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Cover image: Large trunk of fossil wood from Lusitu, Zambia, Upper Permian or Lower
Triassic in age. Field trip in June 2015. Photograph by Steve Tolan.

The macrovertebrate fossil assemblage from the Name Chamber, Sterkfontein: taxonomy, taphonomy and implications for site formation processes

A. Val & D.J. Stratford

Evolutionary Studies Institute, Private Bag 3, WITS 2050, Johannesburg, South Africa
School of Geography, Archaeology and Environmental Studies, University of the Witwatersrand,
Private Bag 3, WITS 2050, Johannesburg, South Africa

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The Name Chamber contains some of the deepest fossiliferous deposits in the Sterkfontein Caves, at ~20 metres below the surface deposits of Members 4 and 5. Recent excavations complemented by detailed studies of the geological context, as well as of the microfaunal and lithic (i.e. Oldowan artefacts) assemblages, have shed some light on the complex history of sediment accumulation in that part of the Sterkfontein karstic system. The Name Chamber has a long and intricate history of deposition that is of particular value for understanding the redistribution of Oldowan-bearing sediments from Member 5 into the deep chamber below. Recognizing sediment movement and sources through multidisciplinary investigations is of key importance to reconstructing primary lithic assemblages and ultimately the behavioural proxies associated with them. Here, we present the results of a taxonomic and taphonomic analysis of the macrofaunal assemblage recovered during excavations of the decalcified sediments of the Western Talus in the Name Chamber. The taxonomic composition of the faunal spectrum is similar to that of Member 5 East Oldowan, with an overrepresentation of medium-sized bovids and the occurrence of taxa associated with grasslands. The taphonomic features of the fossil remains are characteristic of a mixed assemblage with indications of contributions by carnivores, slope wash and gravity collecting bones from the catchment surface (including carnivore-gnawed and butchery-marked specimens). The results independently corroborate lithic and microfaunal analyses and support the hypothesis of multiple origins for the sediments of the Name Chamber, with a main contribution from Member 5 East Oldowan (notably illustrated in the Name Chamber assemblage by the identification of several cut-marked remains and a bone tool), shortly after it accumulated at about 2.18 Ma. There is also indication of a minor contribution from Member 4 but no evidence for a noticeable contribution from Post-Member 6 (L/63 Infill).

Keywords: Sterkfontein Caves, Name Chamber, cave taphonomy, faunal analysis, Plio-Pleistocene, early hominins.

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INTRODUCTION

Continuous work for more than 75 years in the Sterkfontein Caves, in the UNESCO World Heritage Site of the Cradle of Humankind, South Africa (Fig. 1), has led to the recovery of abundant fossils of early hominins and associated fauna, dating back from 3.67 ± 0.16 Ma to the mid-late Pleistocene (Broom 1936; Brain 1981; Kuman 1994a; Reynolds & Kibii 2011; Granger *et al.* 2015). Detailed studies of these fossils have greatly contributed to document the modalities of human evolution in the southern part of the African continent. Member 4 of the Sterkfontein Formation (Partridge 1978) especially has produced the most prolific assemblage of australopithecine remains in the world, found in association with large macro- and microfaunal assemblages. Member 5 has yielded the largest and most complete Oldowan sample in southern Africa associated with *Paranthropus robustus*, and an early Acheulean industry associated with *Homo ergaster* (Brain 1981; Pickering 1999; Kibii 2004; Kuman 1994a,b; Kuman & Clarke 2000; Reynolds & Kibii 2011). As expected in karstic systems, the history of sediment accumulation is complex. The lower subterranean parts of the caves, namely the

Silberberg Grotto, Milner Hall, Jacovec Cavern, and Name Chamber contain deposits that represent intricate and long infilling sequences that have only recently been the focus of dedicated stratigraphic studies (e.g. Clarke 1994; Stratford 2011; Stratford *et al.* 2012, 2014; Bruxelles *et al.* 2014). One of the questions still debated concerns the exact nature of the relationship between the sediments and fossil assemblages recovered from the subterranean chambers (Members 2 and 3 in the Silberberg Grotto) with those found in the exposed deposits of the Sterkfontein main excavation area (Members 4 and 5) (Fig. 1) (Robinson 1962; Wilkinson 1983; Partridge & Watt 1991; Pickering & Kramers 2010; Stratford *et al.* 2014). This research contributes further to the multidisciplinary study of the Name Chamber faunal and archaeological assemblages and their stratigraphic histories in order to help clarify these relationships in this part of the caves.

The Name Chamber is one of the most recent parts of the Sterkfontein Caves to have undergone excavations and received comprehensive geological attention (Avery *et al.* 2010; Stratford 2011; Stratford *et al.* 2012). Early pilot excavations were conducted in 2000, before more extensive

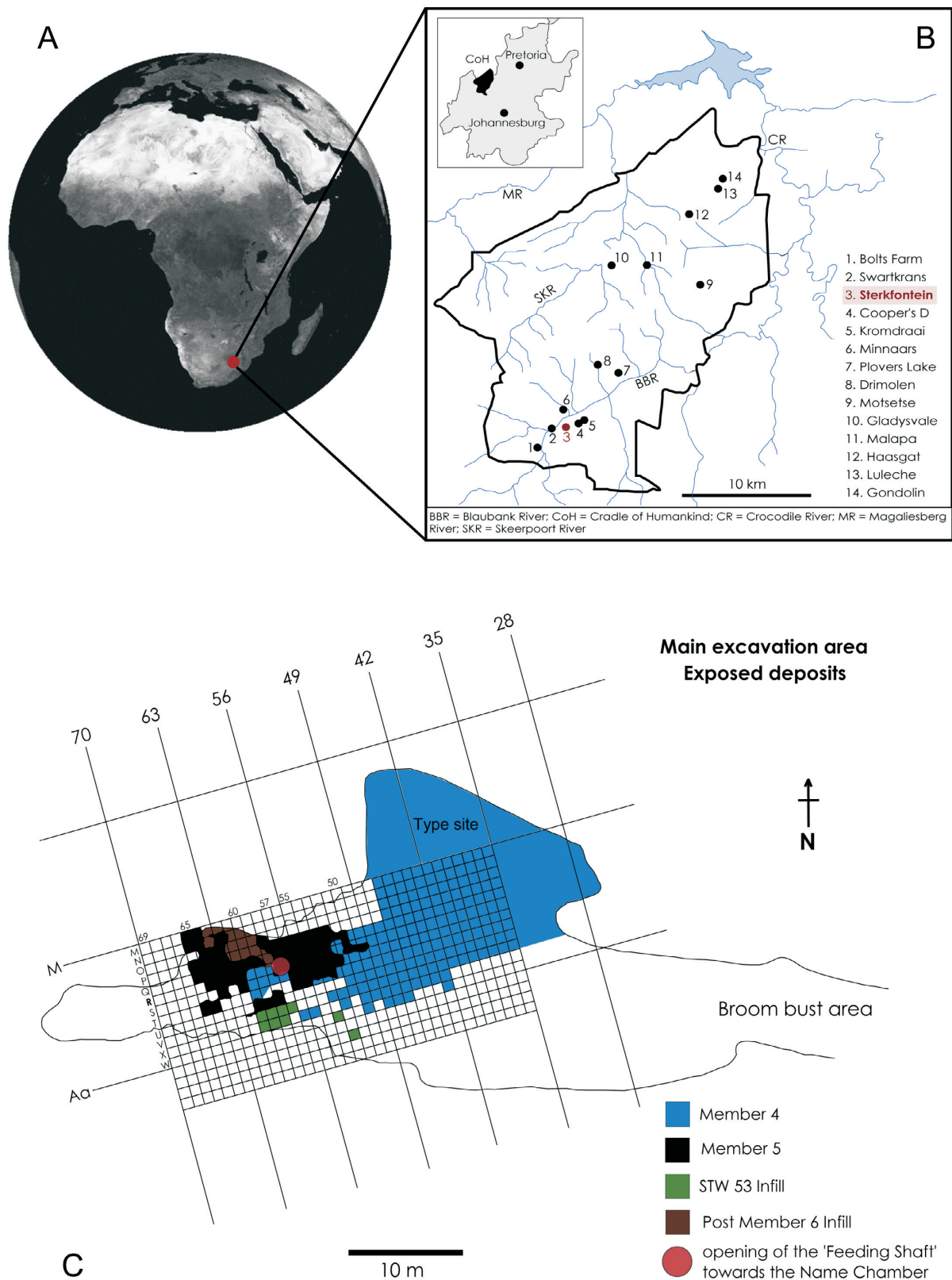


Figure 1. Geographical situation of the Sterkfontein Caves inside the Cradle of Humankind in South Africa (A & B) and location of the Name Chamber (C), from Kuman & Clarke (2000), modified.

excavations took place between 2007 and 2009, under the direction of Clarke and Stratford. The Name Chamber lies directly below the exposed deposits of Member 5 about 20 metres below the landscape surface (Robinson 1962; Clarke 1994). More precisely, the shaft (referred to as the 'Feeding Shaft'), through which most of the sediments from the Name Chamber are thought to originate, opens

directly to the excavated Member 5 deposit in square R57 in the main excavation area, on the western fringe of Member 5 East (Clarke 1994; Figs 1 & 2). The deposits of the Name Chamber consist of calcified and decalcified sediments that have accumulated from the deposits exposed on the surface through the 'Feeding Shaft'. Within the Name Chamber itself, the infills are divided

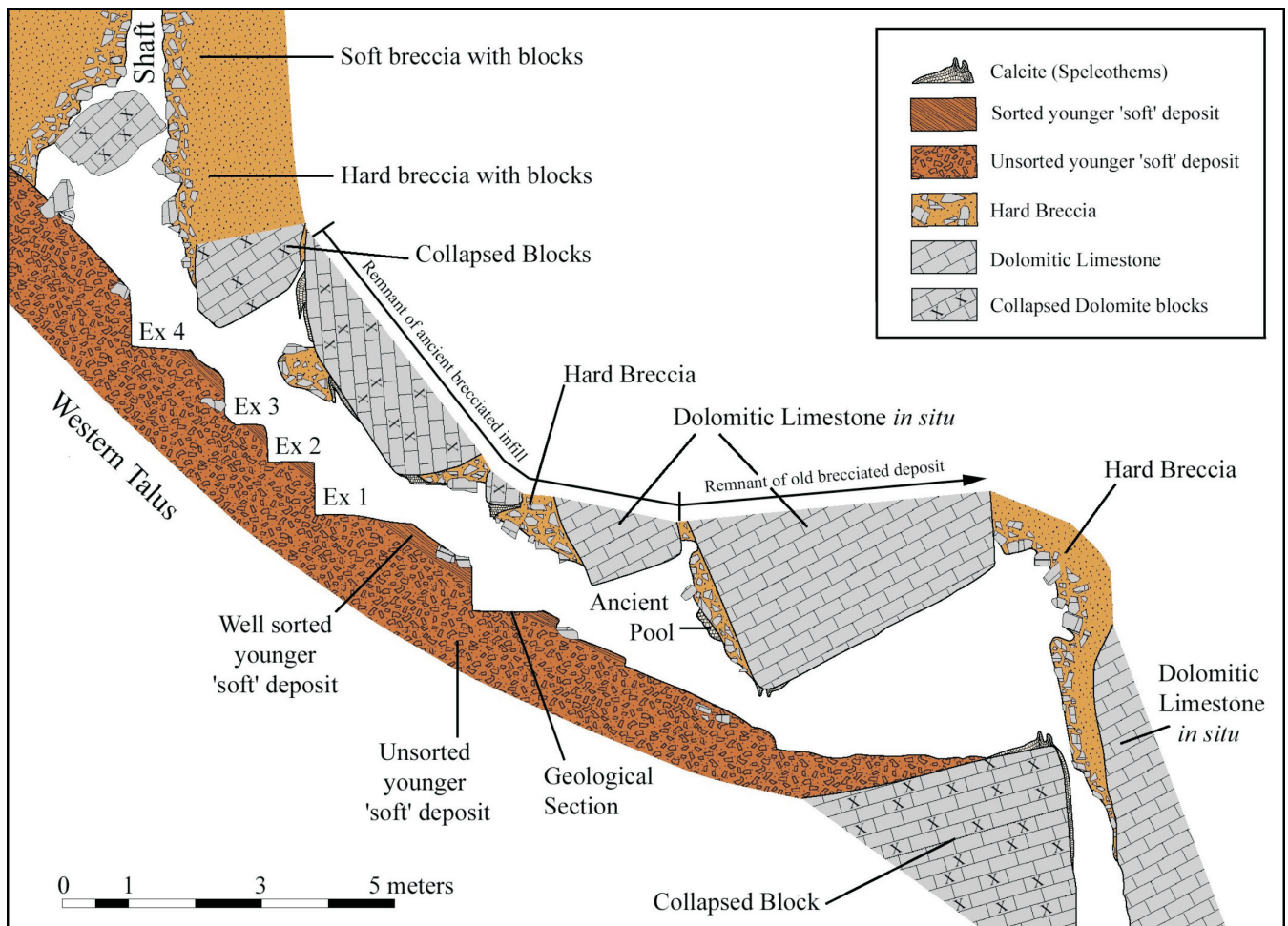


Figure 2. Stratigraphic profile of the Name Chamber.

into two steep talus cone deposits, the Eastern and Western talus deposits, which are separated by a large collapsed dolomite roof block (Fig. 2). Three stratigraphic units have been identified, consistent with successive events of sediments being introduced into the cave. The two first units (the Ancient and Old Brecciated Deposits) have not yet been excavated and are largely represented by calcified remnants preserved on the walls of the chamber. The fossil assemblage presented here comes exclusively from the third unit, called the Younger 'Soft Deposit', and was excavated from decalcified sediments of the Western Talus. The areas focused on for the excavations were chosen based on accessibility and were placed at medial and distal portions of the talus. The Eastern Talus was not excavated because it is significantly steeper and less accessible than the Western Talus. Based on the occurrence, in the Western Talus, of more than a thousand artefacts typologically attributed to the Sterkfontein Oldowan industry, an overrepresentation of the <2 cm fraction in the lithic assemblage (Stratford *et al.* 2012), and the taxonomic composition of the microfaunal assemblage (Avery *et al.* 2010), it has been hypothesized that the sediments from this soft deposit mostly come from Member 5 East Oldowan. Nevertheless, contribution from other parts of the cave system, especially Member 4 and Post-Member 6 (L/63 Infill), cannot be excluded. As identified by Moen and Keyser (Clarke 1994), the 'Feeding Shaft' transects at least parts of the Member 4 deposit.

The aim of this paper is to describe the taxonomic composition of the macrofaunal assemblage recovered from the Western Talus and to propose a thorough analysis of its taphonomic features. Results are compared with taxonomic and taphonomical characteristics of the fauna from Member 5 East Oldowan, Member 4 and Post-member 6 (L/63 Infill), in order to further test the hypothesis that the dominant sediment source is Member 5 East Oldowan and assess the possible degree of contribution of the overlying deposits that are found in close proximity to the 'Feeding Shaft' opening in the Sterkfontein surface excavation (Fig. 1). A brief description of the potential contributing deposits and their macrofaunal assemblages is provided below (see also: Table S1).

Member 4

Member 4 represents the largest deposit exposed on the landscape surface and has been the focus of most excavations at Sterkfontein. It is generally located in the central and eastern areas of the surface excavation site and contains the important 'Type Site' from which the first hominin specimen was discovered in 1936 (Broom 1936). Various dating methods including biochronology, palaeomagnetism, Electron Spin Resonance (ESR), Uranium-Lead and Uranium-Thorium isotopes (Vrba 1976, 1980; Delson 1984, 1988; Schwarcz *et al.* 1994; Partridge 2005; Pickering & Kramers 2010; Herries & Shaw 2011) suggest an age between 2.0 and 2.8 Ma for this large

deposit. Member 4 has yielded over 750 australopithecine specimens representing a minimum number of 87 individuals (Pickering *et al.* 2004a), attributed to *Australopithecus africanus* and *Au. prometheus* (Clarke 2006, 2013). The hominin remains were found in association with abundant faunal remains. The fauna recovered from Member 4 was first studied by Brain (1981) and more recently re-examined by Kibii (2004), who analysed the non-hominin remains, and Pickering and colleagues (2004a), who focused on the taphonomy of the hominin assemblage. Other extensive and diverse studies have been conducted on macrofaunal assemblages yielded from Member 4 (e.g. Broom *et al.* 1950; Ewer 1956; Vrba 1976, 1980; Brain 1981; Delson 1984; Clarke 1988, 1994; Turner 1987, 1997; Pickering 1999; Lockwood & Tobias 2002; de Ruiter 2004; Kibii 2004; Curnoe & Tobias 2006; Moggi-Cecchi *et al.* 2006; O'Regan & Reynolds 2009). The occurrence in the fossil assemblage of the large extinct caprid species *Makapania broomi*, as well as fossilized lianas that require large trees for support (*Dichapetalum mombuttense*; Bamford 1999), indicates moister and more wooded habitats around the site at that time, while species associated with grassland and drier conditions such as *Equus*, *Pedetes* and *Struthio* are absent (Brain 1981; Kuman & Clarke 2000; Reynolds & Kibii 2011). These results are mostly corroborated by analyses of stable carbon isotopes from fossil tooth enamel (see for instance: van der Merwe *et al.* 2003; Codron *et al.* 2005; Lee-Thorp *et al.* 2007).

The taphonomy of the Member 4 assemblage is complex, largely because of the lack of stratigraphic resolution and the enormous 600 000 year time frame represented by the deposit, which is generally analysed as a single entity. The accumulation of the faunal remains inside the deposit is better explained by the combined action of several biotic and abiotic agents; the possible existence of several entrances to the cave; and the repeated introduction of animal remains over a long period of time rather than as a single event (Brain 1981; Kibii 2004; Pickering *et al.* 2004a; Reynolds & Kibii 2011). Large carnivores using the cave as a den combined with a natural death trap scenario seem to explain the origin of most carnivore and bovid remains, while a few individuals might also have been introduced by slope wash (Brain 1981; Kibii 2004). The majority of bone surface modifications observed on the bovid remains are due to carnivore chewing and numerous large carnivore cranial elements together with spotted hyaena coprolites were identified in the assemblage. However, the presence of low-density elements such as ribs and vertebrae, including those of juveniles, which lack any evidence of carnivore activity, indicates that some animals entered the cave via a natural death trap. This is confirmed by the presence of two partial australopithecine skeletons, Sts 14 and Stw 431 (Toussaint *et al.* 2003 and references therein). The carnivore-collecting hypothesis was postulated by Brain (1981) and is supported by more recent studies (Pickering *et al.* 2004) to explain the abundance of hominin remains in Member 4. There seems to have been a predator selection towards smaller individuals that is, females and juveniles. The overrepresentation of cranial material and underrepresentation of postcranial

material is interpreted as a consequence of feeding on the hominin carcasses by large carnivores (felids and/or hyaenids). There is no evidence that the cave was used by the hominins: stone artefacts, burnt or cut-marked bones are absent from the assemblage (Brain 1981).

Member 5 East Oldowan

Member 5 formed on the irregular erosional surface of the Member 4 deposit and is found in the western areas of the surface exposed breccias. The basal part of Member 5 has yielded a large and informative Oldowan industry (Kuman 1994a,b; Kuman & Field 2009) and is mainly restricted to the eastern part of the Member 5 deposit. Based on biostratigraphy, lithic industry, ESR, isotopic analyses and palaeomagnetism, Member 5 East Oldowan deposits have been dated to 2.0–1.1 Ma (Kuman & Clarke 2000; Herries *et al.* 2009; Herries & Shaw 2011). A recent study proposes an earlier age for the deposits, with a new cosmogenic date at 2.18 ± 0.21 Ma (Granger *et al.* 2015). The faunal assemblage, largely dominated by bovids, and especially medium-sized bovids (i.e. class II), comprises 28 274 remains. The occurrence of *Equus*, *Pedetes* and *Struthio* is consistent with grassland habitats and drier conditions in the vicinity of the site (Brain 1981; Kuman & Clarke 2000; Lee-Thorp *et al.* 2007). Five hominin specimens were recovered, including at least three attributed to *P. robustus* (Pickering 1999; Kuman & Clarke 2000).

A detailed taphonomic study of the fauna was conducted by Pickering (1999), who proposed the accumulation of animals falling inside the cave via a natural death trap, complemented by a few individuals and/or bones being washed directly from the landscape. This hypothesis is supported by the extremely low percentage of carnivore-modified material, representing only 0.6% of the faunal assemblage, as well as by skeletal survival patterns for bovids consistent with a natural death trap scenario rather than accumulation by mammalian predators. The presence of one cut-marked bovid scapula fragment is consistent with the practice of butchery activities by hominins in the cave catchment area. The abundant Oldowan stone tools ($n = 3245$) recovered from Member 5 East are also considered by Kuman (1994a,b; Kuman & Field 2009) to have been washed into the cave from the surface. Member 5 has yielded the only bone tool documented at Sterkfontein so far.

Post-Member 6 (L/63 Infill)

The L/63 Infill of Post-Member 6 is one of the recent deposits of the Sterkfontein Formation. Biochronological data and some of the artefacts recovered (i.e. Middle Stone Age stone tools) point towards a mid- to late Pleistocene deposit (Reynolds *et al.* 2007), while ESR dating proposes an age between 0.5 and 0.3 Ma (Herries & Shaw 2011). The sediments from Post-Member 6, similar to those of Lincoln Cave, are poorly calcified. Large carnivores are absent from the faunal assemblage ($n = 5584$), which comprises mostly ungulates and small to medium-sized carnivores, associated with a few remains of archaic *H. sapiens* (Reynolds *et al.* 2007). The faunal spectrum also includes *Equus* and *Pedetes*, generally associated with open habitats.

Compared to other deposits from Sterkfontein, the faunal sample is characterized by a relatively high percentage of remains gnawed by porcupines, with 1.86% of the assemblage modified by this rodent. A few hyaena coprolites were collected from the deposits but the absence of large carnivore remains together with the very low incidence of carnivore damage suggest a negligible carnivore contribution to the assemblage. No anthropogenic modifications, whether in the form of cut-marks, percussion marks or burning, were observed (Reynolds & Kibii 2011).

MATERIALS AND METHODS

The faunal sample analysed here was recovered during excavations conducted between July 2000 and September 2001 of an initial two-square-metre test pit inside the Young 'Soft Deposit' of the Western Talus (i.e. decalcified sediments) of the Name Chamber (Ex1 in Fig.2). Sediments excavated were systematically wet- and dry-sieved using 2 mm screen-meshes (Stratford *et al.* 2012). Results of the study of the mammalian microfaunal remains from this sample and further excavations (Ex 2, 3 & 4; Fig. 2) have been published elsewhere (Avery *et al.* 2010). The present work focuses therefore on the complete mammalian macrofauna and bird assemblage, with the exception of the dental remains, which could not be located. The impossibility to include teeth in the analysis has several limitations both in terms of degree of taxonomic identification and understanding of the fossil assemblage taphonomy. For instance, taxonomic attribution of bovid remains to species level relies almost exclusively on dental material, given the high degree of morphological similarities of postcranial elements between the various bovid species. Furthermore, the absence of dental material can mean the loss of potentially informative elements, such as carnivore deciduous teeth, typically associated with the use of the cave by carnivores as a denning site, especially in the case of hyaenids.

Preliminary taxonomic attributions, anatomical descriptions, and macroscopic bone surface analyses on the macrofaunal material have been conducted by several people (i.e. T.R. Pickering, S. Reynolds & K. Fatherley), but the results of these various ongoing studies were never published. Existing bone identifications were verified using the comparative collections of modern and extinct mammals hosted at the Evolutionary Studies Institute, as well as modern bird skeletons from the Ditsong Museum in Pretoria. Bone surfaces of all identifiable elements and all non-identifiable elements larger than 2 cm were systematically inspected using an Olympus SZ61 microscope (magnification up to $\times 45$). For the non-identifiable elements smaller than 2 cm, a gross inspection of bone surface damage using a hand lens was conducted. Although this type of inspection may not always allow for superficial cut mark or insect damage identification, it is sufficient to recognize acid etched remains through digestion as well as bone percussion flakes. Breakage patterns have been described for long bone fragments, using criteria proposed by Villa & Mahieu (1991) for human long bones. The influence of abiotic processes potentially removing or limiting the visibility of informative animal and human-

induced modifications on bones (e.g. cut marks and tooth marks) were quantified. These include: degree of manganese invasion, weathering stage (following Behrensmeyer 1978), water abrasion, chemical dissolution, presence/absence of matrix concretions, and decalcification. Five stages in the extent of precipitated manganese dioxide on the bone surface were recognized, from none, slight (only a few spots), slight to moderate (abundant spots covering less than 50% of the surface), moderate (>50% the surface of the specimen is covered) to heavy (whole surface of the specimen is covered). Various types of damage caused by biotic agents (root etching, carnivore and rodent gnawing, bird of prey beak and talon impacts, mammalian and/or avian digestion, insect boring and gnawing, animal trampling and hominin butchery) were recorded. The criteria used to distinguish between stone tool, carnivore tooth and trampling marks are based on the definitions proposed by Shipman & Rose (1983), Domínguez-Rodrigo and colleagues (2009) and others (Binford 1981; Behrensmeyer *et al.* 1986; Lyman 1994a). Data available in the literature concerning carnivore (e.g. Maguire *et al.* 1980; Binford 1981; Brain 1981; Shipman & Rose 1983; Lyman 1994a), rodent (Maguire *et al.* 1980; Binford 1981; Brain 1981; Shipman & Rose 1983), insect (Lyman 1994a; Britt *et al.* 2008; Backwell *et al.* 2012) and bird of prey (Andrews 1990; Bocheński & Tomek 1997; Bocheński *et al.* 1997, 1998; Laroulandie 2000, 2002; Bocheński & Tornberg 2003) damage were used for comparative purposes. Definitions of the quantitative units used (i.e. NISP, MNE, MNI and percentage of survival) are those found in Lyman (1994b and references therein).

Due to the absence of dental material and the high degree of fragmentation, the majority of ungulate remains were only attributed a class size (following Brain 1974). Reconstitution of mortality profiles relies on age estimates of the individuals present in the faunal assemblage. In our case, given the absence of dental material, age estimates could rely only on the degree of fusion of long bones and phalanges, with three identifiable distinct stages: juveniles (epiphyses not fused at all), young adults (epiphyses fusing), and adults (epiphyses completely fused).

RESULTS

The total sample comprises 5828 bone fragments. Of this sample, 63 tooth fragments that had been mixed with non-identifiable long bone shaft fragments (small fragments of enamel of molar and premolars of ungulates) are excluded for the analysis since the rest of the tooth sample is missing. Another 27 remains of small rodents are also excluded from the analysis as the majority of the small rodent specimens have already benefitted from thorough descriptions (Avery *et al.* 2010). The sample studied here comprises therefore 5738 bone remains, including 554 specimens identified at least to the family level, 1973 non-identifiable fragments smaller than 4 cm and 3211 non-identifiable fragments smaller than 2 cm.

Composition of the faunal spectrum

The faunal assemblage is largely dominated by bovids, which compose 83% of the identified bone assemblage,

Table 1. Composition of the faunal assemblage from the Name Chamber.

ORDER	FAMILY	SPECIES	NISP	MNE	MNI
PRIMATES	Cercopithecidae	<i>Cercopithecoides williamsi</i>	1	1	1
		<i>Papio</i> sp.	7	7	1
		Large <i>Papio</i>	2	2	1
		Total primates	10	10	3
CARNIVORES	Felidae	<i>Panthera pardus</i>	6	5	1
		<i>Felis</i> sp. (size wild cat)	3	2	1
		Felids indet.	2	2	–
	Canidae	<i>Canis</i> sp. (size black-backed jackal)	2	2	1
		<i>Canis</i> sp. (size wild dog)	5	5	1
		Canids indet.	1	1	–
	Hyaenidae	<i>cf. Parahyaena brunnea</i>	1	1	1
		Hyaenids indet.	1	1	–
	Herpestidae	Herpestids indet. (size marsh mongoose)	2	2	1
		Carnivores indet.	9	9	–
		Total carnivores	32	30	6
ARTIODACTYLAE	Bovidae	<i>Connochaetes</i> sp.	7	7	1
		<i>Damaliscus</i> cf. <i>dorcas</i>	1	1	1
		<i>Alcelaphus</i> sp.	2	2	1
		<i>Tragelaphus strepsiceros</i>	1	1	1
		Bovids indet. Class I	7	7	2
		Bovids indet. Class II	317	134	5
		Bovids indet. Class III	115	56	5
		Bovids indet. Class IV	4	4	1
		Total bovids	454	212	13
	Suidae	Suid indet.	2	2	2
PERISSODACTYLAE	Equidae	<i>Equus</i> sp.	6	6	3
		Total ungulate indet.	94	–	–
RODENTS	Pedetidae	<i>Pedetes capensis</i>	3	3	1
	Leporidae	<i>Lepus</i> sp.	1	1	1
HYRACOIDS	Procaviidae	<i>Procavia transvalensis</i>	2	2	1
		<i>Procavia</i> sp.	1	1	1
BIRDS	Galliformes	<i>Numida meleagris</i>	1	1	1
	Colombiformes	<i>Columba</i> sp.	2	2	1
	Strigiformes	<i>Tyto alba</i>	7	7	2
	Charadriiformes	Indet.	1	1	1
	Falconiformes	Small kite/goshawk	1	1	1
	Passeriformes	<i>Corvus</i> sp.	1	1	1
		Passeriformes indet.	6	6	3
		Birds indet.	18	18	–
		Total birds	37	37	10
TOTALS	Total identifiable remains		554	304	41
	Total non-identifiable remains		5184	–	–
	GRAND TOTAL		5738	–	41

with class II bovids being the most numerous (69.3% of the bovid assemblage). Birds are also abundant in the assemblage with the second most numerous NISP and MNI. Carnivores and primates, even though relatively abundant in terms of MNI (with a carnivore/ungulate ratio of 33.3%), are only represented by a few remains and characterized by low taxonomical diversity (Table 1). Taxa consistent with open and dry conditions (i.e. *Equus* sp. and *Pedetes capensis*) occur in the faunal sample alongside taxa usually associated with woodland and more humid conditions (i.e. *Tragelaphus strepsiceros*) (Sponheimer *et al.* 2003; Skinner & Chimimba 2005) (Table 1). *Cercopithecoides williamsi* is represented in the assemblage by one tooth; based on morphological analyses and isotopic data, this

cercopithecoid is regarded as an ‘open mixed’ species, practising terrestrial locomotion and including a significant amount of savanna-based C₄ resources in its diet (Elton 2000, 2001; Codron *et al.* 2005).

General preservation

The vast majority of the faunal sample is composed of non-identifiable remains (90.3%). The material is highly fragmented, with complete elements ($n = 85$) representing only 1.5% of the assemblage and including exclusively short compact bones, namely phalanges, sesamoids, carpals and tarsals. Despite the presence of large taxa (ungulates such as equids and bovids class III and IV), there is a clear overrepresentation of the small fraction

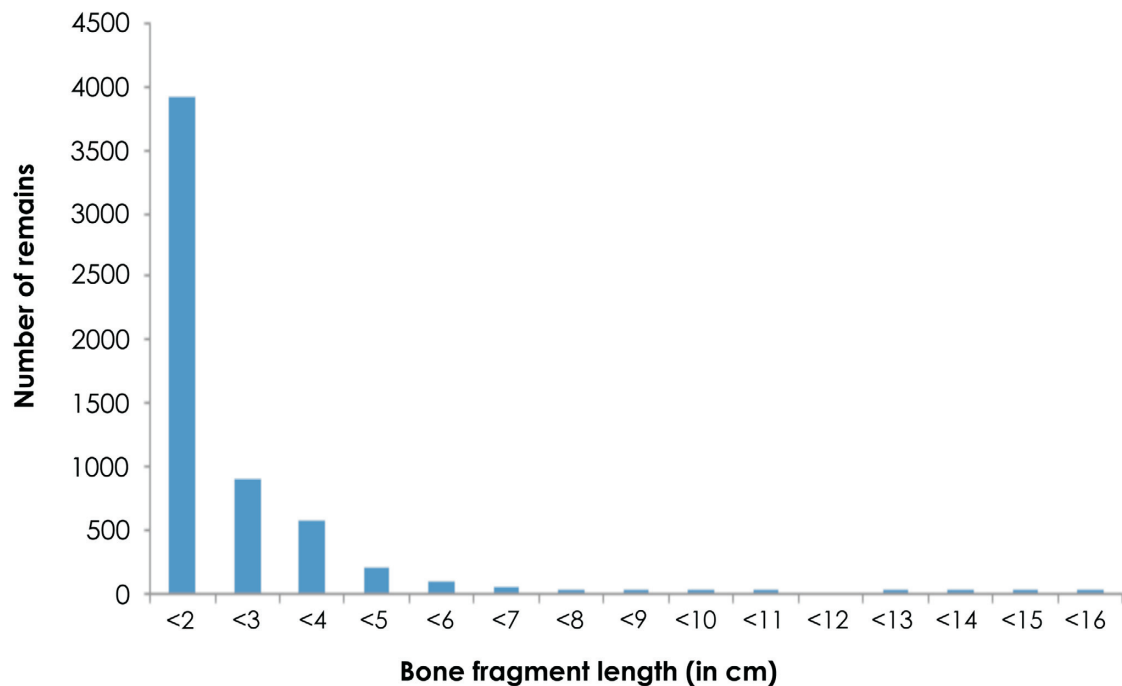


Figure 3. Distribution of the faunal remains from the Name Chamber according to their length.

with elements smaller than 2 cm constituting 56% of the assemblage and the existence of a dramatic decrease in size above 4 cm (Fig. 3). Elements preserved in articulation as well as antimeric bones are absent from the assemblage. No refitting between broken specimens was possible.

Breakage patterns could be observed on 1780 long bone fragment edges and are mostly consistent with dry fractures ($n = 1524$ or 85.6%). Green breakages were observed in 233 cases (13.7%), while 23 edges (1.3%) show evidence for recent breakage, probably occurring during excavations and/or curation of the material. Bone cylinders (i.e. long bones preserving most of the shaft but lacking the epiphyses), typical of carnivore-accumulated assemblages (Cruz-Urbe 1991; Pickering 2002; Kuhn *et al.* 2010) are absent from the assemblage.

32.2% of the elements for which this information was recorded ($n = 2013$) have undergone a decalcification process whereby the calcium initially present in the bone has disappeared, leading to a white chalky aspect of the fossils (Fig. 4). Manganese coating is present on the majority of the remains, from only a few dots (stage 1) to complete covering (stage 4), obscuring in the last case previous bone surface modifications (Table 2). The majority of the remains

Table 2. Distribution of bone remains according to the degree of manganese coating.

Manganese cover	0	1	2	3	4	Total
NR	62	425	936	527	56	2006
%	3.1%	21.2%	46.6%	26.3%	2.8%	100%

Table 3. Distribution of bone remains according to their degree of weathering (following Behrensmeyer 1978).

Weathering stage	1	2	3	4	Total
NR	1116	324	249	117	1806
%	61.8%	17.9%	13.8%	6.5%	100%

falls within stage 1 of weathering, with only superficial cracks visible on the surface of the cortical bone, but specimens characterized with deeper cracks, flaking and removal of the cortical bone consistent with stages 2 and 3 are also present (Table 3).

Fluvial action has produced rounding on 40 specimens, including 39 non-identifiable bone fragments, and one small fragment of bovid metapodial (Fig. 4).

Body part representation

Most skeletal parts (limb, axial, cranial and distal elements) are present in the assemblage, with the exception of the sacrum. The general pattern of body-part representation seems to be slightly density mediated. Hence, in the bovid sample (Table 4), compact elements such as long bones,

Table 4. Bovid skeletal part frequencies in the Name Chamber assemblage.

Element	NISP	MNE	% Survival
Skull	66	7	53.8
Mandible	10	5	19.2
Scapula	4	1	3.8
Pelvis	3	3	11.5
Humerus	14	5	19.2
Radius	13	5	19.2
Ulna	16	4	15.4
Femur	7	3	11.5
Tibia	18	7	26.9
Metacarpal	21	6	23.1
Metatarsal	20	5	19.2
Patella	2	2	7.7
Carpal	8	8	5.1
Tarsal	19	15	11.5
Phalanx	72	59	18.9
Rib	31	11	3.2
Cervical	16	4	4.4
Thoracic	21	4	2.4
Lumbar	7	4	4.4
Vertebra tot.	46	14	2.4
Sacrum	0	0	0



Figure 4. General state of preservation of the Name Chamber faunal assemblage: **A & B**, superior and inferior views of specimen BP/3/29064, metatarsal shaft fragment, bovid class II, showing abrasion by water; **C & D**, closed up views of the abraded surface; **E–J**, superior and inferior views of non-identifiable bone fragments abraded by water; **K**, specimens BP/3/25618–25641, typical non-identifiable bone fragments smaller than 2 cm; **L & M**, different types of manganese coating; **O–R**, highly weathered remains (**O**, long bone shaft fragment; **P & Q**, superior and inferior views of specimen BP/3/27968, metatarsal shaft fragment, bovid class II; **R**, specimen BP/3/28833, proximal right ulna, bovid class II); **S & T**, specimen BP/3/25917, complete proximal phalanx, bovid class II, completely covered by sedimentary concretions; **U & V**, posterior and lateral views of specimen BP/3/29033, near complete talus, bovid class II, showing decalcification.

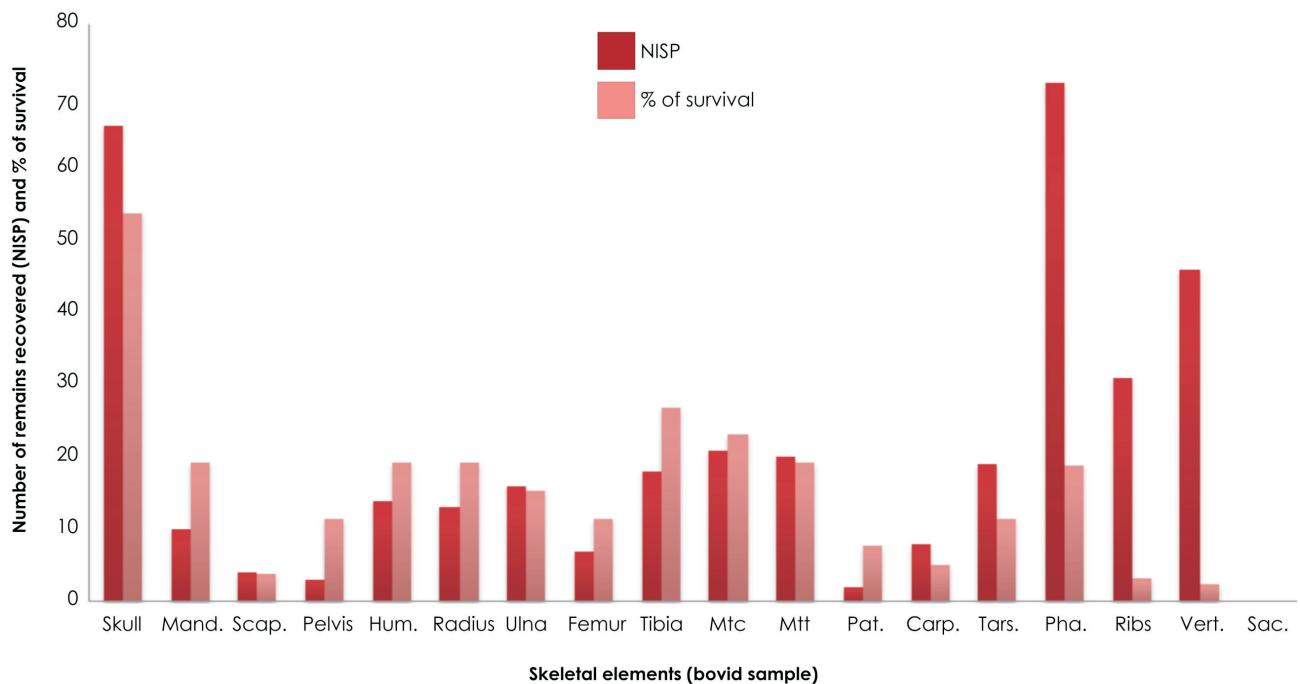


Figure 5. Body part representation pattern for the bovid sample (Mand: mandible; Scap: scapula; Hum: humerus; Mtc: metacarpal; Mtt: metatarsal; Pat: patella; Carp: carpals; Tars: tarsals; Pha: phalanges; Vert: vertebra; Sac: sacrum).

and especially long bone diaphyses, as well as short bones (phalanges, tarsals, carpals and sesamoids) (Lyman 1984; Kreutzer 1992; Lam *et al.* 1999) are the most abundant elements, just after cranial elements. However, low-density skeletal parts, namely ribs, vertebrae and patellae are also present (Table 4; Fig. 5), together with fragile and spongy bones such as non-fused long bone epiphyses of juveniles. Elements from the skull dominate, but this is largely due to the relative abundance of horn core fragments.

Mortality profile

As pointed out previously, age estimates are limited by the absence of dental specimens. Based on postcranial material, carnivores and primates seem to be represented only by adult individuals. The minimum number of 13 individuals composing the bovid sample is distributed as follows: two juveniles (one from class II and one from class III), three young adults (one from class I, one from class II and one from class III) and eight adults. The equid sample

contains six remains, two of which belong to juvenile individuals and four to adults.

Bone surface modifications caused by biotic agents

Carnivore damage

There is clear indication of carnivore damage (Fig. 6; Table 5) in the assemblage ($n = 94$ or 1.6% of the whole assemblage). Specimens affected by pits, punctures and furrows include bovid, carnivore (one canid pelvis fragment and one felid humerus fragment), equid (one phalanx of a juvenile) and non-identifiable remains (Table 5). These modifications occur on various parts of the skeleton: long bones, phalanges, scapula, pelvis, ribs and tarsals. The majority of the digested remains are small fragments (<3 cm) of non-identifiable bones, with the exception of one caudal vertebra and an intermediate phalanx attributed to *Papio* sp. (Fig. 6; Table 5).

Other biotic damage

Only two specimens (both non-identifiable bone fragments) show evidence for porcupine gnawing. Bird of

Table 5. Bone surface modifications caused by biotic and abiotic agents observed in the Name Chamber assemblage.

Modification		Ungulate	Carnivore	Primate	Birds	Non-ident.	Total
Decalcification		161	9	1	–	478	649
Fluvial rounding		1	–	–	–	39	40
Trampling	striae	58	9	2	2	92	163
Root	etching	21	1	–	–	21	43
Carnivore	pits	20	2	–	–	30	52
	punctures	–	–	–	–	1	1
	scores	10	–	–	–	15	25
	crenulated edges	3	–	–	–	–	3
	digested remains	4	–	2	–	48	54
Porcupine	gnawing	–	–	–	–	2	2
Bird of prey	beak/talon impact	–	–	–	–	–	–
Insect damage		18	1	–	–	12	31
Anthropogenic	cut marks	10	0	0	–	6	16

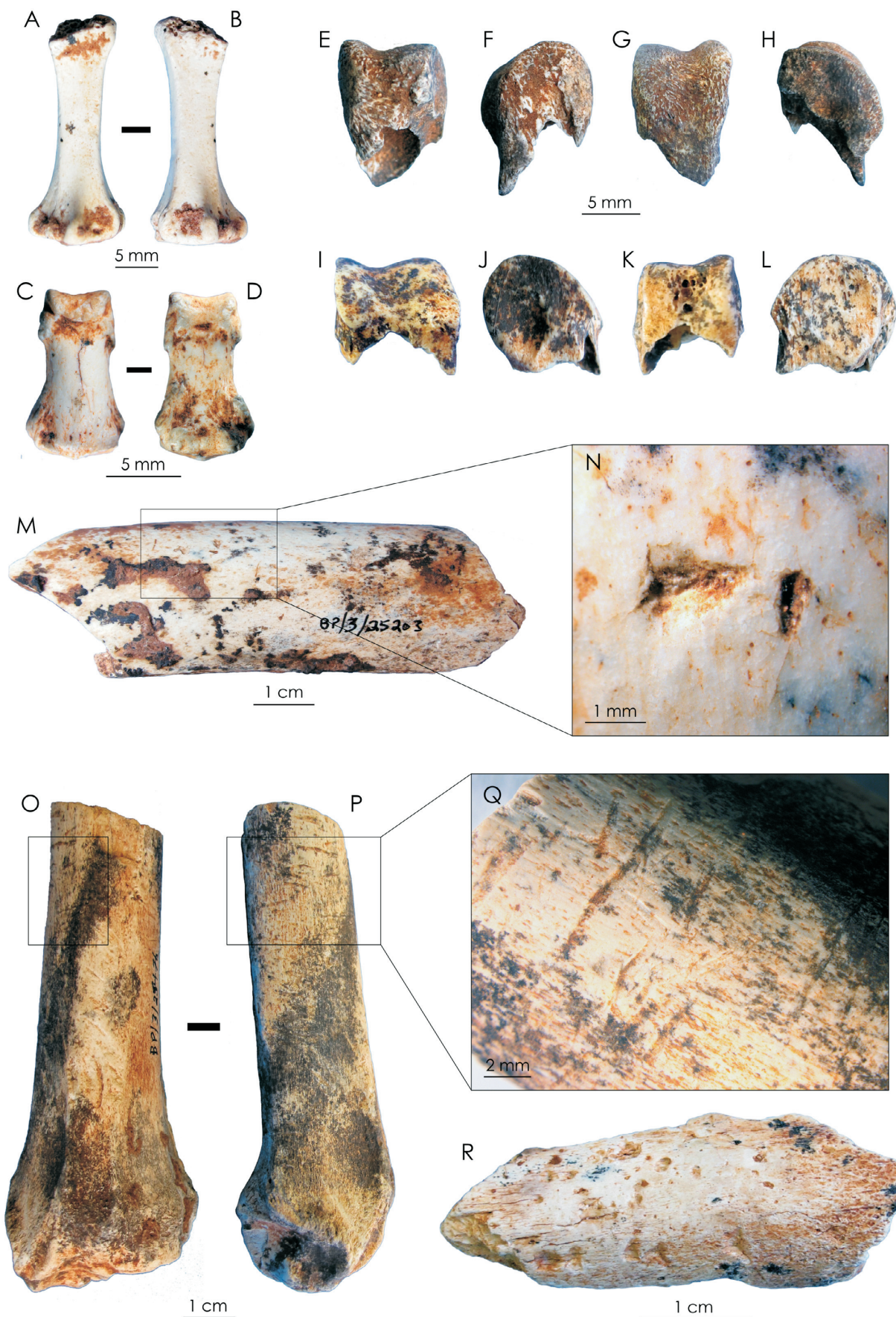


Figure 6. Bone fragments showing evidence of carnivore damage. **A–L**, examples of digested bones: **A & B**, specimen BP/3/31160, caudal vertebra, *Papio* sp.; **C & D**, specimen BP/3/31156, intermediate phalanx, *Papio* sp.; **E–H**, specimen BP/3/28239, proximal phalanx, bovid class I; **I–L**, specimen BP/3/29927, proximal phalanx, bovid class I; **M**, specimen BP/3/25203, femur shaft fragment, non-identifiable mammal, with carnivore pits and scores; **N**, close-up of the carnivore pits; **O & P**, anterior and lateral views of specimen BP/3/25476, distal radius, bovid class II, with carnivore scores; **Q**, close-up of the carnivore scoring; **R**, specimen BP/3/29436, long bone shaft fragment, non-identifiable mammal, with carnivore tooth pits and scores.

prey damage is not documented in the assemblage. Modifications produced by insects in the form of star pits, bore-holes, parallel and intersecting striae are observed on 31 specimens. While it is not possible to determine with certainty the identity of the species at the origin of these modifications, it is possible to point out similarities between these modifications and those experimentally-created for termites (Backwell *et al.* 2012).

Anthropogenic modifications

Bone surface modifications linked to hominin butchery are visible in the assemblage in the form of 16 cut-marked bones (Fig. 7; Table 5). Unsurprisingly, no burnt bone was identified. The cut marks occur on bovid (class II and III) phalanges, metatarsal, tibia shafts, lumbar vertebra, ribs and taxonomically non-identifiable long bone shaft fragments. One distal fragment of a bovid tibia bears evidence both for carnivore (pitting) and anthropogenic damage (cut marks) (Fig. 7). As the modifications do not intersect, it is difficult to estimate the chronology of events in terms of carcass consumption by carnivores and hominins.

One non-disputable bone tool (specimen BP/3/28232) was identified in the assemblage. It is a 9 cm long, 3 cm wide fragment of non-identifiable flat bone of a large mammal (most likely class III/IV ungulate), which has been appointed on one end. Detailed descriptions of this specimen and other bone fragments modified during butchery by hominins will be presented elsewhere (Val *et al.*, in prep.).

DISCUSSION

Taphonomy of the Name Chamber fauna: accumulation agents

The characteristics of the Name Chamber fauna (1) indicate contribution by and impact from multiple biotic and abiotic taphonomic agents, and (2) confirm the mixed origin of the sediments from which the material was recovered – in other words, the secondary depository location of these sediments. Both carnivore and anthropogenic modifications are present in the assemblage, as well as indication of fluvial rounding. High (>20%) carnivore/ungulate ratio, using the MNI, is one of the criteria considered as indicative of bone assemblages accumulated by hyaenids (Cruz-Uribe 1991; Pickering 2002; de Ruiter *et al.* 2009). The high ratio (33.3%) observed in the Name Chamber could reflect hyaenid contribution, even though carnivore-modified bones (i.e. digested and gnawed remains) only account for a small percentage of the assemblage. Besides, elements usually associated with cave use by hyaenids (e.g. Brain 1981; Cruz-Uribe 1991; Pickering 2002; Kuhn *et al.* 2010) such as presence of juvenile carnivore remains and coprolites are lacking. The occurrence of bone cylinders, a consequence of carnivores feeding preferably on long bone epiphyses rather than shafts, can be used to distinguish carnivore-accumulated assemblages from hominin-accumulated ones (Binford 1981; Brain 1981; Cruz-Uribe 1991; Pickering 2002; Kuhn *et al.* 2010). In the Name Chamber assemblage, bone cylin-

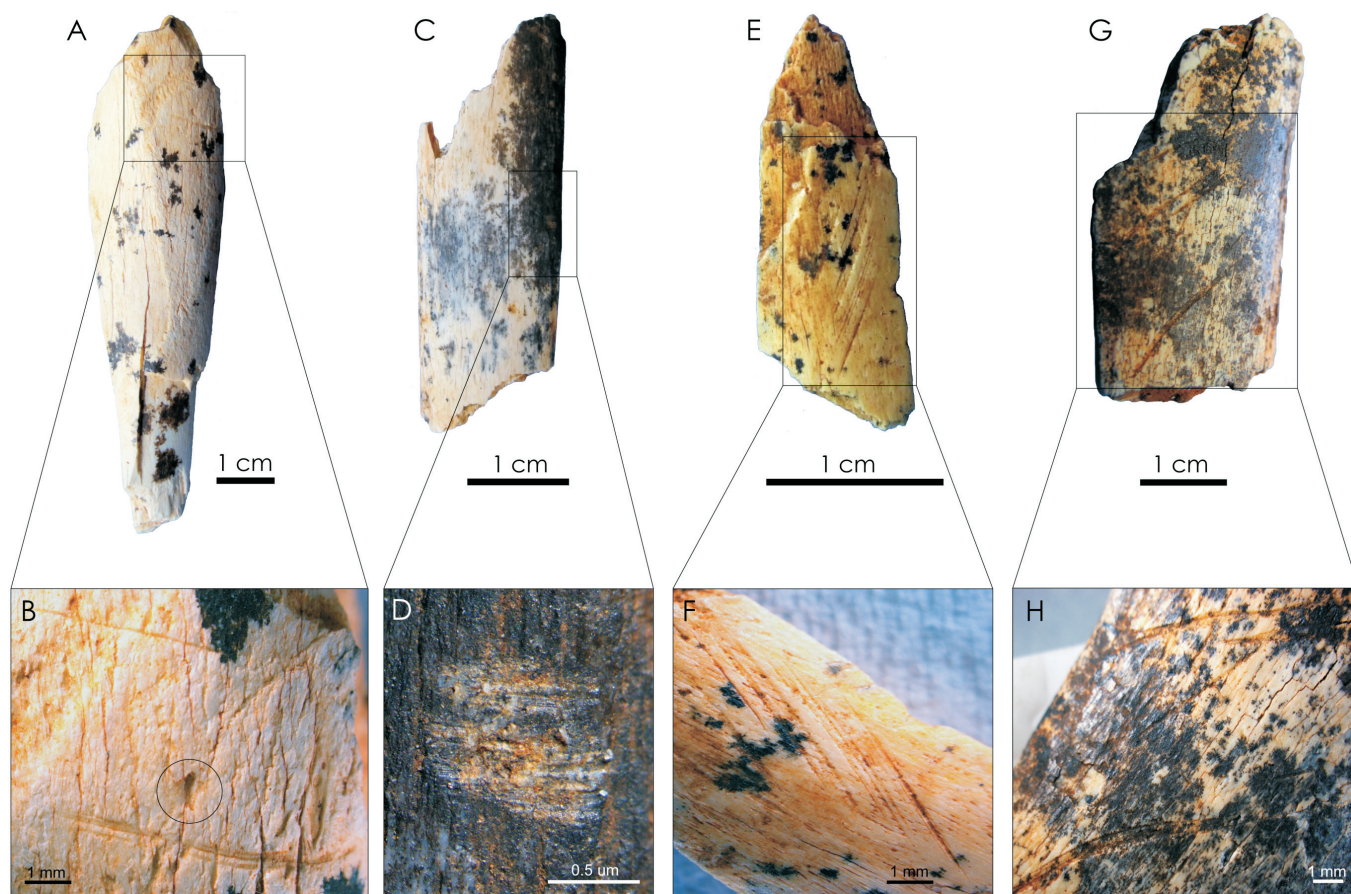


Figure 7. Examples of cut-marked bones: **A & B**, specimen BP/3/28485: tibia shaft fragment, bovid class II (note the co-occurrence of butchery marks and carnivore tooth pit); **C & D**, specimen BP/3/28455: rib fragment, non-identifiable mammal; **E & F**, specimen BP/3/28689: long bone shaft fragment, non-identifiable mammal; **G & H**, specimen BP/3/29062: long bone shaft fragment, non-identifiable mammal.

ders are absent and/or could not be identified given the high degree of fragmentation. Interestingly, the fact that some of the digested remains are carnivore bones could indicate a situation whereby carnivores trapped in the cave practiced scavenging. This is more consistent with a natural death trap scenario. The high carnivore/ungulate ratio has been questioned by some as not necessarily characteristic of hyaenid accumulations (Kuhn *et al.* 2010) and carnivore remains are also found in abundance in natural death trap assemblages, alongside other animals with good climbing proclivities such as primates (see for instance Cooke 1991; Wang & Martin 1993; Costamagno 1999; Pickering *et al.* 2004b; Val *et al.* 2015). The presence of low-density parts also supports a natural death trap scenario where it is expected to find at least some animals entering the cave as complete individuals. Evidence for water abrasion on some specimens suggests the introduction of some fossils from the surface by slope wash.

The occurrence of specimens showing different stages of weathering can suggest either different times of exposure on the surface before the introduction of the remains inside the cave or small variations inside the cave chamber in terms of air circulation or light exposition. However, as the Name Chamber is one of the lowest chambers at Sterkfontein, it seems more likely that conditions in that part of the karstic system will be stable (same degree of humidity, temperature, and constant darkness). Consequently, the lack of homogeneity in terms of weathering can probably be attributed to the introduction into the cave of different types of bones (from fresh carcasses/bones to isolated weathered elements). A similar process has been proposed for the introduction of the stone tools by slope wash (Kuman 1994a,b; Kuman & Field 2009). The high degree of fragmentation of the fossils together with the overrepresentation of the small fraction (<2 cm) can be explained firstly by the methods of recovery chosen, namely excavations of decalcified sediments and systematic sieving using small meshes. Secondly, it also most likely indicates a selective bias during transport of sediments from the exposed deposits into the Name Chamber via the 'Feeding Shaft', a phenomenon already described for the lithic assemblage (Stratford *et al.* 2012).

Comparisons with fauna from Member 4, Member 5 East Oldowan and Post Member 6

The majority of the faunal material known from Member 4 was recovered during excavations conducted by Hughes between 1982 and 1991 (Clarke 2012) in a decalcified area in the centre of the deposit; the fauna from Member 5 East was collected during excavations of both calcified and decalcified sediments (Tobias & Hughes 1969; Kuman 1994a; Clarke 2012). Direct quantitative comparisons with the material from the Name Chamber might not be relevant since systematic taphonomic analysis of the small fraction was not conducted and focus was most likely given to larger, readily identifiable remains (Brain 1981). For instance, in the Name Chamber, the water-abraded, digested and some of the cut-marked remains might be overrepresented as they are generally associated with

small non-identifiable bone fragments. In the L/63 Infill, fossils were recovered from loose sediments. Unfortunately, limited data on the characteristics of the faunal assemblage is available and does not allow in-depth comparisons with our results. Differences in sample sizes (e.g. MNI for Member 5 East is 67, while it is 546 for Member 4) and quantitative units used in the literature (e.g. both NISP and MNI are available for the Name Chamber and Member 5 East, while only the MNI is provided for Member 4 and post-Member 6) prevent testing the statistical significance of differences and similarities observed between the four samples considered. Nevertheless, several lines of data can be compared, in particular: (1) the general composition of the faunal spectrum; and (2) main taphonomic characteristics of the three samples (Table 6; Table S1)

Taxonomic composition

The composition of the faunal assemblage from the Name Chamber is most similar to Member 5 East. In the two assemblages, bovids, and especially class II bovids, largely dominate the faunal sample both in terms of number of remains and minimum number of individuals (Fig. 8), while non-hominin primates and carnivores are much more poorly represented (Fig. 8). Hominin remains from Member 5 East are very few; they are absent from the Name Chamber. This is greatly contrasting with the fauna from Member 4, characterized by a significant overrepresentation of australopithecines and non-hominin primates. Furthermore, in this deposit, the most abundant bovids belong to classes III and IV (76% of the bovid sample in number of remains: Kibii 2004) rather than class II. Regarding palaeohabitat associations indicated by the taxa present in the different fossil assemblages, the Name Chamber is also most similar to Member 5 East. Hence, grassland species recovered from Member 5 East and absent from Member 4 are also present in the Name Chamber (*Pedetes* and *Equus*). Yet, it is worth noticing the occurrence of *C. williamsi* ($n = 1$) and *T. strepsiceros* ($n = 1$) in the Name Chamber, two taxa only found in Member 4. In Member 4, carnivores are represented by a wide range of species (at least 14 different taxa, including various large felid and hyaenid, as well as several canid species), some of them being considered to have made use of the cave as a den, while Member 5 East has only yielded a few carnivore taxa, and their contribution to the faunal assemblage is limited. In that regard, the carnivore sample from the Name Chamber is more similar to what is observed in Member 5 East (Table 6).

Taphonomy

While the faunal assemblage from Member 4 seems to be completely non-anthropogenic (i.e. no stone tools recovered and no butchery damage) with a significant contribution by large carnivores combined with the introduction of some animals via a natural death trap, the sample from Member 5 East has yielded more anthropogenic elements (i.e. lithic assemblages and presence of one cut-marked bone) with a limited contribution by carnivores. The main taphonomic features from post-member 6 (L/63 Infill) are

Table 6. Taxonomic composition of the faunal assemblages recovered from Member 4, Member 5 East Oldowan, post-Member 6 (L/63 Infill) and the Name Chamber at Sterkfontein (data from: Brain 1981; Pickering 1999; Kuman & Clarke 2000; Kibii 2004; Reynolds & Kibii 2011; this paper).

FAMILY	Taxon	M4	M5 East	Post-M6	Name Chamber
HOMINIDAE	<i>Homo</i> sp.	–	–	X	–
	<i>Australopithecus</i> sp.	X	–	–	–
	<i>Australopithecus africanus</i>	X	–	–	–
	<i>Paranthropus robustus</i>	–	X	–	–
CERCOPITHECIDAE	<i>Theropithecus oswaldi</i>	–	X	–	–
	cf. <i>Cercopithecoides williamsi</i>	X	–	–	X
	<i>Parapapio jonesi</i>	X	–	–	–
	<i>Parapapio whitei</i>	X	–	–	–
	<i>Parapapio broomi</i>	X	–	–	–
	<i>Parapapio</i> sp.	X	–	–	–
	<i>Papio izodi</i>	X	–	–	–
	<i>Papio cynocephalus</i>	–	–	X	–
	<i>Papio</i> sp.	–	–	–	X
FELIDAE	<i>Dinofelis barlowi</i>	X	–	–	–
	<i>Dinofelis</i> sp.	–	–	–	X*
	<i>Megantereon cultridens</i>	X	–	–	–
	<i>Homotherium latidens</i>	X	–	–	–
	<i>Panthera leo</i>	X	X	–	–
	<i>Panthera pardus</i>	X	–	–	X
	<i>Felis</i> indet.	X	X	X	X
CANIDAE	<i>Canis</i> sp.	X	X	–	X
	<i>Canis mesomelas</i>	X	–	X	–
	<i>Canis brevirostris</i>	X	–	–	–
	<i>Canis antiquus</i>	X	–	–	–
HYAENIDAE	<i>Chasmaporthetes nitidula</i>	X	–	–	–
	<i>Chasmaporthetes silberbergi</i>	X	–	–	–
	<i>Pachycrocuta brevirostris</i>	X	X	–	–
	<i>Crocuta crocuta</i>	X	–	–	–
	<i>Parahyaena brunnea</i>	X	–	–	X
	<i>Hyaenidae</i> indet.	X	X	X	X
HERPESTIDAE	cf. <i>Mungos</i> sp.	–	X	–	–
	<i>Suricata</i> sp.	–	X	X	–
	<i>Herpestes ichneumon</i>	–	–	X	–
	<i>Herpestidae</i> indet.	–	X	–	X
BOVIDAE	<i>Alcelaphini</i> indet.	–	X	X	X
	<i>Connochaetes</i> sp.	X	–	–	X
	<i>Damaliscus parmularius</i>	X	–	–	–
	<i>Damaliscus</i> cf. <i>dorcas</i>	–	–	–	X
	<i>Damaliscus</i> sp.	–	X	X	–
	<i>Antidorcas bondi</i>	X	–	–	–
	<i>Antidorcas recki</i>	X	–	–	–
	<i>Antidorcas</i> sp.	–	X	X	X*
	<i>Tragelaphus strepsiceros</i>	X	–	–	X
SUIDAE	<i>Phacochoerus africanus</i>	–	–	–	X*
	<i>Metridiochoerus modestus</i>	–	X	–	–
	<i>Suidae</i> indet.	X	–	–	X
EQUIDAE	<i>Hipparion lybicum</i>	X	–	–	–
	<i>Equus</i> sp.	X ¹	X	X	X
HYRACOIDAE	<i>Procavia transvaalensis</i>	X	X	–	X
	<i>Procavia capensis</i>	–	–	X	X
RODENTIA	<i>Hystrix africaeaustralis</i>	X	–	X	X*
	<i>Pedetes capensis</i>	–	X	X	X
	<i>Lepus</i> sp.	X	–	X	X
BIRDS	<i>Struthio camelus</i>	–	X	–	–

*Identified only by S. Reynolds and K. Fatherley (most probably based on dental material).

¹The presence of *Equus* sp. in Member 4 is mentioned by Brain (1981) but Kuman & Clarke (2000) suggested that the provenance of the equid remains was not clear; they argued that these remains are more likely to have come from Member 5 instead. However, the study conducted by Kibii (2004) on more recently excavated material confirms the occurrence of *Equus* sp. in Member 4 (two remains identified with secure provenance).

