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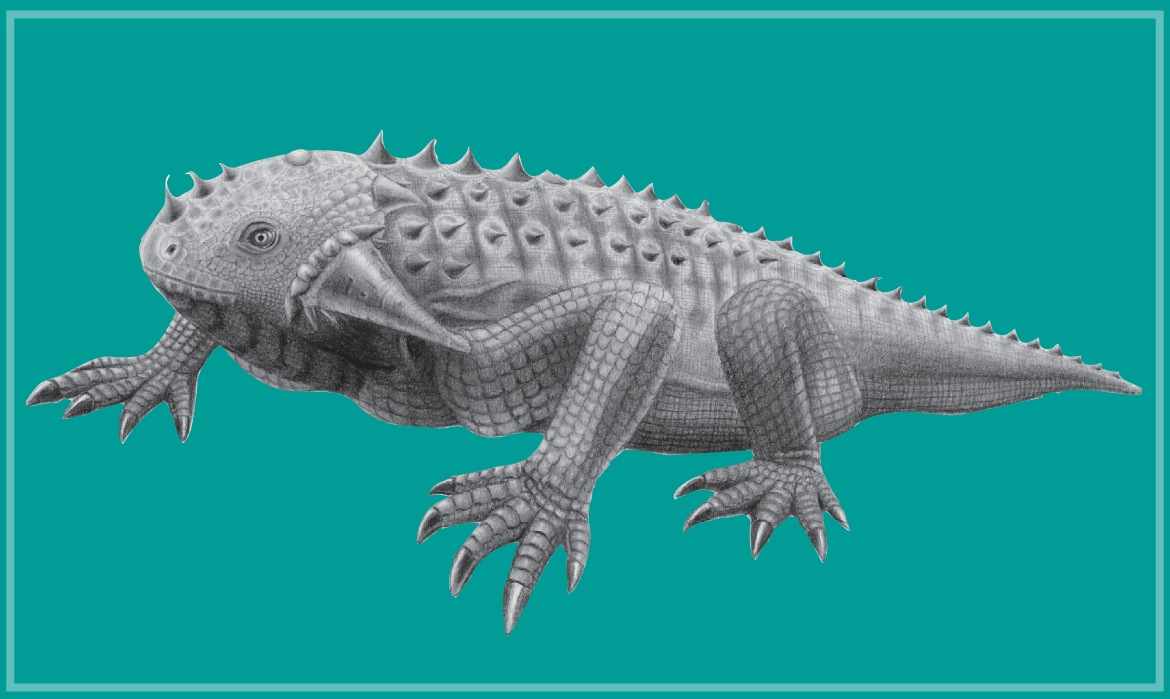

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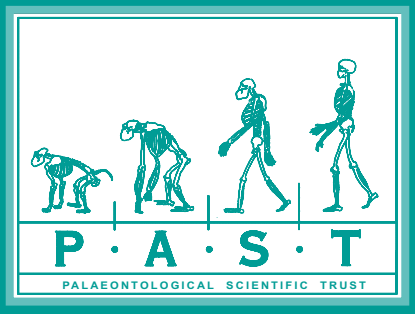

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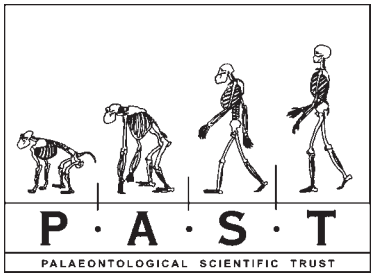

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A new cynodont record from the *Tropidostoma* Assemblage Zone of the Beaufort Group: implications for the early evolution of cynodonts in South Africa

J. Botha-Brink[1*] & F. Abdala[2]

[1]*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 South Africa*

[2]*Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Private Bag 3, WITS, Johannesburg, 2050 South Africa*

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A new specimen of cynodont has been recovered from the lower Upper Permian levels of the *Tropidostoma* Assemblage Zone of the South African Karoo Basin. A series of characters, including the presence of an interpterygoid opening, triconodont postcanine teeth, which are circular in crown view, a probable lingual cingulum, and most significantly, the presence of a masseteric fossa high on the coronoid process, allows this specimen to be assigned to the Procynosuchidae. However, unlike most procynosuchids, precanine teeth are absent and the incisors are represented by four left and five right upper and probably, three lower teeth. Considering the small size of the new specimen from the *Tropidostoma* Assemblage Zone we identify it as a juvenile *Procynosuchus delaharpeae*, the only species currently recognized in the genus. The low number of incisors and absence of precanines in this specimen are interpreted as ontogenetic variation (i.e. juvenile characters). This discovery extends the biostratigraphic range of *Procynosuchus*, as it is now recorded in three assemblage zones, indicating that this taxon is the longest-lived cynodont in the Karoo Basin. The new specimen of *Procynosuchus* and the recently described *Charassognathus gracilis*, are the oldest global records of cynodonts, and indicate an earlier initial radiation of this lineage than was previously thought.

Keywords: *Procynosuchus*, Cynodontia, South Africa, biostratigraphy, Late Permian.

INTRODUCTION

The importance of non-mammaliaform cynodonts in understanding the origin and evolution of mammals is well established. They display several features that illustrate the gradual acquisition of mammalian characteristics and are closely related to Mammaliaformes (=mammals of many authors including for example Hopson & Barghusen 1986 and Kielan-Jaworowska *et al.* 2005). Until recently, the earliest representatives of this group were known from the latest Late Permian (Wuchiapingian-Changhsingian, Catuneanu *et al.* 2005) of South Africa, Zambia, Tanzania, Germany and Russia (Kemp 1979; Tatarinov 1968, 1987, 2004; Sues & Boy 1988; Van Heerden & Rubidge 1990; Rubidge 1995; Battail & Surkov 2000; Abdala & Allinson 2005). A maximum of five non-mammaliaform cynodont taxa (although two are dubious; see Abdala & Allinson 2005: Table 1) are found in the *Dicynodon* Assemblage Zone (AZ) of the Karoo Basin, representing one of the most diverse Late Permian fauna. However, a new cynodont, *Charassognathus gracilis* from levels of the older *Tropidostoma* AZ (Teekloof Pass near Fraserburg) of the Karoo Basin was recently described (Botha *et al.* 2007). In addition, the record of *Procynosuchus*, previously restricted to the *Dicynodon* AZ (Rubidge & Sidor 2001; Sidor & Smith 2004), has recently been extended to the uppermost *Cistecephalus* AZ (Botha *et al.* 2007).

Here we present a new cynodont record consisting of a skull and articulated mandible recovered from Leeu Kloof 43, Beaufort West District, Western Cape Province, South Africa by J.W. Potgieter in 2002. The new material was collected from the *Tropidostoma* AZ and has features that allow it to be identified as a procynosuchid. The new record indicates an early phase of cynodont diversification in the *Tropidostoma* AZ, suggesting a more ancient origin of this group in South Africa than was previously thought.

*Author for correspondence. E-mail: jbotha@nasmus.co.za

MATERIALS AND METHODS

The new specimen (SAM-PK-K10138) consists of a complete skull of a small individual. It is dorso-ventrally compressed and cracked. Both upper dental series are visible, but the left teeth are better preserved.

Material of the following taxa was examined for comparison:

Charassognathus gracilis: SAM-PK-K10369; *Cynosaurus suppostus*: AM 4947; BMHN R1718; SAM-PK-4333; BP/1/3926, 4469; *Dvinia prima*: casts of the holotypic snout (UMZC T.1016) and of the complete skull of the holotype of *Permocynodon sushkini* (UMZC T.299); *Nanictosaurus kitchingi*: TM 279; RC 47 and *Procynosuchus delaharpeae*: BP/1/226, 591, 650, 1545, 1559, 2600, 3758, 5832; OUMNH TSK34; RC 5, 12, 72, 92, 132; SAM-PK-K-338, K8511, K10395; UMCZ T.810.

Table 1. Cranial measurements of SAM-PK-K10138 (in mm).

Basal skull length	56.1
Snout length	27
Orbital length	11.4
Temporal region length	18.6
Interorbital distance	17
Transverse process width	17.7
Maxillary bicanine width	21.7
Upper postcanine row length	12.2
Mandibular length	51

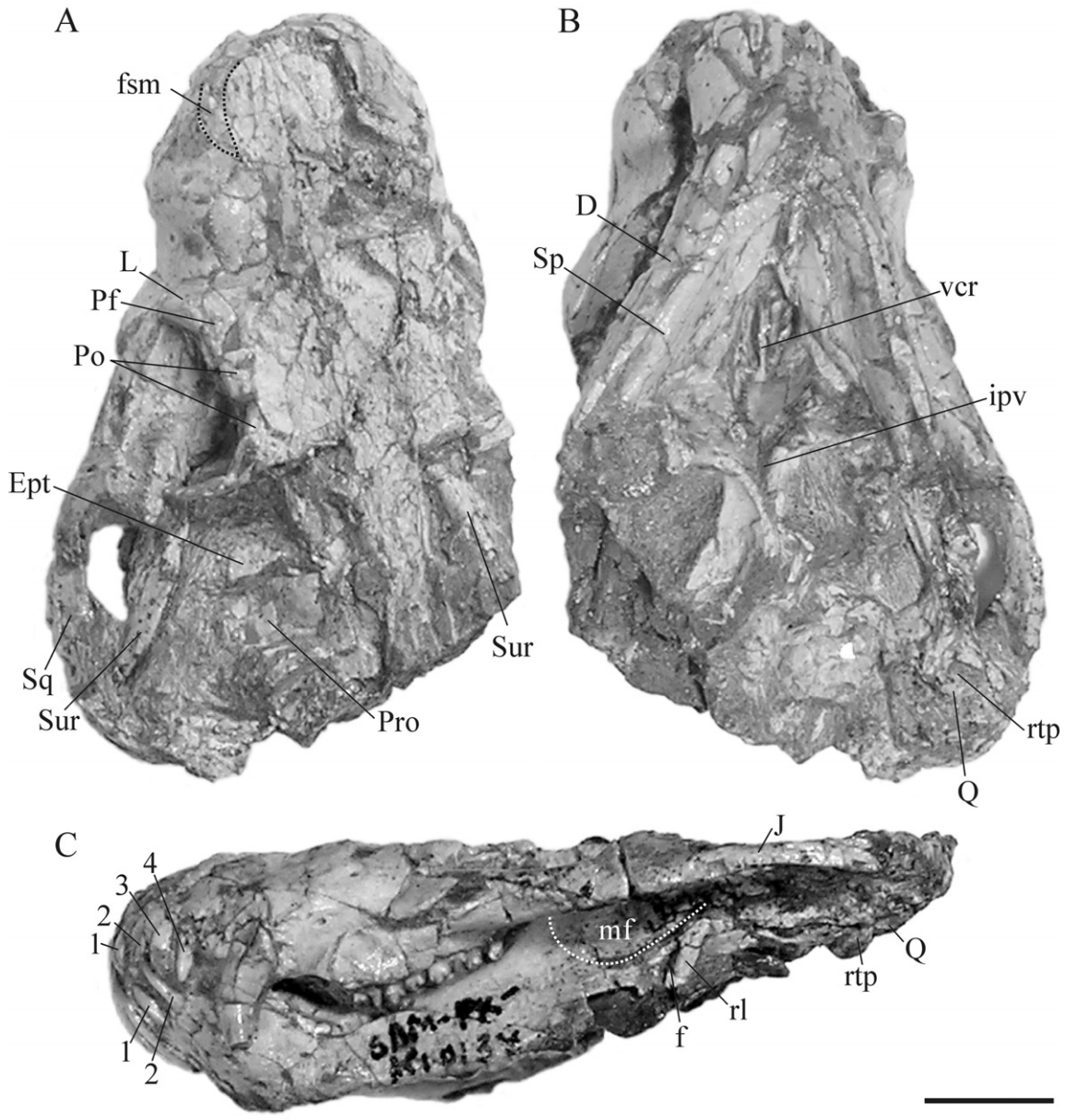

Figure 1. SAM-PK-K10138. **A**, dorsal, **B**, ventral, and **C**, left lateral views. Abbreviations: D, dentary; f, foramen between the dentary and the angular; fsm; facial process of the septomaxilla; ipv, interpterygoid vacuity; L, lacrimal; mf, masseteric fossa; Pf, prefrontal; Po, postorbital; rl, reflected lamina of the angular; Sp, splenial; Sq, squamosal; Sur, surangular; vcr, vertical crest of the vomer. Arabic numbers indicate left upper and lower incisors. Scale bar = 10 mm.

DESCRIPTION

The small (56.1 mm long) skull has a triangular overall morphology, with the snout somewhat longer than the temporal region (see Table 1) and the maximum width located in the middle of the temporal region (Fig. 1A). The skull is dorso-ventrally crushed with most of the bones showing fractures (see Fig. 1), although some sutures can be observed. The lower jaw is tightly occluded to the skull, but some preparation was possible around the upper postcanine series that allowed an almost complete view of the crowns.

In anterior view, the internasal process of the premaxilla is extended between the nasals, and a well-developed facial process of the septomaxilla can be observed on the left side of the skull (Fig. 1A). There are a series of nutritive foramina on the maxilla in the region adjacent to the canines and one large foramen placed posteriorly to these. The lacrimal is particularly short and the inter-orbital region is wide (Fig. 1A). The parietal foramen is not visible, probably due to crushing. A slender left zygomatic arch is preserved, lacking a suborbital angulation or descendent process (Fig. 1C). Only a small fragment of the left epipterygoid is preserved as a laminar bone. The prootic is visible on the left side and consists of a flat bone situated below the parietal.

In palatal view (Fig. 1B), a wide posterior portion of the vomer is visible and the median crest is directed ventrally. The palatal processes of the palatines do not meet in the midline, indicating that a complete secondary osseous palate was absent. A triangular interpterygoid vacuity is present, followed by a wide basicranial girder. The craniomandibular articulation on the left side is poorly preserved, but a remarkably large quadrate/quadratojugal complex is observed.

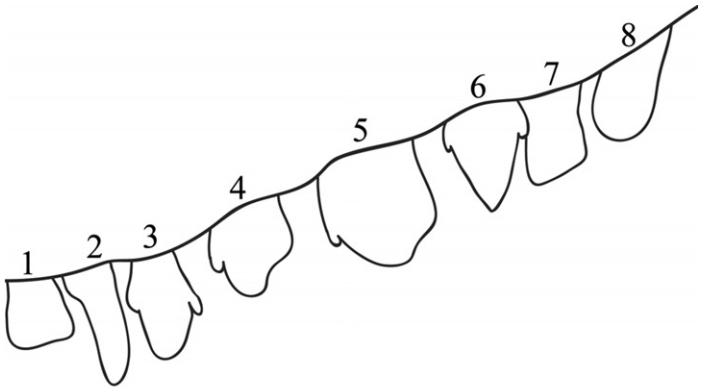

Figure 2. Left upper postcanine series of SAM-PK-K10138. Scale bar = 2 mm.

The anterior lower jaw has an unfused symphysis and many nutritive foramina. The coronoid process of the dentary is low and the masseteric fossa, which lies high on the coronoid process, can be observed on both sides of the lower jaw (Fig. 1C). The posterior margin of the dentary extends to approximately the middle of the temporal fossa. The surangular is a narrow strip of bone dorsal to the angular, extending back to the level of the craniomandibular joint (Fig. 1C). The anterodorsal portion of the left reflected lamina of the angular is preserved, showing a well-developed upward and posteriorly directed crest. A small fossa between the dentary and the angular is present. The posterior portion of the reflected lamina is not preserved and the lateral face of the angular can be seen below the surangular. The left postdentary bar is complete, showing a rounded and well-developed retroarticular process of the articular in ventral view (Fig. 1B, C). On the ventral margin of the horizontal rami, sutures separate the dentary laterally from a large splenial medially.

Four conical upper incisors are observed on the left side of the premaxilla (Fig. 1C), whereas on the right side there is a space with an erupting first incisor, followed by three incisors, and a small tip of an erupting fifth tooth. Two leaf-shaped lower incisors are preserved on both sides, but there is additional space for a third. The fourth upper incisor is smaller than the previous three and there is a small diastema between this tooth and the upper canine (Fig. 1C). Serrations are absent from both the incisors and canines. There is no evidence of precanines. A diastema is also visible between the upper canine and the postcanine dentition. Eight left (Fig. 2) and six right tricuspidate upper postcanines are preserved. The first, seventh, and eighth left postcanines are poorly preserved and do not provide any useful information. The second postcanine is cone-shaped and appears to have only an anterior accessory cusp. Anterior and posterior accessory cusps are present on the third, fourth and fifth postcanines. The sixth postcanine is in eruption and has a high, upwardly directed main cusp, with anterior and posterior accessory cusps placed at the same height on the crown (Fig. 2). On the right maxilla, most of the postcanine crowns are only partially preserved, but it is possible to observe that they are expanded lingually (i.e. circular in occlusal view), suggesting the presence of a lingual cingulum.

DISCUSSION

The record of a second cynodont from the *Tropidostoma* AZ represents an important increase in our knowledge of early cynodont evolution. The triconodont pattern of the postcanines seen in labial view, i.e. a dominant main cusp, with anterior and posterior accessory cusps (also present in *Charassognathus gracilis*), is the oldest postcanine morphology in cynodonts.

Late Permian cynodonts from South Africa and Russia are diverse, with at least four species in each region (Abdala & Allinson 2005). South Africa contains *Procynosuchus delaharpeae, Cynosaurus suppostus, Nanictosaurus kitchingi* and, the recently described, *Charassognathus gracilis* (Botha *et al.* 2007). Russia includes *Cyrbasiodon vladimiriensis, Uralocynodon tverdokhlebovae, Dvinia prima* and *Nanocynodon seductus,* although due to their dental similiarities, the first two species may in fact represent a single taxon.

Procynosuchids (including *Procynosuchus delaharpeae, Cyrbasiodon vladimiriensis* and *Uralocynodon tverdokhlebovae,* see Tatarinov 1987, 2004; Battail & Surkov 2000) have bucco-lingually expanded postcanines that are circular in occlusal view, whereas those of *Dvinia prima* are transversely ovate. In *Nanictosaurus kitchingi* and *Nanocynodon seductus,* the ellipsoid postcanines are clearly more laterally compressed than in procynosuchids and *D. prima,* but they also display cingular cusps on the lingual margin (Van Heerden & Rubidge 1990; Battail & Surkov 2000). In *Cynosaurus suppostus,* the postcanines are simple, ovoid in shape and lack a cingulum. In *Charassognathus gracilis,* the occlusal morphology of the upper postcanines cannot be determined because the upper teeth are preserved in tight occlusion with the lower postcanines.

Most of these early cynodonts show triconodont postcanines when observed labially. *Charassognathus gracilis, Nanictosaurus kitchingi* and *Nanocynodon seductus* have high main cusps with smaller anterior and posterior accessory cusps low on the crown (Van Heerden 1976; Van Heerden & Rubidge 1990; Battail & Surkov 2000; Botha *et al.* 2007). However, some variation does exist in the height of the main cusp and the development of the accessory cusps on the crown. In *C. gracilis,* the accessory cusps are exceptionally tiny and the anterior accessory cusp is placed slightly higher than the posterior accessory cusp (Botha *et al.* 2007). In *Nanictosaurus kitchingi* and *Nano-*

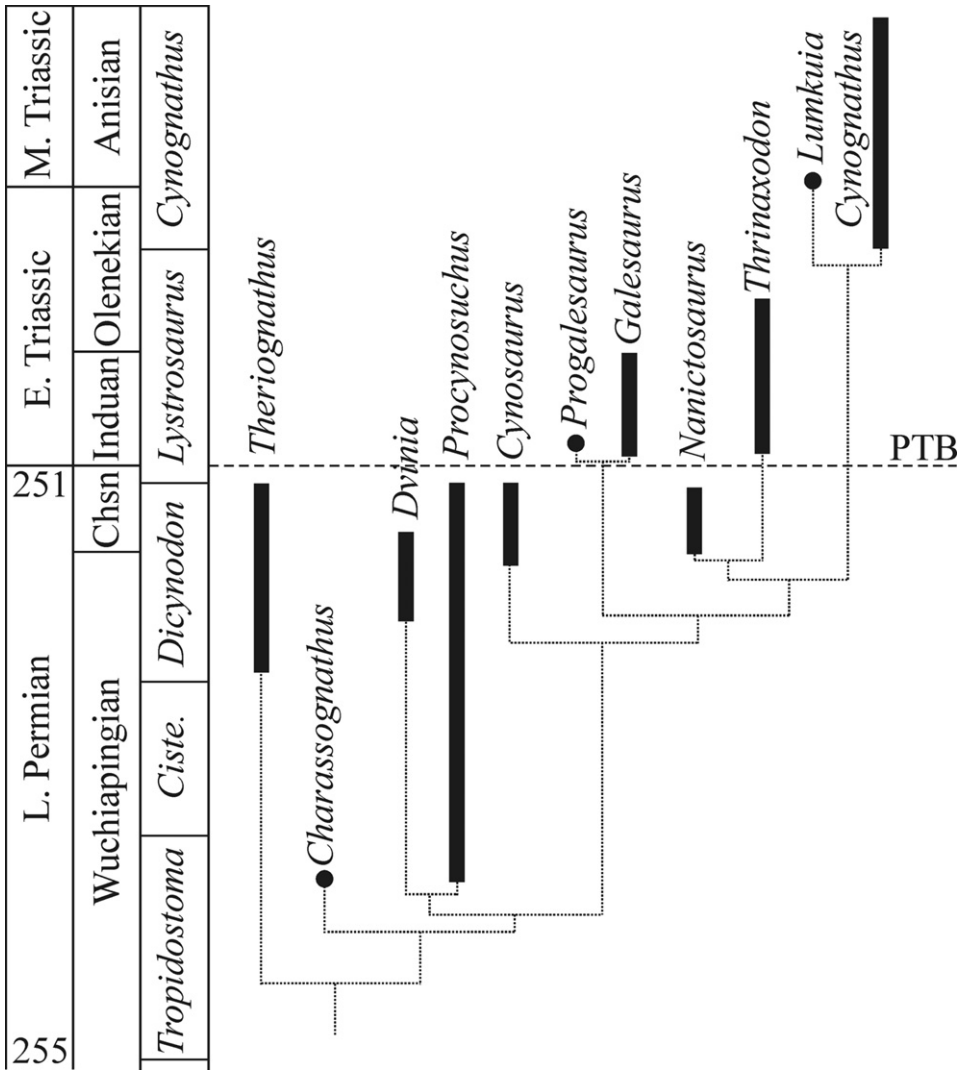

Figure 3. Extended biostratigraphic range and phylogenetic position of *Procynosuchus* plotted against the South African Permo-Triassic biostratigraphy. Vertical bars and solid circles indicate taxon ranges and single specimen occurrences, respectively. Abbreviations: Chsn, Changhsingian; *Ciste., Cistecephalus* Assemblage Zone; PTB, Permo-Triassic boundary. Numbers indicate million years ago. Stratigraphic chart follows Catuneanu *et al.* 2005. (Modified from Botha *et al.* 2007.)

cynodon seductus the accessory cusps are more distinctive and are placed at the same level on the crown (Van Heerden & Rubidge 1990; Battail & Surkov 2000). In contrast, the postcanines of *Cynosaurus suppostus* have a posterior accessory cusp, and even a second posterior accessory cusp in the posterior-most teeth, whereas the anterior accessory cusp is barely visible (see Van Heerden, 1976: figs 14–19). Procynosuchids also have three cusps visible in labial view, but the main cusp is not very high compared to the accessory cusps.

Some variations in features of the anterior dentition of basal cynodonts are well known. *Procynosuchus delaharpeae* and *Dvinia prima* have five or more upper and four or more lower incisors, whereas the majority of cynodonts have four upper and three lower incisors (Hopson & Barghusen 1986; Hopson & Kitching 2001). This is also the case in *Charassognathus gracilis, Nanictosaurus kitchingi, Cynosaurus suppostus* and *Nanocynodon seductus*; the latter species are known only from a mandible with three incisor alveoli (Tatarinov 1987; Van Heerden & Rubidge 1990; Botha *et al.* 2007). In addition, *P. delaharpeae* and *D. prima* are the only cynodonts in which the presence of upper precanine teeth on the maxilla in front of the canine was reported (Tatarinov 1968; Hopson & Kitching 1972; Hopson & Barghusen 1986; Kemp 1979).

The triconodont morphology can be clearly observed in the third and erupting sixth postcanines of SAM-PK-K10138. They exhibit a high main cusp, and anterior and posterior accessory cusps placed at the same height on the crown (Fig. 2). The right postcanine crowns are broken, and careful preparation revealed that the teeth were expanded lingually, suggesting the presence of a lingual cingulum. This morphology closely resembles that observed in postcanines of *Procynosuchus* (Kemp 1979). The presence of the postcanine pattern described above, combined with primitive cynodont features such as the interpterygoid vacuity, a masseteric fossa high on the coronoid process and incomplete secondary palate indicate that SAM-PK-K10138 is a specimen of *Procynosuchus delaharpeae*. However, notable differences exist between the anterior dentition of the new individual and *P. delaharpeae.* SAM-PK-K10138 has five right and four left upper incisors, most likely three lower incisors, and no precanines. Hopson and Kitching (1972) synonymized

several species of basal cynodonts proposed mostly by Broom, as members of *Procynosuchus delaharpeae.* This lumping exercise resulted in a neater taxonomy because many species erected by Broom were based on poorly preserved fossils with no proper diagnostic features or size related characters that may have been related to ontogeny. Hopson & Kitching's (1972) proposal presented a general diagnosis for cynodont families and a list of valid species with synonymy, but individual variations in valid taxa were not thoroughly discussed. Five or more upper and four lower incisors, as well as the presence of precanines were considered as diagnostic features of procynosuchids by Hopson & Kitching (1972) and are widely accepted as typical characters of this group (e.g.; Hopson & Barghusen 1986; Sidor & Hopson 1998; Sidor & Smith 2004). BP/1/650 is a small specimen (approximately 5 mm in basal skull length) originally described as *Protocynodon pricei* by Broom (1949; see also Mendrez 1972), and was included in the synonymy of *P. delaharpeae* by Hopson & Kitching (1972). This specimen was described originally as having six incisors and no precanines (Broom 1949), whereas Mendrez (1972) redescribed the specimen indicating the presence of five or six incisors and one or two precanines. First hand examination of BP/1/650 demonstrates the presence of five upper incisors and no precanines on the right side (the anterior dentition is not preserved on the left side). However, examination of other juvenile and adult specimens assigned to *Procynosuchus delaharpeae* (Rubidge Collection and the Bernard Price Institute Collection) indicates that precanines are usually present and can vary from one to three teeth. SAM-PK-K10138 and BP/1/650 are about the same size (approximately 60 mm), well below the 140 mm skull length of the largest specimens of *P. delaharpeae.* Considering these skull size differences, we interpret the unexpected features in the anterior dentition of SAM-PK-K10138 and BP/1/650 as individual variation, probably related to ontogeny.

IMPLICATIONS FOR EARLY CYNODONT DIVERSITY

Procynosuchus, the most abundant cynodont amongst the Late Permian *Dicynodon* AZ fauna of South Africa, was also recently reported from the uppermost *Cistecephalus* AZ (Botha *et al.* 2007). The discovery reported here results in *Procynosuchus* being the first and only cynodont to have crossed two assemblage zone boundaries in the Karoo Basin. In addition, it is also the only cynodont to have had a global distribution at the end of the Permian, when this group was represented by at least six different taxa in a clear diversification phase (Abdala & Allinson 2005). The discovery of this taxon in the older *Tropidostoma* AZ represents an important biostratigraphic extension of its range, and confirms that it is the longest-lived cynodont from the Karoo Basin. This finding also has important implications for early cynodont diversity, when results of recent phylogenies proposing sister group relationships between *Procynosuchus* and the Russian *Dvinia* (Abdala 2007; Botha *et al.* 2007; Fig. 3) are considered. The record of *Procynosuchus* in the *Tropidostoma* AZ suggests a ghost extension of the Russian taxon to the same age, indicating that cynodonts had already begun a process of incipient diversification and dispersion, by the early Late Permian, far earlier than previously thought.

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INSTITUTIONAL ABBREVIATIONS

AM	Albany Museum, Grahamstown.
BMNH	Natural History Museum, London.
BP	Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg.
OUMNH	Oxford University Museum of Natural History, Oxford.
RC	Rubidge Collection, Wellwood, Graaff-Reinet.
SAM-PK	Iziko South African Museum, Cape Town.
TM	Transvaal Museum, Northern Flagship Institution, Pretoria.
UMZC	University Museum of Zoology, Cambridge.

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Taxonomic status of the reptile genus *Procolophon* from the Gondwanan Triassic

Juan Carlos Cisneros*

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

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The specific composition of the genus *Procolophon* in Brazil, South Africa and Antarctica is discussed in the light of new data. It is found that *P. pricei* and *P. brasiliensis,* two species described from Brazil, fit within the pattern of ontogenetic variation of the type species *P. trigoniceps,* and they are here considered junior synonyms. The South African species *P. laticeps,* characterized by the presence of a temporal fenestra, is no longer considered valid. The peculiar temporal openings of this species are regarded here as an anomalous condition without taxonomic significance. The only complete skull known from Antarctica shows a unique feature consisting of an elliptical depression in the palate. The interpretation of this structure is ambiguous because it may also be attributable to individual variation, and this specimen is provisionally kept within *P. trigoniceps.* Therefore, only the type species, *P. trigoniceps*, is recognized in Gondwana. This species occupies a wide geographic range, from the Paraná Basin to the Transantarctic Mountains.

Keywords: Procolophonidae, *Procolophon*, temporal fenestrae, Triassic, Gondwana.

INTRODUCTION

Procolophon is a member of the Procolophonidae, a clade of small parareptiles that flourished across all Pangaea during the Triassic, becoming extinct during the time of the T/J boundary. *Procolophon* is known from hundreds of specimens, most of them found in the Lower Triassic of the South African Karoo, were it is outnumbered only by the ubiquitous dicynodont *Lystrosaurus* (Kitching 1977; Groenewald & Kitching 1995). The genus possesses a robust, wide torso and enlarged chisel-like teeth, both adaptations suggesting a high-fibre diet (Hotton *et al.* 1997); prominent quadratojugal processes confer a bizarre, triangular shape to the head (Fig. 1). Limb adaptations suggest that *Procolophon* was capable of burrowing (deBraga 2003) and burrow casts from the *Lystrosaurus* Assemblage Zone (AZ) of South Africa have been ascribed to this genus (Groenewald 1991). The genus is noteworthy because of the presence of some individuals with temporal openings, sometimes regarded as representing a different species (Hamley & Thulborn 1993). *Procolophon* has also been recovered from the Fremouw Formation of the Transantarctic Basin (Kitching *et al.* 1972; Colbert & Kitching 1975) and the Sanga do Cabral Formation of the Paraná Basin in Brazil (Barberena *et al.* 1981; Lavina 1983). Two *Procolophon* species have been described from Brazil (Lavina 1983; Cisneros & Schultz 2002). In the light of new data, this study reviews the taxonomic status of the Antarctic material, the Brazilian species, and the specimens with temporal openings from South Africa.

TAXONOMIC HISTORY

Together with the description of the type species *Procolophon trigoniceps* (by page priority, Fig. 2), Owen (1876) proposed *P. minor* based on a juvenile skull. This was followed by five more species proposed by Seeley (1878, 1905): *P. griersoni, P. cuneiceps, P. laticeps, P. platyrhinus* and *P. sphenorhinus.* Some of the features used to distinguish these species are better explained by taphonomic, ontogenetic or individual variation. Besides, all seven of Owen's and Seeley's holotypes were collected by D. White from Donnybrook Farm, in the Eastern Cape Province of South Africa, leading Broom (1936) to recognize only the type species, *P. trigoniceps.* The non-validity of the additional species has been virtually unquestioned by later authors. Broom (1905) in turn, proposed another species, *P. baini*, based on a well-preserved, almost complete skeleton collected by J.M. Bain or T. Bain at an unknown locality. This species was said to differ from *P. trigoniceps* mainly in the number of marginal teeth, but this character is known to be ontogenetically variable in the genus (Gow 1977). *P. baini* was also sunk into junior synonymy with *P. trigoniceps* by Colbert & Kitching (1975).

The discovery of a *Lystrosaurus* fauna in the Fremouw Formation of Antarctica yielded the first *Procolophon* remains from that continent (Kitching *et al.* 1972). These remains were represented by one well-preserved, articulated skeleton plus a number of fragmentary specimens. Colbert & Kitching (1975) noted a number of peculiarities in the best Antarctic specimen, including very small quadratojugal horns and relatively robust limbs, but decided that it fitted within the range of variation of the South African *P. trigoniceps* and referred all Antarctic material to this species. In Brazil, *Procolophon* was reported by Barberena *et al.* (1981) in the Sanga do Cabral Formation, in the state of Rio Grande do Sul, southern Brazil. This find consisted of one partial cranium and mandible, a second mandible and non-associated vertebral elements. These specimens were later described by Lavina (1983) as a new species, *P. pricei.* A *Procolophon* cranium collected subsequently from a different locality was described by Cisneros & Schultz (2002) as *P. brasiliensis.* Both Brazilian species were founded mainly on characters relating to the arrangement of the palatal dentition.

