ISSN 0077–8554

PALAEONTOLOGIA AFRICANA

ANNALS OF THE BERNARD PRICE INSTITUTE FOR
PALAEONTOLOGICAL RESEARCH
UNIVERSITY OF THE WITWATERSRAND
JOHANNESBURG

VOLUME 35, 1999

ISSN 0078-8554

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JOHANNESBURG

VOLUME 35, 1999

ACKNOWLEDGEMENTS

The Bernard Price Institute for Palaeontological Research gratefully acknowledges financial support for its programmes and for publication of this journal by

THE COUNCIL'S RESEARCH COMMITTEE, UNIVERSITY OF THE WITWATERSRAND.
NATIONAL SCIENCE FOUNDATION (NSF)

BERNARD PRICE INSTITUTE
for
PALAEONTOLOGICAL RESEARCH

University of the Witwatersrand
Johannesburg
1999

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PALAEOBIOLOGY OF EARLY CARBONIFEROUS LACUSTRINE BIOTA OF THE WAAIPOORT FORMATION (WITTEBERG GROUP), SOUTH AFRICA.

by

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ABSTRACT

The Early Carboniferous (Viséan) Waaipoort Formation (Cape Supergroup, Witteberg Group) is a heterolithic sandstone dominated formation containing apatite-rich and calcite-rich fossiliferous nodules. Exposures of the Waaipoort Formation (Lake Mentz Subgroup) are not common and are found within the Cape Fold Belt in the Eastern and Western Cape. Fossils in the formation include palaeoniscoid fishes, sharks, acanthodians, ichnofauna, thin-shelled unionid bivalves, two genera of plants, and a cyrtoctenid eurypterid. The salinity of the Waaipoort dual basin depository is interpreted as being fresh to brackish water with some minor fluctuations. The palaeoenvironment is interpreted as being lacustrine.

KEYWORDS: Waaipoort Formation; Witteberg Group; *Palaeoniscoidea; Acanthodii; Chondrichthyes.*

INTRODUCTION

The Waaipoort Formation (Lake Mentz Subgroup, upper Witteberg Group) is the only significant fossiliferous succession of Early Carboniferous (Viséan) age in southern Africa. One of the most important aspects of the Waaipoort Formation is therefore the fossil assemblage which is often used in palaeoenvironmental studies, e.g. the recognition of lacustrine settings (Pickard & High 1972). A number of previous workers have discussed the palaeontology of the Waaipoort (e.g. Theron 1962; Marais 1963; Jubb 1965; Gardiner 1969; Jubb & Gardiner 1975), but palaeobiological studies incorporating sedimentology were not attempted. In a recent study (Evans 1997) fossil assemblages were used in conjunction with sedimentological and taphonomic data to reconstruct the palaeobiology of the Waaipoort biota and to infer a lacustrine depositional setting. Waaipoort fossil material in previous collections was reviewed and substantial further collections were made from 12 localities (Figure 1), yielding important new specimens of unionid bivalves, acanthodian spines, shark scales, palaeoniscoids, vascular plants, ichnofauna and Problematica.

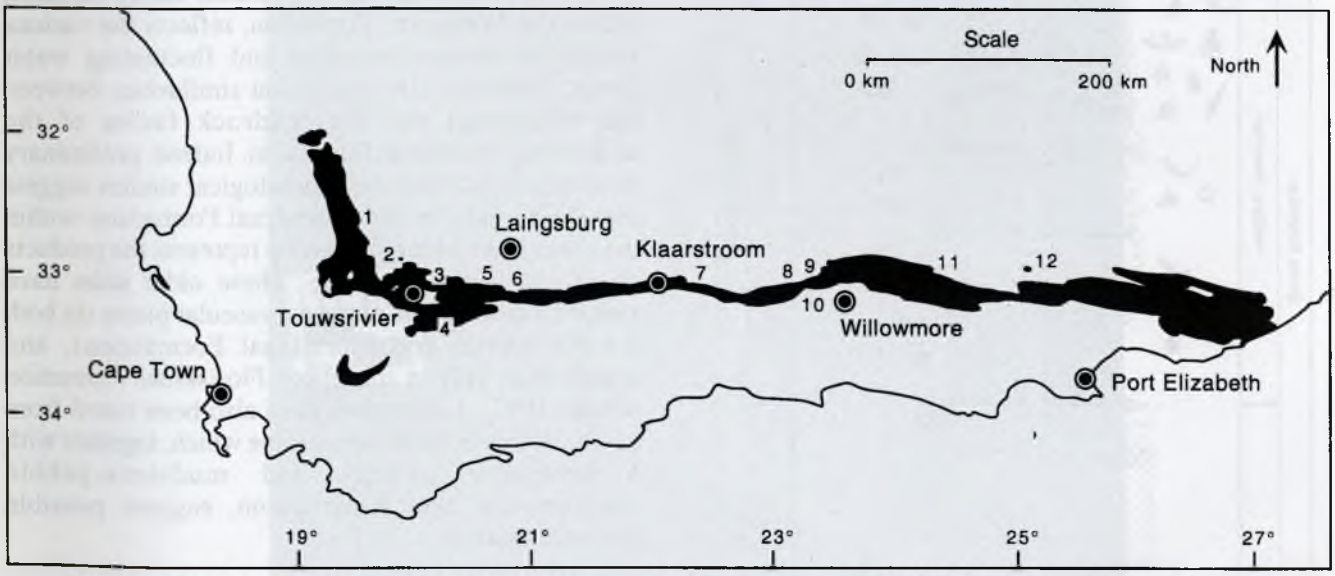

Figure 1: Map of the outcrop area of the Waaipoort Formation and the fossiliferous localities mentioned in the text.

OUTCROP AREA

In the Western Cape the Waaipoort Formation outcrops within the north-south trending western branch of the Cape Fold Belt from north of Inverdoorn (Ceres Karoo) to west of Touwsrivier, and along the east-west trending southern branch of the Cape Fold Belt as far as Grahamstown in the Eastern Cape. Exposures are poor in most places, due to the generally recessive weathering pattern and vegetation or drift cover. Because of the heterolithic nature of the subfeldspathic, mica-rich sediments, the softer-weathering mudrocks and fine-grained sandstones of the mid- to upper Waaipoort Formation (usually the most fossiliferous units) exposures are present at only a few localities.

GEOLOGICAL SETTING AND SEDIMENTOLOGY

Deposition in the Cape Supergroup Basin of southern South Africa commenced in the Ordovician (Broquét 1992). By the Early Carboniferous the basin had decreased to one third the original size (Cloetingh *et al.* 1992), when it consisted of two sub-basins of unequal size (Rust 1973; Veevers *et al.* 1994) situated in subpolar latitudes (Scotese & McKerrow 1990). The subdivision of the Cape Basin is also partly reflected in the palaeobiogeographical distribution of fossil species within the Waaipoort Formation (see below).

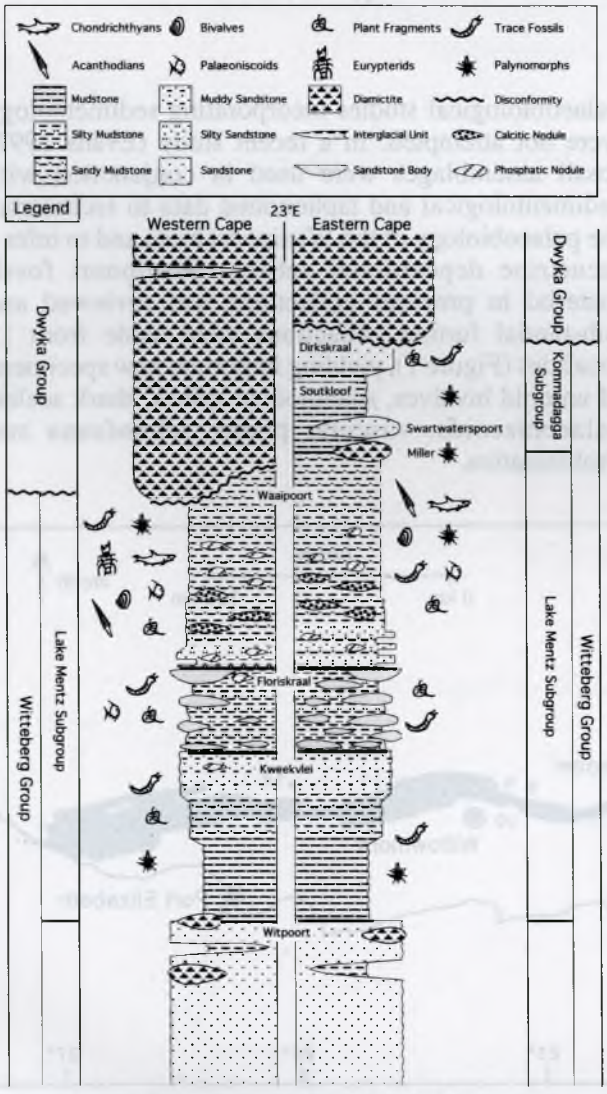

Figure 2. Stratigraphic summary of the upper Witteberg Group, Cape Supergroup of South Africa, also showing the Kommadagga Subgroup which intervenes between the Waaipoort Formation and Dwyka Group in the Eastern Cape Province, pinching out in the Western Cape.

The Waaipoort Formation forms the uppermost unit of the Lake Mentz Subgroup of the Witteberg Group (Figure 2). West of longitude 23°E, the Mid-Carboniferous glacial rocks of the lower Dwyka Group directly overlie the Waaipoort Formation (Johnson 1976), with "stepwise" erosion westwards into progressively lower formations of the Witteberg Group (Loock 1967). To the east of longitude 23°E the Kommadagga Subgroup consisting of four formations (Swart 1982; Johnson 1994) intervenes between the Lake Mentz Subgroup and the Dwyka Group.

Previous interpretations of the depositional setting of the Waaipoort Formation include estuarine (Theron 1962), non-deltaic shelf (Johnson & le Roux 1994), upper prodelta slope and outer delta front (Johnson 1976), lagoonal to mudflat (Theron 1993), continental (Broquét 1992) and lacustrine (Marais 1963; Gardiner 1969). On the basis of recent palaeontological and sedimentological work (Evans 1997) the Waaipoort Basin is interpreted here as an extensive open lake influenced at times by possible glacial and storm processes. Some evidence for nearshore, current- and particularly wave- influenced sedimentation (e.g. oscillation and current rippled bedding planes), and offshore turbidite deposition within a sub-lacustrine fan environment (e.g. thin beds of repeated upper Bouma sequences at some localities) can be seen in detailed sedimentary sections which concentrated around fossiliferous nodule-bearing units in the Eastern and Western Cape (see Evans 1997 for more detail). Extensive lateral and vertical facies variation within the Waaipoort Formation, reflects the various lacustrine sub-environments and fluctuating water levels. There are also significant similarities between the Waaipoort and the mudrock facies of the underlying Floriskraal Formation. Indeed, preliminary palaeontological and sedimentological studies suggest that the Kweekvlei and Floriskraal Formations within the lower Lake Mentz Subgroup represent the products of an extensive, open lake. These older units have yielded a sparse biota of traces, vascular plants (in both the Kweekvlei and Floriskraal Formations), and acanthodian fish in the upper Floriskraal Formation (Evans 1997). Lonestones have also been noted from two localities in the Western Cape which, together with a lenticular quartz- and mudstone-pebble conglomerate near Klaarstroom, suggest possible glacial influence.

Fauna, Flora and Taphonomy

Fish and vascular plant fossils are found predominantly within phosphate- and calcite- rich nodules, but plant material also occurs less commonly

Figure 3: Latex cast of *Willomorichthys striatulus* Gardiner 1969 from the Willowmore district, a laterally preserved, fusiform palaeoniscoid with anterior portion of skull and posterior portion of body missing. Note the large ridge scales anterior to the dorsal fin and the distinctive ornamentation on the dermal plates of the skull. SA Museum 13541. Scale bar in cm.

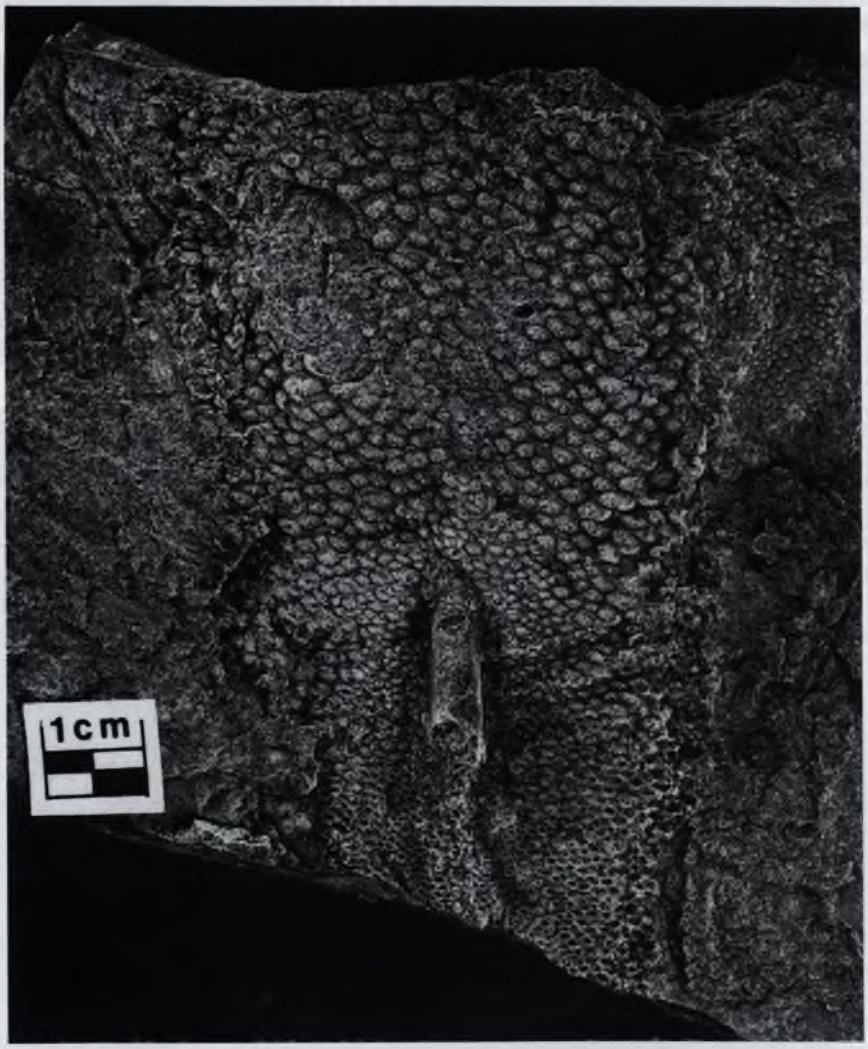

Figure 4: From the Willowmore district, an articulated ?protacrodontid shark body situated within a nodule, with the base of the dorsal neck spine *in situ* (anterior towards top). Council for Geoscience (Bellville) B.0351.

"floating" in the fine-grained sandstone matrix. Geochemical analysis reveals significant amounts of the phosphatic mineral apatite, particularly in one type of nodule. Other nodule types which have been defined on the basis of process of formation and fossil content (Evans 1997) are lenticular, calcite-rich, and may extend up to several tens of meters laterally. They often contain dense horizons of transported, fragmentary plant material. Fossiliferous nodules may include several layers of fish material and mud pebbles, representing thin fining-up sequences, while many of the apatite-rich nodules contain articulated palaeoniscoid fishes (Figure 3), and other biota, including shark (Figures 4-5) and acanthodian fish fragments (Figures 6-7), bivalves (Figure 8), eurypterids, and traces representing various, mainly soft- bodied organisms (Figure 9). Exposures on Schiethoogte near Darlington Dam (previously Lake Mentz), Eastern Cape, are characterised by a layer of densely - packed, fully articulated palaeoniscoid fish (Figure 10). Sedimentological evidence indicates that this mass mortality horizon occurs at the top of a sequence of storm beds in the lower Waaipoort Formation. It is suggested here that mass mortality was probably related to an anoxic event, perhaps caused by overturning of the deep, seasonally-induced thermally-stratified Waaipoort lake triggered by a storm event.

In addition to palaeoniscoids, Waaipoort Formation ichthyofaunas comprise subordinate chondrichthyans (Figures 4-5) and acanthodians ("spiny sharks") (Figures 6-7). Additional examples of both groups have recently been recognised from previous and new collections (Evans 1997). Fragmentary and articulated remains (scales, teeth, fin spine) of ctenacanthiform sharks, including a semi-articulated possible protacrodontoid (Figure 4), have been collected from the Klaarstroom and Willowmore Districts (Oelofsen 1981). At least three acanthodian genera, including the advanced climatiiform *Gyracanthides* (Figures 6-7) and probable acanthodiforms, are represented by fin spines and scales (eg. Gardiner 1973). This material has been briefly described for the first time on the basis of the ornamentation of both these elements (Evans 1997). Acanthodian material is rare in the eastern Waaipoort sub-basin, but is relatively common in the western outcrop of the Waaipoort Formation (from Touwsrivier to Laingsburg and in the Willowmore district itself). A variety of palaeoniscoid actinopterygians (primitive bony fish) represent the most common fauna in the formation and are the only order of fish represented at the fish mass mortality horizon at Schiethoogte 279 in the Eastern Cape. The palaeoniscoids are often well-articulated, and eight genera were recognised by Gardiner (1969), who placed several in families which also occur in the Carboniferous of Scotland. These include several deep-bodied and fusiform genera. Extensive palaeoniscoid material in new and previous collections is currently being reviewed systematically and there are several new or previously misidentified species from the Waaipoort.

The Waaipoort invertebrate biota includes a single specimen of giant cyrtoctenid eurypterid (ca. 1,5m long, enclosed within a nodule) collected near Klaarstroom (Waterston *et al.* 1985) and two forms of rare smooth, thin-shelled bivalves (possibly unionids) from Soetendalsvlei, near Willowmore, shown in Figure 8. Low diversity trace fossil assemblages have been recorded from rocks of the Waaipoort Formation for the first time (Figure 9). Burrowing often occurs within discrete horizons and indicates changing patterns of bioturbation, sedimentation rate and bottom oxygenation, including periods of anoxia. The traces can be ascribed to the activity of infaunal bivalves, arthropods and indeterminate "worms".

Waaipoort floras are markedly low in diversity compared with those recorded from the slightly older Witpoort mudrocks (Gess & Hiller 1995), perhaps due to the influence of colder climates at high, subpolar palaeolatitudes. Longitudinally-ridged plant stems of problematic, possibly progymnosperm, affinities (*Praeramunculus striatiramus*) are very common, especially within the calcareous lenses, while a small variety of lycopods (e.g. *Archaeosigillaria caespitosa*) also occur. New collections are revealing a somewhat greater lycopod diversity than have been recorded by Anderson & Anderson (1985).

Despite some conflicting palaeontological evidence, the salinity of the Waaipoort depository and also the whole Lake Mentz Basin is tentatively interpreted as being fresh to brackish water in a lacustrine system. The fish groups present, including the primitive sharks, contain both marine and non-marine members, and there are differences in ichthyofauna between the sub-

Figure 5: Latex cast of semi- articulated scales (unornamented) of an unidentified ?shark from Zwartskraal. Magnification x3. R. Oosthuizen Collection A.63.

Figure 6: Latex cast of an incomplete fin spine of the climatiiform acanthodian, *Gyracanthides*, from Laingsburg clearly showing nodes on the ridges which are arranged in a distinct chevron pattern. Magnification x2. Geology Dept., University of the Free State, Bloemfontein. 97.123

Figure 7: Latex cast of disarticulated scales of *Gyracanthides* within a nodule from Koega, showing the distinct ridged ornamentation on the crowns. Magnification x3. SA Museum BW.214

Figure 8: Articulated, elongate, possibly freshwater, thin-shelled bivalves (Family Unionidae?) from the Willowmore district, arranged in a clump within a small phosphatic nodule. Magnification x3. R. Oosthuizen Collection F.99.

Figure 9: Polished section through a thinly-laminated mudrock from the Waaipoort Formation at Koega, showing a lined horizontal intrastratal burrow. Council for Geoscience (Bellville) TW.016.

Figure 10: Fossiliferous block from the mass mortality fish horizon at Schiethoogte, Eastern Cape showing density and high degree of articulation of the palaeoniscoids. Council for Geoscience (Bellville). B0354.

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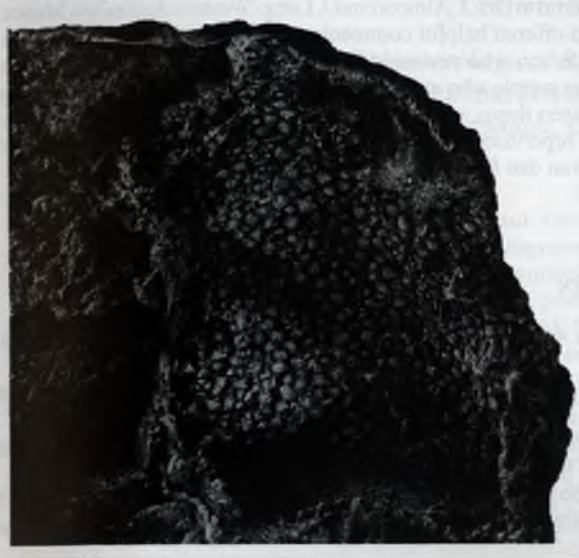

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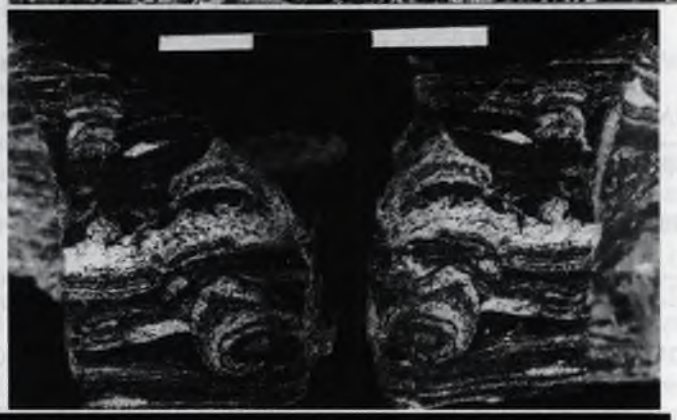

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basins of the Waaipoort. Scottish Carboniferous palaeoniscoids from the same families as Waaipoort genera were apparently freshwater inhabitants. Fully marine salinities are unlikely in view of the very restricted invertebrate biota (stenohaline marine phyla absent) and ichnofauna (cf. Buatois & Mangano 1992) as well as the absence of marine algae (cf. Witpoort estuarine floras; Gess & Hiller 1995). The abundance of allochthonous vascular plant material, with occasional thin-shelled bivalves and eurypterids favours a restricted (hyposaline) to freshwater environment. The latter view may also be supported by isolated gyrogonites (reproductive structures of brackish-freshwater Charophyta) from the Klaarstroom area, although the provenance of this material from the Waaipoort requires confirmation and identification is incomplete. Salinities may have varied during Waaipoort times; small scale fluctuations are suggested by locally abundant synaeresis cracks.

ACKNOWLEDGEMENTS

My thanks go to the Foundation for Research and Development for their financial support during 1995 and 1996, and to Dr J. Almond (Council for Geoscience) for photography. I am very grateful to Drs. J. Almond and J. Long (Western Australian Museum) who offered helpful comments on this paper, and J. Loock and E. Anderson who reviewed this paper. I would like to thank many other people who made great contributions during the course of my Masters thesis, which forms the basis of this paper, and in particular my supervisors Drs R.M.H. Smith (South African Museum) and J. A. van den Heever (University of Stellenbosch).

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Palaeont. afr., **35**, 7-19 (1999)

OBSERVATIONS ON THE STRUCTURE OF THE EARLY PERMIAN REPTILE *STEREOSTERNUM TUMIDUM* COPE

by

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ABSTRACT

New information on the mesosaur *Stereosternum tumidum* is derived from a nearly complete skeleton and other material. Two autapomorphies are identified for *Stereosternum*: (1) presence of an 'odontoid' axial process, formed probably by co-ossification of the atlantal pleurocentrum to that of the axis, and (2) the presence of a posterior supraneural process on the neural arch of dorsal vertebrae. Temporal fenestration appears to be absent in *Stereosternum*, marginal teeth are determined to be subcircular rather than oval in cross section and in this respect resemble those of *Mesosaurus*, and there is no sign of fracture planes in the caudal vertebrae that could be indicative of caudal autotomy. A phylogenetic analysis, based on a slightly modified data matrix from the literature, identifies Mesosauridae as the sister group of Parareptilia within the reptilian clade Anapsida (*sensu lato*). As a consequence of this rearrangement of amniote tree topology, the stem-based taxon Sauropsida is regarded to be in abeyance, because it now includes exactly the same taxa as Reptilia. Mesosaurs, at more than 275 million years of age, can be recognised as the oldest known anapsid reptiles.

KEYWORDS: *Stereosternum*, mesosaurs, Anapsida, phylogeny, Permian

INTRODUCTION

Stereosternum tumidum was described in 1886 by E. D. Cope on the basis of specimens collected from limestones of the Irati Formation, Sakmarian of Brazil. These initial materials preserved only the posterior half of the skeleton, but the following year he (Cope 1887) published a brief description of a skull that, unfortunately, lacked an illustration. Cope recognized that *Stereosternum* shared several characteristics with the aquatic reptile *Mesosaurus tenuidens* (Gervais 1865), known then only from a single specimen from the white-weathering black shales of the Whitehill Formation of southern Africa. Interestingly, *Mesosaurus* was later collected in great quantities from the black shales of the Irati Formation less than three decades later (MacGregor 1908), whereas a century passed before *Stereosternum* was described also from the limestones of the Whitehill Formation (Oelofsen & Araújo 1987).

Following Cope's (1886, 1887) early descriptions, only Osborn (1903) published a detailed description of *Stereosternum*. Osborn's material was only slightly more complete than that available to Cope, and thus many aspects of the anatomy of *Stereosternum* still remain poorly known, especially that of the skull. Current knowledge of mesosaurid anatomy is derived almost exclusively from specimens of *Mesosaurus* (Seeley 1892; MacGregor 1908; Wiman 1925; Huene 1941; Oelofsen 1981). This is surprising, considering that specimens of *Mesosaurus* must be studied from natural moulds that, prior to the adoption of latex casting technology (Heaton 1982), necessitated their study via relatively poor plaster and gutta percha casts. The friable nature of the black shale matrix also limits the number of specimens preserving the greater part of the skeleton. Thus, most of our knowledge of mesosaurid anatomy is based on relatively meagre materials. In strong contrast, complete skeletons of *Stereosternum* of exceptional preservation have been collected from the Irati Formation limestones. One of the best prepared specimens is reposited in the Black Hills Museum of Natural History in Hill City, South Dakota. This individual preserves an almost complete, well preserved skull, a rarity among most museum specimens of *Stereosternum*. A detailed description of the specimen is provided here, with supplementary information from less complete juvenile material.

MATERIALS

The specimens used in this study, BHM 999 (formerly 'BHI 999') and AMNH 11009, from the Black Hills Museum of Natural History and the American Museum of Natural History in New York, respectively, are from the Irati Formation of Brazil. No locality information is available. The Irati is thought by Oelofsen & Araújo (1987) to be Sakmarian in age (roughly 275 million years old). It was divided into two geographical zones by Barberena (1972): zone A consists mainly of black shales with exposures in the Brazilian states of Paraná, Santa Catarina, and Rio Grande do Sul, which have produced mainly *Mesosaurus brasiliensis*; fragmentary skeletons and

isolated elements attributable to both *Stereosternum tumidum* and *Brazilosaurus sanpauloensis* have been collected from interbedded limestones at the Passo de São Borja locality in Rio Grande do Sul (Oelofsen & Araújo 1983). Zone B is comprised predominantly of limestone with exposures in the Brazilian states of Paraná and São Paulo, and have produced complete skeletons of *Stereosternum tumidum* and *Brazilosaurus sanpauloensis*. As the study specimens are reasonably complete, they probably come from localities in the latter two states. A complete specimen (NMS R4710) of *Stereosternum tumidum* in the Natur-Museum Senckenberg, Frankfurt was also examined, but because circumstances did not permit its illustration, mention of this specimen is limited to brief commentary on pedal morphology.

The genera *Mesosaurus*, *Stereosternum*, and *Brazilosaurus* are monotypic. Accordingly, these generic names are used henceforth in preference to their respective specific binomens.

DESCRIPTION

BHM 999 was exposed by previous workers who split the encasing limestone in order to produce a part and a counterpart. Most of the skeleton is present in the available block; it lacks part of the right side of the skull roof, the vertebral column distal to the twelfth cervical through to the first caudal, the tail distal to caudal 14, and portions of the hind limbs. The truncated tail ends at the edge of the block, and nothing can be said of the length of the tail. The other missing areas are presumably to be found on the counterpart, the whereabouts of which is unknown, but their former presence is marked by impressions. Missing elements of the right hind limb have been built up with bone-colored putty, presumably for display purposes. The veracity of these cosmetic restorations is uncertain, and so their outlines are not reproduced in Figure 1. The carpals and tarsals are well ossified, indicating that the skeleton is adult.

Skull (Figures 1 & 2)

The skull is roughly equal in length to the neck, a characteristic unique to *Stereosternum* among mesosaurs (Oelofsen & Araújo 1987). The antorbital region comprises just under three-quarters the total length of the skull. The external naris is positioned approximately at the halfway point of the skull roof. Accordingly, the snout is not as long in relative dimensions as that seen in *Mesosaurus*. Apart from some parasagittal grooves on the premaxilla, the skull roof is devoid of sculpturing. What appear to be lateral excavations at the bases of the premaxillary teeth are the result of crushing of the relatively thin bone forming the lateral walls of the tooth pits. What is visible of the right squamosal and left jugal suggests that a lower temporal opening was not present, unless it was very small. Well-preserved skulls of *Mesosaurus* reveal that a temporal opening was not present in that mesosaur either (Oelofsen 1981; pers. obsv.).

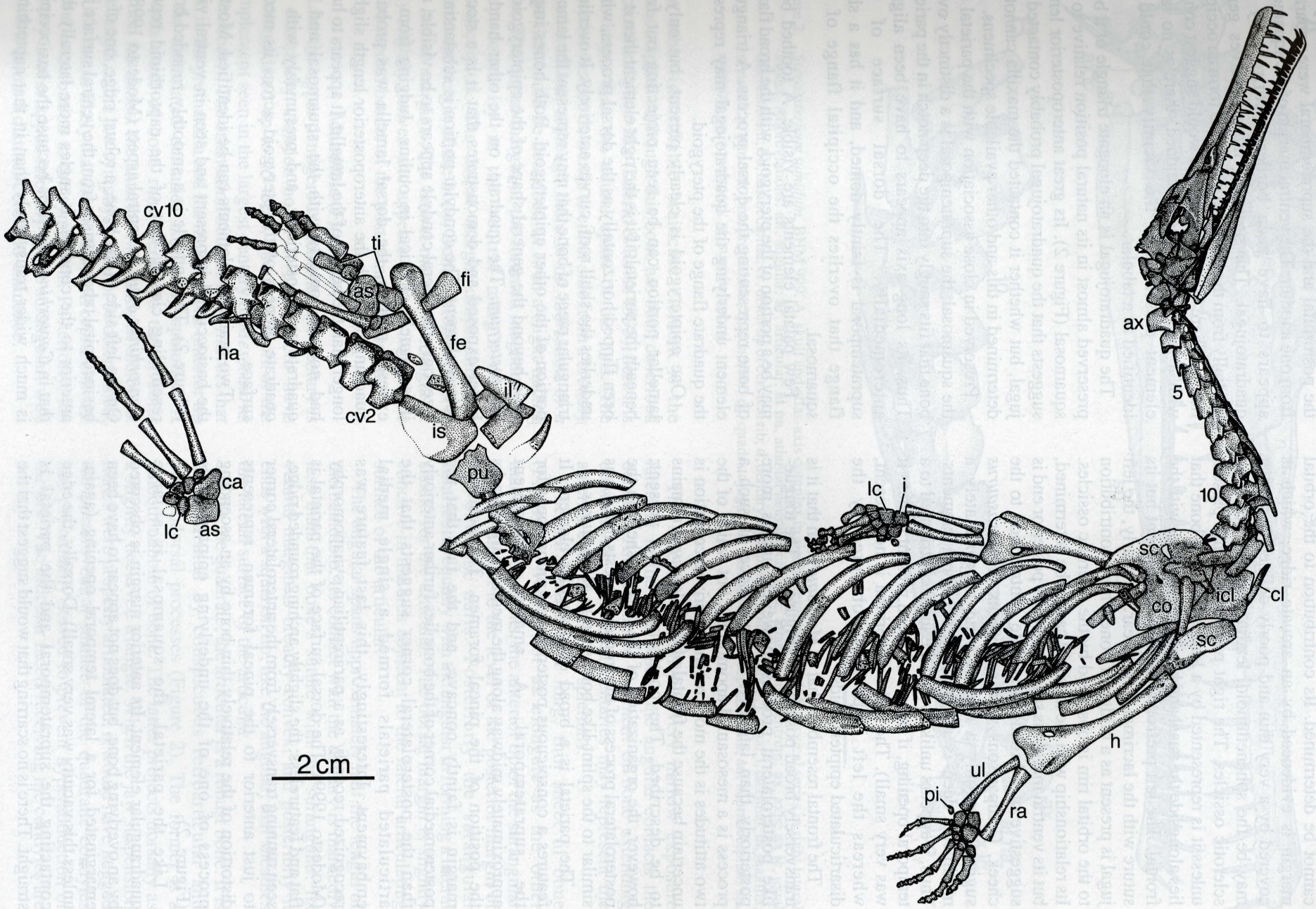
The premaxilla dominates the snout. It accommodates 12 teeth, with room for two or three additional teeth. This complement falls well short of the number (20+) found in the premaxilla of *Mesosaurus*. The teeth fall into two main types: long and short teeth, with the latter no longer than half the length of the former. The shorter teeth may be replacing teeth that were moving into position. Four of the long teeth are each preceded by shorter teeth and collectively they suggest a pattern of alternating long and short teeth. The anteriormost teeth extend almost directly ventrally, with no suggestion of the procumbency seen in *Mesosaurus*. Tooth morphology is described below.

The maxilla is a distinctly triangular bone in lateral view. As preserved it accommodates 14 teeth, with room for three more as evidenced by gaps. One or two additional teeth may have been present on the missing posterior portion. The specimen shows clearly that the anterodorsal margin was overlain slightly by the premaxilla. The primitive condition for amniotes is for the maxilla to overlap deeply the posterior process of the premaxilla. Thus, it appears that in association with the development of an extensive anterior process of the maxilla in mesosaurs, the nature of the suture with the premaxilla was modified as well. On average, the maxillary teeth are shorter than those in the premaxilla, with only a single anterior tooth rivalling the longest premaxillary teeth. However, it would be inappropriate to designate this tooth a caniniform in view of the similarly sized premaxillary teeth.

The septomaxilla comprises an elongate anterior footplate and a posterior facial process (Figure 2). A medial flange extends horizontally into the nares from the footplate. A prominent V-shaped excavation at the base of the facial process probably represents the external opening of the septomaxillary foramen.

Little can be said of the nasal apart from the observation that it shares a strongly serrate suture with the premaxilla that ranges the same anteroposterior extent as the external nares. At the posterior end, slight crushing has exaggerated the nature of the contact with the frontal, which is essentially a simple overlapping suture.

Figure 1. *Stereosternum tumidum*, BHM 999, skeleton with skull and vertebrae visible in right lateral view and appendicular elements seen largely in dorsal aspect. Note the gastralia dispersed among the dorsal ribs, along the ventral midline. Abbreviations: **as**, astragalus; **ax**, axis; **ca**, calcaneum; **cl**, clavicle; **co**, coracoid portion of scapulocoracoid; **cv2**, second caudal vertebra; **cv10**, tenth caudal vertebra; **fe**, femur; **fi**, fibula; **h**, humerus; **ha**, haemal arch and spine; **i**, intermedium; **icl**, interclavicle; **il**, ilium; **is**, ischium; **lc**, lateral centrale; **pi**, pisiform; **pu**, pubis; **ra**, radius; **sc**, scapular blade of scapulocoracoid; **sp**, splenial; **ti**, tibia; **ul**, ulna. Arabic numerals denote cervical vertebrae.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The left lacrimal is present and exposed in medial view, but its sutures with neighbouring elements cannot be determined. Its contribution to the orbital margin is evidenced by an arcuate ridge, which is covered by a very thin and poorly defined bone that may be the sphenethmoid, leading up to a series of sclerotic ossicles. The right prefrontal is not present unless it is represented by a long splinter of bone that lies alongside the nasal and has a small contact with the frontal. The left prefrontal is probably present but its suture with the lacrimal is not clear. Similarly, the left jugal is present as a bridge of bone whose contribution to the orbital rim is obscured by the sclerotic ossicles. Its relationship with the lacrimal cannot be determined, but its ventral margin is straight, and its posterior end is suggestive of a broadly spatulate contribution to the cheek. Comparisons with specimens of *Mesosaurus* suggest that only a narrow band approximately a millimeter deep is covered by overlying elements. Thus, it appears unlikely that the jugal contributed to a temporal opening, if one was indeed present (unless it was very small). The right postorbital is not present, whereas the left is probably obscured by the disarticulated epipterygoids.

The frontal resembles that of *Mesosaurus* in that it is transversely broad posteriorly (Figure 2). The tongue-like posterolateral process, however, angles more posteriorly than laterally. The presence of such a process is a mesosaurid apomorphy, but which of the two attitudes is the more recently derived condition is uncertain because the frontal of *Brazilosaurus* remains to be described. The postfrontal is not present; however, the organization of the narrow shelf on the posterolateral process of the frontal suggests that it was similar to the splint-like bone seen in *Mesosaurus*.

The parietal is a broad quadrangular element. It features a conspicuous posterolateral embayment for the supratemporal. A smaller embayment approximately midway along the medial margin marks the position of the pineal foramen. The posterior margin is faintly concave, and the fact that the posteromedial corner of the bone lies further anteriorly than the posterolateral corner suggests that the articulated parietals formed a single medial embayment. Interestingly, this last feature was recognized recently as a parareptilian synapomorphy (Modesto 1999). The dorsal surface of the parietal is flat and featureless; the slightly arching rounded ridge, seen running transversely from the anterolateral corner to just anterior to the pineal foramen, represents distortion of the relatively thin bone by an ascending process of one of the underlying epipterygoids (Figure 2).

Like the parietal, the squamosal is a large quadrangular element. Its anterior margin is obscured by an overlying bone, but does not appear to have been emarginated for a lateral temporal opening (again, unless this vacuity was very small). Dorsally, the edge contacting the supratemporal and the parietal is straight. There is no scarring that would suggest that the postorbital might have overlain the squamosal in order to contact the supratemporal; thus, it seems likely that the postorbital and the supratemporal were separated from one another. The ventral margin of the squamosal appears to have been bordered entirely by the quadratojugal. The posterior margin curves gently medially from the temporal portion to form an occipital flange. There is no scarring that would suggest contact with a large tabular bone. Indeed, there is no large element preserved in the vicinity that could be identified as a tabular.

The quadratojugal is an elongate triangle of a bone preserved almost in its natural position relative to the squamosal (Figure 2). Its great anteroposterior length suggests that the quadratojugal probably contacted the jugal, but whether it contacted the maxilla cannot be determined in this and other available specimens.

Preserved in close association with the parietal and the squamosal, the supratemporal is a distinctly ovoid bone that fits snugly into the deep notch in the parietal. Thus, its long axis appears to have been aligned anteromedially. The dorsal surface of the supratemporal is faintly domed, and it has a short flange that overlies the occipital flange of the squamosal.

Few palatal elements are visible. A toothed bone may be a portion of the pterygoid, with the broad flange of bone representing the dorsal process. A triangular element underlying the quadratojugal may represent the quadrate flange of the pterygoid.

One epipterygoid is clearly present, but only its lamellar portion can be seen projecting out from beneath the parietal; if it is the right element then it has been flipped horizontally as the dorsal process, which underlies the skull roof, curves anteriorly. It overlies a triangular piece of bone that may represent the lamellar portion of the other epipterygoid. Both bones impart little beyond the general shape of the epipterygoid in *Stereosternum*. The quadrate, on the other hand, is better exposed and demonstrates that it is a stocky, robust element. The condylar portion is substantial in size; only the lateral condyle appears to be visible, and it is vaguely elliptical in outline. Judging from the exposed portion, the dorsal lamella was probably quadrangular, with the anteroposterior length slightly longer than the height of the lamella. It appears to have had normal contacts with the squamosal and the quadratojugal posteriorly, and presumably with the quadrate process of the pterygoid across its medial surface.

Two braincase elements can be identified. Most of the basioccipital is present and seen in ventral view (Figure 2). The condyle is a smoothly rounded boss, resembling closely that of the captorhinid reptile *Captorhinus aguti* in ventral aspect (Modesto 1998b). On the left side of the bone, a robust ridge, one of the basioccipital tubera, arises from the ventral surface just anterior to the condyle. It angles more laterally than that in *Captorhinus*, perhaps because the basioccipital is much wider transversely than in that captorhinid.

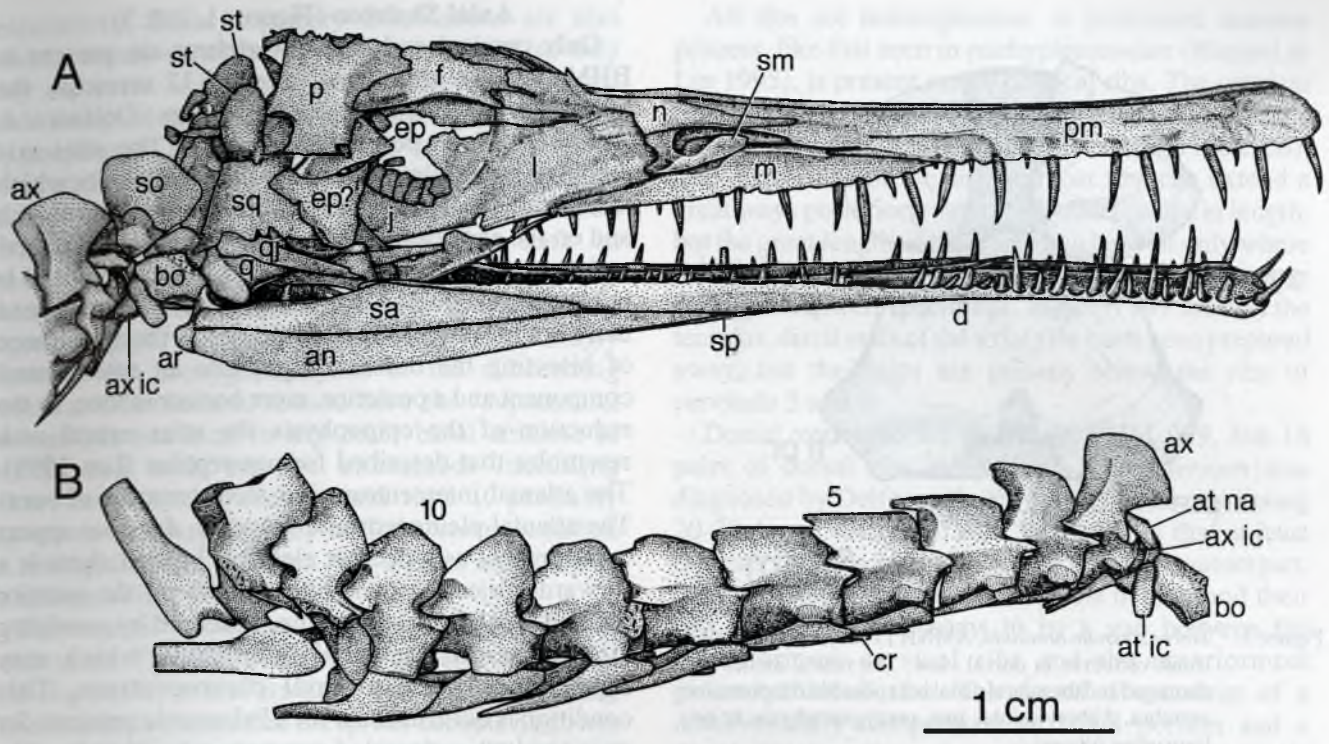

Figure 2. *Stereosternum tumidum*, BHM 999. A, skull and atlas-axis complex in right lateral view, and B, cervical series in right lateral aspect. Abbreviations: **an**, angular; **ar**, articular; **at na**, atlantal neural arch; **at ic**, atlantal intercentrum; **ax**, axis; **ax ic**, axial intercentrum; **bo**, basioccipital; **cr**, distal tip of cervical rib; **d**, dentary; **ep**, epipterygoid; **f**, frontal; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **p**, parietal; **pm**, premaxilla; **q**, quadrate; **qj**, quadratojugal; **sa**, surangular; **sm**, septomaxilla; **so**, supraoccipital; **sp**, splenial; **sq**, squamosal; **st**, supratemporal.

The other identifiable braincase element is the supraoccipital. Although this bone has been described as broad and plate-like (Laurin & Reisz 1995), here it is little larger than the neural spine of the axis. The posterior surface descends to either side from a broadly raised midline, although there is no indication of a ridge that could be described as even a slight nuchal crest. The dorsal margin of the foramen magnum is a deep concavity in the ventral margin of the supraoccipital. The dorsal margin drops almost a quarter the height of the bone, from a midline peak to the lateral margins. The lateral margin is straight or only slightly convex and appears to have formed the entire medial border of the post-temporal opening.

Mandible (Figure 2)

Like the upper dentigerous elements, the dentary is an extremely slender bone. It appears to have accommodated up to 45 teeth, about 10 short of the complement seen in the largest dentary of *Mesosaurus* (pers. obsv.). The orientation of these teeth mirrors that seen in the premaxilla and the maxilla. The anterior tip of the articulated dentaries is slightly spatulate. A smooth shelf of bone runs medial to the alveolar portion for almost the anterior two-thirds of the bone. The length of the jaw symphysis cannot be determined, but it is seems likely that the medial shelf represents the dorsal contribution to the symphysis. Posteriorly, the dentary is overlapped laterally by the surangular, with which it forms a distinct coronoid eminence.

The splenial has only a very narrow exposure laterally in the area where the angular contacts the dentary. An acuminate fragment of bone extending between the articulated dentaries may represent the anterior end of one of the splenials.

The surangular is a long, thin sheet of bone (Figure 2). While not as elongate as the other mandibular elements, the anterior tip of the surangular extends almost to the level of the posterior margin of the external naris. Posteriorly the surangular contributes equally with the angular in forming a lateral sheath for the articular. The dorsal margin is slightly concave in the area adjacent to the lateral articulating surface of the articular.

The angular spans approximately half the length of the mandible. Its contact with the dentary is markedly less than that bone's suture with the surangular. Its ventral margin is broadly convex, and posteriorly it ends with a squarish tip, like the angular, that sheathes the lateral surface of the articular.

Like the quadrate, the articular is a robust bone. It is distinguished by conspicuous retroarticular and posterodorsal processes (Figure 2). The former is a smooth nubbin of bone. The latter projects dorsally as a slightly decurved triangle. When the jaw suspension bones were properly articulated, it would have hugged the posteroventral surface of the quadratic condyles and presumably served to prevent hyperadduction of the jaw. The articular facets receiving the condyles are

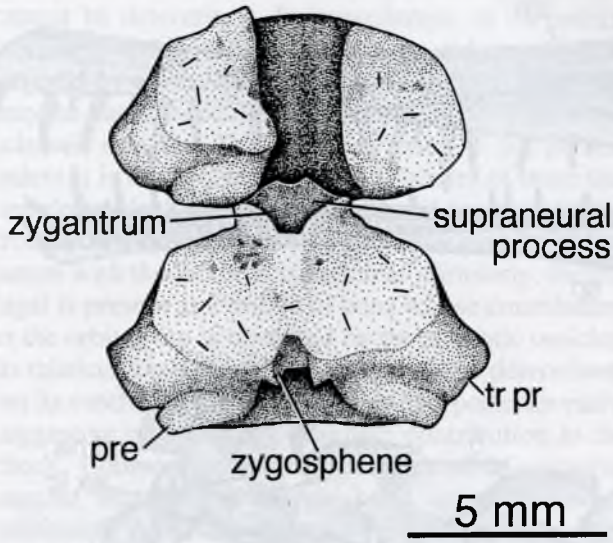

Figure 3. *Stereosternum tumidum*, AMNH 11009, two articulated trunk vertebrae in dorsal view. The neural arches are damaged and the neural canal is exposed in the posterior vertebra. Abbreviations: **pre**, prezygapophysis; **tr pr**, transverse process.

not well exposed, but what is visible suggests that it facilitated only orthal movements of the lower jaw.

Dentition (Figure 2)

The homodont marginal teeth are slender with sharply pointed, slightly recurved tips. The longest teeth are roughly three tooth positions in length (measured from base to tip), and so are absolutely shorter than those in *Mesosaurus* where they exceed five tooth positions in length (pers. obsv.). Basal tooth diameter is about 14 percent total tooth length. Oelofsen & Araújo (1987) described the teeth as oval in cross section. However, the tooth bases of all teeth are subcircular in cross sections. Some of the larger teeth do appear laterally compressed (distal to their subcircular bases), but close examination under light microscopy reveals that this is an artifact of crushing: the teeth are expanded slightly anteriorly and posteriorly and there is a conspicuous furrow that runs down the lateral surface, features strongly suggestive of transverse compression of the teeth. Uncrushed teeth display a gradual decrease in diameter from base to tip. There is the expected reduction in length and diameter towards the posterior end of the dentition in each jaw, in addition to the alternation between long and shorter teeth observed for upper and lower jaws. The shorter teeth may represent replacement teeth, but their is no evidence of remodeling of the alveolar bone, as characteristic of newly ankylosed or ankylosing replacement teeth in other early reptiles (e.g., Modesto 1996a). The marginal teeth appear to be implanted in subthecodont fashion in shallow, regularly spaced sockets. The palatal teeth that can be examined are much smaller than the majority of marginal teeth. They are sharp, straight, homodont structures with subcircular cross sections.

Axial Skeleton (Figures 1, 2 & 3)

Only cervical and caudal vertebrae are present in BHM 999. An articulated series of 12 cervicals, the normal complement for *Stereosternum* (Oelfosen & Araújo 1987), is present (Figure 2B). The atlas-axis complex is complete except for the proatlas, for which there is an articulating facet on the atlantal neural arch and on the exoccipital (Figure 2B). The atlantal neural arch has a small transverse process, although no rib is preserved. There is no distinct epipophysis, and instead there is a low angular mound that gives the appearance of bisecting the dorsal margin into an anterodorsal component and a posterior, more horizontal one. In the reduction of the epipophysis the atlas neural arch resembles that described for parareptiles (Lee 1997). The atlantal intercentrum is a stout crescent of bone. The atlantal pleurocentrum, however, does not appear to be present as a distinct element. Instead, there is a forward-projecting cone-like process on the anterior tip of the axial pleurocentrum, obscured by overlying atlantal neural arch and intercentra, which may represent a fused atlantal pleurocentrum. This condition is quite unusual for a Palaeozoic amniote, for primitively the atlantal pleurocentum is either fused to the anterodorsal surface of the axial intercentrum or it is a discrete element positioned immediately dorsal to the intercentrum, and thus the organization of the atlas described here appears to be unique to *Stereosternum*. In specimens of *Mesosaurus* in which this area is adequately exposed, a single structure comprising a fused atlantal pleurocentrum and axial intercentrum is present (pers. obsv.), the primitive condition for amniotes (Sumida *et al.* 1992).

The axis comprises a small pleurocentrum with co-ossified neural arch and a discrete intercentrum (Figure 2B). The neural spine is hatchet-shaped. A conspicuous ridge arises on its lateral surface and curves posteroventrally onto the postzygapophyses. The ridge may be serially homologous with the mammillary processes that surmount the postzygapophyses in succeeding vertebrae. Postaxial vertebrae lack intercentra. The third cervical appears to have an organization transitional between the axis and the fourth cervical vertebrae. Neural spine height decreases dramatically over the succeeding three vertebrae, and then increases again posteriorly from the seventh cervical. The axial pleurocentrum is the shortest cervical, and the centra gradually increase in sagittal length posteriorly along the series (Figure 2B).

BHM 999 is missing the entire series of dorsal vertebrae. Examination of other referred specimens of *Stereosternum* indicates that, outwardly, the dorsals of this mesosaur do not differ from those of *Mesosaurus* (von Huene 1941). However, a fortuitous horizontal section through two dorsals in the articulated vertebral column of a juvenile, AMNH 11009, reveals two important anatomical features of the neural arch (Figure 3). The first is the presence of zygosphenes and zygantra, small accessory articulations that flank the supraneural pits anteriorly and posteriorly,

respectively. These accessory articulations are also seen in dorsal vertebrae of *Mesosaurus*, and so they may represent a mesosaurid synapomorphy (neural arch morphology of *Brazilosaurus* is unknown). Zygosphenes and zygantra are present also in mosasaurs, where they are thought to have helped to dampen twisting movements of the column (Russell 1967). The second vertebral feature seen in AMNH 11009 is a narrow but broad tongue-like process that floors the zygantra and posterior supraneural pit, and projects posteriorly to fit snugly between the prezygapophyses of the succeeding vertebra. This feature, termed here the 'supraneural process', is not seen in any other basal amniote in which this area can be examined, including *Mesosaurus* (pers. obsv.), and thus it probably represents an autapomorphy of *Stereosternum* (albeit an ambiguous one, because this area is unknown in *Brazilosaurus*).

The caudal vertebrae (Figure 1) are robustly constructed. The anterior six of the preserved series are missing their neural spines, but the succeeding vertebrae demonstrate that the spines become narrower and increase slightly in height posteriorly. The tips of several spines are slightly curved anteriorly. Only the anteriormost preserved member of the series (the second caudal) is visible in dorsal aspect and reveals that the arch is approximately as wide as long; mammillary processes are present on this and the succeeding caudal, but are absent on the remainder of the series. Ribs were borne by the proximal 11 caudals, but all ribs are damaged and little can be said of their morphology apart from the observation that they are dorsoventrally compressed anteriorly but become subcircular in cross section in the posterior four of the series. Intercentra are absent and haemal arches are fused indistinguishably to the preceeding vertebra. There is no evidence that caudal intercentra have fused with the pleurocentra (if such intercentra were ever present). The posterior part of each caudal centrum is accentuated by a slight trough that runs down the lateral surface of the centrum, an excavation that was interpreted as a fracture line for facilitating caudal autotomy (Osborn 1903; Broom 1904). However, the fine cracks representing lines of weakness in extant lizards that can autotomize the tail (Etheridge 1967; Bellairs & Bryant 1985) are absent here, suggesting strongly that caudal autotomy was not present in *Stereosternum*.

Haemal arches are present from the fourth caudal to the last preserved vertebra. They have the appearance of slightly swollen wishbones. The haemal spines are short and the tips of some are conspicuously expanded anteroposteriorly. The haemals of caudals 12 and 13 are twisted and co-ossified for most of their length. This may be a result of ankylosing spondylitis (Stuart Sumida, pers. comm.) or may have resulted from some trauma to the underside of the tail. Either conjecture lends support to the idea that *Stereosternum* was incapable of caudal autotomy.

All ribs are holocephalous. A prominent anterior process, like that seen in pachypleurosaurs (Rieppel & Lin 1995), is present on all cervical ribs. The cervical ribs are slender, rod-like structures, except those on the last two cervicals, which are broad and flat (Figure 2B). The distal ends of the anteriormost ribs can extend a great ways posteriorly, up to 4 cervical centra in length, but the great length of these ribs can be seen only where the cervical vertebrae have been carefully prepared as in several AMNH specimens. In BHM 999 most of the tenuous, distal ends of the axial ribs have been prepared away, but their tips are present below the ribs of cervicals 5 and 6.

Dorsal vertebrae are absent in BHM 999, but 18 pairs of dorsal ribs are present. *Stereosternum* was diagnosed by Oelfosen & Araújo (1987) as possessing 20-22 dorsal vertebrae, so it seems likely that at least two pairs of ribs ended up on the missing counterpart. Possible candidates are anteriormost dorsals and their ribs, because there seems to be a gap between the posteriormost cervical ribs and the anteriormost preserved dorsal ribs. The dorsal ribs consist of a dorsoventrally compressed proximal portion and a distal, thickened portion. The latter is essentially circular in cross section, but crushing has left prominent grooves in many of the ribs from overlying, missing portions of other ribs. An elongate dimple is present on the posterior surfaces of well-preserved ribs. It may mark the former attachment site for intercostal cartilage. The posteriormost left dorsal rib is oriented laterally, in parallel with the sacral ribs. This suggests that the last pair of dorsal ribs are fused to their vertebra in adult *Stereosternum*, as in *Mesosaurus* (pers. obsv.).

The two left sacral ribs are partially preserved and maintain their contact with the ilium. Both are dorsoventrally compressed and subequal in anteroposterior breadth. The fragment of the second sacral rib is smaller than that of the first, to which it is firmly attached for almost all of its preserved length.

Gastralia litter the former ventral midline of the trunk between the left and right series of dorsal ribs. Most are preserved loosely in their former area, but several remain in articulation and collectively are suggestive of the imbricate pattern seen in other early reptiles. Each dermal riblet is a dorsoventrally flattened splint of bone, and there is no evidence of chevron-shaped midline elements (as seen in neodiapsids). Most riblets are no longer than a typical metacarpal, but a few exceed the length of the longest manual digit.

Appendicular Skeleton (Figure 1)

The shoulder girdle is well-preserved apart for the clavicle, of which only a fragment remains of the right element. No cleithrum is in evidence, but, considering the state of the remaining clavicle, the absence of the cleithrum may be either taphonomic or an artefact resulting from the manner in which the specimen was exposed by the original collectors. The well preserved interclavicle comprises a diamond-shaped head and a posterior parasternal stem. The former is flat and

featureless, and the latter is slightly constricted proximally and ends posteriorly with a truncated tip.

The scapulocoracoid is present as a single unit. The scapular portion is dorsoventrally short and curves posteriorly almost as far as the posterior end of the coracoid. There is no supraglenoid foramen. The anterodorsal margin of the scapula merges almost indistinguishably with the anterior margin of the coracoid; a faint notch (partly obscured by two gastralia) may mark the border between the two component elements. The coracoid is large and plate-like. Anteriorly it is suboval in outline, but the posterior end appears quadrangular, albeit with broadly rounded corners. Just anteromedial to glenoid angle, the coracoid is pierced by the coracoid foramen. Subcoracoscapular and coracoid fossae and their associated ridges, prominent in other early tetrapods, are absent.

Among non-mesosaurid amniotes the humerus resembles most closely that of romeriid reptiles (*sensu* Gauthier *et al.* 1988) in relative slenderness. The diameter of the shaft is about 10 per cent the total length of the bone. The distal width of the bone is comparable to that seen in romeriids, being slightly less than 35 per cent the total length of the humerus. The distal end is angled slightly more postaxially, resulting in a relatively straight anterior margin and a slightly more concave posterior margin. The proximal head of the humerus is only slightly expanded compared to the shaft, and it is set at a right angle to the distal end; a small tubercle visible on its dorsal surface may have served for the insertion of the scapulohumeralis muscle. The entepicondyle is relatively small and, as in other reptiles, the supinator process is directed distally.

Both the radius and the ulna are rod-like, narrowly waisted elements that are just under half the length of the humerus (Figure 1). The shafts of both are smooth and featureless, with truncated proximal and distal ends.

The manus is well ossified. In dorsal aspect the curved digits and their metacarpals describe an almost perfect ovoid; it probably formed a stout paddle. The carpus is comprised of nine elements. The three largest are the ulnare, the intermedium, and the lateral centrale. The perforating foramen resembles more the spindle-shaped passage that has been restored for the synapsid *Ophiacodon*, rather than the distinctly circular opening bounded by the intermedium and ulnare that is seen in the reptiles *Labidosaurus* and *Petrolacosaurus* (Sumida 1997). The radiale is unossified, judging from the conspicuous gap between the end of the radius and the first distal carpal, whereas the medial centrale was either unossified as well, or it was entirely absent. Five distal carpals are present, of which the first is the largest. A pisiform is present, well ossified, and larger than the fifth distal carpal. The metacarpals and phalanges are relatively much shorter than those of other amniotes. Those of the first digit are fairly robust, whereas the metacarpals and phalanges become more slender postaxially. The phalangeal formula differs from the plesiomorphic amniote pattern of 2·3·4·5·3 with the loss of a single phalanx from the fourth digit. The unguals are spade-shaped. The first four digits curve postaxially, whereas the fifth is strongly divaricate, as in some mosasaurs (Russell 1967).

The pelvic girdle did not survive as well as the pectoral elements the splitting process used to expose the specimen originally (Figure 1). The entire right side of the girdle is missing, as are portions of the left pubis and ischium, although the associated ilium is very well preserved. None of the remaining pelvic elements are co-ossified. The medial portion of the pubis is absent and the remaining dorsal part has rotated almost 90 degrees from its normal position; the larger of the two notches neighbouring the ischium represents part of the formerly enclosed obturator foramen. Most of the ischium is present and the extent of the missing portion can be restored from its impression. This bone does not differ notably from those of other basal amniotes, apart from having a more gracile dorsal margin. Although it is well preserved, the ilium is not well exposed. The dorsal margin is only marginally longer than the region receiving the sacral ribs and is slightly roughened for muscle attachment. The posterior process tapers abruptly. The ventral portion contributing to the acetabulum appears to be the thickest part of the bone.

Only the left femur is present and it is visible in anteroventral aspect. It is notably more slender than those of contemporaneous terrestrial amniotes; the widths of the proximal and distal ends are both roughly one-fifth, and the shaft about one-tenth, the total length of the bone. The internal trochanter is a weak, rounded ridge and the shaft is smooth and devoid of the adductor ridge system that characterizes terrestrial forms. The distal end is broadly rounded; the medial and lateral condyles are subequal and conjoined with no sign of the notch that separates the condyles of terrestrial basal cotylosaurs. The distal condylar surfaces together form a single, hourglass-shaped articulating surface.

The tibia is about two-thirds the length of the femur. The proximal end appears to be no broader than one-fifth the total length of the bone. Its articulating surface is broadly elliptical and moderately convex in side view. The fibula is as long as the tibia but is broader than that bone throughout most of its length, with the proximal end conspicuously expanded. The fibula is dorsoventrally compressed for most of its length apart from the slightly thicker proximal end. These two elements are essentially indistinguishable from those of *Mesosaurus* (pers. obsv.).

Although the right propodial and epipodials are missing, the right tarsus is well preserved with the exception of the first distal carpal, of which only its impression remains. Of the disarticulated left tarsus only the astragalus, two of the larger distal tarsals, and the calcaneum can be seen, the last of which is mostly obscured by the left tibia. The right astragalus is a distinctly quadrangular bone, with the proximal end slightly narrower than the distal margin. There is no

dorsal component to the articulating surface for the tibia. The lateral margin bears a small notch, the astragalar contribution to the perforating foramen, approximately midway along its length, whereas the distal margin is slightly convex for the reception of the lenticular lateral centrale. The left astragalus is less quadrangular in outline, marginally broader, and conspicuously longer proximodistally than its counterpart in the right tarsus. The distal margin is mostly obscured by overlying metapodials and so the left astragalus was marginally longer than what is visible. It is at least equal in length to the articulated astragalus and lateral centrale in the right tarsus, suggesting strongly that the astragalus and laterale centrale in the left pes were indistinguishably fused. Augmentation of the astragalus by incorporation of the lateral centrale is invariably seen in *Mesosaurus* (Rieppel 1993; Modesto 1996b), and so this individual of *Stereosternum* appears to be polymorphic with respect to the two conditions. The same polymorphism appears to be present in NMS R4710, where the left lateral centrale is distinct but the right is co-ossified with its respective astragalus (pers. obsv.).

The calcaneum is markedly smaller than the astragalus. It is triangular in outline, with broadly rounded corners (Figure 1), and thus differs dramatically in both shape and size from the distinctly plate-like calcanea of terrestrial basal amniotes (Rieppel 1993). The notch for the perforating foramen is positioned just distal to the midway point of the margin contacting the astragalus.

Of the four distal tarsals present in the right tarsus, the fourth is only slightly larger than the second and third elements, which are subequal in size; the fifth distal tarsal is by far the smallest of the series. The impression of the first distal tarsal suggests that it is intermediate in size between the fifth element on one hand and the second and third elements on the other. However, the first distal tarsal is always the largest in specimens of *Mesosaurus*, doubtless because it is associated with the most robust metatarsal (Modesto 1996b), and so the unexpectedly small size of the impression is most likely an artifact resulting from when the specimen was exposed by the splitting of its encasing matrix.

Four of the five metatarsals are preserved between the two pedes. The first metatarsal is present on the left side. It is the broadest and shortest of the series, and is distinctly flattened dorsoventrally. The remaining metatarsals are elongate rods that increase in length postaxially. Between the two pedes the phalangeal formula can be determined to be 2·3·4·5·5, the standard pedal formula for mesosaurs (Modesto 1996b). The digits increase in length postaxially. The phalanges comprising each digit become narrower as one progresses postaxially, such that the longest, the fifth toe, is also the most gracile. The unguals of the first three toes are, as in the manus, spade-like, with the fourth somewhat less so, and the fifth present as tiny claw that resembles the unguals of terrestrial reptiles. The toes were embedded in a web of skin that was strengthened by rays, or fibres, which run parallel to the toes in rare specimens that preserve skin fragments (Rösler & Tatizana 1989). Presumably this condition also applied to the manus.

DISCUSSION

Study of BHM 999 supports most of the identifying characteristics that have been observed for *Stereosternum* by previous workers. The most salient of these is the head to neck ratio of approximately 1:1 (MacGregor 1908; Oelofsen & Araújo 1987). The trunk ribs and haemal arches are also conspicuously thickened, or pachyostotic, as recognized by Oelofsen & Araújo (1983, 1987). However, the pachyostotic nature of the former is shared also with *Mesosaurus*, whereas the condition of thickened haemal arches is shared with *Brazilosaurus*. In contrast to statements by Oelofsen & Araújo (1987) that the marginal teeth of *Stereosternum* are compressed transversely (i.e., the teeth have oval cross sections), the slightly compressed appearance of the teeth appears to be an artifact of crushing in BHM 999; the teeth of this individual were circular in cross section throughout their entire length, as described for *Mesosaurus* (Oelofsen and Araújo 1987).