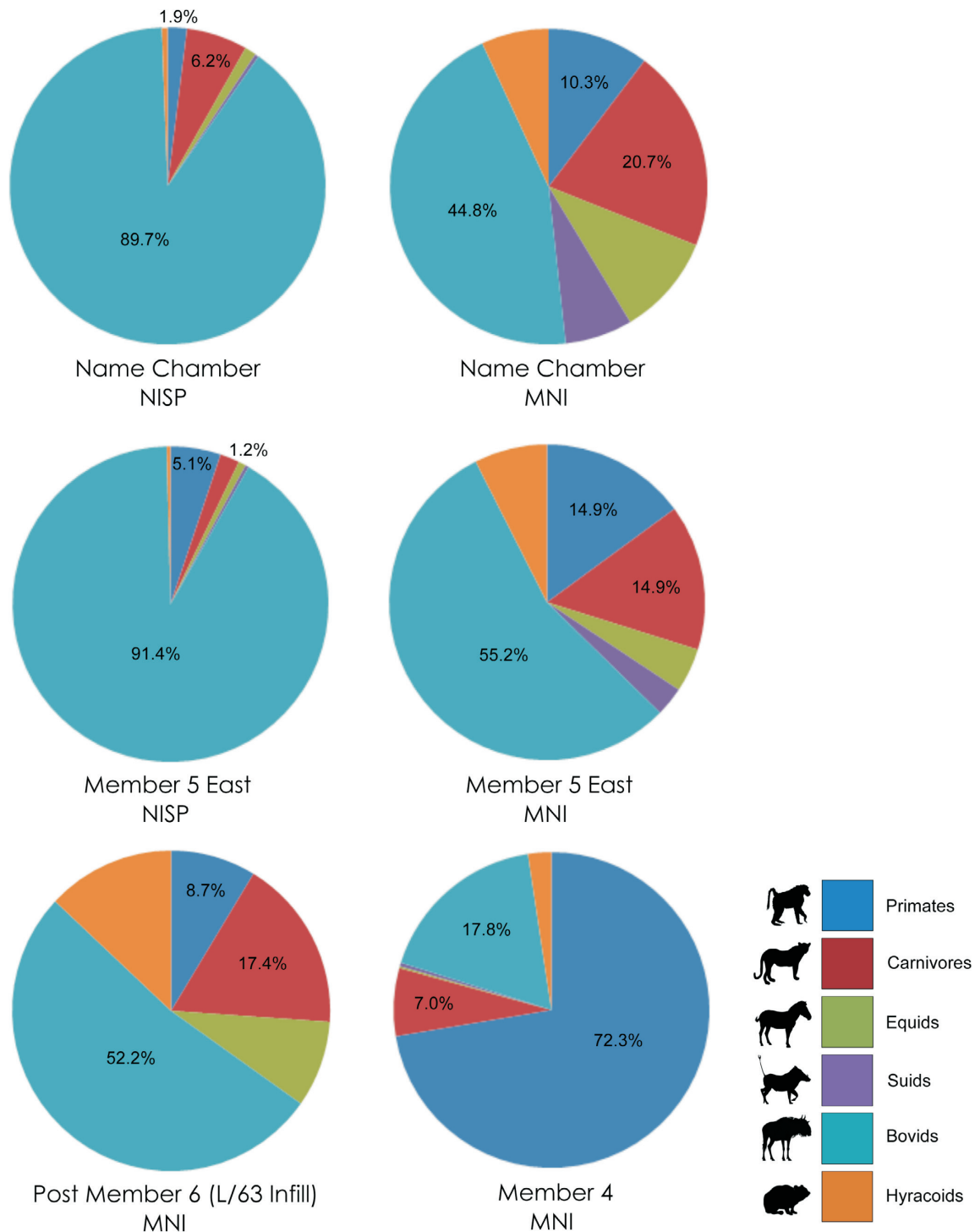


Figure 8. Taxonomic composition of the faunal assemblages from the Name Chamber, Member 4 (data from Brain 1981; Kibii 2004; Pickering *et al.* 2004a), Member 5 East Oldowan (data from Pickering 1999) and the L/63 Infill, Post-Member 6 (data from Reynolds *et al.* 2007).

the notable degree of porcupine damage on the one hand and the low incidence of carnivore damage on the other hand. Evidence for human occupation of the cave at that time is absent. We argue that the mixed taphonomic features of the fauna from the Name Chamber are consistent both with Member 5 East and Member 4, combining carnivore damage, hominin butchery modifications and indications for slope wash. Interestingly, the Name Chamber sample has a higher percentage of both carnivore-damaged remains and butchery modified bones than what is observed for Member 4 and Member 5 East, which is mostly due to sampling biases. Porcupine damage at the

Name Chamber is only illustrated by the presence of one single gnawed bone.

Finally, the identification of a bone tool in the Name Chamber assemblage is worth noting since it supports Robinson's find (1959) and confirms the presence of such implements at Sterkfontein, a presence that is debated by Kuman (2005).

Comparisons with existing studies on the Name Chamber

Previous research on material recovered from the Name Chamber (artefacts and microfaunal remains) combined

with stratigraphic analyses have suggested a scenario whereby the sediments present today in the cave accumulated from exposed deposits via a 12.5-metre-deep vertical shaft (i.e. the 'Feeding Shaft') located just below square R57 in the surface excavation and associated with Member 5 East Oldowan deposit. The presence of numerous blocks of dolomite along this shaft would have led to the filtering of larger elements and the selection of the small fraction (>2 cm) of the lithic assemblage (Stratford *et al.* 2012). Similar observations were made for the macrofaunal assemblage, largely dominated by highly fragmented, small elements (95% of the remains are smaller than 4 cm and 56% are smaller than 2 cm). The taxonomic composition of the microfaunal assemblage from the Name Chamber points out towards a major contribution from Member 5 East, while the identification of a few taxa also suggests contributions from both Member 4 (transected by the 'Feeding Shaft'; Stratford *et al.* 2012) and post-Member 6 (Avery *et al.* 2010). Taxonomical attributions and taphonomic analysis of the macrofauna confirm that the sediments of the Name Chamber mostly come from the Member 5 East Oldowan deposits. Contribution from post-Member 6 was suggested by the presence of *Crociodura*, *Saccostomus* and *Thallomys* in the Name Chamber sample (Avery *et al.* 2010) but this is not supported by clear indication in the macrofaunal assemblage. Some features of the large faunal sample, however, suggest the introduction of sediments and associated fossil material from Member 4, as illustrated by the relatively high incidence of carnivore damage and the presence of *C. williamsi*.

CONCLUSION

Taxonomic and taphonomic analysis of the faunal assemblage recovered during excavations of the soft sediments from the Western Talus in the Name Chamber at Sterkfontein highlights evidence for a mixed assemblage, in a secondary depositional context. The fossil sample, characterized by a generally poor degree of cortical surface preservation and a high level of fragmentation, comprises a significant percentage of small (>2 cm) non-identifiable fragments. Some of these features might easily be explained by the excavation procedures employed, namely the use of a small mesh during sieving, and the type of sediments excavated (i.e. decalcified), leading to the recovery of abundant small elements. The assemblage is characterized by various taphonomic signals, including carnivore damage and water abrasion. Systematic microscopic investigation of bone surfaces also revealed the presence of several butchery marks, which are of special interest since this type of modification is rarely recorded in Plio-Pleistocene faunal assemblages from the Bloubank Valley cave deposits. The taxonomic composition and taphonomic characteristics of the faunal sample are in favour of a major contribution to the sediments of the Name Chamber from Member 5 East Oldowan, and to a much lesser degree from Member 4. The results of this study confirm results of previous studies on the lithics and microfaunal remains and support the initial stratigraphic connection between the Member 5 area initially

proposed by Robinson (1962), further explored by Clarke (1994) and refined by Stratford and colleagues (2012).

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REFERENCES

- ANDREWS, P. 1990. *Owls, Caves and Fossils*. Chicago, University of Chicago Press.
- EVERY, D.M., STRATFORD, D.J. & SÉNÉGAS, F. 2010. Micromammals and the formation of the Name Chamber at Sterkfontein, South Africa. *Geobios* **43**, 379–387.
- BACKWELL, L.R., PARKINSON, A.H., ROBERTS, E.M., D'ERRICO, F. & HUCHET, J.-B. 2012. Criteria for identifying bone modification by termites in the fossil record. *Palaeogeography, Palaeoclimatology, Palaeoecology* **337–338**, 72–87.
- BAMFORD, M. 1999. Pliocene fossil woods from an early hominid cave deposit, Sterkfontein, South Africa. *South African Journal of Science* **95**, 231–237.
- BEHRENSMEYER, A.K. 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* **4**(2), 150–162.
- BEHRENSMEYER, A.K., GORDON, K.D. & YANAGI, G.T. 1986. Trampling as a cause of bone surface damage and pseudo-cutmarks. *Nature* **319**, 768–771.
- BINFORD, L.R. 1981. *Bones. Ancient Men and Modern Myths*. London, Academic Press.
- BOCHENSKI, Z.M. & TOMEK, T. 1997. Preservation of bird bones: erosion versus digestion by owls. *International Journal of Osteoarchaeology* **7**, 372–387.
- BOCHENSKI, Z.M. & TORNBERG, R. 2003. Fragmentation and preservation of bird bones in uneaten food remains of the gyrfalcon *Falco rusticolus*. *Journal of Archaeological Science* **30**, 1665–1671.
- BOCHENSKI, Z.M., KOROVIN, V.A., NEKRASOV, A.E. & TOMEK, T. 1997. Fragmentation of bird bones in food remains of imperial eagles (*Aquila heliaca*). *International Journal of Osteoarchaeology* **7**, 165–171.
- BOCHENSKI, Z.M., HUHTALA, K., JUSSILA, P., PULLIAINEN, E., TORNBERG, R. & TUNKKARI, P.S. 1998. Damage to bird bones in pellets of gyrfalcon *Falco rusticolus*. *Journal of Archaeological Science* **25**, 425–433.
- BRAIN, C.K. 1974. Some suggested procedures in the analysis of bone accumulation from southern African Quaternary sites. *Annals of the Transvaal Museum* **29**(1), 1–8.
- BRAIN, C.K. 1981. *The Hunters or the Hunted? An Introduction to South African Cave Taphonomy*. Chicago, University of Chicago Press.
- BRITT, B.B., SCHEETZ, R.D. & DANGERFIELD, A. 2008. A suite of dermestid beetle traces on dinosaur bone from the Upper Jurassic Morrison Formation, Wyoming, USA. *Ichnos: An International Journal for Plant and Animal Traces* **15**(2), 59–71.
- BROOM, R. 1936. New fossil anthropoid skull from South Africa. *Nature* **138**, 486–488.
- BROOM, R., ROBINSON, J.T. & SCHEPERS, G.W.H. 1950. Sterkfontein ape-man *Plesianthropus*. *Transvaal Museum Memoir* **4**. Pretoria, Transvaal Museum.
- BRUXELLES, L., CLARKE, R.J., MAIRE, R., ORTEGA, R. & STRATFORD, D. 2014. Stratigraphic analysis of the Sterkfontein StW 573 *Australopithecus* skeleton and implications for its age. *Journal of Human Evolution* **70**, 36–48.
- CLARKE, R.J. 1988. A new *Australopithecus* cranium from Sterkfontein and its bearing on the ancestry of *Paranthropus*. In: Grine, F. (ed.), *Evolutionary History of the 'Robust' Australopithecines*, 287–292. New York, Aldine de Gruyter.
- CLARKE, R.J. 1994. On some new interpretations of Sterkfontein stratigraphy. *South African Journal of Science* **90**, 211–214.
- CLARKE, R.J. 2006. A deeper understanding of the stratigraphy of Sterkfontein fossil hominid site. *Transactions of the Royal Society of South Africa* **61**(2), 111–120.
- CLARKE, R.J. 2012. A brief review of history and results of 40 years of Sterkfontein excavations. In: Reynolds, S.C. & Gallagher, A. (eds), *Perspectives on Hominin Evolution*, 120–142. Cambridge University Press.
- CLARKE, R.J. 2013. *Australopithecus* from Sterkfontein Caves, South Africa. In: Reed, K.E., Fleagle, J.G. & Leakey, R.E. (eds), *The Paleobiology of Australopithecus, Vertebrate Palaeobiology and Palaeoanthropology*, 105–123. Springer, Dordrecht.
- CODRON, D., LUYT, J., LEE-THORP, J.A., SPONHEIMER, M., DE

- RUITER, D. & CODRON, J. 2005. Utilization of savanna-based resources by Plio-Pleistocene baboons. *South African Journal of Science* **101**, 245–248.
- COOKE, H.B.S. 1991. *Dinofelis barlowi* (Mammalia, Carnivora, Felidae) cranial material from Bolt's Farm, collected by the University of California African expedition. *Palaeontologia africana* **28**, 9–21.
- COSTAMAGNO, S. 1999. Coudoulous II: taphonomie d'un aven-piège. Contribution des accumulations d'origine naturelle à l'interprétation des archéofaunes du Paléolithique moyen. *Anthropozoologica* **29**, 13–31.
- CRUZ-URIBE, K. 1991. Distinguishing hyena from hominid bone accumulations. *Journal of Field Archaeology* **18**, 467–486.
- CURNOE, D. & TOBIAS, P.V. 2006. Description, new reconstruction, comparative anatomy, and classification of the Sterkfontein Stw 53 cranium, with discussions about the taxonomy of other southern African early *Homo* remains. *Journal of Human Evolution* **50**, 36–77.
- DELSON, E. 1984. Cercopithecoid biochronology of the African Plio-Pleistocene: correlation among eastern and southern hominid-bearing localities. *Courier Forschungsinstitut Senckenberg* **69**, 199–218.
- DELSON, E. 1988. Chronology of South African australopithecine site units. In: Grine, F.E. (ed.), *Evolutionary History of the 'Robust' Australopithecines*, 317–324. New York, Aldine de Gruyter.
- DE RUITER, D.J. 2004. Undescribed hominid fossils from the Transvaal Museum faunal collections. *Annals of the Transvaal Museum* **41**, 29–40.
- DE RUITER, D.J., PICKERING, R., STEININGER, C.M., KRAMERS, J.D., HANCOX, P.J., CHURCHILL, S.E., BERGER, L.R. & BACKWELL, L.R. 2009. New *Australopithecus robustus* fossils and associated U-Pb dates from Cooper's Cave (Gauteng, South Africa). *Journal of Human Evolution* **56**, 497–513.
- DOMÍNGUEZ-RODRIGO, M., DE JUANA, S., GALÁN, A.B. & RODRÍGUEZ, M. 2009. A new protocol to differentiate trampling marks from butchery cut marks. *Journal of Archaeological Science* **36**, 2643–2654.
- ELTON, S. 2000. *Ecomorphology and evolutionary biology of African cercopithecoids: providing an ecological context for hominid evolution*. Unpublished Ph.D. thesis, University of Cambridge, Cambridge.
- ELTON, S. 2001. Locomotor and habitat classifications of cercopithecoid postcranial material from Sterkfontein Member 4, Bolt's Farm and Swartkrans Member 1 and 2, South Africa. *Palaeontologia africana* **31**, 115–126.
- EWER, R.F. 1956. The fossil carnivores of the Transvaal Caves: Canidae. *Proceedings of the Zoological Society, London* **126**(1), 97–100.
- GRANGER, D.E., GIBBON, R.J., KUMAN, K., CLARKE, R.J., BRUXELLES, L. & CAFFEE, M.W. 2015. New cosmogenic burial ages for Sterkfontein Member 2 *Australopithecus* and Member 5 Oldowan. *Nature* **522**, 85–88.
- HERRIES, A.I.R. & SHAW, J. 2011. Palaeomagnetic analysis of the Sterkfontein palaeocave deposits: implications for the age of the hominid fossils and stone tool industries. *Journal of Human Evolution* **60**, 523–539.
- HERRIES, A.I.R., CURNOE, D. & ADAMS, J.W. 2009. A multi-disciplinary seriation of early *Homo* and *Paranthropus* bearing palaeocaves in southern Africa. *Quaternary International* **202**, 14–28.
- KIBII, J.M. 2004. *Comparative taxonomic, taphonomic and palaeoenvironmental analysis of 4–2.3 million year old australopithecine cave infills at Sterkfontein*. Unpublished Ph.D. thesis, University of the Witwatersrand, Johannesburg.
- KREUTZER, L.A. 1992. Bison and deer bone mineral densities: comparisons and implications for the interpretation of archaeological faunas. *Journal of Archaeological Science* **19**, 271–294.
- KUHN, B., BERGER, L.R. & SKINNER, J.D. 2010. Examining criteria for identifying and differentiating fossil faunal assemblages accumulated by hyenas and hominins using extant hyenid accumulations. *International Journal of Osteoarchaeology* **20**, 15–35.
- KUMAN, K. 1994a. The archaeology of Sterkfontein – past and present. *Journal of Human Evolution* **27**, 471–495.
- KUMAN, K. 1994b. The archaeology of Sterkfontein: preliminary findings on site formation and cultural change. *South African Journal of Science* **90**, 215–219.
- KUMAN, K. 2005. Bone tool mimics from an early hominid site in South Africa. In: *Congress of the Pan African Association for Archaeology and Related Studies*, 12th, July 3–10, Gaborone, Abstract 20 pp.
- KUMAN, K. & CLARKE, R.J. 2000. Stratigraphy, artefact industries and hominid associations for Sterkfontein, Member 5. *Journal of Human Evolution* **38**, 827–847.
- KUMAN, K. & FIELD, A.S. 2009. The Oldowan industry from Sterkfontein caves, South Africa. In: Schick, K. & Toth, N. (eds), *The Cutting Edge: Approaches to the Earliest Stone Age*, 151–170. Stone Age Institute Press, Bloomington, Indiana.
- LAM, Y.M., CHEN, X. & PEARSON, O.M. 1999. Intertaxonomic variability in patterns of bone density and the differential representation of bovid, cervid, and equid elements in the archaeological record. *American Antiquity* **64**, 343–362.
- LAROU LANDIE, V. 2000. *Taphonomie et archéozoologie des oiseaux en grotte: applications aux sites paléolithiques du Bois-Ragot (Vienne), de Combe Saunière (Dordogne) et de La Vache, (Ariège)*. Unpublished Ph.D. thesis, University of Bordeaux, France.
- LAROU LANDIE, V. 2002. Damage to pigeon long bones in pellets of the eagle owl *Bubo bubo* and food remains of peregrine falcon *Falco peregrinus*: zooarchaeological implications. *Acta zoologica cracoviensia* **45** (special issue), 331–339.
- LEE-THORP, J.A., SPONHEIMER, M. & LUYT, J. 2007. Tracking changing environments using stable carbon isotopes in fossil tooth enamel: an example from the South African hominid sites. *Journal of Human Evolution* **53**, 595–601.
- LOCKWOOD, C.A. & TOBIAS, P.V. 2002. Morphology and affinities of new hominid cranial remains from Member 4 of the Sterkfontein Formation, Gauteng Province, South Africa. *Journal of Human Evolution* **42**, 389–450.
- LYMAN, R.L. 1984. Bone density and differential survivorship of fossil classes. *Journal of Anthropological Archaeology* **3**, 259–299.
- LYMAN, R.L. 1994a. *Vertebrate Taphonomy*. Cambridge University Press.
- LYMAN, R.L. 1994b. Quantitative units and terminology in zooarchaeology. *American Antiquity* **59**(1), 36–71.
- MAGUIRE, J.M., PEMBERTON, D. & COLLETT, M.H. 1980. The Makapansgat limeworks grey breccias: hominids, hyaenas, hystricids or hillwash? *Palaeontologia africana* **23**, 75–98.
- MOGGI-CECCHI, J., GRINE, F.E. & TOBIAS, P.V. 2006. Early hominid dental remains from Members 4 and 5 of the Sterkfontein Formation (1966–1996 excavations): catalogue, individual associations, morphological descriptions and initial metrical analysis. *Journal of Human Evolution* **50**, 239–328.
- O'REGAN, H.J. & REYNOLDS, S.C. 2009. An ecological reassessment of the southern African carnivore guild: a case study from Member 4, Sterkfontein, South Africa. *Journal of Human Evolution* **57**, 212–222.
- PARTRIDGE, T.C. 1978. Re-appraisal of lithostratigraphy of Sterkfontein hominid site. *Nature* **275**, 282–287.
- PARTRIDGE, T.C. 2005. Dating of the Sterkfontein hominids: progress and possibilities. *Transactions of the Royal Society of South Africa* **60**(2), 107–109.
- PARTRIDGE, T.C. & WATT, I.B. 1991. The stratigraphy of the Sterkfontein hominid deposit and its relationship to the underground system. *Palaeontologia africana* **28**, 35–40.
- PICKERING, R. & KRAMERS, J.D. 2010. Re-appraisal of the stratigraphy and determination of new U-Pb dates for the Sterkfontein hominid site, South Africa. *Journal of Human Evolution* **59**, 70–86.
- PICKERING, T.R. 1999. *Taphonomic interpretations of the Sterkfontein early hominid site (Gauteng, South Africa) reconsidered in the light of recent evidence*. Unpublished Ph.D. thesis, University of Wisconsin, Madison.
- PICKERING, T.R. 2002. Reconsideration of criteria for differentiating faunal assemblages accumulated by hyenas and hominids. *International Journal of Osteoarchaeology* **12**, 127–141.
- PICKERING, T.R., CLARKE, R.J. & MOGGI-CECCHI, J. 2004a. Role of carnivores in the accumulation of the Sterkfontein Member 4 hominid assemblage: a taphonomic reassessment of the complete hominid fossil sample. *American Journal of Physical Anthropology* **125**, 1–15.
- PICKERING, T.R., CLARKE, R.J. & HEATON, J.L. 2004b. The context of Stw 573, an early hominid skull and skeleton from Sterkfontein Member 2: taphonomy and paleoenvironment. *Journal of Human Evolution* **46**, 279–297.
- REYNOLDS, S.C. & KIBII, J.M. 2011. Sterkfontein at 75: review of palaeoenvironments, fauna and archaeology from the hominid site of Sterkfontein (Gauteng Province, South Africa). *Palaeontologia africana* **46**, 59–88.
- REYNOLDS, S.C., CLARKE, R.J. & KUMAN, K.A. 2007. The view from Lincoln Cave: mid- to late Pleistocene fossil deposits from Sterkfontein hominid site, South Africa. *Journal of Human Evolution* **53**, 260–271.
- ROBINSON, J.T. 1959. A bone implement from Sterkfontein. *Nature* **184**, 583–585.
- ROBINSON, J.T. 1962. Sterkfontein stratigraphy and the significance of the Extension Site. *South African Archaeological Bulletin* **17**(66), 87–107.
- SCHWARCZ, H.P., GRÜN, R. & TOBIAS, P.V. 1994. ESR dating studies of the australopithecine site of Sterkfontein, South Africa. *Journal of Human Evolution* **26**, 175–181.
- SHIPMAN, P. & ROSE, J. 1983. Early hominid hunting, butchering, and carcass-processing behaviours: approaches to the fossil record. *Journal of Anthropological Archaeology* **2**, 57–98.
- SKINNER, J.D. & CHIMIMBA, C.T. 2005. *The Mammals of the Southern African Subregion*. Cambridge, Cambridge University Press.

- SPONHEIMER, M., LEE-THORP, J.A., DE RUITER, D.J., SMITH, J.M., VAN DER MERWE, N.J., REED, K., GRANT, C.C., AYLIFFE, L.K., ROBINSON, T.F., HEIDELBERGER, C. & MARCUS, W. 2003. Diets of southern African Bovidae: stable isotope evidence. *Journal of Mammalogy* **84**(2), 471–479.
- STRATFORD, D.J. 2011. *The underground central deposits of the Sterkfontein caves, South Africa*. Unpublished Ph.D. thesis, University of the Witwatersrand, Johannesburg.
- STRATFORD, D.J., BRUXELLES, L., CLARKE, R.J. & KUMAN, K. 2012. New stratigraphic interpretations of the fossil and artefact-bearing deposits of the Name Chamber, Sterkfontein. *South African Archaeological Bulletin* **67**(196), 159–167.
- STRATFORD, D., GRAB, S. & PICKERING, T.R. 2014. The stratigraphy and formation history of fossil- and artefact-bearing sediments in the Milner Hall, Sterkfontein Cave, South Africa: new interpretations and implications for palaeoanthropology and archaeology. *Journal of African Earth Sciences* **96**, 155–167.
- TOBIAS, P.V. & HUGHES, A.R. 1969. The new Witwatersrand University excavation at Sterkfontein: progress report, some problems and first results. *South African Archaeological Bulletin* **24**(95/96), 158–169.
- TOUSSAINT, M., MACHO, G.A., TOBIAS, P.V., PARTRIDGE, T.C. & HUGHES, A.R. 2003. The third partial skeleton of a late Pliocene hominin (Stw 431) from Sterkfontein, South Africa. *South African Journal of Science* **99**, 215–223.
- TURNER, A. 1987. New fossil carnivore remains from the Sterkfontein hominid site (Mammalia: Carnivora). *Annals of the Transvaal Museum* **34**, 319–347.
- TURNER, A. 1997. Further remains of Carnivora (Mammalia) from the Sterkfontein hominid site. *Palaeontologia africana* **34**, 115–126.
- VAN DER MERWE, N.J., THACKERAY, J.F., LEE-THORP, J.A. & LUYT, J. 2003. The carbon isotope ecology and diet of *Australopithecus africanus* at Sterkfontein, South Africa. *Journal of Human Evolution* **44**, 581–597.
- VAL, A., DIRKS, P.H.G.M., BACKWELL, L.R., D'ERRICO, F. & BERGER, L.R. 2015. Taphonomic analysis of the faunal assemblage associated with the hominins (*Australopithecus sediba*) from the early Pleistocene deposits of Malapa, South Africa. *PLOS ONE* **10**(6), e0126904.
- VILLA, P. & MAHIEU, E. 1991. Breakage patterns of human long bones. *Journal of Human Evolution* **21**, 27–48.
- VRBA, E.S. 1976. The fossil Bovidae of Sterkfontein, Swartkrans and Kromdraai. *Transvaal Museum Memoir* **21**. Pretoria, Transvaal Museum.
- VRBA, E.S. 1980. The significance of bovid remains as indicators of environment and predation patterns. In: Behrensmeyer, A.K. & Hill, A.P. (eds), *Fossils in the Making*, 247–271. Chicago, University of Chicago Press.
- WANG, X. & MARTIN, L.D. 1993. Late Pleistocene, paleoecology and large mammal taphonomy, natural Trap Cave, Wyoming. *National Geographic Research & Exploration* **9**(4), 422–435.
- WILKINSON, M.J. 1983. Geomorphic perspectives on the Sterkfontein australopithecine breccias. *Journal of Archaeological Science* **10**, 515–529.

Permo-Triassic palynology and palaeobotany of Zambia: a review

Natasha Barbolini^{1*}, Marion K. Bamford¹ & Stephen Tolan²

¹Evolutionary Studies Institute and School of Geosciences, DST-NRF Centre of Excellence in Palaeosciences, University of the Witwatersrand, Private Bag 3, WITS 2050, South Africa

²Chipembele Wildlife Education Centre, P.O. Box 67, Malama Road, Mfuwe, Zambia

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Permian and Triassic deposits in Zambia have been sporadically researched since the beginning of the 20th century, but there have not been many detailed works on the palaeobotany and palynology of these Karoo-aged rocks. Studies that have been published, suffered from a lack of inter-basinal correlation, which was also hampered by differing stratigraphic subdivisions. We review previous records of palynomorphs, megafloral remains and fossil wood in Zambian Permo-Triassic deposits, present a synthesis of micro- and macrofossil occurrences throughout the country, and propose a standardized subdivision for the Luangwa Valley. This will aid in future correlations between different Karoo basins and act as a framework for future palaeobotanical research in both Zambia and Gondwana.

Keywords: palaeobotany, palynology, Zambia, Permian, Triassic, Karoo.

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HISTORICAL SETTING

The famous missionary explorer, David Livingstone, crossed the Luangwa River from the east in December 1866, and reported finding fossil wood in what is now the Munyamadzi Corridor of the Mid Luangwa Valley (Waller 1874). In 1894, the explorer Edward Glave found fossil trees close to the Munyamadzi River and the escarpment in the Mid Luangwa Valley, and another explorer, Cyril Hoste, in 1896, visited the same area and described fossil trees running south for many miles along the foot of the Muchinga Escarpment (Hoste 1898). In 1905, missionary Henry Masters and his wife found fossil trees in the Lukasashi Valley, a minor arm of the Luangwa Valley (Masters & Masters 1920).

Frank Dixey, geologist from the Nyasaland Geological Survey, was the first true fossil hunter to come to the Luangwa Valley. His initial visit in 1928 was a short reconnaissance to the Upper Luangwa Valley around the Sitwe area, collecting a number of Karoo tetrapod and tree fossils (Dixey 1929). In 1935, Dixey returned with a full portered expedition for 4 weeks to the Upper Luangwa Valley, during which time he collected 'well over a ton of fossils', which were carried out on the heads of porters for 60 miles over mountainous country (Dixey 1937). Forty-three samples of fossil wood were sent to the British Museum (Natural History) in London where a report was completed on the fossil wood by W.N. Edwards, entitled 'Fossil woods from the upper Luangwa Valley' (1937).

The Geological Survey Department (GSD) of Northern Rhodesia came into existence in the latter half of 1950 and their geologists were responsible for documenting fossil plants and trees up until the late 1970s. In the early 1950s coal exploration was carried out during the dry season in

the mid-Zambezi Valley by GSD geologists Harry Gair and Ron Tavener-Smith. Both men found fossil wood in abundance, Gair in the area of what is now known as Chirundu Fossil Forest, a proposed World Heritage site (Fig. 1), and Tavener-Smith at two areas southeast of Gwembe.

Two GSD geologists, Reichwalder and Brandon, worked in the Luano Valley between 1972 and 1974, where they found fossil plants and silicified trees in Karoo sediments (Reichwalder & Brandon 1978).

Between 1959 and 1973 British biologist William Astle worked with the National Parks & Wildlife Department, and he and his Scouts were responsible for finds of fossil plants and trees in the Mid Luangwa Valley area (Fig. 2), many inside South Luangwa National Park (Astle 1999).

Most recently, Professor Tom Kemp and others carried out a fossil recce in 2000 to several of the fossil tetrapod localities visited by the Oxford University Museum expedition in 1974, and found an extensive fossil tree site between the Mwaleshi and Mulandashi Rivers in North Luangwa National Park (Kemp 2000).

GEOLOGICAL CONTEXT

Karoo-aged deposits are widespread in Zambia, and fossils are known from the Permian and Triassic rocks of the mid-Zambezi and Luangwa-Lukasashi-Lunsemfwa Basins, shaded in dark grey (Fig. 3).

Over the years various authors have made use of slightly different naming conventions for the different sub-divisions of the Luangwa Valley, complicating correlation. In this paper a standardized division of the Luangwa Valley is proposed as follows (Fig. 4):



Figure 1. Transporting pieces of fossil wood from Chirundu Fossil Forest to display outside the Geological Survey Department, Lusaka, Zambia. Photographs by Harry Gair.



Figure 2. Fossil wood in the Mid Luangwa Valley. Photographs by William Astle.

- Upper Luangwa Valley – source (Mafinga Hills) to northern boundary of North Luangwa National Park (NLNP) (=‘North Luangwa Valley’ of Utting).
- Mid Luangwa Valley – North Luangwa National Park (NLNP), Munyamadzi Corridor, South Luangwa National Park (SLNP) to Ndevu Gorge, Kampeketa Range.
- Lower Luangwa Valley – Ndevu Gorge to Zambezi confluence.

The Upper Luangwa Valley was previously subdivided by Banks *et al.* (1995) into a northern and southern sub-basin separated by a wide transfer zone, but the authors did not clearly delineate the southern boundary of the northern sub-basin. The southern sub-basin is shown as ending in the vicinity of the Ndevu Gorge, meaning that the Luangwa deposits south of Ndevu Gorge stretching down to the Zambezi confluence (some few hundred kilometres) were not recognized by Banks and colleagues, despite the fact that extensive Karoo outcrop exists there.

The demarcation of Upper and Mid sections is to create a much-needed division between the classic ‘Upper Luangwa Valley’ of Drysdall & Kitching, Dixey, and Utting, and the middle reaches of the Luangwa Valley north of the Ndevu Gorge. The northern boundary of North Luangwa NP was chosen to form an expedient physical boundary (within the northern extremity of the ‘transfer zone’ of Banks *et al.*) to the west of the Luangwa River for the Upper Luangwa Valley division.

Ndevu Gorge is a natural geographical and geological end to the classic rift-like Luangwa Valley upstream of it, in that the wide, flat rift valley-like floor comes to an abrupt end with the Kampeketa range of hills, and the Luangwa is funnelled into a narrow rocky gorge before emerging just upstream of the confluence with the Lunsemfwa River, a major tributary. Accordingly it has been selected to form the southern boundary of the Mid Luangwa Valley.

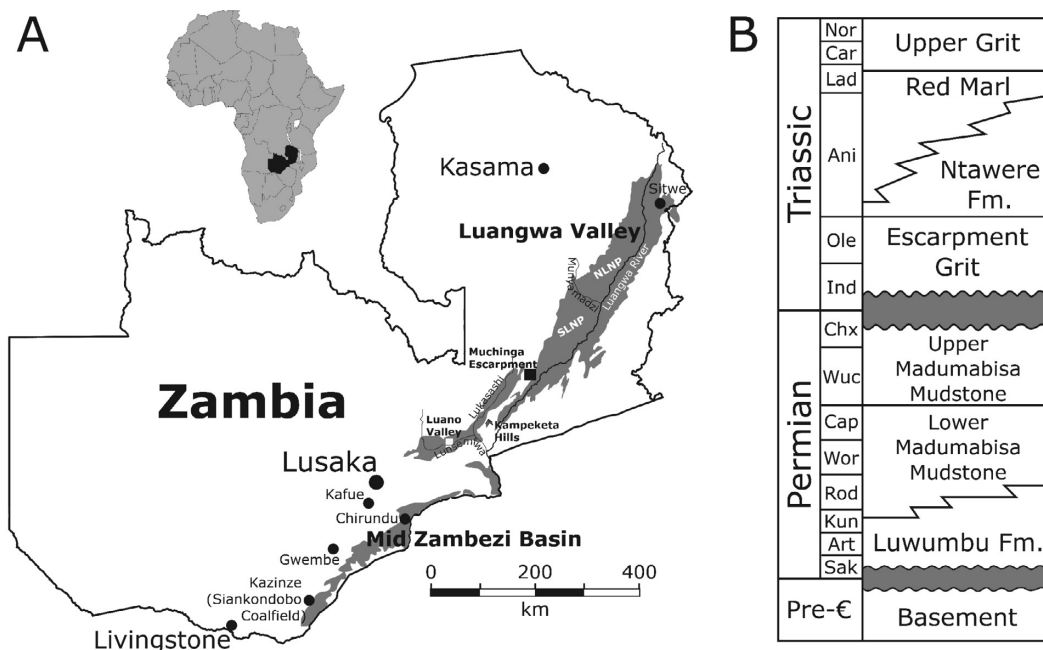


Figure 3. A, Map of Karoo fossil localities referred to in the text; B, generalized stratigraphy of Permo-Triassic rocks in Zambia (modified from Angielczyk *et al.* 2014 and Sidor *et al.* 2014). Karoo deposits are shaded in dark grey.



Figure 4. Proposed subdivision for the Luangwa Valley, showing delineations of the Upper, Mid and Lower Luangwa areas. Karoo deposits are shaded in dark grey.

PALYNOLOGY

Palynological research has mostly been carried out in Zambia by John Utting. He did his Ph.D. thesis in 1970 on the stratigraphy and palynology of the Upper Luangwa Valley, and palynology of the Siakondobo coalfield of the mid-Zambezi Valley. As well as pollen samples, Utting also collected megafloal remains, petrified wood and lamellibranchs (Fig. 5; palaeobotany discussed later in the

text), of which the former two were identified by C.S. Smith and W.S. Lacey.

Samples from Upper Karoo rocks (Escarpment Grit, Ntawere Formation, Red Marl and Upper Grit; Fig. 3) in the Upper Luangwa Valley were palynologically barren, while the Lower Karoo formations were more productive (Luwumbu Coal Formation and Lower and Upper Madumabisa Mudstone). In the Luangwa Valley, the lowermost productive unit, the Mukumba Siltstone Member, is dominated by monosaccate pollen (approximately 80%) along with trilete spores (13%) and the remainder comprising non-striate bisaccate, monocolpate and alele forms.

The monosaccates *Elilasaccites elilaensis*, *Cannanoropollis obscurus*, *Plicatipollenites indicus* and *Scheuringipollenites ovatus* (*Vesicaspora ovata*) are common, as are *Punctatisporites gretensis*, *Granulatisporites micronodosus*, *Retusotriletes diversiformis*, *Apiculatisporis filiformis*, *Acanthotriletes tereteangulatus* (recombined to *Anapiculatisporites tereteangulatus* by Playford & Dino 2002), *Cycadopites cymbatus* and *Quadratisporites horridus* (Table 1). These forms are also all found in the overlying Mpwashi Carbonaceous Member, but quantitatively this unit is very different. The lower Mpwashi Carbonaceous Member contains trilete, monolete, monosaccate, bisaccate (striate and non-striate) and polyplicate forms, none of which exceeds 25% of the assemblage. This changes in the middle part of the Mpwashi Carbonaceous Member to a predominance of triletes and striate bisaccates, with approximately 10% colpate forms (mainly *Marsupipollenites striatus*). The upper part of the Mpwashi Carbonaceous Member has common bisaccate striate and non-striate forms, the latter of which are mainly *Scheuringipollenites* (= *Vesicaspora*), and triletes make up 20–25% of the assemblages (Table 1).

Borehole samples from the Siakondobo coalfield of the mid-Zambezi Valley, Gwembe Coal Formation were also examined, and this unit displays marked qualitative

Zambian Stratigraphy	Plants	Wood	Vertebrates	Lamellibranchs	Palynomorphs	South African Correlatives
Upper Grit		cf. <i>Dadoxylon bougheyi</i> cf. <i>Araucarioxylon</i> sp. A				Stormberg
Red Marl						Molteno
Ntawere Formation	cf. <i>Schizoneura carreri</i> cf. <i>Lepidopteris africanum</i> cf. <i>Dicroidium narrabeensis</i>					Upper Beaufort Cynognathus Zone
Escarpment Grit						Middle Beaufort Lystrosaurus Zone
Upper Madumabisa Mudstone	<i>Glossopteris</i> sp. <i>Glossopteris</i> cf. <i>indica</i> ? <i>Glossopteris decipiens</i> / <i>Gangamopteris cyclopteroides</i> <i>Noeggerathiopsis hislopi</i> , <i>N. stoliczkana</i> <i>Samaropsis</i> sp.	cf. <i>Dadoxylon bougheyi</i>	Dicynodonts	Lamellibranchs Lamellibranchs	<i>Guttulapollenites hannonicus</i> <i>Lueckisporites nyakapendensis</i> <i>Vittatina africana</i> <i>Densipollenites indicus</i>	Lower Cistecephalus Zone Beaufort Endothiodon Zone Tapinocephalus Zone
Lower Madumabisa Mudstone		<i>Dadoxylon nicolii</i> <i>Dadoxylon lukugense</i>			<i>Guttulapollenites hannonicus</i> <i>Vittatina africana</i>	
Fimbia Grit Member						
Mpwashi Carbonaceous Member	<i>Vertebraria indica</i> , <i>V.</i> sp. <i>Glossopteris browniana</i> , <i>G.</i> sp., <i>G.</i> cf. <i>ampla</i> , <i>G.</i> <i>indica</i> , <i>G.</i> <i>stricta</i> ? <i>Gangamopteris</i> <i>Noeggerathiopsis hislopi</i> , <i>N.</i> sp. <i>Paracalamites australis</i> , cf. <i>Phyllothea</i> <i>Stellothea robusta</i> ? <i>Schizoneura goudwanensis</i> <i>Sphenopteris</i> sp. <i>Cordaicarpus</i> sp. cf. <i>Annularia sphenophylloides</i> <i>Samaropsis</i> cf. <i>etheridgei</i>				<i>Protohaploxypinus limpidus</i> <i>P. amplus</i> <i>Pityosporites leschiki</i> <i>Striatopodocarpites lemniscata</i> <i>S. goudwanensis</i>	E C C A
Mukumba Siltstone Member					<i>Elilasaccites</i> cf. <i>elilaensis</i> <i>Quadrifurcites horridus</i> <i>Cannanoropollis obscurus</i> <i>Plicatipollenites indicus</i>	DWYKA / ECCA
Musipizi Conglomerate Member	Indet. fragments	Indet. fragments				

Figure 5. Stratigraphic occurrences of palynomorphs, macroplant and vertebrate fossils in Karoo deposits of Zambia (redrawn from Utting 1970 with taxonomic modifications by Lacey & Smith 1972; Lacey 1974).

differences between the upper, middle and lower parts. The lower Gwembe Formation is dominated by trilete spores, with small proportions of monoletes, monosaccates and bisaccates. In the middle Gwembe Formation, triletes decrease markedly and non-striate bisaccate forms, mainly *Scheuringipollenites* (= *Vesicaspora*) are dominant in some samples. The upper Gwembe Formation contains common triletes again as well as alete forms, while all other groups are either present in minor proportions or entirely absent. Utting attributed these marked quantitative changes to a change of facies that occurs from the top to the bottom of the Gwembe Formation. Megaspores were also recovered from the Gwembe Coal formation, and tentatively identified by Dr E. Spinner of the Department of Geology, University of Sheffield. Taxa include *Carruthersiella* cf. *trivedii* Pant and Srivastava, 1962 (= *Biharisporites trivedii* (Dykstra) Pierart 1961), *Duosporites* sp., *Cystosporites* sp., and *Mammilaespora* cf. *superba* Pant and Srivastava, 1961.

The Lower Madumabisa Mudstone is quantitatively very different from the underlying Mpwashi Carbonaceous Member and dominated by *Guttulapollenites hannonicus* and *Vittatina africana*, along with other bisaccate striate and non-striate taxa such as *Protohaploxypinus amplus*, *P. limpidus*, *P. goraiensis*, *Striatopodocarpites lemniscata* and *Scheuringipollenites ovatus* (Table 1). Upper Madumabisa Mudstone samples were from the area mapped by Drysdall and Kitching in 1963, said to be from the *Cistecephalus* zone. They are dominated by taxa such as *Lueckisporites nyakapendensis*, *Vittatina africana*, *Guttulapollenites hannonicus*, *Protohaploxypinus limpidus* and *Densipollenites indicus* (Table 1). Both the Lower and Upper Madumabisa assemblages are similar in species composition, but can be differentiated on the high

proportion of *L. nyakapendensis* in the Upper unit.

The Mukumba Siltstone assemblage can be correlated with that of the Elila River glacial and periglacial beds, Congo (Bose & Kar 1966). Palynomorphs of the Mpwashi Carbonaceous Member in the Luangwa Valley are similar to those of the lower and middle Gwembe Coal Formation, mid-Zambezi Valley, Zambia. The upper Mpwashi Carbonaceous Member and lower to middle Gwembe Coal Formation are palynologically comparable to the K₂e₂ complex, Ketewaka-Mchuchuma coalfield, Tanzania (Hart 1965), and the lower part of the Mpwashi Carbonaceous Member is similar to K₂e₁. Assemblages from the upper part of the Gwembe Coal Formation resemble those from the Black Shales of Lukuga, Congo (Kar & Bose 1967). Palynomorphs of the Madumabisa Mudstone assemblages can be correlated with those from the Lower Sakamena Beds of Madagascar (Goubin 1965). In particular, the *Cistecephalus* zone of the Upper Madumabisa Mudstone has been tentatively correlated with zone IsC in the upper part of the Lower Sakamena beds, Madagascar.

Utting (1976) extended his doctoral research by sampling the type sections of the Mpwashi Carbonaceous and Mukumba Siltstone members of the Upper Luangwa Basin. In a paper published in 1976 he described two distinct palynological assemblages, with the lower Mukumba Siltstone Member dominated by the monosaccates *Cannanoropollis* and *Plicatipollenites*, and the overlying Mpwashi Carbonaceous Member (containing thin coal seams) yielding a diverse microflora dominated by striate and non-striate bisaccate pollen and trilete spores, but also containing monosaccates, polyapertures, colpates, monoletes and alete spores (Table 2). The most common taxa are *Protohaploxypinus*, *Scheuringipollenites* (= *Vesicaspora*) and *Acanthotriletes*, while *Cannanoropollis* is abun-

Table 1. Palynomorphs of the Upper Luangwa and mid-Zambezi Valleys. Redrawn from Utting (1970).

	LUANGWA VALLEY		MID-ZAMBEZI VALLEY	LUANGWA VALLEY	
	Mukumba Siltstone Member	Mpwashi Carbonaceous Member	Gwembe Coal Formation	Lower Madumabisa Mudstone	Upper Madumabisa Mudstone
<i>Anapiculatisporites tereteangulatus</i> Playford & Dino 2002 (= <i>Acanthotriletes tereteangulatus</i> Balme & Hennelly 1956)	X	X	X		
<i>Anaplanisporites levis</i> Balme & Hennelly 1956		X	X		
<i>Baculatisporites bharadwaji</i> Hart 1963		X	X		
<i>Brevitriletes cornutus</i> (Balme & Hennelly) Backhouse 1991 (= <i>Apiculatisporis cornutus</i> (Balme & Hennelly) Høeg and Bose 1960)		X	X		X
<i>Boutakoffites elongates</i> Bose & Kar 1966		X	X		
<i>Cannanoropollis</i> (= <i>Virkkipollenites</i>) <i>corius</i> Bose & Kar 1966			X		
<i>Cannanoropollis janaki</i> Potonié & Sah 1960 (= <i>Virkkipollenites obscurus</i> Lele 1964)	X	X	X		
<i>Converrucosisporites pseudoreticulatus</i> (Balme & Hennelly) Modie 2007 (= <i>Verrucosisporites pseudoreticulatus</i> Balme & Hennelly 1956; <i>Pseudoreticulatispora pseudoreticulata</i> (Foster & Waterhouse) Millstead 1999)		X	X		
<i>Cycadopites cymbatus</i> (Balme & Hennelly) Segroves 1970	X	X	X		
<i>Cycadopites nevesii</i> (Hart) Hart 1965		X	X		
<i>Deltoidospora lukagaensis</i> (Kar & Bose) Falcon 1975 (= <i>Leiotriletes lukagaensis</i> Kar & Bose 1967)			X		
<i>Deltoidospora directa</i> (Balme & Hennelly) Norris 1965 (= <i>Leiotriletes directus</i> Balme & Hennelly 1956)		X	X		
<i>Densipollenites indicus</i> Bharadwaj 1962					X
<i>Diatomozonotriletes</i> sp. (Naumova) Playford 1963			X		
<i>Elilasaccites elilaensis</i> Bose & Kar 1966	X	X			
<i>Granulatisporites micronodosus</i> Balme & Hennelly 1956	X	X	X		
<i>Granulatisporites trisinus</i> Balme & Hennelly 1956		X	X		X
<i>Greineriellites</i> sp. Bose & Kar 1967			X		
<i>Guttulapollenites hannonicus</i> Goubin 1965				X	X
<i>Horriditriletes filiformis</i> (Balme & Hennelly) Backhouse 1991 (= <i>Apiculatisporis filiformis</i> Balme & Hennelly 1956; <i>Acanthotriletes filiformis</i> (Balme & Hennelly 1956) Tiwari 1965)	X	X	X		
<i>Horriditriletes ramosus</i> (Balme & Hennelly) Bharadwaj & Salujha 1964 (= <i>Neoraistrickia ramosa</i> (Balme & Hennelly) Hart 1960)		X	X		
Incertae sedis A			X		
Incertae sedis B			X		
<i>Kraeuselisporites apiculatus</i> Jansonius 1962		X	X		
<i>Laevigatosporites desmoinesensis</i> (Wilson & Coe) Schopf, Wilson & Bentall 1944		X	X		
<i>Lophotriletes rectus</i> Bharadwaj & Salujah 1964		X	X		
<i>Lueckisporites nyakapendensis</i> Hart 1960		X		X	X
<i>Lycospora</i> sp. A Schemel 1951			X		
<i>Marsupipollenites striatus</i> (Balme & Hennelly) Hart 1965		X			
<i>Microbaculatisporites gondwanensis</i> Bharadwaj 1962			X		
<i>Parasaccites</i> sp. Bharadwaj & Tiwari 1964	X	X	X		
<i>Pilasporites calculus</i> Balme & Hennelly 1956		X	X		

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Table 1 (continued)

	LUANGWA VALLEY		MID-ZAMBEZI VALLEY	LUANGWA VALLEY	
	Mukumba Siltstone Member	Mpwashi Carbonaceous Member	Gwembe Coal Formation	Lower Madumabisa Mudstone	Upper Madumabisa Mudstone
<i>Pityosporites fuscus</i> Utting 1970				X	X
<i>Pityosporites leschiki</i> Hart 1964		X	X		
<i>Plicatipollenites indicus</i> Lele 1964	X	X	X		
<i>Potonieisporites granulatus</i> Bose & Kar 1966		X	X		
<i>Primuspollenites levis</i> Tiwari 1964		X	X		
<i>Protohaploxypinus amplus</i> (Balme & Hennelly) Hart 1964		X	X	X	X
<i>Protohaploxypinus goraiensis</i> Hart 1964		X	X	X	X
<i>Protohaploxypinus limpidus</i> (Balme & Hennelly) Balme & Playford 1967		X	X	X	X
<i>Protohaploxypinus perfectus</i> (Naumova ex Kara-Murza) Samoilovich 1953			X		
<i>Protohaploxypinus samoilovichii</i> (Jansonius) Hart 1964		X			
<i>Punctatisporites gretensis</i> Balme & Hennelly 1956	X	X	X		
<i>Quadrisporites horridus</i> (Hennelly) Potonié & Lele 1961	X		X		
<i>Retusotriletes diversiformis</i> (Balme & Hennelly) Bharadwaj 1962	X	X	X		
<i>Scheuringipollenites maximus</i> (Hart) Tiwari 1973 (= <i>Vesicaspora potoniei</i> Lakhanpal, Sah & Dube 1960)		X	X	X	X
<i>Scheuringipollenites ovatus</i> (Balme & Hennelly) Foster 1979 (= <i>Vesicaspora ovata</i> (Balme & Hennelly) Hart 1960)	X	X	X	X	X
<i>Striatopodocarpites communis</i> (Wilson) Hart 1964		X			X
<i>Striatopodocarpites gondwanensis</i> (Lakhanpal, Sah & Dube) Hart 1964		X	X		
<i>Striatopodocarpites lemniscata</i> (Wilson) Hart 1964		X	X	X	X
<i>Striatopodocarpites secretus</i> (Bharadwaj) Hart 1964		X			
<i>Striomonosaccites</i> sp. Bharadwaj 1962					X
<i>Tetraporina horologia</i> (Staplin) Playford 1963			X		
<i>Triquitrites verrucosus</i> Alpern 1958			X		
<i>Verrucosiporites triseatus</i> Balme & Hennelly 1956			X		
<i>Vestigisporites hennellyi</i> Hart 1960		X			
<i>Vestigisporites methoris</i> Hart 1960		X	X		
<i>Vestigisporites thomasi</i> (Pant) Hart 1960		X			
<i>Vittatina africana</i> Hart 1966		X		X	X
<i>Vittatina africana</i> Hart 1966 (withdrawal of intexine)					X
<i>Vittatina subsaccata</i> (Samoilovich) Jansonius 1962		X			
<i>Zinjispora zonalis</i> Hart 1963		X			

dant in the lower section of the younger assemblage. The microfloras show similarities to the upper part of the Lower Coal Measures of the Ketewaka/Mchuchuma coal-field of Tanzania, but an age for the Luwumbu Coal Formation was not able to be confidently determined based on the palynology.

A species comparison of the palynological assemblages obtained by Utting in 1970 and 1976 (Table 3) shows 8 species in common for the samples from the lower

Mukumba Siltstone (combined total of 43 species), and 26 species in common from the overlying Mpwashi Carbonaceous Member (combined total of 107 species). This low overlap of taxa suggests localized microhabitats in the Luangwa Valley during Permian times.

Utting (1978) recorded the palynology of three boreholes in the Lower Karoo Siankondobo Sandstone and Gwembe Coal formations (comprising the Maamba Sandstone Member, Main Coal Seam and Carbonaceous

Table 2. Qualitative comparison of the Mukumba and Mpwashu assemblages of the Upper Luangwa Valley. Redrawn from Utting (1976).

	Mukumba Siltstone Member	Mpwashu Carbonaceous Member
<i>Botryococcus</i> sp. Kützing 1849	+	–
<i>Cannanoropollis densus</i> (Lele) Bose & Maheshwari 1968	+	–
<i>Høegiasaccites transitus</i> Bose & Kar 1966	+	–
<i>Lunatisporites brevis</i> Bose & Kar 1966	+	–
<i>Pityosporites</i> cf. <i>P. lucidus</i> Hart 1965	+	–
<i>Plicatipollenites trigonalis</i> Lele 1964	+	–
<i>Converrucosporites naumoviae</i> (Hart) Backhouse 1991 (= <i>Verrucosporites naumovae</i> Hart 1963)	+	–
<i>Vittatina</i> sp. Luber ex Jansonius 1962	+	–
? <i>Granulatisporites trisinus</i> Balme & Hennelly 1956	+	+
<i>Anapiculatisporites tereteangulatus</i> Playford & Dino 2002 (= <i>Acanthotriletes tereteangulatus</i> Balme & Hennelly 1956)	+	+
<i>Cannanoropollis</i> (= <i>Virkkipollenites</i>) <i>corius</i> Bose & Kar 1966	+	+
<i>Cannanoropollis mehtae</i> (Lele) Bose & Maheshwari 1968	+	+
<i>Cannanoropollis janaki</i> Potonié & Sah 1960 (= <i>Virkkipollenites obscurus</i> Lele 1964)	+	+
<i>Cycadopites cymbatus</i> (Balme & Hennelly) Segroves 1970	+	+
<i>Cyclogranisporites gondwanensis</i> Bharadwaj & Salujha 1964	+	+
<i>Deltoidospora directa</i> (Balme & Hennelly) Norris 1965 (= <i>Leiotriletes directus</i> Balme & Hennelly 1956)	+	+
<i>Deltoidospora lukagaensis</i> (Kar & Bose) Falcon 1975 (= <i>Leiotriletes lukagaensis</i> Kar & Bose 1967)	–	+
<i>Deltoidospora</i> (= <i>Leiotriletes</i>) <i>plicatus</i> Maheshwari & Bose 1969	+	+
<i>Granulatisporites micronodosus</i> Balme & Hennelly 1956	+	+
<i>Horriditriletes filiformis</i> (Balme & Hennelly) Backhouse 1991 (= <i>Apiculatisporis filiformis</i> Balme & Hennelly 1956; <i>Acanthotriletes filiformis</i> (Balme & Hennelly 1956) Tiwari 1965)	+	+
<i>Neoraistrickia congoensis</i> Kar & Bose 1967	+	+
<i>Parasaccites bilateralis</i> Tiwari 1965	+	+
<i>Pilasporites plurigenus</i> Balme & Hennelly 1956	+	+
<i>Plicatipollenites gondwanensis</i> Lele 1964	+	+
<i>Plicatipollenites indicus</i> Lele 1964	+	+
<i>Protohaploxylinus limpidus</i> (Balme & Hennelly) Balme & Playford 1967	+	+
<i>Punctatisporites gretensis</i> Balme & Hennelly 1956	+	+
<i>Punctatisporites minutus</i> (Kosanke) Peppers 1964	+	+
<i>Scheuringipollenites ovatus</i> (Balme & Hennelly) Foster 1979 (= <i>Vesicaspora ovata</i> (Balme & Hennelly) Hart 1960)	+	+
<i>Converrucosporites pseudoreticulatus</i> (Balme & Hennelly) Modie 2007) (= <i>Verrucosporites pseudoreticulatus</i> Balme & Hennelly 1956; <i>Pseudoreticulatispora pseudoreticulata</i> (Foster & Waterhouse) Millstead 1999)	+	+
<i>Vestigisporites methoris</i> Hart 1960	+	+
<i>Zinjisorites eccensis</i> Hart 1965	+	+
<i>Acanthotriletes bellus</i> Bose & Kar 1966	–	+
<i>Acanthotriletes</i> sp. Naumova ex Potonié & Kremp 1954	–	+
<i>Brevitriletes cornutus</i> (Balme & Hennelly) Backhouse 1991 (= <i>Apiculatisporis cornutus</i> (Balme & Hennelly) Høeg and Bose 1960)	–	+
<i>Baculatisporites bharadwaji</i> Hart 1963	–	+

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Table 2 (continued)

	Mukumba Siltstone Member	Mpwashi Carbonaceous Member
<i>Brevitriteles levis</i> (Balme & Hennelly) Bharadwaj & Srivastava 1969 (= <i>Apiculatisporis levis</i> Balme & Hennelly 1956)	–	+
<i>Cirrabaculisporites praeclarus</i> Maheshwari & Bose 1969	–	+
<i>Cirratriletes africanensis</i> Hart 1963	–	+
<i>Cycadopites nevesii</i> (Hart) Hart 1965	–	+
<i>Grandispora dwoykensis</i> Hart 1963	–	+
<i>Greineriellites</i> sp. Bose & Kar 1967	–	+
<i>Hamiapollenites karrooensis</i> Hart 1964	–	+
<i>Hamiapollenites</i> sp. (Wilson) Tschudy & Kosanke 1966	–	+
<i>Laevigatosporites minor</i> Loose 1934	–	+
<i>Latosporites colliensis</i> (Balme & Hennelly) Bharadwaj 1962	–	+
<i>Lueckisporites nyakapendensis</i> Hart 1960	–	+
<i>Marsupipollenites striatus</i> (Balme & Hennelly) Hart 1965	–	+
<i>Horriditriteles ramosus</i> (Balme & Hennelly) Bharadwaj & Salujha 1964 (= <i>Neoraistrickia ramosa</i> (Balme & Hennelly) Hart 1960)	–	+
<i>Piceapollenites</i> sp. Potonié 1931	–	+
<i>Pityosporites leschikii</i> Hart 1964	–	+
<i>Protohaploxypinus amplius</i> (Balme & Hennelly) Hart 1964	–	+
<i>Protohaploxypinus goraiensis</i> Hart 1964	–	+
<i>Protohaploxypinus micros</i> Hart 1964	–	+
<i>Retusotriteles diversiformis</i> (Balme & Hennelly) Bharadwaj 1962	–	+
<i>Scheuringipollenites maximus</i> (Hart) Tiwari 1973 (= <i>Vesicaspora potonieii</i> Lakhapal, Sah & Dube 1960)	–	+
<i>Striatoabieites</i> sp. (Zoricheva & Sedova) Hart 1964	–	+
<i>Striatopodocarpites cancellatus</i> (Balme & Hennelly) Hart 1965	–	+
<i>Striatopodocarpites communis</i> (Wilson) Hart 1964	–	+
<i>Striatopodocarpites indicus</i> (Bharadwaj) Hart 1964	–	+
<i>Striatopodocarpites lemniscata</i> (Wilson) Marques-Toigo 1972	–	+
<i>Striomonosaccites brevis</i> Bose & Kar 1966	–	+
<i>Thymospora cicatricosus</i> (Balme & Hennelly) Hart 1965	–	+
<i>Thymospora</i> sp. Wilson & Venkatachala 1963	–	+
<i>Vesicaspora milvinus</i> (Balme & Hennelly) Hart 1965	–	+
<i>Vestigisporites gondwanensis</i> (Mehta) Hart 1965	–	+
<i>Vestigisporites hennellyi</i> Hart 1960	–	+
<i>Vittatina africana</i> Hart 1966	–	+
<i>Vittatina saccata</i> (Hart) Jansonius 1962	–	+
<i>Welwitschiapites simplex</i> Tiwari 1965	–	+

Mudstones), Kazinze, mid-Zambezi Basin. A threefold zonation was erected (Fig. 6) and these zones were correlated to the lower and upper units of the Luwumbu Coal Formation, 1000 km to the northeast, in the Upper Luangwa Valley, Zambia. Utting noted that it was not possible to recognize the three subdivisions of Zone 1 of Falcon (1975) in either the Kazinze or Upper Luangwa areas.

The Siankondobo Sandstone Formation (Zone IO) is dominated by monosaccates (*Cannanoropollis* and

Plicatipollenites) with smaller proportions of trilete spores (Fig. 6). These proportions are reversed in the Maamba Sandstone Member and the base of the Main Coal Seam, which are dominated by *Punctatisporites*, *Acanthotriletes* and *Apiculatisporis* (Zone LP). In the remainder of the Main Coal Seam and overlying Carbonaceous Mudstones, striate and non-striate bisaccates become common, particularly *Protohaploxypinus* and *Scheuringipollenites* (= *Vesicaspora*), respectively (Zone LP). The topmost beds of

Table 3. Species common to both investigations (Utting 1970, 1976) of the Mukumba Siltstone and Mpwash Carbonaceous members of the Luangwa Valley.

MUKUMBA SILTSTONE MEMBER	MPWASHI CARBONACEOUS MEMBER
<i>Anapiculatisporites tereteangulatus</i> (= <i>Acanthotriletes tereteangulatus</i>)	<i>Anapiculatisporites tereteangulatus</i> (= <i>Acanthotriletes tereteangulatus</i>)
<i>Cannanoropollis janaki</i> (= <i>Virkkipollenites obscurus</i>)	<i>Brevitriletes cornutus</i> (= <i>Apiculatisporis cornutus</i>)
<i>Cycadopites cymbatus</i>	<i>Baculatisporites bharadwaji</i>
<i>Granulatisporites micronodosus</i>	<i>Cannanoropollis janaki</i> (= <i>Virkkipollenites obscurus</i>)
<i>Horriditriletes filiformis</i> (= <i>Apiculatisporis filiformis</i> ; <i>Acanthotriletes filiformis</i>)	<i>Converrucosisporites pseudoreticulatus</i> (= <i>Verrucosisporites pseudoreticulatus</i>)
<i>Plicatipollenites indicus</i>	<i>Cycadopites cymbatus</i>
<i>Punctatisporites gretensis</i>	<i>Cycadopites nevesii</i>
<i>Scheuringipollenites ovatus</i> (= <i>Vesicaspora ovata</i>)	<i>Deltoidospora directa</i> (= <i>Leiotriletes directus</i>)
	<i>Granulatisporites micronodosus</i>
	<i>Granulatisporites trisinus</i>
	<i>Horriditriletes filiformis</i> (= <i>Apiculatisporis filiformis</i> ; <i>Acanthotriletes filiformis</i>)
	<i>Lueckisporites nyakapendensis</i>
	<i>Marsupipollenites striatus</i>
	<i>Neoraistrickia ramosa</i>
	<i>Pityosporites leschiki</i>
	<i>Plicatipollenites indicus</i>
	<i>Protohaploxypinus amplus</i>
	<i>Protohaploxypinus goraiensis</i>
	<i>Protohaploxypinus limpidus</i>
	<i>Punctatisporites gretensis</i>
	<i>Retusotriletes diversiformis</i>
	<i>Scheuringipollenites ovatus</i> (= <i>Vesicaspora ovata</i>)
	<i>Scheuringipollenites maximus</i> (= <i>Vesicaspora potonieii</i>)
	<i>Vestigisporites hennellyi</i>
	<i>Vestigisporites methoris</i>
	<i>Vittatina africana</i>

GS 31 (Zone AV) contain an incursion of acritarchs (referred to as Incertae sedis by Utting) including *Tetraporina* sp., *Circulisporites* sp., *C. parvus*, *Pilasporites plurigenus*, *Quadrisporites horridus* and *Peltacystia* sp., as well as zonotrilete spores such as *Gondisporites vrystaatensis* (Fig. 6). Rare elements include the bisaccates *Alisporites tenuicarpus* and *Hamiapollenites* sp., and the polyplicate pollen *Vittatina africana*. This zone is not recognized in the Upper Luangwa and most likely represents a localized damp terrestrial environment (Barbolini 2014).

The work of Utting (1978) was supplemented by further palynological investigations by Nyambe & Utting (1997) who also sampled the younger Madumabisa Mudstone and Interbedded Sandstone and Mudstone formations as well as the subordinate Karoo formations of Kazinze area, mid-Zambezi Basin, Zambia. Monosaccate palynomorphs dominate the *Plicatipollenites indicus*–*Cannanoropollis obscurus* Zone, encompassing the basal Siankondobo Sandstone Formation (Fig. 7). Utting (1978) correlated this lowermost zone to Zone 1 of Falcon (1975); however, Césari (2007) suggested that due to the presence of *Vittatina* sp. and *Converrucosisporites confluens*, Zone IO is better correlated with Subzone C, Zimbabwe (Falcon 1975). The overlying *Apiculatisporis levis*–*Vesicaspora potonieii* (LP) Zone of Utting (1978), which spans the Gwembe Coal Formation, is renamed the *Brevitriletes levis*–*Scheuringipollenites maximus* Zone by Nyambe & Utting (1997) to reflect updated taxonomy (Fig. 7). Microfloras indicate ages of late Carboniferous (Gzhelian) to early

Permian (Asselian to early Sakmarian) for the Siankondobo Sandstone Formation, early Permian (Artinskian to Kungurian) age for the Gwembe Coal Formation, late Permian (Lopingian) age for the Madumabisa Mudstone, and early or Middle Triassic (late Scythian or Anisian) age for the Interbedded Sandstone and Mudstone (Nyambe & Utting 1997). The early Permian (Artinskian to Kungurian) age assigned to the Gwembe Coal Formation stems from palynological correlations with Assemblage zone III of the mid-Zambezi Valley, Zimbabwe (Falcon 1975) and the Mchuchuma Formation (K2) of Tanzania, of middle Ecca age (Wopfner & Kreuser 1986). MacRae (1988) correlated the upper part of the *Brevitriletes levis*–*Scheuringipollenites maximus* Zone with Biozone D of the Waterberg, South Africa, indicating a late Artinskian to Kungurian age for the Gwembe Coal Formation. The late Permian age assigned to the overlying Madumabisa Mudstone, which can be correlated with the Tatarian-aged *Cistecephalus* reptile zone of the Upper Luangwa (Utting 1979), is equivalent to strata in southern Africa on the basis of microfloral correlation, including the Madumabisa Shale Formation of Zimbabwe (Nyambe & Utting 1997).

