ABSTRACTS

Trends in metazoan body size, burrowing behaviour and ichnodiversity across the Precambrian–Cambrian boundary: ichnoassemblages from the Vanrhynsdorp Group of South Africa

J.E. Almond[1], L.A. Buatois[2], P.G. Gresse[3] & G.J.B. Germs[4]

[1]*Natura Viva CC, Cape Town, South Africa*
E-mail: naturaviva@universe.co.za

[2]*Department of Geological Sciences, University of Saskatchewan, Canada*

[3]*Trans Hex Group, Parow, South Africa*

[4]*Department of Geology, University of Johannesburg, South Africa*

Rich assemblages of small-bodied metazoans with mineralized skeletons first appeared during the Early Cambrian, notably from the Tommotian Stage onwards (= 530 Ma). Several less diverse 'small shelly fossil' (SSF) assemblages have been recorded from the earliest Cambrian interval (Manykaian Stage). A very limited range of older shells are known from the latest Proterozoic or Ediacaran Period. They include calcified cone-in-cone and flask-shaped skeletons (*Cloudina, Namacalathus*), sandy agglutinated tubes (*Archaeichnium*), and colonial aggregations of tubules (*Namapoikia*), all of which were first recorded from limestones and siliciclastic sediments of the latest Ediacaran Nama Group of Namibia and the South Africa (key references in Frimmel *et al.* 1998; Grotzinger *et al.* 2000; Wood *et al.* 2002). Primitive sponge-like animals (*Otavia*) have been isolated from Otavi Group limestones in Namibia that are older than 720 Ma (Cryogenian Period) as well as from much younger Ediaracan horizons in the Nama Group (Brain *et al.* 2008, this volume, and references therein).

Molecular clock evidence suggests that bilaterally-symmetrical animals (bilaterian metazoans) had already evolved by 600–630 Ma, if not considerably earlier (Erwin 2001; Narbonne 2005; Peterson *et al.* 2005). Early bilaterians were probably very small and lacked mineralized skeletons, so their fossilization potential was extremely low. Trace fossils provide a useful proxy for mobile early bilaterians – or at least for sizeable, bottom-living animals – because the ability to penetrate and rework sediment implies a sophisticated nervous and muscular system as well as some sort of skeleton. Convincing trace fossils have not been recorded before 560 Ma (Ediacaran Period), although several tantalizing claims from older rocks have been made (Narbonne 2005; Jensen *et al.* 2006). Ediacaran trace fossil assemblages worldwide are typically sparse, very low in diversity and dominated by small, fairly simple horizontal burrows generated within shallow marine to offshore settings (Seilacher *et al.* 2005; Jensen *et al.* 2006). The variety, size, abundance, density, complexity and ecological range of trace fossils all increase markedly during the latest Precambrian/Early Cambrian time interval. There is a significant acceleration during the Early Cambrian in step with the explosive diversification of macroscopic body fossils of metazoans and the evolution of sophisticated foraging and other behaviours.

Seilacher & Pflüger (1994) have emphasized the pivotal role played by infaunal bioturbators in driving a profound 'agronomic revolution' on shallow marine bottoms during the Precambrian/Cambrian boundary interval. This entailed the widespread demise of well-laminated, poorly-oxygenated sea beds of the Proterozoic that were bound and sealed by cohesive microbial mats at the sediment-water interface. These archaic substrates supported shallow-tier horizontal burrowers feeding on or beneath the surface mats. With the advent of widespread vertical bioturbation in the Early Cambrian or shortly before, Precambrian 'matgrounds' were largely replaced by better-ventilated 'mixgrounds', especially in shallow marine settings. At the same time, the proliferation of macroscopic zooplankton and nekton may have substantially increased the supply of organic nutrients to bottom-living communities, fuelling the benthic substrate revolution. This was because faecal pellets generated by these floating and swimming animals were large enough to sink rapidly through the water column without being entirely consumed by microbial decomposers *en route* (Peterson *et al.* 2005). With an abundant supply of food and oxygen extending well beneath the sediment-water interface, and less cohesive sediments to penetrate and rework, an infaunal lifestyle became an attractive new option for a wide range of benthic invertebrates, especially in view of rapidly escalating predation pressures during the Cambrian explosion. Compared with their Ediacaran precursors, early Palaeozoic mixgrounds supported a much higher density and variety of infauna, including animals that hid, resided and foraged below the sediment surface, as shown by their far richer ichnoassemblages and higher bioturbation indices.

The thick, relatively undeformed Vanrhynsdorp Group of the Western and Northern Cape Provinces, South Africa, is emerging as a key succession for documenting important developments in ichnodiversity, ichnostratigraphy, body size and burrowing behaviour among infaunal metazoans across the Precambrian/Cambrian boundary (Seilacher *et al.* 2005; Buatois *et al.* 2007; Almond 2008 and references therein). Overall ichnodiversity is low, as is typical for marine sediments of Ediacaran/earliest Cambrian age, but preservation is good and trace fossils are often very abundant, especially in the upper parts of the succession.

So far the basal Flaminkberg Formation, characterized by coarse pebbly alluvial quartzites, has not yielded well-substantiated fossils of any kind. Within the Kwanous Subgroup, limestones of the Grootriet Formation – a probable correlative of the thick Huns Member of the Nama Group to the north – show abundant evidence for microbial binding of fine-grained carbonate (platy-clast limestone breccias, oncolites) but no discernible trace fossils. Narrow, straight to curved, horizontal burrows of the *Helminthopsis* ichnoguild are associated with wrinkly microbial mat textures within dark mudrocks of the overlying Hoedberg Formation. These traces typify inshore as well as deeper water settings in the Ediacaran Period and reflect shallow tier exploitation of superficial matgrounds by 'grazing' metazoans. Enigmatic tubular structures,

tentatively identified as decalcified, reworked *Cloudina,* occur within the lower Hoedberg. The heterolithic Arondegas Formation at the base of the Knersvlakte Subgroup also contains well-preserved horizontal burrows of the *Helminthopsis* ichnoguild (Fig. 1) associated with microbial mat textures and poorly preserved vendotaenids (cyanobacterial 'strings'). However, the stratigraphic position of these Ediacaran-type assemblages (also possibly uppermost Hoedberg) requires confirmation.

Large, one to 2.3 cm wide, horizontal burrows (Fig. 2) occur abundantly within the heterolithic upper Gannabos Formation, interpreted as an offshore, storm-influenced marine succession. The hypichnial wash-out burrows, which remain in taxonomic limbo, have a distinctive subrectangular cross-section and preserve occasional relicts of coarse meniscate back-fill. The gently to tightly curving burrows show frequent overlaps, but a crude meandering or 'scribbling' foraging pattern and even possible avoidance behaviour are also seen. The Gannabos Formation also yields microbial wrinkle marks, clusters of pyrite pseudomorphs, and comb-like tool marks that might have been generated by storm-entrained, finely-ribbed vendobiontans. An Ediacaran age for the Gannabos Formation is provisionally inferred from the notable absence of *Treptichnus* type probe burrows that characterize comparable storm-dominated shelf facies in the Early Cambrian. If correct, the Gannabos burrows would demonstrate that large-bodied (over 2 cm wide) infaunal metazoans appeared before the end of the Precambrian.

Further evidence for substantial infaunal animals, complex burrow infill and primitive meandering behaviour close to the Precambrian/Cambrian boundary is provided by as yet undescribed traces from the Nama Group in the Fish River Canyon, southern Namibia (Fig. 3). They come from thin-bedded micaceous sandstones within the carbonate-dominated upper Spitskop Member (Urusis Formation, Schwarzrand Subgroup). This stratigraphic unit has been radiometrically dated to 543 ± 1 Ma and has also yielded complex traces of the *Treptichnus*-like ichnogenus *Streptichnus* (Jensen & Runnegar 2005). The Fish River Canyon burrows, mostly preserved as positive, washed-out hypichnia, are up to 12 mm across and occasionally retain evidence for a crude meniscate backfill. They range from straight to strongly curved, show frequent internal overlap, and sometimes adopt tightly-coiled, 'pretzel-like' configurations that are unknown in Ediacaran ichnofossils described so far. Abundant comb-like tool marks, possible finely-pleated vendobiontans and a range of other problematic biogenic structures occur in the same beds.

Returning to the Vanrhynsdorp succession of South Africa, complex subhorizontal burrow systems of the distinctive Cambrian ichnogenus *Oldhamia* are recorded from finely laminated mudrocks – probably distal turbidites – of the Besonderheid Formation in the Bokkeveld Escarpment. The Besonderheid specimens co-occur with microbial wrinkle textures and have been assigned to *O. geniculata,* also known from the Early Cambrian of Argentina (Seilacher *et al.* 2005). Well-preserved South African specimens clearly show complete, asymmetrical hair-pin loops at the terminations of closely paired radial burrow sections, demonstrating that these are not blind-ending tunnels (Fig. 4). Systematic centrifugal and centripetal movement of the trace-maker, alternately away from and towards the burrow axis, is also demonstrated by the finely-developed meniscate back-fill (*not* a cleavage artefact, as previously suggested). This sophisticated foraging behaviour may well be common to all *Oldhamia* burrow systems (a controversial point), but complete terminal loops and meniscate backfill are rarely observed so clearly. *Oldhamia* characterizes, but is not restricted to, the Early Cambrian and demonstrates the persistence of shallow tier mat-feeding in deeper water, offshore settings following the agronomic revolution.

Prolific but low-diversity trace assemblages within the younger formations of the Vanrhynsdorp Group (upper Knersvlakte Subgroup *plus* Brandkop Subgroup) are heavily dominated by intrastratal probe-burrows of the *Treptichnus* type. These have been tentatively attributed to priapulid worms (Jensen *et al.* 2006). Microbial wrinkle structures are also common. A spectrum of shallow marine, wave-dominated to tidal settings have been recognized here (Buatois *et al.* 2007). The Vanrhynsdorp treptichnids display considerable preservational, morphological and hence behavioural plasticity, with frequent intergradations between typical *T. pedum* and other *Treptichnus* ichnospecies within the same burrow system (Fig. 5). These systems range from strictly linear (perhaps indirectly current-orientated) to curved, coiled or irregular. The lower surface of individual burrow probes is variously smooth, bi- or tri-lobed, and/or transversely ridged. Transitions with *Curvolithus*-, *Saerichnites*-, *Arthrophycus*- and *Cruziana*-like morphs are observed, but with no discernible temporal succession. This plasticity and lack of stratigraphic pattern seriously undermine the utility of *Treptichnus* spp. for the biostratigraphic zonation of Ediacaran/Early Cambrian boundary successions (Buatois *et al.* 2007). The presence of *Treptichnus pedum* – often treated as a zone fossil for the basal Cambrian – as well as the absence of unequivocal arthropod scratch burrows such as *Rusophycus*/*Cruziana* strongly suggest an earliest Cambrian (Manykaian/Nemakit-Daldynian) age for the entire upper Vanrhynsdorp succession (*Monomorphichnus*-like comb marks are reported from the upper Brandkop Subgroup, but their identity and arthropod origin are controversial). A similar conclusion was reached by Geyer (2005) for the thick Fish River Subgroup (uppermost Nama Group) of Namibia and Gordonia. However, precise correlation of the Nama and Vanrhynsdorp successions remains elusive pending detailed sequence stratigraphic, sedimentological and palaeontological analysis of the South African successions in particular.

We are grateful to Hedi Stummer, Erwin Stummer and Madelon Tusenius for logistical support and assistance with fieldwork

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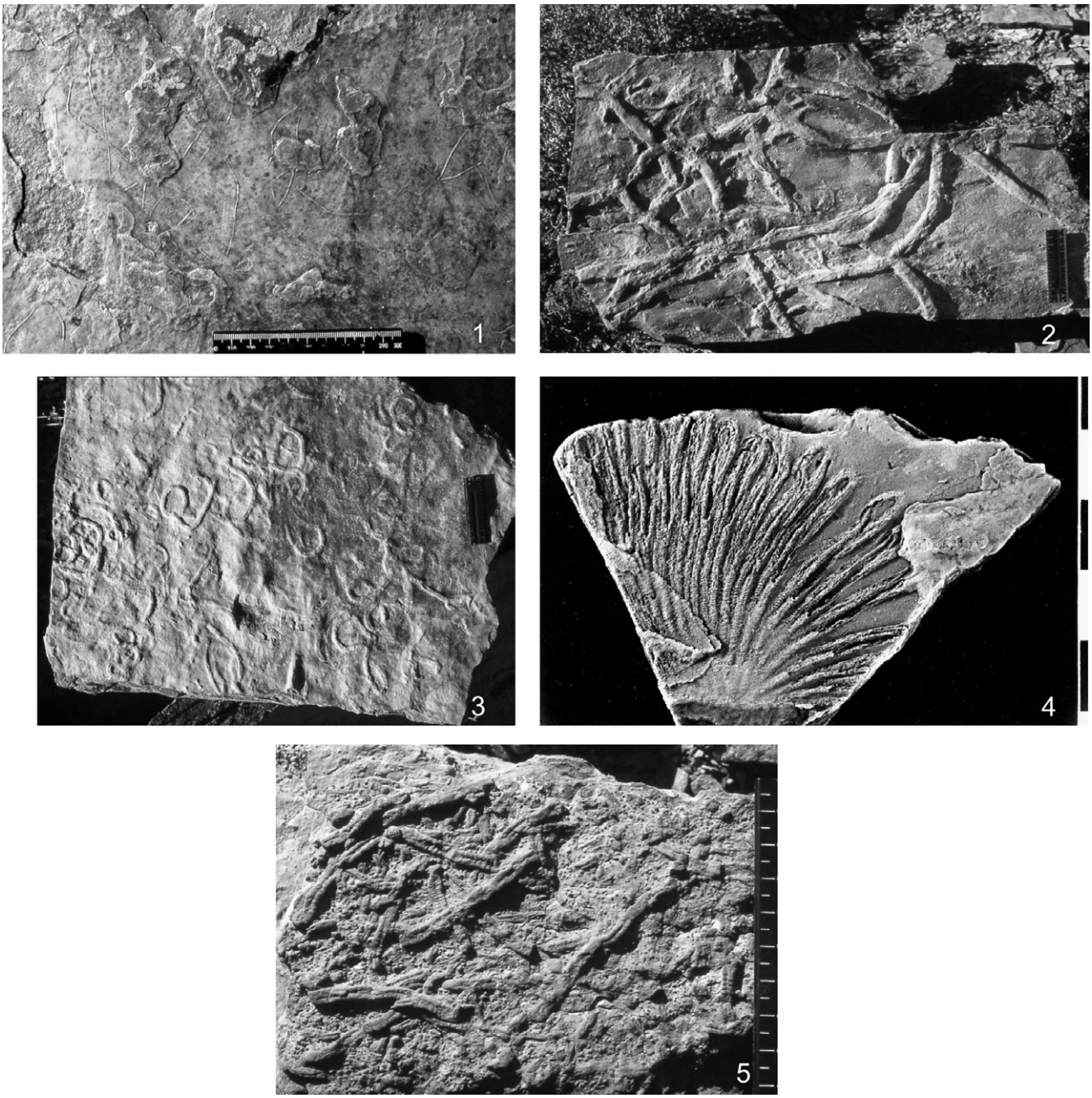

Figures 1–4. **1**, *Helminthopsis* ichnoguild horizontal burrows, Arondegas Formation. Scale 10 cm. **2**, Large horizontal hypichnial burrows, Gannabos Formation. Scale 10 cm. **3**, Large horizontal scribbling traces, Spitskop Member. Scale 10 cm. **4**, *Oldhamia* looped burrow system, Besonderheid Formation. Scale units 0.5 cm. **5**, Treptichnids from the Knersvlakte Subgroup. Scale units 0.5 cm.

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Fossil woods from the early Pleistocene hominin site, Area 1A, Ileret, northern Kenya

Marion K. Bamford

Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa
E-mail: marion.bamford@wits.ac.za

On the eastern side of Lake Turkana in northern Kenya are extensive Plio-Pleistocene deposits containing a rich diversity of fossil mammals, hominins and flora within the radiometrically dated tuffaceous, lacustrine and fluvial sequence. These sediments also contain stone artefacts and hominin-modified bone which greatly increases their interest as far as early hominin behaviour and landscape use are concerned. Reconstruction of this landscape and palaeoenvironment are part of an ongoing multinational and multidisciplinary human evolution project in the eastern Turkana Basin. Today there is a huge lake in the Rift but it has fluctuated from lake to various river systems and deltas of the Omo River, with associated flora and fauna, since the early Pliocene. Silicified wood is fairly common in some areas of the Koobi Fora Formation. One such site is FwJj14E alongside one of the tributaries of the Ileret River. Hominin hand and arm bones have been excavated from here in the Okote Member and dated at 1.52 Ma. The fossils are associated with hominin and bovid footprints. Thirty of the over 100 wood specimens collected have been sectioned and identified. In general the woods have large vessels and an average vulnerability index of 37 which implies a mesic environment with little or no water stress. Taxonomically the woods belong to large African families: Caesalpiniaceae (*Afzelia bipindensis, Didelitia* sp.), Euphorbiaceae (*Drypetes* sp.), Malvaceae (*cf. Sterculia* sp.), Rhamnaceae (*Ziziphus mauritiana*), Sapindaceae (*Blighia* sp.), and Palmae. Most of these taxa do not occur in the area today because now it is much drier and the local vegetation is predominantly *Acacia–Commiphora–Salvadora.* The reconstruction of the palaeovegetation supports the interpretation from the fauna, namely, a tall gallery forest and wooded grassland and more open bushland in the vicinity.

Reconstruction of the cervical vertebrae of *Massospondylus*: implications for neck movement and feeding envelope of the Prosauropoda

Natasha Barbolini & Adam Yates

Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa
E-mail: natasha.barbolini@students.wits.ac.za

Introduction

Massospondylus is a moderately derived prosauropod from the Early Jurassic, notable for its highly elongated neck of over a metre in length. The animal's dentition suggests a primarily herbivorous diet (Galton 1986), perhaps with opportunistic carnivory (Barrett 2000). Otherwise, little is known about its lifestyle. We attempted to deduce the type and range of movement for the neck of *Massospondylus.* Information on feeding behaviour, body posture and habitat was integrated with neck posture, in order to infer the ecological niche of the animal. No previous work had been done on the neck position of prosauropods. Conversely, recent studies have overturned the belief that the related clade, Sauropoda, possessed swan-like, vertically curved necks (e.g. Stevens & Parrish 2005; Christian & Dzemski 2007; Berman & Rothschild 2005). These researchers have concluded that the neck posture of most sauropods was actually closer to the horizontal, and while they possessed a good range of lateral and ventral movement, their dorsiflexion was limited. This has implications for prosauropods, which have also been conventionally reconstructed with swan-like necks. Many prosauropods were thought to be quadrupedal, but a new study has showed that *Massospondylus* was habitually bipedal (Senter & Bonnan 2007). Such discoveries ask for a revision of prosauropod body and neck posture.

Methods and research design

Plasticine models of each cervical vertebra were cast using a well-preserved, articulated specimen (BP/1/4934) as a template. Numerous dimensions were taken to ensure accuracy of the finished models, which were statistically re-evaluated against the original fossils to ensure that models and fossils were not significantly different. Models of nine cervicals (excluding the axis) and the first dorsal vertebra were fitted together in the neutral pose, according to the zygapophyseal alignment technique of Stevens & Parrish (2005). Models were then manipulated to determine the maximum ranges of dorsal, lateral and ventral movement.

Manipulation of models

Feeding envelope

The zygapophyseal alignment technique reconstructs the neutral posture as angled slightly upwards, with a curve in the posterior region (Fig. 1). It is clear that *Massospondylus* was limited in dorsal neck movements (Fig. 2), with the maximum dorsiflexion being only 45 cm higher than in the neutral pose. The vertebrae of *Massospondylus* are so elongate and flattened that only a small amount of dorsiflexion is possible without disarticulation. However, this design permits extensive lateral movement, which would have allowed for browsing from side to side on medium-height plants (Fig. 3). It also was capable of very good ventriflexion, aided in this regard by the distinctive downward curve of the axis and first dorsal vertebra (Fig. 4). This would have allowed it to reach ground vegetation. The habitually bipedal posture

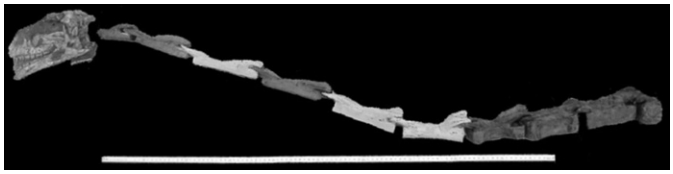

Figure 1. Neutral pose of *Massospondylus* reconstructed using the zygapophyseal alignment technique. Margins of the centra are parallel and centred, with the pre- and postzygapophyses superimposed. The skull is from the same specimen used to build the models of cervical vertebrae. Scale bar = 1 m.

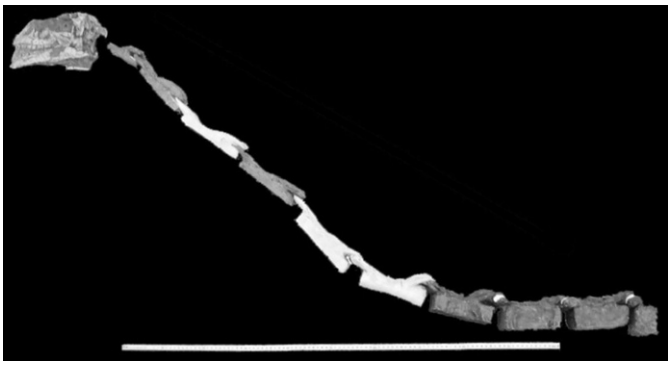

Figure 2. Maximum degree of dorsiflexion in *Massospondylus.* Zygapophyseal facets are overlapping by 50% in both the lateral plane and the plane parallel with the zygapophyses (the minimum degree of overlap before disarticulation occurs in extant birds and mammals). Scale bar = 1 m.

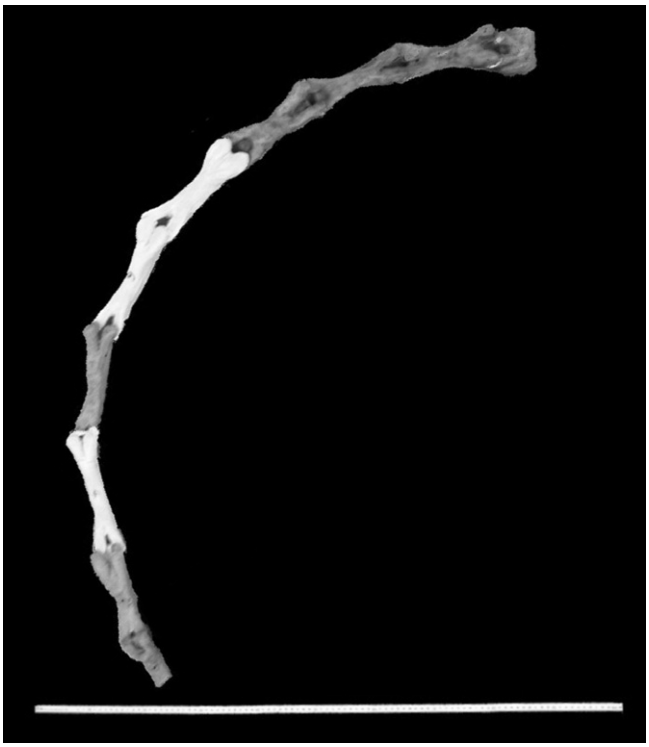

Figure 3. Maximum degree of lateral flexion in *Massospondylus*. Pre- and postzygapophyses rotate freely in the lateral plane, while still overlapping by 50% in both the lateral plane and the plane parallel with the zygapophyses. Axis is to the bottom left. Scale bar = 1 m.

of *Massospondylus* would have increased both its mobility and feeding envelope, especially aiding in dorsal movements. *Massospondylus* could also have adopted a tripodal position, permitting the animal to browse on taller vegetation that could have been present around local water sources (Parrish & Falcon-Lang 2007). The environment in which *Massospondylus* lived was strongly seasonal, and probably resource-limited for parts of the year. Thus, the animal could have adopted a variety of feeding behaviours depending on the nutritional value of the different types of plants, and whether or not they were available.

Research supported by University of the Witwatersrand, and the NRF (through Lucinda Backwell). Many thanks go to Adam Yates for mentoring throughout the year, Marion Bamford for use of her photographic room and references on fossil vegetation, Nkosinathi Sithole who cast the plasticine models, and Fernando Abdala for comments on a final draft.

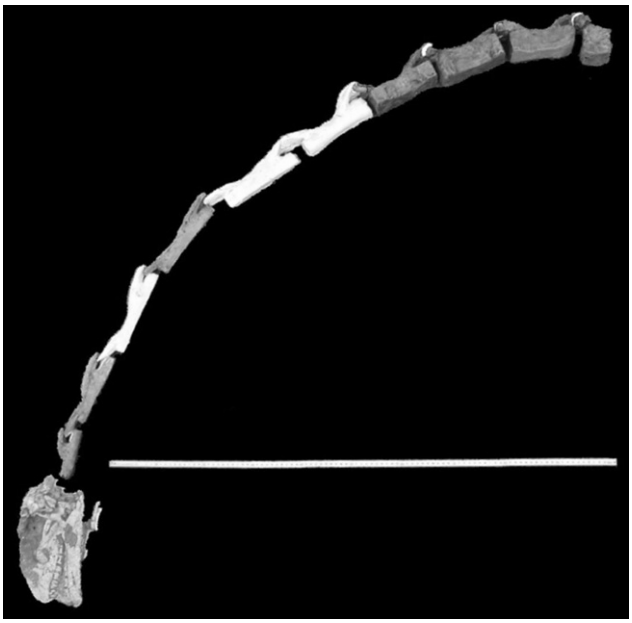

Figure 4. Maximum degree of ventriflexion in *Massospondylus*. Zygapophyseal facets are overlapping by 50% in both the lateral plane and the plane parallel with the zygapophyses. Scale bar = 1 m.

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Dicynodon from South Africa, '*Dicynodon*' from Russia and *Dicynodon*(?) from southeast Asia

Bernard Battail

Département Histoire de la Terre, Muséum National d'Histoire Naturelle, USM 0203 – UMR 5143, Case Postale 38, 57 rue Cuvier, 75231 Paris cedex 05, France
E-mail: bbattail@mnhn.fr

Introduction

The genus *Dicynodon* was erected in 1845 by Owen, with *Dicynodon lacerticeps,* from the Upper Permian of South Africa, as type species. Owing to the fact that *Dicynodon* lacks conspicuous specialized characters, and if we take into account that the genus was erected very long ago, it is

not surprising that many species were attributed to it. A certain number of species were ultimately transferred to other genera, mainly to *Diictodon* Broom 1913, and *Oudenodon* Owen, 1860 (see Keyser 1975, and Cluver & Hotton 1981). On the contrary, a few species were initially attributed to genera (*Daptocephalus,* for example) which are often nowadays regarded as synonyms of *Dicynodon.* On the list established by King 1988 (pp. 89–93), fifty-nine *Dicynodon* species are still found, but the author mentions that they are not necessarily all valid. Indeed, many are known only by incomplete and badly preserved specimens, making detailed comparisons impossible. Moreover, the genus *Lystrosaurus* might well be rooted in the genus *Dicynodon,* rendering the latter paraphyletic.

A rather detailed diagnosis of the genus *Dicynodon* was given by Cluver & Hotton (1981, pp. 106–107), and a slightly modified and expanded one by Cluver & King (1983): 'Medium-sized to large' dicynodonts (average skull length 100 mm to over 400 mm), single pair of maxillary tusks in upper jaw, lower jaw edentulous. Postorbitals tend to cover parietals behind parietal foramen. Septomaxilla merges smoothly with outer surface of snout, does not meet lacrimal. Low boss formed over external nares by nasals. Palatal rim sharp edged, uninterrupted by notch. Palatal portion of palatine large and flat, making short contact with premaxilla. Vomers form long, narrow septum in interpterygoidal fossa. Anterior border of interpterigoidal fossa formed by a crest that joins the vomerine septum. Ectopterygoid small, displaced laterally. Labial fossa present between maxilla, palatine and jugal. Pterygoid makes short contact with maxilla. Basioccipital tubera separated by intertuberal ridge. Fused dentaries carry narrow dentary tables. Dorsal edge of dentary carries deep sulcus behind dentary tables. Rear of dentary extended dorsally to form weak posterodorsally directed process. Mandibular fenestra large, bounded dorsally by lateral dentary shelf. Occipital surface of opisthotic carries depression above paroccipital process.' (Cluver & King 1983, pp. 234, 237).

The above mentioned diagnosis provides a frame which can accommodate all species traditionally attributed to *Dicynodon,* whether from South Africa or from Russia. But it is all too clear that many characters listed in that diagnosis are not restricted to *Dicynodon.* A dentition reduced to a pair of maxillary tusks, for example, is also observed in *Lystrosaurus,* in *Kannemeyeria* and in many other genera. And most characters are described in rather general terms, leaving room for a wide range of possible variations.

Dicynodon from South Africa, *'Dicynodon'* from Russia

Several recent authors reviewed the systematics and phylogeny of late Permian dicynodonts. Their works, undertaken from a cladistic perspective, deal with many more characters than earlier articles (see for example Angielczyk 2001; Maisch 2002; Angielczyk & Kurkin 2003a,b; Fröbisch 2007). However, some of the newly considered characters can seldom be observed, and others could easily have been altered by weathering or distortion, and their real value can therefore be questioned. Fröbisch (2007) established a list of 100 characters, most of which had been used in previous phylogenetic analyses, and particularly in that of Angielczyk & Kurkin 2003a. This list will be used hereafter as a basis for discussion.

The phylogenetic analyses by Angielczyk & Kurkin (2003a,b) and Fröbisch (2007) tend to consider *Dicynodon* as a paraphyletic genus, and to separate the South African form *Dicynodon lacerticeps* from the Russian forms, the latter being provisionally attributed to '*Dicynodon*' rather than to *Dicynodon* proper. The phylogenies presented by Angielczyk & Kurkin (2003a) and by Fröbisch (2007) differ slightly, but both consider *Dicynodon lacerticeps* as the sister-taxon of a clade containing *Lystrosaurus, Kannemeyeria* and the Russian *'Dicynodon'*, and both keep two Russian species , *'Dicynodon' trautscholdi* and *'Dicynodon' amalitzkii.* Out of the hundred characters retained and coded by Fröbisch (2007), fourty-seven can be observed in both '*D.' trautscholdi* and *'D.' amalitzkii,* but only two are coded differently. The canine would be anterior to the level of the anterior margin of the orbit in *'D.'trautscholdi,* at the same level in *'D.' amalitzkii* ; this character is, in my opinion, debatable, because the way it is appreciated depends largely on the orientation given to the skull. And secondly, the interparietal would contribute to the intertemporal skull roof in *'D.' trautscholdi,* but not in *'D.' amalitzkii.* The difference, however, is extremely inconspicuous, and could easily be only the consequence of a slight distortion or weathering. Therefore I tend rather to consider *'D.' amalitzkii* as a junior synonym of *'D.' trautscholdi,* a position already expressed, in particular by Battail & Surkov (2000).

A few anatomical differences have been noted between *'D.' trautscholdi* and the South African *D. lacerticeps.* The septomaxilla is recessed within the naris in *'D.' trautscholdi,* it has a broad facial exposure in *D. lacerticeps.* The dorsal surface of the preparietal is relatively flat and flush with the skull roof in *D. lacerticeps,* it has a depressed dorsal surface relatively to the skull roof in *'D.' trautscholdi.* The postorbitals overlap the parietals nearly completely in *D. lacerticeps,* they are exposed on the skull roof between the postorbitals in *'D.' trautscholdi.* The palatal surface of the palatine is highly rugose in *'D.' trautscholdi,* moderately rugose in *D. lacerticeps.* On the basis of this set of characters, *D. lacerticeps* appears as significantly different from the Russian *'Dicynodon',* and Angielczyk & Kurkin (2003 a) could write: '…we consider it worth noting that in our personal observations of over 600 dicynodont specimens collected in Russia, South Africa, Tanzania, and Zambia, we have only observed the diagnostic suite of features that characterize *D. trautscholdi* and *D. amalitzkii* in specimens collected in Russia. We have not identified any Russian specimens that are referable to species of *Dicynodon* other than *D. trautscholdi* and *D. amalitzkii.* Likewise, we have only observed the diagnostic suite of features that characterizes *D. lacerticeps* in southern African specimens.' (Angielczyk & Kurkin 2003a, pp. 165–166).