The most unusual and intriguing feature of BHM 999 is the structure of the atlas-axis complex. Whereas *Mesosaurus* displays a normal organization of a distinct and well ossified atlantal pleurocentrum and crescentic atlantal and axial intercentra, and the anterior end of the axial pleurocentrum is normally developed in *Brazilosaurus* (pers. obsv. of the holotype), there is no distinct atlantal pleurocentrum in BHM 999. In its place is a conspicuous anterior process protruding from the axial pleurocentrum. Although this process resembles the odontoid of mammals, it is clearly not the relatively small, peg-like process of the mammalian axis. Because only the base of the 'odontoid' of *Stereosternum* is known, its functional significance is far from clear. It may correlate with the presence of a long skull on a long neck in *Stereosternum*. The head of *Mesosaurus*, being larger both in absolute and relative terms, is mounted on a relatively shorter, slightly more robust neck, and the neck of *Brazilosaurus* is relatively longer and it supports a skull that is absolutely smaller (Oelofsen & Araújo 1987). The 'odontoid' process of *Stereosternum*, therefore, may have served to minimize movement at the junction between skull and neck. Although the skull must have been fairly hydrodynamic, it was relatively large in relation to the neck and still had to plough through water as the animal moved forwards, quite possibly with the jaws making lateral sweeps during foraging maneuvers.

Fortuitous breakage of dorsal vertebrae in a juvenile specimen reveals a second autapomorphy for *Stereosternum*: the presence of a supraneural process on the neural arch of trunk vertebrae. This feature must be regarded for the time being as an ambiguous

autapomorphy of *Stereosternum*, as the vertebral column of *Brazilosaurus* remains to be described in detail. Similarly, the presence of accessory vertebral articulations, zygosphenes and zygantra, are considered an ambiguous apomorphy uniting *Stereosternum* and *Mesosaurus*, given that the presence of these accessory articulations cannot be determined in *Brazilosaurus* using the available materials.

In addition to the absence of a maxillary caniniform tooth and a supraglenoid foramen, there are two features in BHM 999 that are suggestive of parareptilian affinities for mesosaurs. The first is the modification of the posterior margin of the parietals to form a single median posterior emargination of the skull roof. This character, present also in *Mesosaurus* (pers. obsv.), was identified only recently as a parareptilian synapomorphy (Modesto 1999). The second is the absence of an atlantal epipophysis, identified by Lee (1997) as a synapomorphy of parareptiles (regarded by Lee 1995, only as a potential parareptilian apomorphy). It should be noted here that, *contra* Lee (1997), an epipophysis is indeed present in millerettids: personal examination of BP/1/3821, the most complete skeleton of *Milleretta rubidgei* (and the only millerettid specimen that preserves the atlas-axis complex), reveals that a small epipophysis is present on the left atlantal neural arch, as reconstructed by Gow (1972); the right arch is damaged and its epipophysis appears to have been spalled off.

In the first phylogenetic analysis to include mesosaurs with other amniote taxa (Gauthier *et al.* 1988), they were grouped together with millerettids, pareiasaurs, and procolophonids. A subsequent study by Laurin & Reisz (1995) grouped the last three taxa together in a clade to which the authors applied Olson's (1947) nomen 'Parareptilia'; mesosaurs were regarded as the sister group of Reptilia and thereby thought to be only distantly related to Parareptilia. However, in an alternate tree that was only a single step longer than their most parsimonious resolution, Laurin & Reisz (1995) acknowledged that mesosaurs subtended a clade formed by millerettids, pareiasaurs, and procolophonids, thereby resurrecting the basic complement of taxa grouped together as 'parareptiles' by Gauthier *et al.* (1988). The two additional parareptilian synapomorphies, present in BHM 999 and not utilized by Laurin & Reisz (1995), therefore have the potential to alter the topology of the most parsimonious tree of those authors by grouping mesosaurs with parareptiles. Furthermore, a redescription of the skull of the basal eureptile *Captorhinus aguti* (Modesto 1998b) revealed that two of the reptilian synapomorphies identified by Laurin & Reisz (1995) are problematic and, therefore, might not serve to exclude mesosaurs from Reptilia. The first of these concerns the breadth of the parasphenoid wings (their character 51): new material demonstrates that the captorhinid parasphenoid differs little in general dimensions from those of mesosaurs and basal synapsids (Modesto 1998b; *contra* Laurin & Reisz 1995). The second, the presence of supraoccipital anterior cristae (their character 54), is in all likelihood a saurian apomorphy that does not apply to Paleozoic reptiles (Modesto 1998b). Considering the doubtful nature of these two characters in barring mesosaurs from Reptilia, the admittedly weak position of mesosaurs as the most basal sauropsids (Laurin & Reisz 1995), and the identification of two additional potential parareptilian apomorphies that are shared also with *Stereosternum*, it would appear that there is a good case for parareptilian affinities for mesosaurs.

With this in mind, the two new characters were added to the data matrix of Laurin & Reisz (1995), one of their characters (character 51) was modified by recoding captorhinids as '0', and the other problematic character (no. 54) was deleted entirely; distributions of states for the two new characters are listed in the appendix. The modified data matrix was analyzed by PAUP 3.1 following all the options outlined by those authors, except that all characters were run unordered. A single most parsimonious tree of 330 steps was discovered (Figure 4*a*), in which mesosaurs form a sister-group relationship with parareptiles (*sensu* deBraga & Reisz 1996). The topology of the preferred tree of Laurin & Reisz (1995), where mesosaurs are excluded from Reptilia, is replicated in an alternative tree of 332 steps. Thus, with only minor additions and modifications to the data matrix of Laurin & Reisz (1995), a slightly different picture of mesosaurid relationships arises. This re-analysis is not intended to serve as a critical re-evaluation of the interrelationships of early reptiles; that is the subject of a forthcoming paper. It does, however, suggest that there is strong evidence that mesosaurs are reptiles and that their closest relatives are most likely to be found among the reptilian taxa now known formally as the Parareptilia (deBraga & Reisz 1996).

Following the tenets of phylogenetic taxonomy (De Queiroz & Gauthier 1990, 1992) and the principle of priority, Williston's (1925) term 'Anapsida' can be applied to the clade of mesosaurs and parareptiles. That nomen was defined by Gauthier *et al.* (1988, p. 142) to include 'extant turtles, and all other extinct reptiles that are more closely related to them than they are to other reptiles'. Thus, Anapsida is the nomen that should have been applied to the clade that Laurin & Reisz (1995) named Parareptilia, which was defined by the latter authors as a stem-based group that includes all reptiles related more closely to Testudines than to other reptiles. Accordingly, Parareptilia *sensu* Laurin & Reisz (1995) can be considered to be preoccupied by Anapsida *sensu* Gauthier *et al.* (1988). The node-based redefinition of deBraga & Reisz (1996) is regarded here as the valid definition of Parareptilia.

The realignment of turtles with the taxa that Gauthier *et al.* (1988) regarded as 'parareptiles' has the potentially confusing effect of removing from the group taxa that have long served as exemplary anapsids (*e.g.*, captorhinids). Moreover, the phylogenetic

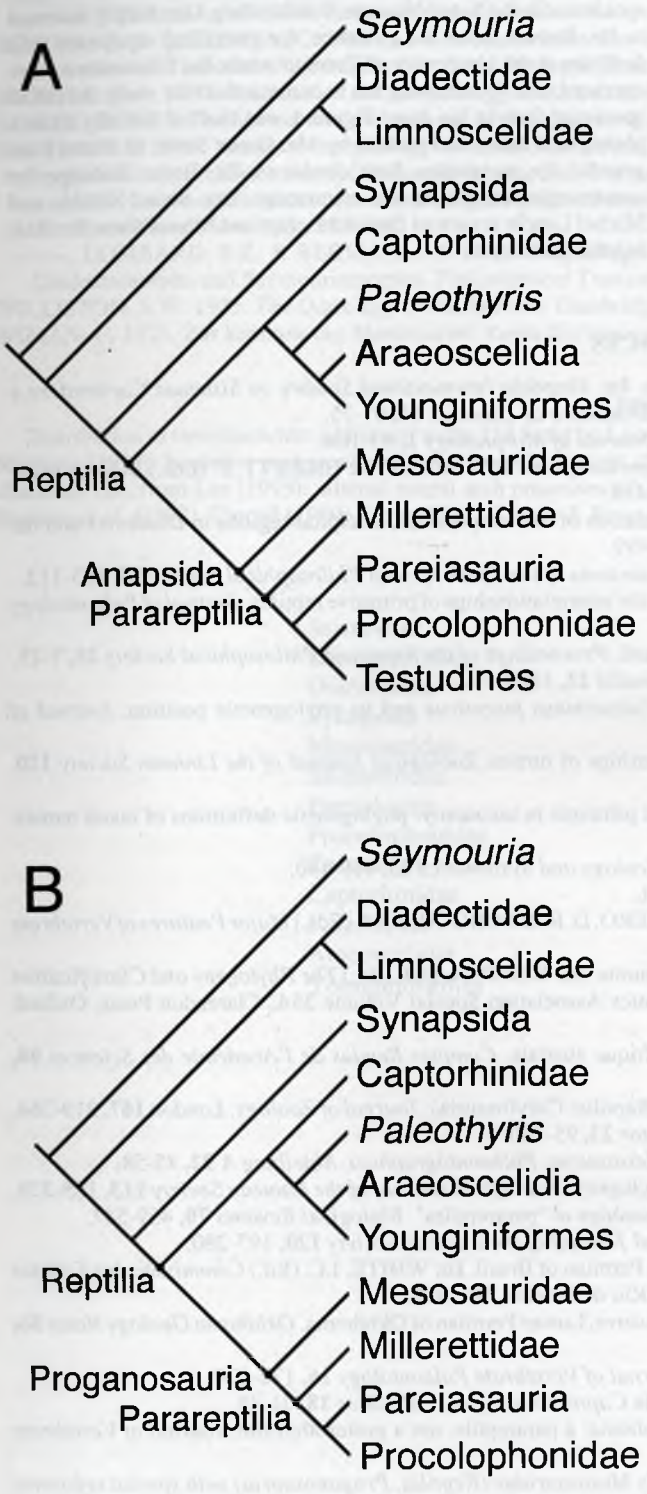

Figure 4. A. Cladogram illustrating the most parsimonious tree obtained from a PAUP 3.1 analysis of a data matrix modified slightly from Laurin & Reisz (1995). Anapsida is diagnosed by characters 24, 25, 91, 97, 113, and 125 of Laurin & Reisz (1995) and the appendix. B. Corresponding phylogeny in which turtles are recognised as diapsid reptiles, illustrating the alternative nomenclature for major amniote groups necessitated by the repositioning of Testudines and the tenets of phylogenetic taxonomy.

definition of a taxon that has long been regarded as unnatural may not be well received by many workers, and it is not inconceivable that a move may be made to suppress the name 'Anapsida' under the aegis of the International Committee for Zoological Nomenclature. However, such an action may be moot given the current controversy over the phylogenetic position of turtles within Reptilia. If the hypothesis that turtles are aberrant diapsid reptiles (Rieppel & deBraga 1996; deBraga & Rieppel 1997) comes to represent the consensus view, Gauthier *et al.*'s (1988) definition of Anapsida may have to be abandoned, for turtles would be nested well within the reptilian crown group. Should this unorthodox view come to pass, then the clade of mesosaurs and parareptiles will be without a name. In contingency, Baur's (1887) nomen 'Proganosauria' would serve as a appropriate name for this 'turtleless' sauropsid clade. Created by Baur (1887) to receive mesosaurs and their close relatives, the taxon included only mesosaurs for most of its history. Proganosauria is defined here as a stem-based group that includes all amniotes related more closely to *Mesosaurus tenuidens* than to saurian reptiles. The alternate nomenclature is labelled on a phylogeny in which turtles are not members of Parareptilia (Figure 4*b*). Thus, Anapsida is the correct name for the clade of mesosaurs and parareptiles, but only as long as turtles are included in the latter group. For the time being, *Stereosternum* and other mesosaurs can be recognised as the most basal anapsid reptiles.

Finally, as a consequence of this minor rearrangement of amniote phylogeny, the nomen 'Sauropsida' now encompasses exactly the same complement of taxa as Reptilia as the latter is regarded in the present work. The former nomen was defined as a stem-based taxon (Gauthier 1994), whereas the latter was defined as a crown-group (node–based) taxon (Gauthier *et al.* 1988). Reptilia clearly has priority here, both as a phylogenetically-defined taxon and as the older, more established taxonomic name. Accordingly, the nomen 'Sauropsida' is regarded to be in abeyance, bearing in mind that that there is no longer a non-synapsid amniote taxon that falls outside of the reptilian crown group. However, the discovery of such a taxon would allow 'Sauropsida' to be resurrected again as one of the two major clades of Amniota.

The identification of mesosaurs as the closest relatives of the parareptiles has two important consequences. The first is that it eliminates the substantial ghost lineage for Mesosauridae that is necessitated by the 'sauropsid' tree of Laurin & Reisz (1995): according to that tree, mesosaurs must have originated sometime during the Westphalian, implying that over 40 million years of their evolutionary history is unknown (Laurin & Reisz 1995: Figure 9). The preferred tree of the present analysis (Figure 4) suggests that such a severe estimate of unrecorded history is unwarranted. If one distinguishes between 'ghost taxa' and 'ghost lineages' (*sensu* Norell 1992), then a ghost lineage for Mesosauridae is absent, and the

ghost taxon for anapsids extends from the late Westphalian until the first appearance of mesosaurs in the late Sakmarian. The oldest known parareptiles are the acleistorhinids from the South Grandfield and Richards Spur localities in Oklahoma (Modesto 1999), which appear some 7 or 8 million years after the mesosaurs. Consequently, the anapsid identification of mesosaurs also reduces the ghost lineage for Parareptilia, which now extends from the late Sakmarian to the early Artinskian.

ACKNOWLEDGEMENTS

I thank Drs. Peter Larson, David Burnham, Eugene Gaffney and Yukimitsu Tomida for the loan of specimens from their respective institutions, and Gerhard Plodowski for allowing me to examine specimens in the Natur-Museum Senckenberg. I am deeply indebted to Dr. Robert Reisz for guidance, for providing equipment and facilities at the University of Toronto where the illustrations were executed, and for allowing me to commandeer for study the BHM specimen then in his care. Figure 1 was drafted initially from a photograph taken and printed by Ms. Diane Scott, to whom I am grateful for assistance. *Baie dankie* to Dr. Bruce Rubidge for constructive remarks on the manuscript. Drs. Stuart Sumida and Michel Laurin reviewed the manuscript and I thank them for their helpful comments.

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APPENDIX

Distribution of two characters additional to the 124 listed by Laurin & Reisz (1995). Their description is as follows: character 125, from Modesto (1999): posterior margin of skull roof roughly straight (0), with a single, median embayment (1), or embayed bilaterally (2); character 126, from Lee (1995): atlantal neural arch possesses (0) or lacks (1) an epipophysis. Sources, in addition to the present work: Berman *et al.* (1992), Carroll (1969), Gow (1972), Laurin & Reisz (1995), Lee (1995), and Sumida (1990).

	125	**126**
Seymouria	0	0
Limnoscelidae	1	0
Diadectidae	2	0
Synapsida	2	0
Mesosauridae	1	1
Millerettidae	1	0
Pareiasauria	1	1
Procolophonidae	0	1
Testudines	0	1
Captorhinidae	2	0
Paleothyris	2	1
Araeoscelidia	2	0
Younginiformes	1	0

Palaeont. afr., **35**, 21-23 (1999)

THE TRIASSIC REPTILE *PALACRODON BROWNI* BROOM, SYNONYMY AND A NEW SPECIMEN

by

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ABSTRACT

Palacrodon browni Broom 1906 (=*Fremouwsaurus geludens* Gow 1992) is a small enigmatic diapsid reptile from the *Cynognathus* Assemblage Zone of South Africa and Antarctica whose dentition is very similar to that of coeval procolophonids.

KEYWORDS: *Palacrodon*, *Fremouwsaurus*, procolophonids, *Cynognathus* Zone.

INTRODUCTION

In 1906 Broom published a description of a small partial left jaw ramus with six teeth of a reptile from the *Cynognathus* zone which he called *Palacrodon browni*. The specimen was collected by Alfred ('Gogga') Brown of Aliwal North, and as with so many Brown localities, the exact provenance of the specimen could not be determined. With his usual intuitive flare, Broom placed the specimen in Rhynchocephalia (which at that time included sphenodontians). He also felt that the specimen was an adult as the last tooth in the dentary is fully formed. Hoffstetter (1955) and von Huene (1956) put *Palacrodon* in the Sphenodontidae. Malan (1963), added the important observation that the teeth in profile are pyramidal, with slightly concave sides, and pointed out the resemblance of the teeth to those of procolophonids; she also remarked on the fact that the *Palacrodon* jaw is far more slender than those of procolophonids, but this is a juvenile character also seen in procolophonids. She concluded that it "could be an aberrant procolophonid or lizard just as easily as an aberrant rhynchocephalian" (sphenodontid).

When examining this material recently I was surprised to find that there are two specimens: SAM-PK-5871 is a block containing the left lower jaw of the holotype, which in addition to the six cheek teeth already described shows evidence of the former presence of five smaller anterior teeth which have broken off, and a small shed thecodont tooth; SAM-PK-6215 is a fragment of right maxilla bearing six teeth – another two teeth have been lost (Figure 1D).

Gow (1992) described the partial skull of a small diapsid from Antarctica, ostensibly from *Lystrosaurus* zone equivalent rocks, as *Fremouwsaurus geludens* (Figure 1E). Comparison of this specimen with the holotype of *Palacrodon* (Figure 1D) shows that they are identical, which implies that *"Fremouwsaurus"* came in fact from *Cynognathus* Zone-equivalent rocks.

The lower, tetrapod bearing, part of the Fremouw Formation equates with the *Lystrosaurus* Zone of the Beaufort Group (Elliot *et al.* 1970a, Kitching *et al.* 1972), but Elliot *et al.* (1970b) noted the occurrence of *Dicroidium* in the upper part of the Fremouw. *Dicroidium* in South Africa occurs in the Early Stormberg Molteno Formation, which lies *above* the *Cynognathus* assemblage zone of the Beaufort. Hammer (1995) records a typical *Cynognathus* Assemblage zone fauna from 200 meters higher in the Fremouw Formation than the *Lystrosaurus* Zone localities. It therefore seems probable that *"Fremouwsaurus"* came from *Cynognathus* Zone equivalent rocks.

During a field excursion in September 1996, a student, Catherine Marshall, collected a partial right maxilla and right dentary, both with teeth, amongst the surface float at a Lower *Cynognathus* Zone locality known as Driefontein in the Paul Roux district. This locality may be expected to yield *inter alia* rhynchocephalians, sphenodontians, and procolophonids. It was while reading the rhynchocephalian literature that I realised that these little jaws, though slightly larger, were extraordinarily similar to Broom's *Palacrodon*, and also *"Fremouwsaurus"*.

DESCRIPTION OF NEW SPECIMEN

The material BP/1/5672(Figure 1A-C) consists of a right maxillary fragment bearing four acrodont teeth and a dentary fragment bearing five. It is not certain whether they belonged to the same animal, but they were found in close proximity and they fit well. They belonged to an individual/s larger than the holotype of *Palacrodon browni*. The bones are not very informative: the maxillary fragment has a few internal grooves which would no doubt serve to match it with a more complete specimen; the dentary has a pronounced Meckelian groove, while on the labial surface, apart from the usual nutrient foramina, there are pits below the four posterior-most teeth. The dentary teeth are not set back from the dorsal edge of the dentary, but swell beyond it as in procolophonids. The teeth, which are broadened labio-lingually, are closely packed together with firm mesiodistal contact, something not seen in procolophonids (some illustrations in Gow 1977 are

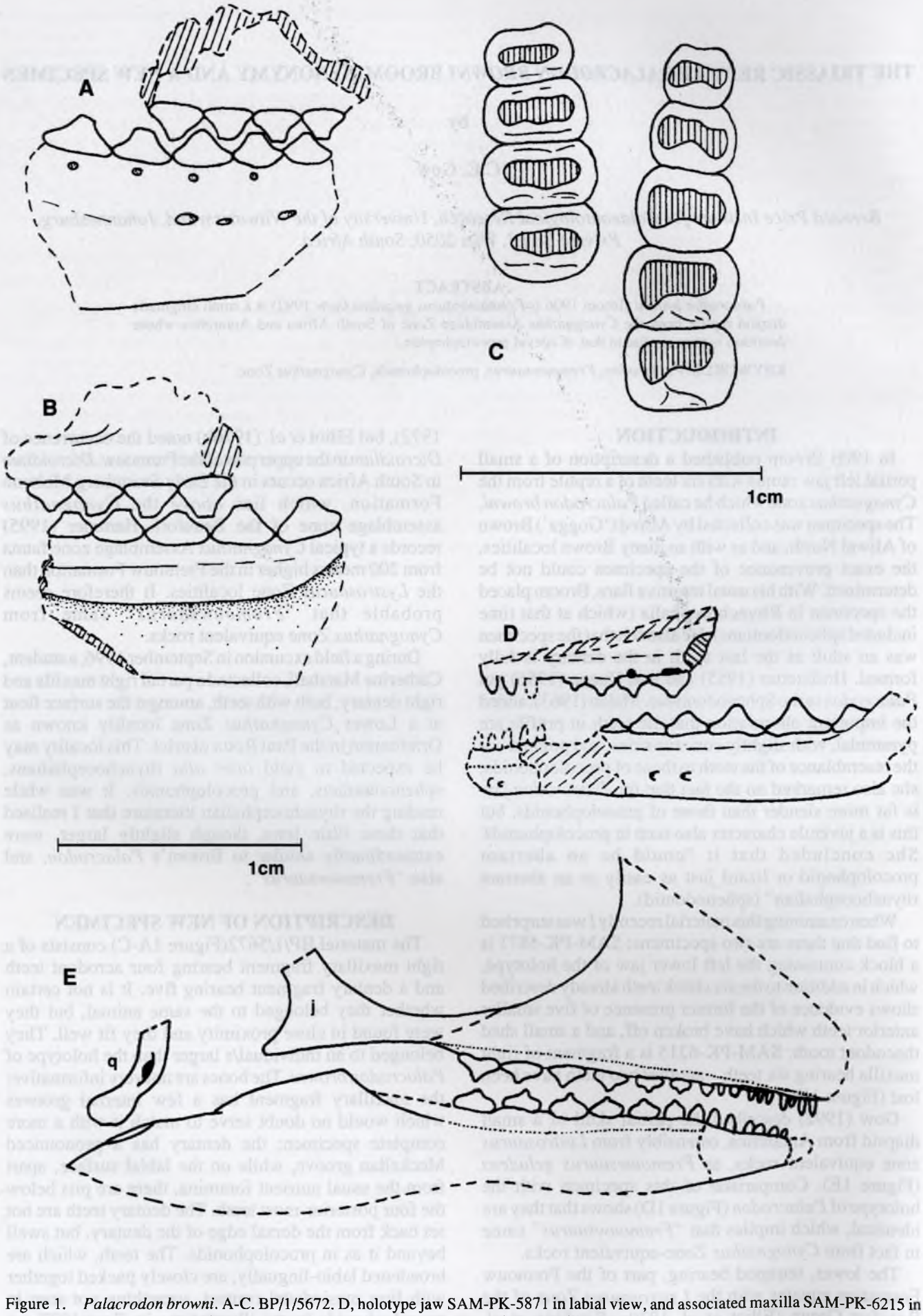

Figure 1. *Palacrodon browni*. A-C. BP/1/5672. D, holotype jaw SAM-PK-5871 in labial view, and associated maxilla SAM-PK-6215 in buccal view. E, holotype of *Fremouwsaurus geludens*. (Note: larger scale applies only to C.)

misleading in this respect). Mesial and distal slopes of the teeth are slightly concave; the transversely broadened tips are lightly abraded, which reveals that the enamel is extremely thin. The upper and lower teeth probably intermeshed at rest, while some propalinal movement was possible during the feeding cycle. Upper teeth have a slight distal shelf and all but the first have a very slightly developed mesial shelf, both shelves running almost the full width of the tooth. Upper wear facets are transversely concave: lower wear facets are more flat in the linguolabial plane; they have a marked mesio-distal convexity, and a noticeable tendency for the facets to extend down the distal slope in more posterior teeth. The teeth decrease in size from back to front, which indicates that the missing more anterior, incisiform, teeth would have been considerably smaller.

DISTINGUISHING *PALACRODON* JAWS AND TEETH FROM THOSE OF PROCOLOPHONIDS

The teeth of *Palacrodon* are very similar to those of *Cynognathus* Zone procolophonids in being acrodont, and having similar morphology, occlusion and wear; however, they can be distinguished by 1) mesiodistal contact between cheek teeth in mature specimens, and 2) mesial and distal crown surfaces are concave.

SYSTEMATIC PALAEONTOLOGY

Diapsida *incertae sedis*

Holotype *Palacrodon browni* Broom 1906

Synonym *Fremouwsaurus geludens* Gow 1992

Refered material: SAM-PK-6215, a right maxilla with teeth, and BP/1/5672, right maxillary and dentary fragments with teeth.

Diagnosis. Small diapsid reptile with breached lower temporal bars and acrodont dentition. Teeth small and peg-like anteriorly, becoming broad posteriorly with crowns biconcave in profile. Posterior cheek teeth of mature individuals having broad mesial and distal contacts with their neighbours.

SUMMARY

Palacrodon (=*Fremouwsaurus*) is an extremely rare component of the *Cynognathus* Assemblage Zone fauna. Its diapsid nature is established on the basis of: jugal with posteroventral spur, quadrate with curved lateral profile and foramen, and absence of quadratojugal (Gow 1992). Although the diagnostic premaxillae and palatines are unknown, the animal cannot be a sphenodontid as in sphenodontids the quadrate foramen lies between the quadrate and quadratojugal.

Palacrodon is characterised by the following: procolophonid-like dentition, but differing in that adjacent cheek teeth contact each other and their mesial and distal slopes are concave. In addition to small size, the following are here regarded as juvenile characters: i) narrow (shallow) dentary, and ii) teeth set back from the lateral margins of the jaws, with iii) distinct ridges on the dentaries and maxillae for the attachment of soft tissue.

ACKNOWLEDGEMENTS

The Director and Staff of the South African Museum are thanked for the loan of the holotype of *Palacrodon*. Catherine Marshall found the new specimen.

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Palaeont. afr., **35**, 25-40 (1999)

PERMO-TRIASSIC FOSSIL WOODS FROM THE SOUTH AFRICAN KAROO BASIN

by

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ABSTRACT

The Karoo Basin extends over more than half of the South African land surface and incorporates sediments deposited over a period of more than 100 million years, from the Upper Carboniferous to the Lower Jurassic. Biozones have been established on the basis of the abundant vertebrate fauna. Fossil plant deposits are numerous but best represented by the Lower Permian *Glossopteris* floras and Middle to Upper Triassic *Dicroidium* floras. Fossil woods occur throughout the sequence. In this paper previously described woods are discussed, newly collected woods are described and an attempt is made to correlate the woods with the Formations and vertebrate biozones. *Prototaxoxylon africanum* (Walton) Krausel and Dolianiti is common but restricted to the Permian (Ecca and Lower Beaufort Groups). *Prototaxoxylon uniseriale* Prasad has the same distribution but is rare. *Australoxylon teixeirae* Marguerier extends from the Ecca to the middle Beaufort. *Araucarioxylon* occurs throughout the Karoo but there are several species that have different ranges. *Araucarioxylon africanum* Bamford sp. nov. occurs throughout the Beaufort and into younger deposits. *Araucarioxylon karooensis* Bamford sp. nov. occurs in the Normandien Formation of the Beaufort Group. Woods with podocarpacean affinities, recognized as *Mesembrioxylon*, first occur in the uppermost Beaufort and extend into the Cretaceous. The woods can, therefore, be used as broadscale biostratigraphic indicators but further data need to be collected.

KEYWORDS: gymnosperm woods, *Araucarioxylon, Australoxylon, Mesembrioxylon Prototaxoxylon*, biostratigraphy.

INTRODUCTION

The first good description of Karoo fossil woods was by Warren (1912) on collections in the Natal Museum but woods had been recorded earlier than that. Atherstone (1857) described the "wood beds" of the Uitenhage area (now Kirkwood Formation, Lower Cretaceous) and Mellor & Leslie (1906) described fossil root casts of *Stigmaria* in the Vaal River near Vereeniging which is in the Ecca Group. Bancroft (1913) described the unusual wood *Rhexoxylon africanum* from the Molteno Formation. The locality and whereabouts of the holotype are unknown but several *Rhexoxylon* species have been described from other Gondwana Triassic deposits. A taxonomic revision of the genus is needed as well as a more feasible interpretation of the growth form of the plant. Walton (1923, 1925, 1956), Rodin (1956), Marguerier (1973) and Erasmus (1976) have also described fossil woods from the Karoo. These woods are summarised in Table 1 together with this author's interpretation and updating of nomenclature.

Dadoxylon is the most common genus in Palaeozoic deposits but this is a most unsatisfactory taxon because there are several interpretations of its diagnostic features and no consensus. Endlicher erected this genus in 1847 and included specimens described by Lindley & Hutton (1831) and Witham (1833). The type species is usually considered to be *D. withamii* which has a homogeneous pith, but this feature was not noted in the original description. There is considerable nomenclatural confusion and Philippe (1993) also showed that the genus is invalid according to the Botanical Code of Nomenclature because Endlicher (1847) included all the syntypes of *Pinites* Witham 1833. *Dadoxylon* is, therefore, a synonym of *Pinites* but *Pinites* is not a homoxylous wood. Furthermore the diagnostic features are in contention; species have been described with or without pith and primary xylem, and with or without multiseriate rays. Revisions of *Dadoxylon* tend to be lengthy because the original diagnosis is too general. *Araucarioxylon* Kraus is another genus with which there is much confusion and some authors synonymise *Araucarioxylon* and *Dadoxylon* or use the names together with one or other genus in parentheses (see Giraud 1991).

The present author prefers the use of "*Dadoxylon*" as a catch-all for woods with araucarian tracheid pitting and pith, which do not fit into the described woods with characteristic or distinctive pith types. With so much new data and more narrowly defined taxa, *Dadoxylon* is of limited biostratigraphic or phylogenetic application as a genus. Perhaps Lepekhina's (1972) group Dadoxyleae has greater use because she made a clear distinction between woods with secondary xylem only and woods with secondary xylem and associated pith. *Araucarioxylon* and *Agathoxylon* Hartig (1848) are useful designations for woods which have secondary xylem with araucarian tracheid pitting and

TABLE 1

Previously described Karoo woods from South Africa. The right hand column shows the most recent taxonomic status. * specimen is redescribed in this paper.

STRATIGRAPHY	NUMBER	LOCALITY	AUTHOR	WOOD	COMMENT
MOLTENO Formation	AM619	Modderpoort	Walton 1925	*Dadoxylon sclerosum*	pith
	SAM 2954	Kromme Spruit	Walton 1925	cf *Dadoxylon sclerosum*	
	--	Dordrecht	Walton 1925	*Rhexoxylon priestleyi*	
BEAUFORT Group	--	Empangeni	Erasmus 1976	*Dadoxylon arberi*	*Australoxylon teixeirae*
	SAM 1089	Klipgat	Walton 1925	*Dadoxylon arberi*	*Australoxylon teixeirae*
	AM 508	Van Wyk's Vlei	Walton 1925	*Dadoxylon arberi*	*Australoxylon teixeirae*
	NM 219	Umkomaas	Walton 1925	*Dadoxylon arberi*	*Australoxylon teixeirae*
	NM 11	Umkomaas	Walton 1925	*Dadoxylon arberi*	*Australoxylon teixeirae*
	SAM 4354	Weltevreden	Walton 1925	*?Dadoxylon arberi*	*?Australoxylon teixeirae*
	*SAM 2945	Hamsfontein	Walton 1925	*Spiroxylon africanum*	
	NM 160	Natal	Warren 1912	*Dadoxylon* sp.2	*Protophyllocladoxylon?*
ECCA Group	AM 2296	Van Wyk's Vlei	Walton 1925	*Dadoxylon arberi*	
	--	Tete	Marguerier 1973	*Australoxylon teixeirae*	
	--	Natal	Marguerier 1973	*Australoxylon natalense*	
	SAM 2946	Noro Kei Pan	Walton 1925	*Dadoxylon* sp.	
	SAM 2947	Van Wyk's Vlei	Walton 1925	*Dadoxylon arberi*	*Australoxylon teixeirae*
	NM (23 specimens)	Natal Coal Measures	Warren 1912	*Dadoxylon* sp.1	*Australoxylon teixeirae* *Australoxylon natalense* *Araucarioxylon spp.*

no additional distinguishing characteristics, such as the ray border cells of *Dammaroxylon* (Schultze-Motel 1966), clustered pits of *Australoxylon* (Marguerier 1973) or traumatic resin canals of *Brachyoxylon* (Hollick & Jeffrey 1909). Philippe (1993) said that *Araucarioxylon* (also a synonym of *Pinites*) was invalid and *Agathoxylon* or *Brachyoxylon* should be used. This author (and many others) consider that *Brachyoxylon* should be restricted to taxa with traumatic resin canals. *Agathoxylon* is rarely used but has abundant axial parenchyma and so could be used for woods with parenchyma which is not confused with resin-filled tracheids. This could mean that *Araucarioxylon* could be emended for woods with secondary xylem only and little to no axial parenchyma. Pant & Singh (1987) have also reviewed this group of woods but came to no conclusion about their affinities.

MATERIALS AND METHODS

Fossil woods have been collected from all over South Africa but only those from known biozones will be considered here. The specimens, localities and stratigraphy are summarised in Tables 2 and 3 in the Discussion.

Polished thin sections have been made of all the samples using the standard method for the transverse, radial longitudinal and tangential longitudinal sections: the polished surface of a small block was mounted on a petrographic glass slide and the rest of the block was cut using a discoplan. The newly cut surface was then ground and polished to the required thickness, usually 25-80 μm, depending on the cell size and crystal size, and studied under a transmitted light microscope. Most woods are silicified but some are calcified.

TABLE 2

Fossil woods studied by the author and used for the biostratigraphy. All specimens are housed in the Bernard Price Institute.

Group FORMATION Member	LOCALITY	SPECIMEN NUMBERS BP/16/ –	COLLECTOR	FOSSIL WOOD
CLARENS	Rhebokhoek	351-363	M. Bamford	*Mesembrioxylon sp. (?)*
MOLTENO	Kannaskop Boesmanshoek Sterkstroom	728-729 727 392	H. Anderson P. J. Hancox	*Araucarioxylon sp.* *Araucarioxylon sp.* *Araucarioxylon sp.*
Beaufort BURGERSDORP	Sterkstroom	490 395		*Mesembrioxylon cf rajmahalense* *Mesembrioxylon sp.*
NORMANDIEN	Thukela, Natal Harrismith McFie's donga	550 551, 552 311, 312 313-315 316 302	C. Gow C. MacKnight T. Mason	*Araucarioxylon karooensis* *Araucarioxylon africanum* *Araucarioxylon africanum* *Australoxylon teixeirae* *Araucarioxylon africanum*
BALFOUR	Aberdeen	721	P. Karpeta	*Australoxylon teixeirae*
TEEKLOOF Poortjie Member	Stellenboschvlei	303-308	J. Loock	*Australoxylon teixeirae*
ABRAHAMSKRAAL Koornplaats Member	Wildheuvel Swaerskraal	281, 282a, 283d 284a 298, 299 300	B. Rubidge R. Heard	*Prototaxoxylon africanum* *Prototaxoxylon uniseriale* *Australoxylon teixeirae* *Prototaxoxylon uniseriale*
Ecca WATERFORD FORT BROWN	Laingsburg	387	B. Rubidge	*Prototaxoxylon africanum*
KOOKFONTEIN	Paardekraal	285, 286f	B. Rubidge	*Prototaxoxylon africanum*
COLLINGHAM	Ecca Pass	469	M. Bamford	*Australoxylon teixeirae*

The thin sections were studied under a Zeiss Axiophot microscope, measured and photographed. Descriptions of the taxa are given below. All specimens and slides are catalogued and housed in the Bernard Price Institute, Johannesburg.

DESCRIPTION OF FOSSIL WOODS

Prototaxoxylon africanum (Walton) Kräusel & Dolianiti 1958

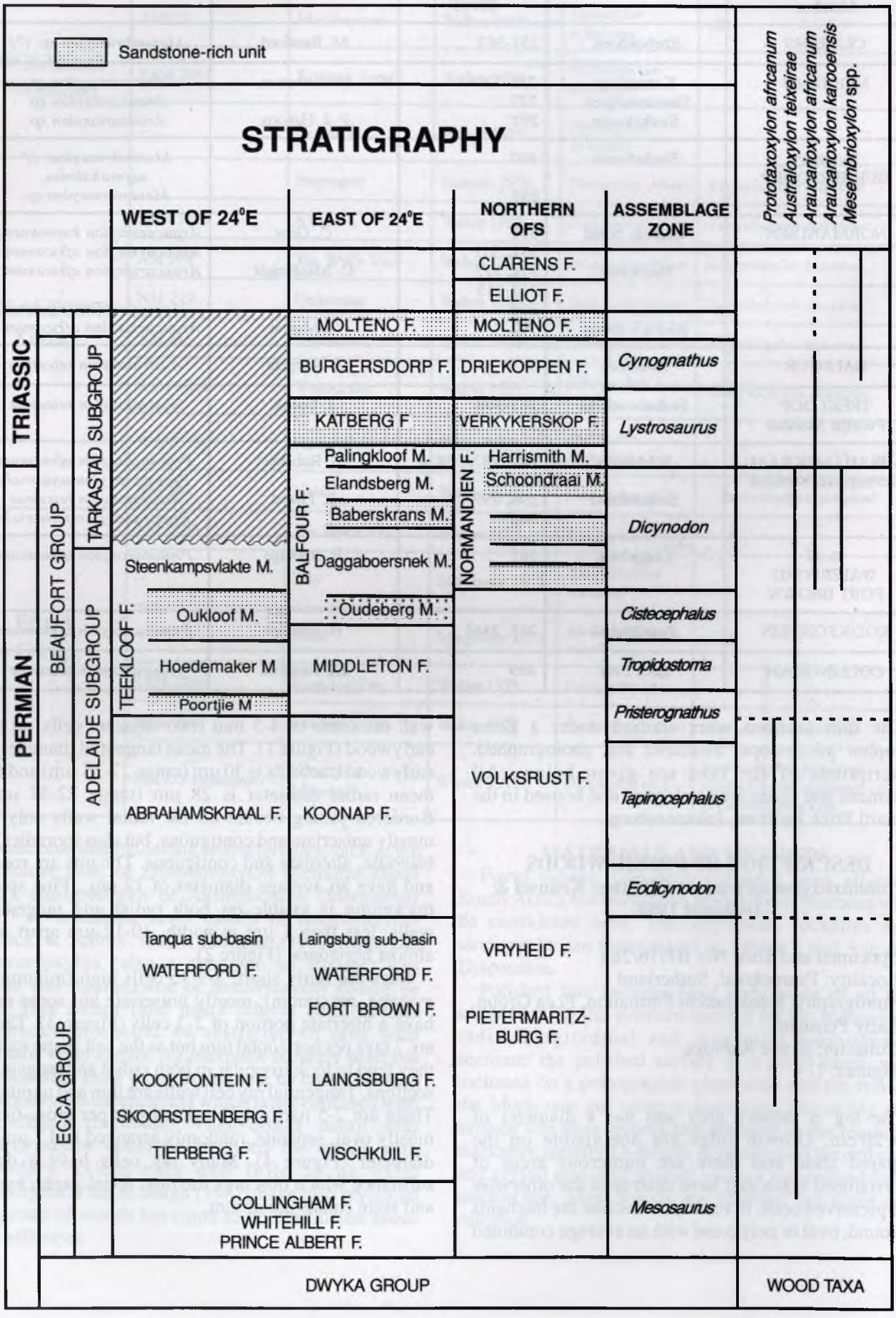
Specimen and Slide No: BP/16/285
Locality: Paardekraal, Sutherland
Stratigraphy: Kookfontein Formation, Ecca Group, Early Permian
Collector: Bruce Rubidge
Figures: 1- 4

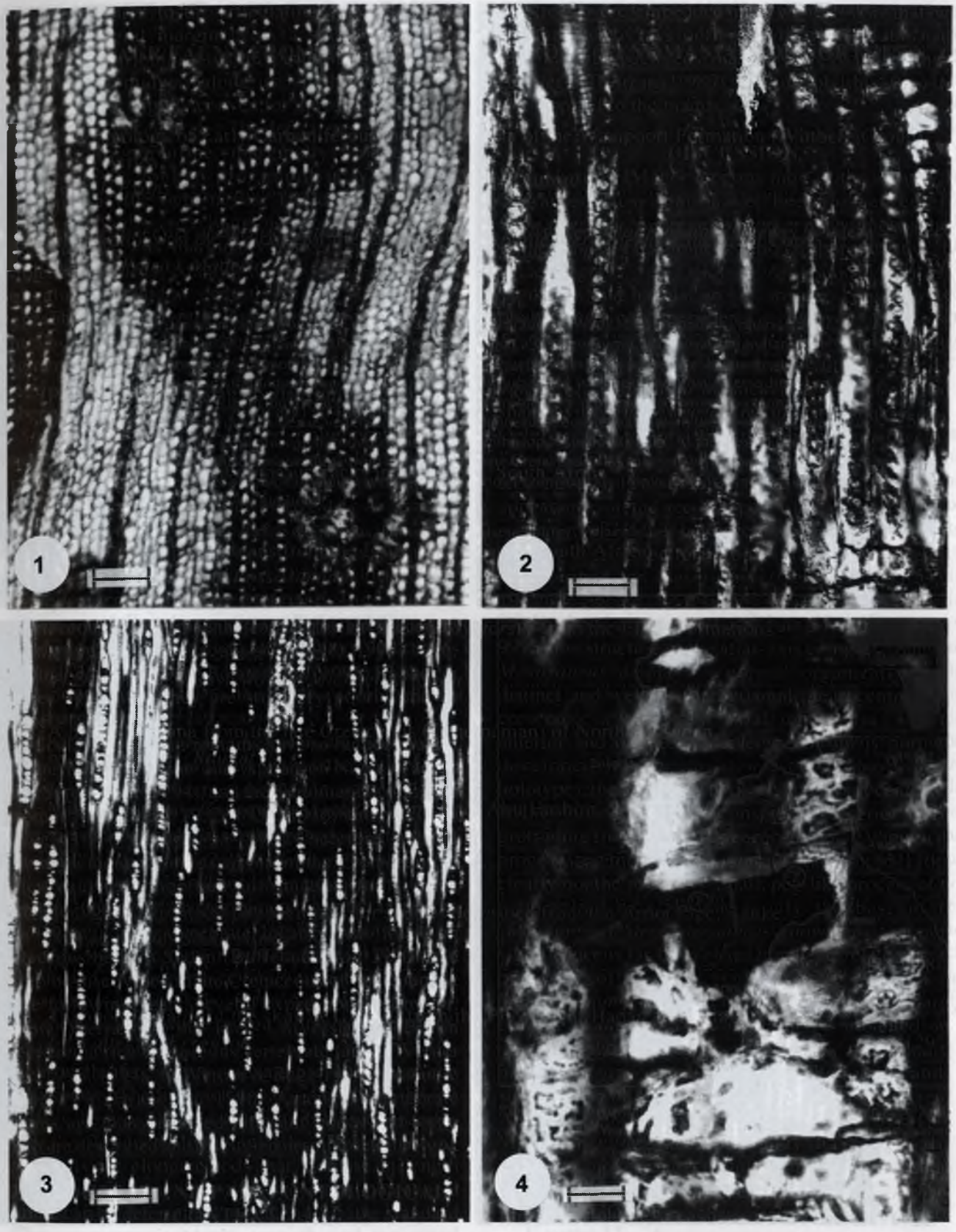
The log is streaky grey and has a diameter of 25 x 20 cm. Growth rings are not visible on the prepared slide and there are numerous areas of recrystallised silica that have destroyed the otherwise well preserved cells. In transverse section the tracheids are round, oval or polygonal with an average combined wall thickness of 4-5 mm (two adjacent cells) in the earlywood (Figure 1). The mean tangential diameter of earlywood tracheids is 30 µm (range 27-35 µm) and the mean radial diameter is 28 µm (range 22-32 µm). Bordered pitting occurs on the radial walls only, is mostly uniseriate and contiguous, but also sporadically biseriate, alternate and contiguous. The pits are round and have an average diameter of 12 µm . Fine spiral thickening is visible on both radial and tangential walls, less than 1 µm in width, 10-12 µm apart and almost horizontal (Figure 2).

Rays are fairly short, 2-9-15 cells high (minimum, average, maximum), mostly uniseriate but some rays have a biseriate portion of 2-3 cells (Figure 3). There are 7 rays per horizontal mm but as the cell shape varies they tend to look irregular in both radial and tangential sections. Tangential ray cell walls are thin and unpitted. There are 2-5 narrowly bordered pits per cross-field, mostly oval, separate, randomly arranged and 7 µm in diameter (Figure 4). Many ray cells have a dark substance which obscures the pits. Axial parenchyma and resin canals are absent.

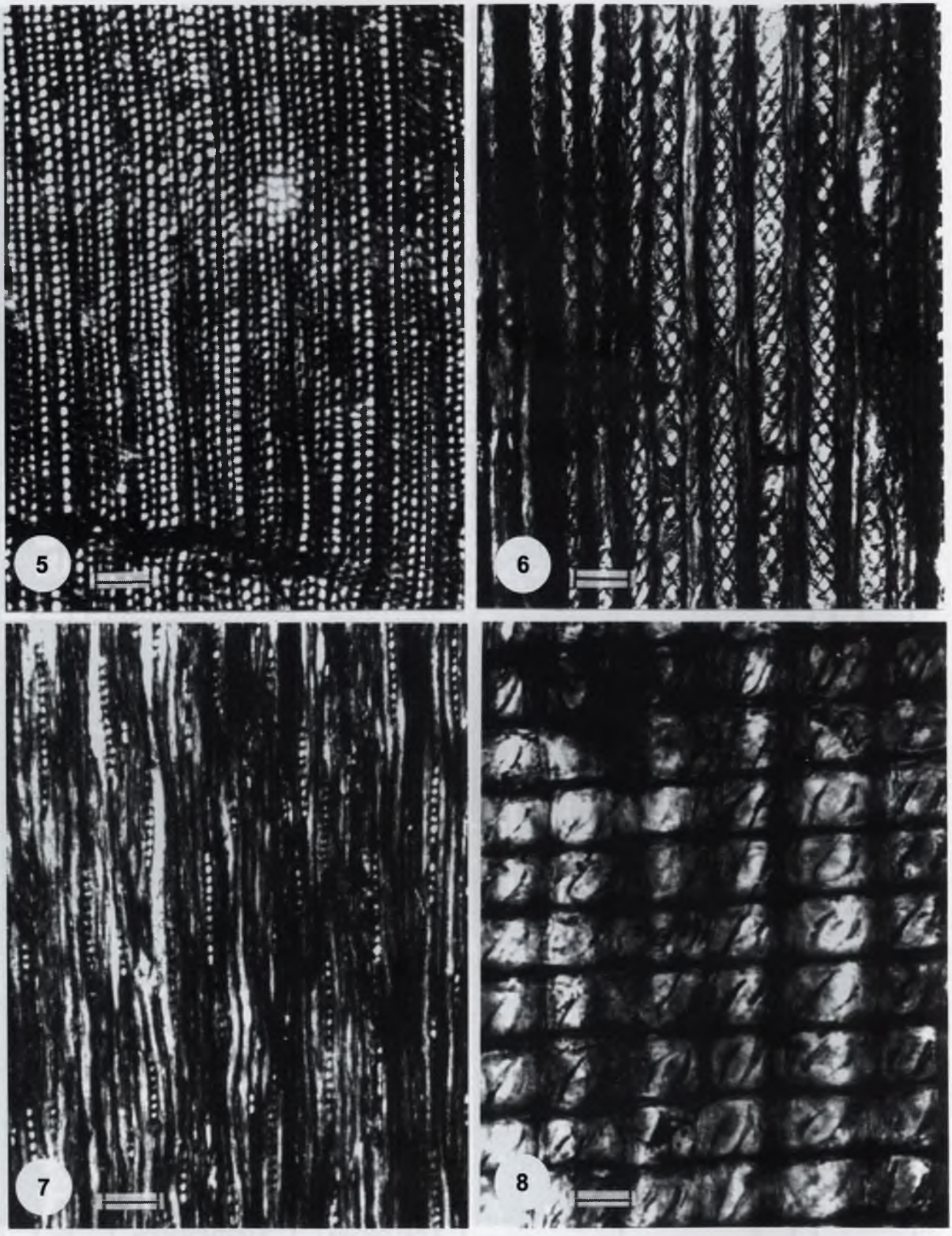
TABLE 3

Stratigraphy of the Permian and Triassic Karoo Basin. Ecca stratigraphy from Wickens (1994). Beaufort stratigraphy from Rubidge *et al.* (1995) and SACS (1980). Ranges of fossil wood taxa from this study.





FIGURES 1-4. *Prototaxoxylon africanum* BP/16/285. **1:** TS (transverse section) showing regular tracheids and no growth rings. The dark patches are a preservational artefact. Scale bar = 150 μm. **2:** RLS (radial longitudinal section) showing the uniseriate and biseriate alternate bordered pits and fine spiral thickenings on the radial walls of the tracheids. Scale bar = 30 μm. **3:** TLS (tangential longitudinal section) showing uniseriate rays and fine spiral thickenings on the tracheid walls. Dark deposits in the cells are probably resiniferous. Scale bar = 200 μm. **4:** RLS showing narrowly bordered pits in the cross-field. Scale bar = 15 μm.



Figures 5-9. *Prototaxoxylon uniseriale* BP/16/300. **5:** TS showing a partial (false) growth ring. Scale bar = 130 μm. **6:** RLS with heavy spiral thickening criss-crossing on the tracheid walls, and uniseriate bordered pits. Scale bar = 50 μm. **7:** TLS uniseriate rays. Scale bar = 130 μm. **8:** RLS with single, oblique cross-field pits partially obscured by the spiral thickening. Scale bar = 15 μm.

Prototaxoxylon uniseriale Prasad 1982

Specimen No: BP/16/300
Locality: Swaerskraal, Laingsburg
Stratigraphy: Koornplaats Member, Abrahamskraal Formation, Beaufort Group, Late Permian
Collector: Rob Heard
Figures: 5 - 8

The log is 9 x 6 cm in diameter and 4 cm in length, beige and browns in colour. Growth rings are distinct but the earliest earlywood is distorted and crushed, compacted into the latewood, so growth rings are difficult to measure; they range from 1-3 mm. In transverse section (Figure 5) the tracheids have roundish lumina and square to polygonal outlines (but the corners are not thickened). Wall thickness is 3-5 µm. The earlywood tracheid mean tangential diameter is 26 µm(range 17-35µ m) and mean radial diameter is 26 µm (range 20-35 µm). Bordered pits occur on the radial walls only, are uniseriate, contiguous and not compressed, with a diameter of 20 µm. Spiral thickening is biseriate, criss-crossing over the pits, 3-5 µm thick and 7-10 µm apart (Figure 6). The spirals are about 45° to the horizontal.

These are definitely spirals; wall degradation was seen in some specimens and the markings are at a steeper angle and appear more broken up and erratic.

Rays are uniseriate, homogeneous, 7-10-20 cells high and there are 10 rays per horizontal mm (Figure 7). Cross-field pits are mostly single, bordered and oblique and also covered by the spiral thickening (Figure 8). Very rarely there are two pits per field. The pits are 7 x 17 mm. There are no resin canals or axial parenchyma.

Discussion

This genus, *Prototaxoxylon,* was first described as *Spiroxylon africanum* by Walton from Harmsfontein, Cape (1925, unknown age) but, as the generic name had already been used, Kräusel and Dolianiti (1958) transferred it to their new genus *Prototaxoxylon.* Although Walton's slides cannot be traced, the type specimen, SAM 2945, was borrowed from the South African Museum and new thin sections made. There is no doubt that the Paardekraal and other specimens (Table 2) belong to the same taxon.

Prototaxoxylon africanum - description of holotype SAM 2945
Figures: 9-12

The specimen is black, smooth and measured 8 x 4 x 3 cm but had already been sectioned. In transverse section the tracheids are square to polygonal with fairly thick walls, 7-10 µm. Growth rings are 4-7 mm wide, indistinct, with very little latewood, and the earlywood tracheid mean tangential and radial diameters are 41 and 40 µm respectively (Figure 9). Bordered pits occur on the radial walls, 1-2 seriate, contiguous, alternate and with a diameter of 12-14 µm (Figure 10). The same pitting occurs on the tangential walls but much less frequently. Rays are uniseriate with occasional biseriate portions of 1-3 cells, 2-9-14 cells high (Figure 11). Cross-field pits are round to oval with a thick, poorly preserved border. The aperture is 5-7 µm and the border 1-2 µm (total diameter 6-8 µm). There are 2-8 of these pits, which are between cupressoid and dacrydioid, per field (Figure 12). Walton described them as "There are two to eight small pits per field. No border can be seen to the pits, though it is possible that a border may have been present." (1925, p. 19). The spiral thickening is very delicate, less than 1 µm in thickness, 10-14 µm apart, almost at right angles to the vertical tracheid walls and passing between the tracheid pits (Figures 10-12).

Emended diagnosis:

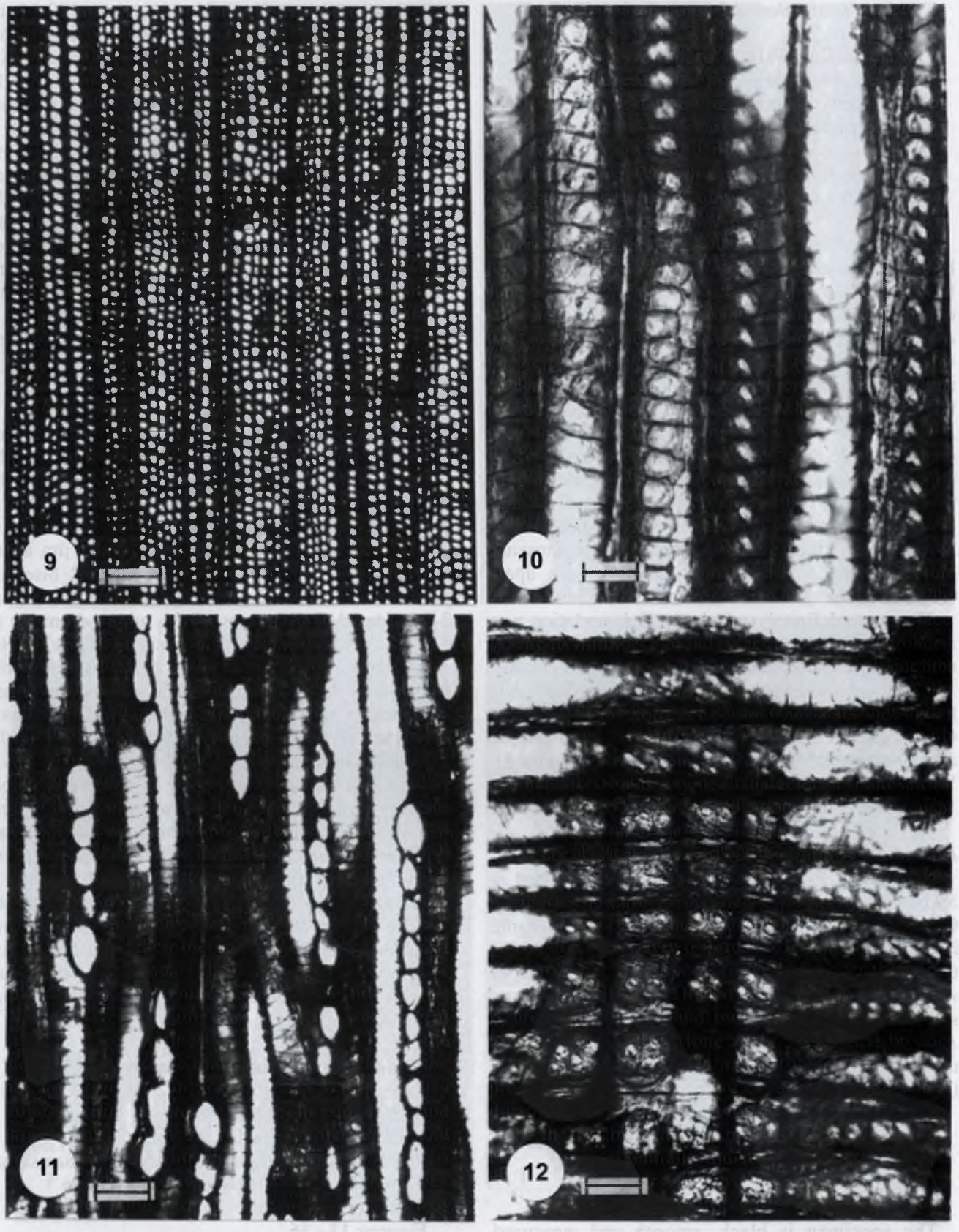
Secondary xylem wood with 1-2 seriate alternate bordered pitting on radial walls of the tracheids. The pits are 12-14 µm in diameter and also occur on the tangential walls but less frequently. Fine spiral thickening on the tracheids is almost at right angles to the walls, less than 1 µm thick and 10-14 µm apart. Rays are low, uniseriate with occasional biseriate portions and the walls are thin and unpitted. There are 2-8 bordered pits per cross-field, with a diameter of 6-8 µm. Axial parenchyma and resin canals are absent.

Prototaxoxylon africanum has been described only from South Africa. Several other species have been documented, mostly from India but also from Russia and Brazil (Prasad 1982). They range in age from the Carboniferous to "Mesozoic". *P. intertrappeum* (Prakash & Srivastava 1962) is of questionable Tertiary age. *Prototaxoxylon uniseriale* was first described from the Upper Permian of India (Prasad 1982) and is quite distinct from *P. africanum* as it has much heavier spiral thickening. *P. africanum* is common in the South African Karoo with occurrences in the Waterford, Fort Brown (Ecca) and Abrahamskraal Formations (Lower Beaufort) which are Lower Permian. In South Africa, *P. uniseriale* has to date only been recorded in the Abrahamskraal Formation.

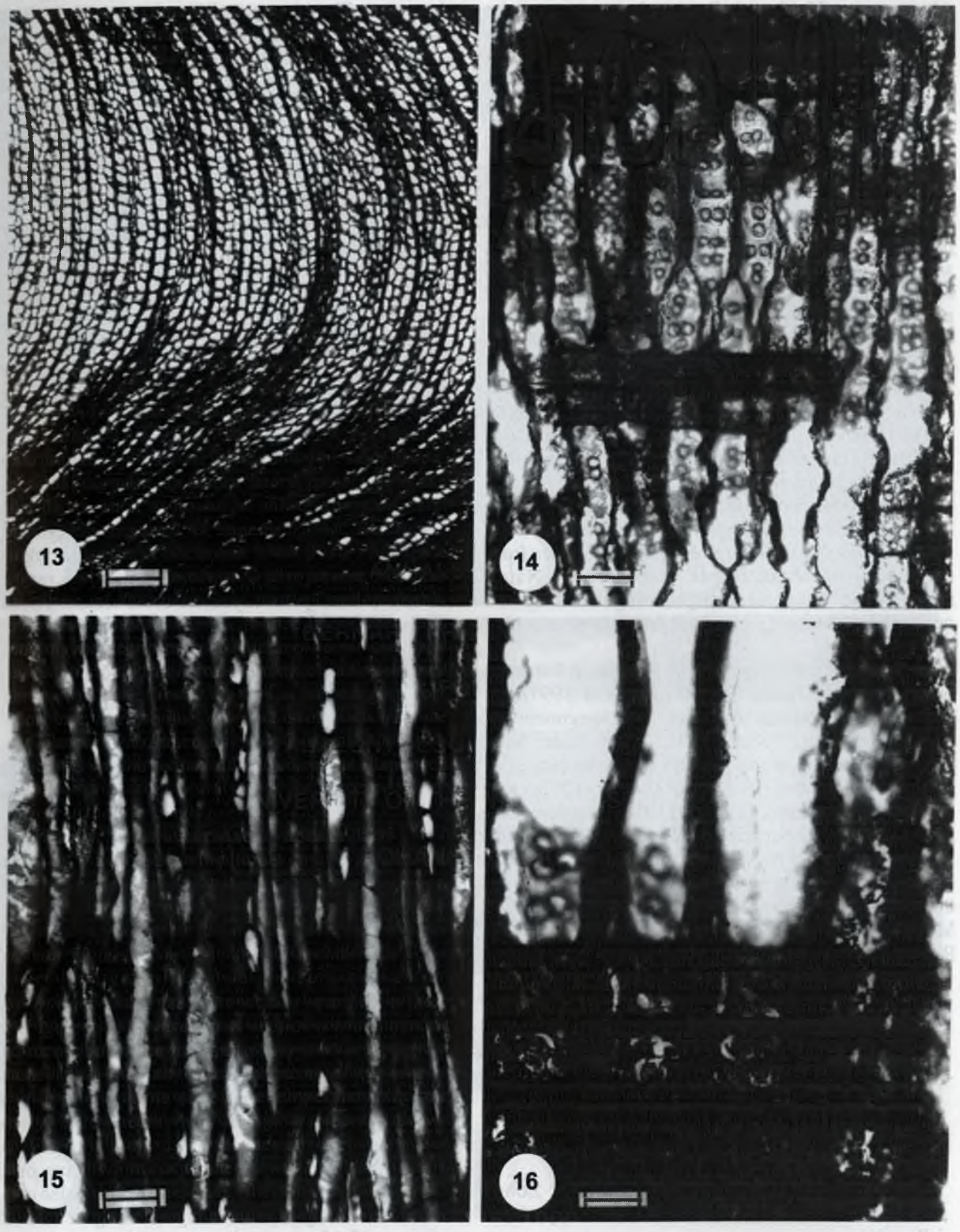
Australoxylon teixeirae Marguerier 1973

Specimen No: BP/16/298
Locality: Swaerskraal, Laingsburg
Stratigraphy: Koornplaats Member, Abrahamskraal Formation, Beaufort Group, Late Permian
Collector: Rob Heard
Figures: 13 - 16

The log measures 10 x 5 x 6 cm and is beige with orange streaks. Growth rings are distorted. Tracheids are square to rectangular in transverse section and the cell walls are 5-7.5 µm thick (Figure 13). The earlywood tracheid mean tangential diameter is 39 µm (range 35-55 µm) and the mean radial diameter is



Figures 9-12. *Prototaxoxylon africanum SAM 2945* (type specimen). **9:** TS with growth ring. Scale bar = 200 µm. **10:** RLS showing uni- and biseriate pitting and fine spiral thickening. Scale bar =30 µm. **11:** TLS with uniseriate rays, some with resin deposits, and fine spiral thickening. Scale bar = 60 µm. **12:** RLS showing narrowly bordered cross-field pits. Scale bar = 10 µm.



Figures 13-16. *Australoxylon teixeirae* BP/16/298. **13:** TS with distorted preservation. Scale bar = 200 μm. **14:** RLS with clusters or stellate groups of pits. Scale bar = 50 μm. **15:** TLS with uniseriate rays and occasional biseriate portions. Scale bar = 100 μm. **16:** RLS with narrowly bordered pits in the cross-field. Scale bar = 20 μm.

44 µm (range 25-60 µm). Bordered pits occur on the radial walls only, are mostly 1-2 seriate, very rarely 3-seriate, opposite or alternate, and mostly in distinct clusters (Figure 14). When contiguous, the pits are still round with no compression. The pits are 10 µm in diameter with an aperture of 5 µm.

Uniseriate rays predominate and occasionally there are biseriate portions of 1-4 cells. The rays are 3-8-21 cells high, homogeneous and there are 10 rays per horizontal mm (Figure 15). The cross-field pits have narrow borders, are round to oval, 7.5 µm in diameter, and there are 3-7 pits randomly arranged in the cross-field (Figure 16). There are no resin canals or axial parenchyma.

Discussion

This species occurs in the Permian of southern Africa. It is very common in the Abrahamskraal Formation and the lower part of the Teekloof Formation (Lower and Middle Beaufort Group). The youngest specimen is from the contact of the *Aulacephalodon* and *Cistecephalus* Assemblage Zones in the Aberdeen area. Marguerier (1973) described two species, *Australoxylon teixeirae* and *A. natalense* from the Karoo of Mozambique and Ecca of Natal, respectively. They are easily distinguished by the quadriseriate tracheid pitting and presence of crassulae in *A. natalense*.

Twenty one other species of *Australoxylon* have been described (Giraud 1991, Weaver et al. 1997) and all are from Permian deposits. The specimens of *Dadoxylon arberi* (Warren 1912) from Natal have definite clustering of the pits and should be placed in *Australoxylon teixeirae* (Marguerier 1973, and personal observation). Erasmus (1976) also described *Dadoxylon arberi* but from the Beaufort Series of the Empangeni district in Natal. His material also has the characteristic stellate groups or clusters of tracheid pits of *Australoxylon* but he overlooked the work of Marguerier. Thus, the restriction of this genus to Permian sediments in southern Africa is to be expected.

Araucarioxylon Kraus 1870

Type species: *Araucarioxylon carbonaceum* (Witham 1833) Kraus

Araucarioxylon africanum Bamford sp. nov.

