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The Intramandibular Joint in Squamates, and the Phylogenetic Relationships of the Fossil Snake *Pachyrhachis problematicus* Haas

Olivier Rieppel
Hussam Zaher

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The Intramandibular Joint in Squamates, and the Phylogenetic Relationships of the Fossil Snake *Pachyrhachis problematicus* Haas

Olivier Rieppel

Hussam Zaher

Abstract

A review of the morphology of the lower jaw in varanoid squamates, including mosasaurs, and basal snakes (scolecophidians, anilioids, basal macrostomatans) reveals a greater degree of variability in the differentiation of the intramandibular joint than had previously been recorded. In particular, the mandibular joint of mosasauroid squamates and snakes differs fundamentally. In mosasaurs, the dentary is primarily suspended from the prearticular and the posteriorly concave splenial receives the anteriorly convex angular. In snakes, the dentary is primarily suspended from the surangular portion of the compound bone, and the angular is the receiving part in the mobile contact with the splenial. Characters of the intramandibular joint, along with those resulting from a review of the cranial anatomy of the fossil snake *Pachyrhachis* from the basal Upper Cretaceous of Ein Jabrud, are used in a review of squamate interrelationships. The results corroborate macrostomatan affinities of *Pachyrhachis* and do not support the hypothesis that snakes originated from mosasauroids, a clade of marine varanoid squamates from the Cretaceous.

Introduction

Mosasauroids are a clade of fossil marine squamates related to extant monitor lizards. Their earliest fossil occurrence is in shallow marine deposits of early Cenomanian age (lower Upper Cretaceous) of southern Europe. These stem-group taxa, variously referred to as Aigialosauridae and/or Dolichosauridae, remain relatively poorly known compared to later members of the clade, the Mosasauridae. The crown-group mosasaurs adopted fully pelagic habits and include species that were among the largest predators of the late Cretaceous seas. Mosasaurs became extinct at the close of the Cretaceous.

The intramandibular joint has played a prominent role in discussions of mosasauroid relationships with snakes ever since Cope (1869) commented on the ophidian affinities of his order Pythonomorpha. In the Pythonomorpha, Cope (1869) included two families of mosasaurs, the Clidastidae and the Mosasauridae. The ophidian

affinities of the Pythonomorpha were established by Cope (1869) on the basis of similarities of dentition, the suspension of the lower jaw, and intramandibular kinetics.

More recently, cladistic support has been building in support of a monophyletic clade Pythonomorpha that would include platynotan (varanoid) squamates and mosasauroids as well as snakes (Lee, 1997). Configuration of such a clade has been corroborated by the redescription of a fossil snake with hind limbs from the basal Upper Cretaceous of the Middle East (Caldwell & Lee, 1997; Lee & Caldwell, 1998). Originally described by Haas (1979, 1980), the status of this fossil snake taxon, *Pachyrhachis problematicus*, remains problematic. Although already considered by some to be the ideal fossil link between snakes and mosasauroids (Carroll, 1988), it was also noted that those characters that are snakelike in *Pachyrhachis* resemble relatively advanced (macrostomatan) snakes instead of more basal members of the group (Haas, 1979, 1980; Rieppel,

pel, 1994). This controversy is still alive, as a re-analysis of the cladistic relationships of *Pachyrhachis* showed it to be the sister taxon of macrostomatan snakes rather than a primitive snake providing a link between this group and mosasaurs (Zaher, 1998).

Considering *Pachyrhachis* as the most primitive snake and “an excellent example of a transitional taxon” (Scanlon et al., 1999) between mosasauroids and snakes (Lee, 1998) has important consequences, as this pattern of relationships suggests that snakes had a marine rather than terrestrial (fossorial) origin. Shared derived characters that have been used in support of a monophyletic Pythonomorpha recall Cope’s (1869) analysis and were derived from braincase morphology and its relation to jaw suspension, lower jaw anatomy, and characters of the dentition (Lee, 1997; Lee & Caldwell, 1998). We have previously critically assessed the characters derived in these latter studies from squamate tooth implantation and replacement (Zaher & Rieppel, 1999) and from braincase morphology and its relation to jaw suspension (Rieppel & Zaher, in press). The intramandibular joint has traditionally been an important character in discussions of snake relationships (Camp, 1923). In their classic monograph, McDowell and Bogert (1954) compiled a large number of characters in support of an anguimorph, or varanoid, relationship of snakes, among which the intramandibular joint figured prominently. Many of the characters enumerated by McDowell and Bogert (1954) came under severe criticism (Underwood, 1957), but anguimorph, or varanoid, relationships of snakes continued to be discussed (McDowell 1972; Schwenk, 1988; see also Rieppel, 1988, for a review). Interestingly, the first large-scale cladistic analysis of squamate interrelationships (Estes et al., 1988) did not provide strong support for anguimorph, or varanoid, relationships of snakes, which in this study were classified as Scleroglossa (all non-iguanian squamates) incertae sedis. However, parsimony analysis of this data set put snakes close to fossorial or burrowing squamates such as dibamids and amphisbaenians (see also Rage, 1982). Whereas this latter hypothesis has recently gained further support from morphological evidence (Hallermann, 1998), molecular data support anguimorph relationships for snakes (Forstner et al., 1995; Reeder, 1995). An as yet unpublished total evidence approach, combining molecular (DNA) and morphological data, unambiguously supported a

((Snake + dibamid) amphisbaenian) clade (Reeder, 1995).

As is true for every phylogenetic analysis, hypotheses of relative relationships are only as good as the character evidence they are based on (Rieppel & Zaher, in press). We propose to review, in this study, the lower jaw anatomy of varanoid squamates and snakes in detail, bearing in mind that superficial and potentially misleading resemblances can result from two factors. One is that increased mobility in the lower jaw, as much as increased cranial kinesis in general, results from a reduction in bone overlap, which in turn is likely to result from paedomorphosis (assuming the aknetic condition to be plesiomorphic; Irish, 1989). The other factor results from structural constraints in the development of an intramandibular joint. As Gauthier (1982, p. 46; see also Underwood, 1957, p. 25) pointed out, “some similarity is to be expected, especially since there is but one place in a squamate mandible where a mobile joint could form—between the dentary–splenial and the postdentary bones.” This point is particularly well borne out by comparison with the convergently differentiated intramandibular joint in *Hesperornis*, a fossil bird (Gregory, 1951; Gingerich, 1973). The splenial, for example, will always show a reduced posterior extent in those taxa that develop an intramandibular joint (Estes et al., 1988). Reference to the intramandibular joint in the analysis of snake relationships will therefore have to transcend superficial similarities or mere reduction characters in order to reveal details of morphology. The characters of Lee (1997) will, in the following, be referenced as L97; the character evidence of Lee and Caldwell (1998) will be referenced as LC98.

Materials and Methods

The specimens examined for this study are listed below. Institutional abbreviations are BMNH, British Museum (Natural History); FMNH, Field Museum of Natural History; HJU-Pal., Paleontological Collections, Hebrew University, Jerusalem. Drawings were made with a Wild binocular M-8 equipped with a camera lucida.

Anilius scytale, FMNH 11175, 35688, uncatalogued

Boa constrictor imperator, FMNH 22353, 22363

Calabaria reinhardtii, FMNH 31372

Charina bottae, FMNH 31300
Cylindrophis ruffus, FMNH 13100, 131780
Cylindrophis maculatus, BMNH 1930.5.8.48, un-
 catalogued
Lanthanotus borneensis, FMNH 74711
Leptotyphlops emini, FMNH 56374
Lichanura trivirgata roseofusca, FMNH 8043
Melanophidium punctatus, BMNH 1930.5.8.119
Pachyrhachis problematicus, HNJ-Pal. 3659
Platycarpus sp., FMNH UC 600
Platyplecturus madurensis, BMNH 1930.5.8.111
Plecturus perroteti, BMNH 1930.5.8.105
Pseudotyphlops philippinus, BMNH 1978.1092
Python reticulatus, FMNH 31281, 31329
Typhlops sp., FMNH 98952
Varanus komodoensis, FMNH 22199
Varanus sp., FMNH 195576
Xenopeltis unicolor, FMNH 11524

The Intramandibular Joint in Squamates

The Intramandibular Joint in *Varanus* and *Lanthanotus*

Among extant varanoids (*Heloderma*, *Lanthanotus*, and *Varanus*), the intramandibular joint shows various degrees of differentiation, least developed in *Heloderma*, most developed in *Lanthanotus*.

In *Varanus* (Fig. 1), the posterior ends of the dentary and of the splenial lie entirely in front of the apex of the coronoid process (L97: char. 72). In lateral view, the posterior end of the dentary shows a more or less distinctly developed biconcave posterior margin. A smaller, dorsally located concavity or indentation receives the anterior tip of the coronoid. The broad and, in some species, shallow concavity below the coronoid–dentary contact broadly overlaps the anterior end of the surangular. The ventral margin of the dentary is drawn out into a short posterior process that overlaps with the anterior end of the angular. The principal element on which the dentary is supported is the surangular.

In lateral view, the splenial and angular form a broadly overlapping, obliquely oriented contact in *Varanus*. More precisely, the tapering posterior end of the splenial superficially overlaps the broad anterior end of the angular and curves around its ventral margin (L97: char. 74; LC98: char. B12).

Sutural relations between the dentary and

splenial and the postdentary bones are more complex in medial view of the tooth-bearing shelf of the mandible of *Varanus*. The anterior tooth-bearing part of the dentary forms a gentle slope (a discrete subdental shelf is absent; L97: char. 67), which in front of the splenial projects ventrally, thus overhanging Meckel's canal in medial view. The anterior part of Meckel's groove opens ventrally relative to the sagittal plane of the mandibular ramus, as it is defined by the lateral wall of the dentary and the medial tooth-bearing shelf (L97: char. 69; LC98: char. B13). The anterior end of Meckel's groove opens medioventrally in the live animal because the lower jaw is rotated around its long axis in such a way as to bring the tooth row into an upright position and to expose Meckel's cartilage medioventrally for the insertion of anterior intramandibular muscles. More posteriorly, the tooth-bearing shelf merges into the septum that separates Meckel's canal from the more dorsolaterally positioned canal for the alveolar ramus of the mandibular division of the trigeminal nerve. The ventral part of the posterior margin of this intramandibular septum is deeply concave. Its concavity defines the dorsal and anterior margin of the anterior inferior alveolar foramen, the posterior and ventral margin of which is defined by the splenial as it contacts the medial surface of the dentary. Above the posterior concavity of the septum, the dentary is broadly overlapped by the splenial in medial view. Dorsal to the dentary–splenial overlap, the dentary forms a very short coronoid process defining a posteroventral recess (notched in lateral view but not in medial view) into which fits the anterior dorsal tip of the coronoid.

The splenial (Fig. 2C) itself is roughly of an arrowhead shape in medial view. A slender and pointed posteroventral projection overlaps the anterior end of the angular (L97: char. 73; LC98: char. B12). A broad posterior dorsal projection provides the medial closure of Meckel's canal at the level of the anterior end of the surangular. Posterodorsally, the splenial contacts the anterior process of the coronoid (L97: char. 77; LC98: char. B14), anterodorsally it contacts the posterior end of the dentary, and posteriorly it defines the anterior margin of the subcoronoid fossa (L97: char. 79; LC98: char. B11), below which it overlaps the anterior end of the prearticular. Anteriorly, the splenial is drawn out into a tapering process that reaches to about the midpoint of the dentary. Along the posterior two thirds of the length of the splenial, a horizontal shelf projects from

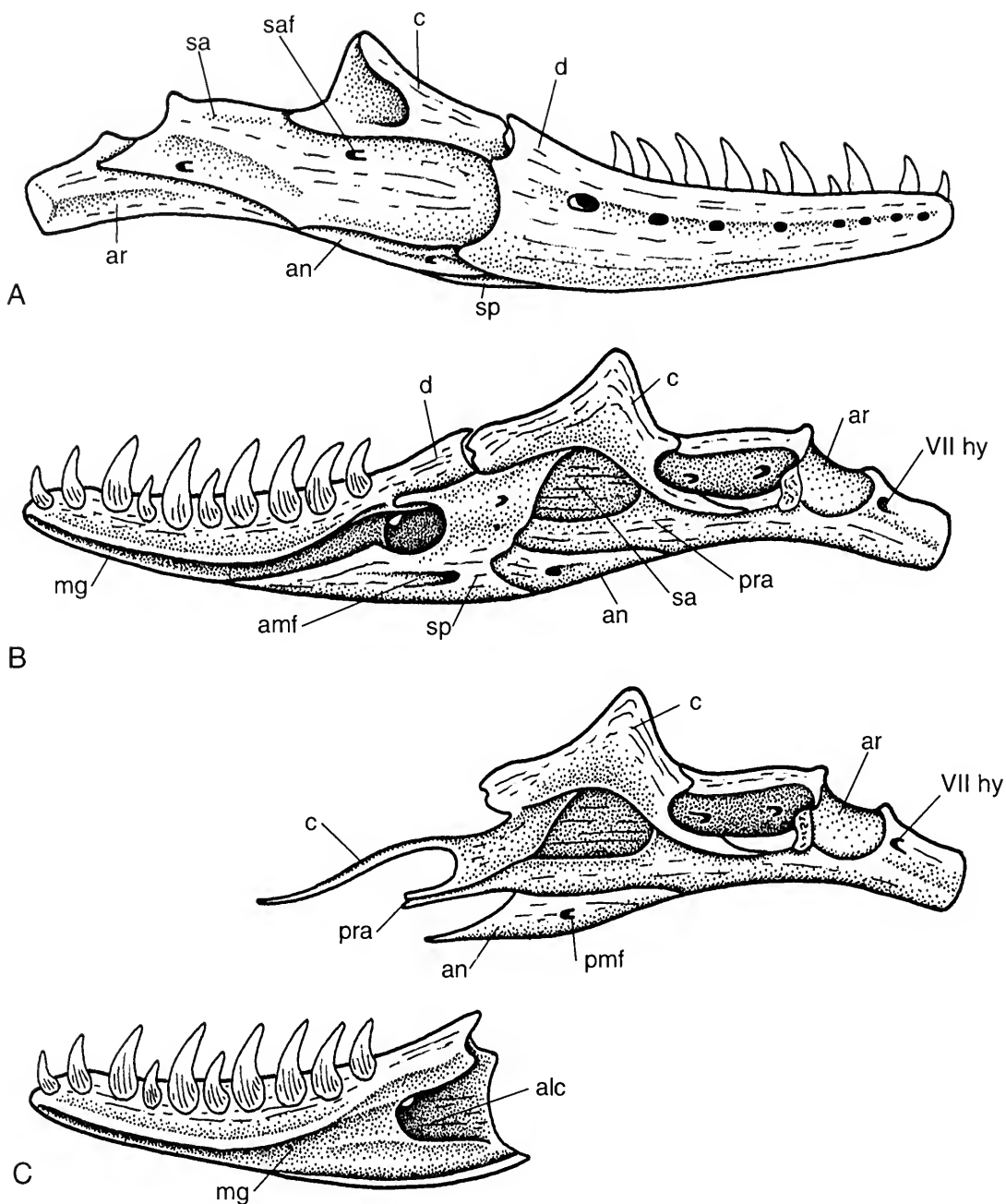


FIG. 1. The lower jaw of *Varanus* (based on *Varanus komodoensis*, FMNH 22199). A, lateral view; B, medial view; C, disarticulated medial view. Not to scale. Abbreviations for all figures: alc, alveolar nerve canal; amf, anterior mylohyoid foramen; an, angular; ar, articular; c, coronoid; cp, compound bone; d, dentary; mf, mental foramen; pl, palatine; pmf, posterior mylohyoid foramen; pra, prearticular; sa, surangular; saf, anterior surangular foramen; sp, splenial; mc (or Mc), Meckel's cartilage; mg (or Mg), Meckel's groove; VII hy, chorda tympani foramen.

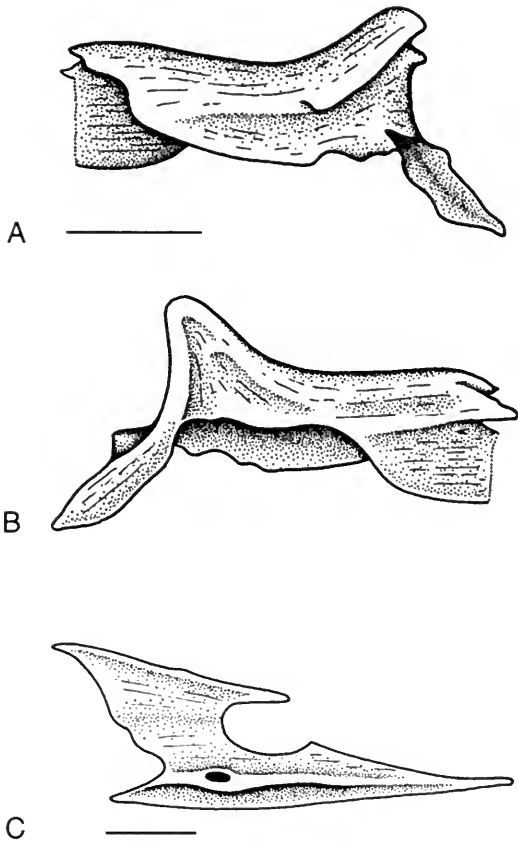


FIG. 2. The coronoid and splenial of *Varanus* sp. (FMNH 195576). A, coronoid, lateral view; B, coronoid, medial view; C, splenial, lateral view. Scale bar = 10 mm.

the lateral surface of the splenial at a level just below the anterior mylohyoid foramen. This horizontal shelf underlies Meckel's cartilage and creates a groove between itself and the laterally curved ventral margin of the splenial, which receives the medially curved ventral margin of the dentary. The anterior mylohyoid foramen opens medially, but a small slitlike opening between the medial vertical wall of the splenial and its laterally projecting shelf at the level of the anterior mylohyoid foramen allows a branch of the anterior mylohyoid nerve to pass into the groove that receives the ventral margin of the dentary. The splenial tapers off at the ventral margin of the dentary (L97: char. 70).

The coronoid (Figs. 2A, 2B) shows a V-shaped outline in medial view, the apex pointing upward and forming the coronoid process. Its ventral margin is concave and defines the subcoronoid fossa

located between the coronoid and the prearticular. In transverse section, the coronoid forms an inverted V, the apex pointing upward, and the base straddling the dorsal rim of the surangular. The main body of the coronoid carries a distinct anteroventral process, the anterior tip of which fits into a recess at the posterior end of the dentary. Below and shortly behind the coronoid–dentary contact, the coronoid forms a medial sheet of bone that extends in an anteroventral direction deep (i.e., lateral) to the broad posterodorsal extension of the splenial but medial to the surangular and to Meckel's cartilage. The coronoid enters the posterior margin of the anterior inferior alveolar foramen lateral to the splenial, where it becomes drawn out into two slender and delicate processes that follow the dorsal and ventral margins, respectively, of this foramen. The dorsal process of the coronoid is more extensively developed than the ventral one, as it follows the dorsal margin of the anterior inferior alveolar foramen medial to the dentary and ventral to the tooth-bearing shelf to the level of the midpoint of the dentary; the ventral projection of the coronoid reaches up to the midpoint of the lower margin of the anterior inferior alveolar foramen.

At the posteroventral base of the coronoid process, the medial shank of the coronoid is drawn out into a posteroventral process, medially overlapping the ascending process of the prearticular, which, together with the coronoid, forms the anterior and medial margin of the adductor fossa (L97: char. 78; LC98: char. B10). Because the medial margin of the adductor fossa is lower than the lateral margin in *Varanus*, the fossa is exposed in both dorsal and medial views of the lower jaw (L97: char. 80; LC98: char. B15).

The prearticular forms the floor of the adductor fossa behind the angular and its medial wall deep to the coronoid. At the anterior margin of the adductor fossa, the prearticular forms a dorsal process extending upward between the (lateral) surangular and the (medial) coronoid, thereby defining the posterior margin of the subcoronoid fossa. The prearticular continues anteriorly below the subcoronoid fossa. Its anterior end slips beneath the posterodorsal extension of the splenial in medial view (i.e., passes lateral to the splenial). Below (i.e., lateral to) the splenial, the anterior end of the prearticular tapers to a thin and pointed process, located ventral to the anterior ventral process of the coronoid, which runs along the ventral margin of the anterior inferior alveolar foramen.

In summary, the dentary and splenial, on the

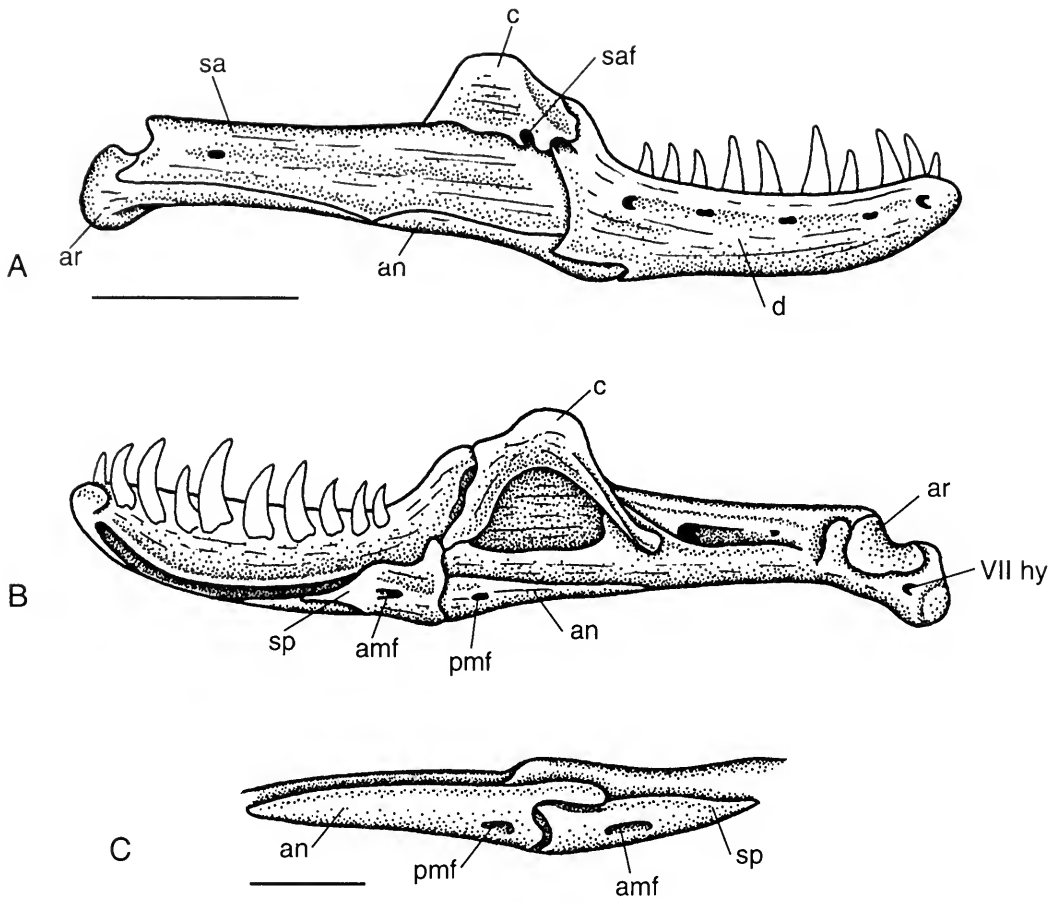


FIG. 3. The lower jaw of *Lanthanotus borneensis* (FMNH 13711). A, lateral view; B, medial view; C, angular and splenial, ventral view. A, B: scale bar = 5 mm; C: scale bar = 2 mm. Abbreviations as in Figure 1.

one hand, and the postdentary bones on the other show a complex and extensive pattern of overlap with one another in *Varanus*, even though this overlap is not revealed by the superficial suture pattern. Lateral to Meckel's cartilage, the dominant overlap is between the dentary (superficial) and the surangular. Medial to Meckel's cartilage, the dominant overlap is between the splenial (superficial) and the coronoid plus prearticular.

The lower jaw of *Lanthanotus* (Fig. 3) differs from that of *Varanus* by an extended contact of the coronoid with the dentary, in both lateral and medial views of the lower jaw. Unlike in *Varanus*, the anterior end of the coronoid is essentially bifurcated, as it embraces the posterior end of the dentary both laterally and medially. The lateral anterior prong of the coronoid is shorter than the medial anterior prong, which extends anteroventrally to establish a broad contact with the anterior

end of the prearticular and the posterodorsal corner of the splenial (L97: char. 77; LC98: char. B14). Behind that anterior bifurcation, the coronoid straddles the longitudinal dorsal shoulder of the surangular, as it does in *Varanus*. A posteroventral process of the coronoid descends on the medial side of the lower jaw, medially overlapping an ascending process of the prearticular, which itself forms the anterior and medial margin of the adductor fossa (rather than the coronoid itself; L97: char. 78; LC98: char. B10) and, at the same time, the posterior margin of the subcoronoid fossa.

The surangular establishes a broad overlap with the dentary lateral to Meckel's cartilage; the posteroventral corner of the dentary also overlaps the anterior end of the angular laterally. The splenial gains no exposure in lateral view, and in medial view it shows a reduction of the posteroventral

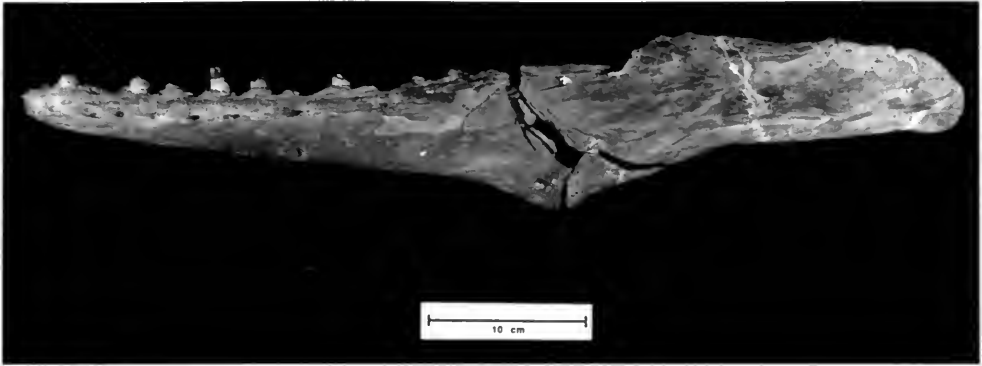


FIG. 4. The lower jaw of *Platecarpus* sp. (FMNH UC 600) in lateral view.

process, which in *Varanus* is distinct and overlaps with the angular. Reduction of this process results in a superficially vertical suture at the contact between angular and splenial in medial view of the lower jaw. The posterodorsal extension of the splenial is again less developed than in *Varanus*, which reduces but does not obliterate the overlap with the anteroventral process of the coronoid.

Whereas the vertical suture on the medial side of the lower jaw suggests a relatively simple and mobile contact between splenial and angular, the ventral aspect of the lower jaw (Fig. 3C) reveals that the angular–splenial contact is more complex (L97: char. 73; LC98: char. B12). The ventral margin of the splenial is concave, receiving the convex ventral margin of the angular. More importantly, the angular forms a distinct anteroventral process, which extends lateral to the posterior end of the splenial, intercalated between the latter and the dentary (L97: char. 74; LC98: char. B12). As in mosasaurs (see below), the splenial is the receiving part, the angular the received part in the intramandibular articulation of *Lanthanotus*. Unlike in *Varanus*, the anterior tip of the relatively short splenial lies dorsomedial to the ventral margin of the dentary (L97: char. 70), and in front of it Meckel's canal opens ventrally relative to the sagittal plane of the lower jaw between a lateral flange of the dentary and the prominent tooth-bearing shelf (L97: char. 69; LC98: char. B13). The splenial of *Lanthanotus* was not disarticulated. It was therefore not possible to assess the presence of a horizontal shelf projecting from the lateral surface of the splenial, which together with the ventral margin of the splenial would form a groove to receive the ventral margin of the dentary, as is seen in *Varanus*. If present, however, such a medial crest must be confined to the posteriormost part of the splen-

ial, as its anterior tapering end lies above the ventral margin of the dentary.

The Intramandibular Joint in Mosasaurs

The lower jaw of mosasaurs was described by Camp (1942) and, in more detail, by Russell (1967). Relevant information is also provided by Bell (1997). The main difference in the lower jaw of *Varanus* and mosasaurs is that the latter have mobilized the intramandibular joint to a greater degree, largely through a reduction of bone overlap (probably due to pedomorphosis, which is common in secondary marine reptiles; Rieppel, 1993a). In lateral view, the posterior end of the dentary of mosasaurs (*Platecarpus*, FMNH UC 600) appears truncated relative to that of *Varanus*, with a more or less straight posterior margin that slopes posteroventrally (Fig. 4). The posteroventral corner of the dentary forms an extensive lateral overlap with the splenial. There is, however, no evidence for any significant anterior extension of the surangular deep to the dentary. Instead, the surangular appears to be truncated at its anterior end and consequently fails to overlap with the dentary. In *Platecarpus* (FMNH UC 600), the dentary does not overlap with the surangular at all.

The contact of the splenial with the angular again is not an overlapping one (Fig. 4). Instead, the two elements abut against each other in a ball-and-socket joint (Bell, 1997; Russell, 1967), which in lateral and medial views translates into a more or less vertically oriented contact between the two elements (L97: char. 74; LC98: char. B12). The posterior surface of the splenial is broadened and round or elliptical in outline. It is concave and forms the socket into which the

rounded and convex anterior surface of the angular fits. In the intramandibular joint of mosasaurs, therefore, the splenial is the receiving part, the angular is the received part.

In medial view, the lower jaw of mosasaurs again differs significantly from *Varanus*. As described previously (Zaher & Rieppel, 1999), the teeth are set in a groove that runs along the dorsal margin of the splenial. As a consequence, a dentary shelf overhanging Meckel's canal is not differentiated in mosasaurs (L97: char. 67). Meckel's canal is open along the anterior third of the length of the mandibular ramus, but unlike in *Varanus*, it opens on the medial surface of the lower jaw because the dentary forms a ventromedial flange in its anterior half, which wraps around the ventral surface of Meckel's cartilage and rises up again on the medial side of the lower jaws (L97: char. 69; LC98: char. B13). More posteriorly, the splenial closes Meckel's canal in medial view. In front of its articulation with the angular, the splenial develops into a high flange of bone, almost completely covering the medial exposure of the dentary. The anterior inferior alveolar foramen is not conspicuous in mosasaurs. A broken lower jaw of an unidentified mosasaur (Mosasauridae indet. FMNH PR 674) shows that, unlike in *Varanus*, the splenial forms no longitudinal crest projecting from its lateral surface, which together with the ventral margin of the splenial would form a groove to receive the ventral edge of the dentary. The broken cross-section of the splenial reveals it to be a simple vertical lamina of bone. Its posterior part lies medial and ventral to the vertical lamina formed by the posterior end of the dentary. The ventral margin of the splenial becomes increasingly thickened posteriorly, as the bone forms the socket to receive the anterior head of the angular. Anteriorly, the splenial tapers to a blunt tip that terminates at a level above the ventromedial dentary flange that wraps around the ventral surface of Meckel's cartilage, i.e., not along the ventral margin of the dentary, as in *Varanus* (L97: char. 70), but on the medial surface of Meckel's cartilage.

The coronoid is reduced in mosasaurs as compared to *Varanus*. A posteromedial process may still be present, but if so, it always remains small (Bell, 1997; L97: char. 78; LC98: char. B10). In front of the apex of the coronoid process, the element extends as a relatively broad anterior process that, as in *Varanus*, "is a saddle-shaped bone straddling the longitudinal 'shoulder' . . . of the surangular which is enclosed in a deep sulcus"

(Russell, 1967, p. 53). It approaches, but does not contact, the dentary, and it remains widely separated from the splenial (L97: char. 75; LC98: char. B14).

The height of the prearticular is greatly increased in mosasaurs, and together with the coronoid the prearticular completely conceals the surangular in medial view of the lower jaw in front of the adductor fossa (L97: char. 79). As noted by Gauthier (1982), the prearticular is the principal element from which the dentary is suspended in mosasaurs, as it extends anteriorly as a high blade that enters between the equally high posterior part of the splenial (medially) and the dentary (laterally).

As in *Varanus*, the adductor fossa of mosasaurs is characterized by a medial margin (formed by the prearticular) that is lower than the lateral margin (formed by the surangular). As a consequence, the adductor fossa opens dorsally as well as medially (L97: char. 80; LC98: char. B15).

By comparison to *Varanus*, mosasaurs have lost the dentary–coronoid contact, lost the broad overlap of surangular and dentary lateral to Meckel's cartilage, and transformed the overlapping splenial–angular contact into a ball-and-socket joint. Medial to Meckel's cartilage, mosasaurs have lost the splenial–coronoid overlap due to a reduction of the coronoid, but the relative height of the splenial and prearticular is increased. In summary, mosasaurs have increased one area of support, the prearticular–splenial–dentary overlap, at the expense of two other areas of support that are well developed in *Varanus*, the splenial–coronoid overlap and the dentary–surangular overlap.

The increased mobilization of the intramandibular joint in mosasaurs is correlated with a loosening of the mandibular symphysis. There is no sutural contact between the anterior tips of the dentaries. Instead, their anterior tips are smooth and rounded, and the dentaries must have been in syndesmotomic or ligamentous connection with each other (Cope, 1869; L97: char. 68; LC98: char. B8).

The Compound Bone of the Ophidian Mandible

In snakes, the surangular, prearticular, and articular fuse to form a single "compound" or "mixed" bone during embryonic development (Bellairs & Kamal, 1981; DeBeer, 1937), incorporating both dermal and chondral elements. Among other squamates, a similar compound

bone is only found in dibamids (Greer, 1985; Rieppel, 1984a) and in amphisbaenians (Montero et al., 1999; Zangerl, 1944). Many details of the embryonic development of the lower jaw of snakes remain to be determined, but it is clear that the elements contributing to the compound bone fuse during embryonic development (Bellairs & Kamal, 1981; Parker, 1879). Few authors had critical embryonic stages available to them, which would show the dermal elements of the compound bone present but not yet fused (Brock, 1929; Haluska & Alberch, 1989; Kamal et al., 1970; Peyser, 1912); or consideration of the development of the dermal bones of the lower jaw was not included in the study (Genest-Villard, 1966). Several studies of cranial development in snakes do not address the ossification sequence and pattern of dermal bones (see reviews in Bellairs & Kamal, 1981; Rieppel, 1993b).

However, Bäckström (1931) described in detail the development of the dermal bones in the lower jaw of *Natrix natrix* and noted that the first elements to appear are the dentary and splenial, followed by the surangular. All five dermal elements are present in the 6.8-mm stage (Bäckström, 1931, Fig. 17) but are still separate from one another. The prearticular is confined to the medial aspect of the lower jaw (of Meckel's cartilage). It entirely conceals the surangular in medial view, and wraps around the ventral surface of Meckel's cartilage below the mandibular articulation. The surangular develops on the lateral and dorsal aspect of Meckel's cartilage, and it is the surangular that forms the large anterior projection that enters between the two posterior prongs of the deeply bifurcated dentary. This interpretation is supported by the position of the homologue of the anterior surangular foramen (at least in alethinophidians), and it is also in accordance with the observation of Estes et al. (1970) that it is the surangular portion of the compound bone that provides the main support for the dentary in the fossil snake *Dinilysia*.