Dicynodon(?) from southeast Asia

In southeast Asia, late Permian dicynodonts are known from limited outcrops of purple beds situated North of

Luang Prabang, Laos. The presence of dicynodonts in Laos was first reported more than one century ago by Counillon (1896). The only specimen collected at that time, the anterior half of a skull, was very briefly described by Repelin in 1923 as *Dicynodon incisivum* sp. nov. The attribution of the specimen to the genus *Dicynodon* was very convincingly confirmed by Piveteau (1938). Unfortunately, many authors referred it, without any anatomical (or stratigraphical) basis, to *Lystrosaurus* sp. (see Battail 1997); this specimen is now considered as lost.

In recent years, many specimens of dicynodonts were collected in the same beds of the same area during annual Franco-Lao expeditions led by Philippe Taquet (Muséum National d'Histoire Naturelle, Paris, France) (Battail *et al.* 1995). The collected dicynodont skulls are not all alike, and differ mainly in their proportions, in the shape of their tusks and in the shape of their occiput. However, all of them conform, in their observable characters, with the definition of *Dicynodon* as given by Cluver & Hotton (1981, pp. 106–107), or by Cluver & King (1983, pp. 234, 237). Indeed, a close examination of these specimens, now being described, rules out that they could belong to any other late Permian (or early Triassic) genus of dicynodonts whose dentition is reduced to a pair of upper tusks (*Aulacephalodon, Idelesaurus, Elph, Interpresosaurus, Delectosaurus, Lystrosaurus*). But a question arises: are they closer to the South African *Dicynodon lacerticeps* or to the Russian *'Dicynodon' trautscholdi*?

In fact, most specimens from Laos display some characters regarded as typical of the South African *Dicynodon*, and some regarded as typical of the Russian *'Dicynodon'*. A common association is that of a preparietal depressed relatively to the skull roof (as in *'D.' trautscholdi*), and postorbitals overlapping the parietals nearly completely (as in *D. lacerticeps*) (Fig. 1). Our knowledge of the anatomy of the dicynodonts of Laos remains unfortunately limited because, even in well-preserved specimens, the sutures are not clearly seen.

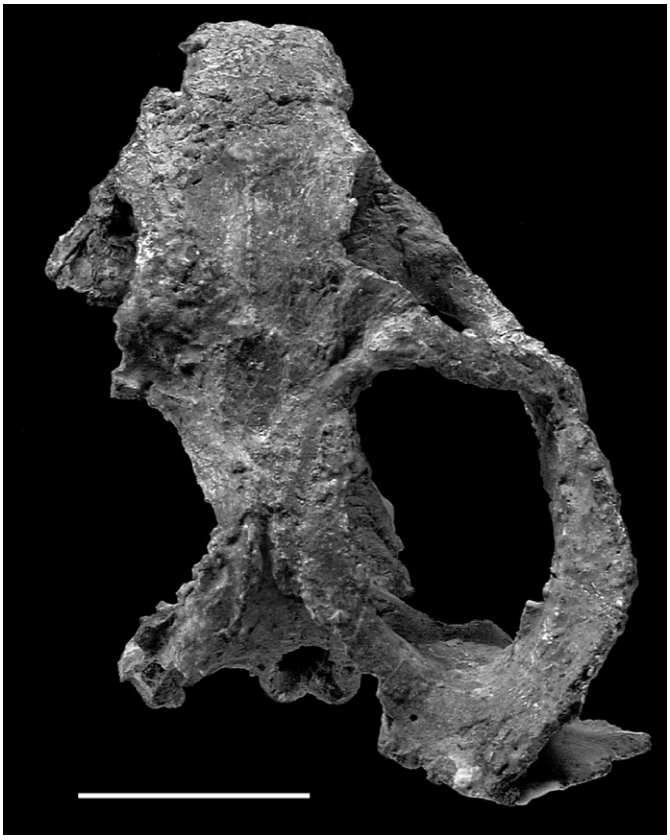

Figure 1. *Dicynodon* sp., skull, dorsal view. Late Permian, area of Luang Prabang, Laos. Musée de Savannakhet, Laos, specimen No. LPB 1993 – 2. Scale bar = 5 cm

Conclusions

The present paper is only a preliminary account of the difficulties encountered when dealing with the genus *Dicynodon* at a world level. No attempt has been made at this stage to establish a new phylogeny of *Dicynodon* and related genera that would include the forms from southeast Asia. It nevertheless appears that the relatively clear-cut distinction between Gondwanan forms (South African *Dicynodon*) and Laurasian forms (Russian *'Dicynodon'*), which could be expected on the basis of recent works, does not seem to be sustained by the analysis of *Dicynodon* material from southeast Asia.

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Taphonomy and taxonomy of the rare Triassic dinosaur *Eucnemesaurus* based on an articulated skeleton from the Eastern Cape

Marc Blackbeard
Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa
E-mail: blackbeardm@gmail.com

The subject of this paper is based on a specimen found on the farm of Cannon Rock in the Eastern Cape and has been informally named the cannon rock dinosaur. The taphonomy of the cannon rock dinosaur BP/I/6234 has been undertaken.

The skeleton is completely articulated and associated, it was found lying on its left side with the right side exposed to weathering. The left side is in good condition as it has been protected and is therefore relatively unweathered compared to the right side. It shows a first stage of weathering in Behrensmeyers six-stage categorization of bone weathering (Behrensmeyer 1978). This site fits the channel fill mode proposed by Behrensmeyer (1988), which includes two taphonomic modes of attritional vertebrate accumulations in fluvial channels based on taphonomic features on bones and their sedimentary context. Some of the bones are deformed this is likely to have been largely due to sedimentary loading during final burial. The ontogenetic evidence of BP/I/6234 shows that the individual was mature. Specimen BP/I/6234 was located on the farm of Cannon Rock approximately 30 km south of Aliwal North in the Eastern Cape. This area is located within the *Euskelosaurus* range zone in the lower Elliot Formation (Kitching *et al.* 1984). The skeleton consists of the posterior end of the dinosaur and includes a number of thoracic vertebrae, the ilia, ischia and pubes, the hind limbs and caudal vertebrae (these are not in very good condition and have not been completely prepared) the anterior end is completely missing as the sandstone in which it was found had been partly eroded away. The lower Elliot Formation consists typically of multi-storeyed, asymmetrical channel fill sandstones. They are characterized by planar and trough cross-stratification and massive beds that are interpreted as perennial moderately meandering fluvial systems (Bordy *et al.* 2004). The sandstone in which BP/I/6234 was found is a typical lower Elliot Formation sandstone. A description of this rare dinosaur (previously known from a few highly fragmentary specimens) has been undertaken, using this information a re-examination and comparison has been done as to ascertain its position within dinosaur phylogeny. This dinosaur has a number of femoral synapomorphies which include a large round turbercle protruding from the proximal end of the femur, the fourth trochanter is rounded rather than sub-rectangular, and is separated from the from the femoral shaft by a rounded notch (Yates 2006). These synapomorphies are quite distinct and are seen within the Riojasuaridae. *Riojasaurus* is a sauropodomorph dinosaur from the late Triassic of Argentina (South America) and was discovered in the Los Colorados Formation (Galton *et al.* 2004). It is now apparent that *Euskelosaurus* is a 'wastebasket' name or nomen dubium that has been hiding a diversity of Triassic sauropodomorph dinosaurs.

Figure 1. The locality where the BP/I/6234 was discovered and excavated on the farm of Cannon Rock.

Figure 2. The prepared posterior end of BP/I/6234 on its left side showing a number of caudal vertebrae, the sacrum and some dorsal vertebrae.

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Variation in anomodont growth patterns across the Permo-Triassic boundary in South Africa

J. Botha-Brink

Karoo Palaeontology, National Museum, P.O. Box 266, Bloemfontein, 9300, South Africa; and Department of Zoology and Entomology, University of the Free State, Bloemfontein, 9300

E-mail: jbotha@nasmus.co.za

The Anomodontia, which includes the dicynodonts, is a well-known group of non-mammalian synapsids that had a particularly long phylogenetic lineage from the middle Late Permian to the Late Triassic. The dicynodonts had remarkably specialized feeding modifications that allowed them to radiate globally to become one of the most diverse terrestrial vertebrates in Earth's history. Their worldwide distribution and abundance has allowed them to play a particularly significant role in global correlations (e.g. King 1992; Angielczyk & Kurkin 2003). They are important as biostratigraphic indicators (Rubidge 1995; Smith & Ward 2001) and they can be used in ecological studies where large sample sizes are required (e.g. Sullivan *et al.* 2003).

These and more traditional studies such as morphological descriptions have provided significant information about the palaeobiology and palaeoecology of this group. However, valuable information can also be gained by studying the bone microstructure or histology of these animals. Early studies, such as those of Enlow & Brown (1957), Ricqlès (1972, 1976) and Chinsamy 7 Rubidge (1993), and more recent, comprehensive works (e.g. *Oudenodon,* Botha 2003; *Diictodon,* Ray & Chinsamy 2004; *Lystrosaurus,* Ray *et al.* 2005; *Tropidostoma,* Botha & Angielczyk 2007), which included multi-element, detailed analyses, have provided important contributions to understanding the biology of dicynodonts. However, a broad overview of the changes in dicynodont bone histology (and hence biology) during their lineage is still lacking. This information is relevant because the dicynodonts were one of the few groups to survive the End-Permian extinction, the most catastrophic mass extinction in Earth's history, and they include the only genus that is known to have crossed the Permo-Triassic boundary, namely *Lystrosaurus.*

This study compares the bone histology of 12 South African anomodont taxa. It includes one non-dicynodont anomodont and 11 dicynodont anomodonts (including three species of *Lystrosaurus*), ranging from some of the earliest known forms, such as *Eodicynodon* from the middle Late Permian *Tapinocephalus* Assemblage Zone to some of the latest forms such as *Kannemeyeria* from the Middle Triassic *Cynognathus* Assemblage Zone.

The bone tissue of all the genera studied consists of fibro-lamellar bone interrupted by annuli and/or LAGs, indicating seasonal growth. However, the degree and pattern of vascularization varies between different genera, allowing some genera to be distinguished from others on the basis of bone histology alone. Enlarged erosion cavities in the peri-medullary region were observed in *L. murrayi,* as previously noted (Ray *et al.* 2005), but also in *L. declivis*, *L. maccaigi*, *Aulacephalodon* and *Dicynodon.* Many of the older individuals display poorly vascularized parallel-fibred tissue at the bone periphery, indicating a decrease in growth rate, but not a complete cessation, suggesting indeterminate growth.

Interestingly, all the genera studied exhibit a remarkably thick cortex, irrespective of the size of the taxon. Where possible, the relative bone wall thickness (RBT) of the bones was calculated, and apart from *Cistecephalus,* all the taxa studied had an average RBT of more than 30%. A free medullary region is absent in many of the genera and is instead filled with trabeculae even in the midshaft regions. These characteristics and their implications regarding lifestyle and phylogeny are discussed.

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Progress in the evaluation of sponge-like fossils from Neoproterozoic limestones of Namibia

C.K. Brain[1], A.R. Prave[2], K-H. Hoffmann[3], A.E. Fallick[4], A.J. Botha[5], D. Condon[6], D. Herd[2], I. Young[7] & C.J. Sturrock[7]

[1]*Transvaal Museum, Northern Flagship Institution. P. O. Box 413, Pretoria, 0001 South Africa*

E-mail: brainnew@iafrica.com

[2]*School of Geography and Geosciences, University of St Andrews, Fife KY16 9AL, Scotland*

E-mail: ap13@st-andrews.ac.uk; dah@st-andrews.ac.uk

[3]*Geological Survey, Ministry of Mines and Energy, Private Bag 13297, Windhoek, Namibia*

E-mail: khhoffmann@mme.gov.na

[4]*Scottish Universities Environmental Research Centre, Rankine Avenue, East Kilbride, Glasgow G75 OQF, Scotland*

E-mail: t.fallick@suerc.gla.ac.uk

[5]*Laboratory for Microscopy and Microanalysis, University of Pretoria, Pretoria 0002, South Africa*
[6]*NERC Isotope Geosciences Laboratory, Keyworth, NG12 5GG, UK*
E-mail: dcondon@bgs.ac.uk
[7]*Simbios Centre, University of Abertay Dundee, Bell Street, Dundee DD1 1HG Scotland*
E-mail: i.young@abertay.ac.uk / c.sturrock@abertay.ac.uk

For the last ten years, one of the authors (C.K.B.) has been conducting a search for microfossils of ancestral animals (here defined as 'multicellular heterotrophs') in limestones and cherts of the Otavi and Nama Groups of Namibia. This has proved to be a very slow and labour-intensive occupation, involving the examination of thin-sections of the rocks, of which about 860 have been prepared thus far by Laura Brain, and the sorting of insoluble residues after samples of the limestone have been dissolved in acetic acid (about 350). A variety of interesting microfossils have been found, most of them preserved with calcium phosphate, as has been shown by analyses undertaken by A.J.B. The commonest of these microfossils appear to be ancestral sponges, referred to here by the informal name Otavia, which vary in overall length or breadth from 0.3 to 5 mm. However, there are various problems in the interpretation of these ancient fossils, as outlined by Brain *et al.* (2001).

When such fossils have been found in limestones from a particular locality by C.K.B., it is of course necessary to establish just where this outcrop fits into to the Neoproterozoic sequence of Namibia. All such outcrops have been examined in detail by A.R.P. and K-H.H. who have also taken samples for stable isotope analysis by A.E.F. Whenever ashbeds have been found, attempts have been made by D.C. to obtain absolute dates from zircon crystals that the samples might contain. We have now obtained *Otavia* fossils from a very long stratigraphic sequence, going back in time to limestones of the Ombambo Subgroup, in the Kaokoveld, which are below the older of the two 'Snowball Earth' glacial episodes, represented there by the Sturtian Chuos diamictite at about 720 million years, then through limestones of the Abenab Subgroup, up to the Marinoan Ghaub glacial deposits at 635 million years. Further to the south in the Nama Group, similar Otavia fossils have been found in a limestone of the Mara Formation at about 550 million years, indicating that these marine organisms survived the harsh climatic conditions associated with glacial episodes.

Although the shape of individual *Otavia* fossils varies, the overall structure of each remains similar, consisting of a hollow container, with several large openings to the outside, often on raised mounds, reminiscent of the exhalent oscula of later sponges. The outer walls of the organisms were also pierced by many smaller holes, similar to sponge ostia, leading into a 'peripheral labyrinth' that had many connections with the large internal cavity, which is reminiscent of a sponge's paragastric chamber. The smallest Otavia individuals may not have been particularly efficient at drawing nutrient-rich water into their bodies, but larger *Otavias* would have had no such difficulty.

When a formal description of *Otavia* species was recently drawn up and submitted for publication, comment from reviewers insisted that more detail of the internal structure should be provided. A complication in this regard is that, in thin petrographic sections, the phosphatized wall-structure appears opaque. For this reason we have established the current collaboration of specialists. Donald Herd, who runs the Electron Microscope Unit at St Andrews University has recently been obtaining exceptional back-scatter and cathode luminescence images of *Otavia* fossils, while at Abertay University in Dundee, Scotland, Iain Young and Craig Sturrock have used their High Resolution X-ray computer tomography (CT) apparatus to produce remarkable images of structural detail. We had the pleasure of showing some of these images to Rachel Wood, the fossil sponge expert, at Edinburgh University and she has generously agreed to be our adviser on this ongoing project.

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Morphological and trophic distinction in the dentitions of two early alcelaphine bovids from Langebaanweg (genus *Damalacra*)

J.S. Brink[1] & D.D. Stynder[2]
[1]*Florisbad Quaternary Research, National Museum, P.O. Box 266, Bloemfontein, 9300 South Africa*
E-mail: jbrink@nasmus.co.za
[2]*Natural History Department: Cenozoic Studies, Iziko South African Museum, P.O. Box 61, Cape Town, 8000 South Africa*
E-mail: dstynder@iziko.org.za

The early Pliocene fossil bovids from Langebaanweg are of interest, as they represent among the earliest well-defined members of modern tribes, such as Reduncini, Bovini and Alcelaphini (Gentry 1980; Vrba 1997). In these fossils typical tribal morphology appears to be in an early stage of evolution, which on the one hand hinders diagnosis, but on the other hand offers a unique opportunity to investigate ancestral morphological states and adaptations. We focus here on the two alcelaphine species from Langebaanweg, *Damalacra neanica* and *D. acalla.* They were of the size of the blesbok, *Damaliscus pygargus,* but their skulls and dental morphologies are underived, representing an early stage in the appearance of distinctive alcelaphine characteristics (Gentry 1980). The dentitions of the two species a very similar and difficult to distinguish, especially when dealing with individual teeth (Gentry 1980). The aim of this study was to define the morphological characters that differentiate the dentitions of the two species and to use this distinction as the basis for assessing their trophic niches.

The Alcelaphini and Caprini are thought to have evolved from an antilopine ancestry in the later Miocene (Gentry 2000). Pleistocene and modern alcelaphine species can be broadly classified into two morphological groupings; those with antilopine body proportions, such as hartebeest, blesbok and tsessebe (genera *Alcelaphus* and *Damaliscus*) and those with more advanced caprine-like body proportions, such as wildebeest (genera *Connochaetes* and *Megalotragus*), reflecting the common ancestry of the

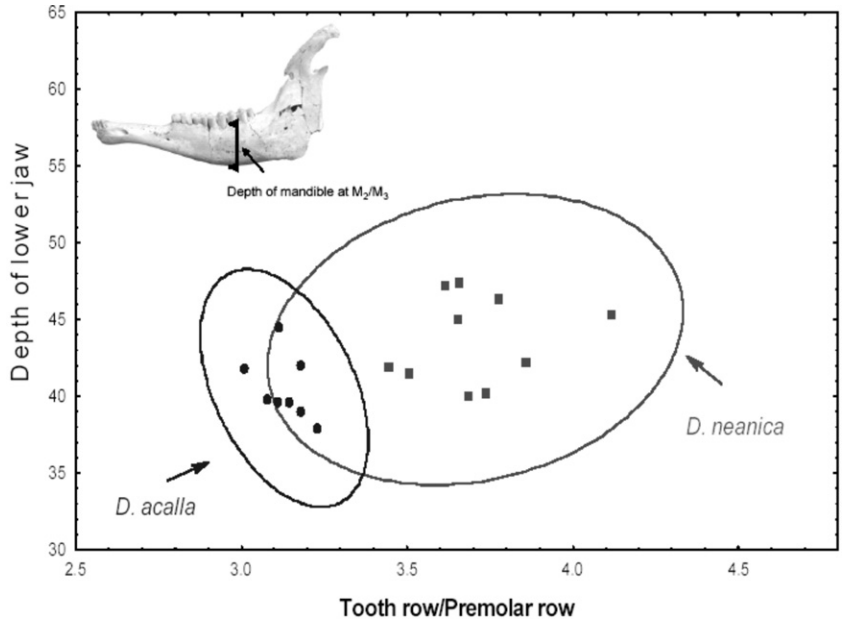

Figure 1. Plot of toothrow/premolar ratios against the depth of the lower jaw at the M_2–M_3 junction of *Damalcra neanica* and *D. acalla.*

Caprini and the Alcelaphini. This two-fold division is also evident in the dentitions of extant and Pleistocene Alcelaphini, where the genera *Damaliscus* and *Alcelaphus* tend to have less hypsodont tooth crowns, longer premolar rows and more complicated enamel folds in the molars. In spite of the underived nature of the alcelaphine dentitions from Langebaanweg, it was possible to classify the dentitions into two morphological groups. *D. neanica* has more derived and caprine-like dentitions, while the dentitions of *D. acalla* are more generalized, typical of what one might expect of an early alcelaphine. This is in accordance with Gentry's observation that the skulls of *D. acalla* are less derived than those of *D. neanica.* The dental characters distinguishing the two species of *Damalacra* can be summarized as follows:

The dentitions of *D. neanica* are generally slightly larger than those of *D. acalla* (Figs 1 & 2).

The premolar rows of *D. neanica* are shortened, the P_2 is absent and in the P_4 the tooth as a whole is distally shortened, giving it a very a caprine-like appearance (Fig. 1). In *D. acalla* the premolar row is longer, the P_2 is present and the P_4 is less squared off distally, more like in extant *Damaliscus* or *Alcelaphus.*

The lower jaws of *D. neanica* are deeper than in *D. acalla* (Fig. 1), suggesting greater hypsodonty. In both species there is a tendency for the metaconid-paraconid fusion to be incomplete, which is an underived character.

In comparison with *D. acalla,* the upper molars of *D. neanica* tend to have a more squared, blocky outline in occlusal view, they tend to expand more bucco-lingually towards the base of the crown, they have larger infundibulae, the styles are robust, ribs tend to be less well developed and basally on the M^3 the metastyle tends to flare distally. The general impression of the upper molars of

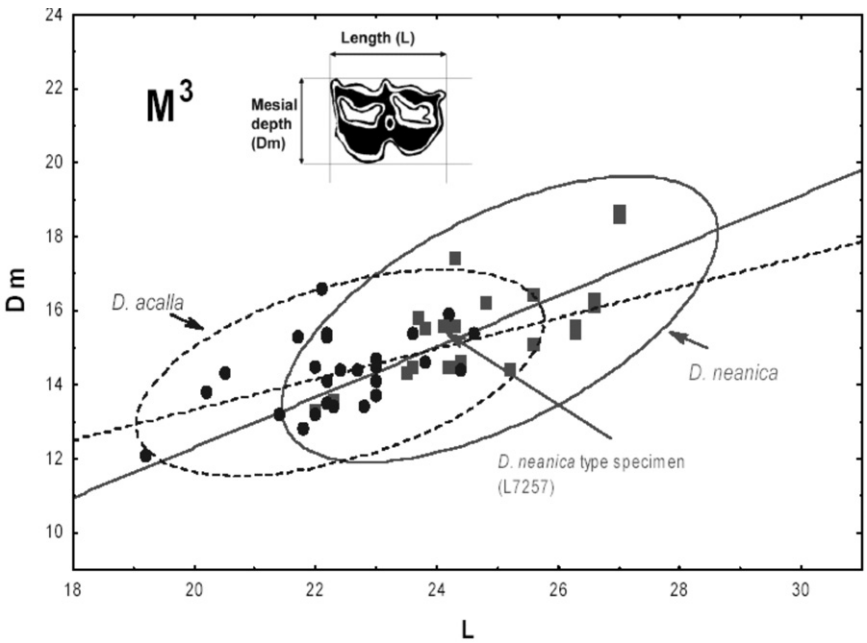

Figure 2. Plot of the occlusal length of the M3 against its bucco-lingual (mesial) depth of *Damalcra neanica* and *D. acalla.*

D. neanica, but in particular the last two characters mentioned, is caprine-like, whereas *D. acalla* has a less derived and more generalized alcelaphine appearance.

The dental characteristics of the two species of *Damalacra* agree broadly with Gentry's assessment of the skull morphologies. It appears that *D. neanica* was more derived and caprine-like in its morphology than *D. acalla.* If mandibular depth may be taken as a proxy for hypsodonty, then it appears that *D. acalla* (37.9–44.5 mm) is only marginal less hypsodont than *D. neanica* (40.0–47.4 mm) (Fig. 1), while both are very similar to the extant blesbok, *D. pygargus* (38.9–43.9 mm). This is somewhat unexpected, given the partly fused state of the metaconid and paraconid of the P_4, and suggests the need to test hypsodonty further by means of direct measurements on unworn M_3s.

If the mandibular depth data reflect hypsodonty then one would expect the trophic niches of both species of *Damalacra* to have tended towards grazing, as in the case of the blesbok. However, a mesowear analysis of the upper molars of *Damalacra* spp. suggests that this was not the case. *D. acalla* clusters with the sample of known mixed feeders and is closest to the bushbuck (*T. scriptus*) in mesowear pattern. *D. neanica,* on the other hand, clusters with the sample of known browsers and is closest to the mule deer (*O. hemionus*) in mesowear pattern. Unlike modern alcelaphines then, grass appears to have been a less important component in the diets of these two early alcelaphine species. The mesowear results are in good agreement with a microwear study of an undifferentiated sample of *Damalacra* teeth (Ungar *et al.* 2007), which suggested feeding niches ranging from browsers to mixed feeders. The apparent lack of agreement between the morphological analysis and the mesowear and microwear results is of interest and will be the focus of further research.

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Some factors leading to the good preservation of trilobite fossils within nodules of the lower Bokkeveld, Steytlerville district, Eastern Cape

C. Browning

Department of Earth Science, Nelson Mandela Metropolitan University, P.O. Box 77000, Port Elizabeth, 6031 South Africa

E-mail: browning.claire@gmail.com

Introduction

Invertebrate fossils and fossiliferous nodules within the Bokkeveld Group (Cape Supergroup) were documented before the turn of last century, although their discovery is likely to have preceded this date considerably (Theron 1972). In general the preservation of fossils within the Bokkeveld is considered good.

Some nodules especially have been known to contain very well-preserved invertebrate fossils (Theron 1972; Oosthuizen 1984), many of which are described as type specimens. Preservation is usually in the form of impressions or hollow moulds with actual fossil material rarely preserved (Oosthuizen 1984). Fresh fossil samples often display pyritic encrustations (Theron 1999). However, very little attention has been paid to the nodular structures themselves and to the possible reasons for better preservation of fossils within them compared to within the surrounding shales. The following short note aims to highlight some macro-, micro-structural and mineralogical differences between trilobite material within shales and nodules. The lower Bokkeveld shales were deposited by prograding deltas bordering an epeiric sea at the margin of a shallow Devonian cratonic basin (Broquet 1992; Theron & Johnson 1991). These lithologies were subjected to advanced stages of diagenesis grading into low-grade metamorphism (de Swardt & Rowsell 1974). Nodular structures within them are considered to be early diagenetic in origin (Theron 1972).

Materials and methods

Some limitations of this study should be noted from the outset. In the absence of equipment needed for detailed chemical and isotope analysis, it was decided to adopt a different approach to nodule examination. Nodules were collected from the Gydo Formation within the Ceres Subgroup at various localities in the Cockscomb/Steytlerville area. Where possible, nodules were collected *in situ* and their GPS locations were recorded. Limited chemical analysis in the form of XRD (XRay diffraction) was carried out on both nodules and shale. However, the majority of the work entailed petrographic analysis of thin sections together with careful observations and photography of macrostructural features and field observations.

Results

Macro-structure

The preferential weathering of nodules indicates that they are more resistant than surrounding shales. Nodular cross-sections usually reveal a series of colouration zones which mimic their roughly circular to elliptical shape. The colouration of these zones varies from burnt orange to deep purple-maroon (Fig. 1). Fossil material within nodules varies but is usually dark grey in colour (Fig. 2). Fossil material within shales also varies but is typically burnt orange in colour and often associated with the growth of fine mica crystals.

Nodules contain a higher percentage of quartz, while the surrounding shale typically contains a higher mica percentage (Table 1). Feldspar is present within the shale. It was, however, not found within nodules (at least not within the detectable limit of the XRD equipment.

Petrography

The minerals replacing trilobite carapaces in shales and nodules differs. Within nodules the typical replacement

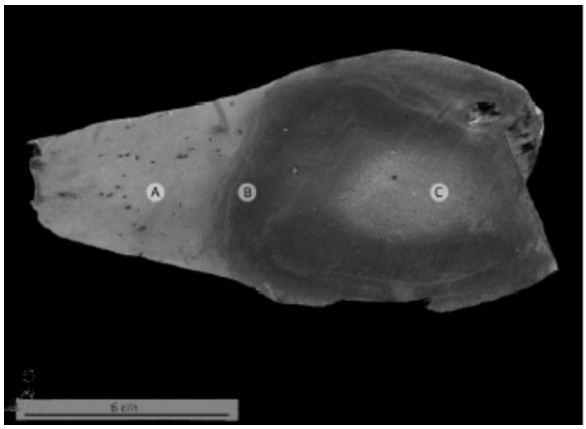

Figure 1. Macro-photograph of a sliced surface of a nodule and surrounding shale. Colouration varies from light grey in surrounding shale (A) through orange at the margin (B) to dark grey/purple in the centre.

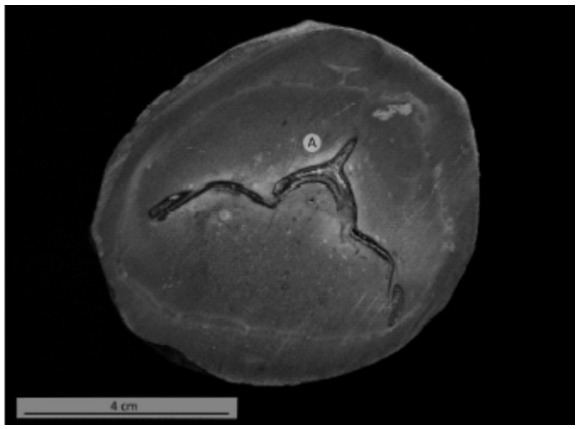

Figure 2. Macro-photograph of a sliced surface of a nodule containing a trilobite carapace (A).

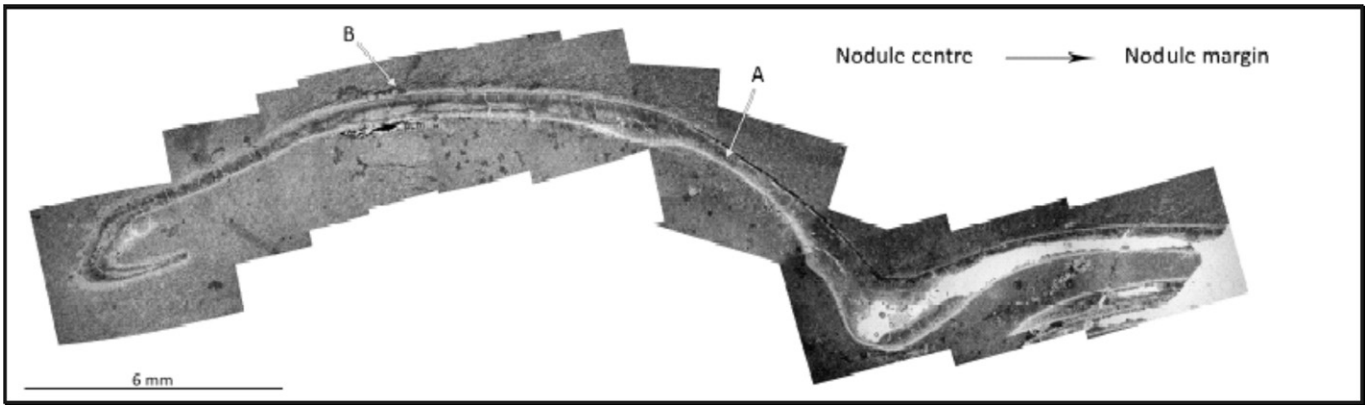

Figure 3. Photomicrograph composite composed of various images of a trilobite carapace within a nodule. Quartz is the dominant replacement mineral (A). The images were taken under PPL .Note the excellent preservation of the carapace and the formation of cleavage near the upper surface of the fossil (B).

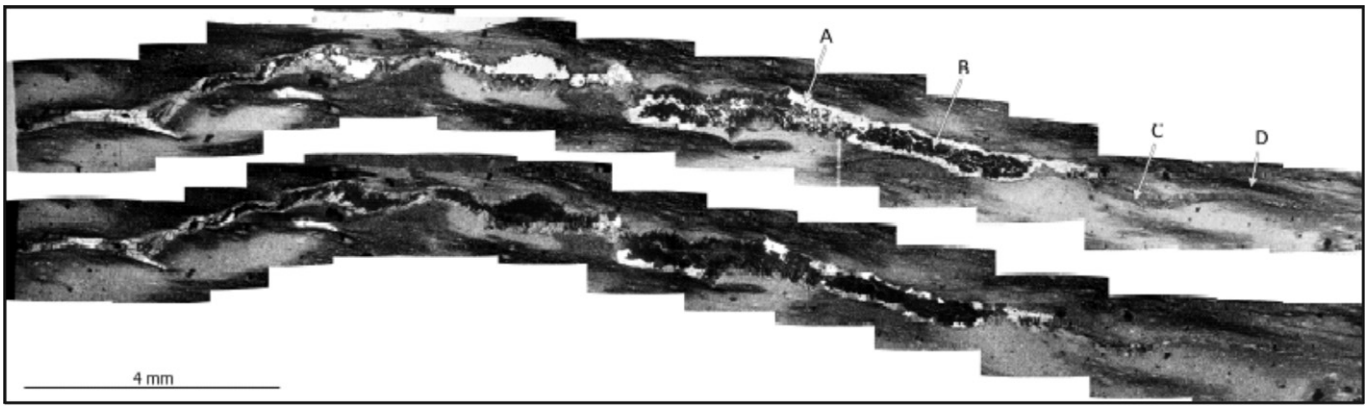

Figure 4. Photo-composite image composed of photomicrographs taken of a trilobite carapace within shale. The upper composite was taken under PPL while the lower one was taken under CPL. The general shape of the carapace can still be seen although deformation is evident. Replacement minerals include quartz (A), hematite (B) and biotite (C). Minor amounts of other white micas are found in association with biotite. Biotite seems to develop preferentially at the thinner margins of the fossil. Hematite is mostly found in the central portions of the carapace and generally shows a close association with quartz. Cleavage can clearly be seen in the shale matrix surrounding the carapace (D). Cleavage intensity varies as do colouration zones within the shale.

texture of aragonite by quartz is seen and quartz as well as some minor opaque minerals are the only replacement minerals (Fig. 3). Within shales the trilobite carapace material was composed to equal proportions of quartz, hematite and biotite (Fig. 4). Opaque minerals were also present as minor constituents. Hematite was found in the central portions of the carapace while quartz and biotite often replaced the thinner and outer portions of the

Table 1. XRD results showing the percentage of dominant minerals found within shales and nodules

	Nodule	Shale
Quartz %	62.6	28.31
Chlorite %	25.68	36.–7
Sericite %	11.72	30.29
Feldspar %	–	5.33

carapace. Deformation of fossil material is higher at the nodular margin than the centre.