PALAEOBOTANY

Megafloras

The first account of Permian fossil plants in Zambia seems to have been Molyneux (1909), who reported species

<i>Plicatipollenites indicus</i> - <i>Cannanoropollis obscurus</i> Zone (IO)	<i>Apiculatisporis levis</i> - <i>Vesicaspora potonieii</i> Zone (LP)	<i>Vittatina africana</i> - <i>Gondisporites vrystaatensis</i> Zone (AV)
<i>Anapiculatisporites tereteangulatus</i> (= <i>Acanthotriletes tereteangulatus</i>) <i>Brevitriletes cornutus</i> (= <i>Apiculatisporis cornutus</i>) <i>Cannanoropollis</i> (= <i>Virkkipollenites</i>) <i>corius</i> <i>Cannanoropollis</i> (= <i>Virkkipollenites</i>) <i>densus</i> <i>Cannanoropollis janaki</i> (= <i>Virkkipollenites obscurus</i>) <i>Cycadopites cymbatus</i> <i>Deltoidospora directa</i> (= <i>Leiotriletes directus</i>) <i>Granulatisporites micronodulosus</i> <i>?Granulatisporites trisinus</i> <i>Laevigatosporites minor</i> <i>Incertae sedis A</i> <i>Parasaccites bilateralis</i> <i>Pilasporites plurigenus</i> <i>Plicatipollenites indicus</i> <i>Plicatipollenites trigonalis</i> <i>Protohaploxypinus limpidus</i> <i>Protohaploxypinus goraiensis</i> <i>Protohaploxypinus micros</i> <i>Striatopodocarpites</i> sp. <i>Protohaploxypinus varius</i> <i>Punctatisporites gretensis</i> <i>Scheuringipollenites ovatus</i> (= <i>Vesicaspora ovata</i>) <i>Tetraporina</i> sp. <i>Converrucosiporites pseudoreticulatus</i> (= <i>Verrucosiporites pseudoreticulatus</i>) <i>Vestigisporites methoris</i> <i>Vittatina</i> sp. <i>Zinjisorites eccensis</i>	<i>Horriditriletes filiformis</i> (= <i>Acanthotriletes filiformis</i>) <i>Acanthotriletes</i> sp. <i>Baculatisporites bharadwajii</i> <i>Brevitriletes levis</i> (= <i>Apiculatisporis levis</i>) <i>Cirratiradites africanensis</i> <i>Cycadopites nevesii</i> <i>Granulatisporites</i> sp. <i>Laevigatosporites collensis</i> <i>Lophotriletes rectus</i> <i>Marsupipollenites striatus</i> <i>Horriditriletes ramosus</i> (= <i>Neoraistrickia ramosa</i>) <i>Pityosporites leschikii</i> <i>Potonieisporites granulatus</i> <i>Protohaploxypinus amplus</i> <i>Protohaploxypinus diagonalis</i> <i>Protohaploxypinus lemniscata</i> <i>Retusotriletes diversiformis</i> <i>Scheuringipollenites maximus</i> (= <i>Vesicaspora potonieii</i>) <i>Striatopodocarpites cancellatus</i> <i>Striatopodocarpites rarus</i> <i>Striomonosaccites</i> sp. <i>Vitreisporites pallidus</i> <i>Vittatina saccata</i>	<i>Alete</i> type I <i>Alisporites tenuicarpus</i> <i>Circulisporites parvus</i> <i>Circulisporites</i> sp. <i>Gondisporites vrystaatensis</i> <i>Hamiapollenites</i> sp. <i>Ouadrissporites horridus</i> <i>Peltacystia</i> sp. <i>Vittatina africana</i> <i>*(species) = form common, but less frequent than dominant group</i>
Monosaccates *(triletes)	Triletes *(monosaccates)	Triletes and bisaccates dominant
Siankondobo Sandstone Formation	Maamba Sst Member	Main Coal Seam
Carbonaceous mudstones with thin coal seams		
77m	58m	53m
		47m
		13m
		0m

Figure 6. Concurrent range zones of the Siankondobo Sandstone and Gwembe Coal formations, Kazinze, mid-Zambezi Basin, Zambia. Redrawn from Utting (1978).

of *Gangamopteris* McCoy 1847, *Glossopteris* Brongniart 1828 and *Schizoneura* Hartig 1837 from the Luano area, and *Glossopteris indica* (Brongniart) Schimper 1869 from the Lufua River valley and its tributaries south of Kafue in the mid-Zambezi Valley. *Glossopteris* and *Gangamopteris*

specimens from Zimbabwe, Zambia and Malawi are small compared to those from South Africa (Arber in Andrew & Bailey 1910; Lacey 1961), possibly due to climatic amelioration in the more northerly areas of Gondwana.

Later authors recorded macroplants from various locali-

System		Stage	Lith. Unit	Palynomorph Zone	Characteristic Taxa	Rock Unit	
Triassic	Mid	Anisian	Stormberg	?			
	Early	Scythian		Unnamed	<i>Pityosporites</i> sp., <i>Falcisporites stabilis</i> , <i>Alisporites</i> sp., <i>Sulcatisporites</i> sp., <i>Platysaccus queenslandi</i> , <i>Rimaesporites aquilonis</i> , <i>Lunatisporites pellucidus</i> , <i>Apiculatisporis</i> sp., <i>Calamospora</i> sp., <i>Verrucosisporites</i> sp., <i>Uvaesporites</i> sp., <i>Aratrisporites fischeri</i> , <i>Playfordiaspora crenulata</i> (<i>Guthoerlisporites cancellosus</i>)	Interbedded Sandstone and Mudstone Fm	
Permian	Late	Tatarian	Beaufort	Unnamed	<i>Guttulapollenites hannonicus</i> , <i>Corisaccites alutas</i> , <i>Protohaploxypinus limpidus</i> , <i>Protohaploxypinus goraiensis</i> , <i>Striatopodocarpites</i> sp., <i>Sulcatisporites prolatus</i> , <i>Vitreisporites pallidus</i> , <i>Reticuloidosporites warchianus</i> , <i>Polypodiisporites mutabilis</i> , <i>Weylandites lucifer</i> , <i>Botryococcus</i> sp.	Madumabisa Mudstone Fm	
		Kazanian					
		Ufimian					
	Early	Kungurian	Mid-Ecca		<i>Punctatisporites gretensis</i> , <i>Deltoidospora directa</i> , <i>Cirratriradites africanensis</i> , <i>Brevitriletes levis</i> , <i>Horriditriletes filiformis</i> , <i>Protohaploxypinus limpidus</i> , <i>Protohaploxypinus amplus</i> , <i>Striatopodocarpites cancellatus</i> , <i>Striatopodocarpites rarus</i> , <i>Plicatipollenites indicus</i> , <i>Scheuringipollenites maximus</i> , <i>S. ovatus</i> , <i>Vittatina saccata</i> , <i>Cycadopites cymbatus</i> , <i>Pilasporites plurigenus</i> , <i>Circulisporites</i> sp.	Gwembe Coal Fm	
		Artinskian					
		Sakmarian	Dwyka		<i>Plicatipollenites indicus</i> - <i>Cannanoropollis obscurus</i>	<i>Plicatipollenites indicus</i> , <i>Cannanoropollis obscurus</i> , <i>Brevitriletes cornutus</i> , <i>Acanthotriletes tereteangulatus</i> , <i>Zinjisporites eccensis</i> , <i>Microbaculispora micronodosa</i> , <i>Converrucosisporites pseudoreticulatus</i> , <i>Cycadopites cymbatus</i>	Siankondobo Sandstone Fm.
		Asselian					
	Carboniferous	Late	Gzhelian				

Figure 7. Palynozones of the Dwyka, Ecca, Beaufort and Stormberg groups of the mid-Zambezi Valley, southern Zambia (redrawn from Nyambe & Utting 1997). Dotted lines represent uncertainty about how far zones extend. Not to scale.

ties, including the Upper Luangwa (Dixey 1937), Lower and Upper Karoo beds at Gwembe (Gair 1959; Tavener-Smith 1958, 1960), and the Western Luano (Gair 1960). Gair (1959) recorded *Glossopteris* sp. from the Gwembe Coal Formation. Bond (1954) and Gair (1959, 1960) reported *Glossopteris indica* from the Lower and Upper Beds of the Madumabisa Mudstone in the Luano and Luangwa areas, along with *Phyllothea* sp. Brongniart 1828 in the Upper Bed. Drysdall & Kitching (1963) identified *Schizoneura* sp. and *Phyllothea* sp. from the Luwumbu Coal Formation and lowest beds of the Madumabisa Mudstone in the Upper Luangwa Valley.

Bond (1954, 1955) described lamellibranchs in association with a *Glossopteris* flora in limestones from the Gwembe area, and Lacey (1974) noted a similar assemblage from the Kafue Valley, consisting of paper shales with poorly preserved leaves (cf. *Taeniopteris* sp. Brongniart 1828) and lamellibranchs of *Palaeomutella oblongata*, *P. neglecta* and *Palaeonodonta wadei* (det. Bond).

Lacey and Smith (1972) and Lacey (1974) made slight modifications of the Ecça flora originally described by Utting (1970), consisting of 17 taxa from the Luwumbu Coal Formation and the Lower Member of the Madumabisa Mudstone in the Upper Luangwa Valley. These taxonomic modifications are presented earlier in the text (Fig. 5). The discovery of the fossil tentatively identified as *Annularia sphenophylloides* Zenker 1833 (Utting 1970; discussed by Lacey 1974) represented the first occurrence of a late Carboniferous–early Permian Russian/North American/European species in an African *Glossopteris* flora at the time. *Annularia* has since been identified in Permian deposits of South Africa (Anderson & Anderson 1985; le Roux & Anderson 1977; Prevec *et al.* 2010), Zimbabwe (Bond 1973) and Argentina (Archangelsky & Cúneo 1984). Other fossil plants collected in the Luwumbu Coal Formation are generally similar to those of other African Ecça-equivalent assemblages, but Utting (1970) and later authors (e.g. Lacey & Smith 1972; Lacey 1974) considered the presence of *Noeggerathiopsis hislopi* Feistmantel 1879 in the Upper Madumabisa Mudstone (correlated with the Lower Beaufort) to be anomalous, being that this species was thought to be restricted to the Ecça Group. To date, *N. hislopi* has been found in the Lower Beaufort Estcourt Formation (Anderson & Anderson 1985) and in Indian Permian coal fields (Srivastava & Agnihotri 2013) so cannot be used as a biostratigraphic marker.

Fragmentary fossil plants were occasionally noted in the boreholes studied by Utting (1978), and a well-preserved *Glossopteris damudica* Feistmantel 1879 leaf was identified by W.S. Lacey in borehole GS 70 of the Siankondobo Coalfield (Gwembe Coal Formation). Lacey & Lucas (1984) listed 9 fossil taxa from new collecting in the Upper Luangwa Valley: *Glossopteris indica*, *G. browniana* Brongniart 1892, *G. cf. communis* Feistmantel 1876, *G. cf. stricta* Bunbury 1861, *G. cf. ampla* Dana 1849, *G. cf. damudica*, cf. *Gangamopteris* sp., cf. *Noeggerathiopsis hislopi*, and *Neomariopteris* (= *Sphenopteris*) cf. *polymorpha* (Feistmantel) Maithy 1974. Megafloral remains indicate an Upper Ecça–Lower Beaufort age and probably derive from the Lower Madumabisa Mudstone.

Less diverse assemblages have been recovered from Triassic deposits in Zambia. Du Toit (1954) made reference to ‘typical species of *Dicroidium*’ present in the mid-Zambezi Kafue Valley (Upper Karoo), and the Western Luano Valley. Utting (1970) recorded unidentifiable plant fragments from the Ntawere and Upper Grit formations in the Upper Luangwa Valley. Lacey & Smith (1972) noted fragments similar to *Schizoneura carreri* Zeiller 1903 (= *Neocalamites carreri* (Zeiller) Halle 1908¹), *Lepidopteris africanum* (Du Toit) (= *L. stormbergensis* (Seward) Townrow 1956¹) and *Dicroidium* (= *Thinnfeldia*^{1,2}) *narrabeenensis* (Walkom) Jakob & Jakob 1950 in the Triassic Ntawere Formation, and these taxa are known from Middle Triassic ‘Molteno’ beds in other Karoo deposits of Africa (Lacey 1974). This is confirmed by the extensive records published by Anderson & Anderson (1983, 1985).

Lacey & Lucas (1984) suggested a Triassic age for deposits in the Mid Luangwa Valley on the presence of cf. *Paracalamites australis* Rigby 1966 and *Dadoxylon* cf. *sclerosum* Walton (syn. *Kaokoxylon* cf. *sclerosum* (Walton) Kräusel 1956). *Dicroidium* cf. *odontopteroides* (Morris) Gothan 1912 and *D. cf. zuberi* (Szajnoch) Archangelsky 1968 (= *Zuberia zuberi* Frenguelli 1943; Artabe 1990; illustrated in Fig. 8), *Neocalamites* cf. *foxii* Lele 1956, *N. cf. carreri* and *N. cf. horensis* (Schimper) 1908 were collected from the Luano Valley and Lacey & Lucas (1984) thought these specimens probably indicated a ‘Molteno age’ for the deposits (the Molteno Formation is currently thought to be Carnian – Hancox 1998).

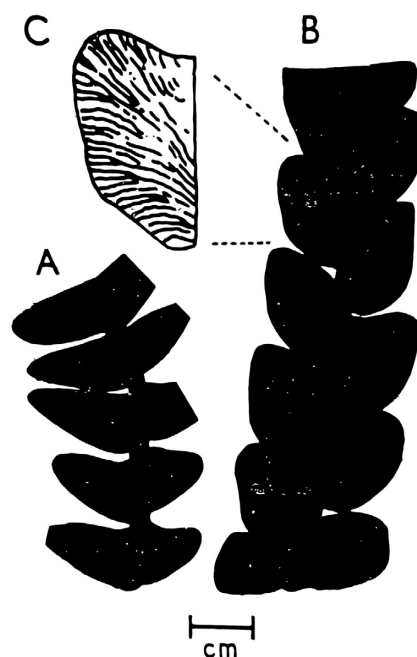


Figure 8. *Dicroidium* from the Luano Valley (reproduced from Lacey & Lucas 1984). **A**, *Dicroidium* cf. *odontopteroides* (Morris) Gothan 1912. **B**, *Dicroidium* cf. *zuberi* (= *Zuberia zuberi* Frenguelli 1943, Artabe 1990). **C**, enlargement of a single pinna from (B), illustrating shape of the pinna, wide basal attachment with numerous veins entering the pinna and dichotomous branching of the veins. Scale bar: 1 cm.

¹Synonym according to Lacey & Lucas (1972), who did not publish figures of the fossil material for re-evaluation by the present authors

²The genus *Thinnfeldia* was historically used for *Dicroidium*-like foliage until Doludenko (1971) demonstrated that the holotype for the type species was a *Pachypteris*. However, Kirchner & Müller (1992) suggested retention of the genus due to unique reproductive structures that differ slightly from those associated with *Pachypteris* (Taylor *et al.* 2009).

Fossil wood

Early geologists described fossil wood in the Luangwa Valley formations: L.A. Wallace (1907) reported 'much silicified wood' in the Mlembo and Lukasashi valleys, J.C. Molyneux (1909) reported that, 'silicified wood in fragments, or in prostrate trunks as long as 9 feet, is found in all [Karoo System] beds up to the Forest Sandstone'.

F.P. Mennell (1930) reported that silicified wood occurs in some abundance in the Upper Shales above the coal seams at various localities, particularly the Lufua River in the mid-Zambezi Valley, and stated that '[s]ilicified wood occurs in these beds in some abundance ... Near the Lusangashi River pieces can be picked up full of holes made by boring insects and looking so exactly like ordinary bits of decayed timber that their weight always gives one a sensation of surprise'.

In 1931, George Reed Downs, an American geology student, spent several months walking in the Lukasashi Valley and found Permian therapsid fossils, as well as well-preserved fossil wood (Downs 1935). He states: '[s]ilicified wood is especially abundant in the district north and northwest of Manchiti. One specimen from half a mile north of N'Kanga village along the Boma path as identified by Mr. Eltar Nielson as representing a primitive cordaitales genus'.

Dixey (1937) described 'large masses of fossil wood' from the Grey Shales and Sandstones, and the Red Pebbly Grits and Grey Grits of the Upper Luangwa Valley (thought by Lacey (1961) to be equivalent to the upper Ecce / base of the Beaufort and the lower and upper Escarpment Grit, respectively). Woods were identified by Edwards (1937) as *Dadoxylon sclerosum* (Walton) Kräusel 1956 and *Dadoxylon arberi* Seward 1919. The genus *Rhexoxylon* Bancroft 1913 was not represented. Dixey also noted abundant fossil wood material in the Red Sandstones of the Upper Luangwa Valley, equivalent to the Forest Sandstones of other areas (Lacey 1961).

In 1941, T.D. Guernsey wrote a report on the geology of the concession areas of Luangwa Concessions (N.R.) Limited, 'based on data gathered by 166 geologists who prospected and mapped approximately 156,000 square miles within Northern Rhodesia'. In the Zambezi-Kafue section of Karoo sediments, the report mentions 'fossil wood ... up to 7 ft. in diameter and 100 ft. long, is abundant'. (However, it is believed by the authors that these figures are exaggerated or a mistake).

Fossil wood was also noted by Gair (1959) and Tavener-Smith (1960) in the Madumabisa Mudstone and Escarpment Grit formations exposed in the Gwembe valley. Gair reported 'abundant fossilised logs, up to 4 feet in diameter, probably including *Dadoxylon* sp. Endlicher 1847 and *Rhexoxylon africanum* Bancroft 1913', and Tavener-Smith describes 'abundant silicified tree-trunks, up to 2 feet in diameter, with annual rings and radial structures well preserved, spread over many acres' in the Escarpment Grit Formation (The authors visited Tavener-Smith's main site in 2015 and found far bigger specimens.) Additionally, Gair (1960) noted fossil wood in Lower Karoo beds of the Western Luano Valley.

Petrified wood collected by Utting (1970) from the

Lower Madumabisa Mudstone was rarely found *in situ*, explaining why the different species suggest varying ages. *Dadoxylon sclerosum* Walton (syn. *Kaokoxylon* cf. *sclerosum* (Walton) Kräusel 1956) and *D. bondii* have been found elsewhere in Africa from Triassic beds, whilst *Dadoxylon nicolii* Seward 1917, nom. illeg. (= *Dadoxylon arberi* Seward 1919) has been found in Permian localities of Gondwana. *D. bougheyi* Williams was one of the only specimens to be found *in situ* from the Upper Madumabisa Mudstone.

In the Kafue Valley, Lacey (1974) noted *Rhexoxylon africanum* Bancroft from the sandstone/grit unit overlying the cf. *Taeniopteris*-lamellibranch assemblage contained in a paper shale unit. As *Rhexoxylon* was considered to be consistent with an 'Upper Madumabisa Mudstone age', the sandstone/grit unit was thought by Lacey (1974) to be the equivalent of the Escarpment Grit elsewhere in Zambia.

Most recently, Lacey & Lucas (1984) recorded *Dadoxylon* cf. *sclerosum* from Triassic deposits in the Mid Luangwa Valley. These woods need to be revised because the genus *Dadoxylon* is now treated as a junior synonym of *Agathoxylon* Hartig (Rößler *et al.* 2014) and there is confusion over *D.* (= *Kaokoxylon*) *sclerosum* and its age range.

CONCLUSIONS

The Karoo deposits of Zambia preserve a rich record of fossilized plants, pollen and wood. John Utting investigated the palynology of both the mid-Zambezi and Luangwa Valleys, while William Lacey was mainly responsible for publications on Permian and Triassic fossil plants. The fossil wood has not been comprehensively researched, with only a few identifications made by Edwards and Lacey, but for the most part, simply noted as occurring over wide areas throughout the country. The palaeobotanical record of Zambia would benefit greatly from a detailed study into both Permian and Triassic woods, as well as further research on the macroplants and pollen to augment existing studies. A new standardized subdivision for the Luangwa Valley is proposed herein, which clarifies naming discrepancies in previous works and should assist in future correlations between different Gondwana basins.

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REFERENCES

- ANDERSON, H.M. & ANDERSON, J.M. 1983. Palaeoflora of southern Africa: Molteno Formation (Triassic), Vol. 1: Part 1, Introduction, Part 2, Dicroidium. Rotterdam, Balkema. 227 pp.
- ANDERSON, H.M. & ANDERSON, J.M. 1985. *Palaeoflora of Southern Africa: Prodomus of South African Megaflores, Devonian to Lower Cretaceous*. Balkema, Rotterdam.
- ANDREW, A. & BAILEY, T. 1910. The geology of Nyasaland. *Quarterly Journal of the Geological Society* 66(1-4), 189-237.
- ANGIELCZYK, K.D., STEYER, J.S., SIDOR, C.A., SMITH, R.M.H., WHATLEY, R.L. & TOLAN, S.C. 2014. Permian and Triassic dicynodont (Therapsida: Anomodontia) faunas of the Luangwa Basin, Zambia: taxonomic update and implications for dicynodont biogeography and biostratigraphy, pp. 93-138 In: C. F. Kammerer, K. D. Angielczyk, & J. Fröbisch (eds), *Early Evolutionary History of the Synapsida*. Springer, Dordrecht.

- ARCHANGELSKY, S. & CÚNEO, R. 1984. Zonacion del Permico continental de Argentina sobre la base de sus plantas fosiles. *Memoria III Congreso Latinoamericano Paleontologia*, 143–158.
- ARTABE, A.E. 1990. Revalidación del genero triasico *Zuberia* Frenguelli 1943, familia *Corystospermaceae*. *Revista del Museo de la Plata (NS), Paleontologia*, **9**(55), 145–157.
- ASTLE, W.L. 1999. A history of wildlife conservation and management in the mid-Luangwa Valley. *British Empire & Commonwealth Museum*, 149.
- BANKS, N.L., BARDWELL, K.A. & MUSIWA, S. 1995. Karoo rift basins of the Luangwa Valley, Zambia. *Geological Society of London Special Publication* **80**, 285–295.
- BARBOLINI, N. 2014. *Palynostratigraphy of the South African Karoo Supergroup and correlations with coeval Gondwanan successions*. Ph.D. thesis, University of the Witwatersrand, Johannesburg, South Africa.
- BOND, G. 1954. Lamellibranchia and plants from the lower Karoo beds of Northern Rhodesia. *Geological Magazine* **91**(03), 189–192.
- BOND, G. 1955. The Madumabisa (Karoo) Shales in the Middle Zambezi region. *Transactions of the Geological Society of South Africa* **58**, 71–99.
- BOND, G. 1973. The palaeontology of Rhodesia. *Geological Survey of Rhodesia Bulletin* **70**, 1–121.
- BOSE, M.N. & KAR, R.K. 1966. Palaeozoic Sporae Dispersae from Congo: Part I – Kindu-Kalima and Walikale Regions. *Koninklijk Museum Voor Midden-Afrika – Tervuren, België Annalen – Reeks in-8 – Geologische Wetenschappen* – no. **53**, 1–169.
- CÉSARI, S.N. 2007. Palynological biozones and radiometric data at the Carboniferous–Permian boundary in western Gondwana. *Gondwana Research* **11**(4), 529–536.
- DIXEY, F. 1929. The Karoo of the Upper Luangwa Valley. *Nyasaland Geological Survey Annual Report for 1928*, 12.
- DIXEY, F. 1937. The geology of part of the upper Luangwa Valley, north-eastern Rhodesia. *Quarterly Journal of the Geological Society* **93**(1-4), 52–76.
- DOLUDENKO, M.P. 1971. *Thinnfeldia* – mladsii sinonim *Pachypteris*. *Paleontological Journal* **2**, 99–104.
- DOWNS, G.R. 1935. *The geology of the Lukasashi Rift Valley, Northern Rhodesia*. Unpublished Ph.D. thesis, Minnesota University, Minnesota, U.S.A.
- DRYSDALL, A.R. & KITCHING, J.W. 1963. A re-examination of the Karoo succession and fossil localities of part of the Upper Luangwa Valley. *Memoir of the Geological Survey of Northern Rhodesia* **1**, 1–62.
- DU TOIT, A.L. 1954. *The Geology of South Africa* (3rd edn). Edinburgh, Oliver and Boyd.
- EDWARDS, W.N. 1937. Fossil woods from the upper Luangwa Valley. *Quarterly Journal of the Geological Society, London* **93**, 75–76.
- FALCON, R. 1975. Palynostratigraphy of the Lower Karoo Sequence in the Central Sebungwe District., Mid-Zambezi Basin, Rhodesia. *Palaeontologia africana* **18**, 1–29.
- GAIR, H. 1959. The Karoo System and coal resources of the Gwembe District, north-east section. *Geological Survey of Northern Rhodesia Bulletin* **1**, 1–88.
- GAIR, H. 1960. The Karoo System of the Western End of the Luano Valley: explanation of Degree Sheet 1431, NE. Quarter. *Report of the Geological Survey of Northern Rhodesia* **6**.
- GOUBIN, N. 1965. Description et repartition des principaux pollenites Permians, Triassiques et Jurassiques des sondages du Basin de Morondava (Madagascar). *Revue de l'Institut Français du Pétrole* **20**, 1415–1461.
- GUERNSEY, T.D. 1941. Synopsis of summary report on the geology of the concession areas of Loangwa Concessions (N.R.) Limited and Rhodesia Minerals Concession Limited Northern Rhodesia. Unpublished manuscript, Broken Hill, N.R., 34 pp.
- HANCOX, P.J. 1998. *A stratigraphic, sedimentological and palaeoenvironmental synthesis of the Beaufort-Molteno contact in the Karoo Basin*. Ph.D. thesis, University of the Witwatersrand, Johannesburg, South Africa.
- HART, G. 1965. The systematics and distribution of Permian miospores. 252 pp. Witwatersrand University Press, Johannesburg.
- HOSTE, C.D. 1898. Explorations west of the Loangwa River. *The Geographical Journal* **XI**, 624–628 + map.
- KAR, R.K. & BOSE, M.N. 1967. Palaeozoic Sporae Dispersae from Congo: Part III – Assise des schistes noirs de la Lukuga. *Koninklijk Museum Voor Midden-Afrika – Tervuren, België Annalen – Reeks in-8 – Geologische Wetenschappen* – no. **54**, 1–60.
- KEMP, T.S. 2000. Report on a field trip to the fossil localities of the North Luangwa N.P. and Munyamadzi corridor GMA – November 2000. Unpublished report, 7 pp.
- KIRCHNER, M. & MÜLLER, A. 1992. *Umkomasia franconica* n. sp. und *Pteruchus septentrionalis* n. sp., Fruktifi kationen von *Thinnfeldia* Ettingshausen. *Palaeontographica* **224B**, 63–73.
- LACEY, W.S. 1961. Studies in the Karoo Floras of Rhodesia and Nyasaland. Part 1. Geological account of the plant-bearing deposits. *Proceedings and Transactions of the Rhodesia Scientific Association* **XLIX**, Part 1–1961, 26–53.
- LACEY, W.S. 1974. Some new African Gondwana plants. *Symposium on stratigraphic palaeobotany, Birbal Sahni Institute of Palaeobotany, Lucknow*.
- LACEY, W.S. & LUCAS, R.C. 1984. Fossil plants from the Luangwa and Luano Valleys of Zambia and their bearing on age determination. *Evolutionary Botany and Biostratigraphy (A.K. Ghosh Commemorative Volume)*, 451–461.
- LACEY, W.S. & SMITH, C.S. 1972. Studies in Karoo Floras. Part 4. Karoo Floras from the Upper Luangwa Valley, Zambia. *Proceedings of the Second International Gondwana Symposium, South Africa*, 1970.
- LE ROUX, S.F. & ANDERSON, H.M. 1977. A review of the localities and flora of the Lower Permian Karoo strata at Vereeniging, South Africa. *Palaeontologia africana* **20**, 27–42.
- MACRAE, C.S. 1988. Palynostratigraphic correlation between the lower Karoo Sequence of the Waterberg and Pafuri Coal-bearing basins and the Hammanskraal plant macrofossil locality, Republic of South Africa. *Memoirs of the Geological Survey of South Africa* **75**, 1–217.
- MASTERS, H. & MASTERS, W.E. 1920. In *Wild Rhodesia*. F. Griffiths, London. 300 pp.
- MENNELL, F.P. 1930. The Karoo system in East and Central Africa. *Int. Geol. Congress, South Africa* **XV 1929 (ii)**, 263–291.
- MOLYNEUX, A.J.C. 1909. On the Karoo system in Northern Rhodesia, and its relation to the general geology. *Quarterly Journal of the Geological Society* **65**(1-4), 408–439.
- NYAMBE, I.A. & UTTING, J. 1997. Stratigraphy and palynostratigraphy, Karoo Supergroup (Permian and Triassic), mid-Zambezi Valley, southern Zambia. *Journal of African Earth Sciences* **24**(4), 563–583.
- PREVEC, R., GASTALDO, R.A., NEVELING, J., REID, S.B. & LOOY, C.V. 2010. An autochthonous glossopterid flora with latest Permian palynomorphs and its depositional setting in the Dicynodon Assemblage Zone of the southern Karoo Basin, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* **292**(3), 391–408.
- REICHWALDER, P. & BRANDON, A. 1978. The geology of the Luano Valley area (Pt.1 The Gneiss complex and Mpanshya Group) (Pt.2, The Karoo System). *Report of the Geological Survey No. 61, Lusaka*, 1–85 + maps.
- RÖSLER, R., PHILIPPE, M., VAN KONIJNENBURG-VAN CITTERT, J.H., McLOUGHLIN, S., SAKALA, J. & ZIJLSTRA, G. 2014. Which name(s) should be used for Araucaria-like fossil wood? Results of a poll. *Taxon* **63**(1), 177–184.
- SIDOR, C.A., ANGIELCZYK, K.D., SMITH, R.M., GOULDING, A.K., NESBITT, S.J., PEEOCK, B.R., STEYER, J.S. & TOLAN, S. 2014. Tapinocephalids (Therapsida, Dinocephalia) from the Permian Madumabisa Mudstone Formation (Lower Karoo, Mid-Zambezi Basin) of southern Zambia. *Journal of Vertebrate Paleontology* **34**(4), 980–986.
- SRIVASTAVA, A. & AGNIHOTRI, D. 2013. Coal seam correlation of an Indian Gondwana coalfield: a palaeobotanical perspective. *International Journal of Coal Geology* **113**, 88–96.
- TAVENER-SMITH, R. 1958. Recent Exploration in the Kandabwe Coal Area. *Transactions of the Geological Society of South Africa* **61**, 5–17.
- TAVENER-SMITH, R. 1960. The Karoo system and coal measures of the Gwembe District, South-west Section. *Bulletin of the Geological Survey of Northern Rhodesia* **4**.
- TAYLOR, E. L., TAYLOR, T. N., & KRINGS, M. 2009. *Paleobotany: the Biology and Evolution of Fossil Plants*. Cambridge, Academic Press.
- UTTING, J. 1970. *Karoo Stratigraphy and palynology of the Upper Luangwa Valley and Lower Karoo Palynology of the Mid-Zambezi Valley, Zambia*. Ph.D. thesis, Sheffield University, Sheffield.
- UTTING, J. 1976. Pollen and spore assemblages in the Luwumbu Coal Formation (Lower Karoo) of the North Luangwa Valley, Zambia, and their biostratigraphic significance. *Review of Palaeobotany and Palynology* **21**, 295–315.
- UTTING, J. 1978. Lower Karoo pollen and spore assemblages from the coal measures and underlying sediments of the Siankondobo coalfield, Mid-Zambezi valley, Zambia. *Palynology* **2**(1), 53–68.
- UTTING, J. 1979. Pollen and spore assemblages from the Upper Permian of the North Luangwa Valley, Zambia. Paper presented at the IV International Palynological Conference, Lucknow (1976–77), 1979.
- WALLACE, L. 1907. North-Eastern Rhodesia. *The Geographical Journal* **29**(4), 369–400 + map.
- WALLER, H. 1874. *The Last Journals of David Livingstone in Central Africa from 1865 to His Death*, Volume 1. John Murray, London. 360 pp.
- WOPFNER, H. & KREUSER, T. 1986. Evidence for Late Palaeozoic glaciation in southern Tanzania. *Palaeogeography, Palaeoclimatology, Palaeoecology* **56**(3), 259–275.

Petroleum of the Deep: Palynological proxies for palaeoenvironment of deep offshore upper Miocene-Pliocene sediments from Niger Delta, Nigeria

Moshood A. Olayiwola^{1,2*} & Marion K. Bamford¹

¹Evolutionary Studies Institute (ESI), and School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS 2050, Johannesburg, South Africa

²Natural History Museum, Obafemi Awolowo University, Ile-Ife, Osun State, Nigeria

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Better understanding of the palaeoenvironments under which the lithologies of the deepwater petroleum systems were deposited is necessary to unravel the problem surrounding the deep offshore petroleum exploration and production. Therefore, the integration of palynological, lithological and gamma ray log data of ditch-cutting samples from wells A and B from the Niger Delta region are utilized to delineate the upper Miocene-Pliocene depositional environments. The detailed palynological analysis revealed diverse and abundant palynomorph assemblages, which consisted of angiosperm pollen 85.7%, monolete spores 5%, fungal elements 4%, trilete fern spores 4%, freshwater algae 1% and marine elements 0.3%. Eight informal palynological assemblage zones (PAZ I–PAZ VIII) with corresponding eustatic sea level changes are delineated in Wells A and B. Four lithofacies, namely sandstones, siltstones, claystones and mudstones, are recognized in association with three depositional environments in the studied wells. Distributary channels are characterized by the erosive base and filled with moderate to fine, uniform and blocky sand-grain size sediments that are of good reservoir quality. Mud-rich sediments, which are of excellent sealing rock potential, capped this sand formation. Moreover, tidal channels are typified by the erosive base and filled with fining-upwards sand sequences with tops covered by muddy sediments. Finally, the regressive barrier sands are filled by coarsening-upwards sediments with basal organic-rich deposits that are likely to be good quality source rock. The oil potential of these sites is of interest to the oil company and the reconstructed palaeoenvironments will be useful for deepwater exploration and exploitation, and probably remove or minimize the risks that are commonly involved in this task.

Key words: palynological proxies, palaeoenvironments, lithofacies, deep offshore, ditch-cuttings, late Miocene-Pliocene, petroleum systems, Niger Delta

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INTRODUCTION

The pursuit of petroleum resources has driven exploration and production from onshore terrains into offshore environments, which are geographically and geologically complex.

Deep-water exploration and production is a high-risk venture (Fadiya 2014). These include harsh offshore environments such as severe weather, ice and storms that pose engineering challenges to offshore drilling equipment, and risk due to incidents that may represent challenges for emergency preparedness. In addition, there are risks due to major hazards, occupational injury and illness (Vinnem 2010). The extremely high cost of maintenance of drillship/semisubmersibles, installation, and the decommissioning of the offshore structures also pose another problem to the deep-water exploration and production (Saifullah & Pudjihanto 1996; Byrd *et al.* 2014). Target missing and subsea blowout due to overpressured shale during drilling further complicates the risk and expenses for the oil and gas industry in the offshore terrain. The 2010 deepwater horizon drilling rig explosion and oil spills in the Gulf of Mexico are a typical example of this

scenario, where many lives were lost and several billions of dollars were spent to stop and clean oil spillage.

Therefore adequate knowledge of the palaeoenvironment of the petroleum system, such as source, reservoir, and cap or seal rocks of the deep offshore area, is essential to guarantee the safety of the rig personnel and marine life in particular, and to reduce the overall cost of deep offshore exploration and production (Magoon & Dow 1994; Magoon & Schmoker 2000). In order to achieve this goal, it is imperative for us to have a better understanding of the environment under which the lithologies of this petroleum system were deposited.

The common deep offshore petroleum system was the shale-sandstone interaction where shale formed the source and seal rocks and sandstone formed the reservoir rock. The Gulf of Mexico (McDade *et al.* 1973; Hood *et al.* 2002), Niger Delta (Ekweozor & Daukoru 1994; Kulke 1995; Tuttle *et al.* 1999) and Bengal (Shamsuddin *et al.* 2001) basins are typical examples of this system. However, limestone occasionally can serve as both cap rock, when its matrix is tightly connected, and reservoir rock when it is fractured (Shamsuddin *et al.* 2001). Evaporite is, in addi-

tion, a potential deep-water reservoir rock (Hood *et al.* 2002). The shale-sandstone facies which generally make up the petroleum system elements occur either as transgressive-regressive sequences during the gradual rise and fall of the sea level relative to the land, or as turbidite deposits in deepwater offshore (Tuttle *et al.* 1999; Hood *et al.* 2002).

During the sea level rise the fining- or deepening-upward sediment sequences will be formed in the subaerial delta plain as channels, inter-distributary bay, crevasse splay and levee deposits (Horne *et al.* 1978; Coleman & Prior 1981). In contrast, coarsening- or shallowing-upward sediment sequences will be deposited during sea-level fall in the subaqueous delta plain that comprises distributary-mouth-bar, river-mouth tidal-ridge and subaqueous slump deposits (Coleman & Prior 1981). High representation of coastal miospores such as those from mangrove, beach, brackish and rainforest environments compared to minimal hinterland miospores, i.e. savanna and montane types, characterize subaerial sediments that were deposited during sea level rise; the opposite represents sea level fall (Morley 1995; Rugmaia *et al.* 2008).

Variations in the abundance of some spore and pollen taxa relate well to changes in eustatic sea-level and hence palynological analyses offer a proxy for the understanding of sea-level rise and fall (Poumot 1989; Morley *et al.* 2004). For instance, low eustatic sea level that is correlated with dry climatic conditions is characterized by an abundance of Poaceae pollen whereas mangrove pollen is predominant during transgressive-highstand that suggests humid climatic intervals (Morley & Richard 1993). For instance, low eustatic sea level that is correlated with dry climatic conditions is characterized by an abundance of Poaceae pollen, whereas mangrove pollen is predominant during transgressive-highstand that suggests humid climatic intervals (Morley & Richard 1993), or retreat of mangroves with rising sealevel and humid conditions (Ellison 1993, 2008).

Many other authors have also successfully employed the relative diversity and abundance of palynomorphs that make up the lithologies of different petroleum systems to reconstruct the palaeoenvironment of their deposition in different basins worldwide. Prominent among these are the Niger Delta Basin (Obob 1992, 1995; Obob *et al.* 1992; Durugbo *et al.* 2010), Sergipe Basin (Carvalho 2001, 2004), Barmer Basin (Tabaei & Singh 2002), McMurray Formation (Demchuk *et al.* 2008), Bornu Basin (Ola-Buraimo & Boboye 2011; Ayinla *et al.* 2013), Anambra Basin (Ola-Buraimo & Akaegbobi 2012), Dahomey Basin (Durugbo & Aroyewun 2012; Adeigbe *et al.* 2013), Larsen Basin (Carvalho *et al.* 2013) and the Gulf of Mexico (Barron & Obob-Ikuenobe 2014). In particular, Obob (1992) used palynomorphs from the middle Miocene onshore Kolo Creek Field to show that the depositional conditions were similar to today's but the climate was somewhat drier. Pollen and dinoflagellate cysts from cores from the western Niger Basin (Durugbo *et al.* 2010) showed that the Plio-Pleistocene (5.0–1.3 Ma) environment was mostly dry and there were two cooling events, possibly related to global glacial events, at –2.7 Ma and

2.0 Ma. In depth correlations by Evamy and colleagues (1978) and Morley & Richard (1993) are used as the framework for correlations in this project.

Data other than palynology have also been helpful for palaeoenvironmental reconstructions (Morley 1986). For example, gamma ray log and lithological data have been employed to delineate sub-environments of deposition such as distributary channel fill, lagoon and tidal delta, coastal barrier and delta fringe in the Niger Delta Basin, Nigeria (Obob 1990, 1991, 1992, 1993, 1995). Seismic data is another useful tool for delineating the depositional environment (Owoyemi & Willis 2006).

The value of palaeoenvironmental interpretation in oil exploration is immense and is a major contributor to the characterization of facies, which may be of reservoir, source and seal rock potentials. Therefore palaeoecological studies will significantly increase the precision and resolution of the palaeoenvironmental interpretation that can provide templates for the distribution of lithologies and reservoir qualities to aid in the vertical and horizontal planning of wells' development (Bann *et al.* 2004; Powell & Riding 2005; Gregory *et al.* 2007).

Most previous research has been concentrated on the onshore deposits. The aim of this study, therefore, is to use the integration of palynological, lithological and gamma ray log data of ditch-cutting samples from Wells A and B from the deep offshore Niger Delta to delineate the past depositional environments or shoreline positions. This will provide a better understanding of the complex nature of the subsurface geology that is usually associated with the deep offshore settings. The findings of this study will enhance the exploration and exploitation of hydrocarbon in particular, and basin analysis in general, in the deep-water environments.

Geological setting of the study area

The study area is situated within the deep offshore (>200 m) part of the Niger Delta Basin that is located in the Gulf of Guinea, on the edge of the West African continental margin (Doust & Omatsola 1990). This basin lies between latitudes 2° and 7° N and longitudes 3° and 9° E and it is in contact with the older Cretaceous sedimentary rocks in the north, the 4000 m (13 100 ft) bathymetric contour line in the south, and the Benin and Calabar Flanks in the west and east, respectively (Tuttle *et al.* 1999; Fig. 1). This basin originated because of the tectonic activities that led to the opening of the South Atlantic in the Gulf of Guinea in the Late Jurassic-Cretaceous period. This is evidenced by the fractured zones along the oceanic crust, e.g. the Charcot fracture zone, expressed as trenches and ridges that are associated with the basin (Wolak 2011; Fig. 1).

Stratigraphically, the Niger Delta is made up of three diachronous formations, namely, in descending order: Benin Formation (continental sediments), Agbada Formation (transitional sand/marine sediments) and Akata Formation (marine sediments) (Short & Stauble 1967; Knox & Omatsola 1989; Doust & Omatsola 1990; Fig. 2). These formations are filled with time-transgressive regressive sequences of siliciclastic sediments that prograded basinward, forming depo belts, namely, Northern Delta,

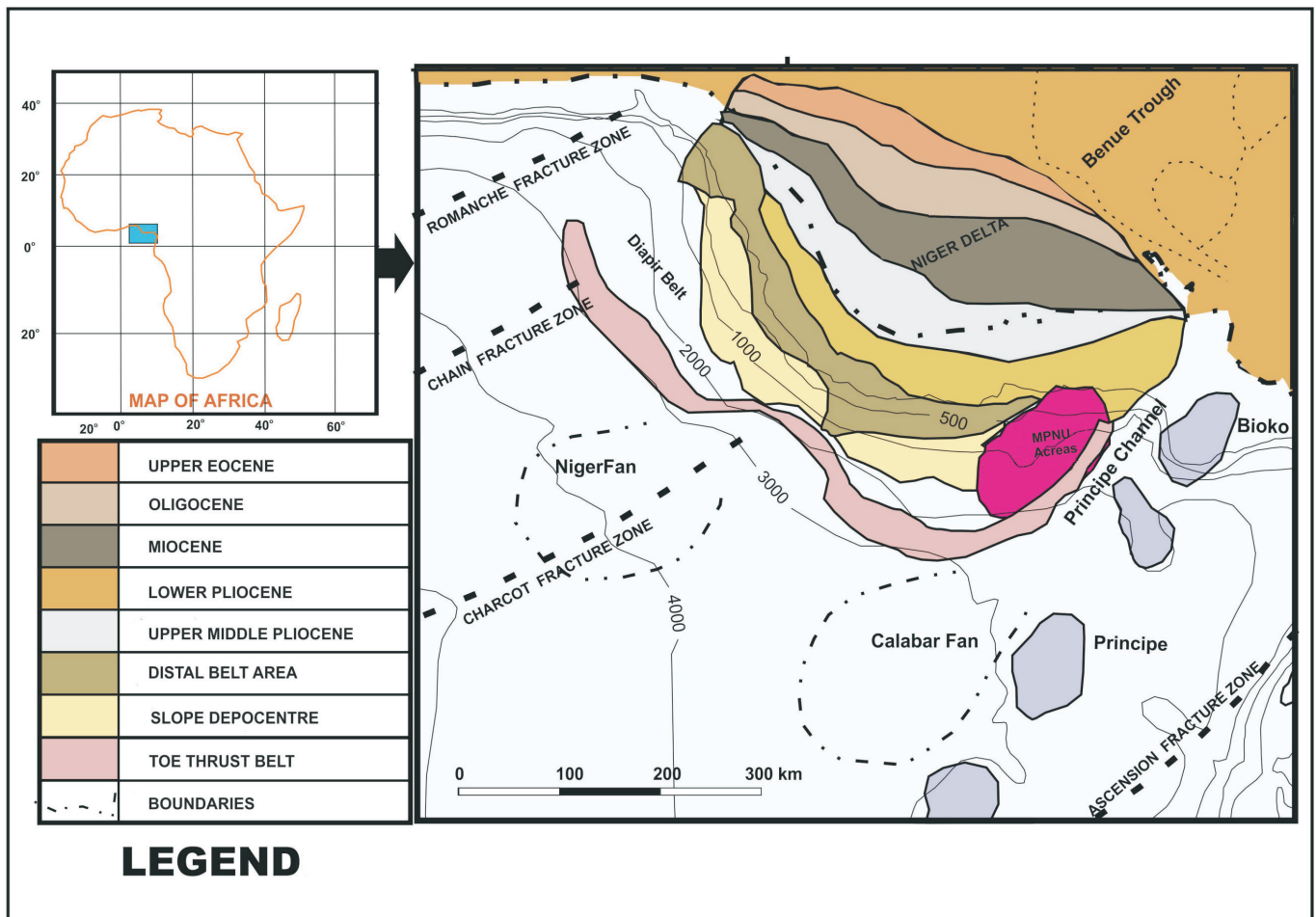


Figure 1. Location of the study area within the MPNU acreage in the southeastern offshore Niger Delta (modified after Wolak 2011).

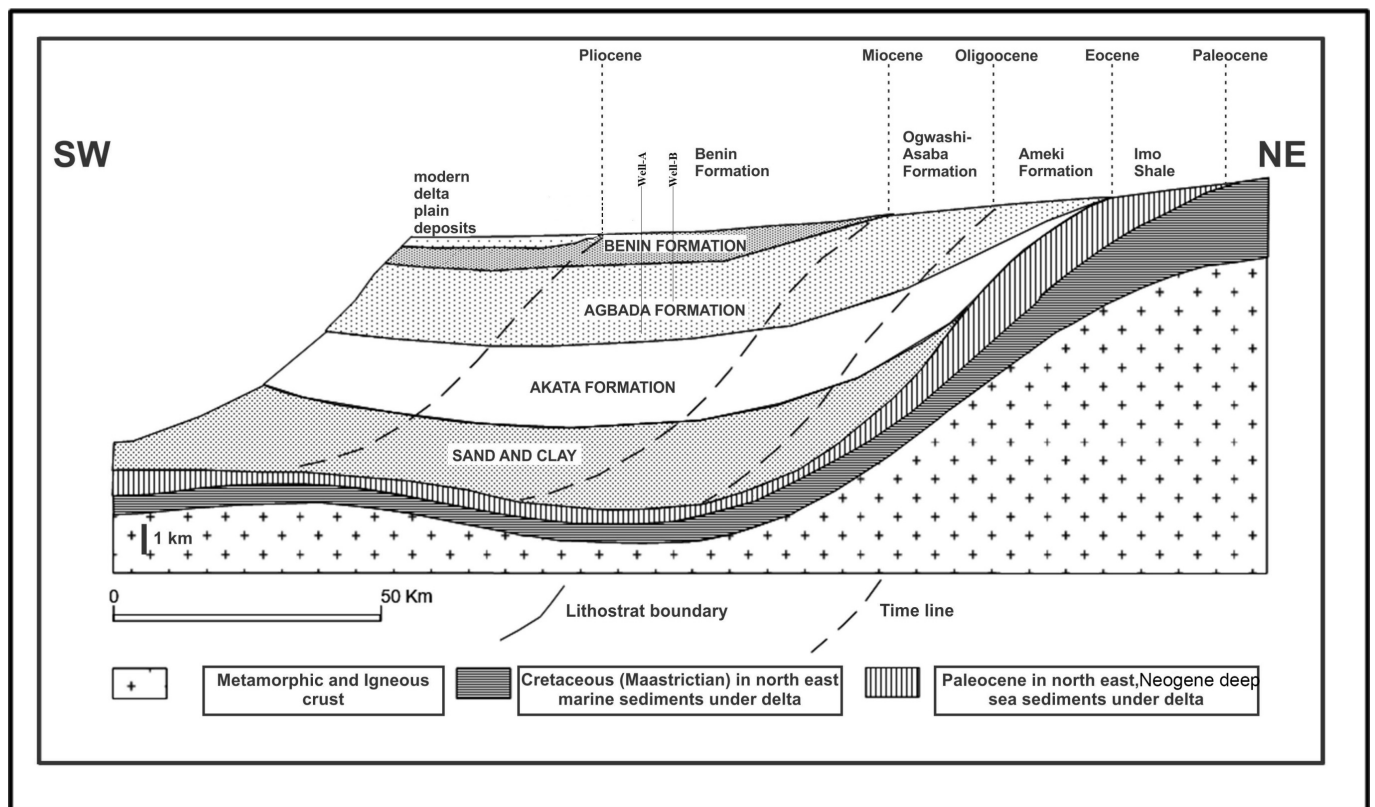


Figure 2. Stratigraphic equivalence of facies in the subsurface Niger Delta with the inferred locations of Wells A and B (modified after Wright *et al.* 1985).

Greater Ugheli, Central Swamp, Coastal Swamp, Shallow Offshore and Deepwater.

METHODS AND MATERIALS

Fifty and forty ditch-cuttings samples with Gamma ray logs of sedimentary rocks from Wells A and B, respectively, were acquired from the deep offshore Niger Delta, Nigeria. The names and locations of these wells are confidential for proprietary reasons. Therefore, these wells have been code-named Wells A and B and are located within the Mobil Producing Nigeria Unlimited (MPNU) acreage in the southeastern offshore Niger Delta (Fig. 1). MPNU acreage has been previously described (see Olayiwola & Bamford 2016). The Department of Petroleum Resources (DPR) and National Petroleum Investment and Management Services (NAPIMS) granted permission to MPNU to provide the material for the study. These acquired ditch-cuttings samples are mostly paralic Agbada Formation sediments while a few are likely to be continental Benin Formation sediments (Fig. 2).

Sample preparation for palynological data

Ninety samples from Wells A and B were used for this study. Ditch-cuttings samples are usually loose sediments and hence crushing was not needed. These samples were processed for palynomorphs following standard procedures (Faegri & Iversen 1989), which includes the addition of HCl, HF, KOH and heavy liquid separation within a saturated ZnCl₂ solution. Identification, counting and description were performed with a light microscope under $\times 400$ and $\times 1000$ magnification with the aid of reference photomicrographs published in the literature, namely: Clarke (1966); Hopping (1967); Germeraad *et al.* (1968); Legoux (1978); Salard Cheboldaëff (1979, 1990); Oboh & Salami (1989); Moore *et al.* (1991); Wood *et al.* (1996); Traverse (2007) and Durugbo *et al.* (2010). Approximately 250 pollen grains spores are counted per sample, excluding marine palynomorphs.

Species identification and pollen diagram

The identified palynomorphs are shown in Figs 3–5 with ranges and zones in Figs 6 & 7 which are based on previous work by Evamy *et al.* (1978) and Morley & Richards (1993).

The percentage abundance and the microfloral distribution trends of Wells A and B are illustrated in the Tilia (version 1.7.16) pollen diagrams (Grimm 1987; Locatelli 2011; Figs 8 & 9).

Pollen diagrams are divided into palynological assemblage zones (PAZ) for ease of interpretation. PAZ is a reflection of palynomorph compositions that can be interpreted by following an individualistic approach or CONISS (Olayiwola & Bamford 2016). Recovered pollen and spores were classified into ecological groups, namely, mangroves, brackish water swamp, freshwater swamp, lowland rainforest, savanna, freshwater algae, fungal elements and marine origin species (Table 1; Figs 6 & 7). The classification of palynomorphs into different ecological groups was based on the general assumption that nearly all the botanical families that existed during Paleogene

times have an affinity with their present-day living relatives (Muller 1981).

The palaeoenvironment is herein reconstructed by reference to the models of Posamentier *et al.* (1988) as modified by Poumot (1989) and Morley (1995), which assumed landward shifting of coastlines during sea level rises and resultant deposition of marine sediments in the subaerial delta plain. There was also shifting of the mangrove and other coastal swamp plant belts during these periods due to their preference for saline water. Therefore, high representation of mangrove, other coastal swamp plants (from beach, brackish, freshwater swamp, rainforest and palm) miospores, fungal elements, freshwater algae and marine origin species characterized this depositional environment (Poumot 1989; Morley 1995; Morley *et al.* 2004; Rugmaia *et al.* 2008). In contrast, as sea level fell the coastline shifted basinward and the shelf area which was initially covered by marine water, was exposed and probably incised due to erosion caused by fluvial activities. Deposition of terrestrial sediments occurred in the subaqueous delta plain and was characterized by widespread savanna vegetation belts. Maxima spectra of savanna and montane pollen characterized this depositional environment (Poumot 1989; Morley 1995; Morley *et al.* 2004; Rugmaia *et al.* 2008).

Palynostratigraphy

The palynostratigraphical biozonation of Wells A and B are based on the recovered floral events and diagnostic bio-event species as defined by Evamy *et al.* (1978) and Morley & Richards (1993) (Figs 6 & 7). Evamy *et al.* (1978) used pollen abundance and diversity to subdivide the Palaeogene-Neogene periods of the Niger Delta Basin into eight super zones comprising P200–P900 Zones. Moreover, sixteen palynological zones were further erected for the Middle Eocene to Plio-Pleistocene segment of the Niger Delta Basin (G1–J3) by Legoux (1978); Morley & Richards' (1993) floral zonation scheme further subdivided the Miocene-Pleistocene epochs into 21 floral zones.

Sample preparation for lithological data

This analysis was carried out to provide the detailed lithological description of the strata penetrated by Wells A and B. An average of 80 g of each of the ditch-cutting samples were soaked in 250 ml aluminum containers with hot water and Sunlight™ liquid detergent for about 24 hours to disaggregate the material. The soaked samples were efficiently washed under a distilled water nozzle tap using a 63 μ m mesh sieve. The retained samples on 63 μ m sieve were dried over hot plates and enclosed in well-labelled drug dispensing cellophane bags.

The lithologic description followed a standard laboratory procedure whereby the washed samples, which were spread on a black anodized aluminum foraminiferal picking tray, were viewed using the binocular reflected light microscope. Gamma-ray and resistivity logs enhanced descriptions, since high and low values of GR-log and RES-log signified shale and sand lithologies, respectively (Adegoke 2002). The essential parameters studied were

grain size, textures and facies changes. These lithological data were plotted, with the aid of SEDLOG™ software, to generate the vertical lithofacies profiles that were embedded in Figs 8 & 9.

Gamma ray logs (GR-logs) data

Acquired GR-logs from Wells A and B are utilized for the understanding of depositional environment changes. Natural radioactivity of rocks, which can be determined by GR-logs, shows generally a close relationship to grain size. The naturally radioactive elements are normally concentrated in shales (clay-size grains; Rider 1990). Clay is herein used in a textural sense, i.e. grain size less than 0.002 mm, which can also be used to describe lithologies, following the format of Rider (1990). Grain size and bedding of sedimentary rocks have an influence on the shape of the gamma ray log curve (<https://www.spec2000.net/2-1-strat1.htm-01/12/2015>). Therefore, GR-log allows the qualitative distinction of zones of shale lithology (high gamma values) from sand lithology (low gamma values). The values of these GR-logs ranged from 0–150 API units (American Petroleum Institute).

There is usually no fundamental relationship between gamma ray log data and the palynology. However, the palynological assemblages and gamma ray log exhibit cyclic changes, which have been used previously to correlate the sedimentary evolution (Sarah *et al.* 1995; Ziegler *et al.* 1997; Wagstaff *et al.* 2006; Adebayo 2014).

Hence, gamma ray curve shapes in association with vertical lithological profiles are used to subdivide the main subaerial and subaqueous delta plains, previously defined by palynomorph assemblages, into sub-environments (Selley 1985; Oboh 1995). The trend of changes of GR-log curve is herein used for the interpretation of the sedimentary depositional environments (Figs 8b & 9b).

RESULTS

The top of Well A is 716 m below sea level and the base is 3024 m below so the core represents 2308 m. Well B is presumably farther from shore and its top is 1472 m below sea level and extends down to 2542 m, so the core is 1070 m long. Nonetheless, the cores represent more or less the same time frame (based on the palynology) although core A is more than twice the length of core B. The core material from the two wells will be presented and discussed together.

Palynology

Thirty-one and 29 palynomorph species belonging to 33 genera are recorded in Wells A and B, respectively, and the palynomorph assemblages are dominated by angiosperm pollen that comprises 85.7% (Figs 8a & 9a). Monolete spores (5%), fungal spores (4%), trilete fern spores (4%), freshwater algae (1%) and marine palynomorphs (0.3%) followed this in abundance.

Palynostratigraphy

Since the palynomorphs recovered from Wells A and B were the same as those described by Evamy *et al.* (1978) and Morley & Richard (1993), their zonation schemes are

used here to determine the age of the strata as well as the palaeoenvironment. The palynostratigraphic biozonation of the wells was defined using the recovered diagnostic markers and ecologically significant species. The first two informal subzones, which are established in these wells, are correlated with P860–P870 Subzones of Evamy *et al.* (1978) (Figs 6 & 7).

P800 Zone and subzone P860 (late Miocene)

The P860 Subzone is the older subzone of zone P800 in Wells A and B with the tops marked at 2548 m and 2185 m, respectively, by the quantitative base occurrence of *Retistephanocolpites gracilis*. The bases were tentatively marked at 3024 m and 2542 m which are the deepest samples analysed in Wells A and B, correspondingly. This subzone may continue below. The continuous co-occurrences of *Gemmamonoporites* sp., *Nymphaeapollis clarus*, *Peregrinipollis nigericus*, *Stereisporites* sp. and *Cyperaceapollis* sp. characterized this subzone and, therefore, their presence indicates a late Miocene age according to the schemes of Evamy *et al.* (1978) and Morley & Richard (1993).

P800 Zone and subzone P870 (early to late Pliocene)

P870 was the youngest subzone documented in the analysed intervals of Wells A and B (Figs 6 & 7). The tops of the subzone were tentatively marked at 716 m and 1472 m which are the depths of the first samples analysed in these wells, respectively. The bases are marked by the quantitative base occurrence of *Retistephanocolpites gracilis* at 2548 m and 2185 m in Wells A and B, respectively. Co-occurrence of *Gemmamonoporites* sp. and *Retistephanocolpites gracilis* together with regular occurrences of *Nymphaeapollis clarus* and the absence of *Podocarpus milanjanus* confirmed early–late Pliocene age in this subzone.

Floral Zonation for Wells A and B

Secondly, the P860 and P870 Sub-zones of Evamy *et al.* (1978) in Wells A and B are further subdivided into seven floral zones of Morley & Richards (1993). P1 (914–716 m), Upper P3–Upper P2 (1487–914 m), Lower P3 (1679–1487 m), P4 (2045–1679 m), P6–P5 (2393–2045 m), P7 (2548–2393) and M1 (3024–2548 m) comprised floral zones in Well A (Fig. 6) while Well B comprised Upper P3 (1609–1472 m), Lower P3 (1692–1609 m), P4 (1774–1692 m), P6–P5 (1993–1774 m), P7 (2145–1993 m), M1 (2350–2145 m) and M2 (2542–2350 m) floral zones (Fig. 7).

Palynological, lithological and gamma ray data and the palaeoenvironmental reconstruction

Thirdly, eight informal palynological assemblage zones and eustatic sea level changes are recorded in Wells A and B which are designated as PAZ-1 to PAZ-VIII from the base to the top (Figs 8 & 9). Four lithofacies comprised of sandstones, siltstones, claystones and mudstones are well represented in Well A, whereas mudstones are predominant in Well B. Eight and five depositional sequences accompanied by nine and seven inferred depositional environments are recognized in Wells A and B, respec-

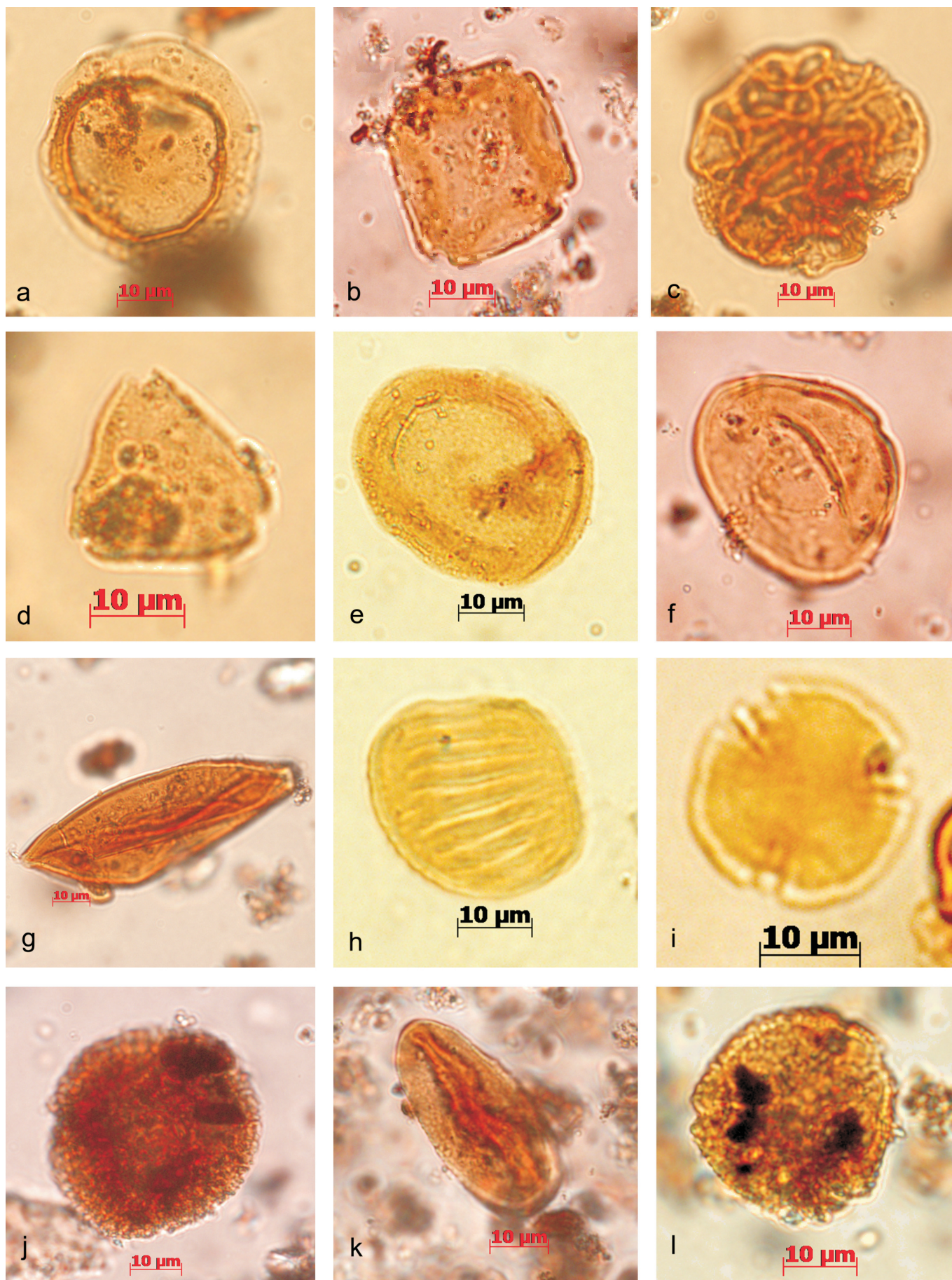


Figure 3. Common palynomorphs from Wells A and B from Niger Delta. (a) *Nymphaeapollis clarus*; (b) *Pachydermites diderixi*; (c) *Peregrinipollis nigericus*; (d) *Proteacidites cooksonii*; (e) *Proxapertites cursus*; (f) *Psilatricolporites crassus*; (g) *Psilamonocolpites* sp.; (h) *Psilastephanocolpites* sp.; (i) *Psilatricolpites operculatus*; (j) *Retitricolporites irregularis*; (k) *Retimonocolpites* sp.; (l) *Retibrevitricolporites obodoensis*.

