

THE PALAEOECOLOGY OF THE PRIMITIVE SNAKE *PACHYRHACHIS*

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The palaeoecology of the primitive, limbed snake *Pachyrhachis* is reevaluated. Previously considered to have been preserved in a shallow bay with a nearby freshwater source, it is here demonstrated to have inhabited an inter-reef basin. Evidence for this comes from the position of the nearest palaeo-shoreline (450 km away), the finely laminated carbonate mudstones, and the absence of bioturbation, alluvium, and unequivocally terrestrial or freshwater taxa. Marine adaptations of *Pachyrhachis* include the laterally compressed body and heavily ossified (pachyostotic) vertebrae and ribs. Hydrodynamic considerations indicate that it was a slow swimmer, and thus an ambush rather than pursuit predator. Morphology of the anterior vertebrae suggests that the strike muscles were well-developed. The narrow head and neck might have been adaptations to reduce water resistance during rapid lunges, and/or to forage in burrows or tight crevices.

Keywords: Paleoecology; *Pachyrhachis*; Cretaceous; Squamates; Snakes.

INTRODUCTION

The origin of snakes from lizard-like ancestors was a major event in vertebrate evolution, and remains rather poorly understood despite much effort. For a long time, the nearest lizard relatives of snakes remained uncertain, and no transitional taxa were known. Recently, however, several independent studies have concluded that large marine mosasauroids are the nearest relatives of snakes (Scanlon, 1996; Lee, 1997, 1998; Caldwell, 1998; Rage, 1997), and a well-preserved transitional taxon, *Pachyrhachis problematicus*, has been identified. (Caldwell and Lee, 1997). Here, we discuss the ecology of this important intermediate and its implications for the evolutionary biology of snake origins

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Pachyrhachis is a long-bodied, marine squamate with reduced limbs, from the Middle Cretaceous of the Middle East. It is known from two largely complete, articulated specimens, both from the same quarry at Ein Jabrud (= Ein Jabrud or Ain Yabrud), north of Jerusalem. They were initially interpreted as two distinct taxa, *Pachyrhachis problematicus* and *Ophiomorphus colberti* (Haas, 1979, 1980a, b). Subsequently, the taxon name *Ophiomorphus* was found to be preoccupied, and it was replaced with *Estesius* (Wallach, 1984). However, a recent detailed study of the two specimens (Lee and Caldwell, 1998) revealed that, aside from a slight size difference, they are in all respects almost identical. *Estesius* (= *Ophiomorphus*) *colberti* therefore became a junior synonym of *Pachyrhachis problematicus*.

Recent study of *Pachyrhachis* revealed that almost every skeletal element is represented in at least one of the two specimens, providing a basis for a very complete understanding of its morphology and relationships. *Pachyrhachis* is the most primitive snake, being the sister group to all other snakes (Lee, 1998; contra Zaher, 1998). It is an excellent example of a transitional taxon, exhibiting most, but not all, of the derived features that are diagnostic of snakes. In particular, it possesses many cranial and postcranial specialisations of snakes, such as those connected with a highly kinetic skull and long slender body. Unlike all other snakes, however, it retains a normal iliosacral contact, and a small but well-developed hindlimb (Figure 1).



FIGURE 1 Body reconstruction of *Pachyrhachis problematicus* showing small head, slender neck region, elongate body, and minute hindlimbs. Only the proximal end of the tail is known, the remainder of the reconstructed tail is conjectural. Scale bar = 10 cm

Because *Pachyrhachis* occupies a crucial phylogenetic position and is very completely known, its palaeoecology is important. The original descriptions by Haas (1979, 1980a, b) did not include any detail, beyond mentioning that the animal was aquatic. The recent detailed study of this animal by Lee and Caldwell (1998) concentrated on anatomy and systematics. Some preliminary remarks about the mode of life of *Pachyrhachis* had already been included in an unpublished thesis by Scanlon (1996), based on existing (but brief and partly inaccurate) descriptions of the holotype (Haas, 1979, 1980a). Scanlon assumed, following Haas, that *Estesius* was distinct from *Pachyrhachis*, so he did not consider the former specimen in his discussion. Here, Scanlon's interpretations are

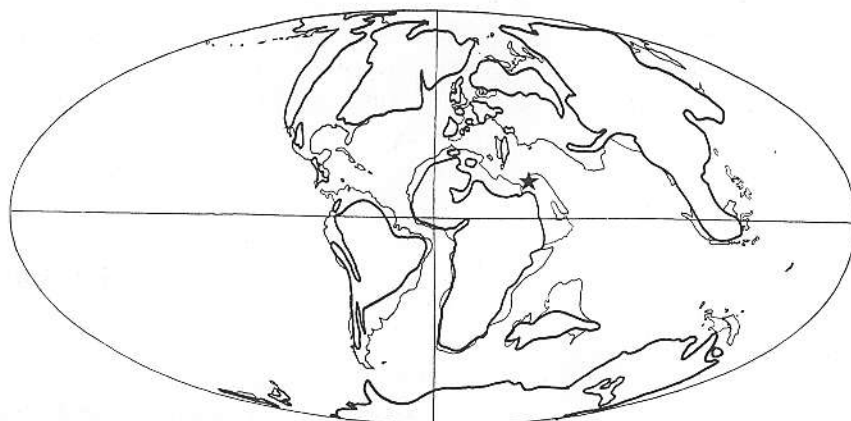


FIGURE 2 Lower Cenomanian palaeogeographic map. The location of Ein Jabrud is indicated by a star. Heavy lines indicate palaeocoastlines, thin lines indicate coastal margins of modern continents

modified and extended in light of the new understanding of the morphology of *Pachyrhachis*.

The general morphology of *Pachyrhachis* is shown in Figures 1, 3, 4 and 6. There is a small, lightly built skull, a slender cervical region, and a long, laterally compressed trunk. The forelimbs and shoulder girdle are absent; the pelvis and hindlimb are greatly reduced in size but still well-formed. Only aspects of the anatomy relevant to the inferred ecology of this animal will be discussed here.

PALAEOENVIRONMENT

Locality and Stratigraphy

Both specimens of *Pachyrhachis problematicus* were found in limestone beds exposed in stone quarries near the town of Ein Jabrud, situated near the West Bank city of Ramallah, 20 km north of Jerusalem (Figure 2). All fossils referred to as the "Ein Jabrud flora and fauna" come from a single horizon within the Amminidav Formation (middle portion of the Judea Group; Arkin *et al.*, 1965). Descriptions of actual quarry sections are currently not available. However, the type section of the formation, located 10 km west of Jerusalem near the village of Amminidav, is an 83 m thick section of dolomites locally interbedded with thin limestones. Based on stratigraphic correlations of Braun (1970) and Shachnai (1969), Chalifa (1985) indicated that the fossil-bearing horizon in the Ein Jabrud quarries is from the lower part of the section.

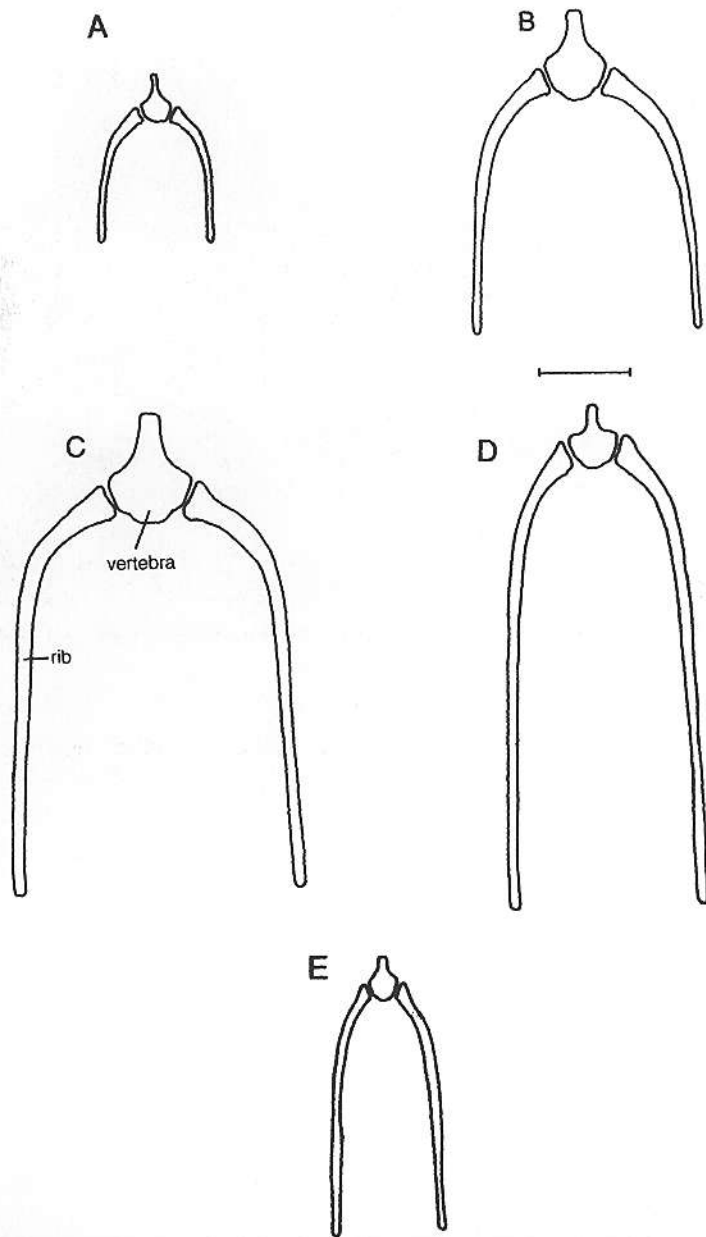


FIGURE 3 Reconstructed cross-sections of *Pachyrhachis*, arranged from anterior to posterior. Scale bar = 2 cm. Approximate regions of the vertebral column are as follows. (A) 5th presacral ("cervical"). (B) 35th presacral (anterior dorsal). (C) 70th presacral (mid-dorsal). (D) 105th presacral (posterior dorsal). (E) 140th presacral (posteriormost dorsal).



