A second primitive marine snake: *Pachyophis woodwardi* from the Cretaceous of Bosnia-Herzegovina

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(Accepted 11 November 1998)

Abstract

The fossil of a second primitive snake from Cretaceous marine sediments is identified and redescribed: *Pachyophis woodwardi* Nopcsa. This snake was similar to *Pachyrhachis* in having pachyostotic vertebrae, a slender neck and a small head. However, *Pachyophis* differed from *Pachyrhachis* in being even more aquatically adapted: the mid-dorsal vertebrae and ribs are more swollen (pachyostotic), the body was more laterally compressed, and the dentary contains more teeth. The hindlimb (well developed in *Pachyrhachis*) cannot be confirmed as present or absent in *Pachyophis*. A cladistic analysis demonstrates that *Pachyophis* and *Pachyrhachis* form a clade. This grouping, here termed the Pachyophiidae, forms the most basal group of snakes so far known and is the sister group to all other well-known snakes.

Key words: fossil snakes, *Pachyophis woodwardi*, Cretaceous, cladistic analysis

INTRODUCTION

Until recently, the fossil record of primitive snakes has been assumed to be relatively poor, and to shed little light on snake origins (e.g. Rage, 1984, 1987; McDowell, 1987; Rieppel, 1988). However, the recent identification of *Pachyrhachis problematicus*, an elongated marine squamate from the middle Cretaceous of the Middle East, as a primitive snake (Caldwell & Lee, 1997) has prompted a study of other similar taxa.

Here, we re-evaluate *Pachyophis woodwardi*, a problematic form from the middle Cretaceous of Bosnia-Herzegovina. This taxon is known from an articulated postcranial skeleton, and some cranial fragments. It was originally described by Nopcsa (1923), who interpreted it as a primitive snake. However, the evidence proposed for this arrangement was not compelling, and later workers have been reluctant to accept this view. Rage (1984) concluded that *Pachyophis* was a lizard 'based on the morphology of the vertebrae', but did not elaborate further. The taxon was discussed again by Rieppel (1988) in a detailed review of snake origins, but no conclusions regarding its affinities were reached. In particular, it remained an open question whether this snake-like marine squamate was genuinely related to snakes, or convergently snake-like. To our knowledge, the specimen has not been closely re-examined since Nopcsa's description 75 years ago.

Our restudy of the fossil reveals some important morphological features not recognized, or misinterpreted in the original study, and provides the first compelling evidence that *Pachyophis* was a very primitive snake. Although the presence of many snake characters cannot be ascertained because of incomplete preservation, many characters uniting *Pachyophis* with *Pachyrhachis* can be recognized. *Pachyrhachis* is well known and has recently been demonstrated to be a snake (Caldwell & Lee, 1997; Lee, 1998; Zaher, 1998). Hence, it can be concluded that *Pachyophis*, being the nearest relative of *Pachyrhachis*, was also a snake. These two very similar marine taxa form the most basal clade of snakes thus far discovered.

METHODS AND MATERIALS

Illustrations of the holotype of *Pachyophis* were made using a binocular dissection microscope with camera lucida attachment, and from specimen photographs taken by the authors. Measurements were made using digital callipers.

The data set used in the cladistic analysis (Appendix) is based on a recent character-by-taxon matrix available for squamates (Lee, 1998), which combines information from several earlier studies (e.g. Estes, de Queiroz & Gauthier, 1988; Reynoso, 1998). *Pachyophis* has been added to the data set. Full descriptions of characters 1–230 can be found in that study. Characters 231–232 are

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new characters identified in this study which have been added to the data set and scored for all terminal taxa. The enlarged data matrix consists of 23 terminal taxa of extant and fossil squamates, and 232 osteological characters. The number of terminal taxa meant that the data could only be analysed using the heuristic search function of PAUP Version 3.1.1 for Macintosh (Swofford, 1993). As discussed by Lee (1998), multistate characters which did not form clear morphoclines were left unordered (49, 54, 59, 60, 61, 63, 77, 89, 130, 150, 151); the remainder were ordered. Cladograms were rooted and characters polarized using an ancestral outgroup taxon constructed based on the distribution of character states in *Sphenodon*, *Marmoretta* and kuehneosaurs. Characters were optimized using delayed transformation.

Locality and stratigraphy

The holotype was collected from a quarry in Selista (Selisca, Selisce), an eastern suburb of Bilek (Bileca), in East Herzegovina about 40 km inland (NE) from Dubrovnik (Nopcsa, 1923). A distinct but possibly related form, *Mesophis nopcsai*, came from the same locality (Bolkay, 1925), but as the only known specimen is apparently now lost (Rage, 1984) it is not considered further here. The 'Plattenkalk' (laminated limestone) in which both are preserved is characteristic of a sheltered, possibly near-shore environment with limited wave action (Katzer, 1918 cited in Nopcsa, 1923), analogous to the Ein Jabrud locality of *Pachyrhachis* (Scanlon *et al.*, 1998).

Along with the Comen (Komen, Comeno) and Lesina (Hvar) vertebrate localities in Slovenia and Croatia, Bilek was considered of 'Neocomian' (Lower Cretaceous) age by Katzer (1918). Langer (1961) considered the aigialosaur localities to be Cenomanian–Turonian, i.e. possibly somewhat younger than the Selisca–Bilek locality which is middle, or more probably late, Cenomanian (Sliskovic, 1970).

Revised taxonomy

SQUAMATA Oppel, 1811
PYTHONOMORPHA Cope, 1869
OPHIDIA Brongniart, 1800
PACHYOPHIIDAE Nopcsa, 1923
Pachyophis woodwardi Nopcsa, 1923

Original diagnosis

Nopcsa (1923: 139) diagnosed the taxon 'Pachyophidae' (more correctly Pachyophiidae; see Cannatella, 1990), containing the single species *Pachyophis woodwardi*, as follows. Skull small, upper jaw not snake-like but lizard-like; lower jaw as in Dolichosauridae and Uropeltidae; jaw region small; teeth needle-shaped, snake-like; about 160 to 180 vertebrae, of which 123 are known

including 46 cervical and 77 (?) trunk vertebrae. Cervical vertebrae elongate, somewhat laterally compressed, neural spines remain slender. Trunk vertebrae square, neural spines broad and short, anterior trunk pachyostotic and osteosclerotic. All ribs without tuberculum costae, anterior ribs curved only proximally and thin, trunk ribs uniformly curved. Shoulder and pelvic girdles at most rudimentarily present. Ventral scales developed as small, narrow transverse shields.

Revised diagnosis

An elongated, limb-reduced marine squamate with a small skull and slender neck. Forelimb and shoulder girdle are absent, presence of hindlimb and pelvis cannot be confirmed. Very similar to the closely related *Pachyrhachis problematicus*. However, it is smaller, and has a greater development of pachyostosis in the mid-dorsal ribs and vertebrae. In this region, the proximal and middle portions of the ribs are very thick, such that the intercostal space is almost obliterated. The distal ends of the ribs are round rather than flat in cross-section. Based on the rib morphology, the body appears to be more laterally compressed. The neural arches and bases of the neural spines are more swollen. There are also differences in the dentition: although smaller, *Pachyophis* has many more teeth on the dentary (approx. 23) than *Pachyrhachis* (12). The other tooth-bearing elements are not preserved in *Pachyophis* and comparisons cannot be made.

