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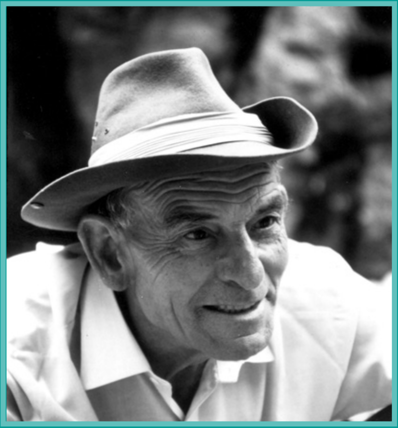
1922–2003



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CONTENTS

Articles

Historical Review

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James William Kitching (1922–2003): a tribute

Michael A. Raath & Bruce S. Rubidge

Bernard Price Institute for Palaeontological Research, School of Geosciences, University of Witwatersrand, Johannesburg

ON 24 DECEMBER 2003, JAMES WILLIAM KITCHING, REGARDED by many as one of the world's greatest fossil finders, died at his home in Johannesburg. His passing marks the end of a pioneering era of palaeontological giants in South Africa.

James Kitching was born on 6 February 1922 in Graaff-Reinet, in the heart of the world-famous Karoo. At a very early age he was inducted into the fundamentals of field palaeontology when he went with his father and younger brothers collecting fossils for the legendary Dr Robert Broom in the mountains around the village of Nieu Bethesda, where he grew up. He found his first fossil at the age of six, and only a year later he found what turned out to be his first holotype specimen, which Broom named *Youngopsis kitchingi* in his honour. It was the first of many new species which he was to present to science over the next seven decades and more.

When in the early 1940s Robert Broom presented a lecture at the University of the Witwatersrand decrying the loss of the country's rich palaeontological heritage to erosion, he struck a receptive chord in one particular member of his audience, the financier Dr Bernard Price. Price responded with an offer of funds to establish a fossil collecting unit at the University, which culminated in the establishment of the Bernard Price Institute for Palaeontological Research (BPI) in 1945. When it sought candidates for its first staff appointment, Robert Broom had no hesitation in recommending his stripling fossil-finder from the Karoo, James Kitching.

Kitching had just been demobilized from active service in Italy at the end of World War II and started his work at Wits as the first – and at that time only – BPI staff member on 26 October 1945. Within weeks he was off on his first field trip, back to the Graaff-Reinet district where he had grown up and which he knew so well. Today there are few places in the Karoo which have not felt the tread of Kitching's boots in his search for fossils. In the process he spent many years away from home, walked many thousands of kilometres, often in the blistering heat of the parched Karoo, and collected many thousands of fossils which today grace major museum collections on all the major continents. Of the 53½ years that Kitching served the BPI, 215 months (just short of 18 years) were spent in the field collecting fossils.

Through his dedication and tireless exertions, the BPI today houses one of the largest fossil collections in the southern hemisphere. More than ninety per cent of the fossils making up those collections were collected by Kitching himself, assisted over the years by a number of field assistants, but especially his long-time field companion and friend, the late Regent Lukas Huma. These collections are today a strong research magnet drawing visiting palaeontologists to Wits from all continents of the globe, and they represent a lasting monument to his work and an abiding tribute to his memory.

His collecting of fossils of Karoo age was not confined to South Africa alone – he collected also in Zambia, Zimbabwe and Lesotho, as well as the U.S.A., Brazil and Argentina. One of the many highlights of his long and productive career was in 1970 when he was invited to Antarctica as part of the U.S.A.-Antarctic Research Programme. Here he was responsible for the first identification of fossil therapsids in Antarctica, identical to those he was accustomed to collecting in South Africa, thus providing further strong palaeontological evidence of former close continental links between southern Africa and Antarctica. One outcome of his spectacular successes in Antarctica is that one of its highland features is now officially named 'Kitching Ridge' in his honour.

Nor was Kitching's palaeontological work confined to the Karoo. On his appointment to the staff of the BPI, the brief given to him was that he should divide his time between collecting Permo-Triassic fossils in the Karoo and Plio-Pleistocene mammalian fossils from the dolomitic cave deposits at Makapansgat in the north of the country. At the latter locality he was involved with investigations at the Cave of Hearths and the famous Limeworks deposits, where in 1947 he made an important discovery – the first specimen of the 'ape-man', *Australopithecus*, to come from that site. Together with Raymond Dart he undertook pioneering taphonomic research on the bone accumulations at Makapansgat. This work led to visits to the Netherlands, Belgium and France to study Palaeolithic mammalian faunas, and he was also involved in the analysis of fossils from Pinhole Cave in Derbyshire, England.

Although he did not have a standard undergraduate academic background, Kitching was granted special permission by the Senate of the University of the Witwatersrand to register for an M.Sc. degree based on his work in the Karoo. When his dissertation was submitted, its quality and comprehensiveness so impressed his examiners that they pressed for the university to award him a doctorate instead, which they did. At the time of his formal retirement at the age of 69 in 1990 he held appointments as Reader in Karoo Biostratigraphy and Acting Director of the Bernard Price Institute for Palaeontological Research at Wits University – ending up heading the institution which he had helped found as its first and most junior staff member. Following his retirement he was invited to become an Honorary Research Professorial Fellow of the Institute, an appointment he held up to his death.

Generations of students and palaeontologists from many parts of the world benefited from his encyclopaedic knowledge of the Karoo and its palaeontology, and many enjoyed his warm hospitality and friendly companionship on camping trips into the field, where he was ever ready to share his depth and breadth of knowledge and experience. Although not a prolific writer, his publications spanned a long and active career, and most have stood the test of time. He was active in publication right up to the end, the last paper to bear his name appearing just months before his death.

During his long career he received numerous awards, including honorary doctorates from the universities of Port Elizabeth (1981) and Wits (1996), the Gold Medal of the Zoological Society of South Africa (1993), the Draper Award of the Geological Society of South Africa (1993), and honorary life membership of the Society of Vertebrate Paleontology in the U.S.A. (1993) as well as the prestigious Morris Skinner award of that Society three years before his death. He was a founder member of the Palaeontological Society of Southern Africa, served a two-year term as its President, and was elected an Honorary Member (the highest honour the Society can bestow) in 1992. He was elected a Fellow of the Royal Society of South Africa in 1987.

Kitching remained a humble, self-effacing man throughout his life, despite the many accolades and honours bestowed on him by his peers during his long career. Above all, he was a family man, devoted to his wife of more than 50 years, Betty, and their three children. He lost his long battle with cancer on Christmas Eve, 2003.

We thank James Kitching's son, Matthew, for photographs used in this tribute.

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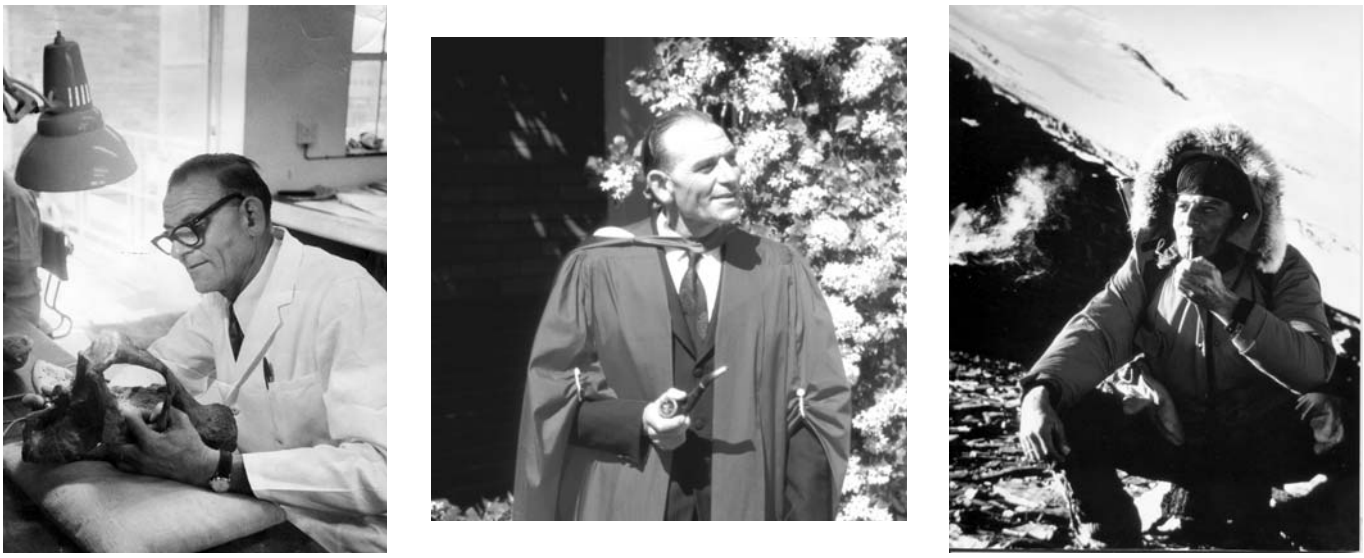
Kitching (far left) with other members of the US Antarctic Research Program team at Amundsen Glacier (1970).

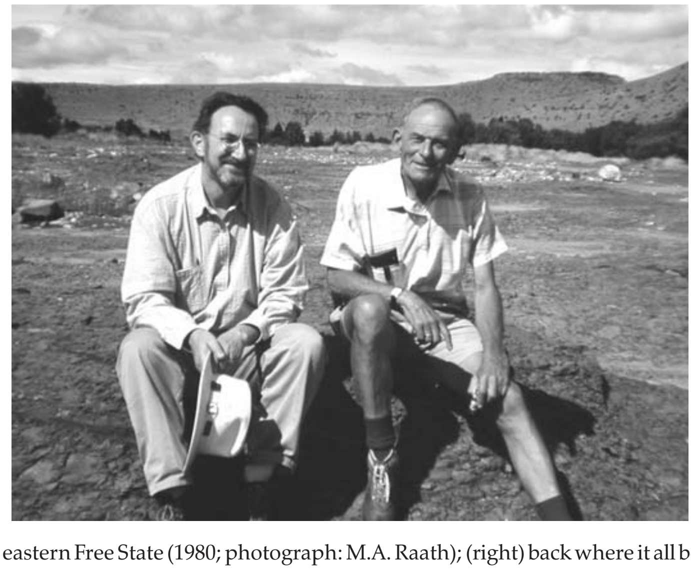
(left) Ever ready to share his knowledge with a young enquiring mind; (right) with a gorgonopsian skull collected from the Luangwa Valley, Zambia (1960/61; photograph: Die Suid Afrikaanse Stem).



(left) At work preparing a large *Theriognathus* skull (mid 1970s); (middle) Ph.D. graduation (1974); (right) smoke-break in the Antarctic (1970).

(left) With the world's oldest dinosaur eggs and embryos which he discovered in 1976; (right) with his field assistant and friend, Lukas Huma, on the occasion of his award for 25 years service to the university (1970).

Attentive group at Makapansgat Limeworks: Brian Maguire (extreme left); unknown (back to camera, wearing hat); Kitching; unknown (back to camera, hatless); Revil Mason; Raymond Dart; Phillip Tobias; unknown (extreme right, wearing hat) (late 1960s).



(left) Searching for tiny cynodonts in the Elliot Formation, eastern Free State (1980; photograph: M.A. Raath); (right) back where it all began for him, at Doornplaas in the Karoo, with a colleague from Canada, Robert Reisz (1997; photograph: B.S. Rubidge).

A new deep-bodied Late Permian actinopterygian fish from the Beaufort Group, South Africa

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A new genus of actinopterygian (ray-finned) fish, *Blourugia seeleyi* is described from Late Permian (Tatarian) fluvio-lacustrine, siltstone-dominated deposits within the lower Beaufort Group of South Africa. It was originally provisionally assigned to the globally known genus *Atherstonia* by Woodward (1893), but indications are that the genus is distinct from *Atherstonia* on the basis of its deep-bodied form and the associated skull characters; thus *Blourugia seeleyi* is placed in Gardiner & Schaeffer's (1989) *Platysomus* Group. The new genus is characterized by a uniquely shaped prominent high triangular posterior blade of the maxilla, dermosphenotic triangular shaped, pointed marginal teeth, 8–10 branchiostegal rays, flank scales that exhibit a well-developed dermal ornamentation consisting of numerous transverse ganoine ridges, and the presence of a dermopterotic that contacts the nasal. *Blourugia* appears to be a primitive deep-bodied form, basal to lower actinopterygian deep-bodied forms such as *Adroichthys, Amphicentrum, Cheirodopsis, Paramesolepis* and *Platysomus.* As a member of Gardiner & Schaeffer's *Platysomus* Group, it is therefore derived relative to stem-actinopterans such as *Howqualepis, Mimia* and *Moythomasia,* and also derived relative to earlier southern African Palaeozoic actinopterygians such as *Atherstonia scutata, Mentzichthys jubbi, Namaichthys schroederi* and the newly/recently described lower Beaufort Group taxa *Bethesdaichthys kitchingi* and *Kompasia delaharpei,* but basal to stem-neopterygians such as *Australosomus* and *Saurichthys.*

Keywords: *Blourugia,* deep-bodied palaeoniscid, Late Permian, Tatarian, Beaufort Group, Actinopterygii.

INTRODUCTION

The type specimen of the proposed new genus of deep-bodied actinopterygian fossil fish, *Blourugia seeleyi,* was originally provisionally assigned by Woodward (1893) to *Atherstonia seeleyi* based on a single incomplete specimen from Klipfontein, Fraserburg district (*Dicynodon* Assemblage Zone), Northern Cape, South Africa. Subsequently Jubb & Gardiner (1975), in their preliminary catalogue of South African fossil fish, referred a number of specimens from Blourug, Victoria West district (*Tapinocephalus* Assemblage Zone) to *A. seeleyi.*

Actinopterygian fishes are bony fishes particularly characterized by the morphology of the fins that are supported by stiff bony spines (Patterson 1982; Romer 1966). They constitute the largest group of living fishes, with a least 29 000 living species (M. Gomon, pers. comm.). The major actinopterygian groups diverged before the end of the Palaeozoic, with the early or 'lower' actinopterygians representing the 'primitive' or basal members of the Teleostei (Patterson 1982).

Blourugia seeleyi gen. nov. belongs to a group of early actinopterygian taxa which, owing to uncertain phylogenetic position, are usually grade-classified as 'palaeoniscids' (see Coates 1998), or consigned to the paraphyletic 'palaeonisciforms' (Coates 1999).

These 'palaeoniscid' early actinoptgerygians are generally characterized by thick, ganoine-covered scales articulated by interlocking peg and socket joints, a heterocercal tail, and a maxilla with an extended postorbital blade attached to the cheek (Gardiner & Schaeffer 1989). Traquair (1877–1914) was the first to use the term 'palaeoniscid' to refer to Palaeozoic ray-finned fishes, which he assigned to the genus *Palaeoniscus*). These palaeoniscids, palaeonisciforms, or 'Palaeoniscimorpha' (Lund *et al.* 1995), consist of mostly Palaeozoic, globally distributed actinopterygians (Coates 1993). The work of Patterson (1982), Gardiner (1984), Coates (1998, 1999), Gardiner & Schaeffer (1989), Poplin & Lund (2000), Cloutier & Arratia (2004) and Gardiner *et al.* (2005) showed that these 'palaeoniscids' include stem-taxa related to the Actinopterygii, Actinopteri, Chondrostei and Neopterygii. The Permo-Triassic Beaufort Group of the Karoo Basin of South Africa is world-renowned for its diverse and abundant therapsid ('mammal-like reptile') fauna (Rubidge 1995), but a fair number of fossil actinopterygian fish specimens have also been collected (Jubb & Gardiner 1975; Bender 1998, 2001). Egerton (1856) was the first to publish on lower Beaufort fish remains collected from the Graaff-Reinet district. More than a hundred years later, Jubb & Gardiner (1975) provided a comprehensive revision and update of the Beaufort Group fossil fish remains described by various researchers in the intervening years. A total of ten lower Beaufort Group actinopterygian species are now known, including *Blourugia seeleyi* gen. nov., and the recently described *Kompasia delaharpei, Bethesdaichthys kitchingi* and *Westlepis kempeni* (Bender 2001, 2002). Fossil fish are relatively rare, but where present are useful biostratigraphic indicators, and have palaeoenvironmental and global correlative potential (Bender *et al.* 1991; Hancox & Rubidge 1997).

MATERIALS AND METHODS

More than 27 laterally compressed *Blourugia* gen.nov. specimens were recovered by the author from a *Tapinocephalus* Assemblage Zone locality on the farm Blourug, Victoria West district (Abrahamskraal Formation,

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Adelaide Subgroup), Beaufort Group (referred to by Jubb & Gardiner 1975). Ten specimens were collected from a *Dicynodon* Assemblage Zone locality on the farm Wilgerbosch, New Bethesda district (Adelaide Subgroup). The formational designation of the Wilgerbosch site is uncertain (Cole *et al.* 2003) but appears to be situated in roughly the stratigraphic equivalent of the Balfour Formation. The specimens at Blourug are contained in a single, thin (on average 10 cm thick), buff-coloured, fine- to medium-grained, sandstone 'fish-bearing' unit, and occur over a lateral distance of 70 m. The fish are generally laterally compressed, occur throughout the unit, and tend to be preserved as fairly complete specimens. They are generally concentrated in areas or 'pockets' within the fish-bearing unit, with over 150 well-preserved specimens collected in total. The specimens at the Wilgerbosch roadside site were derived from a greenish mudstone/ siltstone/fine-grained sandstone horizon, 4.5–13 cm in thickness. Over 350 specimens have been collected from an area of approximately 10 m^2. As with Blourug, the fish are generally laterally compressed, and occur throughout the unit. Examination of the geology at the two study localities and the nature of the fossil fish deposits, indicates that the fishes were deposited in riverine overbank-type environments, preserving the fossils at the Blourug and Wilgerbosch roadside study localities in isolated 'palaeoponds'.

A number of the referred specimens required mechanical and chemical preparation (see Bender 2001, for preparation details). Latex rubber casts or peels, enhanced by whitening with ammonium chloride, were used to illustrate underlying morphological detail. Thin sections of scales were prepared and studied for histological analysis using a Zeiss standard petrographic microscope with polarized light. Interpretive drawings were made using a Leica MZ6 microscope with drawing tube. Photographs were taken using a Nikon FM camera mounted on a copy stand; for the thin sections, a Zeiss polaroid camera was used. The phylogenetics and interrelationships of *Blourugia seeleyi* gen. nov., are investigated using the Gardiner & Schaeffer cladogram III as a basis (Gardiner & Schaeffer 1989), since this is the most recent comprehensive early actinopterygian phylogenetic analysis (Coates 1999).

SYSTEMATIC PALAEONTOLOGY

Class Actinopterygii Woodward 1891
Infraclass Actinopteri Cope 1871

Blourugia gen. nov.

Type species. Blourugia seeleyi (Atherstonia seeleyi) Woodward 1893.

Derivation of name. Named after the paratype locality, privately owned farm 'Blourug'. Blourug means 'blue ridge' in Afrikaans, probably the most commonly used language of the region.

Diagnosis

Medium-sized, deep-bodied fish up to 200 mm in total length with a terminal mouth and almost upright suspensorium. Dermopterotic is a fairly broad, elongated bone, which contacts the nasal as does the triangular dermosphenotic. Premaxilla (or premaxillo-antorbital) is rectangular and is partially excluded from the jaw margin by the maxilla. Jugal is elongated and broad, the lachrymal is relatively short and narrow. Maxilla has a prominent, high triangular postorbital blade. Dentition consists of a median row of larger conical teeth surrounded by more numerous smaller teeth, also present are marginal peg-like teeth. Preopercular is a single large upright triangular to wedge-shaped bone. Two rounded suborbitals and a broad elongated dermohyal are present. Opercular is broad, rounded and articulated on the subopercular. Subopercular is broader and slightly higher than the opercular, and tapers ventrally. Suspensorium is upright. There are 8–10 branchiostegal rays. All the fins are large. Pectoral fin is very elongate with the fin-rays closely jointed over the entire length of the fin. Distal bifurcation is present on at least some of the fins. Heterocercal caudal fin has an elongated body lobe. Flank scales exhibit a well-developed dermal ornamentation consisting of numerous transverse ganoine ridges. Enlarged ridge scales present along the entire dorsal margin. Scale histology consists of a laterally continuous, multilayered ganoine layer, overlying dentine basal bony layers.

Remarks and comparisons

This genus was originally described as *Atherstonia seeleyi* by Woodward (1893), who indicated that the fish was only provisionally referred to the genus *Atherstonia* because of the extremely fragmentary nature of the holotype. Subsequently, Jubb & Gardiner (1975), on the basis of additional well-preserved specimens from Blourug, Victoria West, confirmed the generic and specific designation. Most recently the author recovered ten deep-bodied specimens from Wilgerbosch, which are now also assigned to *Blourugia seeleyi.* Indications from the present study are that the genus is distinct from *Atherstonia,* because of the following characteristics: its deep-bodied form; dermopterotic which contacts the nasal; no antorbital; reduced triangular postorbital blade of the premaxilla; upright wedge-shaped preopercular; high, broad subopercular, which tapers ventrally and is higher and broader than the opercular and branchiostegal rays reduced below the primitive 12–13.

On the basis of its deep-bodied form and the associated skull characters, which are found in deep-bodied lower actinopterygian taxa (such as the triangular postorbital blade of the maxilla, upright triangular preopercular, upright suspensorium), *Blourugia seeleyi* can be placed in the *Platysomus* Group of Gardiner & Schaeffer (1989). *Blourugia* has marginal conical teeth, and an absence of crushing toothplates, which suggests it is comparable with taxa such as *Platysomus superbus* and *Paramesolepis tuberculata,* and distinct from the deep-bodied forms with crushing toothplates such as *Amphicentrum crassum* and *Adroichthys tuberculatus* (see Coates 1988; Gardiner 1969; Moy-Thomas & Dyne 1938) for reference to comparative taxa). The presence of a dermopterotic that contacts the nasal in *Blourugia seeleyi* appears to distinguish it from other *Platysomus* Group taxa. This character is however present in an undescribed Late Permian deep-bodied form from the Bowen Basin, Australia (Bender 1999).

Blourugia seeleyi Woodward 1893

Derivation of name. Named after Professor H.G. Seeley, who discovered the holotype. Although the generic designation is emended, the species name *seeleyi* is retained (see Woodward 1893).

Holotype. P.8613 in the Natural History Museum, London (NHM). The locality is Klipfontein, SW of Fraserburg, Nieuwveldt Range, W Cape, *Dicynodon* Assemblage Zone, Lower Beaufort Group (Jubb & Gardiner 1975).

Paratypes. AK/76/7 and PB/96/5, housed at the Council for Geoscience, Pretoria. The locality is Blourug, Victoria West district, *Tapinocephalus* Assemblage Zone, Lower Beaufort Group.

Referred specimens. V63 and V64 housed in the Victoria West Museum, Victoria West; BPI/1/4373/27,28a,29,30,31, 34,35,36, housed at the BPI Palaeontology, Johannesburg; AK/76/2,3,4,5,6,8; PB/95/5; PB/96/1–4, 6, 8, 9,10,11,13a, housed at the Council for Geoscience, Pretoria.

Horizon and locality. V63, V64, AK/76/2–8, PB/96/1–4, 6, 8, 9, 10, 11, 13a are from Blourug, *Tapinocephalus* Assemblage Zone, Lower Beaufort Group. BPI/1/4373/27, 28a, 29, 30, 31, 34, 35, 36, and PB/95/5 are from the Wilgerbosch roadside locality, *Dicynodon* Assemblage Zone, Lower Beaufort Group.

Diagnosis

Only one species.

Remarks and comparisons

Blourugia seeleyi is the most abundant species at Blourug with in excess of 20 specimens recorded, and10 specimens recorded from Wilgerbosch.

DESCRIPTION

Skull roof

The skull roof region was analysed on the basis of specimens PB/96/4, 5, 9, AK/76/1,7 (see Figs 1–3). It is made up of broad paired parietals, frontals, extrascapulars, and a dermopterotic and dermosphenotic on either side of the frontals. All of the bones of the skull roof are ornamented with well-developed dermal ganoine ridges and denticles. The sensory line system appears to be well developed, with a canal, pits and pit-lines visible.

Parietals (Figs 1, 3 & 4). Most of the left parietal is preserved in PB/96/5 (Fig. 1B, pa) and is a relatively large, broad and subrectangular to ovate, slightly greater than half as long as the frontal. It tapers anteriorly to where it sutures with the frontal bone, posteriorly it is overlapped by the extrascapular. The posterior section of the supraorbital canal terminates in a triradiate canal system.

Frontals (Figs 1, 3 & 4). The frontals (Fig. 1B, fr) are elongate, forming approximately one third of the total length of the skull roof, meeting the median rostral and the nasals anteriorly. The supraorbital canal is marked by as a prominent series of pits in specimen number PB/96/9 (Fig. 3). Dermal ornament consists of a distinctive anteroposteriorly aligned pattern of ribs and denticles except at the posterior margin where they are aligned dorsoventrally.

Dermopterotic (Figs 1–4). The dermopterotic (Fig. 1B, dpt) is a prominent, elongate bone, which is broad posteriorly, tapering anteriorly over the dermosphenotic where it contacts the nasal. It is approximately the combined length of the parietal and the frontal. The infraorbital canal is situated low down on the lateral surface of the bone, towards the ventral margin, where a line of pits and pit-lines appear to trace the passage of the canal dermally. A cluster of pit-lines are present above the dermohyal. The infraorbital canal curves dorsally above the dermosphenotic, and then turns ventrally to enter the dermosphenotic towards the anterior margin. The nasal contact is unusual in deep-bodied lower actinopterygian forms since in most other deep-bodied forms the dermopterotic terminates against the dermosphenotic and is thus separated from the nasal by the dermosphenotic.

Dermosphenotic (Figs 1–4). This bone (Fig. 1B, dsph) is damaged in all of the study specimens in which it is visible but appears to be a fairly large relative to the other bones making up the orbital region, roughly triangular bone, which contacts the nasal anteriorly, underlying the dermopterotic along its entire dorsal margin. The infraorbital canal is visible on the dermal surface as a series of pits and pit canals, which enter the dorsal bone margin from the dermopterotic approximately midway along the margin, and curve ventrally close to the anterior margin before exiting at the narrow ventral margin.

Extrascapulars (Figs 1, 2 & 4). The left extrascapular (Fig. 1B, exsc) is well preserved in PB/96/5 (Fig. 1) and is an elongate, narrow bone overlapping the posterior margin of the skull. It is situated between the parietal and the post-temporal, overlying the post-temporal. The lateral line canal extends along the ventral border, where a number of sensory pits are visible. Dermal ornamentation consists of horizontally inclined ridges, which are distinct from those of the post-temporal in that the ridges are smaller and narrower.

Snout

The snout region is distorted and incomplete but is visible in specimens AK/76/7, PB/96/9, PB/98/3 and appears to consist of a median rostral bone, paired premaxillae and a nasal on either side of the rostral.

Premaxilla (or premaxillo-antorbital) (Figs 2 & 4). The premaxilla (Fig. 2B, pmx) is seen in medial view, poorly preserved in AK/76/7. It appears to be a rectangular bone and seems to be part of the upper jaw margin, at least anteriorly, and does not appear to bear teeth. The rostral bone is situated anterior to the premaxillae and is thus excluded from the jaw margin. Posteriorly the premaxilla sutures with the lachrymal and the nasal.

Nasal (Figs 2 & 4). Narrow and elongate, the nasal (Fig. 2B, na) forms the anterior dorsal margin of the orbit. It contacts the tapered anterior margins of the dermopterotic and the dermosphenotic above the posterior

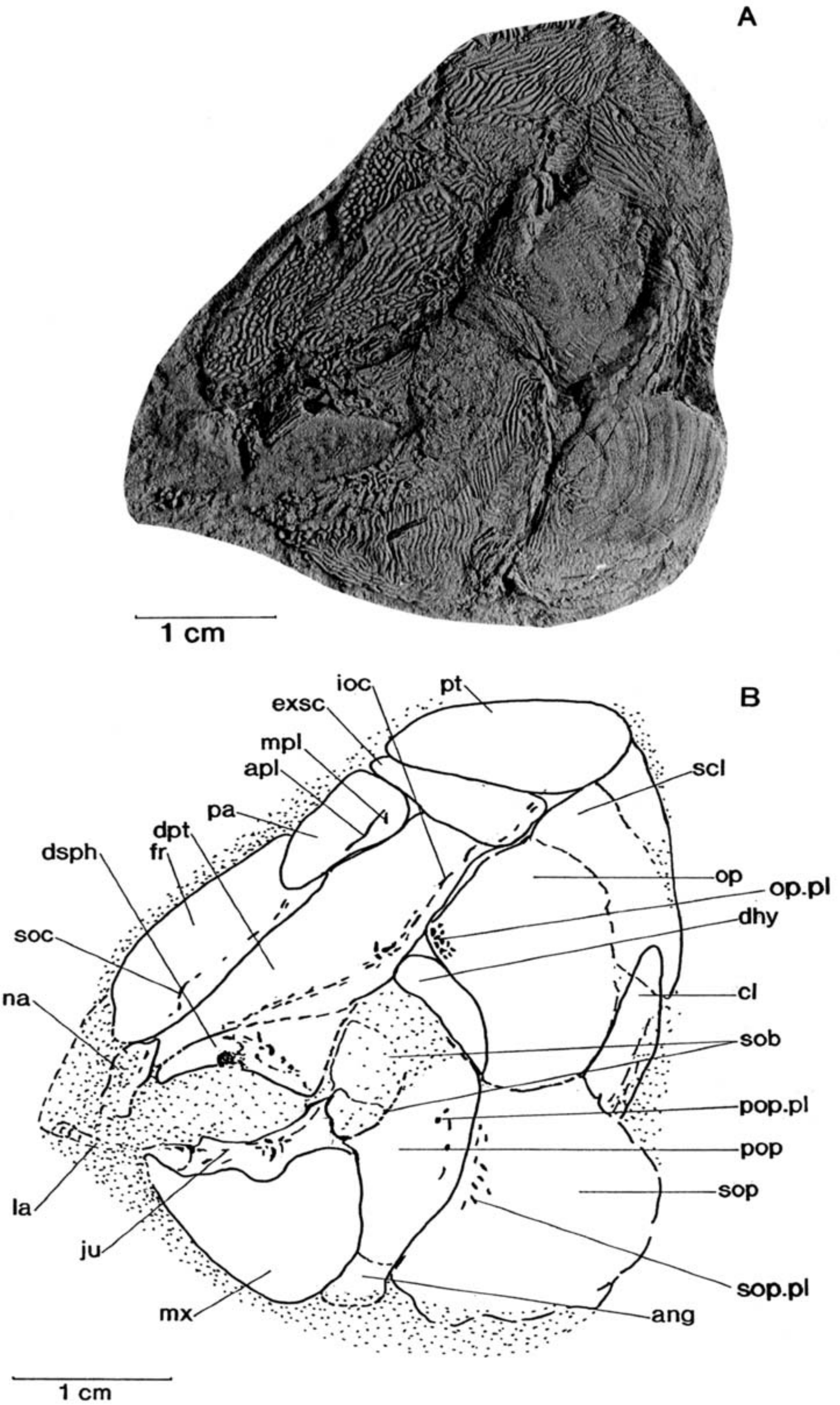

Figure 1. *Blourugia seeleyi* paratype PB/96/5. **A**, Photograph in lateral view showing skull region dermal detail. **B**, Camera lucida reconstruction.

dorsal margin of the orbit. Ventrally the nasal contacts the lachrymal. A single, rounded posterior naris is clearly visible in specimen AK/76/7, situated approximately a third of the distance up from the ventral border; the anterior naris is faintly visible on the inner margin.

Rostral (Figs 2 & 4). The rostral (Fig. 2B, ro) is poorly preserved, but appears to be a single median bone. In AK/76/7 its ventral margin appears to contact the premaxilla some distance above the jaw margin, and is thus removed from the jaw articulation.

Cheek and infraorbitals

The infraorbital region is not well preserved but is visible in specimens PB/96/2, PB/96/5, and AK/76/7, consisting of a large jugal and slightly smaller lachrymal, The cheek region consists externally of a prominent maxilla, preopercular, suborbital complex, an inner palatoquadrate and dermal bones of the mouth, and is best represented in specimens PB/96/5 and AK/76/7.

Jugal (Figs 1, 3 & 4). A large, elongate, crescentic bone (Fig. 1B, ju), which forms most of the posterior margin of

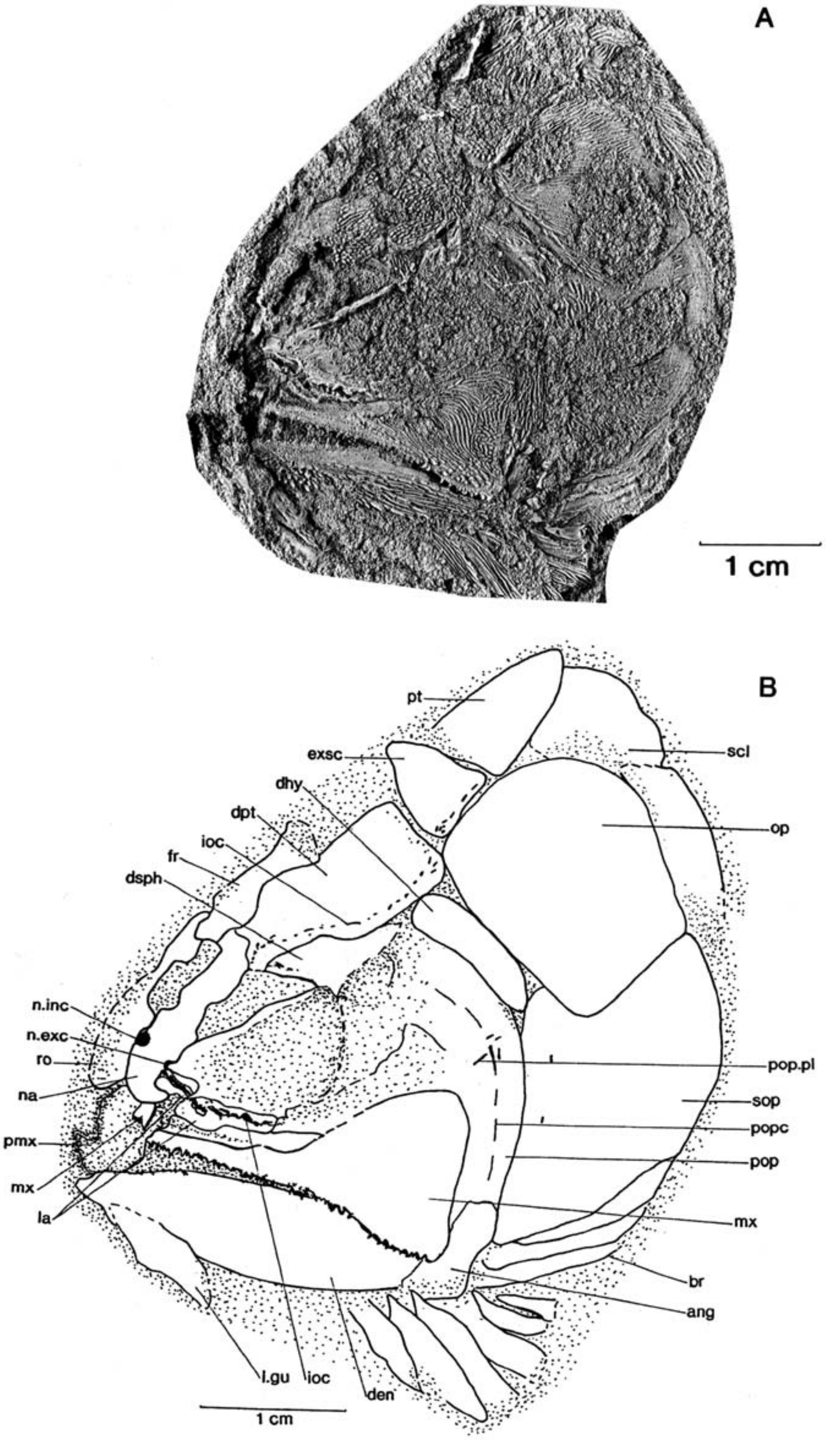

Figure 2. *Blourugia seeleyi* paratype AK/76/1. **A**, Photograph in lateral view showing cheek and snout region detail. **B**, Camera lucida reconstruction.

the orbit, and contacts the dermosphenotic dorsally and the lachrymal ventrally. A well-developed infraorbital canal, with associated posteroventral branchlets, is visible in specimen PB/96/2. A series of pits associated with the infraorbital canal are also visible. Dermal ornament in the form of ridges can be seen towards the dorsal margin of the bone.

Lachrymal (Figs 1–4). The lachrymal (Fig. 2B, la) can be seen in median view in specimen AK/76/7, although it is fractured and somewhat distorted. It is slightly narrower than the jugal and shorter with a broad well-developed infraorbital canal present. Anteriorly it sutures with the premaxilla and the nasal, ventrally it borders the infraorbital blade of the maxilla.

Maxilla (Figs 1–4 & 6). The maxilla (Fig. 2B, mx) consists of a triangular postorbital blade, which is high and rounded dorsally, and a tapered sub-infraorbital blade, which is approximately half of the total maxilla length which appears to be fairly robust. Anteriorly the maxilla appears to suture with the premaxilla, which forms the terminal margin of the skull. The dermal ornament on the postorbital blade is well developed and consists of

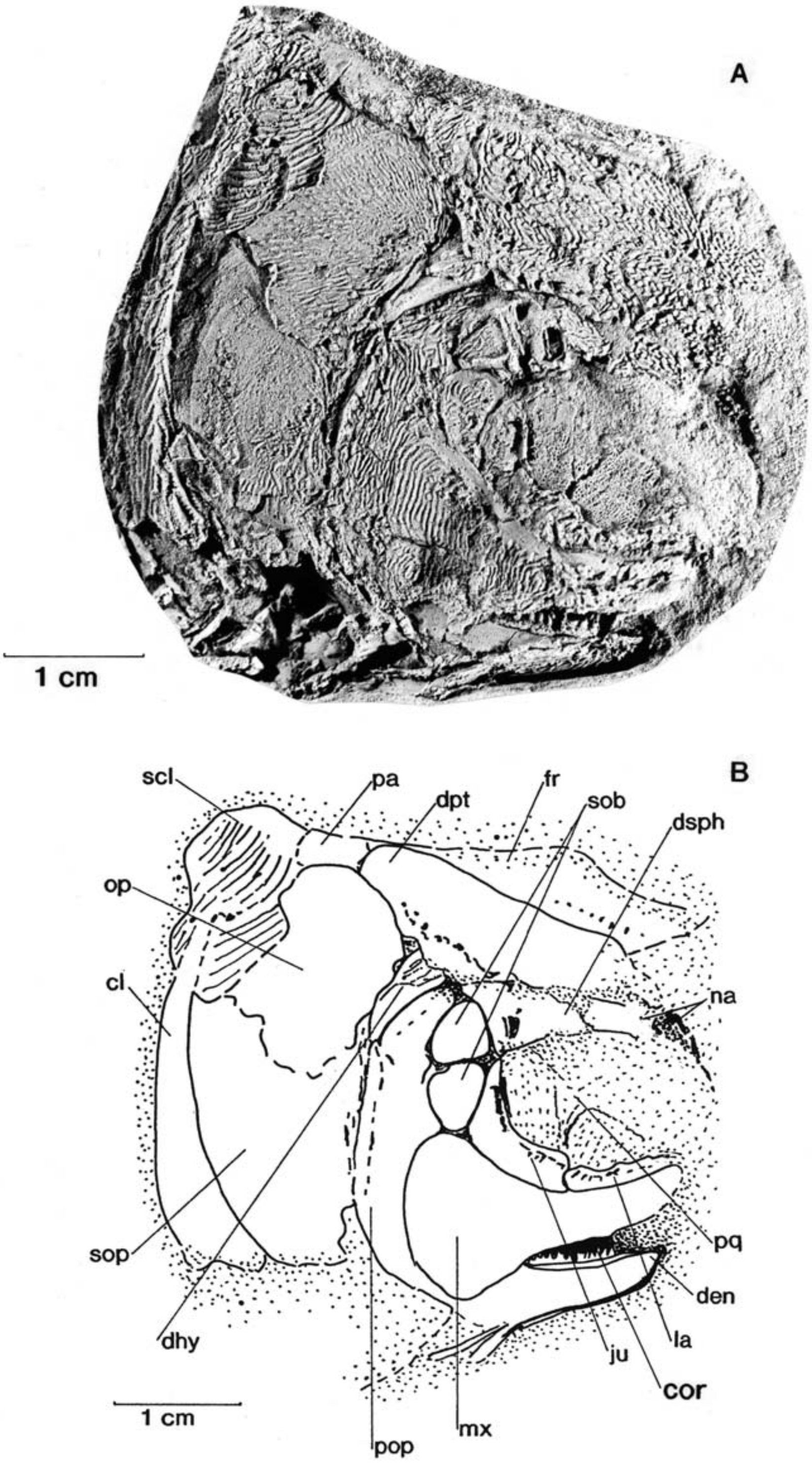

Figure 3. *Blourugia seeleyi,* specimen PB/96/9. **A**, Photograph in lateral view showing suborbital complex in particular. **B**, Camera lucida reconstruction.

numerous vertical or slightly inclined ridges on the body of the blade, and laterally orientated ridges close to the jaw margin.

Dentition (Figs 2 & 4). The occlusal margin of both the maxilla and the mandible consists of a single row of large conical medial teeth (*c.* 1 mm in height) surrounded, at least in certain areas of the jaw margins, by smaller marginal teeth. The dentition pattern seems to be a mixture of the primitive dental pattern and the apparently more advanced type that occurs in *Platysomus* (Poplin & Heyler 1993), characterized by a single row of marginal peg-like teeth. Also present are tooth-like rows of denticles on the dermal bones of the palate (Fig. 8) and the coronoids of the mandible (Fig. 3).

Preopercular (Figs 1–4). The preopercular (Fig. 3B, pop) consists of a single, upright, bar-like, sickle-shaped bone situated between the opercular and subopercular posteriorly, and the suborbitals and maxilla anteriorly. It tapers to form a blunt, rounded ventral margin; the dorsal half of the bone is slightly curved to fit over the posterior margin of the maxilla and contact the suborbitals. The sensory canal system consists of a preopercular canal and a horizon-

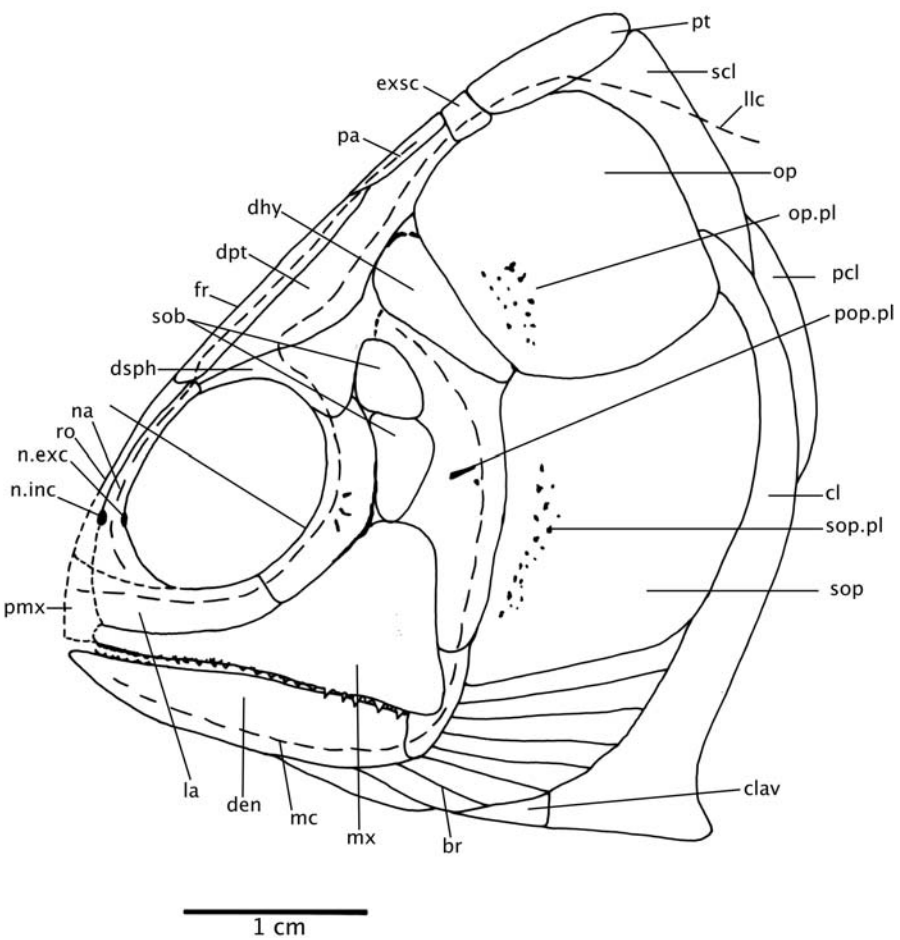

Figure 4. *Blourugia seeleyi*, restoration of the head in lateral view.

tally aligned pit-line groove, which is situated at approximately the inflexion point of the bone; immediately ventral to this a vertical pit-line extends into the preopercular canal. Above the upper horizontal pit-line the preopercular canal continues up to end midway along the dorsal limb and close to the dorsal margin. A series of pits are present close to and also parallel to the posterior margin. The dermal ornament is well developed, and consists of a series of vertically aligned ridges.

Suborbitals (Figs 1, 3 & 4). The suborbital complex (Fig. 3B, sob) consists of two vertically aligned wedge-shaped suborbital bones with rounded margins, situated between the preopercular posteriorly, and the dermosphenotic and the jugal anteriorly.

Palatoquadrate and the dermal bones of the mouth. Portion of the palatoquadrate (Fig. 3B, pq) was observed in specimen PB/96/9. Dermopalatine teeth are visible along the lateral margin of the palatoquadrate in specimen V63 (Fig. 8, ent).

Operculo-gular system

The opercular-gular system is well preserved in a number of specimens, and comprises the dermohyal, opercular, subopercular, branchiostegal rays and the gular plates. The suspensorium is inclined at an angle of approximately 70° to the horizontal. The dermal ornament consists of well-developed ganoine ridges.

Dermohyal (Figs 1, 2, 3 & 4). The dermohyal (Fig. 1B, dhy) is a relatively large, broad, roughly triangular bone, which extends approximately two-thirds of the length of the adjacent opercular.

Opercular (Figs 1–4). The opercular (Fig. 2B, op) is an almost square bone with rounded margins, which is slightly higher than broad and inclined at an angle of *c.* 60° to the horizontal. It is slightly shorter than the subopercular, overlapping and articulating with the subopercular, so that the anterior margin of the subopercular extends dorsally between the dermohyal and the opercular. A series of pits extend along the anterior margin.

Subopercular (Figs 1–4). The largest bone in the skull (Fig. 2B, sop), it is subrectangular with a diagonal length almost as long as the skull roof. The subopercular is dorsally broader than the opercular, and slightly taller. A series of sensory pits are visible along the anterior margin.

Branchiostegal rays (Figs 2, 4 & 6). The branchiostegal ray series (Fig. 2B, br) is not completely preserved in any specimen but appears to consist of 8–10 elongate rays. The posterior-most three are angled diagonally upwards towards the mid-flank region. The dermal ornament consists of ridges running the length of the bones.

The *gulars* are not clearly preserved in any of the study specimens, a lateral gular fragment is preserved in AK/76/7 (Fig. 2B, l.gu).

Lower jaw

The lower jaw was studied in specimens AK/76/7 and PB/96/9. It appears to be well ossified and moderately deep. The dermal ornament is clearly developed in the

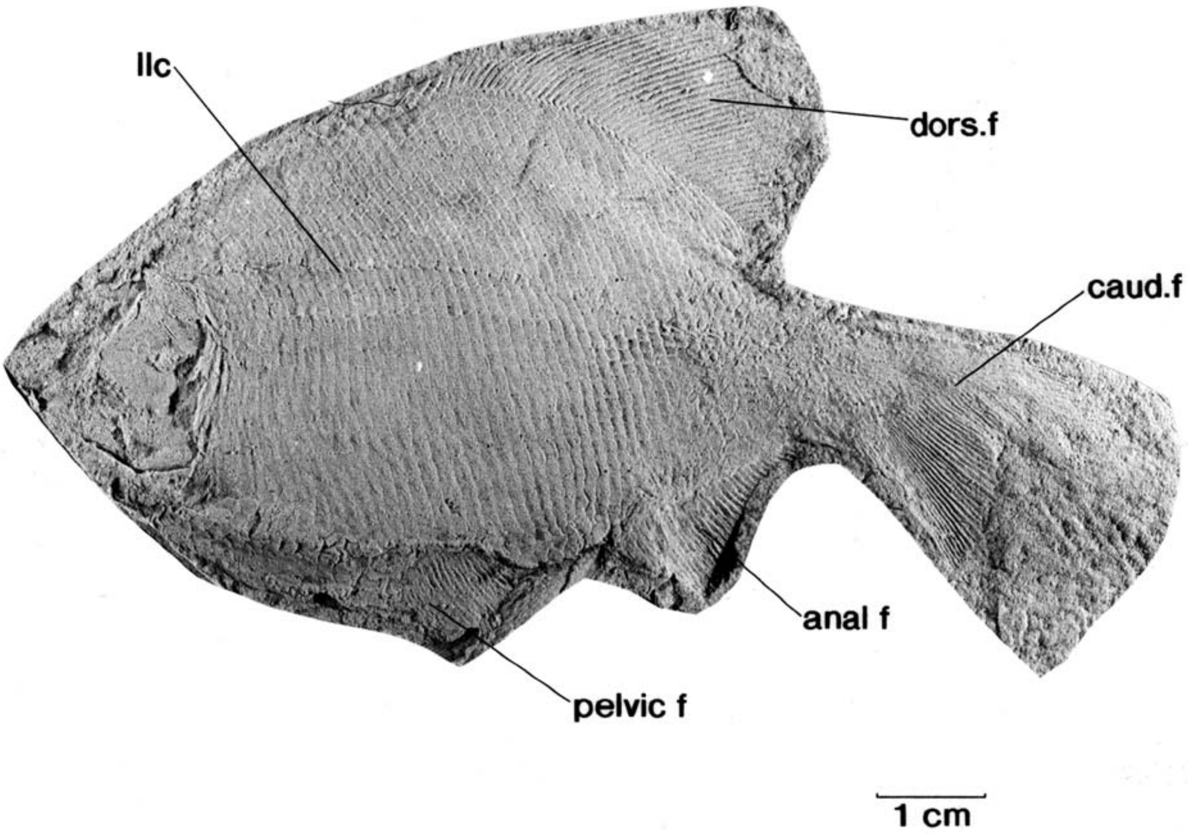

Figure 5. Photograph of *Blourugia seeleyi* specimen AK/76/2 in lateral view, showing the body and fins.

form of narrow, laterally orientated ganoine ridges and short broader denticles. In PB/96/9 a coronoid fragment containing teeth is visible (Fig. 3).

Dentary (Figs 2–4). The dentary (Fig. 2B, den) is fairly Hrobust and deepest in its centre, tapering anteriorly. The depth/length ratio is approximately 1:3.5 (PB/96/9), which indicates a fairly deep dentary relative to fusiform taxa such as *Atherstonia scutata,* and comparable in this regard to other deep-bodied taxa such as *Paramesolepis.* A prominent mandibular sensory line is partially preserved in specimen PB/96/9, represented by a pit-line, usually present on the angular.

Angular (Figs 1, 2 & 4). This bone has a high posterior blade that articulates dorsally with the ventral margin of the preopercular; anteriorly it sutures with the posterior margin of the dentary. In specimen AK/76/7 (Fig. 2) the dentary canal can be seen close to the dorsal margin of the angular where it continues up into the preopercular.

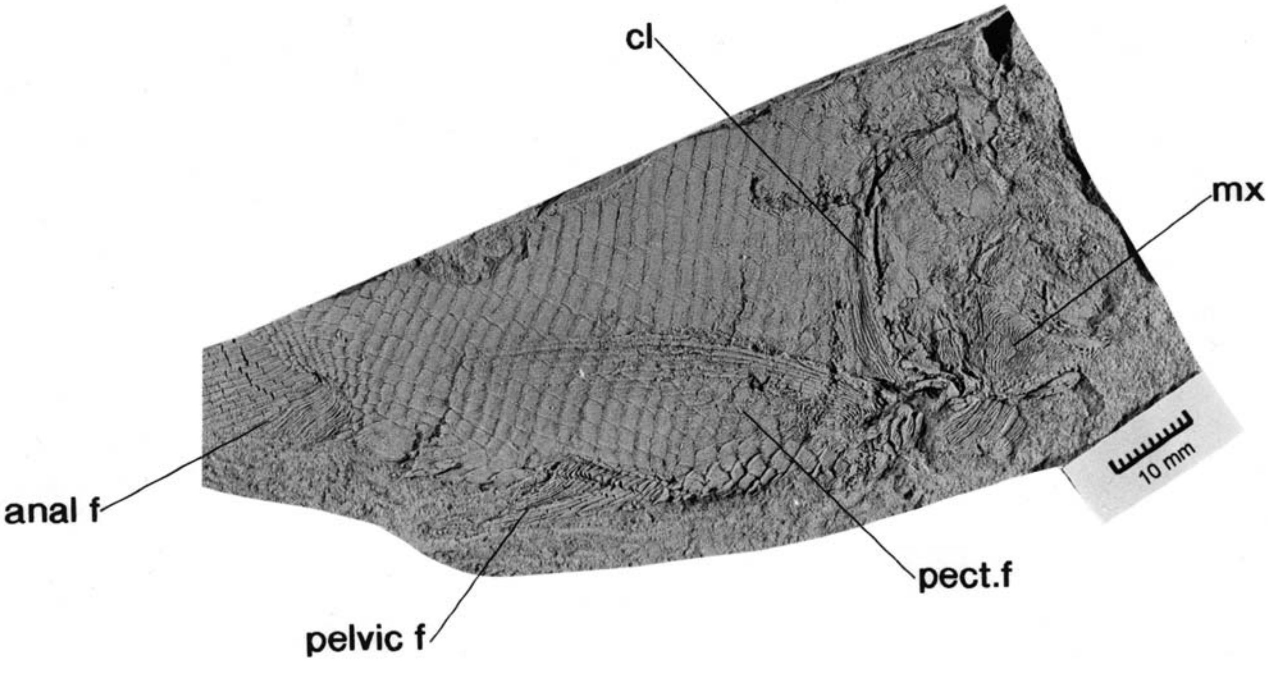

Figure 6. Photograph of *Blourugia seeleyi* specimen PB/96/1 in lateral view, showing pectoral fin and skull region detail.

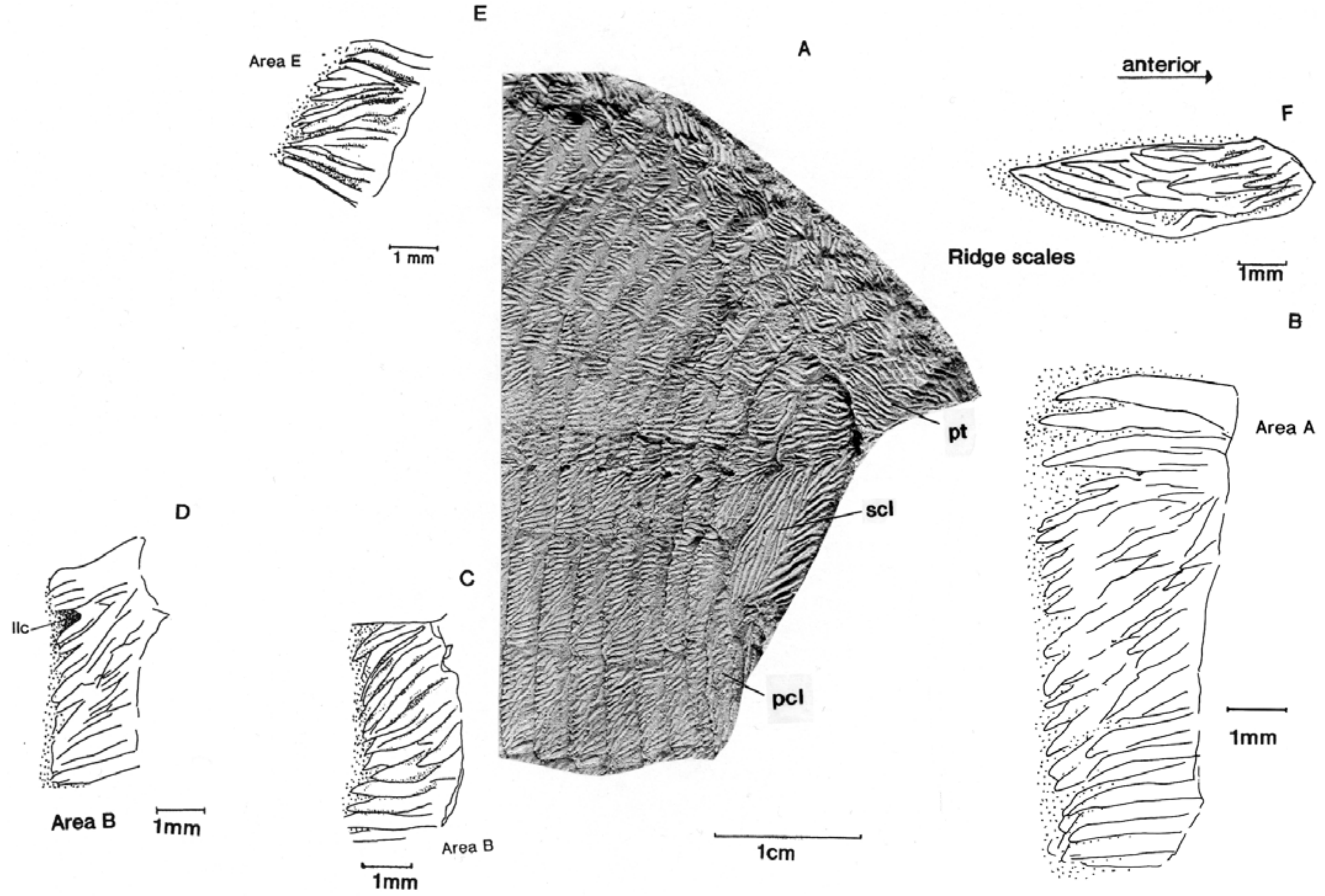

Figure 7. *Blourugia seeleyi* specimen PB/96/13a in lateral view, photograph and camera lucida reconstructions showing scale morphology detail.

Pectoral girdle

The pectoral girdle was studied in specimens PB/96/1 and 5, and consists of paired post-temporals, and a cleithrum, postcleithrum and a supracleithrum on either side of the skull.

Post-temporals (Figs 1, 2, 4, 7 & 8). The left post-temporal (Fig. 1B, pt) is well preserved in PB/96/5 (Fig. 1). It is a large, triangular bone that tapers dorsoventrally towards the posterior margin. It has a straight anterior margin which overlaps the extrascapular The lateral-line canal can be seen close to the ventral margin, where it enters the supracleithrum approximately halfway along the ventral margin of the post-temporal. The lateral-line canal is preceded by a number of pits at the anteroventral border. Dermal ornament consists of ridges horizontally aligned along the length of the bone, and parallel to the inclined dorsal margin.

Supracleithrum (Figs 1–4, 7 & 8). Well preserved (Fig. 1B, scl), but some of the margins are incomplete in a range of specimens. Large with a broad dorsal end where it is overlapped by the post-temporal bone (this overlap is particularly noticeable in Fig. 7), tapering to where it contacts the cleithrum. The lateral-line canal, with associated sensory pits, enters approximately halfway along the posterior margin and exits approximately halfway along the dorsal margin. The dermal ornamentation consists of well-developed ridges, which generally are aligned along the length of the bone, but are horizontally inclined towards the ventral margin (see in Fig. 7).

Postcleithrum (Figs 4 & 7). A narrow, elongated postcleithrum (Fig. 7A, pcl) bone is visible in specimen PB/96/13a, situated at the posteroventral margin of the supracleithrum. It has well-developed horizontal ridges that constitute the dermal ornamentation, similar to those found on adjacent flank scales, but more robust.

Cleithrum (Figs 1, 3, 4, 6 & 8). The cleithrum (Fig. 3B, cl) consists of a slender, elongated vertical blade and a expanded ventral region anterior to the pectoral fin insertion area. It is almost upright in attitude with a slightly curved tapered dorsal blade, and a horizontally inclined ventral blade, which is not clearly preserved. The dermal ornament on the dorsal blade consists of more than five dermal ridges orientated along the length, and on the anterior surface a series of robust 'studs' or denticles.

Body and fins

The body is on average less than twice as long as it is deep, giving *Blourugia seeleyi* a deep-bodied shape (Figs 5, 8 & 9). The total fish length ranges from approximately 115 mm in AK/76/2 (Fig. 7), to 200 mm in V63 (Fig. 8). The total body length ranges from about 80 mm in AK/76/2, to 125 mm in V63. The head length is contained almost six times within the total body length.

The fins are large compared to those of other deep-bodied lower actinopterygians; all apart from the pectoral fin are triangular. All fins have a number of short fin-rays at the fin insertion immediately anterior to the main body of the fin, with fringing fulcra present on the leading

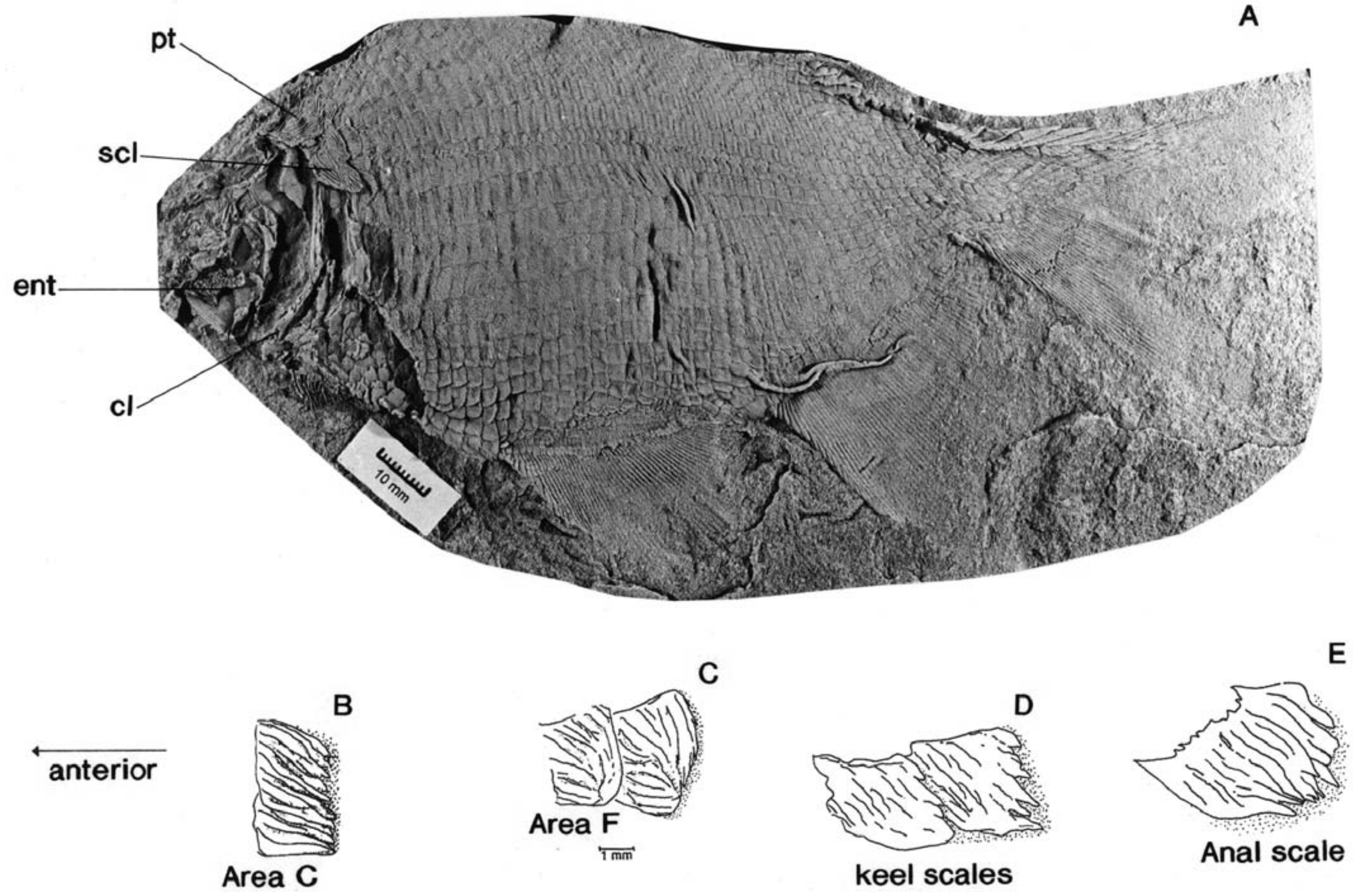

Figure 8. *Blourugia seeleyi* specimen V63 in lateral view, showing body and scale detail.

edges. Fin-rays are numerous and closely articulated throughout their length with unpaired fins and the pelvic fins exhibiting distal birfurcation. The presence of a prominent dermal ornamentation in the form of a rib running lengthways is particularly visible on the pectoral and dorsal fins but also present on the other fins.

Pectoral fin (Figs 6 & 9). Clearly visible (Fig. 6, pect.f) , re-curved over the body in PB/96/1 (Fig. 6), appearing to extend back to the vicinity of the anal fin insertion (scale row *c.* 25), although the distal margin is not preserved it is obviously a very elongate fin. Part of the first or marginal fin-ray is preserved and seems to be a thick, elongate bone. The fin-rays are closely articulated or jointed, apparently throughout the fin length (proximally and distally), with a fin-ray segmentation count of 25–30 close to the leading edge.

Pelvic fin (Figs 5, 6, 8 & 9). The pelvic fin (Fig. 5, pelvic f) is well preserved in V63 (Fig. 8) although the distal margin is not clearly visible. It is a large fin with a fin-ray number of *c.* 50–52. Fin base length is approximately 32 mm in specimen V63, which is particularly long compared to other deep-bodied lower actinopterygians. The fin starts in most specimens at scale row 7, and is located about halfway between the pectoral girdle and the insertion of the anal fin. The fin-rays are up to 30 mm long, with the longest located at the 14th fin-ray.

Anal fin (Figs 5, 6, 8 & 9). This fin (Fig. 5, anal f) is fairly well preserved in V63 (Fig. 8), although the distal margin is not clearly visible. It is a large fin with a fin base length of *c.* 40 mm in specimen V63. This fin starts in most specimens at scale row 26, and comprises more than 60 fin-rays. The fin-rays are up to *c.* 30 mm long, with the longest at the 9th fin-ray.

Dorsal fin (Figs 5 & 9). The dorsal fin (Fig. 5, dors.f) is situated in the anterior half of the body opposite the pelvic fin; it is incompletely preserved in specimen AK/76/2. It is a relatively large fin with a fin-base length of approximately 35 mm and the fin inserted on average at scale row 24. The fin is made up of more than 32 fin-rays, with the longest fin-ray more than 20 mm and the 12th fin-ray from the anterior fin margin. A series of *c.* 7 shorter fin-rays are situated anteriorly on the dorsal fin, preceding the first full length fin-rays of the dorsal fin.

Caudal fin (Figs 5, 8 & 9). The caudal fin (Fig. 5, caud.f) is heterocercal, with an elongated dorsal hypochordal lobe; the longest fin-ray is situated at the 8th fin-ray and is *c.* 45 mm long. The fin starts on average at scale row 41. Caudal fin length (cl) to total fish length (tfl) ratio in specimen V63, cl/tfl = approximately 80:200 mm = 1:2.5, which is relatively large for deep-bodied lower actinopterygians. There is a visible cleft in the tail between the dorsal and ventral lobes situated at approximately the 16th fin-ray.

Scales and squamation

The scale cover and squamation was studied in specimens V63, PB/96/2, 13a and AK/76/2 (see Figs 5–9). The scales are rhombic and have peg and socket articulations, with particularly the mid-flank scales anterior to the pelvic fin elongated and large. The flank scales, particularly in scale cover Areas B to D, undergo a size reduction dorsally

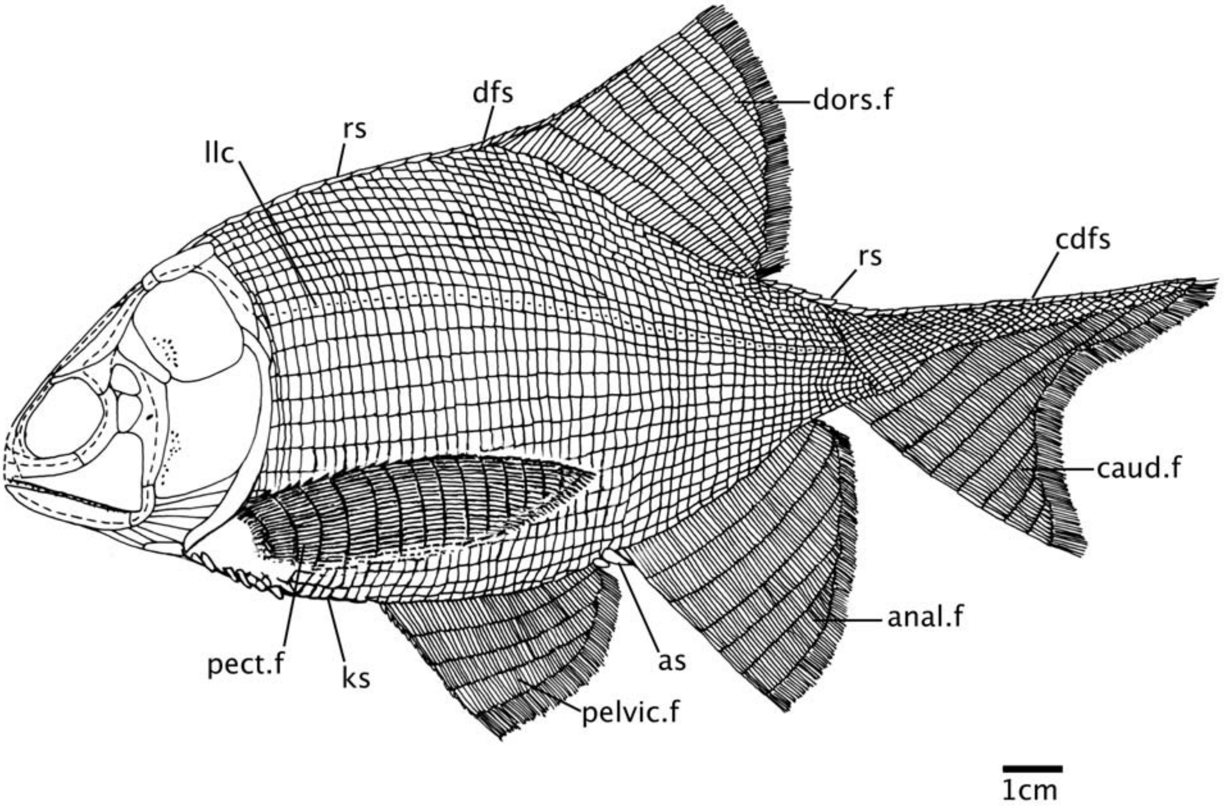

Figure 9. *Blourugia seeleyi*, restoration of fish in lateral view.

and ventrally from the mid-flank region outwards. In PB/96/18 the medial scale morphology was observed, showing a prominent rostrodorsal process or anterodorsal angle present, this character is typical to the palaeoniscids but absent in deep-bodied forms with specialized squamation such as *Amphicentrum, Platysomus* and the bobasatraniids (Coates 1988; Traquair 1879).

Topographic variation of the *Blourugia seeleyi* scale cover (after Esin 1991)

Area A (Figs 7–9). Area A appears to be a small area immediately behind the pectoral girdle, consisting of 5–7 rows of scales. The scales are elongate rectangular, with a height to length ratio of about 3:1. The anterior and posterior scale margins are steeply inclined. The dermal ornamentation on the free field consists of *c.* 16–18 horizontally inclined ridges, most of which terminate in a posterior denticle.

Area B (Figs 7–9). Scales of this area are situated between the pelvic and dorsal fin insertions. As in Area A, they are also elongate rectangular, with a height to length ratio of about 3:1. The anterior and posterior scale margins are also steeply inclined, as in Area A. The free field consists of *c.* 13–16 horizontally to diagonally inclined ridges in the dorsal two-thirds of the scale, which terminate in *c.* 13 posterior denticles. This dorsal series of dermal ridges is separated from a group of ventral ridges, by a diagonal series of ridges running ventroposteriorly. Below the diagonals there are *c.* 8–12 generally horizontally inclined ventral ridges, some of which can be traced into ridges of the abovementioned dorsal series. The ventral *c.* 5 ridges terminate in posterior denticles.

Area C (Figs 8 & 9). The scales in this region are rectangular, becoming square as they taper progressively off in size towards the caudal fin. The height to length ratio is approximately 2:1 near the Area B region, and almost 1:1 close to the caudal region area D border. The free field consists of *c.* 8–15 diagonally to horizontally inclined ridges that terminate in *c.* 4–12 posterior denticles.

Area D (Figs 5, 8 & 9). Scales in the caudal region are reduced, rectangular to diamond-shaped posteriorly with a h/l ratio of approximately 2:3. A series of *c.* 2–4 faint diagonal ridges and grooves are visible on the free field. In the scales near Area C, 1–2 posterior denticles are visible, with the posterior margin becoming entire further back in area D.

Area E (Figs 7, 8 & 9). Area E is a narrow area consisting of approximately 3–4 rows of reduced scales, situated above Areas A and B. The scales are inclined at a steeper angle than the scales of areas A and B, giving them an almost triangular appearance; however, the h/l ratio of approximately 3:2 is indicative of a rectangular shape. The free field consists of *c.* 4–6 prominent enamel ridges in the upper third to quarter of the scale, and then ventrally in the lower three-quarters to two-thirds of the scale there are *c.* 6–8 sub-horizontal ridges. Posterior denticles are not well preserved but there appear to be *c.* 7–10.

Area F (Figs 6, 8 & 9). This area, situated between the pectoral girdle and the insertion of the anal fin consists of 2–4 rows of scales, reduced in size relative to the scales from areas A and B, with a rounded posteroventral margin. The h/l ratio is almost 1:1. The dermal ornament on the free field consists of c. 8 ganoine ridges, which are more diagonally orientated across the body of the scale than in any of the previous areas, terminating in *c.* 4 posterior denticles.

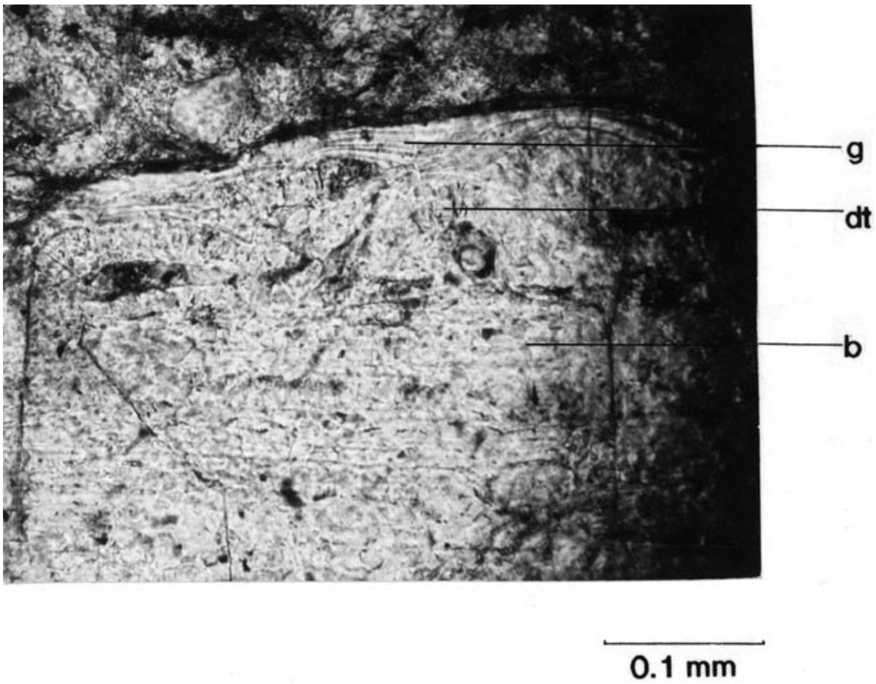

Figure 10. Thin-section photograph of *Blourugia seeleyi* specimen BP/1/4373/35, showing the morphology of the scale layers.

Areas G (Figs 6, 8 & 9). This area consists of *c.* 3–6 rows of very small, slightly elongated, overlapping scales in the regions of the dorsal, pelvic and anal fins. The free field dermal ornamentation consists of *c.* 2–4 diagonal ridges that terminate in *c.* 2 posterior denticles.

Anal scales (Figs 6, 8 & 9). There appears to be one enlarged, ovate anal scale preceding the insertion of the anal fin. The dermal ornamentation is similar to that found on the keel scales.

Ridge scales (Figs 5, 7 & 9). A row of *c.* 12 enlarged triangular ridge scales precede the dorsal fin, with an h/l ratio of approximately 1:3. A row of *c.* 4–5 poorly preserved, enlarged ridge scales are present behind the dorsal fin. The free field ornamentation consists of *c.* 10–12 well-developed parallel ridges along the length of the scales.

Keel scales (Figs 6, 8 & 9). A marginal row of *c.* 10 poorly preserved, enlarged, triangular scales is present between the pectoral and pelvic fins. A further *c.* 5 enlarged, triangular scales are present along the ventral margin between the pelvic and anal fins. The dermal ornament consists of ganoine ridges aligned parallel to the ventral margin.

Basal fulcra

Dorsal fin, basal fulcra (Figs 5 & 9). A series of *c.* 5 small, triangular scales are situated between the ridge scales and the short fin-rays, which constitute the insertion of the dorsal fin.

Caudal fin, dorsal basal fulcra (Figs 8 & 9). A series of *c.* 12–14 elongated and enlarged, acute, triangular scales are situated above the caudal fin.

Caudal fin, ventral basal fulcra (Figs 8 & 9). There appear to be 2–3 triangular scales preceding the insertion of the caudal fin.

Squamation

The scale row configuration can be seen in a number of specimens, including V63 (see Figs 5–9). Scale rows have a slightly sinusoidal arrangement, which can be seen immediately posterior to the pectoral girdle. There is a marked caudal inversion approximately four fin-rays back from the caudal fin insertion.

Scale counting data

Scale rows to pelvic fin (BP/1/4373/36, V63, V64, AK/76/2, PB/96/1, PB/96/8, BP/14373 27):	*c.* 7, 7,7, 7, 7, 8, –.
Scale rows to dorsal fin:	*c.* 25, –, 24, 23, –, 24, 25.
Scale rows to anal fin:	–, 26, *c.* 27, 26, *c.* 25, 26, –.
Scale rows to caudal fin:	*c.* 41, 41, 41, –, –, 42, +40.
Scale rows to caudal inversion:	*c.* 49, 49, 47, –, –, –, +47.

Number of scales in a single scale column:

In front of pelvic fin (V64, PB/96/8, BP/1/4373/27):	*c.* 18, *c.* 22.
In front of anal fin:	*c.* 25, *c.* 27, –,.
In front of dorsal fin:	*c.* 28, *c.* 26, –.
In front of caudal fin:	*c.* 17, –, 17.
In front of caudal inversion:	*c.* 12, *c.* 12, –.

Scale histology

The histological structure of the scale of *Blourugia seeleyi* is shown in Fig. 10. The bottom, bony layer constitutes more than half of the scale thickness. The middle dentine layer appears to laterally overlap in a number of places, but still fairly laterally extensive, with upright branched dentine tubules in a laterally continuous plexus. The ganoine layer is multilayered, and varies in thickness laterally. The scale structure is different to that in *Platysomus,* in which there are only two layers, a compact basal bony layer and upper bone layer (Aldinger 1937). The configuration of the ganoine and dentine layers is similar to the elonichthyid type, and possibly more similar to *Gonatodus* and *Pseudogonatodus* with respect to their variation of thickness in the ganoine layer. It is certainly very different to the *Playsomus* type of scale histology, indicating that, although deep-bodied, *Blourugia seeleyi* may not be related to *Platysomus.* Clearly more detailed analysis of the scale structure, in relation to that in other taxa, is needed.

Laterosensory system

The laterosensory canal system (Fig. 5, llc) was studied in specimens V63 (Fig. 8), PB/96/2, 13a (Fig. 7) and AK/76/2 (Fig. 5). It consists of a well-developed canal system carried by a single row of flank scales over the entire body length (*c.* 6–7th scale row ventral to the dorsal margin in front of the pelvic fin). The lateral line can be seen as a prominent rounded ridge that underlies the dermal manifestation of the canal. The lateral-line scales (see Fig. 7) consist of an enlarged posterior aperture situated on the posterior scale margin. A number of slit-like canal pores were observed in the mid-flank region in specimen PB/96/2. Sensory line pits were observed on the suboperculum and the operculum?

PHYLOGENETIC POSITION OF *BLOURUGIA* GEN. NOV.

Phylogenetic analyses of the study taxon was carried out using cladistic methods, on the basis that most recent comprehensive lower actinopterygian phylogenies utilize cladistics to analyse interrelationships (Gardiner 1984; Gardiner & Schaeffer 1989; Coates 1999; Poplin & Lund 2000; Cloutier & Arratia 2004; Gardiner *et al.* 2005)). The comprehensive lower actinopterygian phylogenetic analysis of Gardiner & Schaeffer (1989) (see Bender 2001, fig. 14) was used as a basis for phylogenetic analysis, since their analysis largely utilizes the visual comparison of dermal skull characters, an essential analytical tool within the context of the present study, owing to the lack of well-preserved endoskeletal characters. In addition, the Gardiner & Schaeffer (1989) analysis is probably the most comprehensive phylogenetic basis for examining lower actinopterygian interrelationships, although, as indicated by Cloutier & Arratia (2004), a number of the taxa are based on poorly known characters.

Gardiner & Schaeffer (1989) produced a large-scale cladistic analysis of primitive actinopterygians, expanding the cladistic phylogenetic study of the lower actinopterygians to include approximately 60 of the best known genera. The Gardiner & Schaeffer (1989) cladogram III (Bender 2001, fig. 14) shows the following: Nodes A–G are represented by relatively primitive lower actinopterygians with separate intertemporal and supratemporal bones and include the genera *Cheirolepis, Polypterus, Mimia, Moythomasia, Kentuckia, Pteronisculus, Boreosomus* groups and *Palaeoniscus.* Node H is characterized by the presence of a dermopterotic and essentially separates primitive lower actinopterygians from more advanced forms including the stem-neopterygians. However, Node H is also a polytomy apparent in Gardiner & Schaeffer's (1989) Cladogram I (referred to by them as the 'H polytomy'), providing a resolution of the 'H polytomy' by carrying out a PAUP analysis, resulting in Cladogram III. Cladogram III thus incorporates the data for the 'H polytomy', and presents evidence for two divergent transformation series related to the H Node. One leads to the *Bobasatrania–Dorypterus* groups (which includes Lower Beaufort Group taxon *Kompasia*), and the other to the Neopterygian Groups. According to Gardiner & Schaeffer, both transformation series are rooted to the *Watsonichthys–Amblypterus* complex. The stem-group neopterygians are defined by Gardiner & Schaeffer based on a single character namely, numerous irregular anamestic supraorbital bones between the nasal and the keystone-shaped dermosphenotic. Taxa such as *Mesopoma, Aeduella* and most other Palaeozoic lower actinopterygian taxa, including *Blourugia* gen. nov. and the deep-bodied early actinopterans such as *Platysomus,* are excluded from the neopterygian group and appear as plesion stem-lineage actinopterans (*sensu* Patterson 1982). However, more recently the comprehensive phylogenetic analysis of Coates (1999) indicated that the stem-neopterygians diverged earlier than indicated by Gardiner & Schaeffer (1989), and on that basis *Blourugia* could be termed a stem-neopterygian.

Blourugia seeleyi shares the following Gardiner & Schaeffer (1989) cladogram III characters (Bender 2001, fig. 14: the following nodal characters are derived from Table 1 of the original article), which are typical of basal actinopterygians: Node A characters: 2. Dermohyal covering head of the hyomandibular which notches the dermosphenotic. 3. Dermal bones with buried layers of ganoine. 4. Shield-shaped rostral with ethmoid commissure. 6. Dermosphenotic in contact with nasal bone. 8. One or two pairs of extrascapulars. 9. Two infraorbitals including a lacrymal and jugal, and no postorbital. 18. Tail with hinge line (caudal inversion). 19. Basal fulcra bordering upper lobe of caudal fin. 20. Rhomboidal scales with anterodorsal angle plus peg and socket articulation.

At least one character at each of Nodes B, C, D, E, H, I, K, L and M is shared by *Blourugia*: Node B Acrodin crown on all teeth and separated from the collar enamel of the tooth shaft. Node C. Fringing fulcra on leading rays of all fins. Node D. Supra-angular on mandible. Node E. The presence of suborbital bones. Node H. Dermopterotic present and overlaps or abuts dermosphenotic. Node I. Reduction in number of branchiostegal rays below primitive 12–13. Dermopterotic normally never overlaps more than one-third of dermosphenotic. Node K. Suspensorium more or less vertical. Preopercular reduced and sickle-shaped. Node L. Snout blunt and rounded. Node M. Body deep and laterally compressed; flank scales deepened.

Blourugia seeleyi shares no further characters at any subsequent nodes and is therefore rooted at Node M, and is thus contained in the *Bobasatrania–Dorypterus* transformation series of the Gardiner & Schaeffer (1989) cladogram III (Bender 2001, fig. 14), which is a side-branch separate from the main chondrostean–neopterygian lineage. Accordingly, *Blourugia* and all taxa situated on the above-mentioned side branch are derived relative to stem-actinopterygians such as *Cheirolepis,* and stem-actinopterans such as *Howqualepis, Mimia* and *Moytho-*

masia, but basal to stem-neopterygian taxa such as *Australosomus, Birgeria, Palaeoniscum* and *Perleidus.*

Bender (2001, 2002) suggested that a revision was required of the original Gardiner & Schaeffer (1989) cladogram III, in particular revision of all the nodes contained on the *Bobasatrania–Dorypterus* side-branch, including the *Platysomus* Group node (Bender 2001, fig. 15). Recently significant new cladistic analyses of lower actinopterygians have included taxa on the *Bobasatrania–Dorypteryus* side branch (Cloutier & Arratia 2004; Gardiner *et al.* 2005), although no Carboniferous or Permian deep-bodied taxa have been incorporated. For this reason these analyses have not been utilized within the framework of the present study. Node M is unchanged from the original Gardiner & Schaeffer node M, which gave rise to the *Platysomus* Group terminal group (M1). The *Platysomus* Group contains members of two families originally assigned to the Platysomoidei, namely the Platysomidae and the Amphicentridae (Gardiner & Schaeffer 1989). The amphicentrids consist of forms with a crushing dentition of broad toothplates, and the platysomids of forms with more conventional, pointed, marginal teeth. The nodal characters are as follows (as for the original node M): marginal teeth peg-like or absent; crushing toothplates present; two sets of radials in median fins; long basal radials fewer in number than distal radials; body deep and laterally compressed, flank scales deepened. Terminal node M1 may be characterized by the same set of characters used to define the *Platysomus* Group: maxilla approaches a right-angle triangle with curved corners; premaxillo-antorbital enlarged and elongated dorsally; mandible deep posteriorly, tapering markedly toward the premaxillo-antorbital. The following taxa are rooted at node M: *Adroichthys, Amphicentrum, Cheirodopsis, Paramesolepis, Platysomus, Plectrolepis, Proteurynotus.*

Poplin & Veran (1996) and Lund & Poplin (1997), in discussion of the interrelationships of various lower actinopterygian taxa, utilized a system of listing and ranking characters in terms of their basal, derived or more specialized nature, in order to clarify the primitive and/or derived nature of the characters that typify specific taxa. Similarly, the character states of the study taxon are documented below using this type of system to assist in defining the primitive/derived morphological nature of the study species. The study taxon shares primitive actinopterygian characters such as fringing fulcra, rhomboidal scales a with peg-and-socket articulation and anterodorsal angle, and shares the stem-neopterygian presence of a dermopterotic, and suborbitals.

The *Blourugia* characters can be summarized as follows:

- *Blourugia seeleyi stem-actinopteran characters*: elongate body lobe of the tail; large pelvic fin.
- *Blourugia seeleyi stem-neopterygian characters*: dermopterotic present; less than 12–13 branchiostegal rays; suborbitals present; subopercular taller than opercular; preopercular upright and sickle-shaped; maxilla postorbital blade reduced.
- *Blourugia seeleyi specialized characters*: elongate pectoral fin jointed throughout.

What these study taxon character sets show is that *Blourugia* displays more stem-neopterygian than stem-actinopteran characters. On the basis of the earlier, more traditionally based lower actinopterygian studies of Gardiner (1967) and Schaeffer (1973), *Blourugia seeleyi* appears to be related to members of a group of mostly Carboniferous forms that are close to 'the central stem group of palaeoniscid evolution' (Gardiner 1967), and Schaeffer's (1973) unspecialized 'core' of Devonian–Permian lower actinopterygians.

SUMMARY AND CONCLUSIONS

A new genus and species of deep-bodied early actinopterygian is described from the Late Permian lower Beaufort Group of South Africa. *Blourugia seeleyi* is part of a Beaufort Group, Late Permian (Tatarian) high-latitude, freshwater ichthyofauna which consists essentially of extinct lower actinopterygian taxa. Phylogenetic analysis is based on a comprehensive phylogenetic study conducted by Gardiner & Schaeffer (1989), revised by Bender (2001, fig. 15) which reveals that *Blourugia,* as a deep-bodied lower actinopterygian form belongs to Gardiner & Schaeffer's (1989) Platysomus Group. On the basis of its marginal dentition and no crushing toothplates, *Blourugia* is more closely allied to *Platysomus* and similarly dentitioned deep-bodied taxa; and basal to the stem-neopterygians such as *Australosomus, Palaeonisum* and *Perleidus.* The platysomid-like deep-bodied lower actinopterygians form a speciose group, including Permo-Carboniferous taxa from Australia, China, England, Europe, North America, Russia, Scotland and South Africa. *B. seeleyi* has a deep body and deepened flank scales, marginal dentition and no crushing toothplates and thus is contained within the *Platysomus* Group, and can be more closely allied to the 'platysomid-like' taxa such as *Platysomus* on the basis of its marginal dentition and absence of crushing toothplates, but basal to more advanced lower actinopterygian deep-bodied forms such as *Bobasatrania, Ebenaqua* and *Dorypterus,* in which the maxilla is free from the cheek bones.

It is a privilege to participate in this volume honouring the late James Kitching who was indeed a constant source of inspiration. Thanks are due to the referees for their time, commitment and invaluable input, and to the journal editors for all their efforts; as this article was part of a Ph.D. study, I would like to thank project supervisors Bruce Rubidge and John Long for their invaluable support and advice over a number of years. I would also like to thank Mike Coates and the late James Kitching for their invaluable comments and advice: James Kitching forever willing to share his considerable knowledge of the Karoo and its fossil treasures, Mike Coates for providing essential fish-morphology guidance to me throughout the duration of the Ph.D. study. Thanks to my employers, the Council for Geoscience, including the directors and other colleagues, for their support; appreciation is also expressed to colleagues at the BPI Palaeontology, Wits University, for their support and assistance. Thanks also to Lionel de la Harpe at Wilgerbosch, and JP and Hester Steynberg at Ganora, for their hospitality, help and enthusiasm; Geoscience Museum Artist Anke Raath, and artists Marinda Smith and Mike Tobias, for providing the diagrams; and last but not least Bernice McLean for invaluable field assistance.

ABBREVIATIONS

ada	anterodorsal angle
anal f	anal fin
ang	angular bone

ant	antorbital bone
apl	anterior pit-line groove
art	articular bone
as	anal scale
b	bony layer
bf	basal fulcra
br	branchiostegal rays
caud.f	caudal fin
cdbf	caudal fin dorsal basal fulcra
clav	clavicle bone
cl	cleithrum
cor	coronoid
cvbf	caudal fin basal fulcra
dbf	dorsal fin basal fulcra
den	dentary bone
df	depressed field
dhy	dermohyal bone
dors.f	dorsal fin
dpl	dermopalatine
dpt	dermopterotic bone
dsph	dermosphenotic
dsph.pl	dermosphenotic sensory pits and pit-line grooves
dt	dentine layer
ent	entopterygoid
exsc	extrascapular bone
fr	frontal bone
frf	fringing fulcra
g	ganoine layer
ioc	infraorbital sensory-line canal
ju	jugal bone
ks	keel scalela – lachrymal
l.gu	lateral gular bone
llc	lateral-line canal
ll.pl	pit-line for main lateral-line
mc	mandibular sensory-line canal
mx	maxilla bone
na	nasal bone
n.exc	excurrent or posterior naris
n.inc	incurrent or anterior naris
op	opercular bone
op.pl	opercular sensory pits and pit-line grooves
p	peg
pa	parietal bone
par	prearticular
pcl	postcleithrum
pect.f	pectoral fin
pelvic f	pelvic fin
pmx	premaxilla bone
pop	preopercular bone
popc	preopercular sensory canal
pop.pl	preopercular sensory pits and pit-line grooves
pt	post-temporal bone
ro	rostral bone
rs	ridge scale
scl	supracleithrum bone
sob	suborbital bone
ssoc	supraorbital sensory-line canal
sop	subopercular bone
sop.pl	subopercular sensory pits and pit-line grooves

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On the stratigraphic range of the dicynodont taxon *Emydops* (Therapsida: Anomodontia) in the Karoo Basin, South Africa

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The dicynodont specimen SAM-PK-708 has been referred to the genera *Pristerodon* and *Emydops* by various authors, and was used to argue that the first appearance of *Emydops* was in the *Tapinocephalus* Assemblage Zone in the Karoo Basin of South Africa. However, the specimen never has been described in detail, and most discussions of its taxonomic affinities were based on limited data. Here we redescribe the specimen and compare it to several small dicynodont taxa from the *Tapinocephalus* and *Pristerognathus* assemblage zones. Although the specimen is poorly preserved, it possesses a unique combination of features that allows it to be assigned confidently to *Emydops.* The locality data associated with SAM-PK-708 are vague, but they allow the provenance of the specimen to be narrowed down to a relatively limited area southwest of the town of Beaufort West. Strata from the upper *Tapinocephalus* Assemblage Zone and the *Pristerognathus* Assemblage Zone crop out in this area, but we cannot state with certainty from which of these biostratigraphic divisions the specimen was collected. Nevertheless, SAM-PK-708 is an important datum because it demonstrates that the stratigraphic range of *Emydops* must be extended below its widely-accepted first appearance in the *Tropidostoma* Assemblage Zone. This range extension is significant because it implies that the divergence between the emydopid and dicynodontid lineages must have occurred no later than *Pristerognathus* Assemblage Zone times, and that most of the major lineages of Permian dicynodonts had emerged by a relatively early point in the history of the group.

Keywords: *Emydops,* Karoo Basin, biostratigraphy, *Pristerognathus* Assemblage Zone, *Tapinocephalus* Assemblage Zone.

INTRODUCTION

The Emydopidae (*sensu* Angielczyk & Kurkin 2003) is a clade of dicynodont therapsids known from the Late Permian to Middle Triassic of South Africa (e.g. King 1988), India (Kutty 1972; Ray 2001), Tanzania (von Huene 1939, 1940, 1942; Cox 1972), Zambia (Drysdall & Kitching 1962; 1963; Kitching 1963), and Antarctica (Cosgriff & Hammer 1979; Hammer & Cosgriff 1981; DeFauw 1989). Although they never achieved the taxonomic diversity of their sister taxon, the dicynodontids, emydopid dicynodonts are noteworthy because some members of the group show diverse and very distinctive modifications of the skull and postcranial skeleton. For example, *Cistecephalus, Cistecephaloides,* and *Kawingasaurus* are highly specialized for a fossorial mode of life (Cox 1972; Cluver 1974, 1978), whereas *Kingoria* shows some of the strongest adaptations for an upright hind limb posture of all dicynodonts (Cox 1959; King 1985; DeFauw 1986). The emydopids also are survivors of the end-Permian mass extinction, with two separate lineages, *Myosaurus* and *Kombuisia,* occurring in the Early and Middle Triassic (Fröbisch and Reisz 2004). Finally, they have played a role in Late Permian terrestrial biostratigraphy for nearly a century (e.g. Broom 1906; Watson, 1914; Kitching 1977; Rubidge 1995).

The most extensively studied emydopid fossil record is found in the Karoo Basin of South Africa. Most recent biostratigraphic studies of the Karoo have suggested that the stratigraphic range of the clade begins with the first appearance of *Emydops minor* in the Late Permian-aged *Tropidostoma* Assemblage Zone or its equivalents (e.g. Kitching 1977; Keyser & Smith 1977–1978; Rubidge 1995), and emydopid-bearing strata outside the Karoo generally have been regarded as coeval with or younger than the *Tropidostoma* Assemblage Zone (e.g. Drysdall & Kitching 1963; Anderson & Cruickshank 1978; Smith & Keyser 1995a,b; Gay & Cruickshank 1999; Ray 2001; Angielczyk 2002a). This pattern of stratigraphic occurrence is somewhat surprising because recent phylogenetic studies (e.g. Angielczyk 2001; Angielczyk & Kurkin 2003) suggest that the lineage including the emydopids and dicynodontids must have diverged by *Tapinocephalus* Assemblage Zone times (Fig. 1). If the phylogenetic hypothesis is accurate, then the apparent absence of stem members of the lineage, or emydopids and dicynodontids themselves, in strata older than the *Tropidostoma* Assemblage Zone in the Karoo implies that the earliest history of these lineages either has been overlooked in the South African fossil record or occurred in a different geographical region.

Here we discuss a single dicynodont specimen, SAM-PK-708, that fills in at least part of the ghost range of the lineage including the dicynodontids and emydopids. SAM-PK-708 is a poorly preserved skull and jaw that Robert Broom described as the holotype of *Opisthoctenodon brachyops* in 1905. Since that time the specimen has been referred to the dicynodont taxa *Pristerodon* and *Emydops* on various occasions (Broom 1915, 1932; Kitching 1977; Cluver & King 1983; King 1988; Keyser 1993; King & Rubidge 1993; Angielczyk & Kurkin 2003), but none of these authors provided a detailed justification for their

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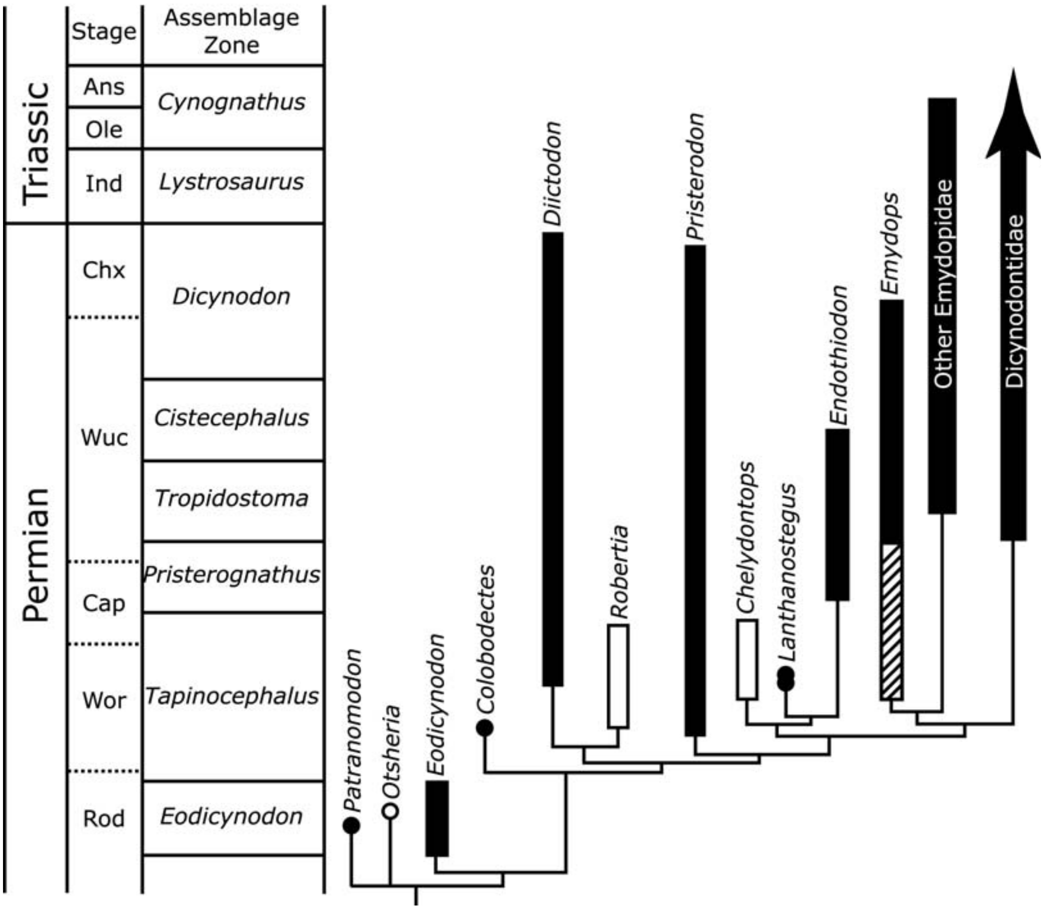

Figure 1. Cladogram drawn to show stratigraphic ranges of *Emydops* and other dicynodonts from the *Tapinocephalus* and *Pristerognathus* assemblage zones. The solid bar for *Emydops* represents its currently-accepted stratigraphic range, whereas the hatched box represents an estimate of the maximum ghost range of the taxon. SAM-PK-708 partially fills this gap, although it is uncertain whether the specimen originated in the *Tapinocephalus* or *Pristerognathus* zones. Topology modified from Modesto *et al.* (2002, 2003) and Angielczyk & Kurkin (2003). Biostratigraphic divisions are based on Rubidge (1995), and ranges of taxa are taken primarily from Rubidge (1995). Correlations of Permian assemblage zones with marine stages are approximate. The stratigraphic occurrences of taxa known from single specimens are represented by dots, whereas ranges of taxa known from multiple specimens are shown by boxes. *Lanthanostegus* is known from two specimens. Ranges for taxa represented by open symbols are poorly constrained.

attributions. We demonstrate that SAM-PK-708 possesses a combination of several features that is found in *Emydops* and no other coeval small dicynodont. Moreover, although the locality data associated with the specimen are vague, it is clear that SAM-PK-708 must have been collected in strata of either the *Tapinocephalus* Assemblage Zone or *Pristerognathus* Assemblage Zone. This finding pushes back the range of the emydopids, and the age of their divergence from the dicynodontids, to at least the *Pristerognathus* zone (Fig. 1). However, we cannot state with certainty that *Emydops* was present in the *Tapinocephalus* Assemblage Zone (contra King 1990; King & Rubidge 1993).