FIGURE 4 Dorsal vertebrae and ribs of *Pachyrhachis* (HUI PAL-3659) showing heavy ossification and roughened surfaces (pachyostosis). Scale bar = 2 cm

Biostratigraphic correlation based on fish faunas from other Tethys margin localities initially indicated an earliest Lower Cenomanian age (Chalifa and Tchernov, 1982). This has since been revised by Chalifa (1985, 1989a,b), following further investigation of the fish fauna. The fossil horizon now appears to be of uppermost Lower Cenomanian age. This places the Ein Jabrud fishes as contemporaries of fish faunas from nearby deposits in Lebanon, and from the northern margins of the Cenomanian Tethys (Comen, Slovenia, and the English Chalk).

Lithology and Sedimentology

Previous Investigations

Most descriptions of units at Ein Jabrud and in surrounding outcrops have focused on major units in the Amminidav Formation (Arkin *et al.*, 1965; Shachnai, 1969; Braun, 1970; Begin, 1975). These indicate that the limestone member, and limestone interbeds found within the dolomitic member, are "...grey, pink, or red, and more thinly bedded than the dolomite." (Begin, 1975: p. 8).

In more easterly outcrops the formation thins and the lower part of the Amminidav is marked by a carbonate breccia. In sections to the west, the Amminidav thickens (up to 120m) as does the breccia unit at the base; the limestone portion of the upper member increases to about 40% of the formation (Begin 1975). No evidence of a clastic component in the Amminidav limestones has been reported.

Gayet (1980), in a paper describing a fossil fish from Ein Jabrud, briefly characterized thin-sections made from the fossil-bearing limestones. She published no figures but did identify several important features: 1) microcrystalline limestone with microsparite-sparite; 2) total absence of organic elements; 3) microsparite and sparite between laminations; 4) presence of "sheetcracks", a fabric whose genesis Gayet suggested was produced by "bulles d'air" (air bubbles trapped in the sediments that would communicate with each other, increase in size, and escape the sediments); 5) presence of calcite (microsparite and sparite) filling the sheetcrack fabric. Gayet (1980) interpreted the finely laminated limestones as indicating that "...de courants bien que l'energie du milieu soit faible" (...the current energy in that environment was weak.). Finally, Gayet (1980) does not mention the presence of any clays in the limestones she examined.

Recent Observations

One of us (MC) examined the fossil-bearing limestones of Ein Jabrud in hand-sample. In color, the thinly bedded limestones are pinkish-tan on fresh surfaces and they weather pink to reddish-orange. Fine horizontal laminae were the only primary sedimentary structures observed. Biogenic structures and bioclastic inclusions were not observed (grain inclusions were less than 10%). Thin-sections of the Ein Jabrud rocks were not made.

Palaeogeography

Beginning in the Aptian and Albian, and continuing through the Cenomanian and Turonian, what is now the modern Middle East was submerged during a major transgressive phase to form an extensive carbonate platform (Follmi, 1989). Numerous patch-reefs and intra-platform basins formed on this enormous shallow-water platform. A loosely comparable modern analogue is the Great Barrier Reef on the northeast shelf margin of the Australian plate. However, this does not match the scale of the epeiric sea and reef system that extended across the Middle East platform during the Cenomanian. The Ein Jabrud locality lies well away from the margin of this platform (Figure 2). The shoreline of northeast Africa was approximately 450 km to the southwest, near the southern end of the

modern Sinai Peninsula (Smith *et al.*, 1995). To the west, along the shelf margin, there was an extensive barrier reef system. Similar shelf-reef complexes occurred along the north and south margins of the Tethys Seaway. (Jurkovsek *et al.*, 1996). Throughout the Albian and Cenomanian, European and African epeiric carbonate platforms supported extensive reef complexes formed by rudist bivalves and scleractinian corals (Bein, 1971; Saint-Marc, 1981; Jurkovsek *et al.*, 1996).

Fauna and Flora

The carbonate rocks at Ein Jabrud contain a rich and superbly preserved vertebrate fauna of fishes and reptiles. Among the fishes, pycnodonts, skates, and rays are well represented, as well as a large number of actinopterygian fishes, many of which have been described (Chalifa, 1985, 1989a,b; Chalifa and Tchernov, 1982; Gayet, 1980, 1982, 1985). With the exception of an amiid, interpreted by (Chalifa and Tchernov (1982) as having been washed into the depositional environment of Ein Jabrud, all the other fishes are considered to have inhabited shallow to deeper water marine environments.

Reptiles are represented by several lizard taxa, one snake, one pteryodactyl, and two turtles. The lizards were mentioned by Haas (1980b) but currently remain undescribed. Our examination of this material indicates that it consists of fragmentary remains of mosasauroids, a group of squamates with definite marine habits (Carroll and deBraga, 1992; Caldwell *et al.*, 1995). The pterodactyl also remains undescribed. The Ein Jabrud turtles are two species of pelomedusid pleurodires described by Haas (1978a,b).

The fossil bed at Ein Jabrud also contains an assemblage of disarticulated and disassociated floral elements. All plant fossils mentioned in the literature are isolated vegetative structures such as leaves and stalks or stems (Chalifa and Tchernov, 1982; Chalifa, 1985).

Taphonomy

Vertebrate Taphonomy

The vertebrate fossils from Ein Jabrud show little or no evidence of scavenging or post-burial bioturbation. Almost all specimens are in close to perfect articulation. This suggests several important biostratigraphic characteristics: 1) absence of an active epifauna and infauna (no evidence of scavenging or bioturbation); 2) low energy environment (little or no bottom currents, or sediments deposited below storm wave base).

Haas (1978a,b) suggested that the Ein Jabrud turtles were elements of a freshwater fauna. This conclusion was extrapolated from the occurrence of extant

pelomedusids in freshwater environments (for a review see Pritchard & Trebbau, 1984). Recent investigations on the taphonomy of turtles indicate that it would be very unlikely for these turtles to have remained articulated if they had washed in from some remote fluvial source, or from a beach (Meyer, 1988; 1991). Meyer (1991) examined the preservation of turtles in marine intertidal zones and in the deeper water of a subtidal lagoon influenced by the daily exchange of oxygenated waters through tidal channels. In both environments, turtle skeletons were quickly disarticulated. In the intertidal zone, wave action and intertidal detritivores swiftly disarticulated the skeletons. In deeper water, decomposition and activities of detritivores soon led to their complete disarticulation.

However, ad hoc taphonomic hypotheses may not be needed to explain the presence of pelomedusid turtles and amiid fishes at Ein Jabrud. The fossil record indicates that many pelomedusids might well have been marine (Wood, 1974; Pritchard and Trebbau, 1984). A number of fossil forms are found only in marine rocks and one modern African species lives in landlocked saline waters (Wood, 1974). The pelomedusids of Ein Jabrud may well have been marine turtles living in the same reef-lagoon environments as *Pachyrhachis* and the mosasauroids. Likewise, amiid fishes are derived from marine holosteans (Carroll, 1988) and most certainly colonized freshwater habitats secondarily. Wilson (1995) described amiid vertebrae from a probable brackish water environment in the Paleocene of Saudi Arabia and questioned the assumption that early amiids were freshwater fish. Their habitat shift might have evolved much later within the group. At this point, we cannot be certain whether *Pachyamia* was a freshwater element that washed out to sea, or a member of the local marine fauna.

Floral Taphonomy

The absence of relatively complete, articulated terrestrial plant structures, or both reproductive and vegetative parts of the same species, also suggests that the locality was far from the nearest landfall (Behrensmeyer *et al.*, 1992). As at Solnhofen, where only fragmentary plant fossils are present, plant taphonomy indicates that the shoreline was some distance away (Barthel *et al.* 1990). It is simplest to assume that the plant fossils were washed in from some distant source and that only vegetative structures were able to float far out on the platform.

It has been suggested for Solnhofen (Barthel *et al.*, 1990) that there may well have been reef islands produced at high points in the patch-reef complex. The possible existence of islands on the Cenomanian Middle East platform, formed by aerially exposed reef mounds, can neither be refuted nor corroborated by current evidence. However, if reef islands did exist, such terrestrial environments could be a source of plant debris. Depending on the distance of such islands from the deposits at Ein Jabrud, the plant debris could still be transported over considerable distances.

