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FIRST RECORD OF TRIASSIC RHYNCHOSAURIA (REPTILIA: DIAPSIDA) FROM THE LOWER ZAMBEZI VALLEY, ZIMBABWE

by

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ABSTRACT

True rhynchosaurids are described from Zimbabwe for the first time. The fossils occur as partially associated skeletons and scattered isolates in upward-fining, micaceous fluvial sandstones of the Pebbly Arkose Formation (late Triassic) in the Western Cabora Bassa Basin, Lower Zambezi Valley. On the grounds that the dentary of the Zimbabwean form possesses a row of small, conical lingual teeth in addition to a palisade row of penicillate teeth on the occlusal surface, it is concluded that the taxon present is *Hyperodapedon* sp., and that it is closely related to a rhynchosaurid described from Tanzania. One bone identified as a prosauropod dinosaurian femur was found associated with the Zimbabwean rhynchosaurids. The late Triassic age suggested by the presence of advanced rhynchosaurids is supported by the occurrence of the typical Triassic fossil plant genus *Dicroidium*, and by the general stratigraphy of the beds which contain the fossils (i.e. the fossil-bearing beds are underlain by beds of mid-Triassic age or younger, and are overlain by beds of latest Triassic or early Jurassic age).

INTRODUCTION

In the course of mapping by the second author in the Lower Zambezi Valley, Zimbabwe, over the past five years, fossils have been recovered from a number of new localities in the Dande Communal Lands situated between the southern valley escarpment and the vicinity of the main east-west access road along the valley floor (Figures 1,2; see also Oesterlen 1989: Figure 1). The sedimentary rocks exposed here vary in age from late Palaeozoic to early Mesozoic (Broderick 1984, 1989; Oesterlen, 1989).

One bone-bearing sample from beds mapped as Pebbly Arkose Formation was referred to the third author in 1988, who recognised amongst the material the characteristic tooth-studded maxillary dental plate of a rhynchosaur. Before this, no rhynchosaur material was known from Zimbabwe. Gow and Raath (1977) identified a few tiny jaw fragments recovered from a dinosaur-rich exposure of Forest Sandstone Formation (late Triassic-early Jurassic) in the Chitake River, some 60 km west of the study area, as belonging to "sphenodontid rhynchocephalians". However, modern opinion is that the term Rhynchocephalia should lapse, being too broad to be useful, and that there is "no close relationship between rhynchosaurs and sphenodontids" (Benton, 1985; he classifies sphenodontids as Lepidosauria along with the squamates).

The discoveries reported here therefore represent the first record of Rhynchosauria from Zimbabwe.

Because of the significance of these initial finds it was decided to follow up with a search for more specimens, in an attempt to identify the rhynchosaur taxa concerned and date the deposits. Accordingly, in May 1990 two of us (PMO and MAR) visited the area, which lies between the Manyame and Angwa rivers (Figures 1,2), and collected more rhynchosaurian material from Oesterlen's sites. One locality also yielded an isolated fragment of a dinosaurian femur, loosely associated with one of the rhynchosaur specimens.

PREVIOUS PALAEONTOLOGICAL WORK IN THE MID AND LOWER ZAMBEZI VALLEY

Previous fossil vertebrate finds in the Mid and Lower Zambezi Valley have consisted almost entirely of representatives of two faunas dominated by dinosaurs: an earlier one of terminal Karoo age (from the Forest Sandstone Formation - latest Triassic to early Jurassic), and a later one of Morrison age (late Jurassic) (Bond, 1965; Raath, Smith and Bond, 1970; Raath, 1977; Raath and McIntosh, 1987).

The terminal Karoo fauna is distinctive and ubiquitous, essentially identical or closely comparable faunas being known from southern Africa, Asia, Europe, and North and South America (Tucker and Benton, 1982; Olsen and Galton, 1984). The age of this fauna straddles the Triassic-Jurassic boundary (Olsen and Galton, 1984), and in South Africa, where it is especially well represented, it in turn comprises two readily recognised constituent faunal assemblages,

TABLE 1

Stratigraphy of the Karoo Supergroup and younger rocks in the Cabora Bassa and Mid-Zambezi Basin, Northern Zimbabwe

Era	Period	Group	Formations: Cabora Bassa Basin	Formations: Mid Zambezi Basin	South African Equivalents
Cenozoic	Quaternary Tertiary		Jesse Sands	Jesse Sands	
Mesozoic	Cretaceous		—?— —?— —?— —?— —?—		
	Jurassic		Dande Sandstone	Kadzi Beds Ntumbe Beds Chenje Beds	
	Triassic	Upper Karoo	Forest Sandstone	Batoka Basalt Forest Sandstone	Stormberg Group
			Pebbly Arkose (*rhynchosaur horizon)	Pebbly Arkose	
			Angwa Sandstone	Fine Red Marly Sandstone Ripple Marked Flags Escarpment Grit	
Palaeozoic	Permian Upper	Lower Karoo	Mkanga	Madumabisa Mudstone	Beaufort Group
			—?— —?— —?— —?— —?—		
	Permian Lower		—?— —?— —?— —?— —?— Kondo Pools	Upper Wankie Sandstone Black Shale and Coal Lower Wankie Sandstone	Ecca Group
	Upper Carboniferous			Glacial Beds	Dwyka Formation
Authorities			Oesterlen 1990, 1991	Bond 1967, Broderick 1990	

an earlier one and an apparently slightly younger successor. The earlier fauna is considered to be of late Triassic (pre-late Norian) age and is characterised by the presence of large euskelosaurid prosauropod dinosaurs and capitosaurid labyrinthodont amphibians. The later assemblage is considered early Jurassic (Liassic) in age and is characterised by abundant remains of the dinosaurs *Massospondylus* (prosauropod), *Syntarsus* (theropod), several taxa of fabrosaurid ornithischians, several taxa of advanced therapsids including abundant remains of the specialised herbivorous cynodont *Tritylodon* (in the northeastern parts of the Orange Free State, South Africa, they are often found concentrated in a well-marked acme zone), several taxa of protosuchid crocodilians, and rare occurrences of early morganucodontid mammals such as *Megazostrodon* and *Erythrotherium* (Kitching and Raath, 1984; Olsen and Galton, 1984). Kitching and Raath (1984) defined two successive biozones in the Elliot Formation of South Africa on the basis of these two faunas - the *Euskelosaurus* Range Zone below, and the *Massospondylus* Range Zone above.

A depauperate version of the Liassic *Massospondylus* Range Zone fauna, so far lacking any ornithischian

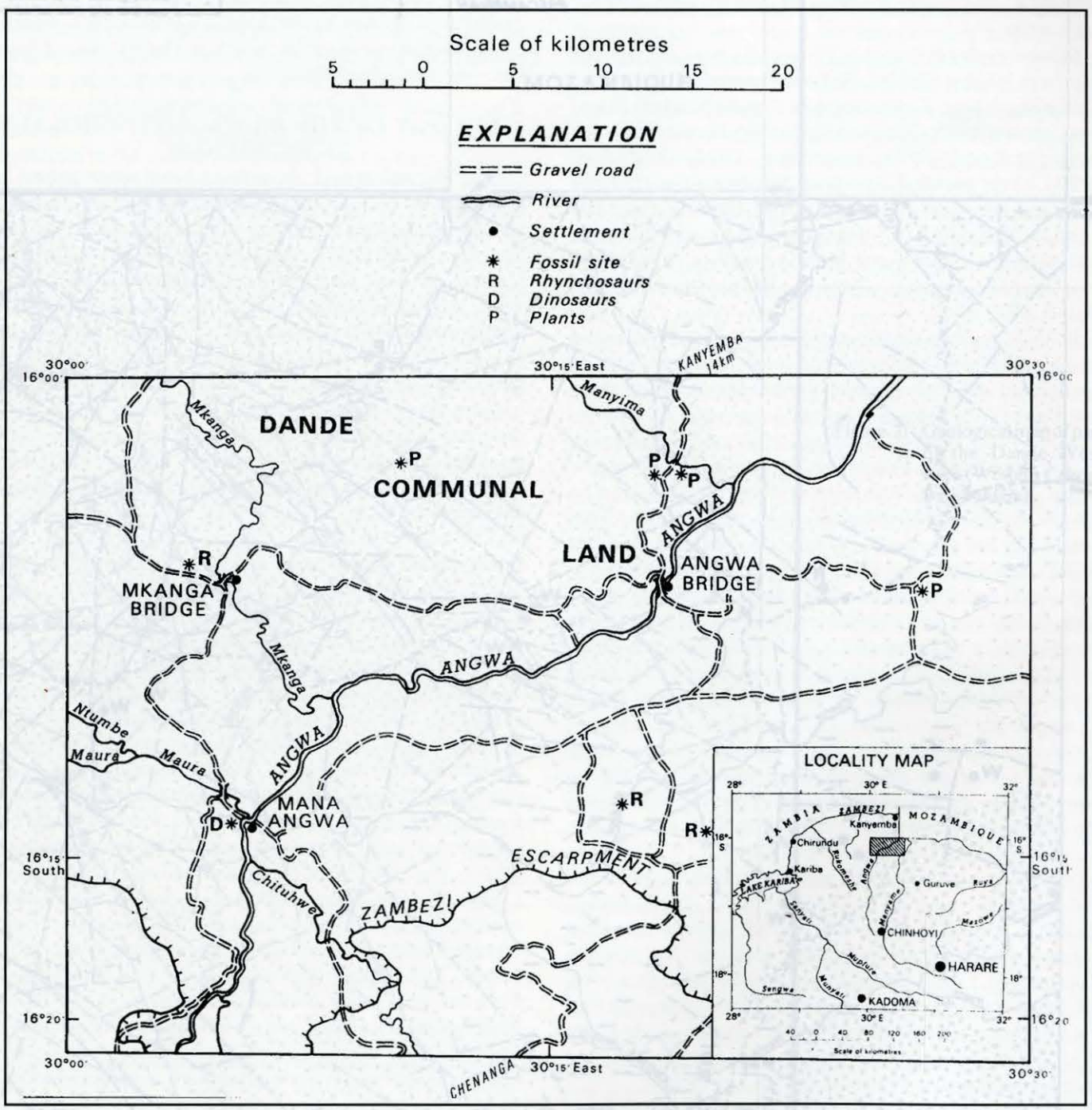


Figure 1: Location of rhynchosaur fossil sites.

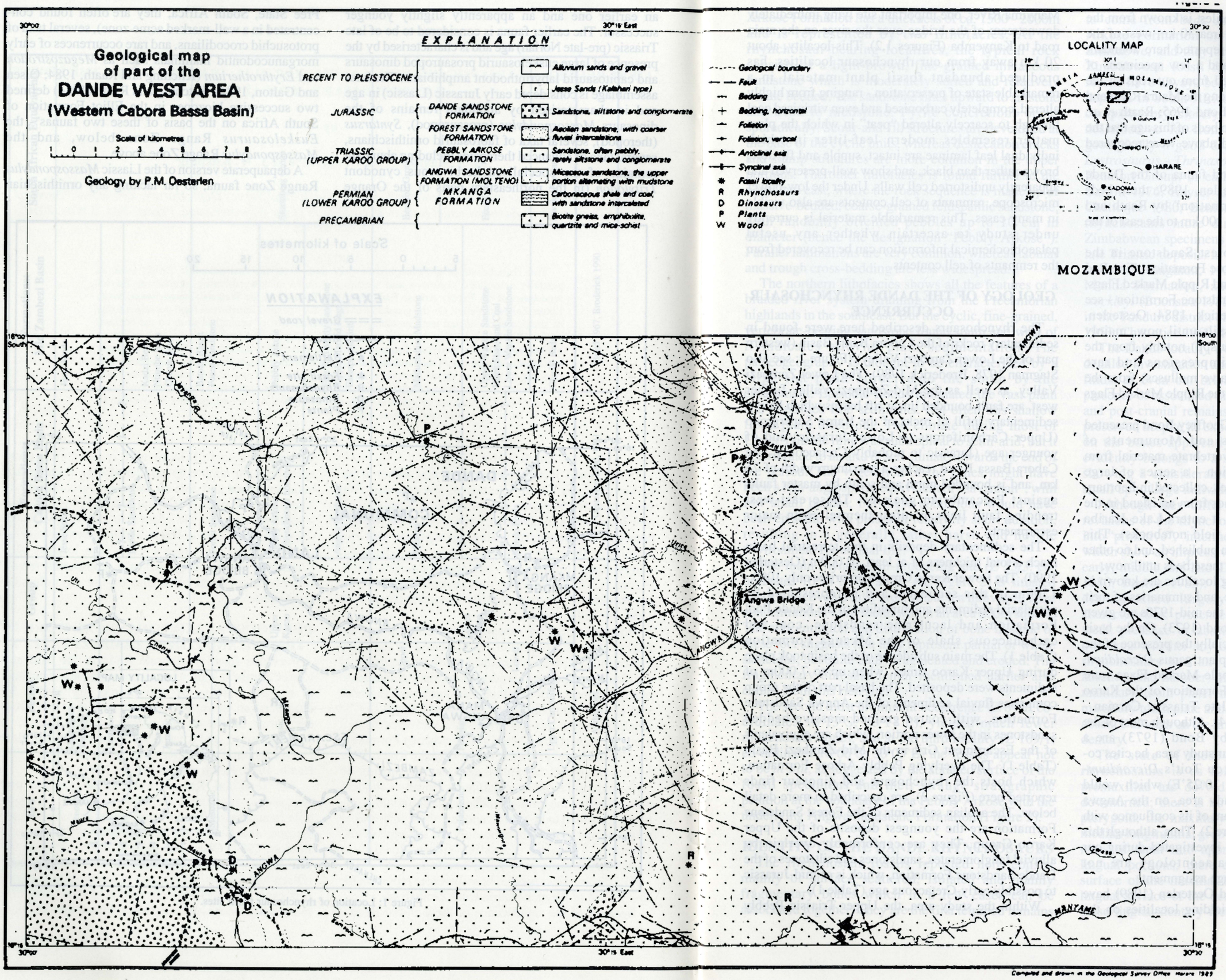


Figure 2: Geological map of part of the Dande West Area (Western Cabora Bassa Basin).

GEOLOGICAL MAP OF PART OF THE DANDE WEST AREA (WESTER CABORA BASSA BASIN)

Erratum: PALAEONTOLOGIA AFRICANA Volume 29, 1992.
M.A. Raath *et. al.* First Record of Triassic Rhynochosauria (Reptilia: Diapsida) from the Lower Zambezi Valley, Zimbabwe pp. 1-10.

Figure 2

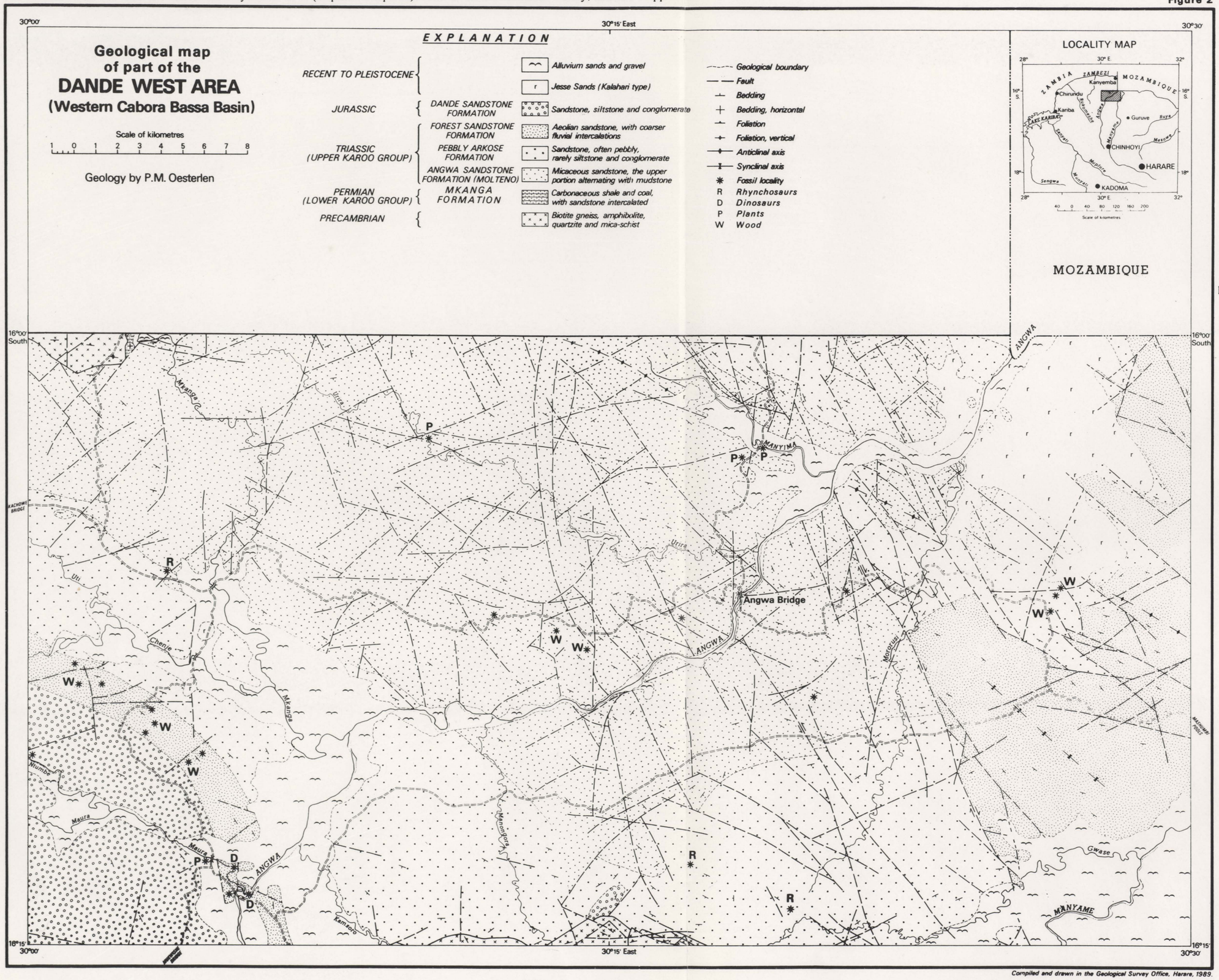


Figure 2: Geological map of part of the Dande West Area (Western Cabora Bassa Basin).

Compiled and drawn in the Geological Survey Office, Harare, 1989.

dinosaurs or mammal-like reptiles, is known from the general vicinity of our study area 30 km west of the rhynchosaur-producing sites reported here abundant remains of *Massospondylus* and a few specimens of *Syntarsus* have been recovered from outcrops of the Forest Sandstone Formation along the Maura River and its tributaries (Figures 1, 2) (Bond 1965; Raath *et al.* 1970; Raath 1977). It was from beds of this age that the sphenodontid jaws mentioned above were recovered from the Chitake River.

The later Jurassic sauropod fauna of the Dande Sandstone Formation (Oesterlen, 1989; these beds were termed the "Kadzi Formation" by Raath and McIntosh, 1987) occurs about 100 km to the east of the study area.

Strata underlying the Forest Sandstone in the Zambezi Valley (Pebbly Arkose Formation, Fine Red Marly Sandstone Formation and Ripple Marked Flags, now known as the Angwa Sandstone Formation - see Table 1; Bond, 1973; Broderick, 1984; Oesterlen, 1989) have yielded few fossils until now, mainly silicified logs (cf. *Dadoxylon* spp) notably from the Pebbly Arkose, and leaf impressions and rare invertebrates (freshwater bivalve molluscs) from the beds beneath, especially from the Ripple Marked Flags (Bond, 1973).

In 1974 the late Professor Geoffrey Bond presented to the National Museums and Monuments of Zimbabwe the only known vertebrate material from the Pebbly Arkose Formation - a series of large dipnoan (lung fish) tooth plates, collected in February of that year by Mr Frank Junor from an island in the Bumi River estuary where it enters Lake Kariba (16°51'S; 28°28'E) (Raath, field notebooks). This record has not previously been published, and no other vertebrates were known from these beds until now.

Several fossil plant-bearing localities are known in beds of this age in Zimbabwe, and summaries of their fossil content as known up to the mid-1970s are given in Lacey (1961, 1970) and Bond (1973). On the basis of the contained fossils, especially the presence of the characteristic Triassic fossil plant genus *Dicroidium*, Bond concluded that the Ripple Marked Flags were equivalents of the Molteno Formation of the Karoo Sequence in South Africa (late Triassic: Carnian - Anderson and Anderson, 1984). Although most of the Molteno localities listed by Bond (1973) are a considerable distance from our study area, he cites co-ordinates for one of A. L. du Toit's *Dicroidium*-yielding localities (16°01'S; 30°25'E) which would place it right within our study area, on the Angwa River about 11 km downstream of its confluence with the Manyima River (see Figure 2). Thus, although this locality was not specifically investigated during our visit, the geology and palaeontology are not inconsistent with a Molteno age assignment.

Both Broderick (1984) and Oesterlen (1989) have reported other *Dicroidium*-yielding localities on the Manyima River, one important site lying immediately downstream of the bridge over the river on the main road to Kanyemba (Figures 1,2). This locality, about 20 km away from our rhynchosaur localities, has produced abundant fossil plant material in a remarkable state of preservation - ranging from highly altered, completely carbonised and even vitrinised coal through to scarcely altered "peat" in which the plant matter resembles modern leaf-litter in which individual leaf laminae are intact, supple and flexible, brown rather than black, and show well-preserved and apparently undistorted cell walls. Under the low-power microscope, remnants of cell contents are also visible in many cases. This remarkable material is currently under study to ascertain whether any useful palaeobiochemical information can be recovered from the remnants of cell contents.

GEOLOGY OF THE DANDE RHYNCHOSAUR OCCURRENCE

The rhynchosaurs described here were found in sedimentary rocks of the Cabora Bassa Basin (western part of the Lower Zambezi Valley) (Figure 2; see also Stagman 1978, Broderick 1989). The Lower Zambezi Valley, as well as the Mid-Zambezi Valley further west, are fault-bounded linear rift basins which have a sedimentary infill of rocks of the Karoo Supergroup (Upper Carboniferous to Lower Jurassic) and of younger age (Jurassic to probably Cretaceous). The Cabora Bassa Basin reaches a maximum width of 75 km, and is bounded north and south by master faults against Precambrian gneisses. These east-west trending fault lines manifest themselves in major escarpments.

The sedimentary deposits in this terrestrial basin reach a total thickness of at least 10 000m (Oesterlen 1990). The Lower Karoo Group comprises only 1000 - 1500m of this sequence, and is represented by periglacial sediments and turbidites of the Kondo Pool Formation and lacustrine sandstone, coal and carbonaceous shale of the Mkanga Formation (Table 1). The main subsidence of the basin took place during Upper Karoo times, when up to 7 000m of sediments were deposited. The basal part of the group comprises fluvial sediments of the Angwa Sandstone Formation, with coarse grained massive-bedded sandstones in the lower portion, which are equivalents of the Escarpment Grit in the Mid-Zambezi Basin (Table 1). The overlying Pebbly Arkose Formation, which hosts the rhynchosaur and dinosaur finds reported here (Figure 2), are described in more detail below. The aeolian sediments of the Forest Sandstone Formation are the youngest deposits of the Upper Karoo Group. They are conformably overlain by alluvial fanglomerates, sandstones and siltstones of the Dande Sandstone Formation, which is of mid-Jurassic to possibly early-Cretaceous age (Table 1).

