYMOLOGY: *Goanna*, a modification of "iguana" (derived from *iwana*, Arawak). Goanna is a common name for some members of the genus *Varanus*, especially in Australia. *Sauros*, (Greek) reptile. This taxon name is applied such that it is complementary to the Monstersauria within the Varanoidea. Thus, monstersaurs are Gila monsterlike varanoids and goannasaurs are goannalike varanoids.

DIAGNOSIS: Goannasaurs are diagnosed by 2(1) presence of pre-septomaxillary rostrum, 8(0) absence of dermal sculpturing on the maxilla, 31(1) neochoanate condition, 47(1) jugal curved (rather than angulated), 65(1) frontals with an anterior maxillary contact, 113(0) absence of a distinct choanal groove, 178(1) straight main axis of dentary, 214(2) "modified pleurodont" dentition (sensu Zaher and Rieppel, 1999a), and 233(1) presence of precondylar constriction of the vertebrae.

COMMENTS: Traditionally, no name has been given to the clade containing all the taxa more closely related to monitor lizards than to *Heloderma*. Recently, Gao and Norell (1998, 2000) redefined Varanoidea for this purpose, but this usage has not gained wide acceptance (see Platynota and Varanoidea above), nor did those papers specifically address mosasaurs. However, given the current topology (figs. 54E, 55E, 56E) (and some of previous analyses), naming this well supported clade seems helpful. The name Goannasauria is used here to balance the other varanoid stem, Monstersauria. Note that mosasauriforms may be goannasaurs or they may fall outside of Varanoidea. Goannasauria retains its general meaning (taxa more closely related to monitor lizards than *Heloderma*) regardless of this topological variability. Note that the strict consensus tree (fig. 54E) collapses the node containing *Lanthanotus borneensis* and *Varanus* exclusive of helodermatids. This is because of uncertainty regarding the phylogenetic placement of *Palaeosaniwa canadensis*, which is a monstersaur in many trees, but sometimes falls on the goannasaur lineage (for further discussion, see the comments for the clade *Parasaniwa wyomingensis* + *Parviderma inexacta* + Varanoidea, above).

Varaniformes comb. nov.
(figs. 54E, 55E, 56D)

DEFINITION: All taxa sharing a more recent common ancestor with *Varanus varius* than with *Heloderma suspectum* or *Mosasaurus hoffmanni*.

COMMENTS: Because the interrelationships of Varaniformes, Mosasauriformes, and Monstersauria are unresolved in this analysis, Varaniformes and Goannasauria are identical in their taxonomic content in the consensus trees presented here (see figs. 54–56). Many of the principle trees support a sister-group relationship between dolichosaurs and a clade containing varanids (usage below) and their fossil outgroups. In order to communicate easily about the nature of the latter group, the name Varaniformes is being applied as a stem-defined taxon name. Note that the principle trees recovered in this analysis always support the placement of *Saniwides mongoliensis* and *Telmasaurus grangeri* as proximal outgroups to Varanidae. *Proplatynotia longirostrata*, *Necrosaurus cayluxi*, and ''*Saniwa*'' *feisti* are always goannasaurs, but, in some trees, are the outgroup to a clade containing mosasauriforms and varaniforms, and in others are basal varaniforms (fig. 54E; indicated also by the Adams consensus tree fig. 55E). Thus, although varaniforms cannot be diagnosed from other goannasaurs based on the current Adams consensus, it is a useful group based on goannasaur interrelationships.

Telmasaurus grangeri + Varanidae
(figs. 55E, 56D)

DIAGNOSIS: Varanidae sensu stricto (below) forms a clade with *Telmasaurus grangeri* based on 9(0) absence of dermal sculpturing on the prefrontal, 43(1) presence of paired lacrimal foramina, 124(1) ectopterygoid contacting the palatine in the suborbital fenestra and 140(1) entocarotid fossa indistinct/absent.

COMMENTS: This clade fits exactly with the definition Gao and Norell (1998) gave to the taxon name Varanoidea. Varanoidea as defined above and used by prior authors (e.g., Rieppel, 1980a; Pregill et al., 1986; Lee, 1997; Bernstein, 1999; Conrad, 2004a, 2006a, 2006b) is much more inclusive than the definition implemented by Gao and Norell (1998).

Varanidae Gray, 1827
(figs. 55E, 56D)

DEFINITION: *Varanus varius*, *Lanthanotus borneensis*, and all descendants of their last common ancestor.

DIAGNOSIS: Varanids are united by 115(1) absence of palatine teeth, 118(1) pterygoid teeth arranged in a single line, 149(1) presence of an expansive crista tuberalis (see character description above), and 151(1) anterior location for the spheno-occipital tubercle.

COMMENTS: The present definition of Varanidae follows that of common usage and previous phylogenetic definitions (Estes et al., 1988; Pianka, 1995; Lee, 1998; Bernstein, 1999; Conrad, 2004a, 2006a, 2006b). The clade as defined here was left unnamed in Lee (1997), a study in which the name Varanidae was defined as all taxa sharing a more recent common ancestor with *Varanus* than with *Lanthanotus borneensis*. Caldwell (1999a) produced a hypothesis of relationships differing from that of the current analysis (fig. 8), but that is one of the only recent studies to do so.

Lanthanotinae Steindachner, 1878
(figs. 54E, 55E, 56D)

DEFINITION: All taxa sharing a more recent common ancestor with *Lanthanotus borneensis* than with *Varanus varius*.

DIAGNOSIS: Lanthanotines are diagnosed by 3(1) presence of a blunt muzzle, 37(1) prefrontal-postfrontal/postorbitofrontal contact present, 83(1) presence of a nuchal fossa on the parietal, and 193(0) absence of a labial flange of the coronoid.

Aiolosaurus oriens + *Cherminotus longifrons*
(figs. 54E, 55E, 56D)

DIAGNOSIS: This unnamed lanthanotine clade is diagnosed by 12(2) mediolateral breadth of the premaxillary nasal process less than the dorsoventral depth and 43(0) presence of a single lacrimal foramen (a reversal).

COMMENTS: The current analysis is the first to cladistically test the position of *Lanthonotus borneensis* with respect to fossil taxa such as *Aiolosaurus oriens* and *Cherminotus longifrons*. *Cherminotus longifrons* was

originally considered to be a close relative of *L. borneensis* (Borsuk-Białynicka, 1984; Gao and Norell, 1998), but the specific position for *A. oriens* within Varanidae was not hypothesized in its original description (Gao and Norell, 2000). Gao and Norell (2000) showed that *C. longifrons* does not possess some of the character states that were used to join it with *L. borneensis* in the studies of Borsuk-Białynicka (1984) and Gao and Norell (1998). Despite this, the current analysis suggests that both *C. longifrons* and *A. oriens* are lanthanotines.

Varaninae Camp, 1923
(figs. 54E, 55E, 56D)

DEFINITION: All taxa sharing a more recent common ancestor with *Varanus varius* than with *Lanthanotus borneensis*.

DIAGNOSIS: Varanines are diagnosed by 42(1) presence of a posterolateral flange on the lacrimal, 44(1) enlarged lacrimal foramen (see character description above), 107(1) rod-shaped vomer, 194(0) anterior end of the coronoid clasping (rather than abutting) the dentary, 235(0) absence of true zygosphenes-zygantra, 257(1) presence of expansion/flattening of the anterior presacral ribs, and 281(1) absence of an intermedium in the manus.

Varanus White, 1790
(figs. 54E, 55E, 56D)

DIAGNOSIS: The species of *Varanus* included in this study form a clade diagnosed as primitively possessing the following synapomorphies: 1(2) elongate antorbital snout, 12(2) nasal process of premaxilla narrowest mediolaterally, 17(1) presence of a premaxilla-maxilla aperture, 69(1) presence of a frontal-palatine contact, 74(1) presence of frontal tabs on the parietal dorsally, 118(2) absence of pterygoid teeth, and 243(2) fusion of the cervical intercentra to the posterior part of the preceding centrum.

COMMENTS: Extant *Varanus* (e.g., fig. 49) are extremely diverse morphologically and ecologically (Mertens, 1942a; Irwin, 1994; Pianka, 1995; Ast, 2001, 2002; Pepin, 2001) and numerous monophyletic groups have been identified in separate morphological and molecular studies with a fair degree of consistency (Fuller et al., 1998; Ast, 2001, 2002; Pepin, 2001). Although these clades are often considered "subgenera," they are typically geographically and morphologically distinct and could be considered relatively speciose genera of their own. Although this issue is not further addressed here, it is a topic deserving more attention.

The current analysis is the first to analyze the relative phylogenetic positions of *Varanus rusingensis* and *Megalania prisca* with respect to numerous extant species. Both are within the extant *Varanus* radiation. *Varanus rusingensis* is nested within a basal clade of *Varanus*. "*Megalania*" *prisca* (hereafter referred to as *Varanus priscum*) is actually a species of *Varanus* (as the name is applied here) and deeply nested within that clade. In this analysis, *Varanus priscum* is suggested to form a clade with *V. salvadorii*, with *V. komodoensis* (fig. 49A) as the sister-taxon to that clade.

The phylogenetic positions of the major *Varanus* clades will be further analyzed using morphology and incorporating more complete taxon sampling elsewhere.

Mosasauriformes comb. nov.
(figs. 54E, 55E, 56D)

DEFINITION: All taxa sharing a more recent ancestor with *Mosasaurus hoffmanni* (fig. 41) than with *Varanus varius* or *Heloderma suspectum*.

DIAGNOSIS: Mosasauriforms are united by 61(0) subolfactory processes present as simple ventral downgrowths, 107(1) rod-shaped vomers, 172(1) absence of a distinct anterior surangular foramen, 178(1) straight main axis of dentary, 218(0) absence of plicidentine, and 303(1) deeply imbricating scales.

COMMENTS: Cope (1869, 1870, 1872, 1878) erected Pythonomorpha to include mosasauroids to the exclusion of his Ophidia (snakes) which he thought to be their nearest relatives. Recently, the taxon name Pythonomorpha has been revived and defined to receive mosasauroids and snakes (Lee, 1997, 1998; Caldwell, 1999a; Lee and Caldwell, 2000; Rage and Neraudeau, 2004). That usage of Pythonomorpha is synonymous with Autarchoglossa in the present phylogenetic hypothesis. The definition given by Lee

(1998) is not tenable given the present topology. Implementation of Cope's term Pythonomorpha would be preferable to creating a new taxon name or new combination for this clade, but the ubiquity of the recent usage of Pythonomorpha sensu Lee (1997) would be difficult to overcome. Therefore, rather than trying to reformulate or redefine Pythonomorpha to restore it to monophyly, the name Mosasauriformes is used here.

Paravaranus angustifrons + Mosasauria
(figs. 55E, 56D)

DIAGNOSIS: These taxa are united, to the exclusion of *Eosaniwa koehni*, by 6(1) posteriorly elongated nares, 8(0) absence of dermal sculpturing on the maxilla, 9(0) absence of dermal sculpturing on the prefrontal, 10(0) absence of dermal sculpturing from the frontal and parietal, 47(1) jugal curved (rather than angulated), 55(1) fused frontals, 115(1) absence of palatine teeth and 189(0) a shortened splenial (see character description above).

Mosasauria Marsh, 1880
(figs. 54F, 55F, 56D)

DEFINITION: *Dolichosaurus longicollis*, *Coniasaurus crassidens*, *Coniasaurus gracilodens*, *Adriosaurus suessi*, *Mosasaurus hoffmanni*, and all descendants of their last common ancestor.

DIAGNOSIS: Mosasaurs are united by 66(0) prefrontals with large contributions to the orbitonasal fenestra, 69(1) presence of parietal tabs on the frontal, 168(1) adductor fossa with a distinct vertical flange, 191(1) presence of an intramandibular joint in which the splenial receives the angular, and 214(2) "modified pleurodont" dentition (sensu Zaher and Rieppel, 1999a).

COMMENTS: There is no existing phylogenetic definition for Mosasauria. Traditionally, this taxon has been treated as an equivalent of Pythonomorpha (Marsh, 1880; Cope, 1900; Fürbringer, 1900a; Osborn, 1903a, 1903b, 1904; Hay, 1905; Camp, 1923; Russell, 1967), but given the current definition of that taxon (see Mosasauriformes above) a distinction between the two is worthwhile. All of the taxa included in this clade according to the current analysis are

generally believed to be semi- to fully aquatic and are universally considered close relatives of mosasaurids; thus the name Mosasauria is defined here such that these taxa are included.

Dolichosauridae Gervais, 1852
(figs. 54F, 55F, 56D)

DEFINITION: All taxa sharing a more recent common ancestor with *Dolichosaurus longicollis* than with *Mosasaurus hoffmanni*.

DIAGNOSIS: Dolichosauridae as defined here in the context of the present analysis includes only *Dolichosaurus longicollis* and *Aphanizocnemus*, and is united by 243(2) cervical intercentra fused to the posterior part of the preceding intercentrum.

COMMENTS: Lee and Caldwell (2000) coded Dolichosauridae based on *Coniasaurus* and *Dolichosaurus longicollis*, but their analysis does not resolve the position of *Aphanizocnemus* with respect to their Dolichosauridae, *Adriosaurus*, and/or snakes. Carroll (1988b: 618) included *Adriosaurus*, *Dolichosaurus longicollis*, *Eidolosaurus trauthi*, and *Pontosaurus* in his Dolichosauridae, but placed *Coniasaurus* tentatively with the Aigialosauridae.

The current analysis offers no unambiguous character support for uniting *Coniasaurus* and *Dolichosaurus longicollis*. The principle trees recovered in this analysis always recover a basal position for a clade containing *Dolichosaurus longicollis* and *Aphanizocnemus*, but the relative phylogenetic placement of *Coniasaurus* is more problematic. *Coniasaurus* is recovered as the sister taxon to *Dolichosaurus longicollis*, as the sister taxon to all other mosasaurs, as a nested mosasauroid (above the level of adriosaurids), or as the sister-taxon to *Opetiosaurus* within mosasauroids. Note that the existing cranial remains are very limited in most of the basal mosasaur taxa and that *Coniasaurus* is known primarily from partial skulls. Future inclusion of a *Judeasaurus tchernovi*, recently described by Haber and Polcyn (2005), may help to resolve this problem.

Mosasauroidea Camp, 1923
(figs. 54F, 55F, 56D)

DEFINITION: All taxa sharing a more recent common ancestor with *Mosasaurus*

hoffmanni than with *Dolichosaurus longicollis*.

DIAGNOSIS: Mosasauroids are united by 163(1) presence of a quadrate suprastapedial process, 187(1) dentary suspended primarily from the prearticular, 249(1) lateral compression and dorsoventral deepening of the tail into a sculling organ, and 265(1) scapula shorter than the coracoid.

COMMENTS: Marsh (1880) discusses "mosasauroids" in an informal fashion referring to *Tylosaurus*, *Lestosaurus*, and *Holosaurus* (the latter two taxa probably synonymous with *Clidastes*). Camp (1923) formalized Mosasauroidea and originally included only Mosasauridae. Recently, the name Mosasauroidea has been used to refer to clades of varying inclusiveness. Most treatments of the group have included "aigialosaurs" and Mosasauridae (Caldwell et al., 1995; Bell, 1997, 2002; Dal Sasso and Pinna, 1997; Lee, 1997, 1998; Caldwell, 1999a; Lee and Caldwell, 2000; Bardet et al., 2003). This is problematic because the monophyly of "aigialosaurs" has been questioned with respect to Mosasauridae, *Adriosaurus*, and Dolichosauridae (Bell, 1997; Dal Sasso and Pinna, 1997; Lee, 1997, 1998; Caldwell, 1999a; Lee and Caldwell, 2000; Bardet et al., 2003) and, consequently, because the composition of the "aigialosaur" group is uncertain. As originally conceived, Aigialosauridae included, among other taxa, *Pontosaurus* (Kramberger, 1892). Carroll (1988b) includes *Coniasaurus* in Aigialosauridae and places aigialosaurids in Mosasauroidea. Some of the studies mentioned above questioning the monophyly of the "aigialosaur" group have specifically omitted *Dolichosaurus longicollis* and/or *Coniasaurus* from their Mosasauroidea (Caldwell, 1999a; Lee and Caldwell, 2000) and others have specifically included them in discussing mosasauroids (Lee et al., 1999a).

Obviously, anchoring Mosasauroidea to "aigialosaurs" leaves a great deal of ambiguity; few studies have analyzed the monophyly of the clade and there is little support for it in general. Here, Mosasauroidea is defined as a stem-based taxon to help alleviate some of this uncertainty and to attempt to retain all of the "aigialosaurs" as mosasauroids (figs. 55F).

Adriosaurus + *Pontosaurus*
(figs. 54F, 55F)

DIAGNOSIS: These taxa form a clade diagnosed by 33(0) maxillary tooth row extending posteriorly beyond the anterior one-fourth of the orbit, 207(1) retroarticular process that is posteriorly expanded (broadened), and 245(1) presence of pachyostotic dorsal vertebrae and ribs.

Aigialosaurus + *Carsosaurus marchesetti* +
Eidolosaurus trauthi + Mosasauridae
(fig. 55F)

DIAGNOSIS: The clade containing mosasauroids exclusive of *Adriosaurus*, *Opetiosaurus*, and *Pontosaurus* is diagnosed, in this analysis, by 13(1) premaxilla possessing an external contact with the frontal and 46(1) jugal extending well anterior to the level of the orbit.

COMMENTS: The current analysis offers only very weak support for an aigialosaurid clade. Instead, "aigialosaurs" are a paraphyletic assemblage that is intermediate between dolichosaurids and mosasaurids. Some of the principle trees in this analysis support close relationships between *Carsosaurus marchesetti* and *Opetiosaurus*, between *Carsosaurus marchesetti* and *Aigialosaurus*, or between *Aigialosaurus*, *Carsosaurus marchesetti*, and *Opetiosaurus*. However, these relationships are not supported in the strict or Adams consensus trees (see comments below).

Eidolosaurus trauthi + Mosasauridae
(figs. 54F, 55F)

DIAGNOSIS: *Eidolosaurus trauthi*, *Tethysaurus nopcsai*, and Mosasauridae form a clade diagnosed by 288(1) lack of distinction between the distal femoral condyles and 289(1) femur flattened and shortened such that the ends are more than one-quarter the length of the ends.

Mosasauridae Gervais, 1853
(figs. 54F, 55F)

DEFINITION: *Halisaurus platyspondylus*, *Tylosaurus proriger*, *Mosasaurus hoffmanni*, and all descendants of their last common ancestor.

DIAGNOSIS: Mosasaurids are diagnosed by two unambiguous synapomorphies: 247(1) absence of a functional sacrum and 275(1) presence of a flattened "hourglass-shaped" humerus.

COMMENTS: The definition of Mosasauridae implemented here follows that of Bell (1997) who divided mosasaurids into *Halisaurus* and Natantia. The sister-group relationship of *Halisaurus* and all other mosasaurids has been recovered in several analyses (DeBraga and Carroll, 1993; Caldwell, 1996; Bardet and Suberbiola, 2001; Bardet et al., 2003, 2005), but has been questioned recently (Bell and Polcyn, 2005; Polcyn and Bell, 2005). This problem will require further examination given the recent description of new taxa such as *Russellosaurus coheni* (Polcyn and Bell, 2005) and *Dallasaurus turneri* (Bell and Polcyn, 2005). Note, however, that although some existing phylogenetic studies of mosasauroids have sampled densely for species than the current analysis (Bell, 1997; Bell and Polcyn, 2005; Polcyn and Bell, 2005), they have limited their taxonomic sampling to mainly North American and European taxa. The current analysis benefits from more complete taxonomic sampling from all over the world (e.g., *Lakumasaurus antarcticus* from Antarctica and *Goronyosaurus nigeriensis* from Africa), but does not include many of the American species represented in earlier analyses. A more definitive phylogenetic and taxonomic analysis should include all of these data.

Halisaurinae Bardet et al., 2005
(figs. 54F, 55F)

DEFINITION: All taxa sharing a more recent common ancestor with *Halisaurus platyspondylus* than *Mosasaurus hoffmanni*.

DIAGNOSIS: *Halisaurus platyspondylus*, *H. arambourgi*, and *Eonatator sternbergii* are united in this analysis by five unambiguous synapomorphies. These are 151(1) anterior location for the spheno-occipital tubercle, 164(2) presence of an infrastapedial process (also within plioplatecarpines), 172(0) presence of a distinct anterior surangular foramen, 235(0) absence of true zygosphenes-zygantra, and 288(0) presence of two distinct

distal femoral condyles (a reversal of a synapomorphy uniting Mosasauridae and *Eidolosaurus trauthi*).

COMMENTS: Halisaurinae is problematic. All of the halisaurines in this analysis have been considered *Halisaurus* at some point. Recently, Bardet et al. (2005) proposed a new genus, *Eonatator*, to receive the species originally described as *Clidastes sternbergii* and later placed in *Halisaurus*. The apparent reason for this change is strictly taxonomic. Bardet et al. (2005) found *Eonatator sternbergii* to be the sister-taxon to the clade *Halisaurus*; thus, the species *sternbergii* might as easily be retained in *Halisaurus*. However, it is not problematic to separate *sternbergii* at the generic level in their analysis or in the context of other recent analyses (Bell and Polcyn, 2005; Polcyn and Bell, 2005), because they also support *sternbergii* as the sister-taxon to other "*Halisaurus*." The current analysis does not resolve the interrelationships between the three included halisaurine species (figs. 54F, 55F), but the future inclusion of the *Halisaurus ortliebi* might clarify these relationships.

The name Halisaurinae was recently defined as a stem-based name including taxa closer to *Halisaurus* than to *Mosasaurus* (Bardet et al., 2005), a definition maintained here but with more specific anchor taxa. Bell and Polcyn (2005) applied the name Halisauromorpha to a clade containing all of the taxa they considered to belong to *Halisaurus* (including *Eonatator sternbergii*) and cite the usage in Bell's unpublished dissertation (Bell, 1993), but do not formally define the group.

The current analysis leaves the placement of *Tethysaurus nopcsai* unresolved with respect to halisaurines and natantians (figs. 54F, 55F). The principle trees recovered in this analysis recover the placement of *Tethysaurus nopcsai* as the sister-taxon to Mosasauridae, as a basal halisaurine, or as a basal natantian. Bardet et al. (2003) originally recovered a sister-taxon relationship between *Tethysaurus nopcsai* and Mosasauridae. Two more recent analyses have suggested that *Tethysaurus nopcsai* forms a clade with *Russellosaurus coheni* and *Yaguarasaurus columbianus* near the base of Russellosaurina (see comments for Russellosaurina below).

Natantia Owen, 1849–1884
(figs. 54F, 55F)

DEFINITION: All taxa sharing a more recent common ancestor with *Mosasaurus hoffmanni*, *Tylosaurus proriger*, and *Plioplatecarpus marshi* than with *Halisaurus platyspondylus*.

DIAGNOSIS: Mosasaurids exclusive of halisaurines form a clade diagnosed in this analysis by 88(0) anteroposteriorly short supratemporal, 183(3) absence of a separate anterior inferior alveolar foramen, 212(0) teeth straight and pointed (conical), and 234(0) absence of oblique vertebral condyles.

COMMENTS: Bell (1997) revived this name first proposed by Owen (1849–1884) to receive all of the non-*Halisaurus* taxa he (Bell) included in his analysis, but did not formally define the taxon name. It is unclear whether Bell (1997) meant for Natantia to include only his "Russellosaurinae" (=Russellosaurina of Polcyn and Bell, 2005 and Bell and Polcyn, 2005) and Mosasaurinae or if he meant for stem-taxa of this radiation to be included as well. Although this question does not affect the taxonomic inclusiveness of Natantia under the current topology, it would become important were members of the stem-group (currently unknown) to be discovered. Because the apparent intention of Owen (1849–1884) was for the name to apply to all of the then-known mosasaurs, the more inclusive, stem-based, definition is implemented here. Natantia is used with some reservation given the absence of a clear Natantia in the strict consensus tree. However, the current definition allows Natantia to become a junior subjective synonym to Mosasauridae if *Halisaurus* is nested within Mosasauridae as suggested by some recent analyses (Bell and Polcyn, 2005; Polcyn and Bell, 2005).

Note that the name Natantia has also been applied to a group of decapods (Boas, 1880), but Owen's (1849–1884) usage has priority.

Mosasaurinae Gervais, 1853
(figs. 54F, 55F)

DEFINITION: All taxa sharing a more recent common ancestor with *Mosasaurus hoffmanni* than with *Tylosaurus proriger* or *Plioplatecarpus marshi*.

DIAGNOSIS: Mosasaurines are united by 53(1) frontal possessing an anterior constricted neck, 177(1) anterodorsal buttress for the coronoid, 250(2) humerus flattened with expanded, but equal, ends, 251(1) divided deltoid and pectoral crests joined by a lamina, 255(2) ulna possessing a facet articulating with the intermedium, and 257(1) notably robust first metacarpal of the manus.

Moanasaurus mangahouangae + *Mosasaurus hoffmanni* + *Globidens dakotensis* + Plotosaurini
(figs. 54F, 55F)

DIAGNOSIS: In the present analysis, mosasaurines exclusive of *Clidastes* are united by 28(2) dorsal and ventral margins of the maxilla subparallel and 69(2) presence of large parietal tabs of the frontal that extend well onto the dorsal surface of the parietal (see fig. 34).

Mosasaurus hoffmanni + *Globidens dakotensis* + Plotosaurini
(figs. 54F, 55F)

DIAGNOSIS: The present analysis recovers only one synapomorphy to support this clade: 219(1) striated tooth crowns.