Hamley & Thulborn (1993) reviewed the status of the species *P. laticeps.* This species was said to differ from

*Present address: Departamento de Paleontologia e Estratigrafia, Universidade Federal do Rio Grande do Sul, and CNPq, Porto Alegre, CP 15001, 91501-970, Brazil.
E-mail: cisneros.jc@gmail.com

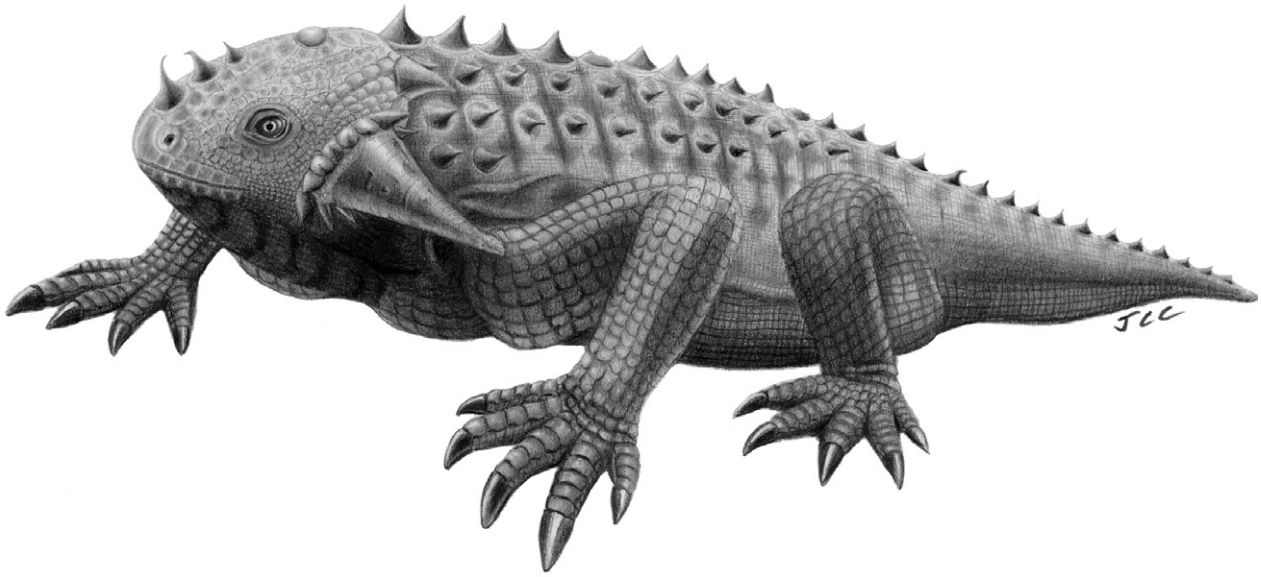

Figure 1. Life reconstruction of *Procolophon trigoniceps*. Note the presence of quadratojugal processes covered by long keratinous spines and large digging-claws. The skeleton of *Procolophon* supports these features (Carroll & Lindsay 1985; deBraga 2003). Numerous minor keratinous spines are common over large or stocky-bodied modern lizards; these structures do not leave traces in the skeleton (e.g. *Iguana, Phrynosoma, Uromastix;* pers. obs.). The long quadratojugal and supratemporal spines of *Procolophon* may have acted as an anti-predatory mechanism, as in phrynosomatid lizards (Young *et al.* 2004).

P. trigoniceps by the presence of a small temporal fenestra (Seeley 1878, 1905). However, the authenticity of these small openings, which are present only in the holotype and a referred specimen of a genus that in South Africa is known from several specimens, was questioned almost from the beginning. They were regarded by some authors as an artefact of preparation or preservation (Broom 1936; von Huene 1912) and the species was neglected, a view endorsed by most later authors (e.g. Colbert 1946; Kuhn 1969; Colbert & Kitching 1975; Carroll & Lindsay 1985). Nevertheless, Hamley & Thulborn (1993) supported the view that the temporal openings were a natural feature in the hypodigm. The temporal fenestra was shown to be particularly well preserved in the holotype, and these authors resurrected the species *P. laticeps.* In addition, Hamley & Thulborn (1993) found four additional apomorphies to support the diagnosis of *P. laticeps.* Recent fieldwork by Johann Neveling in the *Lystrosaurus* AZ of South Africa has provided a new *Procolophon* specimen in which the presence of small temporal fenestrae is unequivocal; this specimen is discussed here.

MATERIALS AND METHODS

Preparation by conventional methods (i.e. mechanical preparation using air-scribes and fine needles) was carried out on several specimens, including recently collected material and the holotypes of *P. trigoniceps*, *P. laticeps* and *P. pricei*. A large number of *Procolophon* specimens were examined, most of them in South African collections, although only some are cited in the text. Specimens from other taxa studied for comparative purposes include the following: BP/1/4299, holotype of *Teratophon spinigenis,* BP/1/4587 paratype of *Teratophon spinigenis,* BP/1/4586 paratype of *Thelerpeton oppressus,* BP/1/4538 holotype of *Thelerpeton oppressus,* IVPP V6064 holotype of *Eumetabolodon bathycephalus,* IVPP V6175 *Eumetabolodon bathycephalus.*

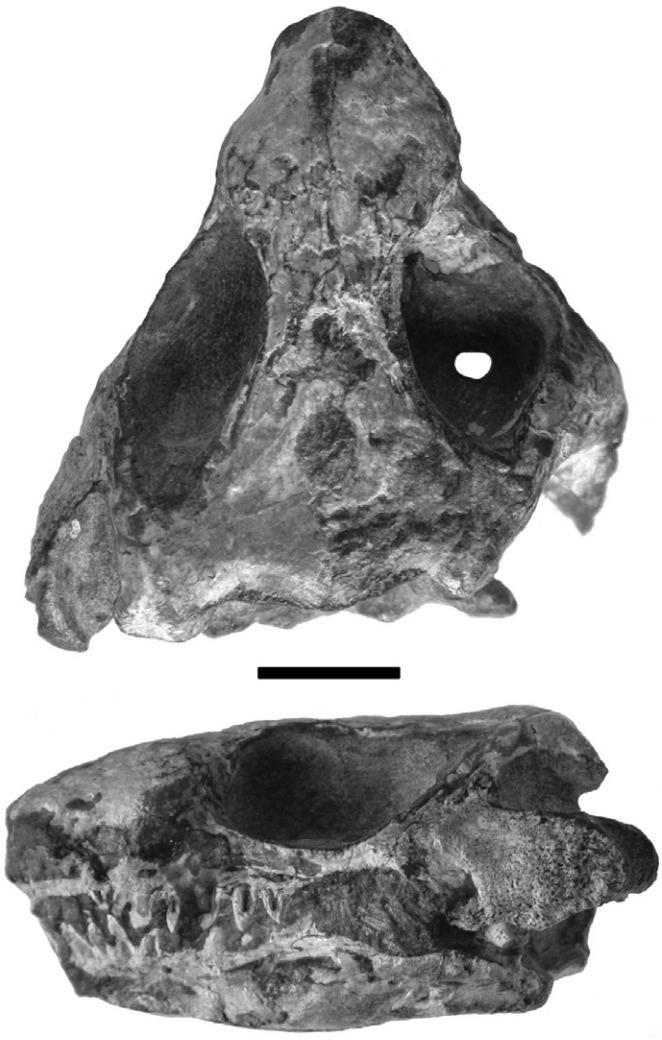

Figure 2. BMNH R1726, holotype of *Procolophon trigoniceps*, cranium in dorsal and left lateral views. Scale bar = 10 mm.

COMPARISONS AND DISCUSSION

The genus *Procolophon* in the Paraná Basin

The genus *Procolophon* is commonly found in the conglomeratic layers of the Sanga do Cabral Formation of Rio Grande do Sul State, southern Brazil (Langer & Lavina 2000; Dias-da-Silva *et al.* 2006). However, these remains consist of disarticulated and reworked bones. The finding of two partial skulls from different localities, that differed from each other mainly in the arrangement of the palatal dentition, was the basis for the proposal of the new species *P. pricei* (Lavina 1983) and *P. brasiliensis* (Cisneros & Schultz 2002). These holotypes are discussed below.

Lavina (1983) distinguished *P. pricei* (Fig. 3A) from *P. trigoniceps* by the following characters: (i) snout shorter and more rounded; (ii) vomerine dentition arranged as an inverted 'V'; (iii) posteromedial palatine tooth row not extending to the anterolateral region of the pterygoid; and (iv) interpterygoid vacuity distinctly larger.

The first character is an artefact of taphonomy because the premaxillae of UFRGS PV0231T have been weathered, giving the snout a more rounded aspect. Character (ii) is consistent with the morphology of several *P. trigoniceps* specimens (Fig. 4), being distinctive only when compared with the stylized reconstruction of the palate of *P. trigoniceps* provided by Broili & Schröder (1936, fig. 6). Character (iii) is variable, and is found in juvenile *P. trigoniceps* specimens (e.g. AMNH 5693, NM QR1447, Fig. 4D,E). An enlarged interpterygoid vacuity (character (iv)) is also seen in some *P. trigoniceps* specimens, especially in juveniles and subadults (e.g. specimen CGP 1-89, Fig. 4A). Thus, the supposedly diagnostic characters of *P. pricei* can be rejected as of a taphonomic nature, or due to individual variation or ontogeny.

Cisneros & Schultz (2002) distinguished *P. brasiliensis* (Fig. 3B) from other species of *Procolophon* by the following characters: (i) vomer possessing a single tooth row extending over the entire bone, and reaching the pterygoid–vomer contact; (ii) a small diastema (or hiatus) in the posterior third of the row; and (iii) three vomerine fangs in the anterior part of the bone, arranged in a 'V' shape, pointing forwards. Characters (i) and (ii) result from a misinterpretation of the position of the vomer–pterygoid contact in MCN PV1904. This suture was erroneously traced on what is in fact a transverse fracture of the anterior part of the pterygoid. The actual suture occurs anteriorly, in the place interpreted by these authors as a tooth hiatus of the vomerine row. Thus, the vomerine tooth row does not reach the vomer–pterygoid suture. Character (iii) is somewhat subjective. The three anterior vomerine teeth are large elements in the vomerine tooth row, but the anteriormost tooth is the largest element, its diameter at the base exceeding by *c.* 50% that of the two following enlarged teeth. The number of enlarged teeth in the vomer is actually variable in *P. trigoniceps*, and some old individuals have a number of them (e.g. BP/1/966, BP/1/4248, Fig. 4C,F). Thus, character (iii) is not a valid autapomorphy.

Re-examination of both diagnoses shows that there are no current grounds to retain *P. pricei* or *P. brasiliensis* as valid species. Both Brazilian holotypes fit within the range of individual and ontogenetic variation of *P. trigoniceps*. The arrangement of the palatal dentition is particularly variable in *P. trigoniceps* and juveniles differ substantially from adults (pers. obs.). A comprehensive description of the pattern of tooth succession in the palate of *P. trigoniceps* is in preparation.

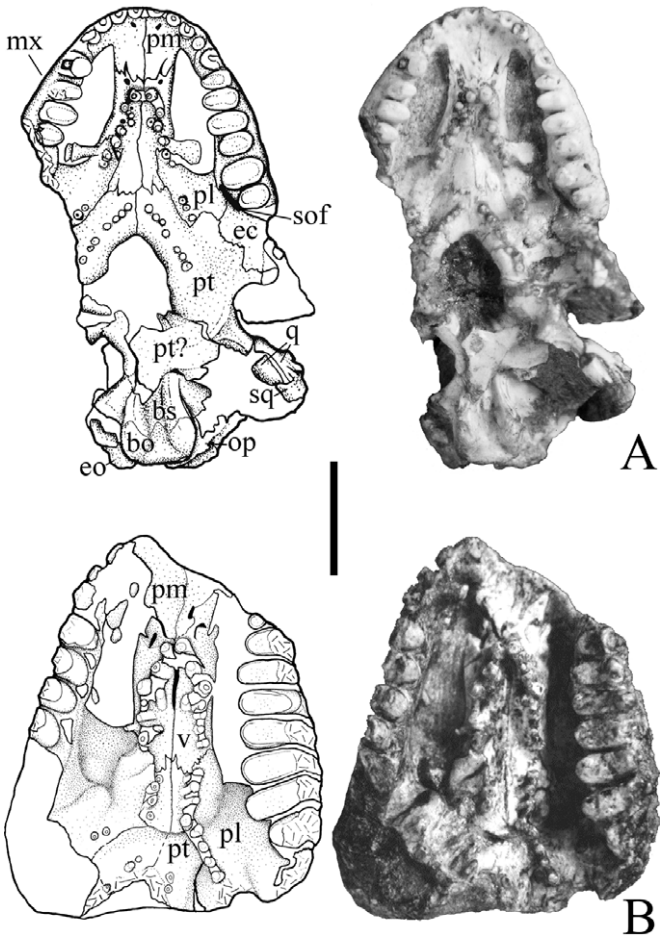

Figure 3. **A**, UFRGS PV231T, holotype of *Procolophon pricei*, cranium in palatal view. **B**, MCN PV1904, holotype of *Procolophon brasiliensis*, cranium in palatal view. Scale bar = 10 mm.

Specimens with temporal fenestrae from the Karoo Basin

The species *P. laticeps* was resurrected by Hamley & Thulborn (1993) on the basis that the temporal fenestrae noted in the two known specimens were real features. In addition, these authors pointed out four further autapomorphies for this taxon. The temporal region of these two individuals, and of a new specimen showing temporal fenestrae recently collected, all from South Africa, is discussed below.

BMNH R3583. The holotype of *P. laticeps* is a weathered but otherwise unaltered cranium and mandible (Fig. 5C). The temporal region is better preserved on the left side of the skull, where the fenestra can be seen. This region is not visible on the right side of the cranium, where it is covered with resin. The temporal fenestra (Fig. 6E,F) is subcircular, located between the postorbital, jugal, quadratojugal and squamosal bones. These bones contribute almost equally to the margins of the temporal opening. The postorbital

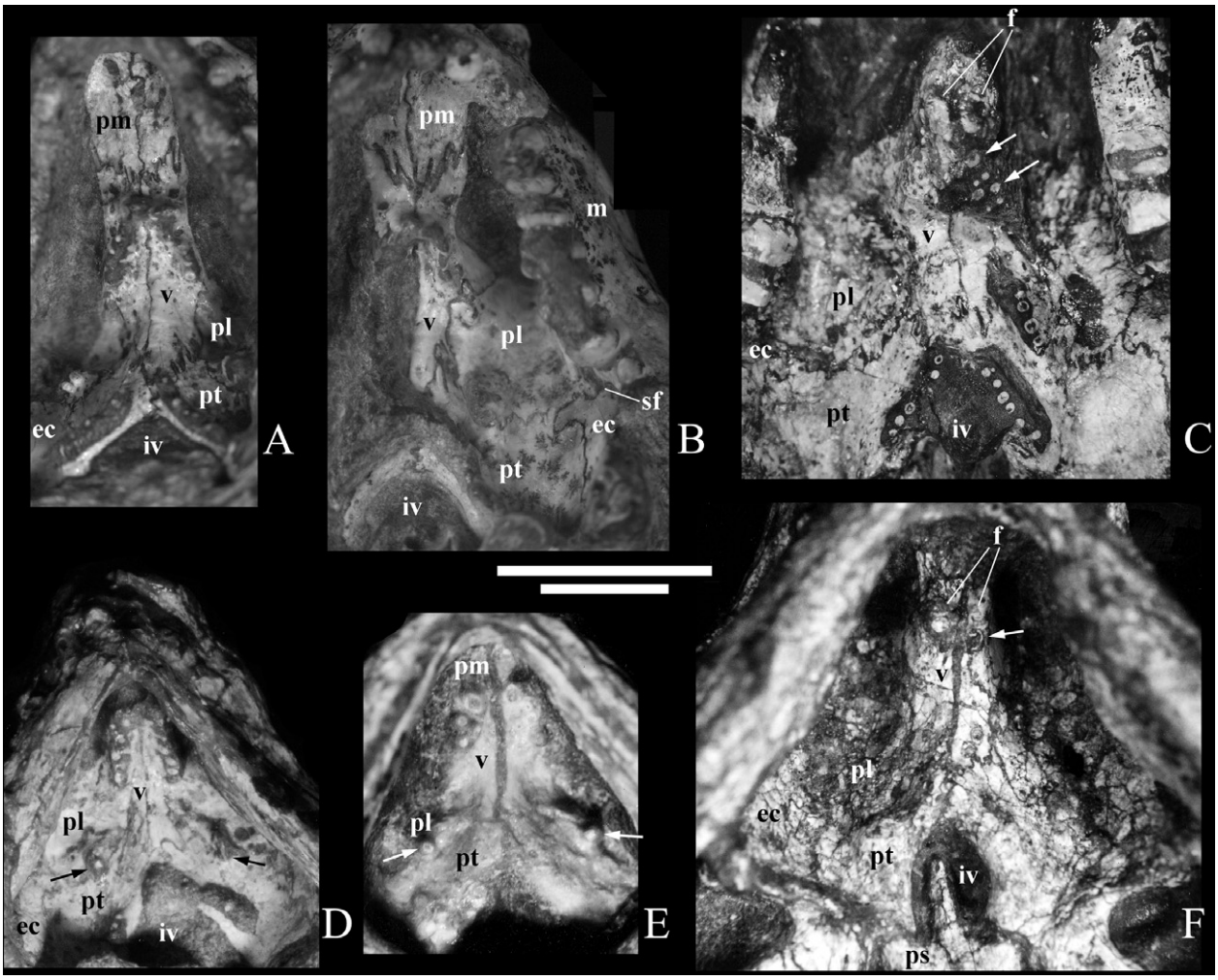

Figure 4. Palate of *Procolophon trigoniceps* specimens from the South African Karoo. **A**, CGP 1-89; **B**, BP/1/4014; **C**, BP/1/4248; **D**, NM QR1447; **E**, AMNH 5693; **F**, BP/1/966. Arrows in C and F indicate posterior enlarged vomerine teeth. Arrows in D and E indicate the last tooth in the pterygoid-palatine tooth row. The mandible is in occlusion in BP/1/4248, NM QR1447 and AMNH 5963. Scale bars = 10 mm, smaller scale bar is for F.

bone forms the anterodorsal margin of the fenestra. Ventrally, this bone has a thin contact with the jugal, which forms the anteroventral edge of the opening. The quadratojugal forms the posteroventral border, and the squamosal the posterodorsal border. As noted by Hamley & Thulborn (1993), part of the dorsal rim of the opening, between the postorbital and squamosal bones, was slightly damaged in preparation. The rest of the structure is, however, well preserved.

BMNH R1949. This specimen was referred to *P. laticeps* by Seeley (1905) and Hamley & Thulborn (1993), and it has been repeatedly illustrated and discussed (see Seeley 1889, 1905; von Huene 1912; Carroll & Lindsay 1985). The specimen consists of an articulated partial skeleton of a large-sized individual (Fig. 4B). The cranium lacks the tip of the snout and the left quadratojugal process, and some areas are weathered. The temporal fenestra (Fig. 6F–I) is preserved on both sides of the cranium. This structure is elliptical, and elongated in a posterodorsal to anteroventral direction. It is located between the postorbital, jugal and squamosal bones. The postorbital delimits the anterior and anterodorsal borders of the fenestra. On both sides of the skull the margins of this bone have been slightly damaged by over-preparation. The openings should therefore be moderately more constricted than they appear now. Anteroventrally, the fenestra is bordered by a basin of the posterodorsal projection of the jugal. The jugal contribution to the margin of the fenestra is the shortest of the three bones that form this structure. The squamosal contribution is the longest, delimiting the posterodorsal to posteroventral margins. Posterodorsally, the squamosal contribution to the margin is concave, and ventrally it forms a straight, thin ventral projection that contacts the jugal. This process excludes the quadratojugal from the margin of the opening.

CGP 1-127. A well-preserved medium-sized specimen (Fig. 5A), consisting of cranium and anterior part of postcranium, collected by Johann Neveling (for stratigraphic context, see Neveling 2004). The temporal region is well preserved on both sides of the cranium. The opening (Fig. 6A–D) is subcircular and smaller than in other specimens, composed by the margins of the postorbital, jugal and squamosal bones. The postorbital forms the anterodorsal rim of the opening. Dorsally, this bone has a short contact with the squamosal that prevents the supratemporal from contributing to the dorsal margin of the fenestra. The squamosal forms the posterior border of the opening, and is less convex than the other two bones that form this structure. The squamosal sutures ventrally to the jugal, this short contact excludes the quadratojugal

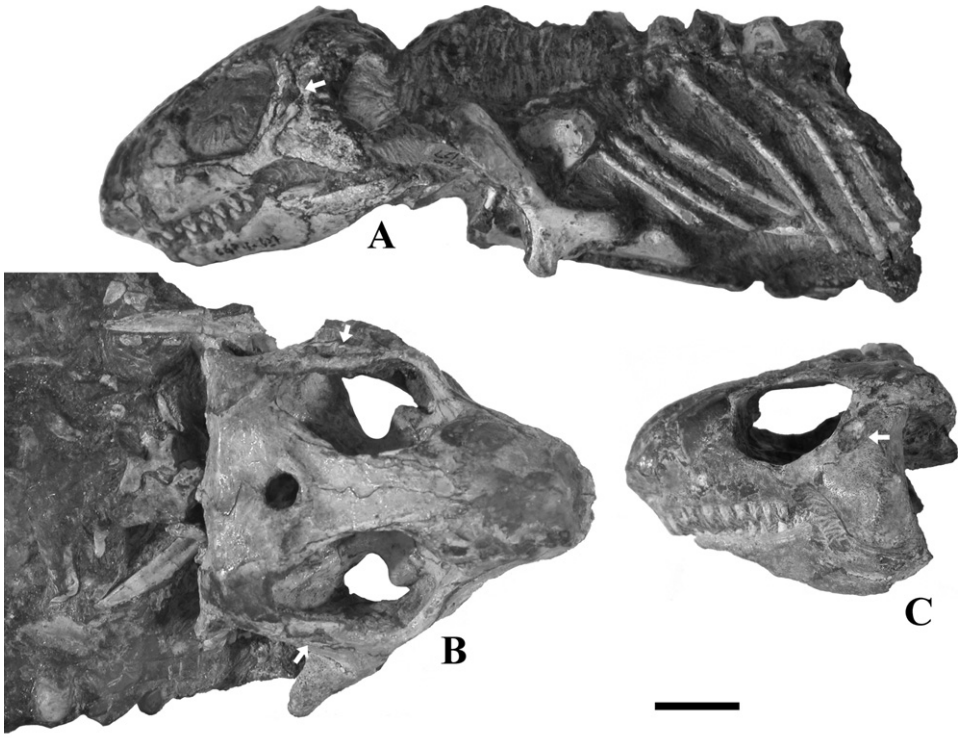

Figure 5. *Procolophon* specimens with temporal fenestrae. **A**, CGP 1-127; **B**, BMNH R1949; **C**, BMNH R 3583 holotype of *P. laticeps.* Scale bar = 10 mm, arrows indicate temporal fenestrae.

from the rim. The jugal forms the markedly convex ventral border of the orbit. In the right fenestra, this bone is positioned slightly more anteriorly than on the left side.

On the validity of *Procolophon laticeps*

The temporal fenestrae show clear discrepancies in the specimens discussed here. In the holotype, the temporal fenestra is considerably wide, being some 50% larger than in CGP 1-127. This difference does not seem to be ontogenetic, because the skulls of both individuals are of comparable length (maximum cranial length: BMNH R3583 = 41.5 mm; CGP 1-127 = 42.4 mm), suggesting comparable ontogenetic stages. In the much larger cranium BMNH R1949, the temporal openings are elongated, being longer dorsoventrally than in the holotype, but shorter anteroposteriorly. The quadratojugal contribution to the rim of the orbit is present only in the holotype. Furthermore, in this specimen the quadratojugal contributes to the rim to a larger extent than the jugal or the squamosal. In the remaining specimens, the temporal openings are formed exclusively by the jugal, the squamosal, and the postorbital. It is difficult to infer an ontogenetic mechanism that can account for this variation in size, shape and composition of the temporal openings in all specimens, and it seems unlikely that they can be regarded as merely due to individual variation.

Besides the presence of temporal fenestrae, Hamley & Thulborn (1993) proposed four additional autapomorphies for *P. laticeps*. Because the bone surface of the skull of the holotype of *P. laticeps* is heavily weathered, these characters were mostly obtained from BMNH R1949, and presumably, by contrast with the holotype of *P. trigoniceps* and other specimens held at the Natural History Museum in London. Taking into account the new specimen with temporal openings, CGP 1-127, as well as a broader sample of *P. trigoniceps*, however, none of these characters seems diagnostic. These characters are: (i) contact between parietal and squamosal bones; (ii) ventrolateral extension of parietal on occipital surface; (iii) arched tip of paroccipital process; and (iv) contact between prefrontal and postfrontal. A contact between parietal and squamosal bones (character (i)) is not obvious in BMNH R1949. On both sides of this specimen, the anterodorsal margins of the squamosals are not well preserved, nor are the lateral margins of the parietals. No contact can be traced between these bones. The bone labelled as "parietal" in Hamley and Thulborn (1993, "pa" in fig. 3) is in fact the supratemporal. Character (ii), ventrolateral extension of parietal on occipital surface, is in fact present in BMNH R1949, but is also present in specimens with no temporal fenestrae, e.g. BMNH R4087 (see Carroll & Lindsay 1985, fig. 5). The character is, therefore, not confined to specimens that bear temporal openings. With regard to character (iii), BMNH R1949 does posses an arched tip of the paroccipital process of the opisthotic (Fig. 7A), but this character is not present in the new specimen CGP 1-127 (Fig. 7B), where the paroccipital process is well preserved and has been carefully prepared. Hence, this character cannot be considered diagnostic for *P. laticeps*. The peculiar morphology of the opisthotic in BMNH R1949 may be due to individual variation. In ventrolateral view, a very short contact is present between the tips of the prefrontal and postfrontal bones (Character (iv)) in BMNH R1949. This prefrontal–postfrontal contact is a highly variable character in *Procolophon*. It is not present in all specimens with temporal openings, and it is present in some specimens that do not possess temporal openings (e.g. CGP 1-108, pers. obs.).

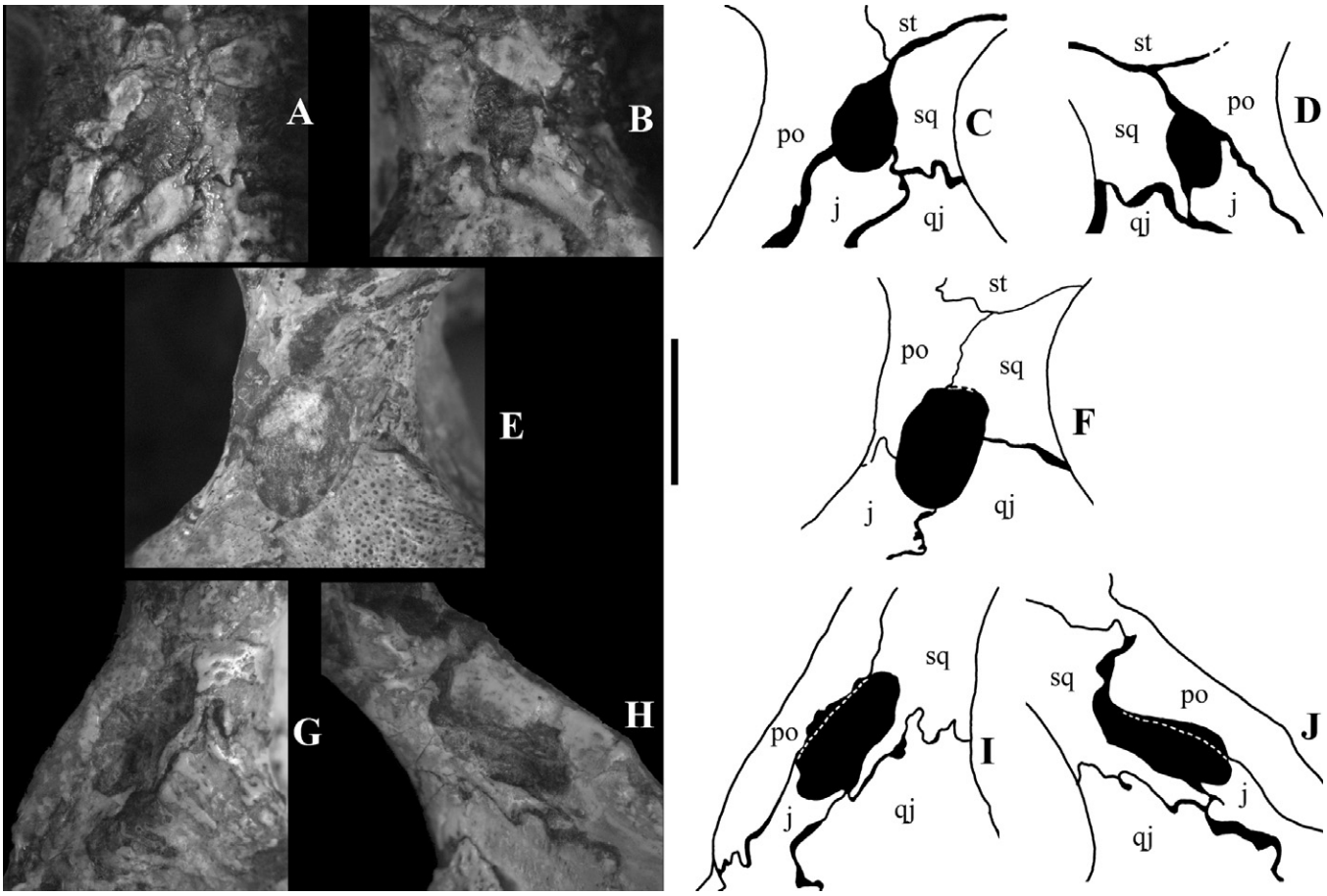

Figure 6. Temporal fenestrae in *Procolophon*. **A–D**, CGP 1-127. **E**, **F**, BMNH R3583 holotype of *P. laticeps.* **G–J**, BMNH R1949. A, C, E, G, I, left lateral views. B, D, F, H, J, right lateral views.

Specimen CGP 1-127 was collected from the same locality and horizon as CGP 1-256 (J. Neveling, pers. comm. 2005), the latter being a *Procolophon* specimen with no temporal fenestrae. Furthermore, the holotypes of both *P. trigoniceps* and *P. laticeps* were collected by D. White at Donnybrook Farm, Queenstown District, presumably from the same localized band of dark red mudstone, approximately one metre thick, within the Katberg Formation. This is the only stratum where *Procolophon* is known to occur at Donnybrook (Kitching 1977). Unfortunately, no precise locality information is available for BMNH R1949. Thus, at least two of the three specimens referable to *P. laticeps* come from sites and horizons that have also produced *P. trigoniceps.* This implies sympatry for the two species, at least in two localities in the Eastern Cape Province of South Africa.

A number of factors, when combined, strongly suggest that *P. laticeps* is not a valid species: (1) the rarity of specimens with temporal openings, within a genus that is known from several well preserved crania; (2) the high variation in the morphology of the temporal openings among the specimens that have them; (3) the absence of additional autapomorphies for *P. laticeps;* and (4) the co-occurrence with *P. trigoniceps* of at least two of the three individuals known.

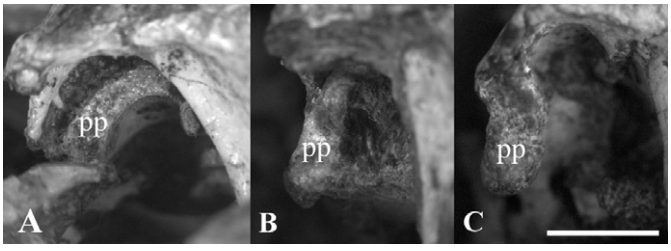

Figure 7. Paroccipital process of the right opisthotic in *Procolophon*, in lateral view. **A**, BMNH R1949. **B**, CGP 1-127. **C**, BMNH R4087. A and B are individuals with temporal openings. Scale bar = 5 mm.

The phenomenon of sympatry is known to occur when there is a non-geographical mechanism of reproductive isolation among the species populations (Mayr 1970; Dobzhansky 1970). Sympatry, however, is an exceptional event in nature. Brooks & McLennan (2002) report a frequency of only 9.1% of sympatric speciation, and sibling species are more likely to occupy different geographic areas (Mayr 1970; Dobzhansky 1970).

Thus, *P. laticeps* is here regarded as a junior synonym of *P. trigoniceps*. The temporal fenestration of *Procolophon* is considered herein to represent an anomalous or pathological feature of the three individuals in which it is known. When considering a large sample of individuals – as is the case in *Procolophon* (some hundred well preserved crania recovered at the Karoo Basin) – anomalous specimens should be expected. The temporal openings of *Procolophon* are smaller and much simpler than those of the procolophonoid *Candelaria barbouri* (see Cisneros *et al.* 2004), and no more than a small genetic change would be necessary to activate the development of these openings in *Procolophon*. The mere embryological failure to close sutures of the relevant bones in the temporal region

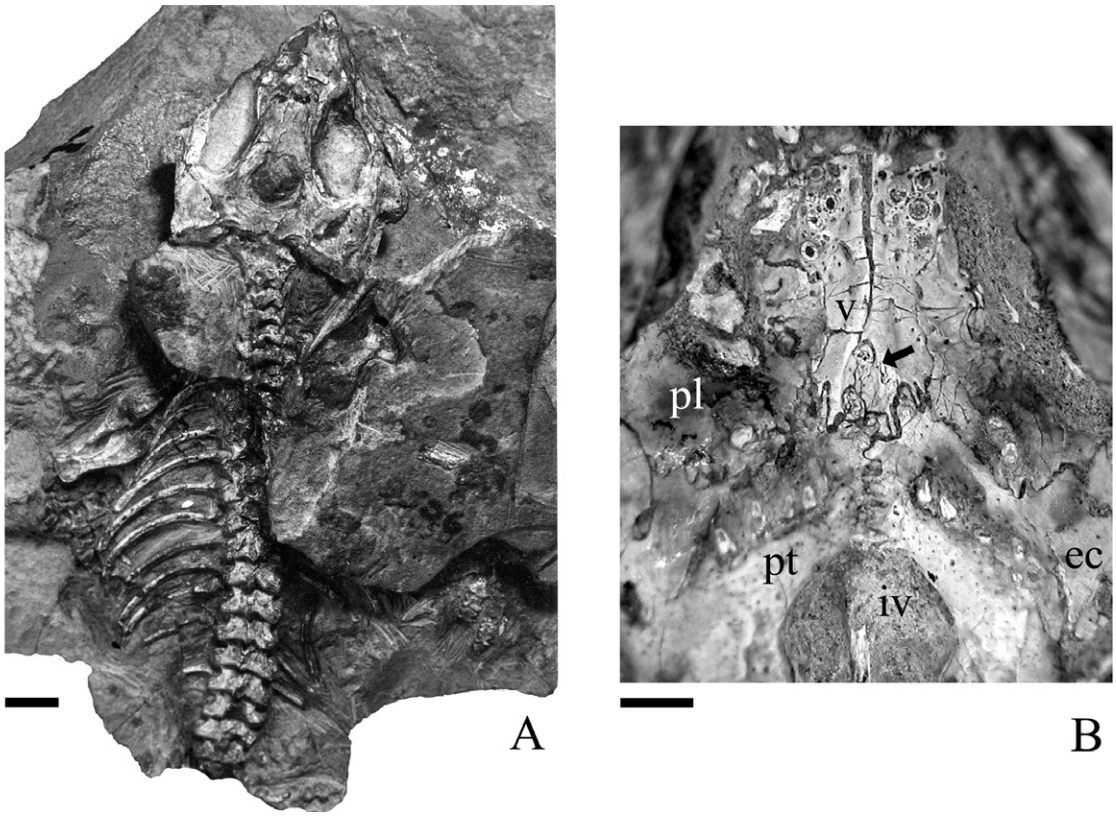

Figure 8. AMNH 9506, *Procolophon trigoniceps* from Shackleton Glacier, Transantarctic Mountains. **A**, skeleton in dorsal view. **B**, detail of palate in ventral view, arrow points to the depression between the vomers. Scale bars = 5 mm (A) and 2 mm (B).

would result in this feature (Tarsitano *et al.* 2001). This unusual condition was not necessarily disadvantageous, because judging by its size, BMNH R1949 represents an old individual.