Within the study area, the Upper Triassic Pebbly

Arkose Formation has a thickness of ca. 1500 - 2000m and is represented by two lithofacies. At the rhynchosaur-bearing localities, the typical rock consists of a light-brown, fine-grained micaceous sandstone which is moderately sorted and relatively coarse bedded. The sandstone fines upward to siltstone and even to mudstone. Pyrite concretions occur sporadically. Scour-and-fill structures are developed at the base of the cyclic units, whereas desiccation cracks and slump structures are more common in the upper portions. The other lithofacies is found further to the north and east, where the rock sequence is made up of massive-bedded, coarse-grained feldspathic sandstone, with randomly oriented pebbles up to 10 cm in diameter (hence the designation "Pebbly Arkose"). Parallel laminations are very common, whereas tabular and trough cross-bedding are less widespread.

The northern lithofacies shows all the features of a braided river system draining from the Precambrian highlands in the southeast. But the cyclic, fine-grained, vertebrate-bearing sandstone found south and west of it indicates alluvial plain sedimentation. The palaeogeography is thought to be characterized by a large flat plain bordered to the south by the escarpment. Episodic floods inundated the vast plain and deposited fine sediments. But often this shallow flood plain dried out. The climate during most of Upper Triassic time was subtropical to semi-arid, but it deteriorated to an arid desert climate towards the end of the period. The vegetation of the times might have been a non-angiosperm equivalent of "savannah", with few small bushes; but these conditions would have been episodic with pulses of relatively short duration, resulting in a generally rather harsh and hostile environment for animal life.

The main rhynchosaur-producing site (Z 53/3, co-ordinates 16°14'S; 30°20'E; see Figure 2) is situated on a grass-covered hilly area, where ten individual bone concentrations were found within an area 200m square. The concentration and distribution of bone in some of these loci suggests that they represent partial or whole skeletons, but quite badly fragmented and eroded. The fragmentary dinosaur femur mentioned earlier also comes from this rich site.

The second most prominent occurrence (Z 64/1, co-ordinates 16°13'S; 30°17'E), yielded much fewer rhynchosaur bones, and at the third locality (Z 109/1, co-ordinates 16°06'S; 30°03'E) the fossils appear not to be *in situ*, as suggested by the abraded surface of the fossil specimens and their strange stratigraphic position at the boundary of the Pebbly Arkose with the underlying Angwa Sandstone Formation (Figure 2).

IDENTITY OF THE DANDE RHYNCHOSAURS

The rhynchosaur fossils reported here consist mainly of surface scattered, isolated and mainly fragmentary bones which in a few cases can be associated together. They are the first tetrapod remains to come from beds assigned to either the Pebbly Arkose Formation or Molteno-equivalent beds in Zimbabwe, and they bring a new perspective to the Zimbabwean fossil fauna. Hitherto, Zimbabwean fossils have always been compared with fossils from deposits in South Africa, with which they seemed to compare very closely. But the only rhynchosaurs described so far from South African deposits are geologically a good deal older, from as low as the *Lystrosaurus - Thrinaxodon* Assemblage Zone in the Beaufort Group, of early Triassic age (Malan 1963; Carroll 1976; Keyser and Smith 1978; SACS 1980; Chatterjee 1980; Benton 1985). On the other hand, rhynchosaurs more directly comparable with the Zimbabwean specimens are known from middle- and late Triassic deposits in Tanzania - *Stenaulorhynchus stockleyi* Haughton, 1932 from the middle Triassic Manda Formation, and the large *Supradapedon stockleyi* (Boonstra 1953) from late Triassic deposits in the Tunduru district of southern Tanzania (Boonstra 1953; Chatterjee 1969, 1980; Benton 1983).

The Dande locality would undoubtedly repay more detailed investigation and controlled excavation of the finds, as even our brief reconnaissance proved the presence of associated material, including both cranial and post-cranial remains, some of it reasonably well preserved despite its exposure, and many of the breaks on the bones apparently fresh. What we recovered evidently belongs to a single taxon of rhynchosaur, showing a considerable size-range from relatively small up to large individuals.

Although they differ in matters of detail, recent revisions of the rhynchosaurs agree in dividing them into "primitive", "intermediate" and "advanced" forms which show an impressive correlation with deposits of early, middle and late Triassic age (Chatterjee 1969, 1980; Benton 1983). These "clusters" of forms are distinguished largely on the basis of dental characteristics: presence or absence of premaxillary teeth; presence or absence of palatal teeth (Benton questions whether any of the middle or late Triassic rhynchosaurs had any palatal teeth); presence or absence (and number) of longitudinal grooves on the maxillary tooth plate; number of toothrows on the maxillary tooth plate and on the mandible; presence or absence of teeth on the lingual surface of the maxilla or dentary.

The state of these characters in the Dande rhynchosaurs is as follows (Figures 3,4,5): the premaxillae are devoid of teeth and are strongly downturned; there is no sign of palatal teeth on the pterygoid; the maxillary dental battery has a single median longitudinal groove which divides the multiple rows of teeth into approximately equal labial and lingual portions; there are no teeth on the lingual surface of the maxilla, but teeth are present on the lingual surface of the dentary. It is not clear whether these lingual dentary teeth are arranged in a distinct

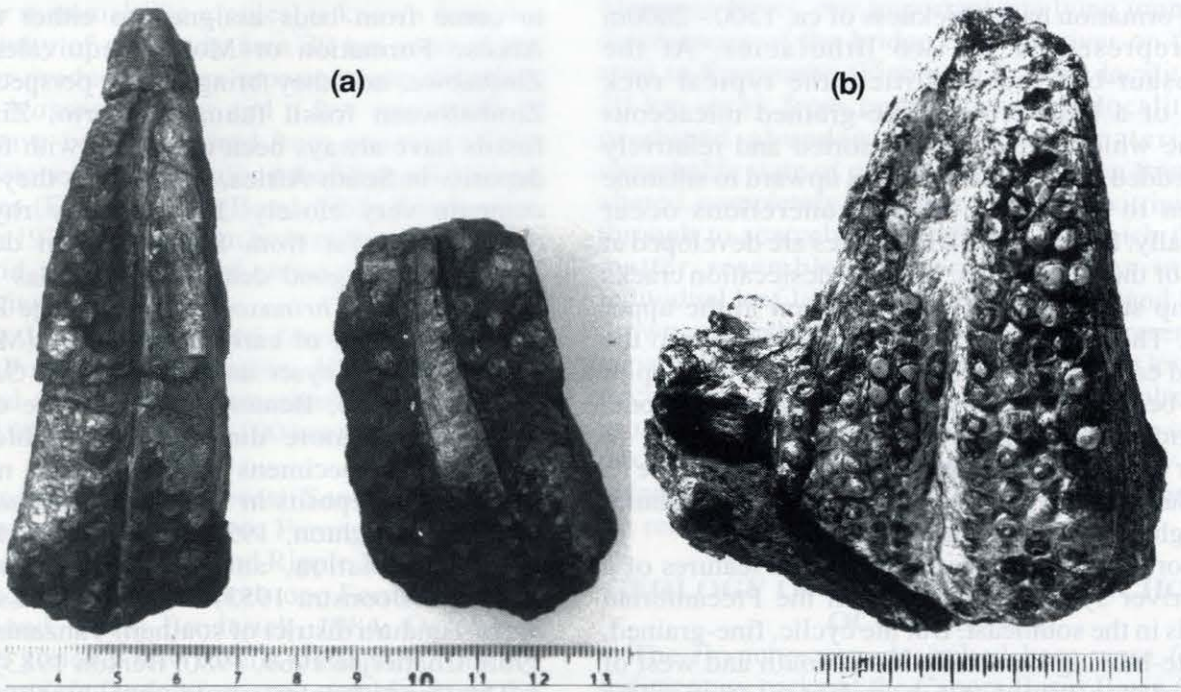


Figure 3:
(a) Occlusal view of (l-r) right and left maxillary dental plates of rhynchosaur specimen from site Z 53/3 (1), Lower Zambezi Valley, Zimbabwe (? adult specimen). These tooth plates were associated with more cranial and postcranial remains (see also Figure 6);
(b) Occlusal view of left maxillary dental plate of *"Supradapedon" (? = Hyperodapedon) stockleyi* (Boonstra, 1953), from the Late Triassic of Tanzania (SAM 11704: courtesy South African Museum, Cape Town; photo C. Booth).
Smaller scale divisions = mm.

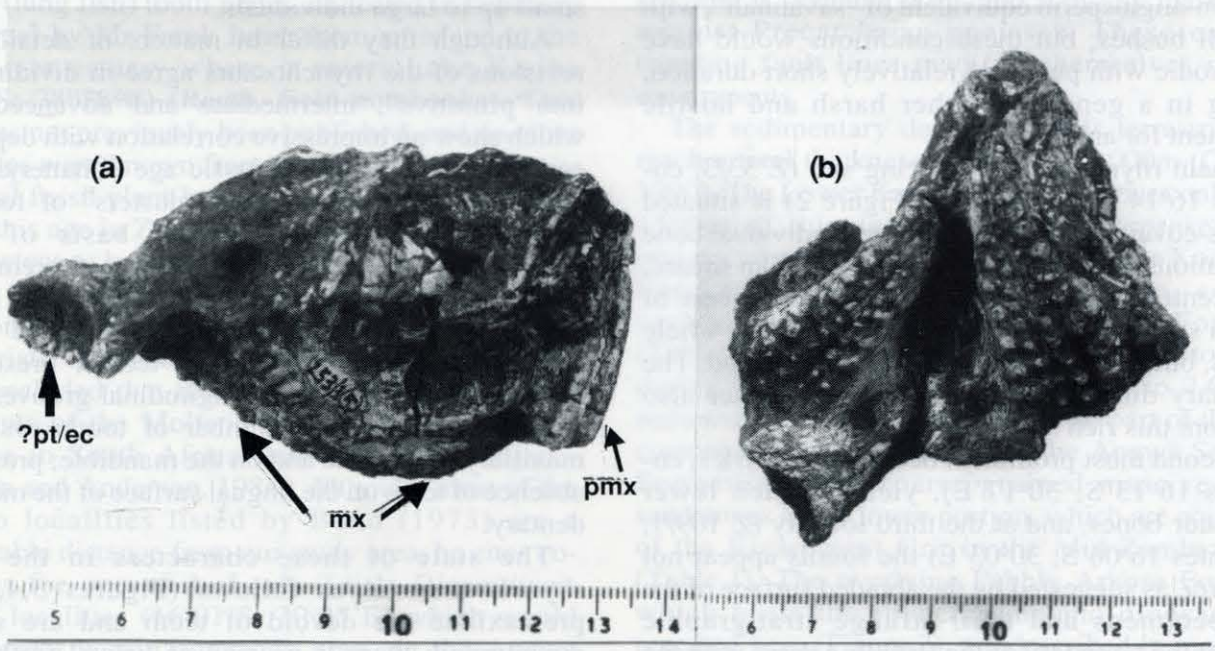


Figure 4:
Portion of snout of a smaller individual from site Z 53/3 (5):
(a) right lateral view. The down-curved premaxillae (pmx) are visible along the right side of the specimen; the curved maxillary dental plate (mx) defines the lower edge; the cup-shaped bone protruding to the left is part of the palatal complex, probably the pterygoid/ectopterygoid (?pt/ec); the dorsal parts of the specimen are eroded away.
(b) palatal view of the same specimen.
Smaller scale divisions = mm.



Figure 5: Dentary of small specimen from site Z 53/3 (5):
(a) labial view, with occlusal palisade of penicillate teeth arrowed (the gap in the row is an artifact due to breakage);
(b) buccal view, with two small conical labial teeth arrowed (t).
Smaller scale divisions = mm.

row or are scattered, as only two teeth are preserved in one section of jaw recovered so far (Figure 5b). The main row of occlusal dentary teeth along the apex of the labial margin are deep-rooted, narrow, penicillate teeth which are tightly packed in the "palisade row" typical of advanced rhynchosaurs.

In terms of Benton's (1983) analysis, this character state places the Dande rhynchosaurs unquestionably within the sub-family Hyperodapedontinae of the family Rhynchosauridae. This sub-family is typical of the late Triassic (Chatterjee 1980; Benton 1983). Within that sub-family Benton (1983) includes the genera *Hyperodapedon*, *Paradapedon*, *Scaphonyx*, *'Supradapedon'* and forms as yet undescribed from the Dockum Group of Texas, USA (Benton 1987). He regards *'Supradapedon'* from Tanzania as possibly a large *Scaphonyx* or *Hyperodapedon* (Benton 1983: p. 712), and having examined the specimen itself (Figure 3b) in the South African Museum, we agree. Benton goes on to suggest that the relationship between *Hyperodapedon*, *Paradapedon* and *Scaphonyx* is so close that they might well be congeneric, although as he points out the lack of lingual teeth on the dentary of *Scaphonyx* might prove to be a valid character separating it from the others.

On these grounds, therefore, it seems safe to refer the Dande rhynchosaur to a species in the *Hyperodapedon* / *Paradapedon* group; since *Hyperodapedon* Huxley 1859 has priority over *Paradapedon* von Huene 1938, the Dande form is provisionally referred to *Hyperodapedon*. On the tentative and imprecise grounds that the longitudinal groove on the maxillary tooth plate divides the tooth rows into roughly equal labial and lingual portions, as is seen in the Indian form *H. huxleyi* (=*Paradapedon huxleyi*), the Dande form is provisionally referred to *Hyperodapedon* sp., cf. *H. huxleyi* Lydekker 1881.

However, it should also be noted that according to Benton's view, *Hyperodapedon* might well prove to be monotypic, with Huxley's original species (*H. gordoni* from the Lossiemouth Formation of Scotland) the only valid species, and the Dande specimens would therefore be referable to *Hyperodapedon gordoni* Huxley 1859.

AGE OF THE DANDE RHYNCHOSAURS

Part of the interest in rhynchosaurs lies in their apparent usefulness for dating sedimentary deposits (Benton 1983; Chatterjee 1969, 1980). The assignment of the Dande rhynchosaurs to the Hyperodapedontinae identifies them as belonging to a group characteristic of and apparently confined to the late Triassic. This accords well with the age indicated by the plant fossils from the area (*Dicroidium*), and is further supported by the discovery of the fragment of dinosaurian femur from the same site as rhynchosaur specimen Z 53/3. On the basis of fourth trochanter morphology, this femur seems to belong to a prosauropod (Figure 6).

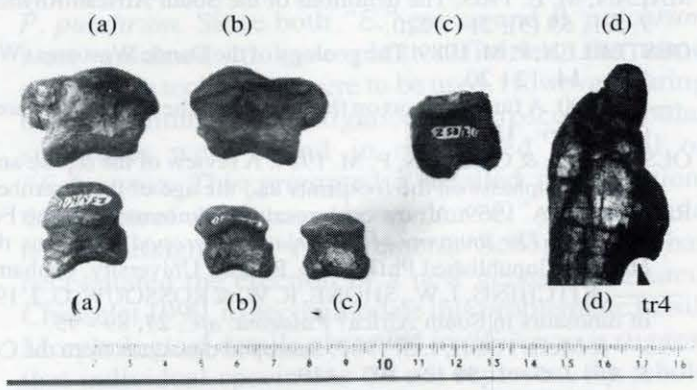


Figure 6:
(a,b) Metatarsals of specimen from site Z 53/3 (1);
(c) Centrum of ?caudal vertebra (Z 53/3 (1));
(d) Fragment of femur of ?prosauropod dinosaur (fourth trochanter arrowed "tr4"), from site Z 53/3 (7);
(e-g) Phalanges (Z 53/3 (1)).
Smaller scale divisions = mm.

Prosauropods are characteristic of the Triassic-Jurassic transition – especially the Elliot Formation in South Africa and its equivalents worldwide and they are not known from beds older than the late Triassic (Carnian) (see discussion on age of dinosaur-bearing deposits in Olsen and Galton, 1984).

Recently, tridactyl bipedal dinosaur tracks have been recorded in Molteno-age (late Triassic) *Dicroidium*-bearing beds in the northeastern Cape of South Africa (Raath, Kitching, Shone and Rossouw, 1990), proving the presence of dinosaurs (although not necessarily of prosauropods) in beds of this age.

Thus the three separate palaeontological indicators - plants, dinosaurs and rhynchosaurs - all converge in indicating a Late Triassic age for the Dande deposits, which is in accord with age deductions based on general stratigraphy.

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DISARTICULATED REMAINS OF AN ORDOVICIAN METAZOAN FROM THE CEDARBERG FORMATION, SOUTH AFRICA: A RE-INTERPRETATION OF *EOHOSTIMELLA PARVA* KOVÁCS 1986.

by

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ABSTRACT

Small pointed axes previously described as a non-vascular Palaeozoic plant, *Eohostimella parva* Kovács 1986, are assigned to *Siphonacis parva* (Kovács) Chesselet 1990 n. comb. These carbonaceous compressions are indicator fossils for assemblages of *Promissum pulchrum* Kovács 1986, which was initially interpreted as a land plant and is now thought to be a giant conodont. These fossils occur with invertebrates and algae in the Late Ashgillian Soom Shale Member of the Cedarberg Formation, in the Table Mountain Group. *E. parva* has a distinctive internal structure which invalidates its assignment to *Eohostimella* Schopf and casts doubt on its placement in the plant kingdom. Presently these small axes are of uncertain affinity although it seems likely that they are the disarticulated remains of a problematic Ordovician metazoan.

INTRODUCTION

Fossils initially identified as belonging to the genus *Eohostimella* Schopf are found in association with bedding plane assemblages and isolated elements of *Promissum pulchrum* Kovács 1986. The abundant, needle-shaped "*Eohostimella*" *parva* Kovács 1986 is an indicator fossil for the rare assemblages of *P. pulchrum*. The systematic position of the unique *P. pulchrum* has been a contentious issue in palaeontological circles. Its spiny axes were initially interpreted as the remains of a creeping land plant which was either the earliest known vascular plant, or an ancestor of the tracheophytes (Theron and Kovács-Endrödy 1986; Kovács-Endrödy 1986). Theron *et al.* (1990) proposed an entirely different interpretation based on morphological and chemical characteristics. The fossil is now thought to be the remains of a giant conodont. *P. pulchrum* and *"E". parva* co-occur with invertebrates and algae in the Soom Shale Member of the Cedarberg Formation in the Table Mountain Group, which is the lowermost unit of the 8 000m thick, Lower Paleozoic, Cape Supergroup (Tankard *et al.* 1982). The Table Mountain Group is conformably overlain by the Devonian Bokkeveld Group and rests unconformably on the Lower Cambrian Cape Granite Complex, which has been radiometrically dated at 553 + 8 Ma (Cocks & Fortey 1986).

A problematic plant fossil from Lower Silurian deposits in northern Maine was assigned to the new genus *Eohostimella* Schopf *et al.* 1966. *E. heathana* Schopf *et al.* 1966 is characterized by an upright growth habit, a hollow dichotomously branched axis and a unistratose cortex covered by minute spines. Schopf *et al.* (1966) suggested that *Eohostimella* might represent an incipient land plant. This suggestion relies on the erect habit of the plant and the nature of the outer cortex which may have had a mechanical role in maintaining the upright position. This hypothesis is corroborated by analyses of organic chemical constituents which suggest the presence of suberin-cutin and lignin polymers thus implying a "vascular-like" plant chemistry (Niklas 1976).

The work presented here was initially undertaken in preparation to an anatomical investigation of *P. pulchrum*. Since both *"E." parva* and *P. pulchrum* were assumed to have plant affinities, the same preparative techniques were to be used. However, during these preliminary investigations, microscopic tubular structures were found in macerated material of *"E." parva*. This prompted a detailed investigation, the results of which have shown that *"E." parva* should not be assigned to *Eohostimella* Schopf. This has necessitated the erection of a new genus, *Siphonacis* Chesselet 1990, to accommodate this problematic fossil. Morphological details observed in *"E." parva* suggest that individual specimens do not represent the whole organism and cast doubt on the placement of these fossils in the plant kingdom.

GEOLOGICAL SETTING

Lithologically, the Soom Shale Member is a fine-grained, thinly laminated micaceous shale (Cocks *et al.*

1970), which is black when fresh, and rarely exposed (Rust, 1967). It underlies the Disa Member, which constitutes approximately 90% of the Cedarberg Formation and comprises thin-bedded argillaceous dark grey and buff siltstone, fine-grained sandstone and mudstone (Cocks *et al.* 1970).

An age bracket of Upper Ordovician to Lower Silurian (±439 Ma) is estimated for the Soom Shale Member on the basis of invertebrate fossils (Cocks *et al.* 1970) and spore tetrads (Gray *et al.* 1986). The size of spore tetrads described as *Tetrahedraletes* cf. *medinensis*, from the Soom Shale at Swartleikloof, led Gray *et al.* (1986) to suggest an earliest Silurian age, but a late Ordovician age is indicated by chitinozoans from the same locality (Cramer *et al.* 1974). According to Cocks and Fortey (1986) the trilobite *Mucronaspis olini* Temple, from the Soom Shale Member at Buffels Dome in the Hex River Mountains, provides strong evidence for a late Ordovician age for this stratigraphic unit. *Mucronaspis olini* is characteristically of Late Ashgill (Late Rawtheyan or Hirnantian) age and none of the other elements of the fauna contradicts this. In

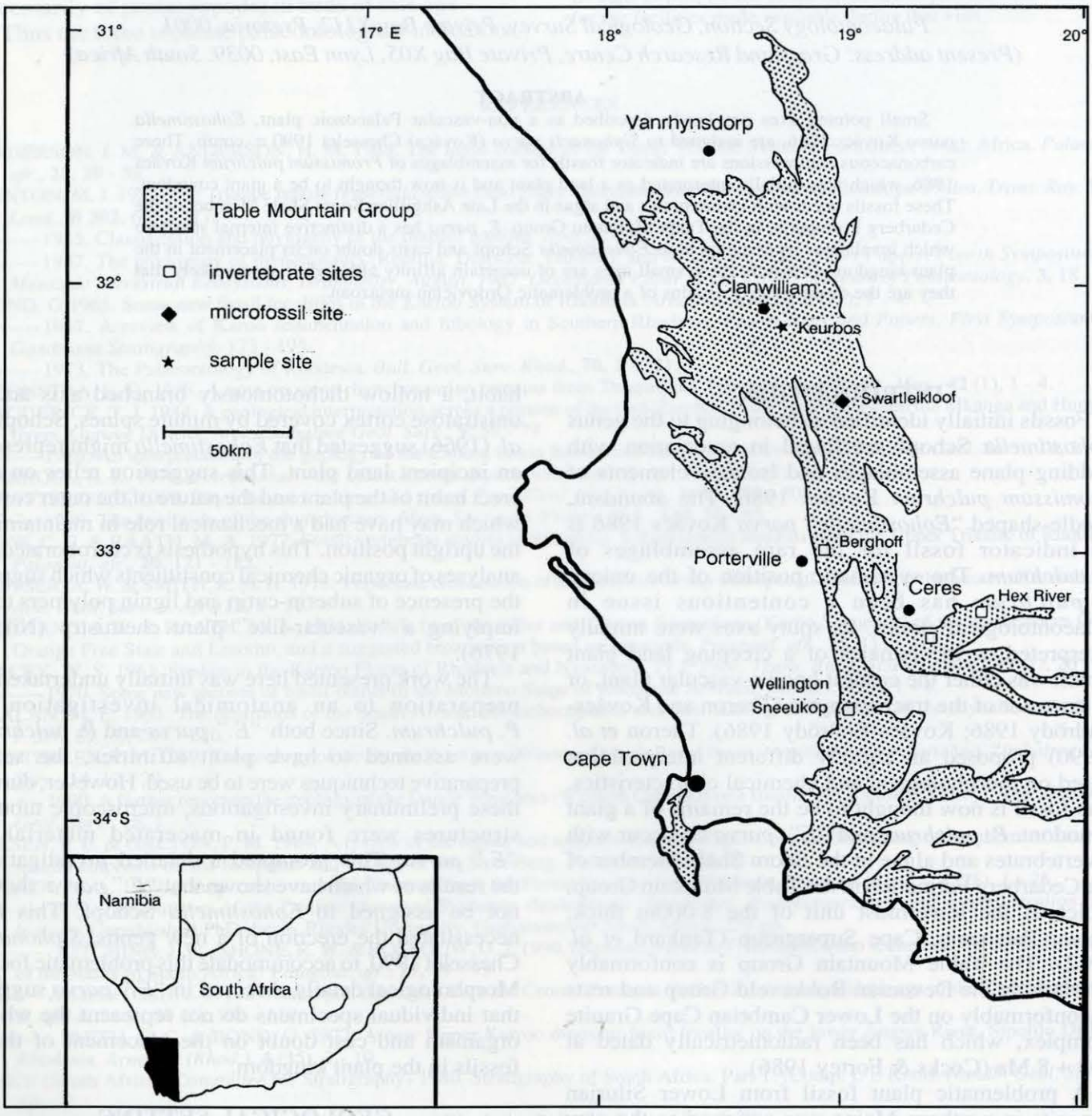


Figure 1. Locality map showing fossil-bearing sites of the Soom Shale Member and the distribution of the Table Mountain Group. (Modified from Theron *et al.* 1990 with permission).

addition, Theron *et al.* (1990) view the late Ordovician age as more likely than the Silurian age for *P. pulchrum*.

