ADRIOSAURUS AND THE AFFINITIES OF MOSASAURS, DOLICHOSAURS, AND SNAKES

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ABSTRACT—The poorly-known, long bodied, limb-reduced marine lizard *Adriosaurus suessi* Seeley, 1881, is reassessed. *Adriosaurus* and a number of other marine lizards are known from Upper Cretaceous (Upper Cenomanian-Lower Turonian) marine carbonate rocks exposed along the Dalmatian coast of the Adriatic Sea, from Komen, Slovenia, to Hvar Island, Croatia. A revised vertebral count reveals 10 cervical, 29 dorsal, and at least 65 caudal vertebrae. The projections previously interpreted as hypapophyses are instead transverse processes. Openings on the anterior part of the skull, previously described as external nares, are probably internal nares. Important features not noted previously include accessory articulations on all presacral vertebrae, pachyostosis of dorsal vertebrae and ribs, and the presence of two pygal vertebrae. Phylogenetic analysis of 258 osteological characters and all the major squamate lineages suggests that *Adriosaurus* and dolichosaurs are successive sister-taxa to snakes. This is consistent with their long-bodied, limb-reduced morphology being intermediate between typical marine squamates (e.g., mosasaurs) and primitive marine snakes (pachyophiids). The analysis further reveals that up to five successive outgroups to living snakes (pachyophiids, *Adriosaurus,* dolichosaurs, *Aphanizocnemus,* and mosasauroids) are all marine, suggesting a marine (or at least, semi-aquatic) phase in snake origins. These phylogenetic results are robust whether multistate characters are ordered or unordered, thus refuting recent suggestions that snakes cluster with amphisbaenians and dibamids (rather than aquatic lizards) if multistate characters are left unordered. Also, the recent suggestion that *Pachyrhachis* shares synapomorphies with advanced snakes (macrostomatans) is shown to be poorly supported, because the reinterpretations of the relevant skull elements are unlikely and, even if accepted, the character states proposed to unite *Pachyrhachis* and advanced snakes are also present in more basal snakes and/or the nearest lizard outgroups, and are consequently primitive for snakes.

INTRODUCTION

DURING THE Cretaceous, within the coastal habitats of the southern European epicontinental Tethys, there was an extensive radiation of marine squamates that included the medium-sized eel-like pachyophiids, the small, long-necked dolichosaurs, and the larger aigialosaurs and mosasaurs. These forms were suggested long ago to be closely related to each other and possibly to snakes (e.g., Cope, 1869; Kramberger, 1892; Nopcsa, 1923), a view which has been supported by some recent phylogenetic analyses (e.g., Lee, 1998; Caldwell, 1999a). While a number of these groups, such as coniasaurs (Caldwell, 1999b; Caldwell and Cooper, 1999), dolichosaurs (Caldwell, in press), mosasaurs (e.g., DeBraga and Carroll, 1993; Lingham-Soliar, 1994; Bell, 1997), aigialosaurs (Carroll and deBraga, 1992; Caldwell et. al., 1995; Polcyn et al., 1999), and *Aphanizocnemus* (Dal Sasso and Pinna, 1997), have recently been studied and described, a number of others have not been studied since early this century. The affinities of these latter taxa, and their implications for the possible evolutionary relationship between snakes and aquatic lizards, remains unknown.

Adriosaurus suessi is one such taxon. It is a small, elongate Upper Cretaceous marine lizard with a long laterally compressed tail and reduced limbs. Seeley (1881) described the taxon based on a single specimen from near Comen, Slovenia, consisting of the posterior half of the vertebral column, the pelvis and hindlimbs. Nopcsa (1908, 1923) later described a nearly complete skeleton and placed it within his broadly defined Dolichosauria. This referred specimen comes from rocks of similar age exposed on the island of Hvar, Croatia ([Nopcsa (1908)] used the Italian name Isola di Lesina).

Nopsca's (1908) systematic conclusions are not robust since phylogenetic reconstruction was largely intuitive at the time. He grouped together all the dolichosaur-like forms on the basis of aquatic habits, long bodies, and limb reduction. The possibility that some or all of these forms might be related to other squamates (on the basis of other characters) was not explicitly investigated. The two specimens of *Adriosaurus* have not been studied in detail since. Here, we redescribe the more complete specimen of *Adriosaurus,* compare it to the type, and undertake a phylogenetic analysis to ascertain its position, and that of other dolichosaur-like forms, within squamates. The results place these long-bodied aquatic forms very close to snakes, and hold whether multistate characters are ordered or unordered. However, there are several other potential biases that make this interpretation tentative.

MATERIALS AND METHODS

The specimen of *Adriosaurus suessi* described here (NHM R2867) required some minor re-preparation. All work was completed by technicians at the Natural History Museum (=British Museum, Natural History), London, England. Specimen drawings were made using a microscope with camera lucida attachment. Photographs were taken by technicians employed by The Natural History Museum, London. Measurements were made using digital calipers.

Museum abbreviations for specimens figured: (NHM), Natural History Museum, London, England; (NMW) Naturhistorisches Museum, Vienna.

SYSTEMATIC PALEONTOLOGY

Monophyletic Rankless Hierarchy
(de Queiroz and Gauthier, 1992)
SQUAMATA Oppel, 1811
VARANOIDEA Camp, 1923
PYTHONOMORPHA Cope, 1869
ADRIOSAURUS Seeley, 1881
ADRIOSAURUS SUESSI Seeley, 1881
Figures 1–7

Revised Diagnosis.—Small marine squamate with elongate neck, body, and tail. Ten cervical, 29 dorsal, and at least 65 caudal vertebrae. Zygosphenes and zygantra present throughout presacral region. Tail deep and laterally compressed. Forelimbs
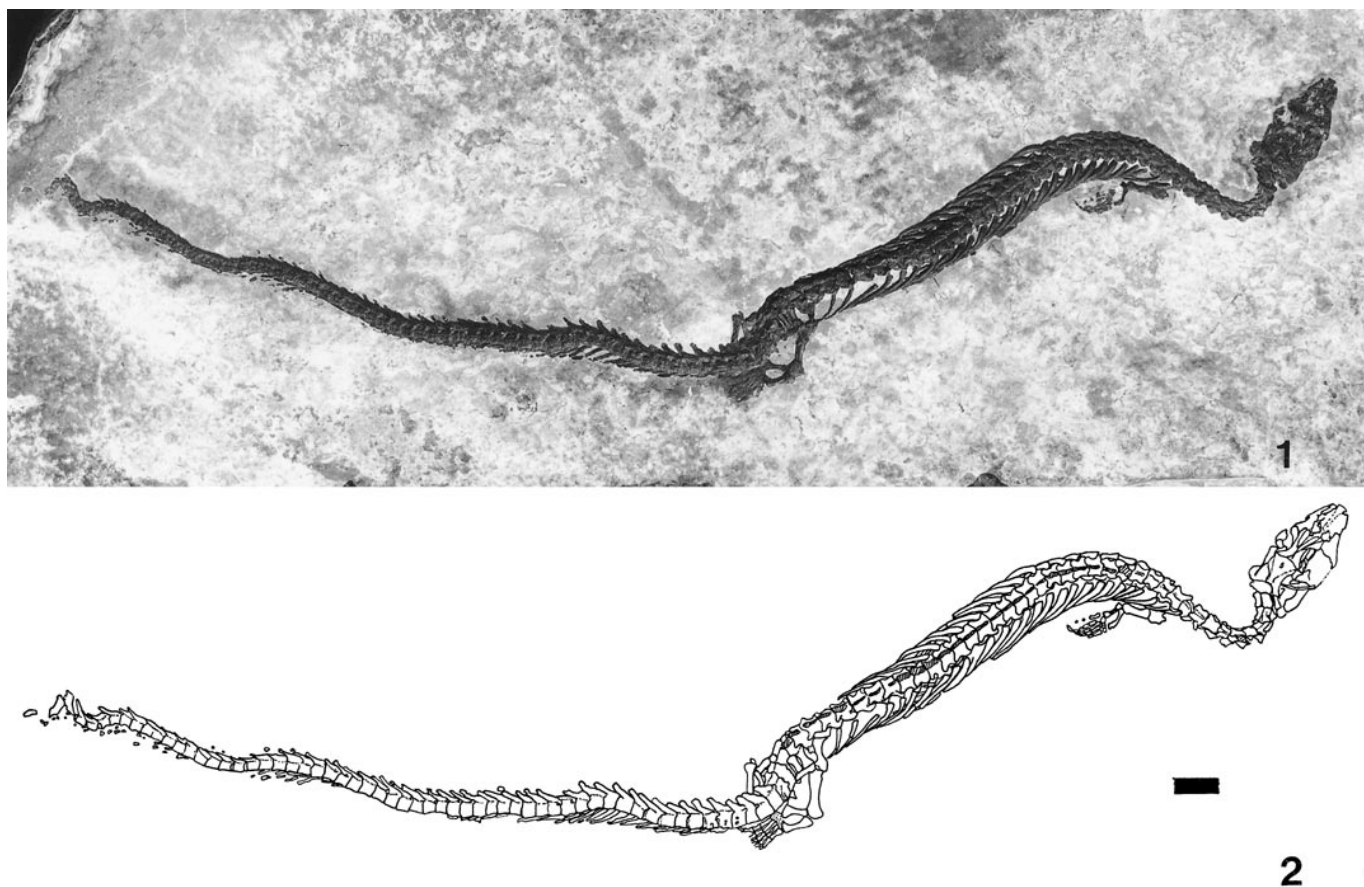
FIGURE *1*—*Adriosaurus suessi,* NHM R2867, specimen as preserved. *1*, Photo; *2*, interpretative drawing. All structures are labelled in the illustrations of each region (see Figs. 3–6). Scale bar = 10 mm.

and hindlimbs reduced in size; forelimbs much shorter than hindlimbs. Differs from other lizard-grade squamates in exhibiting the following unusual characters: laterally compressed trunk region, pachyostotic dorsal vertebrae and ribs, and very elongate tail skeleton.

Type.—The ''Vienna'' specimen, unnumbered, in the Naturhistorisches Museum,Vienna (see Seeley, 1881; Nopcsa 1908). Slab with posterior trunk region, pelvis, hindlimb, and tail (Fig. 2). Locality: Near Komen, Slovenia (Upper Cenomanian, Upper Cretaceous), from the Komen Platey Limestone.

Referred material.—NHM R2867: complete specimen on slab, described by Nopcsa (1908, 1923). Locality: Hvar Island (=Isola di Lesina), 43°10′N, 16°30′E, Croatia, in the local Plattenkalken (Upper Cenomanian-Upper Turonian; Upper Cretaceous). This specimen is re-evaluated here and compared to the type (Figs. 1, 3–6).

Description.—The specimen is almost complete and fully articulated; however, the last few caudals are missing and many of the elements on the ventral surface are not visible, but could be revealed if the slab were embedded in resin and prepared from the reverse side. The skull and presacral region are exposed in dorsal view. The body then twists at the sacrum so that the tail is exposed in right lateral view. The right limbs and girdles are well exposed, the left hindlimb and pelvis are partly covered by the axial skeleton, and the left forelimb and shoulder girdle are completely hidden. The backbone is preserved in an S-shaped curve in the cervical region. The dorsal region is relatively straight and there is a slight bend in the anterior caudal region and a slight bend in the distal caudal region.

Skull.—The skull is crushed dorsoventrally, and elements of the snout and temporal region are poorly preserved (Fig. 3). The only elements that can be identified with certainty are the premaxilla, maxilla, frontal, prefrontal, postorbitofrontal, parietal, and supraoccipital. The posterior end of the right mandible is also clearly identifiable but the boundaries of the elements are unclear. The jugal, ectopterygoid, epipterygoid, pterygoid, squamosal, and supratemporal appear to be visible but identification of these elements remains tentative.

The premaxilla is a small, single element with no trace of a median suture. It is flat anteriorly. A tooth is visible on the left, projecting ventrolaterally. Based on the size of this tooth, the premaxilla could have borne at most four alveoli.

The maxilla is best preserved on the right side. It is a large element, highest in the posterior third. It tapers both anteriorly (reaching the premaxilla) and posteriorly (under the orbit). Dorsally, it meets the prefrontal at its highest point. There is a smoothly concave margin anteriorly that forms the ventral border of the external naris. The left maxilla is badly damaged and adds little information, but contains three visible teeth and another tooth fragment (see later).

Two vacuities in the snout region were interpreted by Nopcsa (1908) as external nares. However, the region is so badly damaged that this is uncertain. A more likely possibility is that the nasals and dorsal process of the premaxilla have been eroded, exposing the palate in this area. This is consistent with the observation that teeth from the mandibles and palate are exposed here; such teeth would not be expected if the exposed part of the snout region were the skull roof. If this area is the palate rather than the skull
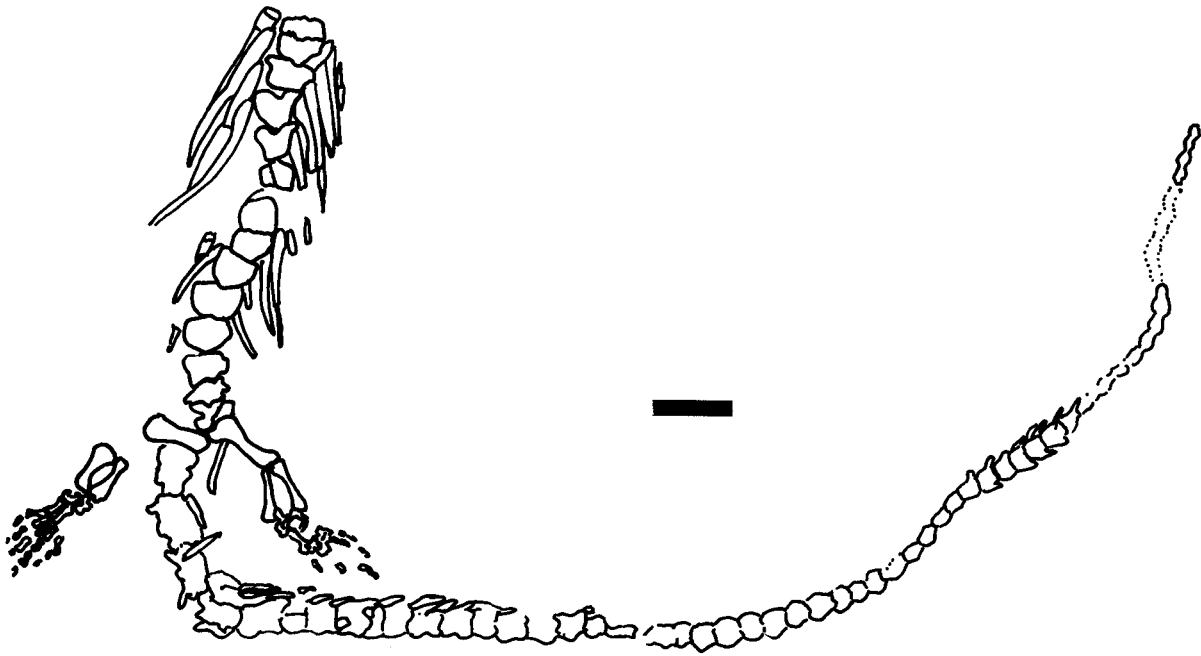
FIGURE 2—Holotype, *Adriosaurus suessi,* NMW, unnumbered specimen, line drawing of specimen as preserved. Scale bar = 10 mm.

roof, the two vacuities would represent the internal nares rather than the external nares.

The margins of the nasals are unclear. Several oblique discontinuities in the anterior region of the frontals might be nasal sutures; Nopsca interpreted some of these as sutures but did not specify which ones. None are particularly likely to be the real sutures, since they would all imply unusually short frontals and unusually long nasals, opposite to the pattern found in marine squamates such as mosasaurs (long frontals, nasals vestigial to absent).

The frontals are clearly visible. They are large, paired elements, constricted in the middle, greatly expanded posteriorly, and at least slightly expanded anteriorly. The anterior boundary with the nasals is unclear. The suture with the parietal is transverse, and appears to be M-shaped rather than straight. The frontals form much of the dorsal margin of the large orbits.

The prefrontals are large sickle-shaped bones. Each is widest ventrally, near its contact with the maxilla, and tapers posterodorsally, extending along the lateral margin of the frontals and forming part of the orbital margin.

The parietal is a large, single element, widest anteriorly, tapering posteriorly, and centrally bearing a large teardrop-shaped foramen. A large descending flange is visible on the right; this walled the brain cavity dorsolaterally and presumably attached to the prootic ventrally. Presence of posterolateral (suspensorial) rami of the parietal cannot be determined due to poor preservation.

The left postorbitofrontal is clearly visible. A similar element on the right might represent the dorsal part of the right postorbitofrontal, but preservation is too poor to be certain. No suture is visible between the postfrontal and postorbital, but again, genuine absence of the suture cannot be confirmed due to poor preservation. The postorbitofrontal is forked medially. The anterior ramus is narrow and extends along the lateral margin of the frontal, forming part of the orbital margin. The limits of the posteromedial ramus are less clear; however, it appears to be long, and wider than the anterior process. There is a distinct ventral process

that formed the posterior margin of the orbit, and presumably met the jugal.

The jugal and ectopterygoid are probably represented by an amorphous mass under the left orbit. However, the boundaries between the two elements are unclear. The posterior half of the mass probably represents the jugal, which is a large bone that curves anteroventrally to meet the ectopterygoid. The ectopterygoid, presumably represented by the anterior half of the mass, is large and curves anteriorly to meet the posterior end of the maxilla.

The identification of the supratemporals is tentative. Two indistinct shapes can be seen extending posterolaterally from the parietal, tapering distally. These are symmetrical, and either represent the suspensorial rami of the parietal, or distinct supratemporals. As they both appear to be separated from the main body of the parietal the latter interpretation is preferred. This would imply that the supratemporals are large and lie on top of the parietal, as in snakes, rather than partially beneath the suspensorial rami as in other squamates (lizards).

The right squamosal might be represented by a boomerang-shaped element that is located immediately lateral to the right ''supratemporal.'' If correctly identified, it would have extended anteriorly to meet the postorbitofrontal, forming a complete upper temporal arch.

The right pterygoid might be represented by a long curved plate of bone in the palatal region, visible lateral to the frontals and parietal; it is not possible to determine the presence or absence of teeth. A medial bulge near the parietal might represent the basipterygoid articulation. From this region the element extends both anteriorly and posterolaterally, but further details cannot be discerned.

The supraoccipital is a tranversely broad element. It appears to be situated behind, rather than below, the parietal, but this might be due to crushing. In any case, the contact between the two elements is extensive and firm.

The right epipterygoid might be represented by a columnar element exposed between the separated right postorbitofrontal
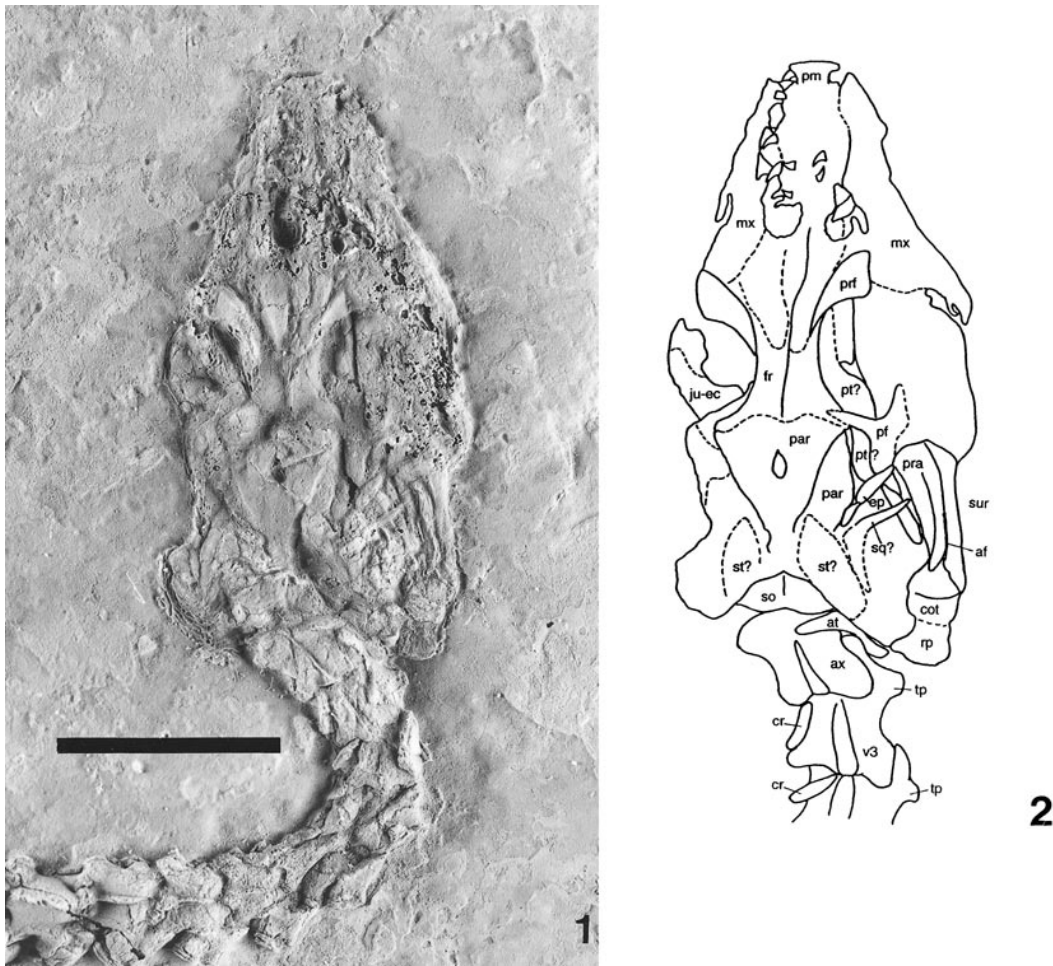
FIGURE 3—*Adriosaurus suessi,* NHM R2867, details of skull and anterior cervical vertebrae. *1,* Photo; *2,* interpretative drawing. Abbreviations: af—adductor fossa, at—atlas, ax—axis, cot—articular cotyle of mandible, cr—cervical rib, ep—epipterygoid, fr—frontal, ju-ec—jugal and/or ectopterygoid, mx—maxilla, par—parietal, pf—postorbitofrontal, pm—premaxilla, pra—prearticular, prf—prefrontal, pt?—probable pterygoid, rp—retroarticular process, so—supraoccipital, sq?—probable squamosal, st?—probable supratemporal, sur—surangular, tp—transverse process, v3—third presacral. Scale bar = 10 mm.

and "squamosal." It is the appropriate shape (a simple rod) and in the expected position on the dorsal surface of the pterygoid, immediately behind the basipterygoid articulation, and lateral to the braincase wall (parietal flange).