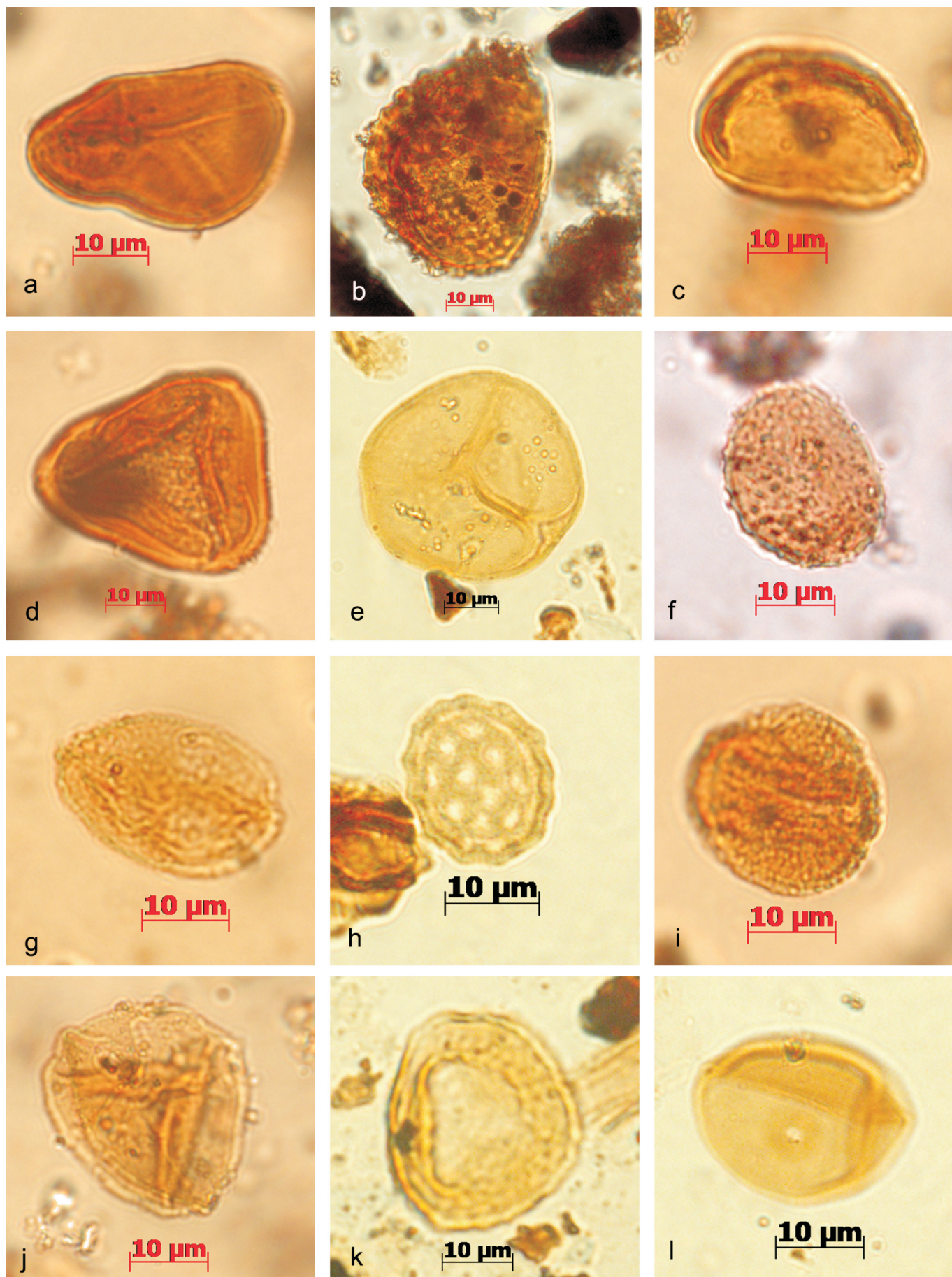


Figure 4. Common palynomorphs from Wells A and B from Niger Delta. (a) *Acrostichum aureum*; (b) *Crassoretitriletes vanraadshooveni*; (c) *Laevigatosporites* sp.; (d) *Polypodiaceoisporites* sp.; (e) *Stereisporites* sp.; (f) *Verrucatosporites* sp.; (g) *Arecipites exilimuratus*; (h) *Chenopodipollis* sp.; (i) *Crototricolpites densus*; (j) *Cyperaceapollis* sp.; (k) *Gemmamonoporites* sp.; (l) *Monoporites annulatus*.

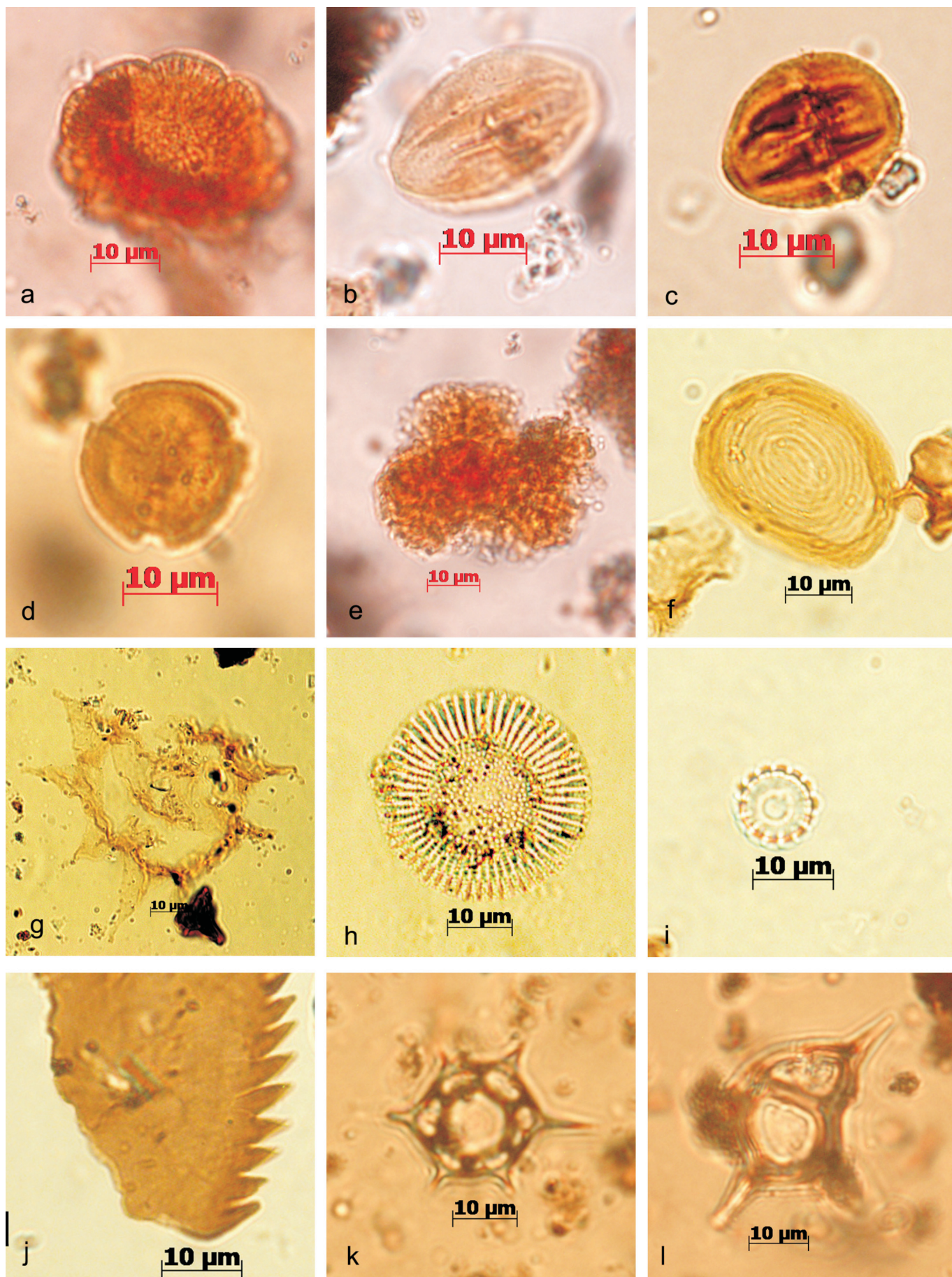


Figure 5. Common palynomorphs from Wells A and B from Niger Delta. (a) *Retistephanocolpites gracilis* (b) *Striatricolpites catatumbus*; (c) *Zonocostites duquei*; (d) *Zonocostites ramonae*; (e) *Botryococcus braunii*; (f) *Concentricytes circulus*; (g) *Pediatrums* sp.; (h) Diatom frustule 1; (i) Diatom frustule 2; (j) Scolecodont sp.; (k) *Distephanus boliviensis* (Silicoflagellate sp. 1); (l) *Naviculopsis robusta* (Silicoflagellate sp. 2).

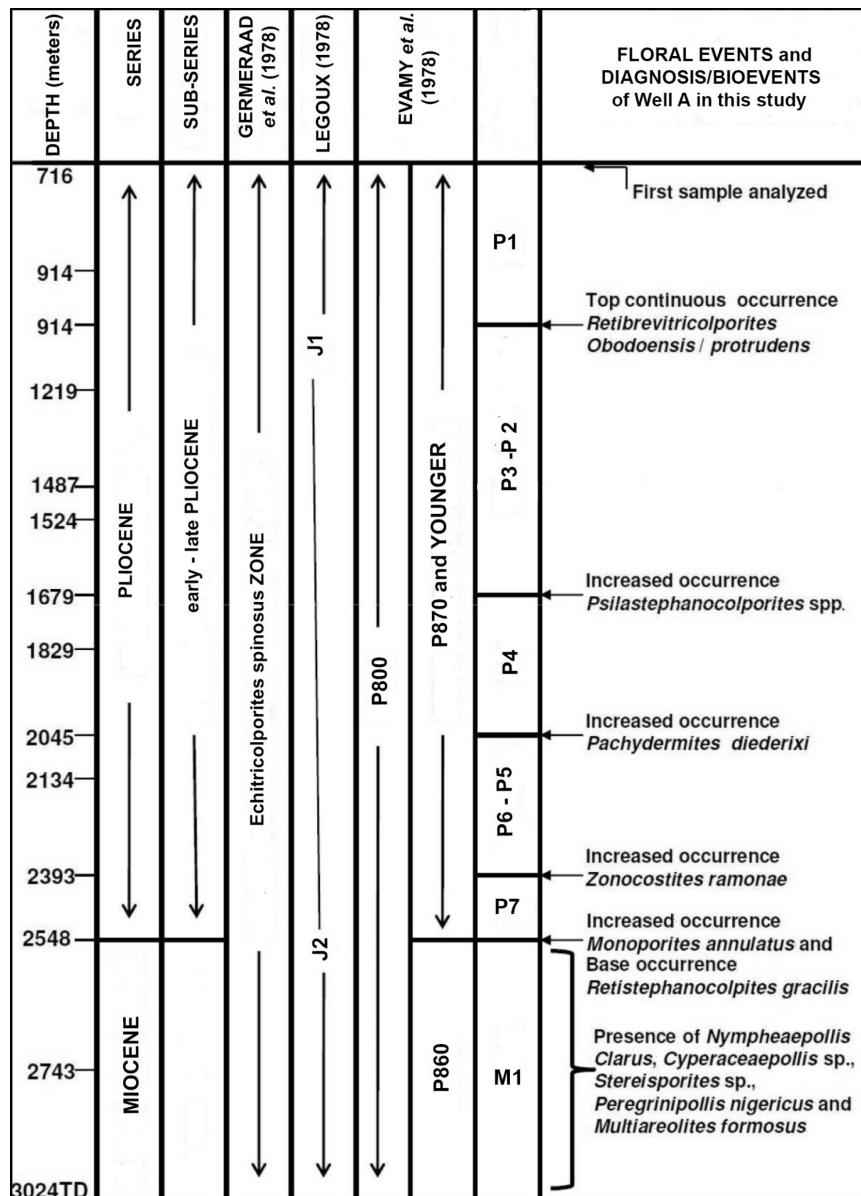


Figure 6. Chart showing palynomorph zones and subzones recognized in well A based on the frameworks of Evamy *et al.* (1978) and Morley & Richard (1993).

tively (Figs 8 & 9). These PAZs with their allied lithologies and likely inferred depositional environments are described below.

It should be noted that the ecological interpretations of the palynomorphs by Germeraad *et al.* (1968), Evamy *et al.* (1978) and Morley & Richards (1993), who have worked on the Niger Basin, have been followed here. There are other interpretations, however, for example, palms producing *Arecipites* pollen can grow along the beach (Povilaskas 2013) and inland along water courses. *Verrucatosporites* spp. represent several families of ferns (Stuchlik 2001). Cyperaceae grow in a range of poorly drained soils from permanent wetlands to dambos to patches in savanna and brackish wetlands. The Chenopodiaceae also grow in a variety of habitats but overall they indicate dry environments

PAZ-IA (2728–2289 m) and PAZ-IB (2542–2516 m); P860 Subzone (late Miocene)

PAZ-IA (from Well A) and -IB (from Well B; Figs 8 & 9) are

the basal parts of the studied sections of Wells A and B. These palynofloral assemblages are correlated with P860 Subzone (of Evamy *et al.* 1978). Hence, the age of these palynozones are likely to be late Miocene. PAZs-IA and IB bases are defined by the first quantitative base increase of *Zonocostites ramonae*. The tops of this zone are marked by the first quantitative decrease of *Zonocostites ramonae* and increase of *Psilatricolporites crassus*, *Monoporites annulatus* and *Verrucatosporites* sp. PAZ-IA and IB are dominated by mangrove, freshwater swamp, freshwater algae and marine palynomorphs (Figs 8a & 9a; Table 1). The rare occurrence of savanna pollen, fungal elements and low-land rainforest characterized this zone. Mudstone lithologies and bell-shaped gamma-ray curves are recorded for this zone.

PAZ-IIA (2899–2469 m) and PAZ-IIB (2515–2457 m); P860 Subzone (late Miocene)

These palynofloral zones are located within the uppermost parts of P860 Subzone of the analysed interval of

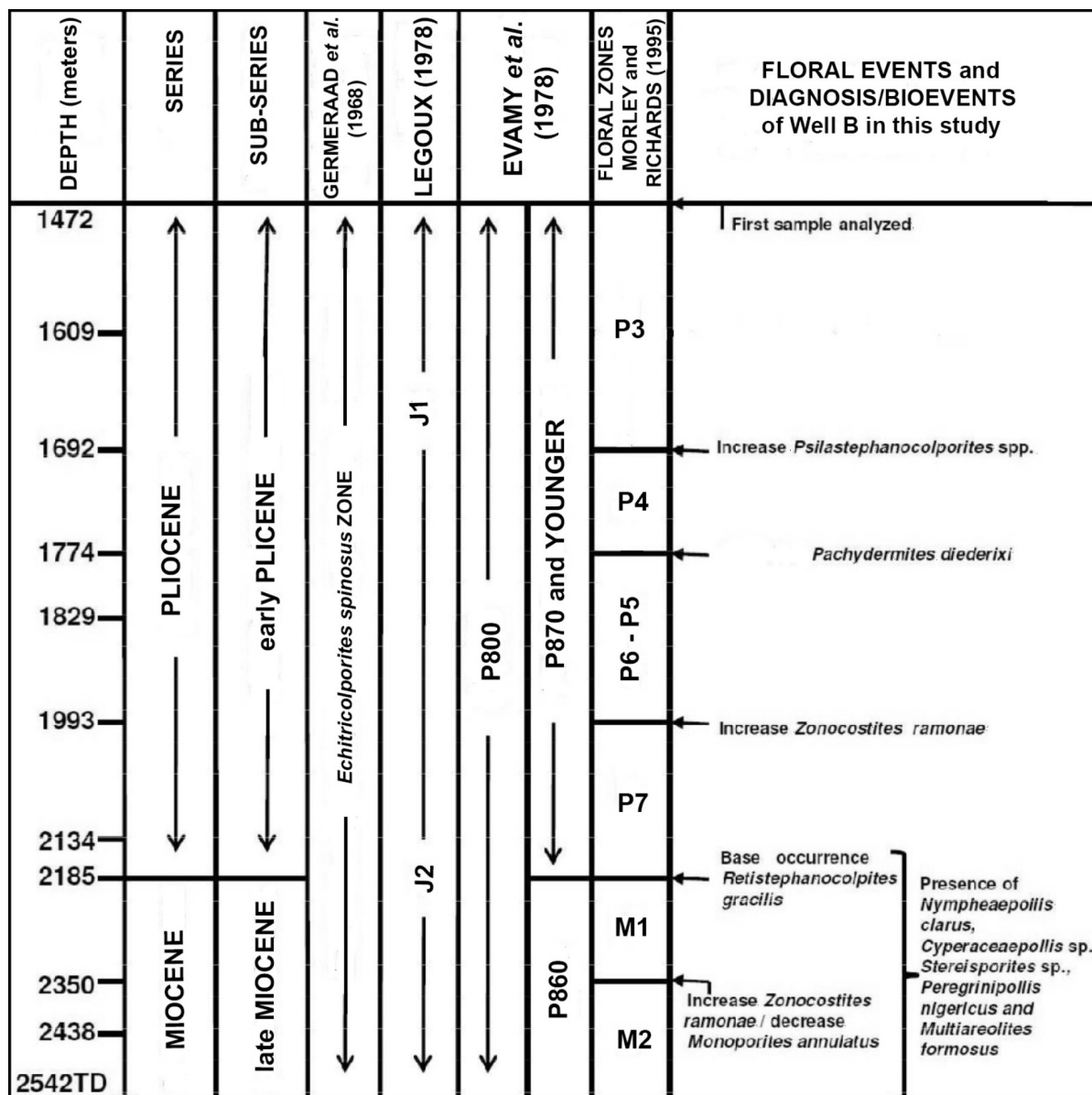


Figure 7. Chart showing palynomorph zones and subzones recognized in Well B based on the frameworks of Evamy *et al.* (1978) and Morley & Richard (1993).

Wells A and B and occurred within the uppermost late Miocene. PAZ-IIA and IIB (Figs 8 & 9) bases are marked by the first quantitative decrease of *Zonocostites ramonae* and increase of *Psilatricolporites crassus*, *Monoporites annulatus* and *Verrucatosporites* sp., while the quantitative increase of *Zonocostites ramonae* and the quantitative decrease of *Psilatricolporites crassus*, *Verrucatosporites* sp. and *Monoporites annulatus* defined the tops. These zones are characterized by the predominance of *Monoporites annulatus*, *Cyperaceapollis* sp. *Verrucatosporites* sp. and *Acrostichum aureum* with reduced proportions of *Zonocostites ramonae*, beach and brackish miospores, algae and marine palynomorphs (Figs 3–5). Sandstone lithologies and boxcar gamma ray signatures are recognized in these zones.

PAZ-IIIA (2469–2335 m) and PAZ-IIIB (2463–2350 m); P870 Subzone (early Pliocene)

These zones that are located within P800 Zone and occurred within the early Pliocene (Zanclean) period of

the analysed interval of Wells A and B. Base boundaries of these palynofloral zones are marked by the quantitative increase of *Zonocostites ramonae* and the quantitative decrease of *Psilatricolporites crassus*, *Verrucatosporites* sp. and *Monoporites annulatus*, while the quantitative decrease of *Verrucatosporites* sp. and quantitative decrease of fungal elements defined their tops. The overall prevalence of mangroves, *Laevigatosporites* sp., *Verrucatosporites* sp. and fungal elements, with reduced percentages of savanna palynomorphs, characterized these palynological zones. In these zones mudstone facies were recorded in Well A, while sandstones were upgraded to siltstone lithologies in Well B, with bell and funnel-shaped gamma ray curves, respectively, in these wells.

PAZ-IVA (2335–2155 m) and PAZ-IVB (2350–2179 m); P870 Subzone (early Pliocene)

These zones occurred in zone P800 within the early Pliocene (Zanclean). The base boundaries of these palynofloral zones are defined by the quantitative decrease of

Table 1. Distribution of recovered palynomorphs in Wells A and B.

S/No	Ecological	Genera	Species	Botanical affinities
1	Mangrove	<i>Zonocostites</i>	<i>ramonae</i>	Rhizophoraceae
			<i>duquei</i>	
		<i>Psilatricolporites</i>	<i>crassus</i>	Euphorbiaceae
2	Beach	<i>Arecipites</i>	<i>exilimuratus</i>	Arecaceae
3	Brackishwater swamp	<i>Pachydermites</i>	<i>diederixi</i>	Guttiferae - <i>Symphonia globulifera</i>
		<i>Acrostichum</i>	<i>aureum</i>	Pteridaceae
4	Freshwater swamp	<i>Nymphaeapollis</i>	<i>clarus</i>	
		<i>Retibrevitricolporites</i>	<i>obodoensis</i>	Rubiaceae
		<i>Retitricolporites</i>	<i>irregularis</i>	Euphorbiaceae - <i>Amanoa</i>
		<i>Gemmamonoporites</i>	sp.	-
		<i>Verrucatosporites</i>	sp.	Polypodiaceae
		<i>Laevigatosporites</i>	sp.	-
		<i>Striatricolpites</i>	<i>catatumbus</i>	-
		<i>Crototricolpites</i>	<i>densus</i>	-
		<i>Psilatricolpites</i>	<i>operculatus</i>	-
		<i>Crassoretitrites</i>	<i>vanraadshooveni</i>	-
5	Lowland rainforest	<i>Psilastephanocolpites</i>	sp.	-
		<i>Stereisporites</i>	sp.	?Sphagnaceae- <i>Sphagnum</i>
		<i>Polypodiaceoisporites</i>	sp.	Adiantaceae - <i>Pteris</i>
6	Savanna	<i>Monoporites</i>	<i>annulatus</i>	Gramineae
		<i>Cyperaceapollis</i>	sp.	<i>Cyperus</i>
		<i>Proxapertites</i>	<i>cursus</i>	Araceae- <i>Nypa</i>
		<i>Chenopodipollis</i>	sp.	Chenopodiaceae/Amaranthaceae
		<i>Proteacidites</i>	<i>cooksonni</i>	Proteaceae
		<i>Peregrinipollis</i>	<i>nigericus</i>	Caesalpinioides -Brachystegia cf. peltophorum
		<i>Retistephanocolpites</i>	<i>gracilis</i>	Rubiaceae-Borreria
		<i>Retimonocolpites</i>	sp.	-
7	Freshwater Algae	<i>Botryococcus</i>	<i>braunii</i>	Not applicable
		<i>Concentricytes</i>	<i>circulus</i>	Not applicable
		<i>Pediastrum</i>	sp.	Not applicable
8	Marine	<i>Distephanus</i> (<i>Silicoflagellate</i> sp.)	<i>boliviensis</i>	Not applicable
		<i>Naviculopsis</i> (<i>Silicoflagellate</i> sp.)	<i>robusta</i>	Not applicable
		<i>Scolecodont</i>	sp.	Not applicable
		<i>Diatom</i>	<i>frustule 1</i>	Not applicable
		<i>Diatom</i>	<i>frustule 2</i>	Not applicable

Verrucatosporites sp. and fungal elements, with the upper boundaries marked by the quantitative decrease of *Psilatricolporites crassus*, *Monoporites. annulatus*, peak of *Verrucatosporites* sp. and the peak of fungal elements. This palynofloral zone was characterized by the dominance of savanna, spores (*Verrucatosporites* sp. and *Acrostichum aureum*) and freshwater algae with corresponding low occurrences of mangrove, brackish water swamp, freshwater swamp, and fungal elements. Mudstones with

intermittent claystones were deposited and accompanied with bell-shaped gamma ray signatures (Figs 8 & 9).

PAZ-VA (2155–1798 m) and PAZ-VB (2179–1996 m); P870 Subzone (early Pliocene)

These palynofloral assemblages are correlated with P870 Subzone within the early Pliocene (Zanclean stage). PAZ-VA and VB (Figs 8 & 9) bases are defined by the quantitative decrease of *Psilatricolporites crassus*, *Monoporites*

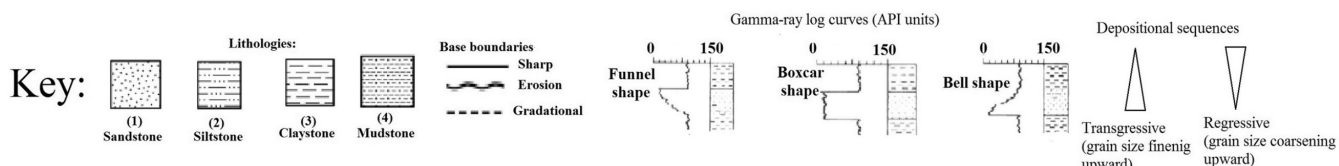
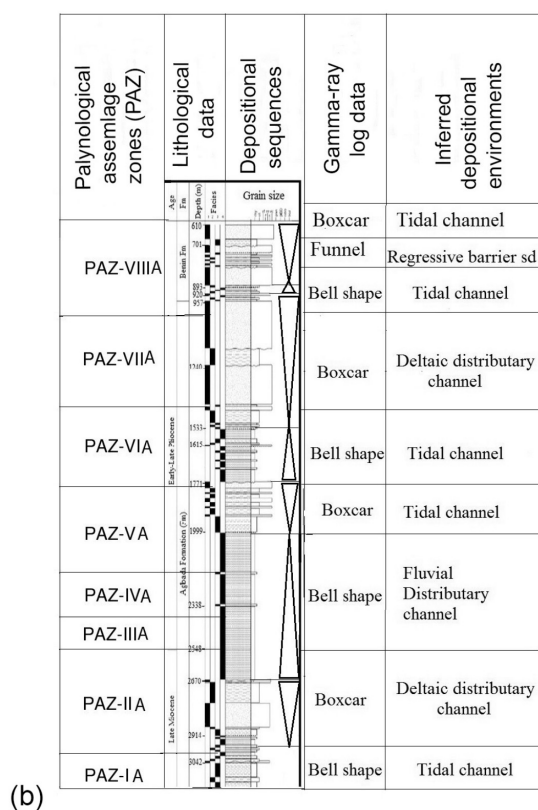
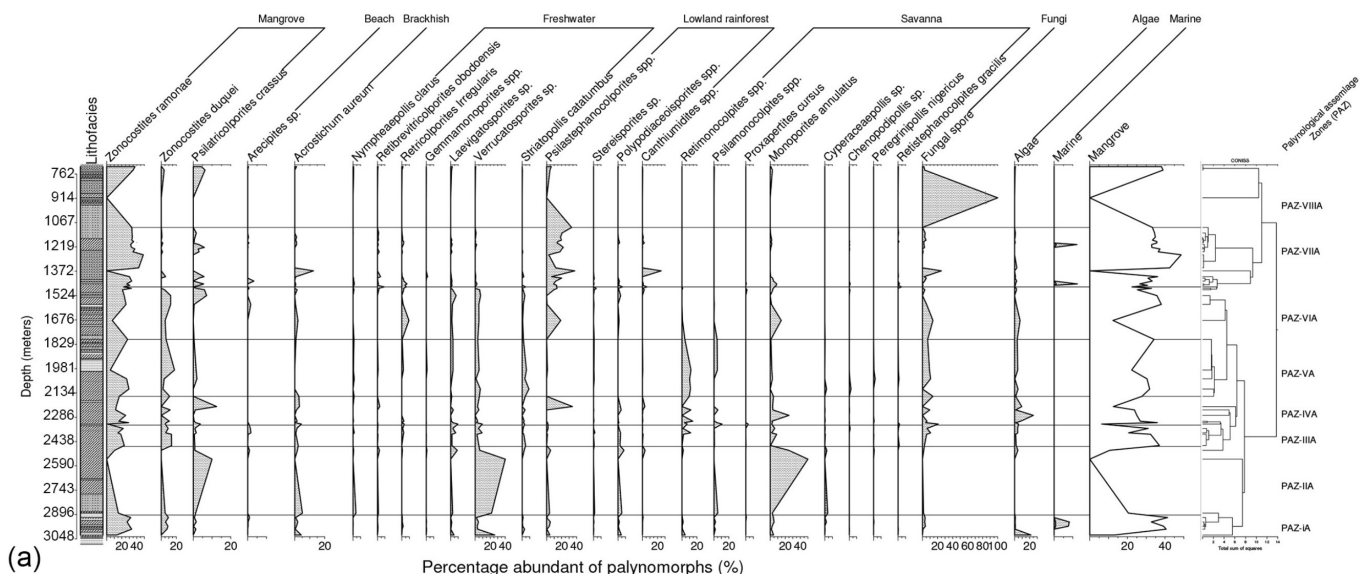


Figure 8. Chart showing integration of palynological, lithological and gamma ray log data with inferred depositional environments in Well A.

annulatus, peaks of *Verrucatosporites* sp. and fungal spores, while the quantitative peak of *Zonocostites ramonae*, quantitative increase of *Monoporites annulatus* and fungal spores marked their tops. PAZ-VA and VB are dominated by mangrove, brackish water swamp, freshwater swamp, freshwater algae, fungal elements and marine palynomorphs with the rare occurrence of savanna. Mudstones upgraded to sandstones are recognized in Well A, while

mudstones facies are recorded in Well B. The accompanied gamma ray curves recorded in these zones are boxcar and bell-shaped in Wells A and B, respectively.

PAZ-VIA (1798–1469 m) and PAZ-VIB (1996–1710 m); P870 Subzone (mid-Pliocene)

These palynofloral zones are located in the middle parts of P870 Subzone of the analysed interval of Wells A and B

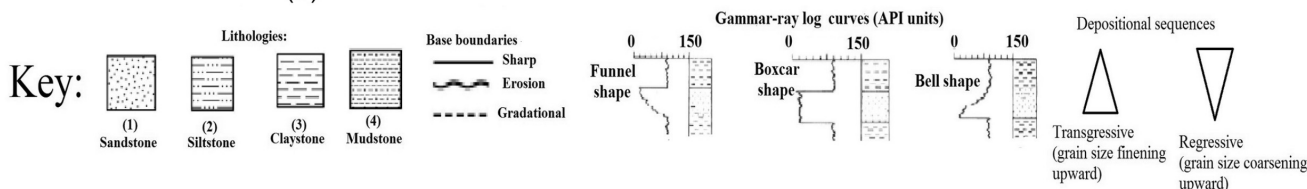
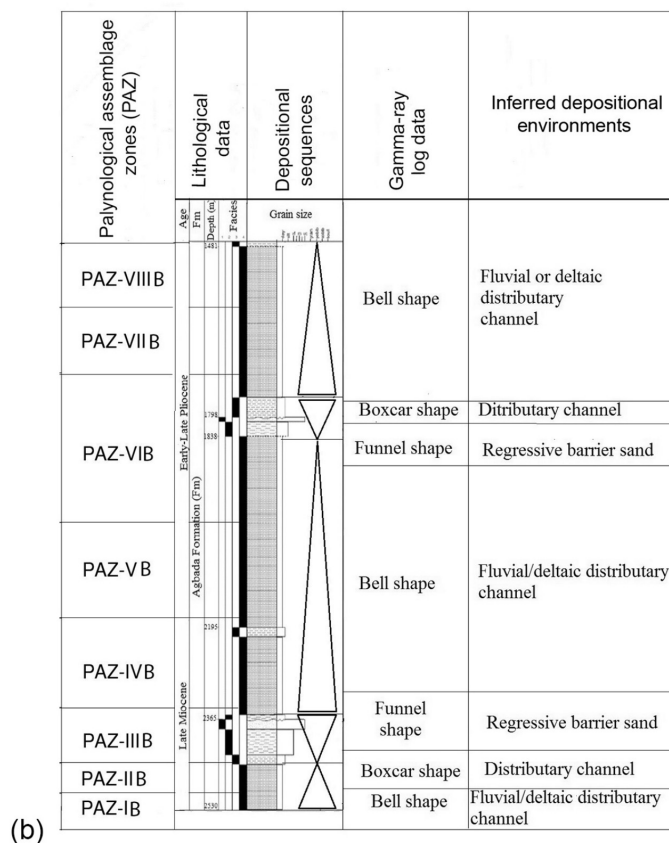
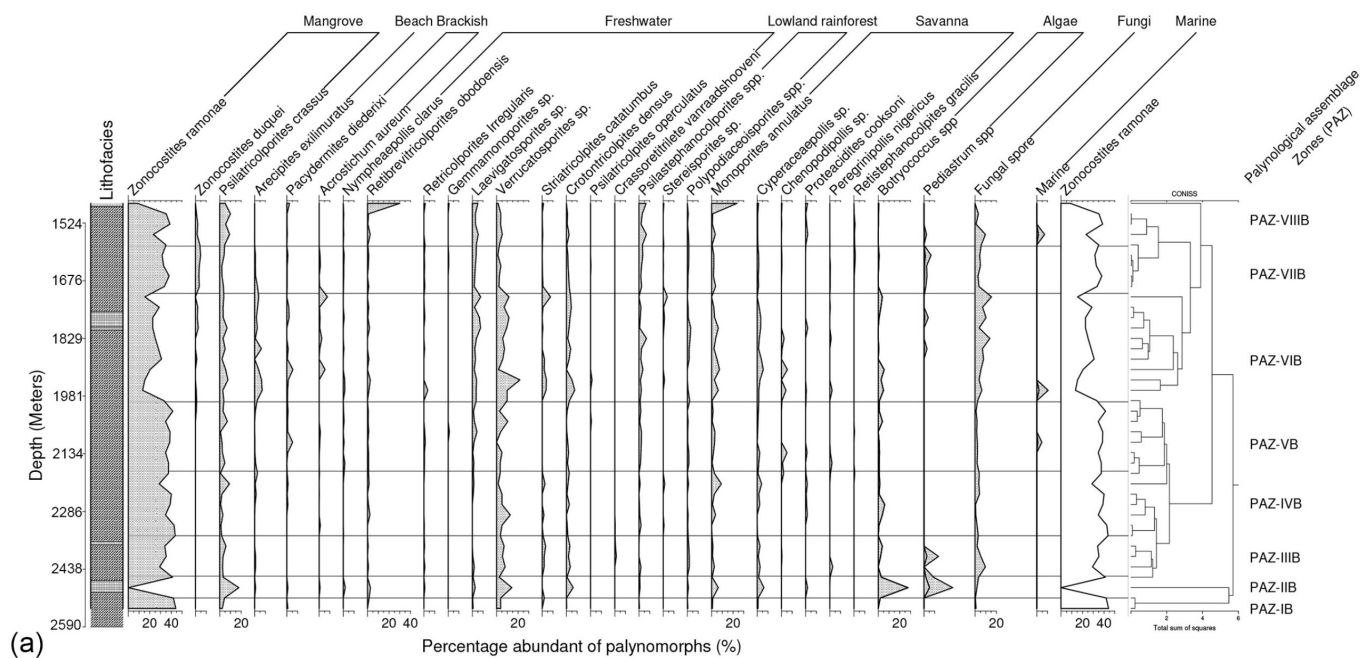


Figure 9. Chart showing integration of palynological, lithological and gamma ray log with inferred depositional environments in Well B.

(Figs 8 & 9), and occurred in the mid-Pliocene. The bases of these micro-floral zones are marked by the quantitative peak of *Zonocostites ramonae*, the quantitative increase of *Monopores annulatus* and fungal elements, while the quantitative decrease of *Verrucatosporites* sp., the quantita-

tive increase of *Monopores annulatus* and the decrease of fungal elements defined their tops. PAZ-VIA and VIB are characterized by the predominance of *Monopores annulatus*, *Cyperaceapollis* sp., *Chenopodiopollis* sp., fungal elements, *Verrucatosporites* sp., *Acrostichum aureum*, fresh-

water algae and marine palynomorphs with a reduced proportion of *Zonocostites ramonae*, beach and brackish miospores. The basal parts of these zones are dominated by deposition of mudstones while sandstones/siltstones lithologies were deposited in the upper parts. Bell-shaped gamma-ray signatures are recorded in these micro-floral zones (Figs 8 & 9).

PAZ-VIIA (1469–1097 m) and PAZ-VIIB (1710–1585 m); P870 Subzone (mid-Pliocene)

These palynological zones that are located within P870 Subzone and occurred within the mid-Pliocene period of the analysed intervals of Wells A and B. Base boundaries of these palynological zones are marked by the quantitative decrease of *Verrucatosporites* sp., the quantitative increase of *Monoporites annulatus* and the decrease of fungal spores. The quantitative decrease of *Zonocostites ramonae* and quantitative increase of fungal spores defined the tops of these floral zones. The overall prevalence of *Zonocostites ramonae*, *Psilastephanocolporites* sp., fungal spores and marine palynomorphs (silicoflagellates and diatoms), with rare to absent savanna, freshwater swamp, freshwater algae palynomorphs characterized these palynological zones. In these zones, sandstone facies were deposited in Well A, while mudstone lithologies were deposited in Well B. Boxcar and bell-shaped gamma-ray curves are recorded in Wells A and B, respectively, (Figs 8 & 9).

PAZ-VIIIA (1097–701m) and PAZ-VIIIB (1585–1463 m); P870 Subzone (late Pliocene)

These palynofloral zones are the uppermost part of Wells A and B and are the youngest stratigraphical zones recorded in these wells. The palynofloral assemblages occurred within P870 Subzone and dated to late Pliocene (Piacenzian stage). PAZ-VIIIA and VIIIB (Figs 8 & 9) bases are defined by the quantitative decrease of *Zonocostites ramonae* and quantitative increase of fungal elements, while the quantitative decrease of *Zonocostites ramonae*, fungal elements and quantitative increase of *Monoporites annulatus* tentatively marked their tops. PAZ-VIIIA and VIIIB are dominated by mangrove, freshwater swamp, lowland rainforest, fungal spores and marine palynomorphs (silicoflagellates and diatoms) with the rare occurrence of savanna. These zones are typified by the deposition of sandstones in Well A, while mudstone facies were deposited in Well B. The accompanied gamma ray curves in these zones are funnel and bell-shaped in Wells A and B, respectively.

DISCUSSION

The detailed palynological analysis revealed that palynomorphs form diverse and abundant assemblages in Wells A and B from the deep offshore Cenozoic Niger Delta and is supported by the previous reports from the Niger Delta (Obboh 1992; Ige 2011; Ige *et al.* 2011; Adebayo *et al.* 2012; Ojo & Gbadamosi 2013; Adebayo & Ojo 2014). The age of Wells A and B ranges from late Miocene (P860 Subzone) to Pliocene (P870 Subzone) (Evamy *et al.* 1978). The quantitative base occurrence of *Retistephanocolpites gracilis* at 2548 m and 2185 m in Wells A and B, respectively,

defined the boundary between late Miocene and Pliocene that suggests the age is around 5.2 Ma (*Discoaster quinqueramus*, Morley & Richard 1993; Olayiwola 2014).

Palynofloral assemblages of Wells A and B are similar to those of West Africa and farther afield, for example, subzones P860 and P870 are correlated with the pan-tropical *Echitricolporites spinosus* Zone of Germeraad *et al.* (1968) and J2–J3 Zone of Legoux (1978). The base of micro-floral zone P3 of subzone P870, defined by increased occurrences of *Psilastephanocolporites* sp. at 1679 m and 1692 m in Wells A and B, respectively, suggest an age of about 4.1 Ma (*Gephyrocapsa demitre*, Morley & Richard 1993; Olayiwola 2014).

The palynological assemblages revealed that there is a landward shifting of the mangrove vegetation due to the sea level rise as shown in PAZ-IA, PAZ-IB, PAZ-IIIA, PAZ-VB, PAZ-VIIB and PAZ-VIIIB. Thick bodies of mudstone/claystone lithologies recorded at depths 2768 m, in Well A, 2469 m, and 1807 m, in Well B, on top of sandstones bodies, are likely to be overpressure zones in the studied wells. Conversely, the palynological assemblage zones PAZ-IIA, PAZ-IIB, PAZ-IIIB, PAZ-VA, and PAZ-VIIA revealed that there is a shifting of the savanna vegetation seaward during sea level fall. PAZ-VIIIA does not show any significant change in savanna pollen. It should be noted that Poaceae, e.g. *Monoporites annulatus*, can grow in diverse habitats, e.g. close to the coast (Rebata *et al.* 2006), and not only in savannas, although for Germeraad (1968) *M. annulatus* is a savanna element. There is no new evidence to contradict this.

Palynological assemblages in PAZs-1A, 1B, IIIA, IIIB, VA, VB, VIIA, VIIB, VIIIA and VIIIB suggested deposition in a subaerial delta plain during sea level rise, while those of PAZs-IIA, IIB, IVA, IV, VIA and VIB suggested deposition in a subaqueous delta plain during sea level fall. The sedimentological analysis revealed two to three lithologies. The sandstones facies are recognized to have been deposited as the regressive sequences in the palynofloral zones PAZs-IIA, IIB, IIIB, IVA, IVB, VA, VIA and VIB (upper part), VIIA and VIIIA. In addition, mudstones or claystone are delineated to have been deposited as the transgressive sequences in palynozones PAZs-IA, IB, IIIA, VB, VIA and VIB (basal parts), VIIB, and VIIIB. In addition analysis of the gamma-ray signatures showed three patterns. These are bell, funnel, and boxcar-shaped, which indicated tidal channel (in PAZs-IA, IB, IIA, IVA, IVB, VB, VIA, VIB, VIIB and VIIIB), deltaic distributary channel (in PAZs-IIA, IIB, VA and VIIB), and regressive barrier (in PAZs-IIIB and VIIIB) depositional environments. The deltaic distributary channel that belongs to the deltaic system complex is recorded in Wells A and B and was previously interpreted to have been formed during the first stage of prograding sea level fall (Emery & Myers 1996). It usually has an erosive base that is interpreted as a sequence boundary and is commonly filled with moderate to well-sorted, uniform and blocky sand-grain size sediments with a good reservoir quality (Unukogbon *et al.* 2008). In addition, tidal channels, which are usually dominated by moderate to well-sorted sand deposits (Obboh *et al.* 1992; Emery & Myers 1996), are recognized in this

study. They are characterized by an erosive base that is commonly filled with fining-upward sand sequences in association with the muddy sediments in the topmost part. The tidal channel sand usually forms a good quality reservoir rock with a sealing rock capacity on top (Unukogbon *et al.* 2008). Furthermore, the regressive barrier sand that formed when there is a drop in the base level of the sea, are recorded in Wells A and B. This sub-environment is characterized by deposition of coarsening-upwards sediments ranging from basal marine shale to continental coarse-grained sand at the top (Selley 1985). The basal organic mud-rich deposits underlying the regressive barrier sand are likely to be of a high-quality kerogen supply in the study area (Chow *et al.* 2005).

Many earlier authors have used a combination of palynologic, lithologic and well-log data to outline different sub-environments in the onshore portion of the Niger Delta. Amongst these are Oboh (1991, 1992a,b, 1993, 1995); Kulke (1995), Unukogbon *et al.* (2008) and Oyedele *et al.* (2012). They reported distributary and tidal channel fills that contained few palynomorphs (chiefly Poaceae) and were associated with erosive based, fining-upward and bell-shaped to blocky gamma-ray patterns. The regressive barrier has equally been described to be rich in palynomorphs (mainly grass, mangrove and ferns spores) in association with coarsening-upward and funnel-shaped patterns. However, three categories of interbedded shale, namely clay smears along faults, interbedded sealing units, and vertical seals, were previously recorded in the Agbada Formation that formed the chief seal rock in the Niger Delta (Doust & Omatsola 1990).

Overpressure zones have earlier been reported to be associated with young Tertiary basins such as the Niger Delta, Gulf of Mexico, Nile Delta and Baram basins (Nwozor *et al.* 2013). This is as a result of high rates of sediment accumulation, which rapidly generated sufficiently thick intervals of shales that commonly characterize these basins. However, the tops of the overpressure zones vary greatly from depo-belt to depo-belt in the Niger Delta (Krusi 1990). Consequently, some authors tried to detect and predict overpressure zones in this region by applying different methods. Amongst these are well logs (Owolabi *et al.* 1990; Osinowo *et al.* 2007) and seismic data (Alao *et al.* 2014; Omolaiye *et al.* 2011; Ayuku & Olorunniwo 2004).

CONCLUSION

The Late Miocene-Pliocene Niger Delta is characterized, in order of abundance and diversity, by angiosperm pollen, monolete spores, fungal elements, trilete fern spores, freshwater algae and marine palynomorphs. The alternation of sandstones and mud/claystone lithologies typified Wells A and B in this study. The sandstone lithologies likely served as reservoir rocks while mud/claystones are suggested to be the good source and seal rocks in the study area. Three different depositional sub-environments, namely, distributary channel, tidal channel, and regressive barrier sands, are delineated in this study. The findings of the multi-pronged approach used here will encourage further studies on offshore wells and help the exploration geologists in recognizing

oil-prone deposits from sub-environments such as the distributary channel, tidal channel, and regressive barrier sands and in detecting/predicting the overpressure zones. Therefore, this will help to reduce the costs and risks that are usually associated with deepwater exploration and exploitation of petroleum sources.

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REFERENCES

- ADEBAYO, O.F., ORIJEMIE, A.E. & ATURAMU, A.O. 2012. Palynology of Bog-1 well, southwestern Niger Delta Basin, Nigeria. *International Journal of Science and Technology* 2(4), 214–222.
- ADEBAYO, O. F. 2014. Well log sequence stratigraphic and palynological analysis of Late Miocene to Pliocene Agbada Formation, Southwestern Niger Delta Basin, Nigeria. *Review of Environment and Earth Sciences* 1(4), 77–98.
- ADEBAYO, O.F. & OJO, A.O. 2014. Miocene-Pliocene vegetation and climate dynamics of the Niger Delta Basin based on palynological signatures. *Journal of Environment and Earth Science* 4(12), 58–67.
- ADEGOKE, O.S. 2002. High resolution biostratigraphy, sequence stratigraphy and 3-D modelling: Indispensable tools for E and P in the New Millennium. *Nigerian Association of Petroleum Explorationists Bulletin* 16(1), 46–65.
- ADEIGBE, O.C., OLA-BURAIMO, A.O. & MORONHUNKOLA, A.O. 2013. Palynological characterization of the Tertiary offshore Emi-1 Well, Dahomey Basin, southwestern Nigeria. *International Journal of Scientific and Technology Research* 2(1), 58–70.
- ALAO, O., OFUYAH, W. & ABEGUNRIN, A. 2014. Detecting and predicting over pressure zones in the Niger Delta, Nigeria: a case study of Afam Field. *Journal of Environment and Earth Science* 4(6), 13–20.
- AYINLA, H.A., OLA-BURAIMO, A.O., ADEIGBE, O.C., BANKOLE, S.A. & ADEBOWALE, M. 2013. Biostratigraphy and high-resolution paleoenvironmental reconstruction of part of Kemar-1 well, Bornu Basin, Northeastern Nigeria. *Journal of Research in Environmental Science and Toxicology* 2(3), 53–63.
- AYUK, A.M. & OLORUNNIWO, M.A. 2004. The use of seismic velocities for the prediction of abnormal pressures: a case study onshore Niger Delta, Nigeria. *Journal of Applied Geology and Geophysics* 3, 64–67.
- BARRON, A. P. & OBOH-IKUENOBE, F.E. 2014. Paleoenvironmental interpretations of Paleogene to early Neogene marine and terrestrial palynomorphs in the Deep Gulf of Mexico. GSA Annual Meeting in Vancouver, British Columbia Paper No. 218-18.
- BYRD, R.C., MILLER, D. J. & WIESE, S. M. 2014. Cost Estimating for Offshore Oil & Gas Facility Decommissioning. AACE®, *International Technical Paper*, 29 pp.
- CARVALHO, M.A. 2001. *Paleoenvironmental reconstruction based on palynology and palynofacies analyses of upper Aptian-middle Albian succession from Sergipe Basin, northeastern Brazil*. Doctoral thesis, Ruprecht-Karl Universität, Heidelberg.
- CARVALHO, M.A. 2004. Palynological assemblage from Aptian/Albian of the Sergipe basin: paleoenvironmental reconstruction. *Revista Brasileira de Paleontologia* 7(2), 159–168.
- CARVALHO, M.A., CABRAL RAMOS, R.R., CRUD, M. B., WITOVISK, L., KELLNER, A.W.A., SILVA, H.P., GRILLO, O.N., RIFE, D. & ROMANO, P.S.R. 2013. Palynofacies as indicators of paleoenvironmental changes in a Cretaceous succession from the Larsen Basin, James Ross Island, Antarctica. *Sedimentary Geology* 295, 53–66.
- CHOW, J. J., MING-CHING LI, & FUH, S. 2005. Geophysical well log study on the paleoenvironment of the hydrocarbon producing zones in the Erchungchi Formation, Hsinyin, SW Taiwan. *Journal of Terrestrial, Atmospheric and Oceanic Sciences (TAO)* 16(3), 531–543.
- CLARKE, R.T. 1996. *Peregrinipollis nigericus* – A new palynomorph from the upper Tertiary of Nigeria. *Grana Palynologica* 6(3), 540–554.
- COLEMAN, J. M. & PRIOR, D. B. 1981. Deltaic environments of

- deposition. In: Scholle, P. A. & Spearing, D. (eds), *Sandstone Depositional Environments*, 139–178. American Association of Petroleum Geologists Memoir 31.
- DEMCHUK, T.D., DOLBY, G., MCINTYRE, D.J. & SUTER, J.R. 2008. The utility of palynofloral assemblages for the interpretation of depositional paleoenvironments and sequence stratigraphic systems tracts in the McMurray Formation at Surmont, Alberta, 6. In: American Association of Petroleum Geologists Hedberg Conference, Banff, Alberta.
- DOUST, H. & OMATSOLA, E. 1990. Niger Delta. In: Edward, J.D. & Santogrossi, P. A. (eds), *Divergent/Passive Margin Basins*, 201–238. American Association of Petroleum Geologists Memoir 48.
- DURUGBO, E.U. OGUNDIPE, O.T. & ULU, O.K. 2010. Palynological evidence of Pliocene-Pleistocene climatic variations from Western Niger Delta, Nigeria. *International Journal of Botany* 6(4), 351–370.
- DURUGBO, E.U. & AROYEWUN, R.F. 2012. Palynology and paleoenvironments of the Araromi Formation, Dahomey Basin, Nigeria. *Asian Journal of Earth Sciences* 5(2), 50–62.
- ELLISON, J.C. 1993. Mangrove retreat with rising sea-level, Bermuda. *Estuarine, Coastal and Shelf Science* 37, 75–87.
- ELLISON, J.C. 2008. Long-term retrospection on mangrove development using sediment cores and pollen analysis: a review. *Aquatic Botany* 89, 93–104.
- EKWEOZOR, C.M. & DAUKORU, E.M. 1994. Northern delta depobelt portion of the Akata-Agbada(!) petroleum system, Niger Delta, Nigeria. In: Magoon, L.B. & Dow, W.G. (eds), *The Petroleum System – From Source to Trap*, 599–614. American Association of Petroleum Geologists Bulletin, v. AAPG Memoir 60.
- EMERY, D. & MYERS, K.J. (eds). 1996. *Sequence Stratigraphy*. Oxford, Blackwell Science.
- EVAMY, B.D., HAREMBOURE, J., KAMERLING, P., KNAPP, W.A., MOLLOY, F.A. & ROWLANDS, P.H. 1978. Hydrocarbon habitat of the Tertiary Niger delta. *American Association of Petroleum Geologists Bulletin* 62, 1–39.
- FADIYA, S.L. 2014. Impact of well site biostratigraphy on exploration drilling in the deepwater offshore Nigeria. *Journal of African Earth Sciences* 100, 60–69.
- FAEGRI, K. & IVERSEN, J. 1989. Textbook of pollen analysis (4th edn by Faegri, K., Kaland, P. E. & Krzywinski, K.). Chichester, John Wiley and Sons.
- GERMERAAD, C.A., HOPPING, J.H. & MULLER, J. 1968. Palynology of Tertiary sediments from tropical areas. *Review of Palaeobotany and Palynology* 6, 189–348.
- GRIMM, E.C. 1987. CONISS: A FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers and Geosciences* 13, 13–55.
- HOOD, K. C., WENGER, L. M., GROSS, O. P. & HARRISON, S. C. 2002. Hydrocarbon systems analysis of the northern Gulf of Mexico: Delination of hydrocarbon migration pathways using seeps and seismic imaging, In: Schumacher, D. & Leschack, L.A. (eds), *Surface Exploration Case Histories: Applications of Geochemistry, Magnetic, and Remote Sensing*, 25–40. AAPG Studies in Geology No. 48, and SEG Geophysical References Series No. 11, .
- HOPPING, C. A. 1967. Palynology and the oil industry. *Review of Palaeobotany Palynology* 2, 23–48.
- HORNE, J.C., FERM, J.C., CARUCCIO, F.T. & BAGANZ, B.P. 1978. Depositional models in coal exploration and mine planning in Appalachian region. *American Association of Petroleum Geologists Bulletin* 62, 2379–2411.
- IGE, O.E. 2011. Vegetation history of the Late Tertiary Niger Delta, Nigeria, based on pollen record. *Research Journal of Botany* 6(1), 21–30.
- IGE, O.E., DATTA, K., SAHAI, K. & RAWAT, K.K. 2011. Palynology studies of sediments from North Chioma-3 well, Niger Delta and its palaeoenvironmental interpretations. *American Journal of Applied Sciences* 8(12), 1249–1257.
- KNOX, G. J. & OMATSOLA, E. M. 1989. Development of the Cenozoic Niger Delta in terms of the 'Escalator Regression' model and impact on hydrocarbon distribution. In: van der Linden, W.J.M., Cloetingh, S.A.P.L., Kaasschieter, J.P.K., van der Graff, W.J.E., Vandenbergh, J. & van der Gun, J.A.M. (eds), *Proceedings KNGMG Symposiums Coastal Lowlands, Geology and Geotechnology*, 181–202. Amsterdam, Kluwer Academic Publishers.
- KULKE, H. 1995. Nigeria. In: Kulke, H. (ed.), *Regional Petroleum Geology of The World, Part II: Africa, America, Australia and Antarctica*, 143–172. Berlin, Gebru Borntraeger.
- LOCATELLI, E.R. 2011. Vegetation history of the Late Holocene in East Glacier National Park, Montana: a paleoenvironmental study. Honors Projects. Paper 9. Online at: http://digitalcommons.maclester.edu/geology_honors/9
- LEGOUX, O. 1978. Quelques espaces de pollen caractéristiques du Neogene du Nigeria. *Bulletin Centres Recherche Exploration-Production d'Elf-Aquitaine* 2(2), 265–317.
- MAGOON, L.B. & DOW, W.G. 1994. The petroleum system. In: Magoon, L.B. & Dow, W.G. (eds), *The Petroleum System – From Source to Trap*, 60. American Association of Petroleum Geologists Memoir 3–24.
- MAGOON, L.B. & SCHMOKER, J.W. 2000. The total petroleum system—The natural fluid network that constrains the assessment unit: In: U.S. Geological Survey World Energy Assessment Team (ed.), *U.S. Geological Survey World Petroleum Assessment 2000—Description and Results*. U.S. Geological Survey Digital Data Series DDS-60.
- MCDADE, E. C., SASSEN, R., WENGER, L. M. & COLE, G. A. 1993. Identification of organic-rich Lower Tertiary shales as petroleum source rocks, south Louisiana. *Gulf Coast Association of Geological Societies Transactions* 43, 257–267.
- MOORE, P.D., WEBB, J.A. & COLLINSON, M.E. 1991. *Pollen Analysis* (2nd edn). London, Blackwell Scientific Publication.
- MORLEY, R.J. 1986. New approaches to stratigraphic and palaeoenvironmental modeling in Neogene deltaics, with emphasis on the Niger Delta. Proceedings of the Third Annual Conference. Nigerian Association of Petroleum Exploration. 2(1), 29–30.
- MORLEY, R.J. 1995. Biostratigraphic characterization of systems tracts in Tertiary sedimentary basins. *Proceedings of the International Symposium on Sequence Stratigraphy in S.E. Asia*, 49–71.
- MORLEY, R.J. & RICHARDS, K. 1993. Gramineae cuticle: a key indicator of Late Cenozoic climatic change in the Niger Delta. *Review of Palaeobotany and Palynology* 77, 119–127.
- MORLEY, R.J., MORLEY, H.P., WONDERS, A.A.H., SUKARNO & VAN DER KAARS, S. 2004. Biostratigraphy of modern (Holocene and Late Pleistocene) sediment cores from Makassar Straits. In: Noble, R.A., et al. (eds), *Proceedings Deepwater and Frontier Exploration in Asia and Australasia Symposium*, 361–371. Jakarta, Indonesian Petroleum Association.
- MULLER, J. 1981. Fossil pollen records of extant angiosperms. *The Botanical Review* 47 (1), 1–142.
- NWOZOR, K.K., OMUDU, M.L., OZUMBA, B.M., EGBUACHOR, C.J., ONWUEMESI, A.G. & ANIKE, O.L. 2013. Quantitative evidence of secondary mechanisms of overpressure generation: insights from parts of onshore Niger Delta, Nigeria. *Petroleum Technology Development Journal* 3(1), 64–83.
- OBOH, F.E. 1990. *Palaeoenvironmental reconstruction of the E2.0 reservoir in the Kolo Creek field, Niger Delta, Nigeria*. Ph.D. thesis, University of Cambridge.
- OBOH, F.E. 1991. Recognizing environments in the deposits of the Niger delta (abstract). *American Association of Petroleum Geologist Bulletin* 75, 647.
- OBOH, F.E. 1992. Middle Miocene palaeoenvironments of the Niger Delta. *Palaeogeography, Palaeoclimatology, Palaeoecology* 92, 55–84.
- OBOH, F.E. & SALAMI, M.B. 1989. Lithostratigraphical and palynostratigraphical studies of Igbomatoru-1 Well, Niger Delta. *Journal of African Earth Sciences* 9, 531–540.
- OBOH, F.E. SALAMI, M.B. & CHAPMAN, J.L. 1992. Palynological interpretation of the palaeoenvironments of Miocene strata of the well Igbomatoru-1, Niger delta. *Journal of Micropalaeontology* 11, 1–6.
- OBOH, F.E. 1993. Depositional history of the Middle Miocene E2.0 Reservoir in the Kolo Creek Field, Niger Delta. *Journal of Petroleum Geology* 16, 197–212.
- OBOH, F.E. 1995. Sedimentological and palynological characteristics of E2.0 reservoir (Middle Miocene) in the Kolo Creek Field, Niger Delta. In: Oti, M.N. & Postma, G. (eds), *Geology of Deltas*, 243–256. Rotterdam/Brookfield, A.A. Balkema.
- OJO, A.O. & GBADAMOSI, A.O. 2013. Sequence palyno-stratigraphical study of Del-2 well Southwest of the Niger Delta Basin Nigeria. *Research Journal in Engineering and Applied Sciences* 2(2), 86–94.
- OLA-BURAIMO, O.A. & BOBOYE, O.A. 2011. Palynological investigation of the Albian to Lower Cenomanian Bima Formation, Bornu Basin, Nigeria. *World Applied Science Journal* 12(7), 1026–1033.
- OLA-BURAIMO, A.O. & AKAEGBOBI, I.M. 2012. Neogene dinoflagellate cysts assemblages of the Late Miocene-Pliocene Ogwashi/Asaba sediments in Umuna-1 well, Anambra Basin, southeastern Nigeria. *Journal of Petroleum and Gas Exploration Research* 2(6), 115–124.
- OLAYIWOLA, M.A. 2014. *Palynostratigraphy and correlation of three wells in the deep offshore Cenozoic Niger Delta*. Unpublished Ph.D. thesis, University of the Witwatersrand, Johannesburg.
- OLAYIWOLA, M.A. & BAMFORD, M.K. 2016. Palynology: A useful tool in understanding palaeoclimatic changes through the Pliocene-Pleistocene from the deep offshore Niger Delta, Nigeria. *Revue de micropaléontologie* 59, 41–55. Online at: <http://dx.doi.org/10.1016/j.revmic.2015.09.003>.
- OMOLAIYE, G. E, OJO, J. S, OLADAPO, M. I. & AYOLABI, E.A. 2011.

- Overpressure prediction of the Efomeh field using synthetic data, onshore Niger Delta, Nigeria. *Exploration Geophysics* **42** (1), 50–57.
- OSINOMO, O.O., OLADUNJOYE, M.A. & OLAYINKA, A. I. 2007. Overpressure prediction from seismic data: implications on drilling safety. American Geophysical Union, Fall Meeting, Abstract.
- OWALABI, O.O., OKPOBIRI, G.A. & OBOMANU, I.A. 1990. Prediction of abnormal pressure in the Niger Delta using well logs. CIM/SPE International Technical Meeting, Calgary, Canada.
- OWOYEMI, A.O. & WILLIS, B. J. 2006. Depositional patterns across syndepositional normal faults, Niger Delta, Nigeria. *Journal of Sedimentary Research* **76**, 346–363.
- OYEDELE, K.F., OLADELE, S., OGAGARUE, D.O. & BAKARE, K. 2012. Sequence stratigraphic approach to hydrocarbon exploration in Bobsaa field, onshore Niger Delta. *Journal of Petroleum and Gas Exploration Research* **2**(6), 106–114.
- POSAMENTIER, H.W. & VAIL, P.R. 1988. Eustatic controls on clastic deposition. II—sequence and systems tract models. In: Wilgus, C.K., Hastings, B.S., et al. (eds), *Sea-Level Changes: An Integrated Approach*, 124–154. Special Publication of the Society of Economic Paleontology and Minerals **42**.
- POUMOT, C. 1989. Palynological evidence for eustatic events in the tropical Neogene. *Bulletin Centres Recherche Exploration-Production d'Elf-Aquitaine* **13**(2), 447–453.
- POVILASKAS, L. 2013. Palinología de angiospermas de la formación Monte Chico (Cretácico Superior) de la Provincia de Santa Cruz, Argentina. *Revista brasileira de paleontologia* **16**(1), 115–126.
- REBATA-H., L.A., RÄSÄNEN, M.E., GINGRAS, M.Y.K., VIEIRA Jr, V., BARBERI, M. & IRION, G. 2006. Sedimentology and ichnology of tide influenced Late Miocene successions in western Amazonia: the gradational transition between the Pebas and Nauta formations. *Journal of South American Earth Sciences* **21**, 96–119.
- RUGMAIA, W., GROTEA, P.J., CHONGLAKMANIC, C., ZETTERD, R. & FERGUSON, D.K. 2008. A Late Pleistocene palynoflora from the coastal area of Songkhla Lake, southern Thailand. *Science Asia* **34**, 137–145.
- RIDER, M.H. 1990. Gamma-ray log shape used as a facies indicator: critical analysis of an oversimplified methodology. In: Hurst, A., Lovell, M.A. & Morton, A.C. (eds), *Geological Applications of Wireline Logs*, 27–37. Geological Society Special Publication No. **48**.
- SHAMSUDDIN, A.H.M., BROWN, T. A., LEE, S. & CURIALE, J. 2001. Petroleum Systems of Bangladesh. South East Asia Petroleum Exploration Society, Exploration Conference, Orchard Hotel, Singapore 35 p.
- SAIFULLAH, S. S. & PUDJIHANTO, S. 1996. Cost study for offshore exploratory drilling operation; The AAPG/datapage combined publication database: Indonesian Petroleum Association, *25th Annual Convention Proceedings* **3**, 31–42.
- SALARD-CHEBOLDAEFF, M. 1979. Palynologie Maestrichtienne et Tertiaire du Cameroun. Etude qualitative et répartition verticales des principales espèces. *Review of Paleobotany and Palynology* **28**, 365–388.
- SALARD-CHEBOLDAEFF, M. 1990. Intertropical African palynostratigraphy from Cretaceous to Late Quaternary times. *Journal of African Earth Sciences* **11**(1/2), 1–24.
- SARAH, J., McLEAN, D. & OLIVER, D. 1995. Development of a sequence stratigraphic framework for an Upper Carboniferous Basin – New concepts using spectral gamma-ray response and palynology. AAPG Search and Discovery Article #91020 1995 AAPG Annual Convention, Houston, Texas.
- SELLEY, R. C. 1985. *Elements of Petroleum Geology*. New York, W.H. Freeman and Company.
- SHORT K.C. & STAUBLE, A.J. 1967. Outline of the geology of Niger Delta. *American Association of Petroleum Geologist Bulletin* **51**, 761–779.
- STUCHLIK, L. (ed.). 2001. *Atlas of Pollen and Spores of the Polish Neogene*. Kraków, W Szafer Institute of Botany, Polish Academy of Sciences.
- TABAEI, M. & SINGH, R.Y. 2002. Paleoenvironment and paleoecological significance of microforaminiferal linings in the Akli Lignite, Barmer Basin, Rajasthan, India. *Iranian International Journal of Science* **3**(2), 263–277.
- TRAVERSE, A. 2007. *Paleopalynology* (2nd edn). Dordrecht, Springer.
- TUTTLE, M.L.W., BROWNFIELD, M.E. & CHARPENTIER, R.R. 1999. Tertiary Niger Delta (Akata-Agbada) Petroleum System (No. 701901), Niger Delta Province, Nigeria, Cameroon, and Equatorial Guinea, Africa. U. S. Geological Survey Open File Report 99-50H.
- UNUKOGBON, N.O., ASUEN, G.O. & EMOFURIETA, W.O. 2008. Sequence stratigraphic appraisal: Coastal Swamp Depobelt in the Niger Delta Basin, Nigeria. *Global Journal of Geological Sciences* **6**(2), 129–137.
- VINNEM, J.E. 2010. Risk indicators for major hazards on offshore installations. *Safety Science*, **48**, 778–787.
- WAGSTAFF, B. E., GALLAGHER, S. J. & LANIGAN, K. P. 2006. Late Cretaceous palynological correlation and environmental analyses of fluvial reservoir facies of the Tuna Field, Gippsland Basin, southeast Australia. *Review of Palaeobotany and Palynology* **138**, 165–186.
- WOOD, G.D., GABRIEL, A.M. & LAWSON, J.C. 1996. Palynological techniques – processing and microscopy. In: Jansonius, J. & McGregor, D.C. (eds), *Palynology: Principles and Applications*, **1**, 29–50. Association of Stratigraphical Palynologists Foundation.
- WRIGHT, J.B., HASTINGS, D.A., JONES, W.B. & WILLIAMS, H.R. 1985. *Geology and Mineral Resources of West Africa*. London, Allen and Unwin.
- ZIEGLER, K., TURNER, P. & DAINES, S.R. 1997. Petroleum geology of the southern North Sea: future potential. *Geological Society Special Publication* **123**. London, Geological Society.

