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Anatomy and relationships of *Pachyrhachis problematicus*, a primitive snake with hindlimbs

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CONTENTS

The anatomy of *Pachyrhachis problematicus*, an elongate, limb-reduced squamate from the Upper Cretaceous of Israel, is described and evaluated in detail. Previously considered a snake-like ‘lizard’ of uncertain affinities, it is here shown to be the most primitive snake, and the sister-group to all other snakes. *Pachyrhachis* exhibits numerous derived characters uniting it with modern snakes (scolecophidians and alethinophidians): e.g. mobile premaxilla–maxilla articulation, braincase enclosed by frontals and parietals, sagittal parietal crest, absence of tympanic recess, single postdentary bone, over 140 presacral vertebrae, and complete loss of shoulder girdle and forelimb. However, it is more primitive than all modern snakes in retaining some strikingly primitive (lizard-like) features: presence of a jugal, squamosal, normal sacral attachment, and well-developed hindlimb composed of femur, tibia, fibula, and tarsals. *Pachyrhachis* provides additional support for the hypothesis that snakes are most closely related to Cretaceous marine lizards (mosasauroids). Almost all of the derived characters proposed to unite snakes and mosasauroids are highly developed in *Pachyrhachis*: the mobile mandibular symphysis, intramandibular joint, long and

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recurved pterygoid teeth, quadrate suspended by the supratemporal, loosely united pelvic elements (ilium, ischium, and pubis), and separate astragalus and calcaneum.

Keywords: squamates; Cretaceous; osteology; mosasauroids; snakes; lizards

1. INTRODUCTION

Snakes exhibit highly distinctive cranial and postcranial specializations, and are one of the most diverse and important groups of living vertebrates. As a result, their affinities with other squamates—lizards, amphisbaenians and dibamids—have been the subject of numerous investigations. Most of these studies, as emphasized in recent reviews (Rage 1987; Rieppel 1988), were unable to resolve conclusively the position of snakes within Squamata. The intractability of the problem was attributed to high levels of convergent evolution among the numerous lineages of elongate, limb-reduced squamates. The origin and relationship of snakes therefore remains one of the main unsolved problems in tetrapod evolution.

Recently, Caldwell (1998) reanalysed the phylogeny of the entire Squamata, revising and extending the data set in Estes *et al.* (1988) by adding several important fossil taxa. Lee (1997*a*) and Scanlon (1996) analysed relationships within a more restricted group of squamates (Platynota), supplementing the data set of Pregill *et al.* (1986) through addition of important fossil taxa and new characters. All three studies found strong evidence uniting snakes with mosasauroids, a group of Cretaceous marine lizards. Until these studies, no rigorous phylogenetic analysis of squamate interrelationships had simultaneously considered both mosasauroids and snakes. As a result, previous studies failed to identify the snake–mosasauroid association and the numerous derived characters supporting this arrangement.

Despite these studies, many aspects of the problem of snake relationships remain contentious. In particular, whereas there was agreement on the mosasauroid–snake grouping (Pythonomorpha), there was disagreement on the position of this clade within Squamata as a whole. Caldwell (1998) found that the mosasauroid–snake clade occupied a rather basal position within Squamata, as the sister-group to scleroglossans (non-iguanian squamates), while Lee (1997*a*) and Scanlon (1996) both placed Pythonomorpha deep within anguimorph scleroglossans, as relatives of Varanus and *Lanthanotus* (see figure 15).

Another unresolved problem is the phylogenetic position of some enigmatic squamate taxa that have not been included in any recent cladistic studies because they were too poorly known. Two such taxa are *Pachyrhachis* and *Estesius* (formerly '*Ophiomorphus*': see paper by Wallach (1984)); long-bodied marine squamates from the Cretaceous of the disputed West Bank, between Israel and Jordan. These animals are not only very similar, but were discovered in the same locality at almost the same time. Both are known from well-preserved, largely complete, articulated skeletons, and were described as showing a curious mixture of varanoid and ophidian characters (Haas 1979, 1980*a*,*b*). However, the original descriptions were brief, and written when the specimens were only partly prepared. In particular, the ventral surface of the skull of *Estesius* was not prepared, while part of the dorsal surface was covered by ribs. Interpretation of the crushed skull of *Pachyrhachis*, and the disarticulated skull of *Estesius*, was therefore extremely difficult.

Haas (1980*b*) was uncertain whether the two animals were related to snakes—and thus intermediate between varanoid lizards and snakes—or were only convergently snake-like. Haas also concluded that *Pachyrhachis* and *Estesius* were distinct taxa, and described numerous differences between the two fossils. In view of the potential importance of these animals to clarify the affinities and origin of snakes it is surprising that they have not been restudied since the original descriptions were published, and their affinities remain enigmatic (Rage 1987; Carroll 1988; Rieppel 1988).

Here we present a detailed description and reinterpretation of these two fossils. Further preparation has revealed much additional information about the morphology of the skulls of these animals. In particular, preparation of the ventral surface of the skull of *Estesius* has revealed much more of the skull, and demonstrated that many of the elements on this animal were misidentified in the original description.

Our restudy of *Pachyrhachis* and *Estesius* indicates that they belong to the same species and are the most primitive known snakes (Caldwell & Lee 1997). The two specimens possess a striking combination of derived snake-like features (e.g. highly kinetic skull, greatly elongated body) along with primitive lizard-like features (e.g. functional pelvis and hindlimbs). This interpretation of *Pachyrhachis* (including *Estesius*) as the sister-taxon of all other snakes clarifies the lizard–snake transition and the origin of many of the most distinctive specializations of snakes.

2. LOCALITY AND STRATIGRAPHY

Both of the known specimens of *Pachyrhachis problematicus* were found in the limestone quarries of Ein Jabrud, near the West Bank town of Ramallah, 20 km north of Jerusalem, Israel. Quarrying activities at Ein Jabrud have exposed a sequence of carbonate rocks that have been attributed to the Bet-Meir Formation (Lower Cenomanian; Early Upper Cretaceous). The fossil-bearing horizon is composed of finely laminated, platey carbonates that weather to a pink to reddish-orange colour. Few primary sedimentary structures were noted while examining slabs bearing *Pachyrhachis* or other vertebrates.

Stratigraphic correlation between the Ein Jabrud section, and the type section of the Bet-Meir Formation at Nahal-Kesalon, 20 km east of Jerusalem, has not yet been completed (Chalifa & Tchernov 1982). However, based on a review of various elements of the fish faunas, Chalifa & Tchernov (1982) concluded that exposures at Ein Jabrud are lowermost Cenomanian. Comparisons with other Cenomanian rocks deposited in the late Mesozoic neo-Tethys suggest that the Ein Jabrud section is slightly older than similar deposits in Lebanon (Chalifa & Tchernov 1982), Comen, Slovenia, and the English Chalk (Patterson 1967).

3. ASSOCIATED FAUNA AND DEPOSITIONAL ENVIRONMENT

The Cenomanian deposits at Ein Jabrud contain a rich vertebrate fauna. Most fossils, including the two specimens of *Pachyrhachis*, are found largely undisturbed and articulated. Among the actinopterygian fishes, pycnodonts are particularly well-represented. Among the elasmobranchs, skates and rays are the most common components (Haas 1979). Both pycnodonts and skates are usually considered shallow-water forms. The remains of lizards (Haas 1980*b*) have so far not been described; our examination of this material indicates that it consists of fragmentary remains of mosasauroids, a group of marine squamates. Terrestrial forms are not represented among the lizard fauna. Turtles are represented by *Podocnemis*, a pelomedusid (Haas 1978*a*,*b*).

Previous interpretations have suggested that the Ein Jabrud platey limestones were deposited in quite anoxic marine environments such as a shallow marine bay (Chalifa & Tchernov 1982). Bays however are characterized by coastline topography and there is little evidence to suggest the proximity of a palaeoshoreline to the Ein Jabrud locality.

Detailed sedimentological descriptions and interpretations of the Ein Jabrud locality are not yet available. Hence, alternative evidence must be used to provide a robust interpretation of the depositional environment. Our new interpretation is based on personal observation of the platey carbonates containing the Ein Jabrud Fauna, sedimentological studies of nearby localities of the same age and environment (Lebanon), potentially similar environments of a different age (Solnhofen), alternative interpretations of the habits of pelomedusid turtles, and turtle taphonomy.

The platey carbonates containing fossils from Ein Jabrud lack primary sedimentary structures such as wavy laminations or ripple marks; all observable structures were fine-bedding structures on a laminar scale. Such structures, and the absence of wavy laminations or ripple marks, indicates that deposition was taking place below storm wave base, or else was occurring in unusually placid waters.

No bioturbation structures were noted. Their absence would suggest anoxic conditions within the carbonate muds i.e. infrequent exchange with larger, more highly oxygenated, bodies of water. Anaerobic bacteria would have dominated within deeper sediments effectively blocking the decomposition of organic remains (leading to good preservation) and excluding the usual infaunal component (thus limiting bioturbation).

These features are all characteristic of lagoonal depositional environments built-up on epeiric carbonate platforms (Tucker & Wright 1990). The lagoons form as small, isolated basins between reef mounds, similar to the Upper Jurassic patch reef and inter-reef lagoons characterizing the Solnhofen Plattenkalke (Meyer & Schmidt-Kaler 1984). Throughout the Albian and Cenomanian, the margins of the European and African Tethys were characterized by epeiric carbonate platforms supporting extensive reef complexes formed by rudist bivalves and scleractinian corals (Bein 1971; Saint-Marc 1981; Jurkovsek *et al.* 1996). The trend throughout the Cenomanian Tethys, and in fact globally, initiated in at least the Albian, was an upward-deepening cycle of transgressions, spurred by increased global tectonism (Follmi 1989). The platforms were slowly drowned as water deepened. The mid-Cretaceous carbonate rocks in Israel and Lebanon record this upward-deepening cycle.

The Lower to Middle Cenomanian platey limestones of Hakel, Lebanon (just north of Beirut), famous for spectacular fossil fishes, have already been compared to the platey Jurassic limestones of Solnhofen, Germany (Hückel 1970, 1974). This comparison was based on microfabrics and geochemistry, and concluded that the depositional environments producing the platey limestones of Lebanon were similar to those of Solnhofen. Therefore, in association with similarities in regional geology and sedimentology (epeiric carbonate platforms and reef mounds), the less intensively studied deposits of Ein Jabrud may also have been deposited under similar conditions to those in Lebanon and Solnhofen.

The Ein Jabrud pelomedusid turtles have been interpreted as indicating the presence of a nearby river (Chalifa & Tchernov 1982), based on the fact that extant forms live in freshwater environments (Haas 1978*a*,*b*; Pritchard & Trebbau 1984). Such a fluvial source would introduce a clastic element that is not observed in the fossil-bearing horizon. An alternative interpretation is that there was no river, and that the turtles were marine. The fossil record of pelomedusids indicates that members of this group may well have evolved adaptations to marine environments (Wood 1974; Pritchard & Trebbau 1984). A number of extinct forms are found in marine rocks, while others show cranial adaptations for molluscivory. One living African form still lives in landlocked saline waters (Wood 1974).

Finally, recent taphonomic investigations suggest that it would have been very unlikely for the articulated specimens described by Haas (1978*a*,*b*) to have washed in from some remote fluvial source, or from a beach (Meyer 1988, 1991). Meyer (1991) examined the taphonomy of turtles in marine intertidal zones, and in the deeper water of a subtidal lagoon with a rich infauna and daily exchange of oxygenated waters through tidal channels. In both environments the turtles' skeletons were quickly disarticulated. In the intertidal zone, detritivores and wave action swiftly disarticulated the skeleton. In the deeper water, detritivores and decomposition completely disarticulated the second skeleton.

Thus, most reasonable interpretation is that the sediments preserving the Ein Jabrud fauna were deposited in an isolated lagoonal environment. This lagoon was nested within the reef mound–lagoonal complexes of the slowly drowning, isolated, epeiric platform located in the south-east Tethys Seaway. This model is very similar to that proposed for the lagoonal deposits of Solnhofen (Meyer & Schmidt-Kaler 1984). The pelomedusids of Ein Jabrud may well have been marine turtles living within the same reef communities as *Pachyrhachis*.

4. SYSTEMATIC PALAEONTOLOGY

REPTILIA Linnaeus 1758
SQUAMATA Oppel 1811
OPHIDIA Brongniart 1800
Pachyrhachis problematicus Haas 1979

(The monospecific genus '*Pachyrhachis*' is redundant with *Pachyrhachis problematicus*, and, being currently uninformative, has not been formally recognized (see § 4f).)

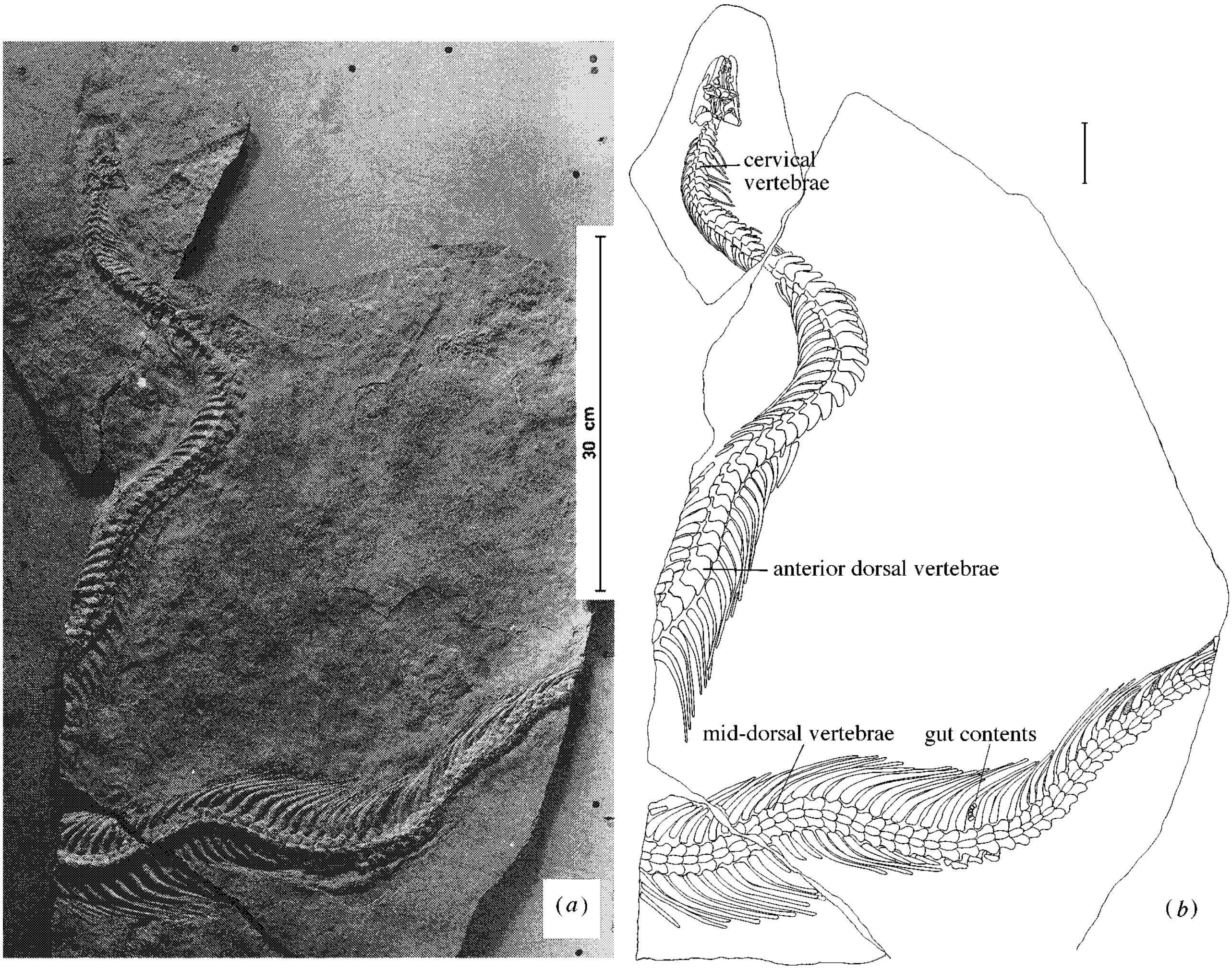


Figure 1. *Pachyrhachis problematicus*. (*a*) Dorsal view of slabs containing holotype (HUJ-PAL 3659), as photographed during the late 1970s. (*b*) Drawing of specimen in its current condition. Since *a* was taken, the dorsal surface of the skull and cervical vertebrae has been embedded in resin, making photography of the specimen impossible. However, as can be seen by comparing *a* and *b*, the specimen was already almost fully prepared when *a* was taken: further preparation has consisted mainly of exposing some more ribs. Also, parts of the slab have been removed but other parts have been re-united. (*a*) Scale bar: 30 cm. (*b*) Scale bar: 5 cm.

(a) ***Synonymy***

Pachyrhachis problematicus (Haas 1979)
Ophiomorphus colberti (Haas 1980*b*)
Estesius colberti (Wallach 1984)

(b) ***Diagnosis***

A long-bodied marine squamate. The head is small, and the cervical region narrow. The shoulder girdle and forelimbs are absent, a small pelvis and hindlimbs are present. It exhibits the following autapomorphies not found in other squamates: (i) the frontal is extremely long and narrow; (ii) the quadrate is sheet-like, being greatly expanded anteroposteriorly; (iii) there is a large rectangular coronoid process; (iv) the coronoid bone has an extremely long anterior flange which extends horizontally along the medial surface of the dentary; (v) the splenial–angular joint is located very far anteriorly, approximately mid-way between the symphysis and the coronoid process; and (vi) the middle trunk vertebrae and ribs are pachyostotic.

(c) ***Type locality and horizon***

Quarries at Ein Jabrud, near the West Bank town of Ramallah. Upper Cretaceous (Lower Cenomanian).

(d) ***Holotype***

Hebrew University of Jerusalem, Palaeontology Collections (HUJ-PAL) 3659 (figures 1, 3 and 4), preserved on three contiguous limestone slabs. Slab 1 contains the articulated skull elements and 22 articulated anterior presacral vertebrae and ribs. The skull is complete but dorsoventrally compressed. Slab 2, the largest slab, has two series of articulated vertebrae. The more anterior portion is contiguous with the block containing the skull and is composed of 36 presacral vertebrae and ribs, representing vertebrae 23 to 58. The more posterior series continues onto slab 3. It is an articulated series of 43 posterior dorsal vertebrae and ribs. In total, there are 101 vertebrae preserved, with a missing section in the mid-body region. The posteriormost dorsals, pelvis and hindlimb, and caudals are not preserved. Slab 1 (containing the skull) has been prepared on the dorsal and ventral surfaces; the dorsal surface has been embedded in clear resin. Slabs 2 and 3 have been prepared only on the dorsal surface.

