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UNIVERSITY OF THE WITWATERSRAND
JOHANNESBURG

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1995

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PREFACE

Most of the papers published in this volume were presented at the 8th biennial conference of the Palaeontological Society of Southern Africa. This gathering, attended by 70 delegates, was hosted by the Albany Museum, Grahamstown from 5th to 7th September, 1994. Not all papers presented at the conference were submitted for publication in this volume of Palaeontologia africana. A programme of events is printed hereunder.

8th BIENNIAL CONFERENCE OF THE PALAEONTOLOGICAL SOCIETY OF SOUTH AFRICA
5th — 7th SEPTEMBER 1994

PROGRAMME

Monday 7 September

Morning Session

CHAIR: DR W. DE KLERK

Presidential Address

B Rubidge — The PSSA – keeping our eyes open to the future

Keynote Address

J Long — New discoveries of Late Devonian fishes from the Gogo Formation, Western Australia.

CHAIR: DR B RUBIDGE

C K Brain — Late Proterozoic micro-organisms from cherts in the Nama Group of Southern Namibia.

J Almond, & P Gresse — Traces and dubiofossils from the late Precambrian – Cambrian of South Africa.

J Theron, R Aldridge, S Gabbot, & S Braddy — New Discoveries from the Soom Shale (Latest Ordovician), Clanwilliam district.

J Almond — Shallow marine invertebrates & traces of the Bokkeveld Group (Devonian, South Africa): an overview of recent work.

E Anderson, N Hiller & R Gess — New discoveries of Devonian fishes at Grahamstown.

N Hiller & R Gess — Algal fossils in the South African Devonian.

Afternoon Session

CHAIR: DR E ANDERSON

B Millsteed — Continents, climates and things that go bump in the desert: A palynological look at environmental changes in the late Permian of Gondwana and their effects on the biosphere.

G Aitken — Permian palynomorphs from the Number 5 coal seam, Ecca Group, Witbank/Highveld coalfields, South Africa.

J Loock, J Kitching & B Rubidge — The stratigraphy of the Lower Beaufort Group in the area surrounding the DR3 uranium anomaly north of Laingsburg

E Latimer — Permian rhinesuchid amphibians from the Karoo

F Durand — A description of *Hewittia albanensis*.

CHAIR: DR M RAATH

L. Firm — A morphological study of the braincase of a sectioned early therocephalian.

B Rubidge & J Kitching — A new biarmosuchid mammal-like reptile from the lower Beaufort Group.

C Gow — *Eunotosaurus*, cladistics and common sense.

J van den Heever & J Hopson — *Blattoidealestes gracilis*, a supposed scaloposaurid therocephalian (Amniota: Therapsida) from the Upper Permian Beaufort Group of South Africa.

B Cox — The jaw function, diet and adaptive radiation of the dicynodont mammal-like reptiles.

Tuesday 6 September

Morning Session

CHAIR: PROF T MASON

R Smith — Changing fluvial encironments across the P-Tr boundary in the main Karoo basin, S. Africa and possible causes of the tetrapod extinctions.

J Hancox — A new dicynodont from the Beaufort Group of South Africa. Implications for the biostratigraphy of the *Cynognathus* Assemblage Zone.

J Kitching — On the occurrence of the *Tritylodon* Acme Zone within the middle Elliot Formation and the fossil content of the zone.

D Dilkes — Phylogenetic and biostratigraphic significance of Early Triassic rhyncosaurs (Reptilia: Diapsida) in South Africa.

M Pickford — A new proterosuchian from Namibia

J Welman — *Euparkeria* and the origin of birds.

CHAIR: J VAN DEN HEEVER

B Newman & M Raath — How to build a dinosaur: Methods used to construct a flesh restoration of the camarasaurid sauropod, *Algoasaurus*, in the Port Elizabeth Museum.

A Cruikshank — A Lower Cretaceous pliosaur from South Africa rediscovered.

H Klinger — Terrestrial elements in the marine Cretaceous of Natal and Transkei.

M Bamford — Palaeobiogeography of Cretaceous and Tertiary fossil wood in southern Africa.

T Mason — Ichnofossils as palaeoenvironmental indices.

A Cadman — Onshore and off – What the Tertiary pollen of the west coast is telling us.

Wednesday 7 September

Morning Session

CHAIR: N HILLER

M Pickford & B Senut — Recent discoveries in the Miocene of Namibia.

B Senut, M Pickford & Y Dauphin — Fossil eggshells of the Sperrgebiet and the Namib Desert: Implications for Biochronology.

R Smith, T Mason & J Ward — Flash-flood sediments and ichnofacies of the late Pleistocene Homeb silts, Kuiseb River, Namibia.

E Van Dijk — Fossil African Lissamphibia.

P Haarhoff — An update of the Early Pliocene birds from Langebaanweg (Cape Province) with particular reference to the raptors and owls.

D L Roberts — Palaeontological aspects of Late Pleistocene aeolianites – Swartklip, southwestern Cape.

CHAIR: C K BRAIN

M Avery — Micromammals, and environments past and future.

J Brink — A new bovid species from the late Quaternary of the southern Cape.

G Watson & I Plug — *Oreotragus major* (Wells, 1952) and *Oreotragus oreotragus* (Zimmerman, 1783), Family Bovidae: two species?

J McKee — Further chronological seriations of Pliocene and Pleistocene faunal assemblages of southern Africa.

G Rossouw — The early inhabitants of South America.

C MacRae — Fossils of South Africa.

Afternoon Session

CHAIR: J MCKEE

K Kuykendall & J McKee — Preliminary report on recent excavations at Buffalo Cave, Makapan Valley, Northern Transvaal.

C Lockwood & K Kuykendall — Age-related changes in the mandible of *Australopithecus africanus*.

K Reed — Environmental reconstruction in modern death assemblages and Plio-Pleistocene hominid localities.

F Thackeray, S Helbig & S Moss — Quantifying morphological variability within and between extant mammalian species: implications for hominid taxonomy.

L Berger — New hominid discoveries and recent advances in palaeo-anthropology in South Africa.

L Berger & C Menter — The potential for testing faunal seriations at southern African hominid bearing deposits through the examination of fossils from horizontally bedded strata at the Gladysvale site.

CHAIR: J F THACKERAY

C K Brain — The past, present and future weaknesses, strengths and opportunities of South African palaeontology (including hominid evolution).

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A PRELIMINARY ASSESSMENT OF THE MICROMAMMALIAN REMAINS FROM GLADYSVALE CAVE, SOUTH AFRICA

by

D.M. Avery

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ABSTRACT

New micromammalian material from Gladysvale Cave has recently been collected by L.R. Berger and A.W. Keyser. The sample contains representatives of 29 species, of which five are insectivores, seven are bats and the remainder are rodents. Apart from one specimen which is possibly referable to the extinct species, *Proodontomys cookei*, the material appears to belong to extant species. Proportional representation of species varies between units. This may indicate different environmental conditions and therefore different ages for the deposits concerned. It could equally reflect different agents of accumulation. Taphonomic work should establish whether this is the case. In general terms, environmental conditions were apparently similar to those of today.

KEYWORDS: Micromammals, Pleistocene, systematics, environments

INTRODUCTION

Gladysvale Cave (2527DC) is one of a series of caves located in the Nascot Private Nature Reserve (previously the John Nash Game Reserve and, before that, the Jack Scott Private Nature Reserve), which mainly comprises the farm Uitkomst 499 JQ, in the Krugersdorp District of Gauteng, South Africa (Martini & Keyser 1989). The site is approximately 13 km northeast of the better-known Plio-Pleistocene hominid localities in the Sterkfontein valley, at an altitude of about 1600 m. The landscape is rugged with streams in heavily incised valleys draining northwards into the Skeerpoort River (Berger & Keyser 1992). The vegetation ranges from open grassland with scattered trees and bushes to more densely wooded valleys.

The caves are developed in a chert-rich dolomitic limestone, overlain by dolomite with shale intercalations (Berger & Keyser 1992). There are two caves, one with upper and lower chambers, that are linked below ground. The cave fill consists of the basal collapse breccia comprising dolomite and chert blocks cemented by flowstone. This breccia is overlain by a flowstone which is fossiliferous in places and is in turn overlain by highly fossiliferous layers of siltstone interbedded with flowstone. Above the bedded silts in the upper chamber there is unconsolidated cave soil overlain by another flowstone. Because much of the fossiliferous material was removed when the caves were mined for calcite it was necessary to collect palaeontological samples from isolated units of *in situ* deposit and from the dumps of discarded material. The various units discussed below are probably of different ages, with the unconsolidated units D5 and L5 perhaps younger than the Pink Breccia and S18/19 units (L.R. Berger, pers. comm.).

Collection of fossil material was originally undertaken by R. Broom (University of the Witwatersrand) in 1937 and a faunal list was published by Cooke (1963); current collection was begun in 1991 by L.R. Berger (University of the Witwatersrand) and A.W. Keyser (Council for Geoscience). Modern micromammalian material has been collected from the area by Vernon (1972) and Rautenbach (1982). As an interim measure, the present study provides an annotated list of the micromammalian taxa recovered thus far from Gladysvale Cave. The environmental implications of the micromammalian material will be considered in a separate paper and are therefore only briefly discussed here.

METHODS

Taxonomic arrangement is according to Meester *et al.* (1986) for extant taxa, and the extinct taxon is interpolated in the appropriate place. Identifications and minimum numbers of individuals (MNIs) are based on maxillae and mandibles only. The method used to calculate MNIs has been explained elsewhere (Avery, 1982). Briefly, however, this involves counting only those jaws that possess a particular, frequently preserved element, which has been determined for each species or group of species, to avoid counting the same jaw twice. The minimum number is the maximum count for any one jaw in individual samples as supplied by the excavators. These minimum numbers were summed to provide totals for seven larger units or collecting localities (Table 1).

The Shannon index of diversity, which takes into account both the number of species and the extent to which they are equally represented, is routinely calculated as a means of assessing general climatic

conditions because a higher value for the index equates with more equable climatic conditions. The index takes the form $H = - (P_i \ln P_i)$ where P_i is the proportion of the sample represented by each species. Table 1 gives a preliminary list of taxa identified and the percentage representation of each taxon in various units. Figure 1 shows this information in visual form as well as giving summary information for each unit or group of units. Lists of species collected in the area in recent times were extracted from Vernon (1972) and Rautenbach (1982), and are listed in Table 2. In the following systematic accounts distributional and habitat data are from Rautenbach (1982) unless otherwise stated.

(NB. It has been decided to retain the name Transvaal when referring to Rautenbach's [1982] monograph because redefining his distributional information to conform to present political boundaries would have introduced unnecessary complications.)

NUMERICAL RESULTS

The total sample comprises 355 individuals representing 29 micromammalian taxa (Table 1). Of these, four taxa are insectivores, seven are bats, 17 are rodents and one is an elephant shrew. The majority of the taxa are represented in less than half the seven units analysed and the number of taxa per unit varies (Table 1; Figure 1) from 6 in L31 (with 15 only individuals) to 19 in S18.E6 (with 119 individuals). The best represented species is *Mystromys albicaudatus*. This taxon is dominant in most units at Gladysvale, as it is at the Sterkfontein valley sites, although it constitutes a smaller proportion of the sample at Gladysvale than it does in the latter area. Percentages are slightly over 50% for Kromdraai and Sterkfontein (Pocock 1987) and for Swartkrans (Avery in prep.) whereas at Gladysvale they are generally less than half that. *Aethomys chrysophilus* is the second best represented species. *Mastomys* sp. and *Elephantulus myurus* occur in all units but in lower numbers whereas *Otomys karoensis* occurs in only five units but in generally high proportions (Table 1). Values of the diversity index range between 1.71 for unit L31 and 2.31 for unit D5 (Figure 1).

SYSTEMATIC ACCOUNTS

INSECTIVORA

Soricidae

Myosorex Gray, 1838 Forest shrew

Myosorex sp. is represented in units S16.E11 and S18.E6 as well as the Pink Breccia. It has been accepted

TABLE 1

Percentage representation of micromammalian taxa in samples from various depositional units at Gladysvale Cave.

No	Species	English common name	D5	L5	L31	S10 to S17	S18.E6	S19.E6	Pink Breccia
1	*Myosorex* sp.	Forest shrew					2.5	1.7	3.1
2	*Crocidura* sp.	Musk shrew	10.0	6.1					1.0
3	*Suncus varilla*	Lesser dwarf shrew	13.3	21.2					
4	*Amblysomus gunningi*	Gunning's golden mole					2.5		1.0
5	*Rhinolophus clivosus*	Geoffroy's horseshoe bat					2.5	4.8	4.1
6	*Hipposideros caffer*	Sundevall's leaf-nosed bat		6.1					
7	*Miniopterus schreibersii*	Schreiber's long-fingered bat		3.0					
8	*Myotis tricolor*	Temminck's hairy bat						0.8	
9	*Eptesicus hottentotus*	Long-tailed serotine bat						0.8	4.8
10	*Eptesicus capensis*	Cape serotine bat							4.8
11	*Scotophilus dinganii*	Yellow house bat							4.8
12	*Cryptomys hottentotus*	Common molerat			13.3	2.5	6.7	19.0	10.3
13	*Otomys karoensis*	Karoo vlei rat	3.3		20.0	22.5	23.5		15.5
14	*Otomys sloggetti*	Sloggett's vlei rat					1.7		
15	*Desmodillus auricularis*	Short-tailed gerbil					0.8		
16	*Tatera* sp.	Gerbil	3.3	3.0		2.5	0.8	4.8	1.0
17	*Mystromys albicaudatus*	White-tailed rat	6.7	3.0	20.0	20.0	29.4	19.0	27.8
18	*Saccostomus campestris*	Pouched mouse					0.8	4.8	1.0
19	*Dendromus melanotis*	Grey climbing mouse	10.0	3.0			0.8		5.2
20	*Steatomys* sp.	Fat mouse	13.3	33.3		2.5	1.7	4.8	
21	*Proodontomys cookei*								1.0
22	*Acomys spinosissimus*	Common spiny mouse	3.3			5.0	1.7		2.1
23	*Lemniscomys rosalia*	Single-striped mouse	3.3						
24	*Rhabdomys pumilio*	Striped mouse				2.5	0.8		2.1
25	*Dasymys incomtus*	Water rat				2.5	1.7		
26	*Mus minutoides*	Pygmy mouse	23.3	12.1		2.5	2.5		1.0
27	*Mastomys* sp.	Multimammate mouse	3.3	3.0	13.3	10.0	5.0	4.8	5.2
28	*Aethomys chrysophilus*	Red veld rat	3.3	3.0	26.7	15.0	11.8	19.0	13.4
29	*Elephantulus myurus*	Rock elephant-shrew	3.3	3.0	6.7	5.0	6.7	4.8	5.2
		SAMPLE SIZE	30	33	15	40	119	21	97

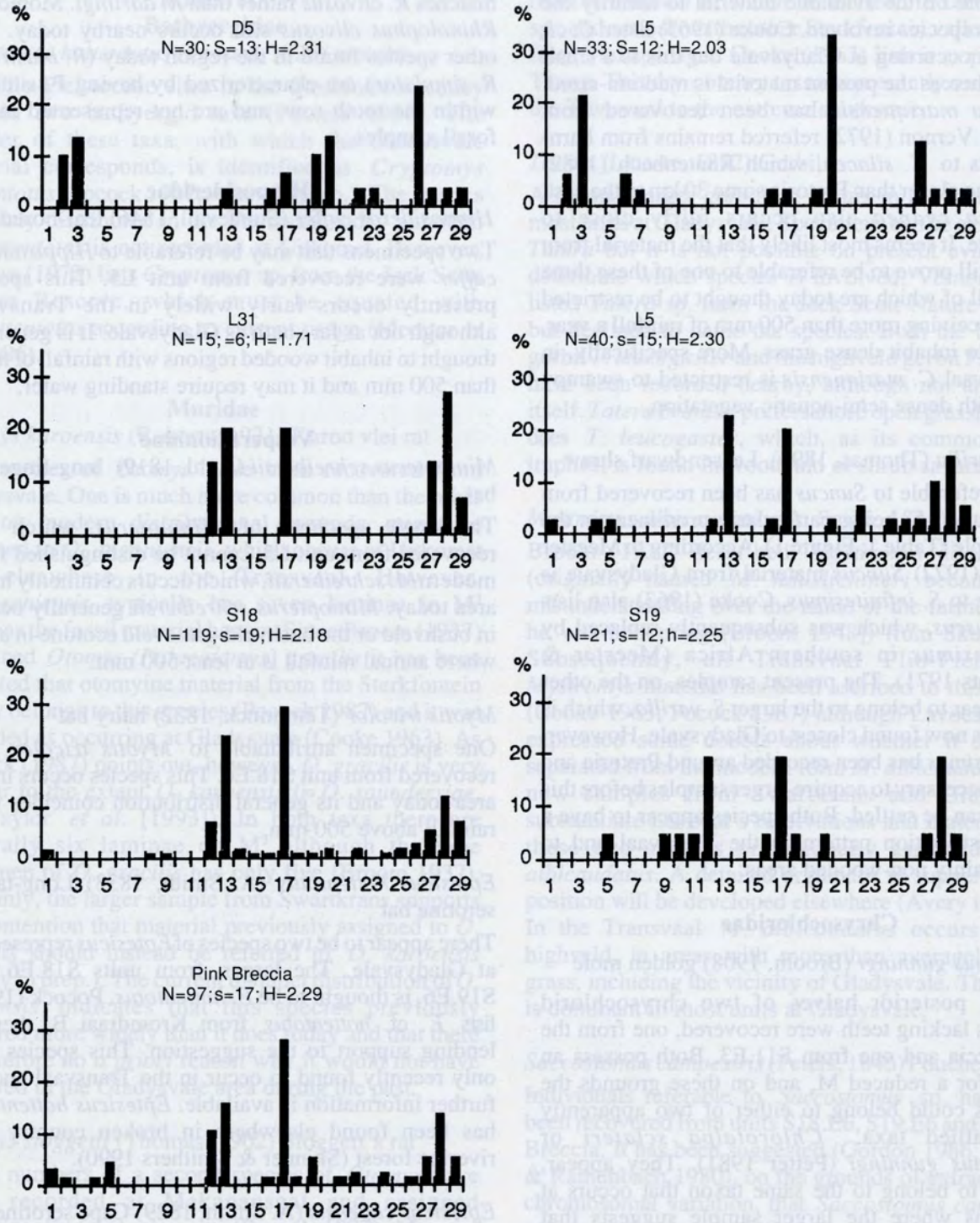

Figure 1. Percentage representation of species in various units at Gladysvale. N=minimum number of individuals; s=number of species; H=Shannon index of general diversity. See Table 1 for species name.

for some time that the species represented in the Gauteng Plio-Pleistocene sites is *M. robinsoni* (Meester 1955; Butler & Greenwood 1965; Butler 1978) and this species has previously been listed for Gladysvale (Cooke 1963). Recent examination of new samples from Swartkrans suggests, however, that *M. robinsoni* may not warrant more than subspecific separation from *M. cafer* (Avery, in prep.). The specific designation of the Gladysvale material must therefore await completion of the Swartkrans study. Vernon (1972) listed *M. cafer* from the Jack Scott Nature Reserve but this specific identification was apparently discounted by Rautenbach (1982) who recorded only *M. varius* from the area. Both species indicate dense moist grass, probably along a stream bank, with *M. cafer* generally indicating a more forested environment than does *M. varius* in the Transvaal today.

Crocidura Wagler, 1832 Musk shrew

Material assignable to *Crocidura* sp. has been recovered from units D5, L5 and the Pink Breccia. It is

not possible on the available material to identify the *Crocidura* species involved. Cooke (1963) listed *C.* cf. *bicolor* as occurring at Gladysvale but this is a small species whereas the present material is medium-sized. *Crocidura mariquensis* has been recovered from Uitkomst. Vernon (1972) referred remains from barn-owl pellets to *C. silacea*, which Rautenbach (1982) recorded no closer than Pretoria some 30 km to the east. *Crocidura cyanea* also occurs fairly close to Gladysvale. It seems most likely that the material from this site will prove to be referable to one of these three species, all of which are today thought to be restricted to areas receiving more than 500 mm of rainfall a year, and tend to inhabit dense grass. More specifically, in the Transvaal *C. mariquensis* is restricted to swampy ground with dense semi-aquatic vegetation.

Suncus varilla (Thomas, 1895) Lesser dwarf shrew

Material referable to *Suncus* has been recovered from units D5 and L5, being particularly prominent in the latter sample (Table 1; Figure 1). According to Meester & Meyer (1972) *Suncus* material from Gladysvale is assignable to *S. infinitesimus*. Cooke (1963) also lists *S.* cf. *etruscus*, which was subsequently replaced by *S. infinitesimus* in southern Africa (Meester & Lambrechts 1971). The present samples, on the other hand, appear to belong to the larger *S. varilla*, which is the species now found closest to Gladysvale. However, *S. infinitesimus* has been recorded around Pretoria and it will be necessary to acquire larger samples before this question can be settled. Both species appear to have a similar distribution pattern in the Transvaal and to inhabit mainly non-wooded areas.

Chrysochloridae

Amblysomus gunningi (Broom, 1908) golden mole

Only the posterior halves of two chrysochlorid mandibles lacking teeth were recovered, one from the Pink Breccia and one from S11.E3. Both possess an alveolus for a reduced M_3 and on these grounds the specimens could belong to either of two apparently closely allied taxa, *Chlorotalpa sclateri* or *Amblysomus gunningi* (Petter 1981). They appear, however, to belong to the same taxon that occurs at Swartkrans where the larger sample suggests that *A. gunningi* is the species represented (Avery in prep.). Neither taxon has recently been recorded from near Gladysvale and little is known of their habitat requirements beyond the fact that both have been collected in forest and in montane areas.

CHIROPTERA

Rhinolophidae

Rhinolophus clivosus Cretzschmar, 1828 horseshoe bat

Mandibles referable to the genus *Rhinolophus* have been recovered from S17.E11, S19.E6 and the Pink Breccia. They appear to belong to a single species. This is probably *R. clivosus* because the alveolus for a very small P_3 is located outside the tooth row, and the size matches *R. clivosus* rather than *R. darlingi*. Moreover, *Rhinolophus clivosus* still occurs nearby today. The other species found in the region today (*R. blasii* and *R. simulator*) are characterized by having P_3 situated within the tooth row, and are not represented in the fossil samples.

Hipposideridae

Hipposideros caffer (Sundevall, 1846) leaf-nosed bat

Two specimens that may be referable to *Hipposideros caffer* were recovered from unit L5. This species presently occurs fairly widely in the Transvaal, although not as far south as Gladysvale. It is generally thought to inhabit wooded regions with rainfall of more than 500 mm and it may require standing water.

Vespertilionidae

Miniopterus schreibersii (Kuhl, 1819) long-fingered bat

The single specimen of *Miniopterus*, which was recovered from unit L5, cannot be distinguished from modern *M. schreibersii*, which occurs commonly in the area today. *Miniopterus schreibersii* generally occurs in bushveld or the bushveld-grassveld ecotone in areas where annual rainfall is at least 500 mm.

Myotis tricolor (Temminck, 1832) hairy bat

One specimen attributable to *Myotis tricolor* was recovered from unit S18.E6. This species occurs in the area today and its general distribution coincides with rainfall above 500 mm.

Eptesicus hottentotus (A. Smith, 1833) Long-tailed serotine bat

There appear to be two species of *Eptesicus* represented at Gladysvale. The larger, from units S18.E6 and S19.E6, is thought to be *E. hottentotus*. Pocock (1987) lists *E.* cf. *hottentotus* from Kromdraai B, thereby lending support to the suggestion. This species was only recently found to occur in the Transvaal and no further information is available. *Eptesicus hottentotus* has been found elsewhere in broken country and riverine forest (Skinner & Smithers 1990).

Eptesicus capensis (A. Smith, 1829) Cape serotine bat

The smaller *Eptesicus* material, which was found only in S19.E6, has been assigned to *E. capensis*. This species, which occurs today in the general area, is widespread and has wide habitat tolerance, although it is attracted to open water.

Scotophilus dinganii (A. Smith, 1833) Yellow house bat

One specimen identified as *Scotophilus dinganii* was recovered from unit S19.E6. This bushveld species, which often feeds over open water, presently occurs close to Gladysvale.

RODENTIA

Bathyergidae

Cryptomys hottentotus (Lesson, 1826) molerat

The Plio-Pleistocene sites in the Sterkfontein valley contain two bathyergid taxa (Pocock 1987). The smaller of these taxa, with which the Gladysvale material corresponds, is identified as *Cryptomys hottentotus* (Pocock 1987; Avery in prep.). The species is widely distributed in the Transvaal today although *C. hottentotus* is not recorded at Uitkomst. However, Vernon (1972) lists *Cryptomys* sp. from the Jack Scott Nature Reserve, which must be equated with *C. hottentotus* according to current usage (Meester *et al.* 1986).

Muridae

Otomys karoensis (Roberts, 1931) Karoo vlei rat

Two species of *Otomys* have been recovered from Gladysvale. One is much more common than the other and, on modern distributional grounds, might be assigned to *O. angoniensis*, which occurs at Uitkomst and elsewhere in the Transvaal. However, *O. angoniensis* typically has seven laminae in M^3 whereas the fossil material has six. Since Broom (1937) described *Otomys (Palaeotomys) gracilis* it has been accepted that otomyine material from the Sterkfontein valley belongs to this species (Pocock 1987) and it was recorded as occurring at Gladysvale (Cooke 1963). As Pocock (1987) points out, however, *O. gracilis* is very similar to the extant *O. karoensis* (= *O. saundersiae*, see Taylor *et al.* [1993]). In both taxa there are generally six laminae on M^3 although the type specimen of *O. gracilis* has only five (Broom 1937). Certainly, the larger sample from Swartkrans supports the contention that material previously assigned to *O. gracilis* should instead be referred to *O. karoensis* (Avery in prep.). The current disjunct distribution of *O. karoensis* indicates that this species previously occurred more widely than it does today and that there is therefore no *a priori* reason why it would not have occurred in the Gladysvale area during the past.

Otomys sloggetti (Thomas, 1902) Sloggett's rat

Small numbers of a second species of *Otomys* have been recorded at Makapansgat and assigned provisionally to *O. sloggetti* (Pocock 1987). Material that may belong to this species has also been recovered from unit S18.E6 at Gladysvale. In the Transvaal the species has only been recorded from montane grassland at Wakkerstroom in the extreme southeast, although it is said to inhabit karroid vegetation in the eastern Karoo. There is no inherent reason why this high altitude species should not have previously occurred further north of its present limit.

Desmodillus auricularis (A. Smith, 1834) gerbil

One specimen attributable to *Desmodillus auricularis* was recovered from S18.E6. It is clearly a rare species since Pocock (1987) only recorded two individuals from Kromdraai B, which he ascribed to *Desmodillus* sp., and none from the other Sterkfontein valley sites or from Makapansgat. Cooke (1963) lists it as present at Taung. This dry-country taxon is presently restricted in the Transvaal to the extreme southwest.

Tatera (Lataste, 1882) Gerbil

A second, larger gerbilline occurs in low numbers in most units at Gladysvale. Specimens can be assigned to *Tatera* but it is not possible on present evidence to determine which species is involved. Vernon (1972) listed *Tatera* sp. from the Jack Scott Nature Reserve but declined to name the species. Both the bushveld gerbil *T. leucogaster* and the highveld gerbil *T. brantsii* have been recorded nearby, although not at the site itself. *Tatera brantsii* prefers more open grassland than does *T. leucogaster*, which, as its common name implies, is found in woodland or shrub savanna.

Mystromys albicaudatus (A. Smith, 1834) rat

Broom (1937) described *Mystromys hausleitneri* (originally named *M. hauslichtneri* because of a misunderstanding over the name of the farmer whom he was honouring [Broom 1948]) from Skurveberg. Subsequently, all Transvaal Plio-Pleistocene *Mystromys* material has been ascribed to this species (Cooke 1963; Pocock 1987) although Lavocat (1956) expressed some doubts about whether it could be separated from the modern form *M. albicaudatus*. The new samples from Swartkrans and Gladysvale substantiate Lavocat's reservations and material from these two sites is provisionally assigned to *M. albicaudatus*. A detailed argument in support of this position will be developed elsewhere (Avery in prep.). In the Transvaal *M. albicaudatus* occurs on the highveld, in areas with more than averagely dense grass, including the vicinity of Gladysvale. This taxon is dominant in most units at Gladysvale.

Saccostomus campestris (Peters, 1846) Pouched mouse

Individuals referable to *Saccostomus* sp. have only been recovered from units S18.E6, S19.E6 and the Pink Breccia. It has been suggested (Gordon 1986; Gordon & Rautenbach 1980), on the grounds of extraordinary chromosomal variation, that *Saccostomus campestris* as presently accepted (Musser & Carleton 1993a) actually comprises two or more species. Already one species (*S. mearnsi* in East Africa) has been differentiated on the basis of karyotypic and morphological differences (Hubert 1978). Even if more species are formally recognized in southern Africa, their description will also require a morphological element before they can be distinguished osteologically. For the present, the material from Gladysvale is therefore perforce referred to *S. campestris*. It has not been listed as occurring in the other Plio-Pleistocene sites; neither does it occur today very close to Gladysvale. In a general way, it is documented as inhabiting woodland while, in the

Transvaal at least, its distribution shows a negative correlation with that of *Mystromys albicaudatus*. The occurrence of both forms at Gladysvale is therefore of some interest. It may also prove significant that a correlation exists between diploid number and biotic zone, with the 2n=46 form found primarily in the Southern Savanna Woodland, including the Transvaal, and the 2n-28-44 forms predominantly in the South West Arid zone (Gordon 1986).

Dendromus melanotis (A. Smith, 1834) climbing mouse

Dendromus specimens from Gladysvale appear referable to *D. melanotis*, as are those from Sterkfontein and Kromdraai (Pocock 1987). Vernon (1972) records the presence of *Dendromus* sp. in the Jack Scott Nature Reserve but Rautenbach (1982) shows no species of this genus closer than Pretoria. The presence of this species indicates stands of dense tall grass.

Steatomys (Peters, 1846) Fat mouse

Gladysvale *Steatomys* sp. molars are relatively broad, thereby suggesting that the species represented may be *S. pratensis* rather than *S. krebsii*. Pocock (1987), on the other hand, refers Kromdraai and Sterkfontein material to *S. krebsii* and this species apparently occurs rather closer to Gladysvale today than does *S. pratensis*. Given, however, that the present species identification is not certain and that the genus is in need of revision (Meester *et al.* 1986), it is thought preferable to follow Vernon (1972) in not assigning the material to a particular species. Although *S. pratensis* and *S. krebsii* apparently do not overlap in the Transvaal they are sometimes found together in dry sandy grassland elsewhere (Skinner & Smithers 1990).

Proodontomys cookei (Pocock, 1987)

One mandible without teeth, which possibly represents *Proodontomys cookei* , was recovered from the Pink Breccia. Further material is required to confirm the presence of this extinct taxon at Gladysvale.

Acomys spinosissimus (Peters, 1852) spiny mouse

According to the current situation (Dippenaar & Rautenbach 1986) the *Acomys* material from Gladysvale should be assigned to *A. spinosissmus* but this will require confirmation. Pocock (1987) declined to identify the material from the Sterkfontein valley and Makapansgat to species. *Acomys spinosissimus* is associated with rocky woodland areas in the Transvaal but in Mozambique it is also found on alluvium along rivers in savanna (Smithers & Lobão Tello 1976).

Lemniscomys rosalia (Thomas, 1904) Single-striped mouse

Only one specimen probably attributable to *Lemniscomys rosalia* was recovered from unit D5. This species (previously *L. griselda*) is today associated with savanna woodland at altitudes below about 1200 m. Gladysvale lies some 400 m higher than this but a record of *Lemniscomys* sp. from Kromdraai B (Pocock 1987) supports the suggestion that this genus occurred on the highveld in the past.

Rhabdomys pumilio (Sparrman, 1784) Striped mouse

Several specimens from Gladysvale were identified as *Rhabdomys pumilio*. This species occurs in the Sterkfontein valley today and in the Transvaal generally it is associated with short dense grass in open savanna above about 1200 m.

Dasymys incomtus (Sundevall, 1847) Water rat

Specimens attributable to *Dasymys incomtus* were recovered from S16.E11 and S18.E6. *Dasymys* sp. has been recorded from Kromdraai and Sterkfontein (Pocock 1987) but has not been collected from the region in recent times. Modern distributions coincide with mean annual precipitation above 500 mm and with dense grass or semi-aquatic vegetation in swampy areas.

Mus minutoides (A. Smith, 1834) Pygmy mouse

Small numbers of *Mus minutoides* were recovered from most units. This species still occurs at Uitkomst and *Mus* sp. has been recorded in the Plio-Pleistocene sites of the Sterkfontein valley and at Makapansgat (Pocock 1987). Although it has a wide habitat tolerance *M. minutoides* generally requires good ground cover, usually in the form of grass.

Mastomys (Thomas, 1915) Multimammate mouse

The *Mastomys* material from Gladysvale is either *M. coucha* or *M. natalensis*. These two taxa were initially distinguished on cytogenetic grounds in Zimbabwe (Gordon 1978) and subsequently by multivariate analysis of cranial characters in South Africa (Dippenaar *et al.* 1993). Dippenaar *et al.* (1993) caution, however, that reliable identification is unlikely to be simple, thereby implying that it may prove impossible to identify incomplete fossil material. Modern distributions suggest *M. coucha* as the most likely species to be represented (Dippenaar *et al.* 1993; Green *et al.* 1980). Both Rautenbach (1982) and Vernon (1972) list *Praomys natalensis*. However, their work was undertaken at a time when neither *Mastomys* nor *coucha* was in use as a valid taxon so that their *P. natalensis* potentially includes both *M. coucha* and *M. natalensis* as presently accepted. Pocock (1987) lists *Praomys* sp. (= *Mastomys* as understood in current taxonomic usage) for the Sterkfontein valley and Makapansgat.

Thallomys (Thomas, 1920) Tree rat

No material referable to *Thallomys* has so far been recovered from the samples examined although Cooke (1963) lists *T. debruyni* from the site. Pocock (1987) did not record the taxon from Sterkfontein or

TABLE 2

Species recorded from the farm Uitkomst and surrounds by Rautenbach (1982) and from the Jack Scott Nature Reserve by Vernon (1972).

Species	Common Name	Uitkomst	Surrounds	Jack Scott
Myosorex varius	Forest shrew	x		
Myosorex cafer	Dark-footed forest shrew			x
Crocidura mariquensis	Swamp musk shrew	x		
Crocidura cyanea	Reddish-grey musk shrew		x	
Crocidura silacea	Lesser grey-brown musk shrew			x
Suncus varilla	Lesser dwarf shrew		x	
Rhinolophus clivosus	Geoffroy's horseshoe bat	x		
Rhinolophus blasii	Peak-saddle horseshoe bat	x		
Rhinolophus simulator	Bushveld horseshoe bat		x	
Miniopterus schreibersii	Schreiber's long-fingered bat	x		
Myotis tricolor	Temminck's hairy bat	x		
Eptesicus capensis	Cape serotine bat		x	
Scotophilus dinganii	Yellow house bat		x	
Sauromys petrophilus	Flat-headed free-tailed bat		x	
Tadarida aegyptiaca	Egyptian free-tailed bat		x	
Cryptomys hottentotus	Common molerat		x	
Cryptomys sp.	Molerat			x
Otomys angoniensis	Angoni vlei rat	x		
Otomys irroratus	Vlei rat		x	
Otomys sp.	Vlei rat			x
Tatera leucogaster	Bushveld gerbil		x	
Tatera brantsii	Highveld gerbil		x	
Tatera sp.	Gerbil			x
Mystromys albicaudatus	White-tailed rat		x	
Dendromus sp.	Climbing mouse			x
Malacothrix typica	Large-eared mouse			x
Steatomys sp.	Fat mouse			x
Lemniscomys griselda	Single-striped mouse		x	
Rhabdomys pumilio	Striped mouse		x	
Mus minutoides	Pygmy mouse	x		
Praomys natalensis	Natal multimammate mouse	x		x
Thallomys paedulcus	Tree rat	x		
Aethomys chrysophilus	Red veld rat	x		
Aethomys namaquensis	Namaqua rock mouse	x		
Aethomys sp.	Veld rat/ rock mouse			x
Rattus rattus	House rat		x	
Graphiurus murinus	Woodland dormouse		x	
Elephantulus myurus	Rock elephant-shrew		x	x

Kromdraai but De Graaff (1961) listed *T.* cf. *paedulcus* from Kromdraai. *Thallomys* also occurs at Swartkrans (Avery in prep.). At the time Broom (1948) described *T. debruyni* three extant species of *Thallomys* were recognized. Subsequently, Meester *et al.* (1986) accepted only one species, *T. paedulcus*, as occurring in southern Africa. Thereafter, Gordon (1987) showed that there were two species, with *T. paedulcus* being replaced in the more arid west by *T. nigricauda*. The most recent treatment of the genus (Musser & Carleton 1993b) resurrects a third species, *T. shortridgei*, which is known only from the south bank of the Orange River near Upington. *Thallomys paedulcus s.l.* (and presumably *sensu stricto.* as well) has been recorded at Uitkomst in recent times and may yet be found in the Gladysvale deposits.