Discussion

There are clearly differences in the nature of minerals which replace fossil material in the shales and within nodules. The colour zoning within nodules is probably as result of varying levels of oxidation of opaque and iron minerals within the nodule matrix. The fact that these minerals are often found in association with fossiliferous material supports this idea. It appears that the presence of quartz within both the nodule structure and as a replacement of the trilobite carapace within the nodule makes these structures more resistant to weathering than surrounding shales. These results could be clarified by the investigation of a wider variety of faunal groups as well as a more extensive chemical analysis of a range of nodules.

Conclusion

Although preservation of invertebrate fossiliferous material is better within nodular structures, material within the shales of the Bokkeveld are not as deformed and poorly preserved as would be expected for lithologies subjected to known levels of diagenesis and metamorphism. The reason for this appears to be mineralogical, with variations in both replacement minerals and overall nodule composition being the main contributing factors. These findings need to be clarified with more detailed analysis of general as well as isotope chemistry.

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Bone microstructure studies of southern African dinosaurs

Anusuya Chinsamy-Turan

Zoology Department, University of Cape Town, Private Bag, Rondebosch, 7700 South Africa

E-mail: zoo-act@uct.ac.za

During life the bones of vertebrates record various aspects of the individual's life history. Soon after death, organic components of vertebrates decompose, but it is well documented that even after millions of years of fossilization, the microscopic structure of bone generally remains intact. Analyses of the texture and organization of the microstructure of fossilized bone, provides unparalleled insight into various aspects of the biology of extinct animals, particularly with regard to growth and development. This analysis provides a review of previous studies of the bone microstructure (osteohistology) of various Southern African dinosaurs.

Early studies of Southern African dinosaurs such as, *Euskelosaurus, Massospondylus carinatus* and *Syntarsus* (now referred to as *Megapnosaurus*) formed part of broader studies aimed at the documentation of types of bone tissue (histology) present among nonavian dinosaurs. Subsequently more focused and comprehensive studies of Southern African dinosaurs were conducted firstly on the Early Jurassic theropod, *Syntarsus* (*Megapnosaurus*) from Zimbabwe and South Africa, and later on the contemporaneous prosauropod, *Massospondylus* from South Africa. These landmark studies provided an analysis of the histological changes in bone microstructure during ontogeny and led to the deduction of the first growth curves for dinosaurs using bone microstructure.

More recent histological analyses were conducted on the coelurosaur, *Nqwebasaurus thwazi* from the Early Cretaceous, Kirkwood Formation of the Algoa Basin. The osteohistology of juvenile basal iguanodontians from the same deposits have also been analysed and new work is currently expanding our understanding of their biology. In addition, current studies, involves the assessment of the bone microstructure of a new prosauropod dinosaur from the Early Jurassic of South Africa.

Studies of the bone microstructure of southern African dinosaurs have made a significant contribution to understanding various aspects of the biology of the Dinosauria

Juan Carlos Cisneros, Paula Camboim Dentzien-Dias, Ana Emilia Quezado Figueiredo & Alexandre Liparini

Departamento de Paleontologia e Estratigrafia, Universidade Federal do Rio Grande do Sul, Porto Alegre, founded by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Brazil

E-mail: cisneros.jc@gmail.com

Introduction

The Rio do Rasto Formation of the Paraná Basin outcrops in the southern states of Brazil. This formation is currently interpreted as a sequence of fluvio-lacustrine deposits (Menezes 2000) and has produced continental vertebrates of Middle to Late Permian age, including paleoniscoid fishes, sharks, lungfishes, temnospondyles, dicynodonts, dinocephalians and pareiasaurids (Würdig-Maciel 1975; Barberena *et al.* 1985; Richter & Langer 1998; Langer 2000; Dias & Barberena 2001; Malabarba *et al.* 2003; Cisneros *et al.* 2005). In southern Brazil, fossil outcrops typically consist of very small exposures, usually human-made, isolated by dense vegetation. Stratigraphic correlations, even among sites that are separated by only a few hundreds of metres, are often impracticable. Here we present a preliminary report on new fossil finds at the Rio do Rasto Formation, including new fossil sites, that resulted from recent prospecting in the state of Rio Grande do Sul.

Figure 1. Map of the state of Rio Grande do Sul, in southern Brazil. 1, Posto Queimado site; 2, Aceguá site.

Aceguá

The municipality of Aceguá (Fig. 1) has produced two important sites, the type localities of the pareiasaurid *Provelosaurus americanus* and the temnospondyle *Bageherpeton longignathus* (Araújo 1995; Dias & Barberena 2001). The type specimen of *Provelosaurus americanus* was recovered from an exposure along RS 153 highway, less than three kilometres northeast from the border between Brazil and Uruguay. Fossils have not been recovered from this site for more than two decades, but during fieldwork in 2008 a new skull (Fig. 2A) and a scapula-coracoid of *Provelosaurus* were collected. In addition, a new fossil outcrop was discovered at the Farm Santo Antônio, in Aceguá, six kilometres east from the type locality of *Provelosaurus americanus.* The new site is characterized by a sequence of reddish siltstone interbedded by lenses of white fine-grained sandstones and intraformational conglomerate. Cranial (Fig. 2B,C) and postcranial elements of *Provelosaurus* were recovered, including previously unknown elements for this genus such as the first mandible, cervical vertebrae and interclavicle. Spiral coprolites referable to chondrichthyans, containing small bones and scales, were also recovered. Fossil gymnosperm wood was located *in situ* and a horsetail (Sphenopsida) was found in association with *Provelosaurus* bones.

São Gabriel (Posto Queimado)

A site in the municipality of São Gabriel, within the Posto Queimado geological sheet, has produced remains of lungfishes, sharks, temnospondyles, dinocephalians and the pareiasaurid *Provelosaurus americanus* (Langer 2000; Malabarba *et al.* 2003; Cisneros *et al.* 2005). A new fossil locality was located 7 km to the east, at the Farm Boqueirão. The outcrop is bent towards the southeast, being characterized by a sequence of siltstones interbedded by lenses of intraformational conglomerates and packages of sandstones. Fragmentary fossil vertebrates occur in high concentration within these conglomerates (Fig. 3). Preliminary investigation has allowed to recognize several labyrinthodont and shark teeth, paleoniscoid scales, and chondrichthyan spiral coprolites.

Discussion

The fossil content of the Rio do Rasto Formation in the State of Rio Grande do Sul at present supports the model

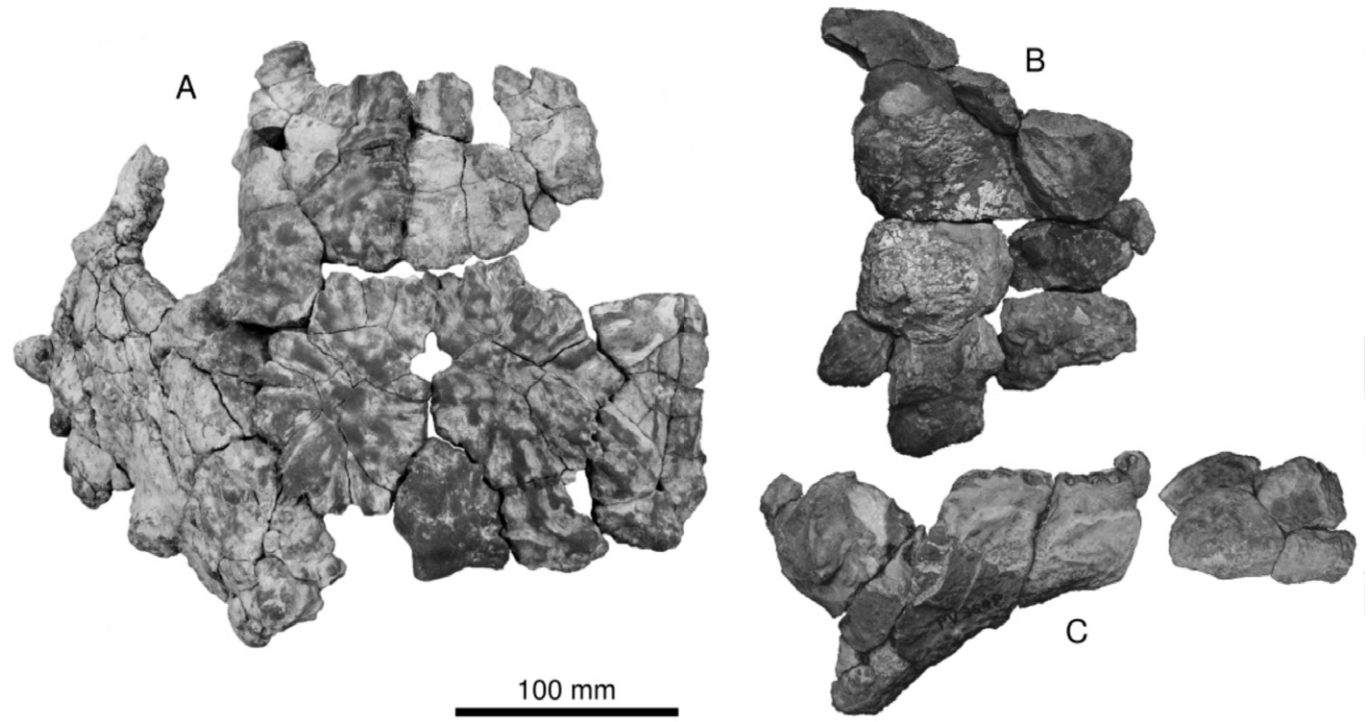

Figure 2. New specimens of the pareiasaurid *Provelosaurus americanus* from Aceguá. **A**, skull in dorsal view, from the type locality; **B**, right posterior portion of skull, in right lateral view, from Santo Antônio Farm; **C**, right mandible in lateral view, from Santo Antônio Farm.

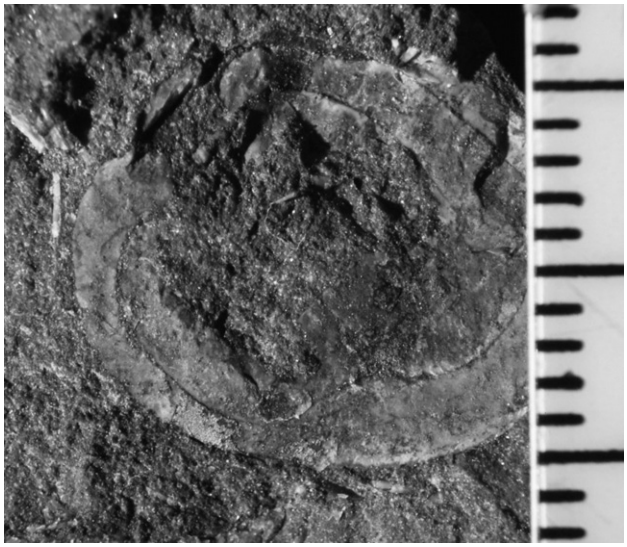

Figure 3. Chondrichthyan spiral coprolite in transverse section, within conglomerate, from Boqueirão Farm, Posto Queimado.

of a fluvio-lacustrine origin for the sedimentation of this stratigraphic unit. The local faunas of Aceguá and Posto Queimado share the presence of the pareiasaurid reptile *Provelosaurus* and are probably of Guadalupian (Middle Permian) age, due to the record of dinocephalians at Posto Queimado (Cisneros *et al.* 2005). Pareiasaurids and dinocephalians are known to co-occur elsewhere only in the *Tapinocephalus* Assemblage Zone of South Africa (Rubidge 1995). This biostratigraphic correlation, however, conflicts with preliminary data from radiometric dating of a bentonite layer from a *Provelosaurus* site in Aceguá (Rocha-Campos *et al.* 2006), which yielded an age of 275.1 ± Ma (Artinskian-Kungurian boundary, Cisuralian). This age is below Olson's Gap (Lucas 2004) and at least ten million years older than any known global record of a pareiasaurid.

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What's new in the world of Devonian tetrapods?

Jennifer A. Clack

University Museum of Zoology, Cambridge, Downing St., Cambridge CB2 3EJ, U.K.

E-mail: j.a.clack@zoo.cam.ac.uk

The past 20 years has seen an exponential increase in the number of known Devonian tetrapod taxa, and a corresponding increase in geographical and environmental ranges that they are know to have inhabited. Recent finds of Late Devonian tetrapod-like fish and tetrapods with limbs are serving to close the morphological gap between finned and limbed tetrapodomorphs. Reviews of the climate during the mid and Late Devonian have suggested scenarios for the emergence of tetrapods, and new techniques are allowing fresh analyses and conclusions to be drawn from earlier collected material.

To date 11 genera of Devonian tetrapod have been named, with other material still awaiting description or publication. As recently as 1993 only three genera were known, two from Greenland and one from Russia. A record from Australia of a fourth remained controversial, though acknowledged tetrapod trackways were known. Since then tetrapods have been discovered in North America, Scotland, Latvia, China and Belgium, and the Australian record has been confirmed. Further finds from other Russian and other localities have also been recorded (Clack 2005, 2006). Thus they are known to have occurred in most of the major continental masses, including Gondwana, by the end of the Devonian. It is therefore not impossible that they will be discovered in other regions including southern Africa and South America. Southern Africa has already yielded an extensive fauna of Late Devonian fishes, some of which, such as a *Soderberghia*-like lungfish, accompanied the tetrapods in most of the other known tetrapod-yielding localities.

The environments that the tetrapods inhabited range from fully freshwater, to marginal marine, encompassing estuarine and lagoonal sites. The implication here is that the earliest tetrapods were euryhaline and could move around continents along their margins or through shallow interconnecting seas. The localities in which the tetrapod-like fish, *Elpistostege, Tiktaalik* and *Panderichthys* have been found are of this estuarine type (Daeschler *et al.* 2006), as well as that of the most primitive tetrapod with limbs, *Ventastega* (Ahlberg *et al.* 2008). The environment represented by the Late Devonian deposits around Grahamstown is also marginal marine/ estuarine (Gess *et al.* 2006). It has been considered that these localities may have been too far south and near to existing glaciated sites thus too cold to have suited tetrapods, but this is not certain.

During the mid- to Late-Devonian, the Earth apparently underwent a climate crisis in which oxgyen level dropped precipitously from over 25% to about 13%, much lower than today's (21%). At the same time, temperatures and carbon dioxide levels were both considerably higher than today. During this period, the area covered by terrestrial plants as well as their size and diversity also increased, resulting in increased organic matter content in the water. Its decay caused widespread anoxia in both marine and riverine systems, at a time of exceptionally low oxygen content in the atmosphere. This was the time during which the tetrapod stem group also diversified, and it is a notable fact that modifications to breathing, support and locomotory apparatuses took place also during this time. It may be that the climatic conditions of the time directly or indirectly affected or effected the emergence of tetrapods from the water (Clack 2007). Recently discovered or newly described taxa of tetrapod-like fish (*Panderichthys, Tiktaalik*) are beginning to show the sequence of character acquistion in the origin of limbed tetrapods (Shubin *et al.* 2004, 2006).

Recently recognized as the most primitive tetrapod known to have had limbs is *Ventastega.* Its skull bears close comparison with that of the tetrapod-like fish *Tiktaalik* from the Frasnian of Canada, especially in the posterior region, where both exhibit an enlarged spiracular notch. Although *Ventastega* is not known from limb material, its girdles are sufficiently similar to those of the better-known *Acanthostega* to infer the presence of limbs with digits. Its occurrence in Laurussia is consistent with a Laurussian origin for limbed tetrapods, although it is among the latest (late Famennian) of the known limbed forms (Ahlberg *et al.* 2008).

The iconic genus *Ichthyostega* has been reassessed in recent years. Three valid species are now recognized, occurring in separate geological formations in the same area in East Greenland (Blom 2005). Its ear region has been interpreted as adapted for underwater audition (Clack *et al.* 2003), whereas its postcranial skeleton shows a mixture of aquatic (paddle-like hind limb, finned tail) with terrestrial (robust shoulder and forelimb, differentiated axial skeleton with broad thoracic ribs) adaptations (Ahlberg *et al.* 2005).

Much of the latter information has been gathered by the use of the relatively new technique of computer-assisted tomography (CT scanning), which is allowing unprecedented access to previously intractable specimens (Callier, Clack and Ahlberg, work in progress). Application of such techniques at finer and finer resolutions will allow us to pose and answer questions that would have been considered impossible by earlier workers, such as the position and more importantly direction of muscle attachments.

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Stratigraphic correlation between the Karoo Supergroup and the Gondwana sequence of India

Doug Cole

Council for Geoscience, Bellville

E-mail: dcole@geoscience.org.za

The retroarc foreland Karoo Basin contains up to 12 km of sedimentary strata in the foredeep overlaid by at least 1.4 km of basaltic lava. The oldest strata are latest Carboniferous (312 Ma) and the lava Early Jurassic (184 Ma). In India, five basin belts are present, which are filled with up to 6 km of sedimentary strata overlaid by to 3 km of basaltic lava (Fig. 1). The strata are Permian (300 Ma) to middle Cretaceous (100 Ma) in age and the lavas (Deccan Traps) earliest Cenozoic (65 Ma). Only the correlation up to latest Jurassic (160 Ma) is described here.

Correlation is based upon Gondwanide-wide marine flooding events and other events such as the P-T extinction and widespread hiata. Seven sequences or time-slots have been recognized in South Africa and India (Fig. 2). Sequence 1 has a basal unconformable boundary and an upper conformable boundary at 290 Ma. The strata are glaciogenic and form the Dwyka Group in South Africa starting at 312 Ma and the Talchir Formation in India starting at 300 Ma. The upper boundary coincides with final rapid melting of ice sheets and an extensive marine transgression. Sequence 2 contains marine shale and in the northeast Karoo Basin, fluvio-deltaic sandstone of the lower Ecca Group in South Africa and wave-dominated deltaic sandstone and shale overlain by fluvio-deltaic sandstone of the Barakar Formation in India. The upper conformable boundary marks the start of another Gondwanide-wide marine flooding event at 271 Ma (Fig. 2). Sequence 3 begins with marine shale in both countries overlaid by a major regressive succession. Submarine fan sandstone is present in the Karoo foredeep. This is followed by a transition into deltaic shale and sandstone. These strata form the upper Ecca Group in South Africa and various formations in India (see Fig. 2). In South Africa, the regressive succession continued up into terrestrial mudstone and sandstone of the lower Beaufort Group. The upper conformable to disconformable

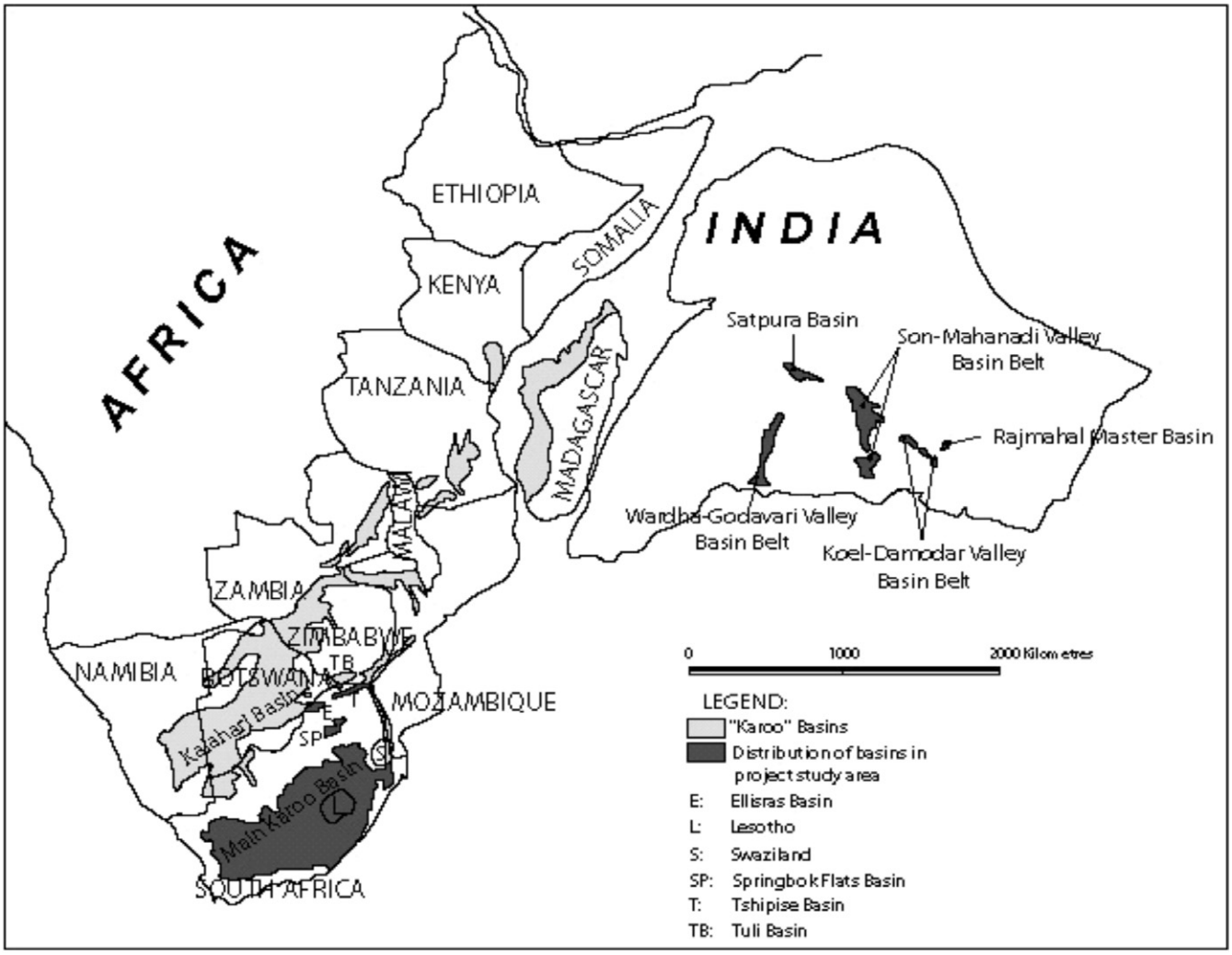

Figure 1. Reconstruction of central Gondwanaland during Permo-Triassic times showing distribution of basins investigated in South Africa and India.

boundary is placed at the Permian/Triassic contact (251 Ma), which is recognized by the appearance of the fossil mammal-like reptile *Lystrosaurus* and in most basins, the influx of prominent fluvial sandstone units (Fig. 2). Sequence 4 is characterized by terrestrial sandstone and predominant red mudstone indicative of semi-arid conditions. Fluvial sandstone is abundant in the lowermost part, but gives way to floodplain mudstone. The strata form the upper Beaufort Group in South Africa and various formations in India (see Fig. 2). Deposition ceased as a result of epeirogenic uplift and was followed by a widespread lacuna (Ladinian vacuity). The upper disconformable to unconformable boundary occurs at 228 Ma and marks the start of renewed accommodation space and deposition of Sequence 5 sediments (Fig. 2). Sequence 5 begins with fluvial sandstone that gives way to floodplain muds uplift and erosion. The strata form the lower Stormberg Group in South Afritone and minor fluvial sandstone. Several short hiata are present as a result of episodic tectonicca and the Supra-Panchet Formation in India. The upper conformable to disconformable boundary is placed at the base of a widespread hiatus (206 Ma), which was caused by epeirogenic uplift related to final coalescence of Pangea. In South Africa, it marks the break between the upper and lower Elliot Formation and a change in basin development from compressional tectonic processes to extensional tectonic processes (Fig. 2). In contrast, Indian basin development was entirely controlled by extensional tectonic processes. Sequence 6 was mostly a period of non-deposition in India apart from some terrestrial sandstone and mudstone and lacustrine shale of the Dhamarum Formation in the Wardha-Godavari Valley Basin (Fig. 1). In South Africa, floodplain mudstone and minor fluvial sandstone of the upper Elliot Formation were deposited after a short (6 million years) hiatus and these grade up into desert sandstone and minor mudstone of the Clarens Formation under an increasingly more arid climate (Fig. 2). The upper conformable boundary is drawn at the base of the extrusive lavas of the Drakensberg Group and the Letaba Formation dated at 184 Ma (Fig. 2). Sequence 7 is represented by basaltic lavas in South Africa, which terminated developments in all the basins at about 180 Ma. In India, few deposits of Sequence 7 are now preserved, as a result of subsequent erosion (Fig. 2), an exception being terrestrial sandstone and mudstone and lacustrine shale of the Kota Formation in the Wardha-Godavari Valley Basin (Fig. 1). The upper unconformable boundary is placed at 160 Ma, which marks the start of the separation between East and West Gondwanaland.

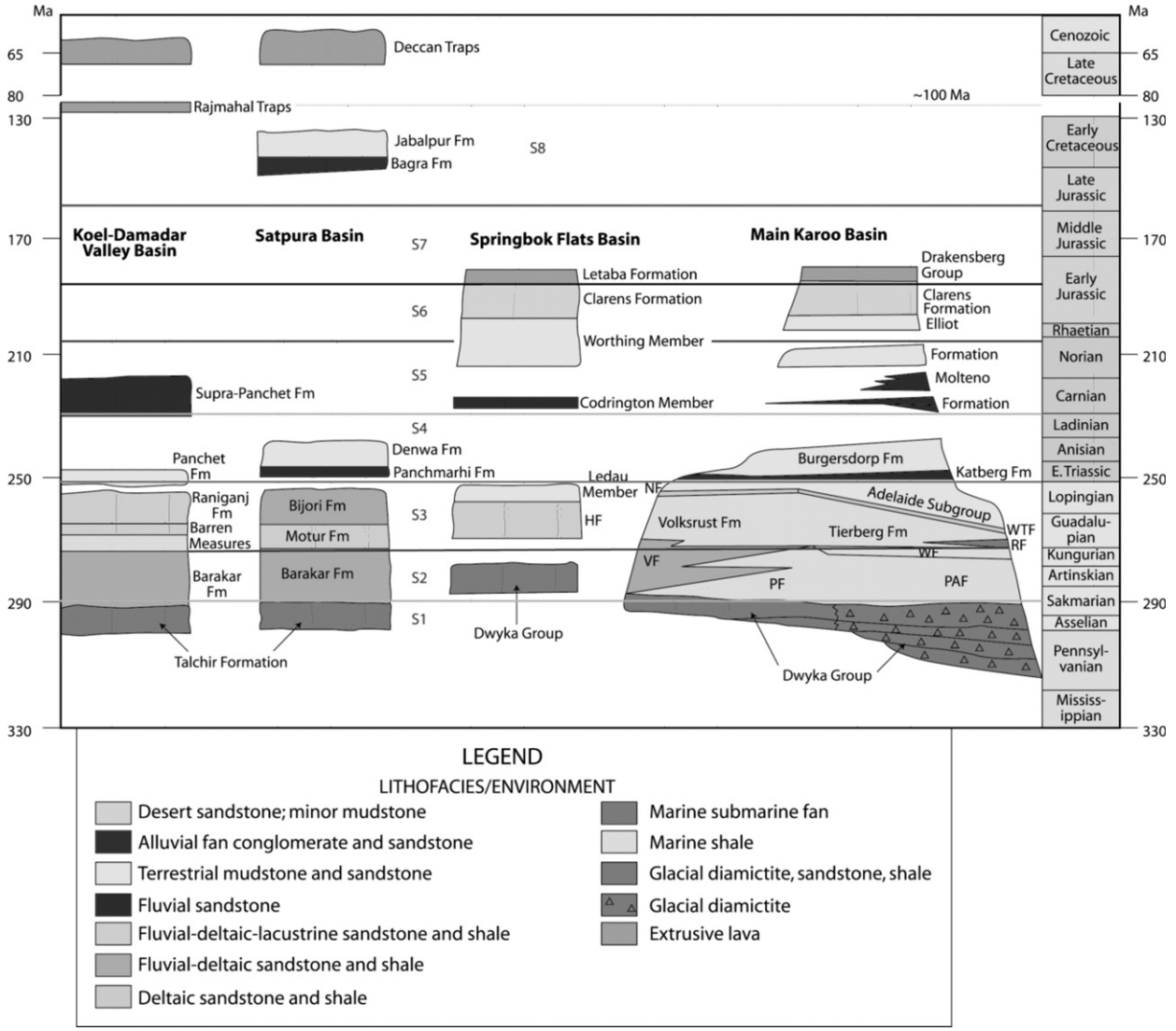

Figure 2. Time–space diagram of central Gondwanaland showing lithofacies/environment of stratigraphic units and their correlation in South Africa and India. S1 to S8 refer to the delineated stratigraphic sequences or time-slots.

Modern human origins and the Cave of Hearths Bed 3 mandible

Darren Curnoe

Human and Primate Origins Program, School of Biological, Earth and Environmental Sciences, Faculty of Science, University of New South Wales, Sydney, NSW 2052, Australia
E-mail: d.curnoe@unsw.edu.au

Introduction

The evolution of modern humans remains among the most important topics of hominin palaeontology. Most palaeoanthropologists consider Africa to have been the centre of origin for both *Homo sapiens* and later 'anatomically modern' members of this taxon (for a review of competing models see Curnoe 2007). Opinions differ about the details of fossil taxonomy and aspects of evolutionary history: ranging from a single, long-lived, slowly evolving and widely dispersed species (*H. sapiens*) containing three diachronic stages in the process of 'modernisation' (e.g. Bräuer 2008), through to five or six temporally shallow, rapidly appearing (speciating) and geographically narrowly distributed species (see reviews by Rightmire 1998; Stringer 2002; Bräuer 2008). Despite this diversity of opinions, the predominant view is that the human species began with the *H. sapiens-H. neanderthalensis* cladogenetic event (genetically clocked to ~370 thousand years ago (or ka): Noonan *et al.* 2006), while anatomically modern humans appeared in the fossil record about 170 ka later (i.e. at ~200 ka: see Stringer 2002).

The fossil-bearing deposits of southern Africa have provided some of the earliest examples of *H. sapiens* under a narrow definition of the species (see Stringer 2002). For example, the Florisbad cranium dated to around 260 ka is argued to be an example of the widely distributed although exclusively African early *H. sapiens.* Other examples include the Laetoli Hominid 18 fossil from Tanzania, Ileret (KNM-ER 3884) cranium from Kenya, Singa specimen from Sudan and Jebel Irhoud remains from Morocco. All of these fossils are thought to be from the period ~300 ka to ~170 ka (Bräuer 2008). Under the single-species model they all form part of the late archaic *H. sapiens* morphological-temporal grade (Bräuer 2008).

Less than a decade ago southern Africa was argued to provide some of the earliest evidence for anatomically modern humans at around 100 ka (Stringer 2002). Now, however, attention has shifted to East Africa where early

modern human fossils are now known to be almost 100 ka older than those in southern Africa. Fossils from the localities of Omo-Kibish and Herto in Ethiopia, Singa in Sudan and Mumba in Tanzania date to between ≤195 ka and ~110–130 ka (see a review in Trinkaus 2005). Thus, current dating evidence suggests that the appearance of early modern humans in southern Africa (i.e. Klasies River Mouth LBS ~100–120 ka: Trinkaus 2005) is broadly coincident with their earliest dispersal out of Africa and may form part of a broad exodus from East Africa.