(e) ***Referred specimen***

HUJ-PAL 3775 (figures 2, 5 and 6), holotype of *Ophiomorphus* (later *Estesius*) *colberti*. Single slab. Most elements

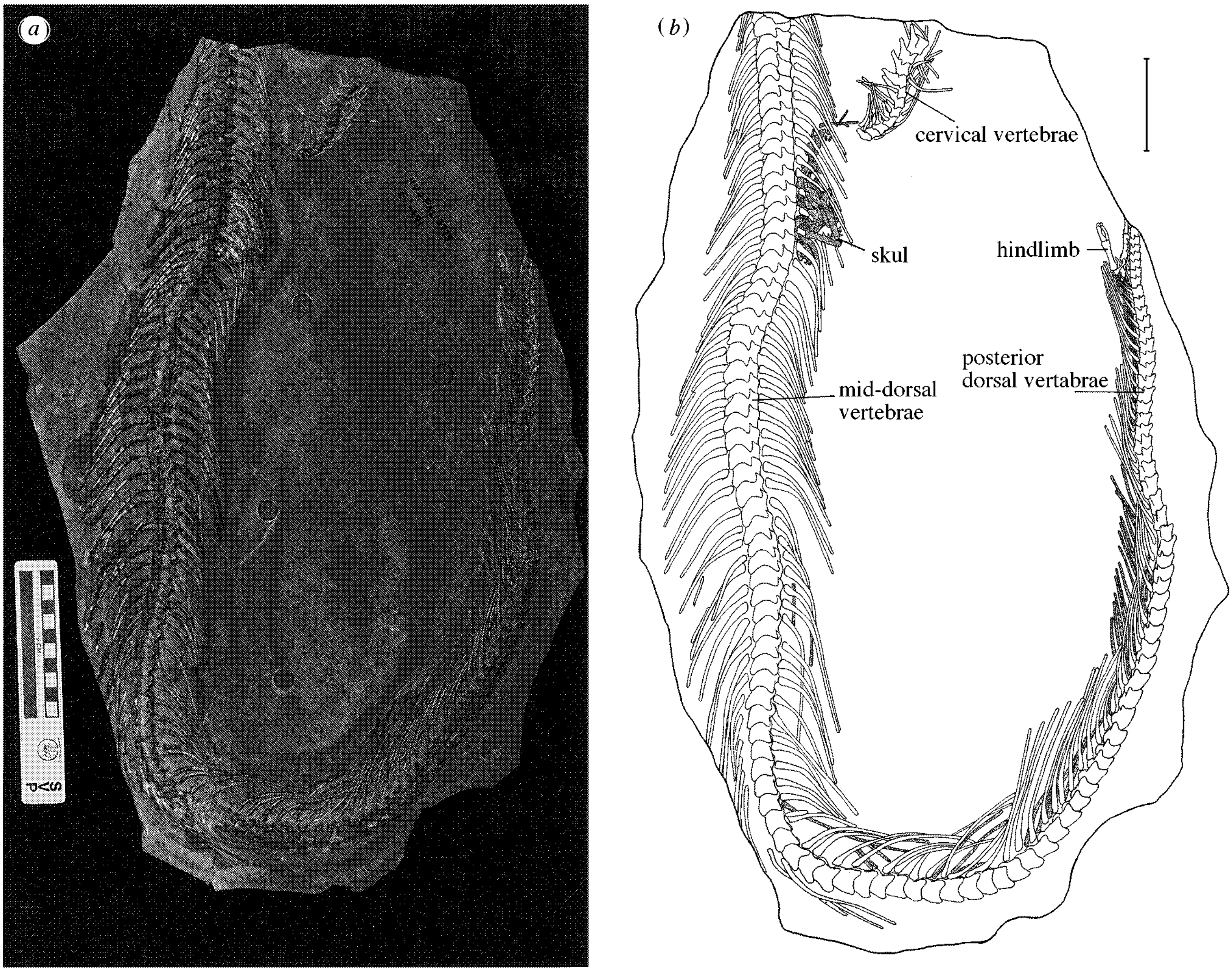
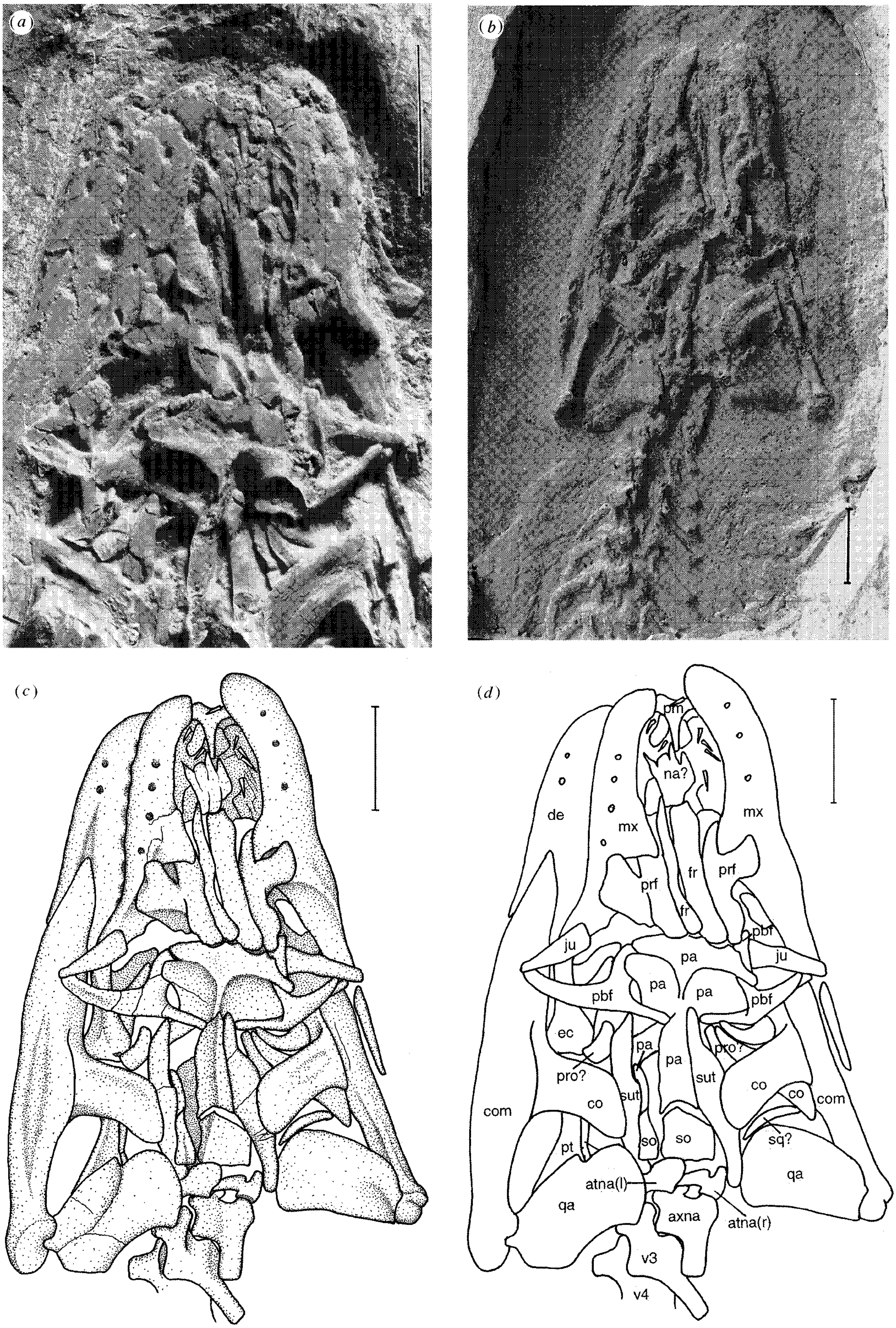


Figure 2. *Pachyrhachis problematicus*. (*a*) Photo and (*b*) drawing of dorsal view of slab containing referred specimen (HUJ-PAL 3775). Both are of the specimen in its current condition. (*a*) Scale bar: 10 cm. (*b*) Scale bar: 5 cm.

of the skull and lower jaw are preserved, but are disarticulated and crushed beneath the anterior ribs. A total of 131 vertebrae and associated ribs are preserved in three distinct regions: six disarticulated anteriormost presacral ('cervical') vertebrae, an articulated series of 11 anterior presacral ('cervical') vertebrae, and a final, main articulated series of 108 middle and posterior presacral ('dorsal') vertebrae and five anterior caudal vertebrae. The complete pelvis is preserved, along with the right and left femora, right tibia, right fibula, and right tarsal elements. The skull and anteriormost six vertebrae are preserved between and under the right ribs near the anterior end of the main series of vertebrae. The region of the skull has been prepared on both dorsal and ventral surfaces, the rest of the slab has been prepared only on the dorsal surface. Some previous workers (see, for example, Rage 1987; McDowell 1987; Rieppel 1988) have questioned whether the skull is part of the main animal or gut contents. However, both the skull and the postcranium are almost identical to corresponding parts of the holotype, and can thus be definitely associated.

(f) *Remarks*

As the following description demonstrates, the holotypes of *Pachyrhachis problematicus* (HUJ-PAL 3659) and *Estesius* (*Ophiomorphus*) *colberti* (HUJ-PAL 3775) do not exhibit any taxonomically significant differences, and can be united on the basis of many distinctive derived characters not found in any other squamates (including mosasauroids and snakes); these characters are listed in the previous diagnosis. Despite the fact that both specimens are known from fairly complete skeletons, we can find no significant differences apart from a slight size difference: the linear dimensions of *Pachyrhachis* are approximately 1.5 times those of *Estesius*. As discussed next, previously cited differences (Haas 1980*b*) are not valid. The postulated skull differences appear to be the result of misidentification of cranial elements in one or both specimens. Venom grooves were reported to be present on the teeth of *Pachyrhachis*, but not *Estesius*. However, grooves are absent from both specimens: instead both specimens possess labial and lingual carinae. Haas (1980*b*) claimed that *Estesius* differed from *Pachyrhachis* in lacking pachyostosis of the middle vertebrae. However, both specimens are pachyostotic in this region; the only difference is the degree of pachyostosis (greater in the larger individual, the holotype of *Pachyrhachis*). In other pachyostotic amniotes, the amount of pachyostosis increases with age and size. This occurs in mesosaurs (M. S. Y. Lee, personal observation), the diapsid *Claudiosaurus* (de Buffrénil & Mazin 1989), and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sirenians (Doming & de Buffrénil 1991). The only other postcranial difference mentioned (Haas 1980*b*) is taphonomic: the pelvis and hindlimb are absent in HUJ-PAL 3659 because the posterior dorsal, and caudal regions are not preserved. We therefore assign both taxa to the same species, and *Estesius* (= *Ophiomorphus*) *colberti* becomes the objective junior synonym of *Pachyrhachis problematicus*.

5. MORPHOLOGY OF *PACHYRHACHIS*

(a) *Cranium*

The skull of the holotype of *Pachyrhachis problematicus* is largely complete, and prepared on both dorsal and ventral surfaces (figures 3 and 4). All elements, including the lower jaws, are preserved in their approximately natural position. The dorsal and ventral surfaces of the snout region are poorly preserved, the rest of the cranium is well-preserved. However, dorsoventral crushing has caused some elements (maxillae, lower jaws, quadrates, pterygoids, and left palatine) to splay laterally.

In the referred specimen, disarticulated skull elements are scattered under the anterior dorsal ribs. Both sides of this area of the block have now been fully prepared (figures 5 and 6). In anteroposterior order, the main recognizable elements are: probable ectopterygoids, complete right lower jaw, quadrate, elements of the skull table (parietal, frontals, a possible supratemporal), complete left lower jaw, maxillae, and a probable palatine.

In the following description, the 'dorsal' surface of the referred specimen is the surface of the slab where the dorsal surface of the articulated postcranial skeleton is exposed, and the 'ventral' surface, the surface of the slab where the ventral surface of the postcranial skeleton is exposed. Thus, some of the disarticulated skull elements are actually exposed in ventral view on the 'dorsal' surface, and vice versa.

(i) *Skull roof and dermatocranium*

Premaxilla

The premaxilla is exposed in dorsal view on the holotype skull (see figures 3 and 7). It is a small, lightly built, triradiate element. The anterior margin is slightly concave. The posterodorsal (nasal) process is short, narrow, and tapers distally. It extends less than half the distance to the prefrontals. The lateral (maxillary) rami are obscured by the articulated maxillae. They were, however, presumably short, because the right and left maxilla are very close together and do not appear to have undergone much *post mortem* disturbance. The contact with the maxilla was probably mobile rather than sutural (see *Maxilla* below).

The ventral surface of the premaxilla is not exposed on either specimen. Our identification of the premaxilla in dorsal view corresponds with that of Haas (1979). However, in his description of the ventral surface of the holotype, Haas (1980*a*) interpreted as the premaxilla the toothed element exposed in ventral view between the separated dentary tips. Superimposition of dorsal and ventral views of the skull shows that this is actually the anterior portion of the left maxilla. The ventral portion of the premaxilla, if exposed, would be positioned anterior to the tip of the right dentary.

Maxilla

The external surfaces of both maxillae are exposed in the holotype, along with most of the alveolar margin (ventral edge) of the right maxilla and the anterior portion of the alveolar margin of the left maxilla. The external and internal surfaces of the right maxilla, and the external surface of the left maxilla, are exposed in the referred specimen (see figures 3–7) .

The maxilla is a long, low element. The middle region bears a prominent antorbital process that is clasped firmly by two processes of the prefrontal. Anteriorly, the maxilla tapers gradually and curves medially towards the premaxilla. The anterior tips of both maxillae are completely exposed in the referred specimen and are rounded and covered in smooth, finished bone. The contact with the premaxilla was therefore non-sutural and presumably mobile. Behind the antorbital process, the maxilla narrows abruptly in its vertical dimension, but becomes much wider horizontally, extending as a shelf along the ventral margin of the orbit to meet the jugal posteriorly and presumably the ectopterygoid posteromedially. The latter contact is not definite as no ectopterygoid is preserved *in situ* (see *Ectopterygoid* in § 5aii).

The maxillary foramina are exposed on the external surfaces of both elements in the holotype. A total of three foramina are visible on the right, four on the left. On the referred specimen, three are visible on the right maxilla, the surface of the left element is damaged. The foramina are equal in size, evenly spaced anteroposteriorly, and located approximately midway between the dorsal and ventral edges of the maxilla. They represent the lateral exits for the maxillary canal, which in living squamates contains the maxillary branch of the fifth cranial nerve, the inferior orbital artery, and the maxillary vein (Bahl 1937). Posterior to the dorsal process, on the antorbital rim, there is a large foramen that represents the posterior entrance to the maxillary canal. This is visible on the right maxilla of the referred specimen.

The internal surface of the anterior region of the maxilla is smooth and featureless. In particular, septomaxillary and vomerine processes, and an indentation for the margin of Jacobson's organ, are all absent. The maxilla presumably did not suture with the septomaxilla and vomer (although a non-sutural contact is possible), and did not enter the margin of the opening for Jacobson's organ. The presence and morphology of the palatine process cannot be determined because the

Figure 3. (*opposite*) (*a*) Dorsal surface of anterior portion of the skull of holotype (HUJ-PAL 3659), as photographed during the late 1970s. (*b*) Photo of plaster cast and (*c*), (*d*) drawings of the dorsal surface of the skull of the holotype in its current condition. Since *a* was taken, the dorsal surface of the skull and anterior vertebrae has been embedded in resin, making photography of the specimen impossible. For this reason, a photograph of the low-fidelity plaster cast, with numerous air bubbles, has been provided (*b*). As can be seen by comparing *a* with *b*, the specimen was already almost fully prepared when *a* was taken, and further preparation has consisted mainly of removing very small areas of matrix around some elements. (*a*) Scale bar: 2 cm. (*b*–*d*) Scale bar: 1 cm.

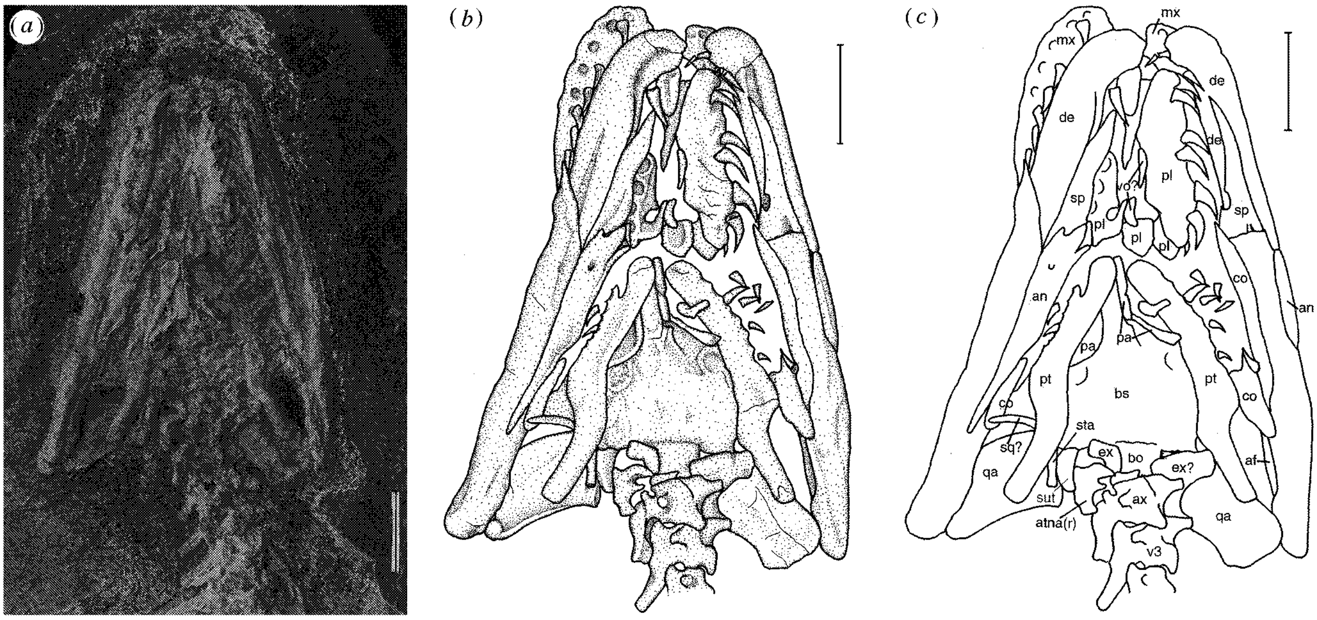

Figure 4. (*a*) Photo and (*b*, *c*) drawings of ventral surface of skull of holotype (HUJ-PAL 3659). Both are of the specimen in its current condition. (*a*) Scale bar: 2 cm. (*b*,*c*) Scale bar: 1 cm.

middle region of the internal surface of the maxilla is only exposed on the right element of the holotype, where it is damaged.

The dorsal margin of the maxilla, anterior to the ascending process, forms the ventral and posterior margin of the external naris. The entire shape of the opening cannot be determined as the nasals are very poorly preserved. The maxilla does not contact the frontals, and is unlikely to have contacted the nasals (see figures 3 and 7). Thus, the naris was probably 'fully retracted' (see Lee 1997*a*), i.e. it probably extended posteriorly to separate the nasal and frontal from the maxilla.

In palatal view the maxilla formed the lateral margin of the internal naris anteriorly and the anterolateral margin of the suborbital fenestra posteriorly.

A total of 13 alveoli (tooth sockets) are visible on the left maxilla of the referred specimen; there is space for about three more near the posterior end, resulting in a probable total of 16 alveoli. The anteriormost eight alveoli are visible on the right elements of both specimens. The alveoli, and preserved maxillary teeth, are all approximately the same size. On the holotype, six long, recurved teeth (see § 5av) are preserved in or near their sockets on the right maxilla; the alveolar ridge of the left maxilla is obscured by the articulated dentaries. On the referred specimen, three teeth are preserved on the right maxilla, and four on the left.

Our identification of the maxillae on the holotype corresponds partly with that of Haas (1979). However, Haas interpreted the posterior part of the right maxilla as the 'ectopterygoid'; there is no evidence of any suture separating this part of the maxilla from the anterior part. In ventral view, the anterior tip of the left maxilla was misidentified as the 'premaxilla' (see *Premaxilla* above). On the referred specimen (Haas 1980*b*), the right maxilla was identified as the palatine (anterior portion) and pterygoid (posterior portion). However, the true identity of this element is unequivocal as the two structures are continuous, forming an element that is identical in shape to the other maxillae recognized, and which bears the maxillary foramina. These foramina allow the lateral and the medial surface of the element to be determined and thus, confirm its identity as the right element. The other maxilla, identified by Haas (1980*b*) as the 'right maxilla', is therefore the left maxilla. The element interpreted by Haas as the 'left maxilla' appears to be the right dentary (see *Dentary* in § 5aiv).

Prefrontal

The right and left prefrontals are preserved in the type but neither could be identified in the referred specimen (see figures 3 and 7). The prefrontal is large triradiate element. The anterior process is narrow and extends anteroventrally along the internal surface of the ascending process of the maxilla. The anterior margin of this process appears to form part of the margin of the external naris. The ventral process is much wider and extends ventrally behind the ascending process of the maxilla.

The posterior process forms part of the skull table. It is a long horizontal plate that extends posteriorly to contact the parietal and postorbital, excluding the frontal from the orbital margin. The parietal is notched for articulation with the posterior process. The medial margin of the posterior process has a long parasagittal contact with the frontal. The lateral margin of the posterior process bears a slight horizontal flange that extends laterally over the orbit.

Haas (1979, 1980*a*) interpreted the anterior and posterior processes of the left prefrontal as the 'left frontal', and the ventral process alone as the left prefrontal. However, the presumed suture between these putative elements is an irregular crack. Haas' interpretation also leaves unexplained the element medial to the putative 'left frontal', and he concluded that this medial element was the septomaxilla. However, the latter element is part of the skull roof, the left frontal. The 'prefrontal' identified by Haas (1980*b*) on the referred specimen appears to be the right coronoid (see *Coronoid* in § 5aiv).