Globidens dakotensis + Plotosaurini
(figs. 54F, 55F)

DIAGNOSIS: This derived mosasaurine clade is united by 46(0) jugal extends no further anteriorly than if forming the anterior margin of the orbit.

Plotosaurini Russell, 1967
(figs. 54F, 55F)

DEFINITION: All taxa sharing a more recent common ancestor with *Plotosaurus bennisoni* than with *Mosasaurus hoffmanni* or *Globidens dakotensis*.

DIAGNOSIS: Plotosaurins are united by 61(1) subolfactory processes of the frontal(s) partly surrounding the olfactory bulbs.

COMMENTS: Bell (1997) synonymized Mosasaurini with Plotosaurini based on the paraphyly of the nominal taxon *Mosasaurus* as Russell (1967) and several others had

conceived of that clade. However, no taxon name at the level of ''superfamily'' or below may contain the type species of *Mosasaurus* (*M. hoffmanni*) and have their basis in a generic name other than *Mosasaurus* (International Commission for Zoological Nomenclature, 2000).

The current topology would yield Mosasaurini Gervais, 1853 exclusive of a Globidensini Dollo, 1924 and Plotosaurini Russell, 1967 monogeneric. Similarly, the current topology and taxonomic sampling would yield a Globidensini exclusive of *Mosasaurus* and Plotosaurini monogeneric (although *Carinodens* almost certainly would belong to Globidensini). Thus, neither Mosasaurini nor Globidensini are used here, and Plotosaurini is redefined. Russell (1967) originally included only *Plotosaurus* in his Plotosaurini. The name is applied here to all taxa that would not be subsumed by Globidensini or Mosasaurini if those clades are someday deemed necessary.

Goronyosaurus nigeriensis + *Plotosaurus bennisoni* (figs. 54F, 55F)

DIAGNOSIS: *Goronyosaurus* and *Plotosaurus* form a clade to the exclusion of ''*Mosasaurus*'' *lemonnieri* diagnosed by 15(0) absence of a rostrum anterior to the premaxillary teeth, 33(0) maxillary tooth row extending posteriorly beyond the anterior one-fourth of the orbit, 65(1) frontals with an anterior maxillary contact, 89(0) contact between the supratemporal arch bones and frontal and parietal unforked, 146(1) posterior opening of the Vidian canal located on the sphenoid-prootic suture, 235(0) absence of true zygosphenes-zygantra, and 276(2) distinct and completely separate deltoid and pectoral crests on the humerus.

Russellosaurina Polcyn and Bell, 2005 (figs. 54F, 55F)

TENTATIVE DEFINITION: All taxa sharing a more recent common ancestor with *Russellosaurus coheni*, *Plioplatecarpus marshi*, and *Tylosaurus proriger* than with *Mosasaurus hoffmanni*.

DIAGNOSIS: Russellosaurinans, defined here in the context of the present analysis,

are united by 83(0) absence of a parietal nuchal fossa and 249(0) dorsoventral height of tail vertebrae and chevrons less than three times the length of the associated centrum.

COMMENTS: Bell (1997) applied the name Russellosaurinae to the radiation including *Tylosaurus*-like and *Plioplatecarpus*-like natantians, explaining that the name was based on a forthcoming description of a new taxon, ''Russellosaurus.'' Polcyn and Bell (2005) described *Russellosaurus coheni* and, recognizing the illegitimacy of Russelosaurinae as conceived of by Bell (1997), proposed the taxon name Russellosaurina for a clade minimally containing *Plioplatecarpus* and *Tylosaurus*. Unfortunately, the definition Polcyn and Bell (2005) intended for Russellosaurina is frustratingly ambiguous. Polcyn and Bell explicitly define the taxon name as, ''Plioplatecarpinae, Tylosaurinae, their common ancestor and all descendants,'' in their abstract (Polcyn and Bell, 2005: 321); a clear and concise, node-based definition for the clade name. However, under the ''definition'' for the taxon name, they define it as, ''[a]ll mosasaurs more closely related to Tylosaurinae and Plioplatecarpinae, the genus *Tethysaurus nopcsai*, their common ancestor and all descendants than to Mosasaurinae,'' (Polcyn and Bell, 2005: 322); an explicitly stem-based definition. Subsequently, they include plioplatecarpines, tylosaurines, ''and closely related forms'' (Polcyn and Bell, 2005: 322). Then, they define it to include some closely related forms (Polcyn and Bell, 2005), but in a way that is incongruous with the stem-based definition they offered on page 322. Further complicating the issue is the usage of Russellosaurina in Bell and Polcyn who first treated mosasaurines and russellosaurines as apparent sister-taxa (Bell and Polcyn, 2005: 188), then considered Russellosaurina to be limited to ''Plioplatecarpinae plus Tylosaurinae'' (Bell and Polcyn, 2005: 189). In their preferred cladogram, Bell and Polcyn (2005: fig. 7) included plioplatecarpines, tylosaurines, *R. coheni*, *Tethysaurus nopcsai*, and *Yaguarasaurus columbianus* in Russellosaurina.

The definition offered above is in keeping with that given in the definition of Polcyn and Bell (2005), but anchored to different taxa so that the taxon name retains its

meaning regardless of the position of *Tethysaurus nopcsai*. The sister-group relationship between a *Plioplatecarpus* group and a *Tylosaurus* group exclusive of *Mosasaurus* is stable and, given the current definition, Russellosaurina will always be referable to that clade. Should new data suggest that *Mosasaurus* is nested within the *Tylosaurus-Plioplatecarpus* dichotomy, then Russellosaurina would be invalidated. This is acceptable given that the clade intended and understood when the Russellosaurina is invoked would be changed beyond recognition.

Tylosaurinae Williston, 1897
(figs. 54F, 55F)

DEFINITION: All taxa sharing a more recent common ancestor with *Tylosaurus proriger* than with *Mosasaurus hoffmanni* or *Plioplatecarpus marshi*.

DIAGNOSIS: Tylosaurines are united by 15(2) presence of an elongate, cylindrical, premaxillary rostrum, 162(1) short tympanic crest on the quadrate, 262(0) absence of anterior coracoid fenestra, and 279(2) presence of a short preaxial ridge on the radius.

Hainosaurus bernardi + *Lakumasaurus antarcticus*
(figs. 54F, 55F)

DIAGNOSIS: *Hainosaurus bernardi* and *Lakumasaurus antarcticus* are united in this analysis (to the exclusion of *Tylosaurus*) by 12(1) nasal process of the premaxilla narrowest mediolaterally and 192(1) presence of a tall, narrow, coronoid process.

COMMENTS: Novas et al. (2002) found *Lakumasaurus antarcticus* to be a basal tylosaurine, an issue that deserves further attention given the differing paleobiogeographical implications of the two hypotheses. Inclusion of *Tylosaurus nepaeolicus* may be helpful in resolving this issue.

Plioplatecarpinae Dollo, 1884
(figs. 54F, 55F)

DEFINITION: All taxa sharing a more recent common ancestor with *Plioplatecarpus marshi* than with *Tylosaurus proriger* or *Mosasaurus hoffmanni*.

DIAGNOSIS: Plioplatecarpines are united by 41(2) fusion of the lacrimal and prefrontal, 152(0) presence of a canal or groove for the basalar artery, 216(1) procumbent anterior marginal teeth, 275(3) presence of a flattened, rhomboid, humerus, and 283(1) manual digit V set off from other digits by 70 degrees or more.

Plioplatecarpus primaevus + *Ectenosaurus clidastoides* + *Prognathodon*
(figs. 54F, 55F)

DIAGNOSIS: Five plioplatecarpines species were included in this analysis and *Platecarpus tympaniticus* is the basalmost taxon. The other four species are united by 72(1) anteroposteriorly broad lateral tabs of the parietal, 146(1) posterior opening of the Vidian canal located on the sphenoid-prootic suture, 164(2) presence of an infrastapedial process and 240(1) lateral processes of the atlas reduced.

Ectenosaurus clidastoides + *Prognathodon*
(figs. 54F, 55F)

DIAGNOSIS: *Ectenosaurus* and *Prognathodon* are united to the exclusion of *Plioplatecarpus* in a clade diagnosed by 37(0) absence of a prefrontal-postorbitofrontal contact, 89(0) contact between supratemporal arch bones and frontal and parietal unforked, and 192(1) presence of a tall, narrow, coronoid process.

Prognathodon solvayi + *Prognathodon overtoni*
(figs. 54F, 55F)

DIAGNOSIS: These two species of *Prognathodon* included in this analysis form a clade diagnosed by 178(0) dentary ventrally convex along its long axis and 219(1) striated tooth crowns.

SECONDARY ANALYSES
OSTEOLOGY-ONLY ANALYSIS

Some recent analyses based on subsets of this data set have recovered somewhat different phylogenetic hypotheses for specific parts of the squamate tree. Among these are analyses of Iguania (Conrad and Norell,

2007a; Conrad et al., 2007), Gekkonomorpha (Conrad and Norell, 2006a), and Anguimorpha (Conrad, 2006b). Because these analyses each focused on the placement of specific fossil taxa, they relied heavily upon osteological characters. These differing phylogenetic hypotheses (when compared with the current analysis) are also important because the current phylogenetic hypothesis is based on data obtained, in part, while researching those studies. Additionally, the current analysis relies heavily upon fossil taxa and nonosteological characters cannot be scored for those fossils. Because of all these things, both individually and in concert, I performed an osteology-only analysis. The results of this analysis are presented as fig. 60 (note that, where the osteology analysis is identical with the full analysis, some taxa have been collapsed into larger clades in the figure). Areas of divergence between the osteological analysis and the full analysis will be highlighted below.

The osteology-only analysis was run exactly as was the full analysis of all the characters and taxa. A total of 3,973 equally short trees were recovered, each with a length of 3,034 steps. Each of these trees had a consistency index (excluding uninformative characters) of 0.1371 and a retention index of 0.7100. Note that because the character/taxon ratio has decreased, a decrease in consistency index is also expected.

IGUANIA (FIG. 60A): Most cladistic analyses (morphology-based and molecular) have suggested a basal dichotomy between non-acrodontan iguanians (= Pleurodonta; = Iguanidae sensu lato) and Acrodonta (see figs. 2, 3, 6, 7, 13; see also Conrad et al., 2007, Conrad and Norell, 2007a), but analysis of this hypothesis has generally been relatively weak. However, the full analysis presented above suggests that Acrodonta is nested within non-acrodontan iguanians. The osteology-only analysis reproduces the hypothesis of a basal dichotomy between Acrodonta and Pleurodonta (sensu Schulte et al., 2003; Conrad and Norell, 2007a; Conrad et al., 2007), but still suggests that hoplocercids are close to acrodontans. Additionally, this analysis supports the presence of a Cretaceous radiation of iguanians from the Gobi (Conrad and

Norell, 2007a), a hypothesis that was neither supported nor denied by the full analysis (figs. 54–56).

Opluridae is problematic. Opluridae is the monophyletic sister-taxon to a monophyletic Tropiduridae sensu Frost and Etheridge (1989) in the full analysis. Recent analyses have questioned this hypothesis (Conrad and Norell, 2007a; Conrad et al., 2007), as does the osteological data presented here (fig. 60A). Indeed, the osteology-only analysis suggests that *Chalarodon madagascariensis* is nested within Polychrotidae sensu Frost and Etheridge (1989) and that *Oplurus* is nested within Tropiduridae. Given the distribution of extant iguanians, this topology implies separate invasions of Madagascar by American clades of iguanians. However, many nested fossil ''pleurodontans'' are from Asia (e.g., *Ctenomastax*, *Igua*, *Polrussia*), suggesting that the biogeography of the group is more complex than it might appear based on extant taxa alone. Although this cannot be considered an argument in favor of oplurid polyphyly, it does offer some plausibility to the hypothesis.

The osteology-only analysis shows more complete resolution of the iguanian clades than the full analysis. For instance, it demonstrates the Cretaceous Gobi clade and resolves the tree supporting a hypothesis that *Igua* and *Polrussia* form a clade close to the tropidurid-*Oplurus* clade.

GEKKONOMORPHA (FIG. 60B): The full analysis suggested that *Parviraptor* (*P. estesi* and *P.* cf. *estesi* as described by Evans, 1994a) is a basal genus of gekkonomorph, falling between AMNH FR21444 and *Gobekko cretacicus* on the tree (figs. 54–56). However, Conrad and Norell (2006a) suggest that *Parviraptor* is a basal member of the lineage including Autarchoglossa and its stem taxa (Evansauria; see above). The osteology-only analysis, instead, suggests that *Parviraptor* is a scincogekkonomorph basal to the gekkonomorph-evansaur split at the level of (and in a polytomy with) *Scandensia ciervensis*. *Gobekko cretacicus* and AMNH FR21444 are recovered as basal gekkonomorphs and the topology within Gekkota is identical to that of the full analysis.

Conrad and Norell (2006a) also suggest that *Gobekko cretacicus* is nested within

Gekkota and that pulls the minimum divergence time of the primary gekkotan lineages fall in the Cretaceous. The placement of *Gobekko cretacicus* as a proximal outgroup to Gekkota does not refute that hypothesis, but it does remove all of the evidence supporting it.

SCINCOMORPHA (FIG. 60B): The osteology-only analysis does not recover a monophyletic Scincomorpha. Instead, *Tepexisaurus tepexii*, Scincoidea (including snakes, amphisbaenians, dibamids, acontids, and feyliniids), and a clade composed of Lacertoidea, Cordyloidea, *Pseudosaurillus becklesi*, "*Pseudosaurillus*" sp. sensu Estes, 1983, and Anguimorpha form a polytomy. In this topology, *Parmeosaurus scutatus* is a scincoid, *Slavoia darevskii* is the outgroup to Scincophidia, and Bainguidae is a basal radiation of Lacertoidea. Inclusion of bainguids in Lacertoidea and of *Parmeosaurus scutatus* in Scincoidea based on osteology is more in line with the traditional views of these taxa.

CARUSIOIDEA AND ANGUIDAE (FIG. 60C): Conrad (2006b) did not recover a monophyletic Carusioidea, but suggested that *Carusia intermedia* was a basal member of Anguimorpha (outside of the crown group). The current full analysis and the osteology-only analysis each recovers a Carusioidea, but the placement of that group varies between the two phylogenetic hypotheses. The full analysis places carusioids and anguids as a clade exclusive of Platynota, but the osteology-only analysis suggests that Carusioidea and the anguid clade (including glyptosaurs, see below) are successively more proximal outgroups to Platynota. The latter hypothesis is more similar to that of Gao and Norell (1998) (fig. 11) and Conrad (2005a, 2006b). Note that *Shinisaurus* is never a carusioid in the current analyses (figs. 54–56, 60) (contra Gao and Norell, 1998). The differences in topology between the present and previous analyses are probably related to the inclusion of numerous basal anguimorphs and/or scincomorphs (e.g., *Becklesius*, *Paramacellodus*, *Parmeosaurus scutatus*, *Pseudosaurillus*) and their effects on character polarities near the base of the anguimorph tree.

The full and osteology-only analyses show numerous minor differences in the placements of fossil anguids (including glypto-

saurs). The phylogenetic placements of *Apodosauriscus* and *Parophisaurus* are unresolved in the osteology-only analysis. *Parophisaurus* is recovered in a trichotomy with Anguidae sensu stricto and glyptosaurs. Numerous differences exist between the two trees in the placements of specific glyptosaurs. Notably, the osteology-only analysis suggests that the "melanosaurs" are more closely related to *Glyptosaurus* and *Proglyptosaurus* than the latter two taxa are to the *Helodermoides*-clade. The addition of data for *Placosaurus* and related, non–North American glyptosaurines, may help resolve this issue.

The full analysis suggests that glyptosaurs are deeply nested within Anguidae, the sister group to diploglossines (fig. 54D, 55D, 56D), but the osteology analysis suggests that glyptosaurs fall outside of the anguid crown group. If the latter is true, then taxonomy becomes an issue for this group. As described above, anguids traditionally are defined as a crown clade, but glyptosaurs are usually considered anguids. Camp (1923) considered Anguidae and Glyptosauridae to represent distinct "families" (fig. 1), but that distinction has not been widely followed since McDowell and Bogert (1954). Regardless, this semantic issue will be investigated further elsewhere.

PLATYNOTA (FIG. 60D): The osteology-based analysis is generally quite similar to the full analysis for Platynota. *Dorsetisaurus* and shinisaurs remain platynotans in both hypotheses. Minor differences include the placement of some taxa and polytomies, such as the specific placement of *Primaderma*, within monstersaurs and of "*Saniwa*" *feisti* and *Necrosaurus cayluxi* within goannasaurs. Importantly, the osteology-only analysis does not recover a mosasauriform position for *Eosaniwa* and leaves the placement *Paravaranus* unresolved with respect to varaniforms and mosasauriforms. However, the placement of mosasaurs within Goannasauria is confirmed.

DEFORMATION COMPARISONS

Several previous analyses of squamate relationships are described above and major differences between the phylogenetic hypotheses are highlighted. The current phylogenetic hypothesis was further compared with two

A

CHAMAELEONTIFORMES #
HOPLOCERCIDAE (see text) #
PHRYNOSOMATIDAE
Igua †
Polrussia †
Oplurus AMNH R47944
Oplurus cyclurus
Oplurus AMNH R71452
TROPIDURINAE
Stenocercus
Liolaemus
Leiocephalus
IGM 3/858 †
Ctenomastax †
Temujinia †
Zapsosaurus †
Anchaurosaurus †
CROTAPHYTIDAE
IGUANIDAE
Anolis vermiculatus
A. occultus
A. heterodermus
amber anole †
FMNH PR2379 †
ANISOLEPINAE
LEIOSAURINAE
Chlarodon
Polychrus guttosus
P. marmoratus
P. femoralis
CORYTOPHANIDAE
Hoyalacerta †
Huehuecuetzpalli †
Ardeosaurus †
Bavarisaurus †
Eichstaettisaurus †
Parviraptor †#
Scandensia †
AMNH FR21444 †
Gobekko †
GEKKOTA #
EVANSAURIA

SQUAMATA

Fig. 60. **(A–D)** Hypothesis of squamate relationships based on the current data matrix with non-osteological characters omitted; Adams consensus. Some taxa have been collapsed where the topology of the clade in this analysis is identical to that presented for the full data matrix (see fig. 55); those taxa have been marked with pound signs (#). Fossil taxa denoted by daggers (†).

B

Fig. 60.   Continued.

morphological analyses (Evans and Barbadillo, 1999; Lee and Caldwell, 2000) and two molecular analyses (Townsend et al., 2004; Vidal and Hedges, 2005) through deformation analyses of tree topology and length. Branches of the tree were manipulated and changes in tree length given the current data matrix were reported in the computer program Mesquite (Maddison and Maddison, 2006). Only the branches that were represented in each cited analysis (e.g., Evans and Barbadillo, 1999) were moved; the rest of the topology stayed as is within the current Adams consensus hypothesis (fig. 55).

MORPHOLOGY: The current phylogenetic hypothesis, reformed such that it is consistent with that of Evans and Barbadillo (1999),

lengthens the tree by 72 steps. To retrieve the topology presented by Lee and Caldwell (2000) requires an additional 106 steps. Making the limbed, Cretaceous, snakes form a basal clade outside of crown-group snakes (and changing nothing else) requires a tree 22 steps longer. Moving this clade into a position as the sister group to a polytomy with dolichosaurids, the *Adriosaurus-Pontosaurus* clade, and higher mosasauroids requires another 37 steps, for a total of 59 steps longer than the Adams tree presented here. Forcing shinisaurs into the more traditional position of being xenosaurids requires the addition of 10 steps.

MOLECULAR DATA: Only subtle differences are present between the studies of Town-

C

Fig. 60.   Continued.

send et al. (2004) and Vidal and Hedges (2005), but the taxonomic inclusiveness does vary. Forcing the current topology to reflect that of Townsend et al. (2004) requires an additional 175 steps. Deforming the Adams consensus of the current analysis to resemble that of Vidal and Hedges (2005) adds 171 steps to the tree.

BREMER SUPPORT

Numerous fossil taxa (e.g., *Chamops*, *Sakurasaurus shokawensis*, *Restes*) included in this analysis are so poorly known that only a few characters may be scored for them. These taxa were included if they were diagnostic from all other taxa in some way

D

Dorsetisaurus †
SHINISAURIA #
Parasaniwa †
Parviderma †
Colpodontosaurus †
HELODERMATIDAE #
Paraderma †
Palaeosaniwa †
Gobiderma †
Primaderma †
"*Necrosaurus*" *eucarinatus* †
Eosaniwa †
Proplatynotia †
Paravaranus †
"*Saniwa*" *feisti* †
Necrosaurus cayluxi †
Saniwides †
Telmasaurus †
VARANIDAE #
MOSASAURIA †#

PLATYNOTA
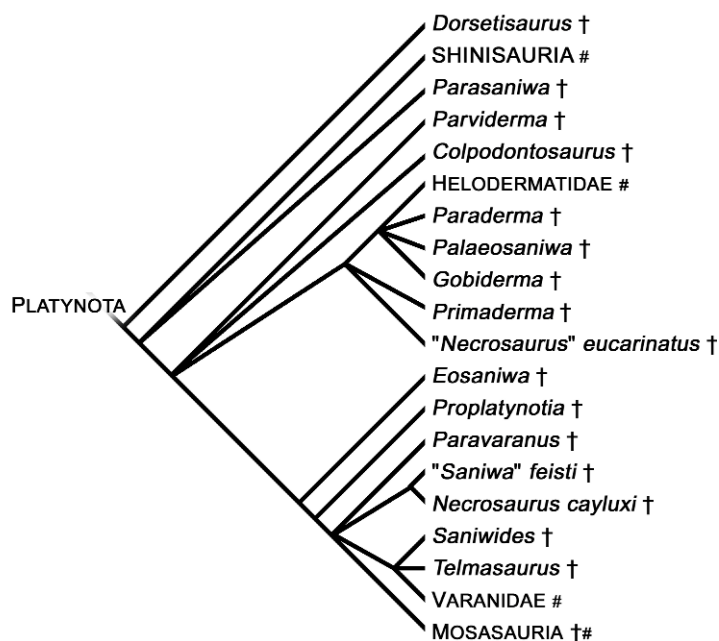
Fig. 60.   Continued.

for reasons described above in the materials and methods section. However, the incomplete nature of these fossils means that they may be somewhat volatile within the phylogenetic tree (as evidenced in comparing the strict and Adams consensuses; figs. 54, 55). In many cases only one additional step is necessary to change their position in the phylogenetic topology and, thus, collapse a number of nodes. One way to deal with this problem would be to delete these problematic taxa. However, again as described above, their deletion might be deleterious to the analysis as a whole and is not desirable. Bremer supports are listed for the strict consensus tree (fig. 55).

DISCUSSION AND CONCLUSIONS

PHYLOGENETIC HYPOTHESIS

Squamate relationships as identified from the present analysis differ somewhat from all previous analyses. Some of the major differences will be highlighted below.

BASIC TREE STRUCTURE: Importantly, if all extinct taxa are ignored, the basic structure of the tree (fig. 61) is similar to that of Estes et al. (1988) (fig. 2) with similarly applied names to the major clades. Iguania, Scleroglossa, Gekkota, Autarchoglossa, Scincomorpha, Lacertoidea, Scincoidea, Amphisbaenia, Dibamidae, Serpentes, and Anguimorpha are recovered as monophyletic. However, the current analysis resolves the position of amphisbaenians, dibamids, and snakes whereas Estes et al. (1988) does not (fig. 2A). Moreover, several new clades are recognized, including the Bainguidae and the Scincophidia.

GEKKONOMORPHS, SCINCOMORPHS, AND SNAKE ORIGINS: In contrast to the hypotheses put forward by Evans and Barbadillo (1998, 1999), the amphisbaenian-dibamid-snake clade is not closely related to geckos in this analysis. Xantusiidae are basal members of the Lacertoidea, in contrast the findings of some recent analyses (Presch, 1988; Evans and Barbadillo, 1998; Lee, 1998, 2000; Lee and Caldwell, 2000; Vicario et al., 2003).

Scincomorpha is found to be monophyletic, in contrast to some more recent analyses (Lee, 1998, 2000; Lee and Caldwell, 2000; Townsend et al., 2004; Vidal and Hedges, 2005). According to the present study, Scincomorpha includes Dibamidae, Amphis-

baenia, and Serpentes. Thus, the present analysis does not support a close relationship between snakes and mosasaurs as has been suggested by some morphological analyses (Lee, 1997, 1998, 2000; Caldwell, 1999a; Lee and Caldwell, 2000; Lee and Scanlon, 2001; Scanlon and Lee, 2002; Caldwell and Dal Sasso, 2004) or with an anguimorph-iguanian group as suggested by molecular data (Townsend et al., 2004; Vidal and Hedges, 2005). Instead, snakes are nested in a group of limbless and limb-reduced scincoids, including feyliniids, acontids, dibamids, and amphisbaenians. Numerous synapomorphies support this hypothesis, but the lack of a fossil record for most clades is somewhat worrisome. It is possible that future discovery of basal members of any of those clades (Feyliniidae, Acontidae, or Dibamidae) may show that the known extant taxa are convergent in their morphology. Additionally, more inclusive taxon sampling will be necessary to analyze the position of limb-reduced gymnophthalmids and lacertids with regard to amphisbaenians, dibamids, and snakes.

ANGUIMORPHA: Among anguimorphs, Xenosauridae is decidedly distinct from shinisaurs. Shinisaurs are found to be basal platynotans.

Although Caldwell (1999a) suggested that mosasaurs might fall outside of Scleroglossa, the current analysis supports the more common placement of mosasaurs as derived varanoids (contra Caldwell, 1999a). Importantly, some "necrosaurid" taxa are more closely related to the mosasaur clade than to any extant radiation (e.g., Varanidae or Shinisauridae).