Aethomys chrysophilus (De Winton, 1897) veld rat

All *Aethomys* specimens from Gladysvale that can be identified to species apparently belong to *Aethomys chrysophilus* as currently accepted. There is, however, cytogenetic, electromorphic and spermatozoan

evidence to show that *A. chrysophilus* comprises two distinct species (Gordon & Rautenbach 1980; Gordon & Watson 1986; Visser & Robinson 1986). These are *A. chrysophilus s.s.* and another species that has yet to be formally identified (Musser & Carleton 1993). The genus is currently under review (C.T. Chimimba, pers. comm.) and it is to be hoped that morphological differences will be found that will enable the identification of the fossil material. *Aethomys chrysophilus*, as presently understood, inhabits wooded plains almost exclusively. No specimens have so far been found that are clearly referable to *A. namaquensis* although both species have been recorded from Kromdraai and Makapansgat (Pocock 1987) and recently from Uitkomst. Vernon (1972) did not distinguish his material to species.

MACROSCELIDEA
Macroscelididae

Elephantulus myurus (Thomas & Schwann, 1906)
Rock elephant-shrew

Specimens referable to *Elephantulus* appear to belong to the species *E. myurus*, which has also been recorded from the Jack Scott Nature Reserve by Vernon (1972). Rautenbach (1982) confirms that it is the only species currently found nearby although he did not find it at Uitkomst. Pocock (1987) has recorded *E.* cf. *brachyrhynchus* and the extinct *E. antiquus* from the Sterkfontein valley and Makapansgat. This latter form is described by Broom (1948) as having a sectorial P^2 very similar to that found in *E. capensis* (= *E. edwardii* [Corbet & Hanks 1968]). *Elephantulus edwardii*, in turn, shares this feature with *E. myurus* (Corbet & Hanks 1968) and it may well prove impossible to distinguish the fossil and modern forms at the species level. *Elephantulus myurus* is generally a grassland species (Corbet & Hanks 1968) but it is locally restricted to rocky outcrops.

DISCUSSION AND CONCLUSION

This preliminary analysis indicates that the micromammalian fauna from Gladysvale is almost entirely composed of extant species, many of which still occur at no great distance from the site today. Nearly the same number of species has been recorded within approximately 20 km of the site in recent times (Table 2) as was recognized in the fossil sample (Table 1). In general terms proportions of various groups are also similar although there are differences at the level of individual taxa, as would be expected. As a preliminary observation, it may therefore be noted that the taxa represented do not suggest conditions greatly different from those of the present. There is a strong indication that rainfall was above 500 mm, as it is today, and ground cover was clearly good, with bush and relatively extensive dense grass. Several species indicate moist riverine vegetation, which may suggest that rainfall was less seasonal than it is at present. Also interesting is that several species seem to indicate the presence of open water.

Percentage representation of certain species varies between units (Table 1; Figure 1). It is clear, for instance, that units D5 and L5 have different proportions, and in some cases different species, from the remainder of the units. Noticeable are the high proportions of various small species (*Crocidura* sp., *Suncus varilla*, *Dendromus melanotis*, *Steatomys* sp. and *Mus minutoides*) and low proportions of the two species (*Otomys karoensis* and *Mystromys albicaudatus*) that are prominent in the other samples. The straightforward interpretation of this is that vegetation was relatively open and climate probably drier at the time units D5 and L5 were deposited than was the case when other units were accumulated. These differences carry the further implication that the units are of a different age from the others, a conclusion supported by their unconsolidated nature, which marks them out as different from the other units.

Straightforward interpretations may, however, be very far from the truth unless they take into account a number of possible biases. For instance, the very fact that the D5 and L5 deposits differ from the others in being unconsolidated could be significant since varying post-depositional histories may have influenced preservation of the material. It is also necessary to determine whether different predators may have been responsible for the collection of the material as has been detailed in cave sites elsewhere (Andrews 1990; Fernández-Jalvo 1995), and whether the micromammal species could have been living in the cave. The differences between samples from units S18.E6 and S19.E6, which are physically contiguous (L.R. Berger, pers. comm.), may be explainable in such terms. Unit S19 contains a noticeably high number of bat species, which are likely to have been living and dying naturally in the cave. Unit S18, on the other hand, includes many more non-volant micromammals, which will almost certainly have been brought in by one or more predator species. Interpretation of the data will have to take into account such differences, which may have information potential of their own. There has, for instance, to be an explanation for why there are more bats at some times than others and why the predators and their preferences change. Conversely, the absence of the generally prominent *Otomys karoensis* from even small samples such as L5 and S19 requires an explanation, regardless of the agent of accumulation.

General diversity is fairly high in most units (Figure 1), apparently due more to high numbers of species than to equability. Apart from unit L31 where small sample size has reduced the value of the index, variation in diversity is not solely due to differing sample sizes and requires explanation. However, it will first be necessary to determine whether the variation has to do with changes in predator preferences or reflects real differences in general conditions. It would therefore not be useful to comment further at this stage.

It is clear, even from this preliminary study, that the rich micromammalian fauna from Gladysvale has the potential to provide useful information on the

environment of the site. This will have particular significance to studies aimed at establishing the conditions in which early hominids developed. By comparing the Gladysvale material with new samples from Swartkrans and Sterkfontein that are under investigation to determine it should also be possible to understand better the ecology of the early hominids at these sites.

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FURTHER CHRONOLOGICAL SERIATIONS OF SOUTHERN AFRICAN PLIOCENE AND PLEISTOCENE MAMMALIAN FAUNAL ASSEMBLAGES

by

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ABSTRACT

Mammalian fossil assemblages from Pliocene and Pleistocene sites of southern Africa have recently been seriated in order to establish a relative chronology (McKee *et al.* 1994). Although an order was inferred for 17 site assemblages of fossil mammals, only ten sites could be seriated at a time. The logistical seriation method has now been modified to handle a greater number of sites at once. Seriations were run on a matrix of Faunal Resemblance Index values for an updated list of time-sensitive mammals of 18 fossil site assemblages. In addition, each assemblage was systematically excluded from analysis in successive seriations to test the robusticity of the method against the influence of individual assemblages. The seriations gave largely consistent results, with the exception of the terminal Pleistocene sites. The most likely chronological sequence inferred from the logistical seriations alone, with corrections for stratigraphic considerations, is: Makapansgat Member 3, Makapansgat Member 4, Taung Hrdlička deposits, Sterkfontein Member 4, Kromdraai B, Sterkfontein Member 5 (in part), Kromdraai A, Swartkrans Member 1, Swartkrans Member 2, Swartkrans Member 3, Gondolin, Plovers Lake, Cornelia, Elandsfontein Main Site, Florisbad/Equus Cave, Cave of Hearths and Klasies River Mouth.

INTRODUCTION

Temporal context is critical for assessing the possible evolutionary roles and associations of fossil mammals. Southern African fossil sites representing the Pliocene and Pleistocene have been problematic in that the nature of most sites has inhibited successful dating by available geochronological techniques (see reviews in Partridge 1986; McKee 1993; McKee *et al.* 1995). Thus our current conception of the temporal framework for these sites is largely reliant on biochronological assessments of the fossil fauna.

Previous approaches to faunal chronologies of southern Africa sites have relied on establishing faunal spans (e.g. Ewer & Cooke 1964; Cooke 1964), or relied on sequences within taxonomic families (Hendey 1974; Vrba 1975, 1982, 1985; Harris & White 1979; Delson 1984; Turner 1990). In order to update the earlier approaches, and use all identified fossil mammals to test the within-family chronologies, a data base of identified mammal species from southern African Neogene sites was compiled and an initial attempt was made to seriate the fossil assemblages (McKee *et al.* 1995). Although a chronological sequence was established for 17 fossil sites, the logistical seriation technique was limited to dealing with only ten sites at a time. The final site sequencing was then compiled from multiple seriations. It was also found that the inclusion or exclusion of particular site assemblages could affect the results of the seriations. In order to overcome these difficulties, the seriation technique has been modified and the new results are reported herein. Additionally, the data base has been updated to accommodate recent developments in Plio-Pleistocene palaeontology.

MATERIALS AND METHODS

A data base of identified mammals from southern African fossil sites (SAFAUNA) was updated from that reported in McKee *et al.* (1995). The updates included the addition of a faunal list from Gondolin (Watson 1993), a modified faunal list for Makapansgat Members 3 and 4 based on the recent assessment by Reed (1995), and the synonymy of *Oreotragus major* with *Oreotragus oreotragus* (Watson & Plug, 1994). The fossil site assemblages used in this analysis are listed in Table 1.

TABLE 1

Fossil site faunal assemblages and codes used in Tables 2-3.

Makapansgat Member 3	MAK3
Makapansgat Member 4	MAK4
Taung Hrdlička deposits	TAUH
Sterkfontein Member 4	STS4
Sterkfontein Member 5	STS5
Kromdraai A	KROA
Kromdraai B	KROB
Swartkrans Member 1	SWT1
Swartkrans Member 2	SWT2
Swartkrans Member 3	SWT3
Gondolin	GOND
Plovers Lake	PLOV
Cornelia	CORN
Elandsfontein Main Site	EFTM
Cave of Hearths (Acheulian levels)	COHA
Florisbad springs	FLOS
Equus Cave (MSA levels)	EQUU
Klasies River Mouth (MSA I & II levels)	KLAS
Extant species in southern Africa	EXTA

New developments in the seriation technique did not change the basic assumptions and methods detailed in McKee *et al.* (1995). Here only an outline of the technique is provided, along with more explicit details of the modifications employed.

Seriations of faunal assemblages must be limited to "time-sensitive" fauna in order to limit the effects of the non-temporal factors that may determine the presence or absence of a species at a fossil site, such as environmental and taphonomic factors. Time-sensitive species are defined as those species which are not overly sensitive to environmental constraints, which do not appear throughout the entire sequence, and which appear in more than one fossil assemblage. These 64 species are listed in Table 2 along with site occurrences. The sources for the data are detailed by McKee *et al.* (1995). The modifications from the earlier list are the exclusions of *Panthera pardus* (which appears throughout the entire sequence), *Simatherium kohllarseni* (dropped from Makapansgat faunal list), and *Oreotragus major* (since synonymized with *Oreotragus oreotragus*), along with the inclusion of *Gigantohyrax maguirei* (now found in more than one deposit).

TABLE 2: Time-sensitive mammalian species with site assemblage occurrences marked by asterisks. Site codes are listed in Table 1, and are ordered here in the optimal sequence determined by the logistical seriation but corrected for known stratigraphic order. Data sources are listed by McKee et al. (1985).

	MAK3	MAK4	TAUH	STS4	KROB	STS5	KROA	SWT1	SWT2	SWT3	GOND	PLOV	CORN	EFTM	EQUU	FLOS	COHA	KLAS	EXTA
ARTIODACTYLA																			
Alcelaphus buselaphus															*		*	*	*
Antidorcas australis												*		*					
Antidorcas bondi				*	*		*					*			*	*	*		
Antidorcas marsupialis								*	*	*	*				*	*			*
Antidorcas recki				*	*	*	*	*	*	*	*		*	*					
Connochaetes gnou													*	*	*	*			*
Damaliscus dorcas											*				*	*			*
Damaliscus niro													*	*		*			
Hippotragus cookei	*			*															
Hippotragus leucophaeus														*				*	*
Makapania broomi	*	*		*															
Megalotragus priscus												*	*	*	*	*	*		
Pelea capreolus							*	*		*		*			*			*	*
Pelorovis antiquus													*	*		*	*	*	
Raphicerus campestris								*	*	*					*				*
Redunca arundinum							*	*			*		*	*			*	*	*
Redunca darti	*	*		*															
Redunca fulvorufula															*			*	*
Syncerus caffer															*			*	*
Taurotragus oryx							*		*	*	*	*	*	*	*	*	*	*	*
Tragelaphus strepsiceros							*	*		*	*	*		*	*		*	*	*
Kolpochoerus paiceae													*	*					
Metridiochoerus andrewsi									*	*	*	*		*					
Notochoerus scotti	*	*	*																
Phacochoerus aethiopicus															*	*	*	*	*
Phacochoerus modestus					*	*	*	*	*	*			*						
Potamochoeroides shawi	*	*		*															
RODENTIA																			
Mystromys antiquus	*		*	*	*														
Proodontomys cookei	*	*	*	*	*		*	*											
Hystrix makapanensis	*						*												
Elephantulus antiquus	*	*	*	*	*	*	*												
Myosorex robinsoni	*			*			*	*											

	MAK3	MAK4	TAUH	STS4	KROB	STS5	KROA	SWT1	SWT2	SWT3	GOND	PLOV	CORN	EFTM	EQUU	FLOS	COHA	KLAS	EXTA
CARNIVORA																			
Lyacon pictus														*	*	*			*
Vulpes pulcher							*	*											
Dinofelis barlowi	*			*				*											
Homotherium crenatidens				*		*	*												
Megantereon cultridens				*	*	*	*	*		*									
Chasmaporthetes silberbergi				*		*		*											
Chasmaporthetes nitidula				*		*		*	*	*									
Hyaena brunnea				*			*	*	*	*				*	*			*	*
Pachycrocuta bellax	*			*		*	*												
Aonyx capensis								*	*	*				*	*	*		*	*
Mellivora capensis														*	*			*	*
Atilax paludinosus															*	*		*	*
Herpestes ichneumon								*						*	*		*	*	*
Suricata suricatta									*	*				*	*				*
PRIMATES																			
Australopithecus africanus	*	*		*															
Australopithecus robustus					*			*	*	*									
Homo sapiens													*	*	*	*	*	*	*
Cercopithecoides williamsi	*	*	*	*	*			*											
Papio izodi			*	*															
Papio angusticeps					*		*												
Papio robinsoni					*		*	*	*	*		*							
Papio cynocephalus															*		*	*	*
Parapapio broomi	*	*		*															
Parapapio whitei	*	*		*															
Parapapio jonesi	*	*		*	*		*	*											
Theropithecus oswaldi								*	*	*				*					
PROBOSCIDEA																			
Elephas recki				*		*													
PERISSODACTYLA																			
Equus burchelli						*	*			*					*	*	*		*
Equus capensis						*	*	*	*	*	*	*	*	*	*	*	*		
Hipparion libycum	*						*	*	*	*	*		*						
HYRACOIDEA																			
Gigantohyrax maguirei	*	*																	
Procavia transvaalensis		*					*	*	*	*	*	*							

Logistical seriation of the assemblages was based on Simpson's (1960) Faunal Resemblance Index (FRI), a robust measure of the degree of similarity between assemblages of time-sensitive fauna. For each pair of sites, the FRI is calculated by taking the number of species shared (C) divided by the total number of species found in the smaller sample (N_1), or simply $FRI=C/N_1 \times 100$. This standardizes site comparisons, and limits the effect of differential sampling of mammal species from the fossil assemblages. These values were calculated for every pair of sites, resulting in the matrix displayed in Table 3.

Optimally seriated matrices should have successively greater FRI values running toward the diagonal (where each assemblage, compared with itself, has an FRI value of 100). In other words, adjacent sites in the sequence should have assemblages that are more similar to each other than to more chronologically distant sites. Although the choice of time-sensitive species and the calculation of FRI values is meant to minimize the effects of non-temporal factors, a perfect logistical seriation is highly improbable given the incomplete nature of the fossil record (see McKee 1995). The seriation technique must minimize deviations from a

series of values increasing toward the diagonal; these deviations are called "backward steps". A "score" is calculated for each ordering of the matrix by summing the absolute value of differences between adjacent sites in a row showing "backward steps". The matrix with the site sequence yielding the lowest score, or the fewest deviations from an ideal matrix, is deemed to represent the optimal seriation.

Computerized logistical seriation techniques used previously were able to seriate only ten assemblages at a time. This is because the number of total orderings of a matrix of ten sites is a factorial ten, or 3,628,000 possibilities, taking about 1.5 hours on a personal computer. Larger matrices would continue to multiply the time needed to try every possible site sequence. However, once a preliminary sequence is established it is not necessary to try every possible order. For example, it is not logical to bother scoring a matrix in which a Pliocene site such as Taung is placed between two Late Pleistocene sites such as Florisbad and Equus Cave. Yet there is value in seriating the entire matrix of 18 sites at once, so that the influence of all the documented sites can be used to determine the optimal order.

A matrix of all 18 sites was seriated with an iterative method by testing permutations of orderings for ten assemblages of the matrix at a time. Thus, while a score was calculated on the basis of all sites, all possible sequences were attempted by reordering sites 9 through 18. Once an optimal seriation was found (as measured by a minimal score), all possible sequences of sites 1 through 10 were tested (holding the remaining sites in a constant order). This process continued iteratively until no improvements in the score were found for either sets (1-10 or 9-18). In this way all reasonable sequences were tested, and the remaining possible site sequences were assumed to be less than optimal.

The final aspect to be considered was that the inclusion or exclusion of a site assemblage could affect the seriation. Thus after the entire matrix of 18 sites was seriated, the process was repeated 18 times on matrices of 17 assemblages, each time excluding a different site assemblage. This systematically tested the robusticity of the seriation against the influence of individual assemblages.

RESULTS

In Table 3 the optimal sequence of 18 site assemblages of time-sensitive mammals is listed along with the matrix of FRI values. Out of the subsequent 18 seriations of 17 sites, each with one successive site assemblage eliminated, 12 yielded the same optimal sequence. Variant sequences of the remaining six seriations included a reversal of the positions of Florisbad and Equus Cave (five seriations), one reversal of Cave of Hearths and Florisbad, and one reversal to correct stratigraphic order of Swartkrans Members 2 and 3.

Out of all the logistical seriations, Makapansgat 3 and 4 were consistently in the incorrect stratigraphic order. Likewise, Swartkrans Members 2 and 3 were reversed in all but one of the seriations. However, when the seriation was rerun with these sites forced into their correct stratigraphic order, there was no effect on the relative positions of any other sites.

DISCUSSION

New developments of the logistical seriation technique, in which all of the 18 sites could be seriated in a single matrix, resulted in a chronology that is largely consistent with that reported by McKee *et al.* (1995). Moreover, the relative consistency of results achieved with the sequential exclusion of individual site assemblages attests to the robusticity of the seriations against the influence of particular sites. However, whereas most of the earlier conclusions regarding the inferred chronology of fossil site assemblages still hold, there are a few noteworthy changes in the sequence.

The relative position of Kromdraai B consistently fell before Sterkfontein Member 5, whereas previously the reverse order was more common. This discrepancy points to the problem noted earlier that the fauna from Sterkfontein Member 5 may represent an extended time period, as confirmed by the archaeological analysis of Kuman (1994). The most reasonable conclusion would be that part of the Sterkfontein Member 5 deposit is penecontemporaneous with Kromdraai B.

It should be cautioned as well that the seriation technique does not have the statistical power to differentiate between the positions of any of the penecontemporaneous sites. This is because sites that lie within 100,000 years or so of each other would probably not sample a distinctly different faunal community, given the slow rates of speciation and extinction (McKee 1995). This is illustrated by the reversals of stratigraphic order seen in the seriations of Makapansgat and Swartkrans. Thus, although the Taung Hrdlička deposits consistently seriate before Sterkfontein Member 4, this alone does not provide sufficient evidence that the sites differ significantly in time. Likewise, the relative positions of the Middle Stone Age (MSA) sites of Equus Cave, Florisbad and Klasies River Mouth do not necessarily reflect a clear chronology.

Mammalian fossils from the Cave of Hearths still present an interpretive problem. Despite the presence of Acheulian artefacts in the deposit, the faunal assemblage consistently seriates among MSA sites. Cooke (1988) also noticed that the fauna were typical of the MSA. Although it is tempting to propose ecological or cultural explanations for this anomaly, it would perhaps be more wise to reassess the Cave of Hearths fauna in light of more recent advances in mammalian taxonomy.

CONCLUSION

Evaluation of the logistical seriations of time-sensitive mammals from 18 faunal assemblages, correcting for known stratigraphic order, suggests the following optimal chronological sequence: Makapansgat Member 3, Makapansgat Member 4, Taung Hrdlička deposits, Sterkfontein Member 4, Kromdraai B, Sterkfontein Member 5, Kromdraai A, Swartkrans Member 1, Swartkrans Member 2, Swartkrans Member 3, Gondolin,

Table 3

List of shared species at southern African faunal assemblages, in optimal seriated order. A) Absolute frequencies of shared species. B) Faunal Resemblance Index (FRI). (Site codes are listed in Table 1).

A

	MAK4	MAK3	TAUH	STS4	KROB	STS5	KROA	SWT1	SWT3	SWT2	GOND	PLOV	CORN	EFTM	EQUU	FLOS	COHA	KLAS
MAK4	12	12	10	4	1	3	3	0	0	0	0	0	0	0	0	0	0	0
MAK3	12	19	5	15	5	2	7	7	1	1	2	0	1	0	0	0	0	0
TAUH	4	5	7	5	4	1	3	4	1	1	1	1	0	0	0	0	0	0
STS4	10	15	5	24	8	8	10	11	4	3	1	1	1	2	2	1	1	1
KROB	4	5	4	8	12	4	9	9	5	4	1	2	2	1	1	1	1	0
STS5	1	2	1	8	4	11	8	6	6	4	2	1	3	2	2	2	2	0
KROA	3	7	3	10	9	8	23	15	12	8	8	7	6	6	7	4	6	5
SWT1	3	7	4	11	9	6	15	26	16	13	7	5	5	8	8	3	4	6
SWT3	0	1	1	4	5	6	12	16	20	16	8	7	5	9	10	5	4	5
SWT2	0	1	1	3	4	4	8	13	16	16	7	5	5	8	7	4	2	3
GOND	0	2	1	1	1	2	8	7	8	7	11	5	5	6	5	4	4	3
PLOV	0	0	1	1	2	1	7	5	7	5	5	10	3	6	6	4	5	3
CORN	0	1	0	1	2	3	6	5	5	5	5	3	11	9	4	6	5	3
EFTM	0	0	0	2	1	2	6	8	9	8	6	6	9	21	12	9	8	10
EQUU	0	0	0	2	1	2	7	8	10	7	5	6	4	12	24	13	11	14
FLOS	0	0	0	1	1	2	4	3	5	4	4	4	6	9	13	15	8	6
COHA	0	0	0	1	1	2	6	4	4	2	4	5	5	8	11	8	13	9
KLAS	0	0	0	1	0	0	5	6	5	3	3	3	3	10	14	6	9	17

B

	MAK4	MAK3	TAUH	STS4	KROB	STS5	KROA	SWT1	SWT3	SWT2	GOND	PLOV	CORN	EFTM	EQUU	FLOS	COHA	KLAS
MAK4	100	100	57	83	33	9	25	25	0	0	0	0	0	0	0	0	0	0
MAK3	100	100	71	79	42	18	37	37	5	6	18	0	9	0	0	0	0	0
TAUH	57	71	100	71	57	14	43	57	14	14	14	14	0	0	0	0	0	0
STS4	83	79	71	100	67	73	43	46	20	19	9	10	9	10	8	7	6	6
KROB	33	42	57	67	100	36	75	75	42	33	9	20	18	8	8	8	0	0
STS5	9	18	14	73	36	100	73	55	55	36	18	10	27	18	18	18	0	0
KROA	25	37	43	43	75	73	100	65	60	50	73	70	55	29	30	27	29	29
SWT1	25	37	57	46	75	55	65	100	80	81	64	50	45	38	33	20	35	35
SWT3	0	5	14	20	42	55	60	80	100	100	73	70	45	45	50	33	31	29
SWT2	0	6	14	19	33	36	50	81	100	100	64	50	45	50	44	27	15	19
GOND	0	18	14	9	9	18	73	64	73	64	100	50	45	55	45	36	36	27
PLOV	0	0	14	10	20	10	70	50	70	50	50	100	30	60	60	40	50	30
CORN	0	9	0	9	18	27	55	45	45	45	45	30	100	82	36	55	45	27
EFTM	0	0	0	10	8	18	29	38	45	50	55	60	82	100	57	60	62	59
EQUU	0	0	0	8	8	18	30	33	50	44	45	60	36	57	100	87	85	82
FLOS	0	0	0	7	8	18	27	20	33	27	36	40	55	60	87	100	62	40
COHA	0	0	0	8	8	18	46	31	31	15	36	50	45	62	85	62	100	69
KLAS	0	0	0	6	0	0	29	35	29	19	27	30	27	59	82	40	69	100

Plovers Lake, Cornelia, Elandsfontein Main Site, Florisbad/Equus Cave, Cave of Hearths, and Klasies River Mouth. The true chronology may vary slightly, for the seriations cannot effectively differentiate between penecontemporaneous sites. Nevertheless, the robusticity of the method suggests that the seriated sequence can provide a generally sound chronological framework for interpreting the southern African fossil record.

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A NEW FIND OF *MEGALOTRAGUS PRISCUS* (ALCELAPHINI, BOVIDAE) FROM THE CENTRAL KAROO, SOUTH AFRICA

by

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ABSTRACT

We document the occurrence of the Florisian, or late Quaternary, form of the giant alcelaphine, *Megalotragus priscus*, from dongas on the Ongers River, near Britstown in the central Karoo. This is significant as it confirms the occurrence of the species in the Karoo and it suggests significantly wetter environments and productive grasslands in the central Karoo in pre-Holocene times. The present-day Karoo environment did not maintain populations of large ruminant grazers similar to *M. priscus*, and other specialized Florisian grazers, prior to the advent of agriculture and pasture management. Aridification in recent times is the likely cause of changes in grassland quality and the local dissappearance of these animals, if not their extinction.

KEY WORDS: Alcelaphine evolution, Florisian mammals, Late Pleistocene extinction

INTRODUCTION

The giant alcelaphine antelope, *M. priscus*, is one of six extinct species which define the Florisian Land Mammal Age (Brink 1994; Hendey 1974). The species is known from a variety of late Quaternary sites in the interior of southern Africa as well as from the Cape Ecozone in pre-Holocene times (Brink 1987; Bender & Brink 1992; Klein 1980, 1984; Klein & Cruz-Uribe 1991). Ecologically the Florisian *M. priscus* is a specialised grazer on the basis of its dental morphology and its association with grassland faunal elements (Brink 1987, 1988; Brink & Lee-Thorp 1992; Klein 1980). The fossil record of *M. priscus* is best documented in the Orange Free State, the North-Western Cape, Transvaal and in the Cape Ecozone (Klein 1980). Apart from the identification of metapodial remains from Blydefontein, Northern Karoo (Bousman *et al.* 1988), the giant alcelaphine is unknown from fossil localities in the Karoo region (Klein 1980). In this paper we report on fossil mammal material from the Britstown district which includes remains of the Florisian species *M. priscus*. This find confirms the presence of the giant alcelaphine in the Karoo during the late Quaternary and suggests a much wetter palaeoenvironment compared to the modern semi-arid conditions of the Karoo.

In Africa the spread of grasslands was a key factor in the evolution and dispersal of open-habitat taxa such as alcelaphine bovids and equids (Churcher & Richardson 1978; Gentry 1978). A feature which seems to characterize bovid evolution in the Plio-Pleistocene of sub-Saharan Africa is the tendency towards regional differentiation through time. In southern Africa this is evidenced by an increase in endemism towards the late Quaternary, of which the modern bovid fauna is the product (Vrba 1976, 1979; Bigalke 1978; Gentry 1978; Gentry & Gentry 1978). One example of this increase in endemism is the evolution of *M. priscus*. An ancestral form, *M. katwinkeli*, is known from East Africa and possibly some southern African Plio-Pleistocene sites, but in the Middle and Late Pleistocene the genus *Megalotragus* is only found in southern African fossil assemblages (Gentry & Gentry 1978; Klein 1984; Marean 1992). Within the genus *Megalotragus* there also appears to be an evolutionary development from the Middle Pleistocene to the Late Pleistocene, in accordance with a general trend towards increased regional differentiation as also seen in other alcelaphine bovids, such as the black wildebeest *Connochaetes gnou* (Brink 1993). In contrast to the view of Gentry (1978), who recognises only one species, i.e. *M. priscus,* in southern African fossil assemblages, we consider the earlier Cornelian specimens to be sufficiently distinct from the later Florisian ones to warrant specific distinction. The earlier Cornelian species, *M. eucornutus,* tends to have horns which are more vertically inserted and horn bases with unfused pedicels, while the later Florisian forms show a tendency towards greater horn divergence and well developed fused horn pedicels, which is considered to be an advanced feature in bovids (Gentry & Gentry 1978, Vrba 1979; Bender & Brink 1992). Ecologically this development is mirrored by an increased grassland component of the large mammal faunas from the Middle to the Late Pleistocene (Cooke 1974; Klein 1984; Brink 1987). This trend reached its climax in the interior of southern Africa during the late Quaternary and it appears that the Florisian Land Mammal Age was characterised by a complex grazing system, reminiscent of the

Serengeti grazing succession (Brink 1987; Brink & Lee-Thorp 1992).

LOCALITY AND GEOLOGY

The fossil material was found in one locality in erosional gullies ("dongas") in the bank of the Ongers River, approximately 70 km north of Britstown in the Northern Cape Province. The area is known as the T'Kuip Hills and forms an elevated landscape (Figure 1). The Ongers River, which forms the border between the districts of Britstown and Prieska, follows a fault east of the high ground that forms the T'Kuip hills. Denudations of the river bank exposed the fossil material. The exposed sediments, from which the fossil material was collected, consist of fine grained silts in which calcrete occurs. The fossil material was collected during a student excursion of the Department of Geology, University of the Orange Free State, in 1993.

FOSSIL MATERIAL

The fossil material is accessioned in the collections of the Florisbad Quaternary Research Department of the National Museum, Bloemfontein and is numbered as follows; ONG-1 horncore, ONG-2 dentary, ONG-3 distal tibia.

Bovidae
Alcelaphini
Megalotragus priscus (Broom, 1913)

The material consists of the lower part of a right horncore (Figure 2) and a partial right dentary of a sub-adult individual (Figure 3). Although the horn base is only partially preserved, it is clear that the horn pedicels were fused at the midline, as in *M. priscus* from Florisbad. The pedicels of Cornelian specimens are incompletely fused, which is considered a primitive feature (Vrba 1979; Bender & Brink 1992). However, it is likely that the horns were less laterally orientated (Figure 2) than in the Florisbad specimens. Gentry & Gentry (1978) noted that horncores from Cornelia appear to be more vertically inserted and speculated that this may be a primitive feature or that it may reflect ontogenetic age, where younger individuals have less divergent horncores. Another possible explanation for the variability in horncore diversion in Florisian specimens is that it reflects sexual dimorphism. A plot of basal dimensions of Florisian horncores in the collections of the Florisbad Quaternary Research Department of the National Museum shows that the smaller specimens had less compressed bases (Figure 4). Apart from two complete specimens from Florisbad (FLO 2273 and FLO 2899), we were able to measure

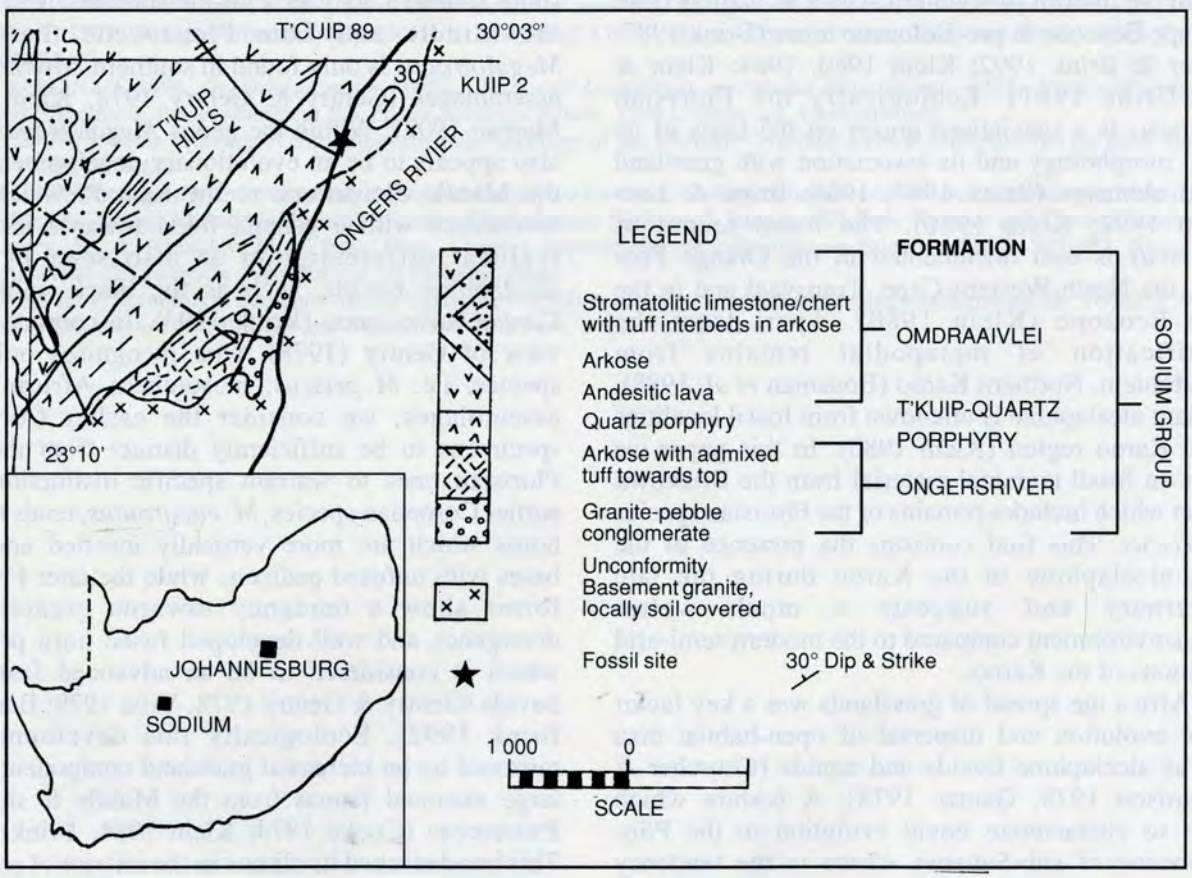

Figure 1. Maps showing the locality of the fossil material and surrounding bedrock geology where the Ongers River flows across an elevated landscape to the north of Britstown, Northern Cape Province.