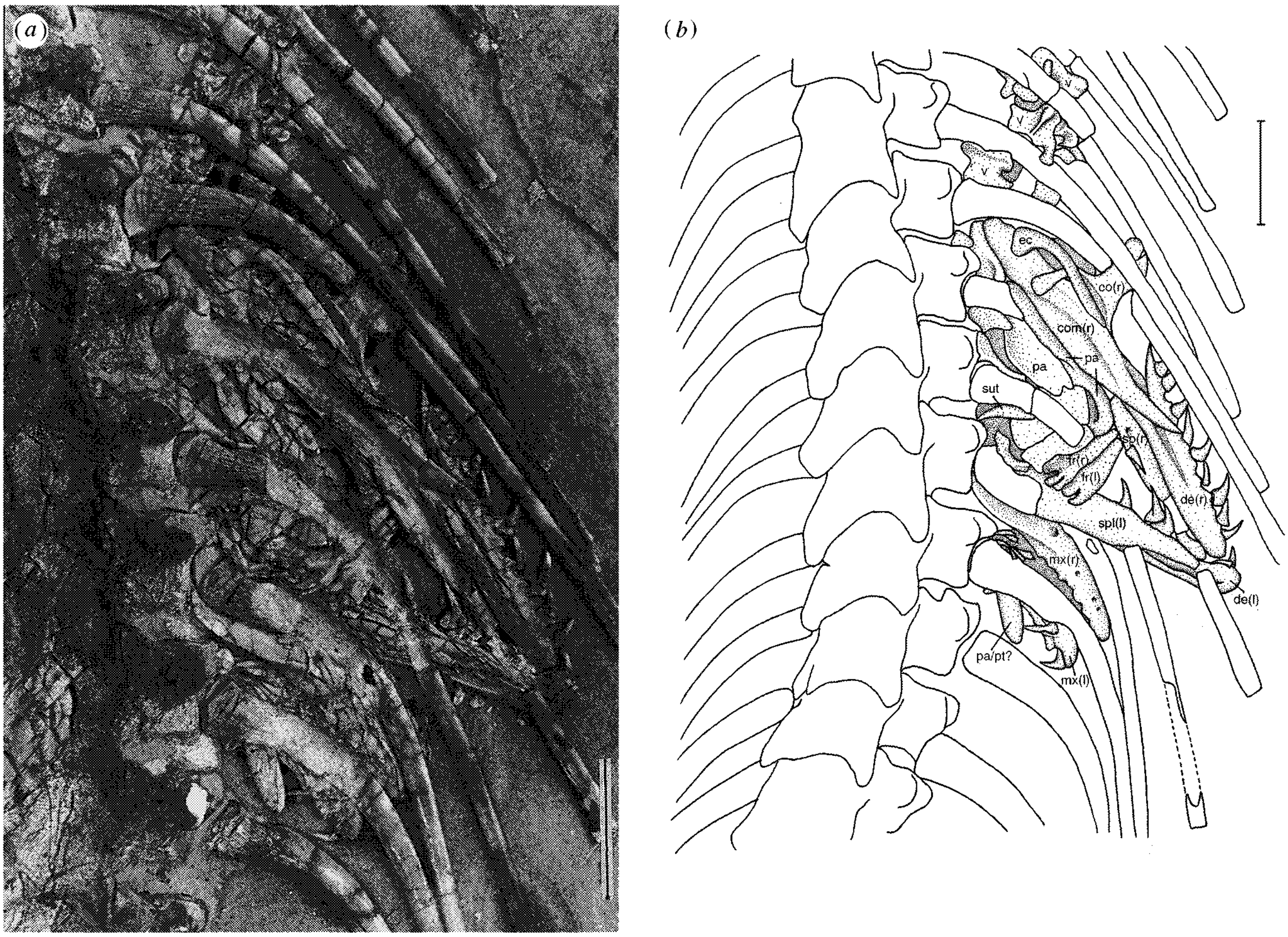

Figure 5. (*a*) Photo and (*b*) drawing of dorsal surface of the region of the referred specimen containing skull fragments (HUJ-PAL 3775). Both are of the specimen in its current condition. (*a*) Scale bar: 2 cm. (*b*) Scale bar: 1 cm.

Lacrimal

The lacrimal is definitely absent. It is not preserved as a separate element, nor is there space for it between the prefrontal and maxilla.

Frontal

Both frontals are exposed in dorsal view on the holotype, and in ventral view on the dorsal surface of the referred specimen (see figures 3, 6 and 7). The frontals are paired, each consisting of a dorsal portion which forms part of the skull table, and a ventral portion (the subolfactory process or descensus frontalis) which forms part of the lateral wall of the braincase.

The dorsal portion is long and rectangular. It sutures medially with its counterpart and laterally with the prefrontal. Posteriorly, it fits into a shallow notch on the anterior margin of the parietal. The frontoparietal suture is a transverse contact. The anterior contact with the nasals is not well-preserved. Anterolaterally, the frontal probably forms a small part of the margin of the external naris, which appears to extend as a slit between the frontal and prefrontal.

The lateral surface of the left subolfactory process, and the medial surface of the right, are exposed on the referred specimen (figure 5*b*). Each subolfactory process is a vertical, parasagittal flange that extends ventrally from the skull table. It is deepest posteriorly and gradually becomes shallower anteriorly. There is a deep notch in the posterolateral margin for the exit of the optic (II) nerve into the orbit. Posteriorly, the subolfactory process probably contacted the descensus parietalis. However, this portion of the descensus parietalis is not preserved. Ventrally, the processes of the right and left frontals probably either contacted the lateral margins of the cultriform process, as in modern snakes, or one another, as in some lizards (e.g. *Heloderma*).

Our interpretation of the right frontal of the holotype corresponds with that of Haas (1979). However, the structure identified by Haas (1979) as 'left frontal' is part of the left prefrontal (see *Prefrontal* above). Instead, the structure identified as the 'nasal' represents part of the left frontal. This structure is much too posterior to be a nasal, being adjacent to the parietal. Furthermore, it is continuous with the piece of bone in front (the boundary identified by Haas is a crack), the two structures together forming the left frontal, identical in shape to the right element. The two frontals on the referred specimen were illustrated (Haas 1980*b*, fig. 10.4), but not identified.

Nasal

The nasals are not preserved clearly on either specimen. On the dorsal surface of the holotype there are scattered fragments of bone between the premaxilla and the frontals (see figure 3). These are likely to be parts of the nasals. Nothing about the shape or size of the nasals, or whether they were fused or paired, can be determined. Haas (1979,

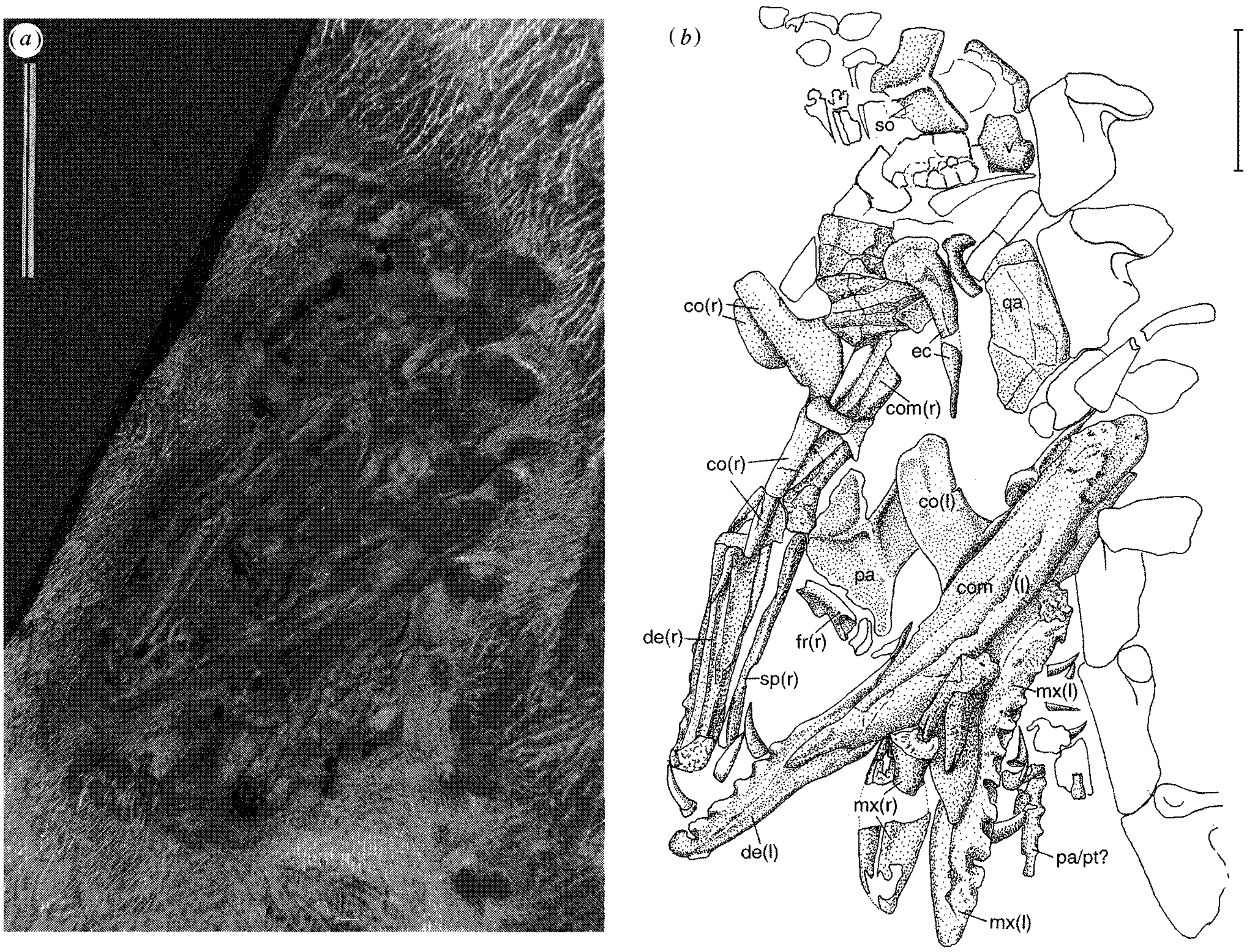

Figure 6. (*a*) Photo and (*b*) drawing of ventral surface of the region of the referred specimen (HUJ-PAL 3775) containing skull fragments. Both are of the specimen in its current condition. (*a*) Scale bar: 2 cm. (*b*) Scale bar: 1 cm.

1980*a*) tentatively identified a bone fragment on the holotype as the 'nasal'; this is part of the left frontal (see *Frontal* above). The element identified as the 'nasal' on the referred specimen (Haas 1980*b*) appears to be the palatine or ptergyoid (see *Palatine* in § 5aii).

Parietal

The parietal is preserved in dorsal view in the holotype, and in dorsal and partly in ventral view in the referred specimen (see figures 3, 5, 6 and 7). It is a single, complex element. Anteriorly, it consists of a short, wide parietal table. Posteriorly, it consists of a long sagittal crest, with descending flanges on both sides.

The anterior margin of the parietal table has four shallow concavities. The medial pair articulate with the frontals, the lateral pair with the prefrontals. Laterally, the parietal table is clasped anteriorly and posteriorly by the two medial processes of the postorbitofrontal. A pineal foramen is not present (contrary to Haas 1979): instead, the entire dorsal surface of the parietal table is shallowly concave. Posteriorly, the parietal table extends backwards as a long, narrow sagittal crest; there are no posterolateral (suspensorial) rami.

The descending processes of the parietal extend ventrolaterally from both sides of the sagittal crest to contact the lateral margins of the parabasisphenoid. The external jaw adductors presumably originated on the dorsolateral surfaces of the descending processes, on both sides of the sagittal crest. The dorsal portions of the descending processes are visible in the holotype and referred specimen: enough is exposed to indicate that the descending process was an extensive vertical wall. The ventral margins, which contact the lateral margins of the parabasisphenoid (including cultriform process), are visible on the ventral surface of the holotype. The right flange (i.e. on the left in ventral view) is intact but slightly obscured by the right pterygoid; the left is broken into three sections, the posteriormost being displaced slightly anterolaterally. The middle portion of the descending process of the parietal is not exposed: it presumably contacted the prootic posteriorly and the descending process of the frontal anteriorly.

The posterior margin of the parietal is concave and has a firm transverse suture with the supraoccipital, which has been incorporated into the skull roof (see *Supraoccipital* in § 5aiii). The sagittal crest of the parietal overlaps the supraoccipital.

Our interpretation of the parietal in the holotype, including the ventral edges adjacent to the parabasisphenoid, corresponds with that of Haas (1980*a*). In the referred specimen, Haas (1980*b*) identified three widely scattered elements as fragments of the parietal. The observation that skull bones in this specimen are never broken into widely separated pieces (although being disarticulated

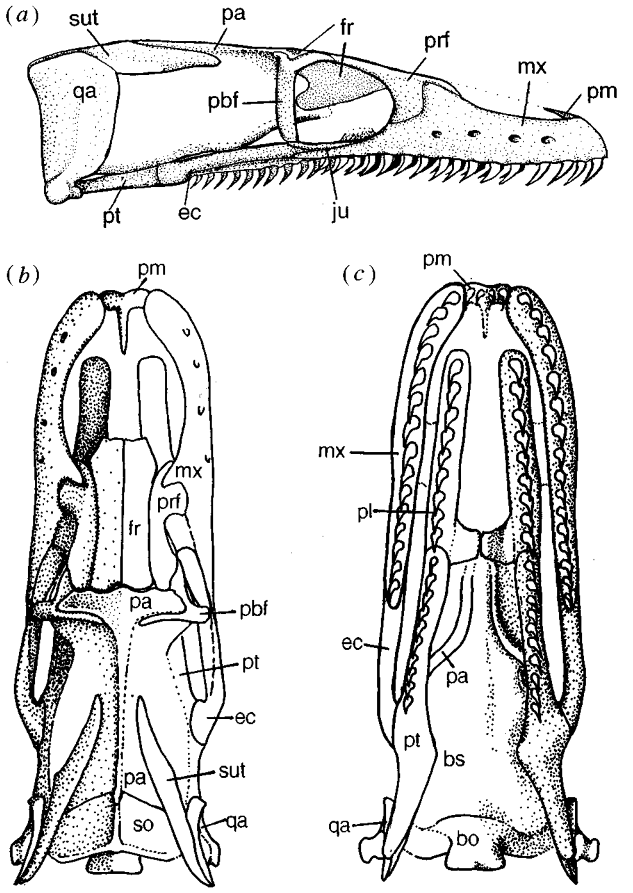

Figure 7. Reconstruction of skull of *Pachyrhachis* in (*a*) lateral, (*b*) dorsal and (*c*) ventral view. Based on information from both specimens (HUJ-PAL 3659 and 3775); there is no scale bar since the specimens differ slightly in size.

and crushed) makes this interpretation implausible for taphonomic reasons. The largest fragment represents the entire parietal. The smallest element is probably a supratemporal (see *Supratemporal* below). The identity of the remaining element remains uncertain.

Postorbitofrontal

Both postorbitofrontals (fused postorbitals and postfrontals) are preserved in external view in the holotype (see figures 3 and 7). The element is triradiate. A long ventral process forms the posterior margin of the orbit, and contacts the jugal; the posterior orbital margin was therefore complete. There are two medial processes. The anterior medial ramus extends anteromedially along the lateral margin of the parietal and prefrontal, forming part of the dorsal border of the orbit. The posterior medial ramus extends along the posterior margin of the parietal table. There is no posteriorly projecting process, which in typical squamates ('lizards') forms part of the upper temporal arch. In *Pachyrhachis* the probable squamosal is small and could not have contributed to a temporal arch (see *Squamosal* below). The upper temporal arch was therefore absent.

Haas (1979) identified the combined postorbitofrontal as the 'postorbital' alone. However, the observation that the element clasps the skull table, and forms the posterior border of the orbit, indicates that it must include the postfrontal. It occupies the area occupied by the postfrontal (skull table) and postorbital (orbital margin) in squamates which retain separate elements. The element Haas (1979) identified as the postfrontal is here interpreted as the jugal (see *Jugal* below).

Jugal

Both jugals are preserved in dorsal view on the holotype (see figures 3 and 7). The jugal is a small horizontal plate that tapers posteriorly towards its contact with postorbitofrontal. It forms the ventral portion of the orbital margin. The contact with the postorbitofrontal appears to have been at a sharp angle, resulting in a distinct 'corner' in the posteroventral region of the orbital margin. Anteriorly, as shown in the left element, the jugal overlies the posterior end of the maxilla. Posteroventrally, the jugal presumably contacted the ectopterygoid, but this is not certain because the ectopterygoids are either not exposed, or are displaced on both specimens. As in all squamates, there is no posterior horizontal process, which in typical diapsids contributes to the lower temporal arch.

Haas (1979) interpreted both jugals in the holotype as 'postfrontals'. However, they are preserved in the wrong position to be the postfrontals, lying on the ventral (instead of dorsal) margin of the orbit. Their shape is also inconsistent with this interpretation, because postfrontals in squamates are usually forked elements clasping the frontoparietal joint (see *Postorbitofrontal* above). The element on the referred specimen identified as the 'jugal' (Haas 1980*b*) is here interpreted as the right splenial (see *Splenial* in § 5aiv).

Quadratojugal

The area which the quadratojugal would have occupied is well-preserved on both sides of the holotype. No quadratojugals are present, and there are no obvious facets or sutural areas on the quadrate or jugal for the element. The quadratojugal is thus definitely absent.

Supratemporal

Both supratemporals are visible on the dorsal surface of the holotype. The posterior end of the right element is also visible in ventral view. A similarly shaped element on the dorsal surface of the referred specimen might also be a supratemporal (see figures 3, 4, 5 and 7).

The supratemporal is an elongate plate of bone, extending posterolaterally from the skull table. It is widest in the middle, tapering anteriorly to a sharp point, and posteriorly to a blunt rounded end. The anterior half overlies the posterior portion of the parietal, and the anteroventral edge closely abuts fragments tentatively identified as parts of the prootic (see *Prootic* in § 5aiii).

The posterior portion of the supratemporal projects freely a considerable distance behind the skull table and braincase, articulating with the cephalic condyle of the quadrate. The contact is visible in dorsal and ventral views on the right side of the holotype. It is smooth and simple; there is no peg-and-socket arrangement.

The supratemporals in the holotype were identified as the 'squamosals' by Haas (1979, 1980*a*). However, each element has a long contact with the parietal, like the supratemporal in all squamates, but unlike the squamosal. A sliver of bone on the right of the holotype was identified as the 'supratemporal'; this appears to be the squamosal (see *Squamosal* below). The fragment of bone between the left quadrate and coronoid interpreted as the 'left supratemporal' cannot be the left supratemporal as the latter element can be identified elsewhere.

Squamosal

An element tentatively identified as the squamosal is visible in both dorsal and ventral views of the holotype (figures 3 and 4). It is a small, curved sliver of bone preserved between the right coronoid and right quadrate which resembles the reduced squamosal in taxa which have lost the upper temporal arch, such as *Heloderma* and *Lanthanotus*. In such taxa, the reduced squamosal (which otherwise contributes to the temporal arch) is instead pressed tightly against the supratemporal. The morphology of the postorbitofrontal indicates that the upper temporal arch was absent in *Pachyrhachis* (see *Postorbitofrontal* above), which is consistent with the interpretation of the sliver of bone as the reduced squamosal.

The element would have fitted against the lateral surface of the large supratemporal. There is no ventral ramus. The squamosal, if correctly identified, has separated from the supratemporal and slipped anterolaterally and ventrally, so that its anterior end abuts the medial surface of the lower jaw (figure 4).

This element was identified as the 'supratemporal' by Haas (1979). However, it cannot be the supratemporal if our identification of the supratemporal is correct (see *Supratemporal* above).

Quadrate

Both quadrates are exposed on the holotype in lateral (external) and medial (ventral) views. They are splayed laterally because of dorsoventral compression. In addition, the left quadrate is split longitudinally. On the referred specimen, a crushed plate of bone on the ventral surface is identified as the left quadrate (see figures 3, 4, 6 and 7).

The quadrate is a rectangular plate, twisted so that the main (dorsal and middle) section is orientated parasagittally, while the ventral end is orientated transversely. This twisting is most clearly shown on the right quadrate of the holotype. In lateral view, the anterior edge is convex and the posterior edge is concave.

The shaft and the tympanic conch are not distinct; rather, they merge gradually so that the entire external surface of the quadrate is a smooth, flat surface. The tympanic recess is therefore absent.

The medial surface of the dorsal end bears the cephalic condyle. This has a parasagittal articulation with the lateral edge of the posterior end of the supratemporal. The articulatory surface is smooth and featureless. The ventral end of the quadrate bears the mandibular condyle, which is orientated transversely. This is a smooth, saddle-shaped area that is concave transversely. There is no anteromedial (pterygoid) process, or sutural area for the pterygoid, indicating that this contact was fibrous and mobile.

Our identification of the quadrates of the holotype corresponds with that of Haas (1980*a*). The 'quadrate' identified in the referred specimen (Haas 1980*b*) is too small to be a quadrate, although its exact identity remains uncertain.

(ii) *Palate*

Vomer and septomaxilla

In the ventral view of the holotype, several crushed fragments of thin bone are preserved between and anterior to the palatines (figure 4). They almost certainly represent portions of the vomer and/or septomaxilla, the elements that occupy this region in other squamates. One of the fragments was identified as the vomer by Haas (1980*a*). However, preservation is so poor that none of the fragments can be readily assigned to either element.

Palatine

Both palatines are exposed on the ventral surface of the holotype (see figures 4, 5 and 7). The left palatine is splayed slightly laterally, and is thus preserved in ventromedial view. The right element is undisturbed, and is thus preserved in ventral view. However, the anterior portion is covered by the lower jaw. On the dorsal surface of the referred specimen the rounded anterior end of a plate-like, tooth-bearing element is preserved. It represents either the anterior or posterior end of a palatine, or the anterior end of a pterygoid (see *Pterygoid* below).

The palatine is a vertical, parasagittal plate that bears an alveolar ridge along its entire ventral surface. It is triangular, being highest (deepest) in the middle and gradually tapering anteriorly and posteriorly. The anterior portion and tip of the palatine, visible in the holotype, is smoothly rounded and covered in finished bone. This is also consistent with the morphology of the possible palatine on the referred specimen. On the posterior end, a plate of bone, the medial process, projects medially to meet its counterpart. This process is approximately rectangular, but tapers slightly distally. The entire ventral surface of this process is fully exposed on the left palatine of the holotype, but there is a parasagittal break. The distal (medial) portion of the process is thus preserved as an isolated piece of bone. However, its identity as the distal end of the medial process is clear because its lateral edge is a rough broken margin that matches the adjacent, broken margin of a short medial flange from the palatine. Its other edges are of finished bone. Only the posterior edge of the right medial process is exposed. The exposed ventral surface of the left process, and posterior edge of the right process, indicate that the medial process is deeply concave transversely. Thus, it projects horizontally from the main body of the palatine and then gradually curves ventrally.