Palaeoenvironmental Interpretation

In the literature there are currently two different interpretations of the depositional environment of the Amminidav Formation. Arkin *et al.* (1965) and Begin (1975, p. 9) have characterized the general shelf/platform environment as follows: "The Amminidav Formation was deposited in a shallow, highly saline sea, as indicated by the abundance of stratigraphic dolomite. The breccia at its base and the burrowings within its rock indicate a shallow sea."

Chalifa (1985) synthesized and interpreted the observations and interpretations of Haas (1978a,b, 1979, 1980a,b), Gayet (1980), and Chalifa and Tchernov (1982), to produce a second model, which focuses on the origin of the thinly bedded fossil bearing limestones. He concluded that the Ein Jabrud sediments were deposited in a shallow marine bay, bordered to the west by patch reefs that did not block communication with the open sea (so anoxic conditions did not exist). Land was close by, supplying the bay with great quantities of alluvium, plant debris, and a limited number of carcasses of freshwater and terrestrial vertebrates. Chalifa (1985) emphasized that the water was very muddy, due to great quantities of alluvium, and that this "muddiness" suppressed the benthonic fauna, hence explaining the absence of bioturbation and scavenging. The great quantity of alluvium was also inferred to have promoted the rapid burial of the animal and plant remains.

Revised Interpretation

In contrast to Chalifa's (1985) interpretation, we support elaboration of the depositional environment as proposed by Begin (1975), with qualifications based on our own observations and those of Gayet (1980).

1. The sediments of the Judea Group generally, and the Amminidav Formation in particular, were deposited in a shallow water marine environment typical of the Cenomanian carbonate platform. This platform sea supported a barrier reef system to the west, and an unknown number of patch reefs and patch reef islands across its expanse. Between the patch reefs and/or patch reef islands, were a large number of variably isolated and interconnected inter-reef basins. Sediments in the basins included reef detritus (including sediments from reef islands), and carbonate mud precipitates. Across the carbonate platform, conditions in each basin would have been extremely variable. Differences in the exchange of sea water between basins and the open sea would have varied the amount of evaporation, precipitation of carbonate muds, and solute concentrations in each basin.
2. The fossil bearing horizon at Ein Jabrud is interpreted as having been deposited in a low energy, quiet water, inter-reef basin. The sediment is a fine

grained, crystalline limestone that precipitated as carbonate mud, forming thin laminae. The bottom waters and/or sediments were probably anoxic as there is no evidence of bioturbation, nor of scavenging by infaunal/epifaunal organisms.

Discussion

The hypothesis that the Ein Jabrud sediments were deposited in a bay close to a freshwater source (Chalifa and Tchernov, 1982; Chalifa, 1985) can still hold if the bay and freshwater source are reconsidered as a carbonate island. If not, the hypothesis fails as there is no evidence of terrestrial clastic sediment in the fossil bearing rocks of Ein Jabrud. The "mud" at Ein Jabrud is a carbonate mud. Carbonate muds are produced either by concentrations of calcareous algae or as chemical precipitates (Tucker and Wright, 1990). Gayet (1980) describes a crystalline carbonate, not a terrigenous mud with calcite cement. The shoreline of North Africa was at least 450 km to the south and there is no evidence to suggest it was ever any closer during the later part of the Cenomanian, either in vertical or lateral facies successions within the Judea Group (see Arkin *et al.*, 1965; Begin, 1975).

There is also no evidence of rapid sedimentation. Rather, the lithology indicates exactly the opposite. The laminae of the fossil bearing limestone are very fine, regular and thin. This indicates that chemical precipitation of carbonate muds was frequent but limited. There are no thick laminae suggesting changes in rate of sedimentation.

It seems likely that some special condition, such as anoxia, was responsible for the absence of bioturbation, scavenging, and other evidence of infaunal/epifaunal activity. Chalifa (1985) proposed highly turbid water as an agent of rapid burial, but the lack of clastics at Ein Jabrud, and the presence of benthos in muddy waters at delta mouths make this implausible. Gayet (1980) noted a sheetcrack microfabric produced by the aggregation of "air" bubbles in the carbonate muds. Gases produced by bacterial metabolism commonly bubble out of organic-rich mud; these bubbles could have aggregated to form the fabric Gayet (1980) observed. Anaerobic bacterial metabolism is highest when anoxic conditions occur in bottom waters and sediments.

In summary, on a regional scale, we consider the palaeoenvironment of Ein Jabrud to be similar to those proposed for Hakel, Lebanon, and Solnhofen, Germany: lagoonal environments located between patch reefs, in an epeiric sea on a carbonate platform (Hückel, 1970; 1974; Meyer and Schmidt-Kaler, 1984). Specifically, the data so far available suggest a quiet water inter-reef basin/lagoon with anoxic bottom waters.

FUNCTIONAL MORPHOLOGY

Body form and locomotion

The postcranial skeleton of *Pachyrhachis* provides compelling evidence that it was an aquatic snake (Figure 1), consistent with the palaeoenvironmental evidence presented above. Three features in particular support this interpretation: the lateral compression of the body, the pachyostosis of its vertebrae and ribs, and the marine fish found preserved as its gut contents.

In almost all squamates, including snakes with a round cross-section, the ribs are uniformly curved along their entire length, forming a smooth arc. In laterally compressed squamates, the ribs are straight distally (Figure 3). This body form has evolved independently three times in extant forms, always in aquatic snakes: in acrochordids (file-snakes), laticaudines (sea-kraits), and hydrophiines (true sea-snakes). The long ribs of *Pachyrhachis* also have this shape. The proximal end is curved but the remainder of the element is straight. When articulated in their natural position, the ribs project laterally from the centrum for a short distance and then immediately curve ventrally, so that the long straight portions form the parallel or converging sides to a deep, narrow body. The proximal portion of the anterior ribs is longer and its curvature is less pronounced compared with that of more posterior ribs. Thus, the anterior ribs projected further laterally before eventually curving ventrally, and the vertical distal portion (forming the sides of the body) is shorter. This indicates that the anterior end of *Pachyrhachis*, though laterally compressed, was wide and not very deep. Posteriorly, the body gradually became relatively deeper, remaining laterally compressed up to the region of the pelvis. The tail of *Pachyrhachis* is not preserved in either specimen, but, based on the gradual anteroposterior change in body cross-section, is likely to have been even narrower and deeper than the pelvic region. This is the situation in extant laticaudine and hydrophiine sea snakes. However, not all obligatorily aquatic snakes have such morphologies; acrochordids, for example, have flattened bodies but tapering tails. Thus, a paddle-like tail in *Pachyrhachis* is likely but not definite.

The body shape of *Pachyrhachis* as indicated by the postcranial skeleton is consistent with taphonomic evidence. In both specimens (see Haas, 1979, 1980a, b), the anterior and middle part of the body is preserved approximately upright between bedding planes. The anterior region has therefore been compressed dorsoventrally. The individual elements are not distorted, but they are displaced slightly with respect to each other. The left and right ribs are splayed out on both sides of the vertebral column. However, the body gradually twists so the posterior portion is preserved on its side between bedding planes. This region is there-

fore compressed laterally. Again, the individual elements are displaced but not distorted. The left and right ribs are preserved on the same side of the vertebral column and pressed against each other. This shows that, in death, both specimens of *Pachyrhachis* rested in the same twisted position, with the anterior portion of the body upright, and the posterior portion on its side. This is consistent with the morphological evidence (the shape of the ribs) indicating that the anterior part of the body was wider (thicker), and thus more likely to rest upright, but the posterior portion was very narrow, and hence likely to rest on its side.

Among squamates, the laterally compressed body is found only in highly aquatic snakes, acrochordids, laticaudines, and hydrophiines. Such forms swim by axial undulation or subundulation (Massare, 1994), propelling themselves by sinusoidal lateral undulations of the posterior portion of the body. In such locomotion, the anterior portion of the body should be held straight and rigid for maximum efficiency. Movements of the anterior region increase drag and also cause the animal to move in a zig-zag fashion, rather than in a straight line (Lingham-Soliar, 1991; see below). The shape of *Pachyrhachis* is consistent with this interpretation. The anterior portion is sub-cylindrical, so more rigid, while the propulsive posterior portion is laterally compressed. Modern sea snakes, which swim in this way, have a very similar shape. Conversely, the laterally compressed posterior body and probably narrow ventral surface in *Pachyrhachis* would have made terrestrial locomotion laborious and slow, as in modern marine snakes (Heatwole, 1987; Cogger, 1992). There is no evidence bearing on the mode of reproduction in *Pachyrhachis*. However, if oviparous, like modern sea-kraits (laticaudines), it would have had to return to shore periodically to lay eggs.