WHY THE DIFFERENCES?: Differences in topology between this and other recent analyses of squamate phylogeny (e.g., Estes et al., 1988; Wu et al., 1996; Evans and Barbadillo, 1997, 1998; Lee, 1998, 2000; Caldwell, 1999a; Lee and Caldwell, 2000) probably result from more taxon sampling in this analysis and, perhaps to a lesser degree, from character selection. Character selection probably bears less of the impact on differences in the topological tree than does taxonomic selection for many reasons. First, the present analysis and all those listed above draw heavily from the data set of Estes et al.

(1988). Second, in addition to the inclusion of several new characters, the present analysis has been designed with the intention of including all of the nonredundant, informative, characters used in the described earlier studies. Thus, there is extensive overlap between previous analyses and this analysis. Third, taxonomic selection has varied widely in the previous analyses described and the current analysis has been designed with the intention of including all of the previously analyzed taxa. Fourth, new taxa have been incorporated in this analysis (e.g., *Lakumasaurus*, *Parmeosaurus scutatus*, *Temujinia*) that were not available to those researchers creating the earlier data matrices.

SCINCOPHIDIA, TAX. NOV.

According to this analysis, Feyliniidae and Acontidae, and the more problematic Dibamidae, Amphisbaenia, and Serpentes form a clade termed Scincophidia within Scincidae sensu lato. This topology seemingly represents a marriage of thought between the traditional anatomical studies suggesting that dibamids and amphisbaenians are scincomorphs and the recent cladistic studies identifying a potential relationship between dibamids, amphisbaenians, and snakes. It is unsurprising that the scincophidian clade has been previously unrecognized given the taxonomic sampling of earlier analyses.

Lee (1998, 2000) argues that the similarities between snakes, dibamids, and amphisbaenians is an example of convergence influenced by a fossorial lifestyle. He states that "nearly all of the characters supporting this arrangement are correlated with head-first burrowing … and invariably co-occur in other tetrapods with similar habits" (Lee, 1998: 369). It follows, then, that the unusual suite of characteristics associated with burrowing will cause unrelated fossorial forms to cluster together on a cladogram and that all fossorial squamates would share most or all of these character states, possibly recovering an erroneous topology. This is certainly a legitimate concern requiring analysis.

Importantly, the only specialized headfirst burrowers Lee (1998, 2000) includes in his analyses are Pygopodidae, Amphisbaenia,
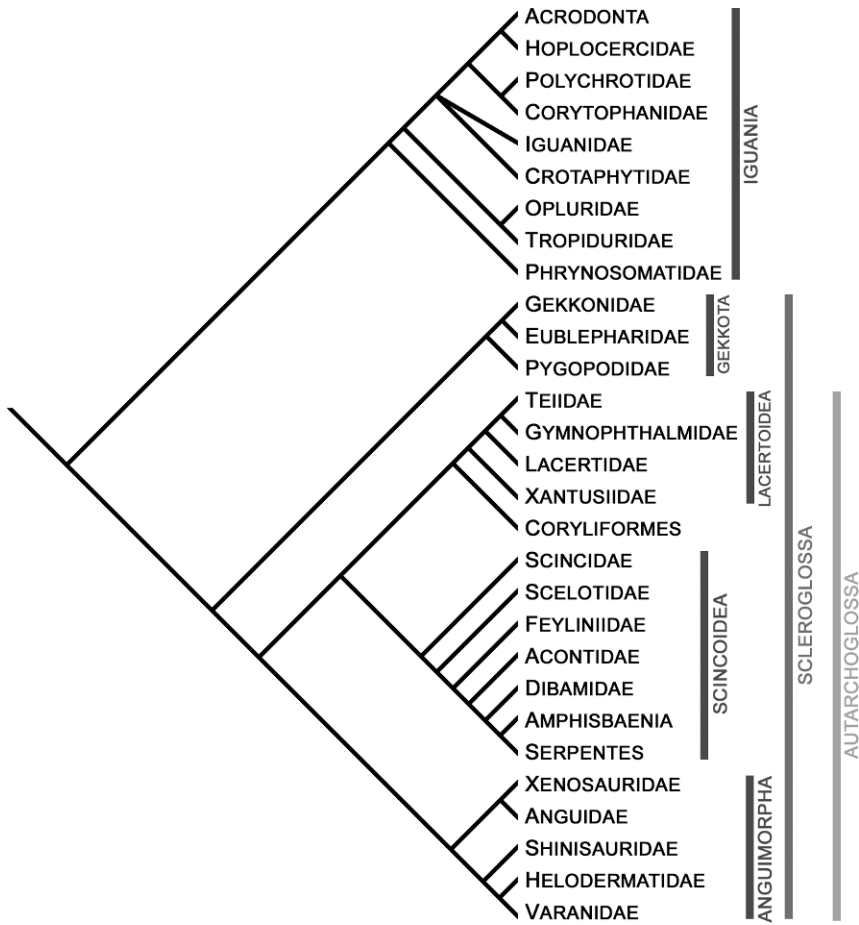
Fig. 61. The current phylogenetic hypothesis (Adams consensus) reduced to display only the major extant squamate clades. The accompanying higher taxonomy (in shades of gray along the right side of the cladogram) demonstrates that the taxonomy proposed here would create minimal disturbance for herpetologists and other neontologists.

and Dibamidae. He codes scincids sensu lato, Anguidae, and Serpentes (exclusive of *Pachyrhachis problematicus*) without breaking them into constituent clades. In doing so, he eliminates four major fossorial squamate radiations included here (Feyliniidae, Acontidae, anguines, and Scolecophidia) that could be used to further analyze his hypothesis of a convergent ecomorph. He also constrains *Pachyrhachis problematicus* to fall outside of crown-group Serpentes and, through his character codings, indicates his a priori assessment that fossorial snakes are not basal. Finally, Lee's (1998, 2000) answer to the perceived problem of the fossorial

ecomorph is to downweight all of the characters he considers to represent fossorial adaptations. This requires an a priori judgment about which characters are associated with headfirst burrowing.

A NEW TEST FOR THE FOSSORIAL ECOMORPH: The phylogenetic analysis above presents a hypothesis in which headfirst, limb-reduced burrowing appears no fewer than four times (within Gekkota, twice within Anguidae, and within Scincoidea), demonstrating that Lee's (1998, 2000) ecomorph problem is not a major concern for the current data matrix; and even this hypothesis neglects to assess the placement

of the limbless lacertoids and cordyliforms. A further analysis of the current data matrix was used here to determine the role of the fossorial ecomorph in the current analysis.

If Lee's (1998, 2000) strategy of down-weighting characters contributing to the fossorial ecomorph is accepted, then making assumptions about which character states to include and therefore which characters to downweight or delete is problematic. In the context of the present analysis, it is unnecessary to determine exactly which characters might contribute to a fossorial lifestyle because extant forms are readily recognized as fossorial or not. Nullifying the impact of the fossorial ecomorph may be accomplished by deleting all taxa in the current analysis except for the limb-reduced, fossorial forms (extinct or extant and fossorial; see below). This was accomplished in two analyses by deleting taxa of variable limb robustness and two analyses including only those taxa that are suspected of being closely related to snakes. The limbed outgroup Rhynchocephalia was always retained. All limbless snakes were always retained because even snake taxa that are not exclusively fossorial practice some head-first burrowing. (The strictly marine hydrophiines do not burrow, but are universally considered derived colubroids and were not specifically considered here.) Four analyses were then run with taxonomic inclusions as listed below.

1. The first analysis included the ingroup taxa Acontidae, Amphisbaenidae, Anilioidea, *Blanus*, Dibamidae (*Anelytropsis papillosus* and *Dibamus*), *Dinilysia patagonica*, Feyliniidae, limbless anguids (*Anniella*, *Anguis*, *Dopasia*, *Ophiodes*, ''*Ophisaurus*'' *attenuatus*, *Ophisaurus ventralis*, and *Pseudopus*), limbless macrostomatans, Pygopodinae (*Aprasia*, *Delma*, *Pletholax*, and *Pygopus*), Rhineuroidea, Scelotidae, Trogonophidae, and *Wonambi naracoortensis*.

2. The second analysis included all the taxa from the first analysis and the bipodal taxa *Bipes* and pachyrhachids.

3. The third analysis was used to analyze the position of mosasaurs when most limbed forms are deleted. All taxa were deleted except for those listed in the first two analyses and all of the Mosasauria.

4. The final analyze excluded the limbless anguids, but included all of the other taxa included

above and added the limbed gekkotans (Diplodactylinae, Eublepharidae, and Gekkonidae), Scelotidae, and Scincidae.

Snakes, amphisbaenians, and dibamids formed a clade in all of these analyses. Successively more distant outgroups in the first three analyses were pygopodines and a clade including Acontidae, Feyliniidae, and Scelotidae. The fourth analysis recovered a clade containing Scincidae sensu lato as the sister group to the snake-amphisbaenian-dibamid clade with a monophyletic Gekkota as the next outgroup. Limbless anguids were invariably monophyletic, but were found to be closer to the other limbless taxa than to the mosasaurs in the third analysis. Mosasaurs were monophyletic in both analyses in which they were included and always represented the basalmost ingroup lineage.

These results demonstrate the cohesiveness of the amphisbaenian-dibamid-snake clade even after nullification of fossorial/limbless characters. Snakes are not mosasaurs or even anguimorphs in any iteration of these analyses. Although the topology of the tree is somewhat different from that of the full analysis, this is not unexpected given the number of deleted taxa.

Certainly, being fossorial is a contributing factor to the morphology of scincophidians, but ecology is expected to be represented in morphology and phylogeny. Varanoids are usually predators of relatively large prey, chameleons are specialized for an arboreal existence, and gekkonids are typically crepuscular or nocturnal predators. These animals show heritable morphological adaptations for these behavioral and ecological aspects of their biology. The same should not be surprising in the fossorial clade Scincophidia.

BASAL SCINCOGEKKONOMORPHS AND EVANSAURS

The current phylogenetic hypothesis invites re-interpretation of some known squamate radiations pursuant to more precise understandings of geckos, scincomorphs, and necrosaurs. Based on current evidence, the traditional understanding of the diagnostic characters of these groups is insufficient for

referral of many fossil taxa. That is to say, for example, that many taxa that have been described as scincomorphs do not represent members of a monophyletic Scincomorpha. Instead, these misidentified taxa are important transitional forms representing intermediate morphologies between the major squamate clades. These misidentified taxa demonstrate the incremental acquisition of character states along a much broader span of squamate phylogeny than to which they are usually attributed. For example, *Ardeosaurus* and *Eichstaettisaurus* represent not true geckos, but basal scincogekkonomorphs possessing some characteristics usually attributed to the Gekkota.

Ardeosaurus, and *Eichstaettisaurus* are representative examples of many taxa close to the main trunk of the squamate family tree whose morphologies show a mosaic pattern of primitive and derived character states when placed in the context of Scincomorpha proper and Gekkota proper.

BASAL GEKKONOMORPHA?: Identification of "ardeosaurs" and "bavarisaurs" as basal scincogekkonomorphs rather than as stemgeckos demonstrates the poor quality of the gecko fossil record. *Gobekko cretacicus* remains the only well-preserved basal gekkonomorph described to date, but even this taxon seems very like modern geckos (see Borsuk-Białynicka, 1990; Conrad and Norell, 2006a) and offers little in the way of a transitional form between the basal scleroglossan condition and Gekkota. However, a new taxon from the Aptian-Albian of Mongolia (AMNH FR21444) was included in the current analysis and helps to polarize character states for Gekkonomorpha. This currently unnamed taxon possesses primitive characteristics such as a complete supratemporal arch and a toothed pterygoid, but also possesses characteristics shared with geckos and *Gobekko cretacicus*. Intermediate taxa such as this reduce the number of character states that may be used to diagnose a given clade by expanding the distribution of some characters and helping to bridge morphological gaps between previously known taxa. They also offer important insights into the relative timing of synapomorphy acquisition for clades and character evolution.

It is worth noting that Sereno (2006) does not consider AMNH FR 21444 (fig. 62) to represent a basal gekkonomorph, but suggests it as a possible basal squamate. He bases his assertion on "the narrow width of the nasals, the simple transverse frontoparietal suture, broad pyriform recess, and absence of [a] pterygoid-vomer contact" (Sereno, 2006:124A). Because Sereno (2006) is the only other study currently addressing this specimen, I will discuss this hypothesis and the characters used to support it here.

Nasal width is difficult to assess outside the context of some comparison (that is, narrow relative to what?). Evans and Barbadillo (1998) compared nasal width to the width of the external nares, but it is unclear if Sereno (2006) is also making that comparison. Regardless, no other group or species otherwise hypothesized to be near the basal squamate condition (by this or other studies) has particularly narrow nasals (e.g., iguanians, *Bavarisaurus*, *Eichstaettisaurus* (fig. 29), dibamids (fig. 31), or basal rhynchocephalians (fig. 32)); indeed, narrow nasals seem to be a varanoid characteristic. Moreover, the nasals are not preserved in AMNH FR 21444.

The suggestion that AMNH FR 21444 has a transverse frontoparietal suture (Sereno, 2006) is erroneous (see illustrations and CT data in Conrad and Norell, 2006a, 2007b). Instead, this animal possesses a gently anteriorly arched frontoparietal suture.

A broad pyriform recess (as defined above, character 123) is plesiomorphic for iguanomorphs, gekkonomorphs, scincomorphs, and anguimorphs, with reversals in most of these groups. Presence of this character state in AMNH FR 21444 does not suggest that it is close to the basal squamate.

The specimen AMNH FR 21444 lacks as vomer-pterygoid contact as described by Sereno (2006). However, this character state is present in the majority of squamates (reversals within chamaeleontiforms and amphisbaenians, and in polyglyphanodontids and *Shinisaurus crocodilurus*).

Thus, none of the character states suggested by Sereno to place AMNH FR 21444 "just outside Squamata…" or "…at a basal position within Squamata," (Sereno, 2006: 124A) actually support that hypothesis.
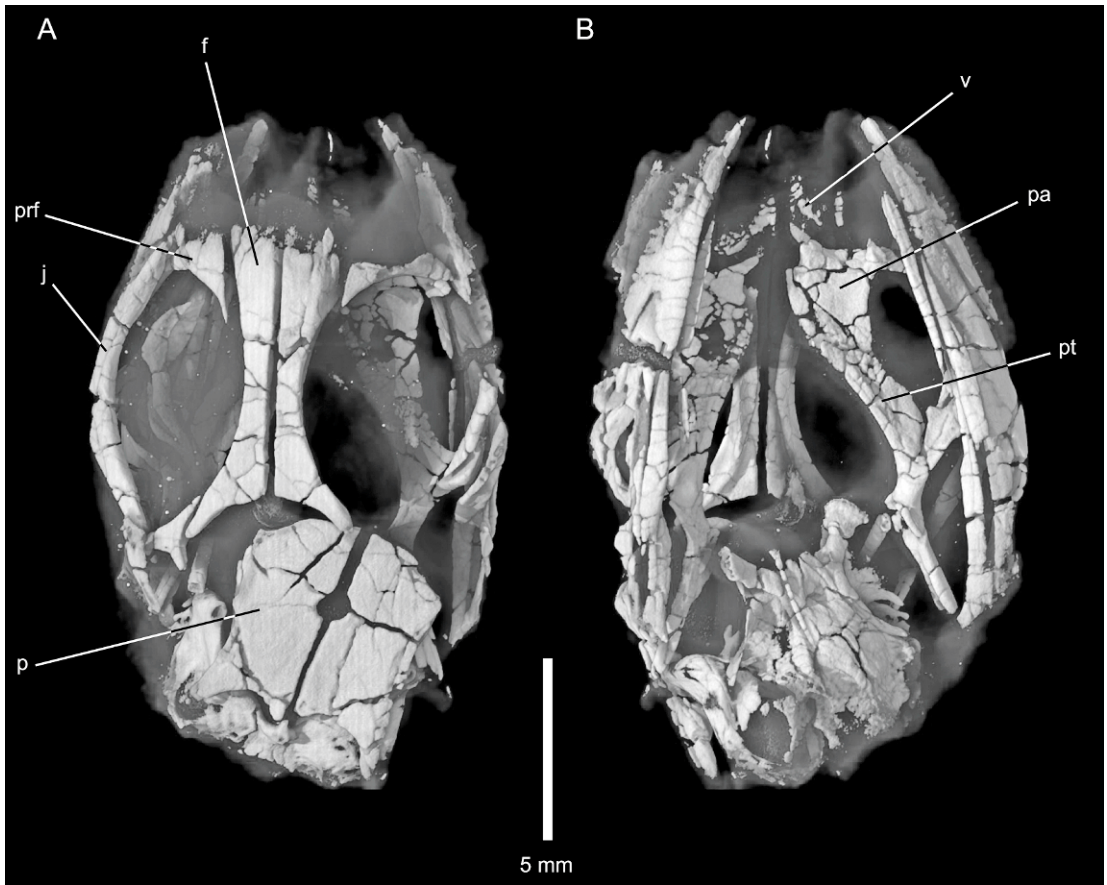
Fig. 62. AMNH FR21444, a basal gekkonomorph whose morphology was recently described by Conrad and Norell (2006b). These are **(A)** dorsal and **(B)** ventral views of high-resolution x-ray computed tomography scans of the skull (anterior toward the top). The scans from which this figure was constructed are available online (Conrad and Norell, 2007b).

Indeed, these character states would not be useful for placing any taxon at the base of Squamata. Given the six unambiguous synapomorphies uniting AMNH FR 21444 with other gekkonomorphs listed above, it currently is most prudent to consider AMNH FR 21444 a basal gekkonomorph.

TAXONOMIC CONSIDERATIONS

STRINGENCY: Taxonomy is a tool for communicating about groups of things. Phylogenetic taxonomy has been, and will continue to be, an important tool with which to discuss organisms in a phylogenetic framework. Ideally, a single taxonomic scheme would be used for every given taxonomic group and that taxonomy would be based on the one true phylogeny of the group. Unfortunately, we are unlikely ever to know the one true phylogeny for any group with more than a few species. Therefore, taxonomists must be careful to make their nomenclatural schemes strict enough to be meaningful, but not so rigid that they are useless if some taxonomic content changes based on new discoveries and/or analyses.

Lee (1998) presents a taxonomic scheme in which any shifting of taxa between groups invalidates the meaning of two or more taxon names. This, or any similar stringency in
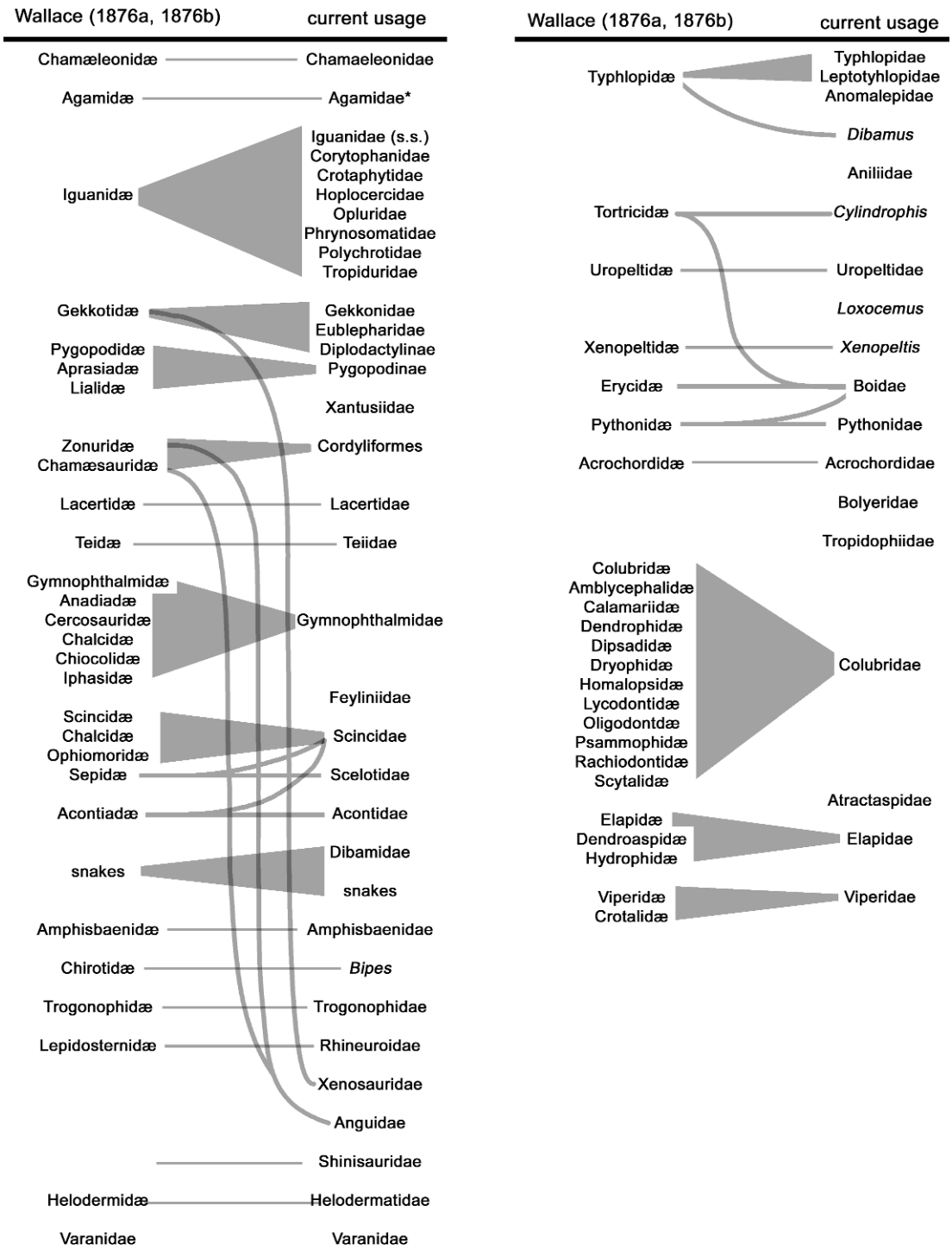
Fig. 63. Comparison of "family"-level squamate taxonomies from Wallace (1876a; 1876b) and current usage (modified after Behler and King, 1979, Whitfield, 1982, Bauer, 2003, Gans, 2003, Pianka and Vitt, 2003, Shine, 2003, and Uetz, 2007). There is remarkable consistency between the two lists, especially given
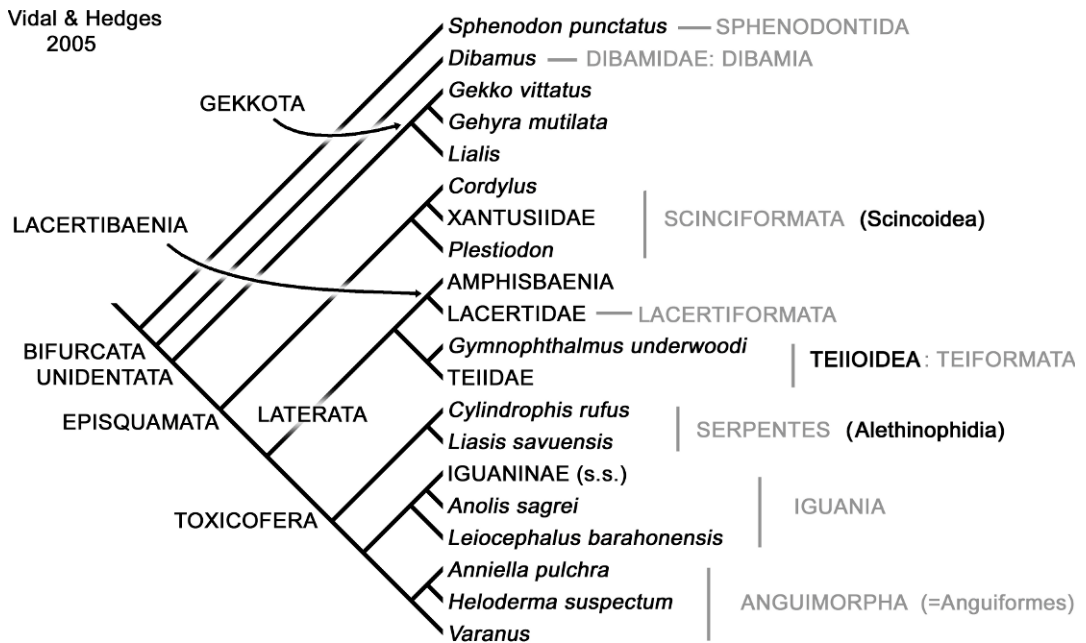
Fig. 64. The taxonomy of Vidal and Hedges (2005) as they apply it to their phylogenetic hypothesis. Taxonomy in gray to the right of the cladogram highlights redundant taxa and taxa applied inappropriately with respect to the content included in the analysis.

taxonomy, makes taxonomy less useful as a tool for discussion of ideas or phylogeny.

CONTINUITY AND SUPERFLUOUS TAXONOMY: New phylogenetic hypotheses sometimes require revisions in taxonomy, but the taxonomy of the squamate "families" has been relatively stable for well over 100 years.

Wallace (1876a, 1876b) supplied a then-comprehensive list of squamate taxa including 2,256 species in 52 families. There is a remarkable correlation between that family list and the current understanding of squamate families, despite the fact that around 8,000 species of squamates are currently named (Uetz, 2007) (fig. 63). Of course, there are some differences, but most of these include further subdivision of currently recognized families by Wallace (1876a, 1876b),

or vice versa rather than substantive differences in the included taxa. Other major differences include the recognition of the families Anguidae and Dibamidae, but Wallace's (1876a, 1876b) system remains useful even now. Similarly, Camp's (1923) suprafamilial taxonomy remains useful (see part of it in fig. 1).