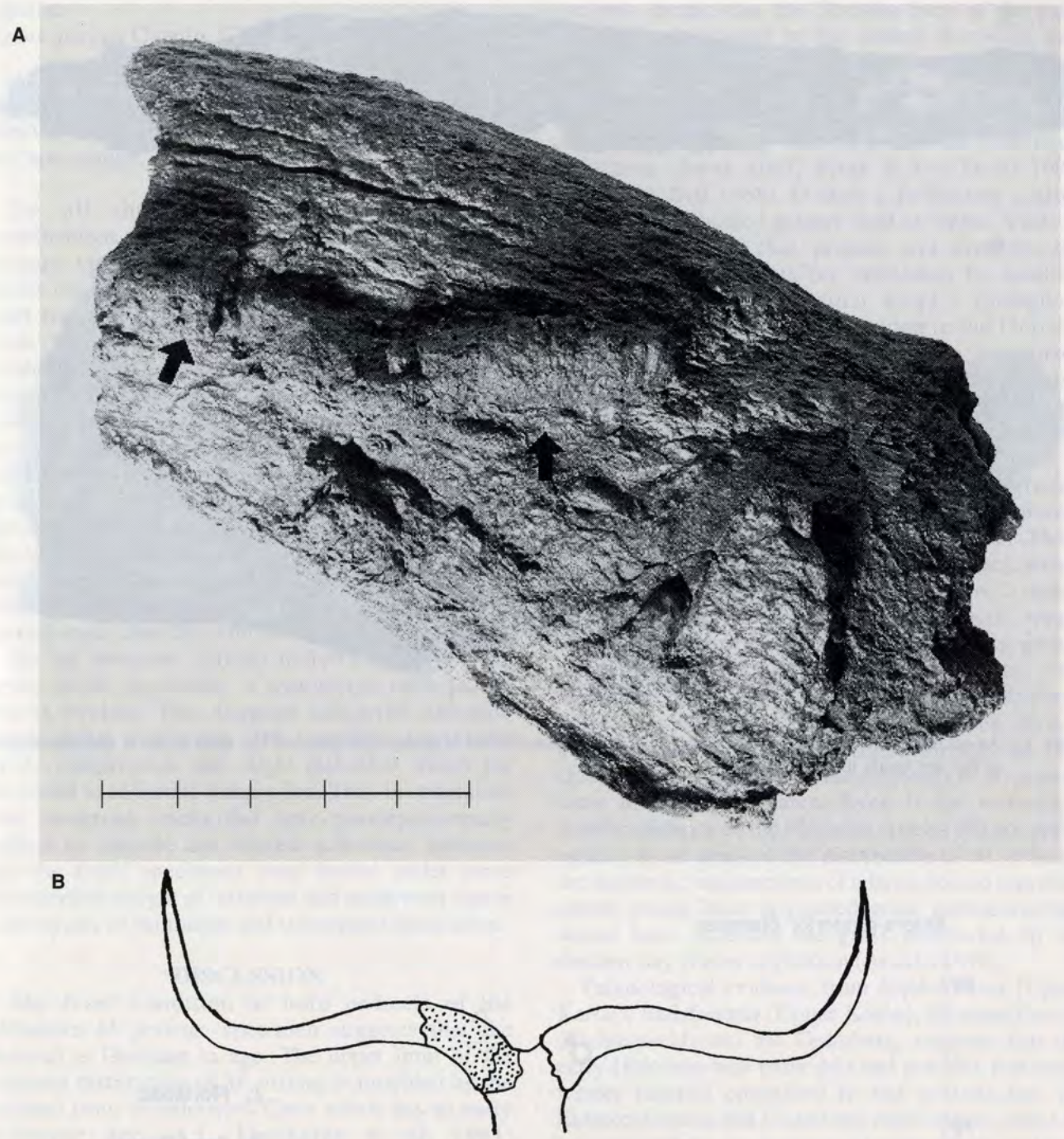

Figure 2. (A) Right horncore fragment of *Megalotragus priscus* (scale in centimetres). The illustration (B) shows the approximate natural position of the fragment .

additional specimens from the Sand River (catalogue number C. 1711) and from the Modder River (catalogue number C. 1607). The specimen from the the Sand River is a virtually complete horncore pair which shows well-developed fused pedicels, but more vertically inserted horncores than the much larger Florisbad specimens. If the small size of the Sand River specimen is taken as an indication that it is female, then pronounced basal compression and wide diversion in Florisian *Megalotragus* horncores could be taken as male characteristics. It is likely that the Sand River specimen is adult, since the horncores are virtually complete and show fully developed curvatures. In this context the Britstown specimen was probably a female.

The partial right dentary comprises only the horizontal ramus that contained milk premolars and developing molars. It is broken between M_2 and M_3, and lacks the symphysial region and the ascending ramus; dP_3 and most of dP_4 are missing. The hypoconid of dP_4 shows a stage of late wear, M_1 is in mid-wear, M_2 in early wear and M_3 is about to erupt, but is within the crypt. The short premolar row and the absence of P_2 are both apomorphic features characteristic of *Megalotragus priscus* (Gentry & Gentry 1978).

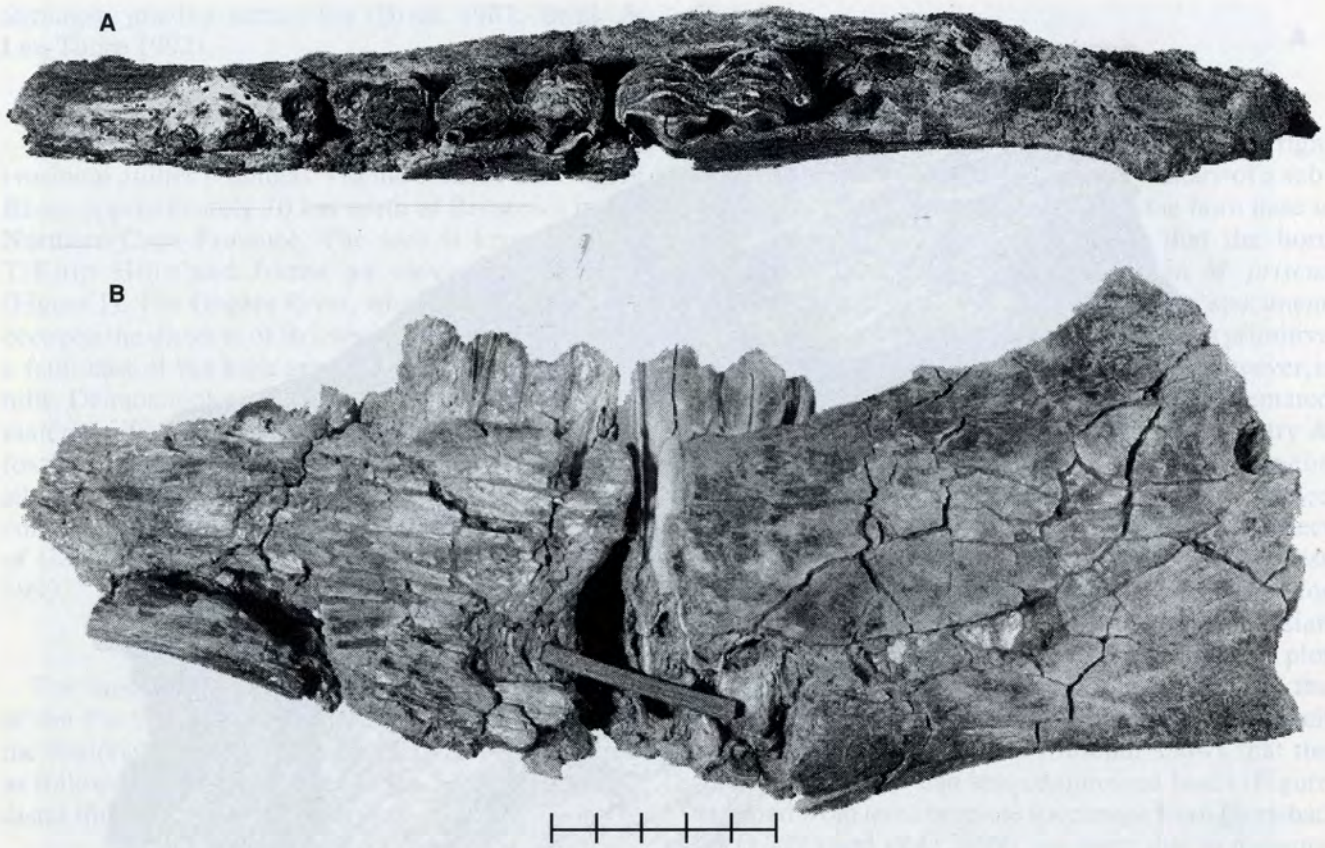

Figure 3. An occlusal view (A) and lingual view (B) of a right mandible of *Megalotragus priscus*. The third molar is still embedded in the jaw (scale in centimetres).

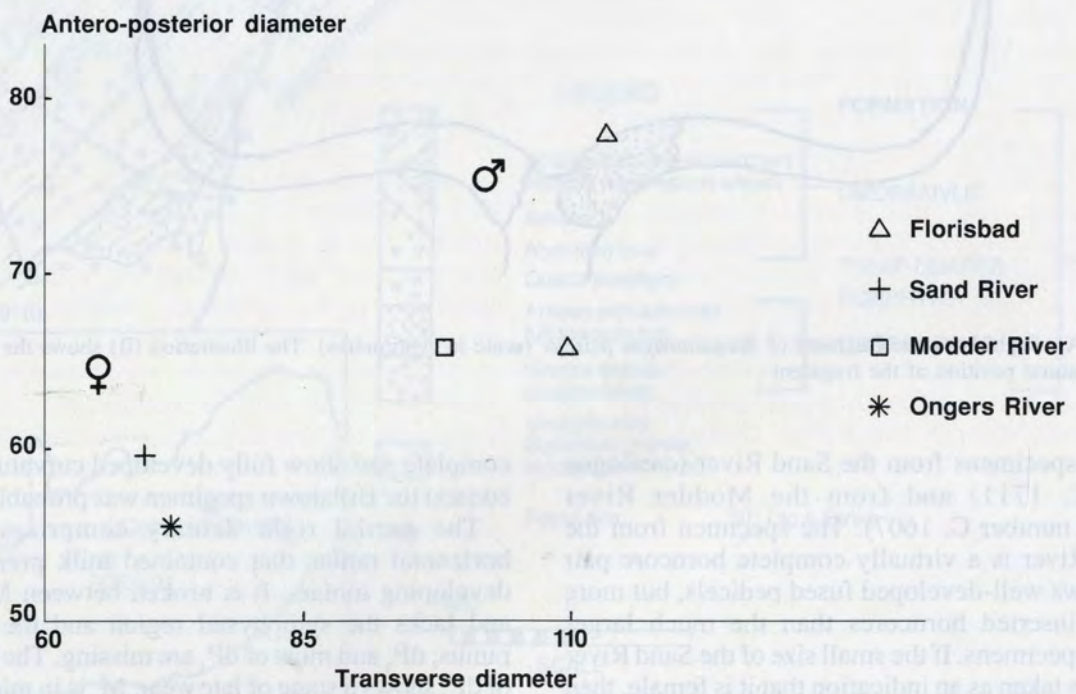

Figure 4. A scatter plot of *Megalotragus* horncore measurements. The two clusters are interpreted as representing sexual dimorphism.

Equidae
Equus quagga Gmelin, 1788

A distal fragment of an equid tibia, although large (distal maximum breadth: 73.8 mm; distal maximum depth: 54.0), is tentatively assigned to the plains zebra or Cape quagga.

TAPHONOMY

On all three specimens postdepositional modifications virtually obliterate possible traces of primary taphonomic agents. Only the equid tibia shows evidence of pre-depositional breakage, as the shaft was clearly shattered when the bone was still fresh. This may have been the result of the bone-crushing activities of either humans or carnivores. However, the extent of postdepositional alteration to the specimen precludes the identification of stone tool cutmarks or carnivore toothmarks. Unfortunately not much is known about the sedimentary context of the specimens and therefore, the primary agents of accumulation cannot be established. However, the typical reddish-brown colour of the specimens and calcrete adhesions suggest a matrix of aeolian soil which had become saturated by calciumcarbonate-rich ground water after deposition.

On the horncore, infilled hollows caused by the larvae of the horn moth, *Ceratophaga vastella*, are clearly evident. This suggests sub-aerial exposure before burial took place. The mandible specifically shows compression and slight distortion which are attributed to sediment compaction. This, in conjuction with numerous cracks that were postdepositionally infilled by calcrete and calcrete adhesions, indicates that the fossil specimens were buried under some considerable weight of sediment and underwent one or more cycles of saturation and subsequent dessication.

DISCUSSION

The fused condition of horn pedicels of the Britstown *M. priscus* specimen suggests that the material is Florisian in age. The upper limit of the temporal distribution of *M. priscus* is provided by the material from Wonderwerk Cave which has an early Holocene age (A.I. Thackeray et al. 1981; J.F. Thackeray 1983). From the Cape coastal zone giant alcelaphine material from Nelson Bay Cave dates to ca. 12 000 years ago (Klein 1984). The lower age limit of the Florisian Land Mammal Age is not firmly established, but a reasonable consensus is an age of not much older than end Middle Pleistocene, which is the assumed age for the Florisbad Spring assemblage (Klein 1984; Brink 1987). Although it is not possible to give a more precise age estimate of the fossil material than to suggest that it is of pre-Holocene late Quaternary age, it is likely, judging from its relatively unmineralised state, that the material is not old and probably not much older than terminal Pleistocene.

Even if the precise age of the specimens is not known, the value of the material lies in the fact that we are now certain that the Florisian form of the giant alcelaphine occurred in the central Karoo in pre-Holocene times. Ecologically this is significant, since the species has been associated with a range of other Florisian grazers in a grazing system resembling the present-day grazing succession of the Serengeti grasslands (Brink 1987; Brink & Lee-Thorp 1992; Gwynn & Bell 1968). In such a facilitating grazing system larger-bodied grazers feed at higher levels in the grassland and thus prepare and stimulate the individual grass plants for utilisation by smaller-bodied grazers. The extinct Bond's springbok, *Antidorcas bondi*, has a key position in the Florisian grazing system as the smallest of the specialized grazers and can be seen as a reliable indicator of highly productive grasslands (Brink & Lee-Thorp 1992). As the smallest of the specialised grazers, the presence of *A. bondi* in the fossil record may well be used to predict the geographical limits of the Florisian grazing system, which probably included at least the present highveld and most of the Karoo (Brink & Lee-Thorp 1992). *M. priscus*, as a large grazing ruminant, would have acted as one of the coarse grass feeders in such a grazing system. Grazing by larger animals would cause regeneration of nutrient-rich grass plants necessary for smaller-bodied ruminants. The hypothesis that virtually the entire interior of southern Africa, including the Karoo, accomodated such a grazing system at certain times during the late Quaternary is supported by the discovery of *M. priscus* from the Britstown area. Even if the ecological interdependance of the Florisian species did not apply equally in all areas of the distribution of *M. priscus*, the metabolic requirements of a large-bodied ruminant grazer would have demanded grass production that would have exceeded the grass production in the modern-day Karoo vegetation (Acocks 1975).

Palynological evidence from Blydefontein (Upper Karoo), Badsfontein (Upper Karoo), Eksteensfontein (Richtersveld) and the Cedarberg, suggests that the early Holocene was more arid and possibly had more winter rainfall compared to the present-day. At Eksteensfontein and Cedarberg aridification seems to be indicated by an increase of "succulent" pollens. Modern patterns of seasonality and rainfall were probably only established from the middle Holocene (Bousman et al. 1988; Scott 1992; Scott 1994; Scott in press). The existence of *M. priscus* in the Karoo could be seen as additional evidence for wetter conditions in pre-Holocene times and it is probable that its dissappearance from this area and elsewhere in central southern Africa at the end of the Late Pleistocene reflects early Holocene aridification on a wide-scale.

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QUANTIFYING MORPHOLOGICAL VARIABILITY WITHIN EXTANT MAMMALIAN SPECIES

by

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ABSTRACT

In this study we attempt to establish a baseline for measuring species variability in the palaeontological record by using linear regression analysis on sets of measurements from extant mammalian species (males and females within species). In particular, this study explores the standard error of the m-coefficient ($s.e._m$), derived from linear regression analyses associated with equations of the form $y = mx + c$, to quantify the degree of morphological variability within extant mammalian species. The slope m generally centres around 1.00. Even though the species in this study range in size from small rodents to large ungulates, $s.e._m$ values show a normal distribution around a mean of 0.035. The approach outlined here has potential application in palaeontological contexts where there is uncertainty about any two specimens being conspecific.

One of the most pressing problems in palaeontology concerns the question whether certain specimens are attributable to a single species. Central to this taxonomic issue is how to quantify morphological variability. Previous attempts to tackle this have included the use of multivariate techniques of the kind that have been used recently by Shea *et al* (1993). Here, a simple technique has been developed whereby the degree of morphological variability in modern species can be quantified, using material that is unquestionably representative of single species. The intention is to compare measurements from a single specimen against a comparable set of measurements from another specimen of the same species; we undertake linear regression analyses for several such comparisons, and determine whether there is any regularity in the standard error of the slope m in equations of the form $y = mx + c$, when dealing with modern mammalian species. The main objective is to explore the potential of using $s.e._m$ to address taxonomic problems.

TABLE 1.
List of species analyzed in this study.

Order	Family	Species
Rodentia	Muridae	*Otomys irroratus*
		Otomys angoniensis
		Aethomys chrysophilus
		Aethomys ineptus
Hyracoidea	Procaviidae	*Procavia capensis*
Lagomorpha	Leporidae	*Lepus saxatilis*
		Prolangus capensis
Carnivora	Hyaenidae	*Hyaena brunnea*
	Felidae	*Felis lybica*
		Felis caracal
		Felis nigripes
		Panthera leo
Primates	Cercopithecidae	*Cercopithecus aethiops*
		Cercopithecus mitis
	Lorisidae	*Galago crassicaudatus*
		Galago moholi
Artiodactyla	Suidae	*Phacochoerus aethiopicus*
		Potamochoerus porcus
	Bovidae	*Damaliscus lunatus*
		Taurotragus oryx
		Tragelaphus scriptus
		Hippotragus niger
		Kobus ellipsiprymnus
		Bos taurus

MATERIALS AND METHODS

Twenty five extant non-hominid mammalian taxa, listed in Table 1, were chosen to represent a broad range of taxonomic groups and body sizes. The taxa encompass 6 mammalian orders (Rodentia, Hyracoidea, Lagomorpha, Carnivora, "Primates", and Artiodactyla), with representatives from 9 families. The species range in average adult body mass from 0.1 to 650 kg, data derived primarily from Skinner and Smithers (1990).

Initially, linear measurements were taken on 5 males and 5 females of each species represented in collections at the Transvaal Museum in Pretoria, South Africa. For each species, only adult individuals of known sex were chosen. Ten measurements per specimen were taken, of which seven were craniofacial and three mandibular (Table 2). These measurements were considered to be generally representative of overall size of the cranium and mandible. For purposes of this exploratory study, data from the largest male and smallest female for each species were used in regression analyses, with data for females on the x axis. By utilizing the extremes rather

TABLE 2.
Measurement definitions

1. Maximum cranial length: greatest length of the skull from the anterior edge of the nasal aperture to the most posterior point on the occiput.
2. Maximum cranial width: greatest width of the braincase at the dorsal root of the squamosals.
3. Interorbital breadth: least breadth between the orbits.
4. Zygomatic arch length: greatest arch length.
5. Greatest cranial height: greatest height of skull perpendicular to the horizontal plane and through the bullae.
6. Mandibular height: measured from the ventral margin of the jaw to the alveolar border between the last two molars.
7. Greatest vertical diameter of the foramen magnum.
8. Length of mandible: from the posterior surface of the condylar process to the anteroventral edge of incisor alveolus.
9. Tooth row length: maximum length of the maxilla, from the anterior edge of incisor alveolus (where present; alternatively, from the most anterior extent of mid-sagittal maxillary bone, as in ruminants without incisors), to the posterior surface of M^3 (or last molar) alveolus.
10. Length of jaw: greatest length of the mandible from the anterior edge of I_1 to the posterior surface of the angular process.

than species means, we hope to document variation within samples for each of the 25 mammalian species ranging in size from small rodents to large ungulates, for purposes of determining whether there is any patterning in the standard error of slope *m* in equations of the form $y = mx + c$, irrespective of variability in body size. The standard error of the slope *m* is designated $s.e._m$.

High $s.e._m$ values can be expected to relate to high morphological variability when comparing any two specimens, reflected also by a high degree of scatter of measurements around a regression line. By contrast, low $s.e._m$ values can be expected to relate to small morphological differences, or very little scatter around a regression line.

RESULTS

As expected when dealing with specimens attributable to the same species, m-coefficients approximate 1,0 (mean for 25 taxa is 0.997 +/- 0.019). Of particular interest is the fact that $s.e._m$ values for 25 taxa approximate a normal distribution around a mean value of 0.035 (+/- 0.014) when data for all species are analysed (Table 3).

The $s.e._m$ values listed in Table 3 do not correlate with body mass (r=0.19). By contrast, the standard error of the *y*-intercept ($s.e._y$) is correlated with body mass (r=0.78).

CONCLUSIONS

This study indicates that morphological variability within mammalian species, as expressed by $s.e._m$, appears to centre around 0.035, irrespective of variability in body size of the mammalian species included in this exploratory analysis. This result applies to craniofacial variables listed in Table 2, for a

TABLE 3

Values for slopes m and constants c in equations of the form y = mx + c, relating two specimens of the same species against each other, in this instance measurements of the largest male (y-axis) against those of the smallest female (x-axis) in samples included for this study.

	m	*c*	$s.e._m$	$s.e._y$
Felis caracal	0.989	-0.539	0.030	2.976
Felis nigripes	1.007	-0.649	0.037	2.096
Felis libyca	0.988	-0.754	0.045	3.484
Panthera leo	0.987	1.541	0.019	4.481
Hyaena brunnea	0.979	-1.037	0.024	5.209
Galago crassicaudatus	1.009	0.604	0.045	2.520
Galago moholi	0.992	-2.508	0.049	1.500
Cercopithecus mitis	0.996	-2.227	0.054	4.473
Cercopithecus aethiops	1.026	-0.232	0.027	2.185
P. ursinus	1.029	-2.357	0.047	7.105
Otomys irroratus	0.969	-0.754	0.048	1.382
Otomys angoniensis	1.031	-3.631	0.038	0.983
Pronolagus rupestris	0.958	3.280	0.036	0.250
Aethomys chrysophilus	1.012	-1.870	0.020	0.468
Aethomys ineptus	1.004	-0.289	0.056	1.256
Lepus saxatilis	0.999	-0.174	0.010	0.067
Procavia capensis	0.978	-0.607	0.040	2.828
Damaliscus lunatus	0.990	-0.269	0.012	4.849
Taurotragus oryx	1.028	-1.696	0.067	16.950
Bos taurus	1.004	-2.381	0.050	16.730
Kobus ellipsiprymnus	0.996	1.187	0.034	9.496
Tragelaphus scriptus	0.965	0.117	0.025	5.998
Hippotragus niger	1.013	0.463	0.027	11.650
Potamochoerus porcus	0.992	-0.178	0.026	9.464
Phacochoerus aethiopicus	0.990	-1.365	0.019	5.667
MEAN:	0.997	-0.653	0.035	4.963
STANDARD DEVIATION:	0.019	1.441	0.014	4.595

range of species listed in Table 1, but can be tested for other variables for other taxa in future analyses. Such results are of potential value for purposes of testing whether particular specimens are conspecific, especially in cases where this is uncertain in palaeontological contexts.

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PRELIMINARY ANALYSIS OF THE FAUNA FROM BUFFALO CAVE, NORTHERN TRANSVAAL, SOUTH AFRICA

by

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ABSTRACT

Systematic excavations at Buffalo Cave in the Makapan Valley were begun in October 1993. This paper presents our preliminary analysis of the faunal assemblage from this site, including new *in situ* fossils and the collections which have been housed at the Bernard Price Institute, Palaeontology since the 1940's. Our palaeoecological reconstruction suggests that the local environment at Buffalo Cave at the time of deposition was an open country grassland or savanna, including a high proportion of alcelaphine bovids and other grazing fauna. However, the presence of other taxa, particularly of tragelaphines, hippotragines, and reduncines, may indicate that a more wooded habitat including a local water source, could also have been part of the Buffalo Cave environment during some part of its depositional history. The fauna overall indicates that deposition occurred during the Pleistocene, rather than the Pliocene. Thus, the environmental and temporal information presently available suggests that the Buffalo Cave fauna represents an environment and time period distinct from other sites in the Makapansgat Valley (i.e., the Limeworks and Cave of Hearths).

INTRODUCTION

Knowledge of bone-breccia deposits from the Makapan Valley probably dates back to the turn of the century, as a result of the extensive limeworks mining operations throughout the region (Mason 1962, 1988). At the very least, amateur palaeontologists had learned of these fossiliferous beds by about 1920 from locals employed by the limeworks operations (Eitzman 1958).

Although the Makapan Limeworks site has been the major focus of palaeoanthropological research in this region (e.g., Cadman & Rayner 1989; Dart 1925, 1948, 1952, 1957; Ewer 1956, 1958; Gentry 1970; Kitching 1953, 1965, 1980; Maguire B. 1980a; Maguire, J.M. *et al.* 1980, 1985; Partridge 1979, 1986; Rayner *et al.* 1993; Torien 1952; Vrba 1982, 1987; Wells & Cooke 1956; and others), other fossil-bearing sites are present in the valley, and have drawn the interest of palaeontologists, as well as archaeologists (e.g., Broom 1937; Cooke 1962; Mason 1971, 1988; van Riet Lowe 1948). In 1937, from another former mining operation across the valley from the Limeworks, Broom (1937) discovered and described a fossil which he believed to represent an extinct dwarf buffalo. He named the species *Bos makapani*, and the site has become known as "Buffalo Cave". No systematic excavations were ever undertaken there, and the site has only a few mentions in palaeontological literature (Boas *et al.* 1982; Broom and Jensen 1946; Gentry 1978; van Riet Lowe 1948). Periodic excursions by the University of the Witwatersrand since the 1940's (J.W. Kitching and P.V. Tobias pers. comm.) have resulted in a modest collection of bone breccia blocks which are stored at the Bernard Price Institute for Palaeontological Research at the University of the Witwatersrand.

Beginning in October 1993, a systematic palaeontological excavation has been conducted at Buffalo Cave under the auspices of the Hominid Palaeoecology Research Programme (HPRP) at the University of the Witwatersrand. The objective of the HPRP, and therefore of the excavations at Buffalo Cave and elsewhere, is the analysis of evolutionary changes in the fauna and ecosystems of southern Africa during the time period in which early hominids were evolving. The palaeontological remains recovered are thus an important part of an ever-growing database, and have the potential to fill in important temporal gaps in our knowledge concerning environmental changes during the more recent evolutionary history of the southern African region. This report is our preliminary assessment of the Buffalo Cave fauna, including our initial interpretation of the ecological and temporal setting of the site in relation to other South African Plio-Pleistocene localities. Obviously, our interpretation of the palaeoecological conditions at Buffalo Cave is subject to modification following the future recovery of *in situ* materials during our ongoing excavations.

CONTEXT OF BUFFALO CAVE FOSSILS

Buffalo Cave is located in the Makapan Valley at approximately 24° 08'S 29° 11'E, 19 km east-northeast of Potgietersrus in the Northern Transvaal (Figure 1).

Like other palaeontological sites in the valley, Buffalo Cave was subjected to lime mining operations during the 1920's and '30's (Eitzman 1958; Maguire B. 1980b; Mason 1988; van Riet Lowe 1948). Thus, the materials there consist of *ex situ* breccia blocks in various mining dumps, as well as *in situ* stratified breccias which represent the ancient cave fillings. These breccias appear to be of several types (see below), but the geology of the deposits has not yet been thoroughly studied. Buffalo Cave was a dolomitic cave system similar to other Transvaal fossil-bearing breccia localities (e.g., Sterkfontein, Swartkrans, Kromdraai), and geological processes described by Brain (1958, 1976, 1978, 1993) are generally applicable.

Identifications were made as part of an inventory of all materials so far collected, and rely heavily on dental fossils, either isolated or those still encased in breccia blocks. Horn cores were also useful for classification of bovids. For the purposes of this inventory, initial processing of breccia blocks was only carried out to the extent necessary for identification, such as to expose the occlusal surface or crowns of teeth. Postcranial remains are largely unidentified at present, and will certainly augment our analysis in the future.

At present, many of the identifications are only to tribe or family, although specimens were classified to genus or species where possible; these identifications

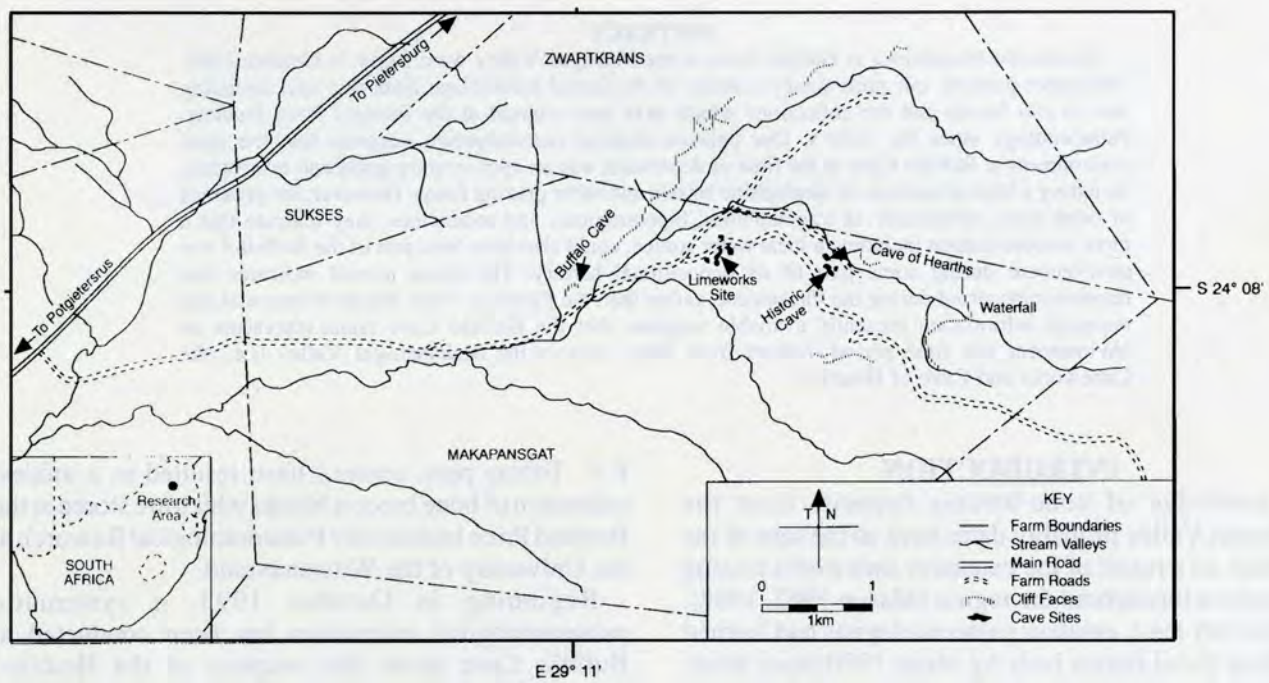

Figure 1. Regional map of the Makapan Valley showing the location of Buffalo Cave in relation to other major cave sites (after Wells & Cooke 1956, and Rayner et al. 1993).

MATERIALS & METHODS

This analysis utilises the collections at the Bernard Price Institute for Palaeontological Research (BPI) and those from the new excavations during 1993-94. To date, the BPI collections include 538 accessioned specimens; a "specimen" may refer to breccia blocks with one or more fossils exposed on the surface, or to isolated fossils (especially teeth). The recent excavations have so far recovered 103 accessioned specimens, most of which are isolated fossil fragments, although fossiliferous breccia blocks are also included. Blocks and isolated fossils are coded separately so that a block "specimen" may include multiple fossils, which may in future be isolated using acid bath or manual techniques. Blocks are catalogued using a "B #" designation; isolated fossils, whether they were extracted from a block or recovered as such during excavation, are catalogued with the designation "BP/17/#", where 17 is the BPI identification number for Buffalo Cave.

must be considered tentative. No attempt was made to determine minimum numbers of individuals at such a preliminary point in the analysis. However, a rough estimate of the relative abundance of different tribes and other taxonomic groups was obtained from tabulated counts of identified specimens (e.g., for Bovidae or Alcelaphini).

Finally, breccia blocks, and where possible, individual specimens were coded by a preliminary matrix type, subjectively identified on the basis of colour, content, and degree of calcification. Although our sample is restricted at present, these data should allow us in future to recognize distinct depositional events and/or processes, possibly representative of changing environments and/or time periods at Buffalo Cave.

FAUNAL ASSESSMENT

Table 1 presents the breakdown of identified specimens from Buffalo Cave. A total of 87 individual specimens have been identified to the taxonomic level

of tribe or lower (e.g., to genus), although many more have been identified to family. Bovidae is the most common family in the assemblage, including at least 6 tribes and 7 genera. No other taxonomic group is as well-represented, but the mammalian fauna also includes the families Suidae, Felidae, Hyaenidae, Equidae, and Cercopithecidae. Although not included in this analysis, fossil rodents, and at least one reptile (a chelonian) have also been recovered from Buffalo Cave.

Bovidae

Bovid remains include isolated teeth, maxillary and mandibular fragments (including dentition), horn cores, and postcranial elements; identifications are based upon dental materials and horn cores. As indicated in Table 1, the most common bovids recovered are alcelaphines, including the genera *Damaliscus* (and perhaps *Parmularius*) and *Connochaetes*. Alcelaphines are typically medium- to large-sized grazers, inhabiting open grasslands or savannas. The other grazer from Buffalo Cave is the bovine *Syncerus*. In contrast, the fossil fauna also include the tribes Tragelaphini (cf. *Tragelaphus*), Reduncini (*Redunca*), and Hippotragini (cf. *Hippotragus*), which typically occupy a closed or perhaps more forested habitat, and require a nearby water supply (Gentry 1978; Vrba 1987). If not indicative of a differing environment, such a habitat may have existed as a nearby gallery forest (which exists presently in the Makapansgat Valley) at some point during the depositional history of Buffalo Cave.

Certain of the bovid genera at Buffalo Cave (*Tragelaphus*, *Redunca*, and *Hippotragus*) range from Pliocene to Recent times (Gentry 1978; McKee *et al.* 1995; Partridge, 1986; Vrba 1976), thus they are of little use for refined dating purposes. However, given the lack of any characteristic Pliocene genera,it appears that our bovid assemblage generally represents a Pleistocene age for Buffalo Cave. Further identifications to species level will in future assist in refining this conclusion.

Bos makapani, the original bovid fossil described by Broom in 1937, and for which the cave is named, is enigmatic for a number of reasons. First, no other fossils of this species have been identified from the Buffalo Cave collections, nor at any other South African sites. However, East African specimens from Olduvai Bed I (Gentry 1978) and at Hadar have been attributed to this species, the latter dating to approximately 3 mya (Boaz *et al.* 1982).

Second, Broom (1937) placed this species within tribe Bovini, and considered it to be a dwarf species. Gentry (1978) later designated *Bos makapani* to tribe Ovibovini (including the modern musk ox and takin, and also the extinct *Makapania broomi*). Thus, this fossil raises questions concerning the age of the site, it's own taxonomic classification, and also the palaeoecological setting of the deposits in which it was found.

Equidae

Two partial mandibles with intact dentition have been assigned to the genera *Equus* and *Hipparion*, on the basis of differences in the complexity of the enamel pattern for the mandibular cheek teeth (Churcher & Richardson 1978). Broom (1937) first reported the presence of *Equus* cf. *capensis* at Buffalo Cave; we have identified the other specimen as *Hipparion* cf. *libycum*. Like the alcelaphine bovids, both equid taxa are suggestive of a more open grassland environment.

Equus capensis is known from many sites throughout southern Africa from the late Pliocene to the late Pleistocene and, like modern members of the genus, probably occupied regions of arid or semiarid savanna (Churcher & Richardson 1978). *Hipparion libycum* is widespread in North, East, and South Africa from the late Pliocene to late Pleistocene. Unlike earlier forest-living hipparions, this species possessed advanced dental specializations indicating "strong reliance on savanna environments and a grazing habit" (Churcher and Richardson 1978:402).

Suidae

A single molar tooth has been attributed to *Phacochoerus*, a genus occupying open habitats such as floodplains or grassland, and which is known to avoid thick bush and forest (Smithers 1983; Bender 1990). Although a species designation has not been made, this genus is known throughout the Pleistocene of North, East, and southern Africa and also includes the living warthogs (Cooke & Wilkinson 1978). An additional partial cranium has also been assigned to Suidae, although a more precise identification will have to await further processing.

Carnivora

Three carnivore specimens have so far been identified from Buffalo Cave, consisting of two isolated teeth and one distal phalanx. One fragmented tooth is an unidentified premolar or molar, and an isolated canine has been placed within Hyaenidae. The phalanx resembles those of the modern felid genus *Panthera*, and is larger than phalanges of any other modern carnivore for which comparisons were available at the Transvaal Museum. Both of these carnivores are grassland or savannah predators, but without more refined identifications these specimens are not useful for establishing the chronological context of the site.