Pachyrhachis, like other pythonomorphs (mosasauroids and modern snakes), possessed tight accessory vertebral articulations, zygosphenes and zygantra. However, the exact shapes of these structures remain unknown because all the vertebrae in both specimens are preserved in tight articulation. In mosasauroids and modern snakes, the zygosphenes and zygantra serve to strengthen the articulations between vertebrae and control the mobility of the vertebral column (Lingham-Soliar, 1991). In mosasauroids, it has been suggested that they facilitated axial subundulatory swimming. The paired zygosphenes and zygantra prevented lateral flexion of the vertebral column when the epaxial muscles contracted, pulling the anterior edges of the left and right zygosphenes tightly against the preceding zygantrum. This presumably happened in the anterior (stiffened) region of the body. However, when relaxed, the geometry of the zygosphene-zygantral articulations allowed lateral flexibility. This presumably happened in the (oscillating) posterior region of the body. The zygosphenes and zygantra might have performed a similar role during swimming in *Pachyrhachis*. Unfortunately, whether or not the zygosphenes and zygantra play a similar role in modern aquatic snakes has yet to be ascertained.

The hindlimbs were clearly too small to be effective locomotory or steering organs (Figure 1). The simplest interpretation of them is that they were in the gradual process of being lost through disuse. If so, they would have been held against the side of the body most of the time, especially during rapid swimming. There are other possibilities, but all are very difficult if not impossible to test. For instance, the males of living boas and pythons use their vestigial limbs to stimulate the female during courtship, and a similar function has been suggested for the small hindlimbs of early whales (Gingerich *et al.*, 1990). Terrestrial lizards with reduced limbs (e.g. certain skinks) still use their tiny rudiments to help in locomotion, although almost all the thrust comes from axial undulation. However, this is unlikely underwater, where buoyancy and softer substrates mean that limbs are unlikely to gain any traction. Another possible use of the limbs might be to anchor the posterior body in a crevice (see section on feeding and foraging below), although lateral curves of the body and tail could be equally or more effective in this role.

Pachyostosis

Pachyrhachis, as its name suggests (pachy – thick, rhachis – spine), exhibits pachyostosis: an increase in the osteogenic activity of the periosteum. This feature is also found in some other, poorly-known squamates, *Simoliophis* and *Pachyophis* (Rage, 1984; de Buffrénil and Rage, 1993), that might be close relatives. Pachyostosis is most pronounced in the middle region of the vertebral column. In this region the vertebrae and proximal portions of the ribs are greatly thickened and swollen in cross-sectional area (Figure 4). Pachyostosis is restricted to secondarily aquatic vertebrates (reptiles and mammals), and functions in buoyancy control. *Pachyrhachis* inhabited shallow-water reefs, and so did not dive deeply enough for its lungs to be compressed. Shallow-diving vertebrates that retain significant air-space in their lungs tend to float. The extra bone deposited in pachyostotic elements provides a means to approach neutral buoyancy (Nopcsa, 1923; Kaiser, 1966; Domning and de Buffrénil, 1991). The increased body density also tends to improve stability in currents and turbulence (Wall, 1983). It is interesting that the increased ossification in *Pachyrhachis* is concentrated in the central part of the body, near the lungs. The extra weight is therefore concentrated where it is required: the otherwise most buoyant section. If the lungs extended anteriorly (or posteriorly) past the region of heavy ossification, the animal would have tended to tilt head up (or tail up), and maintaining the normal horizontal trim would have been more energetically expensive. Similar adaptations are exhibited by sirenians (manatees and dugongs), where extra skeletal weight is appropriately distributed to serve as hydrostatic ballast (Domn-

ing and de Buffrénil, 1991). In both *Pachyrhachis* and sirenians, the extra bone and its distribution imply that (1) the overall density of the animal is very close to that of seawater, and (2) the centre of gravity and the centre of buoyancy (=centre of volume) approximately coincide. Both features are required if an animal is to maintain its depth and trim by passive, hydrostatic means (Domning and de Buffrénil, 1991). Manoeuvrability (yaw and pitch) is maximised if both the centre of gravity and the centre of buoyancy are near the centre of the body, and steering organs are near the extremities (Domning and de Buffrénil, 1991). *Pachyrhachis* satisfies this requirement, the centre of gravity and the centre of buoyancy being very central, with the flattened posterior region being used for propulsion and steering. This hydromechanical constraint appears quite general; while terrestrial snakes use their entire bodies for locomotion, highly aquatic snakes primarily depend on their caudal regions.

In *Pachyrhachis*, there is an ontogenetic increase in the degree of pachyostosis. The ribs and vertebrae are proportionately less thick and swollen in the smaller specimen. This has been observed in other pachyostotic taxa, namely mesosaurs (Lee, personal observation), the diapsid *Claudiosaurus* (Buffrénil and Mazin, 1989), and sirenians (Domning and de Buffrénil, 1990). Lung volume (and thus buoyancy) increases allometrically with weight, such that older, larger animals have proportionately more positive buoyancy (Odell *et al.*, 1981; Bergey and Baier, 1987). The corresponding increase in degree of pachyostosis with age appears to compensate for this (Domning and de Buffrénil, 1991).

Organisms employing anguilliform locomotion (axial undulation and subundulation) are relatively slow, weak swimmers compared with those that employ other methods such as carangiform axial locomotion (tuna-like swimming) or underwater flight (e.g. Webb, 1982). The heavy skeletons of pachyostotic animals also reduce swimming speed and manoeuvrability (de Buffrénil and Mazin, 1989; de Buffrénil and Rage, 1993). The two traits are interrelated: slow swimmers must regulate depth and trim by hydrostatic rather than hydrodynamic means. If an animal falls below a certain ratio of swimming speed to body mass, buoyancy aids (e.g. pachyostosis) are more efficient than hydrofoils (e.g. fins, flippers) in maintaining position in the water column (Alexander, 1990; Domning and de Buffrénil, 1991). *Pachyrhachis* employed anguilliform locomotion and pachyostosis, so it is inferred to have been a very slow swimmer indeed. This conclusion influences interpretations of its possible foraging and feeding ecology.

Feeding and foraging

As a slow swimmer with limited manoeuvrability, *Pachyrhachis* is most unlikely to have been a pursuit predator. No extant aquatic snakes are pursuit

predators. The available evidence suggests that *Pachyrhachis* employed other feeding strategies, such as ambush predation or extracting prey from crevices.

Pachyrhachis possessed prominent blade-like hypapophyses on its first 20 or so vertebrae, a feature unique to snakes. The presence of these hypapophyses in many of the anterior trunk vertebrae implies an ability to strike by rapid release of pre-tensed lateral curves in the neck region (Mosauer, 1935; Gasc, 1974). The main muscles involved (the *musculus transversohypapophyseus*) have only been studied in colubroids, but presumably similar muscles are present in all other snakes which strike. These muscles extend anterolaterally from the hypapophysis to the ventral edge of the transverse process on the preceding vertebra. In ventral view, they form a series of V's (the apices pointing posteriorly). As the hypapophyses gradually get smaller and disappear completely, these muscles change from thick bundles to thin sheets and then finally to connective tissue only. All modern snakes (including marine forms) which strike have hypapophyses on at least the first dozen or so vertebrae. Only in fossorial blindsnakes (scolocophidians) are hypapophyses restricted to the first few vertebrae (Hoffstetter and Gasc, 1969). Scolocophidians do not capture their prey by striking (Webb and Shine, 1993).

Interestingly, the head and neck region of *Pachyrhachis* is narrow in cross-section and light in build. The narrow anterior region that bears the hypapophyses was the part of the body that would have been rapidly extended during the strike. During the strike, drag is much greater in water than in air. In *Pachyrhachis*, the slender cross-section of the anterior region would have reduced drag, facilitating a rapid strike, and the light build would have reduced inertia, permitting rapid acceleration from a stationary state. The aquatic colubrid *Erpeton* has analogous adaptations for reducing water resistance during underwater strikes (Povel et al., 1997).

In comparison to most squamates, though not all snakes, *Pachyrhachis* had a remarkably small head in proportion to the size of its body. The small head and neck region suggest another aspect of feeding in *Pachyrhachis*. Extant sea snakes with narrow heads and necks (some species of *Hydrophis*) feed on eels. This morphology permits the anterior end of the animal to enter and investigate narrow burrows and crevices in search of prey (McDowell, 1972; Voris, 1972; Heatwole and Cogger, 1994). *Pachyrhachis* could have used its small head and slender neck to forage in narrow crevices.

The skull of *Pachyrhachis* is clearly that of a predator. It is lightly built, and highly kinetic. There are long, recurved teeth on the upper and lower jaws, pterygoids, and palatines. Numerous features suggest that the gape was very wide. There is a highly mobile intramandibular joint within each jaw ramus, and the anterior symphysis is also loose. In basal modern snakes such as *Cylindrophis*,

these features combine to increase gape (Cundall, 1995). The lower jaw bows outwards at the intramandibular joint; this causes the two dentaries to open at a more obtuse angle, and such movements are accommodated by the loose mandibular symphysis. The two rami of the lower jaw bulge far apart and allow the passage of large items.

The quadrate in *Pachyrhachis* slopes posteroventrally, as in most modern snakes (Figure 5). This moves the jaw articulation posteriorly, increasing the length of the upper and lower jaws, and thus the gape. Rieppel (1980, p. 561) further suggested that "a posteroventrally sloping quadrate provides for a wider gape than a vertically positioned quadrate at a given angle between the long axes of the quadrate and lower jaw". If there is a maximum angle to which the quadrate-lower jaw joint can open, animals with a posteroventrally slanting quadrate would be able to depress the lower jaw further (Figure 6).