In the adult jaw, the compound bone wraps around Meckel's cartilage. It may be raised into a coronoid process toward its anterior end, and it carries the adductor fossa in its posterior part. The relation of Meckel's cartilage to the adductor fossa differs in important ways in snakes as compared to nonophidian squamates. In squamates other than snakes, Meckel's cartilage is exposed at the bottom of the adductor fossa for approximately half of its length, and fibers of the posterior adductor insert into it. The compound bone

of scolecophidians appears to be a simple tubelike structure, at least in its posterior part. In alethinophidians (at least in anilioids and basal macrostomatans), Meckel's cartilage enters its own canal at the bottom of the compound bone, beginning at the level of the anterior margin of the adductor fossa, and hence is not exposed in the latter. The coronoid is of a much simpler structure in snakes than in nonophidian squamates. It never forms a saddle-shaped structure straddling the dorsal longitudinal shoulder of the surangular. Instead, the coronoid of snakes is a simple sheet of bone that is always applied to the medial side of the dorsal (surangular) portion of the compound bone. It may or may not project beyond the dorsal margin of the compound bone at the apex of the coronoid process. The formation of a compound bone is an autapomorphy of snakes (or a potential synapomorphy shared by snakes, dibamids, and amphisbaenians), and because of its formation, a subcoronoid fossa exposing the surangular between the coronoid and the angular on the medial surface of the lower jaw is a character that cannot be applied or compared to snakes (L97: char. 79; LC98: char. B11).

The Intramandibular Joint in Scolecophidians

Scolecophidians are divergently derived and highly autapomorphic in the structure of their lower jaw, owing to their microphagous habits. In *Anomalepis* (Haas, 1968), the surangular, articular, and prearticular have fused into a compound bone, as in all other snakes. The coronoid is roughly trapezoidal and forms a prominent coronoid process. It is applied against the medial surface of the anterior part of the compound bone and medially overlaps the contact between the posterior end of the dentary and the anterior end of the splenial (List, 1966; angular of Haas, 1968). The anterior end of the compound bone overlaps and thereby supports the dorsal margin of the posterior half of the splenial, which with its anterior half (i.e., in front of the compound bone) underlies and supports the posterior end of the dentary. The posterior part of the dentary meets the dorsal margin of the anterior half of the angular in an oblique plane (L97: char. 73; LC98: char. B12). Meckel's cartilage is wedged between the coronoid medially and the splenial and dentary laterally. In front of the coronoid, Meckel's cartilage comes to lie in a shallow groove that follows the ventromedial margin of the dentary.

The splenial is a simple, flat strip of bone that tapers off along the ventral margin of the dentary (relative to the sagittal plane of the lower jaw). Main support for the dentary is provided by the splenial and by the coronoid in front of the compound bone.

Liotyphlops closely resembles *Anomalepis* in the essential features of the lower jaw, although the shapes of individual elements are different in detail (Haas, 1964). The simple and flat splenial (angular of Haas, 1964) is again underlying the anterior end of the compound bone and the posterior end of the dentary. At the anterior end of the splenial, the Meckelian groove shifts to a position on the medial side of the dentary (Haas, 1964, Fig. 20). The splenial tapers off along the ventral margin of the dentary (relative to the sagittal plane of the lower jaw).

The lower jaw of *Typhlops* typically comprises five elements (Haas, 1930). The largest one is the compound bone, the anterior end of which is again applied against the lateral surface of the large, roughly triangular coronoid. The tapering anterior end of the compound bone reaches the posterior tip of the dentary and may be accompanied up to this level by the anteroventral process of the coronoid. As in anomalepids, a relatively large splenial underlies the contact of the compound bone with the dentary, but in typhlopids it extends anteriorly up to the symphyseal tip of the mandible. At the level of the anterior end of the compound bone, the posterior part of the splenial is located ventral to Meckel's cartilage; in front of the compound bone, the splenial forms a deep trough closed dorsally by the dentary, within which lies Meckel's cartilage. Meckel's canal (groove) is therefore not exposed on the medial side of the lower jaw (L97: char. 69: LC98: char. B13). Other than in anomalepids, most typhlopids show a second element at the ventral margin of the lower jaw, sometimes vestigial, and located behind the splenial, which supports the dentary. The posterior element is identified as angular (List, 1966), but, as in anomalepids, the main support for the dentary is provided by the splenial in typhlopids. In mosasaurs, it is the prearticular that provides principal support for the dentary; in alethinophidians (and leptotyphlopids), it is the surangular as part of the compound bone (Estes et al., 1970, p. 46; see below). In nonophidian squamates, it is the splenial that underlies the dentary, and if so interpreted, anomalepids and typhlopids share a plesiomorphic character in that respect. However, the posterior ex-

ension of the splenial to a level well behind the level of the posterior tip of the dentary may be a synapomorphy shared by typhlopids and anomalepids, whereas the position of the splenial entirely lateral to Meckel's cartilage may be a synapomorphy of anomalepids.

Brock (1932) described five bones in the lower jaw of *Leptotyphlops*, i.e., the dentary, splenial, coronoid, angular, and the compound bone. The splenial is located entirely on the medial side of the dentary, partially closing the posterior part of the Meckelian groove, which is located entirely on the medial aspect of the dentary. The dentary is a relatively large, tooth-bearing element, with a sloping posterior margin that establishes an extended and mobile (Haas, 1930) contact with the compound bone. The latter is shorter and more massively built than in other scolecophidians. An angular underlies the anterior end of the compound bone, which may meet the splenial in a simple abutting contact if the latter projects beyond the posteroventral corner of the dentary (List, 1966). The coronoid is applied to the medial surface of the compound bone and remains widely separated from the splenial. Unlike in anomalepids and typhlopids, it is the compound bone that provides the major support for the dentary in leptotyphlopids. This is also the case in alethinophidians, although in this group, the contact of the compound bone with the dentary is established in a different manner.

The Intramandibular Joint in Anilioids

Anilius shows a weak expression of the posterior bifurcation of the dentary, which is characteristic of alethinophidian snakes (Fig. 5). Posterodorsally, the dentary is drawn out into a short posterodorsal process, which together with the coronoid and the compound bone forms the prominent coronoid process. Medially, the posterior end of the dentary forms a broad concavity that accommodates the anterior end of the compound bone. The mandibular division of the trigeminal nerve, along with Meckel's cartilage, is enclosed in a canal within the compound bone. Further anteriorly, the compound bone opens medially, releasing Meckel's cartilage along with the mandibular nerve into Meckel's groove on the medial side of the dentary. The alveolar ramus of the mandibular division of the trigeminal nerve enters a separate, dorsolaterally positioned canal that leads up to the single mental foramen, which

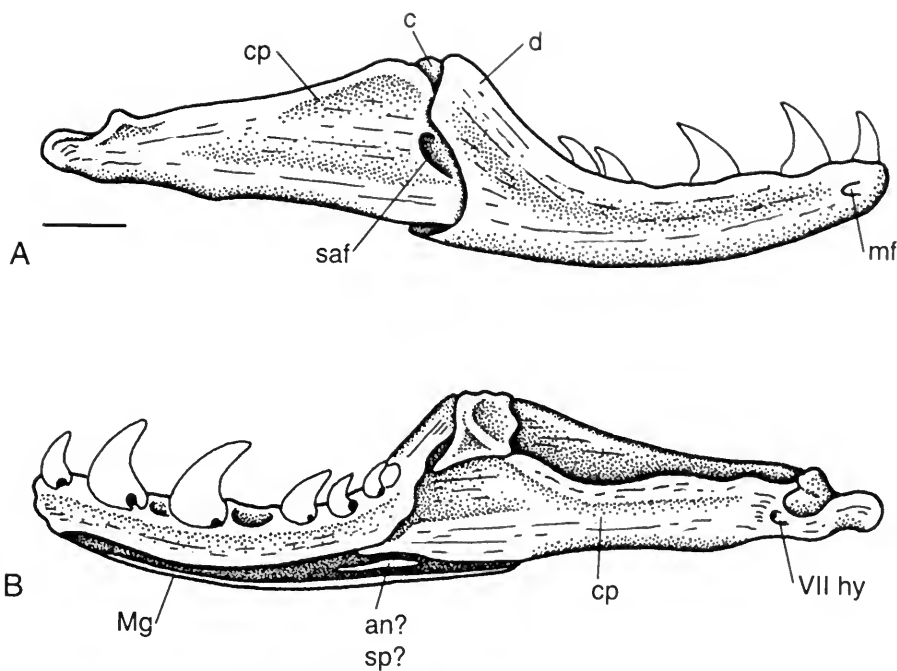


FIG. 5. The lower jaw of *Anilius scytale* (FMNH 35688). A, lateral view; B, medial view. Scale bar = 2 mm. Abbreviations as in Figure 1.

opens at the anterior end of the dentary on its lateral surface (L97: char. 76; LC98: char. C14). Meckel's canal opens ventromedially in its posterior part as the ventral rim of the dentary expands medially below Meckel's cartilage at the level below the anterior end of the compound bone. More anteriorly, however, Meckel's canal opens ventrally (relative to the sagittal plane of the lower jaw), as it does in *Varanus* and other nonophidian squamates except mosasaurs (L97: char. 69; LC98: char. B13). The dorsomedial ledge of the dentary that overhangs the Meckelian groove is closely comparable to the tooth-bearing shelf of *Varanus* (L97: char. 67).

The compound bone of *Anilius* includes, as it does in other snakes, the articular, surangular, and prearticular. It encloses an elongate, deep and wide adductor fossa with a well-defined medial margin. As a consequence, the adductor fossa opens dorsally (L97: char. 80; LC98: char. B15). Deep to the dentary, the part of the compound bone located lateral to Meckel's cartilage extends further anteriorly than the medial cover of Meckel's cartilage, which results in a medial opening of Meckel's canal at the anterior end of the compound bone. The part of the compound bone located lateral to Meckel's cartilage corresponds to

the surangular, and its greater anterior extension corroborates the observation of Estes et al. (1970) in *Dinilysia* and the embryological observations of Bäckström (1931) that, in alethinophidians, it is the surangular that provides the principal support for the dentary.

At the anterior end of the compound bone, between the ventral margin of the latter and the posterior maxillary ledge that wraps around the ventral surface of Meckel's cartilage, lies a small splint of bone. It projects anteriorly to a level slightly in front of the medial component of the compound bone, and it is located ventromedial to the compound bone and, in front of the latter, ventromedial to Meckel's cartilage. By comparison to other basal alethinophidians, this element is perhaps best interpreted as a vestigial angular, although it could also represent a vestigial splenial. Its presence was confirmed in both the lower jaw ramus of *Anilius* FMNH 35688 (Fig. 5) and in a serially sectioned skull (Fig. 6, uncatalogued specimen).

The coronoid is a small element located at the tip of the coronoid process on the medial surface of the compound bone and behind the postero-dorsally ascending process of the dentary. The bone is truncated posteriorly but carries a short

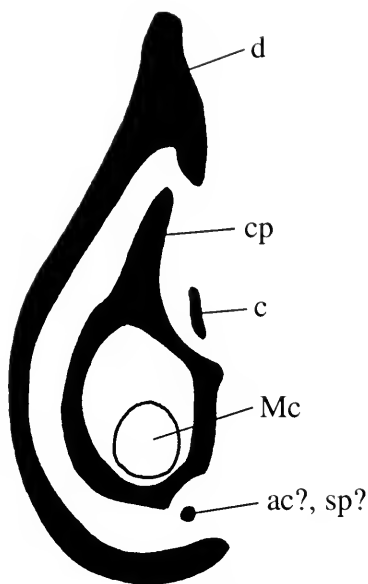


FIG. 6. Transverse section through the lower jaw of *Anilius scytale* (uncatalogued). Abbreviations as in Figure 1.

anteroventral projection, which results in a weakly concave ventral margin. Given the fusion of the surangular and prearticular (and articular) to form the compound bone, a subcoronoid fossa exposing the surangular in medial view is absent in snakes (L97: char. 79; LC98: char. B11).

The intramandibular joint takes on a more complex structure in *Cylindrophis ruffus* (Fig. 7, FMNH 13100, 131780). The function of the intramandibular joint in *Cylindrophis ruffus* has been analyzed in detail by Cundall (1995). The dentary is deeply bifurcated posteriorly, supported by a large anterior projection of the compound bone. As described by Zaher and Rieppel (1999), the teeth are ankylosed to the interdental ridges on the pleura of the dentary. At the anterior end of the dentary, this pleura is again developed into a tooth-bearing shelf (again without marginal thickening) that overhangs the anterior end of Meckel's groove (L97: char. 76). The latter opens ventrally relative to the sagittal plane of the mandibular ramus (L97: char. 69; LC98: char. B13). More posteriorly, the tooth-bearing shelf is developed into the intramandibular septum with a concave medial surface, separating the medial Meckelian groove from the laterally positioned canal for the alveolar ramus of the mandibular division of the trigeminal

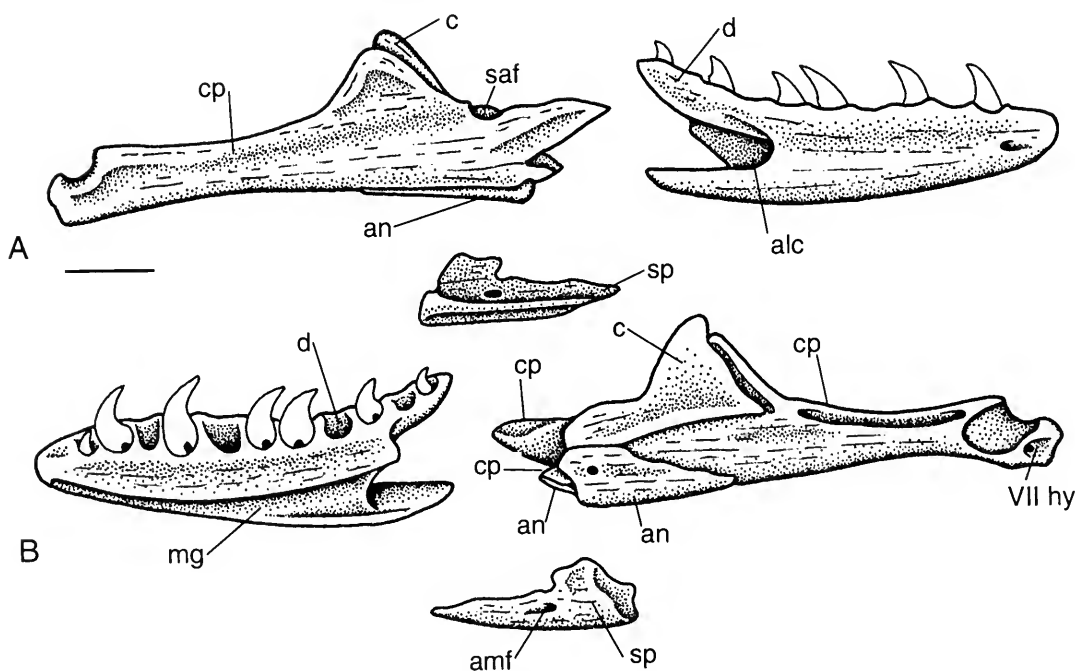


FIG. 7. The lower jaw of *Cylindrophis ruffus* (FMNH 131780). A, lateral view; B, medial view. Scale bar = 2 mm. Abbreviations as in Figure 1.

nerve. Anteriorly, the nerve emerges from the single, laterally placed mental foramen at the tip of the dentary (L97: char. 76; LC98: char. C14). The intramandibular septum reaches backward into the anterior half of the gap between the dorsal and ventral prongs of the posterior end of the dentary. The large, laterally placed anterior prong of the compound bone (surangular portion, see above) thus fits snugly into a recess bounded dorsally by the dorsal prong of the caudally bifurcated dentary, ventrally by the posteroventral process of the dentary, and medially by the intramandibular septum.

Below this contact between the compound bone and the dentary, the vertically oriented suture between angular and splenial is narrowly exposed in lateral view (L97: char. 74). The medial view of the lower jaw exposes the splenial and angular in their full size, pierced by the anterior and posterior mylohyoid foramen, respectively. From the lateral surface of the splenial, at a level narrowly below the anterior mylohyoid foramen, projects a lateral crest. This crest underlies Meckel's cartilage, and, with the ventral edge of the splenial, it forms a distinct groove that receives the ventral edge of the dentary, which itself curves inward. At the level of the anterior mylohyoid foramen, the lateral shelf of the splenial is pierced by a small foramen, which allows a ventral branch of the anterior mylohyoid nerve to slip out of Meckel's canal, entering between the splenial and the dentary. Medially, the splenial forms a dorsal vertical blade that entirely closes the posterior part of Meckel's groove in medial view. More anteriorly, the vertical blade of the splenial gradually tapers to a pointed tip that lies in line with the ventral edge of the dentary (L97: char. 70).

The coronoid is a roughly triangular bone that is received in a shallow facet on the medial side of the compound bone (surangular portion). Together with the compound bone, it forms a prominent coronoid process. The ventral margin of the coronoid is slightly concave. Anteroventrally, the coronoid is extended into a prominent anterior process that remains restricted to the medial surface of the compound bone and hence does not participate in the formation of the large surangular prong that enters between the two posterior processes of the dentary. The anteroventral process of the coronoid establishes an extended contact with the anterior part of the dorsal margin of the angular, but it remains separated from the splenial in our specimens of *Cylindrophis ruffus* (L97: char. 75; LC98: char. B14). The coronoid contacts

the splenial in specimens figured by McDowell (1975, Fig. 6) and Cundall (1995, Fig. 6). (It should be noted that macerating skulls with commercial bleach easily dissolves thin marginal areas of bones.)

In superficial medial view, the anterior end of the angular matches the posterior end of the splenial in height. The two elements meet in a straight, slightly posteroventrally trending suture (L97: char. 73; LC98: char. B12). Disarticulation of the splenial shows that the posterior surface of the posteroventral corner of the splenial is thickened, flat, and sloping posteroventrally, whereas the anterior surface of the angular is similarly thickened, flat, and trending anterodorsally. The two elements meet face to face in a simple abutting contact. Deep to this contact, the dorsomedial edge of the angular forms a small, anteriorly projecting prong that, on its medioventral surface, is lined by a congruent projection of the compound bone. This latter prong originates from the compound bone medioventral to Meckel's cartilage. As described above, the anterior end of the angular is somewhat thickened, and, in addition to the composite medial prong described above, its lateral margin slightly projects anteriorly. As a consequence thereof, the anterior surface of the angular forms a vertically oriented shallow trough that is bounded dorsomedially by the composite prong described above and laterally by the projecting lateral margin of the angular. The posterior end of the splenial fits snugly into that trough on the anterior surface of the angular, while the horizontal crest that projects from the lateral surface of the splenial locks against the ventral surface of the composite dorsomedial prong. Other than in mosasaurs, therefore, the angular is the receiving part in the intramandibular articulation, the splenial is the received part. Posteriorly the angular tapers to a blunt tip, which is located at the ventral margin of the compound bone.

Behind the coronoid process, the compound bone forms the adductor fossa, which is not as deep and wide as it is in *Anilius*. However, its medial margin is only slightly lower than the lateral margin, such that the adductor fossa opens dorsally relative to the sagittal plane of the mandibular ramus (L97: char. 80; LC98: char. B15).

Cylindrophis maculatus (Fig. 8, BMNH 1930.5.8.48; serially sectioned skull, uncatalogued) is closely comparable to *Cylindrophis ruffus* in most of the essential characteristics of the lower jaw. The coronoid process is somewhat lower, but the anteroventral process of the coro-

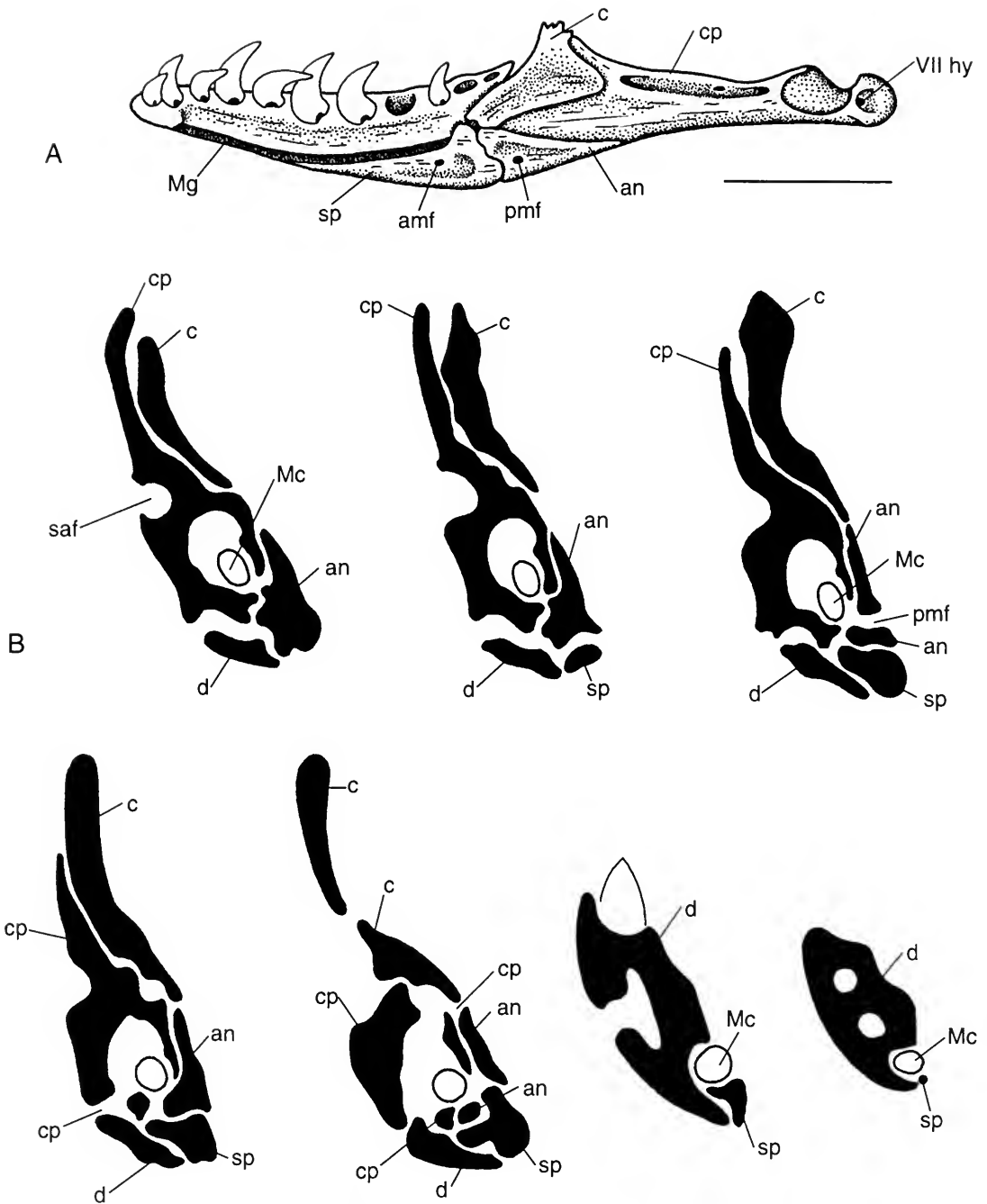


FIG. 8. The lower jaw of *Cyldrophis maculatus* (BMNH 1930.5.8.48; serially sectioned skull, uncatalogued). A, medial view, scale bar = 2 mm; B, serial sections from the coronoid process to the anterior tip of the splenial. Abbreviations as in Figure 1.

noid is larger and approaches the splenial very closely or establishes a contact with it. Also, the superficial splenial–angular suture as exposed in medial view is distinctly concave anteriorly in its ventral part, a trait that is only weakly developed in *Cylindrophis ruffus*. The anterior prong projecting from the medial anterior margin of the angular, and complemented medioventrally by an anterior prong of the compound bone, is also present in *Cylindrophis maculatus*, although perhaps a little less prominently developed than in *Cylindrophis ruffus*. This prong is located at the dorsal margin of the concavity formed by the anterior end of the angular, such that the splenial–angular contact is closely comparable to that described for *Cylindrophis ruffus*.

The lower jaw of uropeltids (Figs. 9, 10) resembles that of *Cylindrophis* quite closely except for characters that result from reduction, probably as a consequence of paedomorphosis related to small overall size. The dentary of *Melanophidium punctatum* (Figs. 9A, 9B; BMNH 1930.5.8.119) retains the deep posterior bifurcation characteristic of althinophidians, but the posteroventral process of the dentary is much reduced in *Platyplecturus madurensis* (Figs. 9C, 9D; BMNH 1930.5.8.111), vestigial in *Plecturus perroteti* (Fig. 10; BMNH 1930.5.8.105), and fully reduced in all other species examined (*Pseudotyphlops philippinus*, BMNH 1978.1092 [Figs. 9E, 9F]; *Rhinophis drummondhayi*, BMNH 1930.5.8.67–68; *Teretrurus rhodogaster*, BMNH 1930.5.8.98, and *Uropeltis woodmansoni*, BMNH 1930.5.8.73–74). The hypothesis that the posteroventral process of the dentary is reduced rather than absent within uropeltids requires corroboration by reconstruction of cladistic relationships within the clade, which is not available at this time. However, *Melanophidium punctatum* is also plesiomorphic with respect to some other characters of its cranial anatomy, such as the presence of teeth on the palatine, the location of the optic foramen, and the retention of sutures in the occipital condyle delineating the basioccipital from the exoccipitals (Rieppel, 1977).

The coronoid, an element of variable size and shape, is always applied to the medial surface of the compound bone and, together with the latter, forms a weakly expressed coronoid process. The coronoid retains relatively distinct anteroventral and posteroventral processes and a concave ventral margin in *Plecturus perroteti* (BMNH 1930.5.8.105) and, to a lesser degree, in *Platyplecturus madurensis* (BMNH 1930.5.8.111). The coronoid usually contacts the posterodorsal process of the dentary

and at least marginally projects beyond the dorsal margin of the compound bone, except in *Pseudotyphlops philippinus* (BMNH 1978.1092), where the coronoid is vestigial, restricted to the medial surface of the compound bone, and has lost the contact with the dentary. The coronoid never contacts the splenial in uropeltids.

In taxa with a reduced posteroventral process of the dentary, the posterior end of this bone wraps around the anterior end of the compound bone in a manner very similar to that observed in *Anilius*. Meckel's groove is open medially in front of the anterior end of the compound bone except in those taxa where the dorsal margin of the splenial establishes a contact, in its posterior part, with the ventral margin of the tooth-bearing shelf of the dentary. Meckel's groove opens on the medial surface of the mandible above the splenial, but it opens ventrally (relative to the sagittal plane of the lower jaw ramus) in front of the splenial, with the exception of *Plecturus perroteti* (BMNH 1930.5.8.105), where the ventral opening of Meckel's groove is restricted to its anterior end.

All uropeltids have a well-developed splenial and angular, each pierced by the anterior and posterior mylohyoid foramen respectively (Figs. 9, 10). The elements meet in a slightly curved, anteriorly concave, but essentially vertically oriented suture apparent on the medial surface of the lower jaw. This suggests a similar articulation of angular and splenial, as is also observed in *Cylindrophis maculatus*. The disarticulated lower jaw of *Pseudotyphlops philippinus* (BMNH 1978.1092), as well as a serially sectioned head of *Plecturus perroteti* (uncatalogued), reveals that the posterior surface of the posteroventral end of the splenial is somewhat thickened, as is the anterior surface of the anteroventral end of the angular. The two elements meet in a simple abutting contact, the splenial with a weakly convex surface, the angular with a weakly concave surface. The composite medial prong formed by the angular and the compound bone and locking the splenial in place in *Cylindrophis* is absent in uropeltids, which therefore are characterized by a somewhat simplified articulation between angular and splenial.

The serially sectioned head of *Plecturus perroteti* (Fig. 10C) shows the posterior mylohyoid nerve leaving Meckel's canal through a small slit-like aperture in the anterior ventral margin of the compound bone to reach the posterior mylohyoid foramen in the angular. In transverse sections, this creates the impression that the compound bone is drawn out into two short anteroventral processes.

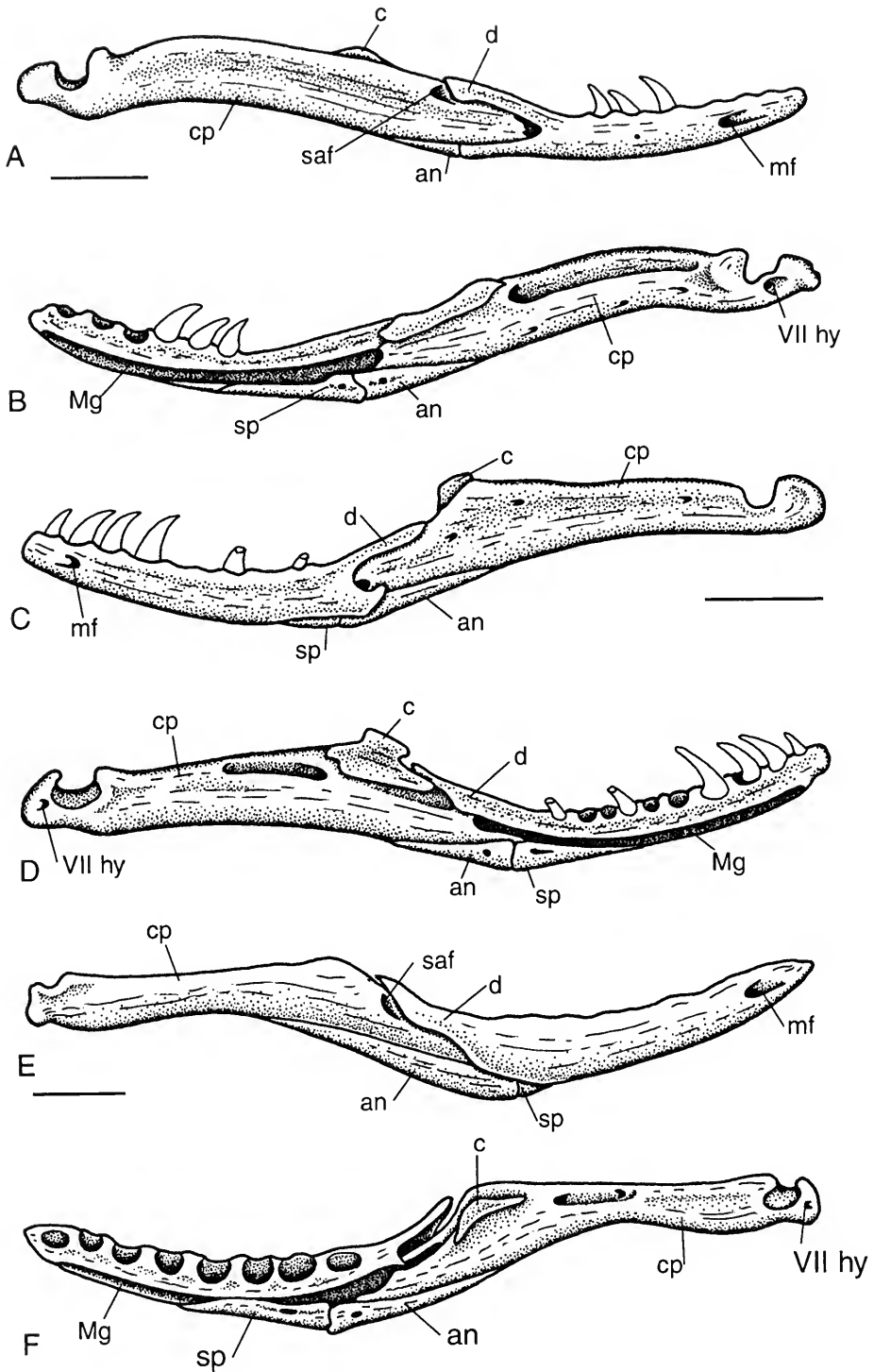


FIG. 9. The lower jaw of *Melanophidium punctatus* (BMNH 1930.5.8.119: A, lateral view; B, medial view; scale bar = 1 mm), *Platyplecturus madurensis* (BMNH 1930.5.8.111: C, lateral view; D, medial view; scale bar = 1 mm), and *Pseudotyphlops philippinus* (BMNH 1978.1092: E, lateral view; F, medial view; scale bar = 2 mm). Abbreviations as in Figure 1.

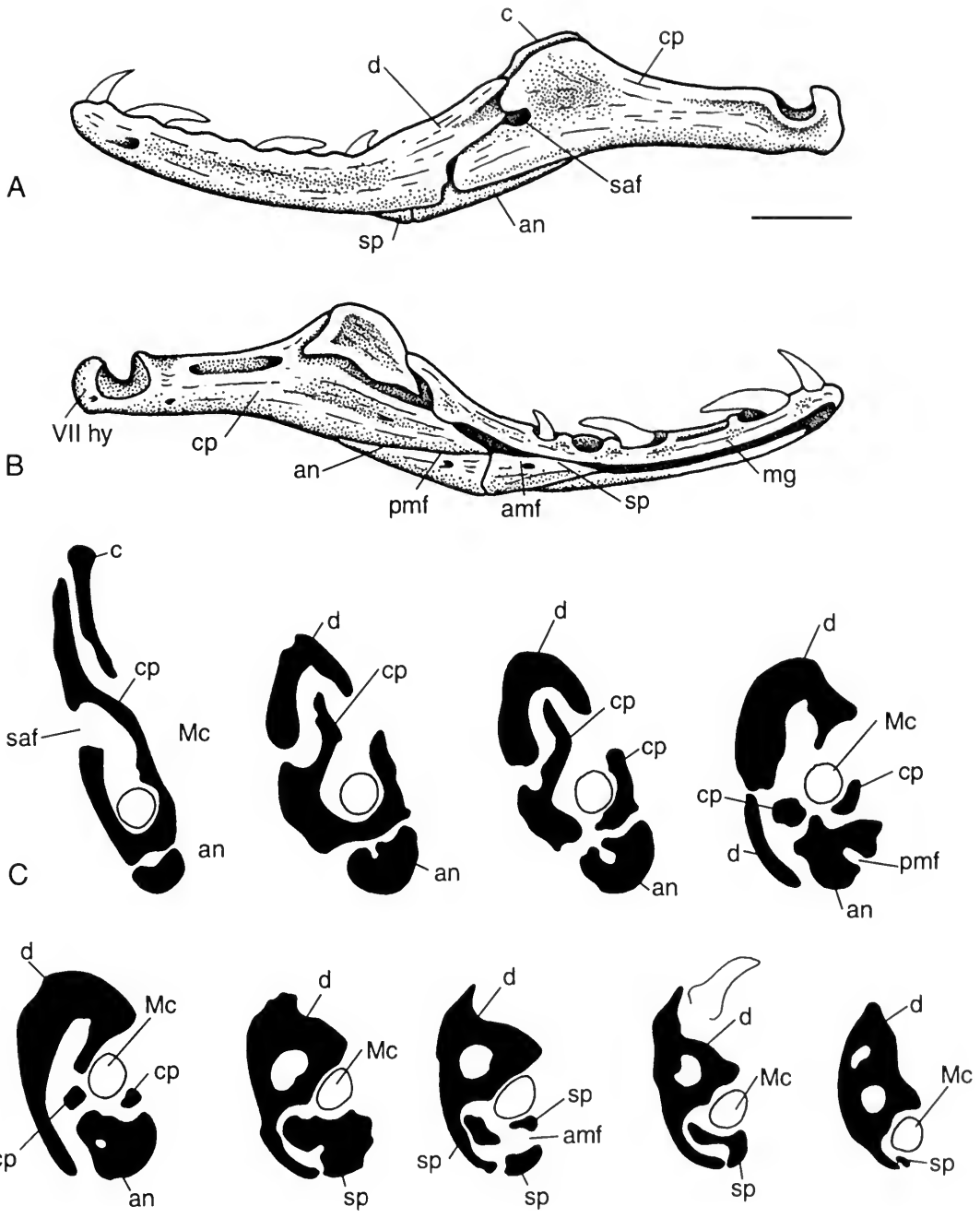


FIG. 10. The lower jaw of *Plecturus perroteti* (BMNH 1930.5.8.105; serially sectioned skull, uncatalogued). A, lateral view; B, medial view; C, serial sections from the coronoid process to the anterior tip of the splenial. Scale bar = 1 mm. Abbreviations as in Figure 1.