Primates

Several fossils have been identified to the primate subfamily Cercopithecinae, including a partial cranium, a distal humerus, and a fragmentary palate with the maxillary tooth crowns embedded in breccia. The cranial remains appear to belong to juveniles, but the humerus is large enough to represent an adult-sized baboon. However, these primate remains are either too fragmentary, or incompletely processed, to identify

whether they represent tribe Papionini or Cercopithecini. As a group, cercopithecine monkeys occupy a wide range of habitats, from dense woodland to open savanna (Melnick & Pearl 1986; Tappen 1968).

Table 1: List of Mammalian fauna from Buffalo Cave.

Taxon	Number of identified specimens
PRIMATES	
Cercopithecidae	
Cercopithecinae indet.	3
CARNIVORA indet.	1
Felidae	
Panthera cf. *leo*	1
Hyaenidae	1
ARTIODACTYLA	
Bovidae indet.	240
Alcelaphini indet.	20
Damaliscus	15
Connochaetes	7
cf. *Parmularis*	1
Tragelaphini indet.	2
cf. *Tragelaphus*	8
Hippotragini indet.	1
cf. *Hippotragus*	1
Reduncini	
Redunca	2
Bovini	
Syncerus	1
Antilopini indet.	1
Ovibovini	
Bos makapani	2
Suidae indet.	1
Phacochoerus	1
PERISSODACTYLA	
Equidae	
Equus	1
Hipparion	1
RODENTIA	40
TOTAL	**351**

SUMMARY AND CONCLUSIONS

The Buffalo Cave fauna appears to represent primarily an open country savanna or grassland environment, dominated by alcelaphine bovids. However, there are elements which suggest the presence of a more forested and wetter habitat at some time during the depositional history of the cave. This evidence may indicate one or both of the following: (a) that a gallery forest existed along local waterways; or (b) that climatic change occurred within the Buffalo Cave sequence. This latter prospect is also supported by the presence of several different breccia types at Buffalo Cave.

We believe that the fauna overall is more indicative of a Pleistocene, as opposed to a Pliocene assemblage, but whether it is early or late Pleistocene cannot yet be determined. Most of the genera identified at Buffalo Cave include modern species (e.g., *Damaliscus, Connochaetes, Panthera, Equus, Phacochoerus*), but many of these have long evolutionary histories, and some (*Redunca, Tragelaphus, Hippotragus*) are also found at Makapansgat (Member 3) which is Pliocene in age (Partridge, 1986). Likewise, the presence of *Hipparion*, and also of the enigmatic *Bos makapani*, may suggest an age during the earlier Pleistocene or Pliocene (Churcher & Richardson 1978; Gentry 1978; Boaz *et al.* 1982).

At present we can produce only a simplified reconstruction of the Buffalo Cave environment. Ecosystems are variable and complex even on a local scale, and there are many factors and lines of evidence--microfauna, sedimentology, pollen analysis, cave geomorphology--which we have not yet had the opportunity to employ, and which will hopefully lead to refinement of our preliminary assessment. Like other South African cave sites (Brain 1981, 1993; Cadman & Rayner 1989; McKee 1991; McKee *et al.* 1995; Partridge 1986; Rayner *et al.*1993; Vrba 1975, 1976, 1987), it is possible that a record of environmental change is preserved in the deposits at Buffalo Cave, and that the fauna as currently known represents a temporally and ecologically mixed assemblage.

The Buffalo Cave fauna appears to represent a time period intermediate between the Pliocene Makapansgat Limeworks site (Members 3 and 4) and late Pleistocene sites in the Makapan Valley, particularly Cave of Hearths and Equus Cave. Furthermore, Buffalo Cave has the potential to provide information concerning the nature of local environmental change during the temporal gap between early and late Pleistocene times.

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FOSSIL EGGS AND CENOZOIC CONTINENTAL BIOSTRATIGRAPHY OF NAMIBIA

by

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ABSTRACT

One kind of aepyornithoid and six kinds of struthious eggshells have been found in Cenozoic deposits of Namibia. Field evidence indicates that the six struthious egg types are time successive, and they thus form a useful basis for determining the relative stratigraphic positions of sites at which they occur. Their placement in the geological time scale has been partly tied down by reference to the biostratigraphic position of mammals that occur in association with them.

INTRODUCTION

Fossil eggshells have been found at more than 70 localities in Namibia. Most of them occur in aeolianite successions of the Namib Sand Sea which crops out extensively in the coastal fringe of Namibia as far inland as 100 km.

Fragments of fossilised 'ostrich' eggs have been known to occur in the region for a long time, but it was only in the 1970's and 1980's that geologists W. Shaw, I. Corbett, J. Teller and J. Ward and ecologist M. Seeley collected specimens for study (Ward and Corbett, 1990). At the invitation of NAMDEB (formerly CDM (Pty) Ltd, the Namibia Palaeontology Expedition has carried out research on the eggs in the hope of learning something about them, since the surface morphology of most of the specimens was clearly different from that of modern ostriches (Corbett, 1989).

Initial estimates of a lower Miocene age for the aeolianites at Rooilepel (Pickford, *in* Corbett, 1989) were based on the presence of incisors of *Parapedetes namaquensis* (initially mis-identified as *Paraphiomys pigotti* on account of the overall similarities in size and morphology of the incisors of these two taxa). Subsequent work by the Namibia Palaeontology Expedition on abundant micromammals associated with the eggshells has confirmed this age estimate (Senut *et al.*, 1994) and has shown that aeolianites were accumulating in the region at intervals throughout the Miocene and subsequent periods, albeit with stratigraphic gaps represented by super bounding surfaces, non-deposition and erosion.

Sauer (1966) had previously described eggshell fragments form a borehole at Beisebvlakte (Etosha), northern Namibia, as belonging to *"Struthio" oshanai*. He estimated a Pliocene age for the species. In the early 1980's, J.D. Ward discovered eggshells of *"S." oshanai* in Tsondab Sandstone at the Elim Gullies, northeast of Sesriem, on the eastern fringe of the Namib sand sea. These fragments were from the base of the aeolianite succession, and a Pliocene age for the specimens seemed unlikely. Further eggshell specimens were found at Schmidtfeld by W. Shaw, at Kolmanskop and Grillental by I. Corbett and later by the authors, at Kahari and Narabeb by M. Seeley, at Nutab and West Pan by J. Teller and J. Ward and at Tjirundo by J. Ward. Prospecting by M. Pickford, R. Swart and J. Gold in the Tsauchab (Sesriem) area in 1992, resulted in the discovery of several more eggshell sites. In 1992, aepyornithoid eggs were found at Elisabethfeld by B. Senut and other members of the Namibia Palaeontology Expedition (Senut *et al.*, 1995). Abundant aepyornithoid eggshells with pores deposed in parallel slit like furrows were found *in situ* in the Kamberg area in 1994 by J. Ward and the authors. From this wide scatter of sites it became evident that fossil eggshells would probably be found throughout the Namib Sand Sea. Such has indeed been the case, these and subsequent surveys having discovered over 70 localities (Pickford and Dauphin, 1993; Pickford *et al* 1993; Senut *et al.*, 1994, in press). Some sites are extremely rich in eggshells (thousands of specimens) while others may be poorly endowed with them. Only a few outcrops of aeolianite are devoid of eggshells.

Thus, in Namibia, fragments of struthious eggs are proving to be ideal for biostratigraphy. They are abundant and widely distributed, their morphology changed through geological time in a way which has now been securely documented, and the species to which they belong is easily determined in the field.

DISTRIBUTION OF FOSSIL EGGSHELLS IN NAMIBIA

Thus far, eggshell fragments have been discovered at more than 70 localities in Namibia (Table 1) (Figure 1), and the number of sites is sure to increase as new areas are prospected. An important point is that several of the localities at which eggshells have been collected have also yielded fossil mammals, which permit the ages of the strata to be determined within reasonable limits. It is clear that the Namib sites span much of the Neogene period.

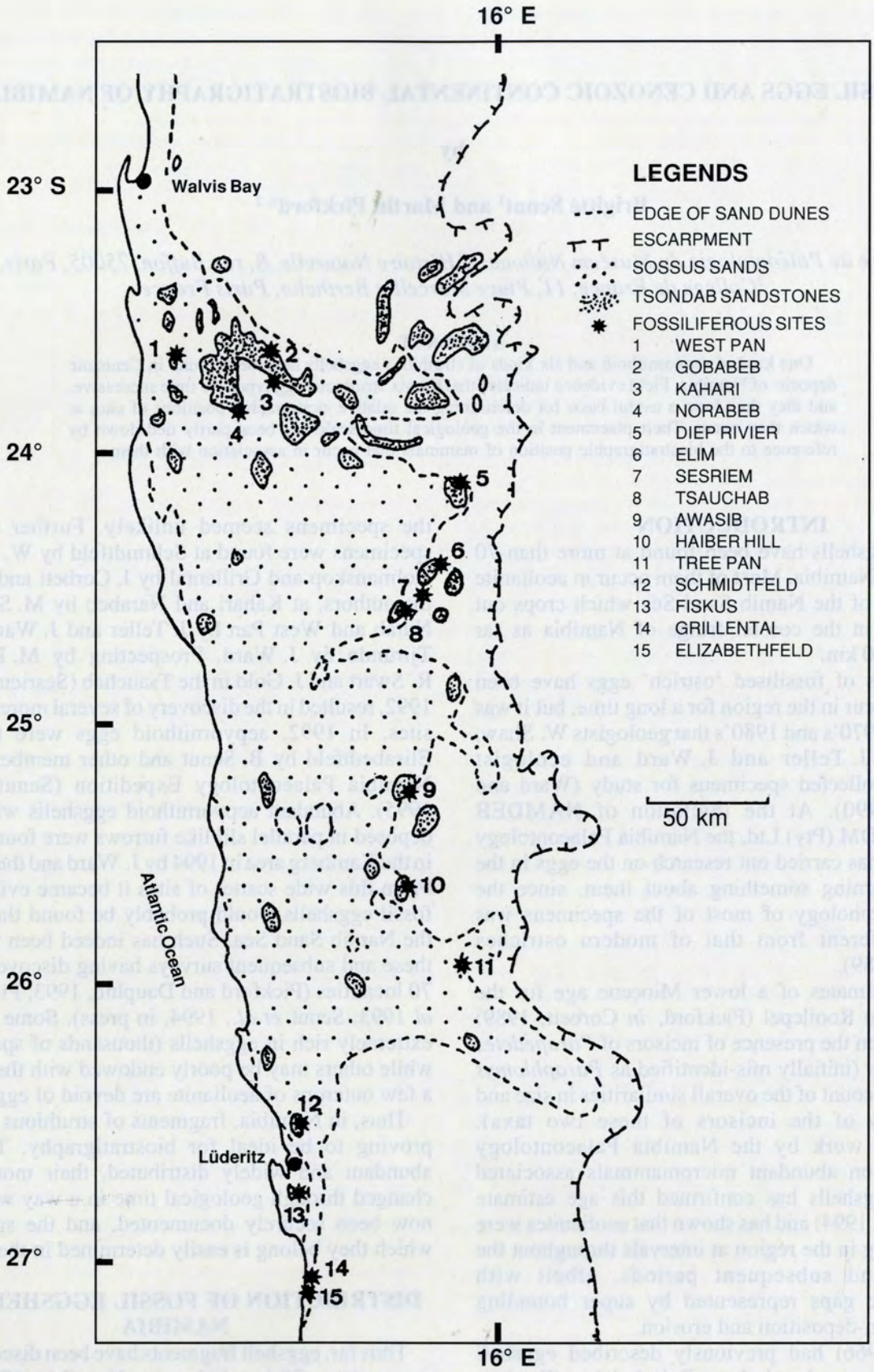


Figure 1: Locality map of the Central Namib showing the disposition of sites which have yielded struthious eggshells

Despite the large number of sites, the diversity of eggshells is low: six of the struthious morphology and one of aepyornithoid structure. Futhermore, where two or more struthious egg types occur in a sequence of aeolianites, they always occur in the same order, but never in the same horizon. On this basis, Pickford *et al.* (1993, 1995); Senut *et al.* (1994) proposed a biostratigraphic ordering of the egg types, even though a complete sequence in superposition had not yet been located. Subsequent surveys in the 120 metre thick

TABLE 1

List of fossil eggshell localities in Namibia.

Aep = Aepyornithoid; D.c. = *Diamantornis corbetti;* D.1. = *Diamantornis laini;* D.w. = *Diamantornis wardi*; N.o. = *Namornis oshanai*; S.c. = *Struthio camelus*; S.d. = *Struthio daberasensis;* ??? = species unidentified

LOCALITIES	SPECIES	AGE
Awasib (Cairn 1, 8-9 km N waterhole)	N.o.	Middle Miocene
Awasib (Cairn 2, 8-9 km N waterhole)	D.c.	Middle Miocene
Awasib (8-9 km N waterhole, low cliffs)	D.w.	Lower Middle Miocene
Awasib (8-9 km N waterhole, mid cliffs)	D.1.	Upper Miocene
Awasib (8-9 km N waterhole, upper cliffs)	S.d.	Post-Miocene
Awasib (8-9 km N waterhole, loose sand)	S.c.	Quaternary
Awasib (10.5 km NNE of waterhole)	D.w.	Middle Miocene
Awasib (9 km NW of waterhole, dune elbow)	S.d.	Post-Miocene
Awasib (8 km W of waterhole, inselberg)	D.w.	Middle Miocene
Buntfeldschuh (loose sand)	S.c.	Quaternary
Daberas (Main aeolianite)	S.d.	Post-Miocene
Daberas (near inselberg)	S.d	Post-Miocene
Daberas (Acheulean deflation surface)	S.c	Quaternary
Diep Rivier (aeolianite)	N.o.	Middle Miocene
Diep Rivier (deflation surface)	S.d.	Post-Miocene
Elbow Dune (9.5 SE of Tree Pan)	D.w.	Middle Miocene
Elbow Dune (loose sand)	S.c.	Quaternary
Elim Gullies (aeolianite)	N.o.	Middle Miocene
Elim (deflation surface)	S.d.	Post-Miocene
Elim (loose sands)	S.c.	Quaternary
Russell's Perch (E-Bay, aeolianite)	S.c.	Quaternary
Elisabethfeld	Aep	Lower Miocene
Etosha (subcrop Beisebvlakte)	N.o.	Middle Miocene
Fiskus (aeolianite)	S.d.	Post-Miocene
Fiskus (green clays)	Aep	Lower Miocene
Gamsberg Pass (conical aeolianite hill)	?Aep	Unknown
Gobabeb (aeolianite)	Aep	Unknown
GP Pan East (aeolianite)	D.w.	Middle Miocene
GP Pan North (aeolianite)	D.w.	Middle Miocene
GP Pan (loose sand)	S.c.	Quaternary
Grillental (green clay)	Aep	Lower Miocene
Haiber Hill (6 km SW)	D.w.	Middle Miocene
Haiber Hill (8 km SW, lower aeolianite)	D.1.	Upper Middle Miocene
Haiber Hill (8 km SW, upper aeolianite)	S.d.	Post-Miocene
Haiber Hill (8.5 km SW)	D.1.	Upper Middle Miocene
Haiber Hill (13.5 km SW)	S.c.	Quaternary
Kahari (8 km S Gobabeb)	S.c.	Quaternary
Kamberg cliff (loose sands)	S.d.	Post-Miocene
Kamberg Mesa	Aep	Lower Miocene
Karingarab (lower aeolianite)	D.c.	Middle Miocene
Karingarab (middle aeolianite)	D.w.	Middle Miocene
Kolmanskop (aeolianite)	S.d.	Post-Miocene
Narabeb (40 km S Gobabeb)	D.w.	Middle Miocene
Nutab (13 km E Gobabeb)	???	Unknown
Obib Gorge (aeolianite)	S.d.	Post-Miocene
Obib (Acheulean deflation surface)	S.c.	Quaternary
Obib (lateral valley aeolianite)	S.d.	Post-Miocene
Rooilepel Depression (Basal aeolianite)	D.c.	Miocene
Rooilepel Depression (middle aeolianite)	D.w.	Middle Miocene
Rooilepel Depression (upper aeolianite)	D.1.	Upper Middle Miocene
Rooilepel (mobile sands)	S.c.	Quaternary
Rooilepel West (aeolianite)	D.w.	Middle Miocene
Rooilepel West (mobile sands)	S.c.	Quaternary
Sesriem (MSA deflation surface)	S.c.	Quaternary
Sesriem North of Windmill (MSA surface)	S.c.	Quaternary
Sesriem North of Airstrip (aeolianite)	D.w.	Middle Miocene
Schmidtfeld (aeolianite)	D.w.	Middle Miocene
Target Pan (aeolianite)	D.1.	Upper Middle Miocene
Target Pan (loose sand)	S.c.	Quaternary
Tjirundo (Omaruru, river silts)	S.c.	Quaternary
Tree Pan (0.5 km E of pan)	D.1.	Upper Middle Miocene
Tree Pan (0.5 km S of pan)	D.1.	Upper Middle Miocene
Tsauchab (aeolianite)	D.1.	Upper Middle Miocene
Tsauchab (upper eaolianite)	S.d.	Post-Miocene
Tsauchab (Acheulean deflation surface)	S.c.	Quaternary
Tsauchab 3 (aeolianite)	S.d.	Post-Miocene
Tsauchab Valley (south)	D.w.	Middle Miocene
Vreemdelingspoort (aeolianite cliffs)	D.w.	Middle Miocene
Vreemdelingspoort (fossil dune, lower)	D.c.	Middle Miocene
Vreemdelingspoort (fossil dune, upper)	D.w.	Middle Miocene
West Pan	D.c.	Middle Miocene
West Pan (50 km S Rooibank)	S.d.	Post-Miocene
Zebra Hill (aeolianite)	Aep	Lower Miocene
Zebra Hill (loose sand)	S.d.	Post-Miocene

aeolianite succession 8-9 km north of Awasib Waterhole during September 1994, by the authors resulted in the discovery of a complete succession of egg types, confirming the preliminary succession worked out on the basis of partial sequences. The order of the various species is given in Table 2, from (1) oldest to (6) youngest.

PHYLOGENY OF EGGSHELL TYPES AND REPLACEMENT OF AVIAN LINEAGES

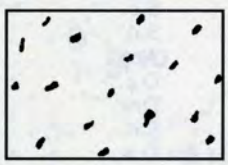
Based on the distribution of the eggshell types in the field, it is evident that only one type of bird laying struthious eggs occurred in the region during any one geological period. Detailed studies of the surface morphology and microstructure of these eggs suggest that *Namornis* probably gave rise to *Diamantornis* and that the three species of *Diamantornis* were derived one from the other in a time successive anagenetic pathway. This lineage gave rise to birds laying *Struthio*-like eggs sometime during the late Miocene, after which eggs of more modern *"Struthio"* type occur in the fossil record. Eggs of *S.daberasensis* may have given rise to *S.camelus* types. This is of interest in view of the usually accepted scenario that *S.camelus* originated in Asia and then migrated to Africa. The new discoveries in the Namib Desert suggest an alternative hypothesis, in which *Struthio* already existed in Africa during the Pliocene and that the extant ostrich is a descendent of this lineage. Further work is needed to confirm this hypothesis.

Aepyornithoid eggshells have been found in Namibia at several sites of pre-Miocene to lower Miocene age (Kamberg, Elisabethfeld) and in surface context in several places (Table 1) which might be younger than lower Miocene, but further work needs to be done to determine their stratigraphic range.

SUMMARY AND CONCLUSION

The recovery of seven kinds of large fossil eggs in the Neogene of Namibia is remarkable, not only for the

TABLE 2
Age, stratigraphic order and surface morphology of struthious eggshells from the Namib Sand Sea, Namibia

Species	Surface Structure of Eggs	Age
(6) *Struthio camelus*		Early Pleistocene to Present
(5) *Struthio daberasensis*		Pliocene (ca 7-2 Ma)
(4) *Diamantornis laini*		Upper Miocene (ca 11-8 Ma)
(3) *Diamantornis wardi*		Middle Miocene (12-11 Ma)
(2) *Diamantornis corbetti*		Middle Miocene (ca 13-12 Ma)
(1) *Namornis oshanai*		Middle Miocene

diversity of eggshell structures encountered but also for their potential for relative dating. Among the six struthious egg types (Table 2) none have ever been found togther in the same stratigraphic interval, indicating that only one bird species producing struthious eggs lived in the Namib at any one geological period. Furthermore, where two or more egg types have been found in superposition, they have always been found in the same order.

At Awasib Cliffs, all six egg types occur in the following stratigraphic order. In the lower slopes leading up to the cliffs, the species *Namornis oshanai* and *Diamantornis corbetti* occur in superposition. At the base of the cliffs, the species *Diamantornis wardi* is found. In the middle section of the cliffs, the species *Diamantornis laini* is very common, while in the uppermost aeolianites at the cliff tops and in sloping ground beyond, the species *Struthio daberasenis* occurs. Finally, in loose sands, eggshells of the modern ostrich, *Struthio camelus* are found.

Fossil struthious eggshells are thus proving to be of great use for correlating strata in the Namib Sand Sea. At several sites, associated mammals have been found, which have yielded information concerning the ages of the various species (Tables 1, 2).

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AFRICAN FOSSIL LISSAMPHIBIA

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ABSTRACT

The Anura (Frogs and Toads) are represented in Africa and associated regions by fossils of every epoch from the Cretaceous to the Holocene. Pipid frogs of African affinity are known from the Early Cretaceous of Israel and Later Cretaceous of South America and Africa; those of Israel and South America have been well-studied, but only one from Africa has been: *Eoxenopoides reuningi* from Namaqualand. Two well-studied Palaeocene frogs of South America, *Shelania pascuali* and *Xenopus romeri*, have affinities with the African pipids. Apart from a Miocene assemblage from North Africa (including pipids, which are now exclusively sub-Saharan) and one species from Namibia, *Xenopus stromeri*, the fossil African anurans remain largely unstudied. Deposits in which the African anuran fossils occur represent crater lakes, other lacustrine deposits, including lacustrine tuffs, river terraces, deltas, estuarine/lagoon zones, karst landscapes and archaeological sites; data are not available for several of the recorded fossils. No fossils in Africa appear to have been definitely ascribed to the Urodela or Caecilia.

INTRODUCTION

At a symposium on African Anura in January 1994 a computerized bibliography programme was demonstrated (Van Dijk, in press). The collection of literature, and the bibliography based on it, was started more than thirty years ago. Many items obtained, although relevant for the study of African Anura, had never been referred to in this connexion, or were only encountered in the reference lists of other articles. This was often the case with references relevant to fossil African Anura or related fossils. What is here presented is a review of the literature extracted from the computerized bibliography, to indicate the state of knowledge of the field and to point out references to fossils which await study.

REVIEW OF DATA

The Lissamphibia include three orders of Amphibia. Of these the legless Caecilia (= Apoda; = Gymnophiona) are known from only a single fossil species from South America, which appears to be related to a living West African species. The Urodela (newts and salamanders) occur in Africa only north of the Sahara, and have not been included in the literature collection or bibliography. There are in fact very few references to fossil urodeles in Africa. The comprehensive study of Estes (1981) lists no described fossil urodele. One Holocene site in East Africa lists Nectridia among the fossils (Andrews *et al.*, 1981). The Nectridia became extinct in the Permian, hence any lower vertebrate fossil with a tail at the site, if it is an amphibian, is more likely to be a urodele, with a remarkable distribution. De Broin, *et al.*(1974) found one specimen or species in the Cretaceous of Niger which they considered to resemble a Urodele – "Il semble d'autre part exister dans le gisement un Urodèle de grande taille dont la position systématique reste à préciser". Estes (op. cit.) refers to urodeles from this site, and to work in progress on them (Estes & Rage, in preparation), but no publication could be traced. (Estes is now deceased). Of the Lissamphibia it is the Anura, the frogs and toads, which are at present overwhelmingly of interest in Africa as fossils, because of their numbers and because of the sureness with which they can be identified as anurans. The distribution of anuran fossils in Africa, and related ones, is summarized in the Table and Map.

DISCUSSION

In this discussion, only the most important diagnostic features will be mentioned. The oldest fossil considered to be an anuran is *Triadobatrachus* (Piveteau 1936a, 1936b, 1937; Estes & Reig 1973; Rage & Rocek 1984), from the Triassic of Madagascar. That it is an amphibian is shown by the presence of only one sacral vertebra. The short tail and small number of presacral vertebrae, reduced ribs, and forward projection of the ilia, are characteristics of Anura.

A fossil of early Jurassic age, from South America, named *Vieraella herbstii*, is very like modern Anura and is in fact assigned to the modern family Ascaphidae. By the Early Cretaceous three modern families, Ascaphidae (from South America), Discoglossidae (from Spain), and Pipidae (from Israel) are known, probably having diverged in the Jurassic. Ascaphidae have not been found in Africa, while living Discoglossidae in Africa are confined to North of the Sahara. A Miocene discoglossid has been reported from Morocco (Sanchiz & Alcover 1984).

The Pipidae, now sub-Saharan in Africa (and South American), occur as fossils in North Africa, while some South American fossils have close affinity to living African genera. The Pipidae are distinguished by loss of

CAENOZOIC				
Holocene				
Late Stone Age, Iron Age	Anura indet.	**archaeological site**	Matupi Cave; **NE Zaire**	van Neer 1984
Middle & Late Stone Age	*Pyxicephalus*+?	**archaeological site** Kumakams, Bremen; **Namibia**	Zebrarivier, Maguams Avery 1984	Cruz-Uribe & Klein 1983;
Pleistocene	amphibia	**lacustrine crystal tuffs**	Olduvai Gorge, Bed I; **Tanzania**	Leakey 1967
Pliocene/Pleistocene	cf. *Xenopus*	**deltaic, estuarine, lagoonal**	Langebaan; **South Afica**	Hendey 1967
	Anura	**calcareous cave breccia**	Transvaal Caves; **South Africa**	
Pliocene				
?Mio-/?Pleistocene	?cf. *Xenopus*	**terrace, volcnaic terrain**	Kleinsee, Namaquland; **South Africa**	Stromer 1931
Miocene	*Xenopus; Ptychadena; Bufo*	**karst landscape**	Beni-Mellal; Morocco	Hecht *et al.* 1961 Vergnaud-Grazzini 1966
	Anura; Nectridia	**muds, marls, silts; ?tuffaceous**	Makobo Island, Lake Victoria; **Kenya**	Andrews *et al.* 1981
	amphibia	**terrace deposits**	Arrisdrift; **Namibia**	Hendey 1978
	Xenopus stromeri	**terrace, ?volcanic terrain**	borehole near Elizabethbucht; **Namibia**	Stromer 1925; Ahl 1926
Oligocene	*Xenopus (Libycus) hasaunus*	?	Jabal al Hasawinah; **C. Lybia**	Spinar 1980
Eocene	amphibians	**lacustrine/fluviatile**	El Kohol, near Brezina; **Algeria**	Mahboubi *et al.* 1986
Palaeocene				
Upper	*Shelania pascuali#*	*?*	*Laguna del Hunco, Chubut;* Patagonia, **Argentina**	*Casamiquela 1960,* ***1961***, 1965; Estes 1982; Baez 1983
Upper	*Xenopus romeri* **	***fissure in limestone***	Sao Jose' de Itabori; **Brazil**	**Estes 1975a; 1975b, 1982**
Mesozoic				
Cretaceous				
Upper	*Eoxenopoides reuningi*	**crater lake**	Banke, Namaqualand; **South Africa**	Haughton 1931; Estes 1977
Upper	pipid; cf. *Eoxenopoides reunigi*	crater lake	Stompoor, Maryvale; Namaqualand, **South Africa**	van Dijk 1985; Smith 1986
	pipid	crater lake	diamond exploration site; **Zaire**	
Upper	*Saltenia ibanezi*	**argillaceous sandstone**	Almenia, Salta; **Argentina**	Reig 1959; Parodi-Bustos *et al.* 1960; Ibanez 1960; Baez 1983
Upper	ranid; 2 pipids cf. *Xenopus* r+;*	continental-marine margin	d'In Beceten, near Tahoua; **S Niber**	de Broin *et al* 1974
Lower	*Thoraciliacus; Cordicephalus* Shomronella jordanica	**lacustrine silt, volcanic terrain laminated shales,**	Makhtesh Ramon; **Israel** Shomron; **Israel**	Nevo 1956, 1968 Estes *et al* 1978

** = *Silurana* * = *Silurana* # cf. *Xenopus muelleri* + cf. *Hymenochirus* *+ cf. *Silurana & Hymenochirus*

TABLE 1.

Fossil Lissamphibia in Africa, and related fossils in South America and Israel.

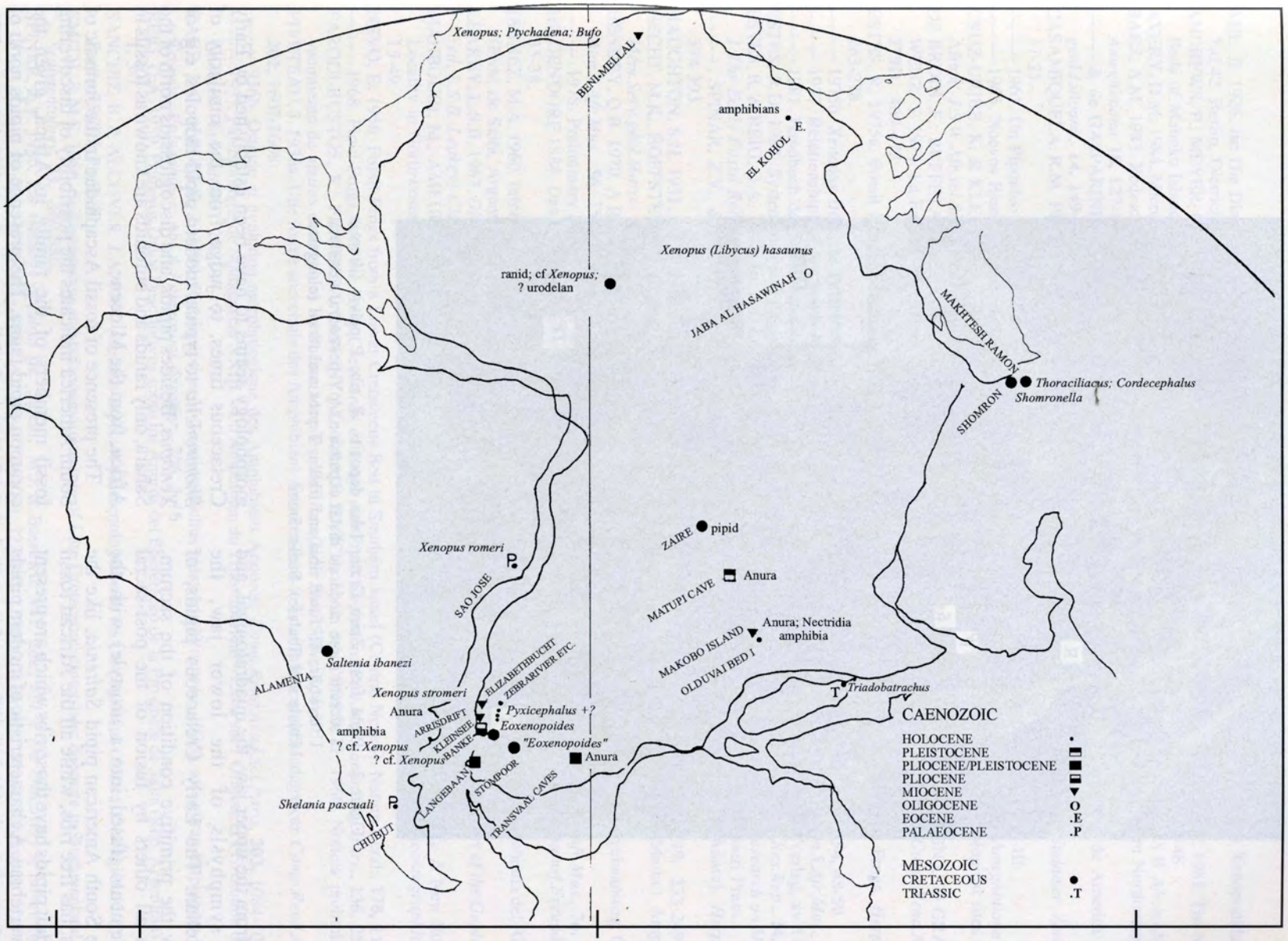

Figure 1. Fossil Lissamphibia in Africa, and related fossils in South America and Israel. Localities are labelled obliquely in Upper Case; the Taxa at the sites are indicated horizontally next to the sites or, where necessary, next to the site labels. Note that there are two sites near Elizabethbucht, and therefore two separate taxon labels. The geological ages of the fossils are indicated by the symbols in the key.

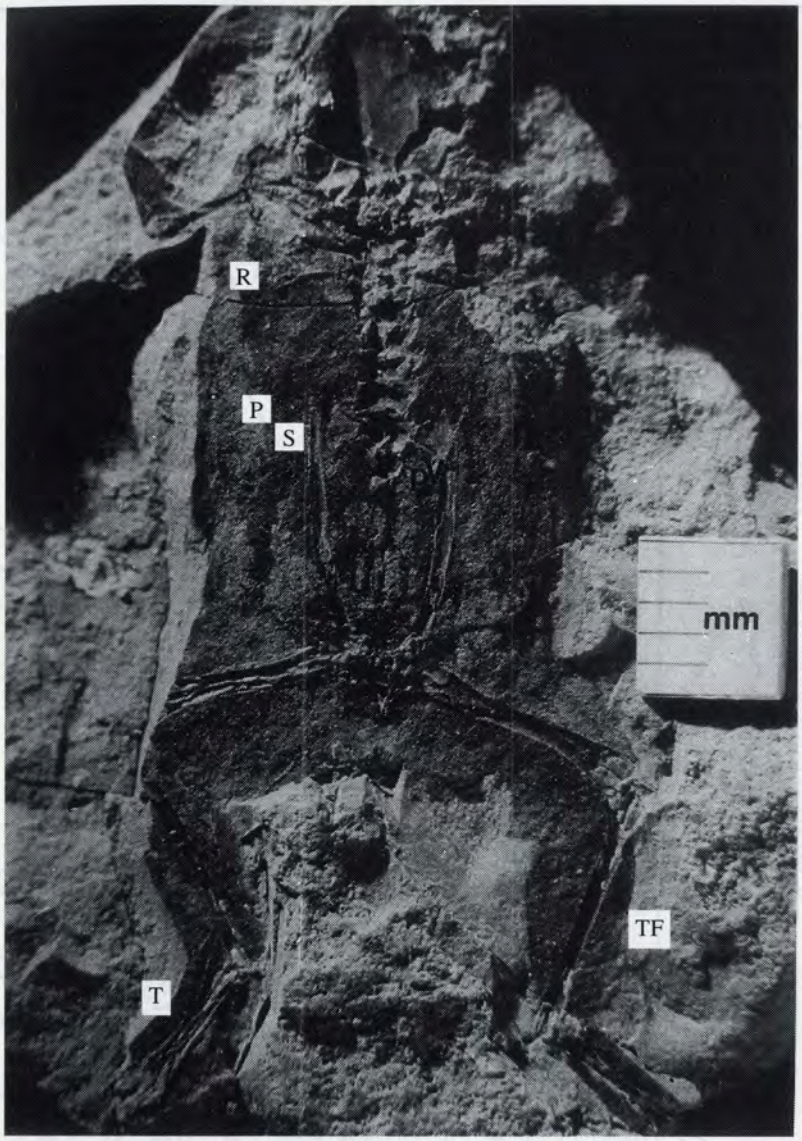

Figure 2. Pipid from Zaire Crater lake deposits. R rib; P pelvis (ilium); S sacrum (note moderate distal expansion); pV postsacral vertebra; U urostyle; TF fused tibia and fibula; T proximal tarsal (elongated tibiale and fibulare). Scale: 5mm.

an element from the upper jaw, the quadratojugal, and from the symphysis of the lower jaw, the Mentomeckelian. The Early Cretaceous pipids, of Israel, show the primitive condition of the sacrum, modified in all others by fusion of the post-sacral vertebral elements (fused into a urostyle) with the sacrum. The South American pipid *Saltenia*, like the Israel pipids, has free ribs, while all the African fossil and living adult pipids have those ribs which are present fused to the vertebrae. A characteristic of modern pipids of both South America and Africa, observed in some fossils, is an expanded sacrum, with straight parallel lateral edges, along which the parallel anterior projections of the ilia can slide; this was discovered in the living genera *Pipá* (South American) and *Xenopus* (African) by Hilgendorf in 1884, to which work no-one seems to have referred, before or after the rediscovery of the phenomenon (in 1960). The ilia may project well anterior to the sacrum. A characteristic pipid tadpole morphology seems to have been established by Early Cretaceous times, to judge from the similarity of *Shomronella* to typical modern pipid tadpoles, e.g. of *Xenopus*. Besides pipids, and discoglossids north of the Sahara, only ranids and bufonids are known as fossils in Africa, from the Miocene.