The genus *Procolophon* in the Transantarctic Mountains

Among the *Procolophon* remains from the Transantarctic Mountains described by Colbert & Kitching (1975), one specimen is notable for its completeness and fine preservation, and offers the best comparisons with non-Antarctic *Procolophon* material. AMNH 9506 is a subadult individual, consisting of a cranium and articulated postcranium, including the 21st presacral vertebrae, ribs, pectoral girdle and forelimbs (Fig. 8A). Colbert & Kitching (1975) noted some peculiarities of AMNH 9506 when compared to known specimens of *P. trigoniceps*; including the fact that it has rather small quadratojugal processes and relatively robust forelimbs. They considered, however, that these traits fitted within the range of ontogenetic, individual or sexual variation of the type species, a view also endorsed here.

Recent preparation of the palate in AMNH 9506 has revealed an unusual feature of this Antarctic specimen, the only one in the collection of AMNH in which the palate is preserved. It consists of a distinctive depression between the vomers (Fig. 8B). This structure is located in the posteromedial region of these bones, is elliptical and symmetrical, and the medial vomerine suture divides it through the midline. It is shallow (less than one millimetre in depth), but taking into account the postmortem dorsoventral compression of the cranium, the depression must have been deeper, although narrower, in life. The surface and margins of this inter-vomerine depression, except for small areas of subperiosteum damaged during preparation, are well preserved. It possesses regular borders and is roughly symmetrical, suggesting that it was a natural feature of the Antarctic procolophonid, not an artefact of taphonomy or preparation. No other *Procolophon* specimen from South Africa or southern Brazil shows this depression. AMNH 9506 is also peculiar because of the large number of foramina in the vomers. Although the number of these foramina is variable in *Procolophon*, no specimen examined in this study possesses a number similar to AMNH 9506. It is possible, however, that the remarkable preservation of the palate in this specimen allows one to see more foramina than in other *Procolophon* specimens where this area has been prepared.

Although it is possible that this depression in the vomers may be of taxonomic significance, especially taking into account the provenance of AMNH 9506, far from both the Karoo and Paraná basins, it is considered unjustified to propose a new species based on this single small feature that could also be a result of mere individual variation. A similar depression was noted by Dias-da-Silva *et al.* (2006) in a large Brazilian specimen, however, its palate is very damaged and the character may not be a natural feature (pers. obs.). As mentioned above, other particular features seen in the Antarctic specimen are considered to fit within the known range of variation of *Procolophon trigoniceps* (Colbert & Kitching 1975). If future work reveals that the palatal depression is characteristic of *Procolophon* specimens from Antarctica, then it may be necessary to propose a new taxon to accommodate them.

SYSTEMATIC PALAEONTOLOGY

Parareptilia Olson, 1947
Procolophonoidea Lydekker, 1890
Procolophonidae Lydekker, 1890
Procolophoninae Lydekker, 1890

Procolophon Owen, 1876

Type species. Procolophon trigoniceps Owen, 1876

Revised diagnosis. Robust procolophonid with adults possessing six to eight large bicuspidate molariform teeth with mesiodistally-compressed, chisel-like crowns. In *Eumetabolodon* from China, and *Thelerpeton* and *Teratophon* from South Africa, adults may posses a similar number of molariform teeth, roughly comparable in morphology to those of *Procolophon*. In these taxa, however, molariform teeth are less compressed and more bulbous than in *Procolophon* (Fig. 9). In addition, the maxillary tooth row of *Procolophon* does not increase distally in labio–lingual breadth as in *Teratophon* and *Thelerpeton*. *Procolophon* can also be distinguished from all procolophonids except *Thelerpeton* by the presence of a single, prominent, posterolaterally directed quadratojugal spine, that does not exceed the orbitotemporal maximum width. Other procolophonids (e.g. *Eumetabolodon*, *Timanophon*) possess a single but much smaller, posterolaterally directed quadratojugal spine. Conversely, *Teratophon* possesses a single spine that greatly exceeds the maximum orbitotemporal width.

Remarks. DeBraga (2003) listed other distinctive, probably diagnostic features for the postcranium of *Procolophon.* Unfortunately this author based his observations largely on SAM PK-7711, a specimen which is unlikely to belong to *Procolophon*. SAM PK-7711 is a huge postcranium collected on the farm Erf 1, near Aliwal North, Free State Province. Erf 1 is the type locality of the archosauromorph *Euparkeria*. The fossiliferous exposures on this farm belong to the Burgersdorp Formation, and are referred to the *Cynognathus* subzone B (Hancox *et al.* 1995). Hence, the age of the specimen is Middle Triassic, exceeding by a considerable margin the LAD of *Procolophon* based on diagnostic material (see below). Four procolophonids, formerly grouped within the genus '*Thelegnathus*', are known from this horizon, all established on cranial characters: *Thelephon contritus*, *Theledectes perforatus*, *Thelerpeton oppressus,* and *Teratophon spinigenis* (Modesto & Damiani 2003). The unusually large size of SAM PK-7711 (see Table 1) suggests that is referable to *Teratophon spinigenis*, the largest procolophonid known from South Africa. A specimen of *Teratophon spinigenis* recently collected by Roger Smith (Fig. 10, Table 1) is closely comparable in size with SAM PK-7711.

Referred material. The *Procolophon* material comprises hundreds of specimens, being too numerous to be listed here. Major collections are held at the following South African institutions: AM, BPI, CGP, NM and SAM.

Localities. Sanga do Cabral Formation (Paraná Basin), Rio Grande do Sul State, Brazil; Katberg and lowermost Burgersdorp formations (Karoo Basin), Free State, Eastern Cape and KwaZulu Natal provinces, South Africa; and Lower Fremouw Formation (Transantarctic Basin), Shackleton Glacier, Transantarctic Mountains. (for a list of localities of specimens cited in the text, see Appendix).

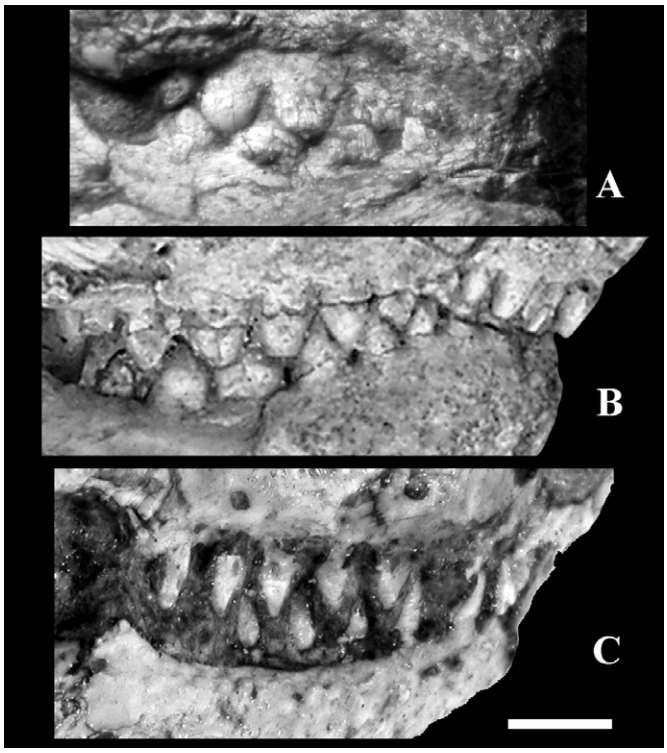

Figure 9. Comparison between **A**, *Teratophon spinigenis* (BP/1/4587), **B**, *Eumetabolodon bathycephalus* (IVPP V6064) and **C**, *Procolophon trigoniceps* (BP/1/5927b); showing differences in dentition. Scale bar = 5 mm for A, B and 3.5 mm for C.

Horizon. The temporal range of *Procolophon* is best documented for the Karoo Basin. The FAD of *Procolophon* is represented by a maxilla (RS 265) recorded at 116 m above the P/T boundary, in the Lower Katberg Formation (Botha

Figure 10. *Teratophon spinigenis* SAM PK-K10174, collected by Roger Smith at the farm Lemoenfontein 44 (Free State Province, South Africa) in the *Cynognathus* subzone B (Middle Triassic). Scale bar = 10 mm.

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Table 1. Selected postcranial maximum measurements (in millimetres) from *Procolophon trigoniceps* (AMNH 9506, CGP 1-127, BMNH R1949, BP/1/962, CGP 1-1), SAM PK-7711 and *Teratophon spinigenis* (SAM PK-K10174). Only adult or subadult material has been included. Maximum transversal length of postzygapophyses was measured on a mid-trunk vertebrae. R, right, L, left.

Specimens	Postzygapophyses transversal length	Interclavicle transversal length	Interclavicle anteroposterior length	Humerus length	Femur length
AMNH 9506	11.7		31.7	~24(R)	
CGP 1-127	9.3	26.7	31.9	25.7(R)/27.2(L)	
BMNH R1949		28.8	36		
BP/1/962		29		25.5(R)	26(L)
CGP 1-1	17			39(R)	~42(L)
SAM PK-7711	19.5	49.5	60	48(R)/50(L)	50(R)/~49(L)
SAM PK-K10174	20				~53(R)

and Smith 2006), being located much higher than the FAD of the dicynodont *Lystrosaurus* (*c*. 41 m below the P/T boundary, Smith and Ward 2001). The LAD of *Procolophon* is represented by a partial maxilla (CGP 1-9) and a partial left mandible (CGP 1-7) found in mudstones at the base of the Burgersdorp horizon 1, a unit that represents the lower part of the Burgersdorp Formation in the proximal sector (Neveling 2004). The genus surpasses the LAD of *Lystrosaurus* and co-existed at least briefly with the reptile *Palacrodon* and the amphibian *Trematosuchus* (Neveling 1999, 2004; Damiani *et al.* 2000), components of the *Cynognathus* Subzone A (Hancox *et al.* 1995). The temporal range of *Procolophon*, therefore, spans the upper part of the *Lystrosaurus* AZ (including the informal '*Procolophon* Abundance Zone' *sensu* Neveling 2004) to the lowermost *Langbergia* Subzone (Early Triassic).

Procolophon trigoniceps Owen, 1876, Figs 2–8, 9C, 10

v*	1876	*Procolophon trigoniceps* Owen p. 25, pl. 20, figs 4–7
	1876	*Procolophon minor* Owen p. 26, pl. 20, figs 8–12
	1878	*Procolophon griersoni* Seeley p. 797, pl. 22, figs 1–3
	1878	*Procolophon cuneiceps* Seeley p. 799, pl. 22, figs 7, 8
v*	1878	*Procolophon laticeps* Seeley p. 801, pl 22, figs 4–6
v	1903	*Procolophon trigoniceps* Broom figs 4–6
	1905	*Procolophon platyrhinus* Seeley p. 226, text-fig. 35
	1905	*Procolophon sphenorhinus* Seeley p. 226, text-fig. 36
v*	1905	*Procolophon baini* Broom p. 332
	1914	*Procolophon trigoniceps* Watson pls 1–3, text-figs 1–5
	1936	*Procolophon trigoniceps* Broili & Schröeder figs 1–10, pls; pl. 3, figs 2–3; pl. 4–6
	1974	*Procolophon trigoniceps* Kemp pl. 1, figs 1–4
	1975	*Procolophon trigoniceps* Colbert & Kitching figs 1–24
vp	1977	*Procolophon trigoniceps* Gow text-figs 1–3, 5, 7 [*non* fig. 6 = new undescribed procolophonid]
p	1974	*Procolophon* van Heerden pls 1,2, 5–8, figs 1, 3–5 [*non* pls 3, 4, fig. 2 = temnospondyl]
v*	1979	*Procolophonoides baini* Ivachnenko p. 13
v*	1983	*Procolophon pricei* Lavina p. 54, figs 1–9
	1985	*Procolophon trigoniceps* Carroll & Lindsay figs 1, 3–14
v*	1987	*Procolophonoides baini* Ivachnenko p. 52
v	1993	*Procolophon laticeps* Hamley & Thulborn figs 2–4
v*	2002	*Procolophon brasiliensis* Cisneros & Schultz figs 1, 2
vp	2003	*Procolophon trigoniceps* deBraga figs 1–3, 6–9, 18 [*non* figs 4, 5, 10–17 = cf. *Teratophon spinigenis*]

Holotype. BMNH R1726, a small, almost complete cranium and mandible in occlusion. Collected by D. White at Donnybrook Farm, Eastern Cape Province, South Africa.

Diagnosis. See generic diagnosis above.

BIOGEOGRAPHICAL CONSIDERATIONS

It is a valid question to ask whether a species of small terrestrial reptile could have such a wide geographic range in Gondwana, through the Paraná, Karoo and Transantarctic basins. Some modern lizards provide examples of wide distributions at species level for small reptiles that are comparable with, or even wider than, the geographic range that is proposed for *Procolophon trigoniceps* in this study. A number of Australian species, including the skinks *Tiliqua scincoides, T. rugosa, T. occipitalis, Menetia grey,* and the gecko *Heteronotia binoei,* have ranges that cover most of the continent, being excluded from the most arid regions of the Australian Desert (Cogger 1979). The fact that these species are spread right across Australia suggests that they could have broader ranges if a larger area was available. An even larger distribution is shown by the agamid *Agama agama;* this species covers all Equatorial Africa (Enge *et al.* 2004). The lacertid *Zootoca vivipara* (formerly *Lacerta vivipara*) has probably the widest range of any modern lizard. It is found all across North Eurasia, from the British Isles east to the Japanese Archipelago (Surget-Groba *et al.* 2002). The range of this species, that is well known for having both viviparous and oviparous populations, includes high altitudes in the Alps, the Pyrénées and the Urals. The modern distribution of *Zootoca vivipara* is far wider than the distribution proposed for *Procolophon trigoniceps* in this study. It would not be unexpected though, that *Procolophon trigoniceps* may yet be found in a yet wider area than that currently known.

CONCLUSIONS

The holotypes of *P. pricei* and *P. brasiliensis* fit within the pattern of individual, and specially, ontogenetic variation of *P. trigoniceps*, and are here considered junior synonyms. The pattern of palatal dentition of *P. trigoniceps,* thus, is more complex than previously suspected, and juveniles may differ substantially from adults. The only complete Antarctic skull known differs from South African and Brazilian specimens in having an elliptical depression in the vomers. The interpretation of this structure is ambiguous as it may also be regarded as due to individual variation, and this specimen is provisionally kept within *P. trigoniceps.* Further evidence from Antarctica would be

necessary to confirm if this structure is present in other specimens, and if it should be regarded as taxonomically important.

The peculiar temporal openings of the South African species *P. laticeps* are here regarded as an authentic feature of these specimens, but their presence is interpreted as anomalous or pathological, and hence without taxonomic significance. The occurrence of temporal openings in *Procolophon* is intriguing, due to their presence in a number of other parareptile lineages (Cisneros *et al.* 2004).

Only the type species *P. trigoniceps* is recognized in Gondwana, on the basis of available evidence. This species occupied a large geographical range, from the Paraná Basin to the Transantarctic Mountains.

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ABBREVIATIONS

Institutional

AM	Albany Museum, Grahamstown, South Africa.
AMNH	American Museum of Natural History, New York, USA.
BMNH	Natural History Museum, London, United Kingdom.
BP	Bernard Price Institute for Palaeontological Research. Johannesburg, South Africa.
CGP	Council for Geosciences, Pretoria, South Africa.
IVPP	Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China.
MCN	Museu de Ciências Naturáis, Porto Alegre, Brazil.
NM	National Museum, Bloemfontein, South Africa.
SAM	South African Museum, Cape Town, South Africa.
RS	South African Museum (field number), Cape Town, South Africa.
UFRGS	Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

Anatomical

bo	basioccipital
ec	ectopterygoid
eo	exoccipital
f	vomerine 'fang'
iv	interpterygoid vacuity
j	jugal
m	maxilla
op	opisthotic
pl	palatine
pm	premaxilla
po	postorbital
pp	paroccipital process of the opisthotic
ps	parasphenoid
pt	pterygoid
q	quadrate
qj	quadratojugal
sf	suborbital foramen
so	supraoccipital
sq	squamosal
st	supratemporal
v	vomer

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Appendix

Provenance of *Procolophon* specimens cited in the text

Specimen	Locality
AMNH 5693	Unknown locality, South Africa
AMNH 9506	Kitching Ridge, E of Shackleton Glacier, Transantarctic Mountains, 85°13'S/177°E
BMNH R1726	Donnybrook, Queenstown, Eastern Cape Province, South Africa
BMNH R3583	Donnybrook, Queenstown, Eastern Cape Province, South Africa
BMNH R1949	Unknown locality, Free State Province, South Africa
BMNH R4087	Haslope Hill, Tarkastad, Eastern Cape Province, South Africa
BP/1/962	Prinsfontein, Tarkastad, Eastern Cape Province, South Africa
BP/1/966	Middelkraal, Tarkastad, Eastern Cape Province, South Africa
BP/1/4014	Hobbs Hill (Windvogelsberg), Cathcart, Eastern Cape Province, South Africa
BP/1/4248	Klipfontein 340 ('*Procolophon* Hill'), Bethulie, Free State Province, South Africa, 30°28'S/26°08'E
BP/1/5927b	Klipfontein 340 ('*Procolophon* Hill'), Bethulie, Free State Province, South Africa, 30°28'S/26°08'E
CGP 1-1	Goedemed prison grounds, Rouxville, Free State Province, South Africa
CGP 1-7	Odendaalstroom, Burgersdorp, Free State Province, South Africa
CGP 1-9	Odendaalstroom, Burgersdorp, Free State Province, South Africa
CGP 1-89	Elandskop 116, Tarkastad, Eastern Cape Province, South Africa
CGP 1-108	Palmietfontein 94, Tarkastad, Eastern Cape Province, South Africa
CGP 1-127	Hill & Dale 156, Tarkastad, Eastern Cape Province, South Africa
CGP 1-256	Hill & Dale 156, Tarkastad, Eastern Cape Province, South Africa
MCN PV1905	Rincão dos Weiss, Mata, Rio Grande do Sul State, Brazil, 29°33'27.35"S/53°26'56.43"W
NM QR1447	Klipfontein 340 ('*Procolophon* Hill'), Bethulie, Free State Province, South Africa, 30°28'S/26°08'E
RS 265	Farm Donald 207, Bethulie, Free State Province, South Africa, 30°24'52"S, 26°15'00"E
UFRGS PV231T	Dilermando de Aguiar, Santa Maria, Rio Grande do Sul State, Brazil, 29°49'37"S/54°13'55"W

Re-evaluation of the postcranial skeleton of the Triassic dicynodont *Kannemeyeria simocephalus* from the *Cynognathus* Assemblage Zone (Subzone B) of South Africa

Romala Govender[1*], Phillip John Hancox[2] & Adam M. Yates[1]

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

[2]*CCIC South Africa, Postnet Suite 81, Private Bag X9, Melville, 2109 South Africa*

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Kannemeyeria simocephalus is probably the best known Middle Triassic dicynodont from South Africa and has been the standard against which other Triassic dicynodonts are compared. In the past studies have concentrated on the cranial morphology of *K. simocephalus* and its implications for Triassic dicynodont taxonomy and phylogeny. There has been little work on the postcranial anatomy of *K. simocephalus,* which remains poorly understood. An analysis of the postcranial skeleton of *K. simocephalus* has identified characters that diagnose the postcranial skeleton. These include a tubercle on the proximo-posterior corner of the medial surface of the acromion; almost straight lateral border of the femur. Material previously described as *K. simocephalus* by Pearson (1924) and Cruickshank (1975) was also included in this study. Some of the material was found to be significantly different from what is understood to be *K. simocephalus* and as a result has been included a separate study. It was therefore concluded that the referred specimen BP/1/5624 is currently the most complete and positively identified as *K. simocephalus.*

Keywords: Triassic, Dicynodont, *Kannemeyeria,* South Africa, *Cynognathus* Assemblage Zone.

INTRODUCTION

Kannemeyeria simocephalus is a medium to large dicynodont from the *Cynognathus* Assemblage Zone of the South Africa. Hancox *et al.* (1995) noted that it is limited to the middle part of the zone, which they labelled as Subzone B (also see Shishkin *et al.* 1995). A recent study of the cranial anatomy of South African *Kannemeyeria* (Renaut 2000) concluded that all known material can be referred to a single species, *K. simocephalus,* and this finding has renewed interest in the postcranial morphology of this species. To date there have only been two studies that have focused on the postcranial skeleton of *Kannemeyeria,* Pearson (1924) and Cruickshank (1975), both of which are incomplete for various reasons. The most serious problem faced by Pearson (1924) was that the elements she studied had suffered considerable damage due to crushing, whereas Cruickshank (1975) provided only a brief description of what was considered a fairly complete specimen.

Although poor preservation has been an issue in previous studies of postcranial material, recent collecting efforts have provided more complete and better preserved specimens. Furthermore, a large proportion of the older material is made up of isolated elements that have been collected over many years, and all of which have been assumed to be *Kannemeyeria.* This assumption is typically based on the premise that *Kannemeyeria* was the only dicynodont present in the *Cynognathus* Assemblage Zone B. An important part of the present study was to identify postcranial autapomorphies of *Kannemeyeria simocephalus* that could be used to refer isolated postcranial material to this species with confidence. Therefore, elements were not used in order to minimize the chance of inadvertently including material that did not belong to *K. simocephalus.*

*Author for correspondence. E-mail: romala@discoverymail.co.za

MATERIALS AND METHODS

The holotype of *Kannemeyeria simocephalus* (HMV 8173) has no known associated postcrania. Therefore the descriptions of the postcranial morphology are based on the following referred specimens of Renaut (2000).

The specimen BP/1/5624 was recovered at the Bethel/Slootkraal locality, Rouxville District, South Africa, *Cynognathus* Assemblage Zone, Subzone B. The skeletal elements are well preserved, but all the bones have experienced some breakage and distortion. Renaut (2000) described the left and right sides of the skeleton of BP/1/5624 as having suffered two different types of distortion. The right femur has been dorso-ventrally flatted so that the natural shape is exaggerated, while the left femur has been rolled and possibly compressed along the anterior and posterior margins. This compression has resulted in the shaft of the femur having a circular shape in transverse section. The scapulae from BP/1/5624 and BP/1/6104 also show different types of distortion; with the scapula of BP/1/5624 twisted so that the anterior dorsal end of the bone approached the distal end. The skeletal material consists of eight vertebrae, a number of rib fragments, all the elements of the forelimb, the scapula, the pelvic girdle and two elements of the hindlimb (left and right femur and right tibia). The postcranial skeleton was found articulated and associated with a complete skull.

Most of the skeleton of BP/1/6160 caudal to the pectoral girdle was lost during the roadworks that exposed the specimen. Only the pectoral girdle, some cervical vertebrae, the forelimbs, and the skull and lower jaw could be collected, but this material was articulated and orientated north–northeast to west–southwest. Locality: Bethel/Slootkraal, Rouxville District, South Africa. *Cynognathus*

Assemblage Zone (subzone B). The specimen was found in green channel sandstone with abundant rip up clasts.

SAM-PK-3017 consists mainly of a skull and a series of vertebrae. Locality: Winnaarsbaken, Burgersdorp District, South Africa. *Cynognathus* Assemblage Zone (Subzone B). The material is well preserved but was not found in articulation; however, it must be noted that although the vertebrae might form a sequence there is no point of reference as to its position in the vertebral column. Although the vertebrae might form a sequence there is no point of reference as to its position in the vertebral column.

ELM 1 consists of a skull and a number of postcranial elements, including vertebrae, ribs, scapulae, coracoids, clavicles, sternum, humeri, radii, ulnae, pelvic girdle (left and right), femora, tibia and fibulae. The mounted material belongs to a single specimen (Courtney-Latimer, 1948), but there are other elements not included in the mount that bear the same catalogue number, indicating that more than one individual is present. Locality: Losberg Mountain on the farm 'Ravenskloof', Tarkastad. *Cynognathus* Assemblage Zone (Subzone B). According to Courtney-Latimer (1948) material that makes up the mounted skeleton was collected in two separate expeditions to the same locality.

Material described by Pearson (1924) housed in the British Museum of Natural History was also re-examined. The following material was included in this study BMNH R3761 the pelvic girdle and R3760 – atlas-axis complex. R3740 consisting of both scapulae and femora. All these specimens came from the Seeley collection of 1910. These specimens were collected in the Burgersdorp district of South Africa.

AXIAL SKELETON

The axial skeleton of *K. simocephalus* is described from both isolated and associated vertebrae. Only vertebrae are described here because the ribs are fragmentary and no complete rib could be reconstructed, despite the fact that the fragments are from a single specimen. BP/1/5624 has eight vertebrae preserved but all have been damaged to some degree. The atlas is the best preserved, whereas the remaining vertebrae are all damaged dorsally. The neural spines, transverse processes, prezygapophyses and postzygapophyses are no longer present. SAM-PK-3017 has at least fifteen vertebrae preserved. The axis is complete and well preserved while the remaining vertebrae are mostly complete with a few that have suffered some damage. Structurally the remaining vertebrae are very similar which suggests that they may belong to the same section of the vertebral column. However, the lack of other associated vertebral columns makes it difficult to determine exactly where these vertebrae fit in.

Cervical region

Atlas. In BP/1/5624 both sides of the atlas are preserved, but it has suffered some damage dorsally and posteriorly. The left and right neurapophyses do not meet in the midline when viewed dorsally (R3760, Fig. 1A). Anteriorly on the medial side of the neurapophysis are two concave facets that lie next to each other producing a 'butterfly' shape, but are separated by a flat, raised ridge. The postero-dorsal border of the posterior facet is higher than the antero-dorsal border, while the antero-ventral border is lower than the postero-ventral border and it most likely that these facets represent the articulation with the occipital condyle (Fig. 1B). The anterior facet is deeply concave in the cranial direction and is C-shape (Fig. 1B). It becomes raised in the medial direction towards in the middle of the bone. The ventral end of the ridge separating the two facets is very broad (Fig. 1B).

Axis. The axis of *K. simocephalus* in SAM-PK-3017 and R3760 is a well preserved, robust and relatively large bone (Fig. 1C,D). The neural spine is short, antero-posteriorly elongated, and thicker anteriorly. When compared with the remaining vertebrae, the axis appears to be more robust. In dorsal view the surface of the neural spine is rugose and transversely flared at its anterior and posterior ends.

In SAM-PK-3017 the prezygapophyses are small, flared and project slightly beyond the anterior end of the neural spine (Fig. 1D). They have smooth, slightly convex articulating surfaces that are directed antero-dorsally. Posteriorly, the postzygapophyses are wide, and are aligned with the posterior end of the neural spine (Fig. 1C,D). Their wide, smooth and convex articulating surfaces are directed ventro-laterally. On the axis the postzygapophyses are positioned closer together than the prezygapophyses. Close to the prezygapophyses, and below them, lie the transverse processes. They are short and become wider towards their free ends (Fig. 1C,D). The transverse processes are narrow and triangular, with a rounded lateral tip.

In lateral view the centrum is antero-posteriorly elongated with the posterior end larger and extending lower than the anterior end. Laterally, the surface of the centrum is concave and extends to the proximal end of the ventral keel (Fig. 1C,D).

The centrum of the atlas of *K. simocephalus* is not fused to the rest of the atlantal components. Instead it is fused to the axis forming the odontoid process (Romer 1956). In anterior view it is crescent shaped (Fig. 1D) with an incomplete dorsal border and three possible articulating sites. Laterally on the odontoid process there are two oval, flat to convex articulating facets, while the third articulating facet is situated ventrally and is oval laterally, with a concave articulating surface. In anterior view the intercentrum of the axis is visible ventrally and is oval. When viewed laterally it is difficult to distinguish between the axis intercentrum and the odontoid process. Ventrally, the intercentrum is triangular when seen in lateral view (Fig. 1C).

Post axial cervical vertebra. BP/1/5624 has two vertebrae in articulation and from the form of the damaged neural spine one is the axis. It is preserved in articulation with another vertebra, which can be assumed to be the first cervical vertebra. Owing to the extent of the damage there are no details of the dorsal part of the vertebrae preserved. The centrum is antero-posteriorly elongated and narrow with no ventral keel.

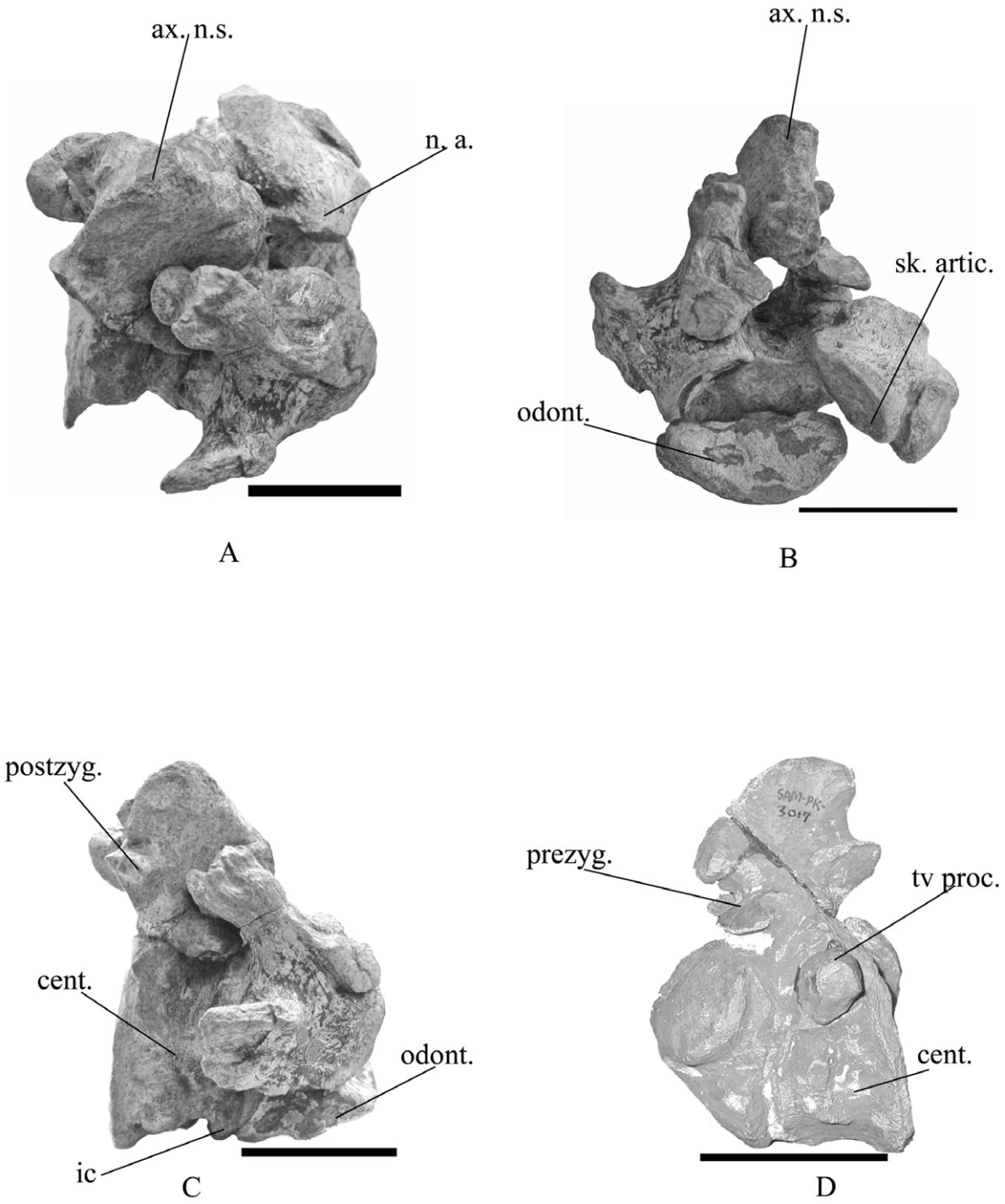


Figure 1. Atlas–axis complex of *Kannemeyeria simocephalus.* **A, B,** right and left lateral views of the atlas, BP/1/5624; **C**, lateral view of the axis, BP/1/3017; **D**, anterior view of the axis, BP/1/3017. Scale bars = 5 cm.