The argillaceous sediments of the Cedarberg Formation, in the predominantly arenaceous Table Mountain Group, were deposited during a period of climatic amelioration following the withdrawal of extensive Gondwana ice sheets that were centered in Africa during Ordovician times (Tankard *et al.* 1982). Glaciogenic deposits grade into shales and the presence of varved sediments implies that initial deposition took place in freshwater proglacial lakes (Tankard *et al.* 1982). The varvites are succeeded by fossiliferous sediments in which the absence of varves is attributed by Tankard *et al.* (1982) to sediment mixing and flocculation in brackish or saline water. Gray *et al.* (1986) pointed out that proximity to the sea, and/or marine incursions, is indicated by the presence of chitinozoans and possible marine phytoplankton in

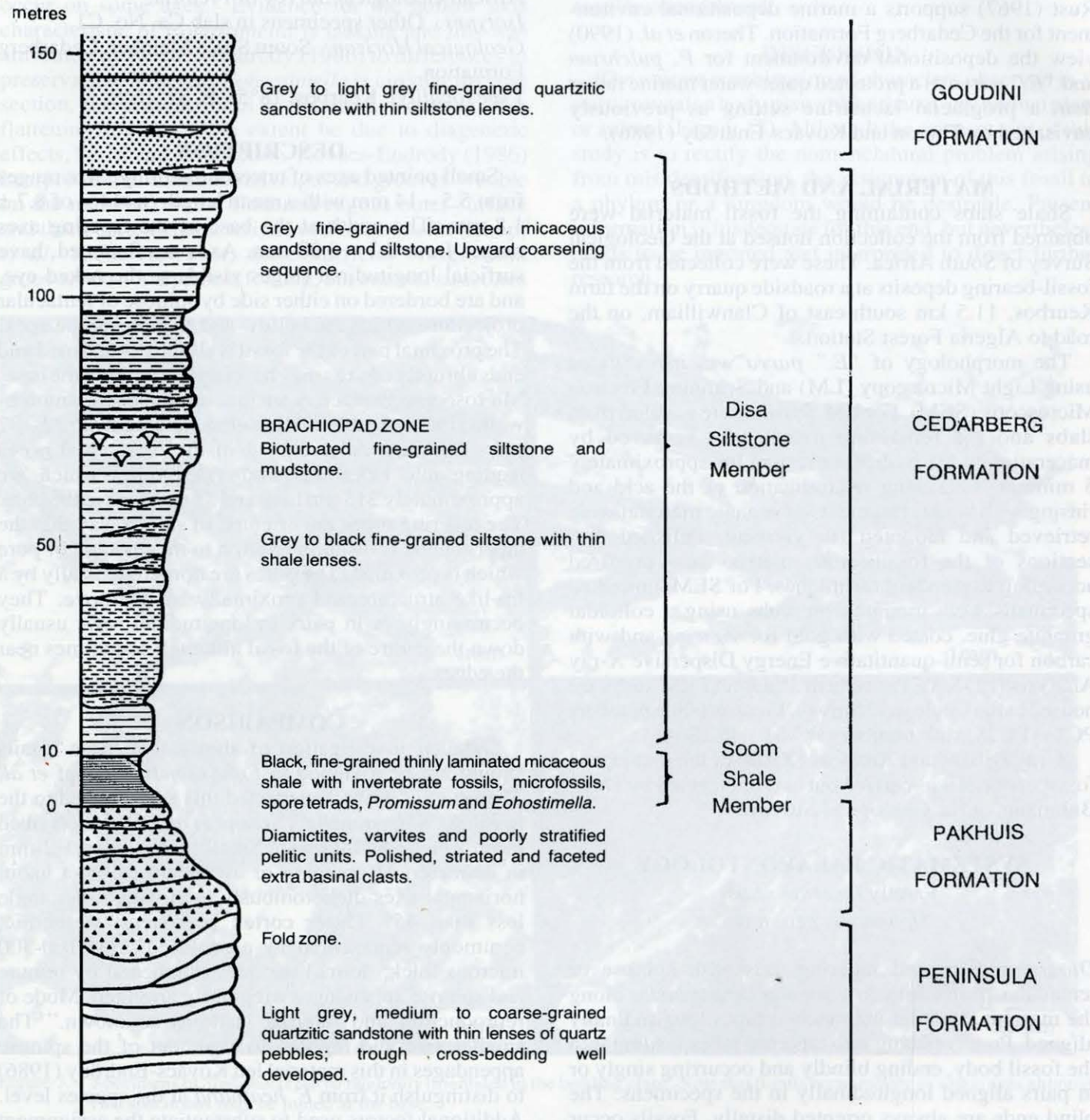


Figure 2. Stratigraphic profile of the Cedarberg Formation. (Modified from Theron *et al.* 1990 with permission).

samples from the Soom Shale Member at Swartleikloof. However, they view the (land plant) spore tetrads, sphaeromorphs and the "absence of normal marine acritarchs" as indicating a possibly "supratidal position during deposition of some of the Soom Shale Member". Trilobites from the base of the Soom Shale Member in the Hex River Mountains (Moore and Marchant, 1981; Cocks and Fortey, 1986) indicate shallow marine conditions. On the basis of lithological evidence as well as the presence of brachiopods in the Disa Member, Rust (1967) supports a marine depositional environment for the Cedarberg Formation. Theron *et al.* (1990) view the depositional environment for *P. pulchrum* and *"E." parva* as a protected quiet-water marine rather than a proglacial lacustrine setting as previously envisaged by Theron and Kovács-Endrödy (1986).

MATERIAL AND METHODS

Shale slabs containing the fossil material were obtained from the collection housed at the Geological Survey of South Africa. These were collected from the fossil-bearing deposits at a roadside quarry on the farm Keurbos, 11.5 km south-east of Clanwilliam, on the road to Algeria Forest Station.

The morphology of *"E." parva* was investigated using Light Microscopy (LM) and Scanning Electron Microscopy (SEM). For LM, fossils were isolated from slabs and the remaining matrix was removed by maceration in 5% hydrofluoric acid for approximately 5 minutes. Following neutralization of the acid and rinsing with water, fragments of organic material were retrieved and mounted for viewing. Polished thin sections of the fossiliferous matrix were prepared according to standard techniques. For SEM, untreated specimens were mounted on stubs using a colloidal graphite glue, coated with gold for viewing and with carbon for semi-quantitative Energy Dispersive X-ray Analysis (EDXA). Permanent slides and EM stubs are housed at the Geological Survey, Pretoria (slide numbers PC1 – PC25, stub numbers PC.S1 – PC.S6).

X-ray Diffraction Analysis (XRD) of the matrix and fossil material was carried out and interpreted by Dr D. Buhmann, at the Geological Survey.

SYSTEMATIC PALAEONTOLOGY

Family *incertae sedis*

Siphonacis gen. nov

Diagnosis Flattened tapering axis with spinose or tentacular projections in a regular arrangement along the margins. Internal unbranched tubes longitudinally aligned. Pores opening into tapering tubes leading into the fossil body, ending blindly and occurring singly or in pairs aligned longitudinally in the specimens. The blind ends are always oriented distally. Fossils occur singly or in pairs in what appears to be an organic connection at the base (or proximal end).

Etymology: *Siphòn* Gr. tube. Refers to the internal structure; *Akis* Gr. a point. Refers to the shape of the fossil.

Siphonacis parva (Kovács) n. comb.

Synonymy. 1986 *Eohostimella parva* Kovács. Kovács-Endrödy (1986) p. 111, pl. 4.1.
Diagnosis: As for genus.
Holotype: C1. V. In the collections of the the South African Geological Survey of Pretoria.
Isotypes: Other specimens in slab Ca. No. C1.
Geological Horizon: Soom Shale Member, Cedarberg Formation.
Type locality: Keurbos, 18°58'E, 32°16'S

DESCRIPTION

Small pointed axes of uncertain affinity. Size ranges from 5.5 – 14 mm with a mean length (n=115) of 8.7 ± 1.8 mm. The width at the base of the tapering axes ranges from 0.3 – 0.08 mm. Axes are flattened, have surficial longitudinal ridges visible to the naked eye, and are bordered on either side by spinose or tentacular projections which are hollow and rounded at the apex. The proximal part of the fossil is slightly broadened and ends abruptly or axes may be joined, in pairs, at the base. Microscopic characters include unbranched, smooth-walled internal tubes of diameters ranging from 22 – 32 µm , longitudinally aligned in the fossil; and pores leading into tapering, blind-ended tubes which are approximately 215 µm long and 35 µm wide at the pore. The tapering tubes are oriented in such a way that the tapering end is distal in relation to the opening or pore which is proximal. The pores are bordered distally by a lip-like structure and proximally by a groove. They occur singly or in pairs in longitudinal rows usually down the centre of the fossil although sometimes near the edges.

COMPARISON

Detailed investigation of shows that these fossils should not be assigned to *Eohostimella* Schopf *et al.* Theron *et al.* (1990) suspected this and referred to the fossil as "*Eohostimella*". Schopf *et al.* (1966) described *Eohostimella* as follows: "Small plants, axes 1-2 mm in diameter, of creeping or ascendant or erect habit, horizontal axes dichotomously branching at an angle less than 45°. Outer cortex persistent, stereomic, commonly represented by a coalified crust 100-300 microns thick; dermal surfaces roughened by minute and spinose appendages irregularly arranged. Mode of reproduction and internal anatomy unknown." The smaller size and regular arrangement of the spinose appendages in this material led Kovács-Endrödy (1986) to distinguish it from *E. heathana* at the species level. Additional factors used to substantiate the assignment of these fossils to *Eohostimella* include the interpretation of superimposed fossils as dichotomously

branched axes and the gradually tapering shape of the fossil. The specific diagnosis for *Eohostimella parva* Kovàcs 1986 p. 112 follows: "Conical axes, 0.5-0.8 mm broad at the base tapering gradually into a long, blunt tip elongated into a point; the axis is more or less 1 cm long. Longitudinal ridges and grooves of different thicknesses and lengths occur on the surface. Minute, spinose appendages in longitudinal rows are confined to one side of the axis. Roundish protuberances of unknown function, at rather regular distances in a row occur on some axes." Evidence for the hollow axis characteristic of *Eohostimella* is lacking and this was attributed by Kovács-Endrödy (1986) to differences in preservation. Whereas *Eohostimella* is circular in cross section, the present fossil is flattened. However, this flattening may to some extent be due to diagenetic effects, burial and compaction. Kovács-Endrödy (1986) interpreted the "longitudinal ridges and grooves" visible on the material as the flattened rugose outer surface and thick cortex characteristic of *Eohostimella* Schopf *et al.* 1966. However, these surficial "ridges and grooves" do not represent folding, but internal structures which have been shown to be smooth-walled tubes and pores leading into tapering tubes. Kovács-Endrödy (1986) noted that the "minute, spinose appendages" are not irregularly arranged as in *Eohostimella* Schopf, nor are they visible on all specimens. Kovács-Endrödy (1986) interprets the uneven distribution of these small spinose structures as their restriction "to one side of the conical axis", rather than to differences in preservation. However, in many specimens the spinose appendages line both edges of the flattened axis in a regular arrangement.

DISCUSSION

The unique combination of characters observed in *S. parva* reveals a body plan unlike that of any known plant or animal (Figure 13). Although the primary aim of this study is to rectify the nomenclatural problem arising from misidentification, the assignment of this fossil to a phylum or a kingdom would be desirable. Present information is inadequate for this end, but nevertheless needs to be reported and interpreted to direct further research.

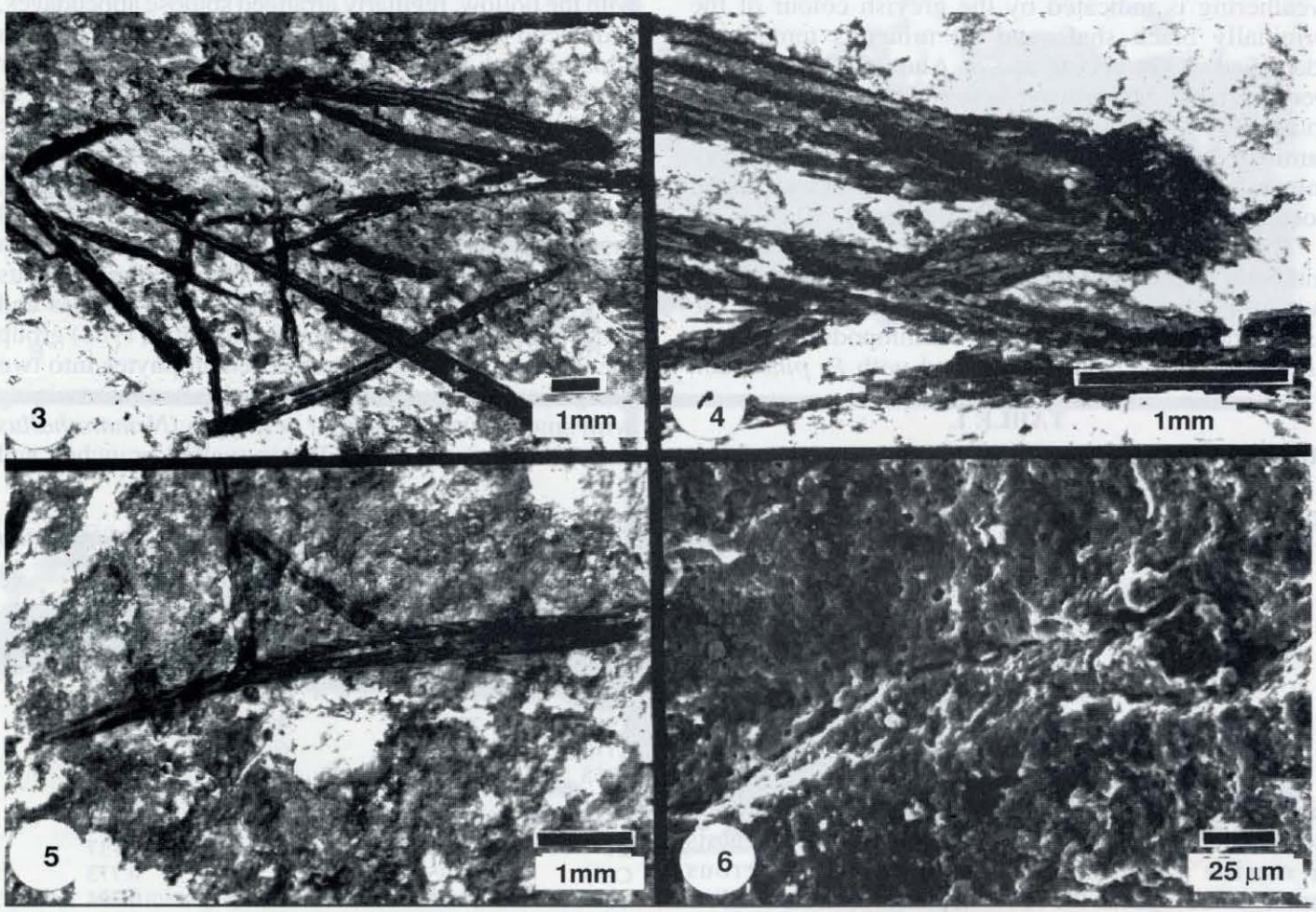


Figure 3. Specimens of *Siphonacis parva* randomly orientated in the bedding plane. Note that fossils occur mostly as single axes although two specimens may be joined at the base.
Figure 4. Two specimens of *Siphonacis parva* which appear to be in organic connection at the base.
Figure 5. A single axis of *Siphonacis parva*. Note minute spinose projections along margin and row of pores in the organic material.
Figure 6. SEM micrograph of pore and tapering tube.

The fossil material is carbonaceous as shown by maceration in hydrofluoric acid. The chemical composition of *S. parva* and the surrounding matrix, as determined by EDXA, is shown in Table 1. The fossil contains higher levels of sulphur than the surrounding matrix (9.9 ± 9.6 for fossil and 3.8 ± 3.3 for matrix) but the high standard deviation indicates some inconsistency in the distribution of sulphur. This sulphur excitation peak is unexplained, but since concomitant higher levels of Fe were not found, the possibility that pyrite may account for the sulphur is excluded. It is also important to note that Theron *et al.* (1990) obtained a sulphur peak in their microprobe analyses of *P. pulchrum* but they did not comment on this result.

X-ray diffraction and petrographic analyses show that the siltstone matrix consists of quartz, muscovite, microcline, an aluminium-rich white mica and two monoclinic micas (polytypes $2M_1$ and 1M), while the fossil contains quartz and mica. The $2M_1$ polytype of mica and the preferred orientation of the shale (F. Hartzer pers. comm.) shows that some metamorphism took place, probably due to deep burial. A degree of weathering is indicated by the greyish colour of the originally black shale and by minerals tentatively identified as Gorceixite and/or Alunite (D. Buhmann pers. comm.). Minor wave action during deposition is indicated by the sometimes disturbed form of the fine laminae in the shale. The accumulation of heavy minerals on bedding planes is indicative of a sediment sorting process (P. Zawada pers. comm.).

The geological context of the Soom Shale Member indicates deposition in an aquatic environment which was probably shallow marine (Theron *et al.* 1990). The association of *S. parva* with brachiopods, trilobites, acritarchs in the Soom Shale and with *P. pulchrum*, unidentified brachiopods, either another conodont or a scolecodonts and a crinoid, at the Keurbos site, suggests a marine environment. In addition, numerous unidentified algae in the bedding planes indicate shallow water, within the photic zone. Furthermore, from the high densities of the fossil in very localized areas of the matrix, their close association with complete conodont assemblages and the relatively quiet depositional environment indicated by preliminary sedimentological observations, it seems likely that the fossils were not transported over large distances. The fossils are randomly orientated in the bedding planes. In slab C.1., which has an area of approximately 190 cm², approximately 150 specimens are preserved together with an assemblage of *P. pulchrum* elements and an unidentified scolecodont or conodont assemblage. Axes also occur singly in some slabs. The range of densities of *S. parva* in the bedding planes is shown in Table 2. Taphonomic studies focusing on the distribution patterns of *S. parva* in the bedding planes would be useful in assessing whether the random orientation of specimens reflects the random dispersion of individuals as would be expected from planktonic life forms, for example, or whether the apparent randomness results from post-mortem disarticulation of a more complex organism.

If the observed morphological details are placed into a functional context, hypotheses regarding the affinities of this enigmatic fossil can be suggested. A small axis bearing a combination of long internal tubes, rows of pores each leading into a blind-ended tube, together with the hollow, regularly arranged spinose appendages, is difficult to interpret functionally as a terrestrial or an aquatic plant. The smooth-walled tubes do not appear to be conducting elements since they do not branch or anastomose. An aquatic plant of such a small size would probably not require vascularization.

An artificial group of plant fossils, the nematophytes, which are grouped on the basis of a structural organization composed of intertwining tubes are known from Silurian (Llandoverian and Wenlockian) deposits (Gray and Boucot 1977; Pratt *et al.* 1978; Niklas and Smocovitis 1983). Niklas and Smocovitis (1983) group the three taxa belonging to the nematophytes into two categories: 1) thin-walled, banded tubes intertwining with smooth-walled tubular cell types (*Nematothallus* and *Nematoplexus*) and; 2) thin-walled branched and

TABLE 1.

Results of EDXA of fossil and matrix showing relative quantities of element oxides (%).

Element Oxides	Sample (n=17) (%)	Matrix (n=6) (%)
MgO	0.607 ± 0.434	0.658 ± 0.483
AlO_3	25.496 ± 5.512	19.312 ± 3.354
SiO_2	51.238 ± 16.168	65.240 ± 7.512
P_2O_5	3.119 ± 1.814	2.315 ± 0.871
SO_3	9.852 ± 9.647	3.767 ± 3.273
K_2O	7.389 ± 1.652	6.612 ± 0.722
CaO	1.575 ± 0.563	1.015 ± 0.125
FeO	0.719 ± 0.221	1.082 ± 0.313

TABLE 2.

Densities (number of specimens per cm²) of *Siphonacis parva* in the bedding planes.

Slab	Area (cm²)	# fossils	number cm-²
C151	-	1	-
C152	-	1	-
C178	49	2	0.041
C260	11.4	2	0.175
C91	20	4	0.200
C119	22.5	6	0.267
C258	42	17	0.405
C251	56	27	0.482
C264	56	38	0.679
C1	190	140	0.737
C259	10.35	8	0.773
C269	31.5	25	0.794
C111	40	39	0.975
C263	4	5	1.250
C262	8	10	1.250
C297	55	78	1.418
C284	60	98	1.633
C111	2	5	2.500

septate tubes intertwined among thicker-walled, large and unbranched tubular elements (*Prototaxites*). In *S. parva* the tubes do not form a plexus, nor are they branched, banded or septate. The possibility that these fossils may be nematophytic is therefore excluded.