Type locality and horizon

Quarry near Bileca, Herzogovina, early Upper Cretaceous (Middle, or more probably Upper Cenomanian; Sliskovic, 1970).

Holotype

Naturhistorisches Museum Vienna A3919 (Figs 1 & 2), articulated postcranium and disarticulated skull fragments preserved on a single limestone block. 101 vertebrae and ribs, and some elements of the lower jaw are visible. Unidentified crushed fragments in front of the cervical vertebrae might be either anteriormost cervicals or skull bones.

Referred material

Nopcsa (1923) described and figured two additional portions of articulated vertebral column and ribs, both from a single slab 'adjacent' to the more complete type. They were preserved in cross-section, and Nopcsa excavated the remaining bone of one to leave a mould from which a temporary cast was prepared using a mixture of gelatine, glycerine, 'joiner's lime', and zinc
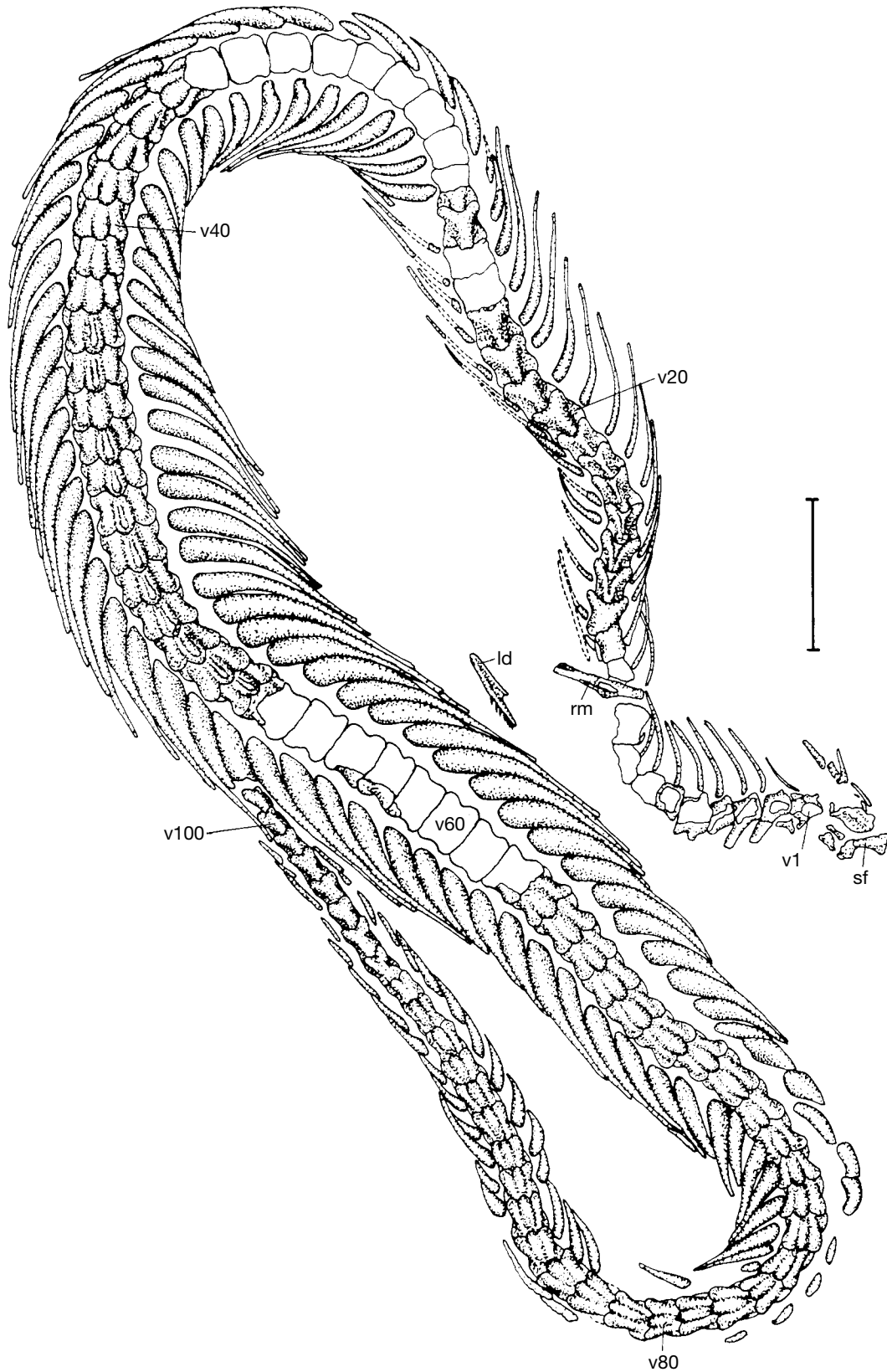
Fig. 1. Holotype of the Cretaceous fossil snake, *Pachyophis woodwardi* (NMW A3919). Scale bar = 2 cm. Abbreviations: ld, left dentary; ns, neural spine; rm, right mandible; sf, possible skull fragments; v = vertebra number. Numbers refer to the number within the preserved series (the atlas and possibly the first few cervical vertebrae are not preserved, see text).
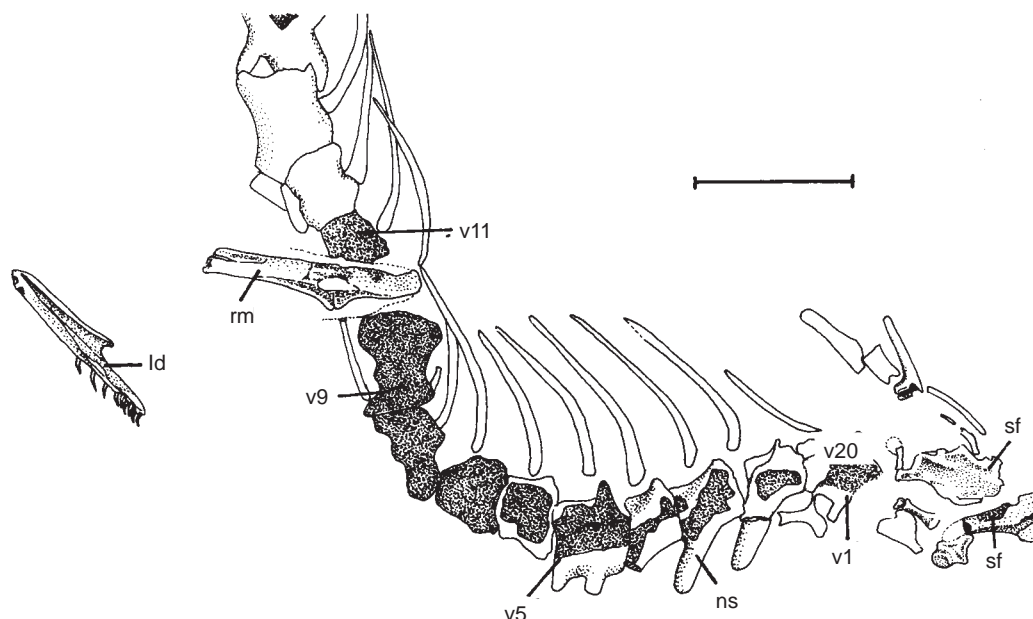
Fig. 2. Details of the anterior region of the holotype of *Pachyophis woodwardi*. Scale bar = 5 mm. Abbreviations as in Fig. 1

oxide paste to get the flexibility of latex and opacity of plaster (p. 118). These casts needed to be kept moist for study, so were presumably temporary. The present location and condition of these specimens is unknown.