Dorsal vertebrae. The dorsal vertebrae of SAM-PK-3017 have a similar morphology and are therefore considered to belong to the same section of the vertebral column. The neural spine is antero-posteriorly narrow, long and inclined posteriorly (Fig. 2A). It projects well beyond the posterior extent of the centrum. In dorsal view the surface of the neural spine is rugose and broad.

Anteriorly, the prezygapophyses are located well in front of the neural spine. The flat articulating surfaces face dorso-medially, and the distal ends of the prezygapophyses almost meet in the midline. This makes the articulating surface appear continuous and that it forms a cup or cradle for the postzygapophyses. The postzygapophyses are very short and do not extend beyond the neural spine in lateral view (Fig. 2A). The articulating surface is flat and directed ventrally, and almost meets in the midline.

The transverse processes are wing-like. They are short and are directed dorsally (Fig. 2A). The lateral ends of the transverse processes are thickened and have rugose surfaces. In dorsal view the surface of the transverse rocess is concave towards the body of the vertebra.

The centrum is antero-posteriorly short with deeply concave sides (Fig. 2A). Along the anterior margin of the centrum there is an elongated, concave facet that extends almost to the ventral end of the centrum. This facet most likely represents the articulation for the rib.

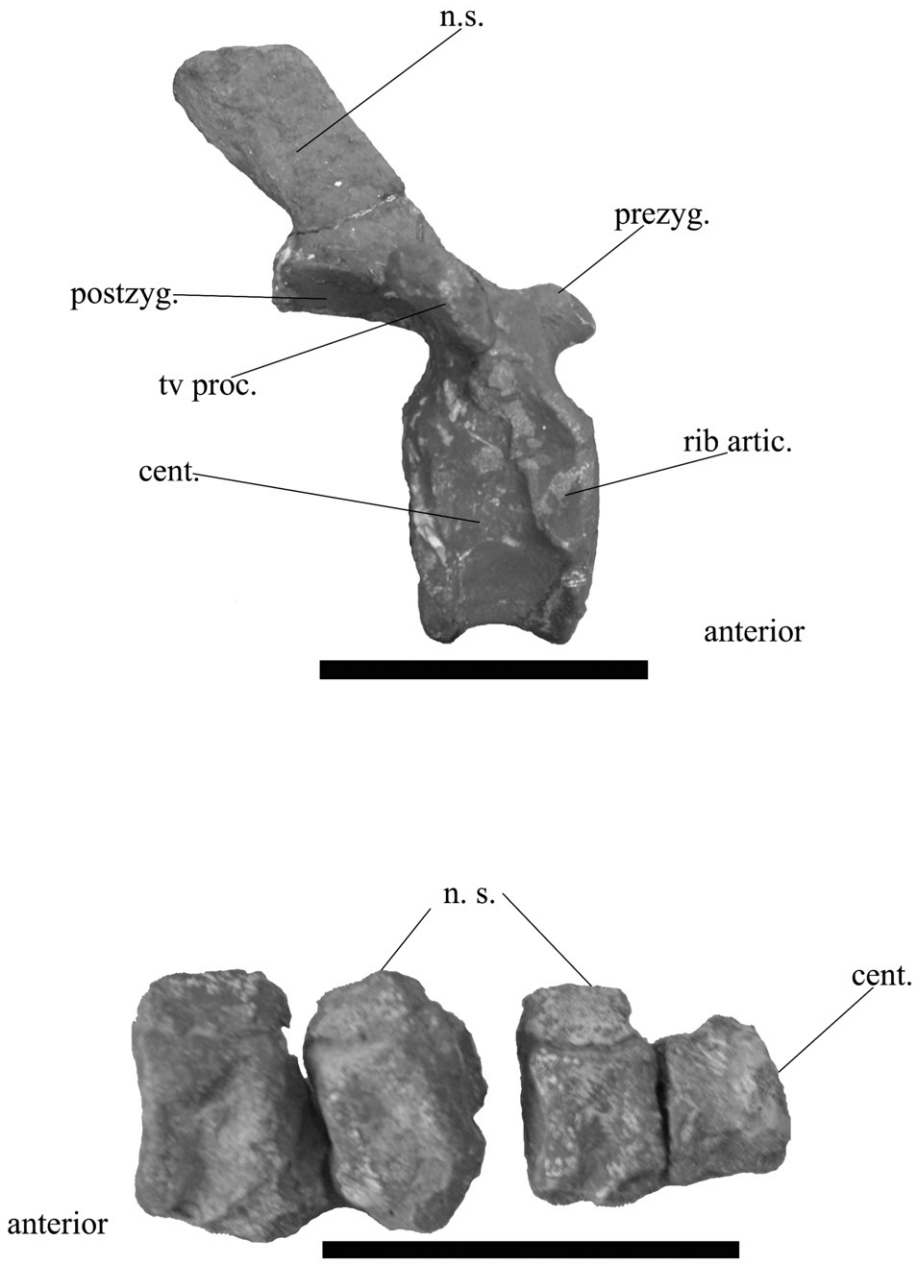


Figure 2. Lateral view of (**A**) dorsal vertebra (BP/1/5624) and (**B**) caudal vertebrae (BP/1/5624). Scale bars = 5 cm.

Caudal vertebrae. There are four poorly preserved caudal vertebrae associated with BP/1/5624 (Fig. 2B). The distal ends of the neural spines are missing. Although damaged, the presence of articulating facets on the anterior and posterior ends of the ventral surface of the centrum suggest the presence of a haemal arche. The centra are very short and round with no evidence for the presence of transverse processes (Fig. 2B). Laterally each centrum is concave. The neural spine of the smallest caudal vertebra is not completely fused to the rest of the vertebra.

Pectoral girdle

Scapula. The scapula blade of *K. simocephalus* is a long and gracile bone that is straight in lateral view but laterally bowed in anterior view (Fig. 3A). It widens distally to form the coracoid plate and glenoid articulations. Approximately a third of the way below the broad dorsal border is the scapula spine which extends to the proximal end of the acromion process. The spine projects beyond the anterior margin and is more prominent in the larger individual (BP/1/5624; ELM 1) (Fig. 3 A,C). The base of the spine is marked by a ridge in ELM 1 and BP/1/5624. On the anterior surface of the scapula is a narrow, concave prespinous region.

The acromion forms a narrow elongated triangle that is directed antero-laterally with a slightly flattened anterior end (Fig. 3C). Below the acromion the lateral surface of the glenoid is concave. The posterior border of scapula is narrow at the level of the acromion and becomes slightly flattened above the glenoid. Distally on the posterior border towards the lateral surface is a small oval to sub-circular tubercle for the origin of the scapula head of the triceps.

Distally the bone flares out to form the glenoid and coracoid articulation. The coracoid articulation is set at an angle to the glenoid. The glenoid and coracoid articulation are separated by a round, thick convex tubercle limited to the lateral side of the glenoid (Fig. 3C,D). The circular

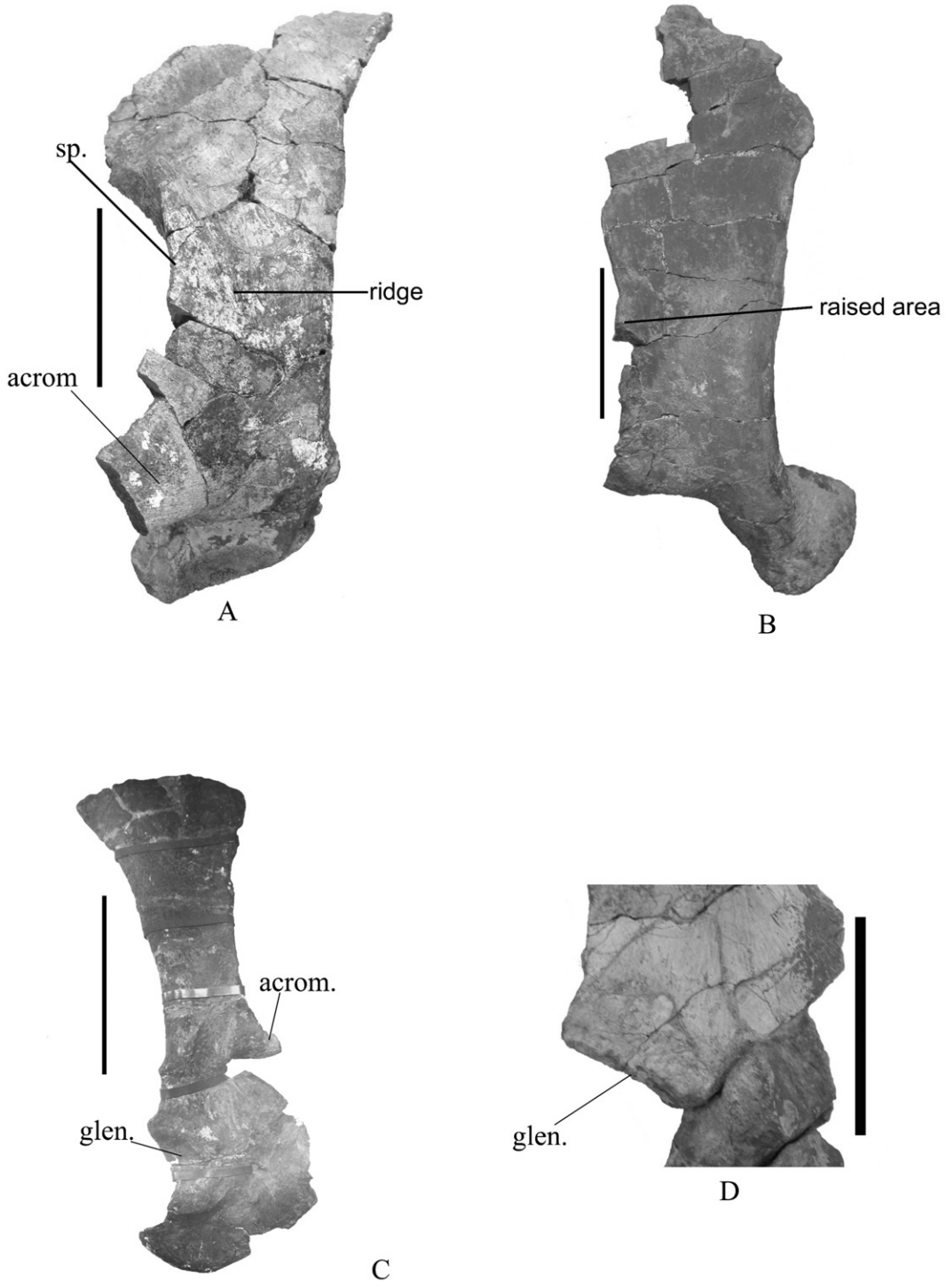


Figure 3. Lateral view of the scapula of *Kannemeyeria simocephalus*. **A**, BP/1/5624; **B**, BP/1/6160; **C**, ELM 1; **D**, BP/1/ 6104 shows the glenoid. Scale bars = 10 cm.

glenoid is directed postero-ventrally with a wide concave surface (Fig. 3C).

Medially, the scapula is shallowly concave to flat (Fig. 4). The medial surface of the acromion process is longitudinally concave. On the postero-dorsal corner of the acromion there is a triangular to U-shaped tubercle (Fig. 4A,B). The surface of the tubercle is low and rugose. A broad, shallow groove runs between the glenoid and the coracoid articulation on their medial surface. This groove probably represents the path where blood vessels and nerves of the shoulder joint pass.

Precoracoid. Based on ELM 1 *K. simocephalus* has a semi-circular precoracoid (Fig. 5A). In this specimen the bone is broken anteriorly and ventrally, perhaps due to its thinness; however, it is unlikely that this has caused the bone's shape to change significantly. Along the posterior border the precoracoid is fused with the coracoid. Although the contact is not very distinct the surface is slightly raised and thickened. Dorsally, the precoracoid forms a distinct sutural contact with the scapula. The coracoid foramen is located in the proximo-posterior 'corner' close to the coracoid and the glenoid, but enclosed entirely by the precoracoid. It is elliptical in the proximo-posterior to antero-ventral direction. The lateral

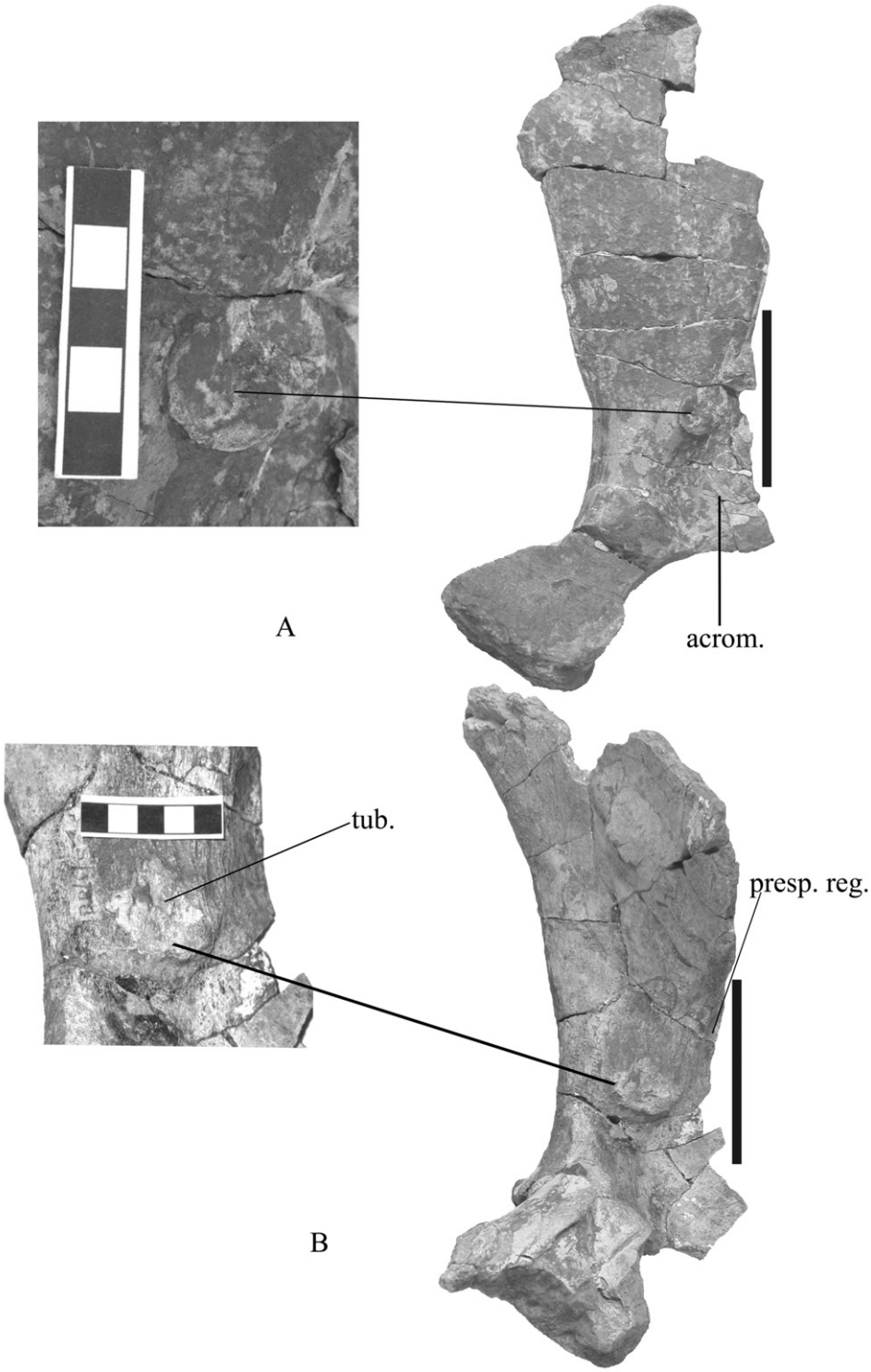


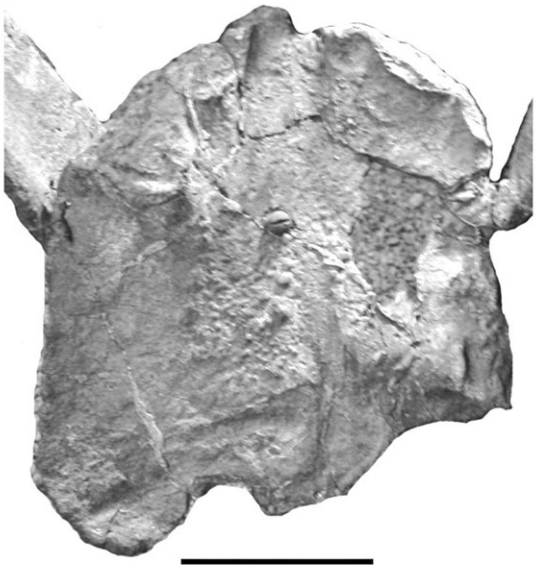
Figure 4. Medial view of the scapula of *Kannemeyeria simocephalus* showing a tubercle on the postero-dorsal corner of the acromion. **A**, BP/1/6160; **B**, BP/1/5624. Scale bars = 10 cm.

surface of the precoracoid is concave in an anterior and ventral direction, resulting in the formation of two possible attachment sites for possibly part of the supracoracoideus and for the coraco-brachialis muscles. On the medial surface there is a groove at the proximal end of the coracoid foramen.

Coracoid. The coracoid (ELM 1) (Fig. 5A) is almost sickle shaped and is thicker than the precoracoid. Most of the dorsal part of the coracoid is made up of the glenoid facet. The facet is triangular and faces laterally and very slightly posteriorly. Its surface is undulating and concave proximally. The distal end of the glenoid facet is bordered by a thin ridge that forms the dorsal margin of a concave area ventral to the glenoid. Posteriorly, the coracoid tapers to a narrow rounded end that is thicker than the anterior end of the bone. It projects beyond the glenoid facet of the scapula. The ventral margin of the coracoid is thickened posteriorly and progressively thins towards the anterior end.

Clavicle. A clavicle is present in ELM 1 (Fig. 5C). It is a thin bone that is expanded proximally and distally. Proximally, the head of the bone is thickened in the dorsal direction

A



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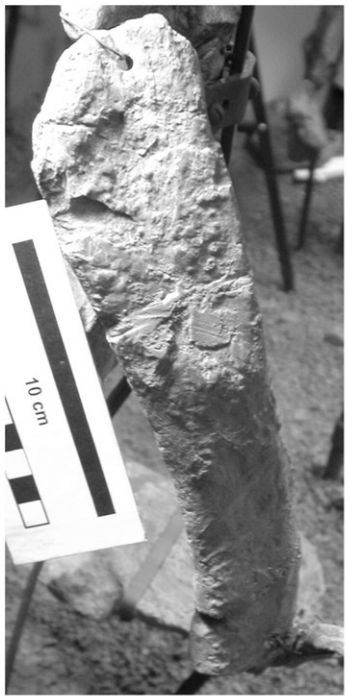

C

Figure 5. **A**, lateral view of the glenoid, ELM 1; **B**, dorsal view of the sternum ELM 1; **C**, ventral view of the clavicle, ELM 1, of *Kannemeyeria simocephalus*. Scale bars = 10 cm.

with a rugose surface. The antero-proximal corner is rounded with a broad, shallow groove on the proximal end. Anteriorly, the surface of the shaft is slightly rugose and thickened. Along the distal end of the clavicle is a broad, shallow groove. Along the posterior surface of the clavicle the lateral border is thickened. In front of this is a groove. The posterior surface of the clavicle shaft is broad and concave. On the proximo-anterior corner of the lateral there is an oval tubercle that projects above the surface of the bone. The dorsal surface of the clavicle is convex, and the posterior border is concave. Distally, the bone is broken but remnants indicate that the bone was flat, broad and thin.

Sternum. The sternum (ELM 1; Fig. 5B) of *K. simocephalus* is a thin, proximo-distally oblong with a thickened anterior end. The anterior end bears a rugose dorsal and ventral surface that bears two oval tubercles on each side of the midline. Each ventral tubercle is flanked by a broad concave area. On the dorsal surface there are two laterally placed, dorsal tubercles and two grooves. The grooves are broad, shallow and lie medial to the tubercles. Posteriorly, the sternum is rounded.

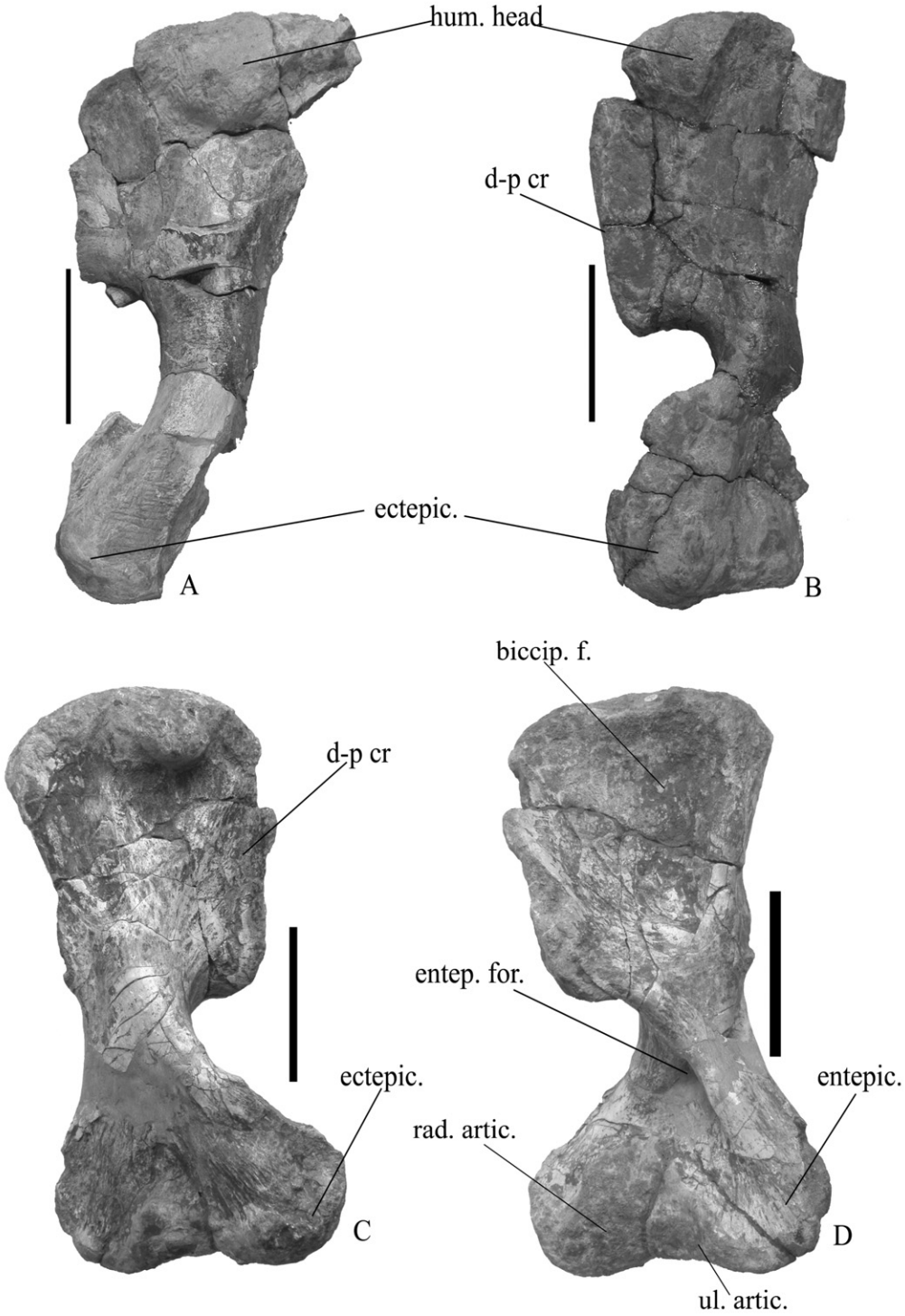

Figure 6. Humerus of *Kannemeyeria simocephalus,* dorsal view: **A**, BP/1/5624; **B**, BP/1/6160; **C**, BMNH R3740; ventral view: **D**, BMNH R3761. Scale bars = 10 cm.

Forelimb

Humerus. The humerus of *K. simocephalus* is a fairly robust bone (Fig. 6). In all the specimens (BP/1/6160; ELM 1; R3740; BP/1/5624) the proximal expansion is rectangular and is wider than the distal expansion. An inverted triangular head of the humerus is located anteriorly along the dorsal border (BP/1/6160; ELM 1; R3740; BP/1/5624) and it is raised above the dorsal surface of the proximal expansion (Fig. 6A,B,C). The dorsal border of the humerus is very rugose and thickened which would suggest that it, including the head, was covered by cartilage (Fig. 6C). Below the head there is a broad, low ridge, which is more prominent in the large individual (BP/1/5624; R3740). There are concave surfaces anterior and posterior to the ridge, with the posterior narrower than the anterior. In the small individual (BP/1/6160) the surface posterior to and below the head is a shallow, concave fossa. This posterior fossa represents the origin of the lateral humeral head of the triceps (King 1981) while the anterior one represents the origin of the scapulo-humeralis anterior (King 1981).

Anteriorly the proximal expansion terminates in the delto-pectoral crest which is rectangular and is 90° to the long axis of the bone (Fig. A–C). The delto-pectoral crest is

dorso-ventrally wide along it entire length and the dorsal surface of the delto-pectoral crest is concave. On the dorsal surface of the delto-pectoral crest is the insertion of the robust deltoideus muscle while on the ventral surface is an area for the insertion of the pectoralis muscle (King 1981) (Fig. 6D). At the proximo-posterior corner of the bone there is a narrow, oval tubercle that thins distally to form the posterior border. A third of the way below the dorsal border in BP/1/5624 there is a small triangular tubercle while in ELM 1 it forms an elongated oval

The shaft of the humerus is not broad and is twisted so that the ectepicondyle is directed anteriorly (ELM 1; BP/1/6160; R3740) while in BP/1/5624 it is directed more dorsally. This feature of the humerus is possibly as a result of varying ages of the various specimens (Fig. A–C).

Almost the entire distal end of the humerus is made up by the olecranon fossa which forms a rather large shallow triangle that is directed posteriorly (Fig. 6A–C). The olecranon fossa it much shallower in BP/1/6160 which again might well be an indication of a variation in the ages of various specimens. Its distal end is marked by the articulating surface of the radius and ulna facets which are reflected onto the distal end of the posterior surface. It is bordered anteriorly and posteriorly by the ectepicondyle and entepicondyle, respectively. The ectepicondyle is not as well developed in BP/1/6160 as it is R3740, ELM 1 and although damaged BP/1/5624 (Fig. 6A–D).

The ectepicondyle is larger and wider than the entepicondyle; however, in BP/1/6160 the condyles are not as well defined as in the other specimens (e.g. R3740; ELM 1; BP/1/5624). Ventrally the ectepicondyle and entepicondyle surfaces are convex.

In ventral view it can be seen that almost the entire proximal expansion is made of the biccipital fossa which forms a rectangle that is fairly deep (R3740; Fig. 6D). It is bordered anteriorly and posteriorly by the delto-pectoral crest and by a broad low ridge, respectively. A ridge runs diagonally across the bone from the delto-pectoral crest to the entepicondyle. This ridge forms the dorsal border of the elongated oval entepicondylar foramen. Below the foramen the surface is slightly concave and extends down posterior to the articulation for the radius and ulna. A shallow groove surrounds the continuous articulating surface for the radius and ulna. The radial articulation (capitulum) is wide, almost rectangular, and appears to extend slightly higher than the smaller triangular ulna articulation (trochlea) (Fig. 6D).

Radius. Although ELM 1consists of a complete forelimb the radius and ulna are considered to be different from those of BP/1/5624 and BP/1/6160 and have therefore been excluded from the description. The proximal expansion of the radius is slightly smaller than the distal expansion. The distal expansion is slightly more expanded than the proximal one.

In both BP/1/5624 and BP/1/6160 the proximal and distal articulating surfaces are medio-laterally narrow and concave. The proximal articulation forms a continuous articulating surface with the sigmoidal facet of the ulna for the distal end of the humerus (Fig. 7). Anteriorly, the proximal end has a straight margin which becomes concave along the shaft. Along the proximo-posterior border of the radius there is an oblong tubercle with a convex surface for articulation with the ulna. Below this articulation the posterior border of the radius is concave. In the large and small specimens the posterior border is more concave than the anterior. Along the anterior border of the proximal expansion is another not as well developed tubercle that probably represents the insertion site for muscles that act on the radioulna joint.

The distal end of the radius is marked by an undulating rim that projects more ventrally closer to the posterior border (Fig. 7). Along the distal third of the anterior border there is a rectangular, medio-laterally and antero-posteriorly narrow tubercle. In BP/1/6160 this tubercle is very narrow when compared with the larger BP/1/5624. There is also a very low, round tubercle along the rim of the distal end of the radius. It is located more towards the middle of the rim in the large individual and closer to the posterior border in the smaller individual.

In medial view there is a groove close to the anterior border (Fig. 7C). This groove extends from below the proximal rim to a third of the bone length above the distal end. The groove is shallow and wide proximally, and narrows towards the distal end. Medially, the distal end is thickened towards the anterior border to form a wide, flattened surface. Although this surface narrows towards the posterior border it is still broad; however, in BP/1/6160 this part of the distal end is very narrow. This part of the rim in the small individual is also directed more proximally, which has made the distal articulating surface visible in medial view. The space of between radius and ulna shafts would have been filled with the blood vessels and nerves that innervated the lower forelimb and foot.

Ulna. The ulna is broad proximally and narrows to form the shaft, which has the same width as the distal end (Fig. 8). The proximal part of the ulna is triangular, and narrows proximally to form the olecranon. The low olecranon is narrow and triangular with a round dorsal border in BP/1/5624 and BP/1/6160. There is no evidence of a sutural contact between the olecranon and the rest of the ulna in either specimen. In lateral view, the ulna of BP/1/5624 is more expanded than BP/1/6160.

The sigmoidal facet is wide and has a slightly concave surface in BP/1/5624 and BP/1/6160 (Fig. 8A,B). In the middle of the sigmoidal facet the surface faces antero-laterally. Part of the articulating surface is directed ventrally and forward toward the anterior border. The sigmoidal facet projects laterally thus forming a thin ridge in BP/1/5624 and BP/1/6160. The surface of the sigmoidal facet in BP/1/6160 and BP/1/5624 is triangular and laterally broad. This lateral projection of the sigmoidal facet merges with the shaft below the distal end of the radial facet.

The radial facet is located below the anterior border of the sigmoidal facet of the ulna, and forms an inverted triangle. Its base is formed by the anterior border of the sigmoidal facet and it narrows distally, ending at the same level as the ridge on the lateral surface. The surface of the radial facet is concave along its entire length and rugose proximally. Distally the surface is not deeply concave and

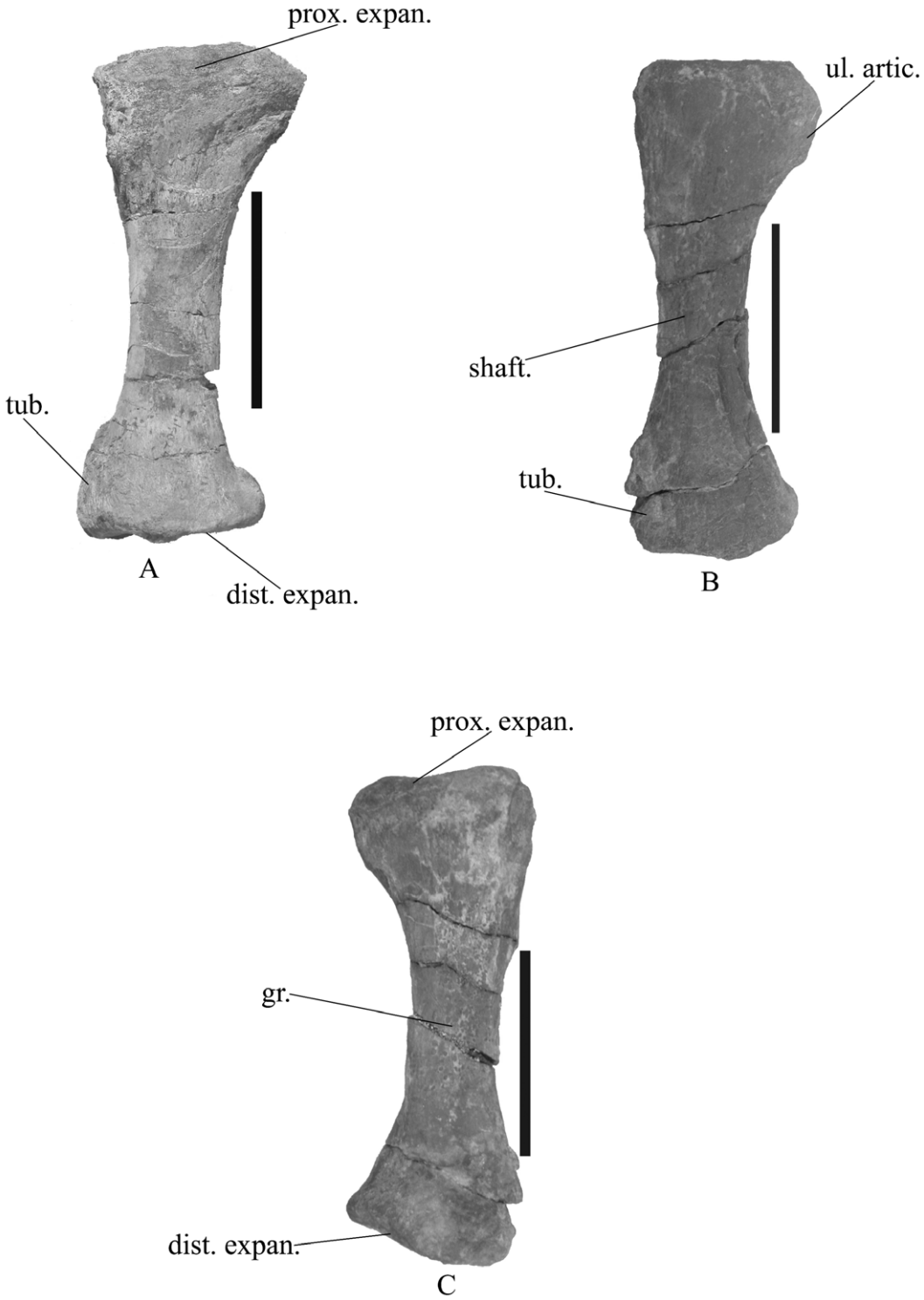

Figure 7. Radius of *Kannemeyeria simocephalus,* lateral view: **A**, BP/1/5624; **B**, BP/1/6160; medial view: **C**, BP/1/6160. Scale bars = 10 cm.

is smooth. The anterior and posterior borders of the radial facet are sharply demarcated.