These do not, however, bridge the angular–splenial contact. As in *Cylindrophis*, the splenial develops a horizontal crest that projects from its lateral surface at a level closely below the anterior mylohyoid foramen and that underlies Meckel’s cartilage. This crest, together with the ventral edge of the splenial, again forms a groove that receives the ventral edge of the dentary. A small foramen located next to the anterior mylohyoid foramen allows a ventral branch of the anterior mylohyoid nerve to pass through the horizontal crest of the splenial and to continue anteriorly between the latter and the dentary. The anterior tip of the splenial again lies at the ventral margin of the dentary. The disarticulated mandible of *Pseudotyphlops philippinus* (BMNH 1978.1092) reveals the same splenial morphology.

The adductor fossa on the compound bone is elongate and deep in *Melanophidium punctatum* (BMNH 1930.5.8.119); this character again seems to represent the plesiomorphic condition, as it is closely comparable to *Cylindrophis*. In other uropeltids, the adductor fossa tends to be reduced to a shallow and relatively short groove located on the anterior half of the bone, behind the coronoid process, and showing a foramen at its anterior and posterior end for the passage of the mandibular division of the trigeminal nerve. The adductor fossa opens dorsally and medially in *Melanophidium punctatum* (BMNH 1930.5.8.119), where it is well developed, but it opens dorsomedially or medially in those taxa where it is reduced to a shallow groove.

The Intramandibular Joint in Basal Macrostomatans

The lower jaw of *Xenopeltis* is highly specialized to allow for extreme mobility (Frazzetta, 1999; McDowell, 1975; Rieppel, 1977). The dentary is short relative to the much elongated compound bone. It is deeply bifurcated posteriorly and carries a much elongated posterior dentigerous process. A sliverlike coronoid is attached to the dorsal surface of the compound bone in front of the adductor fossa, but it does not participate in the formation of a coronoid process (Hoge, 1964). The anterior end of the compound bone enters between the two posterior prongs of the dentary. A small angular and an elongate and pointed splenial are applied to the medial surface of the anterior end of the compound bone. There is no mobile contact between angular and splenial. Indeed, *Xenopeltis* differs from other snakes in that the

intramandibular joint lies between the dentary and the compound bone, angular and splenial being parts of the functional unit represented by the compound bone (Frazzetta, 1999).

No lower jaw of *Loxocemus bicolor* was available for disarticulation, which renders it impossible to comment on the internal structure of the articulation of the splenial with the angular. In its superficial structure, however, the mandible of *Loxocemus* resembles that of other basal alethinophidians and/or macrostomatans (McDowell, 1975; Rieppel, 1977). The dentary is deeply bifurcated posteriorly and carries the elongate posterior dentigerous process characteristic of macrostomatatan snakes. The coronoid is a relatively small sliver of bone that is applied to the medial side of the compound bone, lining the anterior margin of the coronoid process and contacting the dentary anteriorly. The splenial and angular meet in an abutting contact; the superficial suture on the medial surface of the lower jaw is anteriorly concave. An anterior mylohyoid foramen is absent in the splenial. The anterior mylohyoid nerve passes through a notch in its dorsal margin, as is also the case in *Python* (see below). The coronoid narrowly approaches, but does not contact, the splenial. Meckel’s groove opens medially along the splenial but ventrally (relative to the sagittal plane of the mandibular ramus) in front of the splenial. The adductor fossa is elongate and well developed, with a medial margin that is lower than the lateral margin such that the fossa opens medially and dorsally.

The intramandibular joint of *Python reticulatus* (Fig. 11, FMNH 31329) corresponds in its essential traits to that of *Cylindrophis*, although it is somewhat more elaborate. In lateral view, the dentary appears deeply bifurcated, with an elongate posterior dentigerous process overlapping the anterior lateral prong of the compound bone. The presence of such an elongate posterior dentigerous process is a synapomorphy of macrostomatatan snakes (Zaher, 1998). Disarticulation of the mandible (Fig. 11) reveals an intramandibular septum with a concave medial surface, separating the medially open Meckelian groove from the laterally positioned canal for the alveolar nerve. This canal opens anteriorly through the single mental foramen on the lateral surface of the anterior tip of the dentary (L97: char. 76; LC98: char. C14). The intramandibular septum reaches relatively further back into the posterior bifurcation of the dentary than in *Cylindrophis* and, together with the posterior dentigerous process and the posteroventral

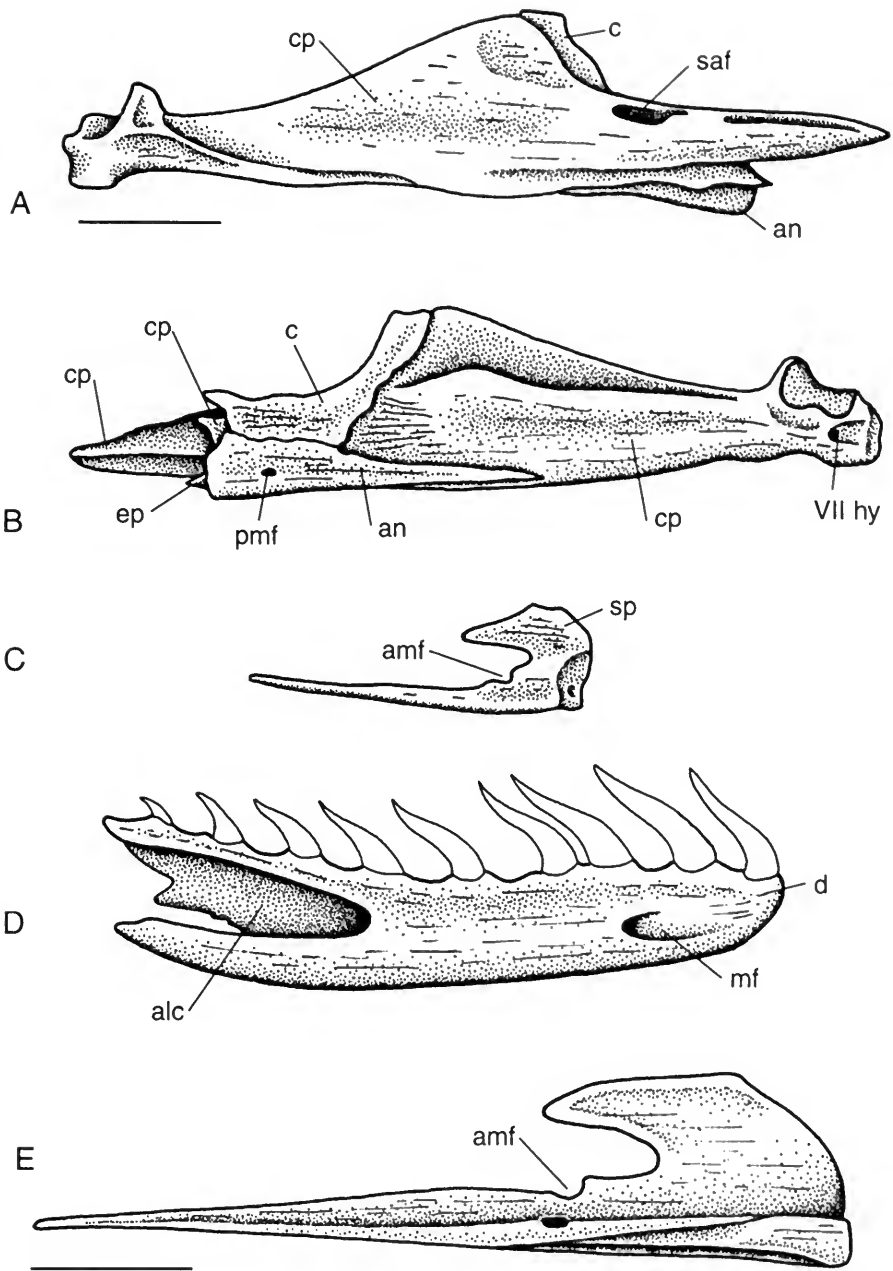


FIG. 11. The lower jaw of *Python reticulatus* (FMNH 31329). A, lateral view of postdentary bones; B, medial view of postdentary bones; C, splenial, medial view; D, dentary, lateral view; E, splenial, lateral view. A-D, scale bar = 2 mm; E, scale bar = 5 mm. Abbreviations as in Figure 1.

process of the dentary, forms a deep recess that receives the prominent anterior and lateral prong of the compound bone (surangular portion).

The medial view of the dentary exposes the Meckelian groove, which opens medially in its

posterior part as the dentary turns inward below Meckel's cartilage but ventrally (relative to the sagittal plane of the mandibular ramus) in front of the splenial (L-97: char. 69; LC98: char. B13). The tall but relatively narrow posterior portion of

the splenial covers only the posteriormost part of the Meckelian groove in medial view. A short and tapering process of the splenial follows the dorsal margin of Meckel's groove, whereas a much longer anteroventral process of the splenial follows the ventral margin of Meckel's groove, tapering off along the ventral margin of the dentary at a more anterior level than is characteristic of anilioids (L97: char. 70). The horizontal lateral shelf that projects from the lateral surface of the splenial is set very low, close to the ventral margin of the element (Fig. 11E). It underlies Meckel's cartilage and, together with the ventral margin of the splenial, forms a groove that receives the medially curved ventral margin of the dentary. Posteriorly, the horizontal shelf gradually tapers off in front of the thickened posteroventral head of the splenial. Again, the lateral horizontal crest of the splenial is pierced by a foramen for the passage of a ventral branch of the anterior mylohyoid nerve, which comes to lie between splenial and dentary. An anterior mylohyoid foramen was not observed in *Python reticulatus* (FMNH 31329); the nerve passed through a notch on the posterior dorsal margin of the splenial, as is also the case in *Python sebae* and *Epicrates cenchrus* (Frazzetta, 1959).

The relatively large and L-shaped coronoid is applied to the medial surface of the compound bone, together with which it forms the prominent coronoid process. All traces of a posteroventral process of the coronoid have disappeared, and its ventral margin therefore is straight (L97: char. 79; LC98: char. B10). The anteroventral process, however, is well developed and broadly contacts the dorsal margin of the angular. Anteriorly, this process of the coronoid is developed into an anterodorsally pointing spur that overlaps the posterodorsal corner of the splenial (L97: char. 75; LC98: char. B14).

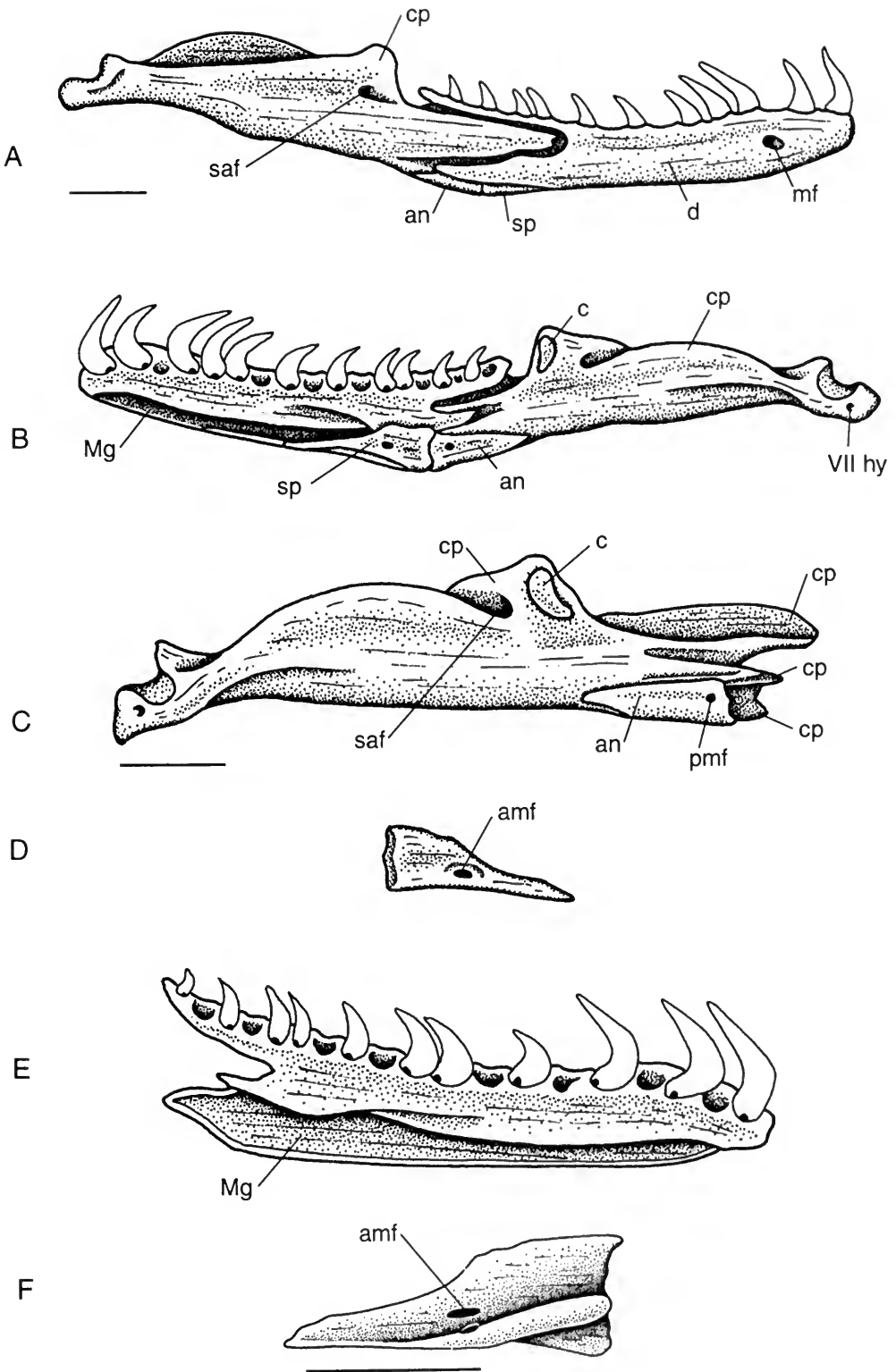
Superficially, the angular meets the splenial in a vertical suture (L97: char. 74), which on the medial margin of the mandible appears slightly convex anteriorly (L97: char. 73; LC98: char. B12). Disarticulation of the dentary and splenial reveals two anterior prongs or processes of the compound bone that, together with the anteriorly projecting lateral margin of the angular, hold the

splenial in place. The larger of these processes is located dorsomedially to Meckel's cartilage, projecting from the prearticular portion ventral and deep to the anterodorsally projecting tip of the coronoid. The smaller ventral process originates from that portion of the compound bone that is located ventromedial to Meckel's cartilage, and it corresponds to the single anterior process of the compound bone seen in *Cylindrophis*. In *Python*, the ventromedial anterior process of the compound bone is not complemented by an antero-medial prong of the angular, as it is in *Cylindrophis*. The two medial processes of the compound bone together with the laterally projecting edge of the angular define a deep, essentially vertically oriented trough into which slides the posterior margin of the vertical lamina of the splenial. The ventral portion of the anterior part of the angular is broadened and forms a distinct socket on its anterior surface. Into this socket fits the equally thickened posteroventral head of the splenial. The intramandibular joint as a whole has reached a greater level of complexity in *Python* as compared to *Cylindrophis* or uropeltids.

The adductor fossa forms a deep and wide trough on the compound bone, with well-defined lateral and medial margins. Of these, the medial margin is lower than the lateral margin, such that the adductor fossa opens dorsally and medially (L97: char. 80; LC98: char. B15).

The lower jaw of basal erycines rather closely matches the pattern established for *Python*. *Lichanura trivirgata roseofusca* (Fig. 12, FMNH 8043) and *Charina bottae* (Figs. 13C, 13D; FMNH 31300), but not *Calabaria reinhardti* (Figs. 13A, 13B; FMNH 31372), show the development of a distinct posterior process from the posterodorsal corner of the intramandibular septum that separates Meckel's groove from the canal for the superior alveolar nerve. This process is only vestigial in *Python* and *Calabaria* (Figs. 13A, 13B), but in *Lichanura* (Fig. 12) and *Charina* (Figs. 13C, 13D), it is distinct and comes to lie in a well-delineated groove or facet on the medial aspect of the anterior prong of the compound bone (surangular portion) that supports the dentary, thus adding to the firmness of the dentary suspension. Only the lower jaw of *Lichanura* was disarticu-

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 FIG. 12. The lower jaw of *Lichanura trivirgata roseofusca* (FMNH 8043). A, lateral view; B, medial view; C, postdentary bones, medial view; D, splenial, medial view; E, dentary, medial view; F, splenial, lateral view. Scale bar = 2 mm. Abbreviations as in Figure 1.



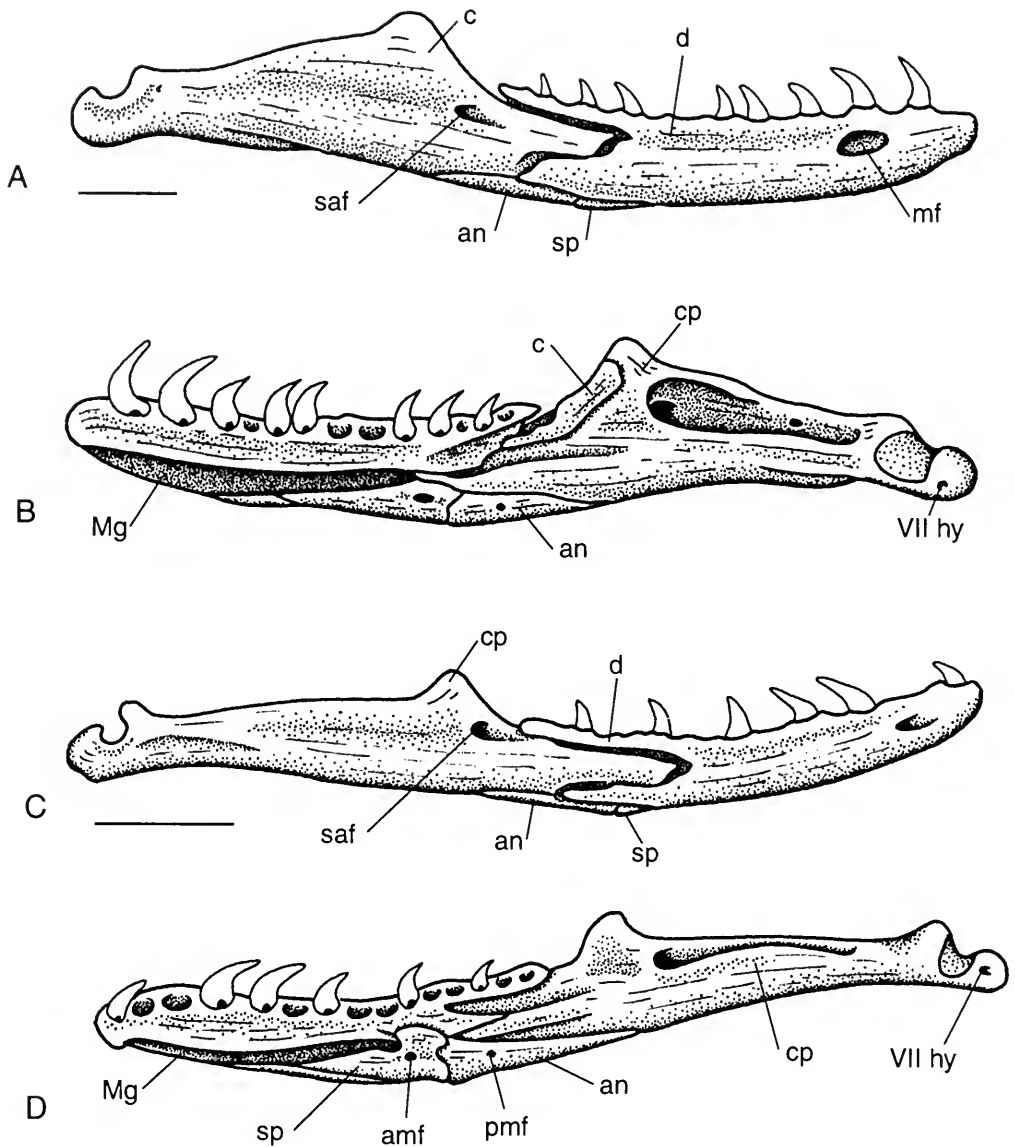


FIG. 13. The lower jaw of *Calabaria reinhardti* (FMNH 31372: A, lateral view; B, medial view) and of *Charina bottae* (FMNH 31300: C, lateral view; D, medial view). Scale bar = 2 mm. Abbreviations as in Figure 1.

lated (Fig. 12), and it revealed some differences in the angular-splenic contact as compared to *Python*. As in the latter genus, an anterior medial prong originates from the compound bone in a position located dorsomedial to Meckel's cartilage and medial to the surangular portion, distinctly projecting beyond the anterior margin of the angular. And again as in *Python*, a second anterior medial prong originates from the compound bone ventromedial to Meckel's cartilage, but whereas this process remains very small in *Python*, it is

elaborated into a tall vertical flange in *Lichanura* and establishes contact with the more dorsally located anterior medial projection of the compound bone (Fig. 12C). This arrangement results in a combined anterior projection of the compound bone medial to the angular, whereas the latter shows an anteriorly projecting lateral margin. Thus, the compound bone and the angular together define a deep vertical trough, into which slides the posterior margin of the posterior vertical lamina of the splenic. The tall ventral part of the

medial anterior projection of the compound bone carries a distinct notch at the depth of the trough that is formed by itself and the anteriorly projecting lateral margin of the angular. Into that notch fits the knoblike posterior head of the horizontal crest that projects from the lateral surface of the splenial (Fig. 12F).

The intramandibular joint of *Boa constrictor* (Fig. 14, FMNH 22363) resembles that of *Lichanura* more closely than that of *Python*, although

important differences are also noted. As in other macrostomatans, the dentary is again deeply bifurcated posteriorly. The two posterior prongs of the dentary, together with the intramandibular septum, form a recess that receives the strongly developed anterior prong (surangular portion) of the compound bone. As in *Lichanura* and *Charina*, the intramandibular septum forms a distinct posteromedial projection. In *Lichanura* and *Charina*, this projection comes to lie in a facet on the

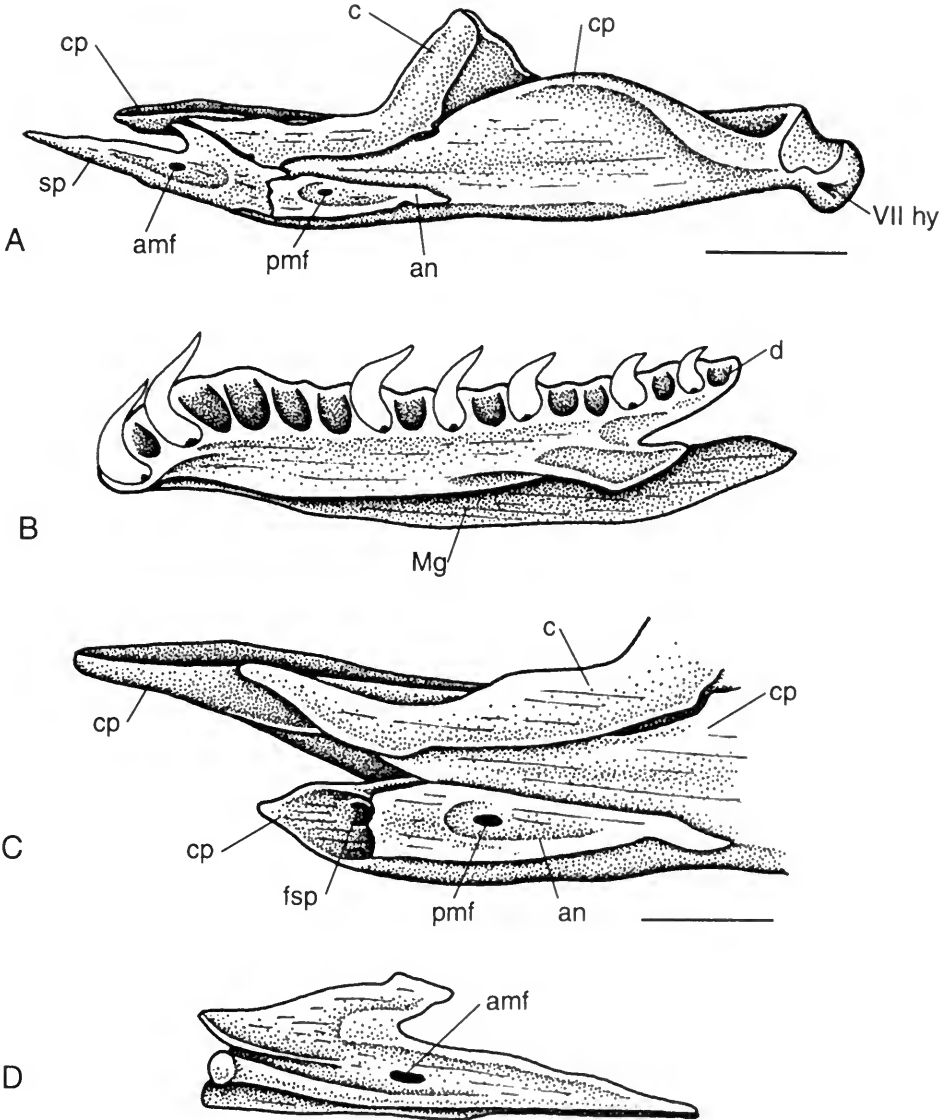


FIG. 14. The lower jaw of *Boa constrictor imperator* (FMNH 22363). A, postdentary bones, medial view; B, dentary, medial view; C, postdentary bones, medial view; D, splenial, lateral view. A, B, scale bar = 10 mm; C, D, scale bar = 5 mm. Abbreviations as in Figure 1.

medial aspect of the compound bone and itself remains superficially exposed in medial view. In *Boa*, this process forms a distinct facet on its medial surface, which receives distinct anterior processes of the coronoid and splenial.

Unlike in *Python*, the angular is applied to the ventromedial surface of the compound bone, with no exposure in lateral view of the lower jaw. Its anterior end is thickened, and its anterior lateral margin is projecting anteriorly. Superficially, the angular meets the splenial in a sigmoidal suture. Unlike in *Python*, the splenial carries a distinct and pointed posterodorsal process that fits snugly into a triangular recess formed by the anterior dorsal margin of the angular and the anterior end of the compound bone (Figs. 14C, 14D).

Medial to the angular, the compound bone forms a pointed, cup-shaped anterior projection that, together with the anteriorly projecting lateral margin of the angular, forms a deep trough that receives the posterior end of the splenial. This arrangement very closely resembles *Lichanura* except for the fact that the two components (dorsal and ventral) that form the anterior projection of the compound bone deep to the angular in the latter genus cannot be distinguished in *Boa* because they are completely fused. At the bottom of the trough between the angular and the anterior medial projection of the compound bone, the latter carries a very distinct notch. Unlike in *Python*, but as in *Lichanura*, the splenial is pierced by the anterior mylohyoid foramen in *Boa*. As in *Lichanura*, a very distinct lateral horizontal crest develops from the lateral surface of the splenial at the level just below the anterior mylohyoid foramen. Together with the ventral margin of the splenial, this horizontal crest forms a groove that receives the medially curved ventral margin of the dentary. A ventral division of the anterior mylohyoid nerve pierces the lateral horizontal shelf of the splenial immediately lateral to the anterior mylohyoid foramen. Unlike in *Python*, the posterior end of the horizontal shelf of the splenial is developed into a distinct articular knob, more distinctly so than in *Lichanura*, which fits into the notch in the anterior medial projection of the compound bone deep to the angular. Of all the snakes described in this study, *Boa* shows the most complex differentiation of the intramandibular joint. The differences observed in the differentiation of the intramandibular joint indicate that a broader survey of its structure could reveal a number of characters that might be useful in the analysis of the interrelationships of basal snakes.

The Skull and Lower Jaw of *Pachyrhachis*

In order to assess the phylogenetic relationships of *Pachyrhachis*, it is necessary to revisit the morphological description and cranial reconstruction given by Caldwell and Lee (1997) and Lee and Caldwell (1998). After the initial description of the dorsal aspect of the skull (Haas, 1979), the specimen was embedded in epoxy and the ventral side of the skull was prepared and described (Haas, 1980). The epoxy resin covering the dorsal surface of the skull renders it difficult to assess some morphological details. Parts of the skull are poorly preserved, such as the nasal complex comprising the nasals, vomers, and septomaxillae, as well as parts of the palate. In general, however, the skull is fairly well known as far as it is preserved, and it will suffice in the present context to review selected parts of its anatomy.

The interpretation of the circumorbital bones in basal snakes has long been controversial (Haas, 1964, 1968), and *Pachyrhachis* is no exception (L97: char. 23; LC98: chars. C7, D3). Haas (1979) described three bones surrounding the orbit of *Pachyrhachis*, a dorsally located postfrontal, a posteriorly located postorbital, and an ectopterygoid that appears to floor the orbit. Lee and Caldwell (1998) considered Haas's (1979) postorbital to represent a postorbital fused with a postfrontal, the latter represented by an elongate anterior process lining the dorsal margin of the orbit and not indicated by Haas (1979). The postfrontal as identified by Haas (1979) was interpreted as a jugal by Lee and Caldwell (1998).

Re-examination of the holotype of *Pachyrhachis* (Fig. 15) showed the postorbital to be a distinct element applied to the lateral wing of the parietal at the posterodorsal corner of the orbit, with a ventral process forming an extensive postorbital bar. The dorsal head of the postorbital is roughly of a triradiate structure. There is a thickened anterodorsal head, which is sutured to the lateral end of the posterior surface of the transverse ridge that is developed on the anterior end of the parietal. From the posterior margin of this dorsal articular head projects a small yet distinct lappet, which is applied against the laterodorsal surface of the lateral parietal wing. Although the dorsal head of the postorbital is smaller than it is in *Python*, its relation to the parietal closely resembles the postorbital–parietal contact in the latter taxon.

At the dorsal margin of the right orbit, an elongate element is exposed that was interpreted as

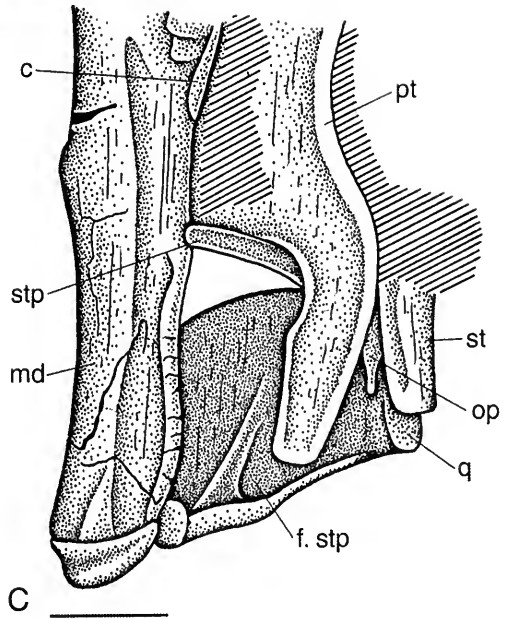
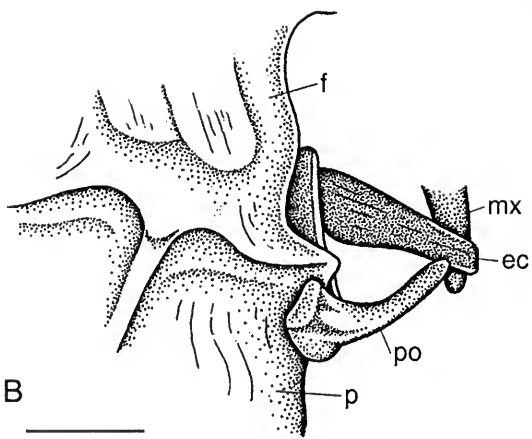
the postfrontal by Lee and Caldwell (1998), who thought it was originally fused to the postorbital and would have lined the dorsal margin of the orbit. Closer inspection reveals, however, that this bony element represents a sheet of bone that exposes its lateral edge dorsally and dips medially as it disappears below the parietal. The bone in question passes below the lateral wing of the parietal and below the proximal head of the postorbital. As such, it cannot represent a postfrontal, which would originally have been fused to the postorbital, but rather corresponds to a broken part of the laterally descending flange of the parietal. We therefore conclude that *Pachyrhachis* lacked a postfrontal.

As preserved, the ventral tip of the postorbital is pushed against the posterior end of an elongated element that lies in the floor of the orbit on top of the posterior end of the maxilla, pointing anteromedially (the postfrontal of Haas, 1979). This element was interpreted as a jugal by Lee and Caldwell (1998), which would appear reasonable, given its topological relation relative to the maxilla and postorbital and its location mostly in front of the latter element (L97: char. 29; LC98: char. D1). However, the element in question shows a distinct broadening of its anterior end, whereas a jugal would be expected to have a tapering anterior process lining the ventral margin of the orbit. For this reason, the element in question could just as well be interpreted as the anterior end of an ectopterygoid that has been broken across the posterior end of the maxilla upon dorsoventral compression of the skull during fossilization. We favor this latter interpretation because it is also supported by parsimony analysis.