If *S. parva* is considered to have animal affinities, what would be the functional implications of the observed morphological details? It seems unlikely that

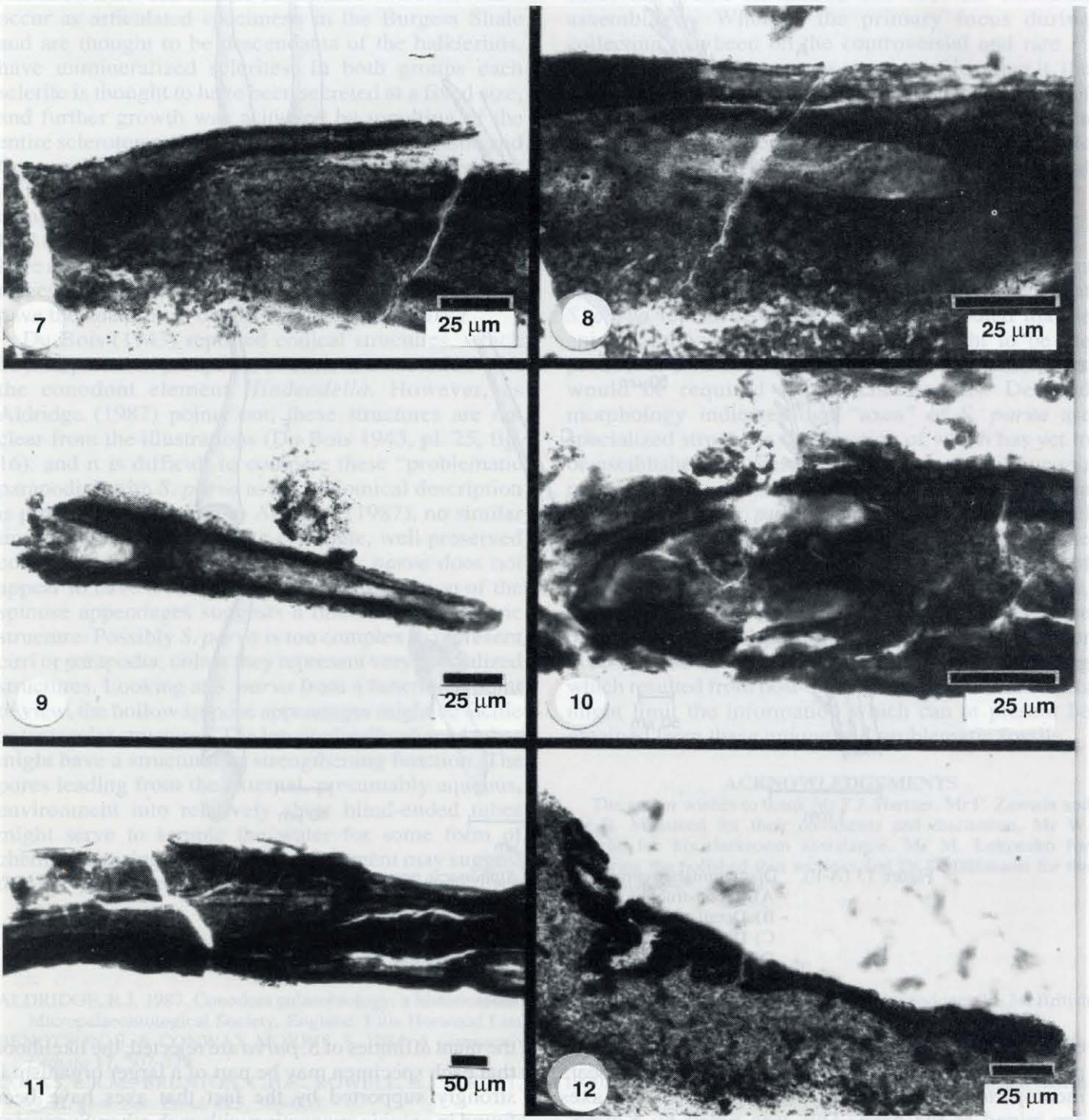


Figure 7. LM micrograph of hollow spinose or tentacular projection at the margin of a macerated fossil.
Figure 8. LM micrograph of spinose projection and lipped pore.
Figure 9. LM micrograph of isolated pore and associated tapering blind-ended tube.
Figure 10. LM micrograph of paired pores and associated tubes. Note groove leading to the pore.
Figure 11. LM micrograph of fragment of macerated carbonaceous material. Note darkened areas showing the positions of smooth-walled internal tubular structures.
Figure 12. LM micrograph of a cross section of *Siphonacis parva*. Note quartz-filled tube and spinose projection.

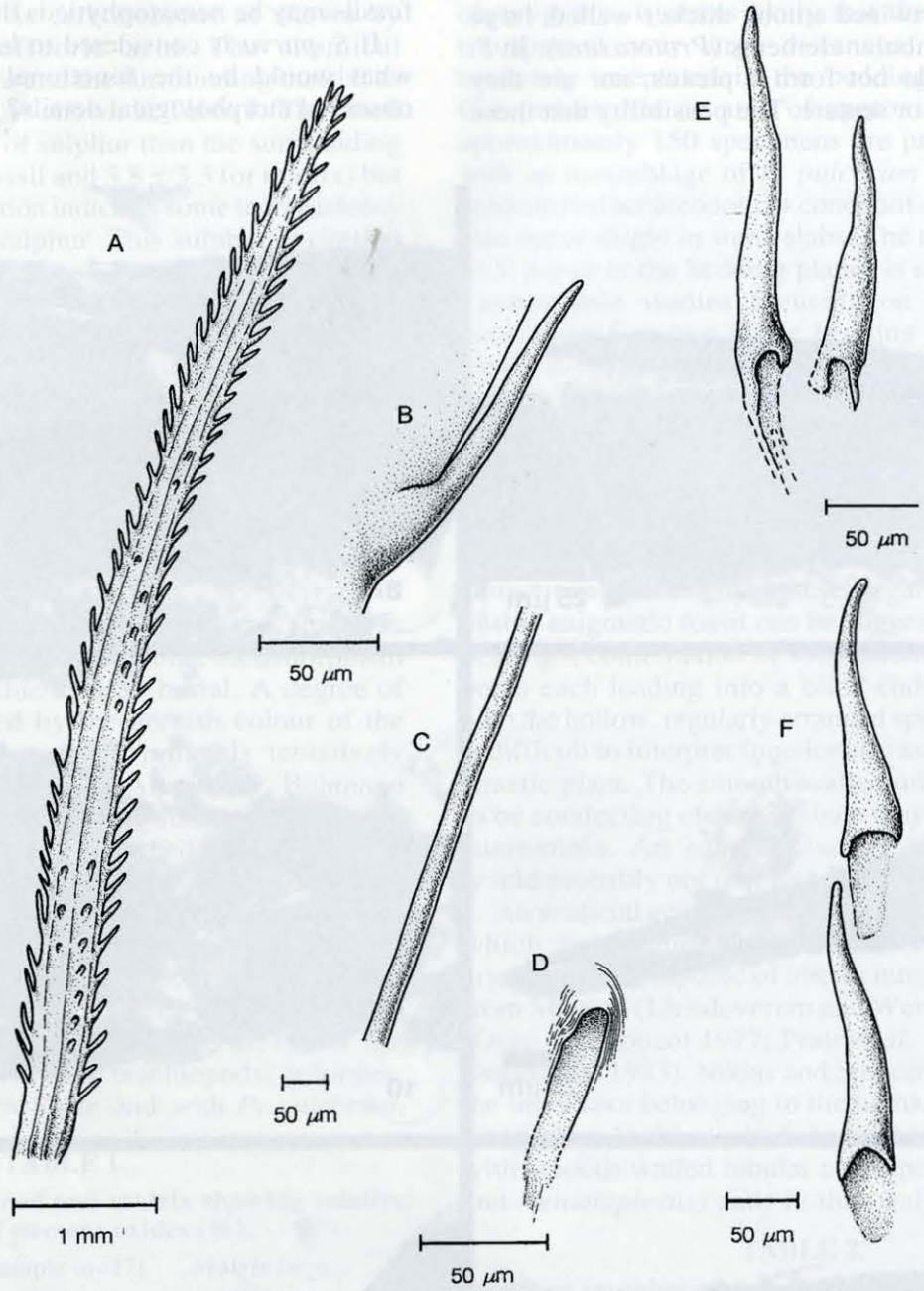


Figure 13 (A-F). Diagrammatic representation of *Siphonacis parva* and structural details.
A) Reconstruction of a whole specimen.
B) Detail of a hollow spinose or tentacular structure.
C) Detail of a smooth-walled tube.
D) Detail of a pore with an elaborate structure on distal side and groove on proximal side.
E) Paired pores and associated tubes.

each specimen represents the whole organism. The proximal end of the fossils, in most cases, appears incomplete and torn; but in a few specimens two axes are joined at the base. This was noted by Kovács-Endrödy (1986) p. 112 who interpreted her observations as follows: "Some of the axes branch dichotomously, and others are attached to one another in such a way that vegetative propagation is indicated. The overwhelming majority of axes without branches might have resulted from the easy separation of branches". If the plant affinities of *S. parva* are rejected, the likelihood that each specimen may be part of a larger organism is strongly supported by the fact that axes have been found in organic connection with each other. Supposing the fossils are disarticulated remains of a larger organism then which part of the hypothetical organism could these fossils be?

A distinctive group of soft-bodied slug-like metazoans is known from the Cambrian Burgess Shale deposits in British Columbia (Conway Morris 1989).

The Lower Cambrian halkieriids are known mainly from disarticulated sclerites composed of calcium carbonate, although articulated specimens are known from Greenland (Conway Morris and Peel 1990). Halkieriid sclerites are thought to have had a primary role in defence. The middle Cambrian wiwaxiids, which occur as articulated specimens in the Burgess Shale and are thought to be descendants of the halkieriids, have unmineralized sclerites. In both groups each sclerite is thought to have been secreted at a fixed size, and further growth was achieved by moulting of the entire sclerotome (Conway Morris 1990; Bengtson and Conway Morris 1984). Whether *S. parva* could represent some form of sclerite is uncertain. The carbonaceous compressions do not contain calcium carbonate (an HCl test showed no reaction). The sclerites of *Wiwaxia* have a "leaf-like" external appearance with longitudinal ridges visible, but it seems unlikely that they would have the anatomical details observed in *S. parva*.

Du Bois (1943) reported conical structures, which he interpreted as parapodia or cirri, in association with the conodont element *Hindeodella*. However, as Aldridge (1987) points out, these structures are not clear from the illustrations (Du Bois 1943, pl. 25, fig. 16), and it is difficult to compare these "problematic parapodia" with *S. parva* as no anatomical description is provided. According to Aldridge (1987), no similar impressions associated with complete, well preserved conodont assemblages are known. *S. parva* does not appear to have a conical shape; the distribution of the spinose appendages suggests a bilaterally symmetric structure. Possibly *S. parva* is too complex to represent cirri or parapodia; unless they represent very specialized structures. Looking at *S. parva* from a functional point of view, the hollow spinose appendages might be tactile or tentacular structures. The longitudinally aligned tubes might have a structural or strengthening function. The pores leading from the external, presumably aqueous, environment into relatively short blind-ended tubes might serve to sample the water for some form of chemical sensing. Such a line of argument may suggest that *S. parva* could represent sensory structures belonging to a soft-bodied animal.

The random orientation of sometimes dense assemblages of *S. parva* contrasts sharply with the often symmetrical arrangement of elements in the bedding plane assemblages of *P. pulchrum*. In some cases the fossils lie around and over the conodont assemblages. Whereas the primary focus during collecting has been on the controversial and rare *P. pulchrum*, using *S. parva* as a means of locating it, the latter has been undercollected and the precise details of their association have not been established. Such data as well as further chemical analyses would be valuable in elucidating the implications of the association of these two fossils.

CONCLUSION

Detailed morphology of *S. parva* indicates that this fossil is not of plant origin and it seems likely that *S. parva* represents remains of a soft-bodied marine animal. Individual specimens are thought to be the product of disarticulation but further taphonomic work would be required to substantiate this. Detailed morphology indicates that "axes" of *S. parva* are specialized structures the function of which has yet to be established. At present the affinities of *Siphonacis parva* are unknown. However, their close association with *Promissum pulchrum*, the similar physical appearance of organic material under LM, some affinities in chemical composition i.e. the presence of a sulphur excitation peak, and their comparable size, suggest that these two fossils could belong to the same organism. This hypothesis would require further investigation and the chemical alteration and flattening which resulted from post-depositional diagenetic effects might limit the information which can at present be obtained from these unique and problematic fossils.

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Palaeont. afr., **29**, 21-23 (1992)

AN ENIGMATIC NEW REPTILE FROM THE LOWER TRIASSIC FREMOUW FORMATION OF ANTARCTICA

by

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ABSTRACT

The partial skull of a new reptile from the Lower Triassic of Antarctica is described: It has a distinctive *procolophon*-like dentition, but other features suggest it is a diapsid. The name *Fremouwsaurus geludens* is proposed for the new animal. It is not possible to place the new form in any known higher taxon, so it is necessary to establish a new Family Fremouwsauridae to receive it.

INTRODUCTION

The Fremouw Formation of Antarctica contains a fossil tetrapod fauna typical of the well known *Lystrosaurus* zone of the South African Karoo, in addition it has yielded an abundance of small "prolacertid eosuchians" (Kitching *et al.* 1972). Our knowledge of the radiation of diapsid reptiles in the Lower Triassic is scanty. Postcranial material, especially at this stage of our knowledge, is of little use.

In 1970 Kitching collected a tiny fragment of grey/green siltstone (40mm x 20mm x 5mm) containing a mixture of white bone and impressions of bone and teeth of a small reptile on an exposure of the Fremouw Formation known as Kitching Ridge (see map in Kitching *et al.* 1972). This little specimen recently came to the author's attention.

MATERIAL

The specimen BP/1/5296 consists of part of the right side of a small skull and lower jaw which would have been approximately 30mm long when complete. The state of the dentition suggests that this was a mature individual. Part of the reason the specimen survived the rigours of the Antarctic climate is that several, mostly indeterminate, postcranial elements lie against the lateral surface of the skull, thus helping to bind the rock together. Preservation is remarkably good, and even the sclerotic ring is preserved. Little mechanical preparation was possible and latex peels were used in the study of the specimen.

SYSTEMATIC PALAEONTOLOGY

Class Reptilia

Subclass Diapsida

Order *incertae sedis*

FREMOUWSAURIDAE fam. nov

Diagnosis: Small diapsid reptile lacking a lower temporal bar but with a backwardly directed jugal spur. Surangular with distinctive crescentic lateral profile. Some sculpting of the lateral surface of the dentary. Dentition heterodont and acrodont with fine, delicate incisiform teeth and large bulbous cheek teeth with linguo-labially broadened crowns which met during occlusion resulting in the formation of wear facets.

Fremouwsaurus gen. nov.

Diagnosis: As for family.
Type species: *Fremouwsaurus geludens* gen. et sp. nov.
Etymology: : After the lower Triassic Antarctic Fremouw Formation from which the specimen was collected.

Fremouwsaurus geludens gen. sp. nov.

Diagnosis: As for genus and family.
Etymology: name from the Latin gelu = frost and dens = teeth : this name is suggested because of the remarkable resemblance of the cheek teeth to blobs of decorative frosting on a cake.
Holotype: BP/1/5296. Partial skull and lower jaw and some fragments of postcranial skeleton. In the collections of the Bernard Price Institute for Palaeontological Research.
Geological Horison: Fremouw Formation
Type horizon and locality: Kitching Ridge, antarctica.

DESCRIPTION

The skull roof is missing. Most of the prefrontal and maxilla, as well as a normally developed lacrimal, are preserved either as bone or impression. An apparently natural edge on the maxilla may indicate the suture with the premaxilla. The lower two thirds of the orbital border and scleral ring are preserved.

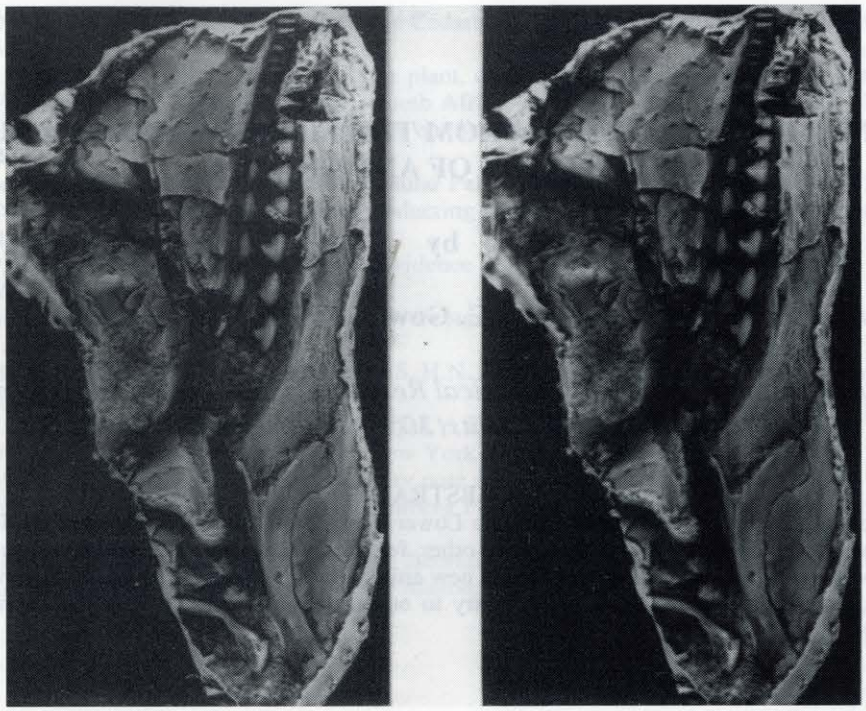


Figure 1: *Fremouwsaurus geludens* – stereophotographs of a latex peel taken from the specimen

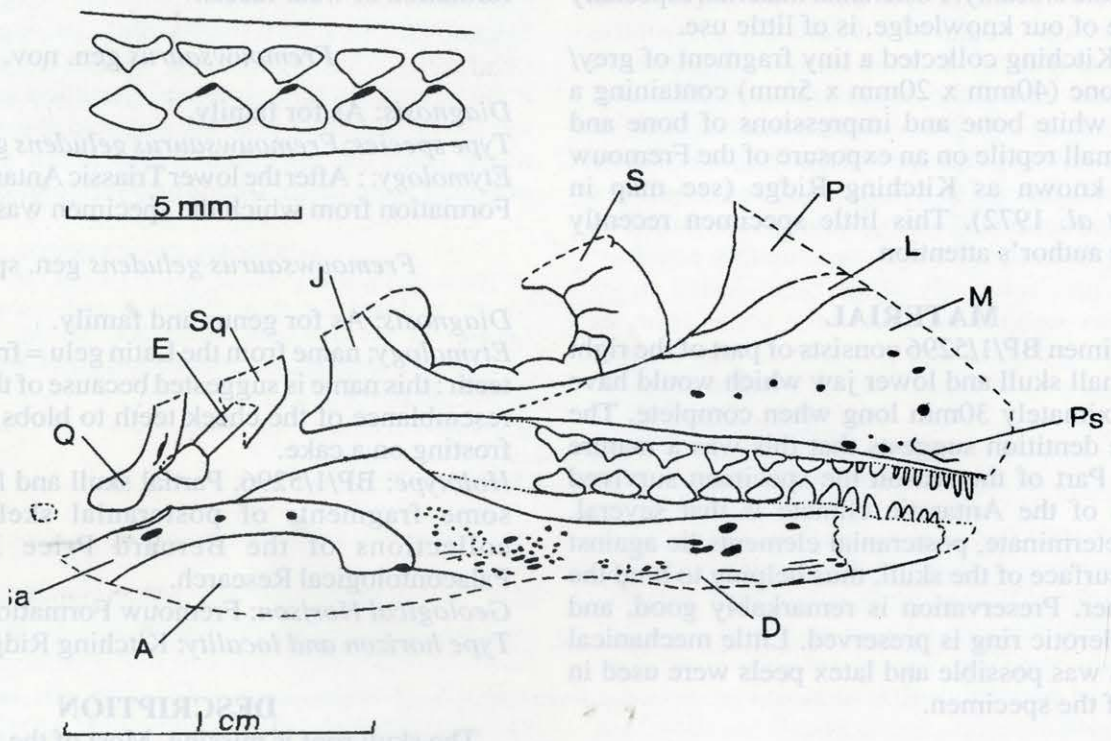


Figure 2: *Fremouwsaurus geludens* expanatory sketch with inset detail of the wear facets and pattern of occlusion of the cheek teeth.
A – angular; P – prefrontal; D – dentary; Ps – suture between premaxilla and maxilla; E – epipterygoid; Q – quadrate; J – jugal; s – sclera; L – lacrimal; Sa – surangular; M – maxilla; Sq – squamosal.

Viewing the specimen medially posterior to the orbit, there is a fragment of pterygoid or ectopterygoid in natural association with maxilla and jugal. Only the lower portion of the jugal is preserved: it has a thin posterior edge and a well developed posteroventral spur. Behind this in an unnatural position, lies a bone consisting of a broad flat shaft and a footplate at an oblique angle to the shaft: its identity is uncertain, but it may be epipterygoid. Lateral to this epipterygoid is a partially exposed sheet of bone which is probably squamosal. Behind this is an excellent impression in lateral profile of a tall strongly bowed quadrate with a deep depression on its posterior (occipital) surface.

The lower jaw has suffered only minor loss at both ends. The lateral surface of the dentary is decorated with ridges and pits. A small coronoid eminence is present. Lateral sutures are well displayed and the surangular has a distinctive crescentic shape.

The remarkable dentition is almost entirely preserved as impression. Most remarkable is the size disparity between the fine anterior teeth and the massive posterior cheek teeth. Tooth attachment is acrodont. A fully formed posterior maxillary tooth is broken in the mesiodistal plane with the labial half of the tooth preserved, this tooth had not yet become attached to the maxilla. The large cheek teeth have linguolabially broadened crowns and a precise occlusal relationship whereby, as the jaws closed, the distal slopes of the lower crowns came into contact with the mesial slopes of the uppers. The resulting wear facets are clearly visible on the lower teeth, but not enough of the uppers is preserved to display the corresponding wear facets.

DISCUSSION

At first sight this little skull has a procolophonid look about it, due to the morphology and mode of attachment of the teeth and the short snout. However, no known procolophonid exhibits such a marked size difference between incisiform amd molariform teeth, and the short snout is a function of the relatively large orbits in skulls of this size. The shape of the posterior edge of the jugal is entirely atypical of this bone in procolophonids; some, such as *Owenetta* and *Procolophon* (Gow 1977) have an upswept jugal, but none has a posteroventral jugal spur. It is extremely unlikely that a procolophonid quadratojugal would become separated from the quadrate; the procolophonid quadrate has a vertical lateral profile, and there is no depression in its posterior surface. Finally, amongst the otherwise unhelpful postcranial elements are two tiny bones which are probably phalanges or possibly caudal centra. These bones are long and slender, whereas the corresponding bones of procolophonids are short and broad.

The jugal as preserved is undisturbed and the posteroventral spur was carefully exposed by the writer. There can be little doubt that this morphology represents a reduction from an ancestral condition in which a lower temporal bar was present. This condition is typical not only of lizards, but also prolacertids (Gow 1975) and some sphenodontids (Carroll 1987). The quadrate is indistinguishable from that of diapsids such as *Prolacerta* (Gow 1975). It is thus very likely that this new form is a diapsid. That it is not a sphenodontid, as the acrodont dentition might suggest, is demonstrated by the presence of a lacrimal bone. Known prolacertids are all carnivorous. There are no characters which would place the specimen unequivocally in lepidosauria and there are no known herbivorous Triassic lepidosaurs. The specimen is best regarded as representative of a previously unrecorded, in all likelihood diapsid, family.