Distally, along the anterior border of the ulna of *K. simocephalus* is a shallow fossa that starts approximately at the midlength of the bone. It is elongated, and is narrowest proximally and widest distally. The entire surface of the fossa is concave, but it is more deeply excavated distally. Its distal border is a round thin ridge. In BP/1/6160 the distal fossa extends onto the medial surface while in BP/1/5624 it is limited to the anterior margin (Fig. 8). On the lateral border of this fossa there is an elongated tubercle with a rugose surface. The position of this tubercle suggests that it may have been the attachment site for the interosseus ligament or possibly interosseus membrane. Posterior to the sigmoidal facet is a narrow, deep groove. In the middle of the shaft is a shallow fossa that extends to the postero-distal end and was separated from the anterior fossa by a narrow ridge.

The medial surface of the olecranon (Fig. 8C) is flattened postero-proximally with a raised rugose surface that extends from the olecranon, and is bound posteriorly by a ridge. A fossa occurs in front of the ridge, which is broad proximally, narrowing distally. A groove begins near the distal end of the fossa and extends to the distal end of the

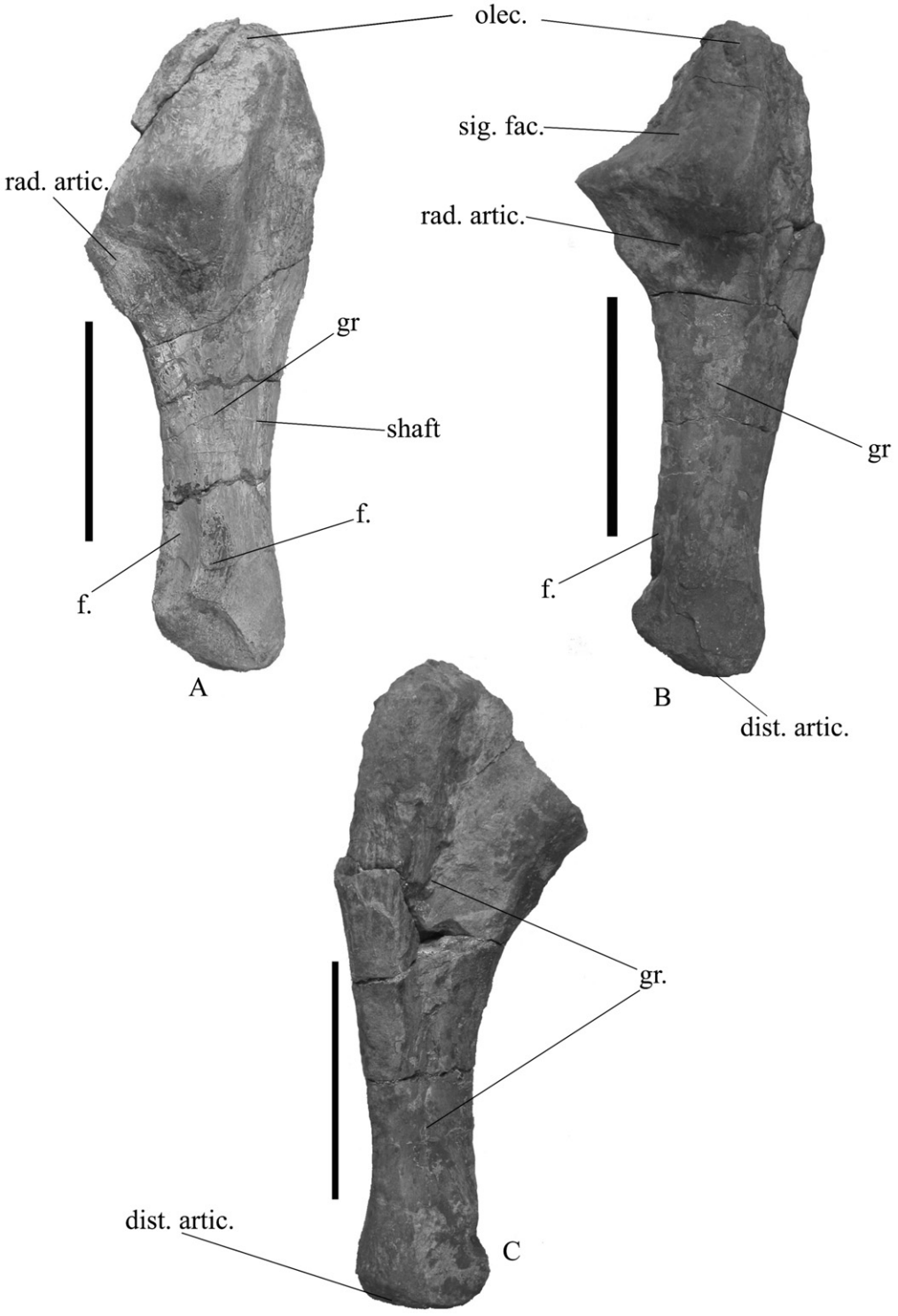

Figure 8. Ulna of *Kannemeyeria simocephalus*, lateral view: **A**, BP/1/5624; **B**, BP/1/6160; medial view: **C**, BP/1/6160. Scale bars = 10 cm.

bone, where it ends as a deep depression. This groove most probably accommodated the tendons of muscles of the forelimb.

The distal articulation is directed ventrally and forms an elongated oval (Fig. 8c). Its surface is concave and broad posteriorly, while it is narrow anteriorly. The articulating surface slopes medially and extends onto the distal medial surface.

Pelvic girdle

The description of the pelvic girdle is based on BP/1/5624 and BMNH R3761 because the pelvic girdle that is part of ELM 1 shows a morphology that is significantly different from the other two specimens.

Ilium. In BP/1/5624 the dorsal border of the ilium is not preserved but this area is preserved in BMNH R3761 (Fig. 9). The dorsal border of that specimen is convex and is slightly lower towards the posterior border (Fig. 9). Laterally, the surface of the blade is concave and the anterior process is directed laterally in BP/1/5624 than in BMNH R3761. The anterior process is antero-posteriorly short and wide when compared with the posterior process and is situated higher than the posterior one. It projects far in front of the pubis. The posterior process is located

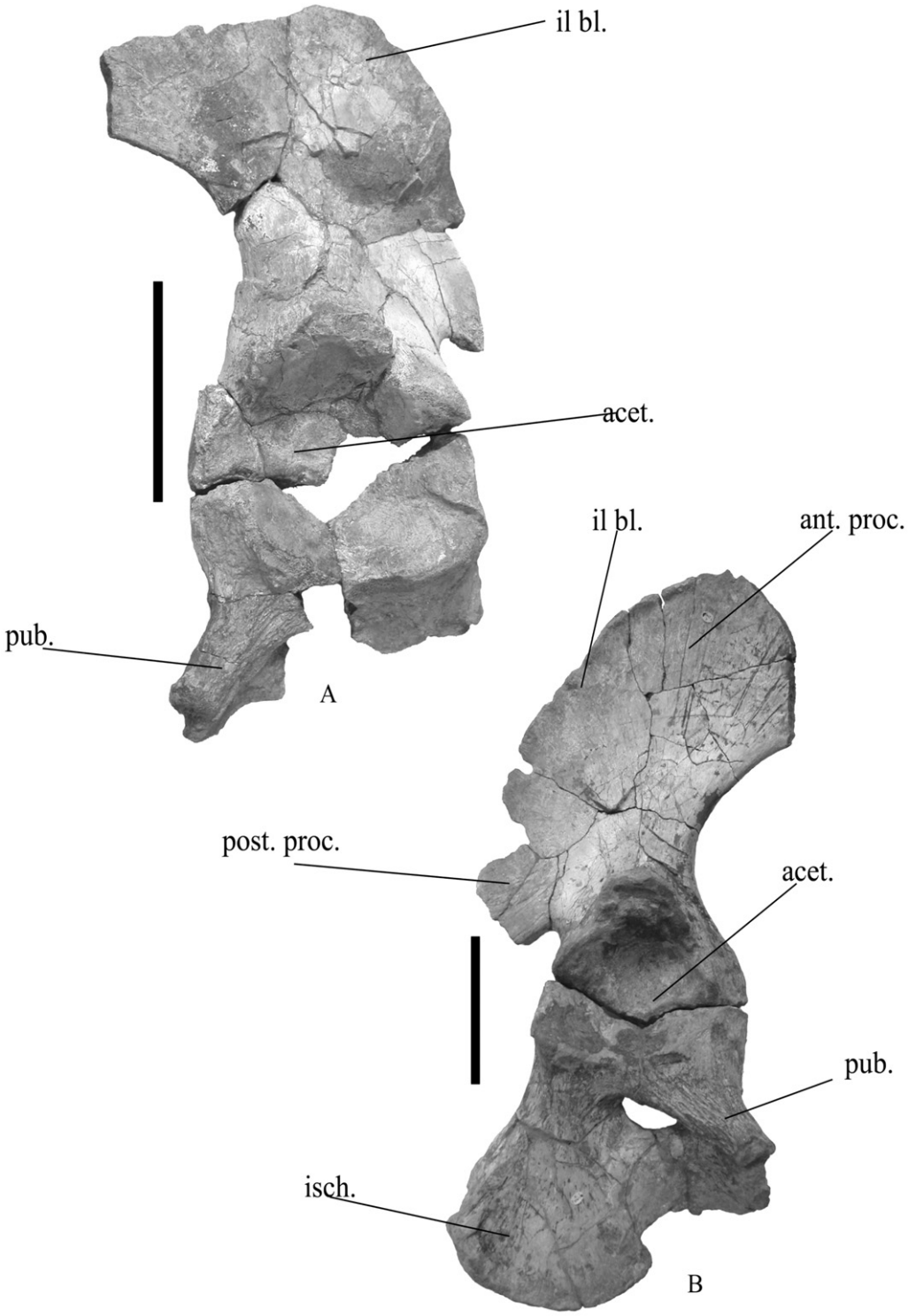

Figure 9. Lateral view of the pelvic girdle of *Kannemeyeria simocephalus*. **A,** BP/1/5624; **B**, BMNH R3761. Scale bars = 10 cm.

close to the acetabulum and the ventral border is concave. It is dorso-ventrally wide and short antero-posteriorly.

Below the anterior process the anterior border of the ilium narrows gradually to form an almost straight border, whereas the posterior border narrows rapidly resulting in a concave border. Anteriorly, the pillar like neck narrows more than it does posteriorly.

The acetabulum is circular, broad, deep and faces laterally (Fig. 9B). Dorsally, the lateral surface of the acetabulum is bordered by supra-acetabular ridge. It is wide and does not project far laterally. The anterior two-thirds of the acetabular facet is separated from the posterior part by the supra-acetabular notch; however, the articulating surface remains continuous. The posterior part of the rim is narrow and sharply demarcated.

Dorsally, the acetabulum facet is bound by the supra-acetabular buttress. This buttress is narrow anteriorly and posteriorly, and broad in the middle. Two-thirds of the way up the posterior border of the supra-acetabular buttress is the supra-acetabular notch, which is narrow and deep in BP/1/5624. The anterior border of the ilium, above the acetabular facet and the dorsal part of the anterior border of the pubis is flattened with a roughened surface.

On the anterior border of the acetabulum, in front of the acetabular facet, is a facet for the pubis. This elongated and concave facet is located on the medial border. Behind the acetabular facet is a concave, almost square facet for the ischium, which is situated higher than the pubic facet. Medially the bone surface of the iliac blade is convex dorsally and becomes concave above the acetabulum. Although the bone has been damaged, five sacral rib facets are visible.

Pubis. The pubis and ischium are fused into a puboischiadic plate in *K. simocephalus* (Fig. 9B). The left pubis of BP/1/5624 is broad proximally and narrows distally. Dorsally, the anterior part of the bone is higher and is directed more medially than posteriorly. The ventral part of the pubis is narrow, and the anterior part of the bone is directed more antero-ventrally. Anteriorly the pubis narrows to form a round tubercle that is directed anteriorly and ventrally. The lateral surface of the tubercle is very rugose in both BP/1/5624 and BMNH R3761. Behind the tubercle the bone extends posteriorly towards the ischium. This part of the bone is thin and the surface is concave.

A small, oval acetabular facet is present on the dorsal surface (Fig. 9B). The surface of this facet is smooth and only slightly concave, and is continuous with the ischial facet.

Laterally, the border of the facet is distinctly lower and the facet faces laterally. The medial wall of the pubic facet extends dorsally to meet the medial wall of the iliac acetabular facet. In front of the acetabular facet is the rectangular, convex facet for articulation with the ilium, which has a rugose surface that projects dorsally creating forming small pillars. This surface matches the surface of the facet anterior to the ilial acetabular facet. It would suggest that these bones interdigitate in order to form a firmly immobile suture. Laterally, the surface below the articulation is rough and is covered by thin ridges. It narrows in the anterior direction to end in a round, concave facet that also has a rugose surface. Along the posterior border of the pubis there is a C-shaped groove that extends across the surface of the bone. It forms the sub-circular anterior border of the obturator foramen.

Ischium. The ischium is triangular and is expanded ventrally (Fig. 9B). Dorsally, the ischial acetabular facet is elongated and has a slightly concave surface. It is separated from the rest of the bone by a ridge. The lateral wall of the facet is lower than the medial one, which rises to form a rugose dorsal border. Posterior to the acetabular facet is the facet that articulates with the ilium. It is a narrow, elongate triangle that has a convex surface. In BP/1/5624 it appears that the ischium is directed medially; however, this may be as a result of the bone being broken and the distal end has been lost. In BMNH R3761 the distal part of the ischium is fairly widely expanded. Along the posterior edge of the distal expanse is a narrow, convex tubercle. Distally the ischium is slightly lower than the pubis.

Anteriorly, the ischium meets the pubis below the acetabular facet to form the concave dorsal border of the obturator foramen. The short, concave, almost circular posterior border of the obturator foramen is formed by the ischium. In *K. simocephalus* the obturator foramen forms a narrow, elongated oval that is slightly wider towards the ischium (Fig. 9B).

Hindlimb

Femur. The femur of *K. simocephalus* is a long, dorsoventrally flattened (Fig. 10B,D) bone with a straight shaft that has concave anterior and posterior borders. The proximal and distal expansions are of equal width. The right femur of BP/1/5624 has been compressed antero-posteriorly, resulting in a dramatically different shape of the bone in comparison to the left femur of the same individual. Owing to its marked deformation the right femur has been omitted from this description (Fig. 10A,C).

The femoral head is round and medially inflected (Fig. 10B). In ventral view the head of the left femur of BP/1/5624 is surrounded by a shallow groove that is steep towards the head. This groove makes the head more prominent in ventral view. In front of the head is a shallow fossa that is broad proximally and narrows distally where it merges with the shaft. The posterior boundary is marked by the presence of the greater trochanter. Below the head of the bone is a low, flat ridge that extends to the posterior border. No internal trochanter is present.

The greater trochanter is elongated and extends along the proximal third of the posterior border of the femur and is almost straight (parallel to the long axis of the bone) (Fig. 10D). It is antero-posteriorly narrow with a rugose surface and is clearly demarcated from the rest of the bone. Dorsally, the greater trochanter is rounded and thick and is not separated from head of the femur and forms a continuous surface along its entire length.

Distally, the articular condyles are separated by a circular intercondylar fossa (Fig. 10D). It is deep and is situated slightly above and between the proximal borders of the condyles. The lateral condyle projects farther onto the dorsal surface than does the medial condyle. It is also directed more ventrally and is slightly lower than the medial condyle in dorsal view. Postero-dorsally to the medial condyle is a broad, shallow groove that terminates at the proximal end of the ventral border. The lateral condyle is smaller than the posterior condyle and its dorsal surface is skewed in the proximal direction. It also is rugose pitted. Distally, the condyles are separated by a broad, deep groove which is steeper towards the posterior condyle.

The ventral articulating surface is present on the distal end of the condyles (Fig. 10B). The articulating condyles are separated on the ventral surface by a broad, antero-posteriorly oblong fossa. This fossa has a shallow, concave surface that is bordered anteriorly and posteriorly by prominent ridges. It extends above the condyles to merge with the shaft above. Distally, the articulating surface of the condyles is directed ventrally and is convex. The articulating surface of the posterior condyle projects more ventrally than that of the anterior condyle. The material studied from the British Museum of Natural History and ELM 1 was found to be significantly different from BP/1/5624 and BMNH R3761.

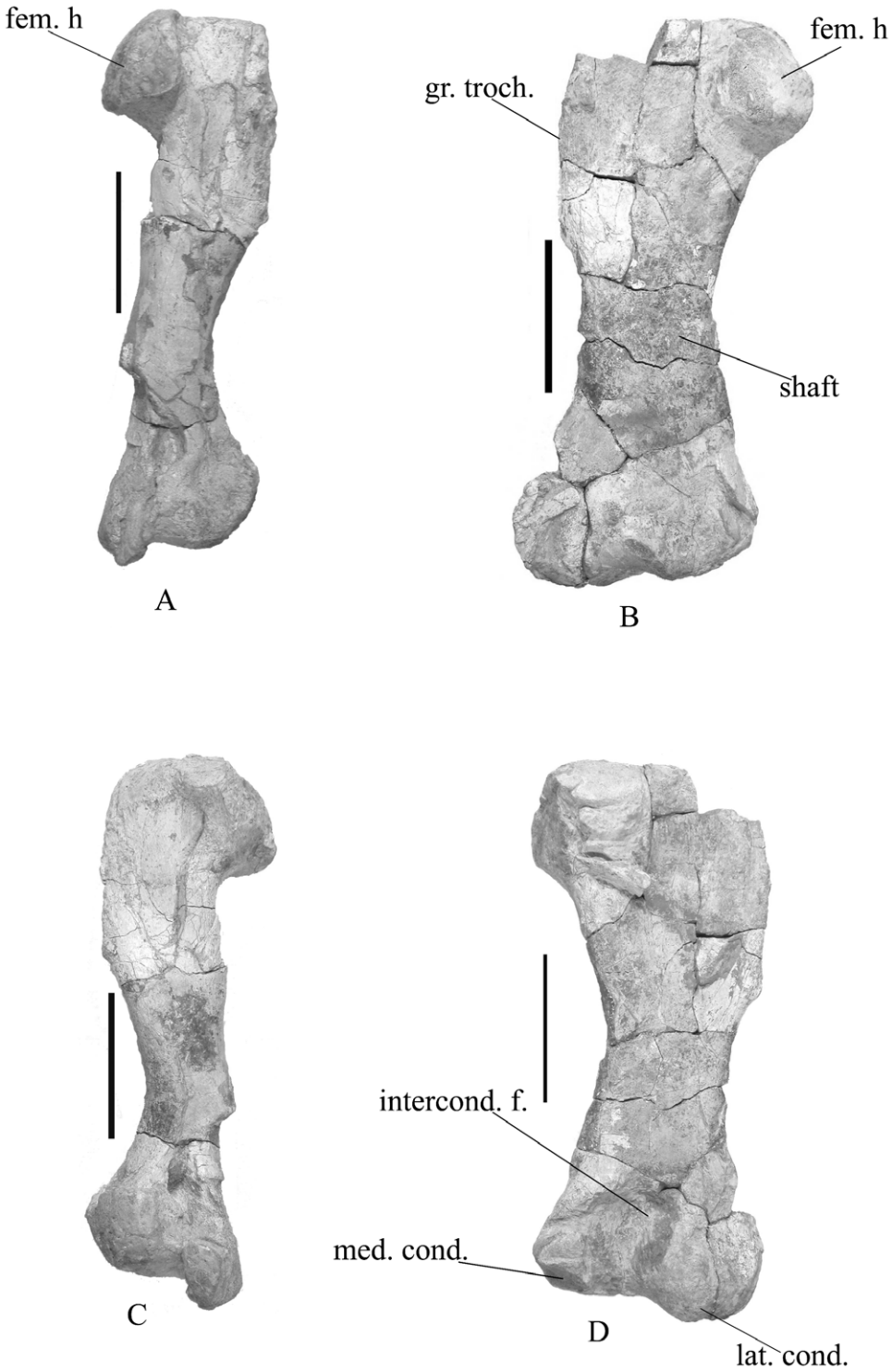

Figure 10. Femur of *Kannemeyeria simocephalus,* dorsal view: **A**, **B**, BP/1/5624; ventral view: **C**, **D**, BP/1/5624. Scale bars = 10 cm.

Tibia. Only the right tibia of BP/1/5624 has been preserved (Fig. 11). It has an almost cylindrical appearance and is flattened antero-posteriorly. Both the proximal and the distal ends are expanded with the proximal being larger than the distal.

Proximally, the tibial tuber faces antero-laterally (Fig. 11A). A round tubercle projects laterally from this surface and is bounded ventrally by a narrow ridge. The surface of the tuberculum is rugose and extends slightly medially. This surface is raised above the rest of the bone and grades down into the anterior margin. Anteriorly, the surface of the margin is broad and roughened.

Lateral to the tibial tuberosity is a shallow groove that extends halfway down the bone (Fig. 11A). It is narrow proximally where the tibial tuberosity projects over this groove and is bound by a lateral ridge. The lateral border of the tibia flares out and a shallow fossa is present below the proximal ridge, which represents the articulation for the fibula. Below this the bone has been damaged. Approximately halfway down the shaft there is a shallow fossa. Distally the bone curves laterally forming a ridge that gives the bone a squared off appearance. Anteriorly the shaft has lost all definitive features due to cracking and damage. Medially the bone was damaged resulting in

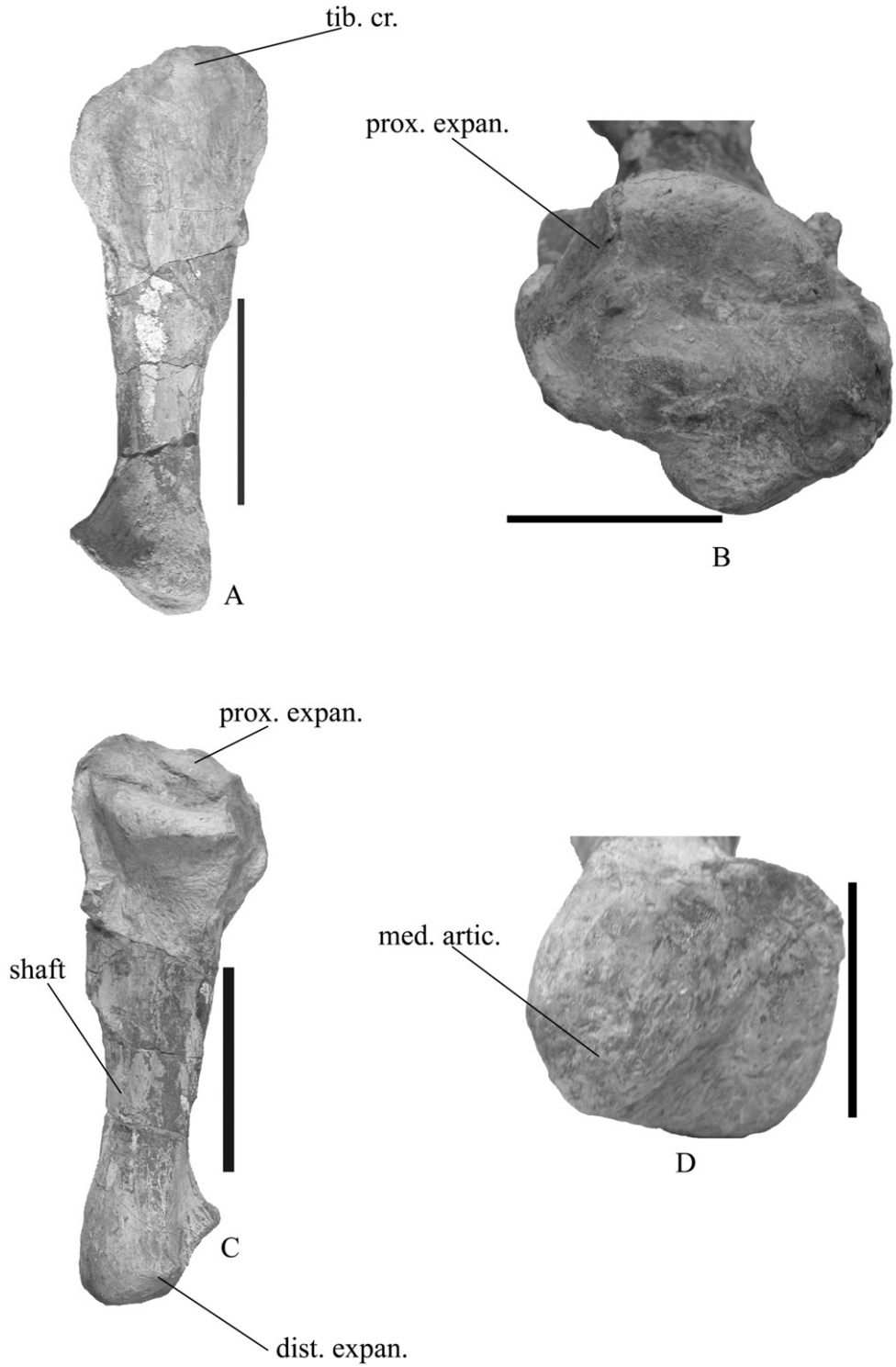

Figure 11. Tibia of *Kannemeyeria simocephalus,* anterior view: **A**, BP/1/5624, **B**, proximal articulation BP/1/5624; posterior view: **C**, BP/1/5624; **D**, distal articulation BP/1/5624. Scale bars = 10 cm.

the middle of the shaft being compressed.

The proximal end of the bone (Fig. 11B) is round and higher anteriorly than posteriorly. It has a single slightly concave articulating surface. Posteriorly, the head is bound by a thick, flat ridge. This structure extends onto the posterior surface and has a roughened appearance. It merges with the surface, which grades into the shaft. Below this the bone is damaged.

Posteriorly, in the middle of the shaft, is a shallow fossa and distally, the concave surface of the shaft ends as a broad ridge above the articulating surface. This distal articular surface is divided into two facets. The medial facet is located more ventrally and has a round, convex surface that is directed ventrally, whereas the lateral facet is a square and directed ventrally with a flat to slightly concave surface (Fig. 11D).

Fibula. The fibula of *K. simocephalus* is along, thin bone and is represented here by BMNH R3761 (Fig. 12). Laterally, the border is concave while the medial border is straight. Proximally, the bone is expanded and a small, hemispherical tubercle rises above the surface. Along the lateral border of the distal expansion is a groove that

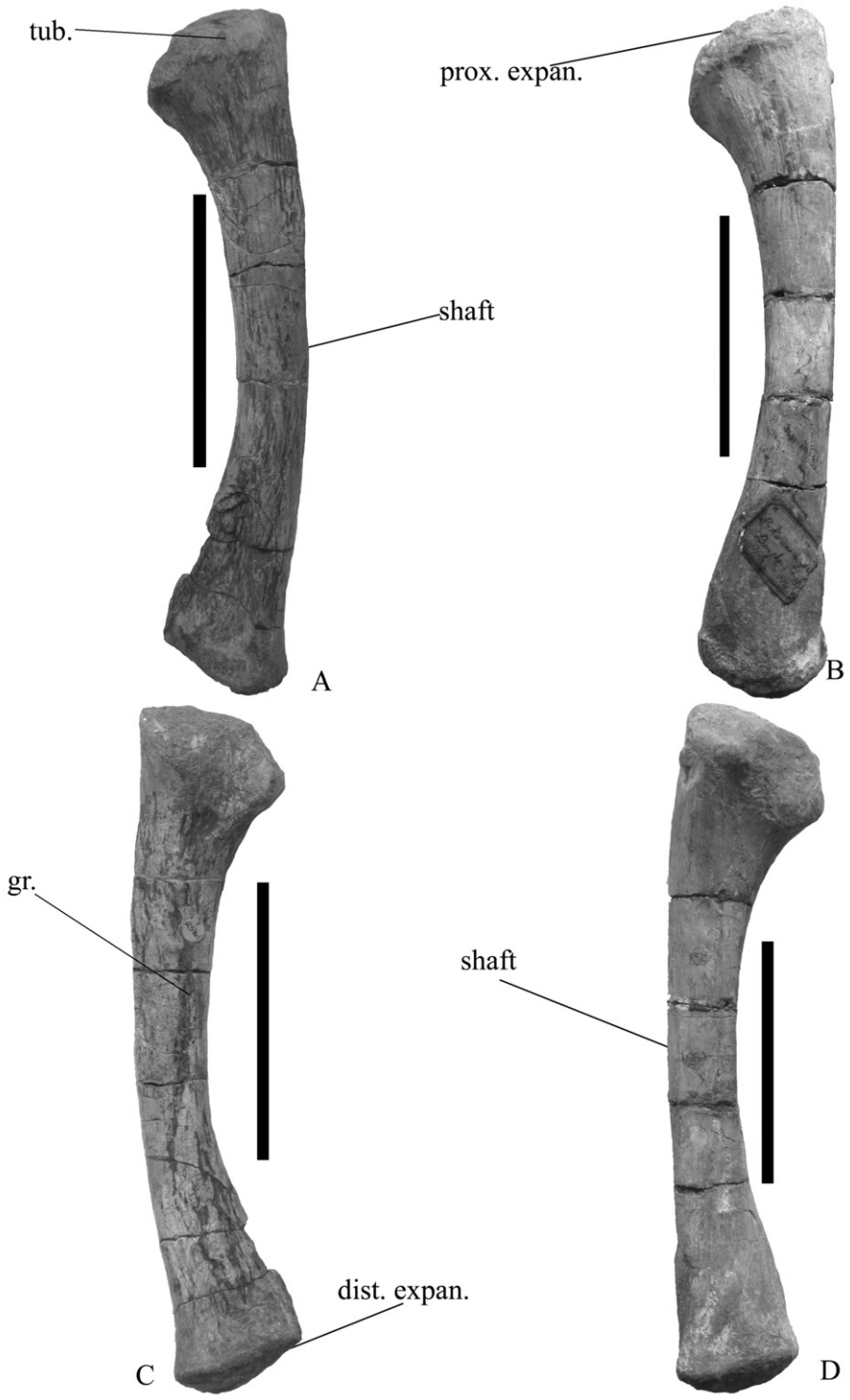

Figure 12. Fibula of the *Kannemeyeria simocephalus,* anterior view: **A, B,** BMNH R3761; posterior view: **C, D**, BMNH R3761. Scale bars = 10 cm.

extends to the distal end. Both the proximal and distal ends have convex surfaces.

DISCUSSION

A detailed analysis of the cranial morphology of *Kannemeyeria* resulted in the identification of a generalist cranial morphology (Renaut 2000) which led to a question as to what kind of postcranial morphology would be seen in *K. simocephalus*. A comparison with other Triassic dicynodonts would also give us an idea as to how *K. simocephalus* fitted into the greater picture that is the relationships of Triassic dicynodonts. The comparison with other Triassic dicynodonts is based largely on the literature available and wherever possible on comparison with actual specimens.

When compared with *Lystrosaurus* the dorsal border of the scapula *K. simocephalus* is not as widely expanded but is rather moderately expanded as seen in other Triassic dicynodonts (e.g. Cox 1965; Bandyopadhyay 1988). The almost straight anterior and posterior borders of the scapula blade of *K. simocephalus* are similar to that of *Lystrosaurus* but more closely resembles that of *Sinokannemeyeria* (Sun 1960; 1963) which also has a tall, moderately wide scapula. It differs from *Wadiasaurus* (Bandyo-

padhyay 1988; Ray 2006) and *Parakannemeyeria* (Sun 1960; 1963) in that the anterior border of these two taxa is slightly concave while other Triassic dicynodonts such as *Tetragonias* (Cruickshank 1967; mounted specimen Tübingen), *Dinodontosaurus* (Cox 1965), *Ischigualastia* (Cox 1965) and *Jachelaria* (Vega-Dias & Schultz 2004) the scapula blades are short, broad with concave anterior and posterior margins.

Kannemeyeria shares an elongated scapula spine on the lateral surface of the scapula with *Placerias* (Camp & Welles 1956) and *Wadiasaurus* (Bandyopadhyay 1988; Ray 2006). Other Triassic dicynodonts have lower scapula spines that are not as prominent and do not project far anteriorly (e.g. *Parakannemeyeria* (Sun 1960; 1963), *Ischigualastia* (Cox 1965), *Tetragonias* (Cruickshank 1967), *Zambiasaurus* (Cox 1969; R9140) and *Rhinodicynodon* (Surkov 1998)) or are absent altogether (e.g. *Dinodontosaurus* (Cox 1965)) and has not been described in *Jachaleria* (Vega-Dias & Schultz 2004).