The parietal of *Pachyrhachis* is pythonomorph in that there is a distinct transverse ridge on its anterior end from which originates a sagittal crest that extends posteriorly (L97: char. 19; LC98: char. C21). The sagittal crest ends in a knoblike projection (the supraoccipital of Haas, 1979), which indicates that the parietal overhung a vertically oriented supraoccipital, just as in *Python*. The dorsolateral surface of the parietal supports the elongate supratemporals (L97: chars. 25–27; LC98: chars. C5, E1), which have free-ending posterior processes from which the quadrates are suspended (Haas, 1979; Lee & Caldwell, 1998). The quadrate of *Pachyrhachis* is autapomorphic as it develops a broad anterior lateral extension. The mandibular condyle of the right quadrate is preserved in articulation with the right mandible, and the cephalic condyle of the same quadrate is

in articulation with the posterior tip of the supra-temporal. From the posterior margin of the right quadrate there projects a distinct medial flange, positioned at a right angle to the broad anterior lateral extension of the quadrate. This posterior medial flange is most prominently developed shortly above the mandibular condyle, but it recedes along the upper half of the posterior margin of the quadrate, tapering off toward the cephalic condyle. The medial surface of the broad anterior lateral extension of the quadrate shows a weakly developed ridge that trends from the anterodorsal corner in a posteroventral direction toward the medially projecting shelf. Below this ridge there is a shallow groove against which the quadrate ramus of the pterygoid is articulated as it extends toward the mandibular condyle of the quadrate. Above this ridge on the medial surface of the quadrate, between it and the medial flange projecting from the posterior margin of the latter, is located a shallow yet distinct notch that must have received the cartilaginous distal end of the stapes. The medial flange projecting from the posterior margin of the quadrate may therefore, in part at least, correspond to the stylohyoideal process on the quadrate of snakes. The morphology of *Pachyrhachis* is again fairly closely comparable to that of *Python*, except that the stylohyoideal process is better defined as it projects from the posterior medial margin of the quadrate in *Python*. Also, the contact between stapes and quadrate seems to be in a more ventral position in *Pachyrhachis* as compared to *Python*. However, the stapes–quadrate articulation of *Pachyrhachis* is distinctly different from the morphology observed in mosasaurs or in basal alethinophidian snakes such as anilioids (L97: 45).

The shaft of the right stapes of *Pachyrhachis* is well preserved as it projects laterally from below the pterygoid between the quadrate posteriorly and the coronoid anteriorly. This element was identified as a supratemporal by Haas (1980) but as a questionable squamosal by Lee and Caldwell (1998). This slender blade of bone cannot represent the supratemporal, as the latter is seen in articulation with the cephalic condyle of the quadrate. Its identification as a possible squamosal followed from the fact that Lee and Caldwell (1998) interpreted another rod-shaped element as the stapes. According to their interpretation, the stapes would project posteriorly, emerging from between the posterior tips of the quadrate ramus of the pterygoid and the supratemporal, respectively. For most of its exposed part, this latter element ap-



pears rod-shaped indeed, but it quickly broadens anteriorly, as is also particularly well shown (on both sides of the skull) on radiographs. In fact, the stapes as identified by Lee and Caldwell (1998) represents a posterior opisthotic process that forms a rudimentary paroccipital process, as is developed in some basal macrostomatans such as *Python*. A comparable paroccipital process is absent in scolecophidians and anilioids. Also, the distal end of the stapes of *Pachyrhachis* forms an elongate, slender, and flattened blade of bone, as is again seen in some basal macrostomatans such as *Python* but which is different from the short and robust stapedial shaft characteristic of anilioid snakes.

Little detail can be identified in the dermal palate and basicranium of *Pachyrhachis* beyond the general contours of the pterygoids and the elongate dentigerous processes of the palatines. However, both lower jaws are comparatively well preserved (Fig. 16) and have been described as being closely similar to the mandibles of mosasauroids (Lee & Caldwell, 1998). The Meckelian canal would be located on the medial surface of the dentary (L97: char. 69; LC98: char. B13), the anterior tip of the splenial would again be located on the medial aspect of the dentary (L97: char. 70), and the splenial would meet the angular in a vertical suture indicative of intramandibular mobility (L97: chars. 73, 74; LC98: char. B12). The coronoid carries a short posteroventral process (L97: char. 78; LC98: char. B10) and a long anteroventral process, which is reconstructed by Lee and Caldwell (1998) to contact the splenial (L97: char. 75; LC98: char. B14).

In fact, the illustration given by Lee and Caldwell (1998, Fig. 4) shows an elongated angular in an overlapping contact with a broad splenial in the right mandible. In the left mandible, the splenial is shown in a position medial to the dentary, but its posterior margin forms a vertical suture with the compound bone rather than with the angular, from which it remains separated.

In the ventral view of the specimen, the compound bone of the left mandible is preserved in medial view. The adductor fossa on its posterior

end faces medially and shows a sharp medial margin almost as high as the lateral margin. In front of the adductor fossa, the dorsomedial margin of the compound bone is lined by an elongate anterior process of the coronoid, which posteriorly is developed into the large coronoid process autapomorphic for *Pachyrhachis*. As in other snakes, the coronoid is applied to the medial side of the compound bone rather than straddling the dorsal margin of the surangular, as is characteristic of nonophidian squamates. The dentary of the left mandible is crushed but exposed in ventral view. Meckel's canal is well exposed toward the anterior end of the dentary, and it is bordered on both sides by sharp edges. This indicates that Meckel's canal originally opened ventrally relative to the sagittal plane of the lower jaw, as is characteristic of other snakes as well. However, the lateral and medial components of the dentary surrounding Meckel's canal have been crushed, as the ventrolateral marginal zone of the dentary can be seen to be broken off from the rest of the bone and flipped medially. This morphology is not comparable to the mosasaur jaw, where Meckel's canal forms a sulcus with smooth, rounded margins on the medial surface of the dentary.

Lee and Caldwell (1998) identified a remnant of the angular along the ventral margin of the left mandible, although it is represented by nothing more than a broken splint of bone and remains separated from the supposed splenial by what appears to be the compound bone. By comparison to the right mandible, the angular thus identified appears to be too narrow, and the bone in question appears to be a crushed remnant of the posteroventral process of the dentary instead. By contrast, there is what appears to be a V-shaped suture line, the apex pointing backward, on the medial surface of the mandible somewhat in front of the posterior end of the coronoid, which may delineate the posterior end of the angular. If correctly identified, the angular represents a relatively broad, elongate, platelike element comparable to, yet somewhat wider than, the corresponding element of the right mandible. If correctly identified, the angular of *Pachyrhachis* would have to

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FIG. 15. A, radiograph of the skull of the fossil snake *Pachyrhachis problematicus* Haas from the lower Middle Cretaceous of Ein Jabrud; B, the right orbit of *Pachyrhachis* and its surrounding bones in dorsal view; C, the left suspensorium of *Pachyrhachis* in ventral view. A, scale bar = 20 mm; B, C, scale bar = 5 mm. Abbreviations: c, coronoid; ec, ectopterygoid; f, frontal; f.stp, facet for stapes; md, mandible; op, opisthotic; p, parietal; po, postorbital; pt, pterygoid; q, quadrate st, supratemporal; stp, stapes.

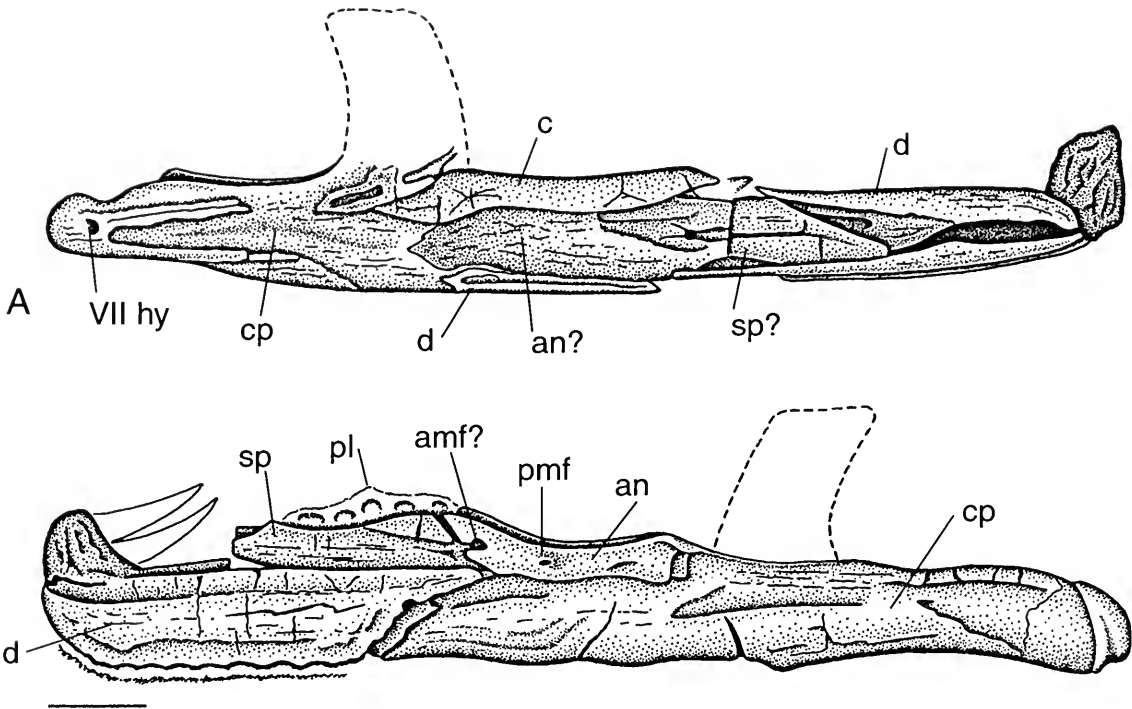


FIG. 16. The mandibles of *Pachyrhachis problematicus* Haas as exposed on the ventral side of the specimen. A, left lower jaw; B, right lower jaw. Scale bar = 5 mm. Abbreviations as in Figure 1.

be reconstructed in broad sutural contact with the coronoid.

Following the angular anteriorly, the relationships of the elements of the lower jaw become more obscured by extensive breakage. There is an anteriorly tapering structure pressed between the lateral and medial margins of Meckel's canal that, in its totality, could represent the angular in articulation with the splenial. However, the vertical posterior end of the splenial, shown in articulation with the compound bone by Lee and Caldwell (1998, Fig. 4), appears to represent a break. Furthermore, the anterior tip of the supposed splenial is separated from the dentary along the dorsal margin of Meckel's canal by what appears to be a very delicate fracture rather than a suture. But even if this were a suture, the splenial would be associated with the wrong (dorsal) margin of Meckel's canal by comparison with other squamates. The exact nature of the angular-splenial contact cannot be unequivocally established on the left mandible. Also, a posterior mylohyoid foramen cannot be identified on the left angular in a comparable position to the one on the right element, although it might be represented by a foramen located more anteriorly in a depression.

The morphology and relations of the angular and splenial are better preserved and more fully exposed on the right mandible.

The preservation of the right mandible is more complicated, but the compound bone is preserved in more or less straight ventral view (the adductor fossa facing upward), and it is exposed to a level far anterior along the lower jaw. The dentary has been twisted during dorsoventral compression of the skull due to the overlying maxilla. The lateral surface of the dentary is therefore more or less exposed in the ventral view of the specimen. There is no indication of a shallow Meckelian groove on the anterior end of the dentary, as is illustrated by Lee and Caldwell (1998, Fig. 4b). Two elongated elements are located along the medial margin of the compound bone and have been interpreted as angular and splenial by Haas (1980) and Lee and Caldwell (1998). The posterior one of these two elements is a fairly broad and elongate, platelike angular with a slightly concave ventral margin and a broken posterior end. The posterior mylohyoid foramen is located somewhat in front of its midpoint. The anterior end forms a distinct and pointed anteroventral projection that overlaps the posterior margin of the adjacent el-

ement, the splenial. Above this anteroventral projection, the sloping anterior margin of the angular is distinctly notched and thus forms the posterior margin of the anterior mylohyoid foramen, which is completed anteriorly by the splenial.

The splenial is an unusually broad element that has been preserved with a broken anterior tip. It seems to taper in its anteriormost part only and must have reached far anteriorly along the ventral margin of the lower jaw. It remains unclear whether a splint of bone lying alongside the dentary represents the thin anterior extremity of the splenial. But even if this possibility is discounted, the splenial of *Pachyrhachis* reaches further anteriorly than is typical of basal alethinophidians and hence is a character that the latter genus shares with macrostomatans. *Pachyrhachis* is autapomorphic, however, with respect to the broad, platelike appearance of the angular and splenial. The two elements also do not meet in a vertical suture but in an overlapping contact, which furthermore appears to enclose the anterior mylohyoid foramen.

Another matter of debate is the number of mental foramina present in the dentary of *Pachyrhachis* (L97: char. 76; LC98: char. C14). Nonophidian squamates typically have a series of mental foramina lining the dentary below the tooth row. By contrast, snakes have a single mental foramen located toward the anterior tip of the dentary. *Pachyrhachis* was described as retaining two mental foramina, another supposedly primitive character of the genus (Lee & Caldwell, 1998).

There is no indication of any foramen on the damaged lateral surface of the right dentary (exposed in the ventral view of the skull). By contrast, two foramina appear to be located toward the anterior end of the left dentary, exposed in the dorsal aspect of the specimen, which is now embedded in epoxy. Of these, the smaller posterior one is an undisputed mental foramen; it is also clearly identifiable in the photograph published by Haas (1979, Fig. 6B). By contrast, the position of the larger anterior foramen corresponds to a notch in the eroded ventrolateral margin of the dentary in the photograph, which shows the specimen before it was embedded in epoxy (Haas, 1979, Fig. 6B). Indeed, the erosion of the margin of the dentary is obscured by the epoxy, on the "ventral" (lower) surface of which a thin film of matrix was left in place, lining the dentary and suggesting a complete lateral (ventral) margin of the supposed foramen. The bone surface is easily distinguished

from the film of matrix, however, not only by its shiny appearance but also by a reddish hue that is absent in the matrix. The impression of a foramen is further reinforced by a bubble, which appears to have formed in the notch of the eroded margin of the dentary as it was embedded in epoxy. In conclusion, *Pachyrhachis* is characterized by the presence of a single mental foramen, as is characteristic of all snakes.

Character Evidence for the Monophyly of the Pythonomorpha

The monophyly of the Pythonomorpha, with *Pachyrhachis* as intermediate between mosasauroids and snakes, has recently been supported by a global analysis of squamate interrelationships (Lee, 1998). In this section, we review the character evidence used by Lee (1998; see this paper for the primary sources of characters, if applicable, and a discussion of characters other than the comments below) for the analysis of squamate interrelationships. For readers who do not have Lee (1998) at their disposal, we give an abbreviated definition of each character as conceived by Lee (1998). Subtleties of character definitions may be lost in our rendering, and the reader is encouraged to refer to Lee (1998) to avoid possible misunderstandings. Our review of this data set (Table 1, pp. 50 *ff.*) is not intended to provide a better understanding of global squamate relationships but rather to test the monophyly of the Pythonomorpha on the same grounds on which it was proposed. If *Pachyrhachis* is indeed the link between mosasauroids and snakes, the consequence could be that snakes have had a marine origin and that the fossorial ecomorph evolved independently among nonophidian squamates and within snakes (Lee, 1998; Scanlon et al., 1999). Our review therefore focuses on those characters that are relevant to the placement of *Pachyrhachis* and to the potential phylogenetic relationships of snakes with varanoid lizards (including mosasauroids), on the one hand, or with amphisbaenians and dibamids on the other.

Character 1: Premaxillary palatal foramina present (0), absent (1). As defined by Lee (1998), the premaxillary foramina in nonophidian squamates are synonymized with the premaxillary channels of snakes (see Kluge, 1989, for terminology).

- Character 2:* Premaxillary lateral foramina present (0), absent (1). There are no such lateral premaxillary foramina in snakes, which therefore cannot be compared and are coded as unknown (?).
- Character 3:* Premaxilla–maxilla contact sutural (0), nonsutural (1).
- Character 4:* Alveolar ridge of maxilla straight (0), upturned at anterior end (1).
- Character 5:* Dorsal process of maxilla at or in front of (0) or behind (1) midpoint of maxilla. The character is redundant, as it combines the information of a retracted naris (character 16) and the degree of posterior extension of the maxilla below the orbit (character 7). *Pachyrhachis* is miscoded: if Lee and Caldwell's (1998) description is correct, the maxillary–prefrontal contact is autapomorphic for this taxon. However, personal inspection of the holotype suggests (especially on the left side of skull) that the “dorsal process of the maxilla” is, in fact, the anterior portion of the prefrontal of similar proportions as seen in anilioids. We therefore code *Pachyrhachis* 0.
- Character 6:* Dorsal process of maxilla extends dorsomedially (0), dorsolaterally (1).
- Character 7:* Posterior process of maxilla long (0), short (1).
- Character 8:* Lacrimal present (0), absent (1).
- Character 9:* Lacrimal separate (0), fused with prefrontal (1).
- Character 10:* Lacrimal foramen single (0), double (1).
- Character 11:* Lacrimal foramen at least partly bordered by facial elements (0), entirely within prefrontal (1). The primitive position of the lacrimal foramen in squamates is between the lacrimal and the prefrontal. Since snakes lack a lacrimal, the lacrimal foramen lies between the maxilla and the prefrontal for those terminals we included. We have been unable to verify Lee's (1998) assessment of the position of the lacrimal foramen in mosasaurs (Camp, 1942; Russell, 1967), but if he is correct, the position of the lacrimal within the prefrontal would be autapomorphic for mosasaurs. As such, the character is uninformative and hence is deleted.
- Character 12:* Jugal present (0), absent (1). Personal investigation of the holotype of *Pachyrhachis* indicates that the jugal sensu Lee and Caldwell (1998) most probably represents the anterior end of the ectopterygoid, which broadly overlaps the posterior end of the maxilla. The ectopterygoid of *Pachyrhachis* appears to be broken across the posterior end of the maxilla on both sides of the skull, a consequence of the dorsoventral compression of the skull. *Dinilyisia* has also been described with a jugal (Estes et al., 1970), an assessment that has been questioned by Lee (1998). We have coded *Dinilyisia* with or without jugal in separate analyses to test the effect of either assumption. Character 12 codes *Dinilyisia* with a jugal (0), whereas character 142 codes *Dinilyisia* without a jugal (1). Using either one of these characters requires deletion of the alternative.
- Character 13:* Jugal does not (0), does (1) extend anteriorly beyond midpoint of orbit. This character again could not be coded accurately for *Dinilyisia* because of the poor preservation of the bone identified as a jugal (Estes et al., 1970).
- Character 14:* Nasals paired (0), fused (1). *Varanus* should be coded polymorphic for this character until the derived nature of paired nasals is confirmed by cladistic analysis of varanid interrelationships. Scolecophidians are polymorphic in this character. The nasal(s) of *Pachyrhachis* is/are not known.
- Character 15:* Nasal–prefrontal contact present (0), absent (1).
- Character 16:* External naris not retracted (0), slightly retracted (1; frontal excluded), strongly retracted (2; frontal enters external naris). *Lanthanotus* has to be coded 1 (Rieppel, 1983) or polymorphic. The nature of the external naris is not known in *Pachyrhachis* (?), although it is most conceivable that it was retracted. Lee (1998) coded snakes 1 for this (ordered) multistate character, but exclusion of the frontal from the posteriorly retracted external naris is most probably a reversal due to the burrowing habits of scolecophidians and anilioids.
- Character 17:* Prefrontal smooth (0), rugose (1) at orbital margin.

Character 18: Frontal(s) single (0), paired (1).

Character 19: Frontal with straight or weakly concave (0), strongly concave (1) lateral margin. Lee (1998) coded *Varanus* 1 for a deeply concave orbital margin of the frontal, yet coded mosasaurs 0 for a slightly concave orbital margin. In fact, the concavity of the orbital margin of the frontal is closely comparable in both groups (1) (Russell, 1967, Fig. 83). A straight frontal margin is derived within mosasaurs (Bell, 1997).

Character 20: Frontal flange underlying nasal absent (0), present (1).

Character 21: Frontoparietal suture complex, interdigitating (0), simple, straight transverse line (1). We propose a redefinition of this character as follows: Superficial delineation of frontoparietal suture complex and distinctly interdigitating (0), essentially a straight transverse line (1), frontal invading parietal (2), frontals posterolaterally embraced by parietal (3). Nonophidian squamates have a frontoparietal suture that superficially forms a more or less straight line (1). In mosasaurs, the frontal tends to develop posterior processes of variable shape overlapping the parietal (2) (Bell, 1997). In basal snakes (Anilioidea), the parietal tends to form anterolateral processes embracing the frontals in a curved suture (3). Scolecophidians (Haas, 1964, 1968; List, 1966) are polymorphic in this character (1 and 3). *Anelytropsis* shows character state 1 (Greer, 1985), but *Dibamus* (Rieppel, 1984b; not *Anelytropsis*: Greer, 1985) shows character state 3. Most amphisbaenians show state 0. *Pachyrhachis* has state 1.

Character 22: Frontal enters (0), is excluded (1) from dorsal margin of orbit. *Pachyrhachis* has to be coded as unknown (?) for this character due to the uncertain nature of the splint of bone exposed at the dorsal margin of the right orbit (see discussion of character 24, below). *Dinilyisia* is coded 0. This character is not applicable to scolecophidians (?).

Character 23: Postfrontal large (0), small (1), absent (2). This character is partially redundant with some of the following. We retain it as coded by Lee (1998) except in *Pachyrhachis* and snakes, which we interpret as lacking a discrete

postfrontal (2). *Pachyrhachis* is coded as unknown (see discussion of character 24, below).

Character 24: Postfrontal separate (0), fused to postorbital in adult (1). This character is problematic, as it makes assumptions about ontogeny in fossils. By comparison to *Varanus*, we agree that the postfrontal and postorbital fuse to form a postorbitofrontal in mosasaurs (Bell, 1997). However, Lee (1998) codes *Pachyrhachis* for a fused postorbitofrontal. This coding is based on the assumption (Lee & Caldwell, 1998) that a splint of bone exposed at the dorsal margin of the right orbit of the holotype of *Pachyrhachis* is the anterior process of the postfrontal, which establishes a contact with the prefrontal at the dorsal margin of the orbit (not present in *Varanus* or mosasaurs). Alternative interpretations would be to identify this splint of bone as postfrontal, separate from the postorbital, or to identify this splint of bone as a supraorbital (present in *Python* [Frazzetta, 1959], with which *Pachyrhachis* shares the crested anterior end of the parietal), lying in front of the postorbital. Re-examination of the holotype of *Pachyrhachis* suggests, however, that neither of these interpretations is correct, as the fragment of bone exposed at the dorsal margin of the orbit seems to be a splint of the laterally descending flange of the parietal (see above). Given the uncertainty of interpretation, we conservatively code *Pachyrhachis* as unknown (?) for this character (as well as for characters 22 and 23). Other snakes lack the postfrontal and hence are not comparable (?). Baumeister (1908) found a sutural separation of the anterolateral process of the parietal that lines the dorsal margin of the orbit in a uropeltid (*Rhinophis*) and considered this process to represent the postfrontal. Although accepted by Rieppel (1977), we here discard this interpretation until the observation of Baumeister (1908) is independently corroborated.

Character 25: Postfrontal not forked (0), forked (1) medially. The postfrontal (postorbitofrontal) is forked dorsally, i.e., clasps the frontoparietal suture in all nonophidian squamates that retain the mesokinetic axis (Rieppel, 1984b), including mosasaurs. Snakes lack a postfrontal, but in *Python*, the dorsal end of the postorbital is forked, without, however, clasping the frontoparietal suture. This morphology is approached by *Pachyrhachis*.

- Character 26:* Palpebral ossification absent (0), present (1).
- Character 27:* Postorbital present (0), absent (1). This character is difficult to interpret without adding the specification of whether the post-frontal is present or absent as a discrete ossification (redundant with character 24). However, as coded by Lee (1998), the character has no bearing on snake relationships and therefore is retained unchanged.
- Character 28:* Ventral process of postorbital long (0), short (1).
- Character 29:* Posterior margin of orbit complete (0), with small gap (1), with large gap (2). Because we interpret the jugal of *Pachyrhachis* as an ectopterygoid, it becomes impossible to decide whether *Pachyrhachis* has a complete or an incomplete postorbital arch. Yet the taxon shows a long ventral process of the postorbital, for which reason we code the taxon as 1.
- Character 30:* Parietal(s) paired (0), fused (1).
- Character 31:* Parietal tabs (triangular flanges extending anteriorly into fossae on ventral surface of frontals) present (0), absent (1). We have some difficulty understanding this character. In *Varanus*, the parietal bears lateral tabs projecting anteriorly that overlap a facet on the frontal as part of the mesokinetic joint (Rieppel, 1979a). A similar relation of these bones, but not as strongly expressed as in *Varanus*, is seen in other nonophidian squamates. This character is absent, however, in *Platecarpus* (AMNH 04909) and in other mosasaurs (Bell, 1977). Comparable anterolateral tabs of the parietal articulating in a facet on the frontal are also absent in snakes (including *Pachyrhachis*), amphisbaenians, or dibamids, which also have lost mesokinesis! However, given our difficulty in understanding Lee's (1998) character definition, we retain the coding he chose for this character.
- Character 32:* Parietal half as long as skull or shorter (0), longer (1) than half of skull length.
- Character 33:* Pineal foramen present (0), absent (1).
- Character 34:* Pineal foramen within parietal (0), on frontoparietal suture (1), within frontal (2).
- Character 35:* Origin of jaw adductor muscles restricted to ventral surface (0), invades dorsal surface (1) of parietal. This character overlaps with character 57. For reasons discussed below (character 57), we retain this character in our analysis but delete character 57.
- Character 36:* Supraoccipital exposed in dorsal view (0), concealed in dorsal view (1) by parietal.
- Character 37:* Posterolateral process of parietal distinct (0), short or absent (1).
- Character 38:* Upper temporal arch complete (0), incomplete (1).
- Character 39:* Jugal does not (0), does (1) contact squamosal.
- Character 40:* Squamosal present (0), absent (1). *Pachyrhachis* is coded for presence of a squamosal, but personal inspection of the holotype confirmed that the squamosal identified by Lee and Caldwell (1998) is, in fact, the stapes and that the stapes identified by Lee and Caldwell (1998) is, in fact, a posterior opisthotic (paroccipital) process, which is also present in a variety of basal macrostomatans (Zaher, 1998; see also Frazzetta, 1959). The squamosal is absent in *Pachyrhachis* (1).
- Character 41:* Dorsal process of squamosal present (0), absent (1). This character is not applicable to *Pachyrhachis* given the reassessment of the previous character.
- Character 42:* Upper temporal fenestra not restricted (0), restricted (1) by postorbital.
- Character 43:* Upper temporal fenestra not restricted (0), restricted (1) by postfrontal.
- Characters 42–43:* These characters were coded 0 for *Pachyrhachis* and snakes by Lee (1998), when in fact they are not applicable to these taxa (?).
- Character 44:* Supratemporal absent (0), present (1).
- Character 45:* Supratemporal on dorsolateral (0), ventrolateral (1) surface of parietal.

Character 46: Supratemporal confined to skull roof (0), forms part of paroccipital process and/or braincase (1). In nonophidian squamates, the supratemporal may or may not contact the distal end of the paroccipital process. The posterior tip of the supratemporal establishes a broad contact with the distal tip of the opisthotic in *Varanus* and a somewhat more extended but otherwise identical contact in mosasaurs (Rieppel & Zaher, in press). In snakes, the paroccipital process is much reduced. If present, it corresponds to a small posterior projection of the opisthotic as seen in some basal macrostomatans, and it is not in contact with the supratemporal (although the slight mobility of the supratemporal may change these relations in dried skulls). Such a paroccipital process is present in *Pachyrhachis*, but its relations to the supratemporal are obscured through dorsoventral crushing of the skull. The posterior tip of the opisthotic (stapes of Lee & Caldwell, 1998) is separate from the supratemporal, however, which indicates lack of a contact. In no case is the supratemporal (a dermal element) part of the braincase (endocranium), although the supratemporal may be superimposed on braincase elements. We conclude that *Pachyrhachis* and snakes have to be coded 0 for this character.

Character 47: Supratemporal less than half (0), at least half (1) of maximum skull width. This character is misleadingly coded for mosasaurs by Lee (1998). In a skull roof of *Platecarpus* (AMNH 01820), the supratemporal is less than half the maximum width of the skull. This is also the case for other mosasaurs (Camp, 1942; Russell, 1967). In basal snakes, the supratemporal is absent or small (scolecophidians and anilioids); it is also small or absent in dibamids and amphisbaenians. In macrostomatans, the supratemporal is elongated and carries a free-ending posterior process, as it also does in *Pachyrhachis* (Zaher, 1998). We therefore propose to modify this character in order to account for the presence of a free-ending posterior process of the supratemporal in *Pachyrhachis* and macrostomatans: supratemporal without (0) or with (1) free-ending posterior process.

Character 48: Supratemporal does not (0), does (1) contact prootic. In *Varanus*, the posterior tip of the supratemporal lies against the lateral surface of the opisthotic at the distal tip of the paroccipital process and is in a loose syndes-

motie connection with the prootic. In mosasaurs, the posterior tip of the supratemporal is somewhat expanded and forms a deeply interdigitating suture with the prootic (Rieppel & Zaher, in press). In snakes, the supratemporal shows very different relations. Due to the relative size increase of the braincase (Rieppel, 1984b), the latter comes to lie in the same plane as the dermatocranium (rather than being suspended within it, as in mosasaurs and other nonophidian squamates). The supratemporal thus comes to lie on top of the otic capsule, lateral to the reduced posterolateral (supratemporal) processes of the parietal, which in turn also lie on top of the otic capsule. The prootic-supratemporal contact in snakes (including *Pachyrhachis*) is therefore the result of a fundamentally different remodeling of the snake skull (Rieppel, 1984b; Rieppel & Zaher, in press) and is not comparable to the morphology seen in mosasaurs and *Varanus*. We therefore delete this character from the analysis (the coding retained in the data matrix is that of Lee, 1998).

Character 49: Quadrate monimostylic (0), streptostylic and suspended from supratemporal, squamosal, and opisthotic (1), suspended mainly from supratemporal (2), suspended mainly from opisthotic (3), suspended mainly from squamosal (4). As worded by Lee (1998), the definition of this character is somewhat confusing. It remains unclear whether character state 1 requires equal participation of the supratemporal, squamosal, and opisthotic in the quadrate suspension and whether character state 2 does or does not allow some participation of the squamosal and opisthotic in the quadrate suspension. As shown by Russell (1967, Fig. 20; see also Rieppel & Zaher, in press), the relation of the paroccipital process (opisthotic) to the supratemporal, squamosal, and quadrate is closely similar in mosasaurs and *Varanus*, where the quadrate articulates with the ventrolateral surface of the distal tip of the paroccipital process by means of an intercalary cartilage. We therefore code mosasaurs as having a squamosal-supratemporal-opisthotic articulation of the quadrate (see also Camp, 1942, p. 35).

Character 50: Quadrate shaft slanting strongly anteroventrally, almost horizontal (0), slanting slightly anteroventrally or vertical (1), slanting slightly or greatly posteroventrally (2). We re-

define this character as quadrate slanting strongly anteroventrally, almost horizontal (0), slanting slightly anteroventrally (1), positioned vertically (2), or slanting posteroventrally (3). These character states reflect an ontogenetic transformation (Bellairs & Kamal, 1981), and their assessment therefore requires that adult material be examined. A posteroventrally slanting quadrate has been designated a macrostomatian character (Rieppel, 1988), and although the reconstructions of *Pachyrhachis* provided by Lee and Caldwell (1998) show a vertically positioned quadrate, it may have had a posteroventrally slanting quadrate in life. As preserved, the quadrates extend posterolaterally from their articulation with the supratemporal, yet the tip of the right lower jaw still reaches the anterior tip of the right maxilla, which indicates that the quadrate and mandible have been shifted slightly forward. We accordingly code *Pachyrhachis* for a posteroventrally sloping quadrate (3).

Character 51: Tympanic crest on quadrate well developed (0), weakly developed (1), absent (2). We code *Varanus* 1 for a reduced tympanic crest, not 0 for a prominently developed tympanic crest, as coded by Lee (1998).

Character 52: Quadrate with (0), without (1) anteromedial lappet.

Character 53: Orbitonasal fenestra wide (0), narrow (1).

Character 54: Ventromedial processes of frontal end free ventrally (0), abutting or sutured to each other below olfactory tracts (1), contact parabasisphenoid (2). As worded by Lee (1998), this character would refer to medially descending flanges of the frontal. These are an autapomorphy of alethinophidians (our character 231), however, which is why we believe that Lee (1998) is, in fact, referring to laterally descending frontal flanges. In amphisbaenians, the lateral ventral flanges of the frontals meet each other and contact the orbitosphenoid ventrally. The coding retained in the data matrix is that of Lee (1998).

Character 55: Orbitosphenoid absent (0), present (1). This character is an autapomorphy of Amphisbaenia and, as coded by Lee (1998), groups *Sineoamphisbaena* with amphisbaenians. Its

presence in *Sineoamphisbaena* must be critically assessed (see character 59).

Character 56: Parietal downgrowths absent or weak (0), prominent (1). The well-preserved parietal of *Platecarpus* (AMNH 01563) is closely comparable to that of *Varanus*. Mosasaurs are here coded 0.

Character 57: Parietal downgrowths pointed ventrally (0), sheetlike (1). Following the character definition of Lee (1998), mosasaurs as well as all varanoids should be coded 1. However, as we understand it, we believe this character is misleading. The parietal may have laterally descending flanges or not: If such flanges are absent, the jaw adductors originate from the ventral surface of the parietal only. If such flanges are present, the jaw adductors “migrate” onto the “dorsal surface” of the parietal (Estes et al., 1988), i.e., they invade the lateral surface of these flanges. This is the same character as character 35. Another character is the presence or absence of a distinct ventral projection from the parietal as seen in some “lizards” such as skinks (Greer, 1970). Redefined along these lines, the character loses its importance for the analysis of snake–mosasaur relationships and is hence deleted from the analysis (the coding retained in the data matrix is that of Lee, 1998).

Character 58: Parietal–prootic contact absent or restricted (0), extensive (1). We believe this character to be poorly defined. Nonophidian squamates in general, mosasaurs included, have an alar process of the prootic made of *Zuwachsknochen* sensu Starck (1979; the term *Zuwachsknochen* refers to a membrane bone extension added to an element, the rest of which is preformed in cartilage) that contacts the parietal. Dibamids (Rieppel, 1984a; Greer, 1985), amphisbaenians (Montero et al., 1999, contra Rieppel, 1984a), and snakes lack the alar process of the prootic, which is also absent in *Sphenodon*. They also have an extensive parietal–prootic contact. We therefore redefine this character as alar process on prootic absent (0), or present (1).

Character 59: Parietal downgrowths end free ventrally (0), contact parabasisphenoid (1), contact orbitosphenoid (2). *Pachyrhachis* should technically be coded as unknown (?), although we agree to code it 1. As such, character state 1 is

a synapomorphy of snakes. The coding used here for *Sineoamphisbaena* is the same as in Lee (1998), although the presence of an orbitosphenoid and its relations to the parietal need to be critically reassessed in this taxon (M. Kearney, personal communication).