The posterior end of the right mandible is exposed in dorso-lateral view. The articular cotyle occupies an extensive area. The region in front of the cotyle bears two longitudinal grooves. One of these must represent the adductor fossa, but it is not certain which one. The sliver of bone on the external edge presumably represents part of the surangular, while the medial sliver presumably represents part of the prearticular. The surangular appears to be distinct from the articular, and does not form part of the articular cotyle. Whether the prearticular was distinct or fused to the articular cannot be determined. The retroarticular process is long and broad. The dorsal surface is smooth and transversely concave. There appears to be a medial projection but this is not certain, as there is a discontinuity between the "projection" and the rest of the retroarticular process.

Several teeth are preserved in the snout region. One is preserved on the premaxilla, and three (plus a fragment) on the left maxilla. Six more teeth can be identified in the middle of the snout region. These presumably belong to the dentaries. However, there is the (less likely) possibility that *Adriosaurus* had large palatine or pterygoid teeth and that the teeth on the snout are thus disarticulated palatal teeth. The teeth on the premaxilla and the anterior tip of the maxilla are small; the teeth preserved in the snout region are mostly intermediate in size, while the two nearer the middle of the maxilla are large. The teeth are pointed, recurved, and widely spaced, but the presence of carinae or plicidentine cannot be confirmed due to poor preservation.

Vertebrae.—Nopcsa stated that the atlas was missing. However, a sliver of bone between the supraoccipital and axis is most probably the right atlas neural arch (Fig. 3). It is a simple curved plate, extending dorsomedially over the neural canal.

The cervical vertebrae are all exposed dorsally (Fig. 1, 3, 4), and are so similar that they can be described together. Including the atlas, there appear to be ten cervical vertebrae. Small ribs are preserved on the left side of presacrals three to nine; these are all short, narrow curved elements. A slightly larger rib is preserved adjacent to presacral ten (Fig. 4). None are pachyostotic. The tenth presacral is positioned immediately in front of the shoulder girdle (Fig. 4), and is followed by vertebrae with large, pachyostotic ribs. Thus, it can be reasonably inferred that the cervical-dorsal boundary was positioned between vertebrae 10 and 11. In contrast, Nopcsa (1908) suggested that there were
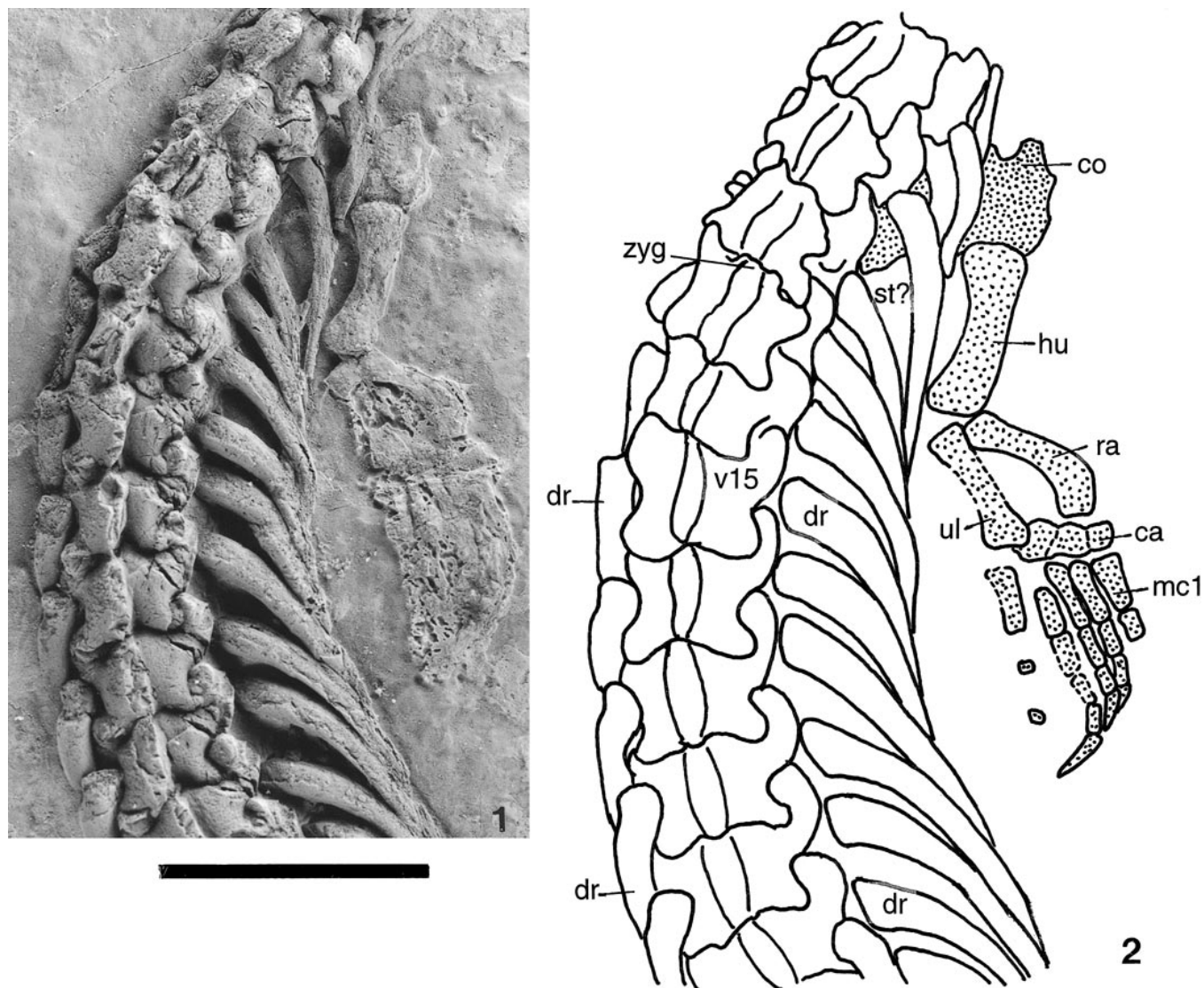
FIGURE 4—*Adriosaurus suessi,* NHM R2867, details of shoulder region and anterior presacrals. *1,* Photo; *2,* interpretative drawing. Abbreviations: ca—carpals, co—coracoid, dr—dorsal rib, hu—humerus, mc1—first metacarpal, ra—radius, st?—probable sternum, ul—ulna, v15—presacral 15, zyg—zygosphene. Scale bar = 10 mm.

most likely 13 (range 11–14) cervicals, but did not justify this. He also stated there were eleven rib-free vertebrae including the atlas. However, as noted above, ribs are visible from the third vertebrae onwards.

On each cervical verterbra, the neural arch is moderately wide with lateral expansions both anteriorly (prezygapophysial) and posteriorly (postzygapophysial). They are not pachyostotic, and the prezygapophysial surfaces are slightly inclined medially. A neural spine extends sagittally along the entire length of the neural arch. It is narrow transversely but long anteroposteriorly. The tips of the neural spines are broken off in all vertebrae. Adjacent neural arches are closely apposed and accessory vertebral articulations (zygosphenes and zygantra) extend between them, though their exact nature cannot be discerned. The transverse process is prominent, and is visible projecting on the left side.

The lateral and ventral surfaces of the centra are not exposed in any presacral vertebra, including the cervicals. Nopcsa's report of ventral "hypapophyses" appears to be a misidentification of the left transverse processes.

There are 29 dorsal vertebrae (Figs. 1, 4, 5) all of which bear large ribs. Nopsca considered the animal to possess 27 dorsals. All dorsal vertebrae are exposed in dorsal view only. As with the cervicals, there is a butterfly-shaped neural arch with a blade-like neural spine, anterior and posterior lateral expansions for the zygapophyses, and zygosphene-zygantral articulations. Nopsca was uncertain if zygosphene-zygantral articulations were present, but suspected they were. They are clearly visible in some vertebrae (Fig. 4), but their exact nature is again uncertain due to the whole column being articulated.

There are some differences between the dorsals and the cervicals. The neural arches of the dorsals are much wider and swollen, so that the dorsal surfaces are convex, rather than flat, transversely. The transverse processes are much less prominent and the ribs articulate flush with the body of the centrum. The centra were also presumably more robust, but this cannot be confirmed as none are exposed.

The dorsal ribs are long and robust, and exhibit a very distinctive L-shape. There is a short proximal section that extends
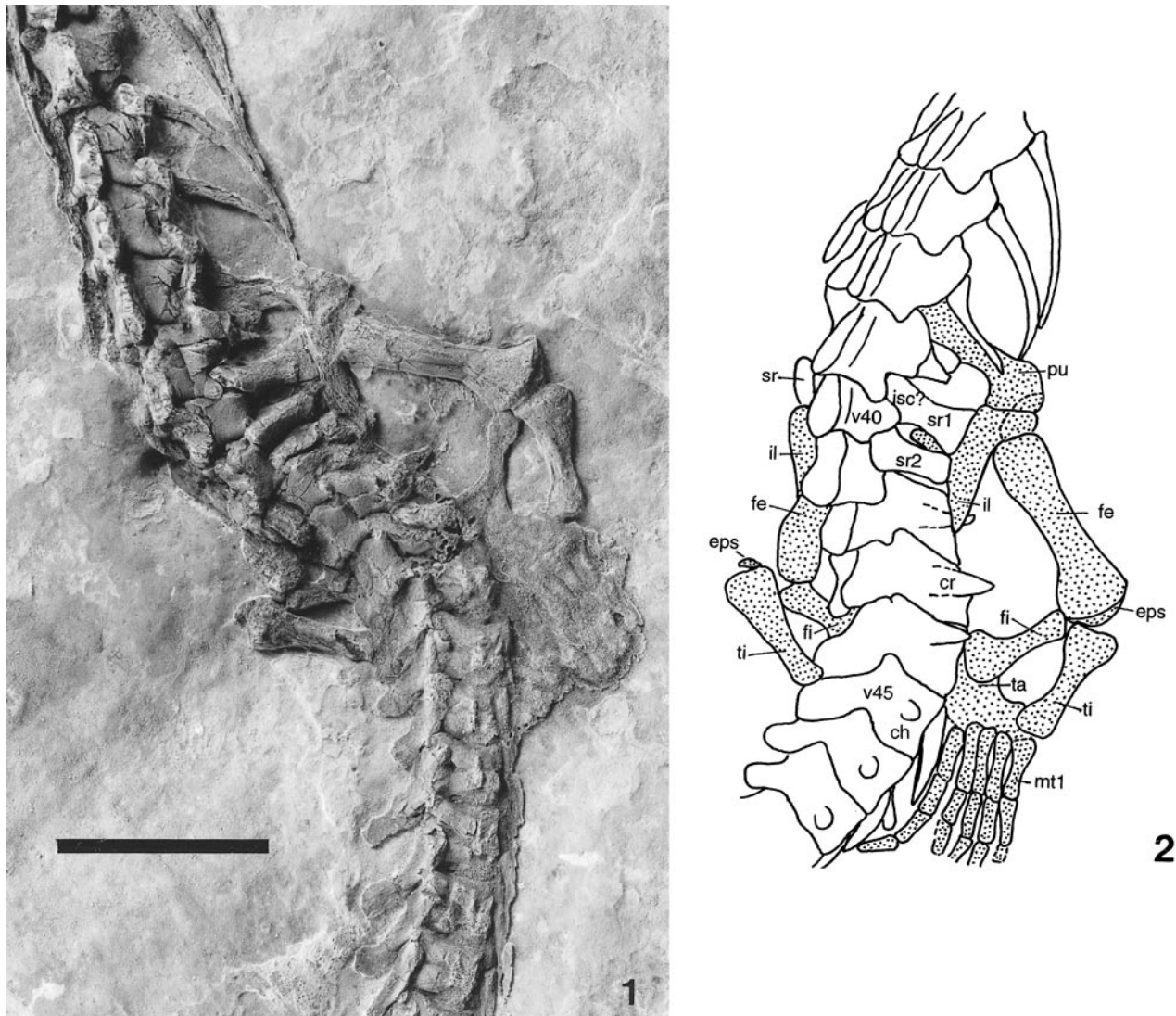
FIGURE 5—*Adriosaurus suessi,* NHM R2867, details of pelvic region and posterior presacral, sacral, and anterior caudal vertebrae. *1*, Photo; *2*, interpretative drawing. Abbreviations: ch—chevron, cr—caudal rib, eps—epiphysis, fe—femur, fi—fibula, il—ilium, isc?—probable ischium, mt1—first metatarsal, pu—pubis, sr1—first sacral rib, sr2—second sacral rib, ti—tibia, ta—tarsus, v40—presacral vertebra 40, v45—presacral vertebra 45. Scale bar = 10 mm.

ventrolaterally from the centrum, followed by a long straight section that extends ventrally and slightly posteriorly. This indicates that the body was laterally compressed. A slight constriction is present just distal to the proximal articulatory surface.

Most ribs are heavily ossified and swollen (pachyostotic), a very prominent feature not noted by Nopcsa. This is most developed at about the middle of the dorsal region but decreases in magnitude anteriorly and posteriorly, so that the anterior and posterior few pairs are almost 'normal' in morphology. Within a rib, pachyostosis is most developed in the proximal half, the distal end of the shaft being narrow and less heavily ossfied.

There are two sacral vertebrae, clearly exposed in dorsolateral view (Fig. 5). These are similar to the dorsals except for the nature of the ribs. The two right sacral ribs are clearly visible; a portion of the left first sacral might also be visible. The sacrals are fused to the centra and are short, blunt, robust elements. They are approximately the same size, but the first is slightly wider distally. They project laterally to articulate with the dorsal process of the ilium.

There are 62 caudal vertebrae (Figs. 1, 4, 5) preserved in a continuous series, followed by a gap, and then an isolated fragment that might represent the 65th. They are all exposed laterally. The caudal vertebrae are all similar in shape but diminish in size gradually. The neural arches appear to be narrow (although this might be due to crushing). Unlike the dorsals and cervicals, the zygapophysial articulations do not project very far laterally. Presence or absence of zygosphene-zygantral articulations cannot be confirmed. There is a long neural spine that extends posterodorsally, tapering distally in lateral view. The centra are exposed in lateral view but are crushed so that their exact three-dimensional shape cannot be ascertained. However, they appear to be long and cylindrical. Articulations between adjacent caudal centra are vertical. Transverse processes are present on the anterior caudals. These are most prominent on the anteriormost caudals, being conical lateral projections. They gradually diminish in size posteriorly and disappear at about vertebrae 27. Caudal autotomy septa are absent.

A chevron is visible under the fourth caudal, near the right
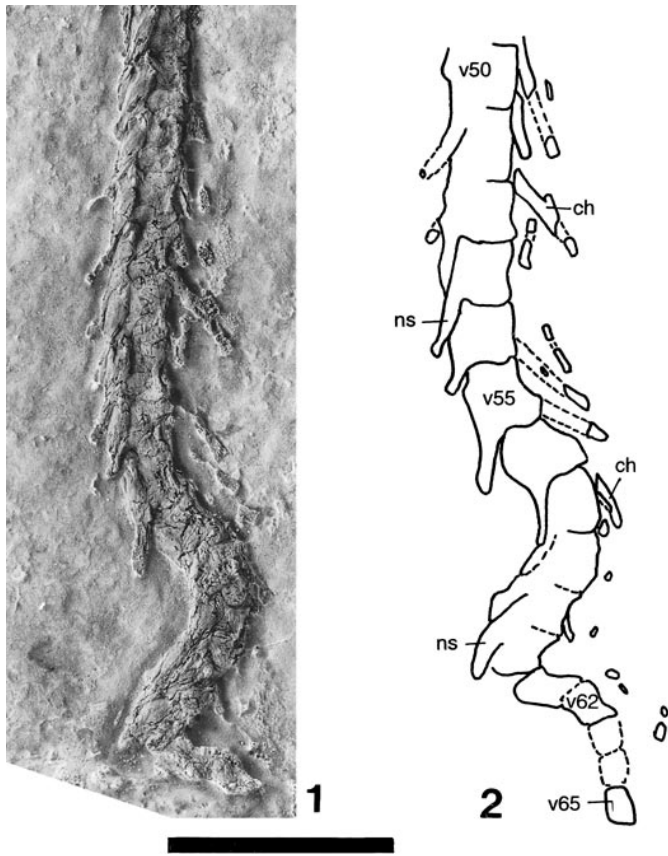
FIGURE 6—*Adriosaurus suessi,* NHM R2867, details of posterior caudal region. The kink near the 55th and 56th caudal vertebra is natural but that between the 60th and 61st vertebrae is probably an artefact (see text). Abbreviations: ch—chevron, ns—neural spine, v55—caudal vertebra 55. Scale bar = 10 mm.

pes, which presumably articulated with the preceding (third) caudal. Thus, chevrons are present from at least the third caudal (Figs. 4, 5), i.e., there were at most two pygals (not including the sacrals). Nopcsa reported chevrons from only the sixth vertebra but suggested they might have been present more anteriorly. The chevrons are long, and project posteroventrally from each centrum. Distinct pedicels on the centra for the chevrons appear to be present at least on the anterior caudals; they are not visible on most other caudals but this might be due to crushing of the centra.

There is a ventral bend in the tail at the level of the 55th caudal (Fig. 1). At the 57th caudal the tail bends the opposite way to resume a horizontal orientation. Between the 60th and 61st vertebrae, there is yet another bend in the caudal column. Nopcsa noted similar bends in the tail of the type specimen of *Adriosaurus* (Fig. 2). The bends in the tail in both specimens might be artifacts (Fig. 6), since the centra are usually slightly separated from one another on the outside of each bend. It is

thus not possible to confirm Nopcsa's interpretation of a ventral tail bend implying a caudal fin. However, the long neural spines and chevrons, and narrow vertebrae with reduced transverse processes, indicate that the tail was certainly deep and narrow (i.e., laterally compressed).

Limbs and girdles.—The anterior and posterior appendages are both reduced in size, with the forelimb being much smaller. Only the right elements of the shoulder girdle are exposed (Fig. 4). The coracoid is preserved immediately anterior to the humerus. There are three embayments in its anterior margins. However, it is uncertain which (if any) of these represent real coracoid fenestra, and which are artifacts of breakage. The coracoid as preserved appears small in comparison to the forelimb and parts of it might missing; however, the complete and well-preserved coracoid of *Aphanizocnemus* (Dal Sasso and Pinna, 1997) is even smaller. A bone fragment partly obscured by a rib, posteromedial to the right coracoid, might represent either the left coracoid or sternum/sternal cartilage; it is unlikely to represent the posterior stem of the interclavicle as it is too broad.