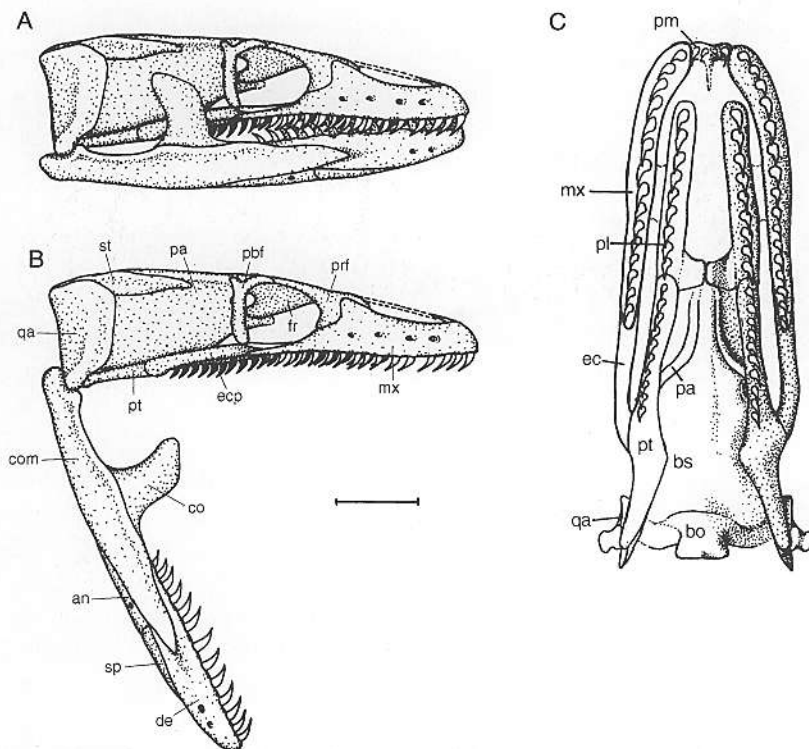


FIGURE 5 Reconstruction of skull of *Pachyrhachis* in lateral view, with jaws closed (A) and open to their inferred maximum extent (B), when the retroarticular process is pressed against the posterior surface of the quadrate and the adductor muscles act at right angles to the coronoid. (C) Reconstruction of the skull of *Pachyrhachis* in ventral view. Scale bar = 1 cm

The very short, broad retroarticular process would also have enabled this snake to open the jaws widely without excessive shortening of the depressor mandibulae muscle, but not with much speed or power. Similar modifications for large gape occur in piscivorous living snakes such as acrochordids.

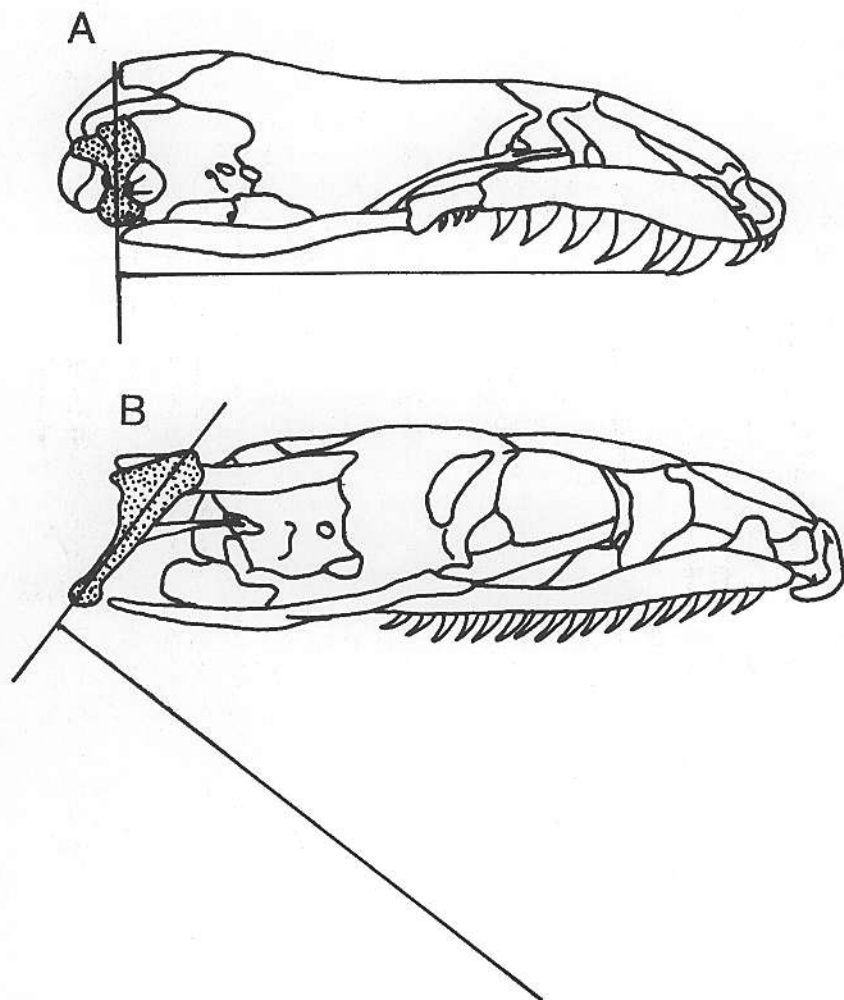


FIGURE 6 Illustration to show how a posteroventrally slanted quadrate (stippled element) increases gape, for a given maximum angle between quadrate and lower jaw (after Rieppel 1980)

The huge coronoid process also suggests a large gape. The adductor muscles inserting on it were presumably large. They would have functioned most effi-

ciently when the jaws were very wide open, acting at right angles to the movement of the coronoid. The great development of the coronoid suggests that rapid and/or powerful closure of the jaws from a wide open position was important, as would be expected in a predator striking and consuming prey that were large in relation to the size of its head.

As in modern snakes, the palatine-pterygoid, palatine-vomer, and probably the palatine-maxilla sutures have been lost, and replaced by mobile articulations (Figure 5C). Also as in modern snakes, the basipterygoid articulation appears to have been a sliding contact. There are no distinct basipterygoid processes; rather, the pterygoids abut the ventral surface of the basisphenoid. The pterygoids and palatine were therefore not immovably connected to any adjacent elements, but were free to move. Again as in most modern snakes, the palatine is a slender parasagittal element, and both the pterygoid and palatine bear a parasagittal row of long, recurved teeth. The palatal elements of *Pachyrhachis* are consequently similar to those in modern snakes, especially basal forms such as aniliids. It is likely, therefore, that the palatal mobility characteristic of modern snakes was at least partly developed in *Pachyrhachis*. Modern snakes transport prey into the oesophagus by alternating movements of the left and right palatal elements, which literally "walk" forwards over the ingested prey item (Bolt and Ewer, 1964; Kardong, 1977). *Pachyrhachis* may have begun to develop this capability.

As noted by Haas (1979), a pycnodont tooth plate is preserved within the abdominal region of the holotype of *Pachyrhachis*. It is surrounded by a large bulge in the ribcage of the animal, suggesting that the remainder of the fish had not yet been fully digested. This toothplate is the only direct evidence of diet for any Mesozoic snake (Haas, 1979), and one of very few in any snake fossils (Greene, 1983). Pycnodonts – deep-bodied, laterally compressed holostean fish – were common elements of shallow marine faunas from the Jurassic to the Eocene. They have been interpreted as inhabitants of quiet reef waters, nibbling on coral with their crushing toothplates (Nursall, 1996). Comparisons with complete pycnodonts found at the same locality as *Pachyrhachis* suggest that the ingested fish was at least 10 cm long and 8 cm deep. This is consistent with the size of the bulge around the toothplate. Few modern reptiles, and no modern snakes, dismember vertebrate prey before swallowing; there is nothing in the anatomy of *Pachyrhachis* to suggest that it did so either. The lightly built, highly flexible skull, large gape and long, narrow teeth suggest that it impaled prey items and swallowed them whole, as do extant piscivorous sea snakes. If the ingested pycnodont was swallowed whole by *Pachyrhachis*, as seems likely, this would indicate the ability to swallow prey items longer and deeper than the skull. This is consistent with the highly flexible nature of the skull and jaws, and the numerous features suggestive of large gape.