The medial surface of the main body of the palatine is smooth and featureless. Most of the lateral surface of the palatine is not exposed, and information on the likely articulation with the maxilla is unavailable. Posteriorly, the palatines contacted the pterygoid. The posterior ends of the palatines are too poorly preserved to determine whether they are sutural or smooth surfaces. However, the morphology of the pterygoid suggests that this contact was loose and mobile (see *Pterygoid* below).

The entire alveolar margin of the left palatine of the holotype is visible. There are discrete sockets for nine teeth. However, only seven teeth, all long and recurved (see § 5av) are preserved in place or closely associated with the sockets. The posterior portion of the right palatine has four sockets and one attached tooth. On the anterior portion of the palatine in the referred specimen, there are four alveoli lacking associated teeth.

The palatines extend almost the entire distance from the pterygoids to the premaxilla. Thus, the vomers could not have been positioned anterior to the palatines, as in non-ophidian squamates, but must have been positioned medial to (i.e. between) the palatines, as in snakes.

Our identification of both palatines on the holotype corresponds with Haas (1980*a*). However, the two pieces of the medial process of the left element, which are clearly continuous with the main portion, were identified by Haas as the 'vomer' and the 'descensus frontalis'. He also interpreted the palatine as 'fairly broad' (p. 98), identifying the medial surface of the left element as the ventral surface. However, this surface faces ventromedially as preserved because the element has been splayed laterally. The element identified by Haas (1980*b*) as the 'palatine' on the referred specimen is interpreted here as the anterior end of the right maxilla (see *Maxilla* in § 5ai). Instead, the element identified as the 'nasal' has alveoli and might be the palatine or pterygoid (see *Pterygoid* below).

Pterygoid

Both pterygoids are preserved in the ventral view of the holotype (see figures 4, 5 and 7). The posterior ends have been pushed apart so that they now diverge posteriorly more than in life, and both elements have been rotated slightly so that the teeth point ventrolaterally instead of ventrally. In the referred specimen, a partly exposed bone on the dorsal surface represents the end of either a palatine or pterygoid.

The pterygoids are the largest palatal component. They are separated along their entire length. Each is a long element that is narrow across the tooth row and comparatively deep dorsoventrally. The anterior (palatine) ramus is the longest portion. It is a parasagittal plate of bone that bears a row of recurved teeth along its ventral margin. At least seven alveoli are preserved in the left pterygoid. The anteriormost is some distance from the anterior tip, so there was probably another alveolus in front of it, assuming the tooth row extended uninterrupted along the palatine and pterygoid. As many as three more alveoli might have been present more posteriorly. A total of four long, recurved teeth (see § 5av) are preserved in or near the alveoli, and four more teeth are preserved nearby. A total of six alveoli are preserved on the right element; two of these have associated teeth. The pterygoid teeth are slightly smaller than those on the palatine. The anterior tip of the pterygoid, which presumably contacted the palatine, is smoothly rounded and covered in finished bone, suggesting that this contact was mobile and non-sutural. The lateral edge of the anterior process is smooth finished bone; this indicates that it formed the margin of the subtemporal fenestra. The ectopterygoid and palatine therefore did not extend along this margin to exclude the pterygoid from the opening.

Posterior to the palatine ramus (and tooth row), the pterygoid bears a lateral flange that probably contacted the ectopterygoid. Immediately behind this flange, the pterygoid again narrows, forming the quadrate ramus. This ramus is shorter than the palatine ramus, and is cylindrical (rather than a vertical plate). It extends posterolaterally towards the quadrate. The posterior end of this ramus is blunt and smooth, and there is no corresponding sutural surface on the quadrate. Thus, the pterygo-quadrate contact was mobile and non-sutural.

Haas' (1980*a*) identification of both pterygoids on the holotype corresponds with ours. However, parts of the left and right coronoids were interpreted by Scanlon (1996) as extensions of the respective pterygoids, and were thus described as transverse flanges of the pterygoids. However, these 'transverse flanges' are continuous with the coronoids. They are separate from the pterygoids and, in ventral view, lie at a deeper (i.e. more dorsal) level than the pterygoids. Thus, the surprising reported presence of large transverse flanges (a primitive reptilian feature lost in squamates) is not accurate. At the time of Haas' description, the pterygoids were not fully prepared (1980*a*, fig. 2), and he stated that they were 'almost toothless' (Haas 1980*a*, p. 99). Additional preparation has revealed the presence of alveoli and teeth.

The 'pterygoid' identified by Haas (1980*b*) on the referred specimen is part of the compound postdentary bone (see *Compound element* in § 5aiv). However, the element identified as the 'nasal' might be the real pterygoid. The element has teeth along one edge, and thus cannot be a nasal. It is flat and plate-like, with a rounded, featureless tip (see figures 5 and 6). Among the toothed elements, it cannot be a dentary or maxilla, as these elements are preserved elsewhere and have tips of a different morphology. It is the wrong shape to be the premaxilla. This leaves only the palatine and the pterygoid. The shape of the element is consistent with it being either the anterior or posterior tip of a palatine, or the anterior tip of a pterygoid. Hence, a more precise identification is not possible.

Ectopterygoid

On the referred specimen, the probable ectopterygoids are visible on the dorsal and ventral surfaces of the block, near the posterior end of the right lower jaw (figures 5–7). They are long, curved elements with a slightly expanded end. They are tentatively identified as ectopterygoids because they are similar in shape to the ectopterygoids of most squamates, especially snakes. Each would also fit snugly into the gap normally occupied by the ectopterygoid: between the lateral flange of the pterygoid and the posterior end of the maxilla. Finally, they are unlike all the well-known elements of the skull. Of the elements not yet identified, or known only in part, they are the wrong shape to be the nasals, prootics, opisthotics, epipterygoids, vomers, and septomaxillae. The only other elements not yet identified are the ectopterygoids, and thus, the process of elimination also supports identity of these elements as the ectopterygoids. Our initial interpretation of these elements as displaced anterior cervical ribs is not tenable because all such ribs, preserved in articulation elsewhere on the block, are much more slender in relation to their length.

Each putative ectopterygoid is a slender, J-shaped element. It has a long, slender anterior ramus which presumably overlapped the maxilla, as in primitive snakes (e.g. *Cylindrophis*) and most other squamates. Posteriorly, the element curves medially to meet the lateral (ectopterygoid) flange of the pterygoid. This end of the ectopteryoid is slightly expanded.

Haas (1980*b*) interpreted the probable ectopterygoid on the dorsal surface of the referred specimen as the 'squamosal'. However, the entire skull roof is preserved in the holotype, and there is no similarly shaped element present. Rather, the element that might be the squamosal in that specimen is a tiny sliver of bone (see *Squamosal* in § 5ai). The other ectopterygoid (on the ventral surface) was not exposed at the time of Haas' description.

Epipterygoid

No epipterygoid can be identified on either specimen; however, as the relevant region is poorly preserved its presence cannot be ruled out.

(iii) *Braincase and chondrocranium*

Parabasisphenoid

The parabasisphenoid is visible on the ventral surface of the holotype (see figures 4 and 7). The surface of the element is poorly preserved, obscuring surface details. In particular, whether the parasphenoid and basisphenoid were separate or fused cannot be determined. In all squamates, however, the elements are fused and *Pachyrhachis* probably had this condition.

The parabasisphenoid is a triangular element, widest posteriorly and tapering abruptly anteriorly into a cultriform process. The cultriform process is parallel-sided rather than tapering, and, as preserved, extends anteriorly beneath (i.e. dorsal to) the right pterygoid. The anterior limit is not visible. The cultriform process is straight, rather than concave dorsally, in lateral view. The basipterygoid 'processes' are located immediately behind the cultriform process, on the anterior end of the wide region of the parabasisphenoid. Each consists of a slightly raised circular area rather than (as in many squamates) a long rod-like projection. The concave articulatory surface faces ventrally and slightly laterally. The corresponding surface on the pterygoid is not exposed.

The anterior portion of the parabasisphenoid, including the cultriform process, is clasped on both sides by the ventral margins of the descending flanges of the parietal (see *Parietal* in § 5ai). Posteriorly, the parabasisphenoid has an indistinct transverse suture with the basioccipital. Our identification of the parabasisphenoid corresponds with that of Haas (1980*a*).

Basioccipital

The basioccipital is preserved in ventral view on the holotype (see figures 4 and 7). The surface is poorly preserved. The element is squarish in ventral view, and much shorter and narrower than the parabasisphenoid. The contact between the two elements is represented by an indistinct transverse groove. The morphology of the occipital condyle cannot be determined. The basioccipital was not discussed in the original description of the holotype because of poor preservation (Haas 1980*a*).

Exoccipital

The right exoccipital is preserved on the ventral surface of the holotype (see figures 4 and 7). It is small, and L-shaped in ventral view, extending along the lateral margin of the basioccipital and the posterior margin of the parabasisphenoid. It also extends dorsally into the matrix. The dorsal portions of this element are not exposed; however, the morphology of the supraoccipital (see *Supraoccipital* below) suggests that the exoccipitals did not meet above the foramen magnum. An indistinct fragment on the left side of the holotype, posterior to the parabasisphenoid and lateral to the basioccipital, may be part of the left exoccipital. Whether the exoccipitals were co-ossified with the opisthotic cannot be determined. The exoccipitals were not identified in the original description of the holotype because of poor preservation (Haas 1980*b*).

Supraoccipital

The supraoccipital is preserved in dorsal view on the holotype, and in dorsal view on the ventral surface of the referred specimen (figures 3, 6 and 7). On the holotype the median (sagittal) crest of the supraoccipital is broken and displaced to the left, partly obscuring the left side of the element.

The supraoccipital is a curved plate. It has been completely incorporated into the skull roof, and lies posterior (rather than ventral) to the parietal. The anterior margin of the supraoccipital is convex, and has a continuous suture with the correspondingly concave posterior margin of the parietal. The posterior margin of the supraoccipital is concave, and consists of smooth finished bone. This edge probably formed the posterior margin of the skull roof and the dorsal margin of the foramen magnum. Thus, the exoccipitals did not meet above the foramen magnum.

The supraoccipital bears a median sagittal crest that is continued anteriorly by the parietal. The anterior edge of this crest is bevelled to receive a posteriorly projecting spur from the crest on the parietal.

At the time of Haas' descriptions, the supraoccipital in the referred specimen was not exposed, whereas the supraoccipital in the holotype was only partly exposed, and not identified (Haas 1979, fig. 4, 1980*a*, fig. 1). The element identified instead as the 'supraoccipital' on the holotype is the atlas neural arch (see *Atlas–axis complex* in 5bi).

Prootic

In the dorsal view of the holotype, two narrow fragments of bone are present beneath and immediately lateral to the right supratemporal (figures 3 and 7). A single wider fragment is present in a similar position on the left. The left fragment is identical in shape to the combination of the two right fragments. They might represent the alar processes of the left and right prootics. The structures are flat plates with blunt rounded ends, and are thus similar in shape to the alar processes of the prootics present in many squamates (e.g. varanoids). They project anterodorsally to overlap the descending flanges of the parietals. This is again very similar to the position of the alar process of the prootic in those squamates which possess them. If this identification is correct, a supratemporal–prootic contact was present in *Pachyrhachis*.

Haas (1979*a*, 1980) also identified one of the right fragments as part of the right alar process of the prootic, but did not discuss the remaining right fragment, or left fragment. Instead, a poorly exposed piece of bone under the left postorbitofrontal was identified as the alar process of the left prootic. This is less likely than our interpretation, as the bone in question is located slightly too anteriorly,

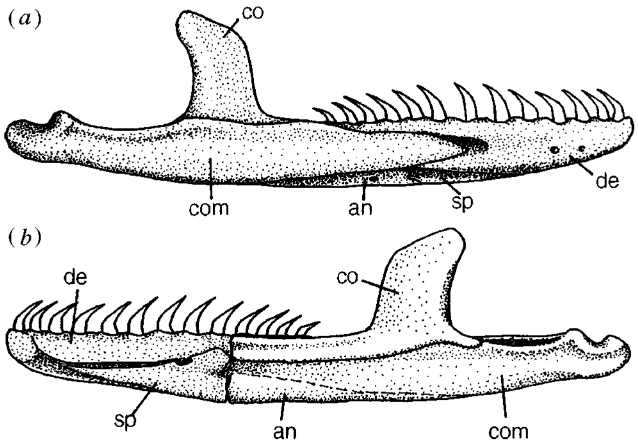

Figure 8. Reconstruction of the lower jaw of *Pachyrhachis* in: (*a*) lateral; and (*b*) medial view. Based on information from both specimens (HUJ-PAL 3659 and 3775), there is no scale bar since the specimens differ slightly in size.

and too deep (under the pterygoid) to be the prootic. The identity of this element remains uncertain.

Stapes

The stapes (columella auris) is exposed only in the ventral view of the holotype (see figures 4 and 9). It is a slender rod-like element that projects posteriorly, between the right pterygoid and supratemporal. The posterior tip is blunt, slightly swollen, and covered in unfinished bone suggesting the presence of a sizeable cartilaginous extra-stapes. Our identification of the stapes corresponds with that of Haas (1980*a*).

(iv) *Lower jaws*

Dentary

Both dentaries are preserved in both specimens (figures 3–6 and 8). On the holotype, the left dentary is preserved in lateral view on the dorsal surface of the block, and in medial view on the ventral surface. The right lower jaw is split longitudinally, so that the lateral (dentary) and medial (splenial, angular) surfaces are both exposed on the ventral surface of the block. On the referred specimen, the right dentary is preserved in lateral view, and the left dentary in medial view, on the dorsal surface of the block. The right dentary is preserved in medial view, and the left dentary in lateral view, on the ventral surface.

The dentary is a long tooth-bearing element that is approximately two-fifths of the total length of the mandible. In lateral (or medial) view, it is deepest posteriorly, and gradually tapers anteriorly, curving medially to meet its partner. The dentary alone forms the mandibular symphysis. The symphysial end of the dentary is shown most clearly on the left elements of the holotype and the referred specimen. It is rounded, and covered in smooth finished bone. There is no discrete flat sutural surface. This indicates that the mandibular symphysis was non-sutural and presumably mobile. Posteriorly, the dentary is deeply notched, being divided into dorsal and ventral processes. The dorsal process is longer, and extends along the dorsal margin of the mandible, nearly reaching the coronoid process. The ventral process is shorter and extends along the ventral margin, reaching the level of the splenial–angular joint.

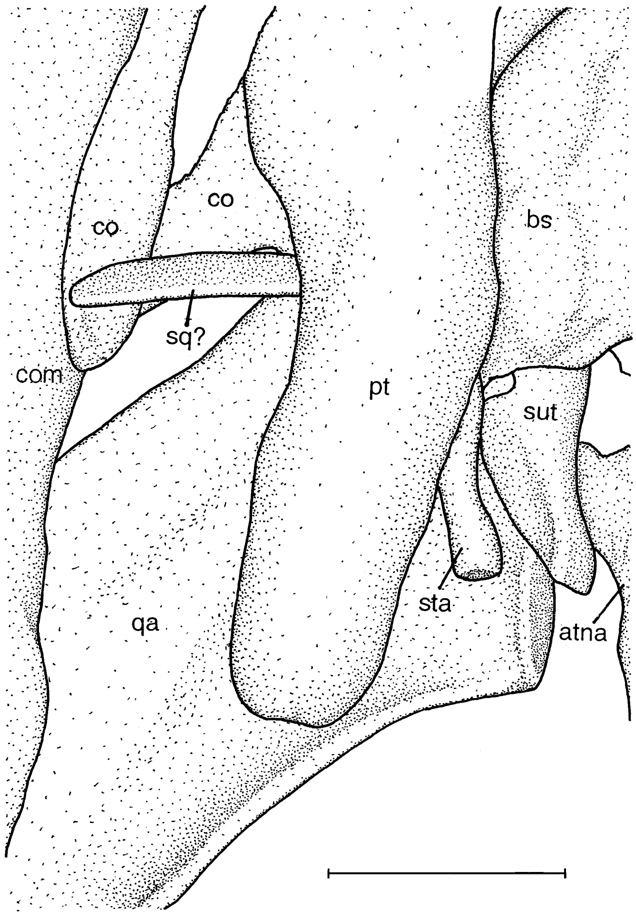

Figure 9. Details of ventral view of posterior right side of skull of holotype (HUJ-PAL 3659) showing details of stapes and the putative squamosal. Scale bar: 0.5 cm.

The lateral surface of the dentary bears a long groove, which extends from posterior edge and gradually tapers to a sharp point just in front of the middle of the dentary. This groove accommodated a similarly shaped anterior flange of the compound element (see *Compound element* below). Two large mental foramina are present on the lateral surface of the dentary. These are clearly visible on the left dentaries of the holotype and referred specimen; the surfaces of the right dentaries are too poorly preserved. Haas (1980*a*) recorded only a single foramen.

Meckel's groove extends along the entire medial surface of the dentary, tapering anteriorly. It is enclosed along most of its length by the splenial. The exposed portion of Meckel's groove is a short canal near the symphyses which is confined entirely to the medial surface of the dentary, and does not encroach onto the ventral edge.

The tooth row extends along the entire dorsal margin of the dentary. On the right dentary of the referred specimen, nearly the entire tooth row is visible. There are 12 alveoli with nine long recurved teeth (see § 5av) preserved *in situ*; another alveolus might have been present more anteriorly, making a possible total of 13. All the teeth on the dentary appear to be similar in size. On the left dentary of the referred specimen, 11 alveoli and three teeth are visible. On the left dentary of the holotype, the eight anterior sockets are visible, the more posterior sockets, and any preserved teeth, are covered by the left maxilla. The alveolar ridge of the right dentary is not exposed.

Our identification of the dentaries on the holotype corresponds with that of Haas (1979, 1980*a*), who also noted the loose symphysis. In the description of the referred specimen, the left dentary was correctly identified in the text (Haas 1980*b*), but the figure labels for the left dentary and splenial were juxtaposed. The right dentary was identified as the 'left maxilla'. However, it is the same shape as the other three dentaries, and is preserved in articulation with the compound element, so its true identity is unequivocal.

Splenial

Both splenials are preserved in medial view on the holotype and on the referred specimen (see figures 4–6 and 8). All are complete except for the right splenial of the referred specimen, which is represented by only a broken sliver of bone.

The splenial is a long triangular plate applied to the medial surface of the dentary. It is deepest (in vertical dimension) posteriorly and tapers to a sharp point anteriorly, a short distance from the symphysis.

The dorsal edge bears a deep notch for the alveolar recess, located near the posterior end. The dorsal and ventral edges are tightly applied to the dentary. The posterior end is overlapped ventrally by the anterior end of the angular. This overlap is best shown on the right mandible of the holotype, and is loose and non-sutural (see *Angular* below). Dorsally, there might have been a short contact with the anterior process of the coronoid. On the left mandible, most of the anterior portion of the angular is eroded away, exposing the straight posterior edge of the splenial. This edge is closely applied to the anterior end of the compound element.

Our identification of the splenials on the holotype corresponds with that of Haas (1979, 1980*a*). The left splenial in the referred specimen was also correctly described in (Haas 1980*b*), although mislabelled (see *Dentary* above). The right splenial was not visible at the time of Haas' description.

Angular

The right angular, and portions of the left, are preserved in medial view on the holotype. Fragments of the right angular, preserved in medial view, can also be tentatively identified in the referred specimen (see figures 4, 6 and 8).

The angular is a long, narrow plate applied to the medial surface of the compound element. It is widest anteriorly, where it contacts the splenial, and gradually tapers posteriorly to a sharp point, terminating well anterior to the articular cotyle. The dorsal and ventral margins are straight and simple. The anterior margin (which overlaps the splenial) is smooth, but bears a pronounced embayment near the middle so that the element has two short anterior prongs. The dorsal prong is slightly longer and wider than the ventral prong. The right angular is slightly displaced from its contact with the splenial. The posterior end of the left splenial is exposed on the holotype. It is vertical and does not have a sutural edge for the angular. The angular–splenial contact was therefore a loose overlap, and was mobile rather than sutural.

A small foramen is present near the anterior end of the angular, midway between the dorsal and ventral margins. It presumably contained the angular branch of the mandibular nerve (Russell 1967).

Our identification of the right angular in the holotype corresponds with that of Haas (1980*a*). However, Haas could not discern the posterior boundaries of this element, and did not identify the fragments of the left angular. The possible right angular on the referred specimen was not exposed at the time of Haas' (1980*b*) description.

Coronoid

Both coronoids are exposed in lateral view on the dorsal surface of the holotype block. The ventral portion of the left coronoid, and the posteroventral end of the right, are also exposed in medial view on the ventral surface of the block. A plate of bone lying deeper in the block, between the right pterygoid and the identified end of the right coronoid, might represent the medial surface of the right coronoid process. On the referred specimen, the right coronoid is exposed in lateral and medial view, and the left coronoid, in lateral view only (see figures 3–6 and 8).

The coronoid consists of a dorsally projecting coronoid process, and a narrow ventral plate applied to the medial and dorsal surfaces of the compound element.

The coronoid process is a large rectangular flange that is taller than it is wide. The anterior and dorsal margins are straight or very slightly convex, whereas the posterior margin is concave. It projects dorsally and slightly posteriorly. The lateral surface bears a shallow vertical groove near the anterior margin. The medial surface is very poorly preserved and no surface details are discernible.