DESCRIPTION

Skull

General

The only cranial elements preserved are the parts of the lower jaw, present near the cervical region. These include the left dentary (described by Nopcsa as a right maxilla), and a fragment tentatively identified as the compound bone, angular, and splenial of the right mandible.

Dentary

An isolated but complete dentigerous element is preserved, fully exposed in medial view (Fig. 3a). Most details of the element are visible, although the anterior tip is slightly weathered. It is here identified as the left dentary, in contrast to Nopcsa's (1923) identification as the right maxilla (see later).

The dentary is a long, tooth-bearing element, deepest at its mid-point, and tapering gradually in depth anteriorly. The posterior portion is more or less rod-like. The exposed internal surface is deeply concave, and formed the lateral wall of the Meckelian canal. The external surface is not exposed. The Meckelian canal tapers anteriorly, not reaching the anterior tip but terminating below the most anterior alveolus. The alveolar ridge is straight and flat. It occupies the entire
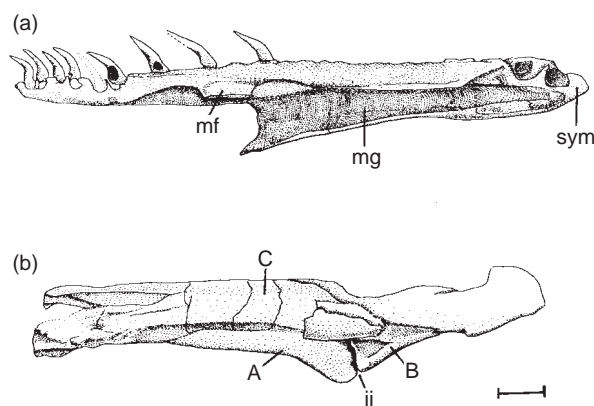

Fig. 3. (a) Left dentary, as preserved in medial view. (b) Jaw fragment tentatively identified as part of the right mandible, preserved in lateral view. Scale bar = 2 mm. Abbreviations: mg, Meckelian groove; mf, medial flange of dentary; sym, symphysis; ij, intramandibular joint; A, putative right angular; B, putative right splenial; C, putative right compound bone.

dorsal margin of the element and projects posteriorly well past the main body of the dentary, resulting in a very long tooth row. A distinct flange is present just posterior to the middle point of the alveolar ridge, projecting ventromedially into the Meckelian canal.

Eight teeth are preserved in the middle and posterior region, ankylosed to the rims of alveoli. The anteriormost four preserved teeth are in alternate alveoli, the intervening teeth having been lost. The posteriormost four teeth form a continuous series. Teeth originally present in the anterior part of the dentary were lost during preservation and/or preparation; they were not mentioned in the original description. There is a gradual decrease in tooth size towards the rear of the element. The anteriormost alveoli are fully exposed due to

weathering, and can be seen to be shallow. The alveoli are difficult to count between the anteriormost two alveoli and the first preserved tooth. There were probably approximately 22. Depending on variation in size and spacing, it is possible that there were slightly more or fewer alveoli, but the number could not have been below 20 or above 24. Nopcsa (1923) estimated a total number of 15 because of the incorrect assumption that the most anterior preserved teeth were in adjacent rather than alternate alveoli.

All teeth are long, slender, and recurved. Nopcsa considered the form of the teeth as 'snake-like', and their attachment to shallow alveoli as 'thecodont'. Certainly, the curvature of the teeth exhibits a condition found only in snakes (among squamates). Each tooth consists of two straight sections: the basal section projects dorsoposteriorly at approximately 70 degrees to the horizontal, while the distal section projects more posteriorly, at approximately 45 degrees. In lizards with recurved teeth, the crowns are smoothly sickle-shaped. The tips are very sharply pointed. The attachment is not the normal thecodont arrangement, where the teeth are deeply implated into sockets. Rather, as shown in the posterior preserved teeth where the jaw margins are weathered away, the teeth are ankylosed to the rims of the sockets. Unfortunately, the teeth are very small and thus were not adequately prepared by workers early this century: presence of carinae or basal fluting cannot be determined. The third and fourth preserved teeth (counting from the front) possess holes near the base. Nopcsa compared these to the small basal foramina teeth of lizards such as *Varanus*, suggesting that they had been enlarged during preparation. Whether these represent basal foramina, resorption pits, or are entirely artefacts of breakage and/or overzealous preparation, can no longer be determined.

Overall, there are strong resemblances to the dentary of the related *Pachyrhachis* (see later), so that each of these specimens provides clues to the interpretation of the other. In this specimen, as in *Pachyrhachis*, the posterior dentigerous process is much longer than the posteroventral process. The medial process under the second preserved tooth in *Pachyophis* is bounded anteriorly by a concavity; this presumably accommodated the rounded dorsoposterior lobe of the splenial, as in *Pachyrhachis* (Caldwell & Lee, 1997: fig. 2j). There is nothing like the medial process in lizards, but in many snakes (e.g. pythons and madtsoiids; Scanlon, 1997) there is a less prominent process, of variable form but with similar relationships to splenial, coronoid and compound bone (fused articular, prearticular and surangular). A horizontal groove extends across the dorsal region of the medial process, parallel to the tooth row; presumably this accommodated the narrow anterior process of the coronoid, as in *Pachyrhachis*.

Nopcsa's interpretation of this element as a right maxilla was based on a general resemblance of its anterior portion and triangular flange to the maxilla of lizards (particularly varanids). The distinct medial laminar projection, level with the first two preserved teeth, was compared to the palatine process of the maxilla found in booid snakes (that of varanids is only weakly developed). Nopcsa also reported that the anterior part of the element showed traces of a vertical suture at the expected contact with the premaxilla.

As discussed above, our interpretation of the specimen as a dentary explains the shape of the element and the medial process, and also explains some additional morphological features which are inconsistent with Nopcsa's (1923) identification of the element as a maxilla. The smoothly tapering concavity extending over the entire medial surface is here considered the Meckelian groove. While lizard (and some snake) maxillae show a medial concavity, it is less regular in shape and does not extend close to the anterior tip. While the anterior part of the specimen is slightly weathered, there is definitely no 'vertical' suture as drawn by Nopcsa. Finally, there is no embayment at the anterior end, along the margin opposite the alveolar ridge. If the element were a maxilla, this margin would be distinctly embayed to form the border of the external naris.