Character 60: Optic foramen not enclosed by bone (0), enclosed partially or entirely by frontal (1), enclosed by orbitosphenoid (2). We believe that this character has to be broken down in order to account for the different positions of the optic foramen in scolecophidians, henophidians, and caenophidians sensu Underwood (1967). The character thus becomes: optic foramen not enclosed by bone (0), enclosed by frontal (1), enclosed by orbitosphenoid (2), enclosed by frontal and parietal (3), enclosed by frontal, parietal, and parasphenoid (4). Acrochordids are autapomorphic for the position of the optic foramen in the parietal, a character that is not relevant to the present analysis and hence is here ignored. *Pachyrhachis* has to be coded as unknown (?). The coding used here for *Sineoamphisbaena* is the same as in Lee (1998), although the presence of an orbitosphenoid and its relations to the optic foramen need to be critically reassessed in this taxon (M. Kearney, personal communication).

Character 61: Anterior brain cavity not floored by bone (0), floored by orbitosphenoid (1), floored by wide cultriform process of parasphenoid (2). We believe this character to be poorly defined. First, the term "anterior brain cavity" is a poor choice of words: since the olfactory tracts and bulbs are part of the brain, the brain cavity extends anteriorly to a level in front of the frontal. As coded by Lee (1998), this character is a synapomorphy shared by mosasaurs and snakes. However, the basicranium of mosasaurs generally resembles that of *Varanus*, with two exceptions: the sella turcica is less recessed below the dorsum sellae, and the dorsum sellae is less developed (Rieppel & Zaher, in press). But mosasaurs, like any other nonophidian squamates, have a sella turcica in front of which the basicranium is abruptly constricted to a short rostrum basisphenoidale, which in turn terminates in a point (or narrow cultriform process), indicating a tropibasic skull. In snakes, the sella turcica lies at the back end of the parabasisphenoid, and the latter extends in front of the sella turcica as a broad

element underlying the brain, with the Vidian canal exposed on the dorsal surface and with the lateral edges sutured to the parietal downgrowths (Rieppel, 1979b). In front of the parietal, i.e., below the frontals, the parabasisphenoid may form a relatively broad (e.g., *Cylindrophis*) or narrow (e.g., *Anilius*) cultriform process. This type of parabasisphenoid (our definition for character state 2) is in fact a synapomorphy of snakes and reflects the fundamental change of skull proportions in snakes versus lizards (much elongated postorbital region, small orbits, short preorbital region). Fossil lizards such as *Anniella* (Rieppel, 1978), amphisbaenians, and dibamids (Rieppel, 1984a) approach the morphology of the ophidian parabasisphenoid because of similar changes in skull proportions.

Character 62: Cultriform process of parasphenoid in lateral view curved upward (0), straight (1). Any aspect of this character that goes beyond the discussion of character 61 is a preservational artifact. The character is therefore deleted from our analysis (the coding retained in the data matrix is that of Lee, 1998).

Character 63: Trigeminal foramen (foramina) open anteriorly (0), bordered anteriorly by parietal (1), bordered anteriorly by orbitosphenoid and parabasisphenoid (2).

Character 64: Alar process of prootic weak (0), extensive (1). This character is redundant with character 58 and therefore is deleted from our analysis (the coding retained in the data matrix is that of Lee, 1998).

Character 65: Alar process of prootic directed dorsally (0), anterodorsally (1). This character is inapplicable to *Pachyrhachis* (unknown [?], contra Lee, 1998), snakes, amphisbaenians, and dibamids.

Character 66: Crista prootica well developed (0), reduced (1). We believe that by comparison to snakes, dibamids, and amphisbaenians, the varanoid genera *Lanthanotus* and *Heloderma*, as well as xenosaurs, should be coded 0. However, we agree to code these taxa for a weakly developed crista prootica (1), but code snakes, amphisbaenians, and dibamids 2 for the absence of a crista prootica.

Character 67: Lateral head vein not enclosed (0), enclosed (1) in bony canal formed by anteroventral continuation of crista prootica.

Character 68: Facialis foramen single (0), double (1). The single or double facialis foramen is variable within *Varanus* (even at the species level), as well as in mosasaurs (Rieppel & Zaher, in press). It is also variable in snakes, where some (scolecophidians, uropeltines) show an intracranial course of the palatine branch of the facial nerve. We therefore delete this character from the analysis (the coding retained in the data matrix is that of Lee, 1998).

Character 69: Hypoglossal foramen well separated (0), close or confluent (1) with vagus foramen.

Character 70: Occipital recess open (0), closed (1) laterally. As defined and coded by Lee (1998), this character requires that the presence or absence of the crista circumfenestralis of snakes is dealt with as a separate character. Otherwise, snakes would have to be coded 1 also (see character 73).

Character 71: Otic capsule not expanded (0), expanded (1) laterally. Lee (1998) codes *Sineoamphisbaena*, *Amphisbaenia*, and dibamids as having a laterally expanded otic region (1). This reflects the relative size increase of the labyrinth organ in miniaturized squamate skulls (Rieppel, 1984b), which is also observed in other fossorial squamates, including snakes. The latter therefore have to be coded 1 also.

Character 72: Stapes light, footplate small (0), robust, footplate large (1). As dibamids and *Amphisbaenia* are coded 1 for a stapes with a robust shaft and a large footplate, basal snakes such as anilioids and some basal macrostomatans (*Xenopeltis*) also have to be coded 1. Scincidae is polymorphic for this character (Rieppel, 1981).

Character 73: Stapedial footplate not surrounded (0), tightly surrounded by bony ridges projecting from lateral surface of braincase (1). As defined and coded by Lee (1998), this character becomes a synapomorphy of mosasaurs and snakes. Note that, in contrast to Lee (1997, character 44) and Lee and Caldwell (1998, p. 1548), Lee (1998, p. 393) notes morphological

differences of this character between mosasauroids and snakes but continues to assume primary homology of these structures in his coding. However, the braincase of mosasaurs resembles that of *Varanus* rather closely and is not comparable to the otic region of snakes characterized by a crista circumfenestralis (Estes et al., 1970; Rieppel & Zaher, in press). We therefore propose to redefine this character as follows: a crista circumfenestralis, enclosing a juxtastapedial recess, is absent (0) or present (1). *Pachyrhachis* has to be coded as unknown (?). The character is a synapomorphy of snakes.

Character 74: Basipterygoid processes long (0), short (1). As defined by Lee (1998), this character is not applicable (not comparable) to snakes because basipterygoid processes of snakes (basal macrostomatans) are not homologous to those of lizards (Kluge, 1991; Rieppel & Zaher, in press). Lee and Caldwell (1998, p. 1534) described short basipterygoid processes in *Pachyrhachis*, and Lee (1998) coded *Pachyrhachis* for short basipterygoid processes (1), despite his claim that the nature of these processes cannot be confirmed for this taxon (Lee, 1998, p. 442) or the claim that distinct basipterygoid processes are absent in this taxon (Scanlon et al., 1999). *Pachyrhachis* should be coded as unknown (?).

Character 75: Articular facet on basipterygoid process subcircular (0), anteroposteriorly elongated (1). The same comments apply to this character as to the preceding one.

Character 76: Basal tubera located posteriorly (0), anteriorly (1). In varanoids and mosasaurs, the basal tubera (sphenoccipital tubercles sensu Oelrich, 1956) are located anteriorly on the basioccipital at the ventral end of the crista tuberalis. In snakes, they are incorporated into the posteroventral part of the crista circumfenestralis, as the latter incorporates the crista tuberalis (Estes et al., 1970; Rieppel & Zaher, in press). As defined by Lee (1998), this character is not applicable (not comparable) to snakes. *Pachyrhachis* should be coded as unknown (?).

Character 77: Posterior opening of Vidian canal within basisphenoid (0), at basisphenoid–prootic suture (1), between prootic and epiphyseal ossification in the region of the basal tubera (2).

Character 78: Posterior opening of Vidian canal situated well in front of (0), near (1) the posterior end of basisphenoid. This is a somewhat vague character, but as the braincase anatomy of mosasaurs is rather closely comparable to that of *Varanus*, they, too, should be coded 0. Snakes should be coded 1 for character 78, yet some snakes should be coded 1 for character 77 (Rieppel, 1979b).

Character 79: Crista tuberalis weakly developed (0), flaring (1). As defined by Lee (1998), this character is difficult to separate from his character 73. As coded, the character is a synapomorphy of *Lanthanotus* and *Varanus*, and as such is irrelevant for the analysis of snake relationships. We retain it as coded by Lee (1998).

Character 80: Supraoccipital separated from (0), in narrow contact with (1), in broad contact with (2) parietal. This character is poorly defined, and we propose to replace it by the following: posttemporal fossae present (0), reduced (1), absent (2).

Character 81: Supraoccipital situated ventrad or posteroventrad (0), at same level (1) as parietal. Scincidae and Pygopodidae are polymorphic for this character.

Character 82: Exoccipital separate (0), fused to opisthotic (1) in adult. Although we retain this character as defined and coded by Lee (1998), we believe its phylogenetic information content to be very limited. The skull of an adult *Varanus komodoensis* (FMNH 22199; condylobasal length: 215 mm) retains a separate exoccipital.

Character 83: Occipital condyle single (0), double (1). Although we retain this character as defined and coded by Lee (1998), we believe its phylogenetic information content to be limited. The double occipital condyle, formed by a posterior projection of the exoccipitals beyond the basioccipital, is strongly expressed within Gekota only (Rieppel, 1984c).

Character 84: Posttemporal fenestrae present (0), absent (1). This character is redundant with character 80 and is therefore deleted from the analysis (the coding retained in the data matrix is that of Lee, 1998).

Character 85: Septomaxilla extensively sutured (0), not sutured (1) to maxilla. Iguanids are polymorphic for this character (Oelrich, 1956; Etheridge, personal communication), yet in most lizards, the main body of the septomaxilla floors the anterior part of the external naris and is sutured to the maxilla, premaxilla, and vomer. In mosasaurs, the thin and bladelike septomaxilla is not in contact with the maxilla but lies dorsal to it and is sutured to the equally thin vomer (Camp, 1942). There does not appear to be any potential for independent mobility of the septomaxilla. Mosasaurs therefore differ from varanoids and other nonophidian squamates in this character. However, in shape and location, the septomaxilla in all nonophidian squamates (including mosasaurs) is radically different from (i.e., nonhomologous to) that of snakes, where the septomaxilla lies lateral to the vomer and, together with the latter, forms a chamber for Jacobson's organ, a synapomorphy of snakes. *Pachyrhachis* has to be coded as unknown (?) because the vomers are not known. Other snakes are also coded ? because the character as defined by Lee (1998) is not comparable (not applicable).

Character 86: Septomaxillae separated by cartilaginous gap (0), meeting on midline (1). We delete this character from the analysis (the coding retained in the data matrix is that of Lee, 1998) because each septomaxilla is associated with its nasal capsule, and the two septomaxillae are always separated by the cartilage of the internasal septum and trabecula communis. Observations to the contrary are artifacts of a dried skull (e.g., Bellairs & Kamal, 1981, Figs. 25, 28, 32, 65).

Character 87: Medial flange on septomaxilla short (0), long (1). Among snakes, anomalepids have no medial flange of the septomaxilla that turns upward (Haas, 1964, 1968).

Character 88: Septomaxillary roof for Jacobson's organ flat (0), domed (1).

Character 89: Opening of Jacobson's organ confluent with choana (0), separated from choana by vomer and maxilla (1), separated by vomer and septomaxilla (2).

Character 90: Vomer(s) paired (0), fused (1).

- Character 91:* Vomer without (0), with (1) extensive contact with maxilla behind Jacobson's organ.
- Character 92:* Vomer less than half as long (0), at least half as long (1) as maxilla.
- Character 93:* Vomer platelike (0), rodlike (1). As defined by Lee (1998), this character is problematic because of the apomorphic vomer configuration in snakes. Although we retain the character, we code basal snakes for a broad vomer (0). *Pachyrhachis* has to be coded as unknown (?).
- Character 94:* Vomer anterior or anteromedial to palatine (0), entirely medial to palatine (1).
- Character 95:* Secondary palate absent (0), present (1).
- Character 96:* Palatine–vomer contact short (0), extensive (1).
- Character 97:* Palatine–vomer contact immobile (0), mobile (1).
- Character 98:* Palatine as long as (0), half as long as (1) vomer. Lee (1998) codes *Pachyrhachis* as unknown (?) for characters 92 and 93 (vomer), appropriately indicating that the vomer of *Pachyrhachis* is not known, but for characters 91, 94, 96, 97, and 98, he codes *Pachyrhachis* 0 when in fact he should code it as unknown again (?).
- Character 99:* Interpterygoid vacuity extending (0), not extending (1) between palatines.
- Character 100:* Palatine without (0), with (1) distinct medial process.
- Character 101:* Choanal groove on palatine short or absent (0), long (1).
- Character 102:* Ectopterygoid–palatine contact absent (0), present (1). Lee (1998) coded mosasaurs as lacking a contact of ectopterygoid and palatine (maxilla enters suborbital fenestra), but Russell (1967) described the ectopterygoid of *Tylosaurus* and *Plotosaurus* as meeting the posterior rim of the palatine (see also McDowell & Bogert, 1954, Fig. 10). The precise disposition of these elements is not known in basal mosasauroids (aigialosaurs), for which reason we code mosasauroids as unknown (?).
- Character 103:* Suborbital fenestra large (0), small (1), absent (2).
- Character 104:* Pyriform recess open and wide (0), open and narrow (1), closed by broad parasphenoid (2).
- Character 105:* Pterygoid–vomer contact present (0), absent (1).
- Character 106:* Pterygoid with (0), without (1) triangular depression on ventral surface, extending from suborbital fenestra toward palatobasal articulation.
- Character 107:* Anterior (palatine) process of pterygoid gradually merges with (0), is distinctly set off from (1) transverse (ectopterygoid) process.
- Character 108:* Anterolateral process of pterygoid extending along lateral margin of palatine absent (0), present (1).
- Character 109:* Epipterygoid present (0), absent (1).
- Character 110:* Mandibular symphysis rigid (0), mobile (1). As coded by Lee (1998), mosasaurs and snakes share a mobile mandibular symphysis, with the anterior ends of the dentaries being smoothly rounded. Although this character is shared with other tetrapods that show an intra-mandibular joint (e.g., *Tyrannosaurus rex*: C. Brochu, personal communication), we accept this character in the present analysis for the lack of better knowledge of mosasaur symphyseal structure. A dentary of *Platecarpus* (FMNH UC 600) shows the anterior end of Meckel's groove to taper out on the medial surface of the straight dentary. It remains unknown what role Meckel's cartilage played in the formation of a mobile mandibular symphysis. In snakes, the anterior tip of the dentary is usually curved inward, and Meckel's cartilage protrudes from Meckel's canal and extends beyond the anterior tip of the dentary as it relates to ligaments, muscle fibers, and accessory cartilages (cartilago symphyseum, derived in snakes) in the formation of a mobile mandibular symphysis (Young, 1998). It is noteworthy that Meckel's cartilages

of the two mandibular ramus fuse with each other to form a true mandibular symphysis in scolecophidians (Young, 1998).

Character 111: Three or more (0), two or less (1) mental foramina on dentary. Personal inspection of the holotype of *Pachyrhachis* reveals rather extensive breakage at the anterior end of the left mandible (lateral view). In spite of retaining the character definition of Lee (1998), we point out that we can identify a single mental foramen only, which is a synapomorphy that *Pachyrhachis* shares with other snakes.

Character 112: Dentary in lateral view with straight (0), concave (1) dorsal (alveolar) margin. As defined and coded by Lee (1998), the straight dorsal margin of the dentary is a synapomorphy shared by *Pachyrhachis* and mosasaurs, but personal inspection of the holotype of *Pachyrhachis* did not allow us to determine the correct character state for this taxon, which is therefore coded as unknown (?). In addition, the dentary is slightly concave dorsally in the lower jaw of *Platecarpus* (FMNH UC 600), and it is distinctly concave in *Prognathodon* (Lingham-Soliar & Nolf, 1989), such that mosasaurs have to be coded polymorphic for this character.

Character 113: Dentary with large (0), small (1), without (2) posterodorsal process extending onto lateral surface of coronoid process. As Underwood (1957) and Gauthier (1982) have emphasized (see discussion above), there is only one logical place to put a joint in the lower jaw, i.e., between dentary and postdentary bones (in the following, all characters correlated with the differentiation of an intramandibular joint will be called dp-characters [for dentary–postdentary relation]).

Character 114: Meckel's canal an open groove (0), closed with dentary lips in sutural contact (1), closed with dentary lips fully fused (2).

Character 115: Anterior end of Meckel's canal at anteroventral margin (0), on medial surface (1) of dentary. The opening of Meckel's canal on the medial surface of the lower jaw, instead of along its ventromedial margin, is a mosasaur (mosasauroid?) autapomorphy. As discussed above, the anterior end of Meckel's canal opens ventral relative to the sagittal plane of the man-

dibular ramus in all snakes (as in all nonophidian squamates). Intramandibular muscles insert into Meckel's cartilage, which, in order to be an effective site of muscle attachment, is exposed ventromedially along the ventral edge of the lower jaw. Inspection of the holotype of *Pachyrhachis* did not reveal a position of Meckel's canal on the medial side of the dentary comparable to the mosasaur condition.

Character 116: Intramandibular septum of dentary does not approach (0), approaches or reaches (1) posteriormost tooth position. In *Varanus*, the posterior margin of the intramandibular septum lies right below the posteriormost tooth; the same is true for mosasaurs (Lingham-Soliar & Nolf, 1989). As defined by Lee (1998), the character is not applicable (not comparable) to scolecophidians (Haas, 1964, 1968). A serially sectioned head of *Anilius scytale* shows the intramandibular septum to terminate just in front of the anterior end of the compound bone, i.e., it terminates well in front of the posterior tooth. The same is true for *Cylindrophis*. In uropeltids (serially sectioned head of *Plecturus perroteti*), the intramandibular septum extends to a level posterior to the posteriormost teeth, which, by comparison to other basal alethinophidians, reflects the shortened tooth row of uropeltids. Macrostromatans become difficult to compare because of the elongated posterior dentigerous process (see character 133, below).

Character 117: Subdental shelf large (0), weak (1), absent (2). As described elsewhere (Zaher & Rieppel, 1999), the subdental shelf is a character that applies only to nonophidian squamates with labial pleurodony. It is absent in *Varanus*, mosasaurs, *Pachyrhachis*, and snakes.

Character 118: Posterior margin of lateral surface of dentary without notch (0), with shallow notch (1), with deep notch (2). This is a dp-character, which loses weight in pulling snakes to mosasaurs plus varanoids if treated unordered, as it should be. The deeply bifurcated posterior end of the dentary of *Pachyrhachis* and snakes (2) is not part of a morphocline, but results from a restructuring of the intramandibular joint, with the compound bone (surangular portion) becoming the supporting element for the dentary. To account for polymorphism in snakes, the character should be further sub-

divided to include the elongated posterior dentigerous process of the dentary, which was defined as a separate character above. In spite of these difficulties, we retain the character as defined and coded by Lee (1998).

Character 119: Overlap of dentary with postdentary bones extensive (0), reduced (1). This is another dp-character that is difficult to understand because the dentary–postdentary articulation is fundamentally different in varanoids, mosasaurs, and snakes. We propose the following redefinition of character states: dentary principally supported by coronoid, surangular, and prearticular (0, nonophidian squamates, including varanoids), by prearticular (1, mosasaurs), by surangular (2, snakes).

Character 120: Splenial large (0), small (1), absent (2). Lee (1998) coded snakes for a reduced splenial, but we code scolecophidians and macrostomatan snakes for a large splenial (0).

Character 121: Splenial overlaps postdentary bones and does (0), does not (1) expand beyond apex of coronoid process, or splenial does not substantially overlap postdentary bones (2). This is another dp-character. We find the splenial to substantially overlap the postdentary bones in *Varanus* in medial view of the mandible. This overlap is reduced in *Lanthanotus*. In ventral view of the mandible, however, the articular carries a long anterior process that broadly overlaps with the splenial. As described above, the posterior margin of the splenial of *Lanthanotus* is concave in ventral view, receiving the convex angular. In mosasaurs, there is no overlap between the splenial and the postdentary bones, but the anterior surface of the splenial is concave, receiving the convex posterior head of the articular. In snakes, the splenial–postdentary relations are as described above, with extensive overlap of the splenial with the postdentary (compound) bone in scolecophidians. In summary, we propose the following redefinition of character states: splenial overlaps with angular (0, all nonophidian squamates except mosasaurs, scolecophidians); splenial meets angular in an abutting contact, the splenial being the receiving, the angular being the received element (1, autapomorphic for mosasaurs); splenial meets angular in an abutting contact, the angular being the receiving, the splenial being the received element (2, alethin-

ophidians). *Pachyrhachis* is coded unknown (?) for this character because the detailed nature of the angular–splenial articulation remains unclear (see discussion above).

Character 122: Anterior tip of splenial on ventral margin (0), on medial surface (1) of dentary. As shown above, the position of the anterior tip of the splenial on the medial surface of the dentary is an autapomorphy (uninformative character) of mosasauroids and is therefore deleted from our analysis (the coding retained in the data matrix is that of Lee, 1998).

Character 123: Extensive (0), reduced (1) contact between splenial and dentary. As defined by Lee (1998), this character is difficult to understand. Mosasaurs have a very extensive splenial–dentary contact. In other taxa, this contact varies according to the degree to which Meckel’s canal is closed medially by the splenial. However, in all squamates examined for this paper except mosasaurs, the splenial carries a lateral shelf, which underlies Meckel’s canal and which, together with the ventral margin of the splenial, locks against the ventromedial margin of the dentary in a solid contact. In view of the autapomorphic relation of the splenial to the dentary in mosasaurs, the character becomes uninformative and is deleted from our analysis (the coding retained in the data matrix is that of Lee, 1998).

Character 124: Splenial–angular contact, in medial view, overlapping and irregular (0), straight (vertical) and abutting (1). As defined by Lee (1998), we find this character to overlap with character 121. The restriction of the view to the medial side of the mandible is artificial and does not account for the complexity and the differences of the splenial–angular relations in the different taxa. As the splenial is the receiving part of the intramandibular articulation in mosasaurs and is the received part in snakes, this character is not simply a synapomorphy linking snakes to mosasaurs as coded by Lee (1998). Given the redefinition of character 121 above, we delete character 124 from our analysis (the coding retained in the data matrix is that of Lee, 1998).

Character 125: Anteromedial process of coronoid long (0), short (1). As defined by Lee (1998), we believe this character to be misleading. As

described above, the coronoid is V-shaped in cross-section (apex pointing dorsally) and straddles the surangular in nonophidian squamates, including mosasaurs. Its anterior contact is reduced in mosasaurs as compared to *Varanus*, as is correctly coded by Lee. In snakes, the coronoid is a simple bony plate that lies against the inside of the compound bone and hence has no chance to overlap with the medial surface of the dentary. In scolecophidians, the dentary lies lateral to the coronoid (Haas, 1964, 1968), while in basal alethinophidians, the posteroventral process of the dentary (if present—vestigial or absent in uropeltids) may extend backward to a level behind the anterior tip of the coronoid (if present) and at a morphological level lateral to the coronoid. As defined, this character is not applicable (not comparable) to snakes.

Character 126: Anterolateral process of coronoid absent (0), present (1). As defined by Lee (1998), this character is not applicable (not comparable) to snakes for the same reasons as those discussed in relation to the previous character.

Character 127: Coronoid contacts (0), does not contact (1) splenial. The coronoid contacts the splenial in scolecophidians and in several basal macrostomatans. The splenial–coronoid contact appears to be variable in *Cylindrophis ruffus*. The specimen discussed above shows the absence of such a contact, which however is shown to be present in another specimen by McDowell (1975, Fig. 6). The drawing of the lower jaw of *Cylindrophis maculatus* discussed above shows the coronoid to approach the splenial very closely; serial sections show the gap between the two bones to be only 0.1 mm, which is only marginally wider than any other skull suture (syndesmosis).

Character 128: Ventral margin of coronoid straight or convex (0), concave (1).

Character 129: Subcoronoid fossa (exposing surangular on medial side of mandible) absent (0), present (1).

Characters 128 and 129: As defined by Lee (1998), dibamids should be coded 1 or polymorphic and amphisbaenians polymorphic for character 128 (straight or concave ventral margin of the coronoid). If this is done, the codings

for characters 128 and 129 become practically redundant. However, a subcoronoid fossa, exposing the surangular on the medial surface of the lower jaw, is a character that is, in fact, not applicable (not comparable) to those taxa that form a compound bone composed of surangular, prearticular, and articular. We opt for the retention of character 128 with corrected coding as indicated above and replacement of character 129 with a new character.

(Our) Character 129: Compound bone formed of surangular, prearticular, and articular absent (0) or present (1, dibamids, amphisbaenians, *Pachyrhachis*, snakes); some amphisbaenians may show incomplete fusion of the postdentary bones (Zangerl, 1944; Montero et al., 1999). *Sineoamphisbaena* shares the presence of a compound bone (Wu et al., 1996).

Character 130: Surangular extends medially to the surface of the dentary terminating in a point (0), terminating with a blunt end (1), surangular terminates with blunt end but does not extend far medial to the dentary (2), surangular extends far into lateral surface of the dentary and terminates in a point (3). This is another dp-character, which was miscoded for mosasaurs by Lee (1998). In *Varanus*, the surangular does extend medial to the dentary and terminates bluntly; probably the same is true for *Lanthanotus* (the lower jaw was not disarticulated). In mosasaurs, the surangular has no overlap at all with the dentary; instead, the overlap is with the prearticular. Dibamids and amphisbaenians should be coded as unknown. As was done by Lee (1998), *Pachyrhachis* is coded like all other snakes except for scolecophidians.

Character 131: Surangular without (0), with (1) dorsal flange overlapping posterior part of coronoid process.

Character 132: Angular present (0), absent (1).

Character 133: Angular with wide (0), with narrow or without exposure (1) on medial side of mandible.

Character 134: Fingerlike angular process present (0), absent (1).

Character 135: Prearticular does not (0), does (1) extend anteriorly past posterior dentary tooth

position(s). This is another dp-character which, as coded by Lee (1998), is a synapomorphy shared by mosasaurs, *Pachyrhachis*, and snakes. However, in mosasaurs, the prearticular extends anteriorly far beyond the posterior teeth (1). *Pachyrhachis* has to be coded as unknown (?). Scolecophidians code as 0, and alethinophidians as not comparable (?).

Character 136: Prearticular crest absent (0), moderately well developed (1), prominent (2).

Character 137: Adductor fossa faces dorsomedially (0), dorsally (1). As coded by Lee (1998), this character is difficult to assess. Following the descriptions above, we propose the following redefinition of character states: medial margin of the adductor fossa on lower jaw is low and rounded (0), developed into a distinct vertical flange (1). The coding for mosasaurs is 1, for *Pachyrhachis* is 1, and for scolecophidians is 0; anilioids are polymorphic (0 and 1), and basal macrostomatans are 1.

Character 138: Adductor fossa narrow transversely (0), inflated transversely (1). This is a synapomorphy of the Lacertoidea that reflects the entry of the posterior adductor into Meckel's canal.

Character 139: Articular fused with prearticular and surangular (0), fused with prearticular (1), separate (2). As defined by Lee (1998), this character is wrongly polarized (see our discussion of character 129).

Character 140: Retroarticular process in line with rest of mandible (0), offset medially (1).

Character 141: Retroarticular process extends straight posteriorly (0), extends posteromedially (1). As defined by Lee (1998), the character states of this character are often difficult to establish and appear to be redundant with character 140. The retroarticular process of mosasaurs is clearly deflected medially. *Varanus* has a rather straight posterior retroarticular process by comparison, but the retroarticular process of *Lanthanotus* is more distinctly medially deflected. Lee (1998) coded Serpentes as 1 but scolecophidians as 0. By comparison to other squamates, *Pachyrhachis* shares with alethinophidians a reduced, knobby retroarticular process,

which should be added as a different character state (2).

Character 142: Dorsal surface of retroarticular process with pit or sulcus (0), smoothly concave (1). Lee's (1998) coding for Serpentes is problematic. Scolecophidians have a retroarticular process that is circular in cross-section (Haas, 1964, 1968), whereas alethinophidians, including *Pachyrhachis*, are not comparable, owing to their short, knobby retroarticular process. Furthermore, the knobby process has a convex, not a concave, dorsal surface. To avoid redundancy with character 141, we propose to treat character 142 as not applicable (not comparable) to *Pachyrhachis* and snakes.

Character 143: Dorsomedial margin of retroarticular process smooth (0), with distinct tubercle or flange (1).

Character 144: Retroarticular process tapering, narrow distally (0), not tapering, broad distally (1).

Character 145: Retroarticular process not twisted posteriorly (0), twisted posteriorly (1). As defined by Lee (1998), this character is not applicable (not comparable) to *Pachyrhachis* and snakes.

Character 146: Marginal tooth implantation acrodont (0), pleurodont (1), thecodont, shallow alveoli (2), thecodont, deep alveoli (3). The premaxillary, maxillary, and dentary teeth of mosasaurs are not thecodont but modified (fully) pleurodont, as are those of varanoids. Scolecophidians likewise are pleurodont. Alethinophidia are derived by the attachment of the tooth base to circular interdental ridges, a character they share with *Pachyrhachis* (Zaher, 1998). According to our analysis of squamate tooth implantation, we propose the following redefinition of character states: tooth implantation acrodont (0), labially pleurodont (1), modified (fully) pleurodont (2, varanoids, mosasaurs, and scolecophidians), or teeth ankyloused to the rim of a shallow socket that is homologous to the interdental ridge of nonophidian squamates (3, *Pachyrhachis*, alethinophidians).

Character 147: Marginal teeth without (0), with (1) sharp carinae. *Varanus* has laterally compressed teeth with anterior and posterior cutting

edges. The same is true for mosasaurs, although their teeth are less laterally compressed. We find carinae to be either very weakly developed or absent in extant snakes. If anything is present, it is a weakly developed anterior cutting edge. *Pachyrhachis* has carinae on the lateral surface of the tooth crown, an autapomorphy of this taxon. As defined by Lee (1998), we find this character misleading and delete it from our analysis (the coding retained in the data matrix is that of Lee, 1998).

Character 148: Plicidentine absent (0), present (1). Lee codes *Pachyrhachis* 1 for the presence of plicidentine and refers to Lee and Caldwell (1998) for justification. However, Lee and Caldwell (1998, p. 1537) state that "marginal teeth are hollow cones," which was confirmed by personal observation of the holotype of *Pachyrhachis* (particularly clear in the broken anteriormost tooth of the left palatine). The presence of weak striations on the enamel surface does not, in itself, indicate the presence of plicidentine, which is the character addressed by Lee (1998). The latter taxon, as all other snakes, therefore has to be coded for the absence of plicidentine, the presence of which is a varanoid synapomorphy.

Character 149: Tooth crowns closely spaced (0), separated by wide gaps (1). As defined by Lee (1998), this character carries little phylogenetic information. The modified (fully) pleurodont teeth of varanoids have a flaring tooth base, and although the teeth meet each other at their base (i.e., narrow spacing of the tooth positions), the flaring of that base still results in a wider spacing of the tooth crowns than is characteristic for nonophidian squamates, which show labial pleurodontology (Zaher & Rieppel, 1999). In addition, the rhythm of tooth replacement in *Varanus* is timed such that the functional teeth tend to alternate with replacement teeth, which creates gaps between the functional teeth, although tooth positions are closely spaced (Edmund, 1960). Mosasaurs again show a basal contact between the teeth, i.e., closely spaced tooth positions, but because of a flaring tooth base, the tooth crowns appear more widely spaced. Flaring tooth bases and a basal contact between teeth are a derived character shared by mosasaurs and varanoids but are absent in other squamates. In spite of these problems, we retain this character in our analysis, although it ap-

pears at least partially redundant with the type of tooth implantation (character 146).

Character 150: Replacement tooth positioned lingual (0) to functional tooth, posterolingual (1) to functional tooth, or absent (2).

Character 151: Resorption pits at base of teeth (0), on bony tooth pedicel (1), absent (2). The development of resorption pits starts at the base of the teeth, i.e., in the bone of attachment, in all squamates (snakes included). However, varanoids lack the development of large resorption pits within which the replacement teeth develop and which extend into the tooth crown. Mosasaur teeth are autapomorphic in that they develop large resorption pits that hold the developing replacement teeth but remain restricted to the tall tooth base formed from the bone of attachment. Scolecophidians develop large resorption pits, but other snakes have small resorption pits, restricted to the basal bone of attachment. In light of these variations, we offer the following redefinition of character states: resorption pits large, extending into tooth crown (0); resorption pits small, restricted to bone of attachment at the base of the tooth (1, varanoids, alethinophidians); resorption pits large, restricted to tall tooth pedicel composed of the bone of attachment (2, autapomorphic for mosasaurs).

Character 152: Replacement teeth erupt upright (0), erupt horizontally (1). The horizontal position of replacement teeth is a synapomorphy of snakes (unknown in *Pachyrhachis*) that is absent in mosasaurs (Zaher & Rieppel, 1999).

Character 153: Five or more (0), four or fewer (1) premaxillary teeth.

Character 154: Median premaxillary tooth absent (0), present (1).

Character 155: Median premaxillary tooth not enlarged (0), enlarged (1).

Character 156: Premaxillary teeth similar in size to (0), distinctly smaller than (1) anterior maxillary teeth.

Character 157: Thirteen or more (0), twelve to nine (1), eight or fewer (2) maxillary tooth positions.

Character 158: Thirteen or more (0), twelve to nine (1), eight or fewer (2) dentary tooth positions.

Character 159: Palatine teeth present (0), absent (1).

Character 160: Palatine teeth small (0), similar in size to marginal teeth (1).

Character 161: Pterygoid teeth present (0), absent (1).

Character 162: Pterygoid teeth small (0), similar in size to marginal teeth (1). As defined by Lee (1998), this character is ambiguous because marginal teeth decrease in size from front to back. Pterygoid teeth, where present, are always smaller than anterior maxillary or dentary teeth in all squamates. For this reason, we delete this character from our analysis (the coding retained in the data matrix is that of Lee, 1998).

Character 163: Egg tooth single (0), paired (1).

Character 164: Centra not constricted (0), slightly constricted (1), strongly constricted (2) in front of condyle.

Character 165: Vertebral condyles facing posteriorly (0), slightly dorsally (1), dorsally (2).

Character 166: Shape of vertebral condyles in middorsal region oval (0), round (1). Lee (1998) coded snakes for a circular vertebral condyle (1), but scolecophidians, various anilioids, and macrostomatans all have a vertebral condyle with an oval outline and are coded accordingly (0).

Character 167: Centra notochordal (0), not notochordal (1).

Character 168: Neural spines tall processes (0), low ridges (1).

Character 169: Zygosphenes and zygantra present (0), absent (1).

Character 170: Articular surface of zygosphene faces dorsally (0), lateroventrally (1).

Characters 169 and 170: As defined by Lee (1998), these characters are redundant and have

to be combined into one: zygosphene-zygantrum absent (0); present with zygosphene articular surface facing laterodorsally (1, Lacertidae, Cordylidae, Gerrhosauridae: Hoffstetter & Gasc, 1969, Fig. 42); present with zygosphene articular surface facing ventrolaterally (2, mosasaurs, snakes, Teiidae, Gymnophthalmidae). We code character 169 accordingly but delete character 170 from the analysis (the coding retained in the data matrix is that of Lee, 1998).