Holotype: BP/16/311
Locality: Near Harrismith
Stratigraphy: *Dicynodon* Assemblage Zone, Normandien Formation, Beaufort Group, Late Permian
Collector: Chris MacKnight
Etymology: named for southern Africa
Figures: 17 - 20

The log is 13 x 10 x 14 cm and is a streaky beige colour. Growth rings are distinct with 8-9 rows of thick-walled radially compressed tracheids comprising the latewood. The average width of the growth rings is 2mm. In transverse section the tracheids are square (Figure 17). The earlywood tracheid mean tangential diameter is 37 µm (range 30-45 µm) and mean radial diameter is 41 µm (range 27-50 µm). The latewood tracheid mean tangential diameter is 36 µm (range 32-48 µm) and mean radial diameter is 13 µm (range 10-20 µm). Bordered pits occur on the radial walls only, are mostly biseriate and alternate, sporadically uniseriate, contiguous to compressed and hexagonal in shape, with a diameter of 12-15 mm and aperture of 5 µm (Figure 18).

Rays are uniseriate only, 2-8-18 cells high and there are 5 rays per horizontal mm (Figure 19). The cross-field pits are araucarioid with narrow borders, 2-4-7 per field and the pits are round to oval and 6-8 µm in diameter (Figure 20). There are no resin canals or axial parenchyma.

Diagnosis

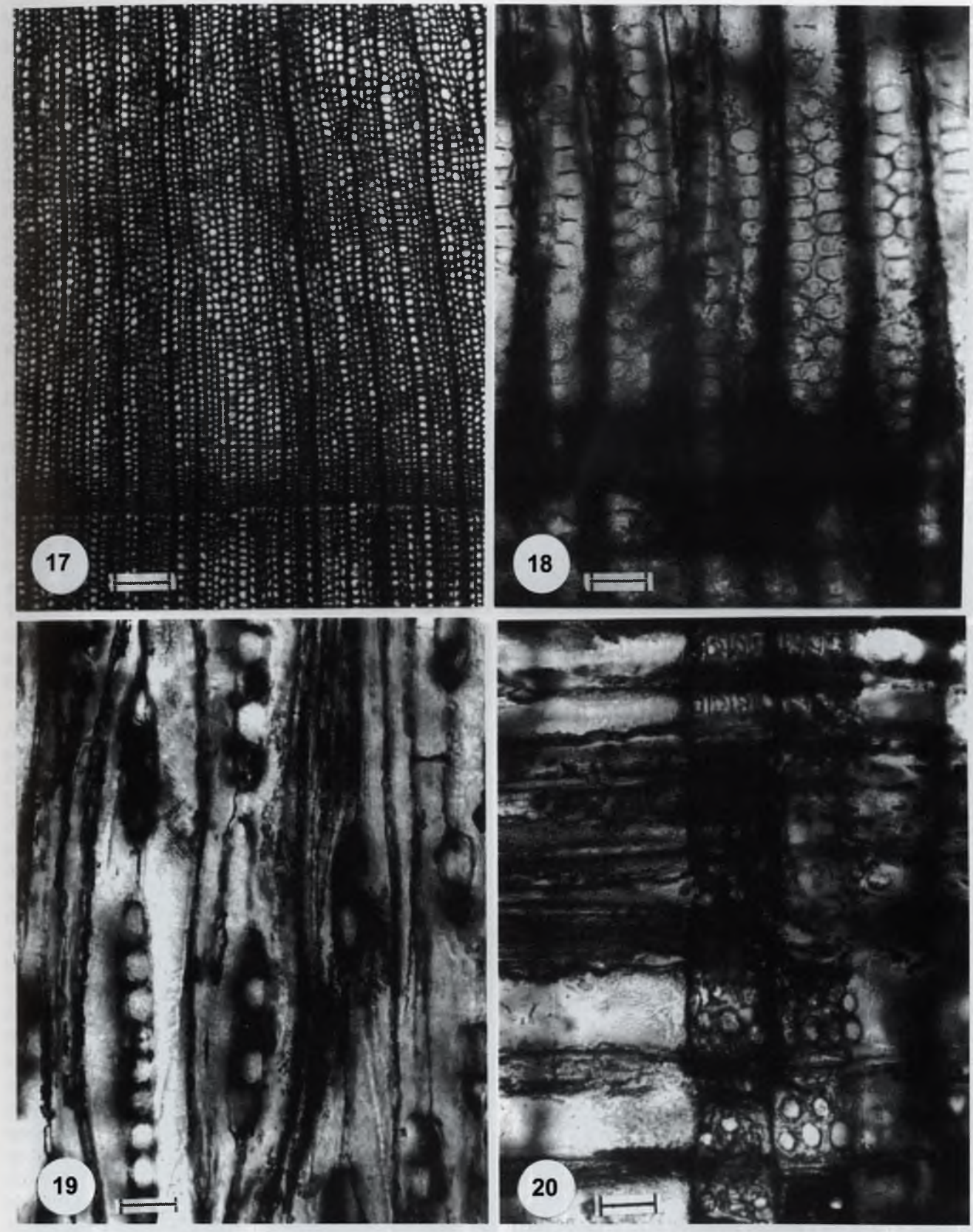
Secondary xylem wood with 1-2 seriate bordered pits on the radial walls of the tracheids, contiguous to slightly compressed, alternate, pit diameter 12-15 µm. Rays are uniseriate and have an average height of 15 cells. Cross-field pits are araucarioid (i.e. narrow border), oval shape, 6-8 µm and 2-4 per field, rarely up to 7. No axial parenchyma or resin canals. Resin in varying amounts in rays and/or tracheids.

Araucarioxylon karooensis Bamford sp. nov.

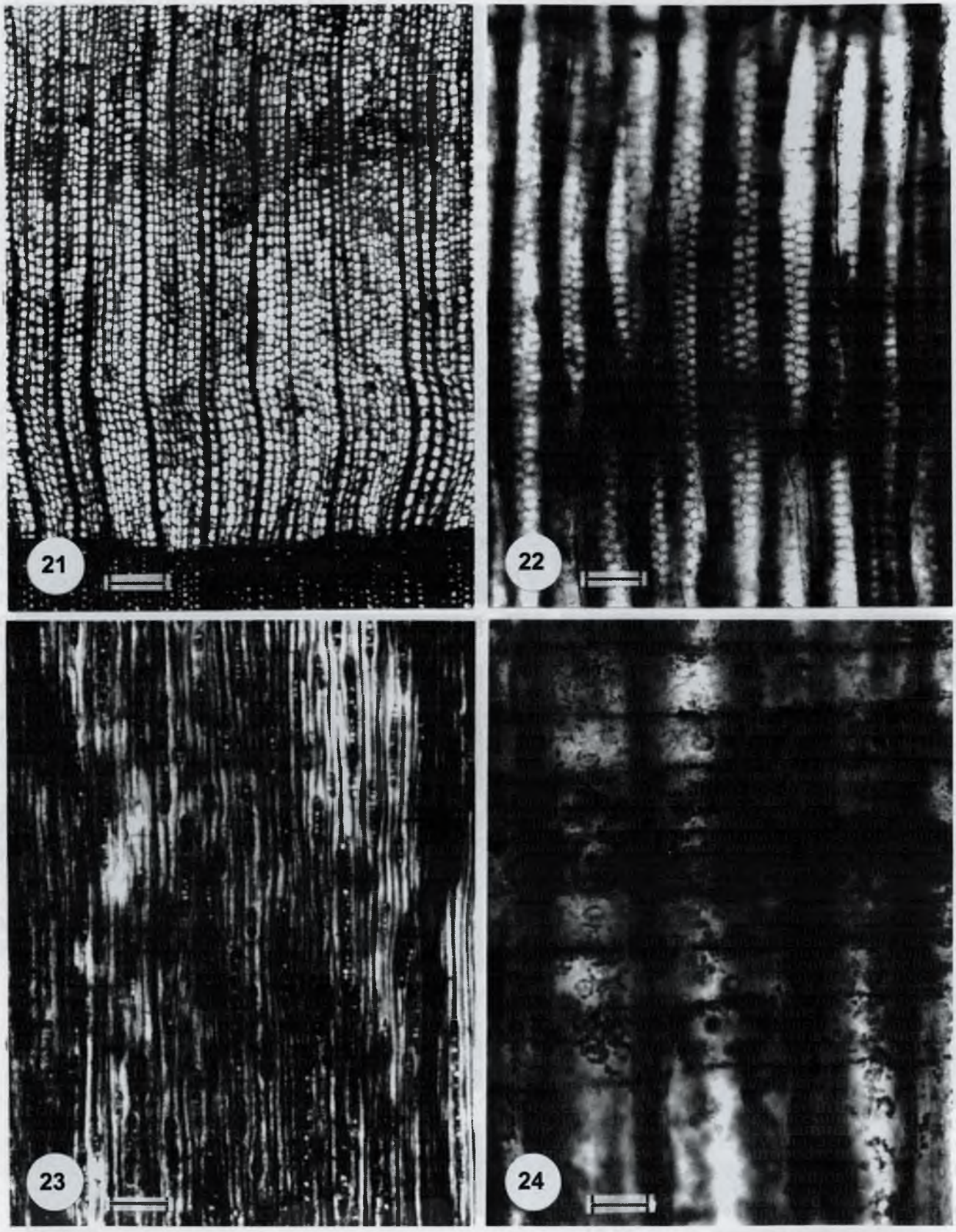
Holotype: BP/16/313
Locality: Near Harrismith
Stratigraphy: *Dicynodon* Assemblage Zone, Normandien Formation, Beaufort Group, Late Permian
Collector: Chris MacKnight
Etymology: named after the Karoo Basin and Karoo Supergroup
Figures: 21 -24

The specimen is 5 x 6.5 x 4 cm and beige with streaks. Growth rings are distinct, on average 6mm wide and terminated by 5-7 rows of latewood cells (Figure 21). In transverse section the tracheids are roundish and the earlywood tracheid mean tangential diameter is 37 µm (range 27-50 µm) and mean radial diameter is 39 µm (range 27-50 µm). The latewood tracheid mean tangential diameter is 30 µm (range 25-38 µm) and mean radial diameter is 17 µm (range 12-25 µm). Alternate bordered pitting occurs on the radial walls only and is mostly biseriate, but also uni- or triseriate, contiguous to hexagonal (Figure 22). The pits are 12-15 µm in diameter with an aperture of 5-7.5 µm.

The rays are uniseriate with sporadic biseriate portions of 1-2 cells, 3-15-25 cells high and there are 5 rays per horizontal mm (Figure 23). The cross-field pits are round to slightly oval with a very narrow border, and there are 2-4 pits per field, 7.5-10 µm in diameter (Figure 24). There are no resin canals or parenchyma.



Figures 17-20. *Araucarioxylon africanum* sp. nov. BP/16/311. **17:** TS with growth ring. Scale bar = 250 µm. **18:** RLS with biseriate, alternate and compressed bordered pitting (i.e. araucarian). Scale bar = 10 µm. **19:** TLS with uniseriate rays. Scale bar =30 µm. **20:** RLS cross-field pits with narrow borders. Scale bar = 15 µm.



Figures 21-24 *Araucarioxylon karooensis* sp. nov. BP/16/313. **21:** TS with growth ring. Scale bar = 200 μm. **22:** RLS showing triseriate araucarian pitting in the central part of the tracheid. Scale bar = 30 μm. **23:** TLS with uniseriate rays and occasional low biseriate portions. Scale bar = 200 μm. **24:** RLS with narrowly bordered cross-field pits. Scale bar = 30 μm.

The pit size varies in some specimens, but this may be an artefact of preservation.

Diagnosis

Secondary xylem wood with araucarian bordered pitting in the radial walls of the tracheids only. Pitting 1-3 seriate, contiguous, slightly compressed, alternate. Triseriate pitting must occur at least 5% of the time in the central part of the tracheid. Pits 12-15 μm in diameter. Rays predominantly uniseriate with occasional low, biseriate portions, average height 15 cells, maximum around 30 cells. 2- 4 cross-field pits, oval with a narrow border (araucarioid), and a diameter of 7.5-10 μm. No axial parenchyma or resin canals. Resin sometimes present in rays and tracheids.

Discussion

The two new species are very similar but *Araucarioxylon africanum* does not have any triseriate pitting whereas *Araucarioxylon karooensis* does have this feature. The rays in both species are similar in height but they are exclusively uniseriate in *A. africanum* whereas in *A. karooensis* there are occasional biseriate portions. Ray features, however, are not usually considered to be as important as pitting. The sizes of the tracheid pits are similar and so are the sizes of the cross-field pits in both species. Their numbers differ: *A. africanum* tends to have more cross-field pits than *A. karooensis*.

New species have been erected because the South African woods show some differences from the previously described species. *A. africanum* is similar to *Dadoxylon (Araucarioxylon) dallonii* (Dupéron-Laudoueneix 1976) from the Cretaceous of Chad. *D. dallonii* has araucarian bordered pitting which is predominantly uniseriate, also biseriate, with diameters of 16-22 μm, the rays are mostly uniseriate with occasional biseriate portions, 1-29 cells high, and there are 1-2 half bordered pits per cross-field with a diameter of 9-10 μm. The differences are in the larger bordered pits of *D. dallonii* and the type and number of cross-field pits. *A. africanum* is also similar to *Dadoxylon (Araucarioxylon) kiliani* (Batton, 1965) from the Cretaceous of Morocco. *D. kiliani* has much larger bordered pits which are predominantly uniseriate and araucarian, but the rays and cross-field pits are the same as the South Africa woods. A third species which is similar to *A. africanum* is *Dadoxylon* sp. 1 (Lemoigne 1981) from the Permian of Saudi Arabia. The difference is again in the more uniseriate nature of the tracheid pitting. No pit sizes are given in the description. The differences described above are sufficient to warrant a new species designation for the South African wood.

Araucarioxylon karooensis is similar to several Indian woods. *A. agathioides* (Kräusel & Jain 1964, Jurassic) has 1-3 seriate araucarian pitting but the pits, 10-23 mm, are larger, and more variable in size than those of *A. karooensis*. The rays and cross-field pits of both species are virtually identical. *D. amraparense* (Sah & Jain 1963, Jurassic) and *D. kharkhariense* (Maithy 1965, Permian) are also very similar but the tracheid pitting is more randomly arranged, with some degree of opposite pitting, unlike the South African specimens. These differences justify the erection of a new species.

There are numerous other species of *Araucarioxylon* and *Dadoxylon* described from Palaeozoic and Mesozoic sediments all over the world, all with fairly minor differences. The taxonomy and affinities have yet to be sorted out, however, careful description is necessary for distinguishing useful biostratigraphic types. *A. africanum* occurs in the Normandien Formation and in younger rocks (unpublished internal reports). *A. karooensis* occurs in the Normandien Formation. The Dwyka woods observed or described in the literature tend to be small, have araucarian tracheid pitting but non-araucarioid cross-field pits, and pith. According to a survey on araucarian woods (Giraud 1991), woods with multiseriate tracheid pitting are older than the biseriate ones and by the end of the Triassic 5-seriate pitting no longer occurred, by the end of the Jurassic 4-seriate pitting no longer occurred, so during the Cretaceous only uniseriate and biseriate araucarian pitting is found. No specimens of *A. karooensis* have yet been found in the younger sediments of South Africa either, but further collecting will confirm or refute these results and the ranges shown in Table 3 will have to be modified.

Mesembrioxylon cf. ***M. rajmahalense*** Jain 1964

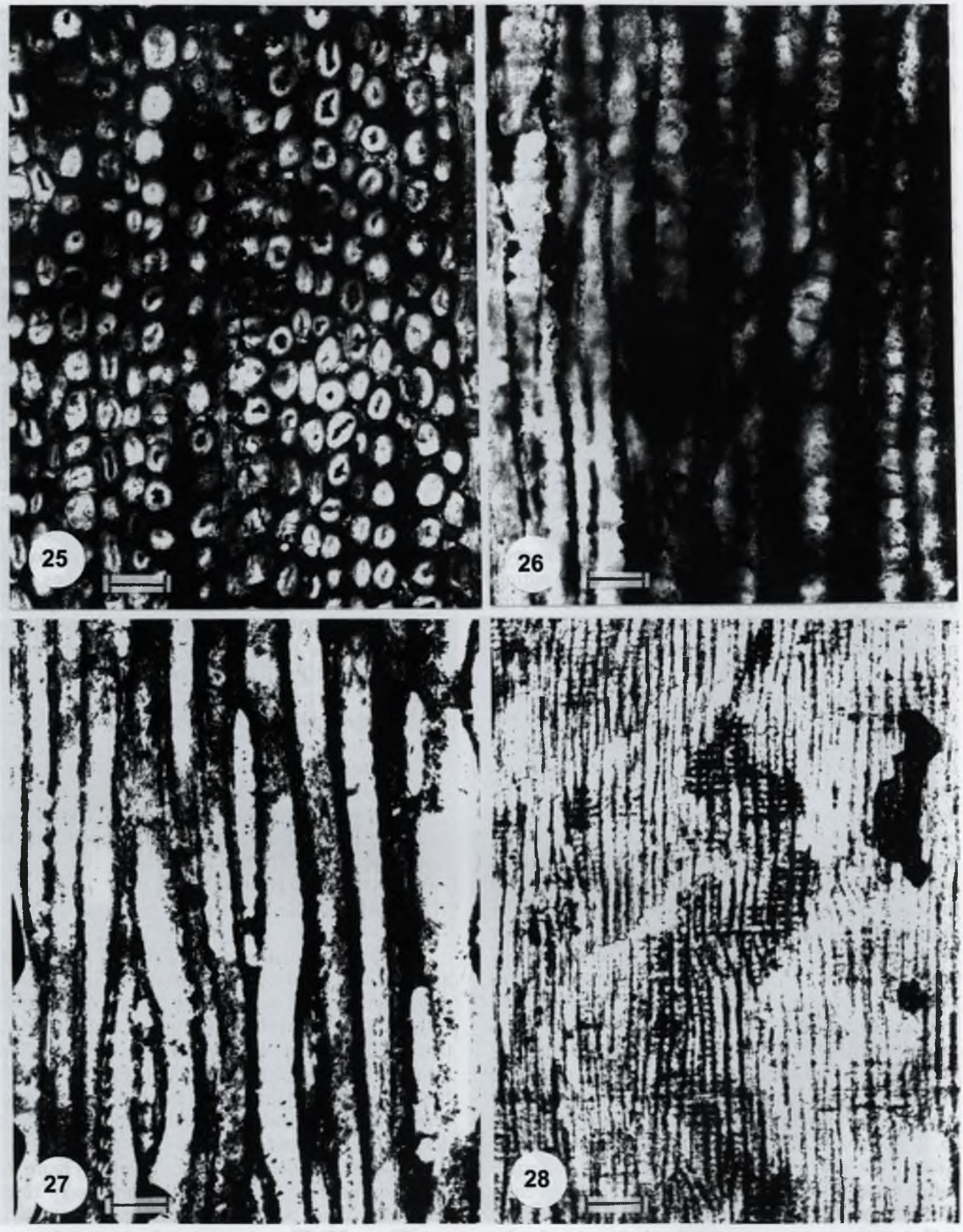
Specimen No: BP/16/470
Locality: Norwood, Sterkstroom.
Stratigraphy: Upper *Cynognathus* Assemblage Zone, Burgersdorp Formation, Upper Beaufort Group, Middle Triassic
Collector: John Hancox
Figures: 25 - 28

The piece of wood measured 5.5 x 5.5 x 3cm and is a milky beige. The tracheids are roundish in outline and neatly arranged in radial rows (Figure 25). Growth rings are not visible. Earlywood tracheid mean tangential diameter is 24 μm (range 20-32 μm) and mean radial diameter is 29 μm (range 22-37 μm). Bordered pitting is uniseriate and contiguous but not compressed, confined to radial walls, with the pit diameters 17-20 μm (Figure 26).

Rays are uniseriate, 1-8-13 cells high (Figure 27). The cross-field pits are round to oval, mostly single, very rarely 2 pits per field, and have a diameter of 12 mm (Figure 28). They are too poorly preserved to see if narrow borders are present. Other ray cell walls are thin and smooth. No resin canals or axial parenchyma occurs.

Discussion

Woods with abietinian pitting (uni- to biseriate, opposite, separate to contiguous but not compressed)



Figures 25-28. *Mesembrioxylon* cf. *rajmahalense* BP/16/470. **25:** TS with no growth rings. Scale bar = 50 μm. **26:** RLS with uniseriate, contiguous but not compressed bordered pits (abietinian). Scale bar = 20 μm. **27:** TLS uniseriate rays. Scale bar = 20 μm. **28:** RLS with single, large, simple cross-field pits. Scale bar = 120 μm.

first occurred in the Upper Triassic (Selmeier & Vogellehner 1968, Mueller-Stoll 1986) as did the Protopinaceae which have "mixed" pitting (araucarian and abietinian). This specimen, BP/16/470, has the features of several abietinian genera, *Podocarpoxylon, Phyllocladoxylon* and *Mesembrioxylon*. These woods have affinities with the Podocarpaceae but *Mesembrioxylon* was erected by Seward (1919) for woods whose cross-field pits are between those of the other two genera. The South African specimen is poorly preserved but is most similar to *M. rajmahalense* from the Jurassic(?) Rajmahal Hills, Bihar, of India (Jain 1964). The Indian wood has mostly uniseriate and contiguous tracheid pitting, 10 x 12 μm in diameter. The rays are 1-10 cells high and there are 1-2 large, simple pits "eiporen" per cross-field, 12-14 μm in diameter, but "sometimes broad, 10 to 20 μm in size". The tracheid pitting in the South African specimen is more regular than the Indian species and a little bigger.

Other specimens have been collected from the Molteno which also appear more podocarpacean than araucarian but the preservation is not good enough to identify them confidently. An example is BP/2/395 from the Burgersdorp Formation. More material needs to be collected and studied.

Fossil woods have also been studied from the Molteno and Clarens Formations but are too poorly preserved to identify to species level. Wood collected by Heidi Anderson from Boesmanshoek and Kannaskop has been distorted and compressed, possibly recrystallized by heat after preservation. The wood is most probably araucarian. John Hancox collected several other samples from the Burgersdorp Formation which also have the same appearance. I collected wood from the Clarens Formation at Rhebokhoek. This wood is unidentifiable because none of the pitting has been preserved but appears to be more like the *Mesembrioxylon* type of wood than araucarian. No wood has been collected and studied from the Elliot Formation.

DISCUSSION

The Karoo Basin vertebrate biostratigraphy has been substantially modified and revised over the last 90 years and in the most recent publication (Rubidge 1995) the ranges of the fish, amphibians and terrestrial vertebrates have been documented within revised Assemblage Zones. No comparable biostratigraphic zonation has been proposed for plant fossils. Although plant material is abundant, most of the material is vegetative which means that the delimitation of taxonomic groups is difficult. In the *Glossopteris* flora for example, there are 40 to 60 leaf species but only half that number of fructifications. These are obviously difficult to reconcile and correlate. The other taxa present are the sphenopsids of which there are several genera, sterile fern fronds, lycopods, ginkgos and gymnosperms of uncertain affinity. As the leaves have not been preserved attached to the wood, the affiliations of dispersed plant organs will remain uncertain.

None of the fossil plant taxa has been thoroughly studied throughout the Karoo of South Africa, and ecological differences also complicate the record, so biostratigraphical correlations have not been made. Fossil woods on the other hand, are more conservative than the leaves, and although they cannot be correlated with any particular plant group, they have a limited distribution through time. The woods, therefore, can be used for a broadscale biostratigraphy.

Based on the fossil woods described above from throughout the Karoo sequence, summarised in Table 2, a preliminary biostratigraphic distribution can be drawn up. *Prototaxoxylon africanum* occurs from the Kookfontein Formation to the Abrahamskraal Formation (Ecca to Lower Beaufort Groups). *Prototaxoxylon uniseriale* is rare and has only been recorded from the Abrahamskraal Formation. *Australoxylon teixeirae* occurs from the Collingham Formation to the Normandien Formation and is very common. *Australoxylon natalense* has been recorded only from the Ecca (Marguerier 1973). *Araucarioxylon africanum* occurs in the Normandien Formation and in even younger sediments (Bamford, unpublished data). *Araucarioxylon karooensis* occurs only in the Normandien Formation. This preliminary biostratigraphy (Table 3) is based on approximately 70 identified woods from known stratigraphic horizons but further collections and studies need to be made in order to check the consistency of this correlation.

ACKNOWLEDGEMENTS

I would like to thank all the geologists and palaeontologists, in particular, Heidi Anderson, Chris Gow, John Hancox, Rob Heard, Paul Karpeta, Johann Loock, Chris MacNight, Tom Mason and Bruce Rubidge, who collected fossil woods from known stratigraphic horizons and allowed me to study them. Richard Lewis is thanked for preparing all the thin sections. Peter Gasson, Kathleen Pigg and an anonymous reviewer are also thanked for their constructive comments on the manuscript.

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Palaeont. afr., **35**, 41-43 (1999)

PRELIMINARY REPORT OF DINOSAUR TRACKS IN QWA QWA, SOUTH AFRICA.

by

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ABSTRACT

We record the presence of tridactyl dinosaur tracks preserved on a siltstone surface in a watercourse in a north eastern Free State game park.

KEYWORDS: Early Jurassic, Elliot Formation, theropod dinosaur, tracks.

INTRODUCTION

Olsen and Galton (1984) reviewed the vertebrate tracks of the Stormberg group of southern Africa (most of them erected by Paul Ellenberger and co-workers during the 'sixties and early 'seventies). They recognised eight ichno-genera, all from the Elliot and Clarens formations, placing all three-toed, bipedal tracks in the ichnogenus *Grallator*, which they believe were "almost certainly" made by theropods: this leaves the small bipedal ornithopods out of consideration. Raath (1972) described tridactyl dinosaur tracks from the then Southern Rhodesia (now Zimbabwe) and attributed them to the theropod *Syntarsus* (Raath 1969). Raath *et al.* (1990) described tridactyl dinosaur tracks from the Molteno Formation which lies at the base of the Stormberg (apart from one small fish the Molteno has yielded no vertebrate fossils); they attributed these to an unknown theropod and suggested that these are the oldest dinosaur tracks in southern Africa. However, these tracks are twice as large as those reported here.

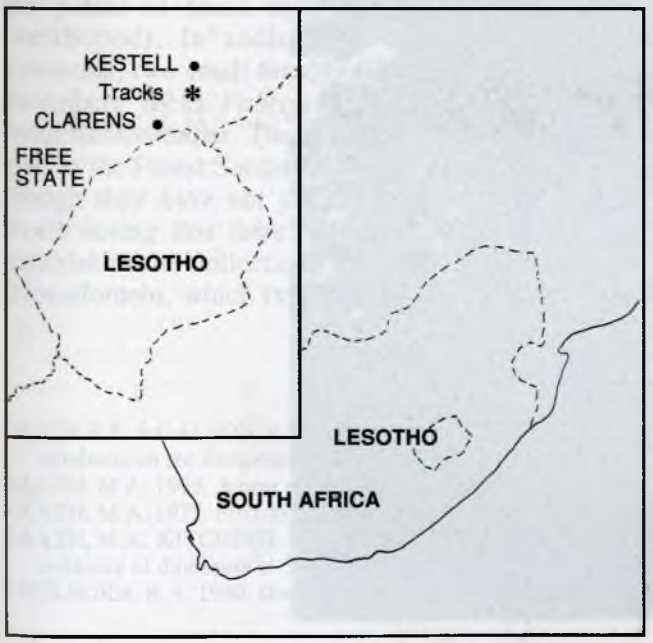

Figure 1. Location of the track site described in this note.

While planning the route for a student field excursion in July 1996, we were shown a superb set of small tridactyl dinosaur tracks in what are probably basal Elliot Formation rocks on the farm Tweedegeluk, in the Qwa Qwa district, north eastern Free State Province (Figure 1). These prints are at an open, level section of an otherwise steep-sided drainage gully where a vehicle track crosses, so they get ridden over by off-road vehicles, albeit infrequently. They also become silted over at times. Ideally a latex impression should be made, and a low wall should be erected at the site to divert storm water.

GEOLGICAL SETTING (Figure 2)

Lack of outcrop makes it difficult to decide whether the tracks are in Molteno or lowermost Elliot rocks. However, in the erosion gully above the tracks all the exposed sediments are fine grained, as is typical of the Elliot. The tracks are either immediately above, or perhaps within, an unusual, locally prominent and easily recognisable, sandstone 'sandwich' with a thick, olive gray, finer grained and more deeply weathered 'filling', representing rapid transition from fining-upward to coarsening-upward episodes. This unusual sandstone sequence lies above the uppermost coarse-grained sandstone with distinctive secondary quartz overgrowths typical of the Molteno Formation, and separated from it by a narrow band of soft weathering fine sediments. According to G.H. Groenewald (pers. comm.), the Molteno Formation is only some 20 metres thick in this area.

DESCRIPTION

Roughly 12 metres of track-bearing pavement are exposed on a gently dipping mud-draped bedding plane of overbank siltstone (Figure 3). Tracks are oriented in two directions along a shallow pond margin, and appear to have been made by one or at most two animals. The tridactyl prints average 8 cm long, with a pace of roughly 20 cm and a stride of 40 cm. Prints were

Figure 2. Students examining the track bearing pavement. Clarens Formation sandstone in the distance. Invasive exotic plants choke the gullies.

Figure 3. Close up view of the palaeosurface seen in Figure 1. The tracks with a geological hammer for scale.

Figure 4. The tridactyl print above the sharp end of the hammer has a worm trail (*Planolites*) superimposed on it.

impressed in soft, saturated mud, such that some of the disturbed sediment fell back into the prints, diffusing the outlines of the toe prints and causing the toes to appear a little wider than they should be. We could find only one short drag mark, and this was more likely made by the middle toe of a partially raised foot, than by a tail.

Other features on the surface include oscillation ripple marks such as are typically left by receding water, and feeding traces of annelid worms, some of the latter superimposed on the dinosaur prints (Figure 4).

THE TRACK MAKERS

Thulborn (1990, p.219) notes that with less than perfect pes prints it is often not possible to distinguish the prints of small theropods and small bipedal ornithopods. In addition to the small theropod *Syntarsus*, two small ornithopod genera are present in Stormberg rocks *Fabrosaurus (Lesothosaurus)* and *Heterodontosaurus*. These may very well be present also in the Forest Sandstone Formation of Zimbabwe, though they have not yet been recorded there. It is worth noting that there is undescribed 'fabrosaurid' material in the collections of the National Museum, Bloemfontein, which is considerably larger than any already described, in fact of an ideal size to have made the prints described by Raath *et al.* (1990).

Our inclination to discount ornithopods in the present case is prompted by the inferred behaviour of the track makers. We suggest these were small theropod dinosaurs, quite likely *Syntarsus* (Raath 1969), moving back and forth parallel to the shore at a leisurely pace, perhaps searching for small vertebrates, similar to the behaviour of modern herons. It could be well worth exposing more of the tracks to try to establish the identity of the track maker.

This record is interesting as the lower Elliot typically yields bones of large animals only: the prosauropod *Euskelosaurus*, the cynodont *Scalenodontoides*, 'rauisuchid' fragments and large amphibians; whereas *Syntarsus*, the only known small theropod, is uncommon and, like the small ornithopods, occurs only in the middle and upper Elliot. These tracks therefore possibly indicate an older extension to the stratigraphic range of *Syntarsus* and or ornithopods.

ACKNOWLEDGEMENTS

We thank Tom Hugo of Qwa Qwa Parks for bringing these tracks to our attention, and Peter Gernetzky for taking us to the site. This note has been much improved by two dilligent referees whom we acknowledge with thanks.

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STEREOSPONDYL AMPHIBIANS FROM THE ELLIOT FORMATION OF SOUTH AFRICA

by

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ABSTRACT

This paper documents the first members of the Chigutisauridae (Amphibia, Stereospondyli) from southern Africa and the first post-Triassic stereospondyls from that region. The material, from the Lower and Upper Elliot Formation, was associated with a diverse fauna including early mammals and dinosaurs. Most temnospondyls known to have survived the Triassic are brachyopoids, with large members of the Chigutisauridae present in the Jurassic and Cretaceous of Gondwana, and smaller members of the Brachyopidae in the Jurassic of Eurasia.

KEYWORDS: Jurassic, Chigutisauridae, Gondwana, Elliot Formation, Stereospondyli

INTRODUCTION

Well documented post-Triassic stereospondyl amphibian remains were first described from the Jurassic of Australia (Warren & Hutchinson 1983), to be followed by several reports from Eurasia (Dong 1985; Nessov 1988; Shishkin 1991; Buffetaut *et al.* 1994), and an Early Cretaceous stereospondyl from Australia (Warren *et al.* 1997). All except one (Warren *et al.* 1998) of the described Jurassic and Cretaceous stereospondyls apparently belong to the Brachyopoidea (Brachyopidae and Chigutisauridae) with the Australian taxa, *Siderops kehli* (Warren & Hutchinson 1983) and *Koolasuchus cleelandi* (Warren *et al.* 1997) identified as Chigutisauridae and the Chinese *Sinobrachyops placenticephalus* (Dong 1985), Mongolian *Gobiops desertus* (Shishkin 1991) and Russian *Ferganobatrachus riabinini* (Nessov 1988, Shishkin 1991) as Brachyopidae. Other fragmentary post-Triassic stereospondyl material has been reported from both geographical areas and a full list of these occurrences was presented in Warren *et al.* (1997). The Chigutisauridae is a Gondwanan taxon, appearing first in the earliest Triassic Arcadia Formation of Australia (Warren 1981), with later representatives in the Late Triassic of Argentina (Rusconi 1949, 1951; Marsicano 1999) and India (Sengupta 1995), while the Brachyopidae were cosmopolitan in distribution with a centre of diversity in Australia. Only two post-Triassic Gondwanan stereospondyls have been recorded apart from the Australian specimens. One is a report of brachyopids from the Upper Elliot Formation of South Africa (Kitching & Raath 1984), while the other is a fragmentary mandibular ramus from the Late Triassic or Early Jurassic of Ethiopia, which alone among late surviving stereospondyls appears not to be brachyopoid (Warren *et al.* 1998). In a list of material from the Elliot Formation, Kitching and Raath (1984) included a total of ten amphibian records, those from the Upper Elliot being listed as brachyopids while those from the Lower Elliot were listed as capitosaurids. During a visit to the Bernard Price Institute for Palaeontology in 1998, the senior author examined all of the Elliot Formation stereospondyl material housed in their collections and identified the available specimens (some had been field identifications only and the material was not collected). All of this material was collected by Kitching and Raath during a field trip in 1982, or by Kitching in field trips in the 1970s and 1980s. The present paper is a description of the better preserved specimens. While all the material described is fragmentary, we have attempted to place it taxonomically because of the importance of documenting which higher taxa of stereospondyls survived beyond the Triassic.

AGE OF THE ELLIOT FORMATION

The Elliot Formation of the Karoo Basin of southern Africa is divided into two biostratigraphical units. The lower unit corresponds to the Lower Elliot Formation and was placed in the *Euskelosaurus* Range Zone in the biozonation scheme proposed by Kitching and Raath (1984). This unit is now thought to be a coeval, distal equivalent of the upper part of the Molteno Formation (Cairncross *et al.* 1995; Anderson *et al.* 1998). Based largely on tetrapod data, the Lower Elliot Formation has traditionally been assigned a Late Triassic (Carnian) age (eg. Olsen & Galton 1984; Gauffre 1993; Anderson *et al.* 1998). This is supported by the presence of a characteristically Triassic *Dicroidium* flora associated with the Lower Elliot Formation (Ellenberger 1972). An unconformity, represented by a distinct palaeosol horizon (Kitching & Raath 1984), separates the Lower Elliot Formation from the Middle and Upper Elliot Formation.

The Middle and Upper Elliot Formation was placed in the *Massospondylus* Range Zone by Kitching and Raath (1984), along with the lower part of the overlying

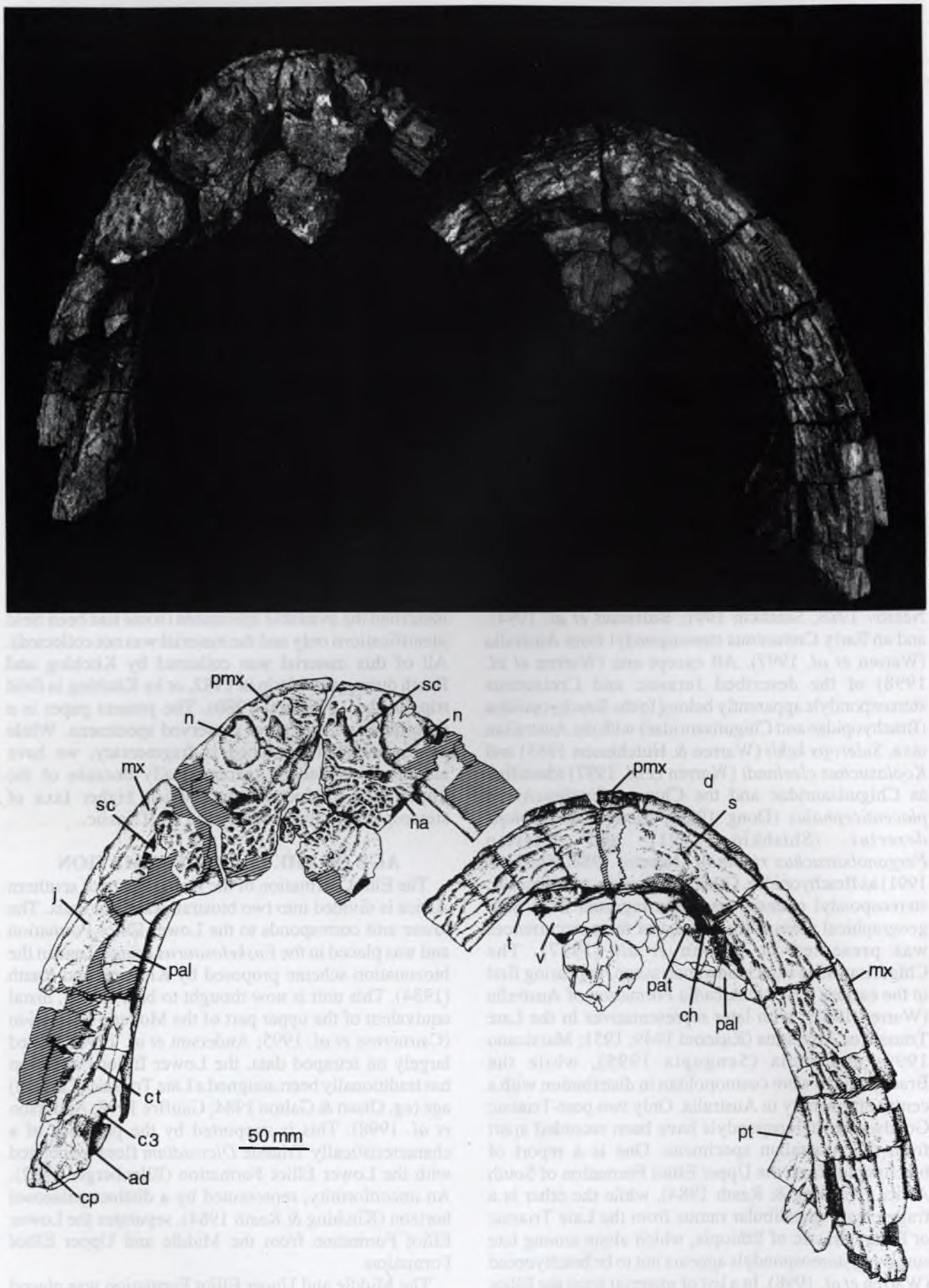

Figure 1. BP/1/5092. Photographs (upper) and drawings (lower) of part of the skull and associated mandible in dorsal (left) and ventral (right) views. Cross hatching indicates broken bone.

Clarens Formation. Based again on tetrapod and floral data (Ellenberger 1972; Olsen & Galton 1984; Anderson *et al.* 1998) the Middle and Upper Elliot Formation has traditionally been assigned an Early Jurassic age. The presence of chigutisaurid temnospondyls in both the Lower and Upper Elliot Formation is not at odds with the presumed ages of both of these faunas, since chigutisaurids occur elsewhere in the Late Triassic of India and Argentina and the Early Jurassic and Cretaceous of Australia (Warren *et al.* 1997).

DIAGNOSES OF HIGHER TAXA

Diagnoses of the Brachyopoidea, Brachyopidae and Chigutisauridae are given below, but in material described in the present paper many of the diagnostic characters were not preserved. It was therefore necessary in most instances to use primitive characters, skull outlines, and differential diagnoses in our taxonomic determinations.

Brachyopoidea Broom 1915

Sensory sulci deeply incised between nostrils and orbits; rounded, stalked exoccipital condyles; ascending ramus of the pterygoid arises from the dorsal surface of the pterygoid as a gently concave lamina; dentition present on the middle and posterior coronoids; postglenoid area (PGA) of the mandible slender and elongated; quadrate rami of the pterygoids strongly downturned forming a U-shaped palate; prearticular extending posterior to the glenoid fossa, covering the medial face of the articular on the PGA; absence of the mandibular sensory sulcus on the labial surface of the PGA; quadrate condyles with two parts of subequal size; atlas elongate; absence of an anterior flange on the dorsal process of the clavicle; width of pectoral girdle considerably less than skull width.

Chigutisauridae Rusconi 1949

Strongly horizontally recurved ascending ramus of the pterygoid; presence of a substapedial ridge on the pterygoid; width of interpterygoid pair less than 90% of the length; posterior meckelian foramen bordered by the prearticular and postsplenial exclusively.

Brachyopidae Broom 1915

Ascending ramus of the pterygoid gently concave and posteriorly recurved in vertical section; absence of a column on the ascending ramus of the pterygoid; posttemporal fenestra as wide as deep; maximum width of the interpterygoid vacuity pair greater than 90% of their length; reduced tooth row on palatines and ectopterygoids; absence of otic notch and tabular horns; postglenoid area of the mandible very elongate and slender; lack of a chordatympanic foramen of the mandible; articular below the level of the dentary tooth row; prearticular process of the mandible absent; rod-like dorsal process of the clavicle slopes posteriorly from its base.

LOWER ELLIOT FORMATION MATERIAL

TEMNOSPONDYLI Zittel 1888
STEREOSPONDYLI *sensu* Yates & Warren, in press
BRACHYOPOIDEA Broom 1915
CHIGUTISAURIDAE Rusconi 1949

BP/1/5252

Material

Partial left and right mandibular rami with some attached and some unattached cranial material. The cranial material includes the left lateral portion of the occiput and part of the posterior end of the palate including a probable exoccipital condyle. A large quantity of fragmentary cranial and mandibular material is associated with this specimen.

Locality

Farm Hollywood (Paardeverlies), Lady Grey District, Eastern Cape, South Africa.

Description

Skull. Cranial material preserved carries coarse ornament similar to that in the other Elliot Formation specimens and includes part of the left and right premaxillae and vomers in articulation with the mandible. Incised into the premaxillae are small parts of the margins of the external nostrils. An anterior palatal vacuity is either absent or very small.

A probable exoccipital condyle is present but is unusual in that it appears to be composed of three superimposed bones. The occipital parts of the squamosal and quadratojugal, which form the characteristic brachyopoid squamosal-quadratojugal trough, are preserved. Small marginal teeth on the premaxillae contrast markedly with a large vomerine tusk (20 mm at the base) and enlarged teeth (15 mm) on the transvomerine tooth row. These transvomerine teeth are attached to a raised area of the vomer as they are in *Siderops* and BP/1/5092.

Mandible. In transverse section the anterolateral parts of the mandible are flattened and of similar transverse section to the equivalent areas in BP/1/5092. The two specimens differ in that the mandibular symphysis is shorter anteroposteriorly in BP/1/5252. An anterior coronoid (C1) bone is preserved and is toothless.

Dentition. Those dentary teeth preserved are a little larger than in BP/1/5092 (10-15 mm at the base) and rounded in section. The vomerine tusks are of a similar size to the dentary teeth.

Taxonomic conclusions

This specimen has a parabolic skull outline, dentary teeth larger than the maxillary teeth, and a squamosal-quadratojugal trough, characteristics not present in the Capitosauridae but found in the Brachyopoidea. Within the Brachyopoidea the specimen is most likely to belong

to the Chigutisauridae because it is extremely similar to the other chigutisaurids described in this paper, but distinguishing characteristics were not preserved.

BP/1/4750

Material

A collection of fragmentary cranial and postcranial material, most of which is too weathered for identification.

Locality

Farm Friesland West, Bethlehem District, Free State, South Africa.

Description

Two segments of skull margin with both marginal and inner tooth rows preserved, an exoccipital condyle and a large number of associated fragments were collected. On the cranial fragments the inner tooth row contains larger teeth than the maxillary row, and an ectopterygoid tusk is present, both conditions not characteristic of capitosaurids. The continuous inner tooth row is not found in the Brachyopidae but is present in the Chigutisauridae.

Taxonomic conclusions

The material is most likely to be chigutisaurid.

TEMNOSPONDYLI Zittel 1888
STEREOSPONDYLI *sensu* Yates and Warren, in press

BP/1/4935

Material

A single fragment of lower jaw ramus.

Locality

Farm Mequatling, Clocolan District, Free State, South Africa.

Description

This single fragment of mandibular ramus is of interest for the presence of two small foramina in its lingual surface. It is not determinable beyond Stereospondyli, in which it can be placed through the presence of coarse ornament on the labial surface.

Taxonomic conclusions

Stereospondyli indet.

UPPER ELLIOT FORMATION MATERIAL

TEMNOSPONDYLI Zittel 1888
STEREOSPONDYLI *sensu* Yates & Warren, in press
BRACHYOPOIDEA Broom 1915
CHIGUTISAURIDAE Rusconi 1949

BP/1/5092

cf. *Siderops* sp. Warren & Hutchinson 1983

Material

A partial skull and attached mandibular rami. Preserved are the anterior half of a left mandibular ramus and the anterior quarter of a right ramus, with the skull margins attached to them. The skull includes part of the left orbit, both external nostrils, and part of the maxilla on both sides. Although the margins of the palate are obscured by the attached mandible, some detail of the palate adjacent to the interpterygoid vacuities is preserved and includes the tusk pairs from vomers, palatines and ectopterygoids.

Locality

Farm Vastrap, Ladybrand District, Free State, South Africa. The specimen came from a playa lake deposit which also yielded almost complete lungfish remains and an abundance of conchostracans.

Description

Skull roof (Figures 1, 2). Preserved is the most anterior part of the skull roof, with a complete left naris and the inner margin of the right naris, the left hand margin of the maxilla and part of the jugal including some lateral orbital margin, and the palate underlying these marginal parts of the skull. The reticulate ornament is relatively fine, especially on the nasal bones, but the remnants of the sensory canal system are broad and deeply impressed. An almost circular left naris is placed far laterally on the skull roof and is farther from the right naris than is typical of chigutisaurids. Most sutures cannot be discerned.

Palate (Figures 1, 2). While much of the palate preserved is obscured by the attached mandible, some of its structure is visible. No trace of an anterior palatal fenestra is evident, but posterior to its expected position

Figure 2. Outline of a chigutisaurid skull with those parts of the skull roof preserved in BP/1/5092 indicated in black.

one transvomerine tooth and a replacement pit are preserved. The left choana is sub-circular and flanked by paired vomerine and palatine tusks, with a few smaller parachoanal teeth on the medial border. A few large palatine and ectopterygoid teeth are present, as is a replacement pit for the ectopterygoid tusk. An isolated portion of the right ectopterygoid, palatine and attached maxilla retains a palatine tusk and replacement pit, an enlarged tooth on the ectopterygoid which might be a tusk, other ectopterygoid teeth and smaller maxillary teeth. Of interest is the presence of a suture running almost parallel to the margin of the interpterygoid vacuity. This must be a suture between a posterior process of the palatine and the ectopterygoid and indicates that the ectopterygoid may be excluded from the margin of the interpterygoid vacuity by a suture between the palatine and the pterygoid. Although almost the entire lateral margin of the right interpterygoid vacuity is preserved, no sutures are determinable. A portion of the left palatine ramus of the pterygoid remains, from which the position of the body of the pterygoid, and hence the approximate size of the skull, could be estimated.

Palatal dentition. All well-preserved teeth of both the skull and mandible are strongly keeled as in the Australian chigutisaurids *Siderops kehli* and *Koolasuchus cleelandi*, and slightly curved lingually towards the tip. In contrast to the situation in *Siderops*, none are serrated. The larger teeth of the mandible are markedly larger (20 mm by 10 mm at the base) than the largest teeth on the maxilla (9 mm by 4 mm). The dentary tusk is 20 mm in diameter while the vomerine tusks are rounded and an estimated 15 mm in diameter. Marginal teeth on the premaxillae and maxillae are of fairly uniform small size with a slight decrease towards the posterior end of the maxilla. Transvomerine and parachoanal teeth are a little larger than the maxillary teeth. Where teeth can be seen in transverse section near the base, labyrinthine infolds having secondary folds (Warren & Davey 1992) are present, with greater complexity in the larger teeth.

Mandible. The mandible is preserved in part, from the symphysis to the level of the adductor fossa, just below the coronoid process. It is markedly flattened dorso-ventrally and is a little anteroposteriorly expanded in the region of the symphysis. Few sutures are discernible. The anterodorsal margin of the adductor fossa is preserved and appears similar to the area in *Koolasuchus*. Just anterior and dorsal to the fossa, a row of coronoid teeth is carried by a ridge on coronoid three.

Mandibular dentition. In common with most brachyopoids, the marginal teeth of the mandible are smaller anterior to the symphyseal area, but increase in size for most of the length of the dentary to decrease in size again near the end of the dentary tooth row. An irregular row of smaller teeth is present on the posterior coronoid (C3), but the presence or absence of dentition on coronoids one and two cannot be determined. Although the area of the symphyseal tusks is obscured by the attached skull roof, one can be seen in transverse section in a break close to the symphysis. Posterior to the tusk a small pit may indicate the presence of a postsymphyseal row of teeth such as was present in *Siderops* and *Pelorocephalus* (Marsicano 1999) but not *Koolasuchus* (Warren *et al.* 1997) or *Compsocerops* (Sengupta 1995).

Taxonomic conclusions

Most characters used in the diagnosis of Brachyopoidea above are not determinable. However, this specimen is clearly a member of the Brachyopoidea through its short, broad and parabolic skull with rounded nares placed close to the anterior margin of the skull. The orbits are situated close to the nares and the sensory canal system is deeply-impressed in this area. Within the Brachyopoidea the specimen belongs to the Chigutisauridae, rather than the Brachyopidae, through the presence of a continuous tooth row between the tusks on the vomers, palatines and ectopterygoids. Its placement within the Chigutisauridae is more tenuous and we place it as cf. *Siderops* sp. until more complete material is available. Its assignment to *Siderops* is based on the presence of teeth on the posterior coronoid. These are absent in other members of the Chigutisauridae. In Figure 2 we have restored the posterior parts of the skull after *Siderops* and using the palatine ramus of the pterygoid as a guide to the position of the occiput. Unless the proportions of BP/1/5092 were quite different from those of *Siderops*, this should be fairly accurate. The resultant skull has orbits placed further posteriorly and nostrils more widely separated than in *Siderops*.

BP/1/5111

Material

Weathered large fragments of skull with attached mandible, weathered neural arches in articulation with centra, a fragment of interclavicle and detached partial ribs.

Locality

Broken Slopes, an annex of the farm Vastrap, Ladybrand District, Free State, South Africa.

Description

Skull. A part of the quadratojugal, occipital part of the squamosal, quadrate and pterygoid are preserved in articulation with the posterior part of the left mandibular ramus. Also present is a part of the basis cranii with parts of the exoccipital, pterygoid and parasphenoid. The quadratojugal is present at the posterolateral margin of the skull but is broken posteriorly so that the presence or absence of the chigutisaurid postquadratojugal process cannot be determined. On the left of the occipital surface parts of the quadratojugal and squamosal bones forming the squamosal-quadratojugal trough are preserved but are

positioned a little anterior to the ventral part of the quadrate with the attached quadrate ramus of the pterygoid. The quadrate may have overlain part of the squamosal-quadratojugal trough.

Mandible (Figures 3, 4). The posterior part of the left ramus is preserved in articulation with the skull, as well as a second section of the left ramus from just anterior to it. The posterior end of the mandible behind the articulation (the postglenoid area) is broken off but in section shows the subcircular cross section characteristic of brachyopoids. A suture running anteroposteriorly along the lingual surface separates the prearticular (above) from the angular (below). In brachyopids the angular is barely exposed on the lingual surface of the mandible whereas in the chigutisaurids *Compsocerops cosgriffi* (Sengupta 1995) and all three species of *Pelorocephalus* (Marsicano 1999) a large angular exposure is present. Australian post-Triassic chigutisaurids were restored with a low angular exposure on the lingual side of the mandible but neither *Siderops kehli* nor *Koolasuchus cleelandi* were well preserved in that area, so in reality the suture could have been higher. A chordatympanic foramen, which is usually found in chigutisaurids but not brachyopids, is present on the lingual side of the ramus below the glenoid fossa. The ornamented angular extends along the ventral surface of both sections of ramus and continues beneath the postglenoid area. While most of the labial surface of the more posterior block is obscured by the quadratojugal, a little of the surangular is present below the glenoid fossa, and on the anterior block the surangular sutures with the posterior margin of the dentary. No teeth are preserved in BP/1/5111.

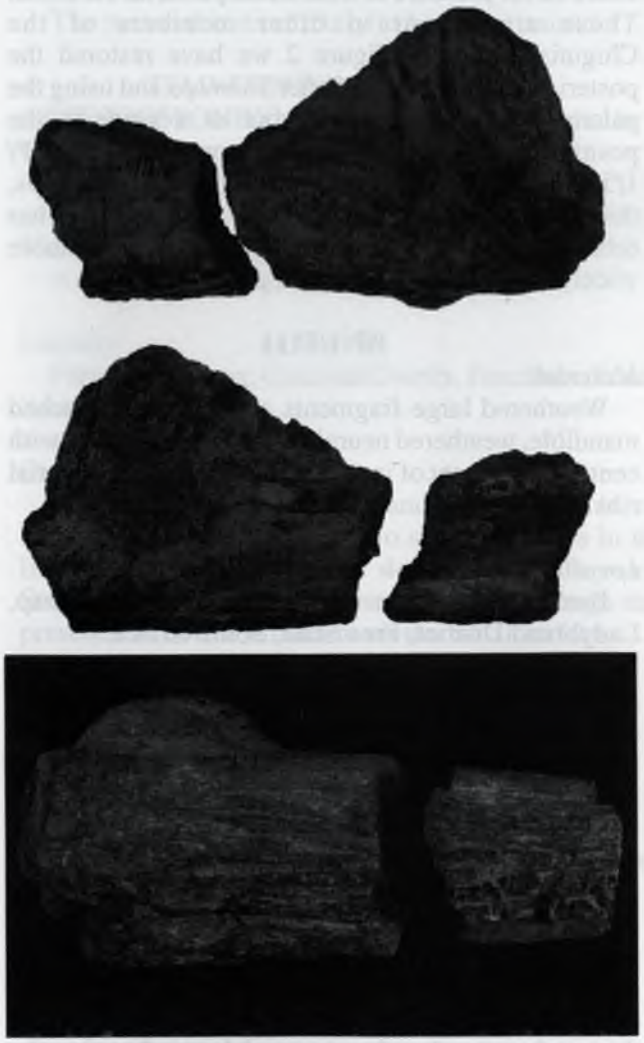

Figure 3. BP/1/5111. Photographs of the posterior part of the left mandibular ramus. Orientation as in Figure 4.

Vertebrae (Figure 5). A total of six neural arches and seven intercentra are preserved in three blocks. The neural arches are extremely abraded but appear to have been robust with stout transverse processes. Among the Chigutisauridae the intercentra are unusual in that they are notochordal, that is, the bone has grown around the sides and dorsal surface of the notochord, leaving a pit. They differ from other notochordal (stereospondylous) intercentra in that they are not circular in anterior or posterior view but are dorsoventrally flattened. In lateral view they have the same wedge-shaped outline as in other chigutisaurid intercentra. While notochordal centra are not normally associated with chigutisaurids and were not present in the Jurassic chigutisaurid *Siderops kehli* (Warren & Hutchinson 1983), notochordal as well as rhachitomous centra were found in the same deposits as the Cretaceous chigutisaurid *Koolasuchus cleelandi* (Warren *et al.* 1997). Sengupta (1995) described a 'pseudostereospondylous' centrum, in which the pleurocentra had fused to the crescentic intercentrum, associated with the Indian chigutisaurid *Compsocerops cosgriffi*, but this fusion is not the case in BP/1/5111.

Ribs. The five rib heads preserved are of varying size and all but one are from the pectoral region.

Interclavicle. The part of the interclavicle remaining is extremely weathered but preserves a small part of the articular area for the left clavicle.

Taxonomic conclusions

The presence of a squamosal-quadratojugal trough is characteristic of the Brachyopoidea. Morphologically, the posterior end of the left mandibular ramus resembles that of brachyopoids in that the postglenoid area is small and rounded in cross section, the angular extends a long way posteriorly on the ventral surface of the mandible, and the prearticular covers the posterodorsal face of the lingual surface so that the articular is not exposed lingually. The presence of a chordatympanic foramen in BP/1/ 5111 indicates that it is chigutisaurid rather than brachyopid.

BP/1/5406

Material

Fragments of skull and attached mandible, intercentrum, neural arch and a section of femoral shaft.

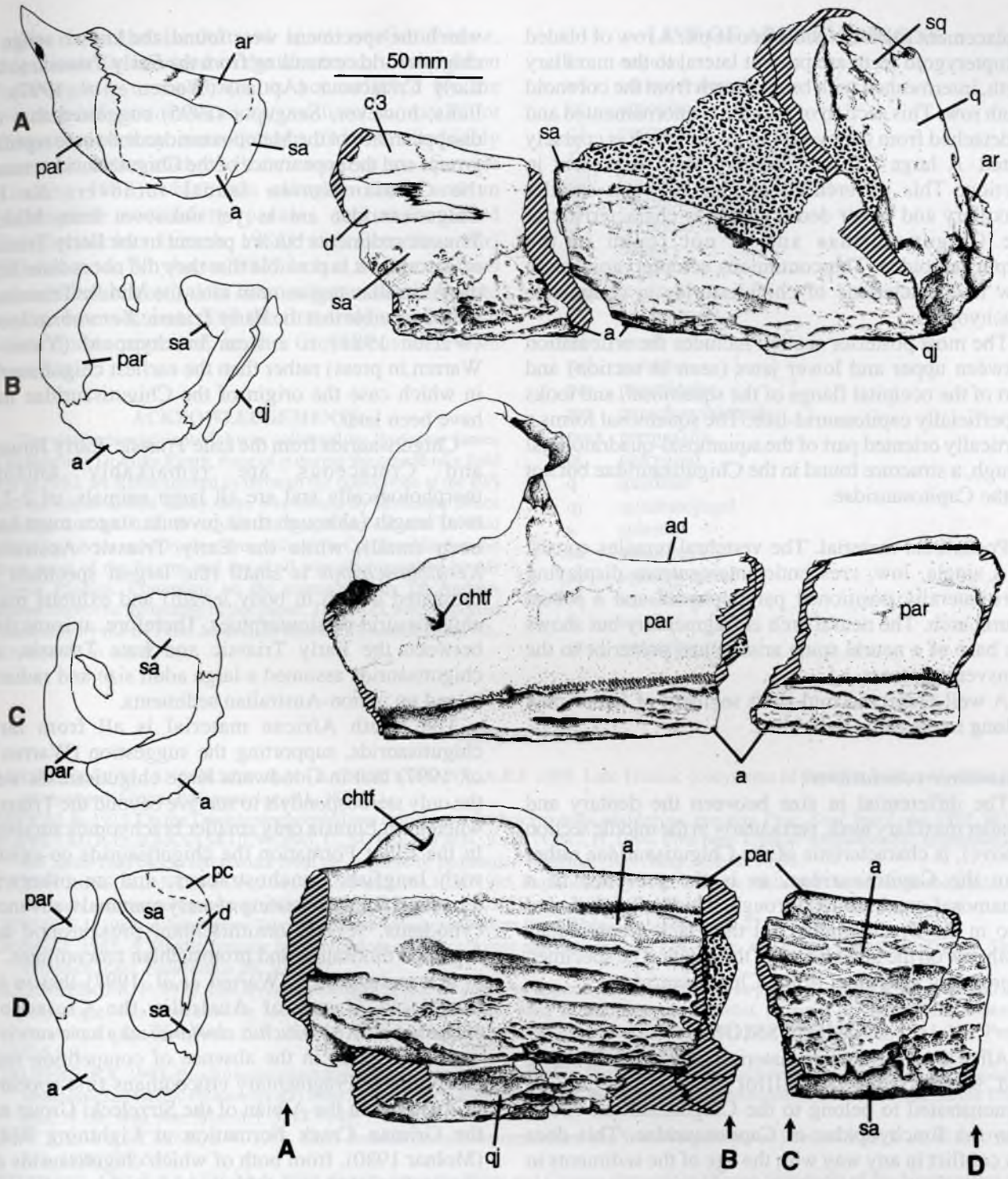

Figure 4. BP/1/5111. Drawings of posterior part of the left mandibular ramus and attached quadratojugal and quadrate, in labial (upper), lingual (middle) and ventral (lower) views. In the labial view anterior is to the left while in lingual and ventral views anterior is to the right. Transverse sections on the left are from the positions indicated (A-D) in the lower drawing, but each is drawn as if looking from behind the jaw. Cross-hatching represents broken bone while coquille hatching represents matrix.

Locality

Farm Vastrap, Ladybrand District, Free State, South Africa.

Description

Skull and mandible. Three pieces containing portions of the left mandibular ramus and cranium are from the region of the choana, towards the posterior end of the maxilla, and the posterior end of the skull. The more anterior piece has a row of four maxillary teeth with pitted ornament above them, a section of a large ?palatine tusk, and dentary teeth in section. The dentary teeth (25 mm in height) are slightly larger than the maxillary teeth (an estimated 22 mm).

The middle section has a maxillary row of ten tooth loci containing eight small (11 mm) teeth. In section a

replacement tooth is visible in one pit. A row of bladed ectopterygoid teeth are present lateral to the maxillary teeth, intermeshed with broken teeth from the coronoid tooth row. This section of maxilla is unornamented and is detached from the overlying jugal, which is coarsely pitted. A large (20 mm) dentary tooth is present in section. This differential in size between smaller maxillary and larger dentary teeth is characteristic of the Chigutisauridae and is not found in the Capitosauroidea. The continuous ectopterygoid tooth row is characteristic of chigutisaurids in contrast to brachyopids.

The most posterior section includes the articulation between upper and lower jaws (seen in section) and part of the occipital flange of the squamosal, and looks superficially capitosaurid-like. The squamosal forms a vertically oriented part of the squamosal-quadratojugal trough, a structure found in the Chigutisauridae but not in the Capitosauridae.

Postcranial material. The vertebral remains consist of a single, low, crescentic intercentrum displaying dorsolaterally positioned parapophyses and a robust neural arch. The neural arch is fragmentary but shows the base of a neural spine arising just posterior to the transverse process.

A well preserved mid-shaft segment of femur may belong to the same individual.

Taxonomic conclusions

The differential in size between the dentary and smaller maxillary teeth, particularly in the middle section (above), is characteristic of the Chigutisauridae rather than the Capitosauridae, as is the presence of a squamosal-quadratojugal trough. This trough is found also in the Brachyopidae but they lack a continuous tooth row on the inner bones of the palate. The specimen is probably a member of the Chigutisauridae.

DISCUSSION

All of the determinable material collected by Kitching and Raath from the Elliot Formation can be demonstrated to belong to the Chigutisauridae rather than the Brachyopidae or Capitosauridae. This does not conflict in any way with the age of the sediments in which the specimens were found, the known range of chigutisaurids extending from the Early Triassic to the Early Cretaceous (Aptian) (Warren *et al.* 1997). In India, however, Sengupta (1995) suggested that the disappearance of the Metoposauridae and some reptilian groups and the appearance of the Chigutisauridae marks the Carnian-Norian faunal turnover. As the Chigutisauridae are as yet unknown from Middle Triassic sediments but are present in the Early Triassic of Australia it is possible that they did not radiate from the Australian region until after the Middle Triassic. It is also possible that the Early Triassic *Keratobrachyops* (Warren 1981) is a stem brachyopoid (Yates & Warren,in press) rather than the earliest chigutisaurid, in which case the origin of the Chigutisauridae may have been later.

Chigutisaurids from the Late Triassic, Early Jurassic and Cretaceous are remarkably uniform morphologically and are all large animals, of 2-3 m total length (although their juvenile stages must have been small), while the Early Triassic Australian *Keratobrachyops* is small (the largest specimen an estimated 40 cm in body length) and exhibits many chigutisaurid plesiomorphies. Therefore, at some time between the Early Triassic and Late Triassic, the chigutisaurids assumed a large adult size and radiated to end up in non-Australian sediments.

The South African material is all from large chigutisaurids, supporting the suggestion (Warren *et al.* 1997) that in Gondwana large chigutisaurids were the only stereospondyls to survive beyond the Triassic, whereas in Eurasia only smaller brachyopids survived. In the Elliot Formation the chigutisaurids co-existed with lungfish, conchostracans, and an otherwise terrestrial fauna consisting of early mammals, advanced cynodonts, several ornithischian, prosauropod and theropod dinosaurs, and protosuchian crocodilians.

It was suggested (Warren *et al.* 1997) that in the Strzelecki Group of Australia the Cretaceous chigutisaurid *Koolasuchus cleelandi* may have survived until the Aptian in the absence of competition from crocodilians. Fragmentary crocodilians first appeared in Australia in the Albian of the Strzelecki Group and the Griman Creek Formation at Lightning Ridge (Molnar 1980), from both of which chigutisaurids are absent. It might be said that no potential crocodile rich strata are present in Australia prior to the Aptian. Nevertheless at least some strata with tetrapods are known in the Early and Middle Jurassic of Australia although they are not abundant. For instance, in the Early Jurassic Evergreen Formation, the chigutisaurid *Siderops* was associated with freshwater plesiosaurs (Thulborn & Warren 1980), while the Middle Jurassic Injune Creek Beds of southern Queensland have yielded remains of the sauropod *Rhoetosaurus brownei* (Longman 1926). In addition, Middle Jurassic theropod dinosaurs and a plesiosaur are known from the Colalura Sandstone of Western Australia (Long & Molnar 1998).