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TAXONOMIC STATUS OF THE PARTIAL CALVARIA A.L. 333-45 FROM THE LATE PLIOCENE OF HADAR, ETHIOPIA

by

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ABSTRACT

The taxonomic status of a partial calvaria, A.L. 333-45, from the late Pliocene of Hadar, in Ethiopia, classified as a hominid and paratype of "*Australopithcus afarensis*" Johanson, White and Coppens 1978 is reassessed. Its total morphological pattern and adaptive affinities agree with the Pongidae, and do not exhibit a single unequivocal hominid character. The evidence in fact suggests that A.L. 333-45 represents a relatively generalized ape, the only pongid calvaria known from the late Pliocene of Africa: and may be the first skull found of *Praeanthropus africanus* (Weinert), 1950. Moreover, this indicates that the fossils assigned to "*Australopithecus afarensis*" do not represent a single taxon: and that the reconstruction of the skull of a male "*A. afarensis*" seems to be a composite of pongid and hominid fossils.

INTRODUCTION

A partial calvaria, A.L. 333-45, from the Late Pliocene of Hadar, in Ethiopia, and assumed to be a hominid, is a paratype of "*Australopithecus afarensis*". Since there is no complete cranium in the collections from Hadar, a composite skull was reconstructed from 13 unrelated parts, including A.L. 333-45, the only and complete calvaria of a presumed male (Kimbel, White and Johanson, 1984).

Johanson and White claim that the Laetoli-Hadar specimens are distinct from apes and from any of the later hominids (Johanson and Edey 1981). "The small A.L. 162-28 cranium emerges as unique among hominids suggesting a common chimpanzee morphological pattern in *A. afarensis*" (Kimbel *et al.* 1984 p.369), yet it supposedly belongs to a "fully bipedal" hominid (Johanson and Edey 1981 p.274).

Washburn described "*A. afarensis*" as having "human bodies topped with heads of apes" (Johanson and Edey 1981p.353). Their heads, which are "more ape-shaped than human-shaped" (Johanson and Edey 1981p.275), exhibit eight features of the calvaria not found in hominids, and share only one derived feature with the robust australopithecines (Kimbel *et al.* 1984). Although Johanson and White observed that A.L. 333-45 fits neither *Homo* nor *Australopithecus* (Johanson and Edey 1981), it was classified as an unequivocal hominid and an *Australopithecus*. Olson (1981, 1985) claims that A.L. 333-45 has advanced basicranial features and represents a primitive robust australopithecine. He transferred it to the genus "*Paranthropus*", and called it "*Paranthropus africanus*", a new combination for *Praeanthropus africanus* (Olson 1981 p.118; Weinert 1950).

Kimbel *et al.* (1984, 1985) countered Olson's claim. They observed that African ape crania match the basal morphology of the A.L. 333-45 mastoid region, and that the overall morphology of this region is strikingly primitive.

In 1983, Ferguson suggested an alternative view, that A.L. 333-45 represents a generalized ape, and that *Praeanthropus africanus*, the Garusi maxilla from Laetoli, is an ape (Ferguson 1986). Kimbel *et al.* (1984) acknowledge that an apelike morphological pattern is indicated in "*A. afarensis*" crania, but nevertheless continue to regard A.L. 333-45 as hominid.

This study reassesses the morphological pattern of A.L. 333-45 in order to determine if the calvaria is indeed an unequivocal hominid, or rather, a relatively generalized pongid.

MATERIALS AND METHODS

The material examined consists of a cast of A.L. 333-45, a partial calvaria that lacks the frontal, most of the right parietal, and the basal portion of the occipital bone, and has only minor plastic deformation. It was described anatomically in detail by Kimbel *et al.* (1982) and reconstructed, except for the upwardly crushed left anterior part of the nuchal plane (Kimbel *et al.*1984). It is unassociated with any fossil dentition. Orientation of the nuchal plane in relation to the Frankfurt Horizontal (F.H.) is after Kimbel *et al.* (1984).

The non-correctable artificial asymmetry of the basicranial region is restored photographically by using a mirror image of the right part, which is undistorted and more complete, and a mirror image of the left occipital condyle which is slightly displaced laterally.

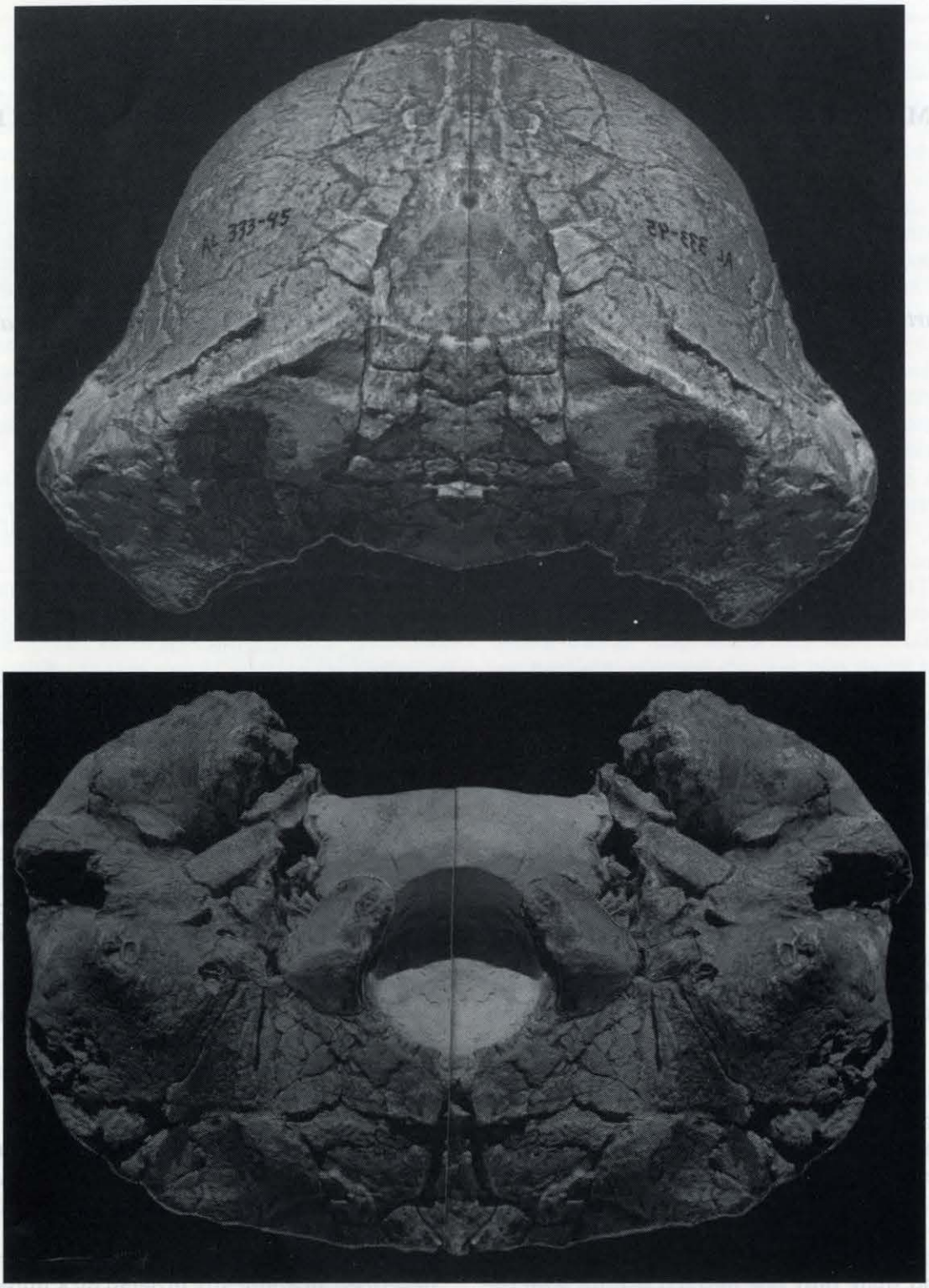


Figure 1. Restoration of the calvaria A.L.333-45. Above, norma occipitalis. Below, norma basalis.

Also examined were casts of *H. erectus*, *A. africanus* Sts 5, *A. boisei* OH 5, *A. walkeri* KNM-WT 17000, (Ferguson 1989) and the occipital fragment "*A. afarensis*" A.L. 162-28, as well as modern skulls of *H. sapiens* (N=20), *Pan troglodytes* (N=10) and *Gorilla gorilla* (N=7). The data base includes the *A. africanus* occipital bone (MLD 1) from Makapansgat and skull I from Sterkfontein, and *A. robustus* skulls SK 48, SK 49 from Swartkrans and the Kromdraai skull (Broom 1936, 1938; Robinson 1954).

The cranial morphology of A.L. 333-45 is compared with criteria by Le Gros Clark (1964) and Tobias (1967) for distinguishing the crania of the Pongidae from those of the Hominidae.

Drawings of the ventral view of A.L. 333-45 are superimposed on those of the gorilla and *Australopithecus* as a new way of determining the development of the occipital torus and comparing the suboccipital features.

RESULTS AND DISCUSSIONS

The morphology of A.L. 333-45 is compared first with the differential diagnosis for the calvaria of the Pongidae and Hominidae (after Le Gros Clark 1964). Numbers 6 under Pongidae and 5 under Hominidae were added by the author.

Pongidae	**Hominidae**
1. Strong muscular ridges	1. Weak muscular ridges*
2. Nuchal area becoming extensive with relatively high position of inion	2. Restriction of nuchal area of occiptal squama, associated with low position of inion*
3. Occipital condyles retain backward position well behind level of auditory apertures	3. Relative displacement forward of occipital condyles
4. Only a limited degree of flexion of basicranial axis associated with maintenance of low cranial height	4. Increasing flexion of basicranial axis associated with increasing cranial height
5. Cranial capacity shows no marked tendency to expansion	5. *Australopithecus* cranial capacity shows a relative or differential expansion. *Homo* shows a relative differential or absolute expansion
6. Inconsistent and late ontogenetic development of flattened mastoid process	6. Consistent, early ontogenetic development of pyramidal mastoid process

* Except *Homo erectus*

A.L. 333-45 has the following characteristics:

1. There is a " strongly apelike arrangement of muscle on the back of the skull " (Johanson and Edey 1981p.259). The nuchal plane exhibits "deeply excavated depressions for the nuchal masculature" (Kimbel *et al.* 1982p.471).
2. The nuchal area is extensive with a relatively high position of inion, which is distinctly above the Frankfurt Horizontal Plane (F.H.P.).
3. The position of the occipital condyles is more posteriorly located than in *A. boisei* Leakey 1959 O.H. 5, and slightly behind the level of the auditory apertures.
4. In view of the low cranial height, posteriorly positioned foramen magnum, horizontal tympanics, and low petro-median angle, it is expected that the associated flexion of the basicranial axis would be limited in degree. However, flexion in *A. walkeri* KNM-WT 17000 is also weak (Walker *et al.* 1986).
5. The cranial capacity, estimated at 500 cc by Holloway (Johanson *et al.* 1982), shows no expansion compared to *A. africanus*, by the lack of

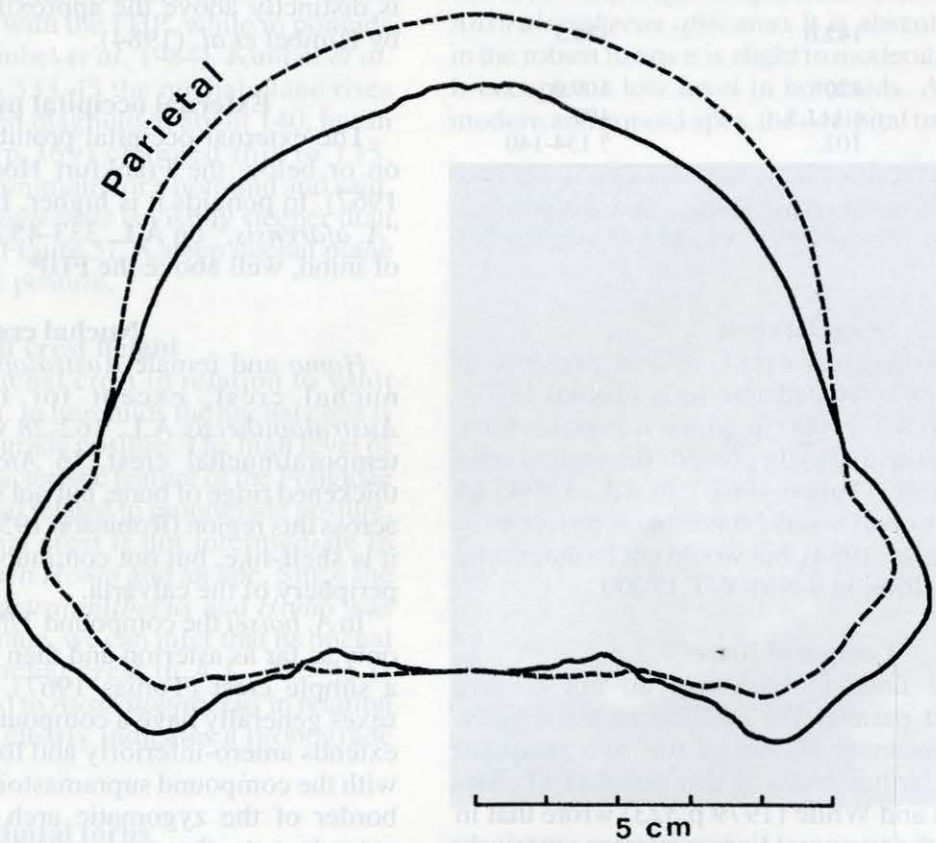


Fig.2. Norma occipitalis of the calvaria A.L. 333-45 (solid line) superimposed on that of *A. africanus* (broken line). Note lack of parietal expansion in A.L. 333-45.

parietal expansion in the coronal plane (Figure 2), and the occipital bone has not rotated downward as seen by the higher position of lambda and inion in relation to the F.H.P. (Kimbel *et al.* 1984, Fig. 14).

6. The flattened mastoid morphology is the "most similar to female *gorillas*" (Kimbel *et al.* 1985 p.122), and is attributed to late ontogenetic development.

In addition to the criteria of Le Gros Clark, many other features are compared, even though several are not diagnostic.

Cranial breadth

In *Australopithecus* the maximum bimastoid breadth is greater than the maximum breadth across the supramastoid crests. In *H. erectus* and pongids the breadth across the supramastoid crests is greater than the bimastoid breadth (except for some gorillas in which the bimastoid breadth is also greater). The maximum breadth in A.L.333-45 is distinctly less than the maximum breadth across the supramastoid crests, unlike *Australopithecus*; it is therefore pongid-like.

TABLE 1

Selected metrics of maximum cranial breadth

Hominoid	Bimastoid	Supramastoid
A.L. 333-45	100 ± 2.0*	126.5 ± 2.0*
A. boisei		
O.H.	142.0	139.5
A. africanus		
MLD/37/38	120*	109.0
Sts 5	c.111.5	107
H.e. erectus	102	? 134-140

* Measured on reconstruction. Metrics *Australopithecus* and *H. erectus* after Tobias (1967): A.L. 333-45 after Kimbel *et al.*, (1982).

Sagittal crest

Homo has no sagital crest. When present in *Australopithecus* it is located anteriorly (Tobias 1967), except for KNM-WT 17000 in which it is posteriorly located (Walker *et al.* 1988). In pongids the sagittal crest is located posteriorly (Tobias 1967.). In A.L. 333-45 an inferred sagittal crest would have been posteriorly located (Kimbel *et al.* 1984), but would not be diagnostic in view of its position in KNM-WT 17000.

Temporal lines

The temporal lines in hominids do not closely approximate and parallel the midline as in pongids. The region of intimate fusion of the two temporal crests is much farther back in the pongids (Tobias 1967). Johanson and White (1979 p.323) wrote that in "*A. afarensis*" " the temporal lines converge anteriorly and closely approximate the midline." This was corrected by Kimbel *et al.*, (1984 p.365) who said, "the temporal lines on the male A.L. 333-45 cranium [sic] more closely approximate and parallel the midline further back on the cranial vault than in any other hominid cranium known," (13.0 posterior to lambda).

The divergence of the temporal lines relative to lambda is not below that in A.L. 333-45, unlike that in *Australopithecus*, except for KNM-WT 17000 (Walker *et al.* 1986), and is thus not diagnostic.

Occipital measurements

Kimbel *et al.* (1984) state that the high occipital scale ratio in males and some females of "*A. afarensis*" is not found in other hominids. The only occipital measurement given by Kimbel *et al.* (1984), that falls outside the range of variation in hominids is the lambda-inion chord. This chord is shorter in apes (*Pan*) than it is in hominids. In A.L. 162-28 the lambda-inion chord is clearly shorter than in hominids, but in A.L. 333-45 and A.L. 288-1 it is virtually the same as the minimum for hominids. The lambda-inion chord A.L. 333-45, however, is relatively small compared to its larger cranial capacity. (Table 2).

Inion

Inion is low in *Homo*, except for *H. erectus* OH 9, in which it is above the Frankfurt Horizontal Plane. In *Australopithecus* inion is low and generally close to the FHP (Tobias 1967), whereas in pongids it is higher, above the FHP. As already noted, in A.L.333-45 inion is distinctly above the approximate FHP, as oriented by Kimbel *et al.* (1984).

External occipital protuberance

The external occipital protuberance in hominids is on or below the Frankfurt Horizontal Plane (Tobias 1967). In pongids it is higher. In the reconstruction of "*A. afarensis*," on A.L. 333-45 it is located at the level of inion, well above the FHP.

Nuchal crest

Homo and female *Australopithecus* have a simple nuchal crest, except for the putative female *Australopithecus* A.L. 162-28 which has a compound temporal/nuchal crest. In *Australopithecus* it is a thickened ridge of bone, but not shelf-like or continuous across this region (Robinson 1954). In KNM-WT 17000 it is shelf-like, but not continuously salient around the periphery of the calvaria.

In *A. boisei* the compound T/N crest extends laterally only as far as asterion and then continues anteriorly as a simple crest (Tobias 1967). Modern apes of both sexes generally have a compound T/N crest. This crest extends antero-inferiorly and forms a continuous ridge with the compound supramastoid crest and the superior border of the zygomatic arch (Olson 1981). It also extends onto the pars mastoidea. In A.L. 333-45 a continuous salient shelf defines the periphery of the calvaria from the compound T/N crests posteriorly to

TABLE 2
Hominid and pongid cranial measurements and indices

	Hominids* (n=23)	A.L. 288-1	A.L.333-45	A.L.162-28	*Pan troglodytes* mean (n=10)
Lamba-inion chord (la-i)	32.0 ± 1.0 - 70.0**	30.7 ± 1.0	31.6	25.1	21.2
Inion-opisthion chord (i-o)	26.0 - 58.0	27.2	38.0 ± 1.0	-	41.6
Index of occipital scale chords (io/la-ix100)	61.9 -120.7	88.6	120.3	>100	192.6
Occipital sagittal chord (la-o)	56.7 - 85.9	51.2 ± 1.0	60.5	-	56.8
Occipital sagittal arc	68.0 -118.2	58.8 ± 1.0	72.0	-	67.6
Occipital sagittal index (chord/arch x 100)	80.0 - 87.6	87.1	84.0	-	84.0
Biasterion chord (ast-ast)	72.5 -125.8	-	94.5 ± 2.0	79.2	79.2

Data after Kimbel *et al.*, 1984.

* *A. africanus*. (n=4), KNM-ER 1805, *A. boisei* (n=4), KNM-ER 1813, *H. habilis* (n=3), *H. erectus* (=*Sinanthropus*) X (n=4), Solo X (n=6)

**After Tobias, 1967

the roots of the zygomatic process anteriorly (Kimbel *et al.* 1982), and extends onto the pars mastoidea (Kimbel *et al.* 1985) (Figure 6).

Nuchal plane angle

The nuchal plane of hominids is not as steeply inclined as it is in pongids. In hominids it faces downward rather than backward as in pongids (Zuckerman 1954a). In hominids it is 139-160, with the FHP, while in pongids (*Pan*) it is 103-138 (Kimbel *et al.* 1984). Kimbel *et al.* (1982) said that in A.L.333-45 the nuchal plane rises steeply from the foramen magnum at about 140, but in 1984, Kimbel *et al.* (p.369) changed this to 135, distinctly less than the minimum for a hominid and said, "the nuchal plane in *A. afarensis* is visibly steeper than in other hominid taxa. (Figure 3). A steep nuchal plane is related to pronograde posture.

Nuchal crest height

The height of the nuchal crest in relation to vault height is also significant. In hominids the nuchal crest is low and related to orthograde posture. The high level of the nuchal crest is a characteristic feature of the Pongidae (Le Gros Clark 1958), and related to pronograde posture. The height of the nuchal crest is not intermediate in *Australopithecus* between *Homo* and an ape. Since the common ancestor of *Australopithecus* and *Homo* was almost certainly orthograde, we can infer that its nuchal crest was low. The nuchal crest in A.L. 333-45 is relatively high compared to *Australopithecus* in relation to the vault height and clearly indicates a pronograde posture (Figure 4).

Occipital torus

At the posterior of the occipital bone on each side of the nuchal crest is a smooth, rounded protuberance or raised portion which projects posteriorly, called the occipital torus (Poirier 1973). In *H. habilis* it is of moderate relief (Day *et al.* 1975). In *H. erectus*, particularly Sangiran IV, it is massive (Le Gros Clark 1964) and enormously thick (Tobias 1967). In *H. sapiens neanderthalensis* it is strong (Le Gros Clark 1972). In some modern populations, occipital tori occur in very high frequencies (Kennedy 1991). In *Australopithecus africanus* it is absent or weak, while in the robust forms it is slight to moderate (Tobias 1967). It occupies a low level in hominids. Among the large modern anthropoid apes, the occipital torus forms a crest



Figure 3 Restoration of the calvaria A.L. 333-45. Left norma lateralis. Note that the steep nuchal plane faces backward more than downward.

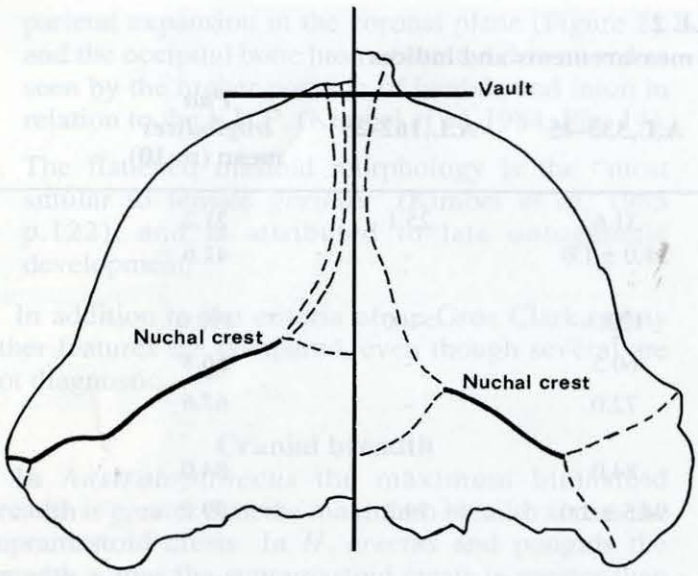


Figure 4 Norma occipitalis of the calvaria A.L. 333-45 (left half) and *A. boisei* O.H. 5 (right half) showing height of compound T/N crest in relation to the vault. Both specimens drawn to the same height. The nuchal crest and occipital torus of A.L. 333-45 are clearly relatively higher and ape-like. Simple crest (broken line), compound crest (solid line).

that reaches high up on the skull (Zuckerman 1954a). Schultz (1965 p.173) notes that "the mechanically disadvantageous location of the occipital joint of adult apes requires such powerful nuchal muscles that their area of cranial attachment has usually to be enlarged with the addition of occipital crests." In A.L. 333-45 the area for nuchal muscles has been expanded by a relatively high compound T/N crest continuous with a salient occipital torus (Figure 5.)