TAXONOMIC HISTORY OF SAM-PK-708

SAM-PK-708 was obtained by Robert Broom from J.R. Joubert on an unknown date. A handwritten note in the accession catalogue of the South African Museum states that Joubert may have collected the specimen in 1881. The locality data, available from subsequent publications and the collections catalogue, are relatively vague and contradictory, and will be discussed in more detail below. In his original description, Broom (1905) made the specimen the holotype of the new species *brachyops,* which he placed in *Opisthoctenodon,* a genus he had only recently erected (Broom 1904). Besides the genotype, *Opisthoctenodon agilis* (AM 4319), SAM-PK-708 is the only specimen that has ever been assigned to this genus. Later, in 1915 Robert Broom re-identified AM 4319 as well as SAM-PK-708 as *Pristerodon.* He based his interpretation on the presence of a number of characters but especially noted the posteriorly serrated 'molars,' which he considered a unique and diagnostic feature of this genus. However, with respect to SAM-PK-708 he stated: 'As the crowns of the molars are unknown it is impossible to be certain that it belongs to *Pristerodon,* but it agrees sufficiently to admit of its being placed here, at least provisionally' (Broom 1915, 358). Several authors (Broom 1932; Haughton & Brink 1954; Kitching 1977; Brink & Keyser 1985) followed Broom's identification of the specimen, but all failed to deliver a detailed diagnosis.

In contrast to the previous authors, Cluver & King (1983) identified SAM-PK-708 as *Emydops,* although they also did not justify their attribution. Moreover, they figured the right lower jaw of the specimen in dorsal and lateral views to show the presence of a short, shallow groove known as the posterior dentary sulcus, a feature that is present in both *Pristerodon* as well as in *Emydops.*

In 1988 King also mentioned SAM-PK-708 in the *Encyclopedia of Paleoherpetology* volume covering the Anomodontia. She referred to the specimen as *Emydops* sp. without ascribing it to any of the eleven recognized *Emydops* species. It is unclear why King (1988) did not use the combination *Emydops brachyops,* but it may be related to the lack of a recent species-level taxonomic revision for the genus at that time.

This situation changed in 1993 when Keyser presented his comprehensive but controversial re-evaluation of what he called the 'smaller Endothiodontidae'. This first and so far only species-level taxonomic revision of emydopids also discussed the two species of the genus *Opisthoctenodon,* called *Pristerodon agilis* and *Pristerodon brachyops* in the paper. Keyser declared the genotype, *P. agilis,* a *nomen dubium,* instead of a synonym of *Pristerodon mackayi,* whereas he regarded the type specimen of *P. brachyops* to be 'an ordinary *Pristerodon*' (Keyser 1993, 24). This statement implies that in his opinion *P. brachyops* (Broom, 1905) is synonymous with *P. mackayi* Huxley, 1868, the only valid species of *Pristerodon.*

In the same year, King & Rubidge (1993) revised the paraphyletic assemblage of small dicynodonts with postcanine teeth at the genus-level and presented generic diagnoses for the taxa they considered valid, i.e. *Pristerodon, Emydops, Eodicynodon,* and *Robertia.* Following Cluver & King (1983) they identified SAM-PK-708 as *Emydops,* but they did not discuss its specific validity. Most recently, Angielczyk & Kurkin (2003) adopted Keyser's (1993) taxonomic identification of SAM-PK-708 as a junior synonym of *Pristerodon mackayi,* but without having personally examined the specimen.

Because of the complex taxonomic history and potential biostratigraphic significance of SAM-PK-708, as well as the fact that most discussions of the specimen have been based on assertions instead of data, we deem it necessary to re-evaluate it in more detail.

COMPARATIVE DESCRIPTION OF SAM-PK-708

SAM-PK-708 consists of a skull and jaw preserved in a single nodule that is broken into four large pieces and a number of smaller fragments. Many of the exposed bone surfaces on the dorsal, anterior and lateral sides of the specimen appear to be weathered, suggesting that they were exposed for some time before the specimen was collected. Because SAM-PK-708 is poorly preserved, we have not endeavored to provide a full description of its morphology. Instead, we focus on documenting features that allow its diagnosis as an *Emydops* specimen, as well as describing similarities and differences between it and other small dicynodonts from the *Tapinocephalus* and *Pristerognathus* assemblage zones.

SAM-PK-708 has a snout–occipital condyle length of approximately 61.2 mm, which is slightly larger than most *Emydops* specimens, but within the known size range of this taxon (e.g. AMNH 5525 = 36.2 mm, BP/1/2366 = 60.0 mm, BP/1/262 = 61.4 mm, SAM-PK-3721 = 47.4 mm, SAM-PK-10148 = 53.0 mm, SAM-PK-10170 = 52.0 mm, SAM-PK-K1671 = 36.1 mm; SAM-PK-K6623 = 52.4 mm). It also is similar to *Pristerodon* (e.g. BP/1/2642 = 67.9 mm, BP/1/2134 = 75.2 mm, BSP 1934-VIII-24 = 77.5 mm, SAM-PK-10153 = 62.6 mm, SAM-PK-K1658 = 55.9 mm), but smaller than is typical for *Brachyprosopus* (FMNH 1561 >107 mm), *Chelydontops* (e.g. SAM-PK-12259 = 128.3 mm), *Colobodectes* (NM QR3329 = 103.3 mm), *Diictodon* (e.g. BMNH R11184 = 95.4 mm, SAM-PK-2354 = 73.1 mm, SAM-PK-10086 = 89.1 mm, SAM-PK-K1242 = 103.2 mm, SAM-PK-K5105 = 91.2 mm), *Robertia broomiana* (e.g. SAM-PK-11461 = 75.0 mm, SAM-PK-11761 = 99.0 mm, SAM-PK-K7807 = 94.1 mm, NMNH 23342 = 103.3 mm), and *Robertia* sp. (e.g. BP/1/1779 = 102.3 mm, NM QR 3145 = 116.5 mm, NMNH 23345 = 113.2 mm). *Lanthanostegus* and *Endothiodon* attain much larger sizes.

The dorsal surface of SAM-PK-708 has been heavily weathered (Fig. 2a), and large portions of the dorsal surface of the snout, interorbital region, and intertemporal region are missing as a consequence. However, it is clear that the intertemporal region of the skull was relatively wide, and the parietals were widely exposed between the postorbitals. A large opening approximately midway along the length of the preserved skull roof likely represents the pineal foramen, whose size has been exaggerated by weathering. A preparietal appears to be present anterior to the pineal foramen, but cracking of the bone in this region of the skull roof makes its exact sutures difficult to trace. The mid-parietal suture can be traced posterior to the pineal foramen, and it meets the suture between the parietals and the postparietal (or interparietal) at the posterior edge of the skull roof. None of the preserved features of the skull roof are exclusive to *Emydops.* However, the fact that the postparietal does not contribute to the dorsal surface of the skull roof argues against the referral of this specimen to *Pristerodon,* a taxon in which the postparietal does contribute to the dorsal surface of the skull roof. The wide exposure of the parietals on the dorsal surface of the skull also is unlike the condition found in *Diictodon,* where the postorbitals nearly completely overlap the parietals.

Little of the occipital surface of the skull is visible when the four main pieces of the nodule are reassembled (Fig. 2d). If the posteriormost piece of the nodule is removed, a transverse section through the occipital plate is exposed (Fig. 2e). Although this does not represent the original external surface of the occiput, some of its characteristics can be inferred. The right side of the occipital plate is damaged so that the lateral profile of the occiput is only preserved on the left side of the skull. The foramen magnum is a large, oval opening that is located to the right of centre on the preserved occipital surface. It is flanked on either side by the posttemporal fenestrae. The left jugular foramen is visible ventrolateral to the foramen magnum. The surface of the bone has undergone extensive cracking, making the sutures between most of the occipital bones difficult to trace. However, the sutures between the opisthotic and the squamosal, and the supraoccipital and the squamosal are visible on the left side. The most diagnostic feature of the occiput is its distinctively squared-off lateral profile (visible only on the left side of the specimen), a morphology that is characteristic of *Emydops* (Fig. 3). Although this morphology can be found

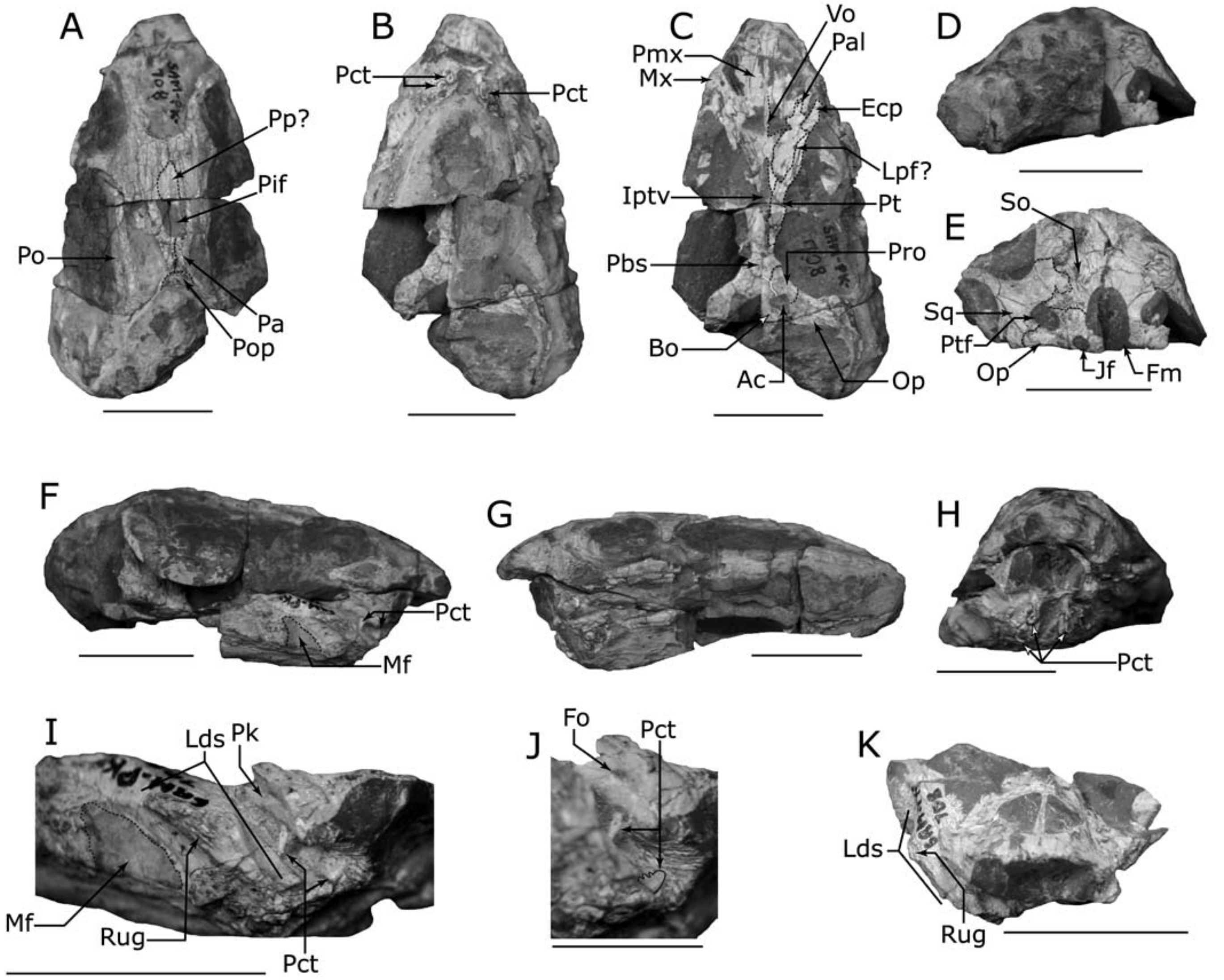

Figure 2. SAM-PK-708. **A**, Dorsal view. **B**, Ventral view, with outer pieces of nodule in place. **C**, Ventral view with outer pieces of nodule removed, exposing coronal section through palate. **D**, Posterior view with outer piece of nodule in place. **E**, Posterior view with outer piece of nodule removed, exposing transverse section through occipital plate. **F**, Right lateral view. **G**, Left lateral view. **H**, Anterior view. **I**, Oblique right lateral view of lower piece of nodule. **J**, Closeup of postcaniniform keel area in I, showing presence of foramen on postcaniniform keel. **K**, Anterodorsal view of the lower piece of nodule, showing dorsal profile of lateral dentary shelf. Scale bar in each panel is 20 mm, except in J, where it is 10 mm. Sutures shown in C and E are as preserved on the specimen, and are not necessarily representative of original sutures that were present on the exterior surfaces of the palate or occipital plate. Note posterior serrations on lower postcanine tooth in I and J.

in some post-*Pristerognathus* zone taxa (e.g. *Myosaurus*), it is not present in any other *Tapinocephalus* or *Pristerognathus* zone dicynodonts (Fig. 3).

Most of the ventral surface of the skull is obscured when the main pieces of the nodule are reassembled, although weathered portions of the postcanine teeth and secondary palate are exposed anteriorly (Fig. 2b). When the two large bottom pieces of the nodule are removed, a section through the ventral surface of the skull is exposed (Fig. 2c). The morphology presented here is typical of dicynodonts. Anteriorly, the secondary palate is formed dominantly by the premaxilla. Its lateral margins are made up by the maxillae, and the palatines and vomer contact it posteriorly. The midventral vomerine plate extends through the middle of the internal nares, and contributions of the palatines and vomer to the dorsal roof of the choanal region also are visible. Ectopterygoids are present lateral to the palatines, and the remains of the lateral palatal foramen may be visible on the left side of the specimen. A relatively large interpterygoid vacuity is present. As is typical in dicynodonts, it is bounded anteriorly by the vomer and laterally and posteriorly by the pterygoids. The remains of the crista oesophagea are present on the median pterygoid plate, and it appears that the crista originally was relatively tall. The anterior pterygoid rami are not well preserved, but appear to have been relatively straight. Posteriorly, the parabasisphenoid is visible between the posterior edge of the median pterygoid plate and the anterior edge of the basioccipital. Contacts between the basioccipital, prootic, and opisthotics, and between the parabasiphenoid and the prootics also are visible. A section through the auditory canal can be seen on both sides of the skull, but is better preserved on the left side of the specimen. Although *Emydops* is characterized by several features of the ventral surface of the skull (e.g. absence of anterior ridges on the

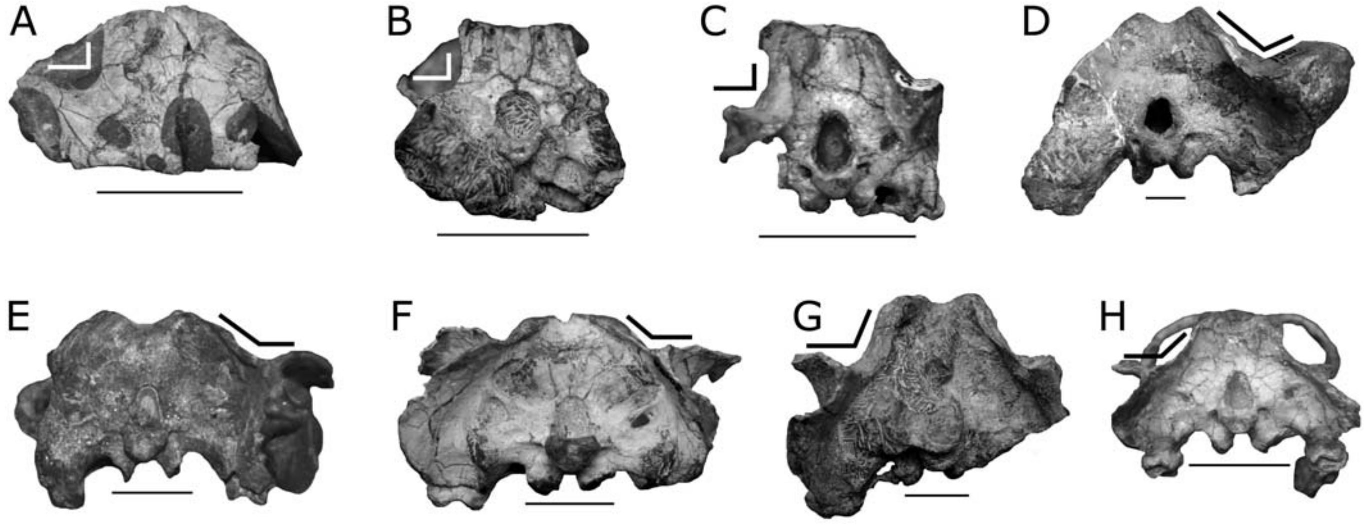

Figure 3. Occipital views of various *Tapinocephalus* and *Pristerognathus* Assemblage Zone dicynodonts for comparison with SAM-PK-708. **A**, SAM-PK-708. **B**, SAM-PK-3721; *Emydops.* **C**, SAM-PK-11060; *Emydops.* **D**, FMNH 1561; *Brachyprosopus.* **E**, SAM-PK-11761; *Robertia.* **F**, SAM-PK-K5105; *Diictodon.* **G**, SAM-PK-11558; *Chelydontops.* **H**, SAM-PK-10153; *Pristerodon.* Compare the distinctively squared-off profile of the occiput in SAM-PK-708 and the two *Emydops* specimens to the more obtuse profile in the other taxa. The occiput of *Colobodectes* is not shown because its lateral margins are highly damaged. Scale bar in each panel is 20 mm.

secondary palate, presence of posterior median ridge on secondary palate, embayment of palatal rim anterior to the caniniform process, square palatal portions of the palatine that are relatively smooth and bear fine vascular foramina), none are preserved or readily visible in the exposed section through the palate of SAM-PK-708.

Anteriorly, much of the snout and all of the dentary symphysis are missing. Thus, the most prominent feature of SAM-PK-708 in anterior view is a large, matrix-filled space representing a transverse section through the buccal cavity (Fig. 2a,h). Sections of the dentary rami also are visible, and weathered sections of several postcanine teeth are present on medial swellings of the dentaries. This postcanine location is typical for most small, toothed dicynodonts of the *Tapinocephalus* and *Pristerognathus* Assemblage Zones. The snout is too damaged to determine whether a nasal boss was present.

Laterally, the left side of SAM-PK-708 is more completely preserved than the right one, but the right side of the specimen retains more diagnostic features. Portions of the snout, suborbital bar, caniniform process, jaw, postorbital bar, and zygomatic arch are present on the left side of the specimen, although they are generally not well preserved or prepared (Fig. 2g). The only potentially diagnostic features preserved on this side of the skull are the presence of a postcaniniform keel and the fact that the caniniform process is at approximately the same level as the anterior margin of the orbit. Both features are characteristic of *Emydops,* but the latter also is found in other *Tapinocephalus* and *Pristerognathus* zone taxa such as *Diictodon* and *Robertia.* The former feature is not present in any of the well-characterized *Tapinocephalus* or *Pristerognathus* zone dicynodonts, although it does occur in several post-*Pristerognathus* zone taxa (e.g. *Cistecephalus, Kingoria, Myosaurus*).

Portions of the snout, suborbital bar, caniniform process, and jaw are visible on the right side of SAM-PK-708 (Fig. 2f). Although the anterior portion of the right caniniform process is damaged, its posterior surface is better preserved than on the left side of the specimen. The postcaniniform keel is particularly pristine, and a single postcanine tooth is present slightly less than halfway along its length. The tooth is well preserved, conical, and appears to lack serrations. Teeth of similar size and morphology can be found along the postcaniniform keel of other *Emydops* specimens (e.g. SAM-PK-11060; Fig. 4c), whereas the upper postcanine teeth of taxa such as *Robertia* or *Pristerodon* tend to be located more medially on the secondary palate.

Just lateral to the postcaniniform keel, a well-developed, round, matrix-filled foramen is present close to the junction of the keel with the ectopterygoid and anterior pterygoid ramus (Figs 2j & 4a). This feature has not been widely reported in descriptions of *Emydops,* although Broom (1905) does refer to it in his original description of SAM-PK-708, calling it a 'depression.' Our personal observations suggest that it is diagnostic for *Emydops* because it is consistently present in specimens in which this region of the skull is preserved and exposed [although the region in question is highly damaged on both sides of the holotype skull of *Emydops* (AMNH 5525)]. A comparable foramen is not found in *Diictodon, Robertia, Pristerodon, Chelydontops, Colobodectes* or *Brachyprosopus* (Fig. 4). A similarly-positioned foramen often is present in *Oudenodon* and *Rhachiocephalus* (e.g. Keyser 1975, p. 24, fig. 18; Maisch 1999), but SAM-PK-708 clearly is not referable to either of these exclusively post-*Pristerognathus* zone taxa. Moreover, we do not consider this foramen to be a potential homologue of the labial fossa or the labial fossa-like features discussed by Cluver (1971), Angielczyk (2001), and Angielczyk & Kurkin (2003) for two reasons. First, the foramen is completely surrounded by the maxilla, instead of a combination of the jugal, palatine, maxilla, pterygoid, and ectopterygoid. Second, the foramen is located farther anteroventrally than is the case for the labial fossa.

Part of the dentary also is well preserved and exposed on

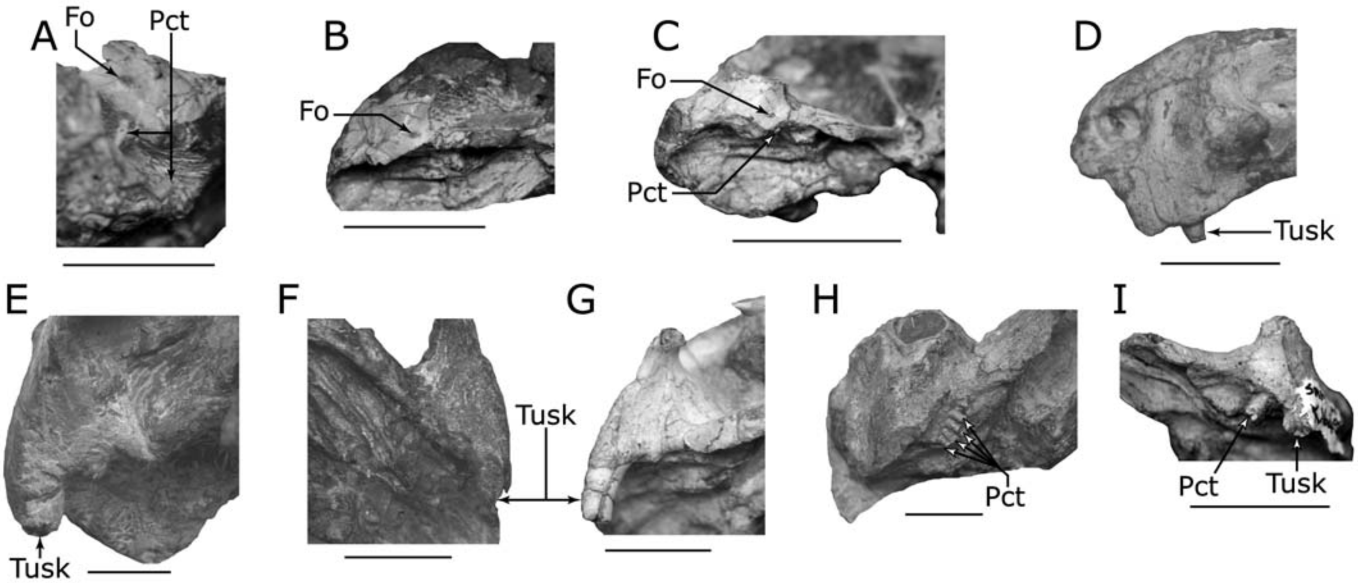

Figure 4. Views of the caniniform process area of various *Tapinocephalus* and *Pristerognathus* Assemblage Zone dicynodonts for comparison with SAM-PK-708. **A**, Right ventrolateral view of SAM-PK-708. **B**, Left ventrolateral view of SAM-PK-6623; *Emydops.* **C**, Left ventrolateral view of SAM-PK-11060; *Emydops.* **D**, Left lateral view of NM QR3329; *Colobodectes.* **E**, Left ventrolateral view of FMNH 1561; *Brachyprosopus.* **F**, Right ventrolateral view of SAM-PK-11761; *Robertia.* **G**, Left ventrolateral view of SAM-PK-K5105; *Diictodon.* **H**, Left ventrolateral view of SAM-PK-11558; *Chelydontops.* **I**, Right ventrolateral view of SAM-PK-K1645; *Pristerodon.* Note that a foramen is present on the posterior surface of the caniniform process in SAM-PK-708 and the two *Emydops* specimens, but in no other taxa. Scale bar in A is 10 mm; in all other panels it is 20 mm.

the right side of the skull (Fig. 2f,i,k). Anteriorly, one postcanine tooth is preserved on a medial swelling of the dentary. It is blade-shaped, larger than the upper postcanine exposed on the right side of the skull, and bears prominent posterior serrations (Fig. 2j). This lower tooth morphology is very similar to that found in several toothed dicynodonts, including *Robertia broomiana, Pristerodon,* and *Endothiodon.* However, it is difficult to determine whether it is also typical for *Emydops* because very few *Emydops* specimens have their lower teeth preserved or exposed. We have personally studied only two *Emydops* specimens with informative lower teeth, SAM-PK-10172 and TM 242 (the holotype of *Emydops minimus*). The lower teeth of SAM-PK-10172 are peg-shaped, whereas those of TM 242 are slightly more blade-shaped. Serrations are not visible in either specimen, but this could be an artifact of incomplete preparation in TM 242. Given these observations, it appears that the lower tooth morphology of *Emydops* was variable. However, the available sample of informative specimens currently is too small to determine whether this variation is of taxonomic or phylogenetic significance.

A shallow posterior dentary sulcus is present lateral to the lower postcanine, and it appears that in life the upper postcanine would have occluded with this sulcus. The lateral wall of the posterior dentary sulcus is slightly taller than the medial wall.

A prominent lateral dentary shelf is present on the lateral surface of the jaw. It begins at the level of the posterodorsal corner of the mandibular fenestra and rapidly expands laterally as it courses anteriorly (Figs 2i,k & 5a). The widest point of the shelf is at the level of the anteroventral corner of the mandibular fenestra, and here its lateral surface bears a prominent rugosity (Fig. 2i,k) that likely represents a muscle scar (presumably for part of the insertion of *M. adductor madibulae externis lateralis*; e.g. Crompton & Hotton 1967; Barghusen 1976; King *et al.*, 1989; Angielczyk 2004). Anterior to its widest point, the shelf narrows and slopes anteroventrally. A weak depression is present on its dorsal surface in this region, and is bounded medially by the lateral wall of the posterior dentary sulcus and laterally by the slightly raised lateral edge of the shelf itself. Little else can be said about the morphology of the jaw because its anterior, posterior, and ventral portions are not preserved on either side of the specimen.

The area of the mandible preserved on the right side of SAM-PK-708 perhaps is the most diagnostic part of the specimen because its morphology is nearly identical to that of the jaws of well-preserved *Emydops* specimens such as SAM-PK-3721 and SAM-PK-6623 (Fig. 5b,c). SAM-PK-6623 has postcanine teeth that are located on a medial swelling, and a shallow posterior dentary sulcus is present lateral to the postcanines (this area is not exposed in SAM-PK-3721). The lateral wall of the sulcus is taller than the medial wall. Both specimens also possess a strong lateral dentary shelf that begins at the level of the posterodorsal corner of the mandibular fenestra and rapidly expands anteriorly. A lateral rugosity is present at the widest point of the shelf in these specimens, and the shelf narrows anteriorly from there. A shallow depression is present on the dorsal surface of the anterior region of the shelf in SAM-PK-6623, but this feature appears to be more weakly developed in SAM-PK-3721.

Moreover, this morphology is different than that of any of the other well-characterized small dicynodonts of the *Tapinocephalus* and *Pristerognathus* Assemblage Zones for which jaws are known (jaw material is not preserved for *Colobodectes* and *Brachyprosopus*). For example, *Diictodon* and *Robertia* lack posterior dentary sulci and have

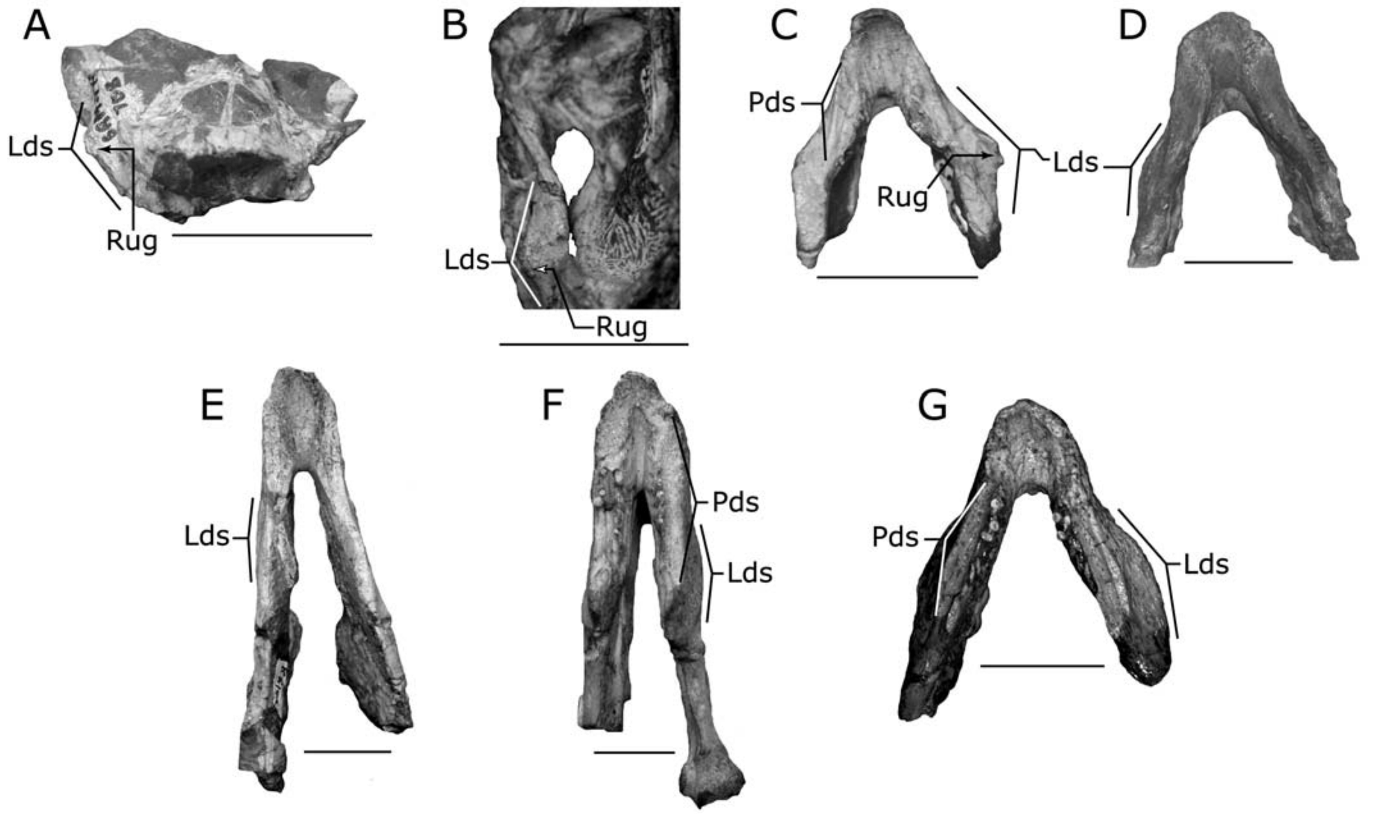

Figure 5. Dorsal views of the jaws of various *Tapinocephalus* and *Pristerognathus* Assemblage Zone dicynodonts for comparison with SAM-PK-708. **A**, Anterodorsal view of the lower piece of nodule of SAM-PK-708, showing dorsal view of right lateral dentary shelf. **B**, Dorsal view of the right jaw ramus of SAM-PK-3721, showing right lateral dentary shelf; *Emydops.* **C**, Dorsal view of SAM-PK-6623; *Emydops.* **D**, SAM-PK-K7807; *Robertia.* **E**, Dorsal view of SAM-PK-K5105; *Diictodon.* **F**, Dorsal View of SAM-PK-12259; *Chelydontops.* **G**, Dorsal view of CGP FL102; *Pristerodon.* Note that SAM-PK-708 and the *Emydops* specimens are the only specimens in which the lateral dentary shelf is strongly developed with a prominent rugosity on its lateral edge. Scale bar in each panel is 20 mm.

much less prominent lateral dentary shelves (Fig. 5d,e). *Chelydontops* does possess a posterior dentary sulcus, but it is more strongly developed in this taxon than in *Emydops* (Fig. 5f). It also lacks a prominent lateral dentary shelf (Fig. 5f). *Pristerodon* has a posterior dentary sulcus and a prominent lateral dentary shelf, but the morphology of these features is different that that of *Emydops* (Fig. 5g). The posterior dentary sulcus in *Pristerodon* is longer and deeper than that of *Emydops,* and bears a closer resemblance to that of *Chelydontops.* Although well developed, the lateral dentary shelf of *Pristerodon* tends to be of a more constant width along its length, instead of narrowing rapidly anteriorly and posteriorly as in *Emydops.* It also lacks the lateral rugosity at its widest point and the shallow depression on its anteriormost dorsal surface. Finally, it is noteworthy that Cluver and King considered the jaw of SAM-PK-708 to be sufficiently typical of *Emydops* to use a drawing of the specimen to illustrate the jaw morphology of this taxon (1983, p. 250, fig. 33a,b).

STRATIGRAPHIC OCCURRENCE OF SAM-PK-708

Broom presents conflicting information about the provenance of SAM-PK-708 in his published accounts of the specimen. In the 1905 paper in which the specimen was first described as the holotype of *Opisthoctenodon brachyops,* Broom states that it likely came from an uncertain locality in the Beaufort West District. However, in 1915 he did not mention a geographic locality for the specimen, but speculated that it likely originated in *Cistecephalus* zone strata. He provided no information about its geographic or stratigraphic occurrence in *The Mammal-like Reptiles of South Africa and the Origin of Mammals* (1932).

A potential clue to the origin of SAM-PK-708 exists in the accession catalogue of the South African Museum. A handwritten note there states that the specimen was collected in the Gough, in the magisterial district of Beaufort West. The Gough (a.k.a., the Koup or the Gouph) is a Khoisan word coined by the early settlers to refer to the expansive, flat, semi-arid scrublands of the Great Karoo. Today the area is fairly accurately delimited by the 'Great Nama Karoo' vegetation type. The southern boundary of the Gough is defined by the East–West trending Groot Swartberge mountains of the Cape Fold Belt; the northern and western margins are clearly defined by the escarpments of the Nuweveldberge and Komsberge mountain ranges. The eastern boundary of the Gough is not defined by any topographic feature; it is based on changes in vegetation at the transition into the 'Eastern Nama Karoo' vegetation zone. Within the collection database and the palaeontological literature of Karoo fossils in South Africa, the term has not been used for any localities east of Beaufort West.

The Gough region contains outcrops of Beaufort Group rocks of the Abrahamskraal and the lower Teekloof forma-

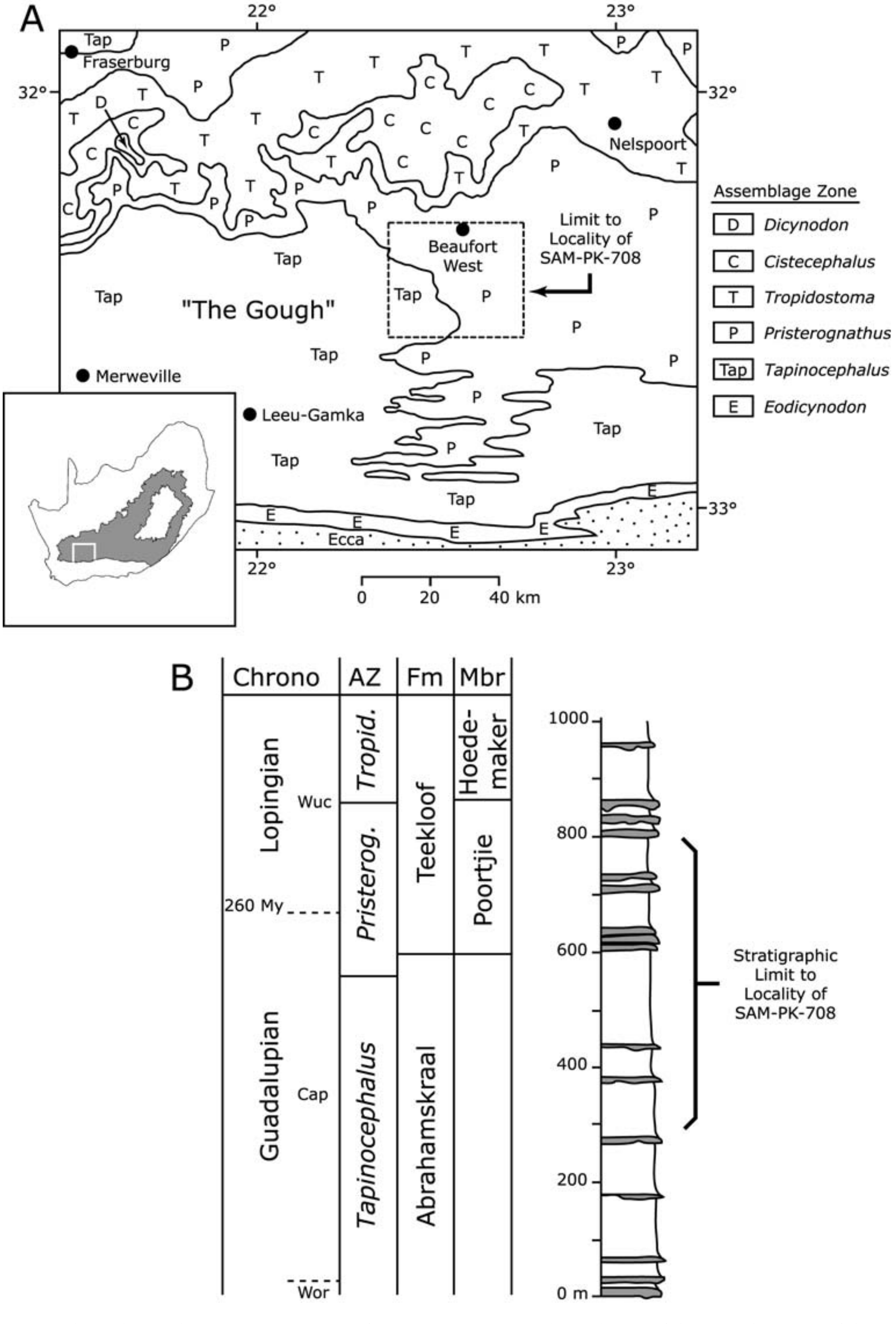

Figure 6. Map and stratigraphic column showing provenance of SAM-PK-708. **A**, Geological map of the Gough region of the Karoo Basin, showing the geographic area from which SAM-PK-708 was collected. Inset map shows the approximate outcrop area of Beaufort Group Strata in South Africa, and the area covered in the geologic map. **B**, Stratigraphic column showing the chronostratigraphy, biostratigraphy, and lithostratigraphy of the Gough region. The portion of the section from which SAM-PK-708 was collected is highlighted.

tions. Kitching (1977) noted that this 'locality' represented a relatively large geographic area, but suggested that most of the material that had been collected there (including the holotype of *O. brachyops*) originated in strata in his *Tapinocephalus* Zone. Since that time the biostratigraphic subdivision of these rocks has been modified, and strata cropping out in the region have been assigned to the *Eodicynodon*, *Tapinocephalus*, and *Pristerognathus* Assemblage Zones (Rubidge 1995). If the data recorded in the accession catalogue are correct, and the specimen SAM-PK-708 was collected in the Gough in the magisterial district of Beaufort West, we can limit its provenance to an area extending some 40 km south of Beaufort West (Fig. 6). It is therefore possible to confine SAM-PK-708 to a 500 m thick stratigraphic interval that spans the top of the *Tapinocephalus* Assemblage Zone and most of the *Pristerognathus* Assemblage Zone. Based on these data we can state that *Emydops*, and by extension the emydopid lineage, appeared in the Karoo no later than *Pristerognathus* Assemblage Zone times, but we cannot rule out the possibility that the first appearance of *Emydops* occurred late in *Tapinocephalus* Assemblage Zone times.

DISCUSSION

Comparison with published diagnoses of *Emydops*

Because SAM-PK-708 is poorly preserved, we have attempted to use several detailed comparisons between it and better preserved specimens of *Emydops* and other small *Tapinocephalus* Assemblage Zone and *Pristerognathus* Assemblage Zone dicynodonts to confirm its identity as an *Emydops* specimen. However, the specimen also compares favourably with published diagnoses of *Emydops* as well.

Nearly all of the species of *Emydops* were described by Broom or Toerien, although the species *Emydops arctatus* (Owen, 1876) is a notable exception. Neither Broom, who erected the taxon *Emydops,* nor Toerien provided a modern-style definition of the taxon. Broom's 'species descriptions' essentially are brief descriptions of individual specimens, but it appears that he considered a broad intertemporal region with wide exposure of the parietals, small size, and the presence of unserrated postcanine teeth to be characteristic of all *Emydops* species (see e.g. Broom 1912, 1913, 1921, 1932, 1935, 1936; Broom & Haughton 1917). Toerien (1953) considered individual variation more thoroughly than Broom, and questioned whether the lack of serration and number of postcanine teeth could be used to effectively distinguish *Emydops* from other taxa. Instead, he suggested that relatively large palatines that contact the premaxilla and the presence of upper postcanines along the alveolar margin were characteristic of the taxon. It also appears that he considered a broad intertemporal region and relatively large postfrontals typical of *Emydops,* if not completely diagnostic.

Several revised diagnoses of *Emydops* have appeared more recently in the literature (e.g. Cluver & King 1983; King 1988; Keyser 1993; King & Rubidge 1993; Ray 2001). Although these diagnoses do not agree on all points, they do share several common features. For example, all of these authors include small size, the presence of a wide intertemporal region with widely exposed parietals, and prominent lateral dentary shelves. Most also incorporate a jaw symphysis that is drawn into a sharp cutting edge, the presence of a shallow posterior dentary sulcus, the presence of an embayment on the medial surface of the palatal rim, relatively straight anterior pterygoid rami, a crista oesophagea that does not extend onto the anterior pterygoid rami, and the presence of a small number of irregularly-placed postcanine teeth.

Although some of these features are not preserved or exposed in SAM-PK-708, many are present, including a wide intertemporal region with wide exposure of the parietals, a prominent, triangular lateral dentary shelf, a shallow posterior dentary sulcus, relatively straight anterior pterygoid rami, the apparently small number of upper and lower postcanine teeth, and the presence of upper postcanines on the postcaniniform keel. When taken together with the detailed similarities noted in the comparative description, we assert that the generally close correspondence between SAM-PK-708 and the published diagnoses of *Emydops* form a strong argument for the referral of this specimen to the taxon. Even if further investigation should show that SAM-PK-708 is not part of *Emydops,* its referral to the Emydopidae is still relatively certain given that it possesses two of the synapomorphies of that clade recognized by Angielczyk & Kurkin (2003) (presence of a postcaniniform keel, straight contour of the squamosal in posterior view; incompleteness and/or poor exposure prevents the assessment of other synapomorphies for the clade).

We have not considered the specific affinities of SAM-PK-708 in detail. As noted above, this specimen is the holotype of the species *Pristerodon brachyops* (Broom, 1905) [= *Emydops* sp. of King (1988) and King & Rubidge (1993)]. In addition, several other species have been referred to *Emydops,* and King (1988) recognized a total of eleven valid species. Keyser (1993) reviewed these species and considered most of them to be synonyms of *Pristerodon mackayi* Huxley, 1868, including the type species of *Emydops, E. minor* Broom, 1912. He recognized only two valid species, *platyceps* Broom & Haughton, 1917, and the new species *tener* Keyser, 1993, both of which he referred to the new genus *Emydoses.* Although we agree with some of his synonymies (e.g. *E. longiceps* Broom, 1913, likely is a synonym of *P. mackayi*) others seem less certain, and we see no need for the erection of the name *Emydoses* because the holotype of *E. minor* (AMNH 5525) is a poorly preserved *Emydops* specimen (also see Ray 2001; Angielczyk & Kurkin 2003). Also noteworthy is the fact that our observations of the type specimen (BMNH R1690) of the species *arctatus* Owen, 1876, suggest that it belongs to *Emydops,* and is not a synonym of *P. mackayi.* This species is considerably older than any of the other described species of *Emydops,* raising the possibility that it may be a senior synonym of names such as *E. minor.* Given these and other taxonomic issues, we consider it premature to speculate on the specific relationships of SAM-PK-708 until the species of *Emydops* are reconsidered, preferably in a phylogenetic framework. However, the early stratigraphic occurrence of SAM-PK-708 does raise the possibility that it might be part of a species lineage that is distinct from later forms.

Stratigraphic range of *Emydops*

Uncertainty surrounds the stratigraphic range of *Emydops* in the Karoo Basin, with different authors placing the first appearance of the taxon in the *Tapinocephalus* Assemblage Zone (King 1990; King & Rubidge 1993) or the *Tropidostoma* Assemblage Zone (Kitching 1977; Keyser & Smith 1977–1978; Rubidge 1995). Some of this ambiguity stems from the question of whether SAM-PK-708 actually is an *Emydops* specimen or not. Although the specimen is poorly preserved, we feel that the question can be answered strongly in the affirmative, eliminating identification as a source of uncertainty.

However, the vagueness of the available locality information for SAM-PK-708 does not allow a complete resolution of the issue. As we have shown, it is possible to narrow down the occurrence of the specimen to a relatively restricted geographic area and stratigraphic interval, but these include strata assigned to both the *Tapinocephalus* and *Pristerognathus* assemblage zones. Thus, although we can state that the first appearance of *Emydops* cannot be younger than *Pristerognathus* Assemblage Zone times, we cannot place a confident lower boundary on the age of the first appearance. Further collecting and/or identification of known locality *Emydops* specimens in museum collections will be needed to determine whether the first appearance of this taxon in South Africa is in the *Tapinocephalus* zone or in the *Pristerognathus* zone. Given that more *Pristerognathus* zone strata crop out in the area from which SAM-PK-708 likely was collected (Fig. 6), it may be most conservative to place the first appearance of *Emydops* in the *Pristerognathus* zone for the time being.

Finally, the identification of SAM-PK-708 has implications for studies of dicynodont phylogeny. Several recent analyses have compared the fit of phylogenetic hypotheses to the fossil record (Angielczyk 2001, 2002b; Angielczyk and Kurkin 2003), and all of these works assumed that *Emydops* appeared during the *Tropidostoma* Assemblage Zone. Pushing the first appearance of *Emydops* back into at least the *Pristerognathus* zone may slightly improve the fit of the phylogenetic hypotheses presented in these analyses, and this range extension must be taken into account in future works. At a broader scale, extending the stratigraphic range of *Emydops* implies that the divergence between the emydopid and dicynodontid lineages must have occurred no later than *Pristerognathus* zone times, and possibly as early as late *Tapinocephalus* zone times. This fact is significant because it means that most of the main lineages of Permian dicynodonts had diverged by a relatively early point in the history of the group.

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ABBREVIATIONS

Institutional

AM	Albany Museum, Grahamstown, South Africa
AMNH	American Museum of Natural History, New York City, U.S.A.
BMNH	The Natural History Museum, London, U.K.
BP	Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa
BSP	Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany
CGP	Council for Geoscience, Pretoria, South Africa
FMNH	Field Museum of Natural History, Chicago, U.S.A.
NM	National Museum, Bloemfontein, South Africa
NMNH	National Museum of Natural History (Smithsonian Institution), Washington, D.C., U.S.A.
SAM	South African Museum, Cape Town, South Africa
TM	Transvaal Museum, Pretoria, South Africa.

Anatomical

Ac	auditory canal
Bo	basioccipital
Ecp	ectopterygoid
Fm	foramen magnum
Fo	foramen
Iptv	interpterygoid vacuity
Jf	jugular foramen
Lds	lateral dentary shelf
Lpf?	lateral palatal foramen?
Mf	mandibular fenestra
Mx	maxilla
Op	opisthotic
Pa	parietal
Pal	palatine
Pbs	parabasisphenoid
Pct	postcanine tooth
Pds	posterior dentary sulcus
Pif	pineal foramen
Pk	postcaniniform keel
Pmx	premaxilla
Po	postorbital
Pop	postparietal
Pp?	preparietal?
Pro	prootic
Pt	pterygoid
Ptf	posttemporal foramen
Rug	rugosity
So	supraoccipital
Sq	squamosal
Vo	vomer

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A new specimen of *Dicynodon traquairi* (Newton) (Synapsida: Anomodontia) from the Late Permian (Tartarian) of northern Scotland

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A recently discovered natural mould of a complete, almost undistorted, skull and lower jaw of a dicynodont (*c.* 237 mm overall length), in a block of Upper Permian sandstone (= Dicynodon Assemblage Zone: Hopeman Sandstone Formation) from Clashach Quarry, Hopeman, Morayshire, is described using novel techniques, including Computed Tomography scanning (CT), Magnetic Resonance Imaging (MRI) and rapid-prototype modelling. It is assigned to the taxon *Dicynodon traquairi* (Newton, 1893). When compared with *Dicynodon lacerticeps* Owen, 1845, it is distinguished principally by having the pineal opening sunk deeply between the diverging parietals, subparallel pterygoid rami narrowly separated, with no transverse flanges, and in addition, a deeply grooved lower jaw symphysis. The southern African fauna lived on river flats in a higher (southern) palaeolatitude than the possibly desert-dwelling Scottish species. The Hopeman Sandstone Formation is of the same age as the better-known Cutties Hillock Sandstone Formation, whose fauna is briefly discussed and reviewed.

Keywords: *Dicynodon traquairi,* Late Permian, Hopeman Sandstone Formation, Computed Tomography scanning, Magnetic Resonance Imaging, rapid prototyping.

INTRODUCTION

During the mid- and late 1990s the National Museums of Scotland undertook a major building and upgrade programme of their flagship building in Chambers Street, Edinburgh. Part of the architectural design was a stone-faced façade to the new extensions, which was to be sourced in the Permo-Triassic quarries (including Hopeman) of Morayshire (Anon 2003), in the north of Scotland (Fig. 1a,b) These (especially the Quarry Wood complex of quarries) had yielded a suite of fossils reptiles and trackways of Late Permian age, in the 19th century (Newton 1893; Benton & Spencer 1995), particularly from Cutties Hillock, near Elgin. These fossils occurred as natural moulds in the rock, and yielded at least three dicynodont species and a pareiasaur (Table 1) (Newton 1893; King 1988; Walker 1973, Benton & Spencer 1995). Hopeman Quarry had previously yielded only trackways (Benton & Spencer 1995). Walker (1973) had assumed a Late Permian-Early Triassic age for both Hopeman and the Cutties Hillock sites, based on the supposedly advanced status of the tetrapod faunas of the latter. Currently they are both believed to be Late Permian in age (see below: and King *et al.* (2005) for summary statements).

In 1997, on splitting a large block of sandstone, the workers at Moray Stone Cutters of Clashach Quarry, near Hopeman, Morayshire (National Grid Reference NJ 163702) observed a cavity broaching the broken surface of the block (Fig. 2). The rock at Hopeman is of a lithology and age very similar to the Cutties Hillock locality (Watson & Hickling 1914; Peacock *et al.* 1968; Walker 1973; Benton & Walker 1985) and C.A. Hopkins had instigated a search programme for possible fossil material appearing at Hopeman (Hopkins 1999). Realising the importance of the discovery, the two-part sandstone block was sent to the Hunterian Museum, University of Glasgow. The identity of the mould in the rock was resolved by means of CT (computed tomography) and MRI (magnetic resonance imaging) scanning techniques. Preliminary reports have appeared (Clark 1999; Clark *et al.* 2004; Hopkins1999; Hopkins & Clark 2000), and this is now the first detailed account of the identity of the mouldic fossil. We assign the fossil skull to *Dicynodon traquairi* (Newton, 1893), a form hitherto known only from the Quarry Wood, Cutties Hillock, locality (NGR NJ 160630). *D. traquairi* can be distinguished from the type species (*Dicynodon lacerticeps* (Owen, 1845)) (King 1988) by the lack of any remnant of the transverse flange of the pterygoids, its deeply sheltered pineal opening and the deeply grooved dorsal surface to its lower jaw symphysis (Table 2).

The taxa in the Cutties Hillock Sandstone Formation fauna, originally described as members of a new genus, *Gordonia,* by Newton (1893), and revised by King (1988), comprise *Dicynodon traquairi* (Newton, 1893), *Dicynodon juddiana* (Newton, 1893), *Dicynodon huxleyana* (Newton, 1893), *Dicynodon duffiana* (Newton, 1893) and *Geikia elegans* Newton, 1893 (Rowe 1980; Cruickshank & Keyser 1984; Maisch & Gebauer 2005), and are assigned to the Synapsida (Dicynodontia; King 1988). *Elginia miribalis* Newton, 1893, is an anapsid; a pareiasaur (Benton & Spencer 1995). (Table 1).

One further specimen from Morayshire, a dicynodont, collected by Alick Walker in 1953, from York Tower Quarry, Knock of Alves (GR NJ 162629), is in the National

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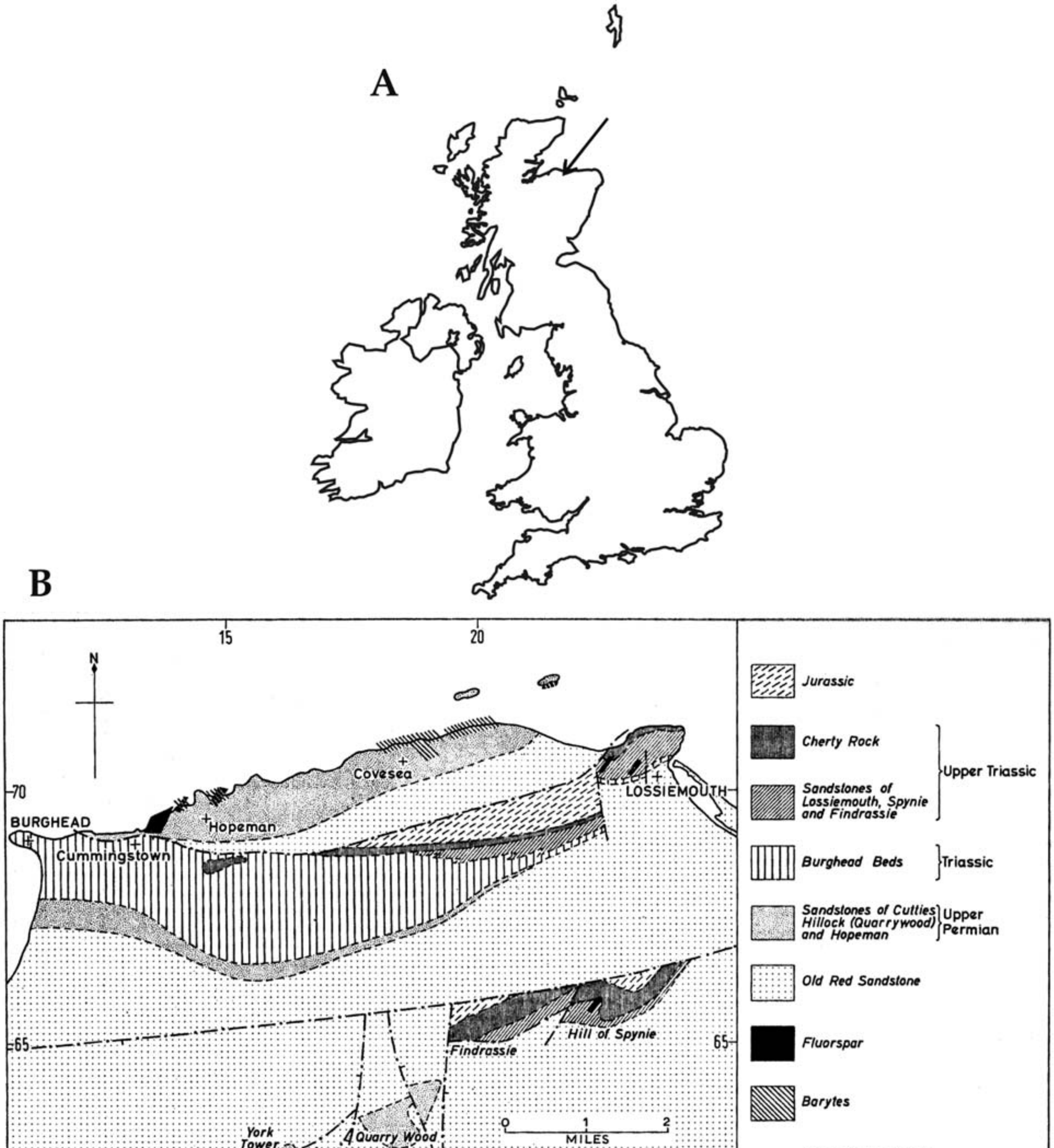

Figure 1. A, Outline map of the British Isles to show location of Hopeman (National Grid Reference NJ 163702). **B**, Geological sketch map of outcrops of the Permo-Triassic rocks in Moray District (Grampian), to show to show positions of Hopeman (Clashach Quarry) and Quarry Wood (Cutties Hillock. Figure 1B modified after Peacock *et al.* (1968).

Museums of Scotland, Edinburgh (NMG G 1984.20.7) (Benton & Spencer 1995).

GEOLOGICAL SETTING

The Hopeman Sandstone Formation has been traditionally assumed to be the broad lateral equivalent of the Upper Permian Cutties Hillock Sandstone Formation (Watson & Hickling 1914; Peacock *et al.* 1968; Benton & Walker 1985), based on the similarity of the trackways found at both localities. Walker (1973) suggested that the Hopeman Sandstone was of earliest Triassic age (= *Lystrosaurus* Assemblage Zone as then understood), based on the presumed equivalence with an assumed Early Triassic age of the Cutties Hillock Sandstone, which in turn was based on the (incorrect) likelihood that the Cutties Hillock fauna was of a later age than the hitherto accepted Late Permian, because of the derived nature of the reptilian fauna. In turn, Cruickshank & Keyser (1984) drew attention to the fact that *Geikia*, a dicynodont and a component of the Cutties Hillock fauna, was a close relative of the South African Upper Permian (*Dicynodon* Assemblage Zone; Groenewald & Kitching 1995) genus *Pelanomodon*, and not

Table 1. List of specimens from Elgin Permian.

Taxon	Number	Specimens	Remarks
Elginia mirabilis	2	GSE 4783–8 ELGNM 1978.550	Newton (1893) Benton & Spencer (1995)
'procolophonid'	1	ELGNM 1978.560 BMNH R4807	Walker (1973) Benton & Spencer (1995)
'Gordonia' traquairi	5	GSE 11703 BMNH R4805–6 ELGNM 1995.5.1 ELGNM 1995.5.2 ELGNM 1999. 22	Newton (1893) Benton & Spencer (1995) This paper skull and humerus
'G'. huxleyana	2	GSE 11704 BMNH R4799-4802	Newton (1893) Benton & Spencer (1995)
'G'. duffiana	1	ELGNM 1978.559	Newton (1893) Benton & Spencer (1995)
'G'. juddiana	1	ELGNM 1890.3	Newton (1893) Benton & Spencer (1995)
'G'. elginensis	1	GSM 90998–901105	Newton (1893) Benton & Spencer (1995)
Specimens indet.	7	BMNH R4794 ELGNM 1935.8 ELGNM 1978.558 ELGNM 1978.886 NMS G 1956.8.3 NMS G 1966.42.1–3 NMS G 1984.20.7	Benton & Spencer (1995) M.A. Taylor & R. Paton, pers. comm., 2004

a lystrosaurid. However, while not being Triassic in age, these two Cutties Hillock reptiles (*Geikia; Elginia*), because of their derived nature, are likely to be of an age later than the *Cistecephalus* Assemblage Zone and with the presence of a member of the genus *Dicynodon,* most probably no later than the *Dicynodon* Assemblage Zone (Groenewald & Kitching 1995). We therefore believe that the Hopeman and the Cutties Hillock Sandstone Formations are the equivalent of the South African (Karoo) *Dicynodon* Assemblage Zone and are of Late Tartarian age (Rubidge 1995).

The Hopeman Sandstone Formation has been variously interpreted as having been deposited under aeolian conditions as part of a substantial transverse dune system (Glennie & Buller 1983; Glennie 2002), or star and crescent dunes (Clemmensen (1987; Anon 2003). There are small areas of fluvial or lacustrine deposits (Peacock *et al.* 1968) and on the foreshore 800 m west of Clashach, an outcrop of thin coarse-grained and pebbly layers, clay clasts and rippled surfaces indicate water-lain horizons (C.A. Hopkins, pers. comm.). Williams (1973) interprets these beds as flash-flood deposits. In the Late Permian, Hopeman was positioned at about 15°N, in the middle of the Pangean supercontinent (King 1992). The South African localities which have yielded the bulk of known dicynodonts, on the other hand, lay at about 60°S palaeolatitude, and this difference, along with differing palaeoenvironments, may well govern their adaptations and, hence, identities (King 1992; Rubidge 1995).

Peacock *et al.* (1968) noted that the first-discovered Elgin reptiles (Newton 1893) occur near the base of the Cutties Hillock Sandstone Formation in a pebbly layer, and that a borehole revealed a layer of pebbles near the base of the Hopeman Formation Sandstone. Discontinuous layers of faceted quartz pebbles are sometimes observed in the base of Clashach Quarry, and stone from the western face also contains occasional scattered pebbles. These pebbles are similar in appearance to the dreikanters from the Cutties Hillock Sandstone Formation, and suggest a comparable horizon.

Clashach Quarry (Hopeman) is composed of sandstone with large-scale cross bedding with foreset dip angles up to 26°, mainly to the SW. The *Dicynodon* skull was found at the extreme top of the western part of the quarry, in a homogeneous block of sandstone with no evidence of internal bedding structures. The fossil was preserved in the form of a mould, and the sediment–cavity interface was heavily stained with dark brown material. The fossils from the Cutties Hillock Sandstone are preserved in the

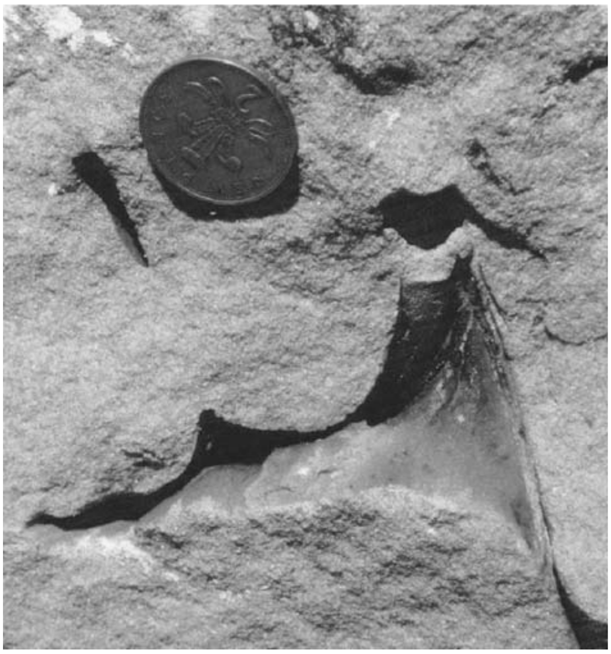

Figure 2. Fractured surface of sandstone block, exposing the mouldic fossil of the new skull of *Dicynodon traquairi* (Newton) (ELGNM 1995.5.1). Coin = 24 mm diameter.

same way, and Newton (1893) noted the presence of a black material coating some cavities, which contains iron, manganese and cobalt.

MATERIALS AND METHODS

Materials

ELGNM 1995.5.1. and ELGNM 1995.5.2. A block of red sandstone from the Hopeman Sandstone Formation, containing a natural mould of a complete skull and lower jaw, from high in the succession at Clashach Quarry (Anon 2003), on the west face (National Grid Reference NJ 163702).

GLAHM 114914. A 'rapid prototype' replica of ELGNM 1995.5.1 & .2. (Clark *et al.* 2004; Figs 3–5 herein).

ELGNM 1999.22. A natural mould of a dicynodont right humerus.

GLAHM 114108. A cast of a natural mould of the humerus associated with the skull.

Methods

The techniques and methodology are described in full in Clark *et al.* (2004), but involve three principal techniques: CT scanning for a preliminary analysis, MRI scanning for a higher resolution image and 'rapid prototyping' to produce a 3-D, solid, model of the space in the rock.

SYSTEMATIC PALAEONTOLOGY

Suborder	**Anomodontia** Owen, 1859
Infraorder	**Dicynodontia** Owen, 1859
Superfamily	**Pristerodontoidea** Cluver & King, 1983
Family	**Dicynodontidae** Cluver & King, 1983
Subfamily	**Dicynodontinae** Owen, 1859
Genus	**Dicynodon** Owen, 1845

Species ***D. traquairi*** Newton, 1893

Locality. Clashach Quarry, Hopeman, Elgin, Morayshire. National Grid Reference NJ 163702

Horizon. Hopeman Sandstone Formation (Upper Level: equivalent of the Tartarian/Dicynodon Assemblage Zone of South Africa (Anon 2003; Rubidge 1995)).

Holotype. 'Newton Specimen Number 1', (GSE 11703). Ascribed to *Gordonia traquairi* Newton, 1893 (Plates 26–28), from Cutties Hillock, Quarry Wood, Elgin, Morayshire. National Grid Reference NJ 160630

Revised diagnosis. A member of the genus *Dicynodon* Owen, 1845 (King 1988), similar in appearance to *Dicynodon lacerticeps* Owen, 1845, with a gracile skull (length-to-width ratio 1.8:1) and the following autapomorphies: anterior palatal rami of the pterygoids horizontal in lateral view, narrowly separated and subparallel, with no evidence of the remains of transverse processes, pineal opening deeply recessed between anteriorly diverging parietals on dorsal surface of skull, and grooved dorsal surface to the lower jaw symphysis.

Table 2. Characters of material described in text.

	Character	Model	CT/MRI
1	Length>100<400	Y	Y
2	Tusks	Y	Y
3	PO covers P	Y	Y
4	SEPT smooth with MX	?	Y
5	SEPT do not meet lacrimal	?	?
6	Low boss over ext. nares	Y	Y
7	Palatal rim sharp, continuous	?	Y
8	Palatal exp. PAL large, flat	?	?
9	PAL short contact with PMX	?	?
10	Very long, narrow	?	Y
11	Ant. border ipt. foss. joins vomerine crest	?	Y
12	Small ECT	?	(Y)
13	ECT displaced laterally	(Y)	Y
14	Labial fossa present	(Y)	Y
15	PT contact with MX short	Y	?
16	BO separated by ridge	Y	Y
17	Fused dentaries with narrow tables	Y	Y
18	Deep dentary sulcus	Y	Y
19	Weak coronoid process	Y	Y
20	Large mandibular fenestra: lateral dentary shelf	Y	Y
21	Occipital surface of OPIS depressed	?	Y

DESCRIPTION OF SPECIMEN

The skull and lower jaw were anatomically complete before fossilization, but have suffered slight distortion post mortem. Information used in creating the reconstruction (Figs 3–5) has been obtained from the CT-scan, MRI and the rapid-prototyping 3-D model. Each provides a unique view of the specimen, and all sources have to be used to obtain a reliable picture of the outline of the skull and its associated lower jaw. Sutures and other bone boundaries are difficult to define, and in spite of the interpretations of Newton (1893), almost impossible to delimit, except in a very few cases, which includes the parietals and postorbital regions of the skull.

The skull is 237 mm long, and 131 mm wide, with a length–width ratio of 1.8:1. The overall appearance of the skull is that of a gracile structure, with delicate postorbitals and zygomatic arches. The lower jaw is significantly shorter than the palatal dimension (155 mm), so that the anterior of the palate is overshot, leaving the tusks standing free and prominent, even when the jaw is in its protracted position (Cox 1998). There are indications of a 'notch' on the midline of the premaxillae, similar to that figured by Newton (1893), and the anterior dorsal surface of the dentary symphysis is deeply grooved, with the possible presence of a midline notch on the anterior face of the symphysis (Figs 3f & 5e).

Low midnasal and supraorbital ridges are present. The parietals are drawn up to a prominent crest, but diverge anteriorly, with the oval pineal sunk between their anterior arms. Little else than this can be seen in dorsal view, though Newton (1893, Plate 28) shows a number of sutures quite clearly, with some having unusual boundaries when compared with conventional material. In dorsal view, the posterior wings of the squamosals obscure their ventral rami and the quadrates, but in this case it may be an artefact of preservation, with the specimen suffering slight asymmetrical dorso-ventral compression (compare Cluver & Hotton 1981; Cluver & King 1983, figs 8 & 23 with Fig. 5a–e herein).

In lateral view the dorsal surface is gently curved (Figs 3c 4c & 5c) and paralleled by the zygomatic arch, which in

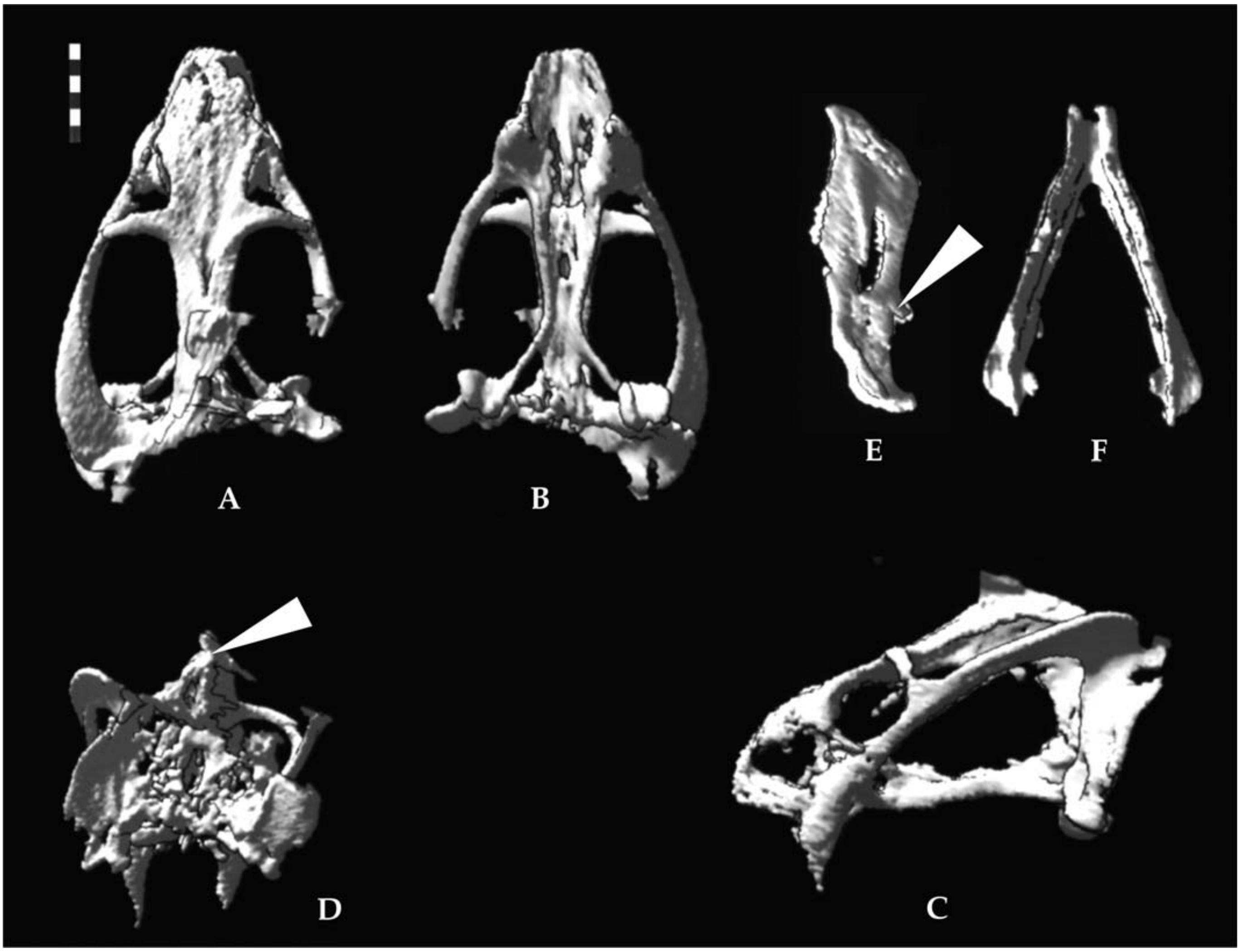

Figure 3. CT scan images of skull of *Dicynodon traquairi* (Newton) (ELGNM 1995.5.1). **A**, Dorsal view. **B**, Palate showing the relatively complete premaxillary surface of the palate. **C**, Right hand side of skull (reversed), note displaced left postorbital and apparent lack of bone in region of external nares. **D**, Occiput, note poor resolution of detail and displaced right postorbital. **E**, Right ramus of the lower jaw, note poor resolution of detail of the reflected lamina (arrowed) of angular. **F**, Dorsal view of lower jaw, note deep groove in the surface of the symphysis (arrowed), and possible notch at the anterior limit of the symphysis. Scale bar = 60 mm.

turn descends more steeply at the level of the orbit, to run into the caniniform process. There is a single pair of tusks. The palatal bars of the pterygoids are straight and on the same level as the rim of the premaxilla. The descending rami of the squamosals lie at almost 90° to the line of the pterygoid bars.

Ventrally, the most important observation is that the anterior rami of the pterygoids are narrowly separated, and do not have any remnants of their transverse flanges (compare Cluver & King 1983, figs 5 & 25 with Fig. 5a,b herein). The interpterygoid vacuity is oval and relatively short but difficult to measure accurately because of lack of precision in the imaging processes. The quadrate rami of the pterygoids diverge widely towards the quadrates. Otherwise the basicranium is very similar to that of *Dicynodon lacerticeps* (Owen), allowing for artefacts of preservation and the different illustrations obtained from these contrasting techniques.

In occipital view there are several areas that are unclear in both MRI and CT scans, and in the model (Figs 3d & 4d), and which has led us to believe that a reconstruction of the occiput would not be informative. Overall it shows no unique characters. The interparietals and the dorsolateral edges of the supraoccipital have marked turned-out rims (Figs 3d & 4d). The quadrate articular surfaces lie slightly below the level of the basioccipital tubera, but both stapes appear to have been lost prior to fossilisation. There are ridges on the surface of the squamosal immediately above the medial condyles of the quadrates for the mandibular depressor muscles (*cf.* Cox 1957, 'tympanic processs').

With the exception of the deeply grooved dorsal surface of the symphysis, the lower jaw is similar to that of *Dicynodon lacerticeps* in most respects, with the lateral shelves on the dentaries lying just above the mandibular fenestrae. The tips of the conjoined dentaries are upturned, with an apparent median notch, which may have matched that proposed for the premaxillae (Fig. 3f) (Newton 1893, plate 28, figs 1 & 2). The reflected laminae of the angulars are apparently broken away (Fig. 3e), but seem to have been close to the main bodies of the jaw rami and did not approach closely to the lateral articular surfaces. The posterior of the dentaries occlude with the palatines and this does not allow the tip of the jaw to fully occlude the anterior surface of the palate (Cox 1998), so

Figure 4. MRI-sourced model of skull *Dicynodon traquairi* (Newton) (ELGNM 1995.5.1). Note the ridged artefact, particularly on the surface of the squamosal, and compare the detail preserved on the dorsal and lateral surfaces of the snout, with those from the CT scan images. **A**, Dorsal view. **B**, Palate, note possible premaxillary notch. **C**, Lateral view. **D**, Occiput. Scale bar = 50 mm.

a substantial thickness of horny bone coverings on the palatal surface is proposed. The presence of dentary sulci (Figs 3e & 5d) give further resemblance to *Dicynodon.*

A single right humerus is preserved in association to the skull as a 2-D, compressed, flattened, shape. Little information can be obtained from it, but the capitellum is larger than the trochlea, and the ventral part of the bone seems to have reasonably complete proportions. However, the proximal portion was damaged post mortem. The delto-pectoral crest is largely broken away and only partially preserves the proximal articulation. Overall length of the humerus, as preserved, is 105 mm, and the distal width is 64 mm.

DISCUSSION

Comparisons of techniques

Of each of the techniques used to illustrate this specimen (Figs 3–5), the CAT-scan images are in many ways the most complete. At the same time they are the least precise. MRI-imaging depends on the use of liquids to penetrate all areas of the fossil, some of which may be so narrow that, unless of great fluidity, the fluids cannot penetrate the finest passages, leaving such areas devoid of any response (Fig. 4a,b). Here the thin-boned areas of the snout, and more particularly the mid-line of the snout roof, have not allowed penetration of the imaging fluid. The 3-D model obtained through the 'rapid prototyping' process shows best the very small degree of distortion suffered by the specimen (Figs 3d & 4d), but cannot improve on the detail preserved. Overall the skull has been obliquely distorted, with the right side being slightly depressed relative to the left. This distortion has caused the postorbitals to be 'lifted' and these are the most clearly outlined bones in the entire skull and lower jaw. Although the best resolution is obtained from the MRI scan, although with even a 2 mm 'slice' interval and a 1 mm overlap, the surface of the imaged bone shows abundant ridging artefacts (Fig. 4a). The completeness of the bone imaged by MRI techniques is also dependent on obtaining optimum 'thresholding' (Clark *et al.* 2004). The optimum thresholding for larger spaces is different to that for narrow spaces, hence a compromise has to be made to produce the best overall image.

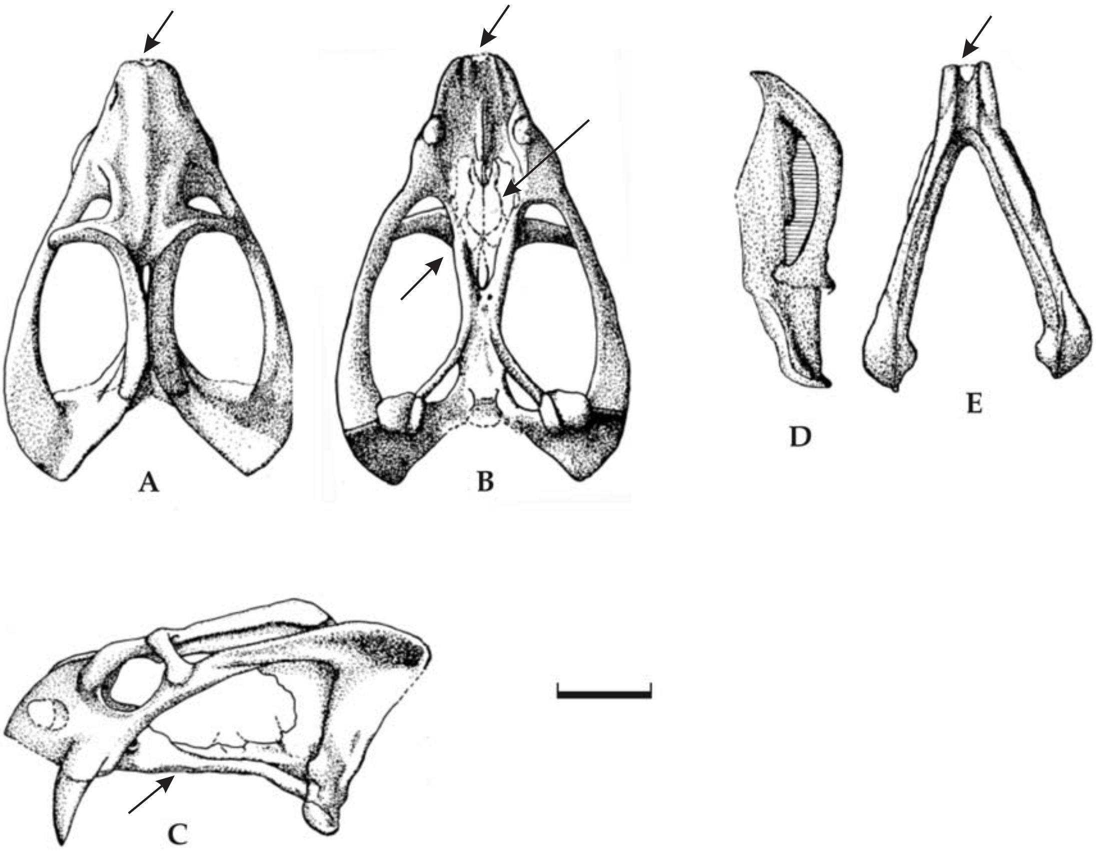

Figure 5. Skull of *Dicynodon traquairi* (Newton) in reconstruction based on information obtained from ELGNM 1995.5.1. **A**, Dorsal view, note possible notch in anterior of premaxillaries (arrowed). **B**, Palate, note possible premaxillary notch, proportions of reconstructed palatines and lack of pterygoid flanges (arrowed). **C**, Left lateral view, note lack of transverse flanges on the pterygoid (arrowed). **D**, Lateral view of lower jaw. **E**, Dorsal view of lower jaw, note deep groove on dorsal surface of symphysis and possible notch on anterior of symphysis (arrowed). Scale bar = 50 mm.

Although the general quality of the CT-scan images is not so good as those obtained from MRI, because the former technique does not rely on penetration of fluid into restricted spaces, an overall more complete surface is seen in the CT-scan images of the snout dorsal surfaces, and the palate (Figs 3a,b & 4a,b). However, definition of the outlines of the skull and lower jaw is not so complete as in the MRI scan. The model, being a direct reproduction of the scanned spaces in the rock, is a 3-D representation of the MRI images, and suffers from the strengths and weaknesses of both the imaging processes and the conversion to the prototyping technique (Clark *et al.* 2004). On the other hand, it is the easiest to handle.

Therefore following on from both scanning techniques, taxonomically important information can be obtained from these and the model (Table 2). The model can be more easily examined, with lighting from different directions, for instance, to show surface detail. From this (using all sources), it is possible to outline the likely limits of the postorbitals, and make possible interpretations of the anterior palatal bones; palatines, ectopterygoids and their relationships with the pterygoid rami. The model is least informative in the occipital region, where 'noise' seems to have obscured much of the detail round the basioccipital tubera, and all but eliminated evidence for presence an intertuberal ridge (Figs 3d & 4d) and the basioccipital condyle. In the region of the external nares, the model shows very little detail of the snout surface (Fig. 4c), although some indication is shown of the possibility of the septomaxillae not being as deeply recessed as in *Dicynodon lacerticeps* (Cluver & King 1983). Examination of the CT-scan and MRI images shows that the narial area is not sunk, and the surface of the snout was smooth (Figs 3c & 4c).

Details of the lower jaw are shown more clearly in the MRI images, compared with both the model and CT-scan images, but in none of the resulting images can any sutures be seen. The reflected laminae of the angulars (Fig. 3e) appear to be broken off and obscured by their closeness to the body of the lower jaw, but do not seem to approach the lateral condyle of the articular at all closely. Their apparent damage may also be the result of being too thin to be resolved by either CT or MRI scanning, in a similar manner to the loss of detail on the snout and palate in the MRI images.

The reconstructions in Fig. 5a–e are a composite of the information obtained from all three techniques. King (1988) lists 21 characters used to define the genus *Dicynodon* (Table 2). From the model, 12 of these characters are seen clearly. Nine are doubtful, or not seen clearly. In combination, from the CT- and MRI-scans, 17 characters agree with King's definition. It is concluded that the specimen in the block of rock is a member of the genus *Dicynodon,* as currently defined. However, closer examination shows that the Hopeman specimen is more gracile than typical members of the genus, and especially of the type species, *D. lacerticeps* (King 1988; Cluver & Hotton 1981; Cluver & King 1983). Other differences are; the deeply recessed pineal opening, the deeply grooved dentary symphysis, and the subparallel and narrowly separated pterygoid rami, leading to reduced contacts between the palatines and the premaxillae. In all of these characters, the Hopeman Sandstone specimen agrees with Newton's original descriptions and figures of *Dicynodon traquairi* (Newton, 1893, plates 26–28).

Scottish Permian amniotes

Dicynodon traquairi (Newton 1893) differs in several notable respects from the types species (*D. lacerticeps*) as recorded here; namely it is more gracile than *D. lacerticeps.* Characters which may be of significance, but which cannot be reliably decided, are the notches postulated for the premaxillae and dentaries (Figs 3f, 4b & 5a,b). The lower jaw cannot occlude the palate in *D. traquairi,* as is also proposed by Cox (1998) for several other dicynodont genera, and this has a bearing on their feeding function and requires that there must have been substantial pads of horn on the palate in order to make an effective bite, which in turn might affect the expression of the notches in palate and snout.

Speculating that the notches on the premaxillae and anterior dentaries were present in life, then the implication is that this species might have possessed a protrusable, prehensile, tongue as proposed by Cruickshank (1978) for the Triassic dicynodont *Dolichuranus*; either to more easily ingest vegetable matter, or to act as a means of apprehending small arthropods. The latter are suggested as a component of the fauna, if only to explain the invertebrate burrows reported previously as 'rainprints' (Brickenden 1859; C.A. Hopkins, pers. comm.).

The other Permian dicynodonts described by Newton (1893) were all subsumed into *D. traquairi* by King (1988) in the latest overall review of the Anomodontia. However, closer examination of Newton's (1893) figures and an opportunity to see casts in the British Geological Survey office in Keyworth, Nottingham, U.K., demonstrated that these synonymies may not all be valid.

For example *D. huxleyana* (GSE 11704) has a flat frontal with a larger pineal than *D. traquairi.* The tusk of the latter seems smaller, but this may be due to the smaller overall size of *D. huxleyana*: 110 mm as opposed to 234 mm for this specimen of *D. traquairi.* These differences therefore may be possibly ontogenetic, or due to sexual dimorphism (*cf Aulacephalodon* Tollman *et al.* 1980: *Diictodon* Sullivan & Reisz 2003).

Dicynodon duffiana (ELGNM 1978.659) has a relatively large pineal, widely separated postorbitals, with substantial exposure of the parietals. It has no mid-nasal ridge and is about 112 mm overall length. It is unlikely that these differences with *D. traquairi* are ontogenetic, and is here regarded as being a separate taxon, until further work can be reported on this taxon. The specimen questionably referred to *D. traquairi* (ELGNM 1978.550) is tuskless and shows ontogenetic differences from *D. traquairi s.s.* It is only 93 mm overall length, and is likely to be referable to one or other of the tuskless families of Dicynodontia (King 1988), but because of its small size, maybe a juvenile. The second *D. huxleyana* (ELGNM 1978.549) is very poorly preserved, but is the same size as the type, and hence possessing a general similarity to it, is likely to be conspecific with it. *D. juddiana* (ELGNM 1890.3) is distorted, has a length of 118 mm and is considered to be another specimen of *D. traquairi.*

Geikia elegans Newton, 1893 is a pelanomodontid (Cruickshank & Keyser 1984) and *Elginia mirabilis* Newton, 1893 a pareiasaur. However, it is timely that these taxa should be revised and the whole fauna reassessed to put it accurately in context with the faunas in Eurasia, China and South Africa.

Sidor *et al.* (2004) suggested that the lack of dicynodonts in a newly recorded Late Permian fauna from the Moradi Formation of northern Niger is due to the desert environment. However, if dicynodont faunas are found in what is now Scotland, and in a desert, then other factors must be found to support their absence in Niger. Notable endemism is seen in both the Scottish fauna and in the other, relatively low latitude faunas of Russia, China and South Africa (Sidor *et al.* 2005), and this may well explain the observed differences.

SUMMARY AND CONCLUSIONS

A recently recovered mouldic specimen of a skull, lower jaw and humerus of one of the species known from Cutties Hillock, near Elgin, Morayshire, *Dicynodon traquairi* (Newton, 1893), is described, using novel techniques. This new specimen is the first from Clashach Quarry, Hopeman, to the north of Elgin. Overall this species of *Dicynodon* is very similar to *D. lacerticeps* (Owen, 1845).

The species *Dicynodon traquairi* is distinct from *D. lacerticeps* (Owen, 1845), in having narrowly separated pterygoids, with no indication of transverse flanges, a pineal sunk deeply between the postorbitals, and a deep groove on the dorsal surface of the lower jaw symphysis. Notches may have been present on the midline of the premaxillae and dentaries.

Of the four described species of *Dicynodon 'traquairi'* from Cutties Hillock, specimens assigned to *D. duffiana* and doubtfully assigned *D. traquairi*, are considered distinct. *D. huxleyi* is possibly a juvenile of *D. traquairi* and *D. juddiana* a distorted adult *D. traquairi. Geikia elginensis* is a pelanomodontid and *Elginia mirabilis* a pareiasaur.

Among the many who have helped progress this project, are particularly grateful to the owners and workers at Clashach Quarry for their enthusiastic support of the work reported here: Drew Baillie for donating the specimens to Elgin Museum, and Bill George, Gavin George and Dave Sim, quarrymen, the discoverers of the skull. Gillian King, Jenny Clack read the draft text, and Dave Norman provided literature and discussion; Michael Taylor and Bobbie Paton confirmed the presence of the York Tower specimen in the National Museums of Scotland, Edinburgh; Mike Howe, Pauline Taylor and Mark Dean at the Geological Survey offices at Keyworth and Edinburgh provided access to comparative material in their care, and checked data relevant to the material. We also acknowledge the help and advice given by Colin MacFadyen and Sue Warbrick of Scottish Natural Heritage, Susan Bennett, lately Director of Elgin Museum (and the curatorial staff of Elgin Museum), Kirsty Ross then of the Western Infirmary, Glasgow, Tristan Lawton, Royal Infirmary, Edinburgh and Debbie Moore of Gartnavel Hospital. The management of The Royal Alexandra Infirmary made available the facilities to carry out the essential scanning procedures that we used. A.R.I.C. is grateful to the Leicester City Museums Service for facilities and to the Department of Geology, University of Leicester for support and encouragement. The original version of this paper was read at the 13th Biannual Symposium of the Palaeontological Society of

Southern Africa, in Johannesburg, July 2004, largely in response to an invitation from Professor Bruce Rubidge. Carol Hopkins of Aberdeen University is thanked for her contributions to an understanding of the co-eval trackways found at Hopeman, and general discussions of the nature of the discovery of the skull, the 'Hole in the Rock'. The final text owes much to Bruce Rubidge (BPI) and John Hancox, of the Geology Department, University of the Witwatersrand and Kenneth Angielczyk. The illustrations were digitially recorded by Richard Forrest.

INSTITUTIONAL ABBREVIATIONS

ELGNM	Elgin Museum, High Street, Elgin, Morayshire, IV30 1EQ Scotland, U.K.
GLAHM	Hunterian Museum, University of Glasgow, University Avenue, Glasgow G12 8QQ, Scotland, U.K.
GSE	British Geological Survey, Murchison House, West Mains Road, Edinburgh EH9 3LA, U.K.
GSM	British Geological Survey, Kingsley Dunham Centre, Keyworth, NG12 5GG, U.K.
NMS	National Museums of Scotland, Chambers Street, Edinburgh EH1 1JF, U.K.

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The taxonomic status of *Parathrinaxodon proops* (Therapsida: Cynodontia), with comments on the morphology of the palate in basal cynodonts

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The holotype and only specimen of *Parathrinaxodon proops,* a cynodont from the Upper Permian Kawinga Formation, Tanzania, is redescribed. Upper postcanines from the middle of the tooth row are ovoid in outline, presenting a large main cusp and tiny anterior and posterior accessory cusps on the sectorial margin. Anterior and posterior lingual cusps on the crown indicate the presence of a lingual cingulum. The overall postcanine morphology is remarkably similar to that of *Procynosuchus delaharpeae,* a Late Permian cynodont particularly common in the lower Beaufort Group of South Africa. The presence of a complete osseous palate and a medial palatal opening between the maxillae (=vomerine fossa) in *Parathrinaxodon proops* remain the main differences previously reported between this species and *Procynosuchus delaharpeae.* Restudy of the palate of *Parathrinaxodon proops* indicates that there exists some degree of deformation, particularly notable in the broken and distorted vomer. The supposed presence of the complete secondary palate and of the medial palatal opening in *Parathrinaxodon proops* are interpreted as resulting from a slight horizontal displacement of the long, and originally free, palatal processes of the maxilla and palatine. It is concluded that *Parathrinaxodon proops* is synonymous with *Procynosuchus delaharpeae.* This synonymy is problematic because *Parathrinaxodon proops* Parrington 1936 would have priority over *Procynosuchus delaharpeae* Broom 1937, but the latter is the best known Late Permian cynodont. Consequently, we propose to conserve *Procynosuchus delaharpeae* as the valid name for this cynodont based on article 23, section 9 (Reversal of precedence) of the International Code of Zoological Nomenclature. An analysis of the Kawinga fauna, using genus as the taxonomic unit for comparison, indicates strong similarity (67%) with faunas from the *Tropidostoma, Cistecephalus* and *Dicynodon* assemblage zones from the South African Karoo.

Keywords: *Parathrinaxodon, Procynosuchus,* Late Permian, Tanzania, cynodonts.

INTRODUCTION

Late Permian cynodonts, besides representing the earliest record of the group, are the phylogenetically most basal members of the Cynodontia, the monophyletic group that includes extant mammals. Ten species of Late Permian cynodonts have been recognized since 1972, the year in which Hopson & Kitching (1972) published their revision of cynodonts, and Mendrez (1972a,b) redescribed and discussed the identity of two South African Late Permian cynodonts. At least six of the 10 Late Permian cynodonts have a disputed taxonomic status (Table 1). Cynodonts of this age are recorded in South Africa (Broom 1938, 1948), Russia (Sushkin 1927; Tatarinov 1968a,b), East Africa (Kemp 1979; Parrington 1936), and, most recently, Germany (Sues & Boy 1988).

In East Africa, basal cynodonts of Late Permian age are known from the Madumabisa Mudstones from the Luangwa Valley in Zambia (Kemp 1979) and the Kawinga Formation (=Usili Formation; Wopfner 2002) of the Ruhuhu Valley, Tanzania (Parrington 1936). The only specimen known from the former rock unit is an almost complete skeleton assigned to *Procynosuchus delaharpeae* Broom by Kemp (1979), and which represents a juvenile individual (Abdala, pers. obs.). Specimens from the Ruhuhu Valley include an incomplete skull described by Parrington (1936) as *Parathrinaxodon proops,* and an incomplete and poorly preserved skull attributed by von Huene (1950) to *Procynosuchus delaharpeae.*

Since its description, the affinities of *Parathrinaxodon*

Table 1. Taxonomy and distribution of Late Permian cynodonts.

Taxon	Country
Cynosaurus suppostus (Owen 1876)	SA
Dvinia prima Amalitzky 1922	R
Cyrbasiodon boycei Broom 1931[a]	SA
Parathrinaxodon proops Parrington 1936	T
Nanictosaurus kitchingi Broom 1936[b]	SA
Procynosuchus delaharpeae Broom 1937	SA, T, Z, G[f]
Protocynodon pricei Broom 1949[c]	SA
Nanocynodon seductus Tatarinov 1968[d]	R
Uralocynodon tverdokhlebovae Tatarinov 1987	R
Cyrbasiodon vladimiriensis Tatarinov 2004[e]	R

[a] Considered a synonym of *Procynosuchus delaharpeae* by Hopson & Kitching (1972), and Battail (1991). Taking into account the poor preservation of the type and only specimen of *Cyrbasiodon boycei,* Hopson & Kitching (1972) retained *P. delaharpeae* as the valid name for the species. Mendrez (1972b) considered *C. boycei* as a valid taxon.

[b] Considered a synonym of *Cynosaurus suppostus* by Hopson & Kitching (1972) and Sidor & Smith (2004), it was regarded as a valid species by Van Heerden & Rubidge (1990). *Nanictosaurus rubidgei* Broom 1940 (regarded as a valid species by Van Heerden 1976) and *Nanictosaurus robustus* Broom 1940 were considered as junior synonyms of *N. kitchingi* by Van Heerden & Rubidge (1990).

[c] Considered a synonym of *Procynosuchus delaharpeae* by Hopson & Kitching (1972) and Battail (1991), it was regarded as a valid species by Mendrez (1972a).

[d] Considered as Galesauridae (at that time including *Thrinaxodon*) by Tatarinov (1968b) and most recently as Thrinaxodontidae by Battail & Surkov (2000). Hopson & Kitching (1972) included it in Procynosuchidae.

[e] *Cyrbasiodon* was considered a synonym of *Procynosuchus* by Hopson & Kitching (1972) and Battail (1991). See 'a' above.

[f] The specimen from Germany was identified as *Procynosuchus* sp. by Sues & Boy (1988).

Abbreviations: G: Germany; R: Russia; SA: South Africa; T: Tanzania; Z: Zambia.

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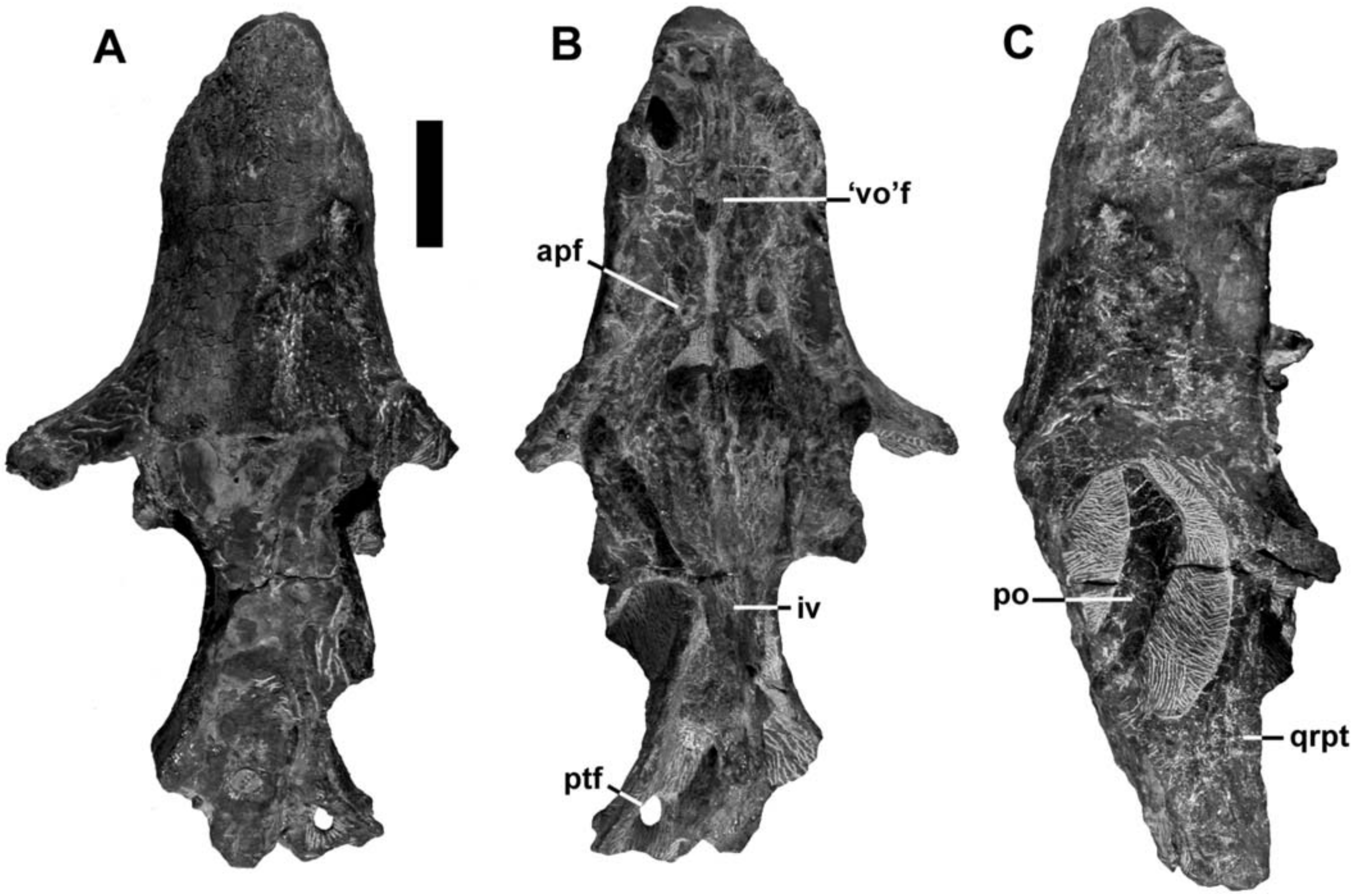

Figure 1. **A**, dorsal, **B**, ventral, and **C**, right lateral views of *Parathrinaxodon proops* holotype, UMZC T.810. Abbreviations: apf, anterior palatal foramen; iv, interpterygoid vacuity; po, displaced portion of the postorbital bar; ptf, pterygoparoccipital foramen; qrpt, quadrate ramus of the pterygoid; 'vo'f: vomerine fossa. Scale bar = 2 cm.

proops have been subject to differing interpretations. Parrington (1936) believed it to be most similar to *Dvinia prima* from the Russian Upper Permian and to *Thrinaxodon liorhinus* from the Lower Triassic of South Africa. Parrington (1936) also suggested that *Cyrbasiodon boycei* was probably related to *Parathrinaxodon proops*. Hopson & Kitching (1972) and Mendrez (1972a,b) included the species in the family Procynosuchidae, whereas Van Heerden (1976) suggested it is a member of the Galesauridae. Battail (1982, 1991) also implied a more derived position for *Parathrinaxodon* than for *Procynosuchus* and *Dvinia,* whereas Hopson (1991; see also Sidor & Smith 2004) considered it indistinguishable from *Procynosuchus.*

Here we present a descriptive update of the holotype and only known specimen of *Parathrinaxodon proops* and discuss its taxonomic identity. We have avoided a complete redescription of the specimen and instead refer the reader to Parrington (1936) for more details. In addition, we propose an explanation for the presence of the 'vomerine fossa' in the palate of Late Permian cynodonts. We also compare the Kawinga fauna with Late Permian faunas from the South African Karoo.