Vidal and Hedges (2005) recently proposed a radically different phylogenetic hypothesis for squamate interrelationships (fig. 12B), and applied new taxonomy to some groups. The phylogenetic hypothesis of Vidal and Hedges (2005), similar to that of Townsend et al. (2004), is important and intriguing given the dissimilarities between those hypotheses and the usual ideas of squamate interrelationships (for example, compare with figs. 2–9, 53–56). However, much of the new

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the separation of approximately 130 years and since more than three times as many squamate species are now recognized. The major differences are mostly the result of identifying new squamate clades (in many cases, through the discovery of species) and subdivision of "families" or lumping them together. Clearly, taxonomy may be relatively constant and remain informative.

taxonomy presented by Vidal and Hedges (fig. 64) is unhelpful and gratuitous. Moreover, Vidal and Hedges (2005) offer no explanation for most of this taxonomy, leading to several problematic situations. Vidal and Hedges (2005) sampled within *Dibamus*, but applied to that branch the name Dibamidae (a name used to describe both *Dibamus* and *Anelytropsis papillosus*) and Dibamia. Thus, the name Dibamia becomes an apparent synonym of Dibamidae or, conceivably, *Dibamus*. Lacertidae is also labeled Lacertiformata. The clade containing teiids and *Gymnophthalmus underwoodi* is labeled both Teiioidea and Teiformata. The clade formed by Teiioidea, Lacertidae, and Amphisbaenia in their tree is labeled Laterata (Vidal and Hedges, 2005), even though this clade is essentially the same as the traditional idea of Lacertoidea (minus xantusiids; but see the usage of Lee, 1998 and Vicario et al., 2003). The Scinciformata of Vidal and Hedges (2005) is essentially the Scincoidea of Vicario et al. (2003) and is almost exactly the Scincoidea of Townsend et al. (2004).

Conclusions

The current study was undertaken with the intentions of supplying an extensive morphological phylogenetic data matrix for squamates, offering a phylogenetic hypothesis based on that matrix, and providing an updated and useful taxonomy. The data matrix provided here is the most taxonomically inclusive so far offered and it may be useful for morphologists as well as for systematists. The provided phylogenetic hypothesis will not be the last word on the subject of squamate phylogeny. Indeed, the matrix is already being expanded both in taxa and characters. Others may well analyze the provided data matrix differently, obtaining a different result. The phylogenetic hypothesis provided herein is no more than an accurate description of the data as it was analyzed. The taxonomy I provide reflects the usage of taxon names as I perceive them to be most often used. The definitions of existing taxon names in this study are offered only as a tool; a reference for the taxonomy as a whole. Taxonomy is most useful as a tool for discussing groups of animals, phylogenetic hypotheses, and ideas about evolutionary history.

Squamata is a clade of extraordinary diversity now and throughout its 210 million - year history. The wide geographic distribution of squamates, their prominence in modern and fossil ecosystems, and their remarkable morphological diversity must rank them as one of the most important vertebrate clades for continued scientific study.

ACKNOWLEDGMENTS

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APPENDIX 1

SPECIMENS USED FOR CODING MORPHOLOGY

INSTITUTIONAL ABBREVIATIONS: AMNH, American Museum of Natural History; FMNH, Field Museum of Natural History; GM, Geiseltal Museum of the Martin-Luther-Universität in Halle/Saale (Germany); IGM, Institute of Geology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; REE, Richard E. Etheridge Collection; TMM, Texas Memorial Museum; UF, University of Florida, Florida State Museum

AMPHISBAENIA: *Amphisbaena alba* AMNH R64884, FMNH 226360; *Bipes canaliculatus* FMNH 105039; *Blanus* sp. FMNH 206116; *Spathorhynchus natronicus* AMNH FR8677

ANGUIMORPHA: *Abronia deppii* FMNH 38523; *Aiolosaurus oriens* IGM 3/171; *Anguis fragilis* AMNH R56193; *Anniella nigra* FMNH 213666; *Bahndwivici ammoskius* FMNH PR 2260; *Barisia imbricatus* FMNH 6526, FMNH 6528; *Carusia intermedia* IGM 3/18, IGM 3/22, IGM 3/23, IGM 3/26; *Celestes costatus* FMNH 13254; *Clidastes propython* FMNH PR 38, FMNH P27324; *Clidastes* sp. AMNH FR14791; *Diploglossus millepunctatus* FMNH 19248; *Dopasia harti* FMNH 24298; *Elgaria* sp. FMNH 23235, FMNH 213397; *Eosaniwa koehni* GM XXXVIII/57; *Estesia mongoliensis* AMNH FR29072 (cast); *Gerrhonotus liocephalus* FMNH 22452; *Heloderma horridum* FMNH 22038, FMNH 250611, FMNH 31366, FMNH 98468, FMNH 98776; *Heloderma suspectum* AMNH R74778, AMNH R142627, FMNH 218077, FMNH 22232, FMNH 22249 FMNH 98774; *Helodermoides tuberculatus* AMNH FR5902, AMNH FR6800, AMNH FR8706; *Lanthanotus borneensis* FMNH 130981, FMNH 134711; *Melanosaurus maximus* AMNH FR5168, AMNH FR5175; *Mosasaurus hofmanni* (including *M. maximus*) AMNH FR1389, AMNH FR2533, AMNH FR5149, TMM 313-1; *Ophisaurus attenuatus* FMNH 98466, FMNH 98467, FMNH 207671; *Ophiodes* sp. FMNH 9270; *Paraderma bogerti* AMNH FR5804; *Paraglyptosaurus princeps* AMNH FR6055; *Parasa-*

niwa wyomingensis AMNH FR22012; *Parophisaurus pawneensis* AMNH FR8711; *Peltosaurus granulosus* AMNH FR42913, AMNH FR1710, AMNH FR8138, FMNH P27072, FMNH UC391, FMNH UC1720; *Platecarpus tympaniticus* (*P: ictericus*) AMNH FR1532; *Platecarpus* sp. FMNH PR 467; *Pseudopus apodus* FMNH 216745, FMNH 22088, FMNH 22359; *Shinisaurus crocodilurus* FMNH 233130, FMNH 234242; UF 57112, UF 61149, UF 61685, UF 62315, UF 62316, UF 62497, UF 62536, UF 62578, UF 68203; *Telmasaurus grangeri* AMNH FR6643; *Tylosaurus proriger* AMNH FR221, AMNH FR1543, AMNH FR3451; *Varanus acanthurus* FMNH 218083, FMNH 98935; *Varanus albigularis* AMNH R47726, FMNH 17142, FMNH 22354; *Varanus bengalensis* FMNH 22495; *Varanus dumerilii* FMNH 223194, FMNH 228151; *Varanus exanthematicus* FMNH 212985; *Varanus gouldii* FMNH 250434; *Varanus griseus* FMNH 31380; *Varanus komodoensis* AMNH R37908, FMNH 22199, FMNH 22200; *Varanus niloticus* AMNH R10524, AMNH R74603, FMNH 12300, FMNH 17144, FMNH 17145, FMNH 17146, FMNH 22084, FMNH 22496, FMNH 45807; *Varanus oliveaceus* FMNH 223181; *Varanus prasinus* FMNH 229907; *Varanus salvadorii* AMNH R59873; *Varanus salvator* AMNH R142471; FMNH 22204, FMNH 31320; *Xenosaurus grandis* FMNH 211833; *Xenosaurus platyceps* UF 43396, UF 43397, UF 45590, UF 53691, UF 56122

GEKKOTA: *Aeluroscalabotes felinus* FMNH 188235; *Coleonyx mitratus* FMNH 5053; *Cyrtodactylus cavernicolis* FMNH 131508; *Cyrtodactylus malayanus* FMNH 188211; *Cyrtodactylus pulchellus* FMNH 209435; *Cyrtopodion scabrum* FMNH 236232; *Gekko gecko* AMNH R-141109, AMNH R-130786; FMNH 14448, FMNH 31013, FMNH 213417; *Gonatodes albogularis* FMNH 209439, FMNH 209440; *Hemidactylus garnoti* FMNH 206754; *Hemitheconyx caudicinctus* AMNH R104409, FMNH 209441; *Lialis burtonis* FMNH 22109; *Myrmecodaptria microphagosa* IGM 3/95; *Pachydactylus bibroni* FMNH 209449, FMNH 209451; *Phyllurus platyurus*; *Teratoscincus microlepis* AMNH R-88524; *Uroplatus* sp. FMNH 250684; unnamed taxon AMNH FR24111

IGUANIA: *Acanthosaura crucigera* FMNH 222259; *Acanthosaura lepidogaster* FMNH 229477; *Aciprion formosum* AMNH FR8717; *Agama agama* FMNH 22189, FMNH 22190; *Amphibolurus barbatus* FMNH 22451, FMNH 51647, FMNH 211265; *Anolis carolinensis* FMNH 229898; *Anolis equestris* FMNH 31312; *Anolis* (*Phenacosaurus*) *heterodermus* AMNH 44987; *Anolis occultus* AMNH 115547, AMNH 147826; *Anolis* sp. FMNH 98636; *Anolis vermiculatus* AMNH 70092, AMNH R63062; *Basiliscus vittatus* FMNH 98361, FMNH 98362, FMNH 98363; *Callisaurus draconoides* FMNH 98364, FMNH 98366; *Chalarodon madagascariensis* AMNH 71461; *Corytophanes cristatus* FMNH 22093, FMNH 206165; *Crotaphytus collaris* AMNH 82297, AMNH 109069, AMNH R-73715, FMNH 637, FMNH 22301, FMNH 22302; *Ctenomastax parva* IGM 3/61, IGM

3/62; *Diplolaemus bibroni* FMNH 7947, REE 2506; *Dipsosaurus dorsalis* FMNH 249785, FMNH 249786; *Enyalioides palbebralis* FMNH 40008; *Enyalioides laticeps* FMNH 31354; *Gambelia* sp. FMNH 211251; *Gambelia wisilizenii* AMNH R-108315; AMNH R-141126; AMNH R-147874; *Hoplocercus spinosus* AMNH 89398, AMNH 90384, AMNH 90658, AMNH 93807; *Iguana iguana* AMNH R74631; *Laemanctus longipes* FMNH 213398; *Leiocephalus carinatus* FMNH 22754; *Leiolepis belliana* FMNH 229470; *Leiosaurus bellii* REE 2410; *Microlophus a: albermarlensis* AMNH R-77624; *Liolaemus alticolor* AMNH 77610; *Liolamus saxitilis* AMNH R-65194; *Liolaemus signifier* AMNH R-90459; *Liolaemus simonsii* AMNH 77625; *Liolaemus zapallarensis* AMNH R-37733; *Morunasaurus annularis* AMNH R-57178; *Oplurus cyclurus* AMNH 138120; AMNH R-71462; *Oplurus quadrimaculatus* AMNH R-47944, AMNH R-71452; *Petrosaurus thalassinus* FMNH 216154; *Plica plica* FMNH 31355; *Polychrus femoralis* FMNH 81405; *Polychrus guttorosus* AMNH R-32675; *Polychrus marmoratus* AMNH R-141130; *Pristidactylus achalensis* REE 2487; *Sauromalus ater* FMNH 22248; *Sauromalus* sp. FMNH 31015; *Sceloporus spinosus* FMNH 98440; *Stenocercus scapularis* FMNH 40612; *Stenocercus arenarius* FMNH 40589; *Temujinia ellisoni* IGM 3/64, IGM 3/65, IGM 3/69; *Tropidurus peruvianus* FMNH 34191; *Uromastyx aegyptius* FMNH 31030; *Urosaurus ornatus* FMNH 98456; *Uromastyx* sp. AMNH R73357; *Urostrophus bibroni* FMNH 28863; *Urostrophus vautieri* REE 2507; *Uta stansburiana* FMNH 98463; unnamed Mongolian taxon IGM 3/858; unnamed FMNH specimen FMNH PR 2379

LACERTIFORMES: *Acanthodactylus pardalis* FMNH 63073; *Ameiva ameiva* FMNH 22294; *Ameiva chrysolaema* FMNH 51622; *Callopistes flavipunctatus* FMNH 8452; *Cnemidophorus motaguae* FMNH 207870; *Cnemidophorus deppii* FMNH 98491; *Dracaena* sp. FMNH 207657; *Kentropyx calcarata* FMNH 31352; *Lacerta lepida* FMNH 229612, FMNH 22267; *Lacerta viridis* AMNH R99684, AMNH R1148; *Podarcis taurica* 213390; *Teius tegu* FMNH 170853; *Tupinambis teguixin* FMNH 217382

RHYNCHOCEPHALIA: *Sphenodon punctatus* FMNH 11113

SCINCOIDEA: *Acontias meleagris* FMNH 187063; *Cordylus giganteus* FMNH 211837, FMNH 257130, FMNH 31283; *Eumeces algeriensis* FMNH 229652; *Eumeces copei* FMNH 98509; *Eumeces fasciatus* FMNH 98512; *Eumeces obsoletus* FMNH 98516; *Gerrhosaurus validus* FMNH 228400, 214858; *Mabuya multifasciata* FMNH 120304; *Scincella melanosticta* FMNH 180970; *Scincus scincus* AMNH R2245; *Sepsina angolensis* FMNH 142793, FMNH 142794; *Sphenomorphus cyanolaemus* FMNH 120244; *Tiliqua scincoides* FMNH 51702, FMNH 51710, FMNH 57520, FMNH 73343; *Tiliqua nigrolutea* AMNH R99684; *Typhlacontias* sp. FMNH 142787; *Typhlosaurus lineatus* FMNH 142756

SERPENTES: *Anilius scytale* FMNH 35683; *Boa constrictor* FMNH 22362; *Cylindrophis maculates* FMNH 13100; *Eunectes murinus* FMNH 31630; *Python reticulates* FMNH 31324, FMNH 99868

XANTUSIIDAE: *Lepidophyma gaigeae* FMNH 98560; *Xantusia* sp. FMNH 22101; *Xantusia vigilis* FMNH 22329

APPENDIX 2
DATA MATRIX

Character state matrix used in this analysis in a Nexus format. Note that suprageneric taxa appear in ALL CAPS. Character 364 (biogeography) was excluded from the analysis, but the data are included here for descriptive purposes. Similarly, *Marmoretta* and Kuehneosauridae are included in this data matrix for comparative purposes, but were not included in the analysis because their relationship to Squamata is not clear (Evans, 1991; Waldman and Evans, 1994; Müller, 2003, 2004b).

#NEXUS
BEGIN DATA;
DIMENSIONS NTAX=225 NCHAR=364;
FORMAT MISSING=? GAP=- SYMBOLS= "0 1 2 3 4 5 6 7 8 9";
OPTIONS MSTAXA=POLYMORPH;
MATRIX
KUEHNEOSAURIDAE 100000-000 02-?00?200 000000-000 00000?0000 0?00000000 000100000? ????00?0?0 000?002?00 0000?00000 0210010000 ???????0?0 0000000000 -000000??0 0?0??????? ????-- 0000 0???-???40 0000?0000? ?????0000 00?00-000? 0?????????? ?00-000000 0000000000 000000??1 00- 00001?? 020001000? 022?00??? ?00?00???? ????00000 ?001-00000 ?0??????? ????0????- -- ??????? ????????? ????????? ????????? ????????? ???4
Marmoretta 110???-000 010?00000? 00?????010 ??00000000 1?00001000 0000100000 0-??0000?? 001?10???? ?????0??0? 0?00?0000? ?????????? ????????? ????????? ????????? ????????? ???0?00??? ?1--??0000 ???20-0??? ?110?0?000 ?????????? 0000000000 ?00000???1 0000??00?? ?????10??? ????????? ????????? ????????? ????????? ????????? ????????? ????????? ???4
RHYNCHOCEPHALIA 100000-000 0102000000 01{12}00000{01}0 0000000000 {12}0000000{01}0 0010100000 0-0-000010 0-11000-00 000000?00 0?10020000 0000?00000 0000000001 -10000?000 0000000000 0000001000 000000?000 110001000- - 0001--001 0{01}300-01-- -00000?--0 000-000000 0{01}0{01}0000{01}0 0000000000 10-0{01}01-02 0{01}00010000 0000?01000 000000?000 000-000000 0001000000 01000001-0 00000-00-- --000?0000 00000----- ?00?0000?0 0???0?0001 00{01}00-0--- 10-4
Huehuecuetzpalli mixtecus 2100?1-000 012?000100 10???00100 ??100000-0 2-00001100 000110200? 0- 0-0-00?001 ?010012?00 0010000000 0100000000 ????1???? ????????1? ????????? ???0?????? ????????? ????????11 ?000?001?? ???????000 01?20-001? ?1?1?1011? ?00-????? 2000000?00 ?00000????

1000101-02 0001000000 0000000000 010?0010?0 000?00000? 000110?000 ?????????? 0???10?0?? ?0???????? ?????????? ?????????? ?????????? ?????????? ???3

AMNHgekkonomorph ?????0-000 ????????0? ??3??????0 0100000010 3-00001100 000?002100 100-111000 0-00-10-10 000001??10 001001100? ????100010 0?10100210 0000000000 1100022010 0011001?0 10?00????? ?????0?00- -011000100 02021?0001 011010?000 000-101101 2000??0000 0??000???? ????????? ????????? ????????? ????????? ????????? ????????? ????????? ????????? ????????? ????????? ????????? ????????? ???8

Gobekko cretacicus 1000?0-000 110?000000 003??00000 ?000000010 3-?0002--- -001002100 110-1110?? 000?-03?10 000-011?1? 0??0?????? 0???10110 101?1-0?11 000100?000 ?10?1?200? ??????10?0 1?001???3? ??????0??? ????????0? 2??????0?? ????????? ????????? ???0????? ??0?????? ????????? ????????? ????????? ????????? ????????? ????????? ????????? ????????? ????????? ????????? ????????? ????????? ???8

DIPLODACTYLINAE 100-00-000 {01}102000000 0130100000 0100000000 3-00002--- -001102100 11??110001 0001-0311{01} 00?-?11-10 0??-1?-011 0000?{01}0110 0011100211 000100?000 1100122010 0?00001000 100011?031 100000000- 000010100 22320-0000 011010?000 010-111101 1000000000 0000000010 {12}0-1001-11 0101000000 0100001011 110101{12}010 0?0100200- 1001101000 311?00?1-1 {01}0000-0--- --010?1010 00100????? 0000{12}10000 0000000??? ????????? ???9

Tepexisaurus tepexii 101?????? ????000??? ?????????? 000?????? ????00110? 0?01?????? 1????????1 ???0-2???0 ???1?10??? ???00?100? ?????0??0 0011100211 000000?000 ??00??2001 0?00?1?0?0 0?0?????11 ?00?00000? ?001?-0?00 02?00-0011 010010?10? ?00-100?11 2000000000 ?000000??1 2001?01-?? 00000????0 03????0?01 110?01?0?? 0?????0000 00?11??00 ?1???0???? 0?0?0-0-?- --???????? ?????????? ????????? ????????? ????????? ???3

Eolacerta 100??00111 110?000000 1130?00000 ??000?00?0 10??000000 0001000100 ????1??011 001?-20000 00?0?1?00 0??00?1001 1???????? ????????2?? ?????0?0?? ??0???????? ??10???000 0??00??1? ????0?000? ?000???000 0001100000 010010?10? ?010100000 0000000000 000000??1 2001221-?? 00??010000 0000000?01 110?00?010 0???00000- 1001100000 01?????20? ?0??1??00 0????????? ?????????? ????????? ????????? ????????? ???4

GYMNOPHTHALMIDAE 1{01}10000?1{01} 1100000000 0030010000 {01}1000000?0 {13}?00000000 0101102100 1{01}0-{01}10011 0012023000 00{02}00{01}0010 000{01}021001 00001{01}0110 0011100{12}11 10{01}0000000 0{01}00002000 002{01}001000 0000010010 200001001- -000??-100 {02}{02}020-001{01} 01101{01}1000 001100000{01} 0300000000 {01}00000{01}101 20012{02}1-?? 0001010000 100000?001 111000{13}00{01} 0?1{12}002000 0000201000 ?10{01}00?201 {01}1000-0-00 0-00004020 00?00????? 0110001101 10001?2011 0000010{01}00 100{23}

Chamops ?0???00?1 1???000??? ??30?1?00? ?0????0?? 1???00???? ?1???????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????0??- -?????00? 02???????? ?????????? ?????????? 0400?{01}0000 ?00000???? ?????????? ?????????? ?????????? ?????????? ?????0??? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ????

TUPINAMBINAE 10{01}0000111 11{01}200{01}000 {01}{01}30{01}10000 00010000{01}0 1100000100 0101102100 0-0-100011 0012{01}23000 0000000100 0200021000 ?000100110 0010100{12}11 1011010000 0000002000 0010011000 0000000010 200000001- -00{01}000000 0202100001 01{01}0100000 0011000000 04000{01}0000 0010000001 2011201-00 0031010000 1000000001 1110001010 0001002000 0000100000 010?00?201 00000-0--- --00004?20 001002???? 0110001101 10001?2011 0000010{01}{01}0 10{01}2

TEIINAE {12}000000111 1102000000 0130010000 0001000000 1{01}0000{01}{01}00 01{01}1102100 0-??000011 0010023000 00?0?00010 0??00?1000 ?000?00110 0010110{12}11 10110{01}?000 00000021-0 0?100{01}1000 000000?010 200000001- -000000000 02020-000{01} 011011?000 0011000000 04000{01}0000 0000001001 20012?1-10 0031010000 1000001001 11100{01}10{01}0 0101002000 0000100000 010?00?201 00000-0--- --00004?20 001002???? 0110001102 10001?2011 00000{01}01{01}0 100{23}

*Pseudosaurillus*SP ?????01?1 ?????????? ??300??10? ?????????? ?????????? ????002100 10?????011 ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????1000? ?000??-100 02010-0000 010010?10? ?00-100001 0000?00000 0???00???1 20011?1-?? ????01???? ?????????? ?????????? ?????????? ??????1-? ?0??1???0 0????????? ?????????? ?????????? ?????????? ?????????? ???4

*Pseudosaurillus*BECK ?????01?? ?????????? ????0?00? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????0?00? 00000?10? 0201??0001 010010?10? ?????????? 0000?00000 0??00???? ?????????? ?????????? ?????????1 ??????010 ????0020?? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ???4

LACERTIDAE 1000000000 1100000000 0010{01}{01}0000 0000000?0 {13}000000000 0{01}01{01}{01}02100 0-??110011 0012-1{03}?01 0??1?10010 0??{01}0?1001 1000?00010 0011100{12}10 00{01}000?000 00000021-0 0?20011000 000000?010 200001001- -00000-000 02020-0000 0100100000 0010000000 0300000000 00{01}0000001 20011{02}1-?? 00{01}10{01}0000 100000?001 110100{01}000 0{01}{01}{01}{12}000000 0001200000 010{01}00?201 00{01}00-0-00 0-00003020 0010001{01}?0 0{01}00001102 10001?0{01}11 0000000000 100-

Ornatocephalus 1001?00111 110?000000 11??0??001 ?0000?00?? 3-??000011 000100010? ????1??0?? ?01?-??11 -??1?100?- 0??0?0001 1?00?????? ???????1?? ?????????? ??0?????? ?????????? ?????????? ?????0????

?000??0000 02?20-000? ?10010?100 0???100111
0000000010 ?00000???? 21???21-?? 0????0???
?2??00???? 1???00???? ????00?00? ?00????00
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CORDYLOIDEA 1000000111 1100000000
0130010000 01000000?0 {12}00000000{01}
0{01}01{01}02100 0-0-{01}100{01}1 001{02}-
2{03}?11 0?01010010 0010021001 {01}000100111
0011100{12}11 0000000000 0000002000
00100{01}1000 0000000011 2000000000
10{01}1010000 {01}23{01}0-0000 0100100100
000-10{01}111 {02}0000000{01}0 000000?001
20011{02}1-?? 0{01}01010000 {12}00000?00{01}
110000{01}000 0001000000 000020{01}000
{02}101000201 {01}010111100 0{01}000010{12}0
00200????? 00{01}0000001 00001?0??? 00????????
???{15}

Sakurasaurus shokawensis ?????001?1 ??????????
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00???????? 2000000010 1??0?????? ??????????
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Parmeosaurus scutatus 101??0-000 010?000000
1030?1000? ??000000?0 1000001100 01?100100?
10??1100?1 0011010??0 01?0000?10 0?1001100?
1???110111 0?1?001011 000?0?0000 ??0??0200?
0020?110?0 0??00???11 ??00000000? ?000??0100
0??10-0001 010010?10? ?00-101?11 0400000000
000000???1 200?02???? 0????????? 01????????
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001?1010?0 00???????? ?????????? ?????????? ??????????
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Xenosaurus 1000000111 1101000000 1130000000
0100000010 1000000011 0011102100 0-0-010001
0010-10101 0?10010010 0-11001000 1000100110
0010101211 0000010000 0000002001
00100{01}1000 0010000011 2000010001 103001-
100 0011100000 0120100000 000-100101
0300000000 1000001101 2001121-{01}0
0021010000 0200000000 1100001000
0{01}01000000 0000201000 {01}1000001-1
0000100000 1000022110 0101?????? 0000?00001
010110000? 100??????? ???3

ExostinusLANC ?????0??1 ??????0??? ??????000
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0300000000? 1??0?0???? ?????????? ??????????
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Carusia 1000?00111 0101000000 01300?0000
0100000010 2000000001 0011102100 0-0-110001
001?-20?00 0100010110 0-11001000 1???100011
1000100111 1000000000 0000002000 0010?11000
00100???11 ?000?10001 103000-100 0001100000
0120100?00 000-000101 2000000000 100001???1
2?0??????? 0?0??????? ?????????? ????????1? ??????????