Nuchal area

As already noted by Le Gros Clark (1972) the nuchal area in pongids is extended, whereas in hominids it is restricted and a "particularly distinctive character of the hominid skull" (Le Gros Clark 1959 p.167). The nuchal area in *H. erectus* is expanded compared to *H. habilis* (Kimbel *et al.* 1984), but its simple nuchal crest is not shelf-like nor is its occipital torus a crest. In A.L. 288-1 the nuchal area is not expanded and there is no indication of an occipital torus. Its postcranial skeleton is clearly orthograde. In apes the mastoid process has a flat posterior surface which represents a lateral extension of the nuchal plane (Schultz 1950). A.L. 333-45 has a relatively high compound T/N crest continuous with an expanded occipital torus and flat posterior surface of the mastoid process, indicating a lateral extension of the nuchal plane as in apes.

Foramen magnum

The relative position of the foramen magnum on the base of the cranium is related to posture. In hominids it is more forwardly placed than in pongids and related to upright posture and bipedalism. The foramen magnum of australopithecines is situated well forward (Tobias 1967), intermediate between ape and man (Tobias 1983a). The opisthion is missing in A.L. 333-45, but the ectobasion is preserved and indicates that the foramen magnum is not as posterior as in modern apes, but more posteriorly located than in *A. boisei* O.H. 5 (Figure 5).

Digastric fossa

The digastric fossa (incisura mastoidea) in hominids (mastoid notch in *Homo*), is short, narrow and oval, and varies from shallow and ill-defined to deep and ridged in *H. sapiens* (De Villiers 1968). In *A. africanus*, "both STS 5 and MLD 37/38 have narrow and deep mastoid notches" (Olson 1985 p.108). Kennedy (1991) says MLD 37/38 "reveals a short and wide mastoid notch." In pongids it is *long*, broadly triangular, oval or V-shaped according to Olsen (1981), and shallow. The digastric fossa in A.L. 333-45 is long, "shallow, triangular and mediolaterally concave" (Kimbel *et al.*, 1985 p.130). The mastoid notch is not a "reliable taxonomic character" (Kennedy 1991) among hominids, but valid between hominids and pongids.

Venous sinus drainage pattern

Kimbel *et al.* (1984) list only one derived feature that A.L. 333-45 shares with the robust australopithecines - the venous sinus drainage pattern. Falk

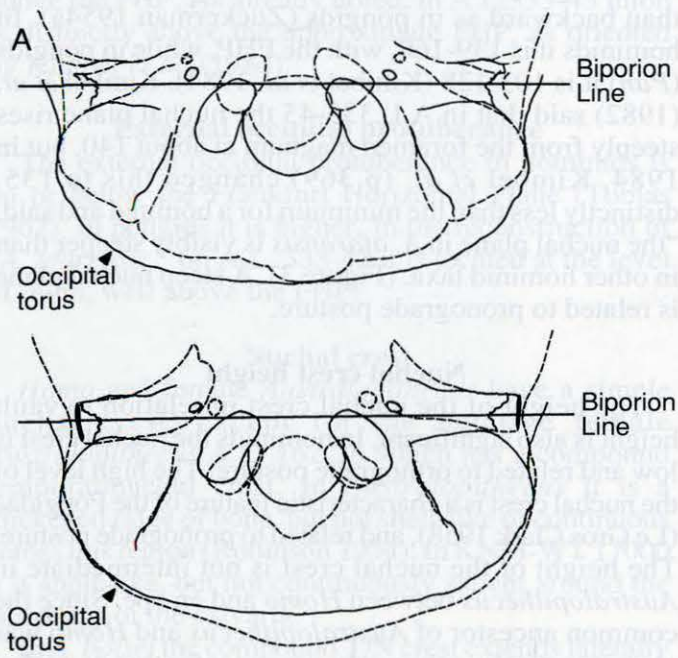


Figure 5 Norma basalis of the occipitomastoid region of A) A.L. 333-45 (solid line) superimposed on that of a female gorilla (broken line), and B) A.L. 333-45 (solid line) superimposed on *A. boisei* O.H. 5 (broken line). Note that occipital tori and mastoid process of A.L. 333-45 and gorilla are nearly identical, unlike O.H. 5, and that the occipital condyles and foramen magnum of A.L. 333-45 are more posteriorly located than in O.H. 5.

and Conroy (1983) suggest that the high frequency of this feature in robust *Australopithecus* has phylogenetic and systematic significance. They say that this feature in A.L. 333-45 is either ancestral to the robust australopithecines, or is shared with a common ancestor. Kimbel *et al.* (1984 p.377) regard the use of this feature for phylogenetic reconstruction as "doubtful owing to the marked temporal and spatial fluctuations in the frequencies of different venous drainage patterns in the *Homo* lineage". In pongids it is undocumented.

Asterionic notch

The asterionic notch is characteristic of pongids and is unknown in hominids. Its presence in the hominid KNM-WT 17000 is "probable" (Leakey and Walker 1988 p.520). The calvaria A.L. 333-45 shares this primitive sutural arrangement with apes (Kimbel *et al.* 1984).

Supramastoid crest

In hominids the posterior part of the temporal ridge from the border of the zygoma arches backward and upward and is called the supramastoid crest. It coincides with the root of the inferior temporal line above the mastoid. In *H. sapiens* it may be slight, moderate or marked (De Villiers 1968). In *A. boisei* O.H. 5 the lateral part of the superior nuchal line continues from the compound T/N crest as a simple nuchal crest onto the inferior surface of the mastoid process (Tobias 1967). It does not join the supramastoid crest, whereas in almost all adult modern great apes the inferior temporal and superior nuchal lines form a robust compound supramastoid crest, the most prominent feature in an occipital view (Olson 1981). In A.L. 333-45 the inferior temporal and superior nuchal lines continue antero-inferiorly as a robust, compound supramastoid crest (Figure 6).

In australopithecines the simple supramastoid crest does not bulge as much laterally as the pars mastoidea (Tobias 1967). In apes the compound supramastoid crest is prominent and is usually, although not always, lateral to the pars mastoidea. The compound supramastoid crest in A.L. 333-45 is prominent and projects slightly more laterally than the *pars mastoidea*, as in A.L. 333-112. The " supramastoid crest of the A.L. 333-45 skull retains the primitive projecting condition found in the great apes" (Olson 1981 p.115).

Supramastoid sulcus

In hominids, between the supramastoid crest and the mastoid crest lies a supramastoid sulcus. Kimbel *et al.*(1985) note that in A.L. 333-45 the supramastoid crest and mastoid crest merge, with no sulcus between them. The supramastoid region of A.L. 333-45 does not share the characteristic occipital profile of *Australopithecus* (Figure 7).

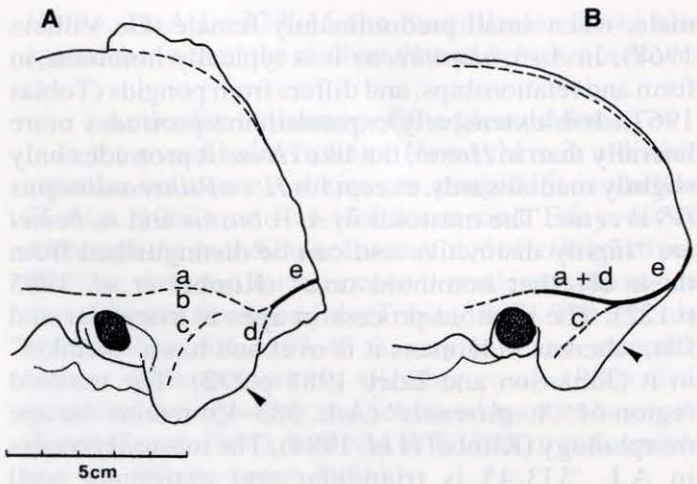


Figure 6 Left norma lateralis of A) *A. boisei* O.H. 5 and B) A.L. 333-45, depicting the occipitomastoid region. Simple crest (broken line), compound crest (solid line). Structures indicated: a) supramastoid crest, b) supramastoid sulcus, c) mastoid crest, d) superior nuchal crest, e) temporal/ nuchal crest. Arrow points to posterolateral face of the mastoid

Mastoid process

In hominids the mastoid process is variably large, medium or small, prominent, pyramidal or cone shaped, and protrudes both laterally and inferiorly. In *H. sapiens* it is mostly medium in size, when large predominantly

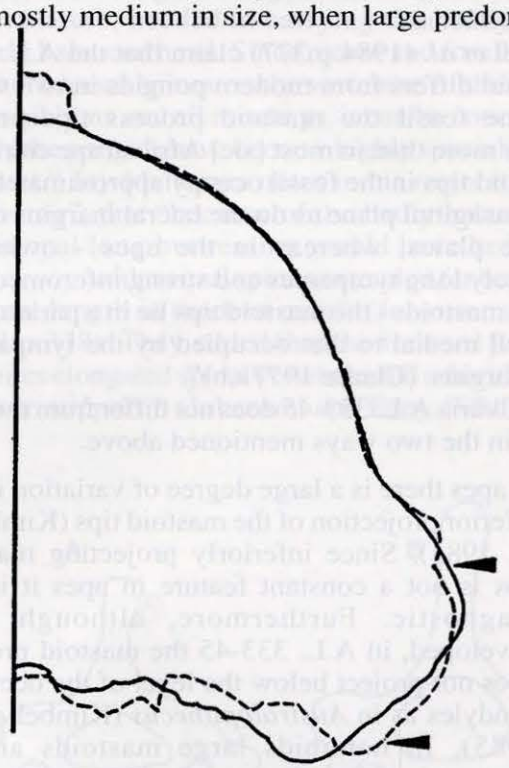


Figure 7 Norma occipitalis of the contour of right half of the calvaria A.L. 333-45 (solid line) superimposed on that of *A. boisei* O.H. 5 (broken line). Note that the supramastoid sulcus is absent in A.L. 333-45, and that the masoid process in O.H. 5 bulges laterally whereas in A.L. 333-45 it is inflected.

male, when small predominantly female (De Villiers 1968). In *Australopithecus* it is typically hominine in form and relationships, and differs from pongids (Tobias 1967). It is extensively expanded and protrudes more laterally than in *Homo*, but like *Homo* it protrudes only slightly medialwards, except for *H. (=Pithecanthropus IV) erectus*. The mastoids in *A. robustus* and *A. boisei* are "highly distinctive and can be distinguished from those of other hominoid taxa" (Kimbel *et al.* 1985 p.122). The mastoid process in apes is triangular and flat, whereas in humans it is oval and has a "wrinkle" in it (Johanson and Edey 1981 p.272). The mastoid region of "*A. afarensis*" (A.L. 333-45) retains the ape morphology (Kimbel *et al.* 1984). The mastoid process in A.L. 333-45 is triangular and extremely well developed. It exhibits a posterolateral face that is flat mediolaterally and slightly concave inferosuperiorly (Kimbel *et al.* 1982 p.122). It has a strong inferomedial inflection not found in hominids (Kimbel *et al.* 1984). "The inferior and lateral projection is not remarkable compared to that of African great apes" and the inflation "does not differ significantly from the condition found to characterize many extant apes, particularly the female gorilla" (Kimbel *et al.* 1985 p.122). The mastoid process in the temporal fragment of "*A afarensis*" A.L. 166-9, however is not flattened but is globular despite the eroded external surface (Taieb *et al.* 1974) as in *Australopithecus*.

Kimbel *et al.* (1984 p.377) claim that the A.L. 333-45 mastoid differs from modern pongids in two ways: 1. "in the fossil the mastoid process tips project inferiorly more than in most [sic] African ape crania; 2. the mastoid tips in the fossil occupy approximately the same parasagittal plane as do the lateral margins of the tympanic plates, whereas in the apes - owing to transversely long tympanics and strong inferomedially inflected mastoids - the mastoid tips lie in a parasagittal plane well medial to that occupied by the tympanic's lateral margins (Clarke 1977a,b)".

The calvaria A.L. 333-45 does not differ from modern pongids in the two ways mentioned above.

1. In apes there is a large degree of variation in the inferior projection of the mastoid tips (Kimbel *et al.* 1984). Since inferiorly projecting mastoid tips is not a constant feature in apes it is not diagnostic. Furthermore, although well developed, in A.L. 333-45 the mastoid process does not project below the level of the occipital condyles as in *Australopithecus* (Kimbel *et al.*, 1985). In hominids large mastoids are an advanced, rather than a primitive feature and hence the "extremely well developed" (Kimbel *et al.* 1982: p.470) mastoids in A.L. 333-45 at such an early date of 3.5 m.y. would be the reverse of the anticipated human evolutionary trend from small mastoids to large (non-projecting mastoid tips notwithstanding).
2. In hominids the tip of the mastoid process is in the same parasagittal plane as the lateral margin of the external auditory meatus. In pongids the tip is medial to the opening of the external auditory meatus (Olson 1981). The mastoid process tip of A.L. 333-84 is about 5.0 mm medial to the lateral tympanic margin, but in A.L. 333-45 the mastoid process tips occupy the same sagittal plane as the auditory apertures (Kimbel et al. 1982). In A.L. 333-45 "most of the anterior lateral portion of the right tympanic (and part of the left) is missing and the entire lateral edge is abraded" (Kimbel *et al.*, 1982 p.470). If the lateral margin of the tympanic plate were intact, the mastoid process would lie medial to it as it does in A.L. 333-48.

Kimbel *et al.* (1985) demonstrated that the mastoid and supramastoid morphology of *A. robustus* and *A. boisei* diverge sharply from A.L. 333-45 and extant African apes.

Postglenoid Process

Postglenoid process in hominids is small or moderate and recessed medially on the same sagittal plane as the tip of the mastoid process. In pongids it is large and inflated (Tobias 1967), and extends laterally, which is the primitive condition. The postglenoid process of A.L. 333-45 is large, extends laterally, and is the most external part of the cranium (Kimbel *et al.* 1982). It is lateral to the sagittal plane of the tip of the mastoid process.

In pongids, the outer part of the tympanic is situated mainly behind the postglenoid process, whereas in hominids it is situated mainly below the postglenoid process, (Broom 1938). The tip of the postglenoid process in the hominid KNM WT 17000 is " completely anterior to the anterior [sic] edge of the external acoustic meatus" (Leakey and Walker 1989 p.9). "In the apes and *A. afarensis* [A.L.333-45] the postglenoid process lies anterior [to] the tympanic plate . . ." (Kimbel *et al.* 1984 p.376) (Figure 8).

Tympanic plates

When viewed basally, the tympanic plate in hominids is squeezed into more of a ridge than a tube, while in apes it resembles a tube (Johanson and Edey 1981). In A.L. 333-45 there is no marked tendency for the auditory meatus to constrict medially and the tympanic plates are tubular (Johanson and Edey 1981), "strongly resembling the pongid condition" (Johanson and White 1979 p.323).

The conformation of the tympanic plate is nearly horizontal in many pongid crania (Tobias 1967). In A.L. 333-45 the tympanic plate tends to be horizontally oriented (Johanson *et al.* 1982).

Styloid process

The styloid process of modern *Homo* does not occur in *H. erectus pekinesis*, australopithecines or pongids

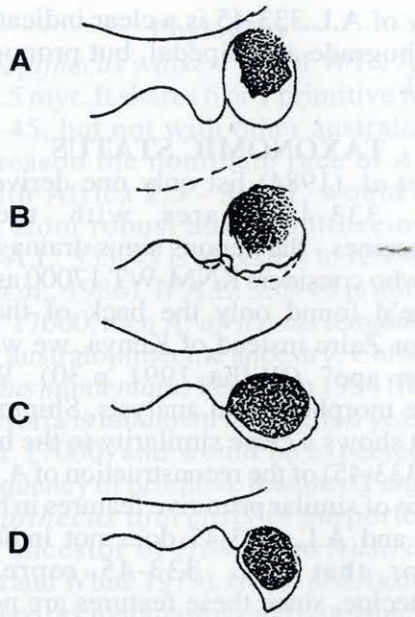


Figure 8 Postglenoid process in relation to the external acoustic meatus in A) *Gorilla*, B) A.L.333-45, C) *A. robustus*, D) *H. sapiens* (after Broom, except A.L. 333-45). In A.L.333-45 the outer part of the tympanic is situated mainly behind the postglenoid process, as in *Gorilla*.

(Tobias 1967). Clarke (1990) records the presence of styloid process in *H. erectus leakeyi* Heberer, 1963 SK 847, which he raises to specific rank, *Homo leakeyi*. Kimbel *et al.* (1982) describe the broken stub of an ossified styloid process in A.L. 333-45, but no styloid process is present in A.L. 166-9 (Taieb *et al.* 1974). The presence or absence of the styloid process is indeterminate as it may not always fossilize.

Pneumatization of the temporal squama

The mean thickness of the temporal squama measured just above the supraglenoid gutter in the robust australopithecines is 5.5, range 4.5 - 6.0 (n=6), in *Pan troglodytes* it is 11.3, range 10.5 - 12.5 (n=3) and in "*A. afaren*sis" it is 9.8, range 9.1 - 10.5 (n=4) (Kimbel *et al.* 1984). The pattern of pneumatization in "*A. afarensis*" was thought to occur only in the extant apes among hominoids (Kimbel *et al.* 1984), but was found in KNM-WT 17000 to be 11.5, (Walker *et al.* 1986) twice as thick as in *A. boisei*, and within the range of apes.

Petro-median angle

Appreciable flexion and anteroposterior reduction of the cranial base is reflected in the high angle between the petrous angle and the median plane (Tobias 1967). The angle in hominids is 32-47.4°, while in modern pongids it is 10 -30° . In A.L. 333-45° the "right petrous angles forward about 30° to the midsagittal line" (Kimbel *et al.* 1982) below the minimum for hominids.

Mandibular (glenoid) fossa

The mandibular fossa approaches nearer the midline in the gorilla than in *A. boisei* (Tobias 1967), or in *Homo*. In A.L. 333-45 the mandibular fossa also approaches nearer the midline than in *A. boisei* or *Homo*.

Articular eminence of the glenoid fossa

In the mandibular fossa of *Homo* there is a distinct articular eminence, whereas in pongids it is shallow (Tobias 1967) or flat (Johanson and Edey 1981). Although the mandibular fossa of *A. boisei* is relatively shallow, the articular eminence is rendered salient, and thus different from pongids (Tobias 1967). The articular eminence in A.L. 333-45 is very low and smoothly convex anteroposteriorly (Kimbel *et al.* 1982). It is described as very weak and not found in other hominids (Kimbel *et al.* 1984). In KNM WT 17000 it is described as weak (Walker *et al.* 1986).

POSTURE AND LOCOMOTION

A lineage is characterized by the main trends of its evolutionary development (Le Gros Clark 1959). The Pongidae are adapted to pronograde posture and quadrupedal locomotion. The Hominidae are adapted to orthograde posture and bipedal locomotion. The skull in apes is supported by a cantilever-like neck, whereas in hominids it is well balanced from below.

Schultz (1968 p.154) wrote that "the dorsal spines of the cervical vertebrae of all great apes have acquired an exceptional length to support their powerful nuchal musculature, needed in carrying the heavy and very poorly balanced head. Since recent and fossil man have as short dorsal spines on the vertebrae of their necks as have gibbons and all monkeys, it can be concluded that "only the pongids have become highly specialized in this respect." Jay Matternes notes in his restoration of "*A. afarensis*", that "because of the badly balanced head, additional long buttressing would have been necessary. . . . . with neural spines extended far beyond their normal length in modern man". (Johanson and Edey, 1981 p.378). They added that the forward jutting face requires elongated spinal vertebrae and a thickly muscled neck to support it (Johanson and Edey 1981).

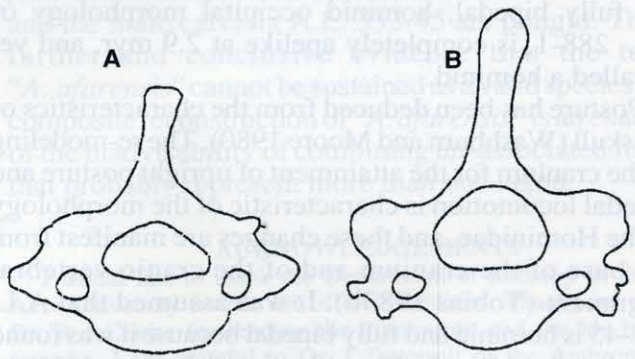


Figure 9 Cervical vertebrae of hominoids (superior view).
A) *Homo sapiens*, 7th cervical vertebra.
B) A.L. 333-106, 6th or 7th cervical vertebra (after Lovejoy *et al.*, 1982). Drawn to the same breadth. Note the very long spinous process of A.L. 333-106.

Although the long cervical spines have been called an adaptation to balancing the head, the major muscles which arise from these spines are for the arms and not to balance the head (Washburn and Moore 1980). Regardless of their function, the long cervical spines are diagnostic of the great apes. It may be significant, therefore that a 6th or 7th cervical vertebra A.L. 333-106 was found at the same site as A.L. 333-45 with a very "long spinous process that is quite distinct" (Johanson and White 1979 p.324) (Figure 9).

According to Bierget (1963) "the kind of locomotion of fossil primates can be determined only from the condition of the post-cranial skeleton". He thus claims that the alterations in the topography of the skull of a hominid in contrast with that of a pongid are not criteria for upright locomotion. The features he refers to are increased kyphosis, which causes increasingly horizontal orientation of the nuchal plane, anterior shifting of the foramen magnum and the more oral position of the occipital condyles. These acknowledged alterations in the topography of the hominid skull, plus the low nuchal height, reduced occipital torus and nuchal area, and weak nuchal masculature are indeed characters correlated with upright locomotion.

The differences in the nuchal and suboccipital regions that distinguish the great apes and hominids are correlated with adaptation to posture (Robinson 1958; Le Gros Clark 1964; Poirier 1973; Tobias 1983). Lovejoy said that animals have to give up one form of adaptation for another (Johanson and Shreeve 1989). Hominids would have lost an apelike occipitomastoid morphology when they adapted to bipedal locomotion. Tobias (1983a p.172) wrote that "all the fossil evidence goes to indicate that elements of this bipedalism complex [including the cranium] were developed early in the history of hominization". This is thought to have occurred between 5 - 7 myr. "The evolution of upright posture was the single most important factor in shaping the derived morphology of the hominid occipitomastoid region" (Olson 1985 p.106). It is inconsistent, therefore, that the occipitomastoid morphology of A.L. 162-28, which is synchronic with the fully bipedal, hominid occipital morphology of A.L. 288-1, is completely apelike at 2.9 myr, and yet is called a hominid.

Posture has been deduced from the characteristics of the skull (Washburn and Moore 1980). The re-modeling of the cranium for the attainment of upright posture and bipedal locomotion is characteristic of the morphology of the Hominidae, and these changes are manifest from the base of the cranium and of the cranio vertebral alignment (Tobias 1983b). It was assumed that A.L. 333-45 is hominid and fully bipedal because it was found near hominid fossils. Classification, however, is based on morphology and not proximity. By including A.L. 333-45 together with undisputed hominid fossils, the significance of its adaptive affinities had been obscured and ignored. The unequivocal apelike occipitomastoid morphology of A.L.333-45 is a clear indication that it was not orthograde and bipedal, but pronograde and quadrupedal.