New specimens of the basal ornithischian dinosaur *Lesothosaurus diagnosticus* Galton, 1978 from the Early Jurassic of South Africa

Paul M. Barrett^{1,2,*}, Richard J. Butler^{2,3}, Adam M. Yates^{2,4}, Matthew G. Baron^{1,5} & Jonah N. Choiniere^{2,6}

¹Department of Earth Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

²Evolutionary Studies Institute, University of the Witwatersrand, Private Bag 3, WITS 2050, Johannesburg, South Africa

³School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, U.K.

⁴Museum of Central Australia, Museum and Art Gallery of the Northern Territory, Corner of Larapinta Drive and Memorial Avenue, Araluen Cultural Precinct, P.O. Box 3521, Alice Springs NT 0871, Australia

⁵Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge, CB2 3EQ, U.K.

⁶School of Geosciences, University of the Witwatersrand

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We describe new specimens of the basal ornithischian dinosaur *Lesothosaurus diagnosticus* Galton, 1978 collected from a bonebed in the Fouriesburg district of the Free State, South Africa. The material was collected from the upper Elliot Formation (Early Jurassic) and represents the remains of at least three individuals. These individuals are larger in body size than those already known in museum collections and offer additional information on cranial ontogeny in the taxon. Moreover, they are similar in size to the sympatric taxon *Stormbergia dangershoeki*. The discovery of three individuals at this locality might imply group-living behaviour in this early ornithischian.

Keywords: Ornithischia, Free State, upper Elliot Formation, ontogeny, sociality.

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INTRODUCTION

The Early Jurassic upper Elliot Formation of South Africa and Lesotho has yielded abundant material of primitive ornithischian dinosaurs and currently represents the best available window on early ornithischian evolution. The fauna includes four heterodontosaurid taxa (*Abrictosaurus consors*, *Heterodontosaurus tucki*, *Lycorhinus angustidens* and *Pegomastax africanus*; e.g. Porro *et al.* 2011; Sereno 2012) and the basal ornithischians *Lesothosaurus diagnosticus* and *Stormbergia dangershoeki* (e.g. Butler 2005). Several of these taxa are represented by multiple individuals and include excellently preserved skull and postcranial material as in *Heterodontosaurus* (Santa Luca *et al.* 1976; Santa Luca 1980; Butler *et al.* 2008a; Norman *et al.* 2011; Sereno 2012; Galton 2014) and *Lesothosaurus* (Thulborn 1970, 1972; Galton 1978; Santa Luca 1984; Sereno 1991; Knoll 2002a,b; Porro *et al.* 2015). However, although *Lesothosaurus* is known on the basis of three-dimensionally preserved skulls and partial postcranial material, complete skeletons have yet to be recovered. Moreover, numerous features of the skull anatomy (e.g. relatively large orbits, lack of fusion between braincase elements), the small size of the material, and some histological evidence suggests that all of the specimens

referred to this taxon thus far are juvenile individuals (e.g. Knoll *et al.* 2010; Porro *et al.* 2015).

The lack of larger subadult or adult material for *Lesothosaurus* poses two problems for our current understanding of early ornithischian diversity and evolution. The first of these is taxonomic: it has been suggested that *Stormbergia* might be an adult morph of *Lesothosaurus* rather than a distinct genus (Knoll *et al.* 2010). *Stormbergia* was distinguished from *Lesothosaurus* on the basis of ischial morphology (Butler 2005), but all of the available specimens of *Stormbergia* represent individuals that are substantially larger than those referred to *Lesothosaurus*. Consequently, it has been suggested that the proposed ischial differences might be of ontogenetic, rather than taxonomic, significance (Knoll *et al.* 2010). Secondly, the lack of adult material may affect the position of *Lesothosaurus* in phylogenetic analyses. *Lesothosaurus* has been recovered in several positions within the ornithischian tree, including as a non-genasaurian ornithischian, a non-cerapodan neornithischian, and a basal thyreophoran (Sereno 1986, 1999; Butler *et al.* 2007, 2008b; Boyd 2015). This instability may be the result of genuine character conflict, lack of key character data, or incomplete lineage sorting close to the base of the ornithischian tree, but it

*Author for correspondence. E-mail: p.barrett@nhm.ac.uk

might also result from the phenomenon whereby juvenile individuals included in analyses cause taxa to move stem-ward due to the absence of more derived, adult morphologies (e.g. Tsuihiji *et al.* 2011; Campione *et al.* 2013).

Here we describe new material of *Lesothosaurus* representing a minimum of three individuals derived from a single bonebed. Two of these are larger than either of the syntype specimens of *Lesothosaurus* or of any of the referred specimens previously reported in the literature (Thulborn 1970, 1972; Santa Luca 1984; Sereno 1991; Knoll 2002a,b; Butler 2005).

LOCALITY AND HORIZON

In 2007, the Keyser family mentioned the presence of dinosaur bones on their property, known as Aushan Grey, to A.M.Y. Subsequent investigations by A.M.Y. in March 2007 revealed that Aushan Grey (formerly part of the farm Landkloof 73: situated at S 28°35'25.6" E 28°03'0.56"), in the Fouriesburg district of Free State Province, South Africa, contained exposures of the upper part of the 'Stormberg group' (the upper part of the Karoo Supergroup) and that the dinosaur bones originated from the upper part of the Elliot Formation (dated as either Hettangian–Sinemurian or Pliensbachian: Olsen & Galton 1984; Yates *et al.* 2004). The bulk of the deposit at this site consisted of laminated overbank siltstones and mudstones. The ornithischian specimens described here were found in a layer sitting on a resistant, bench-forming pedogenic nodule bed, or were found *ex situ* immediately below this bench. The ornithischian fossils were distributed over a 6 m stretch of exposure. No other taxa were found at this level although sauropodomorph dinosaurs and a tritylodontid cynodont were found at other stratigraphic levels.

MATERIAL AND IDENTIFICATION

The majority of the ornithischian specimens were found in situ in a small dense accumulation of bones a few tens of

centimetres across, but one of the specimens (BP/1/6581) was found *ex situ* lying immediately below the level of the bench, although it is likely that it was derived from the same accumulation. Two isolated bones, a surangular (BP/1/6580) and a scapula (BP/1/6583) were found in the same horizon a few metres distant from the main accumulation. At least three individuals are represented within the sample on the basis of scapula size, with scapula midshaft diameters of 11, 18 and 27 mm, in BP/1/6581, BP/1/6582 and BP/1/6583, respectively. It is possible that the isolated surangular (BP/1/6580) pertained to one of the larger individuals present (e.g. BP/1/6582), but it might also represent a fourth individual. Charlton Dube (BP), A.M.Y. and Scott Moore-Fay (formerly NHMUK) prepared the fossils mechanically using an aircscribe. Breaks were repaired with cyanoacrylate glue. Some fossil bones were consolidated after preparation with an approximately 10% solution of Paraloid B-72 solid grade thermoplastic acrylic resin in 100% acetone solvent.

Although the available material of the individuals present is largely non-overlapping, there are no clear differences in morphology that suggest the presence of more than one ornithischian taxon in the sample. Each element in the assemblage is consistent in anatomy with other specimens referred to *Lesothosaurus diagnosticus* (see Thulborn 1970, 1972; Santa Luca 1984; Sereno 1991; Knoll 2002a,b; Butler 2005; Porro *et al.* 2015). Two cranial features support referral of this material to *Lesothosaurus*: the presence of a shallow groove that extends along the dorsal surface of the surangular, backed by a medial ridge (in BP/1/6580: Fig. 1) and the presence of a tongue-in-groove articulation between the maxilla and lacrimal (in BP/1/6581: Figs 2–3). The combined presence of a dorsal groove and medial ridge on the surangular appears to be unique to *Lesothosaurus* and has been proposed as an autapomorphy of the taxon (Butler 2010). Sereno (1991) proposed that the presence of a tongue-in-groove articulation between the maxilla and lacrimal was autapomor-

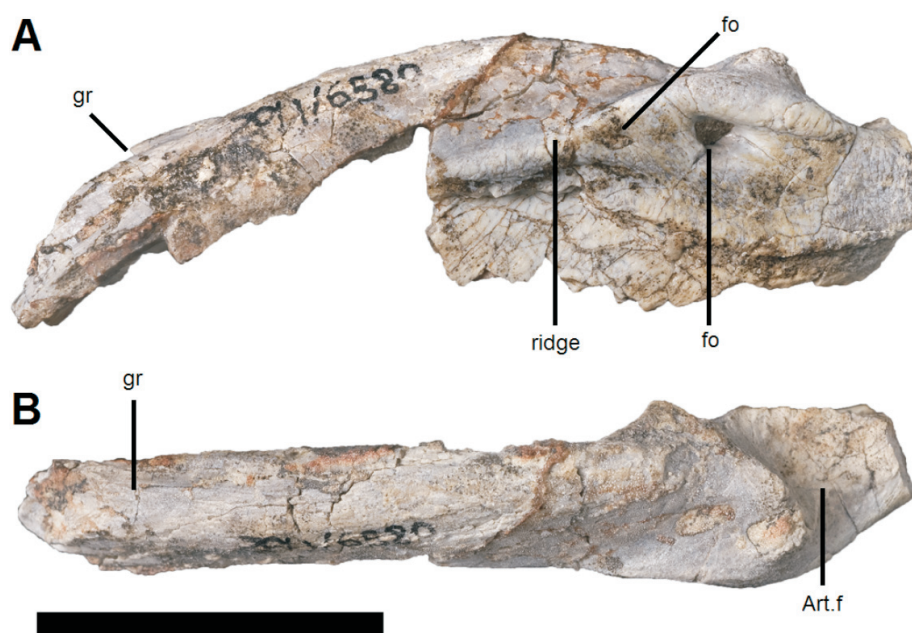


Figure 1. Left surangular (BP/1/6580). **A**, Lateral view; **B**, dorsal view. Scale bar = 20 mm.

phic of *Lesothosaurus*, but this was questioned by Butler (2005) who regarded the distribution of this character as unclear. Nevertheless, no other ornithischians from the Early Jurassic of southern Africa possess this feature (see Sereno 2012) and we regard it as positive evidence for the referral of BP/1/6581 to *Lesothosaurus*. No postcranial autapomorphies currently diagnose *Lesothosaurus* (Butler 2005) and the referral of the two postcranial specimens from this assemblage to this taxon is based on i) their close association with the diagnostic cranial elements and ii) the possibility that the isolated angular might pertain to one of these individuals.

DESCRIPTION

BP/1/6580

This specimen consists of a left surangular that lacks its retroarticular process, rostral-most portion and parts of the ventral margin (Fig. 1). In lateral view, the surangular is shallowly arched and its dorsal margin forms a low coronoid eminence. A strong ridge is present on the caudal part of the lateral surface and extends rostroventrally at approximately 15 degrees to the horizontal, towards the articular surface for the angular (Fig. 1A). The ridge originates at the rostral margin of the articular fossa and extends to a point at least halfway along the length of the coronoid eminence. It delimits the lateral and ventral margins of a dorsally facing concavity that contains a large foramen, which is visible in dorsal view only. Ventral to the ridge, another large foramen is present, which is set within a short, but deep, caudoventrally opening groove. A third smaller foramen lies rostral to the latter, just below the ridge. This lateral ridge is thick and overhangs the anterior part of the articular facet for the angular. This articular facet is striated and depressed relative to the rest of the surangular's lateral surface. The posterior part of the angular articular facet is delimited dorsally by a thin, sharp, horizontally oriented ridge.

In dorsal view, the dorsal surface of the surangular is inflected laterally to form a shallow groove that extends along the element rostrocaudally (Fig. 1B). The medial margin of the groove is formed by a distinct ridge, while the lateral margin is defined by a change in slope. This combination of features is considered to be autapomorphic for *Lesothosaurus* (Butler 2010). Rostrally, the dorsal surface of the surangular is bevelled to form a contact for the coronoid process of the dentary. Immediately caudal to the coronoid eminence, a saddle-shaped sulcus for the reception of the articular is present. This sulcus is delimited rostrally by a prominent transverse ridge, caudally by a low, but distinct, transverse ridge and medially by a low lip of bone, but there is no distinct border laterally. The broken base of retroarticular process has a teardrop-shaped transverse cross-section.

In medial view, the dorsal margin of the surangular overhangs the internal mandibular fossa. This area increases in depth rostrally and its ventral surface is deeply invaginated by the dorsal-most part of the internal mandibular fossa. The area ventral to the articular fossa is shallowly concave for the reception of the prearticular:

this region is separated from the internal mandibular fenestra by a low rostroventrally extending ridge that originates from the rostroventral corner of the articular fossa.

BP/1/6581

General comments

This specimen consists of the rostral part of a crushed skull with associated postcranial material (Figs 2–3). The left-hand side of the skull is the most informative, as the right-hand side has been sheared ventrally with respect to the left, has suffered more crushing and disruption, and is obscured by postcranial elements. The left-hand side of the skull includes an incomplete premaxilla, maxilla, lacrimal, parts of the nasal, prefrontal, jugal and palpebral, as well as a partial dentary and splenial (Figs 2A, 3A). Several partial elements from the right-hand side of the skull are preserved, including the premaxilla, maxilla, lacrimal, prefrontal, jugal, ?frontal, palpebral and dentary. Postcranial elements visible on the right-hand side comprise a vertebra, humerus, ?ulna, scapula and ?rib fragments (Figs 2B, 3B). Due to breakage and the close apposition of many elements, only partial descriptions can be provided. Measurements are provided in Table 1.

Table 1. List of measurements BP/1/6581. All measurements in mm. A ‘**’ indicates measurement of an incomplete element, measured as preserved.

Maximum length of maxilla	51*
Maximum length of dentary	55*
Height of dentary immediately anterior to coronoid eminence	17.5
Length of humerus	72
Distal width of humerus	18
Length of scapula	75*
Scapula midshaft height	11

Premaxilla

The premaxillae are poorly preserved and offer few useful details (Figs 2–3). Parts of both elements are present, with the left slightly better represented, but both are extensively cracked and broken. The premaxillae are in articulation, but sheared off rostrally, to reveal the narial cavity in anterior view. The left premaxilla has an elongate, tapering caudolateral process, which is heavily cracked (Figs 2A, 3A). It articulates with the rostradorsal margin of the maxilla, but breakage obscures the morphology of any premaxillary/nasal/lacrimal contacts. A small sub-triangular flange of bone ventral to the preserved part of the left premaxilla and the rostral border of the left maxilla may represent a strongly deformed caudoventral process. As preserved, the surface of this flange is concave and bounded by a longitudinal ridge along its dorsal margin.

A possible premaxillary tooth is preserved ventral to the right premaxillary fragment. Both the crown and the root are exposed: the root is approximately twice the length of the crown and has a subcircular cross-section, but tapers basally. The root is constricted both labiolingually and mesiodistally immediately basal to the crown. Above this constriction, the crown expands in both directions, but especially mesiodistally. The apicobasal height of the

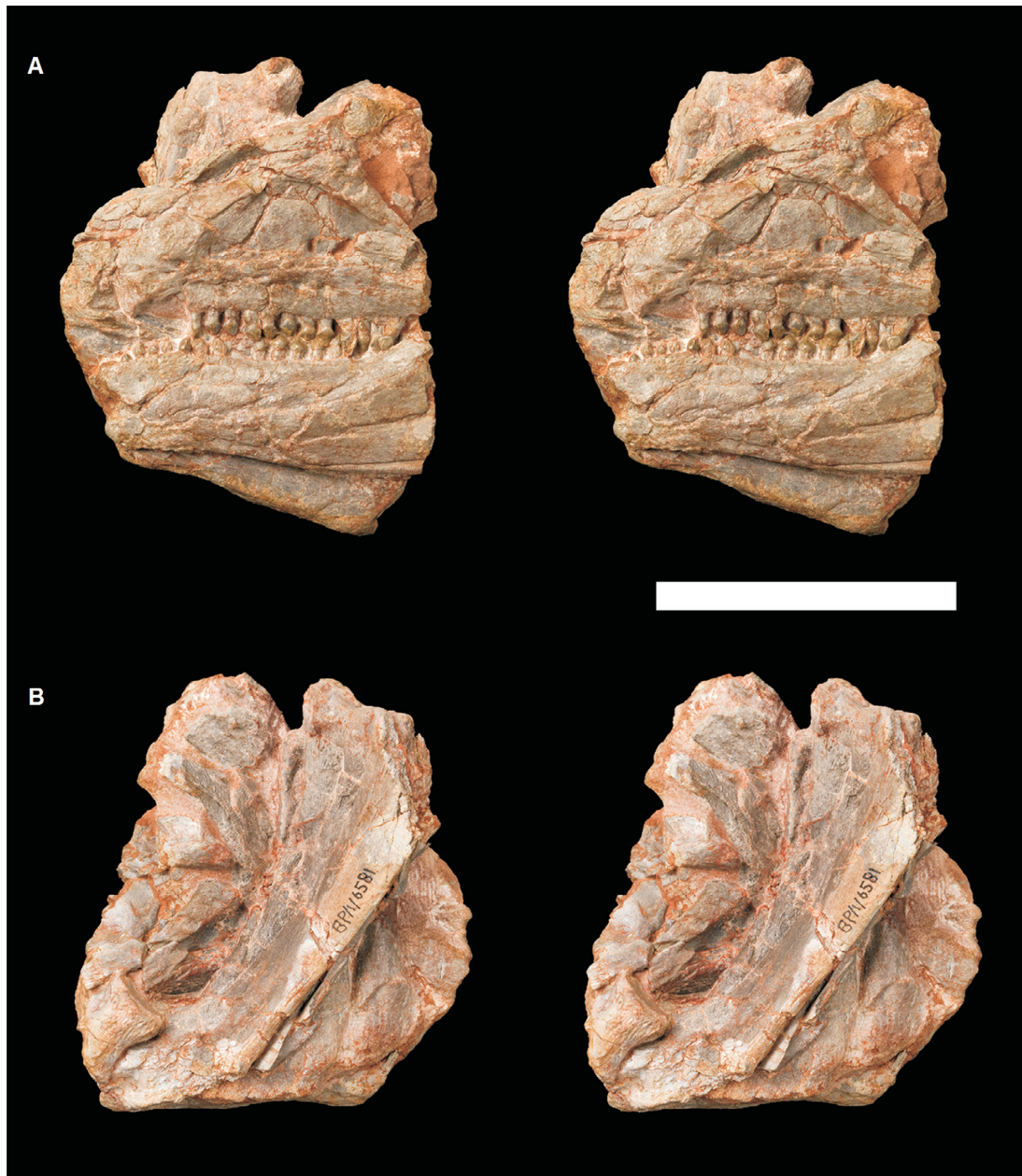


Figure 2. Stereophotographs of partial skull and articulated postcranial elements of BP/1/6581. **A**, Left lateral view; **B**, right lateral view. Scale bar = 50 mm.

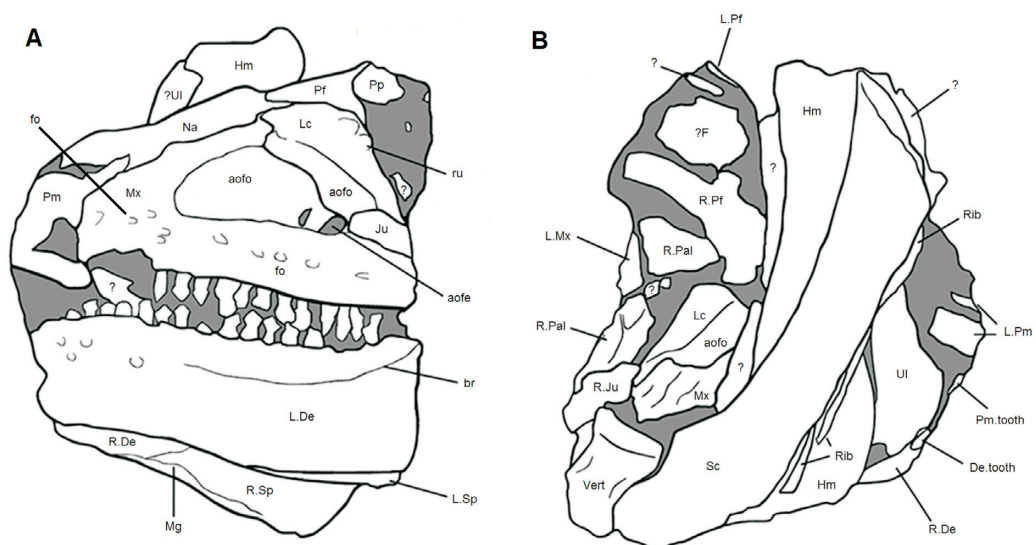


Figure 3. Interpretative line drawings of partial skull and articulated postcranial elements of BP/1/6581. **A**, Left lateral view; **B**, right lateral view.

crown exceeds its mesiodistal width and the crown apex is slightly recurved and lacks denticles.

Maxilla

The left maxilla is missing its rostroventral and caudal-most parts, and the preserved portion has a triangular outline in lateral view (Figs 2A, 3A). The maxilla contacts the premaxilla rostrally, the nasal rostr dorsally, the lacrimal caudodorsally and its tooth-bearing ramus is overlapped by the jugal caudodorsally. Its lateral surface is embayed by a large subtriangular antorbital fossa, which is defined rostrally and ventrally by prominent ridges (the latter corresponding to the 'lateral lamina'). The internal surface of the antorbital fossa is shallowly convex and is depressed in its rostroventral corner and at the point adjacent to its contact with the lacrimal. The maxilla forms an extensive sheet-like medial lamina that closes the fossa medially and which is pierced by a small, elliptical and caudally situated antorbital fenestra. A second smaller elliptical foramen pierces the medial lamina rostral to the antorbital fenestra (Figs 2A, 3A).

In lateral view, the ascending process tapers in rostro-caudal width as it extends dorsally. The apex of the ascending process extends lateral to the rostral part of the lacrimal to form a tongue-in-groove joint with the latter (Figs 2A, 3A). The maxillary toothrow is not inset medially with respect to the rest of the maxillary surface and there is no distinct buccal emargination, although this may have been affected by crushing. There are 13 preserved tooth positions, 12 of which contain teeth. Based on the length of the preserved portion, and comparisons with the proportions of other more complete specimens (e.g. NHMUK PV R8501, NHMUK RU B23), approximately 18 tooth positions would have been present if the maxilla was complete. The tooth-bearing ramus tapers slightly caudally and the dorsal surface of its caudal part is grooved for the reception of the jugal.

Numerous foramina pierce the lateral surface of the maxilla: four of these lie in a distinct cluster rostroventral to the antorbital fossa in the region between the fossa and the premaxillary articulation. These foramina open rostrally and a prominent groove extends rostrally from the dorsal-most foramen to the premaxillary/maxillary articulation. In addition, a line of at least three (possibly four) subcircular nutrient foramina extends parallel to the tooth row (Figs 2A, 3A).

Dental morphology is consistent along the tooth row, although the tooth crowns vary in size. The ninth preserved tooth (counting from the rostral end of the tooth row) is the largest and positioned in the caudal-most third of the tooth row (Figs 2A, 3A). In the rostral half of the preserved tooth row, adjacent tooth crowns do not overlap, although slight imbrication is present between the caudal-most teeth. Tooth crowns are low and triangular in labial view, with apicobasal heights that are subequal to their mesiodistal lengths. The tooth crowns are expanded both labiolingually and especially mesiodistally with respect to the root. The root is slightly constricted in both directions beneath the crown creating a distinct 'neck' and 'cingulum'. The mesial margin of the crown is slightly

longer than the distal margin, so that crown apex is slightly offset distally, but there is no recurvature. Coarse denticles are present on both the mesial and distal crown margins. There are 8–10 denticles along each crown margin, though the number is variable between teeth. No primary or secondary ridges are present on any of the tooth crowns, a distinct central eminence is absent, and the mesial- and distal-most denticles are not supported by strong ridges basally. No other crown ornament is present and there is no evidence for tooth wear. In mesial view, the labiolingual expansion of the tooth crowns is asymmetrical, with the greatest expansion on the labial side. Part of the right maxilla is exposed on the reverse of the skull block, in articulation with the jugal, but it offers no useful details.

Lacrimal

Both lacrimals are present, but the following description is based on the more complete left lacrimal (Figs 2A, 3A). The lacrimal has a quadrangular outline in lateral view and forms the caudal margin of the antorbital fossa, the caudodorsal margin of the antorbital fenestra and the rostral border of the orbit. The rostroventral portion of the lateral surface is deeply embayed to form the rostr dorsolateral section of the antorbital fossa. This embayment is framed by a sharp ridge, which partially overhangs the fossa and extends rostr dorsolaterally from the jugal contact. Ventrally, the lacrimal is overlapped laterally by the jugal, while rostrally its tip bears a 'U'-shaped sulcus that articulates with the ascending process of the maxilla in a tongue-in-groove arrangement, which we consider to be distinctive for *Lesothosaurus* (see above: Sereno 1991). Dorsally, the lacrimal contacts the nasal rostr dorsolaterally and the prefrontal caudodorsally. Ventral to the contact with the prefrontal and adjacent to the palpebral, the lateral surface of the lacrimal is roughened and bears two prominent rugosities or nodes close to the orbital margin.

Jugal

A small subrectangular bone fragment lying dorsal to the caudal part of the left maxilla, and overlapping the ventral part of the lacrimal, probably represents the rostral-most part of the left jugal (Figs 2A, 3A). It forms a small contribution to the caudoventral margin of the antorbital fossa and has a dorsoventrally convex lateral surface. The rostral-most part of the right jugal is also present (Figs 2B, 3B): it is broken into two pieces, with the rostral part preserved in articulation with the right lacrimal and maxilla. The rostral end of the right jugal is slightly embayed by the antorbital fossa.

Nasal

Parts of the left and right nasal are present, positioned between the lacrimal and the caudolateral process of the premaxilla (Figs 2–3). The contact between the nasal and the maxilla is generally a linear butt-joint, although a small, rounded dorsal deviation in the suture appears to be present at the level of the rostrocaudal midpoint of the antorbital fossa. The posterolateral corner of the nasal tapers to a narrow process that extends ventral to the

rostral end of the prefrontal, separating the latter from the lacrimal (Figs 2A, 3A). The lateral surface of this process is faintly rugose. The dorsal surface of the nasal is smooth and bears no foramina or other distinguishing features.

?Frontal

A small, flat quadrangular plate of bone situated between the prefrontals may represent a fragment of one of the frontals, but this identification is based solely on positional evidence (Figs 2B, 3B). It offers no useful anatomical details.

Prefrontal

A triangular plate of bone in contact with the left nasal and lacrimal represents the rostral process of the left prefrontal, but its caudal process is missing and its shape has been affected by crushing and breakage (Figs 2A, 3A). The right prefrontal is also present and incomplete caudally (Figs 2B, 3B). As preserved, the rostral process is broadest caudally and tapers rostrally. Its dorsal surface is shallowly concave rostrally, but planar posteriorly and the whole element is shallowly arched rostrocaudally. The rostral margin of the process extends to a point level with the rostral margin of the lacrimal. Its medial margin, which would have contacted the frontal, forms a straight articular surface. Caudovertrally, the prefrontal is thickened to form the articular region for the palpebral.

Palatine

The right palatine is preserved in dorsal view and lies medial to the right jugal (Figs 2B, 3B). The lateral margin of the element is thickened, forming a distinct ridge. A second subsidiary ridge arises from the lateral margin and divides the dorsal surface into rostral and caudal depressions. The caudal depression is longer and more strongly concave than the rostral depression.

Palpebral

Fragments of both palpebrals are preserved, but include the articular region only (Figs 2–3). The articular region is stout and broad based, with a subpyramidal cross-section.

Dentary

The right dentary is almost completely obscured (Figs 2B, 3B) and the left dentary lacks its rostral and caudal extremities. In lateral view, the dorsal and ventral margins diverge from each other caudally, so that the dentary increases in depth (Figs 2A, 3A). The dorsal expansion of the broken caudal margin indicates that a coronoid eminence would have been present. The rostral-most part of the dentary is slightly downturned and, as a result, the remainder of the ventral margin is sigmoidal, but this may be due to deformation. Rostrally, the tooth row is not inset and the first five teeth are marginally positioned. Caudally, a well-developed buccal emargination is present, which is bounded ventrally by a distinct break in slope. Two large nutrient foramina are positioned ventral to the tooth row, with a third smaller foramen positioned ventral to them: the rostral-most

foramen opens into a short canal that extends rostro-dorsally at the rostral end of the dentary. A fourth foramen is situated ventral to the fifth dentary tooth, on the margin of the buccal emargination, while a final slit-like foramen is placed approximately halfway along the tooth row beneath the ninth and tenth teeth on the buccal ridge.

Thirteen teeth and one empty alveolus are visible in the left dentary. Teeth at the caudal end of the tooth row are obscured by the maxillary teeth and it is possible that at least one, and maybe more, rostrally positioned teeth are missing. Although the exact number of dentary teeth cannot be determined, comparisons with other more complete specimens (e.g. NHMUK PV R8501) suggest that a total tooth count of 18–20 teeth seems likely. The morphology of the dentary teeth is identical to that of maxillary teeth (see above). The largest exposed teeth are in the posterior part of the tooth row, in alveoli 10–12. None of the dentary teeth are worn and there is no overlap between adjacent dentary teeth.

Splénial

Both the left and right splénial are visible in left lateral view, and they are preserved in articulation with their respective dentaries (Figs 2A, 3A). Only a small part of the left splénial is exposed, but most of the medial surface of the right splénial is visible. The right splénial extends for much of the length of the preserved right dentary. It tapers rostrally to a narrow point at the level of the fifth preserved dentary tooth. The medial surface of its ventral margin is faintly rugose.

Vertebra

A small centrum is preserved adjacent to the right jugal (Figs 2B, 3B). One end of the centrum is eroded but the preserved articular surface is concave, with a roughened rugose margin, and the surface is transversely wider than tall (although it cannot be determined if the dorsal margin is the true dorsal margin or broken/obscured). In ventral view, the centrum is hourglass-shaped, has a rounded ventral surface and bears a low midline keel. A small nutrient foramen enters one of the lateral surfaces.

?Dorsal ribs

Several cylindrical bone fragments are present, lying beneath the scapula (Figs 2B, 3B). These are interpreted as the dorsal rib shafts, but offer no useful information.

Scapula

A left scapula is preserved, but can only be observed in medial view (Figs 2B, 3B). The proximal plate is expanded dorsoventrally and has a shallowly concave surface, but most of this area, including the glenoid, is obscured by the presence of a centrum (see above). The acromial region is missing. The dorsal margin of the scapula blade is straight, while the ventral margin is concave, leading to asymmetrical dorsoventral distal expansion of the scapula blade. The medial surface of the blade is strongly convex dorsoventrally. In dorsal view, the scapula blade is almost straight, rather than bowed, but this may be due to crushing.

Humerus

A left humerus lies beneath the scapula and is partially exposed in posterior view (Figs 2B, 3B). Its proximal and distal ends are transversely expanded: the proximal expansion is wider than the distal expansion. Distally, the humerus is divided into medial and lateral condyles that are separated posteriorly by a shallow furrow. The medial condyle extends further distally than the lateral one. In distal view, the medial condyle is longer anteroposteriorly than the lateral condyle.

?Ulna

Adjacent to the humerus another limb element is present that may represent an ulna, as the ?proximal end is transversely expanded in a manner suggestive of an olecranon process. More distally, the shaft tapers ventrally and is subcylindrical in cross-section (Figs 2B, 3B).

BP/1/6582

General comments

This specimen consists solely of postcranial material and incorporates five dorsal and two sacral vertebrae, a ?dorsal neural spine, two partial dorsal ribs, a left coracoid, both scapulae, a right humerus and ulna, a partial left ilium, the proximal end of a right ischium and a left femur (Figs 4–8). Measurements are provided in Tables 2–3.

Dorsal vertebrae

Three of the dorsal vertebrae are preserved in articulation and are held together with matrix, which partially obscures some details of their anatomy (Fig. 4A; Table 2). Each vertebra consists of a complete centrum and partial

neural arch. The centra are amphiplatyan to mildly amphicoelous and are longer than they are high. The anterior articular surfaces are approximately equal in dorsoventral height and mediolateral width. In ventral view, the centra are hourglass-shaped. The first vertebra in the series has a moderately developed ventral keel; the second has a more rounded surface; and the third bears a shallow midline groove. In lateral view, the sides of the centra are lightly excavated and are concave anteroposteriorly and mildly convex dorsoventrally. Several small nutrient foramina are present on each side of the centrum at approximately midlength and midheight. The lateral surfaces immediately adjacent to the articular surfaces are strongly sculpted with short longitudinally extending striations. Neurocentral sutures are filled with a thin line of matrix and are clearly visible.

The neural canal has a circular outline in both anterior and posterior views. Small, subcircular parapophyses are present on the anteroventral corners of the neural arch. The prezygapophyses are angled at approximately 40 degrees to the horizontal in lateral view and probably terminated slightly anterior to the articular surface of the centrum. In anterior view, the articular facets of the prezygapophyses are oriented dorsomedially at an angle of approximately 45 degrees to the horizontal. The prezygapophyses are supported ventrally by stout pedicles that merge with the rest of the neural arch ventrally. A small foramen pierces the base of the left prezygapophysis on the first vertebra, but this foramen cannot be identified on any of the other vertebrae.

The right transverse process is preserved in the second vertebra of the series and is horizontally oriented. The underside of the process bears a swelling along its anterior

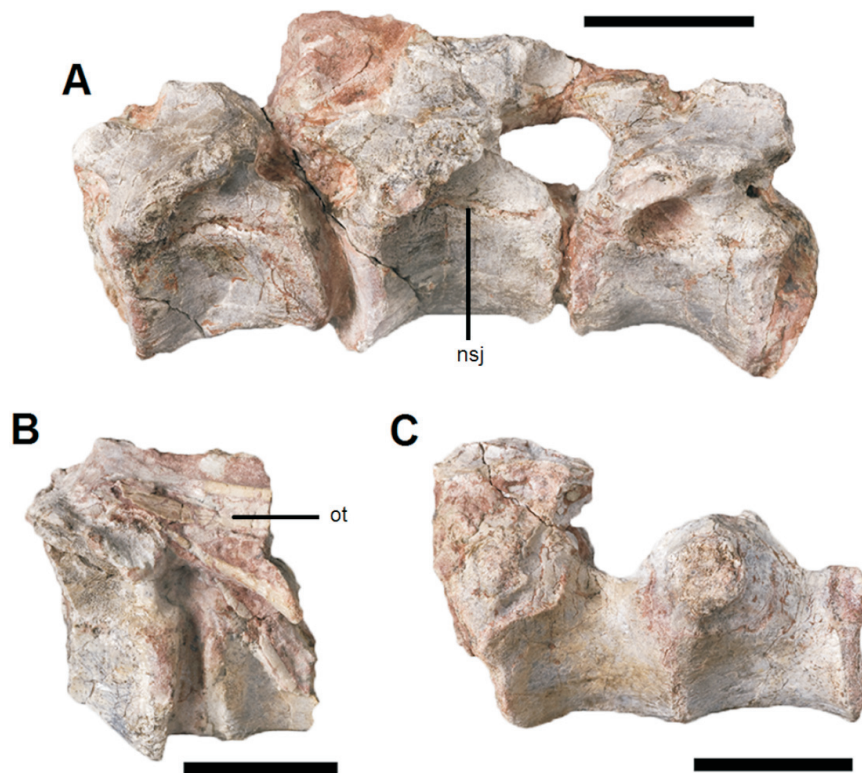


Figure 4. Dorsal and sacral vertebrae of BP/1/6582. **A**, Three articulated dorsal vertebrae in left lateral view; **B**, two partial articulated dorsal vertebrae in left lateral view; **C**, two partial articulated sacral vertebrae in left lateral view. Scale bars = 20 mm.

margin that merges with the base of the arch, in a position equivalent to that of the anterior centrodiaiphyseal lamina. A shallow concavity is present at the postero-ventral corner of the neural arch, which is bounded anteriorly by a stout buttress that is confluent with the posterior margin of the transverse process and dorsally by the base of the postzygapophysis. This buttress is in a position equivalent to that of the posterior centrodiaiphyseal lamina. However, none of the vertebrae show any other evidence of complex neural arch lamination.

Most of the postzygapophyses are broken or obscured by matrix, but those of the second vertebra in the series show that their articular surfaces face ventrolaterally, they extend beyond the posterior articular surface, and they are situated dorsal to the base of the prezygapophysis. There is no evidence for the presence of hyposphenes or hypantra. Small fragments of ossified tendon lie adjacent to the neural arches of the second and third vertebrae. An isolated neural arch is present that cannot be articulated with any of the preserved vertebrae. It is a transversely flattened, subquadrate plate and its posterodorsal corner slightly overhangs its posterior margin in lateral view.

Two additional articulated dorsal vertebrae are included in BP/1/6582, but are poorly preserved. They appear to be identical to the aforementioned vertebrae and are associated with fragments of subcylindrical, rod-like ossified tendons (Fig. 4B). These vertebrae are slightly larger than the other dorsals and the sacral vertebrae, suggesting that they might pertain to the third larger individual in the assemblage that is represented by BP/1/6583, though this cannot be confirmed.

Dorsal ribs

Two dorsal rib heads are preserved. They probably pertain to the anterior part of the vertebral column as the tuberculum and capitulum are widely separated. The base of each rib head is broken just ventral to the area in which the two processes merge and this basal region has a subelliptical transverse cross-section. The tuberculum is broken or obscured in each rib head, although its base can be seen. The capitulum is elongate with a cylindrical cross-section. A partial neural arch is present in the same block of matrix as the rib heads, but offers little information.

Sacral vertebrae

A partial sacrum is preserved consisting of two articulated centra, each of which bears the broken bases of their associated sacral ribs (Fig. 4C; Table 2). The anterior-most centrum bears a partial but very damaged neural arch and the anterior articular surface is damaged and partially obscured by matrix. It is not possible to determine the positions of these vertebrae within the sacrum. The centra are not fully coossified and remain partially separated by a thin line of matrix. The neurocentral sutures and sacral rib articulations of both vertebrae are also unfused.

The anterior articular surface of the anterior sacral is as wide as high with a subcircular outline, whereas its posterior articular surface is wider than high. The lateral surface of the centrum is strongly concave anteroposteriorly

Table 2. List of measurements for selected vertebrae in BP/1/6582. All measurements in mm.

Articulated dorsal series: dorsal 1	
Centrum length	23
Centrum anterior height	19
Centrum anterior width	20
Centrum posterior width	22
Centrum posterior height	20
Articulated dorsal series: dorsal 2	
Centrum length	23
Centrum anterior height	20
Centrum anterior width	22
Centrum posterior width	26
Centrum posterior height	17
Articulated dorsal series: dorsal 3	
Centrum length	26
Centrum anterior height	18
Centrum anterior width	24
Centrum posterior width	19
Centrum posterior height	20
Sacral 1	
Centrum length	23
Centrum anterior width (excluding rib)	23.5
Centrum posterior width	25
Centrum posterior height	19
Sacral 2	
Centrum length	23
Centrum anterior height	19
Centrum anterior width (excluding rib)	25
Centrum posterior width	23
Centrum posterior height	17

and weakly convex dorsoventrally and there is a low, longitudinal break-in-slope that extends along the surface of the centrum approximately one-third of the way up from its ventral margin. Immediately ventral to this break-in-slope, at a point approximately halfway along the centrum, a small elliptical nutrient foramen is present. In ventral view, the centrum is hourglass-shaped and the articular surfaces are subequal in transverse width. The lateral surfaces of the centrum converge ventrally to form a sharp keel that extends along the entire length of the centrum. On the dorsal surface, the neural canal excavates the body of the centrum. Close to the neurocentral suture, at a point immediately posterior to the sacral rib facet, a small depression is present. The sacral ribs are large with a sub-elliptical base but they are broken and no other details can be determined. Although present, the neural arch is too badly preserved to yield any useful information and all of its major processes are missing.

The posterior centrum differs from the preceding one in several respects: its anterior articular surface is wider in ventral view than the posterior articular surface; it lacks a prominent keel (although a slight raised midline eminence is present); it lacks the break-in-slope on the lateral surface and the depression on the neurocentral boundary; and the nutrient foramen is positioned slightly more dorsally on its lateral surface. Both articular surfaces are wider than high and the posterior articular surface has a subelliptical outline. The preserved sacral rib bases are large and cover the anterior two-thirds of the lateral surface of the centrum, and slightly overlap the preceding centrum. Although broken close to their base it can be determined that they tapered distally to some extent. A

small fragment of the succeeding vertebra's left sacral rib adheres to the posterior border of the centrum; an obliquely inclined sub-ovate facet is present along the dorsolateral margin of the posterior articular surface (on the right side) which represents an articular surface for the right sacral rib of the next vertebra.

Coracoid

The left coracoid is preserved in articulation with the scapula (Fig. 5). Its dorsal and anterior margins are broken, but it appears to have been subquadrangular in outline. Most of its lateral surface is shallowly concave (Fig. 5A). A large foramen is positioned in the ventral half of the coracoid, just dorsal to the glenoid fossa and slightly anterior to the articulation with the scapula. A low, horizontally oriented and ventrally positioned ridge divides the lateral surface into a small ventrolaterally facing portion and a much larger laterally facing dorsal portion. The coracoid contribution to the glenoid fossa forms the posterior part of the ventral surface and faces postero-ventrolaterally. The coracoid contributes approximately one-third of the total length of the glenoid fossa. It has a shallowly concave surface and is separated from the ventrolaterally facing portion of the lateral surface by a distinct rounded ridge. Anterior to this, a shallowly concave, ventrally facing surface makes up the remainder of the coracoid ventral surface, which is downturned to form a distinct (though broken) anteroventral (sternal) process.

Most of the medial surface is convex (both dorsoventrally and anteroposteriorly) although small concavities are present adjacent to the anterodorsal and anteroventral corners of the element (Fig. 5B). A low rounded eminence is present adjacent to the scapula articulation at approximately mid-height, which merges with the rest of the medial surface anteriorly. The coracoid is mediolaterally thickest in the region of the glenoid and the area immediately dorsal to it, and it thins slightly anteriorly and markedly dorsally.

Scapula

Both scapulae are preserved and largely complete, with each missing only small sections of the distal blade (Fig. 5; Table 3). The left scapula is preserved in articulation with the coracoid, but they are unfused and separated by a clear line of matrix. The scapula consists of a proximal plate that supports an elongate, posteriorly extending blade. The proximal plate has a sub-trapezoidal outline in lateral view and much of its lateral surface is covered by a shallow concavity that fades out at the point where the proximal plate meets the blade (Fig. 5A). The proximal plate is strongly expanded dorsoventrally and its dorsal margin is expanded into an anteroposteriorly narrow, but elongate, sub-triangular acromial ridge (Fig. 5A). The anterior margin of the proximal plate is slightly concave. A large oval facet on the anteroventral border of the proximal plate forms the scapula contribution to the glenoid fossa and accounts for approximately two-thirds of the fossa's

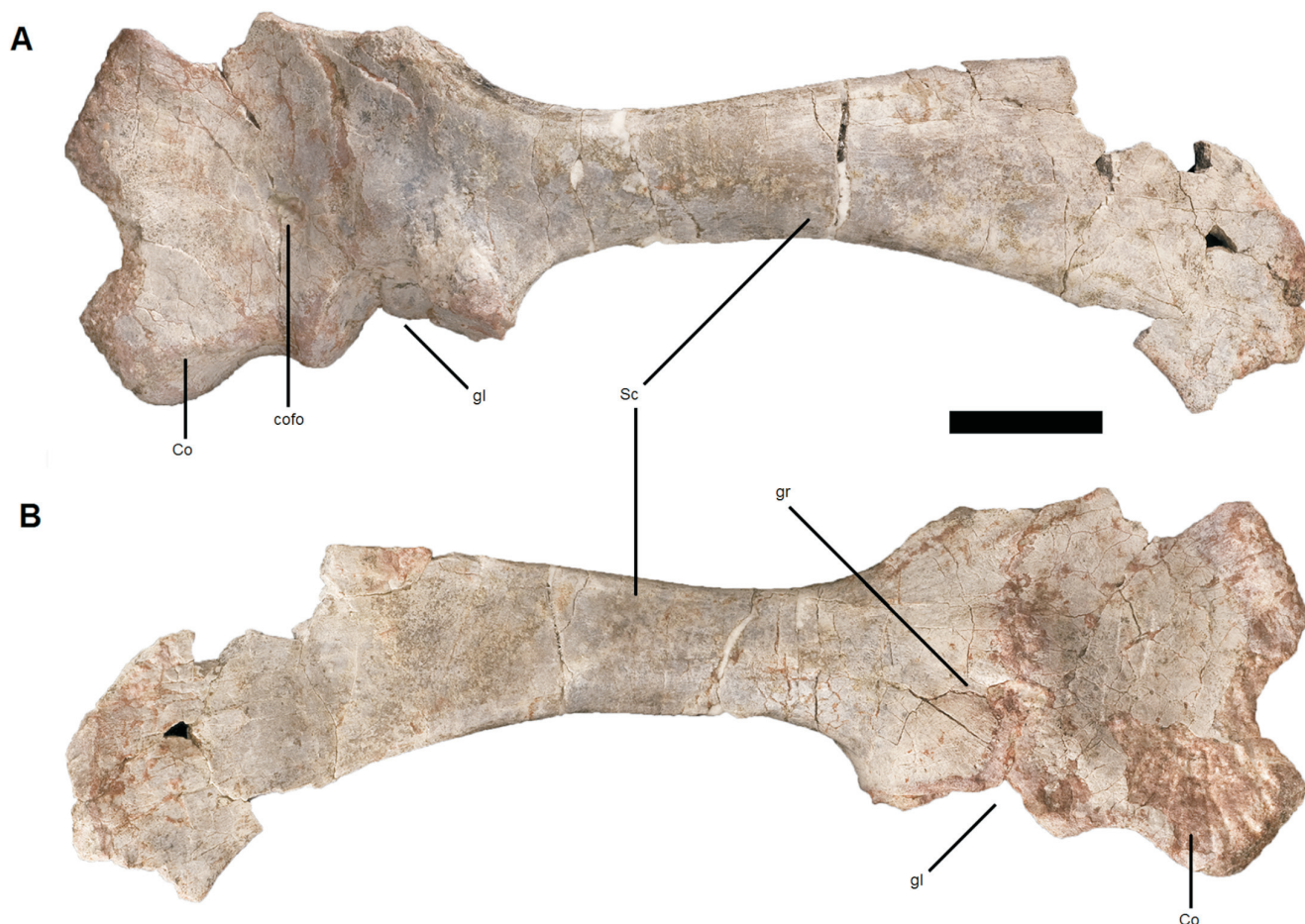


Figure 5. Articulated left scapula and coracoid of BP/1/6582. **A**, Lateral view; **B**, medial view. Scale bar = 20 mm.

Table 3. List of measurements for postcranial elements in BP/1/6582. All measurements in mm. ‘*’ indicates measurement of an incomplete element, measured as preserved.

Left scapula	
Length	132
Maximum height of proximal end	43
Minimum width of blade	18
Right scapula	
Length	127
Maximum height of proximal end	53
Minimum width of blade	19
Expansion of the distal blade	61*
Left coracoid	
Maximum length	41*
Maximum height	48*
Right humerus	
Length	112
Width of proximal expansion	43
Width of distal expansion	29.5
Width of shaft at midlength	15
Distance from head to ventral margin of deltopectoral crest	49
Right ulna	
Length	72.5*
Left femur	
Length	189*
Mediolateral wid	
Anteroposterior width of proximal end	39
Distance to base of fourth trochanter from proximal end	80

total length. This facet is oriented ventrolaterally and is concave both anteroposteriorly and mediolaterally. Medially, the surface of the proximal plate is shallowly convex dorsoventrally and mildly concave anteroposteriorly (Fig. 5B). A short, shallow groove lies close to the ventral border of the coracoid articulation, which likely communicates with the coracoid foramen (Fig. 5B). In anterior view, the dorsolateral portion of the coracoid articulation is concave, while the ventromedial portion is convex.

In lateral view, the anterior part of the elongate scapula blade is dorsoventrally narrow and parallel-sided (Fig. 5A). It expands dorsoventrally in its posterior portion to form a fan-like distal end that is greater in height than the proximal plate. This posterior expansion is asymmetrical as it is caused by divergence of the ventral margin so that most of the expansion lies ventral to the scapula long axis. The ventral tip of the distal expansion is somewhat rugose and the posterior margin of the expansion is slightly thickened relative to the rest of the distal blade. The lateral surface of the scapula blade is strongly convex dorsoventrally in its anterior part, but becomes weakly convex to planar in its distal portions. Medially, the proximal part of the blade is dorsoventrally convex and a distinct break in slope creates a shallow excavation along its ventral border that extends for a short distance posteriorly (Fig. 5B). More distally, the medial surface of the blade becomes flat to very shallowly concave dorsoventrally.

In cross-section, the scapula blade is mediolaterally compressed with respect to the proximal plate. Immediately posterior to the proximal plate it has a sub-elliptical cross-section, which becomes subcrescentic more distally.

In dorsal view, the entire scapula is moderately bowed laterally.

Humerus

The right humerus is well preserved and almost complete (Fig. 6A–C; Table 3). It consists of a narrow shaft that links the mediolaterally expanded proximal and distal ends. The proximal expansion is medially inclined in anterior view and is asymmetrical, so that most of the expansion lies medial to the humeral long axis (Fig. 6A). The proximal expansion is also twisted at an angle of approximately 30 degrees relative to the transverse axis of the distal expansion. The humeral head is positioned slightly medial to the humeral long axis, at the centre of the proximal expansion and forms the dorsal-most point of the humerus. Medial to the head, the dorsal margin of the humerus forms a straight, ventromedially extending slope that terminates in a prominent medial tubercle, which has a quadrate outline. Lateral to the head, the dorsal margin of the humerus is smoothly convex and confluent with the deltopectoral crest ventrally. The deltopectoral crest has a thickened lateral margin, which extends anteriorly and very slightly medially towards its apex (Fig. 6A, 6C), forming an angle of approximately 90 degrees with the anterior proximal surface. The deltopectoral crest is confined to the proximal half of the bone and forms a narrow, smoothly convex flange in anterior view. The anterior surface of the proximal expansion medial to the deltopectoral crest is gently concave mediolaterally (Fig. 6A).

In proximal view, the humerus has a shallow, ‘C’-shaped outline. The humeral head is an indistinct structure that is only slightly thicker than the medial tubercle and it lacks a distinct articular surface. In posterior view, the proximal expansion is transversely convex and the humeral head is supported by a low, indistinct intermuscular line that merges into the proximal end surface at a point level with the dorsal part of the shaft (Fig. 6B). The dorsal part of this surface is striated for muscle attachment areas.

The humeral shaft is slightly crushed, but appears to have had a subelliptical transverse cross-section originally. In anterior or posterior views, the distal expansion is narrower than the proximal expansion and divided into two articular condyles (Fig. 6A–B). Expansion of the distal end is effectively symmetrical around the humeral long axis so that the two condyles are approximately equal in size in anterior and posterior views. The medial condyle is anteroposteriorly expanded relative to the lateral condyle in distal end view and extends slightly further ventrally than the lateral condyle in anterior view. Shallow concavities situated between the condyles on both the anterior and posterior surfaces of the distal expansion expand proximally, although the anterior concavity is the more prominent.

Ulna

The right ulna is present but damaged at its proximal and distal ends and has been slightly crushed. It consists of a narrow, elongate shaft linking proximal and distal ends that are expanded both anteroposteriorly and

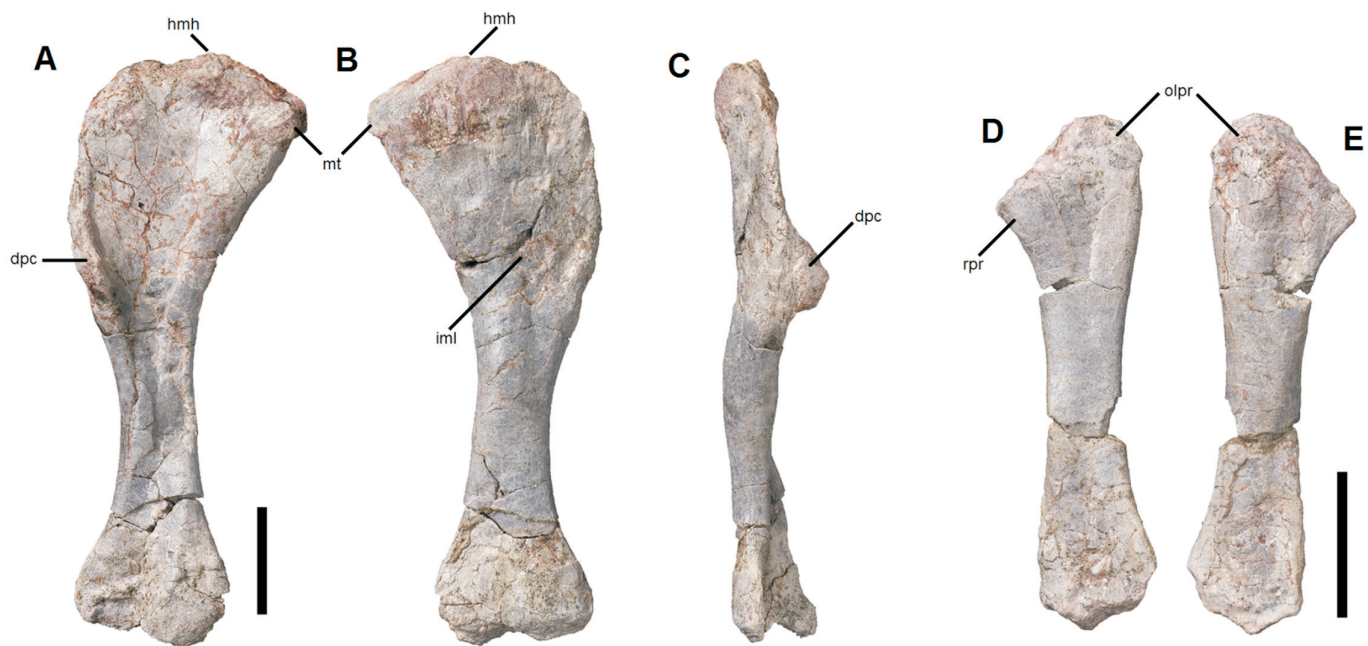


Figure 6. Right forelimb elements of BP/1/6582. A–C, Humerus in anterior (A), posterior (B) and lateral (C) views; D–E, ulna in medial (D) and lateral (E) views. Scale bars = 20 mm.

mediolaterally (Fig. 6D–E; Table 3). The proximal end of the bone is expanded to a greater extent than the distal end in both directions. In lateral view, the ulna terminates proximally in a broad, rounded olecranon process that merges anteriorly with a more ventrally situated, triangular radial process, which projects anteriorly. The humeral glenoid is poorly preserved and the articular surface is damaged. The lateral surface of the proximal end is strongly convex anteroposteriorly. In medial view, the proximal end of the shaft is slightly concave, although this has been accentuated by crushing. The ulnar shaft has a semicircular cross-section close to the dorsal expansion with an almost planar medial surface. This cross-section becomes elliptical more distally as the shaft merges into the distal expansion. The distal end is poorly preserved: the articular region is broken ventrally and offers no useful information.

Ilium

A partial left ilium is present that lacks the preacetabular process, the dorsal margin of the main body, most of the postacetabular process and the pubic peduncle (Fig. 7A–B). The main body is expanded laterally dorsal to the acetabulum to form a well-developed supraacetabular flange: this flange is mediolaterally broadest at the base of the pubic peduncle and narrows posteriorly, grading into the lateral surface of the ilium at a point immediately dorsal to the ischiadic peduncle (Fig. 7A). Most of the acetabulum is backed by a complete, ventromedially extending sheet of bone (Fig. 7A). As a consequence, the acetabulum is only partially open: the fenestra would have been small and confined to the ventral part of the hip socket. The acetabular surface is strongly concave both anteroposteriorly and dorsoventrally. Dorsal to the supraacetabular flange, the lateral surface of the ilium is strongly concave dorsoventrally. The ischial peduncle projects ventrally and slightly posteriorly. The lateral

surface of the peduncle is slightly raised relative to the rest of the acetabular surface and probably represents part of the antitrochanter. In ventral view, the peduncle has an ovate outline, tapering anteriorly, with its long axis extending anteroposteriorly. Its ventral surface is concave, for articulation with the ischium. This concavity is surrounded by a raised lip of bone.

In medial view, the anterior-most part of the brevis shelf is preserved, but its posterior portion is missing and the form of the brevis fossa cannot be determined (Fig. 7B). This shelf extends anteriorly to form the dorsal border of the sacral rib facets. Three separate sacral rib facets are identifiable: the facet for sacral rib two is incompletely preserved and is positioned close to the base of the preacetabular process/pubic peduncle (Fig. 7B). This is separated from the facet for sacral rib three by a low ridge. The latter facet is positioned on the medial surface of the acetabular wall. Posterior to this a larger incomplete facet represents the attachment for sacral ribs four and five, which extends over the medial surface of the ischiadic peduncle and brevis shelf. Another small concavity is positioned dorsal to the scar for sacral rib two, but might represent damage.

Ischium

The proximal end of the right ischium is preserved. It consists of a proximal plate, which is divided into iliac and pubic processes, and a short section of the shaft (Fig. 7C–E). In lateral view, the pubic and iliac processes are separated from each other by an angle of approximately 80 degrees. The pubic process is anteroposteriorly longer than the iliac process is tall dorsoventrally, has a subquadrate outline and extends anteriorly (Fig. 7C). Its lateral surface is shallowly concave anteroposteriorly, whereas the corresponding medial surface is convex. Its anterior margin is transversely compressed, so that it forms a narrow plate in anterior view. The iliac process

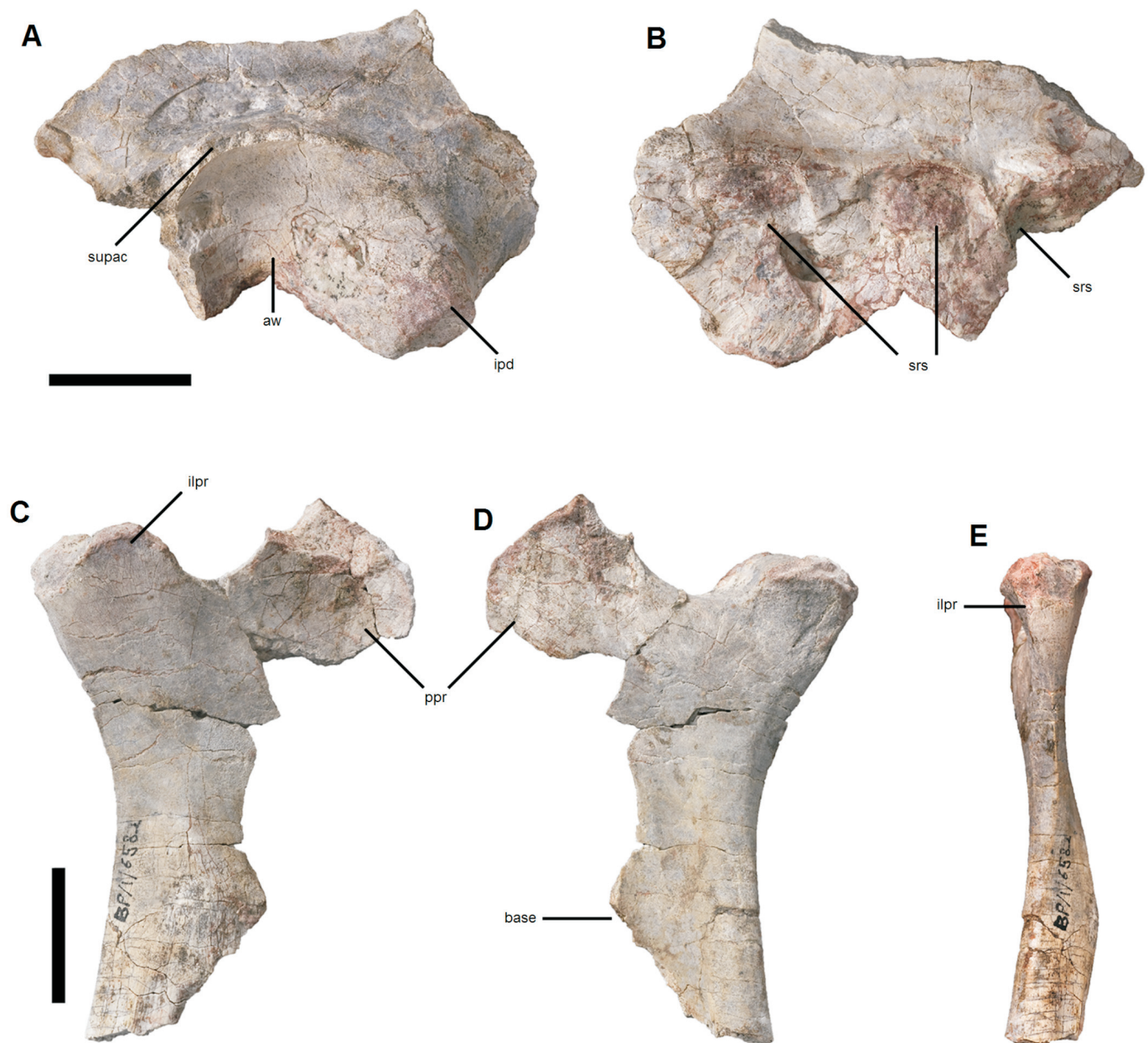


Figure 7. Pelvic girdle elements of BP/1/6582. **A–B**, Left ilium in lateral (**A**) and medial (**B**) views; **C–E**, right ischium in lateral (**C**), medial (**D**) and posterior (**E**) views. Scale bars = 20 mm.

extends dorsally and has a subtriangular cross-section, being broadest anteriorly and tapering posteriorly. Its lateral surface is shallowly convex both dorsoventrally and anteroposteriorly; the corresponding medial surface is slightly concave. The dorsal margin for articulation with the ilium is convex in lateral view. The iliac process exceeds the pubic process in transverse width. The acetabular margin is formed by the dorsal margin of the pubic process and the anterior margin of the iliac process and describes a smooth curve in lateral view. In dorsal view, the acetabular margin is a mediolaterally-expanded shelf, which has a smoothly concave surface.

Posterior to the proximal plate, the ischium narrows dorsoventrally to form the shaft. In lateral view, the proximal-most part of the shaft is dorsoventrally narrow, but the shaft expands ventrally a short distance from the proximal plate, forming a distinctive anteroventral 'shoulder' (Fig. 7C–E). The ventral margin of the shaft is

damaged posterior to this point, so the morphology of this region is somewhat equivocal and it is not possible to determine if a tab-like obturator process was present or absent. The lateral surface of the shaft is strongly convex dorsoventrally. A shallow groove extends along the dorsolateral surface of the shaft, originating at a point level with the anteroventral 'shoulder'.

In medial view, the dorsal margin of the shaft is thickened and the surface ventral to this is strongly convex (Fig. 7D). As a result, the shaft cross-section has an inverted comma-like shape in distal view. In dorsal view, the shaft extends slightly medially with respect to the anteroposteriorly extending proximal plate.