DISCUSSION

Based on the palaeoenvironmental and anatomical evidence now available, we infer that *Pachyrhachis* was a slow-swimming, ambush predator which inhabited shallow reefs and lagoons. This niche is very similar to that occupied by many modern sea snakes. Hence, it is not surprising that *Pachyrhachis* and modern sea snakes are similar in overall body form, despite being only distantly related. Modern piscivorous sea snakes employ two main techniques to capture their prey. The first consists of foraging in crevices and cornering prey. The small head and slender neck of *Pachyrhachis* strongly suggest that it employed this technique. The other strategy involves cruising in areas where prey are abundant, and striking at any individuals that come within range (Heatwole, 1987). The derived hydrophiine *Pelamis* employs a third method to capture its prey. It floats near the surface, mimicking a floating stick, and strikes at small fish that come to shelter under it. However, this method is not employed by any sea snakes which take large prey. Such snakes use one or both of the first two methods, spending the bulk of their time foraging near the sea floor. *Pachyrhachis* probably had a similar mode of life. Pycnodont fish, being durophagous (perhaps analogous to parrotfish on modern reefs), presumably spent much time near the sea floor, so crevice exploration or "cruising" is more likely than surface-feeding. The small head and narrow neck are consistent with crevice feeding, but as discussed above, they might also be adaptations for a fast strike. The pachyostosis exhibited by *Pachyrhachis* is an adaptation for diving in shallow water, and this too argues against a surface dwelling existence.

Haas (1980a, p. 100) commented that in *Pachyrhachis* the "orbit was probably not deep and the eye had probably a rather dorsal position fitting for an animal living in the upper strata of the sea". This suggestion appears to be inconsistent with the above conclusions. However, as shown in Figure 5, the orbit in *Pachyrhachis* is circular, and normal in position. Haas may have meant that the orbit faced dorsally (rather than being located dorsally). However, the dorsal orientation of the orbit in *Pachyrhachis* is an artifact of preservation. The only articulated skull of *Pachyrhachis* (that of the holotype) is crushed dorsoventrally, and the cheek and face elements surrounding the orbit are splayed laterally. The skull therefore appears to be wide and flat. However, the width of the palate, as revealed by the well-preserved pterygoids, suggests that the skull was much narrower. When restored so that the width of the skull roof matches that of the palate, the face and cheek elements, and thus the orbit, face laterally rather than dorsally.

Snakes have long been thought to have evolved from small fossorial ancestors (e.g. Walls, 1940; Bellairs and Underwood, 1951; Underwood, 1967; Rieppel,

1988). Scolecophidians, *Anomochilus*, uropeltids, cylindrophids and aniliids – all small, fossorial forms – are held to be the most primitive living snakes. More advanced snakes are supposed to be secondarily surface-living. The most recent studies of snake phylogeny seem to support this view. The fossorial taxa just mentioned constitute the basal groups of snakes, and the most parsimonious interpretation is that burrowing is primitive in snakes (Cundall *et al.*, 1993; Heise *et al.*, 1995). Our conclusions, that the most primitive snake is the marine *Pachyrhachis*, and that the nearest relatives of snakes are the marine mosasauroids, are therefore unexpected. Neither *Pachyrhachis* nor mosasauroids could have been fossorial. At the very least, this means that fossoriality cannot be primitive in snakes, but rather must have evolved in snakes more derived than *Pachyrhachis*. It suggests that an aquatic origin for snakes, first proposed by Nopcsa (1908, 1923) but now largely ignored, merits serious consideration.

At present, there are two equally parsimonious scenarios (Figure 7A, B). (1) A marine habitat, primitive for pythonomorphs (the mosasaur-snake clade), is retained in mosasauroids and *Pachyrhachis*. More derived snakes reverted to life on land. (2) Pythonomorphs were primitively terrestrial, with convergent marine adaptations evolving separately in mosasauroids and *Pachyrhachis*.

The two hypotheses lead to different predictions for the characteristics of other Mesozoic pythonomorphs. Scenario (1) predicts that basal pythonomorphs found in the future, including snakes more primitive than *Pachyrhachis*, will be aquatic. Discovery of such fossils would imply that marine habits are most parsimoniously interpreted as primitive for pythonomorphs, and reversed (lost) in terrestrial snakes. This hypothesis appears to be supported by the fact that many poorly known taxa – dolichosaurs, *Pachyophis*, *Mesophis*, *Archaeophis*, and *Palaeophis* – which seem to be basal pythonomorphs or basal snakes, are indeed aquatic (Nopcsa, 1908; Scanlon, 1996). Further work on the morphology and relationships of these taxa is therefore required.

Scenario (2) is supported by the observation that while mosasauroids and *Pachyrhachis* are both marine, their swimming adaptations are very different. Mosasauroids are more lizard-like in general body form, with large limbs (flippers in advanced forms). They exhibit no skeletal modifications for buoyancy control, and presumably used hydrodynamic means activity to stay at depth (hydrofoils such as flippers and active swimming). *Pachyrhachis*, on the other hand, is elongate and almost limbless, and used its hydrostatic properties (pachyostosis) to maintain depth. However, such morphological differences may simply represent divergent modifications of an aquatic common ancestor. Scenario (2) would only be unequivocally supported by the discovery of primitive relatives of mosasauroids with terrestrial habits, or of snakes more primitive than *Pachyrhachis*.

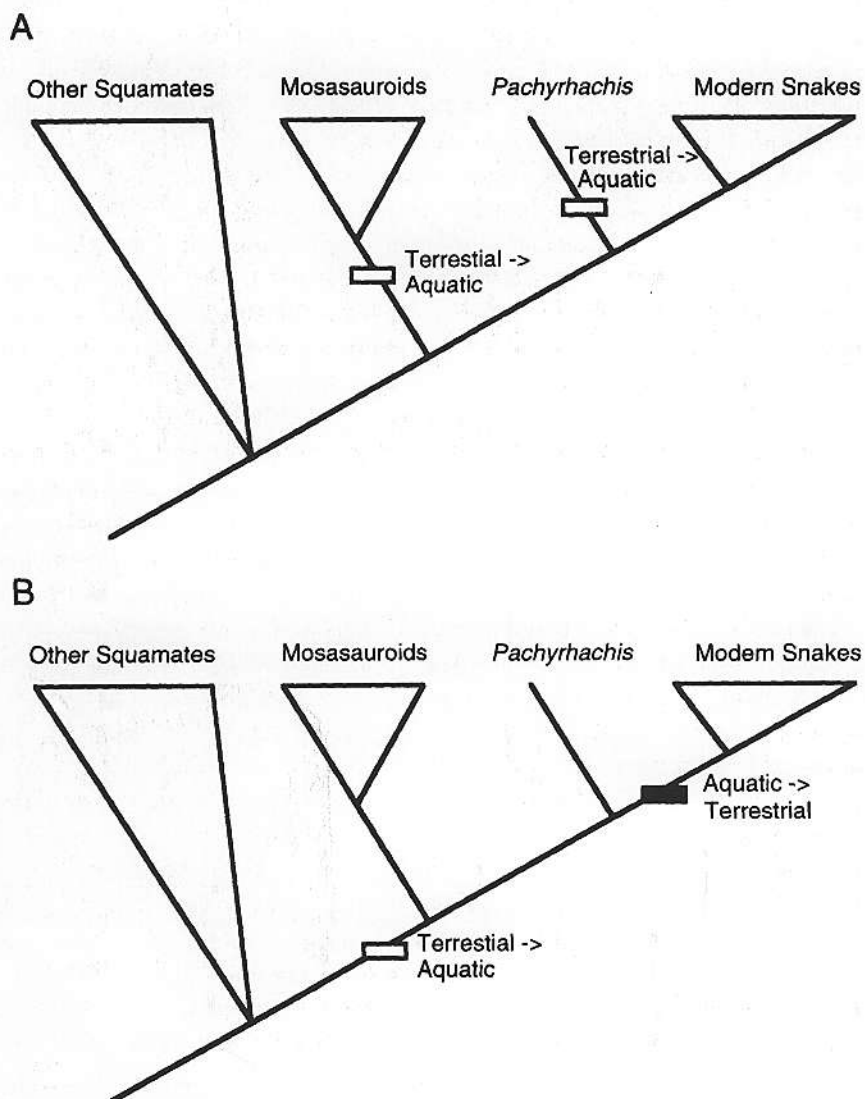


FIGURE 7 Two alternative scenarios consistent with recently proposed phylogenetic relationships among pythonomorphs. (A) Aquatic habits are convergent in mosasauroids and *Pachyrhachis*. (B) Aquatic habits are primitive for pythonomorphs, with modern snakes being secondarily terrestrial

The earliest known snake, from the Barremian of Spain (Rage and Richter, 1994), is poorly known. It could have been either terrestrial or aquatic in its habits, but in any case it was not fully marine as it comes from a continental, fresh-

water deposit. The same can be said of the slightly younger *Lapparentophis*. Although considered terrestrial by Hoffstetter (1960), this inference was based purely on negative evidence: absence of pachyostosis and simplified rib articulations that characterized its presumed close relative *Simoliophis* and comparable forms from the late Albian and early Cenomanian of Algeria (Cuny *et al.*, 1990). The first clearly marine snakes, *Pachyrhachis*, *Simoliophis* and perhaps *Pachyophis* and *Mesophis*, appear in the early Cenomanian (Cuny *et al.*, 1990; Caldwell and Lee, 1997). *Pouitella* from the early to middle Cenomanian of France occurs in marine sediments but its vertebrae resemble those of terrestrial snakes (Rage, 1988). A diverse continental snake fauna from the Cenomanian of Sudan (Werner and Rage, 1994) represents the earliest appearances of several lineages including both terrestrial (Madtsoiidae and ?Aniliidae) and freshwater aquatic (?Nigerophiidae and Russellophiidae) forms.