The shape of the acromion process varies among the Triassic dicynodonts. It is short and directed anteriorly in *Placerias,* while a rectangular acromion process that is directed antero-laterally occurs in *Angonisaurus* (Cox & Li 1983; U12/1), *Sinokannemeyeria* (Sun 1960; 1963) and *Dinodontosaurus* (Cox 1965). An antero-laterally directed triangular acromion process occurs in *Wadiasaurus* (Bandyopadhyay 1988; Ray 2006), *Kannemeyeria, Parakannemeyeria* (Sun 1960; 1963), *Rhinodicynodon* (Surkov 1998), *Tetragonias* (Cruickshank 1967) and probably also in *Zambiasaurus* (Cox 1969; R9140); however, the acromion process is either absent or vestigial in *Ischigualastia* (Cox 1965) and *Jachaleria* (Vega-Dias & Schultz 2004).

Medially the acromion process is longitudinally in all Triassic dicynodonts (Sun 1960, 1963; Cox 1965, 1969; R9140; Cruickshank 1967; Cox & Li 1983; U12/1; Bandyopadhyay 1988; Ray 2006). In *Kannemeyeria* there is a tubercle on the proximo-posterior corner of the medial surface of the acromion. It varies from triangular in the large specimen (BP/1/5624) to round and oval in the small specimen. A review of the literature found that no similar structure has been described in Triassic dicynodonts; however, an examination of the mounted specimen of *Tetragonias* (at Tübingen) shows the presence of the tubercle on the proximo-posterior corner of the acromion's medial surface.

In the forelimb the humerus of the Triassic dicynodonts remains fairly conservative in design and does not change much amongst the taxa. *Kannemeyeria* has a low narrow olecranon that is part of the ulna and does not show any signs of sutural contact with the rest of the ulna, even in the juvenile specimen (BP/1/6160). Thus we infer that the ulna, including the olecranon grew from a single ossification centre in *Kannemeyeria* as it did in earlier dicynodonts. However, in most Triassic dicynodonts (e.g. *Sinokannemeyeria, Parakannemeyeria, Wadiasaurus, Dinodontosaurus, Ischigualastia, Jachaleria* and *Placerias*) the olecranon forms from a separate centre of ossification which may fuse to the rest of the ulna in aged individuals (Camp 1956; Sun 1963; Cox 1969; Bandyopadhyay 1988; Vega-Dias & Schultz 2004; Camp & Welles 1956). The olecranon is either poorly developed or absent in *Lystrosaurus* (Young 1935; Ray 2006), while in *Kannemeyeria, Sinokannemeyeria* (Sun 1960, 1963), *Parakannemeyeria* (Sun 1960, 1963), *Wadiasaurus* (Bandyopadhyay 1988; Ray 2006), *Dinodontosaurus* (Cox 1965), *Ischigualastia* (Cox 1965), *Placerias* (Camp & Welles 1956) and probably *Jachaleria* (Vega-Dias & Schultz 2004) the olecranon is triangular but showing varying states of development.

In *Kannemeyeria* the femoral head is continuous with the major trochanter, as it is in *Wadiasaurus* (Bandyopadhyay 1988; Ray 2006) and many Permian taxa (e.g. *Diictodon, Kingoria,* '*D.*' *trigonocephalus*), whereas it separated from it by a weak groove in *Sinokannemeyeria* (Sun 1960, 1963), *Ischigualastia* (Cox 1965) and *Placerias* (Camp & Welles 1956). The femoral head of *Kannemeyeria* is round and inflected medially as in *Wadiasaurus* (Bandyopadhyay 1988; Ray 2006) and *Dinodontosaurus* (Cox 1965) as compared with the new world stahleckeriids (Cox 1965; Camp & Welles 1956) and sinokannemeyeriids (Sun 1960, 1963) where there is either a distinctly developed neck or the presence of an incipient neck.

Surkov (1998) considered that large Triassic dicynodonts (*Dinodontosaurus* and *Placerias*) had massive limbs and hemispherical humeral heads and that the ectepicondyle extended far distally. *K. simocephalus,* although large, has an inverted triangular head like that seen in *Parakannemeyeria* and *Sinokannemeyeria* and the ectepicondyle does not extend far distally. It points to a possible move to more upright forelimbs which would result in the trunk being raised above the ground. This above observation would suggest that these larger animals were probably predisposed to having more effective and efficient locomotor systems.

Some of the material previously described as *Kannemeyeria* has not been included in these descriptions. It was noted during this study that some of the material previously assigned to *Kannemeyeria* showed significant variation from what is currently known as *Kannemeyeria.* This material includes specimens previously described by Pearson (1924) and Cruickshank (1975). These include many of the elements of the pectoral girdle and forelimb as well as the pelvic girdle and hindlimb.

It has been noted that there are a number of differences between the ulnae of BP/1/5624 and BP/1/6160, and ELM 1. The radial facet of ELM 1 is narrower than that of BP/1/5624 and BP/1/6160 and the laterally projecting ridge on the lateral surface of the ulna is also located further anteriorly in ELM 1 than in BP/1/5624 and BP/1/6160. Also the shape of the olecranon of ELM 1 is round and wide, whereas the olecranon of BP/1/5624 and BP/1/6160 are triangular or wedge shaped. Both BP/1/5624 and BP/1/6160 are associated with skulls that have been identified as *K. simocephalus.* The ulna of ELM 1 is distinctly different from that of BP/1/5624 and BP/1/6160 and suggests that it does not belong to this taxon.

There are also differences between the radii BP/1/6160 and ELM 1. The radius of BP/1/5624 was not considered for all comparisons as it has suffered some damage. The ends of the radius (BP/1/6160) of *K. simocephalus* are expanded, forming narrow articulating surfaces both

proximally and distally. This is different from that of ELM 1, which does not have greatly expanded ends, and which has the proximal and distal articulating surfaces that are wide and nearly circular. On the proximal expansion of the radius facing more posteriorly is the ulna articulation. In ELM 1 the ulna articulation is proximo-distally narrow and triangular, while in both BP/1/5624 and BP/1/6160 the ulna articulation forms a narrow rectangle, with both having a convex surface. Thus we consider the affinities of the radius incorporated into the ELM 1 mount to be uncertain. Although the skull of ELM 1 and most of the postcranial elements have been found to belong to *Kannemeyeria* the above mentioned elements show definite difference from other specimens of *Kannemeyeria.* From notes on the collection of the original (Courtney-Latimer 1948) it would seem that material was collected was incomplete and fragmentary so the mounted specimen was completed with material that had been previously collected (Courtney-Latimer 1948). It is therefore possible that some elements that form part of this specimen may show an anatomy that is different from what is known as *Kannemeyeria simocephalus.*

Scapulae (R3740) described by Pearson (1924) after been examined was found to be significantly different from that described as a part of *K. simocephalus* (BP/1/5624; BP/1/6160) in particular they have a narrower blade, the anterior margin is slightly concave and the prespinous region is much narrower to mention a few of the differences. The femora (R3740) described by Pearson (1924) have wider shafts and the femoral articulating surface is directed more dorsally. The pelvic girdle of ELM 1 shows a morphology that is different from that of BP/1/5624 and R3761 in that the ilium's anterior process is much longer and has a curved appearance. These are just some of the notable differences; however, this material forms the focus of a separate, more detailed analysis.

Diagnosis of *Kannemeyeria simocephalus*

We consider the following characters of the postcranial skeleton to be diagnostic for *K. simocephalus,* and they be added to the current specific cranial diagnosis (Renaut 2000, pp. 114–115,). However, it must be noted that at this time *K. lophorhinus,* the other valid species of *Kannemeyeria,* is poorly represented. Therefore, it is not possible to determine whether the characters listed below are diagnostic of the species *K. simocephalus* or the genus *Kannemeyeria* as a whole. The polarity of the characters was determined by comparison with '*D.*' *trigonocephalus* (based on King 1981 including using figures).

Kannemeyeria simocephalus is a kannemeyeriiforme dicynodont with the following autapomorphies: a U-shaped tubercle at the proximo-posterior corner of the medial surface of the acromion (a similar feature (round) is also present in *Tetragonias* but is not as well developed as seen in *K. simocephalus*); the ventral articulating surface of the lateral condyle of the femur is lower than the medial; lateral border of the femur is almost straight.

Kannemeyeria simocephalus can be further distinguished from all non-kannemeyeriiforme dicynodonts by the presence of the following kannemeyeriiforme synapomorphies: antero-posteriorly expanded dorsal scapula border; scapula spine present; triangular acromion; distal end of scapula flared; distal scapula projects in front of scapula spine; proximal and distal expansions of the humerus are more or less of equal length; anterior process of ilium is wide and posterior process is narrow; anterior process well in front of acetabulum; supra-acetabular notch present; femur has concave posterior border; femoral head is medially inflected; narrow greater trochanter.

It differs from other kannemeyeriiformes by retaining the following pleisomorphic characters: scapula has straight anterior and posterior border; glenoid lower than coracoid articulation; round glenoid articulation; olecranon fused to shaft; triangular olecranon. Supra-acetabular notch present on ilium. Pubis and ischium are fused; oblong obturator foramen; femoral head continuous with greater trochanter; the greater trochanter is parallel to the long axis of the femur; third trochanter absent.

CONCLUSION

An examination of the postcranial skeleton of *K. simocephalus* led to a revision of the postcranial characters that diagnose it. The presence of a U-shaped tubercle on the medial surface of the scapula at the proximo-posterior corner of the acromion and the articulating surface of the posterior condyle is lower than that of the anterior one are found to be unique to *K. simocephalus.* Although there is no mention of a similar feature in the literature describing Triassic dicynodonts, an examination of the mounted specimen of *Tetragonias* showed a round tubercle in a similar position.

Material previously described by Pearson (1924) was also re-examined and some of the material was found to be significantly different from BP/1/5624 in particular the scapulae and femora. The mounted specimen ELM 1 was also studied it was found to contain elements that could be identified as *K. simocephalus* while some long bone elements were found to be significantly different. Courtney-latimer (1948) also stated although a substantial amount of this skeleton comes from a specimen collected in 1948, a fair amount was incomplete and was actually replaced by material that had been collected and housed at the museum. This therefore suggests that ELM 1 is a chimera. The material that was excluded from *K. simocephalus* has been included in a separate study.

It therefore makes BP/1/5624 the most complete positively associated *K. simocephalus* specimen currently known, and thus makes it a suitable standard for the referral of postcranial material to *K. simocephalus.*

We wish to extend our thanks to the National Research Foundation for funding the PhD and Post Doctoral Fellowship that resulted in this work. Many thanks to Alain Renaut for his initial work on the cranial morphology of *Kannemeyeria simocephalus* which spurred the interest in the postcranial skeleton of the species, and for his involvement and assistance at the outset of this project. My thanks to Sandra Chapman at the Natural History Museum, London for allowing me access to the *Kannemeyeria* material housed there. Thanks to Dr Michael Maisch for his hospitality and access to the Triassic material housed at the University of Tübingen, Stuttgart. Thank you to Mr Kevin Cole of the East London Museum, South Africa for allowing us access to the mounted specimen as well as for extra photographs of ELM 1. My thanks to Ms Sheena Kaal of the South African Museum, Cape Town for all her help during my visit to examine Triassic dicynodont material housed there. We express our gratitude to Dr Ken Angielczyk and an anonymous reviewer for their helpful comments.

ABBREVIATIONS

Institutional

BP	Bernard Price Institute for Palaeontological Research, Johannesburg
SAM-PK	South African Museum, Cape Town
BMNH	British Museum of Natural History, London
ELM	East London Museum, East London, South Africa

Anatomical

acet.	acetabulum
acrom.	acromion
ant. proc.	anterior process
atl	atlas
ax.	axis
biccip. f.	biccipital fossa
cent.	centrum
d-p cr.	delto-pectoral crest
ectepic.	ectepicondyle
entepic.	entepicondyle
entepic. for.	entepicondylar foramen
fem. h.	femoral head
glen. f.	glenoid facet
gr. troch.	greater trochanter
hum. h.	humeral head
ic.	intercentrum
il. bl.	ilium blade
intercond. f.	intercondylar fossa
isch.	ischium
lat. cond.	lateral condyle
med. cond.	medial condyle
n. s.	neural spine
n.a	neurapophysis
obt. for.	obturator foramen
odont.	odontoid Process
olec.	olecranon
olec. f.	olecranon Fossa
post. proc.	posterior process
postzyg.	postzygapophysis
prezyg.	prezygapophysis
prox. exp.	proximal expansion
pub. tub.	pubic tubercle
rad. artic.	radial articulation
sig. fac.	sigmoidal facet
sk. artic	skull articulation
sp.	scapula spine
tub.	tubercle
ul. artic.	ulna articulation

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A second specimen of *Blikanasaurus* (Dinosauria: Sauropoda) and the biostratigraphy of the lower Elliot Formation

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

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A second specimen of the rare basal sauropod *Blikanasaurus cromptoni,* is recorded from a site in the Ladybrand district of the Eastern Free State, South Africa. The specimen consists of a right metatarsal 1 that originated from the upper 20 m of the lower Elliot Formation. It can be referred to *B. cromptoni* on the basis of its small size and highly robust proportions, which distinguish this taxon from all other sauropodomorphs. This record extends the geographic distribution of *B. cromptoni* north into the region of the main Karoo Basin where the Elliot Formation is dramatically thinner. It also extends the known stratigraphic range of *B. cromptoni* up from the base of the Elliot Formation into a position near the top of the lower member. This new record, combined with other new discoveries, supports the hypothesis that the thin northern part of the lower Elliot Formation is a condensed section that is largely, if not entirely, coeval with the thicker southern sections.

Keywords: basal sauropod, *Blikanasaurus,* Triassic, biostratigraphy, Karoo Basin, Elliot Formation.

INTRODUCTION

The dinosaur-rich Elliot Formation was deposited during the latest stages of filling of the main Karoo Basin, a large foreland basin to the north of the Cape Fold Belt in southern Africa. The northern third of the basin overlies the Kaapvaal Craton, which is an ancient continental block that influenced the tectonic development of the Karoo Basin during the deposition of the Elliot Formation. As a result the thickness of the Elliot Formation dramatically increases south of the Craton (Bordy *et al.* 2004). The difference in thickness on and off the Craton is particularly strongly marked in the lower part of the Elliot Formation, which is thought to be Late Triassic in age (Olsen & Galton 1984; Lucas & Hancox 2001). It is not known whether the greater thickness in the south represents an expanded section that is coeval with northern sections or whether a greater time span of deposition is represented in the south and no research has been directed towards this question. Until recently the latter hypothesis would have appeared more likely given that there was a set of taxa, including the cynodont *Scalenodontoides macrodontes* and the dinosaurs *Aliwalia rex* and *Blikanasaurus cromptoni,* which had only been found in the southern end of the basin and were apparently restricted to the lowermost part of the lower Elliot Formation (Gow & Hancox 1993; Galton & Van Heerden 1998).

Blikanasaurus cromptoni is a basal sauropod dinosaur (Yates & Kitching 2003; Galton & Upchurch 2004) that was first described as belonging to a new, monotypic family of prosauropods (Galton & van Heerden 1985). Until now this species was known from a single specimen found in the 'passage beds' of Blikana Mountain in the Herschel District (Charig *et al.* 1965), at the southern end of the exposure of the Elliot Formation (Fig. 1). The so-called Passage Beds were named for the beds that are 'lithologically transitional between the typical Molteno Beds below and the typical Red Beds [= Elliot Formation] above' (Charig *et al.* 1965, p. 200). This echoed the thought of several geologists claimed that the Molteno-Elliot contact was conformable and gradational (Du Toit 1939; Turner 1972; Eriksson 1984). However, it is now apparent that there is a regional disconformity between these two formations (Bordy *et al.* 2005). Bone preservation has never been observed in the Molteno Formation below the level of this disconformity (Turner 1972; Bordy *et al.* 2005). Thus it is almost certain that the holotype of *B. cromptoni* originated from the lowest part of the lower Elliot Formation, above the disconformity. This paper records the second known specimen of *B. cromptoni* and demonstrates both its presence in the northern part of the basin and in a stratigraphic position well above the base of the lower Elliot Formation. The stratigraphic range and geographic distribution of other lower Elliot amniotes are also examined and their implications for biostratigraphy and basin development are discussed.

MATERIALS

BP/1/5271 is a group lot of bones that were collected by J.W. Kitching in 1984 and contains a number of sauropodomorph postcranial pieces. Included amongst these is a small, robust right metatarsal I that is identified here as the second known specimen of *B. cromptoni.* The collection appears to be gathering of surface float and there is no indication they represent a single associated individual. The size disparity represented by these elements indicates that more than one individual and possibly taxon is represented. Given the lack of definitive association the metatarsal in question has been designated as BP/1/5271a.

LOCALITY AND HORIZON

The various elements of BP/1/5271 were collected from the lower Elliot Formation outcropping in a large erosional

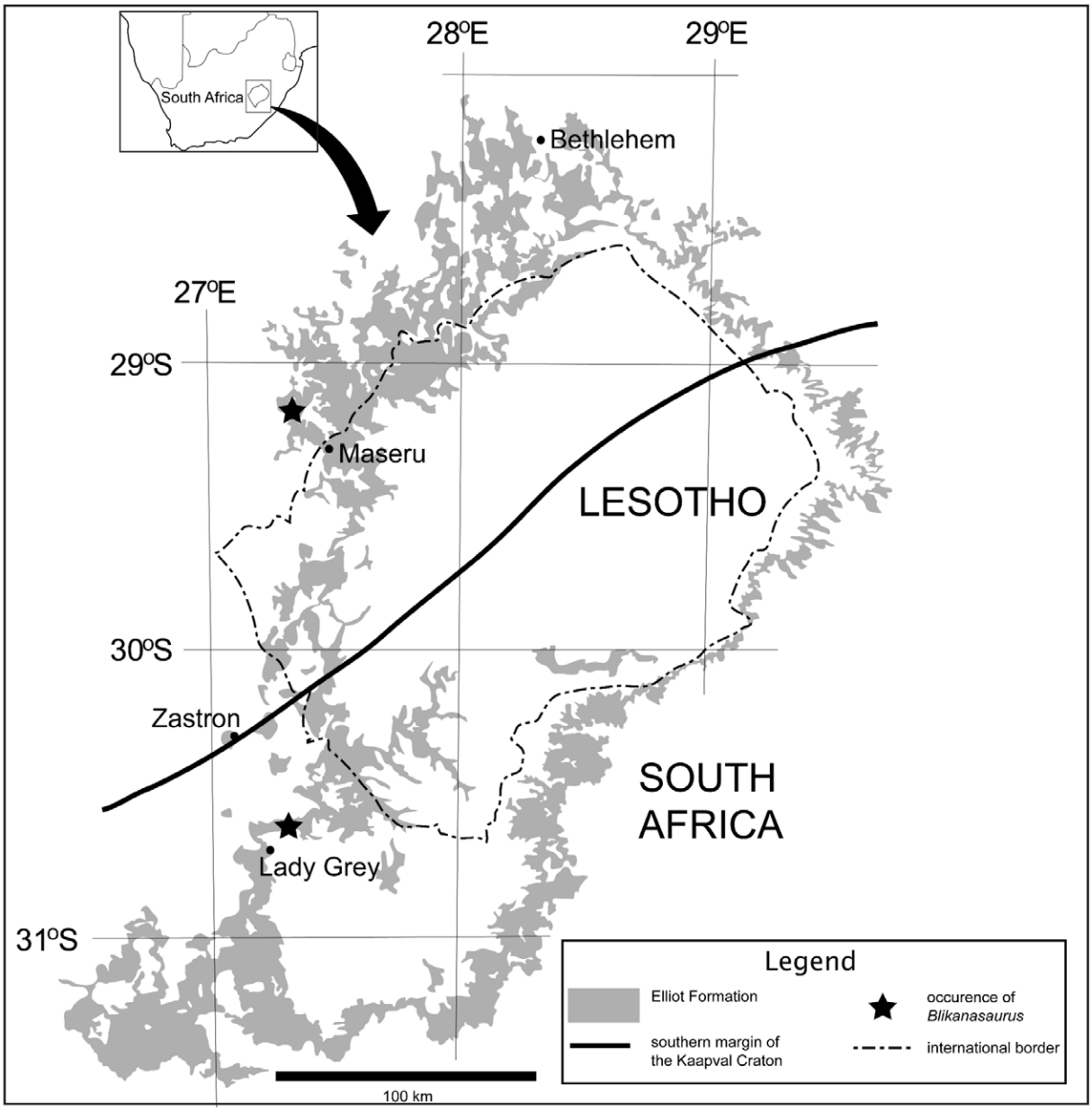

Figure 1. Map of the exposure of the Elliot Formation in the main Karoo Basin of South Africa and Lesotho showing the two known localities of *Blikanasaurus* both on and off the Kaapvaal Craton. Redrawn from Bordy *et al.* (2004).

gully ('donga') on the farm Damplaats in the Ladybrand District of the Eastern Free State. This is the same erosional gully that produced the only known articulated skeleton and skull of *Melanorosaurus readi* (Welman 1999; Yates 2007a; Bonnan & Yates 2007) and the holotype of *Eocursor parvus* (Butler *et al.* 2007). The Ladybrand district is underlain by the Kaapvaal Craton where the lower Elliot Formation is quite thin. Stratigraphic examination of Damplaats places the strata exposed in the donga below the disconformity that separates the upper (Jurassic) and lower (Triassic) units of the Elliot Formation (Butler *et al.* 2007, supplementary material, fig. S1). Complete sections of the lower Elliot Formation in the Ladybrand district are about 60 m in total thickness (Smith & Kitching 1997; Bordy *et al.* 2004) but only the upper 20 m of the Elliot Formation is present at Damplaats (roughly the upper 30% of the unit). Although the precise stratigraphic location of the specimens in BP/1/5271 is not recorded they can only have come from near the top of the lower Elliot Formation because that is all that is exposed at the collection site.

COMPARISON WITH OTHER SAUROPODOMORPHS

The morphology of the distal articular surface clearly identifies BP/1/5271a as a sauropodomorph. The transverse axis of this surface is angled distolaterally, which is a characteristic of Sauropodomorpha more derived than *Saturnalia* (Yates 2007a: character 333). Furthermore the medial distal condyle is highly reduced relative to the lateral distal condyle, while a distinct flexor notch separating the two is maintained. This characteristic is widespread amongst basal sauropodomorphs and basal sauropods and also appears to be diagnostic of Sauropodomorpha more derived than *Saturnalia,* although the character has yet to be used in a cladistic analysis.

An explanation of the phylogenetic taxonomy used in this paper is required before this discussion can proceed.

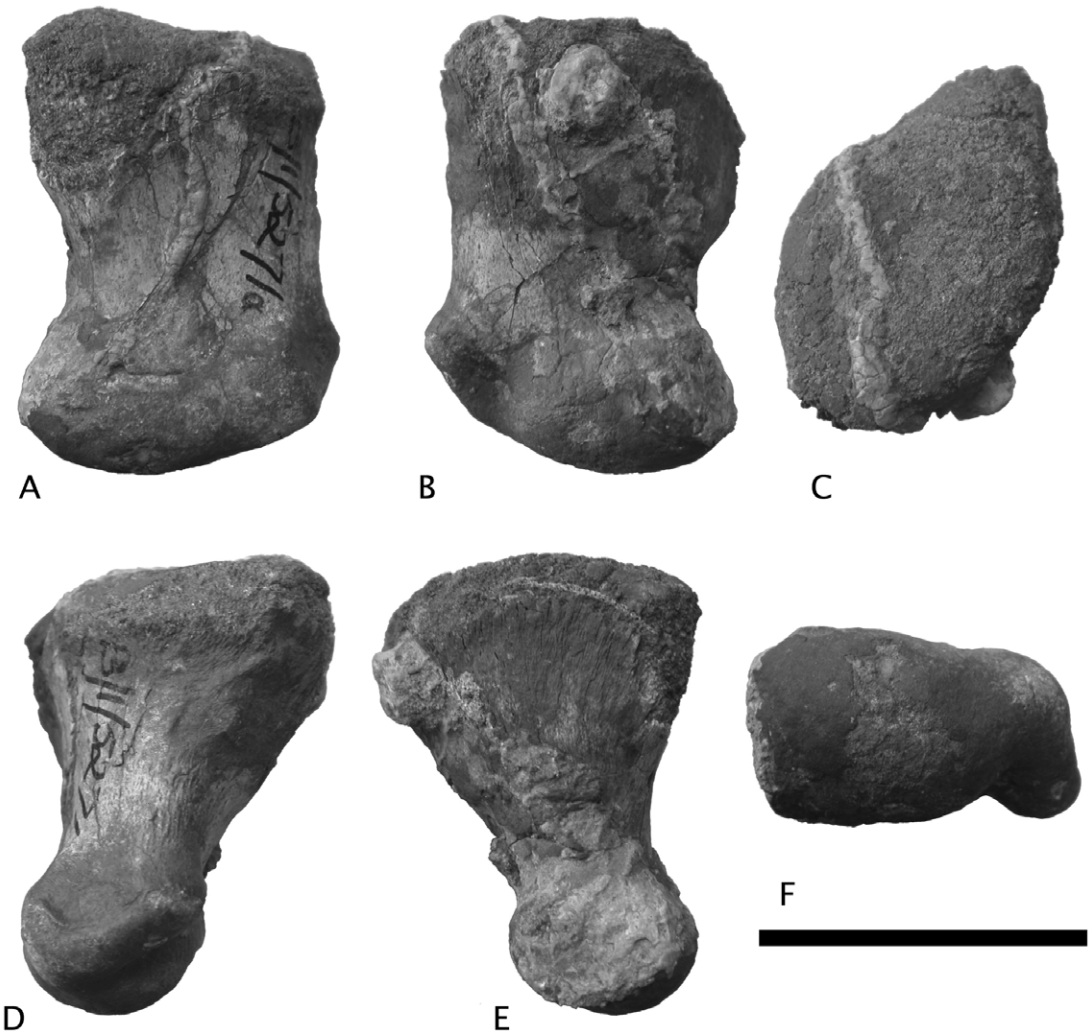

Figure 2. Right metatarsal I of *Blikanasaurus cromptoni* (BP/1/5271a) in (**A**) extensor, (**B**) flexor, (**C**) medial, (**D**) lateral, (**E**) proximal and (**F**) distal views. Scale bar = 50 mm.

A number of definitions of Sauropoda have been proposed over the past decade. The earliest of these is that it is the most inclusive clade including *Saltasaurus loricatus* (a derived Cretaceous neosauropod) but not the familiar 'prosauropod' *Plateosaurus engelhardti* (Wilson & Sereno 1998). However this definition includes numerous traditional 'prosauropods' when applied to phylogenies where basal sauropodomorphs are strongly paraphyletic. Thus the definition of Yates (2007b) is used here. Under this definition Sauropoda is the most inclusive clade including *Saltasaurus loricatus* but not *Melanorosaurus readi* and includes the relatively large obligatory quadrupedal forms and excludes nearly all forms that had traditionally been included in Prosauropoda (with *Blikanasaurus cromptoni* being a notable exception) in all currently viable hypotheses of basal sauropodomorph relationships.

BP/1/5271a is a remarkably robust element in extensor view (the midshaft width is 55% of the total length of the bone) suggesting a position among basal sauropods. The midshaft width is less than half the total length of metatarsal I, in non-sauropod sauropodomorphs, for example it is 40.6 in *Jingshanosaurus xinwaensis* (LV 3), 21% in *Anchisaurus polyzelus* (YPM 208), and 24% in *Lufengosaurus huenei* (Young 1941, fig. 25). Amongst the sauropodomorphs from the lower Elliot Formation similarly stout first metatarsals are found only in the basal sauropods *Antetonitrus ingenipes* (BP/1/4952: 54%) and *Blikanasaurus cromptoni* (SAM-PK-K 403: 53%). The near-sauropod *Melanorosaurus readi* is also somewhat stout-footed but the proportions of its first metatarsal lie firmly in the range of more basal sauropodomorphs (NM 1551: 39%). Although the first metatarsals of the other lower Elliot sauropodomorphs (*Eucnemesaurus fortis, Plateosauravus cullingworthi* and an unnamed taxon from the farm Nova Barletta in the Clocolan district) are currently unknown it is very unlikely that they had stout, sauropod-like metatarsals, like BP/1/5271a, given that their phylogenetic position is basal to the advanced stout-footed forms (Yates 2003, 2007a).

The Damplaats metatarsal differs from *Antetonitrus ingenipes* and shares the following derived similarities with the holotype of *Blikanasaurus cromptoni.* Firstly, the size of BP/1/5271a is close to that of SAM-PK-K 403 and is much smaller than *Antetonitrus ingenipes* (Table 1). A study of the evolution of size in Sauropodomorpha indicates that the small size of *Blikanasaurus cromptoni* is an autapomorphic reversal of the trend towards increased size in the sauropod lineage (Yates 2004). Secondly, the extensor-flexor depth of the distal articular surface is greater relative to the transverse width of the articular

Table 1. Measurements of the first metatarsal of various basal sauropods including BP/1/5271a. All measurements are in mm.

Measurement	*Melanorosaurus* NM 1551	*Antetonitrus* BP/1/4952	*Blikanasaurus* BP/1/5271a	*Blikanasaurus* SAM-PK-K 403
Length	119	120	70	86
Minimum transverse shaft width	47	63	36.5	41
Maximum width of proximal articular surface	69	93.5	56.4	76.5
Width orthogonal to max. prox. width	33	59	36.5	36.5
Transverse width of distal articular surface	67	88.6	46	54
Extensor-Flexor depth of distal articular surface	37	43.7	26	38
Minimum extensor-flexor depth of shaft	23	31.3	21	31

surface in BP/1/5271a (72%) and the holotype of *Blikanasaurus cromptoni* (SAM-PK-K 403: 70%) than in *Antetonitrus ingenipes* (BP/1/4952: 49%). Thirdly, the minimum extensor-flexor depth of the shaft is relatively greater in BP/1/4952 (30%) and SAM-PK-K 403 (36%) than in *Antetonitrus ingenipes* (26%). Based on these comparisons the element can be identified as belonging to *Blikanasaurus cromptoni.*

DISCUSSION

Prior to 2006 there was a small set of amniote taxa that were only known from the lowest beds of the lower Elliot Formation from the south end of the basin where this unit reaches on average 300 metres in thickness (Bordy *et al.* 2004). These included the cynodont *Scalenodontoides macrodontes* and the dinosaurs *Aliwalia rex* and *Blikanasaurus cromptoni. Scalenodontoides* was known from a number of specimens that all derived from the lowest beds of the lower Elliot Formation (Gow & Hancox 1993). As discussed above, the type locality of *Blikanasaurus cromptoni* is located at the very base of the lower Elliot Formation while that of *Aliwalia rex* is recorded as 'Barnard's Spruit (= creek), Ward, 15 miles south of Aliwal North' (Seeley, 1894, p. 317, quoted in Galton & van Heerden 1998, p. 175). No record of 'Ward' as a place-name in the Aliwal North district could be found although Barnard's Spruit is present in the area. Kitching & Raath (1984) note that the directions would place the locality on the farm Ezelsklip. On this farm the creek is deeply incised into the 'Stormberg group' so that if the site is located near the banks of the creek on this farm then it would have to be low in the lower Elliot Formation close to the contact with the Molteno Formation (3026 Aliwal North, 1:250 000 geological map series).

These three taxa hinted at the possibility of a distinct faunal assemblage that preceded the typical fauna of the lower Elliot Formation (usually attributed to the '*Euskelosaurus* Range Zone' [Kitching & Raath 1984]) that was only deposited in the south. However, a skull of *Scalenodontoides macrodontes* has recently been identified that was collected from a site in Lesotho near the northern limit of the Elliot Formation (Battail 2006). Similarly the two dinosaur taxa are now known to occur in sections that lie on the Kaapvaal Craton. *Aliwalia rex* has been recognized as a junior synonym of *Eucnemesaurus fortis*, which is known from two sites at the northern end of the basin: Zonderhout in the Fouriesburg District and Spion Kop in the Senekal District (Yates 2007b). Furthermore the *Eucnemesaurus fortis* collected from Spion Kop was found just over 30 metres above the base of the Elliot Formation, from a site approximately half way up the lower member (recorded as the third vertebrate fossil occurrence from the base in Yates *et al.* 2004, fig. 2). As discussed above the new *Blikanasaurus cromptoni* specimen is also from the northern end of the basin and from a stratigraphic position at least 30 metres above the base of the lower Elliot Formation.

Thus there is currently no evidence for a distinct, early biostratigraphic assemblage that is only present at the south end of the basin. Furthermore the fauna of the lower Elliot Formation would appear to be homogenous for most of its thickness and geographic extent. This suggests that the thinner northern section is a condensed section that is coeval with the southern section. Thus the onset of deposition of the Elliot Formation appears to have been more or less synchronous on and off the Kaapvaal Craton (at least at the level of resolution afforded by vertebrate biostratigraphy). However, it is necessary to collect more diagnostic specimens that are well placed stratigraphically before any sort of biostratigraphic subdivision of the lower Elliot Formation can be ruled out.

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INSTITUTIONAL ABBREVIATIONS

BP Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg.
LV Museum of Lufeng Dinosaurs, Jingshan.
NM National Museum, Bloemfontein.
SAM Iziko South African Museum, Cape Town.
YPM Peabody Museum of Natural History, Yale University, New Haven.

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Makapansgat Limeworks stratigraphy and the singular case of Member X

Alf Latham* **& Ginette Warr**

School of Archaeology, Classics and Egyptology, Liverpool University, Liverpool, U.K.