Posterior lower jaw

A portion of lower jaw overlies the cervical vertebrae (Figs 2 & 3b). Its identity is revealed by the highly visible, vertical intramandibular joint. However, a more precise interpretation is difficult.

It is here tentatively interpreted as fragments of the right lower jaw preserved in lateral view, with element A the right angular, B the right splenial, and C the right compound bone (Fig. 3b). If correct (but see below for other possibilities), the angular (A) is a massive bone, widest anteriorly, which meets the splenial anteroventrally in a vertical joint. The splenial (B) is well preserved only in the region of the joint, and formed a straight vertical surface matching the angular. The intramandibular joint thus formed a bulge on the ventral margin of the lower jaw and was exposed laterally. The proportions of the elements – long angular and short splenial – suggest that the intramandibular joint was situated far anteriorly, as in *Pachyrhachis* (Lee & Caldwell, 1998). The compound bone possessed a flange (C) that projected anteriorly across the intramandibular joint and into the notch in the dentary (Fig. 3a).

An alternative interpretation is that the fragment represents the left lower jaw in lateral view, and thus reverses the anterior and posterior ends. This view was favoured by Nopcsa (1923). Under this interpretation, A is the splenial and B is the angular, with an associated compound postdentary element expanding at the end to form a prominent, 'lizard-like' retroarticular process (Nopcsa, 1923). However, this interpretation cannot readily account for element C, which must still be interpreted as the anterior process of the compound element (unless one assumes it is a displaced bone from elsewhere). This is difficult to reconcile with the observation that C tapers towards the (presumed) posterior end,

instead of anteriorly, and appears to be distinct from the rest of the putative compound element. The expanded end interpreted as a retroarticular process is too badly crushed for any firm identification; the expansion is likely to be an artefact of crushing. Furthermore, its interpretation as the retroarticular process (and thus, the posterior end of the lower jaw) would mean that the intramandibular joint is situated very far posteriorly, in the posterior third of the lower jaw. This is inconsistent with the observation that in the related *Pachyrhachis*, the joint is situated very anteriorly (Lee & Caldwell, 1998).

A third intepretation is possible: that these elements are parts of the *left* lower jaw exposed in *medial* view. This interpretation implies that element A is the left splenial, B the left angular. However, this interpretation cannot readily account for element C, since no element overlies the angular and crosses the intramandibular joint in medial view in either mosasaurs, *Pachyrhachis*, or snakes. In contrast, element C resembles the tapering anterolateral flange of the compound bone in snakes, which overlies the angular and splenial and crosses the intramandibular joint in lateral view.

Postcranial skeleton

General

The bulk of the preserved material consists of a long, S-shaped string of 101 vertebrae and associated ribs (Figs 1 & 2). This series contains the post-atlas 'cervicals' and most of the dorsal region. The most posterior dorsal region, however, including the pelvis and hindlimb (if any), runs under the large mid-dorsal vertebrae and thus cannot be prepared out. In addition, there are some unidentifiable crushed elements at the most anterior end of the animal, which might be either cervical vertebrae or skull bones. The vertebrae change gradually in size, being small and light anteriorly, largest and heaviest in the middle, and small and light again posteriorly (Table 1).

Nopcsa's description of the trunk was based on two additional specimens, representing the anterior region of two other individuals and better preserved (albeit as natural moulds) than the corresponding region of the holotype.

Vertebrae

The most anterior five preserved vertebrae are exposed in left lateral view. The column then twists so that the remaining vertebrae are preserved in dorsal view. Determining the extent of the 'cervical' series in the absence of a preserved head and shoulder girdle is subjective. The ventral surfaces of the vertebrae are not fully exposed and presence or absence of hypapophyses cannot be determined; these structures (typical of cervical vertebrae in many squamates) cannot thus cannot

Table 1. Length-to-width measures of various well-preserved vertebrae from the postcranium of the holotype of *Pachyophis woodwardi*

14th vertebra–length 0.57 mm (prezyg. to postzyg.), width 0.50 mm (across postzyg).
20th vertebra–0.60 mm, 0.57 mm
38th vertebra–0.69 mm, 0.80 mm
52nd vertebra–0.72 mm, 0.86 mm
67th vertebra–0.70 mm, 0.80 mm
77th vertebra–0.65 mm, 0.69 mm
89th vertebra–0.57 mm, 0.48 mm
96th vertebra–0.50 mm, 0.40 mm

be used as a guide. However, the most anterior vertebrae possess several characteristics that can be interpreted as 'cervical-like'. They are smaller and lighter compared to more posterior vertebrae. Also, the ribs articulating with these vertebrae are slender and short compared to those of more posterior vertebrae. The degree of pachyostosis also increases gradually, from none at all in the most anterior vertebrae to maximum development at about the 50th preserved vertebra. Because these changes are gradual, and quantitative rather than qualitative, a precise cervical–dorsal boundary cannot be drawn. A reasonable interpretation is that the 'cervical' region contains approximately the first 19 preserved vertebrae. There was at least one more vertebra in front of this series (the atlas). There were therefore a minimum of 20 'cervical-like' vertebrae. There might have been more cervicals which were not preserved; however, the observation that the very similar *Pachyrhachis* has only 20 cervical-like vertebrae makes it likely that no cervicals apart from the atlas are missing. This suggests that the most anterior preserved vertebra is the axis, and the large fragments in front of it are skull elements. Certainly, the plate-like shape of at least one of these fragments is consistent with this interpretation (Fig. 2). However, this conclusion must remain tentative pending further discoveries.

The first preserved vertebra is too badly damaged to reveal any details (in particular, whether or not it is the axis). However, the second and third are relatively well preserved, although they each contain a large weathered cavity in the centre of the lateral surface. They are small and light, with a narrow neural arch and a long, anteroposteriorly narrow neural spine. This spine projects posterodorsally at 45 degrees, and tapers very slightly distally, ending in a blunt tip. The neural spine of the second vertebra contains a large break near the base, but the spine of the third is completely intact. Morphology of other structures (zygapophyseal and accessory vertebral articulations) cannot be determined.

The next 10 vertebrae (preserved vertebrae 4–13) are too badly weathered to show any useful detail, beyond the fact that they are small and light. The remaining vertebrae (14–101) are mostly well preserved. However, as they are exposed in dorsal view, only the neural arches, neural spines and related structures are clearly visible on most vertebrae. In some vertebrae, the neural

arches themselves are broken off through the horizontal plane, and no surface details are visible: this affects preserved vertebrae 24, 25, 27 (posterior half), 28–35, and 55–62.

A general description of a typical dorsally exposed vertebra follows; the variation along the column will then be discussed. The neural arch is an arched platform from which project the neural spine, pre- and postzygapophyses, zygosphenes and zygantra. In dorsal view each vertebra is 'butterfly-shaped' due to the lateral expansion of the pre- and postzygapophyses. Each arch is therefore widest anteriorly and posteriorly, but narrower in the middle. The articular surfaces are not exposed since the vertebrae are all articulated.