Thus, the present evidence for terrestrial snakes older than *Pachyrhachis* is subject to reasonable doubt. Furthermore, the phylogenetic relationships of these early snakes are uncertain. Terrestrial snakes in the Barremian would not be problematic for scenario (1) if they turned out to be less basal (less "primitive") than the aquatic *Pachyrhachis*, despite their early stratigraphic occurrence. Cope (1869), who supported a mosasauroid-snake relationship, nonetheless favoured scenario (2). He suggested that "terrestrial representatives (of Pythonomorpha) now unknown to us, inhabited the forests and swamps of the Mesozoic continents". At present, however, few known taxa appear to be likely candidates for this role.

Acknowledgements

We thank K. Kardong, J.-C. Rage, O. Rieppel, B. Moon, G. Underwood, and G. Bell for enthusiastic discussion. M. Lee and M. Caldwell are particularly indebted to E. Chernov and colleagues at the Hebrew University, Jerusalem for permission to restudy *Pachyrhachis*, and help and hospitality while in Israel. J. Scanlon, M. Lee and R. Shine are supported by the Australian Research Council, and M. Caldwell by the Natural Sciences and Engineering Research Council of Canada.

References

- Alexander, R.M. (1990) Size, speed and bouyancy adaptations in aquatic animals. *American Zoologist*, **30**, 189–196.
- Arkin, Y., Braun, M. and Starinsky, K. (1965) Type sections of Cretaceous formations in the Jerusalem-Bet Shemesh area. *Geological Survey of Israel. Stratigraphic Sections*, **1**, 1–42.
- Barthel, K.W., Swinburne, N.H.M. and Conway Morris, S. (1990) *Solnhofen: A Study in Mesozoic Palaeontology*. Cambridge: Cambridge University Press.
- Begin, Z.B. (1975) The geology of the Jericho sheet. *Geological Survey of Israel. Bulletin*, **67**, 1–35.

- Behrensmeyer, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, H.-D. and Wing, S.L. (1992) *Terrestrial Ecosystems Through Time: Evolutionary Paleocology of Terrestrial Plants and Animals*. Chicago: University of Chicago Press.
- Bein, A. (1971) Rudistid reef complexes (Albian to Cenomanian) in the Carmel and the Coastal Plain, Israel. *Geological Survey of Israel, Report*, **OD/2/71**, 1-86.
- Bellairs, A.d'A. and Underwood, G. (1951) The origin of snakes. *Biological Reviews*, **26**, 193-237.
- Bergey, M. and Baier, H. (1987) Lung mechanical properties in the West Indian manatee (*Trichechus manatus*). *Respiratory Physiology*, **68**, 63-75.
- Boltt, R. E. and Ewer, R. F. (1964) The functional anatomy of the head of the puff adder, *Bitis arietans* (Merr.). *Journal of Morphology*, **114**, 83-106.
- Braun, M. (1970) Facies changes in the Judea Group in Judea and Samaria. In *Stratigraphic Problems in the Judea Group.*, pp. 29-35. Annual Meeting, Israel Academy of Sciences and Humanities, Jerusalem.
- Buffr nil, V. de and Mazin, J.-M. (1989) Bone histology of *Claudiosaurus germaini* (Reptilia Claudiosauridae) and the problem of pachyostosis in aquatic tetrapods. *Historical Biology*, **2**, 311-322.
- Buffr nil, V. D. and Rage, J.-C. (1993) La "pachyostose" vert brale de *Simoliophis* (Reptilia, Squamata): donn es comparatives et consid rations fonctionelles. *Annales de Pal ontologie (Vert bres-Invert bres)*, **79**, 315-335.
- Caldwell, M. W. (1998) Squamate phylogeny and the affinities of snakes. *Zoological Journal of the Linnean Society* in press.
- Caldwell, M. W., Carroll, R. L. and Kaiser, H. (1995) The pectoral girdle and forelimb of *Carsosaurus marchesetti* (Aigialosauridae), with a preliminary phylogenetic analysis of mosasauroids and varanoids. *Journal of Vertebrate Paleontology*, **15**, 516-531.
- Caldwell, M. W. and Lee, M. S. Y. (1997) A snake with legs from the marine Cretaceous of the Middle East. *Nature*, **386**, 705-709.
- Carroll, R. L. (1988) *Vertebrate Paleontology and Evolution*. New York: W. H. Freeman.
- Carroll, R. L. and DeBraga, M. (1992) Aigialosaurs: mid-Cretaceous varanoid lizards. *Journal of Vertebrate Paleontology*, **12**, 66-86.
- Chalifa, Y. (1985) *Saurorhamphus judeaensis* (Salmoniformes: Enchodontidae), a new longirostrine fish from the Cretaceous (Cenomanian) of Ein Jabrud, near Jerusalem. *Journal of Vertebrate Paleontology*, **5**, 181-193.
- Chalifa, Y. (1989a) New species of *Enchodus* (Pisces: Enchodontoidei), from the Lower Cenomanian of Ein-Yabrud, Israel. *Journal of Paleontology*, **63**, 356-364.
- Chalifa, Y. (1989b) Two new species of longirostrine fishes from the Early Cenomanian (Late Cretaceous) of Ein-Yabrud, Israel, with comments on the phylogeny of the Dercetidae. *Journal of Vertebrate Paleontology*, **9**, 314-328.
- Chalifa, Y. and Tchernov, E. (1982) *Pachyamia latimaxillaris*, new genus and species (Actinopterygii: Amiidae), from the Cenomanian of Jerusalem. *Journal of Vertebrate Paleontology*, **2**, 269-285.
- Cogger, H.G. (1992) *Reptiles and Amphibians of Australia*. Sydney: Reed.
- Cope, E. D. (1869) On the reptilian orders, Pythonomorpha and Streptosauria. *Boston Society of Natural History, Proceedings*, **12**, 250-266.
- Cundall, D. (1995) Feeding behaviour in *Cylindrophis* and its bearing on the evolution of alethinophidian snakes. *Journal of Zoology*, **237**: 353-376.
- Cundall, D., Wallach, V. and Rossman, D. A. (1993) The systematic relationships of the snake genus *Anomochilus*. *Zoological Journal of the Linnean Society*, **109**, 275-299.
- Cuny, G., Jaeger, J.-J., Mahboubi, M. and Rage, J.-C. (1990) Les plus anciens Serpents (Reptilia, Squamata) connus. Mise au point sur l' ge g ologique des Serpents de la partie Moyenne du Cr tac . *Comptes Rendus de l'Acad mie des Sciences, Paris*, **311**, 1267-1272.
- Domning, D. and Buffr nil, V. de (1991) Hydrostasis in the Sirenia. *Marine Mammal Science*, **7**, 331-368.
- Follmi, K.B. (1989) *Evolution of the Mid-Cretaceous Triad: Platform Carbonates, Phosphatic Sediments and Pelagic Carbonates*. Berlin: Springer-Verlag.
- Gasc, J.-P. (1974) L'interpr tation fonctionelle de l'appareil musculo-squelettique de l'axe vert bral chez les serpents (Reptilia). *M moires Mus um national d'Histoire naturelle, Series A*, **83**, 1-182.