The present author recently examined the Cave of Hearths (CoH) Bed 3 mandible (Fig. 1) as part of a broad investigation into the origins of *H. sapiens.* Although the precise age of this specimen is unknown, on geological, faunal and archaeological grounds it is generally considered to be >200 ka and perhaps within the range of ~250–350 ka (Bräuer 2008). Until now, studies of this fossil have emphasized its primitive morphology. Thus, it has mostly been considered to sample the same group as the Kabwe and Saldanha fossils (i.e. archaic *H. sapiens, H. heidelbergensis* or *H. rhodesiensis*: see Tobias 1971; Rightmire 1998; McBrearty & Brooks 2000; Stringer 2002; Bräuer 2008). However, investigations by the present author indicate the presence of a mosaic morphology in this specimen, combining many anatomical features diagnostic of early modern humans with a small number of primitive features. In light of this, there is a need to reassess its taxonomy and to reconsider its possible relevance to reconstructing the emergence of modern humans.

In the discussions that follow, the CoH specimen is compared to mandibular remains from late *H. erectus* and early anatomically modern humans from Africa and West Asia. As there are no mandibles from African archaic hominins (*H. heidelbergensis/H. rhodesiensis*) apart from the CoH specimen, a comparison will also be made with some Middle Pleistocene (non-Neandertal) fossils/samples from Europe. Comparative metric data for African/West Asian early modern humans, the Mauer mandible, a European Middle Pleistocene (non-Neandertal) sample and a late *H. erectus* sample were taken from: McCown & Keith (1939), Tobias (1971), Vandermeersch (1981), Singer & Wymer (1982), Wood & Van Noten (1986), Bräuer & Mehlman (1988), Bermúdez de Castro & Nicolas (1995), and Grine (2000).

It should also be noted that Tobias (1971) described the developmental age of the CoH specimen as juvenile; although, he had doubts about this diagnosis. However, comparisons with modern human dental eruption sequences and molar enamel wear made by the present author actually indicate that the specimen is likely to have been at least a late adolescent (+18 years old) and more probably an adult (+25 years old) (Curnoe, unpublished).

Morphological comparison

Table 1 lists some major anatomical features of the CoH mandible according to their polarity. The vast majority represent the modern morphological condition. Its body is short and thin, most closely resembling modern humans. As Fig. 2A shows, the symphysis thickness value in the CoH specimen is very small (thin) and well below the mean value for late *H. erectus* (difference being statistically highly significant), well below the value for the Mauer mandible (type specimen for *H. heidelbergensis*) and below the mean value for early modern humans. Interestingly, symphysis thickness in the Mauer mandible and the mean for modern humans are both significantly smaller than the mean for late *H. erectus.* This underscores the value of this measurement for systematics. At the level of M_1 (Fig. 2B), the body of the CoH mandible is thin, its value being almost identical to the mean for modern humans. Although the CoH datum is much smaller than the Mauer specimen and the mean for late *H. erectus,* the difference between them is not statistically significant.

When viewed in lateral aspect, late *H. erectus* mandibles tend to maintain even body height anteroposteriorly so that their superior and inferior borders remain approximately parallel (Tobias 1971). However, the CoH body shows anteroposterior reduction in height (or tapering)

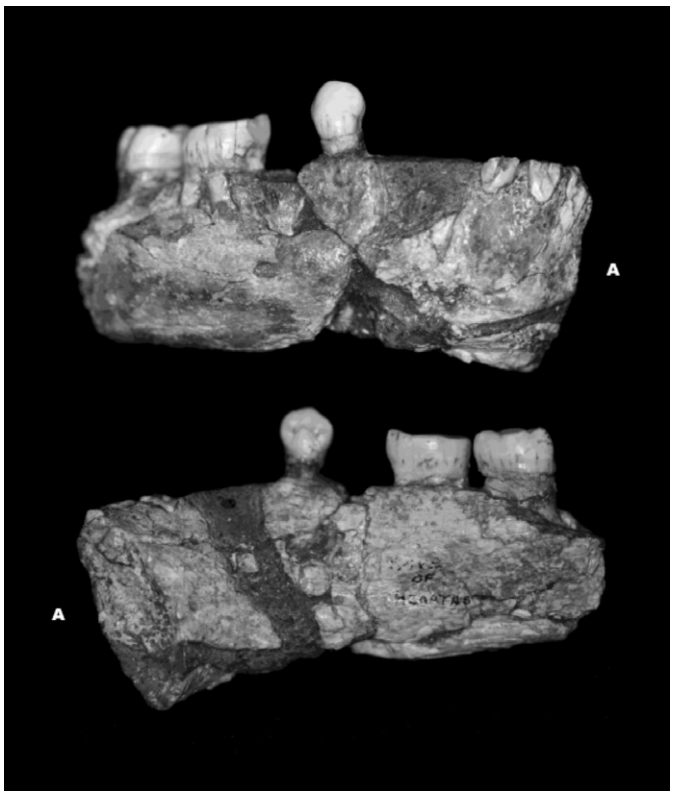

Figure 1. Cave of Hearths Bed 3 mandible in lateral (above) and medial (below) aspects (NB: 'A' denotes anterior).

Table 1. The mosaic morphology of the Cave of Hearths Bed 3 mandible.

Modern features
1. Short and thin body
2. Body tapers (reduces in height) anteroposteriorly
3. Body thickens anteroposteriorly (absolutely and relative to height)
4. Mental foramen located anteriorly (inferior to premolars)
5. Mental eminence (?true chin)
6. Molar crown size reduction ($M_1 \rightarrow M_2$)
7. M_1 crown area more than double P_3 crown
8. Molar crown size reduces anteroposteriorly
9. M_3 agenesis

Primitive features
1. Marked prognathism
2. Taurodont molars

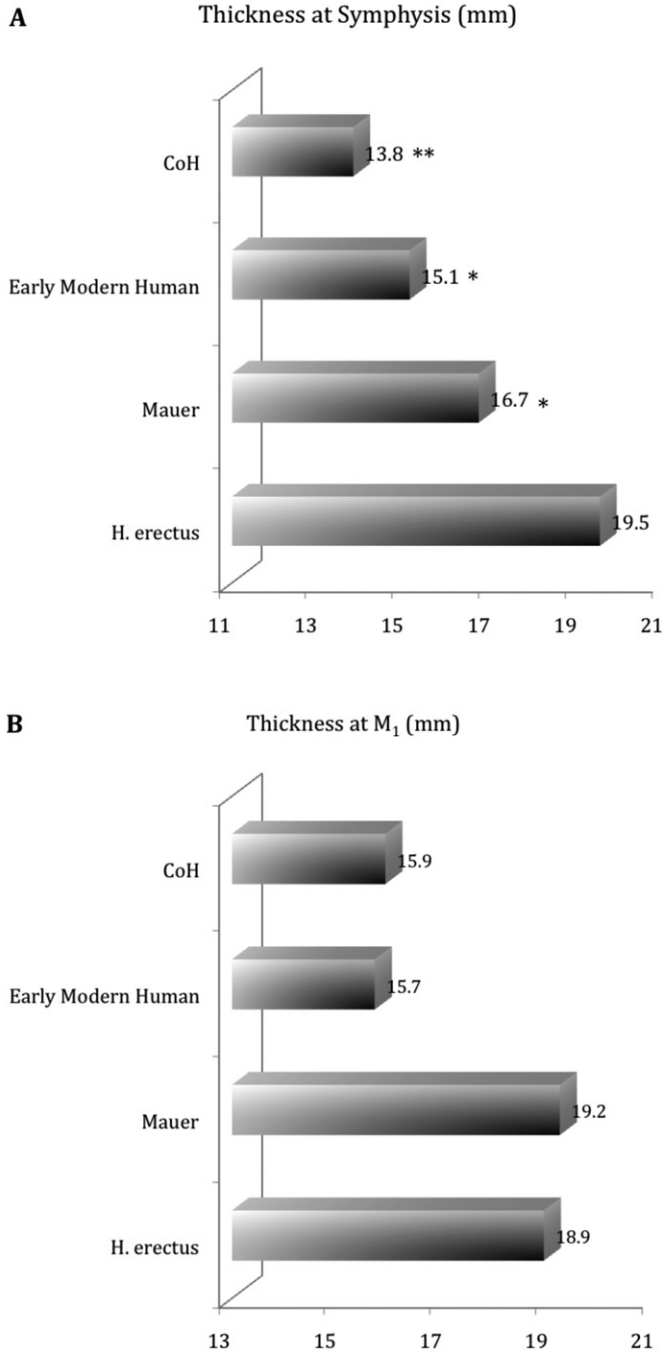

Figure 2. Comparison of mandibular body thickness. Asterisk denotes values as significantly different to the mean value of *H. erectus* using Student's *t*-test).

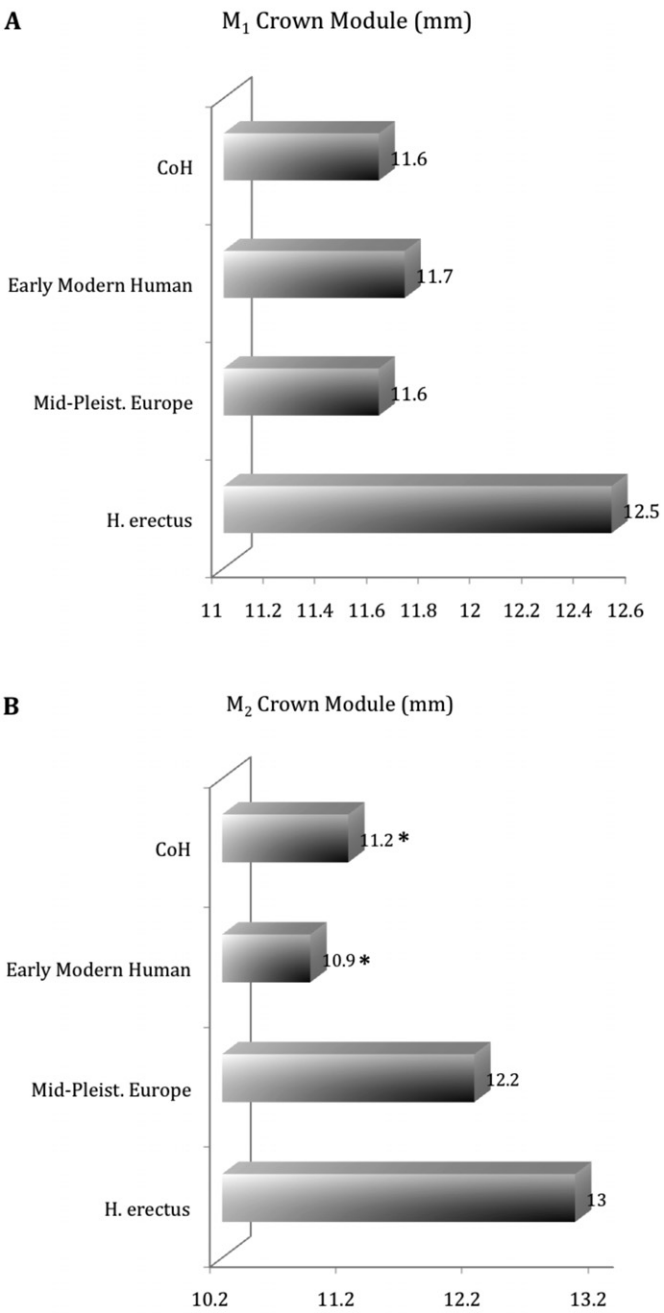

Figure 3. Comparison of molar crown size. Asterisk denotes values as significantly different to the mean value of H. erectus using Student's *t*-test).

the condition seen in early modern humans. Additionally, the body of the CoH specimen thickens anteroposteriorly, as seen in early modern humans, and contrasting with late *H. erectus,* in which it thins.

Another feature frequently cited as characteristic of anatomically modern humans is the anterior placement of the mental foramen. In early modern specimens, this foramen is located mostly inferior to the second premolar (P_4), but in archaic groups including late *H. erectus* and Neandertals it is mostly inferior to P_4/M_1 or M_1 (Lieberman 1995). In the CoH specimen, it is located inferior to P_4 (modern condition).

The presence of a chin is widely considered to be diagnostic of modern humans (e.g. Dobson & Trinkaus 2002; Trinkaus 2005, 2006). Criteria have been developed to distinguish 'true' chins from 'incipient' (developmentally non-homologous) chins (e.g. Lieberman 1995). According to Tobias (1971), the CoH mandible exhibits the components of a true chin (consistent with Lieberman's criteria). However, according to the approach of Dobson & Trinkaus (2002), the CoH chin would not be considered modern, as it lacks anterior projection in the median sagittal plane. Moreover, its very low symphysis angle (high prognathism), a primitive (*erectus*-like) feature, indicates the absence of a true chin.

The teeth of the CoH specimen are also very modern. Its molar crowns reduce in size anteroposteriorly ($M_1 \rightarrow M_2$), and its M_1 crown is more than double the size of its P_3

crown. Both features characterize early modern humans. Its third premolar (P_3) mesiodistal diameter (MD), buccolingual diameter (BL), crown module and crown area values lie outside of (below) the range of late *H. erectus* and sit close to the mean for early modern humans. Its M_1 MD, BL, crown module, crown area and shape index values are identical to or virtually indistinguishable from mean values for early modern humans. Thus, like modern humans, the CoH M_1 is small and characterized by BL narrowing. The CoH M_2 MD, BL, crown module and crown area values lie outside of (below) the range of late *H. erectus* and well within the range of early modern humans. Thus, its M_2 is much reduced in size compared to late *H. erectus* (dental reduction = modern).

As Fig. 3A shows, the CoH M_1 crown module (MD+BL/2) is identical to the mean value for a sample of Middle Pleistocene (non-Neandertal) European hominins; both values being virtually identical to the mean for early modern humans and indicating a common pattern of dental reduction. The mean value for late *H. erectus* is larger, but not significantly so. Figure 3B compares the M_2 crown module for the CoH mandible with comparative samples. Its value is very similar to the mean for early modern humans, but well below mean values for the European Middle Pleistocene sample and late *H. erectus.* When compared using Student's *t*-test the CoH value, early modern human sample mean and European Middle Pleistocene mean are significantly different to the mean for late *H. erectus.* This emphasizes the taxonomic utility of this feature.

The molars of the CoH specimen are characterized by taurodontism or an inferiorly extended pulp cavity. While this is the condition seen frequently in archaic hominins including Neandertals, it is found commonly among early modern specimens (McCown & Keith 1939) and occasionally among contemporary humans (Constant & Grine 2001).

In his description of the CoH mandible, Tobias (1971) argued that the specimen possessed several strong indicators of M_3 agenesis; although, one of them (antero-posterior molar crown size reduction) is suggested here to be a modern trait. Agenesis of the M3s is also a derived feature of later modern humans (Trinkaus 2006).

Discussion and conclusion

On the basis of the present reanalysis, the CoH mandible shows strong affinities to early anatomically modern humans from Africa and West Asia. This finding contrasts with previous studies which have emphasized its primitive morphology and mostly assigned it to *H. heidelbergensis* or *H. rhodesiensis.* However, while it presents as a morphological mosaic, the CoH specimen is overwhelmingly modern in its disposition. The CoH mandible should, therefore, be classified as belonging to *H. sapiens.*

Precisely which sub-group or grade of *H. sapiens* it belongs is a matter of opinion. At the minimum, it should be viewed as representing the 'archaic' grade described by Stringer (2002) or late 'archaic' grade according to Bräuer's (2008) scheme. In both instances, the CoH Bed 3 mandible would belong to the same broad group as the Florisbad cranium, as well as the Laetoli Hominid 18, Ileret, Singa and Jebel Irhoud remains, rather than the Kabwe-Saldanha population.

The alternate view, also consistent with its mosaic morphology, is to consider the CoH mandible to be part of an early anatomically modern group, such as represented by the Klasies River Mouth LBS sample. The lack of chin development in the CoH specimen is similar to the situation within both the later Klasies River Mouth sample (SAS: ~65–90 ka: Trinkaus 2005) and the Israeli Skhul and Qafzeh individuals (Lam *et al.* 1996). However, the CoH specimen is probably much older than these fossils, being either broadly contemporary with the oldest modern humans in East Africa (e.g. Omo-Kibish 1: ≥195 ka) or even pre-dating them by up to ~150 ka (estimated age ~250–350 ka: Bräuer 2008). The implications of such a view are considerable. It implies that modern humans emerged much earlier than is currently believed and that the earliest moderns had a wide distribution across sub-Saharan Africa. While it may be tempting to suggest that southern Africa was the centre of origin for modern humans, this would be unwise at present. First, the geological age of the CoH specimen remains poorly understood. Second, the CoH specimen is only one individual and from a statistical viewpoint a larger sample would be required to support such an argument. Finally, an early emergence for anatomically modern humans would be consistent with archaeologically views that the appearance of the Middle Stone Age marks the origins of modern behaviour (McBrearty & Brooks 2000).

I wish to thank the University of the Witwatersrand for allowing me to study the Cave of Hearths mandible. The University of New South Wales provided funding for the research.

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A study of small-bodied hominims from Palau, Micronesia

Bonita de Klerk & Lee R. Berger
Institute for Human Evolution, BPI Palaeontology, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa
E-mail: bonitadk@hotmail.com

Since the discovery of pygmy elephants in the early 1900s the concept of insular dwarfism has been one of great interest. This phenomenon, by which the size of animals isolated on an island shrinks dramatically over time, has been seen in large reptiles and mammals (Foster 1964). The potential of island effect on body size variation in the genus *Homo* was brought to light with the discovery of *Homo floresiensis.* Brown *et al.* (2004) announced the unearthing of a remarkably small hominid skeleton in Liang Bua cave on the island of Flores, southeastern Indonesia. The remains were dated to the late Pleistocene (95–12 ka) and were described as a new species, *H. floresiensis.* Since the discovery, *H. floresiensis* has been at the centre of a debate regarding its designation as a new hominin species. There are essentially three main arguments within this debate. Brown *et al.* (2004) and Fall *et al.* (2005) argue that *H. floresiensis* represents a case of insular dwarfism from an ancestral population of *Homo erectus.* The second argument by Weber *et al.* (2005) proposes that *H. floresiensis* is a microcephalic *H.* sapiens (i.e. they postulate a pathological condition). Lastly, Jacob *et al.* (2006) suggest that, due to features not unusual in modern pygmoid Australomelanesian *H. sapiens, H. floresiensis* is not a new species, rather a group of small *H. sapiens* that fall within the range of living pygmoid populations. Within the inter-populational variation of human body size polymorphism are a number of cases of 'pygmoid' or dwarfed populations. Typically these populations are known from mainland tropical forests in Africa and island settings in southeast Asia (Richards 2006), and these individuals are considered to be at the bottom of the range for human body size variation. Here we discuss preliminary results of our study of a recently discovered population of small-bodied humans on the island of Palau, Micronesia, which provides additional insight into the issue of dwarfism in human populations. This contribution represents an extension of the announcement paper of this new find (Berger *et al.* 2008), radiocarbon dated to between 1420 and 2890 BP.

Excavation and surface sampling of Ucheliung and Omedokel caves in 2006 and 2007 led to a substantial collection of human material ($n > 1000$). The remains are fragmented and very few associated skeletal elements were recovered due to secondary deposition and disturbance. Of the specimens collected from Palau, only 61 were measurable. Due to the fragmentary nature of the specimens, the measurements taken on individual elements varied. Measurements were taken following Martin (1928), and included for example, anterioposterior diameter of the femoral head, acetabular height and distal maximum breadth of the tibia. The same landmark measurements were taken on a large comparative collection of modern humans, of both 'normal' and small-bodied individuals, including both sexes of adult San from South Africa, pygmoid Andaman and Nicobar Islanders, and a Pygmy from the Democratic Republic of the Congo.

Measurements of the elements from the two Palauan caves indicate body sizes at the lower extreme of modern human variation, and in some cases the range of the small bodied *Homo floresiensis.* This could be seen in the mean estimate derived from the two Palauan femora, namely 43.065 kg, which did not differ significantly from the Andaman Island mean (43.765 kg, $n = 38$). Of the two measurable proximal tibia specimens recovered, one had a bicondylar breadth of 63.1 mm, which falls above, and is not significantly different from the mean of a pooled sex sample of Andaman Islanders (57.8–67.8 mm, $n = 29$). The other tibia specimen has a bicondylar breadth of 53 mm, which falls below the Andaman mean, but reflects an individual of similar size to *Homo floresiensis*, which has a bicondylar breadth of 51.5 mm. All postcranial elements are considered derived. A different observation was made for facial features which showed a combination of primitive and derived features. Primitive features of the Palauan fossils include an inflated glabellar region and the distinct development of a supraorbital torus. Derived features include a distinct maxillary canine fossa, moderate bossing of the frontal and parietal squama and a lateral prominence on the temporal mastoid process. For an extensive list see Berger *et al.* (2008).

The variation seen in the Palauan sample is unlike anything we have seen before. Among this sample are a number of individuals that are small even relative to other pygmy populations. While some individuals plot within the lower end of human variation, there are others that push this limit beyond what is typically considered small for *Homo sapiens.* Even though the Palauan remains exhibit features that are primitive for the genus *Homo,* they are clearly *H. sapiens* due to the craniofacial traits they possess. Colonization of Oceania is thought to have occurred around 4500 years ago by people from the Philippines, but remains of these settlers are rare. Palaeoenvironmental and palynological data support this date (Clarke *et al.* 2006), but archaeological evidence suggests at least one thousand years later (Fitzpatrick *et al.* 2003). Given the relatively recent age of the Palau population they may represent a case of rapid insular dwarfism.

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A review of the occurrence of disarticulated Early Cretaceous sauropod dinosaur fossils from the Kirkwood Formation of the Oudtshoorn and Algoa Basins, South Africa

William J. de Klerk

Albany Museum, Somerset Street, Grahamstown, 6139 South Africa
E-mail: bdeklerk@ru.ac.za

Dinosaur fossils, in the form of disarticulated bones and teeth from various taxa, have been recovered from Early Cretaceous Kirkwood Formation sediments in both the Oudtshoorn and Algoa basins over the past 163 years. During this time only two partly articulated dinosaur specimens have been recovered; the small coelurosaur theropod *Nqwebasaurus* (De Klerk *et al.* 2000) and the nominated holotype of the juvenile ornithopod (iguanodontian) from the Kirkwood Cliff locality (Forster & de Klerk, this volume). It was in 1845 that the first report of a dinosaur fossil discovery was made from South Africa when Mr Andrew Geddes Bain and Dr William Atherstone recovered disarticulated fossil 'bones bigger than those of an ox' from the Bushman's River valley between Grahamstown and Port Elizabeth from a locality that they named 'Iguanodon Hoek'. After a protracted history the material was eventually described by Galton & Combs (1981) as the stegosaur *Paranthodon africanus* (Broom).

Two instances of sauropod fossils material have been identified from the terrestrial Oudtshoorn Basin. In 1927 Broom sent a 3 cm long sauropod tooth that he had recovered from the 'grey-green sandstone' outcrops, to the north of Oudtshoorn, that he had misidentified as Sundays River Formation beds, to Von Heune (1932) for identification. The second report was made by Hoffman (1966) when he described a series of large vertebrae and bone fragments that had been recovered from the Carlitzdorp area in the western part of the Oudtshoorn basin – these fossils he ascribed to a 'gigantic pleisiosaur' which are accessioned at the National Museum Bloemfontein. On investigation of this occurrence in 1999 it was established that there is no evidence to support a marine origin for the Oudtshoorn basin sediments and the fossils are now considered to be from a large sauropod dinosaur.

Disarticulated sauropod fossils in the form of vertebra, partial long bones and numerous isolated teeth have been recovered from at least six localities in the Algoa Basin. The first fragmentary bones were reported by Broom (1904) from a brick quarry at Dispatch (near Port Elizabeth) that he named *Algoasaurus bauri.* Unfortunately the bones that were salvaged, before being made into bricks, were never accessioned into a museum collection and this dinosaur species now sadly languished in the realm of *nomina dubia.* By far the majority of sauropod fossils recovered from the Algoa Basin have come from the general stratotype locality of the Kirkwood Formation in the Sunday River valley 3 km south of Kirkwood village – the site now know as the Kirkwood Cliffs or 'Lookout'. Material recovered thus far includes:

- Large proximal heads of both the humerus and femur from a 'Brontosaurus' now on display at Bay World (Port Elizabeth Museum). The femur end measures 0.6 m across the top.
- Several sauropod teeth were reported by Rich *et al.* 1983) and more have been found since 1995 during successive field seasons, by the author and accompanying students and colleagues.

During the June 1995 field season a well-preserved single diplodocid caudal vertebra (centrum 26 cm) was recovered from the Kirkwood Cliffs. The specimen is now on display at the Albany Museum.

Two additional vertebrae, one a caudal (centrum 15 cm) and the other, thought to be a dorsal (centrum 12 cm) are very likely to have been collected from the Kirkwood Cliffs locality. These specimens were part of the Port Elizabeth Museum and Rhodes University Geology collections. These fossils had in the past been collected by students on field outings.

Recent discoveries of two (possibly three) sauropod vertebrae have been made at Umlilo Hunting Safari reserve some 17 km west of Kirkwood. The vertebra best preserved from this site has been tentatively identified as that of a cervicle from a titanosaurid while the other, displaying distinctive cancellous bone in cross-section is thought to be a dorsal. Both specimens are now nearing completion in their preparation. Several sauropod teeth have also been recovered from the Addo Elephant Park road cuttings since 1995. Within the broader expanse of the Bushmans River valley sauropod material has been recovered from the Shamwari Game Reserve (caudal vertebra and several teeth) and some teeth from the Amakhala Game Reserve ('Iguanodon Hoek' *Paranthodon* site). In summary the sauropod dinosaur taxa are indicated by the seven separate disarticulated vertebrae, a series of fragmentary long bones and numerous disarticulated teeth. Taxa represented by these fossils include diplodocids (possibly *Dicraeosaurid*) and titanosaurids. Diplodocids were previously unknown from the Cretaceous of southern Africa.

Re-evaluating the Jurassic structures identified as termite nests in the Clarens Formation in the Tuli Basin, Limpopo Province, South Africa

J.F. Durand[1] & M. Claassen[2]

[1]*Department of Zoology, University of Johannesburg*
E-mail: fdurand@uj.ac.za

[2]*Department of Geology, University of Pretoria*
E-mail: mclaas@postino.up.ac.za

Clusters of vertical structures discovered in the Clarens Formation sandstones in the Tuli Basin in the Limpopo Province have been identified as termite nests (Bumby *et al.* 2004). These structures have been described by Bumby *et al.* (2004) and Bumby & Bordy (2006) as tall pillar-like structures, some slightly ovoid in cross-section and with differing architecture depending on its level within the structure. They also mentioned fin-like vertical structures which buttressed the cylindrical central section, a basal section honeycombed with small filled-in tunnels and open central spaces. Some structures are described as having a north–south orientation which would have aided with thermoregulation of the assumed termitaria. To support their claim they compare these structures with those built by extant magnetic termites of Australia.

Darlington Munyikwa of the Natural History Museum in Bulawayo (1995) reported rock with a honeycomb-like structure from Zimbabwe similar to those reported by Bumby & Bordy (2006). The presence of enigmatic cylindrical objects in the sandstone was reported south of the Limpopo River, extending from the farms Pontdrift in the west to Schroda (De Villiers 1967; Van Eeden 1969). De Villiers believed that these structures were formed by the action of water and sand during the Jurassic while Van Eeden (1969) argued after revisiting the area and discovering a second site with similar structures on Pontdrift that they were formed by steam percolating through the unconsolidated sand after the deposition of sand on the still hot Drakensberg lavas.

After a study of the structures, microscope slides, mineralogy and comparison with extant termitaria we conclude that these structures were probably formed by means of sedimentary processes and agree in general with the findings of Van Eeden and De Villiers. An explanation for the formation and non-biogenic nature of the structures and a description of the palaeoenvironment are given.

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Large mammals and palaeoenvironmental reconstruction: lessons from a modern bone assemblage in southern Kenya

J. Tyler Faith

Hominid Paleobiology Doctoral Program, CASHP, Department of Anthropology, George Washington University, 2110 G Street NW, Washington, D.C. 20052, U.S.A.
E-mail: tfaith@gwu.edu

The reconstruction of past environments from vertebrate fossil assemblages represents a fundamental goal of paleontology. Faunal analysts have developed numerous quantitative methods for reconstructing paleoenvironments from large mammal remains. These include examination of the presence/absence or relative abundances of particular taxa (Bobe & Behrensmeyer 2004; Klein 1972; Vrba 1980), species diversity indices (Avery 1982; Grayson *et al.* 2001), ecological structure analysis (Andrews *et al.* 1979; Reed 1998), and functional morphology (Kappelman *et al.* 1997; Plummer & Bishop 1994), among others. Paleoenvironmental interpretations are often made in reference to data from present-day faunal communities (Klein 1972; Reed 1997, 1998; Vrba 1980). This reasoning assumes that a death assemblage is a direct reflection of the living vertebrate populations. However, with the exception of Behrensmeyer's long-term taphonomic research in Amboseli Park, Kenya (Behrensmeyer & Dechant Boaz 1980; Behrensmeyer *et al.* 1979), the relationship between living animal communities and their death assemblages has received relatively little attention. Until this relationship is better understood, it will not be clear what exactly one is measuring when reconstructing environmental parameters from fossil assemblages.

This study uses data from a modern landscape bone assemblage in the Shompole/Ol Kiramatian group ranch and conservation area (SOK) of southern Kenya to examine methods of paleoenvironmental reconstruction. Specifically this paper addresses the following questions: (1) Do environmental reconstructions obtained by different methods reflect local (microhabitat) or regional (macrohabitat) vegetational conditions? (2) What methods effectively distinguish habitats within the modern bone assemblage?

The Shompole/Ol Kiramatian group ranch (SOK) is located in southern Kenya along the Kenya–Tanzania border at the base of the Nguruman Escarpment, which marks the western edge of the East African Rift Valley. The semi-arid habitat (~500 mm annual rainfall) supports a rich faunal community that is typical of this region. The principal herbivores include wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*), and Grant's gazelle (*Gazella granti*). Carnivores include lion (*Panthera leo*), leopard (*Panthera pardus*), and striped hyaena (*Hyaena hyaena*), among others.

The SOK bone assemblage was sampled following the taphonomic survey methods developed by Behrensmeyer (Behrensmeyer & Hill 1980; Behrensmeyer *et al.* 1979) in Amboseli Park, Kenya. Transects were surveyed for bones by a team of three individuals across the various habitats that characterize the SOK landscape. This study makes

Table 1. Summary of the results obtained in this study.

Method of environmental reconstruction	Local or regional environmental signal?	Are the reconstructions accurate?	Does the method distinguish SOK habitats?
Presence/absence	Regional	Yes	No
Taxonomic relative abundance	Regional	Yes	Yes
Ecological structure analysis	Regional	Yes	Yes
Diversity indices	–	–	Yes

use of data collected from the following habitats, listed in order of increasing vegetation cover: open grassland (OG), *Acacia tortilis* grassland (AG), *Salvadora* shrubland (SS), and gallery forest (GF). Following the broad habitat classifications described by Reed (1998), these samples within the SOK ecosystem would be classified as grassland (OG & AG), shrubland, and forest, respectively. The broader SOK ecosystem is appropriately classified as a shrubland, which also characterizes the nearby Amboseli and Tarangire (Tanzania) ecosystems (Reed 1998). The minimum number of individuals (MNI) sampled in a given habitat is used as the principal census data.

In a previous study, Reed (1998) compiled taxonomic and ecological data from a number of extant African faunal communities sampling a range of habitats and rainfall regimes (e.g. from the Congo Basin to the Namib Desert). These data are used to 'reconstruct' the vegetation of the four SOK death assemblages using presence/absence data, taxonomic relative abundances, and ecological structure analysis, which classifies faunal communities according to the proportion of species falling into certain locomotor and trophic ecovariables. Faunal similarity is assessed using the Dice/Sorenson coefficient for presence/absence data and Chord distance (converted to a similarity index) for relative abundances of taxa or ecovariables.

A comparison of the SOK death assemblages to extant African faunal communities by means of taxonomic presence/absence, taxonomic relative abundance, and ecological structure analysis consistently links the samples with grasslands (Serengeti Plains) or shrublands (Amboseli NP & Tarangire NP). This is an accurate assessment of the SOK ecosystem. Death assemblages from habitats characterized by extreme differences in vegetation cover (e.g. open grassland *vs* gallery forest) provide a faithful ecological signal of the broader environmental conditions. Because of this 'smearing' of ecological signals across habitats, however, these methods are limited in that they provide little insight into the immediate vegetation from which the death assemblages were sampled. For example, the heavily vegetated gallery forest provides a death assemblage that consistently allies with more open shrubland habitats.