The ventral plate is a long, horizontal flange. It extends anteriorly along the medial and dorsal surfaces of the compound element for a great distance, from the base of the coronoid process to the posterior end of the splenial. This anterior flange tapers very slightly along its length, and terminates in a blunt end. It extends a much shorter distance posteriorly, forming the anterior portion of the medial margin of the adductor fossa. On the medial surface of the lower jaw, the ventral edge of the coronoid is straight.

Apart from the coronoid process, only a small portion of the coronoid is exposed laterally. This consists of a small sliver that extends anteriorly from the base of the coronoid process. It overlaps only the compound element and does not reach the lateral surface of the dentary.

Our interpretation of the coronoid processes of the holotype in lateral view corresponds with Haas (1979, 1980*a*). On the referred specimen, only the lateral surface of the right coronoid was exposed at the time of Haas' (1980*b*) description. This was interpreted as a prefrontal. However, it is identical in shape to the two coronoids on the holotype, and is preserved in its normal position with respect to the other lower jaw elements.

Compound element

The articular, prearticular, and surangular are fused into a single 'compound element' (figures 3–6 and 8). In the holotype, the lateral and medial surfaces of the left compound element are exposed. The dorsal and ventral surfaces of the right element are also visible. In the referred specimen, the lateral surface of the right element is exposed on the dorsal surface of the block. The lateral surface of the left element, and the anterior part of the medial surface of the right element, are exposed on the ventral surface of the block.

The compound element is a long, robust bone that forms the middle and posterior portions of the lower jaw. In lateral view, it is widest in the middle, tapering anteriorly to a sharp point. The long, triangular anterior process fits into a corresponding groove on the lateral surface of the dentary. Posterior to the wide middle portion, the compound element narrows slightly, before expanding again at its posterior end. A long horizontal groove is present in the middle of the lateral surface. This groove is widest in the middle and tapers to a point anteriorly and posteriorly.

The medial surface of the compound element is similar in shape to the lateral surface but, anteriorly, is partly covered by other elements. The dorsomedial edge is overlapped by the long horizontal base of the coronoid. The ventromedial edge is overlapped by the angular. However, a thin strip is exposed medially, between the coronoid and angular. On the left lower jaw of the holotype, much of the angular is eroded away and most of the anterior end of the compound element is exposed in medial view. It is wide and blunt and has a straight vertical contact with the splenial.

The articular cotyle is located on the dorsal surface of the posterior expansion. It is best preserved on the left element of the holotype and appears to be a wide groove that is convex transversely. It forms a saddle-shaped articulation with the quadrate condyle which is concave transversely. There is no distinct retroarticular process. The adductor fossa extends between the articular cotyle and the coronoid process. It is a narrow, anteroposterior slit that opens dorsally. Most of the margin is formed by the compound element; however, the anteromedial portion is bordered by the coronoid.

Haas (1979, 1980*a*) identified the right compound element on the holotype, which he termed the 'mixed bone', and also noted that the articular, prearticular, and surangular were not independent ossifications. However, he did not discuss the boundaries of the left element because it was not as well-preserved. On the referred specimen, only the lateral surface of the right compound element was visible at the time of Haas' description (1980*b*), and this was partly obscured by a rib. Haas (1980*b*) identified it as an 'ectopterygoid'. However, it is now fully exposed and is clearly the right compound element, in articulation with the rest of the right mandible.

(v) *Dentition*

Long, recurved teeth are present on the jaws and on the palate (see figures 3–8 and 10). Each is associated with a discrete shallow alveolus. As already discussed in this paper, there are approximately 16 alveoli on each maxilla, nine on each palatine, ten on each pterygoid, and 12 on each dentary. The ventral surface of the premaxilla is not preserved. However, the element is so narrow that it is unlikely to have contained more than two on each side, unless the premaxillary teeth were extremely minute. The teeth on the maxilla, dentary, and palatine are all approximately the same size, the pterygoid teeth are all slightly smaller.

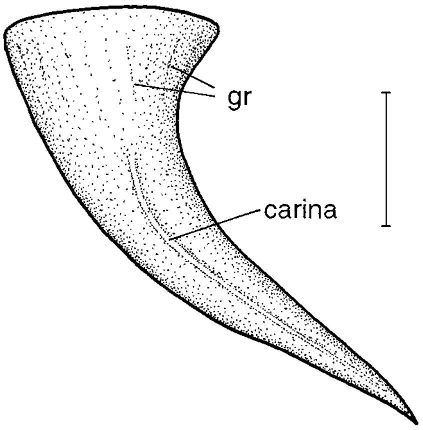

Figure 10. Lateral view of tooth of *Pachyrhachis*, based on palatine teeth preserved on the holotype (HUJ-PAL 3659). The medial surface is the same. Scale bar: 0.1 cm.

The marginal teeth (figure 10) are hollow cones and lack roots. They were not firmly implanted in the sockets, but were ankylosed to the rims. This attachment must have been relatively weak, because many teeth are displaced from their sockets. Some very weak grooves are present near the base of each tooth, oriented parallel to the long axis of the crown. Distally, the tooth gradually tapers to a sharp point. The curvature of the crown is unusual. From the base, the crown extends vertically (ventrally on the maxilla, palatine and pterygoid; dorsally on the dentary) and immediately curves posteriorly. Near the tip, it begins to curve very slightly in the opposite direction i.e. vertically again. Such a curvature is found in many snakes (G. Underwood, personal communication). A long, blade-like ridge extends along the centre of the lateral (labial) surface of the crown, beginning from near the base and extending all the way to the distal tip. A similar ridge is present on the medial (lingual) surface.

(b) ***Postcranial elements***

(i) *Vertebrae and ribs*

The postcranium of the holotype (figure 1) is complete from the atlas to the 58th presacral vertebra. There is then a missing section, considered to have contained approximately 25 presacral vertebrae. This estimate is based on the length of the missing section and the length of the vertebrae in this region, as revealed in the referred specimen. There is then a second, largely continuous string of 43 trunk vertebrae. At this point the slab is broken. Including the missing section, the last vertebra on the holotype is interpreted as being the 126th presacral. Compared to the referred specimen (next paragraph), this means that the holotype specimen is broken approximately 20 vertebrae anterior to the sacral vertebra and pelvic girdle–hindlimb. The anterior 58 presacrals are preserved in lateral view, whereas the posterior 43 are preserved in dorsal view.

The referred specimen contains an unbroken string of 113 trunk vertebrae: 107 presacrals; one sacral; five anterior caudals. Associated with this unbroken main series is an articulated series of 11 cervical-like vertebrae ('nuchals' of Haas (1980*b*)), and six disarticulated anterior cervical-like vertebrae that are scattered beneath the anterior dorsal ribs. The anteriormost (atlas) vertebra, however, cannot be identified. The neural spine of the first vertebra of the main series is short and relatively wide anteroposteriorly. Compared to the holotype, where the first 58 vertebrae are preserved, we interpret the anteriormost trunk vertebra of the referred specimen to be the 38th to 40th presacral. Such identification is possible because there is a gradual change in vertebral shape along the column (see next paragraph). Because 17 anteriormost presacrals excluding the atlas are preserved, this means that the atlas, and approximately another 20 to 22 anterior presacrals, were lost during collection, or initial preservation. The missing vertebrae are the atlas, and approximately three or four between the disarticulated and articulated cervical series; and the remainder (15 to 18) between the articulated cervical series and main series. For the referred specimen, this means that there were at least 151 vertebrae between the base of the skull and the fifth caudal. There were thus approximately 145 presacrals and one sacral.

The six disarticulated cervical-like vertebrae are preserved in ventral view, the 11 articulated cervical-like vertebrae are preserved in left lateral view, and the remaining 113 articulated trunk vertebrae are preserved in right lateral view.

Several characters are common to all the vertebrae of *Pachyrhachis*: centra are procoelous, very short and broad, and exhibit pachyostosis, especially in the middle dorsal region. Varying degrees of pachyostosis are observed in all ribs posterior to the vertebral region identified as cervical-like. In the following descriptions, ribs associated with each region of the axial skeleton are described along with the vertebrae.

The presacral vertebrae are divided into two regions: the anterior cervical-like vertebrae and the dorsal or thoracic vertebrae. In general, the anterior most presacrals are very small vertebrae with relatively tall, thin neural spines. Neither the holotype nor referred specimen shows pachyostosis of the vertebrae or ribs in this region. The more posterior presacrals, or trunk vertebrae, are significantly larger than the anteriormost presacrals. In both specimens, the trunk vertebrae are pachyostotic, though the (larger) holotype shows a slightly greater degree of pachyostosis than the (smaller) referred specimen. This small difference is presumably ontogenetic.

The usual criterion for identifying the posterior limit of the cervical series is the position of the first rib that articulates with the sternum (see, for example, Hoffstetter & Gasc 1969). This definition requires the existence of a pectoral girdle. If the animal has no forelimb or shoulder girdle then by definition it has no neck and no cervical vertebrae. Such a definition is inadequate as it ignores the morphology of vertebrae in favour of non-vertebral characteristics i.e. rib attachment to the sternum. It appears more useful to use intrinsic characters of the vertebrae to define the sacral region. The anterior presacrals of *Pachyrhachis* are clearly differentiated from vertebrae of the main trunk region by size, and by a number of morphological features that are comparable to cervicals in limbed squamates.

Therefore, for the purposes of this study, we differ from Hoffstetter & Gasc (1969) and consider 'cervicals' to be those vertebrae that possess a hypapophysis (representing the fused intercentrum). The following discussion uses 'cervical' in this sense. In the case of *Pachyrhachis*, this also means the putative cervicals are differentiated from the putative dorsals by a marked difference in size, the shape of the neural spine, and the length, robustness and ossification of the associated ribs. The anterior region is well-preserved in both specimens and there is no sign of a pectoral girdle or forelimb. These elements were therefore absent: however, the cervical–dorsal boundary (vertebrae 20–22) presumably represented the approximate original position of the shoulder girdle and forelimb.

Atlas–axis complex

Elements of the atlas–axis complex are preserved in the holotype and referred specimen (see figures 3, 4 and 12). However, their morphology is better revealed in the holotype. The atlas, or first cervical vertebra, consists an intercentrum and the left and right neural arches. The right neural arch is exposed on all surfaces. The base of the arch is small and rises dorsally over the neural canal. As the arch rises dorsally, a small posterior process emerges. There is no neural spine above the arch. On the anteroventral margin there is a rounded margin for articulation with the occipital condyle. The intercentrum is not visible.

On the holotype, the vertebra immediately posterior to the atlas is identified as the axis, or second cervical vertebra. The element is preserved on its side. A small hypapophysis (fused intercentrum) projects to the right in ventral view. Correspondingly, a long, thin blade-like neural spine is preserved on the left. Despite the length of the neural spine, it projects horizontally posteriorly, and thus maintains a low profile above the centrum. A small parapophysis, located near the anterior margin of the cotyle, adjacent to the base of the neural spine, might have articulated with an axis cervical rib (not preserved). On the holotype the axis intercentrum is crushed. On the referred specimen, the axis cannot be positively identified from among the anterior cervical vertebrae present near the base of the skull.

Cervicals

General features of the anterior presacrals observed in both specimens (see figures 1–5 and 12) include the following: anteriormost 'cervicals' (1–6) are very small; they gradually enlarge in size so that the posteriormost 'cervicals' (18–20) have approximately twice the dimensions; neural spines are tall (length approximately 1.5 times the length of the centrum) and narrow (anteroposteriorly); pre- and postzygapophyses of anterior 'cervicals' are large and inclined at an angle of approximately 60°; parapophyses are present and located anteriorly, as well as relatively high-up on the centrum; the intercentrum is fused to the posterior part of the preceding centrum forming a prominent hypapophysis; a median crest that extends the entire length of the ventral surface of the centrum and projects posteroventrally as large bulbous knob (the hypapophysis).

Measurements from the referred specimen illustrate the size variation between anterior and posterior cervicals. The isolated third cervical (figure 5), measured ventrally from the lip of the cotyle to the tip of the condyle, is *ca.* 4.4 mm long, whereas the 17th vertebra (the 11th in the isolated but articulated series), is *ca.* 8.1 mm long.

On the holotype, hypapophyses are observed on at least the anterior 18 presacrals. Posterior to these vertebrae, the ventral surface of the centra are not visible. The first two to three vertebrae on the second section of the holotype show cervical-like characters. The blade-like neural spines are tall, narrow (anteroposteriorly) and approximately 1.5 times the length of the centrum, and the ribs are thin, short and not heavily ossified (pachyostotic). However, a short distance posterior to these vertebrae (presacrals 23 to 25), the size of the centrum and the nature of the ribs, changes markedly. Therefore, based on the holotype, there may be as many as 25 cervical vertebrae, but the most conservative count would be 18.

On the referred specimen there are six small isolated cervicals, and a string of 11 slightly larger articulated cervical–dorsals lying to the right of the body and skull. There is an abrupt difference in size between the last (posteriormost) isolated cervical, and the first (anteriormost) articulated cervical–dorsal. Comparison with the holotype, where this region is complete, indicates that approximately four vertebrae are missing between the two series. This would make the last vertebra in the articulated cervical series the 21st presacral. This vertebra does not appear to possess a hypapophysis, and is thus interpreted as dorsal. The cervical region therefore did not extend past the 20th presacral. Thus, information from both specimens suggests that the cervical region included approximately at least 18 (holotype), but no more than 20 (referred specimen), vertebrae.

Cervical ribs

(See figures 1–5.) On the holotype specimen the first rib preserved is found on the fifth presacral vertebra, even though parapophyses are present on all cervicals posterior to the atlas. This rib is broken, while the next preserved rib (cervical 6) is elongate, gracile and slightly recurved posteriorly. The rib shafts are flattened mediolaterally and widened anteroposteriorly. The distal ends of the ribs are flatter and wider than the middle of the shaft.

On the referred specimen, short cervical ribs are present in association with the disarticulated anterior cervicals. Slightly longer ribs, equal in length to the posterior cervical ribs of the holotype, are present along the length of the isolated series of 11 cervicals–dorsals.

Dorsal vertebrae

Throughout the dorsal region of the presacral column there is a great degree of variation in the size and shape of the centrum bodies, accessory processes, zygapophyses, neural spines, and ribs. The following descriptions of variation in these characters are given as transformations for each feature moving anteriorly to posteriorly along the vertebral column (see figures 1, 2, 11 and 12).

As with all other vertebrae, the dorsal vertebrae are uniformly procoelous, though shallow. The cotyle is broad and forms a rounded to transversely broad oval surface. The dorsal margin of the cotyle very slightly overhangs the ventral margin. However, this does not give an angled appearance (in lateral view) to the joint between articulated vertebrae, rather, this joint remains almost vertical. The condyle is rounded to oval where it can be observed. The centrum surface is differentiated from the condyle surface by a variation in the nature of the bony surface: finished bone on the centrum as compared with endochondral or articular bone on the condyle.

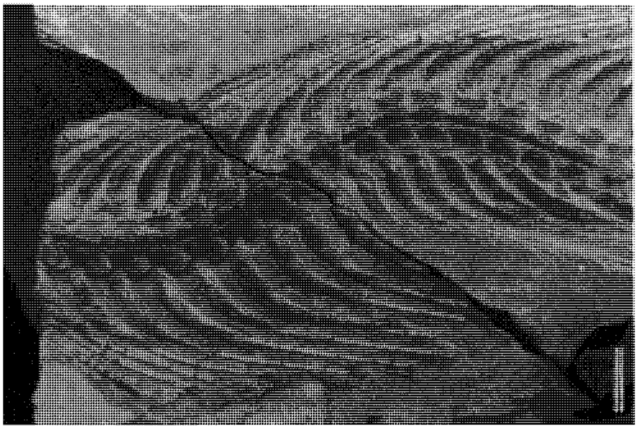

Figure 11. Dorsal vertebrae and ribs of the holotype of *Pachyrhachis* (HUJ-PAL 3659) in dorsal view. Note the roughened surfaces of the pachyostotic proximal portions of the ribs. Scale bar: 2 cm.

In ventral view, the centrum is a short and broad. It is widest near its anterior end, at the parapophyses. It narrows slightly posterior to the parapophyses, but then widens slightly near the condylar surface. However, condyle does not expand laterally past the maximum width of the centrum. A shallow, broad median crest extends along the entire ventral surface of the centrum, from the cotyle to the condyle. As a result the centrum body appears ‘pinched’. On both the holotype and referred specimen, where the ventral surface of the centra are exposed, two small foramina penetrate each centrum at its mid-point, on either side of the ventral ridge. Along the length of the dorsal series, variation in the shape and characters of the centrum involves little more than a change in overall size and degree of pachyostosis.

The trunk centra of the holotype, and to a lesser degree the referred specimen, are pachyostotic. Where pachyostosis is pronounced (from about the 25th presacral to the end of the holotype as preserved), the centrum and neural arch are swollen in all dimensions. Smooth surface bone is absent and is replaced with a porous vascularized bone that is irregular and rough in appearance. This feature is characteristic of pachyostotic regions where resorption and deposition of bone is rapid and ongoing. The centrum is fattened and looses much of its surface detail. The neural arch and base of the neural spine are also swollen above the zygapophyses.

On the anterior part of the lateral surface of the centrum is the parapophyseal process. This process forms the articulation for the ribs and has a distinct bilobate shape throughout the dorsal series. The superior lobe is usually inclined more posterodorsally than the inferior lobe, which is more vertical. The rib appears to articulate mainly with the ventral lobe. The parapophysis represents the greatest lateral expansion of the centrum body, but only projects a slight distance beyond the rest of the centrum. In ventral view, the superior lobe of the parapophysis slightly overhangs the ventral lobe. This overhang creates an angle of articulation for the rib head that affects the orientation of the rib relative to the sagittal

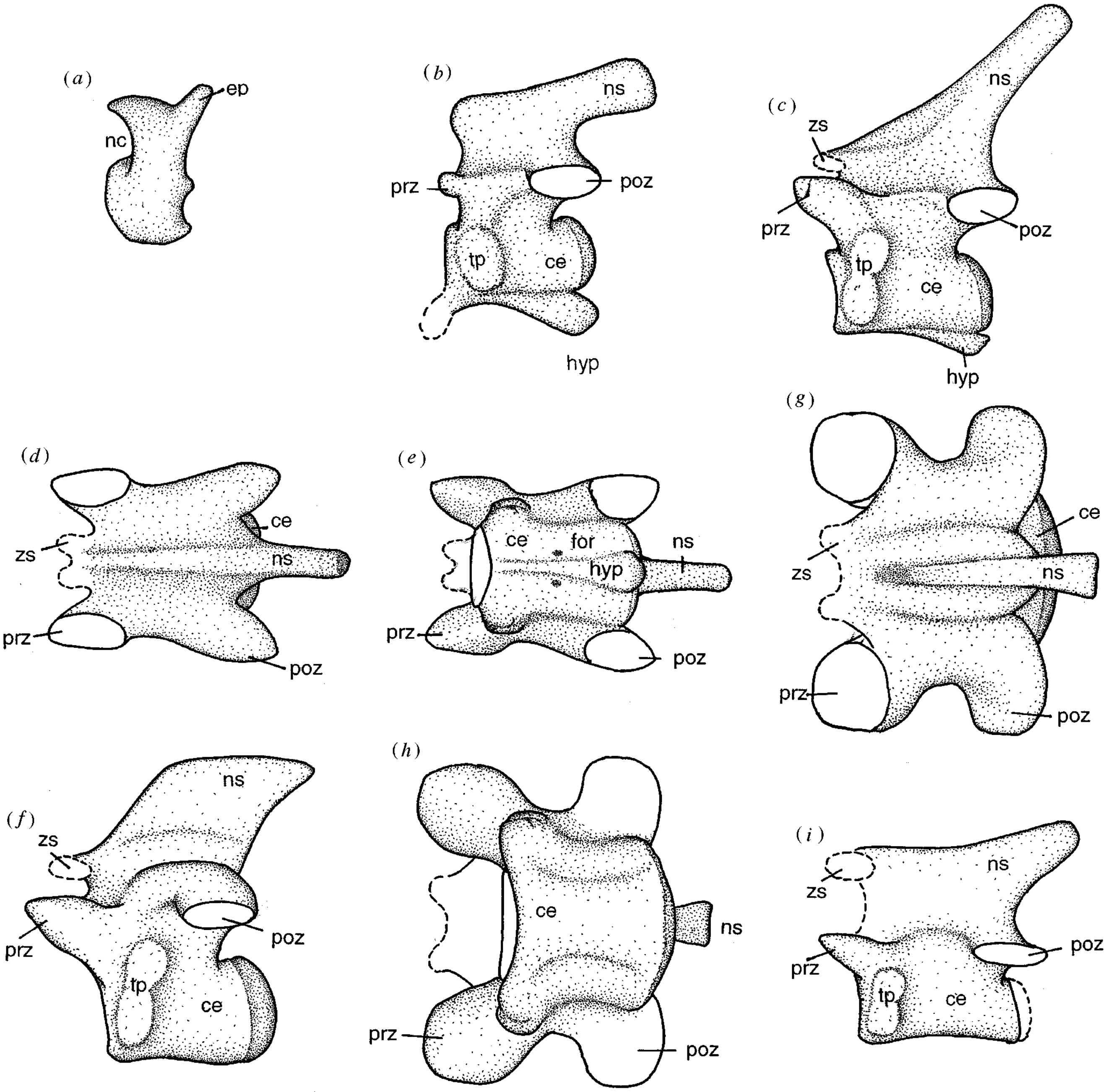

Figure 12. Reconstructions of vertebrae of *Pachyrhachis*, based on information from both specimens (HUJ-PAL 3659 and 3775). There is no scale bar because the specimens differ slightly in size (see specimen drawings). (*a*) Left atlas neural arch in lateral view. (*b*) Axis vertebra in left lateral view. Posterior cervical vertebra in (*c*) left lateral, (*d*) dorsal and (*e*) ventral view. Mid-dorsal vertebra exhibiting pachyostosis in (*f*) left lateral, (*g*) dorsal and (*h*) ventral view. (*i*) Caudal vertebra in left lateral view.

plane of the body. Among presacral trunk vertebrae there is no significant variation in the size and shape of the parapophysis. Dorsal to the centrum, the neural arch expands laterally into a broad, arched platform that supports the pre- and postzygapophyses, the zygosphenes and zygantra, and encircles the neural canal.