The right forelimb is almost completely preserved (Fig. 4). The humerus is a short, simple rod, slightly curved and slightly expanded at both ends. Neither the ectepicondylar nor entepicondylar foramen is visible, but this might be the result of crushing. The radius is straight and slightly expanded at both ends. The ulna projects laterally (preaxially) away from the radius but then curves inward to meet the carpals. The carpals are indistinguishable, being crushed into a single transverse mass. All five metacarpals are large and appear to be wide, though this is probably partly due to compression. Metacarpals 1 to 3 (at least) appear to be widest proximally; this area is not preserved in metacarpals 4 and 5. The phalanges are incompletely preserved. The distal phalanges are only preserved on the second, third, and fourth digits. Digits two and three each had 3 phalanges, digit four has 4, and digit five had at least two. A tentative phalangeal formula is thus? –3–3–4–?. The distally-diverging radius and ulna, and wide manus combine to make the forelimb wide and paddle-like distally.

The pelvis is only partially exposed (Fig. 5). The right ilium is well exposed, and a sliver of bone opposite on the left almost certainly represents the left ilium. The ilium is a large element with a long, tapering posterior ramus articulating with the two sacral ribs. There is no trace of an anterior process. Ventrally, it forms the dorsal margin of the acetabulum and is weakly united with the pubis. The pubis is a large element that projects anteroventrally to meet its partner. Dorsolaterally, it forms the anteroventral portion of the acetabulum. There is a large posterior emargination forming part of a sizeable thyroid fenestra. Presence of a pubic tubercle cannot be confirmed as the anterior margin is eroded. The ischium is not clearly exposed. However, a small fragment of bone exposed between the two right sacral ribs is in the exact place where the right ischium should be, and is provisionally identified as such.

The right hindlimb is fully exposed, while portions of the left (femur, tibia, and fibula) are also visible (Fig. 5). The femur is relatively small and stout compared to typical lizards, and is expanded at each end. A well-developed epiphysis is visible on

FIGURE 7—*Adriosaurus suessi,* life reconstruction. Scale bar = 10 mm.

the distal end. The identities of the tibiae and fibulae are clear as the tibia in squamates is always expanded proximally and the fibula is expanded distally; based on this, on both sides, the lateral element is the tibia and the medial the fibula. This unusual position is because the distal portion of each hindlimb has been rotated posteromedially about the knee joint so that the fibula lies medial to the tibia. On the proximal end of the left tibia, a small sliver of bone is present; this probably represents an epiphysis. As with the radius and ulna, the tibia and fibula diverge distally. The tarsal elements are exposed only on the right, and are all crushed into a single homogenous mass. Hence, the number, identity, and fusion, of astragalus, calcaneum, and distal tarsals cannot be determined. However, it is clear that, like the carpus, the tarsus was very wide transversely. All five metatarsals are preserved; they are large rod-like elements and appear to be wide. The first phalanx is preserved from digit 1, and the first two phalanges are preserved from digits 2 to 4. All three phalanges in digit 5 are preserved, including the ungual. The phalangeal count, based on the more complete pes of the holotype, is 2–3–4?–4?–3 (Seeley, 1881).

PALEOECOLOGY

Numerous features indicate that *Adriosaurus* was highly aquatic. In almost all squamates, the ribs are uniformly curved along their entire length, forming a smooth arc. In laterally compressed squamates, the ribs are straight. This body form has evolved independently at least five times within squamates, always in aquatic elongated forms: in dolichosaurs (extinct marine lizards similar to adriosaurs), in pachyophiids (extinct primitive snakes), acrochordids (living file-snakes), laticaudines (living sea-kraits), and hydrophiines (living true sea snakes). The ribs of *Adriosaurus* also have this shape, and projected laterally from the centrum for a short distance before turning ventrally, so that the long straight distal portions formed the parallel sides to a deep, narrow body. A flattened tail is indicated by the long neural spines and chevrons, and by the poorly developed transverse processes. While it is intriguing to interpret the kink in the caudal series near vertebra 55 as support for an expanded "fin" at the distal end of the tail, there is little solid evidence to support such an interpretation. In a new specimen of a similar taxon under study by Dal Sasso and Caldwell (pers. obs.), there is no evidence of a 'kink' or bend in the tail (see also Dal Sasso and Renesto, 1999). However, the presence of a tail bend and fin in *Adriosaurus* cannot be ruled out, as they occur in a number of marine reptiles, e.g., ichthyosaurs and Jurassic marine crocodilians (Carroll, 1988), and some derived mosasaurs (Schumacher, 1996). Remnants of the soft tissues of the fin have been directly observed in many ichthyosaurs (see Motani et al., 1996).

Adriosaurus exhibits pachyostosis, an anatomical condition resulting from an increase in the osteogenic activity of the periosteum causing a thickening of the periosteal bone. Pachyostosis is most pronounced in the middle region of the vertebral column, where the vertebrae and the proximal portions of the ribs are greatly thickened and swollen in cross-sectional area (Figs. 1, 3, 4). This adaptation creates neutral buoyancy in shallow-diving tetrapods by counteracting the buoyancy created by the air in their lungs (Nopcsa, 1923; Kaiser, 1966; Domning and de Buffrénil, 1991; Wall, 1983; Scanlon et al., 1999). This feature is also found in the related pachyophiids (Rage, 1984; de Buffrénil and Rage, 1993; Scanlon et al., 1999). As in pachyophiids, the extra skeletal weight is concentrated where it is required—the (otherwise) most buoyant section near the lungs (Domning and de Buffrénil, 1991; Scanlon et al., 1999).

Both the forelimb and hindlimb are reduced in size, with the forelimb being smaller than the hindlimb. This reduction in size affects the propodial (humerus and femur) and epipodial (radius/

ulna and tibia/fibula) elements more severely than the manus and pes. As a result the manus and pes are large relative to the remainder of the limb (Figs. 4, 5), and the phalangeal count is not greatly reduced. The distally diverging epipodial elements, and wide manus and pes, mean that the limbs, though small, are broad. The digits of both manus and pes are preserved parallel and undisturbed. One possibility is that they were connected by tight webbing or even enclosed in a fleshy flipper.

For aquatic locomotion the limbs may have been used for very slow swimming and/or for maneouvering; although small, the expanded flat distal regions would have made them effective paddles. For more rapid bursts, lateral undulation was probably used, with the limbs pressed against the sides. The limbs would have been used in terrestrial locomotion if ever the animal needed to move on land—for instance, to deposit eggs. If so, the lateral compression of the body and small limbs would have made for slow and clumsy terrestrial locomotion..

The laterally compressed body, flattened tail, and small limbs (Fig. 7) imply that *Adriosaurus* swam mainly by lateral undulation, and was thus a relatively slow swimmer compared to swimmers that employ other methods such as carangiform axial locomotion (tuna-like swimming) or underwater flight (e.g., Webb, 1982). The pachyostotic skeleton would also have reduced swimming speed and maneouverability (de Buffrenil and Mazin, 1989; de Buffrénil and Rage, 1993). Thus, it can be inferred that *Adriosaurus,* like the pachyophiids (Scanlon et al., 1999), was a relatively slow swimmer, and thus probably confined to near-shore, relatively calm environments. This is consistent with stratigraphic and sedimentological data supporting interpretations of the palaeoenvironment of the southern epicontinental Tethys of Slovenia-Croatia as a near-shore, shallow marine environment dominated by a patch-reef system (Jurkovsek et al., 1996). The sharp, recurved teeth and proportionately large skull (Figs. 3, 7) indicate that it was a predator. Together with its limited swimming abilities, long neck, and elongate body, this suggests it ambushed prey hiding in nooks and crannies, such as small fish or soft-bodied invertebrates.

PHYLOGENETIC RELATIONSHIPS

The two specimens of *Adriosaurus* can be confidently assigned to the same taxon based on anatomy and stratigraphy. Morphologically, the comparable elements preserved in the two specimens are almost identical in size and shape. They share two unusual apomorphies that are rare among squamates: a laterally compressed and very elongate tail (known in aigialosaurs, mosasaurs, dolichosaurs, and *Pontosaurus* [see Kornhuber, 1873]), and straight, pachyostotic ribs (otherwise only found in primitive snakes such as *Pachyrhachis* and *Pachyophis*). No squamate taxon apart from the two specimens of *Adriosaurus* is known to possesses both these features together. Pachyostotic ribs are present in other marine Cretaceous squamates, but these are usually not as straight as they are in the snakes and *Adriosaurus* [the exception is a new, undescribed taxon from Lebanon, mentioned by Dal Sasso and Renesto, (1999), and currently under study by Dal Sasso and Caldwell, pers. obs.].

As to the affinities of this species, *Adriosaurus* is clearly a squamate. Of the squamate synapomorphies identified by Gauthier et al. (1988) and Estes et al. (1988), *Adriosaurus* exhibits the following: fused premaxilla, transverse frontoparietal suture (though this is slightly sinuous), fused parietals, short parietal table, single-headed ribs, eight or more cervical vertebrae, and large thyroid fenestra. Also, it appears to possess some further squamate synapomorphies, though due to poor preservation these are less certain: a humerus lacking an entepicondylar foramen, columelliform epipterygoid with narrow base and not

contacting the quadrate, and sacral and caudal ribs fused to centra (the sacral ribs are clearly fused but the caudal ribs are damaged). Though it lacks two other putative squamate synapomorphies, these are not compelling evidence for excluding it from Squamata: *Adriosaurus* possesses small, short, rather elongate gracile limbs (however, many lizards, and all snakes are also limb-reduced); *Adriosaurus* possesses, rather than lacks, accessory vertebral articulations (however, several lizard families and all snakes have accessory articulations). Conversely, for all the other squamate synapomorphies, *Adriosaurus* exhibits the derived (squamate) condition where it can be coded. It can therefore be confidently concluded that *Adriosaurus* is a squamate.

Accordingly, *Adriosaurus* and well-known marine squamates were added to the most recent phylogenetic analysis of squamates (Lee, 1998). This analysis thus includes all major squamate lineages (''families'') as well as all recently described (or redescribed) marine squamates: mosasaurids, aigialosaurids (Carroll and DeBraga, 1992; DeBraga and Carroll, 1993), *Pachyrhachis* (Lee and Caldwell, 1998), *Pachyophis* (Lee et al., 1999), *Aphanizocnemus* (Dal Sasso and Pinna, 1997), dolichosaurs (recognizing the difficulties of diagnosing *Dolichosaurus* and *Coniasaurus,* we include both genera in the family Dolichosauridae [Caldwell, in press; Caldwell, 1999a, b; Caldwell and Cooper, 1999]), and *Adriosaurus* (this study). In a previous analysis (Lee, 1998), mosasaurids and aigialosaurs were combined into a single terminal taxon (mosasauroids), since it was clear that, relative to the other taxa in that analysis, mosasaurids and aigialosaurs formed a clade. However, in this analysis, with the additional marine taxa, it is by no means certain that aigialosaurs and mosasaurs form a clade relative to all other terminal taxa (e.g., DeBraga and Carroll, 1993; Dal Sasso and Pinna, 1997). Thus, aigialosaurs and mosasaurs were treated as separate terminal taxa in order to allow the possibility that either of these might be most closely related to some other marine squamates. Character codings for all taxa in this matrix, including the marine fossil forms, are based on re-examination of the material. As descriptions of the remaining marine squamates are very old and probably inadequate, they have not been included in the analysis.

The data matrix compiled for this study is in Appendix 1. The characters in Lee (1998) were used here and coded for the additional marine taxa. Codings for other squamates follow Lee with some corrections and clarifications as noted under the relevant character. In particular, some proposed dental synapomorphies between snakes and mosasauroids have recently been questioned (Zaher and Rieppel, 1999a), and these comments are addressed in the Appendix (see also Scanlon and Lee, in press). New phylogenetically informative characters were also identified in this analysis, which help resolve the affinities of the additional (marine) taxa considered here. These characters, like the others, were scored in all other squamate taxa and in the nearest outgroups (rhynchocephalians, *Marmoretta,* and kuehneosaurs). Also, terminal taxa of dubious monophyly used for convenience in earlier analyses (''agamids,'' ''gekkonids,'' and ''xenosaurids'': Estes et al., 1988; Lee, 1998) were here subdivided into smaller units of uncontested monophyly (''agamids'' into leiolepidines and agamines, ''gekkonids'' into eublepharines, diplodactylines and gekkonines *sensu lato,* and ''xenosaurids'' into *Xenosaurus* and *Shinisaurus*). Additional characters that help resolve the relationships between these subdivided terminal taxa were included (unlike in the recent study of Zaher and Rieppel, 1999b—see below). Use of only clades as terminals addresses the criticism of Zaher and Rieppel (1999b) that some terminals used in the analysis of Lee (1998) and Estes et al. (1988) were of dubious monophyly. The dubious monophyly of some terminals was clearly acknowledged by the latter authors, but was not considered relevant in the study of Lee (1998) as none of

these taxa (agamids, iguanids, gekkonids) are potentially related to snakes. Also, these authors also stated that the analysis of Lee (1998) ''fails to recognise variability (polymorphism) of characters within families'' and that the results ''therefore continue to obscure the debate'' (p. 833). However, as was clearly stated in Lee (1998), intrafamilial variability was explicitly considered. The character state present in all basal members of each family was assumed to be primitive for the family, and the family coded for each state. If the primitive state could not be inferred (due to variability in basal members, or poorly resolved intrafamilial relationships), the family was coded with all states that might be primitive—this method of recognizing and accommodating polymorphism was clearly stated in the paper (*contra* Zaher and Rieppel, 1999b) and has been widely used and discussed in the previous papers (e.g., Estes et al., 1988; Caldwell, 1999a).

Snakes are treated as three terminals in the current analysis: *Pachyrhachis, Pachyophis,* and *Serpentes* (all other snakes). There is strong evidence that *Pachyrhachis* and *Pachyophis* are basal to all other snakes, i.e., lying outside a monophyletic Serpentes (Lee, 1998; Scanlon and Lee, 2000). Thus, Serpentes has not been subdivided into smaller component taxa. The basal position of *Pachyrhachis* has again been recently questioned by Zaher and Rieppel (1999b). These authors are finally in agreement with previous studies (Caldwell and Lee, 1997; Lee and Caldwell, 1998) that concluded *Pachyrhachis* is a snake. They are also in agreement regarding the reinterpretations of the most of the elements. However, they present differing interpretations of four elements, and claim that these characters support ''macrostomatan'' affinities of *Pachyrhachis.* They reconstruct *Pachyrhachis* without a forked postorbitofrontal, interpreting the putative anterior ramus as part of the parietal. However, only the identification of the extreme tip of the anterior ramus is questionable. The more proximal part of the anterior ramus, and the entire posterior ramus, is continuous with the rest of the postorbitofrontal. The anterior and posterior rami are clearly exposed on both sides (see photographs in Lee and Caldwell, 1998; Fig. 3). Thus, the suggestion that the postfrontal abutted, rather than clasped, the parietal cannot be supported. Furthermore, even if accepted, the suggestion that this abutting contact represents a macrostomatan synapomorphy is untenable, since some anilioids (e.g., *Cylindrophis*) have a similar contact while the condition in other anilioids, and scolecophidians cannot be scored (since posterior orbital ossifications are absent). Thus, the trait either characterizes alethinophidians, or snakes as a whole.

Zaher and Rieppel (1999b, p. 8343) interpret the putative jugal of Lee and Caldwell (1998) as the ''ectopterygoid,'' because it ''broadly overlaps'' the ''posterior end of the maxilla . . . as in macrostomatan snakes.'' This interpretation is questionable because the element in question lies entirely anterior to the postorbitofrontal on both sides of the skull, whereas the ectopterygoid in snakes invariably lies posterior to the postorbitofrontal (when the latter is present). In contrast, the contentious element is in the correct position to be a jugal: in front of the postorbitofrontal and on the ventral margin of the orbit. Finally, even if the idenfication as the ectopterygoid were accepted, the suggestion that the ''ectopterygoid''-maxilla overlap represents a macrostomatan character of *Pachyrhachis* is not tenable, as anilioids also exhibit this trait, whereas the ectopterygoid and maxilla are so modified in scolecophidians that they should be treated as not applicable. The character applies either to all alethinophidians, or all snakes (depending on how scolecophidians are interpreted).

It was also suggested that the putative squamosal represents the elongated shaft of the stapes, and that the putative stapes instead represents the distal end of a long paroccipital process. However, no further reasons were given for this interpretations.

As emphasised previously (Lee and Caldwell, 1998), identification of the putative squamosal was very uncertain, and the alternative interpretation will warrant careful consideration once the supporting evidence is published. If the squamosal is indeed actually the stapes, then the related interpretation of the putative stapes as the paroccipital process also needs to be considered. However, even if these reinterpretations are correct, the statement that a long stapedial shaft and a pronounced paroccipital process represent ''macrostomatan features'' of *Pachyrhachis* cannot be accepted. Long narrow stapes and large paroccipital processes are found throughout squamates (including the nearest outgroups to snakes) and are presumably primitive for snakes. These symplesiomorphies therefore cannot be used to group *Pachyrhachis* and macrostomatans. Furthermore, macrostomatans, though possessing the long narrow stapes as stated by Zaher and Rieppel (1999b), actually *lack* a sizeable paroccipital processes. The quadrate in macrostomatans is suspended entirely by the supratemporal (e.g., Scanlon and Lee, 2000).

Thus, none of the four new *Pachyrhachis*-macrostomatan synapomorphies proposed by Zaher and Rieppel (1999b) are compelling. For two, the proposed reinterpretation of the preserved elements is dubious. For the remaining two, the proposed reinterpretation is possible (though the supporting evidence has not yet presented); however, even if true the distribution of these characters in the outgroups means that the condition shared by *Pachyrhachis* and macrostomatans is primitive for snakes. In this respect, it is of interest to note that none of these four characters were included in Zaher and Rieppel's (1999b) synapomorphy scheme for snakes (their fig. 2), even though a *Pachyrhachis*-macrostomatan node was presented and (other) supporting characters for this node listed. It seems reasonable to conclude that Zaher and Rieppel's (1999b) analysis does not find these problem characters to be supportive of the authors preferred phylogeny and likely are reconstructed on their cladograms as we suggest above.

Apart from the character data, there are also potential problems in the methods employed in the phylogenetic analysis of snakes by Zaher and Rieppel (1999b), which concluded that *Pachyrhachis* is an advanced snake. In that analysis, the terminal taxon ''modern snakes'' was subdivided into *Dinilysia,* scolecophidians, anilioids, and macrostomatans; however, the relevant characters that help resolve relationships among these new (smaller) terminal taxa were not included (these are listed in Scanlon and Lee, 2000). Thus, these snake taxa were grouped on characters largely chosen to resolve relationships among squamates as a whole, which just happened to also be variable within modern snakes. In subdividing terminal taxa for phylogenetic analysis, it is crucial that the relevant informative characters are included which help resolve relationships among these smaller terminals (as in this analysis). For this reason, the analysis of Zaher and Rieppel (1999b) is incomplete and the results should be treated with caution. Both Lee (1998s) and Caldwell (2000) noted similar methodological problems in an earlier work by Zaher (1998), as well as problems of character choice, character construction, and character interpretation. Subsequent recoding and reanalysis of Zaher's (1998) 'data' by Caldwell (2000), found no support for Zaher's unambiguous assertions that *Pachyrhachis* was a macrostomatan snake. Instead, *Pachyrhachis* was consistently reconstructed as basal to all other included snake terminals.

Based on the above considerations, we continue to treat *Pachyrhachis* and *Pachyophis* as basal to all other known snakes (Serpentes), and thus treat Serpentes as a single monophyletic terminal taxon (Scanlon and Lee, 2000) in the analysis we give here, of overall squamate interrelationships.

Two analyses were performed with the current data matrix.

In the first, multistate characters were ordered into morphoclines where possible, and only those that did not form clear morphoclines were left unordered (see Appendix). In the second, all multistate characters were left unordered. These two analyses were performed to ascertain the effects of character state ordering (if any) on the phylogenetic results. Analysed used the heuristic algorithm of PAUP* (Swofford, 1999) employing 100 random addition sequences. The degree of support for each grouping was ascertained by the support or Bremer index (Bremer, 1988), calculated in PAUP using commands generated by TreeRot Version 2 (Sorenson, 1999), modified so that each search employed 100 rather than 10 random addition sequences. The bootstrapping function in PAUP (1000 replicates each with 20 random addition sequences) was also used to assess the statistical significance of the various groupings found in each analysis. Polymorphism in terminals was interpreted as ''uncertainty regarding the primitive state'' when calculating tree lengths.