Character 171: Dorsal intercentra present (0), absent (1).

Character 172: Presacral vertebrae 22 or fewer (0), 23 to 25 (1), 26 (2), 27 to 50 (3), 50 to 119 (4), 120 or more (5).

Character 173: Cervical vertebrae seven or fewer (0), eight (1), nine or more (2).

Character 174: Hypapophyses present on fourth to sixth presacral (0), on seventh presacral and beyond (1). As defined by Lee (1998), this character is based on arbitrary morphological distinctions. The number of cervical hypapophyses is increased in varanoids because of an elongation of the neck (character 173). Note that *Varanus* has nine cervicals with hypapophyses, whereas mosasaurs have eight or seven cervicals (Russell, 1967). According to Russell, only the anterior six or seven cervicals carry hypapophyses in mosasaurs (in Mososauridae indet., FMNH PR 2103, the last hypapophysis is on the sixth cervical). Snakes are not comparable because they have no easily defined cervical region of the vertebral column and the hypapophyses extend backward far into the trunk, suggesting the presence of dorsal intercentra (absent in nonophidian squamates other than geckos). In the posterior trunk region, the hypapophyses are reduced to a hemal keel, but they may be reduced more anteriorly also in burrowing species (Hoffstetter & Gasc, 1969). A redefinition of character states could account for the number of cervical vertebrae (not applicable, i.e., not comparable to snakes) or the presence versus absence of trunk intercentra. In view of the difficulties of establishing clear-cut character state relations beyond autapomorphies, we delete this character in our analysis (the coding retained in the data matrix is that of Lee, 1998).

- Character 175:* Dorsoposterior flange on atlas neural arch present (0), absent (1).
- Character 176:* Cervical intercentral not sutured nor fused (0), sutured (1), fused (2) to preceding centrum.
- Character 177:* Cervical intercentra neither sutured nor fused (0), sutured (1), fused (2) to following centrum.
- Character 178:* Caudal transverse processes single (0), double (1) in some caudals.
- Character 179:* Caudal transverse processes: two prongs converge (0), diverge (1) distally.
- Character 180:* Caudal transverse processes project laterally or posterolaterally (0), anterolaterally (1).
- Character 181:* Caudal autotomy septa present (0), absent (1).
- Character 182:* Caudal autotomy septa anterior to or within (0), posterior to (1) transverse processes. The distinction of two character states appears arbitrary because, in some nonophidian squamates, the autotomy septum is anterior, in others it is within, and in still others it is posterior to the transverse processes (the coding retained in the data matrix is that of Lee, 1998).
- Character 183:* Pedestals on caudal vertebrae for chevrons weakly developed (0), prominent (1).
- Character 184:* Chevrons articulate with (0), fused to (1) caudal centra.
- Characters 183 and 184:* For reasons discussed below (character 185), we consider chevrons to be absent in snakes rather than co-ossified with the centrum, as was assumed by Lee (1998).
- Character 185:* Caudal chevron positioned at (0), in front of (1) posteroventral margin of centrum. As defined by Lee (1998), this character is not applicable (not comparable) to snakes, which have no chevrons but have hemapophyses instead (Hoffstetter & Gasc, 1969), and these are located at the posterior end of centrum. As coded by Lee (1998), mosasaurs share with varanoids the anterior shift of the chevrons.
- Character 186:* First rib on third (0), fourth (1) cervical vertebra. This character is not applicable to snakes.
- Character 187:* Proximal end of rib without (0), with (1) anteroventral pseudotuberculum.
- Character 188:* Proximal end of rib without (0), with (1) posteroventral pseudotuberculum.
- Character 189:* Lymphapophyses ("forked cloacal ribs" of Lee, 1998) absent (0), present (1). Lee and Caldwell (1998) described a distally expanded sacral rib for *Pachyrhachis* and hypothesized that the appearance of its distal bifurcation might be due to breakage. Lee (1998) codes the distally forked sacral rib of *Pachyrhachis* as comparable to the distally forked cloacal ribs of other snakes, amphisbaenians, and dibamids. Indeed, *Pachyrhachis* shows at least one well-developed lymphapophysis (the sacral rib of Lee & Caldwell, 1998), but the presence of additional, more posteriorly located lymphapophyses cannot be assessed owing to poor and/or incomplete preservation. In those basal snakes that retain limb rudiments, these do not establish contact with the lymphapophyses, and the same might have been true of *Pachyrhachis*.
- Character 190:* Scapulocoracoid large (0), reduced (1), absent (2).
- Character 191:* Emarginations on anterodorsal edge of scapula absent (0), present (1).
- Character 192:* Anterior coracoid emargination absent (0), present (1).
- Character 193:* Posterior coracoid emargination absent (0), present (1).
- Character 194:* Clavicle present (0), absent (1).
- Character 195:* Clavicle follows anterior margin (0), curves anteriorly away from (1) scapulocoracoid.
- Character 196:* Clavicles rodlike (0), expanded proximally with proximal notch or fenestra (1).
- Character 197:* Interclavicle present (0), absent (1).
- Character 198:* Interclavicle cross-shaped (0), simple rod (1).

- Character 199:* Anterior process of interclavicle short or absent (0), long (1).
- Characters 197 and 198:* The interclavicle of nonophidian squamates shows greater complexity than is expressed by these two characters (Camp, 1923). The absence of an anterior process (character 199) may result in a T-shaped or arrow-shaped interclavicle (the coding retained in the data matrix is that of Lee, 1998).
- Character 200:* Ossified (should read calcified) sternum present (0), absent (1).
- Character 201:* Sternal fontanelle absent (0), present (1).
- Character 202:* Five (0), four (1), three (2), two or fewer (3) pairs of ribs attach to the sternum.
- Character 203:* Postxiphisternal inscriptional ribs not united (0), one or more pairs united along ventral midline (1).
- Character 204:* Forelimbs large (0), small or absent (1).
- Character 205:* Ectepicondylar foramen on humerus present (0), absent (1).
- Character 206:* Pelvis large (0), reduced (1), absent (2).
- Character 207:* Pelvic elements co-ossified into single bone (0), strongly sutured to one another (1), weakly united in nonsutural contacts (2). As defined by Lee (1998), this character is difficult to assess throughout squamates. The skeleton of mosasaurs, like that of other marine reptiles, is subject to skeletal paedomorphosis (Sheldon, 1997; see also Rieppel, 1993a), which accounts for the reduced ossification of the pelvic elements (joined together by cartilage in life). However, the pelvic elements are firmly sutured to one another in basal mosasauroids (aigialosaurs: Carroll & deBraga, 1992), which were coded accordingly (1). The pelvis of *Pachyrhachis* is much reduced by comparison to that of mosasaurs, which could be a consequence of its marine habits or of its being a snake, or both. The pelvic rudiments of other snakes are not easily comparable.
- Character 208:* Sacral blade of ilium with (0), without (1) anterior process.
- Character 209:* Pubis short, symphyseal process directed ventrally (0), intermediate in length, symphyseal process directed anteroventrally (1), elongated, symphyseal process directed anteriorly (2). As defined by Lee (1998), this character is difficult to understand. The pubis points anteroventrally in all nonophidian squamates (except mosasaurs), with a medial inclination to form the pubic symphysis. In mosasaurs, the pubis lies horizontally and points medially to form the symphysis (Russell, 1967). The pubis in *Pachyrhachis* is dislocated and its natural orientation unknown. It also remains unknown whether *Pachyrhachis* had a pubic symphysis. To these problems of comparison, we add the observation that coding of the hind limb in *Pachyrhachis* can severely skew the analysis, depending into how many characters the hind limb is atomized. We delete character 209 from our analysis (the coding retained in the data matrix is that of Lee, 1998).
- Character 210:* Pubic tubercle on posterodorsal end of pubis (0), on shaft of pubis (1).
- Character 211:* Hind limbs well developed (0), rudimentary or absent (1). We adopt Lee's (1998) coding (1) for *Pachyrhachis* but note that the incompleteness of its limb (all elements distal to astragalus and calcaneum missing) appears to be an artifact of preservation.
- Character 212:* Femur gracile (0), stout (1). Lee (1998) coded a stout femur as a derived character state shared by *Pachyrhachis* and mosasaurs. Although we retain his coding, we note that the femur of mosasaurs is modified to form the proximal element in a paddle; that of *Pachyrhachis* is crushed (see also character 213, below).
- Character 213:* Femur curved (0), not curved (1) in dorsoventral plane. Lee (1998) coded *Pachyrhachis* and mosasaurs for a straight femur. In fact, the two taxa are not comparable in femur morphology. The femur of mosasaurs is much reduced in length but broadened as a consequence of the limb having been transformed into a paddle. By comparison, the femur of *Pachyrhachis* is elongate and relatively slender (some of the robustness of the femur of *Pachyrhachis* is due to crushing). The diaphysis of mosasaurs retains a distinct biconcave shape, which is not expressed in *Pachyrhachis* (another

er consequence of crushing?). Given the compression of the femur, the character state for character 213 also cannot be identified for *Pachyrhachis*. In view of these differences, and because this character is partially redundant with character 212, we delete character 213 from our analysis (the coding retained in the data matrix is that of Lee, 1998).

Character 214: Distal end of tibia gently convex (0), with notch fitting into a ridge on astragalocalcaneum (1). As defined by Lee (1998), this character is difficult to understand. In fact, this character reflects little more than the absence of separate epiphyseal ossification centers in mosasaurs, which is again due to skeletal paedomorphosis, whereas *Pachyrhachis* may lack separate epiphyseal ossification centers because of its marine habits or because it is a snake, or both (all snakes lack separate epiphyseal ossification centers: Haines, 1969). As such, this character is redundant with character 228 and hence is deleted from our analysis (the coding retained in the data matrix is that of Lee, 1998).

Character 215: Astragalus and calcaneum fused (0), separate (1) in adult. This character is coded by Lee (1998) as another putative synapomorphy of mosasaurs and *Pachyrhachis*, but the lack of fusion of astragalus and calcaneum in mosasaurs is again due to skeletal paedomorphosis (marine). The character is furthermore subject to ontogenetic variation among other nonophidian squamates yet is not applicable (not comparable) to other snakes. To these problems of comparison, we add the observation that coding of the hind limb in *Pachyrhachis* can severely skew the analysis, depending on whether features of the hind limb are lumped into few or split into many characters. In spite of these problems, we retain this character, as it adds to the strength of the test of the phylogenetic position of *Pachyrhachis* as sister taxon of Macrostromata (see further comments below).

Character 216: Dorsal body osteoderms absent (0), present (1).

Character 217: Ventral body osteoderms absent (0), present (1).

Character 218: Separable cranial osteoderms ab-

sent (0), present on periphery of skull table (1), present across entire skull table (2).

Character 219: Separable cranial osteoderms few and large (0), many and small (1).

Character 220: Separable cranial osteoderms tightly connected to skull roof (0), loosely connected to skull roof (1).

Character 221: Rugosities on skull roof formed by overlying cephalic scales absent (0), with vermiculate sculpture (1), without vermiculate sculpture (2).

Character 222: Scleral ossicles present (0), absent (1).

Character 223: Fifteen or more (0), 14 (1), 13 or fewer (2) scleral ossicles.

Character 224: Scleral ossicle shape complex and irregular (0), square (1).

Character 225: Second epibranchials present (0), absent (1) in hyoid skeleton.

Character 226: Second ceratobranchials present (0), absent (1) in hyoid skeleton.

Character 227: Epiphyses on skull and axial skeleton present (0), absent (1).

Character 228: Epiphyses on appendicular skeleton present (0), absent (1).

Character 227 and 228: As defined and coded by Lee (1998), these two characters are redundant and should be coded as a single character. The only difference recorded by Lee (1998) is the polymorphic coding of mosasaurs for the presence of separate epiphyseal ossification centers in the appendicular skeleton of mosasaurs. Bell (1997) describes the variable development of epiphyses on postcranial elements of mosasaurs, but from his description it is not entirely clear what exactly his understanding is of the term epiphysis or, more exactly, of a separate epiphyseal ossification center. We were unable to confirm the presence of separate epiphyseal ossification centers on postcranial elements of mosasaurs in the Field Museum collections. Separate epiphyseal ossification centers are present, however, in stem-group mosasauroids

(Carroll & deBraga, 1992). In summary, characters 227 and 228 are therefore redefined as a single character (227): separate epiphyseal ossification centers present (0, nonophidian lepidosaurs), absent (1, snakes). Because of the ambiguities of description and the presence of epiphyses in stem-group mosasauroids, mosasaurs are coded polymorphic for this character in our analysis. Character 228 is deleted from our analysis (the coding retained in the data matrix is that of Lee, 1998).

Character 229: Epiphyses fuse to diaphyses of long bones at the same time or after (0), before (1) fusion of braincase elements.

Character 230: Postcloacal bones absent (0), present (1).

To those characters of Lee, we add the following three characters, which emerged from the character discussion above:

Character 231: Medial ventral flanges of frontal, separating olfactory tracts from one another, absent (0), present (1). This character is a synapomorphy of Alethinophidia, absent in *Dinilyisia* (Estes et al., 1970), and unknown in *Pachyrhachis*.

Character 232 (new): Cartilaginous processus ascendens of supraoccipital present (0, mosasaurs, *Varanus*, indeed all nonophidian squamates except Gekkota and *Dibamus*), absent (1, Gekkota, *Dibamus*, snakes). Amphisbaenia (and *Sineoamphisbaena*), as well as *Pachyrhachis* and *Dinilyisia*, have to be coded as unknown (?).

Character 233: Elongated posterior dentigerous process of dentary absent (0), present (1). This character is a potential synapomorphy shared by *Pachyrhachis* and macrostomatans (Zaher, 1998).

The list of characters used by Lee (1998) does not include some features that were subject to controversy in the analysis of the relationships of *Pachyrhachis* within squamates by Caldwell and Lee (1997), Lee and Caldwell (1998), and Zaher (1998). We propose to critically review these characters in comparison to those of Lee (1998).

Below follows a list of the characters used by Caldwell and Lee (1997; abbreviated as C1 to C8) in support of a sister-group relationship of scolecophidians and al-

ethinophidians at the exclusion of *Pachyrhachis*. The number in parentheses preceded by a D refers to the corresponding character in Lee and Caldwell (1998).

C1 (D1): Jugal present (0), absent (1). A jugal is here considered to be absent in *Pachyrhachis*. This feature is coded under character 12 (see above).

C2 (D3): Posterior orbital margin complete (0), incomplete (discontinuous) (1). We interpret the purported jugal in *Pachyrhachis* to be part of the ectopterygoid (its anterior ramus). *Pachyrhachis* had an incomplete posterior orbital margin similar to bojids (i.e., with a long postorbital, almost touching the dorsal surface of the ectopterygoid). This character is coded under character 29 (see above).

C3 (D4): Exoccipitals not in contact (0), in contact (1) dorsal to the foramen magnum. As pointed out by Zaher (1998) and acknowledged by Lee (1998, p. 442), this character cannot be scored in *Pachyrhachis* owing to the poorly preserved condition of the skull in this area. This character is thus not included in the present analysis.

C4 (D5): Angular–coronoid contact absent (0), present (1). The contact is absent in *Leptotyphlops* (McDowell & Bogert, 1954, Fig. 13; personal observation), uropeltids (Figs. 9, 10), *Xenopeltis* (Hoge, 1964, Figs. 1, 2), *Corallus* (Kluge, 1991, Fig. 14), and *Candoia* (McDowell, 1979, Fig. 4), and it is variable in *Typhlops* (see Haas, 1930, Figs. 34, 41), *Cylindrophis* (Figs. 7, 8), *Loxocemus* (McDowell, 1975, Fig. 6; Kluge, 1991, p. 37), *Eunectes* (personal observation), and *Boa* (Kluge, 1991, p. 37; Fig. 14). Contrary to Lee's (1998, p. 442) claim that Kluge (1991) indicated "that the contact is present in anilioids," this author (Kluge, 1991, p. 37) pointed out that only some erycines (*Eryx*) and anilioids (*Cylindrophis*) "have a coronoid–angular contact." Personal observations corroborated Kluge's observations on erycines and demonstrated that *Cylindrophis* is variable in respect to this character. All snake terminal taxa (except *Dinilyisia*, as pointed out by Lee, 1998) used in this study, including basal anilioids and basal macrostomatans, are variable with respect to this character, precluding its use in a phylogenetic analysis.

C5 (D6): Mental foramina on dentary, two or more (0), one (1). As already pointed out above (see character 111), *Pachyrhachis* retains only one foramen, as in other snakes. This character is coded under character 29 (see above).

Character 234 (C6 [D8]): When present, the pelvis is external to the rib cage, sacral contacts usually present (0), lies within rib cage, sacral contact absent (1). This feature has been added to the data matrix as character 234. *Dibamids* show state 1.

Character 235 (C7 [D10]): Femur well developed (0), small (1), vestigial or lost (2). This feature has been added to the data matrix as character 235.

Character 236 (C8 [D11]): Tibia, fibula, astragalus, and calcaneum present (0), absent (1). This character has been added to the data matrix as character 236. Dibamids are coded 0, although tibia and fibula only are present in the hind limb of *Dibamus* (Greer, 1985).

Characters 235 and 236: We note that the coding of the limb in *Pachyrhachis* may be problematic because of the potential of oversplitting the character of the presence of a limb. It is obvious that the more limb characters that are included in the analysis, the more *Pachyrhachis* will be pulled toward the root of the ophidian clade, as its most basal member (Lee & Caldwell, 1998). However, in this analysis, we opt for the retention of these limb characters, as they add to the severity of the test of the hypothesis that *Pachyrhachis* is the sister taxon of Macrostromata (Zaher, 1998).

Lee and Caldwell (1998, p. 1550) proposed three additional characters:

D2: Squamosal present (0), absent (1). We interpret the squamosal of *Pachyrhachis* as identified by Lee and Caldwell (1998) as the shaft of the stapes. *Pachyrhachis* lacks a squamosal. This feature is coded in the present study as character 40 (see above).

D7: Neural spines well developed (0), reduced (1). *Pachyrhachis* and macrostomatans share character state 1, whereas the other snakes (including *Dinilysia*) show character state 0. This feature has been coded as character 168 (see above).

Lee and Caldwell (1998, p. 1550) also listed four characters (E1 to E4) found in *Pachyrhachis* and alethinophidian snakes. Among these, three (E1, E2, E3) were discussed by Zaher (1998). Only character E4 is added here as follows:

Character 237 (E4): Palatine short and broad (0), narrow and long (1). As pointed out by Lee and Caldwell (1998), the palatine of *Pachyrhachis* and alethinophidian snakes is a long, narrow element. It is short and broad in *Dinilysia* and short (vestigial?) in scolecophidians. This character is added to the present data matrix as character 237.

Below follows a list of the characters used by Zaher (1998) and retained in the present study:

18: Quadrate anteriorly directed (0), vertically or posteriorly directed (1). This character was discussed above as character 50.

Character 238 (19): Tooth-bearing anterior process of the palatine absent (0), present (1). This character is added to the data matrix as character 238.

20: Free-ending process of the supratemporal absent (0), present (1). This feature has been coded as character 47 (see above).

21: Dorsal surface of the prootic not concealed (0), concealed by the supratemporal (1). This character is here deleted from the analysis, as it is correlated with the elongation of the supratemporal (Lee, 1998).

22: Basipterygoid process well developed, with articulating surface facing more laterally than ventrally (0), reduced, with articulating surface facing ventrally (1). This feature has been discussed under character 74 (see above).

Character 233 (23): Posterior dentigerous process of the dentary absent (0), short (1), enlarged (2). This feature has been modified to a binary character (dentigerous process absent [0] or present [1]) and has been added to the data matrix as character 233.

Character 239 (24): Suprastapedial process of the quadrate present (0), absent (1). Contrary to Lee (1998, p. 443), a suprastapedial process is present and well developed in typhlopids, less developed in anomalepids, and ill-defined or absent in leptotyphlopids. Scolecophidians are thus considered to retain a suprastapedial process. This feature has been added to the data matrix as character 239.

Character 240: Jugal present (0), absent (1). For further details see the discussion of character 12.

Cladistic Analysis

The cladistic analysis presented below is not intended to assess global squamate interrelationships, but should rather be viewed as a test of the conclusions reached by Lee (1998). As indicated in the character discussion above, we believe that

TABLE 1. The data matrix used to analyze the interrelationships of the fossil snake *Pachyrhachis*. Character definitions and discussion are given in the text.

Pachyrhachis 1		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
		ign./de														
1	Kuehneosauridae	?	?	0	0	0	0	0	0	0	?	?	0	0	0	0
2	Marmoretta	0	0	0	0	0	0	0	0	?	?	0	0	?	?	0
3	Rhynchocephalia	?	1	0	0	0	0	0	0/1	0	0	0	0	0	0	0
4	Ancesor	0	0/1	0	0	0	0	0	0	0	0	0	0	0	0	0
5	Iguanidae	0	0	0	0/1	0	0	0	0	0	0	0	0	1	0	0
6	Agamidae	0	0/1	0	0	0	0	0	0/1	0	0	0	0	0/1	0	0
7	Chamaeleonidae	?	?	0	0	0	0	0	0/1	0	0	0	0	1	0/1	0
8	Xantusiidae	1	1	0	0	0	0	0	?	?	0	0	0	0	0	1
9	Gekkonidae	1	1	0	0	0	0	0	1	?	0	0	0	0/1	0	0/1
10	Pygopodidae	1	0/1	0	0	0	0	0	1	?	0	0	0	0	0	0/1
11	Sineoamphisbaena	1	?	0	0	0	1	0	0	1	0	?	0	1	0	0
12	Dibamidae	1	0	0	0	0	0	0	1	?	0	0	1	?	0	1
13	Amphisbaenia	1	1	0	0	0	0/1	0/1	1	?	0	0	1	?	0	1
14	Lacertidae	1	1	0	1	0	0	0	0	0	0	0	0	0/1	0	1
15	Teiidae	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0/1
16	Gymnophthalmidae	1	0	0	1	0	0	0	0/1	0/1	0	0	0	1	0	0/1
17	Cordylidae	0	0/1	0	0	0	0	0	0	0	0	0	0	0/1	0	0
18	Scincidae	0/1	1	0	0	0	0	0	0/1	0	0	0	0	0/1	0	0/1
19	Anguidae	0/1	1	0	0	0	0	0	0	0	0	0	0	1	0	0/1
20	Xenosauridae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
21	Heloderma	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
22	Lanthanotus	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0
23	Varanus	0	0	0	0	1	0	1	0	0	1	0	0	1	0/1*	?
24	Mosasauroidea	0	0	0	0	1	0	1	0	0	0	1	0	1	0	?
25	Pachyrhachis	?	?	1	0	0*	0	0	1	?	?	0	1*	?	?	?
26	Scolecophidia	0	?	1	0	0	0	0	1	?	?	0	1	?	0/1	0
27	Dinilysia	0	?	1	?	0	0	0	1	?	?	0	0*	?	0	0
28	Anilloidea	0	?	1	0	0	0	0	1	?	?	0	1	?	0	0
29	Macrostromata	0	?	1	0	0	0	0	1	?	?	0	1	?	0	0

Pachyrhachis 2		16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
		ord.														
1	Kuehneosauridae	0	0/1	1	0	0	0	0	0	0	0	0	0	0	0	0
2	Marmoretta	0	0	0	0	?	0	0	0	0	0	?	0	0	0	1
3	Rhynchocephalia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0/1
4	Ancesor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0/1
5	Iguanidae	0	1	0	1	1	1	0	1/2	0	0	0	0	0	0	1
6	Agamidae	0	1	0	1	1	1	0	2	?	0	0	0	0	0	1
7	Chamaeleonidae	1	1	0	0	1	0	0/1	2	?	0	0	0	0	0	1
8	Xantusiidae	0	0	0/1	1	0	1	0	0	?	1	0	1	?	0	0/1
9	Gekkonidae	0	0	0	1	0	1	0	0	?	1	0	1	?	2	0/1
10	Pygopodidae	0	0	0	0/1	0	1	0/1	0	?	1	0	1	?	2	0
11	Sineoamphisbaena	0	1	1	0	0	1	1	0	1	0	0	0	0	0	0
12	Dibamidae	0	0	1	0	0	1/3*	0	1/2	?	0&1	0	1	?	2	1
13	Amphisbaenia	0	0	1	0/1	0	0*	0	2	?	0	0	1	?	2	1
14	Lacertidae	0	0	1	1	0	0	0	0	?	1	1	1	?	0	1
15	Teiidae	0	0	0	1	0	0/1	0	0	0/1	1	0	0	1	0	1
16	Gymnophthalmidae	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1
17	Cordylidae	0	0	0/1	1	0	0/1	0	0	0	1	0/1	0	1	0	1
18	Scincidae	0	0	1	1	0	1	0	0	0/1	1	0/1	0/1	1	0	1
19	Anguidae	0	0	0/1	1	0	1	0/1	0	0/1	1	1	0	1	0	1
20	Xenosauridae	0	0	0/1	1	0	1	0	0	1	1	1	0	1	0	1
21	Heloderma	0	0	1	0	0	1	1	0	?	0	0	1	?	0	1
22	Lanthanotus	1*	0	1	0	0	1	1	0	?	1	0	1	?	0	1
23	Varanus	2	0	1	1	0	1	0	0	1	1	1	0	1	1	1
24	Mosasauroidea	2	0	0	1*	0	2*	0	0	1	1	0/1	0	1	0	1
25	Pachyrhachis	?	?	1	0	?	1	?	?	?	?	0	0	0	1	1
26	Scolecophidia	1	0	1	0	0	1&3	?	2	?	?	0	1	?	?	0/1
27	Dinilysia	?	0	1	0	0	0	0	1	0	?	0	0	1	2	1
28	Anilloidea	1	0	1	0	0	3	1	2	?	?	0	0&1	1	2	1
29	Macrostromata	1	0	1	0	0	1	0	2	?	?	0	0	0&1	1&2	1

TABLE 1. *Continued.*

Pachyrhachia		3														
		3 1	3 2	3 3	3 4	3 5	3 6	3 7	3 8	3 9	4 0	4 1	4 2	4 3	4 4	4 5
					ord.	ord.										
1	Kuehneosauridae	1	0	0	1	1	0	0	0	0/1	0	0	0	0	0	?
2	Marmoretta	0	0	1	?	2	?	?	0	0	?	?	0	0	?	?
3	Rhynchocephalia	0	0	0	0	1	0/1	0	0	1	0	0	0	0	0	0
4	Ancēstor	0	0	0/1	0/1	1/2	0	0	0	0/1	0	0	0	0	0	0
5	Iguanidae	0/1	0	0	1	0/1	0	0	0	1	0	0	0	0	1	1
6	Agamidae	0/1	0	0	1	0/1	0	0	0	1	0	0	0	0	1	1
7	Chamaeleonidae	0/1	0	0/1	2	1/2	1	0	0	1	0	0	0	0	1	1
8	Xantusiidae	0	0	0/1	0	0	1	1	0	0	0	1	1	0	1	1
9	Gekkonidae	1	0	1	?	0	0	0/1	1	?	0	1	0	0	0/1	1
10	Pygopodidae	1	0	1	?	0	0	0	1	?	0	1	0	0	0	?
11	Sineoamphisbaena	1	0	1	?	0	0	0	0	1	0	1	1	0	0	?
12	Dibamidae	1	1	1	?	2	0	0/1	1	?	?	1	0	0	?	?
13	Amphisbaenia	1	1	1	0	2	0/1	1	1	?	1	?	0	0	0	?
14	Lacertidae	0	0	0	0	0	1	0	0	0	0	1	0	1	1	1
15	Teiidae	0	0	0	0	1/2	0	0	0	0/1	0	1	0	0	1	1
16	Gymnophthalmidae	0	0	1	?	0/1	0	0	0	0	0	1	0/1	0	1	1
17	Cordylidae	0/1	0	0/1	0	0	0/1	0	0	0	0	1	1	0	1	1
18	Scincidae	0/1	0	0	0	0	0	0	0	0	0	1	0	1	1	1
19	Anguidae	1	0	0	0	0/1	0	0	0	0	0/1	1	0/1	0	0/1	1
20	Xenosauridae	1	0	0	0	0/1	0/1	0	0	0/1	0	0/1	0	0	1	1
21	Heloderma	1	0	1	?	0	0	0	1	?	0	1	0	0	1	1
22	Lanthanotus	1	0	1	?	1	0	0	1	?	0	1	0	0	1	1
23	Varanus	1	0	0	0	1	0	0	0	0	0	1	0	0	1	1
24	Mosasauroidea	1	0	0	0	1	?	0	0	0	0	0/1	0	0	1	1
25	Pachyrhachis	1	0	1	?	2	0	1	1	?	1*	??	??	??	1	0
26	Scolecophidia	1	0	1	?	2	0	1	1	?	1	?	?	?	1	0
27	Dinilysia	1	0	1	?	2	0	1	1	?	1	?	?	?	1	0
28	Anilioidea	1	1	1	?	2	0	1	1	?	1	?	?	?	1	0
29	Macrostromata	1	0	1	?	2	0	1	1	?	1	?	?	?	1	0

Pachyrhachia		4														
		4 6	4 7	4 8	4 9	5 0	5 1	5 2	5 3	5 4	5 5	5 6	5 7	5 8	5 9	6 0
		*		delete		ord.	ord.						delete			
1	Kuehneosauridae	?	?	?	4	1	0	0	0	0	?	0	?	?	0	?
2	Marmoretta	?	?	?	?	1	0	0	0	0	?	0	?	?	0	?
3	Rhynchocephalia	1*	0	0	0	1	0	0	0	0	0	0	?	0	0	0
4	Ancēstor	1*	0	0	0/4	1	0	0	0	0	0	0	?	0	0	0
5	Iguanidae	1*	0	0	1	1	0	0/1	0	0	0	0	?	1	0	0
6	Agamidae	1*	0	0	1	1	0	1	0	0	0	0	?	1	0	0
7	Chamaeleonidae	1*	0	0	1	1	2	1	0	0	0	0	?	1	0	0
8	Xantusiidae	1*	0	0	1	1	0	1	1	0/1	0	1	0	1	0	0
9	Gekkonidae	1*	0	0	3	1	0	1	1	1	0	0	?	1	0	0
10	Pygopodidae	1*	?	?	3	1	0	1	1	1	0	0	?	1	0	0
11	Sineoamphisbaena	??	?	?	?	1	2	1	1	1	1	1	0	0	0/2	1/2
12	Dibamidae	0*	?	?	3	1	2	0/1	1	1	0	1	1	0	0	?
13	Amphisbaenia	??	?	?	3	1*	2	1	1	1	1	1	1	0	2	2
14	Lacertidae	1*	0	0	1	1	0	0	1	0	0	0	?	1	0	0
15	Teiidae	1*	0*	0	1	1	0	0	0	0	0	1	0	1	0	0
16	Gymnophthalmidae	1*	0	0	1	1	0	0	1	0/1	0	1	0	1	0	0
17	Cordylidae	1*	0	0	1	1	0	1	1	0	0	1	0	1	0	0
18	Scincidae	1*	0	0	1	1	0	1	1	0	0	0/1	0	1	0	0
19	Anguidae	1*	0	0	1	1	0/1	1	1	0	0	0/1	1	1	0	0
20	Xenosauridae	1*	0	0	1	1	0	1	1	0	0	0	?	1	0	0
21	Heloderma	1*	0*	0	1	1	0	0	1	1	0	0	?	1	0	0
22	Lanthanotus	1*	0*	0	1	1	1	1	1	0	0	0	?	1	0	0
23	Varanus	1*	0*	0	1	1	1	1	1	1	0	0	?	1	0	0
24	Mosasauroidea	1	0*	1	1*	2	0	1	1	0	0	0*	1	1*	0	0
25	Pachyrhachis	0*	1	1	2	3*	2	1	?	?	0	1	1	?	1	??
26	Scolecophidia	0	0	1	3	0	2	1	1	2	0	1	1	0	1	1
27	Dinilysia	0	0	1	2	2	2	1	?	2	0	1	1	0	1	?
28	Anilioidea	0	0	1	2	2	2	1	1	2	0	1	1	0	1	1/3
29	Macrostromata	0	1	1	2	3	2	1	1	2	0	1	1	0	1	3/4

TABLE 1. *Continued.*

Pachyrhachis	5	6 1	6 2	6 3	6 4	6 5	6 6	6 7	6 8	6 9	7 0	7 1	7 2	7 3	7 4	7 5
		delete	delete		delete				delete							
1	Kuehneosauridae	0	?	0	?	?	?	?	?	?	?	0	?	?	0	0
2	Marmoretta	?	?	?	?	?	?	0	?	?	?	?	?	?	0	0
3	Rhynchocephalia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	Iguanidae	0	0	0	0/1	0/1	0	0	0	0	0	0	0	0	0	0/1
6	Agamidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	Chamaeleonidae	0	?	0	0	0	0	0	0	0	1	0	0	0	0	0
8	Xantusiidae	0	?	0	1	1	0	1	0	0	0	0	0	0	0	0
9	Gekkonidae	0	0	0	1	1	0	0/1	0	0	0	0	0	0	0	0
10	Pygopodidae	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0
11	Sineoamphisbaena	1	?	?	?	?	0	0	0	?	1	1	1	0	0	0
12	Dibamidae	0	?	0	0	?	2*	0	0	1	1	1	1	0	0	0
13	Amphisbaenia	1	1	2	1	?	2*	0	0	1	1	1	1	0	0/1	0
14	Lacertidae	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1
15	Teiidae	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
16	Gymnophthalmidae	0	?	0	1	1	0	0/1	0	0	0	0	0	0	0	0
17	Cordylidae	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
18	Scincidae	0	0	0	1	1	0	0	0	0	0	0	0/1*	0	0	0/1
19	Anguidae	0	0/1	0	1	1	0/1	0	0	1	0	0	0/1	0	0	0
20	Xenosauridae	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0
21	Heloderma	0	?	0	1	1	1*	0	0	1	0	0	0	0	0	1
22	Lanthanotus	0	?	0	1	1	1	0	1	1	0	0	0	0	0	1
23	Varanus	0	0	0	1	1	0	0	1	1	0	0	0	0	0	1
24	Mosasauroidea	0*	1	0	1	1	0	0	1	1	0	0	0	0*	1	1
25	Pachyrhachis	2	1	1	1	?	?	?	?	?	?	?	?	?	?	?
26	Scolecophidia	2	1	1	?	?	2	0	1	1	0	1	1	1	?	?
27	Dinilysia	2	1	1	?	?	2	0	?	?	0	1	1	1	?	?
28	Anilioidea	2	1	1	?	?	2	0	1	1	0	1	1	1	?	?
29	Macrostromata	2	1	1	?	?	2	0	1	1	0	1	0&1	1	?	?