Accessory articulations (zygosphenes and zygantra) are visible throughout the column but can best be seen where the vertebrae have become slightly disarticulated: vertebrae 14–23, 27, 37, 75–78, and 97. The buttress bearing the zygosphene is positioned on the middle of the anterior face of the neural arch. It projects anteriorly to abut the posterior surface of the adjacent neural arch. The latter surface is not exposed on any vertebra, but presumably contained the zygantral articulations. The anterior end of the zygosphenal buttress is visible in the 22nd preserved vertebra: this end is flat, there being no notch separating the left and right zygosphenes. The orientation of the articulatory surfaces cannot be ascertained because not enough of any vertebra is exposed. Presumably, as in *Pachyrhachis* and other snakes, and in mosasauroids, the zygosphenal articular surface faced ventrolaterally and the zygantral articular surface faced dorsomedially.

There is a gradual change in size and shape of the neural arches as one proceeds anteroposteriorly along the vertebral column. In the anterior dorsal region, the neural arches are similar in shape to the cervical neural arches. They are relatively narrow, about twice as long as wide. They gradually change shape, becoming widest in the mid-dorsal region (around the 50th preserved vertebra), where they are slightly wider than long. Further posteriorly, they again become narrower. In the last exposed dorsal (the 101st preserved vertebra), the transverse dimension is again only half the anteroposterior dimension. These changes in neural arch dimensions no doubt reflect similar changes in the size and shape of the dorsal centra. Unfortunately, the orientation of the specimen means that these centra cannot be prepared and exposed easily.

The articulatory surfaces of the pre- and postzygapophyses also change their orientation along the column. In the anterior dorsals, as in the cervicals, they are inclined at about 20 to 30 degrees to the horizontal: the prezygapophyses face dorsomedially and the postzygapophyses face ventrolaterally. In the middle dorsals the surfaces are horizontal, while in the posterior dorsals the surfaces are again inclined.

The degree of pachyostosis also varies gradually along the vertebral column. The cervical vertebrae (1–19) do not show any morphological indications of pachyostosis. By vertebra 20, the first 'dorsal', pachyostosis begins to become apparent, visible signs being a slight swelling of the neural arch. The sloping dorsal surface of the neural arch immediately adjacent to the neural spine changes from being flat to being slightly convex transversely. The degree of pachyostosis gradually increases, reaching a maximum around vertebrae 35 to 65, which are also the largest and proportionally widest vertebrae. In this region, the swellings on the neural arch are so pronounced that they appear as longitudinal ridges on each side of the neural spine, separated from the spine by distinct grooves. In addition, the base of the neural spine is also swollen, being very broad transversely (approximately one-third the maximum width of the neural arch). Further posteriorly, the amount of pachyostosis again decreases, and in the last few preserved dorsals there are no obvious swellings on the neural arch and spine.

Neural spines are broken off from many of the dorsal vertebrae. However, spines are present and complete on preserved vertebrae 31, 32, 34–36, 52, 83 and 89. Anteriorly, the spines are tall and thin in the transverse dimension. In the mid-dorsal region, they are shorter and widen near the posterior edge. Posteriorly, the neural spines become very short, barely projecting above the body of the neural arch. Height and width transitions of neural spines, along the length of the vertebral column, are very similar to those present in *Pachyrhachis* (Lee & Caldwell, 1998).

Ribs

Ribs are preserved in association with almost all the vertebrae. As a result, however, the articular surfaces are not exposed. In the anterior cervical region (which is preserved in left lateral view) only the left ribs are exposed. In the posterior cervical, and dorsal region (which is preserved in dorsal view), the ribs on both sides are exposed. As with the vertebrae, the ribs also exhibit gradual changes in morphology along the vertebral column.

The cervical ribs are all short and appear to be slightly oval in cross-section. They are thickest proximally and taper gradually towards the distal tip. The shaft consists of two relatively straight portions which meet at a distinct 'kink' approximately one-third of the way along the rib. The proximal straight portion comprises approximately one-third of the total length of the rib, the distal straight portion comprises the other two-thirds. When naturally articulated, therefore, the rib shaft projected posteroventrolaterally for some distance, and then bent to extend posteroventrally. Thus, in cross-sectional view, the ribs project ventrolaterally for a short distance before bending to project directly ventrally.

The dorsal ribs vary greatly in morphology along the vertebral column. The most anterior dorsal ribs are very similar to the posterior cervical ribs, being relatively short, very slender, and tapering distally. Again, the shaft consists of two relatively straight portions which

meet at a distinct 'kink' approximately one-third of the way along the rib. However, this 'kink' is less pronounced. Thus, the proximal portion projected more ventrally and less laterally compared with the cervical ribs. The dorsal region was therefore more laterally compressed than the cervical region. As one proceeds posteriorly along the dorsal region, the ribs gradually become even straighter, and thus change to project more directly ventrally. *Pachyophis* therefore was sub-cylindrical anteriorly and gradually became more and more laterally compressed posteriorly.

The mid-dorsal ribs are heavily pachyostotic. A thickening in the proximal half of the shaft begins to be noticeable at about the 20th preserved vertebra (the first 'dorsal'). As one proceeds posteriorly this thickening becomes more and more pronounced, reaching a maximum at approximately the 50th preserved vertebra. This coincides with the region of maximum pachyostosis in the vertebrae. In this region, the proximal ends of the ribs are so swollen that the intercostal spaces are almost absent. The swelling gradually diminishes as one proceeds proximo-distally along the rib shaft. By the middle of the shaft the rib is no longer swollen, and the distal half of the shaft is uniform and narrow in diameter. Towards the posterior end of the animal, the degree of pachyostosis gradually diminishes. By the 100th preserved vertebrae, the rib shafts are again narrow throughout most of their length, though they still appear to taper distally.

The last exposed vertebra is the 101st in the sequence. Since the atlas is not preserved, this must be at least the 102nd vertebra. The more caudal parts of the animal extend beneath the mid-dorsal region and are not amenable to preparation. The related, similar squamate *Pachyrhachis* has 140 presacrals. Assuming that *Pachyophis* had a similar vertebral count, this means that the last exposed vertebra is a posterior dorsal and that a few posteriormost dorsals, and the caudals, are not exposed. This is consistent with the morphology of the last exposed vertebrae, which resemble the posterior dorsals of *Pachyrhachis* in shape and size (relative to the mid-dorsals). This means that the small pelvis and hindlimb, if present (see below), would be located in the part of the animal obscured by the bulky dorsal region.

## PHYLOGENETIC RELATIONSHIPS AND EVOLUTIONARY IMPLICATIONS

Although *Pachyophis* is very similar to *Pachyrhachis* (Lee & Caldwell, 1998), it differs in the following characteristics. The mid-dorsal vertebrae and ribs are much more pachyostotic. The swollen areas of the neural arches beside the neural spine, and the base of the neural spine, are much more convex. The proximal portions of the ribs are much thicker in diameter: in *Pachyrhachis*, the intercostal spaces remain wide, but in *Pachyophis* these spaces are almost obliterated by the expanded ribs. The distal ends of the ribs are narrow and cylindrical, rather than broad and flattened.