In the ''ordered'' analysis, twelve most parsimonious trees were found (length = 659 consistency index = 0.47, retention index = 0.71); the strict consensus of these is shown in Figure 8. In the ''unordered'' analysis, twenty-four most parsimonious trees were found (length = 624, ci = 0.5, ri = 0.71); the strict consensus of these is shown in Figure 9. As will be clear, the two consensus trees are almost identical, differing only in that in the ''unordered'' analysis, relationships of the Lacertoidea are unresolved. Bremer and bootstrap support for each clade is also very similar in the two analyses. Thus, the phylogenetic results are **not** affected by the treatment of multistate characters. However, the phylogenetic results based on a previous, smaller version of this osteological data matrix (Lee, 1998) was noted to be more dependent on assumptions of characters state order. As realised by the author (Lee, unpubl. data), and later by Zaher and Rieppel (1999a, 1999b), in that matrix, snakes clustered with mosasauroids if multistate characters were ordered, but with amphisbaenians and dibamids if multistate characters were unordered. Without extrinsic evidence, it might have been difficult to determine which of these two results is the correct one. However, it is now clear that the ordered results have more support. An independent soft anatomical data set (Lee, in press) agrees with the ordered analysis and not with the unordered analysis, and the present study shows that when additional characters and taxa are added to the osteological data set of Lee (1998), the ''ordered'' result (snakes with marine lizards) is now obtained whether characters are ordered or unordered.

As the basic topology of the trees in both ordered and unordered analyses are unchanged from that in the previous study (Lee, 1998), and most of the clades are discussed in that study, these details are not repeated here. *Adriosaurus* and the other marine taxa fall within pythonomorphs, the mosasaur-snake clade. Pythonomorphs, in turn, are nested within varanoids. The characters diagnosing new clades of immediate relevance to *Adriosaurus* are listed. All the character changes diagnosing these clades that occur under delayed transformation optimisation are listed below. Unequivocal changes (i.e., those that occur under both delayed and accelerated optimisation) are indicated with an asterisk (*).

Clade A: Dolichosauridae, *Aphanizocnemus, Adriosaurus* and Ophidia.

*More than ten cervical vertebrae (190, 0.38, 2 → 3), *Scapulocoracoid reduced (212, 0.71), *interclavicle absent (219, 0.5), *Forelimbs small (227, 0.56), *pelvis reduced (231, 0.6), *hindlimbs small (237, 0.67), *pubis not expanded distally (236, 1.0).

Clade B: *Adriosaurus* and Ophidia.

*Premaxilla-maxilla contact mobile (5, 1.0), *frontals paired

FIGURE 8—The phylogenetic position of *Adriosaurus* within squamates, based on a cladistic analysis of 258 osteological characters, with multistate characters ordered where possible. Strict consensus of 12 trees (length = 660, consistency index = 0.47, retention index = 0.71). The first number at each clade refers to branch (=Bremer) support, the second refers to bootstrapping frequency. Clades directly relevant to the position of *Adriosaurus* are identified by bold font and discussed in the text.

(27, 0.5), postorbitofrontal ventral process large (37, 0.5, 1→ 0), supratemporal superficial (55, 0.5, 1→ 0).

Ophidia (*Pachyrhachis, Pachyophis*, and Serpentes).

*Lacrimal absent (11, 0.75), frontoparietal suture with curved contact (31, 0.67, 1→ 0), *pineal foramen absent (42, 0.56), *parietal table reduced to sagittal crest (44, 0.56, 1→ 0), suspensorial ramus of parietal reduced (46, 0.75), *upper temporal arch incomplete (47, 0.2), tympanic crest absent (61, 0.38, 0→ 2), parietal downgrowths contacing parabasisphenoid (72, 1.0), optic foramina enclosed in bone (73, 1.0), trigeminal foramina bordered anteriorly by parietal (75, 1.0), supraoccipital on skull roof behind parietal (92, 0.67), posttemporal fenestra enclosed (95, 0.5), opening of Jacobson's organ enclosed by vomer and septomaxilla only (100, 0.63, 1→ 2), vomer medial to palatine (105, 1.0), palatine-vomer contact mobile (108, 1.0), palatine with distinct rectangular medial process (111, 1.0), two or fewer mental foramina on lateral surface of dentary (123, 1.0), posterior margin of lateral surface of dentary deeply notched (130, 0.56, 1→ 2), coronoid does not contact splenial (140, 0.5), surangular extends far over lateral surface of dentary (143, 1.0, 2→ 3), articular fused with prearticular and surangular (153, 0.58, 1→ 0), palatine teeth long fangs (176, 1.0), *at least 120 presacral vertebrae (189, 0.18, 3→ 5), *lymphapophyses present (209, 0.5), *scapulcoracoid absent (212, 0.71, 1→ 2), *clavicle absent (216, 0.5), ossified sternum absent (222, 1.0), *forelimbs absent (227, 0.56, 1→ 2), scleral ossicles absent (250, 0.67), *appendicular epiphyses absent (256, 0.67).

It should be noted that the nesting of pythonomorphs within varanoids, as found in the above analysis, disagrees with another study which found that pythonomorphs are basal scleroglossans

(Caldwell, 1999a). The inclusion of *Adriosaurus* in the data matrix of Caldwell (1999a) found it to be the sister-taxon of *Conisaurus* within the pythonomorph clade of the tree, with pythonomorphs still remaining basal to all other scleroglossans. However, inclusion of *Adriosaurus* in an enlarged data matrix currently being derived from that study (Caldwell, in prep.) finds some support for pythonomorphs as basal anguimorphs. Regardless of the uncertainty over the position of pythonomorphs within squamates, the inclusion of *Adriosaurus* within a monophyletic Pythonomorpha (snakes, mosasaurs, *Adriosaurus*, and similar marine taxa), and the nesting of snakes within marine squamates, is common to both data sets. Zaher and Rieppel (1999b; 832) state that Pythonomorpha "includes varanoids, mosasauroids and snakes" but do not justify this statement. This interpretation is puzzling given that Pythonomorpha was explicitly defined by Lee and Caldwell (1998) to include the latest common ancestor of mosasauroids and snakes, and all its descendants. Zaher and Rieppel's (1999b) claim that Pythonomorpha also contains varanoids implies that terrestrial varanoids such as *Varanus, Lanthanotus*, and *Heloderma* (but not other squamates) are nested within the mosasauroid-snake clade, a hypothesis which has not been advanced by anyone to our knowledge. Such claims misrepresent the theoretical implications of cited works but do have the benefit of serving as temporary straw-man arguments.

The Pachyophiidae (Scanlon et al. 1999), consisting of *Pachyrhachis* and *Pachyophis,* is also retrieved in the current analysis, albeit weakly. Zaher and Rieppel (1999: 832) dismiss the characters uniting *Pachyrhachis* and *Pachyophis* as "spurious" but do not give reasons for this claim, nor cite other papers which might contain this information. The current analysis indeed reveals that one of the characters (lateral compression of the body) is also present in other marine pythonomorphs such
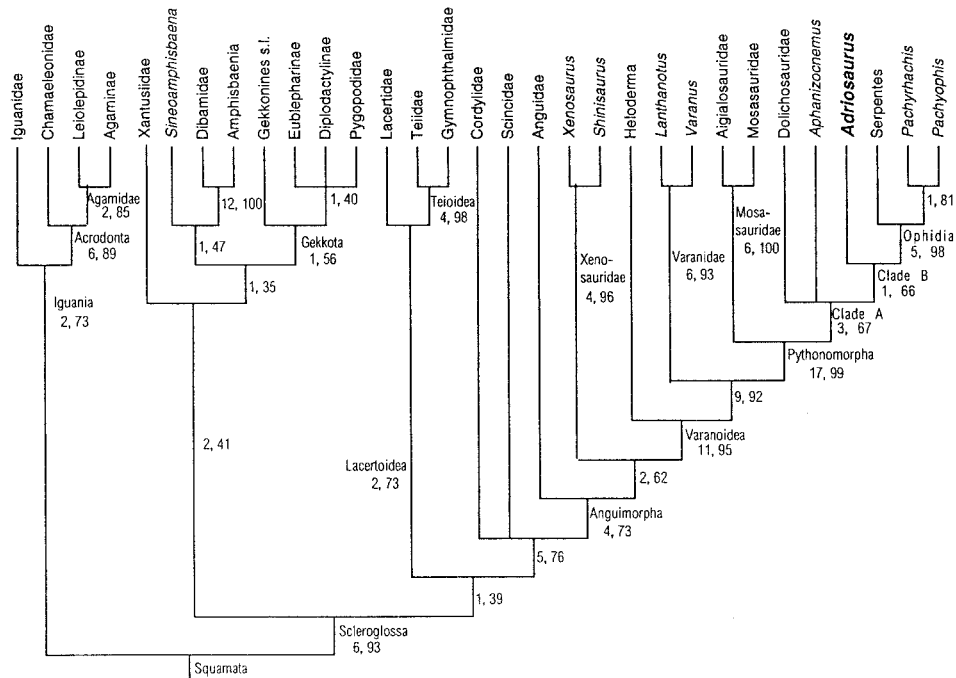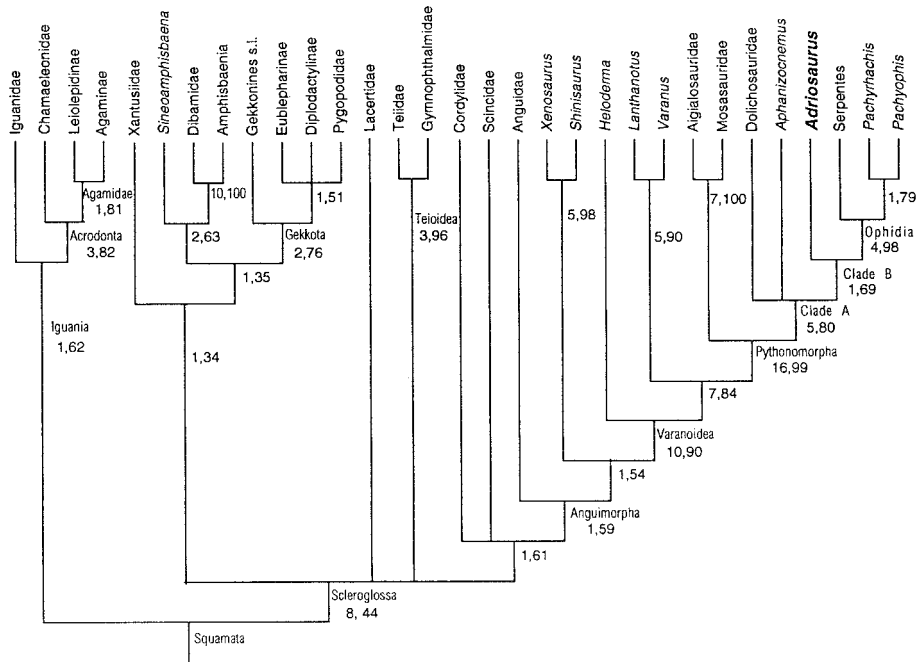
FIGURE 9—The phylogenetic position of *Adriosaurus* within squamates, based on a cladistic analysis of 258 osteological characters, with all multistate characters unordered. Strict consensus of 12 trees (length = 625, consistency index = 0.5, retention index = 0.71. The first number at each clade refers to branch (=Bremer) support, the second refers to bootstrapping frequency. Clades directly relevant to the position of *Adriosaurus* are identified by bold font and discussed in the text.

as *Adriosaurus.* Nevertheless, the remaining synapomorphy (very small head relative to trunk region) remains valid.

The phylogenetic analysis presented here suggests that snakes are nested deeply within a radiation of marine squamates (mosasaurs, aigialosaurs, and similar taxa), and are most closely related to the long-bodied, limb-reduced forms (dolichosaurs, *Aphanizocnemus,* and *Adriosaurus*). Nopcsa (1908, 1923) long ago suggested this arrangement. Previously, recognition of the marine pachyophiids as the most primitive snakes and the marine mosasauroids as the nearest relative of snakes, had merely left the ecology of their origins ambiguous (Scanlon et al., 1999). Only the two nearest outgroups to living (terrestrial) snakes were demonstrated to be aquatic. The recent statement (Zaher and Rieppel 1999b; 832) that this arrangement "implies a marine, rather than terrestrial, origin of snakes" is incorrect. As emphasised in Scanlon et al., (1999), there are two equally parsimonious hypotheses. Snakes might have terrestrial origins (pachyophiids and mosasauroids each independently invading aquatic habitats), or they might have undergone a marine phase (marine habits being acquired in the ancestor of pythonomorphs, retained in mosasauroids and pachyophiids, and lost in more derived snakes). Either scenario implied two habitat shifts in the context of that phylogeny (Scanlon et al., 1999). Considering the repeated invasion of aquatic habitats by tetrapods, and the infrequent transitions in the reverse direction, the first scenario appears more plausible (Scanlon et al. 1999). Thus, that study did not imply or assert an aquatic origin of snakes (*contra* Zaher and Rieppel, 1999b).

This analysis, however, demonstrates that the closest four or five outgroups to modern (terrestrial) snakes are marine (depending on how the polytomy within pythonomorphs is resolved), and in this context there is only one most parsimonious interpretation: marine habits are primitive for pythonomorphs. The corollary is that snakes evolved in a marine environment and are secondarily terrestrial. A similar marine scenario for

snake origins, though popular in the past (e.g., Nopcsa 1908, 1923), appears to have been rejected during subsequent years in favor of a purely fossorial origin (Walls, 1940; Bellairs and Underwood, 1951; Rieppel, 1988).

The aquatic scenario might be considered problematic given that fully terrestrial vertebrates have presumably evolved only once (origin of tetrapods), suggesting that an aquatic-to-terrestrial transition is unlikely and very difficult to achieve. However, it should be noted while most secondarily aquatic tetrapods have paddles for swimming and are thus clumsy on land, dolichosaurs and similar taxa, and primitive (pachyophiid) snakes, possess a body form useful not only for swimming, but also for burrowing, moving through crevices, and traversing open dry ground. Finally, given that primitive mosasauroids (aigialosaurs) were only semi-aquatic (Caldwell et al., 1995), an intermediate scenario might be true. The lineage leading to snakes consisted of semi-aquatic forms—with derived mosasauroids, dolichosaurs and *Adriosaurus* evolving greater aquatic adaptations, and snakes above *Pachyrhachis* shifting towards greater terrestriality.

If snakes had an aquatic or semi-aquatic ancestry, the initial terrestrial phase is also worth exploring. Since several groups of primitive terrestrial snakes (scolecophidians and anilioids) are highly fossorial, one extreme possibility is that the initial colonization of the land involved an aquatic (or semiaquatic) to fossorial transition, without an above-ground terrestrial phase. There are, for instance, many highly terrestrial caecilians with large "amniote-like" eggs and these may have had more aquatic ancestors at some stage, and invaded more terrestrial habitats via a burrowing route. Some extinct long-bodied leposondyl lineages, such as aistopods (see Carroll, 1998) might also have evolved terrestriality in this manner. Another scenario is that the initial colonisation of the land involved surface-active forms: the extant sea-snake *Laticauda* spends long periods on the beach and is a plausible analogue for such a transitional taxon. Indeed,

some primitive terrestrial snakes such as *Dinilysia* and madtsoiids were too large to have been highly fossorial, exhibit no obvious burrowing adaptations, and were presumably active mainly above ground (Scanlon and Lee, 2000).

However, some substantial caveats must be added to these evolutionary scenarios. Apart from mosasaurs and aigialosaurs, all the marine pythonomorphs are very imperfectly known. For instance, dolichosaurs, *Adriosaurus,* and *Aphanizocnemus* can be coded for less than 35 percent of characters. Such an amount of missing information means that support for their phylogenetic positions is not very robust, as indicated by low bootstrap and Bremer support (Fig. 8). Missing information also reduces support throughout the tree, as the poorly-known taxa can fit into many different places with only slight loss in parsimony. Additionally, most of the characters that unite dolichosaurs, *Aphanizocnemus,* and *Adriosaurus* with snakes, to the exclusion of mosasaurs and aigialosaurs, are correlates of body elongation and limb reduction. Thus, the evidence that these taxa are more closely related to snakes than to mosasaurs and aigialosaurs is relatively weak. Indeed, Nopcsa (1908) proposed a similar relationship on the same sort of characters, but this proposal never achieved widespread acceptance. The analysis here shows that these characters still hold up even in a comprehensive cladistic analysis with all squamate taxa and all other informative characters. Although weak, they are at the moment uncontradicted by other characters. More complete finds, and thus information on characters not obviously correlated with body form (e.g., braincase characters), are required before their phylogenetic relationships can be conclusively ascertained and the early evolution of snakes clearly understood. Thus, it is conceivable that the stem lineage leading to snakes consisted entirely of terrestrial forms, but gave off repeated marine offshoots such as mosasauroids and *Adriosaurus.* Due to the taphonomic biases, however, the terrestrial forms may have yet to be found, while the specialized and convergent marine offshoots are well-represented in the fossil record. This bias against the preservation of any terrestrial members of the snake stem lineage could thus lead to the incorrect inference that all members were marine and that snakes passed through a marine phase in their early evolution.

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APPENDIX 1

Character List

The data matrix used in this cladistic analysis. Most characters were discussed in Lee (1998) and are only briefly listed here. However, some codings were changed as discussed under the relevant characters. New characters informative for the slightly different set of terminal taxa here are identified with an asterisk (*). Where necessary, the codings for *Adriosaurus* are discussed under the relevant character.

Skull Roof

 *1. **Premaxilla.** Paired (0); single (1). Estes et al. (1988).

 *2. **Premaxilla.** Does not contact frontals (0); contacts frontals (1)

 3. **Premaxilla with median palatal ramus bearing foramina.** absent (0); present (1).

 4. **Premaxillary lateral foramina.** Present (0); absent (1).

 5. **Premaxilla-maxilla contact.** Immobile and sutural (0); mobile and non-sutural (1). In dolichosaurids, while no premaxilla is preserved, state 0 is inferred as the anterior end of the maxilla has a rough, sutural surface. In *Adriosaurus,* both maxilla are separated by a gap from the premaxilla; while this could be taphonomic, state 1 is provisionally inferred.

 *6. **Maxillae.** Not in contact on palatal surface, behind premaxilla (0); in broad contact on palatal surface, behind premaxilla (1). Some gekkotans approach state 1, but the contact (if present) is very tiny.

 7. **Alveolar ridge of maxilla.** Straight in lateral view, not upturned at anterior end (0); upturned at anterior end near suture with premaxilla, resulting in a distinct notch (1).

8. **Dorsal process of maxilla.** On middle or anterior end of maxilla (0); on posterior half of maxilla (1).

9. **Dorsal process of maxilla.** Extends dorsomedially (0); extends dorsolaterally, overhanging mouth (1).

10. **Posterior process of maxilla.** Long, reaching or extending past middle of ventral margin of orbit (0); short, not reaching middle of ventral margin of orbit (1). The short condition in dolichosaurids is provisional as all known maxilla are worn posteriorly and might have been longer. The maxilla in *Adriosaurus* is distorted but just barely reaches the middle of the orbit, it might possess either state.

11. **Lacrimal.** Present, either permanently separate or fusing with prefrontal during ontogeny (0); absent, never present as a discrete element (1).

12. **Lacrimal.** Separate throughout ontogeny (0); fusing with prefrontal during ontogeny (1)

13. **Lacrimal foramen.** Single opening (0); double opening (1).

*14. **Lacrimal foramen.** Not greatly enlarged (0); greatly enlarged (1).

*15. **Snout shape.** Relatively short, rounded (0), long and very narrow, tapering to point (1). Some pygopodids and *Varanus* have state 1, but state 0 is primitive in both groups (e.g., Greer, 1989; Sprackland, 1991).

16. **Jugal.** Present (0); absent (1). The ventral orbital ossification in some amphisbaenians (e.g., Berman, 1973) is interpreted as a jugal based on positional similarities to jugal of other squamates: like the jugal, but unlike the postorbital, it curves anteriorly to form part of the ventral orbital margin. *Aphanizocnemus* has been coded with state 0, based on the provisional identification of a jugal (Dal Sasso and Pinna, 1997).

17. **Jugal.** Anterior process confined to medial surface of maxilla, jugal does not extend anteriorly beyond middle of orbit in lateral view (0); anterior process on dorsal surface of maxilla, jugal extends anteriorly beyond middle of orbit in lateral view (1).

*18. **Jugal.** Does not extend anteriorly past orbit (0); extends anteriorly past orbit (1). Lee (1997).

*19. **Jugal.** Without large posterior process (0); with large posterior process (1).

*20. **Jugal.** Lacking dermal sculpture (0); with dermal sculpture (1).

*21. **Nasals.** Large (0); greatly reduced or absent (1).

22. **Nasals.** Paired elements (0); single median element (1).

23. **Nasal-prefrontal contact.** Present, nasal-prefrontal contact separating maxilla from frontal (0); absent, nasal and prefrontal separated by maxilla-frontal contact (1).