Further exploration of the SOK data is undertaken to determine whether an ecological signal specific to each habitat can be recovered from the death assemblages. This analysis makes use of presence/absence data, taxonomic relative abundances, the relative abundance of individuals falling into various trophic and locomotor classes, and the Shannon diversity index.

Presence/absence data provides no clear signal that might differentiate faunal communities according to habitat. For example, zebra, wildebeest, warthog (*Phacochoerus aethiopicus*), Grant's gazelle, and giraffe (*Giraffa camelopardalis*) were recovered from all habitats. A contingency table analysis on the taxonomic abundances, however, indicates that relative abundances differ significantly across assemblages and in a manner that is expected given the habitat. For example, there is a clear decline in the abundance of wildebeest and an increase in the abundance of impala as vegetation cover increases. As expected, giraffe are particularly abundant in the *Acacia* grassland and rare in the open grassland. An analysis of trophic and locomotor variables provides similar results. For example, the proportion of grazers declines significantly as vegetation cover increases, whereas mixed feeders become increasingly abundant. Species practicing a mix of terrestrial and arboreal locomotion are particularly abundant in the gallery forest (purely arboreal species were not sampled at SOK). Finally, the Shannon index increases significantly as vegetation cover increases, perhaps hinting at the greater number of food resources that are available.

This study illustrates how taphonomic data from modern bone assemblages can be used to provide an enhanced understanding of paleoenvironmental reconstructions (Table 1). Analysis of the SOK faunal remains show that when comparing a death assemblage to extant faunal communities, one is most likely to recover a broad environmental signal that is characteristic of a particular region as opposed to the immediate habitat from which those bones were sampled. This is true whether one uses presence/absence, taxonomic abundance, or ecological structure analysis. Further analysis shows that different habitats can be reliably distinguished on the basis of relative abundances or the proportions of individuals classified into trophic or locomotor classes. Presence/absence data is of little value for distinguishing the SOK assemblages according to habitat.

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Preliminary report on a new basal iguanodontian dinosaur from the Early Cretaceous Kirkwood Formation, South Africa

Catherine A. Forster[1] & William J. de Klerk[2]
[1]*Department of Biological Sciences, The George Washington University, Washington, D.C., U.S.A.*
[2]*Albany Museum, Somerset Street, Grahamstown, 6139 South Africa*
E-mail: bdeklerk@ru.ac.za

Over the past twelve years ongoing fieldwork in the Lower Cretaceous (Valanginian) Kirkwood Formation in the Algoa Basin, has produced a number of well-preserved vertebrate specimens. This material greatly increases our understanding of the Kirkwood fauna – particularly dinosaurs, known previously from scrappy, fragmentary material. This paper highlights a new taxon of ornithopod dinosaur (basal iguanodontian), consisting of numerous disarticulated elements from at least 20 individuals and a semi-articulated specimen. The first fossil specimens of this new dinosaur species were discovered in 1995 in a 'bone bed' concentration located on the Kirkwood Cliffs ('Lookout') some 3 km south of Kirkwood village. Systematic excavation over four successive field seasons (in 1996, 1997 and 1999) showed that the recovered specimens of this ornithopod are small in size (largest femur = 55 mm), and thus likely representative of juveniles. Several characters (e.g. hatchet-shaped sternal plate, absence of subsidiary ridges on teeth) indicate that this taxon is a derived iguanodontian. Sufficient fossil material from these juvenile ornithopods (hatchlings) has now been recovered and prepared and a new species of dinosaur is currently being described. From a taphonomic perspective the bone concentration appears to represent an accumulation of disarticulated skeletal elements produces by the natural mortality of hatchlings, of varying ages, found at communal nesting site. No eggshell material was found in association with the bones which suggests that the nests were located a short distance from the bone accumulation site.

Evidence for aggradational and degradational landscapes in the Karoo basin during the Early Triassic

Robert A. Gastaldo[1], Johann Neveling[2] & Daniel Pace[3]
[1]*Geology Department, Colby College, Waterville, ME, U.S.A.*
E-mail: ragastal@colby.edu
[2]*Central Regions, Council for Geoscience, Pretoria, Gauteng, South Africa*
E-mail: jneveling@geoscience.org.za
[3]*Mackay School of Earth Sciences and Engineering, Reno, NV, U.S.A.*
E-mail: pacedan@gmail.com

The Early Triassic Katberg Formation (Beaufort Group, Karoo Supergroup) in South Africa is an arenaceous unit that can be traced throughout the basin.

Exposures of its lowermost part at the Carlton Heights locality north of Middelburg provide an opportunity for a detailed sedimentological analysis and evaluation of the controls on its stratigraphy with implications for the paleontological record preserved therein.

Two distinct sandstone geometries co-occur in three thick, resistant benches characterizing the outcrop. Each bench is separated by greenish-grey siltstone. Medium-bedded, planar and/or ripple-laminated sheet sandstone conforms to the traditional description of the Katberg and these geometries are interpreted as ephemeral sheet-flood deposits. The second architectural type consists of thick-bedded, cross-laminated sandstone organized into lenticular multi-lateral geometries that overlie deep erosional scours. Downstream accretionary macroforms and sandy barforms characterize these deposits and are interpreted as representing deeper, sand-bed braided systems. Sandstones of both types amalgamate laterally as the result of landscape degradation, thereby appearing as multi-storied sandstone architectures when exposed within resistant donga or roadcut sections. But, this feature is geographically restricted to distances of only several 100 metres. Intervening siltstones are burrowed heavily by the new ichnotaxon, *Katbergia carltonichnus* (Gastaldo & Rolerson 2008) which normally are restricted to the upper 0.5 m of this lithofacies.

Two distinct populations of pedogenic carbonate concretions occur in the stratigraphy. Pisolith-sized carbonate nodules of various shapes are aggregated within conglomerates that occur intermittently throughout the outcrop and often dominate lenses at the base of sandstone intervals. Larger, *in situ* carbonate nodules are restricted to horizons within thick siltstone intervals, and differ in terms of size, shape, surface texture, and stable isotopic signature. The $\delta^{13}C$ values of the pisolith-sized nodules, restricted to intraformational conglomerates, indicate that these precipitated in equilibrium with atmospheric CO_2. In contrast, the larger, *in situ* nodules indicate that cements were isolated from the influence of atmospheric CO_2 and formed below the water table in wetland paleosols (Tabor *et al.* 2007). Hence, a difference paleoclimatic signature exists for each suite of carbonate nodules. Intraformational conglomerates precipitated under seasonally dry conditions originally as components of aridosols. Seasonal, moist conditions are interpreted for the in situ nodules, a contention supported by the spatial relationship between the large pedogenic nodules and

Katbergia burrows (Hasiotis 2000; Gastaldo & Rolerson 2008).

To date, no physical evidence has been found for pisolithic nodules *in situ* within any paleosol interval of the Katberg Formation, at Carlton Heights or elsewhere. Hence, the only evidence that ardisols (calcisols) ever existed in the study area or other parts of the basin occur as remnants of these Early Triassic phreatic zones that had developed repeatedly across the landscape. Their restricted occurrence in channel-lag deposits indicates that these soils were scavenged during landscape degradation (Allen 1986).

We interpret variation in fluvial channel architectures and isotopic signatures of the carbonate nodules in terms of distinct periods of landscape aggradation, equilibrium, and degradation. Channel and overbank deposits represent deposition during aggradational stages with inceptisol and gleysol (wetland) interfluves dominating the landscape. When the landscape attained equilibrium, the character of interfluvial paleosols changed from seasonally wet gleysols to more seasonably arid calcisols. The latter were scavenged during landscape degradation and deposited within channel lags when there was a return to more seasonably wet conditions. The repetitive shifts between seasonally wet and seasonally arid conditions reflect the impact of strong oscillations of climate rather than pulses of orogenic activity or any ecosystem response to the end-Permian extinction.

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The Vertebrate Fauna of the Late Devonian, Famennian, Witpoort Formation, Waterloo Farm locality, near Grahamstown

Robert Gess

Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa
E-mail: robg@imaginet.co.za

The Witpoort Formation of the Witteberg Group consists of mature quartz arenites, interpreted as having been deposited along a linear sandy, coastline with occasional thin black shales deposited in semi-enclosed lagoonal settings (Hiller & Taylor 1992). Cooper (1986) correlated South African sea level curves to determine the ages of units within the Cape Supergroup. He demonstrated an Upper Devonian (Famennian) age for the Witpoort Formation and a Frasnian age for the underlying Weltevrede subgroup. This is consistent with palaeontological evidence, such as the presence of Late Devonian type plants in the Weltevrede subgroup and lower Witpoort Formation (Plumstead 1967) and the occurrence of the Givetian to Frasnian articulate brachiopod, *Tropidolepis,* near the top of the Weltevrede subgroup (Boucot *et al.* 1983). Further palaeontological evidence comes from the extensive flora (Gess & Hiller 1995) (including the Late Devonian cosmopolitan, *Archaeopteris* (Anderson *et al.* 1995)) and fauna, discussed below, from the upper Witpoort Waterloo Farm locality. In addition, placoderm fish, which make up an important component of the Waterloo Farm fauna, are completely absent from overlying strata. The palaeoniscoid-dominated fauna recorded from the, upper Witteberg, Waaipoort Formation is consistent with an Early Carboniferous interpretation of its age. Cooper (1986) considered the Devonian–Carboniferous boundary to be at, or near, the contact between the clean white quartzites of the Witpoort Formation and the fine black sediments of the overlying Kweekvlei Formation, which he interpreted as a reflection of the Tournasian transgressive cycle.

At Waterloo Farm, a thick horizon of black shale lenses situated near to the top of the Witpoort Formation quartzites was exposed in road cuttings in 1985. It is interpreted as anaerobic sediment that was deposited in an estuarine lagoon, situated behind a sandy barrier bar (Hiller & Taylor 1992). It appears to be coeval with a series of quartzites to its east, interpreted as components of the barrier system. Abundant trace fossils, as well as plant fossils, similar to those found in the black shales, are preserved in the quartzites and in thin reddish shales that are interbedded with them. Fossil fish remains have been found in three lenses, close to the associated barrier-sand deposits. The uppermost of these three has been the richest source of fossils, and the subject of many years of excavation and study. The vast majority of the black shale horizon, stretching for hundreds of metres to the west of these lenses appears to be devoid of vertebrate and arthropod fossils though it contains, in places, large quantities of plant material, often comprised tangles of vascular plant branches. Substantial tree trunks have also been recorded, further suggesting the proximity of a wooded environment. It is likely that the lack of fish and arthropod fossils within these latter beds resulted from low oxygen levels caused by the large volumes of decaying plant matter. The relatively fish-fossil-rich upper lens is somewhat less carbonaceous, than many of the more westerly deposits, and contains isolated, more fragmentary plant remains. An abundance of diverse fish and probably arthropod derived trace fossils suggests that the water column, at this point, was less anaerobic because of its greater proximity to the marine ebb and flow.

Anoxic conditions, within the sediment accumulated below the aerated water, resulted in exceptionally good preservation of some small organisms. Its sulphurous, acidic nature caused poor preservation of large bony elements, generally represented by mineralized compres-

sions. Since exposure in 1985, the outcrop has provided evidence for a growing list of taxa.

Soft tissue compressions of a number of small, unarmoured jawless fish have been collected. These include the holotype of *Priscomyzon riniensis* (Gess *et al.* 2006), the oldest known lamprey, which already exhibited the oral specializations necessary for a parasitic lifestyle and much of the cranial anatomy seen in extant taxa.

The fauna was numerically dominated by groenlandaspid arthrodire placoderms, of which *Groenlandaspis riniensis* (Long *et al.* 1997), which reached a substantial size, was the most abundant. Two other species (including *Africanaspis doryssa* (Long *et al.* 1997)), characterized by extremely high median dorsal plates, were less abundant and more modest in size. Further arthrodire taxa were also present. Antiarch placoderms were represented by *Bothriolepis africana* (Long *et al.* 1997), which was also relatively large. A ptyctodont placoderm has been reported, on the basis of an isolated plate (Anderson *et al.* 1997).

Acanthodians ('spiny sharks') were fairly diverse, though not common, and included a large gyracanthid (Gess & Hiller 1995), at least one diplacanthid (*Diplanthus acus*) (Gess 2001) and an acanthodid. Chondrichthyans included *Antarctilamna,* elsewhere a mid Devonian Gondwanan taxon, *Plesioselachus macracantha* (Anderson *et al.* 1999), and two subadult forms, possibly representing further taxa, of uncertain affinities.

A small actinopterygian (ray-finned fish) was amongst the less common taxa. Sarcopterygian (lobe-finned fish) were more diverse and more numerous. The most abundant of these was a coelacanth (Gess & Hiller 1995), represented by numerous juvenile individuals, which may well have utilized the quiet estuarine environment as a nursary. Long-snouted dipnoans were present, as well as a large tristichopterid (Gess & Hiller 1995), which exhibits some similarities to *Hyneria.* The top predator, represented by fragments, including a large cleithrum, appears to have been a several-metre-long elpisthostegalid-like form.

Waterloo farm represents the only significant high latitude ecosystem known from the latest Devonian, a time when southern Africa formed part of western Gondwana. The palaeolagoon at Waterloo Farm drained into the high latitude, polar, Aghulas Sea, bounded by what is now southwestern South America, the southern Cape coast and West Antarctica. The south pole at the time (Scotese & Barrett 1990), was situated over southwestern Gondwana, most likely in the vicinity of Argentina, on the western shores of the Aghulas Sea. This placement would imply that the Waterloo Farm locality was within 10 to 15 degrees of the south pole.

The movement of Gondwana over the south pole during the Late Devonian and its consequent glaciation may have contributed to a series of global extinction events, that characterize the Famennian, by lowering sea levels and global temperatures. Alternately, or additionally, lowered global temperatures may have resulted from reduced CO_2 levels due to rapid global spread of the first (*Archaeopteris*) forests during the Frasnian, compounded by the colonization of dryer areas by the first seed-plants towards the end of the Famennian. This sudden increase in terrestrial biomass would have increased levels of fixed C entering drainage systems, perhaps helping to account for a series of C-rich anaerobic sediments deposited worldwide during the Famennian (Algeo *et al.* 2001). These sediments appear to be associated with a series of extinction events of variable severity. The most important and widespread two of these events are the Kellwasser extinction event, which approximately coincides with the Frasnian/Fammenian boundary (and mainly affected plant communities), and the Hangenberg extinction event, which coincided with the end of the Famennian and therefore the Devonian/Carboniferous boundary (Algeo *et al.* 2001). This latter extinction event was the finale of the Second Global Extinction Event. This was one of earths five 'major extinction events', and killed a large proportion of marine organisms, including whole groups of fish, such as the Placoderm fish. It may be no coincidence that black anaerobic shales are interspersed through the Witpoort Formation, the second most prominent of which is found near the base of the Witpoort Formation, the probable Frasnian/Famennian boundary at Howisons Poort. The most prominent is that at Waterloo Farm, near the top of the Witpoort Formation and, therefore, immediately preceding the end of the Devonian Period. What we may therefore see at Waterloo Farm, is a record of the protracted demise of the Devonian world in west Gondwana.

The massive explosion of advanced plant life during the Late Devonian, which may well have precipitated the staggered end-Devonian extinction of marine life, created new potential niches for animal life that, during the Early Carboniferous, would be inhabited by tetrapod vertebrates.

Recent studies show that the basic adaptations that permitted life on land were already established in aquatic tetrapods by the end of the Devonian (Clack & Coates 1995). Tetrapod stem group 'Tristichopterid' fish, known from the late Givetian to early Frasnian, coexisted with more crownward 'Elpisthostegalid' fish, from which 'Acanthostegid' tetrapods were probably derived during the Frasnian to Famennian (Clack 2002).

Fossil-bearing Late Devonian rocks are consequently of crucial interest in understanding the emergence of tetrapods and the drastic climatic and environmental changes that helped to drive the process. Waterloo Farm locality was near polar, while better known fossil vertebrate faunas of North America, Europe, China, Australia and Eastern Antarctica were all tropical. Elpisthostegalids and acanthostegids have, so far, only been recorded from Laurasia, (though tetrapod trackways are found in Australian Famennian rocks (Warren & Wakefield 1972)) – leading to the suggestion that tetrapods lived and evolved in the tropical, marginal marine environments of Laurussia before migrating to tropical parts of what is now Australia (Clack 2002). The discovery of an elpisthostegalid-like tetrapodomorph at Waterloo Farm suggests that taxa close to the Late Devonian tetrapod stem were not confined to the

warm tropical waters of Laurasia, but also included large cold-water Gondwanan forms.

The vertebrate fauna of Waterloo Farm is, in general, surprisingly diverse and cosmopolitan considering its high latitude position at a time of nearby glaciation and global cooling. Though retaining a relatively primitive (mid Devonian type) shark fauna, it includes many genera that are absent from mid-Devonian southern African fish faunas, such as the placoderm *Bothriolepis* that radiated out from China during the Devonian. The composition and phylogenetic relationships, of the described placoderm taxa of the Waterloo Farm locality, is most similar to that of East Gondwana (Long *et al.* 1997). Curiously its osteolepiform sarcopterygian fauna, comprising *Hyneria*-like and Elpisthostegalid-like forms, more closely recalls Late Devonian faunas of Laurasia than those of East Gondwanan Australia, which are characterized by more derived Tristichopterids and Rhizodontids. The influence of a warm, southwardly flowing current from the Laurussian tropics cannot be discountered as a mechanism of dispersal, as well as a means of explaining the lush wooded botanical environment adjacent to the lagoon.

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The impact of molecular systematics on palaeontology

Eric H. Harley

Department of Clinical Laboratory Sciences, University of Cape Town
E-mail: harley@chempath.uct.ac.za

In the time before molecular data began to provide novel types of data for phylogeny constructions, morphological data was effectively the only data form available for construction of phylogenies. Molecular data currently consists almost exclusively of DNA sequences, with these sequences consisting of characters which can have any of four different states (A,G,C, or T). These differences allow for a variety of analytical approaches for constructing phylogenetic trees: whereas for morphological data, parsimony is generally the preferred method, since the data can come in many different forms, the simplicity of DNA sequence data, and mode of evolutionary changes over time, allow for a variety of newer and more powerful analytical approaches, with Maximum likelihood and Bayesian methods being popular, and allowing different types of confidence estimates to be calculated for branch points. The presence also of a molecular clock, albeit a stochastic clock, allows for time estimates to be attempted for branch points in the tree, estimates which, however, are only as good as the calibration of the rate of DNA changes over time. Since different genes change at different rates, gene sequences can be chosen to provide appropriate data sets for either closely or very distantly related taxa. The different genomes available for phylogenetic analysis – nuclear, mitochondrial, and (in plants) chloroplast, which follow different modes of inheritance, and differing rates of change, further expand the range of options available for the molecular systematist. Resolution of phylogenetic relationships where the fossil record is problematic (examples will be given for ordinal relationships in the mammalia (Arnason *et al.*, in press), and at the genus/species level in the felidae (Driscoll *et al.* 2007) may be resolved by molecular means if extant taxa are available which are relevant to the question. Ancient but useable DNA can sometimes be extracted from tissues up to maybe 100 000 years old, and can address relationships such as those of recently extinct Proboscidea.

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Comparative feeding biomechanics of *Lystrosaurus* and the generalized dicynodont *Oudenodon*

Sandra C. Jasinoski[1], Emily Rayfield[1] & Anusuya Chinsamy[2]

[1]*Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol, BS8 1RJ, U.K.*
E-mail: s.jasinoski@bristol.ac.uk / e.rayfield@bristol.ac.uk
[2]*Department of Zoology, University of Cape Town, Private Bag, Rondebosch, 7700 South Africa*
E-mail: anusuya.chinsamy-turan@uct.ac.za

Dicynodonts were herbivorous therapsids best represented by fossils from the Permo-Triassic of South Africa. Differences in cranial morphology across Dicynodontia have been correlated with changes in masticatory function, and hence, dietary preference. Although the derived masticatory apparatus of dicynodonts allowed propaliny, it has been previously hypothesized that *Lystrosaurus* primarily utilized powerful orthal jaw movements to process fibrous vegetation. Cranial specializations of *Lystrosaurus,* such as shortened and deepened cranium and a patent premaxilla-nasal suture, have been hypothesized to have increased the efficiency of its masticatory system compared with generalized Permian dicynodonts.

Here we aim to test this assertion using biomechanical modelling techniques. We use finite element analysis (FEA) and a study of cranial functional morphology (including sutures and bone histology) to compare the biomechanical performance of the cranium of *Lystrosaurus* with *Oudenodon,* a generalized dicynodont, during orthal bite simulations. Muscle forces were estimated for each dicynodont using the dry skull method and applied to each cranium to produce a reaction force at a bite point. Patterns and average magnitude of Von Mises stress in each dicynodont cranium and in segmented regions of interest were assessed. During an orthal bite simulation, higher stress occurs throughout the *Oudenodon* cranium, indicating that the cranium of *Lystrosaurus* is more resistant to normal, static feeding loads. Despite this difference in stress magnitude, patterns of stress are similar within both taxa. The FE-stress results, along with mechanical advantage of adductor musculature, a broad symphyseal contact, and other cranial features suggest that *Lystrosaurus* may have employed a snapping bite for processing the tough fibrous vegetation it has been posited to feed on.

Speculations on buoyancy control and ecology in some heteromorph ammonites. 2. The ammonite family Nostoceratidae Hyatt, 1894

Herbert C. Klinger

Iziko South African Museum, Cape Town
E-mail: hklinger@iziko.org.za

In helically coiled ammonites of the subfamily Turrilitinae, buoyancy control is achieved by migration of the siphuncle towards the upper, adapapical edge of the whorls. This results in early decoupling of the cameral fluid, and probably negative or neutral buoyancy. This, in conjunction with apertural modifications, is suggestive of a vagile, benthonic mode of life. In contrast, helically coiled ammonites of the family Nostoceratidae Hyatt, 1894, with a single exception, retain a siphuncle situated at midflank. In addition, the body chamber in these forms is relatively larger than in the Turrilitinae, and the aperture remains simple. It is suggested that the different modes of coiling of the body chambers of helically coiled Nostoceratidae are adaptations to empty the phragmocones of cameral liquid through several stages of coupling and decoupling, and thus to achieve neutral buoyancy for a planktonic mode of life. This is probably an adaptation to a microphagous diet. A benthonic mode of life as suggested by several authors is rejected.

Large mammal butchering experiments using stone tools

Andrea Leenen & Lucinda Backwell

Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa
E-mail: past@fusionreactor.za.net / lucinda.backwell@wits.ac.za

Due to the fact that numerous natural events and human practices modify bones, unequivocal interpretation of bone modifications is sometimes difficult. Further to this, mimics, which are a result of non-human activity, produce the same or qualitatively similar patterns that complicate positive identification of cut marks made by hominins. Reliable measures are required for interpretation of bone modifications, and actualistic experimentation can help towards this. A number of taphonomic processes, including bone modification by various animals and geological processes are recorded in comparative collections housed at institutions in Gauteng. These provide reference material for taphonomists attempting to identify agents responsible for the modification and accumulation of fossil bone assemblages, particularly from early hominin cave sites in the Sterkfontein Valley. However, no reference material exists for hominin modification of bone, and thus motivates for the collection of such traces. The primary goal of this research is to create a modern comparative collection of complete large bovid skeletons that record butchering marks made by stone tools. Four different raw materials commonly found in the southern African archaeological record, namely chert, quartzite, dolerite and hornfels were selected for flake production. Butchery was conducted on three cows by modern Bushmen subsistence hunters skilled in the processing of animals. They form part of a relatively isolated group of !Xo-speaking Bushmen resident in Kacgae village in the Ghanzi district of western Botswana. This study focuses on characterizing stone-generated butchering marks at a macro-and microscopic scale, and documenting their location, number, orientation, size and morphology. Future research will broaden the butchering experiments to include a range of indigenous people processing domestic and wild animals in order to address a number of faunal taphonomy questions. Here we present an account of progress to date.

The Saurichthyidae (Actinopterygii): origin, distribution and interrelationships

Raoul J. Mutter

Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg. Private Bag 3, WITS, 2050 South Africa
E-mail: r.mutter@permotriassicfishes.org

Remains of saurichthyids were first mentioned nearly 300 years ago. The name *Saurichthys* was established by Agassiz in 1834 and refers to the plesiosaur-like appearance of these fish teeth. Three genera are currently accepted, and the validity of a fourth genus is equivocal. The oldest unambiguous member of the family is placed in the genus *Eosaurichthys* Liu & Wei, 1988 from the uppermost Permian of Meishan, China. The genus *Saurichthys* Agassiz 1834 occurs almost worldwide during the Triassic and at least 35 species are diagnosable within this genus. The youngest unequivocal and about coeval saurichthyid remains come from the Lower Jurassic of Canada, England and Germany and are assigned to the genus *Acidorhynchus* Stensiö, 1925. In southern Africa, saurichthyids are reported from various marin Early Triassic sites in Madagascar and Tanzania and from non-marine Middle Triassic sites in South Africa (Mutter *et al.* 2008).

With respect to their record in the southern hemisphere, recent review of saurichthyids revealed intriguing facts about this highly interesting group of primitive actinopterygians. While marine records outnumber non-marine records greatly worldwide and throughout their fossil record, the first unambiguous non-marine species come from the Hawkesbury Series in New South Wales – complete and articulated specimens of *Saurichthys gracilis* and *S. gigas* (Woodward 1890) – and are of Middle Triassic age. South African jaw fragments and isolated teeth, first described by Griffith (1978) were recently revisited by Bender & Hancox (2003) and may be slightly older (Mutter *et al.* 2008). Interestingly, saurichthyids have so far not been positively identified in any non-marine South American formations of Permo-Triassic age (Mutter *et al.* 2008). The apparent occurrence of certain species in non-marine waters have been interpreted as anadromous behaviour (Beltan & Tintori 1980) but preservation in most non-marine sites is fragmentary and remains are likely allochthonous. The South African saurichthyid remains from the Spathian–Ansian boundary of the Burgersdorp Formation are important, because they fill a blank spot on the palaeobiogeographic map, providing evidence for the oldest non-marine occurrence of any saurichthyid.

Patterns of distribution and early saurichthyid evolution are more complex than previously believed, and diversity was already high during the Early Triassic (Mutter *et al.* 2008). However, major traits during long-term saurichthyid evolution can be observed and include reductions of scale rows and skull roof bones, shortening or deepening of the elongate snout and development of various types of dentitions. The genus *Eosaurichthys,* originally confined to the Permian and completely covered by scales, leaped into the Early Triassic. The genus *Saurichthys,* showing various types of reductions in its squamation, existed probably throughout the Triassic and peaked in the Middle Triassic in diversity. A second Triassic genus possesses an extremely short snout, *Brevisaurichthys* Beltan, 1972. The latter genus may be valid but is currently poorly defined and only known from the late Middle Triassic of Europe. A stem group of *Saurichthys* must have given rise to the genus *Acidorhynchus* during latest Middle or in the Late Triassic, and both, *Saurichthys* and *Acidorhynchus* lingered into and coexisted in the Jurassic.

The phylogenetic origin of saurichthyids in the late Palaeozoic is unknown but all previously conducted phylogenetic analyses suspect monophyly and tacitly accept the most widely spread genus *Saurichthys* as the group's 'typical' representative. Early attempts at resolving this issue pointed at a pholidopleurid origin but these studies were based on evaluation of primitive features only (Wade 1935; Nielsen 1935, 1936). Using cladistics, the genus *Saurichthys* is usually non-conclusively classified as an unresolved trichotomy with *Acipenser* and *Birgeria* or with neopterygians and acipenseriforms + *Birgeria* (Gardiner 1984; Rieppel 1992; Grande & Bemis 1996; Bemis *et al.* 1997). Gardiner & Schaeffer (1989) resolved their '*Saurichthys* group' as the sister group of acipenseriforms ('chondrostean group') supported by six apomorphies. A consensus tree using the same matrix, however, left *Saurichthys* as a sister group to *Birgeria* and more advanced actinopterygians (Coates 1999). Coates (1999) presented also three hypotheses with *Saurichthys* in differing phylogenetic positions, overall in a more derived position (unrelated to chondrostean ancestry) than suggested by Gardiner & Schaeffer (1989). The most recent review (Gardiner *et al.* 2005) emphasized the 'old' phylogenetic position for *Saurichthys* – as a sister group to acipenseriforms. Following the latter hypothesis, *Birgeria* + (*Saurichthys* + acipenseriforms) form the sister group of all other more derived actinopterygians.

A single study focusing on intrageneric relationships of *Saurichthys* has so far been conducted (Rieppel 1992). Nine well-known species were chosen and coded using eight well-defined characters. The resulting groups basically mirror the gaps of the fossil record in time and space and support a general but weak evolutionary trend that has recently been even more counterbalanced by the discovery of well-preserved Lower Triassic specimens in the northern hemisphere (Mutter & Cartanyà 2005; Mutter *et al.* 2008).

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Beaufort Group GIS initiative: creating and maintaining an interactive fossil database for palaeontological research

Merrill Nicolas, Cynthia Kemp & Bruce Rubidge
Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa
E-mail: merrill99@googlemail.com

For more than a century, large collections of fossils from the Beaufort Group have been built up in South Africa. Records of these collections have been maintained as separate databases by each of the seven museums which curate them (Kitching 1977; Keyser & Smith 1979; Nicolas 2007). The databases contain a unique time-extensive record of continental vertebrate biodiversity – represented by the fossils of the Karoo Supergroup (Rubidge 1995). As an initiating project, a dataset of records of fossil tetrapods collected from Permo-Triassic Beaufort Group rocks of South Africa was compiled from the seven museum catalogues, and this was linked to a newly created database within the Geographical Information System (GIS). The process required rigorous evaluation of both the quality of the original records, and the degree of collecting bias that may have existed in the different collections. Assessment of quality endorsed the establishment of the two databases and no significant degree of collecting bias was encountered. Thus this new dataset makes possible the determination of terrestrial tetrapod ecological representation from the Middle Permian to Middle Triassic Beaufort Group of South Africa (Nicolas 2007).

GIS offers a spatial map which allows access to more than one map layer simultaneously, giving a multifaceted view of data that shows trends more clearly than tabulated data (Cooper & Netterberg 2004). Thus GIS provides the user with not only data concerning the taxonomy of any record, but also identifies the museum collection and specimen number, as well as giving specimen locality details. For the first time, fossil-collection data can now be viewed on a map of southern Africa which demarcates farm boundaries and shows the topographic and geological signature of farms.

The first five years of the GIS project (2003–2007) was the foundation phase during which all viable tetrapod fossil data from the Beaufort Group was converted to a reputable GIS system, ESRI® ArcInfo® being the system of choice. Suitable map layers were obtained in order to facilitate research relating to distribution patterns of fossil taxa. These map layers include a geological map, farm and farm boundaries, magisterial districts, provincial data, grid-references, and map and satellite imagery for southern Africa. Accessing and importing the data sets took four years (Nicolas 2007).

The second phase (January–December 2008) is current and is a secondary setting-up stage which when complete will provide a streamlined and user-friendly product. It involves rigorous editing and standardization of the seven museum databases. All fields of data content are now identical for each museum: data fields include museum collection name; museum collection number; genus; taxon; province; district; farm name; farm number; commonly used farm name; *x–y* coordinates and assemblage zone. Font and font size are standardized, spelling errors are eliminated, as are records with insufficient or inaccurate data (the latter affect the integrity of the GIS database).

The *x–y* coordinates are important for this phase of product development. Because many older records lacked accurate grid-references, it has been necessary to establish them – for each and every farm in the Beaufort Group where fossils have been discovered. In the past, confusion resulted from farm names being repeated within a given district, but by assigning *x-y* coordinates to farm names and listing the registered farm number, the arbitrary use of popular nicknames is eliminated. Old farm names are not discarded, however, affording researchers as much past-naming information as possible. In the end, all viable fossil records will be identified by a coordinate set which correlates with modern GPS usage.

Maintenance of the database in this new standardized state requires that contributing museums provide updates of new records which comply with the set format. To this end, a manual of procedure for future fossil collection recording is being created. It is anticipated that new contributions to this database will be added on an annual basis. While the pilot project has concentrated on only Beaufort Group data, the concept should be expanded to

incorporate databases of fossils from different stratigraphic successions – and include not only southern African but also international specimens.