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ExostinusSERR ?0???00111 ?10?00???0 ?????0000
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0300000000 1?00?0???? ?????????? ??????????
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Restes ????00111 ???00???0 ?????0000 ??000?00?0
10?0000001 011?1?210? 0-0-??0001 00????????
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?0????????? ?????????? ?????????? 0300000000
1??0?0???1 20010????? ?????????? ?????????? ??????????
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Colpodontosaurus ?????????? ?????????? ??????????
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01020-001? ?????????? ?????????? 1200??1000
1??00???? ?????????? ?????????? ?????????? ??????????
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Eosaniwa 301??01111 ??0??00000 0?????1?? ?0100??0??
10??000100 ?1??0?2100 0-0-??0?1 ??????????
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????0?0??? 0????????? ???0???0?0 0??00????0
?000?1000? ?1--??-100 00?2??001? 0111?1?000 ?00-
101?02 1200000000 2??000???1 2102??1-??
0?1101???? ?1??????? ?????????? ????00?0?? ??????????
?????0?1-? ??1?10??0 01???????? ?????????? ??????????
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Parviderma ??0???0?11 ??0???000 ??30????? ???00?00?0
0??0?????? ????10210? 0-0-0??001 ??10??0????
????0?0??1? 00100????? 1????????? 0?000?0010
000??????? ?????????? ?????1??? ?????????? ?????0?0??
??????0?0? 01020-00?1 001111?001 00??0????
1202??1?0 1???0???? ?????????? ?????????? ??????????
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0????????? ?????????? ?????????? ?????????? ??????????
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Bahndwivici 1011?00111 110?000000 0?10??0000
??010?01?1 10?0000001 010110200? 0-0-0??011
001?010?00 010000011? 00100?100? ????1?????
?????????? ?????1???0 ??00?????? ?????????? ???????11
?100??000? ?????0000 01????00?1 01?010??0?
?0??000101 020000?000 1??0000??1 2001021-??
00??010000 0000000?00 1??00?0?0 0??0000??
?000101000 21??0???? 0?0?10?0?? 01????????
????????? ????????? ?????????? ????????? ???3

Shinisaurus 1011000111 1101000000 011000-000
01010001{01}1 100000000{01} 0101102000 0-0-
010011 0011010000 0110000110 0011011001
1000100110 0010101100 2010010000 0000000021-1
{01}010011000 0010000011 2100000001
2000000000 01{01}1100001 0110100000 000-
000101 0200001000 1010001101 20010{12}1-11
0011010000 0000000000 1100001010 0001000001
0000101000 21000021-1 0000100000 0100022110
0??0????? 00?0?00001 00?0100??? ?????????? ???8

Dalinghosaurus 101??00111 110?000000 0010?0-000
000100011? ????000001 01?1102100 0-0-0100?1
001?010?00 0010000110 00100?1001 ????10????
0?100?10?? ?0????000? 0000??21-? ??100?10?0
00?????10 ?100?0000? ?000?0000 0??1120000
011010?000 ?00-10??1? 020000?000 ?00000??1
2001?21-?? 0??10100?? 0000001??1 010?00?010
0???001000 0000100000 ?1??0???? 0?0?0-0---
01??????? ????????? ????????? ?????????
???8

SaniwaFEIS 10????-0?0 11??00??0? ???????01?
??000?0??? 10??001000 01?1102000 ????1????1
001?0?0?00 0?00000011? ???????0?? 1?????????
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????00??? ?????01?0 ?????????? ?????????? ??0-000???
120?00?100 ???0000??1 2?1?121-?? ????010000
02??00???0 1???0??0?? ????00?00? ?00????000
?1?????1-1 001?1?1??0 01???????? ?????????? ??????????
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NecrosaurusCAYL ????0-000 1?0?0?0?0? 0?30??01?
?0?????0?? ?????????? ????102000 10?1??001
0011110000 ??0000???? ???1?????? 1?????????
????2??1?? ???0?????? ?????????? ?????????? ??????????
?????0??? 1?????10? 010??001? ?????????? ??????????
1202001100 20??00???1 201?1????? 1?1??1??00
0211?????? ?????????? ???????0?? ?????????? ??????????
0?0?0?00 01???????? ?????????? ?????????? ??????????
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NecrosaurusEUCA ????00??1 ?????????? ??30???01?
?01??????? ?????????? ????0?200? 100-??001
?010010000 ??0000???? ?????????? ??????????
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?????0??1 1?????00? 01?22-?0?? ?????????? ??????????
1202001100 ???00???? ?????????? ?????1???? ??????????
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01???????? ?????????? ?????????? ?????????? ??????????
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Proplatynotia 1100?0-011 1101001000 003001?11?
1010100000 1000001101 010?00200? 0-0-110001
?010010?0? 0?0000??10 00100?1??? ?000100110
1100000010 0010010??0 ?00??02000 ??10?110??
???00????? ?????00000 ??????0100 01?22?0011
0011110001 000-000101 1200001?00 201000????
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????????? ???????1-? ?????0??1 0????????? ??????????
????????? ????????? ????????? ???8

Paravaranus ??0??1-000 1?0?0??001 0130???11?
?010000-00 1000001100 01??10210? 0-0-010001
?011010?00 0?10000110 02100?1001 ????101110
1100101011 0000000000 ?00??0?000 ?01??01000
00100???1? ??????000? ??????01?? 01????000?
0????????? ?00-100??1 12{01}0?0{01}?00 2???00????
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*Parviraptor*cf*ES* ??????-??0 ?????????? ??????????
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0021? ??20?1???? ?????????? ?????????? ??????????
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1?????10? 01???????? ?????????? ?????????? 0??2??????
??00???0 20001?1-?? 0??01???0 ?20????????
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*Parviraptor*ESTE 1?0???-0?0 ????00?0? ????0001?
000??0??? ?????????? ????0?1000 1?0-??0??1 0-00-
00110 002001??0? 0010???0?1 ???????1?1
11001?121? ?????????? ?????????? ?????????? ???????1?
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02020??000 1??000???? ?????????? ?????????? ??????????
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???4

Parophisaurus 1010?00100 1?0??0?000 0?30010000
?000?00?0 ????001100 000100200? ??????001 001?-
10000 ???0010110 0??00?1001 1???100?00
00?000?011 0000000000 0?0??????? ??????10??
?0?00???1? ?0???00?01 2010?0000 0021111000?
0110?0??00 000-101102 0000000000 101000??1
20011?1-?? ?????1??00 20???????? ??????????
??????00?? ???02??00? ???????21? ??1?10???0
01??0???? ????????? ????????? ????????? ?????????
???3

Saniwides mongoliensis 1101?10111 1201000000
013001?11? 10101?00?0 10{01}?001100 010100200?
100-110001 ?010010?00 0?0000??10 0-1102100?
????1?1110 110?0?1010 0001000000 000??021-0
?01???1000 00100???11 ?100?0?00? ??????-100
01120-0011 0011110001 000-100101 1202001100
201000???? ?????????? ????????? ?????????? ??????????
????????? ?????????0 ?1?????1-? ????????? ??????????
????????? ????????? ????????? ????????? ???8

Telmasaurus grangeri ???0??-000 ?????????? ??????????
??100?0??0 10100?1100 0111{01}?2211? 10??10001
0010010000 01?0000110 002{01}001001 ?????????0
1100001010 000100?000 000??02001 ??1??11000
00100???11 ?100?????? ?????????0? ?????????? ??????????
?????????? 1?02??1?00 2???0?????1 2?121?1-??
????010??0 ????00???? ????0????? ????0?00??
???1100000 ?1???????? ????????? ????????? ?????????
????????? ????????? ????????? ???8

Lanthanotus borneensis 101-01-000 1101000001
012001?11? 1110001-00 1010001100 0101001000
100-010001 001?013000 001-000110 001-1--011
1000100111 1110101110 0001010000 0000002001
1000011010 1010000011 2100000001 ?010000000
01120-0011 0101110001 000-100101 1202001100
2010001101 2012121-01 02{12}1010000
0211100000 11{01}1003020 0002000000
0001101000 210000?1-1 0000101001 0100024111
01?10001?1 1101?00012 0011?1?0?? 00???????? ???8

Aiolosaurus 111??1-01? 1201001000 01???1?110
??100??0?0 1000?0???? ?1?1?0???? ???????0?1
????????? ?????01?0 ???????001 1000?????? ?1???????
????????? ?????????? ?????????? ?????????? ??00?00???
?011000000 01?20-0010 0000?1??01 ?00-100??1
1202001000 ?0100????? ??1??????? ??????????
????????? ?????????? ?????????? ?????????? ??????????
????????? ?????????? ?????????? ?????????? ??????????
????????? ???8

Estesia 1110?0?001 1101000000 0{01}3001?110
0110001000 1100000100 0101001000 10??010001
001?-13000 1??1010110 0-21011001 1000?00110
1110111210 0001010010 0000002000 0010011001
10100??10 ?000?0000? ?010010000 01?20-00??
000111?001 000-100?01 1202001101 201000??1
2101????? ??1??????? ????????0? ?????????? ????0000??
?????????0 ?????????? ?????????? ?????????? ??????????
????????? ????????? ????????? ???8

Eurheloderma ??1??011?1 ????00?00 ?0?001001?
??1??????? ????0????? ?????????? ?????????? ??10-13000
1?0001???? ?????????? ????1????? ?????1111? ???1?1????
?????????? ?????????? ?????????? ??????0?1 2??????000
01120-001? ?????????1 ?????????? 1202001101
2??0?0???1 2?011?1-?? 0????????? ?????????? ??????????
?????????? ?????????? ??????1-? ?0?1???02 0?????????
?????????? ?????????? ????????? ????????? ???4

Gobiderma 1000?01111 1201000000 0030?1001?
01100000?? 1000000001 0101002000 0-0-010001
0010-10?01 1?00010010 0010021001 ?000100110
1110011011 1?0?0?0010 0?0??02000 ?01??11011
00100??-10 ?000?10000 ???00-000 01020-0011
00?1110?01 000-100101 1202001100 201000???1
21011?1-?? ????01000? ??00000???? ?10?00????
???????0?? ??00101000 21?????1-1 ?????0?002
0????????? ?????????? ?????????? ????????? ?????????
???8

Lowesaurus ??1???11?1 ????????0? ?1????0?? ??1???????
???????00? 1?0?001000 11??01?00? ??10-13???
?????1???? ?????????? ?????????? ?????????? ???10?????
?????????? ?????????? ?????????? ?????????1 2???????0?
01??????? ?????????? ?????????? 120??1101 2???00????
?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ??????1-? ???????12 0?????????
?????????? ?????????? ????????? ???3

Paraderma ?01??011?? 1??10????? ???????01? ??????????
?????????? ?????????? ??????0?? ??1?-1000? ?????1????
?????????? ?????????? ?????????? ???1?????? ??????????
?????????? ?????????? ????????1 2??????000 010?0-?01?
?????????? ?????????? 1?02001100 201000???1 210???1-
?? ?????????? ??0?????? ?????????? ?????????? ??????????
??????1-? ???????12 0????????? ?????????? ??????????
?????????? ?????????? ???3

Primaderma ??1??01??? ??????1??? ???????0?? 1?????0??
??0??????? ?????????? ?????????? ????-????0 ?????10???
?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ????????1 ???????00 010????01?
?????????? ?????????? 120?0?1100 ??1000???1
2?0?0????? ??1??????? ?????????? ?????????? ??????????
?????????? ??????1-? ???????12 0????????? ??????????
?????????? ?????????? ????????? ???3

OphisaurusVENT 1010000000 1101001000 013000-
000 1100000010 1000000000 0001002100 100-
011001 0011-10000 ???1?10010 0??00?1001
1000?00110 0010001010 0010000000 0000002001
0?100?1000 00100??011 ?000000000? ?001000100
0021100001 011010?0? ?00-101102 0000000010
10?00111?1 2011121-11 0?21010000 0002110000
110000-??? 0?0-4----- ---0--1--1 --0000?211
0011101000 00000?2110 0???0????? ?--???????
?????????? ????????? ???3

OphisaurusATTE 1000000000 1101001000 01?00?0000
1100000000 1000000000 0001001000 0-0-011001
0011-10000 ???1?10010 0??00?1001 1000?00110
0010011010 0000000000 00000021-1 0?10011000
00100??011 2100000001 21-0??0100 0011100000
011010?00 000-101102 0000000000 1000001101
2011121-00 0021010000 0002000000 110110-???
0?0?4----- ---2??1--1 --0000?211 0011101000
0000022110 01010????? ?????000?? 0???1?0???
????????? ???3

Dopasia 1000000000 1101001000 01?00?0000
1100001010 100?000000 0001002000 100-011001
001?-10000 ???1?10010 0??00?1001 1000?001?0

0010211110 0000010000 0000002001 0?10011000
00100??011 2100000001 2000??0100 0011110000
011010??00 000-101102 0?00000000 1010001101
2011121-00 0021010000 2002000000 110110-010
0?0?4----- ---22?1--1 --0000?211 0011101000
0000022110 01010????? ?????000?? 0???1?0???
????????? ???8

Pseudopus 1000000000 1101001000 01?0000000
1100000010 1000001100 0001001000 0-0-0100?1
0011-10000 1111010010 0000011001 1000100100
0010001010 0010010000 0000002001 0010011000
0010000011 2100000001 2020000100 0011110000
0010101?00 000-101102 0{02}00000010
1000011101 2011021-11 0021011000 2202010000
110110-000 010-4----- ---0-01001 --0000?211
0011101000 0100022110 01010????? 0??0?00002
0000100??? ??00?????? ???4

Bainguis 10??010?0 11??000?00 0?????00? ?0?00???0
10??001100 0??002100 100-?1?0?? 001?0????0
0????0???? ????0?001 1?????0110 0010???11
10?????00? ??0????00? ??1????010 00?00???1?
?100?????? ????????0? 0?????000? 001010??0?
?01?0??1? 01?00???? ??00????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? -????0?201
001?10?0?0 00???????? ?????????? ?????????? ??????????
?????????? ???8

Anniella 100000-000 1100000000 0110010000 1100-
01000 1000001000 1001001000 110-010001 001?0-
0?00 -0--100110 0110001111 1000100110
0111101210 0010010000 02100-2--1 0020111000
0010000021 2100000001 20001-0110 0020110010
0100100?0 000-101102 1200000000 101000?101
2001121-02 0?2101100? ?00200?000 1---1--1-- 2---
4----- ---2201--1 --0-00?211 11100-0--- --000?2110
11?10????? 0--0?00000 0000100??? ?????????? ???3

Anguis 101000-000 1100001000 0010000000
1100000000 1000001000 0001001000 100-010001
0-1?-10000 00?1010110 0010011001 1000100110
0010101{12}{01}0 0000000000 00000021-1
0010011000 00100?0011 2100000001 20011-0000
0021110010 0100100100 000-101102 1200000000
1010001101 2001121-01 0021011000 200200?000
000-1?2000 010?4----- ---2201--1 --0-00?211 00101-
1-00 0000022110 01?10????? 0??0?00002 0000100???
?????????? ???4

Apodosauriscus ?????000?? ??????1??? ???????00?
?10??0??? ?????????? ????0?2?0? 1?0-???01 ????????0?
?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??????0?1 2??????010
0020110000? ???0?0???? ?????????? 0000?00010
1???1???? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????0?21? 001?1?1??0 00?????????
?????????? ?????????? ????????? ????????? ???3

Celestus 1000001000 1101001000 0030000000
1100000000 1000000000 0001000000 0-0-111001
0010-20000 ???0?10010 0??10?1001 1000?00110
0010100211 0010000000 0000002000 0?10011000
10100??011 ?000010001 203001-0-0 0001110000
011010?0? ?00-101102 0000000010 1010?11101
2001121-11 0021010000 0001001000 1110001010
000100100- 1000200000 01?000?211 1010101000
0000022110 01?10????? 0??0?0???? ?????0???
????????? ???3

Diploglossus 1010001000 1101001000 {01}030000000
1100000010 1000000000 0001000000 0-0-111001

0010-20000 0110?10010 0-?00?1001 1000100110
0010100210 0010000000 0000002000 0?10011010
10100??010 2000010001 203001-000 0001110000
0110100?00 100-101102 0000000010 1010011101
2001121-10 0021010000 0001001000 1110001010
010100000- 1000201000 110000?211 1010101070
0100022110 01?10????? 0000?00011 0000100???
????????? ???2

Ophiodes 1010001000 1101001000 {01}030000000
11000000?0 1000000000 0001000100 0-0-111001
0010-20000 ???0?10010 0??10?1001 1000?00110
0010100210 0010000000 0000002000 0?10011010
10100??011 2000010001 100001-000 0001110000
011010?00 100-101102 0000000010 1010011101
2001121-10 0021010000 2001001000 1110002010
0102---1-- ---0201101 --0000-211 1010101000
0100022110 01?10????? ?????0?0?? 0??1?0011
1001110001 0002

Paragerrhonotus ?00??01100 110?000000 1130?0000
??000?00?0 10??000000 00??102000 1?0-1?001
0??0????? ?????????0 ????????? ???1????? ?????01??
????0????? ???0?????? ????????? ????????? ?0????000?
???????10? 001???000? 0?????0??? ????10??02
0000000000 1??000???? ?????????? ??????????
????????? ????????? ????????? ????????? ??????{12}-
? ?0??1??00 0????????? ?????????? ?????????? ??????????
????????? ???3

Gerrhonotus 1000001??0 1101000000 {01}130?0000
1100000010 1000000000 0001102{01}00 0-0-
{01}11001 001?-10?00 0101010110 0010011?01
1000100111 0010100010 00{01}0000000
0000002000 0010011000 00100?0011
20000{01}0001 2010000100 0011110000
0100100?00 100-101102 0000000010 1000011001
2001121-10 0021010000 2002000000 1100011010
0001000000 0000201000 010000?211 0011101000
0100022110 01010????? 0000?00000 0100100???
????????? ???3

Barisia 1000001??0 1?10000000 11?00?0000
1100000010 1000000000 0001102000 0-0-011001
0010-10?00 0100010110 0010011001 1000100111
0010100{12}11 0010000000 0000002000
0010011000 00100?0011 20000{01}0001
2010000100 0011110000 0100100?00 100-101102
0000000000 1000011001 2001121-10 0021010000
200200?000 11000?1010 000?000000 ?000201000
?1?000?211 0011101000 0100022110 01?10?????
?????0?0?? ????1?0??? ????????? ???3

Abronia 1010001??0 1110000000 1130??0000
1100000010 1000000000 0001102000 0-0-
{01}11001 0010-10?00 0100010110 0010001001
1000100111 0010100210 0000000000 0000002000
0010011000 00100?0011 20000{01}0001
2010000000 0011100000 0110100?00 100-101102
0000000010 1000011001 2001121-10 0021010000
200200?000 11000?1010 000?000000 ?000201000
?1?000?211 0011101000 0100022110 01?10?????
?????0?0?? ????1?0??? ????????? ???3

Elgaria 1000001??0 1100000000 1130?0000
1100000010 1000000000 0001102000 0-0-011001
0010-100?0 0100010110 0010011001 1000100111
0010100011 1000000000 0000002000 0010011000
00100?0011 2000000001 2010000100 00110-0000
0110100?00 100-101102 0000000010 1000011001
2001121-10 0021010000 ?00200?0?0 11000?1010

000?000000 ?000201000 ?1?000?211 0011101000
0100022110 01?10????? ?????0?0?? ????1?0???
????????? ???3

Helodermoides 1000?01111 1?0?000000 ?130?0000?
?0000000?0 10?0001101 01?1001000 100-010001
0010-101?? 1000010?10 0?2001100? ???0000110
00100?001? ??10000000 0000?0?000 00{12}0011000
10100???1? ?0?000000? ?011000100 0011100001
0100100000 100-101102 0600000000 101000???1
2?011?1-?? ??????0??? ?001?????? ???????010
???000000? ??????????0 ?1???0?1-1 0?11101002
21???????? ????????? ????????? ????????? ?????????
???3

Xestops ??????1??1 ?1???????? ?????????0? ??????????
????????? ????0?1000 0-0-????? 0?1??????? ??????????
?????1?0?? ?????????? ????0?0?? ??1?????0 ??0???????
?????????? ?????????? ?????1???1 102??????? ??????????
?????????? ?????????? ?????0010 1???0???? ??????????
?????????? ?????????? ?????????? ?????????? ??????????
???????21? ??1?1???0 2????????? ?????????? ??????????
????????? ????????? ???3

Proglyptosaurus 1001?011?1 1???000?0? ????00000?
?10?0?0??? ?0?00?1101 0?011??00? ??????0?1 0?1?-
101?1 ??11101???0 ???0011001 ?0?0?00?0 ?????????0
00?????0?0 ?10?????0? ?????1??? ?????????? ??????????
?????????0 ?????????? ??0??????? ?????????? ?600?00?0
?01001???? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ??????1-1 0?1?10?002 21????????
?????????? ?????????? ?????????? ?????????? ???3

Paraglyptosaurus ??1??????? 11?1000??? ??????????
?????????? ???0????? ????101000 0-0-??001 0?10-
101?? ???001??0 ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ?????0?00?
????000000 00011000?0 010010?00? ?00-101102
0500?00010 10?000???? ?????????? ??????????
?????????? ?????????? ????0?00?? ?????????? ???????1-?
?0??1??02 2????????? ?????????? ?????????? ??????????
?????????? ???3

Glyptosaurus ?00??01111 110??00000 ?????00000
??00?000?? ?0?00?0001 0??1101000 100-?1?001
0010-101?1 ???1010010 0??00?1001 ?????0????
??1?00?0?? ??????0??0 ??0??????? ??????10??
???00??1? ?????0000? ????00-100 0011110000
0100100?00 100-101102 0600000010 101001???1
210?0???? ????????? ?0??????? ????????? ??0?00??
???????0?? ?????0?1-1 001?101002 21????????
????????? ????????? ????????? ????????? ???3

Melanosaurus ??00?01111 11??000??0 ?????????0
?100?00??? ????000010 0101101000 100-???001
0010-101?0 ????010110 0?10001001 ??????????
????0?0?? ?????????00 000?00?00? ???001?00?
001?????11 ?000?0???? ??????100 0021111000?
01?010??00 ?00-?????? 0600000010 101001???1
2?010?1-?? ?????1??0 2?01????? ?????????? ???????0??
???????00? ???????2?? ????1???0 2??0????? ??????????
?????????? ?????????? ?????????? ???3

Proxestops ??????{01}1?? ?????????? ??30000?0?
?1???0??? ???0????? ????002000 1????1?001 ??1?-
1?000 000?1???? ?????????? ?????????? 0?100??1?
?????????? ?????????? ?????????? ?????????? ?????????1
?020???1?0 ?0?1100??? ?100?0?00? ?00-??????
0600000010 1??001???1 2?01??1-?? ????01????
?????????? ?????????? ?????????? ?????????? ???????1?
001??0?0?0 21???????? ?????????? ?????????? ??????????
?????????? ???3

Odaxosaurus ?0????00?1 11??00???? ??30000000
?10??0??? ????00??0 ????002000 100-?1?001 0010-
10000 100001??1? 0????????? ?????????? ??????01?
?????????? ?????????? ?????????? ?????????? ??????0??1
2??????100 002?1?000? 01??1????? ?00-?????
0600000010 101001???1 20?11?1-?? ??????????
?????????? ?????????? ?????????? ?????????? ??????21?
001?1010?0 00???????? ?????????? ?????????? ??????????
?????????? ???3

Peltosaurus 1000?01111 1100000000 0130010000
1100000010 1000000000 010110200? 10??110001
001?-10000 1101010010 0-11021001 10?0100110
1010100110 0010010000 0000002000 0020?11000
00100??11 ?100010000 1030??-000 0011100000
011010?000 ?00-100102 0600000010 101001???1
2?010?1??? 0????????? ?????????1 11???1?010
0????????? ?????????? ????00?201 0011101000
21??0????? ?????????? ?????????? ?????????? ??????????
???3

Arpadosaurus ?????1??? ?????????? ?????????? ?????0???
?????????? ????10100? 1?0-?1?001 ??10-101?0
??0??101?? ?????????? ?????????0 0?1?0???1? ??????????
0????????? ?????????? ?????????? ?????????0 ??????0???
00???????? ?????????? ?????????? 0600??0010 1???1????
?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????0?{12}1? 001?10?0?0 21????????
?????????? ?????????? ?????????? ?????????? ???3

Ophisauriscus 1000?01000 1101001000 ?23000000?
??000?0??? 1??001000 ??01001000 0-0-?1?001
0010-10000 0111010?10 00000?1001 ????1?????
??0??1?? ?????0??? ?????????? ??????10?? ??00??1?
?????0??? ?????????0 ?????????? ??0??????0 0???101??2
?200000000 101000???1 2?1??21-?? 0??10100?0
?0??00???? ?????-???? ????00?00? ??????1?00
?1??00?211 1011101070 21?0?????? ??????????
?????????? ?????????? ?????????? ???3

Parasaniwa ??????{01}1?1 11??000??? ?????0?00?
?????????? ?????????? ????1?2?00 10?????01
0010010001 000000???? ?????????? ??????????
??????0?? ?????????0 ??0??????? ?????????? ??????????
?????0?1 1?????000 01?20-000? ?????????? ??????????
0200001100 101000???? ??01?????? ??????????
?????????? ?????????? ?????????? ?????????? ??????1-?
????????10 0????????? ?????????? ?????????? ??????????
?????????? ???3