The zygapophyseal articulations are inclined at approximately 15–20° to the horizontal, such that the prezygapophyses face dorsomedially and the postzygapophyses face ventrolaterally. In the mid-dorsal vertebrae of the holotype, the arches are greatly pachyostotic, with two longitudinal swellings beside the neural spine. These swellings are poorly developed in the mid-dorsals of the referred specimen, and all the other dorsals of both specimens. In the mid-dorsals of the holotype, the dorsal surface of each prezygapophysis (excluding facet) is arched and thickened. In the referred specimen the dorsal surface of each mid-dorsal prezygapophysis is flat, similar to the condition observed throughout the rest of the vertebral column in both specimens. The same condition exists for the ventral surface of the postzygapophysis (excluding facet): swollen and arched in the mid-dorsals of the holotype only, and flat in the referred specimen, as in all the other trunk vertebrae of both specimens. In dorsal view the neural arch is wide and forms a flattened butterfly-shape owing to the expansion of the pre- and postzygapophyses. The width of the arch in the mid-centrum region (where it is narrowest) is still wider than the greatest lateral expansion of the centrum (at the parapophyses).

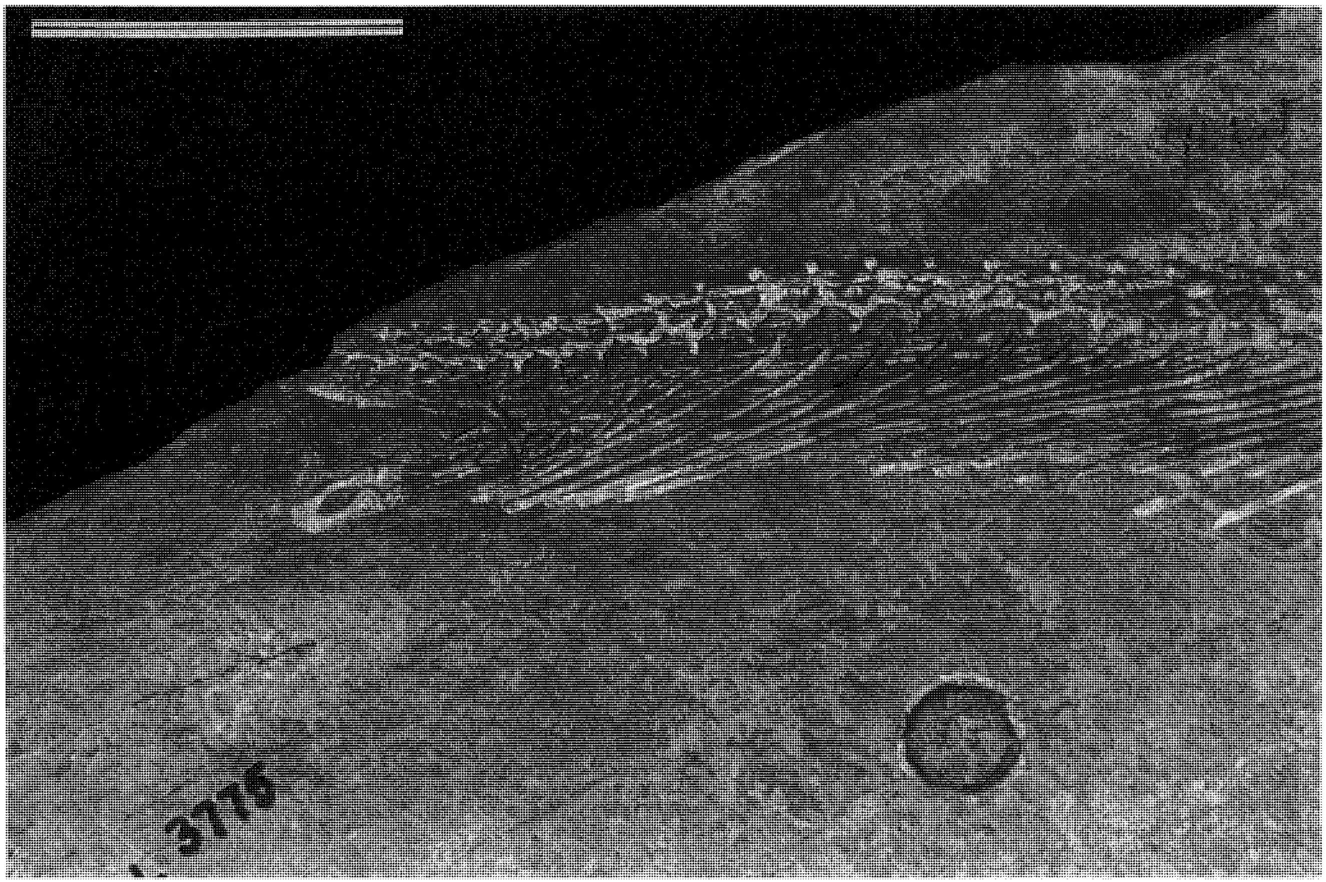

Figure 13. Posterior dorsal region of the referred specimen (HUJ-PAL 3775), showing the relative size of the pelvis and hindlimb. Scale bar: 5 cm.

Tall, blade-like neural spines are present above the neural arch. The most obvious variation observed along the vertebral column are size and shape changes in these spines. Anteriorly, near the cervical–dorsal transition, the neural spines are tall, anteroposteriorly narrow blades that are least twice as tall as the centrum is deep. The dorsal tip of each neural spine is triangular in shape. At the 40th presacral, there is an increase in the anteroposterior dimensions of the spine, making it more robust (there is also an increase in the length and robustness of the ribs at this point). On the holotype, at approximately the 40th presacral, the height of the neural spine therefore appears to decrease; however, this apparent decrease is an artefact of the increased anterior to posterior width of the spine.

A genuine decrease in the height of the neural spines occurs at approximately the 85th presacral vertebra. This transition is not clear on the holotype as the body region with the inferred 85th presacral is exposed in dorsal view and the spines are broken away. However, on the referred specimen, the decrease in neural spine height is obvious in the region of the 42nd to 43rd vertebrae as preserved on the main body section; this region is considered to represent approximately the 85th presacral vertebra. The shape of the dorsal tip of the neural spine also changes, from triangular to rectangular.

From vertebra 85 through to the last presacral, the height of the neural spines continues to decrease. The last presacral has a spine that is approximately equal in height to the depth of the centrum. In this region of the vertebral column, the dorsal tip of the spine is slightly elongate and pointed.

Zygosphenes and zygantra

Well-developed zygosphenes and zygantra appear to be present throughout the column but are not clearly visible in all places (figure 12). Their location on the vertebrae can be identified but their exact morphology cannot be determined. The zygantral facets are present on the posterior, internal faces, of the right and left walls of the neural arch. Zygosphenes are present as accessory processes on the anterior tip of the neural arch lamina, above the neural canal, and between the prezygapophyses. For the zygosphenes and zygantra to meet, it is therefore necessary for the neural arches of adjacent vertebrae to be closely apposed. Throughout the vertebral column of *Pachyrhachis*, the neural spine of each vertebra overhangs the anterior portion of the neural arch of the immediately succeeding vertebra. For this reason, it is also difficult to see the zygosphenes and zygantra throughout most of the column in both the holotype and the referred specimen.

Dorsal ribs

The dorsal ribs are long, rounded in cross section proximally, and flattened distally (see figures 11 and 12). Although the parapophyses of the dorsal vertebrae are bilobate, the dorsal ribs are unicapitate, each possessing a single concave facet for articulation with the parapophysis. The shape of this proximal end closely matches the larger (ventral) lobe of the parapophysis.

The only difference in morphology between the dorsal ribs of the holotype and the referred specimen is the degree of pachyostosis of the proximal portion of the trunk ribs. The proximal ends of the ribs of the holotype are pachyostotic, showing a roughened surface with numerous small pores associated with increased vascularization. Not all of the proximal portion of the rib is transformed in this manner, the maximal amount of this pachyostotic thickening is observed for *ca.* 6–10 mm along the most proximal part of the rib. Distal to this pachyostotic portion there is no difference in rib structure between the holotype and the referred specimen.

Between the two specimens there is no observable difference in the degree of curvature of the ribs at comparable places on the trunk. Each specimen shows similar degrees of curvature and flattening. In the anterior part of the trunk, the rib curves so that the short proximal portion forms a 30° angle to the main straight shaft. The angle of articulation with parapophysis means that the short proximal portion projects ventrolaterally whereas the longer main shaft projects almost directly ventrally. As one proceeds posteriorly, the proximal portion becomes shorter and makes less of an angle with the main shaft. The rib therefore projects almost directly ventrally for its entire length. The posterior trunk region of the animal was therefore very laterally compressed. The expansion created in the anterior part of the trunk by the higher angle of curvature at the neck of the rib would have accommodated the mass of the internal organs.

The following measurements were obtained for the trunk ribs of the referred specimen: average length of mid-dorsal trunk ribs was 66–81 mm; the average length of pre-sacral dorsal trunk ribs, from the tenth to the eighth vertebra anterior to the first sacral, is 54 mm; the length of the rib articulating with the seventh vertebra anterior to the sacral is 51 mm; the length of the rib for the third last dorsal is 32.5 mm; the second last dorsal rib is 21.8 mm; the last dorsal rib is 14 mm in length. Similar measurements were not obtained from the holotype because most of the rib ends have not been prepared free of the matrix.

Sacral vertebrae and ribs

The sacral region is not preserved on the holotype, but is well-preserved on the referred specimen (figure 14). There appears to be a single sacral vertebra. This identification is not based on the morphology of this vertebra, but rather on the modified morphology of the rib, and on the proximity of this rib to the pelvic girdle. This vertebra is very similar to the last dorsal and the first caudal. The neural spine is low, rectangular and overhangs the nextmost posterior vertebra. The pre- and postzygapophyses are large and relatively horizontal. The depth of the centrum is slightly less than the height of the neural spine; the length of the centrum is about equal to the anterior–posterior length of the neural spine.

The sacral rib is short and robust, with a distal expansion that presumably articulated with the medial surface of the ilium, which is preserved immediately adjacent to it. Unlike all other ribs, the distal end of the sacral rib is expanded and plate-like and appears forked; however, this may be the result of breakage.

Caudal vertebrae and ribs

The caudal region is not present on the holotype specimen, and only the most anterior caudals (1–5) are preserved on the referred specimen (figure 14). These five caudal vertebrae cannot be clearly differentiated from the posteriormost presacrals, nor from the sacral vertebra. The height of the neural spines decreases appreciably around the sacrum, and this decrease continues onto the first four caudals. Likewise, the size of the centra decreases.

The only clear difference that demarcates the caudal region from the sacral and presacral region is the immediate change in the morphology and size of the ribs. The preserved caudal ribs are small, short, relatively stubby elements that are *ca.* 5 mm long. They are recurved rods, each with a single tip pointing posteriorly. Haemal arches are not preserved. The overall length of the tail is unknown as the middle and distal regions are not preserved in either specimen.

Gut contents

An element preserved within the ribcage in the posterior dorsal region has been identified as the toothplate of a pycnodont fish (Haas 1979). This suggests that *Pachyrhachis* was piscivorous and capable of ingesting relatively large prey.

(ii) *Pelvis and hindlimb*

Only the referred specimen preserves evidence of the pelvic girdle and hindlimb (figure 14). A very complete right hindlimb is present on the referred specimen. Parts of the left limb are also preserved. The holotype specimen is broken approximately 20 vertebrae anterior to the presumed position of the sacrum, pelvis and hindlimb. Therefore, the following description details the morphology of the appendicular skeleton as preserved in the referred specimen. The three elements of the pelvic girdle are not fused or sutured together. Rather, they appear to have abutted each other, forming a very weak girdle.

Ilium

The right ilium is expanded at both the ventral and dorsal ends, neither of which is well-preserved. The anteroventral end is much wider than the posterodorsal end. Overall, the element is thin lateromedially. The poor preservation of both ends does not allow precise description of either the ventral contribution to the acetabulum, nor the dorsal articulation the sacral ribs. However, the expanded dorsal end closely overlies the distal end of the sacral rib, indicating that the ilium was external to the ribcage and suggesting the presence of a sacral contact.

Pubis

The pubis is the most poorly preserved element of the pelvic girdle. Only two sheet-like fragments are preserved adjacent to the ilium, representing parts of the left and right pubes. The ventral margin of the right element is concave and composed of finished bone, forming the anterior border of the large thyroid fenestra. The pubic symphysis, though poorly preserved, was restricted to the anteroventral end of the pubis, and was thus probably weak.

The element identified as the pubis by Haas (1980*b*) is not a pubis, but rather a fragment of a rib underlying the

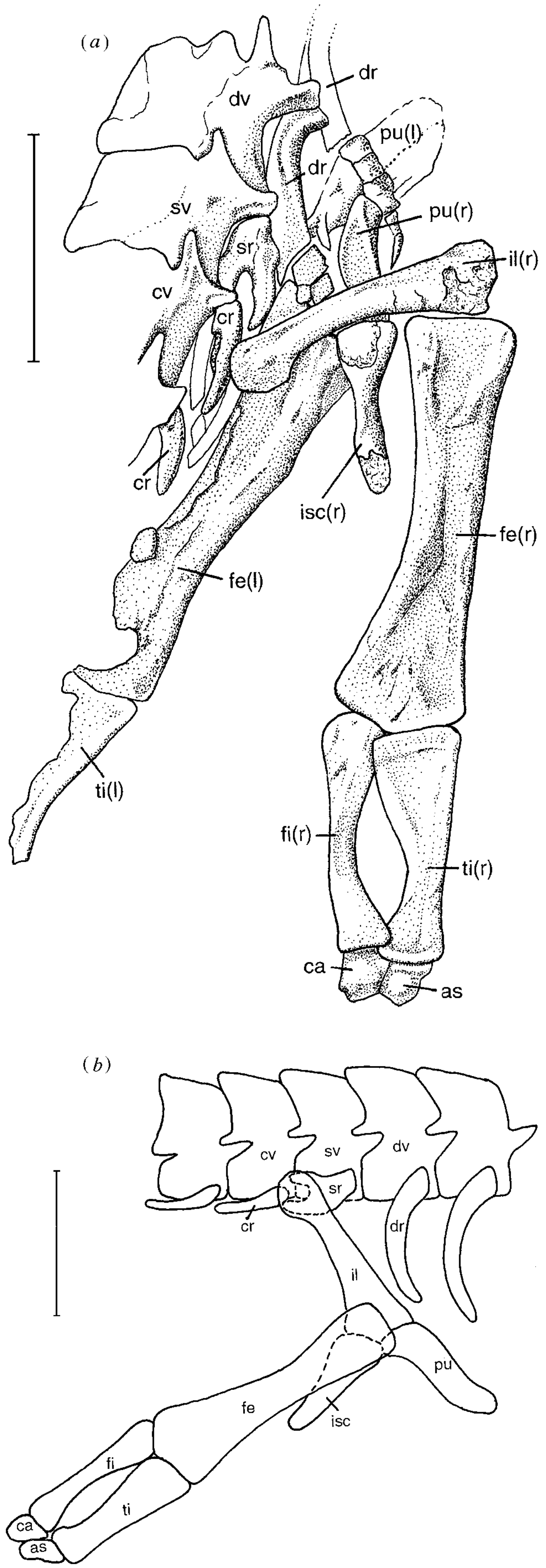

Figure 14. Pelvis and hindlimb of referred specimen (HUJ-PAL 3775). (*a*) Drawing of elements as preserved. (*b*) Reconstruction. Scale bar: 1cm.

trochanter of the femur. The photograph (fig. 10.6) is retouched and does not accurately reflect the element's shape. The real right pubis, as preserved, is a crushed and flattened region of bone fragments adjacent to the ilium.

Ischium

The ischium is approximately half the length of the ilium and is spatula-shaped. The dorsolateral end is much wider than the ventromedial end. The middle region of the bone is rounded in cross-section, whereas the ends are flattened. Neither end is well-preserved, and both ends contribute no information regarding the shape of the acetabulum. The ventral margin is concave and composed of finished bone, forming the posterior border of the large thyroid fenestra. The ischial symphysis was restricted to the narrow ventromedial end of the ischium and was therefore weak.

Femur

Both the right and left femora are preserved. The left femur is exposed in medial view, but is poorly preserved. The right femur is exposed in lateral view and is comparatively well-preserved. The anterior margin is very straight, whereas the posterior margin is concave. The femur is expanded at both ends, the distal end being slightly wider. It is not clear if there was a well-developed articular head on the proximal end. However, the distal margin has distinct surfaces (facets) for articulation with the tibia and fibula. The dorsal surface is smooth. The medial (ventral) surface is also relatively featureless: the intertrochanteric fossa is very shallow and the adductor crest is absent, suggesting that the limb adductor and retractor muscles were poorly developed.

Tibia

Only the right limb of the referred specimen bears a complete tibia. On the left limb, the most proximal end of the left tibia is preserved, but the remainder has been lost. The anterior margin is straight, whereas the posterior margin (bordering the antebrachial space) is deeply concave. The proximal end of the bone is 1.3 times wider than the distal end. The distal end bears an articular facet for the astragalus.

Fibula

The right fibula is of equal length to the tibia. The proximal end is rounded whereas the distal end is flattened in comparison; both ends are of equal size. The anterior or margin (bordering the antebrachial space) is deeply curved, similar to the neighbouring margin of the tibia. The antebrachial space formed between the tibia and fibula is teardrop-shaped. The posterior border of the tibia is straighter that of the fibula.

Proximal tarsal row

The proximal tarsal row, as preserved, contains only two elements: the calcaneum and the posterior (postaxial) portion of the astragalus. The most important feature of these two bones is that they are not fused. A weak line of contact, probably non-sutural, clearly separates the two bones.

The preserved portion of the astragalus is slightly smaller than the calcaneum. The posterior portion of the

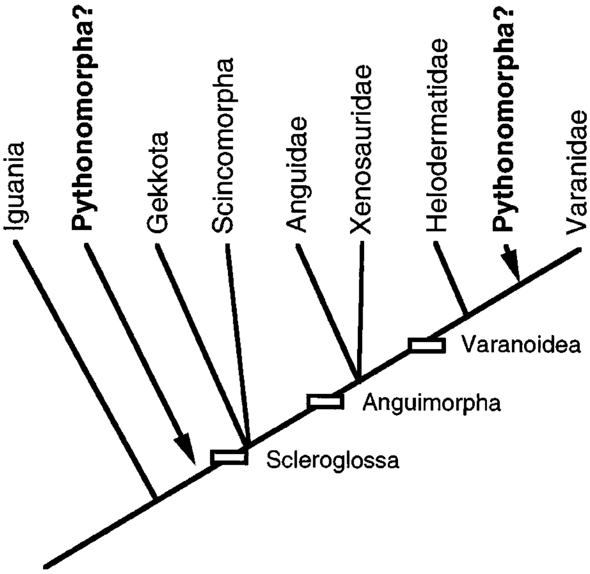

Figure 15. Alternative hypotheses regarding the affinities of pythonomorphs (mosasauroids, *Pachyrhachis*, and modern snakes) within Squamata. Lee (1996*a*) places pythonomorphs within Anguimorpha, as varanid relatives, whereas Caldwell (1998) interprets pythonomorphs as basal scleroglossans, the sister group to all non-iguanian squamates.

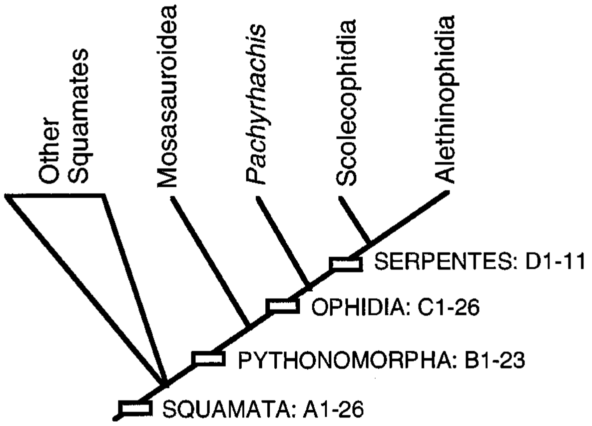

Figure 16. Phylogenetic relationships between *Pachyrhachis* and other squamates. Because of the uncertainty regarding the relationships between pythonomorphs and 'other squamates' (lizards, amphisbaenians, and dibamids), 'other squamates' are here treated as an unresolved but almost certainly paraphyletic grouping. Synapomorphies diagnosing the indicated clades are discussed in the text.

bone, in the position of the 'intermedium' (Caldwell 1996), is rounded and composed of a thicker deposition of bone. There is a small, thin lip of bone that contacts the tibia.