Pachyrhachis	6	7 6	7 7	7 8	7 9	8 0	8 1	8 2	8 3	8 4	8 5	8 6	8 7	8 8	8 9	9 0
		ord.				ord.				delete		delete				
1	Kuehneosauridae	0	?	?	?	?	0	0	0	0	?	?	?	?	?	?
2	Marmoretta	0	0	0	?	?	?	0	?	?	?	?	?	?	?	?
3	Rhynchocephalia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	Iguanidae	0	0	0	0	0*	0	1	0	0	0/1*	0	0	0	0	0
6	Agamidae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
7	Chamaeleonidae	0	0	0	0	0*	0	1	0	0	?	?	?	?	0	1
8	Xantusiidae	0	0/1	0	0	0*	0	1	1	0	0	1	0	1	0/1	1
9	Gekkonidae	1	0	0	0	0/1*	0	1	1	0	0	1	0	1	0	0/1
10	Pygopodidae	1	0	0	0	1/2*	0/1*	1	1	0	0	1	0	1	0	1
11	Sineoamphisbaena	1	?	0	0	1*	0	0	1	0	0	1	0	1	1	0
12	Dibamidae	1	2	1	0	2*	1	0	1	1	0	1	0	1	2	0
13	Amphisbaenia	1	2	0	0	2*	0/1	0	1	1	0	1	0	1	1	0
14	Lacertidae	0	1	0	0	0/1*	0	1	0	0	0	1	0	1	0	0
15	Teiidae	0	0	0	0	0*	0	1	0	0	0	1	0	1	0	0
16	Gymnophthalmidae	0	0	0	0	0*	0	1	0	0	0	1	0	1	0/1	0
17	Cordylidae	0	0/1	0	0	0*	0	1	0	0	0	1	0	1	0	0
18	Scincidae	0	0/1	0	0	0/1/2*	0/1*	1	0	0	0	1	0	1	0/1	0/1
19	Anguidae	0	1	0/1	0	0/1*	0	1	0	0	0	1	0	1	1	0
20	Xenosauridae	0	0/1	0	0	0*	0	1	0	0	0	1	0	1	1	0
21	Heloderma	0	1	1	0	0	0	1	0	0	0	1	0	1	1	0
22	Lanthanotus	1	1	0	1	0*	0	1	0	0	0	1	0	1	1	0
23	Varanus	1	0	0	1	0*	0	1	0	0	0	1	0	1	1	0
24	Mosasauroidea	1	0	0*	0	0*	0	1	0	0	1	1	1	1	0	0
25	Pachyrhachis	?	?	?	?	2	1	?	?	1	?	?	?	?	2	?
26	Scolecophidia	?	1	0	0	2	1	1	0	1	?	1	0&1	1	2	0
27	Dinilysia	?	?	0	0	2	1	1	0	1	?	?	?	?	?	0
28	Anilioidea	?	1	0	0	2	1	1	0	1	?	1	1	1	2	0
29	Macrostromata	?	0	0	0	2	1	1	0	1	?	1	1	1	2	0

TABLE I. *Continued.*

Pachyrhachis		7	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	
															ord.	ord.		
1	Kuehneosauridae	0	0	0	0	0	0	?	?	0	?	0	?	0	0	1	0	
2	Marmoretta	0	0	?	0	0	0	?	0	1	?	0	0	0	0	1	?	
3	Rhynchocephalia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0/1	0	
4	Ancestor	0	0	0	0	0	0	0	0	0	0/1	0	0	0	0	1	0	
5	Iguanidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0/1	1	
6	Agamidae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0/1	1	
7	Chamaeleonidae	0	0	1	0	0	0	0	0	1	0/1	0/1	0	0	0	0	1	
8	Xantusiidae	0	1	0	0	0	0	0	0	0	0	0	1	0/1	0	0	1	
9	Gekkonidae	0	1	0	0	0	0	0	0	0	0	1	0/1	0	0	0	1	
10	Pygopodidae	0	1	0	0	0	0	0	1	0	0	1	0/1	0	0	0	1	
11	Sineoamphisbaena	1	1	0	0	0	1	0	0	0	0	1	1	2	0	0	0	
12	Dibamidae	1	1	0	0	1	1	0	0	0	0	1	1	1	1	1	0	
13	Amphisbaenia	1	1	0	0	0	1	0	0	0	0	1	1	2	2	0/1		
14	Lacertidae	0	1	0	0	0	0	0	0	0	0	1	0	0	0/1	1		
15	Teiidae	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	1	
16	Gymnophthalmidae	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	
17	Cordylidae	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	
18	Scincidae	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	
19	Anguidae	0	1	0	0	0	0	0	0	0	0	1	0/1	0	0	0	1	
20	Xenosauridae	0	0/1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	
21	Heloderma	0	1	1	0	0	0	0	1	0	0	1	1	0	0	0	1	
22	Lanthanotus	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	1	
23	Varanus	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	1	
24	Mosasauroidae	0	1	1	0	0	0	0	1	0	0	1	?	*	0	1	1	
25	Pachyrhachis	?	*	?	?	*	0	?	*	?	*	0	1	1	0	0	0	1
26	Scolecophidia	0	1	0	1	0	0	1	0&1	0	1	?	?	0	0	0	1	
27	Dinilysia	0	1	?	1	0	1	1	0	0	1	1	0	0	0	0	1	
28	Anilioidea	0	1	0	1	0	0	1	0	0	1	1	0	0	0	0	1	
29	Macrostromata	0	1	1	1	0	0	1	0	0	1	1	0	0	0	0	1	

Pachyrhachis		8	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
										ord.	ord.			ord.	ord.		ord.
1	Kuehneosauridae	?	0	0	?	1	0	0	0	0	?	?	?	?	0/1	0	0
2	Marmoretta	0	?	?	0	0	0	0	0	2	0	0	?	0	?	0	?
3	Rhynchocephalia	0	0	0	0	0	0	0/1	0	0	0	0	0	1	0/1	0	2
4	Ancestor	0	0	0	0	0	0	0	0	0/2	0	0	0	0/1	0/1	0	0/2
5	Iguanidae	0	0	0	0/1	0	0	1	2	0/1/2	0/1	0	1/2	1	0	0/1/2	
6	Agamidae	1	0	0	0	0	0	0/1	2	0	0	0	?	1	0	1/2	
7	Chamaeleonidae	1	0	0	1	0	0	0	2	0	0	0	?	1	0	2	
8	Xantusiidae	0	0	0	0	0	0	0	1	2	?	?	0	0	1	0	1
9	Gekkonidae	0/1	0	0	0	0	0	0/1	2	2	?	?	0	0	1	0	1
10	Pygopodidae	0	0	0	0	0	0	0/1	2	2	?	?	0	0	0/1	0	1
11	Sineoamphisbaena	?	?	1	?	0	?	0	2	?	?	?	?	0	0	?	
12	Dibamidae	?	0	1	0/1	0	0	0	0	2	?	?	0	0	0	0	2
13	Amphisbaenia	0/1	?	1	0/1	0	0	0/1	0	0/1/2	1	0	1/2	1	0	1/2	
14	Lacertidae	0	0	0	0	0	0	1	2	0	0/1	0	0	0	1	0	0
15	Teiidae	0/1	0	0	0	0	0	1	2	0/1	0	0	0	0	1	0	0
16	Gymnophthalmidae	1	0	0	0	0	0	0/1	2	0/2	0	0	0/1	0/1	0	0/1	
17	Cordylidae	0/1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	
18	Scincidae	0/1	0	0	0	0	0	1	1	0/1/2	0	0	0	0	1	0	0/1
19	Anguidae	0	0	0	0	0	0	1	1/2	0	0	1	1	1	0	0/1	
20	Xenosauridae	0	0	0	0	0	0	1	1	0	0	1	1	1	0	0	
21	Heloderma	0	0	0	0	0	0	1	2	0	0	1	2	1	0*	1	
22	Lanthanotus	0	0	0	0	0	0	1	2	0	0	1	2	1	0*	1	
23	Varanus	1	0	0	0	0	0	1	2	0	0	1	2	1	0*	0	
24	Mosasauroidae	0	1	0	0	1	0	0/1*	2	0	1	1	2*	0	1	0	
25	Pachyrhachis	?	?	0	?	1	1	?	?	2	0	0	?	2	2	2	0
26	Scolecophidia	1	?	?	0	1	1	1	2	0	0	?	2	0	2	0	
27	Dinilysia	1	0	0	0	1	1	1	2	0	0	?	2	2	2	1	
28	Anilioidea	0/1	1	0	0	1	1	1	2	0	0	0	2	2	2	1	
29	Macrostromata	0/1	1	0	0	1	1	1	2	0	0	?	2	2	2	0	

TABLE 1. *Continued.*

Pachyrhachis	9	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135
		ord.	delete	delete	delete											
1	Kuehneosauridae	?	?	?	?	?	?	?	?	?	0	?	0	?	0	?
2	Marmoretta	?	?	?	?	0	0	?	?	?	?	0	?	?	?	?
3	Rhynchocephalia	?	?	?	?	0	0	?	0	0	0	0	0	0	0	0
4	Ancestor	?	?	?	?	0	0	?	0	0	0	0	0	0	0	0
5	Iguanidae	0*	0/1	0	0	0	0/1	0	1	0*	0	0	0	0/1	0/1	1
6	Agamidae	0*	1	0	0	0	0	0	1	0	0	0	0	0	0	1
7	Chamaeleonidae	0*	?	?	?	0	0	?	0	0	0	0	0	0	0/1	1
8	Xantusiidae	0*	0	0	0	0	0	0	1	0*	0	0/1	1	?	0	1
9	Gekkonidae	0	1	0	0	0	1	0	1	0*	0	0	0/1	1	0	1
10	Pygopodidae	0	1	0	0	0	1	0	1	0*	0	0	1	?	0	1
11	Sineoamphisbaena	?	?	?	?	?	1	?	?	?	0	?	0	?	0	?
12	Dibamidae	0*	?	?	?	1	0	?	0/1	1*	?	?	0	1	?	0
13	Amphisbaenia	0*	1	0	0	0/1	0	0	0/1	1*	?	?	0/1	0/1	0	?
14	Lacertidae	0	0/1	0	0	0	1	0	1	0*	0	0	0	0	1	0
15	Teiidae	0	1	0	0	0	1	0	1	0*	0	0	0	0	1	0
16	Gymnophthalmidae	0*	1	0	0	0	1	0	1	0*	0	0	0	0	1	0
17	Cordylidae	0	0	0	0	0	1	0	1	0*	0	1	0	1	0	1
18	Scincidae	0	0/1	0	0	0	1	0	1	0*	0	1	0	1	0	1
19	Anguidae	0	0	0	0	0	1	0	1	0*	0	0/1	0	1	0	1
20	Xenosauridae	0	0	0	0	0	1	0	1	0*	0	0	0	1	0	1
21	Heloderma	0*	0	1	0	0	1	0	1	0*	1	0	0	0	0	1
22	Lanthanotus	0*	0	1	0	1	0	0	1	0*	2	0	0	0	0	0
23	Varanus	0*	0	1	0	0	0	0	1	0*	2	0	0	0	0	0
24	Mosasauroidea	1*	1	1	1	1	0	1	0	0	2	0	0	0	0	1
25	Pachyrhachis	?	1	1	1	?	?	?	?	0	1*	3	0	0	0	?
26	Scolecophidia	0	1	1	0	?	?	0	0	1	?	1	0	0	0	0
27	Dinilysia	2	1	1	1	?	?	?	0	0	1	3	0	0	0	?
28	Anilioidea	2	1	1	1	?	?	0/1	0	1	3	0	0/1	0	0	?
29	Macrostromata	2	1	1	1	?	?	0/1	0	1	3	0	0	0	0	?

Pachyrhachis	10	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150
		ord.			ord.							ord.	delete			
1	Kuehneosauridae	0	?	0	0	0	0	0	0	1	0	1	0	0	0	0
2	Marmoretta	?	0	?	1/2	?	?	?	?	?	?	1	0	0	0	0
3	Rhynchocephalia	0	0	0	2	0	0	0	0	0	0	0/1	0	0	0	0/2
4	Ancestor	0	0	0	1/2	0	0	0	0	0/1	0	1	0	0	0	0
5	Iguanidae	0	0	0	0	0	0	0/1	0	0	0	1	0	0	0	0
6	Agamidae	0	0	0	0	0	0	0	0	0	0/1	0	0	0	0	2
7	Chamaeleonidae	0	0	0	0	0	0	0/1	0	0	0/1	0	0	0	0	2
8	Xantusiidae	1	0	0	2	0	0	0	0	0	0	1	0	0	0	0
9	Gekkonidae	0	0	0	0	1	1	1	0	1	1	1	0	0	0	0
10	Pygopodidae	0	0	0	0	1	1	1	0	1	0	1	0	0	0	0
11	Sineoamphisbaena	?	?	0	0/1	0	?	?	?	?	?	0	0	0	0	2
12	Dibamidae	0	0	0	0*	0	0	1	0	1	1	1	0	0	0	1
13	Amphisbaenia	0	0	0	0/1/2	0	1	1	0	1	1	0/1	0	0	0	1
14	Lacertidae	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0
15	Teiidae	2	0	1	0	0	0	0	0	0	0	1	0	0	0	0/1
16	Gymnophthalmidae	2	0	1	0	0	0	0	0	0	0/1	1	0	0	0	0/1
17	Cordylidae	0	0	0	0	0	1	0/1	1	1	1	1	0	0	0	0
18	Scincidae	0	0	0/1	0	0	1	1	1	1	1	1	0	0	0	0/1
19	Anguidae	0	0	0	0	0	1	1	0	1	1	1	0	0/1	0	1
20	Xenosauridae	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1
21	Heloderma	0	0	0	0	0	1	1	0	0	1	2*	1	1	1	1
22	Lanthanotus	0	0	0	0	0	1	1	0	0	1	2*	1	1	1	1
23	Varanus	0	0	0	0	0	1	1	0	0	1	2*	1	1	1	1
24	Mosasauroidea	0	1	0	1	0	1	1	0	1	1	2*	1	0*	1	1
25	Pachyrhachis	0	1	0	?	?	2*	?	?	?	?	3*	1	0	0*	?
26	Scolecophidia	0	0	0	?	0	0	?	0	0	?	2	1	0	0	1
27	Dinilysia	0	1	0	?	?	?	?	?	?	?	3	1	0	0	?
28	Anilioidea	0	0/1	0	?	0	2	?	?	0	?	3	1	0	0	1
29	Macrostromata	0	1	0	?	0	2	?	0	0	?	3	1	0	0	1

TABLE I. *Continued.*

Pachyrhachis 11		151	152	153	154	155	156	157	158	159	160	161	162	163	164	165
								ord.	ord.			delete		ord.		ord.
1	Kuehneosauridae	0	?	0	0	?	0	0	0	0	0	0	0	?	?	?
2	Marmoretta	0	?	0	0	?	0	0	0	0	0	0	?	?	?	?
3	Rhynchocephalia	0	0	0	0	?	0	0	0	0	0	0	0	?	?	?
4	Ancessor	0	0	0	0	?	0	0	0	0	0	0	0	?	?	?
5	Iguanidae	0	0	0	1	0	0	0	0	0/1	0	0/1	0	0	0	1
6	Agamidae	?	?	0	1	0	0/1	0	0	1	?	1	?	0	0/1	1
7	Chamaeleonidae	?	?	1	1	0	1	0	0	1	?	1	?	0	0	1
8	Xantusiidae	0	0	0	1	0	0	0	0	1	?	1	?	0	0	1
9	Gekkonidae	0	0	0	1	0	0	0	0	1	?	1	?	1	0	1
10	Pygopodidae	0	0	0	1	0	0	0	0	1	?	1	?	1	0	1
11	Sineoamphisbaena	?	?	0	1	1	0	1	1	1	?	1	?	?	0	1
12	Dibamidae	0	0	0	1	1	0	1/2	1	1	?	1	?	0	0	1
13	Amphisbaenia	0	0	0/1	1	1	0/1	2	2	1	?	1	?	0	0	1
14	Lacertidae	0	0	0	1	0	0/1	0	0	1	?	0/1	0	0	0	1
15	Teiidae	0	0	0	1	0	0/1	0/1	0	1	?	0/1	0	0	0/1	1
16	Gymnophthalmidae	0	0	0	1	0	0	0	0	1	?	1	0	0	0	1
17	Cordylidae	0	0	0	1	0	0	0	0	1	?	0/1	0	0	0	1
18	Scincidae	0	0	0	1	0	0	0	0	1	?	0/1	0	0	0	1
19	Anguidae	0	0	0	1	0	0	0	0	1	0	0/1	0	0	0	1
20	Xenosauridae	0	0	0	1	0	0	0	0	1	?	0/1	0	0	0	1
21	Heloderma	1*	0	0	1	0	1	1	1	0/1	0	0	0	0	0	1
22	Lanthanotus	1*	0	0	1	0	1	1	1	0	0	0	0	?	1	2
23	Varanus	1*	0	0	1	0	1	1	1	1	?	1	?	0	2	2
24	Mosasauroidea	2*	0*	1	0	?	1	0	0	1	?	0	1	?	0	0/1
25	Pachyrhachis	?	?	1	?	?	?	0	0	0	1	0	1	?	0	0
26	Scolecophidia	0	1	1	0	?	?	2	2	1	?	1	?	?	0	0
27	Dinilysia	?	?	?	?	?	?	0	1	0	?	0	1	?	1	?
28	Anliioidea	1	1	1	0	?	?	1	1	0/1	0	1	0	1	0	0/1
29	Macrostromata	1	1	1	0	?	?	1	0	0	0	1	0	1	0	1

Pachyrhachis 12		166	167	168	169	170	171	172	173	174	175	176	177	178	179	180
						delete		ord.	ord.	delete		ord.	ord.			
1	Kuehneosauridae	?	?	0	0*	?	?	1	1	0	0	0	0	0	?	0
2	Marmoretta	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?
3	Rhynchocephalia	?	0	0	1*	0	0	1	1	0	0	0	0	0	?	0
4	Ancessor	?	0	0	0/1	0	0	1	1	0	0	0	0	0	?	0
5	Iguanidae	0	1	0	0/1	1	1	0/1	1	0	0	0/1	0	0/1	1	0
6	Agamidae	0	1	0	0*	?	?	0/1	1	0	0	0	1/2	0	?	0
7	Chamaeleonidae	0	1	0	0*	?	?	1	0	0	0	0	0	0	?	0
8	Xantusiidae	0	1	0	0*	?	?	0/1	2/3	1	0	0	0	0/1	0/1	1
9	Gekkonidae	1	0	0	0*	?	?	0	1/2/3	1	0	0	0	0	?	0
10	Pygopodidae	1	0	0	0*	?	?	1	4	0	0	0	0	0	?	0
11	Sineoamphisbaena	0	1	0	0*	?	?	1	?	1	1	0	0	?	?	?
12	Dibamidae	0	1	1	0*	?	?	1	4/5	0	1	1	2	0	0	1
13	Amphisbaenia	0	1	1	0*	?	?	1	4/5	0	0/1	1	2	0	0	1
14	Lacertidae	0	1	0	1*	0	1	1/2/3	1	0	0	0/1	0/1	0/1	1	0
15	Teiidae	0	1	0	2*	1	1	1/2/3	1	0	0	0	0	1	1	0
16	Gymnophthalmidae	0	1	0	0	1	1	1/2/3	1	0	0	0	1/2	1	1	0
17	Cordylidae	0	1	0/1	1*	?	?	2/3	0/1	0	0	0	0	0	?	0
18	Scincidae	0	1	0	0*	?	?	1	3	1	0	0	1/2	0	0/1	0
19	Anguidae	0	1	0	0*	?	?	1	3/4	0/1	0/1	0	2	0	0/1	0
20	Xenosauridae	0	1	0	0*	?	?	1	2/3	1	0	0	2	0	0	?
21	Heloderma	0	1	0	0*	?	?	1	3	1	0	0	1/2	0	0	?
22	Lanthanotus	0	1	0	0*	?	?	1	3	2	1	0	1/2	0	0	?
23	Varanus	0	1	0	0*	?	?	1	3	2	1	0	2	0	0	?
24	Mosasauroidea	1	1	0	2*	1	1	3	?	1	1	0	0	0	?	0
25	Pachyrhachis	?	?	0	2*	?	?	1	5	?	1	0	2	0	0	?
26	Scolecophidia	0	0	1	2	?	?	1	5	?	?	1	2	0	0	?
27	Dinilysia	?	?	1	2	?	?	1	5	?	?	1	2	0	?	?
28	Anliioidea	0/1	0	1	2	?	?	1	5	?	?	1	2	0	0	?
29	Macrostromata	0/1	0	1	2	?	?	1	5	?	?	1	2	0	0	?

TABLE 1. *Continued.*

Pachyrhachis		13														
		181	182	183	184	185	186	187	188	189	190	191	192	193	194	195
											ord.					
1	Kuehneosauridae	1	?	?	?	?	?	0	0	0	0	0	0	0	?	?
2	Marmoretta	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
3	Rhynchocephalia	0	0	0	0	0	0	0	0	0	0	0/1	0	?	0	0
4	Ancestor	0/1	0	0	0	0	0	0	0	0	0	0/1	0	0	0	0
5	Iguanidae	0/1	0/1	0/1	0	0	1	0	0	0	0	0/1	1	0/1	0	0
6	Agamidae	1	?	0	0	0	1	0	0	0	0	0	1	0/1	0	0
7	Chamaeleonidae	1	?	0	0	0	1	0	0	0	0	1	0	0	1	?
8	Xantusiidae	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1
9	Gekkonidae	0	1	0	0	0	1	0	0	0	0	1	1	0/1	0	1
10	Pygopodidae	0	1	0	0	0	0	1	0	0	1	0	1	0	0	1
11	Sineoamphisbaena	?	?	?	?	?	1	0	0	?	0	?	1	?	?	?
12	Dibamidae	0	0	0	0	0	0	1	1	1	1	?	?	?	1	?
13	Amphisbaenia	0/1	0	?	1	0	0	1	1	1	0/1/2	0	0	0	0/1	1
14	Lacertidae	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1
15	Teiidae	0	0	0	0	0	1	0	0	0	0	0/1	1	1	0	1
16	Gymnophthalmidae	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1
17	Cordylidae	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0/1
18	Scincidae	0/1	0	0	0	0	1	0	0	0	0	0/1	1	0	0	1
19	Anguidae	0/1	0	0	0	0	0/1	0	0	0	0/1	0/1	1	0	0	1
20	Xenosauridae	0/1	0	0	0	0	1	0	0	0	0	0	1	0	0	1
21	Heloderma	1	?	0	0	1	1	0	0	0	0	0	0	0	0	1
22	Lanthanotus	1	?	1	0	1	1	0	0	0	0	0	1	0	0	1
23	Varanus	1	?	1	0	1	1	0	0	0	0	0	1	1	0	0/1
24	Mosasauroidea	1	?	1	0	1	0	0	0	0	0	0	0/1	0	0	?
25	Pachyrhachis	1	?	?	?	?	?	0	0	1	2	?	?	?	1	?
26	Scolecophidia	1	?	?	?	?	?	0	0	1	2	?	?	?	1	?
27	Dinilysia	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?
28	Anilioidea	1	?	?	?	?	?	0	0	1	2	?	?	?	1	?
29	Macrostromata	1	?	?	?	?	?	0	0	1	2	?	?	?	1	?

Pachyrhachis		14														
		196	197	198	199	200	201	202	203	204	205	206	207	208	209	210
								ord				ord.	ord.		delete	
1	Kuehneosauridae	?	?	?	?	?	?	?	?	0	0	0	1	0	0	0
2	Marmoretta	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?
3	Rhynchocephalia	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
4	Ancestor	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
5	Iguanidae	0/1	0	0	0	0	0/1	1/2	0/1	0	0	0	1	0	0	0
6	Agamidae	0	0	0	0/1	0	1	0/1	0	0	0	0	1	0	0	0
7	Chamaeleonidae	?	1	?	?	0	0/1	3	1	0	1	0	1	1	0	0
8	Xantusiidae	1	0	0	1	0	0/1	1	0	0	0	0	0	1	2	1
9	Gekkonidae	1	0	0/1	1	0	0/1	1/2	0	0	0	0	1	1	1	1
10	Pygopodidae	0	1	?	?	0	0	3	0	1	?	1	0	1	?	?
11	Sineoamphisbaena	?	0	?	?	?	?	?	?	0	0	?	?	?	?	?
12	Dibamidae	?	1	?	?	0	0	3	1	1	?	1	0/1	0	?	?
13	Amphisbaenia	?	1	?	?	0/1	0	3	0	0/1	1	1	0	1	?	?
14	Lacertidae	1	0	0	1	0	1	1	0/1	0	0	0	1	0	2	1
15	Teiidae	1	0	0	1	0	1	1	0	0	1	0	0	0	1	1
16	Gymnophthalmidae	1	0	0	1	0	1	1	0	0	1	0	0	1	2	1
17	Cordylidae	0/1	0	0	1	0	0	1/2	0/1	0	0	0	0	0	2	1
18	Scincidae	1	0/1	0	1	0	0/1	1	0/1	0	0	0	0/1	1	2	1
19	Anguidae	1	0/1	0	1	0	0	1/2	0	0/1	0	0/1	0	0/1	2	1
20	Xenosauridae	0	0	0	0/1	0	0	1	0	0	0	0	0	0/1	1	1
21	Heloderma	0	0	1	?	0	0	1	0	0	0	0	1	1	1	1
22	Lanthanotus	0	0	0	1	0	0	3	0	0	0	0	1	1	1	1
23	Varanus	0	0	0	0/1	0	0/1	2	0	0	0	0	1	0	0	1
24	Mosasauroidea	0	0	1	?	0	0	0	0	0	1	0	1*	1	0/1	1
25	Pachyrhachis	?	1	?	?	1	?	?	0	1	?	1	2	1	1	?
26	Scolecophidia	?	1	?	?	1	?	?	0	1	?	1	2	1	?	?
27	Dinilysia	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?
28	Anilioidea	?	1	?	?	1	?	?	0	1	?	1	2	1	?	?
29	Macrostromata	?	1	?	?	1	?	?	0	1	?	1/2	2	1	?	?

TABLE 1. *Continued.*

Pachyrhachis	15	211	212	213	214	215	216	217	218	219	220	221	222	223	224	225
				delete	delete				ord.			ord.		ord.		
1	Kuehneosauridae	0	0	0	0	?	0	0	0	?	?	0	?	?	?	?
2	Marmoretta	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?
3	Rhynchocephalia	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0
4	Ancestor	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0
5	Iguanidae	0	0	0	0	0	0	0	0	?	?	0/1	0	1/2	0	0/1
6	Agamidae	0	0	0	0	0	0	0	0	?	?	0/1	0	2	0	0/1
7	Chamaeleonidae	0	0	1	0	0	0	0	0	?	?	0/1	0	2	0	1
8	Xantusiidae	0	0	0	1	0	0	0	0	?	?	0/2	0	1	0	0
9	Gekkonidae	0	0	0	1	0	0/1	0	0	?	?	0	0	0	1	0
10	Pygopodidae	1	?	?	?	?	0	0	0	?	?	0	0	0	1	0
11	Sineoamphisbaena	?	?	?	?	?	0	0	0	?	?	2	?	?	?	?
12	Dibamidae	1	?	?	?	?	0	0	0	?	?	0	1	?	?	1
13	Amphisbaenia	1	?	?	?	?	0	0	0	?	?	0/2	0/1	2	?	1
14	Lacertidae	0	0	0	1	0	0	0	1	0	0	2	0	1/2	0	0
15	Teiidae	0	0	0	1	0	0	0	0	?	?	0/2	0	1	0	0
16	Gymnophthalmidae	0	0	0	1	0	0	0	0	?	?	0/2	0	1/2	0	1
17	Cordylidae	0	0	0	1	0	1	1	2	0	0	2	0	2	0	0
18	Scincidae	0	0	0	1	0	1	1	2	0	0	0/2	0	1/2	0	0/1
19	Anguidae	0/1	0	0	1	0	1	1	2	0	0	0/1	0	1/2	0	0/1
20	Xenosauridae	0	0	0	1	0	1	0	2	1	0	2	0	1	0	1
21	Heloderma	0	0	0	1	0	1	0	2	1	0	1	0	2	0	0
22	Lanthanotus	0	0	0	1	0	1	0	2	1	1	0	0	2	0	1
23	Varanus	0	0	0	1	0	0/1	0	0/2	1	1	0/1	0	0	0	1
24	Mosasauroidea	0	1	1	0	1	0	0	0	?	?	0	0	1	0	?
25	Pachyrhachis	1	1	1	0	1	0	0	0	?	?	0	1	?	?	?
26	Scolecophidia	1	?	?	?	?	0	0	0	?	?	0	1	?	?	1
27	Dinilysia	?	?	?	?	?	0	0	0	?	?	0	1	?	?	?
28	Anilioidea	1	?	?	?	?	0	0	0	?	?	0	1	?	?	1
29	Macrostromata	1	?	?	?	?	0	0	0	?	?	0	1	?	?	1

Pachyrhachis	16	226	227	228	229	230	231	232	233	234	235	236	237	238	239	240
				delete								ord.				
1	Kuehneosauridae	?	?	1	?	?	?	?	0	0	0	0	0	0	0	0
2	Marmoretta	?	1	?	?	?	?	?	0	0	0	0	0	0	0	0
3	Rhynchocephalia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	Ancestor	0	0/1	0/1	0	0	0	0	0	0	0	0	0	0	0	0
5	Iguanidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	Agamidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	Chamaeleonidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	Xantusiidae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
9	Gekkonidae	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0
10	Pygopodidae	0	0	0	?	1	0	1	0	0	1	0	0	0	0	0
11	Sineoamphisbaena	?	0	0	0	?	0	?	0	0	?	?	0	0	0	0
12	Dibamidae	1	0	0	?	0	0	1	0	1	1	0	0	0	0	1
13	Amphisbaenia	0/1	0	0	1	0	0	?	0	0	2	1	0	0	0	1
14	Lacertidae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
15	Teiidae	0/1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
16	Gymnophthalmidae	0/1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
17	Cordylidae	0/1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
18	Scincidae	0/1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
19	Anguidae	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
20	Xenosauridae	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
21	Heloderma	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
22	Lanthanotus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
23	Varanus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
24	Mosasauroidea	?	0/1*	0/1	?	0	0	0	0	0	0	0	0	0	0	0
25	Pachyrhachis	?	1	1	?	0	?	?	1	0	1	0	1	1	1	1
26	Scolecophidia	1	1	?	?	0	0	?	0	1	2	1	0	0	0	1
27	Dinilysia	?	1	?	?	?	0	?	0	?	?	?	0	0	0	1
28	Anilioidea	1	1	?	?	0	1	1	0	1	2	1	1	0/1	0	1
29	Macrostromata	1	1	?	?	0	1	1	1	1	2	1	1	1	1	1

many of the characters are problematic, yet some were alternatively retained or deleted in the cladistic analysis as coded by Lee (1998) in order to remain as close to the original character evidence as possible. A large number of character states are given as the relative size of continuous variables (e.g., 7, 19, 23, 28, 53, 66, etc.) without reference to some standard. Although this may cause problems for other workers attempting to critically evaluate character-state assignments, we retained these character codings unaltered. The same is true for distinctions of character states that appear to be purely arbitrary, such as “three or more” versus “two or less” in character 111 (see also characters 153, 157, 158, 172, 173, 174, 223). Furthermore, the terminal taxa are coded at the family level, which most probably will result in a substantial degree of polymorphism as greater scrutiny is applied to character coding. As pointed out by Etheridge (personal communication), Iguanidae are coded with a single character state for characters 8, 15, 34, 36, 39, 45, 50, 96, 103, 132, 139, 144, 168, 179, and 180, all of which exhibit two or more states in that taxon. It remains to be seen to what degree polymorphism applies to other terminal taxa. *Anniella*, for example, would greatly affect the coding for Anguidae if it were to be included in that family, and might affect the result of the analysis if it were included as terminal taxon. If a terminal taxon is polymorphic for a given character, then the plesiomorphic character state, if known, should be used for that taxon. Yet the plesiomorphic character state can only be determined by phylogenetic analysis in intrafamilial relationships, and these are often not available. Pleurodont iguanians are a case in point (Frost & Etheridge, 1989), with potentially serious consequences for coding of the Iguanidae. A global assessment of squamate relationships will necessitate breaking up terminal taxa into groups below the family level or rejecting previous analyses of intrafamilial relationships in order to determine the plesiomorphic character state at the family level.

Finally, we also note that work in progress is likely to change several character codings for amphisbaenians as well as for *Sineoamphisbaena* (M. Kearney, personal communication) without threatening to change the major conclusions reached in this paper, however. At this point, our interest is not in the recovery of squamate history (which is beyond the scope of this paper). Instead, our goals are twofold. The first is to test the relationships of *Pachyrhachis* on the basis of the

evidence proposed by Lee (1998), for which reason we propose to split up *Serpentes* as a terminal taxon. The second goal is to test Lee's (1998) conclusion that the burrowing ecomorph evolved convergently in snakes and in dibamids plus amphisbaenians, which is why we critically reexamined the characters relevant to the groups involved, i.e., snakes, varanoids, and the amphisbaenian–dibamid clade.

The cladistic analysis of the modified data set was performed using the software package PAUP, version 3.1.1, developed by David L. Swofford (Swofford, 1990; Swofford & Begle, 1993). The search settings invariably employed the heuristic search strategy with random stepwise addition (10 replications), and branch swapping (on minimal trees only) was effected by tree bisection and reconnection. A number of alternative analyses were performed that varied with respect to three parameters: rooting the analysis on the three outgroup taxa (Kuehneosauridae, *Marmoretta*, Rhynchocephalia) or rooting it on the ancestor reconstructed by Lee (1998); ordering the multistate characters as indicated by Lee (1998; i.e., the characters 16, 23, 29, 34, 35, 50, 51, 77, 80, 103, 104, 113, 114, 117, 118, 120, 121, 136, 139, 146, 157, 158, 164, 165, 172, 173, 176, 177, 190, 202, 206, 207, 218, 221, 223) as well as ordering one of the newly added multistate characters (235) or leaving all multistate characters unordered; and retaining all characters or deleting the ones so designated (i.e., characters 11, 48, 57, 62, 64, 68, 84, 86, 122–124, 147, 162, 170, 174, 209, 213, 214, 228). Characters rendered uninformative by the choice of different outgroups were always ignored if not deleted. Bootstrap (1,000 replications, using identical heuristic search settings) and decay analyses were run for those analyses that most closely approach the search procedure employed by Lee (1998), i.e., with multistate characters ordered, and rooting on the ancestor (our runs 2 and 4 below). All analyses were run in two alternatives. Assuming presence of a jugal in *Dinilysia* required retention of character 12 but deletion of character 240. Conversely, assuming a jugal to be absent in *Dinilysia* required character 12 to be deleted and character 240 to be retained. In those analyses that retained character 240, this character was treated as ordered and unordered, respectively. The values of tree statistics in the discussion below that are not placed in brackets are those obtained by retention of character 12, deletion of character 240 (jugal present in *Dinilysia*); conversely, the values placed in brackets are those

obtained by retention of character 240, deletion of character 12 (jugal absent in *Dinilyisia*). Tree topologies were identical under both assumptions, but the assumption that a jugal is absent in *Dinilyisia* proved slightly more parsimonious.