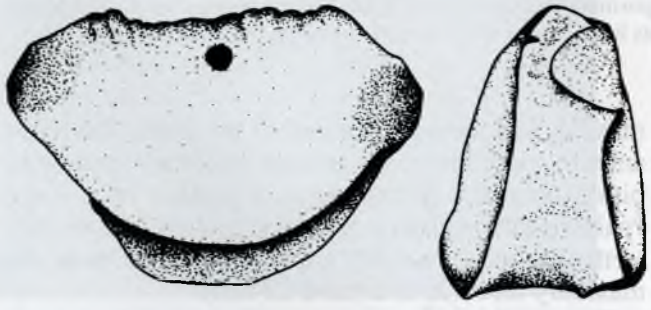

Figure 5. BP/1/5111. Intercentrum in posterior (left) and left lateral views (right).

The hypothesis that, at least in Gondwana, chigutisaurids survived in the absence of competition from aquatic crocodilians, is not nullified by the presence of protosuchian crocodilians in the Elliot Formation as they were thought to be small, highly terrestrial forms such as *Pedeticosaurus* sp. (Gow & Kitching 1988) which has elongate limbs and an incomplete secondary palate, and the related *Terrestrisuchus* (Crush 1984) and *Lesothosuchus* (Whetstone & Whybrow 1983). In fact, all crocodilians were either terrestrial or semi-aquatic but linked to marine environments until the first semi-aquatic fresh water forms appeared in the Cretaceous of North America.

ACKNOWLEDGEMENTS

The stereospondyl material was collected by Professor James Kitching and Dr Mike Raath, most of it during the course of a field trip in 1982. Dr Raath steered us through the collections at the BPI and the senior author's stay there was hosted by Professor Bruce Rubidge and his staff. We thank Dr Ralph Molnar and Dr Paul Willis for advice on all matters crocodilian! Dr Caroline Northwood drew most of the figures and the skull was photographed by Mr Trevor Phillips. Comments on the manuscript by Dr Andrew Milner improved the quality of this paper. This work was supported financially by the BPI and Australian Research Council Grant No. A39602153 to AAW.

LIST OF ABBREVIATIONS

a	angular
ad	adductor fossal
ar	articular
c3	coronoid 3
ch	medial wall of choana
chtf	chordatympanic foramen
cp	coronoid process
ct	coronoid tooth row
d	dentary
j	jugal
mx	maxilla
n	external naris
na	nasal
pal	palatine
par	prearticular
pat	parachoanal teeth
pmx	premaxilla
pt	pterygoid
q	quadrate
qj	quadratojugal
s	splenial
sa	surangular
sc	sensory canal
sq	squamosal
v	vomer
vt	vomerine tusk

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Palaeont. afr., **35**, 55-59 (1999)

FURTHER MATERIAL OF THE CERATOSAURIAN DINOSAUR *SYNTARSUS* FROM THE ELLIOT FORMATION (EARLY JURASSIC) OF SOUTH AFRICA

by

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ABSTRACT

Two further fossils recovered from the Elliot Formation in South Africa are referred to the ceratosaurian genus *Syntarsus*: a partial pelvis and a well preserved and articulated snout.

The pelvic fragment consists of most of the posterior end of the left ilium and sacrum, with a small part of the right ilium attached. The acetabular area and 'brevis shelf' of the left ilium are well preserved, as is the ventral surface of the sacrum. These parts show features characteristic of *Syntarsus* material from Zimbabwe.

The snout has the premaxillae, maxillae, nasals and dentaries from both sides preserved, of which only the premaxillae are more or less complete. The premaxilla has four alveoli and the maxilla nine, and the maxilla bears the characteristic dimpling on its lateral surface also seen in *Syntarsus* material collected in Zimbabwe. The snout also possesses the characteristic small diastema or subnarial gap between the premaxillary and maxillary teeth shown by *Syntarsus* material from elsewhere. The snout is strongly compressed bilaterally and the jaws are tightly closed, so that the dentary teeth are obscured beneath the upper dentition. This compression has crushed the palatal region, obscuring palatal details.

KEYWORDS: Dinosauria, Theropoda, Elliot Formation, Jurassic, Stormberg

INTRODUCTION

The remains of *Syntarsus rhodesiensis*, a small ceratosaurian theropod dinosaur, were first recovered from three sites in the Forest Sandstone Formation of Zimbabwe (?Late Triassic to Early Jurassic), one in the southwest of the country – the type locality at Nyamandhlovu – and two in the north-central region in the Zambezi Valley, on the Chitake and Maura Rivers. The two Zambezi Valley localities have yielded many fossils of a limited number of taxa, mostly prosauropod dinosaurs, and the Chitake River locality in particular has yielded many individual specimens of *Syntarsus* (Raath 1969, 1977; Bond 1973). Material has been recovered in all stages of articulation, from isolated individual bones to fully articulated partial skeletons (Raath 1977).The holotype is an almost complete articulated skeleton.

A second species, *S. kayentakatae*, was described by Rowe (1989) from the Kayenta Formation of Arizona, USA, and there is also evidence of a small theropod very similar to *Syntarsus* from deposits of comparable age in South Wales (D. Warrener, *pers. comm.*, 1980).

Isolated remains of *Syntarsus* from the Karoo Supergroup in South Africa were first reported by Raath (1980), and this was also the first record of ceratosaurian dinosaurs from South Africa. All the South African remains of *Syntarsus* found so far come from within or near the *Tritylodon* Acme Zone, which lies at the top of the Middle Elliot Formation (Stormberg Group, Karoo Supergroup) (Kitching and Raath 1984). This zone is one to three metres thick and is characterised by an abundance of small (<60mm) pedogenic carbonate concretions. There is a fairly high diversity of tetrapod fossils in this zone, dominated by the prosauropod dinosaur *Massospondylus* and the cynodont therapsid *Tritylodon*, from which the acme zone gets its name. In this fauna, apart from *Syntarsus*, are also found fabrosaurid ornithischians, tritheledontid cynodonts, early mammals, protosuchian crocodilians and a chelonian (Kitching and Raath 1984).

The *Syntarsus* material found in South Africa until now has consisted only of isolated fragmentary postcranial remains, including femoral and tibial fragments, isolated bones from the pes and a few vertebrae. This note records the recovery of a partial pelvis and a relatively well preserved snout of *Syntarsus* from two localities on adjoining farms in the northeastern Free State Province, South Africa. They were found by J W Kitching in 1981 and 1985 respectively, the snout on the farm *Paradys*, and the pelvic fragment on an adjacent area between the adjoining farms *Welbedacht* and *Edelweiss* (all localities situated in the Ladybrand District, Free State Province, on 1:50 000 map sheet 2927 AB, Ladybrand) (Figures 1, 2).

The pelvis is uncompressed, but shows extensive fine surface cracking and crazing presumably due to sub-aerial exposure and sun-baking. Haematite coating is much less of a problem in this specimen than in the

case of the snout. The pelvis is relatively small, although the extent of fusion and coalescence of bone in the sacral region suggests that it may be from a mature individual.

The snout is strongly compressed laterally and the jaws are clamped shut. Because of the bilateral compression, the hard mudrock matrix, and a haematite crust which coats much of the specimen, it was decided not to attempt to separate the jaws. Besides, we concluded that the crushing which has affected the specimen would have obliterated virtually all detail in the palatal region, so little would have been gained and much might have been lost had separation been attempted.

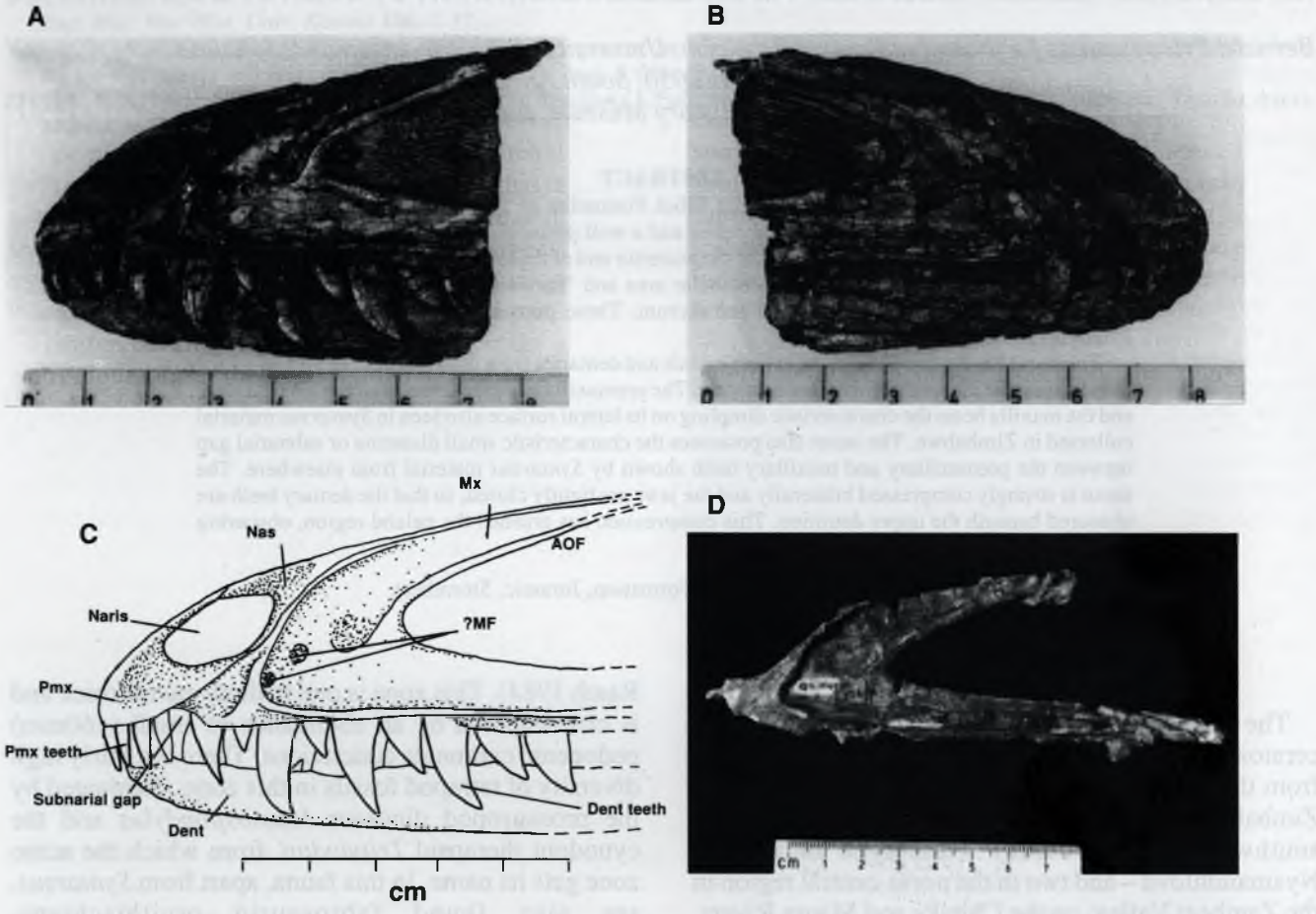

Figure 1. Snout of *Syntarsus rhodesiensis*: a-c. Specimen from the farm *Paradys* (BP/1/5278) a. Left side view; b. Right side view; c. Line drawing of (a) with principal features labelled. (Abbreviations: Mx, maxilla; Nas, nasal; Pmx, premaxilla; Dent, dentary; AOF, antorbital fenestra; ?MF, doubtful maxillary fenestra); d. Left maxilla (QG194) from Chitake River, Zimbabwe, for comparison (Scale divisions = cm).

The external nares and the antorbital fenestrae are filled with a matrix of fine-grained, pinkish-maroon silty mudstone, and the joints and teeth are covered by the haematite coating. Details of the boundaries of the major openings (external nares and antorbital fenestrae) were exposed using pneumatic engraving needles. The haematite coating had one advantage in that it helped to clarify junctions between adjacent bones which were otherwise difficult to recognise in the compressed state, but other finer details remain obscured.

DESCRIPTION OF THE SNOUT

(BP/1/5278, Figure 1)

There are two lateral openings in the snout, the elliptical external naris and the incomplete large, V-shaped antorbital fenestra. The former is bordered by the premaxilla, maxilla and nasal, while the latter is surrounded by the maxilla, except at the open posterior end (which is broken – see Figure 1). The articulations between the premaxilla and nasal, and between the nasal and maxilla are slightly obscured by the haematite coating. There appears to be a loose, movable articulation between the premaxilla and the maxilla. The premaxilla and maxilla bear serrated teeth, four in the former and nine in the latter, and there is a small sub-narial gap, or diastema, between these tooth-bearing bones which is attributable to the loose kinetic joint between them.

The narrow snout tapers towards the tip of the premaxilla, and the premaxilla and nasal are the only bones visible in dorsal view. The dorsal surface of the preserved part of the snout is almost flat, formed by the nasals from either side which meet in the midline in a shallow longitudinal depression. Laterally, the junction of the nasal with the maxilla is sharply

angular, and at the junction there is a slight ridge in the position of the nasal crest described in the American form, *S. kayentakatae* (Rowe 1989).

The long, slender dentary has its teeth largely obscured by the upper dentition. There is no symphysial suture between the lower jaw rami, suggesting a kinetic joint, as in the Zimbabwean *Syntarsus* material and in material of *Coelophysis* from North America (Raath 1977; Colbert 1989).

Description of individual elements

All the bones making up the facial skeleton in this specimen are exceptionally thin, strengthened in a few places by ridges of bone.

Premaxilla

Anteriorly the premaxilla is rounded, and posteriorly it divides into two tapering prongs which form all but the hind border of the external naris. The thin upper process contacts the nasal on the dorsal surface of the snout, overlapping it slightly. The lower process, which forms the lower border of the external naris, contacts the maxilla on its curved anteromedial surface. Their junction is continuous with the line of the subnarial gap, or diastema, between the premaxillary and maxillary teeth. The joint between the premaxilla and maxilla is slightly displaced, suggesting that it was loose and kinetic. An identical loose joint was observed in *S. rhodesiensis* by Raath (1977), and a similar one in *Coelophysis bauri* by Colbert (1989).

The short diastema between the premaxilla and maxilla is largely formed by an embayment on the former. A relatively large tooth on the dentary occupies a position immediately below this gap, but because the lower teeth bite inside the upper teeth it does not seem likely that the gap is to accommodate the tip of this tooth when the jaws are closed.

Because of the crushed and occluded state of preservation, it cannot be established if the small triangular flange on the inner surface above the fourth alveolus noted in the premaxillae of *S. rhodesiensis* from Zimbabwe (Raath 1977) is also present in this specimen.

Maxilla

The maxilla occupies the greater part of the snout in lateral view. The acutely rounded antorbital fenestra divides the maxilla into upper and lower arms, both thin-walled and tapering posteriorly. The upper arm is strengthened by a shallow ridge along its border with the antorbital fenestra, and it tapers posteriorly more quickly than the lower. It contacts the nasal along the dorsolateral angle of the snout in the long, angular, ridged junction described earlier. The front border of the maxilla is curved to form the posterior and (with the lower prong of the premaxilla) the posteroventral border of the external naris. The dentigerous border of the lower arm bears an alveolar ridge that turns dorsally towards the nasal after the second maxillary alveolus, and it borders a dimpled depression in front of the antorbital fenestra, the antorbital fossa (Wittmer 1997). Within this depression the shallow dimples are exceptionally thin-walled, and indeed one appears to be perforated on the left maxilla, forming a sort of 'maxillary fenestra' (Wittmer 1997) ahead of the antorbital fenestra proper (Figure 3c, 'MF'). Whether this fenestra is real or an artefact of postmortem damage to its paper-thin wall is difficult to establish with certainty, because the corresponding position on the right maxilla is damaged. Because of the crushing in the palatal region, the maxillary dimples cannot be observed from the medial side to see if that would resolve the question. Similarly, because the medial surface of the maxilla cannot be observed, it is not possible to say whether the maxilla bears the same small shelf, or 'premaxillary ramp' (Raath 1977), noted on the maxillae of *S. rhodesiensis*.

Nasal

The two nasal elements occupy most of the dorsal surface of the snout. They are elongate, narrow bones which taper towards the tip of the snout where they are overlain by the hindmost tips of the premaxillae. Medially they meet in a long, straight and simple edge-to-edge contact devoid of interdigitating sutures, as in *S. rhodesiensis* and *Coelophysis* (Raath 1977; Colbert 1989).

The nasal terminates anteriorly in a rounded Y-shape, with an upper and a lower tapering prong defining much of the hind half of the external naris. The contact of the upper process with the upper prong of the premaxilla is long and tapering, with the latter overlapping the former. The lower process also tapers down and forwards along the front margin of the maxilla, toward the hind end of the lower premaxillary prong, but not quite reaching it (Figure 1). The naris is therefore bordered by the premaxilla anteriorly, anterodorsally, and antero-ventrally, the nasal dorsally, posteriorly and posteroventrally, and the maxilla contributes mainly to its hind and lower borders.

The contact between the nasals and maxillae laterally is sharp and angular, as noted above.

Dentary

The dentary is long and relatively thin, gently curved, and it tapers slightly towards the front. Laterally it bears a longitudinal groove which extends to the front of the jaw. The number and morphology of the dentary teeth are masked by the state of occlusion of the jaws, besides which the dentary itself is incomplete posteriorly. Shallow pits are associated with the anterior dentary alveoli, opposite the corresponding premaxillary tooth positions.

Dentition

The teeth in the upper jaw are all still in their respective alveoli, unlike the condition in most of the specimens of *S. rhodesiensis* from Zimbabwe, where most of the alveoli were empty (Raath 1977). The tight

closure of the jaws might be of some taphonomic significance. As Colbert notes, one would normally expect that 'after death and the process of disintegration and decay, there would have been some separation of the mandibular rami from their living positions' (Colbert 1989:69). He suggested that the occlusion noted in his sample of *Coelophysis* implied rapid burial soon after death, and this may also have been true of the *Syntarsus* specimen from which the Elliot Formation snout came.

The occlusion of the jaws and their incomplete preservation make the description and determination of the number of dentary teeth impossible.

There are four premaxillary teeth which are slightly curved at their tip. They have serrations on the posterior side. Serrations on premaxillary teeth are also present in *S. kayentakatae* (Rowe 1989) but none were observed in *S. rhodesiensis* or in *Coelophysis* (Raath 1977; Colbert 1989). However, this is of questionable significance as lack of serrations could simply be due to wear.

Nine alveoli are visible in the preserved portion of the maxilla; how many more there were in the missing posterior part cannot be determined. The dentition shows clear evidence of alternate tooth replacement (Figure 1). The maxillary teeth are long and laterally compressed, with strong backward recurvature such that the tip of each tooth curves to a point vertically behind the back of its own alveolus. The same is true in *S. rhodesiensis* (Raath 1977) and *Coelophysis* (Colbert 1989). All the teeth have serrations along the entire posterior edge and the apical part of the anterior edge, except that the first tooth has serrations on the posterior side only. The posterior serrations are larger and more widely spaced than the anterior.

DESCRIPTION OF THE PARTIAL PELVIS
(BP/1/5246, Figure 2)

The pelvic fragment (BP/1/5246; Figure 2) consists of most of the left ilium including the deep almost circular acetabulum with its hood-like dorsal roof, but most of the thin preacetabular flange of the ilium is missing. The 'brevis shelf' on the ventral surface of the ilium behind the acetabulum is well developed, and the ilium in this region is broadly flared laterally as was noted in the holotype and a number of other specimens of *S. rhodesiensis* from Zimbabwe (Raath 1977). The fused posterior sacral centra and the deep circular pits between the adjacent sacral ribs also strongly resemble the holotype of *S. rhodesiensis* (Figure 2a,c). Dorsally the sacral ribs are not complete, but it appears that they were variably fused to form extensive sheets of thin bone like those noted in several Zimbabwe specimens. The neural spines of the sacral vertebrae have also coalesced into a longitudinal blade running almost the full length of the preserved portion of the sacrum. On the right side little is preserved other than the sacrum and a small piece of the ventral brevis shelf behind the acetabulum.

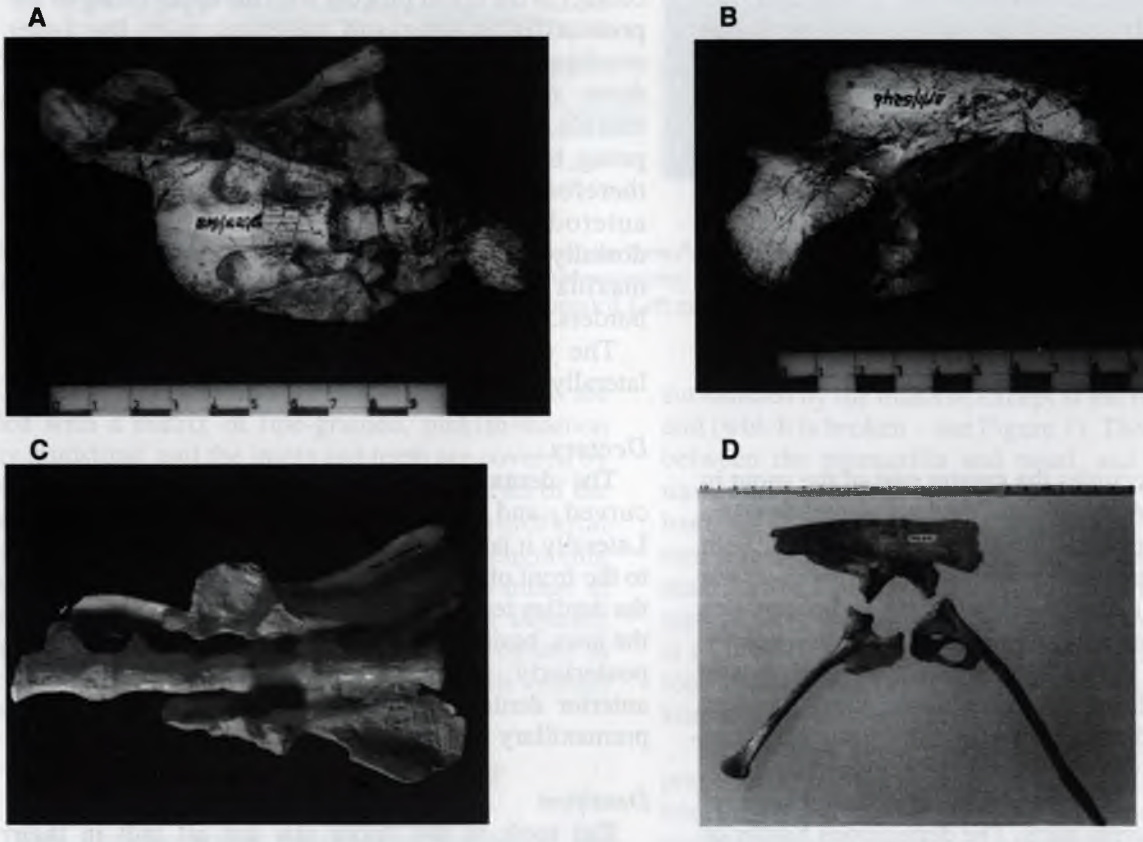

Figure 2. Pelvis and sacrum of *Syntarsus rhodesiensis*: a-b. Specimen BP/1/5246 from *Welbedacht / Edelweiss*, Free State Province, S. Africa a. Ventral view; b. Left side view; c. Cast of holotype pelvis and sacrum (QG1, from Nyamandhlovu, Zimbabwe), in ventral view for comparison (pubes and ischia removed to reveal sacrum); d. Right side view of disarticulated juvenile pelvis (QG691, from the Chitake River, Zimbabwe). (Scale divisions = cm).

DISCUSSION

Comparison of the snout with other ceratosaurs is limited because so little of BP/1/5278 is preserved: only the premaxilla, maxilla, nasal and the dentary are present, and the last three are not complete. The situation is worsened by the compression and tight closure at the tip of the jaws, making study of the palate impossible. However, comparison of the snout with the relevant parts of the skull of *Ceratosaurus nasicornis*, *Dilophosaurus wetherilli*, *Lilliensternus lilliensterni*, *Coelophysis bauri*, *Syntarsus rhodesiensis* and *S. kayentakatae*, shows a close agreement between the characters of BP/1/5278 and those of the ceratosaurs in general (Benton 1990; Colbert 1989; Raath 1977; Rowe 1989; Rowe & Gauthier 1990; Welles 1984), and of *Coelophysis* and *Syntarsus* in particular (Figure 1). The presence a of subnarial gap between the premaxilla and maxilla also unites the snout with members of the sub-clade Coelophysoidea within Ceratosauria (Rowe 1989; Holtz 1994). In these features, and in the presence of the depression of the antorbital fossa in front of the antorbital fenestra, the South African form is inseparable from Zimbabwean *Syntarsus*. The only noted difference between *Syntarsus* from Zimbabwe and the South African snout is the lack of serrations on the premaxillary teeth of the former. However, if the absence of serrations is due to wear, it has no diagnostic value, and in any case *S. kayentakatae* has serrations on its premaxillary teeth.

Although the pelvic fragment (BP/1/5246) is significantly smaller than the holotype pelvis of *S. rhodesiensis*, their morphology, especially in ventral view, is essentially identical.

There seems little doubt that the South African remains reported here belong to the same taxon as the Zimbabwean material, and these specimens are therefore assigned to *Syntarsus rhodesiensis*.

ACKNOWLEDGEMENTS

We are grateful to our colleague, mentor and friend, James W. Kitching, for finding the specimens and entrusting them to us for study. Likewise we are grateful to the Director of the Bernard Price Institute for Palaeontological Research, Professor Bruce S. Rubidge, for permission to study the specimens and for making the Institute's facilities available to us. Finally we thank two anonymous referees for their critical reading of the manuscript and for their helpful suggestions.

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A DINOSAUR FAUNA FROM THE LATE CRETACEOUS (CENOMANIAN) OF NORTHERN SUDAN

by

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ABSTRACT

A dinosaur fauna from the Cenomanian of northern Sudan (Wadi Milk Formation) is described. It comprises at least nine, probably ten to eleven taxa: a dicraeosaurid, a titanosaurid and another undetermined sauropod (possibly a titanosaurid), two charcharodontosaurids, a dromaeosaurid, a probable hypsilophodontid and two iguanodontian ornithopods. It is one of the most diverse dinosaur faunas known from the Cretaceous of Africa. The environment was probably a semiarid savanna with some rivers, lined by dense vegetation, with abundant sauropods, less abundant theropods and rare ornithopods. Gigantic carcharodontosaurids were at the top of the food chain. At the present state of knowledge, the dinosaur fauna from the middle to late Cretaceous of Africa can be characterized by the presence of carcharodontosaurids, spinosaurids, titanosaurids, diplodocoids, and possibly iguanodontian ornithopods.

KEYWORDS: Africa, Cretaceous, Dinosauria, Palaeoecology, Palaeobiogeography

INTRODUCTION

Cretaceous dinosaur faunas from Africa have recently gained more attention (Jacobs *et al.* 1990, 1993, 1996; Sereno *et al.* 1994, 1996; Forster *et al.* 1995; Rauhut & Werner 1995), but they are still very poorly known (Russell 1995).

Articulated dinosaur remains have so far been found only in the ?Barremian and Aptian of Niger (Taquet 1976; Sereno *et al.* 1994), and the Cenomanian of Egypt (Stromer 1915, 1931, 1932, 1934, 1936) and Morocco (Lavocat 1954; Sereno *et al.* 1996). Therefore, isolated skeletal elements of dinosaurs from the Cretaceous of Africa can add important information for a more complete picture of African faunas.

In 1989, a new vertebrate locality was found in Cretaceous beds in Sudan (Buffetaut *et al.* 1990), the first to be discovered in the Cretaceous of this country. In the following years, several expeditions led by Dr. Christa Werner of the Free University of Berlin discovered a rich Cretaceous vertebrate fauna (Werner 1991, 1993, 1994a, b; Werner & Rage 1994; Rauhut & Werner 1995; Evans *et al.* 1996). Among the vertebrate remains are many isolated dinosaur bones and teeth, which are described and discussed in some detail below.

Figure 1. Position of the vertebrate localities in northern Sudan. 1: Wadi Milk Formation, Wadi Abu Hashim; 2: Shendi Formation.

GEOLOGICAL AND PALAEONTOLOGICAL CONTEXT

Localities

Both vertebrate localities are found in northern Sudan, west of the Nile River (Figure 1). The first locality discovered is situated in the Wadi Abu Hashim, some 200 km north-west of Khartoum. Buffetaut *et al.* (1990) recognized two different sites at this positon; however, since the stratigraphic level and sedimentological setting are the same and vertebrate remains have now been found in a large area between these sites, the two localities are now regarded as one (c. Werner, pers. comm. 1994). Werner (pers. comm. 1995) gives the coordinates for this locality as 16°41.77' N; 31°8.7' E.

More vertebrate remains have been found in the Shendi Formation, some 100 km northwest of the city of Shendi. According to Werner (pers. comm. 1996), at least seven different localities with fragmentary vertebrate remains are found in this Formation.

Geological setting

The fossils come from terrestrial sediments, which were deposited in several basins during the Cretaceous. Three different laterally interfingering formations can be distinguished: the Wadi Milk Formation, the Shendi Formation and the Omdurman Formation. The sediments consist mainly of silt- to sandstones, often showing tabular and trough cross-bedding. Some conglomerate layers and rare palaeosols are also present (Bussert 1993a,b).

Bussert (1993a) recognized two different depositional environments: 'braidplain deposits' and 'coastal plain deposits'. The first type is represented mainly by trough cross-bedded sandstones, which are interpreted as deposits of braided rivers, whereas the second type is characterized by finer-grained sediments, derived from meandering rivers, flood plains and lakes. Palaeosols are found in the coastal plain deposits. Palaeocurrent directions are mainly northward in the Wadi Milk Formation.

The Wadi Milk Formation consists mainly of braidplain deposits, which in the north interfinger with coastal plain deposits. The vertebrate locality in the Wadi Abu Hashim is located in the Wadi Milk Formation of the Humar Basin, a large tectonic depression being part of the Central African Fault Zone (Bussert *et al.* 1990). In the Wadi Abu Hashim area, lacustrine sediments form the base of the outcropping parts of the Wadi Milk Formation. Above these fine grained siltstones, sandstones, and coarse cross-bedded sandstones indicate a change in sedimentation from a lacustrine environment to braided rivers. The coarse sandstones are overlain by finer-grained floodplain deposits, and the section ends with more braided river-sediments (Buffetaut *et al.* 1990). The vertebrate remains come from the lacustrine sediments at the base of the outcrop.

Stratigraphy

Since no invertebrates or palynomorphs were found at the vertebrate localities (Werner 1994a), dating of the sediments is difficult. Palynomorphs from other parts of the Wadi Milk and Omdurman Formations indicate an Albian-Cenomanian (Schrank 1990; Schrank & Awad 1990) or Cenomanian - Late Cenomanian (Awad 1994) age. Macrofloral investigations result in an Aptian-Cenomanian age for other parts of the Humar Basin area (Lejal-Nicol 1987). Werner (1994a) dated the locality in the Wadi Abu Hashim as Cenomanian, based on the fish fauna.

In the Shendi Formation, no invertebrates or palynomorphs have been found, but since this unit represents a lateral equivalent of the Wadi Milk and Omdurman Formations, a similar age can be assumed.

Flora and fauna

Based on palynomorphs, the middle Cretaceous formations in northern Sudan can be referred to the microfloral province of Africa/South-America, indicating a palaeoposition close to the equator (Schrank 1990). The presence of fungi, gymnosperms, angiosperms, ferns, aquatic ferns and a high diversity of pteridophytes can be demonstrated on the basis of spores and pollen (Schrank 1990). The relatively high percentage of fern-spores compared to other localities of the same microfloral province, indicates a less arid environment than in other regions. Macrofloral remains are mainly represented by parts of conifers (Lejal-Nicol 1987). The only plant remains found at one of the vertebrate localities is an indeterminable leaf of an aquatic plant (Werner 1994a).

No invertebrate remains have been described from any of the formations so far.

Many of the vertebrates are still under study (e.g. the dipnoans by U. Gloy, the amphibians and reptiles by C. Werner). The following faunal lists are mainly based on Werner (1993, 1994a), modified after the results of the current research (Werner & Rage 1994; Evans *et al.* 1996) and this work.

Floral and faunal list of the Wadi Milk Formation at Wadi Abu Hashim

Plantae:
- indeterminate aquatic plant

Vertebrata:
- Chondrichthyes:
  - Elasmobranchii
    - Euselachii
      - Fam. Acrodontidae
        - cf. *Asteracanthus aegyptiacus*
    - Neoselachii
      - Rajiformes
        - Rajiformes indet.
- Osteichthyes:
  - Actinopterygii
    - Polypteriformes
      - Fam. Polypteridae
        - Polypteridae indet.
    - Lepisosteiformes
      - Fam. Lepisosteidae
        - Lepisosteidae indet.
    - Osteoglossiformes
      - Fam. Osteoglossidae
        - Osteoglossidae indet.
    - Characiformes
      - Characiformes indet.
  - Sarcopterygii
    - Dipnoi
      - Fam. Protopteridae
        - *Protopterus humei*
        - *Protopterus* nov. sp.
      - Fam. Ceratodontidae
        - *Neoceratodus tuberculatus*

Amphibia:
Lissamphibia
Gymnophiona
Gymnophiona indet.
Caudata
Kababisha humarensis
Kababisha sudanensis

Anura
Anura indet.

Reptilia:
Chelonia
Pleurodira
Fam. Podocnemididae
3 taxa Podocnemididae indet.

Squamata
Lacertilia
Lacertilia indet.

Ophidia
Fam. Madtsoiidae
Gen. et sp. indet.

Fam. ?Aniliidae
Gen. et sp. indet.

Fam. ?Lapparentophiidae
Gen. et sp. indet.

Fam. ?Nigerophiidae
Gen. et sp. indet.

Fam. ?Russellophiidae
Gen. et sp. indet.
Ophidia Fam., Gen. et sp. indet.

Archosauria
Suchia
Crocodylomorpha
2 taxa Crocodylomorpha indet.

Fam. Dyrosauridae
Dyrosauridae gen. et sp. nov.

Dinosauria
Saurischia
Sauropodomorpha
Sauropoda
Fam. Dicraeosauridae
Dicraeosauridae gen. et sp. indet.

Fam. Titanosauridae
Titanosauridae gen. et sp. indet.
Sauropoda gen. et sp. indet. (Titanosaurid?)

Theropoda
Tetanurae
Superfam. Allosauroidea
Fam. Carcharodontosauridae
2 taxa Carcharodontosauridae gen. et sp. indet.

Coelurosauria
?Coelurosauria indet.

Fam. Dromaeosauridae
Subfam. Velociraptorinae
Velociraptorinae gen. et sp. indet.

Ornithischia
Ornithopoda
Fam. (?)Hypsilophodontidae
Hypsilophodontidae indet.

Fam. Iguanodontidae
Iguanodontidae gen. et sp. indet.

(?)Fam. Iguanodontidae
cf. *Ouranosaurus* sp.

Faunal list of the Shendi Formation

Vertebrata:
Osteichthyes:
Sarcopterygii
Dipnoi
Fam. Protopteridae
Protopterus humei
Protopterus nov. sp.

Amphibia:
Caudata
Caudata gen. et sp. nov.

Reptilia:
Chelonia
Pleurodira
2 taxa Pleurodira indet.

Archosauria
Suchia
Crocodylomorpha
3 taxa Crocodylomorpha indet.

Dinosauria
Saurischia
Theropoda
Theropoda indet.

DINOSAUR REMAINS FROM SUDAN

The dinosaur remains described here come mainly from the Wadi Milk Formation of Wadi Abu Hashim. Only a few isolated phalanges were found in the Shendi Formation; one of these is described and discussed separately below. The material is stored in the collections of the Institut für Paläontologie of the Free University, Berlin.

SYSTEMATIC PALAEONTOLOGY

Dinosauria Owen 1842
Saurischia Seeley 1888
Sauropodomorpha Huene 1932
Sauropoda Marsh 1878

Sauropod remains are the most common dinosaur fossils in the Wadi Milk Formation. Mainly isolated vertebral centra and fragmentary limb elements have been found; other than teeth, cranial elements are missing. The systematic terms follow Upchurch (1998).

Family: Dicraeosauridae Huene 1927

Gen. et sp. indet.

Material: Three caudal vertebral centra (Vb-856, Vb-857, Vb-892), a proximal end of a left fibula (Vb-884), and the distal end of a right tibia (Vb-879).

Description: Vb-892 is an anterior caudal vertebra (Figure 2A). The centrum is procoelous and relatively short: without the posterior ball, its length is only 70 mm. The ventral side is almost plain, with well developed chevron facets at its posterior end. On the sides, a bony lamina runs from the mid-height of the anterior end to the attachment of the broken transverse process on the dorsal part of the middle of the centrum. The neural arch is broken. It was almost confluent with the anterior end, but slightly offset from the posterior end.

Both other caudal centra are from the middle portion of the tail (Figure 2B-D). The bones are heavily abraded. The vertebrae are amphi-platycoelous with a concave anterior and a plane posterior intervertebral facet. In the ventral half of the facets, a small bulge is found on both facets of Vb-857, but only on the posterior one in Vb-856. The sides of the centra are antero-posteriorly only slightly concave and dorso-ventrally considerably convex in Vb-857, while they are less convex dorso-ventrally but considerably concave antero-posteriorly in Vb-856.

The ventral surfaces of the centra are almost plain transversely. The chevron facets are relatively wide apart, with a shallow longitudinal groove between them. The ventral surface appears concave in lateral view, mainly because of the ventrally projecting chevron facets.

The broken attachments of the neural arches are slightly more than half the length of the centra (70 mm in Vb-857, 57 mm in Vb-856) and their anterior borders are almost confluent with the anterior intervertebral facets in Vb-857 and only a short distance offset from it in Vb-856. In Vb-857, a break on the lateral sides under the posterior end of the neural arch marks the former attachment of the transverse processes; in Vb-856, only a slight swelling is found in this position, indicating that this vertebra is from a more distal part of the tail than Vb-857.

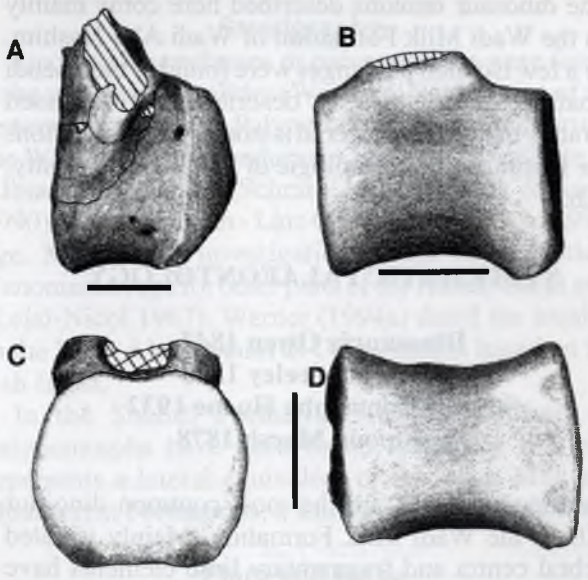

Figure 2. Dicraeosauridae indet., Wadi Milk Formation. A: first caudal vertebra; Vb-892; left lateral view. B-D: mid-caudal vertebra; Vb-856; B: left lateral view, C: posterior view, D: ventral view. Scale bars indicate 5 cm.

Vb-879 is a 200 mm long portion of the distal end of a right tibia (Figure 3A,B). The articular surface is 115 mm wide and 195 mm long. It is relatively narrow anteriorly and flares distally. A well developed latero-ventral indentation is present where the bone widens. The articular surface is slightly inclined proximally in a postero-anterior direction. Laterally, a facet for the articulation of the fibula is present on the posterior half of the bone.

The bone shows a triangular cross-section at the break, with the long side medial. At that point, it is 103 mm wide and 125 mm long.

Vb-884 represents a proximal end of a left fibula (Figure 3C, D). The articular surface is 210 mm long and 72 mm wide, and is widest in the middle. While it narrows only slightly posteriorly, it ends in a relatively sharp, slightly medially pointing tip anteriorly. Both these parts of the bone are inclined distally. The structure of the articular surface resembles that of Vb-848. The bone is broken 130 mm below the articular surface. Along its midline, a broad ridge runs from the broadest part of the surface to the break on the lateral side; the other parts of the bone are very narrow. At the break, the fibula is 154 mm long and 38 mm wide at its widest part.

Discussion: Procoelous anterior caudals, like Vb-892, are usually seen as a typical character of titanosaurids (Powell 1986; McIntosh 1990), but they also occur in diplodocoids and the euhelopodid *Mamenchisaurus* (Hatcher 1901; Janensch 1929; Gilmore 1936; Young 1954). A significant difference between the caudal vertebrae of titanosaurids and the specimen from Sudan

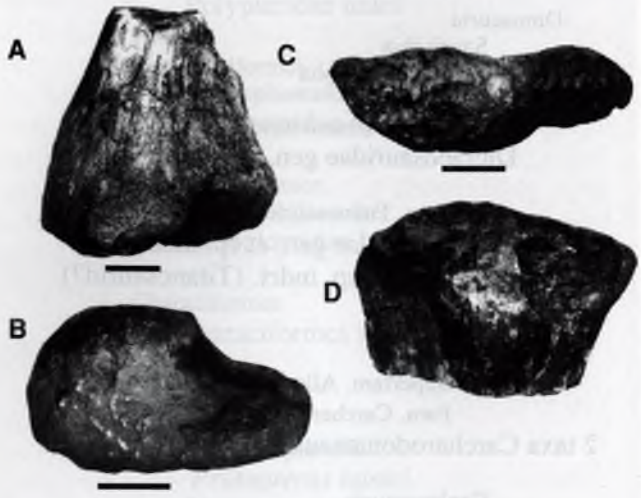

Figure 3. (?)Dicraeosauridae indet., Wadi Milk Formation. A, B: distal end of right tibia; Vb-879; A: lateral view, B: distal view. C, D: proximal end of left fibula; Vb-884; C: proximal view, D: lateral view. Scale bars indicate 5 cm.

is the bony lamina extending from the transverse process onto the centrum. In titanosaurids, this lamina is inclined posteriorly, rather than anteriorly, as it is in Vb-892 (Huene 1929; Powell 1986). Therefore, Vb-892 is referred to the Diplodocoidea.

Within diplodocoids, it differs from *Apatosaurus* in its more pronounced procoelous condition (Gilmore 1936), from *Diplodocus* in its lack of pleurocoels (Hatcher 1901), and there seem to be significant differences from the caudals of *Mamenchisaurus* in the development of the posterior intervertebral facet (Young 1954). On the other hand, the vertebra from Sudan is very similar to the second caudal of *Dicraeosaurus* (Janensch 1929: Taf. III, Figure 2) and is therefore referred to the Dicraeosauridae. The mid-caudals Vb-856 and Vb-857 also show strong resemblances to caudals of *Dicraeosaurus* in respect of their massive shape and widely separated and well developed chevron facets (Janensch 1929: Taf. III, Figure 18, pers. obs.), and for this reason they are assigned to the same taxon. In the tibia fragment, an antero-lateral projection of the fibular facet, such as found in most sauropods (e.g. Gilmore 1936: Figure 23D; Janensch 1961: Beilage K, Figure 3e; Ostrom & McIntosh 1966: Plate 75, Figure 1a), is absent. This projection is also absent from the distal tibiae of *Dicraeosaurus sattleri* and probably *Janenschia* (Janensch 1961). Since there are good arguments for the presence of a dicraeosaurine sauropod in Sudan, this limb fragment is tentatively also assigned to this taxon. The fibula Vb-884 is seemingly more slender than the fibulae of most sauropods (Huene 1929, Gilmore 1936, Janensch 1961, Ostrom & McIntosh 1966), but is similar to that of *Dicraeosaurus* (Janensch 1961).

Family: Titanosauridae Lydekker 1885

Gen. et sp. indet.

Teeth

Material: 53 teeth (Vb-721, Vb-900 to Vb-912).

Description: All the teeth are weakly spatulate to peg-like (Figure 4). The basal cross-section is round in most specimens, but the apical part of the crown is slightly flattened labio-lingually in several, but not all specimens. An unserrated cutting edge is developed mesially and distally. A few teeth show a slightly recurved crown (e.g. Vb-907); in this case, the mesial edge is restricted to the upper two thirds of the crown. The labial side is slightly more convex than the lingual one in all specimens. Enamel ornamentation is often found in the antapical part of the crown; it consists of several very small irregularly shaped ridges running parallel to the edges.

Many teeth show wear facets. While in some teeth the tip of the crown is simply worn away, several others show well defined triangular facets on the mesial or distal carina, sometimes inclined to the lingual, sometimes to the labial side. Janensch (1935-36) described a similar phenomenon in the teeth of *Brachiosaurus brancai*, with the more lingually positioned facets found in the upper jaw and the more labially positioned ones in the lower jaw. If the same was true for the specimens from Sudan, 21 of the teeth showing wear facets represent teeth from the upper jaw and 14 from the lower jaw.

Figure 4. Titanosauridae indet., Wadi Milk Formation. Teeth; A: Vb-721, lingual view, B: Vb-907, labial view, showing triangular apical wear facet, C: Vb-901, distal view, D: Vb-911, tooth of a juvenile individual, lingual view, E: Vb-907, tooth of a juvenile individual with partly preserved root and triangular wear facet, labial view. Scale bars indicate 1 cm.

Discussion: Since the teeth of euhelopodids, "cetiosaurids", brachiosaurids and camarasaurids are much broader than the specimens from Sudan (Wiman 1929; Janensch 1935-36; Bonaparte 1986; McIntosh 1990), the latter must belong to a diplodocoid or titanosaurid, both groups which are characterized by relatively slender teeth (Marsh 1884; Huene 1929; Janensch 1935-36; Kues *et al.* 1980; Powell 1986; McIntosh 1990).

The teeth of diplodocoids are more slender than the elements from the Wadi Milk Formation (Marsh 1884, Janensch 1935-36), while the teeth of the titanosaurids *Laplatasaurus*, *Alamosaurus* and *Malawisaurus* are very similar to the specimens from Sudan (Powell 1979; Kues *et al.* 1980; Jacobs *et al.* 1993). Therefore, the teeth described above are referred to the Titanosauridae. The presence of two slightly different tooth types, one being more spatulate (similar to teeth of *Malawisaurus*; Jacobs *et al.* 1993), the other being very slender and showing an almost circular cross section (similar to teeth of Late Cretaceous titanosaurids; Powell 1979; Kues *et al.* 1980), may indicate the presence of different taxa.

Vertebrae

Material: One presacral (Vb-893) and fifteen caudal vertebrae (Vb-606, Vb-720, Vb-876, Vb-877, Vb-880, Vb-882, Vb-883, Vb-885, Vb-886, Vb-889, Vb-891, Vb-894, Vb-897, Vb-899, Vb-935).

Description: Vb-893 represents the anterior part of a presacral vertebral centrum (Figure 5). The lack of parapophyses on the centrum indicates that it is a posterior dorsal vertebra.

The anterior intervertebral facet is strongly convex, and the centrum is slightly higher than wide. The posterior intervertebral facet is broken away. Just below the former attachment of the neural arch, a pleurocoel

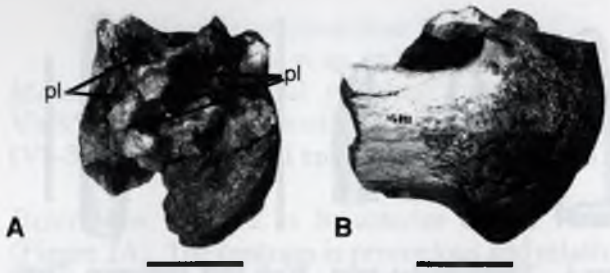

Figure 5. Titanosauridae indet., Wadi Milk Formation. Dorsal vertebrae; Vb-893; A: posterior view of the break, showing the arrangement of the pleurocoels (pl), B: right lateral view. Scale bars indicate 5 cm.

opening is found on both sides. The pleurocoels are longer than high and lead into large excavations in the interior of the centrum. The excavations are irregularly shaped and subdivided by thin laminae of bone. While the right pleurocoel leads into a large chamber extending in an obliquely ventral direction, the left excavation was much smaller and more dorsally placed. At the front end of the pleurocoels, a small, shallow groove in the shape of a recumbent letter 'L' is present on the sides of the vertebra. The neural arch is broken away, but its attachment most probably extended over the whole length of the centrum.

The vertebrae Vb-880 and Vb-883 represent biconvex first caudals.

The centra are wider than high, with a strongly convex posterior ball and a less convex anterior one. Well developed, but broken, transverse processes are present, mainly positioned on the anterior half of the centrum in Vb-880 (Figure 6), extending over the whole length in Vb-883. Below the processes, the centra are strongly convex dorso-ventrally. The ventral side is plain with a very slight depression in the middle in Vb-880, but slightly convex transversely in Vb-883. No chevron facets are present. Several large foramina are found on the lateral and ventral sides. A very large foramen, perhaps representing a vestigeal pleurocoel, is placed just below the attachment of the transverse process in Vb-883. The attachment of the well developed neural arch is situated mainly on the anterior half of the bone.

Vb-720, Vb-876, Vb-877, Vb-891, Vb-897, Vb-899 and Vb-935 represent strongly procoelous anterior caudals (Figure 7). The neural arches are restricted to the anterior half of the centra, but are unfortunately damaged or completely broken away in all specimens. The neural canal was relatively large and more or less circular in cross-section. Well developed, but broken, transverse processes are found in all elements on the anterior dorsal part of the sides. The ventral surfaces are almost plain, with well developed chevron facets. Several foramina are situated on the lateral and ventral surfaces of most elements. While the centra in Vb-876, Vb-877, Vb-891, and Vb-935 are higher than long, those of Vb-720, Vb-897 and Vb-899 are longer than high, indicating that the latter are from a more distal position in the tail.

Vb-882 and Vb-885 represent mid-caudals (Figure 8),

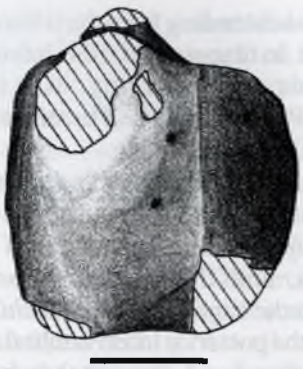

Figure 6. Titanosauridae indet., Wadi Milk Formation. Biconvex first caudal vertebra; Vb-880; left lateral view. Scale bar indicates 5 cm.

while all remaining centra are from the end of the tail (Figure 9). Vb-882 shows an almost rectangular cross-section, but Vb-885, which is obviously from a more distal position, appears to be more or less oval, its width being greater than its height. The centra expand strongly towards the intervertebral facets; this feature is especially striking at the posterior end in Vb-885. In Vb-882, the greatest expansion of the posterior ball lies in the upper half of the centrum. In both vertebrae, there is a small horizontal groove on the posterior ball. The chevron facets are relatively wide apart, more so at the anterior end than the posterior.

The broken attachments of the neural arches are located on the anterior half of the centra and are slightly more than half the centrum length. No transverse processes are present, but in Vb-882, a swelling on the lateral sides beneath the posterior part of the neural arch indicates the insertion of the process in more anterior caudals.

The posterior caudals Vb-606 and Vb-894 are the only other elements well enough preserved to warrant description (Figure 9).

Both vertebrae are relatively slender and show an almost circular cross-section in the middle. In Vb-606, the intervertebral facets are roughly hexagonal. The neural arch was obviously small and restricted to the anterior half of the centrum. As in Vb-885, several small foramina are situated close to the intervertebral facets and the posterior ball shows a shallow horizontal groove. The chevron facets are only weakly developed.

Vb-894 is rod-like, with only two small ridges instead of the neural arch. Although both intervertebral facets are damaged, the procoelous condition is clearly visible. As in the other vertebrae described above, a horizontal groove is present on the posterior face.

Discussion: The presacral vertebra Vb-893 shows irregularly shaped pleurocoels, a character found in titanosaurids (McIntosh 1990), and it is therefore referred to the Titanosauridae. Since biconvex first caudals are also a typical character of titanosaurids (Powell 1986; McIntosh 1990), it is very probable, that Vb-880 and Vb-883 belong to this family, too. The striking differences between these two elements may indicate the presence of more than one taxon.

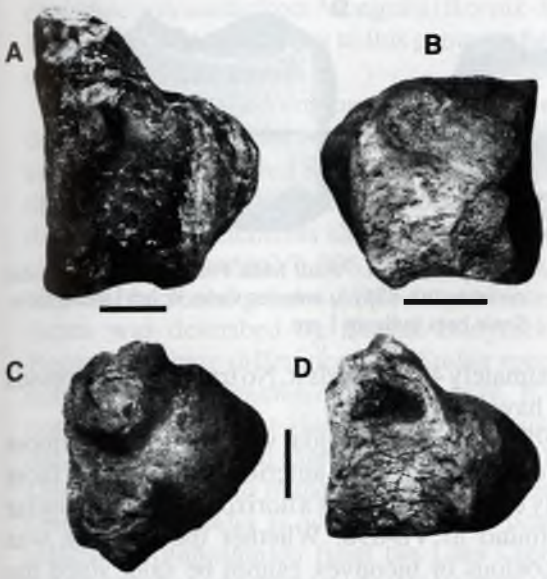

Figure 7. Titanosauridae indet., Wadi Milk Formation. A: anterior caudal vertebra; Vb-876; left lateral view. B: anterior caudal vertebra; Vb-897; right lateral view. C, D: anterior caudal vertebra; vb-899; C: dorsal view, D: left lateral view. Scale bars indicate 5 cm.

Although procoelous anterior caudals are also found in other sauropods (Janensch 1929; Gilmore 1936; Young 1954), the great expansion of the posterior ball in the Sudan vertebrae clearly indicates titanosaurid relationship (Powell 1986; McIntosh 1990). Since the caudal vertebrae are quite similar in different titanosaurids (e.g. Huene 1929; Powell 1986), the fossils from Sudan cannot be referred to a particular genus or species. It is possible that the titanosaurid *Aegyptosaurus*, originally described from the Cenomanian of Egypt (Stromer 1932), is also represented in the Wadi Milk Formation. It should be noted, however, that the taxon from Sudan obviously belongs to the crown group titanosaurids, judging by the procoelous posterior centra. Rod-like caudals like Vb-894 have been described for the genus *Saltasaurus* from the Late Cretaceous of South America (McIntosh 1990).

Because of the great similarity of the caudals of different titanosaurids, it is possible that the elements described above represent more than one species; several different taxa of titanosaurids are often found in one localitiy in the Late Cretaceous of South America, too (Powell 1986; Weishampel 1990).

Limb bones
Material: Distal end of a fibula (Vb-881).

Description: Vb-881 is the distal end of a ?right fibula (Figure 10). The preserved fragment is 210 mm long, its distal dimensions are 128 mm anterio-posteriorly and 107 mm medio-laterally. The cross-section of the bone at the break is semi-circular, with the lateral side rounded and the medial side straight. At this point, the antero-posterior length is 96 mm and the medio-lateral width 57 mm.

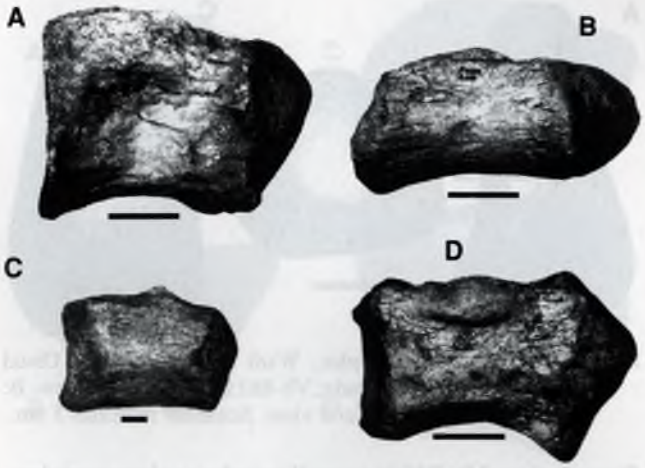

Figure 8. Titanosauridae indet., Wadi Milk Formation. A: mid-caudal vertebra; Vb-882; left lateral view. B, C: mid-caudal vertebra; Vb-885; B: left lateral view, C: dorsal view. D: posterior mid-caudal vertebra; Vb-889; left lateral view. Scale bars indicate 5 cm (A-C) and 1 cm (D).

The medial side is plain up to the distal articular surface, where a horizontal ridge is located. The articular surface is triangular and does not show any notable features, partly due to abrasion.

Discussion: This element is referred to the Titanosauridae because of the triangular shape of the distal articular surface. Such a shape is found in the fibulae of camarasaurids (Ostrom & McIntosh 1966) and titanosaurids, (Huene 1929, 1932). While the triangle is much lower in camarasaurids, the shape of the distal articular surface of a fibula of the South American titanosaurid, *Saltasaurus australis*, figured by Huene (1929: Lámina 16, Figure 5d), is strikingly similar to that of the specimen from Sudan.

Sauropoda indet.

Vertebrae

Material: Three vertebral centra (Vb-719, Vb-895, Vb-896).

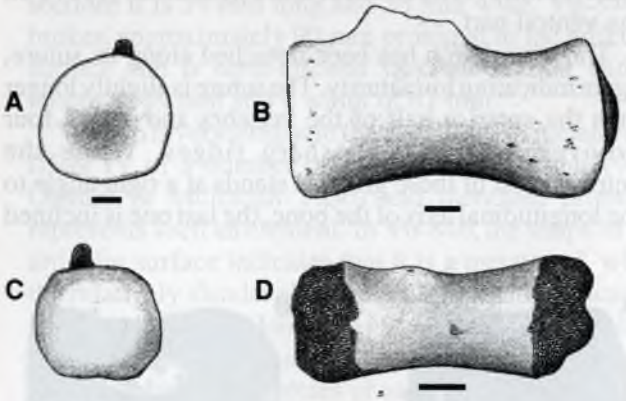

Figure 9. Titanosauridae indet., Wadi Milk Formation. A-C: posterior caudal vertebra; Vb-606; A: anterior view, B: left lateral view, C: posterior view. D: posterior caudal vertebra; Vb-894; left lateral view. Scale bars indicate 1 cm.

Figure 10. Titanosauridae indet., Wadi Milk Formation. Distal end of (?)right fibula; Vb-881; A: (?)anterior view, B: distal view, C: lateral view. Scale bar indicates 5 cm.

Description: Vb-719 is a small opisthocoelous vertebra, which is wider than high (Figure 11). The neural arch is missing; it has been separated from the centrum along its suture, indicating that the element derives from a juvenile individual. This is also supported by its small size, as well as by the cancellous appearance of the bone at the intervertebral facets and clearly visible bone fibres on the sides, both features that are typical for embryonic or very young dinosaurs (Britt & Naylor 1994). The lack of parapophyses implies that it is a dorsal vertebra.

Deep but simple pleurocoel excavations are found dorsally on the sides. These pleurocoels are simple pits which extend from the dorsal and lateral margins of the sides into the bone and reach their greatest depth just above the midline (in lateral view). The ventral side of the centrum is only slightly convex transversely, but strongly concave antero-posteriorly.

The suture of the neural arch extends over the whole length of the centrum. Its detailed structure cannot be described, because of erosion.

Vb-896 is a caudal vertebra with an almost rectangular cross-section (Figure 12). The lateral and ventral surfaces are only slightly concave antero-posteriorly and marginally convex transversely. The vertebra is slightly opisthocoelous, with a bulge on the dorsal part of the anterior intervertebral facet and a horizontal groove on the ventral part.

The neural arch has been detached along its suture, again indicating immaturity. The suture is slightly longer than the anterior half of the vertebra and shows four grooves separated by sharp ridges. While the anteriormost of these grooves stands at a right angle to the longitudinal axis of the bone, the last one is inclined

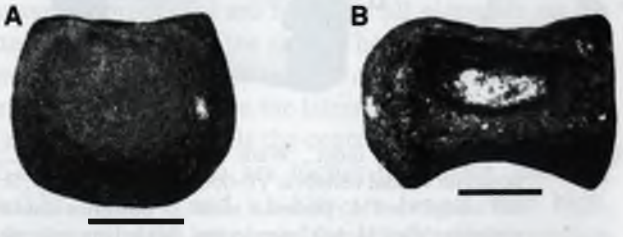

Figure 11. Sauropoda indet., Wadi Milk Formation. Dorsal vertebra of a juvenile individual (?hatchling); Vb-719; A: anterior view, B: left lateral view. Scale bars indicate 1 cm.

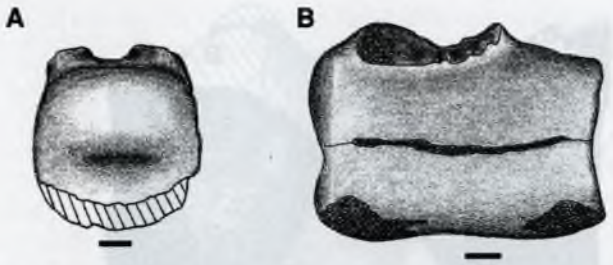

Figure 12. Sauropoda indet., Wadi Milk Formation. Mid-caudal vertebra; Vb-896; A: anterior view, B: left lateral view. Scale bars indicate 1 cm.

at approximately 45° towards it. No transverse processes seem to have been present.

Vb-895 is a posterior caudal vertebra with an almost circular cross-section. The anterior intervertebral facet is slightly convex and shows a horizontal groove similar to that found in Vb-896. Whether the vertebra was opisthocoelous or biconvex cannot be said, since the posterior part is missing. Instead of a neural arch, there are two small ridges dorsally. Although the bone is heavily damaged, it can be said with some certainty that it was probably not much longer than twice its height.

Discussion: The deep pleurocoels characterize the centrum Vb-719 as a saurischian vertebra. In large theropods like *Allosaurus*, the shape of the pleurocoels in the opisthocoelous anterior dorsal vertebrae is different, and these vertebrae show strongly developed parapophyses on the centrum (Madsen 1976). Pleurocoels similar to those in Vb-719 are found in some small theropods, but their dorsal vertebrae are usually not opisthocoelous (e.g. *Deinonychus*; Ostrom 1969). Therefore, the specimen from the Wadi Milk Formation is referred to the Sauropoda.

The element from Sudan differs from juvenile *Apatosaurus* and *Camarasaurus* dorsal vertebrae in showing deep pleurocoels (Carpenter & McIntosh 1994). Although cervical vertebrae of a juvenile *Camarasaurus* are similar to Vb-719 in respect of shape and development of pleurocoels, an important difference is the presence of parapophyses on the vertebral centrum in the former (Carpenter & McIntosh 1994). A dorsal centrum of a juvenile *Phuwiangosaurus* is quite similar in lateral view, but differs in the presence of a faint ventral keel (Martin 1994). A probably juvenile dorsal vertebra of the titanosaurid *Laplatasaurus* is very similar to Vb-719 in its general shape, and perhaps also in the development of the pleurocoels (Huene 1929: Lámina 22, Figure 18).

Since only few juvenile sauropod remains have been found so far, the systematic position of the Sudan specimen must remain unresolved for the present. However, the chances are that it belongs to one of the taxa described above, possibly to a titanosaurid.

The caudal vertebrae Vb-895 and Vb-896 probably belong to the same taxon, judging by the similar morphology of the anterior intervertebral facet. The anteriorly placed neural arch in Vb-896 indicates sauropod relationships for these specimens.

So far, within sauropods, opisthocoelous caudals have been described only in the Late Cretaceous taxon

Opisthocoelicaudia from Mongolia (Borsuk-Bialynicka 1977). A further similarity to this genus is the shortness of the posterior caudals.

However, detailed comparison reveals a number of differences between the vertebrae of *Opisthocoelicaudia* and the specimens from Sudan. In the Asian genus, only the first fifteen caudals are opisthocoelous, but at least the first sixteen elements show transverse processes, a character not found in Vb-896. Furthermore, no character like the horizontal groove on the anterior intervertebral facets was described by Borsuk-Bialynicka (1977). Because of these differences, the Sudan specimens are not referred to *Opisthocoelicaudia* here. It should be noted, however, that Harris & Russell (unpublished data) also recognized sauropod bones with affinities to *Opisthocoelicaudia* in the Cretaceous of Kenya. Since *Opisthocoelicaudia* is now regarded as being closely related to titanosaurids from the Late Cretaceous of other Gondwanan continents (Upchurch 1998), the presence of a closely related taxon from Africa would not be too surprising.

Limb bones

Material: Five limb bone fragments (Vb-845 to Vb-848, Vb-878).

Description and discussion: Vb-848 and Vb-878 are parts of the stylopod. They are referred to the Sauropoda because of their relatively large size and the poorly developed articular surfaces.

Vb-848 (Figure 13A,B) shows a slightly concave, oval proximal articular surface with a transverse width of 104 mm and an antero-posterior length of 135 mm. The surface consists of many small grooves and bumps, as seen in many sauropods. The bone narrows towards the break, which is 100 mm from the articular surface. While the posterior end of the surface is confluent with the shaft of the bone, the anterior end overhangs it, forming a ridge. The cross-section at the break is almost circular, with a width of 62 mm and a length of 64 mm.

This bone probably represents the proximal end of a radius (cf. e.g. Huene 1929: Lámina 11, Figure 4; Ostrom & McIntosh 1966: Plate 50). Because of its poor preservation, nothing further can be said about its identity.

Vb-878 (Figure 13C,D) shows a roughly oval proximal articular surface, which is 115 mm wide and 190 mm long. The bone is heavily eroded. It narrows towards the break, which is approximately 180 mm from the articular surface. At the break, the element is 45 mm wide and 120 mm long antero-posteriorly, with a sharp anterior and a rounded posterior margin.

The fragment from Sudan probably represents the proximal part of a right fibula. It shows similarities with the fibulae of *Saltasaurus australis* and *Apatosaurus louisae* (Huene 1929; Gilmore 1936), but because of its incompleteness and poor preservation, no further conclusions can be drawn.

Figure 13. Sauropoda indet., Wadi Milk Formation. A, B: proximal end of a radius; Vb-848; A: proximal view, B: lateral view. C, D: proximal end of a right fibula; Vb-878; C: proximal view, D: lateral view. Scale bars indicate 5 cm.