Dorsetisaurus ?????00011 1?0??0?000 0?30?00000
?0000?00?? 1?00000???? ????002100 1?0-???011
0010000000 0?00000010 0?1??????? ???????0?0
0??00??0?? ??????0000 000?0?2000 001??11000
00100????? ?????1000- 00001--00? 00?1100011
011011??00 ?00-1???1 0012000000 ???0000????
??????1-?? ?????1???? ?????????? ?????????? ???????0??
?????????? ??????20? ?????????0 ?????????? ??????????
?????????? ?????????? ?????????? ???4

ANILIOIDEA 001011-000 1{12}020{01}0000
0120000010 0100001--0 3-001----- ---1000000 3-
1001-003 0-110-3-0{02} -10-10{01}10- 0---1-11--
0010100111 001{01}2-0{12}11 00000000-0 02211-
1--1 11101?1202 -010000021 1210011{01}00 11--00-
100 0132002011 200100--10 0{01}0-00010-
1003000000 10{02}0001101 200{01}221-??
0?21011100 ?2-201?002 ----2-1-- 2--------- ---2??1-
01 --0000?2-1 ?0100-0--- --0110411? 1?0?0????? ?--
?0000?0 0???1-20?? 01???????? ???{12}

otherMACROSTOMATA 10{01}011-000 1{12}02?1-
000 0{01}30000{02}10 0100000--0 3-001----- ---
10?0000 3-1101-00{13} 0-11{01}-3-{01}2 -?0-
100100 0??-1?{01}1-- 001010121{01} {01}0102-
0{12}11 00000000-0 02211-{01}--1 1110101202 -
010001021 120001110- 100000-000
01{13}21{01}20{01}1 200100?--0 000-00010-
0003{01}0000{01} 10{01}0001101 20{01}1221-??
0?210111{01}0 ?2-201?002 ----2-1-- 2--------- ---
2??1-01 --0000?{12}{01}1 ?0100-0--- --0110411?
1?0?0????? ?--?0000?0 0???1-2{01}?? 01???????? ???0

Xenopeltis 101011-000 1202?1-000 0130000210
0100000--0 3-001----- ---10?0000 3-1101-003 0-110-
3-02 -?0-1001-0 1---1-11-- 0010101111 00102-0111
00000000-0 02211-0--1 1110101202 -01000?021
121001110- 101100-000 0132002011 200100?-00
000-00010- 1003000000 1000001101 2000221-??
0?21011100 ?2-201?002 ----2-1-- 2-------? ---2?-1--
1 --0000?2-1 ?0100-0--- --0110411? 1?0?0????? ?--
??0?0?? ????1-20?? 01???????? ???{78}

Dinilysia patagonica ??1011-000 ??0??1-000
012000?010 01000?0--0 3-001----- ---100100? 0-
??01-002 0-111-3-00 -?0-100110 101-0011--
00?01?0110 1010201111 00000100-0 022?1?1--1
?00??11202 -01??0??21 ?21001?100 ??????-100
01?2102011 20?100-?00 000-00010- 00030?0000
1?0000??1 2010221-?? ?210?1??? 2??010??2 ----2--
1-- 2?-------- ---?????1 ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ???3

Haasiophis terrasanctus 200011-000 1?0201-000
0?20000210 0?000?1--0 3-001----- ---100000? 3-
??01-003 0-111-3-02 -?0-100100 1---0011--
00?0101210 00102-0111 00000010-0 022?1?0--?
?11???12?2 -?1?????21 ?20001110? ?00?00-000
0112002011 21?101?00 ?00-00010- 00030?0000
102000??1 2010221-?? 0?21?11100 ?2-201?002 ----
2--1-- 2--?------ ---2-01000 ?0???????? ???0-0--- --
???????? ?????????? ?????????? ?????-???? ?????????? ???4

Pachyrhachis problematicus 1?1?1?-000 1??0?-???
????00??0 ??000??--0 3-??1----- ---100000?
????0???03 0??1?-3?2 ??0-100?00 1---0001--
00?0?????? ??102-01?? ?2000?0-0 02?????--?
??1??1?2?2 -??????21 ?200?110- ????00-?00 01?20-
2?11 2??101???? 000-?0?10? 00030?0000 1?0000??1
2000221-?? 0?211111?0 ?2-201??02 ----2--1-- 2--
?------ ---2??1000 ?0???????? ???0-0--- --????????
?????????? ?????????? ?????-???? ?????????? ???4

Eupodophis descouensi 10001?-000 1??01-?0? ?????0-
210 ?1000?0--? ?????????? ????0000?? ??1???????
?????????? ?????0100 1?--0001-- ?????01211
00102?1?11 00????1??? ?????????? ?1????????
????????21 ?200001110? ????00-?0? 01?????0??
?10100?-00 00?00010- 00030?0000 ??????????1
20??221-?? 0?210????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ???4

Pachyophis woodwardi ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ??????????
?????????0 ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ????1???? ??????-100
01?211?001 2???????00 00???????? 0003?000??
???000??1 20??2?1-?? 0??1????? ?????0??2 ----2-?1--
????----?- ---??????? ?????????? ????0-0--- --????????
?????????? ?????????? ?????????? ?????????? ???4

Wonambi naracoortensis ????1?-0?0 ?????1-??? ??3000021? ?10??????? ?????????? ????000000 ????0??0?? ?-011-3-02 ???-?0???0 ?????????? ?????????0 0?112???11 10?0?110-0 022?1-1--1 010?101222 -01?-???? ?????1110- 1????-100 01?21120?? 2??????10 010-00010- 0003?00000 10?000???1 20002?1-?? ???1011100 02?101???? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ???9

Bavarisaurus 100??0-000 010?00?000 0?30???0?0 ?0100?00?? ????001000 0001{01}0010? 0-??0??002 0?0?-00??0 ????0?1010 0010010001 1????????? ????????? ???1?0???? ?????????? ?????????? ???????1? ?????00??? ???????100 ?0?21?0??? ?10??0?00 ?0??0?1??1 1200000000 ??1000???0 1?-0?01-0? 0100000?0? 0000???00 0??????00? ??0?0020?? ??????000 ?1??????? ????0-0--- --??????? ?????????? ?????????? ?????????? ?????????? ???4

Ardeosaurus 100??000?1 0?0?000000 0030?00000 ?0000?00?0 3-??001000 000?00000? 0-??1??011 001?-?0??0 0?01010110 0?10010001 1???1????? ????????? ??0??????? ?????????? ?????????? ???????1? ?0???????? ?????????? 0????????? ?????????? ????000?00 ??00??0?? ???00????1 2?00?01-?? ????010??? 0???????00 ?1??0????? ????00?000 ?00?0??000 ??????2?? ?????????0 ?????????? ?????????? ?????????? ?????????? ?????????? ???4

Eichstaettisaurus 101??0-000 010?000000 0????00000 ??000?00?0 3-?0001100 00?110?10? 100-0??001 0000-20?01 0?00010010 0010001001 ????10???? ????1?2?? ??00?????? ???0?????? ?????????? ????????10 ?0?0??00? ??????0??? 0???????? ?1??????? ?0??00??0 0000000000 000000???? 1000021-?? 01??010??? 00??00??01 110001?000 ????00000? ????0??00 ????????? ????0-0--- --??????? ?????????? ?????????? ?????????? ?????????? ???4

Yabeinosaurus ?000?00111 11??00?00? ?????0-000 010000000?? ????001000 000?002000 100-???011 0012000000 010001?710 00100??001 ????1?0??? ???00?00?? ?????0???? ?????????? ?????????? ?????????0 ?000?0?00? ?????0??? ??????0??? ?1?010???? ????000121 0000000010 000000???1 200??1???? 0???010??0 0???00???? ?10?00???? ????00?000 000?0??00 00??0???? ????0-0--- 0????????? ?????????? ?????????? ?????????? ???8

Scandensia ciervensis ?0???0?001 010?000000 ??????01? ???0??0??? ????000010 0??110000? 10???100?? ????-0???? ?????1???? ?????????? ?????????? ?????????? ?????????? ??0??????? ?????????? ?????????? ?????0?00? ???????100 ?2??1000?? 0????????0 ?00-000??0 01??00000 ?000000?0 10-00?1-?? 0000010?00 00??00??01 1100???010 0??000000 000100?000 ?0??????? ?????????? ????0????? ?????????? ?????????? ?????????? ?????????? ?????????? ???4

Aphanizocnemus ???0??-??0 1???0????? ?????????? ?????????? ????0???00 ????10210? ???????0?1 0-1?0???? ?????0??0 0??10?10?1 ?????????? ?????????? ?????????0 ??0??????? ?????????0 0???????1? ??00?0???? ?????????? ??????001 1???????? ?0???????? ?????????? ?????????1 20?1221-?? 0321010001 0211000?00 010?00???? ????00?00? ?002?11100 ?0???????? ?????????? ?????????? ?????????? ?????????? ?????????? ???4

Dolichosaurus longicollis ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ???????0??

?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????00?1 ?????1???? ?????????? ????0????? ?????????1 2001221-?? 032?010?01 011200???0 000???11-- 0??0??0?? ???20?1?0? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ???4

Coniasaurus ?1???1-??0 ??0??0???? ?1??0??110 1?1??00??? ?????????? ?1?11?210? 0-??00011 ?11?????? ?????????0 ?????????? ?01??00??? ????1??11? ????1???? ?????????? ???0????? ?????????? ??????1?? ????0??100 1102--?011 ???1?1-??1 0????????? 1012000000 1??000???1 20012????? ?????????? ?????????? ?00??????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ???3

Adriosaurus 1?00??-??0 1??0????? ??????110 ??0??00?? ????00??0 0???0?21?? ???????11 001?010?00 ?00?00110 0??10???0? 0????????? ?????????? ?????????0 ??0?????? ???0?0???? ???????1? ?????????? ?????????? 1????????? ????1?1??? ????0?1?0 ??00000???1 2001221-?? 03??11?011 021200???? ??????2??? ????0?200? 0002?11000 ?0???????? ?????????? ?????????? ?????????? ?????????? ?????????? ???4

Pontosaurus 2100?1-000 120?000000 1130?11110 ??000?0-10 ????001100 010110210? ????0??1?1 011?1?0?00 ???0?00?10 0??00?1001 ?????????? ?????12?? ?????????? ???00????? ?????11?0 0???????1? ?011?0110? ?1--001100 0102--1001 111101??11 000-101?01 1202001000 ???000???1 2001?21-?? 0311110011 0211000?0? ?10?10?0?? ????00200? ?002??0000 ?0???0?1-? 001??0-?- 00??????? ?????????? ?????????? ?????????? ?????????? ???4

Aigialosaurus 2100?1?000 ??1?000??? ???????110 ??10?0-?0 1???011100 01011?200? ???????111 0010010?00 000000??10 0011021001 ?????????? ?????????? ?????0?0?0 ??0??????? ??1??1??? ???????11 ?01010?10? ?1--?1100 01?2--1001 1?1101?01 000-100101 1202001000 1??000???1 2001221-?? 0?11010?11 0201000??? ?????????? ????00?00- 1001101000 ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ???4

Opetiosaurus 1110?1?000 1??0000??? 1??????110 ??101?0??0 1???001100 010110200? ???????011 0010010??0 001000??1? 0??10?1001 ?????????? ?????????? ?????????? ?????????? ???????11 ?01?0110? ?000??1100 01?2--1001 1??100??01 000-100101 1202001000 100000???1 2?01221-?? ????01??11 020100???? ?00?10???? ????00000- 100???000 ?0???????? ?????????? ?????????? ?????????? ?????????? ?????????? ???4

Tethysaurus nopcsai 3100?1-000 121?000??? ?????0110 ??10000??0 10??010010 010?101010 0-0-000011 ?111000000 0010000110 0?11021001 ?010?????? ???????1?? ???????0?0 0?0?0????? 1?0????100 ??1?????11 ?010?01??? ?1--??0100 01?2--1001 1001????0? ?00-101?01 1202001100 100000???1 20012?1-?? 0?1?01??1 020??????? ?10?10???? ????1?10?? ???2101110 ?????????? ?????????? ????0????? ?????????? ?????????? ?????????? ???4

Carsosaurus marchesetti ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ???????11 ?01??????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????1

20012?1-?? 0?1?01??00 0201000??0 000?1?0010
010?002000 00012?1000 ?????????? ??????????
????????? ????????? ????????? ????????? ?????????
???4

Goronyosaurus 310??0-000 1111000??? ????000210
??00001??0 20??000010 0101101010 11??1000?-
?01?000?00 011000??00 0011021001 ????0?????
?????011?? ??10000000 0?0?0????1 ?01?011000
0?100??1? ?01?701??1 1??????100 01?2--100?
?0???1??1? ?????????? 1002101000 100000???1
20000?1-?? 0?1?01??1 0201?????? ??????????
????3210?? ??1???11? ????????? ????????? ?????????
????????? ????????? ????????? ????????? ???6

Halisaurus ARAM 310??1-000 10?000??? ????????1?
????100??? ????011?0? 0???1?1010 0-0-?00111
001?0?0?00 010000011? ???????0?1 ??????????
???????11? ??????0?? 0?0??????? ??000??1?0
1???????1 ?012?01??? ?000??0100 0102--1001
1011010011 0000100101 1202001?10 ?00000??1
20010?1-?? 0?11011011 0201?????? ??????????
????1010?? ???2??101? ????????? ????????? ?????????
????????? ????????? ????????? ????????? ???6

Halisaurus PLAT 3????1-000 ????0???0? ?1?????10
????1?0??? ?????????? ???110001? 0-??0?0?11
0110000000 0110000011? ?1?????? ??????????
?????011?? ??????0?00 0?0?0????? ?????????0?
1?100???11 ?012?0?10? ?0000011?0 ???????001
1?????-??1 000-100101 ?0??00???? ???00??1
20010?1-?? ??1???1?11 0201?????? ????1?????
????10?0?1 000??1?01? ????????? ????????? ?????????
????????? ????????? ????????? ????????? ???3

Eonatator 3?????000 ?????????0 ?10???11? ?????????
?????????? ???111201? ??0-????11 001?0?0?00
001000011? 0??????0?1 ?????????? ??????????
????????? ????????? ????????? ???????11 ?012?0????
??????1100 ?1?2--10?1 10?1?1-??1 000-100101
????0????? ???00????1 2001021-1? 0?1???1??1
0201?????? ?10?10???? ????101011 010221101?
????????? ????????? ????????? 0????????? ?????????
????????? ????????? ???3

Plotosaurus 310??1-000 1212000000 11-?000210
00001?1-00 1000000100 0101111000 ????1??122
0010002?00 ???0?00000 0??10?1001 ?010?01110
0110101111 101100?000 0000002001 0?1?011100
00000???11 ?011?0110? ??????1100 01?2--10?1
10?101?01? ?00-100101 1002001010 100000???1
2100021-01 0?11011011 0201000??0 100?10?0??
????22202? ?10?????0 ????????? ????????? ?????????
????????? ????????? ????????? ????????? ???3

Globidens 310??1-000 1211100??? ??-?000210 ?0101?1-
?0 200?000100 0101111101? 0-0-000121 0010000000
0110000010 0011021001 ????????0 011010111?
??1?0??0?? 0?0??????? ??1???11?0 00?????11
?012?????? ??????1?? ????????? ????????? ?????????
1512001010 100000???1 20002???10 ??110?1???
????????? ????????? ????1???? ????????? ?????????
????????? ????????? ????????? ????????? ?????????
????????? ???3

Mosasaurus LEMM 310??1-000 1211100??? ??-?000210
00101?1-00 1000001100 0101111010 10??0?002-
0110000000 ???0?00010 0??10?1001 ?????01110
011?10111? ??100??000 000???001 ??1?01100
0??00??1? ?010?01101 ?1--??1100 01?2--1001
101101?011 000-100101 1002001010 100000???1
2000221-?? 0?11011?11 0201????0 100?10?010

????21203? ????2211110 ?0????????? ??????????
????????? ????????? ????????? ????????? ?????????
???4

Mosasaurus HOFF 310??1-000 1211100??? ??-?000210
0010101-?0 1000010000 0101111010 0-??00002-
0010002000 0110000010 0??10?1001 ?01??01110
0110101111 001?00?00? 000???2001 0?10001100
000????11 ?011?01101 11--001100 0132--1001
101101??11 000-100101 1002001010 100000???1
2000221-10 03110110?1 0201000?00 000?10????
????212032 0102211111? ?????????? ??????????
????????? ????????? ????????? ????????? ?????????
???{34}

Moanasaurus mangahouangae 3100?1-000 1211000???
??-?000210 0010101-?0 ????0????? ????111010 0-
??00002- 011?100?00 011000??0 0??102?001
????01110 01101?1111 001????000 0?0?????00?
?????11?0 01??????11 ????0110? ?????1100 01?2--
1001 10?101?01? ?0??100101 1002001000 ?00000??1
2000?????? ?????????? ????????? ????????? ?????????
????????? ????????? ????????? ????????? ?????????
????????? ????????? ????????? ???9

Clidastes 310??1-000 1211100??? ??-?000110 0010100-
?0 1000010100 0101112010 0-0-000011 0010000000
0110000010 0011021001 ?01??01110 011?101110
001?0??000 000???2001 ?01???1100 00?00??11
?010?01101 11--001100 0132--1001 101101??11
000-100?01 1002001000 100000???1 2000221-10
0011011011 0201000?0? ?10?100??? ????212032
0102211?10 ?0???????? ????????? ????????? ?????????
????????? ????????? ????????? ???3

Platecarpus 310??1-000 1211000??? ??-?000110
0010101-?0 2000010000 0101101010 0-0-00011-
0011100000 ?100000010 0010021001 101??01110
011?101110 001000?00? 000???2001 101?001100
01?00???11 ?011101101 1???001100 0132--1001
10?101??01 000-100101 1002011000 100000???1
2000221-?0 0?110?1001 0201000?0? ?10?00?0??
????322031 0012211110 ?0????????? ??????????
????0????? ????????? ????????? ????????? ?????????
???3

Prognathodon OVER 310??1-000 1211000??? ??-
?000110 0010100-?0 ?000010100 01?1101010 0-0-
00012- 0110002000 ???0?00000 0??10?1001
?01??01110 0010101110 001000???? ??????????
????????? ?1?00??11 ?012?01101 1?????1000 0132--
1001 11?101??11 000-100?01 1002011010
100000???1 20000?1-?? 0?110110?? ??????????
????????? ????32203? 0?????11? ????????? ?????????
????????? ????????? ????????? ????????? ?????????
???3

Prognathodon SOLV 310??1-000 1211000??? ??-?00110
0010100-?0 ?00?001100 0101101000 0-0-000001
0110002000 0110000000 0011021001 ????01110
00101?1110 0010000000 000???2??1 001?011100
01?00???11 ?0?2?01101 11--001000 0132--1001
111101??11 000-100101 1002011010 100000???1
2000221-11 0?110110?? ????000??? ??????????
????32203? 0?????11? ????????? ????????? ????0?????
????????? ????????? ????????? ????????? ???{34}

Plioplatecarpus 310??1-000 1211000??? ????000110
0010101-?0 ?0??0?0100 ???1102110 0-0-000111
0110102000 0100000010 0-11021001 ?010?01110
01101?1110 001??0000 000????001 001?011100
01100??11 ?012?01101 1001001100 0112--1001

100101-?01 000-100101 1202011000 100000???1
2000021-11 0?11011??1 0201000??? ?10?00????
????322031 ???22?1??? ?????????? ????????? ??????????
????????? ????????? ????????? ????????? ???3

Ectenosaurus 310??1-000 1111000??? ??-?000110
??101?00?0 200?010000 0101101110 0-??100011
0?010000000 ???0?00?00 0??10?1001 ??????????
???0?????? ?????????0 000???200? ??1???1??0
01?????11 ??12?01101 1???001100 01?2--1001
11?101???1 000-10??01 1202011000 100000???1
2000221-1? 0?1101???? ???000??? ?10?10????
0???322031 0?1??1???? ????????? ????????? ??????????
????????? ????????? ????????? ????????? ???3

Tylosaurus 310??1-000 1211200000 11-?000110
0010101-?0 1000010000 0101101000 0-0-000111
0011000000 0100000010 0011021001 101??01110
0110101111 101000?000 000???2001 1010001100
00100???11 ?111?01101 11--001100 0132--1001
100101??01 000-100101 1002001000 100000???1
210{01}221-10 0011011001 0201000?0? ?0011000??
0???12202? 0002211110 ?0???0???? 0?1??00??-
00??0????? ????????? ????????? ????????? ??????????
???3

Hainosaurus 310??1-000 1111200??? ??-?000110
??10101??? ?0??00010? 0101100010 0-0-000111
0011002?00 011000??10 0011021001 ?????0111?
??????111? ??????0??? ??0????00? ?????????0
0?000???11 ?110?01??1 11--??1100 01?2--10?1
1101?1??01 00??100?01 1002001000 100000???1
20002?1-?? 0?1?01???? ????000??? ?00?10????
????12202? 000??????? ????????? ????????? ??????????
????????? ????????? ????????? ????????? ???4

Lakumasaurus 310???-000 11?1200??? ????000110
00101?1??0 ?0?0?????? ???11?102? 0-0-?0??11
0011?00000 010?00??10 001102?001 ??????????
????????? ????????? ????????? ????????? ????????11
??10?01??? ?001??1100 01?2???0?? ?10101-?0?
0????????? 1002001010 100000??1 20002?1-??
0??????01 02???????? ????????? ????????? ??????????
????????? ????????? ????????? ????????? ??????????
????????? ????????? ???2

Palaeoxantusia ??00?00111 1?????????? ?????100?0
?1100?0000 1000000?11 0001002100 10??1??0?1 0-
0?0?3?12 ??01010000 0-21021001 ????1???0
00?0100211 000001?00? ?0?0???000 ?22???0?0
0?001??1? ?????1?00? ????01-101 22010-0011
0010100100 0010000000 0400000000 00?000????
????????? ????????? ????????? ????????? ??????????
????????? ????????? ????????? ????????? ??????????
????????? ????????? ????????? ???3

Xantusia 1000000111 1{12}00000000
0{01}{23}0000000 0{01}110000000
20000011{01}{01} 0001{01}02{01}00 100-
{01}10011 00{01}2-20{01}{01}1 ???1010100
0?210-0001 0000?10110 0010100211
10{01}{02}010000 0100001000 0001001000
00000?0011 200001000- -00101-101 22110-0011
011010?100 0110000000 0400000000 0000000001
20010?1-11 00110?0000 ?00?00?001 11000?1000
0???000000 0000201000 0101000201 01000-0--0 0-
01011020 00200????? ?????01??2 1???1????? ??????????
???3

Cricosaura 1000000011 1110000000 1120010000
1010000000 2000001100 0001102100 110-110011
0012-23001 ???1010100 0?210-0001 0000?10110

0010100211 0000010000 01000011-0 00210-1000
00001?0011 200001000- -0011--101 22110-0011
011010?100 0110000000 0400000000 0000000001
20010?1-01 00110?0000 ?00?00?001 11000?1000
0???000000 0000201000 0101000201 01000-0--0 0-
01011020 00200????? ?????01??2 1???1????? ??????????
???3

Lepidophyma 100000-000 1100000000 0020011000
0000000000 2000001010 0001001000 0-0-111011
0002-23111 ??21010100 0?210-0001 0000110110
0010100210 0013-10000 0100001000 00210-1000
00000?0011 200001000- -00100-101 22110-0011
011010?100 0110000000 0400000000 0000000001
20010?1-01 00110?0000 ?00?00?001 11000?1000
0???000000 0000201000 0101000201 01000-0--0 0-
01011020 00200????? ?????01??2 1????????? ??????????
???3

Polyglyphanodon 1000000011 110?000000 1030000000
0001000000 1?00001000 0011000000 0-??0000?1 ?-
1?0?2?00 000000--00 0020011001 ????100010
1010100211 111100000?? 0?????????? ???????0?1
0???????1? ?100000001? ?000000100 02020-0001
0100?0000? ?011000100 0714000000 000000????
????????? ????????? 2????????? ?11?1???? ??????????
????????? ????????? ????????? ????????? ??????????
????????? ????????? ????????? ???8

Erdenetesaurus 100???0??1 11??000??? ????0??000
000?0?0??0 10??00110? 0011{01}?220?? ??0-?????1
001?0?0?00 0100000010 0210011000 ????10000?
0010?00?01 111200???0 0????????? ??????????
???00??11 ?000?1001? ???????100 0202100001
010010000? ?????????? 0410000000 000000????
????????? ????????? ????????? ????????? ??????????
????????? ????????? ????????? ????????? ??????????
????????? ????????? ????????? ???8

Adamisaurus magnidentatus 1000000?01 110?000000
0030010000 0000000010 1?00000000 000100010? 0-
??100011 ?012022?00 0100020010 0?10021001
????0001?0 0010100201 -111000?0 0??????????
????0?10?0 0???????1? ?000?0001? ?0001-0001
02000-0000 010010?00? ?011000?00 0114000000
000000???? ?????????? ????????? ????????? ??????????
????????? ????????? ????????? ????????-- 0?????????
????????? ????????? ????????? ????????? ???8

Cherminsaurus 1000?00001 11?000000? 00??1?000
000?0?0??0 1000001?00 00110?200? ?????????1
001?0?0?00 ??00000??10 0210011001 ????100010
00101002?1 1112000??? 0??0?????? ?0?????0??
????????1? ?000?1001? ?1--1--100 0002100001
010010000? ?010000100 0410000000 001000????
????????? ????????? ????????? ????????? ??????????
????????? ????????? ????????? ????????? ??????????
????????? ????????? ????????? ???8

Gobinatus 100??00001 110?000000 0030???01?
?0000?0010 1000001100 01?100200? ????1??001
?01?020000 0010020010 0210021000 ????100010
001010010? -?11000000 0000?????? ?010??10?0
0??00???11 ?0000000?? ?000??0100 00020-0001
01?010000? ?011000000 0010000000 ?01000??1
2?0???1-?? 0?01?1???? ?????????1 010?01????
????00?0?? ????????? ????????? ????????? ??????????
????????? ????????? ????????? ????????? ???8