The calcaneum is slightly larger than the preserved portion of the astragalus. It is polygonal in outline and has a small contact with the tibia. The middle portion of the calcaneum is thicker than the margins. For both bones, the thickened areas are interpreted as initial centres of ossification.

Haas (1980*b*) identified these bones as the fibulare and intermedium. If Haas' (1980*b*) identification of these bones is correct, then homologies must be drawn between the proximal tarsals of *Pachyrhachis* and those of amphibian-grade tetrapods, which possess a tibiale, intermedium and fibulare. However, as *Pachyrhachis* is a squamate, comparisons should be made with other squamates (and other amniotes). All amniotes possess only two elements in the proximal tarsal row: the astragalus and calcaneum (Gauthier *et al.* 1988; Rieppel 1993). These comparisons indicate that the two elements in the tarsus must represent the astragalus and calcaneum.

No distal tarsals, metatarsals, or phalanges are preserved. However, the size and ossification of the more proximal limb elements suggests that they were originally present.

6. THE AFFINITIES OF *PACHYRHACHIS* WITH OTHER SQUAMATES

Previous studies of squamate phylogeny (Estes *et al.* 1988; Gauthier *et al.* 1988; Caldwell 1998; Lee 1997*a*) have provided a robust cladistic framework in which to interpret the relationships of *Pachyrhachis*. We discuss how *Pachyrhachis* possesses traits placing it within the following nested clades in Lee's (1997*a*) scheme: Squamata, Pythonomorpha, Ophidia (figure 16). Within Ophidia, *Pachyrhachis* is the sister-group to Serpentes (Scolecophidia plus Alethinophidia), retaining numerous primitive lizard-like features lost in all other snakes. Lee's (1997*a*) scheme, however, considered a limited selection of taxa (snakes and varanoid lizards). Attempting to fit *Pachyrhachis* into this scheme, therefore, does not test the possibility that *Pachyrhachis* has affinities with other squamate taxa (e.g. amphisbaenians).

We therefore also did a more global analysis of the affinities of *Pachyrhachis*, by including it in the data matrix of Caldwell (1998); this study considered all main fossil and recent squamate taxa, including all families of 'lizards', amphisbaenians and dibamids, and employed a revised version of the character list used in Estes *et al.* (1988). However, this analysis attempted to ascertain the affinities of coniasaurs, and thus, included few characters informative with respect to relationships within ophidians. We thus added characters informative with respect to the relationships between *Pachyrhachis*, scolecophidians, and alethinophidians, identified in Scanlon (1996) and Lee (1997*a*). In this analysis (supplementary information to Caldwell & Lee 1997), *Pachyrhachis* again emerged as the sister-group to all other snakes (scolecophidians and alethinophidians). The assumption that *Pachyrhachis* is the sister-group to all other snakes is supported by both studies.

The position of pythonomorphs within squamates is uncertain. Caldwell (1998) argued that pythonomorphs are a basal squamate lineage, the sister-group to all squamates except iguanians, whereas Lee (1997*a*) argued that they are nested deeply within squamates, being positioned within varanoid anguimorphs (figure 15). As the relationships of pythonomorphs with other squamates are uncertain, in the cladistic scheme discussed here (figure 16), we have treated non-pythonomorph squamates—'lizards', amphisbaenians and dibamids—as an unresolved (but probably paraphyletic) assemblage.

(a) *Squamate features of* Pachyrhachis

Earlier descriptions of *Pachyrhachis* (Haas 1979, 1980*a*,*b*) compared it only to two groups of squamates: mosasauroids (mosasaurs, aigialosaurs and dolichosaurs) and modern (crown-clade) snakes (scolecophidians and alethinophidians). Thus, the taxon was assumed to be a squamate, although the evidence for this assumption was never discussed. Our study confirms Haas' (1979, 1980*a*,*b*) assumption that *Pachyrhachis* is a squamate. Of the extensive list of derived osteological traits diagnostic of Squamata (Estes *et al.* 1988; Gauthier *et al.* 1988), the description here demonstrates that *Pachyrhachis* exhibits the derived (squamate) condition in the following. After each trait, the number in normal font is the number of the character in Gauthier *et al.* (1988), whereas the italicized number is the number used in Estes *et al.* (1988). Some characters were only mentioned in one of these studies. As these traits are all discussed in detail in these studies but they are only briefly described here. However, the condition in *Pachyrhachis* is described in detail, when clarification is required.

A1. Premaxillae fused (25, *67*). Reversed in scincids and gekkonids. In other lepidosauromorphs, the premaxillae are paired.

A2. Frontoparietal suture straight and transverse in dorsal view, and broader than nasofrontal suture (27, *2*). The frontoparietal suture in *Pachyrhachis* is transverse in dorsal view. The nasofrontal suture is not preserved, so the second part of this character cannot be ascertained. Other lepidosaurs have a W- or U-shaped frontoparietal suture which is subequal in length to the nasofrontal suture.

A3. Parietals fused (28, *68*). Reversed in some gekkotans and some xantusiids. In other lepidosauromorphs, except for some rhynchocephalians (Evans 1980; Fraser 1982), the parietals are paired.

A4. Parietal table short, braincase exposed dorsally (*69*). This character was tentatively interpreted by Estes *et al.* (1988) as a squamate synapomorphy, reversed in xantusiids, some xenosaurids, some lacertids and some cordylids. In other lepidosauromorphs, the parietal table extends posteriorly, covering the braincase in dorsal view.

A5. Anteroventral border of orbit formed by jugal (*70*). The immediate outgroups to squamates (kuehneosaurs and rhynchocephalians) have the anteroventral orbit formed by the maxilla. This character is equivocal because many squamates have the latter (outgroup) condition (Estes *et al.* 1988).

A6. Absence of quadratojugal (32) and A7. Absence of posterior process of jugal, which contributes to the lower temporal arch (33). Both traits also occur in kuehneosaurs. Other lepidosauromorphs retain the quadratojugal and posterior process of the jugal. These characters, as noted by Gauthier *et al.* (1988), might be convergent (and thus apomorphic) in squamates and kuehneosaurs, or primitive for lepidosaurs and reversed in rhynchocephalians (sphenodontids) (Estes *et al.* 1988, p. 188).

A8. Loss of ventral ramus of squamosal (30, *4*). The element in the holotype tentatively identified as a squamosal lacks the ventral ramus: it is a small sliver of bone that would have been tightly pressed against the supratemporal. In most other lepidosauromorphs, the squamosal possesses a ventral ramus which extends towards the quadratojugal. We consider this character equivocal, however. Kuehneosaurs also lack a ventral ramus of the squamosal, and absence of this process thus may be a lepidosaur synapomorphy reversed (secondarily present) in rhynchocephalians.

A9. Quadrate lacks anteromedial (pterygoid) lappet, quadrate–pterygoid contact fibrous and mobile (38, *71*). A lappet is present (secondarily) in lacertiforms, helodermatids and some iguanids, although the joint is still fibrous and mobile in these taxa (Estes *et al.* 1988; Gauthier *et al.* 1988). In other lepidosauromorphs, the quadrate lappet is present, and the quadrate–pterygoid union is osseous.

A10. Pterygoids do not meet one another in the midline (35, *7*). In other lepidosauromorphs the pterygoids meet each other anteriorly.

A11. Pterygoid broadly enters suborbital fenestra (36, *8*). In other lepidosauromorphs the palatine approaches or contacts the ectopterygoid, mostly or completely excluding the pterygoid from the suborbital fenestra.

A12. Palatine with choanal groove (37). The median process of the palatine in *Pachyrhachis* (and modern snakes) is concave ventrally, and this anteroposterior groove is considered to be homologous to the choanal groove in other squamates. This character is reversed (groove absent) in some varanids (Lee 1997*a*). In other lepidosauromorphs, the ventral surface of the palatine lacks a groove.

A13. Stapes very slender (40, *12*). If the element in the holotype is correctly identified, *Pachyrhachis* has a slender stapes. Other adequately known lepidosauromorphs (younginiforms, kuehneosaurs, and rhynchocephalians) have a stout stapes.

A14. Angular not extending posteriorly to the level of the mandibular condyle (45, *16*). In other lepidosauromorphs the angular extends posteriorly to the level of the condyle.

A15. Coronoid process large and formed entirely by coronoid bone (part of 46, *17*). In most other lepidosauromorphs, the coronoid process is weakly developed and is formed laterally by the surangular. Some rhynchocephalians have a large coronoid process, but in these forms the process still incorporates the surangular laterally.

A16. Absence of proatlas (character 1 in addendum, *63*). Although the atlas–axis complex is preserved articulated in the holotype, and was carefully examined no proatlas was found. We tentatively conclude that the proatlas was genuinely absent. The proatlas is present in other adequately known lepidosauromorphs.

A17. Procoelous vertebrae (53, *77*). Reversed in some gekkonids and some xanthusiids. Other lepidosauromorphs have amphicoelous centra, except for kuehneosaurs, which have platycoelous centra.

A18. Cervical and posterior trunk ribs all single-headed (47, *18*). Other lepidosauromorphs have double-headed ribs in these regions.

A19. Cervical intercentra modified into prominent, blade-like hypapophyses (48, *19*). Reversed in helodermatids. In other lepidosauromorphs, the hypapophyses are weak swellings or they may be absent.

A20. A total of eight or more cervical vertebrae (49, *20*). *Pachyrhachis* completely lacks a shoulder girdle, and thus a clearly defined cervical region. However, various features of the first 18–20 vertebrae are 'cervical-like', and on this basis we tentatively interpret *Pachyrhachis* as possessing the diagnostic squamate condition. Other adequately known lepidosauromorphs have seven cervicals. Although *Sphenodon* has eight cervicals, more primitive rhynchocephalians have the typical seven (Gauthier *et al.* 1988).

A21. Loss of posterior trunk intercentra (52, *79*). Reversed in some gekkonids. Most other lepidosauromorphs possess trunk intercentra. However, we consider this character equivocal because kuehneosaurs also lack intercentra (Gauthier *et al.* 1988). Loss of intercentra may be convergent (and thus, synapomorphic) in kuehneosaurs and squamates, or it may be primitive for lepidosaurs, reversing (intercentra present) in rhynchocephalians.

A22. Enlarged thyroid fenestra in pelvis, pubic symphysis very short (63, *29*). In other lepidosauromorphs the thyroid fenestra is smaller and the pubic symphysis is more extensive.

A24. Loss of the tibial ridge and astragular groove in the tibio-astragalar joint (64, *31*). Other adequately known lepidosauromorphs have the ridge-and-groove articulation.

A25. Fibulo-astragalocalcanear joint involves most of distal end of fibula (65, *32*). In *Pachyrhachis*, most of the distal end of the fibula articulates with the calcaneum (which is separate from the astragalus). In other lepidosauromorphs only a small portion of the distal end of the fibula articulates with the astragalocalcaneum.

A26. Loss of gastralia (69, *36*). Preparation of portions of the ventral surface of the holotype and referred specimen revealed an absence of gastralia. Other lepidosauromorphs retain gastralia.

The following autapomorphies diagnostic of Squamata, to the exclusion of other lepidosauromorphs, are not applicable in *Pachyrhachis* and thus cannot be assessed in this taxon.

Quadrate supported by expanded paroccipital process rather than squamosal (39, *11*). *Pachyrhachis* and modern snakes have neither condition: they are autapomorphic in that the quadrate is supported entirely by the supratemporal.

Squamosal–quadrate contact a peg-and-socket arrangement, rather than a smooth arrangement (31, *5*). *Pachyrhachis* (and modern snakes) lack the squamosal–quadrate contact, and thus the morphology of the contact cannot be determined.

Elongate, gracile limbs (56, *23*). *Pachyrhachis* lacks forelimbs, and the hindlimbs are so greatly reduced that this character is difficult to interpret objectively.

Pachyrhachis lacks a shoulder girdle and forelimbs, and the following squamate synapomorphies are thus not applicable: anterior coracoid emargination (54, *80*); clavicle articulates dorsally with suprascapular cartilage (55, *81*); absence of entepicondylar foramen in humerus (57, *24*); distal end of ulna hemispherical and articulating with enlarged concavity in ulnare (58, *25*); 'styloid' process on distal end of radius (59, *26*); carpal intermedium reduced or absent (60, *27*); lateral centrale in manus contacts second distal carpal (61, *28*); first metacarpal contacts both medial centrale and second distal carpal (62).

Presence of the following squamate autapomorphies in *Pachyrhachis* cannot be confirmed because of poor preservation or missing elements. Narrow nasals (26, *1*); loss of vomerine teeth (34, *6*); septomaxilla with posteroventral projection extending towards dorsal surface of vomer (23, *9*); septomaxilla invests enlarged vestibule, roofing Jacobsen's organ dorsally and flooring nasal passage ventrally (24, *10*); parasphenoid and basisphenoid fused (character 2 in addendum, 62); opisthotic and exoccipital fused (44, *73*)—reversed in dibamids; columelliform epipterygoid with narrow base, not contacting quadrate (41, *13*); subdivision of fissura metotica into recessus scalae tympani anteriorly and jugular foramen posteriorly (42, *14*); vidian canal fully enclosed posterolaterally (43, *15*); 14 scleral ossicles or fewer (*76*); atlas neural arches cover neural canal dorsally (character 3 in addendum, *64*)—the atlas neural arches are slightly displaced and obscured in the holotype, and are not identifiable in the referred specimen; atlas neural arches fused to first intercentrum at maturity (character 4 in addendum, *65*); neural arches fused to centra in embryo (51, *22*); sacral and caudal ribs fused to centra (50, *21*); tongue-and-groove articulation between calcaneum and fourth distal tarsal (part of 66, *33*); dorsally directed flange on calcaneum (part of 66); hooked fifth metatarsal (67, *34*); loss of second distal tarsal (68, *35*).

A few proposed squamate characters are not present in *Pachyrhachis*. This might be seen as evidence that *Pachyrhachis* lies outside Squamata. However, two of these traits are very dubious, and might not be synapomorphies of squamates. Furthermore, all six of these traits are also absent in modern snakes, and four are also absent in mosasauroids. As most recent studies have shown that mosasauroids and modern snakes are nested within squamates (Estes *et al.* 1988; Scanlon 1996; Lee 1997*a*; Caldwell 1997), these characters must have reversed at least once within squamates, in the lineage leading to mosasauroids and modern snakes. Absences of these traits in *Pachyrhachis* and modern snakes (and mosasauroids) probably therefore represent synapomorphic reversals. These characters are therefore consistent the phylogenetic position of *Pachyrhachis* within Squamata proposed in figure 16.

Supratemporal displaced to a deep position, on the ventral surface of the parietal (29, *3*). In other lepidosauromorphs, the supratemporal, when present, lies in a superficial position on top of the parietal. The supratemporal, however, is superficial in *Pachyrhachis* and in modern snakes, unlike other squamates.

Coronoid overlaps dentary laterally (part of 46, *74*). In other lepidosauromorphs, the coronoid does not overlap the dentary laterally. Iguanids, mosasauroids, *Pachyrhachis* and modern snakes, unlike other squamates, lack the coronoid–dentary overlap.

Medial surface of coronoid with deeply concave ventral edge (new character). In other lepidosauromorphs, the coronoid has a straight or convex ventral edge. Mosasauroids, *Pachyrhachis* and modern snakes, unlike other squamates, also have a straight ventral edge.

Subcoronoid fossa present, surangular exposed on medial surface of lower jaw (new character). In other lepidosauromorphs, the coronoid has a continuous contact with the prearticular, and the surangular is not exposed on the medial surface of the lower jaw. Mosasauroids, *Pachyrhachis* and modern snakes, unlike other squamates, have the latter condition.

Absence of zygosphenes and zygantra (*78*). This character is equivocal as many other lepidosauromorphs lack these structures. Unlike most squamates, some iguanians, some scincomorphs, mosasauroids, *Pachyrhachis* and modern snakes have strongly developed zygosphenes.

Absence of palatine teeth (*75*). All other lepidosauromorphs have palatine teeth. However, this character is highly equivocal because, among squamates, palatine teeth are present in some iguanids, some anguids, helodermatids, *Lanthanotus*, *Saniwa*, *Pachyrhachis* and most modern snakes (Lee 1997*a*).

(b) *Pythonomorph features of* Pachyrhachis

Caldwell (1998), Lee (1997*a*,*b*) and Scanlon (1996) have recently proposed that, within squamates, mosasauroids and modern snakes form a robust grouping, and have applied Cope's (1869) taxon name Pythonomorpha to that clade. Mosasauroids consist of two groups of Cretaceous marine squamates, aigialosaurs and mosasaurs (Bell 1993, 1997; Caldwell 1996). Derived characters diagnosing mosasaurs and aigialosaurs, and relationships within that group, are discussed by Russell (1967), deBraga & Carroll (1993), Bell (1993, 1997), Caldwell (1996) and Lee (1997*a*).

A long list of characters unites mosasauroids, *Pachyrhachis* and modern snakes as a monophyletic Pythonomorpha (Caldwell 1998; Lee 1997*a*,*b*). In this list, the number in normal font refers to the corresponding character in the paper by Lee (1997*a*) the number in italics refers to the corresponding character in the paper by Caldwell (1998). For a few of these characters *Pachyrhachis* cannot be coded.

B1. Parietal with large descending process sutured to the prootic (18). In mosasauroids, the descending process is moderate in size, contacting the dorsal margin of the prootic. In *Pachyrhachis* and modern snakes, this process extends much further ventrally, contacting both the prootic and the parabasisphenoid. Other squamates, and rhynchocephalians, lack the parietal–prootic suture.

B2. Supraoccipital sutured with parietals along its entire dorsal margin (49). This also occurs in *Lanthanotus*. In other squamates, and rhynchocephalians, the supraoccipital is either not sutured to the parietal, or sutured along only part of its dorsal margin.

B3. Quadrate suspended entirely by supratemporal (27). In mosasauroids, *Pachyrhachis*, and those modern snakes retaining a large supratemporal, the quadrate is suspended entirely by this element. Even in modern snakes with a reduced supratemporal, the element is usually intercalated between the quadrate and braincase (Lee 1997*a*). In other squamates, and rhynchocephalians, the squamosal and paroccipital process contribute to the quadrate suspension.

B4. Main body (wide portion) of parasphenoid extends anteriorly some distance in front of the dorsum sella, before tapering into a narrow cultriform process (35). The dorsum sella is not exposed in *Pachyrhachis*. However, it can be inferred to possess the pythonomorph condition because the wide portion of the parasphenoid extends anteriorly well beyond the basipterygoid articulation, and the dorsum sella is never anterior to the basipterygoid articulation. In other squamates, and rhynchocephalians the parasphenoid tapers abruptly into the narrow cultriform process immediately in front of the dorsum sella.

B5. Basipterygoid processes do not project far from body of basisphenoid (33). In most other squamates, and rhynchocephalians, the basipterygoid processes are long, narrow, anterolaterally directed projections.

B6. Cultriform process straight and horizontal in lateral view (36). In other squamates, and rhynchocephalians, the cultriform process is curved in lateral view, extending anteroventrally from the braincase and then curving into a horizontal plane.

B7. Discrete sockets (alveoli) under all marginal teeth (86, *65*). Alveoli are absent in most other squamates and in rhynchocephalians, which have pleurodont or acrodont dentition. Discrete marginal tooth sockets are present in some teiids and most mosasauroids. However, in these squamates the teeth develop within the socket, unlike the condition in snakes where the dental lamina is lingual to the tooth row and outside of the sockets. A recent re-evaluation of *Opetiosaurus* (M. W. Caldwell and M. S. Y. Lee, personal observations) indicates that this primitive mosasauroid had pleurodont teeth and thus lacked alveoli: if so, alveoli probably evolved separately within mosasauroids and in ophidians (*Pachyrhachis* and modern snakes). Alternatively, presence of alveoli might characterize pythonomorphs, their absence in *Opetiosaurus* being secondary.

B8. Highly mobile mandibular symphysis, with rounded anterior tips rather than large symphysial surfaces (68, *62*). In other squamates, and rhynchocephalians, the symphysis is firm and the dentaries meet anteriorly via large flat symphysial surfaces.

B9. Coronoid does not overlap dentary laterally. Reversal of squamate apomorphy.

B10. Coronoid with straight or convex ventral edge (78). Reversal of squamate apomorphy.

B11. Surangular exposed in medial view of lower jaw (79). Reversal of squamate apomorphy.

B12. Highly mobile, simple angular–splenial joint (73, *52*). In other squamates, the angular–splenial joint is less mobile, and is a complex irregular junction. This trait is not applicable to rhynchocephalians, which lack a splenial.

B13. Meckelian canal on medial surface of lower jaw (69, *48*). In most other squamates, the Meckelian canal lies on the ventral edge of the lower jaw. Both conditions occur in rhynchocephalians.

B14. Greatly reduced splenial–coronoid contact (72). Also in *Lanthanotus*. In other squamates, the two elements have an extensive contact. This trait is not applicable in rhynchocephalians, which lack the splenial.

B15. Adductor fossa faces dorsally (80). In other squamates, and rhynchocephalians, the adductor fossa faces dorsomedially.

B16. Long and recurved pterygoid teeth (95). In other squamates, and rhynchocephalians, pterygoid teeth, when present, are small denticles.