- Gayet, M. (1980) Recherches sur l'ichthyofaune Cenomanienne des monts de Judée: "Les Acanthopterygiens". *Annales de Paléontologie (Vertebres)*, **66**, 75–128.
- Gayet, M. (1982) Cypriniforme ou Gonorhynchiforme? *Ramallichthys* nouveau genre du Cenomanien inférieur de Ramallah (Monts de Judée). *Comptes Rendus hebdomadaires des Séances de l'Académie des Sciences. Paris. D*, **295**, 1037–1040.
- Gayet, M. (1985) Gonorhynchiforme nouveau du Cenomanien inférieur marin de Ramallah (Monts de Judée): *Judeichthys haasi* nov. gen. nov. sp. (Teleostei, Ostariophysi, Judeichthyidae nov. fam.). *Bulletin du Muséum national d'Histoire Naturelle. Paris. Ser. 4*, **1**, 65–85.
- Gingerich, P. D., Smith, B. H. and Simons, E. L. (1990) Hind limbs of Eocene *Basilosaurus*: evidence of feet in whales. *Science*, **249**, 154–157.
- Greene, H.W. (1983) Dietary correlates of the origin and radiation of snakes. *American Zoologist*, **23**, 431–441.
- Haas, G. (1978a) A Cretaceous pleurodire turtle from the surroundings of Jerusalem. *Israeli Journal of Zoology*, **27**, 20–33.
- Haas, G. (1978b) A new turtle of the genus *Podocnemis* from the Lower Cenomanian of Ein Yabrud. *Israeli Journal of Zoology*, **27**, 169–175.
- Haas, G. (1979) On a snakelike reptile from the Lower Cenomanian of Ein Jabrud, near Jerusalem. *Bulletin du Muséum national d'Histoire Naturelle, Paris, Series 4*, **1**, 51–64.
- Haas, G. (1980a) *Pachyrhachis problematicus* Haas, snake-like reptile from the Lower Cenomanian: ventral view of skull. *Bulletin du Muséum national d'Histoire Naturelle, Paris, Series 4*, **1**, 87–104.
- Haas, G. (1980b) Remarks on a new ophiomorph reptile from the lower Cenomanian of Ein Jabrud, Israel. In *Aspects of Vertebrate History*, edited by L. L. Jacobs, pp. 177–192. Flagstaff: University of Northern Arizona Press.
- Heatwole, H. (1987) *Sea Snakes*. Sydney: New South Wales University Press.
- Heatwole, H. and Cogger, H. G. (1994). Sea snakes of Australia. In *Sea snake toxinology*, edited by P. Gopalakrishnakone. Singapore: Singapore University Press.
- Heise, P. J., Maxson, L. R., Dowling, H. G. and Hedges, S. B. (1995) Higher-level snake phylogeny inferred from mitochondrial DNA sequences of 12S rRNA and 16S rRNA genes. *Molecular Biology and Evolution*, **12**, 259–265.
- Hoffstetter, R. (1960) Un serpent terrestre dans le Crétacé inférieur du Sahara. *Bulletin de la Société géologique de France, 7e série*, **1**, 897–902.
- Hoffstetter, R. and Gasc, J. P. (1969) Vertebrae and ribs of modern reptiles. In *Biology of the Reptilia*, **1**, edited by C. Gans, pp. 201–310. London: Academic Press.
- Hückel, U. (1970) Die Fischschiefer von Haqwl und Hjoula in der Oberkreide des Libanon. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **135**, 113–149.
- Hückel, U. (1974) Vergleich des Mineralbestandes der Plattenkalke Solnhofens und des Libanon mit anderen Kalken. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **145**, 153–182.
- Jurkovsek, B., Toman, M., Ogorelec, B., Sribar, L., Drobne, K., and Poljak, M. (1996) *Geological Map of the Southern Part of the Trieste-Komen Plateau*. Ljubljana, Slovenia: Institut za Geologijo, Geotehniko in Geofiska.
- Kaiser, H. E. (1966) Functional anatomy of breathing and balance in seacows (Sirenia). *Anatomical Record*, **55**, 246.
- Kardong, K. V. (1977) Kinesis of the jaw apparatus during swallowing in the cottonmouth snake, *Agkistrodon piscivorus*. *Copeia*, **1977**, 338–348.
- Lee, M. S. Y. (1997) The phylogeny of varanoid lizards and the affinities of snakes. *Philosophical Transactions of the Royal Society of London, B, Biological Sciences*, **352**, 53–91.
- Lee, M. S. Y. (1998) Convergent evolution and character correlation in limbless squamates. *Biological Journal of the Linnean Society*. in press.
- Lee, M. S. Y. and Caldwell, M. W. (1998) Anatomy and relationships of *Pachyrhachis*, a primitive snake with hindlimbs. *Philosophical Transactions of the Royal Society of London, B, Biological Sciences*, **353**, 1521–1552.
- Lingham-Soliar, T. (1991) Locomotion in mosasaurs. *Modern Geology*, **16**, 229–248.
- Massare, J. A. (1994) Swimming capabilities of Mesozoic marine reptiles: a review. In *Mechanics and Physiology of Animal Swimming*, edited by L. Maddock, Q. Bone and J. M. V. Rayner, pp. 133–149. Cambridge: Cambridge University Press.

- McDowell, S. B. (1972) The genera of sea-snakes of the *Hydrophis* group (Serpentes: Elaphidae). *Transactions of the Zoological Society of London*, **32**, 189–247.
- Meyer, C. A. (1988) Subtidal lagoon communities of a Late Jurassic turtle-deposit from Northern Switzerland. *Museo Regio Scienze Naturli, Torino*, 107–121.
- Meyer, C.A. (1991) Burial experiments with marine turtle carcasses and their paleoecological significance. *Palaios*, **6**, 89–96.
- Meyer, R. and Schmidt-Kaler, H. (1984) *Erdgeschichte sichtbar gemacht. Ein geologischer Führer durch die Altmühlalb*, Munich: Bayerische geologische Landesamt München.
- Mosauer, W. (1935) The myology of the trunk region of snakes and its significance for ophidian taxonomy and phylogeny. *University of California Publications. Biological Sciences*, **1**, 81–120.
- Nopcsa, F. (1908) Zur Kenntnis der fossilen Eidechsen. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients*, **21**, 33–62.
- Nopcsa, F. (1923) *Eidolosaurus* und *Pachyophis*. Zwei neue Neocom-Reptilien. *Palaeontographica*, **65**, 99–154.
- Nursall, R. J. (1996) Distribution and ecology of pycnodont fishes. In *Mesozoic Fishes: Systematics and Paleoecology*, edited by G. Arratia, and G. Viohl, pp. 115–124. München: Verlag Dr. Friedrich Pfeil.
- Odell, D. K., Forrester, D. J. and 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*, edited by R. L. Brownell and K. S. Ralls, Tallahassee. Florida: Florida Department of Natural Resources.
- Povel, D., Kiene, T. and Kardong, K. V. (1997) The underwater strike of the tentacled snake, *Erpeton tentaculum*. *Abstracts Fifth International Congress of Vertebrate Morphology. Journal of Morphology*, **232**, 309.
- Pritchard, P. C. H. and Trebbau, P. (1984) *The Turtles of Venezuela*. Oxford, Ohio (Miami University): Society for the Study of Amphibians and Reptiles.
- Rage, J.-C. (1984) *Serpentes. Handbuch de Paläoherpetologie, Teil II*, Stuttgart: Gustav Fischer Verlag.
- Rage, J.-C. (1988) Un serpent primitif (Reptilia, Squamata) dans le Cenomanien (base du Crétacé supérieur). *Comptes Rendus de l'Académie des Sciences, Paris*, **307**, 1027–1032.
- Rage, J.-C. (1997) Phylogeny and origin of snakes. In *Herpetology '97: Abstracts of the Third World Congress of Herpetology*, edited by Z. Roček and S. Hart, p. 167. Prague: Durabo Celakovice / Ministry of Environment of the Czech Republic.
- Rage, J.-C. and Richter, A. (1994) A snake from the lower Cretaceous (Barremian) of Spain: The oldest known snake. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, **1994** (9) 561–565.
- Rieppel, O. (1980) The evolution of the ophidian feeding system. *Zoologische Jahrbuch. Anatomie* **103**: 551–564.
- Rieppel, O. (1988) A review of the origin of snakes. *Evolutionary Biology*, **23**, 37–130.
- Romer, A.S. (1966) *Vertebrate Paleontology*. Chicago: University of Chicago Press.
- Saint-Marc, P. (1981) Lebanon. In *Aspects of Mid-Cretaceous Regional Geology*, edited by R. A. Reymont, and P. Bengston, pp. 103–131. London: Academic Press.
- Scanlon, J.D. (1996) *Studies in the Palaeontology and Systematics of Australian Snakes*. Ph.D thesis, University of New South Wales.
- Shachnai, E. (1969) *Geology Map. Ramallah*. Jerusalem: Geological Survey of Israel.
- Smith, A. G., Smith, D. G. and Funnell, B. M. (1994) *Atlas of Mesozoic and Cenozoic Coastlines*. Cambridge: Cambridge University Press.
- Tucker, M. E. and Wright, V. P. (1990) *Carbonate Sedimentology*. Oxford: Blackwell Scientific Publications.
- Underwood, G. (1967) *A Contribution to the Classification of Snakes*. London: British Museum (Natural History).
- Voris, H. K. (1972) The role of sea snakes (Hydrophiidae) in the trophic structure of coastal ocean communities. *Journal of the Marine Biological Association of India*, **14**, 429–442.
- Wall, W. P. (1983) The correlation between high limb bone density and aquatic habits in recent mammals. *Journal of Paleontology*, **57**, 197–207.
- Wallach, V. (1984) A new name for *Ophiomorphus colberti* Haas, 1980. *Journal of Herpetology*, **18**, 329.
- Walls, G.L. (1940) Ophthalmological implications for the early history of snakes. *Copeia*, **1940**, 1–8.

- Webb, P. W. (1982) Locomotor patterns in the evolution of actinopterygian fishes. *American Zoologist*, **22**, 329–342.
- Webb, J. K. and Shine, R. (1993) Prey-size selection, gape limitation and predator vulnerability in Australian blindsnakes (Typhlopidae). *Animal Behaviour*, **45**, 1117–1126.
- Werner, C. and Rage, J.-C. (1994) Mid-Cretaceous snakes from Sudan. A preliminary report on an unexpectedly diverse snake fauna. *Comptes Rendus de l'Académie des Sciences. Paris*, **319**, 247–252.
- Wilson, M. V. H. (1995) Paleocene amiid fish from Jabal Umm Himar, Kingdom of Saudi Arabia. *United States Geological Survey Bulletin*, **2093-C**, 1–5.
- Wood, R. C. (1974) The systematics, ecology, evolution, and zoogeography of African turtles. *National Geographic Society Research Reports*, **1967**, 301–306.
- Zaher, H. (1998) The phylogenetic position of *Pachyrachis* within snakes (Squamata, Lepidosauria). *Journal of Vertebrate Paleontology*, **18**, 1–3.