A first series of tests retained ordered multistate characters as indicated above. Retaining all the characters designated for deletion, deleting the ancestor, and rooting the tree on Kuehneosauridae, *Marmoretta*, and Rhynchocephalia (run 1) yielded two equally parsimonious trees with a tree length (TL) of 645 [644] steps, a consistency index (CI) of 0.462 [0.463], and a retention index (RI) of 0.690 [0.691]. Lack of resolution was restricted to the outside of that part of the cladogram that embraces the anguimorphs, the amphisbaenian–dibamid clade, and snakes. The relative relationships of the latter taxa were fully resolved and read as follows: (Anguidae (Xenosauridae (*Heloderma* ((*Lanthanotus*, *Varanus*) (Mosasauroida (*Sineoamphisbaena* ((Amphisbaenia, *Dibamus*) (Scolecophidia (*Dinilyisia* (Anilioidea (*Pachyrhachis*, Macrostomata)))))))))). Anguimorpha is paraphyletic in this search, mosasauroids being the sister group to a clade including amphisbaenians, Dibamidae, and snakes. Amphisbaenians plus Dibamidae form the sister group of snakes, whereas within snakes, *Dinilyisia* is the sister taxon of Alethinophidia and *Pachyrhachis* is the sister taxon of Macrostomata.

Retaining the ordered multistate characters, retaining all characters designated for deletion but deleting the outgroup taxa Kuehneosauridae, *Marmoretta*, and Rhynchocephalia and rooting the analysis on the ancestor reconstructed by Lee (1998) yielded (run 2) two equally parsimonious trees, again with TL = 622 [621], CI = 0.477 [0.478], and RI = 0.690 [0.692]. The tree topology is the same.

Retaining the ordered multistate characters but deleting all characters so designated and deleting the ancestor but rooting the analysis on the three outgroup taxa Kuehneosauridae, *Marmoretta*, and Rhynchocephalia (run 3) yielded four equally parsimonious trees, with TL = 606 [605], CI = 0.460 [0.461], and RI = 0.683 [0.684]. Resolution of the tree is greatly reduced, but varanoids, on the one hand, and amphisbaenians–dibamids–snakes on the other form monophyletic clades, respectively. The relationships among varanoids are (*Heloderma* (Mosasauroida (*Lanthanotus*, *Varanus*))); those of snakes are (*Sineoamphisbaena* ((Amphisbaenia, Dibamidae) (Scolecophidia (*Dinilyisia* (Anilioidea (*Pachyrhachis*, Macrosto-

mata)))))). Mosasauroids turn out to be the sister group of the *Lanthanotus*–*Varanus* clade, whereas amphisbaenians plus dibamids again form the sister group of snakes, *Dinilyisia* again is the sister taxon of Alethinophidia, and *Pachyrhachis* again is the sister taxon of Macrostomata.

Retaining the ordered multistate characters but deleting all characters so designated and deleting the three outgroup taxa Kuehneosauridae, *Marmoretta*, and Rhynchocephalia but rooting the analysis on the ancestor (run 4) yielded again four equally parsimonious trees, with TL = 584 [583], CI = 0.476 [0.477], and RI = 0.683 [0.685]. The topology of the strict consensus tree is identical to that of the previous run.

A second, parallel set of tests was run but with all multistate characters unordered. Retaining all characters designated for deletion, deleting the ancestor, and rooting the analysis on the three outgroup taxa Kuehneosauridae, *Marmoretta*, and Rhynchocephalia (run 5) yielded a total of four equally parsimonious trees, with TL = 607 [606], CI = 0.486 [0.487], and RI = 0.690 [0.691]. The strict consensus tree differs somewhat for the relationships outside the group that comprises anguimorphs, amphisbaenians, Dibamidae, and snakes, yet the relationships among the latter taxa resemble the first run and are (Anguidae (Xenosauridae (*Heloderma* ((*Lanthanotus*, *Varanus*) (Mosasauroida (*Sineoamphisbaena* ((Amphisbaenia, Dibamidae) (Scolecophidia (*Dinilyisia* (Anilioidea (*Pachyrhachis*, Macrostomata)))))))))). Unordering the multistate characters therefore did not alter relationships among these latter taxa but resulted in a decrease in the tree length and a slight increase in the consistency index and retention index.

The same search but rooted on the ancestor (the three outgroup taxa Kuehneosauridae, *Marmoretta*, and Rhynchocephalia deleted), all multistate characters unordered, and all characters retained (run 6) resulted in two equally parsimonious trees, with TL = 587 [586], CI = 0.501 [0.502], and RI = 0.690 [0.691]. The relationships of the taxa under consideration remain the same, however, as those recovered in the previous search.

Finally, with deletion of all characters so designated, with all multistate characters unordered, and rooting the analysis on the three outgroup taxa Kuehneosauridae, *Marmoretta*, and Rhynchocephalia (deleting the ancestor; run 7), the analysis yielded a total of four equally parsimonious trees, with TL = 567 [566], CI = 0.487 [0.488], and RI = 0.684 [0.685]. The relationships

for the taxa under consideration have slightly changed to a monophyletic Varanoidea that includes the mosasauroids, i.e., (Anguidae (Xenosauridae ((*Heloderma* (Mosasauroidae (*Lanthanotus*, *Varanus*))) (*Sineoamphisbaena* ((Amphisbaenia, Dibamidae) (Scolecophidia (*Dinilyisia* (Anilioidea (*Pachyrhachis*, Macrostomata)))))). Deleting all characters so designated, retaining all multistate characters as unordered, deleting the three outgroup taxa Kuehneosauridae, *Marmoretta*, and Rhynchocephalia, and rooting the analysis on the ancestor (run 8) yielded two equally parsimonious trees again, with TL = 548 [547], CI = 0.502 [0.503], and RI = 0.683 [0.684]. The relationships for the relevant taxa remained the same as in the previous search.

In a final note, we would like to point out that the stability of the (*Sineoamphisbaena* ((Amphisbaenia, Dibamidae) (Scolecophidia (*Dinilyisia* (Anilioidea (*Pachyrhachis*, Macrostomata)))))) clade is not simply due to the addition of the characters 231 through 239 (240)! Running analyses parallel to the ones above with all the characters from 231 through 239 (240) excluded (multistate characters ordered and unordered; characters 1 through 230 all retained, or those so designated deleted; and rooting on the three outgroup taxa Kuehneosauridae, *Marmoretta*, and Rhynchocephalia or on the ancestor) all reproduced that clade, with one difference: *Dinilyisia* invariably falls into an unresolved trichotomy with anilioids and the *Pachyrhachis*-Macrostomata clade. The strict consensus tree thus reads (*Sineoamphisbaena* ((Amphisbaenia, Dibamidae) (Scolecophidia (*Dinilyisia*, Anilioidea (*Pachyrhachis*, Macrostomata))))). And in all these trees, the taxa *Heloderma*, *Lanthanotus*, *Varanus*, and mosasauroids are related to that clade, either as a monophyletic unit or as a paraphyletic assemblage with mosasauroids closest to that clade. In essence, therefore, the addition of new characters (231 through 240) did not influence the basic results other than tree statistics and some increase in resolution among snakes.

Discussion of diagnostic characters is primarily based on DELTRAN character optimization, as it minimizes secondary loss of characters diagnostic at a higher level of inclusiveness. The synapomorphy listings for the (*Sineoamphisbaena* ((Amphisbaenia, Dibamidae) (Scolecophidia (*Dinilyisia* (Anilioidea (*Pachyrhachis*, Macrostomata)))))) are remarkably consistent throughout the eight analyses performed and discussed above (runs 1 through 8), with one exception. Runs 3 and 4 re-

tained the ordered multistate characters but deleted the characters so designated. This resulted in a loss of resolution, the (*Sineoamphisbaena* ((Amphisbaenia, Dibamidae) (Scolecophidia (*Dinilyisia* (Anilioidea (*Pachyrhachis*, Macrostomata)))))) clade falling into a polytomy with other squamates. That result lengthened the list of characters diagnostic for the root of this clade by three characters. The other nodes remained closely similar again to all other analyses performed. In the following, we list all the synapomorphies for the successive nodes in that clade, along with the character state (in parentheses). These lists correspond to run 1; differences in other runs are listed consecutively. Unequivocal synapomorphies (as determined in the first of the eight analyses) optimizing the same way in the ACCTRAN and DELTRAN mode (i.e., with $ci = 1$) are characterized by an asterisk (*). Bootstrap support and decay indices relate to the node characterized by the outermost brackets of the groupings.

(*Sineoamphisbaena* ((Amphisbaenia, Dibamidae) (Scolecophidia (*Dinilyisia* (Anilioidea (*Pachyrhachis*, Macrostomata))))): 19 (0), 25 (0), 33 (1), 51 (2), 54 (1), 56 (1), 58 (0), 60* (1), 71* (1), 72* (1), 75 (0), 80 (1), 98 (0), 149 (0), 155* (1). Run 2 is identical; runs 3 and 4 add 76 (1), 157 (1), 158 (1), 174 (1), 175 (1), and 218 (0) to that list but delete 75, 98, and 149; runs 5 and 6 add 161 and delete 80; runs 7 and 8 add 76 (1), 118 (0), 175 (1), 216 (0), and 218 (0) and delete 75, 80, 98, and 149. Run 2: bootstrap support, 69%; decay index = 5. Run 4: bootstrap support, 80%; decay index = 5.

((Amphisbaenia, Dibamidae) (Scolecophidia (*Dinilyisia* (Anilioidea (*Pachyrhachis*, Macrostomata)))): 8 (1), 12 (1), 23 (2), 29 (2), 35 (2), 37 (1), 38 (1), 40* (1), 46* (0), 49 (3), 66 (2), 80 (2), 81* (1), 84* (1), 116 (0), 129* (1), 168 (1), 172 (4), 189* (1), 190 (1), 194 (1), 197 (1), 204 (1), 206 (1), 211 (1), 222* (1), 232 (1), 235 (1). Run 2 is identical; runs 3 and 4 add 69 (1), 77 (1), 89 (2), 133 (0), 150 (1), 176 (2), 221 (0), 225 (1), and 226 (1) to that list and delete 116; runs 5 through 8 add 157 (2) and delete 190. Run 2: bootstrap support, 77%; decay index = 3. Run 4: bootstrap support, 85%; decay index = 7.

(Scolecophidia (*Dinilyisia* (Anilioidea (*Pachyrhachis*, Macrostomata)))): 3* (1), 16 (1), 45 (0), 54 (2), 59* (1), 61 (2), 63* (1), 68 (1), 73* (1), 89 (2), 94* (1), 97* (1), 100* (1), 106 (1), 110 (1), 111* (1), 119* (1), 152* (1), 153 (1), 154 (0), 167 (0), 169 (2), 172 (5), 190 (2), 200* (1), 207 (2), 227 (1), 234 (1), 235 (2); 236 (1). Run 2 is

identical; runs 3 and 4 add 117 (2), 128 (0), 146 (2), and 181 (1) to that list but delete 89; runs 5 and 6 delete 172 and 235; run 7 adds 128 (0) and deletes 172 and 235; run 8 adds 128 (0) and 181 (1) and deletes 172 and 235. Run 2: bootstrap support, 100%; decay index = 17. Run 4: bootstrap support, 100%; decay index = 21.

(*Dinilyisia* (Anilioidea (*Pachyrhachis*, Macrostromata)): 49 (2), 50 (3), 102 (0), 118 (2), 121 (2), 124 (1), 130* (3), 137 (1), 146 (3), 159 (0), 161 (0). Run 2 is identical; runs 3 and 4 delete character 102 from that list; runs 5 through 8 add character 157 (0). Run 2: bootstrap support, 94%; decay index = 10. Run 4: bootstrap support, 98%; decay index = 8.

(Anilioidea (*Pachyrhachis*, Macrostromata)): 87 (1), 107 (1), 141 (2), 151 (1), 160* (1), 231* (1), 237* (1). Runs 2, 5 and 6 are identical; runs 3 and 4, and 7 and 8, add character 156 (1) to that list. Run 2: bootstrap support, 72%; decay index = 2. Run 4: bootstrap support, 76%; decay index = 2.

(*Pachyrhachis*, Macrostromata): 47* (1), 50 (3), 157 (0), 158 (0), 233* (2), 238* (1), 239* (1). Run 2 is identical; runs 3 and 4 add character 120 (0) to that list; runs 5 through 8 delete character 157. Run 2: bootstrap support, 97%; decay index = 4. Run 4: bootstrap support, 98%; decay index = 4.

The most parsimonious result obtained in this analysis is run 8, which is based on the assumption that *Dinilyisia* lacks a jugal (character 12 retained, character 140 excluded) and had all multistate characters unordered, all characters so designated deleted, and was rooted on the ancestor. The result is ((*Heloderma* (Mosasauroida (*Lanthanotus* (*Varanus*))) (*Sineoamphisbaena* ((*Amphisbaenia*, Dibamidae) (Scolecophidia (*Dinilyisia* (Anilioidea (*Pachyrhachis*, Macrostromata)))))) (Fig. 17). Note, however, that the bootstrap support for the node linking mosasauroids or varanoids (including mosasauroids) to the amphisbaenian–dibamid–snake clade was consistently less than 50%; the decay index for that node is 1.

The Phylogenetic Relationships of *Pachyrhachis*, *Dinilyisia*, and *Dibamus*

Our analysis of snake interrelationships recognizes five terminal taxa, viz. Scolecophidia, *Dinilyisia*, Anilioidea, *Pachyrhachis*, and Macrostromata. The monophyly of macrostromatans is well

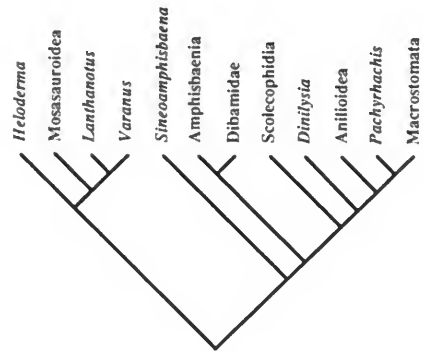


FIG. 17. Cladogram of the interrelationships of snakes obtained by reanalysis of the data of Lee (1998). For further discussion, see text.

corroborated (Rieppel, 1988), but the same cannot be said for scolecophidians or anilioids (Cundall et al., 1993). The test of the monophyly of Scolecophidia is beyond the scope of this paper and it is tentatively accepted here, but the monophyly of the Anilioidea has been corroborated in an independent study (Zaher & Rieppel, unpublished data), which is why we retain this taxon. One character that supports the monophyly of the Anilioidea in this latter work is the configuration of the perilymphatic foramen (Rieppel, 1979b).

Our analysis indicates that, among the terminal taxa used in this context, *Pachyrhachis* is the sister taxon of Macrostromata (Zaher, 1998). This result is very robust, as it was obtained in all analyses performed, with or without inclusion of the newly added characters 231 through 239 (240). Indeed, four unequivocal synapomorphies diagnose the clade including *Pachyrhachis* and Macrostromata, viz. supratemporal at least half of maximum skull width (47, 1), posterior dentigerous process of the dentary enlarged (233, 2), tooth-bearing anterior process of the palatine present (238, 1), and suprastapedial process of the quadrate absent (239, 1). This corroborates Zaher's (1998) earlier findings and removes *Pachyrhachis* from the position of a link between mosasauroid squamates and snakes (contra Carroll, 1988; Caldwell & Lee, 1997; Lee & Caldwell, 1998). The significance of the presence of posterior limbs in *Pachyrhachis* remains elusive at the present time. Either the limb was redeveloped from a rudimentary stage, as is still retained in basal alethinophidians, or relatively complete hind limbs were retained in a variety of fossil alethinophidian snakes that remain unknown (Zaher, 1998). Arguments for the position of *Pachyrhachis*

is that rely on the presence of hind limbs are ad hoc and ignore all the other data.

The relationship of *Dinilysia* as the sister taxon of alethinophidian snakes (Rieppel, 1988) is also well corroborated. Only by deletion of the newly added characters 231–239 (240) does *Dinilysia* fall into an unresolved trichotomy with the Anilioidea and the *Pachyrhachis*–*Macrostomata* clade. Although there is a substantial list of characters supporting this hypothesis of relationships of *Dinilysia*, only one character is an unequivocal synapomorphy: surangular extends far into lateral surface of dentary and terminates in a point (130, 3). In other words, *Dinilysia* shares the alethinophidian intramandibular joint.

Another sister-group relationship that we find well supported is the clade that comprises dibamids and amphisbaenians. The bootstrap support for the node linking dibamids to amphisbaenians is 95% (runs 2 and 4), and its decay index is 6 (runs 2 and 4). These two taxa are linked by an impressive list of characters (DELTRAN character optimization; run 1): 1 (1), 15 (1), 27 (1), 32 (1), 70 (1), 77 (2), 82 (0), 83 (1), 91 (1), 96 (1), 103 (1), 104 (1), 108 (1), 113 (0), 120 (1), 144 (1), 146 (1), 147 (0), 173 (0), 180* (1), 185 (0), 186 (0), 187 (1), 188* (1), 202 (3). Run 2 is identical; runs 3 and 4 add characters 102 (1) and 126 (0) to that list and delete characters 120, 146, and 185; runs 5 and 6 delete characters 103, 104, and 202; runs 7 and 8 add 126 (0) and delete 103, 104, 146, and 185. The two unequivocal synapomorphies linking these two taxa are caudal transverse processes project anterolaterally (180, 1), and proximal end of rib with posteroverventral pseudotuberculum (188, 1). This clade was also obtained by Lee (1998) and other authors (Caldwell, 1999; Evans & Barbadillo, 1998; Hallermann, 1998). We feel less confident, however, accepting other aspects of the cladogram(s) obtained in the present analyses, for reasons discussed below.

Discussion: Snake Origins, and Homology Versus Convergence

Based on his analysis, Lee (1998) concluded that the elongate fossorial ecomorph evolved independently in nonophidian squamates (e.g., dibamids and amphisbaenians) and in snakes. Although he recognized a suite of derived characters shared by snakes, dibamids, and amphisbaenians, he attributed these to miniaturization of fossorial forms (Lee, 1998, p. 415). Characters that diag-

nose the fossorial ecomorph were judged to be correlated, and a case was made that such characters need to be downweighted in order to avoid a “cascade of effects that lead to apparently strong support for a (probably spurious) phylogenetic hypothesis” (Lee, 1998, p. 417). This procedure was justified by reference to the claim that independent a priori evaluation of the potential phylogenetic information content of characters (on the basis of functional anatomy, for example) may be necessary to avoid mistaken conclusions (Lee & Doughty, 1997). That way, a phylogenetic hypothesis is reconstructed that is believed to be better in line with an evolutionary scenario supported, for example, by functional anatomical explanations (of the burrowing ecomorph in this example).

In our view, and contrary to Lee (1998; see also Lee & Doughty, 1997), this procedure is circular because empirically empty a priori assumptions about an evolutionary process are allowed to influence the phylogenetic analysis, when information about evolutionary processes, including functional anatomical explanations, should flow from the reconstructed phylogeny (e.g., Lauder & Liem, 1989). However, we agree with Lee (1998) that there is a serious potential for convergence in the evolution of the fossorial ecomorph owing to structural constraints that correlate with miniaturization and that affect not only dibamids, amphisbaenians, and snakes but also members of other “lizard” families as well, such as *Anniella* (Rieppel, 1984b). However, it remains unclear from Lee’s (1998) arguments why a clade grouping dibamids with amphisbaenians should be retained and even named, although it is supported by characters of the fossorial ecomorph, while the same characters are claimed to support “spurious” phylogenetic relationships of snakes and hence have to be downweighted if snakes are included in the analysis. We acknowledge, however, that the dibamid–amphisbaenian clade survives even more severe downweighting of these characters than is necessary to break the snakes away from that clade.

But just as snakes might group with amphisbaenians and dibamids on the basis of convergent characters correlated with fossorial habits, characters that are correlated with the evolution of the intramandibular joint might lend unjustified support to the snake–mosasaur link. As shown in our analysis of the intramandibular joint, there are enough structural differences in varanoids, mosasaurs, and snakes to justify at least the suspicion

that this functional complex evolved convergently in snakes and nonophidian squamates (Gauthier, 1982).

Several of the characters used in support of a monophyletic Pythonomorpha by Lee (1997, 1998) and Lee and Caldwell (1998) reflect the differentiation of an intramandibular joint. Estes et al. (1988, p. 253) recognized the problem of potential character correlation in association with the differentiation of an intramandibular joint such as the limited posterior extent of the splenial (L97: char. 72; LC98: char. B14). Lee (1997) lists a total of nine mandibular characters that group aigialosaurs, mosasaurs, and snakes. Of these, at least four are correlated with the development of an intramandibular joint: (L97: char. 68, 1; LC98: char. B8) mobile mandibular symphysis; (L97: char. 72, 1) posterior end of the splenial anterior to coronoid process; (L97: char. 73, 1; LC98: char. B12) splenial-angular contact abutting, straight, mobile; (L97: char. 75, 1; LC98: char. B14) coronoid not sutured to splenial. Characters used by Lee (1998) to analyze squamate interrelationships include even more potential synapomorphies that are correlated with the differentiation of an intramandibular joint (our dp-characters in the discussion of the character evidence above). But in contrast to the characters that diagnose the fossorial ecomorph, no attempt or recommendation was made by Lee (1998) to investigate the influence of potential character correlation related to the intramandibular joint on his phylogenetic analysis by downweighting or deleting those. In essence, however, we believe the strategy of downweighting characters to be misguided. In the absence of testability, some kind of correlation (ontogenetic, allometric, functional, etc.) can be invoked for any number of characters, which renders it impossible to establish objective criteria for justifiable degrees of downweighting.

As Lee (1998) postulates convergence of the burrowing ecomorph in the dibamid-amphisbaenian clade and in snakes, the phylogenetic link of snakes to marine mosasaurs becomes essential because it alone documents that snakes could have had a marine origin (Caldwell & Lee, 1997; Lee & Caldwell, 1998; Scanlon et al., 1999) and, consequently, that fossorial habits evolved independently within snakes. The phylogenetic relationships of *Pachyrhachis* thus becomes a key issue in this controversy, and Lee (1998) goes to great lengths to refute Zaher's (1998) conclusion that *Pachyrhachis* is not the most basal snake but

the sister group of Macrostromata (i.e., of relatively advanced snakes) instead.

However, by treating Serpentes as only one terminal taxon, Lee's (1998) analysis did not test Zaher's (1998) hypothesis, because *Pachyrhachis* had nowhere else to go other than being the sister taxon of Serpentes. Breaking up Serpentes as a terminal taxon is therefore important, not only to eliminate polymorphism in this terminal taxon but also to properly test the phylogenetic position of *Pachyrhachis*. Lee (1998) might have thought it unimportant to further test the relationships of *Pachyrhachis* in the context of a global analysis of squamate interrelationships because the position of this genus as the most basal snake had previously been obtained by Lee and Caldwell (1998). Yet the previous analysis of snake relationships conducted by Lee (1997) again constrained the search for the sister group of snakes to varanoid squamates, and many of the characters found in support of a monophyletic Pythonomorpha were used in the subsequent placement of *Pachyrhachis* (Lee & Caldwell, 1998). To provide as broad a basis as possible for the test of the phylogenetic relationships of *Pachyrhachis*, we added to the global squamate analysis presented above those characters that were used by Caldwell and Lee (1997), Lee and Caldwell (1998), and Zaher (1998), but were not included in Lee (1998).

Our discussion of Lee's (1998) evidence above indicates that many of his character definitions are flawed. For some of them, we propose new definitions, for others different codings; some we propose to delete from the analysis; others, which would not seem to directly affect the position of *Pachyrhachis* and the relationships of snakes to the amphisbaenian-dibamid clade, we simply retain. On the basis of only revising character definitions and/or codings as indicated above but without deletion of any character or addition of new characters, *Pachyrhachis* is already found to be the sister taxon of Macrostromata instead of being a link between mosasaurs and snakes, irrespective of whether multistate characters were ordered or unordered. At the same time, snakes group with the dibamid-amphisbaenian clade instead of with mosasaurs and varanoids. The relevant part of the cladogram reads as (varanoids (mosasaurs ((dibamids, amphisbaeniens) snakes))). Upon deletion of the problematic characters listed above, mosasaurs cluster within a monophyletic Varanoidea, which in turn forms the sister group of a clade that includes ((dibamids, amphisbaeniens) snakes). This result, although only very

weakly supported, is interesting, as it corresponds partly to the cladogram obtained by Evans and Barbadillo (1998). However, we believe that different dichotomies of this hierarchy have to be evaluated at different levels of confidence.

The position of *Pachyrhachis* as sister group of Macrostromata is here considered to be very robust. It had been obtained by critical reassessment (Zaher, 1998) of another data matrix previously used by Caldwell and Lee (1997); it is obtained in this study by a critical review of the character evidence used by Lee (1998); and it is corroborated by an independently compiled data set focusing on cranial characters and the interrelationships of basal snakes (Zaher & Rieppel, unpublished data).

With *Pachyrhachis* nested within snakes as sister taxon of Macrostromata, the hypothesis that snakes had an aquatic origin (Caldwell & Lee, 1997; Lee & Caldwell, 1998) loses its empirical basis. The taxa Ophidia and Serpentes as defined by Lee and Caldwell (1998) become redundant. The name to be retained for reasons of priority is Serpentes Linnaeus, 1758 (Linnaeus included caecilians within his Serpentes; as pointed out by Kuhn [1967], the name Serpentes can already be found in the writings of Albertus Magnus). Unless another intermediate fossil is found to relate snakes to mosasauroids, the hypothesis of a terrestrial origin of snakes is more parsimonious. Given our currently poor understanding of the sister-group relationships of snakes within squamates, there is no good basis on which to try to optimize a terrestrial versus an aquatic origin of snakes, however.

In light of our discussion of characters related to squamate dentition (Zaher & Rieppel, 1999), braincase structure (Rieppel & Zaher, in press), and intramandibular joint structure, the putative relationship of snakes with mosasauroids appears to have a weak morphological basis. It is certainly not supported after critical assessment of the data set used by Lee (1998). Conversely, the corrected data set still shows mosasauroids (or varanoids inclusive of mosasauroids) to be pulled into a sister-group relationship with the amphisbaenian/dibamid-snake clade, which indicates similarities shared at some level of the analysis. Corroboration of the monophyly of Pythonomorpha (Lee, 1997) will require new and additional morphological characters but still remains a possibility because molecular data do support a sister-group relationship of snakes and varanoids (Reeder, 1995; Forstner et al., 1995). The same is true of some

soft anatomy characters (McDowell & Bogert, 1954; McDowell, 1972; Schwenk, 1988).

Critical reassessment of the data matrix compiled by Lee (1998) results in snakes being the sister clade to dibamids and amphisbaenians. This clade is very robust in our analysis and conflicts with Lee's (1998) argument for convergence. It is interesting to note that the only total evidence approach to the phylogenetic relationships of snakes reported so far found the same result, i.e., snakes grouping with dibamids and amphisbaenians, although the separate analysis of the same DNA data yielded a grouping of snakes with varanoids (Reeder, 1995). This finding in itself suggests that the morphological data may be subject to convergence, and structural constraints resulting from miniaturization may provide a reasonable explanation for such rampant homoplasy of morphological characters (Rieppel, 1984b). However, the acceptance of convergence cannot be an a priori (and hence empirically empty) assumption but must follow from phylogenetic analysis. The difficulty here is that convergence, if indeed involved in this case, may result in such a strong signal that the node linking snakes to the dibamid-amphisbaenian clade cannot be broken on anatomical grounds. The solution cannot be an arbitrary weighting or ordering of characters. Instead, the analysis of snake relationships among squamates would seem to be a classical case calling for a combination of molecular and morphological data (Reeder, 1995). In addition, it should be noted that almost all of the morphological data that have so far been brought to bear on this question are osteological characters, many of which are particularly subject to structural constraints correlated with miniaturization. In addition to molecular data, it would seem that the inclusion of soft anatomy characters may help to resolve the question of homoplasy versus homology in the comparison of snakes, dibamids, and amphisbaenians (Senn & Northcutt, 1973). Hallermann (1998), for example, used the ethmoidal region (nasal capsule and associated structures) in the analysis of phylogenetic relationships of squamates, and found a sister-group relationship of snakes with the dibamid-amphisbaenian clade on the basis of a character complex that would seem to be less subject to structural constraints resulting from miniaturization than would be the braincase and surrounding structures.

Indeed, the long list of characters shared by *Sineoamphisbaena*, amphisbaenians, dibamids, and snakes (see above, primarily run 1) includes, for

the most part, characters that appear to be related to miniaturization and/or paedomorphosis in fossorial or burrowing squamates. However, there are also some shared characters that would not seem to be related to fossorial or burrowing habits. Recognizing that the interpretation of morphological characters in terms of putative adaptations is fraught with difficulties, we propose the following loose groupings of the characters shared by *Sineoamphisbaena*, amphisbaenians, dibamids, and snakes.

Characters that appear to be related to paedomorphosis coupled with miniaturization in fossorial or burrowing squamates are loss of the lacrimal (8); loss of the jugal (12); loss of the postfrontal (23); postfrontal (postorbitofrontal), where present, not forked medially (25); incomplete posterior orbital margin (29); loss of posterolateral processes of the parietal (37); incomplete upper temporal arch (38); loss of squamosal (40); reduction of crista prootica (66).

Characters that are coupled with structural remodeling of the skull in miniaturized fossorial or burrowing squamates, resulting primarily from an increased relative size of the braincase, are jaw adductor muscles invading the dorsal surface of the parietal (35); quadrate suspension mainly from opisthotic (49); parietal downgrowths prominent (56); alar process on prootic absent (58); otic capsule expanded laterally (71); stapes robust, footplate large (72); closure of the posttemporal fossae (80, 84); neurocranium and dermatocranium positioned at same level (81).

Characters potentially directly related to fossorial or burrowing habits are pineal foramen absent (33); tympanic crest on quadrate absent (51); neural spines are low ridges (168); elongation of trunk (172); scapulocoracoid reduced (190); clavicle absent (194); interclavicle absent (197); forelimbs small or absent (204); pelvis reduced (206); hind limbs rudimentary or absent (211, 235, 236).

Finally, characters that do not appear to be related to miniaturization and/or paedomorphosis nor to fossorial or burrowing habits are frontal with straight or weakly concave orbital margin (19); palatine as long as vomer (98); intramandibular septum of dentary does not approach posteriormost tooth position (116); compound bone in lower jaw present (129); tooth crowns closely spaced (149); medial premaxillary tooth enlarged (155); lymphapophyses present (189); scleral ossicles absent (222); cartilaginous processus ascendens of supraoccipital absent (232). At an early date, Rage (1982) proposed a cladistic relation-

ship of snakes with amphisbaenians and dibamids; this hypothesis continues to be worth testing. A relation to fossoriality does not, after all, preclude any character a priori from being homologous in a clade comprising amphisbaenians, dibamids, and snakes. Although the potential for convergence certainly exists, there exists also the possibility that this clade evolved from a fossorial ancestor, from which the descendants inherited the characters of the fossorial ecomorph.

At this point, we refrain from comments on other parts of the hierarchy obtained by the revision of Lee's (1998) data matrix. The primary reason is that we critically reassessed characters and character states for dibamids, amphisbaenians, varanoids, mosasaurs, *Pachyrhachis*, and other snakes only, in order to test the relative relationships of these key taxa. In order to comment on other aspects of this phylogeny, critical reassessment of the character evidence would have to cover all other nonophidian squamate families, as was pointed out above (problems of varanoid codings have also been highlighted by Gao & Norell, 1998). In this context, we note that a tree only one step longer than the most parsimonious reconstruction results in a dramatic loss of resolution already outside the *Sineoamphisbaena*-amphisbaenian/dibamid-snake clade, and a tree four steps (run 2) or three steps (run 4) longer results in a loss of all resolution outside the latter clade. As discussed in more detail above, the coding of nonophidian squamates at the family level only by Lee (1998) calls for greater scrutiny. This opens an avenue to a long-term project. When a new data matrix is built to investigate squamate interrelationships, the basic topology or the relative support for the different nodes discussed in this paper may change dramatically. At this point, it may suffice to point out that the conclusions reached by Lee (1998)—namely, that *Pachyrhachis* is the most basal snake, linking this group to mosasauroids (Caldwell & Lee, 1997; Lee & Caldwell, 1998); that snakes (therefore) may be inferred to have had a marine origin (Scanlon et al., 1999); and that the fossorial ecomorph (therefore) evolved convergently in dibamids plus amphisbaenians as opposed to snakes—do not pass the test of critical examination of the character evidence he used in their support.

Notes Added in Proof

While this paper was in press, Lee, Bell, et al. (1999) presented a gradualistic model for the evo-

lution of the ophidian feeding mechanism from the ancestral mosasauroid condition, with *Pachyrhachis* as an intermediate stage. Mediolateral flexion of the mandible in mosasaurs (previously described by Telles Antunes [1964, pp. 156 ff. and Fig. 22], in a monograph overlooked by Lee, Bell, et al. [1999]) was interpreted as the starting point for the evolution of ophidian jaw mechanics. However, both the description of the intramandibular joint in squamates given above and the macrostomatian affinities of *Pachyrhachis* invalidate this scenario.

Lee, Caldwell, et al. (1999) also redescribed *Pachyophis woodwardi* Nopcsa (1923) from the Cretaceous of Bosnia-Herzegovina. In order to analyze its relationships, Lee, Caldwell, et al. (1999) used the data matrix in Lee (1998), which we reviewed above, to which they added two characters: pachyostosis of mid-dorsal vertebrae and ribs, and the laterally compressed body. *Pachyophis* was found to be the sister taxon of *Pachyrhachis* on the basis of these two characters, and the two taxa were classified in a family of their own, the Pachyophiidae, again placed as sister taxon to all other snakes.

We were unable at this time to inspect the holotype of *Pachyophis*, but based on the description by Lee, Caldwell, et al. (1999), we doubt the ophidian status of this taxon (see also Rage, 1984). With an estimated 120 presacral vertebrae, the vertebral count is lower in *Pachyophis*. The posterior part of the preserved vertebral column appears to us to closely approach the sacral or cloacal region. *Pachyophis* shows a greater degree of pachyostosis than *Pachyrhachis*, and pachyostosis persists into the posterior dorsal region instead of remaining restricted to the midtrunk as in *Pachyrhachis*. The latter taxon also shows elongated, nonpachyostotic ribs shortly in front of the "pelvic" region, before the last three or four ribs become abruptly shortened. In *Pachyophis*, the ribs gradually decrease in length in the posterior dorsal region, which accordingly would not have been laterally compressed as it was in *Pachyrhachis*.

More important, Lee, Caldwell, et al. (1999) interpret a fragmentary bone as part of the right dentary. Their rendering of this fragment in their Figure 3b shows the anteriorly convex angular being received by the posteriorly concave splenial. We understand from Nopcsa's (1923) description that this element is difficult to identify, but if the interpretation given by Lee, Caldwell, et al. (1999, Fig. 3b) is correct, *Pachyophis* shares the mosauroid

intramandibular joint, which is different from that of snakes and also different from that of *Pachyrhachis* (Lee & Caldwell, 1998, Fig. 4). Given the incompleteness of the material, we believe the best solution is to retain *Pachyophis* (Pachyophiidae) as incertae sedis among squamates.

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