The presence of fossil Ascaphidae in the Jurassic of South America indicates the possibility of discovering fossil members of the family in Africa, given the common pipid fauna. The presence of pipids north of the Sahara in the Miocene suggests that elements of the European fauna, such as those found in North Africa, may also have extended south of the Sahara.

That fossil anuran material in Africa is available for study, is illustrated in the Table and Map. An indication of abundance at one site may be deduced from the recorded presence of "Amphibia" at 22 of 23 sampling spits at Zebrarivier Cave (Avery 1984). A fossil awaiting description is illustrated in Figure 2.

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AN AGGREGATION OF JUVENILE *YOUNGINA* FROM THE BEAUFORT GROUP, KAROO BASIN, SOUTH AFRICA

by

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ABSTRACT

An assemblage of five fully-articulated juvenile skeletons of *Youngina* has been recovered from the Late Permian strata of the south-western Karoo Basin. These 12-cm-long skeletons are not only the first articulated juveniles of this taxon, but also the oldest yet found in the Karoo Basin. They are preserved in overbank mudrocks of the Hoedemaker Member (Beaufort Group, Adelaide Subgroup) on the farm Leeukloof 43 in the Beaufort West district. Although they are estimated to be some three million years older than previously described *Youngina*, these specimens show no significant skeletal differences. The high degree of articulation and the spatial arrangement of these skeletons in a dish-shaped hollow is compelling evidence for them having huddled together within an underground burrow. Taphonomic analysis of associated fossils indicates that this was probably a mechanism to reduce water loss during drought on the ancient Karoo floodplains.

KEYWORDS: *Youngina*, juvenile aggregation.

INTRODUCTION

Younginiforms are a small but well-defined clade of Permo-Triassic diapsid reptiles known from the Late Permian of South Africa (*Youngina*), Tanzania (*Tangasaurus*) and Madagascar (*Hovasaurus, Thadeosaurus* and perhaps *Acerosodontosaurus*), and from the Early Triassic of Kenya (*Kenyasaurus*). Once thought to be related to lepidosaurs (lizards, snakes and their relatives), younginiforms are now considered no closer to lepidosaurs than to archosaurs and are therefore placed closer to the base of the diapsid tree (Laurin 1991).

The fossil record of younginid reptiles in the Karoo Basin of southern Africa is comparatively sparse: only 13 highly distorted skulls and a few disarticulated skeletal elements have been collected to date (Gow 1975). Only one of the skulls has an articulated post-cranial skeleton (BPI 2859) and this is incomplete (Gow 1975). All the *Youngina* specimens collected so far are from Beaufort Group strata assigned to the *Dicynodon* Zone (Smith and Keyser, in press), previously known as the *Daptocephalus* Zone (Kitching 1977). These strata immediately underlie the Permian-Triassic boundary in the southern Karoo Basin (Anderson & Cruikshank 1978). Recently, Roger Smith recovered an unusual assemblage of *Youngina* from strata of the *Tropidostoma* Zone (Smith & Keyser in press), previously known as the lower *Cistecephalus* Zone of Kitching (1977). The new locality is some 700m lower in the Beaufort succession than those described to date making this the earliest recorded occurrence of *Youngina* in the Karoo Supergroup. A very rough calculation of the minimum time involved in accumulating these 700m of fluvial strata, based on 2mm/year for the compacted mudrock intervals and 5mm/y for channel sandstone dominated intervals (Smith 1993) is approximately 3 million years. Based on correlation of the associated *Endothiodon* fauna with similar fossils in the Rio-do-Rasto Formation of Brazil (Keyser 1981), the host strata are estimated to be middle to late Tatarian in age (+/-255-253My). The palm-sized specimen contains at least five fully articulated juvenile *Youngina* skeletons preserved in attitudes and orientations that strongly resemble group denning behaviour of modern lizards.

DESCRIPTION OF *YOUNGINA* ASSEMBLAGE AND EVIDENCE FOR IMMATURITY

The five individuals of SAM K7710 are of similar size (snout-vent lengths 86-94mm) and are all at the same level of skeletal development. In the skull, the elongated posterior process of the post-orbital and U-shaped configuration of the frontoparietal suture identify these animals as youginiforms. Comparing the shape of skull elements such as parietal (posterior process angle and orientation; tabular and supratemporal facets), the dentition, the shape of the humerus and the long shallow ectepicondylar groove – these small skeletons show no marked differences from previous descriptions of the genus *Youngina* (Gow 1975) although they are about half the size of previously described specimens. It is possible that they are a new small morph but it is more feasible that they are immature.

Despite their size, the new skeletons are too well ossified to represent young hatchlings. Neurocentral

sutures are closed; tarsal and carpal elements are ossified; the components of pectoral and pelvic girdles are in close proximity (i.e. there are no large areas of cartilage separating them); and the sacral and caudal ribs are fused to their respective vertebrae (although on one specimen there is the trace of a suture). However, there is also evidence that these small reptiles are not fully mature. In the skull, the roofing bones are unsculptured; the paired frontals and parietals are joined by simple sutures which have separated easily; and the eyes and parietal foramen are proportionally large. The sternal plates are only weakly ossified and remain paired although the coracoid foramen is already enclosed. In the pelvis, the pubis and ischium are separated by a weakly ossified area and the obturator foramen of the pubis is open posteriorly. The ends of the long bones lack joint surfaces. The carpals and tarsals are incompletely preserved. They have ossified centres but are still more rounded than angular in shape; there is no trace of a notch on the calcaneum for the perforating artery.

Developmental stages have been described for two younginiforms- *Hovasaurus* (Currie 1981) and *Thadeosaurus* (Currie & Carroll 1984). *Hovasaurus* was almost certainly aquatic; *Thadeosaurus* at least partially so. Aquatic animals tend to show a retarded level of skeletal development which makes comparison with terrestrial animals difficult. Bearing this in mind, however, the new younginid specimens described here would seem to correspond to age class E or F (H being adult) in the aquatic genera and can be described as juveniles.

SEDIMENTOLOGY AND TAPHONOMY OF YOUNGINA LOCALITY

The new *Youngina* locality is on the border between Beaufort West and Loxton districts of the Cape Province of South Africa within a regionally extensive mudrock sequence (informally termed the Hoedemaker member) that forms part of the Teekloof Formation of the lower Beaufort Group (Adelaide Subgroup). Detailed mapping of sedimentary facies and taphonomic analyses of 243 *in-situ* vertebrate fossils at this locality have been used to reconstruct several floodplain palaeoenvironments (Smith 1993). The younginid fossils were embedded in a 2-metre-thick structureless greenish-grey siltstone, which is interpreted as having accumulated on the proximal floodplain areas flanking a large meandering river (Smith 1987a). Sedimentary structures in the point bars that make up the bulk of the channel sandstones indicate that the rivers were perennial and prone to large discharge fluctuations (Stear 1985). This resulted in flood dominated sedimentation in the main channels and on the channel banks. The structureless siltstone in which the younginids were buried is interpreted as





Figure 1A. Dorsal radiograph of the unprepared younginid specimen revealing the superposition of 5 small skeletons (actual size).

Figure 1B. Dorsal view of prepared specimen SAM K7710 showing the upper three of the group of 5 juvenile *Youngina* skeletons reproduced at actual size.

sheetflood alluvium rapidly deposited by sediment-laden floodwaters that overtopped the channel banks (Smith 1987a). Calcic palaeosols in the associated sediments confirm that floodplain sedimentation was highly episodic and the climate was semi-arid in this part of the basin with highly seasonal rainfall (Smith 1990).

When found, the new younginid specimen (SAM K7710) was completely encased in a thin layer (5mm) of micrite cemented siltstone. Such preferential perimineralisation of fossil bone is common in the proximal floodplain facies of the Hoedemaker Member and is interpreted to be of pedogenic origin (Smith 1990). Both dorsal and ventral surfaces were mechanically prepared with dental drill and needle under magnification (Figure1b). Anatomical details were recorded on transparent film using radiographs (Figure1a) to maintain positional accuracy. These drawings were enlarged in a photocopier and reversed onto clear film thus making it possible to superimpose dorsal on ventral views (and vice versa) to reveal the intricacies of their taphonomic mode (Figures 2 & 3). The five skeletons are preserved in a dorsal-up attitude along the floor of a spoon-shaped depression. Their skeletons are superposed on each other but show no evidence of disturbance other than that attributable to vertical compaction. The high degree of articulation of these very delicate skeletons and the presence of free-floating sternal plates indicate that they were buried with their flesh intact. This, coupled with the spatial arrangement of limbs and parallel orientation of the skeletons in a dish-shaped depression, is compelling evidence for them having been preserved in "life position" as a behaviourally arranged aggregation of juveniles within an underground burrow (Figure3).

To date no fossil eggs or nesting sites have been found in the Beaufort Group although burrow casts containing curled-up skeletons of the small dicynodont *Diictodon* do occur in the vicinity of the younginid locality (Smith 1987b). Interestingly, an aggregation of ten juvenile skeletons of *Diictodon* (SAM K1650) was found within 100m of the younginids and ten more isolated juvenile skulls of *Diictodon* were collected along the 1300m cliff section. The relatively common occurrence of articulated juvenile skeletons of a variety of groups preserved in the proximal floodplain facies possibly indicates that this was a preferred "nesting" area. However, the wide range of disarticulation classes and "clustering" of skeletal elements into shallow scours suggests that the periodicity of flood events and the net floodplain accretion rate in this part of the floodplain were optimal for the preservation of small skeletons.

DISCUSSION OF EVIDENCE FOR JUVENILE AGGREGATION

Possibly the most interesting feature of the new *Youngina* specimens is that they appear to provide evidence for juvenile aggregation in this taxon. This raises questions of why they aggregated and what killed

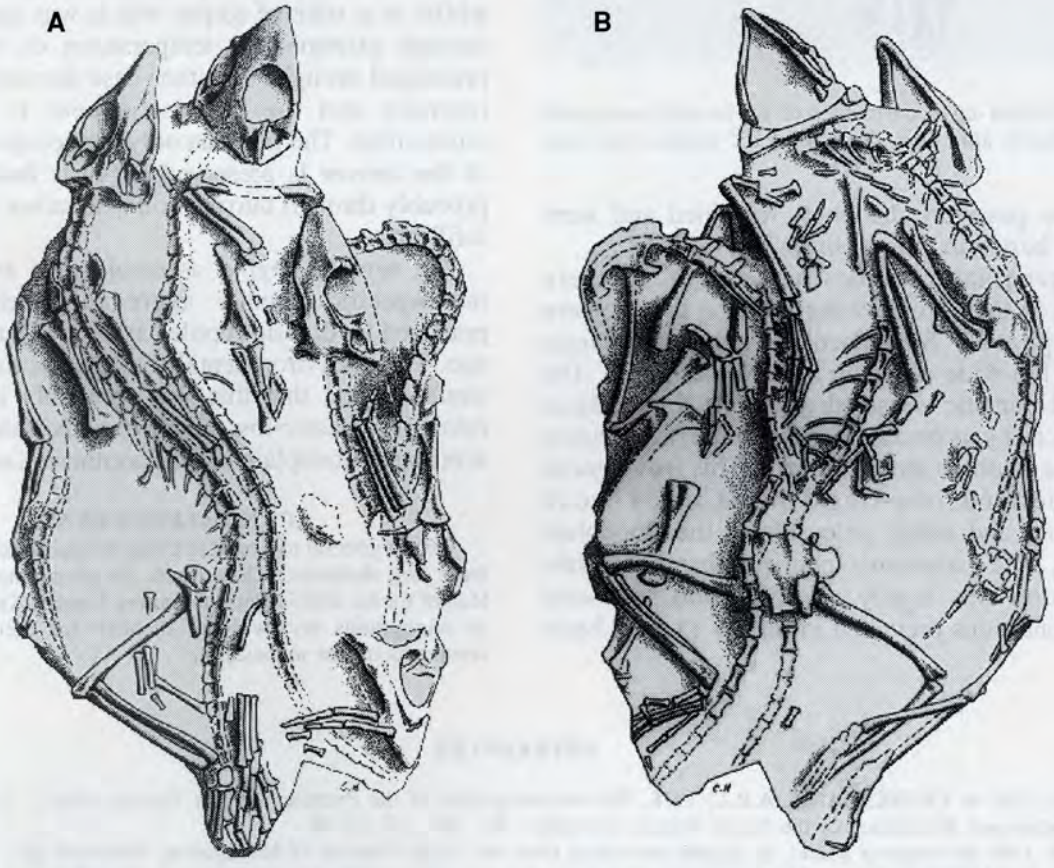

Figure 2. Drawing of dorsal (A) and ventral (B) surfaces of the new younginid specimen. Actual size.



Figure 3. Fleshed -up reconstruction of the juvenile younginids shortly after their death some 255 million years ago.

them all so passively that they remained and were eventually buried in "life position"?.

Palaeogeographic reconstructions of southern Gondwana in the Late Permian position the southern Karoo trough at 55 ° S bounded on the southern margin by a 1000 km-wide orogenic belt (Visser 1991). The aridity and climatic seasonality of the Karoo Basin was enhanced by its continentality and the rain-shadow effect of the southern mountainlands. This is evidenced in well defined tree-rings of silicified wood (*Dicroidium*) and calcic paleosols in the floodplain sediments. The palaeosols confirm that floodplain sedimentation was highly episodic and semi-arid climatic conditions prevailed in this part of the basin (Smith 1990). Comparison of the palaeosol profiles with those of modern soils allows an estimate of mean annual temperatures between 16-20 ^{0}C and highly seasonal rainfall of 500-700mm/y (McPherson & Germs 1979; Smith 1990). In such a setting, large diurnal temperature fluctuations and drought would have been commonplace. It is therefore predictable that ectotherms such as *Youngina* would have some behavioural adaptations, such as aggregating, to regulate their body temperatures. It is also reasonable to assume that these reptiles would aestivate in underground burrows during drought to preserve moisture. Taphonomic analysis of the other 242 *in-situ* fossils found at the younginid locality led to the conclusion that many of the disarticulated dicynodont skeletons had accumulated, during prolonged drought, at watering holes around the margin of a floodplain lake (Smith 1993). Thus it is concluded that drought was the most likely reason that the juvenile younginids went to ground.

The juveniles of some modern species of viviparous lizards, the skinks, huddle together with very similar intertwining and side-by-side disposition. These aggregations involve members of a single brood and are usually found in confined cavities beneath fallen logs or within underground burrows (Shine 1994). Within warm semi-arid climatic conditions the advantages of such behaviour are improved diurnal thermoregulation (Gregory 1982) and more efficient aestivation during drought (Seidel 1978).

It is conceivable that juveniles of both *Youngina* and *Diictodon* died passively within underground burrows whilst in a state of torpor which was induced either through extreme low temperatures or, more likely, prolonged drought. In either case decomposition was retarded and the corpses appear to have been mummified. The fact that only the scoop-shaped floor of the burrow is preserved suggests that burial was probably through burrow collapse rather than gradual infilling.

The new *Youngina* assemblage is evidence that monospecific juvenile aggregation behaviour was practised by diapsid reptiles at least 255 million years ago. Palaeoenvironmental interpretations of the host strata suggest that this was probably a method of minimising water-loss during periods of drought on the semi- arid floodplains of the southern Karoo Basin.

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KAROO SUPERGROUP PALAEONTOLOGY OF NAMIBIA AND BRIEF DESCRIPTION OF A THECODONT FROM OMINGONDE

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ABSTRACT

Karoo strata crop out extensively in Namibia. Numerous and diverse fossils have been collected from three areas – Karasberg, Kalahari and Huab Karoo basins. Although a great deal of research has been done on these strata and their fossil content, the literature is scattered and no publication has been devoted to a detailed review of what has been achieved. This paper presents a review based principally on a literature search allied to personal experience of some of the fossils and field trips to a few localities. It cannot pretend to be an in-depth review. The Namibian Karoo outcrops are so extensive and the palaeontological remains so diverse, that several years of intensive research would be required to achieve such a work. Tragically, many of the fossils mentioned in the text have been lost or their whereabouts are unknown. A small sample of fossils is housed in the Geological Survey Museum, Windhoek, and other fossils are known to be curated by the South African Museum, Cape Town, the Bernard Price Institute for Palaeontological Research, Witwatersrand University and the Geological Survey of South Africa, Pretoria. A thecodont from the Omingonde Formation (Upper Triassic) is described briefly.

INTRODUCTION

Extensive outcrops of late Palaeozoic and Mesozoic sediments occur in southern and northwestern Namibia (Smith *et al.* 1993) (Figure. 1-2). These strata accumulated in intra-cratonic settings, and have not suffered greatly from folding since their deposition. Traditionally these sedimentary rocks have been assigned to the Karoo Supergroup, which is widespread in southern Africa, with important equivalents in South America. (Figure 1).

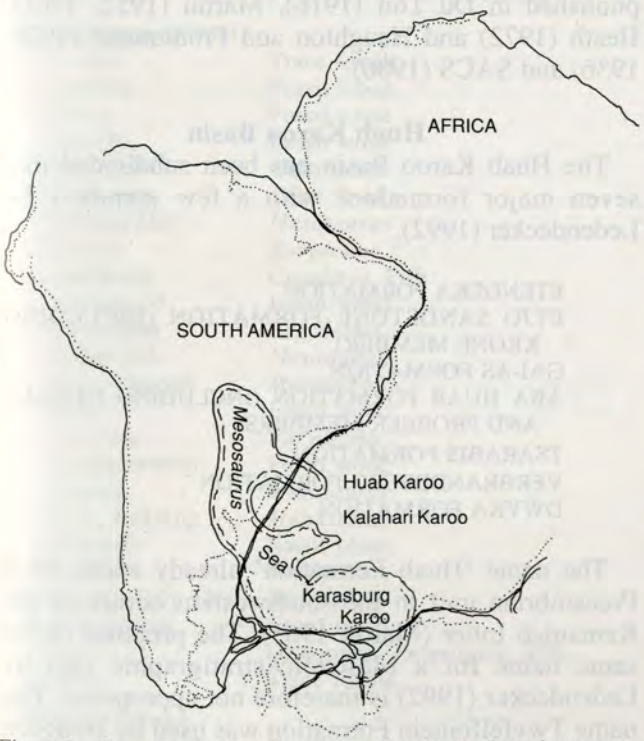

Figure1. Reconstruction of southern Gondwana based on maps by Owen (1983), showing the probable extent of the *Mesosaurus* sea. Note that in this reconstruction the sea does not have the 'central arm' separating Namibia from Brazil (Oelofsen, 1987). *Mesosaurus* sea may have been landlocked, or could have had a limited connection with other oceans of the period.

PALAEOGEOGRAPHY

There has been some debate about the palaeogeography of the Karoo Basins, especially during Whitehill times, recently summarised by Remelin (1994) and Smith *et al* (1993). Most reconstructions, such as the one by Oelofsen (1987) contain a "central sea arm" between South Africa and South America which leads into the ocean that surrounded Gondwana, meaning that the "*Mesosaurus* Sea" would have had direct connections with the ocean. However, sedimentary, volcanological and palaeontological considerations suggest that there was no such "central sea arm" and that there was little likelihood of a major connection to the ocean. Instead the "*Mesosaurus* Sea" appears to have been an isolated, relatively shallow inland sea. Examination of various palaeogeographic reconstructions of southern Gondwana suggests that the "central sea arm" may be an artefact arising from the method of palaeogeographic reconstruction. Reconstructions of Owen (1983), in which the Triassic globe is considered to have had a radius 20% smaller that the modern radius, result in the disappearance of the "central sea arm" and produce a land locked "*Mesosaurus* Sea" (Figure 1). Owen's reconstruction accords better with the geological and palaeontological evidence than do those in which a 500 km wide ocean gap – the central sea arm – existed between Africa and South America.

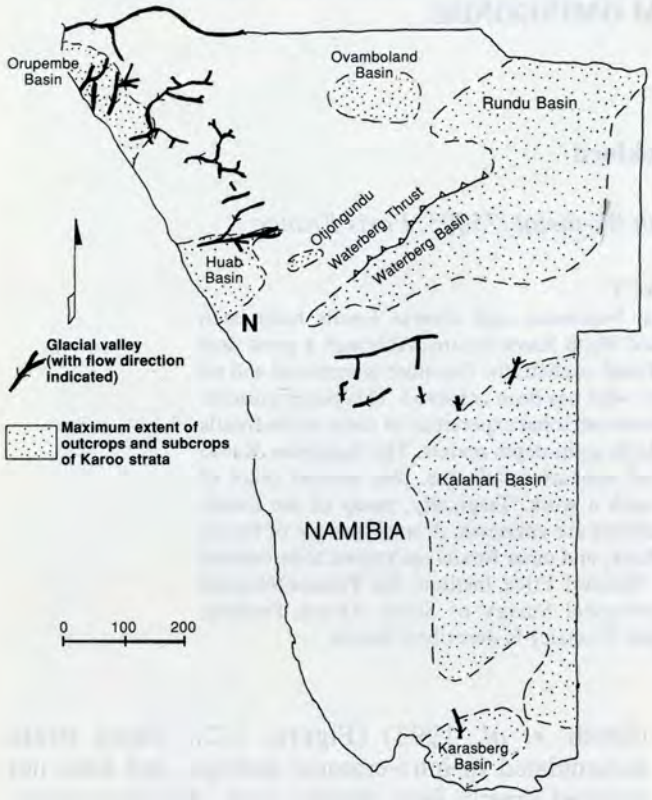

Figure 2. Karoo Basins of Namibia. Karoo outcops and subcrops occur widely in Namibia, the various basins being separated from one another by areas of non-deposition and of erosion. Numerous glacial valleys of Dwyka age occur in the northwest, centre and south of the country. The Waterberg thrust has resulted in Late Proterozoic dolomites being overthrust southwards over Mesozoic strata for distances of at least 4 km.

STRATIGRAPHY

The South African Karoo spans a considerable period of time. The Dwyka is considered to span the Late Carboniferous (Westphalian) to Early Permian (Artinskian) (Visser 1990; Visser *et al.* 1990). The Ecca extends into the early part of the Late Permian (Kazanian) (Rubidge 1991). The youngest rocks admitted to the Karoo are the Etendeka lavas which are early Cretaceous (Erlank *et al.* 1994). The Karoo Supergroup as a whole thus spans the period ca 320 Ma to ca 120 Ma.

Four of the five main stratigraphic groups which comprise the Karoo of South Africa are recognised in Namibia: Dwyka, Ecca, "Stormberg" and Drakensberg Groups. According to Smith *et al.* (1993) the Beaufort Group appears not to be represented in Namibia. However, strata which may be partly equivalent in age to the Beaufort Group of South Africa occur at Omingonde, but these sediments are correlated with the Stormberg by Smith *et al.* (1993).

The Etjo (Plateau) Sandstones are possibly equivalent in age to the Clarens Formation of South Africa (Smith *et al* 1993) although some of them are appreciably younger. In the Etendeka region north of the Huab Basin, lavas of early Cretaceous age overlie aeolianites which may have been active dunes until buried by the lavas. Some of the barchan dunes are intercalated between lava flows and are thus clearly Cretaceous in age (Horsthemke *et al.* 1990; Erlank *et al.* 1984). The fact that several of the Etendeka volcanic units also outcrop in Brazil indicates that break-up of South America and Africa in the latitude of Namibia was achieved later than the Early Cretaceous, (Milner *et al.* 1995; O'Connor & Le Roux 1992).

The extensive outcrops of basalts and intercalated sedimentary rocks in the Mariental region have been mapped as Jurassic. They have not been studied extensively, but could be rewarding from a palaeontological viewpoint as the sediments are of continental affinities. The recent discovery of conchostracans in the Hardap Resort area by R. Swart is of interest in this respect.

Karasburg and Kalahari Karoo Basins

In the south of Namibia, the Karasburg and Kalahari Basin Karoo rocks have been subdivided into four main formations (Oelofsen 1981).

AUSSENKJER FORMATION
WHITEHILL FORMATION
PRINCE ALBERT FORMATION
DWYKA FORMATION

The succession from the Prince Albert Formation to the Aussenkjer Formation is correlated with the Ecca Group. Detailed stratigraphic successions were published in Du Toit (1916), Martin (1952, 1961), Heath (1972) and Haughton and Frommurze (1928, 1936) and SACS (1980).

Huab Karoo Basin

The Huab Karoo Basin has been subdivided into seven major formations with a few members by Ledendecker (1992).

ETENDEKA FORMATION
ETJO SANDSTONE FORMATION (INCLUDING KRONE MEMBER)
GAI-AS FORMATION
ABA HUAB FORMATION (INCLUDING GUDAUS AND PROBEER MEMBERS)
TSARABIS FORMATION
VERBRANDEBERG FORMATION
DWYKA FORMATION

The name 'Huab Formation' already exists for a Precambrian unit in the southwestern corner of the Kamanjab Inlier (Martin 1965). The proposal of the same name for a Mesozoic stratigraphic unit by Ledendecker (1992) is therefore not appropriate. The name Twyfelfontein Formation was used by Hodgson and Botha (1978) for the entire suite of strata between the Dwyka Tillite and the Etjo Sandstone in the Huab region, and is thus not available for a subdivision of the unit. The replacement name Aba Huab Formation proposed here would be an appropriate name for the Huab Formation of Ledendecker (1992).

TABLE 1.
List of Karoo Supergroup Fossil Localities in Namibia.

Ovambo District	
Strata Test N°1	Permian Miospores
Damaraland District	
Doros Crater	*Mesosaurus*
Doros to Gai-as	*Mesosaurus*
Probeer 535	Fossil wood
Krone 721	Fossil wood
Rhino Wash	Trace fossils
Rooiberg 517	Fossil wood
Twyfelfontein 534	Fossil wood
Verbrander Berg	Fossil wood, *Glossopteris*
Vrede 719	Fossil wood, *Paracalamites*
Otjiwarongo District	
Omingonde	cf *Erythrosuchus*
Otjihaenamaperero	Tetrapod tracks
Waterberg Plateau	Tetrapod tracks
Grootfontein District	
Breitenbach 152	Reptilian skull
Neudorf	Tetrapod tracks
Reheboth District	
Schlip	Radiolaria
Vingerbreek Oos 473	Goniatite
Mariental District	
Amalia	*Megaporoxylon zellei*
Goamus	Fossil wood
Hardap Resort	Conchostracans
Hardap 110	*Eurydesma*, Brachiopod, Starfish
Kameelhaar	Stromatolites
Mariental	Starfish, Bryozoa, Gastropoda
Norronaub	Spores
Vipersdorf	*Peruvispira vipersdorfensis*
Keetmanshoop Distirct	
Ai-Ais	Trace fossils
Areititis	Fossil wood
Aurus	Fossil wood
Berseba	Fossil wood
Brukkaros	Gastropods
Chamaites	Trace fossils
Daberas Ost	*Mesosaurus*
Daweb	*Eurydesma*
Ganikobis	*Conularia*, Fish
Garinais 30	Fossil wood
Gavetaams	*Eurydesma*
Gellap Ost	*Mesosaursu*
Gross Daberas	*Mesosaurus*
Huns	Fossil wood
Itsawisis	*Eurydesma*
Keetmanshoop	Fossil wood
Khabus	*Mesosaurus*
Klein Spitzkop	*Mesosaurus*
Mukorob	Fossil plants
Nabaos	*Eurydesma*
Nanebis Berg 120	*Mesosaurus*
Schlangkopf	Fossil wood
Tses	*Orthoceras, Peruvispira*, Fish
Zaris	Trace fossils
Karasberg District	
Aussenkjer 147	Fossil wood
Gooie Hoop	Limulid trace fossil
Haib	*Aphanaia haibensis, Mesosaurus*
Kanabeam	Foraminifera
Kirchberg 13	*Phyllotheca*, arthropods, *Mesosaurus*
Vioolsdrift	Trace fossils
Zwartbas	Trace fossils

The succession from the Verbrandeberg Formation to the Gai-As Formation is included by Ledendecker (1992) in the Ecca Group, while the Etjo Sandstone has been correlated with the Stormberg Group.

The sedimentary succession cropping out at Omingonde spans a period which is not well represented elsewhere in Namibia. It consist of two main formations (Keyser 1973a, b):

ETJO (PLATEAU) SANDSTONE FORMATION
OMINGONDE FORMATION.

The Omingonde Formation was correlated with the *Cynognathus* zone of the Beaufort Group by Keyser (1973 a, b) while the Etjo Sandstone has traditionally been correlated with the Stormberg Group. It is unsure, however, whether the Etjo Sandstone in the type area is really the same unit as the 'Etjo' Sandstones at the base of, and interbedded with the Etendeka Lavas, and furthermore whether it is indeed the time equivalent of the Stormberg Group of South Africa.

Jurassic lavas near Hardap

Extensive outcrops of Jurassic lavas occur in Mariental District. Intercalated between lava flows are sediments of various sorts, in particular evaporites. Few fossils have been found in these strata, perhaps reflecting a lack of prospecting because they are known to yield fossils at Hardap.

PALAEONTOLOGY

The Namibian Karoo Sequence rocks are richly fossiliferous, and have yielded both microscopic and macroscopic fossils at many localities (Table 1). These range from miospores and algae to vascular plants, invertebrates, fish and reptiles.

Karoo fossils provided the first palaeontological evidence to be cited in support of Wegener's theory of continental displacement (Figure. 1). The fossil marine reptile *Mesosaurus* has a restricted distribution in southwestern Africa and Brazil, which indicated to Du Toit (1927) that the two areas had once been much closer together than they are now. Further studies have amply confirmed the overall similarity in depositional successions and fossil content in Brazil and Namibia during Karoo times (Oelofsen & Araujo 1987).

It is convenient to examine the Namibian Karoo fossils in stratigraphic order : Dwyka – Ecca – Omingonde – Etjo – Hardap. Dingle *et al.* (1983) and Anderson & Anderson (1985) considered the Dwyka to be Permian, whereas Oelofsen (1981), regards the Dwyka as late Carboniferous to Early Permian, and the Ecca to be early Late Permian. The Omingonde Formation was considered by Keyser (1973) to be Triassic and the Etjo Sandstones which overlie the Omingonde Formation were reported to be late Triassic to Jurassic. Direct evidence of the age of the Etjo Formation is lacking. However, indurated sand dunes intercalated in the base of the Etendeka Lavas must be of early Cretaceous age (Erlank *et al.* 1984).

TABLE 2
List of organisms and their traces from the Dwyka Group of Namibia (* = holotype from Namibia)

Sporites Potonié, 1983
Triletes Reinsch, 1881
Azonotriletes Luber, 1935
Laevigati Bennie & Kidston, 1886
Punctatisporites foveolatus Maheshwari & Bose, 1969
*Leiotriletes etoshae** Stapleton, 1977
Leiotriletes sup. Naumova, 1937
Retusotriletes diversiformis (Balme & Henneley, 1956)
Apiculati Bennie & Kidston, 1886
Cyclogranisporites sp. Potonié & Kremp, 1954
*Converrucosisporites ovambolandensis** Stapleton, 1977
Verrucosisporites trisectus Balme & Henneley, 1956
Apiculatisporis spiniger (Leschik, 1959)
Anapiculatisporites ericianus (Balme & Henneley, 1956)
*Anapiculatisporites vuureni** Stapleton, 1977
Raistrickia sp. Schopf, Wilson & Bentall, 1944
Horriditriletes concavus Maheshwari, 1969
Horriditriletes novus Tiwari, 1965
Horriditriletes ramosus (Balme & Henneley, 1956)
Convolutispira sp. Hofmeister, Staplin & Malloy, 1955
Zonales Bennie & Kidston, 1886
Zonotriletes Waltz, 1935
Cingulati Potonié & Kaus, 1954
Densosporites sp. Berry, 1937
Cristatisporites mammilatus Maheshwari, 1969
Zonati Potonié & Kremp, 1937
*Kraeuselisporites maior** Stapleton, 1977
Kraeuselisporites minor Stapleton, 1977
Cirratriradites australensis Hart, 1963
Pollenites Potonié, 1931
Saccites Erdtman, 1947
Monosaccites Chitaley, 1951
Cordaitina obscura (Lele, 1964)
Potonieisporites novicus Bhardwaj, 1954
Nuskoisporites rotatus Balme & Henneley, 1956
Striomonosaccites ovatus Bhardwaj, 1962
Disaccites Cookson, 1947
Striatiti Pant, 1954
Protohaploxypinus cf *diagonalis* Balme, 1970
Protohaploxypinus goraiensis (Potonié & Lele, 1961)
Protohaplodypinus sp. Samoilovich, 1953
Hamiapollenites perisporites (Jizba)
Vittatina costabilis (Wilson)
Vittatina ovalis Klaus, 1963
Vittatina saccifer Jansonius, 1962
Vittatina subsaccata Samoilovich, 1953
Vittatina sp. Luber, 1939
Disaccitriletes Leschik, 1955
Illinites pemphicus Klaus, 1963
Disaccimonoletes Klaus, 1963
*Limitisporites rotundus** Stapleton, 1977
Plicates Naumova, 1937
Monocolpates Wodehouse, 1935
Intorti Naumova, 1937
Cycadopites follicularis Wilson & Webster, 1946
Cycadopites nevesi (Hart)
Striaticolpates Bose & Kar, 1966
Monostriocolpites Bose & Kar, 1966
Fusacolpites fusus Bose & Kar, 1966
Sporites Incertae sedis
Schizoporis gondwanensis Hart 1963
Radiolaria
Vascular plants
Foraminifera
Hyperammina
Ammodiscus
Glomospira
Ammobaculites
Spiroplectammina
Trace Fossils
Isopodichnus
Diplichnites Dawson, 1873
Umfolozia sinuousa Savage, 1971
*Punctichnium namibiensis** Ledendecker, 1992
Gluckstadtella cooperi Savage, 1971
Annelida (Scolecodonts)
Conulariida
Conularia
Mollusca
Eurydesma mytiloides Reed, 1932
Eoasianites (Glaphyrites) sp. Ruzhencev, 1936
Orthoceras sp.
*Peruvispira vipersdorfensis** Dickins, 1961
Conchostraca
Bryozoa
Dyscritella cf D.sprinigera (Bassler, 1929)
Porifera
Asteroidea
cf Monasteridae Schuchert, 1915
Crinoidea
Echinoidea
cf *Archaeocidaris* sp.
Pisces
*Namaichthys** *schroederi** Gürich, 1923
*Watsonichthys lotzi** (Gürich, 1923)
Elonichthys? sp.
Rhadinichthys? sp.
Fish Genus V

Dwyka Group

In Namibia Dwyka sediments consist predominantly of diamictites of glacial origin, interbedded with shales, often occurring in glacially sculpted valleys (Martin 1953, 1961). For this reason much of the strata tend to be poorly fossiliferous. However, in southern Namibia fossils have been found in various localities, the bulk of them in Rehoboth, Mariental, Keetmanshoop and Karasberg Districts.

In northern Namibia, there are good exposures of Karoo Supergroup strata in the Huab area. The two basal units have been correlated to the Dwyka (Horsthemke *et al.* 1990). No body fossils have yet been found there, but trace fossils, probably made by arthropods, are known.

Miospores

Stapleton (1977) described miospores from a borehole known as the Strat Test N° 1, which was drilled in the Ovambo Plain immediately north of Etosha Pan. Shales assigned to the Dwyka were encountered between 312 and 527 metres depth. The microfossils were obtained from depths of 368, 377, 436 and 519 metres. These shales overlie 41 metres of diamictite, and thus might belong to the Ecca Group. Additional information is provided by Roveda (1964), summarised in Hedberg (1979). Thirty-nine species of miospores were recorded from this borehole (Table 2), of which six were new to science. The assemblage as a whole indicated to Stapleton (1977) that the shales were of Early Permian age. A Sakmarian correlation

(ca 270 Ma) would satisfy the evidence. Leschik (1959) described a miospore assemblage from the southern part of Namibia, but there were apparently problems of preservation which render many of his determinations suspect (Hart 1963).

Roveda (1964) described three miospore associations from depths of 348, 401, and 483 metres in the Strat. Test N° 1 borehole. At a depth of 348 metres the assemblage is considered to be late Palaeozoic, probably Early Permian (Hedberg 1979). At 483 metres an assemblage similar to that from the Karoo of the Orange Free State is probably of Late Carboniferous age (Roveda 1964).