Femur

The left femur is nearly complete, but has been strongly compressed transversely (Fig. 8; Table 3). It is strongly bowed anteriorly in lateral view, but is straight in anterior

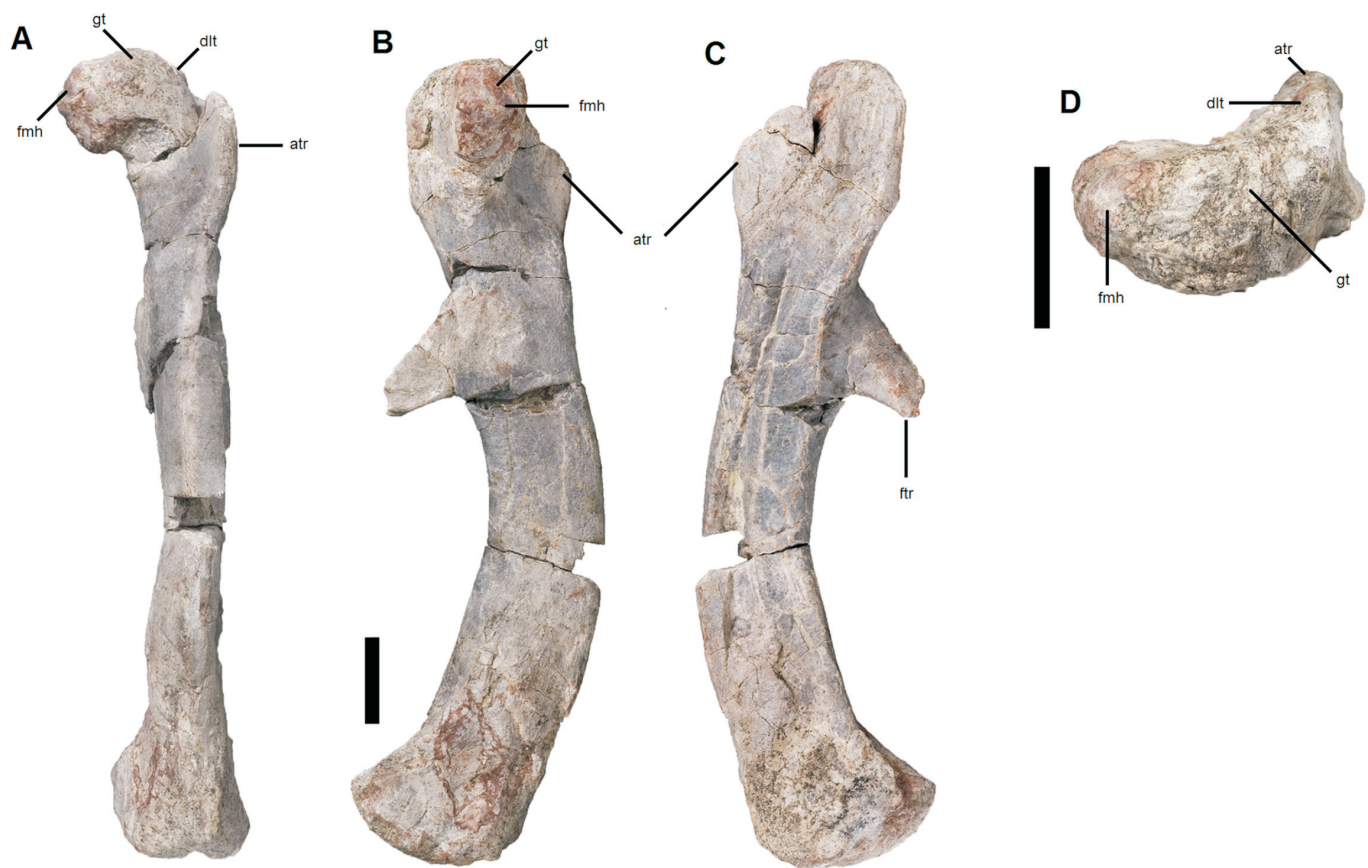


Figure 8. Left femur of BP/1/6582. **A**, Anterior; **B**, medial; **C**, lateral; and **D**, proximal views. Scale bars = 20 mm.

view. In anterior view, the femoral head is in-turned and projects strictly medially. Its dorsal margin is continuous with that of the greater trochanter and their combined dorsal margin is very shallowly convex in anterior view (Fig. 8A). The articular surface of the femoral head is convex: its medial margin is angular in anterior view, with a dorsomedially facing proximal half and a ventromedially facing distal half, although this feature may result from poor preservation. The head is set on a stout neck that is continuous with the greater trochanter. In proximal view, the femur has a slightly convex anterior margin and concave posterior margin (Fig. 8D). A weakly developed groove, the fossa trochantericus, extends across the proximal surface, from the anteromedial corner of the proximal end to the posterolateral corner, dividing the surfaces of the femoral head and greater trochanter. The groove is continuous with a depressed area on the posterolateral corner of the proximal end, the articularis antitrochantericus. There is no development of a medial tuber on the posterior surface. The posterolateral corner of the greater trochanter is thickened and forms a prominent ridge, though this feature may have been accentuated by crushing. Laterally, the greater trochanter is flattened and develops into a small anteriorly extending flange – the dorsolateral trochanter. The dorsal termination of the dorsolateral trochanter lies ventral to the proximal surface of the greater trochanter. In turn, the anterior trochanter is situated anteroventral to the dorsolateral trochanter and is separated from the latter by a deep cleft, which is clearly visible in lateral view (Fig. 8B). The latter

two trochanters have subequal anteroposterior widths in lateral view. The anterior trochanter has a mediolaterally flattened, plate-like cross-section that is slightly wider anteriorly than posteriorly. There is a small foramen on the medial surface of the anterior trochanter, positioned ventral to the notch between the anterior trochanter and the dorsolateral trochanter. The lateral surface of the dorsolateral trochanter is concave anteroposteriorly.

The anterior surface of the anterior trochanter continues distally onto the femoral shaft as an anteriorly convex, mediolaterally robust ridge of bone. This ridge gradually tapers into the femoral shaft, and becomes indistinguishable at its midpoint. A small foramen is present on the medial surface of this ridge at a point level with the dorsal margin of the fourth trochanter. The fourth trochanter is located proximally and is pendant with a triangular outline in lateral view. It arises from the posteromedial margin of the shaft and curves laterally along its length. Its medial surface is scarred for muscle attachment as is the posterior part of its lateral surface, including its dorsal margin and apex. These scars represent the insertions for the *Mm. caudofemoralis longus* (medially) and *brevis* (laterally) (see Maidment & Barrett 2011). A small foramen is positioned in the base of the fourth trochanter laterally. Due to crushing it is not possible to determine the original cross-section of the shaft. The distal end is divided into lateral and medial condyles, each bearing a posteriorly extending epicondyle. Posteriorly, the condyles are separated by a shallow intercondylar groove, but there is no evidence for a groove or fossa on the anterior surface of

the distal end. Due to damage it is not possible to determine the morphology of the distal end surface.

BP/1/6583

This specimen is a partial left scapula, which is lacking its proximal plate and most of the distal expansion. What remains of the scapula blade is identical in morphology to the scapulae included within BP/1/6581 and BP/1/6582. However, it pertains to much larger individual than either of the latter specimens, with a midshaft depth of 27 mm (compare with measurements in Tables 1 & 3) and so provides evidence for the presence of a third individual in the assemblage.

DISCUSSION

Cranial ontogeny

The partial skull preserved in BP/1/6581 is approximately 55 mm in anteroposterior length, but is missing the temporal region and the snout. Comparisons with other specimens (NHMUK RU B17, NHMUK RU B23, NHMUK PV R8501, NHMUK PV R11956, and those described in Knoll [2002a,b]) suggest a total skull length of approximately 100 mm, which is larger than any of the other skulls available for this taxon. As none of the available skulls of *Lesothosaurus* are complete it is not possible to provide proportional comparisons between them (e.g. relative orbit size, snout length), but maxillary length illustrates the range of sizes available. In the majority of specimens, maxillary length is estimated to range between 28 and 35 mm (NHMUK RU B17, NHMUK RU B23, NHMUK PV R8501, NHMUK PV R11956: though it should be noted that many of the maxillae are missing small portions anteriorly or posteriorly), whereas in BP/1/6581 it is a minimum of 52 mm.

Two features of BP/1/6581 may represent ontogenetic variations based on the larger size of this individual and its presumed greater age. Firstly, a series of small rugosities is present on the lateral surface of the lacrimal in BP/1/6581, close to the orbital margin. No other *Lesothosaurus* specimen preserves this feature (NHMUK RU B17, NHMUK RU B23, NHMUK PV R8501, NHMUK PV R11956; Sereno 1991; Knoll 2002a,b; Porro *et al.* 2015). Similar ontogenetic increases in cranial rugosity are known in other small ornithischian taxa, such as the ornithomimid *Jeholosaurus* (Barrett & Han 2009). Secondly, although the maxillary tooth row is incomplete in BP/1/6581, the length of the preserved maxilla (with 13 preserved tooth positions), the extent of the missing posterior process and consideration of tooth size suggests that a minimum of 18 maxillary teeth were present. By contrast, other specimens possess up to 15 maxillary teeth (e.g. NHMUK PV R8501) and might have had a maximum maxillary tooth count of 16–17 when breakage is taken into account. Ontogenetic increases in tooth count are relatively common in dinosaurs and are known in a variety of ornithischian taxa (e.g. Varricchio 1997).

Ontogenetic variation in postcranial characters will be discussed in a separate article providing full redescriptions of the syntype postcrania (NHMUK RU B17; M.G.B. & P.M.B., unpubl. data).

Taxonomic implications

If the Aushan Grey postcranial material is referable to *Lesothosaurus* (see above) it would indicate that larger-bodied individuals of this taxon overlapped in body size with individuals referred to the sympatric taxon *Stormbergia dangershoeki*. Femoral lengths of *Stormbergia* specimens range from 147–202 mm and its minimum scapula shaft widths vary from 18.5–20 mm (Butler 2005), whereas the femoral length of BP/1/6582 is 189 mm and the minimum scapula shaft widths of BP/1/6582 and BP/1/6583 are 18 mm and 27 mm, respectively. However, although this previously undocumented overlap in body size could prove useful in testing the proposed synonymy of these taxa (Knoll *et al.* 2010), as it would remove ontogenetic considerations from the argument, the only preserved ischial fragment in the new assemblage, which is part of BP/1/6582, is incomplete. As a result, it is not possible to determine either the presence/absence of a tab-like obturator process or the relative length of the ischial symphysis, which are the two critical features used to distinguish *Stormbergia* from *Lesothosaurus* (Butler 2005). Nevertheless, at the very least, the new, diagnosable skull specimens described herein offer the possibility of finding other, more completely preserved and large-sized *Lesothosaurus* individuals that might help to resolve this controversy.

Behaviour

The discovery of several *Lesothosaurus* individuals in one locality is potentially significant as it may indicate that these animals formed part of a small social group that perished during the same event. Examples of monotypic ornithischian bonebeds are rare prior to the Cretaceous (Weishampel *et al.* 2004), but a similar discovery of multiple individuals of the Early Jurassic taxon *Laquintasaura* suggests that group-living might have appeared much earlier in ornithischian evolutionary history than usually thought (Barrett *et al.* 2014). Nevertheless, detailed taphonomic information is not currently available for the Aushan Grey locality and it is not clear if the dinosaur assemblage was preserved in a single event, which might support the group-living hypothesis, or whether the remains accumulated over a more protracted period, with different carcasses joining the assemblage at different times. Further sedimentological work is required at the site to distinguish between these possibilities.

CONCLUSIONS

This new material shows that some individuals of *Lesothosaurus diagnosticus* reached similar body sizes to those reported for the sympatric taxon *Stormbergia dangershoeki* and demonstrates the potential for finding other larger individuals that might help resolve the controversial status of the latter taxon. Moreover, these larger specimens document some ontogenetic differences in cranial anatomy, with larger (= older) specimens possessing cranial rugosities that are absent from smaller individuals, as well as higher tooth counts. The discovery of three associated individuals hints at the possibility that *Lesothosaurus* might have lived in small groups, providing

additional circumstantial evidence for the early evolution of sociality in ornithischian dinosaurs.

ABBREVIATIONS

Institutional

BP	ESI Evolutionary Studies Institute (formerly Bernard Price Institute), University of the Witwatersrand, Johannesburg, South Africa.
NHMK	Natural History Museum, London, U.K.

Anatomical

aofe	antorbital fenestra
aof	antorbital fossa
Art.f	articular fossa
atr	anterior trochanter
aw	acetabular wall
base	broken base of ischial shaft
br	buccal ridge
Co	coracoid
cofo	coracoid foramen
De	dentary
dlt	dorsolateral trochanter
dpc	deltpectoral crest
F	frontal
fmh	femoral head
fo	foramen
ft	fourth trochanter
gl	glenoid
gr	groove
gt	greater trochanter
Hm	humerus
hmh	humeral head
ilpr	iliac process
iml	intermuscular line
ipd	ischial peduncle
Ju	jugal
L	left
Lc	lacrimal
Mg	Meckelian groove
mt	medial tubercle
Mx	maxilla
Na	nasal
olpr	olecranon process
ot	ossified tendon
Pal	palatine
Pf	prefrontal
Pm	premaxilla
Pp	palpebral
ppr	pubic process
R	right
rpr	radial process
ru	rugosities
Sc	scapula
Sp	splenic
srs	sacral rib scar
supac	supraacetabular crest
Ul	ulna
Vert	vertebra

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REFERENCES

BARRETT, P.M. & HAN, F.L. 2009. Cranial anatomy of *Jeholosaurus shangyuanensis* (Dinosauria: Ornithischia) from the Early Cretaceous of China. *Zootaxa* **2072**, 31–55.

BARRETT, P.M., BUTLER, R.J., MUNDIL, R., SCHEYER, T.M., IRMIS,

R.B. & SÁNCHEZ-VILLAGRA, M.R. 2014. A palaeoequatorial ornithischian and new constraints on early dinosaur diversification. *Proceedings of the Royal Society B* **281**, 20141147.

BOYD, C.A. 2015. The systematic relationships and biogeographic history of ornithischian dinosaurs. *PeerJ* **3**, e1523 (DOI:10.7717/peerj.1523).

BUTLER, R.J. 2005. The 'fabrosaurid' ornithischian dinosaurs of the Upper Elliot Formation (Lower Jurassic) of South Africa and Lesotho. *Zoological Journal of the Linnean Society* **145**, 175–218.

BUTLER, R.J. 2010. The anatomy of the basal ornithischian dinosaur *Eocursor parvus* from the lower Elliot Formation (Late Triassic) of South Africa. *Zoological Journal of the Linnean Society* **160**, 648–684.

BUTLER, R.J., SMITH, R.M.H. & NORMAN, D.B. 2007. A primitive ornithischian dinosaur from the Late Triassic of South Africa and the early evolution and diversification of Ornithischia. *Proceedings of the Royal Society B* **274**, 2041–2046.

BUTLER, R.J., PORRO, L.B. & NORMAN, D.B. 2008a. A juvenile skull of the primitive ornithischian *Heterodontosaurus tucki* from the 'Stormberg' of South Africa. *Journal of Vertebrate Paleontology* **28**, 702–711.

BUTLER, R.J., UPCHURCH, P. & NORMAN, D.B. 2008b. The phylogeny of the ornithischian dinosaurs. *Journal of Systematic Palaeontology* **6**, 1–40.

CAMPIONE, N.E., BRINK, K.S., FREEDMAN, E.A., MCGARRITY, C.T. & EVANS, D.C. 2013. '*Glishades ericksoni*', and indeterminate juvenile hadrosaurid from the Two Medicine Formation of Montana: implications for hadrosaurid diversity in the latest Cretaceous (Campanian–Maastrichtian) of western North America. *Palaeobiodiversity & Palaeoenvironments* **93**, 65–75.

GALTON, P.M. 1978. Fabrosauridae, the basal family of ornithischian dinosaurs (Reptilia: Ornithopoda). *Paläontologische Zeitschrift* **52**, 138–59.

GALTON, P.M. 2014. Notes on the postcranial anatomy of the heterodontosaurid dinosaur *Heterodontosaurus tucki*, a basal ornithischian from the Lower Jurassic of South Africa. *Revue de Paléobiologie* **33**, 97–141.

KNOLL, F. 2002a. Nearly complete skull of *Lesothosaurus* (Dinosauria: Ornithischia) from the Upper Elliot Formation (Lower Jurassic: Hettangian) of Lesotho. *Journal of Vertebrate Paleontology* **22**, 238–243.

KNOLL, F. 2002b. New skull of *Lesothosaurus* (Dinosauria: Ornithischia) from the Upper Elliot Formation (Lower Jurassic) of southern Africa. *Geobios* **35**, 595–603.

KNOLL, F., PADIANY, K. & DE RICQLES, A. 2010. Ontogenetic change and adult body size of the early ornithischian dinosaur *Lesothosaurus diagnosticus*: implications for basal ornithischian taxonomy. *Gondwana Research* **17**, 171–179.

MAIDMENT, S.C.R. & BARRETT, P.M. 2011. The locomotor musculature of basal ornithischian dinosaurs. *Journal of Vertebrate Paleontology* **31**, 1265–1291.

NORMAN, D.B., CROMPTON, A.W., BUTLER, R.J., PORRO, L.B. & CHARIG, A.J. 2011. The Lower Jurassic ornithischian dinosaur *Heterodontosaurus tucki* Crompton and Charig, 1962: cranial anatomy, functional morphology, taxonomy and relationships. *Zoological Journal of the Linnean Society* **163**, 182–276.

OLSEN, P.E. & GALTON, P.M. 1984. A review of the reptile and amphibian assemblages from the Stormberg of southern Africa, with special emphasis on the footprints and the age of the Stormberg. *Palaeontologia africana* **25**, 87–110.

PORRO, L.B., BUTLER, R.J., BARRETT, P.M., MOORE-FAY, S. & ABEL, R.L. 2011. New heterodontosaurid specimens from the Lower Jurassic of southern Africa and the early ornithischian dinosaur radiation. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **101**, 351–366.

PORRO, L.B., WITMER, L.M. & BARRETT, P.M. 2015. Digital preparation and osteology of the skull of *Lesothosaurus diagnosticus* (Ornithischia: Dinosauria). *PeerJ* **3**, e1494 (DOI:10.7717/peerj.1494).

SANTA LUCA, A.P. 1980. The postcranial skeleton of *Heterodontosaurus tucki* (Reptilia, Ornithischia) from the Stormberg of South Africa. *Annals of the South African Museum* **79**, 159–211.

SANTA LUCA, A.P. 1984. Postcranial remains of Fabrosauridae (Reptilia: Ornithischia) from the Stormberg of southern Africa. *Palaeontologia africana* **25**, 151–180.

SANTA LUCA, A.P., CROMPTON, A.W. & CHARIG, A.J. 1976. A complete skeleton of the Late Triassic ornithischian *Heterodontosaurus tucki*. *Nature* **264**, 324–328.

SERENO, P.C. 1986. Phylogeny of the bird-hipped dinosaurs (Order Ornithischia). *National Geographic Research* **2**, 234–256.

SERENO, P.C. 1991. *Lesothosaurus*, 'Fabrosaurids,' and the early evolution of the Ornithischia. *Journal of Vertebrate Paleontology* **11**, 167–197.

SERENO, P.C. 1999. The evolution of dinosaurs. *Science* **284**, 2137–2147.

- SERENO, P.C. 2012. Taxonomy, morphology, masticatory function and phylogeny of heterodontosaurid dinosaurs. *ZooKeys* **226**, 1–225.
- THULBORN, R.A. 1970. The skull of *Fabrosaurus australis* a Triassic ornithischian dinosaur. *Palaeontology* **13**, 414–432.
- THULBORN, R.A. 1972. The post-cranial skeleton of the Triassic ornithischian dinosaur *Fabrosaurus australis*. *Palaeontology* **15**, 29–60.
- TSUIHIJI, T., WATABE, M., TOGTBAATAR, K., TSUBAMOTO, T., BARSBOLD, R., SUZUKI, S., LEE, A.H., RIDGELY, R.C., KAWAHARA, Y. & WITMER, L.M. 2011. Cranial osteology of juvenile specimens of *Tarbosaurus bataar* (Theropoda, Tyrannosauridae) from the Nemegt Formation (Upper Cretaceous) of Bugin Tsav, Mongolia. *Journal of Vertebrate Paleontology* **31**, 497–517.
- VARRICCHIO, D.J. 1997. Growth and embryology. In: Currie, P.J. & Padian, K. (eds), *Encyclopedia of Dinosaurs*, 282–288. San Diego, Academic Press.
- WEISHAMPEL, D.B., DODSON, P. & OSMÓLSKA, H. (eds). 2004. *The Dinosauria* (2nd edn). Berkeley, University of California Press.
- YATES, A.M., HANCOX, P.J. & RUBIDGE, B.S. 2004. First record of a sauropod dinosaur from the upper Elliot Formation (Early Jurassic) of South Africa. *South African Journal of Science* **100**, 504–506.

Two unrecognized burnetiamorph specimens from historical Karoo collections

Christian F. Kammerer

Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Invalidenstraße 43, 10115 Berlin, Germany, and
Evolutionary Studies Institute, University of the Witwatersrand, Private Bag 3, WITS, Johannesburg, 2050 South Africa
E-mail: christian.kammerer@mfn-berlin.de

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Two historical specimens from Permian rocks of the Karoo Basin represent previously unrecognized members of the rare therapsid group Burnetiamorpha. These specimens cannot be referred to any existing burnetiamorph species, but are left in open nomenclature because of their incompleteness (both are isolated skull roofs). The first specimen is from the *Tapinocephalus* Assemblage Zone (AZ) and is characterized by heavily pachyostosed supraorbital bosses and a low nasal crest. The second specimen is from the *Tropidostoma* AZ and is generally similar to the Malawian taxon *Lende*, but is unique among described burnetiamorphs in having a frontoparietal 'dome' that surrounds the pineal foramen. Phylogenetic analysis of burnetiamorphs recovers support for a split between *Proburnetia* and *Burnetia*-like burnetiids, here named *Proburnetiinae* subfam. nov. and *Burnetiinae* Broom, 1923.

Key words: Synapsida, Therapsida, Burnetiamorpha, Permian, Karoo Basin.

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INTRODUCTION

Burnetiamorpha is an unusual clade of Permian predatory therapsids whose members are characterized by elaborate ornamentation of the skull, often associated with cranial pachyostosis. Until recently, only two burnetiamorph specimens were known: the holotypes of *Burnetia mirabilis* Broom, 1923 from South Africa and *Proburnetia viatkensis* Tatarinov, 1968 from Russia. The new millennium, however, has witnessed an explosion in burnetiamorph richness, with ten burnetiamorph species currently recognized. Of the new additions to the group, two were previously known but only recently identified as burnetiamorphs (*Lemurosaurus pricei* and *Niuksenitia sukhonensis*; Sidor & Welman 2003), but most have been newly described (*Bullacephalus jacksoni* Rubidge & Kitching, 2003, *Lende chiweta* Kruger *et al.*, 2015, *Lobalopex mordax* Sidor *et al.*, 2004, *Lophorhinus willodenensis* Sidor & Smith, 2007, *Pachydictes elsi* Rubidge *et al.*, 2006, and *Paraburnetia sneeubergensis* Smith *et al.*, 2006). Burnetiamorphs have historically been considered very rare components of their respective faunas, as all but one species (*Lemurosaurus pricei*, represented by two definite skulls and an undescribed possible third [Sidor & Welman 2003; Sidor 2015]) are known from a single specimen.

The majority of burnetiamorphs belong to the family Burnetiidae Broom, 1923, defined by Rubidge & Sidor (2002) as the last common ancestor of *Burnetia mirabilis* and *Proburnetia viatkensis* and all of its descendants. Sidor & Smith (2007) recognized two subclades (Fig. 1) of burnetiids: (*Burnetia* + *Bullacephalus* + *Niuksenitia* + *Pachydictes*) and (*Proburnetia* + *Paraburnetia*), with *Lemurosaurus*, *Lobalopex* and *Lophorhinus* representing non-

burnetiid burnetiamorphs. A more recent analysis of burnetiamorph phylogeny (Kruger *et al.* 2015) recovered the former clade ('*Burnetia*-line' burnetiids), but with *Paraburnetia* and *Proburnetia* as successive outgroups (and the new taxon *Lende* in an unstable position, typically as a non-burnetiid burnetiamorph).

Phylogenetic analysis of Burnetiamorpha is hampered by the extreme degree of pachyostosis in the group, typically obliterating cranial sutures and making the identity of skull roofing bones questionable. Numerous characters used in analyses of this clade (Rubidge *et al.* 2006; Smith *et al.* 2006; Sidor & Smith 2007; Kruger *et al.* 2015) relate to various bosses and other cranial excrescences on the skull surface. There is reason to be wary of overreliance on such characters, given that they are often intraspecifically variable in other therapsid groups with extensive cranial pachyostosis (e.g. dinocephalians – see Kammerer 2011; Liu 2013; Boos *et al.* 2015). However, boss morphology appears conserved throughout ontogeny in *Lemurosaurus pricei*, in which the holotype is significantly smaller than the referred specimen and likely represents a juvenile (Sidor & Welman 2003), so these characters may be less variable in burnetiamorphs than in other therapsids. Additional specimens of other burnetiamorph taxa are needed to gauge conservatism in boss morphology with growth in the group as a whole.

Another problematic aspect of burnetiamorph evolution is the fact that the most deeply-nested subclade ('*Burnetia*-line' burnetiids) includes the earliest-known representatives of Burnetiamorpha: *Bullacephalus* and *Pachydictes* from the middle Permian *Tapinocephalus* AZ of South Africa (Rubidge & Kitching 2003; Rubidge *et al.* 2006). This

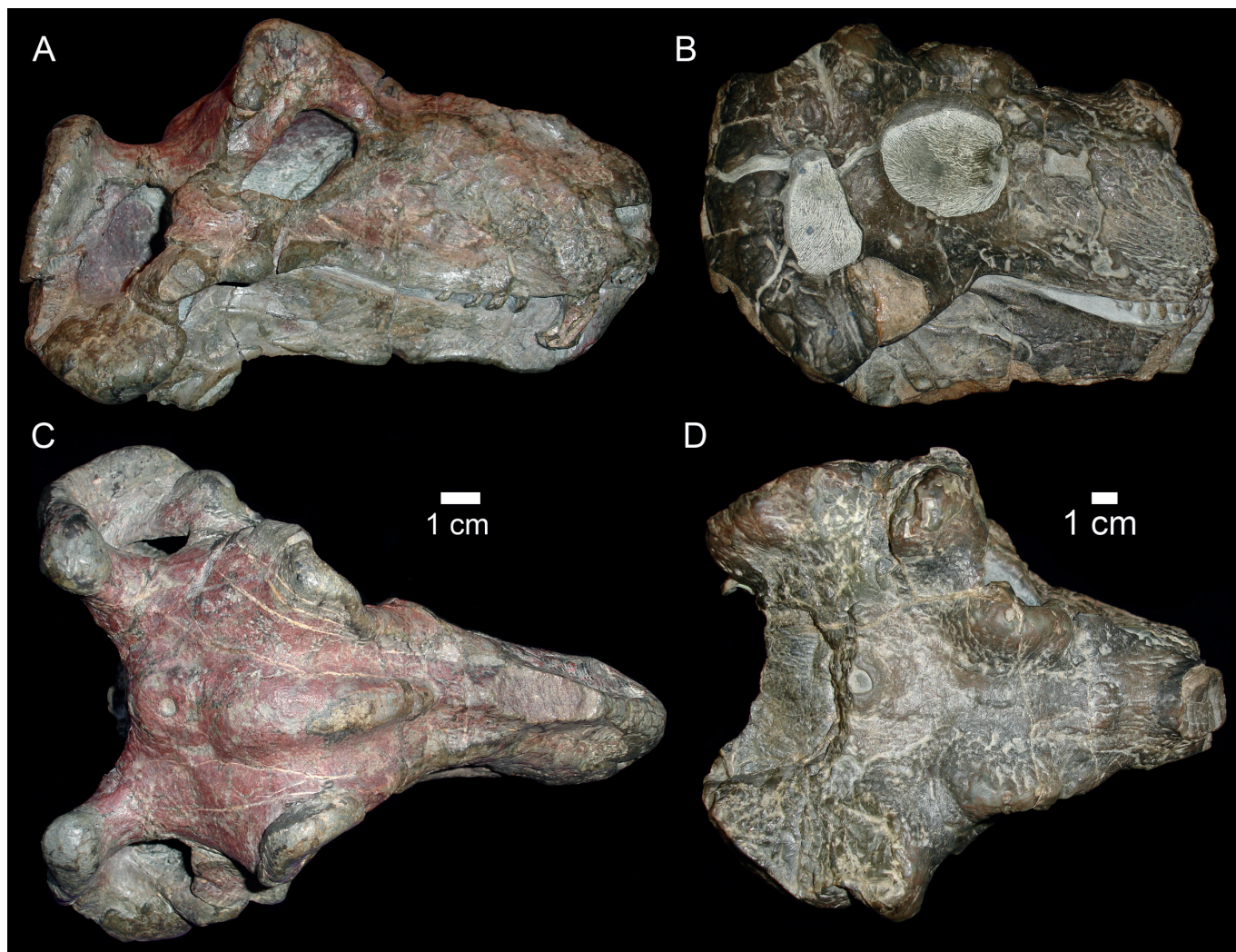


Figure 1. Representative burnetiids, showing exemplars from and characteristics of the two subclades recovered by Sidor & Smith (2007) and the current analysis: *Paraburnetia sneeubergensis* (SAM-PK-K10037) in (A) right lateral and (C) dorsal views; *Bullacephalus jacksoni* (BP/1/5387) in (B) right lateral and (D) dorsal views. In *Paraburnetia*, a single, triangular supraorbital boss is present (directly over the orbits), a massive median interorbital boss is present, and the pineal boss abuts the occiput. In *Bullacephalus*, two supraorbital bosses are present (with the larger one situated above the posterior margin of the orbit), no median interorbital boss is present, and the pineal boss is broadly separated from the occiput.

implies a lengthy ghost lineage between these taxa and the other 'Burnetia-line' burnetiids (*Burnetia* and *Niuksenitia* are from the latest Permian *Daptocephalus* AZ and probable equivalent Russian strata, making them the last known burnetiamorphs [Rubidge & Sidor 2002]) and indicates a significant span of 'hidden' history for the rest of Burnetiamorpha (as the earliest known non-burnetiid burnetiamorphs occur in the late Permian *Tropidostoma* AZ).

Here I describe two previously unrecognized burnetiamorph specimens from historical collections in the Karoo Basin of South Africa: one from the middle Permian *Tapinocephalus* AZ and one from the late Permian *Tropidostoma* AZ. Although fragmentary (both specimens are isolated portions of skull roof), these fossils are not referable to any currently-known burnetiamorph species and suggest higher burnetiamorph diversity in the Karoo than currently recognized. These specimens exhibit a mosaic of features highlighting the complexity of boss evolution in the group and help to fill missing sections of burnetiamorph evolutionary history.

MATERIALS AND METHODS

The following specimens were examined by the author for comparative purposes: *Biarmosuchus tener* (PIN 1758/1, 2, 7, 8, 18, 19, 85), *Bullacephalus jacksoni* (BP/1/5387), *Burnetia mirabilis* (NHMUK R5097), *Herpetoskylax hopsoni* (BP/1/3924; CGP/1/67), *Hipposaurus boonstrai* (SAM-PK-8950, 9081), *Ictidorhinus martinsi* (AMNH FARB 5526), *Lemurosaurus pricei* (BP/1/816; NMQR 1702), *Lobalopex mordax* (CGP/1/61), *Lophorhinus willodenensis* (SAM-PK-K6655), *Lycaenodon longiceps* (NHMUK R5700), *Niuksenitia sukhonensis* (PIN 3159/1), *Pachydictes elsi* (BP/1/5735), *Paraburnetia sneeubergensis* (SAM-PK-K10037) and *Proburnetia viatkensis* (PIN 2116/1). Information on *Lende chiweta* was taken from Kruger *et al.* (2015).

The phylogenetic analysis was run in TNT v1.1 (Goloboff *et al.* 2008) using New Technology search parameters (sectorial searching, parsimony ratchet, drift, and tree fusing) set to find minimum tree length at least 20 times. Support metrics were based on symmetric resampling using 10000 replicates. The data matrix for this analysis is included as Supplementary material for this paper.

SYSTEMATIC PALAEOLOGY

Synapsida Osborn, 1903

Therapsida Broom, 1905

Burnetiamorpha Broom, 1923

Burnetiamorph sp. A

Material. TM 4305, a weathered, largely unprepared partial skull comprising the interorbital region, temporal region and dorsal occiput (Figs 2 & 3).

Locality and horizon. Unknown locality, South Africa; *Tapinocephalus* AZ (Guadalupian). Precise locality data for this specimen has been lost. All that is known is that it is from the *Tapinocephalus* AZ, based on a label found with the specimen.

Description. The dorsal skull roof of this specimen is pachyostosed, and the supraorbital bosses are pachyostotic and massive. It appears that a single supraorbital boss was present on each side of the skull, as is the case for most burnetiamorphs (but not *Bullacephalus* and *Burnetia*). Incomplete preparation complicates the already-difficult delimitation of cranial sutures in this specimen, but a mid-parietal suture can be seen on the posterior half of the pineal boss (Fig. 2) and a mid-nasal suture can be seen in anterior cross-section (Fig. 3C). The pineal boss abuts the back of the skull, unlike the condition in *Bullacephalus* or *Burnetia*. The intertemporal region is very broad (Fig. 2), comparable to that of *Paraburnetia* (Fig. 1C) or *Proburnetia*, but not as broad as in *Bullacephalus* (Fig. 1D). The interorbital skull roof is flat (Fig. 2), similar to that of *Bullacephalus* or *Lobalopex* but unlike *Lende*, *Paraburnetia*, or *Proburnetia* in which there is a massive median boss. A narrow boss is present on the probable back of the nasal, as is visible in anterior view (Fig. 3C). The postorbital bar is pachyostosed and very anteroposteriorly expanded

(Fig. 3A) compared to most biarmosuchians (including other burnetiids – compare with Fig. 1A, B). Ventrally, paired structures at the base of the orbits (Fig. 3D) may represent sphenoid elements. These elements are poorly known in burnetiamorphs, although Sidor & Smith (2007) described a sphenethmoid for *Lophorhinus*. Unlike the paired structures in TM 4305, the sphenethmoid of *Lophorhinus* is a single median ossification. As such, it is possible that these structures could also represent palatal elements, although this is difficult to reconcile with their position in the skull (i.e. intraorbital; compare their position in Fig. 3D with Fig. 3A, B).

Burnetiidae Broom, 1923

Burnetiinae Broom, 1923

Type genus. *Burnetia* Broom, 1923.

Included genera. *Bullacephalus* Rubidge & Kitching, 2003; *Niuksenitia* Tatarinov, 1977; *Pachydictes* Rubidge *et al.*, 2006.

Diagnosis. Burnetiid therapsids characterized by the autapomorphic presence of two supraorbital bosses: a massive, ovoid boss above the anterior edge of the orbit and a more laterally-positioned boss above the posterior edge of the orbit.

Definition. *Burnetia mirabilis* Broom, 1923 and all taxa more closely related to it than *Proburnetia viatkensis* Tatarinov, 1968.

Proburnetiinae subfam. nov.

Type genus. *Proburnetia* Tatarinov, 1968.

Included genera. *Lende* Kruger *et al.*, 2015; *Paraburnetia* Smith *et al.*, 2006.

Diagnosis. Burnetiid therapsids characterized by the autapomorphic presence of a massive, anteroposteriorly elongate interorbital boss.

Definition. *Proburnetia viatkensis* Tatarinov, 1968 and all

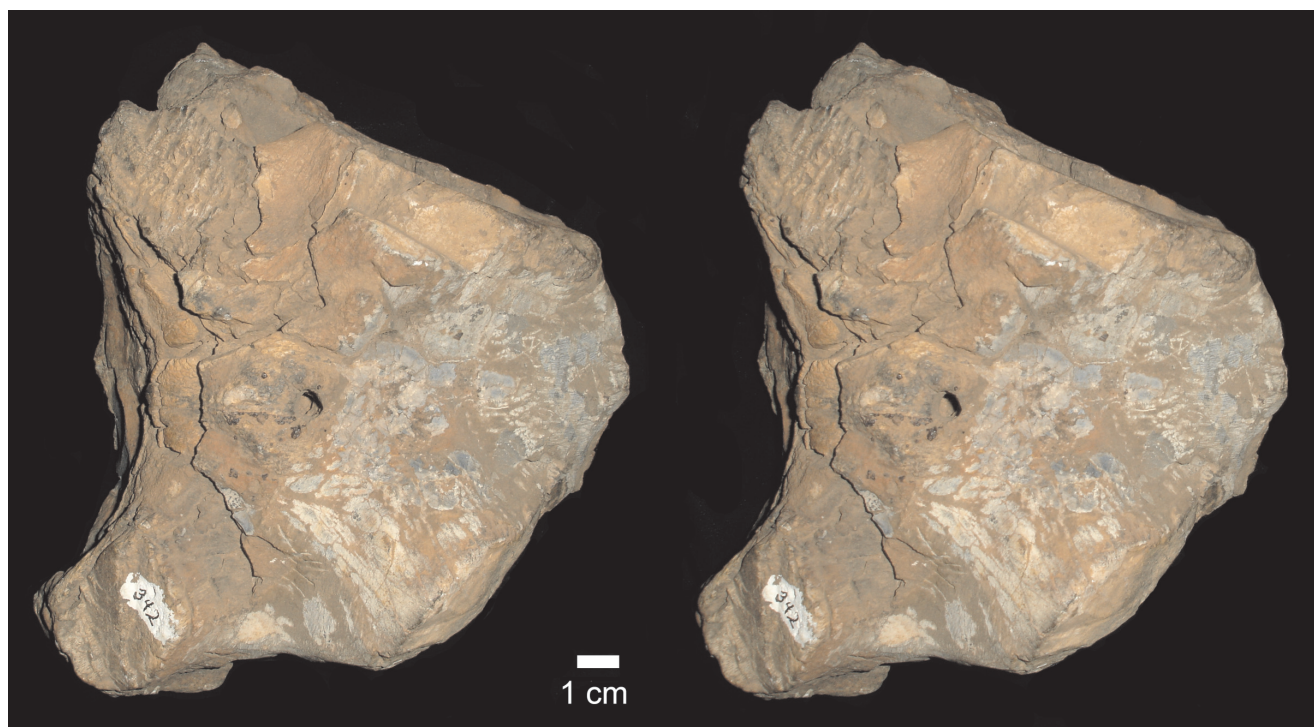


Figure 2. Stereopair of TM 4305 in dorsal view.

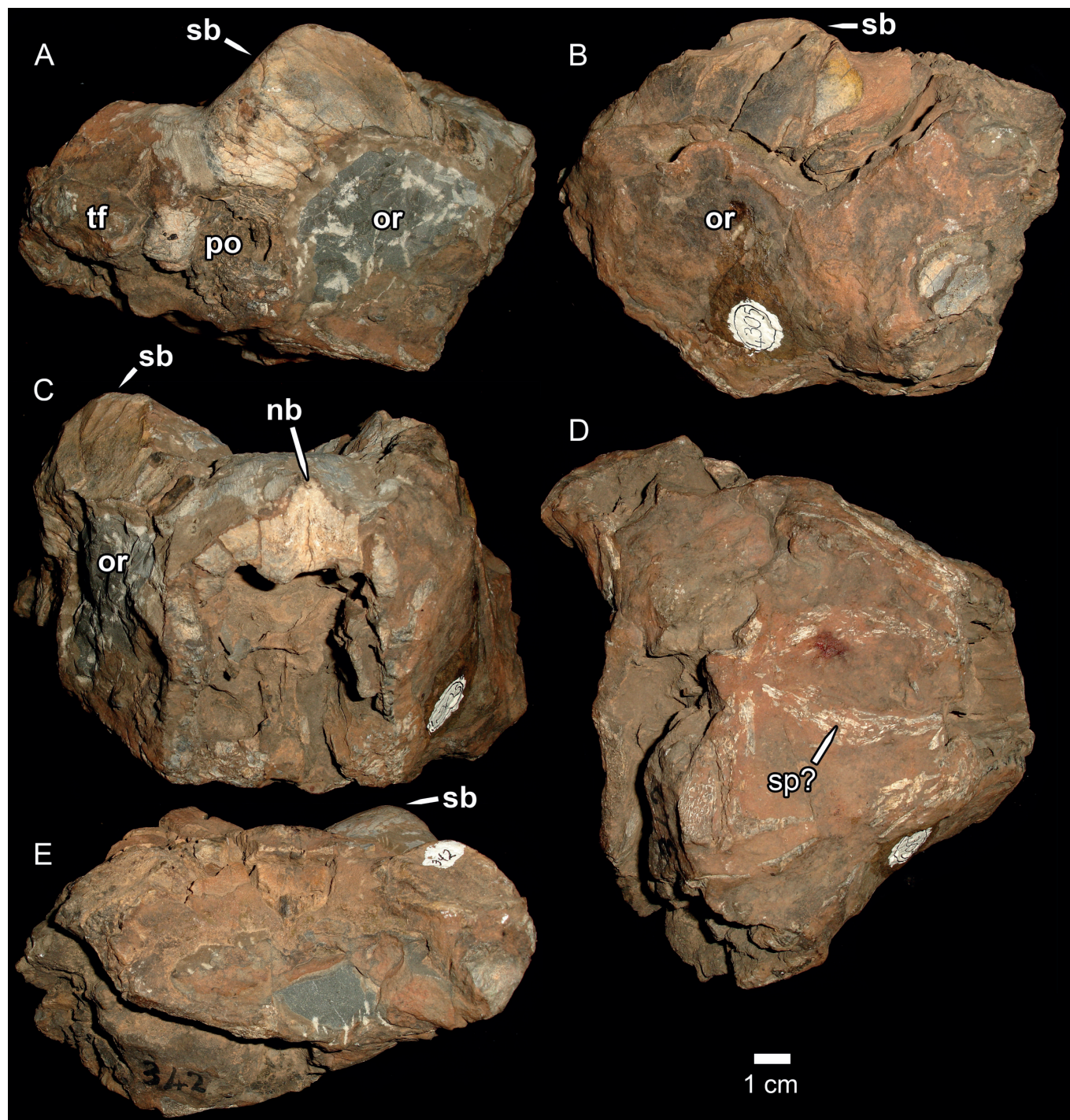


Figure 3. TM 4305 in (A) right lateral, (B) left lateral, (C) anterior, (D) ventral and (E) posterior views. nb, Nasal boss; or, orbit; po, postorbital bar; sb, supraorbital boss; sp, sphenoid element; tf, temporal fenestra.

taxa more closely related to it than *Burnetia mirabilis* Broom, 1923.

Burnetiamorph sp. B

Material. NHMUK R871, a fragment of skull roof preserving the interorbital region and temporal roof to the anterior edge of the pineal foramen (Figs 4–6).

Locality and horizon. Tafelberg, Beaufort West; *Tropidostoma* Assemblage Zone (Lopingian). This specimen was collected by Thomas Bain, at the same locality where he collected the type series of *Tropidostoma* (i.e. the holotypes of *T. dunnii*, *T. microtrema*, and topotypic material [Seeley 1889], all currently considered referable to *Tropidostoma*

dubium [Kammerer *et al.* 2011]). Tafelberg consists of steep exposures near Teekloof Pass spanning (in descending order) the *Cistecephalus*, *Tropidostoma*, *Pristerognathus* and a small portion of the *Tapinocephalus* AZs (B. Rubidge, pers. comm.). As for most historical Karoo collections, precise stratigraphic data for Bain's Tafelberg material is not available. Given that all of this material other than NHMUK R871 is referable to *Tropidostoma*, however, it is reasonable to conclude that this collection originated in the *Tropidostoma* AZ.

Description. This fragment of skull roof was originally labeled 'Theriodont? Reptile' and subsequently relabeled 'Deinocephalian.' The collection of this specimen with

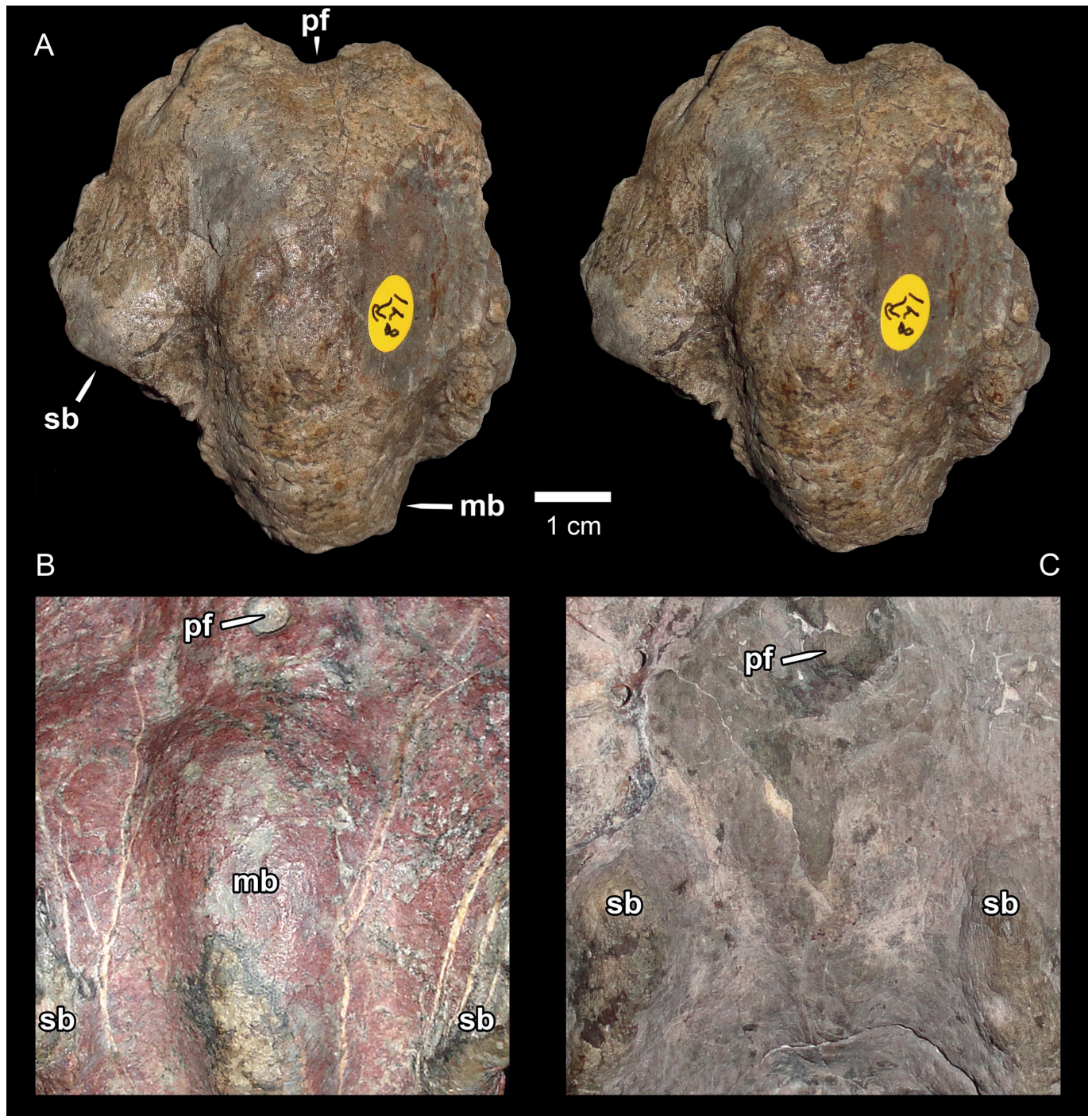


Figure 4. Burnetioid interorbital regions: **A**, Stereopair of NHMUK R871 in dorsal view; close-ups of the interorbital regions of **(B)** *Paraburnetia sneeubergensis* (SAM-PK-K10037) and **(C)** *Burnetia mirabilis* (NHMUK R5097). Note shared presence of a massive median boss in *Paraburnetia* and NHMUK R871 (absent in *Burnetia*), and separation between the median, supraorbital, and pineal bosses in *Paraburnetia* (distinguishing it from NHMUK R871). mb, Median boss; pf, pineal foramen; sb, supraorbital boss.

definitive specimens of *Tropidostoma* makes a dinocephalian identification very unlikely based on established biostratigraphic distributions (Rubidge 1995). Additionally, the high degree of pachyostosis in such a small skull (the preserved portion is 6.3 cm sagittal length, 5.6 cm maximum width) would be remarkable in a dinocephalian, but is typical of burnetiids. In *Anteosaurus* skulls of similar size, there is no development of the frontal boss or supraorbital 'horns' (Kammerer 2011), whereas a median boss and paired, presumed supraorbital bosses are clearly present in NHMUK R871. Among dinocephalians, NHMUK R871 is somewhat similar to *Styracocephalus platyrhynchus*, but

differs from that taxon in the presence of a large median interorbital boss separated from the supraorbital bosses by a narrow channel anteriorly (Fig. 4). In *Styracocephalus*, the massive supraorbital bosses become confluent with a weaker frontal boss located anterior to the orbits (Rubidge & van den Heever 1997).

Among burnetiamorphs, NHMUK R871 is most similar to *Lende*, *Paraburnetia* and *Proburnetia*, which share a massive, anteroposteriorly elongate median boss in the interorbital region. The endocast of *Proburnetia viatkensis* (PIN 2116/1) confirms that this boss overlies the mid-frontal suture (Rubidge & Sidor 2002). In 'Burnetia-line' burnetiids

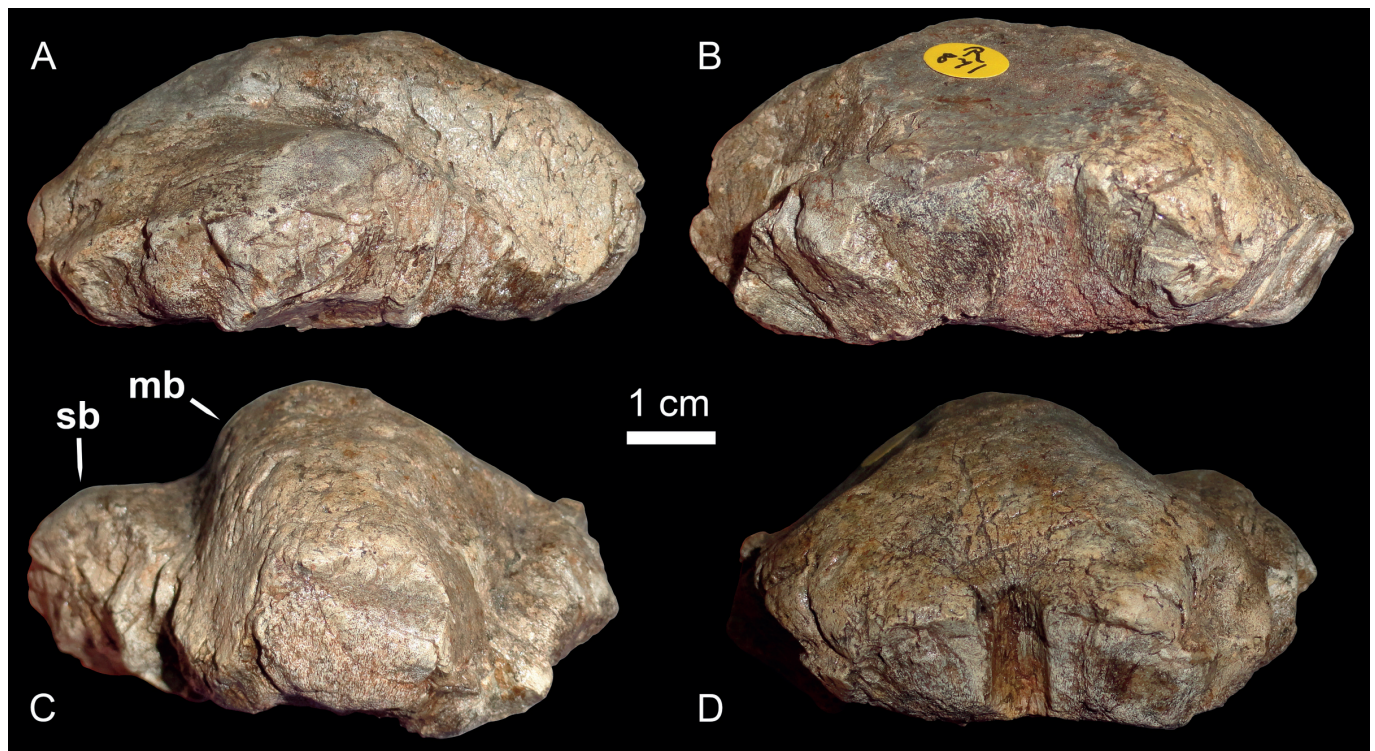


Figure 5. NHMUK R871 in (A) right lateral, (B) left lateral, (C) anterior and (D) posterior views. mb, Median boss; sb, supraorbital boss.

(at least *Burnetia*, *Bullacephalus* and *Pachydectes* – this region is not preserved for *Niuksenitia*), the interorbital region typically bears a weak median ridge (Figs 1D & 4C), but not a massive boss as in NHMUK R871. A broader, but still relatively low, median ridge is also present in the Tanzanian burnetiamorph NMT RB4 (also known solely from an isolated skull roof), which has been considered most similar to *Burnetia* (Sidor *et al.* 2010). The median frontal ridge is extremely weak in *Lobalopex*, and posterior to the contact with the nasals the interorbital region of this taxon becomes almost flat. Although only the anterior edge of the interorbital region is known for *Lophorhinus*, this taxon clearly lacked the sort of massive median boss

present in NHMUK R871 – only a weak median ridge is present. In the other taxa (*Lende*, *Paraburnetia* and *Proburnetia*) with massive interorbital bosses, this structure extends anterior to the orbits, and would be evident in the preserved portion of *Lophorhinus* if present. Finally, *Lemurosaurus* has a distinct median interorbital boss, but it is transversely narrower and anteroposteriorly shorter than that of NHMUK R871 and the other taxa with massive median bosses.

In addition to sharing a massive median interorbital boss, NHMUK R871 also closely resembles *Lende* in the absence of a pineal boss (present in all other burnetia-morphs) and in the morphology of the supraorbital boss.

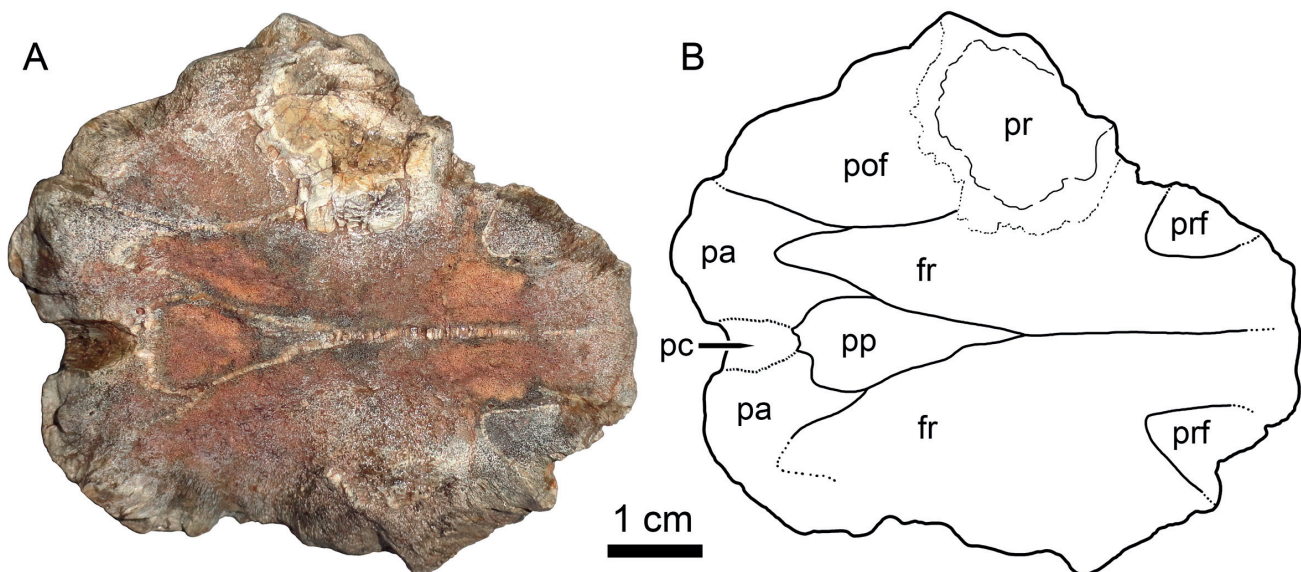


Figure 6. NHMUK R871 in (A) ventral view with (B) interpretive drawing. fr, Frontal; pa, parietal; pc, pineal canal; pof, postfrontal; pp, preparietal; pr, pachyostosed region at base of supraorbital boss; prf, prefrontal.

In *Paraburnetia* and *Proburnetia*, the supraorbital boss, although massive, is topologically restricted to the orbital rim (Fig. 1C), whereas in *Lende*, an attenuate portion of the supraorbital boss extends posteromedially in the direction of the pineal foramen (Kruger *et al.* 2015). The same condition is present in NHMUK R871 (Fig. 4A). However, despite these similarities, NHMUK R871 differs from *Lende* (as well as *Paraburnetia* and *Proburnetia*) in an important regard. In these other taxa, the median, supraorbital, and (in *Paraburnetia* and *Proburnetia*) pineal bosses are all discrete structures, separated from one another by shallow troughs (Figs 1C & 4B). In NHMUK R871, the supraorbital bosses extend far enough posteromedially to fuse with the median boss, forming a diffuse cranial 'dome' in the intertemporal region (Fig. 4A). This 'dome' is penetrated by the pineal foramen, which unlike all burnetiamorphs except *Lende* lacks a raised boss around it. In *Lende*, the pineal foramen is located on a flat surface posterior to the median boss, whereas in NHMUK R871 the median boss (as part of the 'dome') slopes gradually posteriorly, enveloping the foramen. This morphology is similar to that of tapinocephalid dinocephalians, in which the pineal boss becomes absorbed by a pachyostotic dome during ontogeny (Boos *et al.* 2015), and also vaguely resembles the frontoparietal dome of pachycephalosaurian dinosaurs. NHMUK R871 is also unusual in that it appears the median interorbital boss was slightly taller than the supraorbital bosses (Fig. 5C). This is probably an artefact of damage, as the orbital edges of the latter (typically where these bosses are tallest; see Fig. 1C) are not preserved. This said, it is worth noting that the median boss of *Lende* is also unusually tall, proportionally, being nearly equal in height to the supraorbital bosses (Kruger *et al.* 2015).

No sutures are visible dorsally on this specimen (Fig. 4); they have been completely obliterated by pachyostosis. Ventrally, however, clear sutures are visible (Fig. 6), providing some of the only information on the precise positions of the skull roofing bones in a burnetiid. Most of this specimen is made up of the frontals, although a large portion of the left postfrontal is also preserved, making up the supraorbital boss. The posterior tips of the prefrontals are preserved at the anterolateral edge of the specimen, indicating substantial posterior extension of this bone (as is typical of biarmosuchians). Most remarkably, a definite preparietal is present. This element originates immediately anterior to the pineal foramen and is broadest posteriorly, where it is flanked on both sides by anterior processes of the parietals. It strongly attenuates anteriorly between the frontals, giving an elongate triangular shape to the element as a whole. Previously, a preparietal had only been reported for *Pachydictes* within Burnetiamorpha (Rubidge *et al.* 2006), but it is likely that this element was present in many (possibly all) members of the group. Although obscured by pachyostosis, a preparietal-shaped depression is present anterior to the pineal foramen in *Lobalopex* (Sidor *et al.* 2004), and an attenuate element between the frontals in *Burnetia*, although not distinct from the parietals dorsally (Rubidge & Sidor 2002), is very similar in shape to the preparietal of NHMUK R871.

PHYLOGENETIC ANALYSIS

TM 4305 and NHMUK R871 were included in a modified version of the most recent phylogenetic analysis of burnetiamorphs (Kruger *et al.* 2015; itself modified from the analyses of Rubidge & Kitching [2003], Rubidge *et al.* [2006] and Sidor & Welman [2003]) to test their relationships. The analysis of Kruger *et al.* (2015) included 36 characters and 15 operational taxonomic units (OTUs), whereas the current analysis includes 30 characters and 17 OTUs. The following alterations were made to the Kruger *et al.* (2015) matrix for the current analysis:

For character 1 ('length of dorsal process of premaxillae'), Kruger *et al.* (2015) coded *Ictidorhinus martinsi* as having a short dorsal process of the premaxilla (i.e. not extending posterior to the level of the upper canine). However, this portion of the snout is not preserved in the holotype of *I. martinsi* (AMNH FARB 5526) – a damaged section covered in matrix extends between the premaxillae and nasals dorsally. This damaged section extends past the upper canine, so the posterior extent of the premaxilla dorsally is unclear. *Ictidorhinus martinsi* has been recoded as uncertain (?) for this character. Kruger *et al.* (2015) coded *Lophorhinus willodenensis* as being uncertain for this character, but it has been recoded as having a short dorsal process of the premaxilla (state 0). The posterior suture of the premaxilla is preserved in the holotype of *L. willodenensis* (SAM-PK-K6655) and is clearly anterior to the upper canine, as figured by Sidor & Smith (2007).

For character 2 ('lateral surface of lacrimal bears one or more deep fossae'), Kruger *et al.* (2015) coded the non-burnetiamorph biarmosuchians *Lycaenodon longiceps* and *Herpetoskylax hopsoni* as possessing lacrimal fossae, *contra* previous studies (e.g. Sidor & Welman 2003; Sidor & Smith 2007) that considered this fossa autapomorphic for Burnetiamorpha. In my examination of this material (NHMUK R5700, holotype of *Lycaenodon longiceps*, and CGP/1/67 and BP/1/3924, holotype and referred specimen of *Herpetoskylax hopsoni*), no lacrimal fossae were evident, and this character has been recoded as absent (state 0) for these taxa. Kruger *et al.* (2015) coded *Lende chiweta* as lacking a lacrimal fossa, but indicate in their description that this structure is present; this has been recoded accordingly.

For character 3 ('external surface of maxilla'), Kruger *et al.* (2015) coded *Burnetia mirabilis* as having a smooth external maxillary surface. While probably correct, the external bone surface of the holotype of *B. mirabilis* (NHMUK R5697) is so overprepared that this should be considered uncertain (?), and this taxon has been recoded as such.

For character 4 ('shape of dorsal surface of nasals'), Kruger *et al.* (2015) coded *Lende chiweta* and *Proburnetia viatkensis* as having a 'narrow median boss' (state 1). However, the breadth of the nasal boss in *Proburnetia* is nearly equal to (albeit anteroposteriorly shorter than) that of *Paraburnetia* (coded as state 2, 'with transversely expanded median boss') and significantly more transversely expanded than in taxa such as *Lophorhinus* or *Lobalopex* in which it forms a narrow crest. As such, *Proburnetia* has been recoded as state 2 for this character. The nasal boss of *Lende* is also more transversely expanded than that of *Lophorhinus*.

or *Lobalopex*, so it has also been recoded as state 2. This character and character 5 ('shape of dorsal surface of frontals') have been changed to ordered in the current analysis, to reflect the fact that they represent a continuum of increasingly robust cranial bosses.

For character 6 ('posterolateral extension of frontal reaching the level of the midpoint to behind pineal foramen'), Kruger *et al.* (2015) coded *Ictidorhinus martinsi* and *Proburnetia viatkensis* as uncertain. Examination of the holotype of *I. martinsi* (AMNH FARB 5526) and endocast of the *P. viatkensis* type (PIN 2116/1; see also Rubidge & Sidor 2002) indicates that a posterolateral extension of the frontal is present (state 1) in both of these taxa.

The former characters 7 ('supraorbital margin') and 10 ('boss above postorbital bar') of Kruger *et al.* (2015) have been altered to better capture morphological variation among burnetiamorph taxa. These characters are dealing with two related issues: the presence or absence of a supraorbital horn and the shape of that structure. Presence of a supraorbital horn is a burnetiamorph synapomorphy, and is present in all burnetiamorphs in which the skull roof is known. In most taxa this horn is pachyostosed to form a massive boss, but even in *Lobalopex* and *Lophorhinus*, in which the dorsal orbital margin is not pachyostosed, there is a distinct triangular flange above the orbits. Among burnetiamorphs with extensive cranial pachyostosis, two basic supraorbital boss morphologies are present: there is either a single large, triangular boss directly above the orbits (present in *Lemurosaurus*, *Lende*, *Paraburnetia* and *Proburnetia*) or two supraorbital bosses, with a low, massive, ovoid boss above the anterior edge of the orbit and a second, more laterally-positioned boss above the posterior edge of the orbit and the postorbital bar (present in *Bullacephalus* and *Burnetia*; a boss is present above the postorbital bar in *Pachydictes*, but the orbital region of this taxon is too badly damaged to confidently code this character). The new characters 8 ('supraorbital horn') and 9 ('supraorbital boss morphology') reflect these distinctions. For new character 9, taxa lacking a pachyostosed supraorbital boss are coded as not applicable (–).

Character 8 of Kruger *et al.* (2015) ('adductor musculature originates on dorsal surface of postorbital') has been deleted because it was parsimony uninformative (all taxa were coded as either 0 or ?).

For character 11 ('postorbital bar scoop-shaped because temporal fenestra undercuts it'), Kruger *et al.* (2015) coded *Lende chiweta* and *Paraburnetia sneeubergensis* as uncertain. In neither of these taxa does the temporal fenestra undercut the orbit (an anterior expansion of the right temporal fenestra in MAL 290, holotype of *L. chiweta*, represents damage), and they have been recoded as absent (state 0) for this character.