Institutional abbreviations: BMNH, The Natural History Museum, London; BP, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg; OUMNH, Oxford University Museum of Natural History; RC, Rubidge collection, Wellwood, Graaff-Reinet; SAM, Iziko Museums (South African Museum), Cape Town; UMZC, University Museum of Zoology, Cambridge.

MATERIAL

The holotype of *Parathrinaxodon proops* (UMZC T.810) is represented by a partial skull lacking both zygomatic arches, part of the brain case and the lower jaw (Figs 1 & 2). The following comparative materials of *Procynosuchus delaharpeae* were also consulted: BP/1/226, 591, 1545, 1559, 2600, 3758, 5832; OUMNH TSK34; RC 5, 12, 72, 92, 132; SAM-PK-K-338, K8511. Sources of information on the Russian cynodont *Dvinia prima* included Tatarinov (1968b) and casts of the holotype (UMZC T.1016) represented by a snout, and of the complete skull originally assigned to *Permocynodon sushkini* (UMZC T.299; see Tatarinov 1968b).

DESCRIPTION

The basicranial length of UMZC T.810 is estimated to be 130 mm, with a snout length of 53 mm and the palate reaching approximately 45 mm (Table 2). The dorsal bones of the skull are preserved only as far posteriorly as the anterior orbital margin, whereas the skull is almost complete ventrally, lacking only the posterior portion of the basicranium (Figs 1 & 2). Zygomatic arches from both sides are missing. The tips of the dorsal processes of both premaxillae are preserved between the anterior portions of the nasals (Fig. 2A). Additional preparation of the material revealed a displaced portion of the right postorbital bar in

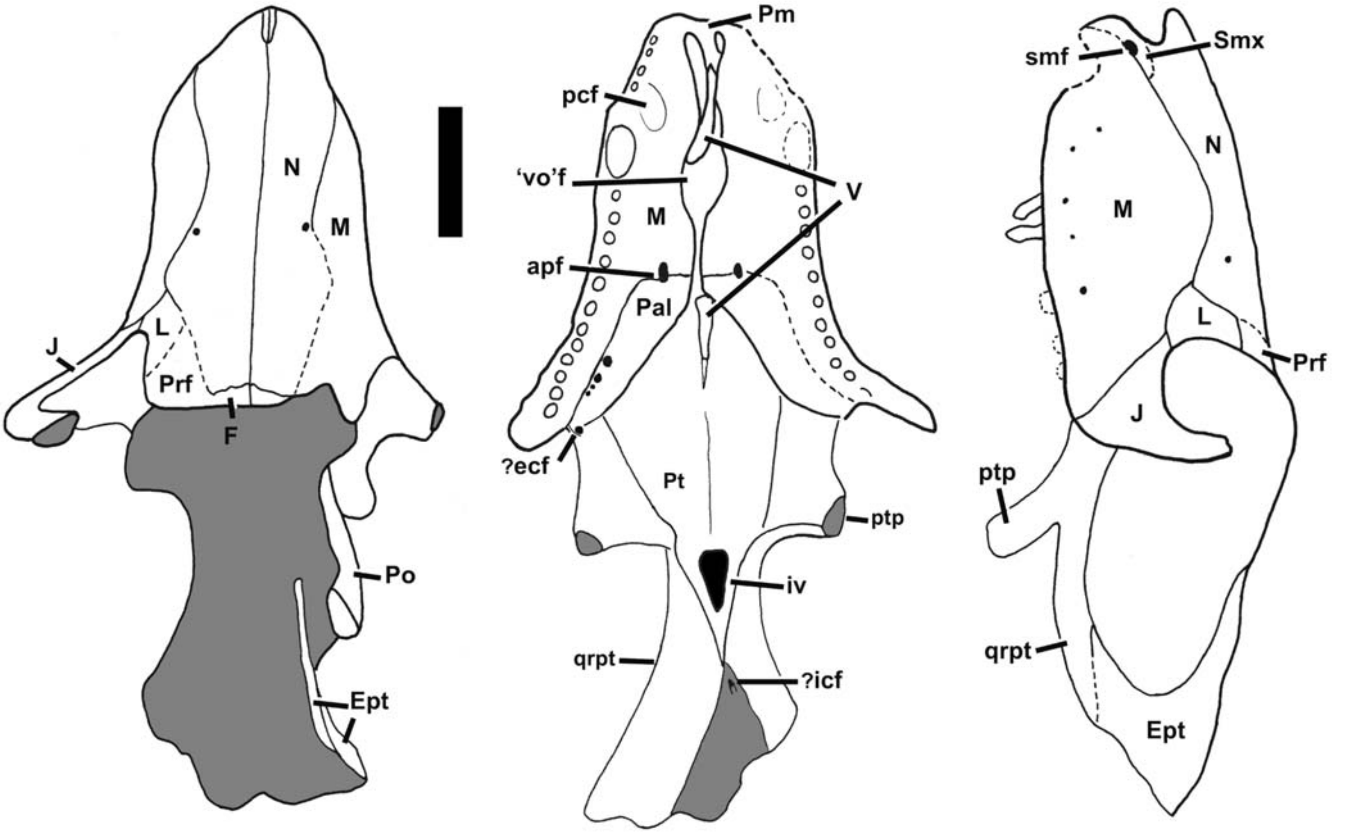

Figure 2. Interpretative drawings of *Parathrinaxodon proops*. **A**, dorsal, **B**, ventral, and **C**, left lateral views. Abbreviations: apf, anterior palatal foramen; ?ecf, ectopterygoid foramen; Ept, epipterygoid; F, frontal; ?icf, internal carotid foramen; iv, interpterygoid vacuity; L, lacrimal; M, maxilla; N, nasal; Pal, palatine, pcf, paracanine fossa; Pm, premaxilla; Prf, prefrontal; Po, displaced portion of the postorbital bar; Pt, pterygoid; ptf, pterygoparoccipital foramen; ptf, pterygoid process; qrpt, quadrate ramus of the pterygoid; smf, septomaxillary foramen; Smx, septomaxilla; V, vomer; 'vo'f: vomerine fossa. Shading indicates broken bone surface; dashed lines indicate broken bone and interpreted sutures. Scale 2 cm.

the middle of the interorbital region (Figs 1C & 2A).

In the anterior portion of the palate, the vomer is broken and somewhat displaced (Figs 2B & 3A). It is not possible to recognize sutures between the premaxilla and the maxilla. A median fossa between the maxillae is observed from the level of the anterior border of the canine, which extends to the level of the third postcanine and appears limited posteriorly by the palatal processes of the maxillae (Figs 2B & 3A). The palatal processes of the maxillae and palatines are very close to, but not in contact with, their counterparts. Well developed anterior palatal foramina indicate the location of the suture between the maxilla and the palatine. The latter bone has very short palatal projections, whose anterior portions lie close to each other, whereas the posterior portions are widely separated, forming part of the ventral margin of the choana (Figs 1B, 2B & 3A). There is a series of foramina in the palatal process of the palatine, close to the suture with the maxilla (Fig. 2B). Similar foramina are also seen in *Procynosuchus* (Kemp 1979: fig. 2; RC 5). A foramen at the base of the transverse process of the pterygoid is interpreted as an ectopterygoid foramen, but sutural margins of the ectopterygoid are not discernible.

Table 2. Skull and snout lengths (in mm), percentage of the snout in relation to the basal skull length and number of upper postcanines in the larger specimens of *Procynosuchus delaharpeae* and in *Parathrinaxodon proops* (in bold).

Specimen	Basal skull length	Snout length	Snout/basal skull length	Postcanine number
RC 5	129	54	41%	10
UMCZ T810	**130***	**53**	**41%**	**10/11**
RC 130	132	56	42%	10/11
BP/1/3748	142	66	46%	10
RC 92	144	64	44%	9/?10

/ : different number of postcanines in left and right sides of the skull;
?: uncertainty in the number of teeth;
*: estimated measurement.

The basicranial girder is wide and an interpterygoid vacuity exists anteriorly between the well-developed ridges of the pterygoid (Figs 1B & 2B). The suture between the quadrate ramus of the pterygoid and epipterygoid is visible on the right side of the skull, and the quadrate ramus of the pterygoid is considerably extended posteriorly.

There are four right incisor-like teeth, and considering the incomplete preservation of the anterior portion of the snout, one or two more teeth could have been present as suggested by Parrington (1936). The anterior extension of the maxilla, as far as the level of the septomaxillary foramen in lateral view (Fig. 2C), indicates that two of these teeth are possibly implanted in the maxilla. It is not possible, however, to identify the premaxilla-maxilla suture in the palate in order to determine if these elements are indeed maxillary precanines. The second incisor-like tooth is the best preserved and is simple and conical. There is no clear evidence, except perhaps the better state of preservation, that this tooth could be in an emergent state as suggested by Parrington (1936). There are 10 left

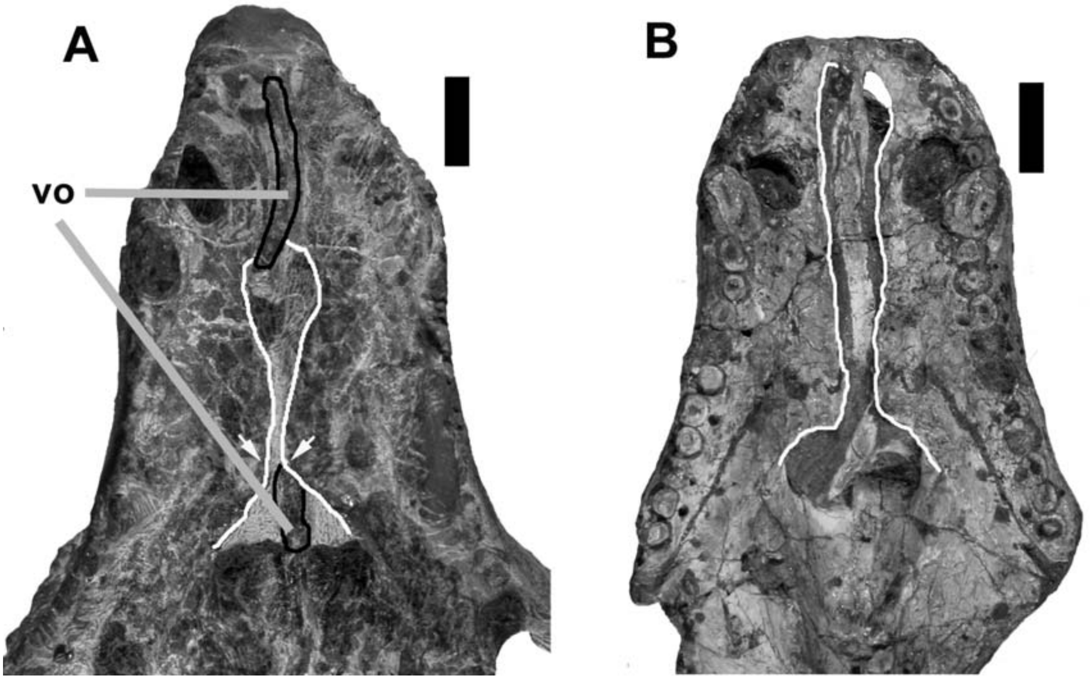

Figure 3. Palate of **A**, *Parathrinaxodon proops* (UMZC T.810), and **B**, *Procynosuchus delaharpeae* (RC 5). The medial borders of the palatal processes are highlighted in white. The arrows in A indicate the region where deformation has brought together the palatal processes of the maxillae and the palatines to produce the vomerine fossa (see text for details). Abbreviations: vo, broken and distorted vomer in *Parathrinaxodon proops.* Scale bars = 1 cm.

and 11 right postcanines, the anteriormost of which (first and third) are simple, possessing a main cusp with small anterior and posterior accessory cusps. A crenulated ridge is observed on the posterior border of the tooth crown. An isolated postcanine crown corresponding to the sixth left postcanine is slightly expanded bucco-lingually and ovoid in crown view (Fig. 4A). The tooth has a broken main cusp, with tiny anterior and posterior accessory cusps at the same level on the crown, both of which are similarly developed. A partially preserved lingual cingulum with one posterior and two anterior cusps is also recognized. Part of the anterior portion of the cingulum is broken, whereas the posterior portion seems to have been affected by wear (Figs 4A & 4B).

DISCUSSION

Parrington (1936) regarded *Parathrinaxodon proops* as being most similar to *Dvinia prima* from the Late Permian of Russia. The similarities included the relatively small snout, the anteriorly oriented orbits, the dental formula, and, in particular, the nature of the postcanine crowns. In addition, he found these two taxa to be similar to the Early Triassic *Thrinaxodon* because of the postcanine tooth morphology (i.e. a large main cusp and small accessory anterior and posterior cusps; lingual cingular cusps), and suggested a close relationship between them. Finally, Parrington (1936) also suggested that *Cyrbasiodon boycei* was related to *Parathrinaxodon, Dvinia* and *Thrinaxodon.* At that time, *C. boycei* was considered a therocephalian; it is currently included with procynosuchid cynodonts, though there is disagreement on its taxonomic identity (see Table 1). After the description of *P. proops,* Broom (1937, 1938, 1948) described several new cynodonts from the Late Permian of South Africa, all of which are now regarded as synonymous with *Procynosuchus delaharpeae* (Hopson & Kitching 1972; Battail 1991). Mendrez (1972a,b) considered *P. proops* to be a procynosuchid and regarded the contact of the posterior portions of the palatal processes of the maxillae, the presence of a narrow median slit in the

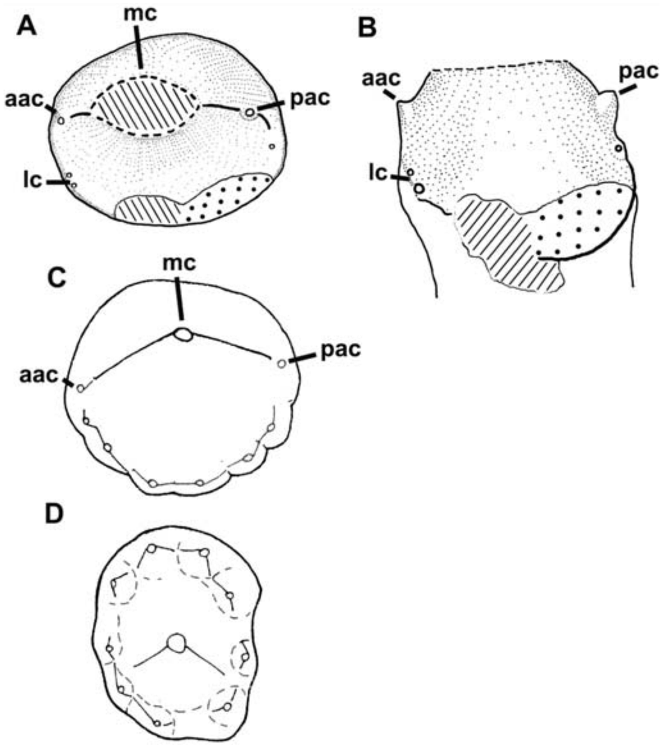

Figure 4. **A**, crown, and **B**, lingual views of the left upper sixth postcanine of *Parathrinaxodon*; **C**, crown view of the left upper second postcanine of *Procynosuchus*; **D**, crown view of left upper twelve postcanine of *Dvinia.* Abbreviations: aac, anterior accessory cusp; lc, lingual cingulum; mc, main cusp; pac, posterior accessory cusp. Hachure indicates broken tooth surface; heavy stipples indicate possible wear facet. In A, C and D anterior is to the left and lingual to the bottom. Figures 3C and 3D after Crompton (1972).

Table 3. Differences previously proposed between *Parathrinaxodon proops* and *Procynosuchus delaharpeae* (Mendrez 1972a,b; Battail 1991) and condition of those characters in *P. proops* after this study (in bold).

	P. proops	*P. delaharpeae*
Osseous secondary palate	Complete/**incomplete**	Incomplete
Median slit in the anterior portion of the palate (=vomerine fossa)	Present/**absent**	Absent
Precanine teeth	Absent/**?**	Present

anterior part of the palate and the absence of precanine teeth as the principal differences from *Leavachia duvenhagei* (=*P. delaharpeae*; see Table 3). Van Heerden (1976) included *P. proops* within the Galesauridae, which at that time also included *Thrinaxodon.* Features in *P. proops* supporting this assignment were the lack of an interpterygoid vacuity, the absence of precanine teeth, the lack of a prominent lingual cingulum on the postcanines and the presence of a complete secondary palate. Battail (1982, 1991) regarded the postcanine morphology of *P. proops* to be very similar to that of *P. delaharpeae,* but he considered the presence of the secondary palate and the absence of maxillary precanines in *P. proops,* as major differences between these species (Table 3).

Parathrinaxodon proops and *Procynosuchus delaharpeae* show ovoid to circular postcanines in crown view, with labial margins lacking cingula and large main cusps and smaller anterior and posterior accessory cusps (see Figs 4A & 4C). The lingual margin of the sixth left postcanine of *P. proops,* the only tooth in which it is possible to observe the lingual face of the crown, is not well preserved, but cusps forming a lingual cingulum are present. These dental features in *P. delaharpeae* and *P. proops* are remarkably distinct from those found in *Dvinia prima* (compare Figs 4A & 4C with Fig. 4D). In addition, the ovoid outline of the postcanine crown and the tiny size of the accessory cusps on the sectorial margin contrast with the anteroposteriorly enlarged postcanines of *Thrinaxodon liorhinus,* in which the accessory cusps are relatively larger (Crompton 1963). The postcanine morphology of *P. proops* thus represents the strongest evidence for conspecificity with *P. delaharpeae.* Other features of UMZC T.810 shared with *P. delaharpeae* are the number of postcanines and the proportion of the snout in relation to overall skull length (see Table 2).

The most intriguing feature remaining in *P. proops* is the presence of an opening in the palate between the maxillae (Parrington 1936: fig. 8), a feature also described in the Russian cynodont *Dvinia prima,* where it was termed the vomerine fossa (Tatarinov 1968b: fig. 2). Careful study of UMZC T.810 shows that although at first sight the snout looks undistorted, the anterior portion of the palate shows that the vomer is broken and displaced from its original position, indicating some degree of deformation of the palate (Fig. 3A). Considering the position of the vomerine fossa in UMZC T.810, we suggest that this 'fossa' is the result of the medial dislocation of the palatal processes of the maxilla. A slight horizontal displacement of the long, and originally free, palatal processes of the maxilla and palatine in specimens of *Procynosuchus delaharpeae* (Fig. 3B) would result in the contact (or quasi contact) of these processes, producing an artefact similar to the vomerine fossa. Examination of a cast of the holotype of *Dvinia prima* (UMZC T.1016) seems to confirm Hopson's (1991) observation that the palatal processes of the maxilla and the palatine do not come into contact in this species (contra Tatarinov 1968b). The sum of evidence suggests that an open secondary palate was the condition present in the Late Permian cynodonts *Procynosuchus, Dvinia,* and *Cynosaurus,* and persisted in the Early Triassic *Galesaurus* and *Progalesaurus* (see Sidor & Smith 2004). On the other hand, *Nanictosaurus* is the only Late Permian cynodont evincing a closed secondary palate, in that there is a contact between the palatal processes of the maxillae and the palatines (van Heerden & Rubidge 1990). The Early Triassic *Thrinaxodon* also exhibits a closed secondary palate (Kemp 1982; Hopson & Kitching 2001; Sidor & Smith 2004), but it should be noted that some well-preserved specimens of this taxon (e.g. BMNH R 511, R 511a, R 3731; BP/1/5208; Fig. 5) show the palatal processes of the maxillae and the palatines adjacent to, but not actually in contact with, their counterparts. Comments about the lack of contact of the halves of the osseous secondary palate in *Thrinaxodon* were also made by Van Heerden (1972). In addition, this condition is also figured in the detailed description of the skull of *Thrinaxodon* (Fourie 1974: figs 1, 8B & 9), although Fourie (1974: 357)

Figure 5. Palate of *Thrinaxodon liorhinus.* **A,** BMNH R.511, **B,** BP/1/5208. Arrow in A indicates palatal processes of the palatines close but not in contact. Note the vomer interposed between the palatal processes of the palatines in B. Scale bars = 1 cm.

Table 4. Tetrapod list and faunal analysis of the Kawinga Formation.

AMPHIBIA	*_Peltobatrachus_	GORGONOPSIA	_Aelurognathus_: CZ _Aloposaurus_: CZ, D _Arctognathus_: C _Dinogorgon_: C, D _Leontocephalus_: D _Scylacops_: CZ _Sycosaurus_: D *_Ruhuhucerberus_ *_Titanogorgon_
PAREIASAURIA	_Pareiasaurus_: T, C, D _Anthodon_: C, D	THEROCEPHALIA	_Theriognathus_: D *_Silphoictoides_
DICYNODONTIA	_Dicynodon_: D _Rhachiocephalus_: T, C _Kingoria_: ?C, D *_Kawingasaurus_ *New genus (=‘_Cryptocynodon_’) _Geikia_	CYNODONTIA	_Procynosuchus_: D

Kawinga taxa	Endemic	Shared with South Africa	Shared with Scotland	Total
Amphibia	1			1
Pareiasauria		2		2
Dicynodontia	2	3	1	6
Gorgonopsia	2	7		9
Therocephalia	1	1		2
Cynodontia		1		1
Total	6 (29%)	14 (67%)	1 (5%)	21

*: endemic taxa.

Abbreviations: C, _Cistecephalus_ Assemblage Zone; CZ: _Cistecephalus_ Zone; D, _Dicynodon_ Assemblage Zone; T, _Tropidostoma_ Assemblage Zone. The gorgonopsia _Tetraodontonius_ is not included because of uncertainty in its taxonomic assignment. Data from King (1988), Sigogneau-Russell (1989), Gay & Cruickshank (1999), Maisch (2002), Maisch & Gebauer (2005) and Angielczyk (pers. comm., 2004). South African faunal assemblages after Rubidge _et al._ (1995), except for _Cistecephalus_ Zone after Kitching (1977).

states ‘the two halves of the palate meet each other in a sutura harmonia’, that is to say, by means of a simple apposition of contiguous rough surfaces (Gray 1988). The unusual condition of the palate found in these specimens of _Thrinaxodon_ can be interpreted as an individual variation not related to ontogeny, since the basal skull length of specimens showing this ‘quasi closed’ palate, ranges between 71 to 84 mm, close to the largest skull size for the species (96 mm). In addition, the palate seems to be completely closed in tiny juvenile specimens described by Estes (1961).

Taxonomic status of _Parathrinaxodon proops_

Recognizing that _Parathrinaxodon proops_ Parrington and _Procynosuchus delaharpeae_ Broom are conspecific raises some concerns about nomenclatural priority. Following article 23, section 1 of the International Code of Zoological Nomenclature (ICZN 1999), _Parathrinaxodon proops_ Parrington 1936 has publication priority over _Procynosuchus delaharpeae_ Broom 1937. However, considering the extensive use of the latter name by most recent therapsid workers (e.g. Kemp 1982, 1988; Hopson & Barghusen 1986; Rowe 1993; Hopson 1994; Sidor & Hopson 1998; Hopson & Kitching 2001; Rubidge & Sidor 2001; Sidor 2001, 2003; Sidor & Smith 2004), and because that taxon represents the best known Late Permian cynodont, we propose to conserve _Procynosuchus delaharpeae_ as the valid name for this cynodont based on article 23, section 9 (Reversal of precedence) of the Code.

Comments on the Kawinga fauna

Parathrinaxodon proops comes from outcrops of the Kawinga Formation, at Stockley’s site B.19 (Stockley 1932) in the Ruhuhu Valley near Mount Kingori. The recorded fauna from the site B.19 also includes the dicynodont genera _Kingoria_, _Rhachiocephalus_, _Kawingasaurus_ and _Pristerodon_; the gorgonopsian genera _Arctognathus_ and _Scylacops_; the therocephalian genus _Theriognathus_ and the dubious _Silphoictoides_; and indeterminate pareiasaurs (Kemp 1969; Gay 1987; Gay & Cruickshank 1999). Tanzanian material of _Pristerodon_ (=_Cryptocynodon parringtoni_ Huene 1942) was recently reassessed as _Diictodon parringtoni_ by Maisch (1995), although Angielczyk (pers. comm., 2004) considers the species _‘Cryptocynodon’ parringtoni_ as a new endemic taxon, different from both _Diictodon_ and _Cryptocynodon._

An analysis of the Kawinga fauna at a generic level indicates six endemic tetrapod taxa and 14 that are also known from localities of the _Tropidostoma, Cistecephalus_ and _Dicynodon_ assemblage zones from the nearby South African Karoo (Table 4). The percentage of endemism at this level (29%) is clearly lower than the percentage of taxa shared with the Karoo faunas (67%). The analysis of endemism in the Kawinga fauna changes radically if we consider taxa at the specific level. Maisch (2002) reports 18 of 26 species (69%) of the Kawinga Formation as being endemic. It is common practice, at least for Permo-Triassic vertebrate faunas, to use the genus (e.g. Lucas, 1998a,b) or even the family (e.g. Shubin & Sues 1991) as index taxa for assessing faunal similarity. Genera, therefore, seem more appropriate than species for analysis of faunal endemism, in which case, species of the Kawinga fauna, which are closely related (i.e. included in the same genus) to taxa from the Karoo and/or other basins, should not be considered as evidence of endemism. Regarding cynodonts, the only taxon represented in east African faunas, _Procynosuchus,_ is also the first cynodont, and the only one of Late Permian age, with a global distribution. This taxon is the commonest cynodont in the *Dicynodon* Assemblage Zone of the South African Karoo, and is also recorded in Germany (Sues & Boy 1988) and Russia (Tatarinov 2004), if we accept Hopson and Kitching's (1972) synonymy of *Cyrbasiodon* with *Procynosuchus.* Other taxa from the Kawinga fauna with widespread distribution are the dicynodonts *Dicynodon* and *Geikia.* The first genus is also known from Zambia, Scotland, China, Laos and Russia (King 1988), although a recent phylogenetic analysis suggest that at least one South African and two Russian species are not closely related (i.e. the genus *Dicynodon* is not monophyletic; Angielczyk & Kurkin 2003). *Geikia* is also represented in the Cuttie's Hillock Sandstone, near Elgin, Scotland, which is considered equivalent with the *Dicynodon* AZ (King 1988; Maisch & Gebauer 2005).

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A juvenile gomphodont cynodont specimen from the *Cynognathus* Assemblage Zone of South Africa: implications for the origin of gomphodont postcanine morphology

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The partial skull and lower jaws of a small gomphodont cynodont from the *Cynognathus* Assemblage Zone of South Africa has a well-preserved postcanine dentition distinctly different from that of contemporaneous adult *Diademodon* and *Trirachodon.* On the basis of its small size and great amount of tooth replacement it is interpreted to be a juvenile individual. The postcanines are compared with those of adults and juveniles of *Diademodon* and traversodontids and is seen to differ from them. Comparison with adults of *Trirachodon* shows some unique postcanine resemblances, such as well-developed anterior and posterior many-cusped cingula and three transverse cusps joined by a prominent ridge. Thus it is identified as a probable juvenile *Trirachodon* of uncertain species. Unlike in *Trirachodon* adults, tall central and internal cusps of the upper postcanines lie close together on the medial side of the crown, separated from the tall external cusp by a deep valley. In these features it shows a striking resemblance to the traversodontid *Scalenodon angustifrons,* but not to more primitive traversodontids. The lower postcanines superficially resemble those of traversodontids in that two cusps (central and internal) are very tall and the posterior basin is elongated, but, unlike in traversodontids, the external cusp is present, though relatively small. Evidence of tooth replacement occurs in the incisors, canines, and postcanines. At least two replacement waves of gomphodont teeth are indicated, as well as replacement of small, possibly sectorial teeth at the rear of the tooth row. Probable homology of (at least) the external and internal cusps in the three gomphodont families suggests that the common ancestor also possessed transversely-expanded crowns developed from an external sectorial position (homologous with the ancestral blade-like tooth) and a hypertrophied internal cingulum.

Keywords: Cynodontia, Gomphodontia, *Trirachodon,* Triassic, *Cynognathus* Assemblage Zone, tooth succession, tooth evolution.

INTRODUCTION

Gomphodonts are a clade of derived non-mammalian cynodonts characterized by the possession of transversely expanded postcanine teeth with crown-to-crown occlusion. These molar-like postcanines, characterized as 'gomphodont' teeth, are generally considered to be specialized for processing a predominantly herbivorous diet (Hopson 1971). If the contentious Tritylodontidae are omitted (see discussions in: Hopson & Kitching 2001; Abdala & Ribeiro 2003), three family-level groups of gomphodont cynodonts are recognized: Diademodontidae, Trirachodontidae and Traversodontidae. In all three families, the expanded postcanines show a progressive decrease in crown wear from the first expanded tooth to the last, indicating that the teeth decrease in age from front to back with no indication of replacement within the row. However, this simple replacement sequence may not be sufficient to explain gomphodont tooth succession, for most taxa show evidence of more complex replacement patterns involving teeth of other morphologies. Furthermore, replacement patterns have been studied in growth series of very few species (e.g. *Scalenodon angustifrons* (Crompton 1955); *Diademodon* sp. (Hopson 1971)), so large portions of the full ontogenetic series are unknown for most taxa.

Diademodontids appear to represent the most primitive condition of dental morphology and replacement pattern among gomphodont cynodonts (Fourie 1963; Hopson 1971; Osborn 1974). In *Diademodon,* the tooth rows end in a series of three or more teeth in which the crown morphology grades from the fully expanded type to a fully sectorial (bladelike) type. *Diademodon* also appears to be primitive among gomphodonts in having the anterior expanded teeth sequentially replaced by simpler, more pointed, non-occluding postcanines (Crompton 1963; Hopson 1971). In trirachodontids and traversodontids, the anterior series of simple teeth is not seen, but sectorial teeth often occur at the rear of the tooth row, though the intermediate morphologies of *Diademodon* do not occur; rather, sectorial crowns usually lie immediately behind fully expanded teeth (Crompton 1955). In more derived taxa of traversodontids, such as *Massetognathus* and *Exaeretodon,* posterior sectorial teeth are unknown and the entire postcanine series appears to consist only of fully expanded teeth.

Disagreement also persists with regard to the homologies of the main postcanine cusps among the three gomphodont families and also between gomphodonts and their carnivorous ancestors with more sectorial postcanines. As noted by Abdala & Ribeiro (2003, p. 534), it appears that the external, sectorial, border of the postcanines in *Diademodon* is homologous with the sectorial postcanines of non-gomphodont cynodonts, with the expanded medial portion of the tooth originating by hypertrophy of the lingual cingulum of the ancestor, as was first proposed by Watson (1913). A similar origin of the postcanine crown pattern in traversodontids, through medial expansion of the lingual cingulum of an ancestral sectorial tooth, was advanced by Goñi & Goin (1987). *Trirachodon,* however, appears to complicate this picture because, as originally noted by Rowe (1986), and recently discussed by Abdala & Ribeiro (2003), the transversely widened lower postcanines seem to result from rotation of the longitudinally elongated posterior sectorial teeth, so that the main fore-aft cusps of the sectorial crown appear to be homologous with the three main transversely-aligned cusps of the more anterior teeth. Thus, two conflicting hypotheses of primary homology exist to account for the occluding postcanines of gomphodonts (Abdala & Ribeiro 2003).

The description of a small gomphodont skull from the collection of the South African Geological Survey (now the Council for Geoscience) in Pretoria provides the opportunity to address some of the problems of tooth succession and tooth homology described above. This specimen, JSM 100, is a partial skull with lower jaws in place of a small, undoubtedly immature, gomphodont from the *Cynognathus* Assemblage Zone of South Africa. Although information on the locality at which it was collected appears to be missing, I consider it to be sufficiently important to warrant description for it shows evidence of active tooth replacement at the time of death and possesses an unusual postcanine crown morphology. I will make the case that the specimen is a juvenile individual belonging to the genus *Trirachodon,* though to which species, *T. kannemeyeri* or *T. berryi,* cannot be determined. If correctly identified, this would be the first juvenile *Trirachodon* known.

MATERIALS AND METHODS

The skull, JSM 100, was borrowed in 1975 and prepared at the University of Chicago by Ms Claire Vanderslice using needles under a binocular microscope. The horizontal ramus of the left dentary was freed from the skull, which permitted the crowns of the left upper and lower postcanine dentition to be fully prepared and illustrated.

The colour of the enamel is noted in the description of the teeth because it is an indication of enamel thickness. The dentine is white, whereas the enamel has been diagenetically darkened, so that the thick enamel on the lateral and posterior surfaces of the larger postcanine cusps is a deep brown, effectively masking the underlying dentine, whereas the thin enamel on the canines and in the postcanine basins is orange to light yellow because it is less effective at concealing the white dentine.

I initially identified the specimen as a juvenile *Trirachodon,* but preparation of the postcanine teeth showed that they were unexpectedly distinct from those of the contemporaneous species, *T. kannemeyeri* and *T. berryi.* Rather, they show similarities to the postcanines of adult traversodontids. However, further study of the postcanines has indicated a number of similarities with the postcanines of adult specimens of *Trirachodon* and differences from those of both juveniles and adults of *Diademodon,* the only other genus of gomphodonts currently known from the *Cynognathus* Assemblage Zone of South Africa, and from juveniles and adults of traversodontids, at present unknown in Beaufort sediments, but known from contemporaneous sediments in Argentina (Bonaparte 1966).

In the descriptions of the dentition, the abbreviation PC (upper case) is used for upper postcanines and pc (lower case) for lower postcanines. In addition, the main cusps of the upper and lower postcanines are designated by upper and lower case abbreviations respectively.

DESCRIPTION

Skull and lower jaws

The outer surfaces of the skull and dentaries are poorly preserved and sutures are not visible. The bone of the palate and all but the outer surfaces of some of the postcanine teeth were still embedded in matrix and so were protected from weathering and erosion and are extremely well-preserved. Several loose teeth lying against the palate (Figs 1 & 2) testify to the fact that the skull was buried with minimum postmortem transport.

The skull is complete back to at least the middle of the temporal fossa. As preserved, it measures about 45 mm at the dorsal midline. The palate is complete to a level just in front of the pterygoid flanges and the postcanine tooth rows are fully preserved. The preorbital length is about 20 mm and orbital diameter about 10 mm (see Table 1). Assuming the midpoint in skull length lay near the centre of the orbit, as in small generalized cynodonts (Hopson 2001, fig. 5), total skull length may have been about 50 mm. This is about half the length of the holotype skull of *Trirachodon kannemeyeri* (Seeley 1895).

The snout is rather low and flat, sloping downward only slightly from the low sagittal crest to the tip of the snout. The last upper gomphodont tooth lies below the anterior half of the orbit. In dorsal view, the snout narrows smoothly to a rounded tip, without a lateral expansion at the level of the canines. Though the area is damaged, the zygomatic arches are parallel to the midline and the temporal fossa is narrow. In ventral view, the secondary palate extends back to the level of the contact between the third and fourth postcanines, indicating that it ends a short distance in front of the orbit. The postcanine tooth rows are set in from the nearly straight lateral margin of the maxilla and the two tooth rows diverge only slightly toward the rear. The contribution of the palatine to the secondary palate is relatively short. The rear of the vomer is exposed in the roof of the choana; its midventral keel is exposed behind the secondary palate. The palatines and anterior ends of the pterygoids are exposed in the primary palate.

The rather massive lower jaw has a smoothly convex lower border that increases in depth from the rounded symphysis to the blunt angular process. The fused symphysis extends back to the level of the upper canines. The outer side of the horizontal ramus is broadly rounded and the lower postcanine row is set in from its outer margin.

The skull shows no special features that ally it with a particular family of gomphodonts. It shows a few resem-

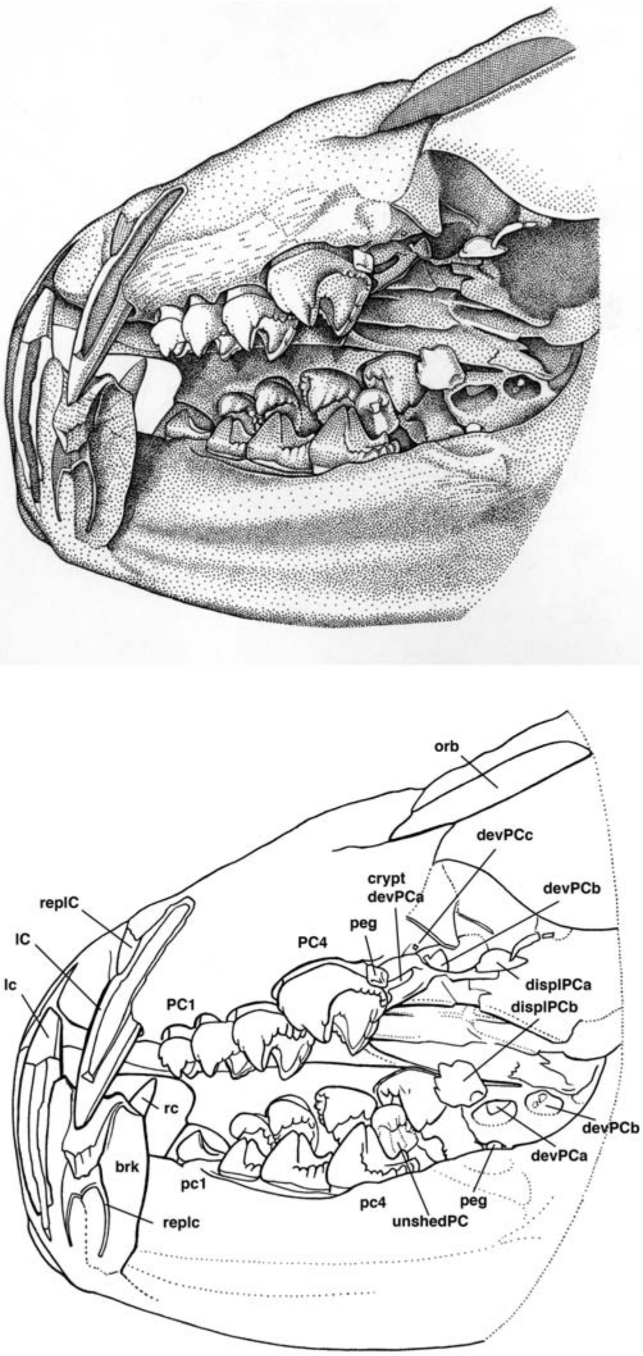

Figure 1. Juvenile ?*Trirachodon* sp. (Council for Geoscience Number JSM 100). Anterior portion of skull in oblique posteroventrolateral view, with left lower jaw removed to show the left upper postcanines and the lingual side of the right upper and lower postcanines. Features are identified in the line-drawing. Because of the oblique view, a scale bar is omitted, but the preorbital skull length is about 20 mm. Abbreviations are at the end of the text.

Table 1. Measurements of JSM 100, juvenile ?*Trirachodon.*

Skull		**mm**
Preorbital length:	Right:	18.8
	Left:	21.6
Interorbital width:		10.6
Dorsoventral diameter orbit:	Right:	9.0
	Left:	10.4
Length secondary palate (from anterior tip of snout):		19.4
Height of snout at level of anterior margin of orbit:		15.3
Width of snout at level of upper canines (estimated):		15.0
Lower jaw		
Length of lower jaw from anterior end to angle:		35.7
Depth of symphysis below upper canines:		7.5
Depth of mandible below pc1:		7.2
Depth of mandible below pc3:		8.7
Canines		
Upper		
A-P diameter at base:	Right:	2.6
	Left:	2.7
Height from alveolus (estimate; tip of tooth missing):	Right:	5.2
Lower		
A-P diameter at base:	Left:	2.3
Height from alveolus:	Left:	5.0
Diastemata behind canines		
Length upper diastema:	Right:	1.4
	Left:	1.7
Length lower diastema:	Left:	3.9
Postcanines		
Length upper (PC1–4) row (parallel to midline of palate):	Left:	12.6
Length lower (pc1–4) row (parallel to midline of palate):	Left:	11.4
(greatest length):	Left:	11.6

Individual upper left postcanines

	PC1	PC2	PC3	PC4
Length:	2.3	2.5	2.9	3.8
Width:	2.5	3.6*	4.9	6.6

Small tooth behind PC4:	Length: 0.8	Width: 1.5
Sectorial tooth at rear of left tooth row ('displPCa' in Figs 1 & 2):	Length: 1.7	Width: 1.0
Developing tooth crown in second alveolus:	Length: 1.9	
Displaced crown behind right PC4: ('displPCa' in Figs 1 & 2):	Length: 2.1	
Small unshed right postcanine ('unshedPC' in Fig. 1):	Length: 1.8	Width: ~2.0

Individual lower left postcanines:

	pc1	pc2	pc3	pc4	Erupting pc 5
Length:	2.3	2.9	3.3	4.3	5.4 (est.)
Width:	1.7	2.0 (est.)	2.6	3.5	3.9
Sectorial tooth behind pc5:	Length: 1.9	Width: 1.4			

*External surface damaged

blances to *Trirachodon* (such as inset of the cheek teeth from the outer margin of the maxilla and dentary) that differ from what is seen in adults of *Diademodon*; however, when comparison is made with juvenile individuals of *Diademodon,* these distinctions are no longer present.

Dentition

Incisors

The incisor regions of the skull and lower jaws are damaged, with only the first and second incisors in the right dentary preserving crown morphology. No incisors are preserved in the left dentary and only incomplete teeth are preserved in the premaxillae.

In the left premaxilla are preserved a cross-section of the root of the first incisor, the exposed wall of the alveolus of the second incisor, and a probable partial section of the root of the third incisor. Evidence of the expected fourth incisor is lacking due to skull damage.

In the right premaxilla are preserved the cross-section of the root of the first incisor and a longitudinal section of the alveolus of the second incisor. Evidence of the third and fourth incisors is lacking due to damage combined with incomplete preparation.

On the lower right are two preserved incisors that are probably the first and second. The matrix-filled space between the second incisor and the lower canine probably held a third incisor, as it does in *Trirachodon* specimens, where the third incisor lies very close to the canine. The second incisor is fully erupted and the tip of the crown of the first incisor is just erupting. Both teeth are spatulate with a convex labial profile and a lingual profile that is convexly-rounded basally and concave more apically. The crown of the second incisor is damaged mesially, but the erupting crown of the first incisor is undamaged and has a mesial ridge separating the more transversely-convex labial surface from the very slightly convex lingual surface. The lingual enamel in this tooth is lighter, therefore thinner, than the labial enamel, which bears fine longitudinal crenulations.

Canines

All four canines are preserved (Figs 1–3). The lower canines lie anterior to the upper canines, their tips extending into palatal fossae that lie anteromedial to the upper canines. The upper canine lies anterolateral to the first postcanine, with a short diastema, about one-third the length of the first postcanine, separating the two teeth.

The lower canine is separated from the lower first postcanine by a long diastema, about twice the length of the first postcanine.

The upper left canine is damaged, with an exposed longitudinal section of root extending nearly to the dorsal margin of the maxilla. The partially damaged crown possesses a distal longitudinal ridge, which appears to lack serrations. An unerupted canine crown is exposed anterior and slightly medial to the functional canine root. Its enamel has fine longitudinal crenulations and is darker, therefore thicker, than that of the functional canine.

The complete right upper canine has a slightly convex anterior profile and a slightly concave posterior profile. It is relatively short with a slight anterior inclination. Its anterior surface is smoothly rounded transversely and the posterior surface forms a sharp ridge showing no evidence of serrations. When viewed from the lingual side, a very narrow ridge is seen to extend up the anterolingual surface, presumably from the unexposed apex of the crown. Toward the upper end of the crown the ridge widens into a broad, low raised area.

The root of the lower left canine is exposed in longitudinal section. The crown is damaged, but shows a posterior ridge and an anterointernal low, thin ridge behind the functional canine. The crown of a replacing canine lies within the jaw behind the functional canine. It extends below the root of the first postcanine (as seen on a transverse break). Its enamel has irregular longitudinal crenulations and is darker (thicker) than that of the functional canine.

The crown of the right lower canine is exposed only on its lingual side. Its enamel is very thin, as on the other functional canines. A thin ridge extends along the anterointernal face of the tooth from its apex to the base of the preserved enamel and the posterior margin of the crown bears a sharp ridge. The tip of the replacement

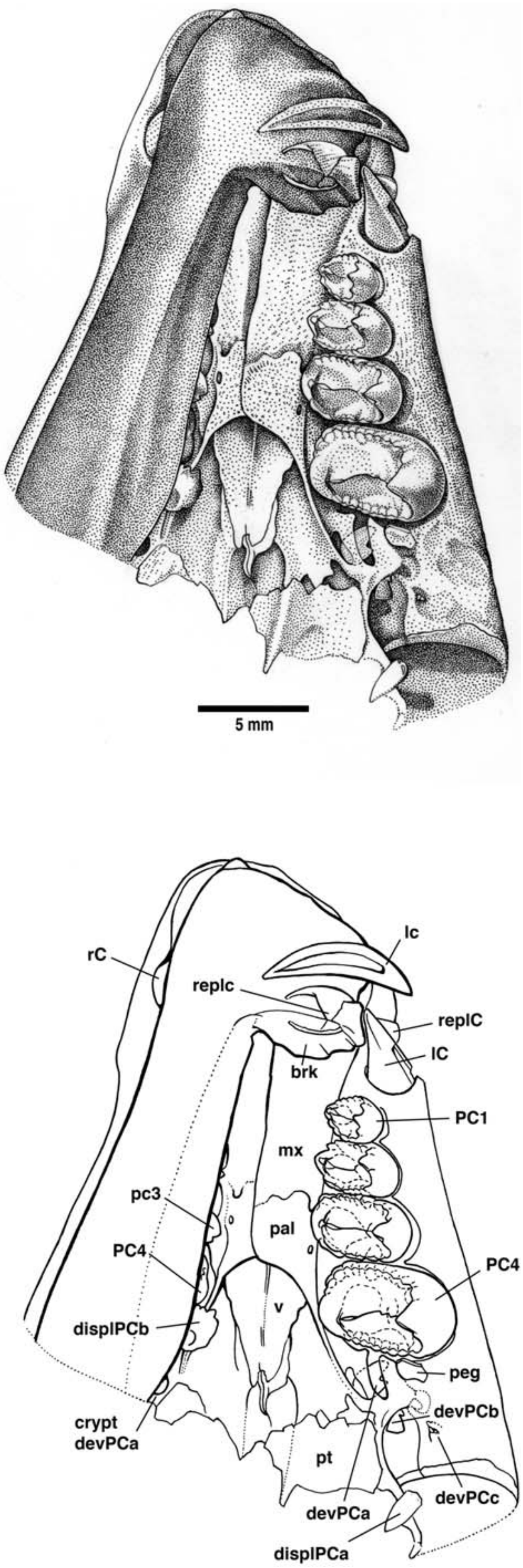

Figure 2. Juvenile ?*Trirachodon* sp. (Council for Geoscience Number JSM 100. Anterior portion of skull in ventral view, with left lower jaw removed to show the left upper postcanines. Features are identified in the line-drawing.

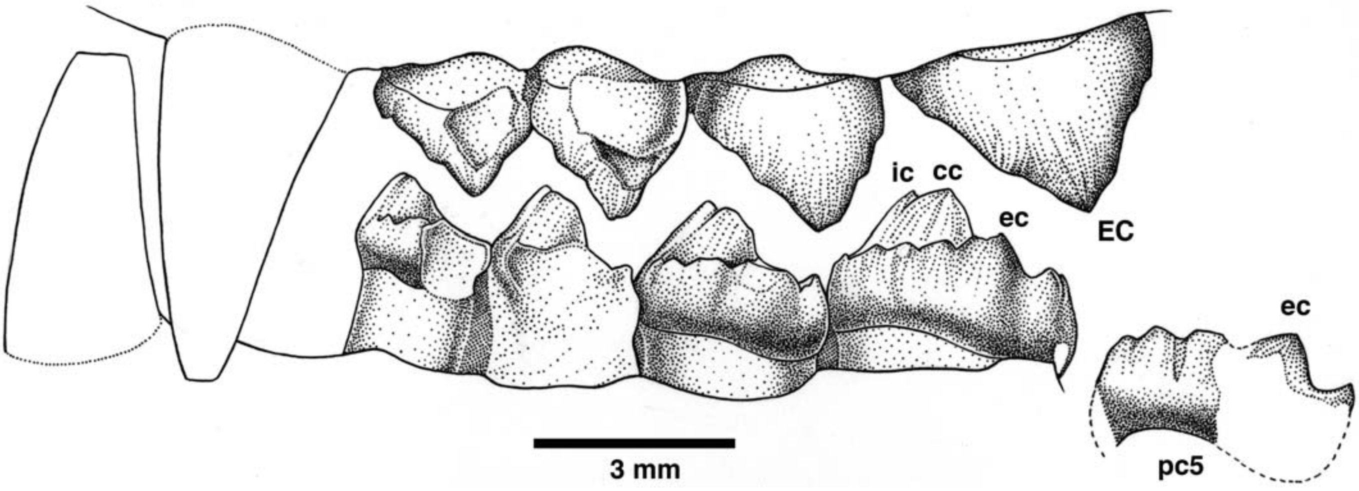

Figure 3. Juvenile ?*Trirachodon* sp. (Council for Geoscience Number JSM 100). Left canines and postcanines in lateral view. Unerupted lower postcanine 5 was exposed through preparation into the jaw.

canine is exposed on the dorsal margin of the jaw behind the functional canine.

Postcanines – general observations

Each postcanine tooth row contains four transversely-expanded functional teeth, which increase in size toward the rear. Additional teeth of differing morphologies lie posterior to the four expanded postcanines, including erupting teeth and developing teeth in their crypts. In the maxilla, a small peg-like tooth (Figs 1 & 2, peg) lies behind the labial half of postcanine 4 on each side. Neither PC4 is fully erupted, that on the right being less erupted than that on the left. Between the partially-erupted right PC4 and the fully-erupted PC3 is a small tooth that partially overlaps the crowns of each (Fig. 1, unshedPC).

Lingual to the small peg-like tooth behind PC4, on both sides, is a crypt containing a developing crown (Fig. 2, devPCa). A second crypt immediately behind the first also contains a forming crown (devPCb). On both sides, posterior to the peg-like tooth and labial to the crypt of the second developing tooth, is a small pit that on the left side contains a tiny isolated cusp (devPCc) but on the right shows no trace of a developing tooth.

Two teeth lie in the matrix against the palate, one behind the second crypt on the left side (Figs 1 & 2, displPCa) and the other behind the inner margin of the erupting PC4 on the right (displPCb). Their original sites in the maxilla (or mandible) cannot be determined. They are described more fully below.

In the right lower jaw, behind the last functional postcanine (pc4), is a bulging area of bone with a possible foramen on its surface. On the left side, behind pc4, was a partially erupted crown, which was further exposed by preparation into the jaw. This large tooth has the same crown pattern as the preceding tooth. The principal external cusp and the posteroexternal accessory cusp behind it were separated from the crown postmortem and lie deeper within the jaw; they are restored in place on the main part of the crown in Figs 3, 7 and 8.

The left lower jaw was prepared free of the skull in order to expose the crowns of the postcanine teeth. The following description is based primarily on the left postcanine series, with some details added from the right series.

Upper postcanines

From PC1 to PC4, the individual teeth increase greatly in size and in transverse relative to longitudinal diameter (Figs 3–6). The crowns are oriented transversely in the skull and each lies more labially than its predecessor. All share the following features:

1) A single tall external cusp at midlength on the crown,

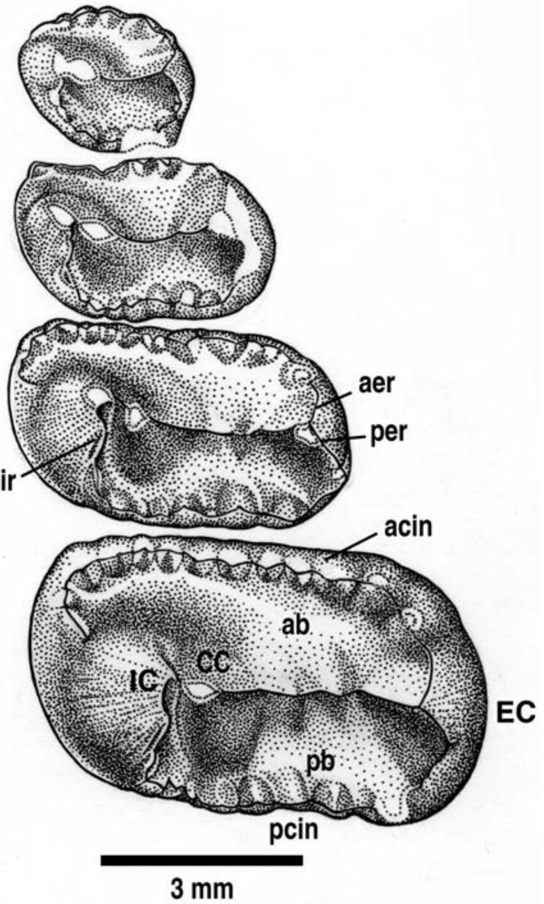

Figure 4. Juvenile ?*Trirachodon* sp. (Council for Geoscience Number JSM 100). Left upper postcanines 1–4 in crown view.

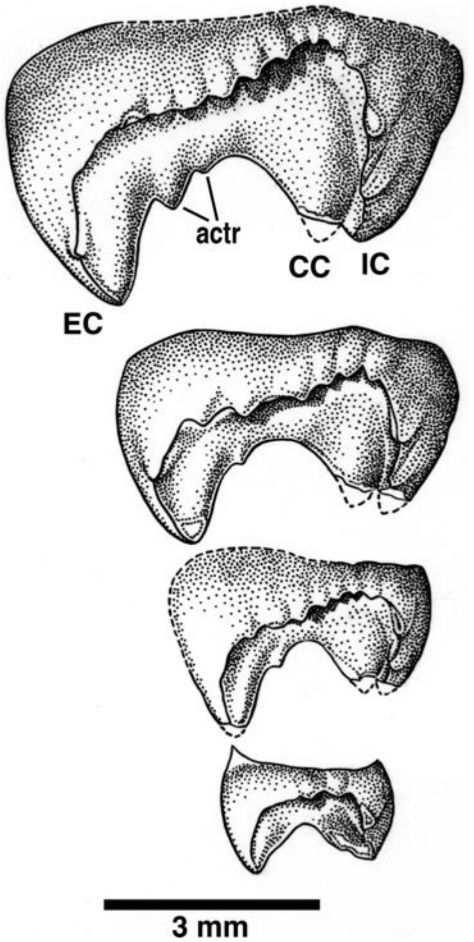

Figure 5. Juvenile ?*Trirachodon* sp. (Council for Geoscience Number JSM 100). Left upper postcanines in posterior view, with PC4 at the top and PC1 at the bottom.

with a ridge sloping anteriorly from its apex that bears a prominent accessory cusp near its base and a posterior ridge bearing a smaller cusp near its base.

2) Two slightly lower cusps on the internal half of the crown, a slightly taller internal cusp and a lower central cusp, separated from one another by a shallow notch. The lingual cusp has a posterior ridge bearing one or two small cusps, but it lacks an anterior ridge.
3) A centrally-located transverse ridge links the apices of the three cusps. From the apex of the external cusp the ridge slopes steeply toward the base of the crown, then curves inward to a low point at about the transverse centre of the crown and slopes more gradually to the apex of the central cusp. A short ridge joins the apices of the central and internal cusps. In PCs 2–4, one or two small cuspules lie on the ridge lingual to the base of the external cusp.
4) A transverse row of cingulum cusps forms the anterior and posterior margins of the crown, enclosing shallow anterior and posterior basins. The cingula are continuous with the anterior and posterior ridges on the main external cusp and with the posterior ridge on the main internal cusp. The anterolingual cingulum ends at the base of the internal cusp, the anterior face of which is smoothly rounded, and the anterior basin extends lingually across the anterior face of the internal cusp. On PC4, the cingulum ridge extends about one-third of the way up the internal cusp and terminates in a small cusp. The cingulum ridge on the anterior face of the external cusp extends to the base of the crown directly anterior to the apex, whereas the ridge on the posterior face of the cusp curves laterally from the apex, then inward toward the base of the cusp, where it joins the cingulum ridge.
5) The anterior face of the twinned central and internal cusps ascends more steeply to the basin than does the posterior face. In crown view, the anterior face is aligned posteroexternally at a low angle to the transverse axis of the crown, whereas the posterior face is oriented anteroexternally at a greater angle to the transverse axis.
6) The anterointernal face of the external cusp, anterior to the transverse ridge, is oriented at an angle of 45 degrees or more to the transverse ridge. The posterointernal face of this cusp is oriented posteroexternally at greater than 45 degrees. This means that the anterior face of the external cusp is oriented more longitudinally than the posterior face.

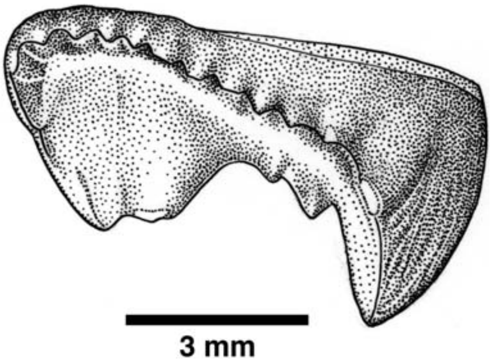

Figure 6. Juvenile ?*Trirachodon* sp. (Council for Geoscience Number JSM 100). Left upper fourth postcanine in anterior view.

From PC1 to PC4, the enamel increases in rugosity on the three main cusps. The anterior and posterior basins are smoother and the enamel is much thinner than on the cusps, appearing a very light yellow, as opposed a rich amber or brown on the main cusps.

Postcanine 1: this small tooth is oval in crown view, being slightly wider than long. The anterior margin is slightly more rounded than the posterior, so the anterior basin is slightly wider than the posterior. Anterior and posterior marginal cingula extend lingually and basally from the ridges on main external cusp. The anterior cingulum has four small cusps (excluding the prominent cusp on the anterior ridge of the external cusp). The posterior cingulum has three or four larger posterior cingular cusps (damage prevents an accurate count) and two small cusps on the posterior ridge of the internal cusp. The central transverse ridge lacks cuspules on its basal portion. On both left and right sides, the posterior internal ridge bears a prominent wear facet on the enamel that extends along the entire ridge.

Postcanine 2: this tooth is about half again as wide as PC1, though only slightly longer anteroposteriorly. The anterior and posterior margins of the crown are nearly straight and parallel to one another. The enamel of the apical part of the posterointernal ridge shows a posteriorly-sloping wear facet. The anterior cingulum has five cusps, the labial- and lingual-most being the largest. (The left PC2 is damaged but the right preserves the cuspules missing on the left.) The posterior cingulum has seven cusps, the second from the external side being the largest. At the base of the external cusp, the transverse ridge bears a single small accessory cusp.

The enamel of the apical part of the posterointernal ridge shows a posteriorly-sloping wear facet. The central portion of the ridge has a well-developed wear facet with longitudinal striations and a central exposure of dentine on the second cusp from the apex. The most lingual two posterior cingulum cusps are also truncated by wear facets. Behind the lateral slope of the central cusp, on the slope toward the posterior valley, is a shallow concavity that may reflect an occlusal area for a lower cusp.

Postcanine 3: this tooth is about one-third wider and longer than PC2. The anterior cingulum has ten cuspules, with the three outermost and two innermost being largest. The anteroexternal ridge bears a small cusp. From the innermost cingulum cusp, a short ridge bearing a small cuspule curves up on to the anterinternal face of the internal cusp. On the posterior cingulum are three large cusps on the labial half and two smaller cusps on the lingual half. On the posterointernal ridge is a small basal cusp, separated from the lingual-most cingulum cusp by a V-shaped notch, and two larger cusps closer to the apex of the internal cusp. On the base of the transverse ridge internal to the main outer cusp is a single small accessory cusp.

Postcanine 4: this tooth is about one-third wider than PC3 and about 40% longer. The anterior ridge on the external cusp has a well-developed accessory cusp (damaged on the left side), but a posterior accessory cusp is not present, although a basal swelling on the posterior ridge may represent this cusp. On the central transverse ridge at the base of the external cusp is a small accessory cusp, as in PCs 2 and 3, with a smaller cuspule lingual to it. The anterior cingulum bears 10 relatively small cusps. A deep V-shaped notch separates the innermost cusp from an anterointernal ridge on the basal half of the main internal cusp. This ridge has a small cusp basally and a larger cusp capping the ridge. On the right side, a definite anterointernal ridge is absent and the basal cusp (here a free-standing cusp) is larger than that on the left. The more apical cusp is separated by a small gap from the basal cusp and forms an elongate low bulge on the side of the internal cusp.

The posterior cingulum and posterior basin slope basally toward the internal side of the crown. A row of five distinctly-spaced cingulum cusps slopes toward the lowest part of the cingulum. At the basalmost part of the cingulum is a very small isolated cusp. More lingually, the posterointernal ridge, which bears two small basal cusps, extends to the apex of the main internal cusp. At about one-third of the distance from the basal cusps to the apex, the ridge bears a prominent cusp (damaged on the left but complete on the right). At about two-thirds of the distance from the basal cusps to the apex the ridge bears a second prominent cusp.

Small gomphodont postcanine: between the partially-erupted right PC4 and the fully-erupted PC3 is a small tooth (Fig. 1, unshedPC) that lies between the lingual halves of the two crowns, partially overlapping each. This small tooth is expanded transversely, but is less than half the width of PC3, being about as wide as PC1. It has a pattern of main cusps that appears similar to that of the upper postcanines, i.e. an external and internal cusp and a probable central cusp adjacent to the inner cusp (all worn or damaged), and an anterior and posterior cingulum of small cusps. Its enamel is very thin and, therefore, lighter than that of the larger crowns. A remnant of root remains on its posterolabial margin. This tooth is interpreted as the last remnant of a preceding functional tooth row that has been almost entirely shed and supplanted by a subsequent replacement wave of larger teeth. There is no evidence of a comparable tooth on the left side, where PC4 is more fully erupted.

Peglike tooth behind PC4: behind the labial half of the upper PC4 on both sides is a small transversely-ovate, peglike tooth (Figs 1 & 2, peg). On the better-preserved right side, the crown has at least two cusps, the labial of which is the larger. The outer side of this tooth is not exposed, so there may be a third, more labial, cusp.

Developing postcanines: lingual to the small peglike tooth, on both sides, is a crypt opening via a foramen that is oval on the right side but, because of damage, is narrower and more elongated on the left (Fig. 1, crypt devPCa). In the crypt on the left side is a developing crown with a large anterior cusp and a smaller cusp behind it (Fig. 2, devPCa). It is possible that the forming crown is a transversely-expanded tooth and that the cusps are the main internal cusp and the adjacent posterior accessory cusp. The inner side of the tooth inclines more ventrolaterally than that of the functional fourth PC, suggesting the more external portion of the forming crown lies deeper within the maxilla, above and partially behind the small peglike tooth. The enamel of the forming crown has longitudinal crenulations and is a slightly darker brown than that of the functional PC4, suggesting it is thicker. In the comparable oval pit on the right side, only the main cusp of the developing crown is visible in its crypt.

Immediately behind the crypt lying internal to the small oval tooth on each side is a second crypt containing a developing crown (Figs 1 & 2, devPCb). On the right side, the crypt is a circular depression in which lies a forming tooth with two small cusps. Along the anterointernal side of the depression is the section of a larger fragment of tooth with thin enamel. Whether it is part of the same crown as the two small cusps is uncertain. On the left, the depression is larger than on the right and has an irregular shape, probably due to damage. It contains a developing crown consisting of a large main cusp joined to a small more anterior cusp. The enamel of this crown is lighter than that of the more fully developed crown anterior to it and is only very slightly crenulated. As the functional upper postcanines lack an anterior accessory cusp, it is uncertain whether the forming crown is part of a transversely-expanded tooth or of a more narrow, sectorial-type, tooth.

On both sides, posterior to the small transversely-ovate functional tooth and external to the crypt of the second developing tooth, is a small pit that on the left side contains a tiny isolated cusp (Figs 1 & 2, devPCc) but on the right shows no trace of a developing tooth. From its position immediately behind the small ovate functional tooth, it appears that this developing crown may be part of the same replacement wave as that tooth and distinct from the wave producing the transversely-expanded (gomphodont) postcanines exposed more medially.

Teeth of unknown original position: two additional posterior teeth are preserved, the original locations of which are uncertain. One is in matrix behind the second unerupted crown on the left (Figs 1 & 2, displPCa). It is a sectorial type tooth with a small anterior cusp and a larger posterior cusp. The labial side of the crown is broadly rounded and the lingual side is more vertical. The root is stout and about twice the height of the crown. It does not seem to be implanted in an alveolus, so may have fallen from a possible alveolus between the ovate peg-like tooth and the small developing tooth behind it.

The second tooth of unknown location has been displaced from its original position and lies against the palate behind the internal margin of the right PC4 and medial to the first crypt containing a developing crown (Figs 1 & 2, displPCb). The tooth lies on its side so the full crown cannot be seen. It is uncertain whether it is an upper or lower tooth. The crown appears to be oval, with a large cusp and two much smaller accessory cusps that curve around the front (as preserved) of the crown, suggesting a basin on the side opposite the main cusp. The tooth lacks a root, which seems to have been eroded away, as matrix on the base of the tooth suggests the root was absent at the time of death.

At present, it is not possible to be sure of the original site of this tooth. If it is an upper, it may have fallen from the round second pit behind the right PC4. As noted above, this pit has a remnant of dentine and enamel along its wall, which may be a remaining part of this tooth. In this case, if the main cusp is labial, the two accessory cusps would be anterior. The upper postcanines have an accessory cusp on the anterior slope of the main cusp and a second accessory cusp anterointernal to the first. However, it is also possible that this tooth is a lower, in which case the main cusp would probably be on the labial side and the accessory cusps would be posterior. There is a possible alveolus on the inner side of the base of the coronoid process from which this tooth may have been shed immediately postmortem.

Lower postcanines

The following description is based mainly on the left postcanine row (Figs 3, 7–9) , which was separated from the upper dentition. As in the uppers, the lower postcanines increase greatly in size from first to fourth, and the unerupted pc5 is much larger than pc4. The crowns are longer than wide and roughly rectangular in outline. Their long axes are parallel to the long axis of the jaw. All share the following features:

1) The anterior two-thirds of the crown bears a large rounded internal cusp closely joined to a slightly lower, oval central cusp that lies posteroexternal to it. A ridge extends from the apex of the lingual cusp to that of the central cusp, the tips being separated by a shallow notch. From the base of the notch anterior and posterior grooves extend down the conjoined cusps and fade into the surface of their common base. The apical ridge crosses the oval central cusp and descends to a basal platform, where it passes posteroexternally and ascends the inner surface of a much lower, but nonetheless prominent, external cusp. The ridge joining the three main cusps is oriented at about 45 degrees to the long axis of the tooth.
2) External and anteroexternal to the conjoined central and labial cusps is a basal cingulum enclosing a narrow basin, which is bounded posteriorly by the main labial

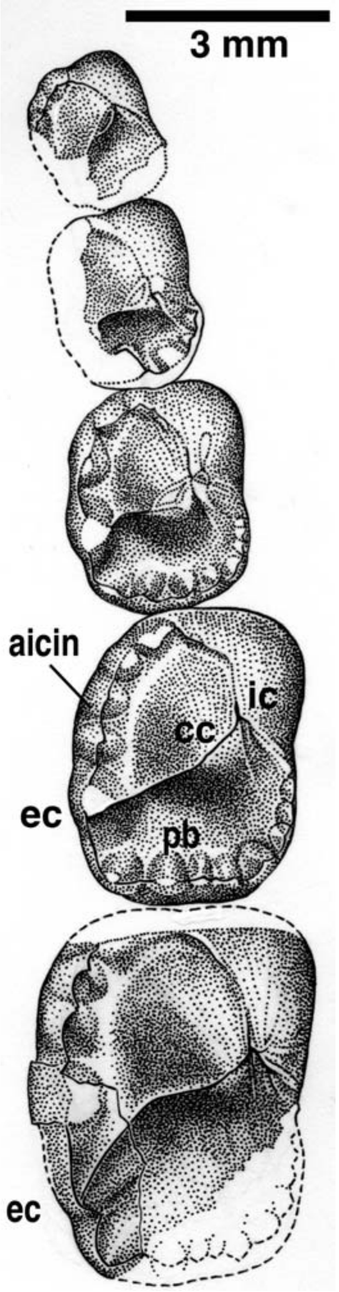

Figure 7. Juvenile ?*Trirachodon* sp. (Council for Geoscience Number JSM 100). Left lower functional postcanines 1–4 and unerupted pc5 in crown view.

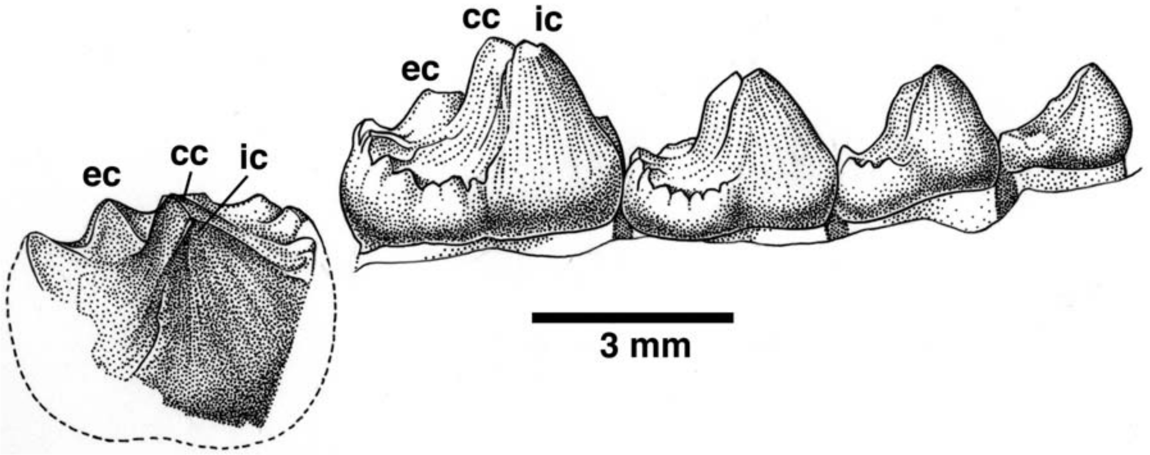

Figure 8. Juvenile ?*Trirachodon* sp. (Council for Geoscience Number JSM 100). Left lower functional postcanines 1–4 and unerupted PC5 in medial view.

cusp (which is the largest cusp on the outer margin of the tooth) and the ridge extending from this cusp to the central cusp. At its narrow anterointernal end, the basin is bounded by a narrow ridge that extends upward a short distance from the inner-most cingulum cusp on to the anteroexternal face of the main internal cusp.

3) Posterior to the three main cusps is a shallow basin bounded posteriorly and posterointernally by a series of cingulum cusps. The basin is about one-third the length of the crown and is slightly concave anteroposteriorly and slightly convex transversely, with its inner side lower than its outer side.

Postcanine 1: on the left side, the posteroexternal part of this tooth is damaged, but, at the time the drawings were made, was otherwise complete (the main internal and central cusps were subsequently broken off). The right pc1 is more complete. The anteroexternal cingulum has two relatively large cusps anterior to the main labial cusp. All of the cusps on the posterior cingulum have been eroded away by tooth wear. The enamel in the central part of the posterior basin on both first postcanines has been worn away, leaving a planar facet on the dentine.

Postcanine 2: the outer side of the left pc2 is heavily damaged and that of the right pc2 is obscured by slight damage and some remaining matrix. Therefore, the number of cusps on the anteroexternal cingulum cannot be determined. On the posterior cingulum of the left pc2, two small internal and two larger, though damaged, posterior cusps are preserved. Probably one and at most two more posteroexternal cusps were present. The apex of the central cusp is truncated by a posteroventrally-sloping wear facet on the enamel; dentine is exposed by wear at the truncated tip of the cusp. The more pointed tip of the internal cusp is also truncated by a flat wear facet.

Postcanine 3: the anteroexternal cingulum has three cusps, a small anterior cusp adjacent to the base of the main internal cusp and two larger more external cusps. The tips of the internal and central cusps are truncated by wear, as in pc2.

Postcanine 4: the large pc4 has four cusps on the anteroexternal cingulum. Posterior to the main external cusp is a notch behind which is a relatively large posteroexternal cingulum cusp. Internal to this cusp are four additional posterior cingulum cusps. On the internal side of the posterior valley are three smaller cingulum cusps, and at the base of the main lingual cusp is a very small cusp. A short distance above this cusp is a low oval cusp with its long axis directed toward the apex of the main cusp.

Erupting postcanine 5: a partially erupted left pc5 was prepared out behind pc4. The apex of its main lingual cusp is at the level of the posterior cingulum of pc4. In order to remove the left lower jaw containing the postcanines from the skull, fine saw cuts were made immediately behind pc4 and across the lower part of the coronoid process. The cut across the horizontal ramus

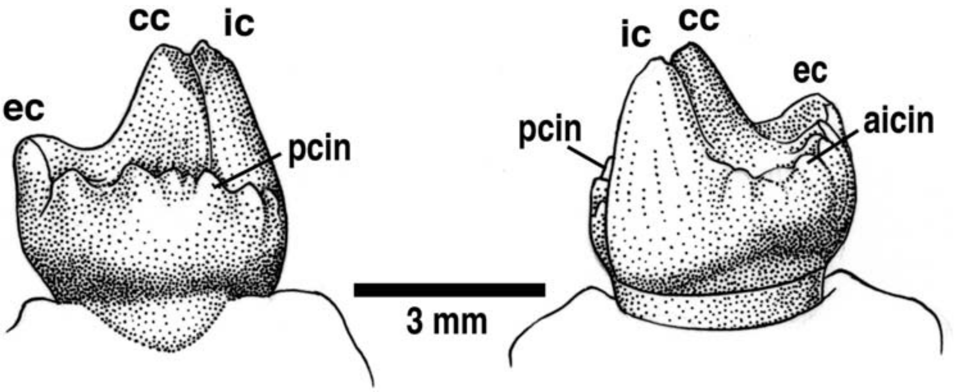

Figure 9. Juvenile ?*Trirachodon* sp. (Council for Geoscience Number JSM 100). Left lower fourth postcanine in posterior (left) and anterior views. In the anterior view, the front of the tooth is rotated slightly to the right so a portion of the posterior cingulum is visible.

removed the anterior-most part of pc5, but most of the crown is intact. The lingual side of the posterior basin is not preserved, but the main labial cusp and the cingulum cusp behind it, though broken away from the crown, are nonetheless well-preserved and restored in place on the crown in the figures. The erupting pc5 is tilted lingually so that the main cusps are inclined inward at about 45 degrees. The crown morphology is of the same pattern as of the preceding teeth, although this tooth differs in having a distinct ascending ridge on the posterointernal side of the main internal cusp. This ridge ends at the posterior groove between the internal and central cusps where it terminates in an oval cuspule. Anterior to this ridge, the enamel of the convex internal surface is very dark and rugose, with dorsoventral crenulations. External to the ridge, the posterior surface of the internal cusp is transversely concave and the enamel is of a lighter colour and is more finely crenulated. The enamel on the transversely convex rear face of the central cusp is of the same character.

The anteroexternal cingulum preserves three external cusps, the remnant of a more anteroexternal cusp, and a small cusp at the base of the very shallow groove between the central and internal cusps. Only the posteroexternal cusp of the posterior cingulum is preserved behind the main external cusp.

Posterior sectorial tooth: behind the centre of the unerupted pc5, above its posteroexternal cingulum cusp, is the remnant of a small longitudinally elongate tooth, the crown of which is very damaged. Its partially exposed root indicates it was mature and in place. An alveolus on the right side, behind the crypt of the unerupted pc5, presumably represents the site for this sectorial tooth. An isolated tooth of comparable size and shape lies on the palate behind the tooth row (Figs 1 & 2, displPCa). This may be the tooth from the empty right alveolus.

Tooth replacement

Incisors and canines of this immature specimen were undergoing rapid replacement at the time of death. Of the two preserved incisors, that interpreted here as the first right incisor is erupting, with only its apex exposed above the alveolar margin, and the second right incisor is fully erupted.

Both upper canines appear to be incompletely erupted, as their alveoli are larger than their crowns and they only slightly overlap the dorsal margin of the dentary. A developing replacement crown lies within the maxilla anterior to the left erupting canine. The right lower canine appears to fill its alveolus more completely than do the upper canines. The tip of a replacement canine is erupting on the dorsolingual side of the jaw behind the functional canine. The left lower canine is damaged and its alveolus is not well exposed, so its degree of eruption relative to the right side is uncertain. A replacement crown is exposed on the left side within the jaw behind the lower canine. Because of difficulty of preparation, it could not be determined whether the tip of this replacing tooth is erupting.

In the postcanine series, the posterior decrease in the degree of wear and of eruption (as indicated by decrease in amount of exposure of roots) demonstrate that the first four teeth have erupted sequentially from front to back. At the rear of both upper and lower tooth rows are unerupted postcanines, the crown morphology of which is similar to that of the functional postcanines (known in the lower dentition and presumed to be the case in the uppers), thus demonstrating that the same sequence of eruption is continuing. In the upper jaw, a second incompletely formed crown lies posterior to the unerupted crown lying immediately behind the fourth postcanine, indicating the likelihood of additional teeth of comparable morphology. Such additional replacement teeth are not seen in the lower jaws, though one would presume they are present within the bone.

As in some other gomphodont cynodonts, small teeth occur at the rear of the functional tooth row, posterior to the main labial cusp. Here, these teeth have a transversely ovate outline rather than the longitudinally ovate outline usual in gomphodonts. Behind this tooth on the left side, lateral to the second developing crown described above, is a small pit containing the apex of a very small ovate cusp with a keeled margin. On the right side is a comparable pit, which lacks a visible crown.

To add to the complexity of the replacement series, a small gomphodont tooth, presumably representative of a previous wave of replacement lies between the right upper PC3 and the erupting PC4.

The crown of the rootless tooth lying in the matrix behind the right PC4 may have belonged to the series represented by the transversely ovate tooth behind PC4. If so it may have been shed from a position in which a replacing tooth is developing. Likewise, it may have been shed from a more medial position, where it would be replaced by a developing PC5. In this case, it may be part of the older series of gomphodont teeth represented by the small tooth lying between right PCs 3 and 4. Finally, it might be part of the older series in the lower jaw, being shed from behind lower pc4 and perhaps lateral to the erupting pc5.

To summarize the inferred pattern of postcanine tooth succession in this individual, the remnant of an earlier wave of gomphodont postcanine replacement is indicated by a small heavily worn upper gomphodont tooth that was about to be shed. The small peg-like tooth behind the outer half of PC4 may be part of this replacement wave, as may be the tiny developing tooth behind the peg-like tooth. A more recent replacement wave is represented by the four functional upper and lower gomphodont teeth and the unerupted fifth and perhaps sixth gomphodont crowns behind them.

DISCUSSION

Identification of JSM 100 as a probable juvenile *Trirachodon*

Specimen JSM 100 is determined to be a eucynodont on the basis of the fusion of its symphysis and a gomphodont cynognathian on the basis of its transversely expanded, occluding postcanines showing a pattern of sequential rather than 'alternate' replacement. It is determined to be a juvenile individual on the basis of the great amount of tooth replacement that was occurring at the time of death and its small size relative to the much larger size of undoubted adult individuals of the gomphodonts *Diademodon* and *Trirachodon,* the only certainly valid genera currently recognized from the *Cynognathus* Assemblage Zone of South Africa (Hopson & Kitching 1972; Kitching 1995).

In its postcanine dentition, JSM 100 more closely resembles adult individuals of *Trirachodon* than of *Diademodon,* notably in the presence of three well-defined transversely-oriented cusps in both upper and lower teeth and in the presence of anterior and posterior cingula usually with a relatively large number of small cusps. In *Diademodon,* the central and internal cusps of the upper postcanines are low and poorly differentiated, the transverse ridge is less well-defined, and, more significantly, the lower postcanines possess only two rather than three principal cusps (Crompton 1972, fig. 3A; personal observation). Finally, immature specimens of *Diademodon* of about the same skull length (about 50 mm) have very different postcanine teeth from those described above, including a series of anterior pointed teeth that replace the gomphodont series and more posterior teeth with oval crowns that are about twice as long as wide and that appear to grade continuously into more posterior sectorial teeth (Hopson 1971).

Comparison of the postcanines of specimen JSM 100 with adult traversodontids, especially *Scalenodon angustifrons* (Crompton 1955, 1972), show some striking resemblances, discussed in detail below. However, when JSM 100 is compared with adult and juvenile individuals of the contemporaneous Argentine traversodontid *Andescynodon mendozensis* (Goñi & Goin 1988), the postcanines are distinctly different, with both the upper and lower crowns of *Andescynodon* possessing a distinctive multicusped sectorial external portion and a single anteriorly-located internal cusp joining the main external cusp by a transverse crest on the anterior margin of the crown.

My conclusion from these comparisons is that JSM 100 is most likely to be a juvenile individual belonging to a species of *Trirachodon.* It will be referred to as ?*Trirachodon* sp. in the subsequent discussion.

Comparison of postcanine crown patterns in gomphodont cynodonts

In Figs 10 and 11 are compared representative upper and lower postcanines of *Trirachodon kannemeyeri,* juvenile ?*Trirachodon* sp. (JSM 100), and *Scalenodon angustifrons,* all drawn from specimens. Only in JSM 100 are the upper and lower teeth known to be from the same individual. The upper row consists of crown views (with the posterior side in the uppers and anterior side in the lowers toward the top of the page) and the lower row of posterior views.

The upper postcanines of all three share the following features:

1) Three main cusps oriented transversely on a crown that is mediolaterally wider than long.
2) A prominent transverse ridge connects the apices of the three main cusps.
3) A well-developed anterior and posterior cingulum, usually joined at each end to the apices of the external and internal cusps and enclosing anterior and posterior basins.
4) The external cusp is the most robust, though not always the tallest.
5) Small accessory cusps on the transverse crest between the external and central cusps (and in adult *T. kannemeyeri* on the ridge between the central and internal cusps as well).

The lower postcanines of all three share the following features:

1) Transverse ridge joining apices of main cusps.
2) Posterior cingulum enclosing posterior basin.
3) Posteroexternal ridge from cingulum to apex of main external cusp (which may not be homologous in all three).

The juvenile ?*Trirachodon* sp. shares with adult *T. kannemeyeri* the following similarity in the upper postcanines:

1) Posterior and (usually in *T. kannemeyeri*) anterior cingulum composed of a continuous row of distinct cusps.

They share the following similarities in the lower postcanines:

1) Three cusps in a transverse row joined by a prominent ridge.
2) Well-developed basin bounded by a cuspidate cingulum extending anterior to the external cusp and its adjacent transverse ridge, though the basin is labially displaced in the juvenile.
3) Complete posterior cingulum formed by a continuous row of distinct cusps that extends between the external cusp and the base of the internal cusp, enclosing a broad posterior basin.

The juvenile ?*Trirachodon* sp. shares with *Scalenodon angustifrons* the following similarities in the upper postcanines:

1) Main cusps much taller than those of *T. kannemeyeri* adult.
2) Central and internal cusps conjoined on lingual side of the crown and separated from the external cusp by a deep valley.
3) Anterior basin anteroposteriorly longer than in *T. kannemeyeri* adult.
4) Small accessory cusps present on transverse ridge near base of notch between external and central cusps.

They share the following similarities in the lower postcanines:

1) Crown longer than wide, with elongation of the posterior basin.
2) Two rather than three enlarged main cusps (of which the homology of the more labial cusp is uncertain).

Major differences nevertheless exist between the juvenile ?*Trirachodon* sp. and *Scalenodon angustifrons*:

1) The external shear between the main lower labial cusp and the longitudinal inner face of the external cusp that characterizes traversodontids is absent in ?*Trirachodon* sp.
2) *S. angustifrons* lacks an external cusp and an anteroexternal cingulum and basin in the lower postcanine

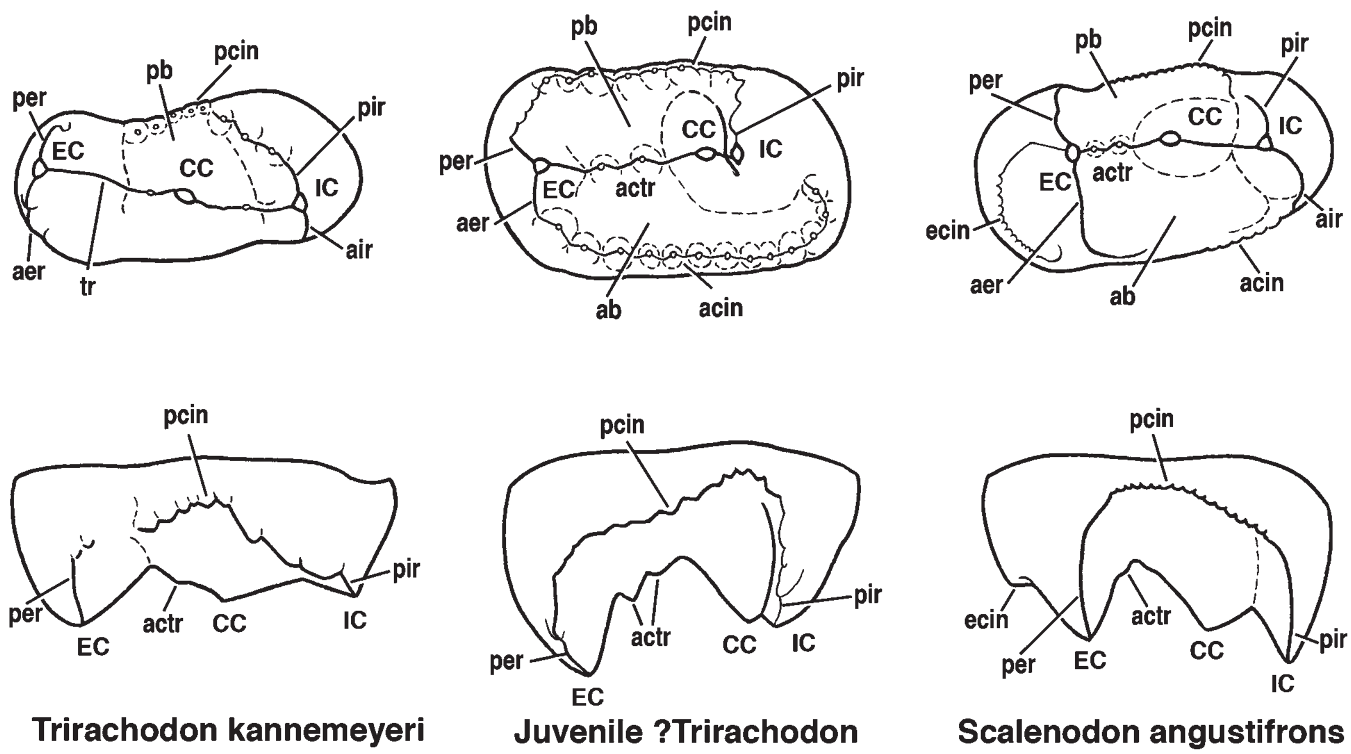

Figure 10. Comparison of upper postcanines in crown and posterior views of *Trirachodon kannemeyeri,* the juvenile specimen of ?*Trirachodon* sp., and *Scalenodon angustifrons.* A distinct anterior cingulum is usually present in *T. kannemeyeri* postcanines. Not to scale.

(although an anteroexternal cusp or narrow anterior cingulum is sometimes present in traversodontids)

Although the dental resemblances of the juvenile ?*Trirachodon* specimen to the traversodontid *S. angustifrons* are striking, their phylogenetic and evolutionary significance is uncertain. As noted above, *Pascualgnathus* and *Andescynodon* as the oldest and probably most basal traversodontids (Abdala & Ribeiro 2003) differ from later traversodontids in having only two main cusps in the upper postcanines and *Andescynodon* differs in having the transverse ridge of the upper teeth on the anterior half of the crown. Thus, it would appear that there is no direct phylogenetic connection between the dental pattern of the juvenile ?*Trirachodon* and the later *S. angustifrons.* Nonetheless, the resemblance in cusp patterns suggests that at least the external and internal upper cusps and the lower internal cusp of trirachodontids and traversodontids may be homologous. This further suggests that, as in *Diademodon* and traversodontids, the postcanine crown pattern of trirachodontids evolved from a primitive sectorial-type tooth by medial hypertrophy of an internal cingulum. Unlike the other two families, trirachodontids modified the external side of the tooth by losing the anterior and, especially, the posterior accessory cusps so that all longitudinal shear on the inner side of the main external cusp was lost.

Under the above interpretation of cusp homologies, only the external cusp of the *Trirachodon* postcanine shares any homology with the longitudinally sectorial crown of the carnivorous ancestor. Thus, the concept of the entire postcanine of *Trirachodon* originating from the entire sectorial tooth rotated 90 degrees (Rowe 1986; Abdala & Ribeiro 2003, fig. 4C) is untenable. The more likely interpretation of specimens in which the posterior two or three 'gomphodont' postcanines appear to be sectorial teeth progressively rotating into a transverse position is that the gomphodont teeth must develop in a longitudinal position at the rear of the narrow mandible; subsequently, as the mandible grows back and increases in diameter, the erupting teeth rotate into a fully functional transverse orientation. The last postcanine, which is oriented in line with the long axis of the dentary, probably is a sectorial tooth, as is commonly seen in both upper and lower jaws of *T. kannemeyeri.*

Under the interpretation of cusp homologies advanced here, the external and internal cusps of the upper postcanine are homologous in the three gomphodont families. A central cusp occurs in *Diademodon,* where it is low and poorly defined, so the three transversely-oriented cusps of the upper postcanines of diademodontids and trirachodontids are probably homologous as well. It is also likely that the two main cusps in the lower postcanines of diademodontids and traversodontids are homologous. This suggests that the central lower cusp of trirachodontids is a neomorph. Therefore, I conclude that the gomphodont postcanines of all three families are homologous as transversely expanded teeth that meet in crown-to-crown occlusion. This is contrary to the interpretation of Goñi and Goin (1987) on the origin of the traversodontid crown pattern directly from a sectorial-toothed Permian or Early Triassic ancestor.

Ontogeny of postcanine tooth function in *Trirachodon*

The transversely expanded postcanines of adult *Trirachodon* appears to be specialized for crushing and grinding, with no longitudinal and little transverse shearing involved. The juvenile specimen described here has taller cusps with steeper sides, suggesting the possibility

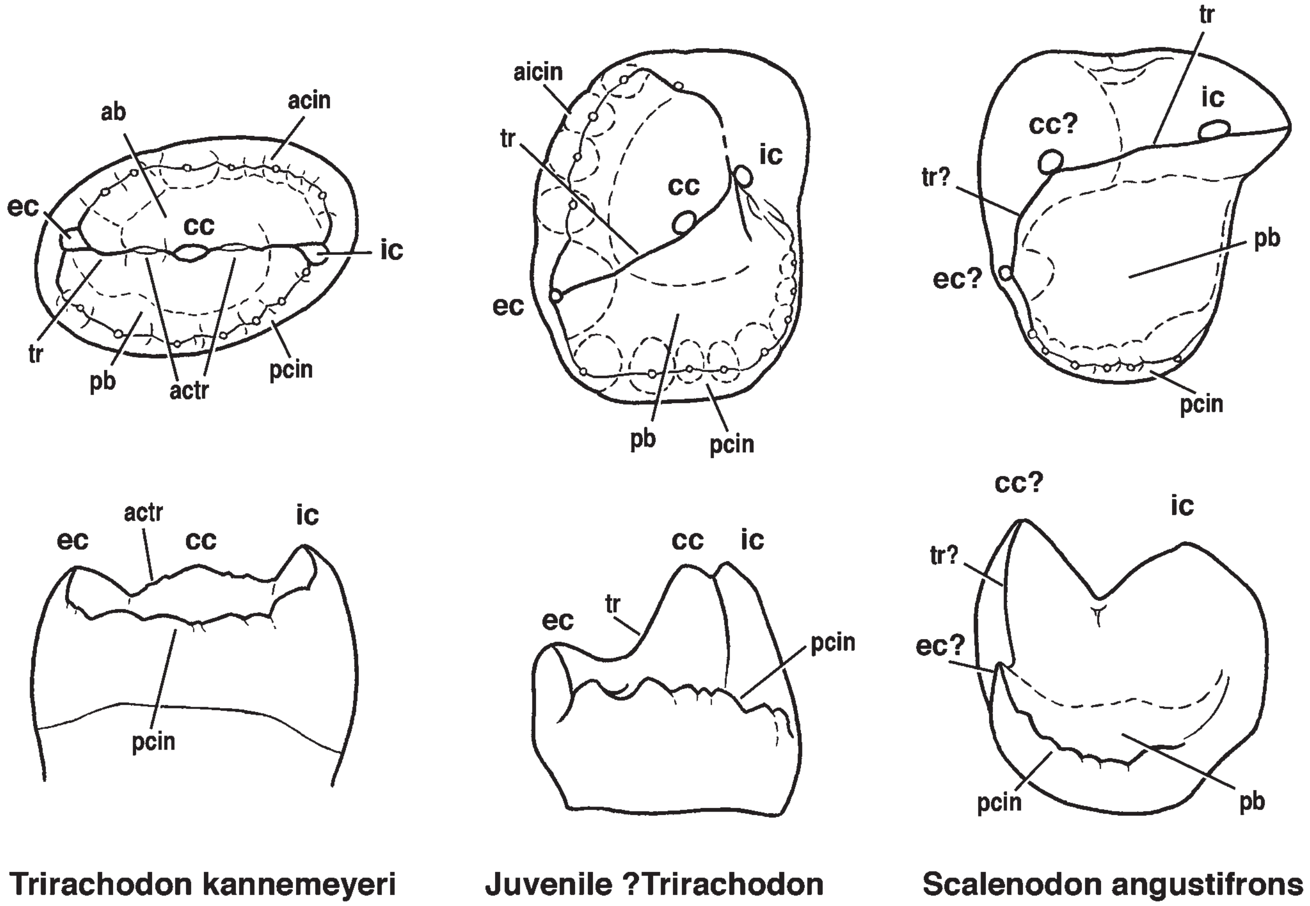

Figure 11. Comparison of lower postcanines in crown and posterior views of *Trirachodon kannemeyeri,* the juvenile specimen of ?*Trirachodon* sp. and *Scalenodon angustifrons.* Not to scale.

of some shear in addition to crushing. Posteriorly-sloping wear facets on the posterointernal ridges of both upper and lower anterior postcanines indicate that the internal cusp of each lower tooth contacted and slid up the rear of the next upper tooth forward, leaving wear surfaces on the posterointernal ridge of that upper tooth. The lower central and internal cusps then moved back across the posterior cingulum of the upper, wearing down its cingulum cusps. Each lower tooth then slid up and back against the anterior face of the next upper tooth back, leaving wear on the posterointernal ridge of the lower. The first part of the chewing stroke would have brought the transverse ridge of the lower to meet, or at least approach, the transverse ridge of the next upper forward, perhaps creating some cutting of the food. During the second, more retractive, portion of the chewing stroke, the main lower cusps (cc and ic) would have moved the food back into the anterior basin of the next upper tooth and then would have ground it against the anterior face of the main upper cusps (primarily CC and IC) by sliding back and down the inclined plane formed by those cusps (see Fig. 3), though probably only for a short distance.

As *Trirachodon* individuals matured, these taller and narrower (with respect to their length) postcanines would have been replaced by broader lower-cusped teeth, presumably with a more exclusively grinding function. Comparison of the posterior views of the postcanine of *T. kannemeyeri* and ?*Trirachodon* sp. (Figs 10 & 11) suggests that the main ontogenetic broadening of the tooth in successive replacements occurred on the medial half of the crown.

I thank Dr André Keyser for facilitating the loan of specimen JSM 100. I also wish to thank M. Claire Vanderslice for both the exceptionally fine preparation and the beautiful drawings of the specimen. My research was supported by National Science Foundation Research Grant BMS75-01159. Finally, I wish to acknowledge the importance to me of Dr James W. Kitching's friendship and support over the years. Wandering through the B.P.I. Karoo fossil collection with James, and listening to the story of each specimen he collected, was one of the great learning experiences of my life.

ABBREVIATIONS

ab	anterior basin
acin	anterior cingulum
actr	accessory cusps on transverse ridge
aicin	anteroexternal cingulum
aer	anteroexternal ridge
air	anterointernal ridge
brk	break
CC	upper central cusp
cc	lower central cusp
cc?	possible homologue of lower central cusp
crypt devPCa	crypt of developing upper postcanine (PC5?)
devPCa	developing upper postcanine (PC5?)
devPCb	developing upper postcanine (PC6?)
devPCc	developing upper lateral postcanine
displPCa	complete sectorial tooth loose in matrix
displPCb	rootless tooth loose in matrix
EC	upper external cusp
ec	lower external cusp
ec?	possible homologue of lower external cusp
ecin	external cingulum
IC	upper internal cusp
ic	lower internal cusp
lC	left upper canine
lc	left lower canine
mx	maxilla

orb	orbit
pal	palatine
pb	posterior basin
PC	upper postcanine
pc	lower postcanine
pcin	posterior cingulum
peg	peg-like upper tooth
per	posteroexternal ridge
pir	posterointernal ridge
pt	pterygoid
rC	right upper canine
rc	right lower canine
replC	replacement left upper canine
replc	replacement left lower canine
tr	transverse ridge
tr?	possible homologue of transverse ridge
unshedPC	unshed small worn gomphodont postcanine
v	vomer

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Late Triassic traversodontids (Synapsida: Cynodontia) in southern Africa

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Scalenodontoides macrodontes was described in 1957 by Crompton & Ellenberger as a new genus and species of the family Traversodontidae. For many years it was known only by its type specimen, a lower jaw from the Upper Triassic of Lesotho. The specimen was redescribed in more detail by Hopson in 1984, who established the close affinities of *Scalenodontoides* with *Exaeretodon.* In 1993, Gow & Hancox described the first skull of *Scalenodontoides,* discovered, together with fragmentary remains, in South Africa. The skull from South Africa looked very much like a skull from Lesotho, housed in the Muséum National d'Histoire Naturelle, Paris, and initially attributed, in an unpublished work, to the chiniquodontid *Belesodon* (Costedoat, 1962). Further preparation of the skull from Lesotho was carried out; the specimen proved not to belong to a chiniquodontid, but to a large traversodontid, described in this paper. A revision of the traversodont remains known from the Late Triassic lower Elliot Formation of Lesotho and South Africa leads to the conclusion that they can all be attributed to the species *Scalenodontoides macrodontes.* Detailed comparisons between *Scalenodontoides* and *Exaeretodon* confirm *Scalenodontoides* as a valid genus, with only one species, *Scalenodontoides macrodontes.* A new diagnosis of *Scalenodontoides macrodontes,* based on an analysis of all available material, is given.

Keywords: traversodontids, Lesotho, South Africa, Late Triassic.