Applications of this database are extremely wide and it is hoped that the palaeontological community will make full use of them. For example, it will afford assessment of geographic and stratigraphic distribution of selected taxa, determination of the number of specimens of individual taxa, relative numbers of specimens of different taxa, co-occurrence of taxa in both a stratigraphic and geographic context, and refining of biozone boundaries. The information will have significant application in basin development studies, environmental impact analyses, as well as in research on ecological and population distribution and biodiversity changes through time.

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Shape variability in the skull of *Aelurognathus* (Therapsida: Gorgonopsia)

L.A. Norton, B.S. Rubidge & F. Abdala

Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa
E-mail: luke.norton@students.wits.ac.za

The infraorder Gorgonopsia Seeley 1894 was initially created to isolate the specimen of *Gorgonops* from other members of the order Therosuchia, on the basis that the, 'temporal vacuities [of the skull were 'roofed over,' (p. 1014). Broom (1910a) recognized that the specimen of *Gorgonops* was damaged and shared cranial features with *Titanosuchus,* and he later (1910b) placed *Gorgonops* in the suborder Dinocephalia. Broom (1913a) reduced the Gorgonopsia to the rank of family, but later (1913b) re-established it as a distinct suborder of the Therapsida, after the discovery of additional specimens.

Between 1913 and 1958 a large number of gorgonopsian specimens were discovered, and many new taxa described, often from poorly preserved and fragmentary material. In 1970 Sigogneau provided an extensive taxonomic revision of the Gorgonopsia synonymizing many of the genera and discarding some taxa based on fragmentary specimens. In her revision, Sigogneau recognized three subfamilies; the Gorgonopsinae, Rubidgeinae and Inostranceviinae.

The Gorgonopsinae as defined by Sigogneau-Russell (1989), contained 18 genera that were grouped together on the basis of sharing several characters, including a narrow interorbital and intertemporal width relative to the total length of the skull, and slender cranial arches. In contrast, the Rubidgeinae, comprising six genera (Sigogneau-Russell 1989), were characterized as having a broad interorbital and intertemporal width relative to the total skull length, and thickened cranial arches. Finally the Inostranceviinae, which contains two Russian genera, has a skull width and length ratio intermediate to that seen in the other two subfamilies.

Gebauer (2007) further revised the taxa of the Gorgonopsia, reducing the number of recognized genera from 26 to 15. Gebauer also performed a phylogenetic analysis on the group, the results of which provided support for only one of the subfamilies proposed by Sigogneau (1970) and Sigogneau-Russell (1989), the Rubidgeinae. The 'Inostranceviinae,' now represented by only a single genus, fell as the sister taxon to the Rubidgeinae, while other taxa are represented as 'evolutionary stages' leading up to the monophyletic group formed by the four genera of the Rubidgeinae: *Rubidgea, Sycosaurus, Clelandina* and *Aelurognathus.*

In this study we are focussing on *Aelurognathus* as it contains the largest number of formally described specimens, 16 in total. This genus is mostly confined to localities of the *Dicynodon* and *Cistecephalus* Assemblage Zones of South Africa, except for one specimen which comes from deposits of a similar age in Malawi. These 16 specimens are currently assigned to six species (Gebauer 2007): *A. tigriceps* (5 specimens), *A. kingwilli* (1 specimen), *A. ferox* (5 specimens), *A. maccabei* (1 specimen), *A. alticeps* (2 specimens) and *A. broodiei* (2 specimens). *Aelurognathus* is a medium- to large-sized gorgonopsians, with a heavy skull and a convex dorsal profile of the snout. The orbits are generally small and temporal opening high. Cranial arches are thick and strong and the posterior of the zygomatic arch has a ventral extension. All these materials are housed in South African collections and most of them were examined first hand by the senior author. Specimens examined so far, vary between 18 to 30 cm in skull length. Approximately 70 cranial measurements will be used to explore changes in skull shape in relation to the size variations of specimens (allometry). This analysis will allow us to determine if there are any major shape variations between different sized individuals and highlight differences that can be attributed to sexual dimorphism in this morphologically conservative genus.

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Expanding the modern reference collection of phytoliths from an *Acacia–Commiphora* grassland in northern Kenya

L.M. Pereira
Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa, and Affiliate of the National Museums of Kenya
E-mail: lucille.pereira@students.wits.ac.za

The site complex of FwJj14 is located in the Okote Member of the Koobi Fora Formation in the Lake Turkana Basin of northern Kenya and dates to *c.* 1.5 million years ago (mya). FwJj14 has yielded faunal remains which include postcranial hominin bones as well as three footprint layers (including a set of hominin footprints), stone tool artifacts and fossil wood. The aim of the current project is to contextualize the remains and behavioural signatures found in the lithological units at FwJj14 within their climatic and vegetational settings through phytolith analysis.

Phytoliths (literally 'plant-stones') are three-dimensional micrometric hydrated opal-A particles that precipitate in cells and/or between cells of the living tissues of certain plants. They are composed of amorphous biogenic silica (opal) and form due to the uptake of dissolved monosilicic acid ($Si(OH)_4$) in ground water during plant growth. Living plants do not make use of the silica in their metabolic processes and the silica is deposited within cavities in the cell lumen or the intercellular space resulting in partial mineralization of some tissues. Not all plants produce phytoliths. However, opal phytoliths have been reported for pteridophyts (Piperno 1988), gymnosperms (Klein & Geist 1978; Sangster *et al.* 1997), Mono- and dicotyledons (for example Twiss 1992; Kealhoffer & Piperno 1998; Rovner 1983). Phytoliths have been observed in different parts of plants such as the leaves, Angiosperm reproductive organs, woody tissues, culms and roots. Their morphologies vary according to the plant organ and plant type.

After the death and decay of plant tissue, opal phytoliths are released into the environment. Phytolith specimens have been identified in sediments dating as far back as the Miocene (Thomassen 1980).

For palaeo-ecologists, phytoliths both supplement and complement palaeoenvironmental information gleaned from other sources and form a useful tool in the reconstruction of past vegetational histories. Several phytolith indices have been developed as aids to environmental reconstructions. These make use of phytolith morphotypes and abundance to discriminate short- and tall- grass abundance, closed or open vegetation community structure, tree cover, the relative abundance of C_3 and C_4 grasses and identify drought stress (Diester-Haas *et al.* 1973; Alexandre *et al.* 1997; Barboni *et al.* 1999).

In order to provide a robust interpretation of past vegetation composition at FwJj14 using phytolith assemblages in palaeo-sediments, a detailed local to regional modern reference collection is required for comparison. In this study, modern vegetation samples were collected from an *Acacia–Commiphora* grassland in northern Kenya and processed using a dry-ashing technique. Observed distinct morphologies where noted and recorded following the International Code for Phytolith Nomenclature (Madella *et al.* 2005). In addition samples of modern sediment in the region were collected and processed to extract phytoliths. This to test whether the sediment samples did indeed reflect the observed modern vegetation. The test and modern reference collection database forms the initial phase of the project which aims ultimately to analyse the phytolith assemblages across all the lithological units at FwJj14. The results of this project are presented.

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The Swartkrans Paleoanthropological Research Project: progress report for 2005–2008

Travis Rayne Pickering[1,2], C.K. Brain[3] & Morris Sutton[2,4]
[1]*Department of Anthropology, University of Wisconsin, Madison, Wisconsin 53706, U.S.A.*
E-mail: tpickering@wisc.edu
[2]*Institute for Human Evolution, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa*
[3]*Transvaal Museum, Pretoria, South Africa*
[4]*School of Geography, Archaeology and Environmental Studies, University of the Witwatersrand, Johannesburg, South Africa*

Swartkrans Cave (Gauteng, South Africa) is one of the most important paleoanthropological sites in the world. Robert Broom and John Robinson's early research at Swartkrans provided large samples of the Pleistocene

hominid *Australopithecus robustus* and demonstrated that the species was synchronous and sympatric with *Homo erectus,* the direct ancestor of modern humans. C.K. Brain's subsequent work at the site resulted in the recovery of large fossil and archaeological samples that, because they were collected with acute regard for stratigraphy and taphonomy, provide essential context for these extinct hominids. In addition, Brain analysed these samples within a robust actualistic framework, allowing him to draw novel inferences about early hominid behavior at Swartkrans between *c.* 1.8 and 1.0 million years (Myr) ago. Included among Brain's most important results were: (1) the recognition that many of the hominid fossils were collected in the cave as the prey of large carnivores; (2) the identification of a hominid bone tool culture; (3) the identification of burned bones from Member 3, indicating the earliest known control of fire by hominids at *c.* 1.0 Myr ago.

Building on this foundation, we initiated the Swartkrans Paleoanthropological Research Project in 2005. Our current excavations are focused in the northeastern portion of the cave. It is here that the Lower Bank, the site's oldest known deposit (*c.* 1.8 Myr old), is in close spatial proximity to Member 4, a Middle Stone Age (MSA) unit and one of the site's most recent deposits. Not only are we interested in defining the contact between these two depositional units, but each contains important archaeological materials in need of better understanding.

Prior to our work, the sample of stone tools from the Lower Bank was very small and less informative behaviorally than the larger assemblages from the more recent Pleistocene units of Swartkrans Members 2 and 3. Our expanded lithic sample from the Lower Bank will allow us to determine if this assemblage belongs to the Oldowan Industrial Complex, the first known stone tool industry in the world or the more technologically advanced Early Acheulean Complex. In addition, the Lower Bank contains a rich, and previously unrecognized, zooarchaeological record – evidence (in the form of stone tool cut- and percussion marks) of the earliest known systematic butchery by hominids in southern Africa.

The MSA is a critical phase in human evolution that heralded the emergence of anatomically modern humans. It is, however, debatable whether these first *Homo sapiens* were cognitively and culturally modern. Technological analysis of artifacts figures prominently in testing the hypothesis that modernity was a complete and simultaneous 'package' of physical and cultural change that appeared first in Africa, at or near the beginning of the MSA. Thus, the Member 4 lithics from Swartkrans are vitally important, especially considering our finding that it is the largest and most complete assemblage from the important Cradle of Humankind area.

Finally, our excavations to determine the geomorphological relationship between the Lower Bank and Member 4 and the vertical extent of the latter yielded unexpected and exciting results. Two stratified layers underlie the MSA level: (1) a large volume of brecciated talus infill that contains an abundance of early Pleistocene fossils (including *A. robustus*); (2) a lower deposit that appears to be a previously unknown extension of the fossil- and archaeology-rich Lower Bank infill. We report here on these findings.

A preliminary assessment of the *Glossopteris*-dominated fossil plant assemblages of the Emakwezini Formation (lower Beaufort, Karoo Supergroup, South Africa) and their palaeoenvironmental setting

Rose Prevec & Emese M. Bordy
Department of Geology, Rhodes University, P.O. Box 94, Grahamstown, 6140 South Africa
E-mail: rose.adendorff@ru.ac.za; e.bordy@ru.ac.za

The Emakwezini Formation crops out in a narrow strip just inland of the eastern coast of South Africa in northern KwaZulu-Natal. The formation is of economic interest as several of its coal seams are being actively exploited at the new Somkhele mine near St Lucia. Although it has been long considered a temporal equivalent of the Normandien Formation (lower Beaufort Group) in the main Karoo Basin, this inference has been based mainly on sparse palaeobotanical evidence and the stratigraphic position of the formation within the Karoo Supergroup. Previously only *Glossopteris* leaves, *Phyllotheca australis* and organs erroneously attributed to *Dictyopteridium* had been described from this formation, on the basis of a few very small, scattered and poorly provenanced collections.

Recent regional-scale investigations of the geology and palaeobotany of the Emakwezini Formation have facilitated a more in-depth interpretation of the floras and depositional environments that persisted in this part of the Karoo Basin during the Late Permian. The formation is characterized by fining-upward successions of medium- to fine-grained sandstones and mudstones that were rapidly deposited in moist, fluvio-lacustrine settings.

Investigations of archived material, several newly discovered and other known plant fossil localities, notably those at KwaYaya railway siding (west of Empangeni) and Emakwezini Station, have led to the recognition of a well-preserved and diverse palaeofloral assemblage. The recovered suite of plant taxa strongly supports a Late Permian age for at least the upper parts of the Emakwezini Formation based on correlation with floras from Upper Permian units in the main Karoo Basin. Key discoveries include the first conclusive occurrences in the region of *Dictyopteridium flabellatum, Rigbya arberioides, Lidgettonia* spp. and *Trizygia speciosa.*

Exploration of the excavations in the open cast mine at Somkhele led to the discovery of a new flora of an as yet undetermined age. The presence of both *Ottokaria* glossopterid fructifications (typical of the Lower Permian in South Africa) and the sphenopsid *Schizoneura gondwanensis* (an index fossil for the Upper Permian in South Africa) in the same stratum may indicate that these deposits are not temporal equivalents of the exclusively Upper Permian strata at KwaYaya and Emakwezini. Alternatively, the prolonged existence of moist fluvio-lacustrine habitats in the region may have promoted the growth and

preservation of plants atypical of floras commonly associated with the Upper Permian in the main Karoo Basin.

In pursuit of Paradise Lost: a call to rekindle palaeontology in Zimbabwe

M.A. Raath
Imhoff's Gift, Kommetjie, Cape Town
E-mail: mickraath@gmail.com

The first report of fossils in what was then called Rhodesia (now Zimbabwe) was in 1901, when one of the first geologists in the newly settled country, A.J.C. Molyneux, reported fossil plants, bivalves and fish from 16 localities in the northwestern parts of the country bordering on the Zambezi Valley (Bond 1969). The fish, a palaeoniscid actinopterygian originally described as *Acrolepis molyneuxi* but now referred to the genus *Namaichthys,* indicated a Late Permian age for those beds.

More than a decade passed before the next significant reports of fossils came in – scrappy dinosaur remains, found in 1914 by H.B. Maufe of the Geological Survey on farms in the Nyamandhlovu District near Bulawayo, and described by S.H. Haughton (Maufe & Haughton 1916). At almost the same time, Ben Lightfoot, also of the fledgling Rhodesian Geological Survey, recovered fossil plants of Ecca age from the shales above and below the just-discovered coal seams at Wankie (Lightfoot 1914).

Little else of palaeontological interest came to light until that other indefatigable pioneer of Rhodesian geology, A.M. Macgregor, appeared on the scene in the 1930s. He soon made his mark, finding Precambrian stromatolites in a limestone quarry near Bulawayo (Macgregor 1941) and a re-visit to Molyneux's Sebungwe localities netted more fish, plants and bivalves, but also some unmistakable tapinocephalid dinocephalian remains (Macgregor 1946). These helped to fix a Lower Beaufort age for Molyneux's locality, specifically the *Tapinocephalus* Zone.

The arrival in 1941 of Geoffrey Bond, as part of a Royal Air Force training group stationed at Heany, near Bulawayo, during the Second World War, soon heralded a new spike in palaeontological activity. Working mainly on his own but sometimes with a few collaborators and colleagues, Bond greatly extended knowledge of Rhodesia's palaeontology and the sedimentology of its largely neglected sedimentary sequences – Rhodesia was, after all, a country occupied and settled mainly for its mineral riches, especially gold, so 'hard rocks' were what all the geologists were after; the sedimentary 'soft rocks' were dismissed as worthless 'overburden'. When the War ended, Bond stayed on and joined the National Museum of Rhodesia as its Keeper of Geology – the quaint almost Dickensian British terminology for curatorial positions in the museums of the colonial outposts – based in Bulawayo, and there he began to assemble an impressive collection of fossils, vertebrate, invertebrate and plant. He was particularly interested in the sedimentology and flora of the extensive coal deposits at Wankie, in the far northwest of the country, and of the associated equivalents of the Lower Karoo in those parts, but his field work extended well beyond that to many other parts of the rest of the country. But one man can do only so much, and despite Bond's efforts (summarized in Bond 1973), large parts of the country remained unstudied or only rather superficially picked over – distances were huge, and infrastructure in the way of roads and availability of supplies were virtually non-existent, not to mention the ever-present threats of the Big Five wild animals and a variety of deadly insect-borne diseases like malaria and sleeping sickness, to name just two.

Just over a decade later, when the University College of Rhodesia and Nyasaland opened in what was then Salisbury (now Harare), Bond became its inaugural Professor and Head of the Department of Geology. This inevitably meant that his work in the field would be severely cut back.

Bond's palaeontological work culminated in his having two fossils named after him, the graceful, gazelle-like extinct springbok *Antidorcas bondi,* and a cockroach, *Rhodesiomylacris bondi*; characteristically, he was especially proud of the latter!

I joined the staff of the National Museums of Rhodesia in 1965, based in Salisbury, and tried to do what little I could to fill the very considerable void left by Bond's departure to the academic world. My main focus was on the dinosaurs and other fauna of the Forest Sandstone Formation, an equivalent of the Upper Elliot Formation of the main Karoo Basin in South Africa, but discoveries of younger fauna in other strata broadened my focus to the overall vertebrate fauna of the Mesozoic beds of Rhodesia.

The Chimurenga War of the 1970s brought all of this to an abrupt end. When I left the country to come to South Africa in 1978, Mike Cooper took over the museum post and continued with the dinosaur work that Bond had started and I had continued. But when Cooper himself emigrated to South Africa, palaeontological work in what is now Zimbabwe virtually came to a full-stop.

Little has been done since then, other than what Tim Broderick, together with his wife, Patricia and colleagues like Phil Oesterlen and Solly Lingham-Soliar, have done, mainly during mapping and exploration in the Zambezi Valley (Ahmed *et al.* 2004). Oesterlen's work for the Geological Survey, mostly conducted while mapping and searching for exploitable hydrocarbon deposits in the Zambezi Valley, produced some surprises, including the first Late Triassic rhynchosaurs in southern Africa which co-existed with the earliest dinosaurs during late Molteno times (Raath *et al.* 1992).

Although the National Museums and Monuments of Zimbabwe have retained a post of Palaeontologist on their staff establishment, filled for several years by Darlington Munyikwa at the Zimbabwe Natural History Museum in Bulawayo – Bond's old department – Munyikwa's ability to make a meaningful contribution was frustrated by an almost total lack of resources in a country whose economy has been in free-fall for almost a decade. Indeed, its decline seems to have been accelerating even beyond the theoretical limit of 'terminal velocity'. The worthless Zimbabwean currency is now the laughing stock of the world, and the people of that country are facing personal hardships undreamed of in the colonial era. So the

chances of rekindling any sort of palaeontological work in Zimbabwe right now seem utterly fatuous and hopeless.

But literally as we speak, talks are under way between the rival political groupings in Zimbabwe aimed at ending the disastrous rule of Robert Mugabe and his ZANU-PF party. Whether or not those talks succeed, one way or another the rot must end in Zimbabwe, and peace and sense must ultimately return, sooner rather than later – it simply cannot continue indefinitely on its current path.

The people of Zimbabwe rose up, stood against, and ultimately defeated, the vastly superior colonial regime of Ian Smith and his Rhodesian Front party in the 1970s; there is no reason why they should not do the same again against their new oppressors. And when the dawn of the new era does finally break, my call is for the members of the PSSA to be ready to grasp the opportunities that are there, ready and waiting. There is huge potential for ground-breaking palaeontological work in Zimbabwe, and our Association is perfectly placed not only to take the lead in exploiting those opportunities, but also to play its part in rebuilding and expanding capacity in our neighbour to the north. We should be actively recruiting and training Zimbabwean students, to work with our own researchers, to reveal the riches that lie hidden beneath the surface of the vast, still almost untapped, Zimbabwean palaeontological treasure-house.

This is the 'Paradise Lost' that I call on us to pursue, before all is indeed forever lost to the grinding finality of erosion.

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Last interglacial fossil trackways in coastal aeolianites at Still Bay

Dave Roberts

Council for Geoscience, P.O. Box 572, Bellville, 7535 South Africa
E-mail: droberts@geoscience.org.za

The impressive Pleistocene coastal aeolianite exposures in sea cliffs east of Still Bay on the west-southern coast of South Africa host a rich archive of fossil mammalian trackways, including the African elephant (*Loxodonta africana*). A new optically stimulated luminescence (OSL) and amino acid racemization (AAR) chronology, the first joint application of OSL/AAR dating in South Africa provides a temporal framework for assessing the palaeoenvironmental significance of dune sedimentation patterns, pedogenesis and ichnology (Roberts *et al.* 2008).

The Pleistocene aeolianite exposures at Still Bay represent the recently wave-eroded remnants of a dune cordon, mainly built by coalesced parabolic dune systems. Sedimentary facies are dominated by large-scale planar cross-stratification formed by foreset progradation in the nose and trailing arms of the dunes and low angle bedding, chiefly representing sedimentation in low relief interdune terrain. The main dune-building wind regime was westerly, associated with cyclonic polar frontal systems (as at the present time). The OSL and AAR dating demonstrate ages ranging from Marine Isotope Stages (MIS) 5e to 5b and termination of Pleistocene aeolian sedimentation at ~90 ka, coinciding with late MIS 5 shoreline regression. The Pleistocene aeolianite is separated from the overlying Holocene dunes (dated to ~8 ka), by a major hiatus recorded by a zone of intense pedogenesis (Roberts *et al.* 2008).

Mammalian footprints were seen in profile, as casts on the underside of beds and as natural impressions. They provide further insights into the Last Interglacial faunas and hence contemporary floras and climate (Roberts *et al.* 2008). The taphonomic processes controlling the morphology and preservation of these unique ichnofossils were found to be complex. The presence of *L. africana* at Still Bay represents the southernmost occurrence of this species recorded to date and possibly, a closer proximity of woodland during MIS 5. This and other observations may indicate a higher moisture regime than at present. There is no available evidence that the elephants were predated by contemporary Middle Stone Age people.

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Biostratigraphic evidence from the central Free State enables a new perspective on Beaufort basin development

Anthony Rutherford

Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa
E-mail: anthony.rutherford@lonmin.com

The Karoo basin was formed as a retroarc foreland basin in front of the Cape Fold Belt in southwestern Gondwana during the Late Carboniferous to mid Jurassic (Catuneanu *et al.* 1998). The highly asymmetrical basin fill is thickest towards its southern provenance area whilst thinning rapidly to the distal north. Loading and unloading produced by the Cape Fold Belt allowed for the depocentre, foresag and forebulge to advance and retreat (distal to proximal) through time. This in turn created simultaneous areas of deposition, erosion and hiatus and a reciprocal or out of phase stratigraphy relative to stratigraphic hinge lines (Catuneanu *et al.* 1998). Accordingly the area in the vicinity of these stratigraphic hinge lines

would have a truncated and relatively rapid changing stratigraphy. This makes regional correlation of local stratigraphic units difficult. Stratigraphic hinge lines relating to the Karoo basin occur largely within the central Free State Province (Catuneanu *et al.* 1998)

Three groups (Dwyka, Ecca and Beaufort) and three additional formations (Molteno, Elliot and Clarens) make up the Karoo sedimentary infill (SACS 1980). Lithological boundaries between these groups and formations manifest changes in depositional style over time. The Beaufort Group has been subdivided into the Adelaide and Tarkastad Subgroups. While the lower Adelaide Subgoup is present only in the proximal sector of the basin the uppermost formations of the Beaufort Group (Balfour, Katberg and Burgersdorp formations), have been correlated across the basin (Groenewald 1989; Neveling 2002).

The Beaufort Group contains a rich tetrapod fossil fauna which has allowed for the Group to be subdivided into eight biostratigraphic assemblage zones (Rubidge 1995). The subdivision of the Beaufort Group into these biostratigraphic units has helped in producing a detailed description of the development of the basin and the regional lithostratigraphy within which they are contained (Catuneanu *et al.* 1998; Hancox 1998; Hancox & Rubidge 2001; Neveling 2002; Rubidge 2005; Botha & Smith 2007). Recent work has allowed for the further sub division of some of the assemblage zones, in particular the *Cynognathus* AZ into A, B and C subzones and the addition of a *Procolophon* biozone within the *Lystrosaurus* Assemblage Zone (Hancox & Rubidge 2001). In addition the change in species of *Lystrosaurus* across time has allowed for a much more finely detailed biostratigraphy for this assemblage zone (Botha & Smith 2007).

It has been argued that the distribution, both geographically and stratigraphically, of the assemblage zones supports the idea that the depocenter, forebulge and foresag advanced and retreated through time (Rubidge 2005). The theory has been shown to hold in both proximal and the distal sectors of the basin (Neveling 2002). However, until now the idea has not been tested in that portion of the basin outcropping in the central Free State and which lies in close proximity to the stratigraphic hinge lines.

In an attempt to understand the effect of the changing depocenter field work was undertaken in the vicinity of the town of Thaba Nchu in the central Free State. Numerous fossils were collected and their lithostratigraphic and geographic position carefully noted. In addition existing fossil collections from the area were accessed and utilized. Most of the fossils collected by previous workers could not be accurately placed within the local stratigraphy as the collection records contained inaccurate coordinates or general localities but they do point to the presence of particular biozones in the area.

Fossils from the *Dicynodon*, *Lystrosaurus* and *Cynognathus* Assemblage Zones were recorded. Three different species of *Lystrosaurus* (*L. murrayi, maccaigi, curvatus*) have been collected from the Thaba Nchu area. The presence of *Procolophon* and taxa belonging to subzones A and B of the *Cynognathus* Assemblage Zone demonstrate the presence of these biozones as well as the proposed *Procolophon* Zone. No taxa from the *Cynognathus* subzone C were recorded.

The combined use of bio- and lithostartigraphy has refined current understanding of the stratigraphy and pointed to great attenuation of the Beaufort Group in the study area.

Stratigraphic gaps have been highlighted, thus supporting the idea of reciprocal infilling of the Beaufort Basin as the forebulge and foresag shifted with time.

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Macroscelidea from the Miocene of the Sperrgebiet, Namibia

Brigitte Senut

Muséum National d'Histoire Naturelle, Département 'Histoire de la Terre', USM 203 et UMR 5143 CNRS, CP 38, 75231 Cedex 05, France
E-mail: bsenut@mnhn.fr

The diamond exploitation in the Sperrgebiet (Southern Namibia) led to the discovery of several Miocene deposits which have yielded a diverse and rich mammalian fauna in different settings. These deposits occur in the fossil loops of the Oranje river (Arrisdrift and Auchas Mine) in the South and in fluviatile and flood plain deposits in the North (Langental, Grillental and Elisabethfeld). Among the mammals, the Macroscelididae (elephant-shrews) are very well represented. The first ones from the area was described by Stromer in the early 1920s.

Oranje River

The first Macroscelideans were discovered at Arrisdrift in the mid-1970s by Corvinus (Corvinus & Hendey 1978) which were later referred (Hendey 1978) to the East African genus *Myohyrax oswaldi,* a very hypsodont species which occurs at Songhor, Rusinga and Karungu in Kenya and at Napak in Uganda (Andrews 1914; Hopwood 1929; Whitworth 1954; Patterson 1965; Butler 1984). New exca-

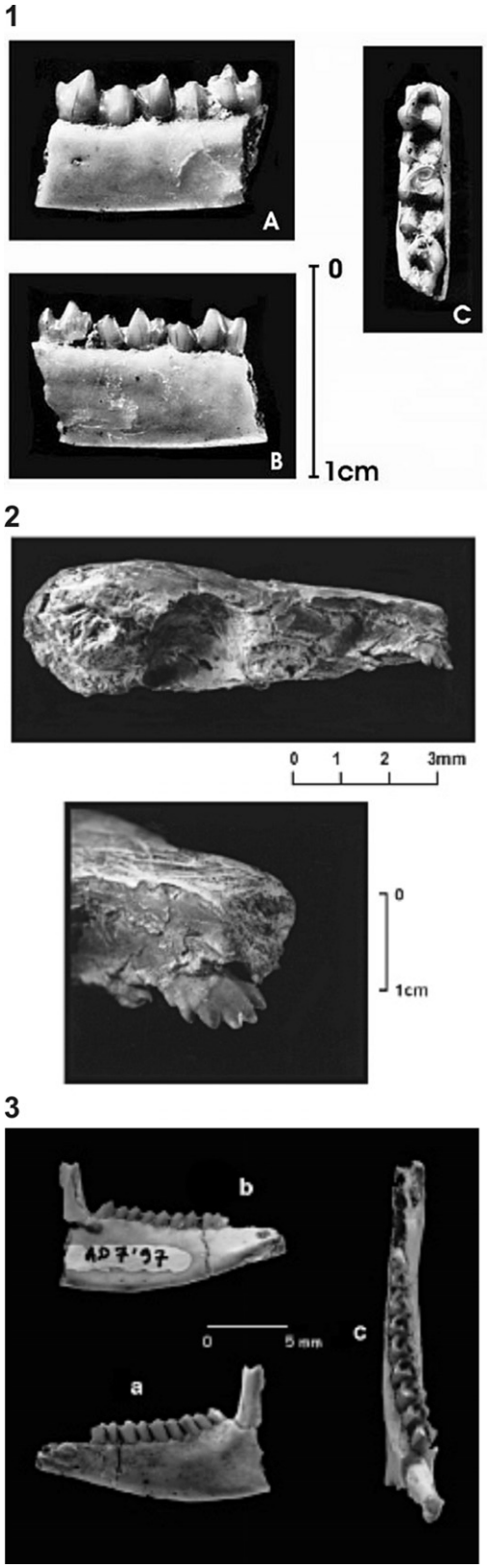

Figure 1. **1**, Mandibular fragment of *Miorhynchocyon gariepensis* (A, labial view; B, lingual view; C, occlusal view); **2**, skull of cf. *Miorhynchocyon gariepensis* (above: lateral view; below: detail of the upper I1); **3**, Mandible of *Myohyrax oswaldi* (a, labial view; b, lingual view; c, occlusal view).

vations were made in the Orange River deposits by the Namibia Palaeontology Expedition and fossils have been unearthed at two sites: Auchas Mine from the Lower Miocene and Arrisdrift from the Middle Miocene (Pickford & Senut 1999, 2003). Two taxa have been described: the

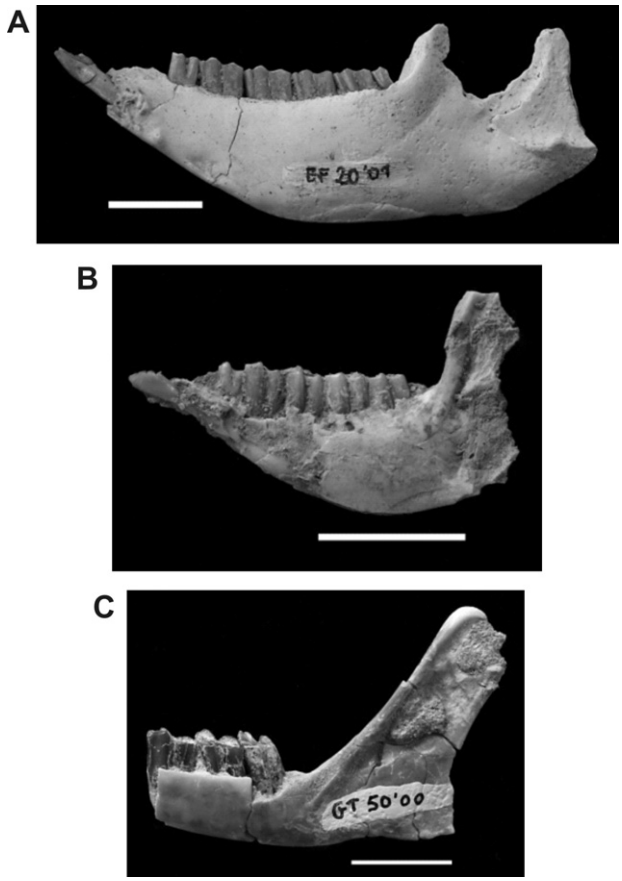

Figure 2. **A**, Left mandible of *Protypotheroides beetz*; **B**, left mandible of *Myohyrax* oswaldi; **C**, left mandible of the large brachyodont species.

abundant hypsodont *Myohyrax oswaldi* (more than 400 specimens) and the poorly represented (3 specimens) brachyodont *Miorhynchocyon gariepensis* (Senut 2003) which recalls the East African miorhynchocyonines described by Butler in 1984, but differs from them by the talonid which is much lower than the trigonid and by the fact that the paraconid is not separated from the protoconid by a deep groove (Fig. 1.1). A large skull and three upper incisors with six main digitations have been tentatively referred to this latter taxon.

However, new discoveries at the Lower Miocene site of Grillental and Langental in the Northern Sperrgebiet suggest that these specimens might belong to a new taxon (Fig. 1.2).