Vascular plants

Pieces of fossil wood have been reported from the Dwyka Group in Namibia (Martin & Wilczewski 1970; Haughton & Frommurze 1928; Heath 1972), but this needs confirmation as Oelofsen (1981) reports that he could not find any such material *in situ*.

Radiolaria

Martin & Wilczewski (1970) reported the prescence of Radiolaria in the so-called *Eurydesma* beds (glacio-marine Dwyka Beds) at Schlip and Ganikobis, but no details are available on the genera and species present.

Foraminifera

Martin & Wilczewski (1970) listed several genera of Foraminifera from the Tses Boulder-Mudstone Member of the Dwyka Group (Keetmanshoop District). These are *Hyperammina. Ammodiscus, Glomospira, Ammobaculites* and *Spiroplectammina* as well as other unidentified forms. Schreuder & Genis (1975) recorded a similar assemblage of Foraminifera from a striated pebble diamictite at Kanabeam 331, Karasburg Basin. The importance of these foraminiferans is that they appear to indicate marine conditions of deposition in this part of southern Namibia during the Permian.

Annelida

Scolecodonts (fossil annelid jaws) were reported, without details from the Tses Boulder-Mudstone Member by Martin & Wilczewski (1970).

Conulariida

Schroeder (1908) reported the discovery at Ganikobis of *Conularia*, a marine organism (possibly a scyphozoan coelentrate but of uncertain affinities) which he thought indicated a Permian age. Range (1912) illustrated a specimen collected at Ganikobis by Gathmann.

Mollusca

The thick-shelled bivalve *Eurydesma mytiloides* has been known from the Namibian Dwyka beds for a long time (Range 1912). Other molluscs reported from the sequence by Martin & Wilczewski (1970) consist of the goniatite *Eoasianites (Glayphyrites)* sp (Du Toit 1916), the gastropod *Peruvispira vipersdorfensis* and the bivalve *Aphanaia haibensis*. All these forms are known from the southern outcrops in Rehoboth, Mariental, Keetmanshoop and Karasberg Districts (Dickins 1961; McLachlan & Anderson, 1973; Heath 1972; Schalk & Germs 1980).

The holotype of *Aphanaia haibensis* Reed 1935, was found by Haughton (Haughton & Frommurze 1928) near Haib (Karasberg District). It consists of a large obliquely elongated mytiliform left valve with only a part of the right valve preserved. The shell is about 85 mm long by about 45 mm wide.

The holotype and paratypes of the gastropod *Peruvispira vipersdorfensis* Dickens, came from Vipersdorf 63 (Mariental District), while additional material was found in Tses Reserve near the main road about 13 km north of Tses Siding. The upper whorl surface of this gastropod is almost straight with the slit-band at the outer edge and approximately vertical. The slit-band is bounded on either side by a distinct ridge, and below it the outline is concave – the concave part being bordered below by a ridge. The outline then joins the base with an arc of low curvature. The columellar lip is distinctly thickened. The species in non-umbilicate and most adult specimens have four whorls, although some have five. Material ranges in height between 8 and 9 mm, in width between 5.5 and 6 mm, and the apical angle ranges between 38° and 46°.

A specimen of the goniatite *Eoasianites (Glaphyrites)* Ruzhencev, was found in a siliceous phosphatic nodule near Schlip (Rehoboth District). Martin *et al.* (1970) assigned it to the subgenus (*Glaphyrites*) and reported that it had 9 whorls and was probably an adult of which the body whorl had broken away.

Brachiopoda

Heath (1966, 1972) illustrated a brachiopod from Hardap 110, but did not describe it in detail. The specimen is probably an example of the bivalve *Eurydesma*.

Bryozoa

Wass (1970, 1972) described some bryozoans *Dyscritella* cf *D. spinigera*, from a locality not far northwest of Mariental (Lane & Frankes 1979).

The specimens on which the record of *Dyscritella* cf *spinigera* (Bassler) is based, were found near Mariental in a calcite-cemented sandstone. The zoaria vary in diameter from 1.08 mm to 1.68 mm, some specimens are oval in section with a width of 1.35-1.40 mm and a length of 1.57-1.75 mm.

Porifera

Sponge spicules were reported from Tses by Martin & Wilczewski (1970) but detailed descriptions have not been published.

Echinodermata

A fragment of starfish was found in a low bluff between Mariental and Hardap (Lane & Frakes 1970).

The specimen is the end of an arm, well preserved but so incomplete that it cannot be assigned to a genus or species. The authors identify it as a member of the family Monasteridae. Heath (1966, 1972) illustrated a virtually complete starfish from Hardap 110, which appears to be the same species as that described by Lane & Frakes. An additional broken specimen has recently been collected from the same site, but it is too fragmentary to add to our knowledge of the species concerned.

Martin (1953) and Martin & Milczewski (1970) record crinoid columnals from the Tses Boulder-Mudstone Member, but details have not yet been published.

Echinoids from near the main road west of Brukaros Siding, north of Tses were recorded by Haughton & Frommurze (1928). They identified the remains as possibly belonging to *Archaeocidaris*. Originally recorded from Dwyka Shales (and thus of Ecca age) this specimen was later considered by McLachlan & Anderson (1973) to have been collected from the Tses Boulder Mudstone, and would thus be of Dwyka age. Martin & Wilczewski (1970) report on the presence of echinoid spines at Tses, but no details are given.

Pisces

Fossil fish have been reported from the Dwyka beds of Namibia since the early part of this century (Gürich 1923; Haughton & Frommurze (1928). Gardiner (1962) provides the most detailed descriptions and analysis of these fossils (Table 2).

Range (1928) summarised the work of Gürich (1923) but identified one of the fish species (genus V by elimination) from the southern Karoo outcrops as *Helichthys loangwae*, although the basis for this identification is not stated. Jubb & Gardner (1975) provide details of repository and discovery horizons of these fish remains. *Namaichthys schroeder* Gürich was first described from Ganikobis (Keetmanshoop District) by Gürich (1923).

Trace Fossils

Arthropod traces from Ai-Ais figured by Abel (1935) and Savage (1971) based on material collected by Haughton, are now preserved at the South African Museum. Anderson (1974) discussed trace fossils from the Warmbad Basin (Ai-Ais, Klipneus and Zwartbas localities). Anderson (1981) dealt with the arthopod trace fossil *Umfolozia* from Klipneus. Other trace fossils were reported from Dwyka beds near Mariental (Lane & Frakes 1970). Horsthemke *et al.* (1990) mention *Umfolozia* in the Dwyka of the Haub Basin. Ledendecker (1992) illustrated ichnofossils from the Dwyka Formation in the Haub Basin which he identified as *Isopodichnus, Diplichnites, Umfolozia sinuosa, Punctichnium namibiense,* and *Glukstadtella cooperi.*

Ecca Group

Strata correlated with the Ecca Group of South Africa are widespread in Namibia (Figure 3),

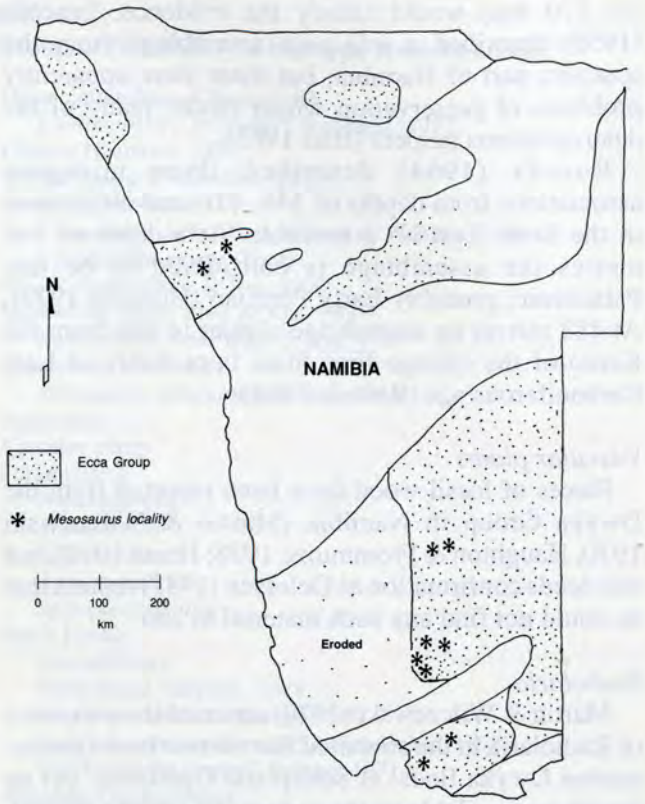

Figure 3. Ecca Group in Namibia. The Ecca Group occurs widely in Namibia, the best exposures being in the south (Kalahari and Karasberg Karoo Basins) and in the northwest (Huab Karoo Basin). *Mesosaurus* is common in these three basins.

occurring in three main outcrop areas: the Kalahari and Karasberg (Warmbad) Karoo in the the south and the Huab Karoo in the northwest. There are also extensive subcrops to the northeast of Etosha.

Numerous plant and invertebrate remains have been collected from the Namibian Ecca Group sediments, which are also rich in stromatolites. Apart from descriptions of *Mesosaurus* and wood, little has been published on these fossils.

Stromatolites

A stromatolite from Kameelhaar (Mariental district) was described by Kräusel (1956). Horsthemke *et al.* (1990) mention that stromatolites are common in the Huab region (Damaraland District) especially in depositional units 5 (Aba Huab Formtion) and 7 (Gai-As Formation). Further information is provided in Horsthemke (1992) and Ledendecker (1992) but detailed descriptions and interpretations have not been published.

Miospores

Ledendecker (1992) illustrated several spores from the Huab Basin Tsarabis formation, including *Calamospora aplata, Vestigisporites* cf *balmei, Vittatina* cf *densa, Gondisporites congoensis* and *Cyclogranisporites* cf *parvus.*

TABLE 3

Fossil Plants from the Huab Karoo Basin (* = holotype from Namibia)

Paracalamites sp. – Doros
Dadoxylon arberi – 16 km S of Quelle Atsab & 5 km west of Awahab Trig. Pt
Taxopitys africana** – Doros Crater
*Solenoxylon wissi** – The holotype is from Rooiberg 517, Damaraland
*Solenoxylon kurzi** – Type specimen is from Rooiberg 517, Damaraland
Solenoxylon oberholzeri – Type is from Rooiberg 517, Damaraland
Solenoxylon sp. – Versteinerter Wald near Khorixas
*Lobatoxylon kaokense** – Holotype was from Rooiberg 517, Damaraland
Megaporoxylon kaokense** – Type specimen from Rooiberg 517, Damaraland
*Kaokoxylon reuningi** – Type material was from Rooiberg 517, Damaraland
*Kaokoxylon durum** – Versteinerter Wald, near Khorixas, Damaraland.

Vascular plants

Fossil wood and leaves are very common in the Namibian Ecca Group sediments, both in the Huab Karoo and the Kalahari and Warmbad Karoo. Kräusel (1928, 1937, 1956a, b, 1959/60) has described much material in detail, while Brown (1977), Rodin (1951), Anderson & McLachlan (1976) and Wiss (1964) provide further information.

The taxa listed in Table 3 are based on fossils from the 'Petrified Forest' west of Khorixas (Kräusel, 1956a) and other Huab Karoo sites such as Doros Crater worked by Range (Kräusel, 1928). Brown (1977) also described material from Doros.

Kräusel (1956b) described fossil wood from the Kalahari Karoo of Mariental and Keetmanshoop Districts (Schlangkopf near Seeheim, Amalia). Other material from Huns, Aurus, Gibeon, Goamus, Mukorop, Berseba, Fish River and Gaibes was also described by Kräusel (1929) (Table 4).

Plant stem fossils, usually casts of the external surface of trunks are common in the Huab area at Verbrandeberg (Damaraland), Ledendecker (1992) recorded an unidentified lycopod, as well as *Cyclodendron leslii*. The latter species was also mentioned as being present in the Karasberg Basin by Schreuder & Genis (1975).

Plant leaves are rare in the Namibian Karoo (Anderson & McLachlan 1976) but *Glossopteris* has been identified at Verbrandeberg, at Gellap Ost (Oelofsen 1981; Anderson & MacLachlan 1976) and at Mukorop (Heinz 1932). The Gellap Ost specimen has a distinct midrib.

An enigmatic leaf-like fossil was found by Oelofsen (1981) on the Farm Aussenkjer (Anderson & McLachlan 1976). It is bilaterally symmetrical with a longitudinal median ridge, which is about 10% of the width of the 'leaf' which itself is 18 mm wide. There is no evidence of secondary venation, but instead there are regular rows of raised dots running obliquely across the impression. The rows of dots, and individual dots, are about 5 mm apart. The outer margin of the impression appears to be irregularly indented, but this may be due to preservation or damage.

Schreuder & Genis (1975) illustrated a sphenophyte leaf (*Phyllotheca*) from sandy shale at the base of the Ecca on Aussenkjer 147 (Karasberg District). The specimen is incomplete, the remaining fragment being some 10.5 cm long and 2.2 cm wide. It has about 10 subparallel 'folds' running along the length of the leaf converging towards the tip. In 1978 *Glossopteris* leaves were collected by Keyser and Smith at the petrified forest site (Smith pers. comm.).

Crustacea

Oelofsen (1981) reported that the crustacean *Notocaris tapscotti* is abundant in the Karasberg and Kalahari Karoo Basins, and at some sites is found in the same beds as the reptile *Mesosaurus*, of which it may have been a food item (Haughton & Frommurze 1928). *Notocaris* has been recorded from Gellap Plateau and the Farm Spitzkop, and Schreuder & Genis (1975) illustrated some material from Aussenkjer 147.

TABLE 4

Fossil Plants from the Kalahari Karoo (* = holotype from Namibia)

Cyclodendron leslii – Goamus
Medullopitys sclerotica** – Weg Huns-Keetmanshoop
*Dadoxylon porosum** – Weg Huns-Keetmanshoop
*Dadoxylon rangei** – Berseba, Weg Huns-Keetmanshoop, Aurus, Road 7 km west of Kalkfontein towards Keetmanshoop, 5 km northeast of Naute towards Keetmanshoop, Keetmanshoop, Itsawisis
*Megaporoxylon scherzi** – Mariental
*Megaporoxylon zellei** – Type specimen from Amalia Mariental District
*Phyllocladopitys capensis** – Ganikobis, Gaibes, Schlangkopf near Seeheim
*Phyllocladopitys martini** – Mariental
Phyllocladoxylon capense – Ganikobis, Goamus, between Tses and Arietites, Mukorop, Berseba and the bed of the Fish River
Abietopitys perforata – Weg Huns-keetmanshoop, Schlangkopf near Seeheim

Mollusca

Haughton & Frommurze (1982) recorded the presence of bivalves and gastropods in Upper Dwyka Shales at Haib, but these may well be Ecca. Ledenecker (1992) recorded two genera, the bivalves *Palaeomutela tanganyikensis* from the Tsarabis Formation, and *Terraia altissima* from the Gai-As Formation.

Pisces

Fish appear to be rare in the Namibian Ecca Group but recently both Oelofsen (1981) and Ledendecker (1992) have recorded scales and teeth. In the Karasberg (Warmbad) Karoo Anderson (1975) documented fish material at Gooie Hoop, and Oelofsen (1981) mentions having found palaeoniscid scales and a bony plate at Aussenkjer. Further fossils were found on the farms Gross Daberas, Asis, and Kirchberg. Ledendecker (1992) illustrated several elasmobranch teeth and bones and actinopterygian bones from the Tsarabis Formation in the Huab Basin. He also found ganoid scales but none of this material has been studied in detail.

Amphibia

McLachlan & Anderson (1973) refer to a fragment of large amphibian bone from Haib (Haughton & Frommurze 1928, 1936). Horsthemke *et al.* (1990) mention coprolites and bone fragments of amphibian in their 'depositional unit 4', equivalent to the Prince Albert Formation. Ledendecker (1992) illustrated some labyrinthodont remains from the Tsarabis Formation, Huab Karoo Basin, one of the few amphibian fossil ever recovered from the Namibian Karoo. The only other known specimen is from the Omingonde Formation (Keyser 1975).

Reptilia

The most common and best preserved vertebrates from the Namibian Karoo rocks are proganosaurian reptiles of the genera *Mesosaurus* (Figure 4) and *Stereosternum* (Oelofsen & Aurajo, 1987). *Mesosaurus* was first recorded from Namibia in 1914 (Stromer 1914; Hennig 1914). The genus *Stereosternum*, well known from Brazil, was recorded from Namibia only recently (Oelofsen & Araujo 1987), its remains having previously been included in *Mesosaurus*. Grote (1984) illustrated disarticulated remains of *Mesosaurus* from Daberas Ost 18, while Schreuder & Genis (1975) illustrated an almost complete specimen from the White Band at Aussenkjer 147.

Von Huene (1925) described what he thought was an isolated mammalian tooth from Doros collected by Reuning, naming it *Archaeotherium reuningi*. Range (1928, 1930) also mentions the specimen in passing, but according to Keyser (1973b), it appears to belong instead to a mammal-like reptile, possibly a cynodont. Keyser (1973b) reported the presence of Dinosauria in the Huab Karoo, 6 km north of Doros, based on a large lumbar vertebra, but detailed descriptions have not been published. Both *Archaeotherium* and the dinosaur are from strata younger than the Ecca.



Figure 4. *Mesosaurus tenuidens* from the White Band at Aussenkjer 147, Southern Namibia. Impression of almost complete skeleton with skull preserved in limestone. Bone has dissolved leaving a natural mould of the skeleton. Scale bar: 50 mm

Trace Fossils

Numerous trace fossils are known to occur in the Namibian Karoo rocks (Haughton & Frommurze 1985) but few have been described. Bather (1927) reported the presence of a U-shaped worm burrow from the Dwyka Shales at Haib, Karasberg District (Haughton & Frommurze 1928, 1936). This fossil was found in the Upper Dwyka Shales, and is thus technically from the

TABLE 5
List of Organisms and their Traces from the Ecca Group in Namibia (* = holotype from Namibia)

Stromatolites

Sporites
Calamospora aplata Bhardwaj & Salujha 1964
Vestigisporites cf *balmei* Hart 1960
Vittatina cf *densa* Anderson 1977
Gondisporites congoensis (Maheshwari & Bose 1969)
Cyclogranisporites cf *parvus* (Lakhanpal Sah & Dube 1960)

Vascular plants
Paracalamites sp. Zalessky
Dadoxylon arberi Seward
Taxopitys africana** Kräusel 1928
Solenoxylon wissi** Kräusel 1956
Solenoxylon kurzi** Kräusel 1956
Solenoxylon oberholzeri** Kräusel 1956
Solenoxylon sp. Kräusel 1956
*Lobatoxylon kaokense** Kräusel 1956
Megaporoxylon kaokense** Kräusel 1956
*Kaokoxylon reuningi** Kräusel 1956
*Kaokoxylon durum** Kräusel 1956
Medullopitys sclerotica** (Gothan 1908)
*Dadoxylon porosum** Kräusel 1928
*Dadoxylon rangei** Kräusel 1928
*Megaporoxylon scherzi** Kräusel 1956
*Megaporoxylon zellei** Kräusel 1956
*Phyllocladopitys capensis** Kräusel 1929
*Phyllocladopitys martini** Kräusel 1956
*Phyllocladopitys capensis** Kräusel 1928
Phyllocladoxylon capense Walton 1925
*Abietopitys perforata** (Gothan 1908)
Filices?
lycopod
Cyclodendron leslii (Seward 1903)
Glossopteris Brongniart 1828
Phyllotheca Brongniart 1828

Trace Fossils
Limulus
Umfolozia Savage 1971
Scolicia
Cruziana
Skolithos Haldeman 1841
Siphonichnus
Diplocraterion or *Teichichnus*
Planolites opthalmoides Jessen 1950

Crustacea
Notocaris tapscotti Broom 1931

Mollusca
*Aphanaia haibensis** Reed 1936
Palaeomutela tanganyikensis Cox 1936
Terraia altissima (Holdhaus 1918)

Pisces
Palaeoniscidae
Elasmorbranchia
Actinopterygia
Ganoidea

Amphibia

Reptilia
Mesosaurus tenuidens Gervais 1864
Stereosternum tumidum

Ecca Group. Anderson (1975) illustrated and discussed limulid tracks, *Koupichnium*, from the Whitehill Formation at Gooie Hoop, north of Vioolsdrif. Oelofsen (1981) mentions trace fossils at Haib and Aussenkjer in the Warmbad Karoo, and at Brandberg. Schreuder & Genis (1975) report a *Limulus* trackway from the boulder shale at Aussenkjer. Some of the Haib *Umfolozia*-type trackways could represent the activity of the crustacean *Notocaris tapscotti* (Oelofsen 1981) because some of the body imprints have such trackways leading up to them. *Scolicia*-like trails occur near the Brandenberg in the Karasberg and Kalahari Karoo Basins. *Cruziana* and *Skolithos* inchnofossils are common in the Karasberg and Kalahari Karoo Basin (Oelofsen 1981). Kingsley (1985), working on cores from drill holes, reported that the genera *Siphonichnus* and *Diplocraterion* or *Teichichnus* occur in the Ecca beds of the eastern part of the Kalahari Karoo Basin. He also mentioned the presence of *Cruziana* and *Skolithos*.

Ledendecker (1992) illustrated a tube-like trace fossil, *Planolites* from the Tsarabis Formation of the Huab Basin.

Omingonde Formation

The Omingonde Formation (Figure 5) is widespread in the Otjiwarongo, Grootfontein and Omaruru Districts. Main outcrops are south of the Waterberg thrust (Lüdke 1970) near Mt. Etjo, Omatakos and north of the Waterberg Plateau.

The first fossil vertebrate discovered in the

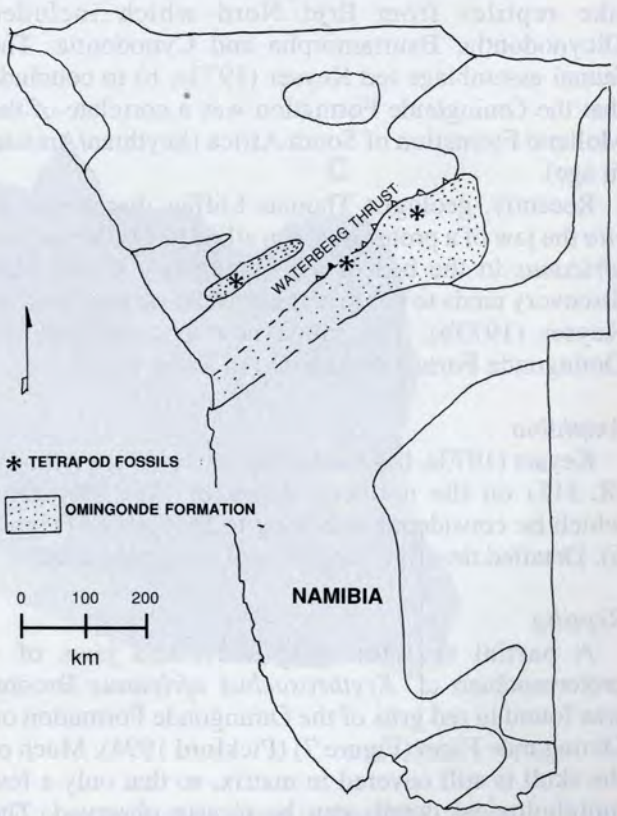

Figure 5. The Triassic Omingonde Formation, Namibia.

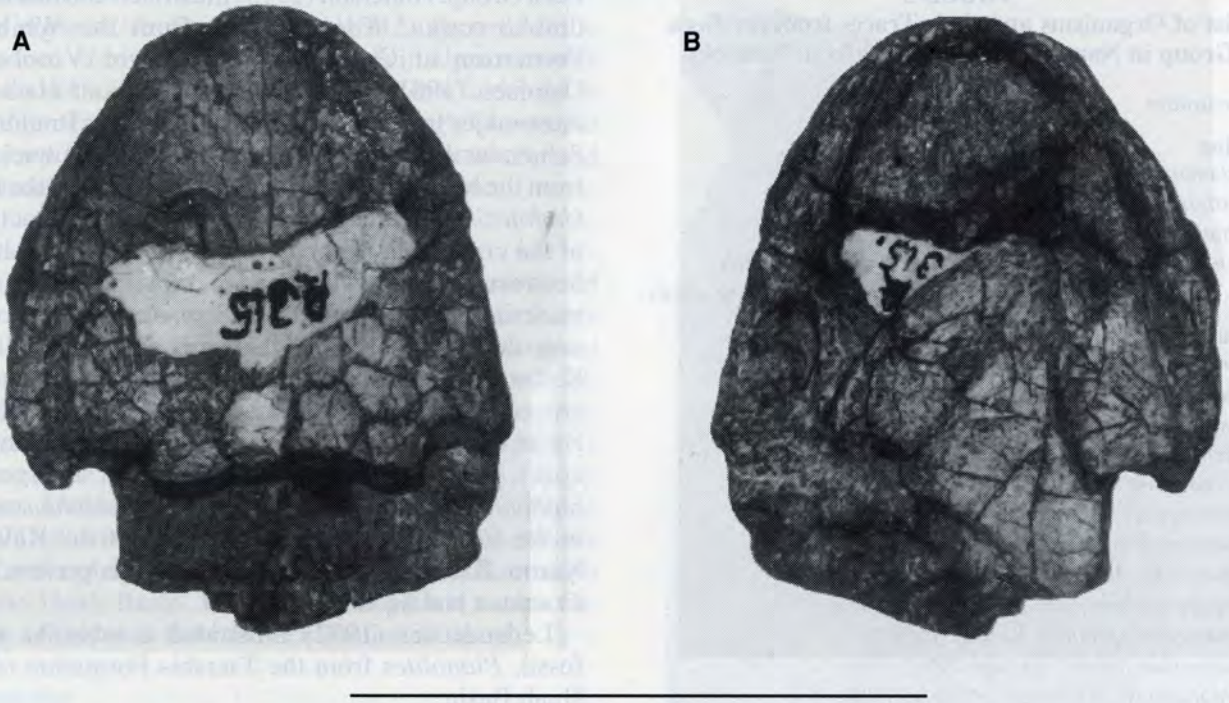

Figure 6. R.315, skull of a small eriopoid amphibian from the Omingonde Formation, northern slopes of Mt Etjo, Central Namibia. **A** – dorsal and **B** – ventral views. Scale bar: 50 mm

Omingonde Formation is considered to have been a reptile skull found on Farm Breitenbach during the 1920's but nothing has ever been published about the specimen, the present whereabouts of which are unknown. Keyser (1973a, b, 1978) recovered a moderately diverse fauna of Amphibia and mammal-like reptiles from Etjo Nord which included Dicynodontia, Bauriamorpha and Cynodontia. The faunal assemblage led Keyser (1973a, b) to conclude that the Omingonde Formation was a correlate of the Molteno Formation of South Africa (Scythian/Anisian in age).

Recently, geologist Thomas Löffler discovered *in situ* the jaw of a proterosuchian allied to *Erythrosuchus africanus* in the bed of the Omingonde River. This discovery tends to confirm the correlation proposed by Keyser (1973b). The fauna now known from the Omingonde Formation is listed in Table 6.

Amphibia

Keyser (1973a, b) found a skull of a small amphibian (R. 315) on the northern slopes of Etjo Mountain, which he considered to belong to Eriopoidea (Figure 6). Detailed descriptions have not been published.

Reptilia

A partial skeleton with skull and jaws of a proterosuchian cf *Erythrosuchus africanus* Broom, was found in red grits of the Omingonde Formation on Omingonde Farm (Figure 7) (Pickford 1994). Much of the skull is still covered in matrix, so that only a few morphological details can be clearly observed. The lower jaws are 62 cm long and 66 mm deep below the

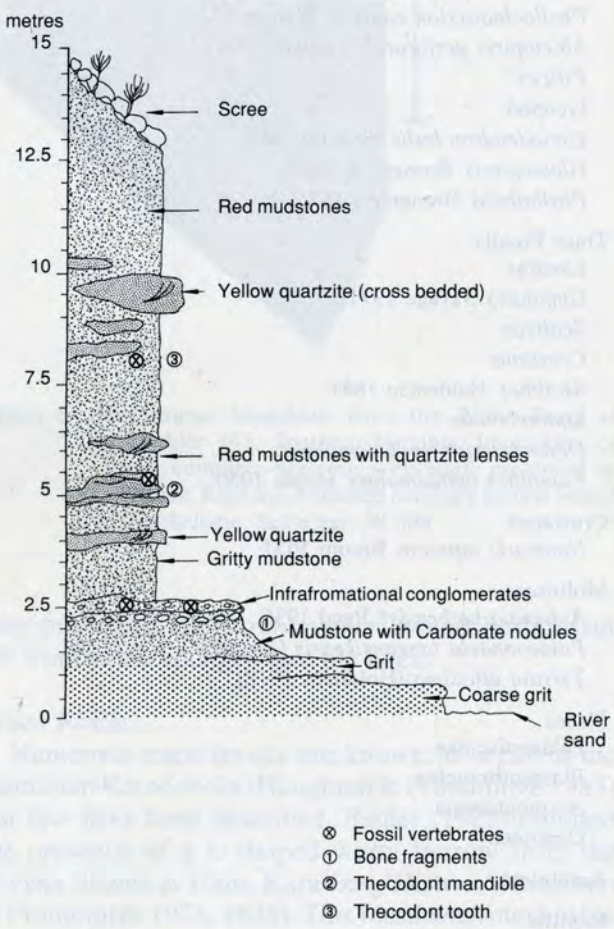

Figure 7. Stratigraphic succession at Omingonde thecodont site.

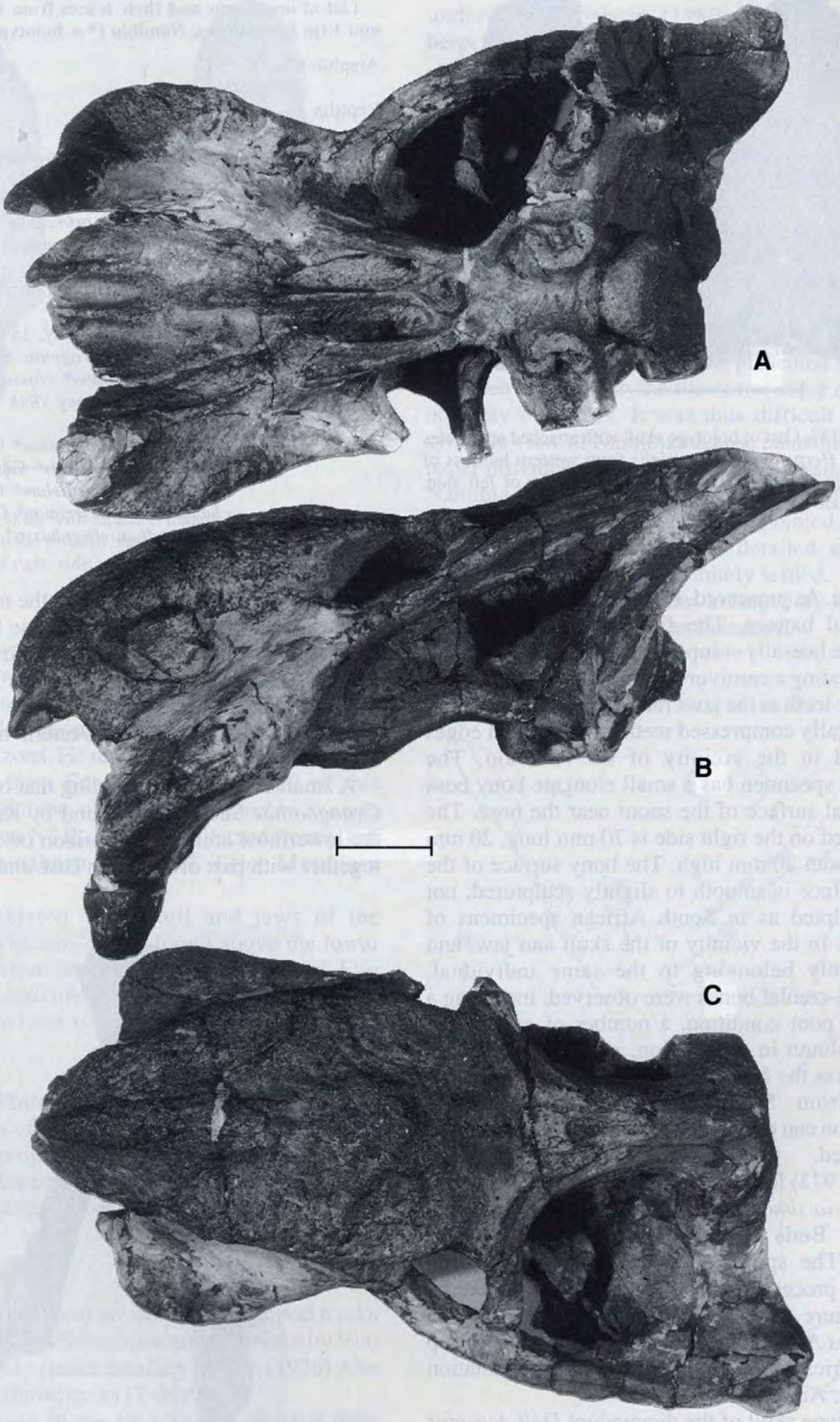

Figure 8. R.313, skull of *Kannemeyeria simocephalus* from the northern slopes of Mt. Etjo, Central Namibia. A – ventral view, B – lateral view of left side, C – dorsal view. Scale bar: 50mm.



Figure 9. R.337, Cast of holotype skull with attached mandibles of *Herpetogale marsupialis* from western buttress of Etjo Mountain. Dorsal and lateral view of left side. Scale bar: 50 mm

TABLE 6
List of organisms and their traces from the Omingonde and Etjo Formations, Namibia (* = holotype from Namibia)

Amphibia
- Eriopoidea

Reptilia
- Proterosuchia
  - cf *Erythrosuchus africanus* Broom 1905
- Dicynodontia
  - *Kannemeyeria simocephalus* Weithofer 1888
  - *Dolichuranus* primaevus** Keyser 1973
  - *Rhopalorhinus* etionensis** Keyser 1973
- Bauriamorpha
  - *Herpetogale* marsupialis** Keyser 1978
- Cynodontia
  - *?Cynognathus* Seeley, 1895
  - *Diademodon tetragonus* Seeley
  - *Titanogomphodon* crassus** Keyser 1973
  - *Trirachodon* Seeley 1894
- Ichnofossils
  - *Saurichnium damarense** Gürich 1926
  - *Saurichnium tetractis** Gürich 1926
  - *Saurichnium parallelum** Gürich 1926
  - *Saurichnium anserinum** Gürich 1926
  - *Tetrapodium elmenhorsti** Gürich 1926

second tooth. As preserved, the lower jaw obscures the upper dental battery. The five teeth rooted in the mandible are laterally compressed and possess serrated edges suggesting a carnivorous life style. The emerged height of the teeth in the jaws ranges up to 50 mm. Four similar laterally compressed teeth with serrated edges were found in the vicinity of the skeleton. The Omingonde specimen has a small elongate bony boss on the lateral surface of the snout near the nose. The knob exposed on the right side is 70 mm long, 20 mm wide and about 20 mm high. The bony surface of the side of the face is smooth to slightly sculptured, not heavily sculpted as in South African specimens of *E.africanus*. In the vicinity of the skull and jaw, and very probably belonging to the same individual, various post-cranial bones were observed, including a humerus in poor condition, a number of gastralia, a vertebral column in articulation, and several ribs. In many respects the Namibian fossil appears similar to material from South Africa, but a detailed determination can only be made after the specimen has been prepared.

Keyser (1973) found a large skull of the dicynodont *Kannemeyeria simocephalus* Weithofer in arenaceous lower Etjo Beds on the northern slope of Etjo Mountain. The specimen (R. 313) has very large caniniform processes and exceedingly wide lateral flanges (Figure 8). This species is known from the *Cynognathus* Assemblage Zone of the Beaufort Group of South Africa and from the Puesto Viejo Formation of Mendoza, Argentine.

The holotype skull of the dicynodont *Dolichuranus primaevus* Keyser was discovered by Keyser (1973) on the southern slopes of a hill north of Etjo Mountain, below the lowermost arenaceous horizon.

The holotype skull of *Rhopalorhinus etionensis* Keyser, was collected by Keyser from the northern slopes of Etjo Mountain between the upper and lower arenaceous horizons of the lower Etjo Beds.