INTRODUCTION

The family Traversodontidae was originally erected in 1936 by Huene to accommodate new forms of gomphodont cynodonts from south America. It is now known by many taxa of various sizes and skull morphologies, which share, in particular, many features in the structure of their postcanine teeth. A cosmopolitan Triassic family, the traversodontids are mostly represented in Argentina (Cabrera 1943; Romer 1967, 1972; Bonaparte 1962, 1963, 1978) and in Brazil (Huene 1935–1942; Barberena 1974; Abdala *et al.* 2002); they are also known from Tanzania (Crompton 1955, 1972), Zambia (Brink 1963; Kemp 1980), Lesotho (Crompton & Ellenberger 1957), South Africa (Gow & Hancox 1993), Madagascar (Flynn *et al.* 2000), India (Chatterjee 1982), Canada (Hopson 1984; Sues *et al.* 1992), the United States of America (Sues & Olsen 1990; Sues *et al*. 1999), Belgium (Hahn *et al.* 1988), France (Godefroit & Battail 1997), and, perhaps, Russia (Tatarinov 1973; Battail & Surkov 2000). Among the many taxa which have been described, some appear to be of dubious validity and a number of possible synonymies were suggested by Battail (1991, 58–60).

In striking contrast with South America, where Late Triassic traversodontids are numerous and relatively diversified, southern Africa has yielded up to now only very few specimens which can be attributed to Late Triassic traversodontids. The purpose of this paper is to provide a short review of the Late Triassic traversodontid material already known from southern Africa, and to describe one more specimen, a skull which, although collected long ago, had been initially misinterpreted, and had never been published. The anatomical characters of the southern African Late Triassic traversodontids are discussed and compared with other representatives of the family. These data are incorporated into a brief systematic and phylogenetic analysis.

REVIEW OF THE LATE TRIASSIC TRAVERSODONTIDS IN SOUTHERN AFRICA

Scalenodontoides macrodontes was described in 1957 by Crompton & Ellenberger as a new genus and species of the family Traversodontidae. The type specimen, the tooth-bearing portions of a huge lower jaw (Figs 1–3), was found on the northern slope of Morobong Hill, Mohale's Hoek district, Lesotho (then, Basutoland), and attributed to 'the upper Molteno Beds'. It has since been established by Turner (1972), that it comes in fact from the base of the Elliot Formation. The type specimen of *Scalenodontoides macrodontes* is housed in the Palaeontology unit of the Muséum National d'Histoire Naturelle (MNHN), Paris, under the number 1957–23. Complements to the original description, comments and comparisons were given by Hopson (1984). A second specimen referred to *Scalenodontoides macrodontes* is the right half of the anterior part of a snout, collected at a short distance from the type, and housed in the South African Musem, Cape Town (SAM K336); it was described and figured by Hopson (1984).

Crompton & Ellenberger (1957) correctly attributed *Scalenodontoides macrodontes* to the Traversodontidae, and compared it to several other genera of the same family. However, they never mentioned the genus *Exaeretodon,* described in 1943 by Cabrera. Hopson (1984) stressed the close affinities of the genera *Scalenodontoides* and *Exaeretodon* which, according to the diagnosis he gave of the genus *Scalenodontoides,* would have differed mostly in their robustness, in their skull proportions and in the relative size of their lower canines and incisors. It must be noted, however, that one of the few characters mentioned by Hopson to distinguish *Scalenodontoides* from *Exaeretodon,* namely, the presence of a chin-like ventral projection of the symphysis of the dentary, found only in *Scalenodontoides,* cannot be retained: a similar feature can indeed be observed in *Exaeretodon argentinus* and in *E. statisticae* (see for

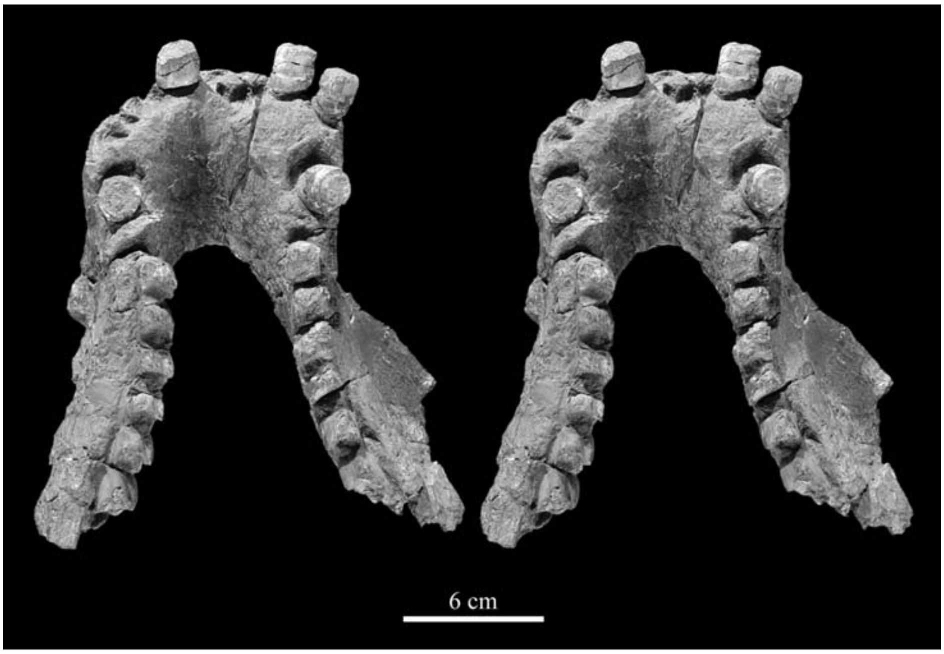

Figure 1. Stereophotograph of the type specimen of *Scalenodontoides macrodontes,* lower jaw (MNHN 1957-23), in dorsal view.

example Chatterjee 1982, figs 2 & 5). Clearly, at that stage of our knowledge of *Scalenodontoides,* the generic distinction between *Exaeretodon* and *Scalenodontoides* could be questioned.

More recently, Hancox discovered relatively abundant material attributed to *Scalenodontoides* and coming from the base of the Elliot Formation of the farm Norwood, Sterkstroom district, Eastern Cape Province, South Africa. The new material, representing at least three individuals of different sizes, was described in detail by Gow & Hancox (1993). It is housed in the Bernard Price Institute, University of the Witwatersrand, Johannesburg, and includes a complete skull (BP/1/5395 A) (Figs 4–7), an isolated parietal fragment (BP/1/5395 B), a fragment of a large snout (BP/1/5395 C), several isolated maxillary postcanines (BP/1/5395 D), and fragments of lower jaws, including one which pertains probably to the complete skull (BP/1/5395 E). The attribution of the South African material to *Scalenodontoides* is certainly correct: the piece of snout from Morobong, Lesotho, is very broad and extremely similar to the corresponding parts of the snouts from South Africa (snout of the complete skull, and isolated snout fragment); the piece of right lower jaw from South Africa has the same size and robustness as the corresponding portion of the type specimen from Lesotho; it has also a posterior mental foramen, and bears five fragmentary postcanine teeth of the same structure as the postcanines of the type. Moreover, the South African material comes from the same stratigraphic level, the base of the Lower Elliot Formation.

The skull described by Gow and Hancox is in good condition, but it has been very dorsoventrally compressed. In its general proportions, it displays a few conspicuous features: the snout is very broad, the skull roof is very broad between the orbits, and the temporal region is remarkably short. These cranial proportions appear as

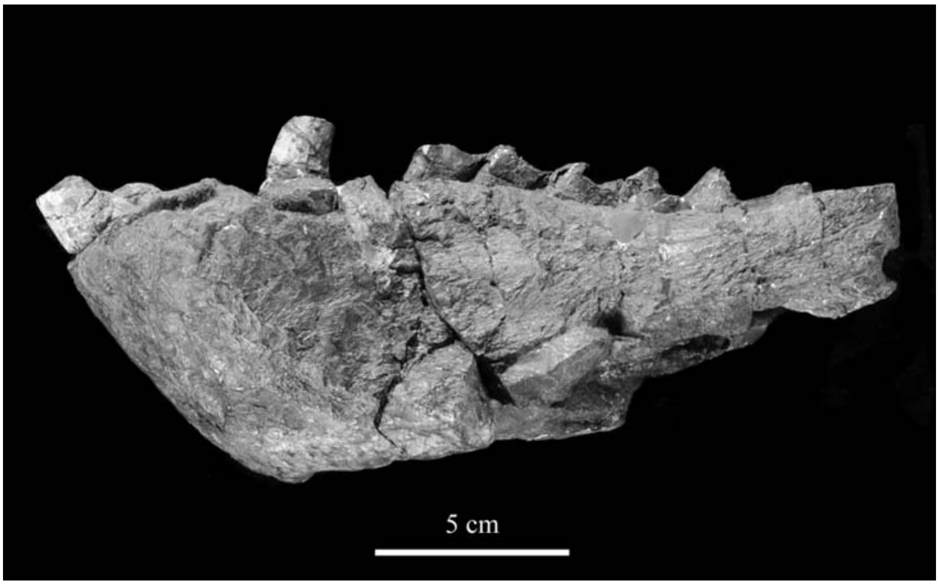

Figure 2. Photograph of the type specimen of *Scalenodontoides macrodontes,* lower jaw (MNHN 1957-23), left lateral view.

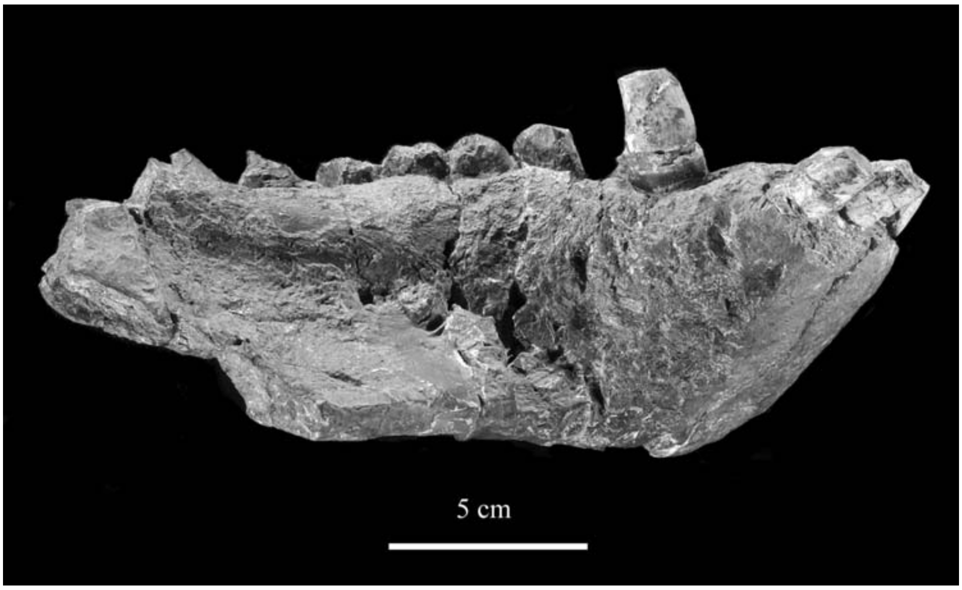

Figure 3. Photograph of the type specimen of *Scalenodontoides macrodontes,* lower jaw (MNHN 1957-23), right lateral view.

quite different from those of *Exaeretodon,* in which the snout is more slender and has a more marked constriction behind the canine, the interorbital width is much more reduced, and the temporal fossae are much more elongated. But the most obvious difference is the existence, in *Scalenodontoides* only, of what Gow & Hancox named a nuchal table: 'In all other cynodonts, parietals, squamosals, and tabulars combine to form a sharp crest separating the

Figure 4. Photograph of the skull of *Scalenodontoides macrodontes* (BP/1/5395 A), dorsal view.

Figure 5. Photograph of the skull of *Scalenodontoides macrodontes* (BP/1/5395 A), ventral view.

occiput from the temporal openings. In *Scalenodontoides* the parietals form a broad, coarsely rugose horizontal shelf, barely overhanging the temporal openings, but forming an extensive shelf above the occiput. Smoothly concave lateral indentations are present where the parietals drop vertically to be overlapped by the squamosals which then wrap around onto the anterior surface as far as the borders of the posttemporal fenestrae.' (Gow & Hancox 1993, 162–164). That unique nuchal table is considered by Gow & Hancox as establishing the generic distinctiveness of *Scalenodontoides.*

The study by Gow & Hancox (1993) of the upper dentition of the South African specimens shows that, as in the snout fragment from Lesotho, there are only three incisors immediately followed by the canine. More important perhaps is the first description of upper postcanines of *Scalenodontoides.* In the skull, only the last postcanine of each row is preserved. In addition, identifiable isolated postcanines include five right uppers and four left uppers. In crown view, the upper postcanines all display a more or less geniculate shape, and can be described as composed of two lobes, one labial lobe and one lingual lobe, which meet in an angle; three in-line labial cusps flank a very steep shearing plane; the central labial cusp is the main one, the anterior and posterior accessory labial cusps are connected to the crest that descends from the main labial cusp; the central part of the crown is occupied by a basin surrounded by a rim which is thicker on the lingual side. The interpretation of the last postcanines which remained *in situ* in the skull is difficult, as 'these teeth had suffered some wear through use, and unfortunately they are impacted into their sockets and have been deformed' (Gow & Hancox 1993, 165). It is worth noting, however, that the last left upper postcanine displays a narrow bridge connecting the labial and lingual lobes, and that the latter is posterior, rather than medial, to the labial lobe (see Gow & Hancox 1993, fig. 8 top right).

THE LARGE CYNODONT SKULL FROM LERIBE (LESOTHO)

Introduction

A large cynodont skull had been found in 1955 by F. Ellenberger near Leribe, northern Lesotho, in the lowermost part of the Elliot Formation (base of the 'Lower Red Beds'). That skull, now housed in the Muséum National d'Histoire Naturelle (MNHN), Paris, under the number 1955–25, is not very well preserved, and was partly

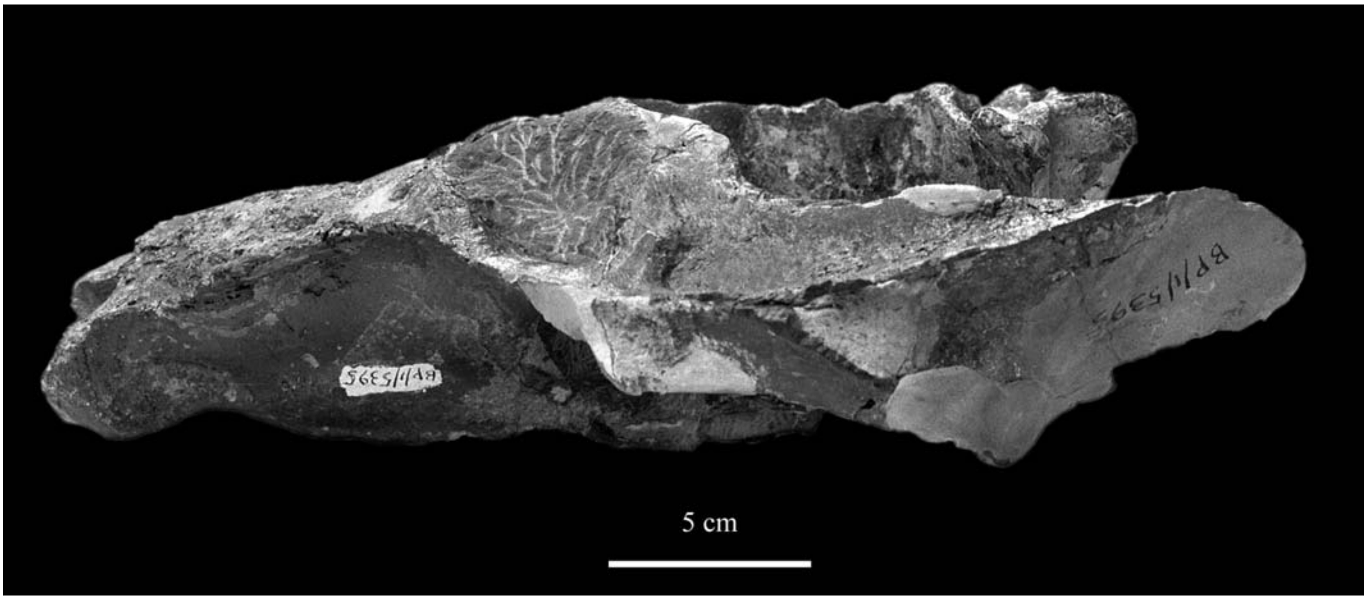

Figure 6. Photograph of the skull of *Scalenodontoides macrodontes* (BP/5395 A), left lateral view.

embedded in an extremely hard matrix. Without any further preparation, it was briefly described in an unpublished work by Costedoat (1962), and compared by her, mainly on the basis of similarities in size and in the structure of the skull roof, with the chiniquodontid *Belesodon* from Brazil.

After the description of the skull of *Scalenodontoides* by Gow and Hancox, I realized that the skull from Leribe, Lesotho, was very similar to it, and that, most probably, it had originally been misinterpreted. Further preparation of the skull from Leribe was carried out; the specimen proved not to belong to a chiniquodontid close to *Belesodon,* but to a large traversodontid.

Description

The state of preservation of the cynodont specimen from Leribe is rather poor. The specimen consists of a large skull without lower jaw (Fig. 8–11). It was found in several pieces. The snout is extremely weathered, and its contact with the rest of the skull is not very good. The skull has not been compressed, but it is distorted, it bears numerous fractures and cracks, and most sutures are not visible. The bone is often difficult to distinguish from the matrix, which is very hard and could not be entirely removed. Only two teeth (right upper postcanines) are preserved.

The basal length of the skull, about 28 cm, is approximately equal to its maximum width. In size and general proportions, the specimen agrees very well with the skull of *Scalenodontoides* described by Gow & Hancox.

Little can be said of the snout, except that it is massive, short and very broad. The dorsal surface of the skull, between the level of the anterior border of the orbits and the level of the posterior part of the temporal openings, is remarkably similar to that of the South African skull: the skull roof is very broad between the orbits (minimum interorbital distance: 12 cm), and the postorbitals have a

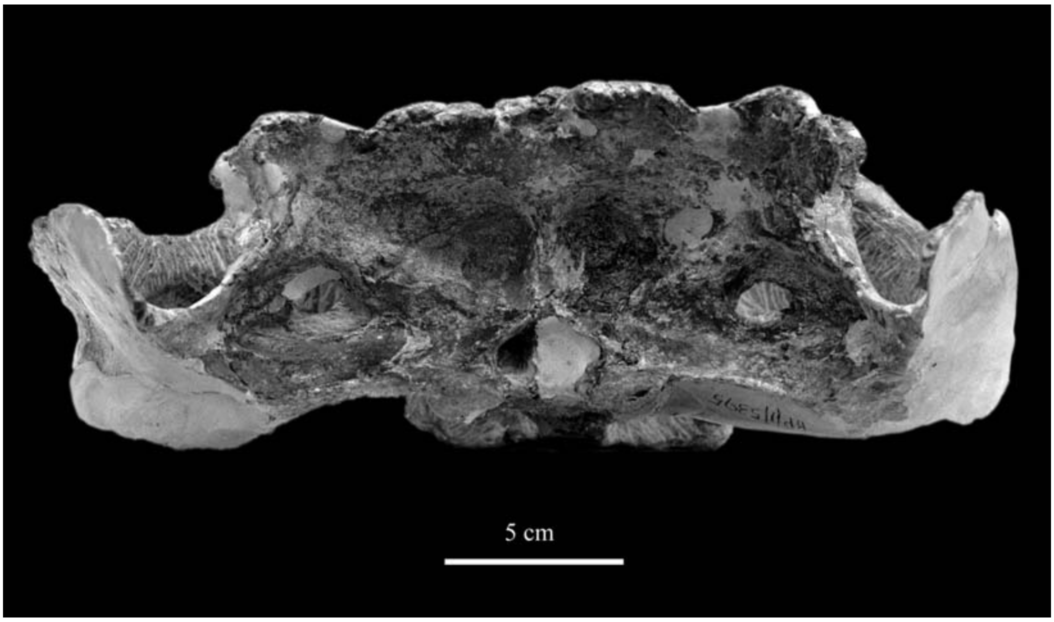

Figure 7. Photograph of the skull of *Scalenodontoides macrodontes* (BP/5395 A), occipital view.

Figure 8. Photograph of the skull of *Scalenodontoides macrodontes* (MNHN 1955-25), dorsal view.

strong dorsal ridge bordering the temporal openings; however, the medial ridge of the frontals is less pronounced than on the South African skull, and no pineal foramen could be found in the Leribe specimen. The temporal region is very short. The cranial arches – suborbital and postorbital bars, zygomatic arch – are extremely robust. As in the *Scalenodontoides* skull from South Africa, the lateral surface of the jugal is depressed behind the orbit. Only the left zygomatic arch is preserved; its posterior surface is weathered, and therefore the posterior process of the squamosal is not preserved.

The occipital region of the skull from Lesotho has been somewhat distorted, but still displays clearly the same structure as that of any other cynodont, with two sharp occipital crests meeting the posterior part of the sagittal crest. The left part of the occipital plate is still coated with a plane layer of very hard matrix, through which one would have expected to see a horizontal shelf of bone protruding, if a nuchal table had been present; the right part of the occipital plate has been partially prepared, and, similarly, no evidence of a nuchal table could be found. The occipital region of the skull from Lesotho is therefore very different from that of the South African skull, even if two common features can be found: the medial part of the occipital crest is almost horizontal (in most cynodonts, the occipital crest descends regularly from the sagittal crest to the squamosal), and, seen in dorsal view, the two occipital crests meet in a very obtuse angle (in most cynodonts, they meet in a more closed angle).

The ventral surface of the skull is neither well preserved, nor fully prepared. The secondary palate is complete and well developed. As in other advanced traversodontids, the postcanine row is displaced medially. Owing to the bad state of preservation of the snout, the total number of the postcanines could not be established. Only two postcanines are preserved, the antepenultimate and the last one of the right side. Behind the pterygoid flanges, the basicranial axis is broad and short. The occipital condyles

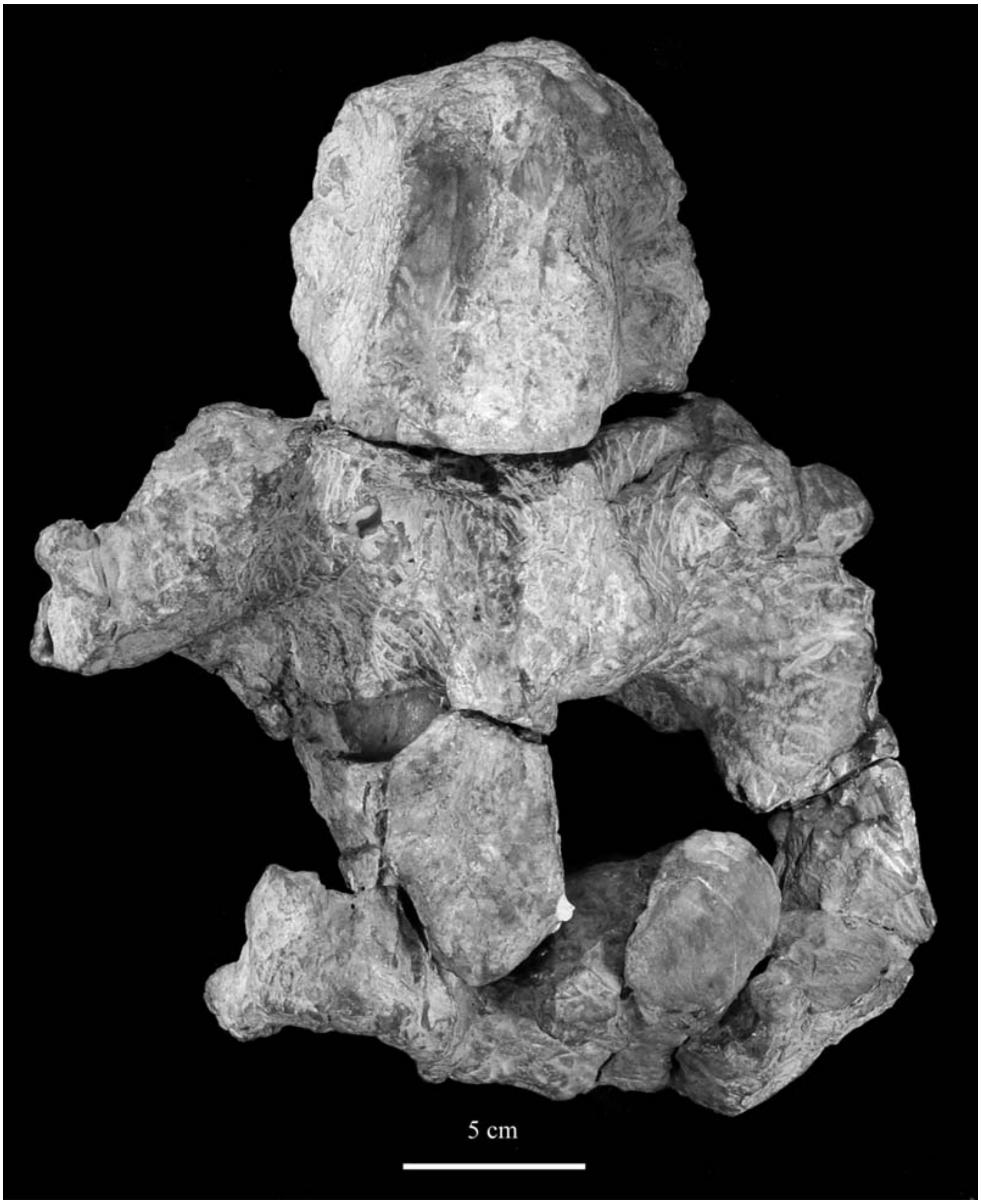

Figure 9. Photograph of the skull of *Scalenodontoides macrodontes* (MNHN 1955-25), ventral view.

are very damaged, especially the right one; they are widely separated. The paroccipital process, relatively well preserved on the left side, is extremely massive.

Dentition. Little can be said of the antepenultimate postcanine, which is very damaged. Its outline in occlusal view is similar to that of the postcanines of *Scalenodontoides* described by Gow & Hancox, 1993, fig. 6e, but it seems to have been narrower anteroposteriorly. The last postcanine (Figs 12–16) has a crown which has suffered only little wear, and it has been fully prepared. Its root is not preserved. Its setting in the tooth row is particular, the main axis of the occlusal surface of the crown being orientated almost anteroposteriorly, rather than obliquely as in the antepenultimate postcanine: the 'lingual lobe' is thus posterior, rather than medial, to the 'labial lobe'. For comparative purposes, the terms labial and lingual have, however, been retained in the description which follows. The two lobes are very well individualized, they are separated by a narrow constriction, marked, behind the posterior accessory labial cusp, by a fold of enamel which penetrates deeply between them. The anterior accessory labial cusp is not very distinct from the main labial cusp. The posterior accessory labial cusp, very small, is situated low on the crown; it rises from a cingulum and is connected to a blunt ridge which descends from the main labial cusp. The lingual lobe bears several ill-defined, low cusps. The postero-external wall of the crown is bordered with a cingulum. The last upper postcanine of the skull from Lesotho is similar to the last left postcanine of the *Scalenodontoides* skull from South Africa in its anteroposterior orientation, and in the presence of a constriction between the two lobes.

Discussion

Owing to its relatively poor state of preservation, the traversodontid skull from Lesotho could not be described in as much in detail as the skull from South Africa. It is higher than the skull from South Africa (but the latter has

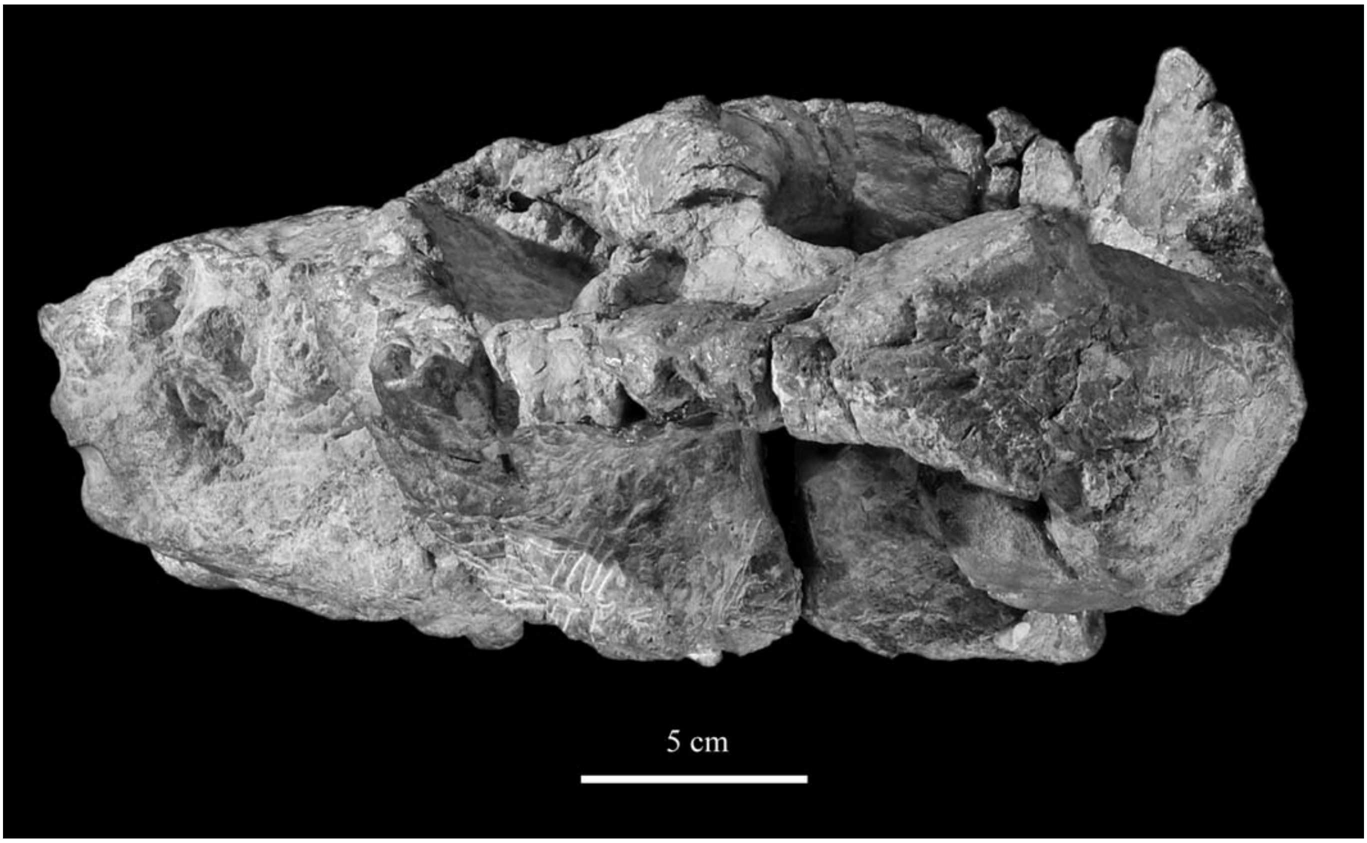

Figure 10. Photograph of the skull of *Scalenodontoides macrodontes* (MNHN 1955-25), left lateral view.

been dorsoventrally compressed), and it has a more massive paroccipital process. Every other character observable on the skull from Lesotho agrees very closely with the corresponding character of the skull from South Africa, with one noticeable exception: a conspicuous nuchal table is present in the skull from South Africa, but totally absent in the skull from Lesotho. Does that only difference, sharp as it may seem, warrant the attribution of the skull from Lesotho to a new taxon? I do not think so, and am inclined to believe that it could rather be ascribed to sexual dimorphism, keeping in mind the fact that, in living tetrapods, sexual dimorphism often expresses itself by a major differ-

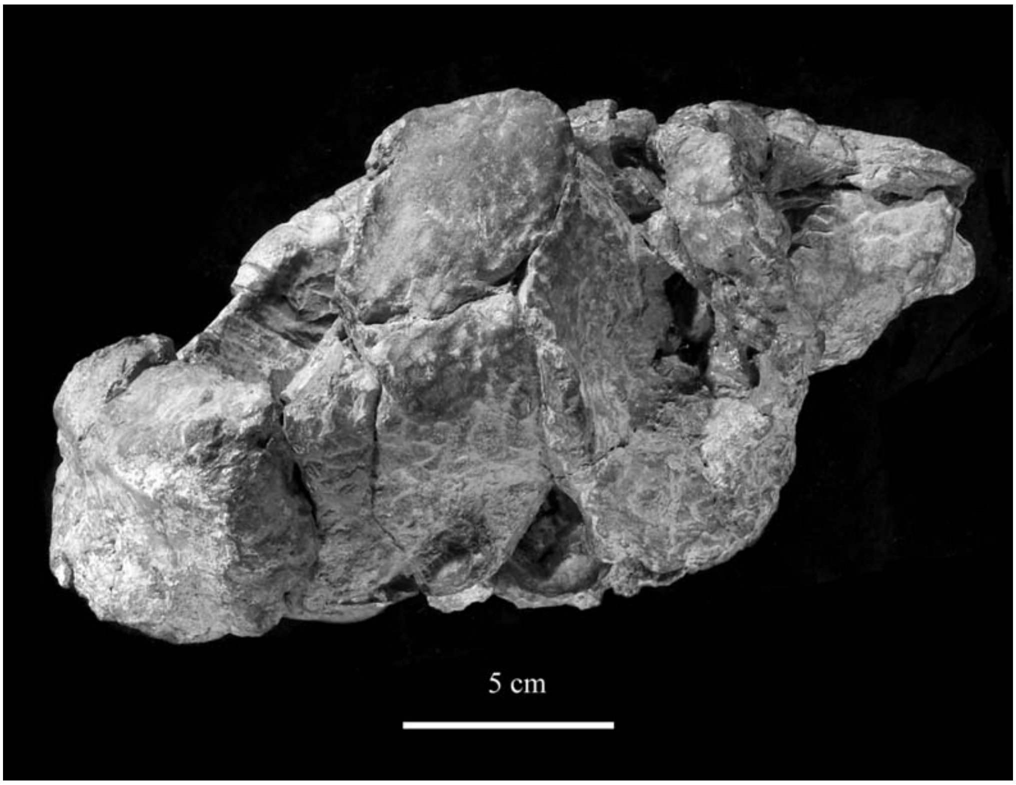

Figure 11. Photograph of the skull of *Scalenodontoides macrodontes* (MNHN 1955-25), occipital view.

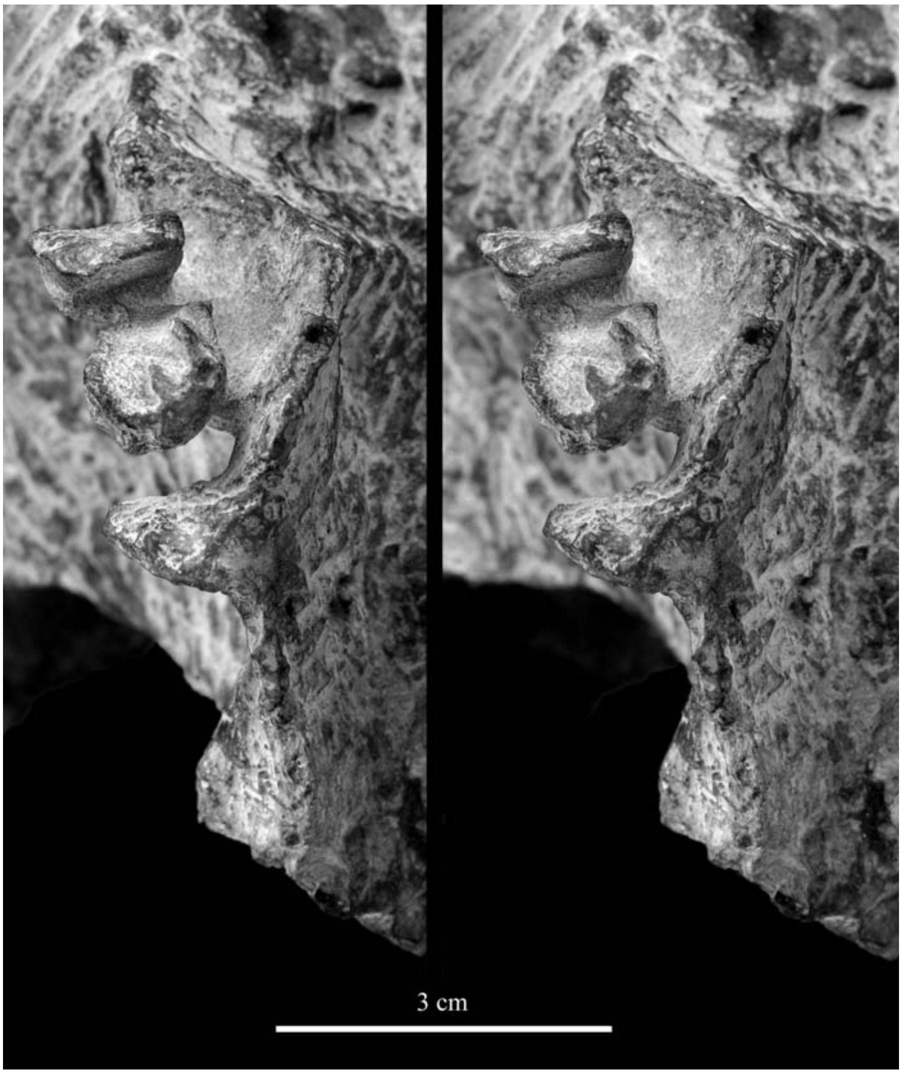

Figure 12. Stereophotograph of the last right upper postcanine of *Scalenodontoides macrodontes* (MNHN 1955-25), occlusal view.

ence dealing with just one character (presence or absence of horns, in many antelope species, for example).

If my conclusions are accepted, all the traversodontid specimens known from the Lower Elliot Formation may be attributed to the species *Scalenodontoides macrodontes.* If they are not, it becomes impossible to determine if it is the skull from South Africa or the skull from Lesotho which belongs to *Scalenodontoides macrodontes.*

THE GENUS SCALENODONTOIDES

Comparisons and phylogeny

In 1984, Hopson re-examined *Scalenodontoides macrodontes,* and convincingly demonstrated that *Scalenodontoides* was a close relative of *Exaeretodon.* In the same paper, he described the fragmentary remains of a huge traversodont found in the Upper Triassic beds of the Wolfville Formation of Nova Scotia, Canada. The largest piece was a partial lower jaw – the horizontal ramus of a right dentary with a small portion of the left dentary adjacent to the symphysis – similar in size and robustness to the corresponding part of the type specimen of *Scalenodontoides macrodontes.* It was chosen as the type specimen of a new species, provisionally placed in the genus *Scalenodontoides* and named ?*Scalenodontoides plemmyridon.* Unfortunately, neither the type specimen, nor the two other dentaries from the same locality, attributed to the same species, had kept their postcanines. An isolated tooth, interpreted as a right lower postcanine, was tentatively assigned to ?*Scalenodontoides plemmyridon.* It is composed of 'a tall, transversely-widened, anterior blade bearing three principal cusps, and a low, anteroposteriorly-narrow, posterior heel' (Hopson 1984, 196).

The problem, well understood and explained by Hopson, was the following: the postcanines of *Scalenodontoides* would have been expected to be similar to those of *Exaeretodon* but, instead, that isolated tooth, wider than long, with anteroposteriorly compressed main cusps, could rather be compared with a lower postcanine of a very different genus, *Massetognathus.* A few years later, a new traversodont tooth, an isolated left upper postcanine, was discovered in the Wolfville Formation of Nova Scotia; it is characterized, in particular, by its anteroposterior compression, by the presence of three large cusps on a vertical transverse ridge, and by a low anterior cingulum. It had then became clear that only one species of large traversodont was represented in the Wolfville Formation and that the isolated postcanines, in view of their sizes and shapes, could be referred to it. These isolated postcanines, upper as well as lower, are far too different, in

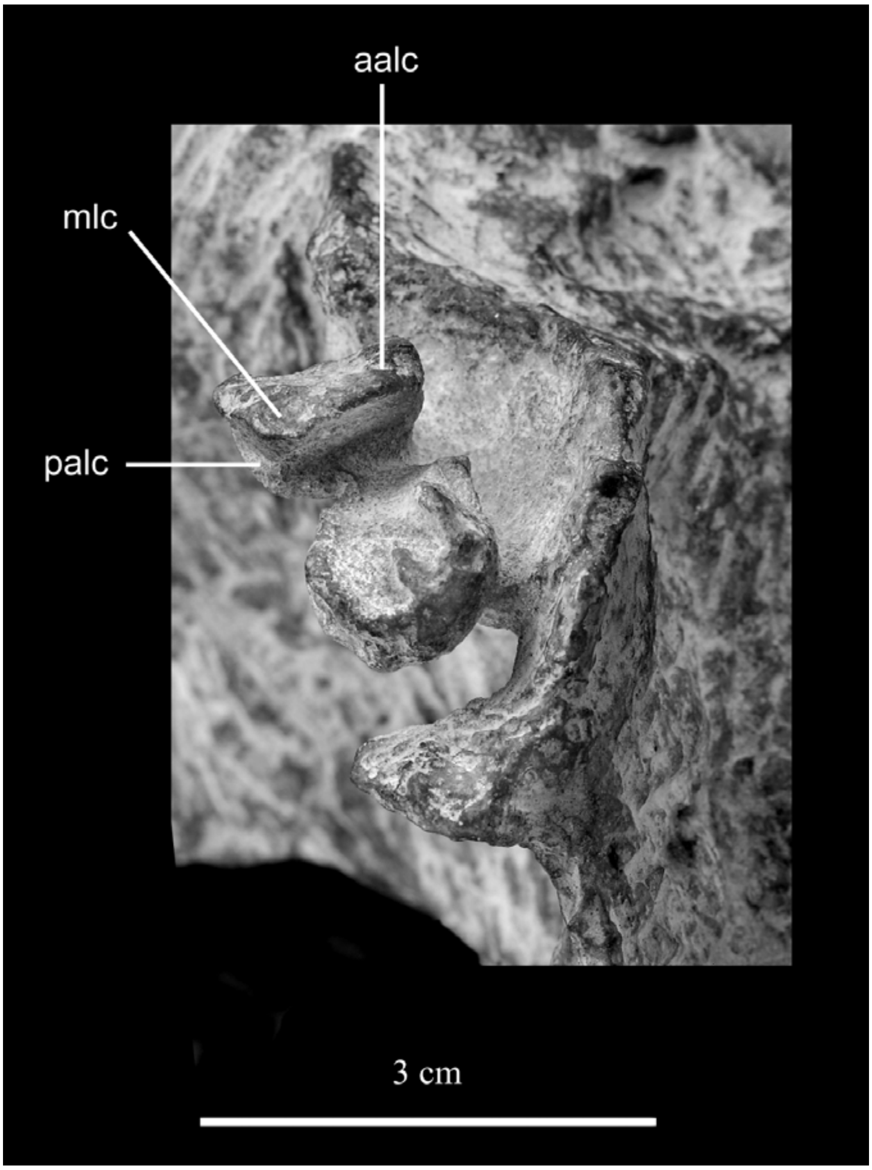

Figure 13. Photograph of the last right upper postcanine of *Scalenodontoides macrodontes* (MNHN 1955-25), occlusal view. Abbeviations: aalc, anterior accessory labial cusp; mlc, main labial cusp; palc, posterior accessory labial cusp.

their structure, from those of *Exaeretodon,* to belong to such a close relative of *Exaeretodon* as *Scalenodontoides.* Consequently, the traversodont from Nova Scotia was transferred by Sues, Hopson & Shubin (1992) to the new genus *Arctotraversodon.* The possibility of a close relationship between the three North American genera *Arctotraversodon, Boreogomphodon* and *Plinthogomphodon* has been suggested by Sues, Olsen & Carter (1999) on the basis of similar features of the upper postcanines. Finally, only one species remains in the genus *Scalenodontoides,* the type species *Scalenodontoides macrodontes.*

Hopson (1984, 1985) could define, within the traversodontids, a clade, comprising *Gomphodontosuchus, Exaeretodon* and *Scalenodontoides,* characterized by the following features of the postcanines: (A) upper postcanines (1) a very oblique orientation of the postcanines in the maxilla; (2) lack of a central cusp on the posterior transverse ridge; (3) a high anterior wall bounding the central basin; (4) a prominent internal ridge anterior to the main internal cusp. (B) Lower postcanines (1) the antero-external cusp is wider than the anterointernal cusp; (2) the anterointernal cusp is inclined obliquely backwards; (3) the crown in occlusal view has a trapezoidal rather than rectangular outline.

The recently described genus *Menadon,* from Madagascar, belong also to this clade (Flynn *et al.* 2000).

Menadon, Exaeretodon and *Scalenodontoides* are united by a few synapomorphies: internarial bar incomplete; enlarged incisors, the lower being procumbent; reduction of upper incisors from four to three. *Exaeretodon* and *Scalenodontoides* have a closer relationship, as they share additional synapomorphies: lack of small anterior postcanines; outline of the upper postcanines geniculate in occlusal view, with very distinct labial and lingual lobes; presence of a posterior accessory labial cusp on the upper postcanines, observable at least on the last ones. As stated by Hopson as early as 1984, *Exaeretodon* appears as the sister genus of *Scalenodontoides.* But thanks to the description of more material since then, the differences between the two genera can now be more clearly pointed out.

The skull of *Scalenodontoides* is different in shape and proportions from that of *Exaeretodon:* its snout is shorter

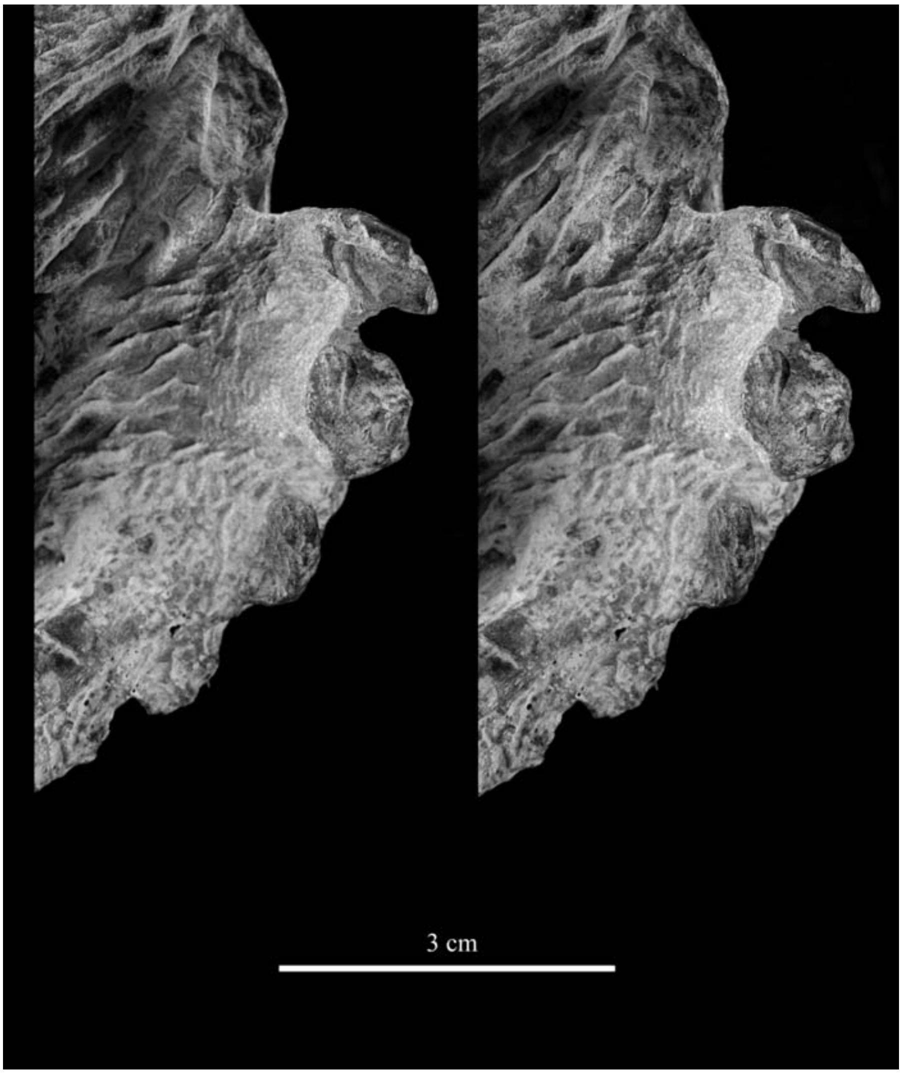

Figure 14. Stereophotograph of the last right upper postcanine of *Scalenodontoides macrodontes*(MNHN 1955-25), postero-external view.

and broader, its temporal region is much shorter; its occipital crests meet in a very obtuse angle; its lower jaw is more massive. A very conspicuous cranial feature, a nuchal table running across the top of the occiput, distinguishes also *Scalenodontoides* from *Exaeretodon;* but it seems to be present only in certain individuals, and could be a character linked to sexual dimorphism (see above).

The dentition is very similar in *Exaeretodon* and *Scalenodontoides.* A few differences can, however, be noted. In all the genera of the clade to which *Scalenodontoides* pertains (*Gomphodontosuchus, Menadon, Exaeretodon* and *Scalenodontoides*), the upper postcanines are orientated obliquely in the maxilla, rather than transversely as in other traversodonts (*Massetognathus,* for example). In *Exaeretodon,* the obliqueness of the orientation of the postcanines increases slightly, but regularly, from front to rear in the tooth row. In *Scalenodontoides,* there is a sharp change of orientation of the last postcanine, which has the main axis of its crown orientated almost anteroposteriorly, rather than obliquely. The labial and lingual lobes of the last upper postcanine, as recorded in both *Exaeretodon* and *Scalenodontoides,* are clearly distinct, being demarcated by an angulation between them, but in *Scalenodontoides* this demarcation is further emphasized by a constriction. On the upper postcanines of *Exaeretodon* and *Scalenodontoides* which have not suffered extensive wear through use, a posterior accessory labial cusp can be seen. It has been described in detail by Abdala *et al.* (2002) in *Exaeretodon:* 'In unworn teeth, the labial posterior accessory cusp is completely isolated from the crest that descends from the main labial cusp .... Thus, two basins characterize the unworn postcanine: the principal one formed by the anterior accessory labial cusp and the main labial cusp, and a posterior small one formed only by the posterior accessory labial cusp.' (Abdala *et al.* 2002, p. 320 and fig. 9). In *Scalenodontoides,* as can be seen on the last postcanine of the skull from Lesotho and on the moderately worn isolated postcanines from South Africa described by Gow & Hancox (1993), the posterior accessory labial cusp, small and very low, is connected by a crest to the main labial cusp and does not form a small basin. The postero-external wall of the crown of the last upper postcanine is bordered by a well developed cingulum in *Scalenodontoides;* such a cingulum does not exist in *Exaeretodon.* The lower postcanines are also slightly different in *Exaeretodon* and *Scalenodontoides.* As noted by Hopson, 'in crown view, the ridge which passes back from the apex of the lingual cusp to the heel describes a distinct curve, concave lingually [in *Scalenodontoides*], whereas in *Exaeretodon* ... the ridge is straight.' (Hopson 1984, 183).

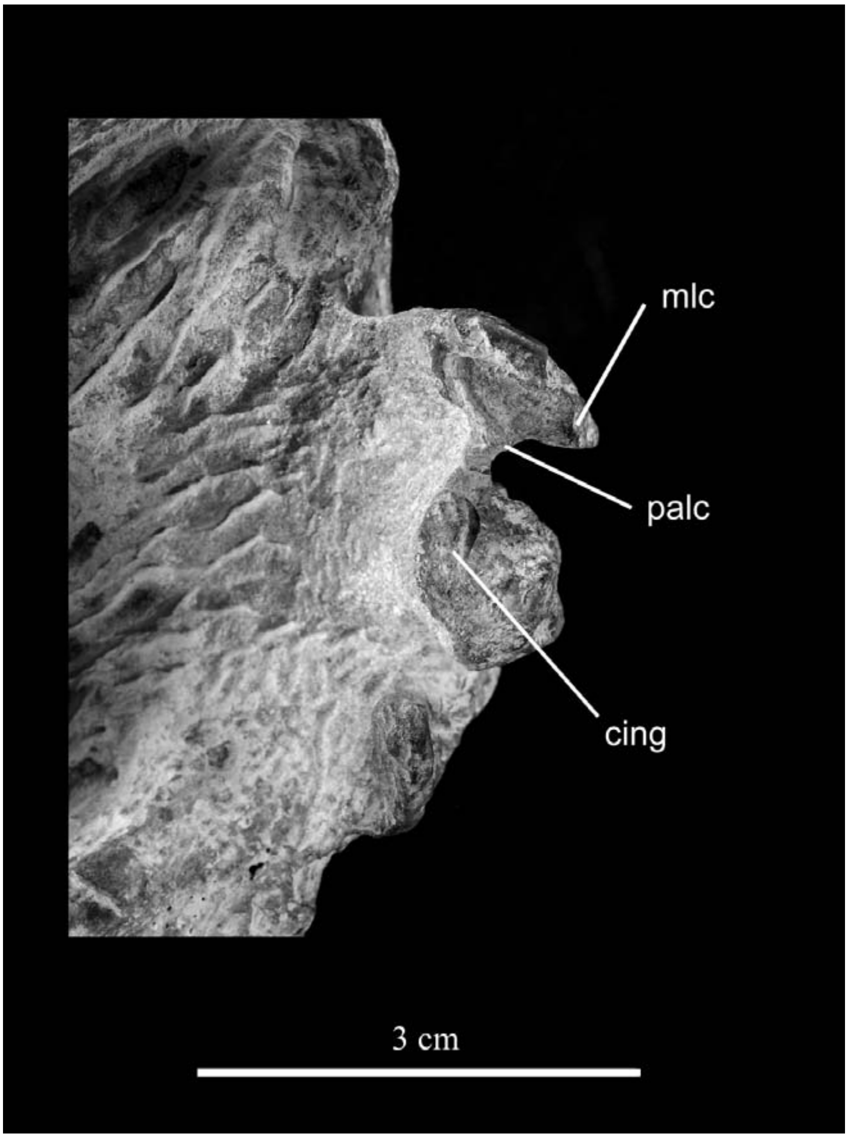

Figure 15. Photograph of the last right upper postcanine of *Scalenodontoides macrodontes* (MNHN 1955-25), postero-external view. Abbreviations: cing, cingulum; mlc, main labial cusp; palc, posterior accessory labial cusp.

SYSTEMATIC PALAEONTOLOGY

Synapsida
Therapsida
Theriodontia
Cynodontia
Traversodontidae

Scalenodontoides Crompton & Ellenberger, 1957

Scalenodontoides macrodontes Crompton & Ellenberger, 1957

Holotype. Specimen No. 1957–23 in the palaeontology unit of the Muséum National d'Histoire Naturelle, Paris. Paired dentaries lacking the region behind the postcanines.

Referred specimens. The right front half of a large snout, No. SAM K336, in the collection of the South African Museum, Cape Town. A complete skull with a fragment of lower jaw, the front part of a large snout, a sagittal crest and isolated postcanines, No. BP/1/5395 in the collection of the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg. A skull lacking the lower jaw, No. 1955–25 in the palaeontological unit of the Muséum National d'Histoire Naturelle, Paris.

Horizon and localities. The type specimen and the partial snout housed in the South African Museum were found a short distance apart; they come from Morobong, Mohale's Hoek district, Lesotho. Originally attributed by Crompton & Ellenberger (1957) to 'the upper Molteno Beds', they are in fact from the base of the Elliot Formation, as shown by Turner (1972). The material housed in the Bernard Price Institute was scattered over a wide area, but comes from only one locality, the farm Norwood, Sterkstroom district, Eastern Cape Province; it was found 'at the base of the Elliot Formation immediately above its contact with the underlying Molteno Formation' (Gow & Hancox 1993). The skull without lower jaw kept in the Muséum National d'Histoire Naturelle was indicated by Ellenberger as having been found near Leribe, Leribe district, Lesotho, at the base of the 'Lower Red Beds', that is to say, in the lowermost part of the Elliot Formation. Thus, all recorded specimens come apparently from the same level: *Scalenodontoides macrodontes* seems to characterize a very narrow stratigraphic interval at the base of the Late Triassic Lower

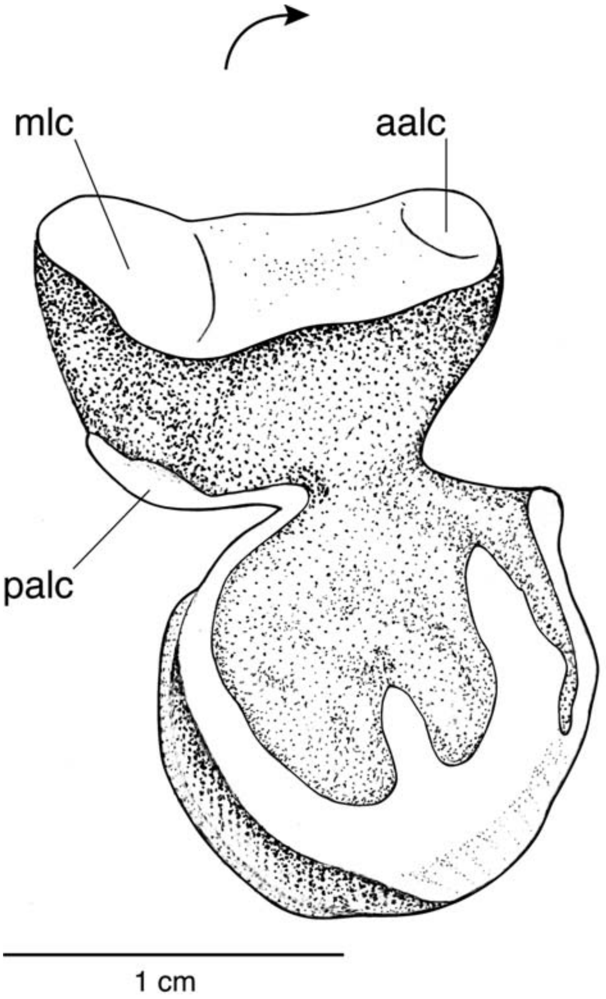

Figure 16. Occlusal view of the last right upper postcanine of *Scalenodontoides macrodontes* (MNHN 1955-25). Abbreviations as in Fig. 13.

Elliot Formation (see Kitching & Raath 1984, fig. 2).

Revised diagnosis. A very large traversodontid. Skull very robust, approximately as broad as long. Snout short and broad. Internarial bar incomplete. Skull roof very broad between the orbits. Temporal region remarkably short. Temporal opening wider than long. Occipital crests almost horizontal in their medial portion, and meeting, in dorsal view, at a very obtuse angle; they can be followed by a robust, overhanging nuchal table composed mostly by the parietal. Occipital condyles widely separated. Lower jaw massive; symphysis broad, long and deep. Upper dentition with only three, large, incisors. Upper postcanines orientated obliquely in the maxilla, except the last one, which has the main axis of its crown orientated almost anteroposteriorly. Labial and lingual lobes of the last upper postcanines clearly distinct and demarcated one from another by a constriction. On the upper postcanines, the posterior accessory cusp is linked by a crest to the main labial cusp, and does not form a basin. The postero-external wall of the crown of the last upper postcanine is bordered by a cingulum. Lower dentition with three very large, procumbent incisors. Lower canine orientated slightly posteriorly. In the lower postcanines, the anterolabial cusp is much larger than the anterolingual cusp; the posterior basined heel is relatively short; in crown view, the ridge which passes back from the apex of the lingual cusp to the heel describes a distinct curve, concave lingually.

CONCLUSIONS

Only one traversodont is known from the Late Triassic Elliot Formation of Lesotho and South Africa, namely *Scalenodontoides macrodontes.* Since the description of this taxon by Crompton & Ellenberger (1957), on the basis of a lower jaw only, additional material, mainly cranial, could be attributed to it. Its study confirms the conclusion drawn as early as 1984 by Hopson, that *Scalenodontoides* is the sister taxon of *Exaeretodon. Scalenodontoides* appears, however, far more different from *Exaeretodon* than could be initially expected. The unique nuchal table, described by Gow & Hancox (1993), the very unusual skull proportions (very broad skull, extremely short temporal region), and distinctive features of the dentition, leads me to consider it indeed as a valid genus. *Scalenodontoides* is also the only cynodont in which pronounced sexual dimorphism can be suggested.

From a biostratigraphic point of view, *Scalenodontoides macrodontes* is interesting, as it characterizes only a short interval in the lowermost part of the Elliot Formation. Finally, the new assignment of the skull from Leribe, Lesotho, has consequences on biogeographical interpretations: as this skull had originally been attributed to a large chiniquodontid, the presence of *Belesodon* sp. in the Upper Triassic of southern Africa was sometimes mentioned in the literature (see for example P. Ellenberger 1970). It appears now that there is no evidence of the existence of such a chiniquodontid in Africa.

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Biostratigraphy of the lower Burgersdorp Formation (Beaufort Group; Karoo Supergroup) of South Africa – implications for the stratigraphic ranges of early Triassic tetrapods

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The Beaufort Group (Karoo Supergroup) of South Africa comprises a thick sequence of fluvio-lacustrine sedimentary rocks that accumulated in a landlocked, intracratonic foreland basin in southwestern Gondwana during the Middle Permian to Middle Triassic. To the south this basin was bounded by the Cape Fold Belt, which acted as the major source of both sediment and discharge. Rocks of the Beaufort Group are renowned for their rich fossil record and eight tetrapod-based biozones are currently recognized. The uppermost two biozones of the Beaufort Group, the *Lystrosaurus* and *Cynognathus* assemblage zones, record terrestrial biotic recovery following the Permo-Triassic mass extinction event. Stratigraphic overlap between these biozones occurs in the proximal sector, but their separation by an unconformity in the distal sector reflects the incomplete preservation of the sequence in this part of the basin. Our results afford chronostratographic control that impacts on current theories on the development of the Karoo Basin, and on the relative age of the sequence.

Keywords: Early Triassic, Karoo Basin, *Lystrosaurus* and *Cynognathus* Assemblage Zones, stratigraphic range, overlap.

INTRODUCTION

Rocks of the Beaufort Group (Karoo Supergroup) outcrop over approximately 300 000 km^2 in South Africa (Smith 1990) and are renowned for their wealth of terrestrial tetrapod fossils, which have enabled the present eightfold biostratigraphic subdivision of this succession (Rubidge *et al.* 1995). This largely uninterrupted record represents a period extending from the Middle Permian to Middle Triassic (Hancox & Rubidge 2001; Rubidge 2005). It fulfils a prominent role in the correlation of terrestrial sequences and Lucas (1998), who advanced a global tetrapod biochronology scheme for the Triassic, based his Lootsbergian and Nonensian land vertebrate faunachrons on fossil assemblages from the Beaufort Group. Owing to the reciprocal flexural profile of the Karoo Basin (Catuneanu *et al.* 1998), the Beaufort Group accumulated in a strongly partitioned foreland basin. Base-level changes in the proximal and distal regions of the basin, corresponding to the southern and northern parts of the basin respectively (Fig. 1), were consequently out-of-phase, and display contrasting stratigraphies.

Triassic strata of the Beaufort Group, encompassing the uppermost Palingkloof Member of the Balfour Formation, as well as the overlying Katberg and Burgersdorp formations (Fig. 2), have been the focus of much research over the past decade (Smith 1995; Groenewald 1996; Hancox 1998, 2000; Smith & Ward 2001; De Kock & Kirschvink 2004; Neveling 2004). The basal part of the Burgersdorp Formation displays thin, weakly lenticular channel sandstones which are dominated by horizontally stratification, indicating strong genetic links with the arenaceous Katberg Formation. This proposed genetic relationship (Marais & Johnson 1965; Groenewald 1996; Hancox 1998), allied to the apparent gradational nature of the contact between these two formations (Johnson & Hiller 1990; Groenewald 1996), prompted several workers to postulate lateral equivalency for the upper Katberg, and lower Burgersdorp formations (Johnson 1976; Stavrakis 1980; Johnson & Hiller 1990; Groenewald 1996; Hancox 1998; Neveling *et al.* 1999).

Biostratigraphically the Triassic rocks of the Beaufort Group incorporate the *Lystrosaurus* and *Cynognathus* assemblage zones (AZs). The fauna and distribution of these biozones have been the focus of much recent research (Hancox 1998; Hancox & Rubidge 2001; Hancox *et al.* 2002; Damiani & Jeannot 2002; Neveling 2002, 2004; Damiani & Hancox 2003; Abdala *et al.* 2005). Various workers have investigated the terrestrial expression of the end-Permian mass extinction at the base of the *Lystrosaurus* AZ (Smith 1995; MacLeod *et al.* 2000; Ward *et al.* 2000; Smith & Ward 2001; Hancox *et al.* 2002 Latimer *et al.* 2002; Retallack *et al.* 2003; Steiner *et al.* 2003; De Kock & Kirschvink 2004). Higher in the succession the recognition of faunal elements of the *Cynognathus* AZ in the northern part of the Karoo Basin (Welman *et al.* 1991) sparked new interest in the latter biozone which resulted in the description of a number of new tetrapod taxa (Damiani 1999, 2001; Neveling *et al.* 2001; Damiani & Jeannot 2002). Of greater significance was a proposal by Hancox and others (Hancox *et al.* 1995; Hancox & Rubidge 1997; Hancox 1998, 2000) for an informal threefold subdivision of the

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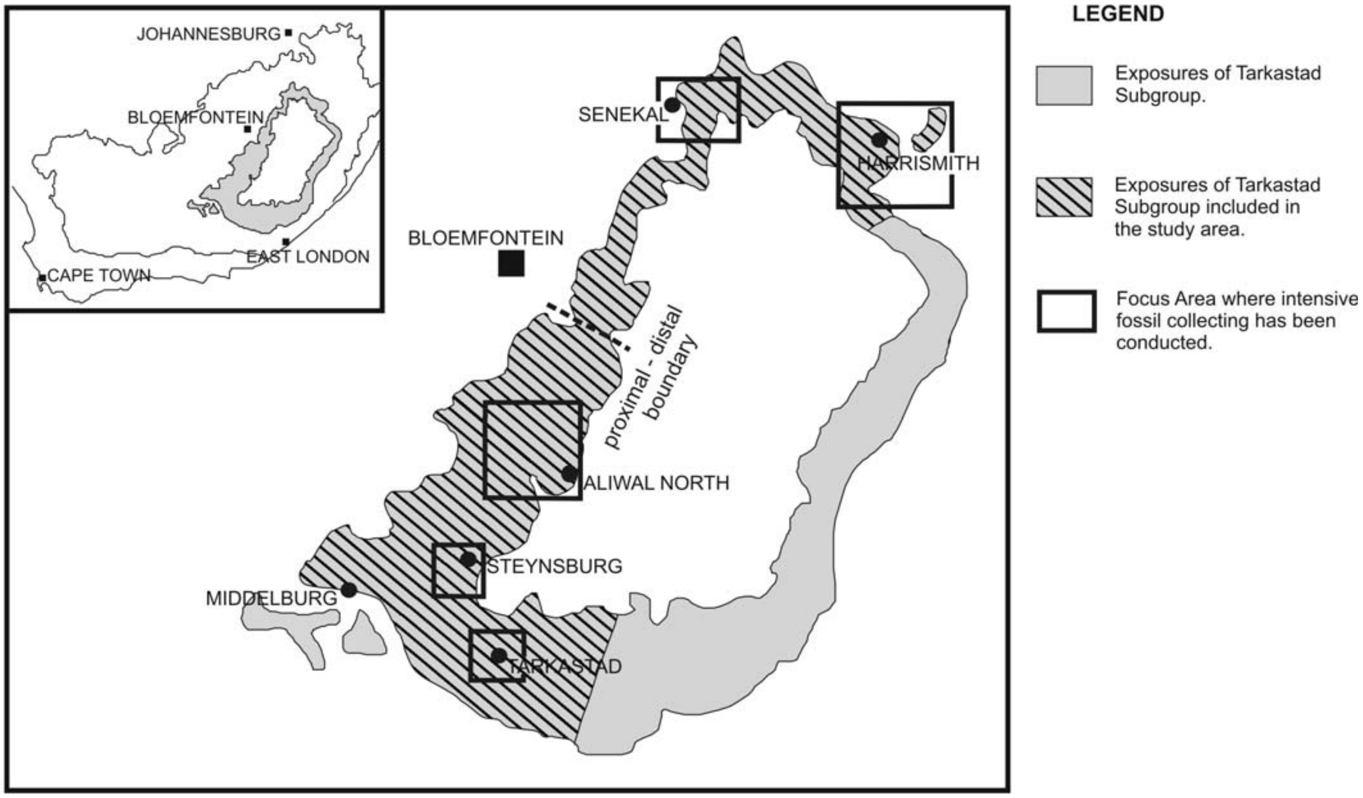

Figure 1. Map showing the distribution of the Tarkastad Subgroup and location of the study area.

Cynognathus AZ, based on the stratigraphic and temporal distribution of key mastodonsaurid (amphibian) genera. Subsequent research further revealed the presence of a more cosmopolitan tetrapod fauna in the uppermost Burgersdorp Formation than previously recognized (Hancox & Rubidge 1994, 1996; Hancox 1998; Hancox *et al.* 2002; Damiani & Hancox 2003; Abdala *et al.* 2005).

The contact between the *Lystrosaurus* and *Cynognathus* AZs, from both a palaeontological and geological point of view, has been a particular focus of Karoo Triassic research in recent years. Kitching (1977) was the first to observe that these are the only two biozones of the Beaufort Group with no common fossil taxa. Later researchers attributed the abrupt nature of this faunal turnover to: the presence of a fossil-barren interval separating the two biozones (Keyser & Smith 1977–78); a stratigraphic gap (Anderson & Cruickshank 1978; Cosgriff 1984; King 1990; Battail 1993); or an extinction event (Lucas 1998). Geological data do not support the existence of a major unconformity within the exposures of the proximal sector, and hypotheses proposing the presence of a stratigraphic gap or fossil-barren zone, have been discredited (Neveling 2002, 2004). In the Rouxville and Burgersdorp districts, stratigraphic overlap has been documented between fossil tetrapod taxa of the *Lystrosaurus* AZ and the lowermost subzone of the *Cynognathus* AZ (Neveling 1998; Neveling *et al.* 1999). Based on the data then available, these authors suggested that an 'Impoverished Zone', encompassing the *Procolophon* Zone of Broom (1906) and part of the lowermost *Cynognathus* AZ as defined by Hancox *et al.* (1995), existed between the *Lystrosaurus* AZ of Groenewald and Kitching (1995) and the *Cynognathus* AZ of Kitching (1995).

NEW BIOSTRATIGRAPHY

An extensive study, incorporating exposures of the Tarkastad Subgroup in both the proximal and distal sectors, and an intensive fossil collecting programme in five selected focus areas (Fig. 1), has enabled us to determine the stratigraphic ranges of various tetrapod taxa and to test earlier hypotheses. Stratigraphic ranges of the fossil tetrapod taxa are summarized in Fig. 3, and it is evident that the patterns differ in the northern (distal) and southern (proximal) parts of the basin.

Our new data do not support the existence of an 'Impoverished Zone' between the *Lystrosaurus* and *Cynognathus* of the proximal sector, but shows the taxa previously reported from this interval to have long stratigraphic ranges extending into the adjacent biozones. The *Procolophon* Zone of Broom (1906) constitutes a very thin horizon that occurs only in isolated geographical localities [for example on the farm Elandskop (S31°57.93′ E26°07.78′) in the Tarkastad district; Neveling 2002] right at the top of the *Lystrosaurus* AZ (*sensu* Groenewald & Kitching 1995). The only two tetrapod genera we recorded from the '*Procolophon* Zone', *Procolophon* and the amphibian *Micropholis,* also occur in traditional exposures of the *Lystrosaurus* AZ lower down in the stratigraphic sequence, with *Procolophon* considered an index taxon of the latter biozone (Groenewald & Kitching 1995). Due to a dearth of distinguishing characters, we are of the opinion that there are no grounds to recognize a distinct and separate '*Procolophon* Zone'. However, the dramatic increase in the number of *Procolophon* fossils towards the top of the *Lystrosaurus* AZ, may in future lead to the recognition of a '*Procolophon* Abundance Zone'.

Our research demonstrates that the range of *Thrinaxodon*

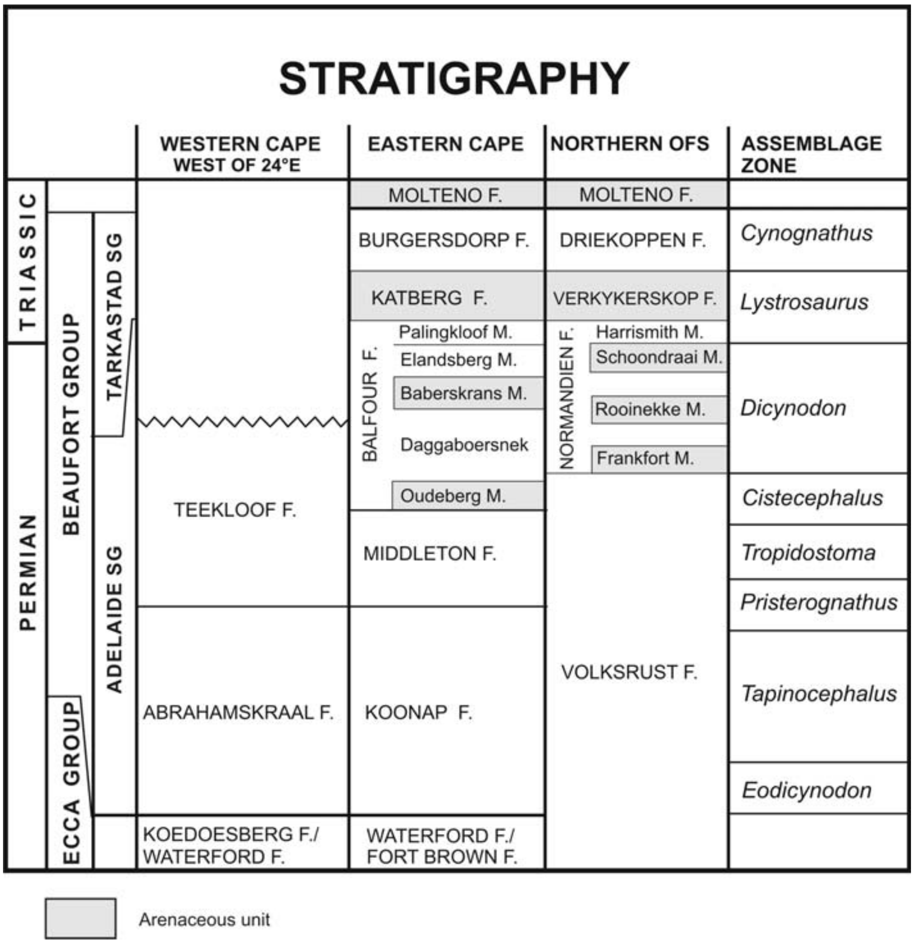

Figure 2. Stratigraphic units of the Beaufort Group. After Rubidge *et al.* (1995).

extends throughout the *Lystrosaurus* AZ; and that *Lystrosaurus* is absent from the very top of this biozone (its last appearance datum [LAD] being more than 50 m below that of *Procolophon* in the proximal exposures of this AZ). *Lystrosaurus* thus disappears before the other elements of the *Lystrosaurus* AZ faunal assemblage (Groenewald & Kitching 1995). The presence of *Thrinaxodon* at the top of the succession in the proximal sector contradicts Groenewald & Kitching's (1995) contention that this genus, together with *Galesaurus*, is restricted to the middle part of the *Lystrosaurus* AZ.

Overlap in the stratigraphic ranges of taxa of the *Lystrosaurus* AZ and the lowermost subzone of the *Cynognathus* AZ is restricted to a very thin stratigraphic interval. In the rocks of the proximal sector the abrupt faunal change-over between the *Lystrosaurus* and *Cynognathus* AZs occurs in the uppermost sandstones of the Katberg Formation and lowermost mudstones of the Burgersdorp Formation (Neveling 2002, 2004; Fig. 3). Our research has also demonstrated that the *Cynognathus* AZ correlates with the entire Burgersdorp Formation, contradicting earlier workers (Keyser & Smith 1977–78; Groenewald & Kitching 1995) who considered the lowest third of the Burgersdorp Formation as part of the *Lystrosaurus* AZ. This means that the latter AZ is restricted to the Palingkloof Member of the Balfour Formation, and the Katberg Formation.

We have traced the lowermost subzone of the *Cynognathus* AZ (Hancox *et al.* 1995) from the northern part of the Karoo Basin (Hancox *et al.* 1995; Shishkin *et al.* 1995) as far south as the Tarkastad and Queenstown districts (Neveling 2002, 2004), and support formal recognition of this biostratigraphic interval. Mastodonsaurid amphibians (Damiani 2001) assignable to the genus *Kestrosaurus* (Shishkin *et al.* 2004) dominate this interval, while the fragmentary medium to large cynodonts from this interval, previously assigned to *Cynognathus* and *Diademodon* (Welman *et al.* 1991; Hancox *et al.* 1995; Hancox 1998) have recently been identified as *Cynognathus* (Hopson, pers. comm., 2002), confirming this faunal assemblage as representing a lower interval of the *Cynognathus* AZ. In the southernmost part of the basin the fauna of this subzone is represented by very scarce amphibian, trirachodontid and archosauriform material from the mudstones and sandstones of the lowermost Burgersdorp Formation. As one proceeds northwards in the basin there is a gradual increase in fossil abundance within this horizon, such that most of the fossils from this interval have been collected from the Senekal and Bethlehem districts in the Free State Province.

Differences between the ranges of taxa in the northern and southern parts of the basin are significant. Overlap between faunas traditionally described from the *Cynognathus* AZ (*sensu* Kitching 1995) and those of the underlying *Lystrosaurus* AZ (*sensu* Groenewald & Kitching 1995) is limited to the southern part of the basin (proximal sector), while no overlap has been recorded in the northern part of the basin (distal sector; see Fig. 3).

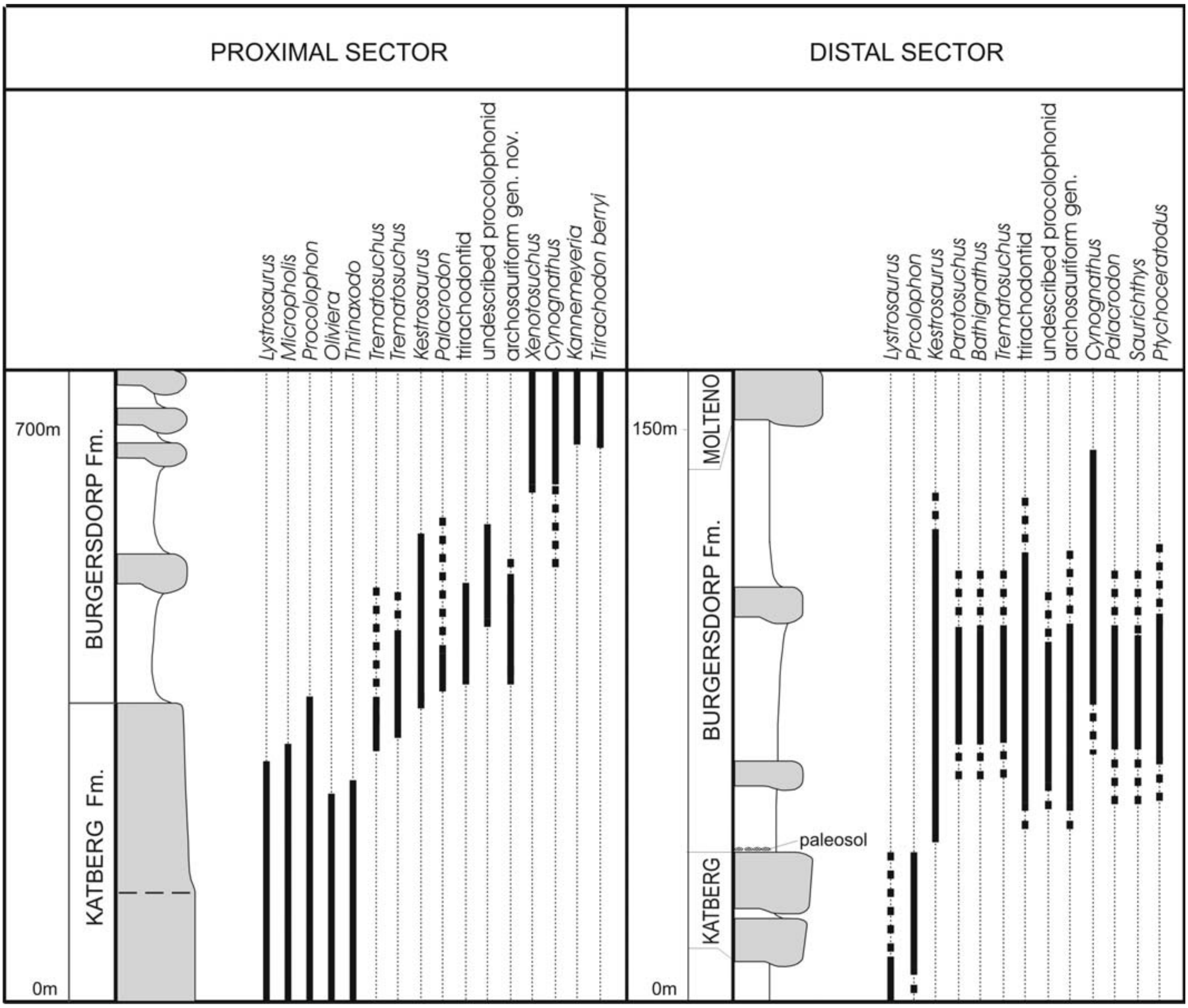

Figure 3. The ranges of important fossil taxa as documented in the studied interval for the proximal and distal sectors of the Karoo Basin. Dashed lines represent inferred stratigraphic ranges based on fragmentary fossil material or literature data. The actinopterygian material is described in Bender & Hancox (2004). (Note sections are not to scale.)

NATURE OF OVERLAP

In the southern half of the study area, west of Aliwal North, the LAD of *Lystrosaurus* is situated in the sandstones of the uppermost Katberg Formation, below the first appearance datum (FAD) of the amphibians *Trematosuchus* and *Kestrosaurus. Procolophon* occurs above the LAD of *Lystrosaurus* and overlaps the ranges of *Trematosuchus, Kestrosaurus* and *Palacrodon,* traditionally considered to be from the *Cynognathus* AZ, by more than 20 metres. Above the LAD of *Procolophon* the fauna of the lowermost *Cynognathus* AZ increases dramatically in abundance with the appearance of trirachodontid cynodonts, procolophonid material that resembles *Thelerpeton* and *Teratophon* in appearance (Cisneros, pers. comm., 2006) and a new erythrosuchid archosauriform. *Cynognathus, Bathignathus, Saurichthys* and *Ptchychoceratodus* have been recorded in the richer northern deposits and do not appear to overlap with *Lystrosaurus* AZ representatives (Neveling 2002). Significantly no dicynodonts, or indeed any medium to large herbivores, have been documented from this subzone, the only interval in the Beaufort Group in which dicynodonts are absent.

LATERAL EQUIVALENCE

Short-snouted (trematosaurine) trematosaurid amphibians are the first elements of a post-*Lystrosaurus* fauna to appear in the stratigraphic record. In the proximal sector an isolated mandible, most likely assignable to *Trematosuchus* (Damiani *et al.* 2000), recovered from the uppermost Katberg Formation in the Burgersdorp district, represents the FAD of trematosaurids. *Trematosuchus* is well documented from the mudstones of the overlying Burgersdorp Formation (Shishkin & Welman 1994; Shishkin *et al.* 1995). As this represented the first record from the Katberg Formation of a taxon previously assigned to the *Cynognathus* AZ (Kitching 1995), it was interpreted as supporting evidence of lateral equivalence of the Katberg and Burgersdorp formations (Neveling *et al.* 1999).

Fossils collected during the course of this study do not support a simple model of lateral equivalence. With the exception of the trematosaurid mandible discussed above and an *ex situ,* tabular fragment assigned to a *Kestrosaurus*-grade mastodonsaurid amphibian, only fossils of the *Lystrosaurus* AZ (*sensu* Groenewald & Kitching 1995) were found in the proximal outcrops of the upper Katberg Formation. *Procolophon* is the dominant tetrapod fossil in the uppermost exposures of the *Lystrosaurus* AZ. Besides two fragmentary *Procolophon* mandibles, only fossils assignable to Subzone A of the *Cynognathus* AZ are found in the lower Burgersdorp Formation of both the proximal and distal sectors of the basin (Fig. 3). The basin-wide correspondence of the *Lystrosaurus* AZ with the Katberg Formation, and the lower *Cynognathus* AZ with the Burgersdorp Formation, seems to suggest that the stratigraphic distribution of these biozones are facies-specific. However, the contact between the two formations is gradational and a detailed sedimentological analysis revealed the presence of similar local depositional environments within both the upper Katberg and lower Burgersdorp formations (Neveling 2002, 2004). Instead, we interpret this association to be indicative of an incomplete stratigraphic record, especially in the distal sector, which resulted from the complex interaction of dynamic subsidence and reciprocal flexure (Catuneanu *et al.* 1998; Pysklywec & Mitrovica 1999; Catuneanu & Elango 2001; Hancox *et al.* 2002; Neveling 2002) in the development of the Karoo Basin.

Our comprehensive biostratigraphic dataset does not support lateral equivalence of the Katberg and Burgersdorp formations, but rather suggests contemporaneous deposition of the lower Burgersdorp Formation in both the southern and northern parts of the basin. From our faunal analysis it is clear that the trematosaurid and mastodonsaurid amphibians, otherwise typical of the *Cynognathus* AZ, are earliest records from the uppermost exposures of the Katberg Formation in the proximal sector and that they predate the appearance of the rest of the *Cynognathus* AZ fauna.

AGE

The stratigraphic overlap between the faunas of the *Lystrosaurus* (*sensu* Groenewald & Kitching 1995) and *Cynognathus* (*sensu* Kitching 1995) AZs has significant consequences for the age determination and duration of the *Lystrosaurus* AZ. Although the earliest record of the genus *Lystrosaurus* is latest Permian (Cheng 1993; Smith 1993, 1995; Smith & Ward 2001), the typical *Lystrosaurus* AZ fauna appears only in the earliest Triassic (MacLeod *et al.* 2000; Smith & Ward 2001; De Kock & Kirschvink 2004; Ward *et al.* 2005). Correlation with *Lystrosaurus*-bearing strata in Russia (Kalandadze 1975; Shishkin *et al.* 2000) and Asia (Romer 1969; Lucas 1993) and more direct correlation with the amphibian fauna in the Andavakoera Formation (Sakamena Group, Madagascar) and Wordy Creek Formation (East Greenland) support an Induan age (Anderson & Cruickshank 1978; Cooper 1982; Ochev & Shishkin 1989; Hankel 1994). Close taxonomic affinities between the rhytidosteid amphibians of the South African *Lystrosaurus* AZ (Kitching 1978; Cosgriff 1984), various Australian assemblages (Cosgriff 1965, 1974, 1984; Cosgriff & Zawiskie 1979; Warren 1991) and the Sticky Keep Formation of Spitzbergen (Cosgriff 1965) also suggest an early Olenekian age (Tozer 1967; Tozer & Parker 1968; Cox & Smith 1973; Foster 1982; Helby *et al.* 1987; Retallack 1997).

The fauna of Subzone A of the *Cynognathus* AZ includes the mastodonsaurid amphibians *Parotosuchus* and *Kestrosaurus*, as well as batrachosuchid and trematosaurid amphibians and archosauriforms which have close taxonomic affinities with taxa from the *Parotosuchus* fauna in the Cis-Urals, and the Middle Buntsandstein in the Germanic basin (Ochev & Shiskin 1989; Shishkin & Ochev 1993; Shishkin & Welman 1994; Shishkin *et al.* 2000; Damiani 1999, 2002; Damiani & Jeannot 2002). This suggests an Upper Olenekian age for the lowermost *Cynognathus* AZ, as previously proposed by Hancox *et al.* (1995). Overlap between faunas of the *Lystrosaurus* and *Cynognathus* AZ's and the presence of a trematosaurid mandible high in the Katberg Formation, suggests that the fauna of the *Lystrosaurus* AZ in southern Gondwana survived up to (or very close to) the end of the Lower Olenekian, while its equivalent fauna in the northern hemisphere disappeared much earlier (Shiskin & Ochev 1993).

CONCLUSION

Detailed bio- and lithostratigraphic research on the contact between the *Lystrosaurus* and *Cynognathus* AZ's has shown that the stratigraphic ranges of faunal elements of both biozones overlap, but this is restricted to the Tarkastad Subgroup in the southern (proximal) part of the basin. In the north (distal sector) these biozones show no faunal overlap. The new biostratigraphic data disprove the previously proposed lateral equivalence of the Katberg and lower Burgersdorp formations and indicates a much longer duration for the *Lystrosaurus* AZ than formerly accepted (Anderson & Cruickshank 1978; Cosgriff 1984; Battail 1993; Lucas 1998). Our research supports the proposed basal subdivision of the *Cynognathus* AZ (Hancox *et al.* 1995) and extends the range of the lowermost subzone A southwards to the Tarkastad district. The entire fauna of the *Lystrosaurus* AZ is replaced by that of the lower *Cynognathus* AZ over a very narrow stratigraphic interval, which indicated the rapid nature of this transition. However, more research is needed to determine the causal factors responsible for the faunal turnover at the interface between these two biozones.

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A fossil peat deposit from the Late Triassic (Carnian) of Zimbabwe with preserved cuticle of Pteridospermopsida and Ginkgoales, and its geological setting

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Well-preserved cuticular material of Pteridospermopsida and Ginkgoales from the Late Triassic of Zimbabwe is described here for the first time. It is preserved within a brown peat-like lens in the Upper Karoo Angwa Sandstone Formation. The locality is on the Manyima River in the lower portion of the mid-Zambezi Valley of Zimbabwe. Using SEM and light microscopy to identify the taxa, the fragmentary cuticles are of Pteridospermopsida type and have been assigned to *Lepidopteris* sp. (Peltaspermales) and *Dicroidium* sp. A, B, (Corystospermales). Cuticles of the ginkgoalean leaf genus, *Sphenobaiera,* are also described. Well-preserved ovules were found in close association with the cuticles, but as the stomata are not visible they cannot be assigned to any genus. Based on their close similarity to the *Dicroidium* flora of the South African Upper Karoo, the plants are considered to be equivalent to the South African Molteno Formation in age (Carnian). The palynoflora supports this age bracket, as does fauna preserved nearby. The taphonomic process was one of transport, sorting and deposition in a fluvial system.

Keywords: cuticle, Peltaspermales, Corystospermales, ovules, Angwa Sandstone, Late Triassic, Carnian, Molteno, Zambezi Valley.

INTRODUCTION

While prospecting for uranium in the Zambezi Valley of northern Zimbabwe, geologists of the German exploration company Saaberg Interplan Uran GmbH, discovered a coaly outcrop in the bed of the Manyima River (Fig. 1), about 4 km from its confluence with the Angwa River. One of us (T.J.B.) paid an early visit to the site in 1984, at which time the significance of a thin layer of apparently unaltered peat-like plant debris within a carbonaceous shale and mudstone layer was recognized. The locality and its geology were briefly described shortly afterwards by Broderick (1984), and then more formally on a regional basis by Oesterlen (1998). Raath *et al.* (1992) referred to it in their description of the geology and palaeontology of the western Cabora Bassa Basin of the Lower Zambezi Valley, noting that the plant fossils at this locality, and the occurrence in related beds nearby of a diagnostically Late Triassic diapsid reptile, the rhynchosaurian *Hyperodapedon,* supported a Late Triassic (Carnian or younger) age for the beds (see also Lucas & Hancox 2001; Lucas & Heckert 2002). Note, however, that Oesterlen's (1998) map places the rhynchosaur occurrence within the Pebbly Arkose Formation, in a slightly higher stratigraphic position than the Manyima plant locality, which he assigned to the Angwa Sandstone Formation and to which he attached a mid-Triassic age. Yet in an earlier publication (Oesterlen & Millsteed 1994), a palynological assemblage from the Manyima locality confirmed a Late Triassic age for these upper coaly beds within the Angwa Sandstone Formation.

The first description of Triassic fossil plants from Zimbabwe was by Seward & Holttum (1921). Further research was carried out by Walton (1927), du Toit (1927), Lacey (1961, 1970, 1976) and Bond (1965). These authors recorded plants typical of the Molteno Formation, including species of *Dicroidium, Lepidopteris* and *Sphenobaiera* and some other genera of doubtful affinity, from several localities along rivers in the Zambezi Valley. The Manyima leaves are fragmentary but have exceptionally well-preserved cuticles that are described here.

Pollen has also been extracted from the material and it too belongs to the pteridosperms.

GEOLOGICAL SETTING

Geology of the Manyima River fossil locality

The fossil locality is in the bed of the Manyima River in the lower section of the mid-Zambezi Valley, seven kilometres due north of the road bridge across the Angwa River on the main road to Kanyemba (Fig. 1), in sedimentary rocks of Upper Karoo age.

Structurally, this Cabora Bassa section of the mid-Zambezi Valley is an east-trending half-graben, its fundamental active fault being the Zambezi Escarpment Fault flanking the southern margin. Here Upper Karoo rocks and the post-Karoo (Late Jurassic) Dande Formation are in direct contact with Precambrian gneisses of the Zambezi

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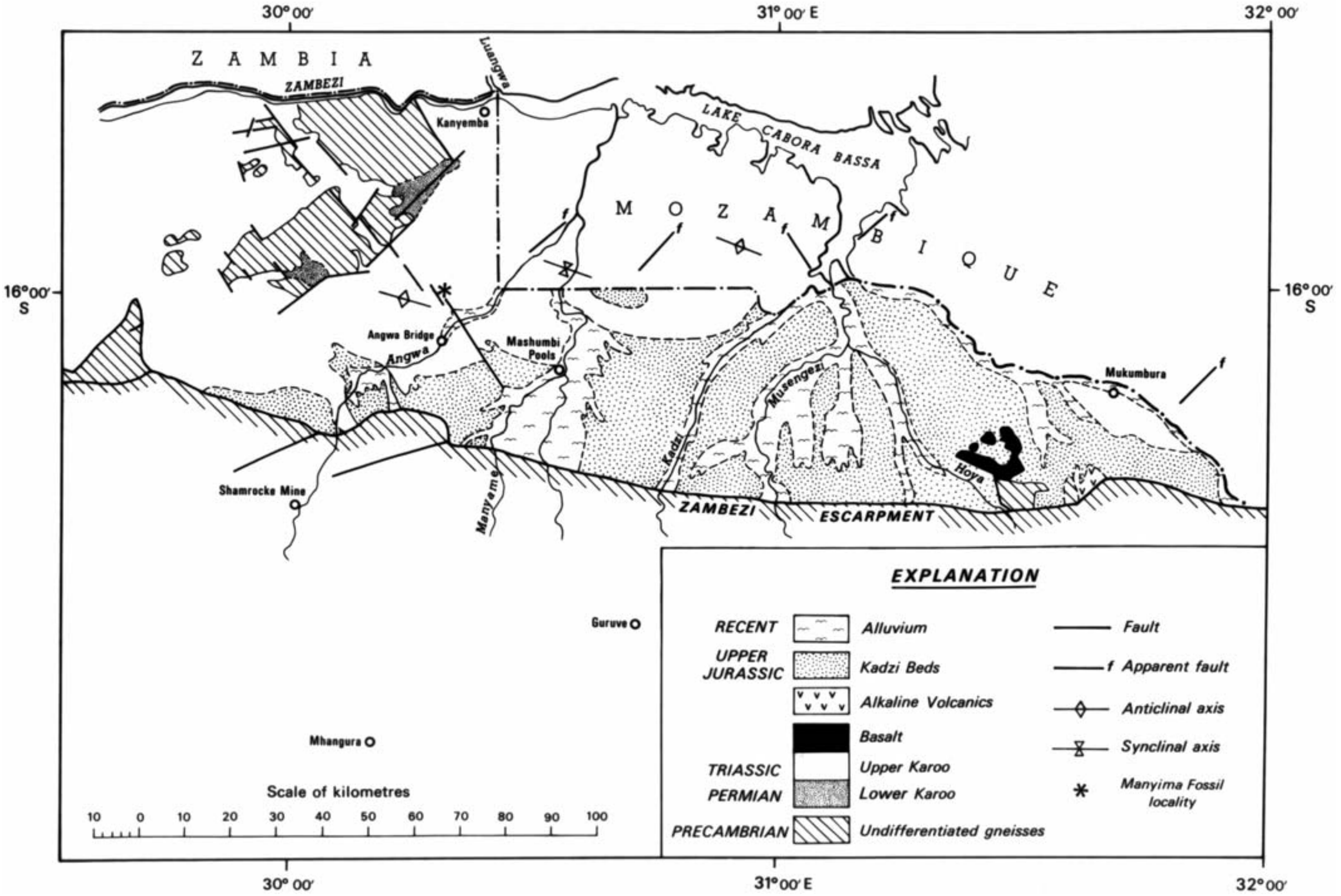


Figure 1. Map showing the geology of the northern portion of the mid-Zambezi Valley, Zimbabwe.

Metamorphic Belt (Fig. 1). Along the northern flank of the Zambezi Valley, in the basin of Lake Cabora Bassa, Lower Karoo glaciogene and Permian coal-bearing sediments appear to overlie the metamorphic basement directly (Broderick 1984). With subsidence, the Karoo sediments have been warped into gentle anticlines and synclines with northwest axial traces lying across the easterly trend of the graben. A number of interference patterns developed within the Upper Karoo sediments, many of them anticlinal or domical and possibly caused by soft sediment slumping during fault movement (L. Zan, pers. comm., 1984). Lower Karoo rocks are rarely exposed in the Zimbabwe section of the Cabora Bassa Basin, but in this area they occur close to and upon gneisses of the Chewore Inliers southwest of Kanyemba (Fig. 1; see also Oesterlen 1998). These horst features were created by northeast and northwest-trending faults operating through post-Karoo times. Farther east, river courses are controlled by northeasterly faults. These may have been responsible for forming secondary cross-graben structures in which a depth to magnetic basement of up to 14 km is reflected (Bosum 1985). Siltstones, sandstones and conglomerates of the post-Karoo Dande Formation have been deposited along the Zambezi Escarpment and over much of the Zambezi Valley east of the Manyame River. Many of the scarp-foot deposits are chaotic boulder conglomerates where the sedimentary sequence has been tilted south towards the Escarpment Fault in the classic roll-back situation found adjacent to graben faulting.

The geology in the vicinity of the Manyima fossil locality is shown in Fig. 2. Upper Karoo sediments underlie the entire area and they show a regional east-southeasterly trend. An older sequence of alternating red to purple or grey mudrocks, commonly ferruginous, and red to brownish-white sandstones are equivalent to the Triassic Molteno Formation of South Africa. They are typical of the Ripple-marked Flags of the Binga District of Zimbabwe and they contain elements of the diagnostic *Dicroidium* flora. Overlying the Molteno-equivalent rocks north of the Manyima bridge are red cross-bedded grits and feldspathic sandstones typical of the Pebbly Arkose Formation of the Middle Zambezi Basin southwest of Kariba. Fine, cross-laminated, biotite-bearing sandstones outcropping at the Manyima site are again seen in outcrop at Angwa Bridge. Two coaly layers were intersected in a water borehole at Chisunga School near the Angwa River 4.5 km east of, and on strike from, the Manyima peat and carbonaceous mudstone outcrop. Four kilometres northeast of the Manyima bridge a domed interference pattern deforms the Karoo sediments. Subsequent faulting has disrupted the Karoo beds and a strong northeast trend is apparent. On the interfluve immediately south of the Manyima River remnants of unconsolidated Kalahari-type or Jesse Sands have been preserved. The river valleys form depositories for thick accumulations of Recent terraced alluvium. However, the Manyima River has incised through this thick cover of alluvium to expose the Karoo sediments in its bed (Fig. 3).