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Within the infilling sequence of the western Limeworks a newly recognized unit, Member X, lies stratigraphically between the Member 1 massive speleothem and the Member 2 red silts. Member X consists firstly of a subaqueous mammillary layer that is ubiquitous to the whole of the Limeworks. It is succeeded by a series of intercalated clastic sediments and calcite-rich layers that is confined to the area between the Original Ancient Entrance and the Classic Section and which is terminated by a second subaqueous carbonate layer. The evidence suggests that surface sediments were washed into a carbonate-rich pool created by seepage water and, from the presence of several articulated skeletons, the Original Ancient Entrance during this phase appears to have acted as an animal trap. There are a few blocks of Member X to be found in the Limeworks dumps that have been placed in the Member 2 rows but which should be prepared separately. From the evidence of the intercalated carbonate and clastic layers it appears that Member X was deposited slowly at first and then speeded up probably because erosion caused retreat of the entrance. Member X has several unusual features including a unique pseudo-breccia layer of co-deposited calcite-mud formations, deposition of aragonite that increases with height, and calcite-aragonite layers that invert the stratigraphy on overhanging walls and ceilings but not on the floors.

Keywords: Makapansgat, Member X, stratigraphy, chronology, Kitching.

INTRODUCTION

The earliest deposits of the Limeworks are the huge stalagmites, flowstones and columns that formed an irregular arc-shaped wall round the outside of the main cavern (Speleothem Arc) and which were extracted by the lime workers in the first half of the twentieth century. Subsequently, as the roof eroded, the precipitation of speleothem was succeeded by collapse blocks and surface runoff from above the cave. Partway through the unroofing phase of the cave, animals such as hyaenas, big cats and porcupines used parts of the cave for denning. One large area on the western side – the Classic Section – is well known for its Grey Breccia (Member 3) the remains of which show that it once contained dense bone accumulations to the local roof. The remains of Australopithecines have been scavenged from the Grey Breccia dump material and from roughly equivalent parts of the central repository that we have called the Central Debris Pile (Latham *et al.* 2003; Latham *et al.* 2007).

A stratigraphy for the Limeworks based on the layer-cake model was constructed by Wells & Cooke (1956), by Brain (1958) and by Partridge (1979) who introduced the Member system for the supposedly successive deposits. Member 1 is the massive speleothems, Member 2 comprises red silts (mainly on the western side). Member 3 is the Grey Breccia, and Members 4 and 5 (which is really one unit) constitute the pink breccia deposited on the inside of the Speleothem Arc in the centre of the fossil cavern. The idea of a single succession was criticized by Maguire *et al.* (1985) who recognized that different areas constituted different repositories of infill. Subsequent stratigraphic reconstructions by Latham and co-workers have concentrated mainly on the fossil-rich western side of the Limeworks and they have used a modified form of the Member notation to describe it. Further work has shown that another episode of deposition occurred between Member 1 and Member 2, sufficiently distinct to have been separated out, and it is here called 'Member X'.

In the area known as the Original Ancient Entrance at the northwest end of the site, the pediment flow of one of these massive Member 1 speleothems is overlain by up to 1 m of sloping and horizontal subaerial flowstones. Member X overlies these speleothem deposits. Latham *et al.* (1999, 2003) showed that the Member 2 red silts of the western Limeworks and the Classic Section were also carried in by periodic floods through an old entrance centred on what is now referred to as the Original Ancient Entrance (OAE). It was in order to resolve ambiguities in the ongoing palaeomagnetic re-analysis that prompted further stratigraphic work, and this has revealed complexities in the layering, including localized stratigraphic inversion of layers in the western deposits.

THE STRATIGRAPHY OF MEMBER 1 TO THE MEMBER 2 RED SILTS

Figure 1 shows the position of the so-called Original Ancient Entrance. This mined feature occupies part of what was once an exit (resurgence) for the original formative stream and then, upon abandonment, a point of ingress for clastic sediments resulting from slope wash. The passage now forms a **U** loop in long section, one arm being the North Alcove to the Main Quarry and the other arm being an upward trumpet-shaped ramp to the exterior surface. This latter arm is now eroded at the surface and, except for the mined western half, is still filled with sediments of Member X and Member 2. The sediments in the actual OAE are at their lowest point and constitute a small, irregular, sedimentary basin. Current excavations on the surface, by T. Crawford, K. Kuykendall, J. McKee & J. Maluleka, for *in situ* bone, have revealed the eastern dolomite wall of this passage and the continuation of the

*Author for correspondence. E-mail: aa09@liv.ac.uk

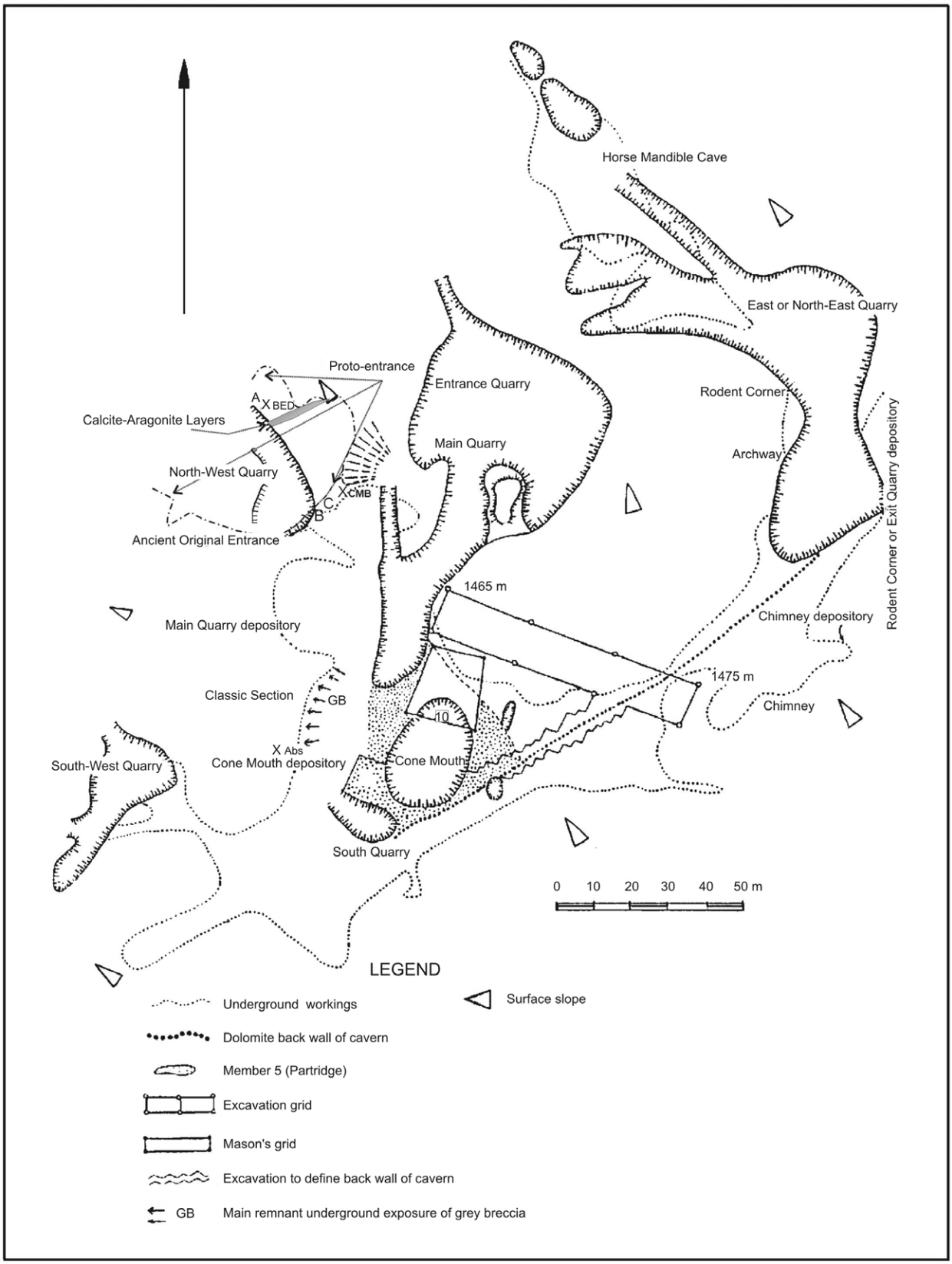

Figure 1. Map of the Limeworks site (after Maguire *et al.*1980), with the proto-entrance centred on the Original Ancient Entrance. The dot-dash line indicates the approximate extent of Member X. The position of the two articulated skeletons and hyrax skull mentioned in the text are marked A, B and C.

roof brow from the western side. Latham *et al.* (2003, 2007) discuss how Member 2 extends along to the end of the Classic Section and upwards onto the faulted buttress of the Main Quarry. This latter is the inner side of the so-called Partridge Block on which the hominid partial cranium MLD 37/38 was found by James Kitching in 1958.

Stratigraphically the sequence in the western Limeworks (excluding the Entrance Quarry) is: (1) massive speleothem of Member 1 with pediment flows down to the basin of the OAE, (2) subaerial flowstones deposited down from the exterior which lap onto the pediment flows, (3) Member X, and (4) Member 2. The latter consists of both red silts

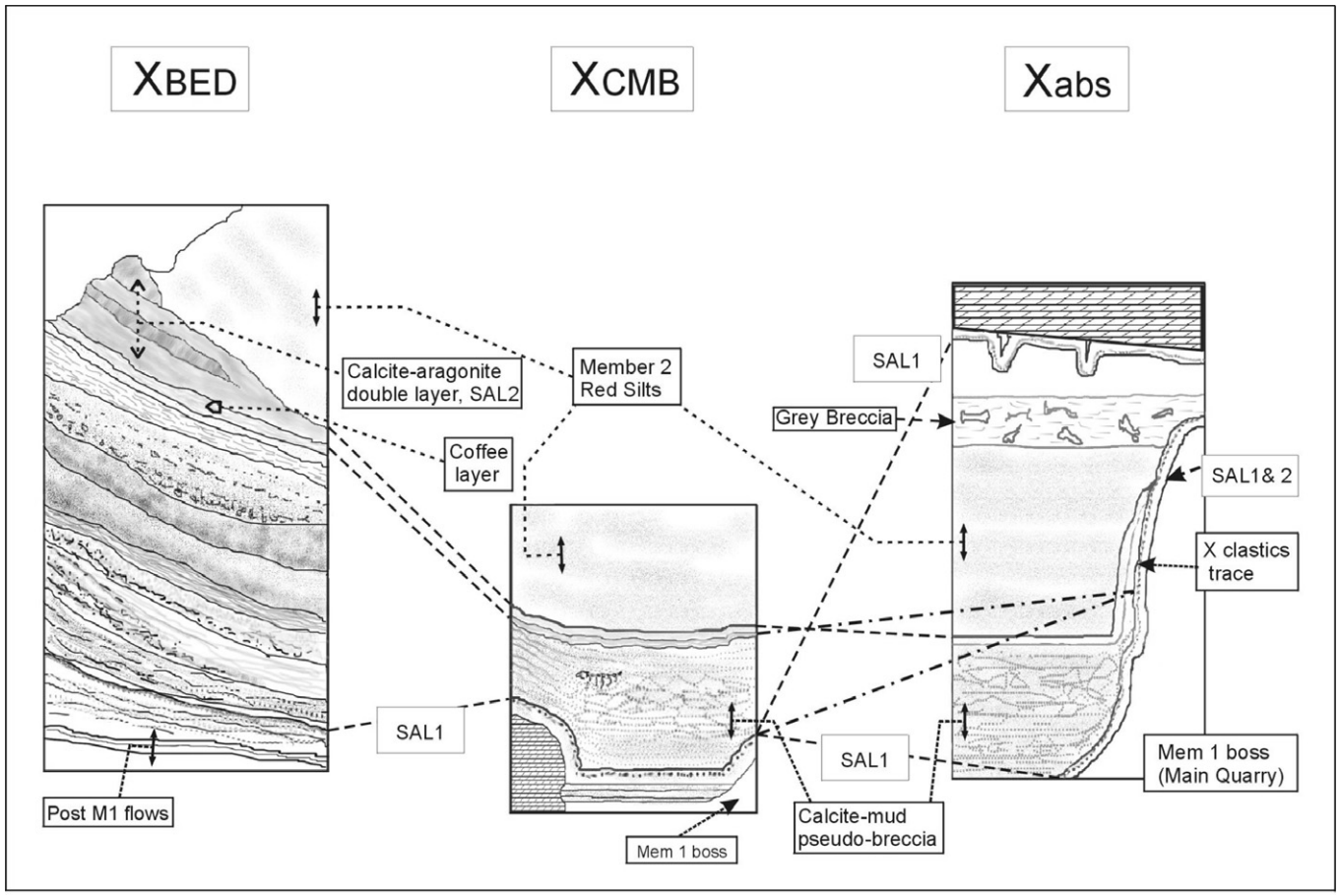

Figure 2. Sketch of the stratigraphy of Member X for three locations, X_{Bed} (bedload), X_{CMB} (calcite-mud breccia) and X_{Abs} (where the clastic layers are absent). Height dimensions are about 5 m bottom to top. The thickness of the strata, particularly Member X clastics, varies widely from place to place and so are approximate in this schematic diagram.

derived as hillwash from above the OAE and several intercalated calcite pediment flows coming from the speleothem bosses in the Main Quarry.

THE STRATIGRAPHY OF MEMBER X

Figure 2 illustrates how the stratigraphic thickness and the sedimentology of Member X are highly varied, and that the Member consists of three fairly distinct sub-units.

Sub-unit 1 – Subaqueous Layer 1 (SAL1)

This begins with about 4 to 7 cm of calcite mammillary layering (subaqueous layer 1, SAL1) that is uniformly deposited over the whole of the Limeworks including the alcoves behind the Collapsed Cone, the Exit Quarry, Rodent Corner and Horse Mandible Cave. This deposit exceeds the height of the Grey Breccia and reaches the level of the overhanging roof in this area. It reaches to within 3 m of the top of the Partridge Block. Sections through SAL1 in the basin of the OAE show that it was laid down fairly evenly (around stalactites as concentric layers) the later layers being progressively contaminated with very fine mud. This layer points to the likelihood that a carbonate-rich pool existed at this time throughout the whole of the former Limeworks cavern.

Sub-unit 2 – Clastic sediments

In the excavated area down to the OAE there follows a series of sloped, fining upward layers of clastic sediments intercalated with sets of calcite raft clasts or thin (<1 cm) subaqueous calcite layers, or both. These clastic layers result from surface runoff ('hillwash' in the Maguire *et al.* [1980] terminology) into a pre-existing pool leaving bedload of angular to subangular clasts (mostly <1.5 cm) and suspended load, each layer becoming finer down-slope. The equivalent interior floor facies contains only the suspended load. Clasts are of dolomite or chert from the country rock in a matrix derived from red-brown soils. The earlier layers outside the OAE are laid down on a slope (near the centre of the former passage) of about 20°. The slope of the last layers has increased to about 30°. This means that the bed load, in being deposited immediately on the slope, served to increase its angle of repose and was set in place by subsequent calcite flows and by calcite cementation, whereas the much finer suspended load of mud was dispersed throughout the rest of the basin, reaching as far as the distal end of the Classic Section. We have found no evidence of slumping or rescouring of the slope deposits.

Sub-unit 2 – Calcite-mud pseudo-breccia

Underneath the OAE the clastic component consists of only the suspended load, and it was laid down at the same time as the calcite. It formed either thin lenticular layers of calcite and mud layers or a pseudo-breccia of calcite in mud and mud in calcite in about equal thicknesses set at mostly low angles (Fig. 3). It is not a normal calcite-raft

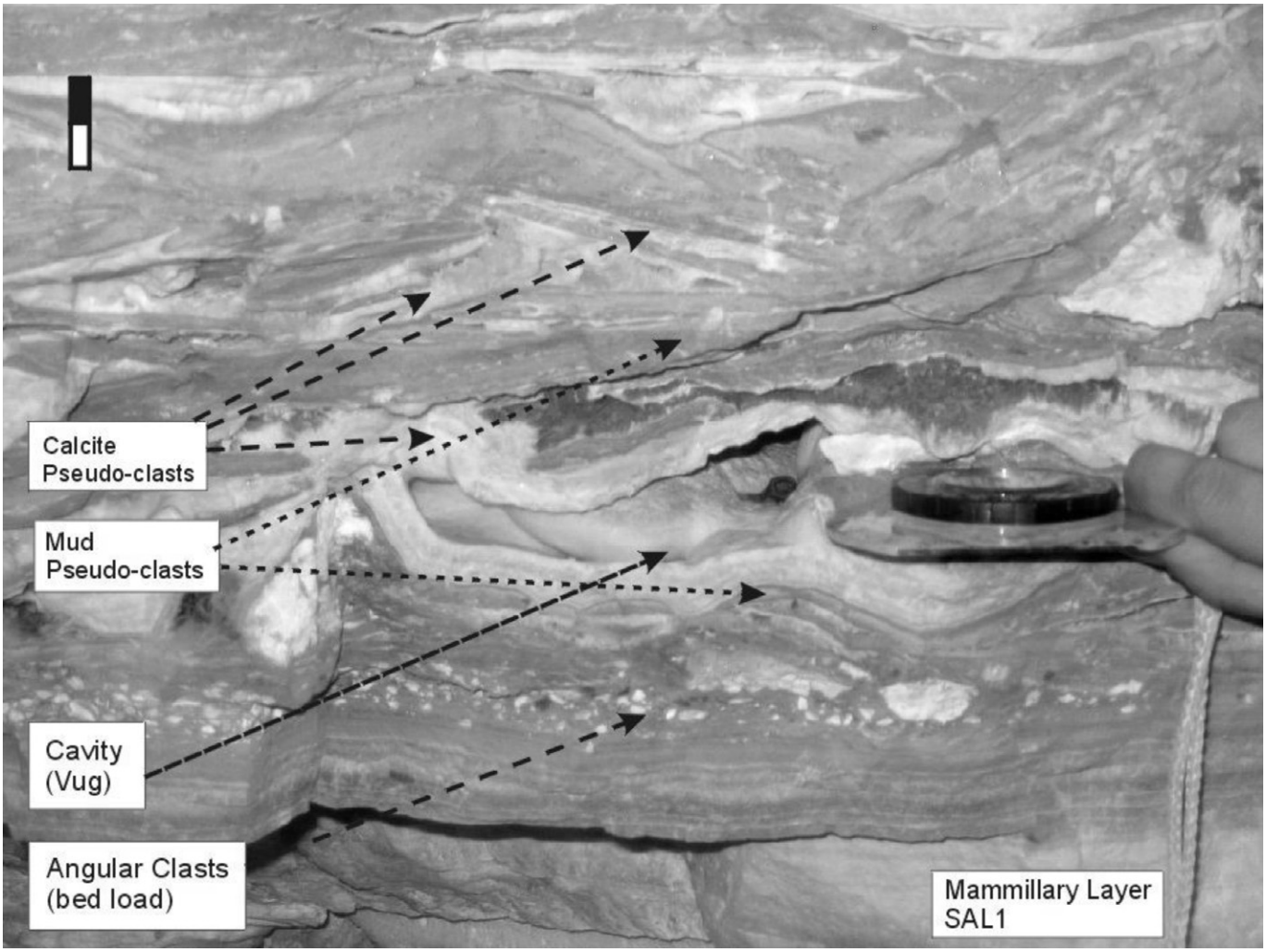

Figure 3. Photograph of the calcite-mud pseudo-breccia. The scale bar is 2 cm.

breccia, as Schrenk (1984) appears to have thought. For the formation of a normal calcite-raft breccia, thin calcite rafts precipitate out on the surface of very still carbonate-rich pools and finally reach a thickness in their growth where surface tension can no longer support the increased weight; they then sink to become incorporated in the sediment. The calcite with mud formations of Member X, however, formed below the surface at the same time as each other so that each is seen to have terminated the other and to have prevented the other from growing as contiguous layers. The calcite formations, sometimes with thicknesses exceeding a centimetre, even enclose quite large holes where there may once have been entirely carbonate solution with no mud at all. The calcite must either have disrupted the normal layering of the mud or the pool was so still that self-attraction by Van de Waal's forces between finest clay particles helped to segregate the mud from the calcite. The extraordinary effect is that the calcite formations do not occur in the mud and the mud does not contaminate the calcite formations – each component is free of the other.

Sub-unit 3 – Calcite-aragonite layers

In the OAE the last sediment layer of Member X is a fine brown mud about 5 cm thick. It coats all horizontal surfaces though, as with all sediments of Member X, it attenuates to a smear on overhanging and vertical surfaces. On top of this coffee-coloured layer is another cream-white calcite layer about 4 cm thick. The extraordinary thing is that higher up in all places of the western Limeworks this last carbonate layer becomes firstly a thicker calcite-aragonite layer up to 15 cm thick and then a calcite-aragonite double layer. It coats all surfaces, including floors (outside on the excavated area of OAE) (Fig. 4) and roofs and existing speleothems of the Main Quarry and it therefore represents a second subaqueously deposited layer (subaqueous layer 2, SAL2) and it formed, as did SAL1, under the surface of a deep carbonate-saturated pool. This time however the pool was not as deep as for SAL1, and the sediments deposited in the pool are confined to this part of the western repository. We have not been able to find it anywhere else in the Limeworks.

STRATIGRAPHIC INVERSION AND THE ABSENCE OF THE CLASTIC STRATA

When slope material representing sub-unit 2 was washed inside the entrance (Fig. 1), the suspended fraction was carried as far as the end of the Classic Section where it was stopped from going any further into the central Limeworks cavern by the massive speleothem boss (part of the Speleothem Arc) that was joined at that point to the dolomite wall. In those places where the pool was confined

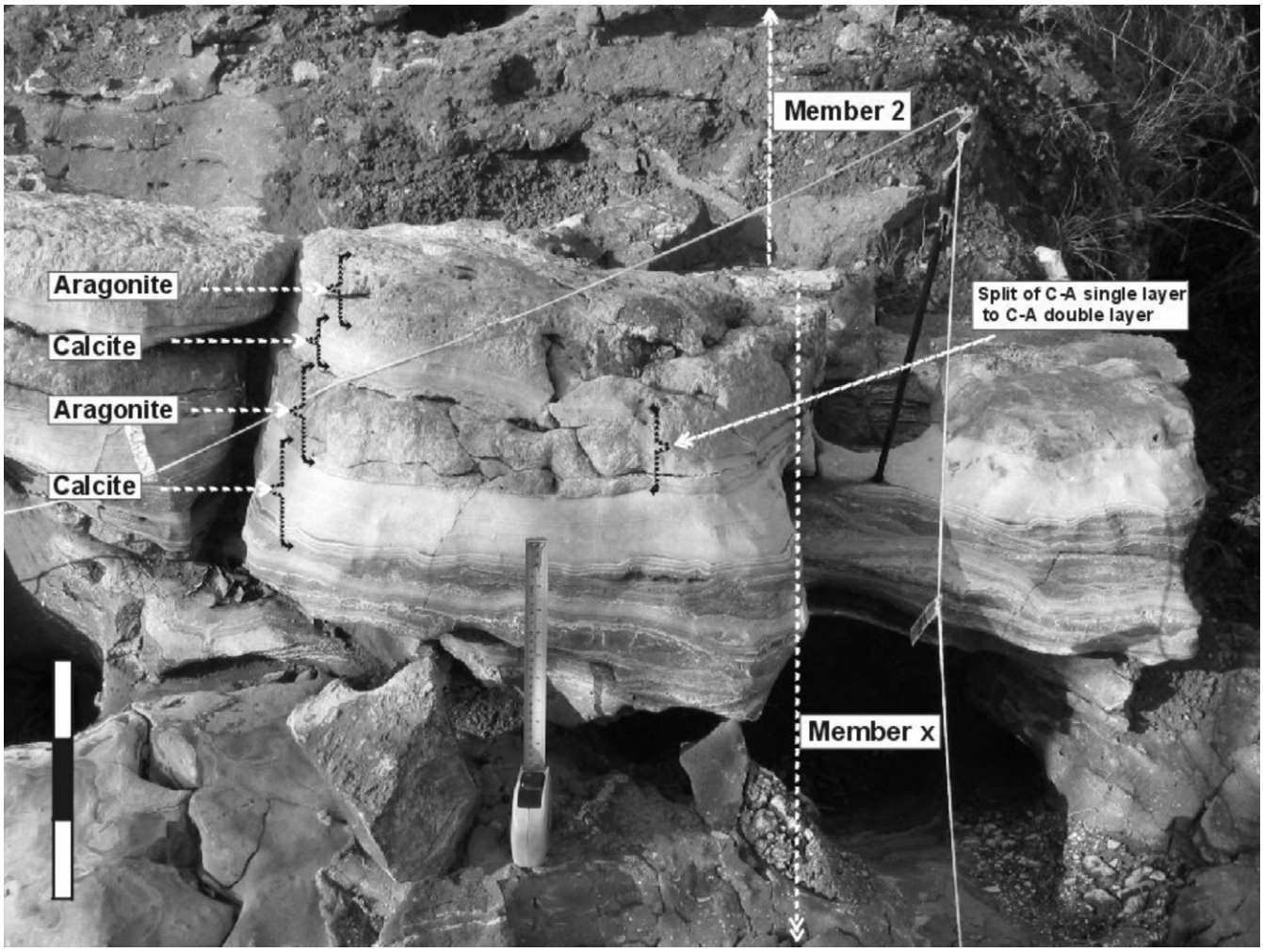

Figure 4. The calcite-aragonite double layer on the bevelled surface of the Original Ancient Entrance. The scale bar is 30 cm.

by vertical walls or vertical speleothem or where there were stalactites there was no clastic deposition at all except for a very fine dark line, less than a millimetre thick, sandwiched between the two subaqueous layers. In effect the dark line is the very finest of the clastic deposits and could easily be missed at a cursory glance. It may also be noted that where the two subaqueous layers are deposited on roof surfaces they therefore represent localized inversions of the stratigraphy. On sub-horizontal slopes the stratigraphic succession including Member X is normal.

CONDITIONS FOR THE FORMATION OF MEMBER X

The formation of all sub-units of Member X could have occurred only under a deep carbonate-rich pool. The impression is of a pool that was formed by copious amounts of drip water coming through the roof of the main cavern (this was some time before the main roof began to collapse) where evaporation was low (the cavern was enclosed except for the early proto-entrances) and where the water could not drain away because of the U-shaped nature of the cave exits or entrances. Then a new configuration of the exit brow in the area of the OAE allowed ingress of sediment from the surface, slowly at first (the first contaminated layers in the SAL1) and then more rapidly (the clast laden debris of the sedimentary layers). Evaporation of water to the outside and ingress of new carbonate water from the interior would ensure that the water stayed saturated, so producing the calcite-mud pseudo-breccia. Then more unroofing of this exit or of the Limeworks cavern itself ensured the rapid evaporation of the pool to produce the calcite-aragonite layers of SAL2 and the start of Member 2 times.

What length of time does Member X represent? SAL1 is finely layered and together with the lower calcite-clastic layers probably formed over a long period of time, in the order of 100 kyr or more. Subsequently, outside the OAE, the fining upwards layers become thicker (0.5 to 2 cm) which strongly suggests that clastic sedimentation speeded up. The metre or so of these later layers may represent just a few thousand years. Inside the OAE the final SAL2 is only 3 cm thick and it probably represents a period as short as a thousand years or less. We conjecture that it represents the ultimate drying out of the former fixed pool as its feed sources were captured elsewhere due to the unroofing of the main cavern.

FAUNAL REMAINS IN MEMBER X

The articulated skeleton of a small bovid, attributed to *Makapania broomi* (Schrenck 1984) in the calcite-mud breccia under the OAE is fairly well known. A few metres away a skull near the inner wall has been identified by Kaye Reed (pers. comm.) in 2003 as that of a hyrax. More bones have been found in this Member X including the

articulated skeleton lying on the sloping strata from the cleared surface that is thought to be of a small bovid (T. Crawford, pers. comm.) and which awaits preparation at the University of the Witwatersrand. These and a few other remains of whole bones or of more-or-less complete skeletons of small animals indicate that the pool acted as a trap. (Bones resulting from denning and predation would be fractured and disarticulated as they are in Members 2 and 3.) One might speculate that animals entering the cave and attempting to drink were not able to get out again. The alternative hypothesis, that the bones represent carcasses brought in by floods, is less likely. There are a few pieces of Member X in the Lime dumps and they should be prepared separately. They have the potential to provide specimens of late Miocene or early Pliocene age in contrast to those from Members 2, 3 and 4 which probably belong to mid to late Pliocene times (Partridge 2000).

After SAL2, the sedimentary regime above, and inside of the OAE changes quite markedly to the red silts of Member 2. Here the input is from surface run-off which created underground pools and dried out after each event; the evidence for this are the repeated generations of mud cracked layers in Member 2 (Latham *et al.* 1999, 2003). Could this sudden change in sedimentation style be due to the beginning of the roof fall of the Limeworks cavern itself? This is a working hypothesis that might be tested by further data. At any rate the bone breccias of Member 2 are, this time, due to denning animals as is evident from the splintered large bovid bones. The den in the Main Quarry lies on a former shelf of a stalagmite pediment flow and the Grey Breccia, representing a quite long period of denning, lies stratigraphically partway through Member 2 (Latham *et al.* 2007).

CONCLUSIONS

The three sub-units of a newly recognized unit, Member X, that was thought to be deposited in the early Pliocene, was formed in a more-or-less permanent pool that in its early stages reached all of the Limeworks cavern. The subaqueous calcite and aragonite testifies to the fact that this pool was supersaturated in carbonate for most of its history. Clastic sediments, confined to the western repository of the Limeworks, were washed into the pool from the direction of the current Original Ancient Entrance and the articulated skeletons of a few small animals appear to indicate that this part of the cave acted occasionally as a trap. The carbonate-rich pool, with its input of fine suspended sediment, resulted in a pseudo-breccia of calcite and mud bodies – a speleothem form that is thought to be unique to this cave. The phase ended when the pool became so saturated that it deposited, at greatest depths, one calcite layer; at medial depths, a calcite-aragonite couplet; and at shallowest depths, a calcite-aragonite double couplet. As the deposition of aragonite is mostly controlled by Mg and, possibly, by elevated temperature, then it is possible that the final calcite-aragonite phase was the result of a significant unroofing of the main cavern, which would have brought in warmer air masses, and increased the evaporation of the pool. The higher levels of the pool would be more concentrated in the lighter Mg that preferentially promotes the growth of aragonite over calcite. There is skeletal material in blocks in the lime dumps that recognizably belongs to Member X. These blocks should be prepared and archived separately from the later Member 2 material.

Member X was first so dubbed by Tafline Crawford who used percussion caps to extract the bovid in the surface exposure of the stratum in 2004. This work and the continuing stratigraphic work at the Limeworks was supported by a U.K. NERC grant (NER/A/S/2000/0034) to Bob Cliff (Leeds) and to Alf Latham (Liverpool), by an NSF grant (BCS-0128770) to Jeff McKee (Ohio State University) and by a Leakey Foundation grant to Alf Latham.

This paper is dedicated to the memory of James Kitching, of the Bernard Price Institute for Palaeontology, University of the Witwatersrand, and his work at the Limeworks over several decades, and is a contribution to his Festschrift. The University of the Witwatersrand Makapansgat acquisitions book amply shows that the majority of hominid fossils known from the Limeworks, were found by him between 1947 and 1958 including MLD 37/38.

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Size and shape of a human foot bone from Klasies River main site, South Africa

Bernhard Zipfel[1]* & Robert S. Kidd[2]

[1]*Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa*

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

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Rightmire *et al.* (2006) recently described three human metatarsal bones of Middle Stone Age antiquity from Klasies River Mouth (KRM) main site, South Africa. One of these, a complete adult left first metatarsal is broadly similar to Late Stone Age (LSA) Holocene skeletons from the southern coastal margins of the Cape, and based on size, was suggested to be from a male. Our analysis subjected the KRM first metatarsal and comparative human samples to selected morphometric analyses, in an attempt to test the hypothesis regarding shape-associated sexual dimorphism as a means to estimate sex in the KRM individual. The results support earlier suggestions that it falls within the range of early Holocene variation, this being very narrow both in size and shape. The size-independent shape-associated morphology, however, suggests that the individual may be female. Even though these findings imply that the KRM individual may have been female based on sexually dimorphic shape-associated discrimination in LSA Holocene people, they are not conclusive and that this individual could probably be assigned to either sex.

Keywords: first metatarsal, Middle Stone Age, Klasies River Mouth, morphometrics, sexual dimorphism.

INTRODUCTION

Rightmire *et al.*'s (2006) recent study of three late Pleistocene human metatarsal bones from Klasies River main site, situated on the southern coast of South Africa provides valuable insights into Middle Stone Age (MSA) occupation of these archaeologically informative deposits. Although there is still some debate on the age of the site (Parkington 1990; Wolpoff 1989), the general consensus is that the early Klasies River humans date between 80 000 and 100 000 years ago. One of these bones, a left first metatarsal (KRM 6113B), was recovered during the 1967–1968 excavations, originally thought to be from a non-human hominin, later regarded as indistinguishable from modern humans (Rightmire & Deacon 1991). Rightmire *et al.* (2006) describe this specimen as broadly comparable in size to that of Late Stone Age (LSA) San males drawn from Cape burials.

The univariate comparison of the dimensions of the Klasies River Mouth (KRM) first metatarsal reveal that the length, proximal and distal dimensions are slightly smaller than average black South Africans. Mid-shaft diameters are comparable to those of black females. All dimensions are close to the averages for early Holocene males from the western and southern Cape (Zipfel 2004; Rightmire *et al.* 2006). The appearance of the KRM specimen is therefore unremarkable and based upon size is suggested to be male. This is also supported by the stature estimates of Rightmire *et al.* (2006) based on the formula by Byers *et al.* (1989), who found significant correlations between metatarsal lengths and stature. Despite Rightmire *et al.*'s well justified hypothesis that the KRM first metatarsal probably belonged to a male based on size, the important question of shape remains unresolved. Shape-associated sexual dimorphism, or in some cases 'dimorphisms' have been reported in foot bones (e.g. Kidd 1995; Kidd & Oxnard 1997; Ferrari *et al.* 2004; Zipfel 2004) in which the intercorrelation between variables reveals more information than individual dimensions or indices on their own. Numerous studies have addressed sex estimation from the hands and feet with varying results (e.g. Robling & Uberlaker 1997; Case & Ross 2007) which require clear identification of the population being considered. Determining the sex of an isolated specimen such as a metatarsal from an extinct group of humans thus poses a challenge.