Vb-847 is the proximal end of a metacarpal (Figure 14A, B). The shape of the articular surface is triangular, with an anterior width of 75 mm, a posterior width of 27 mm and a length of 102 mm. The anterior margin slightly overhangs the shaft of the bone. The bone is broken some 115 mm beyond the articular surface; at this point, it is oval in cross-section with a length of 50 mm and a width of 39 mm.

The element shows great similarities to metacarpal III of *Apatosaurus* and to metacarpal IV of *Janenschia* (Gilmore 1936; Janensch 1961), and therefore most probably represents a 3rd or 4th metacarpal of a sauropod. It cannot be referred to a particular taxon.

Vb-845 and Vb-846 are distal ends of metapodial elements (Figure 14C-H). The articular surfaces are roughly trapeziform, showing the typical small grooves and bumps. The articular surface is relatively narrow in the middle, but expands proximo-distally at the sides, more so medially than laterally. This expansion is especially striking in Vb-846. Vb-845 is broken approximately 140 mm from the articular surface. Here, the bone is relatively slender, showing an oval cross-section. It is 59 mm long and 55 mm wide. Vb-846 is broken approximately 90 mm proximal to the articular surface and is semi-circular in cross-section with a length of 49 mm and a width of 61 mm.

Vb-846 is very similar to the distal ends of metatarsals III or IV of a number of sauropods (Janensch 1961; Ostrom & McIntosh 1966) and therefore probably represents such an element. In Vb-846, the shape of the articular surface indicates that it is a metatarsal, while the relatively slender shaft rather implies identification as a metacarpal (see Janensch 1961; Ostrom & McIntosh 1966). None of the elements can be assigned to a particular genus or species of sauropod.

Theropoda Marsh 1881

Theropod remains are the second most common dinosaur fossils in the Wadi Milk Formation. Some vertebral centra and isolated limb bone fragments have

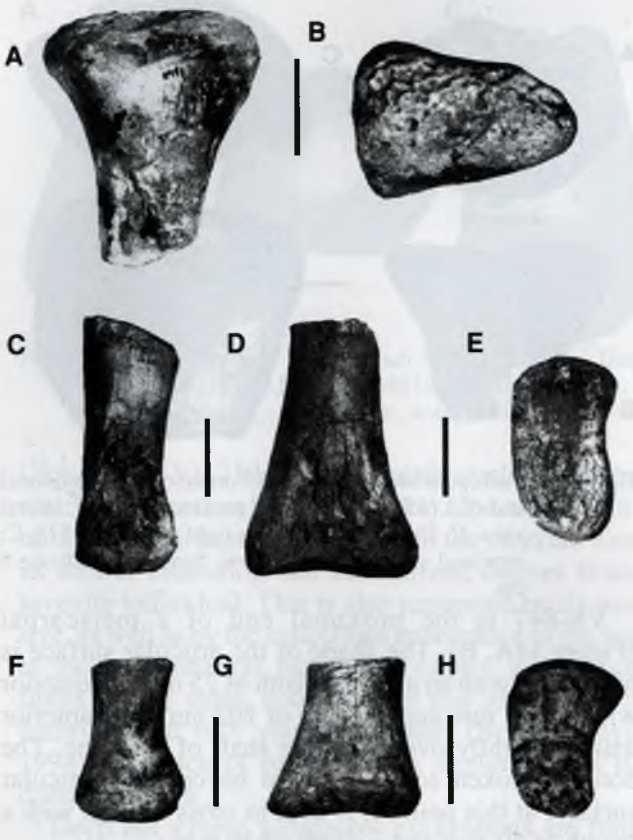

Figure 14. Sauropoda indet., Wadi Milk Formation. A, B: proximal end of a 3rd or 4th metacarpal; Vb-847; A: medial or lateral view, B: proximal view. C-E: distal end of a ?metatarsal; Vb-845; C: ?lateral view, D: anterior view, E: distal view. F-G: distal end of a metatarsal; Vb-846; F: ?lateral view, G: anterior view, H: distal view. Scale bars indicate 5 cm.

been found; teeth are rare in the collections from Sudan. In the following account, the systematic terms follow Sereno *et al.* (1996).

Tetanurae Gauthier 1986
Superfamily: Allosauroidea Currie et Zhao 1993
Family: Carcharodontosauridae Stromer 1931

Gen. et sp. indet.

Material: Three vertebrae (Vb-607, Vb-717, Vb-870).

Description: All these bones are caudal vertebrae, Vb-607 and Vb-717 being from the proximal portion of the tail, while Vb-870 represents a posterior mid-caudal (Figure 15). The vertebral centra are relatively well preserved in these elements, but the neural arches are broken, leaving just the rim of the neural canal in Vb-607 and Vb-717. All vertebra are amphicoelous, with the posterior intervertebral facet being less concave than the anterior one. The shape of the facets is oval to almost circular and the anterior facets are clearly offset above the posterior ones.

The bones are strongly waisted in the middle. In Vb-607 (Figure 15A,B), there are large grooves on either side, which deepen towards the posterior end to a small pneumatic foramen. The sides of this element have collapsed, showing almost identical collapse structures on both sides, suggesting that large pneumatic cavities were present within the bone. Very similarly shaped, though shallower, grooves are also found on the sides of Vb-717 (Figure 15C, D), but no foramina are present and the sides are not collapsed. In Vb-870, only very shallow depressions are found on the sides.

The ventral sides of all the vertebrae are keeled, with a very shallow longitudinal groove in the middle of the keel. Well developed chevron facets are found on both ends.

The preserved part of the neural arch in Vb-607 and Vb-717 is slightly wider than the middle of the centrum at its base, but it narrows dorsally. The neural arches are fused to the centra without any visible suture. Above the lateral grooves, a horizontal ridge, which bends dorsally in its posterior part, is present on the neural arch. No transverse processes are present on the preserved parts of the arches. The neural canal is oval and relatively large. The arches extend over almost the total length of the centra.

Discussion: Vb-606 has been figured by Buffetaut *et al.* (1990) as "large amphicoelous dorsal vertebra ... of a carnivorous dinosaur". However, the presence of chevron facets clearly indicates that it is a caudal vertebra.

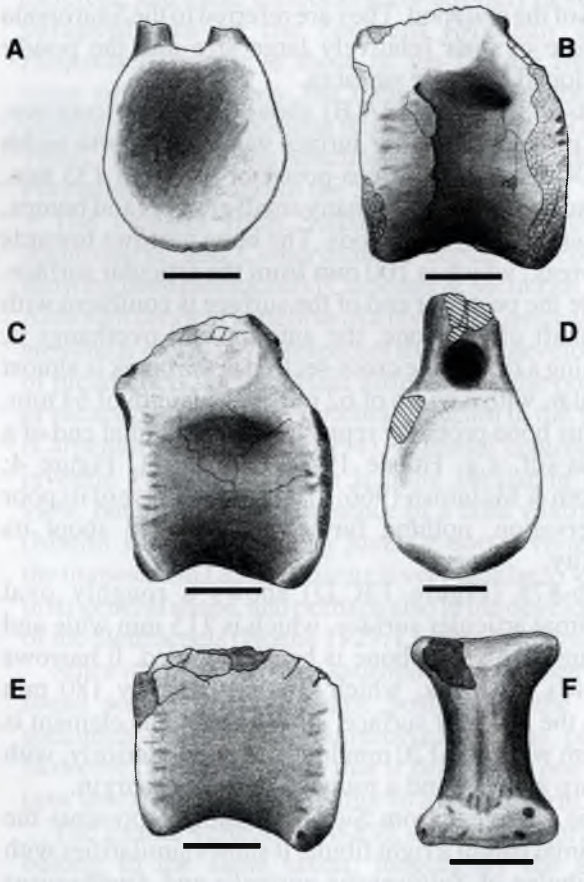

Figure 15. Carcharodontosauridae indet., Wadi Milk Formation. A, B: anterior caudal vertebra; Vb-607; A: anterior view, B: left lateral view. C, D: anterior caudal vertebra; Vb-717; C: left lateral view, D: posterior view. E, F: mid-caudal vertebra; Vb-870; E: left lateral view, F: ventral view. Scale bars indicate 5 cm.

Within well known theropods, the vertebrae from Sudan show greatest similarities to the caudal vertebrae of *Torvosaurus* and allosaurids (Gilmore 1920; Madsen 1976; Britt 1991). As in the elements from the Wadi Milk Formation, the caudals of *Allosaurus* show a ventral keel with a shallow longitudinal groove, a strong constriction at mid-centrum compared with the diameter of the intervertebral facets, an anterior facet which is slightly offset above the posterior one, and a very similar development of the chevron facets (Gilmore 1920; Madsen 1976). The main differences between the vertebrae from Sudan and those of *Allosaurus* is the presence of pleurocoels in the anterior caudal Vb-607.

Within non-coelurosaurian tetanurans, pleurocoelous anterior caudals are found only in carcharodontosaurids (Rauhut 1995; Sereno *et al.* 1996); therefore, the specimens from Sudan are referred to the Carcharodontosauridae. One caudal vertebra referred to *Bahariasaurus* by Stromer (1934: Tafel II, Figure 25) shows great similarity to the elements from the Wadi Milk Formation: the pleurocoels are placed within a lateral groove, which is very similar to that found in Vb-607 and Vb-717, the anterior intervertebral facet is offset above the posterior one, pleurocoels are restricted to the anterior caudals, and a shallow longitudinal groove on the ventral keel is present. However, the type of *Bahariasaurus* may not be diagnostic, and at least some of the elements referred to this genus by Stromer (1934) probably represent a distinct coelurosaurian theropod (Sereno *et al.* 1996; Sereno pers. comm. 1996). According to the pleurocoelous condition of the vertebra figured by Stromer (1934: Tafel II, Figure 25), at least this and the associated specimens (No. 1912 VIII 62; see Stromer 1934: p. 28) represent a carcharodontosaurid, maybe *Carcharodontosaurus*.

(?)Carcharodontosauridae indet.

Vertebra

Material: One caudal vertebra (Vb-871).

Description: This vertebra is the most complete specimen from the Wadi Milk Formation (Figure 16). It shows a part of the neural spine and the transverse processes. The vertebra is amphicoelous, relatively long and strongly constricted in its middle. The sides have collapsed, showing a very similar structure to that found in Vb-607. Only a very faint keel is present ventrally, and the longitudinal groove is slightly more prominent than in the elements described above. Well developed chevron facets are present. The anterior intervertebral facet is strongly offset above the posterior one.

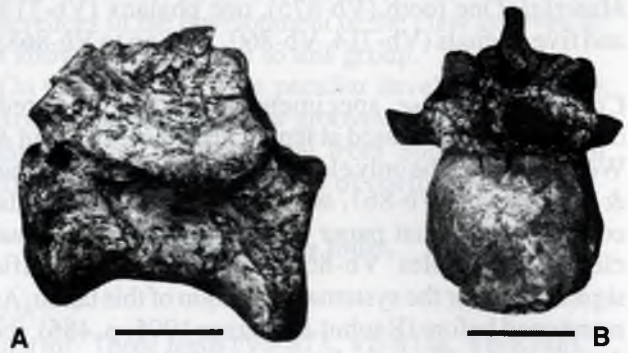

Figure 16. (?)Carcharodontosauridae indet., Wadi Milk Formation. Mid-caudal vertebra; Vb-871; A: left lateral view, B: anterior view. Scale bars indicate 5 cm.

The neural arch occupies the anterior four-fifths of the vertebral centrum. It is fused to the centrum without any visible suture. From the well developed transverse processes, which are located on the posterior half of the arch just above the centrum, a ridge runs to processes at the front end which point antero-dorsally. These processes obviously led to the prezygapophyses, which are broken away. According to the shape of the processes, the prezygapophyses were elongated. Above the transverse processes, the bone is strongly bent medially towards the neural spine. The neural spine extends over the complete length of the neural arch and is 68 mm high in its middle, both ends being extensively damaged. The neural canal is relatively large.

Discussion: This vertebra probably represents a mid-caudal between the 16th and 19th caudal, judging from comparison with *Allosaurus* (Madsen 1976).

Again, great similarities to the caudals of *Torvosaurus* and *Allosaurus* are noted (Gilmore 1920; Madsen 1976; Britt 1991). Differences are the more pronounced offset of the facets and the obvious presence of internal cavities in Vb-871.

Internal cavities and strongly offset facets are found in *Carcharodontosaurus* and a caudal vertebra originally referred to *Bahariasaurus* (Stromer 1931, 1934; see above). Since the shape of the internal cavities also seems to have been very similar to those in Vb-607, Vb-871 can be referred to the Carcharodontosauridae. The differences in the development of the ventral keel and the longitudinal groove, as well as the presence of internal cavities in a posterior mid-caudal indicate that Vb-871 represents a different taxon from the elements described above.

Limb bones

Material: Proximal end of a metatarsal (Vb-849) and a phalanx (Vb-718).

Description: Vb-849 represents the proximal part of a right metatarsal III with a fused distal tarsal III (Figure 17). The proximal end of Vb-849 is 140 mm long antero-posteriorly and 95 mm wide medio-laterally. The bone narrows towards the break, at which it shows an oval cross-section with a length of 85 mm and a width of approximately 51 mm.

The proximal articular surface forms a wide overhanging rim anteriorly, it narrows towards its middle and abruptly widens again posteriorly. The posterior end is offset medially and inclined at an angle of approximately 25° medio-posteriorly against the anterior one.

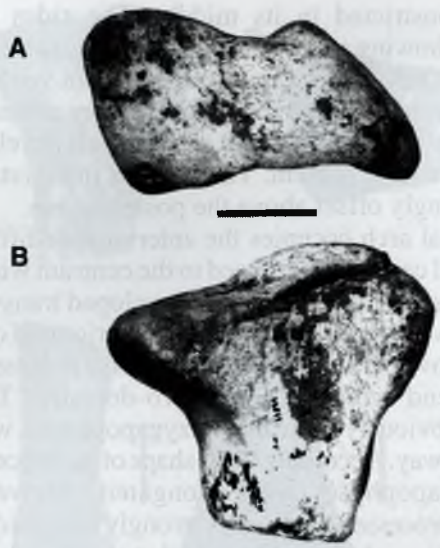

Figure 17. (?)Carcharodontosauridae indet., Wadi Milk Formation. Proximal end of right metatarsal III with attached distal tarsal III; Vb-849; A: proximal view, B: medial view. Scale bar indicates 5 cm.

The medial wall of the bone is more or less straight in its anterior part, but strongly concave posteriorly. The lateral side is more or less straight, with an almost rectangular bulge on its proximo-posterior part. Under the overhanging rim of the articular surface, the anterior side becomes convex transversly. A muscle scar is located directly above the break on this side.

The distal tarsal is heavily abraded, but seems to have been of approximately the same shape as the distal tarsal III of *Allosaurus* (Madsen 1976: Figure 25B,C).

Vb-718 is a well preserved stout pedal phalanx (Figure 18). Its broad proximal articular facet is strongly concave dorso-ventrally, but almost plain transversely. No median ridge is present. The distal articular facet forms a wide ginglymoidal arch which extends further proximally on its ventral side than dorsally. The dorso-ventrally well rounded facet is only slightly concave transversely. The collateral ligament fossae are very deep in the middle of the arch, shallow significantly in a dorso-proximal direction and end above the ventral proximal extension of the articular facet. On the dorsal side, a triangular groove is found proximal to the articular facet. The ventral side is almost plain. A wide area in front of the proximal articular facet is covered with small ridges and grooves, indicating the insertion of the flexor tendon. A similar structure is found to a lesser extent on the dorsal side in front of the proximal facet.

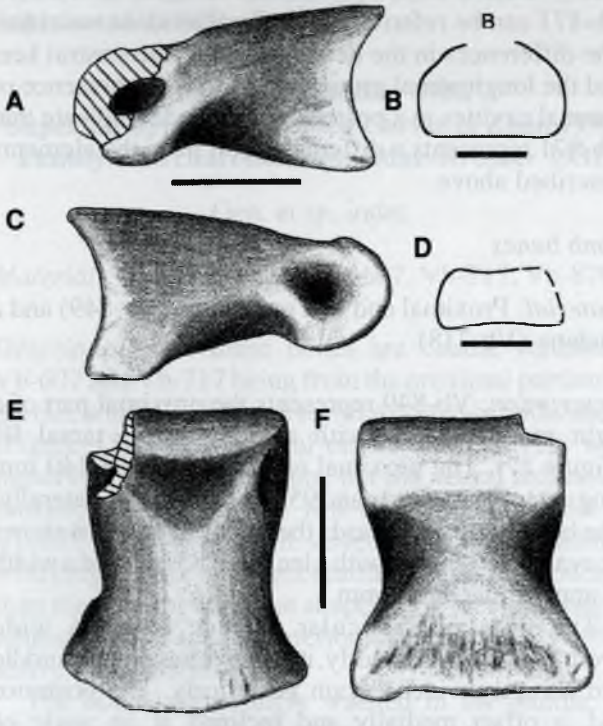

Figure 18. (?)Carcharodontosauridae indet., Wadi Milk Formation. Pedal phalanx; Vb-718; A: left lateral view, B: proximal outline, C: right lateral view, D: distal outline, E: dorsal view, F: ventral view. Scale bars indicate 5 cm.

Discussion: Specimen Vb-849 from the Wadi Milk Formation is very similar to the third metatarsals of *Torvosaurus*, *Sinraptor* and *Allosaurus* (Madsen 1976; Britt 1991; Currie & Zhao 1993). The closest similarity is found in *Sinraptor* (Currie & Zhao 1993: Figure 26B). Since *Sinraptor* and carcharodontosaurids both belong to the superfamily Allosauroidea, and carcharodontosaurids are probably the only large theropods present in the Wadi Milk Formation, Vb-849 is tentatively referred to this family.

The general morphology of phalanx Vb-718 is similar to that of many large theropods and ornithopods (Madsen 1976; Norman 1986; Currie & Zhao 1993). Significant differences to ornithopods are found in the development of the collateral ligament fossae (Taquet 1976; Norman 1986), so the element is referred to the Theropoda.

Within theropods, the pedal phalanges are very similar in widely differing taxa. However, since the only large theropods identified from the Wadi Milk Formation are carcharodontosaurids, Vb-718 is tentatively referred to this family. In comparison with *Allosaurus* and *Sinraptor*, it probably represents phalanx III-2 (Madsen 1976; Currie & Zhao 1993).

Coelurosauria Huene 1914
Family: Dromaeosauridae Matthew et Brown 1922
Subfamily: Velociraptorinae Barsbold 1983

Gen. et sp. indet.

Material: One tooth (Vb-875), one phalanx (Vb-713) and five unguals (Vb-714, Vb-860, Vb-866 to Vb-868).

Comments: These specimens have been figured, described and discussed at length elsewhere (Rauhut & Werner 1995). The only element not described in Rauhut & Werner was Vb-867, which was discovered in the collection after that paper was submitted. The ungual closely resembles Vb-868 and is of no specific significance for the systematic position of this taxon. As mentioned before (Rauhut & Werner 1995: p. 486), the dromaeosaurid from Sudan most probably represents a new genus and species, but the incomplete nature of the remains prohibits the proposal of a new name.

?Coelurosauria indet.

Material: A proximal part of an ungual (Vb-839).

Description: Vb-839 represents the distal portion of a manual ungual (Figure 19). The articular facet is more or less triangular in outline, with its greatest width ventrally. It is strongly concave in lateral view and does not show any medial ridge. The flexor tubercle is very strongly developed. Distal to the articular facet, the bone narrows significantly. On the dorsal margin, a small depression is situated between the articular facet and the claw blade. The claw grooves begin at the articular facet at about half the height of the specimen and run at a steep angle dorsally. They meet on the dorsal margin just 21 mm away from the proximal end. On the ventral side, a longitudinal groove is present, beginning in front of the flexor tubercle. It cannot be stated with certainty whether this groove represents an erosional feature or an original character of the claw. The width of the claw remains constant over its entire preserved length. The claw was obviously not very strongly curved.

Figure 19. ?Coelurosauria indet., Wadi Milk Formation. Manual ungual; Vb-839; A: left lateral view, B: proximal outline, C: ventral outline. Scale bars indicate 1 cm.

Discussion: The very striking flexor tubercle and the morphology of the articular facet indicate that Vb-839 represents a manual claw. A dorsal depression between articular facet and claw blade is a character found in many coelurosaurs (Rauhut & Werner 1995); therefore the claw is tentatively referred to the Coelurosauria. It differs significantly from dromaeosaurid manual unguals in the development of the flexor tubercle and the claw grooves, as well as in the degree of curvature (Ostrom 1969; Barsbold 1983) and can therefore not be attributed to the dromaeosaurid from the Wadi Milk Formation.

Within other coelurosaurs, the specimen from Sudan shows closest similarities to the manual unguals of oviraptorosaurs (Barsbold 1983), but significant differences in the development of the claw grooves do not allow an assignment to this group.

On the other hand, the peculiar development of the flexor tubercle and the claw grooves might represent an autapomorphy of the ungual from Sudan and might therefore indicate a new taxon of coelurosaurs.

Theropoda indet.

Teeth

Material: Three teeth (Vb-873, Vb-874a, Vb-874b).

Description and discussion: Theropod teeth are very rare in the Wadi Milk Formation. The tooth Vb-873 is the most complete specimen in the collection. The crown is 20 mm high and c. 9 mm long. It is strongly compressed laterally, but only slightly recurved. Both carinae show serrations. The denticle count is 3.5 denticles per mm on the mesial carina and 3 per mm on the distal one. The denticles are rounded or slightly inclined apically in the upper parts of the crown. Downward pointing grooves are found between the bases of the denticles. The antapical part of the mesial carina is damaged. The tooth enamel is smooth.

Downward pointing grooves at the bases of the denticles are found in *Allosaurus*, tyrannosaurids and *Carcharodontosaurus* (Stromer 1931; Currie *et al.* 1990; Rauhut & Kriwet 1994). Since the teeth of *Carcharodontosaurus* are also relatively straight (Stromer 1931), Vb-873 might represent a small or juvenile carcharodontosaurid.

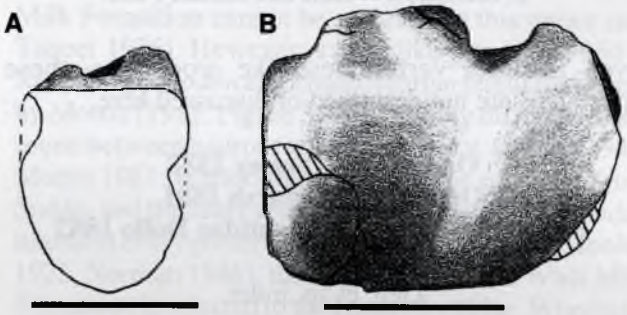

Figure 20. Theropoda indet., Wadi Milk Formation. Two fused sacral vertebrae; Vb-852; A: posterior view, B: right lateral view. Scale bars indicate 5 cm.

Vb-874a and Vb-874b are only apical parts of tooth crowns. The denticles are slightly inclined apically and at least Vb-874b seems to have been strongly recurved. The systematic position of these fragments is unsure. Some other tooth fragments are present, but they are too fragmentary for description.

Vertebrae

Material: Two fused sacral vertebrae (Vb-852).

Description: This specimen is badly damaged (Figure 20). The posterior intervertebral facet of the posterior vertebra is plain, the anterior centrum is broken at its front end. The ventral side is sharply keeled and straight in lateral view. No grooves or pleurocoels are present on the sides. The two centra are firmly fused, the suture forming a horizontal swelling on the sides. The neural arches are not preserved.

Discussion: The specimen shows strong similarities to the fused sacrals of a juvenile tyrannosaurid in the Museum of the Rockies, Bozeman (MOR 533E), and for that reason is referred to the Theropoda.

Indeterminate limb elements

Several isolated phalanges with theropod affinities were found in the Wadi Milk Formation. However, since similar elements are found in other dinosaurs and

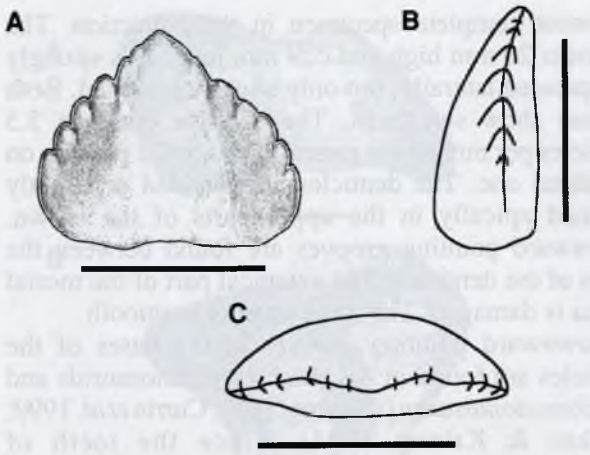

Figure 21. ?Hypsilophodontidae indet., Wadi Milk Formation. Tooth; Vb-936; A: lingual view, B: mesial view, C: occlusal view. Scale bars indicate 1 mm.

even in other vertebrates, like crocodiles, these specimens are not described or discussed here.

Ornithischia Seeley 1888
Ornithopoda Marsh 1881
Family: (?)Hypsilophodontidae Dollo 1882

Gen. et sp. indet.

Material: One tooth (Vb-936).

Description: Vb-936 is a leaf-shaped tooth crown with large marginal denticles (Figure 21). The specimen is very small, with a basal length of 1,43 mm, a basal width of 0,53 mm and a crown height of 1,17 mm. The crown is strongly compressed labio-lingually.

Four large denticles are present mesial to the well developed apical one; on the distal carina, the count is five. On both sides of the apex, two additional smaller denticles are present. Both carinae are slightly bent to the lingual side, making the labial side more convex than the lingual one. A constriction between crown and root is obviously present, but no basal cingulum can be recognized.

Discussion: The leaf-shaped crown and large denticles characterize the specimen from Sudan as an ornithischian tooth. Within ornithischians, very similar teeth are found in the most primitive members of this group ('fabrosaurids', e.g. *Lesothosaurus*) and hypsilophodontids (Galton 1983; Sereno 1991). Since no 'fabrosaurids' have been described from the Cretaceous to date, Vb-936 is tentatively referred to the Hypsilophodontidae. The lack of longitudinal ridges confluent with the marginal denticles, a character seen as a synapomorphy of hypsilophodontids by Weishampel & Heinrich (1992), might be due to the presumably early juvenile ontogenetic stage of the specimen, as has been suggested by Galton (1983).

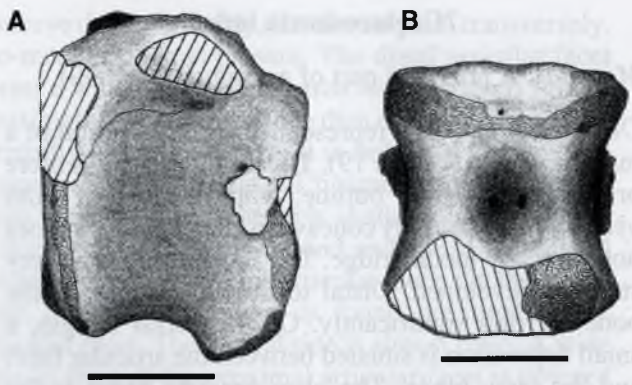

Figure 22. cf. *Oranosaurus* sp., Wadi Milk Formation. Anterior caudal vertebra; Vb-723; A: left lateral view, B: ventral view. Scale bars indicate 5 cm.

Iguanodontia Dollo 1882
Family: ?Iguanodontidae Gervais 1852
cf. *Ouranosaurus* sp. Taquet 1976

Material: Two caudal vertebrae (Vb-723, Vb-853).

Description: Both vertebrae are amphicoelous, with only shallow concavities on the intervertebral facets. While Vb-723 (Figure 22, 23A-C) is a vertebra from the anterior mid-caudal region, Vb-853 (Figure 23D) comes from the posterior portion of the tail.

In Vb-723, the intervertebral facets are sub-rectangular rather than round. The sides are almost plain dorso-ventrally and only weakly concave antero-posteriorly. On the ventral side, there is a deep longitudinal groove between two well developed lateral ridges. Within the groove are two small parallel pits. The well developed chevron facets are especially striking at the posterior end.

The rim of the neural canal and the attachment of the transverse processes are the only remaining parts of the neural arch preserved. The neural arch occupies almost the entire length of the centrum. The transverse processes were directed laterally and slightly posteriorly.

In Vb-853, the cross-section of the centrum is almost hexagonal, due to a weak ridge dividing the sides into two planes, the upper being slightly inclined dorsally, the lower one ventrally. Except for this feature, the sides are almost plain. The ventral side is also plain, showing only very weak indications of the lateral ridges. A single small pit is located in the middle. The neural arch, which originally occupied the entire length of the centrum, is broken away.

Discussion: The subrectangular shape of the vertebrae indicates that they are ornithischian elements. Within ornithischians, the greatest similarities are found in the caudal vertebrae of advanced ornithopods (Ankylopollexia in Sereno 1986; see e.g. Nopcsa 1925; Casamiquela 1964; Taquet 1976; Norman 1986). Caudal vertebrae of *Iguanodon* usually show a plain or slightly convex ventral surface (Hooley 1925; Norman 1986), although Owen (1851) figured a vertebra of this genus

with a ventral groove. This groove, however, is shallower than in Vb-723 and no small pits are present.

A ventral groove like that found in Vb-723 is present in *Ouranosaurus* and hadrosaurids (pers. obs.; see e.g. Nopcsa 1925; Taquet 1976). Since *Ouranosaurus* is found in the Cretaceous of Africa and the elements from Sudan are almost identical to caudal vertebrae of this taxon (pers. obs.; see Taquet 1976), the specimens are tentatively referred to this genus.

Whether *Ouranosaurus* is a representative of the family Iguanodontidae is disputed: while it is placed in this family by Norman (1990) and Norman & Weishampel (1990), Sereno (1986) considers it to be the sister group of hadrosaurids.

Iguanodontidae indet. (?*Iguanodon* sp.)

Material: Distal end of a femur (Vb-850).

Description: Vb-850 represents a heavily damaged distal end of a left femur (Figure 24). Only the posterior part of the medial condyle is well preserved, the anterior side is abraded and the lateral condyle broken. The transverse width of the articular surface is approximately 135 mm. The medial condyle is significantly wider than the lateral one. The postero-proximal extension of the articular surface exceeds the medial height of the condyle, giving the appearance of a cleft between the femoral shaft and the posterior part of the condyle. The distal part of the condyle is only slightly convex over most of its length, but is strongly bent proximally in its posterior part. A ridge runs down from the posterior part of the medial side of the femoral shaft to the bend and widens just above the articular surface.

The extensor groove was obviously relatively deep, as far as this can be judged from the heavily abraded anterior surface.

Discussion: VB-850 shows significant differences from theropod femora in the presence of a cleft between the shaft of the bone and the posterior extension of the medial condyle (e.g. Gilmore 1920; Osmólska *et al.* 1972; Madsen 1976; Ostrom 1976; Currie & Zhao 1993). Although a cleft like this is found in the femur of *Camarasaurus* (Ostrom & McIntosh 1966), significant differences in the general shape, and the shape of the distal outline between Vb-850 and sauropod femora, do not allow an assignment of the former element to the Sauropoda (Huene 1929; Janensch 1961; Ostrom & McIntosh 1966).

Within ornithischians, the femur fragment from Sudan differs from most taxa in the character of the cleft between femoral shaft and posterior extension of the articular surface. For example, this character is not found in *Ouranosaurus*, so the fragment from the Wadi Milk Formation cannot be assigned to this genus (see Taquet 1976). However, a cleft like that in Vb-850 is found in *Iguanodon* and a hadrosaurian femur illustrated by Morris (1981: Figure 3). Since many differences are found between hadrosaurian femora (e.g. Colbert 1948; Morris 1981; Wellnhofer 1994) and the specimen from Sudan, and the latter resembles the femur of *Iguanodon* in almost every preserved detail (see Dollo 1883, Hooley 1925, Norman 1986), the fragment from the Wadi Milk Formation is referred to the Iguanodontidae. Whether it represents the genus *Iguanodon* cannot be said; the presence of the closely related taxon *Lurdusaurus* in the Aptian of Niger (Tacquet & Russell 1999) raises the possibility that the latter taxon is also present in Sudan.

Ornithopoda indet.

Material: One caudal vertebra (Vb-854).

Description: Vb-854 is an amphicoelous distal caudal centrum (Figure 25). The shape of the intervertebral facets is oval to subrectangular. While the lateral sides are strongly convex dorso-ventrally, the ventral surface is almost plain. Chevron facets are only present at the posterior end and they are widely spaced. The neural arch, which originally occupied the anterior three fourths

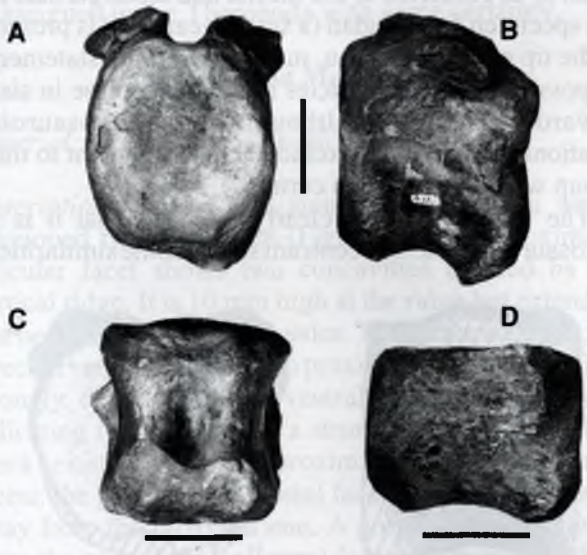

Figure 23. cf. *Ouranosaurus* sp., Wadi Milk Formation. A-C: anterior caudal vertebra; Vb-723; A: anterior view, B: left lateral view, C: ventral view. D: mid-caudal vertebra; Vb-853; left lateral view. Scale bars indicate 5 cm.

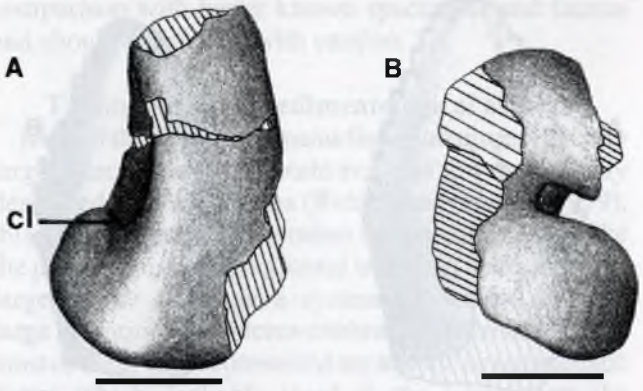

Figure 24. Iguanodontidae indet., Wadi Milk Formation. Distal end of a left femur; Vb-850; A: medial view, note the cleft (cl) between shaft and posterior extension of the condyle B: distal view. Scale bars indicate 5 cm.

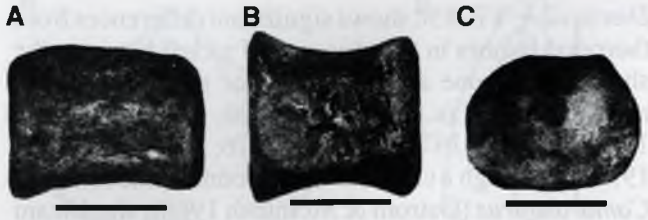

Figure 25. Ornithopoda indet., Wadi Milk Formation. Posterior mid-caudal vertebra; Vb-854; A: left lateral view, B: dorsal view, C: anterior view. Scale bars indicate 5 cm.

of the centrum, has been separated from it along its suture. Nothing can be said about the structure of this suture because of abrasion.

Discussion: The specimen closely resembles distal caudal vertebrae of *Prosaurolophus* (pers. obs.), and it is therefore referred to the Ornithopoda. Since similar vertebrae are found in *Iguanodon bernissartensis*, the element described above may belong to the same taxon as the femur fragment Vb-850.

Dinosauria indet.

Material: One tooth (Vb-722), a vertebra (Vb-855) and a distal end of a femur (Vb-851).

Description: Vb-722 is a leaf-shaped tooth crown with a strong constriction at its base (Figure 26). It is 3,6 mm high and 2,5 mm wide at its widest. It is almost circular in cross-section at its base. Apically the tooth is flattened labio-lingually and slightly bent to the lingual side. Thirteen large denticles are present on the mesial and at least twelve on the distal carina, the lower part of which is slightly damaged. The denticles are inclined apically and are largest in the middle of the carina. There, denticle spacing is 2,5 denticles per mm. Both carinae are slightly bent to the lingual side. On the lingual side are two shallow parallel grooves with a length of approximately 1,5 mm.

Vb-855 represents an amphicoelous caudal vertebra (Figure 27). The intervertebral facets are almost circular and the sides are strongly concave antero-posteriorly, but only moderately convex dorso-ventrally. The ventral surface shows two well developed chevron facets at the posterior end with a shallow groove between them. The neural arch, which originally occupied the anterior three fourths of the centrum, has been separated from it along its suture. Two well developed but broken transverse processes are present on the anterior part of the attachment of the neural arch.

Vb-851 is the poorly preserved distal end of a right femur (Figure 28). The articular surface is approximately 120 mm wide. The medial condyle is wider than the lateral. The articular surface is steeply inclined proximally in its anterior part. The extensor groove is shallow. The cross-section of the bone is subrectangular at the break.

Discussion: Werner (1994a) illustrated the tooth (Vb-722) and referred it to the Ornithopoda.

Large marginal denticles are found in ornithischians, primitive sauropodomorphs and therizinosauroids (e.g. Galton 1983, 1990a, b; Coombs & Maryanska 1990; Russell & Dong 1993). However, the teeth of ornithischians differ significantly in the shape of the crown (Galton 1983, 1990b; Sues & Galton 1987; Coombs & Maryanska 1990), making an ornithischian relationship for Vb-722 seem unlikely. Although the teeth of some prosauropods show a similar shape in combination with large marginal denticles, the fact that no prosauropods are known from sediments younger than the Early Jurassic (Galton 1990a) does not allow an assignment of the Sudan specimen to this group. In the therizinosauroid *Alxasaurus*, a similar tooth shape in combination with large marginal denticles is also found (Russell & Dong 1993). However, the denticles of Vb-722 seem significantly different from those on the teeth of *Alxasaurus*, which do not become significantly smaller towards the apex and even cover the tip in the Mongolian taxon (Russell & Dong 1993), while they seem to be restricted to the mesial and distal carinae in the specimen from Sudan (a small wear facet is present at the tip of this specimen, making a definite statement impossible, but the denticles strongly decrease in size towards the apex). Although a therizinosauroid relationship cannot be excluded, an assignment to this group would be far from certain.

The size of Vb-855 clearly indicates that it is a dinosaur vertebra. The centrum shows some similarities

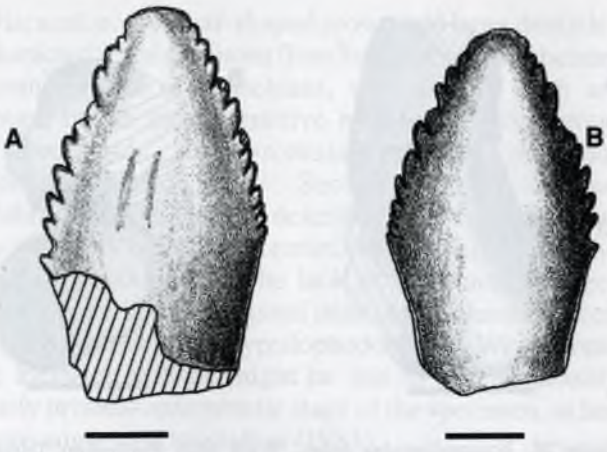

Figure 26. Dinosauria indet., Wadi Milk Formation. Tooth; Vb-722; A: lingual view, slightly rotated mesially, B: labial view. Scale bars indicate 1 mm.

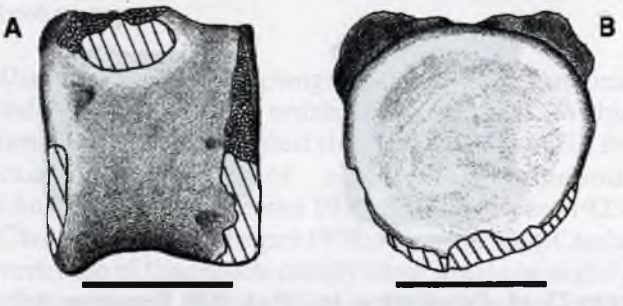

Figure 27. Dinosauria indet. (?Sauropoda), Wadi Milk Formation. Mid-caudal vertebra; Vb-855; A: left lateral view, B: anterior view. Scale bars indicate 5 cm.

Figure 28. Dinosauria indet., Wadi Milk Formation. Distal end of right femur; Vb-851; A: medial view, B: distal view. Scale bars indicate 5 cm.

to caudal vertebrae of brachiosaurids in respect of its general shape (Janensch 1950), therefore it might represent a further taxon of sauropod. However, since there are differences in the attachment of the transverse processes, no assignment of the element is proposed here.

The femur fragment Vb-851 resembles theropod femora in its general shape, but no femur with a similar steep angulation of the articular surface has been observed by the author; therefore, the specimen is assigned for the time being to Dinosauria indet.

Dinosaur remains from the Shendi Formation

Only few of the bones found in the Shendi Formation may be referable to dinosaurs. They are exclusively isolated phalanges. These elements show a proximal articular facet with a medial vertical ridge and a well developed ginglymoidal distal articular facet. Since similar elements are also found in other groups of vertebrates, these specimens are not described or discussed in detail here. Only one of the phalanges can be assigned to the Theropoda with some certainty.

(?)Theropoda Marsh 1881

Material: One phalanx (Vb-861).

Description: Vb-861 is a stout phalanx with a well developed flexor tubercle (Figure 29). The proximal articular facet shows two concavities divided by a vertical ridge. It is 10 mm high at the ridge but extends to a height of 15 mm at the sides. The flexor tubercle is directed ventrally rather than proximally. It is extremely strongly developed. The ventral part is roughened, indicating the insertion of a strong flexor tendon. No 'neck' exists between the proximal and distal articular facets: the ginglymoidal distal facet begins only 5 mm away from the proximal one. A prominent ridge runs from the end of the collateral ligament fossae to the widest part of the proximal facet. While the bone is wide below this ridge, it narrows dorsally. The collateral ligament fossae are L-shaped and situated ventral to the midline rather than dorsal. The distal articular facet is

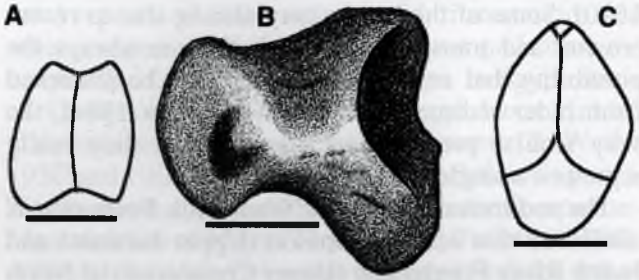

Figure 29. (?)Theropoda indet., Shendi Formation. Pedal phalanx; Vb-861; left lateral view, with distal (left) and proximal (right) outlines. Scale bars indicate 1 cm.

deeply grooved. In front of the facet, a shallow triangular groove is present on the dorsal side. Two small foramina are located within this groove.

Discussion: The strongly developed flexor tubercle indicates that the phalanx described above did not touch the ground during walking. It seems to be well adapted for rapid and/or strong flexion of the digit. Although it cannot be excluded that it represents a manual phalanx of a theropod, its morphology is more consistent with pedal phalanges.

Pedal phalanges showing a strongly developed flexor tubercle in combination with a stout shape are found in troodontids (Osmólska 1987; Osmólska & Barsbold 1990). However, since there are significant differences in the direction of the tubercle and the development of the collateral ligament fossae, the specimen from Sudan is not referred to the Troodontidae here.

In summary, Vb-861 can only be seen as an element of an undetermined small theropod with possible troodontid affinities. It should be noted that a very similar but less well preserved element is also present in the material from the Wadi Milk Formation (Vb-859, not figured).

TAPHONOMY AND PALAEOECOLOGY

The reconstruction of the palaeoecology of the Sudan dinosaurs is difficult, because of the poor preservation of the specimens and the limited data on taphonomy. Therefore, the ideas presented here are mainly based on comparison with better known specimens and faunas and should be viewed with caution.

Taphonomic and sedimentological aspects

Most of the dinosaur remains from Sudan are relatively large. Since small vertebrate remains are more easily destroyed than larger ones (Behrensmeyer *et al.* 1979), this does not necessarily mean that small animals like the probable hypsilophodontid were less abundant than larger ones. Although a systematic search revealed large quantities of microvertebrates (Werner 1994a), most of the groups represented are aquatic or semiaquatic forms which probably lived in the lake where the sediments were deposited, while the dinosaur remains were washed in. The latter conclusion is supported by the signs of abrasion on almost all of the bones, indicating subaerial exposure over some time (Behrensmeyer

1990). Some of the breaks may also be due to recent erosion and transport. Although there is always the possibility that some of the bones may be reworked from older sediments (see Behrensmeyer 1984), the very similar preservation suggests that they really represent a single fauna.

The sedimentology of the Wadi Milk Formation is similar to that of the Morrison (Upper Jurassic) and Judith River Formations (Upper Cretaceous) of North America (Dodson 1971; Dodson *et al.* 1980; Bussert 1993a,b). In all cases, the sediments are dominated by fluvio-lacustrine deposits, showing rapid lateral changes. The climate was warm and there were seasonal changes in the water supply. Since the dinosaur faunas of the Morrison and Judith River Formations are among the best known in the world, and given the similarities in the sedimentology, the taphonomic and palaeoecological data from the North American Formations may be used for comparison with the Wadi Milk Formation.

Differences between the Morrison and Judith River Formations are found in the taphonomy of the dinosaurs: while single articulated or disarticulated skeletons are often found in the Judith River Formation (Dodson 1971), dinosaur localities in the Morrison Formation are characterized by a multispecific assemblage of disarticulated bones (Dodson *et al.* 1980). In comparison, the dinosaur locality from the Wadi Milk Formation is clearly of the Morrison type. Similarities to Morrison dinosaur faunas are also found in the combination of taxa (at higher taxonomic levels): sauropods are most abundant, followed by theropods, and ornithopods are rare. While the relative rarity of theropods might reflect lower population densities compared with the sauropods, the ornithopods possibly lived in a more distal environment (see Dodson *et al.* 1980). Differences between the Morrison and Wadi Milk Formations are found in the higher abundance of aquatic and semiaquatic vertebrates in the latter (Dodson *et al.* 1980; Werner 1994a). This implies a more steady water supply in the Sudanese formation, as is also indicated by palynological and sedimentological data (Schrank 1990; Bussert 1993b). Another difference is the presence of articulated skeletons in the Morrison Formation, as in Dinosaur National Monument, Utah, USA, although this may be more apparent than real and may be due to the different states of research carried out in the wo formations.

In summary, the similarities between the Morrison and Wadi Milk Formations indicate similar, rather uniform landscapes with abundant sauropods, less abundant theropods and rare ornithopods.

Biological aspects

Titanosaurids and dicraeosaurids posess a relatively short neck in comparison with most other sauropods (McIntosh 1990). While feeding in high tree crowns, as suggested by Bakker (1978), seems quite plausible for the giraffe-like brachiosaurids, the shorter neck of titanosaurids may imply that these animals preferred plants growing at moderate heights.

According to Bakker (1978), large iguanodonts probably fed on low growing vegetation. If this was also the case in the iguanodonts from Sudan, they might have lived sympatrically with the sauropods. However, as mentioned above, their rarity implies a more distant habitat.

Hypsilophodontids probably fed on different plants than the larger herbivores. A diet of fruits and seeds might have been suitable for them, and therefore they might well have lived sympatrically with the sauropods, or the iguanodonts, or both.

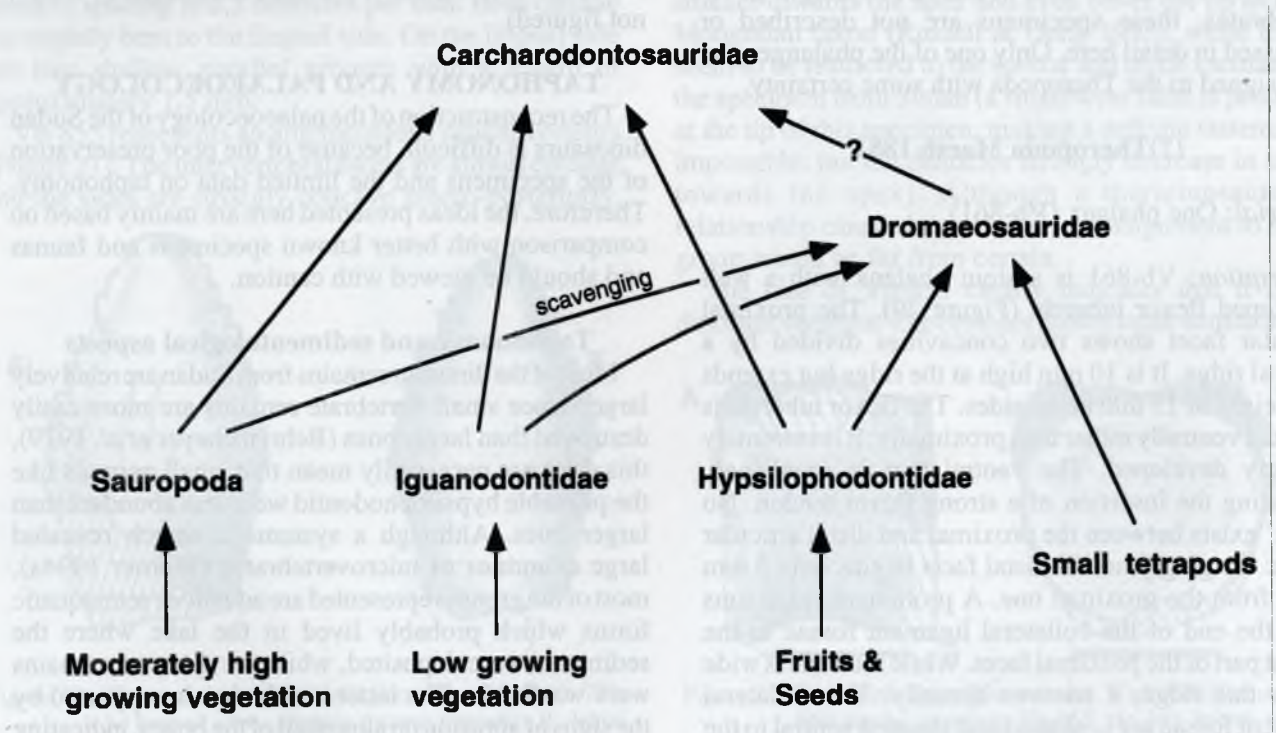

Figure 30. Hypothetical food-chain for the dinosaurs from Sudan. Arrows indicate the direction of energy flow.

Ostrom (1969, 1970) made a strong argument for pack-hunting in the velociraptorine dromaeosaurid *Deinonychus*. If this behaviour also occured in the dromaeosaurid from the Wadi Milk Formation, this taxon might not only have fed on small tetrapods, like the amphibians or lizards, or the hypsilophodontids, but also on the iguanodonts. The sauropods, however, seem to be too large to be killed even by a pack of the rather small dromaeosaurids, although scavenging might well have occurred.

The very large carcharodontosaurids were probably able to bring down any prey. Even if the iguanodonts and sauropods lived in different habitats, the presumed high activity of theropods (Molnar & Farlow 1990) would have allowed them to feed on both.

A hypothetical food chain for the Sudanese dinosaurs is presented in figure 30.

CRETACEOUS DINOSAUR FAUNAS FROM AFRICA

Little is known about African dinosaurs from the early stages of the Early Cretaceous. In the earliest Cretaceous of the Kirkwood Formation in South Africa, remains of stegosaurs, dryosaurids, camarasaurids, brachiosaurids and teeth of titanosaurids and undetermined theropods are found (Rich *et al.* 1983; Forster *et al.* 1995; Forster pers. comm. 1995). In the ?Barremian of Niger, the tetanuran theropod *Afrovenator* and a sauropod with camarasaurid affinities are present (Sereno *et al.* 1994; Sereno & Wilson pers. comm. 1995). The probably latest occurrence of stegosaurids in Africa is in the Early Cretaceous (?Aptian; Mateer *et al.* 1992) of Malawi (Jacobs *et al.* 1990). In the same locality, the primitive titanosaurid *Malawisaurus* and undetermined theropod teeth were found (Jacobs *et al.* 1990, 1993, 1996).

Several dinosaur localities are known from the Aptian and Albian (see Weishampel 1990). Remains of carcharodontosaurids, small theropods (*'Elaphrosaurus' iguidiensis*), the diplodocoid sauropod *Rebbachisaurus*, and iguanodontids are quite abundant, and spinosaurids, brachiosaurids, titanosaurids, dryosaurids, and nodosaurids have also been reported (Lavocat 1954; Lapparent 1960; Bassoulet & Iliou 1967; Taquet 1976, 1984; Schlüter & Schwarzhans 1978; Galton & Taquet 1982; Bouaziz *et al.* 1988; Jacobs *et al.* 1988; Buffetaut 1989; Weishampel 1990; Russell 1996; Sereno *et al.*, 1998; Tacquet & Russell 1999).

Dinosaurs from the early Late Cretaceous of Africa include carcharodontosaurids, spinosaurids, coelurosaurs, including dromaeosaurids, other small theropods (cf. *Elaphrosaurus*; Stromer 1934), titanosaurids, dicraeosaurids, a possible hypsilophodontid, and iguanodontids (Stromer 1915, 1931, 1932, 1934, 1936; Werner 1994a; Rauhut & Werner 1995; Sereno *et al.* 1996; this article). Only very few localities are known from the higher parts of the Late Cretaceous. In the early Senonian of Niger, remains of carcharodontosaurids and titanosaurids were found (Broin *et al.* 1974), and Harris & Russell (unpublished data) report a probable spinosaurid, titanosaurids and other undetermined theropods and sauropods from the unspecified Late Cretaceous of Kenya. In Egypt, strata of Campanian to Maastrichtian age have yielded undetermined theropod remains (Stromer & Weiler 1930) and a titanosaurid sauropod (Wiechmann in prep.). Titanosaurids might have been present in the Campanian-Maastrichtian of Niger (Taquet 1976; Buffetaut 1988). Although western Africa was separated from the rest of the continent by shallow epicontinental seaways several times during the Late Cretaceous, there was probably not much endemism, since land bridges between those two landmasses often existed (Reyment & Dingle 1987). Whether the dinosaur fauna from the Campanian of Madagascar can be regarded as a Late Cretaceous African dinosaur fauna is doubted, since this island might have been isolated during Late Cretaceous times (Besse & Courtillot 1988). Therefore the finds from Madagascar are not taken into consideration here.

In summary, dinosaur faunas from the middle to Late Cretaceous of Africa are probably characterized by the presence of carcharodontosaurids, spinosaurids, titanosaurids, diplodocoids (dicraeosaurs) and possibly iguanodontian ornithopods. Most of these groups probably represent the biological inheritance from Jurassic times.

ACKNOWLEDGEMENTS

This paper is a translated, greatly shortened, and modified version of a diploma thesis at the Free University of Berlin. Special thanks are due to Dr. Bernard Krebs, Berlin, who supervised this work, and to Dr. Christa Werner, Berlin, who allowed me to study the specimens described in this paper and who was always helpful.

The members of the vertebrate working group at the Free University of Berlin, especially Dr. Thomas Martin, Andrea Weigert, Uwe Gloy and Jürgen Kriwet, are thanked for many discussions and critical comments. I also thank Jens Zinke, Berlin, for his help during a trip visiting several museums in the USA in 1992.

I am especially indebted to Dr. Eric Buffetaut, Paris, Dr. Thomas Martin, Berlin, Dr. Ralph E. Molnar, Brisbane, and Dr. Christa Werner, Berlin, and an anonymous reviewer for critical comments on the manuscript.

Many experts helped with the rough identification of the bones described here; I am grateful to all of them, especially Dr. Eric Buffetaut, Paris, and Dr. Peter Dodson, Philadelphia.

For help during visits to several museums and research institutions, I would like to thank Dr. Wolf-Dieter Heinrich, Berlin, Dr. John Horner, Ellen Lamm, Rod Scheetz and Patrick Leiggy, all Bozeman, Dr. John Ostrom, New Haven, Dr. Paul Sereno, Chicago, Dr. Philippe Taquet, Paris, Dr. David Varricchio, Choteau, and Dr. Peter Wellnhofer, Munich. Dr. James Farlow, Fort Wayne, is thanked for sending me unpublished manuscripts and unpublished data on dinosaurs. Dr. José Bonaparte, Buenos Aires, also provided unpublished manuscripts and helped with useful comments.

Thanks are also due to Ellen Drescher, Berlin, who prepared many of the specimens described here, and to Dr. Rolf Kohring, Berlin, who helped solve computer problems.

I would also like to thank my parents for their steady encouragement and especially my father, Dr. Burkhard Rauhut, Aachen, for correcting the German manuscript.

Last, but not least, I thank Dr. Rosemarie Baron-Szabo, Berlin, who encouraged me during the work and often discussed general palaeontological and geological problems with me.

I am now supported by the EC under TMR grant ERBFMBICT 961013, which is gratefully acknowledged.

The field trips to Sudan were supported by the DFG under grant Kr 477/11 "Sudan-Wirbeltiere".

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APPENDIX

Measurements of the dinosaur specimens from Sudan. Vertebral measurements refer to the vertebral centra. All measurements are given in mm.

Dicraeosauridae gen. et sp. indet.:
Vertebrae:

No.	Length	Height	Anterior width	Posterior width
Vb-856	106	89	90+	96
Vb-857	128	110	113+	113+
Vb-892	101	126	146	114

Titanosauridae gen. et sp. indet.:
Teeth:

No.	Crown height	Basal length	Basal width
Vb-721	29	9.5	9
Vb-900	23	7	6.9
Vb-901	17.5	5.1	4.9
Vb-901	10	3.4	3
Vb-903	15.7	5.3	4.6
Vb-907	15.5	7.3	5.7
Vb-910	17.8	7.1	6.1
Vb-911	6.7	2.1	1.9

Vertebrae:

No.	Length	Height	Anterior width	Posterior width
Vb-606	92	44	49	46
Vb-720	249	174	210+	192
Vb-876	172	176	150++	146+
Vb-880	149	133	161	154
Vb-882	176	139	125+	106
Vb-883	135	108+	133+	151
Vb-885	188	84	112+	131
Vb-886	62+	24+	33+	29+
Vb-889	77+	50	47+	41
Vb-891	139	135+	148+	141
Vb-893	-	109+	96	-
Vb-894	67	27	22	21
Vb-897	118	113	113+	106
Vb-899	162	121	135	127

Sauropoda indet:
Vertebrae:

No.	Length	Height	Anterior width	Posterior width
Vb-719	31	21	24	25+
Vb-895	-	33	34+	-
Vb-896	87	58	55	55

Carcharodontosauridae:
Vertebrae:

No.	Length	Height	Anterior width	Posterior width
Vb-607	137	148	131	127
Vb-717	136	129	c. 120	110
Vb-870	130	105	90	87
Vb-871	136	79	76	83

Phalanx:

No.	Length	Proximal height	Proximal width	Distal height	Distal width
Vb-718	105	60	94	42	78

cf. *Ouranosaurus* sp.:
Vertebrae:

No.	Length	Height	Anterior width	Posterior width
Vb-723	96	112	94	90
Vb-853	99	78+	69	70

Ornithopoda indet.:
Vertebra:

No.	Length	Height	Anterior width	Posterior width
Vb-854	88	67	86	83

Dinosauria indet.:
Vertebra:

No.	Length	Height	Anterior width	Posterior width
Vb-855	72	88	87	85

Palaeont. afr., **35**, 85-110 (1999)

MID-CRETACEOUS (CENOMANIAN) SNAKES FROM WADI ABU HASHIM, SUDAN: THE EARLIEST SNAKE ASSEMBLAGE

by

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ABSTRACT

The Cenomanian (mid-Cretaceous) beds at Wadi Abu Hashim (Sudan) have yielded a snake assemblage that is very rich and diverse for its geological age. It is by far the oldest known snake fauna. As the assignment of the hitherto earliest presumed snake (Barremian) to the Serpentes may now be questioned, this diverse fauna is only slightly younger than the earliest certain appearance of snakes (late Albian). The fauna is a surprising mixture of very primitive and comparatively advanced snakes. It includes two forms belonging to the lapparentophiid-grade of snakes ('lapparentophiid-grade snake A' and 'lapparentophiid-grade snake B'), an indeterminate Madtsoiidae, a possible Palaeophiidae, the aniliid *Coniophis dabiebus* sp. nov., *Coniophis* cf. *C. dabiebus*, the nigerophiid *Nubianophis afaahus* gen. et sp. nov., *Nubianophis* cf. *N. afaahus*, the russellophiid *Krebsophis thobanus* gen. et sp. nov., a Colubroidea *incertae sedis* (indeterminate family), and two indeterminate snakes. In sum, at least nine species, perhaps twelve, are present. They represent at least seven families: at least one family of lapparentophiid-grade (?Lapparentophiidae), Madtsoiidae, ?Palaeophiidae, Aniliidae, Nigerophiidae, Russellophiidae, and an indeterminate colubroid family.

The presence of colubroid snakes (Russellophiidae and an indeterminate family) as early as the mid-Cretaceous is especially unexpected. It may be inferred from phylogenies that the higher taxa of snakes (Anilioidea, Booidea, Acrochordoidea, Colubroidea, and obviously Scolecophidia) were already present during mid-Cretaceous times. The diversity of this fauna, coupled with the presence of advanced forms (colubroids), suggest that the origin of snakes markedly antedates the Cenomanian. Africa played an important role in the early radiation and, probably, in the origin of snakes.

KEYWORDS: Cenomanian, earliest radiation, snakes, Sudan.

INTRODUCTION

Snakes were not very diverse during the early and middle parts of the Cretaceous. But this period is very important in the evolutionary history of snakes: 1) the earliest snake, whatever it may be, is expected from this period of time, and 2) the Cenomanian appears as the first phase of radiation of snakes.

The hitherto earliest presumed snake (an unnamed form) was reported from the Early Cretaceous (Barremian) of Spain (Rage & Richter 1994), but new data on mid-Cretaceous varanoid squamates cast doubt on the referral of this fossil to snakes. The Late Albian of Algeria yielded two or three snakes: two unnamed fossils and perhaps *Lapparentophis defrennei* (the geological age of the latter is not definitively settled) (Cuny *et al.* 1990). Cenomanian beds have hitherto produced several snakes: *Lapparentophis defrennei* from Algeria, if it is not of Late Albian age, *Pouitella pervetus* from France (Rage 1988a), *Pachyrhachis problematicus* (= *Estesius colberti*) from the Middle East (Caldwell & Lee 1997), *Simoliophis* (*S. rochebrunei* from France and Portugal and *Simoliophis* sp. from Egypt; Rage 1984), and several unnamed snakes (seven taxa according to Werner & Rage 1994) from Sudan. Moreover, the Cenomanian has produced some snake-like squamates whose relationships are unknown: *Pachyophis woodwardi* and *Mesophis nopcsai*, both from former Bosnia-Hercegovina, remain poorly known.

In this paper we describe in detail the snakes from the Cenomanian (mid-Cretaceous) of Sudan. Werner & Rage (1994) briefly reported on this fauna in a preliminary paper. At that time, seven unnamed species (from six families) were recognized. The present detailed study has shown that in fact at least nine species are present, representing at least seven families. In other words, this Sudanese fauna is the earliest diverse fauna of snakes known and it is the only diverse snake fauna from the Cretaceous; therefore it represents a very important landmark in the early history of snakes.

GEOLOGICAL, STRATIGRAPHIC AND PALAEONTOLOGICAL CONTEXT

The fossils are derived from the Wadi Milk Formation, which is widely distributed in northern Sudan. The Wadi Milk Formation is subdivided into two members: the Wadi Abu Hashim Member at the base and the Jebel Abu Tuweiqiya Member at the top (Bussert 1998). The Jebel Abu Tuweiqiya Member represents sand-dominated braided to meandering river sediments. The Wadi Abu Hashim Member, although prevailing in

subsurface, is exposed exclusively at the plateau-like rim of the source area of the Wadi Abu Hashim, nearly 200 km northwest of Khartoum (Figure 1). It is characterised by very fine-grained sandstone, siltstone and claystone showing such sedimentary features as horizontal- or ripple lamination, calcretes and mottling (Bussert 1993). The depositional environment is interpreted as shallow playa lakes on flood plains near suspended-load meandering rivers (Bussert 1998). The outcropping horizons of the Wadi Abu Hashim Member are 15 m thick, at which a smectite-rich siltstone produces isolated vertebrate remains in abundance.

The age of the Wadi Milk Formation was formerly considered as ranging from Albian to Cenomanian (Schrank & Awad 1990; Schrank 1990; Wycisk 1991). New lithological and biostratigraphic correlation of the surface and subsurface data of the Dongola, Wadi Muqaddam (Schrank 1990) and Khartoum region (Awad 1994) suggests an Albian to Cenomanian age for the Wadi Abu Hashim Member and a Turonian to Santonian age for the Jebel Abu Tuweiqiya Member (Bussert 1998). The presence of the shark *Asteracanthus aegyptiacus* and the lungfish *Protopterus protopteroides*, *Ceratodus humei* and *Ceratodus tuberculatus*, all known from the Cenomanian Bahariya Formation of Egypt, strongly favours a Cenomanian age for the outcropping part of the Wadi Abu Hashim Member (Werner 1994a; Gloy 1997).

Except for one hand-sized leaf of an aquatic plant, all fossils found in the Wadi Abu Hashim Member are isolated vertebrate remains. No articulated skeletons were observed in the field.