Additionally, the mid-dorsal and posterior dorsal ribs in *Pachyophis* appear to be less curved than in *Pachyrhachis*. This suggests that they projected more ventrally (rather than laterally and curving downwards), resulting in this region in *Pachyophis* being more laterally compressed. The more pronounced pachyostosis and lateral compression in *Pachyophis* suggests greater aquatic specialization than in *Pachyrhachis*. There are also differences in the dentition: although smaller, *Pachyophis* has many more teeth on the dentary (*c.* 22) than *Pachyrhachis* (12). Aquatic taxa (e.g. mosasauroids, sauropterygians, ichthyosaurs, pleurosaurs, thalattosaurs, cetaceans), often evolve more numerous teeth, and the higher tooth counts in *Pachyophis* thus also suggests greater aquatic adaptation.

Pachyophis is also much smaller than *Pachyrhachis*, being about half the length, raising the possibility that the above differences are ontogenetic. However, this is unlikely since these differences are in the 'wrong direction'. Pachyostosis functions to increase an aquatic animal's density so that it approaches that of water, and the degree of pachyostosis usually increases with size and age (de Buffrénil & Mazin, 1989; Domning & de Buffrénil, 1990). It appears that lung volume (and thus buoyancy) increases allometrically with weight, such that older, larger animals have proportionately more positive buoyancy (Odell, Forrester & Asper, 1981; Bergey & Baier, 1987). The corresponding increase in the degree of pachyostosis with age appears to compensate for this (Domning & de Buffrénil, 1991). If the differences in pachyostosis were ontogenetic, the small *Pachyophis* would be expected to be less, rather than more, pachyostotic than *Pachyrhachis*. Thus, this small size of *Pachyophis* makes the above differences more, rather than less, significant. Similarly, in squamates where numbers of teeth change ontogenetically, larger and older animals have more teeth (Ray, 1965). Again, if the differences were ontogenetic, the small *Pachyophis* would be expected to have fewer, rather than more, dentary teeth. The two forms differ in one respect which might be allometric, however. The mid-dorsal vertebrae are larger than the cervical and posterior dorsal vertebrae in both forms. The size difference is greater in the larger form (*Pachyrhachis*); this difference might be allometric as a similar pattern is found within many modern snake species (J. D. Scanlon, pers. obs.).

Despite these differences, *Pachyophis* and *Pachyrhachis* are clearly very similar and closely related. The overall proportions of the body and the form of the individual vertebrae and ribs are closely comparable. They can be united on the basis of several derived characters (synapomorphies) absent in other Mesozoic squamates. The mid-dorsal vertebrae and ribs are pachyostotic. No other squamates are pachyostotic, except for poorly known, and possibly related forms such as *Simoliophis*, known only from vertebrae and *Mesophis*, which now cannot be located (Rage, 1984). The pattern of pachyostosis is also unique: only the proximal ends of the ribs are swollen. In other (non-squamate)
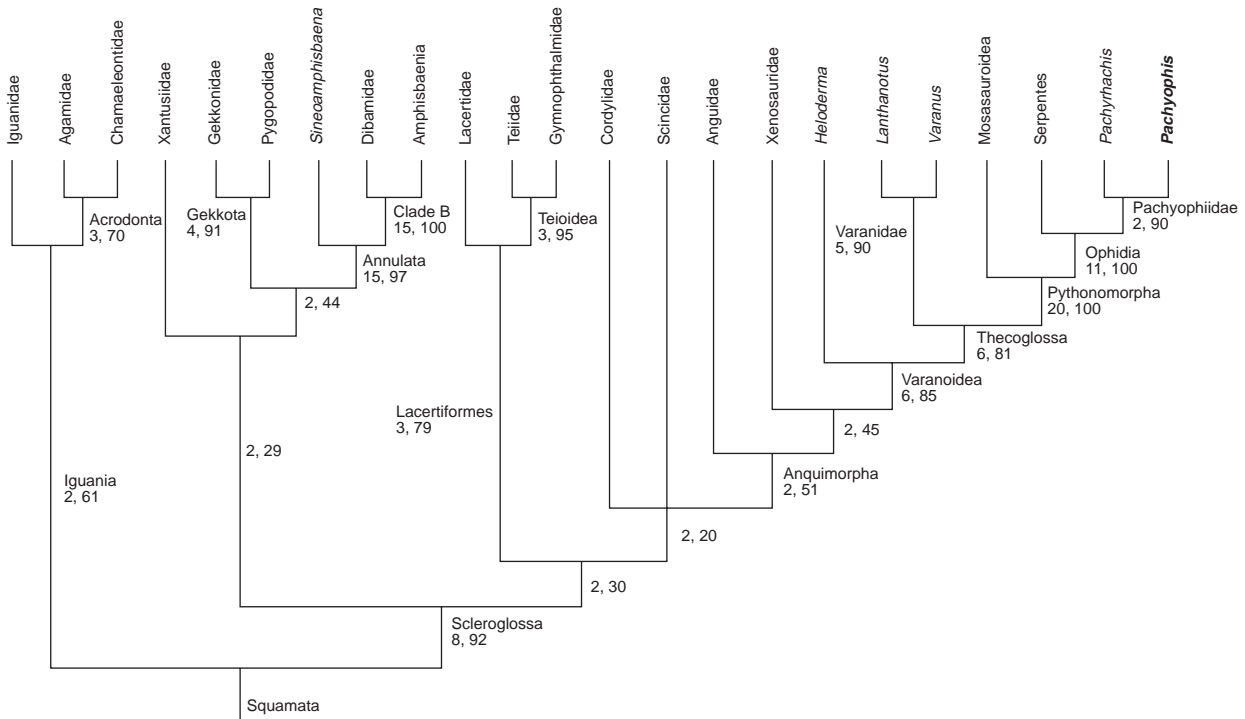
Fig. 4. Strict consensus tree of two cladograms (582 steps) showing relationships of 23 extant and fossil squamate taxa using morphological data (232 osteological characters). The first number next to each clade refers to Bremer support, the second to bootstrapping frequency.

pachyostotic taxa (e.g. mesosaurs, *Claudiosaurus*, and sirenians) the entire ribs are swollen. Finally, the mid- and posterior dorsal region is laterally compressed, as indicated by the shape of the rib shafts (long and vertically straight distally). Again, this body form (and associated rib morphology) is almost unique among squamates; it does not occur in any lizard or well-known primitive snake group. It is, however, found in the poorly-known forms *Archaeophis* (Janensch, 1906) and *Anomalophis* (Auffenberg, 1959), which might prove to be related to each other and to *Pachyophis* and *Pachyrhachis*. It also occurs in some derived macrostomatan snakes: acrochordids and marine elapids (modern 'sea snakes').

The results of the cladistic analysis support this inter- pretation. The analysis resulted in two most parsimonious cladograms (each 582 steps) with a con- sistency index of 0.49, and retention index of 0.65 (Fig. 4). *Pachyophis* and *Pachyrhachis* are sister groups, united by characters 231 and 232 (lateral compression and pachyostosis). Together, they form the sister group of all other (i.e. modern) snakes. The suggestion that *Pachyrhachis*, and by implication *Pachyophis*, fall within modern snakes, as relatives of macrostomatans (Zaher, 1998), was not tested here, since modern snakes were treated as a single terminal taxon. However, the many characters which unite modern snakes to the exclusion of *Pachyrhachis* and *Pachyophis* suggest that this approach can be justified (Lee, 1998). All other clades found in the present analysis are identical to those found in Lee (1998) and are discussed in detail in that

paper. Thus, diagnoses of more inclusive clades that contain *Pachyophis* (i.e. Ophidia, Pythonomorpha, Var- anoidea, etc.) can be found there. It should be noted that this topology is also in broad agreement with the recent analysis by Reynoso (1998).