Character 15 ('preparietal') of Kruger *et al.* (2015) previously had three states ('absent', 'present but is narrowly separated from pineal foramen by parietals', and 'present and forms anterior margin of pineal foramen'), with only *Ictidorhinus martinsi* and *Lycaenodon longiceps* coded as having state 1. However, in *Ictidorhinus*, the preparietal clearly forms the anterior margin of the pineal foramen. For *Lycaenodon*, previous analyses have utilized a composite

coding based on the holotype (NHMUK R5700) and a referred specimen (RC 20; referred to *L. longiceps* by Sigogneau-Russell 1989). However, NHMUK R5700 and RC 20 differ in several regards: for example, RC 20 has broader palatines and significantly narrower choanae than NHMUK R5700. In this feature RC 20 is very similar to *Ictidorhinus*, and it is possible that RC 20 actually represents an adult skull of *I. martinsi*. Given continued uncertainty surrounding the distinction between *Ictidorhinus* and *Lycaenodon* (Sidor & Rubidge 2006), for the purposes of the current analysis the codings for *Ictidorhinus martinsi* and *Lycaenodon longiceps* are based solely on their respective holotypes. Because the pineal region is absent in NHMUK R5700, *Lycaenodon* is here coded as uncertain (?) for preparietal morphology. In RC 20, however, the preparietal forms the anterior margin of the pineal foramen, so even if this specimen was included in the *Lycaenodon* hypodigm it would not warrant use of character state 1 of Kruger *et al.* (2015). This character has been changed to simply reflect presence/absence of the preparietal. It must be noted, however, that in the only taxon coded as lacking a preparietal (*Biarmosuchus tener*), this absence may be autapomorphic. The broad distribution of preparietals among basal therapsids (being common in gorgonopsians and anomodonts in addition to biarmosuchians) suggests that the absence of this element in *Biarmosuchus* may not accurately reflect the ancestral condition for Biarmosuchia.

Character 16 ('vomer') of Kruger *et al.* (2015) has been deleted because it was parsimony uninformative. All known biarmosuchians possess an unpaired vomer. Kruger *et al.* (2015) coded a number of non-burnetiid taxa as uncertain for this character, but an unpaired vomer is clearly present in *Biarmosuchus*, *Hipposaurus* and *Ictidorhinus* and appears to be present in *Herpetoskylax*, *Lemurosaurus* and *Lobalopex* as well. The only taxon Kruger *et al.* (2015) coded as having a paired vomer was *Bullacephalus jacksoni*. However, there is no evidence for a paired vomer in this taxon: although the preserved portion of the vomer is made up of paired ventral ridges, similar structures are present in many other biarmosuchians that have a fused vomer, representing ventral extensions of the lateral vomerine margins. Examining the vomer of the *B. jacksoni* holotype (BP/1/5387) in anterior view, there is no clear suture between these ridges, and I interpret this element as unpaired. Even if this interpretation is incorrect and there is a paired vomer in *Bullacephalus*, this would then be an autapomorphy of that genus. So regardless of the condition in this taxon, this character is parsimony uninformative.

For character 17 ('palatine dentition'), Kruger *et al.* (2015) coded *Niuksenitia sukhonensis* as uncertain. Although the anterior palate is largely missing in the holotype of *N. sukhonensis* (PIN 3159/1), the left palatine boss is well preserved and shows that dentition on this element was limited to a single tooth row along the lateral and medial edges of the boss (state 1). Kruger *et al.* (2015) coded *Bullacephalus* and *Pachydictes* as having extensive palatine dentition (state 0). While these taxa have a dense cluster of palatal teeth on the pterygoid, they have only narrow tooth rows on the palatine, and as such have been recoded (to state 1) for this character.

Character 21 ('shape of postparietal') of Kruger *et al.* (2015) has been deleted because it was parsimony uninformative. Of the three character states ('wider than tall', 'approximately square', and 'taller than wide'), only *Ictidorhinus martinsi* was coded as 'wider than tall' and no taxa were coded as 'taller than wide.'

For character 22 ('ratio of dentary height in canine versus anterior postcanine regions'), Kruger *et al.* (2015) coded *Lende chiveta* as showing a pronounced difference between the canine and postcanine heights of the dentary. The dentary proportions of *Lende* are comparable to those of *Proburnetia*, however, so the former taxon has been recoded as showing nearly equivalent heights for these measures (state 1).

For character 23 ('dentary-angular suture'), Kruger *et al.* (2015) coded *Paraburnetia sneeubergensis* as being uncertain. The mandible of *Paraburnetia* is well preserved and the posterior margin of its dentary is clearly incised (state 1), so this taxon has been recoded accordingly.

Character 24 ('palatine boss size') of Kruger *et al.* (2015) has been deleted because it is vague (no quantitative bounds were provided for the distinction between 'small', 'medium' and 'large' bosses) and inconsistently coded. For example, Kruger *et al.* (2015) code *Hipposaurus* as having a large boss, *Lobalopex* as having a medium-sized boss, and *Lycaenodon* as having a small boss, but the palatine boss is not preserved in *Lycaenodon* (i.e. NHMUK R5700; the palatine boss in RC 20 is present, but too badly damaged to accurately measure) and the relative length of this structure (measured as boss length relative to basal skull length) is very similar in *Hipposaurus* (0.14 in SAM-PK-9081) and *Lobalopex* (0.15 in CGP/1/61) (note also that the boss is actually somewhat smaller in *Hipposaurus* than in *Lobalopex*).

Character state 1 ('nubbin-like boss') has been deleted from character 26 ('squamosal horns') of Kruger *et al.* (2015), because in the only taxon with this character state (*Lemurosaurus pricei*) the boss in question is on the lateral surface of the postorbital, not the squamosal. The coding for *Pachydictes* has been changed from present to uncer-

tain (?), because the back of the skull is damaged in the holotype (BP/1/5735) of this taxon.

Character 27 ('crest on the postparietal') of Kruger *et al.* (2015) has been deleted because this structure (the nuchal crest) is present in all biarmosuchians and the different states ('absent to slight', 'moderate' and 'large') are not readily differentiable. From my examination of these specimens, the primary sources of variation in this character are degree of taphonomic wear and overall skull size. This character has been replaced with a new postparietal character (new character 20), based on the presence or absence of a pair of descending ridges lateral to the nuchal crest, extending from the posterior edge of the parietal onto the postparietal. These ridges are well developed in burnetiids; they are clearly present in *Burnetia*, *Lende*, *Paraburnetia* (Fig. 7A) and *Proburnetia*, and are exceptionally well developed (with rugose surface texture) in *Bullacephalus* (Fig. 7B). Very small but distinct descending ridges are present in the same position in *Lobalopex* but appear to be absent in *Lemurosaurus*.

Character 28 ('dorsal skull angulation above the orbital region') of Kruger *et al.* (2015) has been deleted because variation in this character is primarily due to miscoding or taphonomic distortion. This character refers to the characteristic angle in the dorsal profile of biarmosuchian skulls, which forms an apex above the orbits, with downward slope of both the snout and temporal regions. Kruger *et al.* (2015) coded five taxa as lacking this angulation: *Herpetoskylax*, *Lobalopex*, *Proburnetia*, *Burnetia* and *Bullacephalus*. In *Lobalopex mordax*, the absence of this angulation can be attributed to the extreme dorsoventral crushing suffered by the holotype (CGP/1/61). In the holotype of *Herpetoskylax hopsoni* (CGP/1/67), there is a relatively weak posterior slope to the temporal region, but the characteristic biarmosuchian angulation is definitely present in the referred specimen BP/1/3924. In the burnetiids *Bullacephalus*, *Burnetia* and *Proburnetia*, this angulation is absent, but only because the dorsal margin of the temporal region is expanded due to the presence of pachyostosed squamosal horns. In the absence of these horns, the skull would have the typical

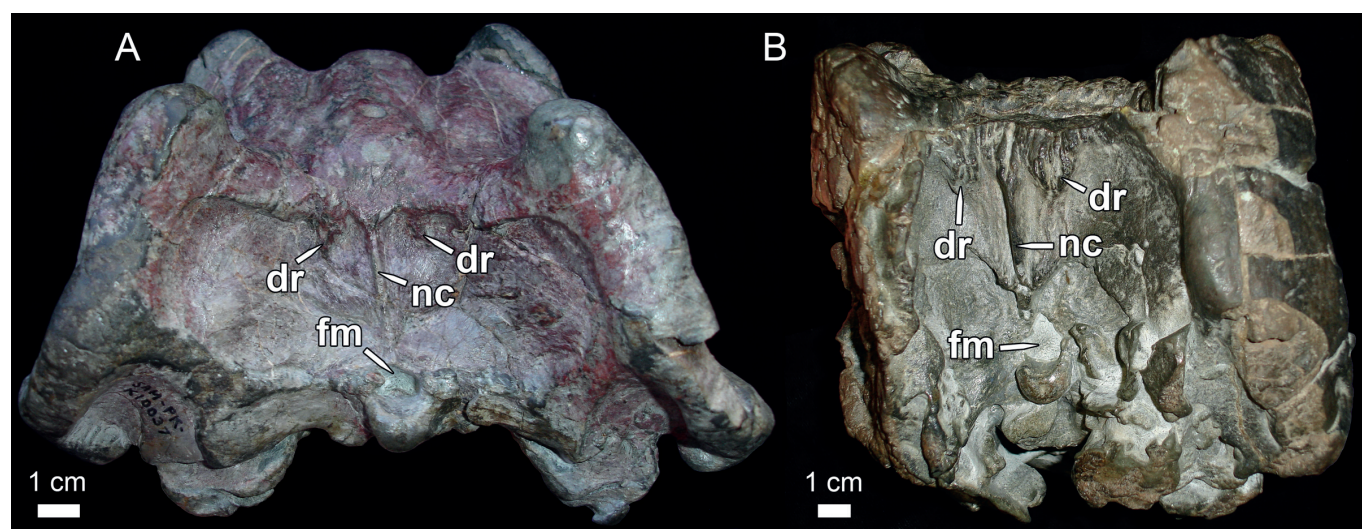


Figure 7. Burnetiamorph occiputs, illustrating presence of paired descending ridges extending between the parietals and postparietal, lateral to the nuchal crest (new character 20): **A**, *Paraburnetia sneeubergensis* (SAM-PK-K10037); **B**, *Bullacephalus jacksoni* (BP/1/5387). dr, Descending ridge; fm, foramen magnum; nc, nuchal crest.

biarmosuchian morphology (as indicated by the relatively ventral position of the temporal fenestra relative to the orbit). As such, the only real morphological variation being captured by this character is redundant with character 26 ('squamosal horns') of Kruger *et al.* (2015).

Character 31 ('arcant ridge extending from anterodorsal margin of orbit towards external naris') of Kruger *et al.* (2015) has been deleted because it was parsimony uninformative. Kruger *et al.* (2015) coded this character as being present in two taxa: *Lobalopex mordax* and *Lende chiweta*. However, the apparent ridge between the orbit and naris in the holotype of *L. mordax* (CGP/1/61) is artefactual – it is the result of dorsoventral crushing creating apparent biplanarity between the maxilla and nasal. There is a real ridge on the lateral surface of the snout in *Lobalopex*, but it corresponds to the underlying canine root and does not extend to the naris. As such, this character is, at best, interpreted as an autapomorphy of *Lende*.

Character 32 ('posterior extension of the postfrontal') of Kruger *et al.* (2015) has been deleted because it was parsimony uninformative. The only taxon for which Kruger *et al.* (2015) coded this as absent is *Biarmosuchus tener*. In the holotype of *Biarmosuchus tener* (PIN 1758/2), the temporal region is poorly preserved and the extent of the postfrontal is difficult to determine. In multiple referred specimens, however (PIN 1758/1, PIN 1758/7, PIN 1758/18), there is clearly a posterior extension of the postfrontal present.

Character 33 ('boss on anterior margin of squamosal') of Kruger *et al.* (2015) previously had three states ('absent', 'small' and 'elongated'). Kruger *et al.* (2015) coded *Lemurosaurus*, *Lende* and *Lobalopex* as having 'small' squamosal bosses and *Burnetia*, *Pachydictes* and *Proburnetia* as having 'elongate' squamosal bosses (*Paraburnetia* and *Niuksenitia* were coded as '?', but these taxa have very prominent squamosal bosses). While this boss is indeed weakly developed in *Lemurosaurus* and *Lobalopex*, the squamosal boss of *Lende* is rather larger relative to its skull size. The squamosal boss morphology among burnetiids varies extensively – 'elongated' does not accurately describe the low bosses of *Proburnetia* or the complex curved structure in *Paraburnetia*, for example. Only in *Burnetia* and *Niuksenitia* are the squamosal bosses nearly identical in morphology. Given the difficulty in firmly demarcating 'small' from 'elongate' bosses in this sample of taxa, this character has been changed to simply reflect presence/absence of the squamosal boss. Kruger *et al.* (2015) coded *Bullacephalus* as lacking a squamosal boss, but although this taxon lacks an anteriorly-projecting boss like that of *Niuksenitia* or *Paraburnetia*, there is clearly a boss on the squamosal below the temporal fenestra. In *Pachydictes* the subtemporal squamosal is not preserved, so its coding has been changed to uncertain (?).

For character 34 ('prefrontal boss'), Kruger *et al.* (2015) coded *Paraburnetia sneeubergensis* as uncertain. A swollen portion of the prefrontal is present at the anterior margin of the orbit in this taxon, so it has been recoded as present (state 1).

For character 35 ('zygomatic arch elevated in lateral view'), Kruger *et al.* (2015) coded *Hipposaurus boonstrai* and *Paraburnetia sneeubergensis* as uncertain. This is a problematic

character; although the zygoma is clearly more elevated in, e.g. *Herpetoskylax* than in *Bullacephalus*, there is not a clear demarcation between these end-members. This character is tentatively retained; as *Paraburnetia* exhibits a morphology comparable to burnetiids in which this character is listed as absent (state 0), it has been recoded as such. Similarly, the morphology of *Hipposaurus* is comparable to that of *Herpetoskylax*, so it has been recoded as elevated (state 1). Kruger *et al.* (2015) coded *Lycaenodon longiceps* and *Lobalopex mordax* as having an elevated zygomatic arch, but this part of the skull is missing in the former and badly crushed in the latter; these have been recoded as uncertain (?).

Character 36 ('palatine teeth') of Kruger *et al.* (2015) has been deleted because it was redundant with their character 17 ('palatine dentition').

Characters 11 ('pachyostosis of zygomatic arch') and 13 ('squamosal thickened along its posterior border with the tabular') of Sidor & Smith (2007) have been added as new characters 16 and 22 in the present analysis. The latter is treated as ordered.

DISCUSSION

Results of the phylogenetic analysis

The full analysis, including the two new specimens, yielded 22 most parsimonious trees of length 45 (consistency index=0.778, retention index=0.882). In the strict consensus (Fig. 8A), TM 4305 is recovered as a burnetia-morph more derived than *Lemurosaurus*, in a polytomy with *Lobalopex*, *Lophorhinus*, all 'Burnetia-line' burnetiids, and a clade made up of the 'Proburnetia-line' burnetiids. NHMUK R871 is recovered in a polytomy with *Lende*, *Paraburnetia* and *Proburnetia* in the 'Proburnetia-line' clade. Deletion of the extremely incomplete new specimens (TM 4305 could be coded for only 4 of 30 characters; NHMUK R871 for 6) from the analysis yielded three most parsimonious trees of length 45. The strict consensus of these trees is a topology similar to that of Sidor & Smith (2007), albeit with *Lende* included within the Burnetiidae (in a polytomy with *Paraburnetia* and *Proburnetia*) and the non-burnetiamorphs *Herpetoskylax* and *Ictidorhinus* collapsed into a polytomy with *Lycaenodon* (Fig. 8B).

Within Burnetiidae, two subclades are formally recognized here, corresponding to the 'Proburnetia-line' and 'Burnetia-line' burnetiids. All previous phylogenetic analyses of Burnetiamorpha have recovered a close relationship between *Burnetia*, *Niuksenitia* and *Bullacephalus* to the exclusion of other burnetiamorphs (Sidor & Welman 2003; Sidor *et al.* 2004; Smith *et al.* 2006), and all analyses that included *Pachydictes* also recovered it as a member of this group (Rubidge *et al.* 2006; Sidor & Smith 2007; Kruger *et al.* 2015). Sidor *et al.* (2004), Smith *et al.* (2006) and Sidor & Smith (2007) also previously recovered *Paraburnetia* and *Proburnetia* as sister-taxa (with this clade in turn forming the sister of 'Burnetia-line' burnetiids). Although Kruger *et al.* (2015) did not recover a monophyletic group of 'Proburnetia-line' burnetiids, this portion of their topology was influenced by character codings disputed here (see above). Here, the 'Burnetia-line' and 'Proburnetia-line'

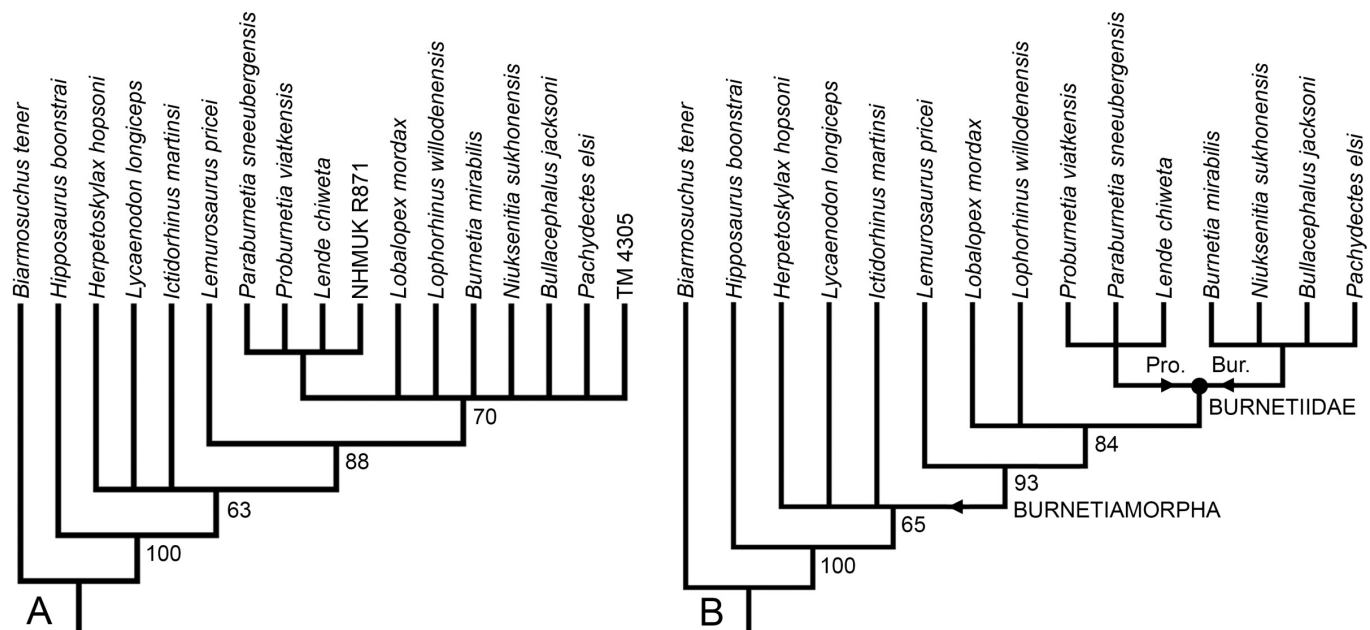


Figure 8. Results of the phylogenetic analysis. **A**, Strict consensus of complete taxon set; **B**, strict consensus with TM 4305 and NHMUK R871 excluded from the analysis. Numbers at nodes represent symmetric resampling values. Pro., Proburnetiinae; Bur., Burnetiinae.

burnetiid subclades are called Burnetiinae Broom, 1923 and Proburnetiinae nov., and make up a node-stem triplet with Burnetiidae.

Burnetiamorph diversity and distribution

Although fragmentary, the new specimens TM 4305 and NHMUK R871 differ from all previously described burnetiamorphs in their overlapping morphology. Because of their incompleteness, these specimens are left in open nomenclature, but they are likely to represent distinct taxa and indicate even higher burnetiamorph richness in the Karoo than currently thought. Although recovered in somewhat uncertain positions in the phylogenetic analysis, these specimens help fill in significant ghost lineages in South African Burnetiamorpha. Though it was recovered in a polytomy with burnetiids, *Lobalopex* and *Lophorhinus*, TM 4305 is likely to be more closely related to Burnetiidae than the latter two genera based on its high degree of cranial pachyostosis, including massive supraorbital bosses and anteroposteriorly expanded postorbital bar. This specimen lacks the median interorbital boss characteristic of proburnetiines and the double supraorbital bosses, very broad intertemporal region, and anteriorly-positioned pineal foramen characteristic of burnetiines (though these characters may also be absent in *Pachydictes*). As such, it could lie immediately outside of Burnetiidae or represent a basal member of either subfamily. This specimen requires additional study (with either new preparation or CT scanning) to solidify its relationships, as it could represent the only proburnetiine or non-burnetiid burnetiamorph known from the *Tapinocephalus* AZ.

NHMUK R871 is recovered as a proburnetiine, representing the oldest African record of the group (*Paraburnetia* is from low in the *Cistecephalus* AZ and, although the correlation is somewhat uncertain, the Chiweta beds that produced *Lende* are generally considered *Cistecephalus* AZ equivalents; Jacobs *et al.* 2005; Smith *et al.* 2006). Though

recovered in a polytomy with all other proburnetiines, several features (absence of a pineal boss, posteromedial expansion of the supraorbital bosses) suggest that NHMUK R871 is most closely related to *Lende* among described burnetiamorphs. Burnetiid biogeography is difficult to assess given their spotty record, but they appear to be broadly distributed even within subclades, with both proburnetiines and burnetiines being present in South Africa (*Paraburnetia*, NHMUK R871, *Bullacephalus*, *Burnetia*, *Pachydictes*), east Africa (*Lende*, NMT RB4) and Russia (*Proburnetia*, *Niuksenitia*). In addition to the published records of east African burnetiamorphs (Sidor *et al.* 2010; Kruger *et al.* 2015), there are currently a number of undescribed specimens referable to this group from the Madumabisa Mudstone Formation of Zambia (Sidor 2015; Sidor *et al.* 2015; Whitney & Sidor in press). Although no burnetiamorphs have yet been recovered from other Permian therapsid-bearing regions (e.g. Brazil, China, India, Scotland), given the general rarity of this group, their absence from these areas should be considered questionable (especially considering that significantly more abundant clades such as Gorgonopsia and Therocephalia have yet to be found there). Greater exploration of these understudied regions will be vital to improving our understanding of early therapsid evolution, but as the specimens described herein indicate, there is clearly still much to be discovered even in the South African fossil record.

ABBREVIATIONS

Institutional

AMNH FARB	American Museum of Natural History, Fossil Amphibian, Reptile, and Bird Collection, New York, U.S.A.
BP	Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa;
CGP	Council for Geoscience, Pretoria, South Africa
MAL	Malawi Department of Antiquities Collection, Lilongwe and Nguludi, Malawi
NHMUK	the Natural History Museum, London, U.K.

NMQR	National Museum, Bloemfontein, South Africa
NMT	National Museum of Tanzania, Dar es Salaam, Tanzania
PIN	Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia
RC	Rubidge Collection, Wellwood, Graaff-Reinet, South Africa
SAM	Iziko Museums of South Africa, Cape Town, South Africa
TM	Ditsong National Museum of Natural History, Pretoria, South Africa.

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REFERENCES

- BOOS, A.D.S., KAMMERER, C.F., SCHULTZ, C.L. & NETO, V.P. 2015. A tapinocephalid dinocephalian (Synapsida, Therapsida) from the Rio do Rasto Formation (Paraná Basin, Brazil): Taxonomic, ontogenetic and biostratigraphic considerations. *Journal of South American Earth Sciences* **63**, 375–384.
- BROOM, R. 1905. On the use of the term Anomodontia. *Records of the Albany Museum*, **1**, 266–269.
- BROOM, R. 1923. On the structure of the skull in the carnivorous dinocephalian reptiles. *Proceedings of the Zoological Society of London* **1923**, 661–684.
- GOLOBOFF, P.A., FARRIS, J.S. & NIXON, K.C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* **24**, 774–786.
- JACOBS, L.L., WINKLER, D.A., NEWMAN, K.D., GOMANI, E.M. & DEINO, A. 2005. Therapsids from the Permian Chiweta Beds and the age of the Karoo Supergroup in Malawi. *Palaeontologia Electronica* **8**, 28A: 1–23.
- KAMMERER, C.F. 2011. Systematics of the Anteosauria (Therapsida: Dinocephalia). *Journal of Systematic Palaeontology* **9**, 261–304.
- KAMMERER, C.F., ANGIELCZYK, K.D. & FRÖBISCH, J. 2011. A comprehensive taxonomic revision of *Dicynodon* (Therapsida, Anomodontia) and its implications for dicynodont phylogeny, biogeography, and biostratigraphy. *Society of Vertebrate Paleontology Memoir* **11**, 1–158.
- KRUGER, A., RUBIDGE, B.S., ABDALA, F., GOMANI CHINDEBVU, E. & JACOBS, L.L. 2015. *Lende chiweta*, a new therapsid from Malawi, and its influence on burnetiamorph phylogeny and biogeography. *Journal of Vertebrate Paleontology* **e1008698**, 1–10.
- LIU, J. 2013. Osteology, ontogeny, and phylogenetic position of *Sinophoneus yumenensis* (Therapsida, Dinocephalia) from the Middle Permian Dashankou Fauna of China. *Journal of Vertebrate Paleontology* **33**, 1394–1407.
- OSBORN, H.F. 1903. On the primary division of the Reptilia into two sub-classes, Synapsida and Diapsida. *Science* **17**, 275–276.
- RUBIDGE, B.S. (ed.) 1995. *Biostratigraphy of the Beaufort Group (Karoo Supergroup)*. South African Committee for Stratigraphy Biostratigraphic Series, **1**.
- RUBIDGE, B.S. & KITCHING, J.W. 2003. A new burnetiamorph (Therapsida: Biarmosuchia) from the lower Beaufort Group of South Africa. *Palaeontology* **46**, 199–210.
- RUBIDGE, B.S. & SIDOR, C.A. 2002. On the cranial morphology of the basal therapsids *Burnetia* and *Proburnetia* (Therapsida: Burnetiidae). *Journal of Vertebrate Paleontology* **22**, 257–267.
- RUBIDGE, B.S. & VAN DEN HEEVER, J.A. 1997. Morphology and systematic position of the dinocephalian *Styracocephalus platyrhynchus*. *Lethaia* **30**, 157–168.
- RUBIDGE, B.S., SIDOR, C.A. & MODESTO, S.P. 2006. A new burnetiamorph (Therapsida: Biarmosuchia) from the Middle Permian of South Africa. *Journal of Paleontology* **80**, 740–749.
- SEELEY, H.G. 1889. Researches on the structure, organization, and classification of the fossil Reptilia.—VI. On the anomodont Reptilia and their allies. *Philosophical Transactions of the Royal Society of London B* **180**, 215–296.
- SIDOR, C.A. 2015. The first biarmosuchian from the upper Madumabisa Mudstone Formation (Luangwa Basin) of Zambia. *Palaeontologia africana* **49**, 1–7.
- SIDOR, C.A. & RUBIDGE, B.S. 2006. *Herpetoskylax hopsoni*, a new biarmosuchian (Therapsida: Biarmosuchia) from the Beaufort Group of South Africa. In: Carrano, M.T., Gaudin, T.J., Blob, R.W. & Wible, J.R. (eds) *Amniote Paleobiology: Perspectives on the Evolution of Mammals, Birds, and Reptiles*, 76–113. Chicago, University of Chicago Press.
- SIDOR, C.A. & SMITH, R.M.H. 2007. A second burnetiamorph therapsid from the Permian Teekloof Formation of South Africa and its associated fauna. *Journal of Vertebrate Paleontology* **27**, 420–430.
- SIDOR, C.A. & WELMAN, J. 2003. A second specimen of *Lemurosaurus pricei* (Therapsida: Burnetiamorpha). *Journal of Vertebrate Paleontology* **23**, 631–642.
- SIDOR, C.A., HOPSON, J.A. & KEYSER, A.W. 2004. A new burnetiamorph therapsid from the Teekloof Formation, Permian, of South Africa. *Journal of Vertebrate Paleontology* **24**, 938–950.
- SIDOR, C.A., ANGIELCZYK, K.D., WEIDE, D.M., SMITH, R.M.H., NESBITT, S.J. & TSUJI, L.A. 2010. Tetrapod fauna of the lowermost Usili Formation (Songea Group, Ruhuhu Basin) of southern Tanzania, with a new burnetiid record. *Journal of Vertebrate Paleontology* **30**, 696–703.
- SIDOR, C.A., KNAUB, C.R., ANGIELCZYK, K.D., BEIGHTOL, C.V., NESBITT, S.J., SMITH, R.M.H., STEYER, J.-S., TABOR, N.J. & TOLAN, S. 2015. Tanzania and Zambia yield an unprecedented fossil record of burnetiamorph therapsids. *Journal of Vertebrate Paleontology, Program and Abstracts* 2015, 213.
- SIGOGNEAU-RUSSELL, D. 1989. Theriodontia I. *Handbuch der Paläoherpetologie*. 17 B/I. Stuttgart: Gustav Fischer Verlag, 1–127.
- SMITH, R.M.H., RUBIDGE, B.S. & SIDOR, C.A. 2006. A new burnetiid (Therapsida: Biarmosuchia) from the Upper Permian of South Africa, and its biogeographic implications. *Journal of Vertebrate Paleontology* **26**, 331–343.
- TATARINOV, L.P. 1968. [New Theriodonts from the Upper Permian of the USSR]. In: Tatarinov, L.P. (ed.) *Verkhnepaleozoiskie i mezozoiskie zemnovodnye i presmykaiushchiesia SSSR*, 32–46. Moscow, Nauka. [in Russian]
- TATARINOV, L. P. 1977. [A new gorgonops from Upper Permian deposits of Vologda Province]. *Paleontologicheskii Zhurnal* **1977**, 97–104. [in Russian]
- WHITNEY, M.R. & SIDOR, C.A. In press. A new therapsid from the Permian Madumabisa Mudstone Formation (Mid-Zambezi Basin) of southern Zambia. *Journal of Vertebrate Paleontology*.

Palynostratigraphy, palynofacies and thermal maturation of the Nsukka Formation from an excavation site in Okigwe, southeastern Nigeria

Ernest Uzodimma Durugbo

Department of Biological Sciences, Redeemer's University, P.M.B. 230, Ede, Osun State, Nigeria

E-mail: ernestduru@yahoo.com / urugboe@run.edu.ng

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There is a dire need to assess the petroleum-generating potential of the Nigerian inland basins. The Nigerian Federal Government has in the last few years demarcated the inland basins, of which little is known palynologically, for oil and gas exploration activities. An input from Nigeria concerning events of the Cretaceous–Paleogene boundary would broaden our knowledge of the global event. This palynological study of the Nsukka Formation from an excavation site in Okigwe, southeastern Nigeria, revealed abundant records of pollen, spores and dinoflagellate cysts. Palm pollen *Longapertites marginatus*, *L. vaneendenburgi*, *L. microfoveolatus*, *Spinizonocolpites echinatus*, *S. baculatus* and *Foveomonocolpites bauchiensis* dominated the microfloral assemblage with common dinoflagellate cysts, especially *Ifecysta* spp., *Cordosphaeridium* spp., *Fibrocysta* spp., *Senegalinium* spp., *Cerodinium* spp., *Phelodinium* spp., *Spiniferites* spp. and *Hafniasphaera* spp., indicating alternating shallow to marginal marine depositional environments. The already published ranges of the palynostratigraphically important taxa such as *Buttinia andreevi*, *Monocolpopollenites sphaeroidites*, *Rugulatisporites caperatus*, *Zlivisporis blanensis*, *Cingulatisporites ornatus*, and the earliest Danian dinoflagellate cyst markers *Damassadinium californicum*, *Carpatella cornuta*, *Hafniasphaera septate* and *Senegalinium bicavatum*, enabled the delineation of the age as Late Maastrichtian–Middle Paleocene. The studied Nsukka sequences consist of alternating successions of fine-grained sandstones, well-bedded dark and sandy shales. The samples were dominated by terrestrial organic components, especially structured phytoclasts, black debris and unstructured phytoclasts/degraded wood elements, indicating deposition in predominantly nearshore environments, coupled with the dominance of peridinoids over gonyaulacoids. However, the basal samples were characterized by common amorphous organic matter co-occurring with dinoflagellate cysts, suggesting brief periods of marine transgressions. Using *Deltoidospora adriennis* as an index, the spore colouration index (SCI) ranged from 4 (golden yellow) to 4.5 (deep yellow), which correlates to vitrinite reflectance values of 0.4–<0.5, indicating that the sediments were immature for oil and gas generation.

Keywords: Nsukka Formation, Okigwe, palynomorphs, spore colouration, phytoclasts.

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INTRODUCTION

Moore *et al.* (1991) defined palynology as the study of pollen grains produced by seed plants (angiosperms and gymnosperms) and spores (produced by pteridophytes, bryophytes, algae and fungi). Previously, however, Hyde & Williams (1944) had provided a broad definition to encompass all entities that survived the maceration process by such corrosive chemicals as HCl, HF, HNO₃, NH₄OH, etc. These entities Tschudy (1961) popularized as 'palynomorphs'. Agashe & Caulton (2009) gave credence to this and further posited that according to geologists palynology entails the study of such microfossils as pollen, spores, dermal appendages, cuticles, vascular elements, diatoms, desmids of plant origin, foraminifera, ostracods, microforaminifera, acritarchs, dinoflagellate cysts and hystrochospherids. Moore *et al.* (1991) enumerated the applications of palynology in different aspects of human endeavor, such as taxonomy, whereby taxonomists infer evolutionary relationships between extant plant populations and their fossil relatives. Under genetic

and evolutionary studies, they reported that palynological studies could refine the taxonomic data by adding a time dimension to it. Melissopalynology is another application of palynology specifically to do with bees, honey and pollen. Forensic palynology is defined as the science of applying modern pollen and spores and other palynomorphs to help solve legal or criminal problems (Bryant & Mildenhall 1990). Furthermore, palynology has been useful in climate change studies. Moore *et al.* (1991) cited Webb (1980) who reported the possibility of erecting mathematical models between fossil pollen data and climatic variables from which past isotherms could be reconstructed. Durugbo *et al.* (2010) used the abundance of Graminae and savanna pollen over mangrove and other wet climate indicators to infer more pronounced dry periods in the Western Niger Delta. Again, combining the pollen data with the occurrence of two saline water tolerant dinoflagellate cysts, *Operculodinium centrocarpum* and *Polysphaeridium zoharyi*, they documented periods of sea level falls (glacial maxima) around 2.0 Ma and 2.7 Ma.

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Several other workers have also used palynomorphs as proxies in understanding the mechanisms of climate change (Morzadec-Kerfourn 1988, 1992; Poumot 1989; Morley 1995; Leroy & Dupont 1997, 2003; Pocknall *et al.* 2001; Molnar & Cane 2004; Sowunmi 2004). Moore *et al.* (1991) mentioned the application of palynological data in the study of human impact on vegetation, tracing vegetation history and correlating deposits and assigning tentative ages/dates and there are numerous other examples.

Palynology is a basic tool for developing stratigraphic and palaeoenvironmental frameworks for rock units. Particulate organic matter when analysed contributes to understanding ore genesis and diagenesis. It also helps in improving engineering practices and recovery of ore. Palynology is of greatest importance in biostratigraphy because pollen, spores, and other palynomorphs are abundant, durable, recognizable and readily available in sediments. Palynofloras from different regions can be correlated and biostratigraphic schemes put in place. The rock samples from different depths are processed in the laboratory, analysed under the microscope and the occurrences of the different palynomorphs recorded. The data so generated is used in determining the age of the rocks and in the interpretation of the palaeoenvironments in which the sediments were deposited.

In this study palynology was utilized for dating the Nsukka Formation from an excavation site in Okigwe, southeastern Nigeria, and to infer the palaeoenvironments based on the recovered palynomorphs and palynofacies. This paper is a further attempt to update our knowledge on the palynology of southeastern Nigeria and document the events of the K/T Boundary from Nigeria and to evaluate the thermal maturity of the Nsukka Formation around

Okigwe as Nigeria desires to explore for hydrocarbons in her inland Basins.

Description of study site

The Anambra Basin, southeastern Nigeria, lies between longitudes 7°00'E and 7°31'E and latitudes 6°14'N and 6°34'N (Fig. 1). The excavation site is located on German Hill, Okigwe, southeastern Nigeria, with bearings N 05° 49'53.6 " and E 007°21'11.2" taken with a Garmin 72 GPS (Fig. 2). The section was freshly excavated for the construction of a petrol station at the time of sample collection, between the 14 and 21 July 2008.

Stratigraphy of the study area

The southern Nigeria sedimentary basin, composed of the Southern Benue Trough, the Niger Delta, the Benin Embayment, the Anambra Basin, the Abakiliki Fold Belt, the Afikpo Syncline and the Calabar Flank, arose from the break-up of the South American and African continents in the Early Cretaceous (Burke 1996; Nwajide 1990; Murat 1972). Three sedimentary phases spanning Aptian-Albian to Plio-Pleistocene have characterized the region. These phases were: (a) the Abakiliki-Benue Phase of Aptian-Santonian age during which the Asu River Group, the Ezeaku and Awgu Formations together with the Benue Valley and Calabar Flank, were deposited. The second sedimentary phase which arose from the Santonian folding and uplift of the Abakiliki Platform and the dislocation of the depocenter into the Anambra Basin and Afikpo region, gave rise to the Nkporo Group, Mamu Formation, Ajali Sandstone, Nsukka Formation, Imo Formation and the Ameke Group, with ages ranging from Campanian to Eocene were deposited (Table 1). Consequently, the third

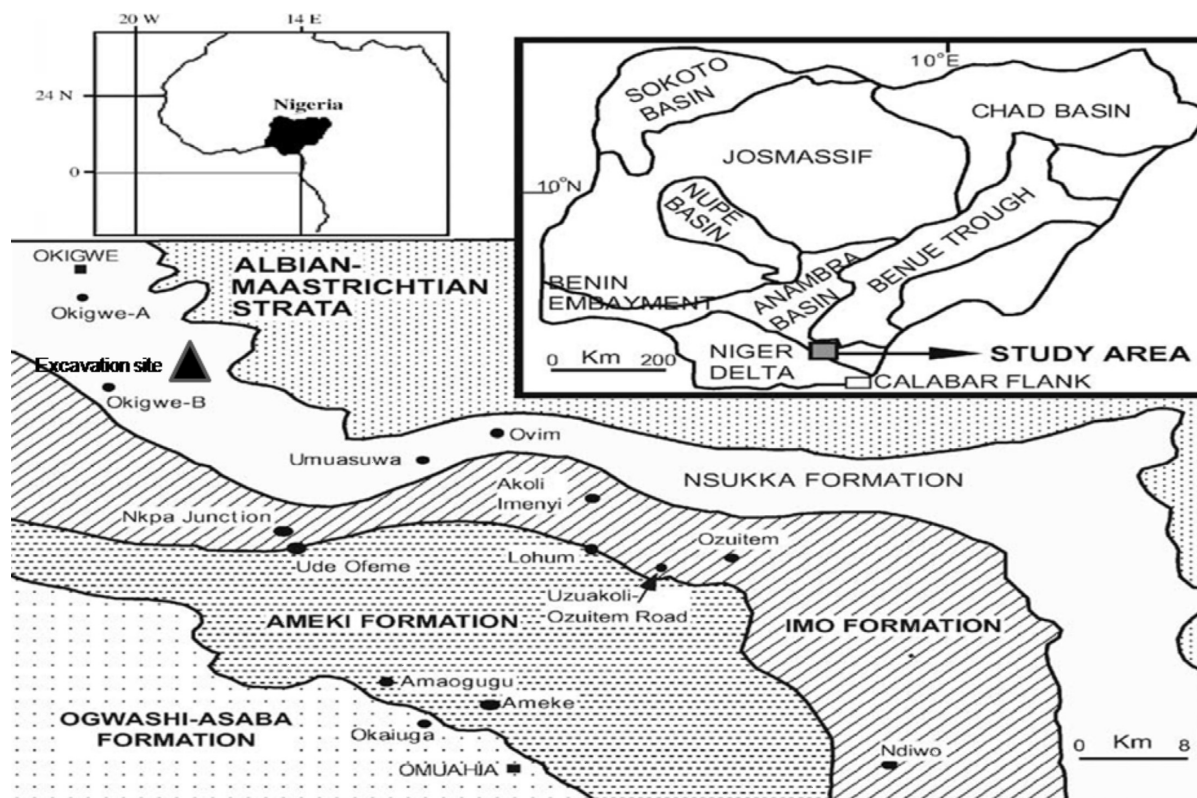


Figure 1. Map of the Anambra Basin showing the studied area. Modified after Umeji & Edet (2008). Large triangle marks excavation site.



Figure 2. The excavation site on German Hill, Okigwe, southeastern Nigeria, with arrows showing the compactly bedded shales.

sedimentary phase which commenced in the Late Eocene led to the formation of the popular petroliferous Niger Delta (Obi *et al.* 2001). The Nsukka Formation which is part of the Anambra Basin and which conformably overlies the Ajali Sandstone, begins with coarse- to medium-grained sandstones and passes upward into well-bedded blue clays, fine-grained sandstones, and carbonaceous shales with thin bands of limestone (Obi *et al.* 2001;

Reyment 1965). Obi *et al.* (2001) used sedimentological evidence to suggest that the Nsukka Formation represented a phase of fluvio-deltaic sedimentation that began close to the end of the Maastrichtian and continued during the Paleocene. According to Adegoke *et al.* (1980), Arua (1980) and Reyment (1965), a Paleocene age is inferred for the basal limestone unit based on ostracod and foraminiferal biostratigraphy, together with the

Table 1. Table of Formations, Niger Delta area (after Short & Stauble 1967).

SUBSURFACE			SURFACE OUTCROPS		
Youngest known age		Oldest known age	Youngest known age		Oldest known age
Recent	Benin Formation (Afam Clay Member)	Oligocene	Plio/Pleistocene	Benin Formation	Miocene
Recent	Agbada Formation	Eocene	Miocene Eocene	Ogwashi-Asaba Formation Ameke Formation	Oligocene Eocene
Recent	Akata Formation	Eocene	L. Eocene Paleocene Maastrichtian Campanian Campanian/ Maastrichtian	Imo Shale Formation Nsukka Formation Ajali Formation Mamu Formation Nkporo Shale	Paleocene Maastrichtian Maastrichtian Campanian Santonian
EQUIVALENTS NOT KNOWN			Coniacian/Santonian Turonian Albian	Awgu Shale Eze Aku Shale Asu River Group	Turonian Turonian Albian

recovered microfauna. Lithology and trace fossils of the basal sandstone unit reflect foreshore and shoreface environments. According to Nfor (2003) the Anambra Basin is dominantly filled with clastic sediments constituting several distinct lithostratigraphic units ranging from Upper Campanian to Recent in age. The lithostratigraphic units have a thickness of up to 2500 m (Reyment 1965) and consist of: Nkporo Shale, Mamu Formation, Ajali Sandstone, Nsukka Formation, Imo Shale, Ameki Formation, Nanka Sands, Ogwashi-Asaba Formation, Benin Formation and the Alluvial Plain Sands. The source of the sediments into the basin is principally from the Cameroon massif and the Abakaliki synclinorium. The Ajali Formation bears false-bedded sandstone with associated clay and shale intervals in the bottom section (Reyment 1965). The Ajali Formation is successively underlain by materials belonging to the Nsukka and Mamu Formations. The Nsukka Formation, which is also called the Upper Coal Measure, bears sandstone, shale and coal, while the underlying Mamu Formation, which Akande *et al.* (1992) called the lower Maastrichtian Coal, conformably overlies the Nkporo Formation is followed successively by the other lithostratigraphic units mentioned earlier.

Previous studies of the sample area

Adebayo & Ojo (2004) using 41 outcrop samples from the Upper Cretaceous strata of the Anambra Basin recognized five informal palynological zones based on pollen and spores within the Maastrichtian. They inferred a swamp environment of deposition fringed by herbaceous vegetation based on the dominance of the trilete spores *Cingulatisporites ornatus*, *Foveotriletes margaritae*, *Verrucatotriletes bullatus* and *Zlivisporis blanensis* with common palm pollen. Oboh *et al.* (2005) studied 14 composite sections of the Paleogene successions outcropping in the Okigwe, Isuikwuato, Umuahia and Ozuitem areas in Imo and Abia States, respectively, of southeastern Nigeria. They documented a comprehensive sequence stratigraphy in the Anambra Basin/Afikpo syncline using data on the stratigraphic succession, textural/lithological variations, and sedimentary structures. They identified the lithofacies associations from the data generated and in addition processed 70 samples from the shale and siltstone horizons and studied their palynological contents. From these data they identified palynofacies assemblages using dispersed organic matter and palynomorph groups. Although there are different schemes for dispersed organic matter, they adopted a simplified scheme adapted to the types of organic components and palynomorph groups present in the sediments. They identified eight types of dispersed organic matter and palynomorph groups including spores and pollen, fungal remains, freshwater algae, marine palynomorphs (dinoflagellates, acritarchs, microforaminiferal inner linings), structured phytoclasts (wood, cuticles, parenchyma), unstructured phytoclasts (resins, comminuted and degraded fragments), black debris and amorphous organic matter. From point counting at least 300 particles of organic debris and palynomorph groups per sample, they converted them to associations based on rock types and five palynofacies assemblages (A–E) deter-

mined by the dominant phytoclast and other associated types.

Antolinez (2006) later studied a set of forty four samples from the early Paleogene interval of Alo-1 well in Anambra State, Nigeria and ODP Hole 959D (Leg 159) in the Côte d'Ivoire-Ghana Transform Margin for their dinocyst contents. He found the dinocyst recovery very good to moderate, and the specimens were commonly well preserved. He compared the stratigraphic and quantitative data with detailed and well-calibrated dinocyst distributions from northwestern Europe and southern hemisphere, Tasmania and New Zealand and identified five informal zones (A to E). Zone A, which was the oldest stratigraphically, was characterized by the consistent occurrence of *Areoligera senonensis*, *Areoligera coronata*, *Palaeocystodinium bulliforme* and *Hafniasphaera septata*. Characteristic of Zone B was the occurrence of *Damassadinium* cf. *D. heterospinosum* in combination with abundant *Fibrocysta/Lanternosphaeridium* spp. and *Cordosphaeridium* spp. The dinocyst assemblages in zone C were characterized by the co-occurrence of abundant *Apectodinium* spp. and *Adnatosphaeridium* spp. Zone D revealed common occurrences of *Glaphyrocysta ordinata*, *Glaphyrocysta divaricata*, *Polysphaeridium subtile*, *Spiniferites microceras* and *Adnatosphaeridium* spp. Finally, the youngest zone, Zone E, was characterized by the occurrence of *Homotriblium abbreviatum*, *Homotriblium* cf. *H. oceanicum*, and *H. pallidum*. Antolinez concluded that his results could have impact on hydrocarbon exploration in tropical areas such as southeastern Nigeria and the Equatorial Atlantic where important hydrocarbon reservoirs occur in Paleocene and Eocene continental and marginal marine rocks and subsidence curves.

The thermal maturation histories and timing of oil migration in this area also rely mostly on palynologically derived ages. Umeji & Nwajide (2007) analysed the stratotype type section of the Nsukka Formation at Ugwu-Nkalagu – Obukpa in Enugu state and the hypostatotype along a road section in Umulolo near Okigwe and established the type section. They recognized two facies, namely the lower shaly facies with coal which Tattam (1944) had called the 'Upper Coal Measures' and an upper sandy facies recognized earlier by Umeji (2000). They reported that both the type section (unit stratotype) and the type locality, lie within the lower shaly facies, while the hypostatotype lies within the type area in the upper non-coaly limestone facies. The coal samples were dominated by the palm pollen *Longapertites marginatus* which accounted for about 70% of the total count. *Proxapertites operculatus* (Arecaceae), which was lacking in the interbedded coal, dominated the mudstone samples, accounting for about 50%. Other components of the samples include other pollen, algal fruiting bodies and monolete and trilete spores, making up 19%, 7% and 4%, respectively. Also common in the mudstone samples were the grass pollen *Monoporites annulatus* (Poaceae) and *Milfordia jardinei* (Restionaceae) especially in the Isi-Ayokpa and Nkalagu-Obukpa mudstones. The Nkalagu-Obukpa mudstones also yielded 2% dinoflagellate cysts made up of four species viz: *Areoligera senonensis*,

Cleistosphaeridium polypes, *Coronifera oceanica* and *Dinogymnium acuminatum*. Umeji and Nwajide dated the type formation latest Maastrichtian–Danian. They also recovered other Paleogene sporomorphs such as *Echiperiporites icacinoides*, *Pachydermites diderixi*, *Verrucatosporites usmensis*, *Cricotriporites fragilis*, *Retistephanocolpites williamsi*, *Ctenolophonidites costatus*, *Echitricolporites spinosus*, *Myrtacidites psilatus*, *Retibrevitricolporites triangulatus*, *Psilatricolporites rotundus*, *Brevicolporites molinae* and *Scabratiporites simpliformis*. Based on the ranges of these recovered palynofloras Umeji & Nwajide (2007) speculated that either these pollens range into the latest Maastrichtian or that sedimentation in the Anambra Basin did not terminate in the Danian but continued into the mid Tertiary. In addition, the Umulolo-1 samples yielded 27% dinoflagellate cysts and 73% sporomorphs. Dinoflagellate cysts such as *Phelodinium gaditanum*, *Exochosphaeridium phragmites*, *E. bifidum*, *Fibrocysta axialis* and *Pterodinium cingulatum* were recovered from the mudstone section. These cysts co-occurred with 30%, 25%, and 20% *Proxapertites operculatus*, *Longapertites marginatus* and *Longapertites microfoveolatus*, respectively. They inferred more marine conditions in the southern Umulolo sections than compared to marsh conditions in the northern type section, due to the absence of the pollen *Monoporites annulatus* in the former. Again, Oboh *et al.* (2007) in their biostratigraphic study of the Early Paleogene in West Africa, recovered six new species and one new combination of dinoflagellate cysts from the Alo-1 well of the lower Imo and upper Nsukka Formation, which were of Paleocene age, from Anambra Basin, Nigeria. These were recovered from the Paleocene–?lowermost Eocene portions of the Imo Formation. The new species were *Ifecysta fusiforma*, *Ifecysta heterospinosa*, *Paleocystodinium rafii* and *Wilsodinium stellatum*. They also transferred *Fibrocysta lappacea* of Drugg (1970) Stover & Evitt (1978) to *Ifecysta* and emended the diagnosis of the latter.

Later Umeji & Edet (2008) reported that exposures of the lower facies of the Nsukka Formation/Unadu River of Reyment (1965), where one or more species dominated the assemblage. Pond weeds (*Azolla cretacea*, *Zlavisporis blanensis* and *Ariadnaesporites nigeriensis*) dominated the Okotokoto samples. These co-occurred with common *Longapertites marginatus* and rare *Proxapertites cursus*, *Longapertites microfoveolatus*, *Longapertites vaneendenburgi*, *Psilatricolporites rotundiporis*, *Syncolporites marginatus*, *Retidiporites magdalenensis*, the algae *Ulvella nannae* and sparse records of the dinoflagellate cysts *Cordosphaeridium inodes*, *Danea californica* and *Exochosphaeridium bifidum*. In contrast, the Aku spring (Ugwu-Nkalagu-Obukpa-Type Section) yielded abundant grass pollen *Monoporites annulatus* with freshwater algae *Pseudoschizaea circula* and the Isi-Ayokpa mudstones also yielded *Monoporites annulatus* with freshwater algae *Pseudoschizaea circula*, common *Echitricolporites spinosus*, *Cyathidites minor*, *Foveotriteles margaritae*, *Leiotriteles adriennis*, *Polypodiisporites* sp., *Stephanocolpites evansii*, *Tripurites iverseni* and *Azolla cretacea*. The assemblages from ripple laminated mudstones from Umulolo (Upper facies) were dominated by

Tertiary palm pollen species *Proxapertites operculatus*, *Longapertites microfoveolatus*, with *Longapertites marginatus*, *L. vaneendenburgi* and abundant dinoflagellate cysts, especially *Ifecysta pachyderma*, *Phelodinium gaditanum*, *Senegalinium bicavatum*, *Ceratiopsis diebelii*, *Exochosphaeridium phragmites*, *Pterodinium cingulatum*, *Cleistosphaeridium diversipinosum*, *C. aciculare*, *Chytroeisphaeridia chytrooides* and *Spiniferites ramosus*. On the other hand, the plastic shale samples from Umulolo were dominated by *Proxapertites operculatus*, *Longapertites marginatus*, *Longapertites vaneendenburgi*, *Cyathidites minor* and *Longapertites microfoveolatus*, together with slightly more dinoflagellate cysts (32%), than in the mudstone section. The most common dinocysts here were *Spiniferites ramosus*, *Hystrichokolpoma rigaudiae*, *Cordosphaeridium inodes*, *Kallosphaeridium orchiesense*, *Phelodinium magnificum*, *Cyclonephelium deconincki*, *Exochosphaeridium phragmites*, *Cleistosphaeridium diversipinosum*, *Danea californica*, *Adnatosphaeridium vittatum* and *Diphyes colligerum*, as well as microforaminiferal wall linings. Sporomorphs made up 68%, while algae were rare. Also recovered from the Umulolo samples were the typical Paleogene sporomorphs *Pachydermites diderixi*, *Echitricolporites spinosus*, *Bacutripurites orluensis*, *Ctenolophonidites costatus*, *Retistephanocolpites williamsi*, *Stephanocolpites evansii*, *Echiperiporites icacinioides*, *Psilatricolporites crassus*, *Psilatriporites rotundus*, *Monoporites annulatus*, *Longapertites microfoveolatus*, *Tripuritetradites hoekeni*, *Proxapertites minutus*, *Zonocostites ramona* and *Verrucatosporites usmensis*. They concluded that the presence of *Dinogymnium acuminatum* in the Nkalagu-Obukpa (type section) restricted the age to Late Maastrichtian, thereby confirming a Late Maastrichtian age to the type section of the Nsukka Formation in the North, while the age is Danian in the south around Umulolo where it is sharply overlain by the Imo Formation. Finally, Durugbo (2013) used the occurrence of abundant palm pollen *Longapertites marginatus*, *L. vaneendenburgi*, *Spinizonocolpites echinatus*, *S. baculatus*, *Retidiporites magdalenensis*, *Mauritidites crassixinus*, *M. crassibaculatus*, together with the dinoflagellate cysts *Paleoperidinium pyrophorum*, *Phelodinium magnificum*, *P. africanum*, *Ifecysta fusiforma*, *I. heterospinosa*, *Fibrocysta lappacea*, *Homotryblium tenuispinosum*, *Diphyes colligerum*, *Cerodinium* spp., *Ceratiopsis* spp., *Apectodinium* spp., *Kallosphaeridium* spp., *Cordosphaeridium* spp., *Exochosphaeridium* spp., *Spiniferites* spp., *Cleistosphaeridium* spp., *Lejeunecysta* spp., *Apectodinium* spp. and *Homotryblium tenuispinosum* to date the Imo shale exposures at the Okigwe/Port Harcourt express road junction as Late Paleocene to Eocene.

Apart from palynological studies, different investigations to evaluate the thermal maturity, foraminiferal content and general hydrocarbon prospectivity of the Anambra Basin have been carried out (Petters 1977; Alix *et al.* 1981; Akande & Erdtman, 1998; Obaje *et al.* 1999; Ehinola *et al.* 2005; Akaegbobi *et al.* 2009; Onuigbo *et al.* 2012).

Akande *et al.* (2011) proposed more studies of the more than 8000 m Cretaceous–Tertiary sediments of the Lower Benue Anambra Basin. They also reported that previous

drilling efforts had revealed both oil and gas reserves in the Anambra Basin at various stratigraphic intervals. The gas finds were in the Cenomanian-Turonian Eze-Aku shales, and dry gas in the Awgu Shale stratigraphic interval coupled with oil and gas in the post-Santonian (Maastrichtian) intervals of the Anambra Basin. Conclusively, they posited that these source rock facies had reached maturity and have generated and expelled hydrocarbons at some stages in the history of basin.

MATERIALS AND METHODS

Thirteen samples at every 20 cm intervals were collected from the excavation site (Fig. 2) in sterile plastic bags. The samples were taken to the Biological Sciences laboratory of Redeemer's University prior to preparation. 30 g of each sample was prepared using the standard palynological techniques of disaggregation and removal of carbonates and silicates with hydrochloric acid and hydrofluoric acid under a fume cupboard (Faegri & Iversen 1989). The samples were further treated with hot hydrochloric acid (HCl) and wet-sieved over a 5 micron mesh polypropylene sieve. The Branson Sonifier 250 was employed during sieving to facilitate complete removal of silt and clay particles. Each residue was oxidized using concentrated nitric acid (HNO₃) and prepared for study as strewn mounts using Loctite. The slides were stained with Safranin O to enhance the study of dinoflagellate cysts. For the palynofacies/kerogen study, the samples were not oxidized with HF acid in order to retain the original nature and colour of the palynomorphs. A Zeiss Axioskop 2 microscope with an attached AxioCam Cc 1 digital camera was used for the analysis at the palynology laboratory of

the Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa. All the species present (pollen, spores, fungal remains, algae, dinoflagellate cysts and foraminiferal linings) were recorded (Supplemental information: Appendix A). The percentage occurrences of the different palynomorph groups are displayed in Fig. 3. Three hundred specimens of the different dispersed organic matter (pollen and spores, fungal remains, freshwater algae, marine palynomorphs, structured phytoclasts (wood, cuticles, parenchyma), unstructured phytoclasts (resins, comminuted and degraded fragments, black debris, and amorphous organic matter) were point counted and converted to percentages and presented in Fig. 4 (Obboh-Ikuenobe *et al.* 2005, 2012). The pollen and spores were identified using local palynological catalogues (Hoeken-Klinkenberg 1964, 1966; Jardine & Margloire 1965; Germeraad *et al.* 1968; Salard-Cheboudaef 1981, 1990; Salami 1983, 1990; Lawal & Moullade 1986; Mahmoud & Schrank 2007). Dinoflagellates and other marine elements were identified based on various monographs (Brinkhuis *et al.* 2003; Edwards 1991; Fauconnier *et al.* 2004; Jan du Chêne 1987; Jan du Chêne & Adeniran 1985; Powell 1992; Williams & Bujak 1977). The nomenclature follows Fensome & Williams (2004). Photomicrographs of the diagnostic palynomorphs were taken at magnifications of $\times 400$ and the sample number and associated England Finder coordinates of the diagnostic palynomorphs are given (Figs 5–9). The slides, residues, unprocessed samples, and duplicate prints are housed in the palynological collections of the Biological Sciences Department, Redeemer's University, Ede, Osun State, Nigeria.

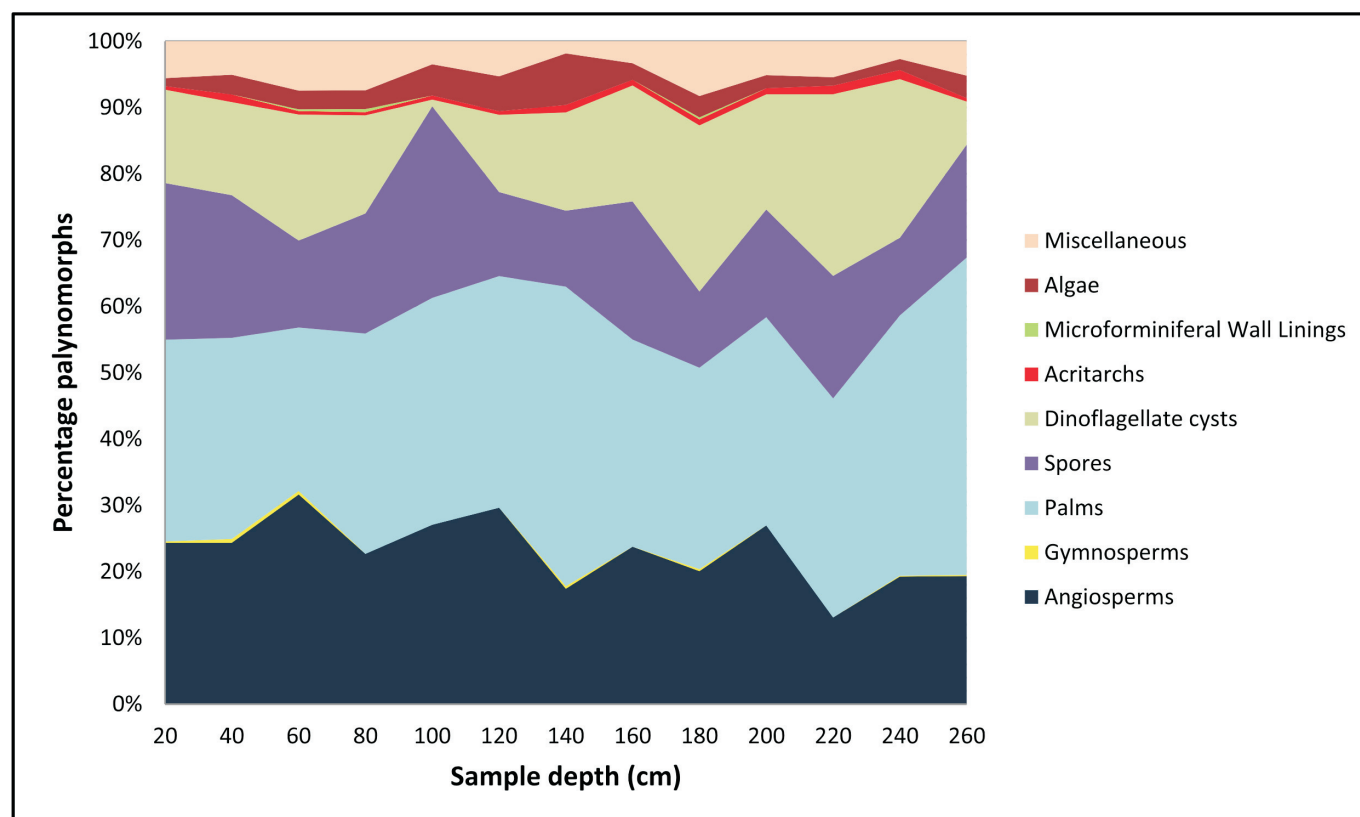


Figure 3. Percentage plot of the different palynomorphs groups in the Okigwe excavation samples.

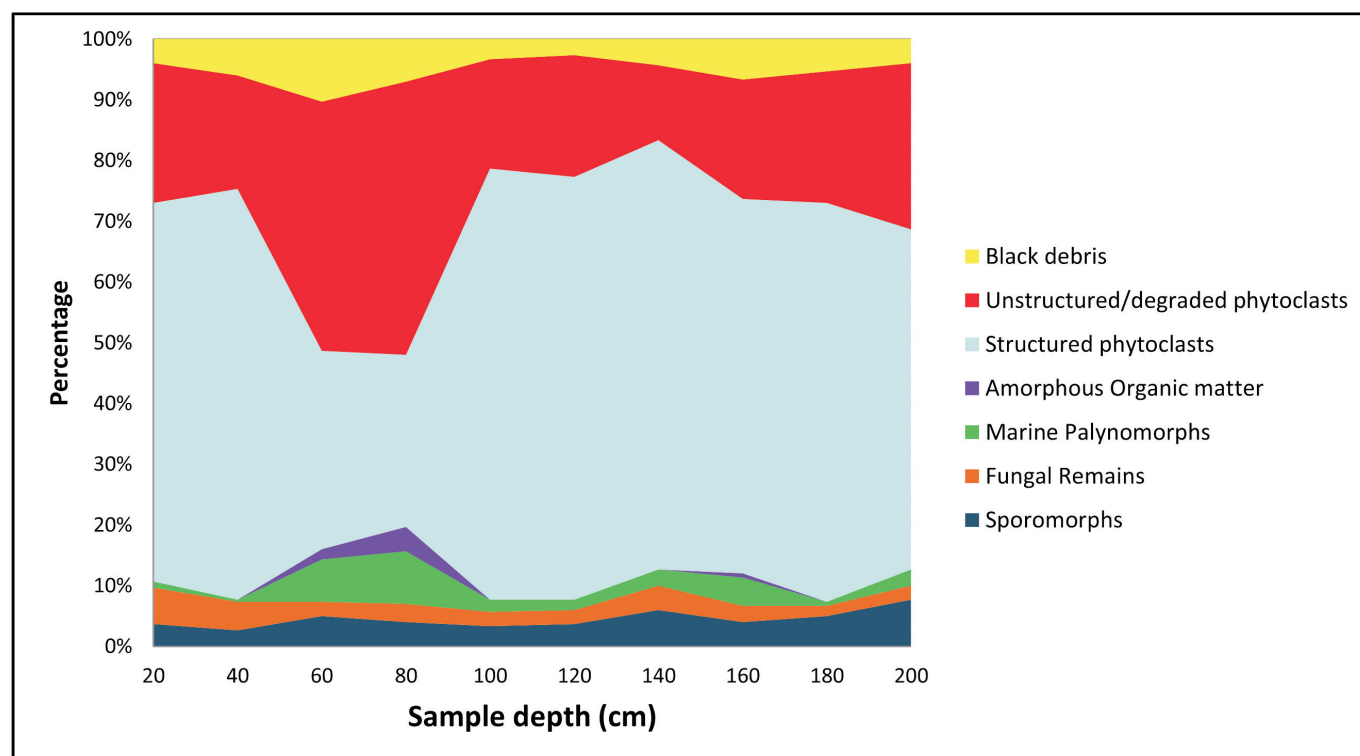


Figure 4. Percentage plot of Palynofacies Groups recorded per sample from the Okigwe samples. Plot on x-axis to 260 cm (depth).