The Cenomanian fish fauna of Sudan is highly diverse. Apart from rare elasmobranchs (e.g. one tooth of a new batoid and a few fragments of the freshwater shark *Asteracanthus aegyptiacus*), indeterminable ichthyoliths and most probably teleostean teeth and vertebrae clearly predominate (Werner 1994a). A characiform, osteoglossids and lepisosteids have been recognized (Werner 1994a). Ranging among the oldest records of polypterids, the fourteen polypterid species of the Wadi Abu Hashim Member show an extraordinary diversity (Werner & Gayet 1997; Gayet *et al.* 1997 a,b). As mentioned above, lungfish are represented in the

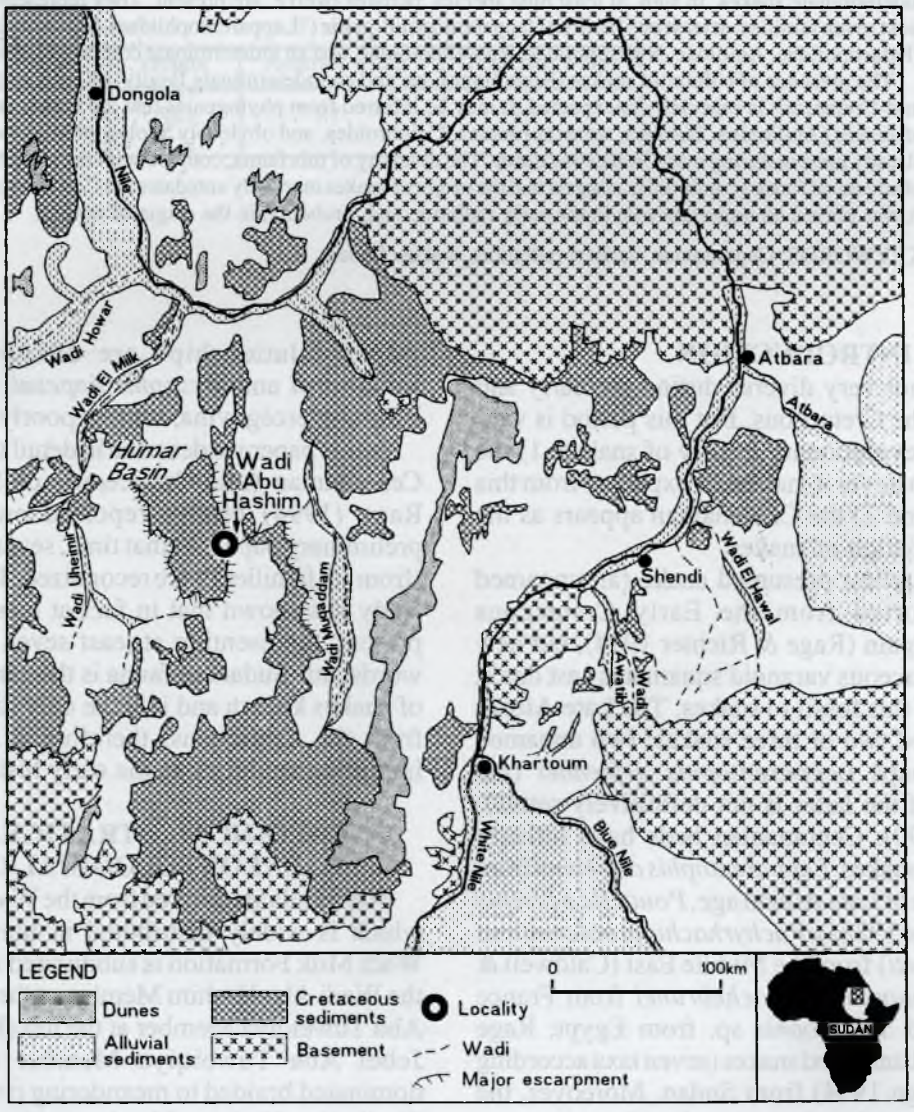


Figure 1. Map of a portion of northern Sudan showing the location of the fossiliferous site.

Cenomanian of Sudan by *Protopterus protopteroides*, *Ceratodus humei*, *Ceratodus tuberculatus*, and a new species of *Protopterus* not yet named (Gloy 1997).

The presence of all three lissamphibian groups in one Cretaceous locality has not previously been reported, but in the Wadi Abu Hashim Member frogs, gymnophionans (Werner 1994 a,b), and salamanders (Evans *et al.* 1996) have been found. Turtle and crocodile remains occur in abundance and have yet to be studied in detail; both groups include three taxa (Werner 1994a). The extraordinary diversity of the dinosaur assemblage is reflected by the occurrence of nine taxa: two titanosaurs, an undefinable other sauropod, two charcharodontosaurs, a questionable hypsilophodontid, *Ouranosaurus*, another indeterminable iguanodontid, and a dromaeosaurid theropod (Rauhut 1999, this volume; Rauhut & Werner 1995). Apart from the snakes studied in this paper, squamates are also represented by several lacertilian osteoscutes.

At present, the disarticulated vertebrate fragments of the Cenomanian Wadi Abu Hashim Member of Sudan, which comprise numerous fish and tetrapod taxa, represent one of the most diverse vertebrate faunas known up to now from Africa.

MATERIALS AND METHODS

A minor proportion of the fossils studied was collected by systematically scanning the weathered surfaces of the vertebrate-bearing layers. In addition, more than seven tons of sediment were collected and screen-washed as already described in detail (Werner 1994a). Inspection of the washing residue yielded the bulk of the snake material.

The terminology for snake vertebral morphology used here is that of Auffenberg (1963) as modified by Gasc (1974), and Rage (1984). The snake material described here is curated at the fossil collection of the Technical University of Berlin - Special Research Project 69 (TUB-SFB69) and bears the following catalogue numbers Vb-662 to Vb-690, Vb-709, Vb-1041 to Vb-1061.

SYSTEMATIC ACCOUNT

According to most recent classifications, living snakes are divided into two groups: the Scolecophidia and Alethinophidia. Nopcsa (1923) erected a third group, the Cholophidia, for old snakes, i.e. the Simoliophiidae. He regarded the Cholophidia as the stem group of both Scolecophidia and Alethinophidia. Other fossil snakes corresponding to an ante-Scolecophidia/Alethinophidia grade are now known (Rage & Prasad 1992; Caldwell & Lee 1997).

There are no scolecophidians at Wadi Abu Hashim. These snakes are generally small and their bones are brittle, and they are very rare in the fossil record. Some of the snakes recovered at Wadi Abu Hashim are perhaps more primitive than the scolecophidians and alethinophidians. Snakes of lapparentophiid grade (i.e. Lapparentophiidae) and the Madtsoiidae were considered as Alethinophidia by Rage (1984, 1987), but such a referral may be questioned today. The recovery of a skull and various skull bones belonging to the Madtsoiidae (Barrie 1990; Scanlon 1996) has shown that this family corresponds to an old lineage (Scanlon 1994, 1996). Madtsoiids have been considered alethinophidians, but this is now being challenged. McDowell (1987) suggested that the Madtsoiidae belong to an ante-Scolecophidia/Alethinophidia radiation. The snakes of lapparentophiid grade are still very poorly known; their relationships cannot be established. However, as they are more primitive than the Madtsoiidae, they might belong to a group more primitive than the Scolecophidia and Alethinophidia. The other taxa found at Wadi Abu Hashim belong to the Alethinophidia.

Lapparentophiid-grade snakes

The Lapparentophiidae are rare mid-Cretaceous snakes known only from isolated vertebrae. The family includes *Lapparentophis defrennei* from the Late Albian or Cenomanian of Algeria (Cuny *et al.* 1990). *Pouitella pervetus* from the Cenomanian of France has been provisionally allocated to this family (Rage 1988a). A possible lapparentophiid from the Late Albian of Algeria was described but not named (Cuny *et al.* 1990). *Simoliophis* (only one valid species named: *S. sauvagei*), which is referred to its own family (Simoliophiidae), is rather frequent in the marine deposits of the Cenomanian. It was regarded as closely related to the Lapparentophiidae (Hoffstetter 1959; Rage 1984); but new material leads to questions about such relationships (Rage, in progress).

The vertebrae of these lapparentophiid-grade snakes are primarily characterized by primitive features, which, coupled with the nature of the fossils, makes it difficult to establish both their interrelationships and relationships with other snakes. These fossils apparently represent a primitive level of evolution within snakes. Two vertebrae from Wadi Abu Hashim represent this level of snake evolution. They probably belong to two distinct taxa.

Lapparentophiid-grade snake A (genus and species new, unnamed)
(Figure 2)

Referred material: one trunk vertebra (Vb-671).

Description.

The vertebra is probably from the mid-trunk region; it lacks the posterior part of the neural arch on the left side, the top of the neural spine, and various salient parts are more or less eroded.

Measurements: length of centrum from cotylar rim to tip of condyle, 6.6 mm; width of interzygapophyseal constriction, 6 mm; width through articular facets of prezygapophyses, 9.4 mm; width of zygosphene, 4.2 mm.

Anterior view: The vertebra is not depressed, nor clearly wide. The articular facets of the prezygapophyses are inclined above the horizontal. The prezygapophyses do not strongly project laterally. Although the lateral tip of both prezygapophyses is damaged, the right side is sufficiently preserved to show that there was no projection which might be considered a prezygapophyseal (or 'accessory') process. This is clearly demonstrated by the regular curvature of the ventro-lateral surface of the right prezygapophysis (Figure 2a, rl). The cross section of the neural canal is rather small. The zygosphene is not very thick; its roof is slightly concave dorsally. The zygosphenal facets define planes which intersect at the zygosphenal centre (= 'centre zygosphénien', Gasc 1974: 53); this centre is situated just below the floor of the neural canal in this taxon. The cotyle appears circular and as wide as the zygosphene; its rim is thick. The two fossae on either side of the cotyle are deep; they appear to lack paracotylar foramina. Parazygosphenal foramina are also lacking. The paradiapophyses are badly damaged; however, it is presumed that they did not project laterally beyond the tip of the prezygapophyses.

Dorsal view: The vertebra is wider than long. Although not deep, the interzygapophyseal constriction is well marked. The bottom of the constriction appears as an obtuse angle which is slightly asymmetric (vertex located somewhat anteriorly). The anterior border of the zygosphene forms a median lobe flanked by two lateral lobes. The prezygapophyseal facets are oval and their major axis is clearly oblique, at about 40° from the vertebral axis. The median notch which indents the posterior border of the neural arch is of moderate depth.

Lateral view. The vertebra appears short and high. The neural spine is restricted to the posterior half of the neural arch; its anterior border rises steeply. The height of the neural spine remains unknown. The facets of the zygosphene are broad and oval. The paradiapophyses were broad, they are rather extended anteroposteriorly. The interzygapophyseal ridge is short, nearly straight, and salient. Lateral foramina are present. The axis of the condyle is oblique.

Ventral view: The centrum appears approximately triangular and poorly delimited by faint subcentral ridges. These ridges are concave posterolaterally. The haemal keel is rather wide and blunt. Anteriorly, it reaches the cotyle rim; it even causes a slight anterior projection of the rim. The keel markedly narrows between the two subcentral foramina.

Posterior view: The neural arch is moderately vaulted. The posterior border of the neural spine and the roof of the zygantrum are thick. The posterior face of the neural arch lacks parazygantral foramina.

Discussion.

The absence of any trace of prezygapophyseal processes represents one of the most noticeable feature of this vertebra. In various aquatic extinct and living snakes, a dorsoventral keel which runs along the prezygapophyseal buttress supersedes the true prezygapophyseal process. Vb-671 has neither a ridge nor a prezygapophyseal process. The lack of any trace of a prezygapophyseal salient characterizes the vertebrae of *Lapparentophis*, *Pouitella*, the Madtsoiidae, *Simoliophis*, and nearly all lizards (Rage 1988a). *Lapparentophis*, *Pouitella*, and *Simoliophis* occur only in the middle part of the Cretaceous, whereas madtsoiids range from the mid-Cretaceous to the Pleistocene (see below). The vertebrae of *Lapparentophis* are very different from that of Vb-671: they are more heavily built, their prezygapophyseal facets are very strongly inclined (the level of their lateral tip lies slightly above the roof of the neural arch), their zygosphene is very narrow and its anterolateral corners are truncated, the zygosphenal centre lies clearly more ventrally (at about the centre of the cotyle), the posterior part of their neural arch clearly slopes anteriorly, their paradiapophyses are elongate dorsoventrally, and paracotylar foramina are present. The vertebrae of *Simoliophis* are very peculiar; a heavy pachyostosis strongly alters their morphology. The overall morphology of Vb-671 is consistent with that of the madtsoiid vertebrae, but it lacks parazygantral foramina, which is the most important vertebral character of this family. Moreover, the lack of paracotylar foramina also argues against a referral to the Madtsoiidae. Finally, the closest resemblance of Vb-671 seems to be with *Pouitella pervetus*, a possible Lapparentophiidae, from the Cenomanian of France. However, it clearly differs from *Pouitella* in lacking parazygosphenal foramina and in having a markedly lower neural spine.

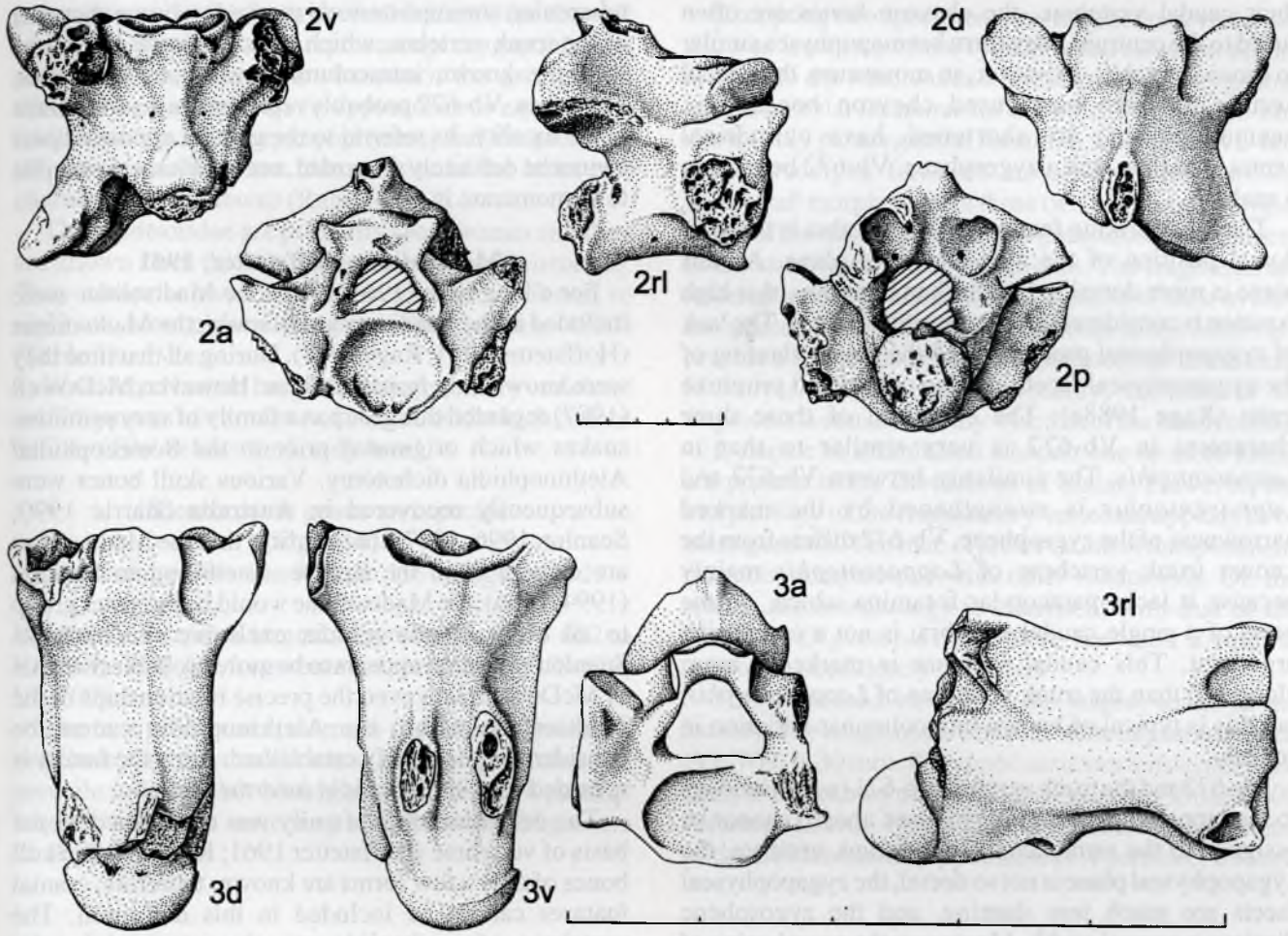
The absence of prezygapophyseal processes, the slanting of the prezygapophyseal facets, and the lack of parazygantral foramina indicate a lapparentophiid level of evolution, but the precise systematic assignment of Vb-671 remains unknown. It might belong to the Lapparentophiidae but this cannot be demonstrated. This vertebra surely represents a new genus and new species, but the single specimen in hand is not complete enough to be a name-bearer of a new taxon. Therefore, we leave this taxon unnamed.

Lapparentophiid-grade snake B (indeterminate snake)
(Figure 3)

Referred material: one caudal vertebra (Vb-672).

Description.

This small caudal vertebra is incomplete: the posterior part of the neural arch, the neural spine, the pleurapophyses (or lymphapophyses), the left prezygapophysis, and the haemapophyses are broken off.



Figures 2-3. Lapparentophiid-grade snakes. 2: Lapparentophiid-grade snake A, trunk vertebra (Vb-671). 3: Lapparentophiid-grade snake B, caudal vertebra (Vb-672). Anterior (a), dorsal (d), right lateral (rl), posterior (p), and ventral (v) views. Scale bars represent 5 mm.

Measurements: length of centrum from cotyle to tip of condyle, 2.7 mm; width of interzygapophyseal constriction, 1.3 mm; width of zygosphene, 0.6 mm; horizontal diameter of cotyle, 1 mm.

Anterior view: The zygosphene is very narrow, comparatively thick, and arched dorsally. The orientation of the zygosphenal facets is nearly vertical; as a result, the zygosphenal centre lies far beyond the ventral surface of the centrum. The transverse section of the neural canal is triangular and wider than the zygosphene. The cotyle is depressed and wider than the neural canal. The zygapophyseal plane lies at a very high level: the level of the medio-ventral limit of the zygapophyseal articular facets is situated just below the ventral limit of the zygosphenal facets. The zygapophyseal facets slant prominently. The zygapophyseal process is absent. The zygapophyseal buttress is strongly compressed; it forms a thick vertical lamina. The vertebra lacks paracotylar foramina.

Dorsal view: The vertebra is very elongate. The anterior border of the zygosphene is somewhat distorted; it apparently formed small lateral lobes and a rather pointed median lobe. The prezygapophyseal facet is elongate and oblique, with its long axis at about 29° to the vertebral axis. The neural spine probably comprised a posterior tubercle, the height of which cannot be estimated, anteriorly prolonged by a faint keel which does not reach the zygosphene.

Lateral view: The neural arch rises moderately posteriorly. The zygosphenal facets are anteroposteriorly short. The vertebra lacks marked interzygapophyseal ridges, but the subcentral ridges are well marked. The axis of the condyle appears to be horizontal or subhorizontal. Lateral foramina cannot be detected.

Ventral view: Subcentral ridges clearly bound the ventral face of the centrum. This surface is narrow, elongate, and its median area forms an elongate anteroposterior bulge; between the bulge and the subcentral ridges the surface is nearly flat. The bases of the haemapophyses are located rather anteriorly, far from the condyle. The subcentral foramina are very tiny.

As Vb-672 lacks the posterior part of the neural arch, the posterior aspect of the vertebra is not informative.

Discussion.

The narrowness of the zygosphene may suggest that this vertebra belongs to mosasaurs. These lizards have generally well-shaped zygosphenes; moreover, on

their caudal vertebrae, the chevron bones are often fused to the centrum, they form haemapophyses similar to those in snakes. However, in mosasaurs, the caudal vertebrae which bear fused chevron bones (i.e., haemapophyses) are shortened, have cylindrical centra, and they lack a zygosphene. Vb-672 belongs to a snake.

The most striking feature of this vertebra is the very dorsal position of the zygapophyseal plane. As this plane is more dorsal in lizards than in snakes, this high position is considered to be a primitive feature. The lack of zygapophyseal processes and the strong slanting of the zygapophyseal facets are also considered primitive traits (Rage 1988a). The condition of these three characters in Vb-672 is very similar to that in *Lapparentophis*. The similarity between Vb-672 and *Lapparentophis* is strengthened by the marked narrowness of the zygosphene. Vb-672 differs from the known trunk vertebrae of *Lapparentophis* mainly because it lacks paracotylar foramina which, on the basis of a single caudal vertebra, is not a conclusive argument. This caudal vertebra is markedly more elongated than the trunk vertebrae of *Lapparentophis,* but this is typical of known intracolumnar variation in snakes.

Vb-672 and the trunk vertebra Vb-671 (which belongs to the lapparentophiid grade too; see above) cannot be assigned to the same taxon. In the trunk vertebra, the zygapophyseal plane is not so dorsal, the zygapophyseal facets are much less slanting, and the zygosphene displays a normal width. Moreover, the neural spine of the caudal vertebra (i.e., Vb-672) was probably tubercular, anteroposteriorly markedly shorter than that of the trunk vertebra, which does not seem consistent with the known intracolumnar variation in snakes. Therefore, Vb-672 probably represents a distinct snake in the locality. Its referral to the genus *Lapparentophis* cannot be definitely discarded, nor does it seem possible to demonstrate it.

Madtsoiidae Hoffstetter, 1961

For a long time (1961-1987), the Madtsoiidae were included in the Boidae as a subfamily, the Madtsoiinae (Hoffstetter 1961; Rage 1987). During all that time they were known only from vertebrae. However, McDowell (1987) regarded this group as a family of very primitive snakes which originated prior to the Scolecophidia/ Alethinophidia dichotomy. Various skull bones were subsequently recovered in Australia (Barrie 1990; Scanlon 1996, 1997) that confirm that the Madtsoiidae are distinct from the Boidae. According to Scanlon (1994, 1996), the Madtsoiidae would be the sister group to all other Alethinophidia exclusive of *Dinilysia*. Scanlon's opinion appears to be more probable than that of McDowell; however, the precise relationships of the Madtsoiidae within the Alethinophidia cannot be considered as definitely established. Here, the family is regarded as Alethinophidia *incertae sedis*.

The definition of the family was established on the basis of vertebrae (Hoffstetter 1961; Rage 1984). Skull bones of only a few forms are known; therefore, cranial features cannot be included in this definition. The vertebrae of madtsoiids are characterized by the combination of the following characters: presence of

TABLE 1.
List of all known Madtsoiidae

Taxa	Geological Ages	Gondwanan areas	Laurasian
Indeterminate genus and species (this paper)	Cenomanian	Sudan	
Madtsoia aff. *madagascariensis*	Coniacian or Santonian	Niger	
Madtsoia madagascariensis	Santonian or Campanian	Madagascar	
Madtsoia laurasiae	Late Campanian or Early Maastrichtian		Spain
Herensugea caristiorum	Late Campanian or Early Maastrichtian		Spain
Alamitophis argentinus	Campanian or Maastrichtian	Argentina	
Patagoniophis parvus	Campanian or Maastrichtian	Argentina	
?Madtsoiid: *Rionegrophis madtsoioides*	Campanian or Maastrichtian	Argentina	
?Madtsoiid	Maastrichtian	India	
?Madtsoiid	Early Palaeocene	Bolivia	
Madtsoia camposi	Middle Palaeocene	Brazil	
Madtsoia cf. *M. bai*	Middle or Late Palaeocene	Argentina	
Indeterminate genus and species	Late Palaeocene	Morocco	
Madtsoia bai	Early Eocene	Argentina	
Patagoniophis cf. *P. parvus*	?Early Eocene	Australia	
Alamitophis cf. *A. argentinus*	?Early Eocene	Australia	
Gigantophis garstini	Late Eocene	Egypt, Libya	
Yurlunggur sp.	Oligo-Miocene	Australia	
Wonambi sp.	Oligo-Miocene	Australia	
Nanowana godthelpi	Early Miocene	Australia	
Nanowana schrenki	Early Miocene	Australia	
Yurlunggur camfieldensis	Middle Miocene	Australia	
Wonambi cf. *W. naracoortensis*	Pliocene	Australia	
Yurlunggur sp.	Pliocene	Australia	
Yurlunggur sp.	Pleistocene	Australia	
Wonambi naracoortensis	Pleistocene	Australia	

parazygantral foramina (a derived feature), the absence of any salient which could represent a prezygapophyseal process (a plesiomorphic character), the great width through the diapophyses (it approaches or exceeds the width through the prezygapophyses), and the presence of paracotylar foramina (the polarity of the latter two characters is unknown) (Rage, 1998).

The Madtsoiidae are primarily Gondwanan and they are known from the late Cretaceous to the Pleistocene. They comprise twelve or thirteen species referred to eight or nine genera (Rage, 1998; Scanlon 1997) (Table 1).

Wadi Abu Hashim has yielded fragmentary vertebrae and fragments of vertebrae of a madtsoiid which cannot be identified below the family level.

Indeterminate genus and species
(Figure 4)

Madtsoiidae: Werner & Rage 1994, Figures 1, 2.

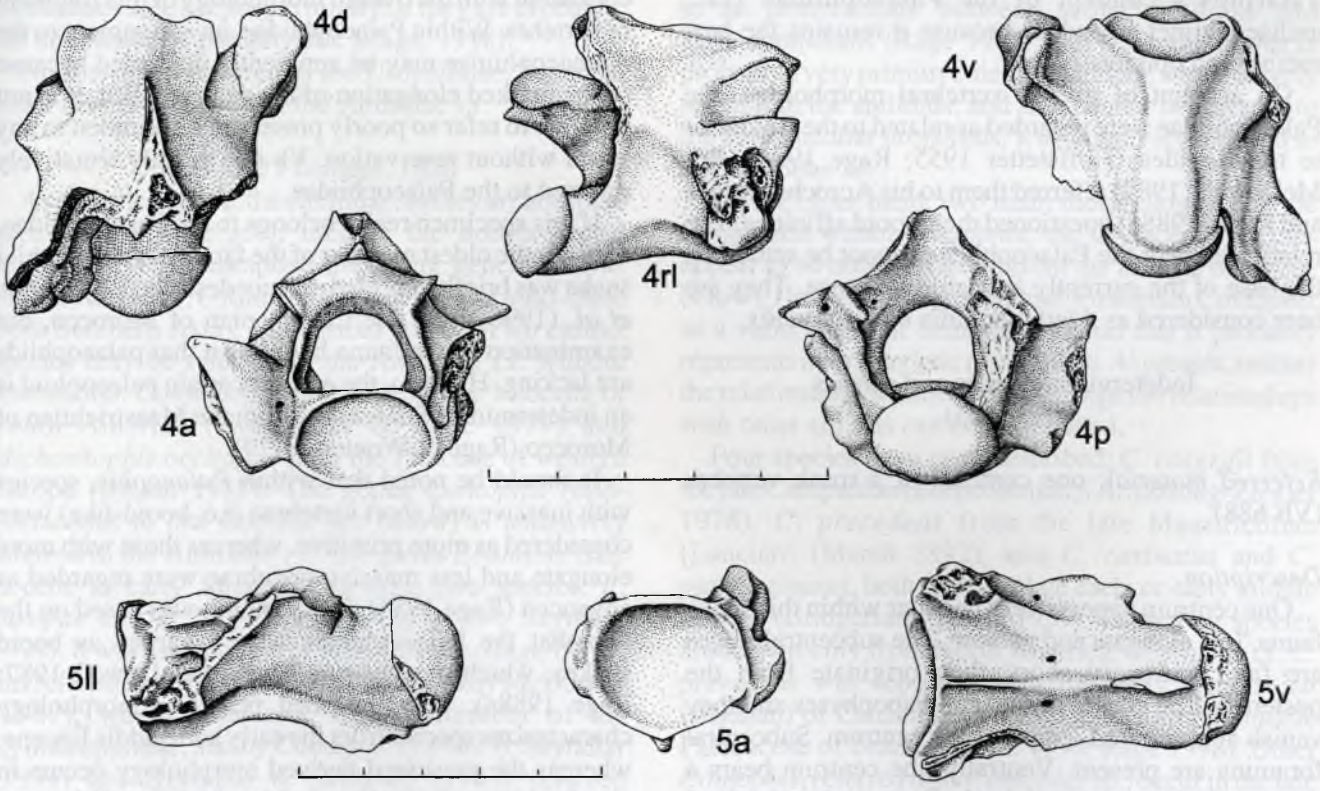
Referred material: 8 fragmentary vertebrae (Vb-662 to Vb-669) and 34 fragments of vertebrae (Vb-670, Vb-709).

The best preserved specimens (i.e., the fragmentary vertebrae) are the smaller ones (including vertebrae of juvenile individuals). Nearly all fragments are parts of large to very large vertebrae; all but one are fragments of centra.

Excepting two specimens, the fragmentary vertebrae show at least two of the typical features which secure referral to the Madtsoiidae (presence of parazygantral and paracotylar foramina; for example, Vb-668). Vb-665 shows only parazygantral foramina whereas in Vb-662 only paracotylar foramina are observable. However, the overall morphology of these two vertebrae is similar to that of the remainder of the sample and their assignment to the same family is beyond doubt. The fragments are referred to the Madtsoiidae on the basis of their overall morphology and, when areas adjacent to the cotyle are preserved, the presence of paracotylar foramina. Moreover, throughout this locality, the size of all fragments is consistent only with that of the Madtsoiidae.

It cannot be established whether one or more forms are present in the Cretaceous of Sudan. However, the morphology of the fragmentary vertebrae appears to be homogeneous. The state of preservation of the specimens prevents comparisons with other madtsoiids. On the whole, the morphology is consistent with that of the *Madtsoia-Gigantophis* complex, but such a referral cannot be confidently proposed.

This madtsoiid is, by far, the largest snake in the locality. The length of the centrum of the largest specimen (Vb-709) is 30 mm. *Wonambi naracoortensis*, the most completely known madtsoiid, had between 350 and 400 vertebrae (Barrie 1990). This number is similar to that of the Boidae (mainly pythonines). Therefore, a rough



Figures 4-5. 4: Madtsoiidae, indeterminate genus and species, juvenile individual, trunk vertebra (Vb-668). 5: ? Palaeophiidae, indeterminate genus and species, centrum of trunk vertebra (Vb-688). Anterior (a), dorsal (d), left lateral (ll), right lateral (rl), posterior (p), and ventral (v) views. Scale bars represent 5 mm.

comparison with pythons indicates that the largest specimen from Wadi Abu Hashim represents a snake probably 6 to 7 m long, perhaps more.

?Palaeophiidae Lydekker, 1888

A possible Palaeophiidae is present at Wadi Abu Hashim. It was not identified in the preliminary article (Werner & Rage 1994). The Palaeophiidae are an extinct family of snakes highly adapted to aquatic life. The family comprises two subfamilies, the Palaeophiinae and the Archaeophiinae. The Palaeophiinae are known only by isolated vertebrae; they include two phenotypic genera: *Palaeophis* (Maastrichtian-Lutetian, perhaps early Bartonian) and *Pterosphenus* (late Lutetian-late Eocene); a third genus, *Vialovophis*, from the late Palaeocene or early Eocene (Nessov & Udovitschenko 1984), is apparently a synonym of *Palaeophis* (Rage 1987). The Archaeophiinae are represented by two articulated specimens from the early Eocene. They belong to two different taxa. *Archaeophis proavus* was redescribed by Janensch (1906); it probably corresponds to a juvenile individual. The second specimen was referred to as *Archaeophis turkmenicus* by Tatarinov (1963); however, it probably belongs to a distinct genus (Rage 1984). Tatarinov (1963) assigned *Archaeophis* to the Palaeophiidae because the vertebrae of *A. turkmenicus* have well developed pterapophyses. The skull of archaeophiines is known (Janensch 1906; Tatarinov 1988); unfortunately, that of the palaeophiines remains unknown, which makes the referral of both groups to the same family uncertain. Here, we follow Tatarinov's concept of the Palaeophiidae (i.e., archaeophiines included) because it remains the best established opinion.

On account of overall vertebral morphology, the Palaeophiidae were regarded as related to the Boidae or to the Booidea (Hoffstetter 1955; Rage 1984). But McDowell (1987) referred them to his Acrochordoidea and Rage (1988a) questioned their booid affinities. The relationships of the Palaeophiidae cannot be settled on the base of the currently available evidence. They are here considered as Alethinophidia *incertae sedis*.

Indeterminate genus and species
(Figure 5)

Referred material: one centrum of a trunk vertebra (Vb-688).

Description.

One centrum appears very peculiar within this snake fauna. It is elongate and narrow. The subcentral ridges are faint and very short; they originate from the posteroventral corner of the paradiapophyses and they vanish at about mid-length of the centrum. Subcentral foramina are present. Ventrally, the centrum bears a deep and sharp sagittal keel. Posteriorly, the keel projects ventrally, thus forming a short hypapophysis. Anteriorly, below the cotyle, it also slightly projects ventrally. As a result of the lack of subcentral ridges, the transverse section of the posterior half of the centrum is approximately triangular. The cotyle is nearly circular, but the dorsalmost part of its rim is somewhat straight; similarly, the dorsal part of the codyle is slightly flattened. In lateral view, the axis of the condyle is nearly horizontal or perhaps horizontal (because of the shape of the outline of the condyle, the orientation of the axis is difficult to estimate).

Discussion.

The overall morphology of this centrum is clearly reminiscent of the Palaeophiidae and Nigerophiidae. The very faint subcentral ridges are consistent with both families. However, the deep sagittal keel and short hypapophysis suggest only the Palaeophiidae. A referral to the Palaeophiidae is also supported by the presence of the slight ventral projection of the anterior part of the sagittal keel (it is sometimes called an 'anterior hypapophysis'). Such an anterior ventral process is present in species of *Palaeophis* interpreted as 'advanced species' by Rage (1984) and in *Pterosphenus*. On the other hand, the morphology of the cotyle and condyle, the dorsal part of which is slightly truncated, also occurs in various species of *Palaeophis*; it is unknown in other snakes. The peculiar orientation of the condyle (axis horizontal or nearly horizontal) is also characteristic of the Palaeophiidae; this condition is approached by the Nigerophiidae and Russellophiidae.

Therefore, several peculiar characters clearly argue for an assignment to the Palaeophiidae, which is consistent with the overall morphology of this fragment of vertebra. Within Palaeophiidae, an assignment to the Archaeophiinae may be apparently discarded because of the marked elongation of the centrum. But, it is not possible to refer so poorly preserved a specimen to any taxon without reservation. Vb-688 is only tentatively referred to the Palaeophiidae.

If this specimen really belongs to the Palaeophiidae, then it is the oldest member of the family. A palaeophiid snake was briefly reported, but not described, by Sereno *et al.* (1996) from the Cenomanian of Morocco, but examination of the fauna has shown that palaeophiids are lacking. Hitherto, the earliest certain palaeophiid is an indeterminate *Palaeophis* from the Maastrichtian of Morocco (Rage & Wouters 1979).

It should be noted that within *Palaeophis*, species with massive and short vertebrae (i.e. booid-like) were considered as more primitive, whereas those with more elongate and less massive vertebrae were regarded as advanced (Rage 1984). This opinion was based on the fact that the Palaeophiidae were regarded as booid snakes, which may be questioned (McDowell 1987; Rage 1988a). The presumed primitive morphology characterizes species from the early and middle Eocene, whereas the presumed derived morphology occurs in clearly older geological levels: Maastrichtian of Morocco (Rage & Wouters, 1979), Palaeocene of Morocco (unpublished), and even Cenomanian if Vb-688 really represents a Palaeophiidae. Obviously, stratigraphic

distribution should not be taken into account in the polarization of characters. However, in the present case, it casts doubts on the previous interpretation.

Anilioidea Fitzinger, 1826

The Anilioidea are an assemblage of primitive alethinophidian snakes that is probably paraphyletic (Cundall *et al.* 1993). They likely form the stem group of the other alethinophidians, i.e., the Macrostomata (Rage 1997). The relationships within the Anilioidea cannot be considered as settled. Traditionally, two families (Aniliidae and Uropeltidae) were recognized within this assemblage. McDowell (1975, 1987) included the Xenopeltidae and Loxocemidae in the Anilioidea, but these two families appear to be closer to the Booidea (Rage, 1998). The Uropeltidae *s.s.* (= Uropeltinae of McDowell 1987), i.e., Cylindrophiinae excluded, unquestionably form a monophyletic group, but the remaining Anilioidea (i.e., the traditional Aniliidae) probably make up a paraphyletic assemblage. Cundall *et al.* (1993) recognized three monophyletic lineages within these non-uropeltid anilioids: each living genus (*Anilius*, *Cylindrophis*, *Anomochilus*) represents one lineage. In order to avoid paraphyletic taxa, they elevated each of these lineages to family rank. But, since it cannot be definitely considered that the traditional Aniliidae are paraphyletic, and because the relationships within this group are not definitely demonstrated, it seems premature to adopt a new classification for non-uropeltid anilioids. It seems preferable to provisionally hold the traditional Aniliidae (which may be labelled 'Aniliidae *s.l.*'), keeping in mind that they are probably, but not certainly, paraphyletic (Rage, 1998).

No fossil was referred to the Uropeltidae, but some fossil taxa are referred to the Aniliidae *s.l.*

Aniliidae Fitzinger, 1826

As indicated above, the Aniliidae, as they are accepted here (= Aniliidae *s.l.*), include the non-uropeltid Anilioidea. They comprise the living genera *Anilius* (South America), *Cylindrophis* and *Anomochilus* (both from Southern Asia), and various fossils. Two extinct species may be referred to the Aniliidae *s.l.* without reservation: *Colombophis portai* from the Miocene of South America (Hoffstetter & Rage 1977) and *Michauxophis occitanus* from the Pliocene of western Europe (Bailon 1988). The genus *Coniophis* (mid-Cretaceous to late Eocene; see below) is tentatively referred to the Aniliidae *s.l.* The genus *Eoanilius* (late Eocene to early Miocene) includes two species: *E. europae* and *E. oligocenicus* (Rage 1984; Szyndlar 1994). It was assigned to the Aniliidae *s.l.* (Rage 1974); this referral has been more or less accepted by McDowell (1987), who considered it as a member of his Cylindrophiinae, and by Cundall *et al.* (1993). Szyndlar (1994) and Szyndlar & Schleich (1993) referred *Eoanilius* to the Aniliidae *s.s.*, that is, to a family which includes only one living genus, *Anilius*.

Vertebrae belonging to *Coniophis* were recovered at Wadi Abu Hashim.

Coniophis Marsh, 1892

Coniophis is known only from vertebrae that are characterized by their comparatively massive construction, their relatively depressed neural arch that does not rise markedly above the zygapophyseal plane, their prezygapophyseal processes that are either very short or lacking, the lack of a median notch in the posterior border of the neural arch (a shallow embayment is often present), their centrum which only slightly widens anteriorly, the more or less oblique long axis of their prezygapophyseal facets, their much reduced neural spine, and their haemal keel generally distinct in at least a part of the vertebral column (Rage, 1998).

The relationships of *Coniophis* are controversial. *Coniophis* was first considered as a snake without a more precise assignment (Marsh 1892; Gilmore 1938). Hoffstetter (1955) erected the family Coniophiidae for the reception of *Coniophis precedens*, the only species known at that time. Hecht (1959) allocated *Coniophis* to the Aniliidae *s.l.* and he considered that its closest relative might be the living *Cylindrophis*. Later, Hecht (1982) suggested that *Coniophis* might be closely related to *Dinilysia* from the late Cretaceous (?Campanian). Subsequently, McDowell (1987) placed *Coniophis* in the Dinilysiidae. The features which characterize the vertebrae of *Coniophis* are either primitive or non-polarizable, which accounts for this uncertainty. *Coniophis* probably represents a paraphyletic assemblage. The vertebral morphology of *Coniophis* corresponds either to that of very primitive Alethinophidia (i.e., to that of Aniliidae *s.l.*) or, perhaps, to an intermediate between scolecophidians and alethinophidians (Rage 1984, 1987). As *Coniophis* is probably a very primitive alethinophidian, we tentatively retain it in the anilioids, and as it cannot be referred to the very peculiar uropeltids, it is tentatively referred to the Aniliidae *s.l.*

On the other hand, two main morphologies may be recognized within *Coniophis*: the Cretaceous species appear to be rather different from the Eocene ones (see below). However, we provisionally maintain *Coniophis* as a valid genus, it being understood that it probably represents a paraphyletic assemblage. At present, neither the relationships within this assemblage nor relationships with other aniliids can be established.

Four species have been described: *C. cosgriffi* from the late Campanian (Edmontonian) (Armstrong-Ziegler 1978), *C. precedens* from the late Maastrichtian (Lancian) (Marsh 1892), and *C. carinatus* and *C. platycarinatus*, both from the late early or early middle Eocene (Bridgerian) (Hecht 1959). These four species are known only from North America. *Coniophis* cf. *C. precedens* was reported from the early Campanian (Aquilan) of Canada (Fox 1975) and from the middle Palaeocene of Brazil (Albino 1990; Rage 1998). Other *Coniophis*, referred to as *Coniophis* sp., occur in the late Albian/earliest Cenomanian (Gardner & Cifelli, 1999), the middle/late Campanian (Judithian) (Breithaupt 1985), the middle Paleocene (Torrejonian) (Estes 1976), the late Eocene (Uintan) (Holman 1979) of the USA, the

late Eocene of France (Rage 1988b), the late Palaeocene (Gheerbrant *et al.* 1993) and early Eocene (unpublished) of Morocco, and the early Eocene of Algeria (unpublished). Moreover, *Coniophis* is perhaps present in a Peruvian locality the geological age of which is either latest Cretaceous or earliest Palaeocene (Rage 1991).

Wadi Abu Hashim has yielded seven vertebrae which correspond to the 'definition' of *Coniophis*. Whatever the precise status of the genus, this fossil represents a new species.

Coniophis dabiebus sp. nov.
(Figures 6, 7, 8)

Holotype: one mid-trunk vertebra (Vb-673).

Type locality: Wadi Abu Hashim, Sudan.

Horizon: Wadi Abu Hashim Member of Wadi Milk Formation; Cenomanian.

Etymology: from Al Dabieb, a local Sudanese name for snakes.

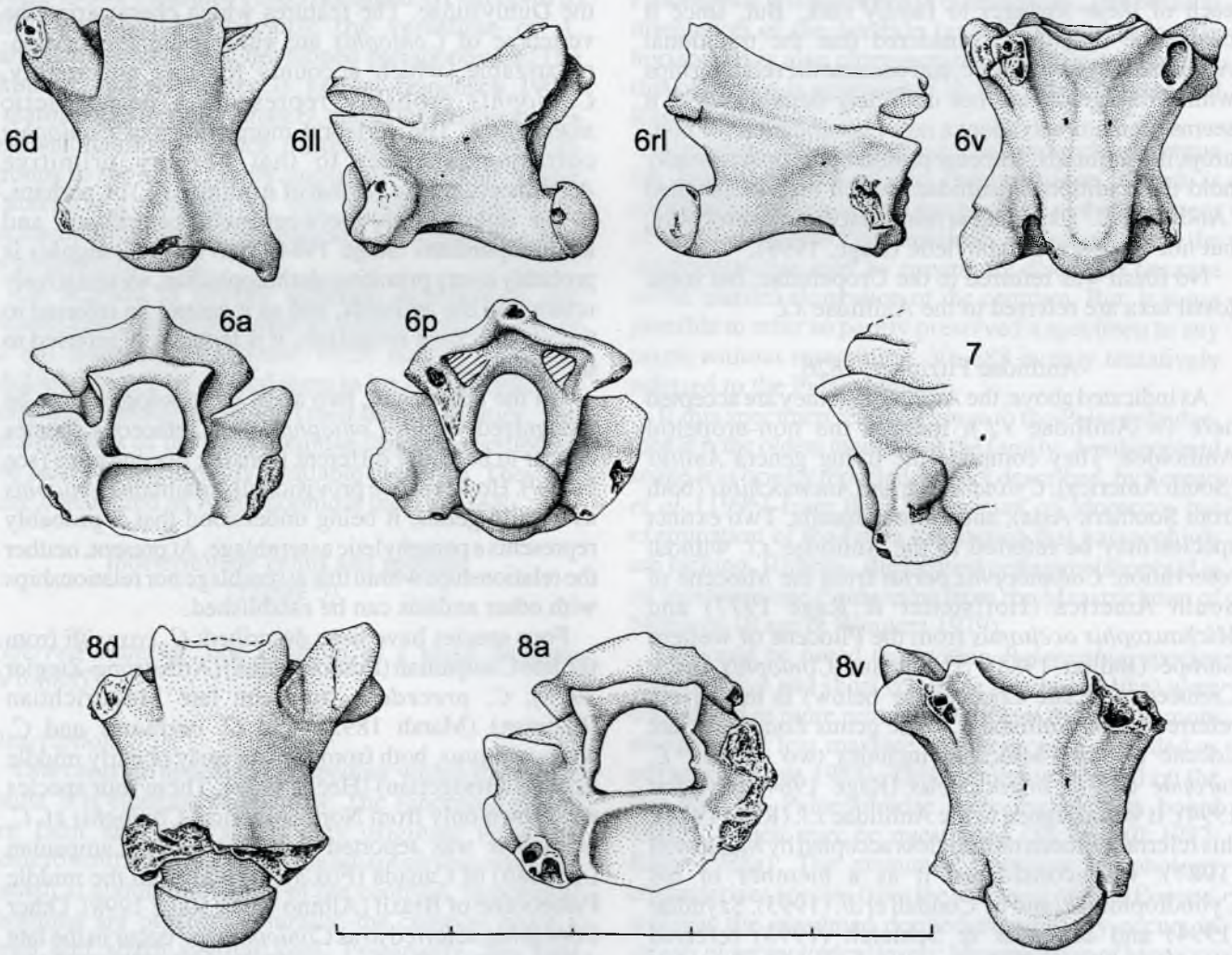
Referred material: 6 trunk vertebrae (Vb-674 to Vb-679).

Diagnosis: *Coniophis dabiebus* differs from the other species of *Coniophis* by its more elongate vertebrae. It is distinguished from *C. precedens*, *C. carinatus*, and *C. platycarinatus* by its less deep interzygapophyseal constriction. It differs from *C. carinatus*, *C. platycarinatus*, and *C. cosgriffi* by its clearly less prominent neural spine. It differs from *C. carinatus* and *C. platycarinatus* by the lack of any indication of prezygapophyseal processes, by its laterally less projecting prezygapophyses, and by its more elongate prezygapophyseal articular facets.

Description of the holotype.

The holotype is a nearly complete mid-trunk vertebra which lacks only the extremities of the left prezygapophysis and the left postzygapophysis.

Measurements: length of centrum from cotylar rim to tip of condyle, 1.9 mm; width of zygosphene, 1 mm; width of interzygapophyseal constriction, 1.3 mm; horizontal diameter of cotyle, 0.9 mm.



Figures 6-8. Aniliidae, *Coniophis dabiebus* sp. nov. 6: mid-trunk vertebra, Holotype (Vb-673). 7: anterior portion of a trunk vertebra showing a well-preserved paradiapophysis, left lateral view (Vb- 674). 8: posterior trunk vertebra (Vb-679); anterior border of zygosphene reconstructed on the basis of Vb-678. Anterior (a), dorsal (d), left lateral (ll), right lateral (rl), posterior (p), and ventral (v) views. Scale bar represents 5 mm.

Anterior view. The vertebra appears rather high and narrow, not massive. The neural canal is ovoid and high. The lateral walls of the canal are thin. The zygosphene is as wide as the cotyle and slightly wider than the neural canal; its roof is thin and slightly arched dorsally. The zygosphenal centre is located in the dorsal part of the cotyle. The cotyle is dorso-ventrally depressed; the dorsal part of its rim is nearly straight. The prezygapophyseal body is high and narrow and the prezygapophyses do not strongly project laterally. The prezygapophyseal facets clearly slant; they lie at a high level, i.e. between two thirds and three quarters of the height of the neural canal. Although the tip of each prezygapophysis is broken off, it may be inferred that the prezygapophyseal processes are absent. The paradiapophyses do not markedly project laterally. The depressions between the cotyle and prezygapophyses do not form well-delimited fossae; they lack paracotylar foramina.

Dorsal view: The vertebra shows a squarish outline. The interzygapophyseal constriction is rather deep and almost symmetrical: its maximum depth occurs at about mid-length of the vertebra. The zygosphene is moderately wide; its anterior border is straight and it forms two small lateral lobes, as a result it appears concave. The articular facets are oval and their major axis is oblique (about 40° to the vertebral axis). No prezygapophyseal process projects beyond the facet. The posterior half of the neural arch gradually slopes anteriorly; the neural arch appears to be somewhat saddle-shaped. The neural spine is a low tubercle (the tip of which is broken) on the posteriormost part of the neural arch; it extends anteriorly as a faint ridge that vanishes in the middle part of the neural arch. The posterior border of the neural arch forms a shallow concavity lacking a median notch. The right postzygapophysis (the only preserved one) markedly projects posteriorly, which is unusual.

Lateral view. The vertebra is moderately elongate. The posterior half of the neural arch clearly rises posteriorly. The neural spine does not appear clearly marked off from the neural arch. The zygosphenal facet is elongate and its long axis is slightly inclined above the horizontal. The paradiapophysis does not markedly extend dorso-ventrally (however, its ventral border is broken). The parapophyseal part is broader than the diapophyseal one. The interzygapophyseal and subcentral ridges are not well-marked. The lateral foramen occupies a low position. The haemal keel is not deep.

Ventral view: The centrum is narrow; it moderately widens anteriorly. Its ventral surface is poorly delimited by weakly defined subcentral ridges. The haemal keel is rather wide and blunt. It is poorly differentiated from the centrum, mainly in the posterior part where its limits become obscure (except its posterior limit which is close to the condyle). Anteriorly, where the haemal keel is defined, the ventral face of the centrum is concave on either side of the keel. Subcentral foramina are present.

Posterior view: The neural arch is very depressed. The neural spine appears low and thick. The roof of the zygantrum and the lateral walls of the neural canal are relatively thin. Parazygantral foramina are absent.

Vertebral variation.

Only mid- and posterior trunk vertebrae are available. Some mid-trunk vertebrae have perfectly preserved prezygapophyses and paradiapophyses. They confirm that the prezygapophyses are without any indication of prezygapophyseal processes (Figure 7, 8a). In the largest vertebrae, the paradiapophyses comprise a hemispherical diapophysis and a broader and rather flat parapophysis (Figure 7). All other features exhibited by these mid-trunk vertebrae are identical to those of the holotype. Two poorly preserved vertebrae are regarded as being from the posterior trunk. They appear more elongate and slightly more depressed than mid-trunk vertebrae. The prezygapophyseal bodies seem less narrow in anterior view. The paradiapophyses are more protruding laterally, they reach the level of the prezygapophyseal tip. The anterior border of the zygosphene forms three lobes. The ventral face of their centrum is even more poorly delimited than in the mid-trunk vertebrae. The haemal keel is hardly distinct. However, if these vertebrae are really from the posterior trunk, it should be noted that they lack the depressions that occur on either side of the haemal keel in the posterior trunk region of most snakes.

Unfortunately, none of these trunk vertebrae retains preserved postzygapophyses. Therefore, it is not possible to establish whether the peculiar posterior projection of the only preserved postzygapophysis in the holotype (Figure 6d, right side) is a specific character or only a peculiarity of this specimen.

Discussion.

The characters exhibited by the *Coniophis* from Sudan clearly show that it represents a distinct species. Apart from the primitive nature of the *Coniophis* features, the most serious problem in the study of this genus is that too many fossils have been referred to as *Coniophis* sp. and remain undescribed. It seems necessary to describe and to name the Sudanese *Coniophis*; the seven available vertebrae permit this.

The vertebrae of *Coniophis dabiebus* are more elongate than those of all other species of the genus. They are narrower and less depressed than those of *C. precedens* and *C. carinatus*. The interzygapophyseal constriction is shallower than that of *C. precedens*, *C. carinatus*, and *C. platycarinatus*. The neural spine does not form a sagittal ridge clearly marked off from the neural arch; by this character, *C. dabiebus* differs from *C. carinatus*, *C. platycarinatus*, and *C. cosgriffi*. Besides, *C. dabiebus* differs markedly from *C. carinatus* and *C. platycarinatus* in lacking any salient which could represent a prezygapophyseal process, in having prezygapophyses less projecting laterally, and articular facets of the prezygapophyses more elongate.

Phenetically, *C. dabiebus* appears to be closer to the other Cretaceous species (*C. precedens* and *C. cosgriffi*) than to the Eocene ones (*C. carinatus* and *C. platycarinatus*). In *C. patycarinatus* and mainly *C. carinatus*, the prezygapophyses stretch markedly laterally and, at their lateral tip, a very short prezygapophyseal process projects slightly beyond the articular facet. This morphology of the prezygapophyses in *C. carinatus* and *C. platycarinatus* is reminiscent of the living Aniliidae (at least *Anilius* and *Cylindrophis*). *C. dabiebus*, *C. precedens*, and *C. cosgriffi* make up an assemblage which is phenetically more distinct from the living forms.

Coniophis cf. *C. dabiebus*
(Figure 9)

Referred material: one vertebra (Vb-680).

A single vertebra displays characters of *C. dabiebus*, but it is shorter than all the vertebrae referred to this species. Such shortness suggests that it might be a very anterior trunk vertebra of *C. dabiebus*. Unfortunately, the posterior part of the centrum is lacking, that is, the presence of a hypapophysis or of a deep haemal keel (which would confirm that the vertebra is an anterior one) cannot be ascertained. On the other hand, the neural arch is not more vaulted and the neural spine is not higher than in the mid-trunk vertebrae, which is not consistent with the usual intracolumnar variation if this vertebra is really a very anterior one. Moreover, the neural spine seems somewhat unusual. It is only a slight thickening of the posterior border of the neural arch which stretches posterodorsally. In lateral view, this thickening resembles a tubercular neural spine (but it is not tubercular); in dorsal view, it projects slightly posteriorly. This vertebra belongs to a juvenile individual as shown by its size and the very depressed cotyle. But this probably cannot account for the differences which distinguish this vertebra from *Coniophis dabiebus*. This specimen cannot be confidently referred to the latter species.

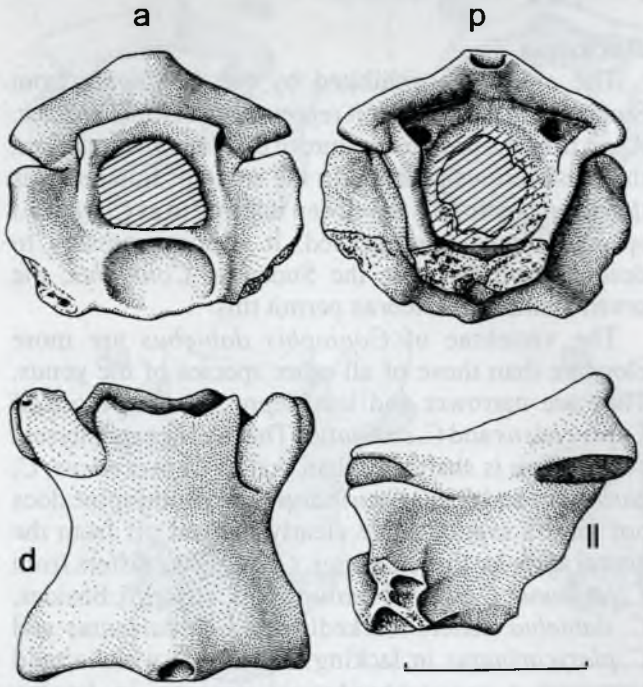


Figure 9. Aniliidae, *Coniophis* cf. *C. dabiebus*. Trunk vertebra (Vb-680). Anterior (a), dorsal (d), left lateral (ll), and posterior (p) views. Scale bar represents 1 mm.

Acrochordoidea Bonaparte, 1838

The Acrochordoidea include the living Acrochordidae and the extinct Nigerophiidae. They are all aquatic snakes. McDowell (1987) assigned the extinct Palaeophiidae to the Acrochordoidea, but they are here considered as Alethinophidia *incertae sedis* (see above).

Nigerophiidae Rage, 1975

The family Nigerophiidae was erected for the single species *Nigerophis mirus* from the Palaeocene of Niger (Rage 1975a). This snake is easily characterized by the overall morphology of its vertebrae which appear to be quite peculiar within snakes. The middle portion of the vertebrae is more or less cylindrical whereas the posterior part is deep. The cylindrical aspect of the middle portion results from the lack, or the weakness, of the interzygapophyseal and subcentral ridges. The vertebrae are posteriorly deep, relative to the anterior and middle parts, because the neural spine (which occupies only the posterior part of the neural arch) is rather high and because the posterior part of the haemal keel is ventrally deflected. This combination of these features is unique within snakes.

Woutersophis novus from the middle Eocene of Belgium (Rage 1980) and *Indophis sahnii* from the latest Cretaceous of India (Rage & Prasad 1992) were tentatively referred to the Nigerophiidae. The vertebrae of *Woutersophis* are reminiscent of both the Nigerophiidae and Palaeophiidae. This genus was referred, with reservation, to the Nigerophiidae because it lacks pterapophyses while these additional apophyses are developed in the Palaeophiidae. *Indophis* shows a rather close phenetic resemblance to *Nigerophis*. However, in *Indophis*, as in *Woutersophis*, the interzygapophyseal and subcentral ridges are clearly defined and the posterior part of the haemal keel is not deflected ventrally. Moreover, in *Indophis*, parazygantral foramina are irregularly present. Therefore, these two snakes cannot be assigned to the Nigerophiidae without reservation.

Wadi Abu Hashim has yielded a snake which appears to be very close to *Nigerophis*. It represents a new genus and species and it may be confidently referred to the Nigerophiidae.

Nubianophis gen. nov.

Type species: *Nubianophis afaahus* sp. nov.

Etymology: from Nubia, the region in which the fossiliferous locality is situated.

Diagnosis: as for the type species and only known species.

Nubianophis afaahus sp. nov.
(Figure 10-12, 13-14)

Holotype: one mid-trunk vertebra (Vb-1041).

Type locality: Wadi Abu Hashim, Sudan.

Horizon: Wadi Abu Hashim Member of Wadi Milk Formation; Cenomanian.

Etymology: from Al Afaa, classical Arabic name for all snakes.

Referred material: 12 trunk vertebrae (Vb-1042 to Vb-1053) and one caudal vertebra (Vb-1054).

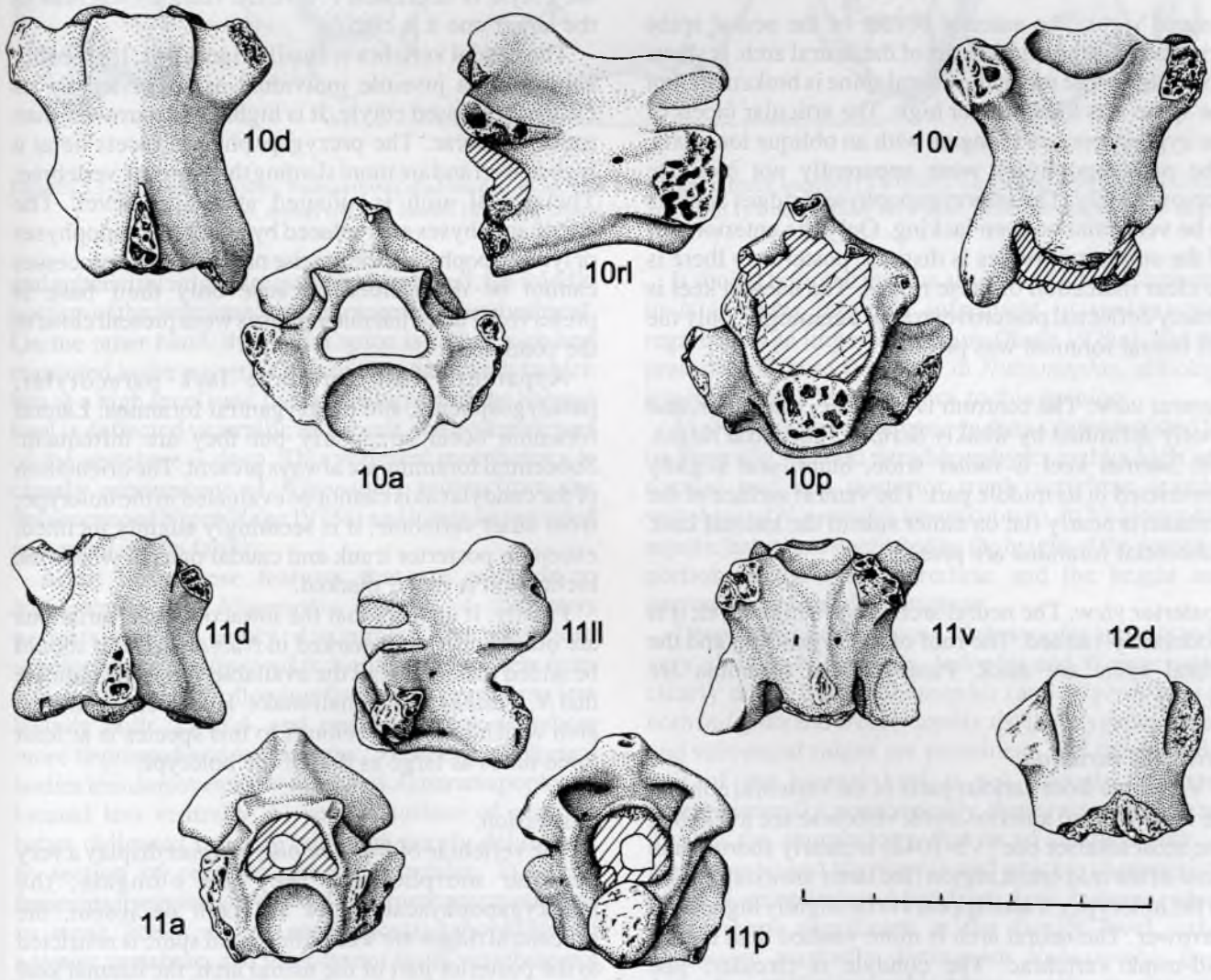
Diagnosis: Snake displaying the unique combination of vertebral features found in *Nigerophis mirus*: interzygapophyseal ridges faint or lacking, subcentral ridges weak, neural spine rather high and restricted to the posterior part of the neural arch, posterior part of the haemal keel deflected ventrally, neural arch lying at a high level. It differs from *N. mirus*, the only other certain nigerophiid, by the following characters: vertebrae more lightly constructed, more depressed and less narrow; prezygapophyseal body less extended dorsoventrally; paradiapophyses situated more dorsally; section of centrum non-subtriangular; ventral surface of centrum weakly bounded laterally; lateral foramina sometimes present; absence of any trace of keel above the postzygapophyses of anterior vertebrae.

Description of the holotype.

The holotype is a mid-trunk vertebra which lacks the tip of each prezygapophysis, the left postzygapophysis, the top of the neural spine, and in which the paradiapophyses and the condyle are eroded. Within the set of available vertebrae, it ranks among the medium-sized ones.

Measurements: width of zygosphene, 1.7 mm; width of interzygapophyseal constriction, 2.4 mm; horizontal diameter of cotyle, 1.5 mm.

Anterior view. The vertebra appears moderately high and narrow. The zygosphene is wide and thin; its anterior edge is nearly straight but its roof bulges slightly dorsally. The zygosphenal centre lies in the



Figures 10-12. Nigerophiidae, *Nubianophis afaahus* gen. et sp. nov. 10: mid-trunk vertebra, Holotype (Vb-1041). 11: anterior trunk vertebra (Vb-1042). 12: mid-trunk vertebra showing a complete zygosphene, dorsal view (Vb-1044). Anterior (a), dorsal (d), left lateral (ll), right lateral (rl), posterior (p), and ventral (v) views. Scale bar represents 5 mm.

ventral part of the cotyle, close to the ventral border. The section of the neural canal is broad, nearly as wide as the zygosphene, and trifoliate. The cotyle is depressed and as wide as the neural canal. The zygapophyseal facets are inclined above the horizontal; the level of the facets lies above the floor of the neural canal (at about one quarter or one third of the height of the canal). The depressions between the cotyle and each prezygapophysis are rather deep; they lack paracotylar foramina.

Dorsal view: The vertebra is elongate. The interzygapophyseal constriction is rather shallow and asymmetrical (its maximun depth is shifted anteriorly). The roof of the zygosphene is rather wide; its anterior border appears to be sinuous, caused by erosion. None of the prezygapophyseal facets is fully preserved. They were apparently narrow and their long axis was oblique, at approximately 55° to the vertebral axis. The neural spine occupies only the posterior half of the neural arch; it is thick posteriorly. The posterior edge of the neural spine fills a narrow median notch in the posterior border of the neural arch; as a result, the vertebra appears to lack such a notch.

Lateral view: The anterior border of the neural spine originates on the middle part of the neural arch. It slants posteriorly. The top of the neural spine is broken off, but the spine was likely rather high. The articular facets of the zygosphene are elongate with an oblique long axis. The paradiapophyses were apparently not elongate dorsoventrally. The interzygapophyseal ridges appears to be very faint or even lacking. Only the anterior part of the subcentral ridges is distinct; posteriorly there is no clear indication of these ridges. The haemal keel is clearly deflected posteroventrally. Seemingly, only the left lateral foramen was present.

Ventral view: The centrum is elongate, triangular, and poorly delimited by weakly defined subcentral ridges. The haemal keel is rather wide, blunt, and slightly constricted in its middle part. The ventral surface of the centrum is nearly flat on either side of the haemal keel. Subcentral foramina are present.

Posterior view: The neural arch lies at a high level; it is moderately vaulted. The roof of the zygantrum and the neural spine are thick. Parazygantral foramina are lacking.

Vertebral variation.

Vertebrae from various parts of the vertebral column are known. Two anterior trunk vertebrae are available. The most anterior one (Vb-1042) is clearly shorter than those of the mid-trunk region (the latter are exemplified by the holotype); it also appears to be slightly higher and narrower. The neural arch is more vaulted than that of mid-trunk vertebrae. The condyle is circular. The zygapophyseal level and the slant of the zygapophyseal facets are similar to those in the mid-trunk region. The neural spine is broken and its height cannot be evaluated; as in the middle part of the trunk, it is restricted to the posterior area of the neural arch. The centrum is markedly shorter than that of mid-trunk vertebrae. A rather deep haemal keel extends from the cotyle to the condyle; its posterior part is broken off; a hypapophysis may have been present.