B17. Four or fewer premaxillary teeth (91). The premaxillary teeth in *Pachyrhachis* are not exposed. However, given the narrowness of the premaxilla in dorsal view, and the size of the marginal teeth, *Pachyrhachis* most probably had four or fewer premaxillary teeth. In most other squamates (see Lee 1997*a*), and in rhynchocephalians (primitively) there are more than four premaxillary teeth.

B18. Presence of well-developed zygosphenes with articular surfaces directed ventrally, and zygantra with articular surfaces directed dorsally (97, *73*). The vertebrae of *Pachyrhachis* are mostly articulated: zygosphenes are visible but their morphology cannot be ascertained. Most other squamates, and rhynchocephalians, lack zygosphenes of this particular morphology: they only occur in some iguanids and teiids (Estes *et al.* 1988).

B19. The three pelvic elements—ilium, ischium and pubis—are not suturally united (130). In other squamates, and rhynchocephalians (primitively) the pelvic elements are suturally united or co-ossified into a single entity.

B20. Astragalus and calcaneum are not suturally united. This occurs in mosasauroids and *Pachyrhachis*, and is of course not applicable in modern snakes. In other squamates, and rhynchocephalians (primitively) the proximal tarsals are fused into a single compound element (the astragalocalcaneum). However, it should also be noted that during development two centres of ossification are noted in the single proximal tarsal cartilage of all squamates. Only late in development do these ossification centres fuse into the single proximal tarsal bone, the astragalocalcaneum. It has been argued by Caldwell (1996) that the astragalus and calcaneum of mosasaurs represent the two ossification centres found within a single proximal tarsal cartilage; *Pachyrhachis* shares this feature with mosasauroids. The paired elements of mosasaurs and *Pachyrhachis* can be interpreted as skeletal paedomorphosis. This is probably a stage in the evolution of limblessness and limb-reduced states.

B21. Absence of epiphyses from skull and vertebral column (140). In other squamates, and rhynchocephalians, epiphyses are present on the skull, in the region of the basal tubera, and on the vertebrae, against the ventral part of the transverse process.

B22. Absence of posterior process on the atlas neural arch (106). In *Pachyrhachis*, there is a dorsally directed process on the atlas neural arch; in mosasauroids and modern snakes there does not appear to be any process at all. Other squamates, and rhynchocephalians, have a posteriorly directed process on the atlas neural arch.

B23. Straight, short femur (135). In most other squamates, and rhynchocephalians (primitively) the femur is typically long and sigmoidally curved. This character is weak as it occurs in many limb-reduced squamates.

The following pythonomorph traits cannot be confirmed in *Pachyrhachis* because of incomplete preservation: lacrimal foramen enclosed entirely by prefrontal (11); basipterygoid processes expanded anteroposteriorly (34); recumbent (horizontal) replacement teeth (90); supratemporal forms part of braincase and contacts prootic (25); crista circumfenestralis encircling footplate of stapes (44); vidian canal is an open groove anteriorly (37); rear opening of vidian canal situated far posteriorly (38); extracolumella with extensive contact with quadrate (45); anterior process of pterygoid distinct from lateral process (62); ribs begin from third cervical vertebra (101).

Lee (1997*a*) interpreted several other characters as pythonomorph synapomorphies: condyles on centra subcircular in shape (110); anterior tip of splenial on medial surface of lower jaw (70), maxilla enters suborbital foramen (66); absence of osteoderms (144). *Pachyrhachis* possesses all of these traits. However, these traits also occur in many squamate lineages, and are thus not compelling synapomorphies uniting pythonomorphs. Lee (1997*a*) concluded that pythonomorphs were nested within anguimorphs: as the listed traits do not occur in most anguimorphs, they were consequently interpreted tentatively as pythonomorph synapomorphies. If pythonomorphs occupy a more basal position within Squamata, as proposed by Caldwell (1998), these traits might diagnose more inclusive groupings of squamates, or might be primitive for Squamata as a whole.

(c) *Ophidian features of* Pachyrhachis

Pachyrhachis and modern snakes (scolecophidians and alethinophidians) form a robust clade, to the exclusion of all other squamates (including mosasauroids), on the basis of numerous derived characters. Many of the traits shared by *Pachyrhachis* and modern snakes were previously thought to be autapomorphies of modern snakes alone (Underwood 1967; Bellairs 1972; Rieppel 1988; Lee 1997*a*). The most recent detailed list of osteological synapomorphies of snakes is Lee (1997*a*), and the number in parentheses after each character refers to the corresponding character in that work.

C1. Mobile premaxilla–maxilla articulation (7). In *Pachyrhachis*, the anterior end of the maxilla is smoothly rounded, and does not have a sutural surface for union with the premaxilla. Presumably, the contact in *Pachyrhachis*, as in modern snakes, was a mobile articulation. In most other squamates, the contact is sutural and immobile.

C2. Descending process of frontal forming at least the anterior margin of optic (II) foramen (40). In other squamates, the optic foramen is not bordered by bone. Some variation also exists between the main groups of snakes. In scolecophidians the entire optic foramen is enclosed by the frontal, whereas in alethinophidians only the anterior border is formed by the frontal.

C3. Descending process of frontal meeting parabasisphenoid (15). In non-ophidian squamates the process does not reach the parabasisphenoid.

C4. Descending process of parietal very extensive, enclosing trigeminal foramen and reaching parabasisphenoid (17). Although most of the descending process in *Pachyrhachis* is not exposed, the ventral edge is exposed and clearly meets the parabasisphenoid. The flange therefore extended all the way down the anterior margin of the prootic to reach the parabasisphenoid, and thus must have enclosed the trigeminal foramen along the way. In other squamates, the descending process of the parietal is either absent, or only meets the dorsal surface of the prootic, not enclosing the trigeminal foramen or contacting the parabasisphenoid.

C5. Supratemporal superficial to parietal. Reversal of squamate apomorphy.

C6. Posterolateral (suspensorial) ramus of parietal greatly reduced (20). In other squamates this process is very long.

C7. Posterior margin of orbit formed by postorbital with long ventral process. *Pachyrhachis*, and modern snakes which possess a postorbital, have this morphology. In other squamates, the postorbital has a short ventral process which does not extend past the centre of the posterior margin of the orbit.

C8. Paroccipital process greatly reduced. In other squamates, the paroccipital process is large and, except in mosasauroids, forms part of the quadrate suspension.

C9. Tympanic recess absent (31). In *Pachyrhachis* and modern snakes, the external surface of the quadrate is smooth and the tympanic recess is absent. In other squamates a distinct tympanic conch projects laterally forming the anterior border of the tympanic recess.

C10. Septomaxilla not sutured to maxilla; mobile septomaxilla–maxilla contact (65). In *Pachyrhachis* and modern snakes, the maxilla is smooth in the region of the ventral border of the external naris. In other squamates, the maxilla bears a sutural surface in this region for the septomaxilla.

C11. Maxilla does not enter margin of opening for Jacobson's organ (52). In *Pachyrhachis*, as in modern snakes, the medial surface of the anterior portion of the maxilla is featureless. Although the opening of Jacobson's organ is not preserved in *Pachyrhachis*, the lack of a medial process on the anterior portion of the maxilla suggests that, as in modern snakes, the maxilla did not enter the margin of the opening. In other squamates, this region of the maxilla bears a prominent medially directed flange that contributes to the margin of the opening for Jacobson's organ.

C12. Vomer positioned medial to palatine (53). In other squamates, the vomer is anterior to the palatine. Though the vomer is poorly preserved in *Pachyrhachis*, the palatine extends so far anteriorly in the palate that the vomer could not have fitted anterior to them. Rather, the vomer must have been positioned medial to the anterior portion of the palatine. The vomer and septomaxilla were probably suspended from the snout complex in the same manner as observed in modern snakes.

C13. Palatine with rectangular medial process, which meets its partner in the midline (59). In other squamates the palatine lacks a distinct medially directed process. This character is not applicable in scolecophidian snakes, where the palatine is greatly reduced.

C14. Dentary with two or fewer mental foramina (76). *Pachyrhachis* has two foramina on the lateral surface of the dentary, modern snakes have one (Scanlon 1996).

C15. Marginal teeth ankylosed to the rims of discrete sockets (86). As described above, discrete marginal tooth sockets are present in teiids and mosasaurs but the teeth are deeply implanted into these sockets and develop from within the socket, unlike the condition in *Pachyrhachis* and modern snakes where the teeth are ankylosed to the rims of the sockets, and the dental lamina is lingual to the sockets.

C16. More than 120 precloacal vertebrae (102). Most other squamates have fewer than 120 presacrals, typically fewer than 30.

C17. Absence of shoulder girdle and forelimb (118, 119, 121, 124, 127). *Pachyrhachis* and modern snakes have both completely lost all traces of the shoulder girdle and forelimb. All other squamates, even limb-reduced forms, retain some vestiges of the shoulder girdle.

C18. Absence of limb epiphyses (138). No epiphyses are present on the hindlimb of *Pachyrhachis* or those modern snakes which retain hindlimbs. Epiphyses are present on the limbs of other squamates, with the exception of mosasaurs. However, they appear to have been lost independently within mosasauroids, because all primitive mosasauroids (aigialosaurs) retain limb epiphyses (see, for example, Carroll & deBraga 1992; Caldwell *et al.* 1995).

There are other derived traits shared between *Pachyrhachis* and modern snakes. These, however, are less compelling as evidence of close relationships because they occur in several other groups of squamates, or because they are not found in all modern snakes.

C19. Absence of lacrimal (10). This trait is weak because it also characterizes gekkotans, dibamids, some iguanians, some scincomorphs and some amphisbaenians. In most other squamates, the lacrimal is present.

C20. External jaw adductor muscles insert on most of the dorsal surface of the parietal (19). This trait is weak because it also occurs in dibamids, amphisbaenians, teiids, mosasaurs, some large varanids such as *Varanus komodoensis*. In other squamates, the external jaw adductors never encroach on more than the lateral edge of the dorsal surface of the parietal.

C21. Parietal table reduced to a sagittal crest (19). This trait is weak because it also occurs in teiids, mosasaurs, and some large varanids such as *Varanus komodoensis*. In other squamates, the parietal table is a wide, flat area. This character is correlated with the morphology of the jaw adductor muscles, as noted in character C20.

C22. Loss of parietal foramen (21). Most other squamates retain this foramen. However, it is also absent in gekkotans, dibamids, most amphisbaenians, gymnophthalmids, *Heloderma*, *Estesia*, and *Lanthanotus*.

C23. Loss of upper temporal arcade (22). Most other squamates retain this arcade. However, it is also absent in gekkotans, dibamids, and *Heloderma*. Absence in some amphisbaenians (see Wu *et al.* 1993) and some lanthanotids (see Lee 1997*a*) is derived within each group.

C24. Surangular, prearticular and articular fused into a single compound postdentary element (81). This trait is equivocal because dibamids also possess a single compound postdentary element, whereas in other squamates the three bones are discrete elements. However, it should also be noted that the condition in dibamids is even more derived: the angular and splenial are either part of the compound bone or are developmentally lost. This is not the condition in snakes, in which the splenial and angular are distinct elements.

C25. Anterior portion of compound postdentary element bears a long, pointed anterior process that extends along the lateral surface of the dentary (83). In other squamates the anterior process of the surangular is shorter and usually less pointed. In some taxa, such as mosasaurs, the surangular is pointed but inserts into the dentary, not along the outside of the element. However, this trait is weak because in scolecophidian snakes the compound bone does not extend past the anterior end of the coronoid; it never bears a long anterior process that extends onto the dentary for any distance past the anterior end of the coronoid.

C26. Reduced pelvis and hindlimbs (129). The pelvis and hindlimb of *Pachyrhachis*, although normal in shape, are reduced, approaching the condition in modern snakes. Whereas most squamates have a much larger pelvis and hindlimbs, similar reduction is found in the numerous groups of elongate forms.

(d) *Advanced features of modern snakes* (*Serpentes*) *absent in* Pachyrhachis

Based on the previous characters, *Pachyrhachis* is clearly the closest relative of modern snakes. However, it retains more primitive characters than any modern snake. The following derived characters unite scolecophidians and alethinophidians, the two clades of modern snakes (Underwood 1967; Rage 1984; Rieppel 1988; Kluge 1991; Cundall *et al.* 1993), to the exclusion of *Pachyrhachis*. In these characters, *Pachyrhachis* retains the primitive condition found in other squamates ('lizards', dibamids, and amphisbaenians). As before, the number in parentheses after each character refers to the corresponding character in Lee (1997*a*).

D1. Absence of jugal. All modern snakes, with a single possible exception, lack a jugal. The primitive alethinophidian snake *Dinilysia* has been tentatively interpreted as possessing a jugal (Estes *et al.* 1970; Frazetta 1970). However, the fragment called the 'jugal' is a horizontal sheet of bone that overlies the posterior end of the maxilla, behind the orbit. In modern snakes, the ectopterygoid has exactly these relationships. For these reasons, presence of a jugal in *Dinilysia* is dubious at best.

D2. Absence of squamosal (28). All modern snakes lack a squamosal. If our interpretation of the sliver of bone in *Pachyrhachis* is correct, this taxon is more primitive than all modern snakes in retaining a squamosal.

D3. Incomplete (discontinuous) posterior orbital margin (24). Among other squamates, this occurs in derived varanids (*Varanus*), derived amphisbaenians and dibamids. However, the first two occurrences are clearly convergent because more primitive varanids (Lee 1997*a*) and primitive amphisbaenians (Wu *et al.* 1993, 1996) retain a complete posterior orbital margin.

D4. Exoccipitals meet above the foramen magnum (48). In all other squamates, the two exoccipitals are separated by the supraoccipital.

D5. Angular–coronoid contact on medial surface of the mandible. In other squamates, the angular and coronoid are separated by the prearticular.

D6. Single mental foramen. Modern snakes have one mental foramen on the mandible. *Pachyrhachis* has two, and all other squamates have three or more (Scanlon 1996).

D7. Reduced neural spines (100). In scolecophidians and basal alethinophidians, the neural spines are reduced to low ridges, making the body perfectly cylindrical. In other squamates, the neural spines are tall blades.

D8. Pelvis lies within ribcage, sacral ribs lost (131). In modern snakes, the sacral contact is lost and the pelvic rudiments, when present, lie within the ribcage. This trait may also occur in mosasaurs (Dobie *et al.* 1986); however, such an occurrence is probably convergent with modern snakes because primitive mosasauroids (aigialosaurs) retain a normal sacral contract (Carroll & deBraga 1992; Caldwell *et al.* 1995). *Pachyrhachis*, like most other squamates, has the normal arrangement where the ilium lies outside the ribcage and contacts the sacral rib.

D9. Two or more forked cloacal ribs (111). *Pachyrhachis* has at most, a single forked cloacal rib (the sacral). Modern snakes have two or more forked clocal ribs (lymphapophyses). Weakly forked ribs also occur in amphisbaenians. Other squamates have normal ribs in this region.

D10. Small femur (134). The femur in *Pachyrhachis* is smaller than in typical limbed squamates. In modern snakes it is even smaller or absent.

D11. Loss of tibia, fibula, astragalus and calcaneum (134). Modern snakes have lost all hindlimb elements except for the femur. Some alethinophidians (pythons and boids) have a single claw-like element of uncertain homology distal to the femur, used in courtship. *Pachyrhachis* is more primitive than modern snakes in retaining a normal tibia, fibula, astragalus and calcaneum.

(e) *Advanced features shared by alethinophidians and* Pachyrhachis

Despite the number of characters supporting our finding that *Pachyrhachis* is the most primitive snake, there are several characters that suggest a close relationship between *Pachyrhachis* and alethinophidians to the exclusion of scolecophidians. This hypothesis therefore merits serious consideration: indeed, the skull of *Pachyrhachis* superficially resembles certain alethinophidians such as boines and pythonines. At present these characters are tentatively considered homoplastic: convergent in *Pachyrhachis* and alethinophidians, or secondarily absent in scolecophidians. However, a comprehensive reanalysis of the main groups of primitive snakes, including *Pachyrhachis* and Dinilysia, is currently underway to rigorously test this interpretation.

E1. Long supratemporal. In *Pachyrhachis* and most alethinophidian snakes, the supratemporal is a long parasagittal element that projects posteriorly behind the parietal. It carries the quadrate (and thus jaw joint) further posteriorly and increases the size of the jaw apparatus. In other squamates the supratemporal does not extend backwards past the parietal.

E2. Vertical or posteroventrally oriented quadrate. In *Pachyrhachis* and the primitive alethinophidian *Dinilysia* (Estes *et al.* 1970; Frazetta 1970) the quadrate is vertical. It is oriented posteroventrally in other alethinophidians. In other squamates, it is oriented anteroventrally (Rieppel 1988).

E3. Large, recurved palatine teeth. The palatine teeth are large and recurved in *Pachyrhachis* and in alethinophidians which possess palatine teeth. In other squamates, palatine teeth, when present, are small denticles.

E4. Long, narrow palatine. The palatine in *Pachyrhachis* and alethinophidian snakes is a long, narrow parasagittal element. In most other squamates, the palatine is a transversely broad, triradiate element. This character is difficult to interpret in scolecophidians, where the palatine is vestigial.

7. A PHYLOGENETIC TAXONOMY OF PYTHONOMORPHA

Our conclusion that *Pachyrhachis* is the sister-group to all known snakes (scolecophidians and alethinophidians) is here formalized in the following indented monophyletic taxonomy. All the taxon names are here given node-based and stem-based phylogenetic definitions (see de Queiroz & Gauthier 1990, 1992), except for the monospecific taxon *Pachyrhachis problematicus*. The 'genus' level taxon *Pachyrhachis* is currently redundant with *Pachyrhachis* *problematicus* and is thus not formally recognized (see de Queiroz & Gauthier 1992).

Pythonomorpha
  Mosasauroidea
  Ophidia (= 'snakes')
    Pachyrhachis problematicus
    Serpentes (= 'modern snakes')
      Scolecophidia
      Alethinophidia

(a) *Pythonomorpha*

Definition: the most recent common ancestor of mosasauroids and ophidians (snakes) and all its descendants (Caldwell 1997; Lee 1997*a*). This taxon contains mosasauroids, *Pachyrhachis*, scolecophidians, and alethinophidians. Diagnosis: see synapomorphies listed here.

(b) *Mosasauroidea*

Definition: the most recent common ancestor of aigialosaurs and mosasaurs, and all its descendants (Lee 1997*a*; Caldwell 1997). The contents of this taxon are listed in Bell (1993, 1997) and Caldwell (1996). Diagnosis: see Lee (1997*a*).

(c) *Ophidia*

Definition: the most recent common ancestor of *Pachyrhachis* and Serpentes (modern snakes), and all its descendants. This taxon contains *Pachyrhachis* and the two groups of extant snakes, scolecophidians and alethinophidians. Diagnosis: see synapomorphies listed in the previous paragraph. We suggest using the vernacular term 'snakes' to apply to this clade.

(d) Pachyrhachis problematicus

Definition: the most inclusive grouping of organisms, inferred to have formed an interbreeding assemblage, that includes HUJ-PAL 3659 (holotype). A species-level taxon, currently containing the specimens HUJ-PAL 3659 and HUJ-PAL 3775. Diagnosis: see autapomorphies listed here.

(e) *Serpentes*

Definition: the most recent common ancestor of scolecophidians and alethinophidians, and all its descendants (Estes *et al.* 1988). A crown-clade definition (see de Queiroz & Gauthier 1992; Bryant 1994; Lee 1996). Diagnosis: see synapomorphies here. We suggest applying the vernacular term 'modern snakes' to this clade.

(f) *Scolecophidia*

Definition: typhlopids, and all taxa more closely related to typhlopids than to alethinophidians. The contents of Scolecophidia are typhlopids, leptotyphlopids, and anomalepidids. Diagnosis: see synapomorphies listed in McDowell (1987) Rieppel (1988), Cundall *et al.* (1993) and Lee (1997*a*).

(g) *Alethinophidia*

Definition: colubroids, and all taxa more closely related to colubroids than to scolecophidians. The contents of Alethinophidia are *Dinilysia*, *Anomochilus*, aniliids, cylindrophids, uropeltids, xenopeltids, boines, pythonines, erycines, trophidophiines, bolyerines, *Acrochordus* and colubroids. Diagnosis: see synapomorphies listed in Underwood (1967), McDowell (1987), Rieppel (1988), Cundall *et al.* (1993) and Lee (1997*a*).

Finally, our use of the vernacular term 'snake' to include *Pachyrhachis* should be justified. The number of evolutionary changes or synapomorphies separating *Pachyrhachis* from modern snakes (Serpentes)—11 is much less than the number of changes separating *Pachyrhachis* and modern snakes from their nearest 'lizard' relatives, mosasauroids—between 18 and 26 (figure 16). Although *Pachyrhachis* is somewhat intermediate between snakes and lizards, it is thus more snake-like than lizard-like. Furthermore, we have shown our drawings and reconstruction of *Pachyrhachis* to numerous non-herpetologists—lay people who will use 'snake' in its vernacular sense—and they have all identified it as a snake rather than a lizard. For these reasons, we prefer to refer to *Pachyrhachis* as a primitive snake, rather than a snake-like lizard. Consequently, we recommend that the informal term 'snake' be used to refer to the formal taxon Ophidia, and the informal term 'modern snakes' be used to refer to the formal taxon Serpentes.

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