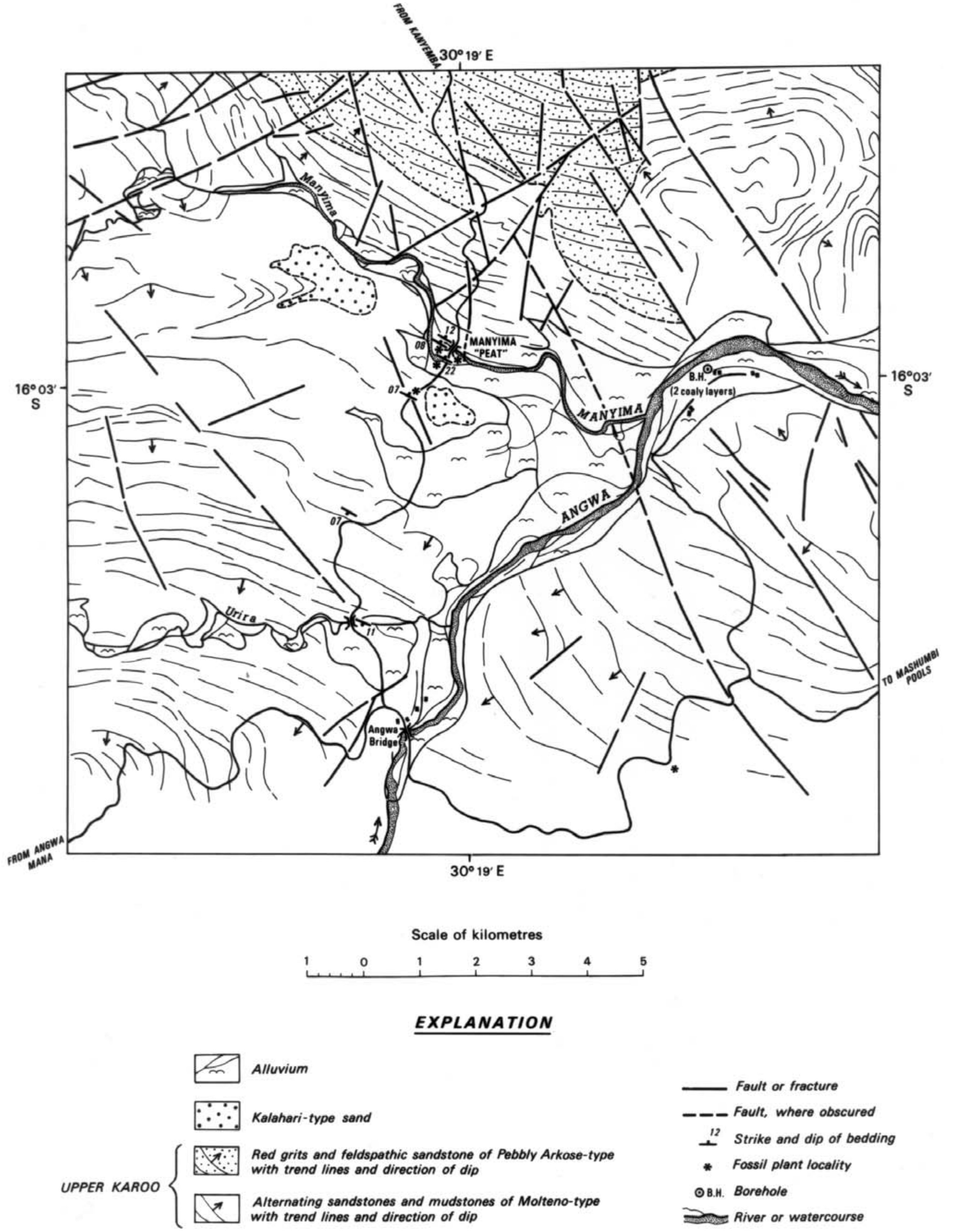


Figure 2. Regional geological map of the area surrounding the Manyima fossil site.

In cliff sections on the meander bends the older dipping sediments are overlain by thick alluvium with an irregular basal contact. A boulder bed about one metre thick marks the base of the alluvium and includes large, disrupted flaggy slabs of the underlying sandstone.

The Karoo beds in the vicinity of the Manyima locality have a consistent strike of 120–125 degrees and they dip at 7–22 degrees to the north-northeast, the greater measurements reflecting oversteepened cross-beds. On the roadside one kilometre south-southwest of the bridge, close to

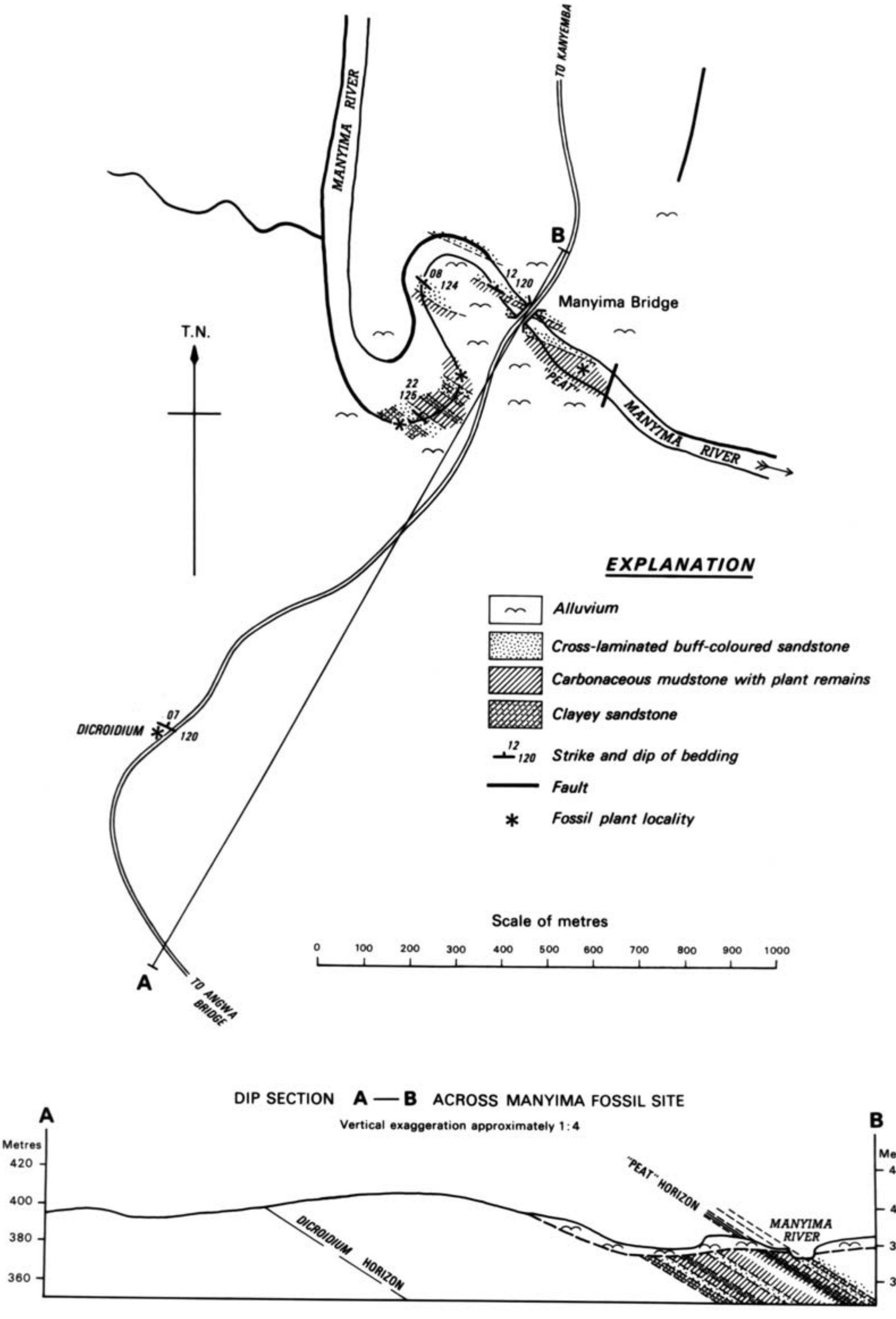


Figure 3. Geological detail at the Manyima fossil locality.

a borrow pit, grey mudstone outcrops with thin fissile, interbedded sandy lenses containing remains of *Dicroidium,* the fructification *Karibacarpon* (Lacey 1976), and *Sphenobaiera*. The relationship of this horizon to the Manyima peat is indicated on the dip section (Fig. 3). The road bridge is founded on two resistant bars of fine- to medium-grained, buff-coloured, finely cross-laminated sandstone in which the laminae are emphasized by the a1ignment of fine flakes of detrital biotite. These sandstones outcrop both upstream and downstream of the bridge and appear as cliff features in the river meander immediately to the northwest. They are flaggy and vertically jointed, which has allowed large slabs to fall away from the face into the river bed. Downstream a north-trending fault with a white siliceous breccia has apparently truncated the sandstone and peat outcrop. The Manyima peat and carbonaceous mudstone unit is sharply overlain by the lower of the two sandstone bars, which is best observed in the river bed and on the right bank directly downstream of the bridge. Here about 1.5 metres of dark grey carbonaceous mudstone gives way downwards to a 1.5 metre-thick layer of finely foliated, friable, carbonaceous material almost entirely made up of plant remains.

An initial examination showed that thin (0.5–2 cm thick) layers and lenses of bright vitrinite having a reflectance value of 0.51 (B. Barber, pers. comm., 1990) are interfoliated within the leafy deposit and, in the more weathered river bank outcrops, they are associated with sulphur encrustation. Vitrinite, indicating diagenesis towards sub-bituminous rank, becomes more apparent towards the base of the plant bed, below which the rock is shaly. Collapse of the overlying sandstone has obscured any further outcrop of the peat in the meander to the northwest, although carbonaceous mudstone was recorded there.

Farther upstream, into the large meander loop which is directed to the south, outcrop has permitted elucidation of the stratigraphy below the peat horizon. The lowest bed exposed comprises a brown, ferruginous clayey sandstone about one metre thick containing poorly preserved specimens of *Sphenobaiera.* This gives way upwards to grey-green mudstone below a 1.5 metre-thick layer of bedded, but weathered, buff-coloured sandstone striking 125 degrees and dipping 23 degrees northeast. A 3.4 metre-thickness of alternating grey and darker carbonaceous mudstone with wedges of fine-grained, yellow, clayey micaceous sandstone occurs below a hard, metre-thick, buff-coloured, cross-bedded and jointed sandstone layer. This jointing has allowed spheroidal weathering to take place and the sandstone beds have broken up in blocky fashion. Above, a thick bed of grey shale containing sandy and carbonaceous lenses is associated with carbon-encrusted plant remains. The relationship of this lower mudstone to the peat horizon above is obscured by alluvium cover.

Palaeoenvironment

There is a repeated sequence of grey to carbonaceous mudstone and shale containing sandy wedges and bars of ripple cross-laminated sandstone in the Manyima deposit. The finer-grained rocks contain abundant plant detritus suggestive of quiet, swampy overbank floodplain and oxbow lake conditions protected by levees, probably in a meandering river system where sandstones are likely to be the product of flood-derived crevasse splays and, to a lesser extent, migrating point bars. The thickest vertical accretion deposit, in which the Manyima peat has been preserved, is in sharp contact with the overlying sandstone. The paucity of well-defined trough cross-bedding, tabular cross-bedding and coarse lag deposits indicates an environment away from any main river channel. The sudden influx of a sand capping allowed for the preservation of the humus-rich accumulation at Manyima, which contains up to 45% of non-combustible ash (W.M. Hamilton, pers. comm., 1984).

MATERIALS AND METHODS

Preservation

The layers of almost pure plant cuticle were collected in blocks upwards through the exposed section by T.J.B. and M.A.R. in 1985.

Their preservation is unusual in that the cuticles have not been lithified and are still brown, flexible and generally translucent. The leaves are fragmentary, the largest ones being incomplete pinnae up to 50 mm long, which is an indication that they have been transported some distance before burial and so represent an allochthonous deposit. The depositional environment was anoxic as there has been little or no degradation of the plant cuticles: there is no evidence of cell wall breakdown, and no discernible fungal, bacterial or insect damage. Mesophyll is absent, but the cuticle fragments are intact.

Preparation of cuticle

The plant material was macerated in the Palaeobotany laboratory of the University of Claude Bernard, Lyon 1, first by addition of 10% HCl to the leaves in a watchglass. Then 20% HF was added in a fume chamber. The material was left in Schultze solution for 3–4 hours to clear the internal organic matter. After neutralising the material with dilute ammonium hydroxide the leaves were carefully teased apart and sorted. Larger leaves were selected because gross morphology is required for identification of taxa. Some leaves were mounted on glass slides in Canada Balsam/glycerine jelly for light microscopy and others were used for SEM.

Scanning electron microscopy

Some pieces of cuticle were selected for observation under the Hitachi S 800 scanning electron microscope at the 'Centre Commun des Microstructures' of the University of Claude Bernard, Lyon 1. After maceration the cuticles were rinsed several times in distilled water. They were mounted on aluminium stubs for SEM by means of double-sided adhesive tape. The samples were then coated with gold in an argon atmosphere to achieve a fine-grained film of 100 Å.

Palynology

Some of the material was prepared for palynological study. It was washed very briefly in 10% HF, neutralized, oxidized with Schultze solution, neutralized with NaOH, then HCl and washed before mounting on glass slides.

SYSTEMATIC STUDY

All the identifiable plant material preserved belongs to the Pteridospermopsida (extinct seed ferns) or the Ginkgoales (maiden hair tree group), which was a more diverse group in the past, with only one species, *Ginkgo biloba* L., remaining today.

Light microscopic study of the cuticular material (Figs 4–23) preceded the SEM studies (Figs 24–32).

Pteridospermopsida
Corystospermales
Dicroidium Gothan 1912

***Dicroidium* sp. A.**, Figs 4 & 5

The fragments of pinnules are broad and show typical venation with a central primary vein and regularly spaced secondary veins arching away to the margins, dichotomising once or twice, close to the midvein and/or close to the margin. The margins are entire and the pinnae taper gradually to an acute apex. This specimen resembles *D. odontopteroides* forma *odontopteroides* (Anderson & Anderson 1983, plates 32, 54) and *D. dubium* subsp. *dubium* (Anderson & Anderson 1983, plates 33, 52). The laminae are 13 mm wide and those of the specimens illustrated by Anderson & Anderson (1983) range from 4–18 mm, with *D. odontopteroides* forma *odontopteroides* having the wider pinnae. The venation, however, is very similar with a well-developed midrib. *Dicroidium odontopteroides* forma *longifolium* (Anderson & Anderson 1983, plate 66) has similar pinnule widths, but greater lengths than the fragments observed in this collection. The incomplete pinnules without connection to a rachis are impossible to attribute to an established species.

***Dicroidium* sp. B.**, Figs 6 & 7

The Manyima River specimens are 6–8 mm wide, elongate and commonly lack apices. The margins are entire but slightly undulating in some specimens. From the midvein secondary veins depart at an acute angle and bifurcate once before reaching the margin. These narrower and more elongate pinnae resemble *D. odontopteroides* forma *lineatum* (Anderson & Anderson 1983, plates 64–65). The recovered material does not preserve the relation between pinnules on the rachis, so specific attribution is not possible.

Cuticle of *Dicroidium* sp.

The best preserved cuticle fragments are small and without distinctive macromorphological features, so it is difficult to distinguish which cuticle belongs to which leaf type as the two macrofossil species (A and B) are so similar. The general features of the cuticle are described below:

Figures 24–28. The epidermal cells are medium to large, polygonal with 4–6 sides, have straight walls and the haplocheilic, monocyclic stomata are evenly scattered but with a random orientation. Each stoma has 4–5 subsidiary cells, usually with two of these being laterally positioned but sometimes either one or both lateral cells are divided into two. In some cases polar cells are divided into two. Guard cells are more regular in shape. The cuticle is thin and has no ornamentation.

Figure 25 shows one stoma with five subsidiary cells and no clearly positioned lateral or polar cells. The epidermal cell walls are slightly sinuous or just nodular. The stoma in Fig. 26 has two large lateral cells which are aligned with the guard cells, but one of the lateral cells is divided in two. There are two polar cells in Fig. 27 but they are not well aligned. Epidermal cells are large with respect to the guard cells and have more or less smooth walls. The cuticle in Fig. 28 is possibly another type as the guard cells are more prominent and the same size as the epidermal cells.

Peltaspermales

Lepidopteris Schimper 1869

***Lepidopteris* sp.**, Figs 9–13

The pinnae are fragmentary but consist of pieces with up to ten pairs of pinnules in an opposite to sub-opposite arrangement. Pinnules range in size from 1–4 mm wide and 3–8 mm long. The base of each pinnule is attached to the rachis completely and there is even some joining of adjacent laminae for a short distance (Fig. 9). The pinnules are at an acute angle to the rachis and the midveins are simple and central with secondary veins also arising at an acute angle, then travelling straight, or with one dichotomy, which arches slightly downwards, to the entire, undulating or crenate margins. Where present, the small teeth have the secondary vein above this tertiary vein. Between the midvein and most secondary veins there are small resin bodies. Resin bodies are also scattered over the lamina (Fig. 12).

These pinnules are similar to *Lepidopteris ottonis* described by Lundblad in 1950 from the Rhaeto-Liassic flora of Sweden. The specimen in her plate 4, fig. 10, is more complete than our material. However, *L. ottonis* is a typical northern hemisphere species and without fertile structures it is unreasonable to place our specimens in this species.

The specimens assigned to *L. madagascariensis* Carpentier by Anderson & Anderson (1989) on the basis of pinnule size and form are almost identical to the Manyima River material, but there is no preserved cuticle for *L. madagascariensis. Lepidopteris stormbergensis* Anderson & Anderson (*L. natalensis* of Thomas 1933 ex Harris 1926) has mostly larger pinnules and markedly serrate margins and acute apices, but the basal pinnae are smaller, entire and with blunt rounded apices. The cuticle of the Zimbabwe material has strongly papillate sunken stomata with 5–6 subsidiary cells over-arching the aperture (Fig. 23). There are also hair bases or papillae on some of the epidermal cells.

Comparing the Zimbabwe cuticle with other specimens, *L. ottonis* (Harris 1926) has one conspicuous papilla on each epidermal cell. Lundblad (1950) described material attributed to the same species, but it has large epidermal cell papillae which are dark areas with no structure. *Lepidopteris natalensis* (Harris 1926; Thomas 1933, fig. 54) cuticle has the same deeply sunken papillate stomata and sparse papillae on the epidermal cells. The material described here is most similar to *L. natalensis,* but it is too fragmentary for specific designation.

Incertae sedis

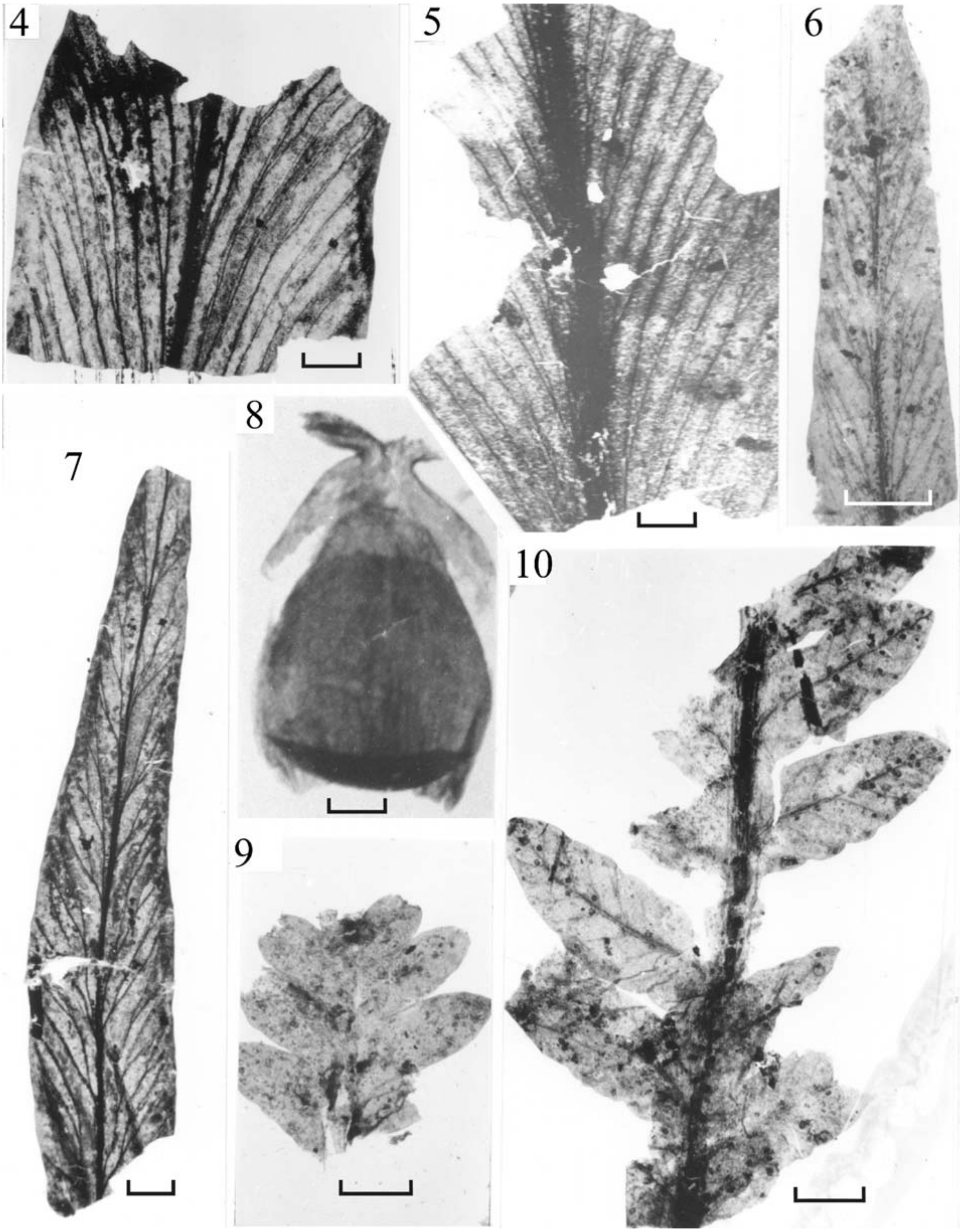
A cross-shaped structure 9 mm in total length, each lobe about 3 mm wide, has a stomatal apparatus identical to that of *Lepidopteris* sp. (Fig. 17) This unknown structure could be a portion of a fertile structure of *Peltaspermum.*

Ginkgoales

Sphenobaiera Florin emend. Harris 1974

***Sphenobaiera* sp.**, Figs 15 & 16

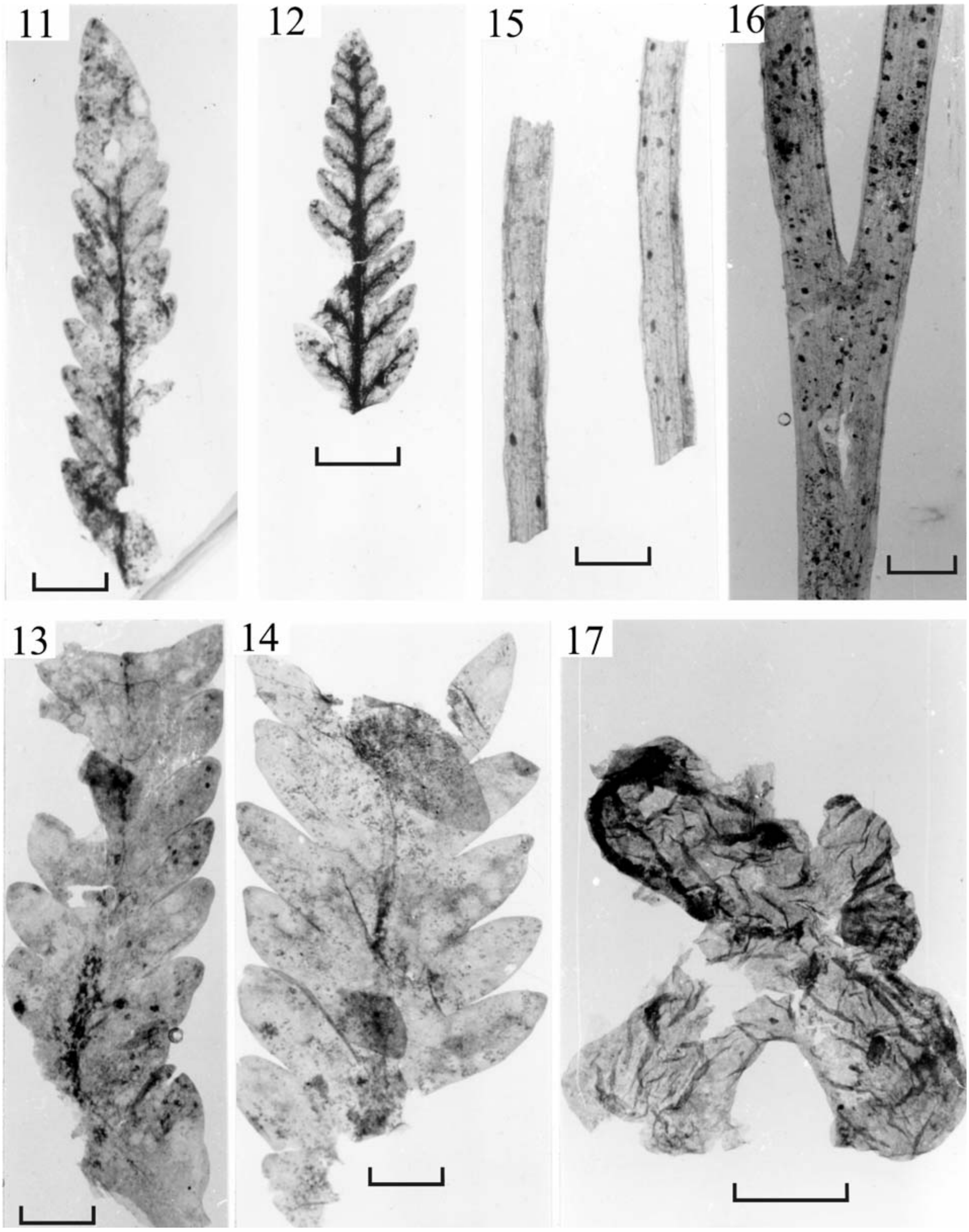
Leaf typically bilobed, narrowly wedge-shaped with basal portion undivided, approximately 10 mm long and 1 mm wide (incomplete fragment). Lobes diverge at about 15 degrees. The lamina is folded longitudinally, so is wider than appears, and no veins are visible. Scattered round to oval resin bodies are present. The cuticle is amphistomatic.



Figures 4–10. Macroplant fossils from the Manyima River. **4**, *Dicroidium* sp. A., fragmentary pinnule showing the venation. **5**, *Dicroidium* sp. A, fragmentary pinnule showing the venation. **6**, *Dicroidium* sp. B., distal part of a pinnule. **7**, *Dicroidium* sp. B., distal part of a pinnule showing venation. **8**, ovule showing the bifid micropylar beak, the integument, nucellus and megaspore. **9**, *Lepidopteris* sp., fragmentary pinna. **10**, *Lepidopteris* sp., fragmentary pinna. All scale bars = 2 mm, except for Fig. 8, which = 500 μm.

Stomata are haplocheilic and arranged in longitudinal bands, probably between veins. Each stoma has elongated subsidiary cells, usually two lateral and two polar, each with rounded or globose papillae over the slightly sunken stoma.

Epidermal cells are also elongated, rectangular, thick and unornamented. Only a few of the epidermal cells are papillate. With the presence of resin bodies in the mesophyll and the linear shape of the leaf, this fragment is characteristic of the Ginkgoales. Because the lamina is divided, the leaf does not belong to the other gingkoalean genera, *Eretmophyllum* Thomas emend. Harris & Millington 1974, *Pseudotoriella* Florin emend. Bose & Manum 1990 or *Nehvidzia* Hlu. *Sphenobaiera* is lobed to

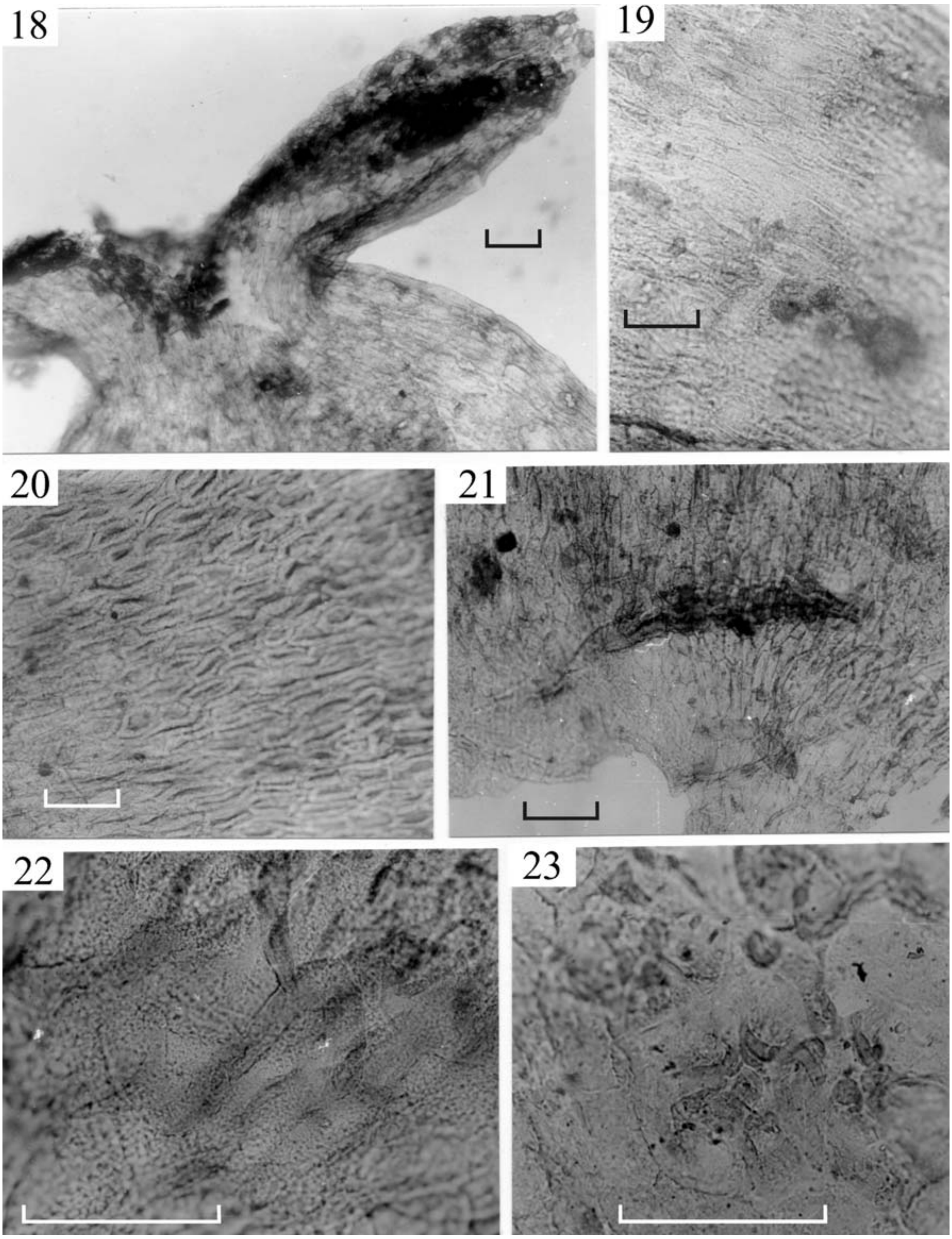


Figures 11–17. Macroplant fossils from the Manyima River. **11**, *Lepidopteris* sp., fragmentary pinna. **12**, *Lepidopteris* sp., fragmentary pinna. **13**, *Lepidopteris* sp., fragmentary pinna. **14**, *Lepidopteris* sp., fragmentary pinna. **15**, *Sphenobaiera* sp., two fragmentary leaves with resin bodies. **16**, *Sphenobaiera* sp., cuticle showing leaf dichotomy with associated resin bodies. **17**, disassociated plant fragment with cuticle showing the characteristics of *Lepidopteris.* All scale bars = 2 mm.

varying degrees. Anderson & Anderson (1989) described many species of *Sphenobaiera,* with six new species from Gondwana. Two of these, *S. pontifolia* and *S. africana* (Baldoni) Anderson & Anderson, have leaves with lobes of the same width. The comparison with northern hemisphere material is more difficult without fertile structures. The cuticles studied here have some affinities with those of *S. africana,* but the stomata seem to differ with the latter having a greater number of subsidiary cells.

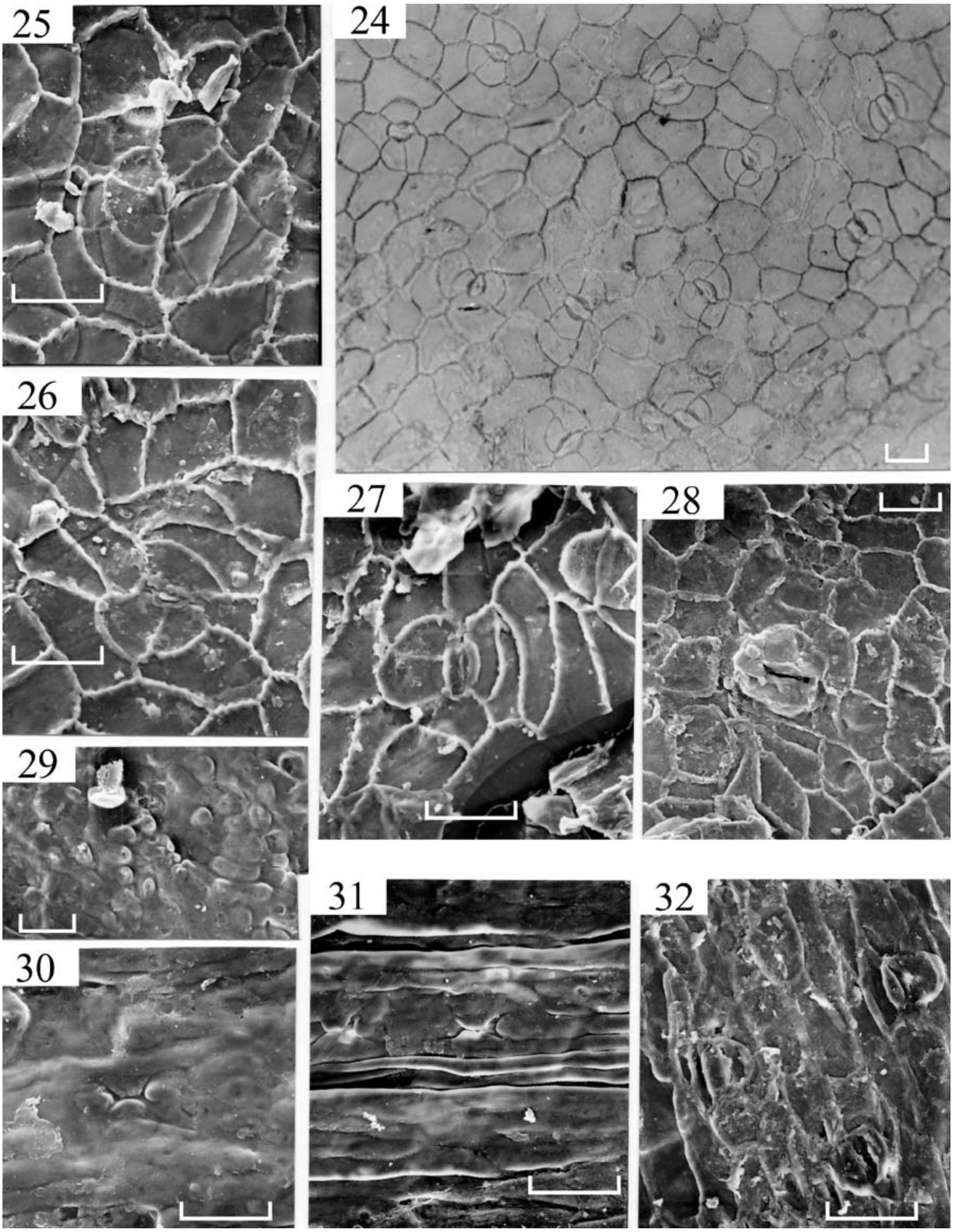
Ovule (Figs 8, 18–22)

These oval structures are 4–7 mm long and 2–4 mm wide, typically with two micropylar beaks at one end, probably flattened (platyspermic) and pear-shaped. Each



Figures 18–23. Cuticular details of the ovule and *Lepidopteris* from the Manyima River. **18**, Epidermal cells near the micropylar beak of the ovule. **19**, integument: epidermal cells of the outer part of the integument. **20**, Nucellus: cells of the nucellus with anticlinal walls. **21**, Integument: the thickened part of the base is of the pollenic chamber. **22**, Megaspore: some folds of the megaspore cuticle are visible but the walls of the cell are not visible. **23**, *Lepidopteris* sp., cuticle showing the stomatal apparatus with papillate subsidiary cells. Scale bars = 100 μm.

ovule consists of an integument with inner and outer cuticles, a nucellus and a megasporangium. Between the inner and outer cuticles of the integument are small resin bodies. The cuticle of the outer integument (Fig. 19) consists of polygonal to rectangular epidermal cells, which at the base of the ovule are irregularly oriented but then converge and eventually are aligned at the micropylar end. The epidermal cells of the inner integument are very delicate. The nucellus comprises polygonal to rectangular cells (3–25 μm wide and 100 μm long), with very thick anticlinal walls (Fig. 20). The base of the pollen chamber is visible as a darker curved ridge or fold (Fig. 21) above which there are pollen grains. The megaspore cuticle is thin and folded but the individual cells are not visible (Fig. 22). The ovules are numerous but not associated with any other particular plant material in this assemblage. In size and shape they strongly resemble seeds of the Corystospermaceae described by Thomas



Figures 24–32. Cuticles of *Dicroidium* and *Sphenobaiera* from the Manyima River. **24**, *Dicroidium* sp., stomatal zone showing numerous scattered stomata (light micrograph). **25**, *Dicroidium* sp., stoma with regular subsidiary cells (internal view of cuticle, SEM). **26**, *Dicroidium* sp., stoma with regular lateral subsidiary and elongated polar subsidiary cells (internal view of cuticle; SEM). **27**, stomata with irregular subsidiary cells (internal view of cuticle; SEM). **28**, *Dicroidium* sp., stoma with broad guard cells (internal view of cuticle; SEM). **29**, *Sphenobaiera* sp., external view of cuticle with papillate epidermal cells (SEM). **30**, *Sphenobaiera* sp., external view of cuticle: stoma with four papillae around the stomatal pit (SEM). **31**, *Sphenobaiera* sp., outer surface of the cuticle showing folds and two stomata with four papillae each (SEM). **32**, *Sphenobaiera* sp., inner surface of the cuticle showing stomata with guard cells (SEM). Scale bars = 50 μm.

(1933, fig. 33) from the Upper Umkomaas Valley in Natal, South Africa. Anderson & Anderson (1983, plate 22) illustrated seeds that have the same morphology, with the characteristic beak and of similar size, but without cuticle preserved. The ovules of *Lepidopteris* figured by Stanislavsky (1976, plate 29, figs 12 & 13) are also similar, but unfortunately they have no preserved cuticle. The ovules described from the Manyima River might also belong to the Peltaspermaceae.

Palynomorphs

Little supra-generic diversity was evident in the assemblage from the Manyima locality, the major miospore component being attributable to non-striate bisaccate pollen. This group comprised 86.5% of all palynomorphs in the samples studied. The balance was composed of striate bisaccates (8%), trilete spores (3%), plicates (2%) and zonates (0.5%). Identification to species level was hampered by the lack of a well-documented taxonomy for Triassic African miospores. However, identification to genus level was possible for several forms, using Australian references. These included *Pteruchipollenites,* which dominated the non-striate bisaccates (95%), and the striate bisaccate *Lunatisporites.* An interesting palynomorph was *Densoisporites* (*Lundbladispora*) *playfordii,* placed in the Upper Triassic by Balme (1964). Balme (1964) reported that pollen grains of the *Pteruchipollenites*-type become common in continental Triassic microfloras from eastern Australia, and that this palynomorph is overwhelmingly the major component of later Triassic sediments. Many sediments containing this microflora are rich in plant macrofossils of which the most characteristic element is the pteridospermic form-genus of *Dicroidium feistmanteli*-type. Earlier, Thomas (1933) had found occasional specimens of a bisaccate grain resembling *Pteruchus papillatus,* in the Kockatea Shale (Molteno Formation) of Natal. Isolated pollen grains of this type were also recorded by Couper (1958) from the British Jurassic, and were assigned to the genus *Pteruchipollenites.*

In Australia Balme (1964) and Dolby & Balme (1976) recognised two major subdivisions for the Triassic, the *Lunatisporites* (*Taeniaesporite)s* and the *Pteruchipollenites* Microfloral subdivisions. Balme stated that the *Taeniaesporites* Microfloral subdivision presents a major break between Permian and Triassic assemblages, and scarcely has a form in common with the *Dulhuntyispora* Assemblage of the Late Permian. A high proportion and diversity of striate bisaccates is indicative of the Australian Late Permian. This is not true of the Triassic, with only *Lunatisporites (Taeniaesporites*) found in reasonably large numbers. Balme (1964) stated that the occurrence of *Lunatisporites* (*Taeniaesporites)* provides a clear link between the Early Triassic floras of the northern and southern hemispheres. Specialization of this flora is suggested by the lack of diversity and the high pteridophytic component of the miospore assemblage. Such specialization could have been climatically controlled, owing to the change to drier conditions at the end of the Permian.

Pollen of the *Alisporites parvus* de Jersey 1962 type has been recovered from a permineralized *Pteruchus* specimen from Antarctica (Yao *et al.* 1995). The authors reviewed other pollen organs of *Pteruchus* and it appears that the associated pollen types are all bisaccates but with varied ornamentation on the corpus, which for isolated pollen samples would probably be assigned to different taxa.

The oldest occurrence of the *Pteruchipollenites* Microflora reported to date is in the Collaroy Claystone near the top of the Narrabeen Group in the Sydney Basin.(Balme 1964). The abundance of this grain in the Manyima River sediments indicates a correlation with the upper part of the Australian Narrabeen Group. A (tentative) age of 220–230 Ma (Carnian Tethys) is suggested by the Manyima pollen assemblage (Balme 1964) but in more recent publications the Narrabeen Group is Early Triassic (White 1986). *Pteruchus* occurs in middle to Upper Triassic sediments (Yao *et al.* 1995). With such a small sample of pollen it is not possible to attempt closer correlations.

DISCUSSION

The assemblage of plants, determined from the fragmentary macrofossil remains and pollen, is not very diverse as there are only pre-spermatophytes. The presence of typical genera such as *Dicroidium, Lepidopteris* and *Sphenobaiera* is indicative of the classic Carnian Molteno flora. Only the genus *Dicroidium* is typical of Gondwana; the other two genera have a much wider distribution. The association of plants described here is typical of other Molteno-equivalent assemblages already described from Zimbabwe (Lacey 1976), but is less diverse. This is probably a consequence of the fragmentary nature of the plant cuticles, which may not be representative of the whole flora.

The preservation of the material, however, is remarkable, in spite of its fragmentary nature. Plants appear to have been fragmented initially, then transported and sorted before being buried and preserved. The accumulation of leaflets, small stems and ovules evidently represents an assemblage of leaf litter. The fragments appear to have been sorted during transportation, because all are within a limited size range: small pieces of sterile material 1 mm to the largest pinnae 50 mm long occur together with isolated fertile material only a few mm in size. As there is little or no associated sediment within the organic matter, we conclude that the sorting was by gentle water transport rather than by wind.

The sedimentary environment is that of a quiet floodbasin swamp and oxbow lakes associated with a meandering river system. The lenses of organic matter are small and separated by barren sandy lenses, which implies separate events of fluvial activity. More material needs to be collected from different levels and lenses to determine if the depositional setting changed over time. Deposition was under anaerobic conditions and in the absence of microbial and fungal activities. Inclusion of sedimentary particles during deposition of the plants within the peat bed was extremely low. Furthermore, the plant layer consists of cuticle only, so there has been some compression and diagenesis which has removed the mesophyll. The ovules are flattened but have some pollen grains within the pollen chamber. Pollen grains adhere to the outside of some of the cuticle fragments even after chemical treatment.

It would appear that deposition of leaf litter occurred in a low energy environment after transport and sorting by fluvial activity. The concentration of organic material and rapid burial by fluvial sediments has produced this remarkable preservation of Molteno plant fragments.

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Preliminary report of a large theropod dinosaur trackway in Clarens Formation sandstone (Early Jurassic) in the Paul Roux district, northeastern Free State, South Africa

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An isolated fallen block of Clarens Formation sandstone near the small northeastern Free State town of Paul Roux preserves part of the trackway of a bipedal dinosaur. Although well known as a local curiosity, this trackway has not previously been formally reported or described. It consists of five successive paces of what is interpreted as a medium-sized to large theropod dinosaur, and represents the largest known theropod trackway in the 'Stormberg' sequence in South Africa. The tracks are assigned to the ichnotaxon *Grallator* sp., and show similarities to North American tracks of comparable age originally described as *Dilophosauripus.* Until now no body fossils of a likely candidate trackmaker were known, but elsewhere in this volume a possible candidate is described by the second author.

Keywords: Dinosauria, tracks, Stormberg, Clarens Formation, Early Jurassic, *Grallator, Kainotrisauropus, Dilophosauripus.*

INTRODUCTION

Unmistakable footprints preserved on a large detached block of sandstone on the farm Uniondale, about nine kilometres southeast of the small northeastern Free State town of Paul Roux (approximate locality coordinates 28°21′47″S, 28°00′05″E), have long been known as a local curiosity. The farmers and townsfolk of the area have long recognized that these markings are the fossilized 'spoor' or tracks of an ancient animal, most accepting the local folklore that the track-maker was 'a dinosaurus'. Although the trackway is well known as a local curiosity and tourist attraction, we are unaware of any formal report or description of these tracks in the scientific literature.

The sandstone block on which the tracks occur (Fig. 1) has come to rest on its side near the base of the adjacent hill from which it has evidently tumbled. It appears to have broken off from a thick, relatively coarse massive sandstone which outcrops near the top of the hill. This sandstone horizon is high in the succession of 'Stormberg' rocks in the area. It is underlain by many metres of coarse, massive sandstone and there can be no doubt that the trackway horizon belongs to the Clarens Formation (Early Jurassic), a conclusion shared by the late James W. Kitching, in whose memory this volume is presented, who visited the site on many occasions over the years.

Dinosaur tracks are known from many localities in 'Stormberg' exposures in Lesotho (Ellenberger 1970) and adjacent areas of South Africa (see e.g. van Dijk 1978; Olsen & Galton 1984; Raath *et al.* 1990; Gow & Latimer 1999), mainly in mudrocks of the Elliot Formation, although Ellenberger (1970) recorded quite a few Lesotho tracksites in what he identified as 'Cave Sandstone', an old name for the Clarens Formation.

Figure 1. Isolated block of Clarens Formation sandstone on the farm Uniondale, preserving five paces of a dinosaur trackway moving from bottom right to top left.

During a brief field excursion by staff and students of the Bernard Price Institute for Palaeontological Research in June 2003 it was decided to take advantage of a stop on Uniondale farm to measure and photograph the tracks (Fig. 2) and formally place them on record.

Because of the way the block has come to rest, the original surface along which the track-maker moved is now

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almost vertical, and therefore rather difficult to measure without some means of climbing the almost vertical five to six metre high face, hence the number of dimensions in Table 1 calculated from scaled photographs, which must therefore be taken as approximations.

DESCRIPTION OF THE UNIONDALE TRACKWAY

The trackway on Uniondale consists of a series of five successive footprints of a large bipedal tridactyl animal (Figs 3 & 4). There is no trace of manus prints associated with any of the pes prints. Because the block is loose and lying on its side, it is no longer possible to determine in which direction the animal originally walked. There are several other scattered, isolated prints of one or more smaller animals on the block, but no clear individual trackways; one such isolated print can be seen slightly below and to the right of R2 in Figure 3a, heading obliquely in the opposite direction to the main trackway.

Each individual print is symmetrically tridactyl, with the central digit (III) the longest (Fig. 4). Each toe print narrows distally, ending in a sharply pointed impression of a narrow claw. Although there has been some weathering of the surface on which the prints are impressed, and no clear details of toe-pad morphology are preserved, their general sharpness and clarity suggests that they are the slightly weathered primary prints impressed directly on the surface on which the animal walked, not underprints.

Table 1 gives the dimensions of the Uniondale trackway, following the methods and terminology of Leonardi (1987) combined with those of Thulborn (1984); where they could not be measured the dimensions were calculated from scaled photographs. Where measurements were physically taken the reference point was the base of the central digit (III).

Figure 2. Measuring stride length from L1 (obscured by bush) to L2 (stride = 2.80 m).

IDENTITY OF THE UNIONDALE TRACK-MAKER

The symmetrically tridactyl prints of the Uniondale trackway agree most closely in shape and size with tracks from beds of comparable age in Lesotho which Ellenberger (1970) named *Kainotrisauropus* spp. Olsen & Galton (1984) referred *Kainotrisauropus* to the ubiquitous tridactyl ichnotaxon *Grallator* (*Eubrontes*), which is generally attributed to bipedal saurischian dinosaurs, notably the theropods (Olsen & Galton, 1984).

The Uniondale track-maker is tentatively identified as a theropod on the grounds that its footprints are longer than broad, that each toe tapers distally, and the toe prints each end in a sharp claw imprint; ornithischian prints in general would be expected to be broader than long, with the toe prints having roughly parallel sides and each ending in a rounded ungual impression rather than the sharply tapering imprint of a claw (Thulborn 1984). The

Table 1. Dimensions of dinosaur tracks.

Dimension	Uniondale trackway	Ntumbe River trackway**	*Dilophosauripus****
Print length	~397 mm (L2*)	400	230
Print width	~323 mm (L2*)	300	280
Ratio of print width to print length	0.81	1.33	0.82
Divarication angle between digits II and III	37 degrees	31	20
Divarication angle between digits III and IV	34 degrees	26	28
Pace length	1.44 m (L1–R1) ~1.50 m (L2–R2*)	1.27 m (ave)	1.06 (isolated print)
Pace angulation	136 degrees (R1–L2–R2) 140 degrees (L2–R2–L3)	135 degrees (ave)	
Stride length	2.80 m (L1 to L2)	1.26–2.62	
Ratio pes length:pace	3.6	3.2	~3

*Measured from scaled photographs.
**Broderick 1984; Munyikwa 1996.
***Welles 1971.

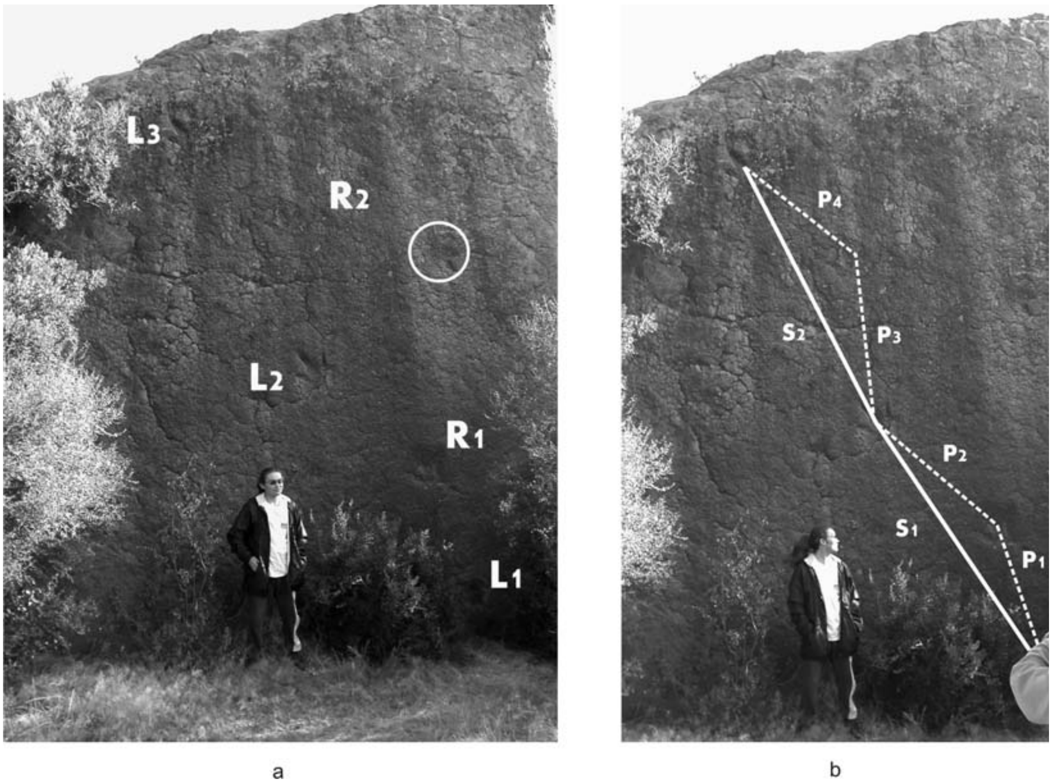

Figure 3. **a**, The full trackway, with figure for scale, and individual prints labelled (note the isolated smaller print [circled] below and to the right of R2, heading in the opposite direction to the main trackway). **b**, Same as (a), with successive strides (S1, S2) and paces (P1–P4) indicated.

lack of manual prints also rules out any quadrupedal dinosaurs such as the prosauropods that dominate the dinosaur fauna of the Elliot and Clarens formations (see e.g. Kitching & Raath 1984), and therefore also rules out attribution of these tracks to the quadrupedal ichnotaxon *Atreipus*.

The tracks reported here agree in general features with unnamed tracks in beds of approximately similar age on the Ntumbe River in northeastern Zimbabwe (Broderick 1984, 1985; Munyikwa 1996) (Table 1), although these prints do not seem to show distinct impressions of narrow, trenchant claws (Raath, pers. obs.). They also agree quite well with tracks recorded by Welles (1971) from the approximately coeval Kayenta Formation of the southwestern U.S.A. (Table 1), which he named *Dilophosauripus*, suggesting possibly another instance of close resemblance between the faunas of the 'Stormberg' of southern Africa and the Kayenta Formation of North America (see e.g.

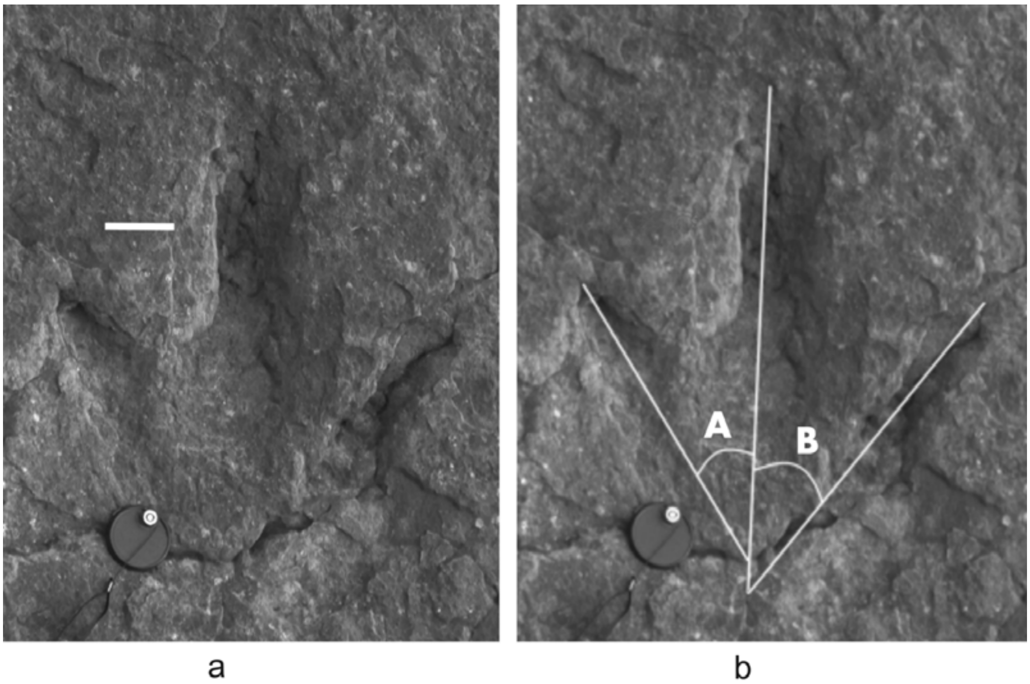

Figure 4. **a**, Individual print (L2) (scale bar = 60 mm). **b**, Same as (a) with lines on which divarication angles were measured between digits II and III (angle B) and between III and IV (angle A). See Table 1 for values.

Olsen & Galton 1984: 92–93).

The animal that made the Uniondale track is considerably larger than any theropod dinosaur known to date by body fossils from either the Elliot or Clarens formations; until now the only theropod represented by bony remains from these deposits is the small form originally named *Syntarsus* (now considered a synonym of *Coelophysis*) (Raath 1980; Paul 1993; Bristowe & Raath 2004). Two footprints attributed to this Gondwana species of *Coelophysis* are known from rocks of Upper Elliot age in Zimbabwe (Raath 1972) and these, together with the abundant, well-preserved foot bones of this animal, make it clear that *Coelophysis* is far too small to have been the Uniondale track-maker. However, elsewhere in this volume, Yates (2005) describes a new large coelophysoid theropod of comparable geological age whose fragmentary remains indicate an animal of the right order of size to have made tracks like those at Uniondale.

We are grateful to the owner of Uniondale for permission to visit and measure the trackway on his farm. The text benefitted from reviews by Drs Claudia Marsicano and Roger Smith, whom we thank for their input.

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A new theropod dinosaur from the Early Jurassic of South Africa and its implications for the early evolution of theropods

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A new theropod, *Dracovenator regenti*, from the upper Elliot Formation is described, based upon a fragmentary skull. It can be diagnosed on the basis of a bilobed fossa on the lateral surface of the premaxilla that is connected to the alveolar margin by a narrow channel, the presence of a deep, oblique, lateral notch on the articular and hypertrophied dorsal processes on the articular. Other aspects of its morphology display a mosaic of coelophysoid and advanced theropod characteristics. A cladistic analysis of basal Theropoda, including the new taxon finds that the new taxon is closely related to *Dilophosaurus wetherilli* and *Zupaysaurus rougieri* although the clade formed by these three taxa is not robustly supported. It also finds that Coelophysoidea *sensu lato* is paraphyletic with respect to Ceratosauria + Tetanurae but that this topology is not a significantly better explanation of the data than an inclusive, monophyletic Coelophysoidea.

Keywords: Theropoda, Coelophysoidea, *Dracovenator,* upper Elliot Formation, South Africa.

INTRODUCTION

Prior to Gauthier's classic (1986) monograph, our understanding of the interrelationships of theropod dinosaurs could be described as murky at best. Most works still adhered to the old notion of a coelurosaur versus carnosaur dichotomy that separated small gracile forms from the larger, more robust, taxa. Nevertheless many had expressed doubts as to the 'naturalness' (monophyly in modern parlance) of these groupings. Gauthier established a basal dichotomy in Theropoda that cut across the big versus small division. The two branches were the Ceratosauria and the Tetanurae. Gauthier's Ceratosauria included the former carnosaur *Ceratosaurus nasicornis* and the small, gracile coelophysoids, while the Tetanurae, included the true carnosaurs and the true coelurosaurs. The monophyly of the Tetanurae as constituted by Gauthier has never been seriously questioned since and it is supported by a number of synapomorphies of the cranial and postcranial anatomy, although the exact node at which these synapomorphies fall on varies between analyses, depending on the basal topology of the Tetanurae and which basal tetanuran taxa are included (Holtz 1994; 2000; Sereno *et al.* 1994, 1996, 1998; Rauhut 2003). The monophyly of Gauthier's Ceratosauria has not been so widely accepted, with suggestions that the larger *C. nasicornis* and its close relatives, the newly recognized Abelisauroidea, share a more recent common ancestor with tetanurans than they do with coelophysoids (Bakker 1986; Forster 1999). However, the closer relationship of *C. nasicornis* to Coelophysoidea than to Tetanurae continued to find support form phylogenetic analyses through the 1990s and into the early years of the new millennium. Several recent analyses that have incorporated substantial amounts of new information have overturned these results (Carrano *et al.* 2002, Rauhut 2003, Sereno *et al.* 2004). It is now the majority view amongst theropod systematists that Ceratosauria contains *Ceratosaurus* spp. and Abelisauroidea and that this clade is more closely related to Tetanurae than it is to Coelophysoidea although Tykoski & Rowe (2004) continue to support the inclusion of Coelophysoidea within Ceratosauria.

The break-up of Ceratosauria is carried further in Rauhut's (2003) comprehensive study of early theropod relationships. He found that, despite a relatively distinctive morphology, the monophyly of the broader coelophysoid assemblage (*Dilophosaurus wetherilli, Liliensternus* spp. and Coelophysidae) was questionable. In particular *Dilophosaurus wetherilli* was found to share a number of derived characteristics with Ceratosauria and Tetanurae not present in other coelophysoids. Nevertheless the position of *D. wetherilli* was unstable and depended upon the inclusion of the enigmatic taxon *Shuvosaurus inexpectatus* which may or may not be a dinosaur (Long & Murry 1995). When *S. inexpectatus* was included *Dilophosaurus wetherilli* formed a clade with Ceratosauria + Tetanurae but when *Shuvosaurus inexpectatus* was excluded it became equally as parsimonious for *Dilophosaurus wetherilli* to be included within Coelophysoidea as for it to form a clade with Ceratosauria + Tetanurae. Other analyses have continued to support the inclusion of *D. wetherilli* within Coelophysoidea (Sereno *et al.* 2004; M.T. Carrano, pers. comm.) but the support for this clade is very weak (M.T. Carrano, pers. comm.). If *D. wetherilli* really does share a more recent common ancestor with Ceratosauria + Tetanurae then it would imply that its coelophysoid-like characteristics such as its elongate and acutely pointed premaxilla, subnarial gap, elongate skull, expanded dentary tip and possibly tall, paired naso-lacrimal crests on the snout were symplesiomorphies of basal Theropoda. In other words, theropods might have passed through a 'coelophysoid'

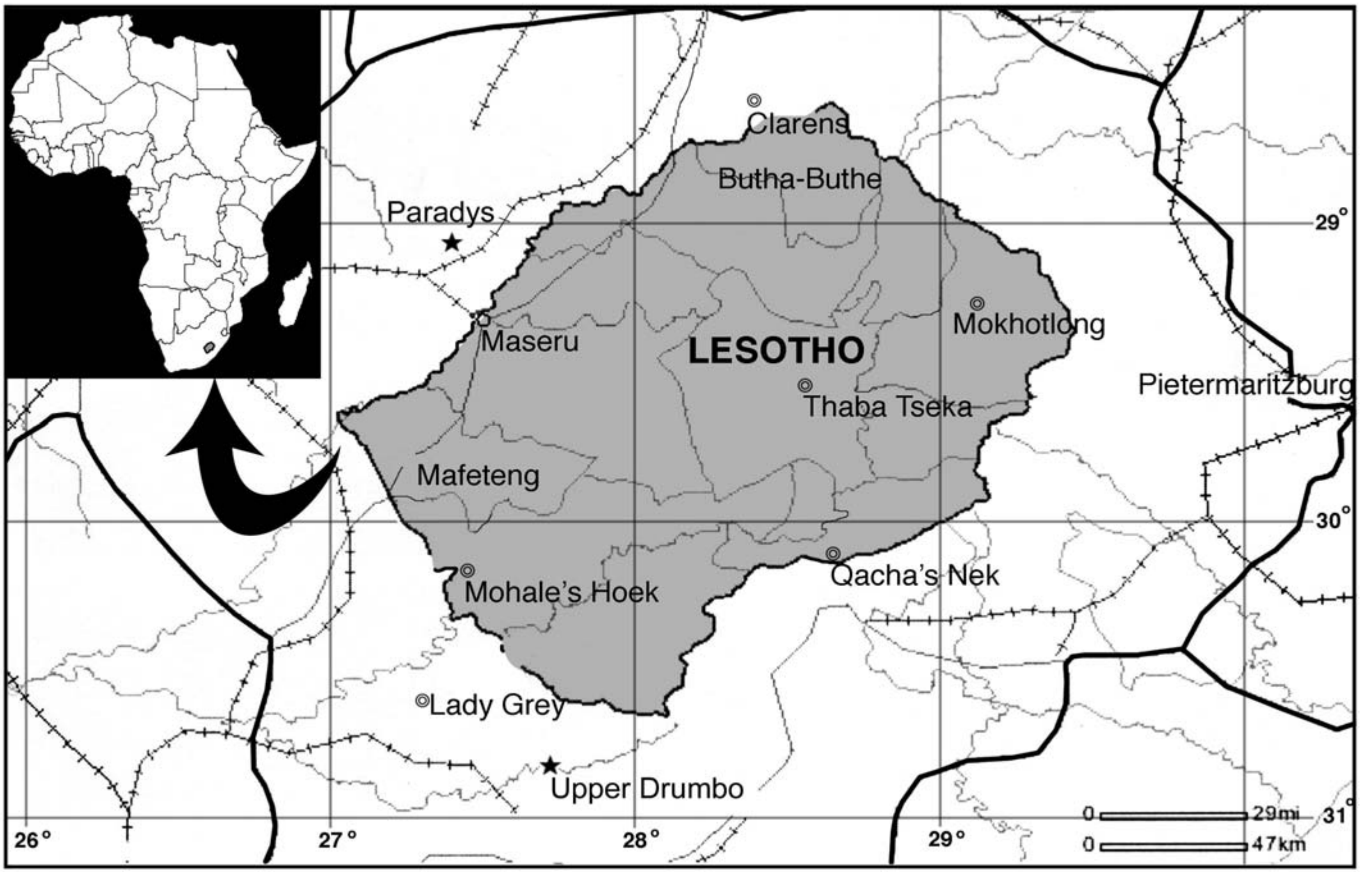

Figure 1. Locality Map for the farms Upper Drumbo and Paradys.

stage in their early evolution. In this respect, the recently described *Zupaysaurus rougieri* from the Late Triassic of Argentina is particularly interesting (Arcucci & Coria 2003). Described as the oldest tetanuran, it shares many characteristics with coelophysoids (most noticeably *Dilophosaurus*-like paired naso-lacrimal crests) as well as sharing some derived characters with ceratosaurian and tetanuran theropods. *Z. rougieri* might add further support to the hypothesis that the broader coelophysoid assemblage is a paraphyletic grade at the base of Neotheropoda. *'Dilophosaurus' sinensis* is yet another taxon that might support this hypothesis (Hu 1993), as it has a number of tetanuran-like characters (Lamanna *et al.* 1998) but it has not yet received an adequate description that allows its phylogenetic position to be accurately assessed.

Here I describe a new taxon of medium-sized (estimated skull length of 500 mm) theropod from the Early Jurassic of South Africa that also displays a mosaic of characteristics.

MATERIAL

J.W. Kitching found the holotype in a sandstone bed in the upper Elliot Formation (*Massospondylus* Range-Zone, Kitching & Raath 1984) on the farm Upper Drumbo in the Barkly East district of Eastern Cape, South Africa (Fig. 1). It consists of a fragmentary, disarticulated skull including both premaxillae, the posterior section of the right maxilla, fragments of the right and left dentary, the right angular, a partial right prearticular, the posterior end of the right mandibular ramus (in two pieces) and numerous unidentified fragments of bone.

A theropod snout (BP/1/5278), also from the upper Elliot Formation (farm Paradys, Ladybrand District, Free State), was described as a South African specimen of *Coelophysis* (= *Syntarsus* Raath) *rhodesiensis* (Munyikwa & Raath 1999) but it might represent a juvenile specimen of the new taxon.

The upper Elliot Formation is Early Jurassic in age but, like most intercontinental deposits of this age, finer resolution than this has proved difficult. It may lie anywhere between the Hettangian and the Toarcian, though a date closer to the younger end of this range is preferred here for reasons given in Yates *et al.* (2004).

SYSTEMATIC PALAEONTOLOGY

Theropoda Marsh, 1881
Neotheropoda Bakker, 1986, *sensu* Sereno 1998

***Dracovenator regenti* gen. et sp. nov.**

Etymology. Draco, dragon (Latin); *venator,* hunter (Latin), refers to both its probable habit of preying on prosauropod dinosaurs and its location in the foothills of the Drakensberg (Dutch: Dragon's Mountain) Range. Species name honours the late Regent 'Lucas' Huma, Prof. Kitching's long-term field assistant and friend.

Diagnosis. A theropod with the following autapomorphic characters: a large bilobed fossa surrounding a large lateral premaxillary foramen that is connected to the alveolar margin by a deep narrow channel; a deep, oblique notch on the lateral surface of the articular, separating the retroarticular process from the posterior

Table 1. Cranial material used in the comparison with *Dracovenator regenti* gen. et sp. nov. Additional information on *Coelophysis rhodesiensis* was obtained from a series of close-up colour photographs of the cranial specimens held at QG. Comparisons with other taxa are based on the literature and are referenced in the text.

Taxon	Specimens
Massospondylus carinatus	SAM PK1314
Liliensternus liliensterni	MB R. 2175
Coelophysis bauri	Unnumbered Ghost Ranch specimens held at the Science Center, Monash University, Melbourne, CM 31374 (cast)
Coelophysis rhodesiensis	QG165 (currently held at the BP)
Dilophosaurus wetherilli	UCMP 37302, 37303, 77270

margin of the glenoid; and particularly well-developed dorsal, tab-like processes on the articular, one on the medial side, just posterior to the opening of the chorda tympanic foramen and the other on the lateral side on the anterolateral margin of the fossa for the m. depressor mandibulae.

It most closely resembles *Dilophosaurus wetherilli* (Table 1) and *Zupaysaurus rougieri* but can be further distinguished from the former (apart from the presence of the autapomorphies described above) by: the presence of a raised ventral margin of the antorbital fossa placed close to the alveolar margin of the maxilla; the presence of unfused, triangular interdental plates on the maxilla; and the lack of a large transversely arched diastema behind the premaxillary row of teeth. It can be further distinguished from *Z. rougieri* by the probable presence of a rectangular anterior ramus of the maxilla offset from the ascending ramus by a prominent inflection. Considering other taxa of coelophysoid grade it can be distinguished from: *Procompsognathus triassicus, Segisaurus halli, Coelophysis bauri, C. rhodesiensis* and *'Syntarsus' kayentakatae* by its greater adult body size; from *Liliensternus liliensterni, Coelophysis bauri* and *C. rhodesiensis* by its probable rectangular anterior ramus of the maxilla; and from *C. bauri, C. rhodesiensis* and *'Syntarsus' kayentakatae* by its buccolingually compressed and serrated premaxillary teeth. It can be distinguished from the unusual, and poorly described, theropod *'Dilophosaurus' sinensis* by the elongate acutely angled body of the premaxilla, the retraction of the external naris to a level posterior to the last premaxillary tooth and the presence of only four premaxillary teeth.

Holotype. BP/1/5243, fragmentary skull.

DESCRIPTION OF THE HOLOTYPE

Premaxilla (Fig. 2)

The right premaxilla is more complete than the left. The main body consists of a subtriangular block of bone that is longer than it is high. In lateral view, the long axis of the nasal process, and the posterior part of the dorsal margin, forms an acute angle of approximately 25° with the horizontal alveolar margin. Anterior to this the dorsal margin curves smoothly downward to meet the alveolar margin and form a rounded anterior margin. A horizontal, elongate, triangular spike forms the posterolateral process. Its dorsal margin forms the ventral margin of the external naris. There is a markedly sharp bend between the ventral margin of this process and the rest of the posterior margin of the premaxillary body unlike *Coelophysis bauri, C. rhodesiensis* and *Dilophosaurus wetherilli* where the two margins are confluent in lateral view. The anterior ramus of the maxilla would fit into the space defined by these two margins and thus was probably rectangular and elongate as it is in basal tetanurans such as *Afrovenator abakensis* (Sereno *et al.* 1994, fig. 3a). An exceptionally long, slender nasal process forms the dorsal margin of the external naris. The nasal process, which has a D-shaped cross-section, maintained a union with its partner up to a point level with the posterior tip of the posterolateral process (about 53 mm along the length of the nasal process). Thereafter the nasal process diverges from the midline and continues for a further 45 mm. The posterior extension of the nasal process is seen in other coelophysoid-grade taxa (e.g. *Dilophosaurus wetherilli, Coelophysis rhodesiensis*). The divergence from the midline indicates that a wedge of the nasal pair was inserted between the left and right nasal processes. The posterior end of the nasal process becomes mediolaterally compressed and a sharp, low dorsolateral crest is developed at its tip. A similar but far deeper crest is developed on the nasal process of the premaxilla in *Dilophosaurus wetherilli* where it is the anteriormost extension of the naso-lacrimal crest. Thus it is probable that *Dracovenator regenti* had a nasolacrimal crest that was lower than that of *Dilophosaurus wetherilli.*

The lateral surface of the premaxillary body bears a distinctive set of foramina that are symmetrical on the left and right premaxillae. There is an especially large bilobed fossa surrounding the foramen above the second alveolus. The foramen is connected to the alveolar margin by a narrow channel, which cuts across the floor of the anterior lobe of the fossa. A large fossa surrounding a foramen in this position is also present in *Dilophosaurus wetherilli* and *Coelophysis rhodesiensis* but this fossa is not bilobed or connected to the alveolar margin by a channel. In front of this fossa there are two smaller foramina, placed vertically above the first alveolus. A fourth small foramen exits above the large bilobed foramen and a fifth above that one, near the dorsal margin. A shallow, subtriangular narial fossa lies anterior the external naris. Dorsal to this fossa there is a distinctive slot-shaped foramen piercing the base of the nasal process as there is in *Dilophosaurus wetherilli.*

The medial symphysis with the opposite premaxilla is extensive and takes up most of the medial surface of the premaxillary body but does not occupy the posteroventral region or the medial side of the posterolateral process.

A narrow medial shelf projects from the ventromedial

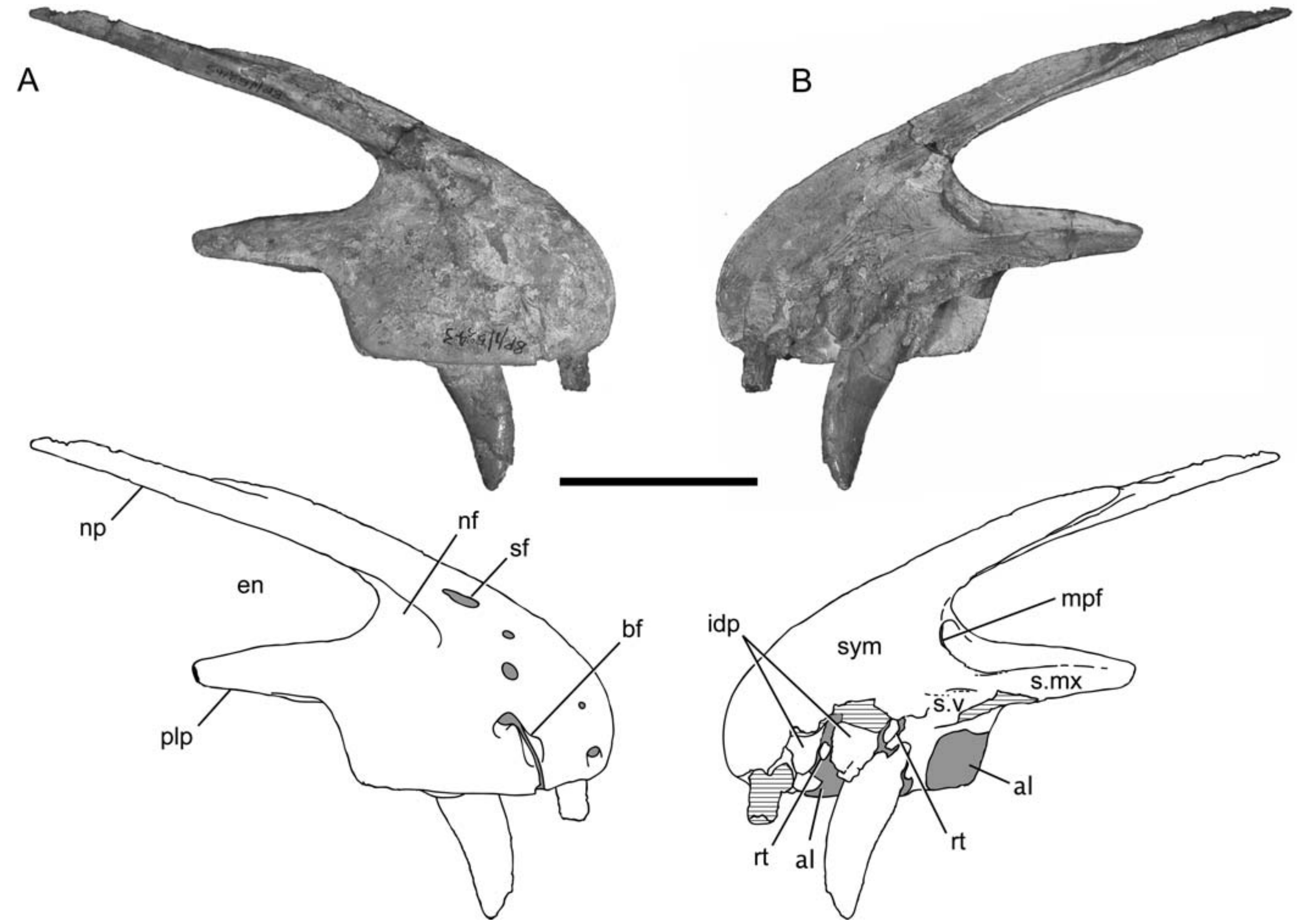

Figure 2. Left premaxilla of *Dracovenator regenti* gen et sp. nov. (BP/1/5243) in (**A**) lateral and (**B**) medial views. Grey areas represent patches of matrix or glue, hatched areas represent broken bone or tooth surfaces. Scale bar = 50 mm.

margin of the base of the posterolateral process. A narrow slot-like foramen pierces the ventrally facing surface created by this shelf. This shelf is presumably homologous with the larger, protrusive posteromedial process observed in many saurischians (e.g. *Massospondylus carinatus; Coelophysis rhodesiensis,* Rauhut 2003, fig. 8; *Sinraptor dongi,* Currie & Zhao 1993, fig. 4). Above this shelf at a point about half way along the posterolateral process is a low ridge. The ridge extends anteriorly and stays parallel to the margin of the external naris. As it curves dorsally, around the anterior rim of the external naris, it defines the anterior rim of the medial premaxillary foramen and the posterior margin of the medial symphysis. The area between horizontal section of this ridge and the ventral margin of the posterolateral process is concave and lightly striated. This is the articular surface for the anteromedial process of the maxilla. A second, much shorter, horizontal ridge begins between the ventromedial shelf and the first ridge, at about the level where the first ridge curves dorsally. The area between the second ridge and the shelf is also striated and probably represents the articulating surface for the anterior end of the vomers.

The premaxilla bears four alveoli, the first of which is smaller than the others. Erupted teeth are present in the first and third alveoli of the right premaxilla, but the first is badly damaged. Both the first and the third teeth have labio-lingually compressed crowns, unlike those of other coelophysoids, where at least the first tooth has a subcircular cross-section (Tykoski & Rowe 2004). The first tooth has a mesiodistal basal length of 10.6 mm and a labiolingual width of 5.1 mm. The crown is directed more or less vertically. The crown of the third tooth is 32.3 mm high and has a mesiodistal basal length of 14.5 mm while the labiolingual width is 7.3 mm. The crown is procumbent and gently curved distally along its length. It has well developed serrations on the distal carina with a density of 14 per 5 mm. The serrations have rounded tips in lateral view and are subrectangular in distal view. The carina begins just a few millimetres above the base of the crown. The mesial margin of the tooth has a weakly developed carina that occupies the apical third of the crown. It has only a few poorly developed, faint serrations.

Maxilla (Fig. 3)

Only a fragment of the right maxilla containing six alveoli is present. Judging from the proximity of the ventral margin of the antorbital fossa to the alveolar margin and the reduction in size of the alveoli towards its posterior end, this fragment comes from the posterior end of main maxillary body, with at most two alveoli missing from the posterior tip. The presence of the attachment scar for the palatine on the medial side also supports this position for the fragment. Interestingly, the depth does not decrease greatly along the length of this fragment,

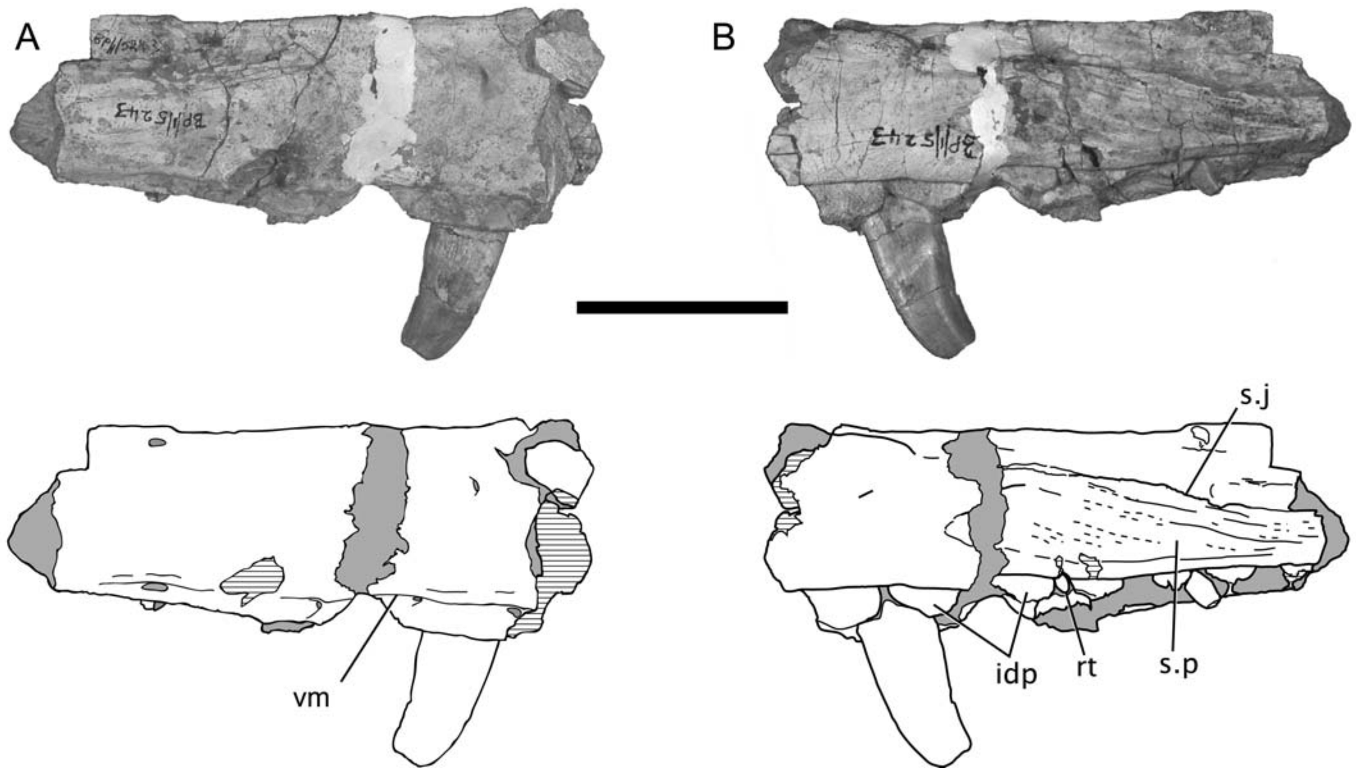

Figure 3. Posterior part of right maxilla of *Dracovenator regenti* gen et sp. nov. (BP/1/5243) in (**A**) lateral and (**B**) medial views. Scale bar = 50 mm.

indicating that the maxilla did not taper to a point at its posterior end.

The lateral surface is shallowly impressed with the antorbital fossa. The ventral margin of the fossa is placed close to the alveolar margin so that the antorbital fossa occupies most of the depth of the maxilla (between 87% and 94%). The ventral margin is also raised into a rounded ridge above the level of the lateral surface of the maxilla, matching the 'alveolar ridge' that is seen in most coelophysoid-grade taxa (Rowe 1989, e.g. *Liliensternus liliensterni, Coelophysis bauri, C. rhodesiensis* and *'Syntarsus' kayentakatae*) except *Dilophosaurus wetherilli* (Welles 1984).

The medial surface is excavated so that there is a thin dorsally projecting lamina on the lateral side that is bounded medially by a shelf that forms the dorsal surface of the main body of the maxilla. The shelf slopes from the dorsal margin, at the anterior end of the fragment to a level just above the posteroventral corner of the maxilla. The dorsal surface of the shelf would have received the anterior end of the jugal. The shelf becomes shallower and less pronounced, with rounder margins, towards the anterior end of the fragment. Below the posterior two thirds of the shelf there is an elongate area of oblique striations that forms the articulating surface for the lateral margin of the palatine. A deep and narrow paradental sulcus extends along the ventral margin, separating the interdental plates from the rest of the medial surface. The interdental plates are unfused, low, sub-triangular plates, unlike the fused, rectangular plates seen in ceratosaurs (e.g. *Ceratosaurus dentisulcatus,* Madsen & Welles 2000; Abelisauridae, Lammana *et al.* 2002) and *Dilophosaurus wetherilli.*

The single erupted maxillary tooth is strongly labiolingually compressed with a mesiodistal basal length of 18.0 mm and a labiolingual basal width of 6.4 mm. The estimated crown height is 40 mm. The apical region is gently curved distally. It has serrated carinae on both the mesial and distal margins. The mesial carina starts 21 mm above the base and has a density of 34 serrations per 10 mm. The serrations are simple, appearing subcircular in mesial view and lacking deep grooves between them. The distal carina starts at the base itself and bears coarser (28 serrations per 10 mm), more strongly developed serrations. The serrations are separated by deeper, broader grooves than those of the mesial carina. The tips of the serrations are rounded in labial or lingual view.

Dentary (Fig. 4)

There are two dentary fragments, one from each dentary. The larger of the two fragments comes from the mid section of the left dentary. It preserves three alveoli but no erupted tooth crowns. A tooth root with strong labiolingual compression is present in the anterior alveolus. The tips of replacement teeth are visible in the anterior and posterior alveoli. These show that the mesial and distal carinae of the dentary teeth were serrated and that the serrations continue over the tip of the tooth. As in the maxilla, the triangular interdental plates are unfused. A narrow and shallow paradental sulcus separates the base of the interdental plates from the medial surface of the dentary. The meckelian sulcus is broad and shallow with rounded margins. It extends along the ventral half of the medial surface. On the lateral side there is a narrower longitudinal sulcus that is located 18 mm down from the alveolar margin. The lateral sulcus fades towards the anterior end of the dentary fragment. Its ventral margin is steep and sharp while its dorsal margin slopes gradually.

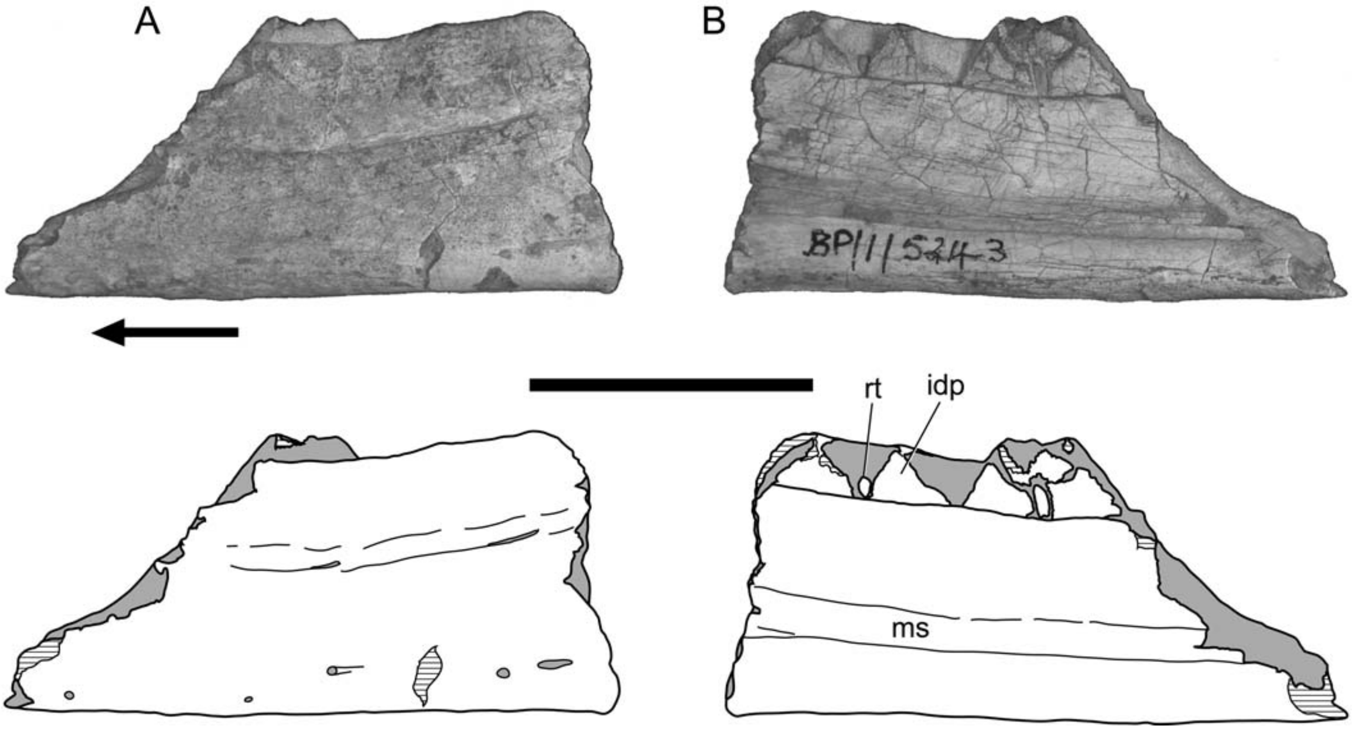

Figure 4. Middle part of left dentary of *Dracovenator regenti* gen et sp. nov. (BP/1/5243) in (**A**) lateral and (**B**) medial views. Arrow in (**A**) points to the anterior. Scale bar = 50 mm.

Elongate neurovascular foramina are placed at irregular intervals along the floor of the lateral sulcus. The smaller right dentary fragment provides no further details.

Prearticular (Fig. 5C,D)

There is a short fragment from near the posterior end of the right prearticular. The fragment consists of a dorsoventrally shallow anterior region that would have formed the ventromedial margin of the adductor fossa and a dorsoventrally expanded posterior region that would have met the glenoid-retroarticular complex; however, the two fragments can no longer be joined.

The lateral surface bears two, tall, sharp-edged ridges, that extend across the length of the fragment, although their height decreases towards the posterior end. At the anterior end these ridges are closely spaced creating a deep, V-shaped sulcus between them. Towards the posterior end they diverge creating a broad, triangular fossa. The upper ridge is placed at the dorsal margin itself, thus creating a laterally projecting shelf that floors the adductor fossa.

The ventral margin of the prearticular fragment widens towards the anterior end. At about the midlength of the fragment a thin, ventrally directed crest arises from the ventromedial margin. This creates a ventrolaterally facing, elongate fossa for the reception of the angular.

Angular (Fig. 5A,B)

The mid-section of the right angular is present. It is a relatively simple, flat bone with a gently convex ventral margin in lateral view. The strongly concave dorsal margin forms the ventral border of the external mandibular fenestra. The ventral margin suggests that the entire fenestra would have been large and ovoid in shape. At its narrowest, the ventral margin of the external mandibular fenestra is just 19 mm from the ventral margin of the angular, and hence the mandible itself. The dorsoventral depth of the angular increases both posteriorly and anteriorly as it does in *Dilophosaurus wetherilli.* More derived theropods (e.g. *Ceratosaurus dentisulcatus,* Madsen & Welles 2000, pl. 13e,f; and *Sinraptor dongi,* Currie & Zhao 1993, fig. 10 e, f) differ in having an anteriorly tapering angular. The articular surface for the dentary is a smooth, flat triangular area on the anterior half of the lateral surface. Its ventral margin is depressed below the level of the lateral surface of the bone. The ventral margin of the angular curves medially to form a sharp-edged medially facing shelf in the posterior half of this fragment. The prearticular would have articulated with the dorsal surface of this shelf. The shelf narrows and disappears at the level that the posterior tip of the dentary would have extended. Anterior to the shelf is a sharp, narrow ridge that extends across the anterior medial surface. A shallow elongate fossa is present between the ridge, which forms its dorsal margin, and the bulging ventral margin of the angular. This fossa would have fitted the posterior end of the splenial. Thin pieces of the posterior-most region of the angular are present on the lateral side of the glenoid-retroarticular complex.

Mandibular glenoid and retroarticular process (Figs 6 & 7)

The posterior end of the right mandibular ramus is preserved. It is a complex of four bones, the articular, surangular, angular and prearticular, preserved in two fragments. The main fragment includes the glenoid fossa and the retroarticular process, while the smaller fragment preserves the ventral crest and a small portion of the

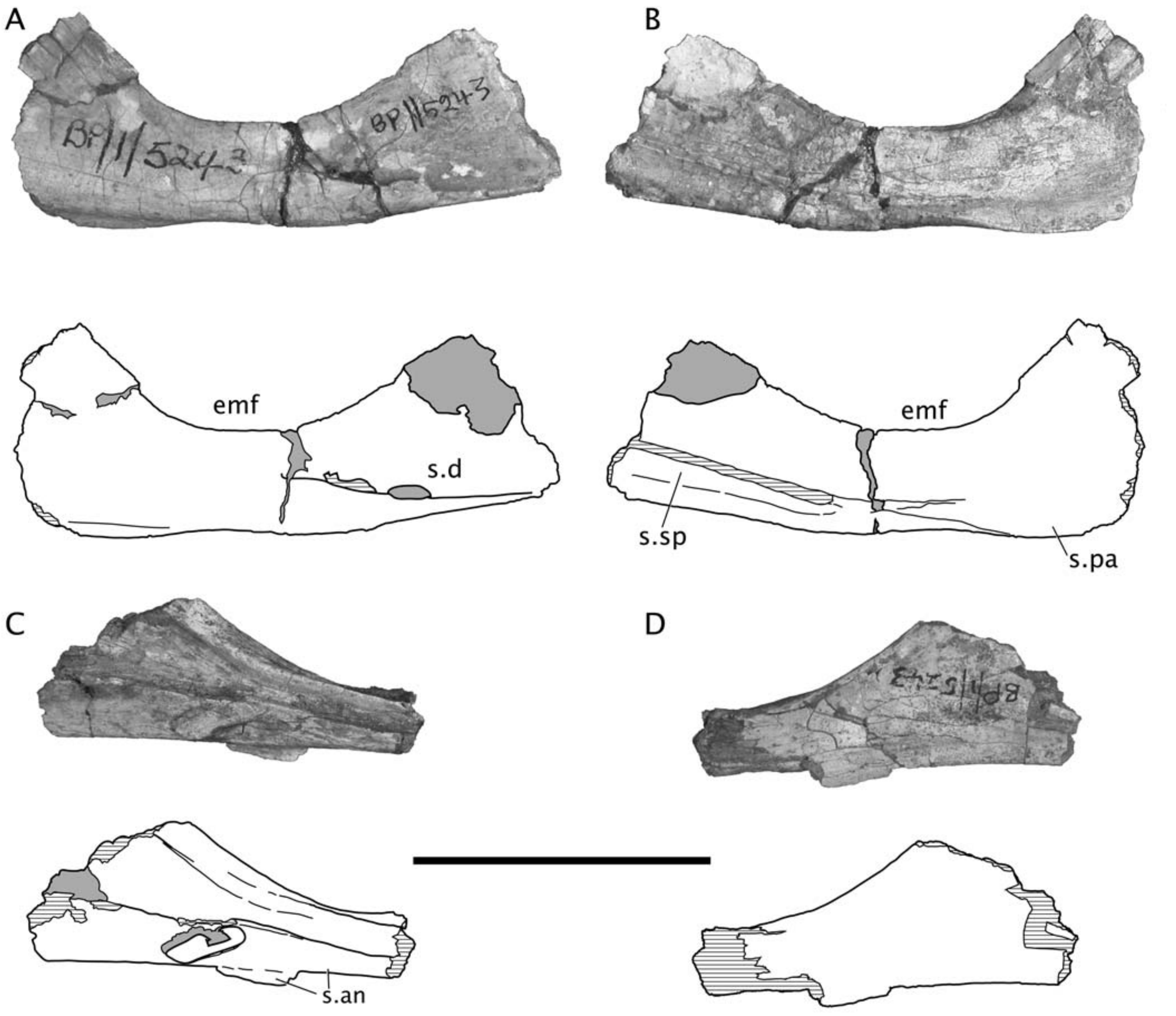

Figure 5. Post dentary bones of *Dracovenator regenti* gen et sp. nov. (BP/1/5243). Middle section of the right angular in (**A**) lateral and (**B**) medial views. Posterior fragment of the right prearticular in (**C**) lateral and (**D**) medial views. Scale bar = 50 mm.

posterior medial wall of the adductor fossa. The angular is represented only by a few thin flakes of bone on the lateral surface of the smaller fragment, anteroventral to the glenoid. It forms part of the deep thin crest that protrudes ventrally. The contact between the angular and the surangular is missing due to a large break along which the bone surface has flaked away. Like much of the damage to this fragmentary specimen, this break appears to have occurred before, or during, burial. The surangular covers much of the ventrolateral surface. It also forms a thick, rounded, laterally protruding ridge that extends forward from the anterolateral corner of the glenoid. A similar ridge is also present in *Dilophosaurus wetherilli* where it extends forward to form a shelf-like ridge on the lateral surface of the surangular (Welles 1984). There is a medial extension of the surangular that forms the anterolateral part of the glenoid and lateral wall of the adductor fossa. The dorsal margin of the lateral wall of the adductor fossa is a rounded ridge that is inset from the lateral ridge described above. Directly ventral to the lateral rim of the glenoid the surangular forms a small fossa. The sharp lateral lip of the glenoid socket forms the dorsal margin of this fossa. Dorsal and posterior to the fossa, the posterior rim of the glenoid forms a laterally protruding, vertically oriented, rectangular process. The surangular–articular suture is difficult to see in this region but it appears to lie close to the ventral end of this process indicating that most of the process is formed by the articular. Posterior to the lateral articular process there is a broad, rounded notch that curves posterodorsally. The suture between the surangular and articular is evident as it traverses the ventral part of this notch. Behind the lateral notch the dorsal margin of the surangular lies close to the rim of the fossa for the m. depressor mandibulae. The surangular terminates just a few millimetres in front of the posterior tip of the retroarticular process. The broad lateral notch mentioned above curves smoothly up onto the dorsal surface of the retroarticular process. The posterior part of the retroarticular process forms an ovoid concave region that faces posterodorsally, as it does in *Dilophosaurus wetherilli* and most tetanurans (Rauhut 2003), where the m. depressor mandibulae would have attached.

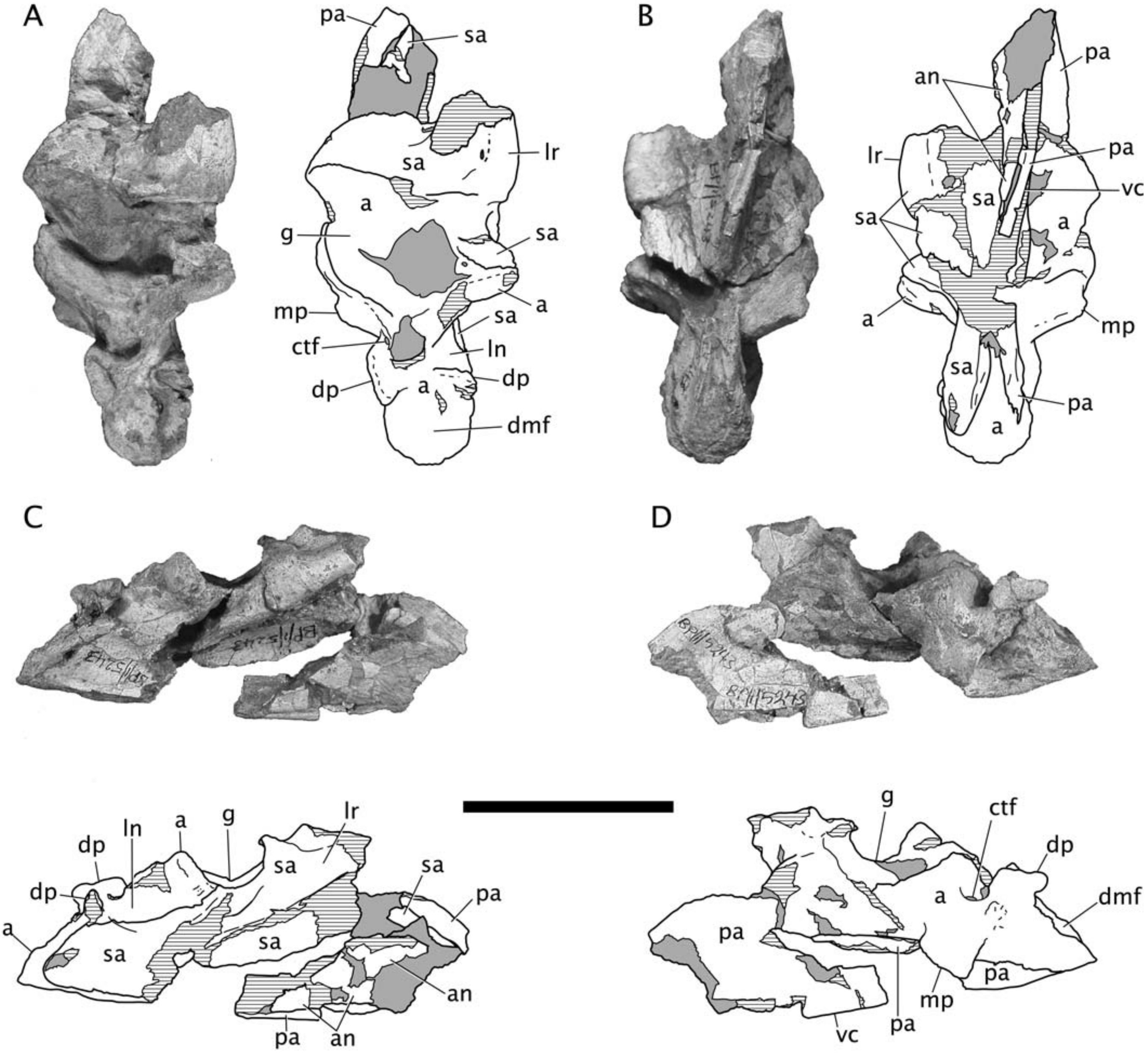

Figure 6. Posterior end of the right mandibular ramus of *Dracovenator regenti* gen et sp. nov. (BP/1/5243) in (**A**) dorsal, (**B**) ventral, (**C**) lateral and (**D**) medial views. Scale bar = 50 mm.