The other anterior trunk vertebra (Vb-1043) is only slightly shorter than those from the mid-trunk region. The haemal keel is deflected posteroventrally and its posterior part projects markedly ventrally, but it does not form a hypapophysis. The other characteristics of this vertebra are similar to those of Vb-1042.

No noticeable variation occurs among mid-trunk vertebrae. Their morphology corresponds to that of the holotype. In only one of them, the anterior border of the zygosphene is well preserved (while it is eroded in the holotype). It forms three lobes which protrude only slightly anteriorly (Figure 12).

In the two known posterior trunk vertebrae, the haemal keel is more clearly outlined and more salient than in mid-trunk vertebrae (Figure 13v). The neural arch is approximately as depressed as that of mid-trunk vertebrae. It should be noted that in the smaller vertebra the cotyle is depressed (?juvenile feature) whereas in the larger one it is circular.

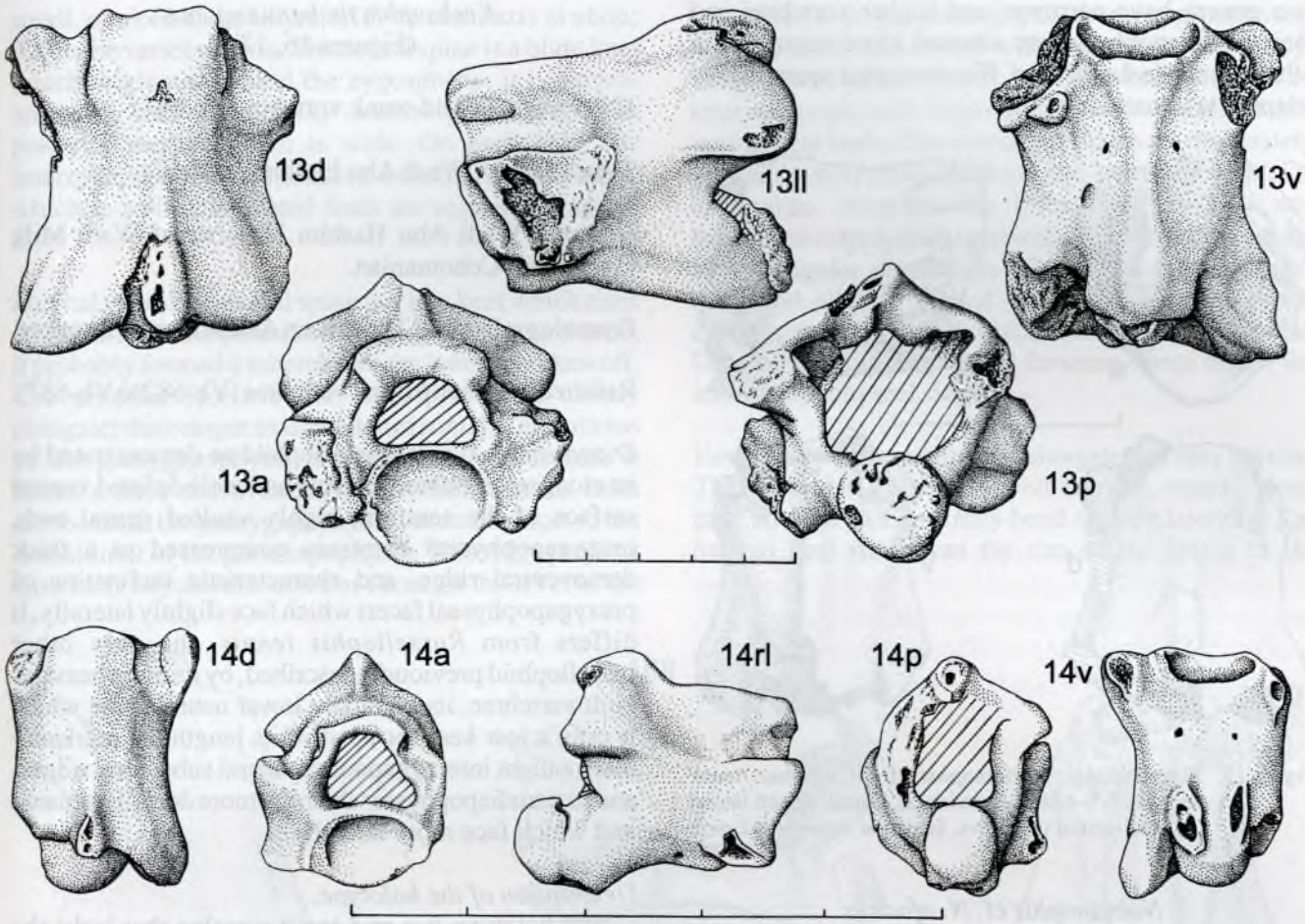
The caudal vertebra is small (Figure 14). It probably belongs to a juvenile individual as suggested by its clearly depressed cotyle. It is higher and narrower than trunk vertebrae. The prezygapophyseal facets lie at a higher level and are more slanting than in trunk vertebrae. The neural arch is situated at a high level. The paradiapophyses are replaced by either pleurapophyses or lymphapophyses; the precise nature of these processes cannot be determined because only their base is preserved. Paired haemapophyses were present close to the condyle.

Apparently, all vertebrae lack paracotylar, parazygosphenal, and parazygantral foramina. Lateral foramina occur irregularly but they are infrequent. Subcentral foramina are always present. The orientation of the condylar axis cannot be evaluated in the holotype; from other vertebrae, it is seemingly slightly inclined, except in posterior trunk and caudal ones in which the inclination is rather marked.

Finally, it appears that the intracolumnar variations are only moderately marked in *Nubianophis*. It should be added that nearly all the available vertebrae indicate that *N. afaahus* was a small snake. However, one neural arch which probably belongs to this species is at least three times as large as that of the holotype.

Discussion.

The vertebrae of *Nubianophis afaahus* display a very peculiar morphology: they are elongate, the interzygapophyseal ridges are faint or absent, the subcentral ridges are weak, the neural spine is restricted to the posterior part of the neural arch, the haemal keel is markedly deflected posteroventrally, and the neural arch is situated at a high level. As the interzygapophyseal



Figures 13-14. Nigerophiidae, *Nubianophis afaahus* gen. et sp. nov. 13: posterior trunk vertebra (Vb-1045). 14: caudal vertebra (Vb-1054). Anterior (a), dorsal (d), left lateral (ll), right lateral (rl), posterior (p), and ventral (v) views. Scale bars represent 5 mm.

and subcentral ridges are not clearly marked, the middle portion of the vertebrae appears more or less cylindrical. On the other hand, the neural spine is rather high and restricted to the posterior part of the neural arch (which lies at a high level) and the posterior part of the haemal keel is deflected ventrally; as a result, the posterior part of the vertebrae is deep. This vertebral morphology is clearly reminiscent of *Nigerophis mirus* from the Palaeocene of Niger (Rage 1975a) and it may be regarded as typical of the family.

Apart from these features that are common to *Nubianophis* and *Nigerophis*, a suite of characters permits one to easily distinguish the Sudanese nigerophiid from *Nigerophis*. *Nubianophis* differs from *Nigerophis* by the following features: 1) vertebrae less heavily built, 2) mid- and posterior trunk vertebrae more depressed and less narrow, 3) prezygapophyseal bodies less dorsoventrally extended, 4) paradiapophyses located less ventrally, 5) ventral surface of centrum better delimited laterally (although poorly delimited), 6) section of centrum not subtriangular, 7) lateral foramina irregularly present, 8) incipient pterapophyses (= weak keels) absent above postzygapophyses of anterior vertebrae, and 9) posterior trunk vertebrae not markedly compressed laterally.

It should be noted that the absence of lateral foramina in *Nigerophis* (absence infrequent in snakes) was regarded as an important feature (Rage 1975a). But the presence of these foramina in *Nubianophis*, although irregular, lends less credence to this opinion.

Nigerophis was an aquatic snake as demonstrated by its ventrally situated paradiapophyses and its high and narrow mid and posterior trunk vertebrae (caudal vertebrae of *Nigerophis* are unknown). In *Nubianophis*, aquatic habits are suggested by the height of the posterior portion of the trunk vertebrae and the height and narrowness of caudal vertebrae.

Despite these differences, *Nubianophis* appears to be very close to *Nigerophis*. *Indophis* and *Woutersophis* clearly differ from *Nubianophis* (and *Nigerophis*). In both *Indophis* and *Woutersophis*, the interzygapophyseal and subcentral ridges are prominent, and the posterior part of the haemal keel is not strongly deflected posteroventrally; consequently, these two snakes do not display the morphology that is so characteristic of *Nubianophis* and *Nigerophis*, and which is characteristic of the Nigerophiidae. Apart from these features, which are perhaps significant at the family level, other characters markedly distinguish *Nubianophis* from *Indophis* and *Woutersophis*. More specifically, the latter

two genera have narrower and higher vertebrae and their paradiapophyses are situated more ventrally; in other words *Indophis* and *Woutersophis* were highly adapted to aquatic life.

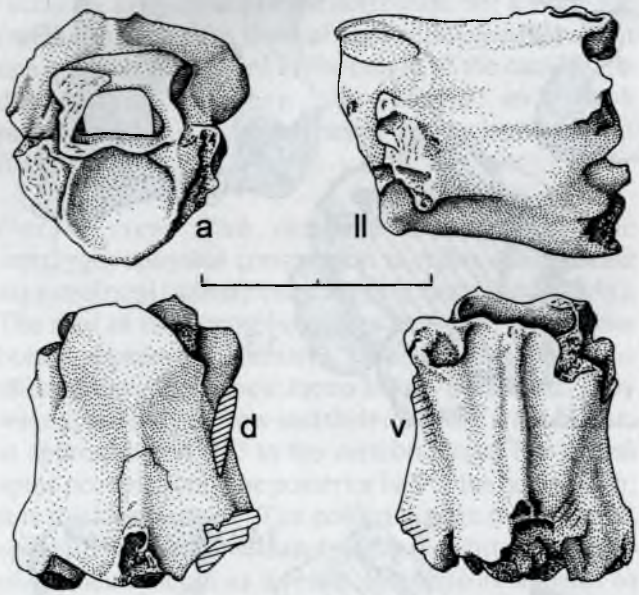


Figure 15. Nigerophiidae, *Nubianophis* cf. *N. afaahus*, trunk vertebra (Vb-1055). Anterior (a), dorsal (d), left lateral (ll), and ventral (v) views. Scale bar represents 2 mm.

Nubianophis cf. *N. afaahus*
(Figure 15)

Referred material: one vertebra (Vb-1055).

One vertebra is fairly similar to those of *Nubianophis afaahus*, but its interzygapophyseal ridges appear to be more prominent, its condyle and cotyle are wider, and its neural canal is smaller than in typical vertebrae of this species. This specimen cannot be confidently referred to *N. afaahus*.

Colubroidea Oppel, 1811

The Colubroidea are considered to be the most advanced snakes. Extant colubroids comprise the Colubridae, Atractaspididae, Elapidae, and Viperidae. Two extinct families, the Anomalophiidae and Russellophiidae, belong to the Colubroidea.

Russellophiidae Rage, 1978

The Russellophiidae, a small family, were hitherto known only in the Palaeogene. They are represented at Wadi Abu Hashim by a new taxon.

Krebsophis gen. nov.

Type species: *Krebsophis thobanus* sp. nov.

Etymology: named in honor of Prof. Dr. Bernard Krebs, Free University of Berlin.

Diagnosis: as for the type species and only known species.

Krebsophis thobanus sp. nov.
(Figures 16, 17)

Holotype: one mid-trunk vertebra (Vb-681).

Type locality: Wadi Abu Hashim, Sudan.

Horizon: Wadi Abu Hashim Member of Wadi Milk Formation; Cenomanian.

Etymology: from Al Thoban, an Arabic name for snakes.

Referred material: 6 trunk vertebrae (Vb-682 to Vb-687).

Diagnosis: A typical russellophiid as demonstrated by its elongate vertebrae, narrow and well-defined ventral surface of the centrum, highly vaulted neural arch, prezygapophyseal butresses compressed as a thick dorsoventral ridge, and characteristic inclination of prezygapophyseal facets which face slightly laterally. It differs from *Russellophis tenuis*, the only other russellophiid previously described, by its more heavily-built vertebrae, its markedly lower neural spine which is only a low keel for most of its length, its markedly more salient interzygapophyseal and subcentral ridges, and its paradiapophyses which are more dorsally situated and which face more laterally.

Description of the holotype.

The holotype is a mid-trunk vertebra that lacks the right prezygapophysis, the left postzygapophysis, and the top of the neural spine. The vertebra is small and elongate.

Measurements: length of centrum from rim of cotyle to tip of condyle, 2.7 mm; width of zygosphene, 1.4 mm; width of interzygapophyseal constriction, 1.7 mm; horizontal diameter of condyle, 0.9 mm.

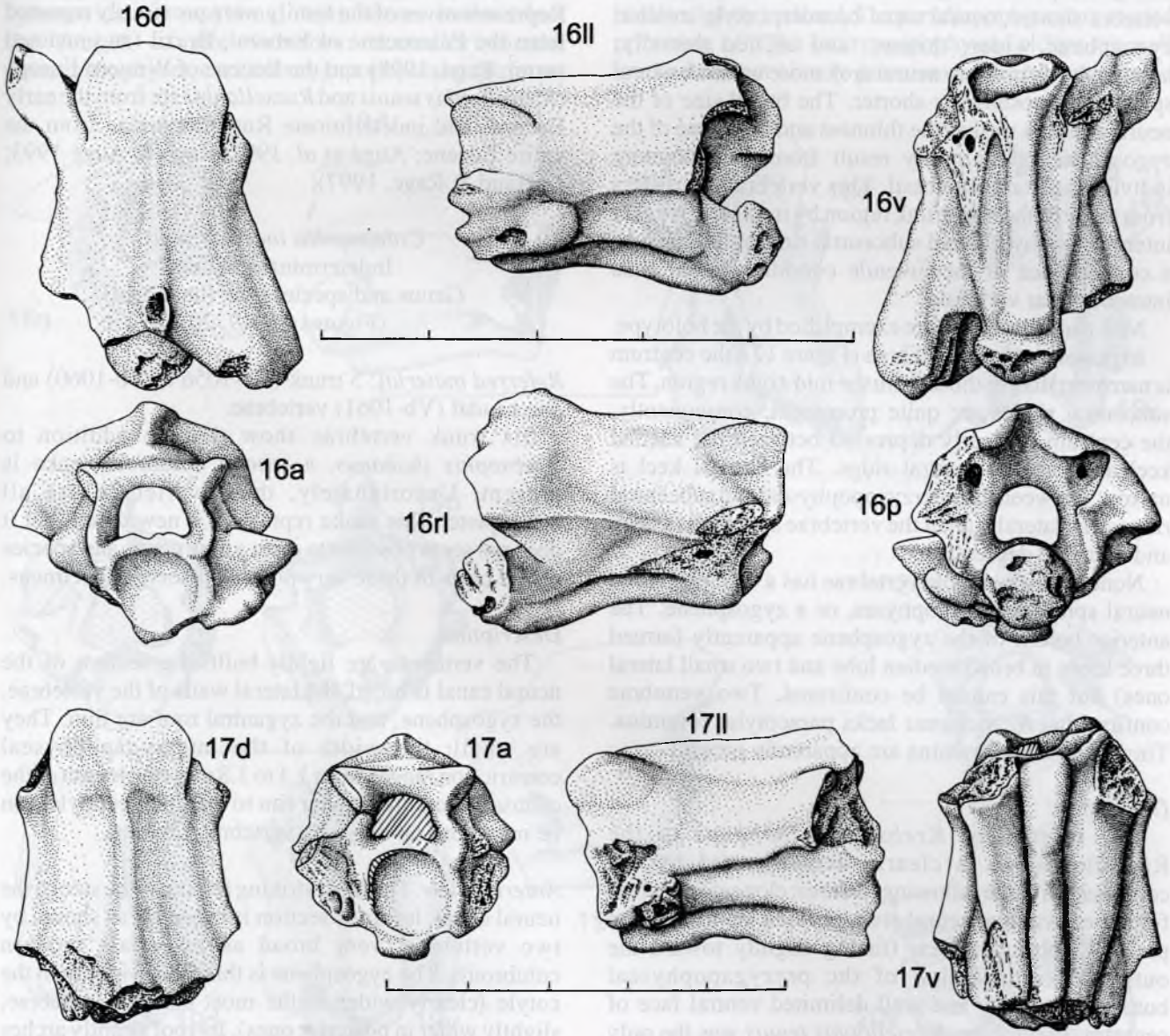
Anterior view: The section of the neural canal is semicircular; as it is rather small, the vertebra does not appear to be lightly-built. The zygosphene is not very thick and it is dorsally flat. It is slightly wider than the cotyle, which is wider than the neural canal. The zygosphenal centre is close to the centre of the cotyle. The cotyle is circular and its rim is thick. The prezygapophyseal articular facet is slightly inclined: it faces somewhat dorsolaterally. The medial border of the facet is approximately level with the floor of the neural canal. The prezygapophysis lacks a prezygapophyseal process. The fossa between the cotyle and the remaining prezygapophysis is deep; it lacks a paracotylar foramen.

Dorsal view: The interzygapophyseal constriction is strongly asymmetrical; its maximum depth is situated quite anteriorly. The zygosphene is broad; its anterior border is convex anteriorly but this shape apparently results from the erosion of small lateral lobes. The articular facet of the remaining prezygapophysis is

small, ovaloid and oblique, with its main axis at about 32° to the vertebral axis. The neural spine is a blunt keel which originates behind the zygosphene; it is narrow anteriorly and it gradually widens posteriorly. The posterior median notch is wide. On each side, the interzygapophyseal ridge forms a flat and narrow stripe which is well demarcated from the rest of the neural arch.

Lateral view: The neural spine is a low keel which rises posteriorly; in the posteriormost part of the neural arch, it probably formed a tubercle but the latter is broken off. The articular facets of the zygosphene are clearly elongate; their major axis is subhorizontal. The buttress of the prezygapophysis is somewhat compressed; it forms a thick dorsoventral ridge which extends from just beneath the prezygapophyseal articular facet to the dorsal limit of the paradiapophysis. This ridge projects anteriorly beyond the articular facet. At the level of the dorsal part of the paradiapophysis, the prezygapophyseal buttress forms a tubercle which protrudes anteriorly. The paradiapophyses are broken off. The interzygapophyseal ridges appear as well-defined and very salient keels. The subcentral ridges are moderately arched dorsally; they are thick and laterally salient. On each side, between the interzygapophyseal and subcentral ridges, the lateral wall of the vertebra appears as a triangular depression. The haemal keel is rather deep and slightly arched dorsally. The axis of the condyle appears to be horizontal or nearly horizontal. On either side, a tiny lateral foramen opens below the interzygapophyseal ridge.

Ventral view: The centrum is elongate and very narrow. The subcentral ridges are well-marked, mainly along their anterior half, and they bend slightly laterally. The haemal keel runs from the rim of the cotyle to the



Figures 16-17. Russellophiidae, *Krebsophis thobanus* gen. et sp. nov. 16: mid-trunk vertebra, Holotype (Vb-681). 17: posterior trunk vertebra (Vb-682). Anterior (a), dorsal (d), left lateral (ll), right lateral (rl), posterior (p), and ventral (v) views. Scale bars represent 5 mm.

condyle. It is blunt, relatively wide, and clearly set off from the centrum. It is slightly constricted along its middle part. Between the haemal keel and the subcentral ridges, the surface of the centrum is depressed. The subcentral foramina cannot be confidently detected.

Posterior view: The neural arch is strongly vaulted. The posterior border of the neural arch lacks parazygantral foramina. The roof of the zygantrum and the lateral walls of the neural canal are comparatively thick.

Vertebral variation.

Anterior, mid- and posterior trunk vertebrae are known but no caudal vertebra is available.

Only one anterior trunk vertebra was found (Vb-687). It probably belongs to a juvenile individual as shown by its small size and depressed cotyle. Its prezygapophyses, paradiapophyses, and neural spine are broken off. This vertebra differs from mid-trunk vertebrae by characters that correspond to known intracolumnar variation: vertebra shorter; neural canal broader; cotyle smaller; zygosphene wider, thinner, and arched dorsally; hypapophysis present; neural arch more vaulted; neural spine anteroposteriorly shorter. The broad size of the neural canal as well as the thinness and the shape of the zygosphene might partly result from the immature individual age of this fossil. This vertebra also differs from those of the mid-trunk region by its clearly weaker interzygapophyseal and subcentral ridges; this may be a consequence of the juvenile condition rather than intracolumnar variation.

Mid-trunk vertebrae are exemplified by the holotype.

In posterior trunk vertebrae (Figure 17), the centrum is narrower than in those from the mid-trunk region. The subcentral ridges are quite prominent; consequently, the centrum is clearly depressed between the haemal keel and each subcentral ridge. The haemal keel is narrow. Between the interzygapophyseal and subcentral ridges, the lateral wall of the vertebrae appears as a deep and elongate depression.

None of the available vertebrae has a well preserved neural spine, paradiapophyses, or a zygosphene. The anterior border of the zygosphene apparently formed three lobes (a broad median lobe and two small lateral ones) but this cannot be confirmed. Two vertebrae confirm that *K. thobanus* lacks paracotylar foramina. Tiny subcentral foramina are apparently present.

Discussion.

The referral of *Krebsophis thobanus* to the Russellophiidae is clearly demonstrated by the combination of the following features: elongate vertebral form, very vaulted neural arch, peculiar slanting of the prezygapophyseal facets (facing slightly toward the outside), compression of the prezygapophyseal buttresses, narrow and well delimited ventral face of centrum. Previously, *Russellophis tenuis* was the only named species allocated to this family (Rage 1975b, 1984).

The vertebral morphology diagnosing the Russellophiidae from other snakes is distinctive. However, within this family, *Krebsophis* may be easily distinguished from *Russellophis*. *Krebsophis* is more heavily-built: the zygosphene, the cotylar rim, the lateral walls of the vertebrae, and the roof of the zygosphene are thicker than in the Eocene taxon. The cotyle and condyle are larger than in *Russellophis*. On the other hand, in *Russellophis* the neural spine is a rather high lamina, while in *Krebsophis* it is a low keel for most of its length. Although the paradiapophyses are not preserved in *Krebsophis*, it may be inferred from the remaining parts that they were more dorsally placed and that they faced less ventrally than in *Russellophis*. The interzygapophyseal and subcentral ridges are markedly less prominent in the latter genus. These differences in vertebral morphology lead to the placement of the Sudanese species in a separate genus.

Krebsophis is the earliest Russellophiidae. Representatives of the family were previously reported from the Palaeocene of Itaboraí, Brazil (an unnamed taxon; Rage, 1998) and the Eocene of Western Europe (*Russellophis tenuis* and *Russellophis* sp. from the early Eocene, and indeterminate Russellophiidae from the entire Eocene; Augé *et al.* 1997; Rage & Augé 1993; Duffaud & Rage, 1997).

Colubroidea incertae sedis
Indeterminate family
Genus and species new (unnamed)
(Figures 18, 19, 20)

Referred material: 5 trunk (Vb-1056 to Vb-1060) and one caudal (Vb-1061) vertebrae.

Six trunk vertebrae show that, in addition to *Krebsophis thobanus*, a second colubroid snake is present. Unfortunately, these vertebrae are all incomplete. This snake represents a new taxon, but it does not seem possible to erect a new genus and species on the basis of these very poorly preserved specimens.

Description.

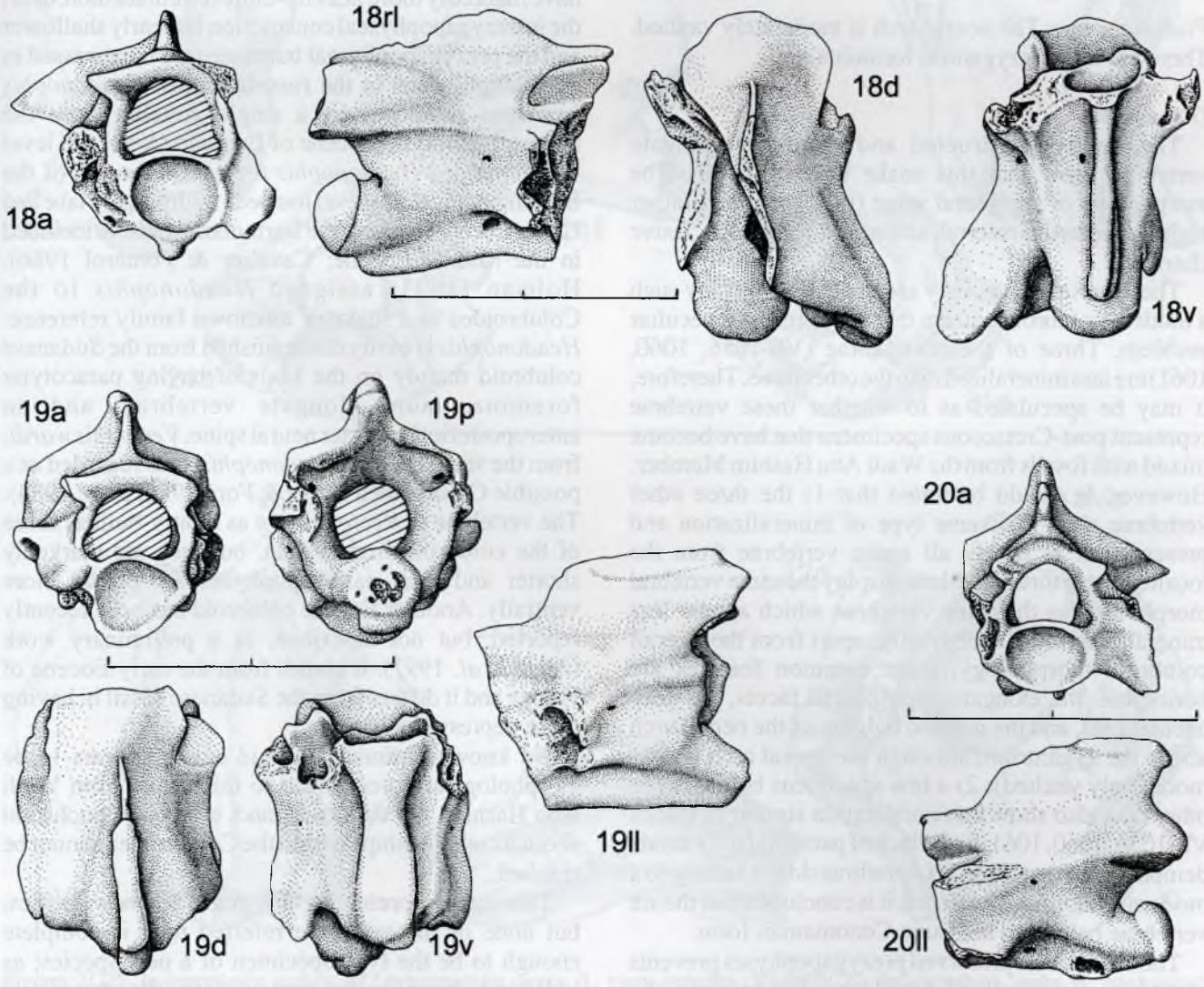
The vertebrae are lightly-built: the section of the neural canal is broad, the lateral walls of the vertebrae, the zygosphene, and the zygantral roof are thin. They are small: the width of the interzygapophyseal constriction ranges from 1.1 to 1.8 mm (the length of the centrum, from the cotylar rim to the tip of condyle, can be measured on only one vertebra: 1.8 mm).

Anterior view. The most striking feature is the size of the neural canal: its cross-section is broad or, as shown by two vertebrae, very broad as in certain modern colubroids. The zygosphene is thin. It is wider than the cotyle (clearly wider in the most anterior vertebrae, slightly wider in posterior ones). Its roof slightly arches dorsally (it is more convex in the caudal vertebra). The cotyle is circular to slightly depressed, small in the most anterior vertebra, broader in the other specimens. None

of the specimens retains a fully preserved prezygapophysis. On the most complete prezygapophysis (Vb-1056), the small preserved part of the articular facet is hardly inclined above the horizontal (Figure 19a); the inclination, if any, is different from that in the Russellophiidae: the facet would face slightly dorsomedially as in practically all snakes in which the facets are not horizontal. The level of the facet lies above the floor of the neural canal, at about one-third of the height of the canal. The precise shape of the prezygapophyseal buttress cannot be determined; however, the remaining parts of the buttress (observable on two vertebrae) show that it was probably not compressed. The paradiapophyses faced ventrolaterally. In the caudal vertebra, the paradiapophyses are replaced by either lymphapophyses or pleurapophyses (Figure 20). Paracotylar foramina are lacking.

Dorsal view. The vertebrae appear elongate. The interzygapophyseal constriction is well-marked and symmetrical; its maximum depth occurs at about half the length of the vertebra. Anterior to the postzygapophyses, each interzygapophyseal ridge forms a narrow and flat area; anteriorly, this flat area reaches only the bottom of the interzygapophyseal constriction, whereas in *Krebsophis* it reaches the posterior limit of the prezygapophysis. The zygosphene is broad; its anterior border forms a very wide central lobe and two small lateral lobes. On the most anterior vertebra available (Vb-1057; Figure 18d), the central lobe strongly protrudes anteriorly. The neural arch swells markedly above the zygantrum. The neural spine is a thin and rather high lamina which extends from the posterior part of the zygosphenal roof to the posterior border of the neural arch. In the only posterior trunk vertebra (Vb-1056), its dorsal edge is slightly thickened; this thickening is very weak in the caudal vertebra. The median notch in the posterior border of the neural arch is shallow. The posterior part of the neural spine overhangs the notch.

Lateral view: The neural spine is comparatively high. Its anterior and posterior borders are inclined posteriorly. The zygosphenal facets are elongate and their long axis is only slightly inclined. The paradiapophyses are eroded or broken off. The interzygapophyseal ridges are well marked but not clearly prominent. The haemal keel is



Figures 18-20. Colubroidea *incertae sedis*, indeterminate family, unnamed new genus and species. 18: relatively anterior trunk vertebra (Vb-1057). 19: posterior trunk vertebra (Vb-1056). 20: caudal vertebra (Vb-1061). Anterior (a), dorsal (d), left lateral (ll), right lateral (rl), posterior (p), and ventral (v) views. Scale bars represent 2 mm.

deep; its ventral border is almost straight. In the most anterior vertebra (Vb-1057), the keel is deep even beneath the cotyle rim where it projects prominently ventrally. In the caudal vertebra, the haemal keel is replaced by paired haemapophyses. The lateral foramina occupy a rather anterior position.

Ventral view: The centrum is elongate, narrow, and rather well delimited by subcentral ridges; however, these ridges are not salient. The haemal keel is well marked off from the centrum and narrow, except in the posterior trunk vertebrae in which it is rather wide and spatulate (as defined by Auffenberg 1963). Anteriorly, the haemal keel reaches the rim of the cotyle and posteriorly it approaches the condyle. The ventral surface of the centrum is approximately flat between the haemal keel and the subcentral ridges, except in the posterior trunk vertebrae in which it is concave and forms a depression on either side of the keel. On the caudal vertebra, paired haemapophyses were present far anteriorly from the condyle (Figure 20 Il). Subcentral foramina are present but they are not visible on all vertebrae.

Posterior view: The neural arch is moderately vaulted. There are no parazygantral foramina.

Discussion.

The lightly constructed and relatively elongate vertebrae show that this snake is a colubroid. The morphology of the neural spine (thin, long, and rather high) supports this referral, although it is not a conclusive character.

These vertebrae, as they are preserved, display such a modern colubroid pattern that they present a peculiar problem. Three of these vertebrae (Vb-1056, 1060, 1061) are less mineralized than the other three. Therefore, it may be speculated as to whether these vertebrae represent post-Cretaceous specimens that have become mixed with fossils from the Wadi Abu Hashim Member. However, it should be noted that 1) the three other vertebrae show the same type of mineralization and preservation as nearly all snake vertebrae from the locality; these three vertebrae display the same vertebral morphology as the three vertebrae which appear less mineralized (more specifically, apart from the overall colubroid morphology, three common features are noticeable: the elongate zygosphenal facets, the deep haemal keel, and the marked bulging of the neural arch above the zygantrnm, although the neural arch is only moderately vaulted); 2) a few specimens belonging to other taxa also show a mineralization similar to that of Vb-1056, 1060, 1061; 3) the lack of paracotylar foramina demonstrates that these six vertebrae do not belong to a modern colubroid. Therefore, it is concluded that the six vertebrae belong to the same Cenomanian form.

The lack of well preserved prezygapophyses prevents comparisons with all colubroid taxa. For example, the overall morphology of this fossil is clearly reminiscent of the Colubridae: as the specimens are preserved, only the absence of paracotylar foramina argues against their referral to this family. The Colubridae range from the late Eocene to the Present (Rage *et al.* 1992). The presence of Colubridae in the middle part of the Cretaceous would be very surprising. Only vertebrae with well-preserved prezygapophyses might permit identification at family level of this colubroid from Sudan.

This snake from Wadi Abu Hashim may be also compared with other extinct Colubroidea: Anomalophiidae, Russellophiidae, *Headonophis*, *Vectophis*. Except the russellophiid *Krebsophis,* all these colubroids come from the Eocene. Although it was indicated in the preliminary report that this colubroid from Sudan might be referred to the Russellophiidae (Werner & Rage 1994: 250), such an assignment should be discarded. This colubroid from Wadi Abu Hashim clearly differs from the Russellophiidae by its notably less vaulted neural arch, normal inclination of prezygapophyseal facets, and probably non-compressed prezygapophyseal buttresses. The Anomalophiidae, represented only by *Anomalophis bolcensis* from the early Eocene of Italy (Auffenberg 1959; Rage 1984), have markedly more heavily-built vertebrae; moreover, the interzygapophyseal constriction is clearly shallower and the prezygapophyseal buttresses are compressed in anomalophiids as in the russellophiids. *Headonophis harrisoni* is known by a single vertebra from the uppermost Middle Eocene of England (*Note:* the level which yielded *Headonophis* represents the top of the Bartonian stage; this level has been traditionally labelled Upper Eocene, but now the Bartonian should be included in the Middle Eocene; Cavelier & Pomerol 1986). Holman (1993) assigned *Headonophis* to the Colubroidea as a snake of unknown family reference. *Headonophis* is easily distinguished from the Sudanese colubroid mainly on the basis of having paracotylar foramina, more elongate vertebrae, and an anteroposteriorly shorter neural spine. *Vectophis wardi*, from the same beds as *Headonophis*, was regarded as a possible Colubroidea (Rage & Ford 1980; Rage 1984). The vertebrae of *Vectophis* are as lightly-built as those of the colubroid from Sudan, but they are markedly shorter and their paradiapophyses are placed more ventrally. Another Eocene colubroid has been recently reported, but not described, in a preliminary work (Augé *et al.* 1997). It comes from the early Eocene of France and it differs from the Sudanese fossil in having more depressed vertebrae.

No known extinct colubroid snake appears to be morphologically very close to this snake from Wadi Abu Hashim. On the other hand, a precise conclusion about its relationships within the Colubroidea cannot be reached.

This snake represents a new genus and new species, but none of the vertebrae referred to it is complete enough to be the type-specimen of a new species; as indicated above, in the present case, the absence of well-preserved prezygapophyses is especially incompatible with the erection of a new taxon. It is

therefore appropriate to leave this new genus and species unnamed for the present.

Indeterminate snakes

Indeterminate snake A
(Figure 21)

Referred material: one mid-trunk vertebra (Vb-689).

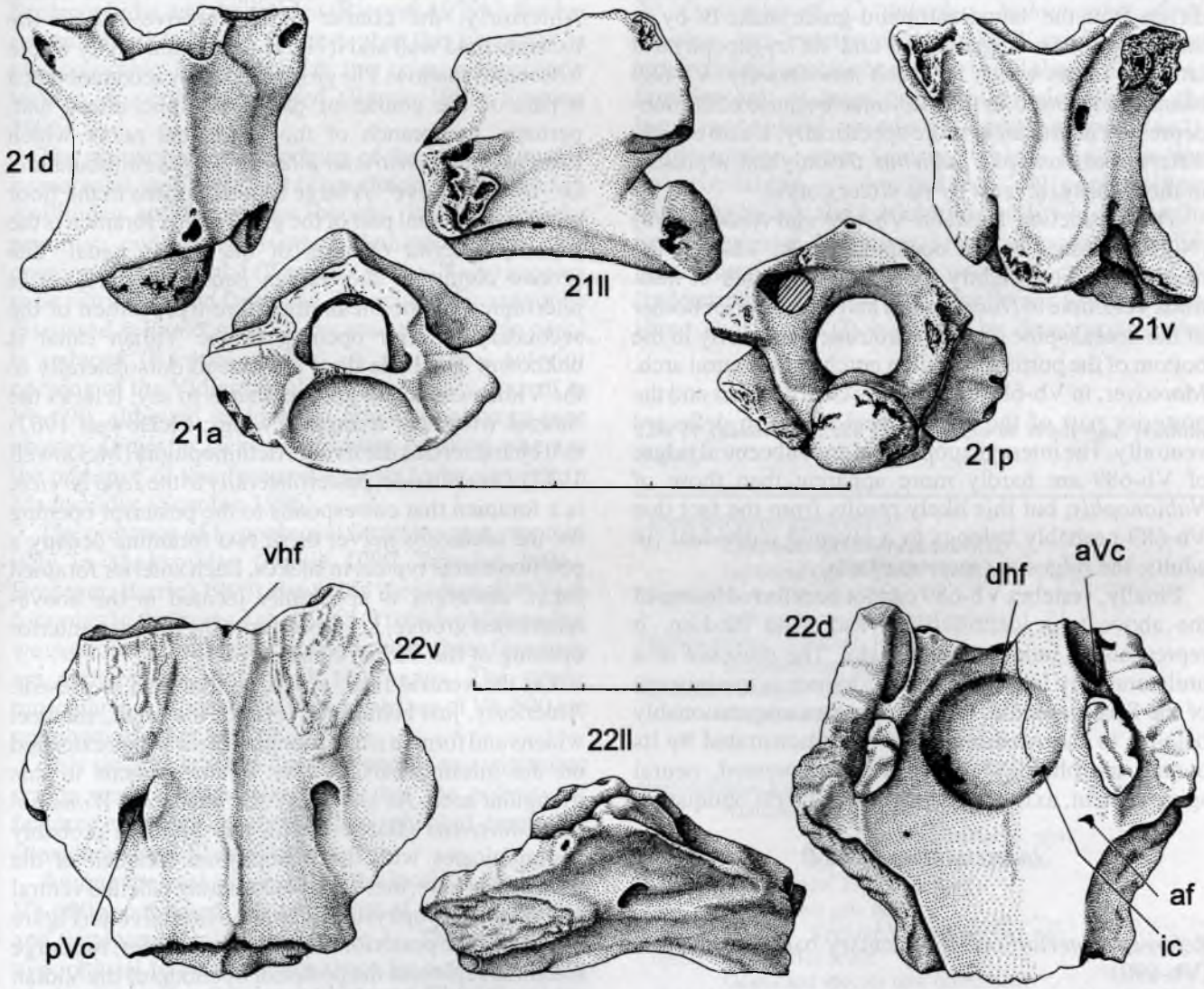
One poorly preserved vertebra cannot be identified. Because of its depressed cotyle and condyle, poorly marked interzygapophyseal and subcentral ridges, and poorly developed postzygapophyseal articular facets, it probably represents a juvenile individual.

Description.

The vertebra lacks the zygosphene, both prezygapophyses, and the right postzygapophysis. The paradiapophyses are eroded.

Measurements: length of centrum from cotylar rim to tip of condyle, 2.5 mm; width of interzygapophyseal constriction, 2.1 mm; horizontal diameter of cotyle, 1.3 mm.

The vertebra is somewhat elongate and, despite its probable juvenile stage, it is rather heavily-built. The depressed cotyle is wider than the neural canal. The size of the zygantrum suggests that the zygosphene was wider than the cotyle. On the anterior face, the depressions, on either side of the cotyle, apparently lack paracotylar foramina. The interzygapophyseal constriction is shallow. The neural spine consists of a long, low and blunt anterior keel with a shorter and higher posterior part (the full height of the latter part remains unknown). The median notch in the posterior border of the neural arch appears as a shallow and wide embayment. The interzygapophyseal and subcentral ridges are rather weak. The axis of the condyle is clearly inclined. Tiny lateral foramina are perhaps present. The



Figures 21-22. Indeterminate snakes. 21: indeterminate snake A, trunk vertebra (Vb-689). 22: Indeterminate snake B, fragmentary basiparasphenoid (Vb-690). Anterior (a), dorsal (d), left lateral (ll), posterior (p), and ventral (v) views. af: *abducens* nerve foramen, aVc: primary anterior opening of Vidian canal, dhf: dorsal hypophysial foramen, ic: internal carotid foramen, pVc: posterior opening of Vidian canal, vhf: ventral hypophysial foramen. Scale bars represent 5 mm.

ventral face of the centrum does not markedly widen anteriorly; it bears a wide and blunt haemal keel which is strongly constricted at mid-length. A very large subcentral foramen opens on the left side; the right foramen cannot be detected. The neural arch is clearly, but not strongly, vaulted. The posterior border of the neural arch lacks parazygantral foramina.

Discussion

Because of the state of preservation of Vb-689, full comparisons cannot be made. This vertebra is comparatively heavily-built, therefore it cannot be referred to the Colubroidea. The vertebrae of the Palaeophiidae display a very peculiar morphology (more specifically, presence of pterapophyses) that differs markedly from that of Vb-689. The absence of parazygantral foramina, as well as the probable lack of paracotylar foramina, are not consistent with the Madtsoiidae. Vb-689 cannot be referred to the 'lapparentophiid-grade snake A' because of the morphology of the neural spine and the shallowness of the posterior median notch in the neural arch. It clearly differs from the 'lapparentophiid-grade snake B' by its markedly wider zygosphene and its zygapophyseal articular facets which lie much less dorsally. Vb-689 cannot be referred to the Aniliidae because of its non-depressed neural arch; more specifically, it also clearly differs from *Coniophis dabiebus*, the only aniliid present in the locality, at least by its wider cotyle.

The distinction between Vb-689 and *Nubianophis* (Nigerophiidae) is less conspicuous. In Vb-689, the neural arch lies slightly more ventrally than in mid-trunk vertebrae of *Nubianophis* and the posterior border of the neural spine does not protrude posteriorly in the bottom of the posterior median notch of the neural arch. Moreover, in Vb-689 the cotyle is clearly wider and the posterior part of the haemal keel is not so deflected ventrally. The interzygapophyseal and subcentral ridges of Vb-689 are hardly more apparent than those of *Nubianophis*; but this likely results from the fact that Vb-689 probably belongs to a juvenile individual (in adults, the ridges are more marked).

Finally, vertebra Vb-689 cannot be referred to one of the above taxa identified at Wadi Abu Hashim. It represents an indeterminate snake. The presence of a unilateral very large subcentral foramen is reminiscent of the Scolecophidia, but this vertebra unquestionably belongs to the Alethinophidia as demonstrated by its overall morphology (vertebra not depressed, neural spine present, axis of zygapophyseal facets oblique...).

Indeterminate snake B
(Figure 22)

Referred material: one fragmentary basiparasphenoid (Vb-690).

This specimen is the only skull bone from the locality belonging to a snake. It is impossible to decide the proper association of this bone with the fossils described above.

Description.

Vb-690 corresponds to the posterior part of a basiparasphenoid, i.e., approximately the basisphenoid part of the bone. Anteriorly, it is missing the cultriform process. The remnant is almost hexagonal.

The dorsal face bears a deep, circular, and well defined *sella turcica* (= hypophyseal, or pituitary, fossa). The wall of the *sella turcica* is subvertical and higher along the posterior half of this fossa than along the anterior half. Posteriorly, this wall is pierced by two foramina for the internal carotids (= cerebral carotids). Anteriorly, a sagittal foramen opens at the base of the wall; this foramen is the hypophysial foramen (Scanlon 1996), awkwardly named cerebral foramen by Barrie (1990) (this foramen is not the cerebral foramen of Underwood 1967: 17). There is no *crista sellaris* posterior to the *sella turcica*. The anterolateral borders of the fragment are very thick; they form the uneven sutural edge for the posteroventral edges of the parietal. Each of these two thick edges is hollowed by a deep longitudinal groove that is open dorsally. The groove is located approximately dorsal to the Vidian canal. Anteriorly, the course of the groove leaves the basisphenoid wall and it enters the cranial cavity where it becomes shallow. The groove probably accommodated a part of the course of the ophthalmic artery and, perhaps, the branch of the trigeminal nerve which innervates the *constrictor internus dorsalis* musculature, i.e., the 'cid nerve'. A large foramen opens in the floor of the intracranial part of the groove; this foramen is the primary anterior opening of the Vidian canal. The groove continues the Vidian canal anteriorly; it is interrupted by the break, therefore the position of the secondary anterior opening of the Vidian canal is unknown. The bone does not extend dorsolaterally to the Vidian canal and groove, that is to say, it lacks the 'lateral wing' (= 'triangular wing'; McDowell 1967) that characterizes the living Alethinophidia (McDowell 1987). On each side, posterolaterally to the *sella turcica*, is a foramen that corresponds to the posterior opening for the *abducens* nerve; these two foramina occupy a position that is typical in snakes. Each anterior foramen for *n. abducens* is apparently located in the above-mentioned groove, i.e. posterior to the primary anterior opening of the Vidian canal.

On the ventral face, a thin sagittal keel is present. Anteriorly, just behind the level of the break, the keel widens and forms a small triangular area which extended on the missing part. A tiny foramen opens in this triangular area. As shown by the madtsoiid *Wonambi naracoortensis* (Barrie 1990), this foramen probably communicates with the hypophysial foramen of the dorsal face; here, these two foramina are labelled ventral and dorsal hypophysial foramina respectively (Figure 22v, d). In the posterior half of the remainder, two large foramina represent the posterior openings of the Vidian canals. The two Vidian canals show similar diameters. As a result of the position of these openings, the Vidian canals are not short. None of the basipterygoid processes is preserved. Obviously, the anterior part of the bone is

broken off, but there is no indication of prominences anteriorly; therefore, it may be questioned whether these processes were present. On each side, a broad corrugated surface extends between the anterior border of the bone and the posterior opening of the Vidian canal. These surfaces probably correspond to the areas of insertion for *m. protractor pterygoidei.*

Discussion.

Vb-690 clearly differs from the basisphenoid of scolecophidians. In these snakes, the *sella turcica* is very close to the posterior limit of the bone and the Vidian canal is a groove (Rieppel 1979a). On the other hand, the lack of lateral wings is a feature known only in scolecophidians (McDowell 1967), Madtsoiidae (Scanlon 1996) and the late Cretaceous *Dinilysia* (Estes *et al.* 1970). According to Rieppel (1979a), it is difficult to demonstrate whether the absence of the wings is a plesiomorphic or derived character; but the above-mentioned systematic distribution argues for a primitive condition.

The absence of a *crista sellaris* characterizes the Scolecophidia and Anilioidea (Rieppel 1979b). Such a systematic distribution suggests that this character is plesiomorphic. In Madtsoiidae, this *crista* is apparently lacking or poorly developed (Barrie 1990; Scanlon 1996).

The primary anterior opening of the Vidian canal is intracranial in Vb-690. This condition is observed in Anilioidea and in various booids; it would be the primitive condition. In other alethinophidians, this opening is extracranial (Rieppel 1979b). It also appears to be extracranial in *Dinilysia*. This character cannot be discussed in Scolecophidia, because their Vidian canal is reduced (Rieppel, 1979a). A secondary anterior opening of the Vidian canal was necessarily present in Vb-690, although its location remains unknown (see above). *Dinilysia* lacks a secondary opening whereas the presence of this foramen appears to be variable in Madtsoiidae (Scanlon 1996).

The presence of hypophysial foramina was reported only in Madtsoiidae (Barrie 1990; Scanlon 1996). However, Barrie (1990) also noted the presence of such foramina in the living *Trachyboa* (Tropidophiidae), but we cannot confirm Barrie's observation; these foramina are perhaps not constant in this genus. The strong muscular insertions on the ventral surface of Vb-690 are unknown in other snakes.

This set of characters does not permit an assignment within snakes, especially given that the polarity of features exhibited by the basiparasphenoid cannot be considered as well established.

Among the snakes present in the locality, the size of Vb-690 is consistent only with that of the Madtsoiidae and 'lapparentophiid-grade snake A'. The presence of hypophysial foramina might argue for a referral to the Madtsoiidae. But differences between Vb-690 and the known madtsoiid basiparasphenoids are marked: the specimen from Sudan has broad muscular insertions on the ventral face and it perhaps lacks basipterygoid processes; however, a referral to this family cannot be definitively ruled out. On the other hand, snakes of the lapparentophiid-grade are known only by vertebrae, therefore we cannot discuss the possible referral of this basiparasphenoid to this assemblage. As a result, Vb-690 may belong to the Madtsoiidae, to a lapparentophiid-grade family, or to a still unknown family.

CONCLUSION

The Cenomanian of Wadi Abu Hashim has yielded a snake fauna that is an amazing mixture of advanced and very primitive forms (Table 2). It comprises at least nine species (perhaps 12), representing at least seven families (perhaps ten). The nine species are: 'lapparentophiid-grade snake A', 'lapparentophiid-grade snake B', an indeterminate genus and species of Madtsoiidae, an indeterminate genus and species presumably belonging to the Palaeophiidae, *Coniophis dabiebus* sp. nov. (Aniliidae), *Nubianophis afaahus* gen. et sp. nov. (Nigerophiidae), *Krebsophis thobanus* gen. et sp. nov. (Russellophiidae), an unnamed colubroid gen. et sp. nov. (indeterminate family), and 'indeterminate snake A'. *Coniophis* cf. *C. dabiebus*, *Nubianophis* cf. *N. afaahus*, and 'indeterminate snake B' might represent either distinct species or species listed above. The seven families are: at least one family belonging to the lapparentophiid grade (Lapparentophiidae?), Madtsoiidae, one family which may be the Palaeophiidae, Aniliidae, Nigerophiidae, Russellophiidae, and a colubroid family which is not the Russellophiidae. Moreover, 1) the two lapparentophiid-grade forms may belong to two distinct families, 2) 'indeterminate snake A' may also belong to a family not listed above, and 3) it cannot be demonstrated that

TABLE 2.
List of snakes from the Cenomanian of Wadi Abu Hashim, Sudan.

Lapparentophiid-grade snakes
Lapparentophiid-grade snake A
Lapparentophiid-grade snake B
Madtsoiidae Hoffstetter, 1961
Indeterminate genus and species
?Palaeophiidae Lydekker, 1888
Indeterminate genus and species
Aniliidae Fitzinger, 1826
Coniophis Marsh, 1892
Coniophis dabiebus sp. nov.
Coniophis cf. *C. dabiebus*
Nigerophiidae Rage, 1975
Nubianophis gen. nov.
Nubianophis afaahus sp. nov.
Nubianophis cf. *N. afaahus*
Russellophiidae Rage, 1978
Krebsophis gen. nov.
Krebsophis thobanus sp. nov.
Colubroidea *incertae sedis*
Genus and species new (unnamed)
Indeterminate snakes
Indeterminate snake A
Indeterminate snake B

'indeterminate snake B', i.e. the basiparasphenoid, belongs to one of the above-mentioned families.

Wadi Abu Hashim has produced the earliest Madtsoiidae, Nigerophiidae, Russellophiidae, and Palaeophiidae – if the identification of the latter family proves correct. The presence of Colubroidea (Russellophiidae and an indeterminate family) was particularly unexpected. Previously, the oldest colubroids were reported from the early Eocene. However, on the basis of molecular and palaeontological data, combined with biogeography, Cadle (1988) presumed that some extant lineages of Colubroidea may have originated during the Cretaceous (without more precision) or earliest Tertiary. The presence of extinct colubroid lineages in the Cenomanian might corroborate Cadle's estimate.

The fauna includes aquatic forms (*Nubianophis afaahus* and the presumed Palaeophiidae), which is consistent with the palaeoenvironment (Bussert, 1998; see above). *Coniophis* was either fossorial or secretive. The other taxa do not show morphological traits which could indicate a peculiar mode of life.

The fossils from Wadi Abu Hashim rank among the oldest known snakes. If the fossil from the Barremian of Spain (Rage & Richter 1994) is not a snake (see above), then the oldest snake remains are only slightly older (late Albian) than those from Sudan. Astonishingly, these Sudanese snakes make up a fauna which is very rich and diverse having regard to its geological age. It is by far the earliest known snake fauna. Apart from Wadi Abu Hashim, other Cretaceous localities yielded at most three taxa represented by rare specimens (e.g., Campanian or Maastrichtian of Cerro Cuadrado, Argentina; Albino 1986). Faunas remain poor and rare in Palaeocene beds. The only rich and diverse faunas from the Palaeocene are those from Itaboraí (Middle Palaeocene, Brazil; Rage 1998) and, to a lesser degree, Adrar Mgorn (Late Palaeocene, Morocco; Gheerbrant *et al.* 1993). Rich and diverse snake faunas are relatively frequent only from the Early Eocene onwards.

From the diversity of the fauna from Wadi Abu Hashim it can be inferred that snakes have had a pre-Cenomanian history, perhaps a rather long one, in Africa. This continent played an important role in the early radiation of snakes. Moreover, if the fossil from the Barremian of Spain is not a snake, the fauna from Sudan may also suggest that Africa is the cradle of snakes, although a snake has been recently recovered from the mid-Cretaceous of North America (Gardner & Cifelli, 1999).

Three of the four higher taxa ('superfamilies') of extant Alethinophidia (Anilioidea, Acrochordoidea, Colubroidea) were therefore present as early as the Cenomanian. But the presence at that time of the fourth 'superfamily', namely the Booidea, and of the sister group of the Alethinophidia, that is the Scolecophidia, may be extrapolated from the recognized phylogenies (Rieppel 1988; Kluge 1991; Cundall *et al.* 1993; Rage 1997). Therefore, the major lineages of living snakes were individualized as early as the mid-Cretaceous. The snake fauna from the Cenomanian of Wadi Abu Hashim documents several of these lineages and thus represents a very important landmark in the history of snakes.

ACKNOWLEDGEMENTS

We wish to acknowledge the financial support of the German Research Foundation (Grant: Kr 477/11-1). Dr Peter Meylan and Dr Van Wallach made helpful suggestions which have improved the text.

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Palaeont. afr., **35**, 111-118 (1999)

RECOGNITION OF NEOTYPE SPECIMENS FOR SPECIES DESCRIBED FROM THE ARNOT PIPE, BANKE, NAMAQUALAND, SOUTH AFRICA.

by

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ABSTRACT

Important palynological studies were completed by Scholtz (1985) on material from the Arnot Pipe on the farm Banke in Namaqualand, Northern Cape Province. The results comprised a rare record of early Tertiary vegetation in southern Africa. The body of Scholtz's research consisted of systematic, descriptive palynology including the description of one new genus and fifteen new species. Ongoing research into South Africa's Tertiary palynology requires that the type specimens from Arnot be used for comparative purposes. However, the microscope slides on which they were founded were not available for examination. Another set of slides, representing two of the seven samples taken at Arnot, was used to search for neotype specimens to replace the missing holotypes. Specimens representing all fifteen new species were found, but were often badly preserved, obscured by debris or trapped between air bubbles as the condition of the decade-old microscope slides had deteriorated. Only specimens in good condition were selected as neotypes, and comprehensively illustrated. Four of Scholtz's new species were transferred to alternative, more applicable, genera.

KEYWORDS: Palynology, Tertiary, Arnot

INTRODUCTION

An important palynological study was completed by Scholtz (1985) on material from the Arnot Pipe on the farm Banke, in Namaqualand, Northern Cape Province, South Africa (Figure 1). The study documented a rare record of early Tertiary vegetation in southern Africa. Such records are sparse because of the paucity of deposits and palynologically productive sites. With continuing research, additional sites are being discovered, creating a demand for comparative studies utilising the Arnot material, especially as far as the type specimens of the genera and species erected by Scholtz are concerned.

However, it was discovered that the Arnot microscope slides were not available as they had not been archived as documented by Scholtz (1985). Their absence, and particularly that of the type specimens, presented a problem for researchers. The current project to nominate neotype specimens was initiated following an extensive search to locate the slides that Scholtz worked on.

Traverse (1996) stated that the loss of type specimens is a common problem in palaeopalynology and it may occur in one of three ways. Firstly, the preservation may not have been adequate or the slides may have deteriorated despite the best attempts at preservation. Secondly, locating the type specimen on a strew slide may not be possible as grains may migrate within the mounting medium with time. Thirdly, researchers may not strictly obey the ICBN rules demanding that slides containing type specimens are archived in a recognised institution because strew slides may contain hundreds of specimens worthy of future research. This last appears to be applicable to Scholtz's slides.

The microscope slides used for the current study are duplicates of those used by Scholtz and prepared by him from the same macerated material but represent only two of the seven samples (52'-58' and Unprovenanced). They are currently archived in the Palaeontology Department at the South African Museum in Cape Town. The ICBN Code provides for neotypification to cater for situations where the holotype has been lost (Traverse 1996). According to Voss *et al.* (1983) in Section 2 on Typification, Article 7, point 8, "a neotype is a specimen or other element selected to serve as nomenclatural type as long as all of the material on which the name of the taxon is based is missing". The specimens nominated in this paper were regarded as being neotypes rather than lectotypes because a degree of uncertainty existed regarding in which sample the original types were found. If the original type had been found in Sample 52'-58', a lectotype must also be recognised from Sample 52'-58'. With the existing information, the exact derivation of the original type specimens could not be confirmed.

A second important facet of the current project was the redesignation of several of the new species to alternative genera. It was discovered during the course of the project that various species were not placed into the most appropriate genus and their transfer was recommended.

The project was successful in locating specimens which could be related to all fifteen new species described by Scholtz (1985). However, many of the

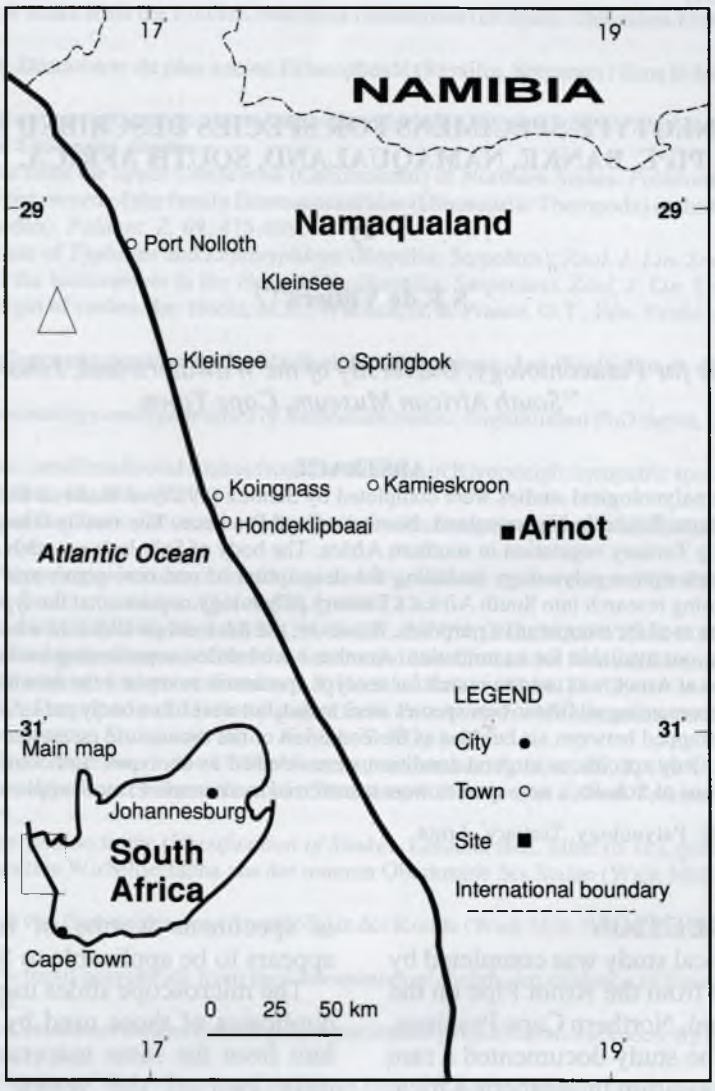


Figure 1. Locality Map

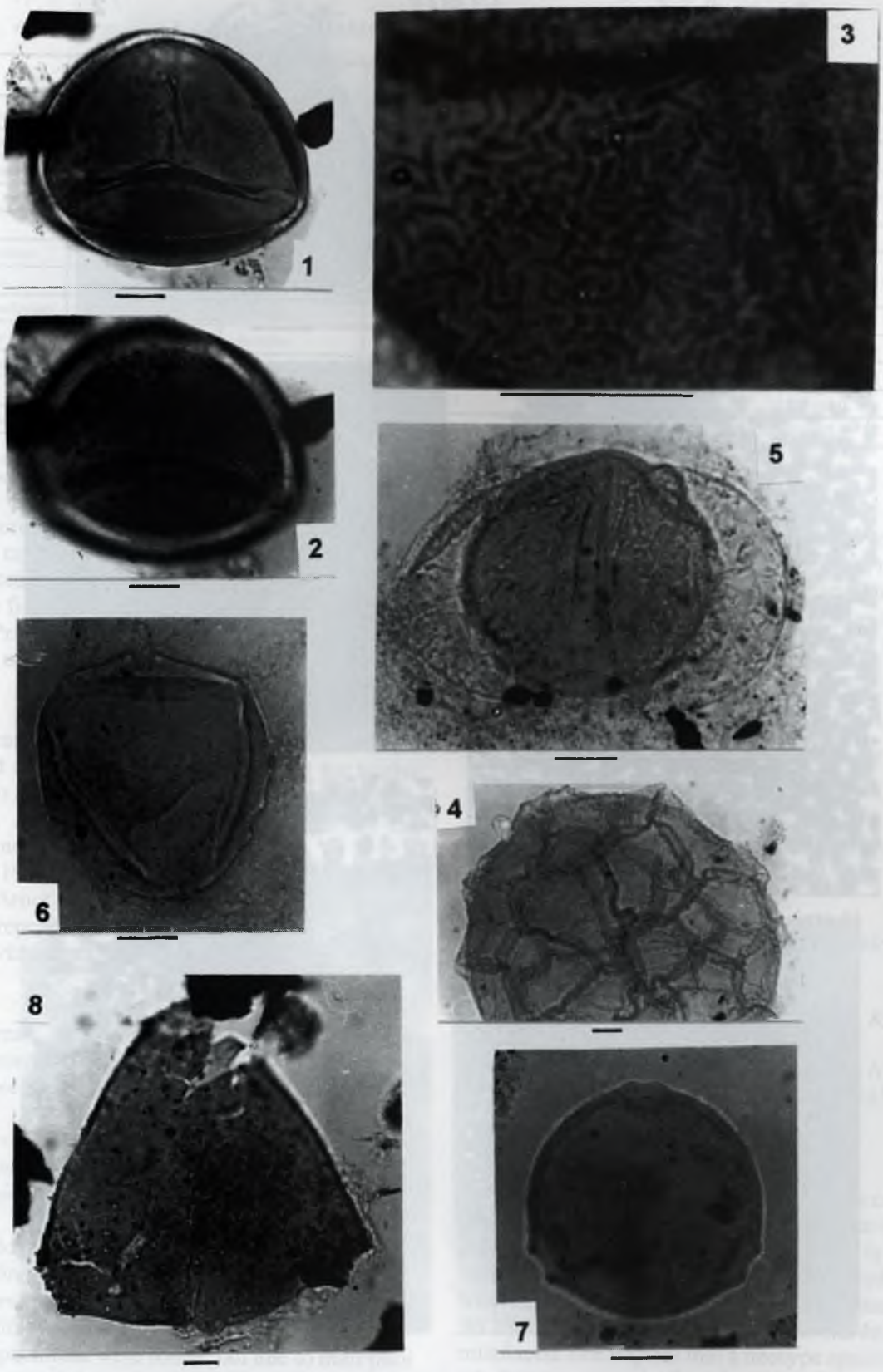
specimens were either badly preserved, obscured by debris or trapped between air bubbles. Only grains in good condition were considered as candidates for nomination as neotype specimens.

MATERIALS AND METHODS

As reported in Scholtz (1985), material was collected from an excavation at the Arnot Pipe during the 1930s by geologists. The samples were archived at the South African Museum and used for various palaeontological studies, including a palynological examination by Kirchheimer (1934).