TAXONOMIC STATUS

Kimbel *et al.* (1984) list only one derived feature that A.L. 333-45 shares with the robust australopithecines - the venous sinus drainage pattern.

Walker, who considers KNM-WT 17000 as *A. boisei*, said, "if we'd found only the back of the skull in Cameroon or Zaire instead of Kenya, we would have called it an ape" (Willis 1991 p.30). Without a comparative morphological analysis, Shipman (1986) states that it shows a close similarity to the back of the skull (A.L. 333-45) of the reconstruction of *A. afarensis*. The presence of similar primitive features in both KNM WT 17000 and A.L. 333-45 does not indicate close affinity, or that A.L. 333-45 represents an australopithecine, since these features are not derived characters of the Australopithecinae, but are either homonoid features shared by pongids and early *Australopithecus*, or due to parallel evolution.

Le Gros Clark (1958 p.66) wrote that "in its general proportion, indeed, the australopithecine skull has a superficial appearance not unlike that of a large ape, but in details of its construction it presents many differences". The calvaria KNM WT 17000 shows the following hominid characters not seen in A.L. 333-45:

1. greater posterior extension of the occipital in relation to brain size
2. greatest breadth bimastoid
3. occipital torus slight or moderate
4. inclination of nuchal plane less steep and restricted
5. mastoid crest lateral to supramastoid crest
6. supramastoid sulcus probably present (damaged)
7. mastoid posterior surface almost, but not flat
8. medial inflection of the mastoids reduced
9. relatively small postglenoid process, not opposite outer tympanic plate
10. coronally placed petrous temporalis

Olson (1985) regards the basicranial morphology of A.L. 333-45 as advanced and highly specialized, while Kimbel *et al.* (1985) say that the occipitomastoid region of A.L. 333-45 is strikingly primitive and resembles that of an ape.

Slowly changing characters are used to characterize the higher categories (Mayr, 1953). The basicranial morphology of hominoids has changed slowly and is thus useful for classification. Olson's (1985) analysis of the cranial morphology of A.L.333-45, in which he claims 3 apomorphic features identify it as a "*Paranthropus*", was shown by Kimbel *et al.*, (1985) to be instead extremely primitive and apelike. The most reasonable classification of A.L.333-45 would be as a member of the Pongidae.

Phylogeny

Australopithecus walkeri KNM WT 17000 is dated at about 2.5 myr. It shares 6 or 7 primitive features with A.L. 333-45, but not with other australopithecines. For this reason the nominate race of *A. africanus* from South Africa 2.5 - 3 myr, would seem to be excluded from robust australopithecine ancestry, assuming A.L. 333-45 is ancestral to KNM WT 17000 (Walker *et al.*, 1986). If A.L. 333-45 is not ancestral to KNM WT 17000, then *A. africanus* remains a candidate for robust australopithecine ancestry. Chronologically, *A. africanus miodentatus* Ferguson 1984 from Ethiopia, whose calvaria is unknown is a million years older than KNM WT 17000, and would be expected to retain a higher frequency of primitive features (Ferguson 1987). *Australopithecus afarensis* is purported to be the common ancestor of *Homo* and *Australopithecus* (Johanson and White 1979). *Homo* and *Australopithecus* share derived occipitomastoid and tympanic morphology not found in A.L. 333-45. The calvaria A.L. 333-45 cannot, therefore, belong to a taxon that was the common ancestor of *Homo* and *Australopithecus*.

SUMMARY AND CONCLUSION

In 1985, Pilbeam wrote that "*Australopithecus afarensis*" resembles *Pan* and *Gorilla* in a few cranial characters. Reassessment of the morphology of the calvaria A.L. 333-45 reveals that it conforms with the Pongidae in its total morphological pattern and differs from the Hominidae in the following characters (even without those related to a steep, nuchal plane).

1. maximum breadth across supramastoid crests greater than maximum bimastoid breadth
2. lambda-inion chord short in relation to cranial capacity
3. strong muscular ridges, particularly in occipital region
4. nuchal crest high in relation to occipital height
5. compound T/N crest shelf-like and extends onto pars mastoidea
6. occipital torus pronounced
7. nuchal area extensive
8. nuchal plane steep relative to FHP
9. foramen magnum (ectobasion) posteriorly located
10. incisura mstoidea long
11. asterionic notch present
12. inferior temporal and superior nuchal lines form compound supramastoid crest
13. supramastoid crest and mastoid crest merge
14. supramastoid crest lateral to pars mastoidea
15. supramastoid sulcus absent
16. mastoid process triangular, posterolateral face flat mediolaterally, slightly concave inferosuperiorly
17. mastoid process inferomedial inflection strong
18. tip of mastoid process medial to opening of external auditory process
19. tympanics tubular in basal view
20. tympanic plate horizontally oriented
21. postglenoid process large, projects laterally
22. postglenoid process anterior to the outer part of tympanic
23. mandibular (glenoid) fossa closely approaches midline
24. petro-median angle low

The calvaria A.L. 333-45 was assumed to belong to a hominid because it came from the same site as hominid fossils. It is sympatric and synchronic with A.L. 333-1, an unmistakable specialized gracile *Australopithecus*. However, A.L. 333-45 is unassociated anatomically with any hominid fossils and I found not a single unequivocal hominid character. Its extremely well developed mastoids are inconsistent with the hominid evolutionary trend from small to large mastoids. Although some of the features are less specialized than in a modern ape, it would be incredibly primitive for a hominid - but not for a pongid.

The hominoid A.L. 333-45 was assumed to be upright and fully bipedal on the basis of its proximity to unassociated hominid specimens. No morphological evidence has been given to support A.L. 333-45 as a hominid. The adaptive affinities of the occipitomastoid morphology of the Pongidae are related to pronograde posture and quadrupedal locomotion. Since the apelike occipitomastoid morphology of A.L. 333-45 is undisputed, its adaptive affinities are related to pronograde posture and quadrupedal locomotion. To conclude that it is a hominid is a *non sequitur*. The calvaria A.L. 333-45 cannot, therefore, belong to a hominid - but belongs to an ape.

I believe A.L. 333-45 is the only known pongid calvaria from the late Pliocene of Africa, and may represent the first known skull of *Praeanthropus africanus*.

The reconstruction of a male "*A. afarensis*" skull is a chimera, a composite of hominid and pongid fossils. The facial fragment A.L. 333-1 is that of a gracile *Australopithecus*, while the female maxillae A.L.200-la and the male calvaria A.L. 333-45 are pongid. This is further and conclusive evidence that the taxon "*A. afarensis*" cannot be sustained as a valid species. The composite reconstruction of "*A. afarensis*" is an example of the inadvisability of combining un-associated fossils that probably represent more than one taxon.

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PREPARATION OF FOSSIL BONE FOR HISTOLOGICAL EXAMINATION

by

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ABSTRACT

A technique for preparing thin sections of fossil bone suitable for histological examination by light microscopy is described.

INTRODUCTION

Palaeo-histology is the branch of palaeontology concerned with the microscopic structure of fossil bone. Researchers entering the field for the first time become aware of a need for a concise description of a technique to prepare thin sections from fossil bone. This note aims to fill that need by describing the procedure used in a recent palaeohistological study (Chinsamy 1988, 1990, 1991, 1992).

The technique described has been successfully applied to the bones of dinosaurs and mammal-like reptiles, as well as to archaeological samples of human bone and also to defatted bone of recent taxa. There is no one 'correct' method of making sections of hard tissues like bones, but all existing techniques share a number of core processes in common (Enlow 1954; Enlow and Brown 1956; Honjo and Fischer 1965; Peabody 1961; Macfall and Wollin 1972; Buffrènil, Ricqlès, Ray and Domning 1990). Although the method described here is specifically intended for use on bone, thin sections of fossilised wood have also been obtained using the same method.

MATERIALS

Many different materials and items of equipment can be used to produce perfectly acceptable results in the sectioning of bones. We list here only those materials used in the processes employed in our laboratory, as a starting point for those who might be entering the field for the first time:

Epofix cold mounting medium; Epotek; Buehler Petrographic slides (27 X 46 mm); for manual grinding, a glass plate (25 X 30 mm) and carbide powder of varying grit size (220, 400, 600, 800, 1000) are needed; for mechanical grinding, a lap wheel grinder and polisher (such as the Buehler Ecomet lll) and waterproof adhesive grinding papers (180, 220, 400, 600, 800, 1000 grit) are required; a section cutting machine such as the "Micro-trim" or any other cutting device with a diamond cut-off wheel and a resectioning vise is suitable.

METHODS EMPLOYED

The procedures we use for preparing sections of fossil bone can be conveniently divided into seven main phases:

1. Measurement and recording of data.
2. Photography.
3. Embedding of specimens for sectioning.
4. Sectioning embedded bone.
5. Grinding one surface to affix to slide.
6. Mounting and labeling the stub.
7. Finishing.

Measurement and recording of data

Because section making is a destructive process, some aspects of the gross morphology and anatomy of the bones will inevitably be lost during the process. It is therefore highly advisable, indeed essential, to record relevant data before the process begins - for example, bone size and shape are often important indicators of age, stature, sex, etc., so data relevant to these factors should be recorded before they are lost irrecoverably once sections have been cut. Making a cast of the original specimen can also provide a valuable store of information.

In order to record precisely where on the bone the section was cut, and in what orientation, and to ensure repeatability and comparability later, it is advisable to standardise any measurements taken (Figure 1). The standards should be set with reference to easily identifiable homologous points on the bone (e.g. trochanters, nutritive foramina, condyles, etc.).

Photography

There are two aspects to photography in our kind of study: first, the need to preserve an unambiguous record of the morphology of the bone before it is sectioned (in combination with the formal documentation mentioned in the preceding paragraph); and second, to compile a photographic record of the end result of the sectioning.

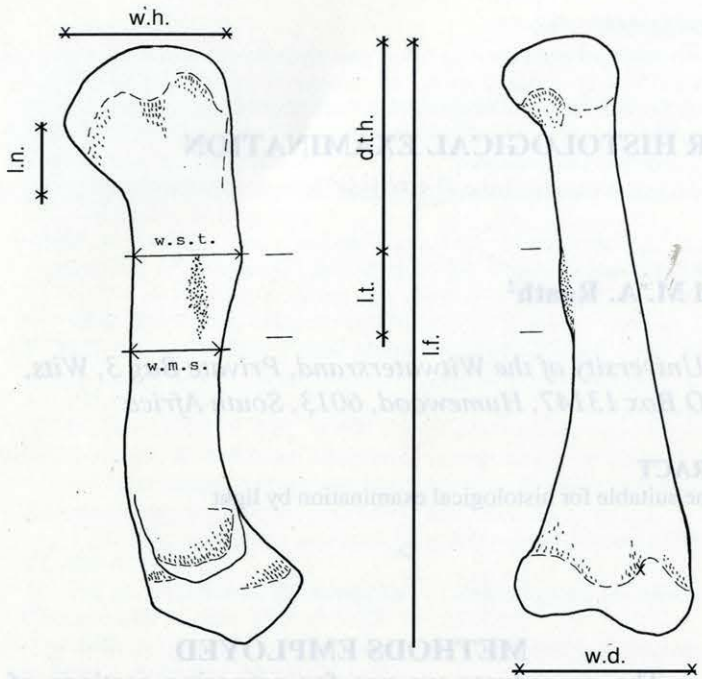


Figure 1: Suggested measurements which should be recorded prior to sectioning.

For the sake of repeatability in both instances, a detailed record of the photography should be kept and should preferably include all relevant technical details such as; film type and speed, camera settings (shutter speed, aperture, lens type, etc.), an indication of the section or slide number, the magnification used, whether or not crossed-nicols or other light-modifying accessories were used, and the light intensity.

Stored with all other relevant notes on the material used, these records become potentially useful archival resources for later reference.

Embedding of specimens for sectioning

Since fossil bones are, in many cases, relatively brittle, they often need to be embedded in resin or some other suitable mounting medium to reinforce the structure of the tissue and prevent them from shattering or disintegrating during the processes of sectioning and grinding.

We use a cold-curing epoxy resin, Epofix, but any resin or other rigid, clear mounting medium which does not interfere with the structure or optical properties of the tissue could be used.

The manufacturer's specifications should be followed meticulously when preparing the resin for use, especially with regard to the mixing proportions for the resin and its hardener; incorrect proportions can lead to disastrous results, including the generation of large amounts of heat during the polymerisation phase which can result in catastrophic damage to the specimen.

Any suitable disposable containers can be used in which to embed the bones in resin; in our laboratory we often use cheap plastic containers of various shapes and sizes. Care should be taken as many plastics are melted by the resins used in the embedding process, but polymerisation of the resin is generally rapid enough for this not to pose a major problem. Experience will soon indicate what kinds of plastic or other containers are unsuitable.

Where bones of a particular size range are often dealt with, it might be advisable to use custom-designed moulds in which to embed the bones. Moulds made of latex or silicone rubber have been found to work well.

To avoid wastage of resin, and also to facilitate easier handling of the specimen, the container chosen should have just sufficient room for the specimen, with not much to spare - about 0.5 - 1cm all around is enough. Prior to embedding the specimen itself, we advise that a layer of resin about 0.5 - 1cm thick be poured into the base of the container and allowed to harden in order to ensure that the bottom of the specimen is well embedded.

Since irritant fumes are generally given off by the resins used, the embedding process should take place in a chemical fume cupboard with the exhaust fan running.

Once the bone is embedded it should be left for the resin to cure until it is hard enough to be removed from the mould (up to about 24 hours, depending on the resin used). Best results are obtained if the embedding takes place under vacuum, as this helps to liberate trapped air bubbles and aids penetration by the resin.

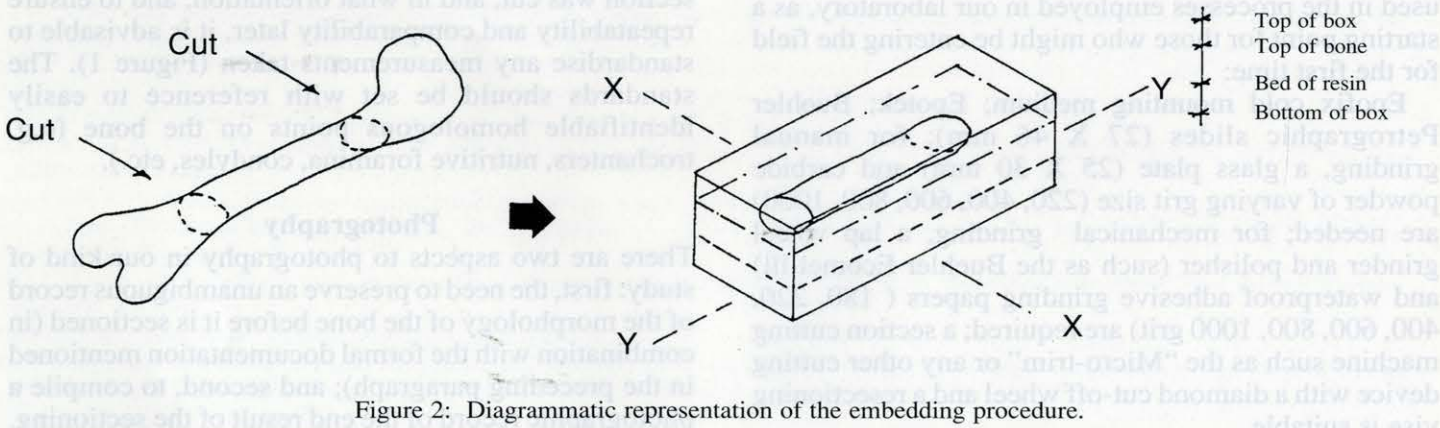


Figure 2: Diagrammatic representation of the embedding procedure.

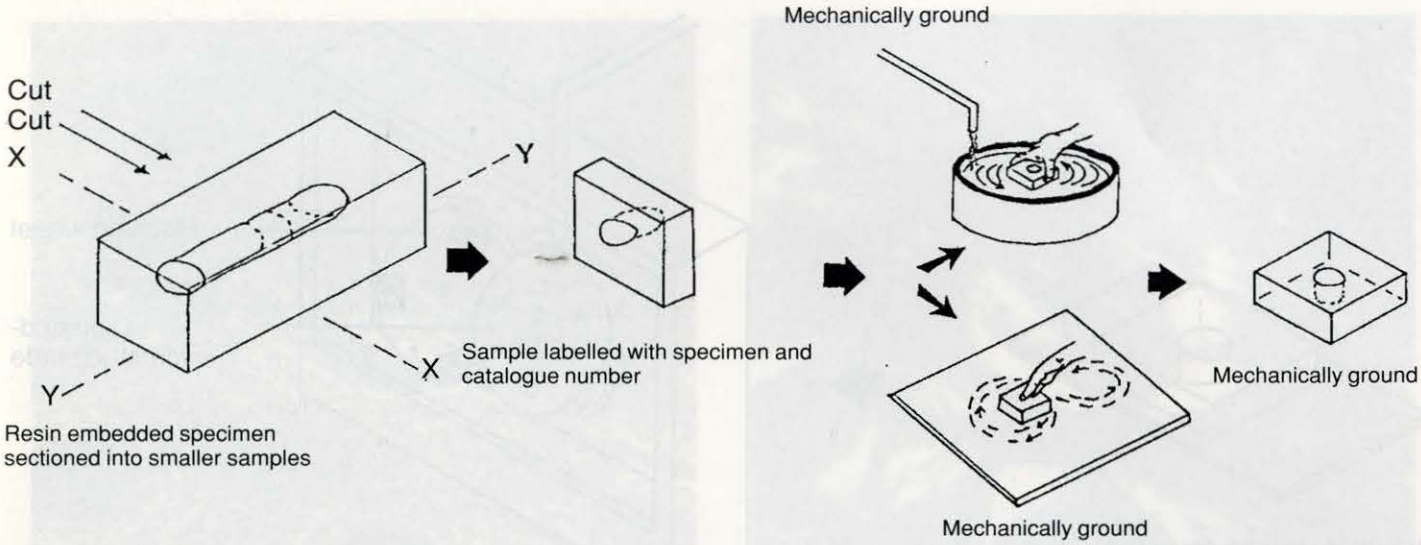


Figure 3: Sectioning of embedded bone and subsequent grinding of specimen.

Sectioning embedded bone

A surprising variation in bone tissue structure occurs in different bones of the same species, and even in different regions of the same bone. It is therefore important to know precisely where along the length of a bone a section has been cut and in what orientation (whether transverse, longitudinal, tangential etc). For this reason, in documenting the sections taken, it is helpful to relate the site of the cut to the standardised measurements of the bone advocated earlier. This facilitates repeatability of observations.

A short stub of bone is cut from the parent specimen using a suitable rock-cutting saw. In our experience a rock-cutter with a water-cooled diamond-studded blade works well. The dimensions (thickness and diameter) of the stub are not critical, but are essentially dictated by what the section cutting machine can accommodate and the size of the glass slides available on which the section is to be mounted; the section should not protrude beyond the edges of the slide.

Each resulting segment of the parent specimen is carefully labelled with its unique specimen number and basic catalogue reference, so that there can be no mistake about its identity and so that it can be easily reunited with its registration details. The way in which the segments are labelled will depend on a variety of factors, not least of which will be the size of individual segments. If the segment is large enough, the catalogue number can be written directly onto it using indelible ink (indian ink) on a small patch of white or other pale paint.

We have found exterior grade PVA paint (e.g. Plascon "Wall-'n-All") an acceptable and durable base on which to write the catalogue number. A satisfactory and relatively permanent label can be produced by writing on good quality paper or opaque polyester foil in waterproof black ink (indian ink), and using Glyptal G1276 cement thinned in lacquer thinners both as an adhesive to stick the label to the specimen and as a protective coating and sealant. If "clear" epoxy resin is used, the specimen and catalogue numbers can be written in pencil on white paper and set in the resin during the embedding.

Grinding one surface to affix to slide

The cut surface is ground down on successively finer abrasive grinding discs, until the surface is completely flat, smooth and free of scratch marks. Grinding can be carried out either manually or mechanically.

The procedure for grinding by hand is both time-consuming and laborious. It involves smoothing the rough cut surface by rubbing it on a glass sheet coated with an abrasive paste. Carborundum powder, in decreasing particle size - e.g. 220, 400, 800, and 1000 grit) - has produced acceptable results in our work. The grinding is carried out by small circular motions, and hand-pressure must be applied to the specimen evenly or wedging can result.

The mechanical procedure is much quicker and more efficient, since it reduces the amount of wedging that may occur, and fairly even surfaces are obtained. The apparatus consists of a rotating lap-wheel onto which waterproof abrasive grinding discs are fixed. Many different models of grinders are available. The grinding discs must be used in a sequence of decreasing coarseness (i.e. increasing grit figures); the sequence of discs we use is 180 grit, 220, 400, 600, 800 and finally 1000 grit. Aluminium oxide powder (0.3 - 0.05 μm) mixed with water is sprinkled onto a cloth-covered lap-wheel for final polishing. Aluminium oxide is also available in paste form, and we have used it sucessfully to obtain a high polish.

After the final polishing, the specimen is washed with water and dried. Excess moisture is removed by placing the specimen onto filter paper or paper towels, thus hastening the drying process.

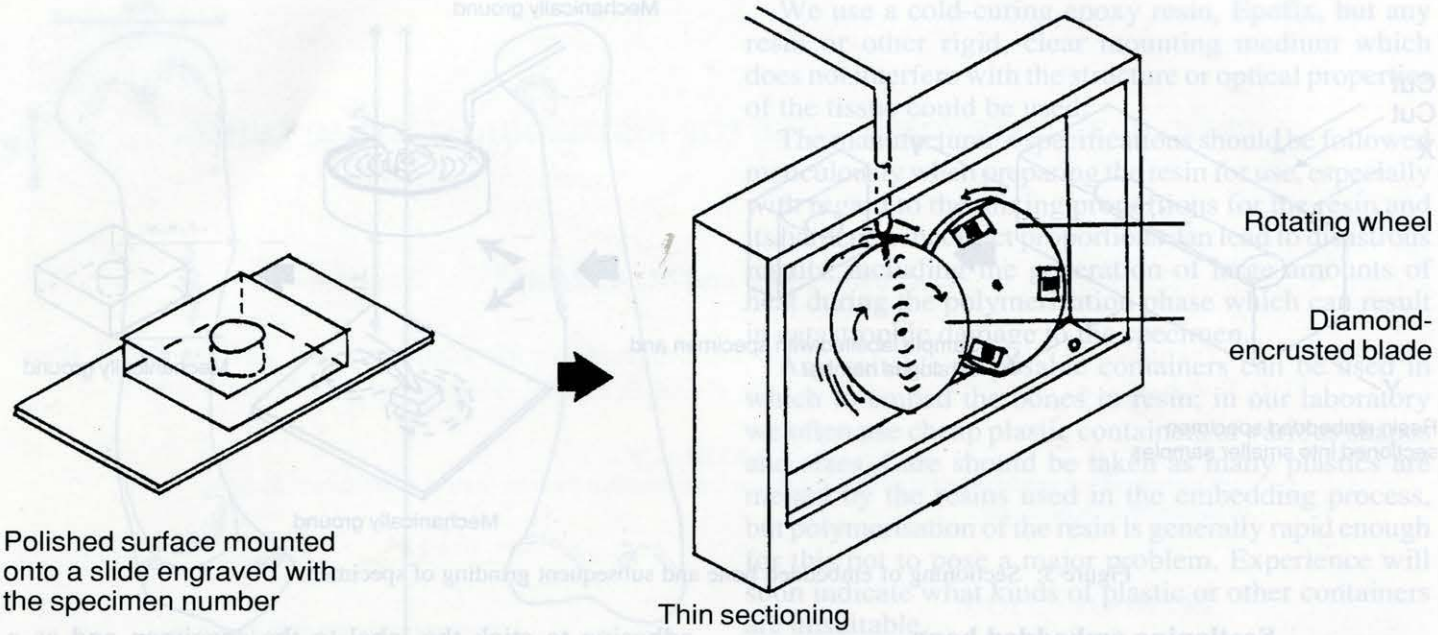


Figure 4: Diagrammatic illustration of the thin sectioning procedure.