Northern Sperrgebiet

In the Northern Sperrgebiet, the Lower Miocene infillings of Oligocene valleys such as Langental and Grillental or flood plain deposits such as Elisabethfeld yielded abundant macroscelidids remains. The macroscelidids are known by two hypsodont species, a small one which is the same as that occurs at Arrisdrift, *Myohyrax oswaldi* (Fig. 1.3) and a large one, *Protypotheroides beetzi* described by Stromer in 1922 and 1926 from Lüderitzbucht in the Sperrgebiet. The 2 taxa are represented at the three main sites by mandibular, dental, cranial and postcranial remains. At Elisabethfeld, a mandible of a Miorhynchocyoninae is present but is bigger than than the one from Arrisdrift. At Grillental and Langental, a few specimens (a mandible and a few upper incisors with several digita-

tions) of a very large brachyodont species have been found and probably belong to a new taxon.

In terms of numbers of individuals, the macroscelidean fauna is largely dominated by hypsodont species which suggest that these animals were adapted to herbivory, eating grass or seeds. We note a strong imbalance between the frequency of hyposodont and brachyodont species, the latter being very rare; as is also the case in the Middle Miocene sites of the Southern Sperrgebiet. At this stage, it is difficult to suggest any explanation; was there any competition between the species? It seems that the brachyodont ones were slightly more diverse in the Lower Miocene sites than in the Middle Miocene ones. A study of Oligocene macroscelidids might shed some light on the matter.

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Vertebrate taphonomy and ichnology of a Permian 'wet desert' in central Pangea

Roger M. H. Smith[1], Christian A. Sidor[2], Neil J. Tabor[3], J. Sébastien Steyer[4] & Dan S. Chaney[5]

[1]*Iziko South African Museum, P.O. Box 61, Cape Town, 8000 South Africa*
E-mail: rsmith@iziko.org.za

[2]*University of Washington, Seattle, Washington, U.S.A.*

[3]*Southern Methodist University, Dallas, Texas, U.S.A.*

[4]*CNRS-MNHN, Paris, France*

[5]*Smithsonian Institution, Washington, U.S.A.*

Paleogeographic models position the vertebrate fauna of the Upper Permian Moradi Formation, northern Niger, approximately 20 °S of the paleoequator in central Pangea (Fig. 1). This basin lies east of the Tethys sea within a 5000 km wide 'corridor' between Gondwana and Laurasia (Gibbs *et al.* 2002; Ziegler *et al.* 1997). Recent field investigations have confirmed that climate was warm, arid with seasonal monsoonal rainfall (Kutzbach & Gallimore 1989; Kiehl *et al.* 2005) and, possibly as a result of these unique physioclimatic conditions, the tetrapod fauna shows a high degree of endemism (Sidor *et al.* 2005).

The Moradi Formation of northern Niger has yielded the only substantial tetrapod fauna from the Upper Permian of central Pangea (de Ricqlès & Taquet 1982)The body fossil record presently consists of two large temnospondyls *Nigerpeton* and *Saharastega*, the pareiasaur *Bunostegos,* the captorhinid *Moradisaurus,* and a possible therapsid (Taquet 1967). This endemic fauna, which is strikingly different in composition from others of the Upper Permian, suggests that the high-latitude southern African and Russian faunas have yielded an oversimplified picture of the distribution of terrestrial faunas in Pangea.

The Moradi sediments accumulated on a flat, semi-arid to arid alluvial plain with large, low angle gravelly alluvial fans prograding from the tectonically active Aïr Massif to the east, which at times impinged on a large stable meandering channel system flowing generally northwards along the axis of the basin.

Taphonomy of 'pareiasaur cemetery' site

Fossil-rich intervals are characterized by wide shallow anastomosing channels conformably filled with a conglomerate of reworked pedogenic carbonate nodules, rhizocretions, and claystone clods overlain by massive sandy siltstone. At Ibadanane 20 km west of Arlit, an area measuring 280 × 50 m was found to contain at least 15 concentrations of dissociated bones comprising ribs, vertebrae and long bones of pareiasaurians (Fig. 3).

Preliminary quarrying revealed disarticulated, but still associated, skeletons of *Bunostegos* as well as amphibians such as *Nigerpeton* and the captorhinid *Moradisaurus.* These 'bone on bone' bonebed occurrences are generally elongated and dip gently towards the channel axis (Figs 4 & 5). The preliminary interpretation of the depositional setting of the pareiasaur 'cemetery' site is of a distal alluvial fan where ephemeral flash-flood streams swept across a silt-dominated loessic plain, scouring through the sparsely vegetated soils to the more resistant calcrete horizons, reworking previously buried bones and burying desiccated drought-stricken cadavers.

Sedimentology and ichnology of Moradi end-point playa deposits

Localized depressions filled with brecciated limestone overlain by finely-laminated calcic siltstone are interpreted as end-point playa deposits (Fig. 6). They clearly demonstrate that this 'wet desert' hosted standing water bodies and preserve a range of insect, arthropod, amphibian and reptile tracks not previously recorded from the Moradi Formation.

The trackway horizons contain an exquisite tetrapod ichnofauna that is preserved within a local, 1.2 to 1.5 m-thick deposit of thinly bedded calcareous siltstone, with polygonal desiccation cracks upon the upper surfaces. The ichnofauna consists of beautifully preserved trackways and isolated footprints made by at least three

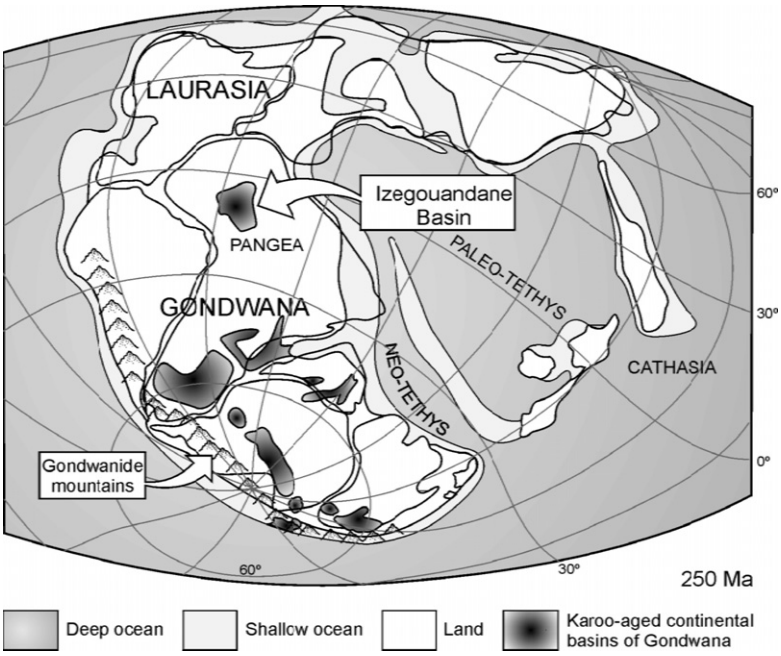

Figure 1. Palaeogeographic setting of the Izigouandane Basin in the latest Permian (after Ziegler *et al.* 1997).

types of amphibians and reptiles, which can be distinguished by their digit number and shape, as well as attributes of their trackways.

The footprints and trackways are preliminary referred to the ichnotaxa *Hylopus* herminatus or *Hyloidichnus* (ascribed to captorhinomorphs or bolosaurs), *Dromopus* or *Rhynchosauroides* (ascribed to lacertoids), and ?*Paradoxichnium* (with parallel digits – possibly therapsid). Interestingly, all of these records suggest Euramerican rather than Gondwanian affinity, as is the case of the associated body fossils outlined above. Importantly, the ichnofauna documents small-bodied tetrapods that have

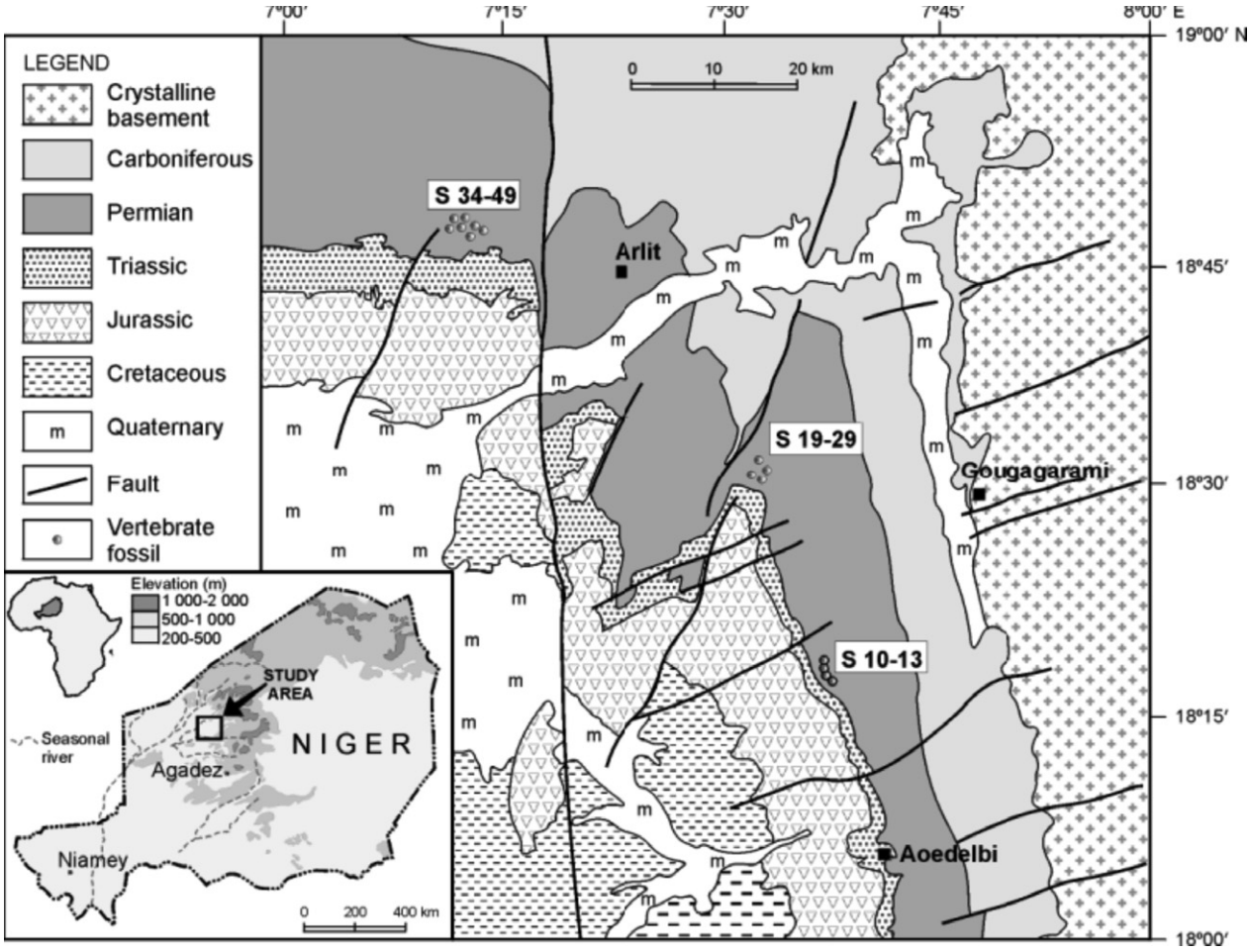

Figure 2. Geology of the study area around Arlit in northern Niger.

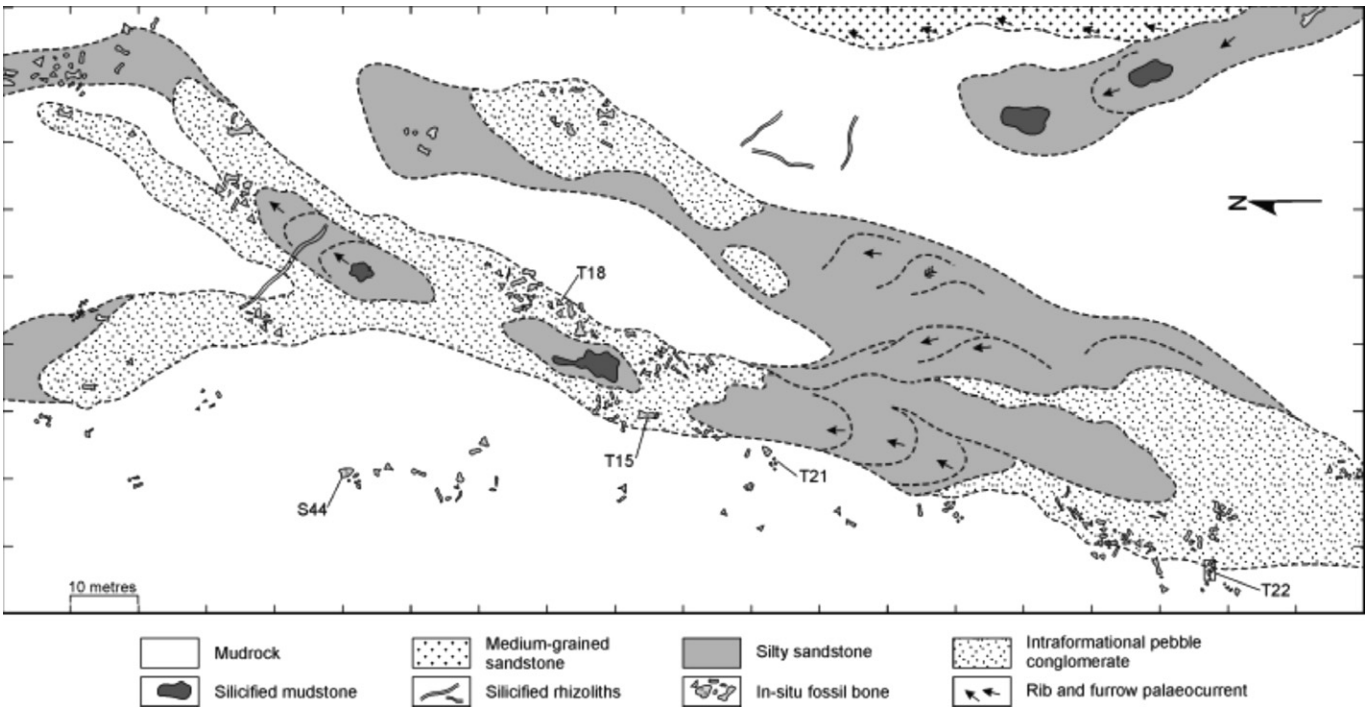

Figure 3. Map of channel-hosted pareiasaur skeletons in the Moradi Fm.

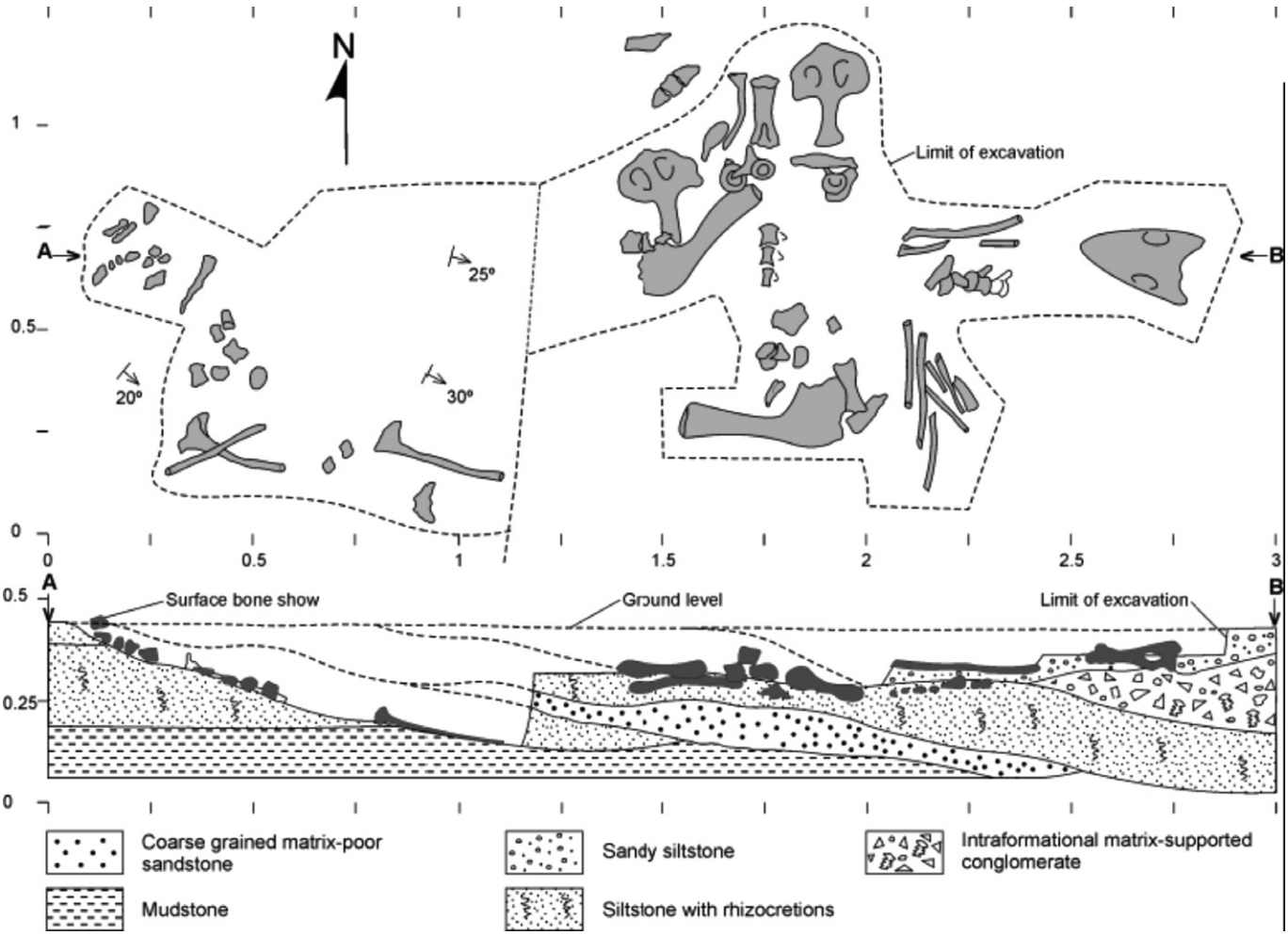

Figure 4. Quarry plan and vertical section through T22 in Fig 3, a scattered *Bunostegos* skeleton in the Moradi Fm.

Figure 5. *Bunostegos* skeleton T22 (Chris Sidor working on the skull).

not yet been recovered from the Moradi Formation as body fossils possibly because of preservational bias but more likely due to lack of sustained and systematic collecting.

The ichnofauna consists of beautifully preserved trackways and isolated footprints made by at least three types of amphibians and reptiles, which can be distinguished by their digit number and shape, as well as attributes of their trackways. The footprints and trackways are preliminary referred to the ichnotaxa *Hylopus herminatus* or *Hyloidichnus* (ascribed to captorhinomorphs or bolosaurs), *Dromopus*or , *Rhynchosauroides* (lacertoids in shape, see Fig. 7), and ?*Paradoxichnium* (with parallel digits). Interestingly, all of these records suggest Euramerican rather than Gondwanian affinity, as is the case of the associated body fossils outlined above.

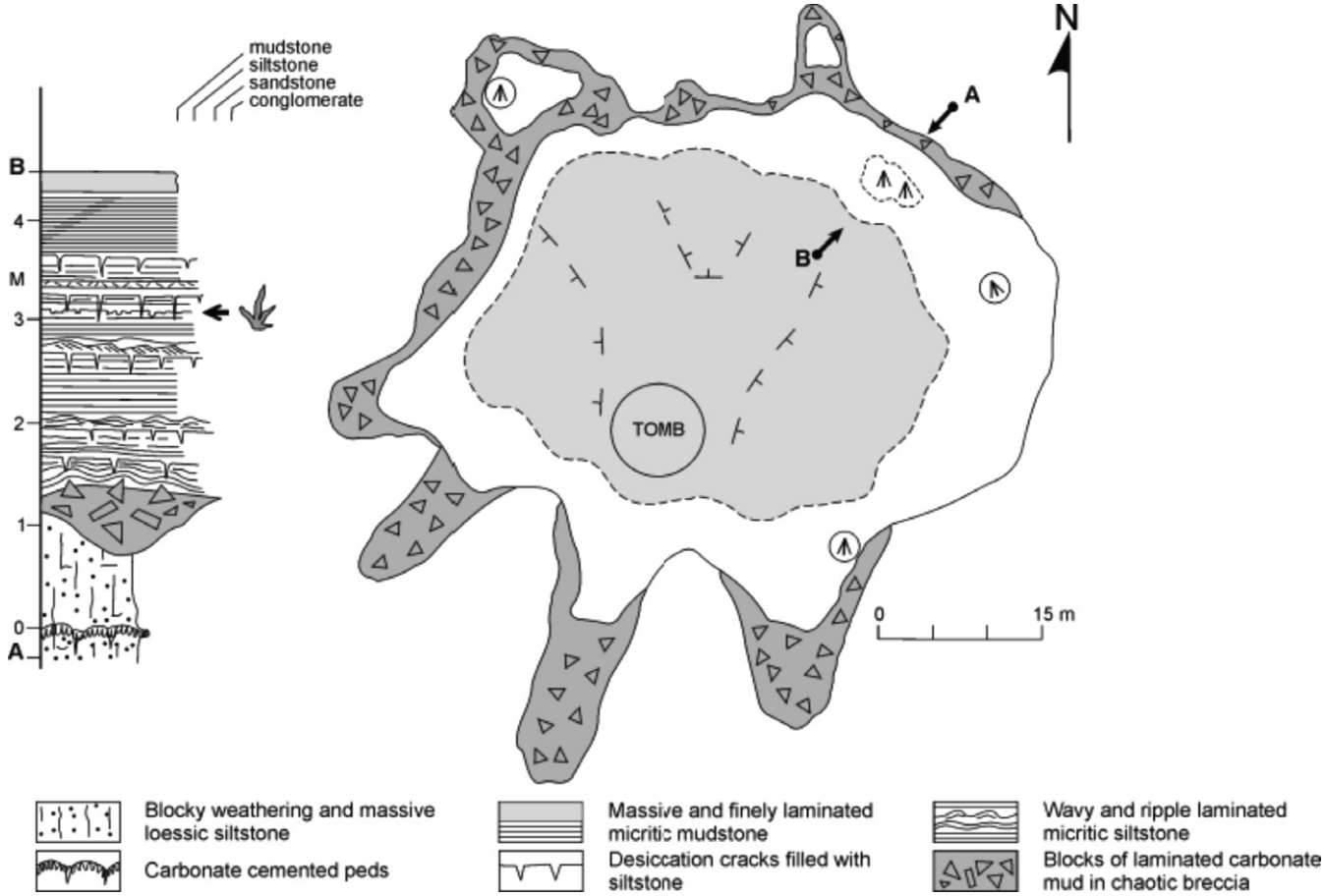

Figure 6. Map and section through a playa-hosted trackway site in the upper Moradi Fm.

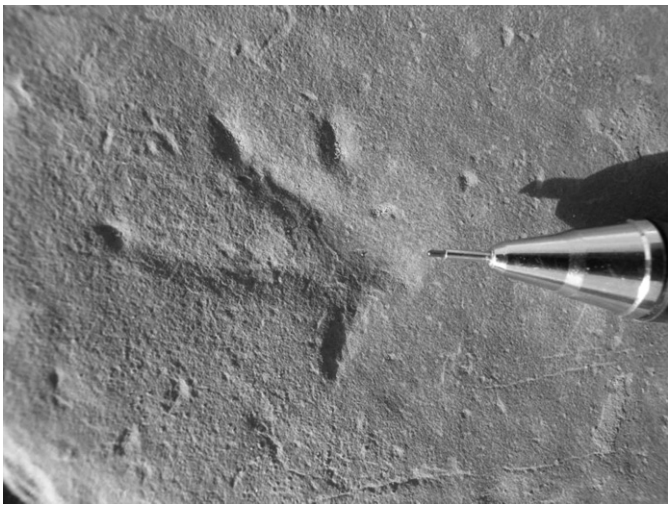

Figure 7. Small trackway with lacertoid affinities tentatively ascribed to *Dromopusor* or *Rhycosauroides*.

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Are bovid dietary preferences integral in understanding past ecosystems?

Christine M. Steininger[1], Peter S. Ungar[2], Nikolaas van der Merwe[3] & Lee R. Berger[4]

[1]*Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa*
E-mail: ihominin@gmail.com

[2]*Department of Anthropology, University of Arkansas, Fayetteville, AK, 72701, U.S.A.*
E-mail: pungar@uark.edu

[3]*Department of Archaeology, University of Cape Town, Rondenbosch, 7701 South Africa*
E-mail: nikolaas.vandermerwe@uct.ac.za

[4]*Institute for Human Evolution, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa*
E-mail: profleeberger@yahoo.com

As primary feeders, bovids have varied diets and occupy a diverse range of ecological niches. They are abundant in modern African ecosystems and prolific in the fossil record. Dietary strategies of modern and fossil bovids are often put into broad categories along the browser/grazer continuum: grazer, mixed feeder and browser. Often reconstructions of ecosystems rely heavily on information about diet at these broad scales. However, are bovid dietary preferences integral in understanding past ecosystems? There has been substantial debate regarding whether these categories are sufficient to explain the full extent of dietary diversity among bovids. Testing dietary hypotheses has often been limited by these broad trophic categories which require arbitrary boundaries. A more informative interpretation of dietary behaviour can only be accomplished by eliminating the circularity of these subjective trophic categories, and examining the full extent of diet variability or flexibility amongst bovid species. The most informative data are not always what the average behaviour of a particular bovid species reflects, but rather what the outliers of the group may imply. Dietary variability or flexibility may be an essential adaptive strategy especially during times of vegetation shifts due to climatic fluctuations. In this regard, intraspecific variations in diet can reveal trends about bovid dietary strategies, and changes in those trends can provide insight into how bovids respond to local climatic change.

This research tests whether the dietary strategy of fossil bovids remained constant at two spatio-temporally similar Plio-Pleistocene South African hominin sites. Dental remains from various fossil bovid species were selected from Swartkrans and Cooper's Caves. Using a multi-proxy approach, stable carbon isotope, dental microwear texture analysis, and mesowear techniques were applied to provide a comprehensive interpretation of the dietary strategies of the bovids. The study was guided by the following research aims: (1) identify the dietary strategies of fossil bovids from two contemporaneous sites, (2) determine the variation or flexibility of dietary strategies, (3) using the data from 1 and 2, compare the dietary strategies of fossil bovids between the different Swartkrans Members (1–3) and Cooper's Cave D locality; and (4) if possible, infer ecological stability or heterogeneity using the dietary strategies of fossil bovids from these various deposits.

To understand the dietary complexity of fossil bovids and their relevance to addressing palaeoecological questions, a multi-proxy approach applied at multiple spatio-temporally similar fossil sites is required. While different techniques have their strengths and weaknesses, when applied together, they are able to result in a solid palaeodietary reconstruction.

This research has been funded by the Palaeontological Scientific Trust. We are grateful to Mike Raath and Bernhard Zipfel from the University of the Witwatersrand along with Francis Thackeray, Teresa Kearney and Stephany Potze from the Transvaal Museum (Northern Flagship Institution) for access to the fossils.

RoA mesowear perspective on the diets of ungulate from the middle Pleistocene levels of Elandsfontein, Western Cape, South Africa

Deano D. Stynder

Iziko South African Museum, Natural History Department: Cenozoic Palaeontology, P.O. Box 61, Cape Town, 8000 South Africa
E-mail: dstynder@iziko.org.za

The dietary regimes of 15 ungulate species from the middle Pleistocene levels of the hominid-bearing locality

of Elandsfontein, South Africa, are investigated using the mesowear technique. Previous studies, using taxonomic analogy, classified 12 of the studied species as grazers (*Redunca arundinum, Hippotragus gigas, Hippotragus leucophaeus, Antidorcas recki, Homoiceras antiquus, Damaliscus* aff. *lunatis, Connochaetes gnou laticornutus, Rabaticerus arambourgi, Damaliscus niro, Damaliscus* sp. nov., an unnamed 'spiral-horn' antelope and *Equus capensis*), one as a mixed feeder (*Taurotragus oryx*) and two as browsers (*Tragelaphus strepsiceros* and *Raphicerus melanotis*). While results from mesowear analysis sustain previous dietary classifications in the majority of cases, five species were reclassified. Three species previously classified as grazers, were reclassified as mixed feeders (*Hippotragus gigas, Damaliscus* aff. *lunatus* and *Rabaticerus arambourgi*), one previously classified as a grazer, was reclassified as a browser (the 'spiral-horn' antelope), and one previously classified as a mixed feeder, was reclassified as a browser (*Taurotragus oryx*). While present results broadly support previous reconstructions of the Elandsfontein middle Pleistocene environment as one which included a substantial C_3 grassy component, the reclassifications suggest that trees, broad-leaved bush and fynbos were probably more prominent than initially thought.

A study of tooth crown form to elucidate niche partitioning in late Miocene/early Pliocene hyaenas from 'E' Quarry, Langebaanweg, South Africa

Deano D. Stynder

Iziko South African Museum, Natural History Department: Cenozoic Palaeontology, P.O. Box 61, Cape Town, 8000 South Africa
E-mail: dstynder@iziko.org.za

The late Miocene/early Pliocene 'E' quarry deposits at Langebaanweg, South Africa, have yielded fossil material of at least four hyaena species *(Ikelohyaena abronia, Hyaenictitherium namaquensis, Chasmaporthetes australis, Hyaenictis hendeyi*). The co-occurrence of four closely related hyaenids at this site raises interesting questions about niche partitioning which have not been sufficiently addressed. In the only previous systematic attempt to tackle this issue, an analysis of M1 lengths, M1 trigonid lengths and P3 widths found evidence for character displacement in the first two variables. While this study suggests that morphological character displacement was a factor in niche partitioning among the 'E' Quarry hyaenas, it was only based on two teeth and three metric variables. In the current study, a geometric morphometric approach is used to compare P2, P3, P4 and M1 (carnassial) crown form to better understand feeding niche partitioning among the four Langebaanweg hyaena species. While results indicate that the four species are very similar in crown shape, *I. abronia* and *H. namaquensis* tend to have slightly shorter, broader cheek teeth than *C. australis* and *H. hendeyi*. This suggests that *I. abronia* and *H. namaquensis* may have been less carnivorous than *C. australis* and *H. hendeyi.* The biggest difference between the species, however, relates to crown size. The four species are evenly spaced with respect to median crown size in all teeth except the P4. These results support a previous suggestion that size-related character displacement was in operation among the 'E' Quarry hyaenas and probably played a major role in reducing inter-specific competition.

Dental size and frequency of pathologies in the teeth of a small-bodied population of mid–late Holocene Micronesians, Palau Micronesia

M.G. Tawane & L.R. Berger

Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa
E-mail: tawanem@yahoo.com

Introduction

The study of the size and shape of teeth has generated more literature than any other aspect of dental anthropology (Wolpoff 1971). The notion of a linear or exponential relationship between crown size and body size is recurrent in the dental and paleontological literature. For some human groups, low but positive correlations between tooth size and body measures have been noted, and some of the correlations are significant (Garn *et al.* 1968), demonstrating that teeth remain in proportion to body size, whatever the body size of a mammal.

However, a recently discovered small-bodied population of hominins from Palau, Micronesia, has been shown to exhibit a number of unusual traits, including extremely small body size, facial size reduction and high degrees of robusticity. They also appear to possess very large teeth and high frequency of certain tooth forms. The presences and absences of these tooth forms are normally observed at very low frequencies in modern human population.

This study intended to compare the size and shape of the teeth of the Palauan population to living humans and fossil hominids, as well as examine the frequency of four apparent pathologies noted in the Palauan samples.

Materials and methods

Four different population groups – namely namely Zulus, Tswanas, Khoisan and Europeans were examined in this study. The teeth of 100 specimens were measured from each population – 50 males and 50 females. Standard measurements of the teeth were obtained using the dimension described by Shaw (1931). In addition, the entire sample of humans from the Dart collection, comprising approximately 2500 specimens, will be used to record the presence and absence of the four pathologies. These pathologies are congenital absence of the third molar, incisiform canines, caniniform premolars and rotated premolars. Degree of expression, orientation and other characters were noted for observed pathologies. Photographs of the pathologies were also taken. Both the measurements and observations were then compared to the Palau sample using statistical analysis. Univariate and bivariate analysis of the Stat view program were used.

Results

The teeth of the Palauens were larger than those of the four population groups, despite having very small stature, and skull, and absence of cheeks. The Khoisan had the smallest teeth of all the groups studied, supporting the fact that they have microdont dentition (Drennen 1925; Haeussler *et al.* 1989). They were followed by the Europeans, in some instances having the same dimensions as the Zulus, and Tswanas, which have mesodont dentition. Megadontia as observed in the Palauen sample could be due to the diet they consumed, or a lag phase in the reduction of the teeth (Berger *et al.* 2008).