However, unlike most tetanurans the fossa for the m. depressor mandibulae remains primitively narrow (its transverse width is 45% of that of the glenoid). The anterolateral rim of this fossa is produced dorsally into a tab-shaped process, with a transverse long axis. A much weaker version of this process is present in *D. wetherilli.* On the opposite, anteromedial corner of the posterodorsal fossa, there is a second, larger tab-like dorsal process. In this case, however, the long axis is oriented obliquely, extending posterolaterally to anteromedially. Again, a weaker version of this process can be observed in *D. wetherilli.* The chorda tympanic foramen opens from the dorsomedial surface of the articular in front of the anteromedial edge of the medial dorsal process. A deep fossa is present in the region enclosed by the chorda tympanic foramen, the medial dorsal process, the lateral notch and the posterior rim of the glenoid. However, this fossa is not floored by finished bone, instead it is largely matrix and scraps of cancellous bone. It is likely that this fossa represents a damaged area that was hollowed out during preparation. The medial surface of the retroarticular process bears a rugose fossa ventral to the medial dorsal process. A large rectangular process, that is directed medioventrally, arises from the space between the rugose fossa and the posteromedial corner of the glenoid, ventral to the chorda tympanic foramen. A similar process, usually described as a pendant process, is also present in allosauroid tetanurans (e.g. *Sinraptor dongi,* Currie & Zhao 1993, fig. 11f) and *Dilophosaurus wetherilli* (where the process itself has broken away but its base is clearly present). The anterior edge of the medioventral process is connected to the posterior wall of the glenoid by a short, thick web of bone. A deep sulcus separates the ventromedial process from the ventral crest. A narrow pointed sliver of the prearticular can be seen on the medial surface of the ventral crest, below the posterodorsal

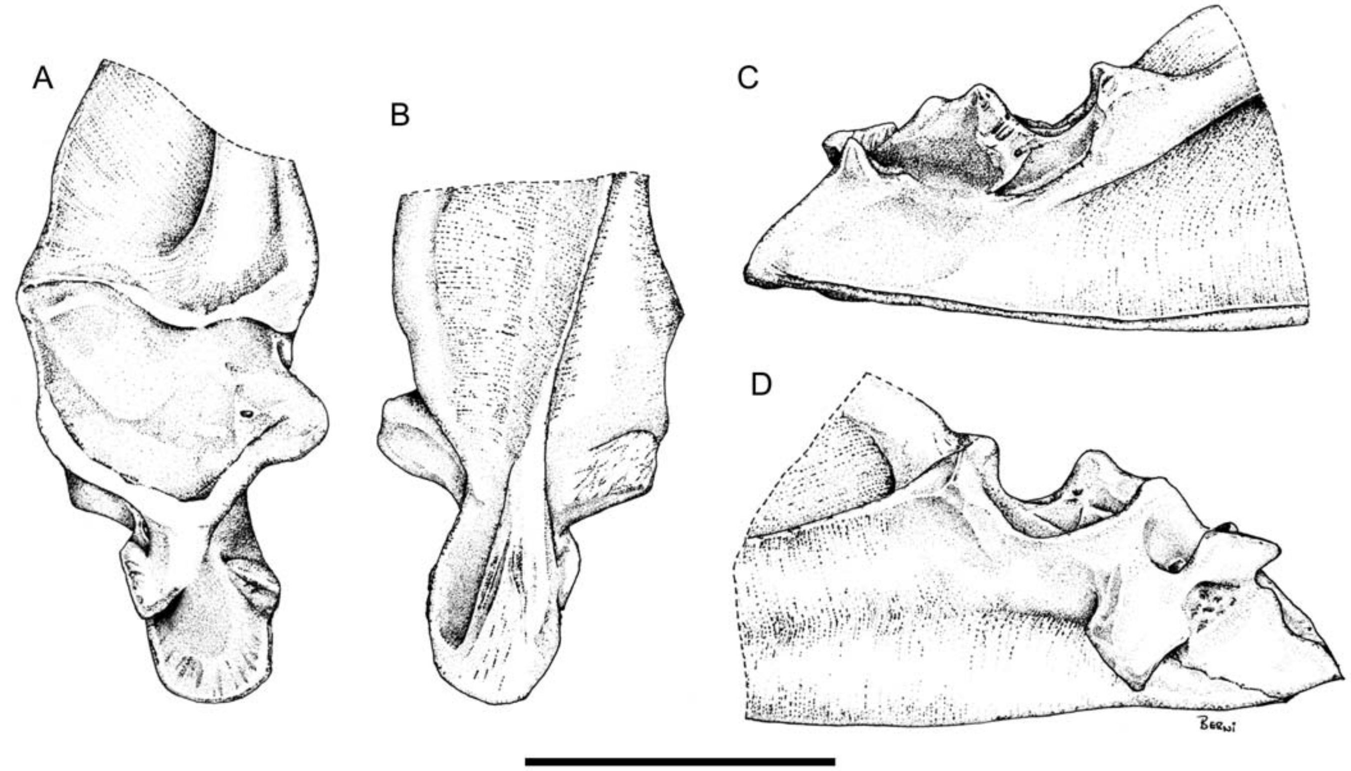

Figure 7. Reconstruction of posterior end of right mandibular ramus of *Dracovenator regenti* gen et sp. nov. (BP/1/5243) in (**A**) dorsal, (**B**) ventral, (**C**) lateral and (**D**) medial views. Scale bar = 50 mm.

articular fossa. It is impossible to trace the articular–prearticular contact anterior to the ventromedial process. In ventral view, the prearticular and the surangular approach each other anteriorly, so that the ventral exposure of the articular is pinched out at the level of the ventromedial process. The ventral crest becomes narrower at this point, with the ventral margin being formed entirely by the prearticular, and the angular being restricted to its lateral surface.

DESCRIPTION OF BP/1/5278 (Fig. 8)

An articulated set of premaxillae, maxillae, nasals and dentaries comprise BP/1/5278. The posterior maxillae, nasals and dentaries are missing. The left side is generally better preserved than the right, though some details are clearer on the right side. Munyikwa & Raath (1999) described the specimen but there are some details and reinterpretations that need to be added to their description.

The nasal processes of the premaxillae extend as far back as the posterior rim of the external naris, thus they extend beyond the posterior tips of the posterolateral processes of the premaxilla. These processes diverge from each other at their posterior ends and are clasped on each side by the bifurcated tips of the premaxillary processes of the nasals. Thus, a w-shaped premaxilla–nasal suture is formed. The shape of the premaxilla–maxilla suture is not well preserved on the left side. It appears that many of margins of the bones have been lost, perhaps due to invasive hematite mineralization. This can be clearly seen along the ventral margin of the maxilla, where the strip of bone below the ventral rim of the antorbital fossa is absent between the third and eighth maxillary tooth. The ventral margin of the anterior ramus of the maxilla, on the left side, slopes anterodorsally to meet the premaxilla. This enhances the appearance of a subnarial notch. However, it appears from the right side that the complete anterior ramus of the maxilla was more rectangular in shape. The ventral margin of the premaxilla is incomplete on both sides, though the slightly better preserved (though less complete) right premaxilla indicates that there was a bend between the ventral margin of the posterolateral process and the posterior margin of the premaxillary body.

The left maxilla displays two small oval fossae on the medial wall of the antorbital fossa, in front of the antorbital fenestra. These match the position of the maxillary and promaxillary fenestra of tetanuran theropods well and are here called the promaxillary and maxillary fossae, respectively. A raised rim along the dorsal margin of the antorbital fenestra curves ventrally at the anterior end of the antorbital fenestra to form a sharp posterior and posteroventral margin to the maxillary fossa – indeed there is a slight recessing of the fossa posteroventrally. The sharp, raised rim is present in coelophysids, although the promaxillary and maxillary fossae are only present as vague shallow depressions. The promaxillary fossa appears to pierce the maxilla but this could easily be a puncture of the extremely thin bone created during preparation. A second hole pierces the medial wall of the antorbital fossa near its anteroventral corner but the rim of this hole is sharp and not depressed as in the fossae described above, so this feature is certainly caused by damage incurred during preparation. Furthermore, the medial wall of the right antorbital fossa shows no foramen in this region. The right maxilla has an extensively damaged external surface making it impossible to observe the fossae. The antorbital fossa is also deeply

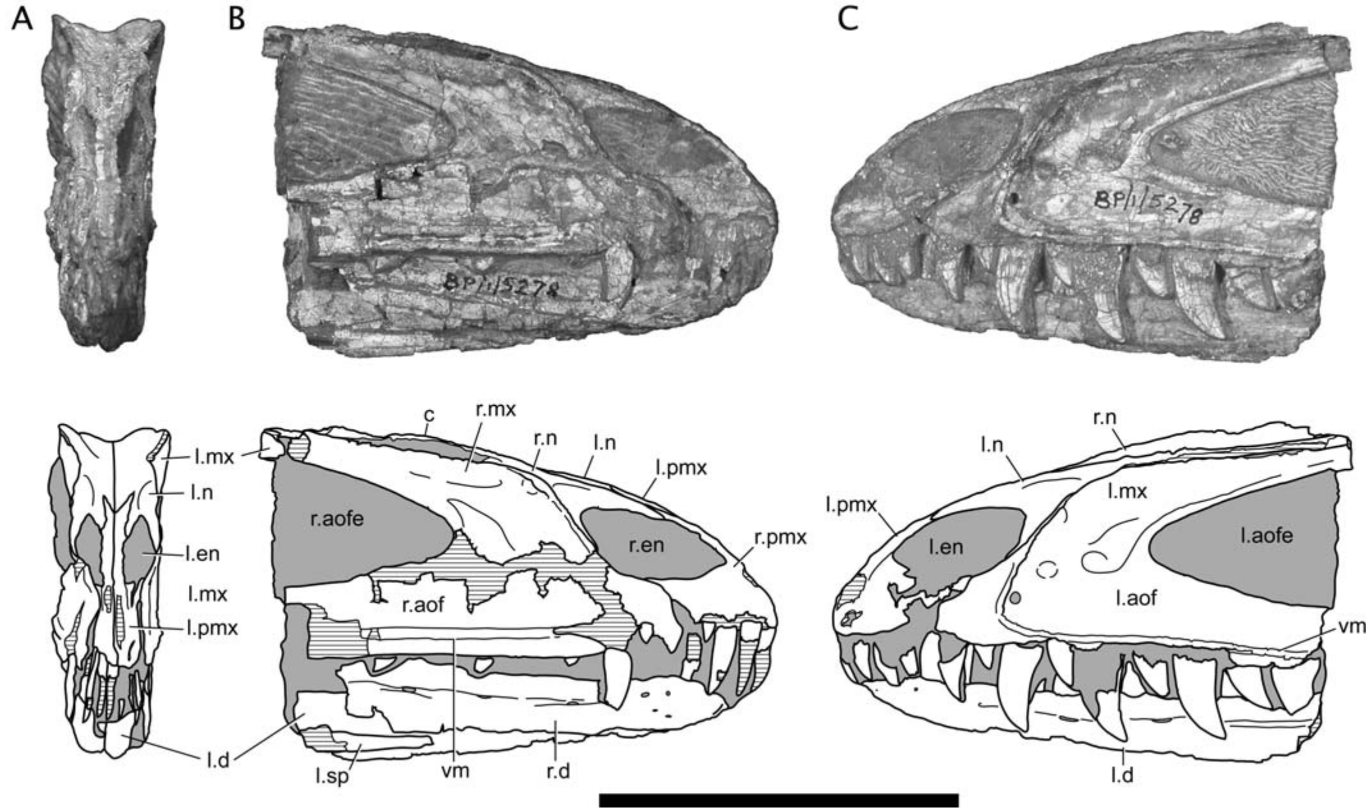

Figure 8. Snout of juvenile ?*Dracovenator regenti* gen. et sp. nov. (BP/1/5278) in (**A**) anterior, (**B**) right lateral and (**C**) left lateral views. Scale bar = 50 mm.

recessed under the anterior rim at the level of the promaxillary fossa.

The anteroventral processes of the nasals are bowed slightly laterally so that the posterior rim is set lateral to the anterior rim. This feature resembles that of ceratosaurs (Rauhut 2003; e.g. *Ceratosaurus magnicornis,* Madsen & Welles 2000, plate 3a) but it is less strongly developed in BP/1/5278 than in these taxa. The dorsolateral margin of the nasals forms a rounded ridge above the posterolateral processes, but posterior to these, where the nasal–maxilla suture reaches the dorsolateral margin of the skull, the nasal flares into a thin, sharp-edged crest that protrudes above the maxilla. This crest is absent on the left side but it is clear that the lateral margin of the nasals is broken here. The crest, which is only two millimetres high, is an incipient version of the crest seen in *Zupaysaurus rougieri, Coelophysis kayentakatae* and *Dilophosaurus wetherilli.*

CLADISTIC ANALYSIS

Dracovenator regenti was included in a modified version of Rauhut's (2003) character-taxon matrix (using only data from the holotype), the most comprehensive analyses of early theropod relationships published to date. Modifications include the collapsing of Coelurosauria more derived than *Proceratosaurus bradleyi* into a single terminal taxon (the interrelationships of this well-corroborated group are of no concern to this work), the separation of '*Syntarsus' kayentakatae* from *Coelophysis rhodesiensis, Acrocanthosaurus atokensis* from Carcharodontosauridae, the addition of 28 new characters and four new taxa in addition to *Dracovenator regenti.* These taxa are the recently described (or re-described) *Masiakosaurus knopfleri* (Carrano *et al.* 2002), '*Poekilopleuron' valesdunensis* (Allain 2002) *Tugulusaurus faciles* (Rauhut & Xu 2005) and *Zupaysaurus rougieri* (Arcucci & Coria 2003). New *Coelophysis* (= *Syntarsus* Raath) *rhodesiensis* material has shown that the supposed clade *Coelophysis rhodesiensis* + '*Syntarsus' kayentakatae* clade cannot be diagnosed by the presence of a postnasal fenestra (Bristowe & Raath 2004). Thus there is little to support the monophyly of *Syntarsus* Raath, or rather its replacement name *Megapnosaurus,* and the two species are treated as separate terminals in this analysis. The synonymy of *Megapnosaurus* and *Coelophysis* (Bristowe & Raath 2004) is provisionally accepted here, while *'Syntarsus' kayentakatae* has a number of unusual character states and deserves a new genus name. Although an exclusive clade *Coelophysis bauri* + *C. rhodesiensis* is not supported by the topology of the most-parsimonious tree found in this analysis (see below) it only takes one extra step to produce such a result. Since the Rauhut's codings for his composite OTU *'Syntarsus'* were based almost entirely on *Coelophysis rhodesiensis* this terminal taxon was simply relabelled for this analysis (with appropriate modifications listed below) and a new terminal for *'Syntarsus' kayentakatae* was created.

The outgroups follow Rauhut (2004) and consist of *Euparkeria, Marasuchus* and Ornithischia. These taxa were included in the analysis in order to polarize the characters but no characters that resolve relationships between the outgroups were considered.

The new characters are as follows (numbers follow on from the character list in Rauhut 2003).

225. Skull length less than (0), or greater than (1), three

times the occipital height of the skull (Sereno 1999).

226. Absence (0), or presence (1), of a foramen on the medial side of the premaxillary body, below the narial margin (Sereno *et al.* 2004).

227. Absence (0), or presence (1), of a slot-shaped foramen at the base of the nasal process of the premaxilla.

228. Posterior tip of the nasal process of the premaxilla level with (0), or extending posterior to (1), the posterior tip of the posterolateral premaxillary process.

229. Posterolateral premaxillary process at least one and a half times longer (0), or subequal (1), to the dorsoventral depth at its base (modified from Carrano *et al.* 2002).

230. Absence (0), or presence (1), of a transversely arched diastema posterior to the premaxillary row of teeth. This character is distinct from the 'subnarial gap' (Rowe 1989). That character refers to an arch or notch at the premaxilla–maxilla contact that is visible in lateral view. This character refers to the transversely concave toothless region behind the premaxillary tooth row. Taxa that have a notched premaxilla–maxilla contact in lateral view do not necessarily display this structure (e.g. baryonychines, Sereno *et al.* 1998, fig. 2a,b).

231. Premaxillary teeth with elliptical (0), or subcircular (1), cross-sections (Tykoski & Rowe 2004).

232. Premaxillary tooth crowns are labiolingually symmetrical (0) or asymmetrical (1) (Sereno *et al.* 1994).

233. Premaxilla–nasal suture on internarial bar is v-shaped (0) or w-shaped (1) (Sereno *et al.* 2004).

234. Subnarial foramen on the premaxilla–maxilla suture is absent (0), present but no larger than the lateral nutritive foramina of the maxilla and located outside the narial fossa (1), or present and larger than lateral nutritive foramina of the maxilla and located on the border of, or inside the narial fossa (2) (Yates 2003a, modified from Sereno & Novas 1993).

235. Promaxillary recess is shallow to absent (0) or extends into the anterior ramus of the maxilla (Sereno *et al.* 1994).

236. Depth of the ventral antorbital fossa less than, subequal (0), or many times greater (1) than the depth of the maxilla between the alveolar margin and the ventral margin of the antorbital fossa (modified from Rauhut 2003).

This character was subsumed into Rauhut's character 15, which described the presence, or absence, of an alveolar ridge. The alveolar ridge is not a neomorphic feature: it is the ventral margin of the antorbital fossa that has become raised above the level of external surface of the maxilla. Although most taxa that have such a raised ventral margin of the antorbital fossa also have a ventrally located margin (the derived state for this character) some taxa with this condition (e.g. *Eoraptor lunensis*) show a plesiomorphic placement of the ventral margin. Thus the two characters are not necessarily correlated and should be coded separately in a matrix.

237. Frontal pair in articulation is longer than wide (0) or wider than long (1) (Allain, 2002).

238. Spur of bone from basisphenoid projecting anteriorly into basisphenoid recess absent (0) or present (1) (Tykoski & Rowe 2004)

239. Dorsoventral expansion of the dentary tip absent (0) or present (1) (Sereno 1999).

240. Pendant medial process of the articular absent (0) or present (1) (Sereno *et al.* 1994).

241. Absence (0), or presence (1), of erect, tab-like dorsal processes on the articular, one immediately posterior to the opening of the chorda tympanic foramen and the other on the anterolateral margin of the posterodorsal fossa.

242. Transversely convex (0) or concave (1) attachment area for the m. depressor mandibulae on dorsal surface of articular. This character was subsumed into Rauhut's (2003) character 73, which describes the width of the attachment area for the m. depressor mandibulae. *Dracovenator regenti* has a concave attachment area, conforming to Rauhut's definition for the derived state for character 73 but it remains narrower than the mandible in front of the mandibular joint, which conforms to his definition of the plesiomorphic state. Clearly the width of the area can be independent of whether or not it is concave. In this analysis, character 73 describes only the width of the attachment area (0 = narrower than the mandible in front of the mandibular joint, 1= wider) whereas character 242 describes the transverse shape of this area.

243. Anterior tip of the axial neural spine in front of (0), level with, or behind (1), the axial prezygapophyses (Tykoski & Rowe 2004).

244. Cervical vertebrae 3–6 subequal to (0), or greater than 10% longer than (1), the length of the axis (Yates 2003a).

245. Cervical vertebrae 7–9 subequal to (0) or greater than 10% longer than (1) the length of the axis (Yates 2003a, modified from Gauthier 1986).

246. Sharp epipophyseal-prezygapophyseal ridge in cervical vertebrae absent (0) or present (1) (Sereno *et al.* 2004).

247. Distal humeral condyles are highly convex (0), or nearly flat (1) (Carrano *et al.* 2002).

248. Distal carpal 1 less than (0), or greater than (1), 120% of the transverse width of distal carpal 2 (Yates 2003a, modified from Sereno 1999).

249. Absence (0), or presence (1) of a distal ischial expansion (Yates 2003a, modified from Sereno 1999)

250. Width of the distal end of metatarsal IV subequal to (0), or less than 50% of (1), of the width of the distal end of metatarsal II (Sereno *et al.* 2004).

251. Astragalus and calcaneum separate (0), or fused (1), in adults (modified from Rowe 1989).

252. Proximal ends of metatarsals II and III separate (0), or fused (1), in adults (modified from Rowe 1989)

Codings for these characters are given in Appendix 1. Codings for characters 1–224 of *'Syntarsus' kayentakatae, Acrocanthosaurus atokensis,* derived coelurosaurs, Carcharodontosauridae, *Dracovenator regenti, Masiakosaurus knopfleri, 'Poekilopleuron' valesdunensis* and *Zupaysaurus rougieri* are given in Table 1.

Further changes include the following modifications to the following characters.

2. Premaxillary body in front of external nares: shorter than body below the nares and angle between anterior margin and alveolar margin more than 75° (0); longer than body below the nares and angle less than 70° (1).

The derived state is divided into two states in this analysis: external naris overlapping with some of the premaxillary body (1) and external naris entirely posterior to premaxillary body (2). *Coelophysis bauri, C. rhodesiensis, Dilophosaurus wetherilli,* Spinosauridae (= Baryonychidae in Rauhut 2003) *'Syntarsus' kayentakatae* and *Dracovenator regenti* are coded as having state 2, otherwise codings are unchanged from Rauhut (2003). Because state 2 is an extreme form of state 1, the character is treated as ordered.

22. Pronounced lateral rims of the nasals, sometimes bearing lateral cranial crests: absent (0); present (1).

As noted by Rauhut (2003) the derived state of this character displays some variability with some taxa exhibiting tall, naso-lacrimal crests. These crests are treated here as a second derived state of this character. *Dilophosaurus wetherilli, 'Syntarsus' kayentakatae* and *Zupaysaurus rougieri* are coded as having state 2. All other codings remain as in Rauhut (2003). As state 2 represents a hypertrophied form of state 1 the character is treated as ordered.

142. Deltopectoral crest: prominent and extending over at least one third of the humerus and well developed (0); strongly reduced in size, extending for much less than one third of the humerus (1).

Rauhut (2003) utilized both size and shape criteria to distinguish state 1 (deltopectoral crest strongly reduced to a small triangular eminence). In practice dinosaurian deltopectoral crests are neither strictly rectangular nor triangular and the difference between the two shape states is rather subjective. I prefer to restrict this character to a simple description of the size differences. Consequently *Deltadromeus agilis* is recoded as having a reduced deltopectoral crest (state 1).

145. Radius: more than half of the length of the humerus (0); less than half the length of the humerus (1).

As it stands, Rauhut's character differentiates the extremely shortened radii of abelisaurids and various basal tetanurans from those of other theropods. However, it fails to distinguish between the moderately short radii of most neotheropods and sauropodomorphs and those of several basal taxa that have radii that approach the humerus in length. Thus the original state 0 is divided into two states: those taxa with a radius more than 80% of the length of the humerus (*Euparkeria capensis, Marasuchus lilloensis, Eoraptor lunensis* and *Herrerasaurus ischigualastensis*) are assigned state 0; while all taxa with a radius that is between 50% and 80% of the length of the humerus (Ornithischia, Sauropodomorpha, *Coelophysis bauri, C. rhodesiensis, Liliensternus liliensterni, Dilophosaurus wetherilli, Piatnitzkysaurus floresi, 'Szechuanosaurus' zigongensis, Allosaurus fragilis, Ceratosaurus* spp., *Acrocanthosaurus atokensis,* and derived coelurosaurs) are coded as having state 1. Those taxa originally coded as having state 1 in Rauhut's (2003) matrix (*Torvosaurus tanneri,* Spinosauridae and Abelisauridae) are now coded as having state 2 (a radius less than 50% of the length of the humerus). The modified character is treated as ordered.

184. Strongly expanded pubic boot: absent (0); present (1).

There are two issues regarding this character. Firstly there is controversy over the state present in Herrerasauridae. Sereno *et al.* (1993) and Rauhut (2003) code herrerasaurids as having a pubic boot whereas Langer (2004) argues, and I agree, that the appearance of a distal expansion in herrerasaurids is caused by the posterior folding of the distal lateral margins of the pubic apron, not the proximodistal expansion of the distal end itself. Secondly Rauhut's character only distinguishes those taxa that have a particularly enlarged boot (at least twice the anteroposterior length of the pubic shafts) from all others. Yet the primitive condition is to have no anteroposterior expansion of the distal end at all, while some taxa coded as 0 in Rauhut's matrix have a small distal expansion. Consequently *Herrerasaurus ischigualastensis* and *Staurikosaurus pricei* are recoded as unknown for this character, reflecting that the transformation by caudal folding has rendered the character indeterminate in these taxa. All other taxa originally coded as 1 are now recoded as having state 2 (a large pubic boot over twice the anteroposterior length of the pubic shafts). Sauropodomorpha, *Coelophysis bauri* and *Liliensternus liliensterni* are recoded from 0 to 1 (a small distal pubic expansion less than twice the anteroposterior length of the pubic shafts).

Finally, the following coding changes were made to the following characters. Changes based upon new evidence have references to that evidence; those that are not referenced represent simple differences of opinion.

4. The posteroventral process of the premaxilla is more widespread amongst early saurischians than Rauhut appreciated. It is certainly present in basal Sauropodomorpha (e.g. *Thecodontosaurus caducus, Massospondylus carinatus*) and Sinraptoridae (Currie & Zhao 1993) so these taxa are recoded as having state 1. Because the process passes medial to the maxilla it cannot be seen in specimens where the premaxilla and maxilla are in articulation. Consequently the following taxa that were previously coded as not having the process (state 0): *Eoraptor lunensis, Herrerasaurus ischigualastensis* and *Monolophosaurus jiangi,* are recoded as being unknown.

6. *Eoraptor lunensis* is recoded as having state 0.

11. *Liliensternus liliensterni* is recoded as having state 0.

22. *Neovenator saleri* is recoded as having state 1 following the discovery of the nasals of this taxon (Naish *et al.* 2001).

23. Rauhut (2004) coded *'Syntarsus'* as having a bluntly

squared anterior tip of the jugal on the basis of QG 278, a specimen of *Coelophysis rhodesiensis.* However, this specimen is probably damaged and a newly prepared specimen shows that the anterior tip of the jugal tapers to a sharp point in this taxon (Bristowe & Raath 2004, fig. 5). Consequently *C. rhodesiensis* is recoded as having state 0.

24. There are no specimens of *Coelophysis rhodesiensis* with a jugal in natural articulation with the maxilla and the lacrimal consequently it is impossible to determine what state is present in this taxon and it is recoded as being unknown (the original coding was based on *'Syntarsus' kayentakatae*).

46. Rauhut (2004) coded *'Syntarsus'* as lacking a squamosal–quadratojugal contact on the basis of *'Syntarsus' kayentakatae.* Since this region is not articulated in any specimen of *Coelophysis rhodesiensis* the character is recoded as unknown in this taxon. Furthermore I disagree with Rauhut's assessment of *'Syntarsus' kayentakatae* and code it as having a squamosal–quadratojugal contact (state 0).

49. New skull material of *Coelophysis rhodesiensis* (Bristowe & Raath 2004) shows that the quadrate foramen is deeply recessed and partly encircled by the quadrate and so it is recoded as having state 1.

67. The basal sauropodomorph *Thecodontosaurus caducus* has a ventral fossa on its ectopterygoid (state 1), although this feature is not present in more derived members of this group (Yates 2003a). Consequently Sauropodomorpha is recoded as polymorphic (states 0 and 1).

102. The basal sauropodomorphs *Plateosaurus engelhardti, Thecodontosaurus caducus* and *Thecodontosaurus antiquus* have large cervical epipophyses that overhang the rear margins of the postzygapophyses (Yates 2003a,b). Consequently Sauropodomorpha is recoded as polymorphic (states 1 and 2).

130. *Deltadromeus agilis* is recoded as having state 0.

131. *Coelophysis bauri, C. rhodesiensis, 'Syntarsus' kayentakatae* and Spinosauridae are recoded as having state 1 following the discovery of furculae in these taxa (Downs 2000; Tykoski *et al.* 2002; Lipkin & Sereno 2002).

140. *Deltadromeus agilis* is recoded as having state 1.

153. The basal sauropodomorph *Thecodontosaurus antiquus* has reduced phalangeal formula for the outer digits of its manus. The fourth finger supports just two phalanges while the fifth finger has none (Benton *et al.* 2000). Consequently Sauropodomorpha is recoded as polymorphic (states 0 and 1).

155. The basal sauropodomorph *Thecodontosaurus antiquus* has a well developed extensor pit on the distal end of at least metacarpal II and a weaker one on metacarpal III (pers. obs. of YPM 2195 and BRSUG material). Consequently Sauropodomorpha is recoded as polymorphic.

165. Several sauropodomorph skin impressions are known and these indicate a scaly skin (Mantell 1852; Czerkas 1994; Chiappe *et al.* 1998), thus the taxon is recoded as having state 0.

204. Rauhut (2003) coded this character as polymorphic for *'Syntarsus'* while noting in the text that it displays a cnemial crest that is confluent with the fibular condyle in proximal view (i.e. state 0) based upon a specimen of *Coelophysis* (= *Syntarsus*) *rhodesiensis.* Since the condition is the same in *'Syntarsus' kayentakatae* (Tykoski & Rowe 2004, fig. 3.9n) Rauhut's coding probably represents a simple typographical error in the data matrix. In any case, both *Coelophysis rhodesiensis* and *'Syntarsus' kayentakatae* are coded as 0 in this analysis.

Procompsognathus triassicus, Ligabueno andesi and *Velocisaurus unicus* were included in Rauhut's complete matrix but were excluded from the analysis for reasons of taxonomic redundancy and they are likewise omitted from this analysis. Rauhut also deleted *Xuanhanosaurus qilixiaensis, Siamotyrannus isanensis* and *'Chilantaisaurus' maortuensis* after an initial analysis because these poorly known taxa greatly increased the number of most-parsimonious trees without changing the relationships between the other taxa in the tree. Consequently, they are also omitted from this analysis. A further poorly known taxon, *Poekilopleuron bucklandi* that Rauhut kept in his analysis (but pruned from the tree he described), is omitted from this analysis for the same reasons. Lastly this analysis excludes the enigmatic taxon *Shuvosaurus inexpectatus* because it probably represents the skull of *Chaterjeea elegans,* a suchian archosaur (Long & Murry 1995).

Collapsing the Coelurosauria into a single terminal taxon (with the exceptions of the basal *Proceratosaurus bradleyi* and *Tugulusaurus faciles*) rendered 62 characters parsimony-uninformative (41 one of these are constant). Nevertheless, these characters are retained so that the character numbering system remains comparable to Rauhut's.

Analysis of this matrix (heuristic search, TBR branch swapping, random addition sequence with 20 replicates) using PAUP 4.0b (Swofford 2002) produced 810 most parsimonious trees that were 522 steps long. The strict consensus of these trees is highly resolved (Fig. 9). Herrerasauridae and *Eoraptor lunensis* are found to be non-eusaurischian saurischians. Coelophysoids in the broad sense are paraphyletic with true Coelophysoidea (*Liliensternus liliensterni, L. airelensis, Coelophysis bauri, C. rhodesiensis, Gojirasaurus quayi, Segisaurus halli* and *'Syntarsus' kayentakatae*) being the sister group of all other theropods. *Dilophosaurus wetherilli* forms a clade with *Zupaysaurus rougieri* and *Dracovenator regenti* which is the sister group of Ceratosauria + Tetanurae. This clade is supported by: paired nasolacrimal crests; a slot-shaped foramen at the base of the nasal process of the premaxilla; a pendant medial process on the articular; and tab-like dorsal processes on the medial and lateral sides of the articular. The basal topology of Tetanurae differs strongly from Rauhut's original analysis. As in that analysis, *'Szechuanosaurus' zigongensis* and *Piatnitzkysaurus floresi* form a basal trichotomy with a clade consisting of all other

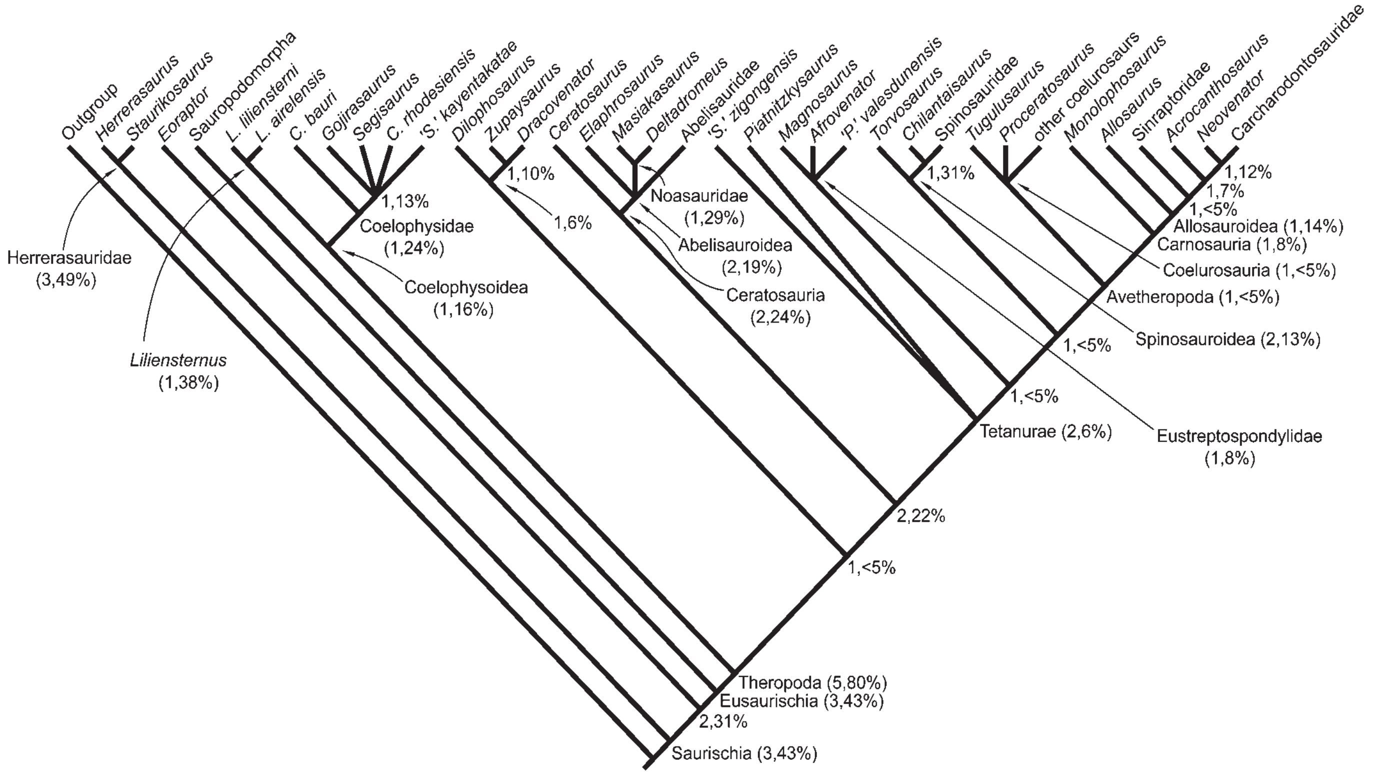

Figure 9. Strict consensus of 54 most-parsimonious trees. Only ingroup relationships are shown, the outgroup taxa (*Euparkeria, Marasuchus,* Ornithischia) are omitted. Numbers at each node indicate support measures, the left is the decay index and the right is the bootstrap support. Tree Length = 513, CI = 0.4893, HI = 0.5107, RI = 0.7152, RCI = 0.3499.

Tetanurae. Unlike Rauhut's analysis, all other non-coelurosaurian taxa do not form a single, highly inclusive, monophyletic Carnosauria. Instead Eustreptospondylidae (consisting of *Afrovenator abakensis, Magnosaurus* spp. and *'Poekilopleuron' valesdunensis*) and Spinosauroidea (*Torvosaurus tanneri, Chilantaisaurus tashuikouensis* and Spinosauridae) form serially closer outgroups to the Avetheropoda (Carnosauria and Coelurosauria). It is interesting to note that *Afrovenator abakensis, Magnosaurus* (as *Eustreptospondylus*) and *'Poekilopleuron' valesdunensis* were also found to form a clade exclusive of all other theropods in a recent analysis of basal tetanuran relationships (Holtz *et al.* 2004).

Very few nodes are robustly supported as can be seen from the generally low decay indices and very low bootstrap supports (Fig. 9). Theropoda is the only strongly supported clade (decay index = 5 steps, bootstrap = 80%) although Saurischia, Herrerasauridae and Eusaurischia are better supported than other nodes in the analysis. This low degree of support is not unexpected given the inclusion of several poorly known taxa (not least of which is *Dracovenator regenti* itself). As the position of *D. regenti* and the relationships of Coelophysoidea are the main questions of this work, a single Templeton test was performed that compared a tree from the set of most-parsimonious trees with one of the shortest trees where *Dilophosaurus wetherilli, Zupaysaurus rougieri* and *Dracovenator regenti* were included in an expanded, monophyletic Coelophysoidea. The difference in length between these two topologies was just one step, and it is unsurprising that the test found that there was no significant difference between them (P = 0.858).

DISCUSSION

The holotype of *Dracovenator regenti* clearly displays a number of synapomorphies of the neotheropod clade (*Coelophysis bauri* + Neornithes and all descendants of their most recent common ancestor, Sereno 1998) despite its incompleteness. Synapomorphies include: anteromedial processes of the nasals that separate the posterior ends of the nasal processes of the premaxilla (creating a w-shaped premaxilla–nasal suture on the internarial bar); a horizontal posterolateral process of the premaxilla that fails to contact the nasal; and a shallow antorbital fossa bordered by a low rounded ridge. Within this clade the specimen displays an intriguing melange of character states. Certain features closely resemble coelophysoids while others are found only in more derived theropods. Coelophysoid-like characteristics of *Dracovenator regenti* include: the low angle between the anterior and alveolar margins of the premaxilla; the retraction of the external nares (also in spinosaurids); the raised ventral margin of the antorbital fossa and its placement immediately above the alveolar margin of the maxilla. Characters found in Ceratosauria + Tetanurae, or included clades are: loss of the posteroventral process of the premaxilla; the probable presence of a rectangular anterior ramus of the maxilla offset from the ascending ramus by an inflection in the anterior profile of the maxilla; a concave attachment area for the depressor mandibulae on the dorsal surface of the retro-articular process; and a pendant medial process on the articular. The shape of the anterior ramus of the maxilla is inferred from the near right-angled bend in the posterior margin of the premaxilla between the main body and the posterolateral process. The pendant medial process of the articular has an intriguing distribution. Its presence in the avetheropod tetanuran clade Allosauroidea has been previously documented but its presence in *Dilophosaurus wetherilli* has remained unnoticed. Nevertheless examination of the referred material (UCMP 77270) shows that the base of a broken pendant process is present. In the present analysis the process is regarded as a synapomorphy of *Dilophosaurus wetherilli* + (*Dracovenator regenti* + *Zupaysaurus rougieri*) that is convergent with Allosauroidea. However, its presence in the basal tetanuran *Cryolophosaurus ellioti* (Sereno *et al.* 1996, table 2) alludes to a broader distribution and the character could diagnose a more inclusive clade.

The cladistic analysis suggests that the broader coelophysoid assemblage may not be monophyletic but this topology is not a significantly better explanation of the data than one where *Dilophosaurus wetherilli, Dracovenator regenti* and *Zupaysaurus rougieri* are included in a broad, monophyletic Coelophysoidea. It is unfortunate that key taxa such as *Dracovenator regenti* and *Zupaysaurus rougieri,* which show a tantalizing mix of typical coelophysoid characters with more derived theropod features, are so poorly known. Hopefully future discoveries of *Dracovenator regenti* will help decide the matter conclusively.

Although the small snout (BP/1/5278) is strikingly similar to *Coelophysis rhodesiensis,* it does display some differences that indicate its referral to that taxon is doubtful. Most noticeably it has compressed, blade-shaped premaxillary teeth with serrations on their posterior carinae (Munyikwa & Raath 1999), as do those of *Dracovenator regenti,* whereas those of *Coelophysis rhodesiensis* do not (Raath 1977). If the anterior ramus of the maxilla is correctly interpreted as being rectangular with an associated sharp bend in the premaxilla–maxilla suture then this would be a further point of agreement between BP/1/5278 and *Dracovenator regenti. Coelophysis rhodesiensis,* like most coelophysoid grade taxa, has an anteroventrally directed first maxillary tooth (Tykoski & Rowe 2004) but in BP/1/5278 it is directed fully ventrally. This character cannot be determined in *Dracovenator regenti* but it does indicate that BP/1/5278 is not referable to *Coelophysis rhodesiensis.* Further differences between BP/1/5278 and *C. rhodesiensis* are subtler. These include more sharply defined fossae within the antorbital fossa, anterior to the antorbital fenestra, the lack of a dorsoventral expansion at the anterior tip of the dentary and the development of a tiny dorsolateral nasal crest. It is telling to note that in all of these features BP/1/5278 resembles *Zupaysaurus rougieri* which is found to be the sister taxon of *Dracovenator regenti* in the cladistic analysis. If BP/1/5278 does belong to *Dracovenator regenti* then it would represent a juvenile individual that is approximately 20% of the size of the holotype individual. Probably the nasal crests would grow into larger structures in adult individuals. Unfortunately the BP/1/5278 lacks the posterior end of the skull, so we cannot determine if the diagnostic features of the articular of *D. regenti* were present, neither is the preservation of the external surface of the premaxillae sufficient to determine if the bilobed fossa was present. The specimen differs from *D. regenti* by having an external naris that is not fully retracted posterior to the premaxillary tooth row and having a nasal process of the premaxilla that does not protrude far beyond the level of the posterior tip of the posterolateral process. However, if BP/1/5278 is truly a juvenile individual then we might expect these features to develop with ontogeny. In any case, there is no unequivocal autapomorphy linking BP/1/5278 to *Dracovenator regenti* and the referral is left as a plausible, but unproven, suggestion.

Dracovenator regenti is the first recorded body-fossil of any theropod, other than *Coelophysis rhodesiensis,* from the *Massospondylus* RZ of southern Africa. However, it has long been known from footprint evidence that theropods larger than *C. rhodesiensis* were present in this biozone. Ellenberger (1970) reported theropod footprints (as *Kainotrisauropus moshoeshoei*), referable to the ichnotaxon *Eubrontes* sp. (Olsen & Galton 1984), that were 34 cm long from the upper Elliot Formation. There is also a large theropod trackway from the overlying Clarens Formation (Raath & Yates 2005). The Clarens Formation contains taxa typical of the *Massospondylus* RZ (Kitching & Raath 1984). These traces come from a theropod similar in size to *Dilophosaurus wetherilli.* The holotype skull of *Dracovenator regenti* is estimated to have been about 500 mm long, and individual elements are comparable in size to those of *Dilophosaurus wetherilli,* so *Dracovenator regenti* is a plausible trackmaker for the large theropod traces of the *Massospondylus* RZ.

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ABBREVIATIONS

Institutional

BP	Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg
CM	Carnegie Museum of Natural History, Pittsburgh
MB	Museum für Naturkunde der Humboldt Universität, Berlin
QG	Zimbabwe Natural History Museum, Bulawayo
SAM	South African Museum, Iziko Museums, Cape Town
UCMP	University of California, Museum of Palaeontology, Berkeley

Anatomical

a	articular
al	alveolus
an	angular
aof	antorbital fossa
aofe	antorbital fenestra
bf	bilobed fossa
c	cranial crest
ctf	chorda tympanic foramen
d	dentary
dmf	fossa for the attachment of the m. depressor mandibulae
dp	dorsal process of the articular
emf	external mandibular fenestra
en	external naris
g	glenoid
idp	interdental plate

j	jugal
l.	left
ln	lateral notch
lr	lateral ridge of the surangular
mp	medial process of articular
mpf	medial premaxillary foramen
ms	meckelian sulcus of the dentary
mx	maxilla
n	nasal
nf	narial fossa
np	nasal process of premaxilla
p	palatine
pa	prearticular
plp	posterolateral process of premaxilla
pmx	premaxilla
r.	right
rt	replacement tooth
s.	surface for articulation of
sa	surangular
sf	slot-like foramen
sp	splenial
sym	symphyseal surface
v	vomer
vc	ventral crest
vm	ventral margin of antorbital fossa

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APPENDIX 1. Character codings for the new characters (225–252) added to this analysis. For polymorphic character states, A = 0,1.

Euparkeria	00000	00000	000?0	00000	000?0	000
Marasuchus	?????	?????	000??	???00	00??0	000
Ornithischia	00000	00000	000?0	00010	00000	000
Eoraptor	0?0?0	00001	000??	0???1	000?0	000
Herrerasaurus	00000	00001	000?1	00011	00000	000
Staurikosaurus	?????	??0??	????0	?0???	0?0?0	0??
Sauropodomorpha	00000	00002	000?0	00011	10011	000
C. bauri	11010	11010	01001	00001	10011	010
Gojirasaurus	?????	?????	??0??	?????	?????	???
L. airelensis	?????	?????	?????	????1	?????	0??
L. liliensterni	?????	??0??	?10?1	????1	1???1	000
Dilophosaurus	11110	11010	00001	11101	100?1	0??
Segisaurus	?1???	?????	??0??	?????	1?0?1	0??
C. rhodesiensis	11010	11010	01011	0000?	10011	011
Magnosaurus	0?0?1	001??	000?0	?????	????1	0??
Monolophosaurus	0?000	00012	10??1	?0?11	1???1	0??
Piatnitzkysaurus	?????	?????	?0000	?????	?00?1	0?0
Proceratosaurus	????0	000??	?0??0	?????	?????	???
‘S.’ zigongensis	?????	?????	?0???	????1	100?1	???
Allosaurus	01001	00012	10000	10111	10011	000
Ceratosaurus	01001	00012	00000	00?01	111??	010
Elaphrosaurus	?????	?????	??0??	????1	111?1	010
Sinraptoridae	01001	00012	10000	10111	100?1	0?0
Torvosaurus	?1001	0011?	?00?0	?????	?00?1	000
Afrovenator	?????	?????	000??	????1	1?011	0?0
Chilantaisaurus	?????	?????	?????	?????	?????	???
Neovenator	??001	000??	?00?0	?????	????1	??0
Deltadromeus	?????	?????	??1??	?????	?11??	?00
Acrocanthosaurus	0?001	00012	100?0	?0111	10011	000
Abelisauridae	01001	00012	00000	00101	111?1	010
Spinosauridae	1?010	01000	10001	0?111	100?1	0?0
Carcharodontosauridae	0???1	0001?	100?0	?????	???11	??0
other coelurosaurs	01000	00012	10000	00111	1001A	000
‘P.’ valesdunensis	0?0??	001??	00??0	?????	?????	???
Masiakosaurus	?????	??0??	?01?0	?????	?11??	110
Zupaysaurus	1????	??01?	01??0	?????	?????	?1?
‘S.’ kayentakatae	1?010	110?0	01011	000??	?????	?11
Tugulusaurus	?????	?????	?????	?????	?????	00?
Dracovenator	?1110	0001?	?1???	111??	?????	???

APPENDIX 2. Character codings (characters 1–224) for the new, or significantly modified, taxa added to this analysis. For polymorphic character states: A = 0,1; B = 1,2; C = 0,2; D = 0,2,3.

Acrocanthosaurus
10?01 10000 01001 11011 01221 10110 11010 00010 00001 00010 020?? ?????
????1 02?12 001?1 01??? 00?00 00111 12101 20010 02100 20110 ???01 0?001
1?101 00111 ?1000 10000 00001 20011 10210 10211 ???1? 1???? ????? ????
01220 00101 00001 01210 011?? 202?? ????1 ????0 ?220

Carcharodontosauridae
?0??? 20?01 11000 10111 10221 10110 1101? 00011 01001 ????? 1B0?? 01111
?000? ????2 0???? 0???? ?00?0 00111 ????1 20010 12100 201?0 ????? ??001
1?10? ?01?? ??00 ????? ????? ????? ????? ????? ????? 101?0 ???00 0?001
01220 00101 00101 01210 011?? 20201 100?? ????0 ????

‘S.’ kayentakatae
02??1 20110 11101 10000 02110 00110 000?0 10000 00000 000?0 0100? ?????
??0?? ????0 00000 00??? 00?10 00100 0?000 000?? ????? ????? ????? ?????
????? ????? 10000 000?? ????? ????? ??1?? ????? ????? ????? ????? ?????
?0?0? ????? ??000 01100 01001 ?0?10 ???00 000?0 ?1??

Other coelurosaurs
0A0A1 20001 01010 11000 A0021 00110 10010 0A000 00C0A 01100 01110 01111
10AA1 03112 00111 0111A 00010 00111 1B0A0 21011 0B100 101A0 11200 0AA01
01010 00111 11000 10010 00001 D011A 10210 10212 00000 10110 10001 0101B
01021 00100 00CA1 012B0 A1111 2220B 10112 11010 0220

‘P.’ valesdunensis
010?1 200?? 21100 11??? ????1 1011? ????? 00?00 10001 ?0??? ?1000 0???0
0000? ?2??? 0???? 0121? 00000 00??? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ????? ????? ????

Masiakosaurus
????? ???0? 00001 00??? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? 0000? ?01?0 00AA1 ????0 ?1010 12100 000?? ?2200 0???1
?1110 00??? ????? ????1 011?? ????? ????? ????? ????? ????? ????? ????0
00120 01??? ???00 00200 11111 102?? ???01 10110 ????

Zupaysaurus
????? ????0 01001 1?000 02020 00110 10000 0?000 00001 0001? 0???? ?????
????? ????1 00?10 00??? ?00?? 00??? ??0?0 ????? ????? ????? ????? ?????
????? ????? ????? 1???? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ?0??? ?01?? ??000 0001? ????

Tugulusaurus
????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
?1??? ????? ????? ????? ????? ??11? ????0 ??2?? ?001? ????? ????? ?????
????? ????? ???00 012B0 01101 212?? ???01 1101? ????

Dracovenator
02001 2???? 21??1 ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ??01? ????? 00?00 00??? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ????? ????? ????

New information on the palate and lower jaw of *Massospondylus* (Dinosauria: Sauropodomorpha)

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Additional anatomical details of the palate and lower jaw of the prosauropod dinosaur *Massospondylus* Owen are documented on the basis of a previously undescribed skull from the upper Elliot Formation. The palate is generally similar to that of other early sauropodomorphs, but can be shown to differ from those of *Plateosaurus, Lufengosaurus* and *Thecodontosaurus* in several respects. For example, *Massospondylus* lacks the well-developed palatine boss seen in *Plateosaurus* and the pneumatic recess that is present on the ectopterygoid of *Thecodontosaurus.* In addition, *Massospondylus* possesses an expanded medioventral premaxillary process that is much larger than that of any other basal sauropodomorph.

Keywords: *Massospondylus*, upper Elliot Formation, Lower Jurassic, palate, mandible.

INTRODUCTION

The basal sauropodomorph (prosauropod) dinosaur *Massospondylus carinatus* Owen is represented by abundant material, including complete skeletons and skulls, from the upper Elliot, Clarens and Forest Sandstone formations of southern Africa (Owen 1854; Cooper 1981; Gow 1990; Gow *et al.* 1990; Sues *et al.* 2004). Indeed, material of this animal is so common that it was selected as the eponymous index taxon of a biostratigraphical unit dubbed the *Massospondylus* range zone (Kitching & Raath 1984), which is thought to be Lower Jurassic (?Pliensbachian and/or ?Toarcian) in age (Yates *et al.* 2004). Although *Massospondylus* was named a century and a half ago (Owen 1854), many aspects of the anatomy and taxonomy of this animal remain unclear. For example, new evidence suggests that some specimens previously ascribed to *Massospondylus* may pertain to another, potentially new, basal sauropodomorph taxon (Barrett 2004).

Cranial material of *Massospondylus* has been described in detail on the basis of a superb series of skulls housed in the collections of the Bernard Price Institute for Palaeontological Research, Johannesburg (Gow 1990; Gow *et al.* 1990; Sues *et al.* 2004). However, preservation and/or the stage of preparation of these specimens has prevented collection of anatomical data from various regions of the palate and from the medial surface of the lower jaw, with the result that these regions have not yet been fully described. In BP/1/4779, for example, the lower jaws are adhered to the skull and remain partly encased in matrix, obscuring the rostral part of the palate. The palates of basal sauropodomorphs are poorly known: only that of *Plateosaurus* has been described in its entirety (Galton 1984), though partial and/or brief descriptions do also exist for other taxa (e.g. *Lufengosaurus*: Young 1951, Barrett *et al.* 2005; *Thecodontosaurus*: Yates 2003; *Massospondylus*: Sues *et al.* 2004). Here, we provide a description of the palatal aspect of the skull and medial surface of the lower jaw of *Massospondylus* based on a previously figured, but undescribed skull in the collections of the South African Museum, Cape Town (SAM-PK-K1314; Figs 1–4).

MATERIALS

In 1967, a joint expedition organised by the South African Museum, Yale University, Birkbeck College (University of London), and the British Museum (Natural History) (now the Natural History Museum, London) collected a variety of vertebrate fossils from the Stormberg Group of South Africa and Lesotho (Attridge & Charig 1967; see also Crompton 1968). During the course of this expedition, C.E. Gow collected an almost complete skeleton of *Massospondylus,* including an excellent skull (SAM-PK-K1314). This specimen pertained to the upper Elliot Formation of Blikana Mountain, Orange Free State (30°34′S, 27°37′E), from an horizon approximately 10–12 m below the contact with the overlying Cave Sandstone (J. Attridge, pers. comm., 2004).

The skull has been compressed dorsoventrally, resulting in midline separation of the palatal elements, some disarticulation of the suspensorial elements, and damage to the nasal region (Figs 1–3). The left mandible (Fig. 4) is essentially complete, but only the rostral part of the right dentary is present. In other respects, the skull is well preserved, with delicate structures such as the left stapes and right sclerotic ring preserved in their correct anatomical positions. SAM-PK-K1314 appears to have been a subadult individual, as evidenced by the presence of discernible sutures between the elements of both the braincase and skull roof.

Initially, preparation was carried out by Ione Rudner of the South African Museum, and was continued by William Amaral and Charles Schaff of the Museum of Comparative Zoology, Harvard University. The left-hand side of the skull has been almost completely prepared, revealing details of all available bone surfaces, whereas the interior of the right-hand side of the skull is still filled with matrix. Both lower jaws are prepared in the round

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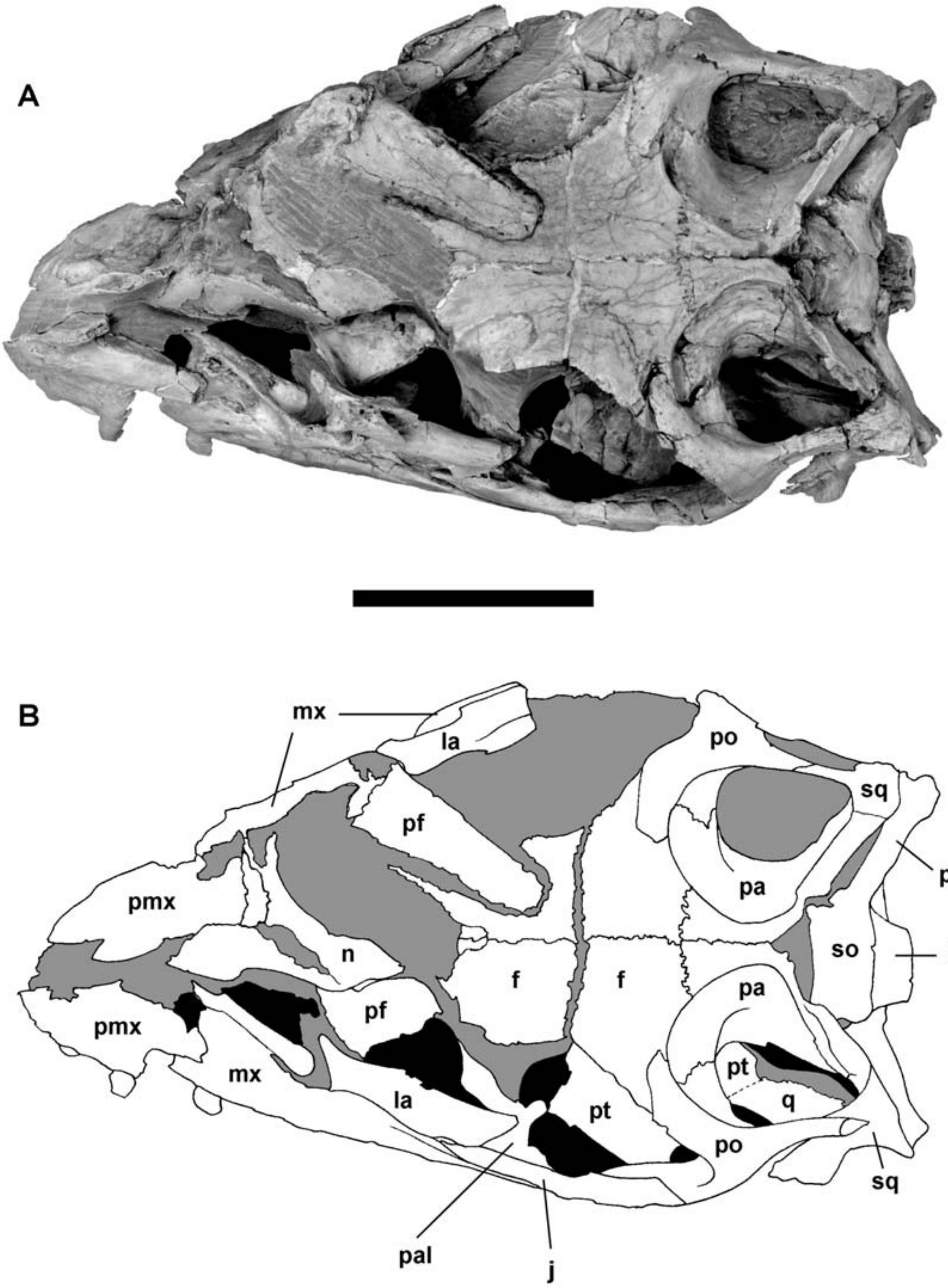

Figure 1. Skull of *Massospondylus carinatus* (SAM-PK-K1314). **A**, Photograph of skull in dorsal view. **B**, Interpretative drawing of the skull. Grey fill represents matrix and reconstruction; black fill represents voids within the skull. Scale bar equals 5 cm.

and are separated from the skull. Although the specimen has never been formally described, it has been figured (e.g. Cooper 1981: figs 1 & 2) and mentioned briefly in several papers (e.g. Attridge *et al.* 1985; Crompton & Attridge 1986). It also formed the basis for the skull reconstruction of *Massospondylus* proposed by Crompton & Attridge (1986: fig. 17.4).

Sues *et al.* (2004) have proposed an emended diagnosis for *Massospondylus* based on a series of cranial autapomorphies (e.g. presence of a lateral boss on the prefrontal and a distinct ridge on the lateral surface of the lachrymal) and a unique combination of other cranial characters (e.g. the combined presence of an ascending maxillary process that is tall, nearly vertical with a narrow medial sheet with an elongate prefrontal). The majority of these features (see Sues *et al.* 2004, for a full list) are present in SAM-PK-K1314, indicating that the latter can be referred to *Massospondylus*, an identification confirmed by comparison with other skulls referred to this genus (e.g. BP/1/4376, BP/1/4779, BP/1/4934 and BP/1/5241).

This description is not intended to be exhaustive, but aims to supplement the recent account provided by Sues *et al.* (2004). In order to avoid excessive duplication of information, the lower jaw will be described in medial view only (Fig. 4), and we will concentrate on those areas of the palate (Fig. 3) that are either unprepared or damaged in the series of *Massospondylus* skulls described by Gow *et al.* (1990) and Sues *et al.* (2004).

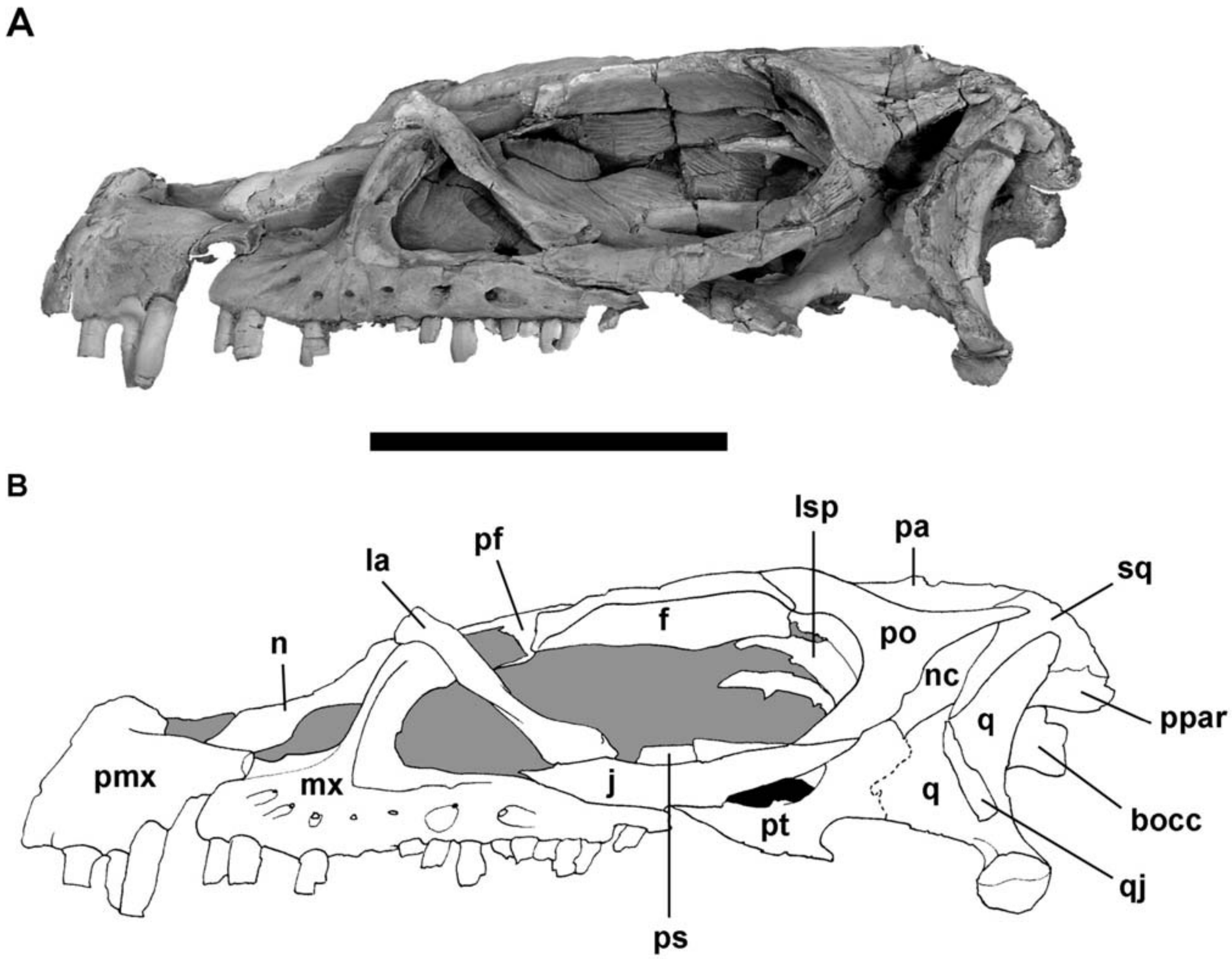

Figure 2. Skull of *Massospondylus carinatus* (SAM-PK-K1314). **A**, Photograph of skull in left lateral view. **B**, Interpretative drawing of the skull. Grey fill represents matrix and reconstruction; black fill represents voids within the skull. Note that breakage of the lower temporal bar reveals some details of the palate in lateral view. Although the braincase can be seen through the dorsal part of the lower temporal fenestra, no suture lines or foramina are discernible. Scale bar equals 5 cm.

DESCRIPTION

Palatal aspect of skull

Premaxilla

Four alveoli are present in each premaxilla, though only three teeth are preserved in life position (right teeth 2, 3 and 4). A sub-circular replacement foramen lies dorsal to each alveolus: the alveoli and replacement foramina were continuous with each other and were not separated by bars of bone. The conjoined replacement foramina/alveoli are separated from each other by rhomboidal interdental plates. The lateral wall of the dental parapet is dorsoventrally deeper than the medial wall: this difference in height remains constant along the length of the premaxilla and the tooth crowns are not obscured in labial view.

The ventral surface of the premaxilla is strongly concave transversely and meets its counterpart at the midline to form a complete premaxillary secondary palate. The caudomedial corner of each premaxilla gives rise to a stout, triangular process that extends caudally parallel to the skull midline, tapering to a bluntly rounded point (referred to hereafter as the medioventral process). This process has a small contact with the rostral margin of the vomer and probably made a small contribution to the rostromedial margin of the internal naris.

Maxilla

In ventral view, the maxilla is dorsoventrally tallest rostrally and tapers caudally to a narrow ramus with a sub-triangular transverse cross-section. A rostromedially directed, stout, cylindrical premaxillary process is present. The medial surface of the maxilla is gently concave dorsoventrally in its rostral part, becoming more planar in the middle section of the bone, before giving rise to a sharp ridge that extends along the caudalmost third of the tooth-bearing ramus, which divides the medial surface into a planar, horizontally oriented surface (lying ventral to the ridge) and a concave area above. This area displays a distinct, strap-like, striated articular surface for the reception of the maxillary process of the palatine.

Rostrally, the lateral margin of the dental parapet is dorsoventrally higher than the medial one. However, the height of the former decreases caudally, until the two margins reach the same height in the caudal third of the tooth-bearing ramus. Small sub-circular replacement foramina are confluent with the medial margins of the alveoli rostrally, but the foramina display a progressive

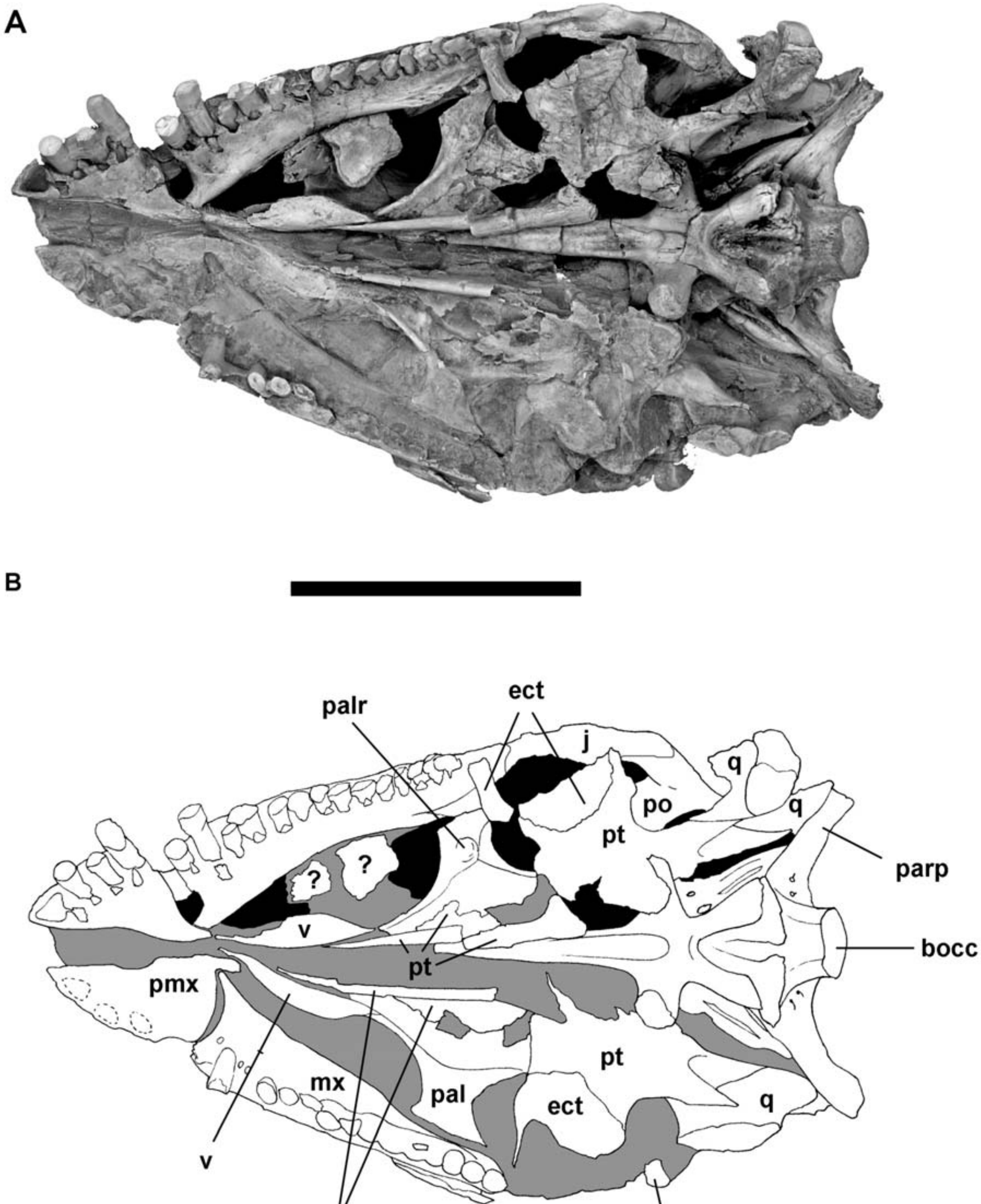

Figure 3. Skull of *Massospondylus carinatus* (SAM-PK-K1314). **A**, Photograph of skull in palatal view. **B**, Interpretative drawing of the skull. Grey fill represents matrix and reconstruction; black fill represents voids within the skull. Most of the braincase elements are unlabelled for clarity. See Gow (1990) and Sues *et al.* (2004) for details of braincase anatomy. Note that scale bar equals 5 cm.

decrease in size caudally, eventually becoming entirely confluent with the alveoli approximately halfway along the tooth row. Alveoli are separated from each other by small rhomboidal interdental plates. The gently concave medial margin of the maxilla would have formed the lateral margin of the large, sub-elliptical internal naris.

Sues *et al.* (2004) mentioned the presence of a small contact between the maxilla and vomer in BP/1/4779 but this contact is not visible due to the presence of matrix surrounding the vomers. There is a small sliver of bone contacting the rostrolateral margin of the right vomer but this is most likely the medioventral process of the premaxilla. Furthermore there is no evidence of any contact between these elements in SAM-PK-K1314. The rostromedialmost part of the maxilla may have made a very small contribution to the secondary palate.

Vomer

The vomers are long, sinous bones in ventral view, which are mediolaterally widest in their central portion

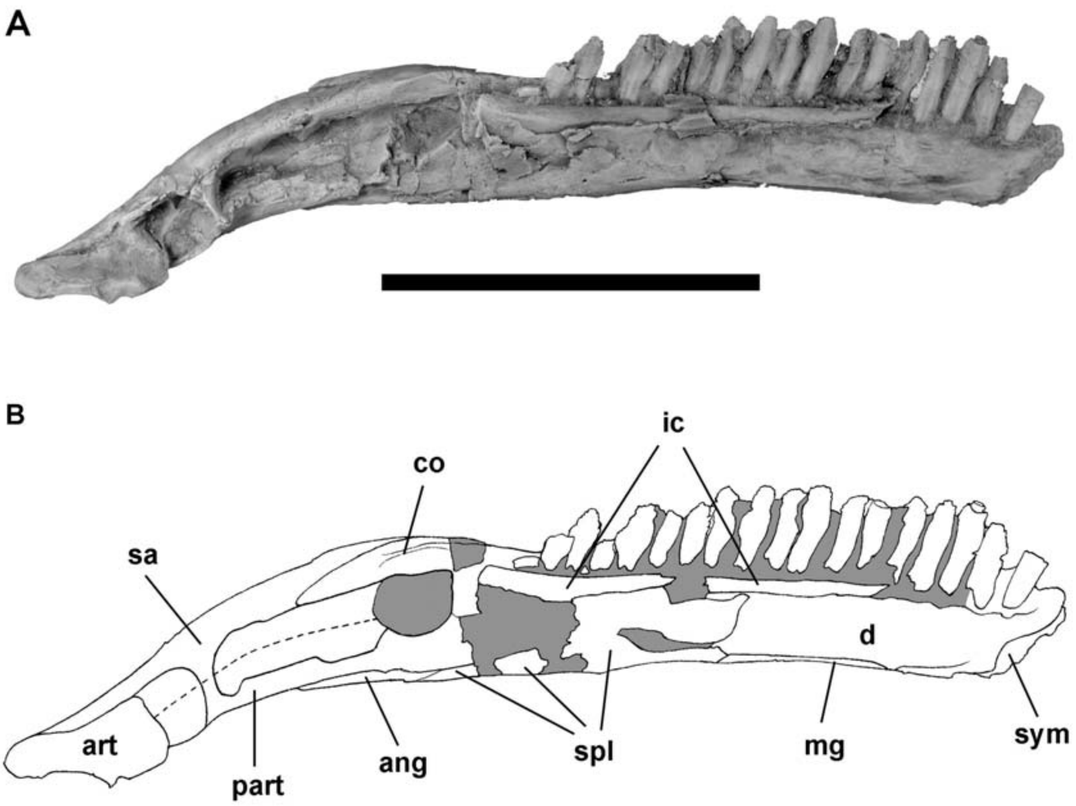

Figure 4. Left lower jaw of *Massospondylus carinatus* (SAM-PK-K1314). **A**, Photograph of lower jaw in medial view. **B**, Interpretative drawing of the lower jaw. Grey fill represents matrix and reconstruction. Dotted line represents the position of likely boundary between the prearticular and surangular. Scale bar equals 5 cm.

and taper both rostrally and caudally. Rostrally, the area that articulates with the premaxilla is flat ventrally, whereas the central and caudal sections of the bone, where the vomer articulates with the pterygoids and palatines (which are the portions visible in BP/1/4779) are transversely convex. The dorsal surfaces of the vomers are obscured by matrix.

Although the vomers have become separated, it is likely that they were in contact along the midline for much of their length, but were separated caudally by the intervention of a narrow rostral extension of the palatine process of the pterygoids. The rostral margin of the vomer and the medioventral process of the premaxilla met along a very short overlapping contact. Caudally, the vomer tapers to a fine point that is clasped between the pterygoid (medially) and palatine (laterally). The concave lateral margin of the vomer comprises the rostral half of the medial margin of the internal naris.

Palatine

There is a small, lightly rugose patch on the ventral surface of the palatine, immediately lateral to the apex of the triangular fossa that occupies the medial side of the ventral surface. This rugosity, which is also present in BP/1/4779, occurs in the same position as the palatine peg seen in *Plateosaurus* (Galton 1984). No other details can be added to the description of Sues *et al.* (2004).

Ectopterygoid

SAM-PK-K1314 permits one new observation on the ectopterygoid in addition to those provided by Sues *et al.* (2004): namely, the ectopterygoid provides a relatively large contribution to the pterygoid flange, accounting for almost all of its lateral portion, or approximately one third of its total surface area.

Pterygoid

As in *Plateosaurus* (Galton 1984), the quadrate process of the pterygoid is subdivided. A long tapering dorsal ramus extends upward along the vertical part of the pterygoid wing of the quadrate and a shorter, stouter ventral ramus extends horizontally along the base of the pterygoid process: this feature is also visible in BP/1/4934 and BP/1/4779, although the distinction between the two rami is not as marked in the latter skull (Sues *et al.* 2004: fig. 5B; pers. obs.). This character cannot be seen in the other skulls in the Bernard Price Institute due to either damage or presence of surrounding matrix. No other details can be added to the descriptions provided by Sues *et al.* (2004).

Mandible

The caudal part of the left mandible has undergone torsion relative to the undeformed rostral part. In particular, the dorsal part of the coronoid eminence is rotated medially, so that in lateral view it appears to be much lower in height than it would have been originally. Also, the articular region has become depressed and rotated medially, so that the articular glenoid faces mainly medially, rather than dorsally, and the level of the craniomandibular joint is situated considerably further ventrally than it would have been in life. The external mandibular fenestra is matrix-filled; the internal mandibular fossa is also partly obscured by matrix and by a small amount of restoration. The internal mandibular fenestra is large and is bounded by the surangular and angular laterally, the prearticular ventrally, the surangular caudodorsally and the coronoid rostrodorsally, with small contributions from the intercoronoid and dentary rostrally. Eighteen tooth positions are present and 15 erupted teeth are preserved *in situ.*

Only the rostralmost part of the right mandible is preserved (from its rostral end up to approximately the level of the 12th tooth position). Its morphology agrees in all respects with that of the left mandible.

Dentary

The lateral dental parapet is higher than the medial one for almost the entire length of the dentary (though this discrepancy is reduced slightly near to the end of the tooth row). In medial view, immediately ventral to the row of alveoli, sub-circular replacement foramina are present, which are separated from each other by small rhomboidal interdental plates. The presence of these foramina can only be confirmed for the first five tooth positions; caudal to this, the region ventral to the tooth row is obscured by the intercoronoid. The symphysis is rostrocaudally narrow, rugose, and approximately elliptical in outline. A very shallow Meckelian groove extends along the ventral margin of the dentary from the base of the symphysis to the articulation with the splenial. Most of the caudal part of the dentary is obscured by contact with the splenial, intercoronoid and prearticular.

Splenial

The splenial is a thin, plate like element that covers much of the caudal part of the dentary in medial view. A sub-rectangular main body, which extends from the ventral margin of the mandible to the level of the intercoronoid, gives rise to a caudally tapering ventral process that extends along the ventral margin of the mandible, underlying the prearticular. The medial surface of the splenial is flat to very gently convex dorsoventrally. The caudoventral process wraps around the ventral margin of the mandible, overlapping the angular, so that a very small sliver of the splenial is visible in lateral view. A small rostral projection from the ventral part of the main body fits into the Meckelian groove that extends along the ventral surface of the dentary.

Intercoronoid

As preserved, the intercoronoid extends from a point level with the rostral margin of the coronoid eminence to the base of the fifth dentary tooth (though it is likely to have extended further rostrally in life). It lies parallel and ventral to the medial dental parapet. It is a dorsoventrally narrow, elongate, rod-like element, which is broken at its rostral and caudal terminals. The medial surface is very gently convex dorsoventrally. Caudally, the terminal part of the intercoronoid is slightly upturned relative to the rest of the bone. Rostrally, it contacts the dentary; in its midsection it also contacts the splenial (ventrally); and caudally it develops an additional contact with the prearticular (ventrally). The intercoronoid may also have contacted the coronoid caudally, but this cannot be confirmed due to damage.

Coronoid

The coronoid is poorly preserved, but it appears to have been a relatively mediolaterally narrow, rostrocaudally short element that comprises the rostral margin of the coronoid eminence in medial view. It is broken rostrally, so it is not possible to determine its contacts with the prearticular, splenial and intercoronoid. It contacts the surangular laterally.

Prearticular

The prearticular is an elongate element with expanded rostral and caudal ends that are connected to each other via a narrow shaft. It forms the ventral margin of the internal mandibular fenestra. It is not possible to see if a foramen is present at the splenial/prearticular junction (as occurs in *Plateosaurus*: Galton 1984) due to crushing of this area and the presence of matrix.

Rostrally, the prearticular contacts the splenial and intercoronoid (in medial view) and dentary laterally. In its middle section, the prearticular contacts the angular and surangular laterally, and caudally it contacts the surangular laterally and the articular dorsally. The rostral expansion is plate-like and its dorsal margin curves caudoventrally to form the rostral margin of the internal mandibular fenestra. The bone narrows caudally before expanding again, both dorsoventrally and mediolaterally, to form the crest-like caudoventral margin of the internal mandibular fenestra (in combination with a medially directed process arising from the surangular). Caudal to this crest, the prearticular thins to form a transversely oriented sheet that contacts the surangular laterally forming a trough for reception of the articular. The prearticular forms the medioventral boundary of a shallow fossa, bounded caudally by the rostral margin of the articular and rostrally by the crest-like ridge marking the caudal margin of the internal mandibular fenestra. This fossa has an irregular surface and many have been filled with cartilage in life: the rostral margin of the articular is composed of smooth finished bone and is not likely to have extended any further forwards, nor has it been displaced caudally.

Surangular

The surangular is the largest post-dentary bone. In lateral view, it contacts the dentary rostrally (though the contact is not clear), the angular ventrally and forms the dorsal boundary of the external mandibular fenestra. Near to its caudal end, the contact with the articular can be seen, and the caudalmost part of the surangular extends almost to the tip of the retroarticular process. It is not possible to see if the large foramen usually present on the rostral surface of the coronoid eminence is present, due to damage. However, a small foramen is present on the lateral surface on the caudal border of the coronoid eminence; this is contiguous with a foramen visible on the medial surface, which enters the internal mandibular fenestra.

In medial view, the surangular forms the lateral boundary of the internal mandibular fenestra and its thickened dorsal border. In the rostral part of this dorsal border, the surangular is overlapped by the coronoid. For most of its length the surangular forms an approximately flat plate (thickened along its dorsal margin, slightly convex laterally and slightly concave medially). It is not possible to determine whether there was any contact with the intercoronoid rostrally, due to damage in the intervening area. The ventral part of the surangular has an extensive contact with the prearticular. Caudally, the surangular thickens mediolaterally to form a medially oriented tapering process that arises at the border of the internal mandibular fenestra to contact the prearticular (forming the crest-like caudal margin of the fenestra, see above). Caudal to this crest, the surangular comprises the lateral boundary of the shallow fossa that lies in front of the articular (see above).

Angular

The angular comprises the caudoventral part of the lateral surface of the mandible and forms the ventral border of the external mandibular fenestra. It is subtriangular in lateral view and contacts the surangular along its length, dorsally. Caudally, it does not extend as far back as the retroarticular process. At its caudalmost point it has a very small contact with the articular. Owing to the torsion of the mandible, the prearticular is visible ventral to the angular (in its caudal part) in lateral view. The lateral surface of the angular is flat to very gently convex, dorsoventrally.

The angular is overlapped medially by the prearticular, which largely obscures it. A very small part of the angular wraps around the ventral surface of the mandible and is visible between the prearticular and the splenial.

Articular

The articular comprises the articular glenoid of the mandible and the majority of the retroarticular process. It fits into a sulcus formed by the surangular and prearticular, which both contact the articular ventrally; in the case of the surangular, this contact continues for the length of the articular, whereas the prearticular terminates more rostrally (although broken in this specimen) allowing the articular to be seen in ventral view. The articular also contacts the angular at its ventrolateral margin. In dorsal view, the articular has a sub-elliptical outline and can be divided into two regions. Rostrally, the dorsal surface is mildly concave both rostrocaudally and mediolaterally and this area represents the glenoid for reception of the quadrate condyle. The glenoid is defined rostrally and medially by the thickened margins of the articular and laterally by the surangular. Caudally, the glenoid boundary is not marked by a ridge, but by a distinct change of slope as the articular curves slightly dorsally to form its second region, the retroarticular process. The glenoid is of approximately the same length as the quadrate condyle. A distinct notch is present medial to the glenoid surface. In dorsal view, the articular tapers caudally to form the short retroarticular process, which has a sub-triangular transverse cross-section. The dorsal surface of the retroarticular process is transversely concave, forming a groove that becomes confluent with the more rounded glenoid cavity rostrally.

COMPARISONS AND DISCUSSION

In most respects, the palate and lower jaw of *Massospondylus* are similar to those of other basal sauropodomorphs, such as *Thecodontosaurus, Lufengosaurus, Plateosaurus* and *Anchisaurus* (Young 1951; Galton 1976, 1984, 1985; Yates 2003; Galton & Upchurch 2004; Barrett *et al.* 2005). Unfortunately, prosauropod palates are very poorly known, so the following comparative comments are far from comprehensive and more detailed investigation must await the description or further preparation of other specimens. However, a number of useful comparisons can be made. For example, *Massospondylus* lacks both the palatine peg (Sues *et al.* 2004), which is considered to be an autapomorphy of *Plateosaurus* (Galton 1984), and the ventrally (?pneumatically) excavated ectopterygoid seen in *Thecodontosaurus* (a possible autapomorphy of the latter: Yates 2003), allowing clear distinctions to be made between the palates of these taxa.

Several other differences are also apparent. In both *Lufengosaurus* (Young 1951; Barrett *et al.* 2005) and *Plateosaurus* (Galton 1984; Galton & Upchurch 2004) the vomers are elongate, parallel-sided elements in ventral view; in *Plateosaurus* vomer length is approximately 27% of total skull length (based on the reconstruction in Galton & Upchurch 2004). By contrast, the central portions of the vomers of *Massospondylus* are mediolaterally expanded relative to their rostral and caudal terminations, giving them a convex lateral outline in ventral view (see above and BP/1/4779). Additionally, the vomers are relatively shorter reaching only 20% of total skull length (based on SAM-PK-K1314). Sues *et al.* (2004) note that the pterygoid of *Massospondylus* lacks the hook-like process that contacts the basipterygoid process in *Plateosaurus*: however, a broad, flattened medial process of the pterygoid, which is separated from the main body of the pterygoid by a deep notch, is present in SAM-PK-1314. In SAM-PK-1314, at least one *Plateosaurus* specimen (HMN XXIV), the skull of '*Massospondylus*' from the Kayenta Formation (A.M.Y., pers. obs. of MCZ 8893), *Lufengosaurus* (Barrett *et al.* 2005) and a basal sauropodomorph skull from the lower Elliot Formation (Welman 1999), the basipterygoid process sits in this notch. The palate of another *Plateosaurus* specimen (SMNS 13200) appears to show a different condition where the hook-like medial process of the pterygoid wraps around the basipterygoid process (Galton 1985). This is reproduced in most reconstructions of the skull of *Plateosaurus* (e.g. Galton & Upchurch 2004), but we suggest that the basipterygoid processes of this specimen are in an unnatural position due to lateral compression and that the condition in SAM-PK-1314 is typical for Prosauropoda.

SAM-PK-K1314 possesses a prominent caudomedial process on the premaxilla, a feature absent in *Plateosaurus*

(Galton 1984; Galton & Upchurch 2004). This feature is not determinable in the *Massospondylus* skulls described by Sues *et al.* (2004), but is clearly much reduced in at least one South African specimen referred to *Massospondylus* (SAM-PK-K388). It is possible that this character may, therefore, be subject to intraspecific variation. Alternatively, this feature may prove to have taxonomic relevance, as it has been suggested that two basal sauropodomorph taxa are present in the upper Elliot Formation dinosaur fauna that can be differentiated on the basis of tooth crown, braincase and skull roof morphology (Barrett 2004). The presence/absence of a caudomedial process may help to further distinguish *Massospondylus* from this second, unnamed, taxon. Interestingly, a skull referred to *Massospondylus* from the Lower Jurassic Kayenta Formation of Arizona, U.S.A. possesses a long caudomedial process (Attridge *et al.* 1985), though a full description and systematic evaluation of this specimen has yet to be published. Similarly, the relative contribution of the ectopterygoid to the pterygoid flange also varies. In SAM-PK-K1314 and *Thecodontosaurus* (Yates 2003), the ectopterygoid comprises most of the lateral portion of the flange, while in *Lufengosaurus* (Barrett *et al.* 2005) and *Plateosaurus* (Galton 1984) the ectopterygoid is restricted to a small portion of the rostrolateral part of the flange. Other specimens of *Massospondylus* (BP/1/4779 and BP/1/4934; Sues *et al.* 2004) show an intermediate condition. Again, it is possible that this feature may either vary within *Massospondylus* or be taxonomically significant. Additional comparative data on prosauropod palates are needed in order to test these suggestions.

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LIST OF ABBREVIATIONS

Institutional

BP	Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg.
HMN	Museum für Naturkunde der Humboldt Universität, Berlin.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, U.S.A.
SAM	South African Museum (Iziko Museums of Cape Town), Cape Town.
SMNS	Staatliches Museum für Naturkunde, Stuttgart.

Anatomical

ang	angular	la	lachrymal
art	articular	j	jugal
bocc	basioccipital condyle	lsp	laterosphenoid
co	coronoid	mg	Meckelian groove
d	dentary	mx	maxilla
ect	ectopterygoid	n	nasal
f	frontal	nc	neurocranium
ic	intercoronoid	pa	parietal
pal	palatine	q	quadrate
palr	palatine rugosity	qj	quadratojugal
part	prearticular	sa	surangular
pf	prefrontal	so	supraoccipital
pmx	premaxilla	spl	splenial
po	postorbital	sq	squamosal
par	paroccipital process	sym	symphysis
ps	parasphenoid rostrum	v	vomer
pt	pterygoid		

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Makapansgat suids and *Metridiochoerus*

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Fossil suid material from Member 3 of the Makapansgat Formation was described as *Potamochoeroides shawi* but some authors have regarded it as an early stage of the *Metridiochoerus andrewsi* lineage. There is no complete cranium so a new reconstruction has been based on combining the data from a number of partial specimens. Comparison with *Metridiochoerus andrewsi* is difficult as there are reasons to suspect that the so-called 'male' and 'female' crania from Koobi Fora could be specifically distinct. An undescribed cranium from the Omo Shungura Formation is morphologically similar to the 'male' and is attributed to *Metridiochoerus jacksoni.* Comparison with the reconstructed Makapansgat suid indicates that the latter already shows an early stage in the distinctive architecture of the *M. jacksoni* cranium, as well as some resemblances in dental features. Accordingly it is suggested that the Makapansgat suid be designated as M*etridiochoerus shawi.* A few teeth from Member B11 of the Shungura Formation, with an age close to 2.95 Ma, are placed provisionally as *M.* cf. *shawi*; previously described molars referred to an early *Notochoerus scotti* are probably from a similar level. While this is suggestive, correlation is not firmly established.

Keywords: suid, *Potamochoeroides, Metridiochoerus,* Makapansgat, Shungura Formation, Koobi Fora Formation, Plio-Pleistocene, Africa.

INTRODUCTION

The Makapansgat Limeworks cave deposits have yielded substantial quantities of fossil remains of Plio-Pleistocene vertebrates, including important specimens ascribed to *Australopithecus africanus.* The deposits represent the consolidated infillings of a large cave system that was developed in the regional dolomitic limestone, The early phase of deposition was subaqueous and resulted in the building of layers of speleothem ('travertine') several metres thick on the floor, walls and roof of the cavern. This high grade calcium carbonate attracted the attention of miners in the 1920s and early 1930s and was removed with the curious result of leaving the former cave fillings as a roof above the galleries that now provide access to the site.

The stratigraphy of the clastic sediments above the travertine is rendered complicated by the existence of several depositories but the sequence of events has been ably reconstructed by Latham, Herries and Kuykendall (2003). Although it is not possible to trace each horizon across the entire area, the 'Classic Section' on the west side provides a useful reference frame and the nomenclature proposed by Partridge (1979, 2000) is still convenient.

The basal speleothem (Member 1) is followed by horizontally stratified red sandy and silty sediments (Member 2). Above this is Member 3, consisting largely of bones and bone fragments in a matrix of grey silty sand, heavily calcified and from 50 cm to as much as 2 m thick. Commonly referred to as 'the grey breccia', this is by far the major source of fossil material. Overlying the bone bed is a thick deposit of pinkish sandy material, sometimes stratified and occasionally rich in clasts of dolomitic material (Member 4); it has yielded a few fossils, notably cercopithecoids but also one specimen of *Australopithecus africanus.*

The purer calcite limestone was removed by the miners and burnt in a kiln on the northwest side of the caves. Any rock that was not pure limestone was discarded and dumped near the kilns, fortunately including blocks and pieces of the grey breccia. Under the direction of Alun Hughes and James Kitching in the 1940s and 1950s the dump material was examined and sorted so that the fossils could be extracted from the easily-recognized grey breccia. Many thousands of bones and teeth were recovered from these dumps whereas only a handful of specimens have been recovered *in situ* from small excavations carried out by Ron Clarke in the 1970s and Jeff McKee in the 1990s. However, the material is so characteristic in appearance that there is little doubt about its derivation from Member 3.

DESCRIPTION

Suid remains

The first account of suids from Makapansgat was given by Maureen Dale (1948) in a brief paper describing two species that she named *Pronotochoerus shawi* and *Potamochoeroides hypsodon.* The type specimen of the latter was a right maxillary fragment with the third molar slightly damaged; the matrix shows that it came from a pinkish deposit. The type specimen of *Pronotochoerus shawi* was a right mandibular ramus from the grey breccia, with lower P3–M3, and it was compared with the material from Omo described by Leakey (1943) as *Pronotochoerus jacksoni.* Subsequently more material was recovered from the grey breccia and one additional specimen from the pink deposit. In 1958, Ewer described the total collection, referring Dale's two species both to *Potamochoeroides* with the species *shawi* having page priority, but she retained the two specific names. Cooke & Wilkinson (1978) considered them conspecific as *Potamochoeroides shawi.* Harris & White (1979) placed the Makapan suid in the genus *Metridiochoerus* as representing Stage I in what they regarded as the *Metridiochoerus andrewsi* lineage, based on the evolution of the third molars. All the cranial material from Makapansgat was re-examined and described by Bender (1992). He constructed a cladogram that he considered as demonstrating the apparent affinity of *Potamochoeroides shawi* with *Potamochoerus porcus* and a lack of affinity with *Metridiochoerus andrewsi* as represented by the fine material from Koobi Fora. This conclusion needs to be reconsidered.

The cranium

There is no complete cranium in the Makapansgat suid collections, the most complete specimen being M1391 which comprises much of the frontal, nasal and maxillary areas and part of the parietals. The snout is broken and the canine flanges and premaxilla are lost, but the palate is almost complete to the back of the third molars. The whole of the occiput is missing and the zygomatic arches are lost. It has been illustrated by Ewer (1958, pl. 2) and by Bender (1992, figs 2 & 3). The specimen shows that there was originally a full set of cheek teeth belonging to a mature animal (Wear Stage 6 of Kullmer, 1999).

Other portions of crania make it possible to effect a reasonably good reconstruction of the cranium, except for the zygomatic arches. M588 is the ventral portion of an occiput and may actually have belonged to M1391. M2062 preserves the braincase behind the nasal/frontal suture, as well as part of the maxilla with an erupting UM2 that shows this to be a young animal. It has been described briefly and well illustrated by Bender (1992, figs 4, 5 & 9). Because of the age difference this specimen cannot simply be integrated with with M1391 but can be used to infer that the braincase was gently arched but not unduly elevated and the orbits rose almost to the roof; the pterygoids protrude ventrally. The morphology of this young cranium accords with the features seen in M305, which preserves the dorsal surface of the frontals from the lachrymal foramina to the occipital crest, as well as part of the parietals and the orbits. Ewer (1958, fig. 2) illustrated the right orbit and lachrymal based on M2062 and M304, showing that the lachrymal was short as in *Potamochoerus.* M2262 is a substantial piece of the braincase from the lachrymal foramina to the occipital condyles but lacking the supraoccipital area and the ventral part of the braincase. Parts of the zygomatic process of the squamosal are preserved, as well as some of the inner surface of the eye sockets. The lower part of the occiput is well preserved, with the foramen magnum, the condyles and the upper part of the paraoccipital proceses, the bullae, the ear region and the basioccipital. The basicranium is also well preserved in M588. Unfortunately the form of the zygomatic arches is unknown, although the maxillary root is seen in the best specimen with the palate (M1391) and seems to resemble the smooth outward sweep of the arch seen in *Hylochoerus* rather than the abrupt lateral projection found in *Potamochoerus.* It also suggests that the zygoma was fairly broad below the orbits. Putting all these pieces together results in the restoration shown in Fig. 1.

The cheek teeth are well preserved in the palate (M1391) and show that the full complement of premolars was present in a mature adult, although only the root impressions of UP1 and UP2 are preserved. UP2 is intact in two other specimens, M321 with UP2–M3, and M353 with UP2–4. The UP3 and UP4 occur together in six other specimens and, although somewhat like these teeth in *Potamochoerus* and *Sus,* are not very close to either but perhaps more like *Sus.* The UP3 has only three roots instead of four. The UM1 is reduced to a stump and UM2 shows the very characteristic *Metridiochoerus* pattern of a rim of enamel enclosing a tract of dentine with scattered 'lakes' of enamel. The teeth are illustrated here in Fig. 2A. In the UM3 there is a distinct gap between the first and second lateral pillars on the buccal side and the lingual pillars have flattened external walls and are rather poorly 'paired' with the buccal pillars. The trigon has only the usual two pairs of lobate lateral pillars and the talon consists of a variable number of smaller, more rounded, pillars that are not obviously paired. Bender (1992) distinguished three groupings in the talon: Group 1 has a single median cusp and 3–4 surrounding styles; Group 2 has 2 medians and 3–5 styles; Group 3 has 3 medians and 5–8 styles. The maximum crown height in the third molars is rarely greater than the anterior basal breadth, the Hypsodonty Index, 100H/B, being close to 120–130 in both uppers and lowers as the lower teeth are narrower than the uppers.

Lower dentitions or partial dentitions are represented in the collections, the best specimen being M2081, which is a mandible with the left ramus broken off behind the LM3 and broken also through the right LM2 (Fig. 2C). The symphysis is virtually intact with the bases of both canines remaining. The anterior border of the symphysis is only gently curved, unlike the projecting central part of the symphysis in the bush pig. There are sockets for six evenly spaced incisors, apparently like those of the bush pig but perhaps a little smaller. The symphysis is not as long as in the bush pig and lacks the small shelf at the back of the symphysis as well as the marked constriction behind the canines that are rather characteristic of *Potamochoerus.* The full premolar series was present. The socket for P1 lies a short way behind the canine, midway to P2. The third molars are in fairly early wear (WS 5 of Kullmer) but M1 is already worn to a featureless tract of dentine. The first lateral pillar on the lingual side of the talonid is larger than that on the buccal side which, however, is in the position to form a third pair of laterals on the crown.

Also shown in Fig. 2D are occlusal and lingual views of the dentition of the original Type of *P. shawi* (M302), which does not appear to have been illustrated since the drawing given with the type description but which unfortunately distorts and elongates the back of the LM3. The lower third molar of the original type of *Potamochoeroides hypsodon* is also illustrated here for comparison (Fig. 2E), as well as a third molar of the extant *Potamochoerus porcus* (Fig. 2F). Dale (1948) recognized the resemblances between the Makapansgat material and the Shungura species *'Pronotochoerus' jacksoni,* now regarded as *Metridiochoerus jacksoni.*

Metridiochoerus from Koobi Fora

After he had listed all the specimens from Makapansgat and described the morphological features of the more complete ones, Bender (1992) tried to evaluate the anatomical features by comparison with actual crania of *Potamochoerus* and *Phacochoerus.* He attempted to include *Metridiochoerus* in his analyses but, not having access to

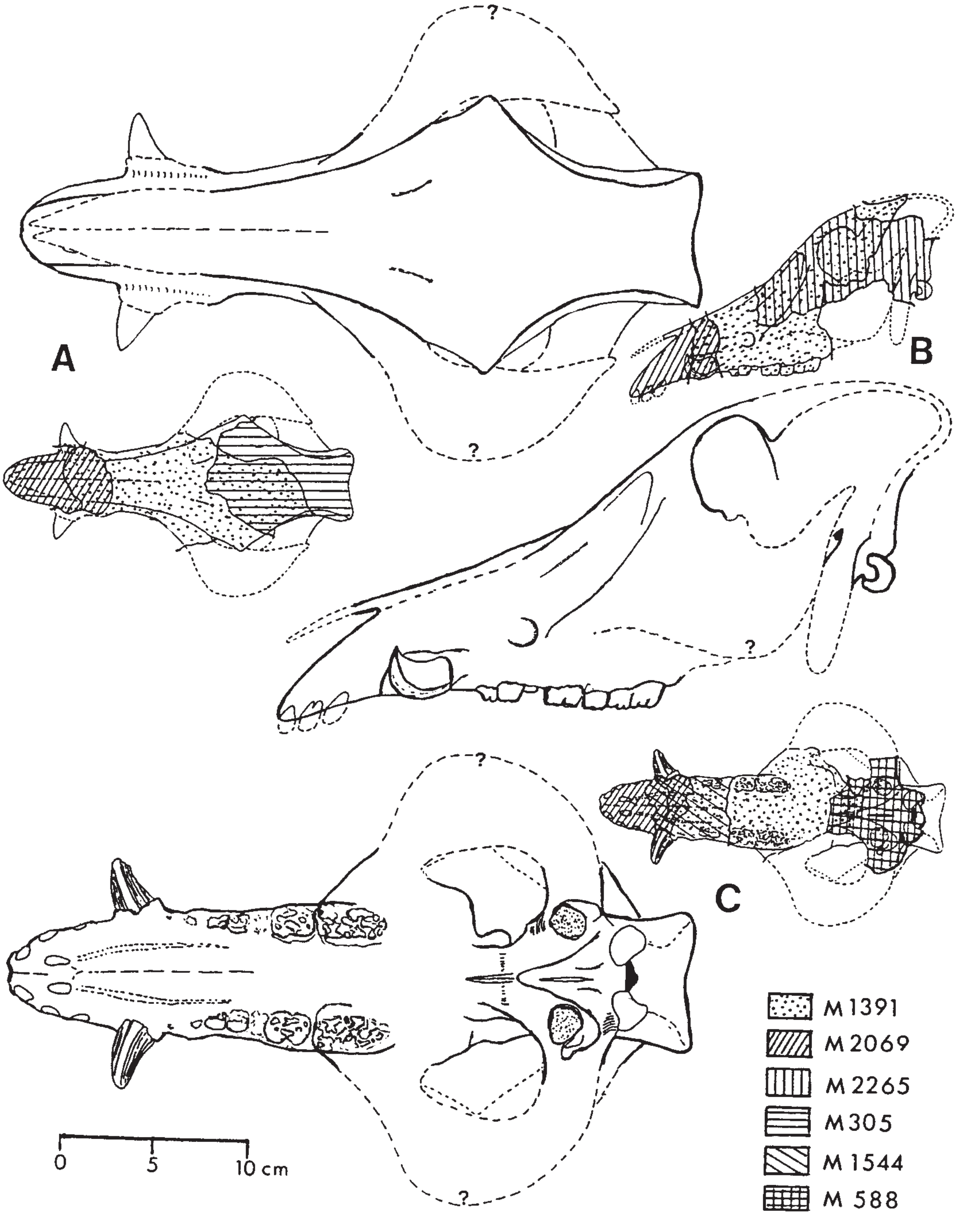

Figure 1. Reconstruction of the cranium of *'Potamochoeroides' shawi* from Makapansgat Member 3, showing the outlines of the specimens used in the synthesis. The form of the zygomatic arches is not known. Isolated canines are potamochoerine but more robust.

the East African material, his concept of *Metridiochoerus* rested largely on the published accounts and illustrations given by White & Harris (1977), Harris & White (1979) and Harris (1983). These authors considered that the two types of crania from Koobi Fora attributed to *Metridiochoerus andrewsi* represented sexual dimorphism with large zygomatic protuberances in the males but none in the females. Two rather poor specimens were reported to have come from the *Notochoerus scotti* zone (below the KBS tuff) while the others are said to be from the *Metridiochoerus andrewsi* zone, above the KBS tuff and thus to occur within a fairly limited time span. The best specimen is an almost complete cranium, KNM ER 228, with some damage to the canine flanges but with well preserved molars and providing a fine model for the 'female' morphology (Harris & White 1979, pl. 13, mislabelled as ER 223). The most complete of the 'male' crania is KNM ER 1210, which has only slight damage in the basicranial area and has lost the front of the nasals and the premaxilla. Very similar but with more damage to the occiput is KNM ER 1644, illustrated by Harris & White (1979) in Plate 14 but mislabelled as KNM ER 1210.