As late Pleistocene human postcranial remains are extremely scarce, further investigation of such remains are justified. The analysis presented here subjects the KRM first metatarsal and comparative human samples to selected morphometric analyses, in an attempt to test the hypothesis regarding shape associated sexual dimorphism as a means to estimate sex in the KRM individual.

MATERIALS AND METHODS

Materials

In addition to the KRM specimen (South African Museum, Cape Town), the first metatarsal elements from both recent (Sotho, Zulu and European) and pre-pastoral Holocene (LSA) skeletal samples were examined for morphological variation. The three recent samples each comprised 30 males and 30 females and the LSA sample of ten males, nine females and 13 of uncertain sex. The recent human specimens were made available courtesy of the University of the Witwatersrand (Raymond Dart Collection, Johannesburg) and the ancient (LSA) specimens by the South African Museum, Cape Town and National Museum, Bloemfontein. The LSA humans were dated between 9720 and 2000 (^{14}C) years B.P. Until about 2000 years ago, all local inhabitants were hunter-gatherers (Hausman 1982; Roberts 1989; Sealy & Pfeiffer 2000; Stock & Pfeiffer 2001) and represent pre-pastoral people with habitual behaviours most closely associated with those of

*Author for correspondence. E-mail: bernhard.zipfel@wits.ac.za

the MSA. Where possible, dimensions were collected from the left side, previous studies demonstrating no significant difference in variation between sides (Steudal 1984; Kidd 1995).

Methods

Linear metatarsal dimensions were defined so as to reflect the general functional shape and size of the bone. These were loosely based on the definitions by Martin & Saller (1957), together with those of, for example, Susman & Brain (1988) and Byers *et al.* (1989). As both distal and proximal portions of the bone are partially damaged, an entirely precise data set is not possible. In this case, two options may be considered. The first, an estimated value for a missing or imprecise dimension could be used. This should be done with caution as an artificial or unrealistic value could easily affect the overall results. Second, the number of variables used in the analyses is reduced. This option, however, is only acceptable when due consideration is given to possible distortion of the results. This depends largely on the type of variable, and the amount of information it contributes to the analyses (Jollife 1972a,b).

Both these options were applied in defining dimensions. A preliminary principal components analysis (PCA) and canonical variates analysis (CVA) of the recent human groups excluding a dimension such as the proximal breadth or inferior distal breadth of the head dimension did not result in any significant change to the results; this was therefore considered an acceptable strategy. Any minor error in estimation, although imprecise, is very small, and the intercorrelation with the remaining variables, which are precise, validates the technique.

For the purpose of this study, eight linear variables were utilized. These were the articular length, proximal articular height and breadth, distal height, total and superior distal breadth and mid-shaft height and breadth. All linear data dimensions were obtained using standard digital sliding callipers. All readings were taken in millimetres and recorded to 0.01 mm. All measurements, except the mid-shaft dimensions, were taken with the bone held and orientated by hand. For the mid-shaft measurements, the metatarsal was placed in a bone vice at the mid-shaft with the proximal articular surface long dimension orientated in the sagittal plane.

Plots of means against their standard deviations revealed a clear positive regression; as a consequence, all data were subsequently transformed to their natural logarithms. 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® 8.2 (2003).

Principal components analysis does not make any *a priori* definitions of interrelationship such as sex differences or the identification of a particular group or groups. It thus shows the distribution shape of the pooled group of organisms and can therefore be used as a cluster finding tool including the KRM specimen within the overall structure. In the current study, the PCA served primarily as an exploratory exercise to validate the data for subsequent canonical variates analysis and to examine the relationship of the KRM specimen to the individuals from the other human sub-groups. As the sex of a number of the LSA individuals is uncertain, the PCA was useful to validate the small LSA sample in terms of determining if the LSA group could be discriminated from the recent human groups. No attempt was made to assign sex via the PCA as this would make the compositions of both males and females in the LSA sample potentially suspect.

Canonical variates analysis defines the maximum discrimination between groups, relative to the variation within the group (Reyment *et al.* 1984) and unlike PCA, requires *a priori* definition of the groups. Therefore, the LSA group was limited to the specimens of known sex only. In the CVA used in this study, the KRM specimen was entered directly as part of the overall canonical structure as a sample size of unity, rather than by interpolation into the matrix of the Holocene comparative samples. A weighted analysis was used. While there is much debate with regards to the relative merits of weighted and unweighted analyses (e.g. Albrecht 1980, 1992), they do serve to maximize the amount of discrimination held within early variates (Kidd 1995).

RESULTS

Principal components analysis

The majority of the variation lies within the first two principal components, together accounting for just over 83% of the total variation. The eigenvectors from the first principal component, are all of positive sign and broadly similar in magnitudes; this suggests that most of the variance contained within this component is associated with size and size-related shape (Jolicoeur 1963) (Table 1). On the second principal component, containing 11.87% of the total variation, the eigenvectors are of both positive and negative sign indicating a large component of size-independent shape content (Table 1).

Even though the variation within the first two principal components does not entirely discriminate any of the groups, the Sotho, Zulu and European groups occupy a

Table 1. The eigenvalues, percentages of variance and eigenvectors for the principle components analysis of the first metatarsal from the five human groups and the KRM first metatarsal.

		PRIN 1	PRIN 2
Eigenvalue:		0.067	0.012
% of variance:		70.50	12.52
Eigenvectors	VAR 1: Articular length	0.272	0.126
	VAR 2: Proximal art. height	0.296	0.175
	VAR 3: Proximal art. breadth	0.386	–0.573
	VAR 4: Distal height	0.357	0.370
	VAR 5: Total distal breadth	0.387	0.306
	VAR 6: Superior distal breadth	0.385	–0.347
	VAR 7: Mid-shaft height	0.348	–0.182
	VAR 8: Mid-shaft breadth	0.377	–0.491

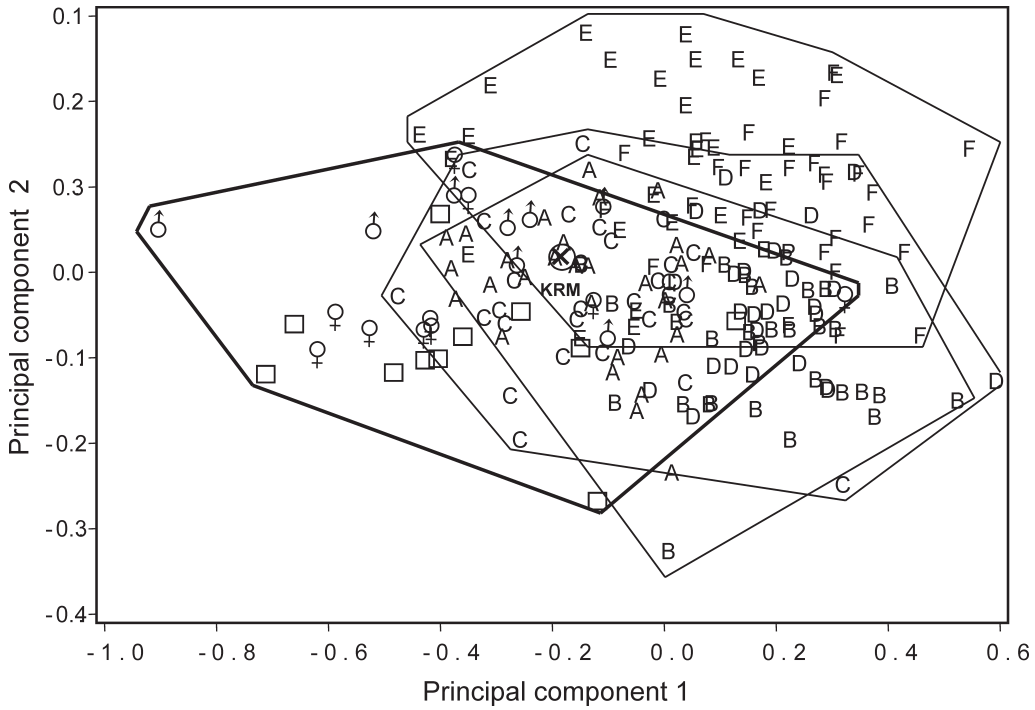

Figure 1. First metatarsal bivariate plot of principal components one and two of log-transformed dimensions including the Holocene human groups and KRM fossil X. **Key**: A = Sotho female; B = Sotho male; C = Zulu female; D = Zulu male; E = European female; F = European male; ♀ = LSA female; ♂ = LSA male; □ = LSA sex indeterminate.

more positive position than the LSA group on the first principal component, with a considerable overlap between all of them (Fig. 1). The spread of males and females in the Sotho, Zulu and European groups are broadly similar. In these groups, on the first principal component, males generally lie more positively than females with a small degree of overlap. There is obvious discrimination by sex in these three groups. In the LSA group, however, there is no clear discrimination between the individuals of known sex. A number of these, including a few of unknown sex lie more negatively than any of the other groups and the most positive portion of the LSA group lies about halfway within the spread of the other three groups.

The KRM specimen lies centrally on the first component, positively within the spread of the LSA group. On the second principal component, the fossil also lies centrally within the entire sample and positively within the LSA group. On this component, of the LSA sample, three females and six males lie positively and six females and three males lie negatively from the KRM specimen (Fig. 1). Both males and females of the LSA group therefore fall within the broad morphology of the KRM first metatarsal. A subsequent canonical variates analysis was thus essential in order to maximize any differences within and between the groups.

Canonical variates analysis

In the analysis of the KRM specimen together with the Holocene human groups, the majority of the discrimination lies within the first two variates, together accounting for almost 90% of the total discrimination. Subsequent variates contain considerably less variation. The third variate contains 6.25% of the total discrimination and the fourth variate 2.59%. The group mean scores along the first, second and third canonical variates are given in Table 2 and Mahalonobis' distance matrix in Table 3.

On the first canonical variate, the group centroids are spread over approximately 4.25 standard deviation units (SDU) with the LSA females on the negative extreme and the European males on the positive extreme. The European centroids lie most positively and the LSA centroids most

Table 2. First metatarsal group means along canonical variates 1, 2 and 3.

Group	Sex	CAN 1	CAN 2	CAN3
% Total discrimination		50.29	37.34	6.25
KRM		–2.28	–0.57	2.35
Sotho	F	–0.87	–0.10	–0.33
Sotho	M	0.34	1.53	0.12
Zulu	F	–1.10	0.22	–0.59
Zulu	M	0.55	1.02	0.43
European	F	0.72	–1.61	0.20
European	M	1.79	–0.51	–0.25
LSA	F	–2.43	–0.64	0.48
LSA	M	–1.84	–1.12	0.61

Table 3. Mahalanobis D^2 distances from the KRM first metatarsal to group centroids of the first metatarsal.

Group	Sex	D^2
KRM		0
Sotho	F	16.01
Sotho	M	23.45
Zulu	F	18.21
Zulu	M	22.39
European	F	22.99
European	M	29.50
LSA	F	10.71
LSA	M	11.78

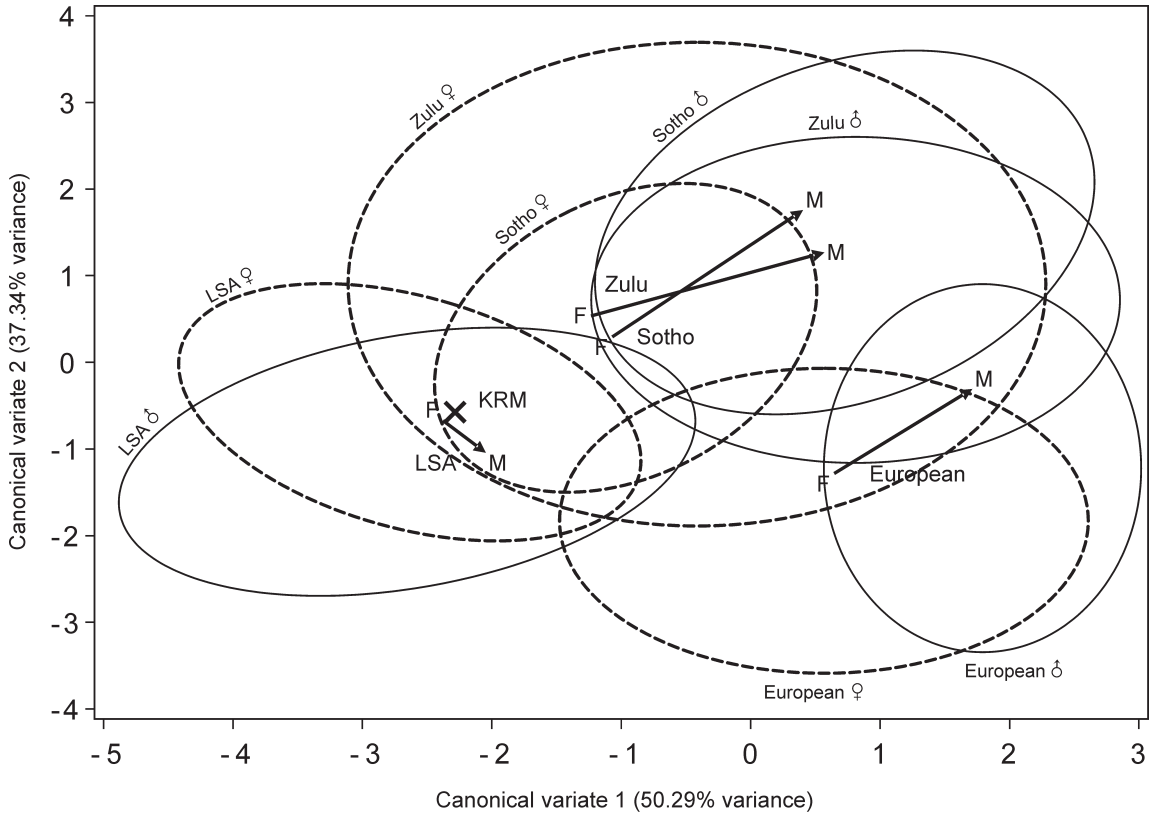

Figure 2. First metatarsal bivariate plot of canonical means and dispersions along canonical variates one and two of log-transformed dimensions including the human fossil KRM. Both the axes are in standard deviation units. F = female. M = male.

negatively with the Bantu-speakers (Sotho and Zulu) between them. On the first canonical variate, the KRM specimen lies well within the spread of the LSA closest to the female centroid (Fig. 2).

On the second canonical variate the group centroids are spread over approximately 3 SDU. The Sotho and Zulu male centroids lie most positively and the European females and LSA males most negatively. The KRM specimen lies closest to the female LSA centroid which lies about halfway between the European males and females (Fig. 2). The KRM specimen is thus not unique and has the greatest affinity with the LSA females. This is also borne out by the Mahalanobis' distance, although the difference in distance between the males and females is only 1.07 (Table 3). The dispersion ellipses, however, show an overlap with LSA males and females as well as Zulu and Sotho females. On the third canonical variate, the KRM specimen lies almost 2 SDU positively to the closest Holocene human centroid (Fig. 3).

DISCUSSION

Based on size only, this is a relatively large human metatarsal, certainly within the range of early Holocene San males. This is not unique among southern African MSA specimens as evidenced by the relatively large, nearly complete right metatarsals IV and V from Border Cave (Morris 1992). Notwithstanding, in the LSA sample, percentage differences between the sexes indicate relatively little size-associated dimorphism (Zipfel 2004). The initial PCA, however, reveals that two of the LSA females are 'larger' than the KRM specimen. The size-independent shape content does not clearly place the fossil within either the LSA male or female morphology as there is no clear discrimination.

Examining the patterns of variation within and between the different groups with canonical variate 2 and canonical variate 1 together, the groups clearly present three areas of discrimination (Fig. 2). One for the European group, one for the Sotho and Zulu groups together, and one for the LSA group. This suggests that the greatest proportion (over 88%) of discrimination may best be described as largely 'genetic'. There are three distinct groups of people, European (Caucasoid) on the one hand, LSA (Khoisanoid) on the other with Bantu-speakers (Zulu and Sotho) between them. The KRM fossil clearly falls within the parameters of the LSA group, close to the LSA female centroid essentially in agreement with the proposed genetic discrimination between the three main human groups (Fig. 2). This suggests, both from the canonical variates plots and to a lesser extent, Mahalonobis' distances, that this individual may have been female, this discrimination being primarily shape-associated. This should however, be considered with the caveat that the range of variation in sexual dimorphism in the LSA sample is very narrow when compared to the other groups. On canonical variates 1 and 2 together, the dispersion ellipses show a distinct overlap of the KRM specimen with male and female LSA and Zulu and Sotho female groups. The fossil could therefore fall into any of these groups at this level of discrimination.

Canonical variates 3 and 1 together present a line of discrimination between the LSA group on the one hand and the recent groups on the other (Fig. 3). This may suggest a largely functional or life-style based discrimina-

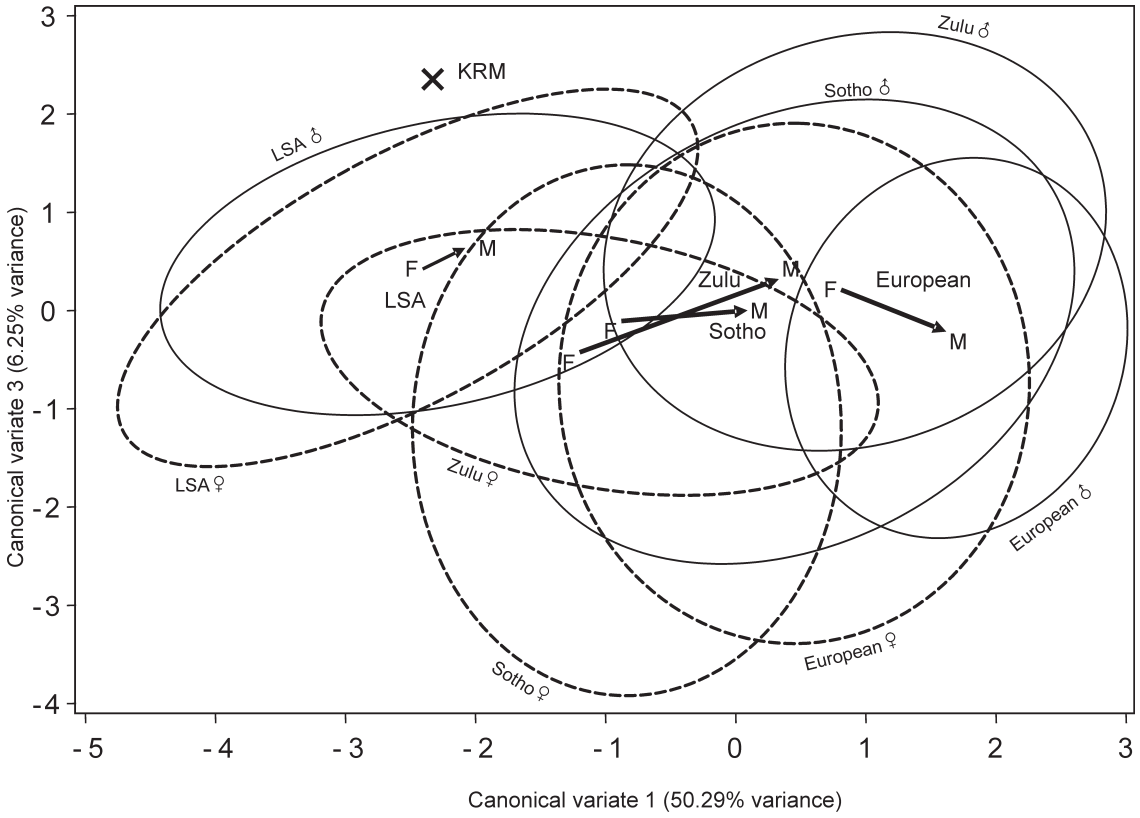

Figure 3. First metatarsal bivariate plot of canonical means and dispersions along canonical variates one and three of log-transformed dimensions including the KRM human fossil. Both the axes are in standard deviation units. F = female. M = male.

tion; habitually unshod LSA individuals walking on natural substrates and shod contemporary people walking on variable substrates. It is, however, possible that canonical variate three reflects residual genetic variation that is not reflected in canonical variate two. With the exception of the European males, the dispersions around the centroids of the other groups overlap to varying degrees (Fig. 3). The KRM fossil, however, lies in a unique position positively on the third canonical variate, clearly discriminated from the other four groups. The canonical coefficients on the third canonical variate including the KRM specimen, have a particularly heavily weighted total distal breadth dimension when compared to the analysis excluding the fossil. There was no indication of macroscopic pathology in this specimen, therefore this is excluded as a reason for this discrimination. There is also no evidence to suggest that the late Pleistocene human populations had life-styles or behaviours that were much different from those of the early Holocene (Hausman 1982). The proportion of discrimination, however, is relatively small representing just over 6% of the total discrimination. It describes in the broadest sense, differences between the KRM specimen on one hand from all other groups on the other. Reasons for this are beyond the scope of this paper. Nevertheless, the majority of the morphological information (87.62%) falls within the range of South African LSA Holocene morphology.

CONCLUSION

All four group samples present with different patterns of sexual dimorphism to some extent, obviously in size, and more subtly in shape. In the LSA group, unlike the recent humans, the first metatarsal shows a size-related dimorphism in which some of the male bones are 'smaller' than those of the females. Therefore, estimating sex based on size alone is not entirely satisfactory. Equally problematic is the relatively small shape-associated sexual dimorphism within the LSA sample. Even though these findings suggest that the KRM individual may have been female based on sexually dimorphic shape-associated discrimination in LSA Holocene people, they are not conclusive. In view of these conflicting, yet equally valid arguments, we suggest that this individual could probably be assigned to either sex.

Our grateful thanks go to G. Avery at the Iziko South African Museum, Cape Town, J. Brink at the National Museum, Bloemfontein, and K.L. Kuykendall, E. Mofokeng and L.R. Berger at the University of the Witwatersrand, Johannesburg, for facilitating access to the skeletal collections. We also wish to acknowledge the reviewers, C. Groves and A. Morris for their helpful comments and suggestions. This work was supported by the Palaeontogical Scientific Trust (PAST).

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Palaeontological Society of Southern Africa – 15th Biennial Meeting, Grahamstown, 2006

Additional abstracts

The following three abstract were inadvertently omitted from the list of abstracts published in *Palaeontologia africana* (2007) **43**, 117–136.

Papers

Evolution in action: documenting hybridization in wildebeest

B. de Klerk[1*] & J.S. Brink[2]

[1]*Bernard Price Institute for Palaeontology, University of the Witwatersrand, Private Bag 3, University of the Witwatersrand, WITS, Johannesburg, 2050 South Africa*
[2]*Florisbad Quaternary Research, National Museum, Bloemfontein*
**E-mail: deklerkb@science.pg.wits.ac.za*

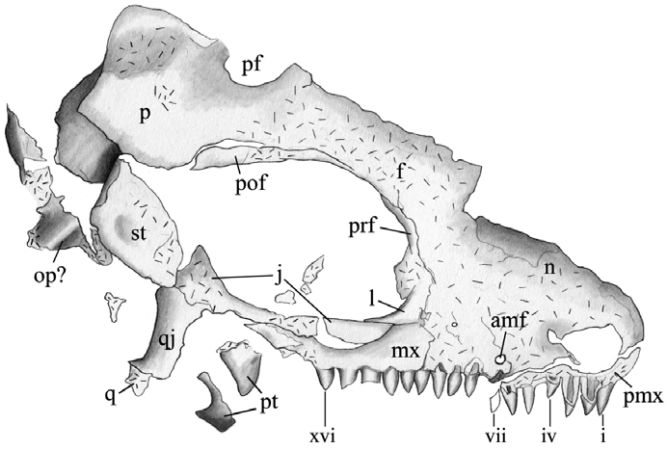
Wildebeest form part of the tribe Alcelaphini and the genus *Connochaetes*. There are two extant species, namely *Connochaetes gnou* (black wildebeest) and *Connochaetes taurinus* (blue wildebeest). From fossil evidence, it is thought that black wildebeest evolved from a blue wildebeest-like ancestor *c.* 1.0 ma ago. Genetic evidence also suggests that the two species of wildebeest diverged in a time less than 1.0 ma. Historically, geographic ranges of these two species have overlapped, but different social behaviour and habitat preferences prevented interbreeding. Black wildebeest, the derived form, is permanently territorial and needs open habitat in order to visually patrol and maintain breeding territories, while blue wildebeest has a flexible reproductive behaviour in being able to reproduce in open grasslands or wooded environments without necessarily occupying territories. It has been proposed that reproductive isolation between *C. taurinus* and *C. gnou* may have been disrupted due to management practices, such as the spatial confinement of black and blue wildebeest within fenced areas and in sub-optimal habitat. This would affect the process of mate selection and allow for interbreeding. Although genetic studies have shown that the blue wildebeest populations are generally 'pure' and that the black wildebeest populations are receiving an influx of blue alleles because of hybridization, the inverse can occur, where black wildebeest males interbreed with blue wildebeest females. In this research, 13 specimens selected at random from a population suspected to be *Connochaetes taurinus* × *Connochaetes gnou* hybrids from the Spioenkop Nature Reserve, KwaZulu-Natal, have been studied. The aim of this project is to test whether a comparative osteological approach can successfully identify hybrids. To this end, hybrid data will be compared, morphologically and statistically, with results from a large reference sample of pure blue and black wildebeest.

New procolophonid parareptile from the Katberg Formation (*Lystrosaurus* Assemblage Zone, Lower Triassic) of South Africa

J.C. Cisneros

Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Private Bag 3 WITS, Johannesburg, 2050 South Africa
E-mail: cisneros.jc@gmail.com

Here a new genus and species of procolophonid is reported. The specimen consists of a partially articulated



skeleton that was collected in the uppermost levels of the *Lystrosaurus* Assemblage Zone, in South Africa (Lower Triassic). The new taxon co-occurs with the well known form *Procolophon trigoniceps*. The cranium of BP/1/1187 (see figure below) displays some primitive features such as a high number of teeth (16 upper marginal teeth) and the lack of quadratojugal spikes, but it possesses derived characters such as the presence of bicuspid teeth. The new taxon is unique in having seven long conical teeth, with the tips slightly recurved, and nine smaller molariform teeth. The dentition is suggestive of insectivorous habits.

The phylogenetic interrelationships of procolophonid reptiles were determined via a comprehensive cladistic analysis using a data matrix of 22 taxa and 66 characters. Besides the new taxon, several other taxa were included for the first time in a phylogenetic analysis, and most of the characters are novel. Information from North American, South American, South African, Chinese and Australian taxa was based on first hand examination. The analysis was performed with the program *Tree Analysis Using New Technology* (TNT) (Goloboff *et al.* 2003). A single most parsimonious tree was found by TNT. The results show that Procolophonidae is a monophyletic group. The new taxon is a basal form, being the sister group of all procolophonoids to the exclusion of the owenettids, *Coletta seca* and *Sauropareion anoplus*. Character optimization indicates that bicuspid teeth were acquired independently by the new taxon, therefore originating twice in the Procolophonidae.

Reference

Goloboff, P.A., Farris, J.S. & Nixon, K.C. 2003. *T.N.T.: Tree Analysis Using New Technology.* Available at http://www.zmuc.dk/public/phylogeny

A remarkable Latest Permian autochthonous flora from Wapadsberg Pass, southern Karoo Basin of South Africa

R. Prevec[1*], R.A. Gastaldo[2], J. Neveling[3] & S.B. Reid[2]

[1]*Geology Dept., Rhodes University, P.O. Box 94, Grahamstown, 6140 South Africa*
[2]*Department of Geology, Colby College, Waterville, ME 04901, U.S.A.*
[3]*Council for Geosciences, Silverton, Pretoria, South Africa*
**E-mail: rose.adendorff@ru.ac.za*

A recent investigation of the well-known Permian-Triassic section at Wapadsberg Pass in the Eastern Cape has led to the discovery of two new autochthonous plant fossil localities. The two exposures probably represent the same fossiliferous horizon outcropping along the new

and old roads through Wapadsberg Pass, and have been correlated to within 10 m across the 1.5 km that separates them. The plant-fossil-bearing horizon is approximately 70 m below the P/T boundary in this area.

The basal 30 m of section along the new road through Wapadsberg Pass consists of fining upwards sequences in which coarse-to-fine siltstone overlies thin sheet sandstone bodies of very fine-to-fine grain size. Sandstone bodies may be imbricated within channel-form geometries, and represent lateral accretion beds within larger channels. Generally, overlying the coarse siltstone is the subsequent channel fill, with other siltstone facies indicative of overbank and interfluve deposits. Pedogenesis of the siltstones is evidenced by the presence of rhizoconcretions and early diagenetic calcareous nodules. One fining upward sequence is capped by a poorly developed paleosol with vertically oriented roots above which fossil plants are preserved in a silty claystone that coarsens to a siltstone.

The flora is represented by impressions within and above an inceptisol (?gleysol) horizon. Plant parts within the paleosol include large *in situ Vertebraria* axes and degraded aerial detritus. Assemblages above paleosols consist of well-preserved aerial debris and ground cover plants concentrated in mats with little intervening sediment between plant parts. These are interpreted to be a leaf litter (O) horizon. Aerial debris becomes less concentrated and more dispersed towards the top of the fossiliferous horizon and represents contribution during aggradation of the landscape. To date, no evidence of erect vegetation has been found in the limited exposures. At least two species of *Glossopteris* leaves, several seed types, and the glossopterid fertile structures *Lidgettonia* sp. and *Eretmonia natalensis* represent contribution from canopy vegetation. Two sphenophyte taxa, *Phyllotheca australis* and *Trizygia speciosa*, associated with sphenopsid cones are found in abundance and represent contribution from ground cover plants. The *Glossopteris* leaf impressions provide abundant evidence of plant–insect interactions, including margin- and hole-feeds, and oviposition scars.

This report represents the first account of a typical Late Permian flora, and the first collection of fertile glossopterid material of any age, from the southern Karoo Basin. Previously, *T. speciosa* had been recorded only as a relatively rare element in the Upper Permian Estcourt Formation floras of the northeastern Karoo Basin, KwaZulu-Natal, and at the Middle to Upper Permian Lawley locality in the northern Karoo Basin. The quality of preservation and abundance of this taxon at Wapadsberg Pass is exceptional.

These findings challenge current perceptions about the quality, abundance, and temporal distribution of fossil floras in the Karoo Supergroup. The role of fossil plants in biostratigraphic studies of the basin has been greatly underestimated in the past. Methodical investigation and accurate characterisation of the floras near the Permian–Triassic boundary can make a significant contribution to our understanding of hypotheses focused on this critical time interval in Earth history.

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Bernard Price Institute for Palaeontological Research
University of the Witwatersrand
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Three orders of headings are used.
FIRST ORDER, printed in bold capitals and left-aligned.
Second order, printed in bold upper and lower case and left-aligned.
Third order, printed in upper and lower case italics and left-aligned.

Headed sections and paragraphs should not otherwise be numbered or lettered in the manuscript.

Tables

Tables must be set out on separate sheets, with their headings in lower case. They are numbered consecutively in arabic numerals. Please indicate the position of each table by appropriate pencil notation in the margin of the text.

When referring to Tables in the text the word 'Table' is spelt out in full and given a capital initial letter, e.g. Table 2.

Illustrations

All illustrations are termed Figures (the word is to be spelt out in full with a capital initial letter), and they are numbered consecutively with arabic numerals. Each illustration must bear in pencil on the reverse side the author's name, a key word(s) from the title, the figure number and the word 'top' in the appropriate position to indicate orientation.

Please mark the position of figures by pencil notation in the margin of the text. When referring to figures in the text the word is abbreviated with a capital initial letter, e.g. Fig. 23.

All artwork should be submitted as camera-ready originals. The use of computer-generated lettering (high-quality laser or ink-jet) or dry transfer lettering is preferred for labelling, and stencil or hand-lettering is to be avoided.

Drawings, maps and diagrams should be in black drawing ink on high quality tracing paper or good quality white card. If drawings are submitted on translucent draughting film, labels and other lettering should *not* be stuck onto the original. Instead they should be clearly written on a submitted photocopy of the original, showing their correct positions clearly, for typesetting by the printers. All illustrations should be designed for same-size printing or slight reduction (by no more than 1/3) in the final form. The maximum acceptable size for illustrations on the printed page is 245 × 175 mm. Tip-ins and fold-outs are not accepted except under very special circumstances, and generally any additional costs will be for the account of the author.

Photographs should be high quality glossy b/w prints of good contrast made from critically focused negatives, and similar constraints on size apply as in the case of drawings.

Good quality digital images in TIF and EPS format (at least 350 dpi for photographs and 1200 dpi for line drawings) may also be accepted. They may be submitted on PC-format disks or CD-ROM.

Scale should be represented by suitably labelled scale bars of appropriate size, with the units of measurement specified in the caption; avoid reference to magnification in captions.

Authors must submit the original of each figure plus two copies, which may be photocopies provided the quality is good and all details are clear.

Numerical data

The metric system (SI units) is to be used throughout for all numerical data. If there is good reason for using units other than metric, the SI metric equivalents must be given in brackets. Authors should familiarize themselves with the standard abbreviations of SI metric units; non-standard abbreviations are not acceptable.

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All manuscripts offered to the Editor are submitted to two or more referees for critical appraisal, and the substance of the referees' comments is forwarded to the author in the event that the manuscript is rejected or requires revision. The Editor will advise the author whether or not the manuscript is accepted for publication.

If the manuscript is accepted, one set of proofs (usually page proofs) will be submitted to the author for careful checking and these must be returned as soon as possible. The cost of any additions or major alterations to the text at proof stage may be charged to the author. Further proofs may be submitted to the author if the Editor considers it to be necessary or desirable, but at this stage any postal charges will be for the account of the author.

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