Frequencies of pathologies were low in the human sample compared to the Palauen sample, and this is mostly due to the less space available for the teeth to develop in. Teeth erupting so close together tend to look more like the teeth next to them (Greenfield 1993).

Estimating body size from tooth size is something that needs to be done carefully, since it is possible that the linear relationship between the two can be lost, as have been demonstrated by the Palauen Micronesians. There is no optimum tooth size that would meet the requirements for all populations. Rather tooth size must be viewed in relationship to other factors, such as diet.

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The identification of fossil herpetological remains from selected Plio-Pleistocene aged fossil-bearing sites in South Africa

Nonhlanhla Vilakazi & Lee R. Berger

Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa
E-mail: nhleiks2002@yahoo.com

Introduction

The abundant southern African animal fossil assemblages have long been recognized as important as a record of ancient life (Lee-Thorp *et al.* 2003). In particular, the Plio-Pleistocene aged fossil deposits are among the most important record of animal evolution during this period on the African continent (Vrba *et al.* 1995). These sites, largely confined to cave breccias in dolomitic regions, have proven particularly important in revealing information about the mode and tempo of human evolution (Hilton-Barber & Berger 2002), as well as the evolution of non-hominin macro- and micro-mammals (Vrba *et al.* 1995). These sites have also been recognized as being important for understanding the recent evolutionary history of other groups including avians (Avery 2001).

Given the intensive research conducted on these fossil assemblages, it is surprising to note that little attention has been given to the herpetological remains that are known to be present in these assemblages. This is even more surprising given the fact that extant herpe-fauna are recognized as being particularly sensitive in their adaptation to specific environments and are often found in very constrained geological environments, plant communities and temperature ranges (Goin & Goin 1971). Thus, the identification of specific forms of fossil herpetofauna at a variety of taxonomic levels could lead to a greater understanding of both the evolution of specific forms of herpe-fauna as well as be a benefit to increased understanding of the palaeoenvironments of these Plio-Pleistocene aged sites. This in turn could lead to insight into changes in environment that affected the mode and tempo of evolution in mammal species.

This study helps in redressing the lack of understanding of the herpe-fauna of selected southern African sites through a detailed study of the fossil herpe-fauna hypothesized to exist in the fossil collections.

The main purpose of this project was to assess the variety and abundance of herpe-fauna (herpetiles) contained in Plio-Pleistocene fossil record of South Africa with the intent of identifying where possible families, genera and species that may give insight into ecology of sites during different temporal periods.

Materials and methods

Examination of the known herpe-fauna and the search for additional material will be conducted in the fossil assemblages of Makapansgat, Swartkrans, Coopers, Gladysvale and Taung. Several of these sites have already been recognized as containing herpe-fauna in varying degrees of abundance, indicating that the condition within these deposits was suitable at the time of accumulation for preserving herpe-fauna. Herpe-fauna was identified through a visual search of the existing material and comparison with modern herpetological material.

Once identified, herpe-fauna was sorted into the highest taxonomic category possible based on the condition and quality of material recovered. Once this material has been sorted, it was then described in detail and compared and contrasted with known extant species where possible.

A broad community of herpe-fauna was then constructed for each of the assemblages. At this point, this study attempts to find meaningful patterns in these communities and examine whether the ancient herpe-faunal communities can give insight into broad palaeo-environments. This is done through comparisons with extant communities of herpe-fauna from known environments.

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An evolutionary explanation why the facial nerve in birds passes lateral to the polar cartilage while in crocodiles it passes medial to the homologous structure

J. Welman[1] & J. Klembara[2]

[1]*Department of Biology, University of Limpopo (Medunsa Campus)*

[2]*Department of Ecology, Comenius University, Bratislava, Slovakia*

One of the classical problems in anatomy is represented by the different path of the facial nerve (palatine ramus) from its exit from the endocranium to its entry into the 'vidian canal' in crocodiles and birds. It seems clear that both the polar cartilages and the palatine rami of the facial nerve are homologous structures and yet, in crocodiles, the nerve pass medial to the polar cartilage but in birds and lizards, it passes lateral to it. Study of crocodile and bird ontogeny confirms the problem but the resolution of recapitulation is inadequate to suggest what happened in the phylogeny. It was the objective to investigate this problem at the hand of direct palaeontological evidence.

Well-preserved, carefully prepared braincases of a phylogenetic series of fossil reptiles linking birds and crocodiles to their reptilian ancestors were studied to obtain direct evidence of what happened in natural history. The path of the palatine ramus relative to the position of the polar cartilage and the dermal basitemporal covering its ventral surface on the basicranium was reconstructed and compared in the various fossil forms.

The path of the palatine ramus of the facial nerve can be reconstructed with some confidence according to foramina and grooves that indicate the path of the nerve in the different fossils. We found that the polar cartilage and the basitemporal shortened over a period of 50 million years and that this opened up a fissure between these elements and the basioccipital about 200 million years ago. The path of the facial nerve coincided with this fissure and the nerve slipped into this crack in some early dinosaurs. When the polar cartilage and basitemporal subsequently expanded again, the nerve became trapped, now following a route medial to the polar cartilage.

This landmark development is documented in the anatomy of all dinosaurs and the earliest crocodilomorphs that made their appearance slightly later in time. On the one hand it strongly suggests that modern crocodiles are true dinosaurs and on the other hand, it confirms that birds are neither closely related to crocodiles nor to dinosaurs.

Evolution of the lateral column of the hominin foot – evidence from the StW 114/115 fifth metatarsal (Sterkfontein)

Bernhard Zipfel[1,2], Jeremy M. DeSilva[3] & Robert S. Kidd[2,4]

[1]*Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa*
E-mail: bernhard.zipfel@wits.ac.za

[2]*Institute for Human Evolution, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa*

[3]*Department of Anthropology, University of Michigan, 101 West Hall 1085 South University Avenue Ann Arbor, MI 48109-1107, U.S.A.*

[4]*School of Biomedical and Health Sciences, University of Western Sydney, Cambelltown, NSW 2560, Australia*

Introduction

A complete, undistorted right fifth metatarsal, StW 114/115 was recovered in August 1982 by the Sterkfontein excavation team under A.R. Hughes. Deloison (2003), in describing early hominin foot bones from South Africa, interpreted the anatomical features of StW 114/115 as being consistent with those of an australopithecine from Member 5. Given the proximity of StW 114/115 to dental remains from Member 4 (Moggi-Cecchi *et al.* 2006), it is reasonable to hypothesize that the metatarsal belongs to *Australopithecus africanus,* though we caution that given the complex stratigraphy of Sterkfontein, there remains the possibility that StW 114/115 is from early *Homo* or from *Paranthropus robustus.*

The hominoid foot consists of a lateral column (that leads to the fourth and fifth digits) and a medial column (that leads to the hallux and the second and third digits) (Aiello & Dean 1990). The medial column of the anterior elements of the foot, best represented by the first metatarsal, has been studied to some extent (e.g. Lewis 1980; Susman & Brain 1988; Deloison 2003; Susman & de Ruiter 2004; Zipfel & Kidd 2006). The lateral column of the anterior foot, however, has received less attention due to the paucity of complete fourth and fifth metatarsals in the fossil record. The StW 114/115 fifth metatarsal, therefore, being the earliest complete hominin fifth metatarsal to date, provides a unique opportunity to further investigate the lateral column of the hominin foot and its evolution.

Materials and methods

The fossil was compared to human and great ape counterparts. Morphological comparisons were made on fifth metatarsals from Victorian British humans (11 females and 16 males). Also included in comparisons were wild-shot great ape individuals comprising chimpanzees (20 females and 19 males), gorillas (20 females and 19 males) and orang-utans (16 females and 11 males). In addition to extant apes and humans, StW 114/115 was compared to the partial fifth metatarsals SKX 33380 from Member 3 of Swartkrans, South Africa (Susman 2004), OH 8 from Bed I, Olduvai Gorge, Tanzania (Day & Napier 1964; Leakey *et al.* 1964; Susman & Stern 1982), AL 333-13 and AL 333-78 from the Afar Locality, Ethiopia (Wood 1974; Grausz *et al.* 1988; Gebo & Swartz 2006) and KNM ER-803f from Koobi Fora, Kenya (Latimer *et al.* 1982).

Morphometric analyses of StW 114/115 are based on the four extant species and females and males were treated as separate groups. Eight variables were chosen so as to reflect the broad morphology of the bone and its functional attributes. The comparative fossils are excluded in the morphometric analysis because of their fragmentary nature. The linear dimensions are based loosely on the definitions by Martin & Saller (1957).

The multivariate objective of the study was to establish patterns of morphological discrimination within and between the groups, initially using principal components analysis (PCA) (Blackith & Reyment 1971; Bryant & Yarnold 2001) and subsequently using canonical variates analysis (CVA) (Reyment *et al.* 1984; Albrecht 1980, 1992). Computations for both analyses were undertaken using PC *SAS*® 9.1.

Non-metric observations of StW 114/115 are the torsion angle of the metatarsal head relative to the base and qualitative assessments of the sagittal and transverse curvatures of the shaft. In addition, plain film radiographs were examined for cortical thickness and pathology.

Results

The general morphology of the bone appears to be very human-like and of an adult. The shaft curves in the transverse plane with the concavity on the lateral side. There is a medial (internal) torsion of the head of approximately 10° measured as the deviation from the vertical axis of the metatarsal head relative to the vertical axis of the base. The shaft is short and stout with a distinct sagittal curvature plane producing a plantar concavity. In profile the shaft has approximately the same dorsoplantar height from just distal to the base, to just proximal to the head giving it a parallel-sided appearance. The base is expanded and the lateral border traces a gentle curve as it passes from the proximal end to the shaft. In profile, the distal articular surface extends well onto the dorsum of the bone and is flanked by prominent epicondyles. On the dorsum there is a shallow sulcus, or depression, between the head and the shaft.

The East African fossils have in common with the Sterkfontein fifth metatarsal an expanded base with the lateral border tracing a gentle curve as it passes from the base to the shaft. In profile, the distal articular surface of StW 114/115 extends onto the dorsum of the bone as in modern humans. The head of StW 114/115 displays an axial torsion which is medial or internal and similar to that of modern humans. In contrast, the apes have a torsion of the metatarsal that is laterally or externally rotated so that the head faces the other metatarsals (Morton 1922; Lewis 1980; Aiello & Dean 1990). The basal articulations for the cuboid and fourth metatarsals are human-like in the acute angle of the articulation with the cuboid with respect to the shaft. The dorsoplantar shape of the proximal articular surface of StW 114/115 is similar to all of the other known hominin metatarsals in being flatter than modern African ape metatarsal facets and falling in the distribution of modern human fifth metatarsal-cuboid facet curvature (DeSilva 2008). The ape proximal articulation with the cuboid is 'elongated' in the mediolateral direction (Susman 1983) and appears also to be more mediolaterally concave than in humans, StW 114/115, OH 8, AL 333-78 and KNM ER-803; this is therefore a distinct feature discriminating the apes from hominins. AL 333-13 has a slightly concave articulation for the cuboid in the mediolateral direction.

Principal components analysis of the eight linear measurements reveals that the majority of the variation lies within the first two principal components, together accounting for just over 76 % of the total variance. The fossil, StW 114/115 lies centrally on the first principal component within the spread of humans. On the second principal component, containing 17.86 % of the total variation, the fossil lies negatively to all the apes, centrally within the humans.

In the CVA of the fossil together with the extant species, the majority of the discrimination lies within the first two variates, together accounting for over 92 % of the total discrimination. Subsequent variates contain considerably less variation, the third, 11.12 % and the fourth, 3.70 % of the total discrimination. Along the first canonical variate, the fossil lies between the human males and chimpanzee females. On the second canonical variate there is a clear discrimination between the fossil, the apes and humans. The fossil is thus of distinct form but has the greatest affinity for humans and chimpanzees. On the third canonical variate the fossil lies broadly between the humans on the one hand, and the apes on the other closest to the human females, gorilla males and orang-utan females.

Discussion

The principal features that distinguish human from ape fifth metatarsals are the sagittal and lateral curvatures of the metatarsal shaft, the torsion of the metatarsal head, and the extension of the distal articular surface onto the dorsum of the head. The dorsal extension of the distal articular surface of StW 114/115 would allow for a human-like metatarsophalangeal dorsiflexion which is essential for successful toe-off during the propulsive phase of bipedal gait (Bojsen-Møller 1979; Bojsen-Møller & Lamoreux 1979). A distinctive feature of the human metatarsal shaft is that it is relatively straight in the sagittal (dorsoplantar plane) and has a slight concavity on the lateral side. In contrast, the ape fifth metatarsal has a sagittal plane curvature with the concavity on the plantar side and a straighter lateral border than in humans. StW 114/115 has a mosaic of these features.

Another compelling feature suggesting a bipedal gait in the StW 114/115 specimen is the internal (medial) torsion of the metatarsal head (Morton 1922; Lewis 1980; Aiello & Dean 1990). This torsion of the metatarsal head in the StW 114/115 individual, which is the same as that of humans, strongly suggests that this hominin had both transverse and longitudinal arches.

The derived (human-like) features in StW 114/115 are therefore: 1) a short robust bone, 2) an internal torsion of the head, 3) a distal articular surface extending onto the dorsum of the metatarsal head with a sulcus or depression between the head and shaft, 4) a transverse plane curvature (lateral concavity) tracing a gentle curve as it passes to

the expanded base and, 5) a dorsoplantar flattened proximal articular surface. Primitive (ape-like) features in StW 114/115 are: 1) a sagittal plane curvature (plantar concavity) of the shaft and 2) a lack of posterior expansion of the plantar shaft at the base.

In the CVA of the morphometric analysis, morphological information is interpreted not only on any single variate, but is jointly held between variates. On a plot of variates one and two, StW 114/115 lies on the line discriminating humans and African apes from orang-utans. This could be interpreted as a broad geographic discrimination between the Homininae of African origin, and the Ponginae of Asian origin.

On a plot of variate one against variate three, the fossil lies on a line discriminating the humans on the one hand and the apes on the other. As the plots of the apes and humans possibly suggest discrimination in terms of locomotion, being quadrupedal terrestrial and arboreal for the apes and habitual bipedalism for the humans, the position of the fossil suggests a unique morphology and perhaps associated function. The isolated fossil does, however, lie closest to the humans and chimpanzees, located in a unique position of the group means along the first two variates.

Skeletal correlates of midfoot stability can be found in both humans and the StW 114/115, which have a mediolaterally 'shortened', dorsoplantarly flat proximal fifth metatarsal articular surface that appears to have evolved for maintaining a stable joint during mid-stance. This morphology results in the midfoot becoming a rigid lever, shifting motion to the metatarsophalangeal joint during the push-off phase of gait. A skeletal correlate of this metatarsophalangeal motion is a dorsally extended articular surface on the distal head of human metatarsals. In contrast, the dorsal-most portion of the metatarsal head of apes appears flat in profile (Susman 1988; Latimer & Lovejoy 1990; Aiello & Dean 1990). The fossil, StW 114/115, displays a very human-like dorsally extended articular surface. Additionally, in the human lesser metatarsals, there is also a depression between the head and shaft (Aiello & Dean 1990). This also relates to an increased potential for dorsiflexion at the metatarsophalangeal joints. This is essential to a bipedal gait where the metatarsophalangeal joint acts as a fulcrum so that the posterior part of the foot can 'roll' over during the toe off phase of gait. This feature is present, though not as well developed in the Sterkfontein specimen as in modern humans.

The human-like functional affinities of this fifth metatarsal, however, do not necessarily indicate that the remainder of the foot would have the same degree of human-like function. In fact, it is unlikely that the gait of the StW 114/115 individual was exactly the same as that of modern humans as the comparatively thicker cortex suggests greater pressure on the lateral column of the foot more closely resembling that of apes (Vereecke *et al.* 2003). Furthermore, the lateral side of the hominin foot may not have evolved in concert with the medial side of the foot (Kidd *et al.* 1996). It would appear that formation of the lateral longitudinal arch, together with increased calcaneocuboid stability was an early evolutionary event in the history of terrestrial bipedalism in hominins. The equivalent modifications to the medial side of the foot, as seen in modern humans, seem to have occurred subsequently, as evidenced in the OH 8 assemblage, and so-called 'Little Foot' assemblage StW 573 (Clarke & Tobias 1995; Kidd *et al.* 1996; Kidd & Oxnard 2005).

Clearly, the StW 114/115 fifth metatarsal is very human-like and the available evidence suggests that the function of this element may not have been much different (if different at all) from that of modern humans. It should, however, be noted that StW 114/115 is only an isolated element of the foot and mixed affinities have been noted in hominin feet suggesting that the medial and lateral columns have not necessarily evolved in concert.

Our grateful thanks go to the University of the Witwatersrand for permission to study StW 114/115 and Jaymati Limbachia of the Helen Joseph Hospital for help with radiography. We thank Stephanie Potze and Lazarus Kgasi of the Transvaal Museum for their help. Thank you to Emma Mbua and Amandus Kwekason. Paul Msemwa, Yohannes Haile-Selassie, David Pilbeam and Michele Morgan for assisting with access to the East-African fossils and casts. We thank the staff of the Smithsonian Institution, Powell-Cotton Museum and British Museum of Natural History for access to human and ape comparative skeletal specimens.

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POSTER ABSTRACTS

The postcranial skeleton of *Galesaurus planiceps*: implications for biology and lifestyle

E. Butler & J. Botha-Brink

Karoo Palaeontology, National Museum, P. O. Box 266, Bloemfontein, 9300 South Africa; andDepartment of Zoology and Entomology, University of the Free State, Bloemfontein 9300

E-mail: elize.butler@nasmus.co.za / jbotha@nasmus.co.za

Galesaurus planiceps is a basal non-mammalian cynodont from the Lower Triassic, *Lystrosaurus* Assemblage Zone (LAZ) of South Africa. The stratigraphic range of *G. planiceps* is relatively short, extending from just above the Permo-Triassic boundary to approximately one third of the way into the LAZ. The range is notably shorter than that of *Thrinaxodon liorhinus,* the better-known sister taxon of *Galesaurus,* whose range extends all the way through the LAZ (Botha & Smith 2006). Both these taxa appeared very quickly after the End-Permian mass extinction event in the Karoo Basin and can be regarded as disaster taxa. The difference in the ranges of these taxa is not fully understood and may be related to lifestyle preferences. Although the postcranial skeletons of *Galesaurus* and *Thrinaxodon* are traditionally considered to be indistinguishable from one another (apart from the ribs) (e.g. Jenkins 1971), newly discovered *Galesaurus* material (associated with positively identified skulls) has come to light allowing this assumption to be tested. Several almost complete skeletons and numerous postcranial elements of *Galesaurus* are currently under study. Preliminary results indicate that the forelimb and pectoral girdle of *Galesaurus* is relatively similar to that of *Thrinaxodon,* particularly where the interclavicle, humerus, radius and ulna are concerned. However, some differences in the scapula-procoracoid-coracoid-complex, the clavicle and manus have been observed. These preliminary results have facilitated in distinguishing these genera using elements other than the ribs or skull. Further study will include examining the rest of the appendiculer skeleton as well as the axial skeleton. The bone histology of *Galesaurus* will also be assessed and compared with that of *Thrinaxodon.*

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An African Origins Platform/West Coast Fossil Park Project

Thalassa Matthews[1], Pippa Haarhof[2], Dave Roberts[3] & Roger Smith[1]

[1]*Iziko Museums of Cape Town*

E-mail: tmatthews@iziko.org.za

[2] *West Coast Fossil Park*

[3]*Council for Geoscience*

The West Coast Fossil Park has been granted three years funding from the African Origins Platform (Department of Science and Technology) to maximize the research, educational and tourism potential of the Fossil Park. The project aims to integrate palaeontological and geological investigations of environmental change over the past 20 million years on the Cape West Coast, focusing on the site of Langebaanweg. Research will be used to develop curriculum based education programmes for schools, foster palaeotourism and create employment opportunities in and around the West Coast Fossil Park at Langebaanweg. A Research Director has been appointed to coordinate a number of on-site research programmes which aim to:

1. Survey and map the extent of the fossil deposits at Langebaanweg
2. Determine the stratigraphy, palaeogeography and age determination of Cenozoic deposits of the Cape West Coast
3. Study the taphonomy and depositional history of the Early Pliocene sivathere-dominated bonebed deposit at Langebaanweg
4. Reconstruct the paleoecology of Langebaanweg using an ecomorphological approach on a number of the taxa (e.g. a study of morphology, isotopes, microwear and mesowear)
5. Reconstruct the Early Pliocene ecosystem of the Cape West Coast using a morphological and taxonomic approach to the fossil micromammals from Langebaanweg

Under the auspices of this programme a number of bursaries have been made available for Honours, Masters and post-doctoral students to work on the geology, geochemistry, palaeoecology and fauna of Langebaanweg. An educational consultant has been appointed to develop and implement a curriculum-based educational programme at the Park, using the unique and exciting fossil and ecological experiences that the West Coast Fossil Park provides.

A comparative study of Late Holocene- and Plio-Pleistocene-aged micromammalian owl accumulations from South Africa

Ceri McCrae

Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa

E-mail: rudget@mweb.co.za

South African Plio-Pleistocene-aged cave deposits often contain well-preserved macro- and micro-mammalian fossil fauna. This is largely due to the taphonomic environment of dolomitic caves, which allow the preservation of fine detail in fossils not found in most other depositional environments (Brain 1981). Microfossils have not received the same attention afforded to macrofossils. Micro-faunal remains are typically intact and well preserved. This is assumed to be due to the way in which the majority of micro-mammalian remains find their way into the fossilization environment, through the introduction of owl pellets into the system (Sparks & Soper 1970; Bunn *et al.* 1982). Owl pellets are essentially neatly packaged death assemblages allowing insight into a particular feed-

ing event (Tarboton & Erasmus 1998). Although, preliminary studies have indicated that it is probable that accumulations of discrete owl pellets can be identified within the consolidated breccias, it has never been given much attention. Despite the abundance and preservation of these micro-mammalian remains, studies of this material have largely been confined to the cranial elements with little regard given to postcranial remains. This leaves open the possibility that fossil taxa have different postcranial morphology to their extant counterparts that has been missed.

If it is possible to recognize discrete owl pellets within fossilized microfaunal deposits, then it is likely that the skeletal elements are associated and the postcrania may therefore legitimately be analysed alongside the cranial remains.

Analysis of modern pellets from both wild and captive owls is expected to contribute to our understanding of taphonomic processes involved in the accumulation of micro- and macro-faunal remains within the dolomitic caves of southern Africa.

An actualistic feeding study conducted on captive owls sheds light on differences in individual and skeletal element representation, as well as the degree of skeletal element association within pellets. This also provides a good mechanism to further understand digestive damage to various skeletal elements.

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A palynological investigation of the mid-Cretaceous Orapa kimberlite pipe in Botswana

Moses Ngcamphalala & Marion Bamford

Bernard Price institute for Palaeontological Research, School of Geosciences, University of Witwatersrand, Private Bag X3, WITS, 2050 Johannesburg
E-mail: ngcamphalala.m@gmail.com

Introduction

The Orapa diamond mine is situated within a large kimberlite pipe approximately 220 km west of Francistown in north-central Botswana.Younger fossilferous sediments filled the resultant craters and have been dated as middle to Upper Cretaceous (Mckay & Rayner 2001), during the time that angiosperms radiated in South Africa.

Previous palynological studies at Orapa suggested that a number of the individual palynomorph assemblages were dominated by *Ephedripites* forms and the occurrence of the genus *Classopollis* which is considered to be mid to Upper Cretaceous in age (Scholtz 1984). Some of these palynomorphs are thin-walled and inaperturate and they may have affinities with the coniferous families Araucariaceae or Cupressaceae. According to Scholtz (1984), they are not useful for precise dating but range from mid to Late Cretaceous. Goldblatt (1978) postulated a warm humid climate for Africa during the mid- to Late Cretaceous, and that tropical forest flora was present over the continent.

Materials and methods

Collection of material

Macroplant samples from Orapa that were collected by staff and students are housed in the BPI herbarium were used. Twenty samples were removed from the blocks from different lithologies. Both reduced and oxidized samples were used to compare numbers of palynomophs in each lithotype.

Pollen extraction

Sediments were crushed with a mortar and pestle to approximately 2 mm fragments and 60 g of each sample was treated. In the fume cupboard carbonates are

dissolved by adding 10% HCl to beakers in a water bath for 2 hours. Washing was carried out by adding distilled water and centrifuging at 3000 rpm for 5 minutes, decanting the supernatant, and repeating the procedure. Organic material was removed by boiling the sample together with 10% KOH and washing as above. Once the pellet was neutral, HF was added to remove silicates and washed again. A saturated solution of zinc chloride was added for density separation and centrifuged at 1800 rpm for 25 minutes.

Some of the supernatant was transferred to the small centrifuge tubes and followed a dehydration series with the increase in alcohol concentration to absolute alcohol and centrifuged at 90 rpm for 3 minutes. The solution was transferred to the cover slip on the Petri dish to dry. After drying the cover slip was mounted on the slide using DPX. Acetone was used to clean the slide.

Pollen slides were studies under a Zeiss petrographic microscope with ×400–1000 magnification. Pollen and spores were identified using the literature. Size, shape, surface texture, number, position of colpi and pores are important features which were used to make the identification in conjuction with reference material.

Results

Palynomorphs found included trilete spores, monolete and tricolpate pollen. Trilete polynomophs are from lower plants, monoletes are from gymnosperm and tricolpates are angiospermous. Angiosperms were the most numerous forms followed by gymnosperms and a few lower plants. According to Bamford (1990) fern macrofossils are numerous and comprise five taxa. The gymnosperm /angiosperm dominance shows that the surrounding environment during deposition was either a fringing forest or shrubland. The pollen yield was too low to allow a reliable interpretation of the past vegetation and climate but the macroplants indicate a small leaved dry and/or cool climate.

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Further light on cranial bone adhering to matrix surrounding Mrs Ples as prepared by Robert Broom

S. Potze & J.F. Thackeray

Transvaal Museum (NFI) & Human Origins and Past Environments (HOPE) Research Unit (HRU)

E-mail: potze@nfi.museum.org

In 1947, Robert Broom and John Robinson of the Transvaal Museum discovered the most complete cranium of *Australopithecus africanus*, nicknamed Mrs Ples (Sts 5). Unfortunately the skull was broken into two pieces due to the fact that dynamite had been used by lime miners. Broom and Robinson mechanically broke the surrounding breccia at the cave, and subsequently used hammer and chisel at the Transvaal Museum to extract the cranium from the surrounding matrix. However, in the process six pieces of matrix were removed that retained the outermost layer of cranial bone. These six pieces were placed in a store at the museum were they remained for about 50 years.

In 1997, Francis Thackeray reported the discovery of these six pieces in the store and was able to demonstrate that they could be refitted back onto the skull of Mrs Ples. These pieces have been labelled Sts 5 (i) – (vi). Sts 5 (ii) was of particular interest because it included a layer of calcite that could be matched with a horizontal band of calcite visible in a photograph of the *in situ* matrix near the wall of the cave, as photographed on the day of the discovery on 18 April 1947. Thackery and Kirschvink have undertaken palaeoamagnetic analyses of the matrix associated with Sts 5 (ii) and demonstrated normal polarity. In the context of other data, it has been suggested that Mrs Ples dates to the time of the Réunion event, 2.15 million years ago.

Sts 5 (i) was a large block of breccia associated with nucchal bone of Mrs Ples. The matrix has been prepared after very careful dissolution in acetic acid. Of great interest is the exposure of temporal lines which had never been seen before. An additional block of breccia Sts 5 (iii) is currently being prepared and is expected to demonstrate how close the temporal line on the left side of the cranium approached bregma. The evidence currently available suggests that the temporal lines on the right and left sides did not meet at bregma, but were relatively close. It is probable that Mrs Ples may have developed a sagittal crest if the individual, a presumed male, had lived into adulthood. The CT scans undertaken by Thackeray and Braga have shown conclusively that Sts 5 was an adolescent at the time of death. The cranial sutures exposed on cranial bone, recently prepared in acid, are distinctly open. This confirms the fact that Mrs Ples was adolescent rather than an adult, as had been suggested by Robert Broom.

Temperature indices based on relative abundances of rodent taxa represented in South African Plio-Pleistocene assemblages from the Cradle of Humankind World Heritage Site: a preliminary study

F. Sénégas

UPR 2147 du CNRS, 44 rue de l'Admiral Mouchez, 75014 Paris, France

E-mail: frank.senegas@evolhum.cnrs.fr

Rodents are among the most common mammals represented in Plio-Pleistocene faunal assemblages excavated from cave deposits in the Cradle of Humankind World Heritage Site and other localities in South Africa. We present temperature indices based on multivariate analyses, using a method previously applied to Late Quaternary microfaunal samples from southern Africa (Thackeray 1987). The indices are calibrated in terms of

temperature expressed in degrees Celsius. The results suggest that assemblages from Kromdraai A, Swartkrans, Bolts Farm, Gladysvale, Haasgat and Drimolen relate to interglacial episodes within the Plio-Pleistocene. The coolest episode represented by samples included in this study is associated with Plovers Lake, dated at about 1 million years ago.

A statistical (probabilistic) definition of a species in palaeontological contexts, based on morphometric analyses of a diversity of modern fauna, using hominid (australopithecine) and therapsid (dicynodont) examples

J. Francis Thackeray
Transvaal Museum, P.O. Box 413, Pretoria, 0001 South Africa
E-mail: mrsples@global.co.za

A major problem in palaeontology is the definition of a species in the fossil record. An approach has been developed whereby probabilities of conspecificity can be assessed, when pairs of specimens are compared (Thackeray *et al.* 1997). As a frame of reference, pair-wise comparisons have been made between measurements of extant vertebrate and invertebrate taxa, using least-squares regression analyses associated with regression equations of the form $y = mx + c$. Of particular interest is the degree of scatter around a regression line, quantified in terms of the standard error of the m-coefficient (s.e.$_m$) associated with the slope of the regression line. Pair-wise comparisons of conspecific pairs of extant taxa show a log-normal distribution of the standard error of the m-coefficient. The mean log s.e.$_m$ value (T) is –1.61, with a standard deviation of 0.23, based on 1424 specimens of extant species. This essentially provides a definition of a species. 1.61 is an approximation of the Golden Ratio. Pairs of hominid fossil crania can be compared using this approach, and assessed in terms of probabilities of conspecificity. For example, when Sts 5 ('Mrs Ples') and Sts 71 (also from Sterkfontein) are compared, a log s.e.$_m$ value of –1.538 is obtained. This is within the 95 % confidence limits of log sem values obtained for conspecific pairs of extant taxa. It is concluded that Sts 5 and Sts 71 are conspecific, contrary to the view expressed by R.J. Clarke. Similarly, when two specimens of *Lystrosaurus* are compared against each other (TM 18 and TM 20), a log sem value of –1.50 indicates a high probability of conspecificity although Brink (1982) thought that they were distinct species (*L. murrayi* and *L. declivis*). It is probable that both TM 18 and TM 20 can be attributed to *L. murrayi* since the latter nomen (described by Huxley in 1859) has precedence over *L. declivis.* (described by Owen in 1860). At least some specimens attributed to *L. murrayi* are probably females and at least some specimens attributed to the larger *L. declivis* are probably males of *L. murrayi* which is also recognized in India as a sexually dimorphic taxon (S. Ray 2005).

Bolt's Farm in the Cradle of Humankind

J.F. Thackeray, D. Gommery, S. Potze, F. Senegas, J. Braga, Lazarus Kgasi & C. McCrae
Human Origins and Past Environments (HOPE) Research Unit (HRU)
E-mail: mrsples@global.co.za

The Bolt's Farm area includes about 20 sites. Some were excavated in 1947 and 1948 by members of the University of California African Expedition. These sites have yielded primates, sabre-tooth cats, pigs, bovids, equids and rodents. Since 2001, the HOPE team has surveyed the area and collected breccia from several sites on Bolt's Farm. Waypoint 160 is about 4.5 million years old. It is the oldest site in the Cradle of Humankind. It was discovered in 1996 by B. Senut, M. Pickford and J. Michaux. The breccia of Waypoint 160 contains a rich microfauna, including extinct rodents. The discovery of *Parapapio* at Waypoint 160 is of particular interest because this extinct primate has been found with hominids at other sites such as Lothagam in East Africa and Sterkfontein, Taung and Makapansgat in South Africa. As yet, Waypoint 160 has not yielded hominids, but it has great potential.