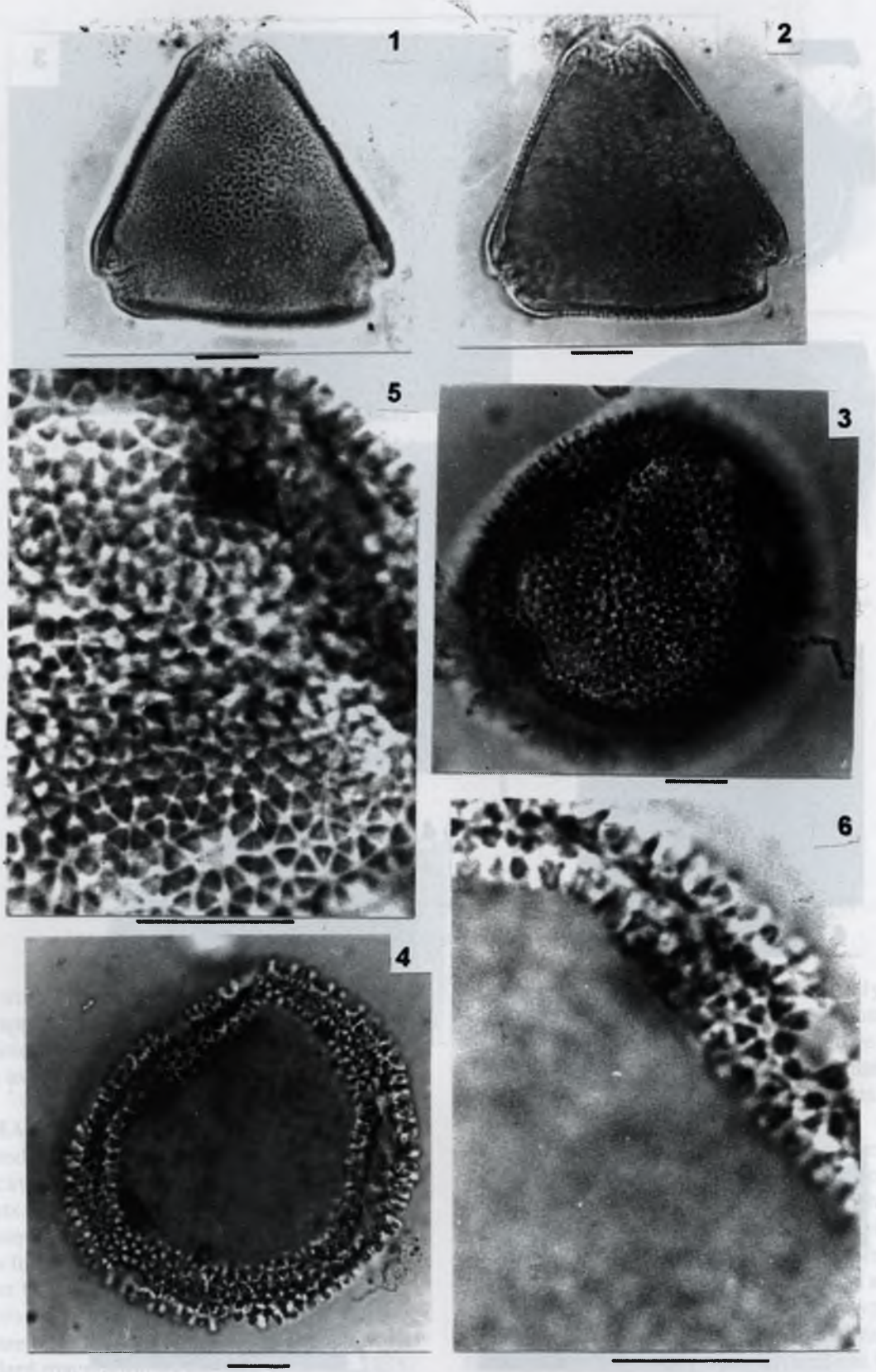
The microscope slides used for the current study were prepared by Scholtz from the above samples using standard maceration techniques (Scholtz 1985). They represent only two of the seven samples from Arnot (52'-58' and Unprovenanced). The slides had deteriorated somewhat since they were prepared a decade ago and contained many air pockets. They were not repaired or remounted for two reasons. Firstly, it was not known whether or not Scholtz had worked on these slides and already isolated important specimens. If the slides were remounted, the location of such specimens would be lost. Secondly, if the repair work was unsuccessful, the only available macerated material might be rendered unusable. It was thus decided to examine the slides before attempting any repair work, in the hope that representatives of the new species could be found and neotypes nominated with no further intrusive action.

The current microscope work was carried out using a Leitz Laborlux 12 POL light microscope equipped with a Wild MPS 51 camera with a Wild Photoautomat MPS 45 light monitor. Photomicrographs of specimens which represented Scholtz's new species were targeted. Each photographed specimen was assigned an individual specimen number. For example, the neotype specimen for *Reticulatasporites grandis* was photographed on film number 315 and the negative of the first shot in which it appeared is 39. The specimen number thus becomes 315-39. A record card was created for each specimen, containing data such as the number of the relevant slide, with its co-ordinates according to the Museum's Leitz microscope. The specimens were compared with the published illustrations and descriptions in Scholtz (1985) to determine whether they conformed to the species and the most representative specimen was chosen as the neotype.



All scale bars = 10µm

Plate 1. Light microscopy: 1. *Camarozonosporites bankiensis*. Psilate proximal face; 2. Same specimen, distal face with hamulate sculpturing; 3. Same specimen, detail of sculpturing; 4. *Reticulatasporites grandis*. Whole grain; 5. *Podocarpidites riembreekensis*. Whole grain, showing distal tenuitas; 6. *Triorites operculatus*. Polar view. Pores do not have operculae; 7. *Triorites sphericus*. Polar view; 8. *Triporopollenites namaquaensis*. Polar view of damaged specimen.



All scale bars = 10μm

Plate 2. Light microscopy: 1. *Propylipollis meyeri*. Polar view, showing sculpturing in polar area; 2. Same specimen, with focus on structure of pores; 3. *Grootipollis reuningii*. Whole grain, showing arrangement of pores; 4. Same specimen, focussing on structure of exine; 5. Same specimen, showing detail of sculpture adjacent to pores; 6. Same specimen, showing detail of exine structure.

TABLE 1
Register of Neotype Specimens

Original genus	New Genus	species name	Neotype specimen no	Sample	Slide no	Co-ordinates*	Plate
Camarozonosporites	No change	*bankiensis*	317-1	"Unprov."	11	5.5 x 126	1 (1, 2, 3)
Reticulatasporites	No change	*grandis*	315-39	"Unprov."	5	11.5 x 131.0	1 (4)
Podocarpidites	No change	*riembreekensis*	313-13	52'-58'	10	10.0 x 115.5	1 (5)
Triorites	No change	*operculatus*	313-24#	52'-58'	9	6.0 x 110.0	1 (6), 4 (1)
Triorites	No change	*sphericus*	315-24	"Unprov."	5	9.5 x 132.0	1 (7), 4 (2)
Triporopollenites	No change	*namaquensis*	315-13	"Unprov."	11	5.0 x 105.0	1(8), 4 (3)
Propylipollis	No change	*meyeri*	310-11	52'-58'	7	3.5 x 101.0	1 (1,2)
Tricolporopollenites	*Simpsonipollis*	*grandis*	314-39	52'-58'	10	15.0 x 120.0	3 (2)
Tricolporopollenites	*Rhoipites*	*brinkiae*	310-27	52'-58'	10	6.5 x 117.0	3 (3)
Tricolporopollenites	*Verrutricolporites*	*coetzeeae*	315-10	"Unprov."	11	3.0 x 132.5	3 (4), 4 (4)
Grootipollis	No change	*reuningii*	314-1	"Unprov."	4	14.0 x 103.0	2 (3-6), 4 (3)
Triporotetradites	No change	*sphericus*	311-26	52'-58'	7	17.7 x 110.5	3 (1)

** On microscope at South African Museum*
 # Not nominated as neotype

The microscope slides were redeposited in the Museum's collection, together with photomicrographs and data from each species. The negatives and specimen cards were filed in the palynological collection of the Bernard Price Institute for Palaeontology at the University of the Witwatersrand.

RESULTS

Specimens of all fifteen species under consideration were found and neotypes were nominated for twelve of them. No amendments to Scholtz's descriptions are suggested. A compilation of information on the nominated neotypes is given in Table 1.

Scholtz (1985) included SEM photographs of several of the new Arnot species, but the images were trimmed. They are reproduced in this paper from Scholtz's negatives without alteration.

Systematic palynology

Trilete spores
Camarozonosporites bankiensis
Neotype specimen 317-1 (Plate 1 nos 1, 2, 3)

Alete spores
Reticulatasporites grandis
Neotype specimen 315-39 (Plate 1 no 4)

Saccate pollen
Podocarpidites riembreekensis
Neotype specimen 313-13 (Plate 1 no 5)
Podocarpidites kamiesbergensis

Several specimens were found, but due to their poor condition none of them were chosen as the neotype. Microphotographs of the specimens and their location on the slides were archived.

Porate pollen
Triorites operculatus

Several specimens were found, but none of them were chosen as the neotype because their pores did not exhibit operculae, which is a diagnostic feature of the species. Scholtz (1985) mentioned in the original description that the operculum is sometimes absent from the pore. Specimen 313-24 (Plate 1 no 6) is a good example of the species, apart from the missing operculae.

NB. Plate 4 no 1 is the same as Scholtz (1985) Fig 13 I.

Triorites sphericus
Neotype specimen 315-42 (Plate 1 no 7)
NB. Plate 4 no 2 is the same as Scholtz (1985) Fig 13 H.

Triporopollenites namaquensis
Neotype specimen 315-13 (Plate 1 no 8)
NB. Plate 4 no 3 is the same as Scholtz (1985) Fig 14 A.

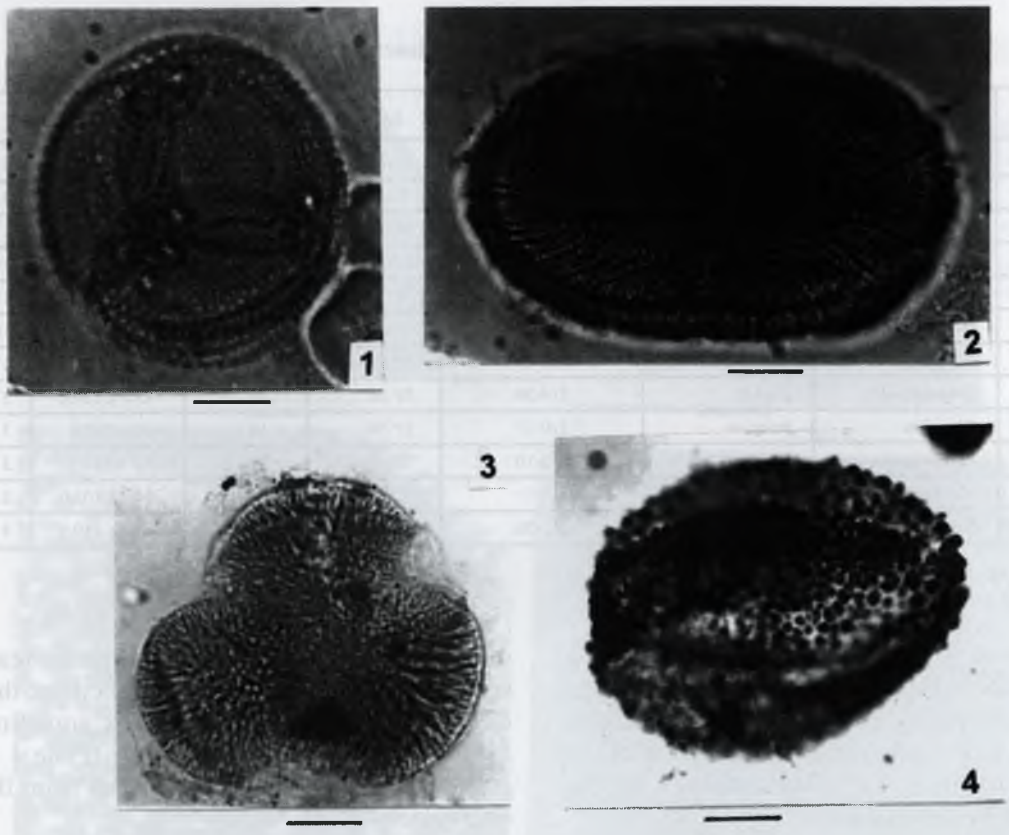
Propylipollis meyeri
Neotype specimen 310-12 (Plate 2 nos 1 & 2)
Grootipollis reuningii
Neotype specimen 314-1 (Plate 2 nos 3 - 6)
NB. Plate 4 no 3 is the same as Scholtz (1985) Fig 19 A.

Colpate pollen
Genus *Spinitricolpites*

Scholtz erected a new genus to accommodate spherical medium to large sized, tricolpate spiniferous pollen grains. The genus included the type species found at Arnot (*S. jennerclarkei*), and another species from New Zealand was transferred to it (*S. latispinosus*). As the type specimen for *S. jennerclarkei* has been misplaced, this implies that a neotype specimen for the whole genus must be found.

Spinitricolpites jennerclarkei

Specimens were found, but due to their poor condition none of them were chosen as neotypes. Microphotographs of the specimens and their location on the slides were archived. The lack of a well-preserved specimen in this case is more significant as it is required to represent a genus as well as a species.



All scale bars = 10μm

Plate 3. Light microscopy: 1. *Triporotetradites sphericus*. Whole grain, showing arrangement and structure of monads within tetrad; 2. *Simpsonipollis grandis*. Equatorial view, showing colpus and zonorate pores; 3. *Rhoipites brinkiae*. Polar view; 4. *Verrutricolporites coetzeeae*, showing verrucate sculpture.

Colporate pollen

Remarks. Scholtz (1985) does not comment on the reason for choosing to place several species within the genus *Tricolporopollenites*. There are two main reasons for challenging this designation. Firstly, according to Jansonius & Hills (1976), *Tricolporopollenites* may be considered a junior synonym of *Rhoipites*. *Tricolporopollenites* was erected in 1953 by Pflug & Thomson (Thomson & Pflug 1953) and *Rhoipites* in 1933 by Wodehouse. Secondly, *Tricolporopollenites* has a very widely circumscribed diagnosis. As the name suggests, it requires only that constituate forms possess three meridional colpi with pores. As such, it could accommodate all fossil tricolporate pollen species. By Tertiary times, palynofloras were dominated by tricolporate pollen, produced bymany families of dicotyledonous angiosperms. It is thus more useful to assign species to genera with more constrained diagnoses, which take into consideration relevant variations in aperture morphology, exine structure and sculpturing, and botanical affinities where possible.

Simpsonipollis grandis

Neotype specimen 314-39 (Plate 3 no 2)

This appeared in Scholtz (1985) as *Tricolporopollenites grandis* and should be transferred to *Simpsonipollis*. Srivastava (1975) established *Simpsonipollis* to accommodate tricolporate grains with a striate sculpture. Kemp & Harris (1977) make further comments on the validity of this genus. Scholtz (1985) indicated that the sculpturing was one of the diagnostic features of this species, so it should be placed within the genus which differentiates striate tricolporate pollen from all other types. However, striate tricolporate grains are common throughout the Tertiary and are produced by many modern families of dicot angiosperms (Muller 1968).

Rhoipites brinkiae

Neotype specimen 310-27 (Plate 3 no 3)

This appeared in Scholtz (1985) as *Tricolporopollenites brinkiae* and should be transferred to *Rhoipites* because *Tricolporopollenites* may be considered a junior synonym of *Rhoipites*. Therefore, this species reverts to the genus with priority.

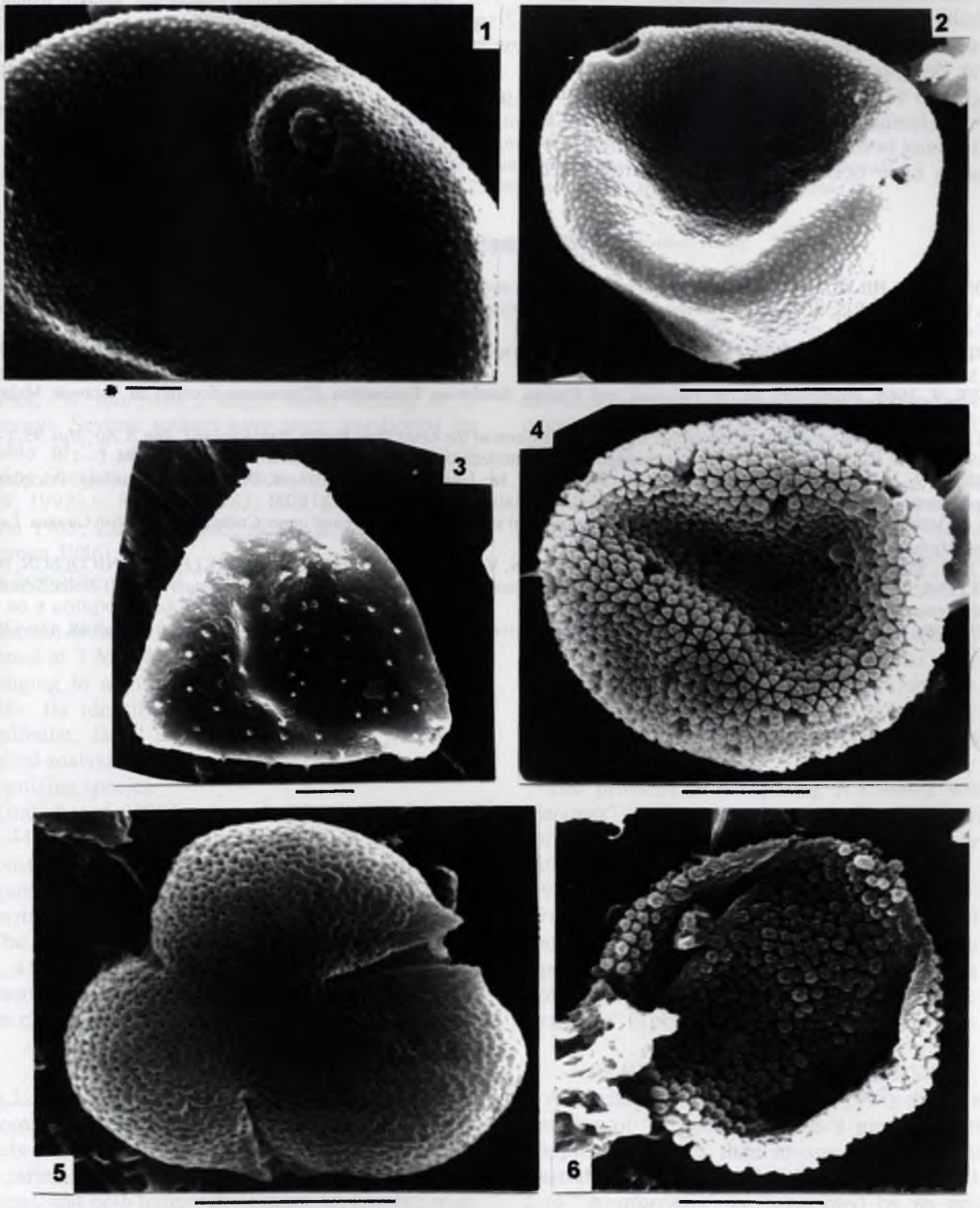
Rhoipites arnotiensis

No neotype nominated because the solitary specimen of the species found was in poor condition. This appeared in Scholtz (1985) as *Tricolporopollenites arnotiensis* and should be transferred to *Rhoipites* for the reason given above for *R. brinkiae*.

Verrutricolporites coetzeeae

Neotype specimen 315-10 (Plate 3 no 4) NB. Plate 4 no 4 is the same as Scholtz (1985) Fig 18 I.

This appeared in Scholtz (1985) as *Tricolporopollenites coetzeeae* and should be transferred to *Verrutricolporites* as this genus was established by van der Hammen & Wymstra (1964) to accommodate tricolporate pollen grains with a verrucate sculpture. As with *Simpsonipollis grandis*, the sculpturing is one of the diagnostic features of this species, so it should be placed within the genus which differentiates verrucate tricolporate pollen from other tricolporate pollen.



All scale bars = 10μu, except * = 1μm

Plate 4. SEM photography: 1. *Triorites operculatus*. Detail of pore with operculum; 2. *Triorites sphericus*. Polar view; 3. *Triporopollenites namaquensis* in Table 1. Polar view; 4. *Grootipollis reuningii*. Whole grain, showing arrangement of pores; 5. *Rhoipites brinkiae*. Oblique view; 6. *Verrutricolporites coetzeeae*, showing verrucate sculpture.

Pollen found as tetrads

Triporotetradites sphericus

Neotype specimen 311-27 (Plate 3 no 1)

DISCUSSION

This project intended merely to replace lost type specimens, not ratify the estimated Palaeocene age of sediments or the reconstruction of the palaeoflora given by Scholtz (1985).

Three of the new species found at Arnot remain without designated neotypes, although specimens belonging to the species are now archived and can be used for reference purposes. The slides used for this project cannot be repaired or remounted as the neotype specimens have been recorded with particular co-ordinates and the condition of the slides cannot now be altered. Neotype specimens for the remaining species await maceration of additional material from Arnot.

The possibility exists that the original slides will be rediscovered, and that the holotypes will thus be reinstated.

ACKNOWLEDGEMENTS

This research project was carried out entirely within the Department of Palaeontology of the South African Museum, Cape Town. I would like to thank the Departmental Staff for the use of microscope and photographic equipment, and for technical help and assistance.

Prof J A Coetzee, Prof L Scott and Dr C Gow kindly reviewed the manuscript.

SEM photography was completed by Mr A Scholtz.

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Palaeont. afr., **35**, 119-129 (1999)

TAXONOMIC STATUS OF THE SKULL A.L.444-2 FROM THE PLIOCENE OF HADAR, ETHIOPIA

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ABSTRACT

A nearly complete hominid skull, A.L.444-2, from the Pliocene of Hadar in Ethiopia, has been attributed to *Australopithecus afarensis* Johanson, White & Coppens 1978. Comparative morphological analysis indicates that it may not conform to this species. Cranial and dental morphology and measurements of A.L.444-2 agree more closely with those of *A. africanus* Dart 1925, to which it could be reassigned.

KEYWORDS: "*Australopithecus afarensis*"; *Australopithecus africanus*; Hadar.

INTRODUCTION

In 1980 Tobias suggested that the Hadar/Laetoli fossil hominoids which had been described as a new species, "*A. afarensis*", might rather belong to *A. africanus*. Several authors have since questioned the validity of "*A. afarensis*" as representing a single species (Leakey 1981; Ferguson 1983, 1986, 1987, 1989, 1992a,b; Schmid, 1983; Falk & Conroy 1983; Olson 1985; Zihlman 1985; Senut & Tardieu 1985, Shipman 1986).

A complete skull of "*A. afarensis*" was not found and so a composite skull was reconstructed by White (Johanson & Edey 1981). A new fossil skull, A.L.444-2, dated at 3 Myr from Hadar, has been identified as belonging to a male "*A. afarensis*" (Kimbel *et al.* 1994). Its identification was based primarily on mandibular, facial and calvarial features without a detailed analysis of the dentition, which is important in recognizing species.

Kimbel *et al.* (1994) assert that the morphology of A.L.444-2 is consistent with that of White's composite reconstruction of a purported male "*A. afarensis*" skull (Figure 1), and that it refutes suggestions that "*A. afarensis*" represents more than one species.

The purpose of this study is to test whether skull A.L.444-2 really confirms the validity of "*A. afarensis*" as a single species, or if it might conform more closely to *A. africanus*.

MATERIAL AND METHODS

A.L.444-2 comprises a partial mandible, right zygomatic, most of the nasal bones and frontal with attached anteromedial segments of the parietals, the left parietal, the occiput with attached posterior right parietal, and both temporals (Figure 1c; Kimbel *et al.* 1994). The anterior cranial base and most of both temporal squamae are missing. The frontal, maxilla and zygomatic are without contacts and their positions relative to each other are uncertain. There is post depositional deformation of the palate, which is compressed along the midline. The right side of the frontoparietal fragment and supraorbital are uplifted. The left zygomatic arch is twisted and the right elevated. The nuchal plane is pushed into the cranial cavity. The endocranial capacity has not yet been determined.

Dentition consists of the right mandibular fragmentary left and right incisors, partial right C and damaged P_4-M_1, the maxillary right I^1, C, P^4-M^3 and left I^1, C, P^3-M^3. Measurements have been obtained for the better preserved maxillary teeth, RC, LP^4, and LM^1-LM^3.

In this study A.L.444-2 is compared with White's composite reconstruction of "*A. afarensis*" and Sts 5 (representing *A. africanus* from Sterkfontein, South Africa) (Figure 1). The data used includes the same information used by Kimbel *et al.* (1994) in identifying A.L.444-2.

The problem in comparing A.L.444-2 with "*A. afarensis*" is that the hypodigm for the latter may comprise more than one species, denial not withstanding (Kimbel *et al.* 1994). Johanson & Taieb (1976) referred some specimens from Hadar to *A. aff. africanus*. In 1979, Johanson and White acknowledged that single specimens can be similar to specimens representing other species. Several specimens have features and measurements that conform to those of "*A. africanus*" (Tobias 1980; Ferguson 1987).

RESULTS AND DISCUSSION

According to Kimbel *et al.* (1994) the character complex of "*A. afarensis*" has a greater number of symplesiomorphies than in any species within the Australopithecinae, and that the attribution of A.L.444-2 to "*A. afarensis*" is "warranted by its primitive constellation of mandibular, facial and calvarial characters". Taxonomic assignment to a new species, however, is not usually based only on symplesiomorphic features, but also on apomorphic or derived characters (Mayr *et al.* 1953). The reason for

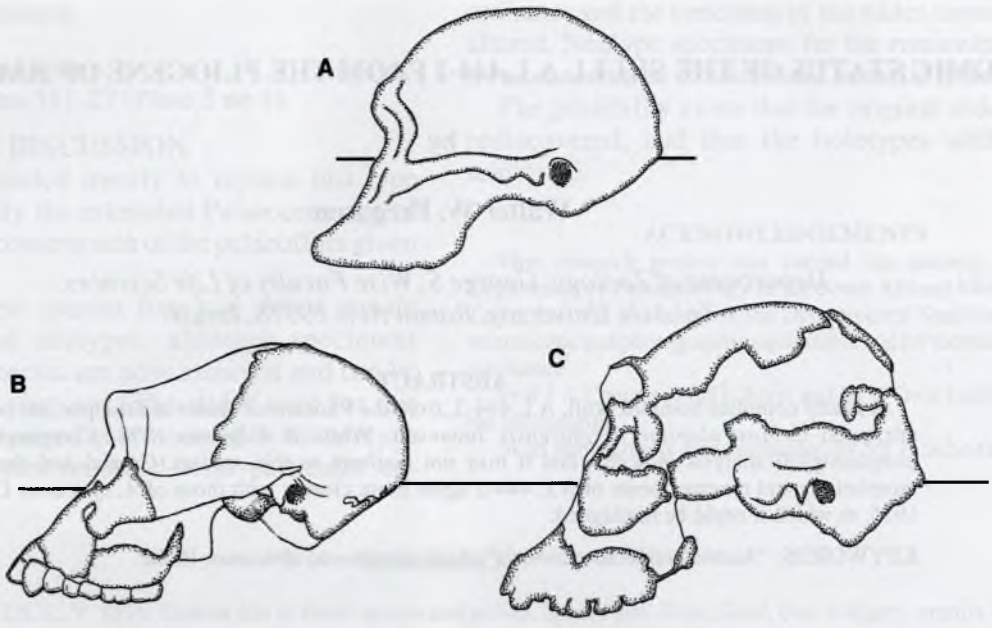

Figure 1: Hominid skulls (left *norma lateralis*). A) *A. africanus*, Sts 5, female; B) Composite reconstruction of male "*A. afarensis*" (after White); C) Reconstruction of male A.L.444-2 (reversed after Johanson & Edgar, 1996). Same relative scale.

the greater number of primitive features in "*A. afarensis*" may not be due so much to its early age, but the possibility that the hypodigm is comprised of pongid as well as hominid fossils (Ferguson 1983, 1986, 1992a,b).

In this study I wish to comment on the primitive mandibular and calvarial features on which Kimbel *et al.* (1994) base their identification of A.L.444-2 as belonging to "*A. afarensis*". Only a single dental feature is given to show its affinity to this "species".

1) Strong prognathism relative to both calvaria (no metrical expression given) and to the P^4-M^1 origin of the zygomatic process of the maxilla. *Comment*: prognathism is strong in *A. africanus* (Tobias 1967), especially in Sts 5.
2) P^4-M^1 origin of the zygomatic process of the maxilla. *Comment*: on "*A. afarensis*" it is also above P^4-M^1 (Kimbel *et al.* 1982); in *A. africanus* the origin of the zygomatic process is variable, above P^4 (Walker *et al.* 1986) or M^1 (Tobias 1967).
3) Marked projection of sagittally and transverse convex premaxilla anterior to the bicanine plane. *Comment*: this is also found in *A. africanus* (Tobias 1980).
4) Nasoalveolar clivus horizontally inclined. *Comment*: not diagnostic for "*A. afarensis*" (Johanson *et al.* 1978).
5) Extensive intranasal component of the premaxilla with step-down to nasal cavity floor. *Comment*: not diagnostic for "*A. afarensis*" (Johanson *et al.* 1978).
6) Inferior lateral nasal aperture margins sharp. *Comment*: this is sometimes found in *A. africanus* (Tobias 1967; Rak 1983).
7) "Canine fossae". *Comment*: such fossae are also found in *A. africanus* (Rak 1983).
8) Zygomaticoalveolar crests curved. *Comment*: this is speculation since the critical parts are missing; in *A. africanus* the crests are straight or slightly curved (Tobias 1967).
9) Palate flat anteriorly. *Comment*: in *Australopithecus* the palate is shallow anteriorly (Tobias 1991).
10) Diastemata 1^2-$\underline{C}$ + C-P_3. *Comment*: this is frequent or common in "*A. afarensis*" (Johanson *et al.* 1982), but not always present. Diastemata are rare in hominids (Le Gros Clark 1972).
11) Temporal lines posteriorly convergent. *Comment*: in "*A. afarensis*" temporal lines converge anteriorly (Johanson & White 1979); in *A. africanus* MLD 1 or MLD 37-38 from Makapansgat temporal lines coverage anteriorly (Tobias 1991).
12) A low, probably bifid, posterior saggital crest. *Comment*: this could occur in large *A. africanus* males (Tobias 1980, 1991).
13) Compound temporal/nuchal crest. *Comment*: this is also found in *A. africanus* (Tobias 1980).
14) Mastoid process massive and inflected beneath the cranial base with tips independent of occipital crests. *Comment*: Kimbel *et al.* (1994) make no mention of a flat posterolateral face as seen in "*A. afarensis*"; the mastoid process is well developed in known australopithecines (Le Gros Clark 1963); rather small in [female] *A. africanus* (Tobias 1991), but would be larger in males. Inferomedial inflection is not diagnostic for "*A. afarensis*" (Johanson *et al.* 1978).
15) Mandibular fossa shallow. *Comment*: it is also shallow in *H. habilis* and *A. africanus* (Tobias 1991), and in KNM-WT 17000 (Walker *et al.*

1986) attributed to "*A. aethiopicus* Arambourg & Coppens 1968", but described as a new species, *A. walkeri* Ferguson 1989.

16) Tubular tympanic plates that sit completely posterior to large postglenoid process. *Comment*: according to Walker *et al.* (1986), the postglenoid in KNM-WT 17000 is anterior to tympanic; in *A. africanus* the tympanic is intermediate and the position of the postglenoid process is variable (Walker *et al.* 1986); the feature is not diagnostic for "*A. afarensis*" (Johanson *et al.* 1978).

17) Maxillary incisors procumbent. *Comment*: this feature is not indicated in "*A. afarensis*" A.L.333-2 (Kimbel *et al.* 1982), and not diagnostic for the species (Johanson *et al.* 1978).

Mandible

Sexual differences in *H. sapiens* are more marked in the mandible than in the cranium (De Villiers 1963). The same may be true in Plio-Pleistocene hominids. Mandibles of presumed males in "*A. afarensis*" are much larger than those attributed to females of the same species, reflecting a high degree of sexual dimorphism (Johanson & White 1979). White (Johanson & Edey, 1981) argues that there is no difference between the large and small jaws from Hadar due to continuous variation. This argument is distorted and undermines the reality of differences between them. Since there is no sharp division, it is claimed there are no differences.

The variation in mandibular corpus robusticity (height/breadth index) in "*A. afarensis*" ranges from 45.5-63.8 per cent, which suggests distinct sexual dimorphism, yet the index of the male A.L.444-2-b (50.9 per cent) is virtually the same as that of the "female" A.L.417-1a (50 per cent). The lack of difference in robusticity between these two specimens does not support strong sexual dimorphism, but may indicate similar robusticity in males of two different-sized species (Table 1).

TABLE 1.
Mandible corpus metrics and index of robusticity of A.L.444-2b compared to those of "*A. afarensis*".

Hominids	Breadth (mm)	Height (mm)	Robusticity (%)
A.L.444-2b	22.0	43.2	50.9
"*A. afarensis*"			
A.L.417-1a.	18.0	36.0	50.0
Hadar sample 1970s	n=13	n=11	n=11
Range	15.6-22.4	28.0-40.5	45.5-63.8

Measured at P_4/M_3 position. Metrics after Kimbel *et al.* (1994).

In *Australopithecus* large, broad teeth are related to large masseter muscles which, in turn, are related to large, high, ascending mandibular rami (Pilbeam, 1972). A.L.444-2 is the largest *Australopithecus* cranium on record (Kimbel *et al.* 1994). The back teeth (P^4-M^3) of A.L.444-2 are 824.80 mm^2, distinctly larger than the maximum for "*A. afarensis*", 708.6 mm^2, and larger than the maximum for *A. africanus*, 733.8 mm^2. It is safe to infer that the ascending ramus of A.L.444-2 would have been at least as large as the maximum for "*A. afarensis*" and within the range of. *A africanus*. The ascending ramus of the female A.L.288-1 is within the lower range of *H. sapiens* (Kimbel *et al.* 1984). If A.L.444-2 and A.L.288-1 were conspecific as claimed, the range of sexual dimorphism of the ascending ramus height in "*A. afarensis*" (31.0-55.0) exceeds those of *A. robustus* (57.0-64.0), *A. boisei* (47.0-65.0) and *H. sapiens* (30.3-41.0).

Endocranial capacity

Tobias (1991) gives the 95 per cent limits of population range of "*A. afarensis*" as 352 - ?493 cm^3, mean ?413.5 cm^3, and *A. africanus* as 391 - 492 cm^3, mean 441.2 cm^3. With the maximum virtually the same, but the mean of *A. africanus* distinctly larger, we may assume that the maximum of *A. africanus* is probably larger than that of "*A. afarensis*". The endocranial capacity of A.L.444-2 probably exceeded 500 cm^3 (Johanson 1996), larger than in "*A. afarensis*".

Frontal

Kimbel *et al.* (1994) note that the frontal is a taxonomically important region, and that "*A. afarensis*" has many primitive features. The frontal in A.L.444-2, however, is not primitive. The supraorbital torus is vertically thick laterally and the low squama and supraorbital sulcus are unlike those of a chimpanzee. As in *A. africanus*, it has no frontal

TABLE 2.
Selected cranial metrics of fossil hominids.

	Postorbital constriction	Biasterionic breadth chord	Difference between max. & min.
A.L.444-2	77.0	106.0	
"*A. afarensis*"			26.8
A.L.162-28	-	79.2	
A.L.333-45	-	94.5	
A. africanus			10.0
MLD 1	-	85.0	
MLD 37/38	-	79.5	
Sts 5	65.5	76.0	
Sts 25	-	?77.0	
Sts 71	71.5	c86.0	
A. boisei			10.8
OH5	-	89.2	
KNM-ER 406	-	c100.0	
H. habilis			24.0
OH 13	-	84.0	
OH 16	75.5	c108.0	
OH 24	74.2	c96.0	
KNM-ER 1470	c80.0	c99.0	
H. erectus			17.0
	-	?113.0-130.0	

Metrics for "*A. afarensis*" after Kimbel *et al.* (1981); A.L.444-2 after Kimbel *et al.* (1994). The rest after Tobias (1967, 1991).

trigon, but the postorbital constriction is as advanced as in *H. habilis* (Table 2).

The postorbital constriction in *H. habilis* is described as moderately developed (Howell 1972). Since the postorbital constriction of A.L.444-2 falls within the range of *H. habilis*, and is greater than in known *A. africanus* (Tobias 1991), it indicates brain expansion, unlike "*A. afarensis*".

Biasterionic breadth

The biasterionic chord breadth gives a good measure of the capacity of the posterior part of the endocranium (Tobias 1991). Although "*A. afarensis*" is supposedly ancestral to *A. africanus* and shows no brain expansion, its biasterionic breadth is on average greater than that of *A. africanus*. This may be due to a sampling error since there are only two values for "*A. afarensis*" and the *A. africanus* sample is mostly females. The biasterionic breadth of A.L.444-2 falls in between *A. africanus* and *H. habilis* (Table 2), and clearly indicates endocranial expansion.

Johanson claims that the brain of "*A. afarensis*" is comparable in size to that of chimpanzees (Johanson & Edey 1981). The marked transverse expansion of the frontal and biasterionic breadth in A.L.444-2 indicates brain expansion greater than that of chimpanzees.

Frontobiorbital breadth index

The frontobiorbital breadth index is the postorbital breadth (constriction) in relation to superior facial breadth. The value for the frontobiorbital index in A.L.444-2 is higher than in any australopithecine or *H. habilis* crania for which data are tabulated, and closest to that of *H. habilis* (Table 3). The index for "*A. afarensis*" is unknown.

Zygomatic

In A.L.444-2 the enormous face, large, flaring cheekbones, and the bone shelf that reflects massive chewing muscles are typical of a 'robust' hominid (McAuliffe 1994). Large, flaring zygomatics are an advanced, not primitive, feature that characterizes the australopithecine lineage, including the least 'robust' member, *A. africanus*. There is no evidence or reason to believe that this specialization arose twice independently in different genera. Its presence in A.L.444-2 is clear evidence of its position early on a 'robust' branch of the Hominidae and more advanced than "*A. afarensis*". It is inconsistent with the claim that "*A. afarensis*" is the most primitive and undifferentiated of hominids (Johanson & White 1979).

Two new species of hominoids older and more primitive than "*A. afarensis*" have recently been described. The first, *Ardipithecus ramidus* (White, Suwa & Asfaw, 1994) from Ethiopia, was mistakenly classified as an *Australopithecus*, but is generally regarded as an ape and was renamed. The second is *Australopithecus anamensis* Leakey, Feibel, McDougall & Walker, 1995 from Kenya, whose holotype is an *apelike* jaw and teeth. To my mind, the only evidence for its being a hominid is a partial tibia anatomically *unassociated* with the jaws and teeth.

TABLE 3.
Frontobiorbital breadth index of hominids.

Hominids	per cent
A.L.444-2	80
A. africanus	
Sts 5	c63.4
A. robustus	
SK 48	c71.7
A. boisei	
KNM-ER 732	65.2
KNM-ER 406	56.0
OH 5	60.1
H. habilis	
OH 24	c74.2

After Tobias (1991); A.L.444-2 after Kimbel *et al.* (1994).

TABLE 4.
Dental metrics of A.L.444-2 compared to those of "*A. afarensis*" and *A. africanus*.

Hominids	C	P^3	P^4	M^1	M^2	M^3
A.L.444-2						
M/D*	10.4	-	10.6	13.7	14.2	14.9
B/L	11.5	-	14.5	15.0	15.8	16.2
"*A. afarensis*"						
M/D	8.9-11.6	7.2- 9.3	7.6- 9.7	10.8-13.7	12.1-13.5	11.4-14.3
B/L	9.3-12.5	9.8-13.4	11.1-12.6	11.2-15.0	13.4-15.0	13.1-15.55
A. africanus						
M/D	8.8-11.2**	8.5-10.0	8.2- 9.9	11.0-14.4	12.7-16.0	11.6-16.4
B/L	8.7-11.8**	10.7-14.5	12.4-13.8	12.6-15.	13.8-18.0	13.9-18.2

*Estimated (Kimbel *et al.*, 1994). *A. africanus* after Tobias (1991).
** Estimated for Sts 3 by Robinson (1956). A.L.444-2 after Kimbel *et al.* (1994); "*A. afarensis*" after Johanson & White (1979).

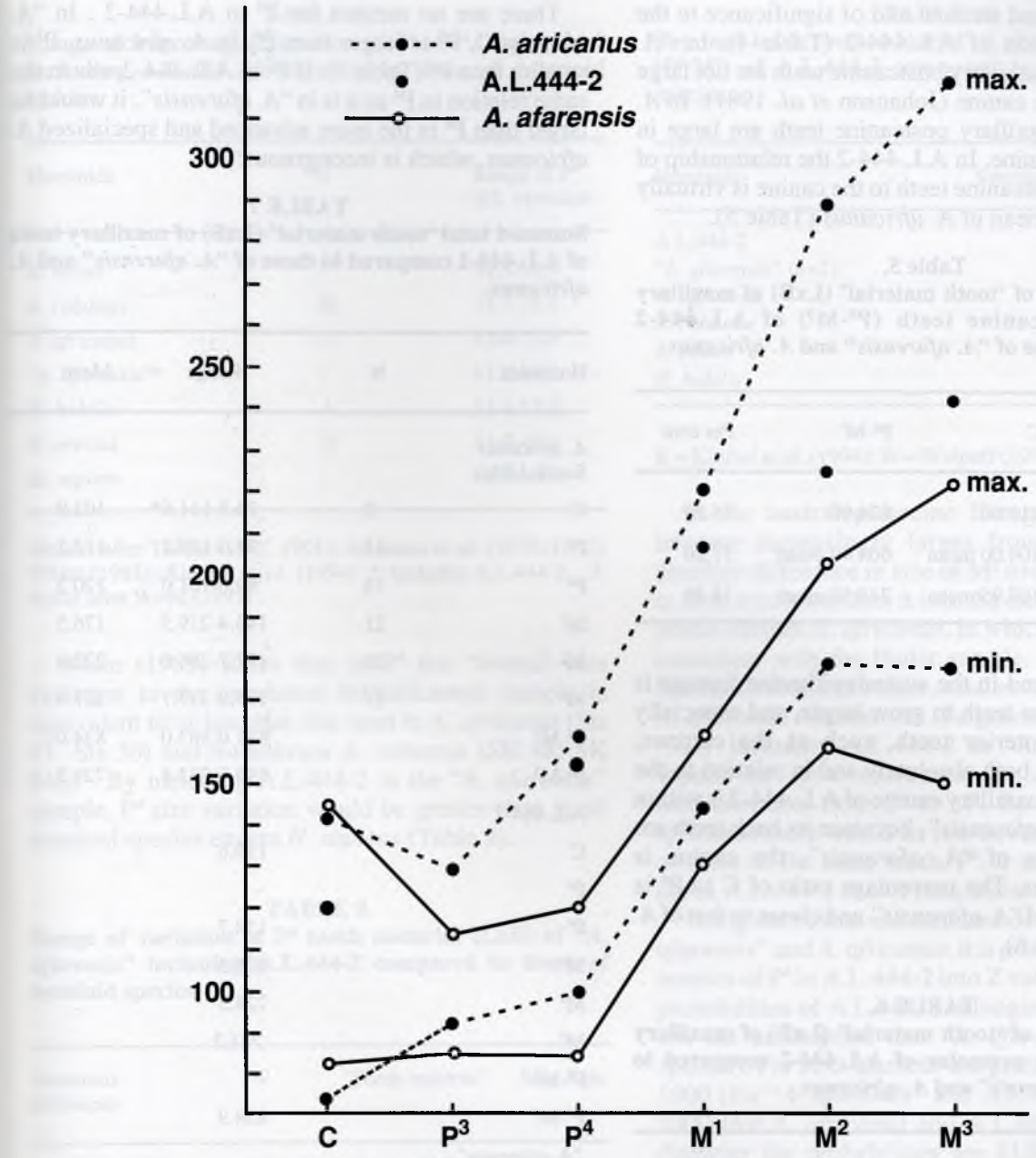

Figure 2: Graphs of maxillary 'tooth material' (C-M^3) of A.L.444-2 compared to the range of variation of *A. africanus* and "*A. afarensis*". Note that A.L.444-2 is in the upper range of *A. africanus*, whereas P^4-M^3 are above the maximum for "*A. afarensis*".

Maxilla

The maxilla and zygomatic fragments of A.L.444-2 are without contacts. In the preliminary reconstruction of A.L.444-2 the maxilla shows greater facial prognathism than in the composite reconstruction of "*A. afarensis*". It seems to be oriented incorrectly, thus creating an apelike nasoalveolar contour and an occlusal line that is unnaturally convergent with the Frankfort Horizontal anteriorly, as in the composite reconstruction of "*A. afarensis*" (Ferguson 1983). If the maxilla would be restored so that the nasoalveolar profile was straighter, then the occlusal line would take its natural, more horizontal inclination and there would be less facial prognathism.

Similarly, the zygomatic has been restored so that in relation to the maxilla the zygomaticoalveolar crest would be curved. Since the critical part is missing, it could just as well have been restored with the zygomaticoalveolar crest straight or slightly curved.

Dentition

Dentition is particularly important in hominid taxonomy. It is surprising, therefore, that apart from noting that the incisors are procumbent, the dentition of A.L.444-2 is dismissed in a single sentence by Kimbel *et al.* (1994) stating, "although the maxillary postcanine teeth are larger than any of those in the limited Hadar and Laetoli sample from the 1970s, relative to canine size they are not unusual". This is not true (Figure 2). The upper postcanine teeth are not only larger than those of "*A. afarensis*" in all M/D and B/L metrics except M^1, but are large in relation to the

canine, thus indeed unusual and of significance to the systematic position of A.L.444-2 (Table 4). In *"A. afarensis"*, the maxillary postcanine teeth are not large in relation to the canine (Johanson *et al.* 1981). In *A. africanus* the maxillary postcanine teeth are large in relation to the canine. In A.L.444-2 the relationship of the maxillary postcanine teeth to the canine is virtually identical to the mean of *A. africanus* (Table 5).

Table 5.
Percentage ratio of 'tooth material' (LxB) of maxillary canine to postcanine teeth (P^4-M^3) of A.L.444-2 compared to those of *"A. afarensis"* and *A. africanus*.

Hominids	C	P^4-M^3	Per cent
A.L.444-2	119.60	824.80	14.50
"A. afarensis"	104.00 mean	604.49 mean	17.20
A. africanus	107.95 mean	746.50 mean	14.46

The dental trend in the australopithecine lineage is for the postcanine teeth to grow larger, and especially broader. The anterior teeth, such as the canines, become smaller, both absolutely and in relation to the back teeth. The maxillary canine of A.L.444-2 is within the range of *"A. afarensis"*, but since its back teeth are above the range of *"A. afarensis"*, the canine is relatively smaller. The percentage ratio of C to P^4 is well below that of *"A. afarensis"* and closer to that of *A. africanus* (Table 6).

TABLE 6.
Percentage ratio of 'tooth material' (LxB) of maxillary canine to fourth premolar of A.L.444-2 compared to those of *"A. afarensis"* and *A. africanus*.

Hominids	C	P^4	Per cent
A.L.444-2	119.6	153.7	77.8
"A. afarensis" Hadar	104.0	100.4	96.0 mean
A.L.199-1	82.7	84.3	98.1
A.L.200-1a	102.5	101.2	101.2
A.L.333-1	124.0	112.8	90.9
A.L.333-2	(?)106.8	113.4	94.1
A. africanus	74.3-141.6	96.6 mean	85.0* mean

Tobias (1967; Table 37) gives the mean for *A. africanus* at 77.0; *A. africanus* after Wolpoff (1978). * Estimated by Robinson (1956:44).

There are no metrics for P^3 in A.L.444-2 . In *"A. afarensis"*, P^3 is larger than P^4. In *A. africanus*, P^3 is smaller than P^4 (Table 7). If P^3 in A.L.444-2 was in the same relation to P^4 as it is in *"A. afarensis"*, it would be larger than P^4 in the more advanced and specialized *A. africanus*, which is incongruous.

TABLE 7.
Summed total 'tooth material' (LxB) of maxillary teeth of A.L.444-2 compared to those of *"A. afarensis"* and *A. africanus*.

Hominids	N	Range	Mean
A. africanus South Africa			
C	7	74.3-141.6*	102.9
P^3	15	92.0-129.2	112.7
P^4	13	99.6-161.0	120.2
M^1	21	143.4-219.5	176.5
M^2	20	177.7-288.0	222.4
M^3	17	177.0-317.7	227.4
P^3-M^3		811.0-863.0	834.0
P^4-M^3		599.6-733.8	721.3
A.L.444-2			
C		119.6	
P^3		-	
P^4		153.7	
M^1		205.5	
M^2		224.3	
M^3		241.3	
P^3-M^3		-	
P^4-M^3		824.9	
"A. afarensis"			
C	10	82.7-145.0	113.8
P^3	7	84.7-124.6	107.8
P^4	6	84.3-119.7	104.1
M^1	9	129.6-162.2	145.9
M^2	3	158.1-210.8	184.4
M^3	5	149.3-215.9	182.6
P^3-M^3		606.0-833.2	724.8
P^4-M^3		521.3-708.6	617.0

Metrics of *A. africanus* after Wolpoff (1978); * Estimated by Robinson (1956); A.L.444-2 after Kimbel *et al.* (1994); *"A. afarensis"* after Johanson *et al.* (1979, 1982).

The buccolingual diameter of P^4 in A.L.444-2 is not only broader than the maximum for *"A. afarensis"* (Table 4), it even reaches the minimum of the range of variation for *A. boisei*, the most specialized of all australopithecines (Table 8).

TABLE 8.
Range of buccolingual metrics of P^4 of "*A. afarensis*" including A.L.444-2 compared to those of hominid species.

Hominids	N	Range of P^4 B/L variation
A. boisei	7	14.3-18.0
A. robustus	20	13.7-16.5
A. africanus	11	12.4-13.9
"*A. afarensis*"*	7	11.1-14.5
H. habilis	4	11.4-12.5
H. erectus	12	11.0-12.3
H. sapiens	-	8.5-10.1

Metrics after Tobias (1967, 1991); Johanson *et al.* (1979, 1982); White (1985); Kimbel *et al.* (1994). * Includes A.L.444-2 . *A. boisei* after Wood (1991).

White (1985) states that in P^4 the "overall size variation in the combined Hadar/Laetoli sample is equivalent to or less than that seen in *A. africanus* (Sts 47; Sts 30) and Swartkrans *A. robustus* (SK 48; SK 845)". By including A.L.444-2 in the "*A. afarensis*" sample, P^4 size variation would be greater than in all hominid species except *H. sapiens* (Table 9).

TABLE 9.
Range of variation of P^4 tooth material (LxB) of "*A. afarensis*" including A.L.444-2 compared to those of hominid species.

Hominids difference	N	'Tooth material'	Max-Min
"*A. afarensis*"*	5	84.3-153.7	69.4
A. africanus	13	99.6-161.0	61.4
A. robustus	30	112-5-181.0	65.5
A. boisei	5	150.9-208.9	58.0
H. habilis Olduvai	10	91.7-103.7	12.0
H. sapiens modern	318	38.5-109.8	71.3

Metrics for "*A. afarensis*" Johanson *et al.* (1979, 1982); * Includes A.L.444-2. *H. habilis* after Tobias (1991); The rest after Wolpoff (1978).

In the primitive "*A. afarensis*" the postcanine teeth average smaller than in *A. africanus*. The back teeth of A.L.444-2, however, are not only significantly larger than in "*A. afarensis*", they are well above the mean for *A. africanus* and even slightly above the mean for *A. robustus* (Table 10), but within the range of *A. africanus* (Table 7).

TABLE 10.
Summed total 'tooth material' (LxB) of maxillary teeth (P^4-M^3) of A.L.444-2 compared to those of hominid species.

Hominids	Summed crown areas (P^4-M^3)
A.L.444-2	824.8[K]
"*A. afarensis*" (n=2)	604.49 mean[K]
A. africanus	746.5 mean[W]
A. robustus	798.5 mean[W]
A. boisei	1161.3 mean[W]
H. habilis	681.24 mean[T]

K = Kimbel *et al.* (1994); W = Wolpoff (1978); T = Tobias (1991).

In the australopithecine lineage molars tend to become increasingly larger from M^1 to M^3. The absolute difference in size of M^2 over M^1 in A.L.444-2 is 18.8, much less than it is in the mean of the nominate South African *A. africanus*, in which it is 45.9. This is consistent with the Hadar sample, part of which has been described as an older, smaller-toothed subspecies, *A. africanus miodentatus* (Ferguson 1987).

By including A.L.444-2 in "*A. afarensis*" there would be new extremes in six out of eight measurements from P^4 to M^3. By including it in *A. africanus* there would be two new extremes, and both of them in the same tooth, P^4. It is obvious to which taxon A.L.444-2 shows the closest dental affinity.

Using the means and standard deviation of P^4 of "*A. afarensis*" and *A. africanus*, it is possible to convert the metrics of P^4 in A.L.444-2 into Z values which give the probabilities of A.L.444-2 belonging to either species (on the assumption that "*A. afarensis*" is a single species). For M/D diameter the probabilities are 11.9 in 1000 (for "*A. afarensis*" and A.L.444-2) and 0.47 in 1000 (for *A. africanus* and A.L.444-2). For the B/L diameter the probabilities are 11.9 in 1000 (for "*A. afarensis*" and A.L.444-2) and 1 in 1000 (for *A. africanus* and A.L.444-2). It may be concluded that on the basis of the standard deviation, it is most improbable that A.L.444-2 belongs to either taxon. One must take into account if the sample of "*A. afarensis*" is not homogenous, the results could be skewed.

In this case the statistics appear to contradict morphological facts. "*A. afarensis*" is claimed to be one of the most primitive of hominids, more primitive than *A. africanus*. In the dentition of A.L.444-2, however: 1) the canine is small in relation to the back teeth; 2) the buccolingual expansion clearly indicates advanced specialization; 3) the buccolingual diameter of P^4 is greater than the maximum known for *A. africanus*; and 4) the very large postcanine teeth reached a stage of molarization greater than in "*A. afarensis*", but within the upper range of *A. africanus*. The dentition of A.L.444-2, therefore, cannot be considered more primitive than in *A. africanus*.

Sexual dimorphism

In *Australopithecus* there is little sexual dimorphism in the size of the back teeth (Robinson 1956). By including A.L.444-2 in "*A. afarensis*", the maximum sexual difference in P^4 would be distinctly greater than in all *Australopithecus* species and closest to that of modern *Homo* (Table 9).

The maximum sexual difference in the post canine teeth (P^4-M^3) of *A. africanus* is 18.3 per cent. In "*A. afarensis*" it is 26.5 per cent without A.L.444-2. The difference between the male A.L.444-2 and the female "*A. afarensis*" A.L.199-1 is a surprising 35.8 per cent. In other words, by including A.L.444-2 in "*A. afarensis*" the sexual dimorphism in the back teeth would be as much as *twice* that of *A. africanus*.On the basis of sexual dimorphism, the back teeth of A.L.444-2 are much too big to belong to the same taxon as A.L.199-1.

Johanson notes that in A.L.444-2 a number of teeth are heavily worn, right down to the dentine, although the individual was only in its thirties at the time of death (McAuliffe 1994). This is inconsistent with the teeth of "*A. afarensis*" A.L.200-1a which, although also an adult, possesses teeth that are not worn flat. The heavily worn teeth of A.L.444-2 are, however, consistent with the moderately rapid rate of flat plane attrition in *A. africanus* (Tobias 1991).

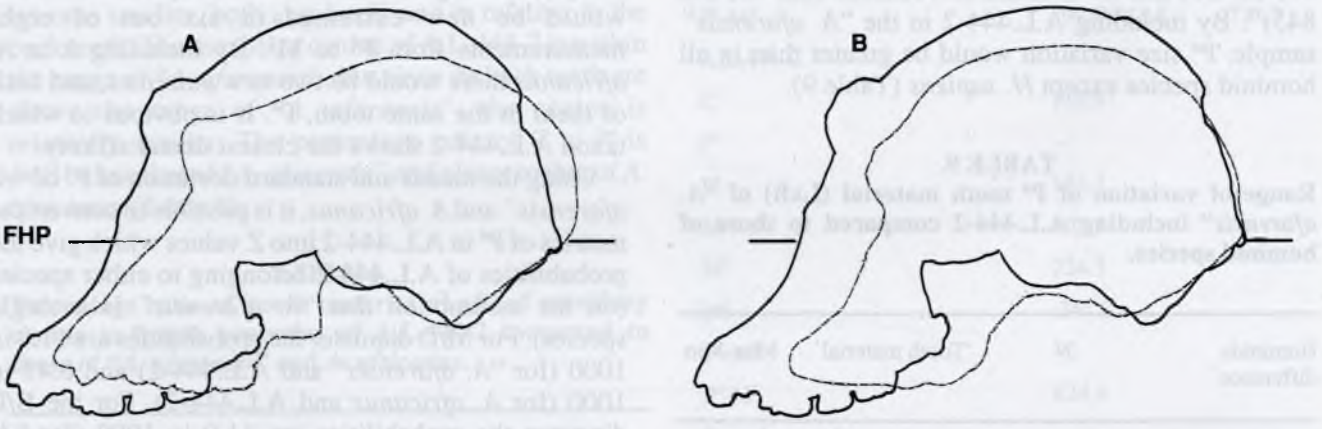

Figure 3: A) The skull A.L.444-2 (thick line) superimposed on composite reconstruction of "*A. afarensis*" (broken line). Drawn approximately to same calvarial length (left *norma lateralis*). Note total non-conformity of overall profile.
B) Male A.L.444-2 (thick line) superimposed on female *A. africanus*, Sts 5 (broken line). Drawn approximately to same relative scale. Note overall similarity of contour allowing for sexual dimorphism.

The composite reconstruction of the skull of "*A. afarensis*"

The new skull A.L.444-2 which supposedly belongs to "*A. afarensis*", does not look like White's composite reconstruction of the skull of "*A. afarensis*". Kimbel *et al.* (1994:449) get around this by saying it "is consistent with the major components" in the reconstruction. This is true insofar as the facial fragment A.L.333-1 is concerned, and that fragment may represent *A. africanus*.

A contour drawing of the skull of A.L.444-2 has been superimposed on the contour of the composite reconstruction of "*A. afarensis*" and on the contour of *A. africanus*, Sts 5, for the purpose of non-metric morphological comparison (Figure 3). The differences between A.L.444-2 and "*A. afarensis*" are striking. A.L.444-2 differs in proportion in the following ways:

1) there is a distinct forehead;
2) the vertex is relatively higher;
3) the occipital is flatter posteriorly (post-depositional deformation);
4) the nuchal plane is not concave, but pushed into the cranial cavity;
5) the face is much deeper and somewhat "dish-shaped";
6) there is greater alveolar prognathism.

When A.L.444-2 is superimposed on a presumed female *A. africanus*, Sts 5, there is overall morphological identity except for size, which can be attributed to a difference in sex. The zygomatic of A.L.444-2 is indeed consistent with the facial fragment A.L.333-1 of the composite in "*A. afarensis*" in its large, flaring zygomatics (greater than in *A. africanus*, Sts 5), broad region of the temporal process of the zygomatic, inferoanterior infraorbital region, and origin of the maxillary process of the zygomatic, all of which conforms with the specialized morphology of *A. africanus*. Unlike *Pan* and *Homo*, it manifestly does not represent the most generalized facial morphology of all hominids as claimed for "*A. afarensis*".

Since there was no complete skull of "*A. afarensis*", a composite reconstruction was made of 12 unassociated parts. Ferguson (1983) suggests that the reconstruction is a synthesis of hominid and pongid fossils. Shipman (1986) thought the reconstruction might belong to two different hominid species, the calvaria to a robust one, and the face to one that is gracile. It was then suggested that the calvaria did not belong to a hominid at all, but to a pongid (Ferguson 1992b), the face to *A. africanus* (Ferguson 1987), and

the jaws mostly from a pongid (Ferguson 1983). Either White's composite reconstruction of "*A. afarensis*" is wrong, or A.L.444-2 does not belong with "*A. afarensis*", or both.

Phylogeny

The skull of A.L.444-2 has been dated at 3 Myr, about 200 000 years younger than the earliest "*A. afarensis*" (Kimbel *et al.* 1994). It is thus synchronic with *A. africanus* from South Africa, dated at 3± 2.6 Myr (Vrba 1985). "*A. afarensis*" is supposedly ancestral to *A. africanus*, yet A.L.444-2 is coeval with *A. africanus*. Kimbel *et al.* (1994) fail to explain this discrepancy. The dating of A.L.444-2 is consistent with the dating of *A. africanus*, especially since an East African taxon, *A. africanus miodentatus* was described from the same location at 3.5 - 3 Myr (Ferguson 1987).

In view of the fact that A.L.444-2 is morphologically outside the range of variation for "*A. afarensis*" and is 200 000 years younger, it might be considered a temporal variant. Kimbel *et al.*(1994) state that the Hadar specimens range from 3.4 - 3 million years in age. They then claim that it constitutes "evidence for about 0.9 million years of stasis in the earliest known hominid species". If A.L.444-2 supposedly represents "*A. afarensis*" and the species was in stasis for almost a million years, it would have to be the same morphologically as earlier "*A. afarensis*", and it is not. A.L.444-2 had already reached the *A. africanus* level of development so it cannot be a temporal variant of "*A. afarensis*".

CONCLUSION

Until recently *A. africanus* was known mainly from female skulls. There is a large male cranium of *A. africanus*, Stw 505 from Member 4, Sterkfontein, but it has not yet been described (Tobias pers. comm.).

In the evolution of *Homo*, the gracile condition is the more advanced, and since the female is more gracile than the male, the female cranium is more advanced than that of the male (Wilfram, 1956). It is manifest that the robust features in a male, the stronger supraorbital ridge, the larger face and bigger canines are primitive features. The very large male skull, A.L.444-2, with more robust features than those of a gracile female *A. africanus*, were apparently mistaken as belonging to a more primitive species.

In this study the skull of A.L.444-2 has been compared morphologically with "*A. afarensis*" in order to determine if it indeed belongs with that taxon as claimed. Thirteen out of seventeen symplesiomorphic features on which the identification of A.L.444-2 as "*A. afarensis*" was based, are shared by *A. africanus*, and thus not diagnostic. The remaining four are not known from *A. africanus*, but neither are they new diagnostic characters for "*A. afarensis*". Before new characters can be added to an original diagnosis, it must be absolutely certain that they represent the same species. The diagnostic characters of "*A. afarensis*" were not based on a single holotype, but on unassociated fragments assumed to belong to the same species. In taxonomy this is a very risky thing to do, as the unassociated fragments might belong to more than one species. Such, in fact, is the case with the composite of "*A. afarensis*", in which the jaw A.L.200-1a belongs to a pongid (Ferguson 1983), the face A.L.333-1 to *A. africanus* (Ferguson 1987), and the partial calvaria A.L.333-45to a pongid (Ferguson 1992).

In a comparison of contours of the crania A.L.444-2 and the composite reconstruction of "*A. afarensis*", the proportions are different and there is no morphological identity. The skull A.L.444-2, however, is comparable to the presumed female *A. africanus*, Sts 5, apart from being larger and more robust. Several calvarial and dental features in A.L.444-2 are inconsistent with the preserved parts of the composite skull of "*A. afarensis*". Metrics and indices of A.L.444-2 are outside the range of variation for "*A. afarensis*".

The dentition of A.L.444-2 is not primitive as claimed for "*A. afarensis*". Measurements of the postcanine dentition (P^4-M^3), except for M^1, are outside the range of variation for "*A. afarensis*", but fall within the upper range of *A. africanus*. Six mesiodistal and buccolingual metrics exceed the maximum for "*A. afarensis*", and are above the mean for *A. africanus*. In "*A. afarensis*" the upper canine is about the same size as P^4 and relatively large compared to the back teeth. In A.L.444-2 , the upper canine is smaller than P^4, and relatively small compared to the back teeth, as in *A. africanus*. Unlike A.L.200-1a, there is no incurvature of M^3. The postcanine teeth indicate flat-plane attrition. Clearly the dentition of A.L.444-2 is not the most generalized yet documented for any unequivocal hominid; rather it should be considered as highly specialized.

Kimbel *et al.* (1994) recognize "*A. afarensis*" as a valid, single species. They then claim that A.L.444-2 belongs with "*A. afarensis*" and that it therefore confirms the unity of the species. An argument that includes the conclusion it hopes to prove as one of its premises is circular. The premise is that "*A. afarensis*" is a valid, single species. The argument could be considered fallacious.

A.L.444-2 had already reached the adaptive plane of *A. africanus* with certain metrics and indices beginning to fall within the range of a robust australopithecine, and thus cannot be conspecific with the more primitive "*A. afarensis*".

Since the morphological pattern of the mandible, cranium, and especially the dentition of A.L.444-2 is inconsistent with "*A. afarensis*", but conforms with *A. africanus*, it is suggested that A.L.444-2 be reassigned to the taxon *A. africanus*. Its apomorphic characters indicate it is early on the australopithecine lineage and the first nearly complete skull of a male *A. africanus* to be recorded from East Africa.

The skull A.L.444-2 has been dated at 3 Myr, within the time period ascribed to some specimens of *A. africanus*. This makes it highly improbable that "*A.*

afarensis" is ancestral to *A. africanus* and supports the determination that A.L.444-2 indeed belongs with *A. africanus*.

A.L.444-2 does *not* confirm the taxonomic unity of "*A. afarensis"* as claimed. There are three possibilities to explain the great variation in the hypodigm of "*A. afarensis":*

1) "*A. afarensis"* is an extremely variable unitary species;
2) "*A. afarensis"* is a composite "species" with *A. afarensis* and one or more other species included;
3) There is no "*A. afarensis"* at all, only other species.

The extreme morphological variation and apelike sexual dimorphism in "*A. afarensis"* are greater than in any species of the Hominidae, which suggests that more than one species is involved. "*A. afarensis"* cannot be one of a composite species unless it can be defined as a valid, new species after the other species are removed from the hypodigm. The true holotype of "*A. afarensis"* is the Garusi maxilla, not the lectotype LH-4 mandible, according to the International Rules of Zoological Nomenclature. The Garusi maxilla, included in the sample of "*A. afarensis"*, already has a name, *Praeanthropus africanus* (Weinert), 1950, which is valid, available and takes priority (Ferguson 1986). "*A. afarensis"* is, thus, an invalid replacement name for *P. africanus*. The mandible LH-4 and the Garusi maxilla are both from Laetoli and about the same geologic age. They are probably conspecific, but this cannot be demonstrated with any certainty as they are unassociated. If it can be shown that LH-4 is not conspecific with *P. africanus* then the name *afarensis* would be available and valid. It is, however, not an *Australopithecus,* but a pongid (Ferguson 1983).

An important point which has been overlooked is that all of the specimens from Hadar/Laetoli do not show the same degree of symplesiomorphic features. Some are apelike, some australopethecine, and some hominine. Due to their primitiveness and fragmentary nature they have been lumped together into a chimera and mistakenly named a single species, "*A. afarensis"*.

The cranial and dental morphology and metrics of A.L.444-2 once again confirm the existence of *A. africanus* at Hadar.

ACKNOWLEDGEMENTS

I would like to thank the Department of Zoology at the Tel Aviv University for the use of their facilities. I also thank Dr. Margaret Yekutiel for help with the statistics and Dr. Brigitte Senut and an anonymous referee for reviewing the manuscript. Many thanks are due to Cynthia Shapiro for typing the manuscript. The drawings were done by the author.

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