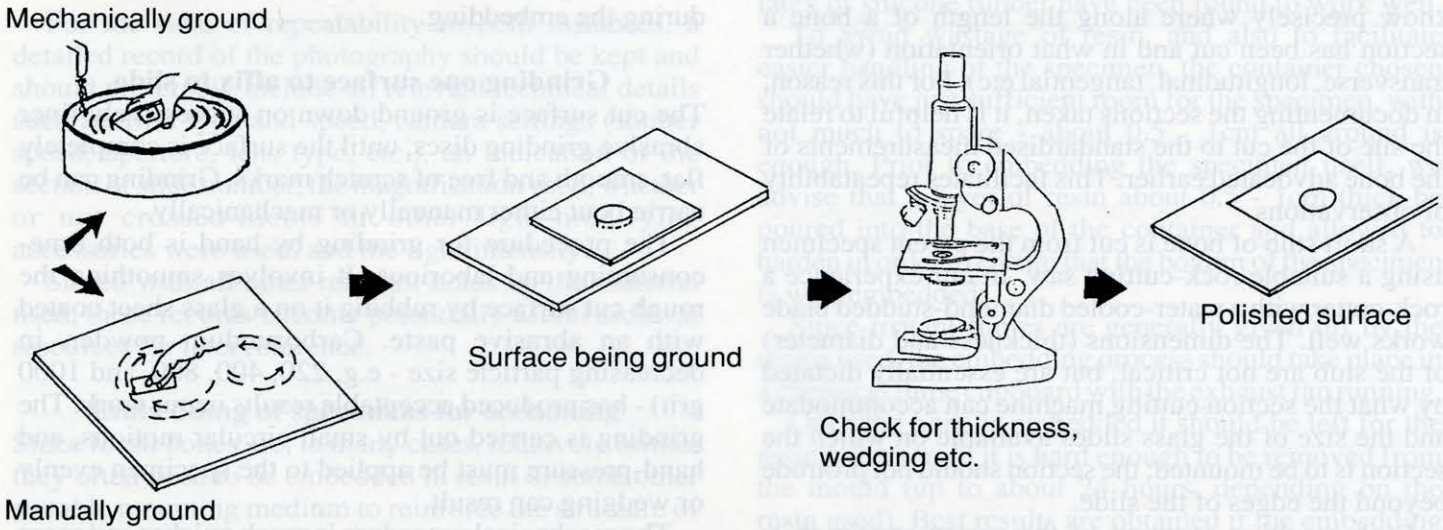


Figure 5: Grinding and polishing of specimen.

Mounting and labelling the stub

The polished surface of the stub of bone is then mounted onto a petrographic glass slide. In our experience frosted slides provide better optical resolution, as well as a better adhesive surface for the mounting medium; clear petrographic slides can be frosted by rubbing them gently on a glass plate with an abrasive paste of 400 grit carborundum powder.

In order to ensure that the slide to which the specimen is affixed remains identifiable during the process of section cutting and in storage afterwards, it must be labelled in some durable way. Indian ink and adhesive labels can be used, but we recommend that the specimen numbers be permanently engraved onto the glass slides using a diamond tipped stylus. We suggest that this be done before the polished specimen is mounted onto the slide since the slides might occasionally break or crack whilst being engraved, which renders them effectively useless. Clearly, if a slide is labelled before a specimen is stuck to it, care must be taken to ensure that the correct stub is stuck to the correct slide. A resin adhesive such as Epotek is used to fix the ground and polished end of the stub to the frosted slide.

The next step is to trim away excess material from the free end of the stub by cutting off slices approximately 1mm thick. This reduces the amount of coarse grinding that will be required. For our section cutting we use a "Micro-Trim" section-cutting machine, which automatically feeds the slides (held by vacuum on a rotating chuck) onto a water-cooled, rotating, diamond-encrusted blade.

Thin sections can also be made satisfactorily using a

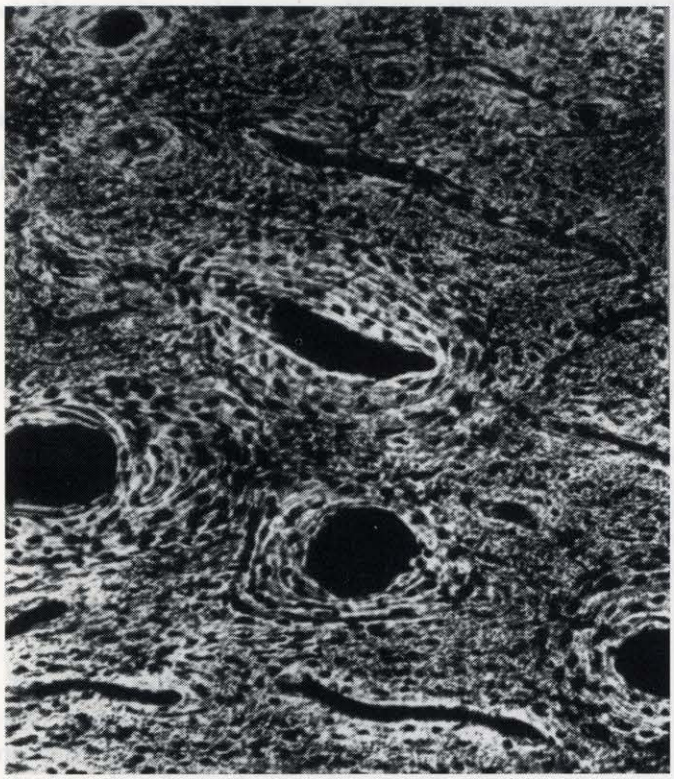


Figure 6: Transverse section of a humerus of the dicynodont *Kannemeyeria* showing primary and secondary osteons in a woven bone matrix. x490. BPI Palaeontlogy, specimen number H2.



Figure 7 Tissue shown in Figure 6, as seen with cross polarisers. X410 BPI Palaeontology, specimen number H2.

variety of other machines and devices, one of the simplest being a diamond cut-off wheel and a resectioning vise.

Finishing

The resulting thin sections will bear distinct cut marks across the free surface, which must be removed by carefully grinding as outlined above. Grinding continues until the cut marks have been removed, the surface is smooth, and the section is of acceptable thinness ready for final polishing. At intervals during grinding the slides should be examined under a low-power microscope to check thickness, amount of wedging or other distortion, and the amount of tissue detail visible (Figure 5). Depending on what is being studied the final thickness of the specimen can vary from about 120 µm to 20 µm (the latter thickness is adequate for histological purposes).

The finished slide is checked to ensure that it is correctly and adequately labelled. We recommend that it be stored together with any left-over fragments or portions of the parent specimen.

Gross microscopic examination of the prepared slide can initially be carried out under low power, e.g. through a dissecting stereomicroscope, to obtain overall information about gross structural features of the tissue More detailed examination is carried out under higher magnification (Figures 6 and 7).

ACKNOWLEDGEMENTS

We thank Armand de Ricqles for his advice and suggestions, particularly in the design and set-up of our laboratory at the Bernard Price Institute, and James Kitching and Matthew Kitching for their technical assistance both in the initial set-up of the laboratory and thereafter. Likewise, we acknowledge Richard Lewis and the late John Molotsi's assistance in preparing many specimens for thin sectioning. We are also grateful to Brigid Ward for her assistance with the illustrations. Robin Reid and Francis Thackery are acknowledged for reviewing this paper.

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A METHOD OF IMPROVING CONTRAST IN ILLUSTRATIONS OF COALIFIED FOSSILS

by

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ABSTRACT

A simple, economic method of enhancing the contrast and, therefore, improving the quality of certain palaeontological photographic illustrations is outlined. The technique, which involves the use of polarising filters, in no way alters the negatives or prints. In recommending this technique, it is hoped some of the confusion arising from inadequate illustrations will be removed.

INTRODUCTION

Real progress in palaeontology can only be made when it is clearly indicated what is both known and knowable about fossil specimens. This is made difficult by the fact that palaeontologists and their collections are spread rather thinly around the world, and the opportunity to become intimately acquainted with type specimens and collections is denied to many. This problem is exacerbated in the southern hemisphere, where the once united Gondwana is now distributed around the globe. Funding is often a problem, and intercontinental stratigraphic correlation is correspondingly hampered. Unambiguous descriptions allied with illustrations of the highest quality are not only desirable, but essential.

It is both a strength and a weakness of palaeontology that, in most cases, the only way we can present data adequately is in the form of a photographic print. This is a strength because a well-taken photograph records faithfully what is preserved on the rock surface, and any unconscious bias is eliminated at source - the fossil becomes the data. The weakness lies in the fact that, although the camera cannot lie, it may be reluctant to reveal the whole truth. Therefore many features can remain hidden or obscured either by a lack of contrast or by persistent glare from a shiny surface.

These photographic difficulties are commonly a problem in palaeobotanical and allied studies, where organic matter may be completely flattened by compression and then coalified (*sensu* Schopf 1976). Frequently, Gondwanan fossil plants are preserved in fine-grained, black carbonaceous shales, the colouring being caused by disseminated plant matter. A black fossil on the surface of a black sediment can be almost impossible to photograph. In other cases, the fossil may be partially or totally transparent. This is particularly true with insect wings which frequently occur in plant collections (Rayner and Waters 1989).

Yet another problem comes with the use of polyvinyl acetate cements which are sometimes used to reinforce delicate specimens. I have encountered this problem in fossils from a particularly significant locality, Orapa. The temperatures at the locality, which is a mine in Botswana, frequently reach into the upper thirties, and to protect the specimens from rapid desiccation, which would destroy them, they are impregnated with cement. However, this acts like a varnish and produces much unwanted reflection from the specimen's surface during photography (Rayner 1987).

In the case of the *Glossopteris* flora, studies have been unnecessarily plagued not only by problems of inadequate, loose descriptions, but also of wholly unacceptable illustrations. In a volume revising the Indian species of *Glossopteris* (Chandra and Surange 1979), the authors stressed that, in the past, "indifferent" illustrations of *Glossopteris* leaves have made the task of diagnosis and identification difficult and confusing. However, in their own revision, many of the photographic illustrations are less than helpful. To overcome the problem, Dr Shaila Chandra has produced some beautiful line drawings. However, drawings are necessarily interpretations and they may be subjective to varying degrees. They can only be considered adequate when a *camera lucida* is used.

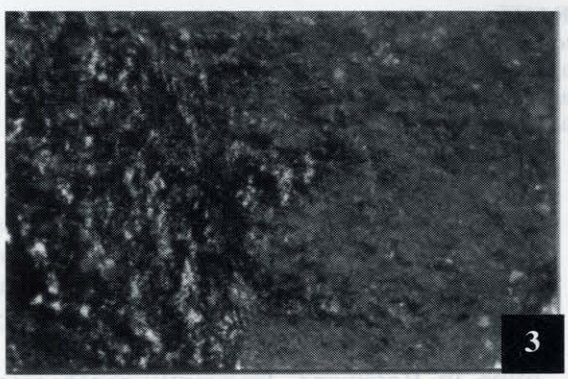
I sympathise with workers faced with the problems of faithfully recording these data, but have been quite astounded at some of the attempts to illustrate indistinct structures. Some examples involve actually drawing lines on photographic prints around certain structures which are otherwise obscure. Clearly, if the organ is that indistinct, then a disbeliever may be justified in suggesting that it is not there at all.

Low-angled, unidirectional lighting is the usual solution to these photographic problems, where surface relief can be easily enhanced. However, with



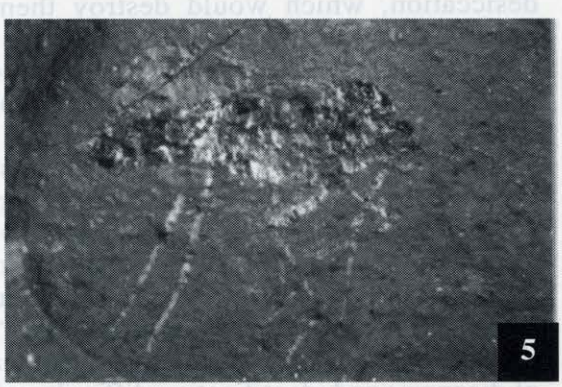


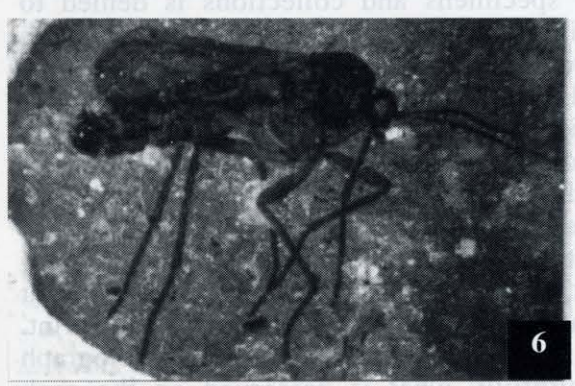
Figs 1 & 2. A middle Cretaceous insect with certain coleopteran affinities; Orapa. x2.5.



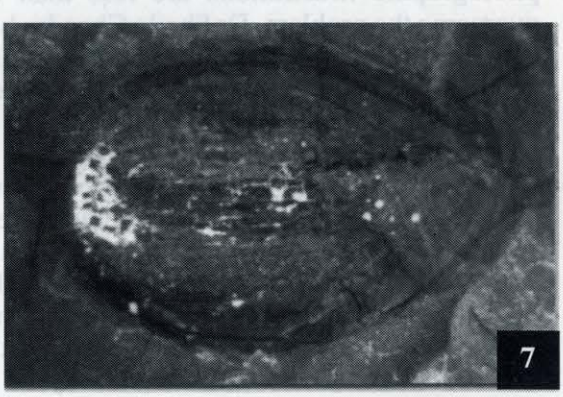


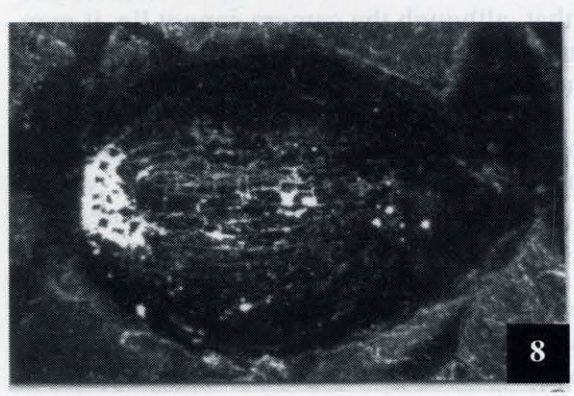
Figs 3 & 4. Enlarged posterior of the same specimen. x10





Figs 5 & 6. Cretaceous dipteran; Orapa. x10.





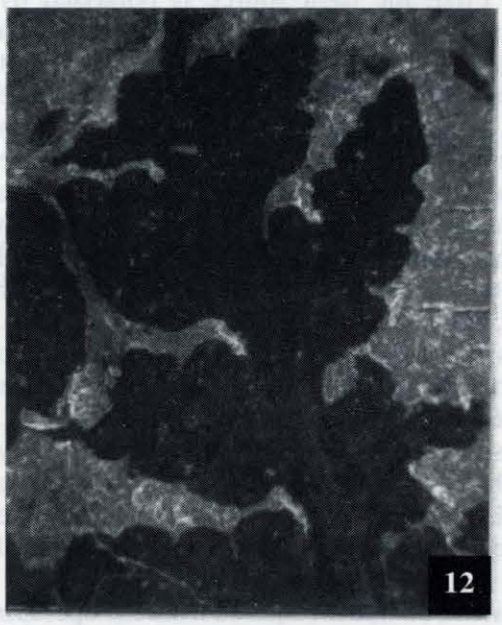
Figs 7 & 8. A dispersed Triassic seed; Little Switzerland. x3.



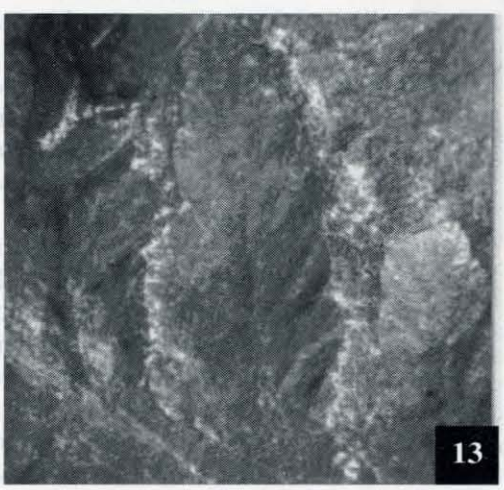


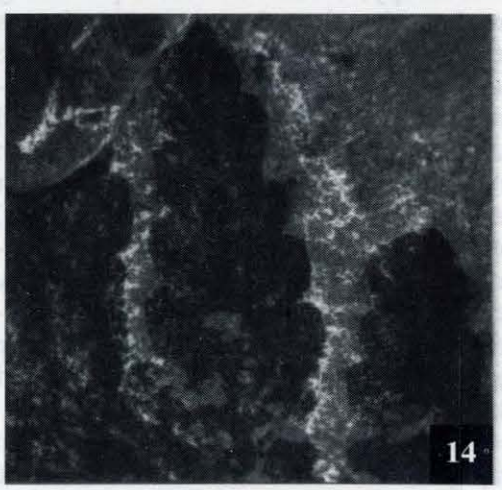
Figs 9 & 10. A cluster of lycopod sporangia; Hammanskraal. x6.





Figs 11 & 12. A portion of a Triassic fern; Little Switzerland. x2.





Figs 13 & 14. Triassic fern foliage; Little Switzerland. x2.

compression material, surface topography is sometimes a luxury, or the shadows cast on the specimen may unavoidably cause confusion. These difficulties, and the sometimes poor results obtained, drove me to seek a solution. The technique I suggest is an easy (and cheap) method of enhancing contrast without retouching the photograph, or altering the specimen in any way.

MATERIALS AND METHODS

The technique I suggest involves using polarised light. This is a tried and tested method of reducing glare (Schaarschmidt 1973), and an acceptable photographic tool. However, the method described here differs in using twice polarised light, similar to that used in transmission light microscopy by optical mineralogists. First, the light source is polarised by means of inexpensive plastic filter(s). Secondly, a filter is placed before the camera such that the light entering the lens is polarised at 90° to that of the original light source. In this way, all light that is directly reflected from the specimen (e.g. from the smooth surface of a coalified compression) will be in extinction, whereas the light reaching the camera from the surrounding matrix will be de-polarised and will pass through the second polarising filter. The latter will, therefore, appear as white light on the final print. The de-polarising of the light from the matrix is also enhanced by the anisotropic nature of the quartz grains which (often) form the bulk of the sedimentary matrix. However, these are the two extreme cases. Reality occurs somewhat in between the two, due mainly to the less than 100% efficiency of the filters, but also to the less than perfect reflectance of the coalified material and the partial reflectance of the matrix.

With this system, all that is required from the operator is the acquaintance of a manufacturer of polaroid sunglasses as a source of filters, and the patience to cut filters the right size and shape to suit the light source(s), and to orientate the filters at right angles to one another.

For photomicroscopy, I cut two small polarising discs which are then placed on the condensing lenses of a fibre optic light source. A polarising filter is also attached to the microscope objective (many microscopes, however, have such filters as accessories). All three filters can be rotated to the optimum position when necessary. Before the specimen is positioned for photography, a highly reflective surface (e.g. a mirror) is placed under the microscope, The filters are calibrated two at a time. When all three filters are correctly positioned, the light from the mirror will be in extinction. The system is now ready for use. Where a single microscope light source is used, the calibration is, of course, much easier.

I have also used this method successfully in macrophotography. Here, there are difficulties with the amount of available light. This is overcome by using long exposures, or a powerful ring-flash unit (or both). I use the latter with a cardboard box which fits closely over a ring-flashlight dish. One end is made up of a 25 cm^2 polarising filter. This distances the plastic from the monitor and flash bulbs and protects it from melting under the heat of the light. The second filter is fitted to the end of the macro lens (again such units are supplied for most cameras). The two are aligned using a mirror (as before) with the monitoring light of the flash. The mirror is removed, and the specimen inserted into the system. I find it necessary, at this stage, to use a second light to focus on the specimen, but this is extinguished during exposure. All ambient light is removed (I find my best results are obtained at night). The camera shutter is locked open, and a series of flashes (the number is of course dependent on the film and light characteristics) completes the exposure.

The lighting arrangement can obviously be used as in normal observation in addition to the production of high contrast photographs. The image produced may sometimes be a little flat. This situation can be improved either by adjusting the light source and producing a shadow effect, or by mis-aligning the filters a little. The greater the intensity of light that is used on a difficult specimen, the more the contrast is enhanced. With plain polarised light, however, increasing the intensity reduces the contrast, and produces more glare. The illustrations (Figures 1-14) were taken, as far as possible, under identical conditions, except for the use of polarising filters in the even numbered ones. It was found, however, that the high light intensity required for the polars produced unnecessary glare, and this was therefore reduced in an attempt to obtain the best results for plain polarised light. All micrographs were taken on a Zeiss SV8 stereo-microscope with Ilford Pan F (50 ASA) film. Films were developed in fresh Ilford ID 11, and printed on Iflospeed glossy paper (grade 3). All photographs were taken and processed in one session to minimise variation.

RESULTS

The illustrations are arranged in matching pairs, the first (i.e. Figures 1,3,5,7,9,11 & 13) has been taken under plain polarised light, the second (i.e. Figures 2,4,6,8,10, & 12) under crossed polars.

Figure 1 is a Cretaceous insect. The specimen has a naturally reflective surface, since the original cuticle remains virtually unaltered. It is the insect equivalent of a coalified compression (*sensu* Schopf 1976). Using polarised light (Figure 2) details of the wing venation are clear - this is essential for reliable identification. The results indicate certain coleopteran affinities, but close examination of the venation, only possible with polarised light, argues against this (McKay 1990). Figures 3 and 4 are an enlarged view of the posterior of the animal. Details of the second wing are revealed only under the cross polars.

Figures 5 and 6 show a small dipteran, probably a bibionid. The specimen is preserved in lateral view,

and details are virtually invisible in the plain light photograph due to excessive reflection. The contrasts between the two photographic methods are obvious. Figures 7 and 8 are of a Triassic dispersed seed, Figures 9 and 10 of a cluster of a Permian lycopod sporangia, and Figures 11, 12, 13 and 14 show parts of Triassic ferns. In each specimen, the black fossil (coalified compression) is preserved on the surface of a dark grey-black carbonaceous shale. The contrast and detail are greatly improved in the polarised photographs.

CONCLUSION

The thick continental accumulations of Gondwanan sediments contain abundant plant remains. Nevertheless, the stratigraphy is currently based on tetrapods. The problems of geography (in that collections are widespread) and of recording difficult data, have combined to retard progress in intercontinental stratigraphy. This technique offers a means to improve the standard of illustrations, and assist an understanding of the complexities of the fossil floras and allied fossils.

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