24. **External naris.** Not retracted, prefrontal and frontal both excluded from posterior narial margin by nasal and maxilla (0); slightly retracted, prefrontal (but not frontal) enters posterior narial margin (1); greatly retracted, prefrontal and frontal enter posterior narial margin (2). Ordered 0–1–2. Dolichosaurs have an embayment in the anterior margin of the frontal, but whether this represented the margin of the naris, or a notch for the nasal, cannot be determined.

25. **Prefrontal.** Smooth (0); with tubercle or rugosities near orbital margin (1).

*26. **Antorbital ridge.** Absent (0); present, extending anteriorly from dorsal margin of orbit (1).

27. **Frontals.** Single median element (0); paired elements (1).

28. **Frontal.** Enters orbital margin, prefrontal does not contact postfrontal or postorbital (0); excluded from orbital margin, prefrontal contacts postfrontal or postorbital (1).

29. **Frontals.** Lateral orbital margin straight or only very slightly concave (0); lateral orbital margin deeply concave (1). Not applicable in taxa where the frontal does not enter the orbit.

30. **Frontal shelf extending anteriorly to underlie nasal.** Absent (0), present (1).

31. **Frontoparietal suture.** In dorsal view, complex curved or interdigitating contact (0); in dorsal view, simple straight transverse contact (1). The contact appears to be slightly sinuous in aigialosaurs (e.g., reconstructions in Carroll and deBraga, 1992) and *Adriosaurus* (pers. obs), and they have been coded with both states.

32. **Postfrontal.** Present and large, extending beyond orbital margin (0); present and small, does not extend beyond orbital margin (1); absent, never present as a discrete element (2). Ordered 0–1–2.

33. **Postfrontal.** Remains separate from postorbital throughout ontogeny (0); fusing with postorbital during ontogeny (1).

34. **Postfrontal** (or dorsomedial portion of single posterior orbital bone). Not forked medially, does not extend a long distance along frontal or parietal (0); forked medially, with an anterior process along the frontal and a posterior process along the parietal (1).

35. **Palpebral (superciliary) ossifications on dorsal margin of orbit.** Absent (0); present (1).

36. **Postorbital.** Present (0), absent (1). Presence of a discrete postorbital during development cannot be determined in most fossil taxa which have (as adults) only a single ''postorbitofrontal''; however, such information is available for mosasaurs (Russell, 1967)

37. **Postorbital ventral process.** Prominent, forming half or more of posterior orbital margin, postorbital primarily an orbital bone (0); small, forming less than half of posterior orbital margin, postorbital primarily a temporal bone (1). If correctly identified, this process is large in *Adriosaurus.*

38. **Posterior margin of orbit.** Present and continuous (0); present but with small gap (1); very incomplete, less than 50% of posterior orbital margin bordered by bone (2). Ordered 0–1–2. Some amphisbaenians retain a complete margin (Taylor, 1951; Berman, 1973).

39. **Parietals.** Paired elements (0); single median element (1).

40. **Parietal tabs** (triangular flanges extending anteriorly into fossae on ventral surface of frontals). Present (0); absent (1).

41. **Parietal.** Approximately half as long as skull, or shorter (0); more than half as long as skull (1). Some amphisbaenians retain a short parietal (Taylor, 1951; Berman, 1973).

42. **Pineal foramen.** Present (0); absent (1). The illustration of *Aphanizocnemus* (Dal Sasso and Pinna, 1997) seems to show a pineal foramen within the parietal, next to a broken edge.

43. **Pineal foramen.** Entirely within parietal (0); on frontoparietal suture (1); entirely within frontal (2). Ordered 0–1–2. Amphisbaenians and gekkonids have an (atavistic) foramen and this is always within the parietal. (e.g., *Eublepharis macularius* CMNH 144941).

44. **Parietal table and jaw adductor muscles.** Parietal table a narrow sagittal crest, jaw adductors extend over entire dorsal surface of parietal (0); parietal table moderately wide, jaw adductors extend onto lateral margin only of dorsal surface of parietal (1); parietal table very wide, jaw adductors restricted entirely to ventral surface of parietal (2). Ordered 0–1–2.

45. **Parietal.** Main body of parietal does not extend far posteriorly, supraoccipital exposed in dorsal view (0); main body of parietal extends posteriorly, supraoccipital covered or nearly covered in dorsal view (1).

46. **Suspensorial ramus (posterolateral process) of parietal.** Well-developed (0); extremely short or absent (1). Some amphisbaenians retain a long suspensorial ramus (Taylor, 1951; Berman, 1973).

47. **Upper temporal arch.** Complete, upper and lower temporal fenestrae separated (0); incomplete, upper and lower temporal fenestra confluent (1). *Adriosaurus* appears to have state 0, but the preservation is too poor to be certain.

*48. **Temporal arch.** Without canthal crest (0); with canthal crest (1). (McDowell and Bogert, (1954) Gauthier, (1982).

49. **Jugal-squamosal contact along upper temporal arch.** Absent (0); present (1).

50. **Squamosal.** Present (0); absent (1). Some amphisbaenians retain a squamosal (Taylor, 1951; Berman, 1973). The single temporal element in some dibamids (Greer, 1985) is interpreted as a squamosal, based on its position dorsal to and overlapping the quadrate.

51. **Dorsal process of squamosal.** Present (0); absent (1).

52. **Upper temporal fenestra.** Not restricted by postorbital (either widely open or restricted primarily by postfrontal), (0); restricted by postorbital (1).

53. **Upper temporal fenestra.** Not restricted by postfrontal (either widely open or restricted primarily by postorbital), (0); restricted by postfrontal (1).

54. **Supratemporal.** Absent (0); present (1).

55. **Supratemporal.** In superficial position, on dorsolateral surface of parietal (0); in deep position, on ventrolateral surface of parietal (1).

56. **Supratemporal.** Confined to skull roof (0); forms part of paroccipital process and/or braincase (1).

57. **Supratemporal.** Small, less than half the maximum width of the skull (0); large, at least half the maximum width of the skull (1).

58. **Supratemporal-prootic contact.** Absent (0); present (1). This character is not yet known in aigialosaurs (*contra* the typographic error in Lee, 1997).

59. **Quadrate suspension.** Sutured to squamosal, pterygoid, and (sometimes) quadratojugal (0); mobile, articulates dorsally squamosal, supratemporal, and opisthotic (1); mobile, articulates dorsally with supratemporal, little or no contribution from other elements (2); mobile, articulates dorsally with opisthotic, little or no contribution from other elements (3); mobile, articulates dorsally with squamosal, little or no contribution from other elements (4).

60. **Quadrate shaft orientation.** Slanting very slightly anteroventrally, or vertical (0); slanting very anteroventrally, almost horizontal (1); slanting slightly or greatly posteroventrally (2). Ordered 1–0–2.

61. **Quadrate.** Tympanic crest (outer conch) directed laterally and a well-developed wall (0); tympanic crest directed laterally but a low ridge (1); distinct tympanic crest absent and external surface of quadrate only weakly concave (2). Ordered 0–1–2. *Sineoamphisbaenia* is coded as unknown because Wu et al. describe it as lacking the conch but illustrate it with what appears to be a conch.

62. **Quadrate.** With anteromedial (pterygoid) lappet (0); without anteromedial lappet (1).

*63. **Quadrate shape.** Without large, posteroventrally curved, suprastapedial process (0). with large, posteroventrally curved, suprastapedial process (1).

*64. **Mandibular articulation of quadrate.** Saddle-shaped, with lateral and medial condyles (0); flat, a single continuous condyle (1).

*65. **Tympanic membrane.** Not ossified (0); ossified (1).

Braincase and associated structures

66. **Orbitonasal fenestra.** Wide, not greatly restricted by either frontals or prefrontals (0); narrow, restricted largely by frontals and prefrontals (1).

67. **Ventromedial processes of frontals.** Not contacting anything below olfactory tracts (0); abutting or sutured with each other below olfactory tracts (1); contacting parabasisphenoid below olfactory tracts (2). Unordered.

68. **Orbitosphenoid ossification.** Absent (0); present (1).

69. **Parietal downgrowths.** Absent or weakly developed ridges (0); prominent flanges (1).

70. **Parietal downgrowths.** Pointed ventrally (0); sheet-like (1).

71. **Parietal downgrowths.** Not sutured to prootic (0); Sutured to prootic (1).

72. **Parietal downgrowths.** Not contacting parabasisphenoid or orbitosphenoid (0); contacting parabasisphenoid (1); contacting orbitosphenoid (2). Unordered.

73. **Optic foramina.** Not enclosed in bone (0); enclosed partly or entirely by frontals (1); enclosed by orbitosphenoid (2). Unordered.

74. **Anterior brain cavity.** Not floored by bone (0); floored by orbitosphenoid (1); floored by large descending frontal flanges (2). Unordered.

75. **Trigeminal foramen or foramina.** Anterior margin not enclosed in bone (0); anterior margin enclosed by descending flange of parietal (1); anterior margin enclosed by orbitosphenoid and parabasisphenoid (2). Unordered.

76. **Alar process of prootic.** Weakly developed (0); long process (1). Iguanids primitively have state 0 (only *Ctenosaurus* and

related forms have state 1); snakes which can be coded for this character (e.g., *Dinilysia,* madtsoiids) have state 1.

77. **Alar process of prootic.** Directed dorsally (0); directed anterodorsally (1). Iguanids primitively have state 0 (only *Ctenosaurus* and related forms have state 1); snakes which can be coded for this character (e.g., *Dinilysia,* madtsoiids) have state 1.

78. **Crista prootica** (ridge on lateral surface of the prootic, overhanging foramen pro nervi facialis). Well-developed lateral flange (0); reduced to weak ridge, or absent (1).

79. **Lateral head vein.** Not enclosed at all in bony canal (0); mostly or entirely enclosed in a bony canal on parabasisphenoid formed by an anteroventral continuation of the crista prootica (1).

80. **Foramen pro nervi facialis** (lateral exit on prootic for hyomandibular branch of the facial or VII nerve). Single (0); double (1).

81. **Hypoglossal (XII) foramen.** Well-separated from jugular (X-XI) foramen (0); located very close to or confluent with jugular foramen (1).

82. **Occipital recess (recessus scalae tympani).** Open laterally (0); closed laterally (1).

83. **Stapes.** Light, with small footplate and slender shaft (0); robust, with large footplate and thick shaft (1).

*84. **Stapedial foramen.** Absent (0); present (1).

*85. **Basisphenoid.** Without long posterolateral flanges (0); with long posterolateral flanges (1).

86. **Basipterygoid process.** Long, i.e., projecting far antero-laterally beyond the body of the basisphenoid (0); short, i.e., not projecting very far beyond the body of the basisphenoid (1).

87. **Basal tubera.** Posteriorly located, very near to occipital condyle (0); anteriorly located, well away from occipital condyle (1). Aigialosaurs appear to have state 1 (Carroll and deBraga, 1992, Fig. 6b).

88. **Posterior opening of vidian canal.** Situated within basisphenoid (0); at basisphenoid-prootic suture (1); situated at suture between prootic and epiphysial ossification in the region of the basal tubera (2). Unordered.

89. **Posterior opening of vidian canal.** Situated anteriorly, well in front of the posterior end of the basisphenoid (0); situated posteriorly, near the posterior end of the basisphenoid (1).

90. **Opisthotic.** Flange extending between basal tubera and paroccipital process weak or absent, most of the stapes exposed in ventral view (0); wide horizontal flange extending posterolaterally from basal tubera to paroccipital process obscuring much of the stapes in ventral view (1).

91. **Supraoccipital.** Does not contact parietal, unossified gap persists between the two elements (0); abuts parietal, the two elements meet but contact is non-sutural, and a tiny gap might remain between the two elements along part of the dorsal edge of the supraoccipital (1); sutural contact with parietal, entire anterodorsal edge of supraoccipital contacts parietal (2). Ordered 0–1–2.

92. **Supraoccipital.** Situated ventral or posteroventral to parietal, does not form part of posterior skull roof (0); situated posterior to parietal, forms part of posterior skull roof (1). *Adriosaurus* has been coded as unknown: although the supraoccipital appears to be behind, rather than below the parietal, this might be a taphonomic artefact (the entire skull is flattened).

93. **Exoccipital.** Discrete element, not fusing with opisthotic until well into postembryonic ontogeny (0); not present as discrete element, fusing with opisthotic within embryo (1).

94. **Occipital condyle.** Single continuous convex projection, posterior surface of condyle straight in ventral view (0); two discrete convex projections arranged horizontally, posterior surface of condyle concave in ventral view (1).

95. **Posttemporal fenestra.** Present as an opening (0); completely closed via sutural contact of the skull roof and otic region of braincase (1).

Palate and associated structures

96. **Septomaxilla-maxilla contact.** Rigid, septomaxilla extensively sutured to the dorsal surface of the palatal flange of the maxilla

(0); mobile, septomaxilla not sutured to maxilla (1). Dolichosaurs lack a distinct sutural area on the dorsomedial surface of the maxilla for the septomaxilla, and thus appear to have state 1.

97. **Septomaxillae.** Separated by cartilaginous gap (0); meeting or nearly meeting on midline in a raised crest (1).

98. **Median flange of septomaxilla.** Short, not reaching level of prefrontal (0); long, extends posteriorly to reach level of prefrontal (1).

99. **Dorsal surface of septomaxilla** (roof of Jacobson's organ). Flat or concave, Jacobson's organ small (0); expanded dorsally and convex, Jacobson's organ large (1).

100. **Opening of Jacobson's organ.** Enclosed partly by maxilla and vomer, confluent posteriorly with choana (0); enclosed fully by maxilla and vomer, sometimes with a tiny contribution from the septomaxilla, not confluent with choana (1); enclosed fully by vomer and septomaxilla only, not confluent with choana (2).

101. **Vomers.** Paired (0); fused (1). Unordered. Not clearly preserved in *Sineoamphisbaena* (Wu et al., 1996).

102. **Vomer.** With little or no sutural contact with maxilla behind opening of Jacobson's organ, most of lateral margin free (0); with extensive sutural contact with maxilla behind opening of Jacobson's organ, entire lateral margin meets maxilla (1). Not clearly preserved in *Sineoamphisbaena* (Wu et al., 1996).

103. **Vomer.** Small, less than half the length of maxilla (0); long, at least half the length of the maxilla (1).

104. **Vomer.** Main portion plate-like (0); main portion rod-like (1).

105. **Vomer.** Anterior or anteromedial to palatine (0); entirely medial to palatine (1).

106. **Secondary palate.** Absent (0); present, formed by medial extension of ventrolateral edge of the palatine (1).

107. **Palatine-vomer contact.** Short, length of contact less than half the length of vomer (0); extensive, length of contact forming at least half the length of vomer (1).

108. **Palatine-vomer contact.** Immobile, sutural contact (0); mobile, non-sutural contact (1).

109. **Palatine.** Long—as long as vomer (0); short—half as long as vomer (1).

110. **Palatines.** Well separated from one another by anterior extension of interpterygoid vacuity (0); contacting or almost contacting one another along most of their midline, obliterating interpterygoid vacuity (1).

111. **Palatine.** Without distinct medially-directed process (0); with distinct rectangular process projecting medially from the middle portion of the palatine to the skull midline (1).

112. **Choanal groove of palatine.** Short or absent (0); long groove leading posteriorly from choana along ventral surface of palatine (1).

*113. **Ectopterygoid.** Does not enter cheek (0); enters cheek as a sliver sandwiched between maxilla and jugal (1). McDowell and Bogert (1954) and Gauthier (1982).

114. **Ectopterygoid-palatine contact.** Absent, maxilla enters suborbital fenestra (0); present, maxilla excluded from suborbital fenestra (1).

115. **Suborbital fenestra.** Present and large (0); present but small (1); absent, i.e., completely closed (2). Ordered 0–1–2. Some xantusiids exhibit state 1 (e.g., *Xantusia riversiana*).

116. **Interpterygoid vacuity** ("pyriform recess" of Estes et al., 1988). Open and narrow (0); open and wide (1); narrow and closed by a broadened parasphenoid (2). Ordered 1–0–2. *Adriosaurus,* if the pterygoid is identified correctly, appears to have state 0.

117. **Pterygoid-vomer contact.** Present, palatal ramus of pterygoid meets vomer anteriorly (0); absent, palatal ramus does not reach vomer (1).

118. **Pterygoid.** With triangular depression on ventral surface, extending from suborbital foramen towards basicranial articulation (0); without such depression (1).

119. **Pterygoid.** Anterior (palatine) process merges gradually, in a gentle curve, with the lateral (ectopterygoid) process (0); anterior process distinctly set off from lateral process, the two portions meeting at a distinct "corner" (1).

120. **Anterolateral process of pterygoid.** Absent, pterygoid with only anterior and lateral processes (0); present, extending along lateral margin of palatine (1).

121. **Epipterygoid.** Present (0); absent (1). A possible epipterygoid has been tentatively identified in *Adriosaurus.*

Lower Jaw

122. **Mandibular symphysis.** Rigid—anterior tips of dentary with a distinct flat symphysial area (0); mobile—anterior tips of dentary smoothly rounded and without distinct symphysial area (1).

123. **Mental foramina on lateral surface of dentary.** Three or more foramina (0); two or fewer foramina (1).

124. **Dentary.** Straight in lateral view, with straight dorsal edge (0); curved in lateral view, with concave dorsal (alveolar) edge (1).

125. **Dentary.** With large posterodorsal extension covering much of the lateral surface of coronoid process (0); with small posterodorsal extension onto anterolateral part of coronoid process (1); does not cover lateral surface of coronoid process (2). Ordered 0–1–2.

126. **Meckel's canal.** Open groove on ventromedial or medial surface of dentary (0); enclosed tube within dentary, upper and lower borders of groove meeting in a sutural contact (1); enclosed tube within dentary, upper and lower borders completely fused together (2). Ordered 0–1–2.

127. **Anterior (symphysial) end of Meckel's canal.** Extends along ventral margin of lower jaw (0); confined to medial surface of lower jaw (1).

128. **Intramandibular septum of Meckel's canal.** Poorly developed, does not approach level of the posteriormost tooth (0); well developed, extends posteriorly to nearly the level of the posteriormost tooth (1). Snakes exhibit state 1 (Scanlon and Lee, pers. obs.). In a dolichosaur (NHM R342), the dentary is fractured at the posterior tooth row to reveal a well-developed septum.

129. **Subdental shelf.** Large (0); weakly developed (1); absent (2). Ordered 0–1–2.

130. **Posterior margin of lateral surface of dentary.** No notch present (0); shallow notch present (1); deep notch present (2). Ordered 0–1–2.

131. **Dentary-postdentary articulation.** Extensive overlap (0); reduced overlap (1).

132. **Splenial.** Large, extending anteriorly past middle of tooth row (0); small, only reaching middle of tooth row (1); absent (2). Ordered 0–1–2.

133. **Splenial.** Extends posteriorly onto postdentary bones, past apex of coronoid process (0); extends posteriorly onto postdentary bones but does not reach level of apex of coronoid process (1); does not substantially overlap postdentary elements (2). Ordered 0–1–2.

134. **Anterior tip of splenial.** On ventral edge of dentary (0); on medial surface of dentary (1).

135. **Splenial-dentary contact.** Extensive bony contact (0); reduced bony contact, much intervening connective tissue (1).

136. **Splenial-angular contact.** In medial view, overlapping, irregular, and with limited mobility (0); in medial view, abutting, straight (vertical), and highly mobile (1).

*137. **Splenial-angular contact.** Not, or very slightly, exposed in lateral view (0); greatly exposed in lateral view (1). The condition in *Pachyrhachis* is uncertain: although the two elements are not exposed in lateral view (dorsal view of slab), examination of the medial surface (ventral view of slab) reveals that both elements appear to be damaged. However, the condition in *Pachyophis* is clear; it has state 1.

138. **Anteromedial process of coronoid.** Long, extensive overlap on medial surface of dentary in front of coronoid process (0); short, coronoid does not greatly overlap medial surface of dentary in front of coronoid process (1).

139. **Anterolateral process of coronoid.** Absent, coronoid does not overlap lateral surface of dentary (0); present, overlapping lateral surface of dentary (1).

140. **Coronoid.** Anteromedial margin contacts splenial (0); anteromedial margin does not contact splenial (1). The provisional

identification of the coronoid in *Aphanizocnemus* (Dal Sasso and Pinna, 1997) seems unlikely, as the element in question is located very posteriorly on the jaw, near the quadrate-mandibular articulation.

141. **Coronoid.** Ventral margin of medial surface straight or convex (0); ventral margin of medial surface concave (1).