Figure 3 compares the dorsal aspects of hemicrania of the 'female' (A) and the 'male' (C), aligned on the infraorbital foramina. The vertex length of ER 1210 is close to 495 mm, compared with 557 in ER 228, while the corresponding figures for the basilar length are 380 mm and 464 mm, respectively. These differences in size are the exact converse of what is usual in the living suids in which the male is consistently larger than the female. This does

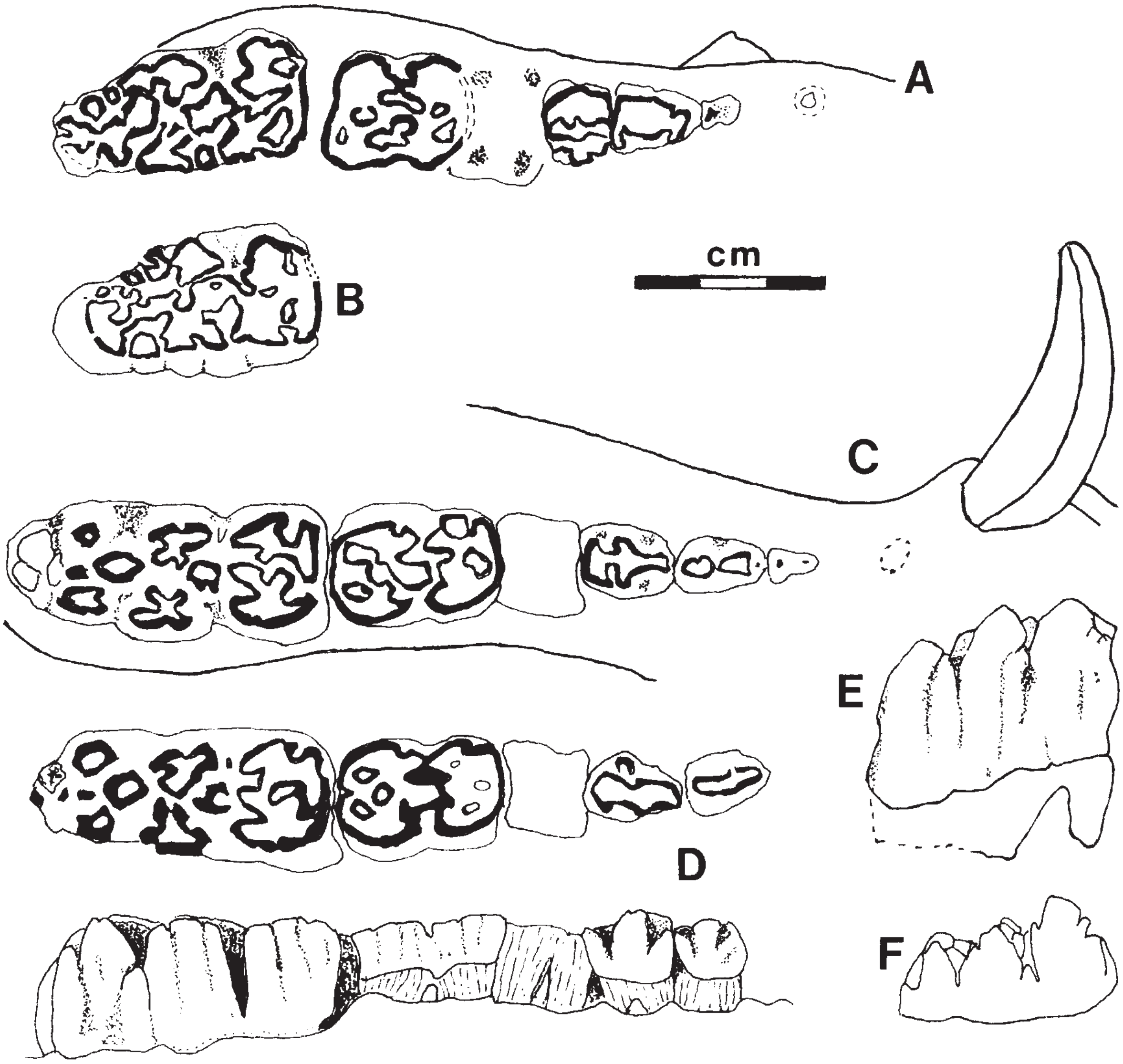

Figure 2. **A**, Occlusal view of RUP3-M3 of *'Potamochoeroides' shawi* in the palate M1391 from Makapansgat. **B**, Occlusal view of crown of RUM3, L1-459, from Member B11 in the Omo Shungura Formation and attributed to *'P.' shawi.* **C**, Occlusal view of LLP1-M3 in a mandible M2081 of *'P.' shawi* from Makapansgat. **D**, Occlusal and inner lateral (lingual) views of LLP3-M3 in incomplete mandibular ramus M302, the type specimen of the species *'shawi'* from Makapansgat. **E**, Lingual view of RUM3 in a maxillary fragment, M303, from Makapansgat, originally the Type of *Potamochoeroides hypsodon,* now absorbed into *P. shawi*. **F**, Lingual view of RUM3 of extant *Potamochoerus porcus.*

not accord with the attractive but simplistic interpretation of mere sexual dimorphism and the possibility that they may be different but related species should be considered.

In the living Suidae, sexual dimorphism is apparent in the upper canines, which are usually significantly larger and more robust in the male than in the female, although in *Hylochoerus* and *Phacochoerus* the female canines are relatively big. However, the morphology of the canines and the general form of the canine flanges are broadly similar in males and females. In the 'males' of *Metridiochoerus* from Koobi Fora the canine flanges are rather like those in the warthog, emerging fairly abruptly from the maxilla at about the same angle or are directed even a little more laterally (Fig. 3C,D). The outer part of the flange is elevated and separated from the main part of the maxilla by a fairly deep parallel groove, much as in *Hylochoerus.* The canine socket is oval with the long axis almost parallel to the palatal plane and shows that the canine was flattened with a broad shallow groove on the dorsal surface and a slightly smaller groove on the ventral surface, very much as in *Phacochoerus.* The nasals widen above the canine flanges and become narrow again above the infraorbital foramen. In the 'female' form the nasals remain narrow and parallel sided. In this form the canine flanges are unusual in that they jut outwards just in front of, or at, the infraorbital foramina. The root portion of the canine is almost parallel to the long axis of the skull and the roots extend so far back that they partly obstruct the nasal passages (Fig. 3A,B). The sockets have a trefoil shape and look rather like an ace of clubs upside down. The two dorsally situated lobes are separated by a fairly shallow groove; the anterior, or medial, groove is also shallow but the posterior groove is deeper. Canines with this morphology exist and are stout and strongly curved, with a slight spiral twist that results in the tips pointing a little upwards and inwards, much as in *Hylochoerus.* These differences in the canines are greater than might be expected with mere sexual dimorphism.

The molars in ER 228 are very similar to the teeth from Kagua, well illustrated by Leakey (1958, pl. 8). Of the

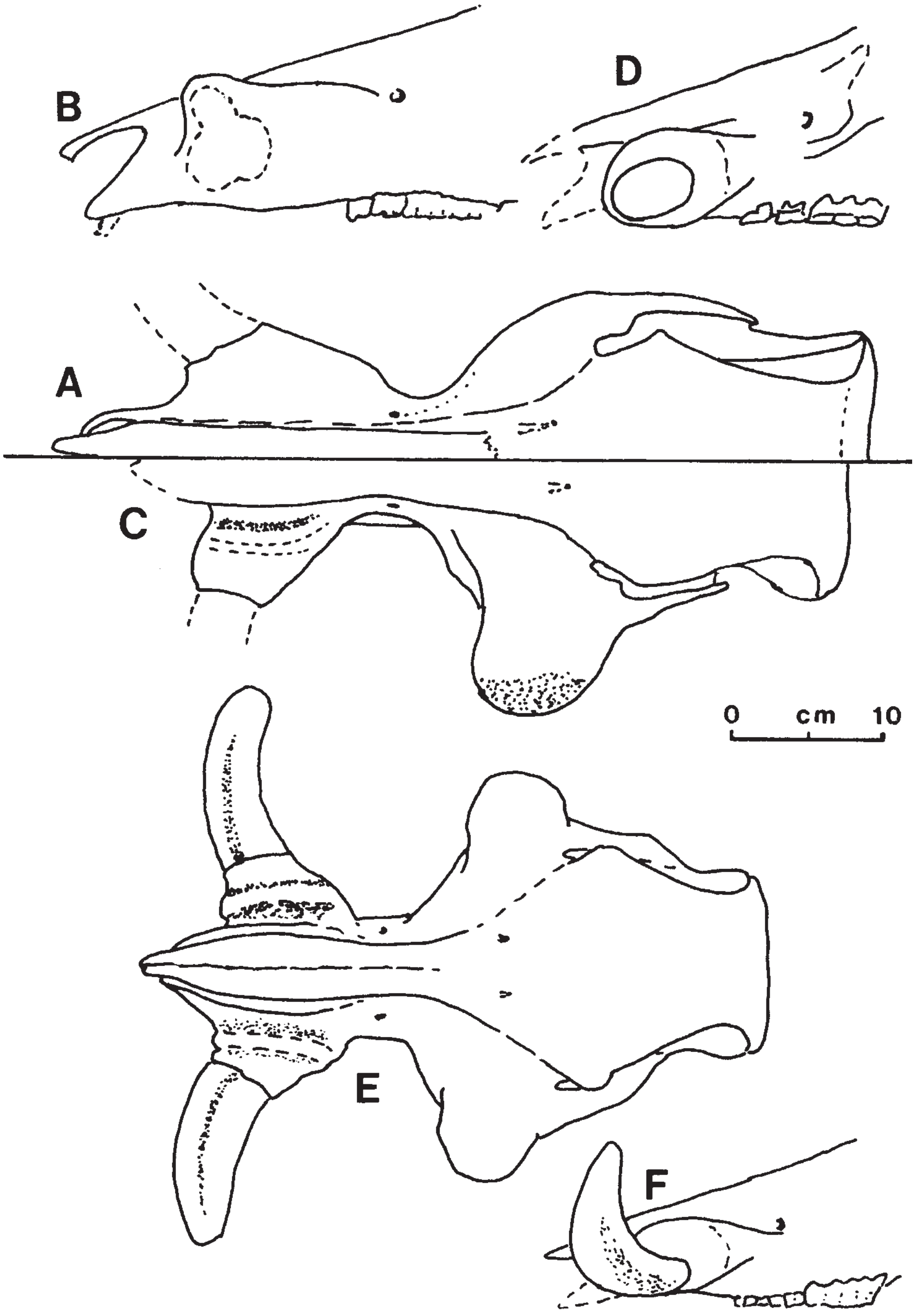

Figure 3. **A**, Dorsal view of hemicranium and **B**, lateral view of canine flange in KNM ER228 from Koobi Fora, supposedly female of *Metridiochoerus andrewsi.* **C** and **D** are similar views of KNM ER1210 from Koobi Fora, supposedly male of *M. andrewsi.* **E**, Dorsal view of cranium O6-332 from lower Member G in the Shungura Formation, attributed to *M. jacksoni.* **F**, lateral view of canine flange of O6-332.

premolars UP4 alone was apparently present in life; only the roots remain but they show that it was a fairly small tooth, later to be shed. Both ER 1210 and ER 1644 were old individuals as the third molars are worn to a border of enamel enclosing a tract of dentine with a number of elongate 'lakes' oriented diagonally across the crown. Despite the advanced age of these two animals, the stumps of moderate sized third and fourth premolars are still present, in contrast to the condition seen in ER 228. These two premolars are very similar to those in the Makapansgat suid but with greater development of the cusps on the lingual side. Even though the 'males' may have come from the lower part of the KBS unit and the 'females' from the upper part, it would be difficult to attribute these morphological difference simply to a time factor; specific separation appears more likely than sexual dimorphism.

Metridiochoerus from the Shungura Formation

In a preliminary assessment of the Suidae from the Lake Rudolf (= Turkana) Basin, Cooke (1976) recognized two species of *Metridiochoerus*, *M. jacksoni* and *M. andrewsi* and presented scatter diagrams showing the length/breadth relationships in the third molars of the samples from the Omo Shungura Formation and the East Rudolf Koobi Fora Formation, some of which came from below the KBS tuff. The age ranges sampled are respectively 3.0–1.9 Ma and 2.0–1.6 Ma. The Omo material was referred to *M. jacksoni*

Table 1. Statistics for metridiochoerine third molars from various horizons in the Koobi Fora Formation, the Shungura Formation and Makapansgat. *n* = sample size; S.D. = standard deviation; min = minimum; max = maximum; mean = mean; HI = Hypsodonty Index = 100 × height/breadth (maximum in sample). Measurements in mm.

			Upper third molars								
Formation	Unit or 'zone'	*n*	Length				Breadth				HI
			Min	Max	Mean	S.D.	Min	Max	Mean	S.D.	
Koobi Fora	*M. andrewsi*	30	50.2	82.3	65.38	6.50	21.1	30.9	25.75	2.33	257
	N. scotti	12	51.9	76.0	59.78	6.29	24.6	28.9	25.98	1.22	206
Shungura	G up	1			53.8				24.5		143
	G lr	14	44.8	54.5	50.80	2.87	22.3	29.9	25.34	2.08	152
	F	3	44.1	56.8	51.57	5.32	24.1	26.2	25.27	0.87	131
	E	4	45.8	48.0	46.67	0.94	24.5	26.5	25.58	0.95	122
	D	5	47.2	53.0	50.40	2.06	24.0	28.7	26.96	1.64	119+
	C	6	42.5	48.1	45.58	2.00	23.0	24.7	23.73	0.61	126
	B11	1			39.5				22.8		68+
Makapansgat		24	40.0	50.5	45.28	3.01	21.0	26.8	23.75	1.56	121

			Lower third molars								
Formation	Unit or 'zone'	*n*	Length				Breadth				HI
			Min	Max	Mean	S.D.	Min	Max	Mean	S.D.	
Koobi Fora	*M. andrewsi*	32	56.5	84.3	66.32	10.92	18.2	24.8	20.13	3.94	328
	N. scotti	5	53.0	64.5	58.78	4.44	19.0	25.0	22.86	2.43	184
Shungura	G up	3	51.5	64.0	60.60	3.26	18.8	22.0	20.20	1.64	191+
	G lr	18	46.0	64.4	56.99	5.00	18.0	24.9	20.99	2.17	209
	F	4	50.6	62.2	56.33	5.24	17.8	23.2	20.95	2.61	172
	E	6	49.0	58.0	53.73	2.89	20.5	23.5	22.43	1.21	181+
	D	2	45.0	59.0	52.00	7.00	19.2	22.5	20.85	1.65	173
	C	5	44.3	57.9	49.92	6.36	18.3	22.5	19.46	1.53	166
Makapansgat		24	39.2	54.8	46.92	3.99	19.3	23.4	20.66	1.11	130

(formerly *Pronotochoerus jacksoni*) and the bulk of the Koobi Fora material to *M. andrewsi.* Morphologically, the molars of *M. jacksoni* and *M. andrewsi* differ in the relative development of the talon, which is shorter than the trigon in *M. jacksoni* and longer in *M. andrewsi* with additional laterals. The lateral pillars are distinctly separated almost to the base of the crown in *M. jacksoni* but in *M. andrewsi* are in closer mutual contact for much of their height and become confluent near the base of the crown. The height of the crown is equal to or less that the basal length in upper third molars of *M. jacksoni* but greater in *M. andrewsi.* A better measure is the Hypsodonty Index, 100H/B, which is below 150 in *M. jacksoni* upper molars, or 200 in the lowers, while in *M. andrewsi* the corresponding figures are 200 in the uppers and more than 300 in the lowers. The premolars are reduced but *M. jacksoni* retains a functional UP3 in the adult, which is lacking or shed early in *M. andrewsi.*

Unfortunately the only upper third molar shown as coming from Member B in Cooke's 1976 scatter diagrams was L1-113. Harris & White (1979) concluded that the specimen had been mislabelled and astutely recognized it as the antemere of a specimen from Member G. (Although mislabelling is fortunately rare, an upper third molar, O158 was illustrated by Harris & White (1979) in their figs 82 & 83 as from Member B but this locality is recorded by De Heinzelin (1983) as Member C8 or lower C9.) The only upper third molar certainly from Member B11 is L1-459, illustrated by Harris & White (1979) in their fig. 84; it is redrawn here as Fig. 2B for comparison with the corresponding molar in the Makapansgat palate M1391, which is strikingly similar. There is some overlap in the size ranges of the third molars from the Shungura and Koobi Fora formations, as was indicated in Cooke (1993, fig. 3). It is suspected that some of the specimens from the lower part of the Koobi Fora Formation (*'Notochoerus scotti'* zone) may belong to *Metridiochoerus jacksoni.* Table 1 sets out the statistical data separately for the material assigned by Harris (1983) to the *'N. scotti'* and *'M. andrews*i' zones, respectively, as well as for the different Members of the Shungura Formation and for Makapansgat. These data are presented graphically in Fig. 4

Cranial material is rare in the Shungura Formation but there are two good crania in Member G. From the base of this unit is O6-332 and from the top of G is O29-2098, belonging to an individual not yet quite mature. O6-332 is almost complete except for slight dorsoventral compression. It is morphologically very similar to ER 1210, although a little shorter (basilar length 360 mm compared with 380 mm) and has a relatively narrower occipital crest (124 mm compared with 163 mm). The parietal area is wide and flat, or even slightly concave, and the rims of the orbits are swollen and elevated just above the parietal surface, The zygomatic arches are expanded and carry thimble-shaped protuberances, the overall bizygomatic breadth being 279 mm as compared with 324 mm in ER 1210, so that the proportions are essentially similar in the smaller cranium, as is seen in Fig. 3E,F. The canine flanges resemble those of *Hylochoerus* and the canines are

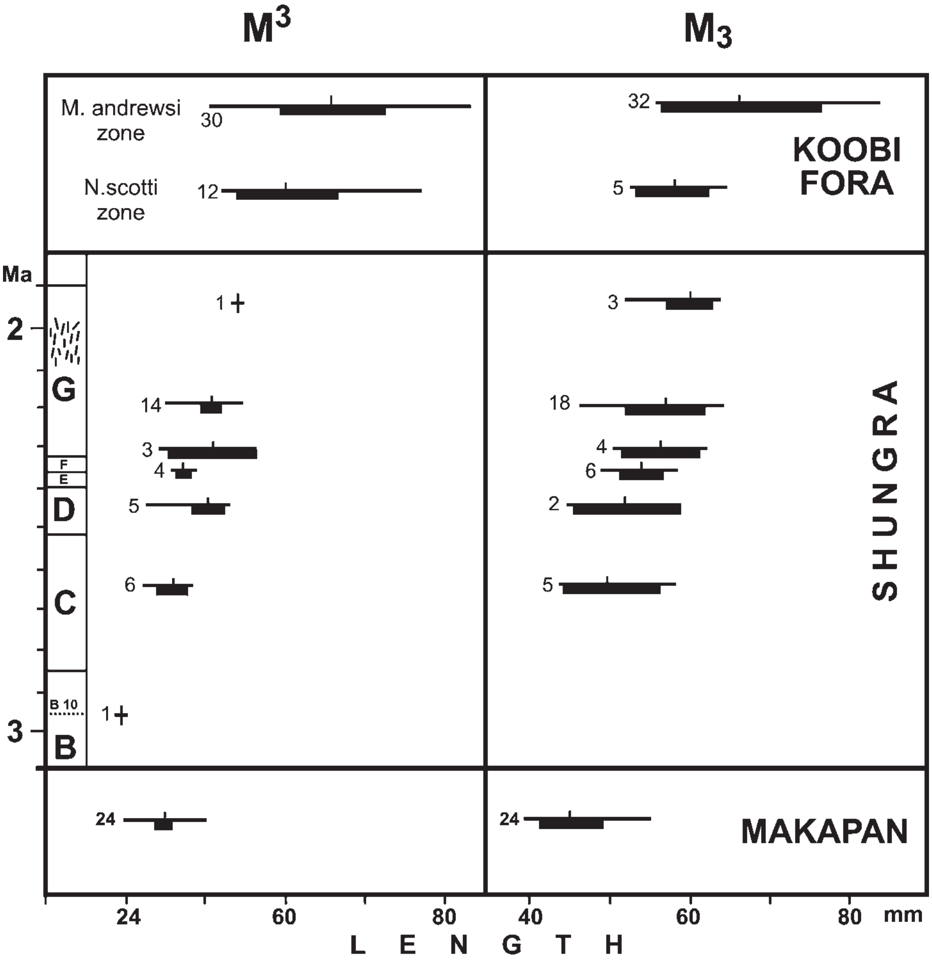

Figure 4. Statistics for third molars referred to *Metridiochoerus jacksoni* from various horizons in the Shungura Formation and comparative figures for metridiochoerine third molars from the Koobi Fora Formation and for Makapansgat Member 3. The figure is sample size, the bar shows range with the heavy bar one standard deviation either side of the mean.

preserved on both sides, very like the tusks of *Phacochoerus* but stubbier and having ribbed enamel on the ventral surface. The palate is damaged but the right UM2 and UM3 are well preserved while on the left side there is a good UM3, a stump of UM1 and intact UP3 and UP4. The teeth are illustrated in Fig. 5A,B, in which the left premolars (C) have been reversed in the occlusal view and transposed to their appropriate positions on the right side to illustrate the appearance of the whole series. The dimensions of the RUM3 are: basal length, 52.8 mm, basal breadth 27.0 mm, and maximum height 31.0+ mm, giving a Hypsodonty Index of 115+. These measurements fit well with the range of other molars from the Shungura Formation attributed to *Metridiochoerus jacksoni* and lie near the bottom of the range for the Koobi Fora sample (see Cooke 1993). Accordingly, this cranium may be taken as representative of *M. jacksoni.* The type specimen of this species is a left lower third molar, M 17083, in the collections of the Natural History Museum, London, and is illustrated here in Fig. 5 in occlusal (G), lingual (H) and buccal (I) aspects.

There are several good mandibles in the Shungura collections that show the retention of both LP3 and LP4, although only LP4 is present in one of the mandibles from the higher levels (Omo 1967 'Type Area Upper'). A good dentition from Member C, O3-126, is illustrated in Fig. 5D and is very similar to the Type specimen in structure but a little less worn. The LP4's are a little smaller and less rectangular than in the bush pig. They have a posterior cingulum and a stout main cone with ridges on either side that produce a cruciform island with wear , sometimes resembling a bird in flight (Fig. 5E,F). The two persistent foveae behind the 'wings' become lakes in more advanced wear. A similar structure is found in the LP4 of the Makapansgat suid (Fig. 2C) and is sufficiently unusual to be of diagnostic value.

Mandibles

The morphology of the mandibles from several different horizons is outlined in Fig. 6 as a series of comparative drawings. *Potamochoerus porcus* is on the left. Next is the Makapan mandible M2081 (with some restoration from M301), which exhibits a wider and shorter symphysis than in *P. porcus* and is not as constricted behind the canines; it also lacks the small shelf at the back of the symphysis which is very characteristic of the bush pig. The Omo mandible O3-126 is shaped rather like the Makapansgat jaw but has a slightly longer diastema behind the canines and also lacks the two anterior premolars. Compared with O3-126 from Member C, the fine jaw that was collected in 1967 from the 'Type Area Upper' (probably Member G but possibly even from Member H) shows greater elongation of the front of the jaw, made more obvious by the fact that the back of the symphysis lies well in front of the anterior

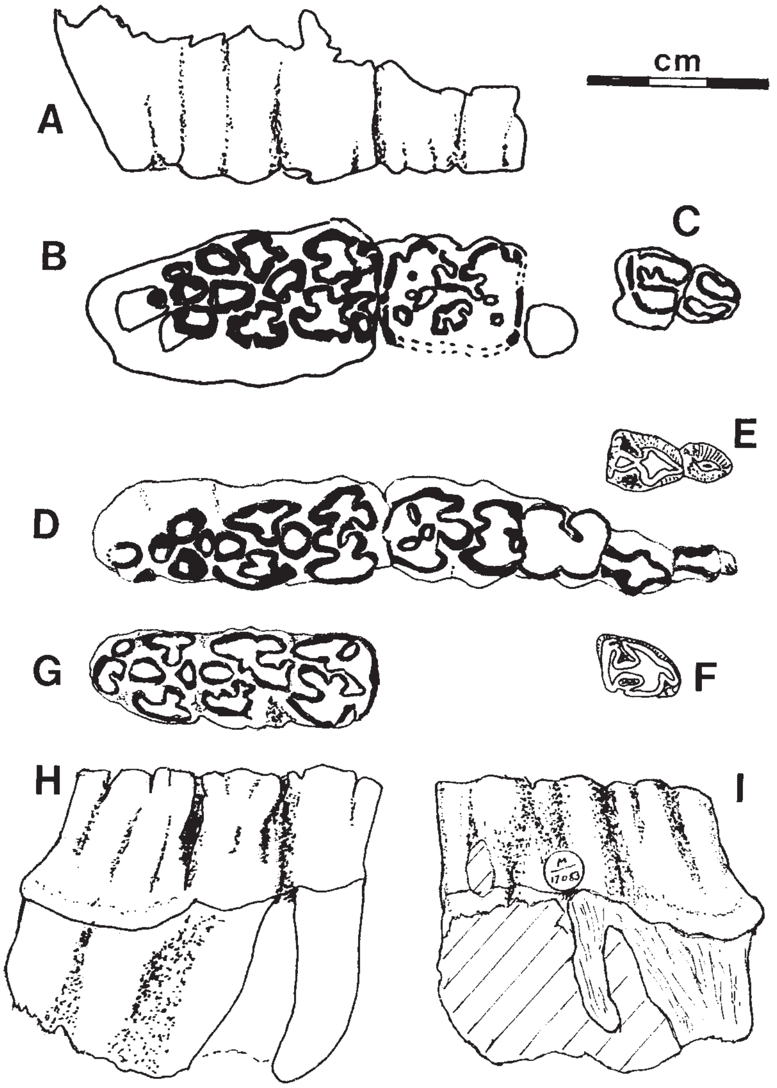

Figure 5. **A**, Outer lateral sketch of UM2-3 in cranium attributed to *Metridiochoerus jacksoni.* O6-332 from lower Member G in the Omo Shungura Formation. **B**, Occlusal view of RUM2-3 shown in A. **C** shows the LUP3-4, drawn reversed and transposed to complete the appearance of the whole series of cheek teeth. **D**, Occlusal view of LLP3-M3 in mandible O3-126 from Member C2 in the Shungura Formation, attributed to *M. jacksoni.* **E**, **F**, Other specimens of LP3 and LP4 from the Shungura Formation to illustrate wear patterns in *M. jacksoni.* **G**, **H**, **I**, Occlusal, lingual and buccal views of LLM3 of the Type of *Pronotochoerus jacksoni* from an uncertain horizon in the Shungura Formation, Natural History Museum, London, M17083.

premolar. The diastema between the canine and the LP4 is substantially increased. Figure 6 also includes one of the most complete mandibles from Koobi Fora, KNM ER222, although the teeth are damaged. The symphysis is long and spatulate. The canine is stout and only gently curved and does not curve back into the body of the ramus but is implanted in the corner of the symphysis and flares upward and outward (Cooke & Maglio 1972, fig. 4). Other mandibles from higher in the Koobi Fora sequence tend to be still more massive. By comparison with Omo 1967, the greater length of the LM3 from Koobi Fora is apparent, with three good pairs of laterals and an incipient fourth pair. In summary, the Makapansgat mandible is morphologically more like the Omo mandible from the lower part of the Shungura Formation than it is like either the mandible of *P. porcus* or that of the Koobi Fora *Metridiochoerus.*

DISCUSSION

In view of the fact that *Potamochoerus* has a very poor fossil record even in the later Pleistocene, it may have been naive to assume that a three million year old ancestor was sufficiently like the extant bush pig for comparison to be meaningful. Specimens from Pliocene deposits that were originally referred to *P. porcus* have subsequently come to be regarded as belonging to *Kolpochoerus afarensis* which, however, may itself be ancestral to *Potamochoerus* (see White 1995, p. 181). In view of the similarity of *K. afarensis* to the bush pig, it may still be reasonable, with caution, to use the living form as a proxy for the ancestor.

The molars of *K. afarensis* are smaller than those of the living bush pig and have thicker enamel and less folding. There are also resemblances in the molars of *K. afarensis* to those of *Metridiochoerus jacksoni* in which the pillars are less bunodont but not yet fully columnar. The Makapansgat material appears to represent one of the members of this early differentiation and mis-assignment of particular specimens within the overall complex is possible. The cranial fragments of the Makapan suid conform to the morphology of a fairly basic suid and *Potamochoerus porcus* provided a somewhat better comparison than *Sus,* which

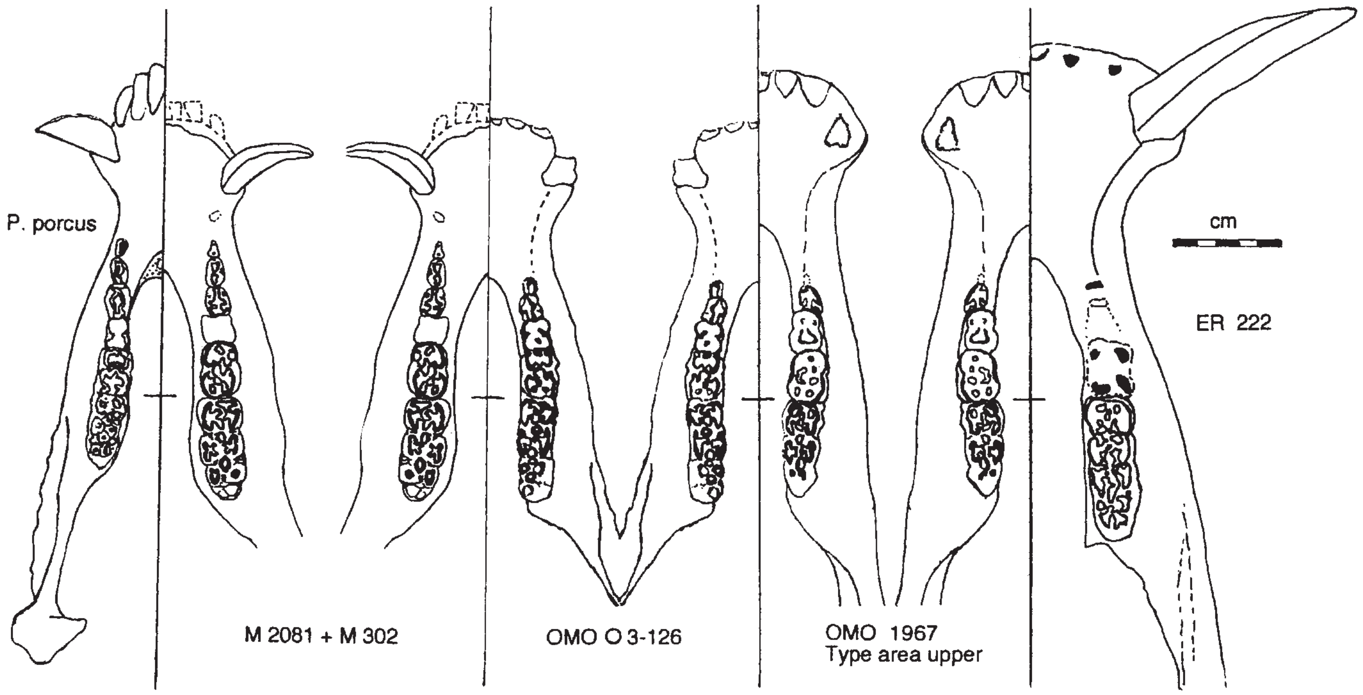

Figure 6. Comparative occlusal views of mandibles, aligned on the M2/M3 boundary. The species represented are, from left to right: extant *Potamochoerus porcus*; Makapansgat *'P.' shawi,* M2081/M302; *Metridiochoerus jacksoni* O3-126 from Member C2 of the Shungura Formation; *M. jacksoni* Omo 1967 from Member G or H of the Shungura Formation; and *M. andrewsi* KNM ER222 from the *M. andrewsi* zone of the Koobi Fora Formation.

led to the designation *Potamochoeroides.* However, the new reconstruction of the Makapansgat cranium provides a slightly different picture.

Figure 7 shows in bold outline the reconstructed cranium of the Makapansgat *Potamochoeroides shawi* compared with (A) *Potamochoerus porcus* and (B) with the Omo cranium O6-332 attributed to *Metridiochoerus jacksoni.* The crania have been aligned on the front of the third molar. Relative to the bush pig, the Makapansgat cranium shows distinct elevation of the occipital condyles and some elevation of the parietal area and orbits as well as backward extension of the braincase and occiput. These features are more developed in the Omo cranium and are characteristic of *Metridiochoerus,* becoming more exaggerated in the Koobi Fora 'female' material and reaching an extreme in *M. compactus.* Thus by comparison with a bush pig, the Makapansgat cranium already shows evidence of the characteristic features of *Metridiochoerus* that are not seen in *Potamochoerus porcus.*

What may be regarded as an important defining characteristic of the cheek teeth of *Metridiochoerus* is the precocious wear on the first and second molars so that by the time the back of the third molar comes into wear, the first molar is reduced to a tract of dentine or is already a mere stump. At this stage the second molars are largely dentine with scattered 'lakes' of enamel. more marked in the upper than in the lower molars. This trend is already apparent in the Makapansgat suid whose cheek teeth are very similar to those attributed to *M. jacksoni* (see Figs 2 & 4). The Omo third molars are a little higher crowned with a Hypsodonty Index of up to 150 in the uppers and up to 200 in the lower third molars as compared with close to 120–130 for both uppers and lowers in the Makapansgat sample. The Makapansgat suid had a complete premolar dentition, although the first premolars may be shed early. *M. jacksoni* retains a functional UP3 in the adult although in some of the later lower dentitions only LP4 is retained. The morphology of both upper and lower P4s is very similar in both the Makapansgat suid and in *M. jacksoni.*

As may be seen in Fig. 4, *M. jacksoni* is a fairly stable species through Shungura Members C to G, showing only a slight increase in the length, most apparent in the lower molars. The solitary upper third molar from Member B (L1-459) is shorter than the later specimens and the enamel pattern is strikingly similar to the corresponding tooth in the Makapansgat palate, M1391 (Fig. 2) and could conveniently be designated *Metridiochoerus* cf. *shawi.* The age of this specimen is close to 2.95 Ma, which would accord with other estimates of the age of Makapansgat Member 3. Although a single specimen would provide a dubious basis for correlation, it may offer a reasonable indication of the age. The only other suid from Member 3 is a *Notochoerus,* represented by a pair of robust lower third molars originally referred by Ewer (1958) to *N. euilus.* In 1993 Cooke referred these mandibles, together with a more recently discovered incomplete lower third molar, to *Notochoerus scotti.* It was pointed out that *N. scotti* was represented by robust specimens in he lowest levels, tending to become narrower and higher crowned in the younger levels and that the Makapansgat specimens accorded best with the samples from Members B and C. Although the evidence is far from conclusive, the two suid species both suggest an age about equivalent to that of Shungura Members B and C.

In the light of this re-analysis of the data, it seems desirable to abandon the genus *Potamochoeroides* and to designate the Makapansgat suid *Metridiochoerus shawi* as an early stage in the evolution of the *Metridiochoerus* complex but

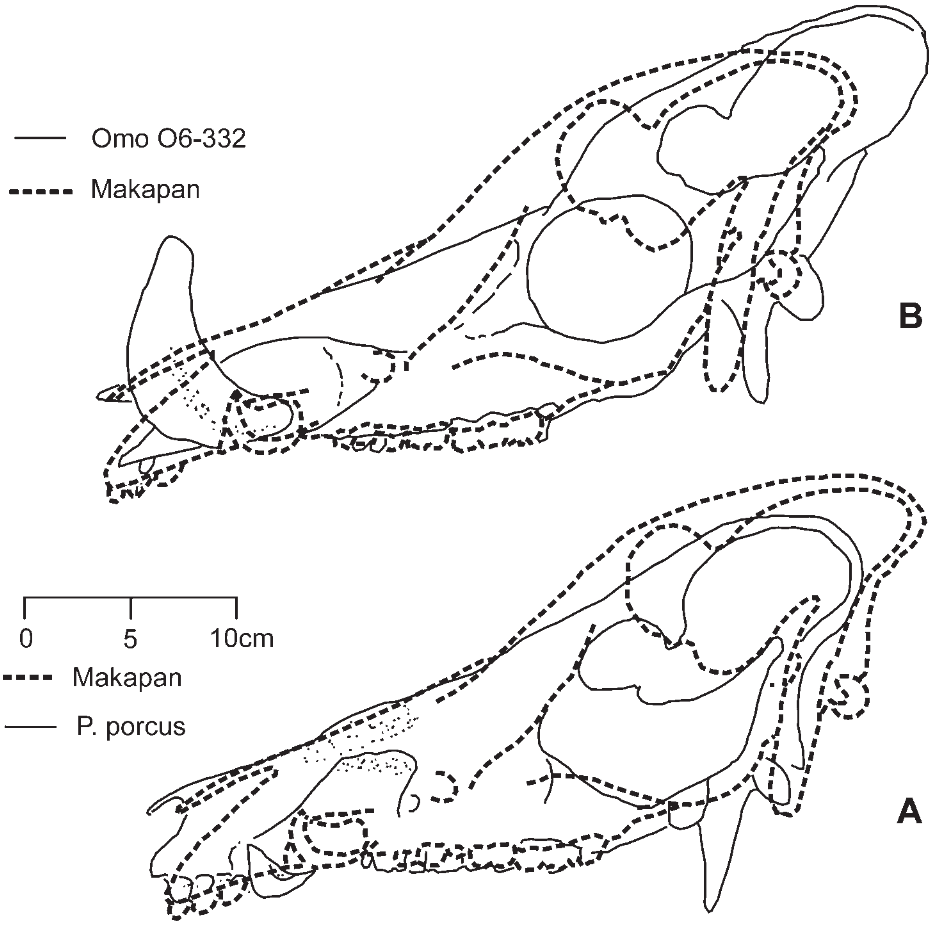

Figure 7. Comparative lateral views of the reconstructed cranium of the Makapansgat suid *'P.' shawi* in bold outline and, in light lines. **A**, Adult male of *Potamochoerus porcus* and **B**, undescribed male cranium, O6-332, attributed to *Metridiochoerus jacksoni* from the Omo Shungura Formation Member G1.

distinguished from *M. jacksoni* by the retention of the anterior premolars, the hypsodonty of the molars, and the different canines.

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Fossil hyraxes (Hyracoidea: Mammalia) from the Late Miocene and Plio-Pleistocene of Africa, and the phylogeny of the Procaviidae

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A palate with much of the dentition from Aragai, Lukeino Formation (6 Ma) Kenya, is the most complete known specimen of a Late Miocene procaviid hyracoid. It shares several features with *Dendrohyrax.* The specimen is as large as the western tree hyrax, *Dendrohyrax dorsalis,* but it is attributed to a new species. *D. dorsalis* ranges through the tropical forests of Central and Western Africa, from Uganda to Gambia. As such the presence of a similar species at Lukeino provides evidence of the humid forest nature of the palaeoenvironment in the Tugen Hills during the Late Miocene. The fossil hyracoid specimens from the Early Pliocene of Langebaanweg, South Africa, are close in morphology to, but somewhat larger than, the extant bush hyrax, *Heterohyrax brucei,* but have some derived characters found in *Procavia capensis.* The cheek teeth are brachyodont, the lower premolar row is complete with a well-developed p/1 and there is a long diastema between the second incisor and the first premolar, all features recalling *Heterohyrax.* However, the depth of the mandible, the hypsodonty of the lower incisor, and the length of the premolar row relative to the length of the molar row are similar to the condition in *Procavia* and attest to the onset of molar enlargement relative to the rest of the dentition. In the overall context of the Procaviidae, *Procavia* is the most derived genus, and the presence of a few *Procavia*-like features in the Langebaanweg fossils indicate that the species concerned was probably already evident on the *Procavia* lineage, but the presence of several plesiomorphic characters reveals that it is a primitive member of the lineage. These also reveal that the specimens do not belong to *Procavia* cf. *antiqua* into which they were previously tentatively classified by Hendey (1976) as they are somewhat more derived. The detailed systematic status of the large extinct hyracoid *Gigantohyrax maguirei,* Kitching, 1965, from Pliocene cave fillings at Makapansgat, South Africa, has not previously been satisfactorily demonstrated, even though it is clear that most authors have considered it to be a procaviid closely related to *Procavia.* Kitching (1965) compared it only to species of *Procavia.* Re-study of the original sample, as well as additional fossils (three partial skulls, isolated upper premolar, fragment of mandible with a premolar) reveal that *Gigantohyrax* shares many features with the genus *Dendrohyrax,* fewer with *Heterohyrax* and even fewer with *Procavia.* It is concluded that among the Procaviidae, *Gigantohyrax* is most closely related to *Dendrohyrax.* The new discoveries of Late Miocene and Pliocene procaviids in Kenya and South Africa, when added to recently described associated upper and lower dental elements of *Meroehyrax bateae* from the base of the Middle Miocene of Uganda, permit a reappraisal of procaviid phylogeny. It is concluded that procaviids probably descended from Saghatheriidae, and that Pliohyracidae did not give rise to procaviids as previously thought by some authors.

Keywords: Procaviidae phylogeny, Lukeino Formation, Makapansgat, Langebaanweg.

INTRODUCTION

Fossil Procaviidae are known from many Plio-Pleistocene localities in East and South Africa (Churcher 1956; Jaeger & Wesselman 1976; Kitching 1965; McMahon & Thackeray 1994; Schwartz 1996, 1997; Schwartz *et al.* 1995; Zeally 1916) but Miocene occurrences are rare, for the moment the only published ones being from Namibia (Rasmussen *et al.* 1996) and Kenya (Fischer 1986). In both the latter occurrences, the procaviids were identified as *Heterohyrax.*

Procaviids have recently been collected at two additional Late Miocene sites in Kenya, Lukeino in the Tugen Hills, and Lemudong'o, near Narok (Hlusko *et al.* 2002). The Lukeino dassies, represented by a palate and some isolated teeth, belong to *Dendrohyrax,* the earliest record of this genus. The Lemudong'o specimens are more fragmentary than the Lukeino material, but they too belong to *Dendrohyrax* (Pickford & Hlusko, in press).

Hyracoids from Langebaanweg were originally attributed to *Procavia* cf. *antiqua* (Hendey 1976, 1981) but no detailed descriptions of the specimens have been published. Examination of the collection, stored in the South African Museum, reveals that they belong to a species that is larger than *P. capensis* (and its probable synonyms *P. antiqua* and *P. robertsi*), but smaller than *P. transvaalensis.* In many features, such as the brachyodonty of the cheek teeth and the presence of p/1 (or lower canine, if Luckett 1990 is correct), the Langebaanweg dassies are close to *Heterohyrax,* but since brachyodonty is probably the primitive condition for procaviids, the decision to classify the remains in *Procavia* is based on the derived morphology of the mandible and dentition which is *Procavia*-like, rather than *Heterohyrax,* even though the quantity of features is not very great. It is possible that *Procavia* diverged from the other extant procaviid genera sometime during the Late Miocene.

The detailed affinities of the giant Late Pliocene procaviid *Gigantohyrax maguirei* from Makapansgat, South Africa, have never been elucidated. Kitching (1965) compared it only to fossil and extant species of *Procavia,* and pointed out a number of ways that the fossils differ morphologically from them. The combination of large size and the morphological differences from *Procavia* provided the basis for erecting the genus *Gigantohyrax.* However, almost all the characters that were used to distinguish *Gigantohyrax* from *Procavia,* occur in the genus *Dendrohyrax.* The only features noted by Kitching that, if true, would continue to distinguish the two genera are the 'massive hypsodont teeth', and the presence of a sagittal crest, neither of which occur in *Dendrohyrax.* A curved maxillo-palatine suture was also listed as a character that distinguished *Gigantohyrax* from *Procavia.*

The aim of this paper is to describe new procaviid fossils and then to review the systematic affinities of the Late Miocene to Pleistocene dassies from East and South Africa. The subject will be tackled in five parts – a general overview of the problems of distinguishing the three extant procaviid genera from each other, as there is a dearth of recent information in the literature, followed by three sections on the fossil hyracoids treated by locality in geochronological order, followed by a section of discussion and conclusions in which the phylogeny of the Procaviidae will be evoked.

MATERIALS AND METHODS

Three hundred and forty seven extant, fully adult procaviid skulls and mandibles were measured with vernier callipers (63 *Dendrohyrax,* 86 *Heterohyrax* and 198 *Procavia*) housed in the Natural History Museum, London, the Transvaal Museum, Pretoria, the Iziko South African Museum, Cape Town, the Bernard Price Institute (Johannesburg) and the Muséum National d'Histoire Naturelle, Paris. Measurements taken included lengths of premolar row, molar row, diastemata, gap between upper incisors, depth of mandible beneath the rear of the first lower molar and temporal crest separation. Dental measurements (length × breadth) of fewer specimens were undertaken. The only measurements that need explanation are mandibular depth and upper molar row length. Because procaviid mandibles increase in depth posteriorly, the callipers were placed with one of its jaws parallel to the base of the mandible, the other jaw being positioned at gingival level between m/1 and m/2. Upper molar row length was measured from the antero-buccal projection of the parastyle of M1/ to the rear of M3/.

Fossils measured included material in the Community Museums of Kenya (*Dendrohyrax samueli*), the Transvaal Museum (*Procavia antiqua, Procavia transvaalensis*), the Bernard Price Institute (*Gigantohyrax*) and the Iziko South African Museum (*Procavia pliocenica* sp. nov.).

Measurements were analysed using Excel to produce bivariate plots (Figs 1–8) the ones retained for this paper being those that showed clear patterns of differences between the three extant genera. Available fossils, except for *Gigantohyrax,* were plotted on these diagrams.

PART I. DIVERSITY OF EXTANT PROCAVIIDAE

The question of generic diversity in extant Procaviidae has been addressed on numerous occasions over the past century and a half (Allaerts *et al.* 1982; Bothma 1967; Brauer 1913; Ellerman & Morrison-Scott 1951; Hahn 1934; Lataste 1886, 1892; Thomas 1892). All authors are agreed that there are at least two genera (*Procavia* and *Dendrohyrax*) and many authors agree that there are three (*Heterohyrax*). Others, however, consider that *Heterohyrax* should be treated as a subgenus of *Dendrohyrax* (Ellerman & Morrison-Scott 1951; Roche 1972, 1978) while yet others have noted morphological and behavioural affinities between *Heterohyrax* and *Procavia* (Hoeck 1978), some even raising the possibility of occasional hybridization between these two genera (Kingdon 1974). The current consensus is that there are three genera, with behaviour [daily life rhythm (nocturnal versus diurnal activity), vocalization], soft anatomy (perineal anatomy, mammary formula) and craniodental, and to a lesser extent skeletal, anatomy (Fischer 1986; Rasmussen *et al.* 1996) serving to distinguish them. Morphometric analysis of several hundred extant procaviids from many parts of Africa and Arabia reveal the presence of three clear groups (*Dendrohyrax, Heterohyrax* and *Procavia*) with a fourth group from Liberia and Nigeria that blends characters and proportions of *Dendrohyrax* and *Procavia.* This group is probably to be referred to *Dendrohyrax,* but the possibility of a fourth genus of extant procaviid requires examination.

For a palaeontologist, only the skeletal source of evidence can be used, but the distinctiveness in cranio-dental morphology between the three genera is not always as clearcut as one would wish. This is because, for many morphological and metric features, *Heterohyrax* is intermediate between *Dendrohyrax* and *Procavia.* An added difficulty is that there is a great deal of geographic variation within each of the genera such that some East African species traditionally attributed to *Procavia* (*ruficeps, johnstoni*) are closer in some dental and cranial features to *Heterohyrax* than they are to the South African species *Procavia capensis.* Churcher (1956), for instance, reported that the p/1 was almost always absent in extant *P. capensis,* and concluded that its presence in the fossil species *P. transvaalensis* and *P. antiqua* was an indication of the primitive status of these two Plio-Pleistocene species. However, in extant East African species of *Procavia,* p/1 is almost always present, and furthermore, the molars are often less hypsodont than those of South African *P. capensis,* and in isolation can easily be confused with those of *Heterohyrax* and even *Dendrohyrax.*

The following features (Table 1) have often been used by neontologists and palaeontologists to distinguish between the skulls and mandibles of the three genera of Procaviidae (Allaerts *et al.* 1982; Bothma 1967; Churcher 1956; Hahn 1934; Skinner & Smithers 1990).

South African specimens of *Procavia capensis* show a wide range of variation in molar hypsodonty, temporal crest anatomy and other craniodental features. This variability is not due to sexual dimorphism, as both males and females are variable in the same way, and it is not solely due to ontogeny, since young adults and aged individuals are also quite variable in these features.

Some distinctions between the mandibles of *Heterohyrax* and *Dendrohyrax*

The mandibles of *Heterohyrax* and *Dendrohyrax* are superficially similar to each other, not only in their dental features but also in most of the mandibular morphology. However, there are a few consistent differences between the mandibles of the two genera. In general, the jaws of *Heterohyrax* are shallower than those of *Dendrohyrax.* This appears to be related to the development of stronger temporalis musculature in the tree hyrax, which often possess well-developed temporal ridges on the dorsal

Table 1. Features often used to distinguish the three extant genera of Procaviidae.

Feature	*Procavia*	*Heterohyrax*	*Dendrohyrax*	Comments
Basal length: jugal breadth	169.7: 100	174.0: 100	180.8: 100	Rarely available in fossil samples, and somewhat variable
Sagittal crest	Often present in adults	Not present	Not present	Varies with age, but overall is a useful criterion, but many *Procavia* do not have one
Frontal bone morphology	Raised close to midline	Raised close to midline	Hollowed near midline	Rarely available in fossils, and in any case somewhat variable in *Procavia*
Infra-orbital foramen position	Above posterior root of P3/	Above contact between P2/ and P3/	Above posterior root of P2/	Somewhat subjective due to difficulties in orienting specimens
Post-orbital bar	Open	Open but some individuals closed	Closed	Not often preserved in fossils, but generally reliable for *Dendrohyrax*
Temporal ridges	Unbeaded	Unbeaded	Beaded	Sometimes incipiently beaded in *Heterohyrax* and even occasionally in *Procavia*
Dorsal profile of skull	Convex	Convex to straight	Concave	Not often preserved in fossils
Premaxillary palatal fossa	Small, shallow	Small, shallow	Large, deep	Not often preserved in fossils
Fossa beneath upper incisive jugum	Small, shallow	Small, shallow	Large, deep	Not often preserved in fossils
Tooth row convergence	Convergent anteriorly	More or less parallel	Convergent posteriorly	Somewhat variable in all genera
Ventral surface of symphysis	Usually smooth	Usually smooth	Often rugose with a basal promontary separated from the rest of the symphysis by grooves	Useful for identifying *Dendrohyrax*
p/1	Usually absent	Present	Present	Tropical species of *Procavia* usually possess this tooth, as do several fossil species
Wear on lower incisors	Tines obliterated rapidly	Tines lost in old age	Tines seldom lost	Not reliable in very worn teeth
Lower incisor hypsodonty	High	Low	Low	Deciduous incisors of *Procavia* are low crowned
Gap between lower central incisor apices	None or narrow (0–1.6 mm)	Narrow to wide (1.3–2.5 mm)	Narrow to wide	Not often preserved in fossils
Upper diastema length	Short	Medium	Long	Some overlap between *Heterohyrax* and *Dendrohyrax*
Upper incisor dimorphism	Strong	Weak	Weak	More difficult to assess in *Heterohyrax* and *Dendrohyrax* than in *Procavia*
Upper molar ectoloph morphology	Almost flat	Undulating	Strongly undulating	Somewhat subjective due to variation caused by wear
Upper molar cingula	Weak	Moderate to weak	Moderate to strong	Not very reliable
Interparietal fusion	None	Yes	Yes	Ontogenetically variable
Gap between upper incisors	Less than width of incisor	Greater than width of incisor	Greater than width of incisor	*Heterohyrax* and *Dendrohyrax* are similar
Molar hypsodonty	Moderate to high	Moderate to low	Low	*Procavia* quite variable, with some individuals overlapping *Heterohyrax*
Upper molar row: premolar row	Premolar row shorter than molar row	Premolar row subequal to molar row	Premolar row longer than molar row	Overlap between *Heterohyrax* and *Dendrohyrax*
Lower molar row: premolar row	Premolar row shorter than molar row	Premolar row subequal to molar row	Premolar row longer than molar row	Generally reliable taking into account loss of p/1
Stylar prominence in upper molars	Weak	Medium	Strong	Variable but reasonably reliable
Dental metrics	Medium to small	Medium to small	Large to medium	Much overlap between the three genera

surface of the skull. Measurements of the mandibular depth below the rear of the first molar plotted against the length of the lower molar row generally differentiates the two genera, at least the adult specimens (Fig. 1). Other measures proposed in the literature concern the length of the premolar row relative to the molar row (Skinner & Smithers 1990) (Figs 2 & 5). There are however, overlaps in the range of variation, so that a few individuals are difficult to classify. Indeed, some specimens appear to be intermediate in morphology between the two genera, blending features of both. Under the circumstances, the identification of some of the extant specimens by the collectors could be in error (many museum labels are inaccurate). In *Dendrohyrax* the ventral part of the symphysis is often marked by rugose bone and two swollen ridges of bone, whereas in *Heterohyrax* the symphysis is smoother

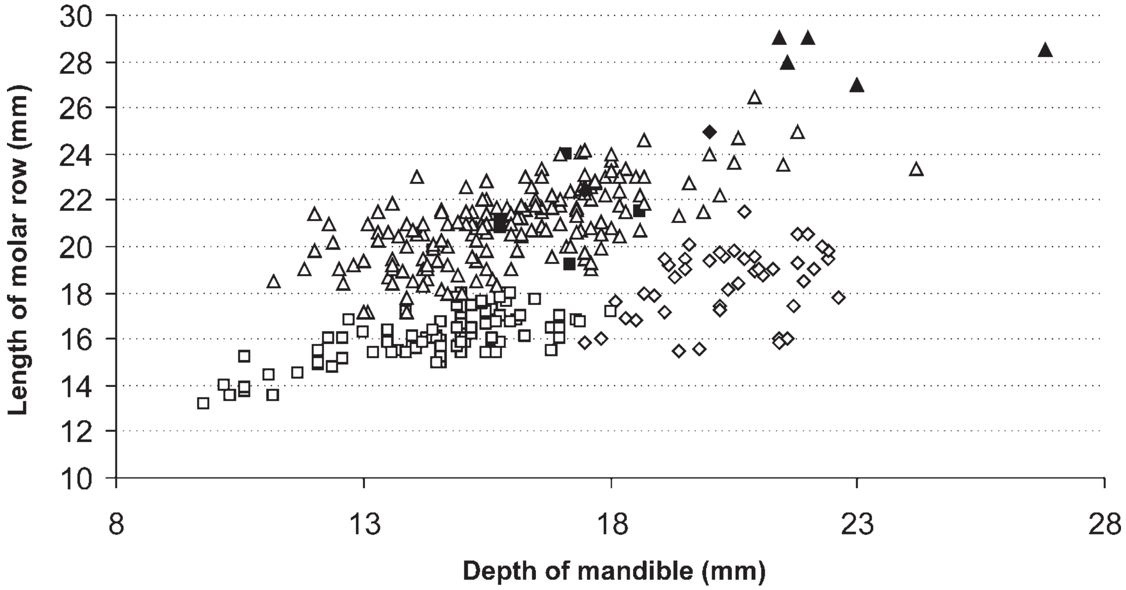

Figure 1. Bivariate plot of depth of mandible beneath the rear of m/1 against length m/1–m/3 in extant and fossil Procaviidae (open symbols, extant species; filled symbols, fossil species) (Δ = *Procavia* species; ✧ = *Dendrohyrax* species; ❑= *Heterohyrax* species; ▲ = *Procavia transvaalensis*; ■ = *Procavia antiqua*; ◆ = *Procavia pliocenica*; ● = *Dendrohyrax samueli*).

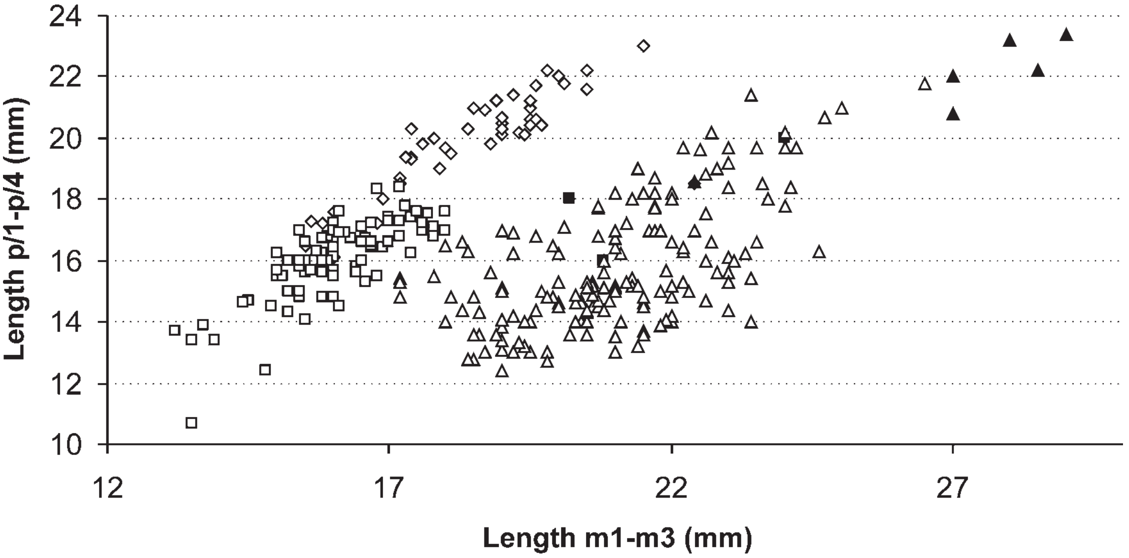

Figure 2. Bivariate plot of length of lower molar row versus length of lower premolar row in extant and fossil Procaviidae (symbols as in Fig. 1).

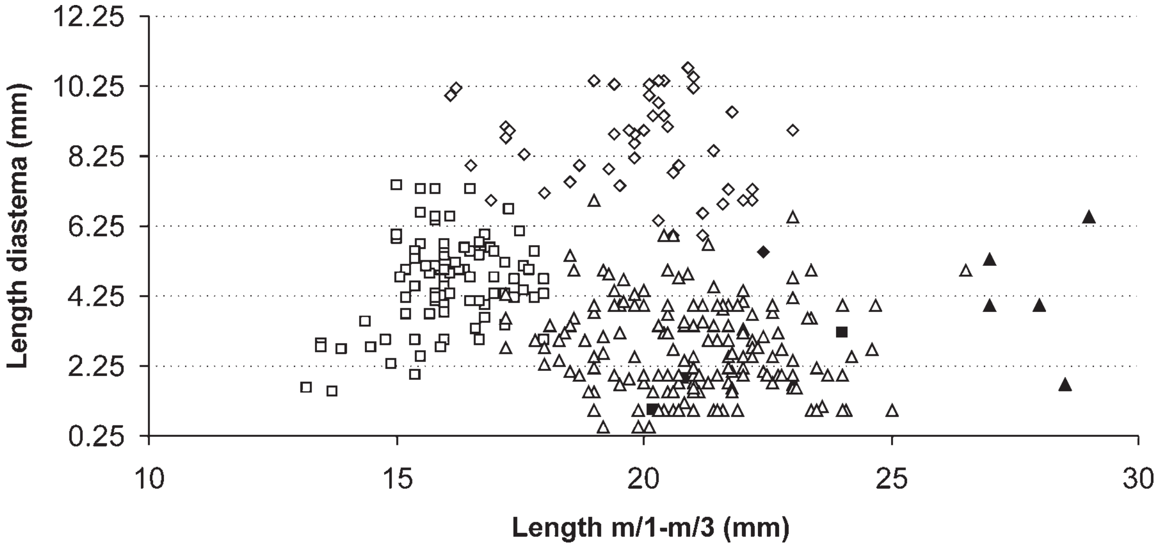

Figure 3. Bivariate plot of length m/1–m/3 versus lower diastema in extant and fossil Procaviidae (symbols as in Fig. 1).

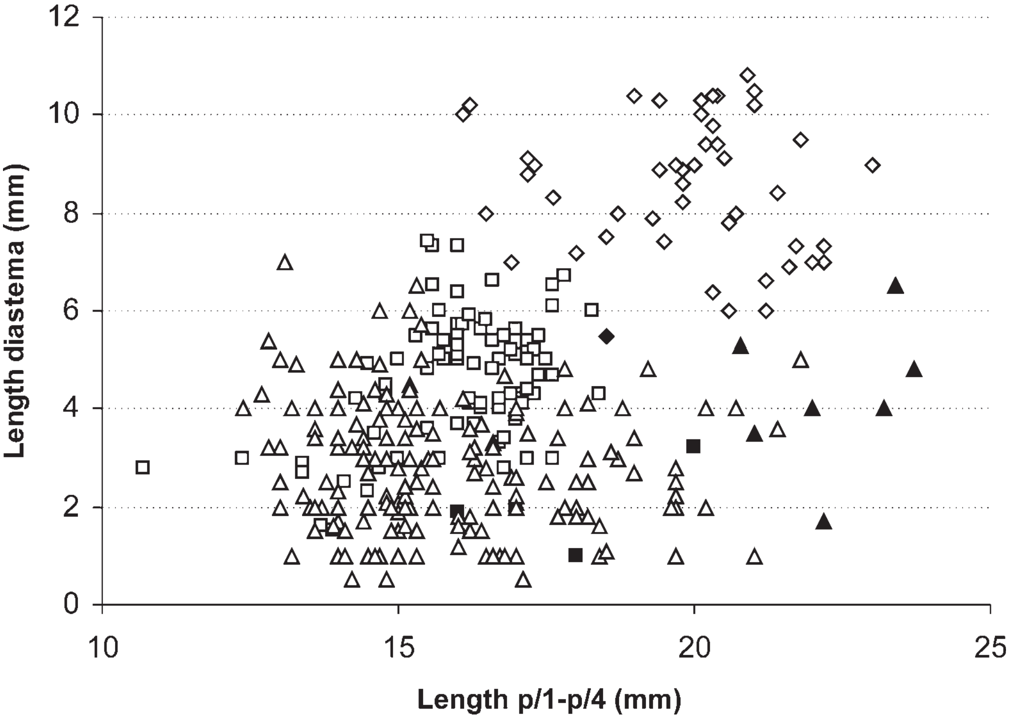

Figure 4. Bivariate plot of lower premolar row versus length of lower diastema in extant and fossil Procaviidae (symbols as in Fig. 1).

and has no ridges. A few specimens of *Dendrohyrax,* especially juveniles, lack the ridges, but if they are present, then the identification of the individuals as *Dendrohyrax* is reliable.

Figures 1–4 are plots of mandibular and dental parameters. Figure 1 deals with mandibular depth against length of lower molar row and reveals the pattern which can be used to distinguish the three genera of extant dassies. The mandibles of *Heterohyrax brucei* are uniformly shallower relative to the length of the molar row than those of *Dendrohyrax* species, which scatter around a separate regression line. The mandibles of *Procavia* species are even shallower relative to the length of the molar row, and they scatter about a third regression line.

Some distinctions between the genera *Procavia* and the *Heterohyrax*/*Dendrohyrax* pair

Because the Langebaanweg dassies combine features of both *Heterohyrax* and *Procavia,* it is necessary to revisit the question of how to distinguish between them and the tree hyrax, *Dendrohyrax.*

Procavia differs in many respects from both *Heterohyrax* and *Dendrohyrax* (Hahn 1934; Sale 1960; Roche 1972). Dentally, the latter two genera are similar to each other, but there are minor differences in premolar-molar proportions, mandibular depth, and cranial morphology. It is difficult, if not impossible, to distinguish isolated lower teeth of these two genera from each other. Table 2 summarizes the main differences between extant *Procavia*

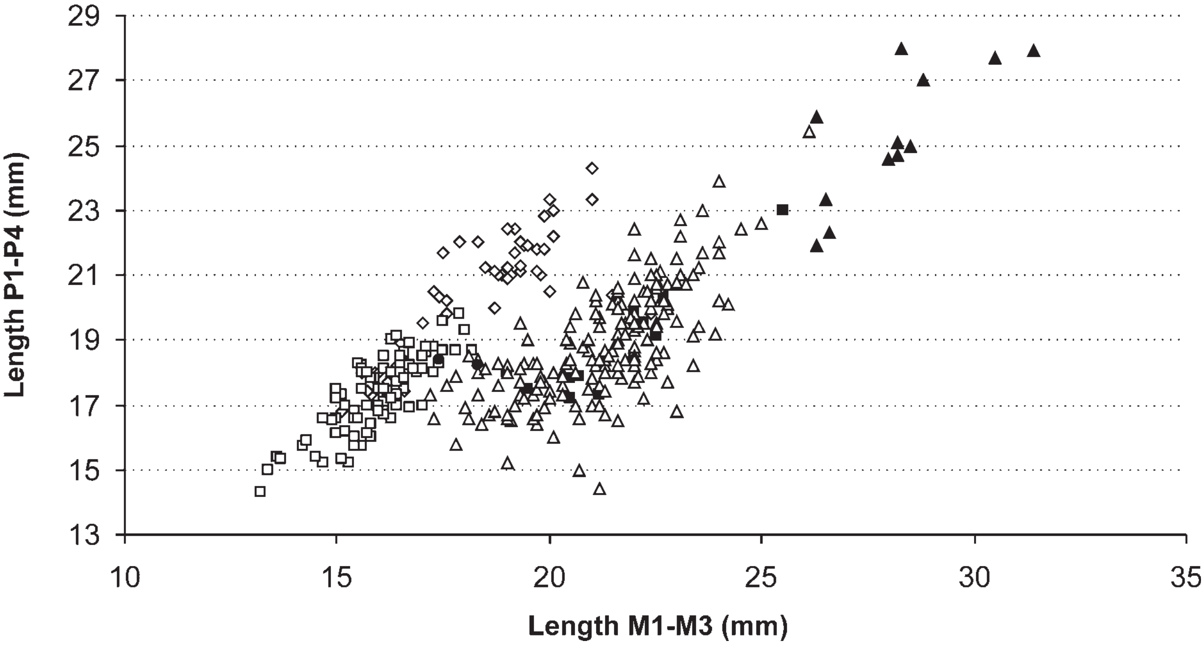

Figure 5. Bivariate plot of length of upper molar row versus length of upper premolar row in extant and fossil Procaviidae (symbols as in Fig. 1).

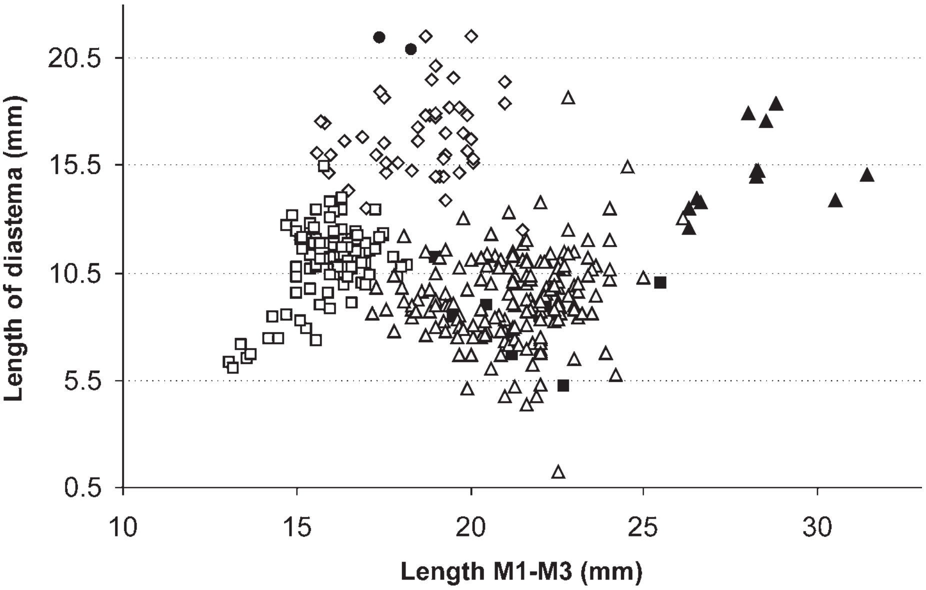

Figure 6. Bivariate plot of length upper diastema versus length of upper molar row in extant and fossil Procaviidae (symbols as in Fig. 1).

on the one hand and the *Heterohyrax/Dendrohyrax* pair on the other.

Variation in fossil and extant *Procavia*

The large degree of morphological variability in *Procavia* has led to some confusion in the literature. Broom (1934, 1936), for instance, created two species of *Procavia* for fossils from karst deposits of South Africa (*Procavia (Prohyrax) antiqua* from Taung, and *P. robertsi* from Uitkomst (= Gladysvale)). The differences between these species related to the hypsodonty of the molars, curvature of the cheek tooth rows and the distance between buccal and lingual cusps in the upper cheek teeth. Some of these features, such as the distance between the buccal and lingual cusps, vary with wear (McMahon & Thackeray 1994) and thus do not represent real morphological differences, but the other features that Broom cited are part of the normal range of variation of the species. Broom appears to have been influenced by the extremes of variation that exist in the extant rock hyrax, his species *P. antiqua* being similar to the more brachyodont specimens of *P. capensis* (which generally have the temporal crests far apart, as in *Heterohyrax*), and *P. robertsi* being similar to the more hypsodont individuals of *P. capensis* (in which the temporal crests are often closer together, even to the extent of forming a sagittal crest). As was demonstrated by McMahon & Thackeray (1994), all the material attributed to *P. antiqua* (including *P. robertsi*) falls within the range of metric variation of *P. capensis,* and on this basis they concluded that all the small fossil dassies from cave deposits

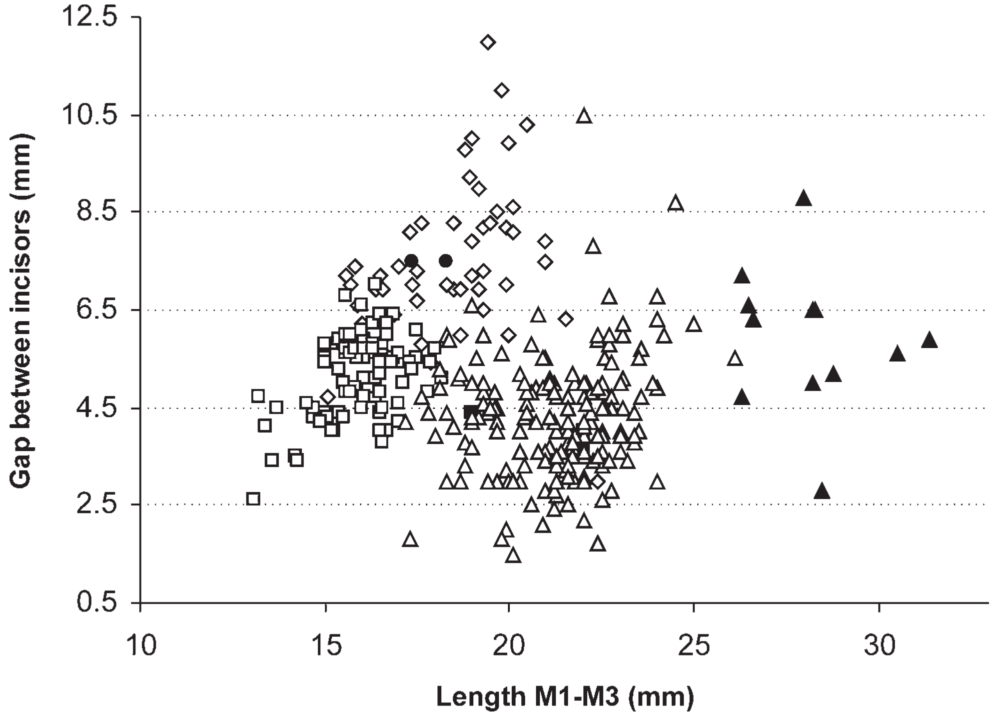

Figure 7. Bivariate plot of length of upper molar row versus length of gap between upper incisors in extant and fossil Procaviidae (symbols as in Fig. 1).

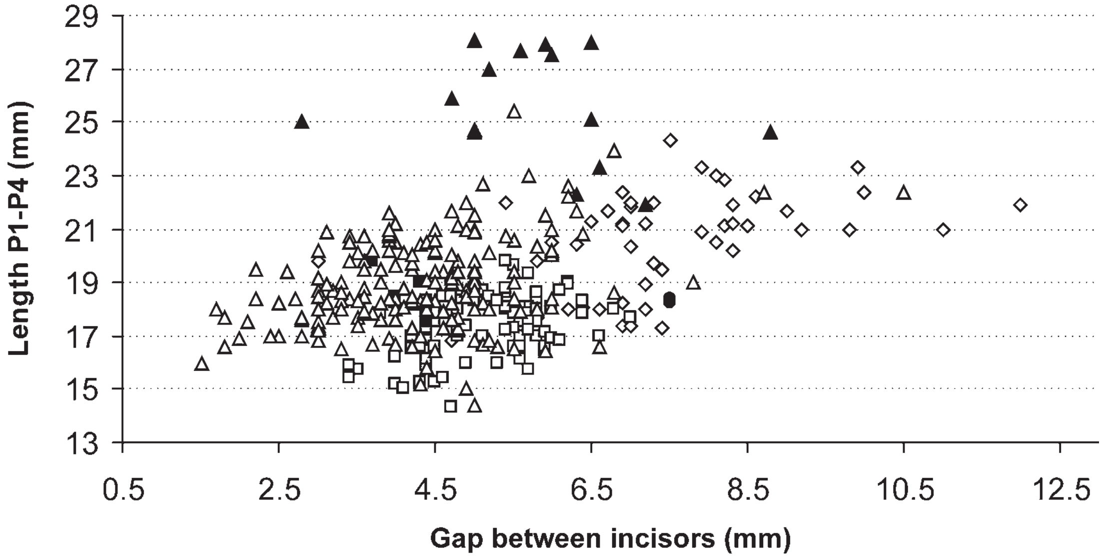

Figure 8. Bivariate plot of length of upper premolar row versus length of incisor gap in extant and fossil Procaviidae (symbols as in Fig. 1).

of South Africa belonged to the extant species *Procavia capensis.* By contrast, Schwartz (1997) upheld Broom's species *P. antiqua,* citing its brachyodonty, a few other odontological features and some metric differences (ratio of ectoloph length to lingual length of upper molars).

While the conclusion of McMahon & Thackeray (1994) is well-founded for the characters that they selected to analyse from a statistical point of view, it does not address the issue of the presence of both brachyodont and hypsodont individuals (populations) in the same species. Nor does it explain the presence of straight and curved tooth rows in the same species, nor of the temporal crest development (wide apart or close together) and other morphological variation. Many of the differences observed are related directly or indirectly to mastication (hypsodonty versus brachyodonty, size of temporal musculature (temporal crest development), loss or retention of p/1, position of the infra-orbital foramen, relative proportions of premolar row to molar row, length of diastemata), from which it is deduced that the diets of the species contain a wide range of plants, with some populations devouring only small quantities of grass, and other populations much more. It is surely no coincidence that the individuals with the most hypsodont molars are also those with the largest areas of origins of the temporal musculature (as reflected in closer temporal crests), and those with the most brachyodont molars tend to have the temporal crests further apart (i.e. smaller areas of origin of the temporal musculature).

Churcher (1956) concluded that *P. antiqua* and *P. robertsi* were synonymous, and reconstructed the cranial and mandibular anatomy of the species on the basis of various fragmentary fossils from a variety of localities. In doing so, he appears to have combined elements of more hypsodont and more brachyodont individuals (see Churcher 1956, p. 496, the list of specific characters is clearly a mixture drawn from hypsodont and brachyodont individuals). Partly because of this the fossil species was considered by him to be a primitive member of the genus, and he positioned it near the base of the *P. capensis* lineage. However, because the fossils possess almost the same range of variation as the extant species, it is in reality just as derived. For this reason, the author agrees with McMahon &

Table 2. Summary of features that have been used to separate *Procavia* from the *Heterohyrax/Dendrohyrax* pair.

Feature	*Heterohyrax/Dendrohyrax*	*Procavia*
p/1	Well formed, two-rooted	Simple peg, tiny single root, often absent except in East African populations
Diastema between i/2 and anterior premolar	Long	Short or absent
Lower incisors	Brachyodont, long times	Hypsodont, short tines
Diastema between lower central incisors	Medium to wide	Absent to short
Distal transverse lophs of lower molars	Short, at right angles to long axis of tooth row	Long, oblique to long axis of tooth row
Mental foramina	Below p/1	Below p/3
Styles on upper molars	Well developed, extending to cervix	Weak, fading out above cervix
Ectolophs of upper molars	Brachyodont	Hypsodont
Buccal cingulum of upper molars	Sub-parallel to occlusal surface	Steeply angled
Increase in size of upper cheek teeth	Regular from anterior to posterior, M3/ slightly smaller than M2/.	Molars abruptly larger than premolars. M3/ large.
Lower molars	Brachyodont	Hypsodont
Premolar row	Long relative to molar row	Short relative to molar row

Thackeray (1994) that *P. antiqua, P. robertsi* and *P. capensis* have similar ranges of metric variation in the dentition, but it is noted that the range of variation in temporal crest separation is greater in the fossil sample than it is in the extant one. This could be due to either of two things; a) the fossil sample is a mixture of two or more species in which case the material from the various sites should not be pooled together into a single species, b) the range of variation in dassies was different in the Plio-Pleistocene than it is today, in which case we cannot use actualism to explain variation in fossil dassies. The former explanation is probably more likely than the latter.

Schwartz (1997) did not mention the fact that extant South African dassies attributed to *P. capensis* are variable in terms of hypsodonty and brachyodonty. My own observations reveal that the species is highly variable, both in terms of hypsodonty and other cranio-dental features, such as the disposition of the temporal crests and curvature of the tooth rows in occlusal view. Fossils from the Gauteng Cave Sites attributed to *P. antiqua* by Churcher (1956) and Schwartz (1997) span a similar range of morphometric variation as *P. capensis.* More detailed analysis of the collections, including undescribed fossils that have been collected in the past two decades may lead to a better understanding of the situation. Pending the results of such a study, I consider that the fossils identified as *P. antiqua* by Churcher (1956) and Schwartz (1997) are better classified as *P. capensis,* but for the purposes of metric analyses which follow, the fossils will be kept separate from extant specimens in order to prevent mixing of material of different geological ages (Figs 1–8).

Even though the more brachyodont individuals of *P. capensis* fall comfortably within the range of metric variation of the species, in terms of some morphological characters they are closer to *Heterohyrax* than to the hypsodont individuals of *P. capensis.* The strong development of the styles and cingula on the ectolophs of the upper molars, for example, is closer to the condition in *Heterohyrax* than to that of hypsodont individuals of *Procavia* in which the ectoloph is flatter (Allaerts *et al.* 1982). The straightness of the palatal tooth rows is another feature by which brachyodont *P. capensis* recall *Heterohyrax,* and there are others, including the relatively great separation of the temporal crests. Because of these similarities, it is sometimes confusing to work on fragmentary material or isolated teeth, and it is possible that some inferences regarding hybridization between *Procavia* and *Heterohyrax* (Kingdon 1974) may be due to the intermediate nature of the brachyodont individuals of *Procavia.*

Inclusion of *Heterohyrax* and *Dendrohyrax* in the analyses reveals an even more complicated situation, with a great deal of overlap in metric and morphological features. Thus, whilst there is little difficulty in correctly identifying complete skulls of *Dendrohyrax* and *Heterohyrax* due to the great differences in temporal crest morphology, post-orbital bar development, length of diastemata relative to the tooth rows, post-orbital closure and proportions of premolar rows to molar rows, it is considerably more difficult to identify fragments of jaws and isolated teeth. This is especially evident when individuals from many populations in different countries and habitats are considered. It is undoubtedly this aspect of *Heterohyrax* and *Dendrohyrax* that underlies the decisions of some researchers to consider *Heterohyrax* to be a subgenus of *Dendrohyrax* (Ellerman & Morrison-Scott 1951; Roche 1972). Nevertheless, there can be little doubt that *Heterohyrax* and *Dendrohyrax* represent separate genera – their biology is so divergent that it is difficult to conceive of them as being congeneric. Not only are their daily rhythms different (diurnal in *Heterohyrax,* nocturnal in *Dendrohyrax*), but also their calls are widely divergent and their social structures dissimilar.

As concerns fossil procaviids, the gradation of morphological features between the three extant genera poses particular problems, especially in fragmentary material. Historically, there has been a tendency to identify brachyodont fossil procaviid remains as *Heterohyrax* (Fischer 1986; Rasmussen *et al.* 1996), but the possibility exists that some of the material could represent *Dendrohyrax* or *Procavia* instead. Only the collection of more substantial specimens will resolve the matter.

At Lukeino, the Aragai palate is complete enough to reveal with little doubt that it belongs to *Dendrohyrax.* The Lemudong'o, Kenya, fossils in contrast are fragmentary and most of the features that are diagnostic for separating *Heterohyrax* from *Dendrohyrax* are lacking. However, a base of a mandibular symphysis preserves morphology that is usually only found in *Dendrohyrax* (presence of a roughened promontary separated from the body of the symphysis by grooves). Metrically the dental remains from Lemudong'o plot within the ranges of variation of both *Dendrohyrax* and *Heterohyrax.* If they are *Heterohyrax* then they represent a large species of the genus, but if they are attributed to *Dendrohyrax,* then they would denote a small species of the genus. The assumption is that only one genus is present at the site, which, if true, means that it should be attributed to *Dendrohyrax* (Pickford & Hlusko, in prep.).

The Langebaanweg (South Africa) dassie possesses mandibular proportions of the genus *Procavia,* and because this morphology is derived among procaviids, the remains are attributed to *Procavia,* even though in several features of the dentititon, they resemble *Heterohyrax.* As such, the Langebaanweg *Procavia* is the earliest known member of the genus in the fossil record. The primitive nature of the cheek dentition, allied to the derived proportions of the mandible suggest that the *Procavia* lineage diverged from those of the other procaviids sometime during the Late Miocene.

PART 2. THE LATE MIOCENE PROCAVIID FROM LUKEINO, KENYA

The site of Aragai in the southern extremity of the Lukeino Basin, Baringo District, Kenya, which is at the base of the Lukeino Formation (Sawada *et al.* 2002) yielded an almost complete palate of a hyrax of modern aspect (Fig. 9). The fossil was collected from rust-coloured sands comprising a palaeosol near the base of the formation. The specimen was heavily encrusted in a hard, red ironstone sand rich in phosphate. The neurocranium is missing and much of the naso-maxillary region is crushed into the nasal cavity but the lateral surfaces of the maxilla are well preserved.

The same site yielded abundant colobine cranial and mandibular material, as well as a juvenile suid mandible (*Nyanzachoerus tulotos*) and remains of impala (*Aepyceros* sp.). The nature of the assemblage and the damage to the specimens indicates that the fossils were probably concentrated in the area by a bird of prey, such as Verreaux's eagle or the crowned eagle, as similar damage has been described in extant bone assemblages recovered from the ground below the nests of the crowned eagle (Sanders *et al.* 2003).

Systematic description

Order Hyracoidea Huxley, 1869
Family Procaviidae Thomas, 1892
Genus *Dendrohyrax* Gray, 1868

Species *Dendrohyrax samueli* sp. nov., Fig. 9

Diagnosis. Upper diastema longer relative to premolar and molar rows than is usual in *Dendrohyrax.* Hypocone of M3/ not greatly reduced, incisive jugum terminates above the P1/.

Holotype. Bar 961'01, palate with much of the dentition.

Type locality. Aragai, Lukeino Formation, Tugen Hills, Kenya.

Age. 6 Ma, Late Miocene.

Etymology. Named in honour of Mr Samuel Chetalam of Rondinin Village and member of the Community Museums of Kenya, who found the holotype.

Description

Lukeino hyrax palate *(Bar 961'01)*

The specimen consists of a palate that was heavily encrusted in a hard red sandstone (Fig. 9). It has the bases of both upper central incisors, the roots of the left P1/ and the right P1/–P3/, the other premolars and all the molars being complete or only slightly damaged and heavily to moderately worn.

The snout is slightly distorted and has suffered a bit of plastic deformation and displacement of bones, especially the nasals which have been pushed into the nasal cavity. The snout flares out abruptly above the P1/ and the zygomatic arch departs from this flared part of the snout at the level of P2/ (Fig. 9). There is a well-developed buccinator ridge just above the roots of the cheek teeth, while on the palatal side of the cheek teeth, especially opposite the molars there is a small shelf of bone, forming a prominent alveolar process. The posterior choanae are broadly U-shaped and invaginate up to the level of the front of M3/ (Fig. 9). The rear of the root of the zygomatic process of the maxilla lies above the middle of M2/.

The upper incisors are triangular in section, the antero-mesial and antero-lateral sides being slightly concave indicating that the individual was probably a male. The lingual surface of the incisor is devoid of enamel, and is slightly convex lingually. The distance between the incisors (7.5 mm) is much wider than the mesio-distal diameter of each of the incisors (4.2–4.5 mm). The central incisors occupy a prominent jugum which extends in the arc of a circle as far back as the P1/ (Fig. 9). The fact that this jugum terminates above the P1/ indicates that it is a relatively long snouted form, unlike *Prohyrax tertiarius* and *Prohyrax hendeyi,* in which the incisor root terminates above the P3/ and other species of *Dendrohyrax* in which it ends above the P2/.

The diastema between the upper incisors and the anteriormost premolar is *c.* 18 mm. The premolar row is *c.* 19.8 mm on the left and 20.5 mm on the right, which is longer than the molar row (18.9 mm left and 19.6 mm right) (Fig. 9; Table 3).

The P1/ roots suggest that the tooth was about the same length as the P2/, and was thus not reduced.

The ectoloph of P2/ is broken and the tooth is heavily worn, but the remaining part of the crown reveals that it was molariform with well-developed protocone and hypocone with large anterior crests leading antero-buccally from each cusp forming prominent protoloph and metaloph, respectively, with a deep valley between them.

P3/ is larger than P2/ and has a well-developed basal cingulum running the length of the ectoloph. The parastyle is strong and projects anteriorly of the rest of the tooth. The paracone and metacone are large and are joined to the ectoloph by well-developed protoloph and metaloph. The parastyle and metastyle form low relief rounded ridges on the outer surface of the tooth. The protoloph and metaloph are separated on their lingual sides by a deep transverse valley, but are strongly joined to the ectoloph.

P4/ is similar to P3/ but is larger, and because it is less worn it is possible to observe an anterior shelf-like cingulum, and a posterior cingulum which overhangs the distal roots. The buccal cingulum is well developed.

The M1/ is larger than the P4/ and differs from it by possessing better developed and more angular styles on

Table 3. Measurements of the teeth (in mm) of Bar 961'01 are as follows.

Tooth	Mesio-distal length	Bucco-lingual breadth
I1/ left	4.5	4.8
I1/ right	4.2	4.8
Gap between I1/s	7.5	–
Diastema left	18.0	–
Diastema right	18.3	–
P2/ left	4.3	–
P3/ left	5.1	6.2
P4/ left	5.6	6.1
P4/ right	5.6	–
M1/ left	6.1	6.3
M1/ right	6.2	6.7
M2/ left	7.1	6.9
M2/ right	7.5	7.7
M3/ left	6.0	6.4
M3/ right	6.3	–
P1/–P4/ left	19.8	–
P1/–P4/ right	20.5	–
M1/–M3/ left	18.9	–
M1/–M3/ right	19.6	–

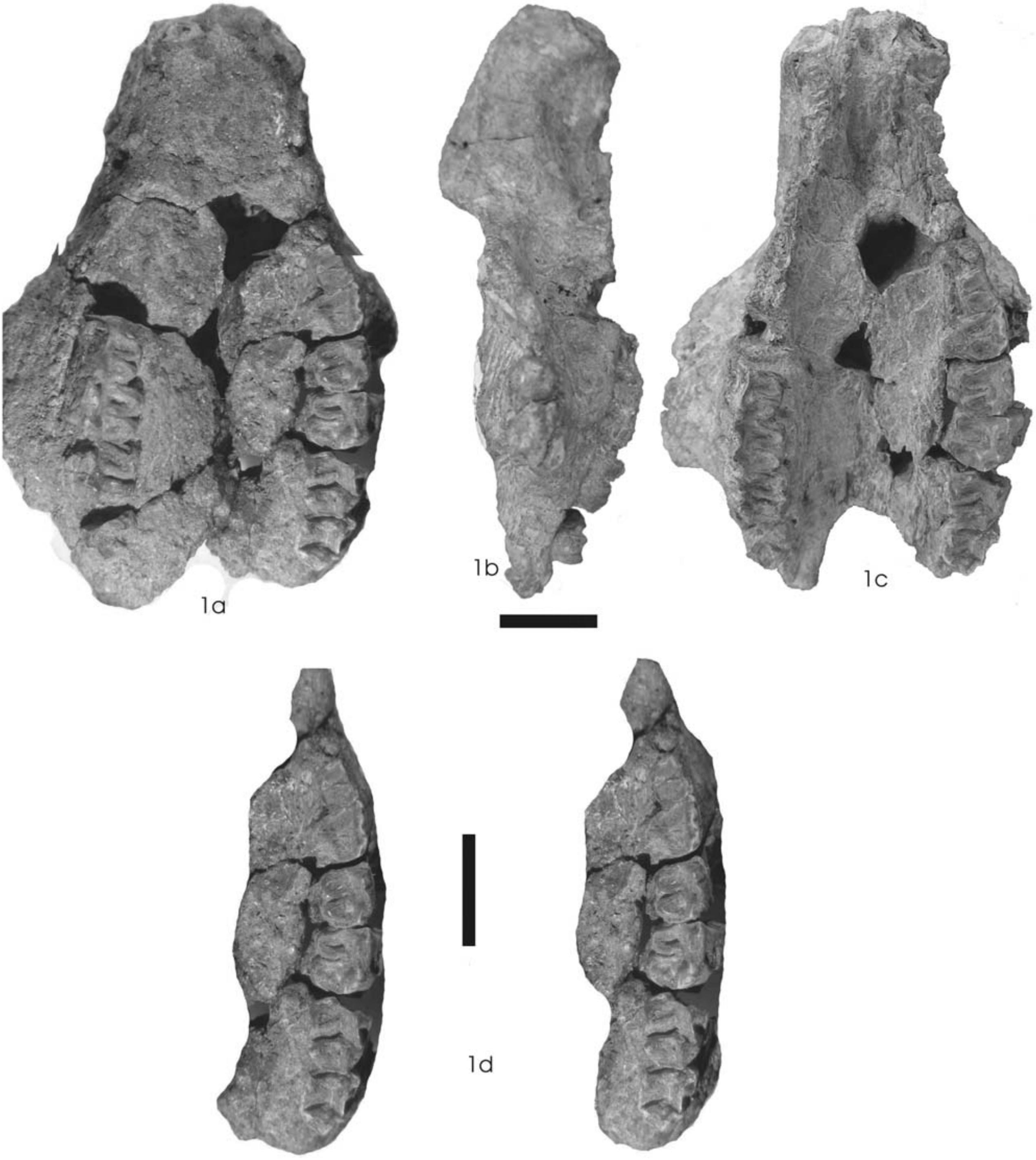

Figure 9. Bar 961'01, *Dendrohyrax samueli* sp. nov. palate with partial dentition from Aragai, Late Miocene (6 Ma), Lukeino Formation, Tugen Hills, Kenya. **1a**, palatal view before cleaning. **1b**, Right lateral view to show incisor jugum. **1c**, Palatal view after cleaning. **1d**, Stereo occlusal view of left cheek tooth row (scale bars = 10 mm).

the ectoloph. It too is deeply worn to the stage where the protoloph and metaloph are confluent with the ectoloph, but still separated from each other lingually. There is a small style at the distal extremity of the ectoloph, and the distal cingulum is well developed. The parts of the ectoloph anterior and posterior to the mesostyle lie in the same plane.

M2/ is the largest tooth in the dentition. It closely resembles the M1/ in morphology, but being less worn reveals that the transverse valley between the protoloph and metaloph is deep. The ectoloph morphology is similar to that of the M1/.

The M3/ is the smallest of the molars and tapers distally more rapidly than the other two, the hypocone being reduced compared with the other cusps. The distal cingulum is much narrower bucco-lingually than it is in M2/, but it still closes off a small fovea between the metaloph and the distal end of the tooth. Despite the reduction of the metacone, the two parts of the ectoloph either side of the metastyle lie in the same plane.

The lingual margins of the tooth rows are virtually parallel, being *c.* 17 mm apart throughout their length. The buccal margins of the toothrow bow outwards slightly, the outer surfaces being 26 mm apart at P4/, 31 mm at M1/ and

Table 4. Comparison of premolar row to molar row proportions of *Dendrohyrax samueli* sp. nov. with other procaviids.

Feature	*Procavia*	*Heterohyrax*	*Dendrohyrax*	Bar 961′01
Premolar row. molar row length (means)	16.18–20.95	15.95–16.42	16.20–16.10	21.2–18.2
Ratio premolars – molars	77%	97%	100.6%	116%

Data for extant hyracoids from Skinner & Smithers 1990.

29 mm at the front of M3/.

In lateral view the occlusal surface of the cheek teeth is slightly convex ventrally.

Comparisons among Procaviidae

Bar 961′01 is definitely not a *Procavia* (the premolar row is longer than the molar row; the molars are brachyodont and have prominent styles, ribs and cingulum; the upper incisors are far apart; the tooth rows are not markedly bowed outwards; I1/ is narrow; the diastema is longer than the length of M2/+M3/, and the molars are more brachyodont than in *Procavia,* in the upper molars the parts of the ectoloph either side of the mesostyle lie in the same plane) (Figs 5–8). Some of these differences in extant genera have been quantified, and it is clear that there is minor overlap in the ranges of variation of these parameters. As a general rule, however, the differences appear to be valid for most individuals.

In overall aspect the Aragai palate and upper dentition is similar to both *Dendrohyrax* and *Heterohyrax*. The craniodental differences between these two genera are subtle, and some are not reliable on a continental basis. However, for southern Africa, where the most thorough comparative work has been done (Bothma 1967; Hahn 1934; Roche 1972), the following criteria are usually valid:

Heterohyrax has the premolar row more or less equal in length to the molar row, the anterior premolars are closer together relative to the molar row and the diastema is much shorter than the length of M2/+M3/. In East Africa there is significant overlap in the range of variation of the premolar/molar measurements, to the extent that a large number of individuals cannot be identified on the basis of the premolar-molar row relationships alone. The length of the diastema relative to the premolar row is a more consistent criterion for distinguishing the genera (Table 4), but there is some overlap in the range of variation. *D. dorsalis* has an elongated diastema that is consistently longer than that in any species of *Heterohyrax.* However, in these features many individuals of *Dendrohyrax arboreus* fall within the range of variation of *Heterohyrax brucei.*

Environmental significance of *Dendrohyrax*

According to Corbet & Hill (1991) there are three extant species of tree hyrax. The largest is *Dendrohyrax dorsalis* which occurs in rainforests extending from Uganda to Gambia. The smaller *Dendrohyrax arboreus* inhabits more seasonal forests and well-wooded areas from Kenya to South Africa, and the coastal species, *Dendrohyrax validus,* is found in Eastern Tanzania and Zanzibar. This distribution translates into a size cline, with large tree hyraxes occurring in rainforest, medium-sized ones in seasonal forests and small ones in woodland and drier areas. When individuals from the three vegetation categories are plotted on bivariate plots a relatively clear pattern emerges supporting the observation. Adding the Aragai specimen onto the same bivariate graph reveals that it plots out consistently with the rainforest individuals.

This identification accords with other evidence that the Tugen region was covered in rainforest during the Late Miocene and Early Pliocene (Pickford *et al.* 2004). Other indications that the Lukeino Formation accumulated under humid climatic conditions are the presence of the water chevrotain, *Hyemoschus aquaticus,* the palm civet (*Nandinia*), the monkey fauna which consists only of colobines, and the bovid fauna which contains duikers, bushbuck and impala. The suids from Lukeino are bunodont, as are some of the proboscideans, including *Anancus kenyensis.* Large browsing mammals are present, including *Ancylotherium cheboitense,* and small giraffids. By contrast, mammals that are classically considered to be adapted to savanna and steppe, such as equids, are rare at Lukeino. Some of the Lukeino mammals are semi-hypsodont, with weak cementum on the cheek teeth (*Primelephas, Ceratotherium, Hippopotamus*). Fossil leaves from the formation are generally large, and many have drip points. Abundant small shards of fossil grass occur in diatomaceous shales (probably disaggregated hippopotamid faeces). The palaeoenvironmental picture that emerges for the Late Miocene of the Tugen Hills, is one of rainforest with open patches of grassland near water bodies, somewhat like parts of the western Rift Valley in eastern Congo and western Uganda.