Pachyophis, therefore, is related to the very similar *Pachyrhachis*, together forming the most basal clade of snakes. The taxon name Pachyophiidae is here applied to *Pachyophis, Pachyrhachis*, and all taxa more closely related to these genera than to modern snakes (scoleco- phidians, *Dinilysia*, alethinophidians). This is a stem- based phylogenetic definition (see de Queiroz & Gauthier, 1992). At present, Pachyophiidae contains *Pachyrhachis* and *Pachyophis*: further study of other superficially similar Cretaceous marine squamates such as *Mesophis* (Bolkay, 1925), *Simoliophis* (Sauvage, 1880, 1897; Nopcsa, 1925) and *Pachyvaranus* (Arambourg & Signeaux, 1952) might also reveal that they are pachyo- phiids (de Buffrénil & Rage, 1993).

Although it is less well known than *Pachyrhachis, Pachyophis* sheds light on the evolution of one impor- tant snake feature not determinable in *Pachyrhachis*. The anterior margin of the zygosphenal buttress is straight in *Pachyophis*, a feature diagnostic of snakes. In lizards, zygosphenes are usually absent. Even when present, as in mosasaurs and some other taxa (Russell, 1967; Estes *et al.*, 1988), each zygosphenal buttress is deeply notched between the two zygosphenal articula- tions. Previously, whether this trait characterized Serpentes (scolecophidians, *Dinilysia*, alethinophidians), or Ophidia (pachyophiids, scolecophidians, *Dinilysia*,

alethinophidians) could not be determined, because the condition in pachyophiids (represented by *Pachyrhachis*) was unknown. Observation of this feature in the clade *Pachyophis* confirms that this feature is present in pachyophiids and must diagnose the more inclusive clade (Ophidia).

Pachyophis exhibited an even stronger development of the aquatic adaptations found in *Pachyrhachis* (pachyostosis, laterally compressed body), and was found in marine sediments. Both members of Pachyophiidae, the most basal clade of snakes, were therefore marine. However, at the moment, whether or not all snakes went through a marine phase in their evolution remains equivocal. Under one scenario consistent with the cladogram in Fig. 4, marine habits are primitive for pythonomorphs, being retained in mosasauroids and pachyophiids, with modern snakes being secondarily terrestrial. This scenario requires two steps. However, another equally parsimonious scenario is that the marine habits in mosasauroids and pachyophiids are (convergent) specializations that evolved within each taxon, and that the modern snakes never went through a marine phase. This scenario also requires only two steps. Further study of other primitive mosasauroid-like or snake-like squamates is required to resolve this issue.

Acknowledgements

REFERENCES

Arambourg, C. & Signeaux, J. (1952). Les vertébrés fossiles des gisements de phosphates (Maroc–Algérie–Tunisie). *Service Géologique du Maroc, Notes et Mémoires* **92**: 1–359.

Auffenberg, W. (1959). *Anomalophis bolcensis* (Massalongo), a new genus of fossil snake from the Italian Eocene. *Breviora* **114**: 1–16

Bergey, M. & Baier, H. (1987). Lung mechanical properties in the West Indian manatee (*Trichechus manatus*). *Resp. Physiol.* **68**: 63–75.

Bolkay, S. J. (1925). *Mesophis nopcsai* n. g., n. sp.; ein neues schlangenähnliches Reptil aus der unteren Kreide (Neocom) von Bilek-Selista (Ost-Hercegovina). *Glasnika Zemaljskog Museja u Bosni i Hercegovini* **37**: 125–136.

Brongniart, A. (1800). Essai d'une classification naturelle des reptiles, 1ère partie. *Bull. Sci. Soc. Philomat. Paris* **35**: 81–82.

Caldwell, M. W. (1998). Squamate phylogeny and the relationships of snakes and mosasauroids. *Zool. J. Linn. Soc.* (in press).

Caldwell, M. W. & Cooper, J. A. (1998). Redescription, palaeobiogeography, and palaeoecology of *Coniasaurus crassidens* Owen, 1850 (Squamata) from the English Chalk (Cretaceous, Cenomanian). *Zool. J. Linn. Soc.* (in press).

Caldwell, M. W. & Lee, M. S. Y. (1997). A snake with legs from the marine Cretaceous of the Middle East. *Nature* **386**: 705–709.

Cannatella, D. C. (1990). Ancient greek and ophidian orthography. *J. Herpetol.* **24**: 322–323.

Cope, E. D. (1869). On the reptilian orders Pythonomorpha and Streptosauria. *Proc. Boston Soc. Nat. Hist.* **12**: 250–266.

de Buffrénil, V. & Mazin, J.-M. (1989). Bone histology of *Claudiosaurus germaini* (Reptilia, Claudiosauridae) and the problem of pachyostosis in aquatic tetrapods. *Hist. Biol.* **2**: 311–322.

de Buffrénil, V. & Rage, J.-C. (1993). La 'pachyostose' vertébrale de *Simoliophis* (Reptilia, Squamata): données comparatives et considérations fonctionelles. *Ann. Paléont. (Vert.-Invert.)* **79**: 315–335.

de Queiroz, K. & Gauthier, J. (1992). Phylogenetic taxonomy. *Annu. Rev. Ecol. Syst.* **23**: 449–480.

Domning, D. & de Buffrénil, V. (1991). Hydrostasis in the Sirenia. *Marine Mammal Sci.* **7**: 331–368.

Estes, R., de Queiroz, K. & Gauthier, J. (1988). Phylogenetic relationships within Squamata. In *Phylogenetic relationships of the lizard families*: 119–281. Estes, R. & Pregill, G. K. (Eds). Stanford, California: Stanford University Press.

Hoffstetter, R. (1959). Un serpent terrestre dans le Cretacé inférieur du Sahara. *Bull. Soc. geol. France* **7**: 897–902.

Janensch, W. (1906). Über Archaeophis proavus Mass., eine schlange aus dem Eocän des Monte Bolca. *Beiträge zur Paläontologie und Geologie Oestrich-Ungarns und des Orients* **19**: 1–33, Pl.I-II.

Langer, W. (1961). Über das Alter der Fischschiefer von Hvar-Lesina (Dalmatien). *N. Jb. Geol. Paläontol. Mh* 1961: 329–331.

Lee, M. S. Y. (1997). The phylogeny of varanoid lizards and the affinities of snakes. *Phil. Trans. R. Soc. Lond. B* **352**: 53–91.

Lee, M. S. Y. (1998). Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate phylogeny. *Biol. J. Linn. Soc.* **65**: 369–453.

Lee, M. S. Y. & Caldwell, M. W. (1998). Anatomy and relationships of *Pachyrhachis*, a primitive snake with hindlimbs. *Phil. Trans. R. Soc. Lond. B* **353**: 1521–1552.