142. **Subcoronoid fenestra on medial surface of the mandible.** Fenestra absent, prearticular expands dorsally and contacts the entire ventral edge of the coronoid, surangular covered by these elements in medial view (0); fenestra present as distinct gap between coronoid and prearticular, surangular exposed in medial view (1).

143. **Disarticulated surangular.** Extends far into the dentary and terminates in a point (0); extends some distance into the dentary and terminates in a blunt end (1); extends a short distance into the dentary and terminates in a blunt end (2); extends over lateral surface of dentary (3). Unordered. Aigialosaurs appear to have state 2 (e.g., Carroll and deBraga, 1992, fig. 8a, d).

144. **Surangular.** Does not extend dorsally to overlap posterior part of coronoid process (0); with flange extending dorsally to overlap posterior part of coronoid process (1).

*145. **Surangular.** Does not form large portion of articular cotyle (0); forms half of articular cotyle (1).

146. **Angular.** Present (0); absent (1).

147. **Angular.** With wide exposure on medial surface of the mandible (0); not exposed, or exposed as only a very narrow splint, on the medial surface of the mandible (1).

148. **"Fingerlike" angular process.** Absent (0); present (1).

149. **Prearticular** (in medial view with dentary and splenial removed). Extends only a short distance in front of coronoid process, not past posterior teeth (0); extends well anterior to coronoid process, past posterior teeth (1).

150. **Prearticular crest.** Absent (0); moderately well-developed (1); prominent, with embedded angular process (2). Ordered 0–1–2.

151. **Adductor fossa.** Faces dorsomedially (0); faces dorsally (1).

152. **Adductor fossa.** Narrow transversely, does not bulge medially (0); inflated transversely, bulges medially (1).

153. **Articular.** Fused with prearticular and surangular (0); fused with prearticular but not surangular (1); separate from both prearticular and surangular (2). Ordered 0–1–2. The descriptions of states 0 and 2 were inadvertantly switched in Lee (1998); this is corrected here.

*154. **Retroarticular process size.** Intermediate, between 1 and 2 times articular cotyle (0); short, < articular cotyle (1); long, >2 times articular cotyle (2). Ordered 1–0–2.

155. **Retroarticular process position.** In line with rest of mandible (0); offset medially, resulting in a lateral "step" where it joins the rest of the mandible (1).

156. **Retroarticular process orientation.** Extends straight posteriorly (0); extends posteromedially (1).

157. **Retroarticular process.** Dorsal surface with distinct sulcus or pit (0); dorsal surface smoothly concave (1).

158. **Retroarticular process.** Dorsomedial margin smooth and featureless (0); dorsomedial margin with discrete tubercle or flange (1).

159. **Retroarticular process.** Tapering, narrow distally (0); not tapering, broad distally (1).

160. **Retroarticular process.** Not twisted posteriorly, posterior dorsal surface directed dorsally (0); twisted posteriorly, posterior dorsal surface directed dorsomedially (1).

Dentition

161. **Marginal teeth.** Pleurodont, teeth set in a continuous groove (0); acrodont, teeth ankylosed to jaw margin (1); thecodont, teeth ankylosed in discrete alveoli and separated by well-developed interdental plates (2). Unordered. The teeth are thecodont in dolichosaurids (pers. obs); there is a deep groove and complete but thin interdental plates separating adjacent teeth. A similar situation also appears to be the case in the aigialosaur *Opetiosaurus* (pers. obs).

It has long been recognised that among squamates, only mosasauroids and snakes have teeth set in discrete alveoli, a condition often described as "thecodonty," "modified thecodonty," "subthecodonty," or "ankylosed thecodonty" (e.g., Edmund, 1969; Bell, 1997; Lee, 1997). Recently, however, Zaher and Rieppel (1999) have argued that this is not the case. They redefine thecodonty very narrowly to refer only to taxa where the teeth are attached to the jaw by ligaments (rather than by bone of attachment) and continually replaced: presence of discrete alveoli alone is not sufficient (thus, even mammals are not thecodont under their definition). They then state that mosasauroids and snakes do not share their character state "thecodonty." However, the presence of discrete alveoli remains a synapomorphy of mosasauroids and snakes, whether one chooses to label it thecodonty or not. Among squamates, only mosasauroids and snakes have extensive interdental plates that divide the alveolar groove into discrete sockets; arguments that such complete plates and discrete sockets are lacking in scolecophidians, but present in some lizards such as *Tiliqua,* are addressed elsewhere (Scanlon and Lee, in press).

162. **Marginal teeth.** Without sharp carinae (0); with sharp carinae (1).

163. **Bases of marginal teeth.** Smooth, dentine not infolded (0); dentine infolded ("plicidentine"), resulting in longitudinal grooves (1). While most snakes lack plicidentine, it is present in some basal forms such as madtsoiids (Scanlon and Lee, in press). Zaher and Rieppel (1999: 6) state that "mosasaurs lack plicidentine." However, the bases of the tooth crowns in mosasauroids typically have either true infoldings of the enamel (e.g., see photographs in Lingham-Soliar, 1994) or at least distinct ridges on the external surface (e.g., Russell, 1967).

164. **Marginal teeth.** Crowns closely spaced (0); crowns separated by large gaps (1). Dolichosaurids are coded as not applicable as tooth bases are widely spaced but the tops (which are anteroposteriorly expanded) closely approach each other.

*165. **Marginal teeth.** Without high pedestals (0), with high pedestals (1).

166. **Position of replacement teeth.** Lingual to functional tooth (0); posterolingual to functional tooth (1); no true replacement teeth (2). Unordered.

167. **Resorption pits associated with replacement teeth.** At base of teeth (0); on bony tooth pedicel (1); absent (2). Resorption pits have not been observed on any aigialosaur teeth (Carroll and deBraga, 1992). Unordered.

168. **Orientation of replacement teeth.** Erupt upright, growing straight upwards into functional position (0); erupt horizontally, and then rotating through ninety degrees about the base into functional position (1). Zaher and Rieppel (1999) question the presence of recumbent replacement teeth in mosasauroids, suggesting that the almost universal occurrence of this feature in mosasauroids is a taphonomic artefact. As discussed more fully elsewhere (Scanlon and Lee, in press), this is unlikely since (a) in the great majority of mosasauroid material (but no specimens of *Mosasaurus*—see below) replacement teeth have this orientation, (b) the non-vertical replacement teeth are always recumbent and never face some other direction (if they were taphonomically displaced some would face medially, etc) , and (c) all specimens of species of *Mosasaurus* always have upright teeth (this consistent exception would not occur if recumbency was a random taphonomic artefact).

169. **Premaxillary teeth.** Five or more (0); four or fewer (1). The narrow premaxilla in aigialosaurs is unlikely to have contained more than four teeth (Carroll and deBraga, 1992), and a similar situation occurs in *Adriosaurus.*

170. **Median premaxillary tooth.** Absent (0); present (1).

171. **Median premaxillary tooth.** Not enlarged (0); much larger than other premaxillary teeth (1).

172. **Premaxillary teeth** (apart from median tooth). Similar size or larger than anterior maxillary teeth (0); distinctly smaller than anterior maxillary teeth (1).

173. **Maxillary teeth.** Thirteen or more tooth positions (0); between twelve and nine tooth positions (1); eight or fewer tooth positions (2). Ordered 0–1–2. Based on the size and spacing of

the teeth, and the probable length of the maxilla, *Adriosaurus* must have possessed between 14 and 10 teeth, i.e., state 0 or 1.

174. **Dentary teeth.** Thirteen or more tooth positions (0); twelve to nine tooth positions (1); eight or fewer tooth positions (2). Ordered 0–1–2.

175. **Palatine teeth.** Present (0); absent (1).

176. **Palatine teeth.** Small conical denticles (0); similar in size to marginal teeth (1).

177. **Pterygoid teeth.** Present (0); absent (1).

178. **Pterygoid teeth.** Small conical denticles (0); similar in size to marginal teeth (1).

179. **Egg teeth.** Single (0); paired (1). Dibamids have paired teeth (NHM 1903.4.13.64).

Axial Skeleton

180. **Centra.** Not constricted anterior to condyle, i.e., condyle not wider than posterior end of centrum (0); slightly constricted anterior to condyle, i.e., condyle slightly wider than posterior end of centrum (1); greatly constricted anterior to condyle, i.e., condyle much wider than posterior end centrum (2). Ordered 0–1–2. *Adriosaurus* is tentatively scored with state 0, based on the illustration in Seeley (1881).

181. **Vertebral articulatory surfaces.** Vertical, condyles (if present) facing posteriorly, much of the articulatory surface is visible in ventral view (0); slightly anterodorsal, condyles facing slightly dorsally, only the ventral edge of the articulatory surface is visible in ventral view (1); anterodorsal, condyles facing very dorsally, none of the articulatory surface is visible in ventral view (2). Ordered 0–1–2.

182. **Shape of articulatory surfaces in mid-dorsal vertebrae.** Oval, horizontal (mediolateral) dimension wider than vertical (dorsoventral) dimension (0); circular (1). Although no vertebra from an aigialosaur has been prepared from all sides, they appear to have state 0 (Carroll and deBraga, 1992). Thus, contrary to Lee (1998), mosasauroids (aigialosaurs 0; mosasaurids 1) and snakes (scolecophidians 0; alethinophidians 1) each exhibit both states.

183. **Centra.** Notochordal, i.e., perforated by persistent notochord in adults (0); not notochordal, i.e., not perforated by persistent notochord in adults (1).

*184. **Centra.** Amphicoelous (0); procoelous (1).

185. **Neural spines.** Tall processes (0); low ridges (1). The spines in *Aphanizocnemus* are well-developed in the cervical and caudal region and reduced in the dorsal region; it has therefore been coded with both states.

186. **Zygosphenes and zygantra.** Present (0); absent (1).

187. **Zygosphenes and zygantra.** Type A, articular surface of zygosphene faces dorsally (0); type B, articular surface of zygosphene faces ventrolaterally (1).

188. **Intercentra on dorsal (thoracolumbar) vertebrae.** Present (0); absent (1). Some pygopodids retain intercentra Kluge (1987).

189. **Number of presacral vertebrae.** 23 to 25 (0); 22 or fewer (1); 26 (2); 27 to 50 (3); 50 to 119 (4); 120 or more (5). Ordered 1–0–2–3–4–5. Although no complete series is preserved in any dolichosaurid, NHM 49002 has 19 cervicals and 6 small (anterior) dorsals while NHM 32268 has 19 large (posterior) dorsals; thus, the presacral count must have been at least 16 cervicals plus 6 small dorsals plus 19 large dorsals. Dolichosaurs have accordingly been coded with states 3, 4, or 5.

190. **Number of cervical vertebrae.** Seven or fewer (1); eight (0); nine or ten (2); more than ten (3). The last state represents a new informative state that is relevant in this analysis. Ordered 1–0–2–3. While snakes cannot be coded due to lack of a pectoral girdle, "cervicals" can be recognised in *Pachyrhachis* and *Pachyophis* based on their small size, lack of pachyostosis, and well-developed hypaophyses.

*191. **Transverse processes of cervicals.** On anterior end of centrum (0); on middle of centrum (1).

192. **Hypapophyses on anterior presacrals.** Only extending to the posterior end of the sixth presacral at most (0); extending to the seventh presacral or beyond (1).

193. **Dorsoposterior flange on atlas neural arch.** Present, directly overlying axis neural arch (0); absent (1). While most snakes lack the flange, some basal snakes retain it (Scanlon, 1996).

194. **Cervical intercentra** (excluding atlas and axis intercentra). Not sutured or fused to preceding centrum (0); sutured to preceding centrum (1); fused to preceding centrum (2). Ordered 0–1–2.

195. **Cervical intercentra.** Not sutured or fused to following centrum (0); sutured to following centrum (1); fused to following centrum (2). Ordered 0–1–2.

*196. **Pachyostosis of mid-dorsal vertebrae and ribs.** Absent (0); present (1).

197. **Caudal transverse processes.** Single processes throughout caudal region (0); double processes in some caudals (1).

198. **Caudal transverse processes.** Two prongs converging distally (0); two prongs diverging distally (1).

199. **Caudal transverse processes.** Project laterally or posterolaterally (0); project anterolaterally (1).

200. **Caudal autotomy septa.** Present in some caudals (0); absent in all (1).

201. **Caudal autotomy septa.** Anterior to, or within, transverse processes (0); posterior to transverse processes (1). Both dibamids and amphisbaenians (e.g., *Rhineura floridana*) have a septum posterior to the transverse process.

202. **Pedestals on caudal vertebrae for chevrons.** Weakly developed, barely raised above the surface of the centrum (0); prominent raised tubercles (1).

203. **Chevrons.** Articulate with caudal centra (0); sutured or fused to caudal centra (1).

204. **Caudal chevron position.** At posteroventral margin of centrum (0); situated more anteriorly, some distance from posteroventral margin of centrum (1).

*205. **Body shape.** Round, ribs smoothly curved (0); laterally compressed, middle and distal regions of ribs totally straight (1).

206. **Ribs.** Begin from third (or more anterior) cervical vertebra (0); begin from fourth (or more posterior) cervical vertebra (1).

207. **Ribs.** Proximal end without anteroventral pseudotuberculum (0); proximal end with anteroventral pseudotuberculum (1).

208. **Ribs.** Proximal end without posterodorsal pseudotuberculum (0); proximal end with posterodorsal pseudotuberculum (1). Snakes have state 1 (*contra* Lee, 1998).

209. **Distally forked cloacal ribs** ("lymphapophyses"). Absent (0); present (1).

*210. **Tail.** Cylindrical or only slightly lateral compressed, transverse processes well-developed, chevrons and neural spines not elongated (0); very laterally compressed, transverse processes reduced anteriorly and absent posteriorly, chevrons and neural spines elongated (1). All outgroups primitively exhibit state 0, though some aquatic rhynchocephalians (pleurosaurs) have state 1. Although only the promixal part of the tail is preserved in *Pachyrhachis,* and no part is preserved in *Pachyophis,* the highly compressed posterior trunk region (more compressed than in other aquatic squamates) suggests they possessed state 1.

*211. **Neural spines of posterior caudal vertebrae.** Projecting dorsally or posterodorsally (0); projecting almost horizontally, highly inclined posteriorly (1).

Shoulder Girdle and Forelimb

212. **Scapulocoracoid.** Present and large (0); present but reduced (1); absent (2). Ordered 0–1–2.

213. **Emargination on anterodorsal edge of scapula.** Absent (0); present (1).

214. **Anterior (primary) coracoid emargination.** Absent (0); present (1).

215. **Posterior (secondary) coracoid emargination.** Absent (0); present (1).

216. **Clavicle.** Present (0); absent (1). Clavicles are provisionally treated as present in both aigialosaurs and mosasaurids because they are present in at least some taxa from both groups (Caldwell et al,. 1995; Russell, 1967); absence in other taxa might not be a genuine loss, but due to non-preservation or poor ossification.

217. **Clavicle.** Follows contour of anterior margins of scapulocoracoid (0); curves anteriorly away from scapulocoracoid (1). The clavicle in *Aphanizocnemus* appears to curve ventrally away from the scapulocoracoid (Dal Sasso and Pinna, 1997), but this interpretation is provisional as this might be due to distortion of a medial curvature.

218. **Clavicles.** Rod-like, at most only slightly expanded proximally and with no notch or fenestra (0); greatly expanded proximally, usually with notch or fenestra (1).

219. **Interclavicle.** Present (0); absent (1).

220. **Interclavicle.** Cross-shaped, with lateral processes (0); simple rod, without lateral processes (1). Contrary to Lee (1998) aigialosaurs exhibit state 0 (e.g., Caldwell et al., 1995) and mosasaurids state 1 (Russell, 1967).

221. **Interclavicle.** Anterior process small or absent (0); anterior process large (1).

222. **Ossified sternum.** Present (0); absent (1).

223. **Sternal fontanelle.** Absent (0); present (1).

*224. **Sternal fontanelle.** Single (0); paired (1). Moody (1980).

225. **Number of rib attachment points to sternum.** Five pairs (0); four pairs (1); three pairs (2); two pairs or fewer (3). Ordered 0–1–2.

226. **Postxiphisternal inscriptional ribs.** None united along the ventral midline (0); one or more pairs united along the ventral midline to form continuous chevron-shaped structures (1).

227. **Forelimbs.** Large (0); small (1), absent (2). Ordered 0–1–2.

228. **Ectepicondylar foramen of humerus.** Present (0); absent (1). The foramen is not visible on the humerus of *Adriosaurus.* However, this interpretation is tentative because the preaxial edge of this element is rough, suggesting that part of the element (which might have borne the foramen) might be missing.

*229. **Epipodials.** Parallel (0); distally diverging (1).

*230. **Forelimb.** "Foot"—olecranon large, carpals well-ossified, digits independently movable and with well-developed joints (0); "flipper"—olecranon small, carpals poorly-ossified, digits joined by webbing or sheath and with poorly-developed joints (1). All outgroups primitively exhibit state 0, though some aquatic rhynchocephalians (pleurosaurs) have state 1. Kuehneosaurs have state 0, though the olecranon is small (Colbert, 1970).

Pelvic Girdle and Hindlimb

231. **Pelvis.** Present and large (0); present and small (1); absent (2). Ordered 0–1–2.

232. **Pelvic elements** (ilium, ischium, pubis). Distinct elements but strongly sutured together (0); co-ossified into a single pelvic bone (1); distinct elements, weakly united in non-sutural contacts (2). Ordered 1–0–2.

233. **Sacral blade of ilium.** With anterior bulge or process (0); without anterior process (1).

234. **Pubis.** Short in length, symphysial process directed ventrally (0); intermediate in length, symphysial process anteroventrally (1); greatly elongated, symphysial process directed anteriorly (2). *Varanus* exhibits both states 0 and 1, xantusiids exhibit state 1, and teiids exhibit state 2. Ordered 0–1–2.

*235. **Pubic plate.** Oriented parasagitally, wide in lateral view (0); oriented transversely, narrow in lateral view (1). All outgroups appear to have a parasagittal pubic plate, hence the transverse pubic plate found in almost all squamates appears to be a squamate synapomorphy. The parasagittal plate found in many aquatic varanoids appears to be a reversal. This character is not applicable in taxa with highly reduced pelves.

*236. **Pubis.** Expanded distally, at symphysial margin (0); not expanded distally (1). This character is not applicable in taxa with highly reduced pelves.

237. **Hindlimbs.** Well-developed (0); reduced (1); absent (2). Ordered 0–1–2.

238. **Femur.** Gracile (0); stout (1).

239. **Femur.** Curved in dorsoventral plane (0); not curved (1).

240. **Distal end of tibia.** Gently convex for astragalocalcaneal articulation (0); with notch fitting into a ridge on astragalocalcaneum (1).

241. **Astragalus and calcaneum.** Co-ossified (0); separate (1).

*242. **Hindlimb.** "Foot"—fifth metatarsal fully hooked, tarsals well-ossified, digits independently movable and with well-developed joints (0); "flipper"—fifth metatarsal partially hooked or not hooked, tarsals poorly-ossified, digits joined by webbing or sheath and with poorly-developed joints (1). All outgroups primitively exhibit state 0, though some aquatic rhynchocephalians (pleurosaurs) have state 1.

Miscellaneous Osteological Characters.

*243. **Body proportions.** Head moderately large with respect to trunk region (0); head extremely small with respect to trunk region (1). *Pachyrhachis* and *Pachyophis* differ from all "lizards" and all basal snakes in having very small heads, a condition approached only in some advanced sea snakes.

244. **Dorsal body osteoderms.** Absent (0); present (1).

245. **Ventral body osteoderms.** Absent (0); present (1).

246. **Separable cranial osteoderms.** Absent (0); present only periphery of skull table (1); present over entire skull table (2). Ordered 0–1–2.

247. **Separable cranial osteoderms.** Few and large (0); many and small (1).

248. **Separable cranial osteoderms.** Tightly connected to skull roof, though separable (0); very loosely connected to skull roof (1).

249. **Rugosities on skull roof bones formed by overlying cephalic scales.** Rugosities absent (0); rugosities present, no vermiculate sculpture (1); rugosities present, along with vermiculate sculpture (2). Ordered 0–1–2.

250. **Scleral ossicles.** Present (0); absent (1).

251. **Scleral ossicles.** Fifteen or more (0); fourteen (1); thirteen or fewer (2). Ordered 0–1–2.

252. **Scleral ossicles.** Complex and irregular in shape (0); square in shape (1). New osteological character from Underwood (1970). Not applicable in taxa with poorly developed, or lacking, scleral ossicles (see character 223).

253. **Hyoid apparatus.** Second epibranchials present (0); second epibranchials absent (1).

254. **Hyoid apparatus.** Second ceratobranchials present (0); second ceratobranchials absent (1).