Lukeino procaviid

The Lukeino hyrax palate is closest in morphology and proportions to the extant genus *Dendrohyrax.* In most measurements it falls within the range of variation of the western tree hyrax *Dendrohyrax dorsalis,* which occurs in rainforest extending from Uganda to Gambia. It is larger than the eastern tree hyrax *Dendrohyrax arboreus,* and the coastal species, *Dendrohyrax validus.* It is definitely not *Procavia,* and is unlikely to represent *Heterohyrax.* This is the first fossil record of *Dendrohyrax.* Because it has a relatively long upper diastema, an unreduced M3/ and the incisive jugum terminates in a position more anterior than is the case in other species of *Dendrohyrax,* the Aragai specimen is classified as a new species, *Dendrohyrax samueli.*

Dendrohyrax, as its name implies, is indicative of trees. It is arboreal, except in a few places where it lives in rocky areas with abundant crannies within forested areas (Corbet & Hill 1991; Roberts 1951). It is mostly nocturnal, but does have some diurnal activity when conditions are

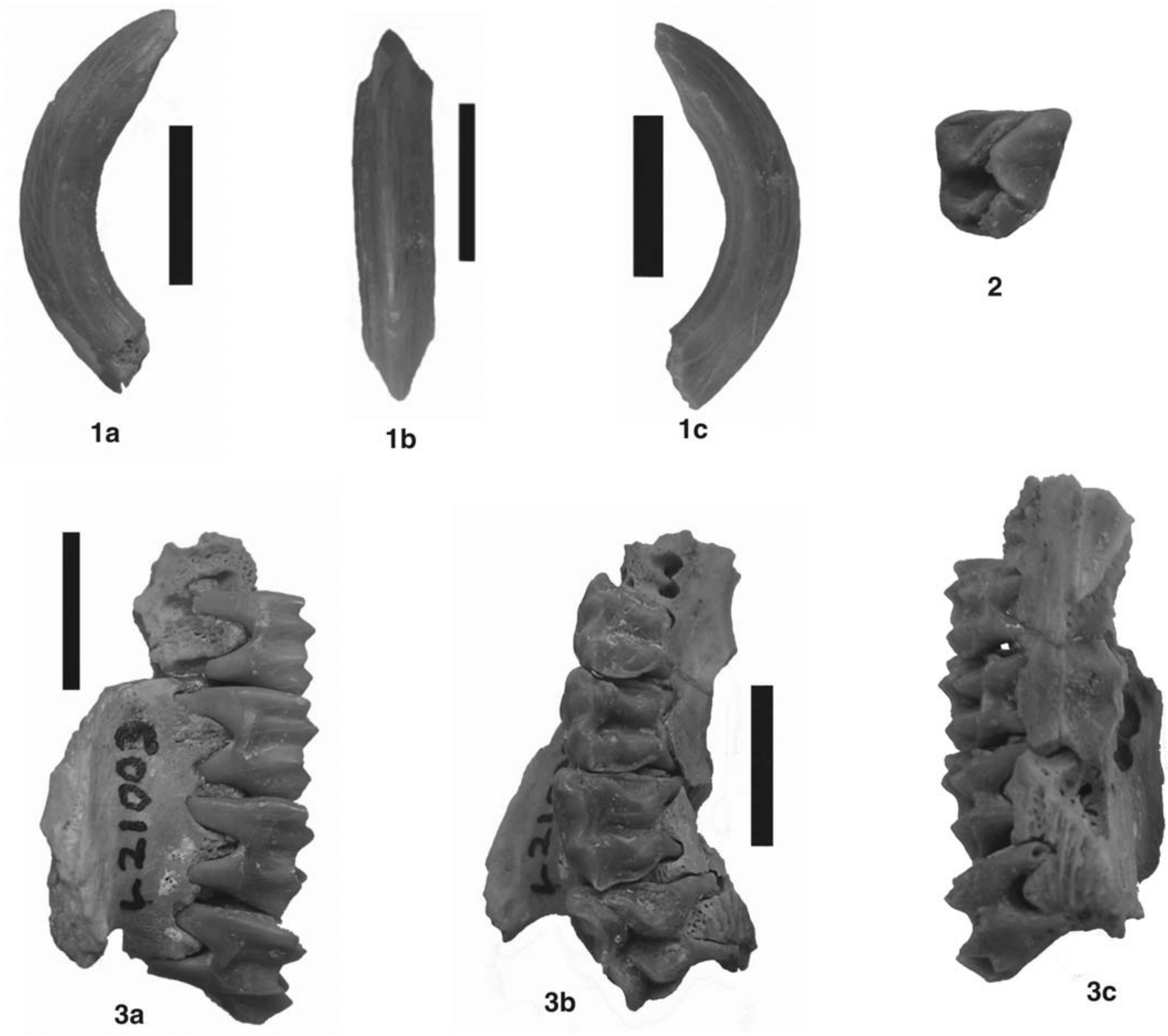

Figure 10. *Procavia pliocenica* sp. nov. from Langebaanweg, South Africa (scale bars = 1 cm). **1**, PQ L 11189, left I1/, **a**) mesial; **b**) anterior and **c**) distal views. **2**, PQ L 21003, left M3/, occlusal view. **3**, PQ L 21003, right maxilla with P3/–M2/ and alveoli of P2/, **a**) buccal; **b**) occlusal and **c**) lingual views.

suitable (Sale 1960). On the basis of the hyrax and other faunal and floral evidence, it is postulated that the Tugen Hills were covered in rainforest during the Late Miocene.

PART 3. THE LANGEBAANWEG PROCAVIID

Langebaanweg is an Early Pliocene site in Western Cape Province, South Africa from which a restricted sample of dassies was attributed to *Procavia* cf. *antiqua* by Hendey (1976, 1981). The bulk of the fossils described herein (Figs 10 & 11), came from the Quartzose Sand Member of the Varswater Formation.

Systematic description

Genus *Procavia* Storr, 1780

Species *Procavia pliocenica* sp. nov., Figs 10 & 11

Diagnosis. Species of *Procavia* with two rooted p/1, species 20% larger than *Procavia capensis* (and its probably synonymous species *P. antiqua* and *P. robertsi*); smaller than *Procavia transvaalensis.*

Synonymy

1976 *Procavia* cf. *antiqua* Broom, 1934 – Hendey, pp. 236, 242.
1981 *Procavia* cf. *antiqua* Broom, 1934 – Hendey, pp. 52, 90.

Holotype. PQ L 23564, mandible with both bodies, but lacking incisors, the right p/1 and ascending rami (Fig. 11.1).

Type locality. Langebaanweg, Cape Province, South Africa.

Stratigraphy. Quartzose Sand Member, Varswater Formation.

Age. Lower Pliocene

Etymology. The species name refers to the Early Pliocene age of the deposits from which the fossils were obtained.

Paratypes

Upper jaws and teeth

L 11189/21, left I1/ (Fig. 10.1).
L 21003, right maxilla with P3/–M2/, plus two isolated upper cheek teeth (Fig. 10.2, 10.3).

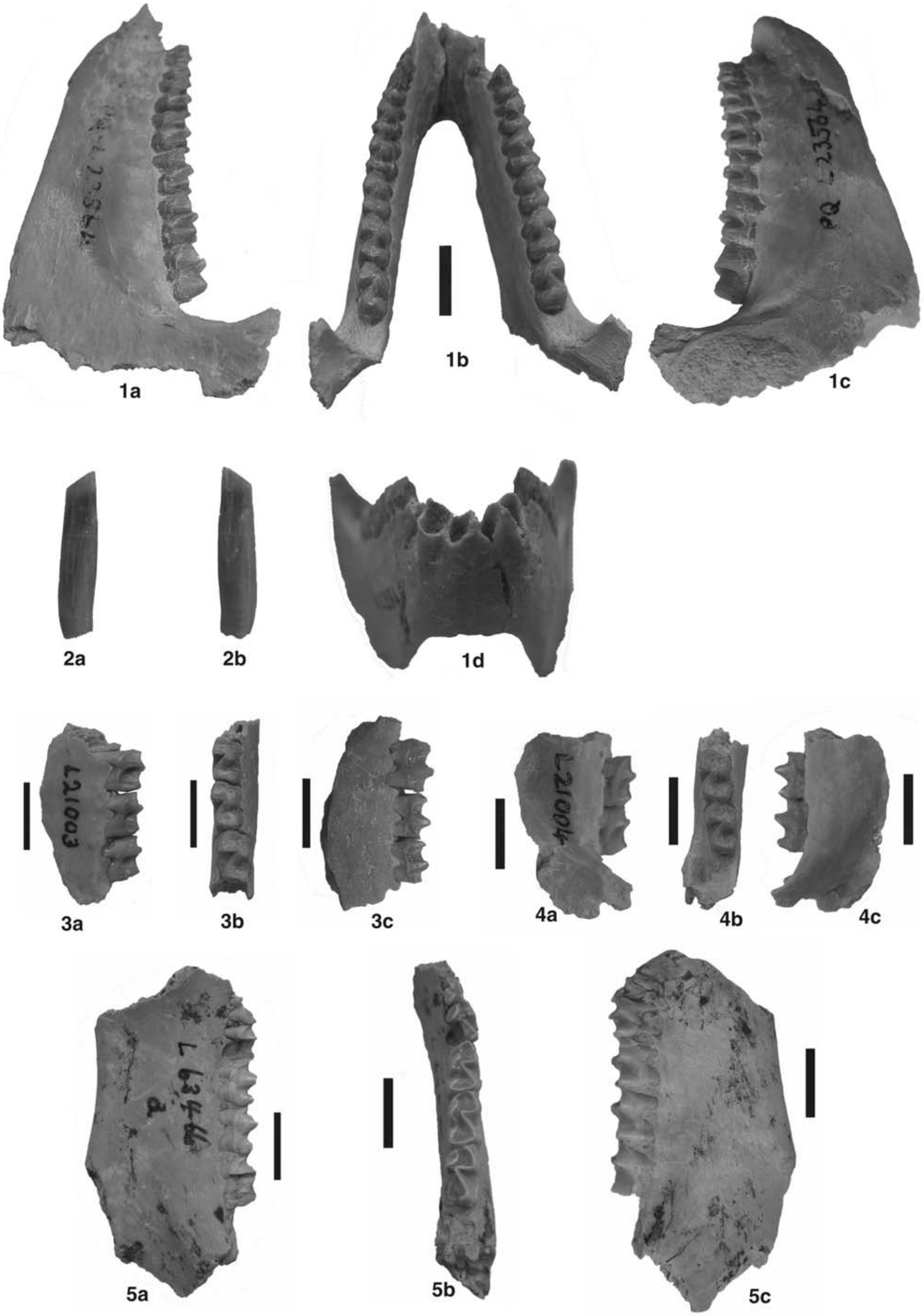

Figure 11. *Procavia pliocenica* sp. nov. from Langebaanweg, South Africa (scales: 1 cm). **1**, PQ L 23564, mandible lacking incisors, right p/1 and ascending rami, **a**) left lateral, **b**) occlusal, **c**) right lateral and **d**) anterior views. **2**, PQ L 21003, right i/2, **a**) anterior and **b**) posterior views. **3**, PQ L 21003, left mandible fragment with p/4–m/2, **a**) buccal, **b**) occlusal and **c**) lingual views. **4**, PQ L 21004, left mandible fragment with m/2–m/3, **a**) buccal, **b**) occlusal and **c**) lingual views. **5**, PQ L 63455, right mandible with p/3–m/2, **a**) lingual, **b**) occlusal and **c**) buccal views.

L 50522, right P3/.
L 63466f, right maxilla with two fragmentary cheek teeth.

Lower jaws and teeth
L 13633, right m/2.
L 21003 (see above) right i/2, plus left mandible fragment with p/4–m/2 (Fig. 11.2).
L 21004, left mandible with m/2–m/3 (Fig. 11.3).
L 24016, left m/2.
L 24605, left mandible fragment with p/2.
L 63466a, right mandible with p/3–m/2, roots p/2 (Fig. 11.5).
L 63466b, left mandible with rear half of m/3.
L 63455c, right mandible with m/1–m/2.
L 63466d, right mandible with p/1–p/2 and front part of p/3.
L 63466e, left mandible fragment with m/2.

Description

Maxilla. The only piece of hyracoid maxilla preserved at Langebaanweg consists of the alveolar process from P2/ to M2/ and part of the root of the zygomatic process of the maxilla (Fig. 10.3). As in *Heterohyrax brucei,* the two lingual roots of the P2/ are close together, being fused near cervix, while those in the P3/ to M2/ are wide apart. In the fossils the rear of the root of the zygomatic process of the maxilla is opposite the rear of M1/, which is further forwards than it usually is in adults of *H. brucei,* in which it is opposite the midline of M2/. However, during ontogeny the dental battery in dassies migrates forwards with respect to the zygomatic arch, and its forward position in the Langebaanweg specimen is due to the youthful status of the individual (M3/ was probably still in its crypt) rather than to a specific difference.

The morphology of the maxillary dentition of the Langebaanweg hyrax is similar to that of extant *Heterohyrax brucei* (Fig. 10.2, 10.3). The cheek teeth differ markedly from those of *Procavia capensis* by having well-developed styles and buccal ribs on the ectoloph. The ectoloph is brachyodont rather than hypsodont as in *Procavia.* In the extant rock hyrax the styles are usually weak and the ribs low and rounded (although the molars are variable in these respects), whereas in the Langebaanweg species the styles project more strongly buccally and the ribs are more prominent and are sharper. The styles in the fossil species are pinched in and sharp apically and swell towards cervix where they are more rounded in profile. The cingula on the buccal surfaces of the upper cheek teeth are sharper and more prominent than they are in the extant species. The hypocone of the M3/ in the Langebaanweg dassie is complete, though relatively smaller than it is in the other molars. In *Procavia capensis,* the hypocone of the M3/ is reduced to absent but similar reduction also occurs frequently in *Heterohyrax* and *Dendrohyrax.* Measurements of the upper teeth are provided in Table 5. In other respects the upper cheek teeth of the Langebaanweg dassie are close to those of the extant bush hyrax.

Table 5. Measurements (in mm) of the upper dentition of *Procavia pliocenica* sp. nov. from Langebaanweg, South Africa.

Catalogue No.	Tooth	Length	Breadth
L 11189/21	I1/	5.0	4.8
L 21003 right side	P3/	5.8	6.2
	P4/	6.4	6.9
	M1/	7.4	7.3
	M2/	7.9	8.0
L 21003 left side	M1/	7.3	7.3
	M3/	7.1	7.6
L 50522	P3/	6.4	6.2

Mandible. There are several mandible fragments of dassies from Langebaanweg, and one specimen, the holotype (Fig. 11.1), consists of a lower jaw lacking only the ascending rami and the incisors. The diastema between the i/2 and p/1 is longer in the Langebaanweg specimen (5.5 mm) than it is in the extant rock hyrax (usually 1–2 mm only). This together with the fact that p/1 is present in the fossil species, and is reduced to absent in *P. capensis,* means that the Langebaanweg species has a proportionally longer mandible than extant rock hyrax, somewhat similar to those of *Heterohyrax* and *Dendrohyrax.* Related to this is the position of the mental foramina, which occur below the p/3 and p/4 in *P. capensis,* but beneath the p/1 and p/2 in *P. pliocenica.* In most other respects the mandibles of the Langebaanweg and extant bush hyrax are similar to each other.

Apart from its greater dimensions, the mandibular dentition of *P. pliocenica* is similar to that of *Heterohyrax brucei.* It differs in several important ways from extant *Procavia capensis* – the p/1 is large and possesses two roots in the Langebaanweg species, whereas in South African *P. capensis* the p/1 is usually absent, or if present is a tiny, single rooted tooth with a single cusp (most individuals of East African *Procavia* retain the p/1). In *P. pliocenica* the p/1 has two crescentic lophs, being a smaller and narrower version of the p/2. The i/2 from Langebaanweg has three terminal pectinations as in the extant species. The lower cheek teeth of *P. pliocenica* have sharp buccal cingula, whereas in South African specimens of *Procavia capensis* buccal cingula are usually absent or are represented by a low rounded swelling near the base of the crown. In East African specimens of *Procavia* there can be sharp buccal cingula in the lower cheek teeth, and the p/1 is more often present than it is in South African populations.

The rear loph of the m/3 in *P. pliocenica* is as well-developed as it is in the m/1 and m/2, whereas in South African *Procavia capensis* it is usually slightly reduced (lower when unworn) in size relative to those of the m/1 and m/2 as well as to the anterior loph of the m/3. A further difference between the lower cheek teeth of the Langebaanweg species and extant *Procavia capensis* is that in *P. pliocenica* the rear loph of the molars is oriented almost at right angles to the long axis of the tooth row, whereas in *P. capensis* it is more oblique, being angled at about 60° to the long axis of the tooth row.

However, the relative depth of the mandible is similar to the situation in *Procavia* rather than *Heterohyrax* and *Dendrohyrax,* the jaw being relatively shallow compared to the length of the molar row. Measurements of the lower teeth are given in Table 6.

Table 6. Measurements (in mm) of the lower dentition of *Procavia pliocenica* sp. nov. from Langebaanweg, South Africa.

Catalogue No.	Tooth	Length	Breadth
L 13633	m/2	7.2	3.8
L 21003	i/2	4.3	2.3
	p/4	6.0	4.4
	m/1	7.4	4.1
	m/2	7.3	4.7
L 21004	m/2	7.9	4.8
	m/3	7.6	4.7
L 23564 left side	p/1	3.4	2.3
	p/2	5.0	3.2
	p/3	5.2	3.9
	p/4	5.6	4.5
	m/1	7.2	3.8
	m/2	7.4	4.5
	m/3	6.8	4.3
L 23564 right side	p/2	4.9	3.2
	p/3	5.5	3.9
	p/4	6.0	4.5
	m/1	7.6	4.3
	m/2	7.2	4.5
	m/3	7.6	4.6
L 24016	m/2	7.1	4.5
L 24605	p/3	5.3	3.6
L 63466a	p/3	5.6	–
	p/4	6.8	5.3
	m/1	7.6	4.9
	m/2	7.6	5.0e
L 63466b	m/3	–	4.7*
L 63466c	m/2	–	4.4
	m/3	7.1	4.4
L 63466d	p/1	3.6	2.3
	p/2	4.5	3.2
L 63466e	m/2	7.3	4.7

*Rear loph of m/3.

Comparisons with other *Procavia* species

Procavia antiqua. The lower cheek teeth of *Procavia pliocenica* are about 20% larger than the mean of *Procavia antiqua* Broom, 1934 (Churcher 1956) (Fig. 1, 2). Some features of the dentition of *P. antiqua* described by Churcher suggest that this species is intermediate between *Heterohyrax* and *Procavia.* In particular, the more brachyodont molars, and the position of the protocone and hypocone relative to the ectoloph are primitive features, as is the presence of a well-formed p/1. However, the smooth ectoloph of the upper molars, the very short lower diastema, the single-rooted nature of the p/1 and the shape and narrow gap between the upper central incisors, and the close proximity of the lower central incisors, are all features typical of the genus *Procavia.*

McMahon & Thackeray (1994) concluded that *P. antiqua* and *P. robertsi* were synonyms of *P. capensis,* as the material is metrically and morphologically similar to the extant dassies from South Africa, but this view was challenged by Schwartz (1997), who considered the differences between the populations to be great enough to warrant separation at the species level. He therefore reinstated *P. antiqua.* However, there are still residual problems with the fossil species, in that the range of morphological variation in dental and cranial features seems to be rather large for a single species, and there may in fact be two species of dassies in the Plio-Pleistocene deposits of South Africa.

Procavia transvaalensis Shaw (1937) and its synonym (*Procavia obermayerae* Broom, 1936) is about 150% the size of *P. capensis* (i.e. 1.5 times larger) (Churcher 1956). It appears to be morphologically close to *P. capensis.*

Identification of the Langebaanweg hyracoids

The dentition of the Langebaanweg dassie differs in several respects from those of extant *Procavia.* The upper and lower molars are brachyodont, the p/1 is not reduced, the diastema is long, and the ectolophs of the upper molars possess well-developed styles and ribs which extend to the cervix, all features that do not occur in extant *Procavia,* but are present in *Heterohyrax* and *Dendrohyrax.* In addition the molar ectolophs are not as hypsodont as they are in living *Procavia.* The main feature by which the Langebaanweg dassie resembles *Procavia* is the depth of the mandible relative to the length of the molar row, the shape of the symphysis and the hypsodonty of the lower incisor.

There are few differences between the upper dentitions of *Heterohyrax* and *Dendrohyrax,* and even traditionally used criteria for distinguishing between them, such as length of the upper premolar row relative to molar row (Bothma 1967; Skinner & Smithers 1990) are sometimes inconclusive for some individuals. Unfortunately there is no complete upper cheek tooth row from Langebaanweg, so this 'test' cannot be applied.

There are differences in cranial morphology, principally related to the development of the temporal crests, which are strongly developed in *Dendrohyrax* and weak in *Heterohyrax.* Correlated to this difference, which suggests that *Dendrohyrax* possesses more powerful masseter and temporal musculature than *Heterohyrax,* is the presence of a deeper mandible in the tree hyrax than in the bush hyrax and the rock hyrax. The functional meaning of this is not clear, as it seems not to be related to chewing power or duration, since the teeth of the two genera are closely similar to each other. It is possible that these features are related to the loud and prolonged calling that typifies *Dendrohyrax,* and the softer, less common calling that occurs in *Heterohyrax.* When tree hyraxes call, they extend the head upwards, tightening the skin beneath the mandible, which, together with the enlarged hyoid apparatus, forms an efficient resonance chamber and 'drum skin'.

Be that as it may, the deeper mandible in *Dendrohyrax* generally serves to distinguish it from both *Heterohyrax* and *Procavia.* The Langebaanweg specimens (two can be measured) indicate that the mandibles are shallow relative to the length of the molar row, and they thus accord better with *Procavia* than with *Dendrohyrax* or *Heterohyrax.* The ventral surface of the symphysis is similar to that of *Procavia,* and the central incisor roots are close together, as in the rock hyrax, and unlike the situation in *Dendrohyrax* and *Heterohyrax.* Furthermore, the lateral lower incisor from Langebaanweg is hypsodont, and the tines are worn off well above the cervix, as in *Procavia,* markedly different from the lower crowned incisors of *Heterohyrax* and *Dendrohyrax.*

Phylogenetic implications of the Langebaanweg dassie

The species *P. pliocenica* provides a link between the extant *Procavia capensis* on the one hand and the genus *Heterohyrax* on the other, including *Heterohyrax auricampensis* from the Late Miocene of Berg Aukas, Namibia (Rasmussen *et al.* 1996). The overall similarity in size and morphology of these species indicates that the procaviids have experienced slow evolution for the past 10 million years.

In four features – the depth of the jaw relative to the length of the molar row, the morphology of the ventral part of the symphysis, the lack of a diastema between the lower central incisors, and the hypsodont i/2 with short tines – the Langebaanweg hyrax falls within the range of variation of *Procavia.* Because of this it is possible that the population is an early member of the *Procavia* lineage, retaining a large quantity of primitive features in the dentition. If this is so, then the genus *Procavia* originated in the Late Miocene rather than earlier. In this case the genus did not evolve its distinctive hypsodont dentition (molars in particular) until the Late Pliocene or Pleistocene. As Churcher (1956) pointed out, the Middle to Late Pliocene species *Procavia antiqua* retains a number of features of the dentition that are present in *Heterohyrax* but not in *Procavia,* including a well-formed p/1, and clear buccal styles and ribs on the upper molars, which are brachyodont (but see discussion above about *P. robertsi* and the results of McMahon & Thackeray 1994).

Geographic origin of the genus *Procavia*

The earliest known member of the *Procavia* lineage is from South Africa (this paper; Churcher 1956), where it has a more or less continuous fossil record from *c.* 5 Ma to the present. In East Africa, *Procavia* is unknown until the Late Pleistocene to Holocene, where it has been found in archaeological contexts at Kapthurin, Bromhead's Site and Gamble's Cave, Kenya (Hopwood 1931, 1939), while in Zimbabwe its earliest known record is Bulawayo (Zeally 1916). It is thus likely that the genus *Procavia* evolved in southern Africa, where it survived for a substantial period before spreading northwards during the late Pliocene, first to Eastern Africa, and eventually to parts of northeast Africa and even the Arabian Peninsula. Undoubtedly, the adaptations of *Procavia* for surviving in semi-arid and arid environments enabled it to colonize East Africa as this region became drier during the Pliocene before local lineages of hyraxes (*Dendrohyrax* and *Heterohyrax*) could themselves adapt to them. Tree hyraxes are still restricted to well-wooded to forested environments, but the bush hyrax (*Heterohyrax*) has managed to adapt to somewhat arid environments, and often occurs side-by-side with *Procavia.* However, in extremely arid regions, such as the Sahara and the Arabian Peninsula, the only hyracoid found is *Procavia.*

Extant South African rock hyraxes are more derived than those that occur in the tropics. In *P. capensis* the molars are more hypsodont, the upper diastema shorter, and the p/1 is generally absent, whereas in the East African species, p/1 is almost always present, the molars are often more brachyodont and the upper diastema longer. Thus, even the extant *Procavia* populations of South Africa are more evolved than those of East Africa.

Langebaanweg procaviids

The fossil dassie from the early Pliocene deposits at Langebaanweg belongs to the *Procavia* lineage, being similar in size to extant *Procavia capensis,* but it retains a large number of primitive features of the cheek dentition usually associated with the genera *Heterohyrax* and *Dendrohyrax.* It is larger than extant *Heterohyrax brucei* and the extinct *H. auricampensis,* and is attributed to a new species, *Procavia pliocenica.* In some features of its dentition it approaches the extinct early Miocene species *Meroehyrax bateae,* indicating that among all the known early Miocene hyracoids, the procaviids are more closely linked to *Meroehyrax* than to any other known genus, *Prohyrax* included. It is thus more likely that procaviids descended from saghatheriids than from any other family of hyracoids.

PART 4. AFFINITIES OF *GIGANTOHYRAX* AMONG THE PROCAVIIDAE

The detailed affinities of the large hyrax from Makapansgat, South Africa, *Gigantohyrax maguirei,* have never been elucidated. Examination of the fossils housed at the Bernard Price Institute (University of the Witwatersrand), South Africa, reveals that the resemblances between *Gigantohyrax* and *Dendrohyrax* are pervasive (Figs 12–14). The cheek teeth are large, concomitant with the dimensions of the skull, but they are by no means hypsodont, being upscaled versions of the teeth in *Dendrohyrax,* with well-formed buccal cingulum, large para-, meso- and metastyles, and relatively low-crowned ectoloph, and the parts of the ectoloph either side of the mesostyle lie in the same plane (Allaerts *et al.* 1982) (Fig. 14). Since Kitching's report, additional material has been collected from Makapansgat, consisting of two partial adult skulls, a juvenile skull that has been severely crushed, an isolated upper premolar and a fragment of lower jaw carrying a premolar. The undescribed fossils are useful in that they reveal variation in temporal crest morphology, some individuals having them close together and others wide apart. Thus the two features that could be taken to distinguish *Gigantohyrax* from *Dendrohyrax* were either incorrectly reported (hypsodont teeth) or are variable (degree of separation of the temporal crests).

Table 7 summarizes the main features of cranial morphology that distinguish adults of the three genera of Procaviidae and *Gigantohyrax.* The list contains observations by Allaerts *et al.* 1982; Hahn 1934; Kitching 1965, and the author.

The position of the infra-orbital foramen in *Gigantohyrax* was evoked by Kitching (1965) as a difference from *Procavia,* but the scoring of this character is somewhat subjective because of difficulties in orienting the reference plane (in lateral view, curvature of the toothrows differs in the three extant genera). In any case the supposed differ-

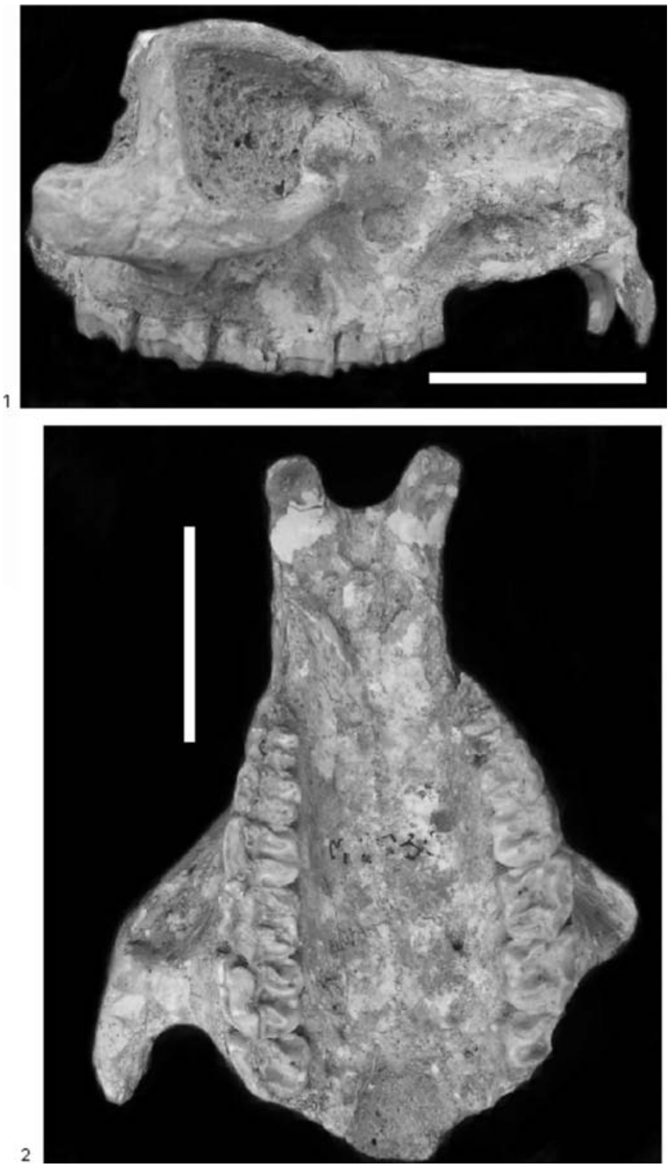

Figure 12. M 8230, snout of *Gigantohyrax maguirei* Kitching, 1965, from the Pliocene of Makapansgat, South Africa ((scale bars = 5 cm). **1**, right lateral view. **2**, Palatal view.

ences between the three extant genera are not great. Likewise, the anterior convergence of the tooth rows in *Gigantohyrax* is not markedly different from that in other procaviids, at least when measured between the lingual edges of the cheek teeth. Hypsodont specimens of *Procavia* sometimes have toothrows that converge more sharply than brachyodont specimens, but in any event the degree of convergence is quite variable in all three extant genera.

Determination of sex in *Gigantohyrax*

In extant procaviids, the upper incisors are sexually dimorphic. In both sexes the incisors are tusk-like, but in males the section is almost an equilateral triangle, often with the two anterior surfaces slightly concave in section, whereas in females, the section is an inequilateral triangle, in which the antero-lateral surface is appreciably broader than the antero-mesial one, and the anterior surfaces are convex.

The incisors in the holotype snout (M 8230) (Fig. 12) are tusk-like and in section have a short mesial side and a long slightly convex labial one as in females of extant procaviids. The other specimens of *Gigantohyrax* lack incisors, so it is not possible to determine their sex.

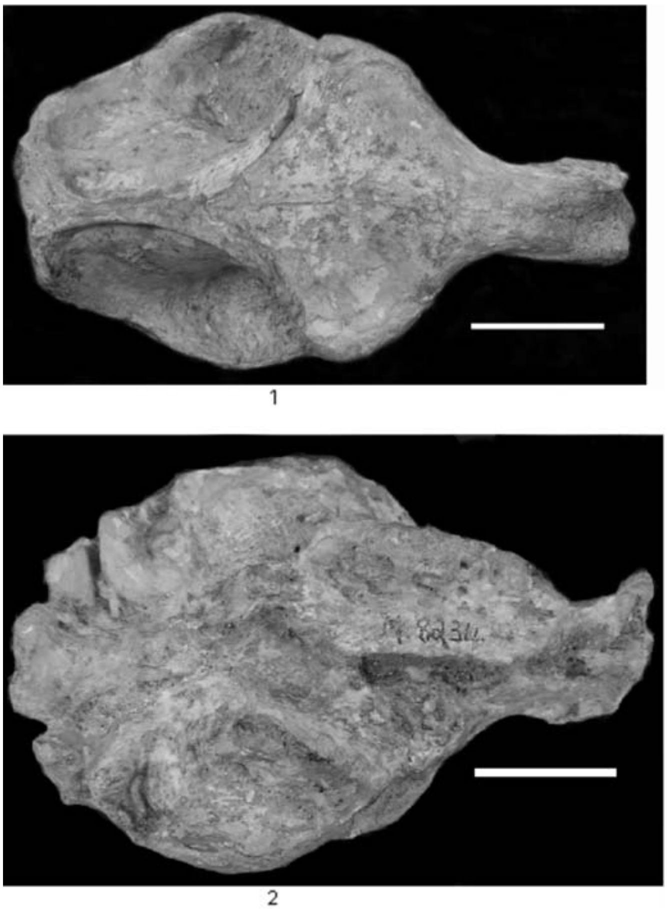

Figure 13. M 8234, skull of *Gigantohyrax maguirei* Kitching, 1965, from the Pliocene of Makapansgat, South Africa (scale bars = 5 cm). **1**, Dorsal view. **2**, Palatal view.

Discussion and conclusions on *Gigantohyrax*

Of the 19 features listed in the table, *Gigantohyrax* shares only a few with *Heterohyrax* (anterior position of incisive foramina, large gap between upper incisors, brachyodont cheek teeth). It shares none with *Procavia*. By contrast, it shares most of them with *Dendrohyrax.* The question that poses itself is whether the Makapansgat fossils should not be classified as *Dendrohyrax* rather than as a separate genus. Apart from the obvious size differences, there are two features by which the fossils described by Kitching (1965) differ from *Dendrohyrax,* the presence of a sagittal crest or temporal crests that are close to each other (Fig. 13.1) and the relative proportion of the lengths of the premolar and molar rows. An undescribed skull of *Gigantohyrax* (M 8416) has the temporal crests separated from each other, thereby not forming a sagittal crest, but they are not as wide apart as is generally the case in *Dendrohyrax.* The difference between the lengths of the molar and premolar rows (molars are 101% of premolars in M 8415, and 110% in M 8230) is less that is usual in *Dendrohyrax* (88–91%), and is closer to *Heterohyrax* (*c.* 100%) and *Procavia* (109–118%).

The fact that adults of *Gigantohyrax* and *Dendrohyrax*

Table 7. Summary of comparison between *Gigantohyrax* and the three extant genera of Procaviidae.

Character	*Procavia*	*Heterohyrax*	*Dendrohyrax*	*Gigantohyrax*
Anterior ventral zygomatic depression	Small or absent	Often present	Variable but often strong	Strong
Maxillo-palatine suture	Usually square (some individuals curved)	Usually square (some individuals curved)	Square to curved	Curved (one specimen)
Orbital margin	Not thickened	Not thickened	Thickened	Thickened
Temporal crest	Not beaded	Not beaded	Beaded	Beaded
Interparietal	Rarely completely fused	Rarely fused	Fused	Fused
Parietal and supra-occipital suture	Not fused	Early fusion	Variable fusion	Fused
Post orbital bar	Open	Open	Closed	Closed
Frontal surface	Convex	Convex	Collapsed	Collapsed
Dorsal profile of cranium in lateral view	Convex	Convex	Concave	Concave
Molar cingula	Weak	Moderate	Strong	Strong
Molar styles	Weak	Moderate	Strong	Strong
Molar ectolophs	Hypsodont	Brachyodont	Brachyodont	Brachyodont
Diastema	Short (length less than P1/–P2/)	Long (length = P1/–P3/)	Long (length = P1/–P3/)	Long (length = P1/–P4/)
Anterior termination of nasals	Behind premaxilla tip	Behind premaxilla tip	Slightly behind premaxilla tip	Above premaxilla tip (one specimen)
Diastemal ridge	Weak	Moderate	Strong	Strong
Gap between incisors	Small	Large	Large	Large
Depression in palatal part of premaxilla	Shallow, small	Shallow, small	Deep, large	Deep, large
Incisive foramina	Opposite or slightly anterior to P1/	Well anterior to P1/	Well anterior to P1/	Well anterior to P1/
Fossa beneath upper incisive juga	Shallow	Shallow	Deep	Deep

show fusion of the sutures of the back of the neurocranium, whereas adults (and even senile) *Procavia* usually do not, indicates that the former two genera are remarkably close, not only in osteology and odontology, but also in growth variables such as fusion of sutures. There can be little doubt that *Gigantohyrax* and *Dendrohyrax* are more closely related to each other than either is to *Procavia* or *Heterohyrax.* By all the cranial criteria listed above, *Gigantohyrax* is furthest morphologically from *Procavia* among the procaviids.

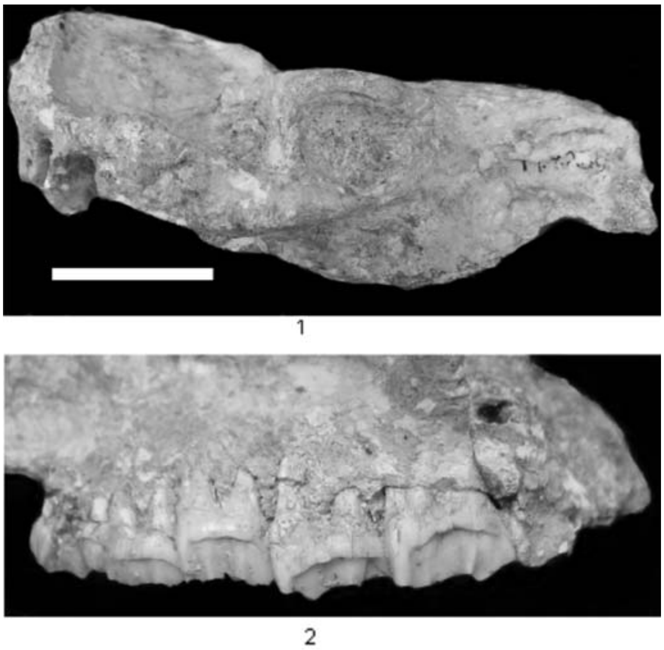

Figure 14. *Gigantohyrax maguirei* Kitching, 1965, from the Pliocene of Makapansgat, South Africa (scale bars = 5 cm). **1**, M 8234, skull, lateral view (note the concave dorsal profile). **2**, M 8230, enlargement of buccal aspect of upper left cheek dentition, P2/ to left, damaged M3/ to right (note strongly developed cingulum and styles).

If *Heterohyrax* is considered to be a subgenus of *Dendrohyrax,* as was suggested by Ellerman & Morrison-Scott (1951) and Roche (1972), then one would be forced to consider *Gigantohyrax* a synonym of *Dendrohyrax.* However, I take the view that *Gigantohyrax* is generically distinct from, although closely related to *Dendrohyrax,* and that *Heterohyrax* deserves full generic rank.

PART 5. DISCUSSION

The earliest known hyraxes of modern aspect (Procaviidae) are from Nakali (Kenya) (Fischer 1986) and Berg Aukas (Namibia) (Rasmussen *et al.* 1996) aged about 10 Ma. Prior to this date all the known African hyracoids were of archaic affinities including forms such as *Parapliohyrax* from Namibia, Kenya and the Maghreb (Pickford *et al.* 1997). Plio-Pleistocene East African hyracoids have been attributed to *Heterohyrax* and *Gigantohyrax* (Jaeger & Wesselman 1976) although, in the absence of complete tooth rows, the identification of the remains as *Heterohyrax* as opposed to *Dendrohyrax* must remain in doubt. *Gigantohyrax* Kitching 1965, first described from South Africa, appears to be most closely related to *Dendrohyrax* among the modern genera (thickened frontal above the orbits; depressed frontals; strongly developed post-orbital bar fused to the jugal; beaded temporal crests; premolar row longer than molar row; upper central incisors wide apart, molars brachyodont, dorsal profile of skull concave in lateral view). The Lukeino hyrax specimen is thus the first tropical African Late Miocene hyrax to be confidently identified to genus (*Dendrohyrax*).

Churcher (1956) considered that the genus *Procavia* included *P. tertiarius* from the Early Miocene of Namibia, which he erroneously thought was Pleistocene, but the discovery of more complete specimens of *Prohyrax tertiarius* and *Prohyrax hendeyi* (Pickford 1994, 2003) indicate that the similarities once considered to link these Early Miocene forms to the extant ones are outweighed by the abundant dissimilarities. As such the few comparable features (such as small size, some aspects of molar morphology) are probably symplesiomorphies, whereas the differences including the presence of hypsodont curved ectolophs with inflated styles in *Prohyrax* are apomorphies that do not occur in procaviids. However, the presence of a distally directed fifth root in the M3/ of some procaviids suggests that the ancestral form may have possessed a third lobe in the M3/ as in pliohyracids, although this lobe no longer occurs in any of the extant procaviids. In procaviids, the upper molars generally have a small fifth root distally, located between the distal pair of roots. Only in the third molars is the fifth root enlarged, inclined and positioned distally from the second pair of roots. The relationships of the procaviids to other East African Early Miocene hyracoids, such as *Afrohyrax* and *Brachyhyrax* (Whitworth 1954; Pickford 2004) are more distant than they are to Pliohyracidae. *Meroehyrax*, however, is of interest, as recent discoveries in the Early Miocene of Uganda (Pickford 2004) reveal that its upper dentition is morphologically intermediate between that of procaviids on the one hand and *Saghatherium* on the other. Out of all the known Early Miocene hyracoids, *Meroehyrax* is the most likely lineage from which the procaviids evolved.

Comparisons with Middle and Late Miocene Pliohyracidae (Pickford & Fischer 1987) and Procaviidae reveal few similarities between them. *Parapliohyrax* is considerably larger than any procaviid, with the exception of *Gigantohyrax,* and it has extremely hypsodont curved ectolophs in the upper molars. There are also major differences in cranial morphology.

The Aragai (Lukeino) tree hyrax palate is much more complete than the fossil from Nakali (a single lower tooth of doubtful position in a mandible fragment) (Fischer 1986). As such it provides useful data about the Late Miocene members of the Procaviidae, and reveals that by this time they were almost modern in most aspects of the upper dentition and in size. This contrasts strongly with the Eurasian hyracoids of the Late Miocene and Plio-Pleistocene which were all pliohyracids of large to gigantic size; Chinese *Postschizotherium* for example, was about the size of a rhinoceros.

Phylogenetic origins of the Procaviidae

In order to uncover the origins of the procaviids, it is necessary to explore the extinct Early Miocene species *Meroehyrax bateae* (Pickford, 2004). The main features that are of interest in a phylogenetic sense are the development of the styles, ribs and cingula on the buccal side of the upper cheek teeth, which in *H. auricampensis* and *P. pliocenica* are well formed, imparting a strongly undulating buccal surface to the teeth, reminiscent of the genera *Saghatherium* and *Meroehyrax.* In particular, the styles in *Meroehyrax* and *Heterohyrax* are pinched in at their apices and bulbous or swollen near cervix, unlike the styles in other hyracoids such as *Prohyrax, Afrohyrax* and *Brachyhyrax* (Pickford 2004).

Despite the resemblances to *Meroehyrax,* there are major differences between the Early Miocene form and *Heterohyrax* including the absence of a third lobe in the lower m/3 in *Heterohyrax.* There is a distal cingulum in the m/3 of *P. pliocenica* which may represent a trace of this structure, which has completely disappeared or is weakly developed in the extant species *H. brucei* and *P. capensis* but is present in Late Miocene *Dendrohyrax* from Lemudong'o, Kenya (Pickford & Hlusko, in press).

In conclusion, the most likely group from which procaviids evolved is the Saghatheriidae, in particular the genus *Meroehyrax* from the Early Miocene of East Africa, the dentition of which is similar enough to that of procaviids to have given rise to them, principally by loss of the third incisor and canine in the upper and lower toothrows, the loss of the upper second incisor and suppression of third lophids in the m/3.

CONCLUSIONS

This revision of the Late Miocene to Pleistocene hyracoids of East and South Africa, fills in some of the gaps that used to exist between the 10-million-year-old *Heterohyrax auricampensis* from Berg Aukas, Namibia, and *Procavia antiqua* of the Plio-Pleistocene of South Africa. The most crucial fossils for throwing light on procaviid phylogeny are from two localities in Kenya which have yielded the earliest known well-identified fossils of *Dendrohyrax,* and material from Langebaanweg of Early Pliocene age which represents an extremely primitive stage of the *Procavia* lineage, retaining a number of plesiomorphic features similar to those that occur in *Heterohyrax.* The inclusion of *Gigantohyrax* from the Middle Pliocene of Makapansgat, South Africa, to the debate provides additional evidence of the affinities of the various genera of procaviids, showing, as it does, many features close to *Dendrohyrax.* For example, if *Heterohyrax* is considered to be a subgenus of *Dendrohyrax* (Ellerman & Morrison-Scott 1951; Roche 1972), then *Gigantohyrax* would have to be identified as *Dendrohyrax,* since it is much closer morphologically to this genus than *Heterohyrax* is. Given its gigantic size, and the presence of a few morphological characters that distinguish it from *Dendrohyrax,* such as the presence of a sagittal crest in some specimens, I accept its generic distinctiveness, in which case, I am forced to agree with most authors (Allaerts *et al.* 1982; Bothma 1967; Hahn 1934; Skinner &

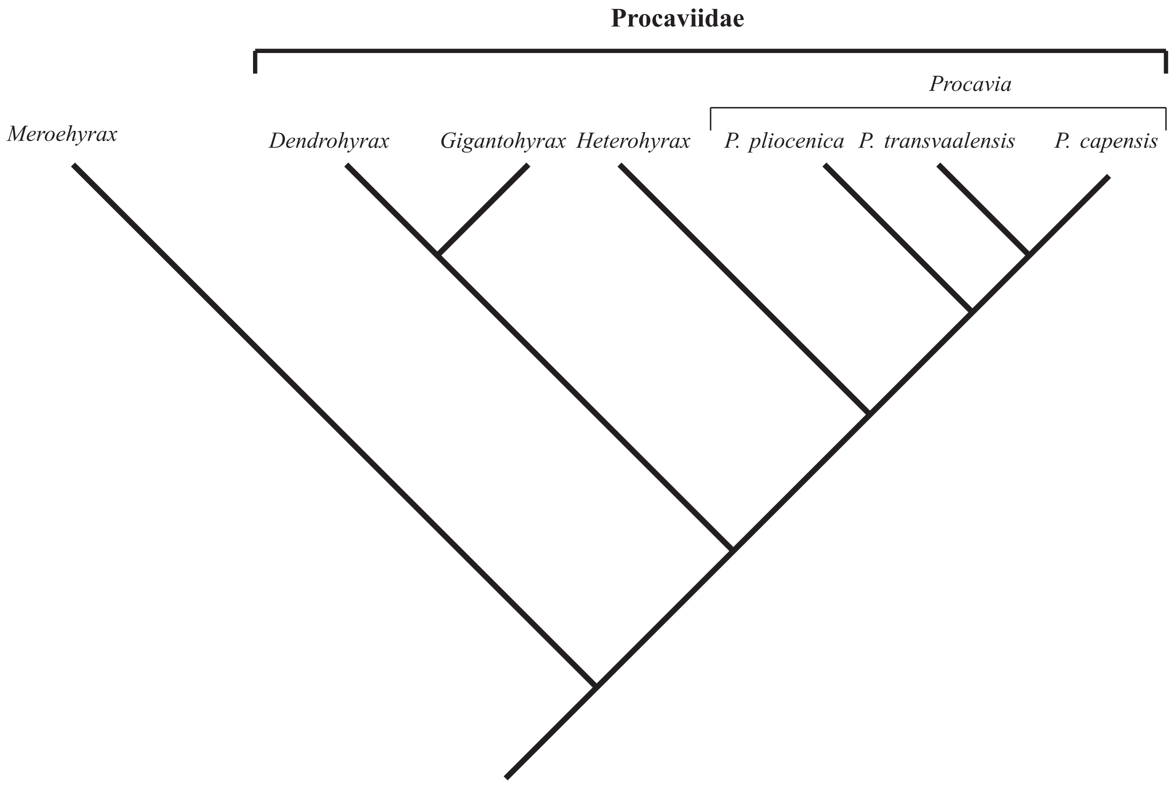

Figure 15. Relationships among Procaviamorpha excluding Pliohyracidae.

Smithers 1990) that *Heterohyrax* is indeed generically distinct from *Dendrohyrax.*

As a result of this study, the relationships between the four known genera of Procaviidae are clearer (Fig. 15). What remains to be determined is the origin of the family Procaviidae. Most recent papers have looked to the Pliohyracidae for the origins of this family (Pickford & Fischer 1987; Pickford *et al.* 1997) despite major differences in cheek tooth morphology. Recent finds, including the discovery of associated upper and lower dental elements of the saghatheriid *Meroehyrax bateae,* from Moroto, Uganda, (Pickford 2004) opens up new possibilities. In several features of the cheek teeth, *Meroehyrax* presages the dental morphology of procaviids. The third lobe in the M3/ and m/3 of *Meroehyrax* is reduced in size. It is absent in the M3/ of procaviids, but in m/3 of *Dendrohyrax* from Lemudong'o, there is a low vertical ridge on the distal surface of the m/3 that could represent the final stages in the disappearance of the third lobe. In *Procavia pliocenica* the distal cingulum rises slightly in the m/3 but does not form a ridge, which could represent an even later stage in its suppression. Very occasionally, extant dassies will grow an m/4 in the mandible, and if so then it is a narrow pillar lodged closely behind the m/3, in a position analogous to the third lobe in *Meroehyrax bateae* (Whitworth, 1954). On the basis of the Moroto fossils, it now seems more likely that the procaviids descended from Saghatheriidae, than from any other family, including the Pliohyracidae (Fig. 15).

I thank Dr R. Smith and his staff at the Palaeontology Division at the South African Museum (Dr M. Avery, Mr K. van Willingh), for access to the fossils. This research was funded by the CNRS (programme ECLIPSE), the Collège de France (Chaire de Paléoanthropologie et de Préhistoire) and the French Ministry of Foreign Affairs (Commission de Fouilles). Particular thanks to Dr F. Thackeray (Transvaal Museum) for additional funds for this research and to Teresa Kearney for access to extant dassie specimens in the Transvaal Museum, and Denise Hammerton for the same at the Iziko South African Museum, Cape Town and Dr M. Raath at the Bernard Price Institute (University of the Witwatersrand). Thanks also to Dr L. Hlusko, for inviting me to examine the fossils tree hyraxes from Lemudong'o. Thanks are also due to Dr D. Hills, Natural History Museum, London, and Mr F. Renoult (Anatomie Comparéé, Muséum National d'Histoire Naturelle, Paris) for access to extant dassies in their care.

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The ownership of the Taung skull and of other fossil hominids and the question of repatriation

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The ownership of fossils, and for purposes of this paper I refer to that of hominid fossils, was long assumed to be vested in the individuals who made the discoveries. The author reviews here a series of case histories with which he has had direct or indirect personal contact, that illustrate claims for ownership. Some have been explicit, some implicit. They are drawn from South Africa, East Africa, North Africa, England, France, Germany, Italy, Russia, the Netherlands, Indonesia and China. This historical essay reviews the replacement of this practice by a policy that fossils are not seen as personal property, but as part of the heritage of the country of origin. During the colonial era, many specimens were removed from former colonies to the 'home countries', where they remained for decades, at least until the subject territories attained their independence from the former imperial powers. The new policy about ownership, in such cases, entails the return (repatriation) of the expatriate fossils to the source country. Examples of success stories and of tardy responses are given. A policy for the future is set forth.

Keywords: national heritage, fossil hominids, repatriation.

AVANT PROPOS

It is a privilege to have been invited to contribute this article in honour of James Kitching. My acquaintance with him goes back to the earliest days of the Bernard Price Institute for Palaeontological Research (and its predecessor) and to the early expeditions organized by the Wits Anatomy Department to Makapansgat from the middle 1940s onwards. Our friendship blossomed from those times and was to last for almost sixty years. With his remarkable powers of observation, indefatigability and dogged perseverance, he went on to make more personal discoveries of fossils than any other person who worked in South Africa, rivalling in this respect even the redoubtable Robert Broom. To the Kitching family thanks for bestowing such a remarkable set of genes as James inherited. Thank you James for your unexampled gifts to palaeontology and for your unique personality.

RAYMOND DART AND TAUNG

Historically, the Taung child skull had provided the world's first striking evidence that the early hominids had evolved in Africa and what manner of creatures our early ancestors were. It was important not only as a beautiful and very well-preserved specimen, but because, historically, it was the recovery of this child skull of what Raymond Dart called *Australopithecus africanus* that effected a revolution in our understanding of human evolution. Its geography was unexpected; its morphology was without precedent; the pattern of early hominid emergence that it compelled on us was totally at variance with what had been expected by the wise ones up to 1924 (the discovery year) and 1925 (the year in which R.A. Dart published the first account of it). If there were doubt that humans had evolved from non-humans beforehand, the features of the Taung skull, as Dart's analysis revealed them to the world, largely dispelled these uncertainties, although it took a number of years for a sceptical community of scholars to accept Dart's claims.

From the beginning Dart, who had achieved instant fame through the Taung find and what he made of it, assumed that he owned the Taung skull. Such visitors as Robert Broom, Ales Hrdlicka, Alfred Sherwood Romer and the Prince of Wales (later and briefly King Edward VIII) enjoyed free access to the Taung skull, usually in Dart's office in the Wits Anatomy Department. For the Prince of Wales, Dart took the skull down to the old Carlton Hotel, Eloff Street, Johannesburg, for the apprisement and delectation of the Prince. Those were the first notable visitors to the Taung child in 1925 and it was in Dart's gift to show it to them.

Not only Dart but his University and the Witwatersrand Council of Education were under the impression that Dart owned the skull. This is confirmed by a passage Dart wrote in his autobiographical *Adventures with the Missing Link*:

> 'Perhaps, like Davidson Black [who had revealed Peking Man to the world], I should have travelled overseas with my specimens to evoke support for my beliefs, and I was presented with this opportunity. The Witwatersrand Council of Education wrote to say they appreciated that, because of the lack of comparative material in the form of anthropoid skulls of corresponding age, it would be impossible for me to perform a satisfactory monographic study of the Taungs [*sic*] skull in South Africa. The Council said they were willing to defray the expenses of my going to England for this study *provided I donated the skull to the university.* After careful thought, I decided I could not be bound by such a conditional undertaking, nor was I prepared to absent myself for so long a time from the young department [of anatomy] and my newly established home.' [emphasis mine]. (Dart with Craig 1959, p. 51.)

With the Council of Education's offer having been refused by Dart, the Taung skull remained to all intents and purposes his personal property. This view persisted from 1925, the year of the announcement of the discovery, to the end of 1958, when Dart relinquished the chair of anatomy to me. At that stage Dart told me that he was handing the custody of the Taung skull to myself. There was no written agreement and, to the best of my recollection, no mention of ownership of the skull. At Dart's behest, I was to be the guardian and keeper of the skull. Thus it has remained. Although the author gladly accepted the responsibility of being custodian of the Taung skull, he has never considered himself to be the owner of the skull. In terms of the policy set out in the Conclusion below, while the fossil is, in the broadest sense, owned by the world – as world treasure, in the narrower and more practical sense, the fossil belongs to South Africa, a viewpoint one has repeatedly stressed over many years. Within South Africa, the direct custodianship of the skull would repose in an appropriately-equipped and expertly staffed Institution, the choice of which – usually a university or a museum – would normally depend on historical factors and the convenience of researchers in the field of palaeo-anthropology. This determination is in keeping with worldwide practice, for example in France, Germany, the United Kingdom, the Czech Republic, Russia, Hungary, Italy, Spain, Indonesia, China, Australia, the Chad, Ethiopia, Kenya, Tanzania, Malawi and South Africa. In terms of these considerations, the Taung skull appropriately reposes in the University of the Witwatersrand, the Florisbad cranium in the National Museum in Bloemfontein, the Swartkrans and Kromdraai hominid fossils in the Northern Flagship Institution (Transvaal Museum), the Makapansgat hominid remains in the University of the Witwatersrand, the Hopefield skull in the Iziko South African Museum). The list is not complete.

In the present context, it should be noted that the term *repatriation* applies to the return of a fossil to the country of origin from another country to which it had been removed. It does not apply to the movement of fossils from one repository to another within the same country (see Conclusions).

It could be argued that Dart's personal claim to ownership rested on his extraction of the skull from the breccia received in his laboratory, and on his remarkable recognition of the unique and hitherto unprecedented complex of traits that pointed to the child's special place in hominid[1] evolution. He had not excavated the specimen from the deposits of the Buxton Limeworks: that had been carried out by a limeworker, M. de Bruyn, while, on the instructions of A.F. Campbell of Johannesburg, the box of specimens had been retained in the site office of the works manager, A.E. Spiers. Other links in the chain of discovery had been forged by E.G. Izod, 'Pat' Izod, Miss Josephine Salmons and Professor Robert Burns Young. On a visit to Taung from the Wits geology department, Young had actually selected the groups of fossils in breccia blocks, including the Taung child skull. Young had arranged for them to be brought to Johannesburg and handed over to Dart on 28 November 1924. With all these interlinking moments, Dart's role was the final and inevitably the most important one (Tobias 1984a).

THOMAS DREYER AND FLORISBAD

Dart's claim of ownership was not unique in those far-off days. When the Florisbad cranium was discovered in 1932 by Professor Thomas F. Dreyer (1935) near Bloemfontein in the Free State Province, the two assistants who helped him in the excavation, A.J.D. Meiring and A.C. Hoffman, were not allowed to come near the Florisbad cranium. According to what Hoffman told me years later when he was Director of the National Museum in Bloemfontein, Dreyer, overcome by emotion, hugged the cranium to his bosom, while sitting on a small elevation close to the excavation site, and threw clods at the two young men when they tried to come nearer to see the fossil! Dreyer's possessiveness and 'ownership' of the cranium were evident from that point. Some twenty two years later, the Annual Conference of the S.A. Association for the Advancement of Science met at the National Museum in Bloemfontein under the presidentship of Hoffman, then Director of the Museum. Dreyer, aged and ill, came from his home to the Museum to show the participants the important Florisbad cranium. That year had earlier been marked by Dreyer's receipt of a doctorate of science *honoris causa* from the Witwatersrand University. This recognition was for Dreyer a high-water mark in his career, for he had long smarted under his perception that the Florisbad cranium had been spurned by Dart's school in Johannesburg and Drennan's in Cape Town. The culmination came with Dreyer's last public showing of the Florisbad skull at the National Museum. Soon after these two signal events, Dreyer died, doubtless a happier man than he had been in the preceding decades of frustration and resentment. To this day Florisbad remains the most important fossil hominid find from the Free State Province.

SERGIO SERGI AND THE ITALIAN NEANDERTALS

Another example of claimed ownership was of the Italian fossils of San Felice Circeo (Monte Circeo) and Saccopastore. These splendid Neandertal skulls reposed in the Institute of Anthropology at the University of Rome under its Director, Professor Sergio Sergi (1878–1972). Sergi told me that during the German occupation of Italy in World War II, he became aware that German officers were seeking fossil treasures for Adolph Hitler and that they wished to obtain these skulls. Some of the following story Sergi himself told me during my visit in the 1960s. Further details were kindly filled in by Professor Giorgio Manzi of Universita di Roma 'La Sapienza', helped by Professor P. Passarello, and Professor A.G. Segre and Mme. Eugenia Segre-Naldini. In the period between July 1943 and June 1944, a German officer called on Sergio Sergi and asked to see these skulls, probably with the aim of sending them to Germany. Sergi told the officer that the specimens were at that time in Messina, Sicily, where his colleague Landogna was making some special studies on the fossils – or so said Sergi. He knew very well that the American forces had already landed in Sicily, so that even if the fossil skulls were down there, access to them by Hitler's agents would have been impossible. In fact Sergi had instructed his technician, Maria Ricca, to take the skulls secretly in an unexceptional shopping basket to a well known church, Santa Maria della Pieta, in Trastevere, Rome, after a clandestine agreement with the clergy of that parish. The place of safe-keeping was below the altar of the church! There they reposed, probably until Rome was liberated by the allied armies in June 1944. At the end of the war, the crania of Saccopastore and San Felice Circeo were safely recovered and restored to the University of Rome.

When S. Sergi retired from the directorship of the Institute of Anthropology, I was told by some Roman colleagues that he was not enamoured of his successor, Venerando Correnti. So Sergi removed the Saccopastore and San

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[1] Hominid' (a member of the Hominidae) has been used almost universally for the family of humankind for the last century. Molecular data have shown that apes are genetically so close to living humans that it would be inappropriate for them to be classified as a separate family. Hence, for many evolutionists apes are also hominids. To distinguish those hominids that are most closely related to humans, many palaeo-anthropologists, especially English-speakers, have adopted the tribe 'Hominini' (conventionally shortened to hominin) within Hominidae. However, numerous authorities continue to use 'hominids' in the old sense, a usage that is followed here. There is as yet no consensus.

Felice Circeo skulls to his private apartment in the city. In order to see the skulls, I had to seek an invitation to visit Sergi's apartment. The wizened octogenarian received me warmly when I arrived by appointment one morning. He had been studying hairs. To measure the diameter of a single hair, he had devised an apparatus (a 'trichonophore') to hold an individual hair. With another piece of equipment he had invented, a 'microtrichonometer', he proceeded to measure the diameters of hairs held by his trichonophore. Another part of the extraordinary study was microtrichonoscopy! When I arrived for what I presumed would be a visit of at most a few hours (I had booked a city tour for the afternoon), Sergi started demonstrating these instruments to me, explaining how they worked and what he did with his results. It was a little heavy going. My mastery of Italian was limited and Sergi had almost no English. So he spoke to me in a kind of pidjin, comprising Italian, German, French, some English – and the remainder in what I took to be pure Latin. I quietly dubbed the composite language 'Sergi-ese'; yet I managed to follow a large part of what he was saying to me. The hours were passing – my city tour ticket was still in my pocket, a little hot and crumpled. I had not yet fulfilled the main purpose of my visit, to familiarize myself with the Italian fossil skulls. Then his daughter, also an anthropologist, whom it is said he had left 'as his eyes and ears' in Correnti's Institute of Anthropology, came in and announced that lunch was ready. This was the last thing I had expected. There followed a simple but delicious repast with Italian red wine. After that my powers of concentration, which had held up in fair to middling style throughout the morning, waned embarrassingly. Another hour or two of microtrichonology ensued (thank goodness, Sergi who knew how to measure any one of my eyelashes, did not notice my drooping eyelids!). In the late afternoon, he was reminded that I wished to see those fossils. Into the bedroom we went, where they were kept in hat-boxes under the bed with one on top of the wardrobe. In a rather soporific state I examined these specimens. Sergi's rapid, soft, high-pitched pitter-patter of conversation accompanied this exercise also. By the time I took my leave at about six in the evening, I was feeling quite punch-drunk. It had been a memorable and unrepeatable experience. My unused city tour ticket was discarded.

Those fossil skulls were most assuredly Sergi's personal property (he believed); after all, had he not saved them from the looting of the German officers – and, for that matter, from the clutches of Correnti? On my visit to Correnti in the Institute, the poor plundered professor, whom I found a very pleasant person, insisted on telling me how he was saddled with the first name, Venerando ('Venerable!'). His grandfather had been a deeply pious man. He insisted that his grandson be given this name under pain of disinheritance. A little archly, Correnti said, 'What could my parents do?'

RALPH VON KOENIGSWALD AND 'JAVA MAN'

A fourth example of a palaeo-anthropologist who firmly believed he owned the fossils for which he was responsible was Gustav Heinrich Ralph von Koenigswald, known to his family and friends simply as 'Ralph'. He had been responsible for discovering and recovering a number of fossils of 'Java Man' along the Solo River, at the boundary between the middle and eastern thirds of Java, in what was then the Dutch East Indies, later Indonesia. Koenigswald later became a good friend of mine, from his first visit to South Africa in the early 1950s soon after my appointment as a young lecturer in Dart's department. He had been born in Berlin in 1902 of Danish-German parentage. When he was only fourteen years of age, he and a friend made a first visit to Mauer near Heidelberg. Only 10 years earlier, in 1907, a fossilized hominid mandible had been recovered from the Grafenrain Quarry at the village of Mauer on the Elzenz River. In a letter to me, many years later, Koenigswald mentioned this visit: 'I did not find a new Heidelberg Man, but a kind workman presented me with a molar of a rhinoceros, the first specimen of my vertebrate collection.' Koenigswald accepted that he owned the rhinoceros tooth and all of the other specimens that were to come later.

Not long afterwards, Koenigswald visited Steinheim an der Murr near Ludwigsburg, 32 km north of Stuttgart in Wurttemberg. It was 15 or 16 years before Karl Sigrist jun. discovered the strange and interesting *Homo* cranium of Steinheim in his father's sand and gravel pit in 1933. On that early visit, Koenigswald recalled in a letter, 'the only mandible of a wolf ever found there I discovered, but left it to old Berckhemer, whom I have known since my school days.' It was Fritz Berckhemer, geologist and palaeontologist of the Wurttemberg Natural History Museum in Stuttgart, who was later to excavate the famous Steinheim human cranium and to publish the first brief record of it in 1933. In both these instances, testified to by Koenigswald's correspondence with me, it is clear that from a tender age he held without question to the maxim, 'finders keepers' much loved of schoolboys in my own youth. It was 'my vertebrate collection' and 'I left it to old Berckhemer'.

The most crucial chapter in Koenigswald's career began in 1930. Here is the story in Koenigswald's simple and unadorned prose:

> 'In the autumn of 1930 my old teacher, Professor F. Broili, [at the University of Munich] received an enquiry from Holland: would one of his students be willing to go to Java as a palaeontologist for the Geological Survey? He asked me; I jumped at the chance; and in January 1931 I landed at Tanjung Priok, the port of Jakarta.' (1956, page 23)

From 1931 to 1941 Koenigswald made some of the most important discoveries of *Homo erectus* specimens ever encountered and contributed appreciably to an understanding of their place in time and in hominid systematics and evolution. The details of these admirable fossils need not concern us here. On two of the Javanese specimens, the Trinil calvaria that Eugene Dubois had recovered in 1891 and the Kedung Brubus mandible of 1890, I had made re-studies that were published in 1966, 1967 and 1971. Here I should like to dwell on the fate of the Javanese fossil hominids.

In December 1941, Japan entered World War II. Within days, the famous original fossils of 'Peking Man' had disappeared, while work in Java had come to a standstill.

A last-minute American offer to move the original Javanese hominids to the United States was not accepted; in any event Koenigswald himself did not learn of the offer until after the war. Instead he took extraordinary measures to ensure that 'his' fossils were secreted and protected. Shortly before the Japanese forces occupied Java, plaster casts were substituted for some of the original hominid fossils. In Koenigswald's words,

> 'The casts were extremely well made and to lay eyes almost indistinguishable from the originals. We had mixed finely ground brick dust with the plaster of Paris, so that even in the event of injury the break would remain nicely dark, as in a genuine fossil. We switched the skulls, so that if the contents of the safe should one day vanish eastwards a few original pieces, at least, would remain in the country.'

When the Japanese overran Java, Koenigswald was taken captive and he spent many months in a prisoner-of-war camp. However, his wife, Luitgarde von Koenigswald, whom he had married at Bandung in 1935, managed with the help of Javanese friends to stay out of the prison camp. The new Javanese fossil finds, some of which had not yet been described, were saved by her. In this operation, she was helped by neutral friends, namely two Swiss geologists from the Shell Company, Doctors Mohler and Rothpletz, and a Swedish journalist, Rulf Blomberg. The specimen that Koenigswald regarded as his most important discovery, namely the maxilla of Sangiran IV with its large palate and diastema (or space between the canine and first premolar), Mrs. von Koenigswald kept in her pocket throughout the Japanese occupation. Other specimens were concealed by Koenigwald's friends, the villagers and the neutrals. On one occasion, the Swedish friend, fearing a house search, put the entire collection of isolated teeth which he was safeguarding, including those of *H. erectus* and *Gigantopithecus,* into large empty milk bottles which he buried in his garden by night!

Because of Koenigswald's foresight, all of the Javanese hominid fossils survived the war. It was a remarkable legacy to posterity and to the post-war flowering of science. His achievement stands in marked contrast to the tragic loss of the Peking Man remains. At the end of hostilities, a weakened Koenigswald was released and he was re-united with his family, Luitgarde, daughter Annamaria-Felicitas and all of 'his specimens', save for one of the Solo skulls from Ngandong. Later, the missing Solo cranium was found by an American officer, Walter Fairservis, in the Imperial Household Museum of the Japanese Emperor. The skull was repatriated to its fellows in Koenigswald's hands. Franz Weidenreich had escaped from the Japanese occupying forces in China and got safely to New York. Following a letter Koenigswald sent to Weidenreich, the latter arranged with the Rockefeller Foundation and the Viking Fund (forerunner of the Wenner-Gren Foundation for Anthropological Research) to bring the Koenigswalds' live and fossil families to America. Koenigswald had no compunction about packing the Javanese fossils and carrying them to the U.S.A. with him. Earlier, he had had no scruple about taking the Javanese fossils to Peking (now Beijing) at Weidenreich's invitation, to make, with the latter, direct comparisons between the *H. erectus* fossils of Java and those of China. The Javanese fossils were in his perception his own: he had led the team that dug many of them up and he had saved them from wartime pillaging.

Since this passage was written, one of the reviewers of this article has kindly drawn my attention to a document in Bandung, which purports to show that Koenigswald 'applied for and obtained formal permission to borrow the Indonesian fossils when he took them from Indonesia'. The reviewer does not indicate whether the Bandung document covers all of the Javan hominid fossils, or only those which had not yet been published; nor whether a time factor was attached; and it is not clear if this document covered the temporary removal of some of the Javan hominid fossils to Beijing, China, during Koenigswald's visit before the war, or the long-term removal with his departure for America after the end of the war. In any event, it is manifest from Koenigswald's subsequent actions that he considered the arrangement as far more than a 'loan', nor did he refer to such formal permission in his partly autobiographical *Meeting Prehistoric Man* (1956).

As a result, when the Rijksuniversiteit of Utrecht in the Netherlands created a new chair of stratigraphy and palaeontology especially for Koenigswald, off he went with his itinerant fossils for a twenty-years' sojourn in Utrecht.

During these twenty years, most highly productive ones from Koenigswald's point of view, he brought the Javanese fossils across to Cambridge in 1964, where, as a visiting professor, I had the originals of the Leakeys' Tanzanian fossils. There followed an 'Afro-Asian Conference – with a difference'! (Tobias & Koenigswald 1964). Once more, Koenigswald felt free to pack 'his' fossils, with his socks and pyjamas, and trundle them across the seas.

At Utrecht, Koenigswald dreamed of establishing a great international centre for the cherishing and safeguarding of 'his' Javanese hominid fossils and for the study of human evolution. His plans were not to be realized in the Netherlands.

Instead, in Germany, the Werner-Reimers Foundation provided the facilities he needed at the Senckenberg Research Institute and Natural History Museum of Frankfurt. Once again, Koenigswald packed his bags, his fossils and his personal library, and without a 'by your leave', or apparently any consultation with the Netherlands authorities, carried them off to Frankfurt, Germany. He still considered them his personal property. There was anger in the Netherlands when they learned that the birds had flown. In this case, they felt strongly: after all the fossils had been discovered in Java when it was still a part of the Dutch East Indies; Koenigswald had been given a position in the Geological Survey and several years later Dutch nationality; the University of Utrecht had created a new chair especially for him. The least the Dutch authorities might have expected was that the fossils from their former colony would remain in the Netherlands 'motherland'!

Koenigswald spent the last fourteen years of his life with his beloved fossils in the Senckenberg. He retained warm and close links with the Indonesian investigators, Teuku Jacob, Sastrohamidjojo Sartono and Pieter Marks. Jacob received his Ph.D. degree at Utrecht and Koenigswald gave the Indonesian scholars much help and encouragement, when they visited him at his Institute in the Senckenberg. The relationship culminated in Koenigswald's last visit to Java in 1976 to receive the honorary doctorate of science of the Gadjah Mada University of Yogyakarta. It was the first honorary degree to have been awarded by that University to a European.

On one of my visits to Indonesia after Koenigswald's death in 1982, my good friend in Yogyakarta, Teuku Jacob, told me that Koenigswald had returned to him the fossil cranium of Mojokerto, a child calvaria from Perning in Java. Jacob had taken it back to Yogyakarta after the Nobel Symposium in Karlskoga in 1978. It was black and almost as round as a large cricket ball, but the face, jaws and teeth were not present. There was a small deficiency of bone in the region of bregma (the point or area where the frontal bone and the two parietal bones approximate one another). Previous workers had taken this gap to be an unclosed anterior fontanelle, and they inferred from this that the Mojokerto individual represented a baby or young child. I had carefully examined the area in question, both in Utrecht and at the Senckenberg, with magnification. It was clear to me that a piece of bone had been broken away in that area, and that the gap was not the unmistakable anterior fontanelle. I re-examined the black 'cricket ball' in Jacob's hands in Yogyakarta. Then he appealed to me: could he be sure that this was the actual fossil specimen? Mindful of the cunningly devised casts that Koenigswald had prepared in Java as the Japanese were getting nearer, Jacob asked: could this not be one of those casts in which brick dust had been mixed with plaster of Paris? I examined it, especially in the region of bregma, and I tested the weight in my hand. I could detect nothing that would disqualify it from being the original. To satisfy Jacob's doubts, the only manner by which it could be proven one way or the other, short of sectioning the specimen which nobody's conscience would allow, was to scan it, that is, to make a CT-scan (Computerized Tomographic Scan) of the specimen. This is a non-invasive method and would leave the specimen intact. I left Teuku Jacob with that suggestion, although at that time neither he nor I knew of the appropriate apparatus anywhere in Indonesia. Japan and Australia might prove to be the nearest countries where this sort of study could be done. There, for the moment, the matter rested.

In reply to my letter of 30 July 2004, seeking more information on this, Teuku Jacob wrote on 26 August 2004. He confirmed that the Mojokerto cast had been cleverly made 'with the same colour and weight as the original'. Then he added that the skull he had doubted before was the original as he had proved by scanning in Jakarta, Paris, Toulouse and Tokyo. The semicircular canals of the inner ear could clearly be seen and, when the black colour in the foramen magnum was scratched away, the natural pumice filling the brain-case was clearly revealed.

When on 20 November 1983 I delivered the memorial address in honour of Koenigswald, at a commemorative function in the Senckenberg Museum, Frankfurt, I ended with these words:

> 'His ever present sense of humour, the naughty twinkle of his eyes, the little chuckle, that over-obvious wink when he made a piquant and sometimes unquotable point about one of his colleagues, his gifts as a raconteur and his seemingly inexhaustible fund of anecdotes, the breadth of his knowledge about eastern lore, the passion of his quest for ancient remains, his probing and punctilious observations, his manifestly endomorphic love of life, his enthusiastic enjoyment of the company of his fellow scientists and of their wives – all add up to a celebrated man, an eminent scientist, a loyal friend, an unparagoned personality, companion of the heart.' (Tobias 1984b, pp. 89–90)

I wondered at the time whether I should have added to the formidable list of attributes – 'staunchest upholder of the private ownership of fossils'. I am glad I left it out because of what I have recently learnt from Teuku Jacob (see below).

FRANZ WEIDENREICH AND 'PEKING MAN'

An interesting contrast may be cited. Weidenreich departed from China several months before the Japanese occupation of Beijing late in 1941 and with his wife went to live and work in New York. He was able to take with him *casts of Peking Man* and of most of the important later Javanese finds, of which he had obtained casts from Koenigswald, during their exchange of visits in 1937 and 1939. Sadly, from one point of view, Weidenreich left the originals of Peking Man behind in China. In contrast, Koenigswald took the *originals of Java Man* with him to America. Those Peking Man fossils disappeared not long afterwards and have never been seen again. The Java Man fossils, which Koenigswald guarded as if they were his own children, survived – although it must be admitted that they are probably the most well-travelled fossils ever! Circumstances did not permit the Peking Man fossils to be removed when it was still tolerably safe to do so. Koenigswald created his own circumstances! These two pieces of historical happenstance should not, of course, be taken by inference as support for the private ownership of fossils.

Other instances are known to me, but I have included here only some with which I had contact.

THE ATTITUDE TOWARDS OWNERSHIP TODAY

It is universally acknowledged that all fossil hominid specimens that are found today belong to, and belong in, the country in which they are found. The array of fossils from northern Kenya, which emanated from the east and west of Lake Turkana, and those from the area of the Tugen Hills just to the south, are the property, the national heritage of Kenya. The Olduvai, Laetoli and Peninj fossils from northern Tanzania are unequivocally Tanzanian treasure. The fossil hominids of Bahr-el-Ghazal and Toros-Menalla in the Chad Republic belong to the Chad. The change came about with the attainment from the 1960s onwards of *uhuru,* independence, decolonization. Earlier, fossils discovered in British, French, German, colonies and protectorates, were automatically taken to the 'home country'. Kenyan fossils discovered before *uhuru* went to the Natural History Museum in London. The same was true of fossils like the Kabwe or Broken Hill remains from Zambia (recovered when that territory was still Northern Rhodesia) and the Singa cranium from the

Sudan. From Algeria, the hominid fossils of Ternifine, and from Morocco, those of Casablanca, Jebel Irgoud and other sites, were taken to Paris where they reposed in either the Museé de l'Homme, the Muséum National d'Histoire Naturelle or the Institut de Paléontologie Humaine. There were similar examples from Eyasi in Tanganyika (before World War II), which were taken to Germany; and from Palestine/Israel from which fossils were taken to London, Paris and the Peabody Museum, Harvard University.

It might be thought of as a delicate and sensitive issue what should happen to the fossil remains which were removed from the far-flung corners of empires, to various 'homelands' (which of course were not really homelands at all, when looked at from the angle of the fossil human populations!). It is accepted today by almost all countries and by UNESCO that such specimens are part of the legacy of their respective territories of origin. The question should therefore be asked: is there any valid reason why this principle should not apply to parts of the heritage discovered when political circumstances were different, for example, before independence? To be consistent, the principle should surely apply retrospectively.

From a purely practical point of view, there are considerable difficulties when a collection of specimens reposes partly in the land of the find and partly in some other country. For example, a scholar who wished to study the Mount Carmel *Homo* fossils from the Tabūn and Skhūl caves would have to travel from the Natural History Museum in London, to the Peabody Museum of Harvard University, Cambridge, Massachusetts, to the Rockefeller Museum in Jerusalem. Then, if casts of these fossils were desired, some were officially obtainable from the University Museum, University of Pennsylvania, Philadelphia.

Next to that wide scattering of the Mount Carmel fossils, the division of the Sterkfontein hominid fossils into some six hundred specimens in the School of Anatomical Sciences at the University of the Witwatersrand Medical School, Johannesburg, and one or two hundred specimens in the Transvaal Museum of the Northern Flagship Institution, in Pretoria, is relatively inconsiderable: the two institutions are about fifty kilometres apart. That division of the collection founded on historical factors is inconvenient but not a serious hardship for the earnest scholar. Moreover, casts of excellent quality can be obtained from both host institutions.

REPATRIATION OF HOMINID FOSSILS

Should there be wholesale repatriation of hominid fossils from their places of enforced exile to their cradlelands? On grounds of principle, there is no doubt that this would be the most ethical solution, other things being equal. However, one must ask: are other things equal? Where we are contemplating the future of objects of such rarity and of such historical and archival world value, we have to ask whether conditions in the source-land are such as to provide adequate protection, security, curatorial skills and custodianship. In some countries, such facilities may not be available. This lack would demand help from a body like UNESCO[2], for the construction of suitable vaults, the provision and training of curators, and the development of a culture of cherishing, appreciating, admiring and valuing the objects in question. UNESCO already has such programmes under way in several parts of the world.

REPATRIATIONS TO ASIA

Java, Indonesia

The return by Ralph von Koenigswald of the 'black cricket ball', the calvaria of the Mojokerto child, to Teuku Jacob of Gadjah Mada University at Yogyakarta, has already been mentioned.

In a recent letter received from Indonesia's most eminent palaeo-anthropologist, Professor Teuku Jacob, more light has been thrown on repatriations to Indonesia. When Teuku Jacob was hospitalized for a few days in Utrecht in 1967, Koenigswald promised him that he would return the collection to Java. In an interview in the *Frankfurter Algemeine Zeitung* in 1974, Koenigswald indicated that he would return the collection to Indonesia. A year later Teuku carried the Ngandong skulls back to Java. In 1997, he had picked up the Sambungmachan skull 3 which he wrote had been 'smuggled away to New York'. Another *Homo erectus* skull had been spirited away from Indonesia and allegedly offered for sale by an antique dealer in Switzerland! Sambungmachan 4, Jacob wrote, was back in Java – in Bandung. All told, according to Teuku Jacob, around two-thirds of the Indonesian *H. erectus* were now in Yogyakarta, Java. Other pre-war Indonesian hominid fossils were still in Leiden and Frankfurt. It is very largely owing to the persistent efforts of Teuku Jacob and the understanding and co-operative attitude of the late Ralph von Koenigswald that this satisfactory outcome has been achieved.

China

It is not part of the theme of this article to discuss the lamentable loss of the 'Peking Man' fossils, that had been discovered at Zhoukoudian near Beijing (formerly Peking). They were casualties of the Sino-Japanese theatre of World War II and their disappearance has never been adequately explained. Despite strenuous efforts by Chinese and U.S.A. colleagues, the missing collection of *Homo erectus pekinensis* fossils has never come to light during the lapse of sixty years. Happily, palaeo -anthropologists at the IVPP (Institute for Vertebrate Palaeontology and Palaeo-anthropology) in Beijing have subsequently made a number of important discoveries of *H. erectus* and other hominids in China.

Another small repatriation is worth mentioning. To the University of Uppsala in Sweden several teeth of 'Peking Man' from Zhoukoudian, Locus A., had found their way in the 1920s. Otto Zdansky in 1923 sent to Uppsala a lower premolar and an upper molar; while Birger Bohlin produced in 1927 a lower molar. In 1978, during the course of a meeting in Sweden, I was delighted to find that the teeth had survived and were still present in Uppsala, and in addition that Birger Bohlin was alive as a professor emeritus of the Institute of Geology at the University of Uppsala. The meeting itself was historical: it took the form

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[2] United Nations Educational, Scientific and Cultural Organisation.

of a Nobel Symposium organized by the Royal Swedish Academy of Sciences, from 21–27 May 1978, and it commemorated the 200th anniversary of the death of Carolus Linnaeus. Carl von Linné, to use the unlatinized version of his name, was the great classifier extraordinaire of living things. Linné braved the wrath of his fellow mortals and claimed that whatever rules were found to apply to other animals should be assumed to apply as well to man. More than a hundred years later, Charles Darwin in *The Origin of Species* did not do as much: in that voluminous book, mankind earned only one small hesitant sentence *on the last page of the book.* In a sense, Linné brought humans down from the angels to join the apes. It was eminently worthwhile that the Academy had brought a goodly selection of scholars together. We met in Karlskoga in Alfred Nobel's house, where the King and Queen of Sweden joined us for one of the sessions of the symposium and for lunch. It was on this occasion that King Carl Gustav conferred on Mary Leakey the Linnean Gold Medal. She was the first female recipient. During a visit to Uppsala, we met old Professor Birge Bohlin and were shown by him those Chinese teeth that had been excavated over half a century earlier. He gave a talk in the form of a postscript to the excavation at Zhoukoudian in 1927 and 1928. During an informal get-together of the symposiasts, in the presence of Bohlin, the organizer, Lars-König Königsson, and Carl Gustav Bernhard, the Secretary-General of the Royal Swedish Academy of Sciences, Richard Leakey used the occasion to challenge the Swedes to return those Zhoukoudian teeth to the Institute of Vertebrate Palaeontology and Palaeo-anthropology (IVPP) in Beijing, China. I was in full agreement with the sentiment, although the way in which it was sprung on the Swedish hosts on such a Linnaean bicentenary occasion was inappropriate. In the event, the teeth were duly returned to China. This was not a case of specimens having been taken away before independence, but the removal of the fossils went back to a period when foreigners had had very few scruples about what they did with specimens from far-off cradle-lands.

THE SITUATION IN AFRICA

South Africa

As one of the self-governing dominions of the British Commonwealth, South Africa was in the fortunate position that its early fossil hominids were not removed to England. This was true of the early finds of the first two decades of the Union of South Africa, such as the calvaria of Boskop and the skull of Taung, and of all the later discoveries. Soon after I took over the custodianship of the Taung, Makapansgat and post-1965 Sterkfontein hominid fossils, I was approached by a representative of a distinguished US university who offered to buy one australopithecine tooth for a considerable sum of money! I was aware that Robert Broom had sold a number of Karoo fossils of reptiles to colleagues in the U.S.A, but I was deeply conscious of the value of fossil hominids to South Africa and strong ethical considerations loomed large in my thinking. I had not a moment's hesitation in rejecting the American offer!

A great number of archaeological and physical anthropological specimens had been removed from South Africa, especially to Europe, in the nineteenth century, but these examples of the plunder of recent human skeletons and cultural objects fall outside the scope of this study.

Like South Africa, Australia fell under the commonwealth dispensation. Hence fossil human skulls recovered there have remained in the country.

East Africa

Sudan – A cranium from Singa on the Blue Nile was early removed to the Natural History Museum in London. It was studied there by Arthur Smith Woodward in 1938, by Lawrence H. Wells in 1951 and by me in 1955 (Tobias, 1962). In 1963, Don Brothwell was making a detailed re-study of the Singa skull. Both he and I agreed that the cranium should be regarded as neandertaloid and not as 'Bushmanoid' as Woodward and Wells had concluded. To the best of my knowledge, the cranium still reposes in the Natural History Museum.

Kenya – a number of the earlier discoveries of Upper Pleistocene *Homo* specimens from Kenya still reposed in the Natural History Museum, London, when I last enquired. These included remains from Kanam and Kanjera, but not those found since the end of World War II, such as the Koobi Fora, West Turkana and Tugen Hills fossils.

In Nairobi, Richard Leakey caused a fine facility to be built with generous support from the Royal Swedish Academy of Science and other international sources. In this were housed all of the fossil hominids from Kenya that had been recovered after *uhuru.* It was initially given the name TILLMIAP, The International Louis Leakey Memorial Institute for African Prehistory. At the opening ceremony, a fine statue of Louis Leakey standing at the entrance of TILLMIAP was unveiled. This was an example of a former colony which had risen admirably to the need for the bones of its earliest citizens to be housed in ideal conditions.

Tanzania – Two or three fossil partial crania were recovered by Kohl-Larsen from Lake Eyasi in northern Tanganyika (as it then was). When I studied these specimens, Eyasi II was represented by an occipital bone in the National Museum, Dar-es-Salaam. Its marked occipital torus was reminiscent of those of Kabwe, Zambia, and Hopefield, Western Cape Province. Eyasi I was still in Germany to where Kohl-Larsen had relocated it. Clearly these Eyasi remains should be re-united in Tanzania, if this has not already been done.

There is an interesting example of a successful local repatriation, where the fossil concerned was an 'expatriate' for a relatively short period. When Mary Leakey discovered the magnificent cranium of *Australopithecus boisei* (called originally by her husband Louis Leakey *Zinjanthropus boisei,* and nicknamed variously 'Zinj', 'Dear Boy' and 'Nutcracker Man' based on proposals respectively by Louis, Mary and myself), it was removed from Tanzania to the Leakeys' base at the National Museum in Nairobi, Kenya. I worked on it there and also in the Witwatersrand anatomy department for some years. When I had completed my major study (Tobias 1967a), but when the finalizing of my manuscript, reading of proofs and so on, were not yet finished, Louis Leakey arranged for 'Zinj' to be returned to the newly independent and re-named Tanzania. From the scientific academies of Beijing, Moscow, Paris, London and Washington, leading figures in palaeontology came to Dar-es-Salaam for the handing-over ceremony. I was invited to be present – although it was stipulated that I attend not as a representative of any organization or country, but as the person who had worked on the fossil for some five years! Here is the point: a special depository was constructed in the National Museum (formerly the George V Museum) in Dar-es-Salaam. This was made exceptionally secure, fire proof, with temperature- and humidity-control. It was a model of how the world's most precious fossils should be housed. President Julius Nyerere, known to his nation as 'Mwalimu' or teacher, took a personal interest in the preparation of the repository and played an active part in the ceremony that took place in the grounds of the Museum. Here was a National Museum that was convinced of the need to erect suitable facilities and, when funds were forthcoming, they did just that.

North Africa

Fossil hominids were originally removed from Algeria and Morocco to France. The most important specimens were: from Algeria – mandibles, teeth and a parietal bone from Ternifine; from Morocco – specimens from Témara, Sidi Abderrahman, Rabat, Jebel Ighoud and Tangier (Mugharet-el-Aliya).

From the Haua Fteah cave in Cyrenaica, Charles McBurney and a team from Cambridge University recovered two mandibles in a Levalloiso-Mousterian horizon. These were studied by J.C. Trevor and L.H. Wells (1953) and in greater detail by Tobias (1967b). When last seen the two jaws were in the Natural History Museum, London.

From the cave of Porc-Epic near Dire-Dawa in Ethiopia, a mandibular fragment was recovered. Its repository was last reported to be the Institut de Paléontologie Humaine, Paris.

Chad Republic – the cranium of Yayo (Koro Toro), discovered by Mme Francoise Coppens, was for many years in Paris where the author examined it jointly with Yves Coppens. Its latest repository was the Museum National d'Histoire Naturelle, Paris. The more recent Chadian finds from Bahr-el-Ghazal and Toros-Menalla were recovered by a joint Franco-Chadian expedition led by Michel Brunet of Poitiers, France. These specimens, like the post-independence discoveries in Kenya and Tanzania, are housed in the Chad.

Central Africa

The finest fossil hominid specimen to emerge, until today, from Zambia was the outstandingly complete cranium of what used to be called 'Rhodesian Man' or Broken Hill Man and after independence came to be known as Kabwe Man, Kabwe being the African name for Broken Hill. This specimen was recovered by a miner, T. Zwigelaar, in 1921, long before independence. From colonial Northern Rhodesia, the cranium went to the Natural History Museum in London. There, when I last looked, it still resided. Word reached me that the Zambian Government had asked the British Museum to repatriate the skull to Zambia. This was apparently declined by the British authorities, for one or other of several reasons one has heard. One does not know if the refusal was because Zambia, as such, did not exist when the cranium was recovered in 1921; for fear that facilities for storage and curating of the skull might not be at par in Zambia; or for the concern that, if this specimen were repatriated, it might prove to be the thin end of the wedge leading to a flood of other requests. This is one of the cases known to me where an official, formal request for repatriation of a fossil hominid specimen has been made to a former colonial power by the fossil's source land.

LOSS DURING REPATRIATION

This is the sad tale of 'Egbert' the neandertal youth from Ksâr 'Akil in the Lebanon. Father Franklin Ewing S.J. had excavated in the cave deposit of Ksâr 'Akil near Beirut in the Lebanon in 1938, and with his colleague J.G. Doherty, had recovered human remains, said to have been 'neandertaloid' in character. The best preserved was the partial skeleton of a child of about eight years old, to which Ewing gave the nickname 'Egbert' because (he told me) of the state of preservation of its cranium – 'like a broken eggshell!' Some other human remains were recovered. Egbert was for the time being in Fordham Catholic University in The Bronx, New York City, where I visited Ewing and 'Egbert' in 1956. Father Ewing allowed me to handle and examine it. It included a good mandible and I was able to obtain a cast of the cranium and mandible of the best specimen. I compared the Ksâr 'Akil jaw with the juvenile jaw that McBurney had invited me to examine, from Haua Fteah in Cyrenaica, a little further around the Mediterranean littoral. There were strong resemblances between the two mandibles and I included photographs of both in my description of the Haua Fteah remains, published as an appendix in Charles McBurney's *The Haua Fteah (Cyrenaica) and the Stone Age of the South-East Mediterranean* (1967). In 1956 I took photographs of Ewing holding Egbert on the steps at the entrance to Fordham University. After Ewing's death, these remains were intended to be repatriated to Beirut. They were sent from Fordham to the Society of Jesus' headquarters in Austria, with a view to their being returned to the museum in Lebanon. The fossil bones have never been seen again, despite fairly rigorous enquiries made by Nancy Minugh-Purvis of Philadelphia and myself as a Visiting Professor at the University of Pennsylvania in the 1990s. So my 1956 photographs of Father Ewing and Egbert may be the last photographs taken of the skull.

LE MOUSTIER AND COMBE CAPELLE SKELETONS, PROBLEMATICAL EUROPEAN REPATRIATIONS

The skeleton of the Le Moustier Neandertal youth was brought to light in August 1908 in the Dordogne district in the south of France. The tools from this cave gave the name Mousterian to the associated archaeological industry

(Klaatsch & Hauser 1909). It seems clear that the skeleton was moved to Germany without the enthusiastic acquiescence of the French archaeologists. In *Fossil Man,* the 1923 English translation of the classical French work, *Les Hommes Fossiles,* by Marcellin Boule, a rather scathing account is given of the exhumation and removal of the Le Moustier skeleton. Essentially the same account is repeated in the 1957 English edition by Boule and Vallois:

> 'In January 1909, a dealer in antiquities, of Swiss nationality, who had only too long exploited, for German profit, the deposits in the Dordogne district, that is to say, the most ancient and the most valuable archives in France, revealed the circumstances under which he had discovered and exhumed a human skeleton at Le Moustier.

The exhumation [by the Swiss dealer, O. Hauser] took place on 10 August 1908, in the presence of a tribunal of scientists from beyond the Rhine – Klaatsch, H. Virchow, von den Steinen, Hahne, Wüst, and others (and, of course, in the absence of any French scientist). Even so the scientific value of this relic is markedly diminished by the poverty of significant stratigraphical or palaeontological data, and especially by the deplorable manner in which it was extricated and restored. The reconstruction of the skull by Klaatsch, a professor of anatomy, is a positive caricature. A second reconstruction, in which several of Klaatsch's distinguished colleagues were called upon to assist, has at least the merit of being more faithful. The monetary value of the skeleton from Le Moustier was, on the other hand, considered beyond compare by the 'Museum für Völkerkunde' in Berlin, which paid Hauser, the dealer, the fabulous price of 125,000 [gold] francs!'

In fairness to Hauser, however, when he brought the first limb-bones to light, he suspended operations for four months and entrusted the excavation of the bones to Hermann Klaatsch (1923).

A year later, Hauser recovered another skeleton, ornamented with sea-shells, in a bed at Combe Capelle in the Dordogne, France. This, too, was acquired by the Berlin Museum, Hauser once again acting as an agent. Combe Capelle was considered to represent 'a variety of the Cro-Magnon Race' (Boule & Vallois, 1957).

Then, for some thirty-five years, the two historical skeletons reposed in the State Museum in Berlin where they were rated as 'two of the most important anthropological artefacts of the Museum für Vor- und Frühgeschichte' (Hoffman & Wegner, 2002). During the Second World War, the bombing of Berlin on 3 February 1945 resulted in the Museum being hit and, in the ensuing fire, the Le Moustier postcranial remains, among others, were severely damaged and partly destroyed. As a young student I grew up with the teaching that the Le Moustier skull had been lost, a casualty of the war. In 1957, Boule and Vallois wrote – not entirely accurately – that the Le Moustier skeleton 'was completely destroyed during the last war' (page 205, footnote 22). In fact, the Le Moustier skull had been taken to the Soviet Union in 1945. Subsequently, the 'lost' skull was located in Moscow, whence it was returned, along with the necklace of Combe Capelle and art objects, to the German Democratic Republic in 1958. For seven more years, the Le Moustier skull remained to all intents and purposes 'lost' in Berlin. Only in 1965 was the Le Moustier skull 're-excavated' in Berlin where it was identified as that of Le Moustier (Hesse & Ullrich 1966; Hoffman & Wegner 2002).

Theoretically, if the Soviet authorities had known of the identity of the skulls, they would have been confronted with a dilemma: to which destination should the remains be returned – to France, from which they were removed almost a century ago, or to Berlin where, by purchase, they had reposed since about 1909? By today's thinking, the Le Moustier skull should have been sent to France. However, the Russians sent it back to the Berlin State Museum from which it had been plundered, presumably by Soviet officers.

This must be an unusual, if not unique, repatriation quandary, where there were two potential claimants for the 'return' of a fossil *Homo* expatriate. However, if that was the theoretical position, it should be added that there was no evidence that the skulls of Le Moustier and Combe Capelle were identified specifically in Moscow, nor that these cranial remains had been closely examined there. They were returned, along with stolen artworks in a packing case, to Berlin from which they had been taken. It was only in 1965 that Henrike Hesse 'rediscovered' the Le Moustier skull (Hesse & Ullrich 1966).

In 1997, I was invited to Berlin by the German palaeoanthropologist, Herbert Ullrich. He gave me the opportunity to examine the somewhat fire-scorched skull of Le Moustier and to confirm its identity. Until then, it had been one of the very few European hominid fossils that I had not personally examined over the previous forty-five years.

At the time of my visit to Berlin in 1997, the skull of Combe Capelle, which Otto Hauser had excavated near Mont Ferrand in the Dordogne on 26 August 1909, was still 'missing'. Strenuous efforts were made by some of the German colleagues to find and identify the fragments of the calvaria, face and mandible. Isolated fragments had to be compared with illustrations and measurements that had much earlier been published (Hoffman 1997). Only on 27 December 2001 could Almut Hoffmann and Dietrich Wegner announce that they had 're-discovered' and identified the skull of Combe Capelle without any doubt (Hoffman & Wegner, 2002).

The cases of Le Moustier and Combe Capelle illustrate dramatically how, under wartime conditions, the purloining of fossils by invaders may add another dimension to the problems of expatriation and repatriation of fossil hominids.

CONCLUSIONS

This article has been concerned, in the main, with a series of case histories that illustrate claims for the ownership of hominid fossils. The coverage has not been universal, but the author has confined his attention very largely to examples with which he has been personally in contact, whether directly or indirectly. The article has dealt with specimens whose hominid (hominin) status is not in doubt. There are, of course a number of taxa whose systematic status is still uncertain; this includes fossils whose generic status has been variously assigned and at deeper, Miocene levels, whose classification as hominids *sensu stricto* has been proposed by some and opposed by other scholars. Examples of such indeterminate genera, or whose determinacy changes with the recovery of new specimens or alterations in the systematics of higher primates, are *Otavipithecus, Kenyapithecus, Afropithecus, Samburupithecus, Nacholapithecus, Morotopithecus, Heliopithecus, Proconsul, Griphopithecus, Ankarapithecus, Oreopithecus, Rudapithecus, Graecopithecus, Sivapithecus, Lufengpithecus.* In the normal course of events, it would be appropriate and judicious for specimens representative of such taxa to be handled, as though they were agreed hominids, at least until consensus was reached on their status. Therefore the author's conclusions below should be applied to such specimens.

The author staunchly supports the idea that fossil hominids belong in and should remain in their country of origin. Where the fossils had been removed to another country, they should be restored to their cradle-land. If there is doubt about whether the facilities in the cradle-land are adequate, the country of 'adoption', perhaps helped by UNESCO, should offer to improve or help provide appropriate facilities for the permanent housing of the fossils in their country of origin. This category of heritage treasures comprises very rare specimens, many of which can fairly be described as unique. Therefore UNESCO should perhaps set up a commission to oversee problems of repatriation of fossil hominids, just as there is a special authority (the World Heritage Centre) to oversee sites and collections that have been placed on the World Heritage list.

This analysis and these recommendations do not necessarily apply to recent human remains, including lightly fossilized skeletal material. A different set of issues may arise in such cases, especially if the bones in question are claimed by living peoples, such as ethnic or tribal groups. Such claims may raise questions, such as the credibility or authenticity of the claimed relationship between the living populations and the skeletal remains: this might apply in cases where the recent skeletal remains have been exhumed from unmarked and unidentified graves. It is less likely to apply to skeletons in anatomy departments of medical schools: under the law of South Africa, for instance, such skeletons may be prepared from bodies legally acquired from state institutions (such as hospitals), bodies, that is, of people who have died in such institutions unclaimed by relatives or bona fide friends. Another category of legally permissible acquisition of human bodies by medical schools is that of persons who have made testamentary provision for their bodies, after death, to be delivered to anatomy departments or other medical school departments, of the institution chosen by the body donor.

In respect of recent or lightly fossilized human material that has been removed from the country, such bones belong to the country of origin and should be repatriated to it. It would not be appropriate for such remains to be handed over to local populations who claim 'ownership' of the remains, if they suspect or have reason to believe that the skulls or skeletons in question had originally been exhumed, or nefariously obtained as by the unlawful killing of human beings, from people living in the 'tribal' land or national territory, or who had belonged to the local population in question. There would always be problems of firmly establishing the provenance of such remains. Instead, on repatriation such remains should be returned to the state, which should be recognized as the appropriate authority to receive the remains and, taking what advice it needs, to determine the most suitable repository for them, be it in a university with a medical or health sciences faculty, or in a museum.

One other problem related to the main theme of this article has been raised by one of the referees and has already been under discussion in South Africa and elsewhere. This relates to requests received from time to time that specific fossils housed in museums and in universities be transferred to an authority close to the discovery site. The term 'repatriated' has even been used in such requests, although the term is clearly not applicable: 'repatriate' means to return to the native land (*Patria,* native land). 'Relocate' or even a borrowing of the genetical and botanical term 'translocate', would be appropriate for a movement from one repository to another within the country.

Basically, the same essential principles should apply in such cases. The fossil in question belongs to the country within which it was discovered. Thus, the Taung skull belongs to South Africa and not to one of its areas or provinces. The second principle is that the specimen should repose in an appropriately-equipped and expertly staffed institution. Thirdly, the choice of institution should depend on historical factors – by whom and where was the specimen recovered, extricated from the entombing matrix or breccia, reconstructed (where necessary) and analysed? Fourthly, another most important factor governing the choice of a suitable institution is this: *the fossils, let it never be forgotten, are research materials.* At which institution would the needs and convenience of researchers and graduate- and postgraduate students be best served?

Regional interests and local tourism can be well served by the provision of superlatively made casts of selected fossil specimens. Experts at the repository should always be willing to help design suitable displays and furnish reliable information for the erection of local exhibits at or near the source site. Successful examples of such local exhibits are those at Olduvai Gorge, Tanzania, type site of *Australopithecus boisei* and *Homo habilis*; Zhoukoudian, near Beijing (where original fossil hominids are housed), the type site of *Sinanthropus pekinensis,* now known as *Homo erectus pekinensis* and still popularly called 'Peking Man'; and San Felice Circeo (Monte Circeo), the cave site on the west coast of peninsular Italy, which has yielded a fine Neandertal skull, – to name one in each of three Old World continents.

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