The articulated skull and mandibles (R. 337) (Figure 9) of *Herpetogale marsupialis* Keyser, a small therocephalian, were found above the uppermost arenaceous horizon on the western buttress of Etjo Mountain.

A small lower jaw resembling that of the cynodont, *Cynognathus* Seeley, was found by Keyser (1973) in the lowermost arenaceous horizon on Etjo Mountain, together with part of the brain case and the occiput.



Figure 10. Mandible of *Diademodon tetragonus* (R321) from the Omingonde Formation, northern slopes of Etjo Mountain, Central Namibia. Occlusal view. Scale bar: 50 mm.

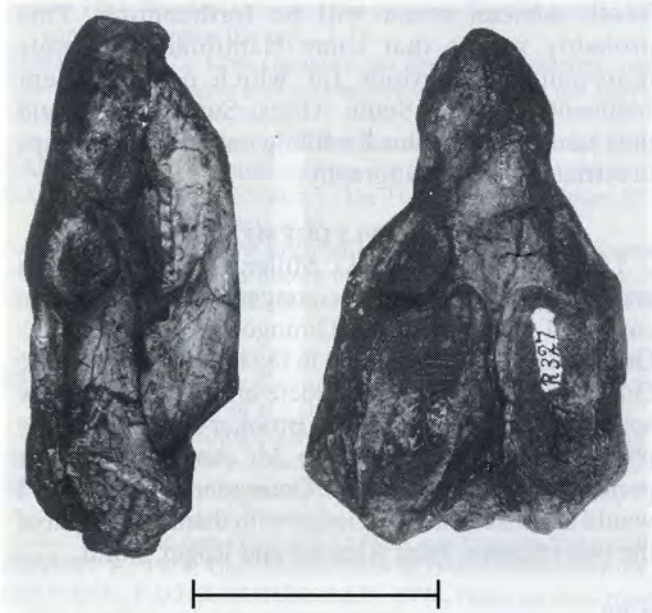

Figure 11. R.327, skull with attached mandibles of *Trirachodon* sp. from the western buttress of Etjo Mountain. Lateral view of right side and dorsal view. Scale bar: 50 mm

A skull, some post-cranial bones and two lower jaws (R. 321: Figure 10) assigned to the cynodont *Diademodon tetragonus* Seeley were found by Keyser (1973) in nodule-bearing shale beds between the two arenaceous horizons. He reported that he could observe no differences from South African material of this species. The holotype of *Titanogomphodon crassus* Keyser, specimen N° R. 322 was collected from a grit bed on the northern slope of Etjo Mountain (Keyser 1973).

A partial skeleton with skull and jaws of the cynodont *Trirachodon* sp was found above the lower arenaceous horizon on the western buttress of Etjo Mountain. The specimen R. 327 (Figure 11) is well preserved but the bone is cracked and deeply impinged by matrix.

Etjo (Plateau) Sandstone Formation

The type area of this formation is the plateau of Mt Etjo. In the group are included aeolianites in the Gamsberg, the Etendeka and Orupembe areas (Figure 12), ranging in age from Late Triassic to Early Cretaceous.

Trace Fossils

At Otjihaenamaperero are abundant tetrapod tracks which were found by Elmenhorst and described by Von Huene (1925) and in more detail by Gürich (1926) who named several ichnospecies (Table 6).

These trackways in the Etjo Sandstone have been interpreted as indicating an upper Carnian to Norian age (Dingle *et al.* 1983).

Tetrapod tracks have also been reported from the Waterberg Plateau (Cosburn 1981) and at Umurumba Omambonde (Wiechmann 1983; Martin 1984; Grote 1985 unpub.) but detailed studies have not been undertaken. Cosburn (1980) listed the following herpetogenera at Waterberg on the basis of ichnofossils – *Massospondylus, Tritylodon, Pachygenelus* and *Gryponyx*, although no details were provided.

Jurassic lavas near Hardap

Swart (pers. comm.) has discovered conchostracans at Hardap, in sediments intercalated in the Jurassic lavas. These small crustaceans, like ostracods, have two shells that are sometimes confused with those of bivalves. The material is currently under study.

SUMMARY

Up to now, much of the data presented in this paper has been scattered in the literature, some of it old and not easy of access. It was thus difficult to obtain a synoptic view of Namibian Karoo palaeontology. This paper provides a gazetteer of Karoo fossil localities in Namibia (Table 1) and lists of taxa reported from the country (Tables 2-6). It should be pointed out that, for some floras and faunas, the detailed stratigraphic positions have not been definitely settled. The lists are thus provisional inventories arranged by stratigraphic positions as reported in the literature.

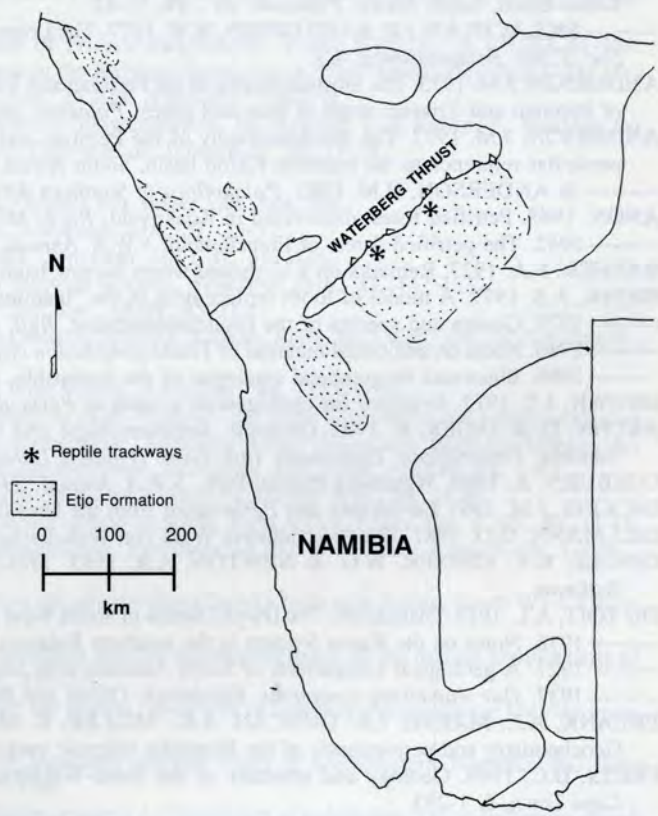

Figure 12. Etjo Formation in Namibia. The aeolian Etjo (or Plateau) Sandstone crops out well in central and northwestern Namibia. The formation comprises aeolianites of various ages ranging from Late Triassic to Early Cretaceous. At serveral outcrops footprints attest to the presence of dinosaurs, including bipedal forms, in Namibia.

It is unfortunate that many of the fossils mentioned in the literature appear to have been lost. Furthermore, the detailed geological context of much of the material was inadequately recorded at the time of collection. Many of the site designations consist of farm names, but Namibian farms tend to be vast, the majority being several thousand hectares in extent. Even if the outcrop or subcrop from which fossils were collected can be identified, the stratigraphic position of the fossils within the outcrop was not always recorded.

Considerable work needs to be done on Namibian Karoo stratigraphy. Up to now, correlations have been made principally southwards with South African Karoo type areas and westwards with Brazilian successions, but it is evident that for some strata, such as the Omingonde Formation and the aelianites in the Etokendeka volcanics, no simple correlations with South African strata will be forthcoming. This probably means that some Namibian sediments represent time periods for which no equivalent sediments occur in South Africa. Such strata would thus assume great value for filling out some of the gaps in African Karoo stratigraphy.

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MORE FOSSIL WOOD FROM THE NAMAQUALAND COAST, SOUTH AFRICA; ONSHORE MATERIAL.

by

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ABSTRACT

Fossil wood was collected from a palaeo-beach sequence on the farms Sandkop, Oubeep and adjacent State land, on the Namaqualand (west) coast of South Africa. Of the 14 samples sectioned only 5 were well enough preserved to describe and identify to species level. The woods are podocarpaceous and have been assigned to the taxa *Podocarpoxylon cf. umzambense, Mesembrioxylon woburnense, M. stokesi* and *Mesembrioxylon sp.* The samples are Lower Cretaceous in age and were most probably reworked a number of times into successively younger palaeoshoreline deposits. The same species occurred in the offshore sediments, therefore indicating a wider area of "woodland" and further evidence of extensive shelf erosion by subsequent marine transgressions and regressions.

KEY WORDS: Podocarpaceae, Lower Cretaceous, South Africa.

INTRODUCTION

Fossil wood is abundant in southern African terrestrial deposits but has been little studied. Previously described gymnospermous wood has mainly been assigned to two genera, *Dadoxylon* Endlicher (Warren 1912, Walton 1925, 1956) and *Araucarioxylon* Kraus (Rodin 1951, Erasmus 1976a). A few woods have been placed in other genera, for example, *Dammaroxylon* (Schultze-Motel 1966, Marguerier 1973, Erasmus 1976b), *Australoxylon* (Marguerier 1973) *Podocarpoxylon* (Schultze-Motel 1966), and several genera with pith, *Rhexoxylon,* (Bancroft 1913), *Tordoxylon, Solenoxylon, Lobatoxylon, Megaporoxylon, Kaokoxylon* and *Phyllocladopitys* (Krausel 1956a,b,c).

The correct use of the genera *Dadoxylon* and *Araucarioxylon* has been discussed at length by several authors (Vogellehner 1964, Maheshwari 1972, Lepekhina 1972, Erasmus 1976a, Pant & Singh 1987) but there is no general consensus. There is a similar problem with the genera *Podocarpoxylon, Phyllocladoxylon* and *Mesembrioxylon. Podocarpoxylon* and *Phyllocladoxylon* were erected (Gothan 1905) for secondary xylem with uniseriate (occasionally biseriate and opposite) tracheid pitting, ray cell walls thin and smooth and podocarpoid crossfield pitting. The distinction between the two genera is based on the cross-field pitting. *Podocarpoxylon* has one, occasionally two, simple pits in the field. *Phyllocladoxylon* has one, occasionally two, large, simple pits in the field. *Mesembrioxylon* (Seward 1919) encompasses both genera because the pits are not always distinguishable (Seward 1919, p. 173). Different authors favour different genera and thus there is a great deal of overlap. The onshore woods belong to different species of two of these genera, *Podocarpoxylon* and *Mesembrioxylon*, but the usage of the genera will not be discussed here.

LOCALITY AND GEOLOGY

Clasts of fossil wood were collected from the surface of a raised palaeoshoreline on the farms Oubeep, Sandkop and adjacent State land, which is known locally within the De Beers offices as the Recent Emergent Terrace (Figure 1). The terrace is a composite feature, cresting between 12 to 9 metres above sea level (masl) in the vicinity of Oubeep. The palaeoshoreline from which the fossil wood comes, therefore, predates the Eemian (± 120 000 BP) palaeoshoreline which crests at about 4 masl. According to Hendey and Volman (1986) the palaeoshoreline at Oubeep predates the Late Pleistocene, and in Kensley and Pether's scheme (1986) it would be Middle Pleistocene.

The clasts of fossil wood occur within the palaeo-beach sequence as well-rounded and polished pebbles and cobbles, but one log of approximately 400mm x 200mm has been recovered. Some cobbles are discoidal, showing that they have spent a considerable time in the nearshore and beach environment. The presence of chattermarks on the surface of the clasts shows that the beach was subject to high-energy conditions.

MATERIALS AND METHODS

The silicified fossil wood was cut and polished to make petrographic thin sections in the normal manner. The sections are somewhat thicker because of the cell and crystal sizes. Three slides in different planes have

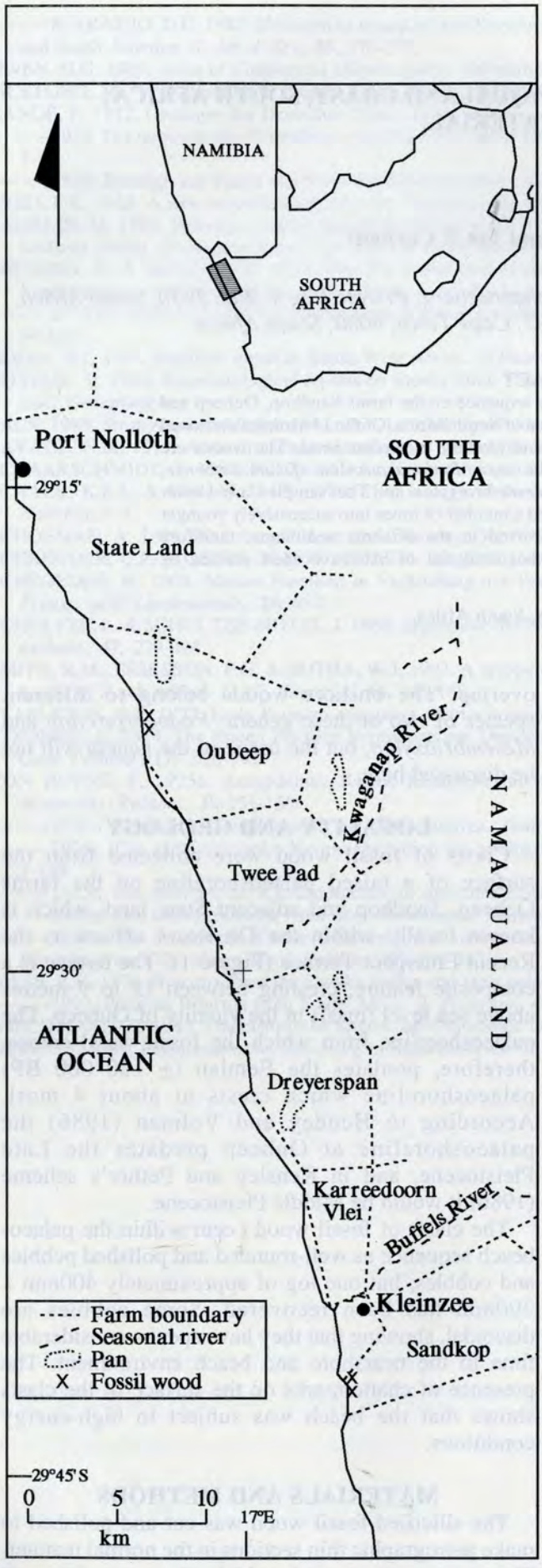


Figure 1: Locality map.

been made for each specimen. The planes are transverse, tangential longitudinal and radial longitudinal.

DESCRIPTION OF MATERIAL
Family Podocarpaceae

Podocarpoxylon cf. umzambense Schultze-Motel, 1966.

BPI Number: BP/16/228
Locality: Farm Oubeep, Namaqualand Coast.
Figures: 2-5
Other specimens: none.

Description

Growth rings are indistinct and comprise 3 - 4 rows of latewood cells with smaller radial diameters (Figure 2).

The tracheids are thin walled (average 7.5µm) and a little distorted. The tracheid mean tangential diameter of earlywood is 40µm (range 27-55µm). The mean radial diameter is 60µm (range 50-67µm). The latewood mean tangential diameter is 39µm (range 35-47µm) and mean radial diameter is 26µm (range 22-28µm). The tracheid bordered pitting is on the radial walls, uniseriate and separate (Figure 3). The pits are round with a diameter of 15µm, and round aperture of 6µm. Resin or gum deposits are common.

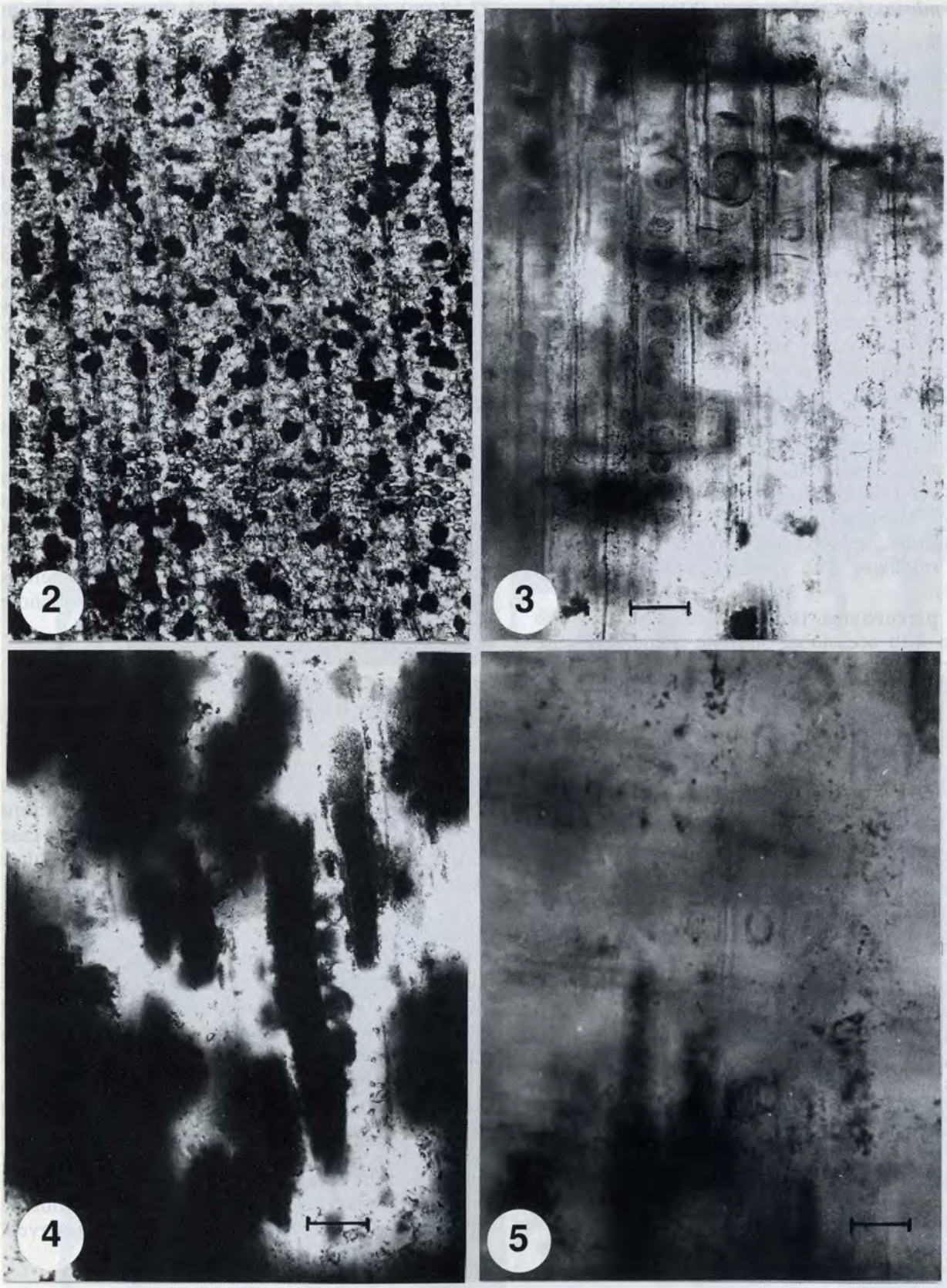
Axial parenchyma is very sparse. The rays are uniseriate and low; their total height is difficult to determine because of the gum deposits in the tracheids but their range is 3-8-18 cells (Figure 4). Ray parenchyma cell walls are thin and smooth, and the cross-field pits single, simple, round to oval and have an average diameter of 10µm. Ray tracheids and resin canals are absent.

Identification

This specimen has typical *Podocarpoxylon* features and is almost the same as *P. umzambense* from the Upper Cretaceous Umzamba beds of the south east coast of South Africa described by Schultze-Motel (1966). The latter specimen has 1-2 opposite tracheid pits on the radial walls, ray height of 1-25 cells and also 1-2 elliptic pits per cross-field. The sizes of all the pits in both specimens are almost the same but the incompleteness of the rays in the Namaqualand onshore specimen means that it cannot be placed in the described species with complete confidence.

This specimen is also similar to *M. gothani* (Seward 1919, Thayn & Tidwell 1984) from the Aptian of the Isle of Wight, except that the latter has very low rays. Both have quite small cross-field pits (*M. gothani*: 7µm).

BP/16/228 is also very similar to BP/16/244 from the Namaqualand Shelf (offshore) deposits (Bamford and Corbett 1994) and also called *P. cf. umzambense*.



Figures 2-5: *Podocarpoxylon cf. umzambense* BP/16/228. **2:** Transverse section. Tracheids are thin-walled and resin is abundant. Magn 50x. Scale bar = 200µm. **3.** RLS. Bordered pits on the radial walls of the tracheids. Magn 270x. Scale bar = 37µm. **4:** TLS. A few ray cells are visible on the right of the photograph but the rest have been obscured. Magn 225x. Scale bar = 44µm. **5:** RLS. Simple podocarpoid pits are just visible in the photograph. The ray cell walls are thin and smooth and some cells have resinous deposits. Magn 550x. Scale bar = 20µm.

Mesembrioxylon woburnense (Stopes) Seward 1919.

BPI Number: BP/16/227
Locality: Farm Oubeep, Namaqualand Coast
Figures: 6-9.
Other specimens: BP/16/231, 233.

Description

What appear to be growth rings on the hand specimen are seen to be cracks when viewed under the microscope. Only two real growth rings are evident on the slide and they are 9mm apart.

The tracheids are regularly aligned and the rays are prominent in transverse section. The tracheids are squarish in outline (Figure 6). The earlywood mean tangential diameter is 39µm (range 32-45µm) and mean radial diameter is 41µm (range 37-48µm). The latewood is inconspicuous and forms only 4-5 cell layers. The mean tangential diameter is 40µm (range 30-50µm) and mean radial diameter is 15µm (range 10-20µm). Tracheid pits occur on the radial walls only, uniseriate, separate and contiguous and have a diameter of 20µm with a round aperture of 12µm (Figure 7).

Axial parenchyma is very rare. The rays are uniseriate with occasional biseriate portions (Figure 8). Their average height is 9-15 cells but they range from 2-25 cells high. The cell walls are thin and smooth. Cross-field pits are single, simple, oval to rounded in outline and 12 x 8µm in size (Figure 9). Some pits are rounder with a thinner rim but this may be due to preservation. The oval pits have an oblique orientation. Resin occurs in tracheids and rays. No ray tracheids or resin canals are present.

Identification

BP/16/227 is *Mesembrioxylon woburnense* because it has the same tracheid pitting, rays and cross-field pitting as the type (Seward 1919). This specimen is very similar to BP/16/46 from the offshore deposits (Bamford and Corbett 1994) and the latter one has only been closely compared to *M. woburnense*. Both the Namaqualand onshore and offshore specimens have crossfield pits that fall within the size range of the original specimen described from the Aptian of England.

Mesembrioxylon stokesi Thayn and Tidwell 1984.

BPI Number: BP/16/223
Locality: State land adjacent to farm Oubeep, close to shore.
Figures: 10-14
Other specimens: none

Description

Growth rings are not visible but the preservation of cells is patchy.

The tracheids are squarish in outline. The mean tangential diameter of the earlywood is 48µm (range 27-58µm) and the mean radial diameter is 38µm (range 35-45µm). Latewood is absent. The tracheid bordered pitting is on the radial walls only and is uniseriate, separate and contiguous. The diameter of the pits is 18-19µm but the size and shape of the aperture is unknown.

Axial parenchyma is absent. The rays are uniseriate with occasional biseriate portions of 2-5 cells, and mostly 10-28 cells high but occasionally rays of up to 48 cells occur. Ray cell walls are thin and smooth and the cross-field pits are single, mostly simple, rounded and have a diameter of 10-13µm. Sometimes the pits have a vague aperture and so appear bordered. Resin is common in tracheids but no resin canals nor ray tracheids were found.

Identification

With the very high rays and podocarpoid cross-field pits this wood is indistinguishable from *Mesembrioxylon stokesi* from the Lower Cretaceous of Utah (Thayn & Tidwell 1988). The onshore Namaqualand specimen does not have the abundant parenchyma that the American specimen has although this may be due to poor preservation. The specimen described here is the same as BP/16/35 described from the offshore deposit (Bamford & Corbett 1994.)

Mesembrioxylon sp.

Specimens: BP/16/221, 222, 224, 225, 226, 229, 230, 232, 265.

The rest of the onshore samples show at least one podocarpoid feature but there is insufficient information to identify them further. This was the case with many of the offshore specimens as well and they have all been placed in this taxon.

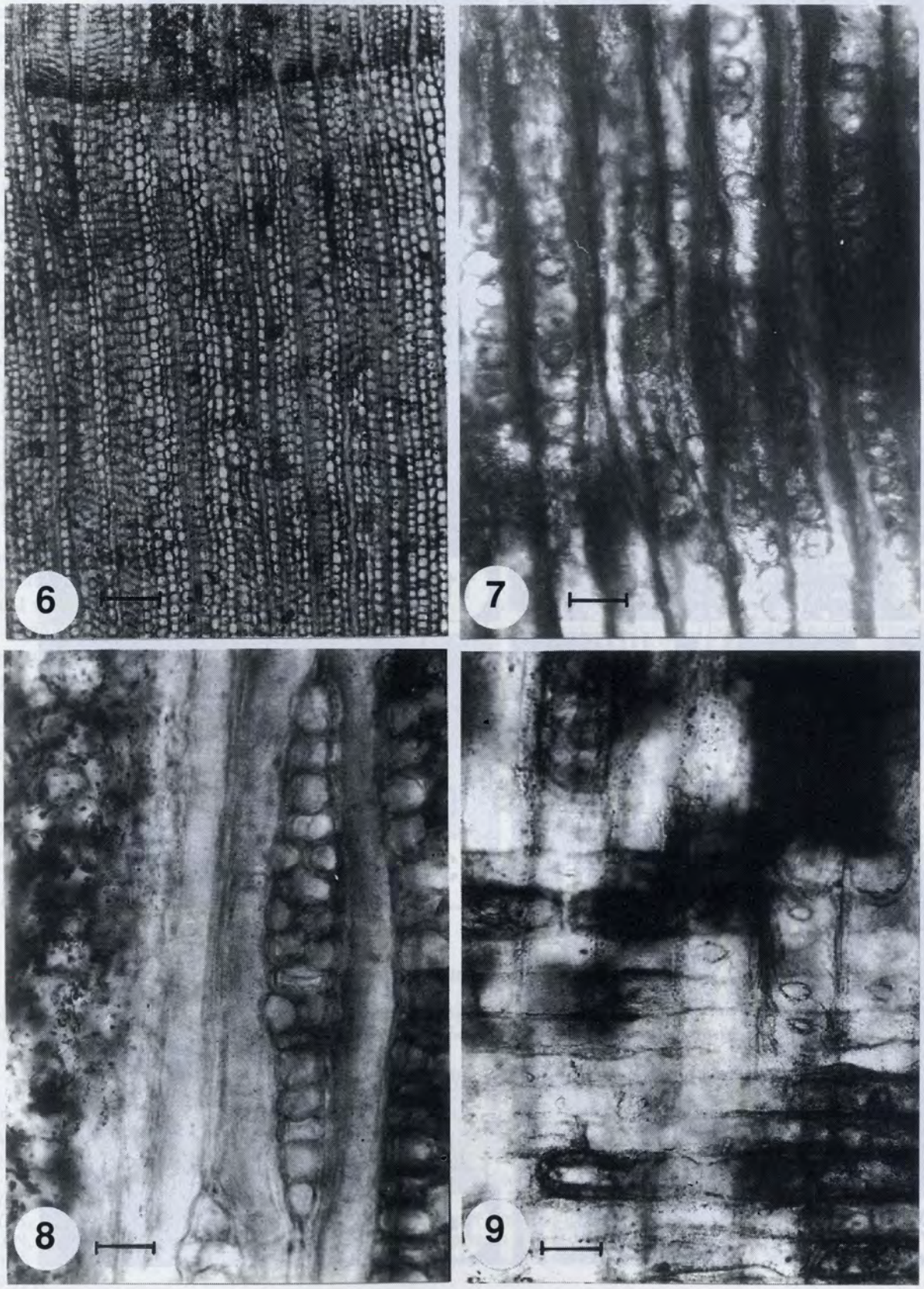
General Description

Growth rings vary from 1-3 mm in width or are absent. Latewood is never more than 4 cells wide. The tracheids are fairly thin-walled and range in tangential diameter from 17-60µm and radial diameter 24-62µm for the earlywood, and the latewood is usually crushed. The bordered pits are on the radial walls only, uniseriate, separate and contiguous and vary from 14-22µm in diameter. The presence of parenchyma is variable but it is never abundant. Rays are mostly uniseriate with occasional biseriate portions, and cell walls are thin and smooth. Ray height falls within the range 5-35 cells. The cross-field pits are not preserved.

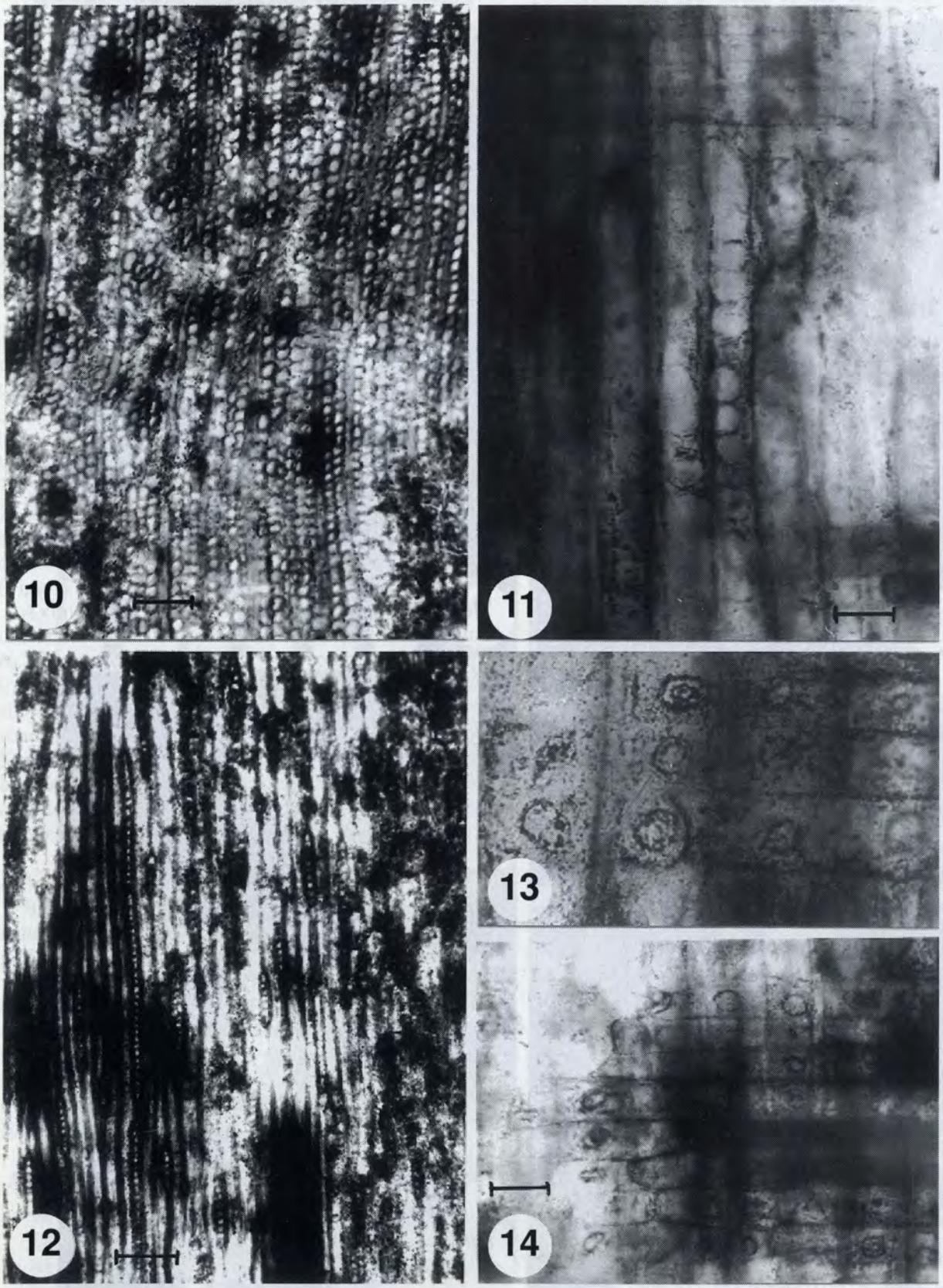
DISCUSSION

Age and Palaeoecology

The Namaqualand coast fossil woods described here are the same as those from the offshore (continental shelf) deposit but there is less variety. This is hardly surprising as the sample size is smaller (14 onshore specimens and 43 offshore specimens). These woods have been compared with both northern and southern



Figures 6-9: *Mesembrioxylon woburnense* BP/16/227. **6:** TS to show regular tracheids and one growth ring. Magn 37x. Scale bar represents 270µm. **7:** RLS. Bordered pits on the radial walls of the tracheids, separate and contiguous. Magn 250x. Scale bar = 40µm. **8:** TLS. Biseriate ray, squarish cells and variable height. Magn 250x. Scale bar =40µm. **9:** RLS. Cross-field pits, single, simple and oval to round. Magn 240x. Scale Bar = 42µm.



Figures 10-14: *Mesembrioxylon stokesi* BP/16/223. **10:** TS. Regular tracheids but patchy preservation. Magn 42x. Scale Bar = 240µm. **11:** RLS. Contiguous bordered pits on the radial walls of the tracheids. Magn 270x. Scale bar = 37µm. **12:** TLS. Very high uniseriate rays. Magn 42x. Scale bar = 240µm. **13:** RLS. Cross-field pits bordered. Magn 800x. Scale bar = 12µm. **14:** RLS. Cross-field pits simple – the most common form. Magn 500x. Scale bar = 20µm.

hemisphere fossil woods and indicate a Lower Cretaceous age (see also Bamford & Corbett 1994).

The two families represented in the fossil record are the Podocarpaceae and Cheirolepidiaceae (offshore deposit, Bamford & Corbett 1994). Podocarpaceae is a well established southern hemisphere family with some 80 extant species. The fossils cannot be compared with any of the extant species although they share many of the family features. Modern podocarps are mostly restricted to wetter regions or higher altitudes. The Cheirolepidiaceae are extinct but extended from the Upper Triassic to the Lower Tertiary (Alvin 1982, Watson 1988). They occupied a variety of habitats but mostly had the ability to survive periods of drought (Francis 1983). Fossil podocarps frequently occupied low-lying plains (Dupéron-Laudoueniex & Pons 1985). The evidence from the growth rings of the fossil woods indicates that the palaeoclimate was a seasonal one with periods of drought. The low-lying coastal plains experienced changing sea levels (Kensley & Pether 1986) and the trees were occasionally flooded and preserved *in situ*. Some specimens may have been transported a short distance during the Cretaceous erosional phase (Ward & Corbett 1991).

Fossil woods have been collected from as far north as the Orange River mouth to just south of Kleinzee, a distance of approximately 150km (Figure 14). The homogeneity of the wood types suggests that the trees were contemporaneous, in geological terms, and this implies an extensive "forested" area. It is not possible to determine if the "forest" was a closed canopy one or more open woodland. Looking at modern vegetation there are variations within any particular region and one part may have been drier and more sparsely vegetated than another. It is not possible to extract such detail from the samples collected offshore. Nonetheless it is significant that there was an extensive wooded area along the west coast during Lower Cretaceous times.

Although the wood is of Cretaceous age, the sedimentary deposits are Pleistocene (Hendey & Volman 1986, Kensley & Pether 1986), thus providing clear evidence that the material in the palaeoshoreline at Oubeep has been derived from an older deposit. Surface drilling on the boundary of the farm Dreyerspan to the north of Kleinzee, and immediately south of Oubeep has delineated a palaeochannel feature. The pollen from a palaeo-channel on the farm Dreyerspan (Figure 1) has been dated as pre-Barremian (Soekor Report 1990). It therefore appears likely that the onshore fossil wood material has been derived through erosion of the Early Cretaceous palaeochannel feature by shoreface incision during transgression(s) across the area (pers. comm. Molyneux 1993). It is possible that the clasts of fossil wood have been reworked a number of times into successively younger palaeoshoreline deposits, as indicated by the extent to which the clasts have been rounded, polished and chattermarked.