255. **Epiphyses on skull and axial skeleton.** Present (0); absent (1).

256. **Epiphyses on appendicular skeleton.** Present (0); absent (1).

257. **Fusion of long bone epiphyses.** Fuses to diaphyses at the same time, or after, fusion of braincase elements (0); fuses to diaphyses before fusion of braincase elements (1).

258. **Postcloacal bones.** Absent (0); present (1).

The following characters in Lee (1998) were not used here:

Cultriform process. Curved in lateral view (0); straight (1). This character is difficult to quantify, subject to distortion during drying, and impossible to score on taxa where the relevant region is unossified.

Lacrimal foramen. Bordered at least partly by facial elements, i.e., lacrimal or maxilla (0); entirely within antorbital flange of prefrontal (1). This was interpreted as a mosasauroid-snake synapomorphy by Lee (1998); however, the lacrimal foramen appears to be absent in mosasaurs, which thus cannot be coded.

Otic region. Region of braincase containing fenestra ovalis not expanded laterally (0); region of braincase containing fenestra ovalis expanded laterally (1). This character was interpreted as diagnosing a *Sineoamphisbaena* + dibamid + amphisbaenian clade (Wu et al., 1996; Lee, 1998). However, the lateral expansion in *Sineoamphisbaena* is correlated with the general broadness of the skull, while in dibamids and amphisbaenians the region is only appears expanded due to allometry (as in all small squamates, the otic region is relatively large).

Footplate of stapes. Not tightly surrounded by ridges projecting from the lateral surface of the braincase elements (0); tightly surrounded by flanges from prootic and opisthotic (1). This was interpreted as a mosasauroid-snake synapomorphy; however, the flanges in mosasaurs tightly encircle only a tiny area around the stapes, while those in snakes encircle a much greater area and might be argued to fail the test of similarity.

Basipterygoid process. Articulatory facet at distal end is a small

subcircular area (0); articular facet at distal end is a large anteroposteriorly elongated area (1). This character is very variable within terminal taxa and very difficult to quantify.
Pubic tubercle. On posterodorsal end of pubis (0); more anteroventrally placed, occupying shaft of pubis (1). This character was interpreted as a scleroglossan synapomorphy (Estes et al., 1988; Lee, 1998). However, there are no clear differences between scleroglossans and other squamates (i.e., iguanians).

APPENDIX 2

The character-by-taxon matrix compiled in this study. ? = missing data, − = inapplicable. Multistate taxa are identified as follows: A = 0 & 1, B = 0 & 2, C = 1 & 2, D = 0 & 1 & 2, E = 2 & 3, F = 0 & 2 & 3, G = 0 & 4, H = 3 & 4, J = 4 & 5, K = 3 & 4 & 5.

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TAXON                                    CHARACTERS

                 1 2 3 4 5 6 7 8 9 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 3 4 4 4 4 4 4 4 4 4 4 5
                                     0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0

Ancestor         0 0 0 A 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 A 0 0 A A A 0 0 0 0 A 0
Iguanidae        1 0 0 0 0 0 A 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 1 0 0 0 1 1 0 C 0 0 0 0 0 0 1 A 0 0 1 C 0 0 0 0 1 0
Leiolepidinae    1 0 0 0 0 1 1 0 0 0 A 0 0 0 0 1 1 0 0 0 0 0 1 0 0 0 1 1 0 2 - 0 0 0 0 0 1 0 0 0 0 1 C 0 0 0 0 1 0
Agaminae         1 0 0 0 0 1 1 0 0 0 A 0 0 1 0 0 A 0 1 0 0 0 0 0 1 1 0 2 - 0 0 0 0 0 1 0 0 0 1 2 0 0 0 0 1 0
Chamaeleonidae   1 0 - - 0 1 0 0 0 0 A 0 0 1 0 0 1 0 1 0 0 A 0 1 1 A 0 A 0 1 0 2 - 0 0 0 0 0 1 A 0 A 2 A 1 0 0 0 1 0
Xantusiidae      1 0 0 1 0 0 0 0 0 ? ? 0 0 0 0 0 0 1 0 0 0 1 0 0 0 A 0 A 0 1 0 - 1 0 1 - 0 A 0 0 A 0 2 1 1 0 0 0 0
Eublepharinae    0 0 0 1 0 0 0 0 0 0 1 - 0 0 0 0 0 0 1 0 0 0 1 0 0 0 0 1 0 1 0 0 1 0 1 - 2 0 1 0 1 0 2 0 0 1 - - 0
Gekkonines s.l.  1 0 0 1 0 0 0 0 0 1 - 0 0 0 0 0 1 0 0 0 1 0 0 0 A 0 1 0 1 0 0 1 0 1 - 2 1 1 0 1 - 2 0 0 1 - - A
Diplodactylinae  0 0 0 1 0 0 0 0 0 0 1 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 1 0 1 - 2 1 1 0 1 - 2 0 0 1 - - 0
Pygopodidae      0 0 0 A 0 0 0 0 0 0 1 - 0 0 0 0 0 1 0 0 0 A 0 0 0 0 A A 1 0 - 1 0 1 - 2 0 1 0 1 - 2 0 0 1 - - 0
Sineoamphisbaena ? 0 ? ? 0 0 0 1 0 0 1 0 ? 0 0 1 0 0 0 0 0 0 1 0 1 1 - 0 1 0 1 0 0 0 0 0 1 0 1 - 2 0 0 0 0 1 0
Dibamidae        1 0 0 0 0 0 0 0 0 0 1 - 0 0 0 1 - 0 - 0 0 0 1 0 0 0 1 0 0 0 1 - 0 1 0 - 1 0 1 - 2 1 1 1 1 - 0 0 A 1 - - A
Amphisbaenia     1 0 0 1 0 0 0 0 A A 1 - 0 0 0 A 1 0 1 0 0 0 1 0 0 0 1 0 A 0 0 2 - 0 0 1 - B 1 1 A 1 0 0 A A 1 - - A
Lacertidae       1 0 0 1 0 0 1 0 0 0 0 0 0 0 0 0 A 0 A 0 0 0 1 0 1 0 1 0 0 0 - 1 1 1 - 0 1 0 0 0 0 2 1 0 0 0 0
Teiidae          1 0 0 1 0 0 1 0 0 0 0 0 0 0 0 1 0 1 0 0 0 A 0 0 0 0 0 1 0 A 0 A 1 0 0 1 0 1 0 0 0 A 0 0 0 0 A 0
Gymnophthalmidae 1 0 0 0 0 0 1 0 0 0 A A 0 0 0 0 1 0 1 0 0 0 A 0 0 0 0 0 1 0 0 0 0 1 0 0 1 0 1 0 0 1 - C 0 0 0 0 0
Cordylidae       1 0 0 A 0 0 0 0 0 0 0 0 0 0 0 0 A 0 1 0 0 0 0 0 0 A 0 1 A 0 A 0 2 A 0 0 0 0 0
Scincidae        A 0 0 1 0 0 0 0 0 A 0 0 0 0 0 A 0 1 0 0 0 A 0 0 0 1 0 1 0 A 1 A A 1 0 1 A 0 0 0 2 0 0 0 0 0
Anguidae         1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 1 0 1 A 0 0 A 0 0 0 A A 1 0 1 0 A 1 1 0 1 0 1 1 0 0 0 C 0 0 0 0 0 A
Xenosaurus       1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 0 0 0 1 0 1 0 1 1 1 0 1 0 1 1 0 0 0 2 1 0 0 1 1 0
Shinisaurus      1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 1 0 1 0 1 1 1 0 1 0 1 1 0 0 0 1 0 0 0 1 0 0
Heloderma        1 0 0 1 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0 1 1 - 0 1 0 - 0 0 1 - 0 1 1 0 1 - 2 0 0 1 - - 0
Lanthanotus      1 0 1 0 0 0 1 0 1 0 0 0 0 1 0 1 0 1 0 0 1 0 2 0 0 1 1 - 0 1 0 - 1 0 1 - 2 1 1 1 - 1 0 0 1 - - 0
Varanus          1 0 1 0 0 0 0 1 0 1 0 0 1 0 0 0 1 0 1 0 0 1 - 2 0 0 1 0 1 0 1 0 1 1 1 0 1 1 1 0 0 0 1 0 0 0 0 0
Serpentes        1 0 1 A 1 0 0 0 0 A 1 - 0 0 0 1 - - - 0 0 A 0 1 0 0 1 A A 0 0 B - 0 0 A 0 C 1 1 A 1 - 0 0 1 1 - - 1
Pachyrhachis     1 0 ? ? 1 0 0 0 0 0 1 - ? 0 0 0 1 0 1 0 ? ? - 2 0 0 1 1 - ? 0 0 1 1 0 1 - 0 0 1 - - 0
Pachyophis       ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
Aigialosauridae  1 1 ? ? 0 ? 0 1 0 1 0 0 ? ? 1 0 1 1 1 0 1 ? - 2 0 1 0 A 1 0 A 0 ? 1 ? ? 1 0 1 ? 0 0 0 1 ? 0 0 0 0 0
Mosasauridae     1 1 1 0 0 0 0 1 0 1 0 0 0 0 0 1 0 1 1 1 0 1 0 - 2 0 1 0 0 0 0 A 0 1 1 A 0 1 0 1 1 0 0 0 1 ? 0 0 0 0 0
Dolichosauridae  ? ? ? ? 0 ? 0 1 0 1 ? ? ? ? ? ? ? ? 0 ? ? ? 0 ? 0 0 1 0 1 ? ? ? 0 ? ? ? ? ? 0 ? ? ? ? ? ?
Aphanizocnemus   1 ? ? ? ? ? ? ? ? ? ? ? 0 0 ? ? ? ? ? ? ? ? ? 0 0 1 0 ? 0 ? 1 ? ? ? ? 1 ? 0 0 0 2 ? ? ? ? ? 0
Adriosaurus      1 ? ? ? 1 ? 0 1 0 A 0 ? ? 0 ? ? ? ? ? ? ? ? 0 0 1 0 1 ? A 0 ? 1 0 ? 0 ? 1 ? 0 0 0 1 0 ? 0 ? 0 ? ? ?
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TAXON                                    CHARACTERS

                 5 5 5 5 5 5 5 5 5 6 6 6 6 6 6 6 6 6 6 7 7 7 7 7 7 7 7 7 7 8 8 8 8 8 8 8 8 8 8 9 9 9 9 9 9 9 9 9 9 1
                 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0
                                                                                                                  0

Ancestor         0 0 0 0 0 0 0 G 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
Iguanidae        0 0 0 1 1 0 0 0 1 0 0 A 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 A 0 1 0 0 0 0 0 0 0 0 0 0
Leiolepidinae    0 0 0 1 1 0 0 0 1 0 0 1 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 1 0 0 0 0 0 0 0 0
Agaminae         0 0 0 1 1 0 0 0 1 0 0 1 0 0 0 A 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 1 0 0 0 0 0 0 0 0
Chamaeleonidae   0 0 0 1 1 0 0 0 1 0 2 1 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 2 0 1 0 0 - - - - 0
Xantusiidae      1 1 0 1 1 0 0 0 0 1 0 0 1 0 0 0 1 A 0 1 0 0 0 0 0 0 1 1 0 1 0 0 0 0 0 0 A 0 0 1 0 1 1 0 0 1 0 1 A
Eublepharinae    1 0 0 A 1 0 0 0 3 0 0 1 0 0 0 1 1 0 0 - 0 0 0 0 0 1 1 0 1 0 0 0 0 1 0 0 1 1 0 1 1 0 0 1 0 1 0
Gekkonines s.l.  1 0 0 0 - - - - 3 0 0 1 0 0 0 1 1 0 0 - 0 0 0 0 1 1 0 1 0 0 0 0 A 0 0 1 1 0 0 1 0 1 1 0 0 1 0 1 0
Diplodactylinae  1 0 0 0 - - - - 3 0 0 1 0 0 0 1 0 0 0 - 0 0 0 0 0 1 1 0 1 0 0 0 0 0 1 1 0 0 1 0 1 0 1 1 0 0 1 0 1 0
Pygopodidae      1 0 0 0 - - - - 3 0 0 1 0 0 0 1 1 0 0 - 0 0 0 0 1 1 0 1 0 0 0 0 0 1 0 0 0 1 0 1 1 0 0 1 0 1 0
Sineoamphisbaena 1 1 0 0 - - - - 1 1 ? 1 0 0 0 1 1 1 0 1 B ? 1 ? ? ? 0 0 0 ? 1 1 ? ? 0 1 ? 0 0 C 0 0 1 0 0 1 0 1 ?
Dibamidae        1 0 0 0 - - - - 3 0 2 A 0 0 0 1 1 1 0 - 0 0 0 1 1 0 0 1 1 0 0 1 1 1 0 0 1 0 2 1 0 1 1 0 1 0 1 2
Amphisbaenia     1 0 0 0 - - - - 3 A 2 1 0 0 0 1 1 1 1 1 1 2 2 1 2 1 1 1 1 0 0 A 1 2 0 0 2 A 0 1 1 0 1 0 1 1
Lacertidae       1 0 1 1 1 0 0 0 1 0 0 0 0 0 1 0 0 0 - 0 0 0 0 1 1 0 0 0 0 0 0 0 0 1 0 0 1 0 1 0 0 0 1 0 1 0
Teiidae          1 0 0 1 1 0 A 0 1 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 1 1 0 0 0 0 0 0 0 0 C 0 1 0 0 1 0 1 0
Gymnophthalmidae 1 A 0 1 1 0 0 0 1 0 0 0 0 0 0 1 A 0 1 0 1 0 A 0 0 0 0 0 0 0 1 0 1 0 0 0 1 0 1 A
Cordylidae       1 1 0 1 1 0 0 0 1 0 0 1 0 0 0 1 0 0 1 0 0 0 0 0 1 1 0 0 0 0 0 1 0 0 A 0 0 1 0 1 0 0 0 1 0 1 0
Scincidae        1 0 1 1 1 0 0 0 1 0 0 1 0 0 1 0 0 A 0 0 0 0 0 1 1 0 0 0 0 1 0 0 A 0 0 A 0 1 0 0 0 1 0 1 A
Anguidae         1 A 0 A 1 0 0 0 1 0 A 1 0 0 0 1 0 0 A 1 A 0 0 0 0 1 1 A 0 0 1 0 A 0 A 0 0 1 A 0 0 0 1 0 0 0 1 0 1 1
Xenosaurus       0 0 0 1 0 0 0 1 0 1 0 0 0 1 0 0 0 - 0 0 0 0 1 1 1 0 0 1 0 0 0 0 1 0 0 0 0 1 0 1 0 0 0 1 0 1 1
Shinisaurus      1 0 0 1 1 0 0 0 1 0 0 1 0 0 0 1 0 0 - 0 0 0 0 0 1 1 1 0 0 1 0 0 0 1 0 0 1 0 1 0 1 0 0 0 1 1
Heloderma        1 0 0 1 1 0 1 0 1 0 0 0 0 1 1 0 0 - 0 0 0 0 1 1 1 0 0 1 0 0 0 1 0 0 1 1 0 0 1 0 0 0 1 0 1 1
Lanthanotus      1 0 0 1 1 0 1 0 1 0 0 0 1 0 0 0 - 0 0 0 0 1 1 1 0 1 1 0 0 0 ? 0 1 1 0 1 1 0 0 1 0 0 0 1 0 1 0
Varanus          1 0 0 1 1 0 1 0 1 0 1 1 0 0 0 1 1 0 0 - 0 0 0 0 1 1 1 0 0 1 1 0 1 0 1 0 0 1 0 1 0 0 0 1 0 1 1
Serpentes        - 0 0 1 0 1 A 1 E D 2 1 0 A 0 1 2 0 1 1 1 1 1 2 1 1 1 1 0 1 1 0 0 0 0 1 1 0 1 0 2 1 1 0 1 1 1 1 1 2
Pachyrhachis     1 0 0 1 0 1 1 1 2 2 2 1 0 ? 0 ? ? 0 1 1 1 1 1 2 1 1 1 ? ? ? ? 0 0 ? 1 ? ? 2 1 ? ? 2 1 ? 1 1 ? ? ? 2
Pachyophis       ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
Aigialosauridae  1 0 0 1 1 ? 1 ? ? 2 0 ? 1 1 1 ? ? ? ? ? ? 0 2 ? ? ? ? ? ? ? ? ? 1 1 ? ? ? ? ? ? 0 ? ? ? ?
Mosasauridae     0 0 0 1 1 1 1 1 2 2 0 1 1 1 1 1 0 0 1 1 1 0 0 2 0 1 1 0 0 1 1 0 1 0 2 0 1 0 0 1 0 0 1 1 1 1 0
Dolichosauridae  ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 ? 2 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 ? ? ? ?
Aphanizocnemus   1 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
Adriosaurus      ? 0 0 1 0 ? 1 ? ? ? ? ? ? ? ? ? 1 1 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 2 ? ? ? ? ? ? ? ?
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APPENDIX 2

Continued.

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TAXON                                                        CHARACTERS

                 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1
                 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 3 4 4 4 4 4 4 4 4 4 4 5
                 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0

Ancestor         0 0 0 0 0 0 0 0 A 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 B 0 0 0 A A 0 B ? ? ? ? 0 0 0 ? 0 0 0 0 0 0 0 0 0 0
Iguanidae        0 0 0 0 0 0 0 0 0 0 0 0 0 0 A 1 0 0 0 A 0 0 1 2 D A 0 C 1 0 D A A 0 0 0 0 A 0 1 1 0 0 0 0 A A 1 0
Leiolepidinae    0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 A 1 1 0 0 0 0 2 0 0 0 - 1 0 2 - 1 0 0 0 0 0 1 0 0 0 0 0 0 1 1 0
Agaminae         0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 1 0 0 0 0 A 2 0 0 0 - 1 0 C 1 1 0 0 0 0 0 1 0 0 0 0 0 0 1 1 0
Chamaeleonidae   1 0 0 1 0 0 0 0 1 A A 1 0 0 1 1 1 0 0 1 0 0 0 2 0 0 0 - 1 0 2 - - - 0 0 0 - 0 0 0 0 0 0 0 A 1 0
Xantusiidae      1 0 1 0 0 0 0 0 0 0 1 0 A A 1 1 0 0 0 0 0 0 0 1 2 - 0 0 1 0 1 1 0 0 0 0 0 0 1 1 0 A - 1 - 0 1 1
Eublepharinae    0 0 1 0 0 0 0 0 0 0 1 0 A 0 1 1 0 0 0 0 0 0 0 2 2 - 0 0 1 0 1 0 1 0 0 0 0 1 0 1 1 0 0 0 0 1 0 1 0
Gekkonines s.l.  A 0 A 0 0 0 0 0 0 0 0 1 0 1 0 1 1 0 0 0 0 0 0 2 2 - 0 0 1 0 C 0 1 0 0 0 0 1 0 1 1 0 0 0 A 1 0 1 0
Diplodactylinae  0 0 1 0 0 0 0 0 0 0 1 0 1 0 1 1 0 1 0 1 0 0 0 0 2 2 - 0 0 1 0 1 0 1 0 0 0 0 1 0 1 1 0 0 0 1 - 0 1 0
Pygopodidae      0 0 1 0 0 0 0 0 1 0 0 1 0 A 0 1 1 0 1 0 0 0 0 A 2 2 - 0 0 A 0 1 0 1 0 0 0 0 1 0 1 1 0 0 0 1 - 0 1 0
Sineoamphisbaena 0 ? 1 0 0 0 1 0 0 0 0 1 0 1 2 1 0 ? - 1 ? 0 ? 0 2 ? ? ? - 0 0 ? ? ? ? 0 ? 1 ? ? ? 0 0 0 ? 0 ? ?
Dibamidae        0 1 1 0 0 1 1 0 0 0 0 1 - 1 1 0 1 - 0 0 A 0 0 0 0 2 - 0 0 0 0 2 - - - - 0 1 0 - A 0 0 0 - 1 - 0 1 0
Amphisbaenia     0 1 1 0 0 0 1 0 0 0 0 1 0 1 2 2 A A - A A 0 0 A 0 D 1 0 C 1 0 C 1 1 0 0 0 A 0 0 A 0 0 A 0 A 0 0 1 0 1 1
Lacertidae       0 0 1 0 0 0 0 0 0 0 0 1 0 0 0 A 1 0 0 0 0 0 1 2 0 A 0 0 1 0 0 0 A 0 0 0 0 1 0 1 1 0 0 0 0 1 0 1 1 0
Teiidae          0 0 1 0 0 0 0 0 0 0 0 1 0 1 0 0 1 A 0 0 0 0 0 1 2 A 0 0 0 1 0 0 0 1 0 0 0 1 0 1 1 0 0 0 0 1 0 1 2
Gymnophthalmidae 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 1 1 0 0 0 0 0 A 2 B 0 0 A A 0 A A 1 0 0 0 0 1 0 1 1 0 0 0 0 1 0 1 2
Cordylidae       0 0 1 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 A 0 0 0 0 1 1 0 0 0 1 0 0 0 1 0 0 0 0 1 0 1 1 0 1 0 0 1 0 1 0
Scincidae        A 0 1 0 0 1 0 0 0 0 0 1 0 0 0 1 1 A 0 0 0 0 1 1 D 0 0 0 1 0 A 0 A 0 0 0 0 1 0 1 A 0 1 0 0 1 0 1 0
Anguidae         0 0 1 0 0 0 0 0 0 0 0 1 0 A 0 1 1 0 0 0 0 0 0 1 C 0 0 1 1 1 0 A 0 0 0 0 0 0 1 0 1 1 0 A 0 0 1 0 1 0
Xenosaurus       0 0 1 0 0 0 0 0 0 0 0 1 1 0 0 1 1 0 0 0 0 0 0 1 1 0 0 1 1 1 0 0 0 0 0 0 0 0 1 0 1 1 0 0 0 1 0 1 0
Shinisaurus      0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 1 0 0 0 0 0 0 1 1 0 0 1 1 1 0 0 0 0 0 0 0 1 0 1 1 0 0 0 1 0 1 0
Heloderma        0 0 1 1 0 0 0 0 1 0 0 1 0 1 0 1 0 1 1 0 0 0 0 0 1 2 0 0 1 2 1 1 1 1 0 1 0 0 0 1 0 1 1 0 0 0 0 0 1 0
Lanthanotus      0 0 1 0 0 0 0 0 1 0 0 1 0 1 0 1 1 0 0 0 0 0 0 1 2 0 0 1 2 1 1 1 2 0 1 0 0 1 0 0 1 1 2 0 0 0 0 0 0
Varanus          0 0 1 1 0 0 0 0 1 0 0 0 0 1 0 1 1 1 0 0 0 0 0 1 2 0 0 1 2 1 1 0 1 0 1 0 0 0 0 1 1 2 0 0 0 0 0 0 0
Serpentes        0 0 1 A 1 0 0 1 A 0 1 1 A 0 1 1 - 0 0 1 1 A 2 0 1 1 A 2 0 1 1 A 1 0 1 0 0 0 3 A - A 0 0 A 0 0
Pachyrhachis     ? 0 ? ? 1 0 0 1 0 0 1 1 0 0 0 1 1 ? 1 0 ? 1 1 0 2 0 1 ? - 2 1 0 2 1 1 1 ? 0 0 1 0 0 3 0 - 0 0 0 1 0
Pachyophis       ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 ? 0 2 0 1 1 - ? 1 ? ? ? ? 1 1 ? ? ? ? 3 ? ? 0 ? ? ? ?
Aigialosauridae  ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 ? ? ? ? ? ? ? 1 0 0 2 0 1 ? - 0 1 0 2 1 ? 1 1 1 0 ? 0 0 2 0 1 0 0 0 1 0
Mosasauridae     0 0 1 1 0 0 0 1 0 0 1 0 0 0 0 1 0 1 0 0 0 1 0 0 2 0 1 1 - 0 1 0 2 1 1 1 1 1 0 1 0 0 0 ? ? ? 0 0 0 1 0
Dolichosauridae  ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 0 2 1 1 1 - 0 ? ? 2 1 ? 1 ? 0 1 0 0 0 ? ? ? 0 0 0 ? 0
Aphanizocnemus   ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 ? ? ? 1 ? ? ? ? ? ? ? ? ? 0 0 ? ? ?
Adriosaurus      ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 ? ? ? ? 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 ? ? ? ?
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TAXON                                                        CHARACTERS