Darchansaurus 101?00111 ??0?000?00 0040???000
00010?0000 1000001101 001100000? ????0??0?1
001?0?0?00 010002??00 021003100? ?0??100010

1110101200 -002000000 ?0000????? ??2???1000
0???????1? ??00?0001? ?000010100 02020-0001
010010000? ?011?0??0? 0400100000 000000????
????????01 ????????? ????????? ????????? ????0??0??
??????00? ????????? ????????? ????????? ?????????
????????? ????????? ????????? ???8

MacrocephCHUL 1000?00111 110?000000 004000-000
00010000?0 1000001010 0011000000 0-0-1000?1
0010022?00 0001000010 0210031001 ?0?0000010
1010100201 -112000000 1000001000 001?011000
00001??0?10 ?000?1001? ?1--1--100 02020-0001
010010000? ?011000100 0400100000 000000??01
2000221-01 0?11010000 2000000?01 011?01?010
0???000000 0000210000 01???????? ??????????
????????? ????????? ????????? ????????? ?????????
???8

Sineoamphisbaena hexatabularis 1010100011
110?000000 00200?0000 10110010-0 2?0?001000
001100000? 11??0110?1 0-00?23?01 ???100--10
0?1?001001 ?00??00010 001010020? -??3-0000?
1????-???? 00?0??1000 000????10 ?000000???
??????0101 0??20-0??? ?1?0?0??0? ?0??000?00
0104000000 ?00000???1 20002?1-?? 001?71????
???00???? ?1?????0?? ????0020?? ?????????? ??????????
????????? ????????? ????????? ????????? ?????????
????????? ???8

Bipes 101010-000 1212000000 1130000001 1000-0-0-0
3-001----- ---100000? 110-1100-- 0-1-0-3002 ???-
101--? 1?--1--011 0000?00010 00101-0201 -013-
1?101 12210-0--1 -?00-111-0 101111?031
120001000? ?1--1--101 21301201-- -10010?000 010-
000101 0000000000 0110000111 2201021-??
0121011100 100211?000 00011031-- 0-0200200-
1002--1-01 --0101?201 01000-0--- --01004010
1?000????? ????0?00?1 0??1?0??? ?????????? ???3

Blanus 000010-000 1112000000 1030000000 1010-010-
0 3-001----- ---1000000 110-110001 0-110-3002 ???-
101--? 1?-----1-- 0000?00010 00101-0201 -013-1?101
12210-0--1 -?20--11-2 -01111?031 120001000?
??????-101 21300-01-- -10000?0?0 0??0000101
0000000000 01100001?1 2201021-?? 0121011100
100211?000 00011031-- 1-0-0--1-- ---2--1-01 --
0101?201 01000-0--- --11004010 1?00010?0 ?-
??0????? ????????? ????????? ???{46}

AMPHISBAENIDAE {01}0{01}010-000
1212{01}00000 1130000000 10{01}0-010-0 3-
001----- ---1000000 110-110001 0-11{01}-3002 ???-
101--- 1?--1--{01}11 0000?00010 00101-0211 1013-
1?101 {01}2210-0--1 -?20-11{01}-0 101111?131
120001000- -0{01}01--101 {12}1301001-- -
10000?000 000-000101 0000000000 01100001-1
2201021-?? 0121011100 1002110002 -0012031-- 1-
0------- ---2--1-2- --0{01}01?201 0{01}010-0--- --
{12}1004010 1?000010?0 ?--?0?00?1 0???1?00??
?0???????? ???-

TROGONOPHIDAE 101010-000 1112100000
1120000001 1000-010-0 3-001----- ---1000000 110-
110001 0-110-3002 ???-101-0- 0?--1--1-- 0000?00010
00101-0211 0013-1?101 022{01}0-0--1 -2{01}0-111-
0 0011101?131 120001000- -0201---101 21300-01-- -
10000?010 010-000101 0001000000 -1000001-1
2201021-02 0121011100 120201?002 -0012031-- 0-
0------- ---2---2- --0{01}01?201 0{01}0{01}0-0--- --
11004010 1?000010?0 ?--?0?00?1 0???1?0???
?????????? ???-

RHINEURIDAE 1010101111 1102{01}00000
{01}130000100 1000001010 3-00001100
0101000000 110-110002 0-110-3002 ???-101-0- 0?--
1--011 0000?00010 00100100201 -013-10101 12210-
0--1 -000-112-0 1011110131 12000{01}000- -
0{01}01-0101 2132100010 01{01}000?000 010-
000101 000{01}000000 0110000?-1 2201021-0?
0121011100 120210?002 ----2--1-- 2--------- ---2----
2- --0001?201 01000-0--- --11004010 1?000010?0 ?--
?0?00?1 0???1?00?? ?0???????? ???3

Cherminotus longifrons 1110?1-000 1201000000
0130?10110 ?1100?1-00 1000001100 010100200?
100-?10001 0010010?00 0110000110 0010011001
?0?01?0110 110020?110 0000010000 ??00?02001
?01??1?010 10100??11 ?100?00001 ?000000000
????0-0011 0001110001 00??1?0101 1202001100
201000???? ?0???????? ????????? ????????? ????????1?
????????? ????????? ????????? ????????? 0?????????
????????? ????????? ????????? ????????? ???8

Zapsosaurus 1?0???0010 ?????????? ?????????0 ??01??????
10??001100 01?110210? ???????0?1 101?002?00
??200001?0 ?1??01?00? ?????00010 00001?1211
00000?0000 000?0??001 0????010?0 0?000???11
?000?0000? ?000000100 10?1100011 0110?0?000
?00-000020 0400?00000 0??000??1 2?????????
???1?????? 01???????? ????????? ????????? ??????????
????????? ????????? ????????? ????????? ??????????
????????? ????????? ???8

Anchaurosaurus 100??0-000 110?000000 0030?1?010
??010000?0 1000001100 01?1102100 0-0-000001
1010002?00 002000001?0 ?????????? ????0?????
?????012?? ??0?000000 0?000??00? ?0?????0?0
00000???11 ?000000000? ?000?0100 11021?0011
011010000? ?00-000020 0400000000 000000??1
2?000?1-?? ?????10?00 0000?????? ?00??0????
????00?0?? ??0?0?000? ?????????? ????0?0?-- --???????
????????? ????????? ????????? ????????? ???8

Ctenomastax 100??00001 110?000000 0130?11010
01010000?0 1?00001100 011110210? 0-??0000?1
001?002?00 0010000110 0210011001 0????00?10
000?1?121? ??000000000 0?0??????? ?00??010?0
00000???11 ?000000???? ?000???000 1?02???001
010010??0? ?00-000020 2000100000 000000????
????????? ????????? ????????? ????????? ??????????
????????? ????????? ????0-??-- --???????? ??????????
????????? ????????? ????????? ???8

Temujinia 1000?00001 110?000000 ??30?11010
01010?0000 1000001100 011110210? ??????0001
001?002?00 0020000010 0210011001 ????0??0?0
00001?1211 00000?0000 00000?0001 001??0?0?0
00000??1? ?000?0000? ?010??0100 1002100011
0110?0?00? ?00-000?20 0400000000 0??000????
????????? ????????? ????????? ????????? ??????????
????????? ????????? ????????-? ????????? ??????????
????????? ????????? ????????? ???8

Rhampholeon 0000002011 11{01}2000000 1130011000
0101000100 3--1000001 0001100000 0-0-000011
0010003?02 --00010000 1---010000 01--010010
0000100011 1010000000 02010001-0 ?0000-10?0
0??10-?041 200001000- -020??-101 01320-01-- -
11000-000 ?000000120 0401000000 -000001101
210??01-00 0101010010 0200000102 -0010031-- 0-
0-00100- 1000001000 3??010?2?0 00000-0--- 0-
00010000 1?00?????? ??0?000???? ????????? ??????????
???5

Brookesia 001?002011 1-02000001 0030011000 0101-
01100 3--1000001 0001100000 0-0-000010 0-
10023?01 0000000000 1---010000 01--010010
0000100111 1010000000 02010001-0 ?0000-10?0
0??10-?041 200001000- -02000-101 01321201-- -
12000-000 ?000000120 0401000000 -000001101
210??01-00 0101010010 0200000102 -0010031-- 0-
0-00100- 1000001000 3??010?2?0 00000-0--- 0-
00010000 1?001????? ?11000???? ??????0???
?????????? ???1

Physignathus 000000-000 1100000000 1030011000
0001000000 1001001010 0011102000 0-0-000001
0110002100 0010000000 1---020000 0000000010
0000101211 1000000000 0000000000 0000001000
0000000001 ?000000000? ?020000001 01-21101-- -
12010000? ?000000020 0101100000 -0-000??01
2????????? ?????????? ?????????? ?????????? ??????????
?????????? ???100?1-0 00000-0--- --000????? 0?????????
?01??????? ?????????? ?????????? ???9

Agama 100001---- 1102000000 0030011000
0101000000 1001000110 0111102100 0-0-000001
0010002200 0010000101 1---010000 0000000010
0000100211 1010000100 0000010100 0000001001
00000?0011 200000000- -020010101 01321001-- -
10010-000 000-000020 0101100000 -0-0000001
2000001-00 0001010000 0200001000 0101002000
011000000- 1001100000 11?100?1-0 00???-?-??
??0?0????? ?????????? ?????????? ?????0??? ??????????
????

Uromastyx 000001---- 1202000000 1030111000
0101000110 3-0000{01}110 0011102100 0-0-
000001 1010002200 0000010000 1---020010
0000010010 0000100202 1100100100 0000010000
0010001001 00000?0011 200000000? ?000000100
01321001-- -110100000 000-000010 0101100000 -
0-0000001 2011001-10 0101010000 0200001000
0110000010 011200000- 1001100000 11?100?1-1
00???-?-?? ??0?0????? ????0?0??? ?????????? ?????0???
?????????? ???6

Phrynosomimus 0011002111 1100000000 1030?11000
01010?0000 1000001111 0111102100 0-??00?0?1
001?-02?00 0000010??0 1?--001000 ????0000010
0000100211 00100?0000 ??0????1-? ?????210?0
0????????? ??00?0000? ?000??010? 00??0-000?
010010?0? ?00-000?20 0101?00000 -??000????
?????????? ?????????? ????????0 1?????000 ??????????
?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ???8

Priscagama gobiensis 1000?02111 111??00000
1130111010 0101?00000 1000000011 01111?210? 0-
??00000?? 001?-02?00 0100010110 1?--011000
0???000010 000?101110 1010000000 0?0????00?
??0???1010 0???????1? ?00??0000? ?000000?00
00020-0001 010010???? ?00-00???0 0101??0000 -
00000???? ?????????? ?????????? ?????????? ??????????
?0???????? ?????????? ??????1-? ?????????? ??????????
?????????? ?????????? ?????????? ???8

Mimeosaurus crassus 0000?02111 110?000000
0030111010 01010?0000 1000001111 001110210?
????0??0?1 001?-02?00 000001?00 1?--011000
????000010 000?1?120? -?10000?00 ??0?0?0???
??1??10?0 0??00???1? ??0??0000? ?000000010?
001????001 010010?0? ?00-0?0?20 0101100000 -
00000???1 2?00?????? ?????1???? ?????????? ??????????

?????????? ?????????? ??????1-? ????????-? ??????????
?????????? ?????????? ?????????? ?????????? ???8

AMNHiguana 0000?00001 110?000000 0030?11010
??010?0000 1000001100 0111102100 ????0??0?1
101?002?00 0010000110 021001?001 ????100???
?0???????1? ?00000????? ??00??000? ?0????????
????????1? ?0???0?00? ??????0??? ?????????? ?1?010????
????000020 040000?000 ?00000???1 2000001-?0
00??0?0?00 01??000??0 111?00?0?0 0??00000-
1000100000 10???????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ???8

CROTAPHYTIDAE {01}000010011 1100000000
003001{01}000 0101000010 1000000001
0111102100 0-0-000001 {01}012002000
0010000101 0--0010000 0001100010
0000{12}01111 0000000000 0000000001
0000001000 0000000011 200000000- -
0100{01}0100 20321{01}0001 0110100000 000-
000020 0400100000 0010000001 2000001-00
0011010?00 0{12}00000000 11100{01}1000
001100000- 1000100000 010{01}0001-1 00000-0---
--00001000 00?00?0?0? ?01??????? ??????{01}???
?????????? ???3

IGUANIDAE 10{01}000001{01} 1100000000
0030010000 01010000{01}0 1000001100
01{01}110{01}100 0-??000001 001000{12}000
???0?00001 01?00?0000 0001?00010 0000101{12}11
10000{01}?000 00000101-0 0?{01}0011000
000000?011 200000000- -000000100
203{01}100010 0110101?00 000-000020
0400000000 0000000001 2000101-10 0001010?00
0000000{01}00 0110011000 001000000-
1000100000 01000001-0 00000-0--- --00001000
00?00?0?0? ?00?????? ?????{01}0?? 00???????? ???-

FMNHpolychrotid 100??0???? 110000?000 ?030??????
??0???0??? ????001?01 0???1021?1 0-?????001
0?10?02??? ???0?0??0? 0??00??00? ??????0010
00???1111? ?????????? ?????????? ?????????? ??????????
?000?0???? ?????????1 ???2??0??? ?1??????0?
?0??000?20 0?00?00000 ?00000???1 2?00?01-??
0???010??0 03000011?1 1??00???? 0???00000?
?000000?000 ?????????? ???0-0--- --???????? ??????????
?????????? ?????????? ?????????? ???3

ANISOLEPINAE 1000000111 1100000000
1030000000 0101000000 100000000{01}
000110210{01} 0-0-000001 0012002000 ???0000000?
0?00010000 0000?10010 0000101111 1010000000
00000101-? 0000001000 0000000011
?0000{01}000- -0{01}{01}010101 2002100011
011010?000 0400000000 0000000001
2000001-10 0001010000 3000000101
111000{12}000 010000000- 1000100000 00?00011-
0 0000{01}-0--0 00000?1000 0???1?1??? ?01???????
?????????? ?????????? ???2

LEIOSAURINAE 1000000111 1100000000
1030000000 01010000{01}{01} 1000000000
00{01}1102100 0-0-000001 0012002000 ???000010?
0?11010000 0000?{01}0010 0000101111
1010000000 0000010{01}01 00{02}0001000
0000000011 ?00000000- -011{01}00101
20{01}2100011 011010?000 000-000020
0{34}00000000 0000000001 2000001-10
0001010000 {03}300001101 11{01}0001000
0000000000 {01}000100000 01?000{01}1-0 00000-

0--- --000?1000 0???1?1??? ??1??????? ??????????
?????????? ???3

PHRYNOSOMATIDAE 10{01}000{02}00{01}
1200000000 1030000000 0101000000
{13}00000{01}100 0111102100 0-0-000001
0010002200 {01}000000100 0??1010000
0000100010 000010121{01} {01}000000000
0000000001 0000001000 0000000011 200000000- -
0{02}0010100 0012100010 01{01}010?000 000-
000020 0{04}00000000 0010000001 2000101-10
0011010?00 010000100{01} 0100012000
011100100- 1000{12}00000 0100{01}001-1 00000-
0--- --00001000 00?00?0?0? ?0{01}???????
?????{01}??? ????????? ???3

CORYTOPHANIDAE 100000001{01} 1100000000
1030010000 0{01}0100{01}{01}{01}00
1000000{01}1{01} 0011102100 0-0-000001
0{01}1{01}{02}10{02}0-0 0--00001{01}0
0?1{01}010000 000000010 0000201111
1010000000 0000010{01}?1 000?001000
0000000011 200000000- -001000100
20321{01}00{01}1 011010?000 000-000020
0400000000 0000000001 2000101-10 0001010?00
{03}{12}0000{01}001 0001001000 000100000-
100{01}{01}000000 00010001-0 ?0000-0--- --
00001000 00?00?0?0? ?01??????? ?????????? ??????????
???{23}

PolychrusMARM 100000{02}011 1110000000 10?0?0-
000 0101000010 1000000111 0001102101 0-0-
?000?1 001?003000 0000000111 1---010000
?0??100010 0000201111 1010000000 00000101-1
00200-1000 0000000011 ?00000000? ?000??0101
20-2120010 011010000? ?00-100120 0400000000
0000000001 2000011-10 0001010000 0?00000100
1110002000 010000000- 1000101000 01??10?1-1
????0-0--- --000?1??? ?????????? ?01??????? ??????????
?????????? ???3

PolychrusFEM 100000{02}011 11?0000000 ?0?000-
000 0101000010 1000000001 0011102101 0-0-
100001 0010002000 0010000111 1---010000
000?100010 0010201{12}11 1010000000
0000010001 0010001000 0000000011 200001000- -
00001-100 2002100010 011010?000 000-000020
0400000000 0000000001 2000001-10 00?1010000
?30000!10? 1100002000 0?0000000- 1000000000
01011001-0 00001-0--0 0000011000 00?01?1???
?01??????? ?????????? ?????????? ???{23}

PolychrusGUTT 100000{02}001 0110000000 103000-
010 0001000000 1000000100 0001102101 0-0-
000001 001?002000 0010000011 1---010000
?00?000010 0000201101 1000000000 00000?01-?
?010?01000 0000000011 ?000?0000? ?001010100
20?20-0011 0110100000 ?00-100020 0400000000
000000???? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ????10?1-0 00?00-0--- --0?0?1???
?????????? ?????????? ?????????? ?????????? ???2

AnoleAMBER 100?00???? ??0?000000 ?030??????
0?01??00?? ????000??? 0???102101 0-0-0000??
?????????? ????0?010? ?1??01?00? 0???0011?0
00001?1211 ?000?0?0?0 0?00??000? ??0????0?0
0???????1? ?000?????? ???????10? ?????????? ?11???????
??0-?00?20 0400000000 ?000000??1 2000??1-??
???1010000 03??000?00 110?00?000 ????00000?
????100000 ?1??00?1-? 00000-0--- 000?0?????
?????????? ?????????? ?????????? ?????????? ???3

AnolisHETE ?00000{01}111 1100000000 103000-010
0101000000 1001000011 0111102101 0-0-000001
0010002001 0000010001 0110010000 ?0??001110
00101?1211 11???0100 00000101-0 0000001000
0000000?11 ?000?0000- -0011-0101 20321201-- -
1?010?00? ?00-?0???? 0400000000 000000????
?????????? ?????????? ????????? ?????????? ??????????
?????????? ???0?011-0 00000?0?-- 0000?11000
0?????????? ?01??????? ?????????? ?????????? ????

Isodontosaurus 000??0-000 1310000000 0030?11000
??0!0?00?0 1000001100 001110210? ????1??001
1010002?00 001000??00 0101010000 ??????????
0???1002?? ?0???00??? 0??00????? ??1????0??
???????21? ?000?00??? ?02000-100 0010?0?0001
011??????? ?010000?10 0500000000 000000????
?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ????????? ???8

AnolisOCC 101000-000 1300000000 003000-010
0101000000 1000000000 0011102101 0-0-000001
0010002001 0000000001 0210010000 ?00?001110
0000101111 1000000000 0000000001 0000001001
0000000011 ?000?0000- -0311-0101 20120-0011
0110101000 000-000020 0400000000 0000000001
2000000-10 0001010000 0300000100 1100001000
000000000- 1000000000 01?0?011-0 00000-0---
00000?1?0? 0????????? ?????????? ?????????? ??????????
???3

AnolisVERM 101?000111 1300000000 0030010110
0101000000 1000000011 0011102101 0-0-100001
0010100?01 0000000101 0110010000 ?00?001110
0000101101 1100000000 0000?01-1 ?000000000
0000000011 ?000?0000- -001010101 2032100010
011010100? ?10-001020 0400000000 0000000001
2000000-10 0?01010000 0?00001??0 1110001000
000000000- 1000100000 01?0?011-0 00000-0---
00000?1?0? 0????????? ?????????? ?????????? ??????????
???3

Leiocephalus 0000000011 1101000100 0030000000
0101000000 1000001100 0011102100 0-0-000001
0010002000 ???0000010? 0?10010000 0001?10010
0000101{12}11 1000010000 00000001-1
0010001000 0000000011 ?00001000- -03001-101
20020-0010 010010?000 000-000020 0400000000
0000000001 200000????? ?????????? ?1????????
?????????? ?????????? ????????? ???0?0?1-0 0????-?-??
??0?0????? 0??0?0??? ?????????? ?????????? ??????????
???3

Stenocercus 0000000011 11{01}0000000
{01}010010000 010{01}000010 1000001100
0111102100 0-0-000001 0010002000 0010000100
0100010000 0000000010 0000101111 1010000100
0000000001 0010011000 0000000011 ?00000000- -
001010101 20020-0010 0110100000 000-000020
0400000000 0000000001 2000001-00 0011010000
0100001{01}00 111?001000 001100?00- 1000100000
00?010?1-1 00?00-0--- --0000???? 0???0?1???
?00??????? ?????????? ?????????? ???2

TROPIDURIDAE {01}0000000{01}{01}
1100000000 {01}0{13}00100{01}0 0101000000
100000{01}1{01}0 0111102100 0-0-000001
0010002200 00200001{01}0 01{01}0010000
0001100010 0000101111 1000000{01}00
0000000001 00100{01}1000 0000{01}00011
200000000- -0{23}101010{01} 20{01}20-0010

0100100000 000-000020 0{24}00000000
00{01}0000001 2000001-10 0011010000
010000?00{01} 11{01}?011000 0{01}1100000?
?000100000 0??1{01}0{01}1-1 00?00-0--- --0000????
0???0?1?0? ?00??????? ??????0{01}1 0001010101
001{23}

Liolaemus 0000000011 1100000100 101000-000
0101000000 1000001101 0111102100 0-0-000001
0010002200 0010001-10 0110010000 0001110010
0000101111 1010000000 0000000001 00000?1000
0000000011 ?00001000- -0011--101 1002100010
0110100000 000-000020 0400000000 0000000001
2000000-11 0?01010000 0100001??0 0110001000
001100?00- 1000200000 00?110?1-1 00???-?-??
??0?00???? 0???0?0??? ?00??????? ?????????? ??????????
???2

Hoplocercus 0000002001 1100000000 1011110000
0001000000 4001001100 0011102101 0-0-000001
0010002000 0000000101 0110010000 ?000100010
0010101110 0010000000 00000101-1 0010201000
1000100010 ?00000000- -020010100 00{01}20-0000
0110100000 000-000120 0400000000 0000000001
2000001-11 0?01010000 0100000100
110000{01}000 001100000- 1001200000 00??20?1-0
00???-?-?? ??0?00?000 0????????? ?????????? ??????????
?????????? ???2

Morunasaurus 0000002001 1100000000 003010-000
0001000000 1001001100 000110210? 0-0-100001
0010002?00 0100000101 0110001000 00??100010
0010101110 0010000000 00000?01-1 10100?1000
0000000011 ?00001000- -02000-100 0002110010
011010000? ?00-000020 0400000000 000000????
?????????? ?????????? ????????? ????????? ??????????
?????????? ?????0?1-0 00???-?-?? ??0?00?000 0?????????
?????????? ????????? ????????? ???2

Enyalioides 0000002011 1100000000 10{01}0000000
0101000000 4001001100 0011102101 0-0-000001
0010002000 0000000101 0110010000 0000100010
0000101111 0010000000 00000101-1 0010001000
0000000011 200000000- -000000100 00020-0010
0110100000 000-000020 0400000000 000000???1
2000001-10 0001010000 0100001100
11000{01}1000 001200000- 1001200000 01000001-
0 00000-0--- --000?1000 00?00?0?0? ?01???????
?????????? ????????? ???2

OplurusQUa 001?000111 1100000000 0030011000
0101000000 0000001100 0101102101 0-0-000001
0110002000 0000000100 ????01?000 00?1100010
0010201111 1000100000 0000010000 0010001000
00001?0011 ?000?0000? ?001010101 20000-0010
011010000? ?00-000020 0400000000 0000000001
2000??1-00 ??01?????? ?1???????? ??0???10??
?0??????? ????????? ???00011-1 00???????? ??0????????
?????0??? ??1??????? ????????? ????????? ???1

OplurusCYCL 001?000111 1100000000 1030011000
0101000000 1000000101 01?1102101 0-0-000001
0110002000 0110000100 1---010??? ?0?1100010
0010201111 1010010100 0000010000 0010001000
0000100011 ?000?0000? ?030010100 00020-0011
011010000? ?00-000020 0400010000 000000???1
20000?1-00 ??01?????? ?1???????? ??0???10??
?0??????? ????????? ??00011-1 00???????? ??0?0?????
???0?0?0?? ?11??????? ????????? ????????? ???1

OplurusQUb 001?000111 1110000000 1030011000
0101000100 1000000100 000110200? 0-0-000001

001?001000 000000??00 0110010000 0???100010
0010201111 1000010000 00000?000? 0010?01000
00000?0011 ?000?0000? ?030010101 20120-0010
011010000? ?00-000020 0400000000 000000????
?????????? ????????? ?1??????? ??0???10?? ?0????????
?????????? ???0001?71 00???????? ??0?0????? ?????0???
??1??????? ????????? ????????? ???1

Chalarodon ?????0?11 ???????0?? ????????? ??010?0?0?
1?00000100 0?1?102101 0-0-???01 1010002000
001000???? ?????????? ????00?1? ?????????? ???????0?
????0?0??? ???0?????? 0?0??????? ??0?0?00?
?001010100 20120-0010 011010000? ?00-?????
04?0???000 0??000???? ????????1? ??????????
?1???????? ??0??20?? ?0???????? ?????????? ???00011-0
00???????? ??0??????? ????0?0??? ?11??????? ??????????
?????????? ???1