CONCLUSION

The fossil woods from the onshore and offshore sediments of Namaqualand are very similar and are of Lower Cretaceous age. They indicate a moister climate than is experienced today because large trees were able to grow in the low-lying coastal plains. The palaeoclimate, however, was seasonal with periods of water shortages. In both cases the woods have been reworked and incorporated into considerably younger palaeoshoreline sequences.

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DENTITION AND FEEDING NICHE OF *ENDOTHIODON* (SYNAPSIDA; ANOMODONTIA).

by

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ABSTRACT

The cranial morphology and extensive dentition of the dicynodont therapsid *Endothiodon* are different from those of any other dicynodont and it clearly had a different feeding niche. Recently prepared material from Mozambique which has relatively well preserved dentition has revealed that the mode of tooth replacement of *Endothiodon* differs in the upper and lower jaws. The very high and narrow vaulted palate with a close fitting, pointed lower jaw indicates that *Endothiodon* had a small mouth with muscular cheeks and extensive cheek pouches, suggesting a browsing feeding niche.

KEYWORDS: Therapsida, Dicynodontia, *Endothiodon*

INTRODUCTION

The anomodont genus *Endothiodon* is known from South Africa, Zambia, Tanganyika (Cox 1964), India (Kutty 1972), and Brazil (Keyser 1981). However, because most of the skull material is fragmentary, relatively little is known about the cranial anatomy of this atypical dicynodont. Several specimens collected in Mozambique in 1956 which are housed in the collections of the Bernard Price Institute for Palaeontological Research have recently been prepared. Comparison of this material with specimens from the Beaufort Group of South Africa reveals important new information on the dentition and possible mode of feeding of *Endothiodon*.

In South Africa, where the majority of *Endothiodon* specimens have been found, the stratigraphic range of the genus extends from the *Pristerognathus* Assemblage Zone to the upper regions of the *Cistecephalus* Assemblage Zone (Smith & Keyser In Press a & b). Because its stratigraphic range is relatively limited the genus has been used as a zone fossil in previous biostratigaphic subdivisions of the Beaufort Group in South Africa (Broom 1906, 1907, 1909; von Huene 1925; Watson 1914 a,b).

The Mozambiquean material was sent to Dr S H Haughton, then director of the Bernard Price Institute, in 1957, by Dr F Mouta, who had collected it in the Lugno area of Niassa Province in 1956.

Cox (1964), in revising the taxonomy of *Endothiodon*, used the palate and dentition to reduce nine species to three. He also speculated that the animal may have fed by grubbing vegetable matter out of swampy ground. In contrast, our research suggests that *Endothiodon* was a specialised browser. The genus is unique among anomodonts in having premaxillary teeth and also has differing modes of tooth replacement in upper and lower jaws.

MATERIAL AND METHODS

The Mozambiquean material consists of several fragmentary skull pieces, of which two snouts are the most complete, and several incomplete jaws consisting of the symphyseal region and considerable portions of one or both tooth rows. All have suffered postmortem damage, including total or partial loss of teeth, but some crowns functional at time of death remain. As this is a surface collection which required no excavating, exposed bone has been weathered but freshly exposed bone is very well preserved.

Most preparation was undertaken mechanically using an air scribe, but as the bone is not adversely affected by acid the carbonate rich matrix was speedily removed in 5% formic acid, the bone being strengthened during preparation with a dilute, penetrating solution of Glyptal Cement.

DESCRIPTION

Lower Jaw

Although the purpose of this paper is to describe the dentition of *Endothiodon*, as the lower jaw of this genus has not been described in detail it is here described briefly as far as preservation of the material permits. In the collection studied only the anterior portions of the jaw rami are preserved and the surangular, prearticular and articular bones are missing.

In the symphyseal region the dentaries are curved upwards into a sharply pointed and narrow beak which fits closely into the highly vaulted palate of the upper jaw. A broad groove is present on the dorsal surface of the dentary lateral to the teeth.

A lateral dentary shelf is absent in *Endothiodon* (Cluver & King 1983), but in all specimens examined a bulbous swelling of the dentary is present on the ventrolateral side of the jaw (Fig. 1 A&D) anterior to

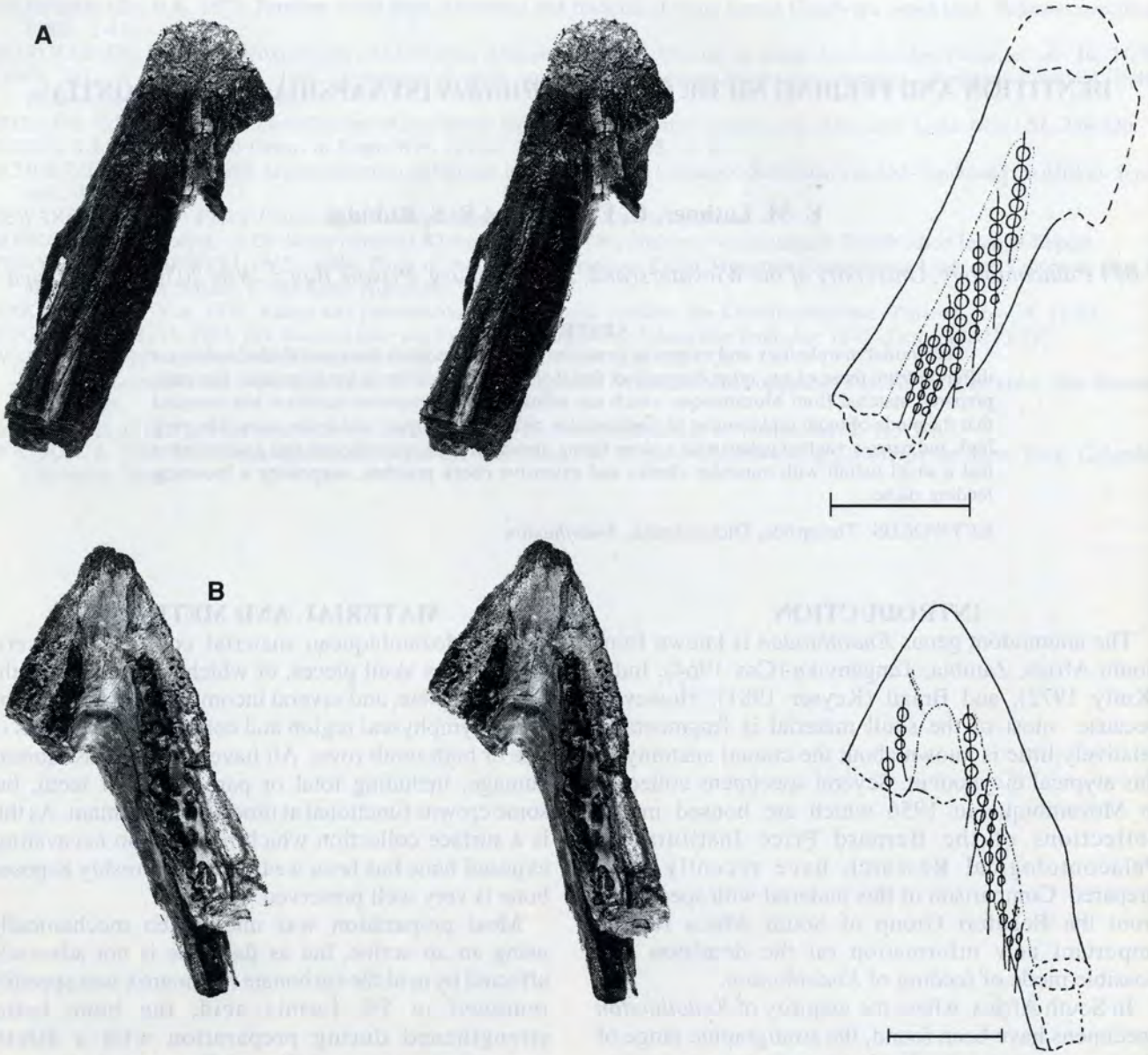


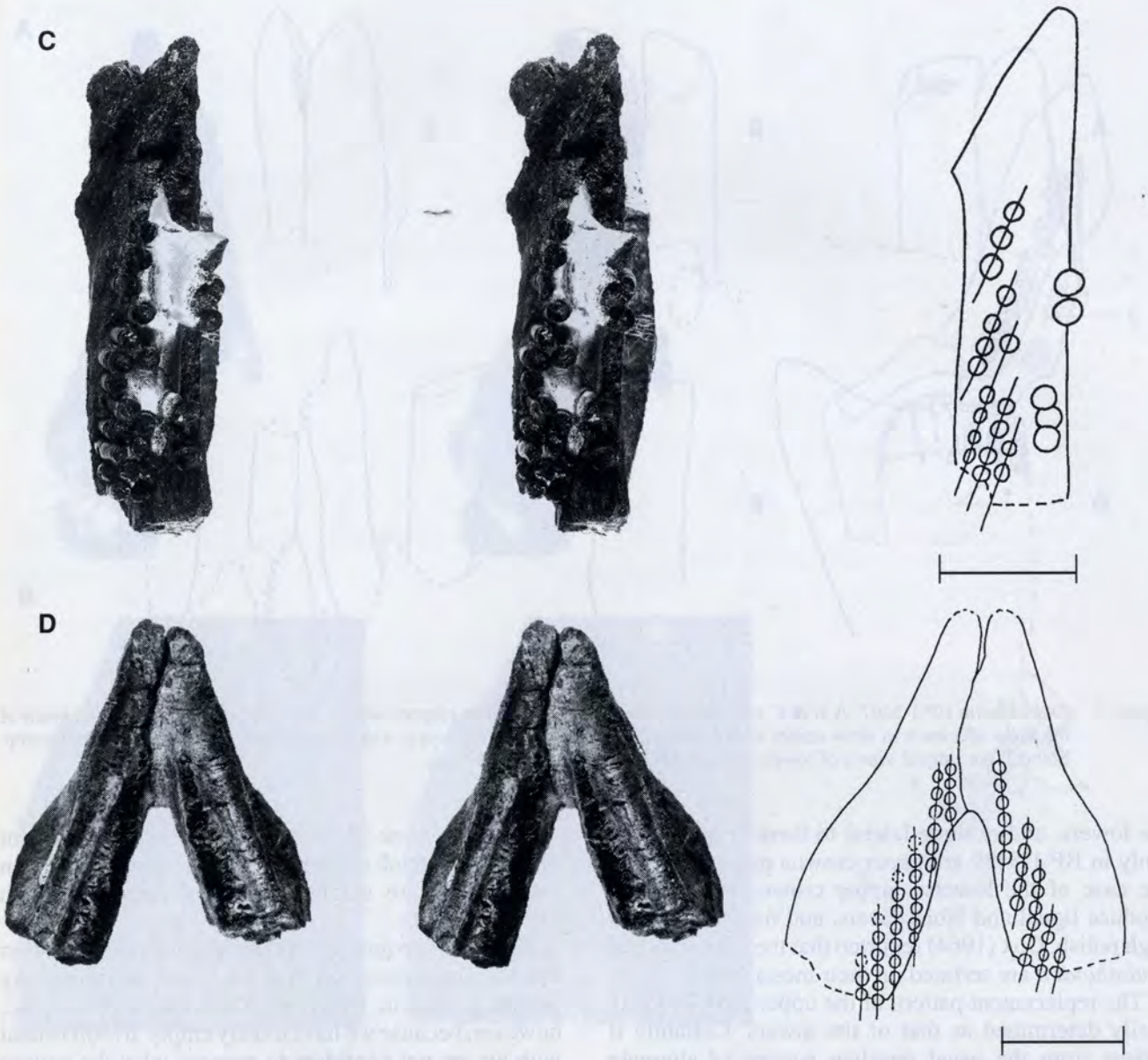
Figure 1. *Endothiodon* Stereophotographs of lower jaws illustrating arrangement of teeth. Lines join members of the same Zahnreihe. B has some upper teeth in natural association in the matrix – these are clearly much thicker than the lowers. A = BP\1\5494; B = BP\1\5492; C = BP\1\5489; D = BP\1\5491; Scales are 50mm.

the intramandibular fenestra. This swelling is not however the same as a lateral dentary shelf and the function is not yet understood.

The splenial is a relatively large bone and typically constitutes most of the ventral surface of the symphyseal region. The splenials form an anterodorsally oriented wedge between the dentaries, and in longitudinal section the splenial shows a distinct undulation within the symphysis at the anterodorsal part of the suture with the dentary. Posteriorly the splenial tapers to a point, low on the medial surface of the dentary.

The angular forms the largest portion of the ventral border of the lower jaw extending forwards as far as a point in line with the posteroventral border of the symphysis, where it forms a pointed contact between the dentary on the lateral side and the splenial on the medial side. None of the fragments have the posterior region of the angular preserved.

Cox(1964) considered that *Endothiodon* has three parallel rows of teeth in the dentary. However it is now apparent that it is not possible to group the teeth in parallel longitudinal rows, rather they fall into obliquely arranged Zahnreihen (Edmund 1969) or replacement waves (Figure 1). Zahnreihen are a series of consecutive replacement waves; each Zahnreihe is a row of teeth in which the oldest is the anteriormost and the youngest the posteriormost, i.e. teeth have erupted sequencially from front to back. Most amniotes have single rows of marginal teeth; such retention of several Zahnreihen is an uncommon phenomenon.Teeth of more posterior Zahnreihen tend to be smaller, as is commonly the case in the marginal dentitions of amniotes generally. In all cases where the dentitions are sufficiently well preserved (BP\1\5489 to 5494 and 5497), it can be seen that new teeth were being added to even the most posterior Zahnreihen, showing that there was active, ongoing replacement throughout the tooth row.



Because of the persisting Zahnreihen the tooth bearing portion of the dentary is a broad zone in which the teeth are held in an area of spongy bone that is continually being remodelled. This area, which broadens posteriorly from the posterodorsal margin of the symphysis, extends medially from the medial margin of the dentary to the lingual edge of the lower jaw. The labial margin of this zone, where it is exposed by loss of teeth, displays deep, concave impressions of the roots (Figure 2D). The lingual margin (Figure 2D) bears a sequence of foramina within (behind) which developing, unerupted teeth can be seen. The margins of these crypts erode upwards as the new tooth grows (Figure 2F); the alveolar border then closes as the tooth moves labiad. As the majority of (especially fully functional) crowns are missing, it is not possible to work out the exact sequence of replacement. However it is apparent that there was no bilateral symmetry to the process (Figure 1). It is clear that replacement waves moved posteriad along the jaw, as shown by the relative maturity of new teeth.

The crowns of unworn lower teeth are broad mesially, tapering towards the distal edge which bears sharp, posteriorly directed serrations extending almost to the tip (Figure 2 B,C,E & F). Roots are cylindrical. Only two undamaged crowns of teeth worn through use are present in the collection (Figure 2 A,B & C). These show that crowns became faceted on their lingual and labial sides. This could only be effected by contact with food. In all cases where they are preserved, the rounded tips of the teeth take on a high polish (like hard objects tumbled in a vegetable fibre medium). The crown facet on the labial side of the second tooth bears fine horizontal striations which are visible under a light microscope and were most probably caused by abrasive particles in the food.

Upper Jaw

Upper Dentition

The teeth of the upper jaw, which are roughly positioned in a single row, are considerably more robust, having at least twice the cross-sectional area of

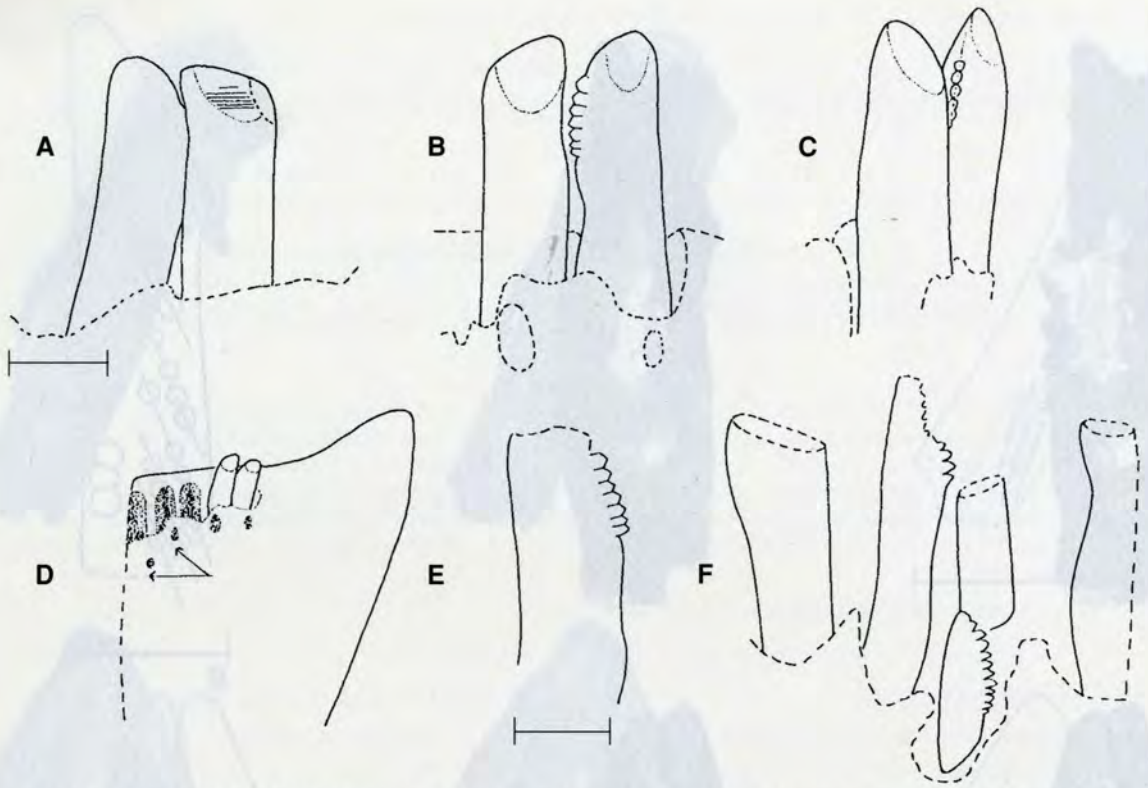


Figure 2. *Endothiodon* BP\1\5497. A,B & C are labial, lingual and distal views respectively of two left lower teeth. D is a sketch of the same specimen to show empty sockets behind these teeth, and the crypts within which new replacement teeth develop. E and F are lingual views of lower teeth of BP\1\5292. Scale bar: 50 mm.

the lowers, and occlude lateral to them (Figure 1 C). Only in BP\1\5489 are upper crowns preserved, as in the case of the lowers , upper crowns are worn to produce ligual and labial facets, and their tips have a high polish. Cox (1964) reported that the upper teeth of *Endothiodon* are serrated on their mesial edges.

The replacement pattern of the upper teeth is not as easily determined as that of the lowers. Certainly it differs from the usual reptilian pattern of alternate replacement. Possibly because they are more robust, the upper teeth did not need replacement as frequently as the lowers. Specimen BP\1\338 (Figure 3 B), which is relatively well preserved, permitted some understanding of the mode of replacement of the upper teeth. In this specimen, as in all the specimens studied where this part of the skull is preserved, the first two teeth are borne by the premaxilla. The first position is occupied by a mature tooth. In the second position are two confluent alveoli, in the more lingual of these the tip of a replacement crown is just visible, while the more lateral cavity represents a tooth recently shed.

The first tooth position in the maxilla bears a mature tooth about to be shed. Resting against its lingual surface is a new tooth in an advanced state of eruption. The next two positions are occupied by the roots of mature teeth, the crowns of which are missing; labiad to these teeth are pits from which previous teeth had been shed. The next two positions are represented by empty, ovate sockets; the next by a mature tooth with an empty socket labiad to it, and the last position by a newly formed but badly damaged tooth.

Lines in Figure 3 B indicate that there is a consistent direction in which teeth migrate in the upper jaw, but in essence there are single, rather irregular rows of teeth in each maxilla.

Hopson has pointed out to us that there is a suggestion that the upper dentition, like the lower dentition, may be interpreted in terms of *Zahnreihen*. We agree, however, because we have mostly empty alveoli to deal with we are not confident to propose what the pattern might be.

FEEDING AND MASTICATORY FUNCTION

As Cox (1964) has suggested, upper teeth were probably opposed by a horny pad occupying the dentary sulcus labiad to the lower teeth (Figure 1); this is a fairly laterally restricted area into which to have to bite, which could just accommodate the degree of lateral drift which occured during the life of the teeth.

Lower teeth were not as restricted. As Cox(1964) pointed out these teeth occluded against the palatines, which presumably were also covered in life by horny pads. The palatine pads would have been shorter than the lower tooth rows: with the jaw fully occluded the pads would lie above the back of the tooth row. Thus for the front of the tooth row to be effective, the jaw would have to be drawn back. This would also allow opposing patterns of upper and lower tooth serrations to effectively slice up food in the mouth. This is excellent supporting evidence for the propalinal jaw movements envisaged for dicynodont anomodonts by Crompton and Hotton (1967) and King, Oelofsen & Rubidge (1989).

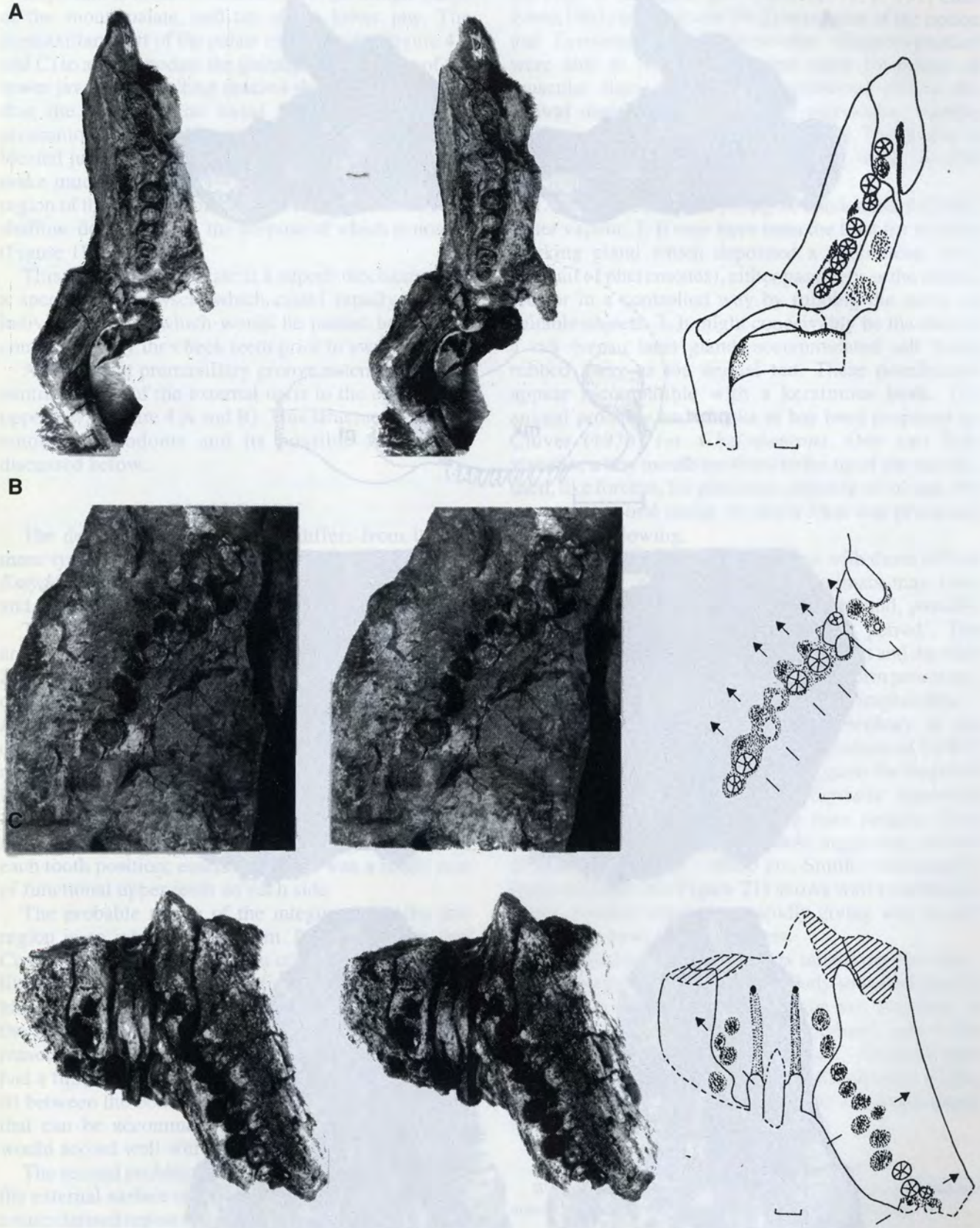


Figure 3. *Endothiodon* Stereophotographs of upper jaws, illustrating arrangement of teeth. Direction of movement of replacing teeth indicated by arrows. A. BP\I\5498 a small individual with a replacing second premaxillary tooth. B. BP\I\998. Right upper dentition. Lines indicate single tooth positions within the row. C. BP\I\5499. Upper dentition - interpretation only possible in the light of B. Scale bar: = 10mm

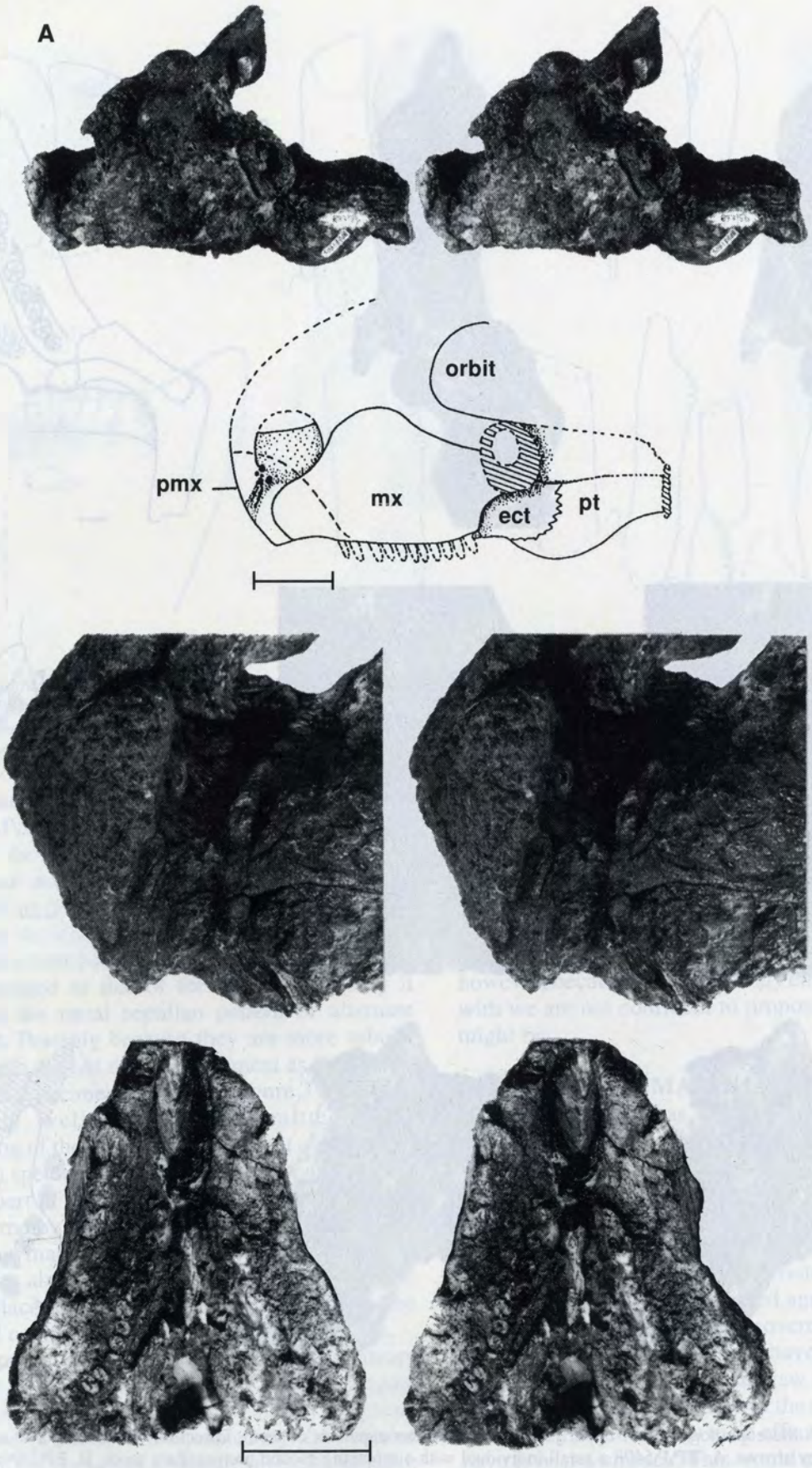


Figure 4. *Endothiodon* A and C Stereophotographs of the large snout BP\1\5505 (B is BP/1/5506).
A. Left lateral view photographs and drawings same scale. B. Snout detail to show ventrolateral groove in premaxilla. C.Palatal view. Scale bar = 50 mm

Important to these considerations is the unique shape of the snout, palate, and tip of the lower jaw. The premaxillary part of the palate rises steeply (Figure 4A and C) to accommodate the pointed, upturned tip of the lower jaw. This vaulting reaches so high (Figure 4A) that the floor of the nasal cavity slopes up to accommodate it and the anterior tip of the upper jaw is located just in front of the external nares. This would make mud grubbing very awkward. The symphyseal region of the sharply pointed lower jaw bears a narrow, shallow, dorsal groove, the purpose of which is unsure (Figure 1B).

This forceps-like muzzle is a superb mechanism for a specialised browser, which could rapidly nip off individual leaves which would be passed back to be comminuted by the cheek teeth prior to swallowing.

A prominent premaxillary groove extends from the ventral border of the external naris to the edge of the upper jaw, (Figure 4 A and B). This structure is unique among anomodonts and its possible function is discussed below.

DISCUSSION

The dentition of *Endothiodon* differs from that in more typical reptiles, including the dicynodont genus *Emydops* (Hopson 1964), in which replacement is rapid and alternate.

The multiple rows of dentary teeth in *Endothiodon* are the result of retention of several members of each Zahnreihe, and it appears that tooth replacement continued throughout the animal's life. Although *Endothiodon* is the only dicynodont to exhibit such a dentition in the lower jaw, similar arrangements are recorded in (for example) *Captorhinus* (Bolt and DeMar 1975), and some procolophonids (Gow 1977).

Replacement in the upper jaw was more usual, with never more than two teeth (of different ages) present at each tooth position; essentially there was a single row of functional upper teeth on each side.

The probable nature of the integument in the jaw region is an intriguing problem. It is interesting that Cox (1964) makes no mention of an extensive turtle-like horny beak as is usual for dicynodonts; he confines himself to proposing horny pads on the palatines and in the lateral dentary groove. There are essentially two reasons why it is difficult to conceive that the animals had a full, turtle-like beak. One is the incredibly close fit between the bones of the upper and lower jaws: all that can be accommodated here is tough skin (this would accord well with a browsing habit).

The second problem is the presence of the groove in the external surface of the premaxilla which runs from a vascularised region at the ventral border of the naris to the edge of the upper jaw. Cluver(1971, p. 191) cites Ewer(1961) and Watson(1912) in support of the notion that *Lystrosaurus* and *Dicynodon* (*Daptocephalus*) were able to close the external nares by means of muscular flaps attached to vascularised pits in the ventral narial border, involving premaxilla, maxilla and septomaxilla, but this is speculative. The groove in *Endothiodon* is clearly quite different; three possible functions suggest themselves.

1.It permitted the recycling of condensed, exhaled, water vapour. 2. It may have been the tract for a scent-marking gland which deposited a pheromone (or a cocktail of pheromones), either passively as the animal fed, or in a controlled way by rubbing the snout on suitable objects. 3. It might conceivably be the duct of a salt (sensu lato) gland, accummulated salt being rubbed away as the animal fed. These possibilities appear incompatible with a keratinous beak. The animal probably had cheeks as has been proposed by Cluver (1975) for *Chelydontops*. One can thus visualise a tiny mouth confined to the tip of the muzzle, used, like forceps, for precision cropping of foliage, but an extensive oral cavity in which food was processed prior to swallowing.

These suggestions are at variance with those of Cox (1964, p.18), who suggested the animals may have 'grubbed vegetable matter out of the ground, possibly in the extensive mud swamps of the period'. The closeness of the nares to the tip of the snout and the total lack of enlarged canines, or even caniniform processes, are additional reasons why we find this implausible.

Modern perceptions of the palaeoecology of the lower Beaufort differ from that of Plumstead (1963) cited by Cox (1964). Smith (1993) regards the Beaufort as consisting of predominantly fluvially deposited rocks, with floodplain accretion rates ranging from 0.4-5.5mm\yr, but with palaeosols suggesting periods of stasis from 5000 – 10000 yrs. Smith's taphonomic reconstruction (his Figure 21) shows well established, dense, riverine vegetation, rapidly giving way to arid conditions away from the rivers.

We visualise *Endothiodon* as inhabiting the dense riverine vegetation (as the most likely source of quality browse), occupying a trophic niche not available to smaller, more fully terrestrial dicynodonts, and would therefore predict that articulated *Endothiodon* skeletons, i.e. those which have fossilised *in situ*, would most likely be found close to fossilised major river courses.

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(v) Volume specification of journal: i.e. series (if any), volume number (in bold) part number (if any), pagination (first and last page).

Examples of reference citations

ANDERSON, H.M. 1976. *A revision of the genus* Dicroidium *from the Molteno Formation*. Unpublished PhD thesis, University of the Witwatersrand, Johannesburg.

------ & ANDERSON, J.M. 1970. A preliminary review of the biostratigraphy of the uppermost Permian, Triassic and lowermost Jurassic of Gondwanaland. *Palaeont. afr.*, **13**, 1-22.

VAN DER MERWE, N.J., LEE-THORP, J.A., THACKERAY, J.F., HALL-MARTIN, A., KRUGER, F.J., COETZEE, H., BELL, R.H.V., & LINDEQUE, M. 1990. Source-area determination of elephant ivory by isotopic analysis. *Nature* **346,** 744-746.

CROMPTON, A.W. 1962. On the dentition and tooth replacement in two bauriamorph reptiles. *Ann. S. Afr. Mus.*, **46**(9), 231-255.

ROMER, A.S. 1966. *Vertebrate Palaeontology* (3rd Ed.). Chicago, University of Chicago Press.

------ 1973. Permian reptiles. **In:** Hallam, A., Ed., *Atlas of Palaeobiogeography*, 159-168. Amsterdam, Elsevier.

HOPSON, J.A. & BARGHUSEN, H.R. 1986. An analysis of therapsid relationships. **In:** Hotton, N., MacLean, P.D., Roth, J.J. & Roth, E.C., Eds, *The Ecology and Biology of Mammal-like Reptiles*, 159-168. Washington, Smithsonian Institution Press.

Reference citations in the text should give the name of the author and the date on each occasion, and substitutes such as *op. cit., loc. cit.*, etc should not be used, e.g. "Smith & Jones (1943) suggest that ...", "extinction rates (Smith & Jones 1972) and other factors ..."

In text successive references should be separated as follows (Brain 1990, 1991; Hughes 1961; Smith & Jones 1992).

Headings

Three orders of headings are used.

FIRST ORDER – printed in bold capitals in the centre of the column.
Second Order – printed in bold upper and lower case in the centre of the column.
Third Order – printed in upper and lower case italics to the left of the column.
Headed sections and paragraphs should not be otherwise numbered or lettered in the manuscript.

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Tables should be typed on separate sheets and their headings typed in capitals. They are numbered consecutively in arabic numerals. **Authors should indicate the position of each table by appropriate pencil notation in the margin of the text.**

When referring to them in the text the word Table should be spelled out in full and given a capital initial letter, e.g. Table 2.

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All illustrations are termed Figures, (the word is to be spelled out in full with a capital initial letter and they are numbered consecutively with arabic numerals. Each illustration should bear in pencil on the reverse side the author's name, a key word(s) from the title, the figure number and the word "top" in the appropriate position to indicate orientation. **Authors should mark the position of figures by pencil notation in the margin of the text.**

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All artwork should be submitted ready for the camera. The use of dry transfer lettering is preferred and stencil or hand lettering is to be avoided. Graphic scale indicators are preferred in all artwork where a scale is appropriate.

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The metric system (SI units) is to be used throughout for all numerical data. If for some good reason units other than metric are used, the SI metric equivalents should also be given in parentheses. Authors should familiarise themselves with the correct abbreviation of SI metric units.

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