                 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2
                 5 5 5 5 5 5 5 5 5 6 6 6 6 6 6 6 6 6 6 7 7 7 7 7 7 7 7 7 7 8 8 8 8 8 8 8 8 8 8 9 9 9 9 9 9 9 9 9 9 0
                 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0

Ancestor         0 0 A 0 0 0 0 0 A 0 0 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 ? - - - 0 0 0 A 0 0 0 0 0 0 0 0 0 0 - 0 A
Iguanidae        0 0 2 0 0 0 A 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 A 0 A 0 0 0 1 0 1 1 0 A 1 1 A 0 0 0 0 A 0 0 A 1 0 A
Leiolepidinae    0 0 2 0 0 0 1 0 0 0 1 0 0 0 0 2 - - 0 1 0 1 0 0 1 - 1 - 0 A 1 0 1 1 0 1 - 1 0 0 0 0 0 0 1 0 0 - 0 1
Agaminae         0 0 2 0 0 0 1 0 0 0 0 1 0 0 0 2 - - 0 1 0 A 0 0 1 - 1 - 0 0 1 0 1 1 0 1 - 1 A 0 0 0 0 C 0 0 - 0 1
Chamaeleonidae   0 0 2 A 0 0 A 0 0 A 1 0 0 0 0 2 - - 1 1 0 1 0 0 1 - 1 - 0 0 1 0 1 1 0 1 - 1 1 1 0 0 0 0 0 0 0 - 0 1
Xantusiidae      0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 1 - 1 - 0 0 1 0 1 1 0 1 - A E 0 0 0 0 A 0 A 1 0 0
Eublepharinae    0 0 2 0 1 0 1 0 1 1 0 0 0 0 0 0 1 0 0 0 0 1 - 1 - 1 0 1 1 0 1 0 1 - 0 2 0 0 0 0 0 0 0 0 0 - 0 0
Gekkonines s.l.  0 0 2 0 1 0 1 0 1 1 0 0 0 0 0 0 0 1 0 0 0 0 1 - 1 - 1 0 - 1 0 0 0 1 - 0 B 0 0 0 0 0 0 0 0 0 - 0 0
Diplodactylinae  0 0 2 0 1 0 1 0 1 1 0 0 0 0 0 0 0 1 0 0 0 1 - 1 - 0 1 0 - 1 0 A 0 1 - 0 B 0 0 0 0 0 0 0 0 0 - 0 0
Pygopodidae      0 0 2 0 1 1 1 0 1 A 0 0 0 0 0 0 1 0 0 0 0 1 - 1 - 1 0 1 1 0 1 0 1 - A 4 1 0 0 0 0 0 0 0 0 0 - 0 0
Sineoamphisbaena ? 0 C 0 0 ? ? ? ? ? 1 0 0 0 0 2 - - 0 1 1 0 1 1 1 - 1 - ? 0 1 0 1 1 0 1 - 1 ? 0 0 ? ? 0 0 0 ? ? ? ?
Dibamidae        0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 1 0 0 0 1 1 0 C 1 1 - 1 - 1 0 1 0 1 1 1 1 - 1 J 1 0 A 1 2 0 0 0 - 1 0
Amphisbaenia     0 0 D A 0 1 1 0 1 1 A 0 0 0 0 0 A 1 1 A 2 2 1 - 1 - 0 0 1 0 1 1 1 1 - 1 J 1 0 A 1 2 0 0 0 - 1 A
Lacertidae       0 1 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 A 0 0 1 - A 0 0 0 1 0 1 1 0 0 0 1 F 0 0 0 0 A A 0 A 1 0 0
Teiidae          0 1 2 0 0 0 0 0 0 0 0 0 0 0 A 0 0 0 1 0 A A 0 1 - A 0 0 A 1 0 1 1 0 0 0 1 1 F 0 0 0 0 0 1 0 1 1 0 0
Gymnophthalmidae 0 1 2 0 0 0 0 0 A 0 0 0 0 0 A 0 0 1 0 0 0 1 - 1 0 0 0 1 0 1 1 0 0 0 1 1 F 0 0 0 0 C 0 1 1 0 0
Cordylidae       0 0 2 0 0 1 A 1 1 1 0 0 0 0 0 0 0 1 0 0 0 0 1 - A 0 0 0 1 0 1 1 A 1 - 1 E A 0 0 0 0 0 0 0 - 0 0
Scincidae        0 A 2 0 0 1 1 1 1 1 0 0 0 A 0 0 0 1 0 0 0 0 1 - A 0 0 0 1 0 1 1 - 1 3 0 0 0 C 0 0 A 0 0 A
Anguidae         0 0 2 0 0 1 1 0 1 1 0 0 A 0 0 1 0 0 0 1 0 0 0 1 0 A 0 0 0 1 0 1 1 0 1 - 1 H A 0 A 0 2 0 0 A 0 0 A
Xenosaurus       0 0 2 0 0 1 0 0 1 0 0 0 0 0 0 0 1 0 0 0 1 0 0 0 1 - 1 0 0 0 1 0 1 1 0 1 - 1 3 0 0 0 0 2 0 0 0 - 0 1
Shinisaurus      0 0 2 2 0 0 1 0 0 1 0 0 0 0 0 0 1 0 0 0 1 0 0 0 1 - 0 0 0 0 1 0 1 1 0 1 - 1 0 0 0 0 0 2 0 0 0 - 0 0
Heloderma        0 0 2 0 0 1 1 0 0 1 0 1 1 1 0 1 2 0 0 1 0 1 1 1 A 0 0 0 0 1 0 1 1 0 1 - 1 3 0 0 0 0 C 0 0 0 - 0 1
Lanthanotus      0 0 2 0 0 1 1 0 0 1 0 1 1 1 0 1 2 0 0 1 0 1 1 1 1 0 0 0 0 0 ? 1 2 0 1 1 0 1 - 1 3 2 0 1 0 C 0 0 0 - 0 1
Varanus          0 0 2 0 0 1 1 0 0 1 0 1 1 1 0 1 2 0 0 1 0 1 1 1 1 - 1 - 0 2 2 0 1 1 0 1 - 1 3 2 0 1 0 2 0 0 0 - 0 1
Serpentes        1 0 0 D 0 1 1 0 0 1 2 1 A 1 0 1 2 1 1 0 - 1 D D A 1 A 1 0 A A A 1 1 1 0 1 1 5 - 0 A A 2 0 0 0 - 0 1
Pachyrhachis     1 0 0 1 - - - - - 2 1 1 1 0 ? 2 ? 1 ? ? ? 0 0 0 1 0 1 ? 0 0 ? 1 0 0 ? 1 5 3 1 0 1 2 0 1 0 - 0 1
Pachyophis       ? ? ? ? ? ? ? ? ? ? 2 ? ? 1 0 ? ? ? ? ? ? 0 ? ? ? ? ? ? 0 ? ? ? ? 1 0 0 ? ? 5 3 0 ? ? ? ? 1 ? ? ? ?
Aigialosauridae  1 0 1 0 0 1 1 0 1 ? 2 1 1 1 1 ? 2 ? 1 ? ? ? 0 0 ? ? ? ? 0 1 0 1 1 0 0 1 1 3 2 1 1 ? 0 0 0 0 - 0 1
Mosasauridae     1 0 1 0 0 1 1 0 1 1 2 1 1 1 1 1 1 - 1 0 0 1 - 0 1 ? 0 A 1 1 1 0 0 1 1 3 2 1 1 1 0 0 0 0 - 0 1
Dolichosauridae  ? ? ? ? ? ? ? ? ? 2 0 0 - 0 1 2 1 ? ? ? ? 0 0 ? ? ? ? 0 1 0 1 1 0 0 1 1 K 3 0 1 ? 2 0 0 0 ? 0 1
Aphanizocnemus   ? ? 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 A 0 ? ? 3 3 0 1 ? 0 0 0 0 - 0 1
Adriosaurus      ? 0 ? 0 0 1 1 0 1 ? ? ? ? 1 0 ? ? ? 1 ? ? 1 A ? ? ? ? ? ? 0 1 ? ? ? 0 0 ? 1 3 3 0 ? ? ? ? 1 0 - 0 1
```

APPENDIX 2

Continued.

TAXON — CHARACTERS (201–250)

Taxon	201–250
Ancestor	0 0 0 0 0 0 0 0 0 0 A 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 - - 0 0
Iguanidae	A A 0 0 0 1 0 0 0 0 0 A 0 0 A 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 - - A 0
Leiolepidinae	- 0 0 0 1 0 0 0 0 0 0 1 A 0 0 A 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 - - 0 0
Agaminae	- 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 - - A 0
Chamaeleonidae	- 0 0 0 1 0 0 0 0 0 1 0 0 1 - - 1 - - 0 A - 3 1 0 1 0 0 0 0 1 0 1 0 0 0 1 0 0 0 0 0 0 0 - - A 0
Xantusiidae	0 0 0 0 1 0 0 0 0 0 0 1 0 0 1 1 0 0 1 0 A 0 1 0 0 0 0 0 1 1 1 1 0 0 0 0 1 0 0 0 0 0 0 - - A 0
Eublepharinae4	1 0 0 0 0 1 0 0 0 0 0 0 1 1 0 0 1 1 0 0 1 0 A 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 1 0 0 0 0 0 - - 0 0
Gekkonines s.l.	1 0 0 0 0 1 0 0 0 0 0 1 1 A 0 1 1 0 0 1 0 0 - 1 0 0 0 0 0 0 A A 1 0 0 0 0 1 0 0 0 0 0 0 - - 0 0
Diplodactylinae	1 0 0 0 0 1 0 0 0 0 0 1 1 0 0 1 1 0 0 1 0 0 - C 0 0 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 0 0 0 0 - - 0 0
Pygopodidae	1 0 0 0 0 1 0 0 0 1 0 0 0 0 1 - 1 0 0 1 0 1 - - 1 - - - 1 - - - 2 - - - - - - - - 0 0 0 - - 0 0
Sineoamphisbaena	? ? ? 0 1 0 0 ? ? 0 ? 1 ? ? ? 0 ? ? ? ? ? 0 0 0 0 ? ? ? ? ? ? ? ? ? ? 0 0 0 0 - - 2 ?
Dibamidae	1 0 0 0 0 1 1 1 0 - 1 - - - 1 - - 1 - - 0 0 - 3 1 2 - 0 - 1 A 0 - - - 1 - - - - - 0 0 0 - - 0 1
Amphisbaenia	1 - 1 0 0 0 1 1 1 0 - D 0 0 0 A 1 ? 1 - - A 0 - 3 0 C 1 0 0 1 1 1 - - - 2 - - - - - 0 0 0 - - B A
Lacertidae	0 0 0 0 1 0 0 0 0 0 0 1 0 0 1 1 0 0 1 0 1 0 1 A 0 0 0 0 0 0 2 1 0 0 0 1 0 0 0 0 0 0 1 0 0 2 0
Teiidae	0 0 0 0 1 0 0 0 0 0 A 1 1 0 1 1 0 0 1 0 1 0 1 0 0 1 0 0 0 1 0 2 1 0 0 0 1 0 0 0 0 0 0 - - B 0
Gymnophthalmidae	0 0 0 0 1 0 0 0 0 0 0 1 1 0 1 1 0 1 0 1 0 1 0 1 0 0 0 1 0 0 0 1 0 0 0 1 0 0 0 0 0 0 - - B 0
Cordylidae	0 0 0 0 1 0 0 0 0 0 0 1 0 0 A A 0 0 1 0 0 - C A 0 0 0 1 0 2 1 0 0 0 0 1 0 0 0 1 1 2 0 0 2 0
Scincidae	0 0 0 0 1 0 0 0 0 0 0 A 1 0 0 1 1 A 0 1 A - 1 A 0 0 0 0 0 A 1 2 1 0 0 0 1 0 0 0 1 1 2 0 0 B 0
Anguidae	0 0 0 0 A 0 0 0 0 0 A A 1 0 0 1 1 A 0 1 0 - C 0 D 0 0 0 A 1 A 2 1 0 A 0 0 1 0 0 0 1 1 2 0 0 A 0
Xenosaurus	0 0 0 0 1 0 0 0 0 0 0 1 0 0 1 0 0 0 1 0 0 - 1 0 0 0 0 0 0 1 0 1 1 0 0 0 1 0 0 0 1 0 2 1 0 2 0
Shinisaurus	0 0 0 0 1 0 0 0 0 0 0 1 0 0 1 0 0 0 1 0 0 - 1 0 0 0 0 0 0 1 1 1 1 0 0 0 1 0 0 0 1 0 2 1 0 2 0
Heloderma	- 0 0 1 0 1 0 0 0 0 0 0 0 0 1 0 0 1 - 0 0 - 1 0 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 0 1 0 2 1 0 1 0
Lanthanotus	- 1 0 1 0 1 0 0 0 0 0 1 0 0 1 0 0 0 1 0 0 - 3 0 0 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 0 1 0 2 1 1 0 0
Varanus	- 1 0 1 0 1 0 0 0 0 1 0 A 0 0 A 0 0 A 0 A - 2 0 0 0 0 0 0 0 A 1 0 0 0 0 0 1 0 0 0 A 0 B 1 1 A 0
Serpentes	- - 1 1 0 0 0 1 1 0 - 2 - - - 1 - - 1 - - 1 - - 1 - - - 0 2 - - - C 2 1 - - - C - - - - - 0 0 0 0 - - 0 1
Pachyrhachis	- ? ? ? 1 ? 0 0 1 1 ? 2 - - - 1 - - 1 - - 1 - - 1 - - - 0 2 - 0 - 1 2 1 1 0 1 1 1 1 0 1 1 1 0 0 0 - - 0 1
Pachyophis	? ? ? 1 ? 0 0 ? 1 ? 2 - - - 1 - - 1 - - 1 - - - ? 2 - ? - ? ? ? ? ? ? ? ? ? 1 0 0 ? ? ? ? ?
Aigialosauridae	- 1 0 1 0 0 0 0 0 1 1 0 0 0 0 0 ? 0 0 0 ? 0 0 - 0 0 0 1 1 1 0 2 1 1 0 0 0 1 1 0 1 1 0 0 0 - - 0 ?
Mosasauridae	- 1 0 1 0 0 0 0 0 1 1 0 0 A 0 0 ? 0 0 1 - 0 0 - 0 0 0 1 1 1 0 2 1 A 0 0 0 1 1 0 1 1 0 0 0 0 - - 0 0
Dolichosauridae	? ? 0 1 0 ? 0 0 0 ? ? 1 - 0 0 ? ? 1 ? ? 0 ? ? ? ? 1 ? ? ? 1 ? ? ? ? ? 1 1 1 ? ? 0 0 0 0 ? ? 0 ?
Aphanizocnemus	- 1 0 1 A ? 0 0 0 1 1 1 - 1 0 0 1 0 ? ? ? ? ? ? ? 1 1 ? 1 1 2 1 1 0 1 1 1 ? ? 1 1 0 0 0 0 - - 0 ?
Adriosaurus	- 1 0 1 1 ? 0 0 0 1 1 1 - ? ? ? ? ? ? ? ? ? ? ? ? 1 1 1 1 2 1 1 0 1 1 1 ? ? 1 1 0 0 0 0 - - 0 ?

TAXON — CHARACTERS (251–258)

Taxon	251	252	253	254	255	256	257	258
Ancestor	0	?	0	0	A	A	0	0
Iguanidae	C	0	A	0	0	0	0	0
Leiolepidinae	2	0	A	0	0	0	0	0
Agaminae	2	0	1	0	0	0	0	0
Chamaeleonidae	2	0	1	1	0	0	0	0
Xantusiidae	1	0	0	0	0	0	1	0
Eublepharinae	0	1	0	0	0	0	1	1
Gekkonines s.l.	A	1	0	0	0	0	1	1
Diplodactylinae	0	1	0	0	0	0	1	1
Pygopodidae	0	1	0	0	0	0	?	1
Sineoamphisbaena	?	?	?	?	0	0	0	?
Dibamidae	-	-	1	1	0	0	?	0
Amphisbaenia	2	?	1	A	0	0	1	0
Lacertidae	C	0	0	0	0	0	1	0
Teiidae	1	0	0	A	0	0	1	0
Gymnophthalmidae	C	0	1	A	0	0	1	0
Cordylidae	2	0	0	A	0	0	1	0
Scincidae	C	0	A	A	0	0	1	0
Anguidae	C	0	A	1	0	0	1	0
Xenosaurus	1	0	1	1	0	0	1	0
Shinisaurus	1	0	1	1	0	0	1	0
Heloderma	2	0	0	1	0	0	1	0
Lanthanotus	2	0	1	1	0	0	1	0
Varanus	0	0	1	1	0	0	1	0
Serpentes	-	-	1	1	1	1	?	0
Pachyrhachis	-	-	?	?	1	1	?	0
Pachyophis	?	?	?	?	?	?	?	?
Aigialosauridae	?	?	?	?	1	0	?	?
Mosasauridae	1	0	?	?	1	1	?	0
Dolichosauridae	?	?	?	?	?	0	?	?
Aphanizocnemus	?	?	?	?	?	?	?	?
Adriosaurus	?	?	?	?	?	0	?	?