McDowell, S. B. (1987). Systematics. In *Snakes: ecology and evolutionary biology*: 3–50. Seigel, R. A., Collins J. T. & Novak, S. S. (Eds). New York: Macmillan.

Nopcsa, F. (1923). *Eidolosaurus* und *Pachyophis*. Zwei neue Neocom-Reptilien. *Palaeontographica* **65**: 99–154.

Nopcsa, F. (1925). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägypten. II. Wirbeltier-Reste der Baharje-Stufe (unterstes Cenoman). 5. Die *Symoliophis*-Reste. *Abh. Bayerisch. Akad. Wiss., Math.-naturw. Abt.* **30**: 1–27.

Odell, D. K., Forrester, D. J. & Asper, E. D. (1981). A preliminary analysis of organ weights and sexual maturity in the West Indian manatee (*Trichechus manatus*). In *The West Indian Manatee in Florida*. R. L. Brownell, R. L., Jr & Ralls, K. S. (Eds). Tallahassee, Florida: Florida Department of Natural Resources.

Oppel, M. (1811). *Die Ordnungen, Familien, und Gattungen de Reptilien*. Munich. [Not seen.]

Rage, J.-C. (1984). *Handbuch der Paläoherpetologie. Teil 11. Serpentes*. Stuttgart: Gustav Fischer Verlag.

Rage, J.-C. (1987). Fossil history. In *Snakes: ecology and evolutionary biology*: 57–76. Seigel, R. A., Collins J. T. & Novak, S. S. (Eds). New York: Macmillan.

Ray, C. E. (1965). Variation in the number of marginal tooth positions in three species of iguanid lizards. *Breviora* **236**: 1–15.

Reynoso, V. H. (1998). *Huehuecuetzpalli mixtecus* gen. et sp. nov: a basal squamate (Reptilia) from the Early Cretaceous of Tepexi de Rodríguez, Central Mexico. *Phil. Trans. R. Soc. Lond. B* **353**: 477–500.

Rieppel, O. (1988). A review of the origin of snakes. *Evol. Biol*. **22**: 37–130.

Russell, D. (1967). Systematics and morphology of American mosasaurs. *Bull. Peabody Mus. Nat. Hist*. **23**: 1–240.

Sauvage, H. E. (1880). Sur l'existence d'un Reptile du type Ophidien dans les couches à *Ostrea columba* des Charentes. *C. r. som. Acad. Sci*. **91**: 671–672.

Sauvage, H. E. (1897). Vertébrés fossiles du Portugal. Contributions à l'étude des poissons et des reptiles du Jurassique et du Crétacique. *Mém. Direction Travaux Géol. Portugal* 1897: 23–24.

Scanlon, J. D. (1997). *Nanowana* gen. nov., small madtsoiid snakes from the Miocene of Riversleigh: sympatric species with divergently specialised dentition. *Mem. Queensl. Mus*. **41**: 393–412.

Scanlon, J. D., Lee, M. S. Y., Caldwell, M. W. & Shine, R. (1998). Taphonomy and palaeoecology of the primitive snake *Pachyrhachis*. *Hist. Biol*. (in press).

Sliskovic, T. (1970). Die stratigraphische lage der schichten mit Pachyophiidae aus Seliste bei Bileca (Ostherzegowina). *Bull. Sc. Yougosl. A* **15**: 389–390.

Zaher, H. (1998). The phylogenetic position of *Pachyrhachis* within snakes (Squamata, Lepidosauria). *J. Vertebr. Paleontol*. **18**: 1–3.

Appendix   Additions to the character list and data matrix of Lee (1998) used in this cladistic analysis. *Pachyophis* was added to the taxon list and coded for the following characters out of the 230; the state exhibited by *Pachyophis* is identified with an asterisk (*). It could not be coded for the other characters due to missing data or the characters being not applicable (e.g. forelimb morphology). In addition, two characters (231 and 232) were added to the character set, and the codings for these new characters for all taxa are listed below.

110. **Mandibular symphysis**. Rigid (0); *mobile (1). Anterior end of dentary appears to be rounded.
112. **Alveolar margin of dentary**. *Straight in lateral view (0); curved in lateral view (1).
113. **Dentary**. With large posterodorsal extension onto coronoid process (0); with small posterodorsal extension (1); *without posterodorsal extension (2).
114. **Meckel's canal**. *Open groove (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 fused together (2).
115. **Anterior (symphysial) end of Meckel's canal**. Extends along ventral margin of lower jaw (0); *confined to medial surface of lower jaw (1).
116. **Intramandibular septum of Meckel's canal**. Poorly developed (0); *well developed (1).
119. **Dentary–postdentary articulation**. Extensive overlap (0); *reduced overlap (1).
124. **Splenial–angular contact**. Overlapping, irregular, and with limited mobility (0); *abutting, straight and highly mobile (1).
130. **Disarticulated surangular**. Extends far into the medial surface of the dentary and terminates in a point (0); extends some distance into the medial surface of the dentary and terminates in a blunt end (1); does not extend appreciably into the medial surface of the dentary and terminates in a blunt end (2); *extends far into the lateral surface of the dentary and terminates in a point (3). This coding assumes our preferred interpretation of the posterior elements of the lower jaw is correct.
132. **Angular**. *Present (0); absent (1).
146. **Marginal tooth implantation**. Acrodont, (0); pleurodont (1); *shallow thecodont (2); deep thecodont (3).
149. **Marginal tooth spacing**. Crowns closely spaced (0); *crowns separated by large gaps (1).
158. **Dentary teeth**. *Thirteen or more tooth positions (0); twelve to nine (1); eight or fewer (2).
168. **Neural spines**. *Tall processes (0); low ridges (1).
169. **Zygosphenes and zygantra**. *Present (0); absent (1).
172. **Number of presacral vertebrae**. 22 or fewer (0); 23 to 25 (1); 26 (2); 27 to 50 (3); 50 to 119 (4); *120 or more (5).
187. **Ribs**. *Without anteroventral pseudotuberculum (0); with anteroventral pseudotuberculum (1).
188. **Ribs**. *Without posterodorsal pseudotuberculum (0); with posterodorsal pseudotuberculum (1).
190. **Scapulocoracoid**. Present and large (0); present but reduced (1); *absent (2).
194. **Clavicle**. Present (0); *absent (1).
197. **Interclavicle**. Present (0); *absent (1).
200. **Ossified sternum**. Present (0); *absent (1).
204. **Forelimbs**. Large (0); *small or absent (1).
216. **Dorsal body osteoderms**. *Absent (0); present (1). E127.
217. **Ventral body osteoderms**. *Absent (0); present (1). E126.
231. **Pachyostosis of mid-dorsal vertebrae and ribs**. Absent (0); *present (1). *Pachyrhachis* and *Pachyophis* have state 1; all other squamates, and outgroups, have state 0.
232. **Body cross-section**. Round, trunk ribs uniformly curved (0); *laterally compressed, distal portions of trunk ribs straight (1). *Pachyrhachis* and *Pachyophis* have state 1; all other squamates, and outgroups, have state 0.