Polrussia 000???-000 1??0000?0? ????00010 ??110?0???
10??00110? 0111102100 0-??000?1 101?00??0
??10??000? 1?--00?000 ????0????0 ?0?01?01??
000000?00? 0?0??????? ???????0?0 0??01?????
????0000? ?001??0100 2??20-0010 011010?00? ?00-
?0??2? 0000??0000 ??0?000???? ?????????? ??????????
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Igua 0?1???-000 ?????????? ?????????? ?????0??? ??????????
????10?1?? ?????????1 101?002000 ????00????
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?0??????? ?????????? ?????????? ?????????? ??????????
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Myrmecodaptria 0010?010?0 01??000?00 ?0???10000
??010?00?0 3?000001100 00111?010? 11?????0?1
001?-20?01 1101-10010 000-1--001 ????1?0?1?
1??01?021? ??11000??? 0?0?0?2??? ?0?????0?0
????????11 ?000?0000? ?000??0001 0?120-0001
01??00?10? ??10000?00 1000000000 ?0?000????
?????????? ?????????? ?????????? ?????????? ??????????
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Eidolosaurus trauthi ??0??????? ?????????? ?????????0
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2?0??21-?? ?3?1110?11 0?0?000?0? ??????????
????0??00? ???2??0110 ?????????? ?????????? ??????????
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SCELOTINAE 0000000000 {01}102000000
0130000000 1100000000 1000000000 0111002000
0-0-110001 0-10-20010 0021010010 0020021001
1000100111 0012100211 1000000000 0000002000
00200-1000 0000010011 200001000? ?0011--100
1201120010 001000?100 000-101111 0000000000
1000000101 2001021-11 00?1011000 ????100001
1?????3010 000200200- 1--0201000 -10000?201
1110111?00 00000?1020 002?0????? ?00???????
?????????? ????????? ???5

ACONTINAE 001000000{01} 0102{01}00000
00{23}0000101 1100001000 1000001100
0101000000 100-111001 00100{12}{03}010
1{01}01{01}00010 001{01}{01}010{01}1
1000100111 0012101211 101{01}100000

0000002000 00100010{01}0 0010010011
21000{01}0000 10101-0101 22200-0010
010010?000 000-{01}01101 0000000000
000000??01 2001021-?? 0??1011?00 020000?0??
?????????? ?-??4-??-- ?--{01}0-1--2 --0000?201
1110111?00 00000?1020 102?0????? ??????????
??????000 ?????????? ???5

SCINCINAE 1000000101 {01}10{02}000000
0130010000 {01}10000{01}010 20000000{01}{01}
00{01}1102100 100-110011 0-12-20{01}10
0021010010 0020{01}01001 1000110111
001{12}100211 10{01}10000000 0000000000
0010011000 {01}000010011 20000100{01}0
100001-101 12010-0000 0000000100 000-101111
0000000000 100000?101 2001021-11 0011010000
0000001001 1100011010 010000200-
100{01}201000 {02}10000?201 1010111100
0000001020 002?0????? ?00??????? ??????01-1
00010{01}1{01}00 {01}{01}0-

FEYLININAE 1010000000 1100000001
00{13}0000100 121000{01}010 20001----- ---
1000100 100-110001 0-10-22010 1021010110 001-
1-?001 1000110111 01121-1211 1000010000
0000002000 00210-1000 0000010011 2000010000
11--??-101 22?10-021- 0000010?100 000-101111
0000000000 100000??01 2001021-?? 00?1010000
????00001 0---2-31-- 0-0------- ---??-?--1 --0000?201
1110111?00 00000?1020 002?0????? ??????????
?????0001 110101111- 00-5

Meyasaurus diazromerali ?000?00?11 110?000000
1?300????0 ??000?0??0 ???000000 0001102100 100-
11?001 0002020000 ??00000?10 0010001000
1??1????0 ??????0?1? ??1??????? ???0?????? ??????????
????????11 ?000??0001 1?????0100 02?11000?0
01?0?0??00 ?010000001 0400000000 000000???1
2001101-12 0001010?00 000?000?01 110?000010
0?01002000 0000001000 ?1?????1-? ????1?1?-- 1-
???????? ?????????? ?????????? ?????????? ?????????? ???4

Slavoia darevskii 2010?00001 {01}102000000
002001?100 1110001000 1000001000 0001000000
0-0-110011 0011-20000 0011010010 0010001001
????000011 0012100111 100?1100?? 1?000?200?
?02????000 0???????11 ?000?1000? ?00001-000
02?10-0011 011000-100 ?00-100111 1000000000
001000??1 2101011-?? 0?01010000 02??00???1
110?00?010 ????00000? ?0?1???000 ?0???????0
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Tchingisaurus multivagus 100???0001 11??000?00
?????10000 ??010?00?? 10??000100 01?100210?
????????11 ?012020?00 001??20?1? 02100?1000
1????????? ?????????? ?????????? ?????????? ??????????
????????11 ?000?0001? ?000010100 0002100000
010010?10? ?011000000 0410000000 000000????
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Dibamus 101010-000 1202000000 1130000101 121000-
0-0 3-001----- ---1000000 100-111003 0-11013?11
100-110--- 1---1--1-- 0000100111 00121-1211
0002010000 022{01}000--1 00001210-0
1011100031 020001000- -0201--101 22-00-021-
010010-000 010-001101 0000000000
{01}000001111 2200021-?? 0-21010100 100011?002
----?-31-- 1-0----1-- ---{01}0-1-02 --2000?2-1 11100-

0--- --1-100010 1??0?????? ?--?0000?? 0???1??1-?
0?01?????? ???8

Anelytropsis papillosus 001010-000 1200000000
1130000100 12100000-0 3-001----- ---1000000 100-
111001 0-10013?11 ???-10001? 0?1-1--1--
0000?00111 00121-1211 1002110100 02200?0--1
00001210-0 1011100031 02??01000- -0001--101 22-
00-021- 010000?000 010-000101 0000000000
{01}00000???1 2200021-?? 0-2?????00 100011????
?????????? ?????????? ?????????? ???{01}00?2-1 11100-
0--- --1-1????? ?????????? ?--?????? ??????????
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Eoxanta lacertifrons 1010?0-000 020?000000
?030010001 0100000010 1000001?00 ?0?1002000
100-110011 ??12-20?00 ??01010010 0020021001
????100011 0010100211 101100000? 010?0??000
??10??000 0??00???1? ?????1000? ????1--000 02010-
000? 01?0?0010? ?010000000 0000?00000 ???00?????
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Hoyalacerta sanzi 100??0-000 0?0??0?0?? ?????0?000
??000????? 10??00?1?? ?????02100 0-???0000?
?????????? ???0?0???? ????0??00? ?????????? ??00??02??
?????????? ??0?????? ?????????? ?????????1 ?000??????
?????????? ?????????? ?????????? ????0000?0 00??0??00
?00??0??1 2000021-?? 0?00010??0 00????1?0?
?10?00???? ????00?00? ??????000 ?????????? ??????????
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Globaura venusta 100??0-000 0100000000 0030110010
01000000?0 1000001100 0011102100 10??110011
?012-20?01 0011010010 0010021001 ????100011
0010100211 100000000? 11000?200? ??00??0?0
0??01??11 ?000?0000? ?0001-0100 02110-0000
011010010? ?010000011 0000?00000 ?00000????
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Palaeosaniwa ??????1?11 ?????????? ?????????? ??????0???
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??1?0101?? 0???0??00? ????1????? ??????10??
?????????? ?0?0?0???? 0?1??1?0?? ??0??????1
?1????0??1 ???????00? 01??0-???1 ?????1?0?? ?00-
????? 12?2001100 1?00????1 21121?1-?? ????0?0?00
0201?????? ?????????? ???00?00? ???1??1000 ?1?????1-
? ?00?1????2 0????????? ?????????? ????????? ??????????
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HelodermaHORR 101-001111 1101000000
0130010000 0010001010 1000000001 01-1000000
110-010001 0010-13000 110-010100 001-1--011
0000101110 1110111210 0002010010 00000021-1
0010011000 0010000010 2000000001 1000000000
01120-0011 000111{01}001 000-100101 1202001101
2010001001 2101121-00 0011010000 0201000000
10010010-1 0-02000000 0001101000 010000?1-1
0000101012 0000023111 0101000?0 0111?000?1
0101110?? ?????????? ???3

HelodermaSUSP 101-001111 110100000{01}
0030010000 0010001010 1000000001 01-1000000
110-010001 0010-13000 110-010100 001-1--011
0000101110 1110111{12}10 0002010010 00000021-
1 0010011000 0010000010 2000000001 1000000000
01120-0011 0001110001 000-100101 1202001101
2010001001 2101121-00 0011010000 0201000000

10010010-1 0-02000000 0001101000 010000?1-1
0000101012 0000023111 0101010001?0 0111?000?1
01011100?? 0????????? ???3

HelodermaTEXA 1?1-?01111 110????00? ?0??1?000
01100?10?0 1000000101 01-1000000 11???10001
??10-13?01 ???-01??0? 0?1-1--011 ?????01110
11101?1210 00?200001? 000??021-? 001????000
0??00??1? ????????? ????????? ????????? ?????????
????????? 1202000111 2????0???? ????????? ?????????
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?0?1???12 0????????? ????????? ????????? ?????????
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Gonatodes 101000-000 1102000000 0030110000
0000000010 3-00002--- -001102100 110-111001
0010-03210 100-011-10 001-1--011 0001110110
0000100211 0001000000 1100121000 0011001000
0000110031 000000000- -0311-0101 22320-0010
011010-000 010-011100 0000000000 0000000010
100-001-12 0?01000000 0100001001 111?001010
010?00000- 1000200000 311?00?1-1 ?0000-0---
00010?1??? 0???1????? ?00?0????? ????????? ?????????
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Gekko 101000-000 1100000000 0030011000
0000000010 3-00002--- -001102100 110-110001
0000-03210 101-011-10 001-1--011 0001110110
0000100211 0001000000 1100102000 0011001000
1000010031 100001000- -1-1--100 2232120010
010010-000 010-011100 0000000000 0000000010
100-001-?? 0101000000 0100001?11 111?001010
000100000- 1000100000 ?11?00?1-1 00001000-0
00010?1010 001?3????? ?00?110000 0??0?0?0???
????????? ???8

Pachydactylus 101000-000 1202000000 0030110000
00000000-0 3-00002--- -001102000 110-100001
00?0-03000 100-011-10 001-1--011 0001110110
0000100211 0001000000 1100122000 0010001000
1000110031 000001000- -1-1--100 2232120010
011010-000 010-111100 2000000000 0000000010
100-001-11 0201000000 0100001011 1101001010
010100000- 1000200000 311?00?1-1 00001000-0
01010?1??0 0???3????? ?00?1?0000 0?????????
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Teratoscincus 000000-000 1100000000 0040111000
0000000000 3-00002--- -001102100 110-010001
0010-03201 000-011-10 001-1--011 0001110110
00001-0211 0001000000 1100121000 0000001000
1000110031 000000000- -0011-0100 2232120010
010010-000 000-111100 0000000000 0000000010
1000001-?? 0101000000 0100001011 110?00?0??
????00000- 100?101000 011?00?1-1 10100-0---
00010?1??0 0???3????? ?00?11???? ?????????
????????? ???6

Aeluroscalabotes 100000-000 1100000000 003010-000
0100010010 3-00002--- -001102100 110-110001
0012-03200 100-010010 001-1--011 0000100110
0010100211 0001000000 1100102000 0011001000
100011??31 000000000- -1--1-0100 2232100010
010010-00? ?00-011100 2310000000 0000000011
2000001-11 0?01000000 010000?01? ?11?00????
????00000- 1000201000 311?00?1-1 00?00-0---
00000?1??? 0???0????? ?0??1????? ????????? ?????????
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Hemitheconyx 100000-000 1100000000 0030110000
0100010010 3-00002--- -001102100 110-100001
0012-03201 100-011-10 001-1--011 0000100111

1 0101-1210 0001000000 1100122010
000{01}001000 1000110031 000000000- -0311-
0100 2232120010 011010-000 ?00-011000
2300000000 0000000010 100-011-?? ??01000000
010000?011 111100???? ???00000- 1001201000
311?00?1-? 00000-0--- 00000?1010 0?1?0?????
?0??110000 0???0????? ????????? ???5

Coleonyx 100000-000 1100000000 003010-000
0100010010 3-00002--- -001102100 110-110001
0012-03201 100-011-10 001-1--011 0000100110
00101-1211 0001000000 1100122000
000{01}001000 000011?031 000000000- -0011-
0100 22320-0010 010010-000 ?00-011101
2000000000 0000000010 100-001-11 0001000000
0100001011 1111001010 000100000- 1000101000
311?00?1-1 00?00-0--- 00000?1?10 0?1?0?????
?0??1????? ????????? ????????? ???3

Paramacellodus ?01???01?? 11?000??? ????01000?
??0??????? ????????? ????????? ????????? ?????????
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00010-000? 01?010?10? ?00-10??01 0100000010
000000???1 20011?1-?? 0???010??0 00????????
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00????????? ????????? ????????? ????????? ????????? ???4

Becklesius ??????01?? ????????00 01??010000 ?0???????
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0000 011010010? ?00-?????? 0000000000 0??000??1
2????????? ?????0??? ????????? ????????? ?????????
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Volivaceus 2100010001 1100001001 0130011110
1010000-00 111100010- 12-1001000 110-010011
0111110000 0100000110 0011021001 100-101110
1100101210 0002010100 000000200? ?0000?1010
1010000011 ?000000000? ?010000000 01120-0001
0110110001 000-101101 0512001100 201000??? 1
20?2021-?? ?2?10100?0 021100?000 11??002000
0??200000- 100??0000 ??0000?1-1 000??0?00?
0?0000???? 0????????? ????????? ????????? ????????????

Veremius 110001-000 1200001000 0130011100 1010000-
?0 111100110- 12-1002000 110-010011 0111010000
0000020110 0011021001 100-101110 0100101210
0001010?00 0000002?0? ?0?00?1010 1010000011
?100000001 1010000000 01120-0011 0110110001
000-100101 1202001100 201000??? 1 20?2021-??
?2?10100?0 021100?000 11??002000 0??200000-
100??0000 ??0000?1-1 000??0?00? 0?0000?????
0????????? ????????? ????????? ????????? ????

Vtristis 2100010001 1110001000 1130011110 1010000-
?0 111100?10- 12-1002000 110-010011 0011010000
0000000110 0011011001 100-101110 0100101210
0001010?00 0000002?0? ?0?00?1010 1010000011
?100000001 1010000000 01120-0001 0110110001
000-100101 1202001100 201000??? 1 20?2021-??
?2?10100?0 021100?000 11??002000 0??200000-
100??0000 ??0000?1-1 000??0?00? 0?0000?????
0????????? ????????? ????????? ????????? ????

Vprasinus 2100010001 1100001000 1130011110
1010000-?0 111100110- 12-1002000 110-010011
0011010000 0010000110 0011021001 100-101110
0100101210 0001010000 00000021-1 0010001010
1010000011 ?000000001 1010000000 01120-00??

011011?00? ?????????? ?????????? ???00????1
201202??00 1????????? ?????????0 111000????
????00000- 100011000?? ?0???????1 0000??????
???0????? ????????? ????????? ????????? ?????????
???9

Vsalvadorii 3110010001 1200001000 0130011110
1110000-00 1111001100 12-10021{01}0 110-
010001 0011010000 0{01}00000110 0011011001
100-101110 0100101210 0001010000 00000021-1
0000001010 1010000011 2100000001 1000000000
01120-0011 0110110001 000-101101 1202001100
2010001101 20220???00 1??1??0??? ??????????
?????????? ????00?0?? ???????000 ???????1-1
000??0?00? 0?000????? 0????????? ????????? ?????????
????????? ????

Megalania ?11???00?1 ?????01??? ??3001?11? 1?????1???
?????????? ????002120 110-?10001 0011110000
???0?0011? 0????????? ????????? ??0?????? ?????????
???0????? 0??0????? ?1??????? ??????0?1 ??????00?
01???????? ?????????? ?????????? 1202001100
2??000???1 20220?1-?? 1???010?00 021100????
???????000 ????00?0?? ???1??0000 ??????????
?????0???3 ????????? ????????? ????????? ?????????
????????? ???9

Vkomodoensis 3110010001 1200001001 0130011110
1110000-00 1111001100 1{12}-1002000 110-
010011 0011010000 0100000110 0011021001 100-
101110 0100101210 0001010000 0000002001
1000001010 1010000011 2100000001 1000000000
01120-0011 0110110001 000-100101 1202001100
2010001101 2022021-01 1221010000 021100100?
?11?002000 0??20000?- 1001100000 ?{01}?????1-1
000??0?003 0?000????? 0????????? ????????? ?????????
????????? ???9

Vvarius 3110010001 1200001001 0130011110 1010000-
00 111100110? 12-1002100 110-010011 0011010000
0000000110 0011021001 100-101111 1100101210
0001010000 00000021-1 1000001010 1010000011
2100000001 1010000000 01120-0011 0110110001
000-100101 1202001100 201000???? ??????????
????????? ????????? ????????? ????00000- 100???000
???????1-1 0000?????? ????0????? ????????? ?????????
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Vrusingensis ?????????? ?????????? ?????1?11? ?01???????
?????????? ?????????? ????????? 0110010000 ???0?0????
?????????? ????????? ????????? ????????? ?????????
????????? ????????? ?????00?0? ??10?0000 01?20-0???
???????01 000-100101 1502001100 ???000???1
20120?1-?? 1???-010000 021?00???? ?11?00????
???0?0000?? ???1??0000 ?1???????? ?????????? ??????????
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Vgriseus 2100010001 1200001001 0130010100
1010000-?0 1111001100 11-1002000 1100010011
0011010000 0100000110 0011021001 100-101110
1100101210 0001010100 0000002001 ?010001010
1010000011 2000000001 1010000000 01120-0001
010011?001 000-100101 1202001100 2010001101
20?2021-01 1221010000 0211001000 1110002000
0?0200000- 1001100000 000000?1-1 000010100?
00000-4111 010101???2 1101?00112 1?11112???
????????? ????

Vniloticus 2100010001 1200001001 1130010110
1010000-00 1111001100 11-1002000 110-010011
0111010000 0100000110 0011021001 100-101110
1100101210 0001010100 00000021-1 1010001010

1010000011 2100000001 1010000000 01120-0001
0110110001 000-100101 1512001100 2010001101
2012021-01 1221010000 0211001000 1110012000
000200000- 1001100000 010000?1-1 000??0?00?
0?0000???? 0????????? ????????? ????????? ?????????
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Vexanthematicus 1100010001 1200000001 1130010110
1010000-00 1111001100 11-1002000 110-010011
0111010000 00{01}0000110 0011011001 100-
101110 1100101210 0001010100 0000002001
1010001010 1010000011 2000000001 1010000000
01120-0001 0110110001 000-100101 1502001100
2010001101 2022021-02 1221010000 0211001000
1110002000 0?0200000- 1001100000 010000?1-1
000??0?00? 0?000????? 0????????? ????????? ?????????
????????? ????

SaniwaENS 1100?10001 110?000001 ?130?1?110
?100000??0 1111001100 ?1?1002000 ????0??001
0010010?00 0100000110 00110?1001 10?-101110
0100201110 0001010??? ??00000020?? ??10???0?0
??1?????1? ??00?0?001 1?????0000 01????00??
?1?011??01 000-101101 1202001100 2??000???1
2012021-01 12110?0?00 0211001000 111?002???
0?0200000- 1001??0000 00???0???? 0?0?0-0-0-
0????????? ????????? ????????? ????????? ????????? ???3

Typhlops lineolatus 001010-000 110201-000 001000-3--
0--000---0 3---1----- ---1000100 3-0-011001 00100-3-
11 -00-101--- 1---1--1-- 001010011- 21101-0210
00010-00-0 12211----1 1000?112-2 -01010?031
120001100- 10-11---00 01320-20-1 -10100-000 0-0-
000100 000200-000 ?020101101 2211221-02
0?210?1100 02-2110002 ----2--1-- 2--------- --22-1-
2- --?000?2-1 10100-0--- -0111????? 1???0?????
????????? ????????? ????????? ???6

Liotyphlops albirostris 001010-000 10-201-001 010000-
3-- 0--0000-00 3---00110- 1--1001000 3-0-011003
00000-3-02 --0-101--- 000????1-- 001010011-
2110100213 00010-00-0 12211----1 1000?112-2 -
01010?031 ?20001100- 11--1---00 01320-20-1 -
10110-000 0-0-000100 000200-000 ?020101101
2211221-02 0?210?1100 02-2110002 ----2--1--
2--------- ---2----2- --?000?2-1 10100-0--- -0111?????
1??0????? ?--??????? ?????????? ?????????? ???{23}

Leptotyphlops goudottii 001010-000 110201-001
004000-010 0--000---0 3---1----- ---1000000 3-0-
011002 00100-3-02 --0-101--- 1---1--1-- 0000100110
10101-0211 00011-00-0 12211----1 1000?112-2 -
01010?031 ?20001100- 10-01---00 01320-20-1
210100-000 000-000100 0002000000 ?021001101
2211221-02 0?210?1100 02-2010002 ----2--1--
2--------- ---2----2- --?000?2-1 11100-0--- -0111?????
1??0????? ?????????? ?????????? ????????? ???{23}

Pygopus 001000-000 1101000000 1130{01}0-000
0010000000 3-00002--- ---1100100 110-110001 0-
00-03?01 0001011-10 001-1--011 0000100110
1111100211 0001000000 1100102000 0021001000
0000110031 100000000- -030??0101 22020-0010
011010-000 000-110101 0000000000 0000000??1
2001021-?? 0001001000 0100101010 100-0031-- 0-
0-4----- ---1--1001 --1100?2-1 10100-0--- --010?10?0
00000????? ?-00210001 000000?0?? ?1???????? ???9

Aprasia 111000-000 1102200000 012000-000
0010001000 3-00002--- ---1100000 110-011000 0-
00013-01 100-121-00 001-1--1-- 0001110110
0011100210 0001000000 11001021-1 ?0200010-2

-000110031 ?10001000- -000??-101 20020-01-- -
11010-000 010-100100 0200000000 0000000??1
20010?1-?? ????????? ????????? ????????? ?????????
????????? ???0???2-1 10100-0--- --010??0?? 0???0????
???02?0001 00000???? ????????? ???9

Delma 100000-000 1102000000 113010-000 00100010-
0 3-001----- ---1100100 110-111000 0000-13?01
0001011-00 001-1--011 0001100110 0010100211
0001010000 1100102000 00110010-2 -0001??031
?10000000- -0011--101 20020-0010 0110100000
010-110101 0000000000 000000???? ??????????
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???0???2-1 10100-0--- --010?10?? 1???0????? ?????????
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Pletholax 111000-000 1112000000 1110?0-010
0?10000110 3-00002--- ---1101000 110-011000 0-
00013-01 0001021-10 001-1--011 00001??11?
?????0021? ?0?1??0000 11001021-1 ?0200010-0
0000110031 ?10000000- -0301-0101 20020-0010
0100100000 010-111101 0200000000 000000????
????????? ????????? ????????? ????????? ?????????
????????? ???0???2-1 10100-0--- --010?0?? 0???0????
???02?0001 00000???? ????????? ???9
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ENDBLOCK;

APPENDIX 3

ANATOMICAL ABBREVIATIONS USED IN FIGURES

a	angular
aif	anterior inferior alveolar foramen
aprf	articular surface for the prefrontal
as	astragalus
asaf	anterior surangular foramen
auf	autotomy foramen
aus	autotomy septum/plane
bc	braincase
bo	basioccipital
bptb	basipterygoid buttress of the pterygoid
c	coronoid
ca	calcaneum
cot	vertebral cotyle
crt	crista tuberalis
d	dentary
dp	descending process of the parietal (decensus parietalis)
dt	distal tarsal
e	epipterygoid
ec	ectopterygoid
ect	ectepicondyle
ef	ethmoid foramen
ep	epiphysis
exc	extracolumnella
f	frontal(s)
fe	femur
fi	fibula
ftb	frontal tab of the parietal
gl	glenoid
gr	groove
il	ilium
is	ischium
isa	infrastapedial arch of the quadrate
j	jugal
l	lacrimal
m	maxilla
mpm	premaxillary-maxillary aperture
mr	medial ridge
n	nasal
nff	nasofrontal fontanelle
np	nasal process
oto	otooccipital
p	parietal
pa	palatine
pap	palpebral
pf	postfrontal
pfo	parietal fossa
ph	phalanx (phalanges)
pif	pineal foramen
pm	premaxilla
pmy	posterior mylohyoid foramen
po	postorbital
pod	postdentary bones of the mandible
pof	postorbitofrontal (fused postorbital-postfrontal)
popr	paroccipital process
poz	postzygapophysis(es)
pr	prootic
pra	prearticular
prf	prefrontal
prz	prezygaphophysis(es)
ps	parasphenoid
pt	pterygoid
ptb	parietal tab of the frontal
ptt	pterygoid tooth/teeth
pu	pubis
pvpr	posteroventral process of the jugal
q	quadrate
ra	radius
sa	surangular
sag	sagittal ridge of the parietal
sm	septomaxilla
so	supraoccipital
sop	subolfactory process of the frontal
sot	sphenoccipital tubercle
spfo	subpalpebral fossa
sph	sphenoid
sq	squamosal
ssa	suprastapedial arch
st	supratemporal
sta	stapes
stp	supratemporal process
syn	synapophysis
ti	tibia
tp	transverse process
v	vomer
vg	venom groove
zgs	zygosphene