RESULTS

Palynological assemblages

The palynomorphs recovered revealed an admixture of both continental and marine forms. The relative frequencies of the angiosperms, gymnosperms, dinoflagellate cysts, acritarchs, pteridophytes, algae and fungal elements, charred gramineae cuticle and *incertae sedis* in the different samples are highlighted in Supplemental information (Appendix A), and displayed in Fig. 3. A total of 6168 palynomorphs were recovered in the 13 samples studied. Pollen species made up of 74 species dominated with a total count of 3537, out of which angiosperms dominated with 99.77%, while gymnosperms accounted for only 0.23% (Table 2).

Successively, the pteridophyte spores followed with counts of 1087; dinoflagellate cysts 1000; acritarchs 52, microforaminiferal wall linings 5; algae 175 and miscellaneous 312, composed of fungal elements, charred gramineae cuticle and *incertae sedis*. An assessment of the pollen species revealed that palm pollen species dominated with about 19 species, and total counts of 2130; gymnosperms represented by two species had a total count of 10, contributing 0.28%, while the other pollen contributed 39.5% (Table 2). Overall, these palms accounted for 60.22% of the total pollen, and 34.53% of the total palynomorphs recovered.

Palynofacies

The visual estimation revealed the occurrence of three

Table 2. Total recovered palynomorphs groups per sample.

Sample number	Angiosperms	Gymnosperms	Palms	Spores	Dinoflagellate cysts	Acritarchs	Microforaminiferal wall linings	Algae	Miscellaneous	Total
20CM	140	1	175	136	81	3	0	7	32	575
40CM	130	3	162	115	75	6	0	16	27	534
60CM	123	2	96	51	74	2	1	11	29	389
80CM	144	0	211	115	94	3	3	18	47	635
100CM	132	0	167	141	5	3	0	23	17	488
120CM	56	0	66	24	22	1	0	10	10	189
140CM	47	1	122	31	40	3	0	21	5	270
160CM	57	0	75	50	42	2	0	6	8	240
180CM	68	1	103	39	85	3	1	11	28	339
200CM	121	0	141	73	78	4	0	9	23	449
220CM	72	0	182	102	151	7	0	7	30	551
240CM	172	1	351	105	214	12	0	15	24	894
260CM	119	1	295	105	40	3	0	21	32	616
Total	1381	10	2146	1087	1000	52	5	175	312	6168

groups of dispersed organic matter and palynomorphs which dominated some of the samples. The most significant groups were the structured phytoclasts, unstructured/degraded phytoclasts and marine elements. The amorphous organic matter appeared to be directly related to the marine elements as they occurred commonly in samples with appreciable numbers of dinoflagellate cysts (Samples 3, 4, 8, 11). The percentage constituents of the different palynofacies assemblages per sample are outlined in Table 3 below.

Kerogen analysis

Using *Deltoisopora minor* as the palynomorph index, the kerogen analysis of the samples revealed a predominantly golden yellow to deep yellow colour of palynomorphs which corresponds to spore colour indices of 4.0–4.5. This is correlated to vitrinite reflectance values ranging between 0.4–<0.5 indicating immature oil and gas generation potentials (Dow 1977; Hunt 1996; Matchette-Downes 2009).

DISCUSSION

Palynostratigraphy

The studied samples are dated Late Maastrichtian–Middle Paleocene based on the presence of *Buttinea andreevi*, *Monocolpopollenites sphaeroidites*, *Zlivisporis blanensis*, *Constructipollenites ineffectus*, *Mauritidites lehmanii*, *Proteacidites sigalii*, *P. dehaani*, *Foveotrilites margaritae*, *Cingulatisporites ornatus*, *Distaverrusporites simplex* and *Rugulatisporites caperatus* (Fig. 11; Hoeken-Klinkenberg 1964; Salami 1983, 1990).

Globally the events of the K/T boundary have been of special interest to palaeontologists. Slimani *et al.* (2010) together with other workers reported that organic walled phytoplankton survived the events of the K/T catastrophes. In the present study, the Cretaceous – (Pg) Tertiary boundary is taken at a depth of 180 cm, due to the Last Appearance Datum (LAD) of the aforementioned palynomorphs, namely *B. andreevi*, *M. sphaeroidites* and *Z. blanensis*, together with *Carpatella cornuta* and *Damassidinium californicum*, between 260–180 cm. In his range chart Salami (1983) highlighted the ranges of *B. andreevi* and *M. sphaeroidites* as terminating at the end of

the Maastrichtian, however, *R. caperatus*, *D. simplex* and *C. ornatus*, continued into the Paleocene. Later, Salami & Atta-Petters (2004) further documented that the former ranged from Campanian to Maastrichtian in Nigeria. Furthermore, Germeraad *et al.* (1968) had given the ranges of *Buttinea andreevi*, *Proteacidites dehaani*, *Retidiporites magdalenensis*, *Longapertites vanendenburgi* and *Foveotrilites margaritae* in Nigeria as not younger than Paleocene. Oboh-Ikuenobe *et al.* (2012) posited that *Achomosphaera allicornu* appeared for the first time in mid-latitudes during the Danian, while *Phelodinium magnificum*, *Hafniasphaera septata*, *Cerodinium diebelii* and *Paleocystodinium golzowense* are all associated with the Danian age. Slimani *et al.* (2010) linked the occurrences of *D. californicum*, *C. cornuta*, *Eisenackia circumtabulata*, *Membranilarnacia tenella* and *Senoniasphaera inornata* with the Danian of Morocco, while the Maastrichtian is characterized by latest occurrences of *Disphaerongenella carposphaeropsis*, *Glaphyrocysta perforata* and *Manumiella seelandica*. In addition, they also recorded some of the species recovered from the Okigwe samples, especially *Cribrasperidinium cooksoniae*, *Cordosphaeridium exilimurum*, *C. inodes*, *Riculacysta* sp., *Apteodinium fallax*, *Spiniferites cornuta*, *Pterodinium cingulatum*, *Fibrocysta bipolaris*, *Areoligera senonensis*, *Glaphyrocysta perforata*, *Phelodinium magnificum*, *P. africanum*, *Isabelidinium bakeri*, *Senagalinium bicavatum* and *S. microspinosum*, among others. This trend reveals the preponderance of these species in the Early Paleocene globally. Moreover, Hamdi *et al.* (2013) reported the presence of the majority of the dinoflagellate cysts reported here in their study of Cretaceous–Paleogene transition deposits from the Ellès section of northern Tunisia. They placed the K–Pg boundary just above the acme of *Manumiella seelandica* and the last appearance of *Dinogymnium* spp., *Alisogymnium euclaense* and *Pterodinium cretaceum* which were directly below the first appearance of the basal Danian markers: *D. californicum*, *Membranilarnacia? tenella*, *Senoniasphaera inornata* and *C. cornuta*. Apart from these they also recorded *Senagalinium bicavatum*, *S. microspinosum*, *Kallosphaeridium yorubaense*, *Cerodinium* spp., *Phelodinium magnificum*, *P. africanum*, *Cordosphaeridium inodes*, *Glaphyrocysta perforata*, *Fibrocysta axialiis*, *F. bipolaris*, *Achomosphaera allicornu*, *A. regiensis*, *Apteodinium fallax*, *Cerodinium diebelii*, *Diphyes*

Table 3. Percentage counts of the different palynofacies groups per sample.

Sample depth	Sporomorphs	Fungal remains	Marine palynomorphs	Amorphous organic matter	Structured phytoclasts	Unstructured/ degraded phytoclasts	Black debris	Total (%)
20CM	3.67	6	1	0	62.33	23	4	100
40CM	2.67	4.67	0.33	0	67.66	18.67	6	100
60CM	5	2.33	7	1.67	32.67	41	10.33	100
80CM	4	3	8.67	4	28.33	45	7	100
100CM	3.34	2.33	2	0	71	18	3.33	100
120CM	3.67	2.33	1.67	0	69.66	20	2.67	100
140CM	6	4	2.67	0	70.67	12.33	4.33	100
160CM	4	2.67	4.67	0.67	61.66	19.66	6.67	100
180CM	5	1.67	0.67	0	65.66	21.67	5.33	100
200CM	7.67	2.33	2.67	0	56	27.33	4	100
220CM	20.67	4	14	2.67	22.66	30	6	100
240CM	19.67	3.67	1	0.33	55	14	6.33	100
260CM	14.67	2.33	1.67	0.67	54.66	19.33	6.67	100

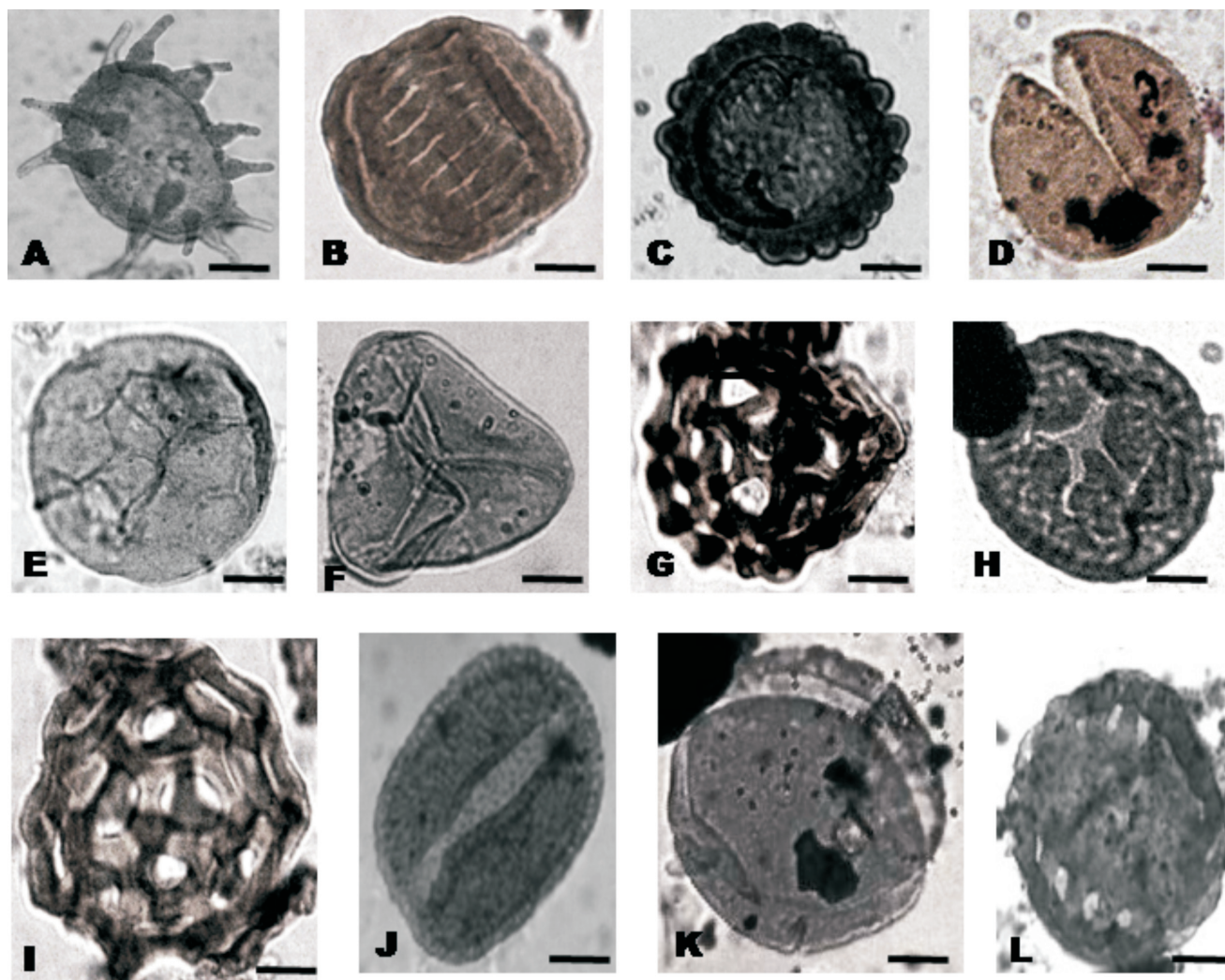


Figure 5. Photomicrographs of pollen and spores recovered from the studied Okigwe samples. **A**, *Spinizonocolpites echinatus* Muller 1968 (Sample 2 G33/3). **B**, *Tubistephanocolporites cylindricus* Salami 1985 (Sample11 G32/2). **C**, *Cingulatisporites ornatus* Martin, 1973 (Sample 12 P40/1). **D**, *Monocolpopollenites sphaeroidites* Jardine & Margloire 1965 (Sample12 G50/3). **E**, *Zlivoisporis blanensis* Pacltova 1961 (Sample13 H41/2). **F**, *Cyathidites minor* Couper 1953 (Sample11 R29/1). **G**, *Buttinia andreevi* Boltenhagen 1967 (Sample13 V56/0). **H**, *Rugulatisporites caperatus* Van Hoeken-Klinkenberg 1964 (Sample 11S34/3). **I**, *Buttinia andreevi* Boltenhagen 1967 (Sample11 G31/1). **J**, *Foveomonocolpites bauchiensis* Jan du Chêne & Adegoke 1978 (Sample 4 R22/0). **K**, *Proxapertites operculatus* van derHammen 1956 (Sample12 K55/1). **L**, *Tubistephanocolporites cylindricus* Salami 1985 (Sample10 C41/2). All photomicrographs taken at $\times 400$; scale bars = 12 μm .

colligerum, *Areoligera senonensis*, *Senegalinium bicavatum* and *S. microspinosum* which were also recovered in the present study. Conclusively, Grandstein *et al.* (2004) highlighted the First Appearance Datum (FAD) of *D. californicum* and *C. cornuta* at the top of Da-1 dated 64.96 Ma, while *C. cornuta* has its FAD in the Selandian at Sel-2 at 60.98 Ma. The reason for the preponderance of these dinocysts is not farfetched because Vadja-Santivaniez (1999) showed that the Upper Cretaceous strata in Venezuela, Brazil and Colombia were mostly marine with common dinoflagellate cysts, just as these studied sediments revealed. This suggests that the marine conditions must have continued into the early Paleogene. Although the typical Late Maastrichtian dinoflagellate marker genus *Dinogymnium* spp. was not recovered, possibly due to more saline conditions, the ranges of the dominant dinoflagellate genera *Ifecysta*, *Fibrocysta*, *Kallosphaeridium*, co-occurring with the aforementioned sporomorphs, concurs with the age assignment already reported for the Umulolo section, which is a few kilometers away from Okigwe town, by Umeji & Nwajide (2007). The

common records of *Fibrocysta* spp., *Ifecysta* spp. and *Cordosphaeridium* spp. agrees with the Zone B of Antolinez (1999). It further concurs with the reports of Umeji & Edet (2008) who inferred a Late Maastrichtian age for the type section in the north, based on the presence of *Dinogymnium acuminatum*, while they dated the southern section around Umulolo, Danian. This Danian age is supported by the presence of most of the dinoflagellate cysts recovered from the Danian of Senegal by Jan du Chêne (1987) especially *Fibrocysta* spp., *Ifecysta* spp., *Cerodinium* spp., *Cordosphaeridium* spp., *Kallosphaeridium* spp., *Spiniferites* spp., except *Tanyosphaeridium* spp. The recovery of some of the new species reported by Oboh *et al.* (2007), dated Paleocene–?lowermost Eocene, especially *Diphyes bifidum*, *Ifecysta fusiforma* and *Ifecysta heterospinosa* which were not recovered by Umeji & Nwajide (2007) and Umeji & Edet (2008), supports the age of the Okigwe excavation samples as ranging into the Middle Paleocene. This age assignment is further supported by the absence of the typical Late Paleocene (Thanetian–Eocene) dinoflagellate cysts, *Homotryblum tenuispinosum* and *Apectodinium*

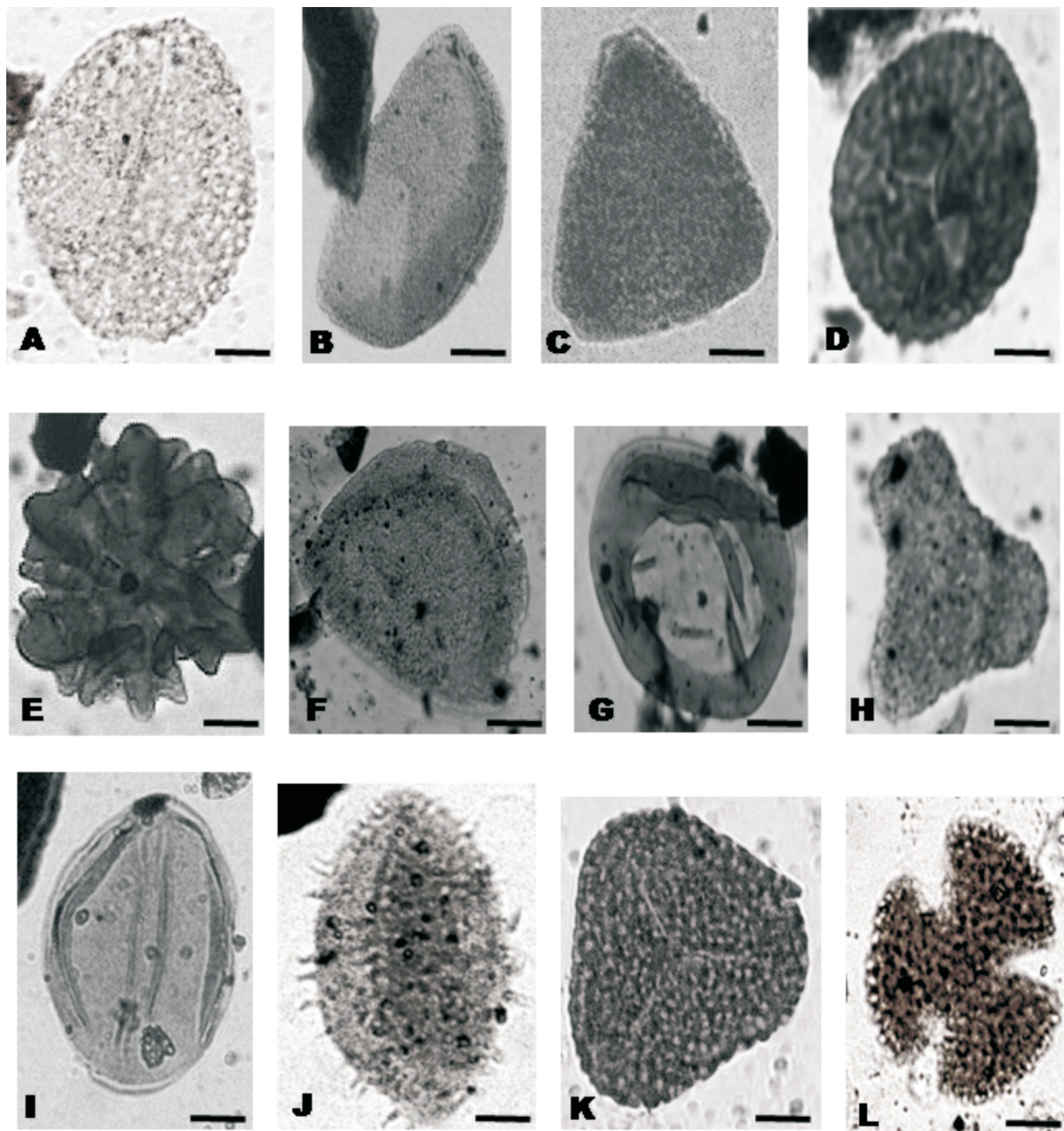


Figure 6. Pollen and spores recovered from the studied Okigwe samples. **A**, *Liliacidites cf. nigeriensis* (Van Hoeken-Klinkenberg 1966) Salami 1985, (Sample 7 T35/4). **B**, *Longapertites marginatus* van Hoeken-Klinkenberg 1964 (Sample 6 G28/3). **C**, *Proteacidites dehaani* Germeraad, Hopping and Muller, 1968 (Sample 12 N42/0). **D**, *Rugulatisporites caperatus* Van Hoeken-Klinkenberg 1964 (Sample 8 S34/3). **E**, *Ctenolophonidites costatus* (van der Hammen & Garcia 1966) Germeraad *et al.* 1968 (Sample 10 Q21/3). **F**, *Longapertites vaneendenburgi* Germeraad *et al.* 1968 (Sample 11 Q35/1). **G**, *Milfordia jardinei* Erdtman 1960 (Sample 11 J36/4). **H**, *Syndemicolpites typicus* Van Hoeken-Klinkenberg 1966 (Sample 11 O44/0). **I**, *Sapotaceoidapollenites* sp. (Sample 1 K54/2). **J**, *Mauritiidites crassixinus* (Jan du Chêne *et al.* Onyike and Sowunmi, 1978 (Sample 3 W34/1). **K**, *Foveotriletes margariae* Germeraad *et al.* 1968 (Sample 1 W46/4). **L**, *Retitricolporites americana* Wymstra 1964 (Sample 1 W46/4). All photomicrographs taken at $\times 400$; scale bars = $12\ \mu\text{m}$.

homomorphum, which were not recorded in the samples studied. Comparing these results with those of Oboh *et al.* (2005) revealed that they had studied sediments younger than Middle Paleocene because they had dated their basal depositional sequence Upper Nsukka, with the overlying Imo Formation still dated Paleocene, while their youngest Formation (Ogwasi-Asaba) is of Eocene age, hence the recovery of such palynomorphs as *Praedapollis africanus*.

Palynofacies

The assemblage is generally dominated by unstructured phytoclasts, structured/degraded phytoclasts, with rare amorphous organic matter, except in Samples 3, 4, 8 and 11, which had appreciable counts of marine elements. The whole assemblage closely resembles palynofacies assemblage C of Oboh *et al.* (2005, 2012) due to the highest percentages of structured phytoclasts, with values ranging

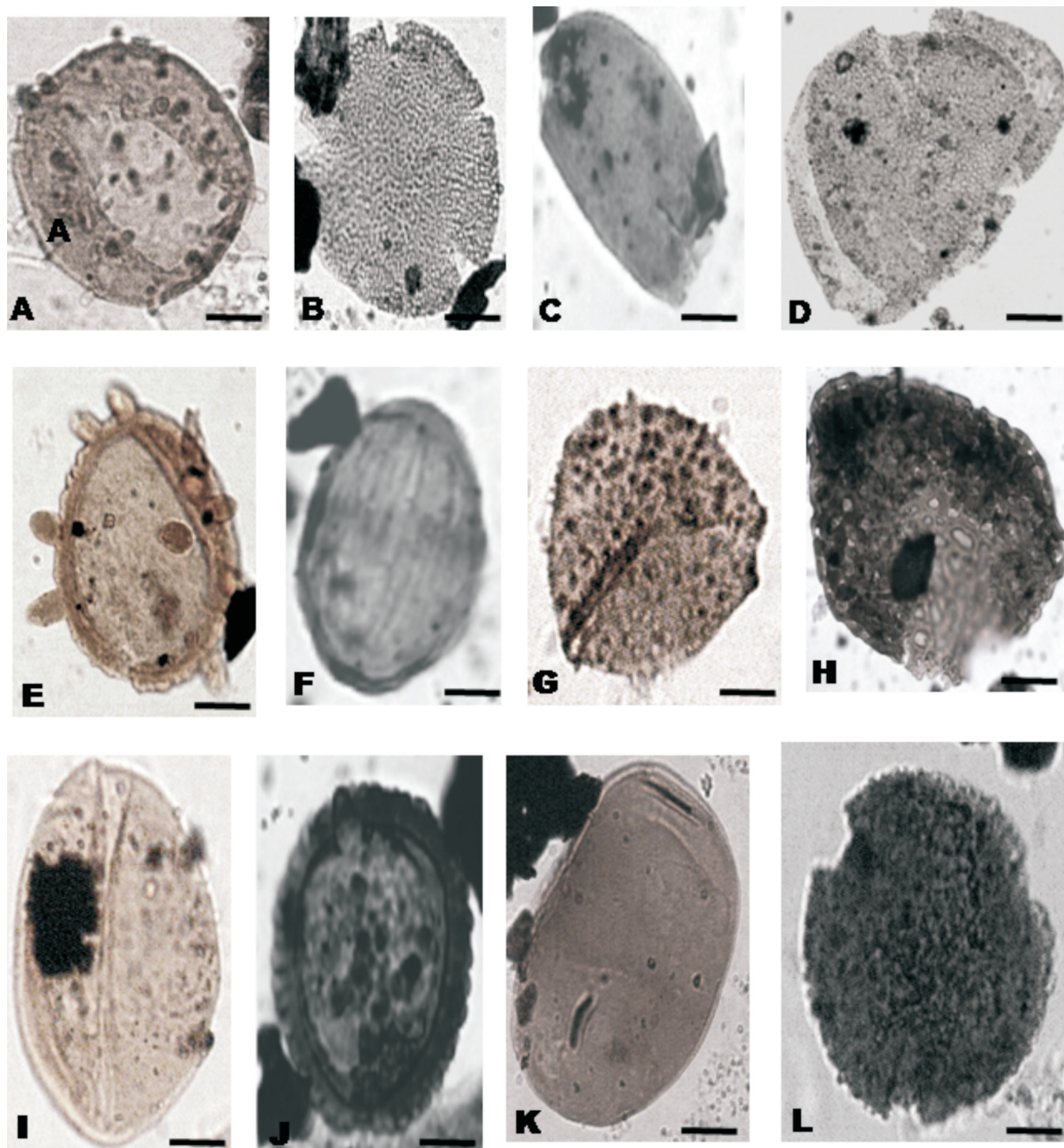


Figure 7. Pollen and spores recovered from the studied Okigwe samples. **A**, *Mauritiidites lehmanii* Salard-Chebouldaeff 1978 (Sample 6 G28/3). **B**, *Arecpites* sp. (Sample 11 S29/1). **C**, *Retidiporites magdalenensis* van der Hammen & Garcia 1966 (Sample 11 K51/4). **D**, *Longapertites vaneendenburgi* Germeraad *et al.* 1968 (Sample 11 Q35/1). **E**, *Spinizonocolpites baculatus* Muller 1968 (Sample 9 S33/4). **F**, *Ephedripites multicostatus* Brenner 1963 (Sample 3 S46/2). **G**, *Echitriporites trianguliformis* Van Hoeken-Klinkenberg 1964 (Sample 2 K51/4). **H**, *Periretisyncolpites giganteus* Kieser & Jan du Chêne 1979 (Sample 8 Q35/2). **I**, *Bombacacidites polanuris* Jaramillo *et al.* 2007 (Sample 13 C41/2). **J**, *Distaverrusporites simplex* Muller 1968 (Sample 3 O53/2). **K**, *Laevigatosporites discordatus* Pflug, 1953 (Sample 3 N36/3). **L**, *Nigeripollis gemmatus* Salami 1985 (Sample 6 S47/2). All photomicrographs taken at $\times 400$; scale bars = 12 μm

from 36% to 65%. However, the percentages of amorphous organic matter were lower here. Although Oboh *et al.* (2005) reported 36% to 65% structured phytoclasts for palynofacies assemblage C, the Okigwe samples yielded a range of 22.67 to 70.67%. Again, in Samples 3, 4, and 11 the structured/degraded phytoclasts were more common than those of the structured; coincidentally, these samples recorded the highest amount of amorphous organic

matter indicating that possibly these samples were undergoing rapid deterioration in deeper water settings. Finally, the palynofacies samples contained more sporomorphs than those studied by Oboh *et al.* (2005); here the range was between 2.67% in Sample 2, to 20.66% in Sample 11. Oboh *et al.* (2005) associated the highest pollen and spore content of 0.3–12% with their palynofacies assemblage D in which amorphous organic matter

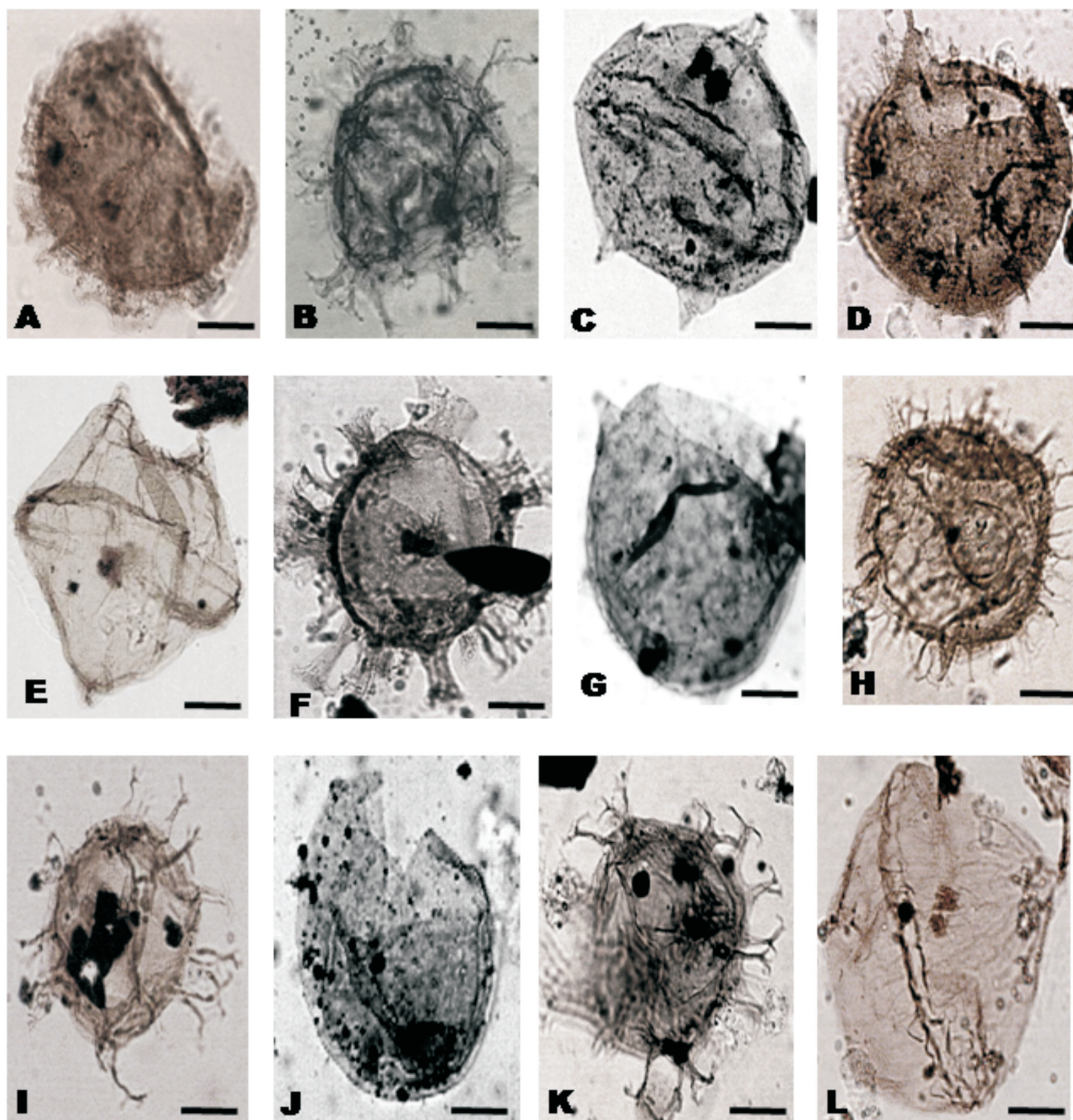


Figure 8. Dinoflagellate cysts recovered from the studied Okigwe samples. **A**, *Kenleyia* sp. (Sample 10 R41/4). **B**, *Damassadinium californicum* (Davey, 1967) Fensome *et al.* 1993. (Sample 13 W36/1). **C**, *Cerodinium* spp. (Sample 6 N49/1). **D**, *Ifecysta fusiforma* Oboh *et al.* 2007 (Sample 11 R29/1). **E**, *Phelodinium magnificum* (Stanley, 1965) Stover & Evitt 1978 (Sample 10 G28/3). **F**, *Cordosphaeridium exilimurum* Davey & Williams 1966 (Sample 10 J40/4). **G**, *Cribroperidinium cooksoniae* Norvick 1976 (Sample 13 P46/3). **H**, *Exochosphaeridium phragmites* (Clarke & Verdier 1973) Clarke *et al.* 1968 (Sample 5 V56/0). **I**, *Achomosphaera* spp. (Sample 10 G28/3). **J**, *Kallosphaeridium yorubaense* Jan du Chêne & Adediran 1985 (Sample 11 R29/1). **K**, *Spiniferites multibrevis* Davey & Williams 1966 (Sample 11 R41/4). **L**, *Phelodinium africanum* Biffi & Grignani 1983 (Sample 5 U29/4). All photomicrographs taken at $\times 400$; scale bars = 12 μm

dominated. Here the samples, as suggested earlier, were deposited not too far from the coast which accounted for the high counts of pollen and spores which generally decrease in number seawards (Shrank 1984; Quattrocchio & Sarjeant 2003).

Paleoenvironmental interpretation

Workers such as Shrank (1984), Quattrocchio & Sarjeant (2003) proposed that terrestrial components (sporomorphs and land derived detritus) in an assemblage decrease as

the marine components (dinoflagellate cysts, foraminiferal linings etc) increase offshore (with distance away from terrigenous influx). In this study sporomorphs, especially palms, dominated the assemblages although microplankton were moderate in most of the samples. The depositional environments fluctuated between Outer/Middle Neritic as indicated by species of *Impagidinium*, *Kallosphaeridium*, *Trichodinium*, *Cribroperidinium*/*Spiniferites*, *Cordosphaeridium* and *Polysphaeridium*, to Coastal Deltaic environments, as inferred from the

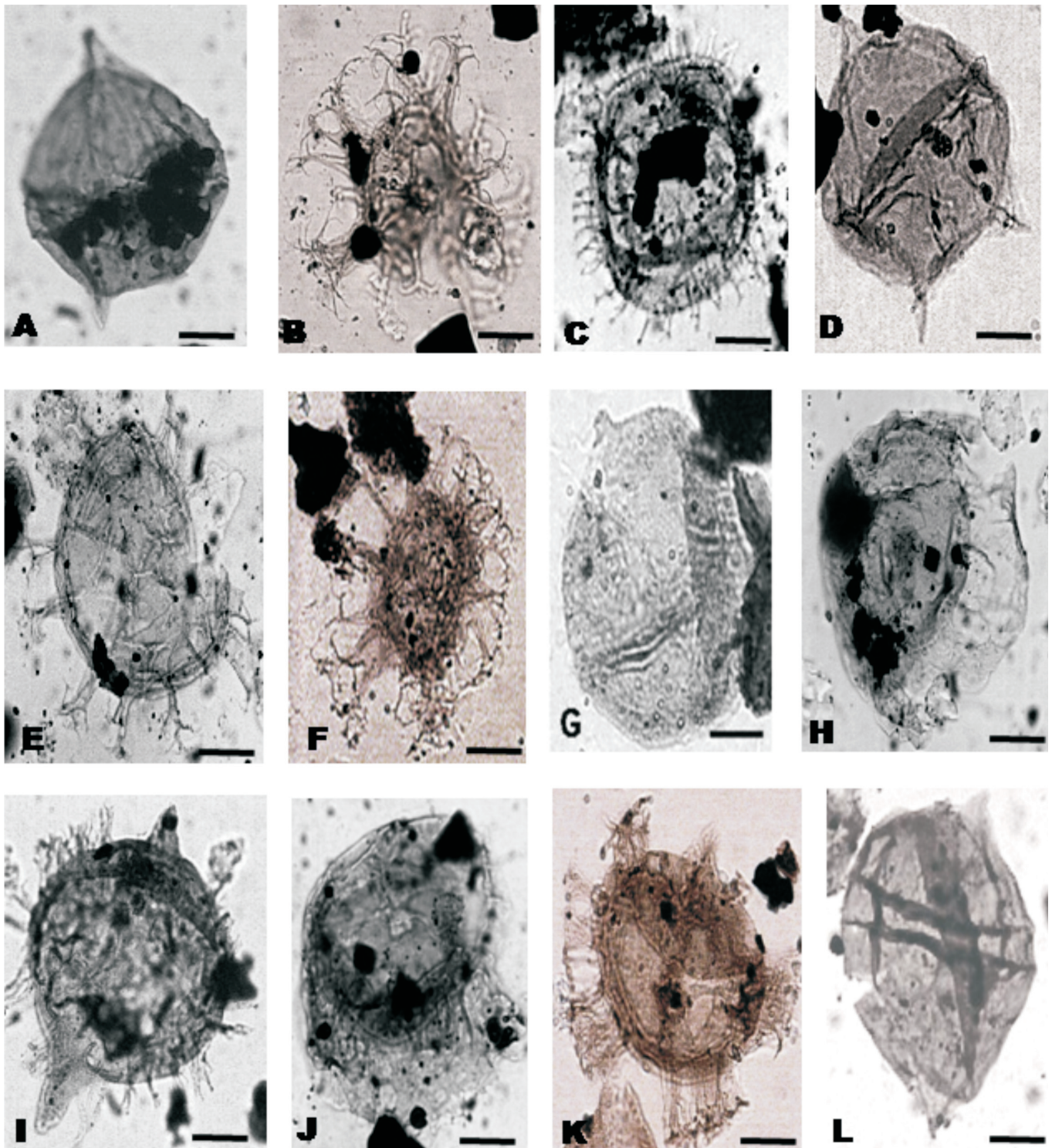


Figure 9. Dinoflagellate cysts recovered from the studied Okigwe samples. **A**, *Carpatella cornuta* Grogorovich 1969 (Sample 11 R41/4). **B**, *Damassadinium californicum* (Davey 1967) Fensome *et al.* 1993 (Sample 13 W36/1). **C**, *Cerodinium* spp. (Sample 6 N49/1). **D**, *Ifecysta fusiforma* Oboh *et al.* 2007 (Sample 11 R29/1). **E**, *Phelodinium magnificum* (Stanley, 1965) Stover & Evitt 1978 (Sample 10 G28/3). **F**, *Cordosphaeridium exilimurum* Davey & Williams 1966 (Sample 10 J40/4). **G**, *Cribroperidinium cooksoniae* Norvick 1976 (Sample 13 K41/2). **H**, *Exochosphaeridium phragmites* (Clarke & Verdier 1973) Clarke *et al.* 1968 (Sample 5 V56/0). **I**, *Achomosphaera* spp. (Sample 10 G28/3). **J**, *Kallosphaeridium yorubaense* Jan du Chêne & Adediran 1985 (Sample 11 R29/1). **K**, *Cordosphaeridium exilimurum* Davey and Williams, 1966 (Sample 10 J40/4). **L**, *Fibrocysta lapacca* (Drugg 1970) Stover & Evitt 1978 (Sample 9 T38/2). All photomicrographs taken at $\times 400$; scale bars = 12 μm .

variations in the percentages of Gonyaulacaceans and Peridinaceae and dominance of palm pollen over other palynomorphs together with common freshwater algae. Just as Oboh *et al.* (2012) observed, the paucity of deeper water associated dinoflagellate cysts such as *Impagidinium* spp. and *Nematosphaeropsis/Adnatosphaeridium* spp. which together with the low diversity and dominance of inner

neritic taxa that they had associated with relative proximity to the shoreline in their study of the Late Maastrichtian–Paleogene palynoflora of southern Missouri, the same trend which was evident in this present study. The results of the palynofacies analysis further corroborates this paleoenvironmental deduction due to the common records of structured phytoclasts, unstructured/degraded

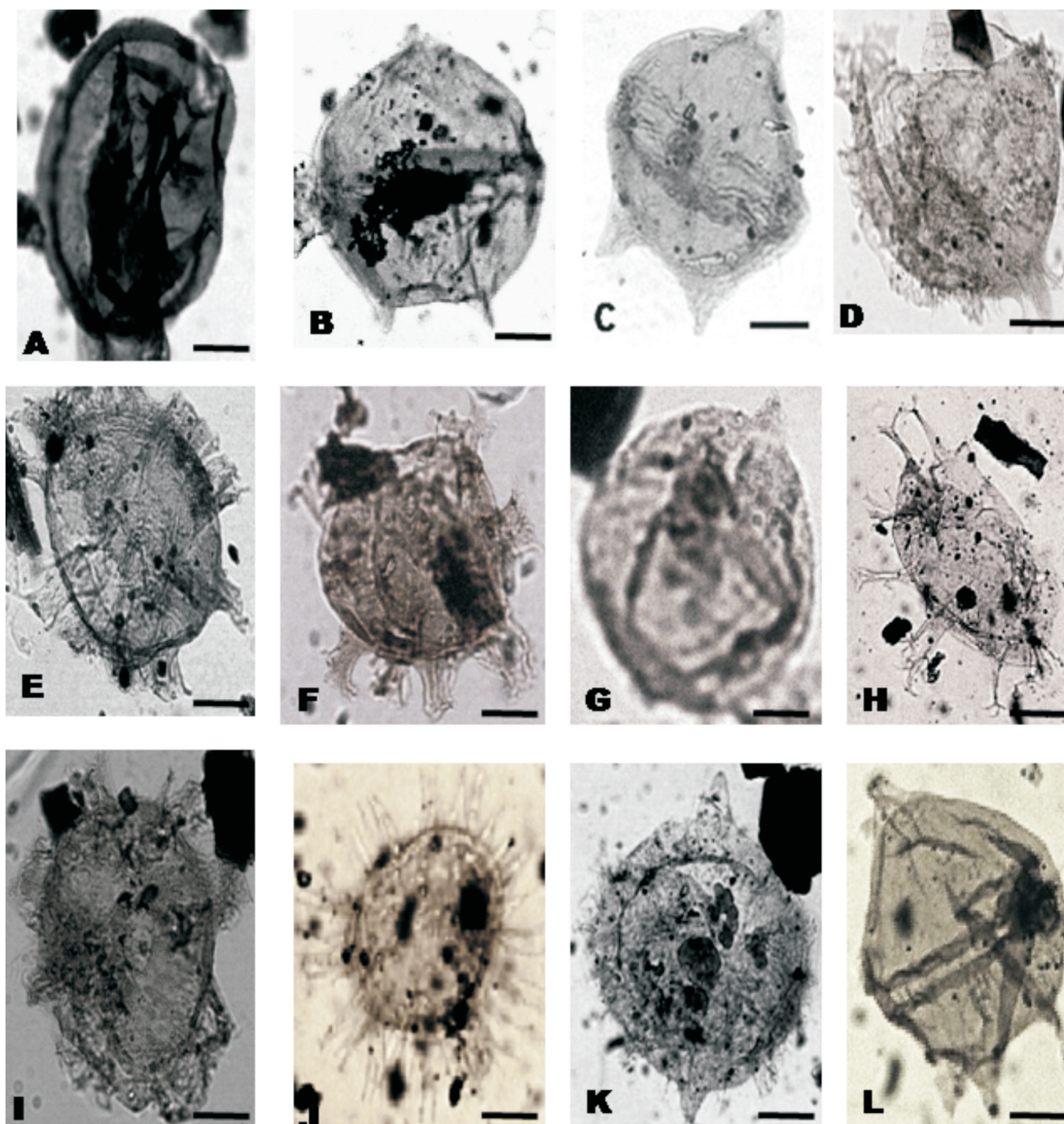


Figure 10. Dinoflagellate cysts recovered from the Ogikwe samples. **A**, *Selenopemphix nephroides* (Benedek 1972) Benedek & Sarjeant 1981 (Sample 4 J43/0). **B**, *Hafniasphaera delicata* Fensome *et al.* 2008 (Sample 11 R41/4). **C**, *Impagidinium* spp. (Sample 6 S47/2). **D**, *Achomosphaera alcornu* Eisenack 1954 (Davey & Williams) (Sample 11 P41/3). **E**, *Adnatosphaeridium multispinosum* Williams & Downie, 1966 (Sample 4 G33/3). **F**, *Senegalinium bicavatum* Jain & Millipied 1973 (Sample 10 N36/3). **G**, *Adnatosphaeridium multispinosum* Williams & Downie 1966 (Sample 4 G33/3). **H**, *Glaphyrocysta semitecta* (Bujak in Bujak *et al.* 1990) Lentin & Williams 1981 (Sample 6 S47/2). **I**, *Fibrocysta bipolaris* (Cookson & Eisenack) Stover & Evitt 1978 (Sample 4 G33/3). **J**, *Riculacysta* spp. Soncini & Rauscher 1988 (Sample 4 J43/0). **K**, *Senegalinium microspinosum* (Boltenhagen 1977) Lentin & Williams 1980 (Sample 11 V56/0). **L**, *Spinidinium* spp. (Sample 1 K41/2). All photomicrographs taken at $\times 400$; scale bars = $12\ \mu\text{m}$

phytoclasts, low amorphous organic matter and moderate records of dinoflagellate cysts. Continentally derived palynodebris (phytoclasts, fungal remains, sporomorphs, etc) and oceanic varieties (dinocysts, acritarchs, foraminiferal linings, marine amorphous organic matter) both occur in marine and marginal marine environments as demonstrated in this study (Jaramillo & Obboh-Ikuenobe 1999; Obboh *et al.* 2012). Furthermore as mentioned earlier, the dominance of terrestrially derived organic compo-

nents in most of the studied samples indicated proximity to the source for those components, and agrees with the reports of Obboh *et al.* (2012). These findings concur with the results of Obi *et al.* (2001) who inferred from sedimentological evidence that the Nsukka Formation represented a fluvio-deltaic sedimentation phase which began close to the end of the Maastrichtian and continued during the Paleocene. The dinoflagellate assemblages of the Nsukka Formation from Okigwe are generally domi-

- BRINKHUIS, H., SENGERS, S., SLUIJS, A., WARNAAR, J. & WILLIAMS, G.L. 2003. Latest Cretaceous-earliest Oligocene and Quaternary dinoflagellate cysts, ODP Site 1172, East Tasman Plateau. In: Exon, N.F., Kennett, J.P. & Malone, M.J., (eds), *Proceedings Ocean Drilling Program Scientific Results*, 189.
- BRYANT, V. M. Jr. & MILDENHALL, D.C. 2002. Forensic palynology: a new way to catch crooks. *Crime & Clues*, 15 pp.
- BURKE, K.C. 1996. The African Plate. *South African Journal of Geology* **99**, 341–409.
- DOW, W.G. 1977. Kerogen studies and geological interpretations. *Journal of Geochemistry and Exploration* **7**, 79–99.
- DOWIE, C., HUSSAIN, M.A. & WILLIAMS, G.L. 1971. Dinoflagellate cyst and acritarch associations in the Paleogene of southeastern England. *Geoscience and Man* **3**, 29–36.
- DURUGBO, E.U., OGUNDIPE O.T. & ULU, O.K. 2010. Palynological evidence of Plio-Pleistocene climatic variations from the western Niger Delta, Nigeria. *International Journal of Botany* **6**(4), 351–370.
- DURUGBO, E.U. 2013. Palynostratigraphy, age determination and depositional environments of the Imo Shale exposures at the Okigwe/Port Harcourt Express Road Junction, Okigwe, southeastern Nigeria. *Greener Journal of Physical Sciences* **3**(7), 255–272.
- EDWARDS, L.E. 1991. Paleocene and Eocene dinocysts from the Salt Range, Punjab, Northern Pakistan. Chapter C of Regional Studies of the Potwar Plateau Area, Northern Pakistan. In: Warwick, P.D. & Wardlaw, B.R. (eds), *U.S Geological Survey Bulletin* 2078-C.
- EHINOLA, O.A., SONIBARE, O.O., FALODE, O.A. & AWOFA, B.O. 2005. Hydrocarbon potential and thermal maturity of Nkporo Shale from Lower Benue Trough, Nigeria. *Journal of Applied Science* **5**, 689–695.
- EISAWI, A. & SCHRANK, E. 2008. Upper Cretaceous to Neogene palynology of the Melut Basin, southeast Sudan. *Palynology* **32**, 101–130.
- ERDTMAN, G. 1969. *Handbook of Palynology. An Introduction to the Study of Pollen Grains and Spores*. New York, Hafner Publishing Company.
- FAEGRI, K. & IVERSEN, J., 1989. *Textbook of Pollen Analysis* (4th edn). Copenhagen, Munksgaard.
- FAGERI, K., KALAND, P.E. & KRZYWINSKI, K. 1989. *Textbook of Pollen Analysis by Knut Fageri and John Iversen* (4th edn). Chichester, John Wiley & Sons.
- FAUCONNIER, D., MASURE, E., BEGOUEN, V., CORNU, P., COURTINAT, B., FOUCHER J.C., HSSAIDA, T., LACHKAR, L., MICHOUX, D., MONTEIL, E., OGG, G., POURTOY, D., RAUSCHER, R. & SOUCINI, M.J., 2004. Les dinoflagellés fossiles. Guide pratique de détermination. Les genres à processus et archéopyle apical. *Bureau de Recherches Géologiques et Minières, Éditions Collection Scientifique*, 600 pp.
- FENSOME, R.A. & WILLIAMS, G.L. 2004. The Lentin and Williams index of fossil dinoflagellates 2004 Edition. *American Association of Stratigraphic Palynologists Contributions Series* **42**, 892 pp.
- GERMERAAD, J.H., HOPPING, C.A. & MULLER, J. 1968. Palynology of Tertiary sediments from tropical areas. *Review of Paleobotany and Palynology* **6**, 189–470.
- GRADSTEIN, F., OGG, J., PALMER, A.R. & GEISSMAN, J., 2004. Geological Time Scale. Exxon Mobil Texas. *Geological Magazine* **135**, 305–309.
- HAMDI, M.A., SLIMANI, H., ISMAIL-LATTRACHE, K.B. & SOUSSI, M. 2013. Dinoflagellate cyst biostratigraphy from the Cretaceous-Paleogene boundary at Ellès, Tunisia. *Revue de Micropaléontologie* **56**, 27–42.
- HANSEN, J.M. 1977. Dinoflagellate stratigraphy and echinoid distribution in the Upper Maastrichtian and Danian deposits from Denmark. *Bulletin of the Geological Society of Denmark* **26**, 1–26.
- HARKER, S.D., MCGANN, G.J., BOURKE, L.T. & ADAMS, J.T. 1990. Methodology of Formation MicroScanner image interpretation in Claymore and Scapa fields (North Sea), In: Hurst, A., Lovell, M.A. & Morton, A.C., (eds), Geological applications of wireline logs. *Geological Society of London Special Publication* **48**, 11–25.
- HARLAND, R. 1978. Dinoflagellate cysts and acritarchs from the Bearpaw Formation (Upper Campanian) of southern Alberta, Canada. *Paleontology* **15**, 665–706.
- HOEKEN-KLINKENBERG, VAN P.M.J. 1964. A palynological investigation of some upper Cretaceous sediments in Nigeria. *Pollen et Spores* **6**(1), 209–231.
- HOEKEN-KLINKENBERG, VAN P.M.J. 1966. Maastrichtian Paleocene and Eocene pollen and spores from Nigeria. *Leidsche Geologie Mededelingen* **38**, 37–48.
- HOROWITZ, A. 1976. Environment of deposition and stratigraphy of the uranium bearing strata around Beaufort West, South Africa. *Atomic Energy Board* (South Africa). P.E L **251**, 27 pp.
- HOROWITZ, A. 1990. Palynology and palaeoenvironment of uranium deposits in the Permian Beaufort Group, South Africa. *Ore Geology Reviews* **5**, 537–540.
- HUNT, J. M. 1996. *Petroleum Geochemistry and Geology*, New York, W.H. Freeman and Company.
- HYDE, H.A. & WILLIAMS, D.A. 1944. The right word. *Pollen Analysis Circular* **8**, 6.
- JAN DU CHÈNE, R. E. 1987. The dinoflagellate cysts from the Danian of the Madeleine Formation, Dakar, Senegal; a systematic study. *Cahiers de Micropaléontologie* N.S. **2**, 3–4.
- JAN DU CHÈNE, R. E. & ADENIRAN, S. A. 1985. Late Paleocene to Early Eocene dinoflagellates from Nigeria. *Cahiers de Micropaléontologie, Centre nationale de la recherche scientifique* No. **1984-3**, 5–38.
- JARAMILLO, C.A., BAYONA, G., PADRE-TRUJILLO, A., RUEDA, M., TORRES, V., HARRINGTON, G.J. & MORA, G. 2007. The palynology of the Cerrejón Formation (Upper Paleocene) of northern Colombia. *Palynology* **31**, 153–189.
- JARAMILLO, C.A. & OBOH-IKUENOBE, F.E. 1999. Sequence stratigraphic interpretations from palynofacies, dinocyst and lithological data of Upper Eocene-Lower Oligocene strata in southern Mississippi and Alabama. U.S. Gulf Coast. *Palaeobiogeography, Palaeoclimatology, Palaeoceanography* **145**, 259–302.
- JARDINE, S. & MAGLOIRE, L. 1965. Palynologie et stratigraphie du Crétacé des bassins du Sénégal et de Côte d'Ivoire. *Memoires du Bureau de Recherches Géologiques et Minières* **32**, 187–245.
- JARZEN, D.M. 1994. Palynological analysis of the Gondar (Ethiopia) Hanging. *Program Abstracts*, 27th Annual Meeting of the American Association of Stratigraphic Palynologists: 20.
- KASKA, H.V. 1989. A spore and pollen zonation of Early Cretaceous to Tertiary non-marine sediments in central Sudan. *Palynology* **13**, 79–90.
- LAWAL, O. & MOULLADE, M. 1986. Palynological biostratigraphy of Cretaceous sediments in the Upper Benue Basin, N.E. Nigeria (1). *Revue de Micropaléontologie* **29**, 61–83.
- LEROY, S.A.G. & DUPONT, L.M. 1997. Marine palynology of the ODP site 658 (N-W Africa) and its contribution to the stratigraphy of Late Pliocene. *Geobios* **30**(3), 351–359.
- LEROY, S.A.G. & DUPONT, L. 2003. Development of vegetation and continental aridity in northwestern Africa during the Late Pliocene: the pollen record of ODP site 658. *Palaeogeography, Palaeoclimatology, Palaeoecology* **109**(2–4), 295–316.
- MAHMOUD, M.S. & SCHRANK, E. 2007. Late Cretaceous pollen and dinoflagellates from two boreholes (Nuqra-1 and 3) in the Aswan area, southeast Egypt. *Revue de paléobiologie, Genève* **26**(2), 593–613.
- MATCHETTE-DOWNES, C. 2009. *Guide to Optical Microscopy in Petroleum Geochemistry*. Marlow, U.K., MDOIL Limited.
- MOORE, P.D., WEBB, J.A. & COLLINSON, M.E. 1991. *Pollen Analysis* (2nd edn). London, Oxford, Blackwell Science.
- MOLNAR, P. & CANE, M. A. 2004. El Niño's tropical climate and teleconnections as a blueprint for pre-ice-age climates. *Palaeogeography, Palaeoclimatology, Palaeoecology* **142**, 51–84.
- MORLEY, R.J. 1995. Biostratigraphic characterization of Systems Tracts in Tertiary sedimentary basins. In: Caghey, C.A., Carter, D.C., Clure, J., Gresko, M. J., Lowry, P., Park, R.K. & Wonders, A. (eds), *Proceeding of the International Symposium on Sequence Stratigraphy in SE Asia*, pp. 49–71.
- MORZADEK-KERFOURN, M.T. 1988. Paleoclimates and paleoenvironments from the Late Glacial to Recent in the eastern Mediterranean, east of the Nile Delta. The contribution of organic-walled microfossils. *Bulletin des centres de recherches et exploration-production Elf-Aquitane*, **12**(1), 267–275.
- MORZADEK-KERFOURN, M. T. 1992. Estuarine dinoflagellate cysts among Oceanic assemblages of Pleistocene deep-sea sediments from the West African Margin and their paleoenvironmental significance. In: Head, M. J. & Wrenn, J. H. (eds), *Neogene and Quaternary Dinoflagellate Cysts and Acritarchs*, 133–146. Dallas, American Association of Stratigraphic Palynologists Foundation.
- MUIR, M.D. (1974). Microfossils from the middle Precambrian McArthur Group Northern Territory, Australia; In: Oro, J., Miller, S.L. Ponnampuruma, C. & Young, R.S. (eds), *Cosmochemical Evolution and the Origins of Life*, 105–118. Dordrecht, D. Reidel Publishing Co.
- MURAT, R.C. 1972. Stratigraphy and paleogeography of the Cretaceous and Lower Tertiary in southern Nigeria. In: Dessauvage, T.F.J. & Whiteman, A.J. (eds), *African Geology*, 251–266. Ibadan, University of Ibadan Press.
- NFOR, B.N. 2003. *Sedimentary Facies and the Diagnostic Characteristics of the Campanian-Eocene, Anambra Basin, S.E. Nigeria*. Ph.D. thesis, Department of Geology, Nnamdi Azikiwe University, Awka, Nigeria.
- NWAJIDE, C.S. 1990. Cretaceous sedimentation and palaeogeography of the central Benue Trough, In: Ofoegbu, C.O. (ed.), *The Benue Trough Structure and Evolution*, 19–38. Braunschweig/Wiesbaden, Friedr. Vieweg and Sohn.
- OBJE, N.G., ULU, O.K. & PETERS, S.W. 1999. Biostratigraphic and

- geochemical control of hydrocarbon prospects in the Benue Trough and the Anambra Basin, Nigeria. *Nigerian Association of Petroleum Explorationists Bulletin* **14**(1), 18–54.
- OBI, G.C., OKOGBUE, C.O. & NWAJIDE, C.S. 2001. Evolution of the Enugu Cuesta: a tectonically driven erosional process. *Global Journal of Pure Applied Sciences* **7**, 321–330.
- OBOH-IKUENOB, F.E., OBI, C.G. & JARAMILLO, C.A. 2005. Lithofacies, palynofacies, and sequence stratigraphy of Palaeogene strata in southeastern Nigeria. *Journal of African Earth Sciences* **41**, 79–102.
- OBOH-IKUENOB, F.E., SPENCER, M.K., CAMPBELL, C.E. & HASELWANDER, R.D. 2012. A portrait of Late Maastrichtian and Paleocene palynoflora and paleoenvironment in the northern Mississippi Embayment, southeastern Missouri. *Palynology* **36**(1), 3–79.
- OLUSOLA, J.O. 2010. Occurrence of some Maastrichtian dinoflagellate cysts from the Upper Cretaceous sediments of Bida Basin Nigeria. Implications for age and paleoenvironment. *Global Journal of Geological Sciences* **8**(3), 217–230.
- ONUIGBO, E.N., ETU-EFEOTOR, J.O. & OKORO, A.U. 2012. Palynology, paleoenvironment and sequence stratigraphy of the Campanian-Maastrichtian deposits in the Anambra Basin, southeastern Nigeria. *European Journal of Scientific Research* **3**, 333–348.
- PETTERS, S.W. 1977. Mid-Cretaceous paleoenvironments and biostratigraphy of the Benue Trough, Nigeria. *Geological Society of America Bulletin* **89**, 151–154.
- POCKNALL, D.T., WOOD, L.J., GEEN, A.F., HARRY, B.E. & HEDLUND, R.W. 2001. Integrated paleontological studies of Pliocene to Pleistocene deposits of the Orinoco Delta, eastern Venezuela and Trinidad; In: Goodman, D.K & Clarke, R.T. (eds), *Proceedings of the 1X International Palynological Congress*, 319–326. Houston, American Association of Stratigraphic Palynologist Foundation.
- POUMOT, C. 1989. Palynological evidence for eustatic changes in the tropical Neogene. *Bulletin des centres de recherches et exploration-production Elf-Aquitane* **13**(2), 437–453.
- POWELL, A.J. 1992. *A Stratigraphic Index of Dinoflagellate Cysts*. London, Chapman and Hall.
- QUATTROCHIO, M.E. & SARGEANT, W.A.S. 2003. Dinoflagellates from the Chorrillo Chico Formation (Paleocene) of southern Chile. *Ameghiniana* **40**, 129–153.
- REYMENT, R.A. 1965. *Aspects of the Geology of Nigeria*. Ibadan, Ibadan University Press.
- SALAMI, M.B. 1983. Upper Senonian and Lower Tertiary pollen grains from the southern Nigeria sedimentary basin. *Revista Española de Micropaleontología* **17**(1), 5–26.
- SALAMI, M.B. 1990. Palynomorph taxa from the “Lower Coal Measures” deposits (?Campanian-Maastrichtian) of Anambra Trough, southeastern Nigeria. *Journal of African Earth Sciences* **11**(1/2), 135–150.
- SALARD-CHEBOLDAEFF, M. 1981. Palynologie Maestrichtienne et Tertiaire du Cameroun. Resultats Botaniques. *Review of Paleobotany and Palynology* **32**, 401–439.
- SALARD-CHEBOLDAEFF, M. 1990. Intertropical African palynostratigraphy from Cretaceous to Late Quaternary times. *Journal of African Earth Sciences* **11**(1-2), 1–24.
- SHORT, K.C. & STAUBLE, A. J. 1967. Outline of Geology of Niger Delta. *American Association of Petroleum Geologists Bulletin* **51**: 761–779.
- SHRANK, E. 1984. Organic geochemical and palynological studies of Dahkla Shale profile (Late Cretaceous) in southeast Egypt. Part A: Succession of microfloras and depositional environments. *Berliner Geowissenschaften Abhandlungen Reihe A* **50**, 189–207.
- SLIMANI, H., LOUWY, S. & TOUFIQ, A. 2010. Dinoflagellate cysts from the Cretaceous-Paleogene boundary at Quled Haddou, southeastern Rif, Morocco: biostratigraphy, paleoenvironments and paleobiogeography. *Palynology* **34**(1), 90–124.
- SOWUNMI, M. A. 2004. Aspects of Nigerian Coastal Vegetation in the Holocene: some recent insights. In: Battarbee, R.W. et al. *Past Climate Variability through Europe and Africa*. Dordrecht, Springer.
- TATTAM, C.H. 1944. A review of Nigerian stratigraphy. *Reports of the Geological Survey of Nigeria*. No. 13, 61 pp.
- TSUCHDY, R.H. 1961. Palynomorphs as indicators of facies environments in Upper Cretaceous and Lower Tertiary strata, Colorado and Wyoming; Wyoming Geological Association. Symposium on Late Cretaceous rocks, Sixteenth Annual Field Conference, pp. 53–59.
- UMEJI, O.P. 2000. Evolution of the Abakiliki and the Anambra sedimentary basins, southeastern Nigeria. *A report of Shell Chair Project submitted to Shell Petroleum Development Company Nigeria Limited*, 155 pp.
- UMEJI, O.P. & NWAJIDE, C.S. 2007. Age control and designation of the standard stratotype of Nsukka Formation of Anambra Basin, Nigeria. *Journal of Mining and Geology* **43**(2), 147–166.
- UMEJI, O.P. & EDET, J. E. 2008. Palynostratigraphy and palaeoenvironments of the Type Area of Nsukka Formation of Anambra Basin, southeastern Nigeria. *Nigerian Association of Petroleum Explorationists Bulletin* **20**(2), 72–88.
- VADJA-SANTIVANEZ, V. 1999. Miospores from the Upper Cretaceous–Paleocene strata in northwestern Bolivia. *Palynology* **23**, 181–196.
- WEBB, T. III. 1980. The reconstruction of climatic sequences from botanical data. *Journal of Interdisciplinary History* **10**, 749–772.
- WILLIAMS, G.L. & BUJAK, J.P. 1985. Mesozoic and Cenozoic dinoflagellates. In: Bolli, H.M., Saunders, J.B. & Perch-Nielsen, K. (eds), *Plankton Stratigraphy*, 847–964. Cambridge, Cambridge University Press.

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The Editor
Palaeontologia africana
Evolutionary Studies Institute
University of the Witwatersrand
Private Bag 3
WITS 2050
South Africa
Telephone: [+27-11] 717-6690/6682
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- CROMPTON, A.W. 1962. On the dentition and tooth replacement in two bauriamorph reptiles. *Annals of the South African Museum* **46**(9), 231–255.
- 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.
- ROMER, A.S. 1966. *Vertebrate Palaeontology* (3rd edn). Chicago, University of Chicago Press.
- ROMER, A.S. 1973. Permian reptiles. In: Hallam, A. (ed.), *Atlas of Palaeobiogeography*, 159–168. Amsterdam, Elsevier.
- VAN DER MERWE, N.J., LEE-THORP, J.A., THACKERAY, J.F., HALL-MARTIN, A., KRUGER, E.J., COETZEE, H., BELL, R.H.V. & LINDEQUE, M. 1990. Source-area determination of elephant ivory by isotopic analysis. *Nature* **346**, 744–746.
- PERIERA, L.M. 2009. The Wits Online Phytolith Database. University of the Witwatersrand, Johannesburg, South Africa. Online at: <http://web.wits.ac.za/Academic/Science/GeoSciences/BPI/Research/WOPD/> (accessed 15 February 2010).

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